

# Peatland plant communities under global change: negative feedback loops counteract shifts in species composition

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**Abstract.** Mires (bogs and fens) are nutrient-limited peatland ecosystems, the vegetation of which is especially sensitive to nitrogen deposition and climate change. The role of mires in the global carbon cycle, and the delivery of different ecosystem services can be considerably altered by changes in the vegetation, which has a strong impact on peat-formation and hydrology. Mire ecosystems are commonly open with limited canopy cover but both nitrogen deposition and increased temperatures may increase the woody vegetation component. It has been predicted that such an increase in tree cover and the associated effects on light and water regimes would cause a positive feed-back loop with respect to the ground vegetation. None of these effects, however, have so far been confirmed in large-scale spatiotemporal studies. Here we analyzed data pertaining to mire vegetation from the Swedish National Forest Inventory collected from permanent sample plots over a period of 20 yr along a latitudinal gradient covering 14°. We hypothesized that the changes would be larger in the southern parts as a result of higher nitrogen deposition and warmer climate. Our results showed an increase in woody vegetation with increases in most ericaceous dwarf-shrubs and in the basal area of trees. These changes were, in contrast to our expectations, evenly distributed over most of the latitudinal gradient. While nitrogen deposition is elevated in the south, the increase in temperatures during recent decades has been larger in the north. Hence, we suggest that different processes in the north and south have produced similar vegetation changes along the latitudinal gradient. There was, however, a sharp increase in compositional change at high deposition, indicating a threshold effect in the response. Instead of a positive feed-back loop caused by the tree layer, an increase in canopy cover reduced the changes in composition of the ground vegetation, whereas a decrease in canopy cover lead to larger changes. Increased natural disturbances of the tree layer due to, for example, pathogens or climate is a predicted outcome of climate change. Hence, these results may have important implications for predictions of long-term effects of increased temperature on peatland vegetation.

*Key words:* bog; bryophytes; climate change; conifers; ericoids; forbs; graminoids; mire; nitrogen deposition; peatland; sedges.

## INTRODUCTION

Peatlands, especially bogs and fens (collectively known as mires) play an important role in the global carbon and water cycles (Nilsson et al. 2008, Loisel et al. 2014, Waddington et al. 2015), contribute significantly to the biodiversity of forest landscapes (Spitzer and Danks 2006) and also deliver various other ecosystem services (Kimmel and Mander 2010, Moor et al. 2015). The soils of mires are organogenic, with the degree of decomposition depending on the degree of near-surface anoxia. Decomposition also depends on the quality of the litter and, therefore, peat formation is strongly affected by the composition of plant communities (Ward et al. 2010, 2015). In addition, both albedo and evapotranspiration of mires are affected by the vegetation (Waddington et al. 2015). Hence, their role in the carbon- and hydrological

cycles, and the delivery of different services such as carbon sequestration and flood attenuation, can be altered by vegetation changes (Moor et al. 2015).

Although most mires in high latitude ecosystems are exposed to relatively low nitrogen deposition (Dentener et al. 2006), recent evidence suggests that the accumulated effects of low annual input rates may result in considerable long-term nitrogen effects (De Schrijver et al. 2011, Phoenix et al. 2012). Moreover, both recorded and predicted increases in temperature tend to be greater at high latitudes (SMHI 2015). Mires are generally open or semi-open nutrient limited environments where nitrogen deposition and climate warming can be expected to cause severe changes (Johansson et al. 2006). Experimental and modeling studies on the impact of warmer climate on mire plant communities indicate that vascular plant species, including trees, increase in abundance while *Sphagnum* species decrease as an effect of both drought and increased mean temperatures (Weltzin et al. 2000, 2003, Wiedermann et al. 2007, Breeuwer et al. 2009, Heijmans et al. 2013). There are indications of life-form specific interactions

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between drought and temperature with respect to shrubs and graminoids. While both life-forms may benefit from higher temperatures, graminoids only do so when a high water-table is maintained (Weltzin et al. 2003). Similar to the effects of increased temperatures, nitrogen deposition experiments on mires have shown that *Sphagnum* species are disfavored and vascular plants increase with increased nitrogen availability (Berendse et al. 2001, Bubier et al. 2007, Wiedermann et al. 2007, 2009, Juutinen et al. 2016). Higher temperature and precipitation may enhance the effects of nitrogen deposition, opening up the possibility of interaction between these two global change factors (Limpens et al. 2011). Based on stratigraphic data, Charman et al. (2013) suggested that higher temperature may be beneficial for peatland plants as an effect of a longer growing season. This probably holds as long as precipitation is sufficient for growth.

The *Sphagnum* species play an important role in peat formation and the hydrology of mires; thus, changes in their productivity due to global change may have long-term consequences for the mire ecosystem. The expected positive effects of both warming and nitrogen on the growth and density of the tree layer may further change the hydrological dynamics of mires, causing the water table to sink, at least periodically. This effect may disfavor many species and cause a positive feedback effect, i.e., increase the effect of warming and nitrogen, on the ground vegetation (Ohlson et al. 2001, Gunnarsson et al. 2002, Heijmans et al. 2013, Waddington et al. 2015). However, the large-scale effects of global warming and nitrogen deposition on mire plant communities along latitudinal gradients are largely unknown.

Sweden has 5.1 million hectares of mires (SLU 2015), constituting >10% of the land area, distributed over a latitudinal range of almost 14°. The latitudinal temperature gradient is negatively correlated with the deposition of nitrogen (Hedwall et al. 2013a), which decreases from ~15 kg·ha<sup>-1</sup>·yr<sup>-1</sup> in southwestern Sweden to close to ambient levels (~2 kg·ha<sup>-1</sup>·yr<sup>-1</sup>) in the far north (Akselsson et al. 2010). Since the late 1970s there has been very little management of these mires due to legal as well as economic restrictions on drainage and harvesting of trees (SFS 1979; Hånell 2009). Hence, there is an opportunity to study the effects of large scale environmental change on mire vegetation without the confounding effects of management.

Repeated surveys of permanent vegetation sample units are invaluable for documenting patterns of change in plant composition and to help us to understand the impacts of multiple and interacting ecosystem drivers (Lindenmayer et al. 2010). Gaining in-depth insights into the general patterns and processes of vegetation change also requires extensive data sets, sampled over large environmental gradients. A combination of a temporal and spatial approach allows the assessment of the relative contribution of local and large-scale factors to changes in community composition (Verheyen et al. 2012, De Frenne et al. 2013, Bernhardt-Römermann et al. 2015). The

Swedish National Forest Inventory (NFI) includes a vegetation survey with permanent plots on peatlands which has now been repeated during a 20-year period (1994–2013, SLU 2015) and covers the entire country. The vegetation survey of the Swedish NFI thus represents one of the most extensive long-term vegetation data sets for mires globally. The survey of the NFI, in combination with the geographical range of Swedish mires, offers an excellent opportunity to study large-scale and long-term vegetation changes, and to analyze impacts of multiple and interacting anthropogenic and environmental drivers.

In this study, we use NFI data to assess the influence of local and large-scale drivers on the flora of Swedish mires. We analyze changes in the most frequent taxa surveyed among vascular plants (forbs, graminoids and woody species), bryophytes and lichens during the 20-yr period, 1994–2013. Specifically, we test the following hypotheses: (1) *Sphagnum* species decrease while vascular plants in the ground vegetation increase over time; (2) tree species increase in biomass over time; (3) these changes are larger in southern than northern Sweden (as a result of differences in atmospheric nitrogen deposition and a warmer climate); and (4) the effects of environmental change on the tree layer will enhance the effects on the ground vegetation in a positive feedback loop, i.e., an increase in density of the tree layer driven by environmental factors will result in additional effects on the ground vegetation.

## MATERIALS AND METHODS

### *The vegetation data of the NFI*

The Swedish NFI collects data on forest structure, composition and environmental variables from a nationwide network of permanent sample plots. The permanent plots are aggregated in square clusters with 4–8 plots in each square, all of which are located along the edge of the square. The edge of each square is 300–1,200 m, which along with the distance between squares varies between five regions. Detailed information about trees and the ground vegetation is collected repeatedly, returning to the same individual plot at intervals of 10 yr (SLU 2015). For further information and critical evaluation of NFI permanent plots and survey methods, see SLU (2015) and Milberg et al. (2008). For this study, we used all permanent plots on land which is defined as mire: peat forming wetlands with an estimated timber production capacity less than 1 m<sup>3</sup>·ha<sup>-1</sup>·yr<sup>-1</sup>. The NFI records ditches within 25 m of the center of the plot. All such plots (6%) were excluded, resulting in a data set including 2,202 mire plots that were surveyed once during the period 1994–2003, and then re-surveyed 10 yr later during the period 2004–2013. Of these plots, 0.1% changed during the study period to a land-use class indicating a higher level of productivity.

In the vegetation survey, the presence of 270 species or species groups, including vascular plants, bryophytes and

lichens (henceforth also referred to as taxa), was noted in circular plots with a radius of 5.64 m (area 100 m<sup>2</sup>), (see Odell and Löfgren 2009 for species nomenclature). Fifty-three taxa in the shrub and ground layers reached an overall frequency of at least 4% in the sample plots during the study period 1994–2013 and were analyzed with respect to change in occurrence over time. In addition, the presence/absence of the three most common tree species (*Betula pubescens*, *Picea abies* and *Pinus sylvestris*) was analyzed. Data on the tree layer were collected from a plot with a radius of 10 m, with the same center point as the vegetation plot. In this study, inventory data on the basal area (BA; m<sup>2</sup>/ha) of the two most common species, the evergreen conifers *P. abies* and *P. sylvestris*, and the summed deciduous broadleaf tree species were analyzed, resulting in a total of 56 taxa being investigated.

### Statistical analysis

All statistical analyses were undertaken in R version 3.2.2 (R Core Team 2015). To analyze how species with different changes in occurrence are distributed along environmental gradients, a non-metric multidimensional scaling (NMS) was performed on the plant community data from the first survey in 1994–2003 (i.e., excluding re-survey data), by applying the metaMDS function in the vegan package (Oksanen et al. 2013). To assist in the interpretation of the gradients in this indirect ordination, we used the BA of all deciduous trees, *P. abies* and *P. sylvestris* together with the total BA and temperature sum (TS) as environmental variables. TS was defined as the long-term average of the yearly summed daily mean temperatures exceeding 5°C (Eriksson et al. 1983). In addition, we calculated the plot mean Ellenberg indicator values (Ellenberg et al. 1992) for light (L), temperature (T), continentality (K), moisture (F), soil reaction (R, correlated with pH; Diekmann 2003) and nutrients (N). The correlations between the ordination and the environmental/indicator variables were analyzed using the envfit function and projected onto the final NMS solution. The output illustrates the strength (length of arrows) and the direction of the strongest correlation. The NMS and projection of environmental variables used Bray–Curtis dissimilarity (BCD) and 999 permutations.

The presence/absence of the 56 taxa data were modeled as an effect of time, temperature sum (TS), and the interaction between these two main-terms, in binomial (logit-link) generalized linear mixed models (GLMM) with region, cluster and plot as random effects. Non-significant ( $P > 0.05$ ) interactions between time and TS were removed from the models. TS was strongly correlated with the deposition of nitrogen (Pearson correlation:  $r = 0.87$ ,  $P < 0.001$ ). Hence, TS was introduced in the GLMMs as an indicator of the common gradient of climatic variation and deposition. The GLMMs of species presence/absence were derived using the glmmPQL function in the MASS package (Venables and Ripley 2002).

The effects of time and TS on the BA of trees were modeled by a zero-adjusted GLMM with region, cluster and plot as random effects. This model consisted of a binomial (logit-link) GLMM for the dichotomized BA (0/1) and a Gamma (log-link) GLMM for the continuous part (BA > 0). These models were created using the glmer function in the lme4 package (Bates et al. 2015) and then merged according to the procedure described by Zuur et al. (2012). A partial model selection was performed on all GLMMs such that non-significant ( $P > 0.05$ ) interactions were removed.

For the vegetation data, BCD between inventories within plots were calculated using the vegdist function in the vegan package. The effects of the tree layer density measured as the total BA, the change in total BA between inventories and the TS on the BCD were modeled by a generalized additive mixed model (GAMM) with region and cluster as random effects, in the mgcv package (Wood 2006). The change in BA was not correlated to the initial BA ( $r^2 = 0.008$ ), implying that these two variables can be interpreted independently. A GAMM is a generalization of a GLMM in which the assumption of a linear relationship between predictors and the (transformed) response variable is relaxed. Our GAMMs were built without prior assumptions about the shape of the relationship between the variables. GAMMs add smooth components to a linear model, and therefore, in principle, no restriction exists with respect to the shapes that they can take. To avoid overfitting and to optimize the smoothing parameter, model complexity was restricted by applying generalized cross-validation. The GAMMs were created with a Gamma distribution and log-link.

### RESULTS

The NMS of all 56 taxa showed a clear separation in ordination space between the fens dominated by graminoids and forbs and dwarf-shrub dominated bog communities along the first dimension, and between open fens and forested bogs along the second dimension (Fig. 1). The variables most closely related with the ordination were Ellenberg's indicator values for light (L), moisture (F), soil reaction (R) and nutrients (N) (Table 1). Among the environmental variables, the total BA of trees had the largest  $R^2$  (0.23) while the  $R^2$  of TS was only 0.01, indicating a much larger impact of local habitat than macroclimate. The BA of *P. sylvestris* and Ellenberg's indicators for temperature, reaction (pH) and nutrients showed the strongest correlation with the first NMS dimension suggesting a gradient from minerotrophic fens to ombrotrophic bog communities. The BA of all tree species separately and in total, indicator values for light, continentality and moisture showed the strongest correlation with the second dimension thus supporting the interpretation of a gradient ranging from open wet fens to bogs with a high tree canopy cover (Table 1). These gradients are also revealed by the position of the taxa, with bog species to the right (pine

TABLE 1. Post hoc fit of environmental variables and plot means of Ellenberg values to the two-dimensional solution from the Non-metric multidimensional scaling (NMS; Fig. 1).

	Dim 1	Dim 2	R <sup>2</sup>	P
	Corr.	Corr.		
Temperature sum	-0.26	0.97	0.01	0.003
BA <i>Pinus sylvestris</i>	0.67	0.74	0.11	0.001
BA <i>Picea abies</i>	<0.01	0.99	0.12	0.001
BA deciduous	-0.46	0.89	0.16	0.001
BA total	0.10	0.99	0.23	0.001
L (light)	-0.19	-0.98	0.76	0.001
T (temperature)	-0.92	-0.38	0.23	0.001
K (continentality)	0.18	0.98	0.13	0.001
F (moisture)	-0.47	-0.88	0.76	0.001
R (soil reaction)	-0.99	0.17	0.48	0.001
N (nutrients)	-0.83	0.56	0.58	0.001

Notes: BA, basal area. The table shows the independent correlations with the two axes separately, together with the R<sup>2</sup> and P-value for each variable in relation to the ordination.

bog species at the top) and minerotrophic indicators to the left.

Out of a total of 56 analyzed taxa, the presence of 28 either increased or decreased significantly over time at locations with low TS according to the GLMMs (Table 2). The majority of these taxa increased (18), while only 10 decreased. Only eight taxa showed a significantly different trend over time depending on TS (significant Time × TS interaction): *Carex echinata*, *Cladonia alpestris*, *Drosera* spp., *Deschampsia flexuosa*, *Empetrum nigrum*, *Scheuchzeria palustris*, *Sphagnum* spp., and *Trientalis europaea* (Table 2, Fig. 2a–h).

The largest turn-over of species was found among the bryophytes, dwarf-shrubs and graminoids. Among the six recorded bryophytes, five taxa increased, including *Sphagnum* spp., and one decreased (*Polytrichum commune*). The positive change with time in *Sphagnum* at low TS was, however, weak and the opposite trend was found at high TS (Fig. 2g). Seven out of 11 dwarf-shrubs increased, whereas none decreased. All seven dwarf-shrubs that increased are species with ericoid mycorrhiza.

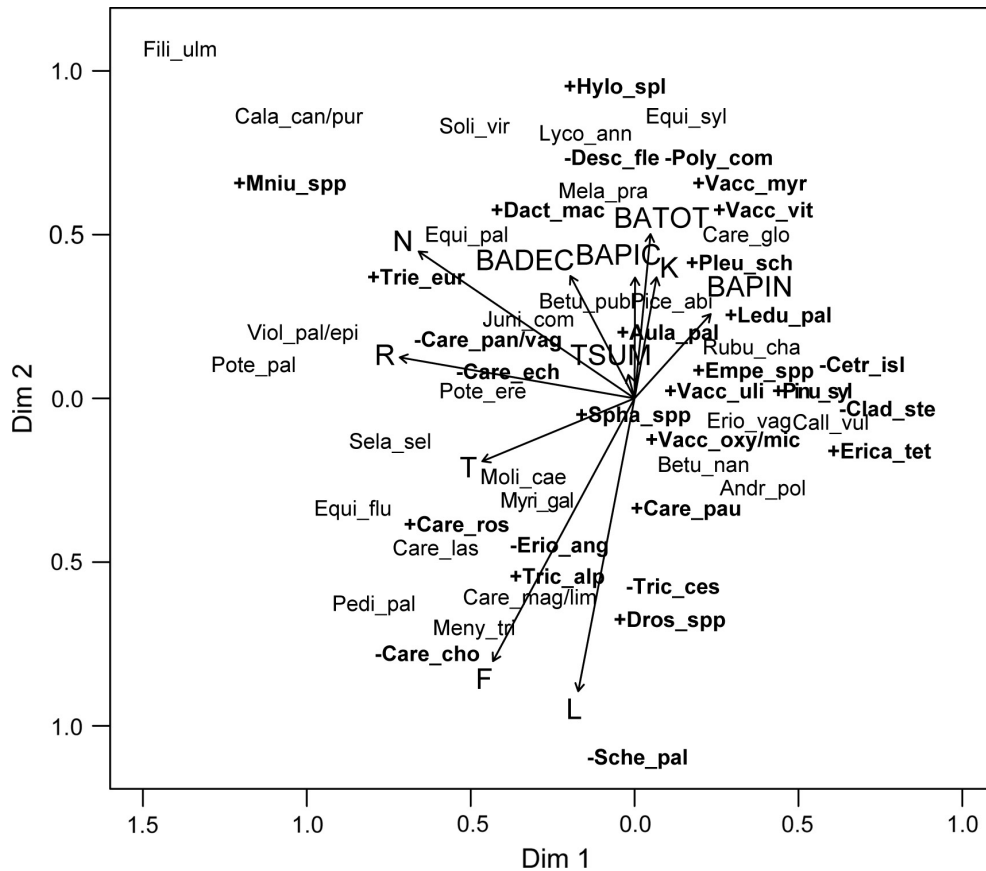


FIG. 1. Ordination diagram showing the two-dimensional result of a non-metric multidimensional scaling (NMS) of the NFI data from 1994 to 2003. Arrows show the post hoc fit of environmental variables: basal area of deciduous trees (BADEC), *Picea abies* (BAPIC), *Pinus sylvestris* (BAPIN), total basal area (BATOT) and temperature sum (TSUM) and plot-means of Ellenberg indicator values for light (L), temperature (T), continentality (K), moisture (F), soil reaction (R) and nutrients (N). Abbreviations for the taxa are given in Table 2 and correlation statistics for the environmental variables in Table 1. Taxa in bold text either decreased (-) or increased (+) in plot frequency during the 1994–2013 period (Table 2).

TABLE 2. List of analyzed taxa with change in probability of occurrence over time, along the temperature sum gradient as indicated by generalized linear mixed models (GLMM).

Taxon	Abbreviation	Life-form	Change over time, T	Temperature sum, TS	Significant T × TS interaction
<i>Polytrichum commune</i>	Poly_com	Bryophyte	–	ns	
<i>Hylocomium splendens</i>	Hylo_spl	Bryophyte	+	–	
<i>Aulacomnium palustre</i>	Aula_pal	Bryophyte	+	–	
<i>Mnium</i> spp.	Mniu_spp	Bryophyte	+	ns	
<i>Pleurozium schreberi</i>	Pleu_sch	Bryophyte	+	–	
<i>Sphagnum</i> spp.	Spha_spp	Bryophyte	+	–	Decrease over time at high TS
<i>Selaginella selaginoides</i>	Sela_sel	Dwarf-shrub	ns	–	
<i>Calluna vulgaris</i>	Call_vul	Dwarf-shrub	ns	+	
<i>Lycopodium annotinum</i>	Lyc_ann	Dwarf-shrub	ns	–	
<i>Andromeda polifolia</i>	Andr_pol	Dwarf-shrub	ns	–	
<i>Vaccinium myrtillus</i>	Vacc_myr	Dwarf-shrub	+	–	
<i>Erica tetralix</i>	Eric_tet	Dwarf-shrub	+	0	
<i>Vaccinium vitis-idaea</i>	Vacc_vit	Dwarf-shrub	+	–	
<i>Vaccinium uliginosum</i>	Vacc_uli	Dwarf-shrub	+	–	
<i>Ledum palustre</i>	Ledu_pal	Dwarf-shrub	+	+	
<i>Vaccinium oxycoccus/microcarpum</i>	Vacc_oxo/mic	Dwarf-shrub	+	ns	
<i>Empetrum nigrum</i>	Empe_nig	Dwarf-shrub	+	–	Weak increase over time at low TS and decrease over time at high TS
<i>Filipendula ulmaria</i>	Fili_ulm	Forb	ns	+	
<i>Melampyrum pratense</i>	Mela_pra	Forb	ns	–	
<i>Potentilla erecta</i>	Pote_ere	Forb	ns	–	
<i>Solidago virgaurea</i>	Soli_vir	Forb	ns	–	
<i>Rubus chamaemorus</i>	Rubu_cha	Forb	ns	–	
<i>Viola palustris/leptopisila</i>	Viol_pal/epi	Forb	ns	ns	
<i>Equisetum palustre</i>	Equi_pal	Forb	ns	–	
<i>Pedicularis palustris</i>	Pedi_pal	Forb	ns	–	
<i>Potentilla palustris</i>	Pote_pal	Forb	ns	+	
<i>Equisetum fluviatile</i>	Equi_flu	Forb	ns	+	
<i>Equisetum sylvaticum</i>	Equi_syl	Forb	ns	–	
<i>Menyanthes trifoliata</i>	Meny_tri	Forb	ns	ns	
<i>Drosera</i> spp.	Dros_spp	Forb	ns	ns	Stronger increase over time at high TS
<i>Dactylorhiza maculata</i>	Dact_mac	Forb	+	–	
<i>Trientalis europaea</i>	Trie_eur	Forb	+	–	An increase over time only at low TS
<i>Molinia caerulea</i>	Moli_cae	Graminoid	ns	–	
<i>Calamagrostis canescens/purpurea</i>	Cala_can/pur	Graminoid	ns	ns	
<i>Carex globularis</i>	Care_glo	Graminoid	ns	ns	
<i>Carex lasiocarpa</i>	Care_las	Graminoid	ns	ns	
<i>Carex magellanica/limosa</i>	Care_mag/lim	Graminoid	ns	–	
<i>Eriophorum vaginatum</i>	Erio_vag	Graminoid	ns	–	
<i>Eriophorum angustifolium</i>	Erio_ang	Graminoid	–	–	
<i>Carex panicea/vaginata</i>	Care_pan/vag	Graminoid	–	–	
<i>Deschampsia flexuosa</i>	Desc_fle	Graminoid	–	–	No change over time at high TS
<i>Carex chordorrhiza</i>	Care_cho	Graminoid	–	ns	
<i>Trichophorum cespitosum</i>	Tric_ces	Graminoid	–	–	
<i>Scheuchzeria palustris</i>	Sche_pal	Graminoid	–	–	Weak increase over time at high TS
<i>Carex echinata</i>	Care_ech	Graminoid	–	–	No change over time at high TS
<i>Carex rostrata</i>	Care_ros	Graminoid	+	–	

(continued)

TABLE 2. Continued.

Taxon	Abbreviation	Life-form	Change over time, T	Temperature sum, TS	Significant T × TS interaction
<i>Carex pauciflora</i>	Care_pau	Graminoid	+	–	
<i>Trichophorum alpinum</i>	Tric_alp	Graminoid	+	–	
<i>Cetraria islandica</i>	Cetr_isl	Lichen	–	–	
<i>Cladonia alpestris</i>	Clad_ste	Lichen	–	ns	Increase over time at high TS
<i>Betula nana</i>	Betu_nan	Shrub	ns	–	
<i>Juniperus communis</i>	Juni_com	Shrub	ns	–	
<i>Myrica gale</i>	Myri_gal	Shrub	ns	+	
<i>Betula pubescens</i>	Betu_pub	Tree	ns	+	
<i>Picea abies</i>	Pice_abi	Tree	ns	–	
<i>Pinus sylvestris</i>	Pinu_syl	Tree	+	+	

Notes: ns, non-significant; sig, significant ( $P < 0.05$ ). The interaction between time and temperature sum (TS) indicates whether there were significantly different trends in changes at high compared to low temperature sums. Species are ordered according to life-form and direction of change.

For one of these, *Empetrum nigrum*, there was a significant Time × TS interaction with a decreasing trend at high TS (Fig. 2e). Among the 16 graminoid taxa, three increased and four decreased (Table 2). All three graminoid taxa with significant interactions showed a weak or no trend at high TS. Forbs were a large group (15 species) with only two species changing (both increased). *P. sylvestris* was the only species among the trees and shrubs that increased in presence and this increase was even over the TS gradient. Most of the declining species were characteristic of the nutrient poor fen community, while increasing species appeared along both gradients (Fig. 1). The bog community had a large share of increasing species, whereas none decreased.

The final zero adjusted GLMM of the BA included only the main terms time and TS. The summed BA of all trees was higher at high TS than at low TS and increased over time (Table 3, Fig. 3). The increase was similar at low and at high TS (non-significant T × TS interaction). The predicted value of BA increased, at intermediate TS (1100), from 3.1 m<sup>2</sup>/ha in 1994 to 4.4 m<sup>2</sup>/ha in 2013 (Fig. 3).

According to the GAMM, the BCD was significantly lower on sites with high initial BA of trees (Fig. 4), implying a smaller change in species composition when there is denser canopy cover. The relationship between BCD and initial BA was non-linear, with the strongest negative effect of BA on BCD occurring at low BA, and above 5 m<sup>2</sup> there was no significant change in BCD along the BA gradient. There was a negative linear relationship between change in BA and BCD, implying that disturbance, measured as loss of tree cover, increased the BCD while an increase in BA due to growth led to decreasing BCD and increasing stability in the ground vegetation composition (Fig. 4). As these two variables were uncorrelated ( $R^2 = 0.008$ ) and the latter effect remained despite the inclusion of the initial BA in the model, it can be concluded that these effects are unrelated. BCD was unaffected by TS over most of the range, but increased strongly at TS > 1200, which may indicate a threshold in the effects of current or accumulated nitrogen deposition.

## DISCUSSION

This study provides evidence of significant temporal changes in mire vegetation along an extensive gradient of climate and nitrogen deposition. During the 20 yr when data were collected, woody vegetation with tree cover and dwarf-shrubs increased along with forest bryophytes. In contrast to our hypothesis, vegetation changes were evenly distributed along most of the latitudinal gradient and a gradually increasing tree canopy cover stabilized the ground vegetation as a result of a negative feed-back loop.

### Changes in species composition

The increase in cover of trees and of the presence of dwarf-shrubs connected to the bog community in our study is in line with the predicted effects of both a warmer climate and nitrogen deposition from experimental (Weltzin et al. 2000, 2003, Wiedermann et al. 2007, Breeuwer et al. 2009, Heijmans et al. 2013) and observational studies in single mires or smaller regions with elevated nitrogen deposition (Nordbakken 2001, Gunnarsson et al. 2002, Gunnarsson and Flodin 2007, Kapfer et al. 2011). One dwarf-shrub, *Empetrum nigrum*, however, displayed this trend in the north while in the south it declined. The species is represented by different subspecies in the north and south (*hermaphroditum* and *nigrum*, respectively). However, both subspecies are associated with open environments and the species may, therefore, have suffered from the increase in tree cover (cf Zvereva and Kozlov 2004), which was somewhat greater in the south. In addition, several bryophytes increased that either, like *Pleurozium schreberi* and *Hylocomium splendens*, are associated with forest habitats or, like *Aulacomnium palustre*, grow in both open and forested habitats. *Polytrichum commune* often grows in shaded, marginal parts of peatlands, and its decline was therefore surprising. The more typical peatland species *Polytrichum strictum* has been found to respond positively to N

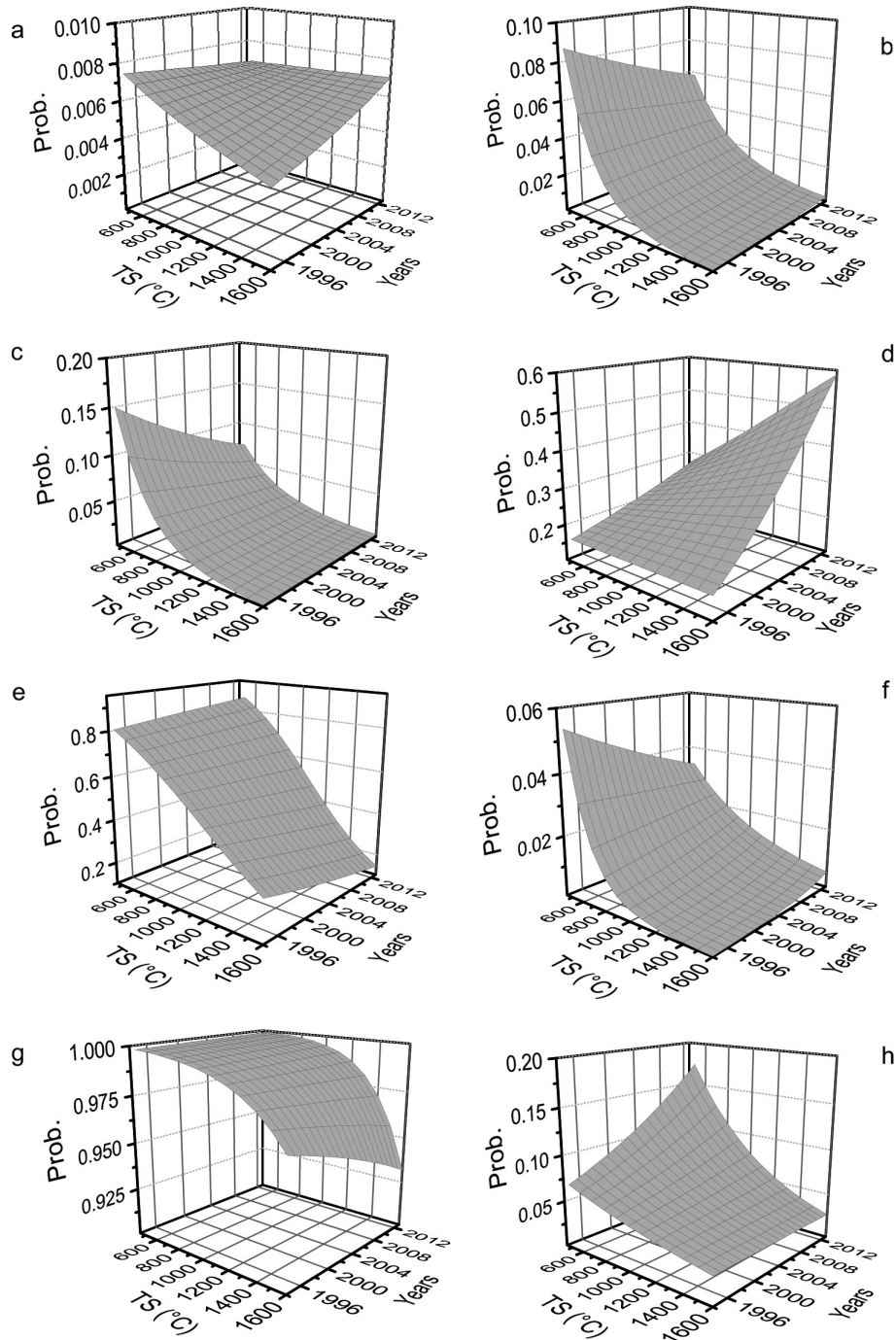


FIG. 2. Predicted probabilities of occurrences from generalized linear mixed models (GLMM) of the eight taxa that showed significant interactions between temperature sum (TS) and time: *Cladonia alpestris* (a), *Carex echinata* (b), *Deschampsia flexuosa* (c), *Drosera* spp. (d), *Empetrum nigrum* (e), *Scheuchzeria palustris* (f), *Sphagnum* spp. (g), *Trientalis europaea* (h). The original time-scale in the analyses, ranging from 0 to 19, has been replaced with calendar years to facilitate the interpretation of the axis.

additions (Mitchell et al. 2002, Juutinen et al. 2016), but experiments suggest that the relationship between species of *Sphagnum* and *Polytrichum* may be altered by changes in temperature and N availability (Mitchell et al. 2002, Bu et al. 2011, Juutinen et al. 2016).

Mire vegetation is spatially and temporally dynamic, and some of the changes we observed resemble the natural succession from fen to bog (for example, the expansion of dwarf shrubs and feather mosses; and the decrease in some fen graminoids). This shift includes acidification

TABLE 3. Zero-adjusted generalized linear mixed models (GLMM) of the effect of time and temperature sum (TS) on the basal area (BA) of trees.

	Binomial component				Gamma component				AIC
	Est. par	SE	Z	P	Est. par	SE	Z	P	
Full model									
Intercept	1.84	0.11	16.60	<0.001	1.33	0.03	39.64	<0.001	22,387.3
Time	0.06	0.04	1.30	0.193	0.11	0.01	7.96	<0.001	
Temperature sum	0.36	0.08	4.58	<0.001	0.12	0.03	3.67	<0.001	
Time × Temperature sum	0.03	0.04	0.65	0.513	0.02	0.01	1.13	0.259	
Reduced model									
Intercept	1.84	0.11	16.60	<0.001	1.33	0.03	39.64	<0.001	22,385.0
Time	0.05	0.04	1.26	0.207	0.10	0.01	7.48	<0.001	
Temperature sum	0.36	0.08	4.58	<0.001	0.12	0.03	3.68	<0.001	

Notes: AIC, Akaike's information criterion. The independent variables were centered and standardized prior to the analyses. The models included a binomial component representing the presence/absence of trees and a gamma component representing the continuous response. The non-significant interaction was removed from the full model.

and hummock formation, in which *Sphagnum* mosses play a major role (Granath et al. 2010), and stratigraphic data show that it can occur as quickly as over a few decades (e.g., Gorham and Janssens 1992). It seems, however, unlikely that these natural processes should be so well synchronized as to explain our results any more than a little, but they could reinforce the effects of increased temperature.

*Deschampsia flexuosa*, a grass associated with the drier forested mires, exhibited a decreasing trend over time. This is surprising, since this species has often been considered an indicator of increased nitrogen availability in boreal forest (e.g., Strengbom and Nordin 2012). During our study period, however, it has decreased in Swedish

forests, probably as a result of increasing stand density (Hedwall et al. 2013b, Hedwall and Brunet 2016). The increase in basal area suggests that the same scenario is relevant for mires. Most other graminoids were

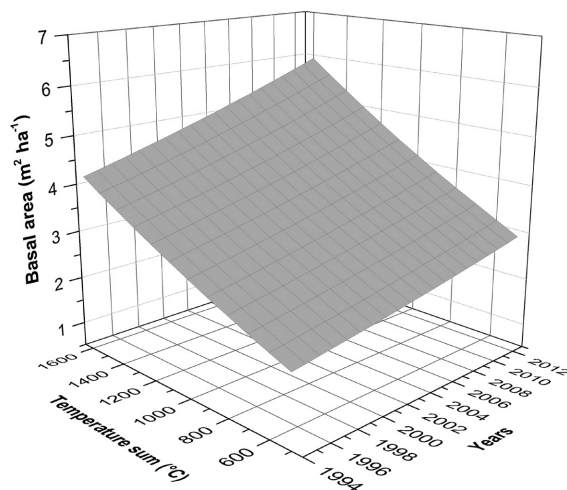


FIG. 3. Predicted basal area of trees from the fixed part of a zero-adjusted generalized linear mixed model (GLMM; reduced model; Table 3). The standardized predictors from the model are shown on their original scale. The original time-scale in the analyses, ranging from 0 to 19, has been replaced with calendar years to facilitate the interpretation of the axis.

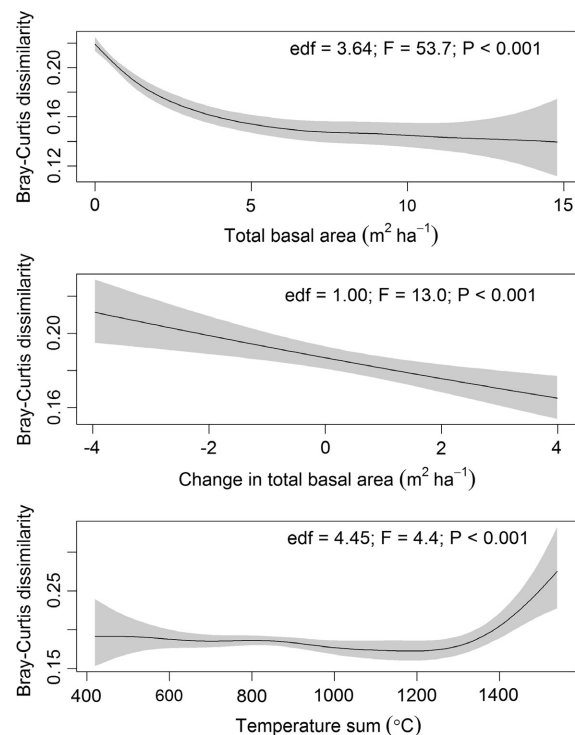


FIG. 4. Smoothers from a generalized additive mixed model (GAMM) of the effects of initial total basal area of trees, change in basal area and temperature sum on the Bray-Curtis dissimilarity (BCD) between inventories (10 yr). The dependent variable is back-transformed to the original scale to facilitate interpretation. Intercept =  $-1.68$  (on the natural log scale;  $t = -106.3$ ;  $P < 0.001$ ). The edf (exact degrees of freedom) indicates the complexity of the GAMM smoother where edf = 1 is a straight line. The shaded areas indicate  $\pm 2$  SE.



associated with the wet fen habitats, which are characterized by low cover of trees and by plant species with high light requirements. This species group exhibited a high turnover, with both increasing and decreasing species and, for two species, the trends also differed along the latitudinal gradient. With respect to this species group, there were only partial overlaps in direction of change with earlier studies (Nordbakken 2001, Gunnarsson et al. 2002, Gunnarsson and Flodin 2007, Kapfer et al. 2011). These studies were, however, all observational from one or a few mires in which mostly local processes were recorded, partly during earlier time-periods.

In contrast to most experiments on warming and nitrogen addition, no general decrease was seen with respect to *Sphagnum* species. Instead, while clearly decreasing in the south, a small increase was indicated in the north. *Sphagnum* mosses constitute a large share of the biomass in mires and were the most frequent group of species in this study. Considering the large sample plot size in the NFI, the decrease in presence of *Sphagnum* in the south is noteworthy. *Sphagnum* mosses incorporate nitrogen in their biomass at low deposition rates (Kooijman 1992, 2012, Bragazza et al. 2005), but the bryosphere may start to leach nitrogen to the roots of competing vascular plants when there is higher deposition (Berendse et al. 2001, Limpens et al. 2003). An increased growth of vascular plants may in turn lower the water table and reduce the competitiveness of *Sphagnum* further (Ohlson et al. 2001). However, different responses among *Sphagnum* species to increased nitrogen (Granath et al. 2009) may delay a general decrease. Hence, threshold effects along nitrogen gradients with positive feedback loops may be expected, with no changes at low deposition while high nitrogen availability may be detrimental. Nitrogen deposition had been ongoing for decades in southern Sweden at the start of our study period and earlier studies have recorded an increase in some *Sphagnum* species (Gunnarsson et al. 2002) that may have been a consequence of this deposition. The NFI aggregates *Sphagnum* species, which leaves us to speculate about changes with respect to individual species; however, it is likely that such a threshold has now been passed in the far south, and that this may have occurred even before our study began.

Drainage of mires may have effects on the vegetation similar to N deposition and warming, including increases in tree encroachment as well as in abundance of dwarfshrubs and forest bryophytes (Laine et al. 1995, Mälson et al. 2008, Punttila et al. 2016). Although we excluded plots directly affected by ditches, drainage elsewhere in the catchments may have contributed to some extent to the observed changes in vegetation. However, most drained mires in Sweden were ditched decades prior to the beginning of our study period (SFS 1979; Hånell 2009). Nevertheless, the initial productivity of our plots was very low ( $<1 \text{ m}^3 \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ ) and by the end of our study only 0.1% of the plots had changed into a more productive land-use class, indicating that any effects of drainage have been very small.

### *Interpretation of the latitudinal gradient*

The latitudinal temperature gradient in Sweden is tightly correlated with the nitrogen deposition (Hedwall et al. 2013a) and was used in the analyses as an integrated vector of these two variables. The nitrogen deposition decreased from  $\sim 15 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$  in the south to close to ambient levels ( $\sim 2 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ ) in the far north (Akselsson et al. 2010). The deposition of anthropogenic nitrogen has continued at these levels for several decades, resulting in an accumulated deposition that is many times larger in the south than in the north. Although even the greatest deposition rates observed in Sweden are far from extreme in an international context (Dentener et al. 2006), the accumulated effects of low annual input rates may result in considerable long-term nitrogen effects (De Schrijver et al. 2011, Phoenix et al. 2012). In addition, there are indications that the effects of nitrogen deposition may increase with increasing temperatures (Limpens et al. 2011). Hence, we expected that the changes in mire vegetation would decrease from south to north. We found very little evidence for such trends when considering individual species, however, and there was almost no effect on the changes in species composition. It has been suggested that increases in temperature will have similar effects on the vegetation as nitrogen deposition (cf. Weltzin et al. 2000, 2003, Bubier et al. 2007, Wiedermann et al. 2007, 2009). One possible reason of the lack of differences along the gradient may be different main drivers of change in the south and north. So far, there has been a greater increase in temperature and vegetation period in the north (SMHI 2015), and these two global change factors may have complementary effects along the gradient.

Two exceptions to the absence of differences between south and north were the effect on *Sphagnum* discussed previously and the non-linear pattern of the Bray–Curtis distance between vegetation inventories along the temperature sum gradient. The Bray–Curtis distance indicates non-linear patterns with a threshold effect and a sharp increase in response at a certain level of environmental impact, i.e., the system may be resistant to low or intermediate impact while a high impact may cause large effects and movement towards an alternative state (Scheffer et al. 2001).

### *Negative vs. positive feed-back loops*

Previous studies indicate that the establishment and expansion of trees and other woody vegetation which reduce the light available to the ground vegetation and lower the water table can induce a positive feed-back loop with respect to the effects of environmental change (Ohlson et al. 2001, Gunnarsson et al. 2002, Heijmans et al. 2013, Waddington et al. 2015). This would imply that changes reinforce each other continuously and the response of the tree layer may increase the effects on the ground vegetation. This is in contrast to the results presented herein, where the increasing density of trees was correlated to a smaller compositional change in the

ground vegetation, independent of the initial tree density. This indicates a negative feed-back loop as the increase in tree cover is a predicted outcome of the same environmental factors that affect the ground vegetation. Similar effects of the tree layer have been found in temperate closed canopy forests, where the tree layer moderated the effects of both increased temperatures and nitrogen deposition on the understory vegetation (Verheyen et al. 2012, De Frenne et al. 2013). Climate change has been predicted to increase frequencies of natural disturbances such as wildfires, gales, pests, and pathogens (Dale et al. 2001). Even if tree cover has increased in general, local and rather drastic tree deaths in peatlands have been described (Gunnarsson and Rydin 1998), probably caused by unusually wet summers leading to anoxia in the root and mycorrhizal zone. Verheyen et al. (2012) and De Frenne et al. (2013) also hypothesized that disturbance of the tree layer could release the effects of, for example, accumulated nitrogen. Our results support this suggestion of interacting effects of local and large-scale drivers as the change in species composition increased when the tree cover was reduced.

#### CONCLUSIONS

This large-scale resurvey study indicates an increase in woody vegetation on Swedish mires, which is probably an effect of nitrogen deposition and increasing temperatures. While nitrogen deposition may be a major driver of vegetation change in southern Sweden, increasing temperatures are probably most important in the north. The observed decrease in *Sphagnum* mosses and a pronounced change in species composition in the far south may indicate a threshold effect due to long-term accumulated nitrogen deposition. This would imply that mire vegetation may be resistant to nitrogen deposition up to a certain level, after which rapid changes towards an alternative state occur. It has been suggested that an increase in tree cover driven by global change may induce additional changes to the ground vegetation in a positive feed-back loop. Instead we found a negative feed-back loop, where the tree cover delays the effects on the ground vegetation. It has been predicted that changes in climate will increase the frequency and severity of natural disturbances of the tree layer due, for example, to pathogens or wind, which in turn may facilitate global change-driven effects on ground vegetation. Hence, our results have important implications for predictions of the long-term effects of global change.

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