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Research article

Vegetation dynamics 1946–2018 in an old-growth conifer forest

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We analysed ground vegetation in 250 plots in 2018 in the old-growth *Picea abies*-dominated forest Säby Västerskog, south-east Sweden as a follow-up of studies in 1946 and 1998 with the same layout of plots. The vegetation changes were not clearly directional: the species composition in 2018 was intermediate between that of 1946 and 1998, whereas in 1998 species richness was higher and with the unique presence of a number of species indicating small-scale disturbances. *Vaccinium myrtillus* increased in cover since 1946 and *Avenella flexuosa* decreased. This goes against regional trends that have been attributed to nitrogen deposition. Regional changes are overshadowed by local dynamics.

Keywords: long-term changes, nature reserve, south-east Sweden, species richness, spruce forest

Introduction

The conifer forests of the boreal zone represent 30% of the world's forested area (Gauthier et al. 2015), and even more when similar boreo-nemoral forests are included. However, only a small part of these forests has had a more or less natural development. In Sweden 3.5% of the productive coniferous forests below the mountain-near forests are protected in national parks and nature reserves (Per-Erik Wikberg unpubl.). How much of these forests are primeval or near primeval forests is unknown. The largest parts are situated in the northern half of Sweden. In Norway less than 2% are estimated to be 'natural forest' (Storaunet and Rolstad 2020). These forests have been under the influence of environmental changes during the last century, notably N deposition, acid rain and climate change (Pihl Karlsson 2021). In successional unmanaged forests, the field layer cover may be gradually reduced due to increasing density of the tree layer until a steady state is reached (Nygaard and Ødegaard 1999, Bergstedt and Milberg 2001).

N deposition is considered a main driver of changes in dominance among species as it alters the competitive relationships (Bobbink et al. 2010), and is the likely cause for shifts from dwarf shrubs to nutrient-demanding species in southern Sweden (Hedwall et al. 2019). The speed of recovery of soil conditions after reduced N deposition is variable (Stevens 2016), and apparently a slow process (Strengbom et al. 2001).

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Effects may persist for a long time, at least 15–18 years with clear-felling in between (Olsson and Kellner 2006), which can be explained as hysteresis effects (Stevens 2016, Bowman et al. 2018).

Soil acidification through deposition of nitrogen and sulfur was documented in southern Sweden when comparing the period 1949–1970 with 1985, with a concomitant decrease in some acid-intolerant species (Falkengren-Grerup 1989). A decrease in abundance of species associated with rich soils was also found in Norway by Økland et al. (2004) over a time period as short as five years (starting between 1988 and 1992), which was interpreted as a response with a long lag-phase in long-lived species to acidification. However, in nutrient-poor soil, N deposition may rather cause eutrophication (Falkengren-Grerup 1989).

Monitoring programmes, such as the National Forest Inventory (NFI) in Sweden, are major sources of evidence for vegetation changes in Nordic conifer forests. However, most plots within NFI fall within managed forests (Hedwall et al. 2013, 2019, 2021, Hedwall and Brunet 2016, Jonsson et al. 2021), which makes it difficult to separate long-term changes from the succession within a rotation period (Tonteri et al. 2016). To avoid management effects, Jonsson et al. (2021) used NFI data from stands that were not managed during the study. They found a decline in species richness. Based on repeated surveys of province floras, Sundberg (2014) concluded that boreal species had declined in southern Sweden during the second half of the 20th century. Changes in nine Norwegian old-growth forests were monitored in 1988–2021 by Økland et al. (2023), and they likewise noted a general decrease in most species groups and a decrease in site species richness.

Even when management is accounted for, time lags in plant responses make interpretations difficult (Økland et al. 2004, Jonsson et al. 2021), and long-term data (published or archived) from the increasingly rare old-growth forests are crucial elements of monitoring programmes (Laweson et al. 2000) and should be included in these types of research (c.f. Økland et al. 2023). Such studies are needed to increase the knowledge of natural processes in conifer forests. Are large-scale trends apparent, or are they overshadowed by internal processes such as gap formation by wind, fire and insect attacks, as suggested by Grandin (2011)? Monitoring programmes cover a selection of species, whereas long-term studies based on complete vegetation analysis are needed to reveal dynamics in community structure and species richness and composition (Hédl et al. 2017).

Although there are numerous descriptions of boreal and boreo-nemoral field and bottom layer vegetation based on vegetation plots from the early 20th century and onwards, few of these plots can be found today for re-sampling. Some rare examples of long-term studies with permanent field-layer plots in Scandinavian boreal forests, e.g. Engelmark et al. (1998) and Nygaard and Ødegaard (1999) do, however, exist. In other cases, plots have been relocated with the help of remaining trees or other features (Hofgaard 1993). A dataset of ca 250 plots exists from the old-growth *Picea abies*-dominated forest Säby Västerskog, collected in 1946 by Arnborg (Arnborg 1946) and in 1998 by Caruso (Caruso 1999). Re-sampling of these plots may add to the sparse knowledge about the long-term dynamics of these types of forests.

Our aim is to investigate change or constancy in frequency and abundance of species as well as in species richness and community composition in a 72-year perspective. It is hypothesised that directional changes exist, including a decline of vascular plant species in general, related to nitrogen deposition, mirroring the results from monitoring programmes. However, these changes could be overshadowed by local processes such as gap creation that would affect the heterogeneity in the field and bottom layers of the forest, rather than lead to directional changes (Grandin 2011).

Material and methods

Description and history of the forest site Säby Västerskog

Säby Västerskog is a small protected coniferous forest in the boreo-nemoral region (Sjörs 1965) of south Sweden (Fig. 1) in the province Östergötland, Vist parish (58°15′05″N, 15°46′46″E). The landscape around the reserve is dominated by managed coniferous forests intersected by open fields. The reserve is a mesic forest dominated by *P. abies* and, to a lesser extent, *Pinus sylvestris*, without a clear spatial separation of these species. The field layer is dominated by *Vaccinium myrtillus.* Elevation is approximately 115–135 m a.s.l. The mean annual temperature measured at Bjärka-Säby, situated approximately 2 km NNW of the forest, was 7.2°C (1945–1983, SMHI 2021a) and the mean annual precipitation was 597 mm (1945–1992; SMHI 2021b). The ground is relatively flat, but with a few rocky outcrops. It is in some places covered with big boulders. Till soil dominates. The humus is in most places a mull, and pH varies from 3.2 in a peaty soil to 6.0 in a herb-dominated site (Arnborg 1947–1954).

Säby Västerskog was superficially described by Sernander (1922, 1925). Its history was tentatively reconstructed as follows by Arnborg (1947–1954), based on age determinations of trees and tree species composition: The forest was probably cut before 1800 with only a few spruces left. It was then used as a grazing area for cattle. Around 1800 the main part of the forest gradually became denser, mainly with *P. abies* and *P. sylvestris*. At the beginning of the 20th century a few big pines were cut, and spruce became more common. As Arnborg (1947–1954) found very few individuals of *Betula* spp. and *Populus tremula*, he concluded that the area had not suffered from forest fires. Also, there was no evidence that the forest had been planted. The trees in the southeast corner of the forest were younger than in the main area and had probably increased in number after grazing ceased around 1885. Up to then, that area was probably a pasture with a sparse *Betula* stand, a vegetation type common in Sweden at that time. A small mire with *Betula* spp. and *Alnus glutinosa* trees in the northeast, where the forest borders a railway, was drained around 1900, resulting in a dense spruce forest.

Arnborg (1947–1954) believed that the forest had not earlier suffered from storm felling, but in March 1943 many

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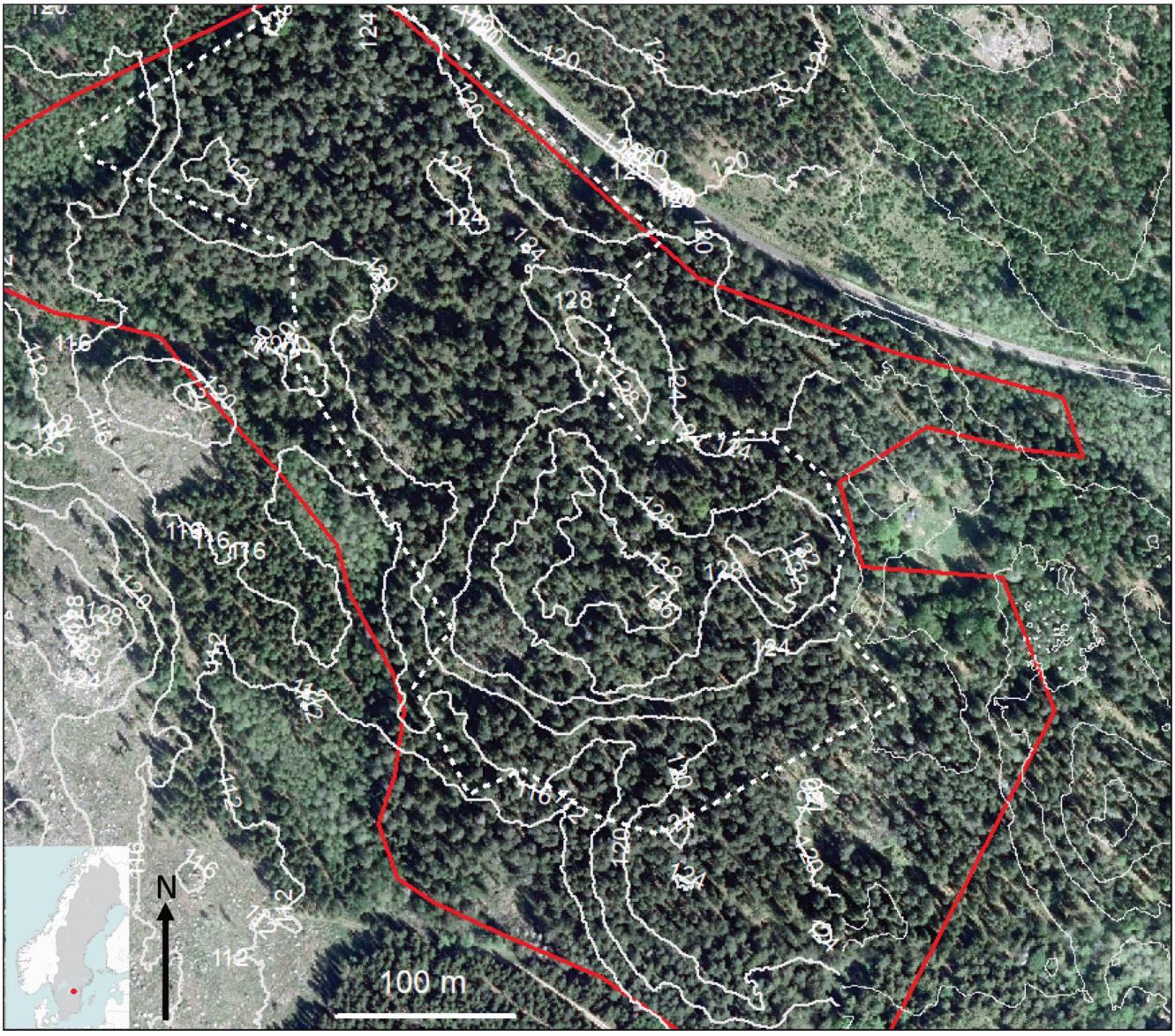


Figure 1. Säby Västerskog. Red line, the current nature reserve; white dashed line, the investigated area (roughly corresponding with the original reserve). Equidistance is 4 m. Air photo ©Lantmäteriet. Elevation data based on laser scanning with 1 m grid (Markhöjdmodell grid 1+, Lantmäteriet 2021).

trees, mainly *P. abies*, fell in a storm (Arnborg 1949). Two storms had large effects on forests in the region: in January 2005 ('Gudrun') and January 2007 ('Per'). Nevertheless, in 2018 only approximately 5% of the field-layer plots were in gaps with fallen trees. Two gaps were of considerable size (ca 1/2 ha). There were also many standing dead trees after a recent attack of spruce bark beetles *Ips typographus*. The oldest individuals of *P. abies* were 200–250 years old, and the oldest *P. sylvestris* tree was ca 160 years old (Länsstyrelsen Östergötlands län 2018). The tree population in the reserve was carefully mapped by Linder (1937), and this mapping was repeated in part of the area in 2022 (Lindstrand 2022).

The forest was protected by the County Board in 1923. The reserve then encompassed 11.9 ha, was fenced and closed to the public. Since 1974 it has been open for public access, and in 1998 the protected area was enlarged to 22.1 ha. In 2018 it also became a Natura 2000 area (Länsstyrelsen Östergötlands län 1974, 1998, 2018).

Field methods

This paper is based on three vegetation surveys at Säby Västerskog. In 1946 Arnborg sampled the field and bottom layer vegetation in 253 plots (0.5 × 0.5 m), distributed in a regular 20 m grid across the whole reserve. Small, field layer individuals of trees and shrubs were not included. His results, including distribution maps of selected species, are only documented in manuscripts (Arnborg 1946, 1947–1954),

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except for a popular article (Arnborg 1949). Arnborg (1946) indicated the southern and northern endpoints of a central line in relation to the corners of the nature reserve.

In 1998 Caruso (1999) repeated Arnborg's investigation. The nature reserve had been expanded the same year, but he relocated the border posts of the original reserve. Individual plots could not be relocated, but he placed plots by use of Arnborg´s scheme. Caruso increased the plot size to 1 × 1 m and sampled 243 plots.

Our own field sampling took place in 2018, again with a plot size of 1 × 1 m. The border posts of the original reserve had by then disappeared. With Arnborg's landmarks we could relocate the coordinates of the northernmost plot of the central line, probably to within less than 5 m. To make sure that we covered the original area, we sampled 308 plots; and, later on, when we could superimpose the plots on a map (using ArcGIS ver.10; ESRI 2011) we reduced the number to 250 plots that covered the same area as the previous surveys. We extracted elevation (m a.s.l.) for all plots from laser scanning with 1 m grid (Markhöjdmodell grid 1+; Lantmäteriet 2021). All three surveys were made in July and onwards, in the same phenological phase.

Our analyses included vascular plants and bryophytes. However, a complete survey of the latter was not attempted. Lichens were not included. Seedlings and saplings of shrubs and trees were included only if they were below 50 cm in height, but they were excluded from the statistical analyses, as they had not been included in Arnborg's sampling. In all three surveys (1946, 1998, 2018), the cover of plant species was estimated by use of the Hult-Sernander-Du Rietz cover scale (Du Rietz 1921): 1, < 6.25% cover; 2, 6.25–12.5%; 3, 12.5–25%; 4, 25–50%; 5, > 50%. We have retained this rather coarse scale which reduces possible errors caused by bias in estimations. Some of the 1998 data are unfortunately lost; we have presence/absence data for all species, but cover data have been retained only for twelve species that were mapped by Arnborg (1947–1954).

In 2018 we also noted if the plot included a big root plate, a root pit or traces of boar activity, and if it was situated in a big gap. By use of the 1–5 cover scale we also estimated the area within each plot covered by a tree base or thick living roots above the ground, as well as litter, open soil, boulders and the number of logs (dead, fallen tree stems with a diameter > 10 cm). From 2018 we also have data on shrub cover from the 1 × 1 m plots, which include woody plants taller than 0.5 m and with a diameter < 10 cm at breast height (1.3 m). Within a circle with a radius of 5 m around each plot we noted the presence of each tree species, and estimated total tree density (stem diameter >10 cm) in the scale: 0, no trees; 1, a few trees; 2, intermediate; 3, dense tree stand.

Nomenclature

We adjusted the species lists for bryophytes so that the taxonomic resolution would be the same as in the earlier surveys. Unfortunately, the two dominant feather mosses *Hylocomium splendens* and *Pleurozium schreberi* were lumped in 1946. *Dicranum* spp. mainly include *D. majus*, *D. polysetum* and *D. scoparium*. *Eurhynchium angustirete*, *Oxyrrhynchium hians* and *Sciuro-hypnum curtum* are lumped and coded as *Brachythecium/Eurynchium*. *Mnium* spp., *Plagiomnium affine*, *P. undulatum* and *Rhodobryum roseum* are lumped as *Mnium* spp. *Polytrichum* spp. include *P. commune*, *P. formosum* and *P. juniperinum*. *Sphagnum* spp. include *S. capillifolium, S. angustifolium/fallax, S. girgensohnii* and *S. palustre*. *Dryopteris dilatata* and *D. expansa* were not separated. Nomenclature follows Dyntaxa (2023). All taxonomic units used in the calculations are referred to as 'species'.

Statistical methods

Changes in cover between 1946 and 2018 were tested with two-tailed t-tests for all species. For all three surveys we only have cover data for twelve species, and for these we tested changes in cover between the three surveys with Anova, followed by Tukey HSD tests to establish which survey(s) differed. For these tests we used significance level $\alpha = 0.05$. As the increase in plot size after the first survey may have caused higher frequency values, we only, somewhat arbitrarily, discuss species showing a change of ≥ 20 plots between any two surveys.

For ordinations we applied global non-metric multidimensional scaling (NMDS) with the *metaMDS* function in the 'vegan' package (Oksanen et al. 2022) in R ver. 4.2.1 (www.r-project.org). We used the Bray–Curtis dissimilarity index. The convergence criterion was set at default (sfgrmin = 10^{-7}) and we ran multiple starting configurations to convergence (maxit = 1000, trymax = 1000). We fitted three dimensions (k = 3, to reduce stress and reach stable solutions). Axes were rescaled to half-change units, and species scores were computed as weighted averages. In ordination diagrams we drew 95% confidence ellipses for groups with the *ordiellipse* function. Vectors for elevation and survey number (time) were fitted with the *envfit* function and we used *ordisurf* to overlay a generalised additive model of plot elevation. Differences between surveys were tested with *adonis2* (difference in position) and *betadispers* (difference in variation). To explore factors that are not related to elevation or time, we ran an ordination based on cover data from 2018, followed by *envfit* models for the variables listed under 'Field methods' in addition to elevation.

Floristic turnover was calculated as Jaccard index (number of shared species divided by total number of species in two surveys) and is illustrated by a Venn diagram produced with the *venn.diagram* function in R (package 'venn.diagram') and plotted by the *plotVenn* function (package 'nVennR'). Species accumulation curves were extracted with the *specaccum* function in 'vegan', adding plots in random order.

Results

Species richness and turnover

The total number of taxonomic units (species and species groups) recorded in the plots was 45 in 1946 (36 vascular plants + 9 bryophytes), 72 in 1998 (64 + 8) and 61 in 2018 (50 + 11). The species accumulation curves (Supporting

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information) reveal that 98% of the total species richness is reached after a random extraction of 231, 225 and 232 plots, respectively, in the three surveys.

Thirty-seven species occurred in all three surveys, and the number of unique species (Fig. 2) was higher in 1998 (17 species) than in 2018 (7) and 1946 (3). Most of the unique species in 1998 are typical of small-scale disturbances: *Campanula persicifolia*, *Chamaenerion angustifolium*, *Epilobium montanum*, *Galeopsis tetrahit*, *Geranium robertianum*, *Hypericum maculatum*, *Moehringia trinervia*, *Poa annua*, *Ranunculus repens*, *Stellaria graminea*, *Urtica dioica*.

The surveys in 1998 and 2018 shared more species and had the highest floristic similarity (Jaccard index) than the other pairwise combinations of surveys (Fig. 2). Only a few relatively rare plants were found: *Circaea alpina*, *Chrysosplenium alternifolium* and the orchids *Coeloglossum viride* and the Red-Listed *Goodyera repens* (VU; SLU Artdatabanken 2020).

Cover changes

Occurrences and cover in individual plots for the twelve species that were analysed in all three surveys are mapped in Fig. 3, with changes in mean cover summarised graphically in Fig. 4.

For the remaining species, cover can only be compared between 1946 and 2018. However, all of those that increased significantly had low plot frequency in 1946 (0–8 plots), and their apparent cover increase may well reflect an increase in plot frequency due to increased plot size. For that reason, we include only three species that decreased significantly in Fig. 3–4.

The distribution of the species within the forest was fairly even, except that some species had a distribution gap in the south–central part of the forest (Fig. 3), coinciding with areas with higher elevation (Fig. 1), where *Vaccinium vitis-idaea* instead had high cover in 1946. *Gymnocarpium dryopteris* and *Pteridium aquilinum* had a stable mean cover, but with some spatial changes. *Gymnocarpium dryopteris* had fewer plots with high cover in 2018, and *P. aquilinum* had no plots with high cover in 1998 (Fig. 3).

Because of the large sample size even small changes in mean cover are significant in some cases, such as the net decrease in *Hepatica nobilis*, *Anemone nemorosa* and *V. vitis-idaea*. All four species that increased from 1946 to 1998 decreased after 1998 (Fig. 4). *Maianthemum bifolium* and *Dicranum* spp. were in 2018 close to the 1946 cover after the 1998 peak (Fig. 4), and there were hardly any plots with a high cover of these species in 2018 (Fig. 3). For the whole period 1946–2018 *Ptilium crista-castrensis* had a net decrease, and *Plagiochila asplenioides* a net increase. For both species, plots with a high cover had become rare in 2018 (Fig. 2).

For the whole period nine species decreased. Most of the decrease took place during the second period for *H. nobilis*,

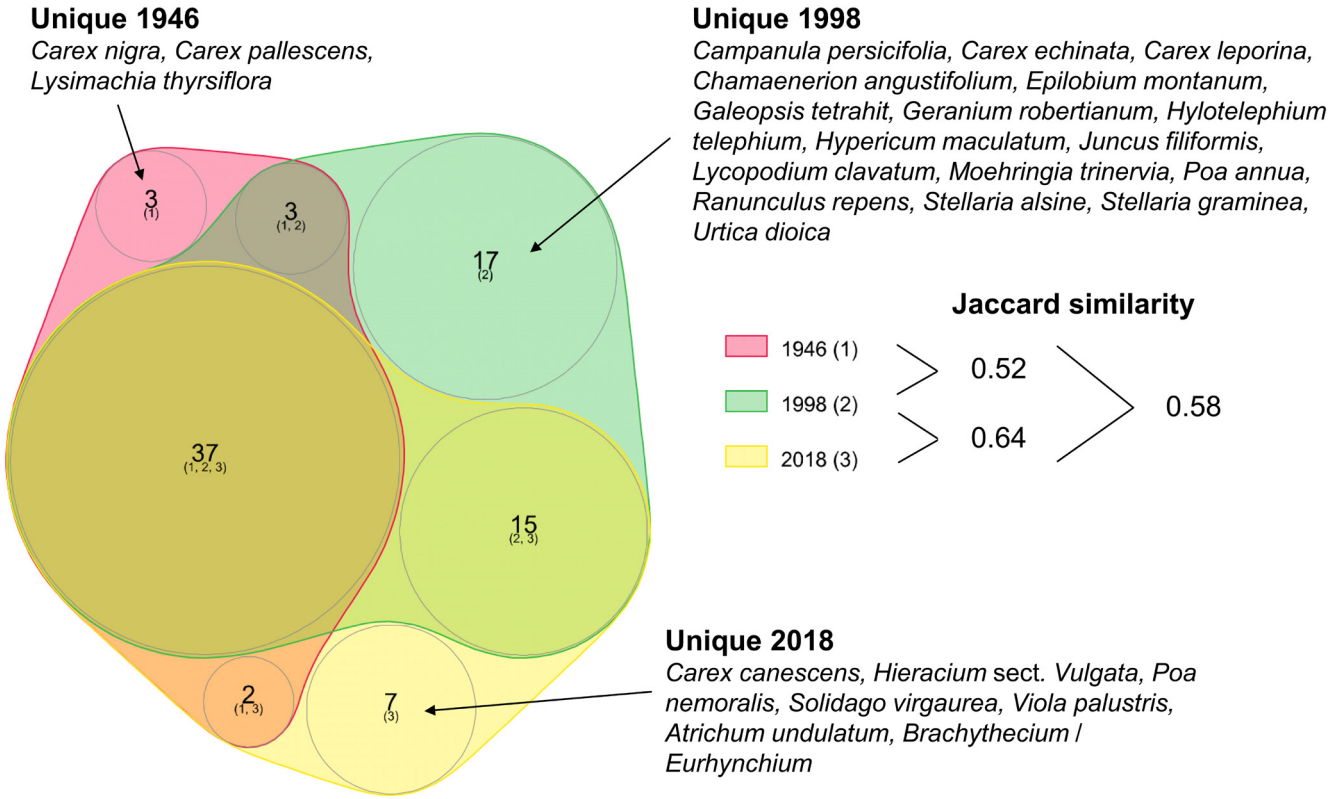


Figure 2. Venn diagram showing the number of species shared by the three surveys, and Jaccard index showing floristic similarity in total species compositions of pairs at time-points.

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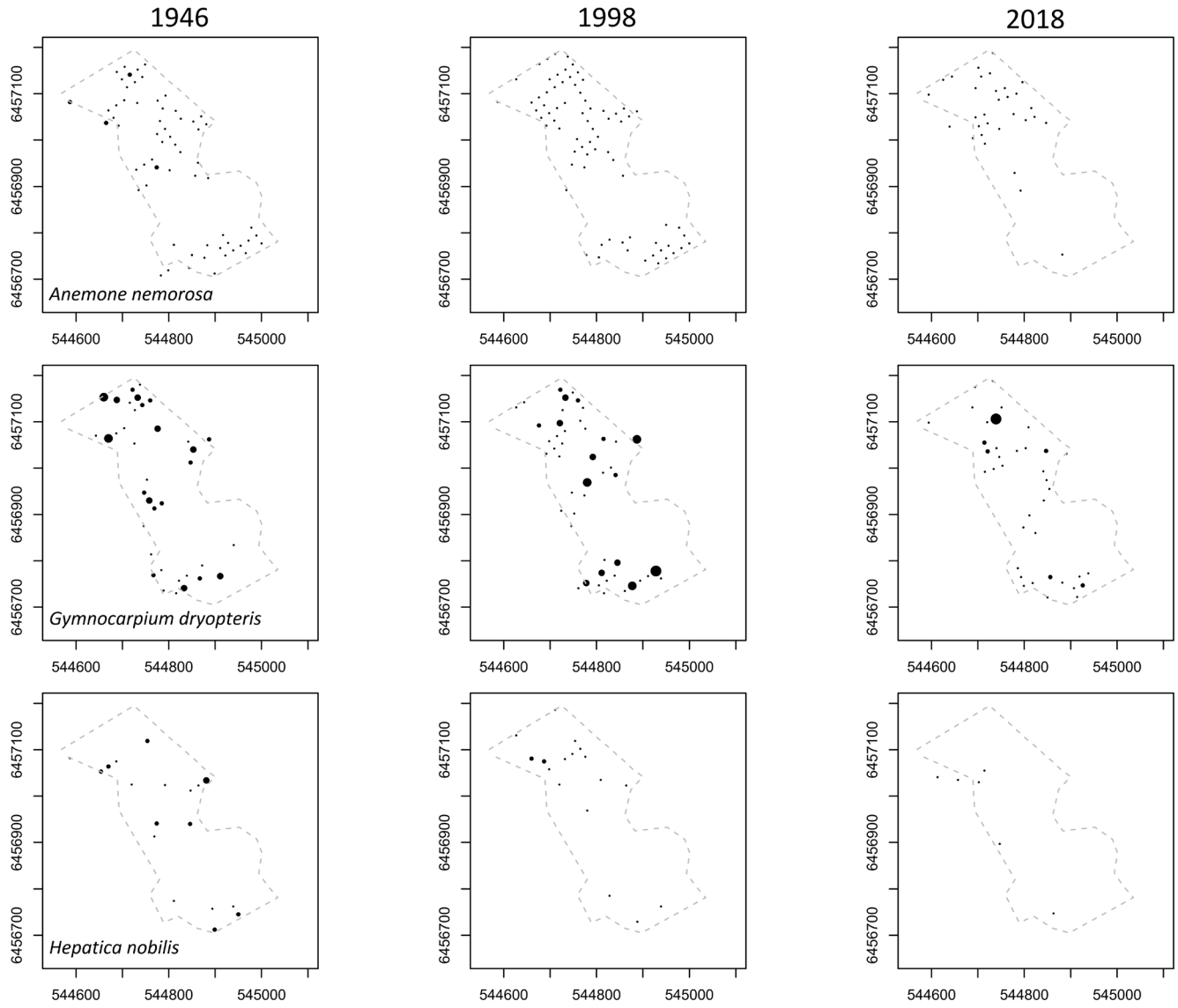


Figure 3. Maps showing cover in 1946, 1998 and 2018 (species in the last panel lack cover data for 1998). Dot size represents cover in the Hult-Sernander-Du Rietz scale (0–5). Coordinates are in metres, in the national grid SWEREF99.

P. crista-castrensis, *H. splendens*/*P. schreberi*, *A. nemorosa* and *Oxalis acetosella*. The other decreasing species were *Rhytidiadelphus triquetrus*, *V. vitis-idaea*, *Avenella flexuosa* and *Luzula pilosa.* Net increase was only observed for *P. asplenioides* and *V. myrtillus*; *V. myrtillus* was the only species with a significant increase after 1998.

Frequency changes

With the criterion to discuss only species with a change of occurrence of ≥ 20 plots between any two surveys, sixteen species increased in frequency between 1946 and 1998 (Table 1). Between 1998 and 2018 only *Dryopteris filix-mas* increased, whereas nine vascular species and four bryophytes decreased. Over the whole investigation period nine species increased their frequency and five species decreased. Among bryophytes, both species indicating relatively nutrient-rich soil (*Mnium* spp.) and nutrient-poor soil (*Dicranum* spp. and *P. crista-castrensis*) decreased in frequency. The two common bryophytes *H. splendens* and *P. schreberi* were recorded separately in 1998 and 2018, but did not change in frequency between these two years (Supporting information).

Seedlings and field layer individuals of trees and shrubs were not included in the 1946 sampling. In 1998 and 2018 eight and ten woody species were registered in the field layer plots, respectively (Table 2). The most common tree species in the field layer in 1998 and 2018 were *P. abies*, *Quercus robur* and *Sorbus aucuparia*. Other species occurred only sporadically.

Vegetation changes

An ordination including cover data from 1946 and 2018 showed that NMDS1 is related to topographical variation

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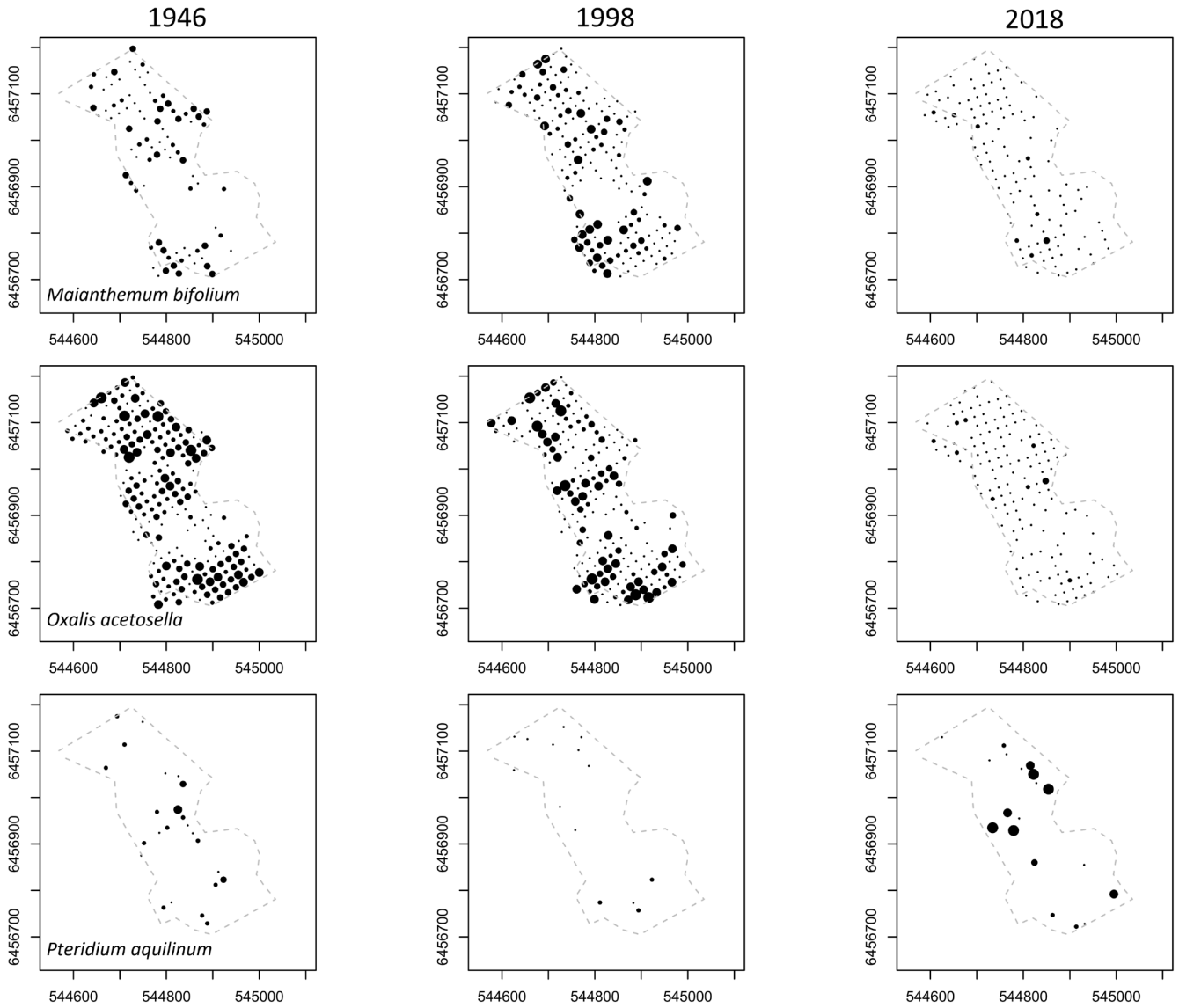


Figure 3. Continued.

with very little variation between surveys (Fig. 5). NMDS2 depicts the directional change as shown by the significant difference in position of plots from the two surveys (adonis: $F_{1, 496} = 39.5$; $p = 0.001$). There was a small, but significant increase in variance in plot scores between 1946 and 2018 (betadispers: $F_{1, 496} = 9.2$; $p = 0.002$).

To extract species that may be influential for the directional change in the ordination, we related the NMDS2 scores to the changes in abundance for the fifteen species in Fig. 4. Increasing species tended to have low NMDS2 scores, and vice versa, leading to a negative relationship between change in cover and NMDS2 scores ($R^2 = 0.31$; $p = 0.047$; $n = 15$; Fig. 6). From left to right along the regression line we find the decreasing *O. acetosella*, *H. splendens*/*P. schreberi*, *L. pilosa*, *R. triquetrus* and *A. flexuosa*; and the increasing *P. asplenioides* and *V. myrtillus*. A deviating species is *H. nobilis* with high NMDS2 score but very little change in cover.

An ordination with all three surveys could only be made with presence/absence data, which is problematic given that plots were smaller in 1946. We therefore first ran an ordination with presence/absence data from 1946 and 2018 to test how well this would resemble the ordination based on cover in Fig. 5. The results (Supporting information) were similar but separated the surveys less well: NMDS1 reflects variation in elevation and NMDS2 separates the two surveys (adonis: $F_{1, 496} = 25.9$; $p = 0.001$), but less clearly than in Fig. 5. This suggests that it is possible to analyse the three surveys with presence/absence data, but that the results should be interpreted with caution.

Again, NMDS1 is related to topographical variation and NMDS2 depicts changes between surveys (Fig. 7; adonis: $F_{1, 739} = 25.5$; $p = 0.001$). However, these changes are not unidirectional; vegetation had changed between 1946 and 1998, but in 2018 appeared more similar to the 1946 vegetation.

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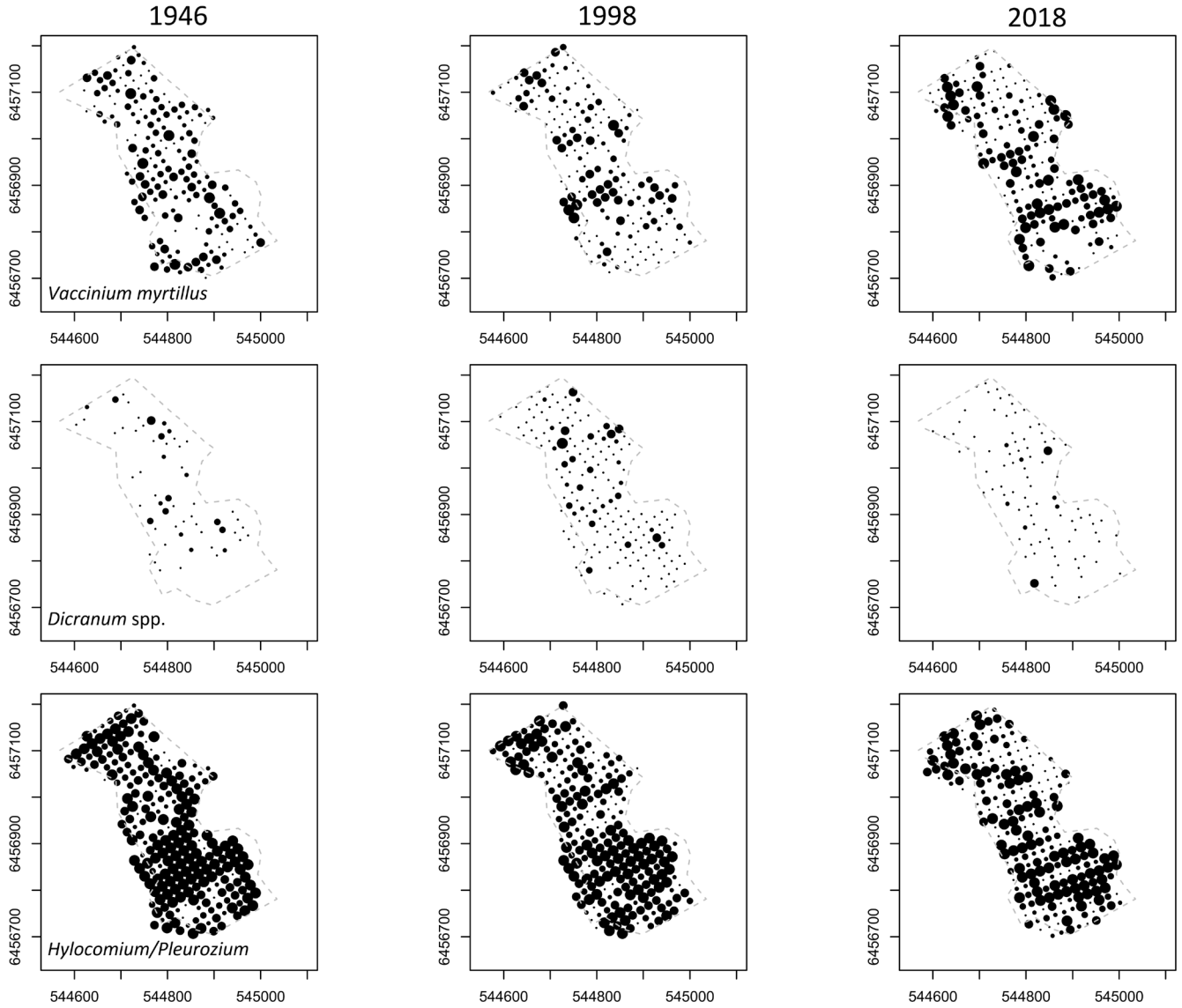


Figure 3. Continued.

The ordination diagram suggests that the difference between 1946 and 1998 was bigger than between 1946 and 2018.

Separate ordination of the 2018 dataset

The separate ordination of the cover and environmental data from 2018 (Fig. 8) shows, in addition to the close relation between axis 1 and elevation, NMDS2 to be positively associated with tree density, litter cover and presence of conifers, and negatively with cover of logs in the plots and presence of oak. The 12 plots situated in gaps all had low NMDS2 scores.

There is a positive correlation between the NMDS2 scores in this 2018 ordination (Fig. 8) and the NMDS2 scores for 2018 in the joint 1946+2018 ordination (green dots in Fig. 5; $r=0.28$; $p < 0.001$; $n=247$), i.e. plots with high tree density in 2018 are the ones that are most similar to the 1946 plots. The NMDS1 scores reflecting elevation are strongly correlated between the two ordinations ($r=0.97$; $p < 0.001$; $n=247$).

We noted 15 species in the tree layer around the field layer plots. *Picea abies* was the most common tree species and was found around approximately 90% of the plots, followed by *P. sylvestris* at more than half of the plots (Table 3). The most common deciduous species were *Q. robur*, *Corylus avellana* and *S. aucuparia*. Birches (*Betula pendula* and *B. pubescens*) were less common.

Discussion

Based on other studies (Sundberg 2014, Jonsson et al. 2021, Økland et al. 2023) we hypothesised the changes in Säby Västerskog to be directional with a decrease in vascular plant species richness. We did observe a decline in species

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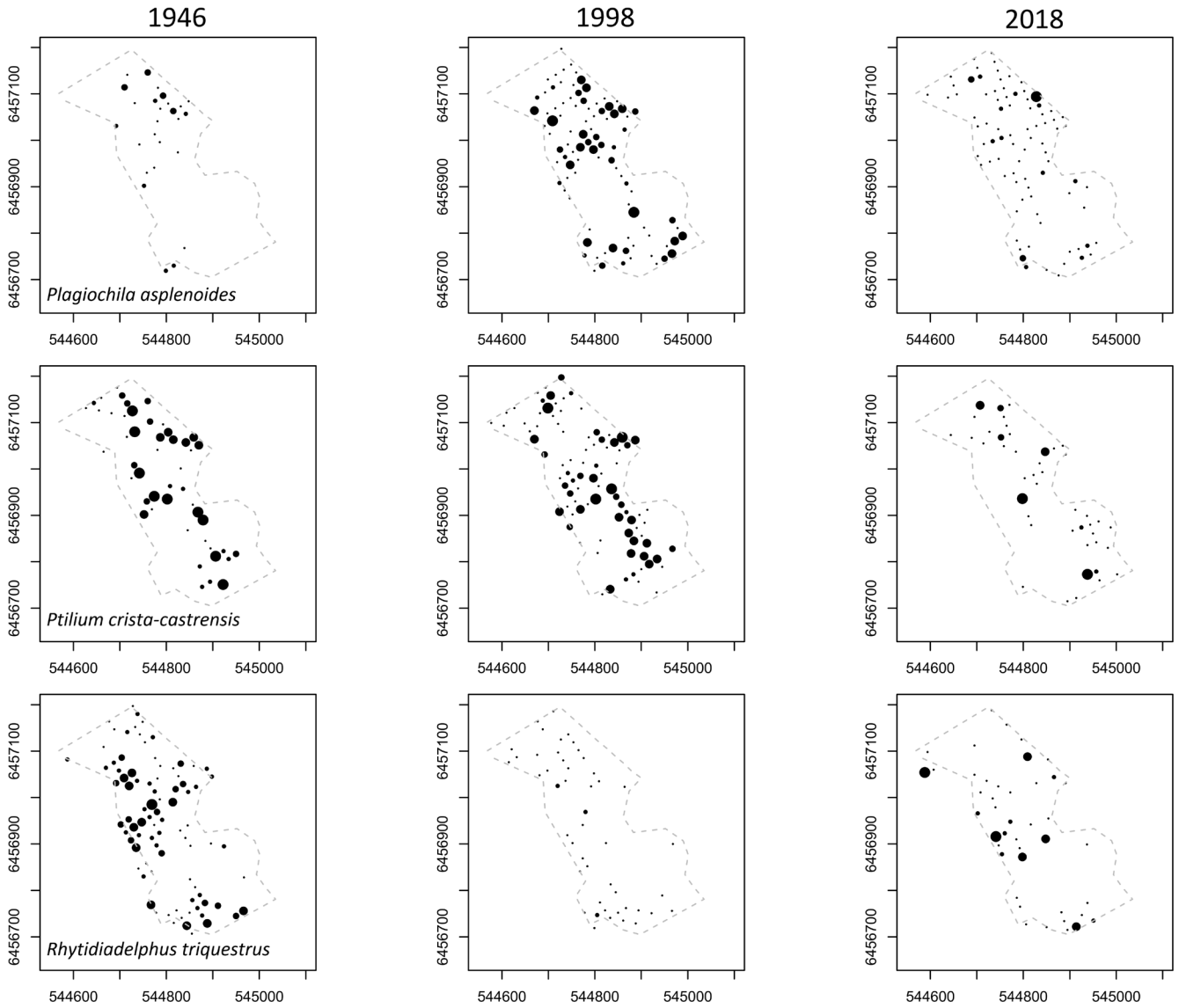


Figure 3. Continued.

richness and in the cover or frequency of several species after 1998; and, in line with Jonsson et al. (2021), very few species increased during this period (*V. myrtillus* in cover and *Dryopteris filix-mas* in frequency). However, the declines represented in many cases a bounce back from increases between 1946 and 1998. Hence, the changes were not directional, as will be further discussed below.

Topography: The main cause of spatial variation

Säby Västerskog is largely a *P. abies–V. myrtillus* forest with some variation strongly related to topography (Fig. 5), which in turn is related to soil depth, and hence to nutrient and water availability. Økland and Eilertsen (1993) have interpreted the complex elevational gradient from spruce to pine dominance as mainly dictated by soil moisture. However, we study variation within the spruce-dominated part of the gradient, which is mostly related to variation in nutrient availability according to Økland and Eilertsen (1993). For example, among the dwarf shrubs *V. vitis-idaea* is found in the direction of a higher elevation in the ordination than does *V. myrtillus*, and among grasses the order is *Festuca ovina* – *A. flexuosa* – *Deschampsia cespitosa*. Our interpretation of the main gradient in species composition is also supported by, for example, *Rubus idaeus* and several bryophyte species found in the lower parts. There is nothing to indicate that the vegetation has changed over time along this gradient, and therefore, given our interpretation of the ordination, no indications of changes in moisture or nutrient conditions. The vegetation was more heterogeneous in 2018 than in 1946, but the difference is small (Fig. 5) and there is no strong evidence for divergent succession.

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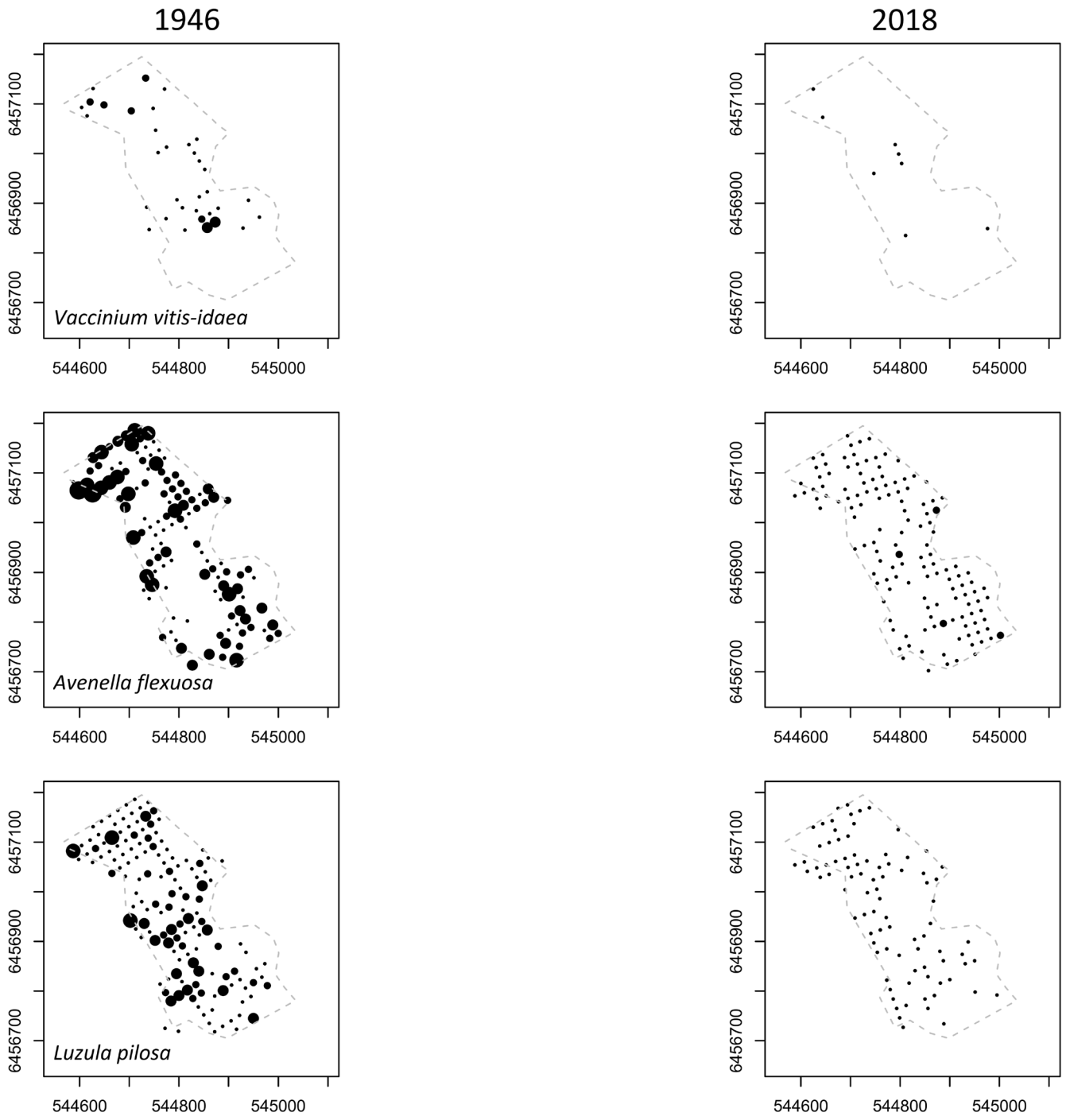


Figure 3. Continued.

Vegetation changes in relation to regional trends

A somewhat surprising result was the increase in cover in *V. myrtillus* and decrease in *A. flexuosa* between 1946 and 2018 (Fig. 6). Based on data from NFI (SLU 2023), Hedwall et al. (2019) suggested that N deposition is the likely cause for shifts from dwarf shrubs to grasses and more nutrient-demanding species during the period 1994–2013 in southern Sweden. Their finding was supported by fertilisation experiments in which *V. myrtillus* and *V. vitis-idaea* decreased and *A. flexuosa* increased under high N doses (Strengbom et al. 2002, Nordin et al. 2005). It has been demonstrated that experimentally high doses of N cause attacks by pathogens on *V. myrtillus* (Nordin et al. 1998, Strengbom et al. 2002).

In Säby Västerskog there was no indication of an increase in the N indicator (Tyler et al. 2021) *Rubus idaeus*. Among herbs *M. bifolium* increased during the first period but returned to

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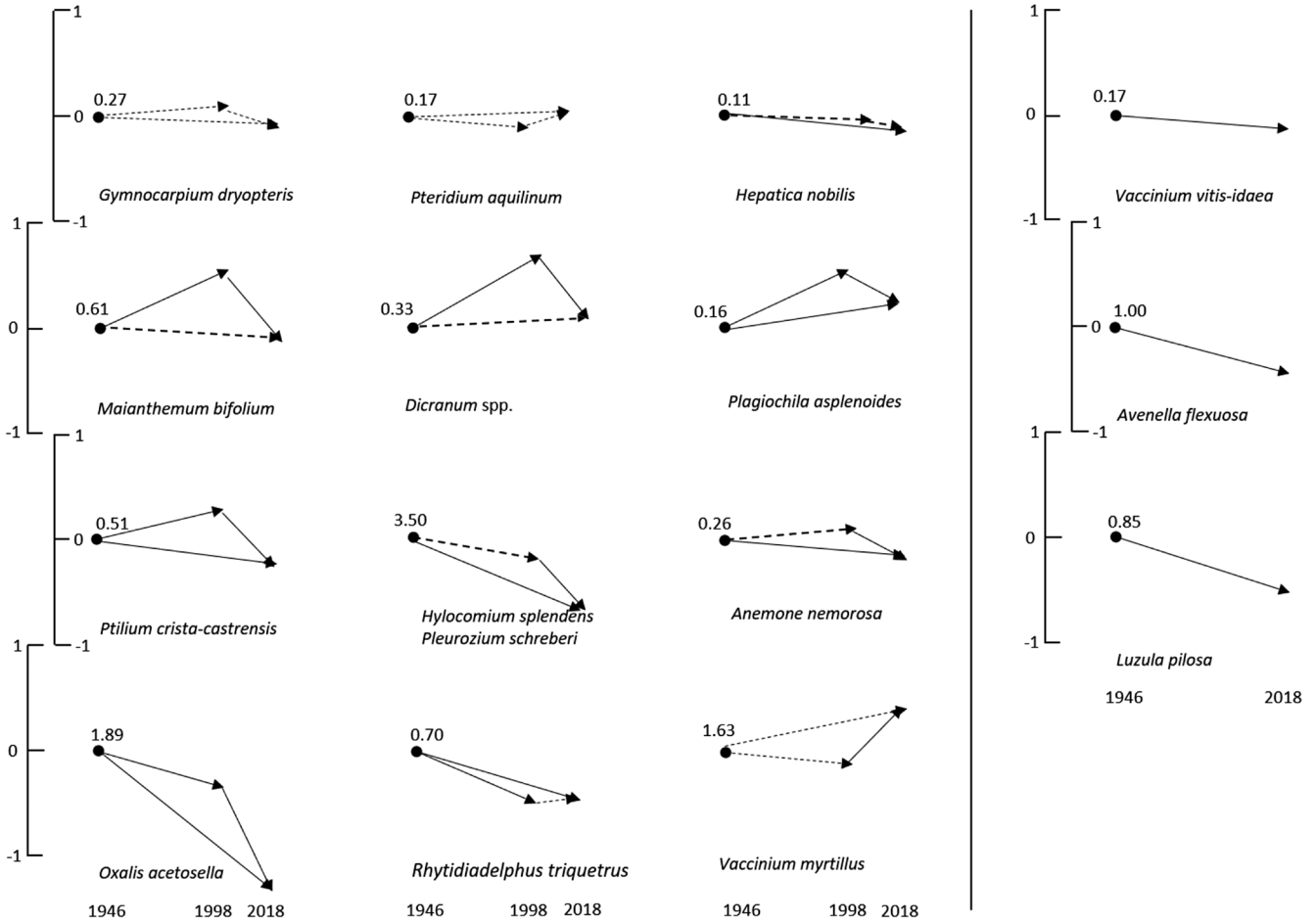


Figure 4. Changes in mean cover after 1946 (y axis is +/− 1 unit in the Hult-Sernander-Du Rietz scale). Cover in 1946 is given and plotted as zero. Solid lines, significant change (Tukey HSD tests following anovas); dashed line, nonsignificant change. To the right of the vertical line are three additional species lacking cover data in 1998 that decreased significantly between 1946 and 2018 (t-tests).

the original cover during the second period. *Oxalis acetosella* decreased during both periods and *A. nemorosa* during the second period. In conclusion, we did not find any general effects of N deposition.

Some studies have documented effects of N deposition on the vegetation composition in boreal forests already at relatively low levels (Kellner 1993, Strengbom et al. 2003, Nordin et al. 2005). Effects on forest floor vegetation were confirmed in a regional study by Strengbom et al. (2003). After N fertilisation at 11 sites, Jacobson et al. (2020) found changes in the proportion of species but few replacements. However, the results are not straightforward: Nygaard and Ødegaard (1999) did not find clear changes caused by N deposition in a south Norwegian forest, and there were no signs of N deposition effects on Norwegian spruce forests monitored by Økland et al. (2023).

A modelling study by Engardt et al. (2017) suggested a moderate increase in N deposition in southern Sweden already in the 1940s (c.f. Granath et al. 2014). In south-eastern Sweden the deposition was high in the 1980s and early 1990s (Andersson et al. 2018). It decreased during the 1990s, and maps by Karlsson et al. (2022) suggest that N deposition in our area was 6–8 kg ha^{-1} $year^{-1}$ in 2001 and approximately 6 kg ha^{-1} $year^{-1}$ in 2018. This is still at the critical load suggested by Nordin et al. (2005). Thus, the N deposition was high during the early part of our time period, somewhat lower during the latter part.

Regional vegetation changes are the result of a complicated combination of climate warming, N deposition and acidification (Hedwall et al. 2021). Interpretation is therefore difficult, particularly as time lags (Økland et al. 2004) and interactions must also be assumed (Jonsson et al. 2021). Specifically, the eutrophication effects of N deposition could be confounded by the acidifying effects of air pollution. Falkengren-Grerup (1989) clearly demonstrated that forest soils in southern Sweden became more acidic during a 35-year period from around 1950, and showed that some species had decreased, but mostly in sites with low pH. One of these species was *O. acetosella* which decreased continuously in Säby Västerskog. Also in southern Norway this species had a strong decline from 1988 to ca 2000 (attributed to acidification; Økland et al. 2004), but showed a recovery from ca 2000 (Økland et al. (2023), in contrast to our results.

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Table 1. Plot frequency and changes in plot frequency for each species. The table includes species with a change of ≥ 20 plots between any two surveys. '<' indicates that the difference was less than 20 plots (see Supporting information for plot frequency for all species).

		Plot frequency			Change		
Species	Abbreviation	1946	1998	2018	1946–1998	1998–2018	1946–2018
Dicranum spp.	Dicr.spp	57	170	91	114	−80	34
Mnium spp.	Mniu.spp	5	108	17	103	−90	<
Maianthemum bifolium	Mai.bifo	86	167	123	81	−44	37
Viola riviniana	Vio.rivi	0	66	39	66	−27	39
Plagiochila asplenioides	Pla.aspl	26	92	85	66	<	59
Avenella flexuosa	Ave.flex	120	177	134	57	−43	<
Polytrichum spp.	Poly.spp	8	62	30	54	−32	22
Carex digitata	Car.digi	38	93	78	55	<	40
Lysimachia europaea	Lys.euro	0	45	12	45	−33	<
Lactuca muralis	Lac.mura	0	42	24	42	<	24
Ptilium crista-castrensis	Pti.cris	49	88	44	40	−45	<
Luzula pilosa	Luz.pil	146	177	87	31	−90	−59
Dryopteris carthusiana	Dry.cart	2	24	33	22	<	31
Melampyrum pratensis	Mel.prat	3	23	0	20	−23	<
Goodyera repens	Goo.repe	0	20	1	20	<	<
Linnaea borealis	Lin.bore	0	20	6	20	<	<
Oxalis acetosella	Oxa.acet	212	188	154	−22	−36	−58
Rhytidiadelphus triquetrus	Rhy.tri	87	48	43	−39	<	−44
Dryopteris filix-mas	Dry.fili	1	7	31	<	24	30
Anemone nemorosa	Ane.nemo	62	74	31	<	−43	−31
Melampyrum sylvaticum	Mel.sylv	11	27	5	<	−22	<
Vaccinium vitis-idaea	Vac.viti	34	25	8	<	<	−26

In managed forests, the rotation period is a main driver of change. Longer rotation periods might favour the dwarf shrub *V. myrtillus*, but Hedwall et al. (2013) found a decrease in dwarf shrubs, probably driven by both eutrophication through N deposition and increasing forest density during the period 1953–2012. To reduce management effects, Jonsson et al. (2021) used NFI data from stands that were not managed during their study. They quantified vegetation changes over 10 years (starting in 1995–2003 for different plots). Several species had decreased, including the grass *Avenella flexuosa* (as in Säby Västerskog) and the dwarf shrub *V. myrtillus* (increased in Säby Västerskog), which would be an expected outcome of increased shading as the stands grow older (c.f. Bergstedt and Milberg 2001).

As for bryophytes, we found a decrease in the large feathermosses (*Hylocomium*/*Pleurozium* group), especially after 1998. In contrast, a shift in cryptogams with large species increasing at the expense of small ones over the last decades was suggested by Økland et al. (2023), probably as a result of increased annual temperature, growing season length and the number of days with precipitation. However, the observations of Økland et al. (2023) indicate that it is necessary to disentangle the group of 'large cryptogams': they found that *H. splendens* had indeed increased, but *P. schreberi* had decreased. Opposite changes over time in reactions of these two common species were found by Jonsson et al. (2021): *H. splendens* increased in the boreo-nemoral and the southern boreal region. *Pleurozium schreberi* also increased in the southern boreal region but decreased in the boreo-nemoral and northern regions. Since the two species were lumped in our data, we can only conclude that at Säby Västerskog the net change was negative for these feathermosses.

Table 2. Number of plots in 1998 (of 243 plots in total) and in 2018 (of 250 plots) with shrub and tree species in the field layer (< 50 cm high). Plot size 1 × 1 m.

Species	1998	2018
Acer platanoides	1	1
Betula pubescens	1	0
Corylus avellana	3	2
Frangula alnus	0	1
Picea abies	8	28
Populus tremula	0	2
Quercus robur	12	15
Ribes alpinum	1	1
Ribes uva-crispa	1	1
Salix caprea	0	1
Sorbus aucuparia	16	18

Økland et al. (2023) found an increase in *P. asplenioides* in contrast with its decrease in our study. They found contrasting responses among *Dicranum* species, and the four *Polytrichum* species tested by Dirkse and Martakis (1992) reacted differently. With the coarse taxonomic resolution of bryophytes in our data it is difficult to evaluate the causes of the decrease since 1998 in *Dicranum* spp. and *Polytrichum* spp. in Säby Västerskog.

Also for bryophytes the role of N has been discussed in the literature, but is difficult to generalize. Based on field experiments, Dirkse and Martakis (1992) found that fertilisation led to a decrease in both *H. splendens* and *P. schreberi,* whereas Jacobson et al. (2020) found that nitrogen significantly increased the total cover of *P. schreberi* but had no detectable effect on *H. splendens*.

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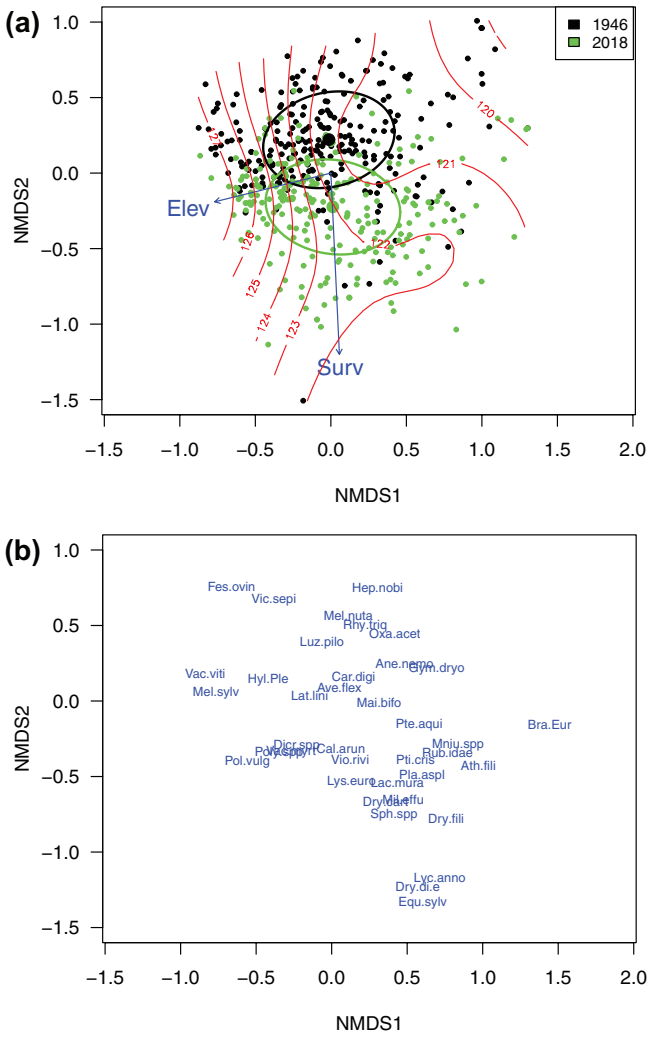


Figure 5. Non-metric multidimensional scaling (NMDS) ordination based on cover in plots in 1946 and 2018 (stress = 0.18). (a) Plot scores with confidence ellipses for the two surveys. The centroids for the two surveys are shown by the larger dots. Vectors are fitted for survey (coded as 1 and 2) and plot elevation (m a.s.l.; also shown as fitted contour lines). (b) Species scores for species with > 6 observations. Full species names are given in Supporting information.

Local dynamics: tree density and treefalls

We found significant, but not pronounced, changes in the vegetation between 1946 and 2018 that were independent of the variation in elevation. The lack of description of variation in the forest structure in 1946 makes it difficult to interpret these changes. However, in the 2018 data (Fig. 8) the variation that is independent of elevation is instead linked to tree density, notably to high cover of *P. abies*. Our interpretation is that variation in canopy cover affected the vegetation changes between the surveys. The ordinations hint that the forest had higher tree density in 1946 than in 2018 (see Results: 'Separate ordination of the 2018 dataset'). However, basal area (particularly in spruce) had increased in Säby Västerskog between 1937 and 2022 (Lindstrand 2022), and

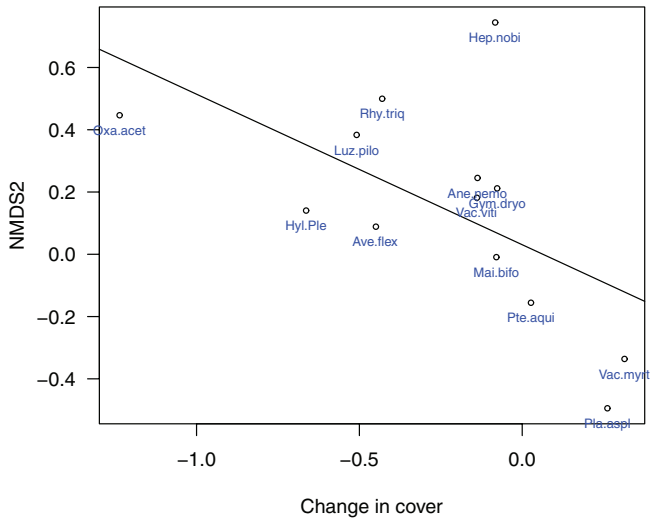


Figure 6. Relationships between changes in species cover (1946–2018) and their NMDS2 species scores from Fig. 5 for the fifteen species in Fig. 4 (full species names in Fig. 3).

to reconcile these contradictory results one can hypothesise that the dynamics is driven by variation in small-scale disturbances and gaps due to treefall rather than by an overall variation in the tree layer.

The trend in our study was not clearly directional: the species composition shifted between 1946 and 1998, but in 2018 again had become more similar to 1946 in the ordination (Fig. 7), and the species composition in 1946 was more similar to 2018 than to 1998 (see Jaccard index in Fig. 2). Total species richness increased between 1946 and 1998, but decreased thereafter. The list of ruderal species that were unique to 1998 (Fig. 2), together with the higher species richness, support the interpretation from the ordinations that the

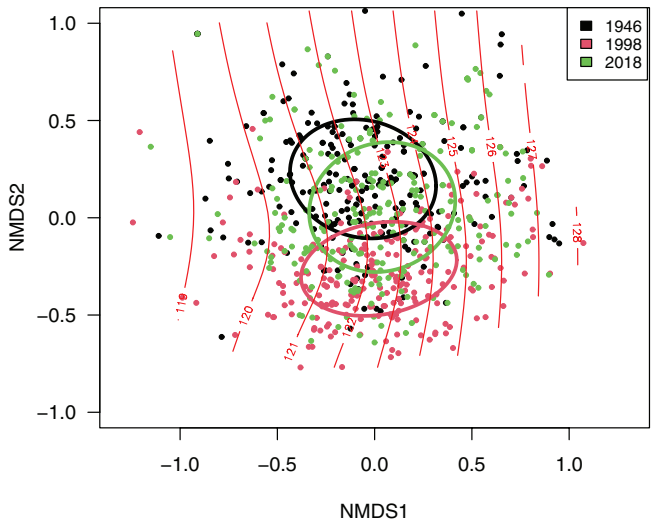


Figure 7. Non-metric multidimensional scaling (NMDS) ordination based on presence/absence in 1946, 1998 and 2018 (stress = 0.15) with confidence ellipses for the three surveys and plot elevation (m a.s.l.) as fitted contour lines.

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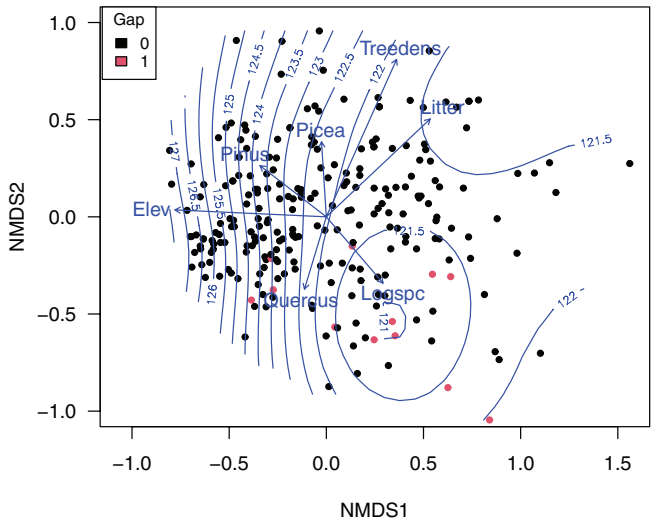


Figure 8. Non-metric multidimensional scaling (NMDS) ordination based on cover in 2018 (stress = 0.14). Vectors shown for variables with $p < 0.05$ in goodness of fit tests with envfit: plot elevation, presence of *Pinus sylvestris*, *Picea abies* and *Quercus robur* and total tree density around the plot, litter cover in plot and coverage of tree logs in plot (%). Elevation is also shown as fitted contour lines. The twelve plots located in gaps are indicated by red dots.

forest was more open and with more small-scale disturbances in 1998 than at the other surveys.

Regional trends versus local changes

Many authors discussing changes in conifer forest that fall within our first survey interval (up to 1998) attributed vegetation changes to N deposition, whereas Økland et al. (2023), who studied changes that fall within our second survey interval (after 1998), attributed their findings to 'complex, cascading effects of the changing climate'. Both lines of reasoning are reasonable, considering that the decrease in N deposition was replaced by an increase in temperature in the 1990s. However, the evidence is often circumstantial and, as we note above, results from different studies are conflicting. Not least, it is difficult to reconcile the observations at Säby Västerskog with some previous studies. One reason could be that regional studies with many sites (Strengbom et al. 2003, Nordin et al. 2005, Økland et al. 2023) can pick up signals of environmental change, which in a long-term study of one site (Nygaard and Ødegaard 1999) would be masked or overruled by internal disturbance dynamics or succession (Engelmark and Hytteborn 1999). Conversely, the importance of internal processes may be underestimated in regional studies.

Reliability of historical data

Historical data on forest floor vegetation spanning over seven decades are rare in the literature, and ecological studies covering such a long time often have to resort to chronosequence approaches with their well-known disadvantages (Austin 1977). Repeating old descriptive studies gives the opportunity to expand the time-scale vegetation changes, but variation in methods is often a problem (Hédl et al. 2017).

Table 3. Number of field layer plots in 2018 (n = 250) surrounded by tree or shrub species within a 5-m radius.

Species	Frequency	%
Picea abies	224	89.6
Pinus sylvestris	134	53.6
Quercus robur	59	23.6
Corylus avellana	46	18.4
Sorbus aucuparia	40	16.0
Betula pendula	10	4.0
Salix caprea	8	3.2
Betula pubescens	5	2.0
Acer platanoides	3	1.2
Populus tremula	2	0.8
Sambucus racemosa	2	0.8
Sorbus intermedia	2	0.8
Frangula alnus	1	0.4
Prunus padus	1	0.4
Prunus sp.	1	0.4

Although we do not have cover data for all species from 1998, we found analyses of changes based on presence/absence and cover to yield similar results and interpretations. The changes in species cover are largely mirrored in the changes in plot frequency, with two exceptions being *V. myrtillus*, which showed a more pronounced increase in cover than in frequency, and *Hylocomium/Pleurozium* which decreased in cover, but maintained presence in almost all plots.

For bryophytes we were forced to use the coarse taxonomic resolution of the earlier surveys. The total number of species in the forest is therefore underestimated, but the comparisons over time are still valid. The initial increase may partly be explained by the increase in plot size. However, the plot size was the same in 1998 and 2018, which, together with the large number of plots, support the conclusion of non-directional changes. The species accumulation curves indicate that all surveys had a good representation of total species richness.

We do not have permanently marked plots, but the number of plots in the original study was considerable and we could repeat the layout. We are, therefore, confident that we have obtained an accurate picture of the changes in flora and vegetation.

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Author contributions

Ingvar Backéus: Conceptualization (equal); Formal analysis (supporting); Funding acquisition (equal); Investigation (equal); Writing – original draft (equal); Writing – review and editing (equal). **Håkan Hytteborn**: Conceptualization (equal); Formal analysis (supporting); Funding acquisition (equal); Investigation (equal); Writing – original draft

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(equal); Writing – review and editing (equal). **Håkan Rydin**: Data curation (lead); Formal analysis (lead); Writing – original draft (equal); Writing – review and editing (equal).

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.0gb5mkm85 (Rydin et al. 2024).

Supporting information

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

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