

# ECOGRAPHY

## Research article

### Changing species dominance patterns of Boreal-Arctic heathlands: evidence of biotic homogenization

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Heathlands are extensive systems often dominated by slow-growing and long-lived woody plants. These systems require longer-term studies to capture if and how they are changing over time. In 2020, we resurveyed species richness and cover of vascular plant communities in 139 heathlands along the coastline of northern Fennoscandia, first surveyed during 1965–1975. The first survey included six heathland types, each with dominance – a cover of 25% or more – of the dwarf shrubs *Calluna vulgaris*, *Kalmia procumbens*, *Betula nana*, *Vaccinium myrtillus* and *Empetrum nigrum*. The two latter heathland types made up 29% and 48%, respectively, of all heathlands. In addition to the dominant dwarf shrubs giving their names to the heathland types, a few other species qualified as dominant. In the resurvey, all the heathland types had *E. nigrum* as the single dominant species, except for the heathland formerly dominated by *B. nana*. Most other species had low cover both at the time of the original survey and the resurvey. Also, the heathland types were species poor at the time of the original survey, with an average of eight vascular plant species per 4 m<sup>2</sup> and were found equally species poor in the resurvey. Species richness differed between heathland types only at the time of the original survey, and the ratio of species exchange between the two surveys was negatively related to the original cover of *E. nigrum*.

Here we provide a half-century perspective on vegetation change, during which several heathland types in northern Fennoscandia have changed to *Empetrum* heathlands, reducing the diversity of heathland types across the Boreal to Arctic landscape. As a native plant, *E. nigrum* cannot be considered invasive, but its allelopathic capacity has likely already modified these heathland ecosystems and will continue to do so, reducing ecosystem multifunctionality across the region.

Keywords: biodiversity change, *Empetrum nigrum*, long-term, regional scale, resurvey, vascular plants



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## Introduction

Biodiversity change and associated ecosystem change is happening as a response to global environmental change (IPBES 2019). Changes in biodiversity over time can be of many types. One type of change, biotic homogenization, is a process whereby genetic, taxonomic or functional similarities of biotas increase over time (sensu Olden and Rooney 2006). Changing biodiversity across larger scales can also take the form of biotic heterogenization, a process in which ecological communities, for instance, become more dissimilar over time (Socolar et al. 2016). To identify whether biotic homogenization or heterogenization is taking place, knowledge of the identity of the biota in communities over space and time is needed. Within the framework of homogenization and heterogenization, communities can lose species and yet still become more heterogenous over time, or communities can gain species and still become more homogenous (sensu Socolar et al. 2016).

Boreal-Arctic heathland ecosystems, mainly covered by clonal dwarf shrubs (Walker et al. 2005), are systems typically influenced by long-lived species. Their clonal growth form and longevity make individual dwarf shrubs able to cover extensive areas and have a stable presence (de Witte and Stöcklin 2010). Boreal-Arctic heathlands dominated by dwarf shrubs also harbor species of forbs, graminoids, vascular and non-vascular cryptogams, and are generally characterized by the presence of few species but several functional groups (Wookey et al. 2009). Plants with faster process rates are expected to benefit from a warmer climate, suggesting that the most nutritious plants, the herbaceous plants such as forbs and graminoids (Niinemets et al. 2015), will have the ability to increase growth rates the most. Such changes in plant species composition of heathlands have consequence to their ecosystem multifunctionality (Liu et al. 2021). Therefore, given the extensive nature of Boreal-Arctic heathlands, climate change can be a driver of modified ecosystem multi-functionality over large geographic areas. Yet, the observed greening of the Arctic suggests deciduous shrubs benefit the most from elevated temperatures (Elmendorf et al. 2012) unless controlled by herbivores (Olofsson et al. 2009, Christie et al. 2015, Bråthen et al. 2017). Also, deciduous shrubs are predicted to respond more strongly to warming than evergreen shrubs, even when browsed by herbivores (Christie et al. 2015). Several empirical studies do, however, report encroachment by native evergreen dwarf shrub species, also under herbivory (Angers-Blondin and Boudreau 2017, Maliniemi et al. 2018, Vowles and Björk 2019, Tuomi et al. 2022). Such horizontal encroachment by evergreen dwarf shrubs causes distinctly different ecosystem processes than that of either herbaceous plants or deciduous shrub encroachment, and is suggested being termed 'evergreening' (Tuomi et al. 2022). Predictions also suggest that alien plants not yet present, but adapted to the novel climates in Arctic areas, are likely to invade (Seebens et al. 2017). Hence, there are several ways by which biodiversity change can take place, causing either biotic homogenization or heterogenization of

the Boreal-Arctic heathland ecosystems. Adding to the complexity, Arctic heathland systems consist of a range of heathland types that vary in regard to dominating dwarf shrub species (Walker et al. 2005), and that also may affect the way the heathlands change (Wiszt et al. 2013).

Recent vegetation resurveys have shown how species compositions can change over time in Fennoscandian Boreal-Arctic heathland systems. In northern Finland, evergreen dwarf shrubs, and particularly *Empetrum nigrum*, have increased whereas lichens have decreased across heathlands over the last five decades (Vuorinen et al. 2017, Maliniemi et al. 2018). Similarly, in northern Sweden, evergreen shrubs have expanded in both shrub heathland and birch forest over the last two decades (Vowles et al. 2017a). These empirical findings suggest, contrary to expectations of evergreen dwarf shrub vulnerability to climate change (Bokhorst et al. 2015), that native evergreen dwarf shrub species are responsive to climate warming (Vowles and Björk 2019), and that there is an evergreening rather than greening in Arctic and Boreal heathland systems. Also, the succession into forests is considered a current threat to treeless Boreal heathland systems in Norway (Hovstad et al. 2018) and to Atlantic *Calluna vulgaris*-dominated heathlands across northern Europe (Løvschal and Damgaard 2022). Tree or larger shrub encroachment into treeless heath may, however, depend on the abundance of *E. nigrum*; no tree or larger shrub encroachment was found in *E. nigrum*-dominated heathlands in Finland (Maliniemi et al. 2018) nor in Atlantic *C. vulgaris*-dominated heathlands where *E. nigrum* was common (Løvschal and Damgaard 2022). Furthermore, after adding 500 birch seeds to a dwarf shrub heathland in the forest ecotone, Vuorinen et al. (2017) found only two surviving birch seedlings. Similarly, González et al. (2021) found no tree establishment in either disturbed or intact dwarf shrub heathlands in the forest ecotone over a period of eight years. These results align with findings that heathlands dominated by evergreen dwarf shrubs, and in particular by *E. nigrum*, are resistant to change (Aerts 2010, Bokhorst et al. 2018, González et al. 2019). Bokhorst et al. (2018) even showed recovery of an evergreen heathland after a caterpillar outbreak that defoliated 81% of *E. nigrum* shoots. This raises the question if biodiversity in Arctic and Boreal heathland systems is likely to change in response to climate change only when not originally dominated by evergreen dwarf shrub species, and particularly by *E. nigrum*.

Here we address the longer-term temporal and large-scale changes in biodiversity in the heathlands across northern Fennoscandia, a region representing the transition between Arctic and Boreal systems. We present results from a vegetation resurvey of heathlands, originally surveyed by Haapasaari (1988) in the late 1960s and early 1970s, and ask if biodiversity homogenization or heterogenization (sensu Socolar et al. 2016) has taken place in these heathlands. If *E. nigrum* has encroached where it was already present in the 1970s, other biodiversity may have declined (Bråthen et al. 2018). With dominant species, species composition and richness becoming more similar among heathland types, this

would be indicative of the process termed subtractive homogenization (sensu Socolar et al. 2016). However, if certain species – in particular dominant dwarf shrubs – have benefitted through facilitation such as wind protection by *E. nigrum* (Pellissier et al. 2010), the heathlands may still be functionally distinct in terms of dwarf shrub dominance. With shared dominance between several dwarf shrub species and with little overall change in species composition, functionality and richness, the process may rather be additive homogenization (sensu Socolar et al. 2016). Last, where deciduous dwarf shrubs such as *Vaccinium myrtillus* or *C. vulgaris* were dominating in the 1970s, we expect deciduous shrubs and trees, especially boreal species, to have encroached (Webb 1998, Vandvik et al. 2005); whereas we expect no change where evergreen dwarf shrubs and *E. nigrum* were dominating, and the overall process to be additive heterogenization (sensu Socolar et al. 2016). Disturbances are expected to enhance any spatial differences in species composition and richness. We focus on dominant species and functional groups (growth forms) to assess changes in species dominance and functionality, and we focus on species composition and species richness to assess changes in overall heathland biodiversity.

## Material and methods

### Study region

In 2020, we resurveyed heathland sites along the coastline of Troms and Finnmark county, northern Norway (69.6°N, 18.7°E–70.5°N, 30.7°E). These sites are north of the Atlantic *C. vulgaris*-dominated heathlands (Løvschal and Damgaard 2022), yet they represent similar heathland types. The sites were originally surveyed by Matti Haapasaari during 1965–1975 (Haapasaari 1988) (Fig. 1, Supporting information). At that time the heathlands were categorized as oligotrophic and with both deciduous and evergreen dwarf shrubs being the dominant plants. The heathlands were all coastal and in

close vicinity to roads and settlements in the forest ecotone, in low alpine landscapes or in landscapes close to the sea-level of exposed coast or inland fjords.

The study region thus has a variable climate, ranging from oceanic to more coastal and continental climate, also affected by the variable topography along the coastline (Fig. 1). Vegetation types vary from northern boreal among the south-western plots to more Arctic conditions among the north-eastern plots. The region has a variable bedrock, ranging from limestone and gabbro to sandstone and granite (Norway's national geological survey). The region has undergone changes in climate over the last decades, in particular a lengthening of the growing season (Tuomi et al. 2022) and an associated shortening of the snow cover duration (Pedersen et al. 2021).

The study region has low density of human settlements, yet there has been an overall increase in population size since the time of the first survey ([www.ssb.no/statbank/table/06913](http://www.ssb.no/statbank/table/06913)). Intensified land use has therefore likely taken place between the original survey and the resurvey, with anthropogenic activities and livestock modulating heathland change across the region. Also, although evidence is scarce in this transition zone between boreal, oroarctic and Arctic systems, it is likely that some of these heathlands have been exposed to anthropogenic fires as part of traditional management systems (Edvardsen et al. 1988). However, no signs of current fire management were found during the resurvey.

### The resurvey

The relocation of sites was based on plot-wise information reported in the original publication, including detailed descriptions of the area, the heathland type and its approximate extent (m<sup>2</sup>), and with data on elevation, slope and aspect (Haapasaari 1988, Maliniemi et al. 2018). Prior to the field resurvey, approximate coordinates were carefully estimated for a total of 150 vegetation plots in 139 sites (Fig. 1), a few sites having more than one plot. We used digital elevation

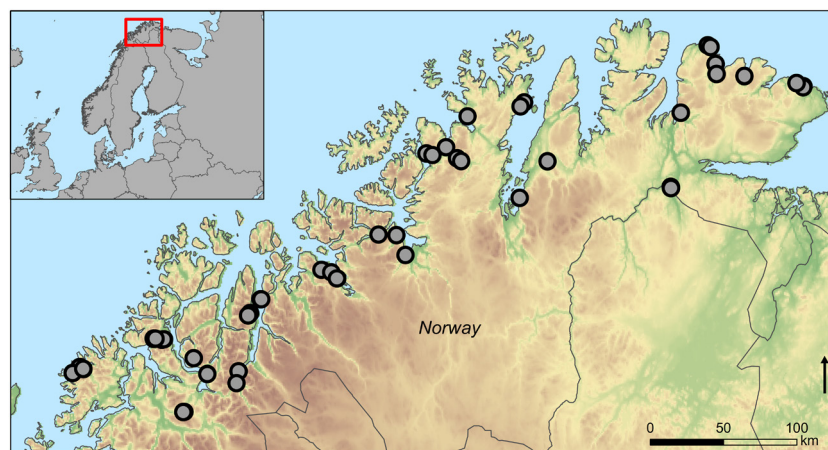


Figure 1. Distribution of the resurveyed vegetation sites ( $n = 139$ ) along the coastal heathlands of northern Norway. Several sites were in heathlands approximately 50 m to one or a few kilometers in proximity, being too close to show up as separate sites on a map of the whole region. Shades of yellow and brown indicate elevation up to a maximum of 1834 m a.s.l. in the region.



models and aerial images which, in most cases, limited the potential plot location to a relatively small area. Plots that could not be given approximate coordinates were left out from this study. In case where coordinates suggested plot placement in an unlikely location – such as in a boulder-field, in a cliff or clearly outside a neighboring, more homogenous heathland – a more accurate relocation of the plot was made in the field based on the plot-wise information. Within each site we established a  $2 \times 2$  m plot. Resembling the original survey, plots were placed so that their vegetation was representative of the average community composition of the studied heathland type. However, because the accurate slope can be difficult to estimate from digital maps or aerial images, we sometimes relocated the plot to the nearest correct slope. Also, in the few heathland sites where Haapasaari surveyed more than one plot, we carefully evaluated the heathland based on his descriptions before final plot placements in the resurvey.

For each plot we estimated the absolute cover (% of plot area covered) of each vascular plant species. We followed the cover scale of the original survey (0.1, 0.25, 0.5, 1, 2, 3, 5, 7, 10, 20, 30 ... 90, 100% cover). We also recorded any visible human influence on each heathland site, such as a fireplace, viewpoint cabins, old buildings, trails, industrial buildings and any signs of herbivory or marine deposits. The resurvey lasted from mid-July to mid-September, corresponding to the timing of the original survey. The resampling was conducted by three principal resamplers, either alone or with assistance.

Similar to earlier experience with another set of original data from Haapasaari (Maliniemi et al. 2018), the resurveyed heathland types were at least partly recognizable by their original community composition and rarely showed complete temporal turnover. Even though relocation error inherently exists for all the resurveyed plots, such as for any quasi-permanent plots, certain criteria should be met in order to use quasi-permanent data for temporal comparisons (Kapfer et al. 2017). These criteria are 1) detailed location information, 2) comparable seasonality between the time periods, 3) use of experienced observers and 4) harmonization of data between the surveys (Kapfer et al. 2017). In our study we ensured these criteria, and hence the magnitude of observed changes in our study is likely to be larger than the relocation error itself (Kopecký and Macek 2015).

The number of heathland sites per heathland type differed, with *Betula*, *Calluna*, *Racomitrium* and *Windswept* heathlands having 4, 6, 12 and 11 sites, respectively, whereas *Myrtillus* and *Empetrum* heathlands had 40 and 66 sites, respectively. Hence, most plots were sampled in what Haapasaari defined as *Empetrum* or *Myrtillus* heathlands. It was also in these heathlands that the relocated sites having more than one plot occurred, with plots in duplicates, triplicates or quadruplicates per site (in a total of eight and four sites in *Empetrum* and *Myrtillus* heathlands, respectively). Finally, the number of sites with disturbance also differed between heathland types (Supporting information), with some heathlands having a lower proportion of disturbed sites than others.

## Data preparation for analysis

First, we harmonized species names between the two surveys. Several species were without reproductive structures during the sampling. For species that are difficult to separate without reproductive structures, such as species of *Calamagrostis*, *Melampyrum* and *Pinguicula*, we replaced the suggested species names with family names. We also harmonized data in terms of cover values. When we compared the cover values sampled in the 1970s with those sampled in 2020, we found that the estimates were overall larger in 2020 (Supporting information). This could be due to a true increase in cover; yet, to omit any potential systematic bias in cover values between the surveys, we calculated the proportional cover of each species within each time period. For each species within each survey we divided its cover by the total vascular plant cover estimated within the respective survey. We present the actual cover values only when displaying the abundance distribution among the dominant, defining species for each heathland type.

For further preparation of the data we identified common, dominant species as defined by the Norwegian Biodiversity Information Centre (biodiversity.no), where species with more than 25% cover are considered dominant and species with occurrence in at least 12.5% of plots are considered common. For each period, the species that were commonly dominant were identified for each of the heathland types and for all heathlands together.

For an assessment of heathland community change we calculated new variables. For functional change we grouped species according to growth form and calculated the cover of forbs, graminoids, vascular cryptogams, deciduous dwarf shrubs, evergreen dwarf shrubs and trees per plot per period. We calculated the species richness per plot for both periods separately and the temporal beta diversity per plot. For the latter we calculated the species exchange ratio based on abundance (SERa) (Hillebrand et al. 2018) (Eq. 1), in which  $p$ , the proportion of abundance (cover) per species 1) per plot is represented in the 1970s and 2020 by  $p_i$  and  $p'_i$ , respectively:

$$\text{SERa} = \frac{\text{Sum}((p - p')^2)}{\text{Sum}(p^2) + \text{Sum}(p'^2) - \text{Sum}(p \times p')} \quad (1)$$

Finally, we calculated an index to account for the change in *E. nigrum* cover between the two surveys by subtracting the original survey cover from that estimated in the resurvey.

The visible signs of human influence, herbivory or marine influence registered in 2020 were categorized as path (13 sites), nearby industry (15 sites), tourist and/or recreational spot (12 sites), herbivory (39 sites) and marine deposits (2 sites) for a total of 81 sites. The remaining sites were categorized as no disturbance. At the time of the original survey there were no recordings of visible signs of human influence or other disturbances (Haapasaari 1988). For the data

analysis, all the disturbance categories were pooled to a binary factorial predictor of disturbance.

## Data analysis

We used a linear mixed-effects model (LMM) framework for the statistical analyses on the change in heathlands from the 1970s until 2020. We fitted LMMs for the response variables cover of 'commonly dominant' species, cover of growth forms and species richness, in which the fixed-effects structure included the interaction among the two categorical predictors survey year (1970s and 2020) and heathland type (Betula, Calluna, Empetrum, Myrtillus, Racomitrium and Windswept). To account for the hierarchical spatial structure of the sites having more than one plot, we specified site as random-effect. Biome and elevation were also specified and tested for importance as random-effects. To assess the change in cover for the 'commonly dominant' species and growth forms we only used the plots where a given species or growth form was present in either one or both periods.

For the response variable SERa we fitted LMM with heathland type as fixed-effect predictor and with site as random-effect, and with biome and habitat specified and tested for importance as random-effects. We also fitted LMMs for assessing species richness in relation to *E. nigrum* cover-change between the surveys, for assessing SERa in relation to *E. nigrum* cover in the original survey, and for assessing both species richness and *E. nigrum* cover in 2020 in relation to the disturbance assessed in 2020. For the latter analysis we pooled heathland types because of their unequal proportion of sites with disturbance, assessing the relation to disturbance in Empetrum heathland to that of other heathlands.

When necessary, data were transformed to meet assumptions of normal distribution. We validated each model by checking for normal distribution of the residuals and linearity between observed and fitted values. Results are presented in figures with model estimates of marginal means (EMMs) and their confidence intervals including raw data of cover either as point data or in violin plots. An extensive overview of results in figures and tables is provided in the Supporting information.

Finally, we assessed the uniqueness of the species composition of the different heathland types during both periods using non-metric multidimensional scaling (NMDS). We applied pairwise permutational multivariate analysis of variance (pairwise PERMANOVA) and the function *adonis* with 999 permutations to compare all heathland types within each period separately. The periods were analysed separately because the ordination did not converge when including both periods.

Data analyses were run in R ver. 4.3.0 ([www.r-project.org](http://www.r-project.org)) with packages 'lmerTest' (Kuznetsova et al. 2017), 'emmeans' for the estimated marginal means of model outputs (Lenth 2023), 'vegan' for the NMDS and PERMANOVA (Oksanen et al. 2022), and 'ggplot2' for graphical presentations (Wickham 2016).

## Results

The distribution of cover values among the species defining the heathland types in the 1970s had changed in 2020. Each of *Betula nana*, *C. vulgaris*, *E. nigrum*, *K. procumbens* and *V. myrtillus* dominated the right tail of the distribution in at least one heathland type in the 1970s, whereas in 2020 all the right tails were dominated by *E. nigrum* apart from in the Betula heathlands (Fig. 2). For a direct comparison between the periods the remaining results are based on relative cover.

Across all heathland sites and both periods, a total of 104 vascular plant species were recorded including trees (5 species), dwarf shrubs (26 species including crowberry), forbs (44 species), graminoids (19 species) and vascular cryptogams (10 species). Out of the 104 species, only one species, *E. nigrum*, was found to be dominant in terms of average abundance (cover  $\geq 25\%$ ) across all heathland types in both the 1970s and in 2020, whereas 20 species were found to be common (occurrence  $\geq 12.5\%$  of plots) in each period (Table 1). Among the latter, *E. nigrum*, *Vaccinium vitis-idaea* and *V. uliginosum* were found to occur in almost all sites of some of the heathland types in the 1970s (occurrence  $\geq 80\%$  of plots), whereas in 2020 *Avenella flexuosa* and *V. myrtillus* were also found to be in this category of 'constant' species (Table 1).

The number of dominant species (cover  $\geq 25\%$ ) within each of the heathland types decreased from two in the 1970s to one in 2020 in the Calluna, Myrtillus and Windswept heathlands. In the Empetrum and Racomitrium heathlands there were only one dominant species in both periods and in the Betula heathlands the number of dominant species increased from one to two, with *B. nana* being accompanied by *E. nigrum* (Table 1). Also, the number of 'constant' species' (occurrence  $\geq 80\%$  of plots) declined in all heathland types but for the Racomitrium heathlands, where they remained stable (Table 1).

### Change in dominant species and dominant functional groups

Combining abundance (cover) and occurrence (presence), the set of species being dominant and common (in at least one heathland type and in either one or both periods) were found to be the evergreen dwarf shrubs *E. nigrum*, *V. vitis-idaea*, *K. procumbens*, *C. vulgaris*; the deciduous dwarf shrubs *V. myrtillus*, *V. uliginosum*, *Arctous alpina* and *B. nana*; and the forbs *Chamaepericlymenum suecicum* and *Diapensia lapponica*.

Significant increases in cover among these species between the 1970s and 2020 were typically within the lower range of mean cover values, remaining below an abundant cover but for *B. nana* (Fig. 3, Supporting information). In contrast, significant declines in cover were typically from higher mean cover values. Mean cover values for *C. vulgaris* in Calluna heathland, for *V. myrtillus* in Myrtillus heathland and for *K. procumbens* in the Windswept heathlands were above 25% in the 1970s and with at least 10% less in 2020 (Fig. 3). For these heathland types *E. nigrum* had significant increases

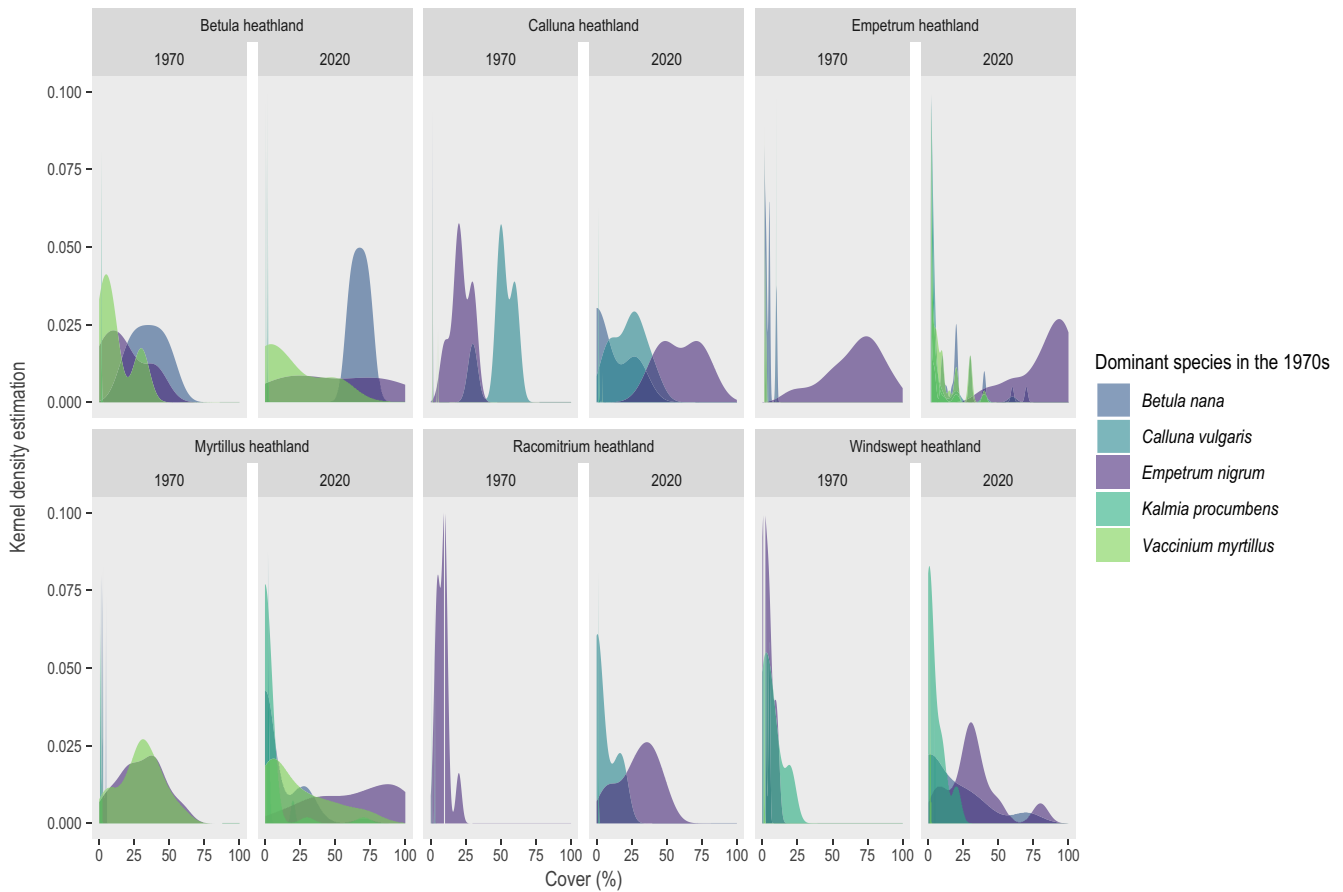


Figure 2. Density of cover values observed in the 1970s and in 2020 for each of the dominant vascular plant species defining the heathland types when observed by Haapasaaari in the 1970s. Note that numbers of sites vary between heathland types, and that this graph is based on cover values as registered within each time period.

Table 1. Number of species in different abundance and occurrence categories as applied by the Norwegian Biodiversity Information Centre (biodiversity.no). Abundance is calculated in average per heathland type or in average across all heathlands, whereas occurrence is calculated as the proportion of plots with species presence.

Heathland type	Period	Number of species			
		In abundance (cover)		In occurrence (frequency of plots)	
		Abundant ≥ 12.5%	Dominant ≥ 25%	Common ≥ 12.5%	Constant ≥ 80%
Betula	1970	2	1	18	6
	2020	2	2	22	3
Calluna	1970	2	2	21	6
	2020	2	1	19	5
Empetrum	1970	1	1	13	2
	2020	1	1	14	1
Myrtillus	1970	2	2	24	3
	2020	2	1	16	2
Racomitrium	1970	2	1	11	2
	2020	2	1	14	2
Windswept	1970	2	2	11	2
	2020	3	1	13	1
All heathlands	1970	1	1	20	3
	2020	1	1	20	5

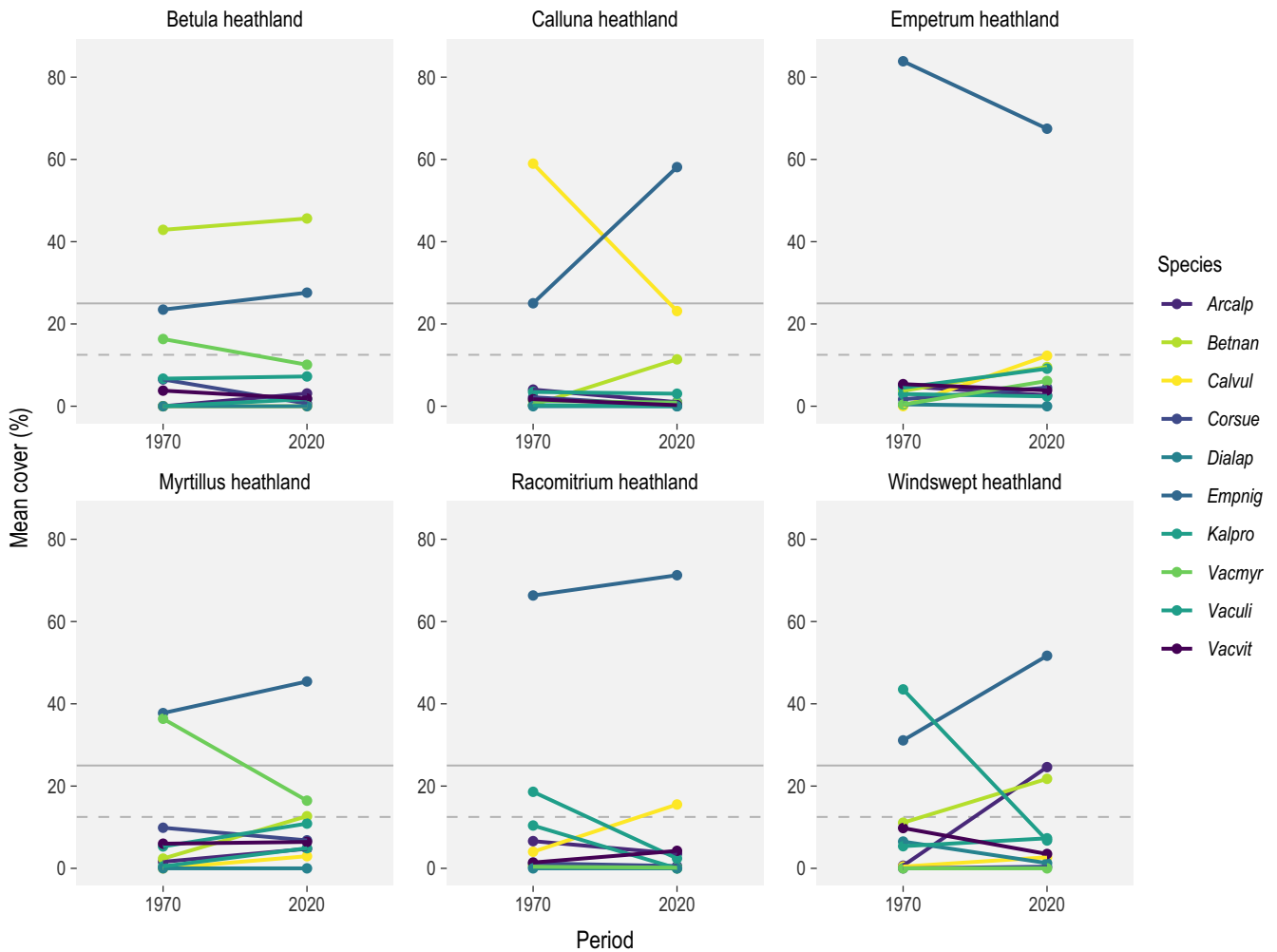


Figure 3. Mean cover of commonly dominant species in each of the heathland types and periods as predicted from mixed effects models. Dashed and solid horizontal lines indicate lower limit of cover for abundant (> 12.5%) and dominant (> 25%) species, respectively, as defined by the Norwegian Biodiversity Information Centre (biodiversity.no). Cover values are backtransformed for all species but *Empetrum nigrum*, which did not need transformation of data to meet assumptions of normal distribution. See Supporting information for model results.

in cover, becoming the sole dominant species. However, *E. nigrum* had a significant decline in Empetrum heathlands (Supporting information), yet with a high mean cover also in 2020 and with no other species becoming dominant (Fig. 3).

The rate of encroachment of *E. nigrum*, assessed as the average change per year, was slow. In Calluna heathlands, where the cover of *E. nigrum* increased the most and more than doubled from an average proportional cover of 25 to 58.1%, the yearly increase was 0.66%. In comparison, the yearly decline of *E. nigrum* in Empetrum heathlands was 0.33%. While we provide an estimate for the annual rates here, the changes in cover may not have been equal over the years.

Mean cover of several of the growth forms changed from the 1970s to 2020 in all heathland types (Fig. 4). However, significant increases in cover of forbs, graminoids, vascular cryptogams and trees were typically in low mean cover values below 5%, and the mean cover of deciduous dwarf shrubs

was subordinate to the evergreen dwarf shrubs in all heathland types but for the Betula heathlands (Fig. 4, Supporting information). The low tree cover in both periods indicates there has barely been any change in tree cover over the last five decades.

### Change in species composition

In the 1970s the species richness differed among heathland types. All heathlands dominated by deciduous shrubs or *C. vulgaris* had approximately four species more than the Empetrum, Racomitrium and Windswept heathland types (Fig. 5 upper left panel), whereas in 2020 any differences in species richness between heathland types were no longer significant (Fig. 5, Supporting information). The Empetrum heathland had a significant increase from an average of 6.47–8.01 species per plot from the 1970s to 2020, while the Myrtillus heathland had a significant decline from an average

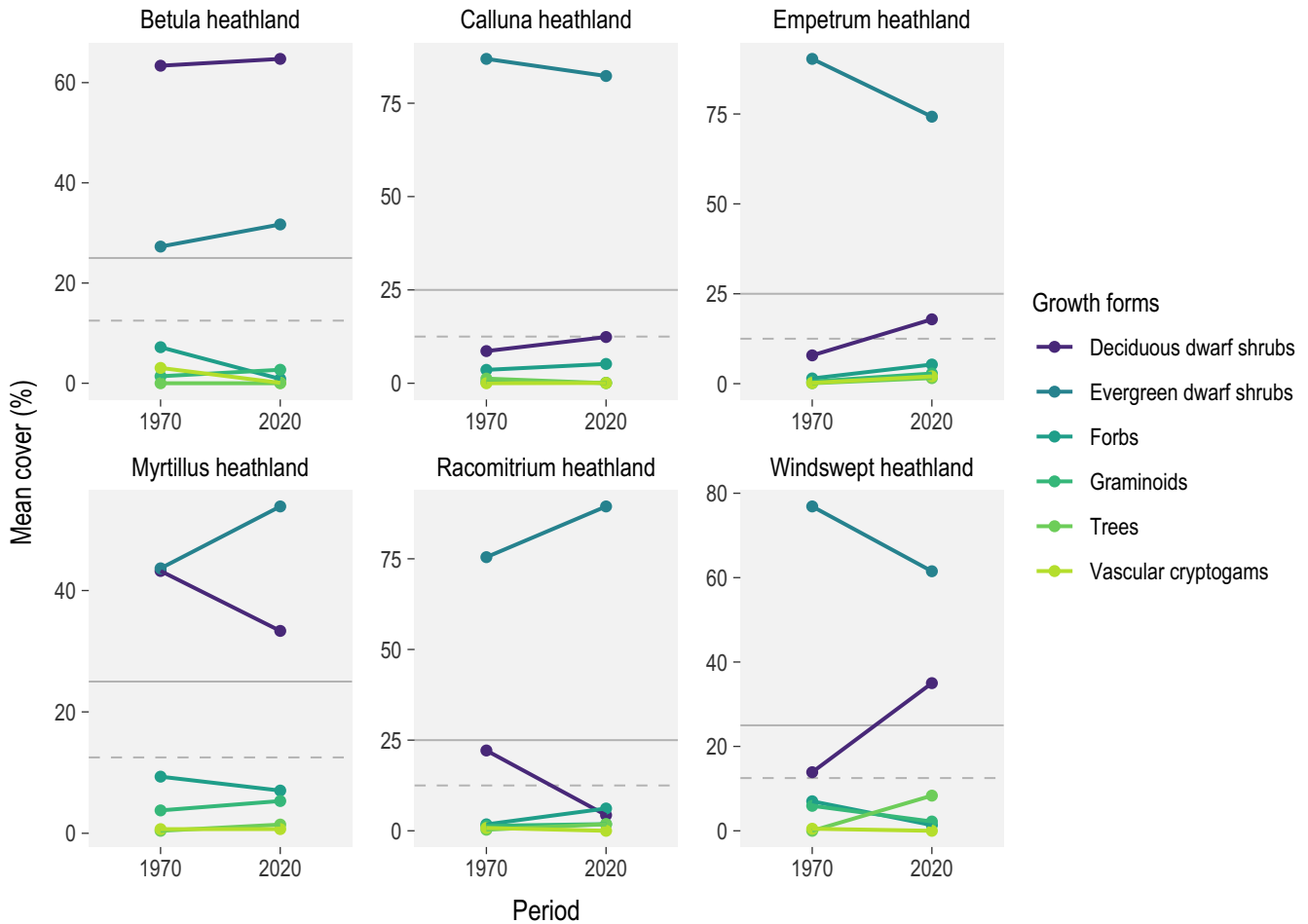


Figure 4. Mean cover of growth forms in each of the heathland types and periods as predicted from mixed effects models. Dashed and solid horizontal lines indicate lower limit for abundant cover (> 12.5%) and dominant cover (> 25%), respectively, as defined by the Norwegian Biodiversity Information Centre (biodiversity.no). Cover values are backtransformed. See Supporting information for model results.

of 10.52–8.9 species (Supporting information). Change in species richness was not related to the original cover of *E. nigrum* in the 1970s [predicted slope of  $-0.016$  ( $-0.038$  to  $0.005$  95% CI)] or to any change in *E. nigrum* cover between the periods [predicted slope of  $-0.019$  ( $-0.041$  to  $0.003$  95% CI)] (Fig. 5 upper right panel).

Species exchange ratio based on species abundance (SERa) differed between the heathland types (Fig. 5 lower panel), with all but the Betula heathland having a higher SERa compared to the Empetrum heathland. This suggests Calluna, Myrtillus, Racomitrium and Windswept heathlands all had a more distinct change in the abundance composition of species from the 1970s to 2020 (Supporting information). Furthermore, SERa was negatively related to the *E. nigrum* cover in the 1970s, with the species compositional change being lower where the original (old) *E. nigrum* cover was higher [predicted slope of  $-0.005$  ( $-0.006$  to  $-0.004$  95% CI)] (Fig. 5 lower panel).

The heathland types explained more of the variation among plots in the 1970s compared to 2020, with a  $R^2$  of

0.59 and 0.28, respectively (Fig. 6), suggesting their species composition was more distinctly different in the 1970s compared to 2020.

### Effect of disturbance

No relation between the species richness and disturbance was found in either Empetrum heathlands or in the other heathland types [mean richness in disturbed 8 (6.8–9.3 95% CI) versus non-disturbed Empetrum heathlands 7.8 (6.4–9.2 95% CI) and mean richness in disturbed 8.6 (7.4–9.8 95% CI) versus non-disturbed other heathlands 7.7 (6.4–8.9 95% CI)]. However, in the other heathland types the cover of *E. nigrum* in 2020 was lower in disturbed plots [mean cover of *E. nigrum* in disturbed 44.8 (38.3–51.4 95% CI) versus non-disturbed heathlands 58.8 (51.8–65.8 95% CI)]. In the Empetrum heathlands the cover of *E. nigrum* was not related to disturbance [mean cover in disturbed 66.5 (59.7–73.2 95% CI) versus non-disturbed heathlands 66.8 (59.3–74.3 95% CI)].



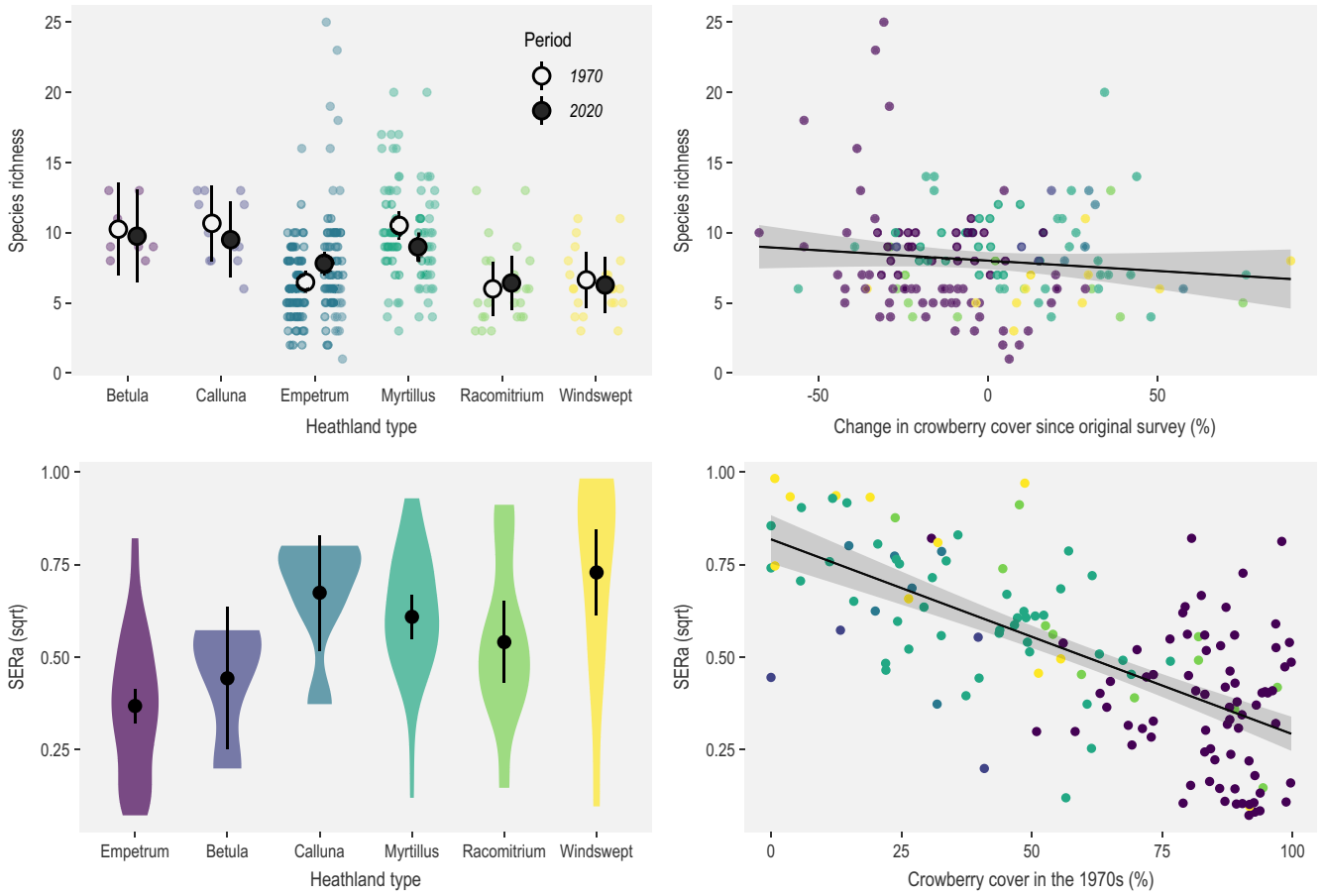


Figure 5. Predicted estimates of species richness and species exchange ratio based on abundance (SERA). Species richness ( $\pm$  confidence intervals) per heathland type and period (upper left panel) and species richness in relation to the change in crowberry *Empetrum nigrum* cover between the two periods (upper right panel). Predicted SERa means ( $\pm$  95% CI) separately for each heathland type and with each violin based on the raw transformed data (lower left panel), and the predicted linear relationship ( $\pm$  95% CI bands) between SERa and crowberry *E. nigrum* cover in the 1970s (lower right panel). Raw values are presented in color per heathland type in all panels, dots being colored according to heathland type as in the left panels. Note that dots in the upper left panel display the large difference in number of sites between heathland types and hence the variation in prediction certainty .

### Discussion

We found a decline in the diversity of heathland types over the last five decades, consistent with a longer-term spatial homogenization among Boreal-Arctic heathlands in northern Fennoscandia. The changed biodiversity patterns documented in our study are most in line with subtractive homogenization (sensu Socolar et al. 2016). Over time *E. nigrum* had gained or retained its dominance in all the heathland types and was also the only dominant plant in all but the *Betula* heathlands. Functionally, the heathlands had remained similar with dwarf shrub dominance, and with the evergreen dwarf shrubs having a higher cover than deciduous shrubs in all heathland types but in the *Betula* heathlands. All other growth forms had remained low in overall cover. The species richness differed between the heathland types in the 1970s, whereas in 2020 the species richness was similar in all types. The temporal beta diversity, assessed as the species exchange ratio based on abundance (SERA), was low in the

*Empetrum* heathland compared to the other heathland types, suggesting a temporal process by which *Empetrum* heathland remained more stable in its species composition whereas the other heathland types changed. Also, as indicated by the ordination analysis, the species composition was more distinct between the heathland types in the 1970s compared to 2020, further suggesting biotic (i.e. heathland) homogenization. In sum, this suggests that most heathland types had changed towards the *Empetrum* heathland type. Such change also implies that ecosystem multifunctionality is reduced, with consequences for regional biodiversity-ecosystem functioning (Mori et al. 2018) and nature’s contribution to people (Supporting information).

We did not find disturbance to have significantly modified spatial patterns in species richness. However, disturbed sites in encroached heathlands had 14% lower cover of *E. nigrum* compared to non-disturbed sites. Because disturbance is related to trampling by humans or mammals, such a reduction in *E. nigrum* encroachment is consistent with

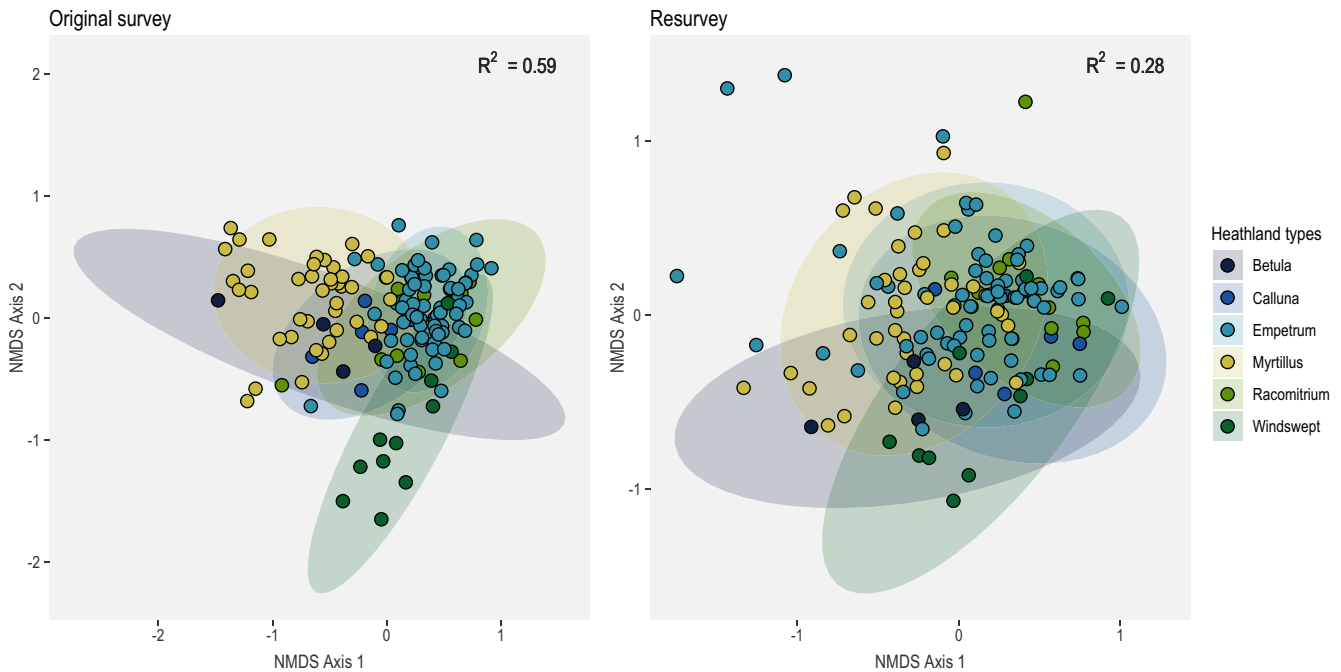


Figure 6. Two-dimensional non-metric multidimensional scaling (NMDS) ordination of plant species cover values separately for the 1970s (original survey, stress=0.16) and in 2020 (resurvey, stress=0.18). Ellipses show 95% CI of the mean. Colors are according to heathland type.

previous findings of *E. nigrum* being vulnerable to trampling (Tybirk et al. 2000), and hence we hypothesize that lack of disturbance may be a driver of *E. nigrum* encroachment. Yet, at the same time, disturbance did not promote species richness. However, *E. nigrum* has allelopathic polyphenolic compounds in its leaves that in turn can significantly retard litter decomposition, soil nutrient fluxes and seedling establishment (Wardle et al. 1998, Bråthen et al. 2010, González et al. 2021), suggesting that conditions under which richness can be enhanced by disturbance are not present where *E. nigrum* is a dominant plant.

Our results do not corroborate predictions from a previous study suggesting a range of species to be facilitated by the presence of *E. nigrum*. In particular, *K. procumbens*, *V. uliginosum*, *A. alpina* and *Rubus chamaemorus*, all suggested to be facilitated by the presence of *E. nigrum* (Pellissier et al. 2010), either remained low in cover, declined or were superseded by *E. nigrum*. In contrast, in the Empetrum heathlands, the increase in species richness, the decline in cover of *E. nigrum* and the slight increase in cover of five dominant species may suggest that in old Empetrum heathlands there is a slight improvement of growing conditions. Also, a tendency for an increase in the cover of *A. alpina* and *C. vulgaris* in the more barren Racomitrium and Windswept heathland types, does suggest that facilitation by *E. nigrum* may be a process; or, vice versa, that these species facilitate *E. nigrum*. Alternatively, in these barren habitats there is no facilitation and no competition due to the open space, with *E. nigrum* being most successful in encroaching the open space, such as has been found in sand dunes in Arctic Canada (Angers-Blondin and Boudreau 2017).

Although trees and deciduous shrubs are abundant species in the Boreal ecosystems bordering the Arctic ecosystems in the study region, and were present in the heathlands in the 1970s, they did not encroach over time. Importantly, the Calluna and Myrtillus heathlands were rather encroached by *E. nigrum*, suggesting a horizontal as opposed to a vertical encroachment. This type of encroachment is likely less visible to people. The slow encroachment rate of *E. nigrum* also suggests it is not a process attracting attention, but rather a shifting ecosystem baseline that may go unnoticed. Because *E. nigrum* is an allelopathic plant, its capacity to limit the establishment of other plant species (González et al. 2015, Pilsbacher et al. 2021) has likely been important to the heathland homogenization. Furthermore, its resistance towards extreme weather incidents (González et al. 2019) has likely been important to its stable presence in the heathlands.

We found that *E. nigrum* had encroached into heathland types varying in total vascular plant cover from 25% to 100% (as described in the original survey). This suggests a versatile capacity of *E. nigrum* to encroach into barren and stressed environments, and into more competitive environments with complete vegetation cover, terminating in a late successional stage of *E. nigrum* dominance. A previous study on the paleoecology of coastal heathland systems does predict such successional trajectories from heathlands dominated by *Racomitrium* and from windswept, barren heathlands to *E. nigrum* dominance, the latter predicted to represent a stable community that is possibly dependent on sea-spray and strong winds (Edvardsen et al. 1988). Indeed, in our dataset we only had the Racomitrium heathland in near-coastal systems, corroborating these predictions.

Paleoecological evidence does, however, also point at *E. nigrum*-dominated heathlands as a more recent heathland type, with evidence of previous burning practices and co-dominance with *C. vulgaris* (heather) being superseded by *E. nigrum* dominance after burning practices were ended (Edvardsen et al. 1988).

The heathlands we resurveyed were all classified as oligotrophic by Haapasaari (1988), hence already considered poor in plant life and nutrient availability in the 1970s. Yet, the dominance of deciduous shrubs in some of the heathland types suggests they differed in nutrient availability and hence ecosystem process rates. Deciduous shrubs such as *B. nana* and *V. myrtillus* are more nutrient rich, with an average leaf nitrogen content of 1.7 and 1.6%, respectively, compared to the evergreen *E. nigrum* with an average nitrogen content of 1.0% (Murguzur et al. 2019). The shift towards *E. nigrum* dominance in deciduous shrub-dominated heathlands thus suggests that the nutrient availability has declined. Furthermore, *E. nigrum* encroachment has likely modified the heathlands for other co-occurring organisms. For instance, a change in dominant species from *C. vulgaris* and *V. myrtillus* to *E. nigrum* is a shift from nectar availability and insect pollination to no nectar production and wind pollination (Bell and Tallis 1973). *E. nigrum*, being an allelopathic plant, also suggests environmental modification is ongoing, with conditions for a reduction in process rates, as has already been documented in boreal forests (Nilsson and Wardle 2005).

Recent vegetation resurveys in Arctic systems shed light on the capacity of heathland systems to shift character, but also on how herbaceous systems are changing. In herbaceous, Arctic vegetation types, there has been a decrease in species richness and a significant increase in the occurrence of particularly evergreen but also deciduous dwarf shrubs over the last nine decades (Kapfer and Popova 2021). Historically these sites were 'species-rich, herbal plant communities of Russian subarctic grasslands and meadows' as described by Aarno Kalela (Kapfer and Popova 2021). Cessation of animal husbandry has likely been a contributor to this change. Also, in a shorter-term study, Vowles et al. (2017b) documented a (severe) expansion of evergreen shrubs into grassland where these shrubs were already abundant (cover approx. 15%) two decades ago. Overall, these findings suggest that a transition from herbal to dwarf shrub communities, or from grasslands to heathlands, is not unlikely. This further implies that change, even in decadal time scales, can be the norm and may confound our understanding of the stability of vegetation types. For instance, the relation between contemporary vegetation cover and soil qualities such as carbon storage is likely not straightforward when also considering legacy effects from former vegetation types and past flora in contributing to carbon stocks. Our empirical findings align with a slow yet continuous dwarf shrub evergreening of tundra grasslands and heathland systems, a process of biotic homogenization. Considering *E. nigrum* is a native plant it cannot be considered invasive, yet it is likely modifying these heathland ecosystems and, at the same time, diminishing ecosystem multifunctionality across the region.

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## Author contributions

**Kari Anne Bråthen:** Conceptualization (lead); Data curation (equal); Formal analysis (lead); Investigation (lead); Resources (lead); Validation (lead); Writing – review and editing (lead). **Maria Tuomi:** Conceptualization (supporting); Data curation (equal); Investigation (lead); Methodology (supporting); Validation (supporting); Writing – review and editing (equal). **Jutta Kapfer:** Conceptualization (supporting); Data curation (equal); Investigation (supporting); Methodology (supporting); Validation (supporting); Writing – review and editing (equal). **Hanna Böhner:** Data curation (equal); Formal analysis (supporting); Validation (supporting); Writing – review and editing (equal). **Tuija Maliniemi:** Conceptualization (lead); Data curation (equal); Formal analysis (supporting); Investigation (equal); Resources (supporting); Validation (equal); Writing – review and editing (equal).

## Transparent peer review

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## Data availability statement

Data are available from the DataverseNO Digital Repository: <https://doi.org/10.18710/YUNHFP> (Bråthen et al. 2024).

## Supporting information

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

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