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Running head: Changes of northern forest vegetation

Half a century of multiple anthropogenic stressors has altered northern forest understory plant communities

Authors: Per-Ola Hedwall[1*], Lena Gustafsson[2], Jörg Brunet[1], Matts Lindbladh[1], Anna-Lena Axelsson[3], Joachim Strengbom[2]

[1]Swedish University of Agricultural Sciences, Southern Swedish Forest Research Centre, P.O Box 49, 230 53 Alnarp, Sweden.

Corresponding author, email: per-ola.hedwall@slu.se, phone: +46 70 560 37 38

[2]Swedish University of Agricultural Sciences, Department of Ecology, P.O. Box 7044, SE-750 07 Uppsala, Sweden

[3]Swedish University of Agricultural Sciences, Department of Forest Resource Management, 901 83 Umeå, Sweden

Abstract

Boreal forests form the largest and least disturbed forest biome in the northern hemisphere. However, anthropogenic pressure from intensified forest management, eutrophication and climate change may alter the ecosystem functions of understory vegetation and services boreal forests provide. Swedish forests span long gradients of climate, nitrogen deposition, and management intensity. This makes them ideal to study how the species composition and functions of other, more pristine, boreal forests might change under increased anthropogenic pressure. Moreover, the National Forest Inventory (NFI) has collected systematic data on Swedish forest vegetation since the mid-20th century. We use this data to quantify changes in vegetation types between two periods, 1953-1962 and 2003-2012. The results show changes in forest understory vegetation since the 1950s at scales not previously documented in the boreal biome. The spatial extent of most vegetation types changed significantly. Shade-adapted and nutrient-demanding species (those with high specific leaf area) have become more common at the expense of light-demanding and nutrient-conservative (low specific leaf area) species. The cover of ericaceous dwarf shrubs decreased dramatically. These effects were strongest where anthropogenic impacts were greatest, suggesting links to drivers such as nitrogen deposition and land-use change. These changes may impact ecosystem functions and services via effects on higher trophic levels and faster plant litter decomposition in the expanding vegetation types. This, in turn, may influence nutrient dynamics, and consequently ecosystem productivity and carbon sequestration.

Keywords: boreal forest biome, ecosystem function and services, forest floor vegetation, functional trait analysis, global climate change, ground vegetation, hemiboreal, vegetation types, temporal vegetation dynamics

Introduction

Boreal forests are the largest forest biome of the northern hemisphere (Keenan et al. 2015). They are under increasing anthropogenic pressure (Potapov et al. 2008, Seidl et al. 2017) which is likely exacerbated by accelerating global environmental change (Moen et al. 2014). Understanding how boreal forests respond to these changes is crucial for mitigating undesired loss of biodiversity and ecosystem functions. In this context, understory plant communities are particularly important because they host most plant species (Gilliam 2007), and play a key role in decomposition, nutrient cycling and successional development (Wardle et al. 2003, Nilsson and Wardle 2005, Cornwell et al. 2008, Wardle et al. 2012).

Environmental changes such as shifts in land use, eutrophication and climate change all influence forest vegetation (Gilliam 2016, Hedwall and Brunet 2016, Naaf and Kolk 2016). Modern intensive forestry has greatly altered landscape dynamics and ecosystem functions (Gilliam 2016). Increased productivity has led to greater timber volumes and denser stands, and landscapes with more evenly-aged forests (Felton et al. 2017). The composition and abundance of the forest understory vegetation are, besides edaphic conditions (Walter 1979), largely determined by canopy tree species composition and closure (Hart and Chen 2006). Thus, changes in forest structure are often important drivers of understory changes (Oberle et al. 2009, Hedwall et al. 2013, Perring et al. 2018).

Nitrogen (N) availability strongly influences the productivity (Tamm 1991) and understory species composition of northern forests (Bobbink et al. 2010). Hence, anthropogenic increases in nitrogen deposition may have large effects on forest vegetation (Bobbink et al. 2010). Climate change, wildfire suppression, ungulate overabundance, drainage, and introduction of exotic species may also all contribute to vegetation changes in forests (Gilliam 2016). The importance and roles of these drivers, and their interactions, depend on factors such as the current forest management system (Chaudhary et al. 2016), former forest use (Vellend et al. 2007), and site conditions (Naaf and Kolk 2016).

How vegetation changes scale to effects on ecosystem processes is determined by to what degree these alterations of species relative abundances come along with changes in functional composition (Suding et al. 2008). Specific leaf area (SLA) is for example strongly associated with nutrient turnover and growth rates (Lavorel and Garnier 2002). Plant-trait composition in North American and European forests has shifted in recent decades toward increased dominance of species with high SLA (Amatengelo et al. 2014, Hedwall and Brunet 2016). This indicates that nutrient-demanding species have replaced nutrient-conservative species such as dwarf shrubs, which could have implications for ecosystems' carbon sequestration dynamics by increasing decomposition rates and carbon turnover (Wardle et al. 2012, Wardle et al. 2004, De Deyn et al. 2008, Jonsson and Wardle 2009).

Despite their potential consequences for biodiversity and ecosystem functions, long-term, large-scale analyses of changes in forest floor vegetation are rare (Lindenmayer et al. 2010, Amatengelo et al. 2014, Hedwall and Brunet 2016, Li and Waller 2016, Verheyen et al. 2017). The few studies examining combined effects of anthropogenic stressors on forest vegetation have focused on trees (Lindbladh et al. 2014, MacIntyre et al. 2015) or the species richness of understory vegetation (Rogers et al. 2008). How understory vegetation composition has changed is little studied, despite its importance to predict future impacts of global environmental change on ecosystem functioning (Lindenmayer et al. 2010).

Sweden has some of the world's most anthropogenically-impacted boreal forests. Within the country, pressure generally declines from south to north. A long history of industrial forestry and nitrogen deposition (Granath et al. 2014; Fig. 1) has considerably increased timber volumes and stand densities. Hence, Swedish forests are a useful model to predict future vegetation changes in other regions that face increasing anthropogenic pressure under global environmental change. Moreover, systematic long-term (>50 years) vegetation data from the Swedish National Forest Inventory (NFI) provide excellent opportunities to assess changes in understory plant communities under persistent pressure from anthropogenic stressors.

In this paper, we investigate how cover of 13 vegetation types, including functionally-important species groups, has changed in Swedish forests over the last 50 years. We anticipate that light-demanding, nutrient-conservative vegetation has decreased due to denser forests and high nitrogen deposition. We also expect the changes to be more pronounced in the south, where these drivers have been, and still are, much stronger than in the north. Finally, to evaluate effects of changes in understory composition on ecosystem function, we examined changes in the abundance of dwarf shrubs and community aggregated SLA. If our expectations concerning changes in vegetation types are confirmed, we anticipate a reduced cover of dwarf shrubs and an increase in mean SLA implying effects on ecosystem processes and services.

Material and methods

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 and 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 ~12.5 kg ha^{-1} yr^{-1} in the far south to just above ambient levels in the far north (Akselsson et al. 2010). Since the 1960s, Swedish forestry has been based on clearcutting, with associated activities like soil scarification, artificial regeneration, and repeated thinning operations (Royal Swedish Academy of Agriculture and Forestry 2015). This type of forestry is currently conducted on >80% of productive forest land in Sweden, and about 90% of the annual growth (ca. 120 million m^3) is extracted each year (SFA 2014). The efficiency of this forest management system has led to productivity doubling since the 1920s (SLU 2017), resulting in denser and darker forests (Hedwall and Brunet 2016). In addition, there has been a substantial change in the age structure of Swedish forests since the 1950s, with young forest (0-20 years) area increasing by 74% and old forest (>80 years) decreasing by 31% (SFA 2014; The National Board of Private Forestry 1959; Appendix S1: Fig. S1).

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). Since 1983, these temporary plots have been supplemented by a network of permanent plots surveyed every 5 to 10 years (Fridman et al. 2014). In our study, we used plots on productive forest land (23.2 Mha), of which ca. 4% is now formally protected in reserves, and around 13% is retained or set aside for conservation by forest owners (Claesson et al. 2015). Between 1953 and 1962 vegetation in all inventoried forest plots (6.64 m radius) was 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 (Table 1). We refer to this as the “old data”. Data collected between 2003 and 2012 (hereafter the “modern data”) include more detailed information on the understory vegetation than the old data, and were collected recurrently in permanent plots at 10-year intervals (Fridman et al. 2014). 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 and Löfgren 2009). For further information and critical evaluation on modern NFI permanent plots and survey methods, see SLU (2015) and Milberg et al. (2008). To compare the old and modern datasets, 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. However, for the vegetation types "Grasses" and "Heather" the documentation from the 1950s was incomplete, so we assumed that the former included all graminoids (e.g. *Poaceae* spp., *Cyperaceae* spp., *Juncaceae* spp.), and the latter included *Erica* spp. (rather uncommon) in addition to *Calluna vulgaris* (common). These assumptions probably had little influence on the results, but possibly, they imply that we might overestimate the cover of these two types in the modern data. The classification into one of the forb types (Table 1) is highly dependent on the presence of indicator species. As the chance of recording the presence of a species increases with plot size, the smaller plots (see above) in the modern data may have led to underestimation of these types.

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 was chosen to cover one inventory cycle, and accordingly no single plot has been included more than once. To account for differences in climate, nitrogen deposition and land-use history we divided Sweden into two regions, boreal and hemiboreal (Fig. 1), and classified the plots into three age classes (0-20, 21-80 and >80 years) based on increment core data from the stand-age assessment done by the NFI. The hemiboreal region in Sweden is a transition zone between the temperate and boreal biomes (Ahti et al. 1968). It covers most of southern Sweden (Fig. 1), except for a small temperate area along the southern and southwestern coasts. The vegetation of these areas has, however, been strongly "borealized" (i.e. converted to coniferous forest) by forest management and other human impact (Lindbladh et al. 2014), so the few temperate plots were merged with the hemiboreal region in our analyses. The vegetation inventories have been restricted to productive forest land (annual timber production capacity >1 m^3 ha^{-1}), whose coverage has increased – slightly in the boreal region (by 0.7%) and substantially (by 11.2%) in the hemiboreal region – between the two inventories in this study according to our analyses.

The plots are clustered into the outline of a square (Appendix S2: Fig. S). 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. Therefore, we summed the forest area that each vegetation type represented within each region (hemiboreal and boreal) and year using pre-calculated area factors from the NFI database, following a previously described procedure (Toet et al. 2007). In brief, we weighted the contribution of each plot by the forest area that it represents. The relative area within each vegetation type was then calculated for each year in the old (1953–1962) and modern (2003–2012) periods. These annual estimates (10 observations per period) were used in the statistical analyses.

Generalized Linear Models (GLMs, with quasibinomial distribution due to underdispersion, and logit link) were used to model the effect of time on the proportion of each vegetation type. In the models, we used time as a categorical variable with two levels, indicating the beginning and end of the study period, respectively. Time was nested within region, resulting in one intercept and one regression slope for each of the two regions (hemiboreal and boreal). Effects on the response variables were deemed significant if $P \leq 0.05$. The share of the bearberry (*Arctostaphylos uva-ursi*) class (Table 1) was too low to allow statistical analyses in any of the regions, and crowberry (*Empetrum* spp.) could only be analyzed in the boreal region.

To clarify the importance of different drivers and to improve our interpretation of the temporal trends by linking changes in composition to specific mechanisms, we used the modern NFI data to calculate mean indicator values for light requirement, nutrient requirement (Ellenberg et al. 2001), disturbance (Tyler et al. 2018), and seed bank longevity (LEDA trait database, Kleyer et al. 2008) for each vegetation type within the two regions. Individual species' indicator values range from 1 to 9 with higher values indicating higher values of each resource requirement or trait. Overall vegetation type values were calculated as arithmetic means of all species present in at least 5% of the plots in a given type. We used non-metric multidimensional scaling (NMS) to illustrate differences in the combined mean indicator values among the 12 vegetation types.

We calculated mean 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). We analyzed change in mean SLA between the old and modern periods using a GLM with a gamma error distribution and log link. Dwarf shrubs are a relatively homogeneous group and important indicator of environmental changes (Hedwall et al. 2017), and cover estimates are available from NFI data. To estimate the change in dwarf shrub cover, we calculated the aggregate cover of all species of *Calluna*, *Empetrum*, *Erica* and *Vaccinium* for the two time periods by using vegetation type-specific values 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). These products were then summed estimate cover at the landscape level, and further analyzed by applying a GLM using a quasibinomial error distribution, following the procedure described above. These analyses assume that cover of dwarf-shrubs was stable within vegetation types over time. To test the validity of this assumption, we used GLMs to examine trends in the yearly mean of dwarf shrub cover between 1994 and 2013 for all 24 combinations of vegetation type (SLU 2015) and region (Ahti et al. 1968). Only four combinations showed a significant trend over time. The cover of dwarf shrubs decreased in the 'Dwarf shrub with low forbs' vegetation type in both regions, and in the bilberry and grass types in the boreal region. This suggests that we may have underestimated the decrease in total dwarf-shrub cover between the 1950s and 2000s, especially in the boreal region. Thus, our reported changes should be regarded as conservative estimates. All statistical analyzes were performed using R version 3.2.2 (R Core Team 2015). The GLMs were done with the glm() function in the stats package (R Core Team 2015) and the NMS was done with the metaMDS() function in the Vegan package (Oksanen et al. 2018)

Results

Nine out of 12 vegetation types in the boreal region, and ten out of 11 in the hemiboreal region, showed significant changes in proportion of forest land between the old and modern periods (Fig. 2, AppendixS3: Table S1). Moreover, the summed changes (increases + decreases) were greater in the southern hemiboreal (85%) than in the northern boreal (56%) region. Six types in the boreal region and five types in the hemiboreal region decreased in extent, while in both regions four types increased. The dwarf shrub with low forbs type decreased most in both regions; its share declined from 31 to 21% in the boreal region, and from 37 to 7% in the hemiboreal region. In both regions, the low forb and tall forb types showed the largest increases.

Shares of the low forb type increased from 2 to 18% and 12 to 31% percent in the boreal and hemiboreal regions, respectively, while those of the tall forb type increased from 1 to 6% and from 4 to 16%, respectively. Diverging patterns between the regions were found for the cowberry and low cover types (Fig. 2). The cowberry type increased in the boreal, but decreased in the hemiboreal region, while the share of the low cover type increased by 9% in the hemiboreal region, but did not significantly change in the north. Overall changes in vegetation types were similar among forest age classes. Of a total of 78 age class comparisons (13 vegetation types x 3 age-classes x 2 vegetation regions), only 8% deviated from the general pattern within the vegetation type (Appendix S4: Fig. S1).

The first ordination axis of the NMS based on mean indicator values orders vegetation types along a spectrum of decreasing light availability and increasing nutrient availability (Fig. 3). Vegetation types whose share increased are generally connected to high nutrient availability and low light availability, except for the cowberry type in the boreal region. Vegetation types with decreasing and stable shares are more evenly spread along axis one, but absent at high values, except for the dwarf-shrub tall-herb type. The positions of the dwarf-shrub types with low or tall forbs along the first axis indicate that these vegetation types have lower nutrient and higher light requirements than the forb types without dwarf shrubs. The second axis orders vegetation types along a gradient of increasing adaptation to disturbance, also indicated by a more persistent seed bank, without a clear pattern concerning temporal trends of different types. The grass type, which decreased, was the only vegetation type that showed clear association with disturbance (Fig. 3).

The cover of all dwarf shrubs combined decreased significantly in both the boreal ($P = 0.014$) and hemiboreal ($P < 0.001$) regions. The change was largest in the hemiboreal region, where the cover decreased from 27 to 14%, while cover in the boreal region decreased from 38 to 32% (Fig. 4). In addition, the abundance-weighted SLA increased markedly over time ($P < 0.001$). Again, the change was larger in the hemiboreal region, where the mean SLA grew from 17.3 to 19.8 mm^2 mg^{-1}, than in the boreal region (15.4 to 16.8 mm^2 mg^{-1}; Fig. 5). The largest changes in the hemiboreal region occurred at low SLA values, and the area with a mean SLA <17 mm^2 mg^{-1} decreased from 68 to 31% (Fig. 5).

Discussion

Our results provide clear evidence of changes in the forest understory vegetation since the 1950s, at scales and magnitudes not previously documented in the boreal biome. The vegetation has changed from dominance by nutrient-conservative and light-demanding species (e.g. dwarf shrubs with low SLA), towards a higher share of shade-adapted, nutrient-demanding species (e.g. forbs with high SLA), which agrees with our expectations. The study period coincides with the introduction and subsequent dominance of mechanized industrial clear-cut forestry and eutrophication from increased nitrogen deposition, which we suggest have been the main drivers of the observed changes. The magnitude of trait composition change suggests that distinct changes in ecosystem functions of Swedish forests have occurred, including increased understory productivity, altered carbon cycling, and reduced berry production.

Drivers

As the forest overstory strongly influences the composition and abundance of the understory vegetation (Hart and Chen 2006), the shift toward more shade-tolerant vegetation types seen in our data is probably caused by increases in timber volume and denser, darker forests (Reinkainen et al. 2000, Sandström et al. 2016, Tonteri et al. 2016, SLU 2017). Support for this hypothesis is also provided by the minor forest age-related variations, as more than 90% of vegetation-type comparisons between the 1950 and 2000 periods revealed similar trends across age classes. Industrial forestry, using the clearcutting system, is practiced on more than 80% of the productive forestland in Sweden (SFA 2014), and there is a longer history of intensive forestry in the Fennoscandian countries than elsewhere in the boreal biome (Hagner 1999). Large-scale planting of nursery-grown seedlings has increased wood production, and resulted in a 70% increase in overall timber volume in Swedish forests during the study period (SFA 2014). This has also caused a shift toward younger and denser forests (Appendix S1: Fig. S1), which is part of a widespread trend in European and North American forests (Rautiainen 2011). However, the trend toward denser forest canopies predates large-scale introduction of plantation forestry in Sweden. Since the 1800s, smaller and less frequent forest fires, conversion of arable land, semi-natural grasslands and heathlands to forest, and cessation of forest grazing by livestock have all contributed to denser tree canopies (Appendix S5; Lindbladh et al. 2011, 2014). Since the start of our time series in the 1950s, ecological legacy effects of these processes may still have contributed to the vegetation shifts we recorded (Eriksson 1996).

According to the ordination analysis, grass was the vegetation type most clearly associated with disturbance. Disturbance by fire has long shaped the structure and composition of boreal forests (Shorohova et al. 2011), but the frequency of fires has decreased dramatically in many boreal regions due to changes in land use and active fire suppression (Appendix S5, Appendix S6; Cumming 2005). In Sweden, the loss of forest fires has led to increased tree densities (Hedwall and Mikuśinski 2016), and to an increase of the shade-tolerant, fire-sensitive Norway spruce (*Picea abies*) in formerly more open Scots pine (*Pinus sylvestris*)-dominated forests (e.g. Linder et al. 1997). This concurs with observations following fire exclusion elsewhere, for example in oak savanna, longleaf pine, ponderosa pine, and Douglas-fir forests in the USA (Peterson and

Reich 2001, Varner et al. 2005, Keeling et al. 2006). Moreover, fire intensity and frequency directly affect the productivity and composition of understory vegetation (Schimmel and Granström 1996). While grasses may benefit from low-intensity fires in the short term, more severe fires can favor dwarf shrubs in the long term as the latter have deeper rhizomes and budbanks than the most common grass, *Avenella flexuosa*, in these ecosystems (Schimmel and Granström 1996). Hence, it is possible that a forest landscape with a large variation in fire frequency and severity can simultaneously have larger shares of both grass and dwarf-shrub dominated vegetation types than we see in Sweden today. Additionally to causing an increase in forest density (i.e. the number, volume or basal area of trees per area unit), the decrease in forest fires may thus also have contributed directly to the decrease of these vegetation types.

Eutrophication from nitrogen deposition decreases the competitive ability of dwarf shrubs in relation to graminoids and forbs (Bobbink et al. 2010). Thus, nitrogen deposition is likely another important driver of the dramatic decline in dwarf shrubs we recorded, especially in the hemiboreal region, where nitrogen deposition rates are considerably higher than in the boreal region (Appendix S7: Fig. S1). Besides the direct eutrophication effects on the forest floor, nitrogen deposition can indirectly affect understory vegetation by enhancing tree growth (Thomas et al. 2010, From et al. 2016), thereby reducing light availability for ground vegetation, although the realization of such effects depends on forest management (e.g. thinning operations). High forest density and low light availability can suppress effects of eutrophication on the understory vegetation (Strengbom et al. 2004, Verheyen et al. 2012), which may explain why the disturbance-favored grass type declined, despite increased nitrogen availability. Responses similar to our observations seem likely under elevated nitrogen input wherever it is a growth-limiting factor, including large parts of the boreal biome (Vet et al. 2014).

Climate change has likely contributed to the observed changes, as the increase in annual mean temperature in Sweden exceeded 1 °C during our study period. At the same time, the period of snow cover has become shorter in southern Sweden (SMHI 2015), a change that may be more important for vegetation than increased temperature per se (Kreyling et al. 2012). The response of the vegetation to a warmer climate will largely resemble that due to nitrogen deposition (i.e. eutrophication effects; cf. Walker et al. 2006, Hedwall et al. 2015), and we cannot exclude the possibility that some of the effects we attribute to eutrophication are due to climate change. As most evidence of climate driven eutrophication effects originates from northern ecosystems with low nitrogen deposition it is, however, largely uncertain how these drivers may interact. While effects of nitrogen deposition decrease with distance from pollution sources (Dentener et al. 2006), climate change is a global phenomenon, and thus will affect remote northern forests.

Functional implications

Shifts in plant community trait composition can lead to changes in important ecosystem processes, such as litter decomposition and nutrient turnover (Lavorel and Garnier 2002, Quested et al. 2007). The 50-year shift toward higher SLA seen in our data has probably induced positive feedback effects on ecosystem productivity and aboveground carbon sequestration. Litter with traits typically associated with high nutrient availability, e.g. high SLA, decomposes and turns over nutrients faster, while litter with nutrient-conservative traits (e.g. low SLA), decomposes more slowly (Wardle et al. 2012, Reich et al. 1995). Hence, changes in trait composition may substantially affect ecosystems' carbon sequestration dynamics (Wardle et al. 2012, Wardle et al. 2004, De Deyn et al. 2008, Jonsson and Wardle 2009). In this context, reduced cover of dwarf shrubs may be especially important, as they significantly contribute to net primary production of Swedish forests (Nilsson and Wardle 2005, Wardle et al. 2012). In addition, replacing dwarf shrubs with vegetation that produces faster-decomposing litter can increase the turnover rates of soil carbon (Nilsson and Wardle 2005), which can have implications for ecosystem-level carbon sequestration as the soil is a major carbon pool in northern ecosystems. Further, dwarf shrubs provide food for many forest species (Atlegrim 1989, Lakka and Kouki 2009, Selås et al. 2011) and produce berries (especially the dominant bilberry *Vaccinium myrtillus* and cowberry *V. vitis-idaea*) that have high potential economical revenue (Miina 2010), and societal value associated with berry picking (Pouta et al. 2006). Hence, beside the potential impacts on biochemical processes and vegetation structure, it is likely that reduced dwarf shrub cover has also had significant impact on populations of other organisms, and ecosystem services associated with berry production.

The future of northern forests?

Our study is among the first to quantify large-scale effects on forest vegetation of changing light and nutrient conditions over a period of several decades. The trend toward understory vegetation adapted to less light and more nitrogen in Sweden during the past 50 years stemmed primarily from combined effects of the introduction of industrial forestry and increased nitrogen deposition. However, climate change, the legacy of past agricultural practices, and fire dynamics may also have contributed to the observed changes.

Forest density is increasing in many northern forest regions (Rautiainen et al. 2011, Bose et al. 2017, SLU 2017), and is often accelerated by climate-change induced increase in forest productivity (Gauthier et al. 2015, Gonsamo et al. 2017). Projected increase in productivity under climate warming may also allow further expansion of industrial forestry operations into areas where productivity is currently too low (Raunikar et al. 2010). Although multiple other trajectories, differing from what we report from Sweden, are possible, global climate change will affect vast areas of the boreal biome currently minimally-affected by anthropogenic pressures.

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Data availability

The data used in this article can be accessed from ResearchGate:

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Table 1. The vegetation classification scheme used in the field by the Swedish National Forest Inventory (NFI) from 1953-1962 and applied in this study to classify NFI plots post-hoc from 2003-2012. Species nomenclature is according to Karlsson and Agestam (2014).

	Vegetation type 1953-1962	**Classification applied to 2003-2012**
1	Rich forb	occurrence of at least one of the indicator species[1]
2	Tall forb	not as 1 and occurrence of at least two of the indicator species[2], one species is enough if its cover ≥ 2 m^2
3	Low forb	not as 1-2 and occurrence of at least two of the indicator species[3], one species is enough if its cover ≥ 2 m^2
4	Dwarf-shrubs with tall forbs	as 2 but dwarf-shrub[4] cover ≥ 1/4
5	Dwarf-shrubs with low forbs	as 3 but dwarf-shrub[4] cover ≥ ¼
6	Grass	not as 1-5 and grass[5] cover ≥ ¼
7	Low vegetation cover	not as 1-6 and dwarf-shrub[4] cover < 1/16
8	Bearberry	not as 1-7 and dwarf-shrub[4] cover ≥ 1/16 and ≥ 1/4 of these is *Arctostaphylos uva-ursi*[6]
9	Crowberry	not as 1-7 and dwarf-shrub[4] cover ≥ 1/16 and ≥ 1/4 of these is *Empetrum nigrum* ssp.[6]
10	Bog-billberry/Labrador tea	not as 1-7 and dwarf-shrub[4] cover ≥ 1/16 and ≥ 1/4 of these is *Vaccinium uliginosum* and *Rhododendron tomentosum*[6]
11	Bilberry	not as 1-10 and dwarf-shrub[4] cover ≥ 1/16 and *Vaccinium myrtillus* > *V. vitis-idaea* and *Calluna vulgaris*/*Erica* spp.
12	Cowberry	not as 1-10 and dwarf-shrub[4] cover ≥ 1/16 and *Vaccinium vitis-idaea* > *V. myrtillus* and *C. vulgaris*/*Erica* spp.
13	Heather	not as 1-10 and dwarf-shrub[4] cover ≥ 1/16 and *C. vulgaris*/*Erica* spp. > *V. myrtillus* and *V. vitis-idaea*

[1] *Anemone ranunculoides*, *Lamiastrum galeobdolon*, *Mercuralis perennis*, *Aegopodium podagraria*, *Galium odoratum*, *Sanicula europaea*, *Actea spicata*, *Cardamine bulbifera*, *Paris quadrifolia*

[2] 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)

[3] *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)

[4] *Vaccinium myrtillus*, *V. vitis-idaea*, *V. uliginosum*, *Calluna vulgaris*, *Erica* spp., *Empetrum nigrum* ssp., *Arctostaphylos uva-ursi*, *Rhododendron tomentosum*

[5] *Poaceae* spp., *Cyperaceae* spp., *Juncaceae* spp.

[6] if more than one of *Arctostaphylos uva-ursi*, *Empetrum nigrum* ssp. or *Vaccinium uliginosum* and *Rhododendron tomentosum* is ≥ 1/4 of the dwarf-shrubs the plot is classified by the most abundant species.

Fig. 1. Map of Sweden showing the gradient of average (2005-2014) total nitrogen deposition (a), and average timber volumes on productive forest land in 1953-1957 (b) and 2012-2016 (c). The dashed line indicates the border between the boreal and hemiboreal regions.

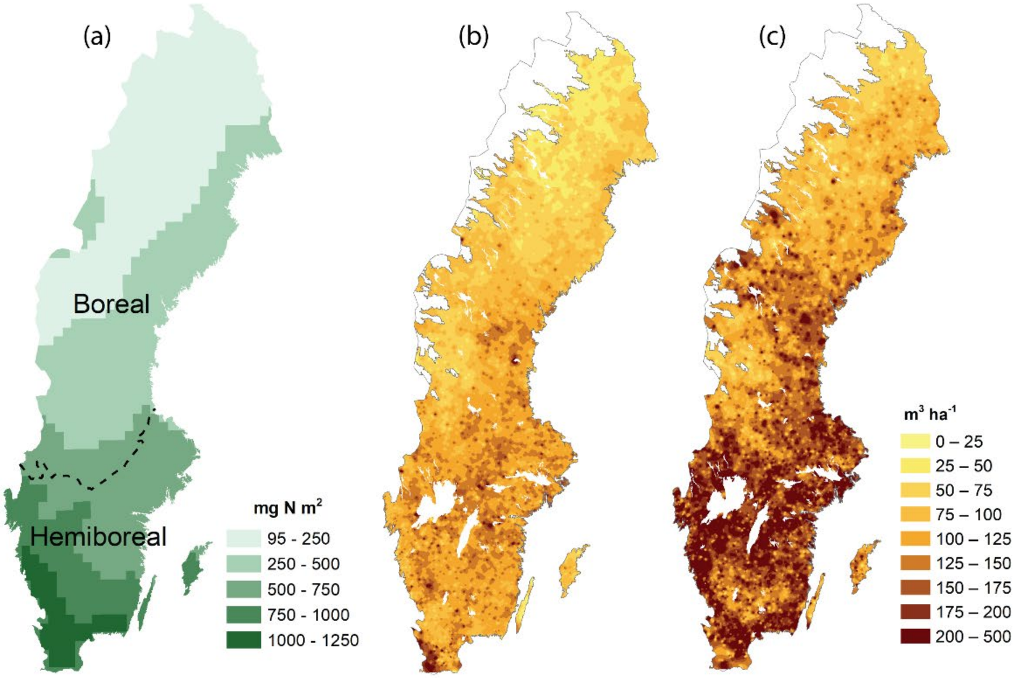
Fig. 2. Change in share of vegetation types in the boreal and hemiboreal regions of Sweden between the 1950s and 2000s. The red bars show decreases from right to left and green hatched bars show increases from left to right, as indicated by arrows. Yellow bars indicate statistically-insignificant changes. The vegetation types are ordered along the SLA gradient in Fig. 5.

Fig. 3. Non-metric multidimensional scaling of community averages of Ellenberg indicator values for light (L) and nutrients (N), as well as for indicators of disturbance dependence and seed bank longevity of the vegetation types in the modern data. Locations of decreasing (red), increasing (green) and stable (black) vegetation types are shown in ordination space, along with positions of the different indicators (blue).

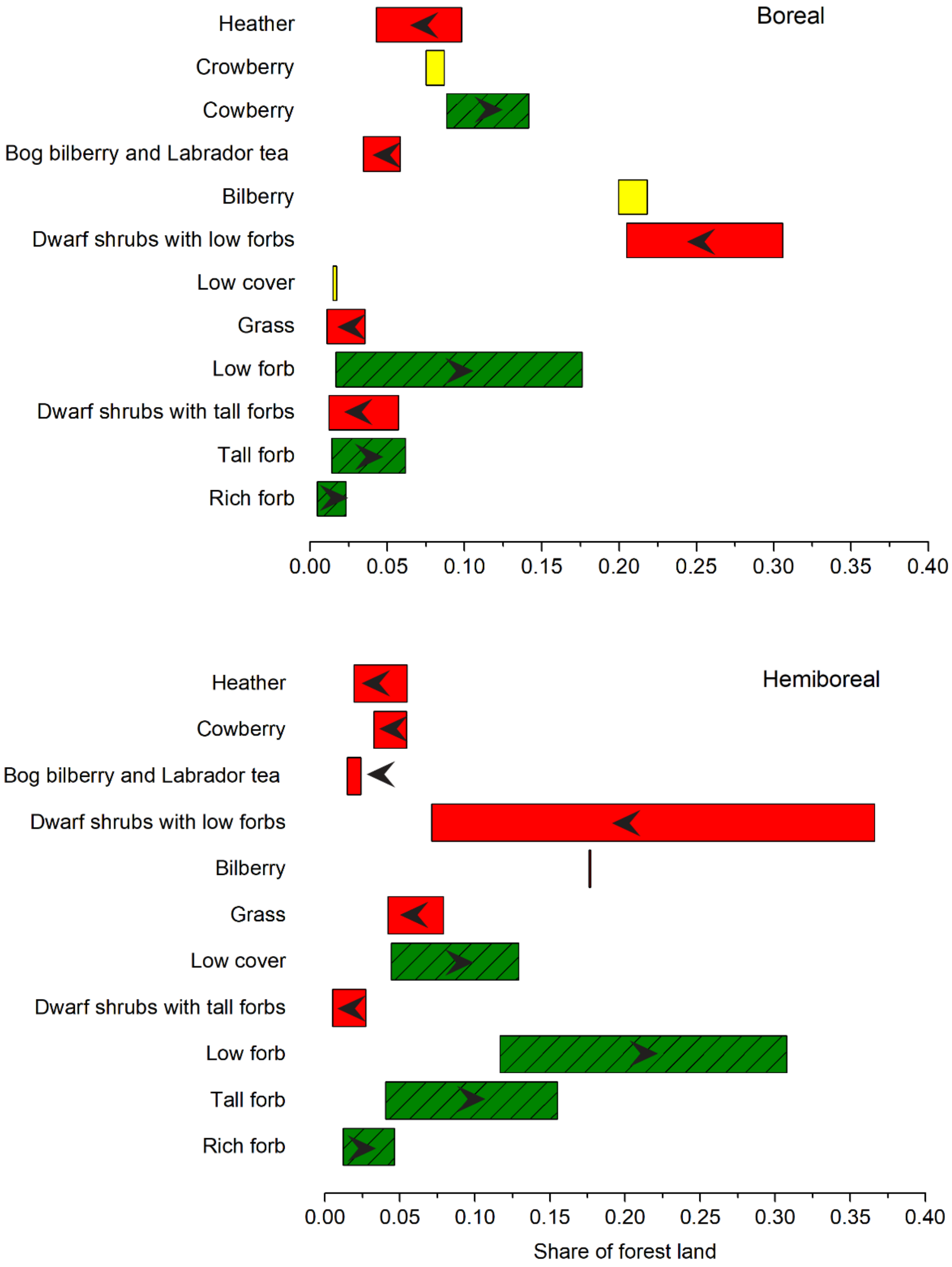
Fig. 4. Mean (±SE) cover of dwarf shrubs (*Vaccinium myrtillus, V. vitis-idaea, V. uliginosum, Calluna vulgaris, Erica spp., Empetrum nigrum ssp., Arctostaphylos uva-ursi, Rhododendron tomentosum*) in the 1950s and 2000s in the boreal and hemiboreal regions of Sweden.

Fig. 5. Changes in abundance-weighted mean SLA (±SE) between the 1950s and 2000s in the boreal and hemiboreal regions of Sweden (upper panel), and cumulative area distribution along the SLA gradient in the two time periods in the boreal region (middle panel) and hemiboreal region (lower panel). The black thick lines show mean values in each time period, while the thin colored lines indicate the variation among the 10 sample years.

Figure 1.

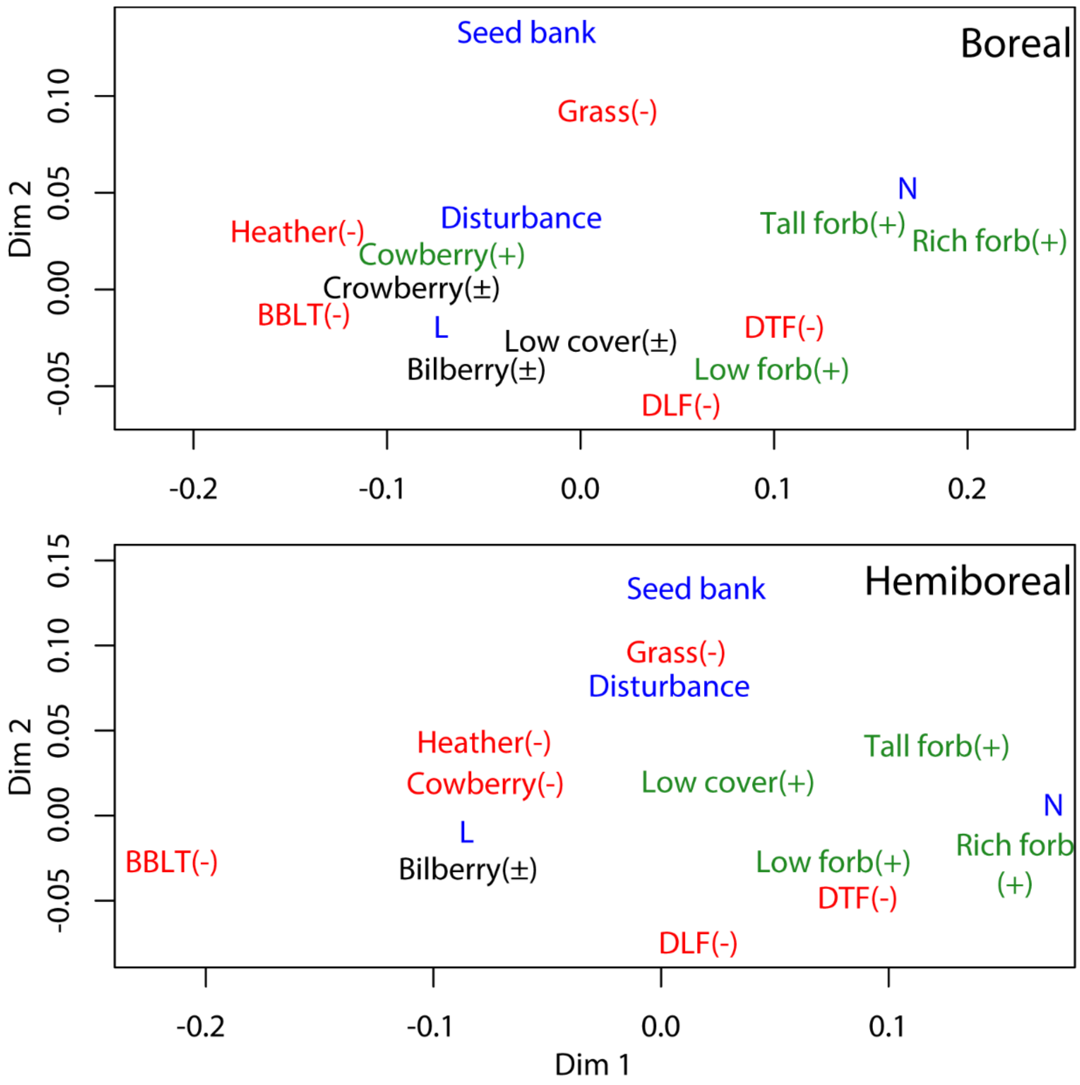

(a)
(b)
(c)
Boreal
Hemiboreal
mg N m^2
95 - 250
250 - 500
500 - 750
750 - 1000
1000 - 1250
m^3 ha^{-1}
0 – 25
25 – 50
50 – 75
75 – 100
100 – 125
125 – 150
150 – 175
175 – 200
200 – 500

666 Figure 2.



667

Figure 3.



Boreal
Seed bank
Grass(-)
N
Heather(-)
Disturbance
Tall forb(+)
Rich forb(+)
Cowberry(+)
Crowberry(±)
BBLT(-)
L
Low cover(±)
DTF(-)
Bilberry(±)
Low forb(+)
DLF(-)
Dim 2
0.10
0.05
0.00
-0.05
-0.2
-0.1
0.0
0.1
0.2
Hemiboreal
Seed bank
Grass(-)
Disturbance
Heather(-)
Tall forb(+)
Cowberry(-)
Low cover(+)
N
L
Rich forb
(+)
BBLT(-)
Bilberry(±)
Low forb(+)
DTF(-)
DLF(-)
Dim 2
0.15
0.10
0.05
0.00
-0.05
-0.2
-0.1
0.0
0.1
Dim 1

Figure 4.

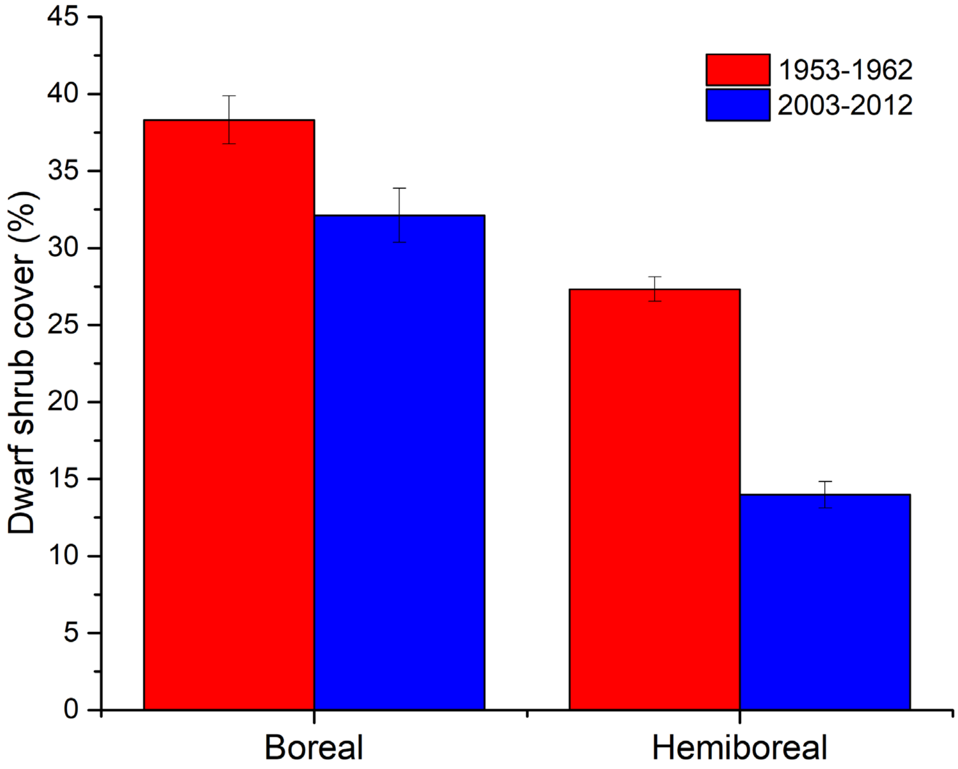
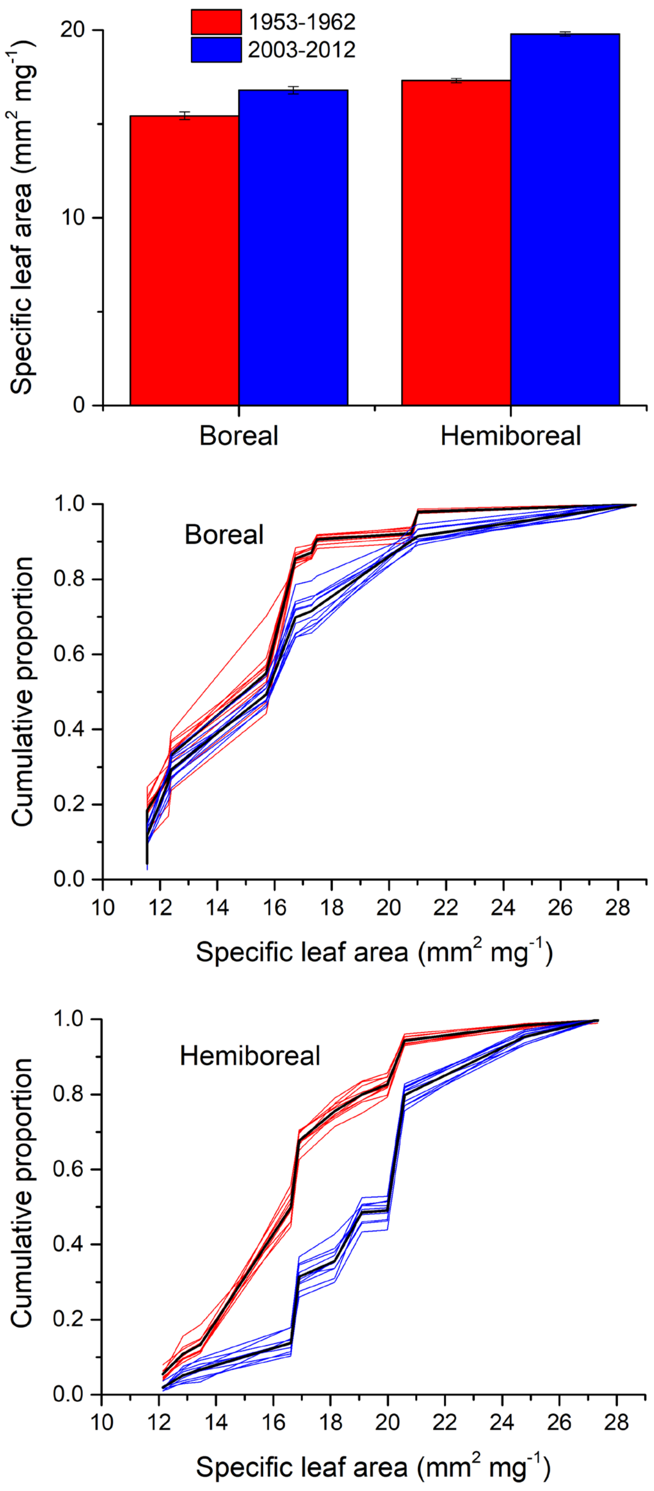

Dwarf shrub cover (%)
0
5
10
15
20
25
30
35
40
45
1953-1962
2003-2012
Boreal
Hemiboreal

Figure 5.



1953-1962
2003-2012
Specific leaf area (mm^2 mg^{-1})
0
10
20
Boreal
Hemiboreal
Cumulative proportion
0.0
0.2
0.4
0.6
0.8
1.0
Boreal
10
12
14
16
18
20
22
24
26
28
Specific leaf area (mm^2 mg^{-1})
Cumulative proportion
0.0
0.2
0.4
0.6
0.8
1.0
Hemiboreal
10
12
14
16
18
20
22
24
26
28
Specific leaf area (mm^2 mg^{-1})