Research article

Dwarf shrub expansion and loss of lichens distinctly dominate multi-decadal changes in northern boreal understory plant communities

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Abstract

Northern boreal forests and treelines are particularly sensitive to the current climate change that has already resulted in increased productivity, shrub expansion and up- and northward shifts of species. However, these changes are expected to be gradual or lagged due to slow process rates, and can be buffered to some extent by large herbivores. Multi-decadal observations of understory change in northern boreal forests remain scarce, particularly those involving bryophytes and lichens despite their importance for biodiversity and ecosystem functions. Here, we analyse temporal changes in understory plant communities of northern boreal forests in Saariselkä, Finland (68.46° N, 27.37° E) that were originally sampled in 1981. We resurveyed plant communities (vascular plants, bryophytes and lichens) at 22 sites (including 88 vegetation plots) in 2014 and at 80 sites (320 plots) in 2022 in different forest site types. Reindeer grazing was moderate throughout the study period (1.5–2.0 reindeer/km^2), while mean annual temperature rose over 1 ^{o}C. We found clear temporal shifts in plant communities towards increasing dwarf shrub dominance and decreasing lichen cover and diversity, which were consistent across the study area and within different site types. However, the increase in dwarf shrubs was species-specific: the cover of bilberry (*Vaccinium myrtillus*), crowberry (*Empetrum nigrum*) and lingonberry (*Vaccinium vitis-idaea*) had increased over time, while the originally most dominant species, heather (*Calluna vulgaris*), had decreased and become subordinate to all the above. The observed changes reflect a shift into moister conditions and are

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likely linked to both succession and climate change. Long-term reindeer grazing is most likely the key driver reducing lichen cover, which may be further affected by the dwarf shrub expansion. The consistency of the observed changes in different site types is indicative of corresponding changes occurring elsewhere in northern boreal forests with comparable environmental conditions and grazing pressure. Importantly, our results raise concerns about the local disappearance of lichens if the declining trend continues.

Keywords: *Calluna vulgaris, Empetrum nigrum, Cladonia spp., reindeer lichen, shrubification, vegetation resurvey*

Introduction

Northern boreal forests and treelines are particularly sensitive to the current climate change (Holtmeier & Broll 2005) that is particularly pronounced in the polar regions (Rantanen et al. 2022). Several studies have reported increases in productivity (Kauppi *et al.* 2014; Zhang *et al.* 2008), shrub expansion (Myers-Smith *et al.* 2011; Rundqvist *et al.* 2011) and upward and northward shifts of treelines (Aakala *et al.* 2014) that have occurred over decades, often in response to climate warming, in high-latitude environments. In contrast, studies of long-term changes and dynamics of understory vegetation in the northern boreal forests are still relatively scarce, even though understory vegetation is ecologically important and affects many ecosystem processes (Nilsson & Wardle 2005). Particularly rare are studies at the plant community level, including non-vascular cryptogams, i.e. bryophytes and lichens. These are important components of understory plant diversity and play a key role in many ecosystem functions in high-latitude environments (Kumpula 2001; Turetsky *et al.* 2012).

Importantly, changes in high-latitude plant communities are likely to be relatively gradual (Chapin *et al.* 2004) or lagged (Jonsson *et al.* 2021) due to slow process rates and dominance of long-lived perennial plant species, and therefore require longer-term data to observe (Vellend *et al.* 2017). Resurveys of historical vegetation data are an essential method for revealing long-term trends in vegetation (Hédl & Chudomelová 2020; Kapfer et al. 2017; Maliniemi et al. 2023) and often serve as the only source of temporal information for areas lacking long-term monitoring. Old documentations of plant communities that include detailed information on non-vascular cryptogams are rare, and most include only vascular plants. It has therefore been relatively uncommon to study simultaneous long-term changes in different plant groups.

Understory vegetation in northern boreal forests is dominated by dwarf shrubs, which are keystone species in these environments, with mosses and lichens being abundant and important attributes of plant communities (Nilsson & Wardle 2005). Wildfires are a key factor in controlling the species composition and successional stages of understory vegetation, especially in unmanaged forests (Nilsson & Wardle 2005). However, wildfires are being strongly controlled or suppressed in certain parts of the boreal zone and fire regimes have changed over time (Gauthier et al. 2015; Granström & Niklasson 2008). This is likely reflected in the understory composition over long time scales as fire has long been a regenerating force in the boreal biome. In the absence of fires, understory vegetation develops towards a late successional stage, characterized by the dominance of crowberry (*Empetrum nigrum*) and feather mosses, which eventually leads to ecosystem regression, where soil microbial activity, decomposition and N mineralization slow down and conditions become less suitable for tree establishment and growth (Nilsson & Wardle 2005).

Reindeer grazing is another fundamental driver that influences high-latitude vegetation. Several studies have shown that grazing can inhibit the expansion of taller shrubs and trees (Olofsson *et al.* 2009; Vowles *et al.* 2017) and, therefore, buffer against climate-driven vegetation changes. However, grazing has less influence on dwarf shrubs, especially on evergreen dwarf shrubs (Vowles *et al.* 2017). Another distinct effect of grazing is its negative influence on lichens (Bernes *et al.* 2015; Kumpula *et al.* 2014,) that reindeer trample and use for winter food (Kumpula 2001). Despite the generally recognized responses of tall shrubs and lichens on reindeer grazing, its effects on other plant groups can be highly context dependent and vary in different habitat types (Bernes *et al.* 2015). Furthermore, these effects are mixed with local and regional climate change effects. Therefore, studies addressing local conditions are needed to advise research and management (Bernes *et al.* 2015).

In 2022, we resurveyed understory plant community data (including vascular plants, bryophytes and lichens) from northern boreal forests in northern Finland that was originally surveyed in 1981. The studied forests have remained outside forest management and other direct human disturbances, like most of the northernmost boreal forests (Gauthier *et al.* 2015), but have been grazed by reindeer the whole study period. In this study we analyse how the composition and diversity of plant communities have changed across the study area and within five different forest site types over the past 40 years. We investigate changes both at the level of the whole community and separately for different plant groups (vascular plants, bryophytes and lichens) and species, as well as in terms of temporal beta diversity. Finally, we include a smaller subset of data, resampled from same sites already in 2014, to explore temporal dynamics of dwarf shrubs and different plant groups in more detail. Based on evidence elsewhere, we expect to observe increases in vascular plant abundance but decreases in lichen abundance over time.

Materials and methods

Study area and vegetation resurvey

Study area is located in Saariselkä region in Northern Finland (68.46° N, 27.37° E), and represents one of the northernmost distributions of boreal forests (Gauthier *et al.* 2015). Mean annual temperature (1990-2021) in the area is -0.7 °C, ranging between -12 °C (mean in January) and +13 °C (mean in July) (Jokinen *et al.* 2021). Mean annual precipitation (1990-2021) is 600 mm, while mean snow cover is 70 cm, snow cover period lasting on average from October to May (Jokinen *et al.* 2021). During the past 30 years, mean annual temperature has risen over 1 °C, mean annual precipitation has increased approximately 90 mm and mean snow cover thickness has slightly decreased in the region, when compared to the reference period of 1960-1991 (data from the nearest weather station at Ivalo airport: Finnish Meteorological Institute 1991).

The study area has remained outside direct human impact (e.g. forestry) that is represented by a few non-paved roadways and a power line crossing easternmost gradient (Fig. 1). None of the sampling sites overlap with these disturbances and we estimated them having only a minor effect on the adjacent sites. However, the area is a part of a year-round reindeer pasture in Ivalo herding district (Kumpula *et al.* 2014). The number of reindeer in the herding district increased sharply during 1970-80s, reached a peak of nearly three reindeer/km^2 in the late 1980s and since stabilized at around 1.5–2 reindeer/km^2 (Appendix S1). To our knowledge, there have been no recent forest fires in the area, and no evidence of forest fires was observed during the resurvey or mentioned in the original publication (Lyytikäinen 1983).

According to Ahti *et al.* (1968), the study area belongs to the northern boreal vegetation zone. Forests in the study area are mostly *Pinus sylvestris* -dominated, relatively open xeric (dry) and sub-xeric (semi-dry) forests (Fig. 1) with *Betula pubescens* ssp. *czerepanovii* forming the altitudinal treeline. Understory vegetation is typical to northern boreal forests; relatively species-poor and dominated by a few dwarf shrubs (*Calluna vulgaris*, *Empetrum nigrum*, *Vaccinium myrtillus*, *Vaccinium vitis-idaea*), with bryophytes and lichens, of which the most dominant are feather mosses (*Hylocomium splendens*, *Pleurozium schreberi)* and reindeer lichens (*Cladonia* spp), respectively. According to Lyytikäinen (1983) plant communities can be classified into *Calluna-Cladonia* type, *Empetrum-Calluna-Cladonia* type (that is the most common and include infertile and fertile variants, and *Betula* variant at the treeline) and *Calluna-Uliginosa* type, representing a continuum from dry to semi-dry types to more fresh types, respectively.

The original vegetation survey was carried out in 1981 by Lyytikäinen (1983) who mapped vegetation from a total of 100 sites along elevational gradients on four forested

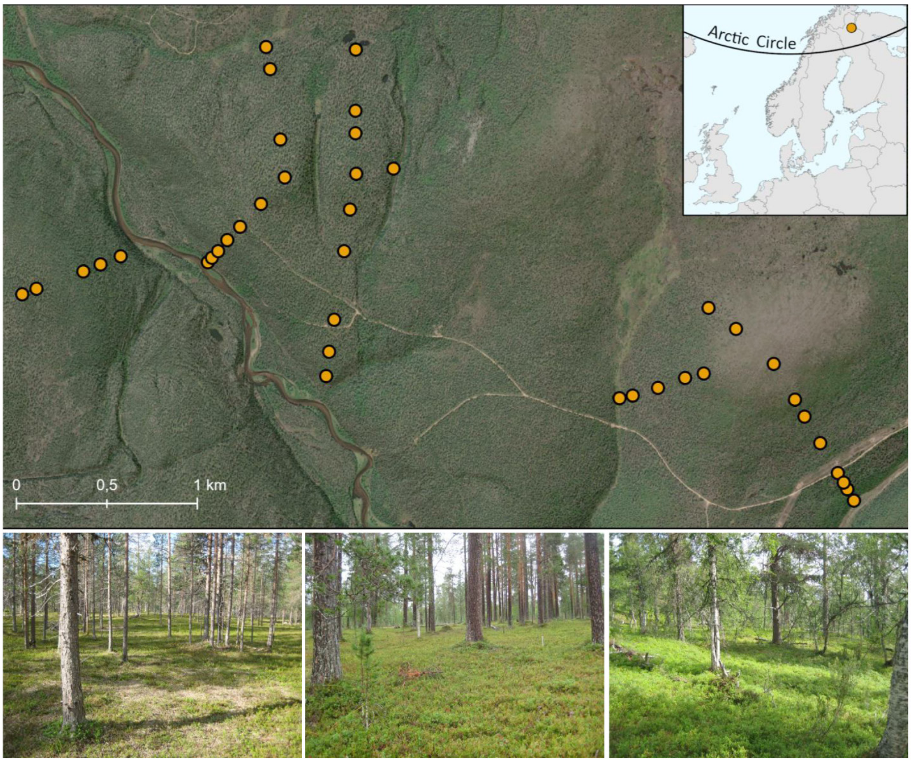

Figure 1. Location of the study plots. Vegetation in the study area is mostly old, open pine dominated xeric (dry) (photo lower left) and sub-xeric heath forests (semi-dry) (lower middle) with patches of old mixed mesic (fresh) heath forests (lower right).

hills (Fig. 1). Together, elevational gradients extend from 190 to 400 m asl. and cover different aspects. Treeline is reached only in the easternmost hill, where there is a small area of treeless heathland. Study sites were established in pairs, i.e., two sites are next to each other, separated by 15 meters. At each site, vegetation was mapped from four 1 x 1 m plots. Plots were placed five meters away from the centre of the site and at an angle of 45 degrees in each direction, in relation to the elevational gradient. In the case of a tree or a large rock, the plot was systematically moved clockwise. Each vascular plant, bryophyte (excluding small liverworts) and lichen species (excluding a few crustaceous species growing on one plot) were identified from the plot and were given a percentage cover value using the following scale: + (< 1 %), 1, 2, 3, 4, 5, 7, 10, 15, 20, 30, 40, … 90, 95, 100 %. Non-vascular cryptogams growing on rocks and tree trunks were not included. For each site, the percentages for each species were averaged across the four 1 x 1 m plots. Basal area was measured from 31 sites.

In the summer 2022, we resurveyed 80 sites (Fig. 1), consisting of total of 320 vegetation plots of 1 x 1 m, using the same methodology as in the original survey, described above. These include 12 sites of *Calluna-Cladonia* type, 31 infertile variant of *Empetrum-Calluna-Cladonia* type, 17 fertile variant of *Empetrum-Calluna-Cladonia* type, 10 *Betula* variant of *Empetrum-Calluna-Cladonia* type and 10 *Calluna-Uliginosum* type. Of the 80 resurveyed sites, 22 sites were resampled already in 2014 for another study (Maliniemi, Happonen & Virtanen 2019). This data also represents different site types and is used in the final analysis of this study to complement interpretation on temporal dynamics of dominant species and plant groups. For all of the analysis, certain bryophyte and lichen species were identified or combined at the level of genus (e.g. *Dicranum* spp., Appendix S2) due to highly similar appearance and to reduce the identification error. Old and new data were harmonized in terms of species taxonomy before the analyses.

The old sites did not have coordinates, so their relocation was based on the original map in Lyytikäinen (1983) where gradients were drawn and the information on elevation, slope and aspect that was given for each site. Thus, sites are quasi-permanent, which is often the case with old vegetation data (Kapfer *et al.* 2017). This inevitably causes some relocation error between the old and the new site locations. However, this error was estimated relatively small in this study because the gradients could be relocated relatively precisely. Moreover, the species-poor and homogeneous vegetation in the study area and the averaging from four vegetation plots reduces the error. In general, comparable resurveys to our study have been shown to be robust to the relocation error (Kopecký & Macek 2015).

Data analyses

We used non-metric multidimensional scaling (NMDS) to explore temporal shifts in plant communities, both across all study sites and within different habitat types. NMDS was calculated with absolute cover values (%) and Bray-Curtis dissimilarity. Covers of dominant species (*C. vulgaris*, *E. nigrum*, *V. myrtillus*, *V. vitis-idaea*) and plant groups (vascular plants, bryophytes and lichens) were fitted into the ordination as correlation vectors. The effect of time on compositional shift across all study sites was tested with permutational manova (PERMANOVA; Anderson 2001). Permutations (n = 999) were not allowed within the paired sites due to repeated measures design. In addition, possible increases in compositional similarity over time, indicating biotic homogenisation, were tested using the homogeneity of multivariate dispersions (PERMDISP; Anderson *et al.*

2006). This was done by comparing site-wise distances to the spatial median of all sites in a multivariate space between the surveys. Analyses above were implemented in R version 4.3.0 (R Core Team 2024) using a 'vegan' package (Oksanen *et al.* 2024).

We used temporal beta diversity index (TBI; Legendre 2019) to estimate the magnitude of temporal turnover in plant communities. TBI was calculated for each pair of sites (original survey in 1981-resurvey in 2022) using species absolute cover values and percentage difference (i.e., Bray-Curtis) as a dissimilarity metric. TBI values range from 0 to 1, indicating completely similar (at 0) or dissimilar (at 1) community composition between surveys, and were further decomposed into species losses and gains. The shares of losses and gains were plotted and tested with permutation tests with 9999 permutations to find out whether gains or losses dominate temporal turnover. TBI was calculated for the whole species composition but also separately for vascular plant, bryophyte and lichen compositions to explore temporal dynamics in different plant groups. To estimate species-level changes over time, we used paired t-tests. P-values were permuted (n = 9999) and corrected for multiple testing using the Holm correction. TBI, the related analyses and t-tests were calculated using R package 'adespatial' (Dray *et al.* 2023).

The effect of site type on the observed changes in the cover of dominant dwarf shrubs and plant groups was tested with linear mixed effects model (LMM), using the package 'nlme' (Pinheiro *et al.* 2023). The time of the survey and the interaction of time and site type were assigned as fixed effects in the models. Hierarchical and temporal structure of the data was taken into account by assigning plot ID, nested within the site (i.e. pair of sites along the gradient), as a random effect in each model. Residual diagnostics were checked for each model and if necessary, response variable was square root -transformed to meet assumptions of normal distribution.

Finally, using the data resampled also in 2014, we explored cover change dynamics in dominant dwarf shrubs and different plant groups, using the three time periods. Of the data from 1981 and 2022 we included only those sites (n = 22, consisting of 88 vegetation plots) sampled in 2014. We ran LMMs for each response variable, using year as a fixed effect and plot ID as a random effect (in this dataset there were no pairs of sites along the gradient but only one site). To analyse if there were significant difference between the pairs of group (year) means, Tukey's post hoc test was run using the package 'multcomp' (Hothorn *et al.* 2023).

Results

A total of 68 species were identified on the study plots during the surveys (Appendix S3). Of the species (or genera considering non-vascular cryptogams), 53 were found in the original survey (33 vascular plant, 8 bryophyte and 12 lichen species or genera) and 63 were found in the resurvey (40 vascular plant, 13 bryophyte and 10 lichen species or genera). There were no considerable gains or losses over time, i.e., species gained or lost were typically recorded once or twice (Appendix S3).

The composition of plant communities changed significantly over time across the study sites (PERMANOVA: F = 11.75, p = 0.001, Fig. 2a), but showed no significant temporal decrease in compositional dissimilarity, i.e. biotic homogenisation (PERMDISP: average distance to spatial median 0.356 in 1981 and 0.328 in 2022, F = 1.83, p = 0.193). Plant communities shifted towards *E. nigrum* and *Vaccinium* spp.

dominance and away from *C. vulgaris* and lichens, and these shifts were consistent across all site types (Fig. 2b). NMDS1 axis generally represents site type gradient from mesic to dry types, according to the classification in the original survey (dashed ellipses in Fig. 2). The driest site type, *Calluna-Cladonia*, no longer exists as it was in 1981 but resembles more *Empetrum-Calluna-Cladonia* types.

Temporal beta diversity index (TBI) was 0.42 across all sites with all species included and the compositional change of plant communities was dominated by species losses (Table 1; Fig. 3a). Of the different plant groups, species gains dominated only in vascular plants, while lichens had the highest TBI value (0.70) that was almost entirely due to species losses (Table 1; Fig. 3b-d).

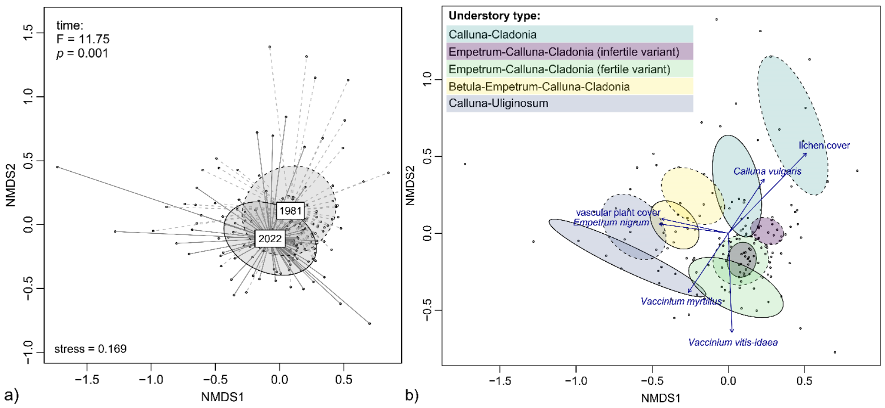

Figure 2. Non-metric multidimensional scaling (NMDS) illustrating temporal shifts in plant community composition, based on Bray-Curtis dissimilarity and species absolute cover values (%). a) Ellipses (1 standard deviation) are drawn across all study sites during both surveys. b) Ellipses are drawn across different habitat types during the original survey in 1981 (dashed lines) and the resurvey in 2021 (solid lines). Arrows represent significant correlation vectors for the cover of *C. vulgaris* (r^2 = 0.166, p = 0.001), *E. nigrum* (r^2 = 0.194, p = 0.003), *V. myrtillus* (r^2 = 0.200, p = 0.001), *V. vitis-idaea* (r^2 = 0.384, p = 0.001), all lichens (r^2 = 0.494, p = 0.001) and all vascular plants (r^2 = 0.185, p = 0.002).

Table 1. Mean temporal beta diversity index (TBI) and its components (losses and gains) calculated across pairs of sites (original survey and resurvey) for all species and different plant groups. Mean change (gains-losses) indicates the direction of change, i.e. whether losses (negative) or gains (positive) dominate. Its associated p-value is tested with 9999 permutations.

Variable	Losses	Gains	TBI	Mean change	Stat	*p.perm*
All species	0.235	0.186	0.421	-0.049	-3.230	0.002
Vascular plants	0.159	0.259	0.418	0.010	3.732	0.001
Bryophytes	0.197	0.198	0.396	0.001	0.037	0.967
Lichens	0.678	0.026	0.703	-0.652	-22.652	0.001

Species-level investigations further confirmed temporal changes in the cover of dominant dwarf shrubs (Table 2). Originally the most dominant species *C. vulgaris* has become subordinate to *E. nigrum*, *V. myrtillus* and *V. vitis-idaea*, of which the former was the most dominant species across the study sites in the resurvey. Evergreen dwarf shrub with more northern distribution, *Arctous alpina*, had also significantly declined, although having small coverage during both surveys. Of bryophytes, the cover of *Pohlia* spp. had increased (although this can be due to more precise observer in 2022, as small *Pohlia* individuals are often found among other bryophyte samples) while that of *Polytrichum* spp. had declined. Reindeer lichens (*Cladonia arbuscula*, *C. rangiferina*, *C. stellaris*) had decreased the most in cover, but the decline was also clear with *Cetraria ericetorum*, minute *Cladonia* spp. and *Stereocaulon* spp. (Table 2). There was no significant difference in the basal area between the surveys (Appendix S4).

Despite the observed general trends above, there were site type-specific responses in the cover changes of dominant dwarf shrubs and different plant groups (Fig. 4). *C. vulgaris* tended to decrease in all but the driest site type (*Calluna-Cladina*), whereas *E. nigrum* tended to increase especially on those types where it was least abundant in 1981. *V. myrtillus* and *V. vitis-idaea* increased particularly in the *Calluna-Uliginosa* type. Vascular plant cover tended to increase in all but the site type typical to treelines (*Betula-Empetrum-Calluna-Cladonia*), where it was influenced by the strong decline in the cover of *C. vulgaris*. Bryophyte cover tended to slightly decrease in all but the driest *Calluna-Cladina* type where it had replaced previously abundant lichens (Fig. 4).

Temporal comparisons including data from 2014 indicate nonparallel temporal dynamics regarding dominant dwarf shrubs and different plant groups (Fig. 5). Whereas the decrease in the cover of *C. vulgaris* seems to have generally taken place before 2014, the strong increase in *E. nigrum* is a more recent event. Decrease in lichen cover have also mostly taken place before 2014. Bryophyte cover shows a decreasing trend until 2014, after which it has recovered, resembling the cover in 1981 by 2022. The cover of vascular plants remained stable throughout the whole study period (Fig. 5).

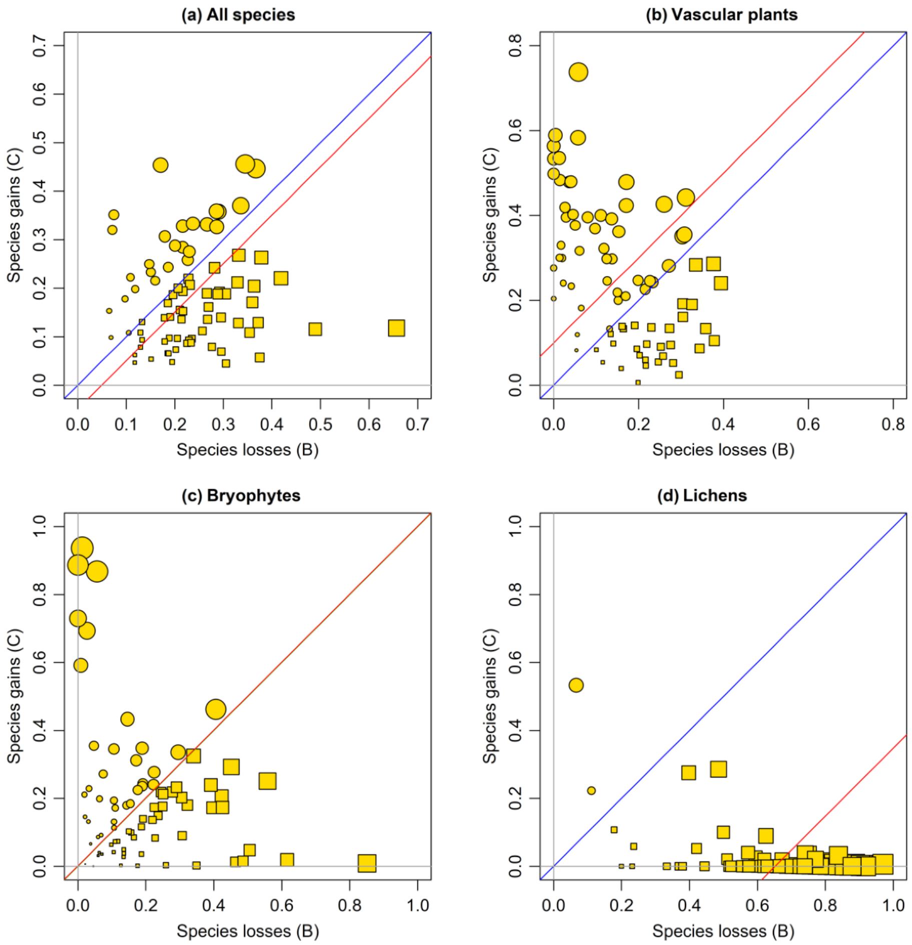

Figure 3. BC-plots illustrate the output of TBI analyses by displaying if temporal changes in plant communities are dominated by gains (circles) or losses (squares). Each symbol represents one site, and its size is proportional to the TBI values. BC-plots are drawn for a) all species and separately for b) vascular plants, c) bryophytes and (d) lichens. The diagonal blue line indicates where there is a balance between gains and losses, while the red line passes the centroids of all the symbols and is placed on the side that dominates temporal changes.

Table 2. Changes in species' frequencies, absolute mean cover (with 95 % confidence intervals) and relative cover across all study plots over time. Only species with significant changes are listed. P-values are based on paired t-tests made for species absolute covers with 9999 permutations (p.perm) and are corrected for multiple testing (p.adjust). *Seedlings only. List of all species in Appendix S3.

species	frequency 1981 / 2022	cover (%) 1981 / 2022	absolute cover change (CI's) (%)	relative cover change (%)	p.perm	p.adjust
Arctous alpina	14 / 6	0.22 / 0.02	-0.20 (-0.38, 0)	-90.9	< 0.001	0.032
Calluna vulgaris	69 / 65	12.78 / 7.68	-5.10 (-7.83, -2.36)	-39.9	< 0.001	0.017
Empetrum nigrum	80 / 80	9.94 / 15.05	+5.11 (2.94, 7.28)	+51.4	< 0.001	0.007
Festuca ovina	6 / 1	0.04 / <0.01	-0.04 (-0.08, 0)	-92.9	0.016	0.799
*Pinus sylvestris**	30 / 41	0.13 / 0.34	+0.21 (0.05, 0.37)	+161.5	0.003	0.135
Vaccinium myrtillus	78 / 78	6.02 / 9.19	+3.17 (1.32, 5.03)	+52.7	< 0.001	0.037
Vaccinium uliginosum	22 / 22	0.33 / 0.85	+0.52 (0.02, 1.02)	+157.6	0.012	0.627
Vaccinium vitis-idaea	80 / 80	4.99 / 8.11	+3.12 (2.07, 4.18)	+62.5	< 0.001	0.007
Pohlia sp.	13 / 33	0.04 / 0.20	+0.16 (0, 0.35)	+400.0	< 0.001	0.017
Polytrichum sp.	35 / 22	0.78/ 0.15	-0.63 (-1.43, 0.16)	-80.8	< 0.001	0.007
Ptilidium sp.	31 / 38	0.91 / 0.31	-0.60 (-1.15, -0.04)	-65.9	0.015	0.770

Cetraria ericetorum	14 / 2	0.15 / 0.01	-0.14 (-0.25, -0.04)	-93.3	< 0.001	0.011
Cladonia arbuscula	79 / 73	6.86 / 0.38	-6.48 (-7.92, -5.04)	-94.4	< 0.001	0.007
Cladonia rangiferina	78 / 77	4.00 / 0.45	-3.55 (-4.47, -2.64)	-88.8	< 0.001	0.007
Cladonia stellaris	68 / 43	2.36 / 0.15	-2.21 (-3.11, -1.31)	-93.6	< 0.001	0.007
Cladonia sp.	80 / 80	3.03 / 1.41	-1.62 (-2.27, -0.97)	-53.5	< 0.001	0.007
Stereocaulon sp.	20 / 3	0.09 / 0.01	-0.08 (-0.12, -0.04)	-88.9	< 0.001	0.007

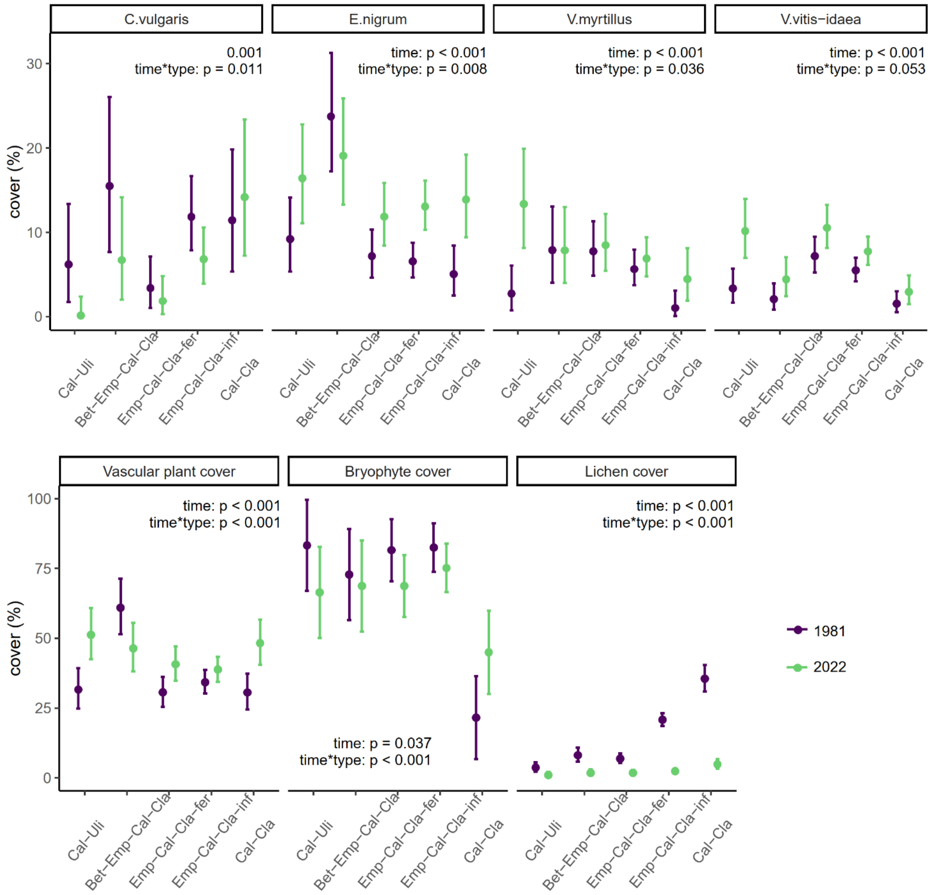

Figure 4. Temporal changes in the mean cover of dominant dwarf shrubs (upper panel) and in the cover of different plant groups (lower panel) in different vegetation types. Means are linear mixed model effects with 95 % confidence intervals. For each variable, the significance of time and the interaction between time and vegetation type are shown (detailed model statistics in Appendix S5).

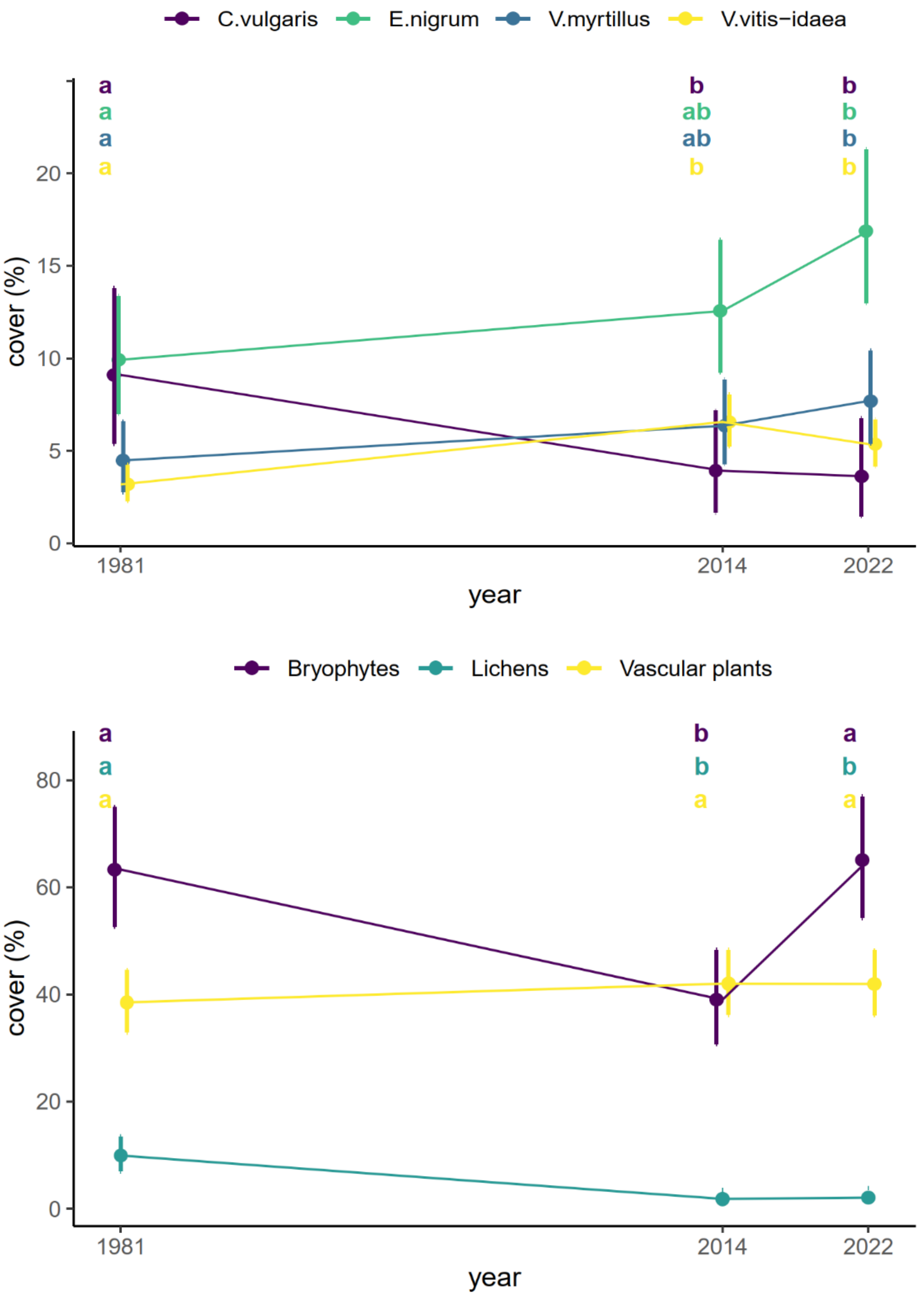

Figure 5. Temporal dynamics in the cover of dominant dwarf shrub species (upper panel) and different plant groups (lower panel) in three time points. Same sample sites (n = 22) were included from each year. Means are linear mixed model effects with 95 % confidence intervals. Letters indicate significant ($p < 0.05$) difference between years and are based on Tukey's post hoc tests (statistics in Appendix S6).

Discussion

We found that the studied northern boreal plant communities have shifted towards more dwarf shrub dominance and have experienced profound losses in lichen cover and diversity during the past 40 years. While these changes were expected based on earlier studies (e.g. Väre *et al.* 1996), the decline in lichens was particularly pronounced, indicating that certain species are close to disappear locally. Recently, the expansion of evergreen dwarf shrub *E. nigrum* have been reported from mountain birch forests, treeless heaths, and tundra (Bråthen *et al.* 2024; Maliniemi *et al.* 2018; Vowles *et al.* 2017; Wilson & Nilsson 2009,), but less from boreal forests, where its strong expansion is indicative of late successional stages and potential ecosystem retrogression (Nilsson & Wardle 2005). However, its relatively rapid increase during the past decade in the study area (Fig. 5) suggests that it can be increasing more broadly also in northern boreal forests. Our study showed that understorey vegetation change is evident over several decades in northern boreal forests with generally slow process rates and that it is important to consider also non-vascular cryptogams (bryophytes and lichens) to gain a comprehensive understanding of the vegetation dynamics and their potential outcomes over the long-term.

The studied plant communities were already characterised by dwarf shrubs 40 years ago. However, their cover had increased over decades, but with species-specific changes. Increased cover of dwarf shrubs is in line with long-term observations of increasing shrub abundance made across the northern hemisphere that have been linked to warmer climate (e.g. in Bråthen *et al.* 2018; Maliniemi & Virtanen 2021; Myers-Smith *et al.* 2011; Tuomi et al. 2024), but also to natural succession in the absence of forest fires (Maliniemi *et al.* 2023). The latter also explains, at least partly, the changes in species dominance patterns from *C. vulgaris* dominated system towards *Vaccinium* spp. and *E. nigrum* dominance, which is indicative of late successional stages in boreal forest understories (Nilsson & Wardle 2005; Tybirk *et al.* 2000). This stage is characterized by moister conditions due to faster accumulation of organic material (Wardle *et al.* 2003). However, tree canopies in the study area have remained rather unchanged (Appendix S4), comparable to findings in Franke *et al.* (2015) from the same area in 1983-2009. Thus, not only succession due to closing canopy, but also changing moisture conditions driven by long-term changes in snow cover duration and thickness most likely co-drive the observed trends (Luomaranta, Aalto & Jylhä 2019). Especially evergreen dwarf shrub *E. nigrum* show a strong response to earlier snowmelt (Wipf & Rixen 2010) that has been observed in the study area during the past decades (Callaghan *et al.* 2011).

Our results clearly show that *E. nigrum* expansion is occurring also in northern(most) boreal forests in Fennoscandia and suggest that this is a rather recent phenomenon (Fig. 5). Similar to what has been reported from treeless heathlands (Bråthen *et al.* 2024), *E. nigrum* expansion has been strongest on sites with originally low *E. nigrum* cover (Fig. 4). As a clonally growing allelopathic species that is a strong nutrient competitor, *E. nigrum* has the advantage of being able to colonize effectively compared to most other accompanying species (Nilsson & Wardle 2005; Tybirk *et al.* 2000). Strong increase in dwarf shrubs and especially *E. nigrum*, has high potential to start slowing down regeneration of *P. sylvestris* (Nilsson *et al.* 1993) and can eventually lead to ecosystem retrogression (Nilsson & Wardle 2005). However, *E. nigrum* is sensitive to disturbance, especially fires, that can prevent its expansion and revert its effects on the ecosystem (Nilsson & Wardle 2005). Evidence from high-latitude environments has shown that *E. nigrum* has a negative impact on many aspects of biodiversity (Bråthen *et al.* 2024;

Salminen *et al.* 2023; Tuomi et al. 2024). Therefore, further expansion of *E. nigrum* could be detrimental particularly to lichens, which were severely declined in the study area compared to 1980s, and these dynamics should be closely monitored.

Reindeer grazing is a key factor driving long-term lichen decline in northern Fennoscandia (Akujärvi *et al.* 2014; Bernes et al. 2015; den Herder *et al.* 2003; Kumpula *et al.* 2014; Stark *et al.* 2023) and the observed lichen decline in this study is in line with this firm evidence. Our results strongly suggest that when considering both frequency and cover, lichen species *Cetraria ericetorum* and *Stereocaulon* spp. have declined close to a level of local disappearance. Although our data do not allow testing the effect of different drivers on the observed lichen decline, it is likely that in addition to grazing, dwarf shrub encroachment further suppresses lichens, as also found by Tonteri *et al.* (2022), and this may be the case especially with pioneer lichens such as *Stereocaulon* species. Taller shrub expansion or increased tree saplings was not observed in this study, similar to other grazed areas in northern Europe, where reindeer inhibit expansion of taller shrubs and tree saplings (Maliniemi *et al.* 2018; Vowles *et al.* 2017; Vuorinen *et al.* 2017). Reindeer grazing has also been shown to have a negative impact on *C. vulgaris* biomass (Väre, Ohtonen & Mikkola 1996) and cover (Kumpula *et al.* 2011), yet some other studies have not observed such effects (Vowles *et al.* 2017). Also, as a by-product of digging for food, reindeer remove the protective snow cover in winter, which can harm *C. vulgaris* (and lichens) but perhaps to a lesser extent some other species, such as *E. nigrum*, that are more adaptable to changing snow conditions (Bienau *et al.* 2014). *C. vulgaris* is particularly sensitive to reduced wintertime snow cover that, when extreme, has been documented to cause *C. vulgaris* diebacks (Bjerke *et al.* 2017; Hancock 2008). However, it is likely that grazing alone does not explain decreased *C. vulgaris* cover, but it is also negatively affected by the long-term succession and changing climatic conditions.

Although temporal changes in dwarf shrub dominance patterns showed a general increase in *E. nigrum* and *Vaccinium* spp. and decrease in *C. vulgaris*, there were some site type specific differences. One of the most distinct compositional changes had occurred in the driest *Calluna-Cladina* site type where the expansion of *E. nigrum* was strongest (Fig. 5) and where bryophyte cover had replaced lichens. Such shift in the cover of non-vascular cryptogams may have occurred in response to grazing (also in Tonteri *et al.* 2022), as shown by Väre *et al.* (1995) in a comparable site type in northern Finland, whereas strong *E. nigrum* expansion is comparable to that occurring in the oligotrophic treeless heathlands of northern Finland (Maliniemi *et al.* 2018). In general, differences between site types seem to have become smaller, as also indicated in the NMDS (Fig. 2), even though biotic homogenisation across the sites was not statistically confirmed. However, our results indicate that if the current trend continues, biotic homogenisation will likely be evident in the future.

Our results also hint at asynchronous temporal dynamics between dominant dwarf shrub species and different plant groups in the studied plant communities (Fig. 5). Lichen loss seems to have taken place earlier in the study period and may have resulted rather soon after the increase and peak in grazing pressure in late 1980s (Appendix S1). As lichens recover slowly (Klein & Shulski 2009), their cover has not restored under grazing pressure that stabilized at the level of circa 1.5-2 reindeer per square kilometer since the peak. However, even though current grazing pressure would no longer substantially reduce lichen abundance, further increases in the number of reindeer might do so, as well as ongoing climate warming that has been shown to have a negative effect on lichen cover and diversity (Klein & Shulski 2009; Lang *et al.* 2012). The increase of *E. nigrum*, in turn, seems to be a more recent phenomenon and coincides with the rapid warming during the later part of the study period. At the same time with the strong *E. nigrum* increase, also bryophyte cover increased substantially, which is characteristic to the late successional stage proceeding to retrogressive phase (Nilsson & Wardle 2005).

Historical vegetation data provide essential baseline information, against which temporal changes can be observed using a resurvey study approach. This approach complements long-term monitoring that is lacking in several areas and habitat types. Whereas two time points can reveal longer-term temporal trends in vegetation, more sampling points are needed to reveal more specific and shorter-term temporal dynamics (see also Hédl & Chudomelová 2020). Also, it should be noted that old site type classifications may no longer be valid as such (see Fig. 2 for temporal shifts in site types from 1981 to 2022) and this should be considered in areas and habitats where classifications dating back decades are used to guide current management and conservation.

Conclusions

Studied northern boreal forest understory plant communities have undergone clear shift in their dwarf shrub and lichen abundance over the past 40 years and currently represent a successional stage that is linked to ecosystem retrogression. Our results indicate that the observed shift, and especially the expansion of *E. nigrum* has occurred recently and relatively rapidly. *E. nigrum* expansion should be further monitored as it has negative effects on many facets of biodiversity and several above- and belowground processes (Nilsson & Wardle 2005). Severely declining lichens appear to be particularly vulnerable, facing multiple threats including reindeer grazing, climate warming and expansion of *E. nigrum*. Although the effects of reindeer on vegetation (other than tall shrubs and lichens) are highly context-dependent (Bernes *et al.* 2015) and further mixed with climate change effects, the consistency of the observed changes suggests that similar changes are occurring elsewhere in northern boreal forests with comparable environmental conditions and long-term grazing pressure.

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