

RESEARCH ARTICLE

Climate change drives substantial decline of understory species richness and abundance in Norway spruce forests during 32 years of vegetation monitoring

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Abstract

Questions: Observations in permanent forest vegetation plots in Norway and elsewhere indicate that complex changes have taken place over the period 1988–2020. These observations are summarised in the “climate-induced understory change (CIUC)” hypothesis, i.e. that the understory vegetation of old-growth boreal forests in Norway undergoes significant long-term changes and that these changes are consistent with the ongoing climate change as an important driver. Seven testable predictions were derived from the CIUC hypothesis.

Location: Norway.

Methods: Vegetation has been monitored in a total of 458 permanently marked plots, each 1 m², in nine old-growth forest sites dominated by *Picea abies* at intervals of 5–8 years over the 32-year study period. For each of the 52 combinations of site and year, we obtained response variables for the abundance of single species, abundance and species density of taxonomic–ecological species groups and two size classes of cryptogams, and site species richness. All of these variables were subjected to linear regression modelling with site and year as predictors.

Results: Mean annual temperature, growing-season length and the number of days with precipitation were higher in the study period than in the preceding ca. 30-year period, resulting in increasingly favourable conditions for bryophyte growth. Site species richness decreased by 13% over the 32-year study period. On average, group abundance of vascular plants decreased by 24% (decrease in forbs: 38%). Patterns of group abundance change differed among cryptogam groups: although peat-moss abundance increased by 39%, the abundance of mosses, hepatics and lichens decreased by 13%, 49% and 67%, respectively. Group abundance of small cryptogams decreased by 61%, whereas a 13% increase was found for large cryptogams. Of 61 single species tested for abundance change, a significant decrease was found for 43 species, whereas a significant increase was found only for 6 species.

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Conclusions: The major patterns of change in species richness, group species density and group abundance observed over the 32-year study period accord with most predictions from the CIUC hypothesis and are interpreted as direct and indirect responses to climate change, partly mediated through changes in the population dynamics of microtine rodents. The more favourable climate for bryophyte growth explains the observed increase for a few large bryophyte species, whereas the decrease observed for small mosses and hepatics is interpreted as an indirect amensalistic effect, brought about by shading and burial in mats of larger species and accelerated by reduced fine-scale disturbance by microtine rodents. Indirect effects of a thicker moss mat most likely drive the vascular plant decline although long-term effects of tree-stand dynamics and former logging cannot be completely ruled out. Our results suggest that the ongoing climate change has extensive, cascading effects on boreal forest ecosystems. The importance of long time-series of permanent vegetation plots for detecting and understanding the effects of climate change on boreal forests is emphasised.

KEYWORDS

abundance decline, bryophyte, climate warming, hepatic, Norway spruce forest, understorey vegetation, vascular plants, vegetation change

1 | INTRODUCTION

The boreal forest biome, which extends across the northern hemisphere and encircles the Arctic, covers about 11% of the Earth's land area and contains about one-third of the total forested area on our planet (Högberg et al., 2022). The boreal forest plays a fundamental role in the global carbon cycle as a sink for carbon (Pan et al., 2011), harbours a diverse biota with tens of thousands of species (Kayes & Mallik, 2021) and provides invaluable ecosystem services, ranging from timber products to arenas for recreation (Pohjanmies et al., 2017).

Although Russia, Alaska and Canada still contain extensive boreal forests without traces of commercial forestry, almost all Fennoscandian forests have legacies from logging and/or other human activities such as livestock grazing. The current condition of Norwegian forests is the result of very intensive exploitation in the period 1850–1920, to the extent that the Norwegian forest authorities feared deforestation (Barth, 1916; also see Breidenbach et al., 2020). After World War I, measures were taken to establish more sustainable forestry practices. Over the period 1900–1930 selection logging replaced the former dimension cutting practice and was itself replaced by rotation forestry (clear-cutting followed by tree planting) after World War II (Storaunet & Rolstad, 2020). As a result, the standing volume of Fennoscandian forests has increased over the past 100 years (Högberg et al., 2021), in Norway by a factor of three (Breidenbach et al., 2020). At present, only 1.7% of the productive forest area in Norway is classified as natural forest according to the strict definition used by the National Forest Inventory, while ca. 30% of the forest area has not been subjected to clear-cutting (Storaunet & Rolstad, 2020).

The understorey species composition of boreal forests in a near-natural state responds to broad-scale (e.g. forest fires; Sirén, 1955, Økland, 2000b) and fine-scale (e.g. windthrows that cause tree upheaval; Schaetzel et al., 1989, Jonsson & Esseen, 1990) natural disturbances; tree-layer dynamics such as gaps created by the death of single trees (Økland et al., 2003); variation along local environmental gradients (Økland & Eilertsen, 1993; Økland, 1996); and regional variation in climatic conditions (Økland, 1996). This makes the understorey vegetation a sensitive indicator of environmental change (Økland & Eilertsen, 1996; Lawesson et al., 2000; Økland et al., 2004).

Although forestry was long regarded as the single major threat to boreal forest biodiversity, this rapidly changed when the so-called “new forest damage” was observed in Central Europe around 1970 (Kubiková, 1991). Linked to long-distance airborne pollution (“acid rain”; Tamm, 1976; Schütt & Cowling, 1985), the new threat triggered the initiation of several monitoring programmes and studies (Brynjulf, 1977). In Norway, very few permanently marked vegetation plots existed that could be re-analysed for assessment of understorey vegetation responses to human-induced environmental change (but see Nygaard & Ødegaard, 1999). Monitoring of vegetation–environment relationships in permanent plots was therefore initiated in 1988. Over the years from 1988 to 1992, eleven monitoring sites in old-growth boreal forests dominated by Norway spruce (*Picea abies* (L.) Karst.), spread over Norway, were established (Økland, 1990, 1996; Økland & Eilertsen, 1993). Later, nine of these sites were integrated in the Norwegian Terrestrial Monitoring Programme (TOV; Framstad et al., 2020). Old-growth forests, all protected by law or in the process of becoming protected, were selected for this monitoring programme to facilitate separation of pollution effects from the



effects of modern forestry (Økland, 1996, cf. Hedwall et al., 2021). This did not, however, exclude legacies from selection and dimension logging performed more than ca. 100 years ago.

Since the start of the monitoring programme, several different patterns of vegetation change have been observed in TOV sites. In the 1990s, a decreasing abundance of vascular plant species restricted to soils richer in nutrients was observed in the southern monitoring areas where the pollution load was highest. This was hypothesised to represent a time-lagged reduction in the recruitment of long-lived, clonal plants due to soil acidification, brought about by deposition of long-distance airborne pollutants (Økland et al., 2004). In the 2000s, the load of airborne pollutants over Norway and other European countries was reduced to below critical limits (Aas et al., 2020) and this vascular plant trend was no longer seen (Økland & Nordbakken, 2004; Halvorsen et al., 2019; Økland et al., 2019b). In the 2000s and 2010s, increasing bryophyte cover (note that the term “bryophyte” is used as a collective term for phyla Bryophyta, “mosses”, and Marchantiophyta, “hepatics”, whereas the term “cryptogam” also includes lichens) on the forest floor was observed (Halvorsen, 2019), apparently resulting from an increased abundance of large, dominating moss species (Økland et al., 2019a). At the same time, reduced species richness and abundance of small bryophytes, hepatics in particular (Halvorsen et al., 2019), and reduced species richness and abundance of most forb species (Økland et al., 2019b) were observed.

These observed changes were tentatively linked to climate change by the following line of reasoning. A vast majority of bryophyte species lack a well-developed cuticle and take up water with dissolved mineral nutrients over their entire surface (Buch, 1947; Tamm, 1953; Hosokawa et al., 1964). Forest bryophytes receive most of their supplies of water with nutrients directly from rainwater although uptake from soil may occur in dry periods with high evapotranspiration rates due to upward water movement (Callaghan et al., 1978; Brown & Brümelis, 1996; Økland et al., 1999). Bryophytes are photosynthetically active as long as they receive sufficient light, are well hydrated and the ambient temperatures allow positive net photosynthesis (Proctor, 2000). In general, boreal forest bryophytes are adapted to a relatively cool climate, as indicated by their relatively low temperature optimum for photosynthesis (Stålfelt, 1937a; Glime, 2020). This does, however, vary among species, regions and seasons (Skre & Oechel, 1981; He et al., 2016). Common boreal forest species, exemplified by *Hylocomium splendens*, may therefore have a positive net C uptake at temperatures below 0°C (Stålfelt, 1937b). Although a wetter climate with longer growing seasons favours bryophyte growth in general, the large, dominating, more-productive species like *Hylocomium splendens*, *Dicranum majus* and *Sphagnum* spp., benefit more strongly from the improved growth conditions than smaller species. In the absence of fine-scale disturbances, the bryophyte layer will therefore grow denser and have an amensalistic effect (Burkholder, 1952) on smaller species, which, in turn, will be overgrown, deprived of light and eventually disappear (Rydin, 1997; Økland, 2000a). Several explanations for

declining forb abundance may apply. Indirect negative effects of a denser bryophyte carpet have been observed on seed germination (Ohlson & Zackrisson, 1992) and clonal bud development (Huber & Stuefer, 1997). Furthermore, Hedwall et al. (2021) indicate a potential role of structural changes in ageing forests. We refer to these lines of reasoning as “the climate-induced understorey change” (CIUC) hypothesis.

Other long-term studies of understorey vegetation in boreal (including boreo-nemoral) forests mostly show trends that differ from observations at the nine TOV sites. Studies based on area-representative data that also include managed forests show strong responses to a combination of a increasing tree-layer density and N deposition: decrease in dwarf shrubs and bryophytes, increase in species with preference for nitrogen-rich sites, decreasing species richness (Hedwall et al., 2013, 2019, 2021; Hedwall & Brunet, 2016; Vacek et al., 2017; Prach & Kopecký, 2018). Particularly strong decline is reported for the key species *Vaccinium myrtillus*. Sundberg (2014) attributed the strong decline in understorey vascular plants, notably small-statured species, in S Sweden to land-use changes, including fertilisation for enhanced timber production. Hedwall et al. (2021), however, pointed to complex interactions between forestry and climate change as drivers of observed vegetation change. Some studies also report that reduced richness is accompanied by homogenisation of the species composition (Prach & Kopecký, 2018). A decline in vascular plants and dominant mosses is also reported in the study of old-growth spruce forests by Nygaard and Ødegaard (1999), but these authors did not observe any response to increased N deposition. This leaves us with important knowledge gaps: Which of the observations made at TOV sites since 1988 represent significant long-term trends? What is their relationship with potential drivers like climate change, acid rain, forestry legacies and other human impacts, past and present?

The main aim of this study is to test the CIUC hypothesis: that the understorey vegetation of old-growth boreal forests in Norway undergoes significant long-term changes and that these changes are consistent with ongoing climate change as an important driver. We accomplish this aim by evaluating seven elements of the CIUC hypothesis, formulated as testable predictions, by using data from the nine TOV sites in boreal forests dominated by Norway spruce, collected between 1988 and 2020: (1) Climatic conditions for bryophyte growth have improved. (2) The species richness and/or abundance of large mosses, especially species with preference for moist sites and/or a humid climate, have increased. (3) The species richness and/or abundance of small cryptogams has decreased. (4) The increase in large mosses and the decrease in small cryptogams are coordinated in time and space. (5) A pattern of vascular plant decline that corresponds with the pattern of deposited long-term airborne pollutants, N in particular, is no longer present. (6) The species richness and/or abundance of forbs has decreased. (7) The increase in large bryophytes and decrease in forbs are coordinated in time and space. The seven predictions are evaluated separately. A discussion of possible mechanistic relationships among substantiated patterns of change underpins the final assessment of the CIUC hypothesis.



2 | METHODS

2.1 | Selection of sites, placement of plots and recording of species

The nine Norway spruce-dominated monitoring sites, which are referred to by the two-letter codes given in Table 1 and Figure 1, were selected to span natural climatic and geographical gradients in Norwegian spruce-dominated forests (Økland, 1996, Økland et al., 2004, cf. Bakkestuen et al., 2008) as well as gradients in the deposition of long-distance airborne pollutants (Aas et al., 2020). All sites include similar ranges of within-site variation along the main local environmental gradients (mineral nutrients, soil moisture, tree influence and topography; Økland & Eilertsen, 1993, Økland, 1996, Økland et al., 2004). Accordingly, the sites are treated as replicate samples from the same population of boreal forests. Only remotely situated, old-growth Norway spruce stands, now protected by law, were selected to minimise successions induced by former logging and husbandry grazing (Økland & Eilertsen, 1993; Økland, 1996).

Within each site, plots for long-term monitoring of vegetation and the environment were established between 1988 and 1992, using a restricted random sampling design (Figure 1). In all sites except SO, ten 5 m × 10 m macro plots, each with five randomly placed 1-m² vegetation plots, were placed to span local environmental gradients (Økland, 1996); i.e. 50 vegetation plots at each site. Three plots hidden under large, downed logs at the last re-analysis (two in BR and one in GU) were removed from the data set prior to analysis. In SO, eight transects were placed to span the local environmental variation in coniferous (Norway spruce and Scots pine [*Pinus sylvestris* L.]) forests. One hundred macro plots, each 4 m × 4 m, were randomly chosen among positions spaced 10 m along the transects (Økland & Eilertsen, 1993). In each of the 61 macro plots dominated by Norway spruce, one 1-m² plot in fixed position was used for this study. All the 458 plots were permanently marked by subterranean aluminium tubes.

Each 1-m² plot was divided into 16 subplots of 0.0625 m² each. In all subplots, the presence or absence of all species of vascular plants <0.8 m high (thus excluding shrubs and trees), bryophytes and lichens were recorded at each forest site with intervals of 5–8 years. The number of times the vegetation was recorded (in the years 1988–2020) at each site varied from five to seven, totalling 52 site-by-year combinations for the nine sites.

For more detailed descriptions of the sites, including environmentally interpreted ordination analyses of variation in species composition along the main local environmental and regional climatic gradients based on data from the first year of analysis (1988–1993), see Økland and Eilertsen (1993), Økland (1996) and Økland et al. (2004).

2.2 | Species groups and traits

The 308 recorded taxa, hereafter referred to as “species” (see Appendix S1 for full taxon list and nomenclatural notes), were

divided into two groups, each with four subgroups, by criteria given in Appendix S2. Vascular plant subgroups were trees and shrubs, dwarf shrubs, forbs and graminoids; cryptogam subgroups were mosses, *Sphagnum*, hepatics and lichens. The division into groups and subgroups was primarily motivated by the species’ ecological and ecophysiological characteristics, but also reflected taxonomic differences. Accordingly, the categories are referred to as taxonomic–ecological groups.

For vascular plants, ecological indicator values for N for Sweden according to Tyler et al. (2021) were used as proxies for the species’ realised optima along a soil nitrogen availability gradient.

Size is an important cryptogam trait (Stanton & Coe, 2021), with high relevance to evaluation of predictions (3) and (4). We therefore assigned to each cryptogam species a value for the size index *S* (Økland, 1995a), which expresses the estimated median surface area, *a* (length × width, in mm²) of the living part of moss shoots, lichen podetia or thalli on the forest floor. For mosses, this typically corresponds to 1 year’s growth (Økland, 1995a, 1995c). *S* values were assigned to each species by combining observations in the SO site with measurements given in the literature. For the current study, some of the index values given by Økland (1995a) were revised to better represent the variation across the nine sites. *S* is expressed on a logarithmic scale:

$$S = \text{floor}(\log_2 a),$$

i.e., $\log_2 a$ rounded down to the nearest integer number. *S* values for cryptogam species recorded in the nine sites, given in Appendix S1, varied between 1 and 9. A species was categorised as small if $S \leq 4$ and as large if $S \geq 8$. The two size groups included 55 and 34 species, respectively.

2.3 | Response variables used in analyses

Data aggregated to combinations of site and year of monitoring (hereafter referred to as site-by-year combinations or, simply, sites) were used as observation units in all analyses. Four categories of response variables were constructed: (1) Single-species abundance, hereafter referred to as species abundance, was obtained for each species in each site-by-year combination as the species’ average subplot frequency (the sum of subplot counts in the n_s plots at the site, divided by n_s). This is a measure of species’ overall frequency in the terminology of Wilson (2011). Abundance values ranged from 0 to 16. Before analyses, $1/n_s$ was added to all species abundance values to also allow logarithmic transformation of absence observations. (2) Group abundance was obtained for each species group in each site-by-year combination as the sum of species abundance values for all species in the group. Group abundance thus expresses the average total number of subplot occurrences per plot for all species belonging to the species group in question. A value of 64 for forbs in a site-by-year combination thus means that the average number of forb species per subplot



TABLE 1 Sites (with abbreviation): geographic position, climate and years analysed. Climate variables are given as annual mean values for the two periods, 1958–88 (period 1) and 1989–2018 (period 2).

Site	Paulen (PA)	Solhom-fjell (SO)	Gryt-dalen (GR)	Rausjømarka (RA)	Bringen (BR)	Otter-stadstølen (OT)	Gutulia (GU)	UR-vatnet (UR)	Gran-neset (GN)
Latitude (°N)	58°18–19'	58°58'	59°15'	59°49'	60°32–34'	60°49'	62°00–01'	63°06–07'	66°30–31'
Longitude (°E)	7°55–56'	8°50'	8°37'	11°02'	9°23–24'	5°45'	12°09–13'	9°48–49'	14°52–53'
Altitude (m)	150–275	350–475	475–550	220–300	600–750	220–350	700–850	300–400	225–325
Area (km ²)	3	2	0.5	0.2	6	2	4	3	0.5
First year analysed	1990	1988	1988	1988	1991	1989	1989	1992	1990
Last year analysed	2018	2018	2019	2016	2014	2020	2017	2015	2013
Number of times analysed	6	7	6	6	5	6	6	5	5
T periods 1 + 2 (°C)	5.7	4.4	3.1	4.5	1.9	4.1	0.2	3.6	1.8
T period 1 (°C)	5.2	3.7	2.5	4.0	1.5	3.5	-0.7	3.1	1.2
T period 2 (°C)	6.3	5.2	3.8	5.1	2.4	4.6	1.1	4.1	2.4
T _{autumn} periods 1 + 2 (°C)	6.4	5.1	3.8	5.0	2.2	4.8	0.9	4.0	2.4
T _{autumn} period 1 (°C)	6.1	4.7	3.4	4.7	2.1	4.5	0.3	3.7	2.0
T _{autumn} period 2 (°C)	6.7	5.5	4.1	5.3	2.4	5.2	1.5	4.3	2.8
P periods 1 + 2 (mm)	1795	1391	1234	1030	762	3744	767	993	1475
P period 1 (mm)	1683	1353	1256	976	745	3426	727	969	1422
P period 2 (mm)	1912	1430	1212	1086	779	4072	808	1018	1530
ΔT [(period 2) – (period 1)] (°C)	1.2	1.5	1.3	1.1	0.9	1.1	1.8	1.0	1.2
ΔT _{autumn} [(period 2) – (period 1)] (°C)	0.6	0.8	0.7	0.6	0.3	0.7	1.2	0.6	0.8
ΔP (% change, period 1 to period 2)	13.6	5.7	-3.5	11.2	4.6	18.9	11.2	5.0	7.6
PRA >0, period 1 (days)	108.3	86.4	79.8	94.8	70.0	118.3	67.1	90.9	71.6
PRA >0, period 2 (days)	135.7	106.4	92.5	107.2	73.9	136.5	71.9	98.9	80.2
ΔPRA [(period 2) – (period 1)] (days)	27.4	19.9	12.7	12.5	3.9	18.1	4.8	8.0	8.7
GSL, period 1 (days with T > 0)	272.5	243.0	225.2	242.1	208.4	252.9	181.8	239.4	213.4
GSL, period 2 (days with T > 0)	296.7	271.4	249.3	263.0	222.7	278.7	197.8	259.6	227.7
ΔGSL [(period 2) – (period 1)] (days with T > 0)	24.2	28.4	24.1	20.9	14.2	25.8	16.0	20.2	14.3

Abbreviations: GSL, growing-season length; P, precipitation; PRA, potential relative assimilation index; T, temperature (see text for further explanation).

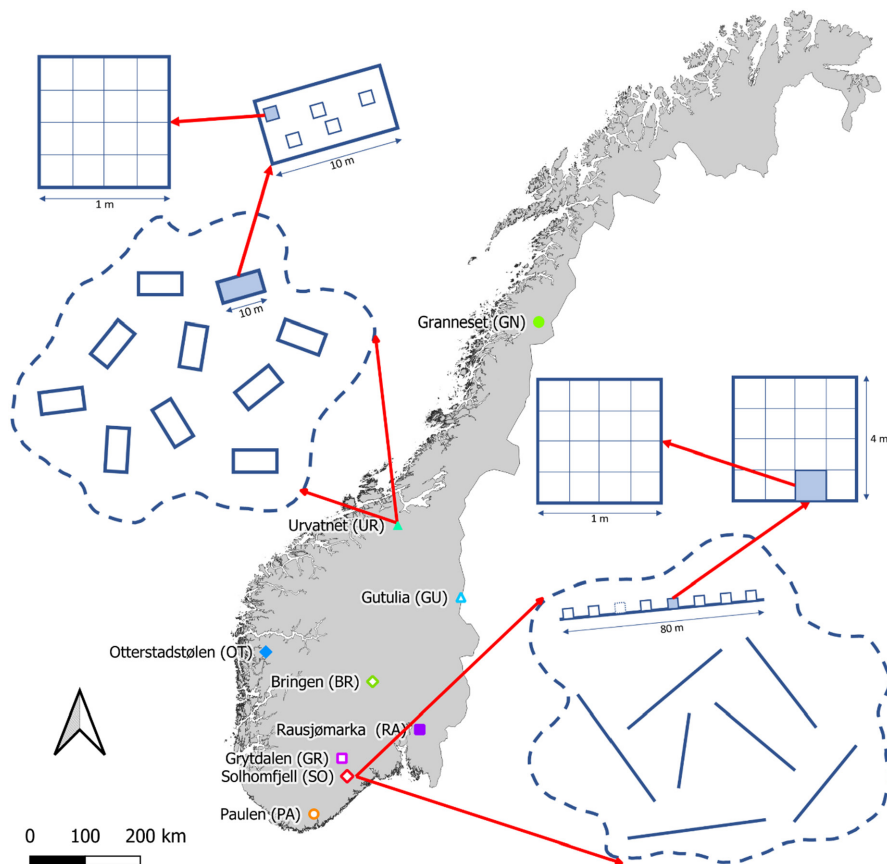


FIGURE 1 Map showing the geographical positions of the nine study sites within Norway and an outline of the sampling designs. A transect sampling design was used in the SO site (bottom right), whereas a block design was used in all other sites (upper left). Note that sites are labelled by use of the same symbols and colours throughout the paper.

in this site-by-year combination, is 4 (16 subplots \times 4 species = 64 subplot presences). (3) Group species density (Grace, 1999) was obtained as the average number of species in a given species group present in each 1-m² plot. (4) Site species richness was obtained as the total number of species recorded in at least one plot in a given site-by-year combination.

Individuals of tree and shrub species less than 0.8 m high were only used for calculation of site species richness. These species were excluded from calculation of the other response variables because they are represented in the data mostly by seedlings and saplings with high mortality and, hence, plot-scale abundances that fluctuate strongly from year to year (Økland, 1995b).

2.4 | Climatic data and indices

Because long-term on-site weather data were not available, we used gridded temperature and precipitation data from the Norwegian Meteorological Institute (<http://www.senorge.no>) with a spatial resolution of 1 km \times 1 km and a temporal resolution of 1 day to characterise variation in the climate in each site during the study period. These data (see Table 1) were subsequently interpolated and corrected for altitude. We estimated annual means, minima and maxima for temperature and precipitation for the period 1958–2018 and separately for the ca. 30-year period before the onset of monitoring (1958–1988) and the bulk of the period covered by our study (1989–2018).

The growth of plants, including bryophytes, is strongly influenced by temperature (e.g. degree-days), and the availability of moisture and light (e.g. sunlight exposure). To assess the potential role of climatic factors for the observed abundance changes, we calculated the “potential relative assimilation” (PRA) index, as defined by Økland (1997), for all days in the period 1958–2018. This index, originally designed to integrate the expected effects of day-to-day weather conditions on the growth of the forest moss *Hylocomium splendens* (a typical large moss in Norwegian boreal forests), is considered equally relevant for other forest bryophytes (Halvorsen et al., 2019). The PRA index expresses potential assimilation on a scale from 0 (complete limitation) to 1 (no limitation). It is obtained as the product of four factors, each of which is also scaled from 0 to 1: radiation r , snow cover s , warmth w and state of hydration h . For a given day i (in a given year), the index is given as

$$PRA_i = r_i \times s_i \times w_i \times h_i.$$

Outside the growing season, when growth is completely limited by one of the four factors, PRA equals zero. The length of the growing season is defined as the number of days with $PRA > 0$ in one calendar year. For the two periods 1958–1988 and 1989–2018, we calculated the mean number of days per year with $PRA > 0$ as well as the difference in number of days with $PRA > 0$ between the first and the second period. A full explanation of the PRA index, including the rationale behind it and calculation details, is given in Appendix S3.



2.5 | Statistical analyses

All response variables are counts (of species or subplot occurrences) or derived from counts by averaging. Their variances are therefore expected to increase with the mean (Crawley, 2013). We therefore subjected all response variables to binary (base 2) logarithmic transformation before analysis. This has the dual effects of homogenising the variances of variables that differ in mean values (e.g. species abundances from different sites) and changing the interpretation from differences in absolute values to differences in relative values, i.e. rates of change in abundance, species density or species richness.

All transformed response variables were subjected to linear modelling (McCullagh & Nelder, 1989; Venables & Ripley, 2002). Five nested models, starting with the null model, were obtained for each response variable by successively adding predictors in the following order: (1) the categorical variable SITE (with up to nine classes); (2) the continuous variable YEAR (of recording; ranging from 1988 to 2020); (3) the quadratic term YEAR²; and (4) the interaction SITE:YEAR. The quadratic term was included to open for a nonlinear temporal pattern. *F*-tests were used to test the null hypothesis that the added predictor did not explain a larger fraction of the residual variation than expected of a random variable. For selected response variables, we also obtained site-specific models, i.e. one model for each site, testing the effect of YEAR.

Transformation of response variables to binary logarithms translates the regression coefficient for YEAR in models with SITE+YEAR as predictors, β_{YEAR} , to estimates of the annual rate of change in the transformed response (unit of measurement: year⁻¹). A difference of one unit in the transformed response then corresponds to a doubling or a halving of the untransformed response variable over the time period. β_{YEAR} values of $\pm 1/32 \text{ year}^{-1} = \pm 0.03125 \text{ year}^{-1}$ then correspond to a doubling ($\beta_{\text{YEAR}} = +1/32 \text{ year}^{-1}$) or halving ($\beta_{\text{YEAR}} = -1/32 \text{ year}^{-1}$) of the untransformed response variable during the 32-year study period. A given value of β_{YEAR} can be converted to percentage relative change (increase or decrease) y in the response variable in the period from year t_0 to t_1 , on the original scale, by the equation

$$y = 100 \times \left(2^{\beta_{\text{YEAR}}(t_1 - t_0)} - 1 \right).$$

Tests of single-species abundances were restricted to the 61 species present at all or all but one monitoring year in six or more sites. Patterns of variation in selected response variables over the study period are illustrated using customised graphics in which each site is represented by the same symbol and colour throughout (Figure 1). Labels on the vertical axis are given in the original units (abundance, species density, etc.).

Significant tests of species abundance ($p < 0.05$ in two-tailed tests, corresponding to $p < 0.025$ in one-sided tests) were sorted into negative and positive changes (decrease or increase in species abundance over the study period, respectively) by the sign of β_{YEAR} . The exact test based upon the binomial distribution (Crawley, 2013) was applied to counts of species with a significant abundance change for evaluation of the null hypothesis that the observed number of

significant tests did not deviate from the expected number of significant tests in a random sample. Because the tests of abundance change were two-tailed, the expected number of significant tests with a given sign is $0.025 \times n$, where n is the number of species tested.

R version 4.1.2 was used for all analyses (R Core Team, R Foundation for Statistical Computing, Vienna, AT) (R Development Core Team, 2021).

3 | RESULTS

3.1 | Growing-season length

The average growing-season length increased from the 1958–1988 period to the 1989–2018 period in all sites (Table 1, Appendix S4). The number of days per year with PRA > 0 increased by 3.9–27.4 days, corresponding to an average over the nine sites of 14.7%. The number of days with $T > 0^\circ\text{C}$ increased by 14.2–28.4 days, averaging 9.0%.

3.2 | Site species richness

In all sites, species richness (the number of species recorded in 1 year) decreased from the initial year (1988–1992) to the last year of recording (2013–2020). The lowest richness reductions were observed in the northernmost site GN (one species) and the two southernmost sites PA and SO (eight and four species, respectively). In the other sites, reductions between 12 and 30 species (in OT) were observed (Figure 2). Although 83.7% of the variation in site species richness was explained by site, more than half of the residual variation (62.5%) was explained by year (Table 2). The estimated rate of decrease was $-0.0063 \text{ species year}^{-1}$, corresponding to an average reduction of 13% over the 32-year study period. The quadratic term was significant, indicating increasing rate of decrease with time.

3.3 | Group species density and group abundance

The patterns of variation in response variables group species density (average number of species per plot) and group abundance (average total number of subplot occurrences per plot) were closely similar, as demonstrated by the correlation coefficient $r = 0.9737$ ($p < 0.0001$, $n = 11$) between corresponding regression coefficients β_{YEAR} in conditional models (Table 2). We therefore restrict our attention to group abundance, which turned out to be the more sensitive measure of abundance change among the two. In particular, this was the case for species occurring in all or nearly all plots in a site.

Group abundance decreased for vascular plants as well as for cryptogams, at rates of $-0.0121 \text{ year}^{-1}$ and $-0.0107 \text{ year}^{-1}$, respectively. This corresponded to 24% and 21% average decrease over the 32-year period, respectively (Table 2). Patterns of decrease were

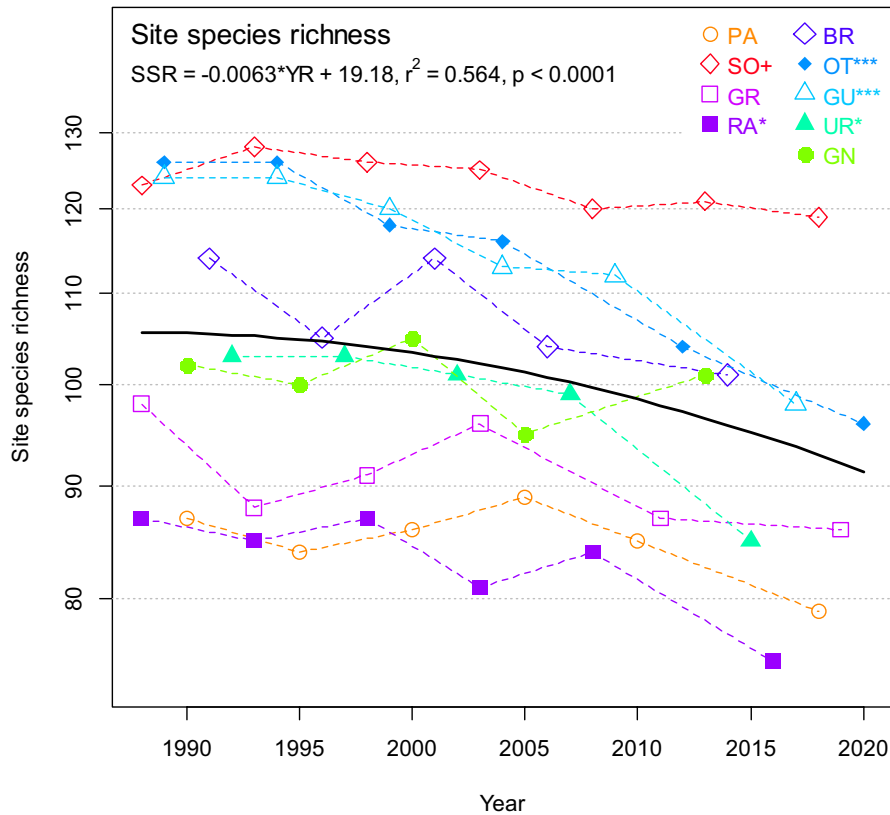


FIGURE 2 Variation in site species richness (SSR) as a function of recording year for nine boreal forest sites in Norway (see Figure 1 for geographic locations and explanations of two-letter site codes). The solid line shows the relationship between SSR and year (YR). Regression coefficients in site-specific models are significantly different from 0 if the site code in the legend is followed by + ($0.05 < p < 0.10$), * ($0.01 < p < 0.05$), ** ($0.005 < p < 0.01$) or *** ($p < 0.005$).

linear for vascular plants (non-significant quadratic term), and significant at $\alpha=0.1$ for all sites. Significantly nonlinear time trajectories were, however, observed for cryptogams (Figure 3a). In all sites except BR, cryptogam abundance increased in the 1990s but was suddenly replaced by strong reduction at the turn of the century. Overall reductions significant at $\alpha=0.1$ were observed in five of nine sites (Figure 3b).

The three vascular plant subgroups – dwarf shrubs, forbs and graminoids – followed the pattern of vascular plants but differed with respect to rate of decrease, from $-0.0212 \text{ year}^{-1}$ for forbs (corresponding to a 38% decrease in 32 years) via -0.0088 for graminoids to $-0.0038 \text{ year}^{-1}$ for dwarf shrubs, corresponding to 18% and 8% reduction in the 32-year period, respectively (Table 2). A significant decrease in forb abundance at $\alpha=0.1$ was observed in all sites except RA, where a slight increase was recorded (Figure 3c). Particularly strongly reduced forb abundance was observed in the southern sites PA and GR, in which the initially low forb abundance was about halved during the study period.

The four subgroups of cryptogams differed considerably in their temporal patterns of variation in group abundance, indicating that the overall pattern for cryptogams resulted from unique subgroup patterns (Figure 3d–f). The highest overall rate of decrease, $-0.0501 \text{ year}^{-1}$ (corresponding to 67% reduction in 32 years), was observed for lichens which, however, had low abundance in all sites and showed inconsistent among-site patterns (Figure 3f). The group abundance of hepatics was significantly nonlinear and as much as 83% of within-site variation was explained by year (Table 2). The rate of abundance decrease

($-0.0306 \text{ year}^{-1}$) corresponded to 49% reduction of the abundance over the study period (Figure 3e). A significant decrease in hepatic group abundance at the $\alpha=0.05$ level was observed in seven sites. Mosses followed the same pattern as hepatics, although with less strong decrease ($\beta_{\text{YEAR}} = -0.0063 \text{ year}^{-1}$, corresponding to 13% decrease in 32 years). *Sphagnum* was the only species subgroup for which a significant abundance increase was found, showing a consistent pattern (53% of within-site variation explained) and a significant effect of year at the $\alpha=0.1$ level in six sites. The group abundance of *Sphagnum* was higher at the end than at the start of the study period in all sites (Figure 3d). The regression coefficient, $+0.0148 \text{ year}^{-1}$ corresponded to 39% increase in 32 years.

Different patterns of variation in group abundance were observed for small and large cryptogams (Figure 4). Hepatics made up the largest subgroup of small cryptogams (Appendix S1), and this size category therefore closely followed the pattern of decrease observed for hepatics, with a significant quadratic term and with an even steeper decline ($\beta_{\text{YEAR}} = -0.0429 \text{ year}^{-1}$, corresponding to a 61% decrease in 32 years). The average number of subplot occurrences decreased from approximately 12 to approximately 5 per plot (Figure 4a). Among the 11 species groups and subgroups, small cryptogams had the lowest among-site variation (51%). Large cryptogams, which included all *Sphagnum* and several moss species, showed a small but consistent and significant increase over the 32-year period ($\beta_{\text{YEAR}} = +0.0057 \text{ year}^{-1}$, corresponding to 13% increase). A significant increase for large cryptogams at the $\alpha=0.005$ level was observed in the two southernmost areas (Figure 4b). Some of the

TABLE 2 Linear modelling of site species richness, species density and group abundance with respect to predictors SITE, YEAR, YEAR² and the interaction SITE:YEAR.

Response variable	Variation explained by predictor				Conditional r^2_{YEAR}	Annual change β_{YEAR}
	r^2_{SITE}	Δr^2_{YEAR}	$\Delta r^2_{\text{YEAR}^2}$	$\Delta r^2_{\text{SITE:YEAR}}$		
Site species richness						
All species	0.837	0.092	0.010	0.031	0.625	-0.0063
Group species density						
Vascular plants	0.947	0.037	0.000	0.006	0.702	-0.0087
Dwarf shrubs	0.959	0.018	0.000	0.014	0.423	-0.0032
Forbs	0.944	0.035	0.001	0.009	0.617	-0.0123
Graminoids	0.948	0.032	0.000	0.006	0.624	-0.0066
Cryptogams	0.653	0.184	0.062	0.051	0.710	-0.0110
Mosses	0.731	0.094	0.073	0.049	0.621	-0.0063
<i>Sphagnum</i>	0.916	0.025	0.001	0.027	0.297	+0.0124
Hepatics	0.688	0.194	0.049	0.049	0.779	-0.0196
Lichens	0.879	0.036	0.001	0.027	0.301	-0.0433
Small cryptogams	0.658	0.192	0.053	0.065	0.715	-0.0255
Large cryptogams	0.987	0.001	0.000	0.002	0.098	+0.0028
Group abundance						
Vascular plants	0.787	0.141	0.001	0.023	0.664	-0.0121
Dwarf shrubs	0.931	0.016	0.001	0.034	0.236	-0.0038
Forbs	0.890	0.064	0.002	0.025	0.583	-0.0212
Graminoids	0.902	0.049	0.001	0.023	0.503	-0.0088
Cryptogams	0.855	0.060	0.036	0.027	0.665	-0.0107
Mosses	0.783	0.059	0.063	0.057	0.562	-0.0071
<i>Sphagnum</i>	0.928	0.038	0.001	0.014	0.532	+0.0148
Hepatics	0.783	0.136	0.044	0.019	0.830	-0.0306
Lichens	0.867	0.045	0.002	0.044	0.340	-0.0501
Small cryptogams	0.510	0.304	0.104	0.035	0.833	-0.0429
Large cryptogams	0.969	0.008	0.001	0.014	0.306	+0.0057

Note: The variation explained by SITE (given as r^2 , the total sum of squared deviation from the mean) and the additional variation explained by the other predictors, is tabulated. Rejection of the null hypothesis that addition of a variable did not explain more variation than expected by chance, as tested by the F -ratio test ($\alpha=0.05$), is indicated by r^2 values in bold. All tests of SITE and YEAR were significant at the $\alpha=0.0001$ level with one exception: the test of YEAR for large cryptogam group species density ($p=0.0400$). Conditional r^2_{YEAR} is the fraction of residual variation explained by YEAR and YEAR², or YEAR only if the variation explained by YEAR² was not significant, after the variation due to SITE was accounted for. β_{YEAR} is the regression coefficient of YEAR in the models with SITE + YEAR as predictors. All response variables were transformed to binomial (base-2) logarithms. Accordingly, β_{YEAR} provides estimates of the annual rate of change in a response variable. $n=52$; $df_{\text{SITE}}=8$, $df_{\text{YEAR}}=1$, $df_{\text{YEAR}^2}=1$, $df_{\text{SITE:YEAR}}=8$. For definition of species groups and subgroups, see Appendix S2.

northernmost sites in which a significant increase for large bryophytes was not observed had relatively high cover of large cryptogams at the start of the study (R. Halvorsen and T. Økland, personal observations).

Significant positive correlations between rates of change in group abundance per year, calculated for the 43 intervals between site-by-year combinations in the nine sites (Appendix S5),

were found between vascular plants and cryptogams ($r=0.347$, $p=0.0225$), and between forbs and graminoids ($r=0.524$, $p=0.0003$). Contrary to expectations, correlation coefficients with a positive sign were also obtained between group abundance change for pairs of species groups with opposite patterns of change: *Sphagnum* spp. and other cryptogams ($0.1 < r < 0.2$; $p > 0.25$), small and large cryptogams ($r=0.361$, $p=0.0176$) and

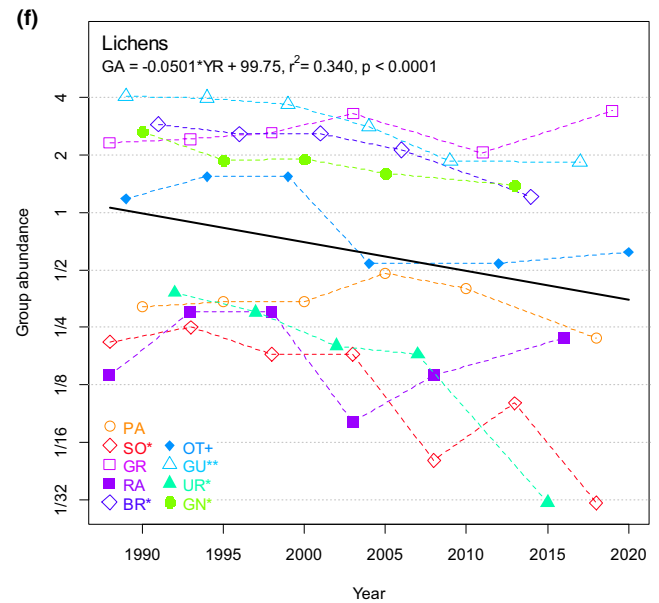
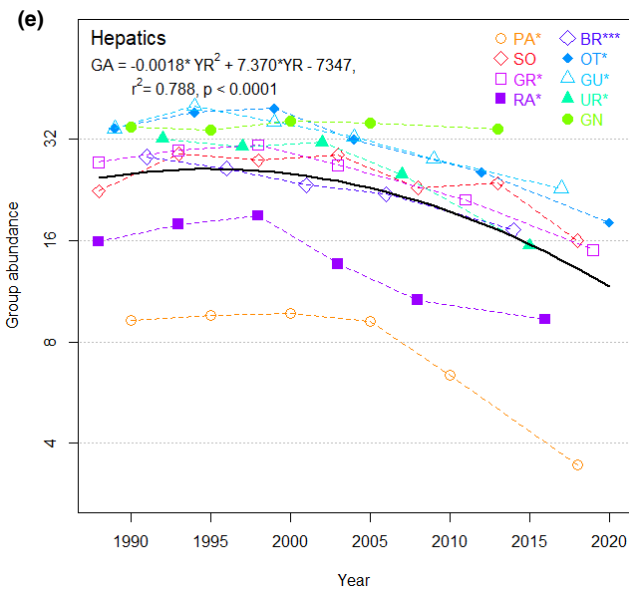
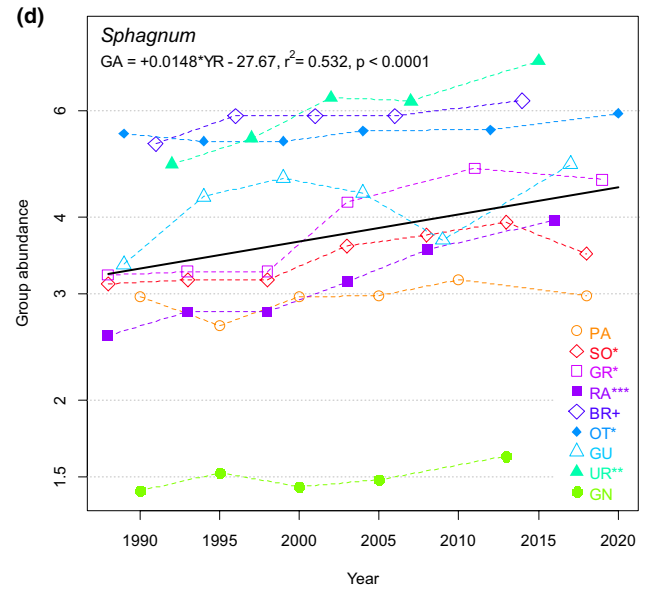
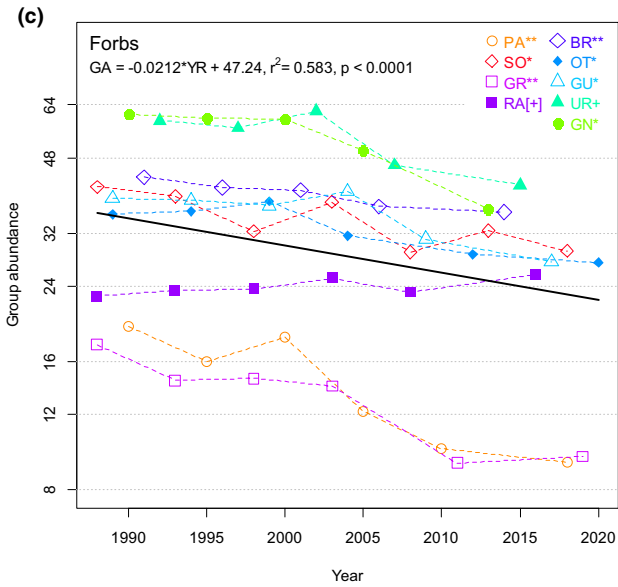
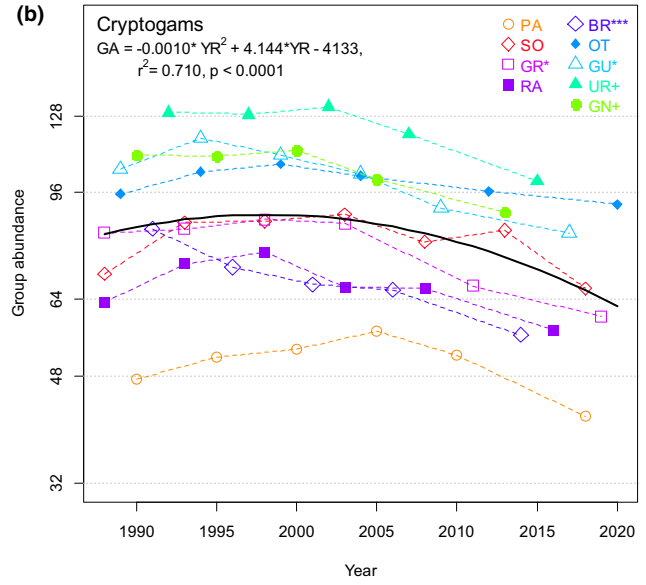
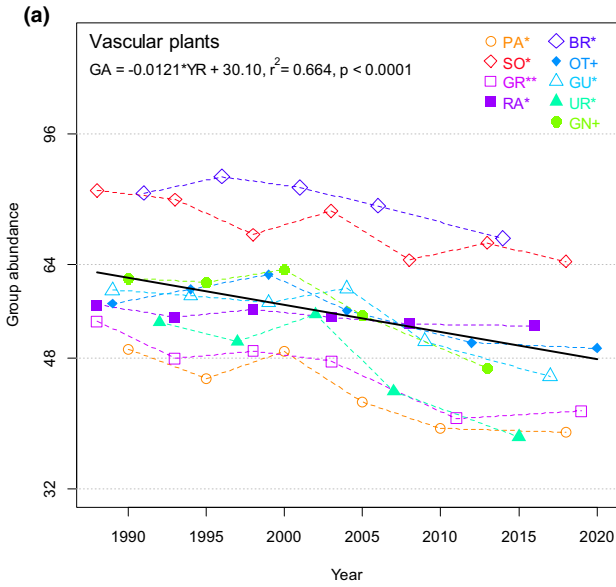


FIGURE 3 Variation in group abundance (GA) for selected taxonomic–ecological species groups and subgroups as functions of recording year for nine boreal forest sites in Norway (see [Figure 1](#) for geographic locations and explanations of two-letter site codes). (a) Vascular plants. (b) Cryptogams. (c) Forbs. (d) *Sphagnum*. (e) Hepatics. (f) Lichens. The solid line shows the relationship between GA and year (YR). Regression coefficients in site-specific models are significantly different from 0 if the site code in the legend is followed by + ($0.05 < p < 0.10$), * ($0.01 < p < 0.05$), ** ($0.005 < p < 0.01$) or *** ($p < 0.005$). Square brackets around a sign indicate a significant trend opposite to the general pattern.

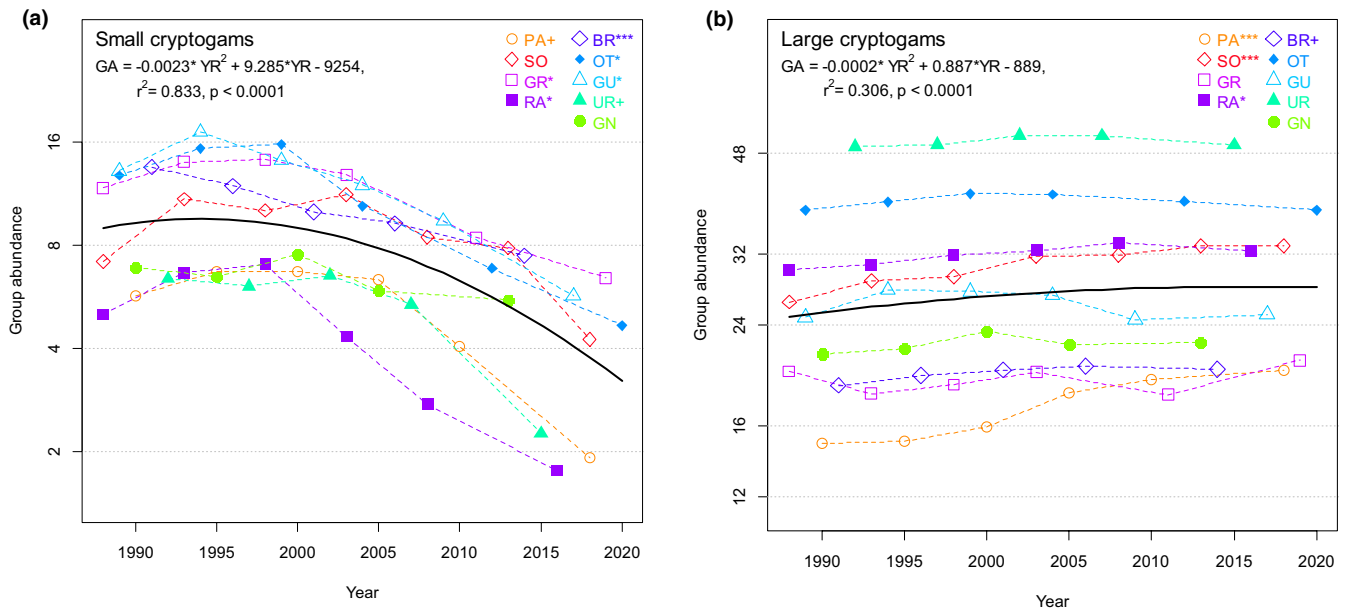
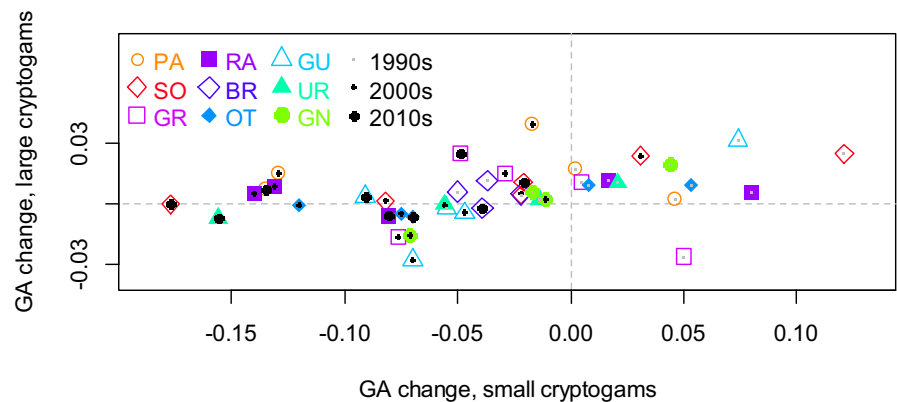


FIGURE 4 Variation in group abundance (GA) for small and large cryptogams as functions of recording year for nine boreal forest sites in Norway (see [Figure 1](#) for geographic locations and explanations of two-letter site codes). (a) Small cryptogams. (b) Large cryptogams. The solid line shows the relationship between the GA and year (YR). Regression coefficients in site-specific models are significantly different from 0 if the site code in the legend is followed by + ($0.05 < p < 0.10$), * ($0.01 < p < 0.05$), ** ($0.005 < p < 0.01$) or *** ($p < 0.005$).

FIGURE 5 Relationship between rates of change in group abundance (GA) per year for small and large cryptogams, calculated for the 43 intervals between recording years in each of the nine sites (see [Figure 1](#) for geographic locations and explanations of two-letter site codes).



forbs and large cryptogams ($r=0.266$, $p=0.0852$). A closer look at the relationship between group abundance change for small and large cryptogams show that the variation in growth rate of large cryptogams was negligible compared with that of small cryptogams, and that the positive correlation resulted from the many cases of concordant increase in the 1990s ([Figure 5](#)). [Figure 5](#) also demonstrates that the rates of decrease in small cryptogams were particularly high in the 2000s and 2010s, in many different combinations of site and period.

3.4 | Species abundance

Of the 308 species recorded in the 458 plots, 61 satisfied criteria for being subjected to modelling of abundance change. Significant abundance change trends ($p < 0.05$) over the 32-year study period were found for 49 species, of which 43 showed negative trends ([Table 3](#)). The six species with a significant abundance increase were equally distributed in the two subgroups mosses and *Sphagnum* ([Table 3](#), [Appendix S6](#)).



Species group	N	n	n ₋	p ₋	n ₊	p ₊
Trees and shrubs	12	-	-		-	-
Dwarf shrubs (woody phanerophytes)	6	2	2	0.0006	0	-
Forbs	74	15	10	<0.0001	0	-
Grasses	29	2	2	0.0006	0	-
Mosses	78	19	13	<0.0001	3	0.0112
Peat mosses	12	3	0	-	3	<0.0001
Hepatics	67	17	13	<0.0001	0	-
Lichens	30	3	3	<0.0001	0	-
Small cryptogams	55	11	8	<0.0001	0	-
Large cryptogams	34	10	3	<0.0001	6	<0.0001

Note: The null hypothesis tested was that the predictor YEAR did not explain more variation in species abundance after the variation due to SITE was accounted for than expected by chance. p -values associated with n_{-} and n_{+} , p_{-} and p_{+} , respectively, were obtained by the exact binomial test.

Species with similar patterns of change over the entire study period differed much in detail, as illustrated by the three significantly declining forbs *Gymnocarpium dryopteris*, *Lysimachia europaea* and *Rubus saxatilis* (Figures 6a,b,d), and the strongly declining moss *Plagiothecium denticulatum* (Figure 6f) and hepatics *Calypogeia neesiana*, *Fuscocephaloziopsis lunulifolia* and *Lophocolea heterophylla* (Figure 6i-k). Although vascular plant species decreased at a near constant rate throughout the study period, as shown by the non-significant quadratic terms for 13 of 19 species, cryptogam species shared a common tendency for near constant abundance in the 1990s, followed by a rapid decrease after the turn of the century. Accordingly, the quadratic term was significant for 22 of 29 significantly declining moss and hepatic species. The highest overall rate of decrease was observed for *Plagiothecium denticulatum*. This species decreased significantly in all six sites in which it occurred initially. In two areas (RA and GU), the species was not relocated in any plot in the last recording year. The $\beta_{\text{YEAR}} = -0.1122 \text{ year}^{-1}$ corresponded to a 92% decline over 32 years.

Figure 6c and l exemplify two species without a significant long-term trend, *Oxalis acetosella* (Figure 6c) decreased in the southeasternmost areas SO, GR and RA in the 1990s, it later recovered (GR) or even increased to higher abundance levels (SO and RA). The largest hepatic, *Plagiochila asplenioides*, was the only species in its subgroup with a positive β_{YEAR} value (Figure 6l).

Species with a significant abundance increase followed more or less the same overall pattern, exemplified by the dominating moss species *Hylocomium splendens* (Figure 6e) and *Rhytidiadelphus loreus* (Figure 6c), and *Sphagnum russowii* (Figure 6h). These species increased strongly in sites with low initial abundance, whereas a small or negligible increase was observed in sites where the species

was present in almost all subplots throughout the study period. The strongest increase observed for any species, $\beta_{\text{YEAR}} = 0.0676 \text{ year}^{-1}$ for *Sphagnum russowii*, corresponded to a 347% increase (Figure 6h).

The rate of vascular plant abundance change, given by β_{YEAR} in single-species models, was negatively, but not significantly, correlated with the N indicator values ($r = -0.406$, $p = 0.0845$, $n = 19$). The rate of cryptogam abundance change, given by β_{YEAR} in single-species models, was positively correlated with cryptogam size ($r = 0.312$, $p = 0.0001$, $n = 42$; Appendix S7).

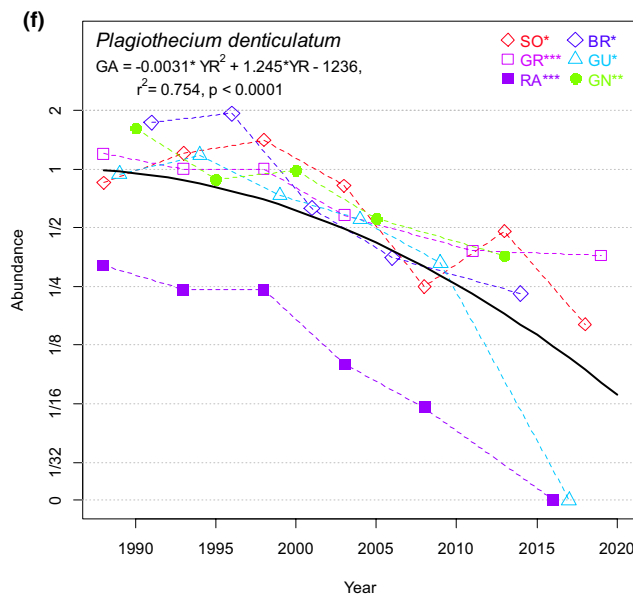
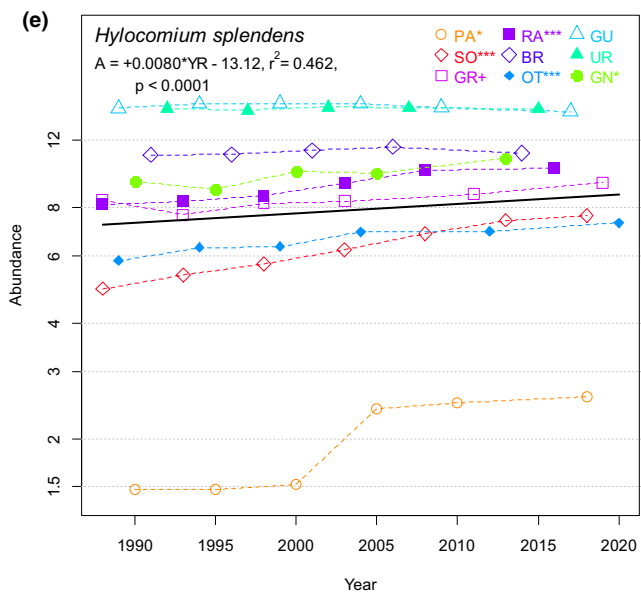
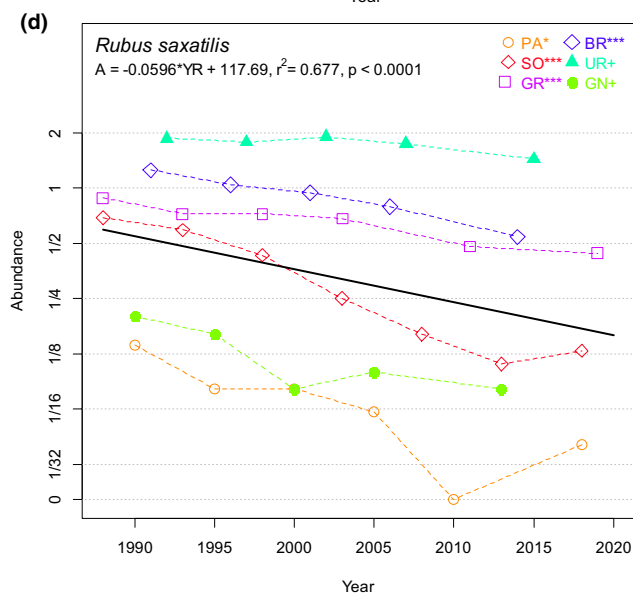
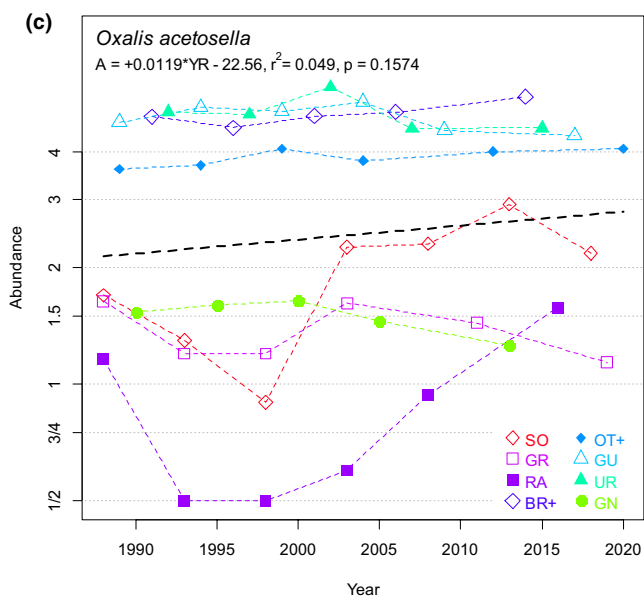
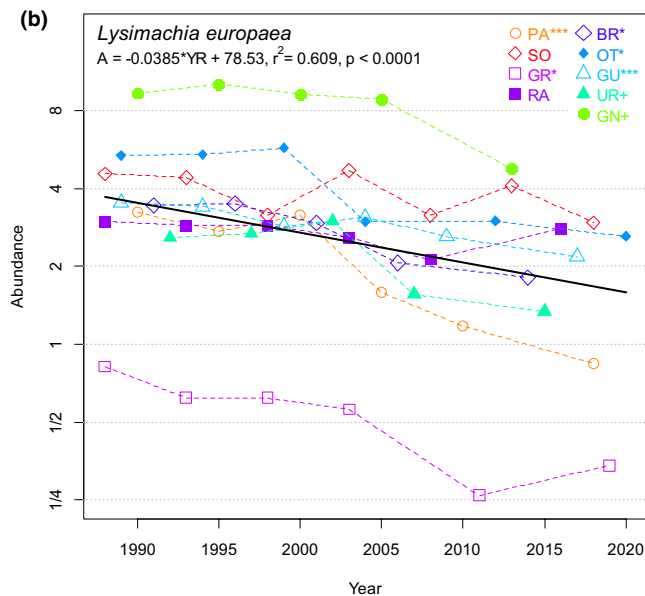
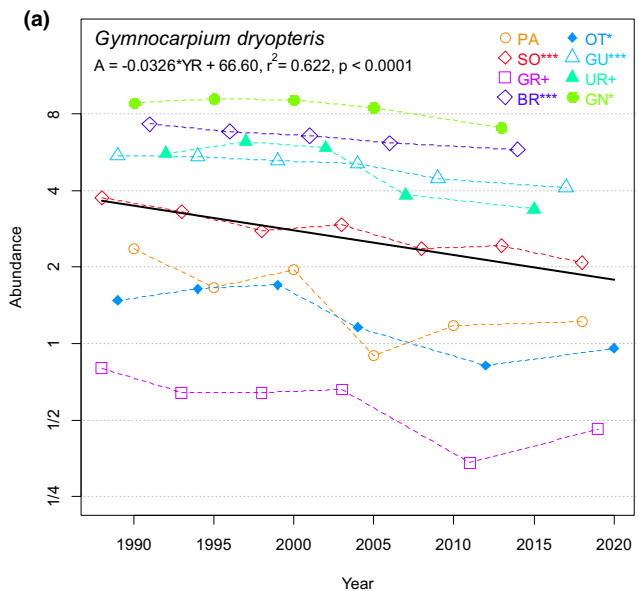
4 | DISCUSSION

We first evaluate the seven predictions from the CIUC hypothesis separately based on our results and relevant literature. Thereafter we broaden the perspective to address potential implications of our results.

4.1 | Prediction 1: Climatic conditions for bryophyte growth have improved

Our results suggest that bryophyte growth has been favoured by an increase in annual mean temperature, growing-season length (days with $\text{PRA} > 0$) and to some degree also annual precipitation. Furthermore, the number of days with rainfall was higher in the study period than in the preceding 30-year period (Framstad, 2021). The increase in the accumulated PRA index results primarily from elevated temperatures and more days with precipitation, most notably in the autumn,

FIGURE 6 Variation in abundance (A) for selected species as functions of recording year for nine boreal forest sites in Norway (see Figure 1 for geographic locations and explanations of two-letter site codes). (a) *Gymnocarpium dryopteris*. (b) *Lysimachia europaea*. (c) *Oxalis acetosella*. (d) *Rubus saxatilis*. (e) *Hylocomium splendens*. (f) *Plagiothecium denticulatum*. (g) *Rhytidiadelphus loreus*. (h) *Sphagnum russowii*. (i) *Calypogeia neesiana*. (j) *Fuscocephaloziopsis lunulifolia*. (k) *Lophocolea heterophylla*. (l) *Plagiochila asplenioides*. The solid line shows the relationship between A and year (YR). Regression coefficients in site-specific models are significantly different from 0 if the site code in the legend is followed by + ($0.05 < p < 0.10$), * ($0.01 < p < 0.05$), ** ($0.005 < p < 0.01$) or *** ($p < 0.005$).



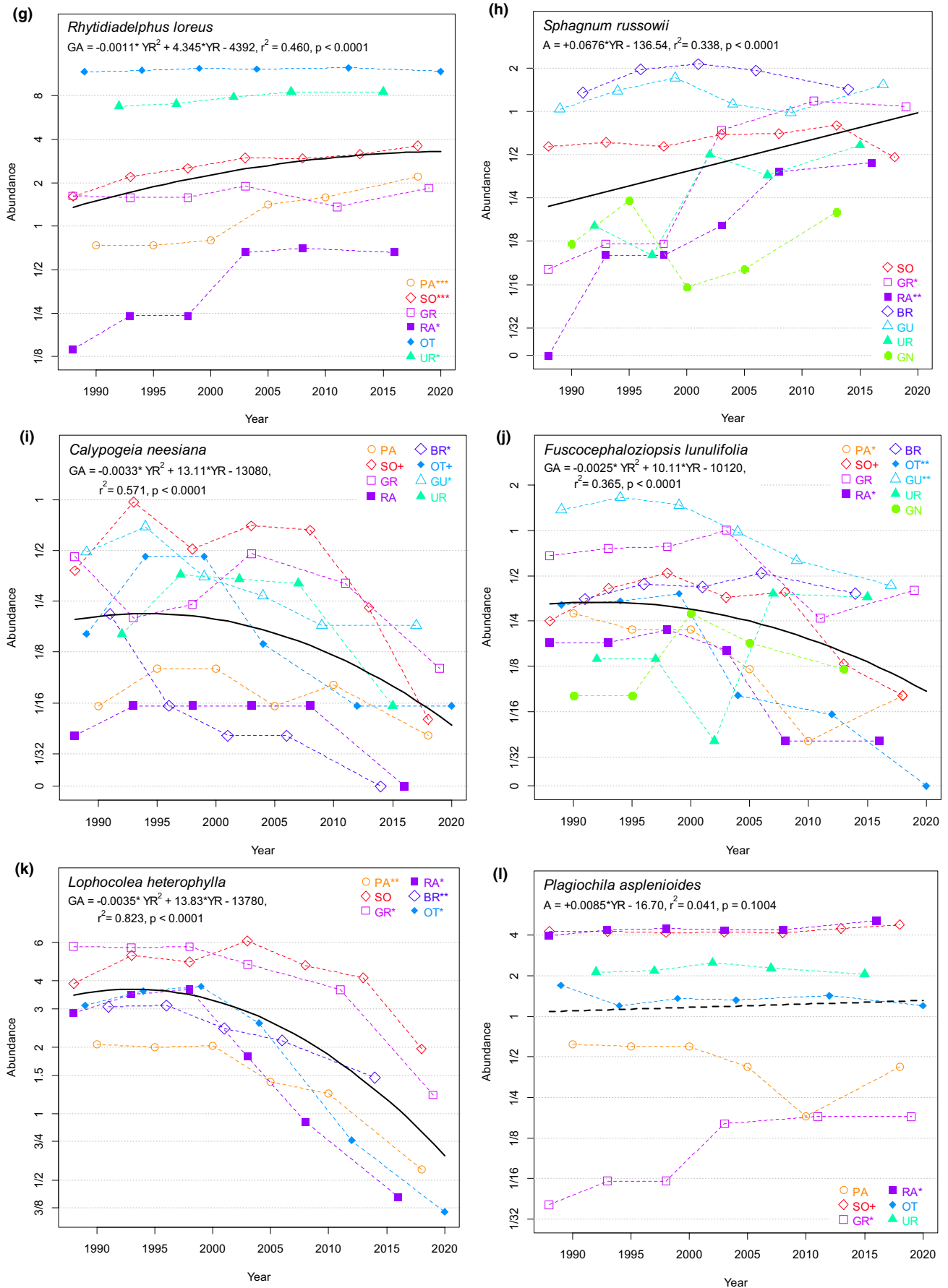


FIGURE 6 (Continued)

which in turn results in longer growing seasons and more favourable conditions for bryophyte growth. For example, autumn (September, October and November) mean temperatures have increased by 0.6–1.2°C from the 1958–1988 to the 1989–2018 period. In late autumn, when shading by above-ground parts of understorey vascular plants is reduced and the soil is kept moist for most of the time because of lower temperatures and more frequent rainfall, growth conditions in boreal forests are near optimal for large forest mosses (Økland, 1997). Prediction 1 is therefore supported by our results.

4.2 | Prediction 2: The species richness and/or abundance of large mosses, species with preference for moist sites and/or humid climate in particular, have increased

The results show a significant increase in species density and group abundance of *Sphagnum* species and an increase in the abundance of some large moss species, notably the (locally) dominating species, *Hylocomium splendens*, *Rhytidiadelphus loreus* and *Ptilium crista-castrensis*. In several sites, a significant increase is also observed for *Dicranum majus* and *Plagiothecium undulatum*. A majority of the bryophyte species that have increased significantly in the total data set either prefer humid climates (e.g. *Rhytidiadelphus loreus* and *Plagiothecium undulatum*; Størmer, 1969) or moist patches on the forest floor (*Sphagnum angustifolium*, *S. girgensohnii*, *S. rubiginosum* and *S. russowii*; Økland, 1996). The increase for these species thus accords with the increase in temperature and number of days with precipitation (see also Framstad, 2021) during the monitoring period, which is expected to result in a more humid climate. The strong increase in *Sphagnum* species suggests that the duration of periods with high soil moisture has also increased over the past decades.

The observed patterns of change for bryophytes accord with their ecophysiological adaptations, as outlined in the Introduction. Bryophytes span considerable variation in morphology, life-history strategy and growth form (During, 1992; Bates, 1998; Rossi et al., 2001), but most species are susceptible to desiccation and favoured by long periods in a hydrated state (Buch, 1947; Hosokawa et al., 1964). Improved conditions for bryophyte growth, as indicated by an increase in the PRA index, is the most likely reason why the abundance of a few, mostly large, mosses has increased considerably over the past three decades. Our results therefore support prediction 2. A contrasting temporal pattern was, however, observed by Nygaard and Ødegaard (1999) in a comparable old-growth forest in the period 1931–1991. They attributed the recorded decrease in several moisture-demanding species to an increased density of the tree layer dominated by Norway spruce.

4.3 | Prediction 3: The species richness and/or abundance of small bryophytes has decreased

This prediction is substantiated by the strong decrease in group species density and group abundance of small cryptogams, of which

most are hepatics, over the 32-year study period. This pattern also contributes strongly to the observed reduction in site species richness. Furthermore, the results add important details to the overall pattern: hardly any decline in small bryophytes took place in the 1990s, and the decrease in small-statured species on the forest floor starting around year 2000 still goes on and apparently accelerates.

The observed decrease in group density for bryophytes that results from the massive decrease in small-statured species accords with the predictions of Walker et al. (2006) and He et al. (2016) that tundra and boreal forest bryophytes will be particularly susceptible to biodiversity reductions due to global warming. Our findings, which indicate that only a few species increase in abundance under the current climate change regime whereas most species decrease, also accord with results of the experimental warming study by Sun et al. (2017) who find that effects of warming are “species and community specific”.

4.4 | Prediction 4: The increase in large and decrease in small bryophytes are coordinated in time and space

At a first glance, our results seem to support this prediction: over the entire 32-year study period, group species density and group abundance have increased for large species (prediction 2) and decreased for small species (prediction 3). However, when the study period is divided into periods of five to eight years, the overall pattern decomposes into incongruent patterns for large and small bryophytes. From the first to the second recording year, i.e. in the first half of the 1990s, the abundance of both small and large bryophytes increased, for the small-sized species most strongly in the southernmost sites PA, SO, GR and RA where the initial bryophyte cover was much lower than further north (see Figure 3b). After about 1995, and most notably after 2000, significant increases for large mosses have taken place in the southernmost sites PA and SO, whereas in the sites further north the increase is restricted to specific species and periods. In the highest- and northernmost-situated sites (GU, UR and GN) hardly any increase in subplot frequency has been observed for large mosses. However, even in these sites the percentage cover of large bryophytes has continued to increase, e.g. for *Hylocomium splendens* (Timmermann et al., 2020; Økland et al., 2021). Meanwhile, from the late 1990s, small mosses have decreased significantly in all sites except GN, at accelerating rates. This is demonstrated by the significant quadratic terms in abundance models. We therefore interpret the observed abundance reduction for small bryophytes as a general, i.e. long-lasting and broad-scale, pattern that occurs all over Norway (although perhaps weaker towards colder climates).

Most small mosses and hepatics in boreal forests tend to occupy open, vertical or frequently disturbed microsites (“pockets”), whereas they are less frequent on the “normal” forest floor (Økland, 1996; Økland et al., 2001, 2003). Økland and Økland (1996) and Økland (2000a) propose a mechanistic explanation for the tendency of small bryophyte shoots, conspecific or not, to disappear from the “normal” forest floor in the absence of recurrent fine-scale

disturbances: small shoots are overtopped by larger shoots and enter a negative spiral of reduced light supply. Reduced growth of the small shoots ends with growth cessation, burial in the bryophyte carpet and, finally, death.

The onset of abundance reduction for small bryophytes observed in our study coincides with the cessation of regular population cycles of lemmings (*Lemmus lemmus*), wood lemmings (*Myopus schisticolor*) and other microtine rodents (e.g. *Myodes rufocanus*). Kausrud et al. (2008) point to 1994 as the year when the formerly regular microtine rodent cycles in alpine and adjacent upper and northern parts of the boreal bioclimatic zones, with a period of about 4 years, were replaced by irregular cycles with considerably longer intervals between peak years. This is substantiated by observations in our study sites: rodent peaks were observed in SO and GR in 1987–1988 and in OT and GN in 1988–1989, just before the start of this study. After the start of this study in 1988, distinct microtine rodent population peaks have only been observed four times: 2000–2001 in GN, and 2010–2011 in GR, GU and GN (Halvorsen, 2019; Halvorsen, personal observations).

When occurring in high numbers, rodents disturb the bryophyte layer by browsing and trampling, causing a temporary reduction of bryophyte cover (Ericson, 1977; Rydgren et al., 2007; Halvorsen, 2014). After rodent population peak years, 25% of *Hylocomium splendens* growing points have been observed to be cut (most probably eaten; Kalela et al., 1963) and another 25% lost (Halvorsen, 2019). The reduced frequency of fine-scale disturbance of the boreal forest floor resulting from the reduced frequency and regularity of microtine rodent population peaks may have triggered the decline in small bryophytes by favouring a long-term build-up of dense carpets of large mosses. Kausrud et al. (2008) hypothesise that the collapse of microtine rodent population cycles is an indirect effect of climate change, operating by the following mechanism: the increasing frequency of mild periods in winter causes frost and ice formation in the subnival air space between the snow layer and the ground, restricts rodent mobility and food supply, and results in higher mortality and lower reproduction rates.

4.5 | Prediction 5: A regional pattern of vascular plant decline that corresponds with the pattern of deposited long-term airborne pollutants, inorganic N deposition in particular, is no longer present

Our results substantiate that the regional pattern of decrease in nutrient-demanding species of vascular plants in the southern sites, as reported by Økland et al. (2004) for the monitoring years between 1988 and 1997, is no longer present. Abundance decrease is observed for vascular plants independent of their demands for mineral nutrients; the only common grass *Avenella flexuosa*, the common forbs in nutrient-poor, submesic spruce forests, *Maianthemum bifolium*, *Lysimachia europaea* and *Solidago virgaurea*, as well as for the more nutrient-demanding species, *Gymnocarpium dryopteris*, *Rubus saxatilis* and *Viola riviniana* (Appendix S6). Furthermore, over the past

two decades, *Oxalis acetosella*, which declined significantly in several sites in the 1990s (Økland et al., 2004), has recovered to higher abundance levels after 2000 in some sites. Further support for prediction 5 comes from the lack of a positive relationship between N indicator values and vascular plant abundance change.

These results accord with the reduced deposition of anthropogenic acidifying compounds (NO_3^- and SO_4^{2-}) in Norway and other European countries during the 30-year study period (Ackerman et al., 2019; Aas et al., 2020). Nevertheless, they do not rule out the possibility that high levels of N deposition in the southernmost sites prior to 1990 have affected boreal forest understorey vegetation. The significant abundance decrease observed for the dwarf shrub *Vaccinium myrtillus* in several sites, as well as in the total data set (Appendix S6), does, for example, accord with the decrease in dwarf shrub cover in Swedish forests since 1950, most strongly in regions with the largest increase in nitrogen deposition and rates of land-use change (Hedwall et al., 2019, 2021). However, an alternative and more likely explanation for the decrease in *Vaccinium myrtillus* observed in southern Sweden is that the trend towards a more nitrophilous vegetation is mainly due to the application of fertiliser to production forests (Sundberg, 2014; Hedwall et al., 2021).

4.6 | Prediction 6: The species richness and/or abundance of forbs has decreased

This prediction is substantiated by the significant decrease in species density and group abundance observed for vascular plants, forbs in particular, resulting from a significant linear abundance reduction for 14 of 19 tested vascular plant species (10 of 15 forbs) over the 32-year study period. In contrast to the nonlinear cryptogam patterns, vascular plant abundance has decreased at a constant rate during the study period; 65–70% of within-site variation in vascular plant species density and group abundance is explained as a linear function of time, higher than for any other group (Table 2).

Reduced forb abundance is observed in many other studies (Nygaard & Ødegaard, 1999; Hedwall et al., 2013, 2019; Sundberg, 2014; Prach & Kopecký, 2018). However, the hypothesised causes of those patterns – forestry measures, fertilisation or tree-layer dynamics – do not apply to the old-growth forests at our sites. Because our explanation for the forb decline involves an increase in large bryophytes (prediction 7), predictions 6 and 7 are discussed together.

4.7 | Prediction 7: Increase in large bryophytes and decrease in forbs are coordinated in time and space

Our results are ambiguous with respect to this prediction. Over periods of five to eight years, rates of large bryophyte and forb abundance change are weakly positively correlated, contrary to the prediction (Appendix S5). However, over the entire 32-year study period, prediction 7 is strongly supported by the increase in large

bryophytes and the decrease in forbs. Our results therefore allow for the hypothesis that the primary mechanism driving vascular plant abundance decline is the climate-driven increase in abundance, and hence, cover and thickness, of moss carpets on the boreal forest floor, brought about by processes that operate on time-scales of decades and on broad spatial scales.

Most vascular plant species in boreal forests are clonal and long-lived (Eriksson, 1989; Økland, 1995b). The observed, national-scale, abundance decline observed for this species group may result from long-term recruitment rates that are lower than mortality rates. A negative relationship between large bryophytes and vascular plants is demonstrated by Brooker and Callaghan (1998) and Gornall et al. (2011) who found that a thick moss carpet structures vascular plant communities by reducing soil temperatures and soil N content. A thick moss layer has a strong insulating effect on the soil (Oechel & van Cleve, 1986) and retains and immobilises N supplied from above (Pearce et al., 2003; Curtis et al., 2005; Cornelissen et al., 2007). Increasing bryophyte carpet thickness also results in decreased root growth (Gornall et al., 2011), decreased rhizome branching (Martin et al., 2020) and a reduced number, size and growth rate of tillers (Slade & Hutchings, 1987; Huber & Stuefer, 1997; Krna et al., 2009). Our observations thus accord with the mechanism suggested for the long-term decrease in vascular plant abundance with increasing bryophyte-layer thickness (Brooker & van der Wal, 2003; Gornall et al., 2011), summarised by Gornall et al. (2011: 780) as follows: "... an increase in moss depth may be viewed as an increase in environmental severity as experienced by a vascular plant, with gradual decreases in soil temperature, soil nutrient availability and length of the growing season". The negative effect of a thick bryophyte layer on vascular plant branching (tillering, etc.) is mediated by the phytochrome system, i.e. a response to the change in the red/far red ratio underneath a dense bryophyte canopy resulting from light absorption by the green moss tissue (Casal et al., 1985; Deregibus et al., 1985; Wan & Sosebee, 1998; Lafarge et al., 2005).

The negative effect of thick bryophyte carpets on vascular plants is, however, not restricted to clonal plants; a thick bryophyte carpet is inferior to naked soil, logs and other microsites as substrates for germination and the survival of seeds from trees, herbs and graminoids and fern spores (Ohlson & Zackrisson, 1992; Hörnberg et al., 1997; Sedia & Ehrenfeld, 2003; Wardle et al., 2008; Drake et al., 2018). Soudzilovskaia et al. (2011) found that *Hylocomium splendens* was among the strongest suppressors of vascular plant seedlings in a field experiment in a North Swedish subarctic forest. Rydgren et al. (1998) demonstrated that microsite availability also matters for clonal, asexually reproducing vascular plants like *Gymnocarpium dryopteris*, which decreased significantly in seven of the nine sites in our study. Other species with a significantly decreasing abundance in several sites, e.g. *Maianthemum bifolium*, *Lysimachia europaea* and *Vaccinium myrtillus*, have been shown by Eriksson and Ehrlén (1992) to be limited by both microsite and seed availability. Expanding carpets dominated by a few large moss species may therefore have a double effect on vascular plants, by creating a less favourable

micro-environment, and by reducing the abundance of microsites suitable for regeneration.

We cannot rule out the possibility that changes in tree-stand structure may have contributed somewhat to the observed patterns of vascular plant decline, as observed in many studies of old-growth (Nygaard & Ødegaard, 1999) as well as managed forests (Hedwall et al., 2013, 2015, 2021). None of the nine sites studied by us was completely unaffected by former dimension and selection logging and/or forest fires, even though their tree populations were characterised as "old-growth" at the start of the monitoring programme (Økland & Eilertsen, 1993; Økland, 1996; Ohlson et al., 2009). Increased tree growth reduces the supply of light to the understorey while, on the other hand, many old trees experience reduced crown density and also give rise to canopy gaps when they die. The balance between these processes in the study sites is not known. Furthermore, older trees take up more nutrients from the soil (Tamm & Hallbäck, 1988) and thus contribute to the reduced availability of nutrients, nitrogen included, to understorey vascular plants. Although we have not observed patterns of species compositional change that can be related to tree-layer changes, effects of tree-stand dynamics cannot be completely ruled out.

4.8 | Conclusions, implications and recommendations

We interpret our results as a complex, cascading effect of the changing climate, in general accordance with the CIUC hypothesis. Increasingly favourable conditions for bryophyte growth facilitate the build-up of extensive, thick moss carpets, which in turn create an increasingly unfavourable habitat for small bryophytes as well as for vascular plants. These effects are strengthened by the collapse of cyclic microtine rodent population dynamics, which is also likely to be driven by climate change (Kausrud et al., 2008). We cannot, however, completely rule out the possibility that other factors, such as tree-layer changes that are legacies of former management, wildfires and so on may add small pieces to this complex puzzle. This accords with the conclusion of Hedwall et al. (2021) that climate change interacts with natural processes in boreal forests in a most complex manner.

Our results add new perspectives on climate change effects on boreal forest biodiversity. Although some organism groups are expected to be favoured and others are expected to be disfavoured by a warmer climate, our study demonstrates a significant, negative resultant effect on understorey vascular plants and cryptogams in Norwegian old-growth boreal forests over the past three decades. If global warming continues, the proposed mechanisms behind these changes are likely to remain active, resulting in further loss of biodiversity. However, several processes may interfere with, or alter, this prediction. The predicted increase in tree pests and pathogens (Ghelardini et al., 2016; Biedermann et al., 2019) may reduce tree-layer density, which may in turn reduce the growth rates of shade-tolerant dominant mosses (He et al., 2016), potentially benefitting

vascular plants (Økland & Eilertsen, 1993). An increased frequency of extreme weather events may trigger higher windfall disturbance frequencies (Venäläinen et al., 2020) which in turn also contribute to a more open tree layer. An additional effect of windfall disturbance is disruption of the bryophyte carpet, which favours regeneration of trees (Hörnberg et al., 1997; Hanssen, 2003) and other vascular plants (Eriksson & Ehrlén, 1992). An increased frequency of summer drought and extreme heat spells affects Norway spruce negatively (Kunert, 2020) and may also have negative effects on understory mosses (Greiser et al., 2021) and the dominant dwarf shrubs (Taulavuori et al., 2013), while elevated temperatures also increase the risk of winter drought, thus contributing to “Arctic and boreal browning” (Bjerke et al., 2017). These partly antagonistic effects make prediction of the long-term outcome of advanced climate warming almost impossible. Continuation of the current trend towards loss of biodiversity is likely to reduce the resilience of boreal forests to external pressures (Hisano et al., 2018) and may thus contribute to the loss of important ecosystem services provided by boreal forests.

More than 30 years of detailed forest understory monitoring in permanent plots has demonstrated that the vegetation, i.e. the set of vascular plants and cryptogams, is a sensitive indicator of the state and condition of the boreal forest ecosystem. The monitoring programme in which the sites in this study were included, thus fulfilled the purpose of giving early warnings of ecosystem change (Økland, 1990; Økland & Eilertsen, 1993; Lawesson et al., 2000). Although the major patterns of change are interpretable in terms of broad-scale environmental change, several minor patterns await detection and interpretation. Continuation of vegetation monitoring, including repeated sampling of tree-layer and soil chemical variables, is necessary to ensure early detection and facilitate understanding of mechanisms behind future changes.

AUTHOR CONTRIBUTIONS

TØ and RH designed the study. TØ, RH and JFN conducted the fieldwork together with several other colleagues and field assistants. All authors contributed to data analyses and interpretations. TØ wrote the manuscript with contributions from all authors. RH performed new data analyses and revised the manuscript. All authors edited and approved the final version.

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DATA AVAILABILITY STATEMENT

The data sets used for the analyses are provided in Appendix S8.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. List of recorded species.

Appendix S2. Taxonomic–ecological species groups and subgroups.

Appendix S3. Explanation of the PRA index.

Appendix S4. Additional climate information.

Appendix S5. Correlations between rates of change in total abundance per year for selected species-group pairs.

Appendix S6. Linear models for single-species abundance.

Appendix S7. Relationship between cryptogam size and rate of annual species abundance change.

Appendix S8. Data (Excel file).

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