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Interactions between local and global drivers determine long-term trends in boreal forest understorey vegetation

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Abstract

Aim: Global change effects on forest ecosystems are increasingly claimed to be context dependent, indicated by interactions between global and local environmental drivers. Most examples of such context dependencies originate from temperate systems, while limited research comes from the boreal biome. Here we set out to test if interactions between climate warming, nitrogen deposition, land-use change resulting in increasing forest density, and soil pH drive long-term changes in understorey vegetation in boreal forests.

Location: Sweden.

Time period: 1953–2012.

Major taxa studied: Vascular plants.

Methods: We used long-term (50 years) National Forest Inventory data on forest understorey vegetation in Sweden to model the combined effects of climate warming, nitrogen deposition, increase in forest density (tree basal area), and soil pH.

Results: Our results identify increasing temperature, nitrogen deposition and denser, shadier forest conditions as the main drivers of understorey vegetation changes during this time period. More importantly, we found that these effects varied with local conditions, that is, that the change towards a more nitrophilic understorey vegetation was more pronounced at low than high soil pH. Forest density was an important modulator of nitrogen deposition and temperature increase, with effects generally decreasing with density. Decreased cover of ericaceous dwarf shrubs was driven by both forest density and nitrogen deposition, with a stronger effect at low than at high pH.

Main conclusions: Our results highlight that to understand forest ecosystems' response to global change, and to make adequate management decisions to mitigate the effects of global change, we need to understand how changes in local environmental factors (forest density and soil pH) interact with global-scale drivers (nitrogen deposition and climate warming). Neglecting such interactions will lead to incorrect estimations of effects. In our case, we would for example, have underestimated the eutrophication effects on acid soils, which constitute a considerable part of the boreal biome.

KEYWORDS
air pollution, environmental change, forest floor vegetation, forestry, interacting drivers, long-term data

1 | INTRODUCTION

Northern forest ecosystems are facing rapid change due to multiple global change drivers, such as climate change, nitrogen deposition and land-use change (Bobbink et al., 2010; Hedwall & Brunet, 2016; Hedwall, Brunet & Rydin, 2017; Hedwall, Gustafsson, et al., 2019; Svensson et al., 2019). These forests are especially sensitive to warming and increased nutrient availability, as most boreal and many northern temperate forest ecosystems are cold-adapted and strongly nitrogen-limited (Bobbink et al., 2010; Hedwall, Bergh & Brunet, 2017; Tamm, 1991). In this context, understorey plant communities are particularly important because they host most of the forest plant diversity (Gilliam, 2007), and play a key role in decomposition, nutrient cycling and forest succession (Cornwell et al., 2008; Landuyt et al., 2019; Nilsson & Wardle, 2005; Wardle et al., 2003, 2012). Although many northern forests are too remote from major emission sources to experience high pollution loads, considerable areas are exposed to low, or intermediate, levels of nitrogen deposition due to long-distance transport and local pollution sources. Additionally, recent evidence suggests that also accumulated low annual inputs can result in substantial long-term eutrophication effects (De Schrijver et al., 2011; Phoenix et al., 2012). A common effect of nitrogen deposition in northern plant communities is a switch from dwarf shrub-dominated communities (Ericaceae family) to graminoid-dominated vegetation types (Bobbink et al., 2010; Hedwall & Brunet, 2016; Hedwall, Gustafsson, et al., 2019; Strengbom et al., 2004), or from low-growing, to tall-growing species (Clark et al., 2019). Similarly, climate warming is predicted to increase nitrogen mineralization (Contosta et al., 2011; Rustad et al., 2001; Sardans & Peñuelas, 2012), and analyses of the effects of a warmer climate on northern vegetation indicate that in addition to favouring thermophilic species (Zellweger et al., 2020), nitrophilous forbs and grasses increase, while dwarf-shrubs and bryophytes with low demands on nitrogen decrease when temperatures increase (Hedwall et al., 2015; Walker et al., 2006).

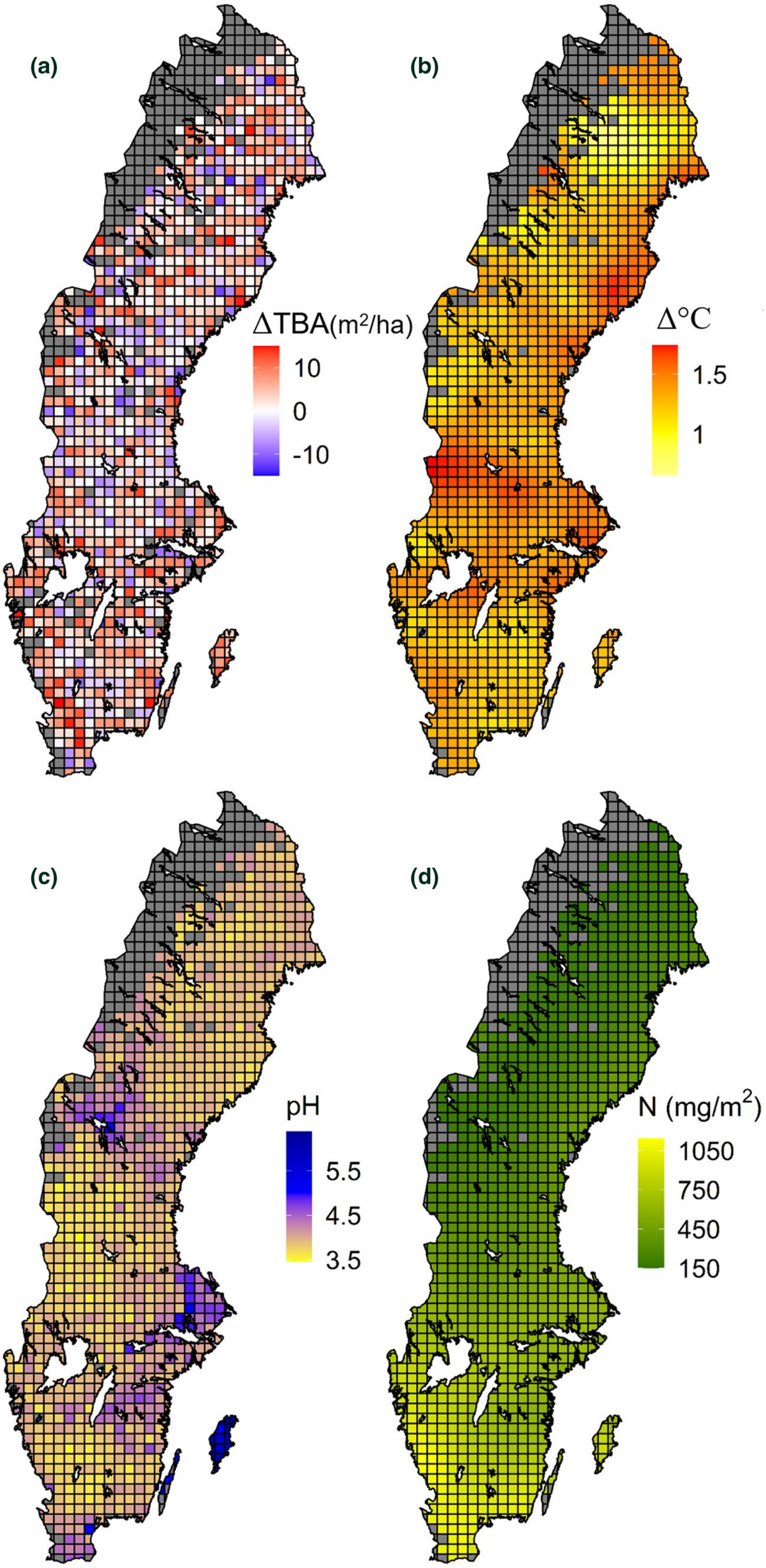
Additionally, land-use change, here defined as intensified anthropogenic use, influences northern forest ecosystems and their plant communities (Gilliam, 2016; Hedwall & Brunet, 2016). Traditionally, livestock grazing, selective cutting, and frequently occurring wildfires resulted in relatively low forest canopy cover (Östlund et al., 1997; Schimmel & Granström, 1996). The introduction of modern forest management (including fire prevention and cessation of livestock grazing) has profoundly changed stand structure and tree species composition during the past century in North American and north European forests (Foster et al., 2002; Hedwall & Mikusiński, 2015, 2016; Lindbladh et al., 2014; McEwan et al., 2011), and thereby influenced landscape dynamics and ecosystem functions (Gilliam, 2016). The introduction of more intensive forest management has led to greater timber volumes and denser stands, and made stands less structurally diverse (Felton et al., 2017; Gold et al., 2006; Kuuluvainen et al., 2012; Rautiainen et al., 2011). As the abundance and composition of the forest understorey vegetation are largely determined by tree species composition and canopy cover (Hart & Chen, 2006; Hedwall, Brunet, et al., 2013; Hedwall, Holmström, et al., 2019), changes in forest structure are important drivers of understorey changes (Hedwall, Brunet, et al., 2013; Oberle et al., 2009; Perring, Bernhardt-Römermann, et al., 2018).

In order to understand and predict how global change will influence our ecosystems and where changes will be greatest, we need to understand if these effects are context dependent, and if so, how. We need, for example, better information on how the effects of climate change and nitrogen deposition vary depending on land-use history, forest structure, and soil conditions (De Frenne et al., 2013; Midolo et al., 2019; Perring, Bernhardt-Römermann, et al., 2018; Perring, Diekmann, et al., 2018; Verheyen et al., 2012). Denser tree layers can for example, at least temporarily, buffer the effects of increasing temperatures and nitrogen availability on the ground vegetation (Verheyen et al., 2012; Zellweger et al., 2020). Adding to this complexity, the context dependency can be multi-layered, so that global change effects on the vegetation may depend on, for example, both forest structure and historical land use concurrently (Depauw et al., 2020; Perring, Diekmann, et al., 2018).

In northern forests, nutrient availability generally increases with soil pH, that is, these factors are closely correlated (Hedwall, Brunet, et al., 2019), and many forest plant species are adapted to low or high values on both gradients (Falkengren-Grerup, 1990). By extension, this implies that low pH can constrain the response of nitrophilic (adapted to high nitrogen availability) plant species to eutrophication. As an example, boreal forests contain few species adapted to high nutrient availability (confined to certain uncommon nutrient rich sites), and fertilization of boreal forests may result in species assemblages with low resemblance to the natural communities (Hedwall, Strengbom, et al., 2013). Such, and other, context dependencies have occasionally been identified in temperate forest systems (Perring, Diekmann, et al., 2018), but the extent in boreal forests is largely unknown (Hedwall, Brunet, et al., 2017). More focus on this knowledge-gap is essential for deeper understanding of forest ecosystem responses to global change.

Forest management has considerably increased timber volumes and stand densities in Swedish forests since the 1950s (Figure 1a), which together with nitrogen deposition (Granath et al., 2014; Figure 1d) has led to a shift in vegetation in southern Sweden (e.g. Hedwall, Gustafsson, et al., 2019). With its long history of industrial forestry and relatively high nitrogen deposition, both greatly

FIGURE 1 Maps of Sweden showing change in total basal area (ΔTBA) of trees on productive forest land between 1953–1957 and 2012–2016 (a), the change in annual mean temperature between 1961–1970 and 2001–2010 (b), the gradient of average (1993–2013) soil pH from the National Forest Inventory (NFI) data (c) and annual modelled total nitrogen deposition between 2005 and 2014 (d). Grey spatial units lack data. Data on N deposition were downloaded from http://www.smhi.se/klimatdata/miljo/atmosfarskemi [Colour figure can be viewed at wileyonlinelibrary.com]



increasing from the 1950s (Granath et al., 2014; Östlund et al., 1997), much of the Swedish forests, especially in the southern part, represent the high end of anthropogenic influence in northern forests. Hence, Swedish forests are useful model systems for how two major global change drivers, nitrogen deposition and intensive land use, may interact with climate change (Figure 1b) and impose vegetation change in other regions facing increasing anthropogenic pressure under global environmental change. An important step forward is also to consider how such large-scale factors interact with local factors such as soil conditions. Moreover, systematic long-term (> 50 year) vegetation and tree data from the Swedish National Forest Inventory (NFI), in combination with more recent soil data, provide excellent opportunities to analyse changes in understorey plant communities.

Our main aim with this study is to increase insights into how changes in environmental factors occurring at a global scale (nitrogen deposition and increasing temperatures) interact with local scale factors (forest density and soil pH) as mechanisms of change of forest understorey vegetation. More specifically, we use national survey data to analyse the effects of increasing temperatures, nitrogen deposition and land-use change (through increasing forest density) during the last half-a-century, and how these effects vary with local soil conditions (pH; Figure 1c). We hypothesize that forest density, through its effects on understorey light availability, influences the understorey vegetation response to increased temperature and nitrogen deposition. More explicitly, we expect the effects of these two large-scale drivers to be larger in open than in closed forests (De Frenne et al., 2013; Verheyen et al., 2012). Furthermore, we hypothesize that low soil pH restricts the effects of both increasing temperatures and nitrogen deposition as well as determines the outcome of an increase in forest density due to species adaptations to light, nutrient availability and pH. To test these hypotheses, we analysed temporal changes in the spatial distribution of four vegetation types that either are adapted to both dark and eutrophic conditions (three forb dominated types), or connected mainly to low light availability (low vegetation cover) (Hedwall, Gustafsson, et al., 2019). These four vegetation types currently cover *c*. 60% of the forestland in southern Sweden, in comparison to *c*. 20% in the 1950s (Table 1; Hedwall, Gustafsson, et al., 2019). Dwarf shrubs are an ecologically relatively homogeneous group associated with mostly nutrient poor, acidic and light environments, and an important indicator group of environmental changes (Hedwall, Gustafsson, et al., 2019). This species group has shown the most drastic change in cover (from 27 to 14%) since the 1950s (Hedwall, Gustafsson, et al., 2019) and, thus, we also tested the hypothesis that the decrease in dwarf shrubs can be explained by changes in forest density, temperature increase and nitrogen deposition. Due to the adaptation of these plants to low pH soils and relatively open forests we hypothesized that they may be more resistant to the large-scale drivers on such sites, than their more nitrophilic shade-adapted competitors.

2 | MATERIAL AND METHODS

2.1 | Study system

Sweden spans almost 14° of latitude (55.3–69.1° N), with annual mean temperatures ranging from about 8 °C in the far south to −3 °C in the far north (Raab & Vedin, 1995). Thus, Swedish forests (total area: 280,000 km^2) fall into both the boreal and hemiboreal biomes (Ahti et al., 1968). There is also a latitudinal gradient in nitrogen deposition, ranging from *c*. 12.5 kg/ha/year in the far south to just above ambient levels in the far north (*c*. 1–2 kg/ha/year, Akselsson et al., 2010; Figure 1d). The mean annual temperature has increased by, on average, 1 °C since the mid-1900s (Kjellström et al., 2014; Figure 1b). Since the 1960s, clearcutting has been applied full-scale on the productive forest land of Sweden, with associated activities like soil scarification, artificial regeneration, and repeated thinning (SFA, 2020). This type of forest management is currently conducted on > 80% of productive forest land in Sweden, and about 90% of the

TABLE 1 Indicator species used in the classification of the forb vegetation types (see Supporting Information Appendix S1: Table S1 for details)

Vegetation type	Indicator species	Δ Hemiboreal (%)	Δ Boreal (%)	SLA	L	R	N
Rich forb	*Anemone ranunculoides*, *Lamiastrum galeobdolon*, *Mercurialis perennis*, *Aegopodium podagraria*, *Galium odoratum*, *Sanicula europaea*, *Actaea spicata*, *Cardamine bulbifera*, *Paris quadrifolia*	3.4	1.8	27.9	5.1	4.7	4.5
Tall forb	Tall ferns except *Pteridium aquilinum*, *Aconitum lycoctonum*, *Lactuca alpina*, *Filipendula ulmaria*, *Urtica dioica*, *Stachys sylvatica*, *Trollius europaeus*, *Silene dioica*, *Rumex acetosa*, *Geranium sylvaticum* (only north)	11.5	4.8	27.0	5.3	3.8	4.1
Low forb	*Hepatica nobilis*, *Oxalis acetosella*, *Anemone nemorosa*, *Maianthemum bifolium*, *Gymnocarpium dryopteris*, *Pyrola* spp., *Fragaria vesca*, *Veronica* spp., *Lysimachia europaea*, *Melampyrum sylvaticum*, *M. pratense*, *Ficaria verna*, *Alchemilla* spp., *Ranunculus* spp., *Geranium sylvaticum* (only south)	19.1	15.9	27.0	5.1	3.3	3.3
Low cover		8.5	0.2	19.7	5.4	2.7	3.1

Note: Δ Hemiboreal/Boreal indicates the change in percentage of the productive forest area between the two time periods (Hedwall, Gustafsson, et al., 2019). L, R and N are the community weighted Ellenberg indicator values for light, soil pH and nutrient availability, respectively, while SLA is the mean specific leaf area. Species nomenclature is according to Karlsson and Agestam (2014).

annual growth (*c*. 120 million m^3) is extracted each year (SFA, 2014). This forest management system has led to a doubling of the standing forest volume since the 1920s (SLU, 2017), resulting in denser and darker forests (Figure 1a; Hedwall & Brunet, 2016).

2.2 | The Swedish National Forest Inventory

The NFI has surveyed Swedish forests since the 1920s. Since 1953, the NFI has used a nationwide network of systematically distributed temporary circular sample plots (Fridman et al., 2014). From 1983, these plots have been complemented by a network of permanent plots surveyed every 5–10 years (Fridman et al., 2014). In our study, we used plots on productive forest land (presently 23.2 Mha, with an annual timber production capacity > 1 m^3/ha), of which *c*. 4% is formally protected in reserves, and around 13% is retained or set aside for conservation by forest owners (Claesson et al., 2015). The coverage of productive forest land has increased, slightly in the boreal region (by 0.7%) and substantially (by 11.2%) in the hemiboreal region since the 1950s (Hedwall, Gustafsson, et al., 2019).

Between 1953 and 1962, all inventoried forest plots (6.64 m radius) were classified as one of 13 vegetation types, using a combination of cover estimates of vascular plant species and occurrence of certain indicator species according to a classification scheme (Supporting Information Appendix S1: Table S1). We refer to this as the ‘old data’. Data collected between 2003 and 2012 (hereafter the ‘modern data’) include more detailed information on the understorey vegetation than the old data and were collected in permanent plots (Fridman et al., 2014). Both inventories also include detailed surveys of tree layer structure and tree species composition. In the modern vegetation survey, the presence of 270 species, or species groups, and coverage of 72 species, including vascular plants, bryophytes, and lichens, is recorded in circular permanent plots with a radius of 5.64 m (Odell & Löfgren, 2009). To compare the old and modern data sets, we converted the modern data into the vegetation types used in the 1950s by applying the instructions from the old inventories to the detailed information on species occurrence and coverage collected between 2003 and 2012. We selected the four vegetation types (‘Rich forb’, ‘Tall forb’, ‘Low forb’ and ‘Low vegetation cover’) that had increased in the hemiboreal zone (Hedwall, Gustafsson, et al., 2019; Supporting Information Appendix S1: Table S1) for further analyses. The classification of the decreasing vegetation types is largely dependent on the cover of dwarf shrubs. Hence the cover of these species was, additionally, chosen to represent the decreasing vegetation types in our analyses, all being associated with more nutrient poor, acidic and high light conditions. The classification into one of the forb types is highly dependent on the presence of indicator species (Table 1). As the chance of recording the presence of a species increases with plot size, the smaller plots in the modern data may have led to underestimation of these types.

We used the modern NFI data to calculate mean indicator values for light requirement, soil pH and nutrient requirement (Ellenberg et al., 2001; Hedwall, Brunet, & Diekmann, 2019). Individual species' indicator values range from 1 to 9 with higher values indicating higher values of each resource requirement. Overall vegetation type values were calculated as arithmetic means of all species present in at least 5% of the plots in a given type. Additionally, we calculated mean specific leaf area (SLA) for each vegetation type by weighting species-specific SLA values from the LEDA trait database (Kleyer et al., 2008) by mean cover estimates within each vegetation type in the modern NFI data (2003–2012). SLA is a plant trait that is strongly associated with nutrient cycling and plant growth rates (Lavorel & Garnier, 2002), and recent shifts towards plant communities with high SLA have been observed both in North American and European forests (Amatangelo et al., 2014; Hedwall & Brunet, 2016; Hedwall, Gustafsson, et al., 2019).

2.3 | Data analyses

We used data for all NFI plots (117,891) that had been classified into vegetation types between 1953 and 1962, and all plots inventoried in 2003–2012 (7,784) for which sufficient vegetation data were available for the post hoc conversion to the old vegetation types. The 10-year window of the modern data represents one inventory cycle, and accordingly no single plot has been included more than once.

The plots are arranged in square-shaped clusters. The length of each square's edge, the number of plots per square, and the distance between squares varies regionally, and has changed over time (Supporting Information Appendix S2: Figure S2). Thus, the inventories can be considered as two temporary separate surveys. To relate changes in understorey vegetation over time to environmental variables, we expressed the relative cover of the vegetation types in a uniform square grid with a side length of 20,000 m. This grid size minimizes the number of grids lacking data (grey spatial units in Figure 1) without sacrificing the high spatial resolution of the nitrogen deposition data and statistical power in the analyses (Supporting Information Appendix S3: Figure S3). From 1,319 spatial units 1,020 have information about forest density and vegetation types. For each of these spatial units, we calculated the forest area covered by each vegetation type using pre-calculated area factors from the NFI database, following the procedure described by Toet et al. (2007). In brief, to account for the differences between inventories, we weighted the contribution of each plot by the forest area that it represents. Since the larger number of plots in the old than in the modern data set potentially could lead to biased estimates of coverages of the vegetation types, we performed a balanced random sampling of plots from the old data. This procedure allows the inclusion of probabilities to ensure the same number of plots in the old and modern data sets while retaining the distribution between vegetation types (Grafström et al., 2012). We then identified spatial units where the vegetation types Rich forb, Tall forb, Low forb or Low cover had increased over the study period, resulting in a binary (0/1) response variable that was used for further analyses.

To estimate the change in dwarf shrub cover, we calculated the aggregate cover estimates of all species of *Calluna*, *Empetrum*, *Erica* and *Vaccinium* for the two time-periods using vegetation type-specific values, one set for the hemiboreal and one set for the boreal zones, computed from the cover estimates of those species in the modern data. The relative cover within each vegetation type was calculated, and then multiplied by the relative cover of the respective vegetation types in both the 1950s (old data) and 2000s (modern data) within the spatial units. These products were then summed to produce an estimate of the dwarf shrub cover at the two time points. These estimates were used to assess the change over time as the difference between the two time points.

The basal area for Norway spruce and the total basal area, at both time points, were calculated for each spatial unit and time period to estimate the change in forest density over time. The change in basal area was correlated (Pearson correlation, $r = .67–.68$) with today's basal area (i.e. a spatial unit with a large increase in basal area over time has a large basal area today) and so we choose to include the latter in our analyses as it includes only positive values, which facilitates the interpretation of the results. Top soil pH (Hedwall, Brunet, & Diekmann, 2019) measurements were available for 23,368 plots in the modern data (1993–2013). We used these plots to create an interpolation map (Kriging) from which a mean pH for each spatial unit was calculated and included in our analyses as a measurement at one time point. For each spatial unit, we also calculated the change in modelled annual mean temperature between the two periods 1961–1970 and 2001–2010 (Figure 1b). Additionally, we assigned every spatial unit a value of total nitrogen deposition. These values were extracted from a map of modelled mean deposition between 2005 and 2014 (Figure 1d). Data on climate and nitrogen deposition were provided by the Swedish Meteorological and Hydrological Institute (SMHI, 2015). These gradients were limited in the models to < 25 and 40 m^2/ha for the basal areas of Norway spruce and total basal area, respectively, and to < 5 for pH. The total basal area and the spruce basal area were positively correlated ($r = .64$) and thus not included in the same models. All explanatory variables were standardized prior to further analysis by subtracting the mean and dividing by the standard deviation. To facilitate the interpretation of the results all diagrams show the scale of the untransformed variables.

We used generalized linear models (GLMs) as implemented in the glmmTMB function in the glmmTMB package (Brooks et al., 2017) in R (R Core Team, 2020) to test the effect of these explanatory variables on the response variables. The probability of an increase in the four selected vegetation types was modelled with binomial error distribution, while a beta distribution was used to estimate the effects of the different models on the change in the proportion of forest land covered by dwarf shrubs. A logit link-function was applied in both the binomial and beta GLMs. In line with our expectations (see Introduction) concerning interactions between the environmental variables, we set up two models differing in whether the total basal area or spruce basal area was included. To avoid spatial dependence in the residuals, we used spatial filtering as implemented in the SpatialFiltering function in the spdep package (Bivand & Wong, 2018). This procedure fits Moran's eigenvectors to the coordinates of the observations, and then selects a subset of these eigenvectors to be included in the GLM as proposed by Kühn and Dormann (2012). To test for remaining spatial autocorrelation in the residuals after this procedure, we performed a Moran's *I* test with the testSpatialAutocorrelation function in the DHARMa package (Hartig, 2020). Equation 1 shows the general structure of these models where the basal area is either the basal area of all trees, or of spruce, and *i* refers to each spatial unit.

$$\begin{aligned} Y_i = {} & \beta_0 + \beta_1 \mathrm{Basal\,Area}_i + \beta_2 \mathrm{pH}_i + \beta_3 N\,\mathrm{Deposition}_i + \beta_4 \mathrm{Temperature\,Change}_i \\ & + \beta_5 \mathrm{Basal\,Area}_i{}^{*}\mathrm{pH}_i + \beta_6 \mathrm{Basal\,Area}_i * N\,\mathrm{Deposition}_i + \beta_7 \mathrm{Basal\,Area}_i{}^{*}\mathrm{Temperature\,Change}_i \\ & + \beta_8 \mathrm{pH}_i * N\,\mathrm{Deposition}_i + \beta_9 \mathrm{pH}_i{}^{*}\mathrm{Temperature\,Change}_i + \beta_{10} \mathrm{Eigen\,Vectors}_{(x,y)i} + \varepsilon_i \end{aligned} \tag{1}$$

The two models were then compared with the Akaike information criterion (AIC). Pseudo *R*-squares, as suggested by Nakagawa and Schielzeth (2013), and the percentage correct predictions (PCPs) were calculated for evaluation of the chosen model. The PCPs were calculated by the performance package (Lüdecke et al., 2020) and the function performance_pcp. All interactions were visualized by plotting the predicted trends along one continuous variable at the 10th and 90th percentiles, and the median of the other variable, while all other variables were kept to their mean values. We also performed a post-hoc test of whether the slopes at these three values differed from zero. These tests were performed using the emtrends function in the emmeans package (Russell, 2021), and the *p*-values were corrected for multiple testing by the false discovery rate method.

3 | RESULTS

3.1 | Rich forb type

The model best describing the probability of an increase (according to AIC) in the Rich forb type (Supporting Information Appendix S4: Table S4) was the model including spruce basal area (Supporting Information Appendix S5: Table S5). All main effects, including pH, spruce basal area, nitrogen deposition, and temperature increase showed a significant ($p = .009$) positive effect on the probability of an increase in this vegetation type (Figure 2). In addition, there also was a significant interaction between spruce basal area and nitrogen deposition ($p = .005$), indicating that nitrogen deposition only had a positive effect at low basal area, while deposition had no effect at high basal area.

3.2 | Tall forb type

The model best explaining (lowest AIC; Supporting Information Appendix S4: Table S4) the probability of an increase in the Tall forb type was the model including total basal area, with significant positive effects of the total basal area ($p = .002$), pH ($p < .001$) and nitrogen deposition ($p < .001$), while temperature increase had no effect

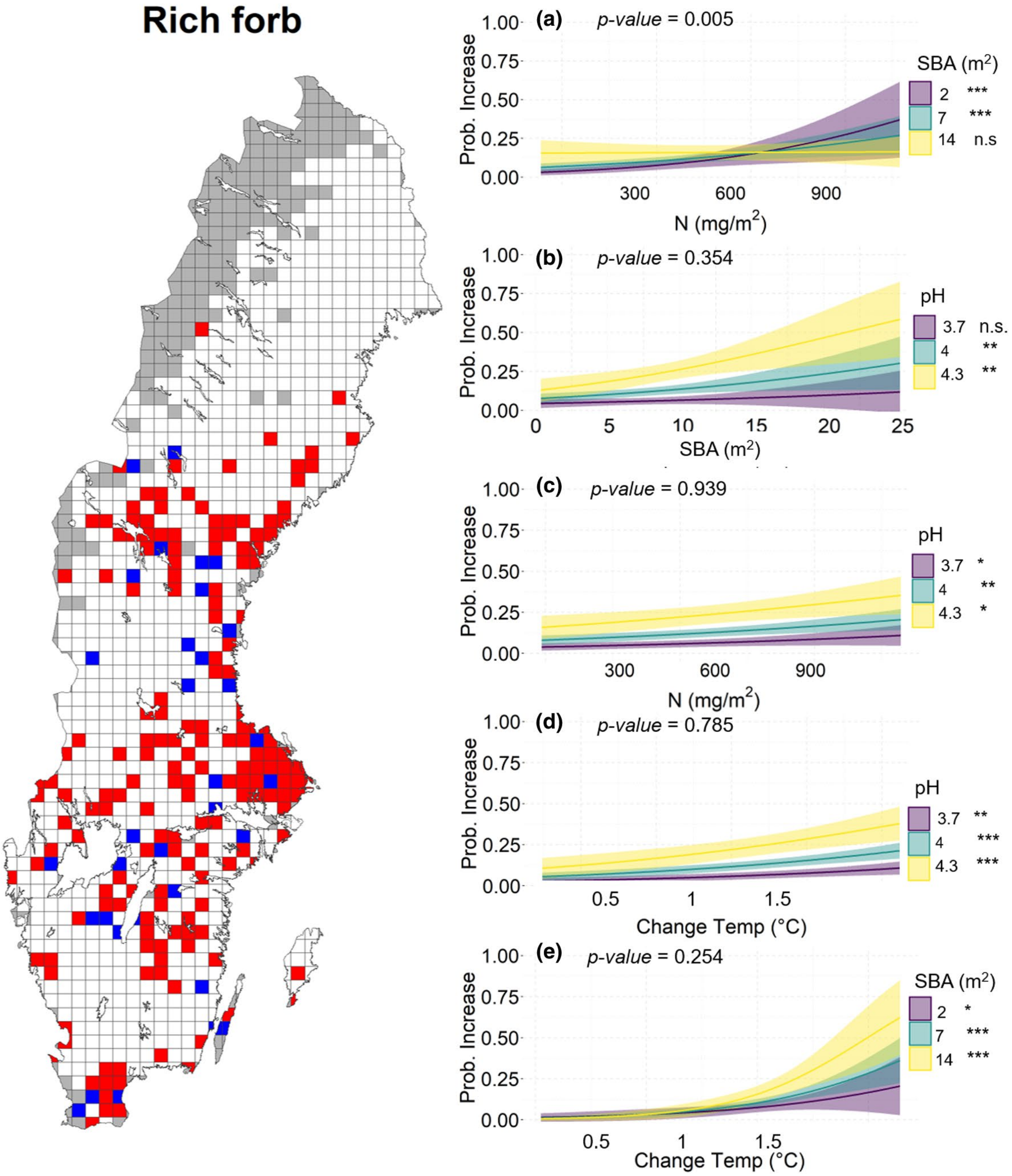


FIGURE 2 Map showing spatial units where the vegetation type Rich forb increased (red), decreased (blue) or was absent (white) from the 1950s to 2010s. Grey units indicate areas without data. The diagrams show the predicted effect (± 95% confidence interval) of the interactions between spruce basal area (SBA) and nitrogen deposition (a), SBA and pH (b), nitrogen deposition and pH (c), temperature increase and pH (d), and temperature increase and SBA (e) on the probability of an increase in the Rich forb type. *p*-values are shown for the omnibus test of the interaction terms. The symbols in the legends indicate the *p*-values from a post-hoc test of the slopes (≠ 0) where n.s. = $p > .05$, *$p \le .05$, **$p \le .01$, ***$p \le .001$ [Colour figure can be viewed at wileyonlinelibrary.com]

(p = .323). The interactions between the basal area and nitrogen deposition (p = .003), between basal area and temperature increase (p = .011), between temperature increase and pH (p = .021), and between nitrogen deposition and pH (p = .005) were all statistically significant (Supporting Information Appendix S5: Table S5). While there was a clear increase with deposition at all levels of basal area, the effect of increasing deposition was more pronounced at low than at high basal area (Figure 3). Similarly, the probability of an increase in cover of the Tall forb type was greater at high nitrogen deposition, but this effect was stronger under low pH than at high pH. The positive effect of climate warming was, additionally, only present at low pH and low basal area.

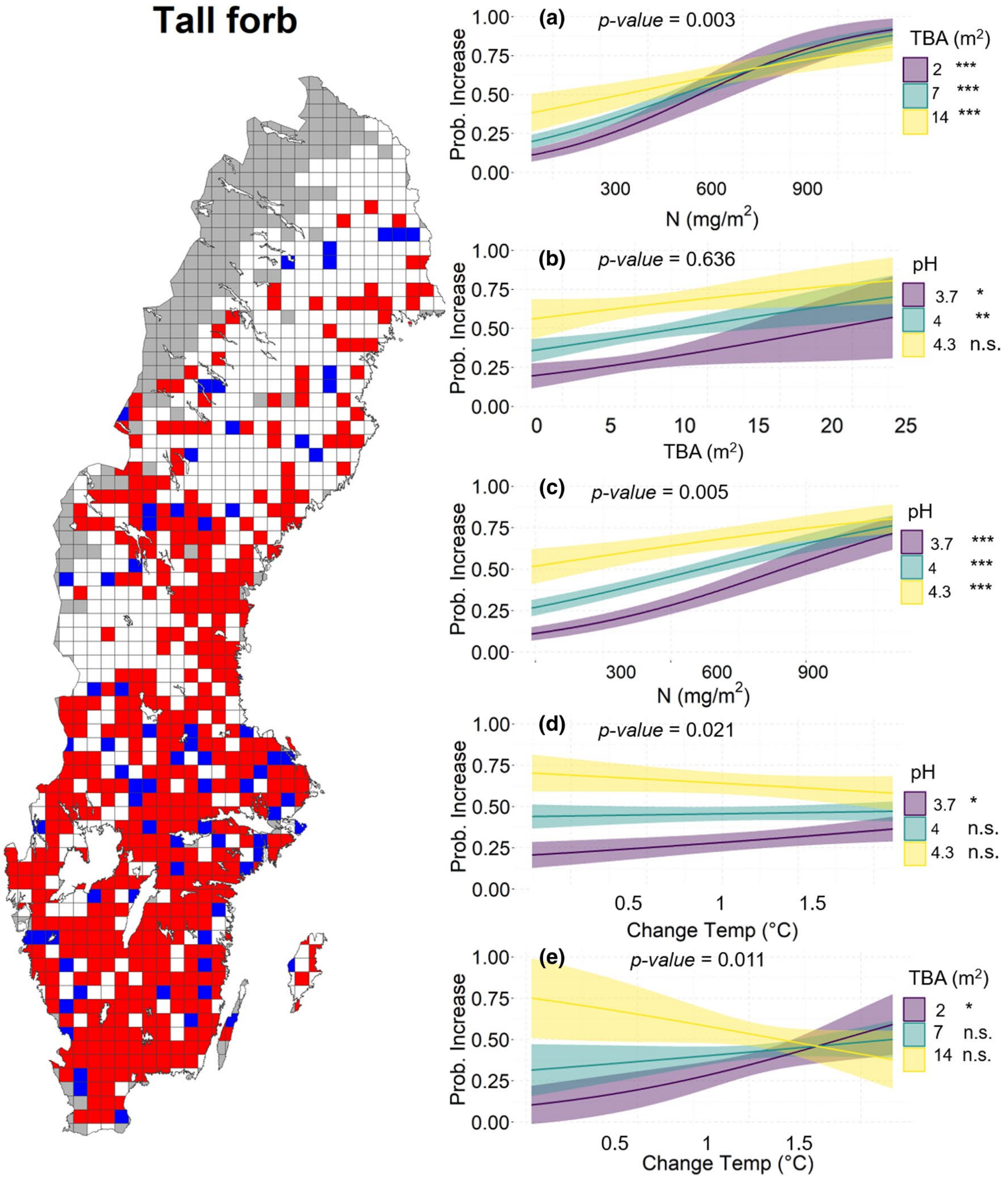


FIGURE 3 Map showing spatial units where the vegetation type Tall forb increased (red), decreased (blue) or was absent (white). Grey units indicate areas without data. The diagrams show the predicted effect (± 95% confidence interval) of the interactions between total basal area (TBA) and nitrogen deposition (a), TBA and pH (b), nitrogen deposition and pH (c), temperature increase and pH (d), and temperature increase and TBA (e) on the probability of an increase in the Tall forb type. The slopes of the variables shown as continuous are predicted for the 10th and 90th percentiles, as well as the median of the other variable in the interaction. *p*-values are shown for the omnibus test of the interaction terms. The symbols in the legends indicate the *p*-values from a post-hoc test of the slopes (≠ 0) where n.s. = $p > .05$, *$p \le .05$, **$p \le .01$, ***$p \le .001$ [Colour figure can be viewed at wileyonlinelibrary.com]

3.3 | Low forb type

The model best explaining an increase in the Low forb type (lowest AIC; Supporting Information Appendix S4: Table S4) was the spruce basal area model with significant ($p < .001$) positive effects of all main factors (Supporting Information Appendix S5: Table S5). In addition, the interaction between nitrogen deposition and pH was highly significant ($p < .001$). The probability of an increase in the Low forb type increased with nitrogen deposition at low pH, while there was no effect of deposition at high pH (Figure 4).

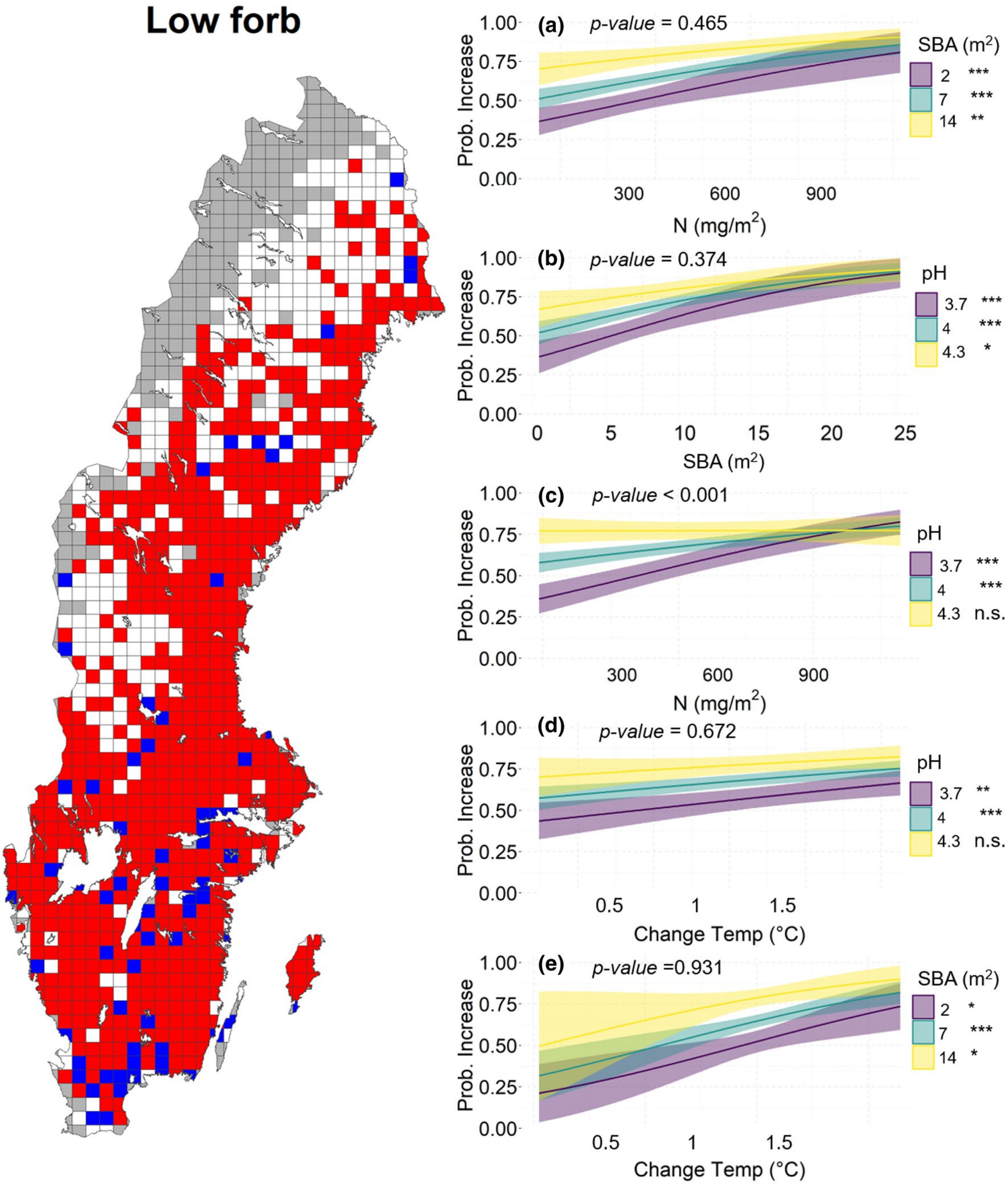


FIGURE 4 Map showing spatial units where the vegetation type Low forb increased (red), decreased (blue) or was absent (white). Grey units indicate areas without data. The diagrams show the predicted effect (± 95% confidence interval) of the interactions between spruce basal area (SBA) and nitrogen deposition (a), SBA and pH (b), nitrogen deposition and pH (c), temperature increase and pH (d), and temperature increase and SBA (e) on the probability of an increase in the Low forb type. *p*-values are shown for the omnibus test of the interaction terms. The symbols in the legends indicate the *p*-values from a post-hoc test of the slopes (≠ 0) where n.s. = $p > .05$, *$p \leq .05$, **$p \leq .01$, ***$p \leq .001$ [Colour figure can be viewed at wileyonlinelibrary.com]

3.4 | Low vegetation cover type

The best model (lowest AIC; Supporting Information Appendix S4: Table S4) for the Low vegetation cover type was the spruce basal area model. This model included a significant positive effect of nitrogen deposition ($p < .001$), and a significant ($p = .023$) interaction between nitrogen deposition and spruce basal area (Supporting Information Appendix S5: Table S5). While there were significant effects of deposition on the probability of an increase at all levels of basal area, the effect was stronger at high basal area (Figure 5).

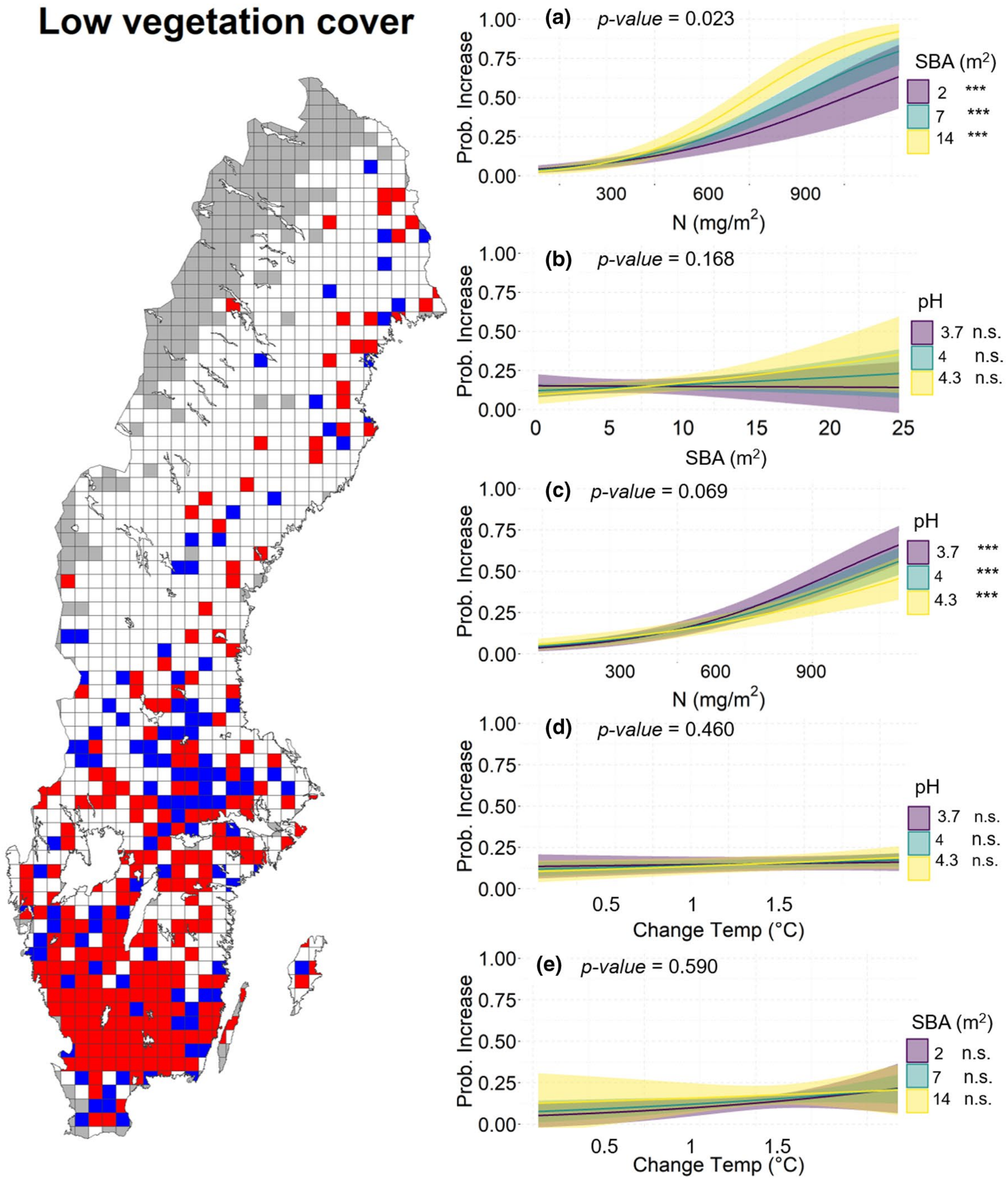


FIGURE 5 Map showing spatial units where the vegetation type Low vegetation cover increased (red), decreased (blue) or was absent (white). Grey units indicate areas without data. The diagrams show the predicted effect (± 95% confidence interval) of the interactions between spruce basal area (SBA) and nitrogen deposition (a), SBA and pH (b), nitrogen deposition and pH (c), temperature increase and pH (d), and temperature increase and SBA (e) on the probability of an increase in the Low vegetation cover type. *p*-values are shown for the omnibus test of the interaction terms. The symbols in the legends indicate the *p*-values from a post-hoc test of the slopes (≠ 0) where n.s. = $p > .05$, ***$p \leq .001$ [Colour figure can be viewed at wileyonlinelibrary.com]

3.5 | Dwarf shrubs

The model best explaining the decrease in dwarf shrubs (Supporting Information Appendix S4: Table S4) was the spruce basal area model. All the main effects were highly significant ($p < .001$). While the decrease in dwarf shrubs was greater at higher values of spruce basal area, nitrogen deposition and pH, it was smaller at high temperature increase (Supporting Information Appendix S5: Table S5). In addition, the interactions between nitrogen deposition and pH ($p < .001$), and between basal area and pH ($p = .012$) were significant, indicating stronger effects of basal area and deposition at low than at high pH (Figure 6).

4 | DISCUSSION

Our study shows clear effects of interactions between the two global change drivers, nitrogen deposition and increasing temperature on one side, and local land-use changes (forest density, indicating intensified forest management) on the other, on vegetation in northern forests. Additionally, it highlights the importance of local settings, as soil pH noticeably influenced the effects of the temperature increase, nitrogen deposition and forest density. This strong context dependency of varying drivers' effects on forest ecosystems is in line with studies in temperate forests (De Frenne et al., 2013; Midolo et al., 2019; Perring, Bernhardt-Römermann, et al., 2018; Perring, Diekmann, et al., 2018; Verheyen et al., 2012), but has so far not been shown for the vast boreal forest. As such, our results stress the importance of accounting for context dependencies when predicting the effects of global change on forest ecosystems and in designing management strategies to reduce negative impacts. Neglecting to account for these context dependencies may lead to incorrect estimations of the effects as well as predicting wrong trajectories of ecosystems under global change.

The importance of nitrogen deposition as a driver of increases in the cover of the forb types found earlier (Hedwall, Gustafsson, et al., 2019) was confirmed by our results. The probability of an increase in any of the forb types was also positively correlated with pH, and in the Tall forb and Low forb types there were significant interactions between nitrogen deposition and pH. This relates to one of our other hypotheses, that the local factor of soil pH may modulate effects of global drivers like nitrogen deposition. Besides the forb types being nutrient demanding, they are also mainly restricted to sites with high pH (Table 1). Our results further indicate that the effect of nitrogen deposition is greater at low pH, which contradicts our hypothesis. This may in turn indicate that higher nitrogen availability somewhat compensates for low pH (Falkengren-Grerup, 1990). However, high pH sites may already contain the even more neutrophilic Rich forb type, limiting the possibility of a N-induced change. In addition, the probability of an increase of the Low cover type was higher at sites with high N deposition and low pH. This effect most likely stems from the same confining factor as for the forb types, that is, that most sites with high pH already contained more neutrophilic and shade tolerant vegetation types.

Soil pH has decreased in forest soils in southern Sweden during the 20th century according to local studies (Falkengren-Grerup, 1987). In addition to eutrophication, nitrogen deposition also results in acidification. In combination with the acidification caused by sulphur deposition, which peaked during our study period (Binkley & Högberg, 1997), this has likely restricted the effects of eutrophication on the vegetation. Based on our results it is evident that soil pH regulates the effect of nitrogen deposition, and it seems reasonable to assume that the changes in forest vegetation would have been much greater if they had occurred under a period with lower sulphur deposition. Thus, it is also possible that the effect of nitrogen deposition may be even greater in regions, or during time periods, with lower sulphur deposition than in Sweden.

The change in land use from agriculture to forestry during our study period was relatively small, and thus of minor importance for the observed vegetation changes (Hedwall, Gustafsson, et al., 2019). The influence of this transition does, however, most likely differ between vegetation types. For example, many of the high pH sites where the Rich forb type has expanded are probably strongly influenced by legacy effects of former livestock grazing or haymaking. Therefore, the observed changes may reflect successional change from light demanding neutrophilic (adapted to low acidity) grassland communities to forest vegetation.

Forest density, indicated by basal area, played a significant role in the increase of the four vegetation types, both by significant main effects, and also by interactions with nitrogen deposition. In both the Rich forb and the Tall forb types the effect of nitrogen deposition was smaller in dense forests than in more open ones, and in line with our hypothesis, a similar response was also indicated by the interaction between the temperature increase and basal area for the Tall forb type. Possibly, the responsiveness to increased N availability from high deposition and higher temperatures is restricted by limited light availability as suggested in other studies (Strengbom et al., 2002, 2004; Verheyen et al., 2012; Zellweger et al., 2020).

Nitrogen deposition can alter the community composition from dwarf shrub dominance towards narrow-leaved grasses, mainly *Avenella flexuosa* (Bobbink et al., 2010). Expansion of this grass depends on high light availability (Strengbom et al., 2004), and a possible explanation behind the observed interaction between density and deposition could thus be that nitrogen deposition has shifted the understorey vegetation on acidic soils to a more light-demanding type. Dense forests can mitigate the effects of nitrogen deposition and climate change (cf. Greiser et al., 2019; Verheyen et al., 2012), by lowering temperatures or restricting competing vegetation. Maintaining a continuous tree canopy cover at special sites has consequently been suggested as a management option to protect sensitive plant communities under pressure from climate change (Greiser et al., 2019; Zellweger et al., 2020). However, according to our results, the mitigation effect will be restricted to communities adapted to high pH in combination with low light environments, while such management may be detrimental to species and ecological functions connected to the understorey under more acid conditions (Hedwall, Gustafsson, et al., 2019).

While dwarf-shrub cover generally decreased more at high basal area, the impact of nitrogen deposition was dependent on pH. In contrast to our hypothesis of dwarf shrub resistance to changes at low pH, our results indicate more complex relationships. At low and intermediate pH, cover decreased with increasing nitrogen deposition, while this effect was absent at high pH. Dwarf shrubs are well adapted to low pH (Ellenberg et al., 2001), and it is possible that nitrogen deposition lowered pH on base-rich soils, and by this counteracted the negative eutrophication effects on these species by disfavouring neutrophilic competitors (Falkengren-Grerup, 1987, 1990). The temporal transition from dwarf shrubs to herbaceous

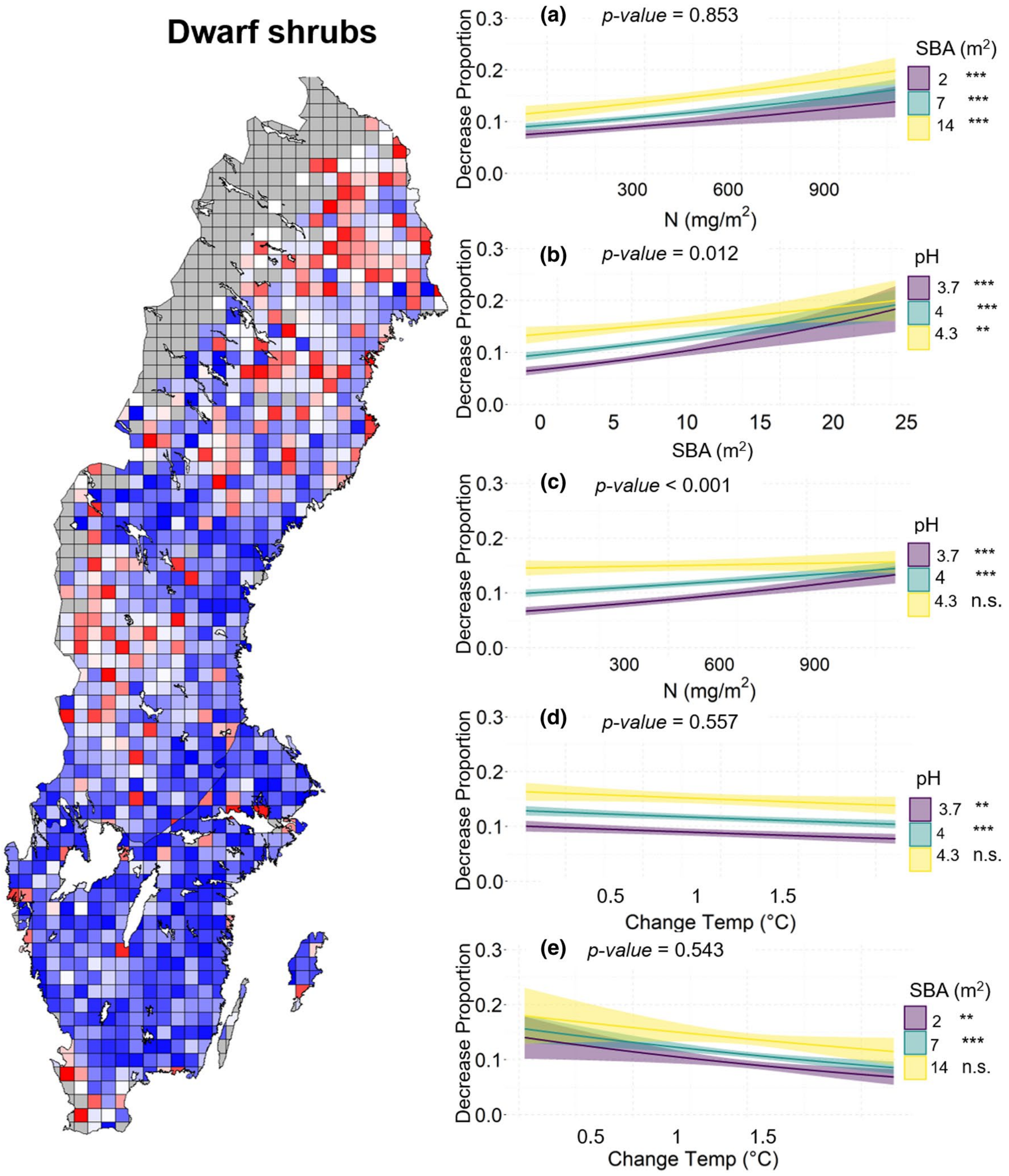


FIGURE 6 Map showing spatial units where the dwarf shrubs increased (red), decreased (blue) or did not change (white). The more intense the blue or red, the larger the change, while grey units indicate areas without data. The diagrams show the predicted effect (± 95% confidence interval) of the interactions between spruce basal area (SBA) and nitrogen deposition (a), SBA and pH (b), nitrogen deposition and pH (c), temperature increase and pH (d), and temperature increase and SBA (e) on the decrease in dwarf shrubs. *p*-values are shown for the omnibus test of the interaction terms. The symbols in the legends indicate the *p*-values from a post-hoc test of the slopes (≠ 0) where n.s. = *p* > .05, ***p* ≤ .01, ****p* ≤ .001 [Colour figure can be viewed at wileyonlinelibrary.com]

vegetation, observed in the southern part of our study area, as an effect of nitrogen deposition and land-use change (see also Hedwall & Brunet, 2016; Hedwall, Gustafsson, et al., 2019), may have reinforced the natural biogeographical differences in cover of herbaceous and dwarf shrub-dominated communities; the latter being more dominant towards the north.

The increase in annual mean temperature in Sweden has exceeded 1 °C during the last 50 years (SMHI, 2015), and the warmer climate is an important variable explaining the observed changes in the Rich forb and Low forb types, and to some extent also the Tall forb type and in the dwarf shrubs. Most of the indicator species in the rich forb type, and many species in the low forb type (e.g. *Anemone nemorosa*, *Ficaria verna*, *Hepatica nobilis*) are more abundant in southern Sweden than in the north, while there is no such geographical pattern among the species of the Tall forb type (Hultén, 1971). It is thus possible that these vegetation types, besides being indicators of soil fertility and light conditions, also are indicative of a warmer climate. In contrast, dwarf shrubs, dominated by *Calluna vulgaris*, *Vaccinium myrtillus* and *Vaccinium vitis-idaea*, are distributed from southern to northern Europe (Hultén, 1971) and may therefore be relatively indifferent to increasing temperatures, or even respond positively to increasing temperatures when other factors are controlled for.

It is possible that the interactions observed in our study may be specific to the gradients in plant composition in our study area. However, as many of the dominant species in our study area are widespread and common in many places in northern Eurasia, and some even have a circumpolar distribution (e.g. *V. vitis-idaea*), it is plausible that similar interactive effects can also be expected to occur in other regions. The degree to which our results can be generalized to other parts of the boreal biome also depends highly on the context of anthropogenic impact. As an example, nitrogen deposition has decreased in the boreal regions of western Europe and eastern North America during recent decades, while increasing in large parts of western Canada and in Siberia (Ackerman et al., 2019). There is a major deficit of knowledge concerning the recovery of forest ecosystems from excess nitrogen levels, but considerable timelags in this process have been proposed (Gilliam et al., 2019; Schmitz et al., 2019; Strengbom et al., 2001). Furthermore, the future trajectories of changes in these ecosystems may be largely dependent on the size of the nitrogen pool, and factors that may mobilize or immobilize this pool (Schmitz et al., 2019), for example increasing temperatures or disturbances. Hence, interactions between different drivers may also in the future be of major importance for the development of the vegetation in areas with decreasing deposition. Most of the boreal areas with increasing deposition, except parts of south-east Siberia, still have rather modest levels of deposition (Ackerman et al., 2019). The development in these areas will be largely dependent on the trends in emissions, but even if they remain at low level, long-term deposition may still induce change due to increasing ecosystem nitrogen pools (De Schrijver et al., 2011).

More than half of the boreal forest globally is affected by forestry (Gauthier et al., 2015), including considerable areas where forest structure and understorey composition are largely determined by choice of management (Strengbom et al., 2018). We suggest that the development of forest understorey communities in managed boreal forest under influence of large-scale drivers like nitrogen deposition and climate change will, as in temperate forests (De Frenne et al., 2013; Verheyen et al., 2012), be strongly affected by management-induced changes in forest density and tree species composition.

In conclusion, neglecting to consider interactions between global change drivers, as well as context dependency when predicting future vegetation development, may lead to both under- and overestimates of the magnitude of change. Here we show that the expected nitrophilization of the forest understorey vegetation under elevated nitrogen deposition is greater at low than high pH. By not including pH in models estimating effects of global change, we risk underestimating the eutrophication effects in forest ecosystems on acid soils, constituting the largest part of the boreal biome. Hence, our results show that vegetation development under global change may take considerably different trajectories due to interactions between drivers. In addition, forecasting global change effects on forest understorey communities, as well as mitigating global change effects, requires that local conditions, in our case soil pH and forest density, are accounted for.

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AUTHOR CONTRIBUTIONS

All authors contributed to developing the ideas and designing the study. JUD did the data handling and statistical analyses. POH led the writing of the paper in cooperation with all authors. All authors have approved the final version.

DATA AVAILABILITY STATEMENT

Data openly available in a public repository that issues data sets with DOIs: https://datadryad.org/stash/share/1xQhq6a1Ugdnzs_EpeBwfQoN8gvtuefFVlgPk3ZyAlw

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BIOSKETCH

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SUPPORTING INFORMATION

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

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