SPECIAL FEATURE: HISTORICAL ECOLOGY

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Changes in subarctic vegetation after one century of land use and climate change

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Abstract

Questions: Have species richness and composition in subarctic vegetation changed over the past ca. 90 years? Are compositional shifts linked to changes in land management or climate? Are observed changes associated with vegetation type, life form, or habitat preference?

Location: Rybachy and Sredny Peninsulas, NW Russia.

Methods: We resurveyed vegetation ca. 90 years after the first sampling in 1927–1930 to study changes in species richness, abundance and composition. Because of missing plot-related environmental measurements we used a weighted averaging approach calculating relative changes in species-specific optimum values for different environmental gradients represented by species indicator values to identify compositional change in relation to the environment. Changes in species composition were visualised using detrended correspondence analyses. Significances of observed changes in species richness and frequency were evaluated using restricted permutation tests. A χ^2 test was used to test if observed changes in abundances were related to species' life form and habitat preferences.

Results: Species composition has changed significantly over the past ca. 90 years, as indicated by significant changes in species' frequencies and values of optima for the environmental gradients temperature, moisture, nutrients and light. Species richness decreased significantly, in particular in nitrophilous and wet growing vegetation. Species typical for grazed grasslands and meadows and species of wet habitats became less abundant, while dwarf shrubs and forest species increased.

Conclusions: Land abandonment, in combination with climate change, is likely to have caused the observed changes in the subarctic vegetation of NW Russia. Shifts in the species dominance ratios and interspecific competition (e.g. for reallocated nutrients) after land abandonment may have been promoted by the subsequent change towards a warmer climate, facilitating the regrowth of previously open meadows with grazing-intolerant tall herbs, forest herbs and dwarf shrubs. This study illustrates clearly the long-term effects of land-use change, the consequences of which are still visible even after almost one century in the subarctic.

1 | INTRODUCTION

Human activity has always had an impact on the environment by influencing directly (e.g. land use) or indirectly (e.g. climate change) on landscapes and their natural components. Numerous studies demonstrate that recent climate warming has driven species' geographic distributions polewards (Forbes, Fauria, & Zetterberg, 2010; Myers-Smith et al., 2011; Sturm, Racine, & Tape, 2001; Tape, Sturm, & Racine, 2006) or up the elevational gradient (Chen, Hill, Ohlemüller, Roy, & Thomas, 2011; Lenoir & Svenning, 2010; Steinbauer et al., 2018) resulting in significant changes in species composition, diversity and structure (Savage & Vellend, 2014; Walther, 2010). In treeless tundras, shrubs in particular were often found to have expanded as a response to increased summer temperatures (Forbes et al., 2010; Myers-Smith et al., 2015). Land-use change as a direct influence on landscapes has caused a worldwide decline in species diversity and ecosystem services (Pereira et al., 2010; Tscharntke, Klein, Kruess, Steffan-Dewenter, & Thies, 2005). Land abandonment has increased dramatically over the past decades in north European mountain areas and at high latitudes. The legacies of management regime shift can mediate or buffer the effects of climate change, thus causing divergent community states over time (García-Valdes, Svenning, Zavala, Purves, & Araujo, 2015; Saccone, Pyykkonen, Eskelinen, & Virtanen, 2014). However, in Northern Europe, particularly North Fennoscandia, where traditional pastoralism has decreased strongly, studies on land-use change impacts on vegetation are rare (but see e.g. Persson, 1984) and long-term mutual relationships with climate are not fully understood (Newton et al., 2009).

Traditional use of grasslands as a natural resource, especially the management by grazing livestock and mowing meadows at moderate cutting intensity, may be beneficial by providing high-quality products (e.g. forage and meat) and at the same time helping to preserve rare and threatened species (Collins, Knapp, Briggs, Blair, & Steinauer, 1998; Henle et al., 2008). Grazing is generally considered an appropriate management tool for lowlands as it may increase habitat and plant species diversity by reducing competitive pressure and by forming gaps to increase the horizontal heterogeneity of sites (Cousins, Auffret, Lindgren, & Tränk, 2015; Dupré & Diekmann, 2001). Accordingly, extensively (i.e. moderately) grazed pastures are among the most species-rich ecosystems in Northern Europe (Herrero-Jáuregui & Oesterheld, 2018). Modifications of long-term pasture management may have dramatic consequences on the biodiversity and ecosystem services (Díaz et al., 2006). As species adapt individually to changes in the environmental conditions (Chapin & Shaver, 1985; Le Roux & McGeoch, 2008; Walther et al., 2002), a change in the environment, such as in the grazing

regime, will modify species composition and diversity. Pasture abandonment may change plant functional traits composition (Díaz et al., 2006; Kahmen & Poschlod, 2008) and foliage structure as grazing cessation favours the development of more dense and patchy vegetation such as tall grasses and nitrophilous herbs (Krahulec et al., 2001; Persson, 1984; Song et al., 2012). The discontinuation of traditional management practices during the 20th century in northern Europe is an important driver of subsequent succession and region-wide afforestation, reverting open grasslands and pastures into scrub and woodland (Newton et al., 2009; Veen, Jeffersen, de Smidt, & van der Straten, 2009). However, long-term studies are lacking that focus on long-term changes in plant species diversity and composition at the fine scale in high-latitude areas that have experienced both land-use change and decades of above-average climate warming (AMAP, 2012; Kattsov et al., 2005).

Here we study long-term vegetation changes in subarctic vegetation at the fine scale over a period with both climate change and cessation of agricultural land use. We present the results of a plant-sociological resurvey conducted in the northwesternmost part of the Russian mainland in 2016, about 90 years after the first sampling. We use ordination methods and an indicator-based approach that relates observed changes in species composition with changes in environmental variables to identify the direction of change in plant communities. To explore potential changes at the ecosystem level, we investigate whether changes in vascular plant species' abundances are in favour of specific plant functional types.

2 | METHODS

2.1 | Study area

The study site is in the northern part of Pechengsky District of Murmansk, representing the northernmost part of continental European Russia (69°33′–69°56′ N, 31°44′–32°07′ E; Figure 1). The study site is divided into two parts: the smaller southern part, Sredny Peninsula, and the larger northern part, Rybachy Peninsula. Sredny is connected by a 4-km-wide land neck with the mainland in the south and with Rybachy in the north. Hence, the study site is almost completely surrounded by water.

The bedrock consists of upper Proterozoic solid (rocks), such as sandstones, shales and conglomerates, unlike the granite-dominated mainland coast of the Murmansk region (Siedlecka & Siedlecki, 1968). The main soil type is podzol rich in aluminium (Al) and iron (Fe). The highest plains rise up to 300 m a.s.l. in the inland, while the coast is abrasional with the pediment plain varying

FIGURE 1 Map of Rybachy and Sredny Peninsulas with locations of 250 vegetation plots resurveyed in 2016 and the meteorological stations closest to the study site (inlay)
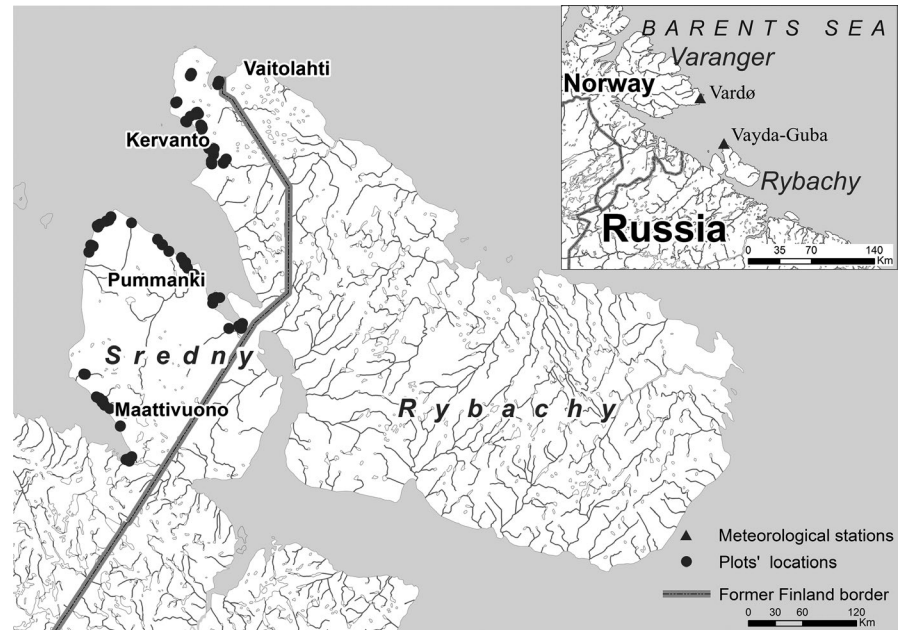
around 50 m a.s.l. (Atlas Miloserdov, 1971). The climate is oceanic. Influenced by the south extension of the North Cape current, the climate is relatively mild compared to other areas at similar latitudes. Climate variables for the time period before the first survey are partly available for mean annual temperature and precipitation (Appendix S1 and S2) from the Vayda-Guba meteorological station, which is located in the northernmost part of the study area (Figure 1). Mean annual temperature has increased from +1.2°C in the period before the first survey (1901–1930) to +2.4°C in the period prior to resurvey (2006–2016; Table 1). The average annual precipitation has increased from 350 mm (1886–1935) to 772 mm (2006–2016; Appendix S1). The vegetation period with daily mean temperatures above +5°C was 113–130 days (1901–1930; Kalela, 1939). Snow cover depth was approximately 20 cm during winter in the time period before the first survey and has decreased to 17 cm (2006–2016).

The study area is within the zone of Subarctic Tundra (Aleksandrova, 1977). It is covered mostly by dwarf-shrub tundra with dominance of *Empetrum nigrum* ssp. *hermaphroditum* and *Vaccinium* species. Large areas of the Sredny Peninsula, especially in the south and in river valleys, are covered by birch krummholz.

The Rybachy and Sredny peninsulas have been used for a long time mainly for fishing and (semi-)domestic livestock husbandry, and several small settlements (villages) have been established for this purpose (Kalela, 1939). The total number of inhabitants in the four villages Vaitolahti, Kervanto, Pummanki and Maattivuono increased from 292 in 1882 to a maximum of 451 in 1939. The largest village on Sredny Peninsula was Pummanki, established in the 1850s and inhabited by a maximum of 200 people and 150 cows in the 1890s. Large areas were used for reindeer herding in summer, and the numbers of reindeer peaked in the beginning of the 20th century. For instance, the village of Maattivuono had up to 3,000 reindeer in 1913. In 1939, almost every farm herded

cattle and sheep, a few also had horses. Birch forests and willow scrubland areas around the yards were cleared efficiently and natural meadows and mires were mown. The resulting meadows were partly fertilised with algae, dung or fish offal every two to four years. Several areas around the villages on the Sredny and Rybachy peninsulas were used for grazing cattle and sheep (herding densities unknown), but domestic reindeer were not kept there (Kalela, 1939). Since 1939/1940 and with the change from Finnish to Russian territory, land utilisation (fishing and sheep/cattle herding) ceased and the villages were abandoned. Today, a meteorological station and a lighthouse are operated there. The land is now part of a military area, which occasionally is grazed by reindeer only.

2.2 | Vegetation sampling and resampling

In the summers of 1927–1930, Aarno Kalela studied the vegetation around the villages that was used for grazing by domestic (sheep and cattle) and semi-domestic animals (reindeer). The aim of Kalela's study was to conduct a plant-geographic and -sociologic investigation in well-developed, species-rich, herbal plant communities of subarctic grasslands and meadows. At a given site within homogeneous vegetation types, plant species composition was studied and species covers were estimated using 1 m × 1 m plots (*n* = 428; Kalela, 1939). These plots were not permanently marked, but the geographic position of each plot was explained and described in detail in Kalela (1939). Plot locations were also indicated on a sketch map.

In 2016, we resurveyed the vegetation on the Sredny and Rybachy peninsulas using the same methods as described by Kalela (1939). A total of 250 plots of 1 m × 1 m size were placed as close as possible to the assumed original locations in

homogenous vegetation of the respective vegetation type of interest (Figure 1). All information about the plots' geographical locations that was available from the original study (e.g. plot location marks on sketch maps, location names, altitude, exposition, position relative to conspicuous landscape elements and landmarks) was carefully taken into account when re-establishing the vegetation plots in order to minimise plot relocation errors potentially caused by the use of non-permanently marked plots (Kapfer et al., 2017).

The nomenclature follows Lid and Lid (2005) for all vascular plants.

2.3 | Statistical methods

Having different observers in the first survey and the resurvey may cause a bias owing to subjective estimates of species covers (Kapfer et al., 2017). Moreover, the lack of permanently marked vegetation plots and the unequal number of plots in the two surveys hampers a direct, plot-by-plot comparison of plots in the calculation of vegetational change over time. The data were therefore standardised and analysed accordingly as described below to minimise potential effects of plot relocation and observer bias on the calculation of change.

2.4 | Species frequencies and richness

We calculated each species' frequency (occurrence in number of plots) and mean cover for both the historical dataset and the resurvey. To minimize potential observer effects on the calculation of change in species covers all cover estimates (both from the historical sampling and the resampling) were first transformed into five cover categories using the Hult–Sernander–Du Rietz abundance scale (Du Rietz, 1921) and then back-transformed into per cent values using the means of each cover class. Because of unequal numbers of plots sampled within the different vegetation types in the old ($n = 428$) and the recent sampling ($n = 250$) we related the number of plots a species occurred in to the total number of plots of the respective sampling period. Then, frequencies/covers of the first sampling were subtracted from frequencies/covers calculated for the resurvey. We applied a restricted permutation test to test whether the observed changes in species frequencies and covers were statistically significant and independent of the vegetation types investigated. Therefore, in the randomisation procedure, the plots of the historic sampling and the resurvey were shuffled randomly with the restriction that only plots from similar vegetation types were randomised. Then, a change was calculated based on the new randomised dataset. A total of 999 permutations were run, and we counted the number of permutations where the absolute change in frequency or cover (calculated from the randomised dataset) was larger than or equal to the observed change value

(calculated from the non-randomised dataset). This number was divided by 1,000 (999 permutations plus the observed change value) to get the significance value. Only species occurring in at least five plots were considered in these analyses (i.e. 159 species for calculation of change in frequency and 105 species for cover). A chi-square test of independence was performed to examine the relationship of species' life form and species' habitat preference with observed changes in species frequencies and covers.

2.5 | Species optima for environmental gradients

The lack of plot-specific environmental data in the historical dataset hinders the direct analysis of change in vegetation composition in relation to environmental change. We therefore applied an indirect approach using a weighted average technique that calculates relative changes in the species' realised optimum value for different environmental gradients (see Kapfer, Grytnes, Gunnarsson, & Birks, 2011), represented by indicator values for light, soil moisture, soil pH, soil nutrients and temperature (Landolt et al., 2010). We compared each indicator value calculated from all species co-occurring with a focus species today and in the previous sampling. A change in a species' optimum value indicates that a species was found to co-occur more (or less) often with species of a higher, or lower, specific indicator value, thus indicating that a change in the plant communities has occurred with respect to the indicator value considered. A restricted permutation test (as described above and in detail in Kapfer et al., 2011) was used to test if changes in species' optimum values were significant. Only species occurring in more than five plots in each sampling period were considered for this analysis in order to reduce the potential effect of rare species on the analysis. A total of 79 such species were analysed.

2.6 | Community composition and richness

To study community-specific changes in species composition and richness (number of species per plot) we applied two-way indicator species analysis (TWINSPAN; Hill, 1979) for vegetation classification. The process of classification was done hierarchically, i.e. samples were successively classified into categories (communities), and species were then classified into categories based on the sample classification. Altogether seven vegetation types were identified for a total of 499 plots. For the classification, only those plots for which a sample score could be calculated to indicate each plot's position along the environmental gradient were chosen. Thus, only those plots were chosen where all species could be allocated an indicator value (Landolt et al., 2010). Detrended correspondence analysis (DCA) was used to visualise and investigate changes in the species composition of all seven vegetation types.

TABLE 1 Change in species' optima for the environmental gradients temperature (Temp), alight, soil moisture, soil reaction (pH) and nitrogen

Taxon	Temp		Light		Moisture		pH		Nitrogen		Occ
Achillea millefolium	−0.71	***	0.05	n.s.	1.26	***	−0.56	**	−0.01	n.s.	169
Alchemilla vulgaris aggr.	−0.06	n.s.	0.43	n.s.	−0.57	**	−0.17	n.s.	−0.76	**	152
Angelica archangelica	−1.23	***	1.73	***	−0.15	n.s.	−0.45	**	−2.49	***	39
Anthoxanthum nipponicum	−0.98	*	0.57	n.s.	−0.27	n.s.	0.92	*	−0.78	*	47
Anthriscus sylvestris	−0.05	n.s.	1.51	***	−0.79	*	−0.57	**	−2.44	***	28
Astragalus alpinus ssp. *arcticus*	−1.00	***	0.29	n.s.	1.83	***	0.05	n.s.	0.80	n.s.	86
Avenella flexuosa	−0.28	n.s.	0.68	n.s.	0.29	n.s.	0.97	***	0.06	n.s.	101
Bartsia alpina	0.63	***	−0.77	***	−0.16	n.s.	0.27	n.s.	0.80	***	101
Betula nana	1.00	***	−0.80	**	1.21	**	−0.08	n.s.	1.11	***	84
Bistorta vivipara	−0.13	n.s.	0.39	***	0.10	n.s.	−0.27	*	−0.16	n.s.	287
Calamagrostis neglecta	0.97	*	−0.59	**	0.56	n.s.	−1.47	*	0.28	n.s.	42
Calamagrostis phragmitoides	−0.94	***	1.33	***	−0.36	*	0.04	n.s.	−1.86	***	45
Caltha palustris	0.84	n.s.	0.05	n.s.	−0.84	*	−0.31	n.s.	0.77	n.s.	41
Campanula rotundifolia	−0.17	n.s.	−0.16	n.s.	0.86	***	0.18	n.s.	0.53	**	123
Carex aquatilis	0.86	*	−0.05	n.s.	−1.00	**	−0.77	*	0.11	n.s.	51
Carex atrata	−0.66	n.s.	0.26	n.s.	1.15	**	0.20	n.s.	0.40	n.s.	53
Carex capillaris	1.29	***	−0.19	n.s.	0.92	**	0.10	n.s.	0.59	*	78
Carex rariflora	1.60	n.s.	−2.04	***	2.62	***	−0.44	n.s.	2.43	***	15
Carex vaginata	0.85	***	−0.25	n.s.	0.87	***	0.21	n.s.	0.79	***	142
Cerastium fontanum ssp. *holosteoides*	0.17	n.s.	−0.27	n.s.	0.60	*	−0.42	n.s.	−0.13	n.s.	50
Chamaepericlymenum suecicum	−0.86	***	0.94	***	1.04	**	1.71	***	1.13	**	70
Chamerion angustifolium	−1.29	***	2.00	***	−0.17	n.s.	0.68	n.s.	−1.38	**	60
Cirsium heterophyllum	−0.52	n.s.	0.73	*	−0.36	n.s.	0.55	n.s.	−1.14	*	33
Comarum palustre	1.14	**	−1.89	***	−0.82	**	−1.46	**	0.22	n.s.	63
Deschampsia cespitosa	−0.08	n.s.	−0.56	n.s.	−0.29	n.s.	−1.03	*	−0.75	**	133
Dianthus superbus	−0.67	*	−0.09	n.s.	1.24	***	−0.33	n.s.	−0.49	n.s.	101
Dryas octopetala	1.67	***	−1.35	*	2.00	**	−0.16	n.s.	1.33	**	24
Dryopteris expansa	−0.89	***	1.03	**	0.97	**	1.06	***	0.53	n.s.	33
Empetrum nigrum ssp. *hermaphroditum*	1.00	***	−0.85	***	1.15	**	0.03	n.s.	1.08	***	120
Epilobium hornemannii	0.34	n.s.	0.59	n.s.	−0.17	n.s.	−0.52	n.s.	−1.21	*	25
Epilobium palustre	2.23	*	−1.56	*	−1.47	n.s.	0.02	n.s.	1.05	n.s.	19
Equisetum arvense	0.68	*	0.46	n.s.	−0.10	n.s.	−0.19	n.s.	0.45	n.s.	106
Equisetum pratense	1.40	***	−0.09	n.s.	0.05	n.s.	1.09	***	1.33	***	94
Euphrasia sp.	−0.09	n.s.	−0.26	n.s.	1.05	***	−0.13	n.s.	0.25	n.s.	163
Festuca ovina	1.00	***	−0.61	***	1.11	***	−0.13	n.s.	0.75	***	237
Festuca rubra	−0.61	n.s.	−0.05	n.s.	0.56	*	−0.51	n.s.	−0.47	n.s.	159
Festuca rubra ssp. *arenaria*	1.16	***	−1.33	***	−0.79	***	−0.80	**	−0.35	*	67
Filipendula ulmaria	−0.18	n.s.	0.61	n.s.	−0.60	***	−0.46	n.s.	−0.66	n.s.	94
Gentianella aurea	−1.10	***	−0.15	n.s.	1.46	***	−0.45	n.s.	−0.62	n.s.	38
Geranium sylvaticum	−0.92	**	0.63	***	−0.64	***	0.51	*	−1.26	***	125
Gymnocarpium dryopteris	−0.37	n.s.	2.06	***	0.39	n.s.	1.36	**	0.29	n.s.	18
Lathyrus japonicus	1.41	n.s.	−1.23	*	−0.35	n.s.	−0.05	n.s.	−0.54	n.s.	31
Leymus arenarius	−0.24	n.s.	0.14	n.s.	0.79	*	0.00	n.s.	−0.14	n.s.	61

(Continues)

TABLE 1 (Continued)

Taxon	Temp		Light		Moisture		pH		Nitrogen		Occ
Oxytropis campestris ssp. sordida	−0.17	n.s.	0.29	n.s.	1.57	***	−0.53	n.s.	0.53	n.s.	58
Parnassia palustris	0.47	*	−0.25	n.s.	0.13	n.s.	−0.10	n.s.	0.57	*	163
Poa alpina	−0.96	*	0.35	*	0.64	*	0.61	**	−0.14	n.s.	91
Potentilla crantzii	0.60	n.s.	−0.22	n.s.	0.73	***	0.29	n.s.	1.00	***	81
Rhinanthus minor	−0.26	n.s.	0.14	n.s.	0.39	n.s.	−0.66	*	−0.33	n.s.	123
Rubus saxatilis	−0.63	n.s.	0.47	n.s.	0.78	**	0.72	*	0.59	n.s.	69
Rumex acetosa	0.16	n.s.	0.41	n.s.	−0.32	n.s.	0.66	**	−0.24	n.s.	179
Salix lanata	0.78	n.s.	−0.42	n.s.	−0.39	*	−1.00	n.s.	0.35	n.s.	38
Salix reticulata	1.87	***	−0.79	*	−0.29	n.s.	0.41	n.s.	1.16	**	30
Saussurea alpina	0.61	**	−0.41	**	−0.06	n.s.	0.29	*	0.71	***	202
Selaginella selaginoides	1.12	***	−0.87	***	0.03	n.s.	−0.03	n.s.	1.12	***	126
Silene acaulis	0.78	***	−1.36	***	−0.19	n.s.	−0.05	n.s.	1.46	***	75
Solidago virgaurea	−0.52	**	1.09	***	0.64	***	0.76	***	0.06	n.s.	154
Stellaria crassifolia	2.55	n.s.	−2.07	*	−0.22	n.s.	−1.00	n.s.	1.74	*	13
Stellaria nemorum	−0.80	***	1.53	***	−0.94	**	0.16	n.s.	−2.25	***	35
Taraxacum sp.	−0.36	n.s.	0.20	n.s.	−0.18	n.s.	−0.32	n.s.	−0.76	*	54
Thalictrum alpinum	1.47	***	−0.47	n.s.	−0.10	n.s.	0.49	*	1.24	***	118
Trientalis europaea	−0.26	n.s.	0.97	*	0.69	*	0.96	***	0.27	n.s.	56
Triglochin maritima	−2.20	***	−0.34	n.s.	−0.27	n.s.	−0.76	n.s.	−1.39	***	52
Vaccinium myrtillus	−1.25	***	1.12	**	0.68	n.s.	1.34	***	0.19	n.s.	43
Vaccinium uliginosum	1.76	***	−1.40	***	1.14	**	0.08	n.s.	1.84	***	56
Vaccinium vitis-idaea	−0.47	n.s.	0.80	*	0.50	n.s.	0.26	n.s.	−0.17	n.s.	73
Vicia cracca	−0.18	n.s.	−0.81	***	0.37	n.s.	−0.32	n.s.	−0.07	n.s.	123

Note: Species occurring in at least five plots in both the historical survey and in the resurvey were tested.

Occ, number of occurrences in plots in total for both surveys.

***, $p ≤ 0.001$; **, $p ≤ 0.01$; *, $p ≤ 0.05$; n.s., not significant; n.p., statistical test not performed.

TWINSPAN and DCA analyses were conducted using the software package JUICE (Tichý, 2002) and PC-ORD (version 6; MjM Software, Gleneden Beach, OR, USA), respectively. All other analyses were run in R, version 3.5.0 (R Core Team, 2018).

3 | RESULTS

The total number of species (both samplings together) was 213, of which 179 and 177 species were recorded in the historical sampling and in the resurvey respectively. The number of species only found in either the historical survey or in the resurvey was 36 and 34 respectively. Species richness per plot decreased from 11.8 species (±5.6) in 1930 to 10.6 species (±5.8) in 2016 ($p = 0.027$) on average for 428 and 249 plots respectively.

Species richness decreased in six of the seven vegetation types identified by TWINSPAN. Statistically significant decreases were found to be strongest for meso- and eutrophic fens ($T = 9.3$, $p < 0.001$), snowbeds with tall herbs and ferns ($T = 5.1$, $p < 0.001$), nitrophilous coastal herb communities ($T = 4.1$, $p = 0.034$) and wet meadows with tall herbs ($T = 3.0$, $p = 0.010$; Figure 2, Appendix S3).

3.1 | Species compositional changes

Species' optimum values changed significantly for 66 out of 79 tested species. The percentage of species that have changed significantly for the different gradients are: 47 (temperature), 46 (moisture), 43 (nutrients), 42 (light) and 32 (soil pH; Table 1). A higher percentage of species has shifted its optimum positively for moisture (69%), soil pH (60%), nutrients (59%) and temperature (57%). This shows that the respective species co-occurred more often with species of a higher indicator value for these variables in the resurvey compared to the first survey. Fifty-five per cent of those species that shifted significantly for the gradient light were found to have changed their co-occurring species for species with lower values for light, indicating a shift towards darker (more shady) conditions for the respective species.

Detrended correspondence analysis (Figure 3) revealed a similar trend over time for the seven vegetation types, whose distribution in
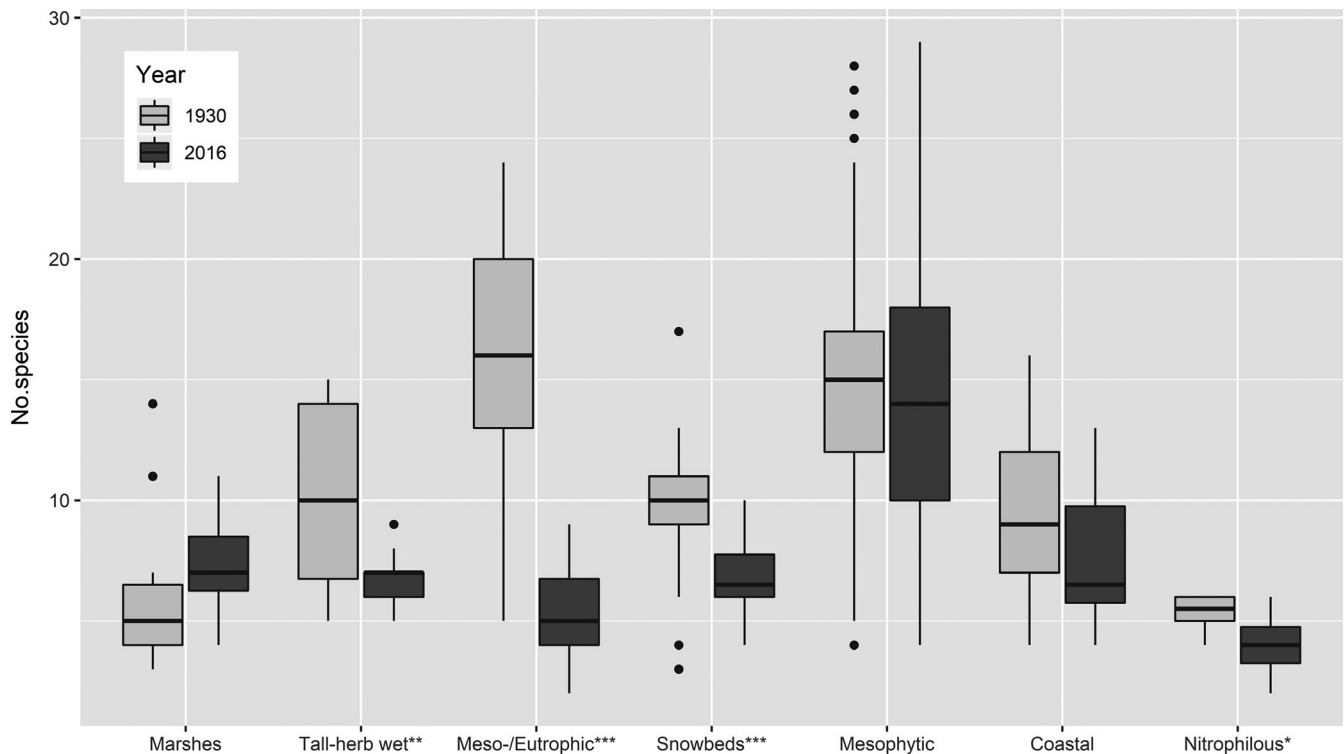
FIGURE 2 Temporal change in number of species per plot (No. species) in the vegetation types Marshes and saltmarshes; Tall-herb wet meadows at floodplains; Mesotrophic and eutrophic fens; Snowbeds with tall herbs and ferns; Mesophytic dry meadows and herbaceous communities; Coastal dry meadows and grasslands on thin soil; Nitrophilous coastal herb communities. Significance levels from two sided t test: ***, $p \leq 0.001$; **, $p \leq 0.01$; *, $p \leq 0.05$ (see details in Appendix S3)

the ordination space is mostly explained by the gradients light (DCA axis 1, $r = 0.611$) and moisture (DCA axis 2, $r = 0.673$).

3.2 | Change in species frequencies and covers

Of 159 species tested for change in occurrence frequency, 66 species (31.0%) were found to have changed significantly (42 species decreased, 24 species increased; Figure 4a, Appendix S4). The species that changed most were the tall herbs *Ranunculus acris* and *Trollius europaeus* (decrease) and the dwarf shrubs *Vaccinium vitis-idaea* and *Empetrum nigrum* (increase). The majority of the species with significant frequency change were forbs (F: 32 species) and graminoids (G: 21 species), of which both had a larger number of species having decreased (F: 20, G: 17) than increased (F: 12, G: 4). For dwarf shrubs (total number of occurrence = 17), the opposite trend was found, i.e., 6% of the species (14% out of those changing significantly) have decreased, whereas 35% of dwarf-shrub species have increased in frequency (86% of the significantly changing species). Two shrub species were observed more (*Betula nana*) and less (*Salix* spp.) frequently in the resampling compared to the historical sampling. Three spore plants have significantly decreased (*Selaginella selaginoides*, *Equisetum pratense*, *Equisetum sylvaticum*) and one has increased (*Gymnocarpium dryopteris*).

Of 105 species tested for change in cover, 35 species (33%) were found to have changed significantly. Greatest changes in cover

occurred in the graminoids *Carex glareosa*, *Carex aquatilis* (increase) and *Calamagrostis neglecta* (decrease) and the herb *Silene acaulis* (decrease; Figure 4b). Changes in species cover were not significantly correlated with changes in species frequency ($r = 0.16$, $p = 0.104$).

A chi-square test found no significant correlation between life form and the number of observed increases or decreases in species frequency ($\chi^2 = 10.4$, $p = 0.240$) and species cover ($\chi^2 = 7.3$, $p = 0.506$; Appendix S5a), nor between species' habitat preference and frequency ($\chi^2 = 10.3$, $p = 0.419$) and cover ($\chi^2 = 4.9$, $p = 0.766$; Appendix S5b).

4 | DISCUSSION

The vegetation on the Rybachy and Sredny peninsulas has changed greatly between 1927–1930 and 2016. Species typical for grazed and mown meadows and species of wet habitats became less abundant, while dwarf shrubs and tall herbs as well as species of drier habitats and forest species increased. Species optimum values for different environmental gradients were found to have changed significantly for the majority of the tested species. This indicates major changes in species composition, as the respective species were found to co-occur with species with different indicator values for environmental factors in 2016 than in the first survey. As significant changes were identified for species regardless of vegetation type, our results indicate an overall compositional turnover at the study
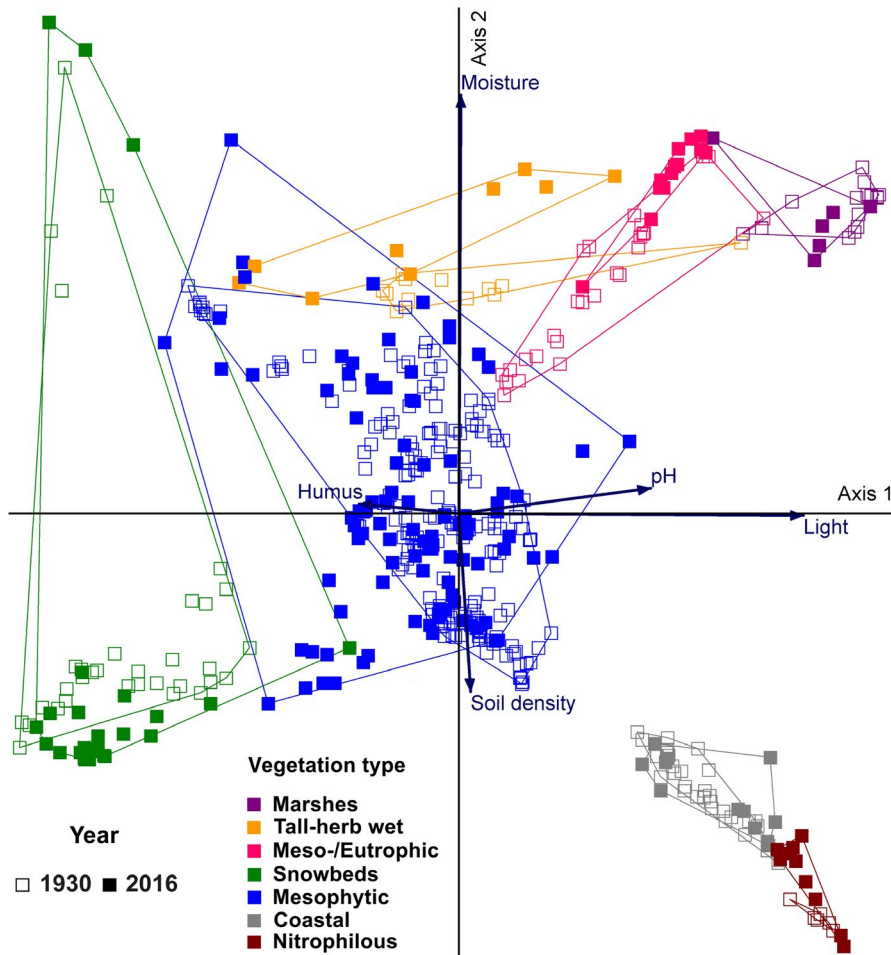
FIGURE 3 Detrended correspondence analysis (DCA) on 499 vegetation plots representing seven vegetation types for the first sampling period (Kalela, 1939) and for the resurvey in 2016. Polygons indicate the range of vegetation types in relation to different environmental gradients represented by indicator values (Landolt et al., 2010). The variables light and moisture were strongest correlated with DCA axes 1 ($r = 0.611$) and 2 ($r = 0.673$) and best explain the distribution of vegetation plots in the depicted ordination space

site. It is most likely that the compositional changes are caused by the combined, probably synergistic effect of climate warming and land abandonment, which both may contribute to the increased growth of predominantly shrubs and forest species, thereby indicating afforestation and over-growth of previously open landscapes (Boutin et al., 2017; Kapfer et al., 2011; Myers-Smith et al., 2015; Walther et al., 2002).

There is reported by several other studies on effects of land abandonment (Collins et al., 1998; Halada et al., 2017; Persson, 1984; Song et al., 2012; Vassilev, Pedashenko, Nikolov, Apostolova, & Dengler, 2011), species richness has decreased also in our study site. This contrasts with the generally described consequences of climate warming, which may have positive effects on species richness. This has been shown e.g. for unproductive areas such as grazed alpine grasslands (Boutin et al., 2017). The observed decrease in the number of species in our study site may therefore indicate the effects of grazing cessation to possibly override the potential positive effects of climate warming on species richness in low-productive tundra habitats.

There is strong evidence for the effects of land-management changes on species distribution and composition (Dupré & Diekmann, 2001; Krause, Pugh, Bayer, Lindeskog, & Arneth, 2016; Song et al., 2012). For instance, increased grazing can cause

a shift in ecosystem states towards grass-dominated vegetation in the subarctic tundra (Bråthen et al., 2007). A decline in grazing activities, in particular abandonment, may reverse this shift and decrease the proportion of grassland species while increasing species of ericoid shrub cover. Such a change was observed on the Sredny and Rybachy peninsulas over the past ca. 90 years. Numbers of grass species and other species typical for grazed grasslands (e.g. the poisonous herbs *Ranunculus acris* and *Trollius europaeus*) decreased and several dwarf shrubs and tall herbs indicating abandonment (e.g. *Geranium sylvaticum*, *Chamerion angustifolium*, *Valeriana sambucifolia*) became more frequent or increased in cover (*Anthriscus sylvestris*, *Filipendula ulmaria*). The increase of these particular tall herb species and shrubs indicate the regrowth of the formerly used land, along with a shift in the shade conditions between species. Such shifts in the dominance ratio of shady plants are supported by the significant changes in species' optimum values for light.

Land abandonment changes the mechanical disturbance regime (e.g. removing nutrients via consumed biomass by grazers or by mowing), soil fertility and the nutrient input rate and richness in soils (Peco, Navarro, Carmona, Medina, & Marques, 2017). This will most likely affect species composition by shifting patterns in species competition and species dominance ratios at the expense
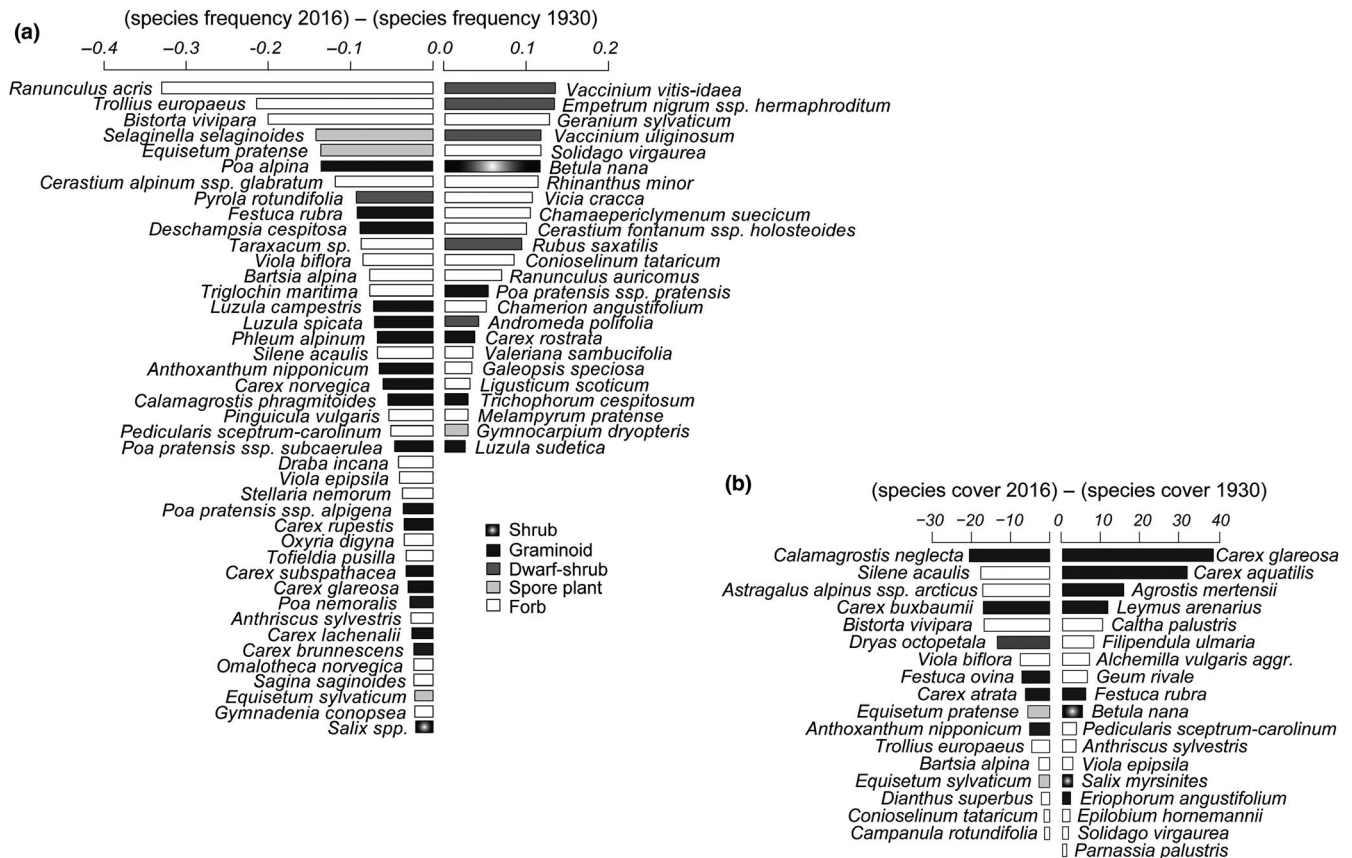
FIGURE 4 Species of different life forms with statistically significant (*p* < 0.05) change in: (a) occurrence frequency; and (b) cover between 1930 and 2016

of less competitive, nutrient-demanding species (Hellström et al., 2003). Such changes may cause an increase in biomass and a decrease in species richness, which may be more pronounced in nutrient-rich areas (Dupré et al., 2009; Song et al., 2012), and accompanied by an increase in more competitive tall herbs (Pärtel, Kalamees, Zobel, & Rosén, 1998; Vassilev et al., 2011). This is confirmed by our results showing the greatest species richness decrease in more nitrophilous vegetation types and an increased growth of, for instance, the tall herbs *Anthriscus sylvestris* and *Filipendula ulmaria*. Furthermore, compositional changes towards less nutrient-demanding vegetation are indicated by the negative changes in the realised optimum for nutrients of several species typical for nutrient-rich habitats (e.g. *Angelica archangelica*, *Anthriscus sylvestris*, *Chamerion angustifolium*, *Geranium sylvaticum*, *Alchemilla vulgaris*, *Taraxacum* sp.). Furthermore, seashore species lacked any response in their realised optimum (e.g. *Honckenya peploides*, *Cochlearia officinalis*, *Carex aquatilis*), which indicates that changes in the soil nutrient regime are likely to drive the observed changes. This may be explained by the seashore being an independent system where species use different nutrient sources (e.g. macro-algae from the sea) than other vegetation types that are directly impacted by e.g. nutrient input from grazing animals. Thus, shifts in the independent seashore vegetation (e.g. decrease in frequency of *Triglochin maritima* and

Carex subspathacea) are more likely to be linked to (recent) climate change (partly also observed for the high Arctic; Kapfer & Grytnes, 1939) rather than by factors such as mowing or grazing.

Our results clearly indicate that land abandonment is a major driver causing some of the observed changes in species diversity and composition. However, the observed increased growth of typical forest species and (dwarf) shrubs may also be related to climate change, as other studies in the Arctic and subarctic have shown (Kapfer & Grytnes, 1939; Maliniemi, Kapfer, Saccone, Skog, & Virtanen, 2018; Myers-Smith et al., 2015; Sturm et al., 2001; Tape et al., 2006). Effects of climate warming are suggested by our results, for instance, in optimum value changes along the moisture gradient. These changes were found to be predominantly positive for several dwarf shrubs (e.g. *Betula nana*, *Vaccinium uliginosum*, *Empetrum nigrum*, *Dryas octopetala*), forest species (e.g. *Rubus saxatilis*, *Solidago virgaurea*, *Trientalis europaea*, *Gymnocarpium dryopteris*) and species of other rather dry habitats (e.g. *Astragalus alpinus*, *Campanula rotundifolia*), whereas negative values were observed for species of moister habitats (e.g. *Carex aquatilis*, *Caltha palustris*, *Comarum palustre*). It can be assumed that wetter habitats were invaded by species of drier habitats having lower optimum values for moisture. These observed changes may imply a change of wet habitats towards drier conditions, which is reported in several recent studies in high-latitude, subarctic Europe to be a consequence of recent climate warming (Britton, Beale, Towers, & Hewison, 2009; Kapfer, Virtanen, & Grytnes,

2012; Matteodo, Ammann, Verrecchia, & Vittoz, 2016; Sandvik & Odland, 2013).

5 | CONCLUSIONS

Land-use change, in particular grazing cessation, is found to be an important driver of the observed changes in species richness, abundance and composition in subarctic vegetation. Promoted by the subsequent effects of a warmer and wetter climate, vegetation has shifted away from grass- and herb-dominated vegetation typical for grazed grasslands and towards an increased growth of species indicating regrowth caused by land abandonment and climate change. This long-term study shows that the combined effect of land abandonment and climate change may lead to dramatic changes in low-productive tundra vegetation, which in the subarctic are still visible after ca. 90 years of environmental change. Further vegetation regrowth and shrubification may be expected with continued climate warming.

AUTHOR CONTRIBUTIONS

JK conceived the ideas, performed the analyses and led the writing; KP conducted fieldwork, prepared the data and contributed to data analyses, interpretation and revising the text.

DATA AVAILABILITY STATEMENT

Primary data and datasets prepared as a part of the study and R codes are stored at the Norwegian Institute for Bioeconomy Research, Tromsø/Ås.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Appendix S1. Climate data for the study site.
Appendix S2. Climate chart for the study site.
Appendix S3. Results of the *t*-test on alpha diversity for vegetation types.

Appendix S4. Species list with species' frequencies and covers in 1939 and 2016.
Appendix S5. Results of the Pearson's Chi-square test on species frequency and cover for life form and habitat preference.