

Fine-scale dynamics and community stability in boreal peatlands: revisiting a fen and a bog in Sweden after 50 years

E. PEDROTTI,¹ H. RYDIN,¹ T. INGMAR,² H. HYTTEBORN,^{1,3} P. TURUNEN,¹ AND G. GRANATH^{1,4,5,†}

¹Department of Plant Ecology and Evolution, Evolutionary Biology Centre, Uppsala University, Norbyvägen 18D, SE-752 36 Uppsala, Sweden

²Eriksbergsvägen 18, SE-752 39 Uppsala, Sweden

³Norwegian University of Science and Technology, NO-7491 Trondheim, Norway

⁴Department of Aquatic Sciences and Assessment, Swedish University of Agricultural Sciences, Box 7050, SE-750 07 Uppsala, Sweden

⁵School of Geography and Earth Sciences, McMaster University, 1280 Main Street West, Hamilton, Ontario L8S 4L8 Canada

Citation: Pedrotti, E., H. Rydin, T. Ingmar, H. Hytteborn, P. Turunen, and G. Granath. 2014. Fine-scale dynamics and community stability in boreal peatlands: revisiting a fen and a bog in Sweden after 50 years. *Ecosphere* 5(10):133. <http://dx.doi.org/10.1890/ES14-00202.1>

Abstract. Multi-decadal studies of community and ecosystem dynamics are rare; however, this time frame is most relevant for assessing the impact of anthropogenic influences and climate change on ecosystems. For this reason, we investigated changes in vegetation and microtopography over 52 years in two contrasting mire ecosystems, one ombrotrophic (bog) and one minerotrophic (fen), representing different successional stages and contrasting hydrological settings. In both peatlands, floristic composition was recorded in the same permanent plots ($n = 55-56$, 0.25 m^2) in both 1960 and 2012 and microtopography was mapped over a large area (ca. 2500 m^2) that encompassed these same plots. We quantified and compared the community-level changes and internal spatial dynamics, tested associations between pH/microtopography and community/species change, and examined how the area and location of hummock microforms had changed over time. The bog exhibited little site level change in vegetation, where few species changed significantly in cover and plot frequency. However, detailed analyses revealed some large within-plot changes over time in the bog, illustrating that bogs can be highly dynamic systems at a fine scale. In contrast, the rich fen experienced a clear directional change; specifically, bryophyte abundance decreased by 70% and brown mosses were almost extinct. Although pH had decreased over time at the rich fen, this decrease at the plot-level was not associated with the decline of brown moss abundance. The microtopographic structure did not change substantially at the bog where $\sim 70\%$ was covered by lawn/hummocks; however, in the rich fen hummocks expanded (from 10% to 16% cover) and moved or expanded down slope. Our study suggests, that at the site-level, the bog ecosystem was more resistant to environmental changes over time compared to the rich fen, as evidenced by shifts in vegetation and microtopography. The contrasting scales of vegetation dynamics observed within a bog (i.e., within-plot changes vs. site-level) indicate that plant-environment feedbacks contribute to the peatland level stability. While in rich fens, internal feedbacks may be weaker and the ecosystem's vegetation and microtopographic structure are vulnerable to shifting hydrological fluxes.

Key words: beta diversity; boreal; microtopography; peatland development; plant population and community dynamics; *Sphagnum*; succession; vegetation change.

Received 24 June 2014; revised 8 August 2014; accepted 27 August 2014; final version received 23 September 2014; **published** 31 October 2014. Corresponding Editor: D. P. C. Peters.

Copyright: © 2014 Pedrotti et al. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited. <http://creativecommons.org/licenses/by/3.0/>

† **E-mail:** gustaf.granath@gmail.com

INTRODUCTION

A pressing question in plant ecology is how to understand the impact of global change on ecosystems (Walker et al. 2006). Peatlands are unique ecosystems in that long-term (millennium) changes in species composition, structure and carbon accumulation rate can be studied by examining peat cores. These paleoecological studies have shown the contrast between stability and rapid change in ecosystem structure (Janssens et al. 1992). Similarly, changes in ecosystem structure have also been observed in vegetation studies over time spans of 5–60 years (Gunnarsson et al. 2000, Nordbakken 2001). Although previous studies provided some understanding of the temporal dynamics of ecosystem structure, little is known about the fine-scale floristic variation over time and how successional stage interacts with susceptibility to change.

Boreal peatlands consist of fens and bogs, where fens receive minerotrophic ground water and bogs rely on precipitation and atmospheric deposition as sources of water and nutrients. The accumulation of peat characterizes both bogs and poor fens (i.e., fens with low pH), which can largely be ascribed to the bryophyte genus *Sphagnum* (peat mosses). With its acidifying and recalcitrant litter, *Sphagnum* rapidly forms peat (Rydin and Jeglum 2013). In rich fens (high pH), other bryophytes dominate and peat accumulation rates are usually much lower (Thormann et al. 1999). If the peat accumulation process continues in a fen, the peat surface will eventually disconnect from the minerotrophic ground water and the fen transforms into a bog. The fen-bog transition (ombrotrophication) has traditionally been described as a unidirectional slow autogenic succession (Zobel 1988), but recent research describes how rapid these shifts may occur (Granath et al. 2010, Tahvanainen 2011). For example, Granath et al. (2010) showed that the absence of flooding can allow *Sphagnum* to expand in rich fens, thereby resulting in an ecosystem shift to a poor fen or bog within decades. However, if *Sphagnum* cover remains sparse in a rich fen, a fen-bog transition may not occur because of the slow peat accumulation rates of other plants.

Peatland vegetation structure and composition varies spatially at multiple scales (from <1 m to

km) largely due to differences in the environmental conditions and spatial aggregation (Andersen et al. 2011, Rydin and Jeglum 2013). The main environmental gradients are pH and height above the water table, the latter often dichotomized as hollows (peat surface closer to the water table) and hummocks (peat surface farther above the water table). Not surprisingly, vegetation changes have also been attributed to changes in precipitation and temperature (Belyea and Clymo 2001, Weltzin et al. 2003, Gunnarsson and Flodin 2007, Breeuwer et al. 2010) and long-term exposure to atmospheric deposition (Gunnarsson et al. 2000, Limpens et al. 2011). The impact of atmosphere deposition is likely most evident in bogs, as they more heavily rely upon atmospheric fluxes than fens.

Microtopographic patterns of hollows and hummocks are directly coupled to the autogenic process of peat accumulation, where hummocks form through the establishment of *Sphagnum* species that produce decay-resistant litter (Johnson and Damman 1993). However, hydrological feedbacks may also play a key role in the distribution and formation of the microtopographic structure (Morris et al. 2013). Recent studies have tried to understand the stability and dynamics of microtopography primarily through modeling approaches (Nungesser 2003, Couwenberg 2005, Eppinga et al. 2010), although ground-penetrating radar has also been applied and indicated that hummocks in peatlands may move downslope over time (Kettridge et al. 2012). Furthermore, Koutaniemi (1999) mapped strings and flarks in a northern boreal fen (66° N) over 21 years, and recorded both downhill and uphill movements as high as several decimeters in some years, mainly due to frost actions. However, in regions less affected by frost action, long-term data that capture these dynamics in bogs and fens are lacking. This lack of data is surprising since microtopography is central to peatland ecology and changes in microtopography have an impact on hydrological and biogeochemical processes (Belyea and Clymo 2001).

The aim of this study is to quantify and compare the community-level changes and internal spatial dynamics in a bog and a rich fen over a half-century, using a unique set of permanently marked plots established in 1960. Specifically, we investigate if there are signs of successional

processes in the rich fen, showing a directional change towards poor fen or even bog vegetation, and compare the amplitude of such changes with that in the bog. Subsequently, we investigate if these changes can be related to pH and water level. We also examine how the area and location (i.e., persistence) of hummock microforms have changed over time. We envisage that hummock expansion may occur in the rich fen as a first stage towards ombrotrophication, but that hummock microforms are likely more stable in the bog.

METHODS

Study area

Florarna is a nature reserve (52 km²) in SE Sweden (Uppsala county), consisting of a complex of peatlands, ranging from rich fens to bogs (Ingmar 1971). The area is ~30 m a.s.l. and has been undergoing land uplift (isostatic rebound) since the last glaciation and emerged from the sea about 2000–1500 BC. Stratigraphic analyses show that many peatlands in this area have undergone a succession from rich fen (shaped under the influence of calcium-rich moraine), via poor fen, to bog (Ingmar 1963). The hydrological history is well documented from the early 17th century when the catchment outlet was dammed (named Pierreslután) for hydro power. The frequency of low water levels were reduced and periods of high water levels were prolonged; however, the maximum high water level was not changed. The dam was razed in 1955 lowering the water level in the lake system by ca 30 cm (Brunberg and Blomqvist 1998) until 2002 when the hydrology was roughly restored to its pre-17th century regime. The fen and bog sites are 600 m and 2000 m away from the nearest lake, respectively. At mean water level, the fen and bog sites are currently, and before 1955, about 1.0 and 3.2 m above this lake system. Additionally, there are no drainage or forestry operations that have affected the study sites.

The mean temperature in January is -3.7°C and in July is 16.4°C , and average annual precipitation is 676 mm (1961–2012, Swedish Meteorological and Hydrological Institute, SMHI, www.smhi.se). Monthly data for the period between vegetation surveys (1961–2012) indicate a slight increase in temperature during

the growing season (average temperature between May 1 to September 30), especially between 1985 and 2005 (SMHI, www.smhi.se; Appendix: Fig. A1). There was no clear trend in monthly precipitation, although there appears to be a cyclical pattern. From precipitation and temperature data, we calculated the ratio between precipitation (P) and potential evaporation (PE; see Oudin et al. 2005 for equation), which was used as a moisture index (P/PE; Prentice et al. 1993), and did not show any trend over time (Appendix: Fig. A1).

The fen site

The open rich fen is virtually horizontal, but with a weak water flow from south to north (Appendix: Fig. A2) and a pH of ~6–7. In the center of the fen, a 25×150 m main plot was established in 1960 in W-E direction (north-west corner at $60^{\circ}16.775' \text{ N}$, $17^{\circ}51.609' \text{ E}$) to capture the spatial heterogeneity within the fen.

The bog site

The slightly raised bog has a pattern of strings of hummocks and hollows in the center, pine covered edges, and a lagg fen bordering the forest on mineral soil in some areas (Appendix A: Fig. A2). A main plot, with the size 40 m (south-north) \times 60 m (east-west), was established to cover the typical boreal pattern of hummocks and hollows, with a pH close to 4 (northwest corner at $60^{\circ}16.977' \text{ N}$, $17^{\circ}49.248' \text{ E}$). The plot has a faint slope with the hollows about 2 dm lower in the eastern than in the western part of the plot.

Plant survey and environmental data

The first survey in 1960 was performed by Ingmar and he also instructed the 2012 survey to ensure consistency in methods. Nomenclature follows Hallingbäck et al. (2006) for bryophytes and Karlsson (1997) for vascular plants.

By random sampling, uncommon species and communities are usually undersampled, or not sampled at all. Therefore, in 1960, a stratified sampling design was set up. Based on dominant species, 10 community types were identified at the rich fen (four of which were separated into subtypes with or without co-dominance by *Myrica gale*) and 15 at the bog. At each main plot, an accurate 5 m \times 5 m grid was established with measuring tapes and each grid intersection

was assigned to a community type. For each community type, sub-plots (0.5 m × 0.5 m) were placed at five randomly selected grid points assigned to that community (less than five grid points for the rarest community types), adding up to 55 and 56 plots in the main plot of the fen and bog, respectively. The plots were marked in 1960 and revisited 1983 when the wooden markers were replaced with PVC tubes to secure the locations. During the survey of the plots in 2012, only seven markers could not be located at the fen site and 19 at the bog site; furthermore, our grid points were always within 5 cm from the old markers. Hence, a high degree of accuracy was achieved during the relocation of the plots, even where markers were lost.

Percent cover of each species was estimated using the same method in 1960 and 2012 with the following scale: 1–5% (1% interval), 7%, 10–95% (5% intervals), 95–100% (1% interval).

The year of 2012 was very wet with the down gradient parts of the mires permanently flooded. Bryophytes growing in the wettest areas in the rich fen were entangled in a gyttja-like material and, as a consequence, it was difficult to find and identify them at the species level. We also feared that the submersion of these bryophytes in algal-rich water led to extensive short-term fluctuations in community composition. Therefore, we re-surveyed bryophytes in the rich fen in the dry year (2013) to assess whether or not their presence was underestimated in 2012. Another person performed this additional survey to avoid bias and it is worth noting that results from the 2013 survey did not affect the statistical results of the comparisons with the 1960 survey. For this reason, we concluded that short-term fluctuations caused by an extreme year or observer bias could be ruled out, and base our analysis on vegetation data from 2012.

To investigate acidification of the rich fen, we examined changes in plot level pH in 2013. The same method was used in both 1960 and 2013, where measurements were made in water from lightly squeezed surface samples. A pH instrument was used in 1960, and in 2013, we used a portable pH meter (Hanna Instruments 98129).

To test if vegetation changes can be related to the water level, we measured surface height above the water table (HWT; Rydin and Jeglum 2013) for all plots in 2013 using a perforated

plastic tube as a dipwell and a plumper to locate the water table. HWT was not measured in 1960, therefore, relating vegetation changes to microtopographic position can only be made for 2013.

Mapping microtopography

In 1960, the 5 × 5 m grid was used to map the microtopographic structure. By using a gridded paper, the structures were mapped (scale 1:200) with a high degree of accuracy (likely within ±10 cm). At the rich fen, microtopographic mapping did not cover the eastern third of the main plot and hummocks were mapped because they were easy to delineate, where they rose above the otherwise flat surface. At the bog, it was easier to delineate the hollows. For the purpose of this investigation, the hummock-hollow border was defined as the rather sharp and easily observable transition between dominance of the brown and red *Sphagnum* sect. *Acutifolia* (*S. fuscum* and *S. rubellum*; hummock) and the lighter colored *Sphagnum* sect. *Cuspidata* (*S. cuspidatum*, *S. balticum*, *S. tenellum*; hollow). To re-map the microtopographic structures, we used a differential carrier-phase GPS (Model: Trimble R7 GNSS, Antenna: Zephyr Geodetic II) in kinematic mode with one recording per second. A local base-station was placed ~1 km from the survey sites and was connected to the Swedish Grid (SWE-POS network of base-stations). The post-processing was done in Trimble Business Center v 2.08 giving an accuracy of ±2 cm in horizontal and ±4 cm in vertical. We also recorded the main plot corners and plot positions with the GPS.

Data analysis

For each species, paired *t* tests were employed to test if changes in abundance between the two time points were significant ($\alpha = 0.05$). Welch approximation of degrees of freedom was used to account for unequal variances. We only included plots where the species was present in at least one of the years and excluded double zeros. The inclusion of all plots would mean including plots (i.e., microhabitats) that fall outside the fundamental niche of the species. Thus, it is easier to interpret the effect sizes instead of using all plots that contain many double zeros. To test if species had changed significantly in plot frequency, we performed Fisher's exact test. Species (S) turnover in the

plots is expressed as a proportion of the species recorded in 1960, i.e., $(S_{\text{new}} + S_{\text{lost}})/S_{1960}$. The liverwort species, *Aneura pinguis* and *Calypogeia sphagnicola*, were excluded since they were difficult to sort out in the gyttja-like material in wetter parts of the fen in 2012 (e.g., *Calypogeia sphagnicola* was not found 2012 but recorded 2013). For the *Cladonia* lichens we distinguished *Cladonia alpestris* and *Cladonia rangiferina*, but treated the remaining *Cladonia* species collectively. For all analyses, *Vaccinium oxycoccos* and *V. microcarpum* were merged since they were not always distinguishable in the field.

To investigate the prediction that changes in species community were different between sites (fen and bog) over time (i.e., differences in directional changes), we tested the time \times site interaction in a Multivariate ANOVA, using the *adonis* function in R package *vegan* ver 2.0-10 (Oksanen et al. 2013, R Development Core Team 2013). This function generates a MANOVA, using a distance matrix (here Bray-Curtis dissimilarities) as response, and a permutation test in order to detect the differences in group means (Anderson 2001). Because of the repeated measurement structure of the data, we did not allow permutations within plots to formulate the correct null-hypothesis for the interaction effect. If differences in within-group variation between groups are large, a significant effect may reflect differences in dispersion rather than different mean values of the groups (Warton et al. 2012). However, it has been suggested that the *adonis* function is less sensitive to dispersion effects than some of its alternatives, e.g., ANOSIM (Oksanen et al. 2013). We explored the differences in dispersion (*beta-diverse* function) to evaluate the results given by the MANOVA, and to analyze whether the vegetation at the two sites had converged (less dispersion) or diverged (larger dispersion). To further compare within plot changes with site level changes (e.g., Benschoter and Vitt 2008), we analyzed changes in dissimilarities (Bray-Curtis index) for each plot (plot dynamics) and for each main plot (site level dynamics, i.e., prior to calculating dissimilarities, mean species abundances were calculated for 1960 and 2012). In addition, we partitioned the Bray-Curtis dissimilarities (BC_{sum}) into two components following Baselga (2013): (1) balanced variation in abundance (BC_{bal}), that is dissimilarity caused by

species abundances change from 1960 to 2012 with different signs for different species so the changes balance, (2) abundance gradients (BC_{gra}), that is species changes their abundance from 1960 to 2012 in the same direction (increase or decrease). The R package *betapart* ver 1.3 was used to calculate BC_{bal} and BC_{gra} (Baselga et al. 2013).

Vegetation changes over time at the two sites, were illustrated by plotting results from a Nonmetric Multidimensional Scaling (NMDS) analyses performed in *vegan*. A separate NMDS was made for the rich fen and a smooth surface (generalized additive model, GAM) for pH was fitted to investigate the relationship between community change and pH.

For structural and spatial changes, the recorded points were retrieved from the GPS, plotted in Quantum GIS version 2.0 (Quantum GIS Development Team 2013) as polygons representing the microtopography in 2012. The 1960 map was georeferenced using main plot corners and two grid points as fix points and structures were added as polygons in a layer representing 1960. Changes in hollow (bog) and hummock (fen) cover were analyzed by calculating polygon area 1960 and 2012, and polygon overlap using the R package *rgeos* ver 0.3-6 (Bivand and Rundel 2013).

Data and R code to conduct the analyses are available as a Supplement in *Ecological Archives*.

RESULTS

Species occurrences and turnover

In the plots, a total of 61 species were recorded in the rich fen (1960: 50, 2012: 47) and 24 in the bog (1960: 23, 2012: 23) (Appendix: Tables A1 and A2). At the rich fen, 13 species were recorded only in 1960 and 11 species were only recorded in 2012. For the bog, one species was only recorded in 1960 and one new species was found 2012. The species turnover in the plots was 48% and 9% for the fen and bog, respectively.

Changes in plot frequency

In the fen, four species were found in significantly more plots ($P < 0.05$) in 2012 than in 1960, with the largest increase in *Eriophorum angustifolium* (25 more plots). Seven species decreased in frequency (Table 1; Appendix: Table

Table 1. Changes in plot frequency and cover (%) for species between 1960 and 2012 at the rich fen and bog. The change columns indicate the direction and magnitude of the change, i.e., an increase or decrease of plots with the species present or the absolute change in percent units. For brevity, only the most abundant species and species with interesting changes are shown. P-values are derived from Fisher's exact test (frequency change) and paired *t* tests (change in percent cover), respectively. *n* equals the number of plots in which the species was present at least one of the years. A complete species list is given in Appendix A: Tables A3 and A4.

Species	Change in plot frequency	Absolute change in cover (%)	Mean cover 1960 (%)	<i>n</i>
Rich fen				
<i>Andromeda polifolia</i>	10	0.6*	0.7	41
<i>Aulacomnium palustre</i>	2	12	1	7
<i>Calliergonella cuspidata</i>	0	-3	6	8
<i>Campylium stellatum</i>	0	-21**	25	33
<i>Carex chordorrhiza</i>	-10*	-1.3***	1.3	10
<i>C. lasiocarpa</i>	-1	-3**	5	55
<i>C. limosa</i>	-27***	-0.9***	1.2	43
<i>C. livida</i>	-6	-1**	2	50
<i>Cinclidium stygium</i>	1	-1	3	16
<i>Drosera intermedia</i>	-11*	-1*	2	25
<i>Eriophorum angustifolium</i>	25***	0.9***	0.2	30
<i>Menyanthes trifoliata</i>	-5	3**	2	46
<i>Myrica gale</i>	10**	9**	11	55
<i>Pseudocalliergon trifarium</i>	-17***	-2*	2	17
<i>Rhynchospora alba</i>	-16*	1*	1	45
<i>R. fusca</i>	5	2.2	0.0	5
<i>Scheuchzeria palustris</i>	-17***	-2**	3	49
<i>Scorpidium revolvens</i>	-5	-2*	2	8
<i>S. scorpioides</i>	-22***	-46**	47	41
<i>Sphagnum centrale</i>	3	17	63	8
<i>S. contortum</i>	16***	-10*	17	34
<i>Trichophorum alpinum</i>	8*	0.8*	0.3	12
<i>Utricularia intermedia</i>	4	1	1	34
<i>Vaccinium oxycoccos</i>	9	1**	1	44
<i>Warnstorfia exannulata</i>	8	0	3	13
Bog				
<i>Andromeda polifolia</i>	5	1	2	53
<i>Calluna vulgaris</i>	8	1	18	34
<i>Cladonia alpestris</i>	-11**	-15*	16	13
<i>C. rangiferina</i>	-4	-8	9	17
<i>Drosera rotundifolia</i>	16**	1.1***	0.8	40
<i>Eriophorum vaginatum</i>	7	-1	4	53
<i>Mylia anomala</i>	1	0	2	40
<i>Pinus sylvestris</i>	10*	2.3	0.5	15
<i>Pleurozium schreberi</i>	-7	-23*	26	12
<i>Rhynchospora alba</i>	-8	-3**	4	12
<i>Sphagnum balticum</i>	7	-2	18	42
<i>S. cuspidatum</i>	0	-19	76	18
<i>S. fuscum</i>	3	23**	37	32
<i>S. rubellum</i>	16*	11*	23	44
<i>Vaccinium oxycoccos</i>	4	-2	4	54

P* < 0.05; *P* < 0.01; ****P* < 0.001.

A3), where *Carex limosa* decreased the most (27 fewer plots) and some of the bryophytes, e.g., *Pseudocalliergon trifarium* (-17) and *Scorpidium scorpioides* (-22) also decreased considerably (Table 1). At the bog changes were less noticeable, three species increased significantly in frequency (*Drosera rotundifolia*, *Pinus sylvestris* and *Sphagnum rubellum*), while only the lichen *Cladonia alpestris* decreased (Table 1; Appendix: Table A3).

Changes in cover

At the rich fen, 18 species showed statistically significant change in cover between 1960 and 2012 (seven increased and eleven decreased) but many changes were small (Appendix: Table A4). Among the more consistent changes, we note the decrease in *Sphagnum contortum*, *Scorpidium scorpioides* and *Campylium stellatum*, and the increase in *Myrica gale* (Table 1, Fig. 1). At the bog, only three species exhibit statistically signif-

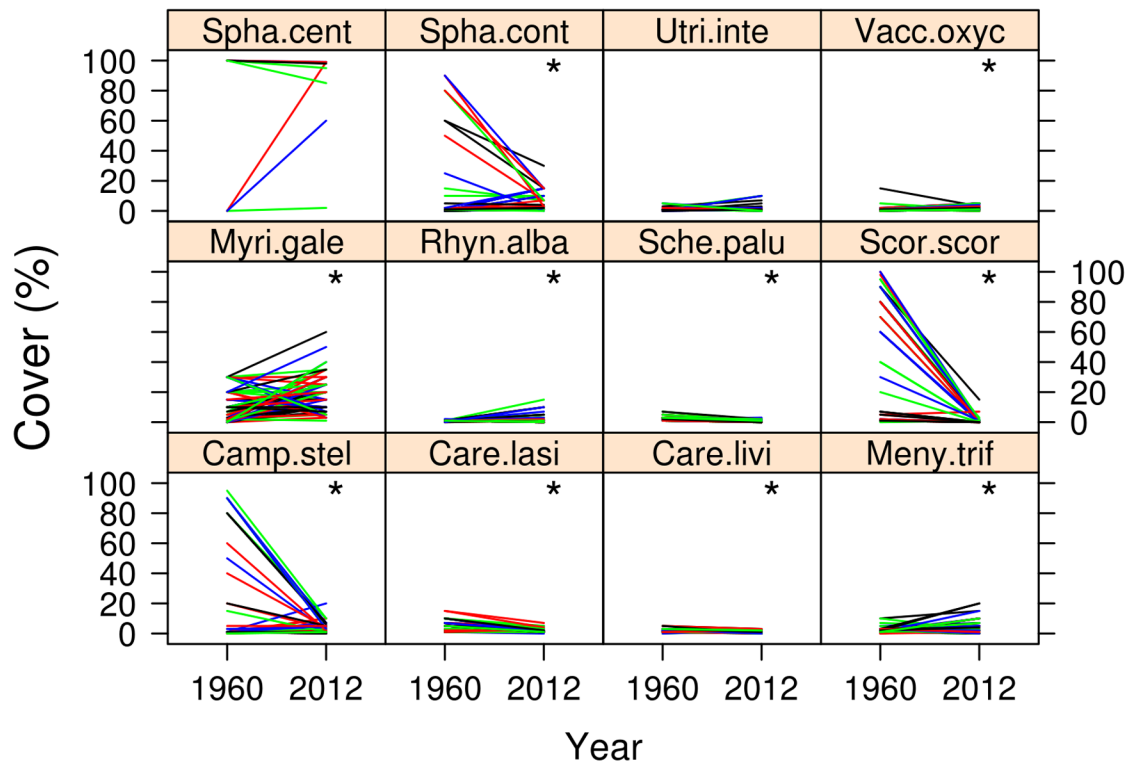


Fig. 1. Changes in cover (%) of the 12 most abundant species at the rich fen between 1960 and 2012. The first four letters of the genus and species epithet is given (see table 1 for full names). Asterisk indicates if the change in abundance is statistically significant ($P < 0.05$). Lines represent plots where the species was recorded at least one of the years.

icant increases in cover, while three species significantly decreased in cover (Table 1). However, for some species, the changes were rather erratic and species that increased on average could display large decreases in some plots (e.g., *Sphagnum fuscum* and *S. rubellum*; Fig. 2). Analyses of changes in abundance for the different life forms at the rich fen showed almost a doubling in dwarf shrubs (from 13% to 24% in cover) while bryophytes were reduced to a third (73% to 23% in cover) (Table 2). At the bog, only minor shifts in cover of different life forms were observed.

Changes in species composition

Permutation MANOVA, based on Bray–Curtis dissimilarity matrices, tested if the species community changed over time and if communities changed differently between sites (fen and bog). An interaction effect between time and site suggests that the two sites have changed differ-

ently over time ($F_{1,108} = 18.0$, $P = 0.001$). The NMDS plot illustrates that the rich fen site has significantly shifted to become more similar to the bog, while the bog site centroids from the two years almost completely overlap (Fig. 3A). Analyses of site dispersion at the two time points of the two sites indicated that the spread of plots in the multivariate space were different between the four groups. The differences were not large, but the PERMANOVA results should be interpreted cautiously. Further analysis of site dispersion showed that the plant communities within each site had converged (not shown).

Analyses of changes in dissimilarity (Bray–Curtis index) for each plot (plot level dynamics) and for each site (site level dynamics) showed large changes within plots over time at both sites (Fig. 4). At the rich fen, the site-level survey showed that it was 33% dissimilar in 2012 compared to 1960 and most plots were more than 50% dissimilar. In contrast, the bog exhib-

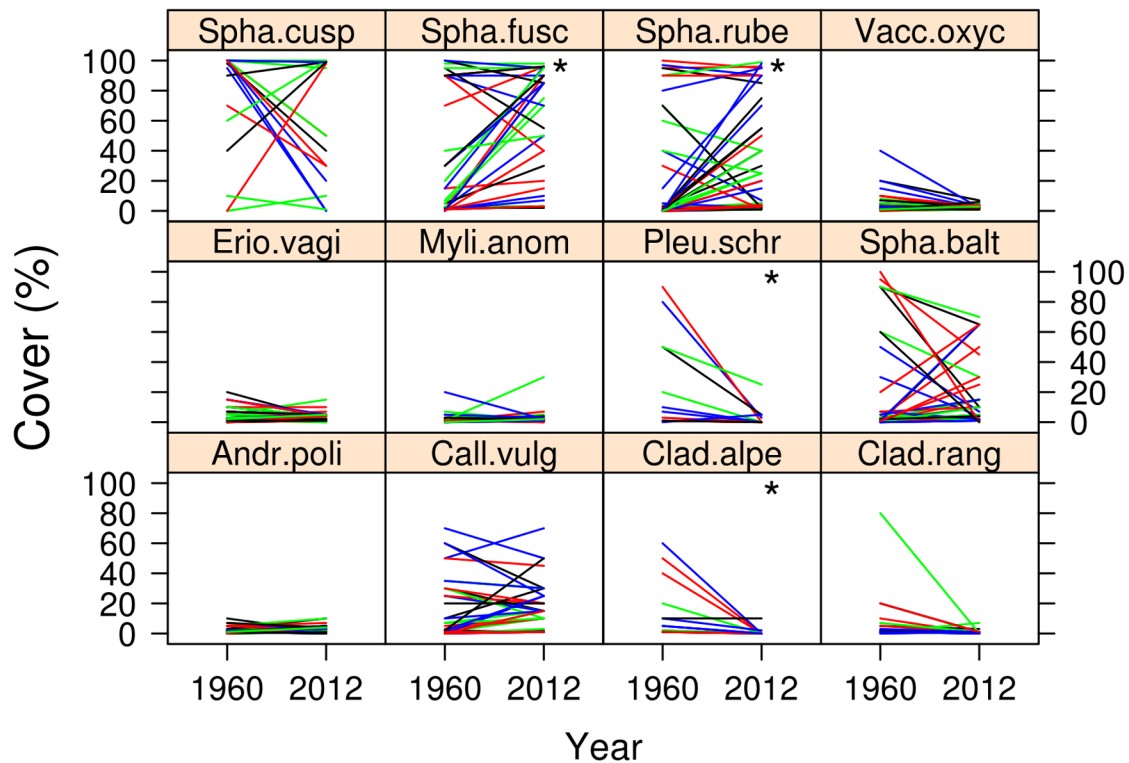


Fig. 2. Changes in cover (%) of the 12 most abundant species epithet at the bog between 1960 and 2012. The first four letters of the genus and species are given (see Table 1 for full names). Asterisk indicates if the change in abundance is statistically significant ($P < 0.05$). Lines represent plots where the species was recorded at least one of the years.

ited little change at the site level (6% dissimilarity), although it exhibited large changes within plots. At the bog, changes in species composition were almost exclusively due to balanced variation, that is, the abundance of some species declined over time in the same magnitude as the abundance of other species increased. In contrast, a significant proportion of the changes at the rich

fen site were due to a directional change (i.e., decline or increase in abundance) and it was even more important than balanced variation at the site level.

Effects of pH and water table position on species changes

In 1960, pH was measured in 39 plots of the 55

Table 2. Changes in cover of life forms between 1960 and 2012 (summed cover of all species within each life form) at the rich fen (n = 55) and bog (n = 56). P-values are derived from paired *t* tests.

Life form	Rich fen		Bog	
	Absolute change in cover (%)	Mean cover 1960 (%)	Absolute change in cover (%)	Mean cover 1960 (%)
Trees	1.1	0.2	0.6	0.1
Dwarf shrubs	11.2***	12.7	-0.1	18.7
Graminoids	-4.8***	13.0	-1.6*	5.5
Herbs	2.7***	4.5	1.0**	1.9
Mosses	-50.0***	72.8	8.8*	83.3
Liverworts	-0.3***	0.4	0.2	1.5
Lichens	0.1	0.0	-7.7*	8.8

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

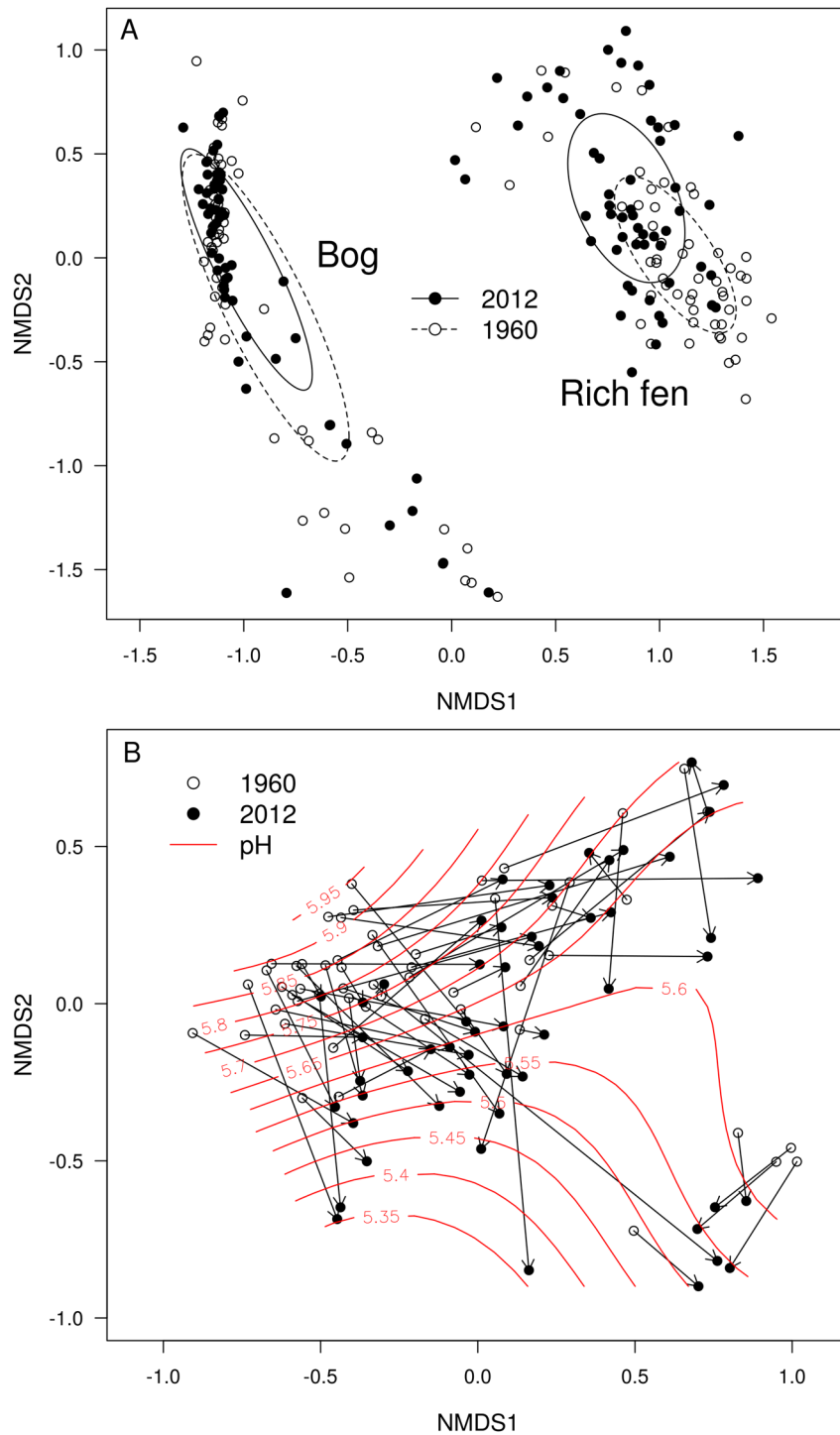


Fig. 3. NMDS ordination showing plots based on Bray–Curtis dissimilarity matrix (stress 0.08). In the upper panel (A) both sites are included in the ordination (stress = 0.08) and the lines represent standard deviation of the groups' centroids. The lower panel (B) is an ordination (stress = 0.08) of the rich fen site with a fitted smooth surface (GAM) for pH (measured in 2013). Arrows illustrate the movements of each plot between the years.

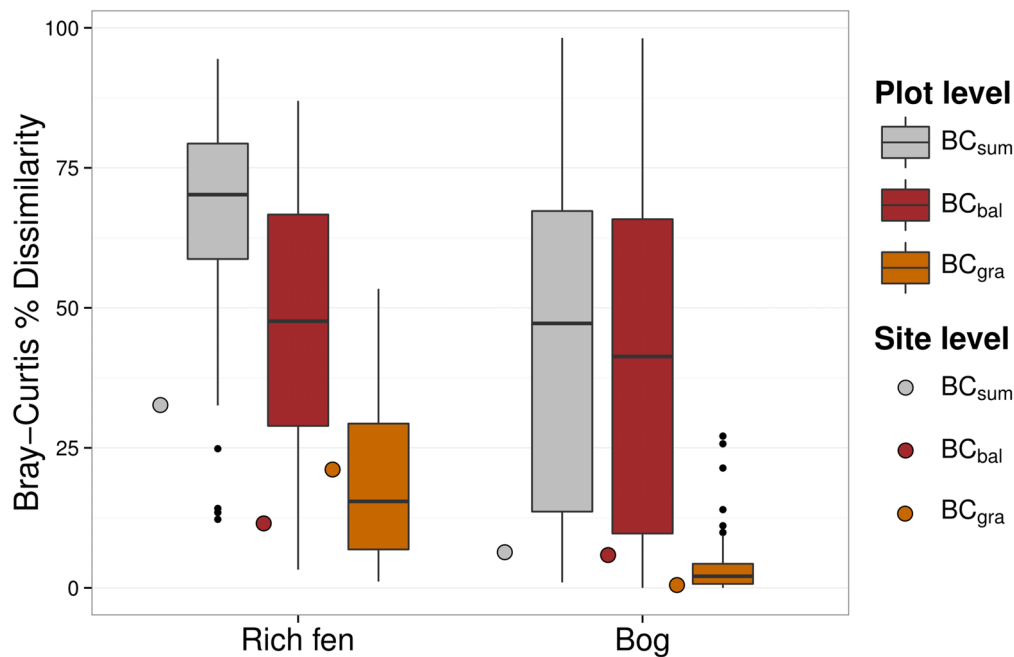


Fig. 4. Dissimilarities (Bray-Curtis, BC) between 1960 and 2012 at each plot for the two sites. Thick line indicates the median value and the box shows lower and upper quartiles, and whiskers cover the 1.5 interquartile distances. Values located outside the whiskers are indicated by black dots. Colors are the different components of BC dissimilarity, where BC_{sum} is the sum of BC_{bal} (balanced variation in abundance, whereby different species increase and decrease equally over time) and BC_{gra} (abundance gradients, whereby species generally increases, or decreases, over time). Filled circles to the left of each box represent dissimilarities between the years at the site level. These dissimilarities are derived using site means of each species (i.e., the mean cover of all plots).

plots in the fen and pH was lower in 38 of these plots in 2012 compared to 1960. On average, pH had decreased by 0.31, from 5.84 to 5.53 (paired t test, $t = 9.8$, $df = 38$, $P < 0.001$). There was no correlation between pH change and height above the water table (HWT) in 2013. An overlay of a pH gradient on an NMDS for the rich fen site supported the hypothesis that species changes were partly associated with changes in pH (Fig. 3B). At the plot level, large changes (quantified as Bray-Curtis dissimilarity between 1960 and 2012) were associated with high HWT at the rich fen, while no such relationship was observed in the bog (Fig. 5). However, individual analyses on pH sensitive moss species that showed a large decrease in abundance (i.e., *Campylium stellatum*, *Scorpidium scorpioides*, *Sphagnum contortum*) revealed no strong correlation between their decrease and pH change, or with HWT measured in 2013.

Changes in microtopographic structure

The analysis of the two polygon layers (1960 and 2012) showed a 73% increase in hummock area at the rich fen, where coverage increased from 9% in 1960 to 16% in 2012 (Fig. 6). About 10% of the hummock area in 2012 was not mapped as hummocks in 1960; hence, some areas decreased in hummock cover between 1960 and 2012. Plots of the two layers further illustrate this dynamic in hummock distribution, where it is noticeable that most hummocks have moved slightly downslope (Fig. 6). At the bog site, observed changes were much smaller, where hollow area had decreased from 34% to 25% and was almost exclusively attributable to some hollows becoming smaller. Moreover, hollows exhibited little expansion into new areas and there were no directional changes (Fig. 6).

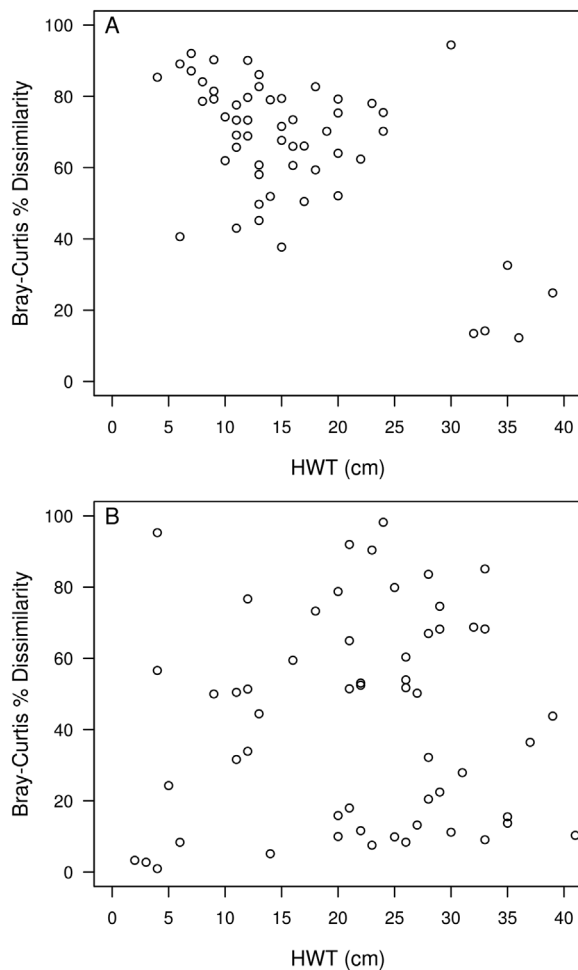


Fig. 5. Dissimilarities (Bray-Curtis, BC) between 1960 and 2012 at each plot, plotted against height above the water table (HWT) measured in 2013 for the (A) rich fen (Spearman rank correlation $r_s = -0.44$, $P < 0.001$), and (B) the bog ($r_s = 0.08$, $P = 0.55$).

DISCUSSION

Changes in species presence and abundance

The most striking results are the changes in the rich fen: the drastic decline in brown mosses (e.g., *Campylium stellatum* and *Scorpidium scorpioides*), the increase of shrubs (mainly *Myrica gale*), the decrease in pH, and the expansion of hummocks. These changes could have been caused by a number of autogenic and allogenic factors that are not easily distinguishable from one another. Calcareous fens will naturally go through a phase of acidification, leading to ombrotrophica-

tion and bog formation. Furthermore, this process can be swift and take place in a matter of decades (e.g., Janssens et al. 1992). Sharp declines in brown mosses and a concomitant drop in pH, which are indicative of rapid transitions, have been observed over the last 50 years at other peatlands in the region. In one instance, a fen had lost most of its brown mosses since the 1950s (Thygesen 1997). Because peatlands in this region are situated where the land emerged after postglacial land uplift, a low altitude indicates that Florarna (30 m a.s.l., this study) is younger and emerged out of the sea later than the fen described by Thygesen (1997) (60 m a.s.l.). Therefore, it is not probable that they both should have reached this stage of quick autogenic change during the exact same decades. Furthermore, similar changes have been documented in distant parts of Sweden (Hedenäs and Kooijman 1996).

The observed changes would be consistent with anthropogenic acid and nitrogen deposition during the 20th century. Acid deposition mimics the natural *Sphagnum*-induced acidification (e.g., Granath et al. 2010) and nitrogen can reduce the growth of bryophytes both directly (N may be toxic at high levels, Paulissen et al. 2004) and indirectly by promoting vascular plants and thereby reducing available light for bryophytes (Kooijman 1992, Mälson et al. 2008). Changes in species composition were indeed associated with reduced pH, however, the trend was not strong for brown mosses and there may be within and between year variation in pH not captured by our study. However, N deposition may not account for changes in species composition for two reasons: (1) Florarna is located in a region with low N deposition ($\sim 0.6 \text{ g m}^{-2} \text{ yr}^{-1}$; Granath et al. 2009) that is far below the present critical limit of $1.5\text{--}3.0 \text{ g m}^{-2} \text{ yr}^{-1}$ for base-rich fens (Bobbink and Hettelingh 2010) and (2) the expanding *Myrica gale* is a nitrogen fixer and is less likely to benefit from high N availability.

Because nutrients are not likely to account for the observed changes in the fen, the occurrence of dry conditions over the last 50 years are likely important. Indeed, temperature has increased over the last 50 years and, although water availability has varied over time, data suggest two particularly dry periods between 1960 and 2012 (Appendix: Fig. A1). The decrease in

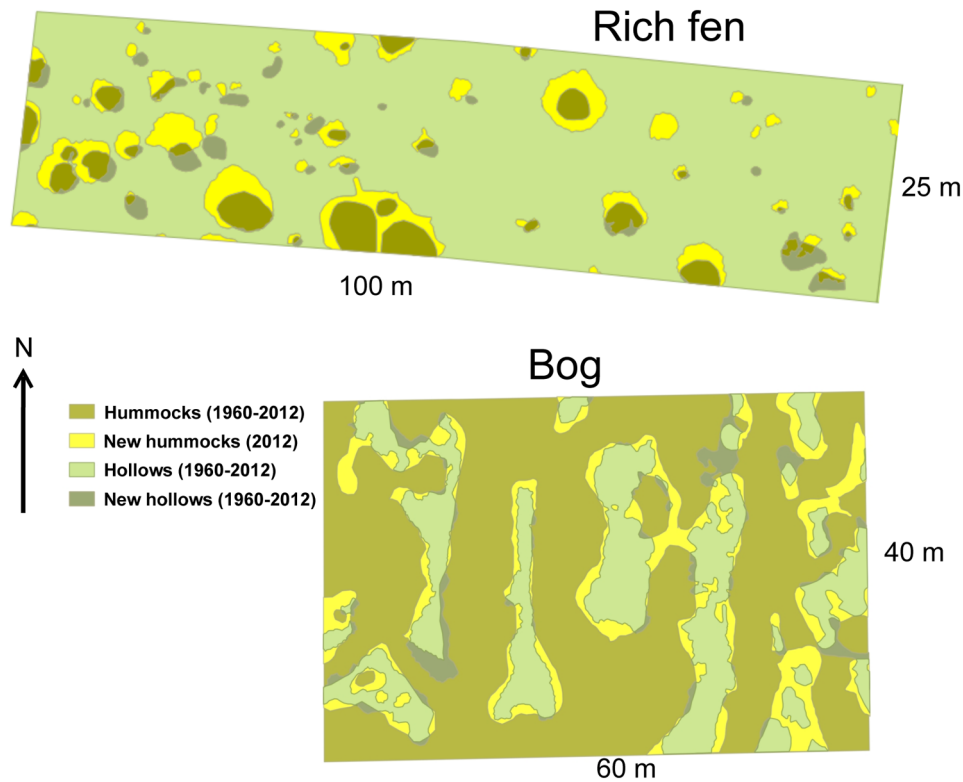


Fig. 6. Upper: Mapped hummocks at the rich fen site. Lower: Mapped hollows at the bog site. The surveyed rich fen plot extends 50 m to the east but that section was not mapped. See Appendix: Fig. A2 for an aerial photo of the sites.

frequency of *Scheuchzeria palustris*, like elsewhere in Sweden (Gunnarsson et al. 2002, Kapfer et al. 2011), provides further support that the occurrence of dry periods explain these shifts because this species is sensitive to prolonged dry periods (Tallis and Birks 1965). Moreover, dwarf shrubs would benefit from drier conditions in the surface peat due to increased availability of oxygen for root respiration and mycorrhiza (Pellerin and Lavoie 2003, Kapfer et al. 2011, Gunnarsson and Flodin 2007). The role of the lake's water regime is somewhat difficult to evaluate. Before 1955, and after 2002, the lake water level was usually about 0.8–1.1 m below the fen site, but occasional peaks in lake water level could probably have risen very close to the fen surface level (T. Ingmar, *personal observation*). In the 1955–2002 period, the lake water level, was roughly 30 cm lower, and even at high-water peaks, would have been at least 30 cm below the fen level. Although we lack detailed data on

water level fluctuations, it is likely that the absence of high-water events over a half-century promoted the expansion *Myrica* shrubs and *Sphagnum* hummocks (cf. Granath et al. 2010). Such changes may be irreversible and we can at least conclude that the changes remain after ten years of restored water levels.

In the bog, a small increase in *Sphagnum* cover occurred in the absence of expansion of vascular plants. This indicates stable ombrotrophic and oligotrophic conditions, making the site more favourable to *Sphagnum* than vascular plants (Malmer et al. 1994). Most of the erratic changes in *Sphagnum* cover took place in plots placed close to the border between hummocks and hollows, where even the small spatial changes in microtopographic structures could lead to quite large changes in species composition (e.g., hummock species being completely replaced by lawn/hollow species in the plot). Such lateral shifts in microtopography have been linked to a

feedback mechanism that increases the resilience of bogs to changes in hydrology and helps to maintain the bog surface pattern under periods of climatic variation (Belyea and Clymo 2001). Studies over the last decades have reported a rapid expansion of trees, shrubs and other vascular plants in bogs and attributed this to increased N deposition and climate change (Gunnarsson et al. 2002, Pellerin and Lavoie 2003, Kapfer et al. 2011). However, this trend was not supported in our study and a larger study area would have been required to observe increases in tree cover. Moreover, the warmer and drier recent period does not seem to have had a significant impact on the bog. By definition, the bog yields a surplus of water and as long as the *Sphagnum* cover is intact, it will be resistant to small climatic fluctuations.

Changes in species composition and peatland stability

The NMDS ordination showed a considerable change in species composition at the fen site between 1960 and 2012 compared to the bog site. As with the changes in individual species, this result suggests a directional change (i.e., decline or increase in abundance) in the fen under the influence of drier and more acidic conditions. The directional change was clearly more important than balanced variation (by which the abundance of some species would decline over time in the same magnitude as the abundance of other species increased) at the site level. However, the change has not caused a major change in the plot floristic heterogeneity, as indicated by the beta-diversity (reflected in the size of the ellipse and the average distance of the plots to the centroid in Fig. 3) that is rather similar at the two time points. In contrast, the plant community at the bog site has not changed substantially. Its position in multivariate space is fairly similar and the sub-plot heterogeneity (beta-diversity) is slightly lower, suggesting a tendency towards internal convergence. However, the decrease in beta-diversity is quite small and should not be over interpreted. This stability is not surprising and Minkinen et al. (1999) found that a bog could retain much of its vegetation even after moderate drainage. This is likely attributable to the absence of groundwater contributions in the bog (i.e., absence of water level above the peat

surface) and the extremely acidic and nutrient-poor conditions that prevent the invasion of most forest species. In contrast to the bog's stability, the fen site changed significantly, but the external force was not large enough to push the system into a *Sphagnum*-dominated state (poor fen). Such shift can occur within decades (Janssens et al. 1992, Tahvanainen 2011), but wet years with flooding by Ca-rich water will prevent the invasion of *Sphagnum* beneath the hummock level (Granath et al. 2010).

The view that bog habitats are stable (Zobel 1988, Gunnarsson et al. 2000) does not preclude internal, fine-scale dynamics. Our study characterized plot-level floristic changes due to balanced variation where the abundance of some species declined over time in the same magnitude as the abundance of other species increased. Earlier long-term studies have emphasized the overall stability of ombrotrophic peatlands (Backéus 1972, Gunnarsson et al. 2000) and fine-scale, short-term studies (5–10 years) have suggested little dynamics in continental bogs (Benscoter and Vitt 2008), but substantial changes in more maritime bogs (Nordbakken 2001). Stochastic, or feedback-driven, hydrological changes can lead to alterations in competitive strength since there is a strong niche partitioning along the water table gradient in bogs (Rydin 1993, Belyea and Clymo 2001). Consequently, interactions between shifting environmental conditions and competitive ability can lead to the observed fine scale (plot-level) dynamics, but community stability at site level. Species coexistence is not only favoured by spatial heterogeneity (Amarasekare 2003), but also by temporal heterogeneity.

Microtopographical structure

The microtopography of peatlands is a well-studied subject due to its link to many ecological processes, such as niche differentiation in *Sphagnum* (Rydin and Jeglum 2013), hydrological processes (Belyea and Clymo 2001) and differential decomposition rates (Johnson and Damman 1993). Hence, it is surprising that our study is one of the first to pair a detailed quantification of the microtopographic structure with long-term changes in fens and bogs. We found that roughly 30% of the bog area consists of hollows. Although this is a small sample of the entire

bog, it contrasts with a sub-arctic bog in Sweden where only 5–7% were classified as hollows (Malmer and Wallén 1996). At the fen site, the proportion of hummocks had increased, indicating that ombrotrophic conditions were slightly enhanced during the investigated time period.

The structure at the bog site was very similar in 1960 and 2012. However, a few areas showed remarkable changes by transitioning from hollow to lawn/hummock, illustrating how stochastic, local processes can rapidly change these habitats at a fine scale (Nordbakken 2001). Our data did indicate that rapid changes are possible (cf. Couwenberg 2005) but they are likely restricted to lower structures (lawns). In contrast, the fen site exhibited signs of rapid turnover, where hummocks degrade on one side while simultaneously expanding on the other. Recent views on the stability of hummocks have focused on biological processes (differential rates of growth and decay; see review in Rydin and Jeglum 2013); however, the dynamics observed within this study suggest that water flow through the peatland is a stronger control on hummock stability, and indicate that hydrological processes have a fundamental influence on the spatial dynamics of hummocks (Koutaniemi 1999, Morris et al. 2013).

Conclusion

Overall changes were rather small emphasizing that peatlands are stable and resistant ecosystems under moderate environmental change. The rich fen habitat exhibited a directional change, in which, an observed decline in brown mosses was likely attributable to periods of drier conditions. This effect is reinforced by the expansion of vascular plants (notably *Myrica gale*) that act in concert with acidification and changes in local hydrology. The bog habitat, although harboring fewer species, remained unaffected but showed some non-directional internal dynamics over time. The difference in stability between the bog and fen was also apparent in changes in their microtopographical structure, where hummocks in the fen expanded or moved significantly over time.

ACKNOWLEDGMENTS

We thank Rickard Petterson who supplied the GPS

instrument and helped us extracting the GPS data. We also thank Max Lukenbach and two anonymous reviewers for valuable comments. This work was supported by the Swedish research council Formas. Andreas Press did the 2013 survey of bryophytes.

LITERATURE CITED

- Amarasekare, P. 2003. Competitive coexistence in spatially structured environments: a synthesis. *Ecology Letters* 6:1109–1122.
- Andersen, R., M. Poulin, D. Borcard, R. Laiho, J. Laine, H. Vasander, and E. T. Tuittila. 2011. Environmental control and spatial structures in peatland vegetation. *Journal of Vegetation Science* 22:878–890.
- Anderson, M. J. 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology* 26:32–46.
- Backéus, I. 1972. Bog vegetation re-mapped after sixty years. *Studies on Skagershultamossen, central Sweden*. *Oikos* 23:384–393.
- Baselga, A. 2013. Separating the two components of abundance-based dissimilarity: balanced changes in abundance vs. abundance gradients. *Methods in Ecology and Evolution* 4:552–557.
- Baselga, A., D. Orme, and S. Villeger. 2013. betapart: Partitioning beta diversity into turnover and nestedness components. R package version 1.2. <http://CRAN.R-project.org/package=betapart>
- Belyea, L. R., and R. S. Clymo. 2001. Feedback control of the rate of peat formation. *Proceedings of the Royal Society B* 268:1315–1321.
- Benscoter, B., and D. Vitt. 2008. Spatial patterns and temporal trajectories of the bog ground layer along a post-fire chronosequence. *Ecosystems* 11:1054–1064.
- Bivand, R., and C. Rundel. 2013. rgeos: interface to geometry engine: open source (GEOS). R package ver 0.3-2. <http://CRAN.R-project.org/package=rgeos>
- Bobbink, R., and J.-P. Hettelingh. 2010. Review and revision of empirical critical loads and dose-response relationships. *Proceedings of an expert workshop, Noordwijkerhout, 23–25 June 2010*. Co-ordination Centre for Effects, National Institute for Public Health and the Environment (RIVM). http://wge-cce.org/Publications/Other_CCE_Reports
- Breeuwer, A., M. M. P. D. Heijmans, B. M. Robroek, and F. Berendse. 2010. Field simulation of global change: transplanting northern bog mesocosms southward. *Ecosystems* 13:712–726.
- Brunberg, A.-K., and P. Blomqvist. 1998. *Vatten i Uppsala län 1997*. *Upplandsstiftelsen*. Uppsala, Sweden.
- Couwenberg, J. 2005. A simulation model of mire patterning—revisited. *Ecography* 28:653–661.

- Eppinga, M. B., M. Rietkerk, L. R. Belyea, M. B. Nilsson, P. C. D. Ruiter, and M. J. Wassen. 2010. Resource contrast in patterned peatlands increases along a climatic gradient. *Ecology* 91:2344–2355.
- Granath, G., J. Strengbom, A. Breeuwer, M. M. P. D. Heijmans, F. Berendse, and H. Rydin. 2009. Photosynthetic performance in *Sphagnum* transplanted along a latitudinal nitrogen deposition gradient. *Oecologia* 159:705–715.
- Granath, G., J. Strengbom, and H. Rydin. 2010. Rapid ecosystem shifts in peatlands: linking plant physiology and succession. *Ecology* 91:3047–3056.
- Gunnarsson, U., and L. A. Flodin. 2007. Vegetation shifts towards wetter site conditions on oceanic ombrotrophic bogs in southwestern Sweden. *Journal of Vegetation Science* 18:595–604.
- Gunnarsson, U., N. Malmer, and H. Rydin. 2002. Dynamics or constancy in *Sphagnum* dominated mire ecosystems? A 40-year study. *Ecography* 25:685–704.
- Gunnarsson, U., H. Sjörs, and H. Rydin. 2000. Diversity and pH changes after 50 years on the boreal mire Skattlösbergs Stormosse, Central Sweden. *Journal of Vegetation Science* 11:277–286.
- Hallingbäck, T., L. Hedenäs, and H. Weibull. 2006. Ny checklista för Sveriges mossor. *Svensk Botanisk Tidskrift* 100:96–148.
- Hedenäs, L., and A. Kooijman. 1996. Förändringar i rikkärrsvegetationen SV om Mellansjön i Västergötland. [Changes in the vegetation of a rich fen in Västergötland, Sweden.]. *Svensk Botanisk Tidskrift* 90:113–121.
- Ingmar, T. 1963. Från havsvik till mosse: något om Florornas utveckling. *Sveriges Natur, Årsbok* 1963:155–177.
- Ingmar, T. 1971. Floran (Florarna) and adjacent mires, Uppsala county (prov.Uppland). In H. Sjörs, F. Björkbäck, and T. Ingmar, editors. A tentative qualitative evaluation of Swedish mires. Suomen Maataloustieteellisen Seuran. Julkaisuja. *Acta Agralia fennica* 123:74–86.
- Janssens, J. A., B. C. S. Hansen, P. H. Glaser, and C. Whitlock. 1992. Development of a raised bog complex in northern Minnesota. Pages 189–221 in H. E. Wright, Jr., B. Coffin, and N. Aaseng, editors. *Patterned peatlands of northern Minnesota*. University of Minnesota Press, Minneapolis, Minnesota, USA.
- Johnson, L. C., and A. W. H. Damman. 1993. Decay and its regulation in *Sphagnum* peatlands. *Advances in Bryology* 5:249–296.
- Kapfer, J., J.-A. Grytnes, U. Gunnarsson, and H. J. B. Birks. 2011. Fine-scale changes in vegetation composition in a boreal mire over 50 years. *Journal of Ecology* 99:1179–1189.
- Karlsson, T. 1997. Förteckning över svenska kärlväxter. *Svensk Botanisk Tidskrift* 91:241–560.
- Kettridge, N., A. Binley, X. Comas, N. J. Cassidy, A. J. Baird, A. Harris, J. Kruk, M. Strack, A. M. Milner, and J. M. Waddington. 2012. Do peatland microforms move through time? Examining the developmental history of a patterned peatland using ground-penetrating radar. *Journal of Geophysical Research: Biogeosciences* 117:G03030.
- Kooijman, A. M. 1992. The decrease of rich fen bryophytes in the Netherlands. *Biological Conservation* 59:139–143.
- Koutaniemi, L. E. O. 1999. Twenty-one years of string movements on the Liippasuo aapa mire, Finland. *Boreas* 28:521–530.
- Limpens, J., et al. 2011. Climatic modifiers of the response to nitrogen deposition in peat-forming *Sphagnum* mosses: a meta-analysis. *New Phytologist* 191:496–507.
- Malmer, N., B. M. Svensson, and B. Wallén. 1994. Interactions between *Sphagnum* mosses and field layer vascular plants in the development of peat-forming systems. *Folia Geobotanica et Phytotaxonomica* 29:483–496.
- Malmer, N., and B. Wallén. 1996. Peat formation and mass balance in subarctic ombrotrophic peatland around Abisko, northern Scandinavia. *Ecological Bulletin* 45:79–92.
- Mälson, K., I. Backeus, and H. Rydin. 2008. Long-term effects of drainage and initial effects of hydrological restoration on rich fen vegetation. *Applied Vegetation Science* 11:99–106.
- Minkinen, K., H. Vasander, S. Jauhiainen, M. Karsisto, and J. Laine. 1999. Post-drainage changes in vegetation composition and carbon balance in Lakkasuo mire, Central Finland. *Plant and Soil* 207:107–120.
- Morris, P. J., A. J. Baird, and L. R. Belyea. 2013. The role of hydrological transience in peatland pattern formation. *Earth Surface Dynamics Discussions* 1:31–66.
- Nordbakken, J. F. 2001. Fine-scale five-year vegetation change in boreal bog vegetation. *Journal of Vegetation Science* 12:771–778.
- Nungesser, M. K. 2003. Modelling microtopography in boreal peatlands: hummocks and hollows. *Ecological Modelling* 165:175–207.
- Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, and H. Wagner. 2013. *vegan: Community Ecology Package*. R package version 2.0-9. <http://CRAN.R-project.org/package=vegan>
- Oudin, L., F. Hervieu, C. Michel, C. Perrin, V. Andréassiana, F. Ancil, and C. Loumagne. 2005. Which potential evapotranspiration input for a lumped rainfall-runoff model? Part 2—Towards a simple and efficient potential evapotranspiration model for rainfall-runoff modelling. *Journal of Hydrology* 303:290–306.

- Paulissen, M. P., P. J. van der Ven, A. J. Dees, and R. Bobbink. 2004. Differential effects of nitrate and ammonium on three fen bryophyte species in relation to pollutant nitrogen input. *New Phytologist* 164:451–458.
- Pellerin, S., and C. Lavoie. 2003. Reconstructing the recent dynamics of mires using a multitechnique approach. *Journal of Ecology* 91:1008–1021.
- Prentice, C. I., M. T. Sykes, and W. Cramer. 1993. A simulation model for the transient effects of climate change on forest landscapes. *Ecological Modelling* 65:51–70.
- Quantum GIS Development Team. 2013. Quantum GIS Geographic Information System. Open Source Geospatial Foundation Project. Version 2.0. <http://qgis.osgeo.org>
- R Development Core Team. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rydin, H. 1993. Mechanisms of interactions among *Sphagnum* species along water-level gradients. *Advances in Bryology* 5:153–185.
- Rydin, H., and J. K. Jeglum. 2013. *The biology of peatlands*. Second edition. Oxford University Press, New York, New York, USA.
- Tahvanainen, T. 2011. Abrupt ombrotrophication of a boreal aapa mire triggered by hydrological disturbance in the catchment. *Journal of Ecology* 99:404–415.
- Tallis, J. H., and H. J. B. Birks. 1965. The past and present distribution of *Scheuchzeria palustris* L. in Europe. *Journal of Ecology* 53:287–298.
- Thormann, M. N., A. R. Szumigalski, and S. E. Bayley. 1999. Aboveground peat and carbon accumulation potentials along a bog-fen-marsh wetland gradient in southern boreal Alberta, Canada. *Wetlands* 19:305–317.
- Thygesen, P. 1997. Vegetationsförändringar i Ryggmossens östra lagg 1947-1993. Thesis. Uppsala University, Uppsala, Sweden.
- Walker, M. D., et al. 2006. Plant community responses to experimental warming across the tundra biome. *Proceedings of the National Academy of Sciences USA* 103:1342–1346.
- Warton, D. I., S. T. Wright, and Y. Wang. 2012. Distance-based multivariate analyses confound location and dispersion effects. *Methods in Ecology and Evolution* 3:89–101.
- Weltzin, J. F., S. D. Bridgham, J. Pastor, J. Chen, and C. Harth. 2003. Potential effects of warming and drying on peatland plant community composition. *Global Change Biology* 9:141–151.
- Zobel, M. 1988. Autogenic succession in boreal mires: a review. *Folia Geobotanica et Phytotaxonomica* 23:417–445.

SUPPLEMENTAL MATERIAL

APPENDIX

Table A1. Complete species list for species occurring in the plots at the two sites rich fen and bog in 1960 and 2012. *Calypogeia sphagnicola* was not found 2012 but was found in 2013. Hence it is not counted as a species that was only recorded in 1960.

Species	Abbreviation	Life form	Rich fen		Bog	
			1960	2012	1960	2012
Vascular plants						
<i>Agrostis canina</i>	Agro.can	Graminoid	X			
<i>Andromeda polifolia</i>	Andr.poli	Dwarf shrub	X	X	X	X
<i>Betula pubescens</i>	Betu.pube	Tree		X		
<i>Calluna vulgaris</i>	Call.vulg	Dwarf shrub		X	X	X
<i>Carex chordorrhiza</i>	Care.chor	Graminoid	X			
<i>C. dioica</i>	Care.dioi	Graminoid	X	X		
<i>C. lasiocarpa</i>	Care.lasi	Graminoid	X	X		
<i>C. limosa</i>	Care.limo	Graminoid	X	X		
<i>C. livida</i>	Care.livi	Graminoid	X	X		
<i>C. panicea</i>	Care.pani	Graminoid	X	X		
<i>C. rostrata</i>	Care.rost	Graminoid		X		
<i>C. viridula</i>	Care.viri	Graminoid	X			
<i>Comarum palustre</i>	Com.palu	Herb	X			
<i>Drosera anglica</i>	Dros.angl	Herb	X			
<i>D. intermedia</i>	Dros.inte	Herb	X			
<i>D. rotundifolia</i>	Dros.rotu	Herb	X	X	X	X
<i>Empetrum nigrum</i>	Empe.nigr	Dwarf shrub		X	X	X
<i>Equisetum fluviatile</i>	Equi.fluv	Graminoid	X	X		
<i>Eriophorum angustifolium</i>	Erio.angu	Graminoid	X	X		
<i>E. vaginatum</i>	Erio.vagi	Graminoid			X	X
<i>Frangula alnus</i>	Fran.alnu	Tree	X	X		
<i>Hammarbya paludosa</i>	Hamm.palu	Herb	X			
<i>Juniperus communis</i>	Juni.comm	Tree	X	X		
<i>Lysimachia thyrsoflora</i>	Lysi.thyr	Herb	X	X		
<i>Menyanthes trifoliata</i>	Meny.trif	Herb	X	X		
<i>Myrica gale</i>	Myri.gale	Dwarf shrub	X	X		
<i>Parnassia palustris</i>	Parn.palu	Herb	X	X		
<i>Pedicularis palustris</i>	Pedi.palu	Herb	X			
<i>Peucedanum palustre</i>	Peuc.palu	Herb	X			
<i>Phragmites australis</i>	Phra.aust	Graminoid		X		
<i>Picea abies</i>	Pice.abie	Tree	X	X		
<i>Pinus sylvestris</i>	Pinu.sylv	Tree	X	X	X	X
<i>Rhododendron tomentosum</i>	Rhod.tome	Dwarf shrub				X
<i>Rhynchospora alba</i>	Rhyn.alba	Graminoid	X	X	X	X
<i>R. fusca</i>	Rhyn.fusc	Graminoid		X		
<i>Rubus chamaemorus</i>	Rubu.cham	Herb			X	X
<i>Scheuchzeria palustris</i>	Sche.palu	Graminoids	X	X	X	X
<i>Trichophorum alpinum</i>	Tric.alpi	Graminoids	X	X		
<i>Trientalis europaea</i>	Trie.euro	Herbs	X			
<i>Utricularia intermedia</i>	Utri.inte	Herbs	X	X		
<i>U. minor</i>	Utri.mino	Herbs	X	X		
<i>U. vulgaris</i>	Utri.vulg	Herbs	X			
<i>Vaccinium myrtillus</i>	Vacc.myrt	Dwarf shrubs	X			
<i>V. oxycoccus</i>	Vacc.oxyc	Dwarf shrubs	X	X	X	X
<i>V. uliginosum</i>	Vacc.ulig	Dwarf shrubs			X	X
Bryophytes						
<i>Aneura pinguis</i>	Aneu.ping	Liverworts	X	X		
<i>Aulacomnium palustre</i>	Aula.palu	Mosses	X	X		
<i>Bryum pseudotriquetrum</i>	Bryu.pseu	Mosses	X			
<i>Calliergon cordifolium</i>	Call.cord	Mosses		X		
<i>Calliergonella cuspidata</i>	Call.cusp	Mosses	X	X		
<i>Calypogeia sphagnicola</i>	Caly.spha	Liverworts	X			
<i>Campylium stellatum</i>	Camp.stel	Mosses	X	X		
<i>Cinclidium stygium</i>	Cinc.styg	Mosses	X	X		
<i>Dicranum spp.</i>	Dicr.spp	Mosses			X	X
<i>D. scoparium</i>	Dicr.scop	Mosses		X		
<i>Hamatocaulis vernicosus</i>	Hama.vern	Mosses	X	X		
<i>Mylia anomala</i>	Myli.anom	Liverworts			X	X

Table A1. Continued.

Species	Abbreviation	Life form	Rich fen		Bog	
			1960	2012	1960	2012
<i>Pleurozium schreberi</i>	Pleu.schr	Mosses			X	X
<i>Pohlia sphagnicola</i>	Phol.spha	Mosses			X	
<i>Pseudocalliergon trifarium</i>	Pseu.trif	Mosses	X			
<i>Sanionia uncinata</i>	Sani.unci	Mosses		X		
<i>Scorpidium revolvens</i>	Scor.revo	Mosses	X	X		
<i>Scorpidium scorpioides</i>	Scor.scor	Mosses	X	X		
<i>Sphagnum balticum</i>	Spha.balt	Mosses			X	X
<i>S. centrale</i>	Spha.cent	Mosses	X	X		
<i>S. contortum</i>	Spha.cont	Mosses	X	X		
<i>S. cuspidatum</i>	Spha.cusp	Mosses			X	X
<i>S. fuscum</i>	Spha.fusc	Mosses			X	X
<i>S. rubellum</i>	Spha.rube	Mosses			X	X
<i>S. tenellum</i>	Spha.tene	Mosses			X	X
<i>Straminergon stramineum</i>	Stra.stra	Mosses	X	X		
<i>Tomenthypnum nitens</i>	Tome.nite	Mosses		X		
<i>Warnstorfia exannulata</i>	Warn.exan	Mosses	X	X		
Lichens						
<i>Cladonia</i> spp.	Cald.spp	Lichens		X	X	X
<i>C. alpestris</i>	Cald.alpe	Lichens			X	X
<i>C. rangiferina</i>	Clad.rang	Lichens			X	X

Table A2. Number of species found at the two sites, divided into seven life forms.

Life form	No. species	
	Rich fen	Bog
Trees	5	1
Dwarf shrubs	6	6
Graminoids	16	3
Herbs	14	1
Mosses	17	8
Liverworts	2	1
Lichens	1	3
Total	61	24

Table A3. Changes in plot frequency for species between 1960 and 2012 at the rich fen and bog for all species. The change column indicates the direction and magnitude of the change, i.e., an increase or decrease of plots with the species present. *P*-values are from Fisher's exact test.

Species	<i>P</i>	Change	No. plots	
			1960	2012
Rich fen				
<i>Agrostis canina</i>	1.00	-1	1	0
<i>Andromeda polifolia</i>	0.09	10	22	32
<i>Aulacomnium palustre</i>	0.72	2	3	5
<i>Betula pubescens</i>	1.00	1	0	1
<i>Bryum pseudotriquetrum</i>	0.50	-2	2	0
<i>Calliergon cordifolium</i>	1.00	1	0	1
<i>Calliergonella cuspidata</i>	1.00	0	7	7
<i>Calluna vulgaris</i>	0.24	3	0	3
<i>Campylium stellatum</i>	1.00	0	28	28
<i>Carex chordorrhiza</i>	<0.01	-10	10	0
<i>C. dioica</i>	0.22	-6	13	7
<i>C. lasiocarpa</i>	1.00	-1	55	54
<i>C. limosa</i>	<0.001	-27	41	14
<i>C. livida</i>	0.22	-6	48	42
<i>C. panicea</i>	0.44	-3	5	2
<i>C. rostrata</i>	0.50	2	0	2
<i>C. viridula</i>	0.50	-2	2	0
<i>Cinclidium stygium</i>	1.00	1	12	13
<i>Comarum palustre</i>	0.24	-3	3	0
<i>Dicranum scoparium</i>	1.00	1	0	1
<i>Drosera anglica</i>	0.24	-3	3	0
<i>D. intermedia</i>	0.04	-11	23	12
<i>D. rotundifolia</i>	0.27	5	5	10
<i>Empetrum nigrum</i>	1.00	1	0	1
<i>Equisetum fluviatile</i>	0.31	-5	48	43
<i>Eriophorum angustifolium</i>	<0.001	25	4	29
<i>Frangula alnus</i>	1.00	1	2	3
<i>Hamatocaulis vernicosus</i>	0.68	-2	4	2
<i>Hammarbya paludosa</i>	1.00	-1	1	0
<i>Juniperus communis</i>	1.00	0	1	1
<i>Lysimachia thyrsiflora</i>	1.00	0	1	1
<i>Menyanthes trifoliata</i>	0.39	-5	43	38
<i>Myrica gale</i>	<0.01	10	45	55
<i>Parnassia palustris</i>	0.36	3	1	4
<i>Pedicularis palustris</i>	1.00	-1	1	0
<i>Peucedanum palustre</i>	0.12	-4	4	0
<i>Phragmites australis</i>	1.00	1	0	1
<i>Picea abies</i>	1.00	0	1	1
<i>Pinus sylvestris</i>	1.00	0	3	3
<i>Pseudocalliergon trifarium</i>	<0.001	-17	17	0
<i>Rhynchospora alba</i>	<0.01	-16	42	26
<i>R. fusca</i>	0.06	5	0	5
<i>Sanionia uncinata</i>	1.00	1	0	1
<i>Scheuchzeria palustris</i>	<0.001	-17	49	32
<i>Scorpidium revolvens</i>	0.16	-5	7	2
<i>S. scorpioides</i>	<0.001	-22	40	18
<i>Sphagnum centrale</i>	0.56	3	5	8
<i>S. contortum</i>	<0.01	16	16	32
<i>Straminergon stramineum</i>	0.68	-2	4	2
<i>Tomenthypnum nitens</i>	1.00	1	0	1
<i>Trichophorum alpinum</i>	0.04	8	3	11
<i>Trientalis europaea</i>	0.50	-2	2	0
<i>Utricularia intermedia</i>	0.57	4	24	28
<i>U. minor</i>	0.18	-8	33	25
<i>U. vulgaris</i>	0.24	-3	3	0
<i>Vaccinium myrtillus</i>	1.00	-1	1	0
<i>V. oxycoccus</i>	0.11	9	31	40
<i>Warnstorfia exannulata</i>	0.07	8	5	13

Table A3. Continued.

Species	P	Change	No. plots	
			1960	2012
Bog				
<i>Andromeda polifolia</i>	0.29	5	45	50
<i>Calluna vulgaris</i>	0.19	8	26	34
<i>Cladonia alpestris</i>	<0.01	-11	13	2
<i>C. rangiferina</i>	0.50	-4	15	11
<i>Dicranum</i> spp.	0.82	-2	13	11
<i>Drosera rotundifolia</i>	<0.01	16	22	38
<i>Empetrum nigrum</i>	0.44	5	20	25
<i>Eriophorum vaginatum</i>	0.11	7	44	51
<i>Mytilia anomala</i>	1.00	1	35	36
<i>Pinus sylvestris</i>	0.01	10	3	13
<i>Pleurozium schreberi</i>	0.09	-7	11	4
<i>Pohlia sphagnicola</i>	0.50	-2	2	0
<i>Rhododendron tomentosum</i>	1.00	1	0	1
<i>Rhynchospora alba</i>	0.06	-8	12	4
<i>Rubus chamaemorus</i>	0.85	2	26	28
<i>Scheuchzeria palustris</i>	1.00	0	9	9
<i>Sphagnum balticum</i>	0.23	7	33	40
<i>S. cuspidatum</i>	1.00	0	16	16
<i>S. fuscum</i>	0.71	3	29	32
<i>S. rubellum</i>	<0.01	16	28	44
<i>S. tenellum</i>	0.68	2	2	4
<i>Vaccinium oxycoccus</i>	0.27	4	50	54
<i>V. uliginosum</i>	0.44	-4	11	7

Table A4. Changes in cover between 1960 and 2012 at the rich fen and bog for all observed species. Only plots where the species were recorded at one of the surveys are included. Absolute change in percent cover is reported together with means at the two survey years. *P* values are derived from paired *t* tests, and *n* equals the number of plots.

Species	<i>n</i>	<i>P</i>	Absolute change	Mean 1960	Mean 2012
Rich fen					
<i>Agrostis canina</i>	1	...	-1.0	1.0	0.0
<i>Andromeda polifolia</i>	41	0.02	0.6	0.7	1.3
<i>Aulacomnium palustre</i>	7	0.19	12.3	0.4	12.7
<i>Betula pubescens</i>	1	...	3.0	0.0	3.0
<i>Bryum pseudotriquetrum</i>	2	...	-1.0	1.0	0.0
<i>Calliergon cordifolium</i>	1	...	5.0	0.0	5.0
<i>Calliergonella cuspidata</i>	8	0.36	-3.0	5.6	2.6
<i>Calluna vulgaris</i>	3	..	20.3	0.0	20.3
<i>Campylium stellatum</i>	33	<0.01	-21.1	25.2	4.1
<i>Carex chordorrhiza</i>	10	<0.001	-1.3	1.3	0.0
<i>C. dioica</i>	15	0.07	-0.5	1.0	0.5
<i>C. lasiocarpa</i>	55	<0.001	-3.1	5.0	1.9
<i>C. limosa</i>	43	<0.001	-0.9	1.2	0.3
<i>C. livida</i>	50	<0.01	-0.6	2.1	1.4
<i>C. panicea</i>	5	0.11	-2.8	3.2	0.4
<i>C. rostrata</i>	2	...	1.5	0.0	1.5
<i>C. viridula</i>	2	...	-1.0	1.0	0.0
<i>Cinclidium stygium</i>	16	0.38	-1.1	2.8	1.7
<i>Comarum palustre</i>	3	...	-1.0	1.0	0.0
<i>Dicranum scoparium</i>	1	..	2.0	0.0	2.0
<i>Drosera anglica</i>	3	-	-1.0	1.0	0.0
<i>D. intermedia</i>	25	0.03	-0.9	1.6	0.7
<i>D. rotundifolia</i>	10	0.82	0.1	1.1	1.2
<i>Empetrum nigrum</i>	1	...	10.0	0.0	10.0
<i>Equisetum fluviatile</i>	51	0.81	0.0	1.0	1.0
<i>Eriophorum angustifolium</i>	30	<0.001	0.9	0.2	1.1
<i>Frangula alnus</i>	3	0.17	15.3	1.3	16.7
<i>Hamatocaulis vernicosus</i>	5	0.37	-0.4	0.8	0.4
<i>Hammarbya paludosa</i>	1	...	-1.0	1.0	0.0
<i>Juniperus communis</i>	1	...	-4.0	5.0	1.0
<i>Lysimachia thyrsiflora</i>	2	1.00	0.0	0.5	0.5
<i>Menyanthes trifoliata</i>	46	<0.001	3.1	2.2	5.4
<i>Myrica gale</i>	55	<0.001	8.5	11.1	19.7
<i>Parnassia palustris</i>	4	0.06	0.8	0.3	1.0
<i>Pedicularis palustris</i>	1	...	-1.0	1.0	0.0
<i>Peucedanum palustre</i>	4	...	-1.0	1.0	0.0
<i>Phragmites australis</i>	1	...	1.0	0.0	1.0
<i>Picea abies</i>	2	1.00	0.0	0.5	0.5
<i>Pinus sylvestris</i>	6	0.34	2.7	0.5	3.2
<i>Pseudocalliergon trifarium</i>	17	<0.01	-1.7	1.7	0.0
<i>Rhynchospora alba</i>	45	0.02	1.3	1.0	2.2
<i>R. fusca</i>	5	...	2.2	0.0	2.2
<i>Sanionia uncinata</i>	1	...	1.0	0.0	1.0
<i>Scheuchzeria palustris</i>	49	<0.001	-2.0	2.8	0.8
<i>Scorpidium revolveans</i>	8	0.05	-1.5	1.8	0.3
<i>Scorpidium scorpioides</i>	41	<0.001	-45.6	46.6	1.0
<i>Sphagnum centrale</i>	8	0.27	17.1	62.5	79.6
<i>S. contortum</i>	34	0.05	-9.7	16.8	7.1
<i>Straminergon stramineum</i>	5	0.37	-0.4	0.8	0.4
<i>Tomenthypnum nitens</i>	1	...	1.0	0.0	1.0
<i>Trichophorum alpinum</i>	12	<0.01	0.8	0.3	1.1
<i>Trientalis europaea</i>	2	...	-1.0	1.0	0.0
<i>Utricularia intermedia</i>	34	0.09	1.0	1.1	2.1
<i>U. minor</i>	36	0.65	0.1	1.0	1.1
<i>U. vulgaris</i>	3	...	-1.0	1.0	0.0
<i>Vaccinium myrtillus</i>	1	...	-7.0	7.0	0.0
<i>V. oxycoccus</i>	44	<0.01	1.3	1.2	2.5
<i>Warnstorfia exannulata</i>	13	0.96	0.2	3.4	3.5

Table A4. Continued.

Species	<i>n</i>	<i>P</i>	Absolute change	Mean 1960	Mean 2012
Bog					
<i>Andromeda polifolia</i>	53	0.08	0.7	2.2	2.8
<i>Calluna vulgaris</i>	34	0.67	1.2	17.5	18.7
<i>Cladonia alpestris</i>	13	0.02	-15.0	15.9	0.9
<i>C. rangiferina</i>	17	0.10	-8.2	9.4	1.1
<i>Dicranum spp.</i>	17	0.27	-1.3	3.1	1.8
<i>Drosera rotundifolia</i>	40	<0.001	1.1	0.8	2.0
<i>Empetrum nigrum</i>	30	0.93	0.1	2.8	2.9
<i>Eriophorum vaginatum</i>	53	0.20	-0.8	4.3	3.5
<i>Mylia anomala</i>	40	0.77	0.3	2.1	2.4
<i>Pinus sylvestris</i>	15	0.13	2.3	0.5	2.7
<i>Pleurozium schreberi</i>	12	0.03	-22.9	26.1	3.2
<i>Pohlia sphagnicola</i>	2	...	-1.0	1.0	0.0
<i>Rhododendron tomentosum</i>	1	...	2.0	0.0	2.0
<i>Rhynchospora alba</i>	12	<0.01	-3.1	3.7	0.6
<i>Rubus chamaemorus</i>	31	0.28	0.5	2.3	2.8
<i>Scheuchzeria palustris</i>	11	0.22	-0.9	3.2	2.3
<i>Sphagnum balticum</i>	42	0.71	-1.9	17.6	15.8
<i>S. cuspidatum</i>	18	0.15	-19.1	75.7	56.7
<i>S. fuscum</i>	32	<0.01	22.9	37.1	60.0
<i>S. rubellum</i>	44	0.04	10.8	22.7	33.5
<i>S. tenellum</i>	5	0.87	0.4	1.6	2.0
<i>Vaccinium oxycoccus</i>	54	0.07	-1.7	4.3	2.6
<i>V. uliginosum</i>	13	0.80	0.4	1.7	2.1

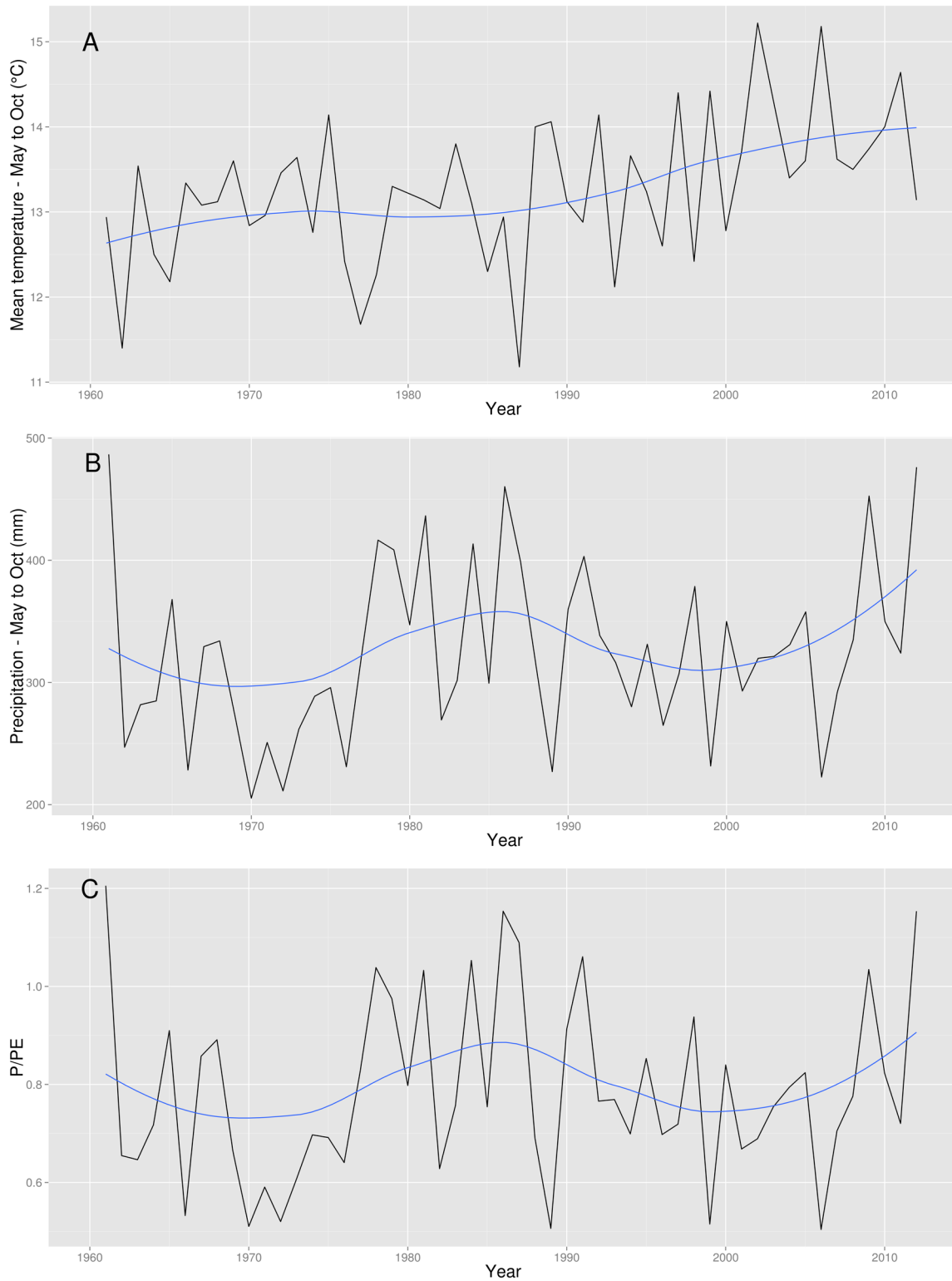


Fig. A1. Temporal trends (1960–2012) for mean temperature, precipitation and the ratio precipitation:potential evaporation over the growing season (May 1st to September 30th). Blue line represents a trend line which is based on a loess function (local smooth).



Fig. A2. Aerial photos of the two sites with the investigated plots marked. The rich fen site to the left and the bog site to the right. © Lantmäteriet, Licence number i2012/921.

SUPPLEMENT

Data and R code needed to conduct the analysis described in the main text and appendix ([Ecological Archives C0005-013-S1](#)).