Bog vegetation re-mapped after 63 and 103 years: expansion of *Rhynchospora alba* (Studies on Skagershultsmossen 2)

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SUMMARY

The vegetation in an area of the ombrotrophic bog Skagershultsmossen, South-Central Sweden, was mapped in 2010. The same area was previously surveyed in 1907 and 1970. Only small changes were found in 1970, in contrast to the situation in 2010, when a large shift in the vegetation was observed. The previously dominating vegetation type, lawns dominated by *Eriophorum vaginatum*, had more or less disappeared and was replaced by carpet vegetation dominated by *Rhynchospora alba*, *Sphagnum tenellum* and *S. balticum*. Also, the carpets dominated by *Scheuchzeria palustris* had decreased to a large extent. There are several possible climatic explanations behind the changes, and we suggest that increased frost action linked to the reduction in snow cover may be important. The shift in the vegetation has most certainly led to a decrease in peat productivity and, hence, a reduction in carbon sequestration by the bog is assumed. Skagershultsmossen is an important reference site for future studies of long-term vegetation changes.

KEY WORDS: frost, long-term study, reduced peat productivity, South-Central Sweden, vegetation shift

INTRODUCTION

There are very few studies of long-term vegetation changes on ombrotrophic bogs prior to the advent of aerial photography, and those are mostly based on peat stratigraphy. An exception is the vegetation mapping of a small part of the bog Skagershultsmossen in South-Central Sweden made in 1907 (von Post & Sernander 1910). Re-mapping of the same area in 1970 (Backéus 1972) has given us an opportunity to follow changes over more than 100 years. We do not know of any other detailed studies on ombrotrophic bogs that cover more than a century.

Only minor vegetation changes were noted at the mapping in 1970 (Backéus 1972). In other long-term studies in northern Europe, bogs have been found to be fairly stable over time (Gunnarsson & Rydin 2000, Gunnarsson *et al.* 2002, Rydin *et al.* 2006, Kapfer *et al.* 2011, Pedrotti *et al.* 2014). However, directional changes have been observed in studies covering shorter timespans (Gunnarsson & Flodin 2007, Granlund *et al.* 2022). Fen vegetation, that is groundwater fed, has more often been attributed with higher rates of vegetation change (e.g., Gunnarsson & Rydin 2000, Gunnarsson *et al.* 2002, Pedrotti *et al.* 2014, Tyler *et al.* 2020) and in some cases vegetation shifts have occurred (e.g., Gunnarsson & Rydin 2000, Pedrotti *et al.* 2014).

The micro-topographic gradient (in vertical distance to the groundwater table) is one of the most important gradients on ombrotrophic bogs, stretching from carpets and mudbottoms via lawns to hummocks (as defined by Sjörs 1948). These levels are defined floristically here, as in Backéus (1972). Changes along this gradient are related to site wetness, but edaphic factors and internal processes may also influence the vegetation gradient.

The aim of the investigation reported here is to detect possible changes in bog vegetation from unique long-term observations over a century and, if there are any changes, to quantify them and determine their direction.

METHODS

Study site

Skagershultsmossen is one of the largest peatland complexes in South-Central Sweden, covering about 1900 ha in total (Figure 1). The north-western part of the complex (~ 600 ha) has been used for industrial peat extraction since 1898 (Svantesson 2010). In the 1960s and 1970s the method used for excavating peat gradually changed from cutting of peat blocks to peat milling. The southern part of the complex developed within a drumlin field. Here, peat milling started on the virgin bog in the 1970s. The central part of Skagershultsmossen is a well-developed plateau bog which was designated as a nature reserve in 1982 and was later also incorporated into the protected EU Natura 2000 network. The nature reserve was expanded south-eastwards to its present extent in 2009. In the landscape west of the bog there has been a reduction of farmland, which has been replaced by tree plantations. The increase of forestry activities has occurred mostly since 1975 (Figure 2).

Previous and recent studies

The first documentation of the investigated area (59.1 °N, 14.7 °E) is a detailed (scale 1:1500) map of the plant communities within a small part of the bog plane, made by von Post in 1907 and published in an excursion guide for the International Geological Congress in 1910 (von Post & Sernander 1910, redrawn in Backéus 1972). This map is reproduced here as Figure A1 in the Appendix. The same area was re-mapped in 1970 (Figure A2) by Backéus (1972) and in 2010 by ourselves (Figure 3). The mapped area is about 180 m × 280 m.

The original selection of investigation area was probably based on a combination of practical considerations and assumed representativeness. A series of Normalised Difference Vegetation Index (NDVI) values was produced in order to assess how representative the study plot is in relation to the surrounding part of the bog (Figure 4, Table A1 in the

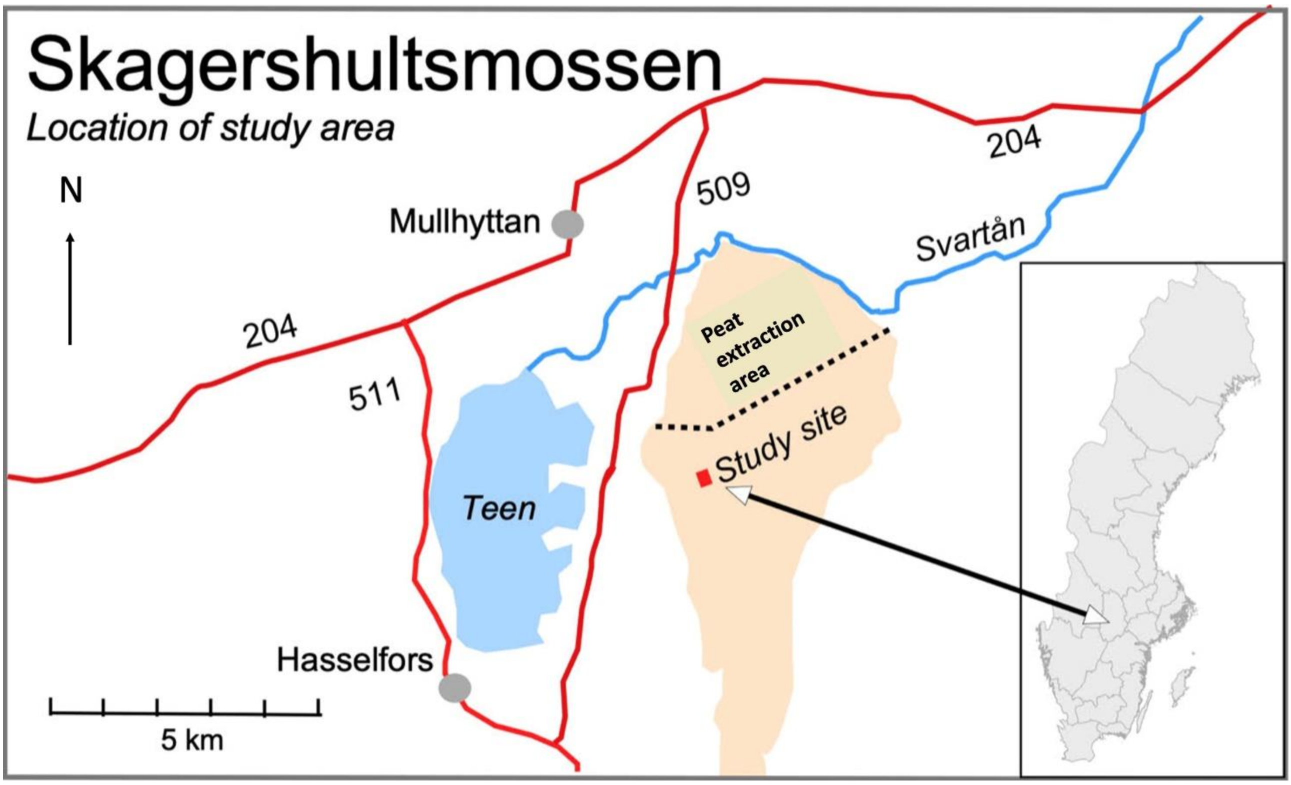

Figure 1. Location of the study site within Sweden.

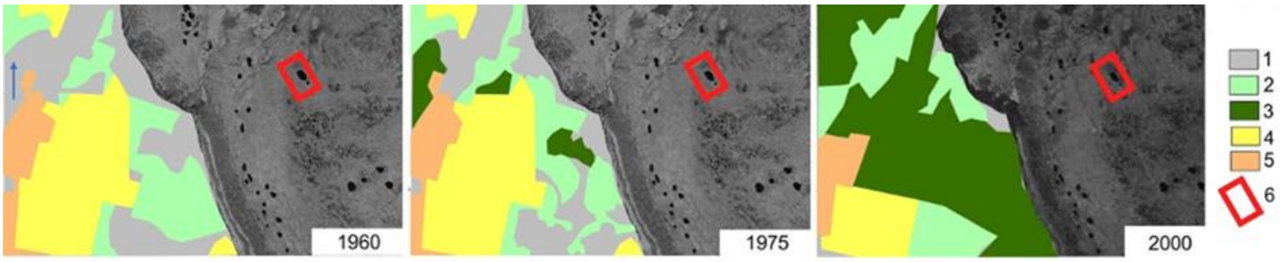

Figure 2. Land use changes 1960–2000 to the west of the study area on the bog Skagershultsmossen. 1: Forested area in 1960; 2: recently logged areas; 3: tree plantation; 4: cultivated land; 5: meadows and homesteads; 6: study plot on the bog. Agricultural activities decreased and forest-related activities (logging and tree planting) increased during the later observation interval (1975–2000).

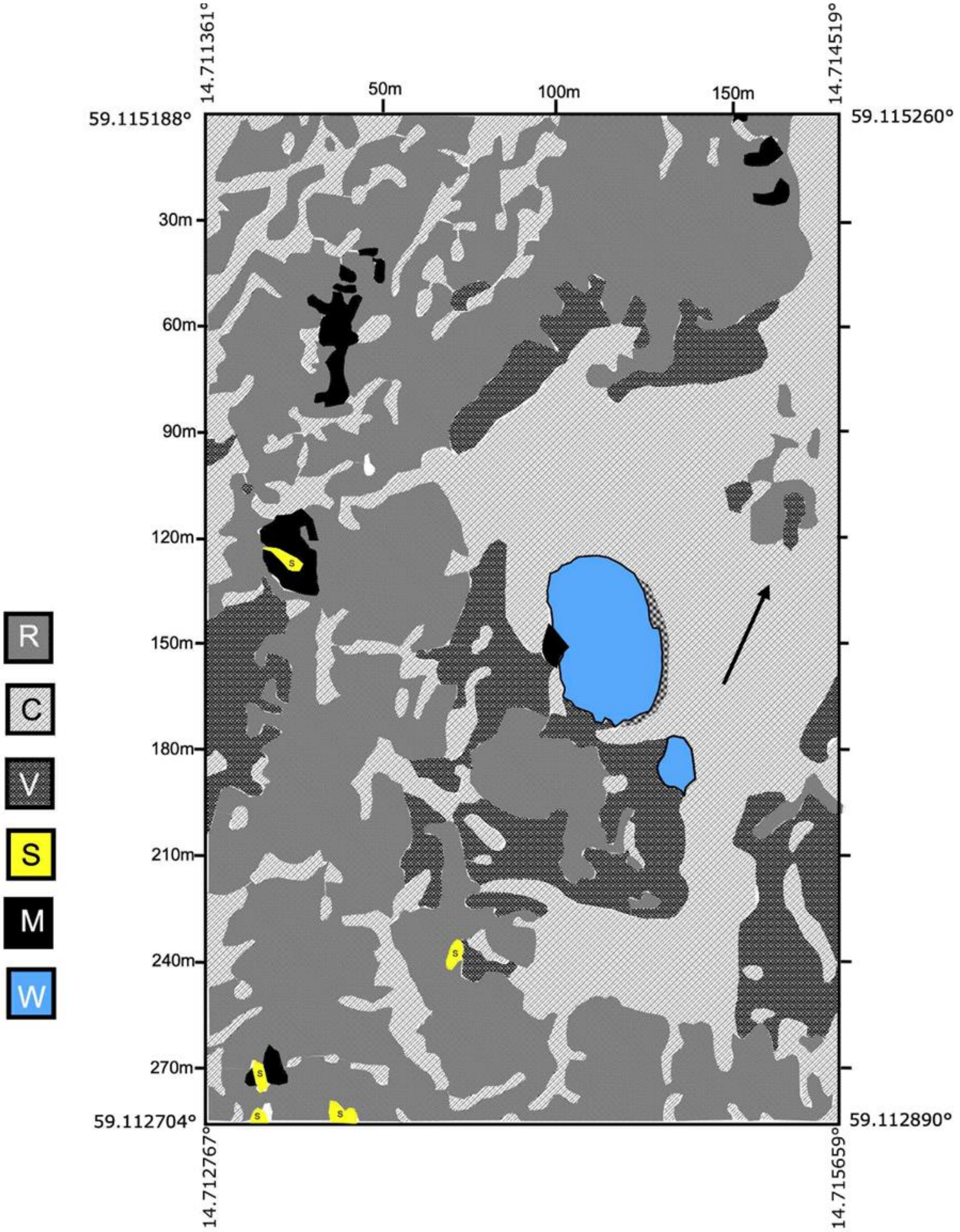

Figure 3. Vegetation of the Skagershultsmossen study plot in 2010. C = Callunetum; M = mudbottoms; R = Rhynchosporetum; S = Scheuchzerietum; V = Vaginetum; W = open water (pools).

Appendix). The NDVI is an index that is used to analyse vegetation from remote sensing data using the formula:

$$\mathrm{NDVI} = (\mathrm{NIR} - \mathrm{Red}) / (\mathrm{NIR} + \mathrm{Red}) \qquad [1]$$

where Red and NIR denote the spectral reflectance of the red (visible) and near-infrared spectral bands, respectively. Calculations of NDVI for a given pixel always result in a number that ranges from -1 to +1. The NDVI is positively correlated with the water table depth on bogs (Šimanauskienė *et al*. 2019).

The homogeneity of the NDVI indicates that the study site is indeed representative for the open bog area of Skagershultsmossen. Figure 4 shows that the lowering of the water level in the drained peat workings does not influence the water level in the bog, except within a narrow strip along the edge of the peat extraction area.

Plant communities

We have retained the plant community names used by von Post & Sernander (1910) and Backéus (1972). The relationship between these community names and later phytosociological classifications is discussed in detail by Backéus (1972). In summary, Callunetum corresponds to hummocks, Vaginetum to lawns, and Scheuchzerietum and Rhynchosporetum to carpets, in the terminology of Sjörs (1948, cf. Rydin & Jeglum 2013).

The publication by von Post & Sernander from 1910 is the origin of the theory of cyclic regeneration on bogs that was a paradigm in mire science during much of the 20th century but has now been largely refuted (Barber 1981, Backéus 1991). According to this theory, Scheuchzerietum constituted the "progressive" carpets and Rhynchosporetum the "regressive" carpets. The regressive vegetation was considered to consist of weakly peat-producing vegetation types including mudbottoms and wet carpet vegetation dominated by *Rhynchospora alba*, while the progressive vegetation contributed to the production of peat with typically lawn and hummock vegetation (except for lichen-dominated hummocks) but also carpets dominated by *Scheuchzeria palustris*.

Field methods in 1907, 1970 and 2010

The 1907 map was most probably based on techniques and equipment used by the Geological Survey of Sweden at the time, i.e., a plane table surveying technique supported by a "distance tube", which was an optical levelling instrument attached to a plate and movable in a vertical direction. Hence, bearings to mapped objects could be set with precision and points could be plotted on the drawing.

Field methods in 1970 were described by Backéus (1972). Mapping was done on the ground in July using base-lines 25 m apart and transverse lines extending from these wherever needed. Fixed points did not exist, but the two bog pools are stable structures and were therefore used as starting points for orientation. The same mapping method was used in August 2010 when, in addition, we used a handheld GPS to get approximate coordinates (with an accuracy of ± 10 m) for some of the more permanent features of the site. A field visit was also made in August 2022 to find out whether the major changes observed in 2010 persisted.

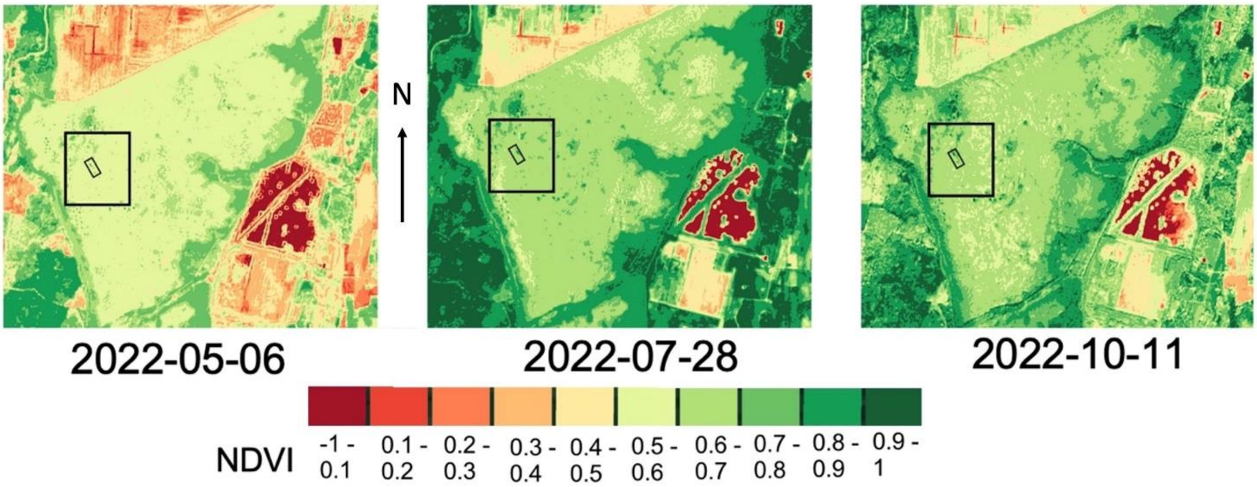

Figure 4. A series of NDVI calculations (Equation 1) for the central part of Skagershultsmossen on three occasions in 2022, derived from Sentinel-2 satellite data with 10 m resolution. The mapped study area (small rectangle) is shown with its surrounding reference area (larger rectangle; see Table A1).

Vegetation sampling was done in late June–July 1970 using 1-m^2 plots in all plant communities (Backéus 1972). Vegetation plots were also sampled in 2022 to investigate whether mapped changes in the distribution of dominating species were linked to distribution changes among accompanying species in the community. Plots were selected subjectively to encompass the variation in vegetation composition. In 2022, percentage cover was estimated but later transformed to the logarithmic 5-degree Hult-Sernander-Du Rietz scale (Du Rietz 1921) in order to conform with previously collected data. The frequencies and means presented are meant only as a descriptive summary of the data and cannot be attributed with strict statistical meanings.

Data extraction

As all of the maps lack marked fixed points and were made by different techniques, digital overlays of the three maps were placed on a modern aerial orthophoto. As the outline of the two bog pools was unchanged over time, the pool outlines were used to align the three maps. Slight discrepancies were found between the maps, in terms of both mapped area and angular geometry. Therefore, the extraction of information for evaluation of changes over time was made by screen digitising the outlines of specific classes on each map to obtain digital area estimates expressed as percentages of total area, which reduced errors arising from the differences in map geometry. As a consequence, strict statistical comparisons between maps are not possible, and only substantial changes can be regarded as meaningful. For this reason, results are presented for Rhynchosporetum and Scheuchzerietum only. The data collection method also permits discussion of changes in distribution of (mainly) the vegetation types dominated by *Calluna vulgaris* (Callunetum), *Eriophorum vaginatum* (Vaginetum), *Rhynchospora alba* (Rhynchosporetum) and *Scheuchzeria palustris* (Scheuchzerietum), as well as open water and mudbottoms (mostly free of vegetation). Individual species were not mapped.

RESULTS

While no major changes in the distribution of communities were identified for the period from 1907 to 1970 (Backéus 1972), we found a drastic spread of Rhynchosporetum across the former Vaginetum habitats during the period 1970 to 2010 (Table 1 and Figure 5).

Table 1. Cover (% of total area) of Rhynchosporetum and Scheuchzerietum through time, digitally estimated from individual field survey maps.

Year	1907	1970	2010
Rhynchosporetum	5	10	50
Scheuchzerietum	2.4	3.7	0.7

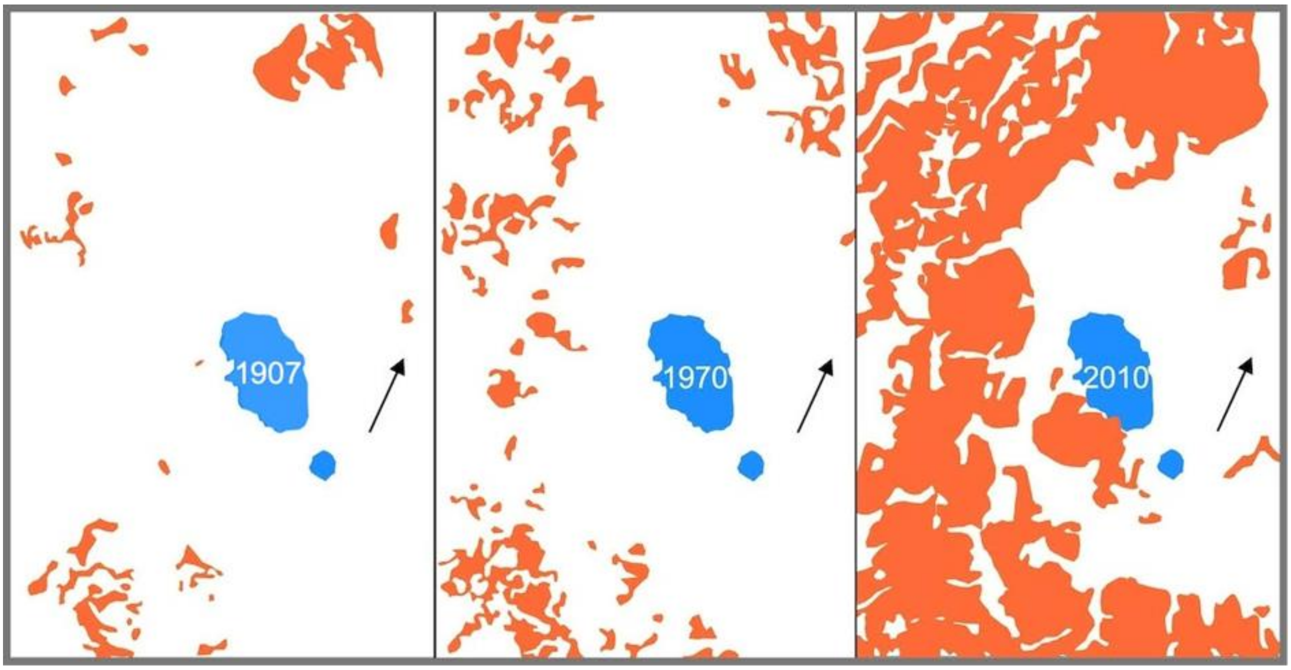

Figure 5. The expansion of Rhynchosporetum (shaded orange) within the study area over time (cf. Table 1).

Comparison of the vegetation data from 1970 and 2022 showed no major differences in species composition within communities (Table 2). Thus, over large areas there has been not just an invasion of the species *Rhynchospora alba* into Vaginetum, but a complete shift in community from Vaginetum lawns to Rhynchosporetum carpets. As a consequence, Vaginetum has decreased and the small areas still mapped as Vaginetum in 2010 had almost completely disappeared by 2022. Although *Eriophorum vaginatum* occurs in all bog communities, the increase of Rhynchosporetum has meant a large reduction in the abundance of *E. vaginatum* (Table 2).

Table 2. Vegetation analyses from 1970 and 2022. Sampling was done in Jun–Jul 1970 and on 18 Aug 2022. [a] Scheuchzerietum in 1970 that had changed to Rhynchosporetum in 2022; [b] Vaginetum in 1970 that had changed to Rhynchosporetum in 2022; [c] Rhynchosporetum in both 1970 and 2022; [d] *Sphagnum medium* was recorded under the name *S. magellanicum* in 1970. Numbers are plot frequency in percent. Integer superscripts are mean cover values transformed into the Hult-Sernander-Du Rietz scale (Du Rietz 1921), where + indicates mean cover < 1 %; 1: 1–6.25 %; 2: 6.25–12.5 %; 3: 12.5–25 %; 4: 25–50 %; 5: > 50 %.

	Callunetum		Vaginetum		Scheuchzerietum			Rhynchosporetum			mud-bottoms
	1970	2022	1970	2022	1970	2022[a]	2022	1970	2022[b]	2022[c]	1970
Number of plots	10	2	10	3	8	3	3	10	5	2	7
Andromeda polifolia	100^1	100^1	100^2	100^+	60^1	70^1	30^+	-	100^1	100^+	40^1
Betula pubescens	10^+	-	-	-	-	-	-	-	-	-	-
Calluna vulgaris	100^5	100^4	40^1	100^2	-	-	30^1	20^+	100^1	100^1	-
Empetrum nigrum	60^1	50^+	-	-	-	-	-	-	-	-	-
Pinus sylvestris	10^+	-	-	-	-	-	-	10^+	20^+	-	-
Vaccinium oxycoccus	80^1	100^1	100^2	100^1	90^1	100^1	100^+	90^1	60^+	50^+	40^1
Vaccinium uliginosum	20^+	-	-	-	-	-	-	-	-	-	-
Drosera longifolia	10^+	50^+	90^1	30^+	80^1	100^1	100^1	80^1	100^1	100^+	40^1
Drosera rotundifolia	80^1	100^1	100^1	100^1	80^1	100^1	30^+	90^1	60^+	100^1	30^+
Rubus chamaemorus	100^4	100^2	60^1	30^1	-	-	-	-	-	-	-
Carex limosa	-	-	60^1	-	100^2	-	30^+	100^1	20^+	-	100^1
Eriophorum vaginatum	100^1	100^1	100^2	100^2	60^1	-	30^+	60^1	100^1	10^+	10^+
Rhynchospora alba	-	50^1	-	70^1	30^+	100^3	100^2	100^2	100^2	100^3	90^1
Scheuchzeria palustris	-	-	10^+	-	100^2	70^1	100^1	20^+	40^+	-	30^+
Trichophorum caespitosum	-	-	10^+	-	-	-	-	-	-	-	-
Dicranum undulatum	30^1	100^1	-	30^+	-	-	-	-	-	-	-
Pleurozium schreberi	-	50^+	-	-	-	-	-	-	-	-	-
Polytrichum juniperinum v. *strictum*	-	20^+	-	-	-	-	-	-	-	-	-
Warnstorfia fluitans	-	-	-	-	40^2	-	-	30^1	-	-	30^1
Sphagnum balticum	10^+	100^1	100^3	100^1	90^4	100^2	100^1	90^2	100^3	100^1	30^+
Sphagnum cuspidatum	-	-	30^+	-	100^4	100^4	100^5	70^4	80^4	100^2	100^1
Sphagnum fuscum	100^4	100^5	30^1	100^2	-	-	-	-	20^1	-	-
Sphagnum medium[d]	20^+	-	80^1	-	80^3	100^1	70^2	90^4	20^1	50^1	60^1
Sphagnum rubellum	50^3	100^2	100^5	100^2	40^3	100^1	30^2	60^1	100^1	50^+	-
Sphagnum tenellum	-	100^1	90^1	100^4	-	70^1	30^+	100^2	100^4	100^1	-
Hepaticae (incomplete)	-	50^1	-	-	-	-	-	100^2	40^+	40^+	-
Cetraria islandica	30^+	-	50^1	30^+	-	-	-	40^1	20^+	-	-
Cladina alpestris	50^1	50^1	-	-	-	-	-	-	-	-	-
Cladina sylvatica coll. + *C. rangiferina*	100^2	100^1	50^1	100^1	-	-	-	-	-	-	-
Cladonia spp.	40^1	-	30^+	-	-	-	-	50^1	-	-	30^+
Cornicularia aculeata	30^+	-	-	-	-	-	-	-	-	50^+	-

Scheuchzerietum decreased after 1970 (Table 1) and has mainly been replaced by Rhynchosporetum. Possible changes in the extent of hummocks (Callunetum) in relation to hollows are not conclusive owing to the character of the data and are therefore not presented here.

The mudbottoms in the NE and NW part of the mapped area (Figure 3 and Figure 6) seem at first sight (compare Figures A1 and A2) to have increased since 1907 but, to a large extent, this reflected only a transition from shallow water to mudbottom depending on the actual water level during mapping. The big hollow in the NE appeared stable and the same applies to the big hollow in the far NW (Figure 6). The southernmost of the big hollows in the NW was covered by shallow water in 1907, whereas in 1970 it was mapped as "floating *Sphagnum*" and Scheuchzerietum (which was completely absent in 1907). Thus, the previous (water-filled) mudbottom had become overgrown. In 2010 (Figure 3), most of the *Sphagnum* had disappeared and we found a mudbottom again, thus returning to the 1907 situation. Scheuchzerietum had also mainly disappeared.

The three deep hollows on the 1907 map (one in the NE and two in the NW part) have remained in the same place (compare Figures A1, A2 and 3). Also, the two bog pools have been stable, with vertical borders and no floating *Sphagnum*. *Nymphaea alba* can be seen in the smaller pool on a photo from 1907 (von Post & Granlund 1926). It was still present in both pools in 1970, but has since then disappeared.

DISCUSSION

The main change observed during the 2010 mapping is the large expansion of Rhynchosporetum carpets and a corresponding reduction of Vaginetum lawns. *Rhynchospora alba* is restricted to carpets and mudbottoms (Table 2). It has now spread onto almost all of the former lawns (Vaginetum), and the whole community has changed from lawn to carpet (Rhynchosporetum). We think that the change of dominating *Sphagnum* species is important in relation to the vegetation shift. *Sphagnum rubellum*, mainly a lawn and low hummock species in this part of the country (Backéus 1972), has been replaced by *S. tenellum* and *S. cuspidatum*. *S. balticum* has remained stable (Table 2).

Økland (1990) placed *Sphagnum tenellum* and *S. cuspidatum* in the category '(C-)S-R strategy' in Grime's (1979) terminology (i.e. a stress tolerator and ruderal species), which is an unusual trait within the *Sphagnum* guild. Traits associated with stress tolerance in *S. tenellum* are low growth rate (Rydin 1985) and high desiccation tolerance, but the species has poor desiccation resistance and can colonise bare peat (Økland 1989; but see Soro *et al.* 1999), which is an R strategy trait. Ability of the species to colonise cutover bogs in the UK is demonstrated by McMullen *et al.* (2004).

The lawns on Skagershultsmossen are dominated by *Sphagnum rubellum*, with *S. balticum* as a co-dominant in places, and with low cover of *S. magellanicum* agg. and *S. tenellum* (Backéus 1972). It has been suggested that *S. tenellum* is fully included in the water level niche of *S. balticum*, being hardly competitive against *S. balticum* at any point within that niche (Rydin 1986). The competitive relationship between *S. tenellum* and *S. rubellum* has not been studied. The latter has a low cover in carpets. The observed changes suggest that conditions in the (previous) lawns have changed so much that *S. rubellum* has been disfavoured (cf. Nordbakken 2001). We suggest that frost action or

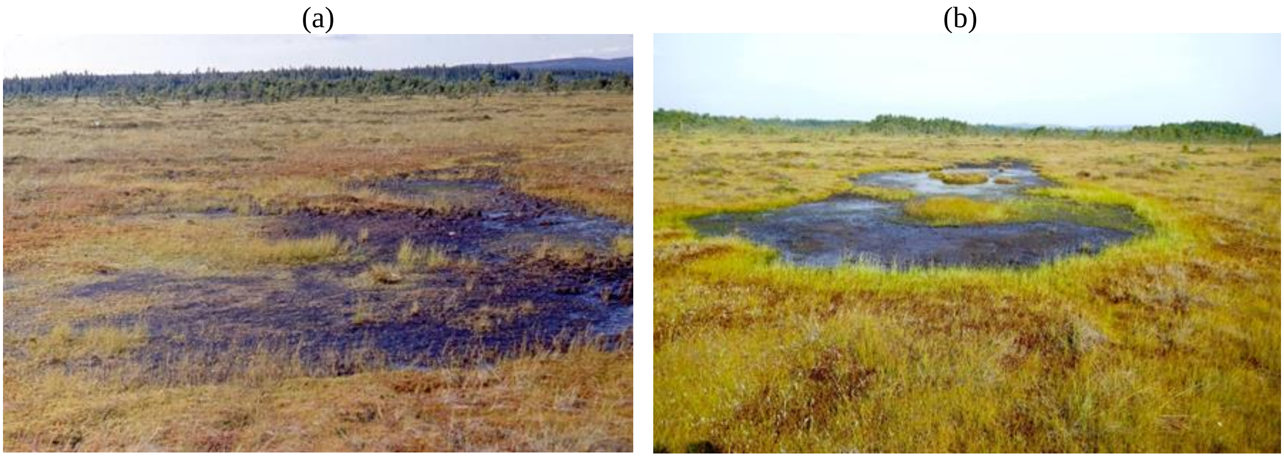
(a) (b)

Figure 6. The mudbottom community in the NW corner of the study site in 1970 (a) and 2022 (b).

drier summers (see below) may be harmful for *S. rubellum* and that *S. tenellum,* as a species with ruderal traits and a capability for rapid establishment (cf. Rydin 1993) has, therefore, taken over. However, as *S. tenellum* has a slow growth rate and low peat-producing ability, the lawns have turned into regressive carpets, in turn favouring *Rhynchospora alba*. Alternatively, *R. alba* may have colonised dying *S. rubellum* habitats directly, before the establishment of *S. tenellum*. *Sphagnum tenellum* may be able to persist together with *S. balticum* in the carpets due to its more rapid recovery after drought (Rydin 1993) or exposure to frost.

Most bog species spread vegetatively by branching from lower, often overgrown, parts of the stems (Backéus 1985). *Rhynchospora alba* is different. Its shoots are annual, with small and shallow root systems which are also annual (Metsävainio 1931). It has been suggested (Sernander 1901, Backéus 1985) that the species is spread mainly by its easily detached vegetative winter buds (botanically bulbs) that act as diaspores and are spread by water. However, the role of these buds in maintaining the population may have been exaggerated. Backéus (1985) found 1.2–1.5 buds per individual in autumn, which had been reduced by about 40 % after winter. This would not be sufficient to maintain the population.

During the field visit in August 2022 we observed the establishment of *Rhynchospora alba* from seeds, producing large green mats of seedlings. Seed establishment has also been observed in other parts of the boreal region (Egawa & Tsuyuzaki 2011, Karofeld *et al.* 2015) but has not, to our knowledge, been reported previously from Sweden. Whether the seedlings had germinated from seeds produced in the same year or from overwintering seeds could not be determined. Seeds are reported not to disperse until September (Egawa *et al*. 2009) and they can survive for at least one year in dry as well as moist conditions (Bourgeois *et al.* 2019). Egawa & Tsuyuzaki (2011) reported that *R. alba* plants do not produce seeds the first year after germination. All visible parts of the seedlings wilt during winter (Backéus pers. obs.), and they apparently also survive the winter as winter buds. Without large seed set and vigorous seedling establishment, *R. alba* could hardly have been able to undergo such a massive increase since 1970.

Seed production is most certainly an important factor for dispersal of *R. alba.* Most probably, the seeds can float on open water (Masing 1955, cited in Karofeld *et al.* 2015), thus enabling dispersal over larger areas during inundated periods on flat open bogs. Such spreading has been recorded on cut-over peat surfaces by Hebda *et al.* (2000) and Nishimura & Tsuyuzaki (2014). After establishment of *Rhynchospora alba* on mudbottoms, it can act as a nurse plant for seedling survival (Egawa & Tsuyuzaki 2011) as well as for *Sphagnum* establishment (Karofeld *et al*. 2015). Establishment of *S. tenellum* may also be facilitated by low interspecific competition in carpets and, particularly, mudbottoms (Ohlson & Malmer 1990).

Several environmental factors may explain the large increase in Rhynchosporetum carpets (Table 3). We discuss first two environmental factors that relate to a changing climate and have already been mentioned as possibly important, namely frost action and changed water supply.

The annual number of days with snow cover in the area has been reduced by ca. 20 days between 1970 and 2010 (Wern 2015). This is coupled to a corresponding reduction in the length of climatic winter. At the same time, the snow cover is likely to have become thinner and more intermittent with temperatures fluctuating around freezing point (Makoto *et al.* 2014). Therefore, it is not totally obvious how the depth of frost penetration and the frequency of temperatures above freezing have changed. However, increased frost action is expected to be harmful for plants with large overwintering root systems and rhizomes whereas species without overwintering root structures, like *Rhynchospora alba*, would be less affected.

Precipitation data are no longer collected in the vicinity of the bog, but it appears from more distant data collected by the Swedish Meteorological and Hydrological Institute, as well as from their small-scale maps, that precipitation has increased by ~ 50 mm to around 700 mm a^{-1} since 1970. This change is unlikely to have caused substantial vegetation change.

Rhynchospora alba has a southern boreal distribution (Hultén 1971) with a northern limit potentially determined by the length of the growing season (Byne & Ryser 2020). It has been shown (Byne & Ryser 2020) that the species is ‘periodic’, so an early start of growth is coupled to earlier senescence and early senescence is slow compared to the later senescence of plants commencing growth in late spring. Byne & Ryser (2020) showed that plants starting late undergo a forced senescence when temperatures become low in autumn, and they produce smaller winter bulbs with reduced nitrogen (N) content. Thus, an early start of growth optimises immobilisation of resources at the end of the season. This trait may not help to spread the plant, but is probably important for maintaining the population.

R. alba may be negatively influenced by hotter summers with increased frequency and duration of dry periods. The *Sphagnum* species in hollows are fairly resistant to drought stress, but if the conditions become so dry that even lawn and hummock species dry out, these may turn out to be less resistant to the stress. The total quantity of (deep) vascular plant roots at 30–40 cm depth is higher during dry summers (Backéus 1990), but *R. alba* roots reach a depth of only 4–6 (rarely 10) cm (Metsävainio 1931). Dry summers may therefore, in theory, result in fluctuating populations of *R. alba*. However, this explanation is not very likely to be valid. Despite long experience, we have never seen wilting *R. alba* plants during the growing season or observed fluctuating populations of this species.

High N deposition may also favour *R. alba*, which has been reported to become the dominant plant after N addition (Heijmans *et al.* 2002). In a five-year study in the oceanic region in SW Sweden (Gunnarsson & Flodin 2007), the vegetation was found to change towards wetter conditions, N demanding species increased, and the frequency of *R. alba* also increased. In the same study the *Sphagnum tenellum* associated with *R. alba* did not change. N deposition may also be a factor in the observed changes at Skagershultsmossen, as deposition levels are still elevated in the area compared to preindustrial levels and the N deposition was still high in 2010 compared to 1970. N deposition has declined during the last 20 years (Karlsson *et al.* 2022), but in 2010 the total N deposition was still as high as ~ 5 kg ha^{-1} year^{-1} (Pihl Karlsson *et al.* 2011). It has been shown that high levels of N deposition reduce the growth of *Sphagnum* in general (Gunnarsson & Rydin 2000). A meta-analysis of *Sphagnum* growth showed that the combination of high N deposition and high summer temperatures was particularly negative for *Sphagnum* growth (Limpens *et al.* 2011).

Table 3. Possible (alternative) reasons for the expansion of Rhynchosporetum carpets.

Possible causes and their ranges of operation				Remarks and references
External influences	Atmospheric deposition	Distant sources/ causes	1. Atmospheric fallout from air pollution	No substantial change in N deposition during recent decades; Danielsson *et al.* (2021), Pihl Karlsson *et al.* (2011).
			2. Forestry activities, e.g. aerial nitrogen fertilisation.	No evidence of such activities in local forests; according to current forestry legislation, in this region a single N dose of 300 kg ha^{-1} per forest generation is allowed in general but fertiliser application is prohibited on or near wetlands, protected areas etc. (source: Swedish Forest Agency).
			3. Deacidification by airborne calcium from lake water	Not applicable for nearby Lake Teen according to County Administrative Board planning information (Grahn 2012).
		Local sources/ causes	1. Agriculture	Not applicable; our air photo inventory shows a reduction of nearby agricultural land through time.
			2. Peat extraction	Unknown; distance from the peat milling site is probably too great (Tissari *et al.* 2006).
On-site effects	Climate related	Snow cover	1. Duration	General trend since ca. 1980 is towards shorter duration of snow-lie and thinner snow cover (Wern 2015).
			2. Depth	
		Frosts	1. Frequency	There are no local recordings of frequency, duration or penetration depth of frosts. A national survey that returned estimates based on field sampling suggests that normal frost penetration in dry peat is 60 cm in the local area (Jansson 1972).
			2. Duration	
			3. Penetration depth	

It has also been suggested that nutrient-rich dust from nearby agricultural fields (Franzén 2006) may hamper *Sphagnum* growth. However, the prevailing wind in the study area is (south-) westerly and, as can be seen in Figure 2, the area of arable land in that direction has decreased and the forest belt close to the bog makes the ingress of dust unlikely. One of many environmental impacts from peat mining is the spread of dust (cf. Winkler & DeWitt 1985) and, in our case, nutrient-poor dust from nearby peat milling could potentially reduce photosynthesis among *Sphagna*. However, the prevailing wind direction and the distance of about 600 m from the active peat extraction site mean that any effect should be quite small (Tissari *et al.* 2006). A small change in groundwater regime south of the peat extraction area can, similarly, not be excluded but any effect is likely to have been minimal.

Eriophorum vaginatum occurs in all bog communities but tends to concentrate in lawns (Vaginetum) where it dominates (Table 2). In spite of its perennial growth form, this species has decreased in cover in the new Rhynchosporetum areas. Competition with the small and weak rival *Rhynchospora alba* is an unlikely reason for its decline, as is the continuing elevation of N deposition (see above) because this is known to favour *E vaginatum* (cf. Nordbakken 2001). Edaphic conditions are apparently less optimal for this species in carpets than in lawns, and it seems most likely that its decline is a secondary consequence of the loss of lawn habitat.

The area covered by *Scheuchzeria palustris* has decreased considerably and the species has almost disappeared from this part of Skagershultsmossen since 1970 (Table 1). This conforms to results from other studies (Gunnarsson *et al.* 2002, Pedrotti *et al.* 2014) and may be a result of high sensitivity to drought (Tallis & Birks 1965, Gunnarsson *et al.* 2002). As mentioned, a warmer climate with dry spells will temporarily cause dry conditions in hollows. Furthermore, Gunnarsson & Flodin (2007) suggest that species adapted to low N levels, like *S. palustris*, decrease when N levels increase.

Calluna vulgaris defines the hummocks, the locations of which appear stable. The total hummock area may have decreased somewhat from 1970 to 2010, but our data are not conclusive. This aligns with the conclusion of Backéus (1972) that cyclic regeneration does not take place on this *primus locus* for the cyclic regeneration theory (von Post & Sernander 1910).

The large shift in vegetation from Vaginetum lawns to Rhynchosporetum carpets may have a large effect on carbon dynamics by considerably reducing the carbon sequestration capacity of the bog, as highly productive lawns are replaced by less productive Rhynchosporetum carpets and mudbottoms (Backéus 1985, Karofeld *et al.* 2015). This transition also implies a change to lower *Sphagnum* cover (Table 2) and higher methane (CH_4) emissions from carpets with small depth to water table (Rydin & Jeglum 2013). On Skagershultsmossen the same vegetation shift is assumed to have occurred on a large part of the bog, as the studied site is representative of the entire bog (Figure 3). Inspection during field visits in 2022 (I. Backéus and U. Gunnarsson, pers. obs.) revealed very little lawn vegetation elsewhere. Similar large areas of Rhynchosporetum carpets have also been found on several other bogs in South and South-Central Sweden (I. Backéus and U. Gunnarsson pers. obs.). Reduced peat accumulation has also been reported in several studies on peat accumulation in south Sweden (Franzén 2006, Gunnarsson *et al.* 2008 among others). Franzén (2006) even suggests that decomposition has occurred in the sub-surface peat, possibly as a result of climatic change or increased nutrient loads in the area.

Modelling the effects of climate change on several species in the British Isles, Berry *et al.* (2003) found *Rhynchospora alba* to be a ‘winner’ and *Eriophorum vaginatum* a ‘loser’. This is in line with our findings. Distinct shifts in bog vegetation may be rapid after a threshold has been exceeded (Eppinga *et al.* 2009), but observations of a shift towards *R. alba* carpets have rarely been reported through actual monitoring of current ombrotrophic vegetation. However, several vegetation shifts have been found in studies of long-term vegetation development in the peat profiles of bogs (e.g., Svensson 1988). Also, Karofeld *et al.* (2015) reported an infilling of open mudbottoms with *Sphagnum* and found that, in most cases, this was accompanied by increasing abundance of *Rhynchospora alba*. Other shifts that have occurred fairly recently in mire vegetation include shifts from intermediate fen to poor fen (e.g., Vitt & Chee 1990, Gunnarsson & Rydin 2000) and from rich fen to bog hummocks (Pedrotti *et al.* 2014, Granlund *et al.* 2022).

CONCLUSIONS

In this study we report a strong shift in bog hollow vegetation which does not have a simple and clear-cut explanation. Several alternative explanations are suggested (Table 3), some of which may operate in the same direction and/or reinforce one another. It is likely that experimental work in combination with detailed field monitoring will be required before any firm conclusions can be drawn about which are the most likely causes of the observed changes in vegetation.

It is generally expected that changes in bog vegetation will be small and slow. However, there are few sites where changes in the structure and communities of bog vegetation can be studied over long periods. Future monitoring is important because the changes we have observed appear to be linked to climate dynamics and/or large-scale N deposition. The long record of change that is already available for the investigated area on Skagershultsmossen makes this an important site that could serve as a reference area for wider studies of change in mire vegetation. Because it is a protected site, no further local anthropogenic impact is anticipated.

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AUTHOR CONTRIBUTIONS

Coordination: IB; fieldwork: IB, UG; remote sensing and GIS: LS; drafting text: IB, UG, LS.

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Appendix

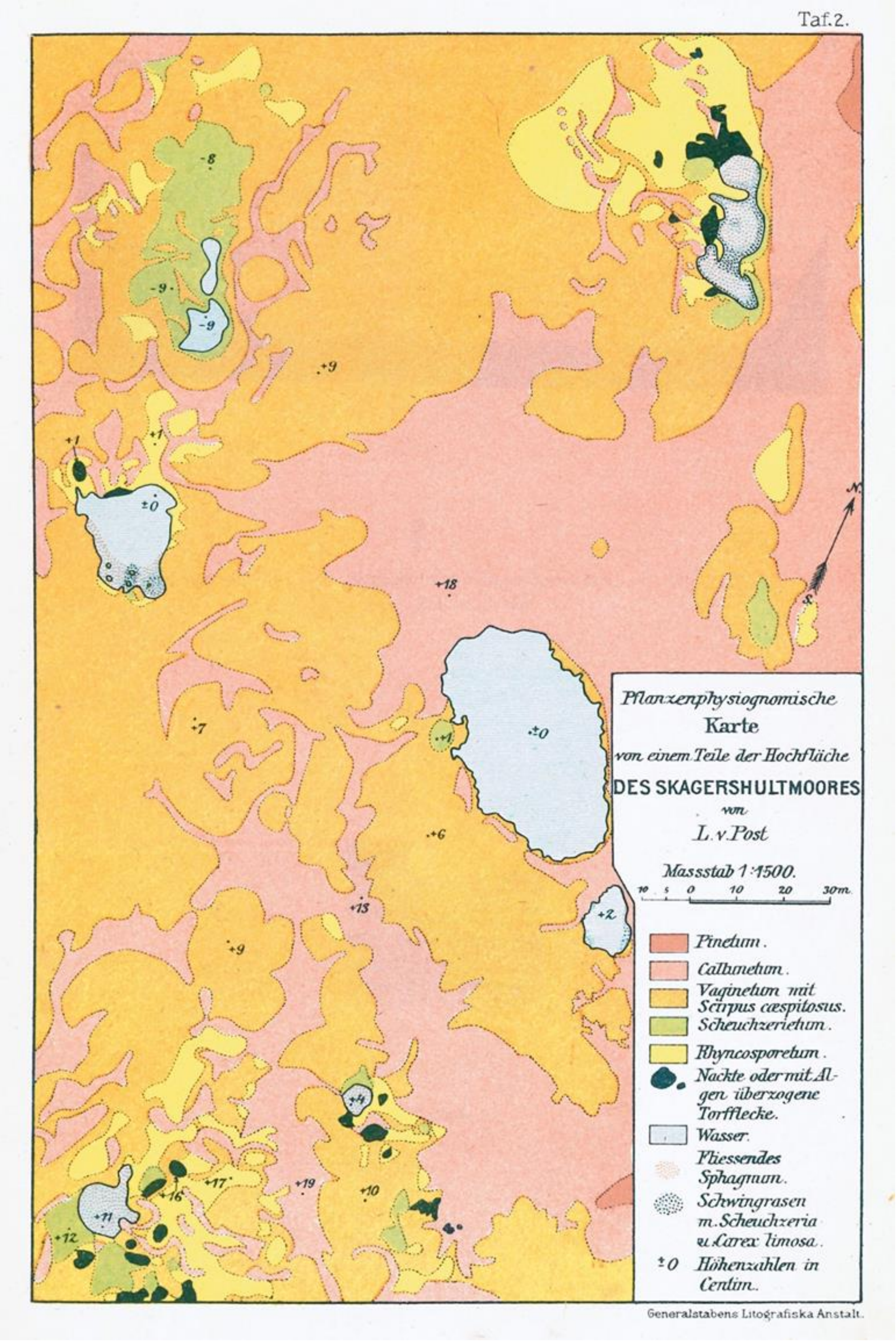

Figure A1. Vegetation map from 1907. Reproduced from Sernander & von Post (1910).

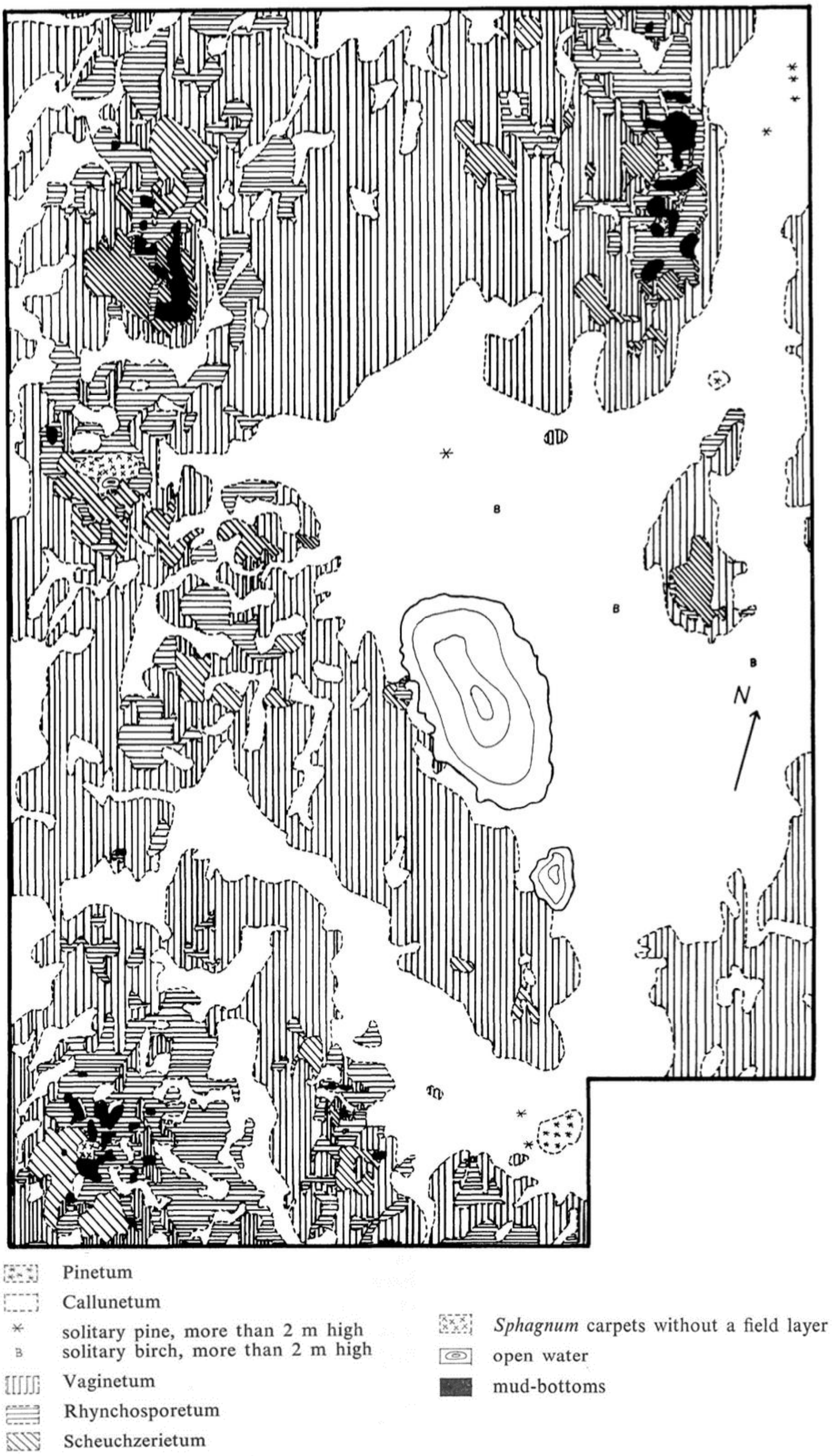

Figure A2. Vegetation map from 1970. Reproduced from Backéus (1972).

Table A1. NDVI frequency distributions (percent of area) observed in the reference area and the studied area on 05 May, 28 July and 11 October 2022 (Figure 4).

	05 May		28 July		11 October	
NDVI	Reference area	Field study area	Reference area	Field study area	Reference area	Field study area
0.9–1.0	0.06	3.23	0.31	3.23	0.81	3.23
0.8–0.9	0.25	0.00	2.24	0.00	2.74	3.23
0.7–0.8	1.43	0.00	10.14	19.35	13.62	19.35
0.6–0.7	10.88	9.68	82.21	67.74	68.78	61.29
0.5–0.6	86.94	83.87	5.1	9.68	14.50	12.90
0.4–0.5	0.93	3.23	0.00	0.00	0.00	0.00
0.3–0.4	0.00	0.00	0.00	0.00	0.00	0.00
0.2–0.3	0.00	0.00	0.00	0.00	0.00	0.00
0.1–0.2	0.00	0.00	0.00	0.00	0.00	0.00
-1.0–0.1	0.00	0.00	0.00	0.00	0.00	0.00