Rapid changes in plant assemblages
on mud-bottom hollows in raised bog: a sixteen-year study

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SUMMARY

Mud-bottom hollows with bare peat surface are common features of raised bogs in the boreal zone. Due to retarded peat accumulation, these hollows promote changes in plant cover, microtopography and carbon accumulation. We undertook a 16-year study of eight permanent plots in mud-bottom hollows to assess their durability, regularities and causes of development. Annual changes in the areas of plant assemblage types in the plots averaged around 20 %, and changes during the entire study period approached 90 %. Bare peat surfaces existed for 3–12 years on average before being overgrown by lateral expansion of the bordering *Sphagnum* carpet (average rate of advance 4.1 ± 1.3 cm yr^{-1}) or by clumps of *Rhynchospora alba*. The annual changes in representation of plant assemblages fluctuated through time and were related to weather factors. The overgrowth of bare peat by *Sphagnum* carpet was favoured by wetter conditions, whereas overgrowth by the *R. alba* dominated plant assemblage was temporally less regular and independent of weather.

KEY WORDS: bare peat; permanent plots; plant assemblages; *Rhynchospora alba*; *Sphagnum* mosses

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INTRODUCTION

The final stage of mire development - ombrotrophic raised bog - is characterised by rather stable environmental conditions and by only slow successional changes in plant cover. Therefore, bogs are considered to be among the climax communities of the boreal zone (Klinger 1996, Zobel 1998). In Estonia, the first mires had already attained the bog stage *ca.* 8,000 years ago (Allikvee & Ilomets 1995) and have since been quite stable with only minor and slow-paced changes in plant cover. Established plant communities dominated by *Sphagnum* mosses may exist for thousands of years (Karofeld 1995). Because future climate change is expected to have greater effects at higher latitudes and in wetlands, and because the response of mires to changing environmental conditions will be partly affected by plant cover and microtopography (Bridgham *et al*. 1995, Waddington & Roulet 1996, Weltzin *et al*. 2001, Yu *et al*. 2001), it is important to understand the nature and controlling factors of these changes.

Raised bogs are noted for their patterned surface microtopography and their heterogeneous plant cover, dominated by *Sphagnum* mosses, which create a specific environment for all other organisms and which play key roles in carbon accumulation within peat deposits (Gorham 1991, Rydin & Jeglum 2006). However, most bogs in the boreal

zone contain patches in which *Sphagnum* mosses are dead, and the bog surface within these patches often consists of blackish leathery algal mats. Mud-bottom hollows have been described and studied in Estonia (Masing 1982, Masing 1984, Karofeld & Toom 1999), in Scandinavia and Finland (Sjörs 1983, Eurola 1962, Malmer 1962, Hosiaisluoma 1975, Nordbakken 2001), in north-west Russia (Bogdanowskaya-Guiheneuf 1969), in western Europe (Boatman & Armstrong 1968, Goode 1970, Hulme 1976, Lindsay *et al*. 1985) and in North America (Damman & French 1987). Terms such as mud-bottom hollow, bare or naked peat area, flark, regressive complex, *etc*. have been used to designate these areas. In this article we use the most common term, mud-bottom hollow. The blackish surfaces of mud-bottom hollows are composed of a dense layer of algae (dominated by *Zygogonium ericetorum*) covering remnants of *Sphagnum* mosses (Karofeld & Toom 1999). The dimensions of mud-bottom hollows vary from tens of centimetres up to tens of metres and their areas can attain several hundreds of square metres. Typically only a few *Rhynchospora alba*, *Drosera anglica* and/or *Andromeda polifolia* plants grow there. The mud surfaces are inundated during wet periods, whereas in dry summers the dried algal mats form a characteristic leathery purple layer - the so-called 'meteoric paper' (Thomson 1924).

The degeneration of *Sphagnum* mosses and the formation of mud-bottom hollows have been attributed to the effects of bog gases, floods, freezing, desiccation, colonisation by algae or lichens and infection by fungi (see Karofeld 1999 for an overview). Several experimental studies have revealed the leading role of micro-fungi in the necrosis of *Sphagnum* mosses (Readhead 1979, Untiedt & Müller 1984, Tsuneda *et al.* 2001a, Tsuneda *et al.* 2001b, Thormann *et al.* 2001, Thormann *et al.* 2002). The necrotic effect of algae and parasitic fungi (particularly *Lyophyllum palustre*) on *Sphagnum* mosses may be initiated by increased N availability (Limpens *et al.* 2003a, Limpens *et al.* 2003b) and, therefore, also occurs near bird colonies in bogs (Tomassen *et al.* 2005). The existence of freshly formed and expanding mud-bottom hollows alongside relatively stable or overgrowing mud-bottom hollows may indicate that the factors triggering their formation are restricted in time and space (Karofeld & Toom 1999), as confirmed by a transplantation experiment at Männikjärve Bog in Estonia (Karofeld 2001). Our personal observations suggest that the formation of new mud-bottom hollows occurs periodically within just a few years. The simultaneous appearance of several mud-bottom hollows on Männikjärve Bog attracted our attention in 1997 and inspired the present study. Since then the formation of new mud-bottom hollows has not been observed in this bog.

Mud-bottom hollows cover considerable parts of the surfaces of some bogs and, therefore, are likely to affect the succession of plant communities and the differentiation of bog microtopography. Peat accumulation is retarded at these locations (Sjörs 1961, Hulme 1976), and replaced by increased peat mineralisation (Sjörs 1990, Karofeld 2004) and methane emission (Crill *et al.* 1992, Frenzel & Karofeld 2000). Therefore, the vertical differentiation between mud-bottom hollows and adjacent areas with *Sphagnum* growth and ongoing peat accumulation increases. The resulting depressions are inundated for longer during wet periods, thereby becoming suitable for hydrobiontic plant species and initiating accelerated changes in plant communities (Masing 1982, Karofeld & Pajula 2005). This development results in a sharp contact in the vertical profile at which the composition of peat changes from hummock or lawn peat to hollow peat *via* a thin slimy interlayer (Karofeld 1998).

Mud-bottom hollows have been described by several authors, but to our knowledge no other detailed long-term studies have been carried out to elucidate their durability and development over time. We followed changes within permanent plots over 16 years in order to elucidate the permanence of mud-bottom hollows and the character and dynamics of their development. We explored: 1) the main pathways for the development, changes between plant assemblage types and overgrowth of mud-bottom hollows; 2) whether the changes and their dynamics are affected by specific meteorological conditions; and 3) how the development of mud-bottom hollows might be affected by future climate change.

METHODS

Study site and permanent sample plots

The study was carried out at Männikjärve Bog (area 320 ha, maximum peat thickness 7.5 m) in central Estonia (58° 52′ 55″ N, 26° 14′ 87″ E). This is a raised bog of limnogenic origin with a well-developed hollow-ridge-pool complex in the centre and forested margins. The mud-bottom hollows were first described by Thomson (1924), followed by Masing (1982, 1984) and others (Karofeld & Toom 1999, Frenzel & Karofeld 2000). In each of eight mud-bottom hollows of different types, the corners of a 1 × 1 m permanent study plot were marked with wooden sticks during autumn in 1998–2000. Plots I, II, III and V were located in mud-bottom hollows with a large area of bare peat and a relatively distinct border with healthy *Sphagnum* carpet; whereas Plots IV, VI, VII and VIII represented hollows with fragmented patches of bare peat within vegetated areas. Each plot was photographed in September or October, at the end of the vegetation period. Before photographing each plot, a wooden frame meshed with string dividing the plot into a 20 × 20 cm grid was placed on the corner sticks and its position adjusted to match the previous year's photograph if necessary. Noticeable differences from the previous year's photograph were described in the field.

Analyses of plant cover patterns

Photographs were scanned and reshaped, and oblique distortions removed, with *Micrografix Picture Publisher 10*. Each image was then vectorised with *MapInfo* using the positions of recognisable objects (e.g., clumps of *Eriophorum vaginatum* or *R. alba*) and the fixed corners of the plots; and five centimetres was cropped from each side of the image to eliminate possible deformation at the edges and to maximise precision, resulting in a plot area of 90 × 90 cm for further analysis. Plant cover maps were created by identifying four different plant assemblage types:

A) healthy *Sphagnum* carpet with some vascular plants (*Sph.*);

B) necrotic, dying *Sphagnum* (necr. *Sph*);

C) almost-bare peat surface, often covered with algal mat or with few vascular plants or *Sphagnum* shoots (bare surf.); and

D) bare peat surface overgrown with clumps of *R. alba* and/or with *Sphagnum* mosses (overgr. bare surf.) (Figure 1).

For the four plant assemblage types, areas and cover percentages were calculated, as well as changes between them since the preceding year and throughout the study period. Changes over areas smaller than 10 cm^2 were excluded from further analysis. Such exclusions constituted < 5 % of the area of any single plot, were caused largely by inaccuracy in digitising or distortion of photographs, and tended to consist of long and narrow bands between the different assemblage types. For example, dried-out *Sphagnum* mosses were often difficult to distinguish from necrotic mosses at this scale. A Markovian chain model (Usher 1981) was used to determine the permanency and probability of transitions between the four assemblage types. Annual changes and percentage of probabilities were calculated to establish how much each assemblage type changed each year.

Changes in plant assemblage types

The increase or decrease in the area of each plant assemblage type within each plot was expressed as a percentage of the area recorded in the preceding year. In order to achieve a near-normal distribution, these percentages were square root transformed before data processing. The presence of relatively clear boundaries allowed us to calculate the speed (cm yr^{-1}) of the lateral expansion of *Sphagnum* carpet over the bare peat surface in Plots I−IV and VI. The distance (n = 6–10) was measured perpendicularly from tangents to the previous year's edge on vectorised photographs using ArcGIS software. To test the synchronicity of *Sphagnum* carpet expansion between plots, we used pairwise Spearman correlation.

Relationships between changes in plant assemblage types and weather factors

Data for monthly rainfall and air temperature covering the whole study period were acquired from the Männikjärve Bog meteorological station, which was located a few hundred metres from the study plots. From these data, mean monthly and total precipitation and mean temperature were calculated for each vegetation period (Table 1). Vegetation period was defined as a six-month long freeze-free period from the beginning of May till the end of October. To elucidate any combined effect of precipitation and air temperature, the Lang's Moisture factor (Stadler 2005) was calculated from total precipitation and mean air temperature during the vegetation period, according to the equation:

$$M_L = P / T \qquad [1]$$

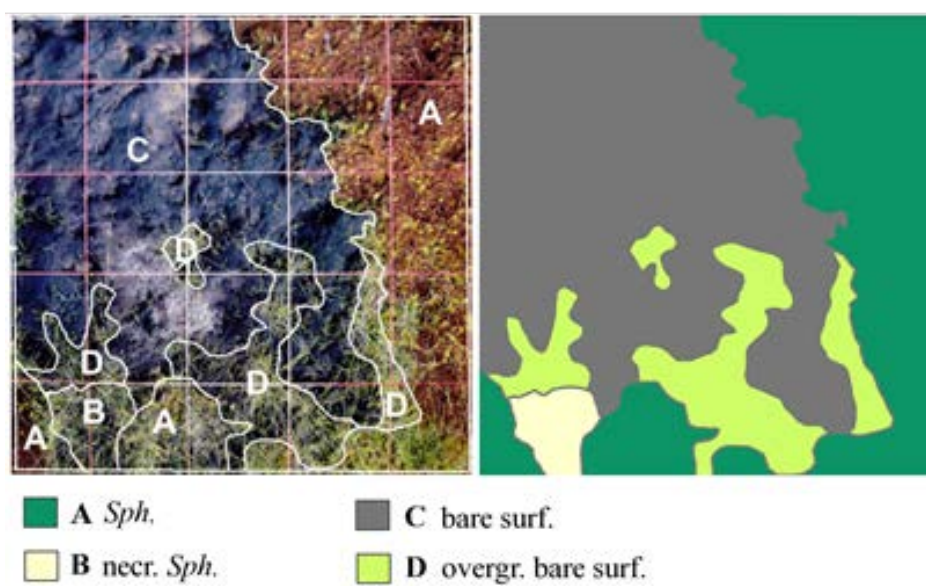where *P* is total precipitation (mm) and *T* is mean daily temperature (°C).

Figure 1. Photograph of Sample Plot I (left) and the plant assemblage types distinguished (right) in October 2002.

General Linear Models (Statistica version 9.1; Statsoft Inc.) were applied to test relationships between the changes in plant assemblage types and the weather factors. One-way ANOVA was used to clarify the effect of the year on the changes and the Tukey HSD test was used to evaluate differences between years. Multiple Linear Regression (standard stepwise method) was used to estimate the effect of weather on the changes in areas covered by the different plant assemblage types. Surface cover changes were square-root transformed before analysis. Total and mean precipitation, mean temperature and Lang's moisture factor *per* vegetation period were entered into the regression model as independent variables, and standardised regression coefficient 'beta' was used to evaluate the importance of changes to each assemblage type.

To assess autocorrelation between successive years and to test whether meteorological variables were correlated with lateral expansion of the *Sphagnum* carpet we fitted a linear model with AR1 autocorrelation structure. R statistical computing software was used, along with the "nlme" package (Pinheiro *et al.* 2014). All relationships were evaluated at significance level $p < 0.05$.

Plant cover within the plots was described at the beginning and end of the study period, identifying all plants (vascular plants and bryophytes) to species level. To reveal the type of bog microform (hollow, lawn or hummock) where mud-bottom hollows had formed, peat samples were taken directly beneath the bare peat surface or algal mat and the dominant *Sphagnum* species were identified under the microscope.

Table 1. Precipitation and temperature at Männikjärve Bog during the vegetation periods (01 May to 31 October) of the study years.

Year	Total precipitation (mm)	Mean monthly precipitation (mm)	Mean monthly air temperature (°C)	Lang's Moisture Factor (M_L)
1999	337.3	56.2	12.8	26.35
2000	370.7	61.8	11.9	31.15
2001	454.7	75.8	13.1	34.71
2002	306.3	51.1	12.6	24.31
2003	521.0	86.8	12.2	42.70
2004	583.0	97.2	12.4	47.01
2005	402.3	67.1	12.9	31.18
2006	276.5	46.1	13.8	20.03
2007	447.0	74.5	13.0	34.38
2008	597.9	99.7	12.5	47.83
2009	502.8	83.8	12.3	40.88
2010	388.6	64.8	13.6	28.57
2011	370.4	61.7	14.1	26.27
2012	519.0	86.5	12.7	40.86
2013	321.8	53.6	14.2	22.66
2014	445.5	74.3	13.2	33.75

RESULTS

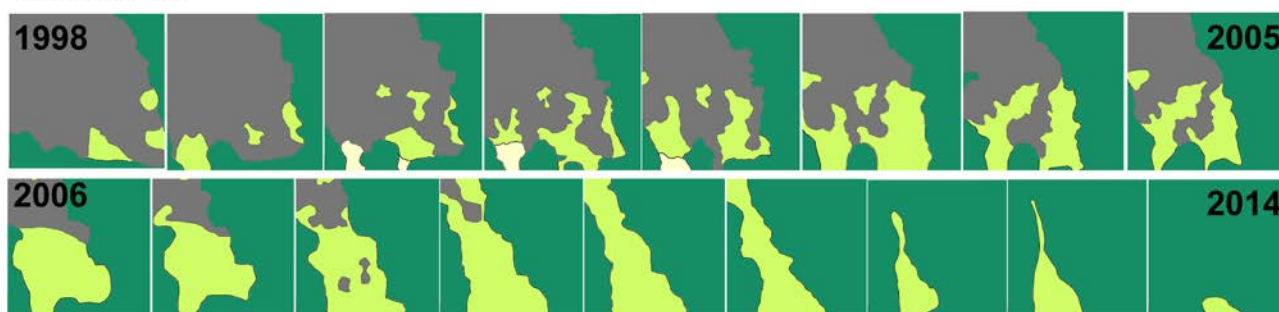**Distinction of plant assemblage types**
In most cases it was relatively easy to distinguish between the four defined plant assemblage types. Figure 1 shows, for illustration, a photograph of Plot I and its plant assemblage types. Whereas Plots II and III were characterised at the start of the study by two dominant assemblages (A and C) separated by rather distinct borders, the other plots were much more diversely patterned. Figure 2 illustrates the patterns of plant assemblages (and changes) recorded in each year of the study period for three plots.
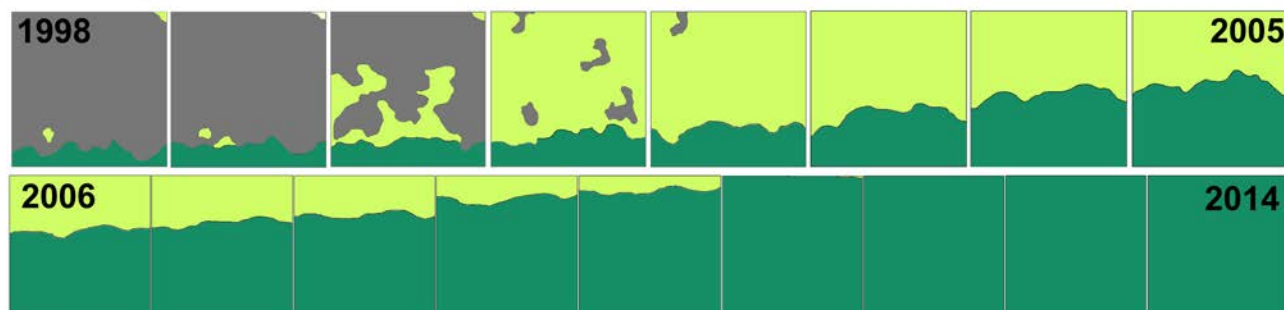
Changes in plant assemblage types
Botanical analysis of the peat directly beneath the bare peat surface or algal mat revealed that four of the mud-bottom hollows had formed in hollows and four in lawns. Former hollows at Plots I, II, IV and V were distinguished by the dominance of *S. cuspidatum* and *S. balticum* with some *S. magellanicum*, whereas former lawns at Plots III, VI, VII and VIII were distinguished by the dominance of *S. magellanicum*.

Changes in the areas of the four plant assemblage types and the dynamics of overgrowth of bare peat surface are shown in Figure 3. The changes in some plots, especially Plots I−III, were relatively simple
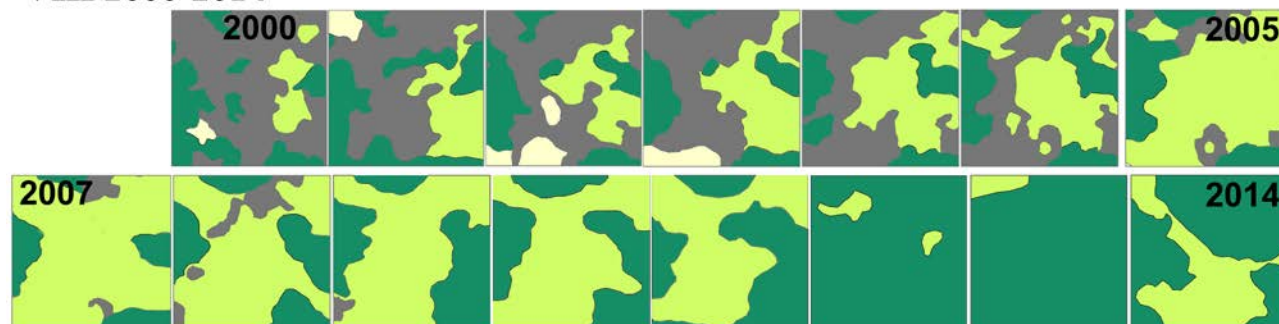

Figure 2. Maps of plant assemblage types in Sample Plots I, III and VIII in consecutive years of this study. See Figure 1 (legend) for key to assemblage types.

and unidirectional, involving the overgrowth of bare peat surface by *Sphagnum* carpet and / or *R. alba* clumps. Changes in the other plots were multifarious and exhibited temporal reversals. Nonetheless, by the end of the study, seven mud-bottom hollows had been totally overgrown and small patches of bare peat surface among *R. alba* clumps remained recognisable only in Plot IV.

Annual mean changes in the areas of plant assemblages on the plots varied > 2.5 times amongst the plots (Table 2). Generally, greater annual changes did not result in greater total change over the whole study period. For example, the greatest annual mean change (in Plot VII) resulted in the second-smallest total change. Only in Plot VIII did

Table 2. Annual (% ± SD) and total change in area between plant assemblage types in the sample plots.

Plot	Annual mean (%)	Period total (%)
I	12 ± 5	88
II	13 ± 14	76
III	11 ± 15	89
IV	17 ± 14	81
V	22 ± 14	82
VI	13 ± 9	66
VII	28 ± 7	70
VIII	26 ± 12	87
Mean	18 ± 11	80

the second-greatest annual change lead to one of the greatest total changes as well. Greater annual mean and smaller total-period changes characterised plots in which greater changes between plant assemblage types took place in smaller areas during the study period.

The annual and total average changes in area of plant assemblage types varied widely and fluctuated in both magnitude and character (Figure 4). During three periods (1998−1999, 2001−2002 and 2004−2005), most changes were smaller than the study-period average. Changes greater than the period average occurred mostly in 2000−2001, 2005−2006, 2007−2008 and 2011−2012. Whereas the first two periods with greater changes were distinguished by extensive overgrowth of bare peat surface with *R. alba* clumps, the later periods were characterised by increase in the area of *Sphagnum* carpet and its expansion over bare peat surfaces. Only in 2002−2003 and 2007−2008 did the total area of the *Sphagnum* carpet decrease (temporarily) to any degree.

The observation period of 16 years was sufficiently long to calculate, at annual intervals, the probability of a plant assemblage type remaining the same or changing to another type (Table 3). Due to the great heterogeneity of some sample plots and difficulties in distinguishing between some assemblage types, these probabilities exhibit large standard deviations. Nevertheless, as suggested by visual observation and by Figures 2 and 3, the most likely transitions were the replacement of necrotic *Sphagnum* with healthy *Sphagnum* carpet and the overgrowth of bare peat surface by *R. alba* clumps / *Sphagnum* carpet. It was most probable that a patch would remain unchanged, because this scenario
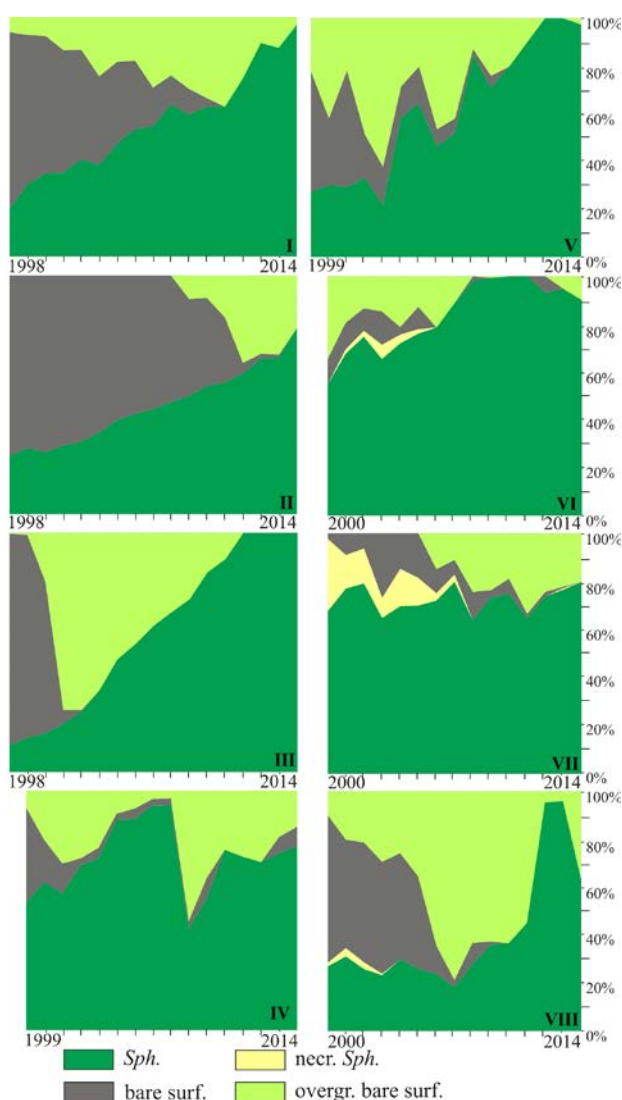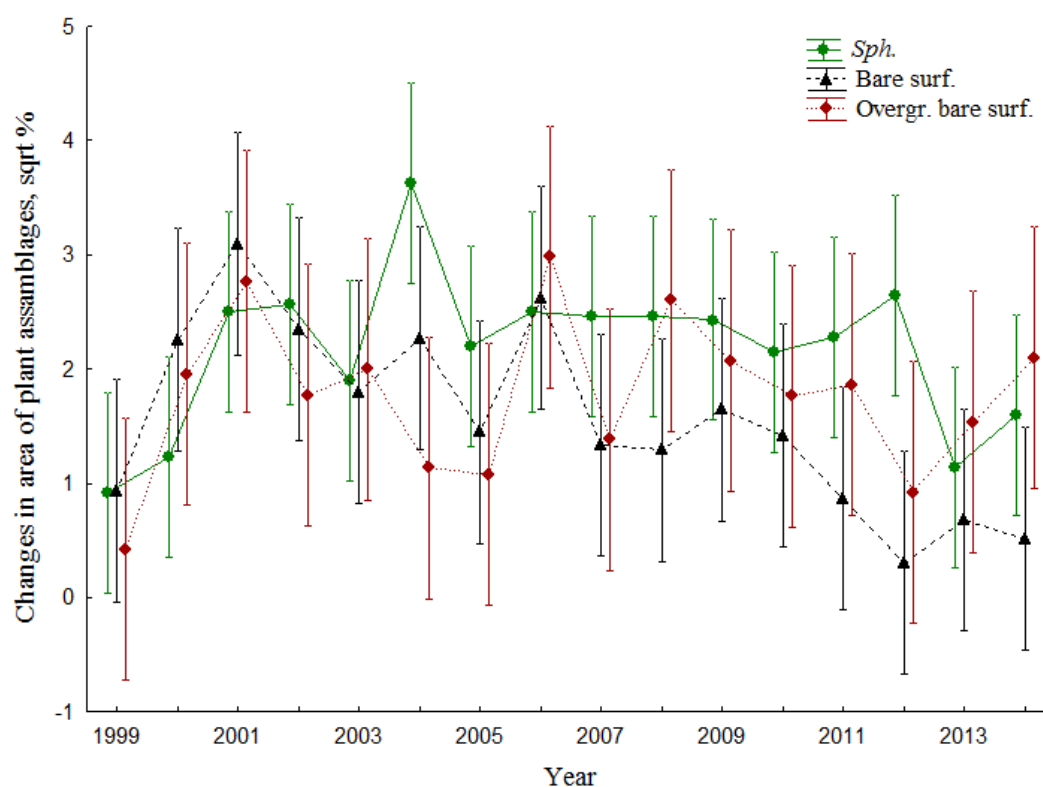

Figure 3. Time course (1998−2014) of percentage of plot covered by each of the four plant assemblage types, in Sample Plots I−VIII.

Figure 4. Changes in the areas (sqrt) of *Sphagnum* carpet *(Sph.)*, bare peat surface (bare surf.) and overgrown bare peat surface (mostly by *R. alba*; overgr. bare surf.) for each year of the study.

characterises single-year transitions; yet even relatively small annual changes between assemblage types could lead to great changes over the complete period (Table 2).

Determination of the dominant *Sphagnum* species beneath the bare peat surface and of plant species in overgrowing plant assemblages showed

Table 3. Probability (% ± SD) of annual transitions within or between plant assemblage types during the study period.

Initial type	End type			
	A	B	C	D
A (*Sph.*)	93 ± 7	4 ± 3	4 ± 4	8 ± 8
B (necr. *Sph.*)	44 ± 30	45 ± 20	< 1	40 ± 30
C (bare surf.)	14 ± 16	< 1	70 ± 26	37 ± 30
D (overgr. bare surf.)	30 ± 27	7 ± 7	20 ± 20	67 ± 25

that lawn communities had been replaced by hollow communities in four plots (Plots III, VI, VII and VIII), whereas hollow communities had persisted in Plots IV and V and had been replaced by wet lawn communities in Plots I and II.

Types and character of bare peat surface overgrowth and expansion of *Sphagnum* carpet

In general, two types of overgrowth of bare peat surface co-existed. The first type was characterised by a distinct border between bare peat surface and an expanding *Sphagnum* carpet approximately 5 cm high, whose outermost shoots 20−30 cm from the border leaned towards the bare peat, encroaching onto it by 10−15 cm. These shoots were not fixed to the bare peat surface and could easily be lifted by hand. The expanding *Sphagnum* carpet and the first patches on bare peat surface typically consisted of two species out of *S. cuspidatum*, *S. balticum* and *S. magellanicum* (in order of probability). The average annual speed of lateral expansion of the *Sphagnum* carpet over the bare peat surface varied greatly in magnitude (from 0 to 13.3 cm yr^{-1}, average 4.1 ± 1.3 cm yr^{-1}) as well as within and among the plots and years (Figure 5). The rate of
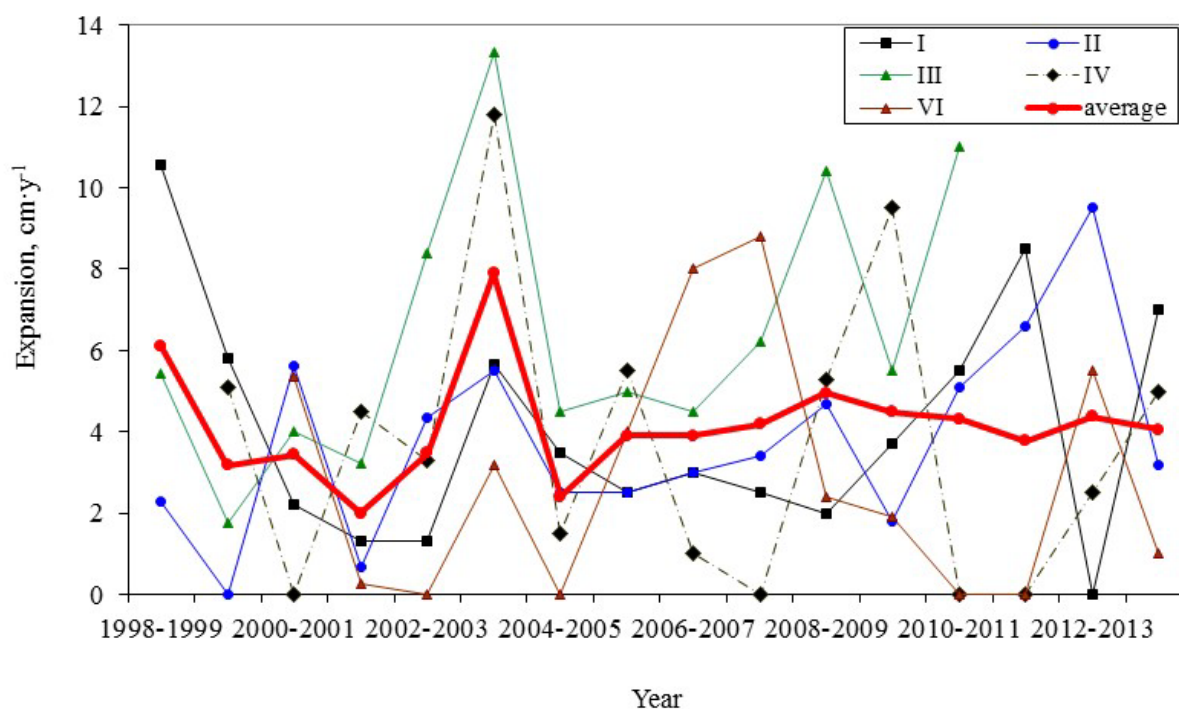
Figure 5. Annual lateral expansion (cm yr^{-1}) of *Sphagnum* carpet over the bare peat surface in five plots and their average.

expansion fluctuated, with periods of consecutive years when expansion in most plots was faster (1998−1999 and 2003−2004) or slower (2001−2002, 2002−2003 and 2004−2005) than the period average. The speeds of *Sphagnum* expansion in different plots were more similar in periods with slower expansion than during faster expansion.

The speed of *Sphagnum* carpet expansion was synchronous only between Plots II and III (correlation coefficient = 0.60, p = 0.03); the other three plots behaved differently. Mean precipitation had a significant positive effect (p = 0.04) on the average expansion rate of *Sphagnum* carpet. The negative value of the autocorrelation parameter of the model residuals suggests that years of faster expansion of *Sphagnum* carpet were followed by a year of slower growth. The confidence interval of the parameter included zero, however, so this effect is not statistically significant.

The second type of bare peat surface overgrowth occurred by single plants or clumps of *R. alba* sprouting and spreading on the bare peat surface. As *R. alba* cover increased it favoured *Sphagnum* mosses by improving the moisture conditions (nurse plant function), leading to continuing overgrowth by *R. alba* and *Sphagnum* in combination. Because this type of overgrowth was distributed and sporadic, it was impossible to measure lateral expansion speed.

Relationships between changes in plant assemblage types and weather factors
Although the rate of decline in the area of bare peat surface due to overgrowth decreased during the study period, it was the only change in the three main assemblage types that exhibited a significant temporal correlation (Table 4). Mean monthly temperature had no effect on the changes in area of these assemblage types, and only the increase in *Sphagnum* carpet area was significantly correlated with precipitation and with Lang's moisture factor. Note that the necrotic, dying *Sphagnum* (necr. *Sph*) assemblage was excluded from the analysis for the total study period due to likely inaccuracies in determination and the short duration of this type.

One-way ANOVA indicated that the year had a significant effect on the increase in area of *Sphagnum* carpet and the decrease of bare peat surface area ($F_{(15,112)}$ = 2.35 and 2.20 respectively; p > 0.01), whereas there was no significant temporal variation in the changes in area of overgrown bare peat surface (Figure 4).

Multiple regression analysis indicated that air temperature and total precipitation during the vegetation period were significant factors in accounting for changes in the area of plant assemblage types in mud-bottom hollows. Weather factors were more significant for changes in the

Table 4. Correlation coefficients (n=128) between changes in plant assemblage types, study year and weather factors. Significant correlation coefficients are in bold.

Cover type	Year	Total precipitation (mm)	Mean monthly precipitation (mm)	Mean monthly air temperature (°C)	Lang's Moisture Factor (M_L)
A (*Sph*)	0.01	**0.19**	**0.19**	-0.07	**0.18**
C (bare surf.)	**-0.35**	0.00	0.00	-0.17	0.04
D (overgr. bare surf)	0.06	0.00	0.00	0.04	-0.01

area of *Sphagnum* carpet, accounting for 25.3 % (p < 0.001) of their variance. Only 20.9 % and 10.2 % of the variance in changes of bare peat surface and overgrowth of bare peat surface, respectively, were attributable to weather factors; however, the total model was insignificant for both factors. Total precipitation had a significant positive effect on the increase in *Sphagnum* carpet area (beta= 0.29), whereas drier conditions with higher temperature retarded the decline of bare peat surface (beta = -0.22). Lang's Moisture factor had a significant effect (beta = 0.23) on the increase in *Sphagnum* carpet area. The changes in overgrown bare peat area were independent of weather factors.

DISCUSSION

Earlier publications and observations indicate that mud-bottom hollows are common in raised bogs, suggesting they may be long-lived. Our results have revealed that annual and longer-term changes in the plant cover of mud-bottom hollows can be substantial (up to 90 % of plot area), and that individual mud-bottom hollows are less stable and enduring than was hitherto presumed. Small bare patches and the edges of larger bare peat surfaces were overgrown within a year, whilst most areas of bare peat were completely overgrown in 3–12 years. The speed of overgrowth fluctuated between years, and slowed towards the end of the study period because most of the bare peat surface had already been overgrown. The greatest annual changes were observed in 2001, in Plots III and V (60 % and 49 % of the plot areas, respectively), when large areas of bare peat surface were overgrown by clumps of *R. alba*; and in 2004 when relatively small changes in fragmented plant cover resulted in significant total changes in Plots V and VI.

Of the four plant assemblage types, *Sphagnum* carpet appeared to be the most enduring and most able to expand at the expense of the other types. The apparent instability of degenerate *Sphagnum* areas was due largely to their strip-like shape and small initial area, as well as observer difficulty in differentiating between necrotic and dried-out *Sphagnum*. Still, our results failed to confirm the anticipated gradual replacement of areas of degenerate *Sphagnum* carpet by bare peat surface, inasmuch as a transition between the corresponding plant cover types appeared unlikely. This transition may still occur, even though it did not occur during our study, because of the intermittent nature of mud-bottom hollow formation. There are no data on the timing of formation of mud-bottom hollows but there are reasons to assume that their formation is periodic. All of the eight mud-bottom hollows included in this study were overgrowing, whereas only 27 of 41 mud-bottom hollows investigated at the same bog in 1998 showed signs of expansion (Karofeld & Toom 1999). A significant expansion of mud-bottom hollows during a specific period has also been documented by Nordbakken (2001).

During the study period the area of bare peat surface decreased, in part because of overgrowth by the expanding *Sphagnum* carpet but also, in the first stage especially, by the development of clumps of *R. alba* (in Plots V, VI and especially III). The bare peat areas in these plots were not initially bordered by carpets of *R. alba* and the new single plants presumably did not appear by vegetative spreading, but mostly by germination of dispersed seeds. The dispersal of relatively heavy *R. alba* seeds by wind is limited to small distances and the seeds are transported more readily by water (Masing 1955). Therefore, the seeds can spread relatively easily and far on bare peat areas, which are often inundated after rains, and germinate during the next spring season (Maas 1989, Shipley & Parent 1991). *R. alba* seeds are noted for their ability to sprout on bare peat surfaces (Masing 1955), which often offer even more favourable habitats than *Sphagnum* carpet.

Seeds that fall onto *Sphagnum* and fail to sprout during the first few years will be buried in the *Sphagnum* mat, whereas seeds lying on bare peat can remain viable at the surface (where conditions are more favourable for germination) for several years (Grime *et al*. 1981, Baskin & Baskin 1998, During 2001, Jurado & Flores 2005). Once the first plants of drought-tolerant *R. alba* (Egawa & Tsuyuzaki 2015) establish on a bare peat surface, the number of clumps and the overgrowth of bare peat surface is enhanced by increased seed rain *in situ* and, to an even greater degree, by vegetative spreading. Therefore, this type of overgrowth proceeded gradually and sporadically during the first years of our study then accelerated rapidly, resulting in total overgrowth of the mud-bottom hollows involved.

Bog is not a favourable habitat for the establishment of *Sphagnum* mosses by sprouting from spores (Sundberg & Rydin 2002). Therefore, shoots of *Sphagnum* mosses expand over bare peat surfaces mostly from the bordering *Sphagnum* carpet. The average annual lateral expansion during this study was slightly greater than a previously measured rate (2.4 ± 1.3 cm yr^{-1}, Karofeld & Toom 1999). It is not necessarily affected directly by the annual length increment of *Sphagnum* mosses which was measured in 2013–2014, for *S. magellanicum* in the same bog, at only 0.96 ± 0.53 cm yr^{-1} (n = 31; Vellak & Karofeld, unpublished data); and earlier for *S. cuspidatum* at $1.0-1.7$ cm yr^{-1} (Karofeld 2001). Nonetheless, the annual length increment in *Sphagnum* carpet expanding over a bare peat surface could be greater than in a dense *Sphagnum* mat because shoot density is lower, meaning greater exposure to light and thus enhanced photosynthesis. *Sphagnum* carpet expands over a bare peat surface mostly from its border, thereby inducing more consistent change between plant cover types than occurs by the appearance of *R. alba* clumps on bare peat. Years with fast lateral expansion of *Sphagnum* carpet do not correspond to those with notably large total increase in *Sphagnum* carpet area, whereas slower *Sphagnum* expansion in 2001–2002 and 2004–2005 occurred simultaneously with a smaller increase in the area of *Sphagnum* carpet. The growth of *Sphagnum* mosses is enhanced in wet conditions; Thomson (1924) noted their expansion over bare peat surfaces mostly during wet summers. Our results confirmed that the expansion of *Sphagnum* carpet over bare peat was significantly affected by precipitation during the vegetation period. The fluctuations in rate of lateral expansion were mostly simultaneous in different plots. The fluctuations may have been caused by a hysteresis of the joint

effects of more favourable meteorological conditions inducing faster length increment followed by the *Sphagnum* shoots subsiding towards the bare peat surface during subsequent year(s) because they were not supported from this direction. Leaning of *Sphagnum* shoots over the bare peat surface can be promoted by heavy rainfall, snowpack and other factors that make this process irregular and not entirely predictable. This explains why meteorological conditions explained only 9.1 % of the *Sphagnum* carpet expansion but were significant for the increase in area of *Sphagnum* carpet. An additional contribution to this increase arose from sprouting of *Sphagnum* under 'nurse' clumps of *R. alba* (Egawa & Tsuyuzaki 2011, Pouliot *et al*. 2011, Ma *et al*. 2015).

Although large changes were evident in the mud-bottom hollows, these changes showed little uniformity or consistency in terms of magnitude and character. For example, Plots II and III were similar at the beginning of the observation period (bare peat surface bordered by *Sphagnum* carpet, Figure 3) but their subsequent development differed. In Plot II the bare peat surface was gradually overgrown by *Sphagnum* carpet and, only during the final years, also by the *R. alba* dominated plant assemblage; in contrast Plot III experienced fast and almost total overgrowth by *R. alba* clumps which later created suitable conditions for their own replacement by *Sphagnum* carpet. This difference is probably due to the near-absence of *R. alba* from the vicinity of Plot II, whereas Plot III had *R. alba* plants within the *Sphagnum* carpet and a few individuals on the bare peat surface that initiated vegetative spreading and overgrowth.

The multifarious nature of the changes in mud-bottom hollows makes it difficult to identify and quantify the underlying factors. The presumed association between changes in plant assemblages and weather factors appeared not to explain all developments, suggesting manifold relationships which were sometimes delayed, prevented or obscured by other factors. For example, warm and dry summers favour pollination and seed production by *R. alba* but inhibit transport of the seeds by water, their germination on bare peat surfaces (these being dried-out), and the growth of *Sphagnum* mosses. Conditions of higher rainfall and lower temperatures, resulting in the inundation of bare peat surfaces and enhanced transport and sprouting of *R. alba* seeds as well as *Sphagnum* growth are, on the other hand, unsuitable for successful flowering and seed production. Sprouting of bog plants from seed can take several years, especially on bare peat surfaces, thereby obscuring any correlation between

meteorological conditions and changes in plant cover (especially overgrowth by *R. alba* in the present context). Inasmuch as warmer and drier conditions seem to retard the overgrowth of mud-bottom hollows, future climate warming could further slow down overgrowth, thereby increasing the longevity of mud-bottom hollows and the associated effects on changes in plant cover and microtopographical differentiation of bogs.

Although individual mud-bottom hollows are generally short-term features, some bare peat areas can exist for at least ten years. According to measurements at the same bog, arrested peat accumulation and intensive peat mineralisation cause these areas to sink relative to their *Sphagnum*-covered surroundings by a few millimetres annually (Karofeld 2004). Since the water table is only a few centimetres below the surface, even a relatively short period of enhanced mineralisation caused by the presence of bare peat surfaces may lead to changes in plant cover and microtopography. In this study the four mud-bottom hollows that originated on lawns were transformed into hollows after overgrowth. The overgrowth of mud-bottom hollows has to be relatively fast in otherwise very stable bogs to maintain their *status quo* - "one has to run fast to stay in the same place".

CONCLUSIONS

1. The mud-bottom hollows that are common features of raised bogs in the boreal zone appear to form periodically within a few years, are in a state of constant change, and generally end through overgrowth by clumps of *R. alba* or by *Sphagnum* carpet. However, some areas of mud-bottom hollow can exist for at least ten years.

2. The decrease in bare peat surface and increase in *Sphagnum* carpet areas are affected by the amount of precipitation, and the overgrowth of mud-bottom hollows slows in drier and warmer years.

3. Still, the opposing effects of several factors make it difficult to establish significant correlations between the nature and speed of mud-bottom hollow development and all of the possible causative factors.

4. Because of retarded peat accumulation, persistent mud-bottom hollows trigger rapid changes in plant cover and a consequent differentiation in microtopography and, potentially, carbon balance.

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