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Dynamics or constancy in *Sphagnum* dominated mire ecosystems? A 40-year study

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Traditionally mire ecosystems (especially bogs) have been viewed as stable systems with slow changes in the vegetation over time. In this study the mire Åkhultmyren, south-central Sweden was re-investigated in 1997 after 40 yr of continued natural development. The results show a high degree of dynamics in a *Sphagnum* dominated bog and fen. Altogether 97 vascular plant and bryophyte species were recorded in the two inventories of the bog and poor fen vegetation. pH and electrical conductivity in the mire water were also surveyed. In 1997 we found 10 new species and that 8 species had disappeared since 1954 but the over-all mean number of species per plot (size 400 m²) had hardly changed. However, 21% of the species increased and 21% decreased significantly in frequency. Most of the species that decreased in frequency were low-grown vascular plants, most common in wet microhabitats. Vascular plant species that increased in frequency included trees (defined as > 1.3 m in height) and were generally taller than the unchanged or decreasing species. The frequency of dwarf shrubs and hummock bryophytes increased too. Areas with an initial pH of 4.5–5.0 showed the strongest decrease in pH, coinciding with an enlarged distribution of some *Sphagnum* species. The species diversity increased on the bog, but decreased in the wettest parts of the fen, where the pH also decreased. Species with unchanged or increasing frequency often showed high capacity to colonise new plots. On average the sum of gains and losses of species in the plots in 1997 was ca 50% of the species number in 1954. The vegetation changes indicate a drier mire surface and an increased availability of nitrogen. The increased tree cover may have triggered further changes in the plant cover.

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Mainly based on studies in peat stratigraphy, plant successions in *Sphagnum* dominated peat-forming mire vegetation have been viewed as directed by autogenic processes leading towards a more or less predictable, stable system (Weber 1902, Zobel 1988). In the micro-topographical pattern of hummocks and hollows on ombrotrophic bogs, stability has been demonstrated both over several decades (Backéus 1972) and for periods from several centuries to millennia (Barber 1981,

Svensson 1988a, Rydin and Barber 2001). However, in peat cores both changes in dominance among species and appearance of new species have been documented from macrofossil records (Svensson 1988b, Kuhry 1997, Malmer and Wallén 1999). Further, succession leading to a transition from a minerotrophic fen to an ombrotrophic bog means the disappearance of many species and the species turnover may then for a short period be relatively high (Svensson 1988b). Otherwise, we expect

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that in *Sphagnum* dominated mire vegetation changes in species composition are slow processes compared to those regularly occurring in terrestrial environments.

In addition to internal dynamics, recent studies on ombrotrophic bogs have shown considerable directional changes over the last 50 yr (e.g., Lütke Twenhöven 1992, Mackay and Tallis 1996, Risager and Aaby 1997, Risager 1998, Frankl and Schmeidl 2000). The vegetation on mires seemingly untouched by drainage and cultivation is influenced by diffuse anthropogenic changes to the environment such as a lowered regional ground water level (Malmer and Wallén 1999) or an additional supply of nitrogen and sulphur due to atmospheric pollution (Lee 1998). In southern Sweden a lower ground water level has been suggested as a reason for a reduction in species richness in fens (Tyler and Olsson 1997) and on bogs, for an increased growth of trees (Åberg 1992, Ihse et al. 1992, Malmer 1998) and a reduced *Sphagnum* cover (Malmer and Wallén 1999). High levels of nitrogen deposition would disfavour species adapted to a low nitrogen supply rate like several *Sphagnum* species (Gunnarsson and Rydin 2000). In addition, increased nutrient availability may increase the aboveground biomass and litter production of vascular plants, and thereby reduce species richness among bryophytes (Berendse 1999). Reduced growth of *Sphagnum* mosses may also facilitate the growth of vascular plants (Berendse et al. 2001, Ohlson et al. 2001, Malmer et al. 2003). Raised levels of acidifying compounds in the atmospheric deposition may reduce the pH in the mire water, which particularly will affect bryophytes with specific pH requirements (Gignac 1993, Rydin 1993, Gunnarsson et al. 2000).

In a recent study, Gunnarsson et al. (2000) presented data from a reinvestigation of the vegetation after 50 yr on Skattlösbergs Stormosse, an untouched mire situated in an area with a low level of air pollution in central Sweden. For most species, a decrease in frequency was observed during that period and species richness decreased in plots with a pH > 5 in the first survey.

In the present study, we present the results from a similar reinvestigation after 40 yr of the mire Åkhultmyren, situated in southern Sweden. The mire is exposed to higher levels of anthropogenic pollutants than Skattlösbergs Stormosse and we therefore expected greater changes in the vegetation. The flora, vegetation and environmental conditions on this mire were studied in the 1950s (Malmer 1962a, b) and the study was partly repeated in 1997. The results from these two inventories of *Sphagnum* dominated mire vegetation are compared with the following objectives: 1) to trace the plant population dynamics and changes in species diversity over several decades, 2) to estimate mobility and turnover of species at a large scale (400 m²) for comparisons with other vegetation types and 3) to identify the possible autogenic and allogenic (includ-

ing anthropogenic) causes behind any observed changes in species frequency and distribution.

Material and methods

Study site

The vegetation on the mire Åkhultmyren (57°05'N, 14°30'E, 230 m a.s.l., total area 1.1 km²) was described in detail by Malmer (1962a). The mean annual precipitation at Aneboda, ca 2 km from the mire, was 716 mm for the period 1919–1960 (Malmer 1962a) and 789 mm for the period 1983–1998 (Swedish Environmental Research Institute, < <http://www.ivl.se> >). The mean annual temperature is ca 6°C and the vegetation period (temperature > 3°C) is ca 210 d (Malmer 1962a). The mean annual wet deposition of nitrogen increased from 0.48 g m⁻² yr⁻¹ during the period 1947–1962 to 0.72 g m⁻² yr⁻¹ in 1962–1976 and sulphur deposition increased from 0.96 to 1.28 g m⁻² yr⁻¹ between these two periods (Malmer and Wallén 1980). The wet deposition has not continued to increase. The mean annual wet deposition of nitrogen and sulphur were during the period 1983–1998 at Aneboda 0.72 and 0.65 g m⁻² yr⁻¹, respectively (Swedish Environmental Research Institute, < <http://www.ivl.se> >).

From field investigations in 1953–1955 (mainly 1954) Malmer (1962a) described one part of the mire, the Stattute area (size 560 × 300 m), in detail with distribution maps of most vascular plants and bryophytes together with measurements of water pH and conductivity. These studies were repeated in 1996–1998 (mainly 1997). The main part of the area is a wide topogenous fen, with a gradual transition to an ombrotrophic bog towards southwest. A row of brook pools divides the fen area into an inner part (the Inner Fen) bordering the surrounding forest (mainly *Picea abies*) on mineral soil and an outer part (the Outer Fen) with the transition to the bog (Fig. 1). The brook pools, as well as the rest of the fen, are supplied with water coming from areas north of the investigated part of the mire. No important drainage has been made in the area, but large parts of the surrounding forests were clear-cut around 1970. Cattle grazing occurred earlier in the forests and along the margin of the mire but ceased around 1950.

Based on the distribution of the plant species, Malmer (1962a) divided the Outer Fen into two parts, the *Nartheicum ossifragum* and the *Eriophorum angustifolium* zones next to the bog and the row of brook pools, respectively (Fig. 1). In the Inner Fen the marginal parts were separated as the mire margin zone while the rest together with the parts along the row of brook pools formed the *Menyanthes trifoliata* zone (Fig. 1).

The 1954 inventory

For the first inventory, the Stattute area was divided into a grid of 20 × 20 m plots (Malmer 1962a: Map 1) with plot corners marked with wooden sticks. The presence or absence of all vascular plants and bryophytes was noted for each plot. The following widespread and abundant species: *Andromeda polifolia*, *Calluna vulgaris*, *Empetrum nigrum*, *Vaccinium oxycoccos*, *Drosera rotundifolia*, *Eriophorum vaginatum* and *Sphagnum rubellum*, were not as intensely recorded as the other species. For the tree species, *Betula pubescens*, *Picea abies* and *Pinus sylvestris*, only individuals > 1.3 m in height was recorded although seedlings and individuals < 1.3 m were widespread.

Distribution maps of the investigated species were published in Malmer (1962a), but for the present study we used the unpublished original maps and field notes. Levelling of the water surface and other hydrological measurements in 1954 (Malmer 1962a), confirmed that the limit between ombrogenous and geogenous soil wetness (Sjörs 1948, 1950), coincided with the limit for the continuous distribution of *Narthecium ossifragum* towards the bog, i.e. the fen plant limit sensu Du Rietz (1949). The position of the *N. ossifragum* limit in 1940 was also indicated on a map made by B. Collini (Malmer 1962a: Fig. 13).

The pH and conductivity of the mire water were monitored at several positions during the growing season of 1954 (with supplementary measurements carried out in the following years; Malmer 1962b: Fig. 9) and surveyed in ca 140 points (hollows with open water) over the entire area in August 1954. The weather in 1954 was normal except for the months June to August, which were wetter than normal (Malmer 1962b). The pH was measured using a glass electrode and the conductivity was reduced for H⁺-activity according to Sjörs (1950).

The 1997 inventory

For the 1997 inventory several of the plot corners marked with wooden sticks in 1953 were retrieved mainly on the ombrotrophic part. The positions of these corners were captured using a differential Global Positioning System (GPS). From the GPS positions and the map positions of these points combined with the positions of boulders in the Inner Fen, we were able to reconstruct the 1954 grid, using a rectifying linear mapping function (Richards 1986). The new grid was put out on the mire using GPS equipment. This method produced a small deviation (< 1 m) from the old grid in the central parts of the area, when comparing positions of old sticks, not used for the rectification, with the new grid. For plots at the margin of the study area, the deviation between the grids might be somewhat higher.

The floristic data in the plots of the new grid were recorded using the same method as in the first inventory. The data also included the less intensely studied species in the 1954 study, and comprised 245 of the central plots of the Stattute area, that is ca 70% of the plots studied in 1954 (Fig. 1). The distributions of *Eriophorum angustifolium* and *Narthecium ossifragum* were re-mapped using GPS in 1996. The limit between the area with *Sphagnum magellanicum* and the area with *S. papillosum* as dominants in the lawn communities (Fig. 21 in Malmer 1962a) was also re-mapped.

The pH and conductivity of the mire water were monitored during the period 11 June–24 July 1997 at four of the points monitored by Malmer (1962b). The four sampling points formed a gradient from the row of brook pools to the ombrotrophic bog (Fig. 1). Precipitation occurred mainly during the nights and the water table was slightly above the average level during the monitored period. On 7 July 1997, we surveyed the pH and conductivity over the study area. As the 140 measurement points from 1954 could not be re-located, we measured in small hollows with open water close to the plot corners. The measurements were carried out in the same way as in the first inventory.

Taxonomic notes

The nomenclature follows Karlsson (1997) for vascular plants and Söderström and Hedenäs (1998) for bryophytes. Since 1954, *Sphagnum imbricatum* has been split into *S. affine* and *S. austinii* (Flatberg 1984). *Sphagnum austinii* occurs mainly on bog hummocks and *S. affine* in fen areas. This difference was recognized by Malmer (1962a) and it was therefore possible to reconstruct the distribution of the two taxa, for 1954. *Sphagnum flexuosum* was in 1954 recorded on the mire but only outside the Stattute area. In 1997 it was recorded from eleven plots in the area along the north-eastern mire margin. It is possible that corresponding stands in 1954 were identified as *S. apiculatum* (= *S. fallax*) and therefore we have merged *S. flexuosum* into *S. fallax* in all calculations.

In both inventories *S. auriculatum* (= *S. denticulatum*) and *S. inundatum* were distinguished as separate taxa in the field. However, the variation in the field characters is rather continuous and we are not sure that we have used them in the same way for both inventories. Therefore, we treat these taxa together as *S. denticulatum* in the present study.

Data analysis

Species richness denotes the number of plant species recorded in each 20 × 20 m plot. To estimate the degree of change in species richness for each plot between the

inventories, we calculated the change in richness and a turnover index, T , using the formula

$$T = 100 \times (G_{97} + L_{97})/S_{54} \quad (1)$$

where S_{54} is the number of species recorded in the plot in 1954 and G_{97} and L_{97} the number of species that were Gained and Lost in the plot between the two surveys, respectively. In these calculations, the three tree species (*Betula pubescens*, *Picea abies* and *Pinus sylvestris*) were excluded while the seven widespread and abundant species dealt with less intensely in 1954 were included under the conservative assumption that their occurrences were the same as in the 1997 inventory.

The frequency of occurrence of each species, i.e. the number of 20×20 m plots ($n = 245$) in which a species was recorded, was calculated for each inventory. The significance of the difference in frequency between the two inventories was tested with Wilcoxon rank sum test using presence/absence values for each plot.

To obtain a measure for the dispersal capacities of the species, we calculated a mobility index, M , for each species according to

$$M = 100 \times N_{97}/F_{97} \quad (2)$$

where F_{97} is the plot frequency for species in 1997 and N_{97} the number of new plots in which the species was recorded in 1997.

As an indirect indication on which environmental changes had occurred on the mire, we calculated the changes in Ellenberg indicator values for the plots. For each plot and year we calculated the mean indication (as suggested by Ter Braak and Gremmen 1987) for nitrogen (N), pH (reaction, R), light (L) and moisture (M, Ellenberg et al. 1991). The values for N are only based on the vascular plants, since no figures occur for bryophytes.

Results

Changes in the tree layer

Three tree species, *Betula pubescens*, *Picea abies* and *Pinus sylvestris*, were found on the mire. They also occurred widely as saplings (that were not mapped). The frequency of tree reaching heights above 1.3 m increased significantly between the inventories (Table 1) and all three species expanded their distribution (Fig. 2). For *Picea* the change was from 0 to 16 plots. *Alnus glutinosa*, *Salix aurita*, *S. cinerea* and *Frangula alnus* only occurred as shrubs (< 1.3 m in height) and were treated together with the other investigated species.

Species richness and turnover

Altogether, 97 species were noted in the two inventories, 53 vascular plants and 44 bryophytes (Table 1). In addition to the three tree species, the number of species recorded in each inventory was nearly the same, 83 and 87 in 1954 and 1997, respectively. Six species were observed only in one plot and at one of the inventories and may be looked upon as occasional on the mire. However, except for *Deschampsia caespitosa*, they were all mire species. The total number of species per plot (400 m^2) ranged from 13 to 44. The range was 7–26 for vascular plants and 3–21 for bryophytes. Both inventories revealed a general decrease in species number per plot from the mire margin and the row of brook pools to the bog (Fig. 3). Seen over the whole investigated area, the mean number of species per plot decreased slightly from 1954 to 1997 resulting from a decrease of vascular plant species (Table 2). The plots in the bog showed an increase in total number of species as well as in bryophytes (Table 2, Fig. 3). For all other parts of the mire the number of vascular plants per plot decreased, while the number of bryophytes increased (Table 2). The greatest changes in total species number per plot, both increases and decreases, were found along the row of brook pools and in the mire margin (Fig. 3).

Eleven new species, eight vascular plants and three bryophytes, were noted in 1997, while seven species, two vascular plants and five bryophytes were not found again. The turnover index calculated according to eq. (1) indicates that in an average plot the sum of new or disappeared species in 1997 compared to 1954 was ca 50% of the number of species found in the plot in 1954 (Table 2). Both for vascular plants and bryophytes the turnover was largest in the mire margin zone and along the row of brook pools and less on the bog and the adjacent part of the Outer Fen (Table 2). However, even on the bog a few plots showed turnover values > 50% (Fig. 3). Bryophytes showed a higher turnover than the vascular plants (Table 2).

Species frequency and mobility

Among the 76 species (trees excluded) recorded in both inventories 36, i.e. 47%, showed a change in frequency between the inventories, 17 increased and 19 decreased (Table 1). Most of the new or disappeared species in the second inventory were found only in few plots (Table 1). A conspicuous exception was *Scheuchzeria palustris* (Fig. 4), which in 1954 was recorded from 102 plots but could not be found in the area in 1997. Among other species not seen in 1997 were *Hammarbya paludosa* and *Aneura pinguis*, which in 1954 were noted in 6 and 11 plots, respectively. Some other species, e.g., *Lycopodiella inundata*, *Carex echinata* and *C. panicea*,

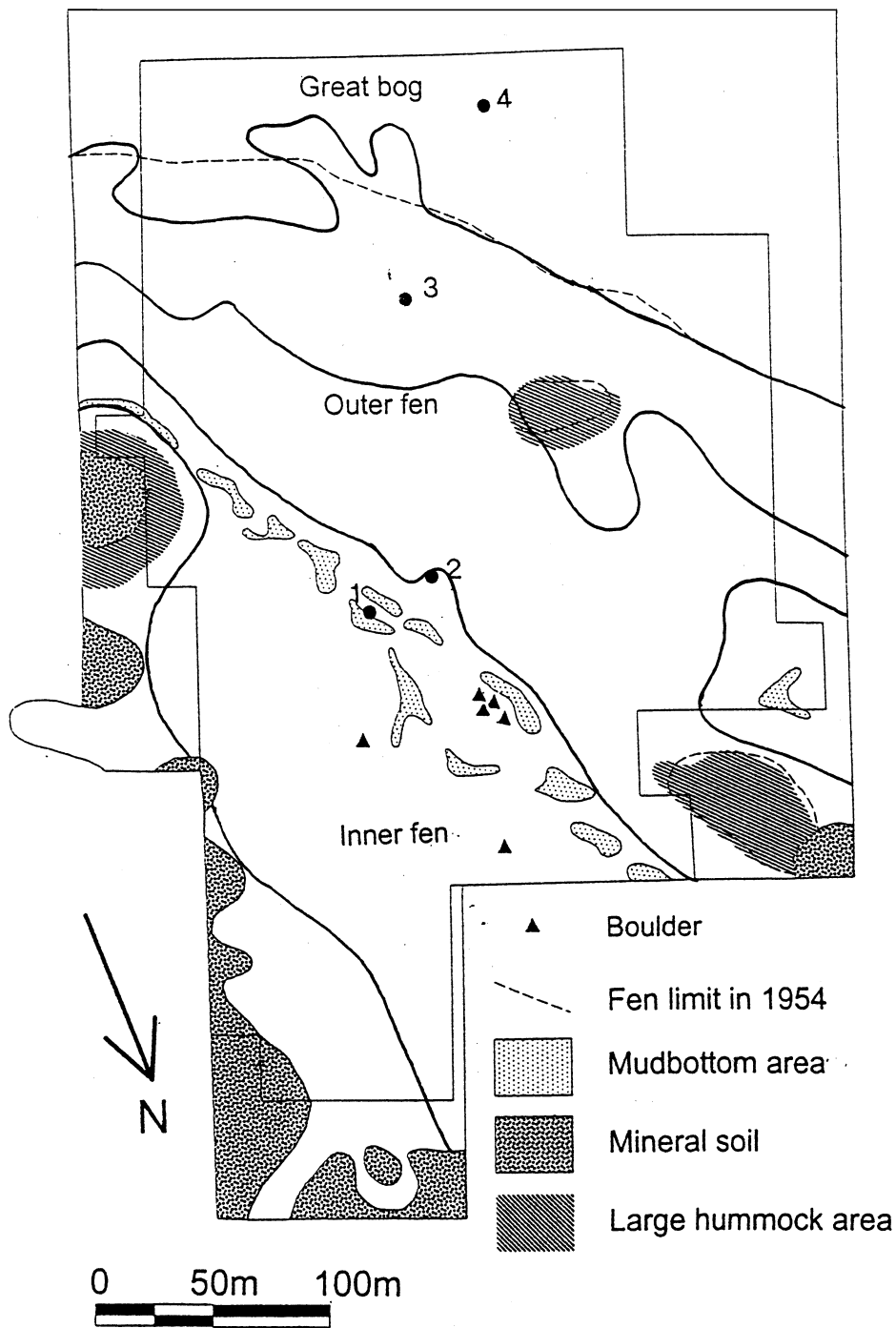


Fig. 1. Map over the Stattute area on the mire Åkhultmyren. The inner, framed area shows the part of the mire investigated in 1997, the numbered points show the positions monitored for pH in 1954 and 1997. The limit between fen and bog (broken line) was determined from hydrological measurements in 1954. The solid lines shows the limits between the zones, which are arranged from the lower left to the upper right corner as follows: the mire margin, the *Menyanthes trifoliata* zone, the *Eriophorum angustifolium* zone, the *Narthecium ossifragum* zone and the bog. The area at the right corner belongs to the *Menyanthes trifoliata* zone. Redrawn from Malmer (1962b).

Table 1. Frequency as number of plots (size 20 × 20 m, n = 245) in which the species occurred at each of the inventories, the change in frequency between the inventories, the number of plots which the species entered (Gains) or disappeared from (Losses), and the Mobility of the species calculated according to eq. (2). The significance of the difference in frequency was tested with Wilcoxon rank sum test using presence/absence values for each plot. The species are ordered by decreasing percentage change within each growth form. For the trees only individuals > 1.3 m was recorded.

Species	Plot frequency		Change in plot frequency		Losses	Gains	Mobility (%)
	1954	1997	Net	%			
Trees (> 1.3 m)							
<i>Picea abies</i>	0	16	16 ^{n.p.}	new	0	16	100
<i>Betula pubescens</i>	15	123	108 ^{***}	720	3	111	90
<i>Pinus sylvestris</i>	72	156	84 ^{***}	117	5	89	57
Shrubs							
<i>Betula nana</i>	0	2	2 ^{n.p.}	new	0	2	100
<i>Salix cinerea</i>	0	1	1 ^{n.p.}	new	0	1	100
<i>Juniperus communis</i>	2	15	13 ^{***}	650	2	15	100
<i>Frangula alnus</i>	1	7	6*	600	1	7	100
<i>Salix aurita</i>	8	9	1 ^{n.s.}	12.5	4	5	55
<i>Alnus glutinosa</i>	3	2	-1 ^{n.p.}	-33	2	1	50
Dwarf shrubs							
<i>Rhododendron tomentosum</i>	0	1	1 ^{n.p.}	new	0	1	100
<i>Vaccinium uliginosum</i>	6	18	12*	200	2	14	78
<i>V. myrtillus</i>	7	18	11*	157	2	13	72
<i>V. vitis-idaea</i>	10	18	8 ^{n.s.}	80	3	11	61
<i>Erica tetralix</i>	114	141	27*	24	9	36	25
<i>Salix repens</i>	133	110	-23 ^{n.s.}	-17	35	12	11
<i>Andromeda polifolia</i>	Not rec.	244	-	-	-	-	-
<i>Calluna vulgaris</i>	Not rec.	243	-	-	-	-	-
<i>Vaccinium oxycoccos</i>	Not rec.	243	-	-	-	-	-
<i>Empetrum nigrum</i>	Not rec.	188	-	-	-	-	-
Herbs							
<i>Trientalis europaea</i>	0	4	4 ^{n.p.}	new	0	4	100
<i>Corallorhiza trifida</i>	0	1	1 ^{n.p.}	new	0	1	100
<i>Viola palustris</i>	10	14	4 ^{n.s.}	40	4	8	57
<i>Potentilla erecta</i>	24	31	7 ^{n.s.}	29	11	18	58
<i>Narthecium ossifragum</i>	201	212	11 ^{n.s.}	5	4	15	7
<i>Galium palustre</i>	1	1	0 ^{n.p.}	0	1	1	100
<i>Menyanthes trifoliata</i>	96	86	-10 ^{n.s.}	-10	14	4	7
<i>Rubus chamaemorus</i>	141	114	-27*	-19	45	18	16
<i>Comarum palustre</i>	18	10	-8 ^{n.s.}	-44	9	1	10
<i>Drosera intermedia</i>	171	73	-98 ^{***}	-57	106	8	11
<i>D. anglica</i>	158	55	-103 ^{***}	-65	114	11	20
<i>Utricularia minor</i>	38	9	-29 ^{***}	-76	31	2	22
<i>U. intermedia</i>	42	7	-35 ^{***}	-83	37	2	29
<i>Lycopodiella inundata</i>	20	2	-18 ^{***}	-90	19	1	50
<i>Hammarbya paludosa</i>	6	0	-6 ^{n.p.}	-100	6	0	-
<i>Drosera rotundifolia</i>	Not rec.	234	-	-	-	-	-
Graminoids							
<i>Agrostis capillaris</i>	0	2	2 ^{n.p.}	new	0	2	100
<i>Deschampsia caespitosa</i>	0	1	1 ^{n.p.}	new	0	1	100
<i>Carex rostrata</i>	22	35	13 ^{n.s.}	59	6	19	54
<i>C. canescens</i>	4	5	1 ^{n.p.}	25	3	4	80
<i>Eriophorum angustifolium</i>	164	201	37 ^{***}	23	0	37	18
<i>Carex nigra</i>	29	26	-3 ^{n.s.}	-10	18	15	58
<i>Trichophorum caespitosum</i>	215	189	-26 ^{**}	-12	37	11	6
<i>Rhynchospora alba</i>	200	145	-55 ^{***}	-28	69	14	10
<i>Carex pauciflora</i>	152	104	-48 ^{***}	-32	60	12	12
<i>C. lasiocarpa</i>	86	52	-34 ^{***}	-39	37	3	6
<i>Rhynchospora fusca</i>	42	16	-26 ^{***}	-62	38	12	75
<i>Agrostis canina</i>	15	4	-11 ^{**}	-73	12	1	25
<i>Carex limosa</i>	113	29	-84 ^{***}	-74	89	5	17
<i>Equisetum fluviatile</i>	21	4	-17 ^{***}	-81	18	1	25
<i>Carex panicea</i>	18	2	-16 ^{***}	-89	16	0	0
<i>C. echinata</i>	54	5	-49 ^{***}	-91	50	1	20
<i>Scheuchzeria palustris</i>	102	0	-102 ^{n.p.}	-100	102	0	-
<i>Eriophorum vaginatum</i>	Not rec.	218	-	-	-	-	-
Bryophytes (exc. Sphagnum)							
<i>Dicranum majus</i>	0	3	3 ^{n.p.}	new	0	3	100
<i>D. leioneuron</i>	0	2	2 ^{n.p.}	new	0	2	100
<i>Polytrichum strictum</i>	11	103	92 ^{***}	836	4	96	93
<i>Hypnum cupressiforme</i>	1	7	6 ^{n.p.}	600	1	7	100
<i>Aulacomnium palustre</i>	30	135	105 ^{***}	350	6	111	82

Table 1. (Continued).

Species	Plot frequency		Change in plot frequency		Losses	Gains	Mobility (%)
	1954	1997	Net	%			
<i>Dicranum bergeri</i>	32	99	67***	209	20	87	88
<i>Pleurozium schreberi</i>	42	99	57***	136	18	75	76
<i>Warnstorfia fluitans</i>	12	28	16**	133	8	24	86
<i>Polytrichum commune</i>	10	15	5 ^{n.s.}	50	3	8	53
<i>Dicranum fuscescens</i>	2	3	1 ^{n.p.}	50	2	3	100
<i>Hylocomium splendens</i>	6	8	2 ^{n.s.}	33	6	8	100
<i>Warnstorfia exannulata</i>	2	2	0 ^{n.p.}	0	2	2	100
<i>Dicranum bonjeani</i>	3	2	-1 ^{n.p.}	-33	3	2	100
<i>Straminergon stramineum</i>	114	71	-43***	-38	49	6	84
<i>Dicranum scoparium</i>	15	7	-8 ^{n.s.}	-53	15	7	100
<i>D. drummondii</i>	1	0	-1 ^{n.p.}	-100	1	0	-
<i>Riccardia latifrons</i>	3	0	-3 ^{n.p.}	-100	3	0	-
<i>Aneura pinguis</i>	11	0	-11 ^{n.p.}	-100	11	0	-
<i>Sphagnum</i>							
<i>Sphagnum girgensohnii</i>	0	5	5 ^{n.p.}	new	0	5	100
<i>S. fimbriatum</i>	1	3	2 ^{n.p.}	200	0	2	67
<i>S. palustre</i>	3	7	4 ^{n.p.}	133	1	5	71
<i>S. lindbergii</i>	12	21	9 ^{n.s.}	75	7	16	76
<i>S. russowii</i>	3	5	2 ^{n.p.}	67	1	3	60
<i>S. majus</i>	100	143	43***	43	26	69	48
<i>S. tenellum</i>	151	214	63***	42	3	66	31
<i>S. pulchrum</i>	112	155	43***	38	6	49	32
<i>S. balticum</i>	124	164	40***	32	15	55	34
<i>S. fuscum</i>	157	202	45***	29	18	63	31
<i>S. cuspidatum</i>	128	150	22*	17	6	28	19
<i>S. affine</i>	44	47	3 ^{n.s.}	7	27	30	64
<i>S. papillosum</i>	214	222	8 ^{n.s.}	4	18	226	12
<i>S. austinii</i>	4	4	0 ^{n.p.}	0	3	3	75
<i>S. magellanicum</i>	244	241	-3 ^{n.s.}	-1	3	0	0
<i>S. angustifolium</i>	49	42	-7 ^{n.s.}	-14	27	20	48
<i>S. fallax</i>	90	76	-14 ^{n.s.}	-15	40	26	34
<i>S. denticulatum</i>	140	113	-27*	-19	52	25	22
<i>S. compactum</i>	35	15	-20**	-57	30	10	67
<i>S. molle</i>	5	2	-3 ^{n.p.}	-60	5	2	100
<i>S. subsecundum</i>	3	1	-2 ^{n.p.}	-67	3	1	100
<i>S. capillifolium</i>	10	3	-7 ^{n.p.}	-70	10	3	100
<i>S. subnitens</i>	6	1	-5 ^{n.p.}	-83	6	1	100
<i>S. squarrosom</i>	1	0	-1 ^{n.p.}	-100	1	0	-
<i>S. subtile</i>	3	0	-3 ^{n.p.}	-100	3	0	-
<i>S. rubellum</i>	Not rec.	237	-	-	-	-	-

Not rec. = not recorded on plot basis; n.p. = statistical test not performed; n.s. = not significant, $p \geq 0.05$; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

seem to be close to disappear (Table 1). *Trientalis europaea* and *Sphagnum girgensohnii* were the most widespread ones among the species new to the area.

Among the vascular plants, species with significantly increasing frequency were generally taller than those with unchanged or decreasing frequency (Fig. 5). Herbs and graminoids decreased significantly in plot frequency between the inventories while shrubs, dwarf shrubs and *Sphagnum* species changed less in frequency than the other groups (Table 3). No herbs, and only *Eriophorum angustifolium* among the graminoids increased significantly in frequency (Table 1). On the other hand, bryophytes other than *Sphagnum* showed an increase in plot frequency (but with highly varying responses among species, and therefore not significant for the group). Only three bryophytes species decreased significantly in frequency (Table 1). Some species with a decreased frequency, viz. *Carex panicea*, *Sphagnum sub-*

nitens and *S. subsecundum* form together with the disappeared *Hammarbya paludosa*, *Aneura pinguis* and *Sphagnum squarrosom*, and the unchanged *Warnstorfia exannulata* a rather distinct group of species more typical for rich fen than for poor fen vegetation in this region (Malmer 1962a, Rydin et al. 1999). The percentage of plots with an occurrence of at least one of these species decreased from 1.2 to 0.2% from the first to the second inventory.

Calculated according to eq. (2) species mobility presents a relative measure of the extent to which a species had entered new plots at the second inventory. Nearly all species with a significant decrease in frequency showed a low mobility (< 25%). However, *Rhynchospora fusca*, *Straminergon stramineum* and *Sphagnum compactum* were striking exceptions, combining a decrease in frequency with a high mobility. Several of the species with a non-significant change in frequency

also showed a mobility > 50%. Bryophytes showed on average, a greater mobility than did the vascular plants (Table 1). For species with a continuous distribution the mobility will always be low.

Species distribution

Changes in species frequencies and changes in species distributions did not always follow each other (Table 1, Fig. 4). Many species changed in frequency, either increasing, mainly filling in gaps within their distribution areas, like *Erica tetralix*, *Rubus chamaemorus* and *Warnstofia fluitans*, or decreasing but still occurring in the same core area in 1997 as in 1954, like *Utricularia intermedia*, *U. minor*, *Straminergon stramineum* and *Sphagnum compactum* (Fig. 4). In contrast, four low-grown species decreased in frequency (*Carex limosa*, *C. pauciflora*, *Rhynchospora fusca* and *Trichophorum caespitosum*) and had more or less disappeared from the Inner Fen and the row of brook pools. Four others (*Drosera anglica*, *D. intermedia* and *Rhynchospora alba*) had also disappeared from large parts of the Outer Fen but maintained their frequency on the bog and the adjacent part of the fen (Fig. 4). Except for *Carex limosa*, all these low-grown species now have a distribution more centred towards the bog than in 1954 (Fig. 4).

Along the row of brook pools and in the Inner Fen, *Scheuchzeria palustris* disappeared completely, while the distribution of *Carex lasiocarpa* and *Equisetum fluviatile* contracted (Fig. 4). In 1954 there was only one population of *Carex rostrata* outside the mire margin. In 1997, *C. lasiocarpa* was largely restricted to the marginal

parts of the Inner Fen, while *C. rostrata* occurred along the row of brook pools. The species increasing in frequency and expanding to new plots (Fig. 4), included particularly hummock species such as *Vaccinium myrtillus*, *V. vitis-idaea*, *Aulacomnium palustre*, *Dicranum bergeri*, *Hypnum cupressiforme*, *Pleurozium schreberi* and *Polytrichum strictum*. Along with the expansion of the hummock forming *Sphagnum fuscum*, three other more wet growing *Sphagnum* species (*S. cuspidatum*, *S. balticum* and *S. tenellum*) expanded in the Outer Fen, along the row of brook pools and even in the Inner Fen. These three species occurred in 1954 only on the bog and in the Outer Fen (Fig. 4). Two other *Sphagnum* species, *S. majus* and *S. pulchrum*, expanded both in the Inner Fen towards the mire margin and in the Outer Fen towards the bog (Fig. 4). It is notable that neither *Menyanthes trifoliata* nor any other species that in 1954 were confined to the mire margin or the Inner Fen had expanded to the Outer Fen or to the bog.

From 1940 to 1996 the *Narthecium* limit moved southwards towards the bog in the southeastern part of the study area (Fig. 6), altogether ca 40–50 m. Otherwise this limit remained in the same position. More conspicuous is that *Eriophorum angustifolium* from 1954 to 1996 had expanded its continuous distribution in the Outer Fen up to 60 m approaching the *Narthecium* limit (Fig. 6). There were in 1996 also a few scattered occurrences of these two species even on parts of the mire that for hydrological reasons must be viewed as truly ombrotrophic.

In 1954, it was easy to divide the Outer Fen into two parts, one southern toward the bog, where *Sphagnum magellanicum* dominated in the lawn communities and

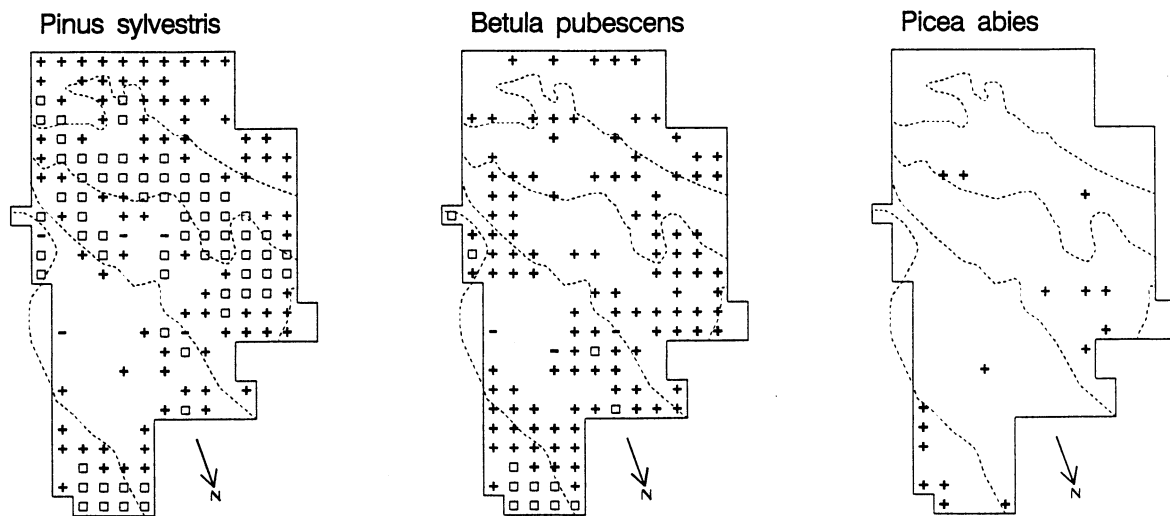


Fig. 2. Distribution maps for 1954 and 1997 showing the presence of trees (> 1.3 m high) in 20 × 20 m plots. The plots are marked according to: the species was found as a tree in both surveys (□), the species was only found in 1954 and disappeared between the surveys (-), the species was new in the 1997 survey (+). The broken line shows the different zones as described in Fig. 1.

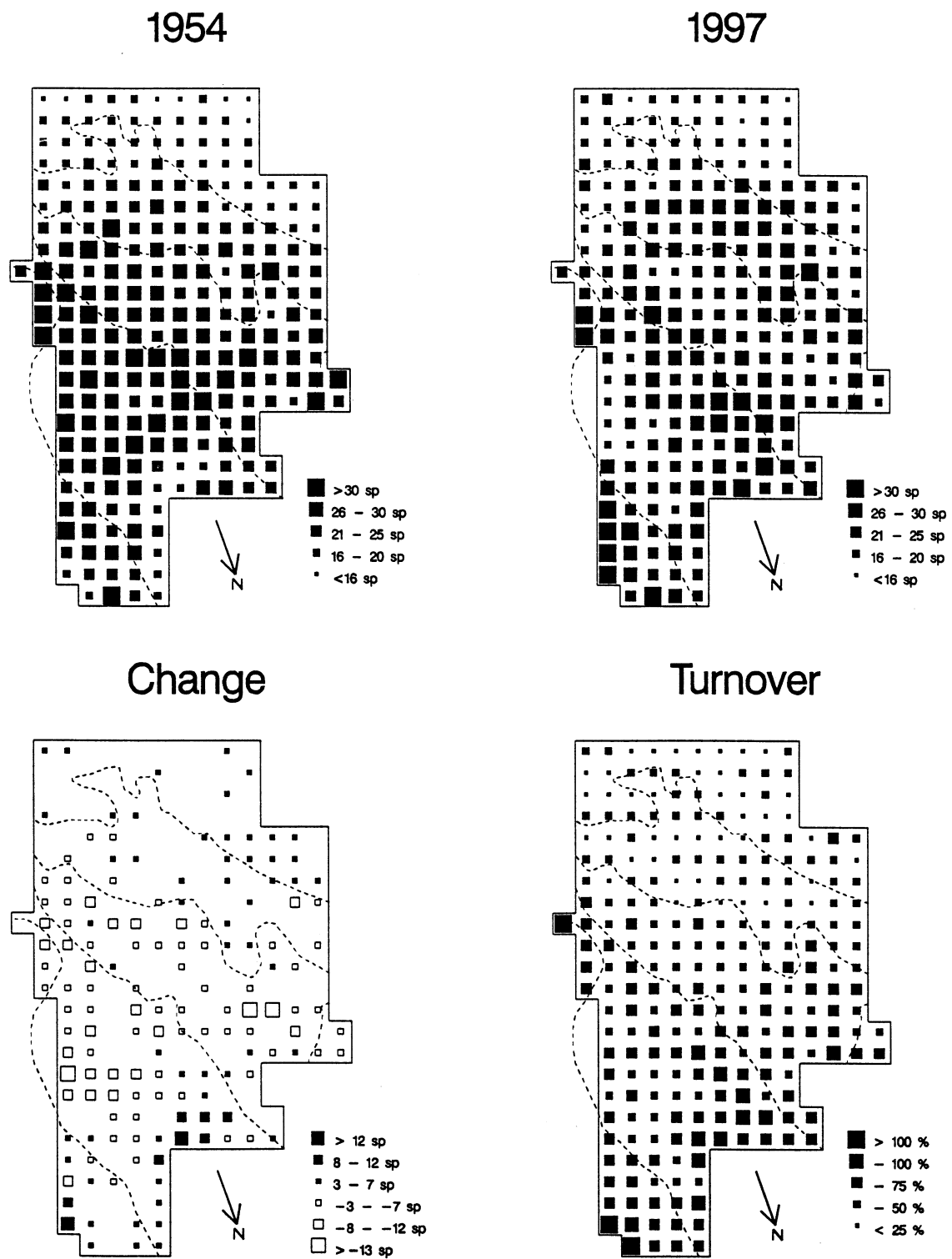


Fig. 3. The total number of investigated species per plot in 1954 and 1997, the change in species number between the investigations and the species turnover calculated according to eq. (1) in the investigated area on Åkhultmyren. The broken line shows the different zones as described in Fig. 1.

one northern where *S. papillosum* dominated. This limit rather closely followed the distribution limit for *Eriophorum angustifolium* in 1954 (Malmer 1962a). In 1997 the two limits did not coincide, as *E. angustifolium* had expanded, while the limit between dominant *S. magellanicum* and *S. papillosum* in the lawns remained at the same position as in 1954.

pH and conductivity

The survey of pH in the water in 1997 indicated that the pH in the ombrotrophic parts of the mire was about the same as in 1954 (pH < 4.1, Fig. 7). However, in the fen area the pH was lower in 1997, especially along the brook pools, where it had decreased from values in the range 4.7–4.9 to near 4.3 (Fig. 7). The four sample points monitored for pH all had lower mean values in 1997 compared with the corresponding samples from the period 1954–1958 (Fig. 8, a reduction by 0.2–0.5 pH units).

At the monitored points, the conductivity (reduced for H⁺-activity) increased by > 25 µS cm⁻¹ when compared to the 1954–1958 period (Fig. 8). On the day when conductivity was measured in 1997, the monitored points had values below the mean for the monitored period (ranging from 5 to 36 µS cm⁻¹ below the mean), but still the conductivity was ca 20 µS cm⁻¹ higher than in 1954 over all the mire (Fig. 7). The relationship between pH and electrical conductivity changed between the two inventories (Fig. 9), reflecting a changed ionic status in the mire water. It was not

possibly to record changes in the water table, since the most sticks used as measuring references had disappeared or been broken.

Indicator values

The indirect indications of the environmental conditions obtained by the Ellenberg indicator values (Ellenberg et al. 1991) gives both for 1954 and 1997, the same picture as the observed environmental variation demonstrated for the vegetation gradients (Malmer 1962a, b, 1986). This means that the indicator values for nitrogen (N) and pH (reaction, R) increases from the bog to the mire margin, while there is a slight decrease for light (L) values because of an increasing tree cover (Table 4). For moisture (F) the highest figure is found in the *Menyanthes* zone in 1954 and drier conditions were indicated both in the mire margin and on the bog.

For all plots taken together the indicator values show increased nitrogen values from 1954 to 1997, while pH, light and moisture decreased (Table 4). The values also indicate that the ground conditions became darker and the mire surface drier both on the bog and in the four zones in the fen. As demonstrated by the measurements of the water pH (Figs 7 and 8) the changes in the indicator values indicate a distinct decrease in pH in the wettest parts of the fen. The indicator values also indicate a slight increase on the bog because of the establishment in 1997 of new species on the bog with rather high R-values (Table 4). The indicated increase

Table 2. Species turnover in the plots calculated according to eq. (1) and the total number of species (vascular plants and bryophytes) per plot in 1954 and in 1997. Mean values (SE) given separately for all plots and for plots within the different zones (see text). The significance of the differences in species number tested with paired t-tests.

	Turnover	n	Mean number of species per plot			Paired t
			1954	1997	Difference	
All species						
All plots	45.2 (1.2)	245	24.4 (0.3)	23.7 (0.3)	-0.7 (0.3)	-2.23*
Bog plots	28.2 (1.4)	48	17.3 (0.3)	19.1 (0.4)	1.8 (0.4)	4.80***
<i>Narthecium</i> zone	29.8 (1.2)	47	23.5 (0.4)	24.0 (0.5)	0.4 (0.5)	0.93 ^{n.s.}
<i>Eriophorum</i> zone	48.2 (1.6)	62	27.0 (0.4)	24.3 (0.5)	-2.7 (0.6)	-4.63***
<i>Menyanthes</i> zone	57.9 (1.8)	68	26.9 (0.6)	25.0 (0.5)	-1.9 (0.8)	-2.52*
Mire margin	69.6 (5.7)	20	27.6 (1.5)	27.9 (1.0)	0.3 (1.5)	0.22 ^{n.s.}
Vascular plants						
All plots	33.8 (1.0)	245	15.6 (0.2)	12.8 (0.2)	-2.7 (0.2)	-12.38***
Bog plots	21.2 (1.9)	48	10.2 (0.2)	10.5 (0.3)	0.3 (0.3)	1.32 ^{n.s.}
<i>Narthecium</i> zone	22.0 (1.5)	47	14.0 (0.2)	13.3 (0.2)	-0.7 (0.3)	-2.60*
<i>Eriophorum</i> zone	36.7 (1.3)	62	17.4 (0.2)	13.0 (0.3)	-4.4 (0.3)	-15.83***
<i>Menyanthes</i> zone	42.5 (1.3)	68	17.9 (0.4)	13.2 (0.3)	-4.7 (0.4)	-10.64***
Mire margin	53.8 (4.5)	20	18.5 (0.7)	15.5 (0.9)	-3.0 (0.9)	-3.19**
Bryophytes						
All plots	70.0 (3.0)	245	8.9 (0.2)	10.9 (0.2)	2.0 (0.2)	10.17***
Bog plots	38.6 (2.8)	48	7.0 (0.1)	8.5 (0.2)	1.5 (0.2)	6.44***
<i>Narthecium</i> zone	41.0 (2.7)	47	9.6 (0.3)	10.7 (0.4)	1.1 (0.3)	3.46**
<i>Eriophorum</i> zone	74.2 (4.8)	62	9.5 (0.4)	11.2 (0.3)	1.7 (0.4)	4.27***
<i>Menyanthes</i> zone	96.3 (6.7)	68	9.0 (0.3)	11.8 (0.3)	2.8 (0.4)	6.39***
Mire margin	110.2 (11.1)	20	9.1 (1.1)	12.5 (0.3)	3.3 (0.9)	3.55**

n.s. = not significant, p ≥ 0.05; * = p < 0.05; ** = p < 0.01; *** = p < 0.001.

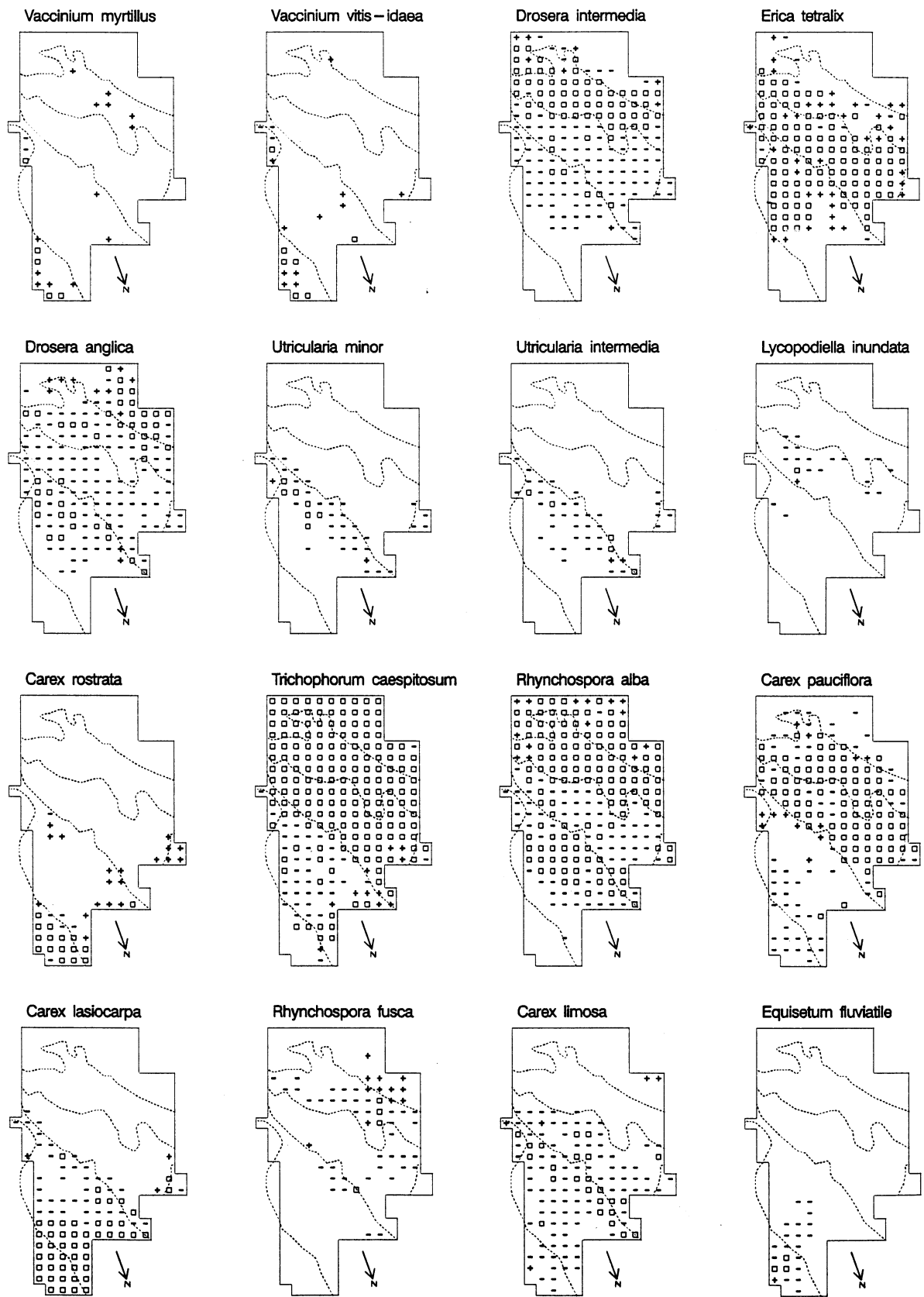
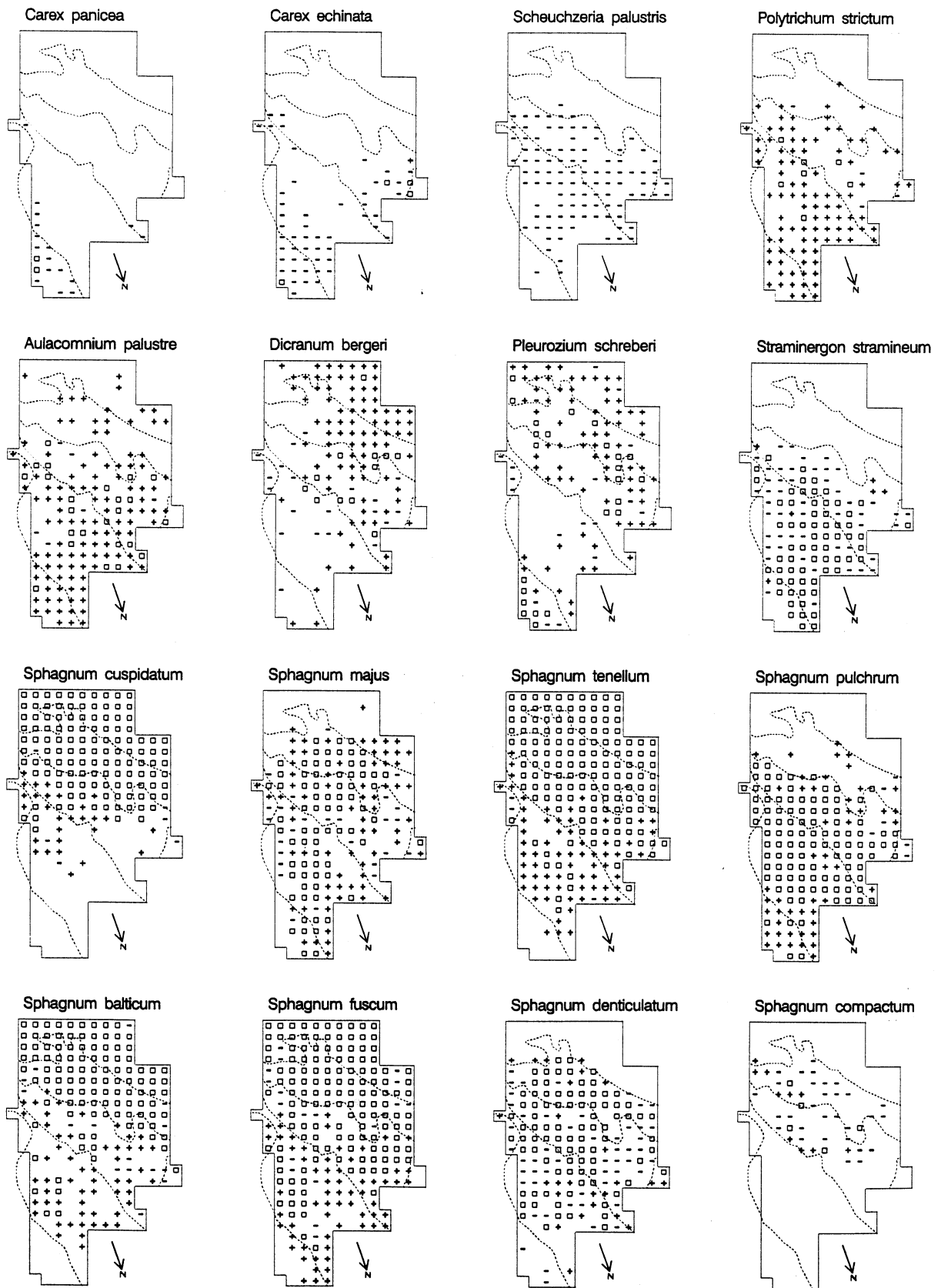


Fig. 4.



in the availability of nitrogen is greater on the bog than in the fen zones.

Discussion

Plant cover dynamics

The plant sociological approach in the 1954 survey did not include permanently marked plots at a finer scale, which makes comparisons on the community level impossible. However, all the plant communities distinguished in 1954 (Malmer 1962a) were easily recognised also in the 1997 inventory. Neither the positions of nor the limits between the five zones in the vegetation along the gradient from the margin to the bog have changed considerably. The second author (N.M.), also performed the 1954 survey, and can make some unquantified comparisons: for instance an increased abundance of dwarf shrubs on the hummocks on the bog and an increased dominance of *Narthecium* in the lawns in the Outer Fen are obvious. Despite the increase in plot frequency of most *Sphagnum* species (Table 1) the general impression is that the cover of *Sphagnum* nowadays is less continuous than in 1954 (Malmer 1998, Malmer and Wallén 1999).

In contrast to this seemingly stable situation at the community level we found a highly dynamic situation regarding the plant populations. A high mobility was demonstrated not only for species increasing in frequency, but also for several species with no significant change or even decreasing in frequency. A low mobility for a species reflects a low dispersal capacity, which may in a changing environment result in decreased occurrence.

The high mobility among the species and the high species turnover were unexpected, particularly because of the large plot size (400 m²). Moreover, all vascular plants in bog and poor fen vegetation are perennials and nearly all are clonal (Backéus 1985, Sjörs 1988). The features of clonal species should favour their persistence and give a high resistance to environmental changes. It is therefore surprising that *Scheuchzeria palustris* could disappear entirely and that *Rhynchospora fusca* demonstrated such a high mobility in spite of its decrease in frequency, as both species have large underground rhizomes. Evidently, even over a period of less than half a century a high mobility is important to counteract local disappearances within a fen or a bog.

Most studies on species turnover in plant communities have been performed in small plots (< 4 m²), over short periods of time (e.g. van der Maarel and Sykes

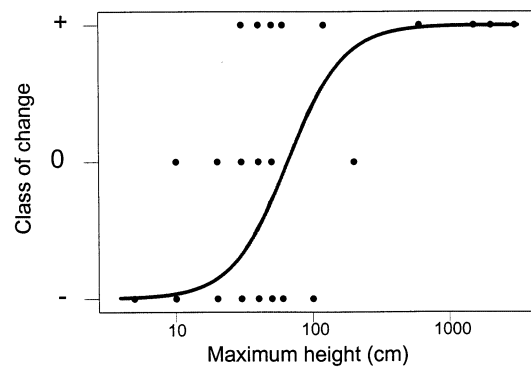


Fig. 5. Ordinal logistic regression model (Anon. 1998) showing the vascular plant maximum heights (dots) for species significantly increasing (+), unchanged (0) or significantly decreasing (-) and the predicted probability from the logistic regression (solid line). The literature data for the plants maximum heights were from Lid and Tande Lid (1994). The axis for maximum height was \log_{10} -transformed prior to the analysis and the parameter estimate for $\log_{10}(\text{maximum height})$ was -2.44 ($p < 0.01$).

1993, Økland 1995). The large plot size in this study hides small-scale turnover, which was found in a study of bog vegetation by Nordbakken (1997), but reveal a considerable mobility and turnover of species in large plots (400 m²) and in *Sphagnum* dominated mire vegetation when the study period is extended to several decades. Compared to the successional changes observed in forests and woodlands over similar spatial and temporal length (e.g. Rydin and Borgegård 1988, Brunet et al. 1997) our data may indicate a low rate of change. However, considering the assumed slow natural changes in boreal peatlands (e.g. Backéus 1972) our investigation points at considerable internal dynamics, seen both in species turnover in the plots and in the distributional changes of many species.

Diversity changes

It is well known that the number of plant species per unit area decreases along both the mire margin–mire expanse and the rich–poor vegetation gradients (Sjörs 1948, Malmer 1962a, Anderson and Davis 1997). This was also confirmed in the present study for combined species richness as well as for the vascular plants and bryophytes taken separately (Table 2, Fig. 3). However, for vascular plants, the difference in species richness between bog and mire margin plots decreased from 1954 to 1997, while it increased for bryophytes (Table 2). The changes resulted in a flora of less conservation value as a number of regionally less common mire

Fig. 4. Distribution maps for 1954 and 1997 showing the occurrences of species in 20 × 20 m plots. The plots are marked according to: the species was found in both surveys (□), the species was only found in 1954 and disappeared between the surveys (-), the species was new in the 1997 survey (+). The broken line shows the different zones as described in Fig. 1.

species (e.g. *Hammarbya paludosa*, *Lycopodiella inundata* and *Rhynchospora fusca*) have been replaced by widespread forest species (cf. Risager 1998). On Skattlösbergs Stormosse, species diversity (plot size 100 m²) decreased over a similar period (Gunnarsson et al. 2000). However, that decrease was mainly found in sites with pH > 5.0. On the sites with lower pH (com-

parable to Åkhultmyren) the diversity hardly decreased at all.

Diversity in vascular plants and bryophytes has changed in different ways. The decrease in vascular plant diversity along the mire margin was more than compensated for by an increase in bryophyte diversity. The bog and the adjacent parts of the Outer Fen

Table 3. Mean frequency (SE) as number of plots (20 × 20 m) for species of different growth forms in 1954–1997 and the mean difference (SE) in plot frequency between 1954 and 1997. The significance of the differences was tested with paired t-tests, where n is the number of species.

Growth form	Mean number of plots		Difference	Paired t	n
	1954	1997			
Shrubs	2.3 (1.2)	6.0 (2.2)	3.7 (2.1)	1.75 ^{n.s.}	6
Dwarf shrubs	45.0 (24.9)	51.0 (24.0)	6.0 (6.8)	0.89 ^{n.s.}	6
Herbs	61.7 (18.4)	41.3 (15.4)	-20.4 (9.1)	-2.24*	15
Graminoids	72.7(17.5)	48.2 (16.5)	-24.5 (8.5)	-2.88*	17
Bryophytes (except <i>Sphagnum</i>)	16.3 (6.4)	32.4 (10.8)	16.1 (9.0)	1.78 ^{n.s.}	18
<i>Sphagnum</i>	65.6 (14.9)	73.4 (17.1)	7.8 (4.4)	1.77 ^{n.s.}	25
All species	50.4 (7.0)	48.3 (7.2)	-2.1 (3.6)	-0.57 ^{n.s.}	87

n.s. = not significant, $p \geq 0.05$; * = $p < 0.05$.

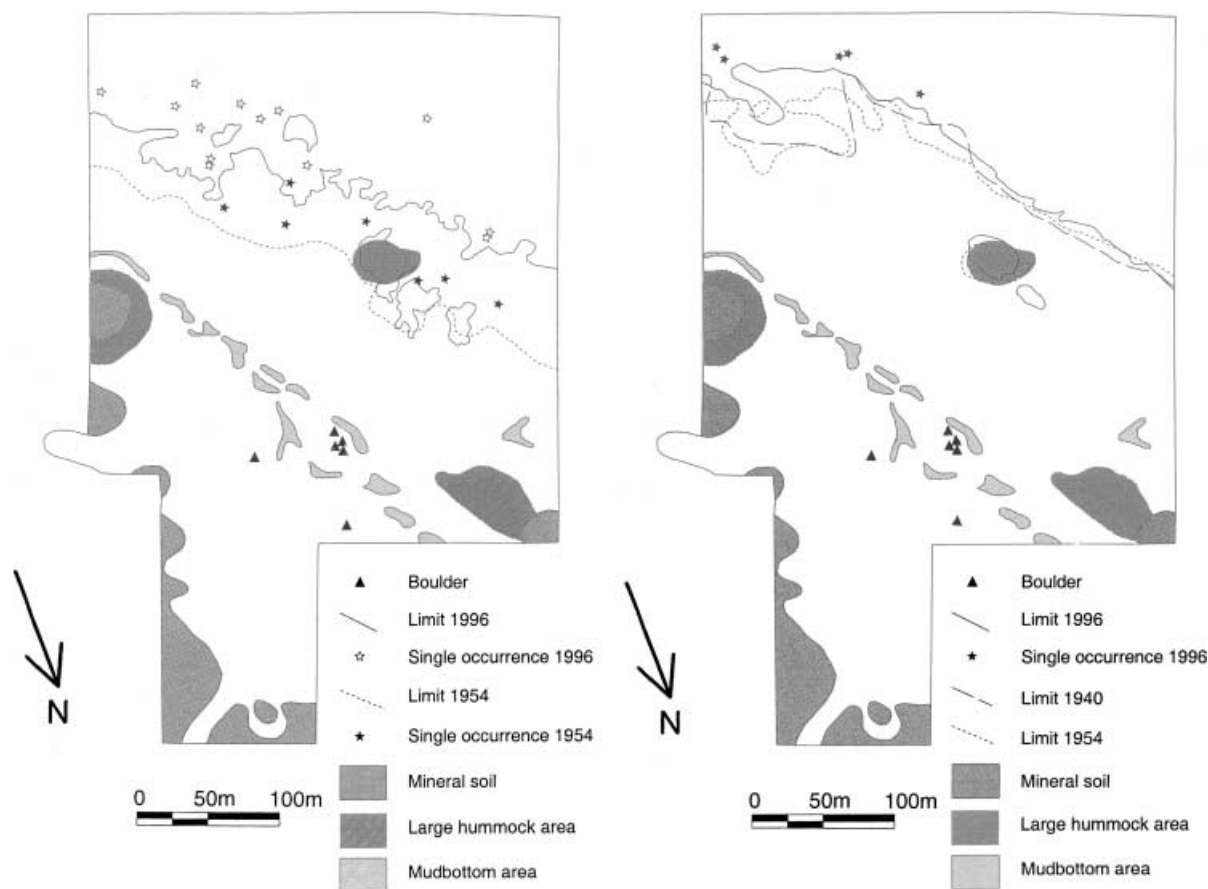


Fig. 6. The continuous distribution limits towards the bog for (left) *Eriophorum angustifolium* in the Outer Fen in 1954 and 1996 and (right) *Narthecium ossifragum* in 1940, 1954 and 1996. Stars mark isolated occurrences outside the continuous limit.

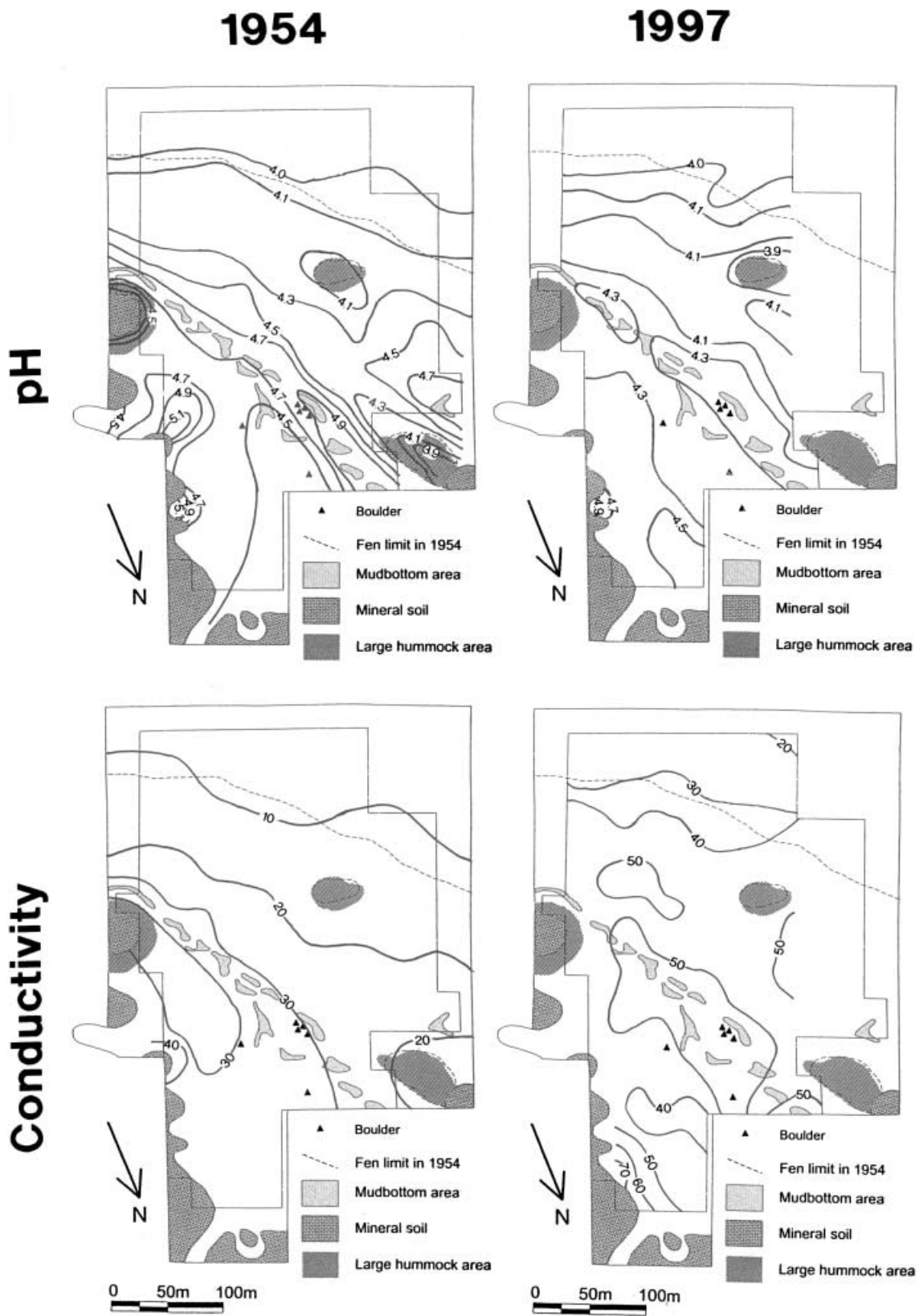


Fig. 7. Isoclines in the study area for pH and electrical conductivity reduced for H^+ -activity ($\mu S\ cm^{-1}$) in 1954 and in 1997.

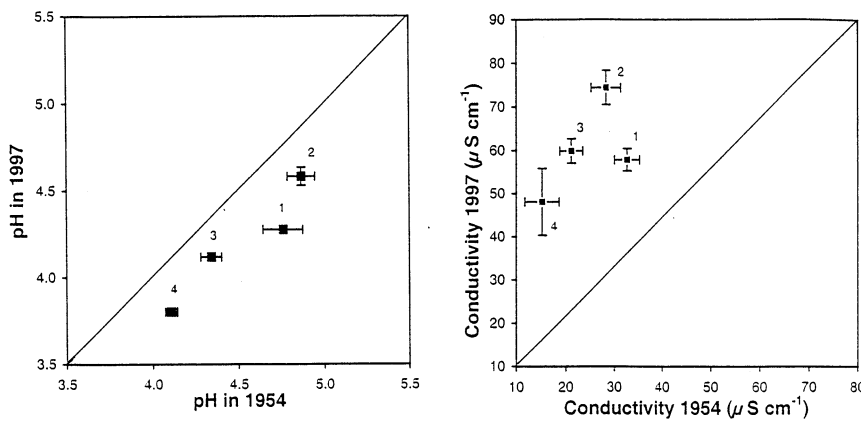


Fig. 8. pH (left) and conductivity (right) in water from four points where open water was sampled in May–September 1954 ($n = 11$) and in June–July 1997 ($n = 28$). For each sample point the mean value (\pm SE) is presented for each period. The positions of the sample points are indicated in Fig. 1. The solid line represents $y = x$.

showed no change in vascular plant diversity, but still the bryophyte diversity increased. In contrast, in the central part of the fen with *S. papillosum* as dominant in the lawn communities, the decrease in vascular plant diversity was not compensated for by the increase bryophyte diversity. Here the decrease in frequency and even disappearance of low grown herbs and graminoids particularly influenced the species diversity.

Two processes seem to have been important for the changes in species diversity. Firstly, the increased cover of trees may have increased the environmental heterogeneity, especially on hummocks and along the mire margin. Therefore, today many plots hold both light-demanding mire bryophytes and shade tolerant forest species, both vascular plants and bryophytes. Secondly, a considerable number of species, mainly small grown

vascular plants and a few bryophytes, have failed to find new, suitable habitats, at the same time as they disappeared from existing sites, particularly in the central part of the fen.

Internal processes or environmental changes?

Studies on macrofossils in peat have demonstrated that changes in the peat-forming vegetation take place both gradually over centuries and rapidly over shorter periods (e.g. Svensson 1988a, b, Ellis and Tallis 2000). Rapid changes, including even changes in the dominant *Sphagnum* species, have been contemporary with climatic shifts. Gradual changes, on the other hand, could more often be interpreted as mainly autogenic, caused by internal processes in the vegetation (Clymo 1964, Vitt and Kuhry 1992, Malmer and Wallén 1999 and unpubl.).

In this study the changes represent a gradual development and some of the changes were noted as ongoing already at the time for first inventory (Malmer 1962a). The high species mobilities represent an internal (autogenic) process in the vegetation. On the other hand, even on this nearly pristine mire, the changes in the Ellenberg indicator values suggest that external (allogenic) processes have affected the vegetation.

The peat stratigraphy in the study area indicates that the position of the fen plant limit (the boundary between fen and bog) during the Sub-Atlantic period (the last 2000 yr) has shifted to its present position from a position closer to the row of brook pools (G. Svensson, pers. comm.). This shift may have resulted from the combined effects of changes in the flow of the water from the surroundings to the fen area and/or changes in the peat accumulation rate within the area, particularly a decreased accumulation rate in the ombrotrophic parts (Malmer and Wallén 1999). The change in the position of the fen plant limit from 1940 to 1997 as indicated by the distribution of *Narthecium ossifragum* and the expansion of *Eriophorum angustifolium* in the Outer Fen may be considered in this context. New

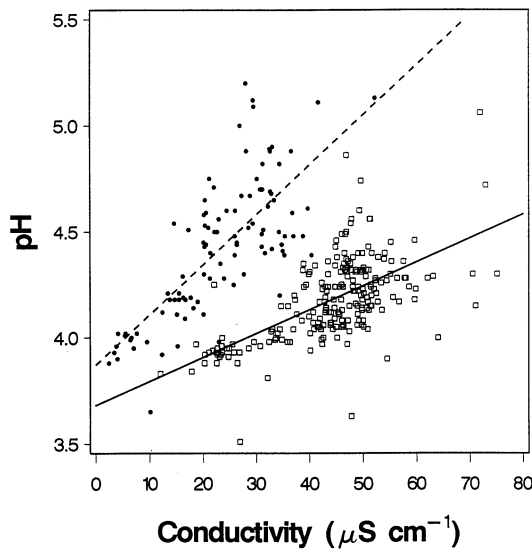


Fig. 9. Relationship between pH and conductivity reduced for H^+ -activity ($\mu S cm^{-1}$) at Åkhultmyren in 1954 (dots, broken line) and in 1997 (squares, solid line). The regression lines follows the equations $pH_{54} = 3.87 + 0.023 \times cond_{54}$ ($R^2 = 0.55$, $n = 100$) and $pH_{97} = 3.68 + 0.011 \times cond_{97}$ ($R^2 = 0.38$, $n = 220$).

Table 4. Ellenberg indicator values in 1954 and 1997 calculated per plot for nitrogen (N), pH (reaction; R), light (L) and moisture (F). Mean values (SE) together with the difference between the years given separately for all plot and for plot means within the different zones. The significance of the differences was tested with Wilcoxon signed rank test for paired observations (S). The mean values for nitrogen are only based on the vascular plant species, while the other mean values are based on both vascular plants and bryophytes.

	n	Mean Ellenberg figures per plot			S
		1954	1997	Difference	
N values (nitrogen)					
All plots	245	1.69 (0.02)	1.79 (0.02)	0.10 (0.01)	6811***
Bog plots	48	1.36 (0.03)	1.60 (0.03)	0.24 (0.04)	423.5***
<i>Narthecium</i> zone	47	1.49 (0.01)	1.60 (0.02)	0.11 (0.02)	288.5***
<i>Eriophorum</i> zone	62	1.61 (0.02)	1.60 (0.02)	-0.01 (0.02)	-69.5 n.s.
<i>Menyanthes</i> zone	68	1.96 (0.03)	2.06 (0.03)	0.10 (0.02)	556***
Mire margin	20	2.32 (0.06)	2.41 (0.05)	0.09 (0.04)	56*
R values (pH)					
All plots	245	2.04 (0.03)	1.87 (0.02)	-0.17 (0.02)	-7652.5***
Bog plots	48	1.51 (0.02)	1.64 (0.02)	0.13 (0.03)	375***
<i>Narthecium</i> zone	47	1.76 (0.02)	1.79 (0.01)	0.03 (0.02)	129 n.s.
<i>Eriophorum</i> zone	62	2.10 (0.04)	1.80 (0.02)	-0.30 (0.03)	-945.5***
<i>Menyanthes</i> zone	68	2.44 (0.04)	2.03 (0.03)	-0.41 (0.04)	-1032***
Mire margin	20	2.41 (0.05)	2.22 (0.06)	-0.19 (0.05)	-75**
L values (light)					
All plots	245	8.20 (0.02)	8.00 (0.02)	-0.20 (0.01)	-11 787.5***
Bog plots	48	8.57 (0.02)	8.24 (0.03)	-0.33 (0.03)	-5485***
<i>Narthecium</i> zone	47	8.23 (0.02)	8.09 (0.03)	-0.14 (0.03)	-422***
<i>Eriophorum</i> zone	62	8.20 (0.01)	8.04 (0.02)	-0.16 (0.02)	-864***
<i>Menyanthes</i> zone	68	8.05 (0.02)	7.91 (0.02)	-0.14 (0.03)	-763***
Mire margin	20	7.71 (0.06)	7.42 (0.08)	-0.29 (0.09)	-72**
F values (moisture)					
All plots	245	7.99 (0.02)	7.63 (0.02)	-0.36 (0.02)	-12 808.5***
Bog plots	48	7.69 (0.03)	7.52 (0.04)	-0.17 (0.04)	-302.5***
<i>Narthecium</i> zone	47	7.89 (0.03)	7.75 (0.03)	-0.14 (0.03)	-339***
<i>Eriophorum</i> zone	62	8.06 (0.03)	7.63 (0.03)	-0.43 (0.03)	-924.5***
<i>Menyanthes</i> zone	68	8.25 (0.03)	7.70 (0.02)	-0.55 (0.04)	-1168***
Mire margin	20	7.89 (0.07)	7.47 (0.05)	-0.42 (0.08)	-86***

n.s. = not significant, $p \geq 0.05$; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

isolated occurrences of *E. angustifolium* have also been noted on several bogs in southern Sweden during the latest decades (Malmer 1998).

The expansion of trees may well have been triggered allogically, but once established an increased tree cover can have rapid autogenic repercussions on the ecosystem (Frankl and Schmeidl 2000, Ohlson et al. 2001), e.g. by increasing the shading. In 1954, a tree layer occurred only along the mire margin and on a few large hummocks in the Outer Fen, but today only few plots lack trees altogether. The tree cover (mainly *Pinus sylvestris*) has generally increased on virgin mires in southern and central Sweden at least during the last 50 yr (Åberg 1992, Gunnarsson and Rydin 1998). For Åkhultmyren aerial photographs from the period 1947–1977 show that already during that period the increase in cover of trees and hummocks had begun (Ihse et al. 1992). The increased nitrogen deposition could be a reason for the increased tree cover, but a position well above the ground water table is essential for the survival of pine seedlings (Gunnarsson and Rydin 1998), and a lowered ground water table may be one of the main reasons for the increased occurrences of trees on mires (Malmer 1998, Malmer and Wallén 1999, Frankl and Schmeidl 2000). Combined with a

lower water level the improved tree growth may have prepared the way for the increasing or new species that are true hummock inhabitants (e.g. *Dicranum bergeri* and *Polytrichum strictum*) or common under forest canopies (e.g. *Vaccinium myrtillus*, *V. vitis-idaea* and *Pleurozium schreberi*, Ohlson et al. 2001). These two groups comprise nearly 40% of the new or increasing species on Åkhultmyren.

The decreases in frequency among small growing herbs and graminoids could also be an effect of a lowered ground water table, as most of these species have their greatest abundance in the wettest microhabitats. Among them is *Scheuchzeria palustris*, whose disappearance from many parts of Europe has been explained by its sensitivity to long dry periods (Tallis and Birks 1965). Two of the three bryophytes that have decreased significantly also occur in these microhabitats (e.g. *Sphagnum denticulatum* and *S. compactum*). These changes affect the diversity and turnover in the central part of the study area, i.e. the row of brook pools and its surroundings. It is evident from mapping of the row of brook pools in 1954 that the hydrology in this area has changed. In 1954 the area with open water surface was much larger than today, which is also indicated by the large decrease in the Ellenberg moisture indicator in

the *Menyanthes trifoliata* zone. In contrast to the decreasing *Utricularia* species and *Sphagnum denticulatum*, the dense carpet formers *S. majus* and *S. pulchrum* have increased in frequency, and it appears that these carpet species have expanded over open water and other formerly wet microhabitats. Lawn communities with a high abundance of *Narthecium ossifragum* may also have expanded over such communities, although it is impossible to trace it from this study. This expansion is particularly observed in the central parts of the fen where *S. papillosum* dominates the lawn communities.

An acidification was observed along the row of brook pools and in the Inner Fen indicated by the reduced pH and Ellenberg pH indicator. In these parts *Sphagnum balticum*, *S. cuspidatum* and *S. tenellum* have expanded since 1954 when they were confined to the most acid parts. In addition, bryophytes more common in moderately rich than in poor fens (e.g. *S. subsecundum*, *S. subnitens*, *Riccardia latifrons*) have decreased in frequency or disappeared. Also at Skattlösbergs Stormosse and other mires a reduction of pH in sites with rich fen vegetation coincided with a loss of rich fen bryophytes (Thygesen 1997, Gunnarsson et al. 2000). Since *Sphagnum* species can acidify the environment (Clymo 1964), such changes can be autogenic. The observed increment in conductivity of the mire water may mainly reflect an increase in sulphate ions, indicating atmospheric deposition, but the increased sulphate levels are unlikely to have had any effects on the plant populations.

We do not have data on the cover of *Sphagnum*, but there are several observations of decreasing *Sphagnum* cover on bogs in southern Sweden and Denmark during the latest decades (Malmer 1998, Risager 1998). Moreover, experimental studies have demonstrated that growth of important peat producing hummock *Sphagnum* species decreased with increasing nitrogen influx (Gunnarsson and Rydin 2000). The increased nitrogen deposition during the period between the inventories gives a good reason to expect a corresponding decrease in productivity and vitality among several of the dominant *Sphagnum* species and less sensitive species may then get an opportunity to expand. For example *S. fallax* has expanded its distribution on bogs in western Europe that are much more exposed to airborne pollutants than Åkhultmyren (Lütke Twenhöven 1992, Mackay and Tallis 1996, Risager and Aaby 1997).

In bog and poor fen vegetation, the structure of the plant communities depends on the competition between the vascular plants and *Sphagnum* for light and for mineral nutrients (Malmer et al. 1994, 2003). There are clear indications that the balance is shifting in favour of the vascular plants (Berendse et al. 2001, Ohlson et al. 2001). A lower mean water level will increase mineralisation in the peat, but that will only increase the availability of nutrients for the vascular plants, as *Sphagnum* only has access to minerals from atmo-

spheric deposition (Malmer et al. 1994, 2003, Svensson 1995). This would be especially important for vascular plants like dwarf shrubs and *Narthecium ossifragum* that lack aerenchymatic tissue in their belowground parts (Daniels 1975). Slow-growing vascular plants and bryophyte species may under such conditions be replaced by more nutrient-demanding and productive vascular plants (Aerts and Berendse 1988), and this is probably what we observe at Åkhultmyren. An expansion of *Narthecium ossifragum* and other vascular plants forming dense or tall grown stands triggered by an increased availability of mineral nutrients will also reduce the diversity among the low grown herbs and graminoids. Additionally, when the aboveground biomass and the litter production increase, the regeneration by seeds may be hampered, further reducing species richness (e.g. Redbo-Torstensson 1994, Foster and Gross 1998).

The Ellenberg indicator values for nitrogen indicate that the availability of mineral nutrients is higher in the mire margin than in the mire expanse vegetation (Malmer 1962b, 1986). An increased nutrient availability may explain the expansion of *Phragmites australis* (cf. Harding 1993, Güsewell and Edwards 1999, Gunnarsson et al. 2000), which was found along the northern margin of the mire just outside the study area. *Phragmites australis* may reach the study area within the next ten years or so.

In conclusion, although the bog and poor fen ecosystem on Åkhultmyren is more or less untouched, it is remarkable that we have found great changes in the frequency and distributional patterns for nearly 50% of the species in plots as large as 400 m² during the last 40 yr. Some changes may be autogenic but there is strong evidence that much of the changes were allogenic and caused or enhanced either directly or indirectly by the combined effects of increased surface dryness, acidification and increased nitrogen supply. The roles of these factors cannot be fully disentangled in the present study but the unexpected great mobility among the species has perhaps reduced the effects of environmental changes on the species richness.

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