Changes in the abundance of keystone forest floor species in response to changes of forest structure

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Abstract

Question: Does the abundance of keystone forest floor species change in response to changes in the forest structure?

Location: Sweden

Methods: We used data from the Swedish National Forest Inventory to investigate changes in the abundance of three common species, as well as the total abundance of all understorey vascular plants (the field layer) in forests in the boreal and temperate parts of Sweden. GLMs and GAMs were used to relate species abundance and temporal changes in abundances to forest structure and forest structural change.

Results: Productivity, measured as the site index, was the most important determinant of individual species' abundance. The volume of *Picea abies,* the density of tree stems and forest age were among the most important forest structural variables. We found that the dwarf shrub *Vaccinium myrtillus,* the narrow-leaved grasses (mainly *Avenella flexuosa*) and the total field layer cover decreased in boreal Sweden from 1994 through 2010 and that these changes coincided with an increase in forest density and with a reduction in forest age.

Conclusions: Changes in Swedish forests to higher tree layer density and younger age appear to contribute significantly to current changes in forest floor vegetation. The use of more intensive thinning practices to reduce the total density of the forest and to increase the proportion of broad-leaved tree species and *Pinus sylvestris* would favour the forest floor species in this study. Moreover, increasing forest age (i.e. the length of rotation periods) might favour *V. myrtillus* in particular, for which the time since disturbance is important for the recovery of pre-disturbance abundance. However, increased thinning intensity and forest age will reduce the potential for wood production, implying a trade-off between production of wood and maintenance of well-developed forest floor vegetation.

Introduction

The vegetation of the forest floor contains a large fraction of the plant species in temperate and boreal forests (Gilliam 2007). The forest floor vegetation is also important for nutrient and carbon cycling in forests (Nilsson & Wardle 2005; Kolari et al. 2006) and as a food source for herbivores (Selås 2001; Selås et al. 2011). The tree layer is a key factor influencing the abundance and the species composition of forest floor vegetation (Hart & Chen 2006). Therefore, changes in forest structure are expected to affect the forest floor vegetation. However, this effect is not one-sided; dense forest floor vegetation may deprive seedlings of tall-growing woody species of light and thus influence the development of the tree layer (George & Bazzaz 2003; Royo & Carson 2006).

Over wide areas of boreal and temperate biomes, changes in both land use and forest management have altered stand structure and tree species composition (Östlund et al. 1997; Hessburg et al. 2000; Etheridge et al. 2005; Rogers et al. 2008; Moen & Keskitalo 2010; Verheyen et al. 2012). Industrial forestry traditionally targets monospecific, even-aged and fast-growing forests (Puettmann et al. 2009) through the use of genetically improved seedlings, soil scarification and fertilization. These measures bring about increased growth rates, increasing stand density and shorter rotation periods. Additionally, a change to a warmer and wetter climate

may result in increased net primary production (Boisvenue & Running 2006; Bergh et al. 2010; McMahon et al. 2010). Consequently, many countries presently report an increase in volumes of standing wood (Gold et al. 2006; Anonymous 2009; Rautiainen et al. 2011). Simultaneously with changes in forests used primarily for production, tree density may increase in forest reserves because of fire control and general lack of management (Linder et al. 1997; Verheyen et al. 2012).

Sweden has the second largest areal cover of forests in Europe, surpassed only by Russia (Zanchi et al. 2007). The southern third of the country is a part of the temperate vegetation zone (the hemiboreal and temperate zones according to Ahti et al. 1968), which contains natural occurrences of *Quercus* spp. and other temperate hardwood species. The northern part of the country belongs to the boreal zone and is dominated by the coniferous species *Picea abies* (L.) H. Karst. and *Pinus sylvestris* L. Because of active forest management, these species also dominate the forests of southern Sweden. The standing volume of Swedish forests has increased by ca. 80% since the 1920s (Anonymous 2011a). In the temperate part of the country, this increase has been accompanied by a change in tree layer structure to forests with high canopy cover, while less favourable growth conditions limit the density and height of the tree layer in parts of boreal Sweden. Odell & Ståhl (1998) reported negative abundance changes for the most important vascular plant species of the forest floor over a 15-year period from 1983 to 1997, but they did not discuss if this decline was related to structural forest changes.

The main objective of this study is to relate changes in forest floor vegetation to changes in forest structure in Sweden, and to test if these changes differ between the temperate and boreal parts of the country.

Methods

Data from the Swedish National Forest Inventory (SNFI) were used to investigate changes in the forest floor vegetation and to model species–environment relationships. Response variables in this study were the abundances (measured as percentage cover, visually estimated) of three species or species groups [*Vaccinium myrtillus* L., *V. vitis-idaea* L. and narrow-leaved grasses (dominated by *Avenella flexuosa* (L.) Drejer); referred to as *species*], as well as the total cover of the field layer (all understorey vascular plants with an approximate maximum height of 1 m or less).

Selected species

The most common forest floor vascular plants in Sweden are the deciduous dwarf-shrub *V. myrtillus*, the evergreen dwarf-shrub *V. vitis-idaea* and the grass *A. flexuosa* (Odell &

Ståhl 1998). The two *Vaccinium* species are more abundant in mature than in younger forests. *V. myrtillus* abundance is reduced by clear-cutting (Kardell 1980; Atlegrim & Sjöberg 1996; Bergstedt et al. 2008; see, however, Bergstedt & Milberg 2001), whereas *A. flexuosa* is favoured by clear-cutting (Bergstedt & Milberg 2001). In boreal Europe, *V. myrtillus* often dominates the forest understorey where it functions as a keystone species because of its influence on the population dynamics of bank voles (*Myodes glareolus*) and capercaillie (*Tetrao urogallus*), and its role as an important food source for ungulates such as moose (*Alces alces*; Selås 2001; Selås et al. 2011), red deer (*Cervus elaphus*; Hegland et al. 2010) and roe deer (*Capreolus capreolus*; Mysterud et al. 1997).

Swedish National Forest Inventory

The SNFI collects data on forest structure and environmental variables in a nationwide network of permanent and temporary sample plots. Detailed information on the forest floor vegetation is collected recurrently in permanent plots at intervals of 10 yr. For this study, we used plots outside of formally protected areas (nature reserves and national parks) and on productive forest land (estimated production capacity >1 m$^3 \cdot$ha$^{-1} \cdot$yr^{-1}); which made up a subset in which ca. 97% of the Swedish productive forest area is represented, and of which ca. 5% was voluntarily set aside for nature conservation by the forest owners (Anonymous 2010). The plots were aggregated in square-shaped clusters with eight plots in each square, all of which are located along the border of the square. The edge of each square was 300–1200-m long, and the distance between squares varied between regions (Fig. 1; Ranneby et al. 1987), with an average of 14 800 m between the square centres in the northernmost region and 6200 m in the south of Sweden.

Each SNFI plot has a radius of 10 m. For this study data on the volumes of each tree species, stand age and stem density were used together with data on soil properties (Table 1). Some topographic variables, such as the slope and ground surface structure, were estimated in plots with a radius of 20 m with the 10-m plot in the centre (Table 1). The cover of forest floor species was estimated in one circular permanent plot with a radius of 5.64 m (and area 100 m^2), with the same centre as the 10- and 20-m plots. Cover was estimated as the vertical projection of each species/group of species, in 1% classes. Ground without a proper forest floor, such as roads, ditches and disturbed soil resulting from soil scarification, were excluded when cover was estimated. For further information on SNFI vegetation survey methods, see Odell & Ståhl (1998) and Anonymous (2011b). Arithmetic averages across regions (sampling strata) were made by weighting each plot by the forest area it represents, in order to compensate for uneven sampling
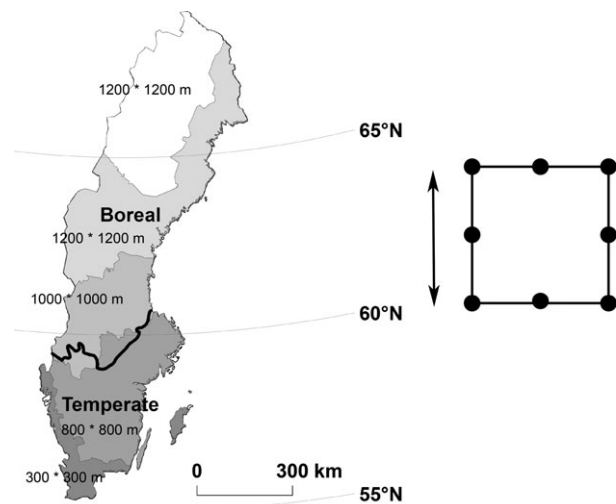
Fig. 1. A map of Sweden showing regions in which different edge lengths of sample clusters were used in the Swedish National Forest Inventory. The thick black line marks the border between the boreal and temperate vegetation zones according to the National Atlas of Sweden (1996).

intensity. Averages for the basal area weighted age were also calculated by weighting the age with the basal area of the geographical units (boreal, temperate). To avoid (potential) spatial correlation in the data, cluster means were used in all analyses of temporal trends.

Modelling of species–environment relationships

The shape of species–environment relationships often departs from the frequently assumed unimodal shape towards skewedness or bimodality (Austin 2002; Rydgren et al. 2003). More flexible functions than symmetric, bell-shaped curves have therefore been advocated (Austin 2007). In this study, we used Generalized Additive Models (GAMs) (Wood 2006) as implemented in the mgcv (Wood 2006) package in R 2.15 (R Development Core Team, R Foundation for Statistical Computing, Vienna, AT). A GAM is a generalization of a Generalized Linear Model (GLM) in which the assumption of a linear relationship between predictors and the (transformed) response variable is relaxed. Our GAM models were built without prior assumptions about the shape of the species–environment relationship. GAMs add smooth components to a linear model and therefore, in principle, no restriction exists in the shapes that they can take. To avoid over-fitting, model complexity was restricted by applying the procedure for generalized cross-validation in mgcv, to optimize the smoothing parameter.

Data from permanent SNFI plots sampled between 2000 and 2009 were used for modelling the responses of *V. myrt-illus* and *V. vitis-idaea*, narrow-leaved grasses and field layer abundance. Because our objective was to model the relationship between species abundances and forest structure, we excluded plots with a mean tree height of <3 m. The

Table 1. Variables used in modelling, with descriptive statistics; see Anonymous (2011b) for more detailed information.

Variable	Description	Unit	Range in inventory data	
			Min	Max
Age	Basal area weighted age	Years	0	200
Broad-leaved tree volume	Volume of all broad-leaved deciduous trees, primarily *Betula* spp.	$m^3 \cdot ha^{-1}$	0	400
Picea abies volume	Volume of all *Picea abies* trees	$m^3 \cdot ha^{-1}$	0	400
Pinus spp. volume	Volume of all trees of the genus *Pinus*, primarily *P. sylvestris*	$m^3 \cdot ha^{-1}$	0	400
Stem density	Number of stems of all tree species with a DBH >5 cm	Stems·ha^{-1}	0	4000
Ground surface structure	5 Classes, ranging from even to uneven		1	5
Site index	The dominant height of *P. abies* at a total age of 100 yr, estimated according to Hägglund & Lundmark (1977)	m	8	39
Slope	6 Classes, increasing steepness		1	6
Soil moisture	5 Classes, ranging from dry to wet		1	5
Soil texture	8 Classes, ranging from boulders/rocks to clay		1	8
Soil water mobility	3 Classes, ranging from seldom/missing to longer periods		1	3
Thickness humus layer	Thickness of the humus layer in cm	cm	0	99
Altitude	Meters above sea level	m	0	780
Latitude	Coordinates in RT90, increasing northwards		6 141 403	7 591 577
Longitude	Coordinates in RT90, Increasing eastwards		1 231 255	1 876 551

data set therefore consisted of ca. 6500 plots. Model selection was made by backward elimination; variables individually significant at the α = 0.01 level were retained in the model. Additionally, a hierarchical variation partitioning (HP) was performed to quantify each variable's contribution to the models. To prevent the remaining variables from compensating for the exclusion of a variable in the HP, the exact degrees of freedom (EDF) of the final models were used. The EDFs describe the complexity of the species–environment relationship in terms of the number of smooth parameters, where EDF = 1 is a straight line. By repeatedly applying HP and rebuilding the models, we excluded variables that contributed less than 1% of the total explained deviation of the model. Based upon a pre-analysis graphical data exploration, the Gaussian distribution with identity link was chosen for analysis of field layer abundance and the γ-distribution with log link for the species. Model residuals were checked for normality (Gaussian distribution) using Q-Q plots, and homoscedasticity was checked by plotting Pearson residuals against the linear predictor. For each model, the variables included and their significance, the EDFs, or in the case of linear terms, the estimated parameter, are reported.

Analyses of temporal trends

The GLMs (Venables & Ripley 2002) were used to investigate temporal trends (1994–2010) in the cover of *V. myrtillus*, *V. vitis-idaea*, narrow-leaved grasses, field layer abundance and the volumes of broad-leaved tree species, *P. abies* and *Pinus* spp., tree stem density and stand age. The GLMs were performed using the MASS package (Venables & Ripley 2002) in R 2.15 (R Foundation for Statistical Computing). A pre-analysis graphical exploration of the response variables revealed non-normal distributions for all species/species groups except for the field layer abundance. A Gaussian distribution with identity link was used for the latter while a γ-distribution with log link was used for the remaining variables. Analyses of forest floor vegetation were based upon 744–960 permanent plots yr^{-1}, while analyses of forest structure were based on 5696–7774 permanent and temporary plots yr^{-1}. We expected temporal trends to differ among regions due to latitudinal differences in species abundances, land-use history and forest structure. Accordingly, separate analyses were made for the southern (temperate) and the northern (boreal) data subsets by including interactions with region in the GLMs (Fig. 1).

Results

The GAMs explained between 24.8% and 44.5% of the total deviance of the response variables (Table 2). The site index was the most important explanatory variable in all models except models for field layer abundance, in which site index was the second most important variable after the volume of *P. abies*. Volume of *P. abies* was the most important forest structural variable in all models except the model for narrow-leaved grasses, in which stand age was the most important variable (Table 2).

Field layer abundance was positively related to the site index (Fig. 2), but the increase in cover with increasing site index tended to level off at site indices above 20. Abundances of narrow-leaved grasses, *V. myrtillus* and *V. vitis-idaea* were unimodally related to the site index. *Vaccinium myrtillus* abundance peaked at a lower value of the site index than the abundance of narrow-leaved grasses, and *V. myrtillus* was more abundant over a broader spectrum of site index values. *V. vitis-idaea* abundance increased with the site index up to values of 15–20, above which it rapidly decreased. With an increasing volume of *P. abies*, field layer abundance first decreased but levelled off at 200 m^3·ha^{-1}. Similarly, *V. myrtillus* and *V. vitis-idaea* abundance both decreased with increasing spruce volume up to 200–300 m^3·ha^{-1}. The abundance of narrow-leaved grasses decreased rapidly with increasing stand age (Fig. 2). The second most important forest structural variables were tree stem number (field layer, narrow-leaved grasses), age (*V. myrtillus*) and the volume of broad-leaved tree species (*V. vitis-idaea*). The field layer abundance decreased with increasing tree stem density (up to ca. 2500 stems·ha^{-1}; Fig. 2). The abundance of narrow-leaved grasses decreased rapidly with increasing stem density (up to ca. 1500 stems·ha^{-1}). *Vaccinium myrtillus* increased with increasing forest age up to 80–100 yr of age (Fig. 2). An almost linear negative relationship was found between the *V. myrtillus* abundance and the volume of broad-leaved tree species. As for other species abundance variables, a slight decrease was observed for volumes >200–300 m^3·ha^{-1}.

The GLMs for *V. myrtillus*, narrow-leaved grasses and field layer abundance revealed significant decreases from 1994 through 2010 (Table 3). For *V. myrtillus* and the total cover of the field layer, significant interactions between year and zone were also found, which indicate that temporal change differs between the temperate and boreal zones. The sign of the interaction term indicates that the strongest decrease took place in the boreal zone (Fig. 3). The GLMs for forest stand variables revealed positive temporal trends (increase with time) for the number of tree stems, the volume of broad-leaved tree species, the volume of *Pinus* spp. and the total volume, while forest age decreased with time (Fig. 4). Significant interactions between year and zone were found both for forest age and for stem number. Figure 4 shows that the decrease in forest age and the increase in stem number were stronger in the boreal than in the temperate zone.

Table 2. GAMs for the response of species abundance (cover) to explanatory variables (see Table 1 for explanation). For each model, the following are given: distribution, link function and total explained deviance. For each environmental variable, are given: P-value, exact degrees of freedom (df), the parametric coefficient (Pc) estimate for linear variables and explained variation as percentage of the total explained deviance.

| Variable	Field layer Gaussian distribution, identity-link Explained deviance 24.8%				Narrow-leaved grasses Gamma distribution, log-link Explained deviance 32.6%				Vaccinium myrtillus Gamma distribution, log-link Explained deviance 31.1%				Vaccinium vitis-idaea Gamma distribution, log-link Explained deviance 44.5%			
	P	df	Pc	expl.	P	df	Pc	expl.	P	df	Pc	expl.	P	df	Pc	expl.
Intercept	<0.001		44.6		<0.001		2.0		<0.001		3.0		<0.001		2.0	
Age	<0.001	8.8		4.0	<0.001	8.7		10.4	<0.001	7.1		5.8	<0.001	7.9		2.0
Picea abies volume	<0.001	3.2		34.7	<0.001	7.2		5.2	<0.001	6.0		6.1	<0.001	6.6		6.3
Pinus spp. volume	<0.001	2.7		3.2	<0.001	8.5		5.2	<0.001	3.0		3.9	<0.001	7.0		1.6
Broad-leaved tree volume	<0.001	4.9		3.6	<0.001	6.3		5.2	<0.001	7.7		2.9	<0.001	3.6		3.1
Stem density	<0.001	5.5		4.8	<0.001	3.1		6.7	<0.001	6.7		2.3	n.s			
Ground surface structure	<0.001		−1.5	1.6	n.s.				n.s.				n.s.			
Site index	<0.001	4.9		11.3	<0.001	8.7		17.2	<0.001	5.6		20.9	<0.001	7.6		10.3
Slope	n.s.				n.s.				n.s.				n.s.			
Soil moisture	n.s.				<0.001		−0.2	2.5	n.s.				n.s.			
Soil texture	n.s.				n.s.				<0.001		−0.1	2.6	n.s.			
Soil water mobility	n.s.				n.s.				n.s.				n.s.			
Thickness humus layer	<0.001	6.4		5.2	<0.001	5.4		7.7	<0.001	6.4		4.8	<0.001	6.7		1.6
Altitude	<0.001	4.8		7.3	<0.001	4.3		11.7	<0.001	1.0		9.3	<0.001	3.5		1.6
Latitude	<0.001	8.4		12.1	<0.001	8.6		3.4	<0.001	8.3		4.2	<0.001	7.4		2.7
Longitude	n.s.				0.005	1.9		2.8	<0.001	8.7		3.9	<0.001	8.0		2.5

n.s. = variables not included in models.

Discussion

This study indicates that the field layer abundance, as well as the abundance (cover) of three important species/ species groups decreased in boreal Sweden in the period 1994–2010. This finding is in agreement with the results of other recent studies (Anonymous 2011c). In this time period, a 4% decrease in forest age has taken place, as well as an increase in average tree volume per hectare by ca. 15%. Slight increases in tree volume and forest age have also taken place in the temperate zones, accompanied by a decrease in narrow-leaved grass abundance. Our results for boreal Sweden thus accord with results of Odell & Ståhl (1998), who recorded negative trends for all forest floor species included in our study for the period 1983–1997. They did not analyse the cause of this decline, but the strong decrease in plant cover found by Odell & Ståhl (1998) was associated with a strong increase in tree volume, especially in the temperate zone and in old-growth forests in which V. myrtillus tends to be most abundant (Anonymous 2011c). Our results further accord with results of earlier studies (Kardell 1980) hypothesizing that an increase in forest age has a positive effect on V. myrtillus abundance.

Decreasing trends similar to those found in our study are reported for V. myrtillus and A. flexuosa in Germany (Jandt et al. 2011) and in Finland (Reinikainen et al. 2000). Økland et al. (2004) report a decrease in abundance of several forest floor species in southern Norwegian spruce forests, while inconsistent patterns of change were reported from northern Norway. Reinikainen et al. (2000) attribute these changes to changes in forest structure mediated by forest management and also mentions increased reindeer grazing as a potentially important cause of changes observed in Finland. In both the Norwegian and German studies the authors discuss environmental pollution, acidification and eutrophication as possible explanations of the observed forest floor vegetation change. A gradient of decreasing N deposition runs from south to north in Sweden, and the contribution of anthropogenic N is minimal in large parts of the boreal area (Pihl-Karlsson et al. 2011). Nitrogen deposition and forest fertilization have been hypothesized to favour narrow-leaved grasses and affect Vaccinium species negatively (Nordin et al. 2005, 2009). Our results only partly accord with this; both V. myrtillus and narrow-leaved grasses decreased in the boreal region where the N deposition is low, while in the temperate region with higher N deposition, the cover of V. myrtillus remained unchanged but the abundance of narrow-leaved grasses decreased. Our data thus do not support the hypothesis that N enrichment explains the observed patterns or temporal vegetation change.
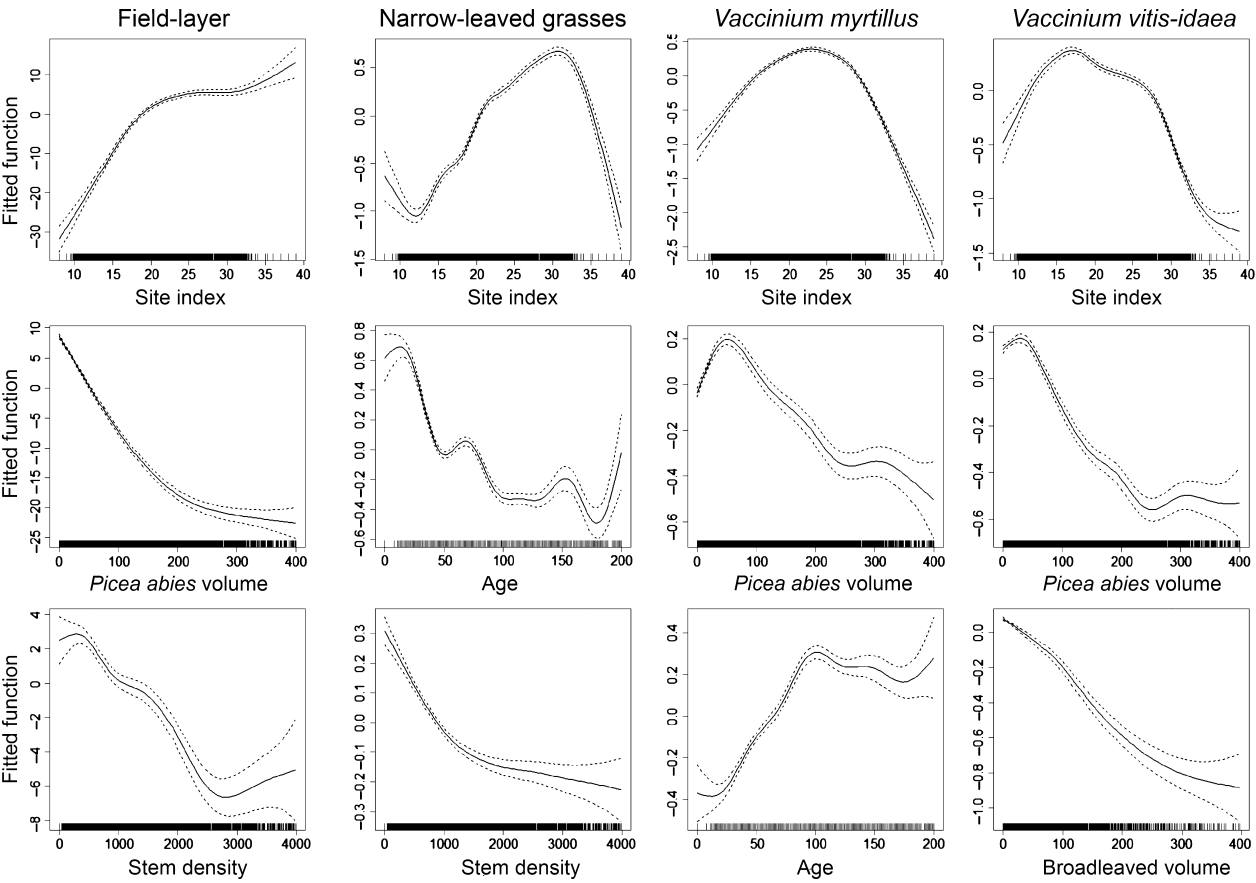
Fig. 2. Partial contributions of the generally most important explanatory variables (top) and two of the most important forest structural variables (middle and bottom) in the models of species abundance. Dashed lines show ±2SE. Values for individual sample plots are shown above the x-axis.

Table 3. GLMs for temporal change between 1994 and 2010 for species abundance (cover) and forest structural variables (see Table 1 for explanation). The zone variable is a factor-type variable with two levels; temperate and boreal zones.

	Year		Zone		Year*zone	
	t	P	t	P	t	P
Narrow-leaved grasses	−6.593	<0.001	8.413	<0.001	n.s.	n.s.
Field-layer	−8.216	<0.001	−5.736	<0.001	5.689	<0.001
Vaccinium myrtillus	−6.291	<0.001	−9.617	<0.001	9.540	<0.001
Vaccinium vitis-idaea	0.094	0.925	−3.409	<0.001	3.289	0.001
Age	−3.026	0.002	−6.448	<0.001	6.305	<0.001
Volume of broad-leaved tree species	8.168	<0.001	50.892	<0.001	n.s.	n.s.
Volume of *Picea abies*	n.s.	n.s.	34.910	<0.001	n.s.	n.s.
Volume of *Pinus* spp.	5.204	<0.001	5.108	<0.001	n.s.	n.s.
Volume of all tree species	6.655	<0.001	56.129	<0.001	n.s.	n.s.
Stem density	9.519	<0.001	7.197	<0.001	−7.206	<0.001

n.s. = variables not included in models.

Alternatively, the expected effects of N deposition on south Swedish forest vegetation took place earlier in the pollution history, and N saturation (e.g. Tamm 1991) now

occurs in which further N addition has small or no effects. The apparent absence of eutrophication effects may also be due to strong variation in our data (and in Swedish forests
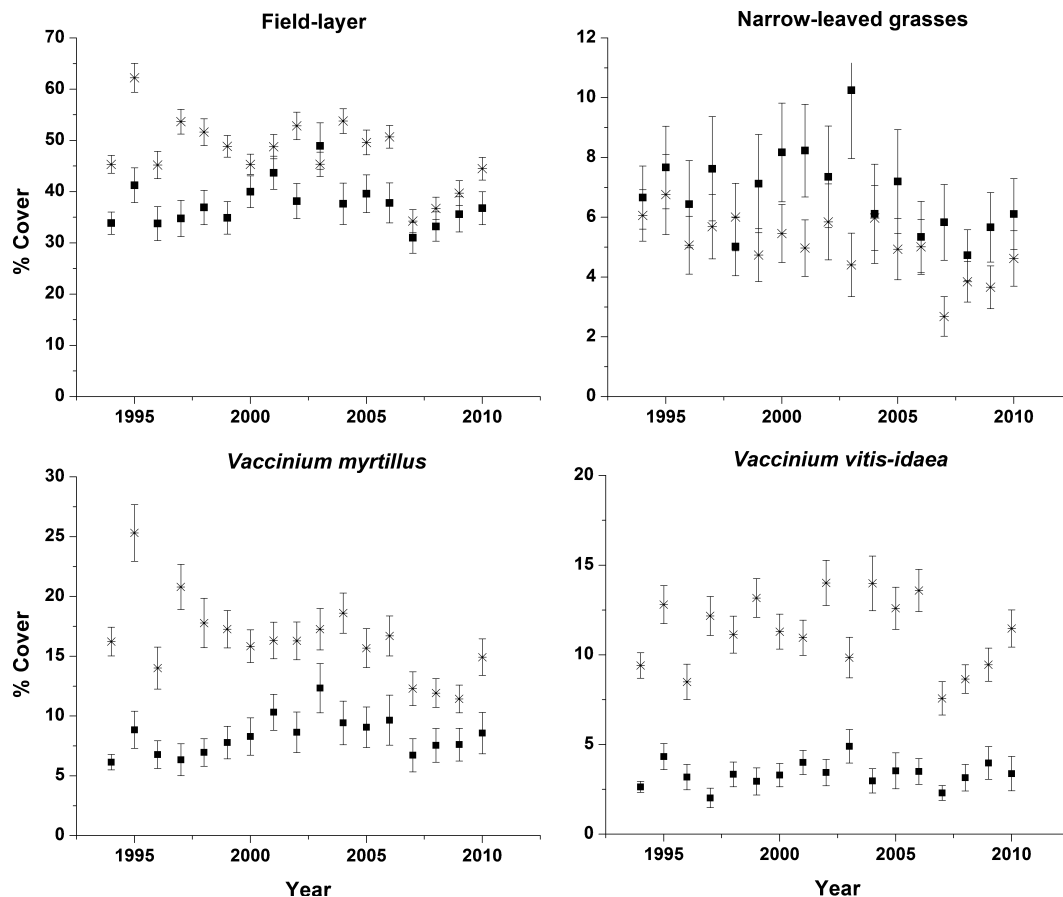
Fig. 3. Average area-weighted cover of *Vaccinium myrtillus*, *V. vitis-idaea*, narrow-leaved grasses and field layer abundance in each year between 1994 and 2010 in each zone (square = temperate; asterisk = boreal). Error bars indicate ±2SE.

in general) with respect to tree species, age, successional stage and management regime. Therefore, we cannot completely rule out the possibility that effects of N deposition remain after all of these factors are corrected for.

Site productivity, here measured as the site index, is an indirect measure of soil conditions and climate that constitute the conditions that determine the composition of the forest floor vegetation (Prentice et al. 1992). The ordering of the species by peak abundance relative to variation in site productivity, *V. vitis-idaea* < *V. myrtillus* < narrow-leaved grasses, were according to our expectations (Hägglund & Lundmark 1977). Our results indicate that the factors that limit site productivity also influence the abundance of forest floor species up to a productivity level beyond which other limiting factors take over.

According to our modelling results, the volume of *P. abies* and stand age (for narrow-leaved grasses) are the most important forest structural variables explaining variation in abundance (cover). This accords with light

(radiation) being one of the most strongly limiting resources for forest floor vegetation, influencing both composition and several aspects of biological diversity (Keith et al. 2009; Oberle et al. 2009; Hedwall et al. 2010). The late-successional species *Picea abies* greatly influences the light regime in forests (Johansson 1987), with its high shade-casting ability (Vandekerkhove & Hermy 2004). However, results reveal no increase in *P. abies* volume between 1994 and 2010. Negative relationships are also found between species abundances and the volume of broad-leaved tree species, as well as with stem density. This result indicates that broad-leaved tree species may influence light availability less strongly than *P. abies*, although the increase in density of these species is also negative.

Our models indicate that two key processes – increased forest density and changes in the age structure of forests – are responsible for the observed changes in forest floor vegetation. The most pronounced changes with time are observed for *V. myrtillus*, a species that is expected to be disfavoured both by increased forest density and lower
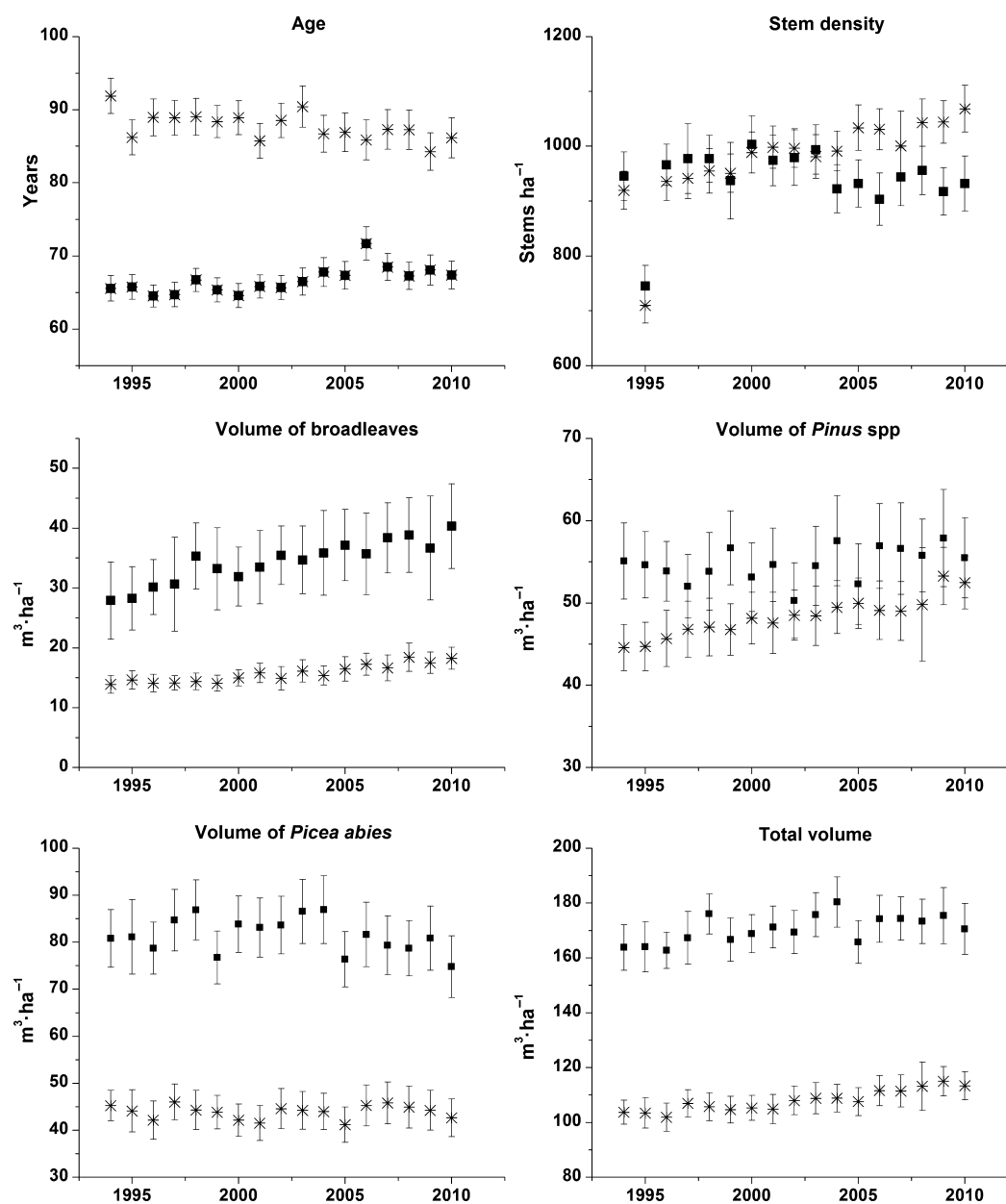
Fig. 4. Average forest age, stem density and the volumes of broad-leaved tree species, *Pinus* spp. and *Picea abies* and the total volume in each year between 1994 and 2010 in each zone (square = temperate; asterisk = boreal). Error bars indicate ±2SE.

forest age. Narrow-leaved grasses are observed to decrease in abundance in both zones. The most abundant species in this group is *A. flexuosa*, which usually increases when forests are clear-cut, but decreases under light-reduced conditions under a dense canopy, even if the availability of nutrients is high (Hedwall et al. 2010). The decrease of *A. flexuosa* is most pronounced in boreal Sweden, where this species is less abundant than in temperate Sweden. Although the proportion of young forest has increased in Sweden over the last decades, simultaneous increase in forest productivity may limit the time window available

for *A. flexuosa* to increase after clear-cutting. The expected increase in the temperate zone due to increased area covered by young forests may, therefore, be counteracted by shorter periods of high abundance after clear-cutting and by an increased density of mature forests.

Increased forest productivity leads to shorter rotation periods and larger fractions of the forest area are covered by clear-cuts at a given time point. Average rotation periods in Swedish forestry are now 60–100 yr, the longest being in the north. While narrow-leaved grasses are considered to be favoured in clear-cuts, *V. myrtillus* is consid-

ered to be negatively affected (Kardell 1980; Atlegrim & Sjöberg 1996). These relationships are substantiated by the modelled responses to stand age. According to Kardell (1980), *V. myrtillus* has a recovery period of 80–100 yr following clear-cutting. Our results indicate that shortened periods of recovery between severe disturbances (e.g. clear-cutting) will affect the *Vaccinium* species negatively.

Unless large portions of the trees are removed by thinning during the rotation period, canopy cover will increase during tree stand maturation. Thinning (i.e. a removal of 25–35% of tree volume at stand level on two to three occasions during the second third of the rotation period) is common practice in modern forestry, performed to enhance timber quality. Changes in the forest floor observed in this study indicate that the present thinning regime is not sufficient for full recovery of forest floor vegetation.

It is suggested that vascular plants in *P. abies* forests benefit from an increased proportion of broad-leaved tree species (Hart & Chen 2006, 2008; Felton et al. 2010) and Miina et al. (2009) found that *V. myrtillus* abundance is higher in *P. sylvestris* forests than in *P. abies* forests. Accordingly, Miina et al. (2010) suggest that a management regime for the dual purpose of timber production and production of *V. myrtillus* berries should include increased proportions of *P. sylvestris*, higher thinning frequencies and intensities than are normally the case today, and longer rotation periods. Our results, however, indicate that high forest density has negative effects on the forest floor vegetation regardless of whether other tree species than *P. abies* dominate.

Even though the models explained a considerable fraction of the total deviance of the response variables, several causes of noise are likely to be present in the data. The data on forest structure, such as volumes of different tree species, number of tree stems and age, are probably less affected by observer bias than the cover estimated for forest floor plants in large plots (100 m^2). Observer bias in individual cover estimates is likely to be present despite extensive calibration taking place between field staff (Bergstedt et al. 2009). However, we argue that errors are most likely stochastic and non-directional, so that the large data set and the large number of observers involved levels out error and bias in individual observations (cf. Bergstedt et al. 2009).

The decrease observed for the keystone species in boreal forests, *V. myrtillus*, in this and earlier studies (Odell & Ståhl 1998), may have long-term implications for higher trophic levels of the forest ecosystem (Selås 2001; Baines et al. 2004; Selås et al. 2011). Our results show that optimization of timber production is likely to have negative long-term side effects on berry production and other ecosystem functions of the field layer.

Conclusions

Results of this study indicate that the cover of two of the most common species on the forest floor is currently decreasing in Sweden. Our analyses suggest that this decrease is an effect of changes in the forest structure. Furthermore, results of our study indicate that maximizing carbon storage in forest biomass to mitigate climate change is incompatible with maintenance of well-developed forest floor vegetation. This study indicates that in order to favour species of the understorey, forests could be managed by intensified thinning, by favouring tree species (*P. sylvestris*, *Betula* spp.) with crowns that are open or that allow more light to reach the ground for other reasons and, for *V. myrtillus*, by extended rotation periods. Because these measures are likely to impact timber production (and the economic revenue) negatively (Nilsson et al. 2010) , a trade-off exists between timber production and conservation of forest floor vegetation.

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