Bachelor Thesis

Stockholm University

Degree Project in
Marine Geology 15 hp

Fen-bog transitions

A case study from Store Mosse in Småland, Sweden

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Stockholm 2020

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Abstract

Peatlands play a vital part in the Earth's climate system. They store around a third of the worlds soil organic carbon. Two important peatland ecosystems are fens and bogs which differs a lot regarding environmental variables (e.g. pH, vegetation, height above water table, nutrient input etc.). Allogenic and autogenic factors influence the development and general succession of a peatland with the typical succession being from fen moving towards bog. This project set out to reconstruct past changes in peatland species diversity over the last 8000 years at the largest southern bog complex in Sweden, Store Mosse (The *Great Bog*). Based on macrofossil data and other proxies (e.g. bulk density) the peatland development in the SM B sequence was established. The fen-bog transition occurred at 5800 cal years BP. The sequence showed that a retrogression towards fen-like conditions occurred at 4100 cal years BP. The peatland gradually recovered from 3100 cal years BP and moved into a final bog stage at 2100 cal years BP. Allogenic factors (mainly shifts in climate towards drier or wetter condition) together with autogenic factors seems to always be working together, depending on the general state of the peatland, driving the development. Large peatland complexes (such as Store Mosse) has an ability to buffer against allogenic changes but after some time changes are inevitable. This is alarming due to the changes in climate we are already facing today, widespread drying of peatlands could initiate retrogressions from bogs to fens, which in turn could be a part of a positive feedback cycle of warming climate.

Keywords

Fen-bog transition, peatland succession, peat, macrofossils, paleoclimate

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Introduction

Peatland ecosystems play an important role in the Earth's climate system and the global carbon cycle. Peatlands are estimated to store around one third of the world's the soil organic carbon (Gorham, 1991). Peatlands are considered to be a CO_2 sink while at the same time being a significant source of CH_4 emissions (Mathijssen et al., 2016). In a general sense there are two main categories of peatlands, fens and bogs. While there are other types (e.g. marshes and swamps) fens and bogs are the main producers of deep peat soils. Fens usually produce more CH_4 emissions than bogs and due to the higher levels of humification and decomposition of organic matter, they normally do not accumulate as much carbon as bogs (Mathijssen et al., 2016). *Sphagnum* dominated bogs on the other hand are linked with lower decomposition rates resulting in an increase in carbon stored in the peat (Korhola et al., 1996). In the northern hemisphere *Sphagnum spp.* are accountable for approximately 50% of all peat (Bengtsson et al., 2016). Looking at peatland development over time, there is a correlation between the rapid vertical peat growth occurring during the *fen-bog transition* and higher levels of carbon uptake together with declining CH_4 emissions (Mathijssen et al., 2016). With global climate change, which is, leading to changing patterns of precipitation and drought and more unreliable seasons, understanding peatlands and factors affecting their succession has become of greater importance.

Terminology and definitions:

To be able to talk about fen-bog transitions an understanding of the different types of peatlands is necessary but complicated by the fact that definitions vary depending on scientific discipline. It is also important to have in mind that the vocabulary associated with peatlands have definitions in different languages that sometimes overlaps with each other which can make direct translation and interpretation complex. An example of this is the word *mire* which in Swedish translates to *myr.* The word mire is defined, a little problematically, as "wet terrain dominated by living peat-forming plants" (Rydin & Jeglum, 2013). This definition poses a problem in that the development of peat is normally associated with particular species but can development among most plant species (Rydin & Jeglum, 2013). The term *mire* is commonly used in biology and ecology where the focus is on the species and vegetation and not necessarily on the soil. In Swedish however, the word *myr* is often used as a collective term for fens and bogs. In addition to that, there is another term in Swedish which can add more confusion to the term *mire, norrlandsmyr* (*Norrlands mire*) also called *blandmyr* (*mixed mire*). *Norrland mires* or *mixed mires* are most commonly found in the northern parts of Sweden and consists of complex peatlands altering between fens and bogs.

While the term mire is defined by the process of peat formation the term *peatland* is defined by the thickness of the peat layer. Considering that the minimum depths of peat defining a *peatland* are different around the world this term is also problematic. Most countries use a minimum depth of 30 cm to define a peatland but Canada, for example, uses a minimum depth of 40 cm (Rydin & Jeglum, 2013). In Sweden a 30 cm thick peat layer defines a peatland, but most soil maps only show peatlands that have a 50 cm thick peat layer due to soil mapping as a rule being done at 50 cm depth. The Swedish National Encyclopaedia defines peatlands as areas with a 50 cm depth of organogenic soils. Organogenic soils is a term that includes gyttja soils and is therefore not strictly considering peat only. These are examples of how the definitions of the terminology regarding peatlands can vary more or less depending on the authors background and knowledge about the possible inconsistency in the usage of terms and definitions.

Definitions of fens and bogs:

The most commonly used attribute to distinguish a fen from a bog and vice versa is the nutrient regime of the peatland. The nutrient regime naturally goes hand in hand with the moisture regime of a peatland. The nutrient regime in fens are minerotrophic and the peatland has contact with the groundwater which supplies minerals and nutrients from the surrounding soils (Ronkainen et al., 2014). Fens can be more or less rich in nutrients ranging from eutrophic to oligotrophic. Bogs have an ombrotrophic nutrient regime and due to the loss of contact with the groundwater they only get influxes of nutrients from precipitation and mineral dust (Ronkainen et al., 2014). Bogs can have a pattern of microtopography with hummocks, hollows, lawns, mud-bottoms and bog-pools where the moisture gradient and the height above the water table varies between the different microtopographies (Howie et al., 2020). These differentiations in microtopography have given rise to adaptation among species (e.g. *Sphagnum*) that thrive in specific types of microtopography due to the different hydrological niches they can offer (Howie et al., 2020) (Bengtsson et al., 2016).

There are other characteristics that separate fens from bogs. These include for instance, the type of vegetation, the type of peat (which depends on the peat-forming plants) and the pH. Bog peat is usually less decomposed compared to fen peat (Ronkainen et al., 2014). Fens normally have a higher pH and greater biodiversity among species while bog are acidic with a low pH and less species diversity (Granath et al., 2010). The pH definitions of fen and bogs is a further division into the bog – poor fen – rich fen series (Table 1). A series where the term *rich* is an indication of richness in flora (correlated with higher pH) and not necessary a richness in nutrients (Rydin & Jeglum, 2013).

Table 1: Table showing the pH range in the bog – poor fen – rich fen series.

Type:	Bog	Poor fen	Intermediate & moderately rich fen	Rich fen
pH:	3.5 – 4.2	4 – 5.5	5 – 7	6.8 – 8

Fen-bog transitions:

The development of a peatland is strongly connected to the succession of the vegetation. Primary succession happens when an area is first colonized by organisms, such as in Store Mosses case, when the last ice sheet retreated. What drives the further development of a peatland is secondary succession. Secondary succession can be influenced by various change-driving factors. Allogenic factors that have an influence on the succession can be climate change (affecting precipitation, evapotranspiration, temperature, seasonal changes, wind strengths and/or directions), fires, deposition of eroded material and even human impact (e.g. draining and fertilization) (Hughes & Barber, 2003). Autogenic factors are imposed by changes in the internal ecosystem itself, for example by influence and alterations caused by the vegetation, organisms and different substrates (Granath et al., 2010). Some types of peatlands are more influenced by allogenic factors while others are more influenced by autogenic factors. For fens both allogenic and autogenic factors pose an influence on the succession and development (Rydin & Jeglum, 2013). On the other hand, ombrotrophic bogs are highly dominated by the autogenic factors but at the same time changes in for example climate or atmospheric dust can affect the bog (Rydin & Jeglum, 2013).

There are two main processes which leads to peatland formation, infilling and paludification. Infilling is a process where an aquatic environment (e.g. a lake) is overgrown by fen vegetation and paludification is a process where previously less moist mineral soils becomes wetter (e.g. forest developing into swamp forest) (Rydin & Jeglum, 2013). The typical succession of peatlands follows a long-term development from a minerotrophic fen towards ombrotrophic bog conditions where a decrease in the base saturation occurs at the same time as the acidity increases (Rydin & Jeglum, 2013). For ombrotrophication to happen the active surface of the peatland needs to loose contact with the underlying water table (Hughes & Barber, 2003). Ombrotrophication can be realised either through lowering of the water table (allogenic) or rapid vertical peat accumulation (autogenic) (Hughes & Barber, 2003). When a peatland moves into ombrotrophic conditions it is very unusual for the ombrotrophication to transpire in every corner of the peatland. There are practically always some areas, such as the margins or bog pools, that still are in contact with the groundwater and mineral soil. Even though an ombrotrophic bog in general is looked on as the “final stage” in peatland succession, instabilities and events can occur that can trigger a bog to retrogress into a fen, often as a consequence of allogenic changes (Rydin & Jeglum, 2013).

Studies have shown that indicator species have great importance when it comes to identifying the fen-bog transition (Väliranta et al., 2017). But it can be problematic to draw hasty conclusions given the presence or absence of specific species. If the indicator species have been established in one area it can be problematic to apply the same species to another area. An example of this being *Eriophorum augustifolium* and *Sphagnum papillosum* which in the northern and eastern parts of Sweden are sensitive indicators for minerotrophy while they concurrently are found in bogs in the southwest of Sweden (Rydin & Jeglum, 2013). Another study from Finland suggests that the fen-bog transition only should be recognised where the species dominating the vegetation changes from *Eriophorum* to wet or dry ombrotrophic *Sphagnum spp.* (Väliranta et al., 2017). If considering locations even further away, peatlands in the southern hemisphere can pose as an extreme example of how specific succession related species varies with geographical location. In many Subantarctic peatlands *Sphagnum spp.* are entirely absent or lack significant influence in the peat-forming process (Van der Putten et al., 2012). An interesting example is New Zeeland where *Empodisma minus* (wire rush) have been suggested to play a larger key role in autogenic fen-bog transitions than *Sphagnum spp*. (Hodges & Rapson, 2010). Peatlands are often classified as oligotrophic to eutrophic fens in the Subantarctic which suggest that the hydrological system and the nutrient regime are of high importance when it comes to classification (Van der Putten et al., 2012).

The fen-bog transition can be identified using other proxies than macrofossils, for example, bulk density, humification, geochemical profiles of mobile elements (e.g. Ca, Sr, Fe) and ash content, a combination of different proxies is preferred. Bulk density, a proxy of the degree of peat decomposition which can indicate past surface moisture conditions, tends to be lower when the peat is well-preserved (Chambers et al., 2011). Well-preserved peat is normally deposited during productive and/or wet conditions promoting rapid burial of organic matter (Chambers et al., 2011). Humification is a proxy of the degree of decomposition of peat and can be used to indicate the bog surface wetness which is thought to primarily be driven by precipitation, reinforced by temperature (Chambers et al., 2011).

Store Mosse (The *Great Bog*) and previous research:

Store Mosse is the largest bog complex in southern Sweden (77 km^2). The area is protected as one of Sweden's 30 national parks. Store Mosse is since 1974 considered internationally valuable wetland according to the Ramsar Convention and is also under EU protection as a Natura 2000 site.

Store Mosse has been studied for decades. Macrofossil analysis was done in 1988 by Svensson but only with 4 age dates and consequently the age model has a lot of uncertainty in changes over time. Since then studies have been done on changes in mineral dust deposition and hydrology at Store Mosse (Kylander et al., 2013, 2016 and 2018). These studies were done on SM O core and provided an understanding of the fen-bog transition based on bulk density and geochemical indicators. More research needed to be done on the macrofossils to better understand the development of Store Mosse and the cores SM A and SM B were recovered. SM A and SM B were recovered close to each other in order to look at variations in species between different microtopographies within the bog. This project is mainly focusing on SM B but will use previously published data from SM A (Ryberg et al., 2019) as well as key proxies from SM O to compare and evaluate results from SM B.

Aim and objectives:

This project aims to reconstruct past changes in peatland species diversity over the last 8000 years at the largest southern bog complex in Sweden, Store Mosse (The *Great Bog*). Based on macrofossil data, when does the fen-bog transition take place and what are the influencing factors driving the transition? Which species are dominating at what stages in the peatland development? What are the main driving factors in the development of the peatland and is the typical fen-bog succession story always applicable?

Methods

Site description and sampling:

Store Mosse is located in the western part of the province of Småland and is the largest bog complex (77 km^2) in southern Sweden (Figure 1). The area has a mean annual temperature of 5,9°C (SMHI, 2020a) and a mean annual precipitation of 756 mm/year (SMHI, 2020b). The development started when the Weichsellian ice sheet retreated. The area was then covered by an ice-dammed glacial lake, Lake Fornbolmen. Due to isostatic rebound Fornbolmen was tilted to the south which made the northern parts of the lake drain and dry out (Kylander et al., 2013). The establishment of peat-forming vegetation started in the northern parts of drained lake (Svensson, 1988). Today, the bog is still sloping roughly 1.2 m/km to the south as a consequence of the isostatic rebound (Svensson, 1988). Typical hummock and hollow microtopography is visible over the raised bog plain (Svensson, 1988). The hummocks form strings which run perpendicular to the southward slope of the bog (Kylander et al., 2013).

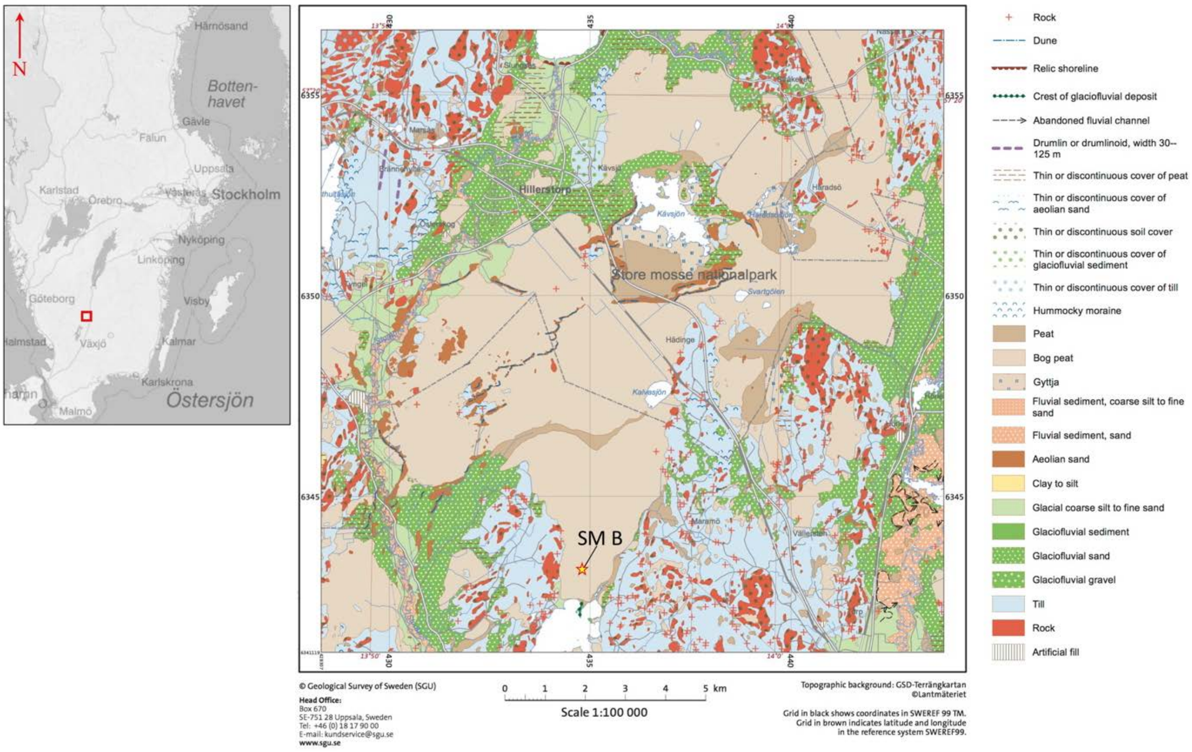

Figure 1: Map over the study area. The coring site for SM B is indicated with a star. White areas on the map of Store Mosse are lakes.

In November 2018 several cores were recovered from the south part of the bog (Figure 1). The cores, SM A and SM B were purposely recovered very close to each other with the motivation to get at broader picture of vegetation changes within the same small area (Lat: 57º13'38.22"N, Long: 13º55'10.86"E). The cores were recovered with a 1 meter long Russian corer with the diameter of 7.5 cm. SM B was recovered from a lower hummock and eight one-meter sections with 25 cm overlap were recovered from two adjacent parallel holes (Figure 2). Species found growing around the core site included *Sphagnum medium*, *S. balticum*, *S. cuspidatum/majus, Cladonia spp.* (reindeer lichens), *Empetrum nigrum* (crowberry), Sedges *sensu lato* (e.g. *Carex spp*., *Eriophorum vaginatum*), *Calluna vulgaris* (heather) and *Erica tetralix* (cross-leaved heath).

Cores were sub-sampled in contiguous 1 cm slices using a stainless-steel knife. Approximately 1 cm^3 from each slice was freeze-dried while the remaining material from each sample was left wet.

Figure 2: Photograph of the core site of SM B with the two adjacent parallel core holes. Dominated by Sphagnum medium. Photo courtesy of Eleonor Ryberg.

Bulk density and age dating:

To calculate the bulk density the dimensions of the freeze-dried 1 cm^3 samples was measured using callipers and the dry weight of the sample was divided with the estimated volume. Using the calculated bulk density values the alignment of the overlapping adjacent cores was corrected for a composite sequence depth of 600 cm.

Age dating was done at the Tandem Laboratory at Uppsala University. Plant microfossils from eight depths were analysed for ^{14}C dates were established (Table 2). The CLAM program (v. 2.2) developed by Blaauw (Blaauw, 2010) was used to generate the age-depth model. The program included a calibration of the ^{14}C dates using the IntCal13.14C calibration curve (Reimer et al., 2013). A smoothed spline was deemed the best fit for the curve and no statistical outliers were present. The peat accumulation rate (PAR, $g/m^2/yr$) was calculated using the bulk density (g/cm^3) and the accumulation rate (yr/cm) derived from the age model. For this study the raw data was then analysed in Microsoft Excel version 16.16.7.

Table 2: Table showing the ^{14}C dates obtained using plant microfossils and the CLAM program developed by Blaauw (Blaauw, 2010)*. The table also shows the calibrated age model dates that were obtained using IntCal13.14C calibration curve (Reimer et al., 2013).*

Sample Depth (cm):	***Laboratory no.:***	***Material dated:***	***14C yr ± 1SD:***	***Calibrated Age Range:***
60	Ua-64326	*Sphagnum (Majus,* sect. *Cuspidatum* mix*)* stems, charred plants, sedges *sensu lato*	422±31	435-525
128	Ua-64327	*Sphagnum (Austinii,* and sect. *Cuspidatum* mix*)* stems and leaves	956±31	795-929
197	Ua-64328	*Sphagnum (Austinii)* stems and leaves	1879±32	1726-1886
272	Ua-64329	*Eriophorum Vaginatum* remains, bark, charred plants	3006±33	3075-3258
354	Ua-64330	*Sphagnum (Fuscum* and *Rubellum*) stems, *Eriophorum vaginatum* remains, bark, wood	4295±34	4827-4893
440	Ua-64331	*Sphagnum (Fuscum* and *Rubellum*) stems, sedges *sensu lato*, wood	4452±34	4959-5144
510	Ua-64332	Sedges *sensu lato*, charred plants, wood	5929±36	6666-6806
595	Ua-64333	Sedges *sensu lato*, phragmites	7357±39	8038-8223

Macrofossil Analyses:

Twenty samples from the SM B sequence were analysed to generate a low-resolution record. Using a 120 µm mesh sieve approximately 5 ml peat from each sample was washed gently. Each sample was analysed in a petri dish under a stereo-zoom microscope under magnification ranging X10-40. Following methods developed by Mauquoy and Van Geel (2007), Väliranta et al. (2007; 2012; 2017) and Birks (2017) plant coverage percentages were estimated using a graph paper with a 10 x 10 mm grid as scale. A high-power microscope analysis using a modified Quadrat Leaf Count protocol (QLC) (Mauquoy & Van Geel, 2007) (Väliranta et al., 2007) could establish identification on species level of different *Sphagnum* species.

When establishing the plant coverage percentages four central categories of vegetation were used: *Eriophorum spp.*, sedges *sensu lato* (e.g. *Carex spp*.), *Ericaceae* (roots) and Bryophytes (separated into *Sphagnum* and brown mosses). Unidentified organic matter (UOM) was also established using coverage percentage. *Ericaceae* seeds, leaves and flowers, spindles, mycorrhiza and pieces of charcoal were counted in absolute numbers. Pieces of charcoal were subdivided into two categories depending on their size, one for charcoal pieces greater than 1 mm and one for charcoal pieces smaller than 1 mm. Occurrence of wood, bark and insect remains (along with other plant occurrences that were less than 1%, e.g. *Calluna vulgaris*) were noted on a three-part scale of + (rare), ++ (occasional) and +++ (abundant). For this study the raw data was then analysed and organised in Microsoft Excel version 16.16.7 and Tilia version 2.6.1.

Description of Persons Responsible for Data Collection:

The collection of the data used in this BSc project was done by people other than the author herself as described in Table 3. All figures and interpretations are the authors own however.

Table 3: Table showing the people responsible for the data collection.

Previous work performed on SM B:	
Sampling and field work	Dr. Malin Kylander, Terese Kumlin, Austin Stout, Jenny Sjöström, Eleonor Ryberg
Sub-sampling and freeze drying	Eleonor Ryberg, Fredrik Bogren
Macrofossil analyses	Eleonor Ryberg
^{14}C-dating and age-depth modelling	Eleonor Ryberg

Results

SM B begins at 8000 cal years BP with a period (unit 1) dominated by *Eriophorum spp., Carex spp., Ericaceae* and unidentified organic matter (UOM) (figure 3). At around 7000 cal years BP there is a steadily increase in the bulk density and PAR (figure 3). At around 5800 cal year BP there is a sharp drop in the bulk density and PAR together with a change in the dominating vegetation type (figure 3). This second period (unit 2) is reasonably stable until around 4100 cal years BP when a clear difference can be seen in the signal from the macrofossils and the bulk density (figure 3). Around 4780 cal years BP during the second period, lasting from approximately 5800 cal years BP to 4100 cal years BP, there is a significant decline in *Sphagnum spp.* while *Eriophorum* and *Ericaceae* increases rapidly (dashed red line in figure 3). Macrofossil charcoal and UOM is found at the same depth in the sequence (figure 4). The second period is dominated by *Sphagnum fuscum* and *Sphagnum rubellum* (figure 5).

At roughly 4100 cal years BP there is a significant increase and stronger fluctuations in the bulk density in SM B (figure 3). At the same time a pronounced increase of the sedges, especially Eriophorum, and *Ericaceae* (roots) together with a total absence of *Sphagnum spp.* can be seen (figure 4). There is also a significant amount of UOM and findings of wood and bark (figure 4). The initiation of the third period at around 4100 cal years BP is relatively sharp, conversely the transition from the third section to the fourth section is diffuse (figure 3). The third period is therefore divided up in 3a and 3b. In unit 3b there is a gradual transition from around 3100 cal years BP to 2100 cal years BP where the bulk density is fluctuating but with another character (fewer but still strong fluctuations) than during the period of unit 3a (figure 3). There are gaps in the macrofossil data during the time of unit 3b but shortly after the initiation, around 2800 cal years BP *Sphagnum medium* and *S. acutifolia* are showing up in the sequence (figure 5). A weak gradual trend towards lower bulk density (lower lows and lower highs) is seen during in unit 3b (figure 3).

Around 2100 cal years BP there is a fairly sharp drop accompanied with a change in character observing both the PAR and the bulk density (figure 3). This change marks the beginning of a more stable period with lower bulk density values with the exception of a few sharp peaks. The fourth period (unit 4) is considered the last main stage in the sequence and is ongoing in present time. There is a significant increase in the *Sphagnum spp*. simultaneously occurring with a decrease in sedges and *Ericaceae* (roots) distinguishing the fourth period (figure 4). Around 400 cal years BP there are significant amounts of charcoal in the macrofossil data (figure 4) matching with a very high and sharp peak visible in the bulk density and PAR (figure 3). The *Sphagnum* species are changing during the fourth period, the bottom half of the section is mostly *S. medium* and *S. austinii* while *S. balticum*, *S. majus*, *S. cuspidata*, *S. fallax* and *S. austinii* show up in varying extents in the top half of the section (figure 5).

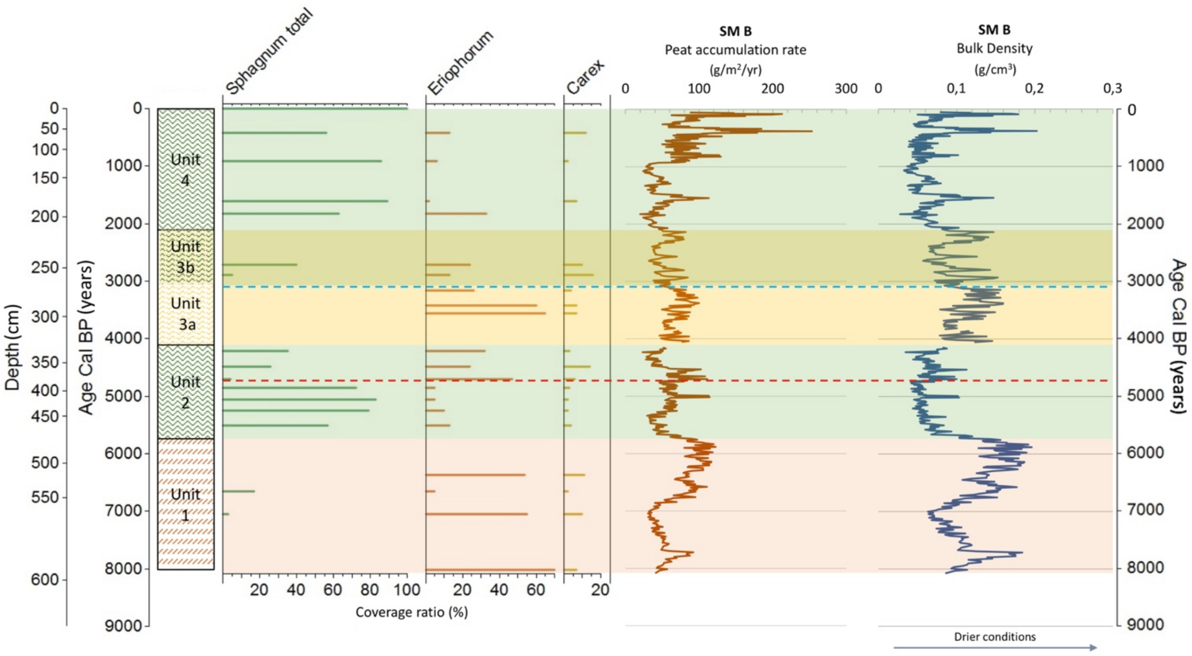

Figure 3: Data from SM B (from left to right): lithology and unit division, the three main macrofossil indicators; Sphagnum spp., Eriophorum spp. (mainly Eriophorum vaginatum) & Carex spp., PAR and bulk density. The background colours indicate the different sections in the lithology. The dashed red line indicates possible disturbance. The dashed blue line indicates the transition from unit 3a to unit 3b. Unit 3b is marked as a period with no sharp boundaries.

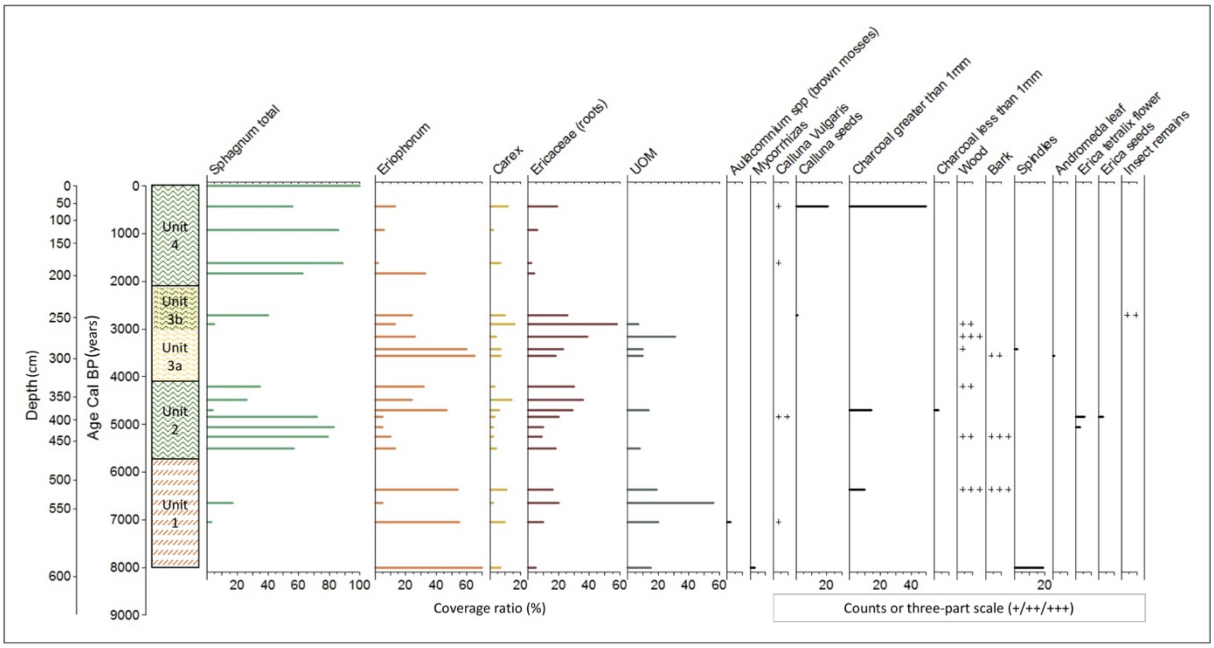

Figure 4: Data from SM B (from left to right): lithology and unit division and following that all categories of macrofossils except the Sphagnum species (figure 5). Sphagnum spp., Eriophorum spp. (mainly Eriophorum vaginatum), Carex spp., Ericaceae (roots), UOM (unidentified organic matter), Aulacomnium spp. (brown mosses) and Mycorrhizas are analysed as coverage percentages. Calluna seeds, charcoal, spindles, Andromeda leaves, Erica tetralix flowers and Erica seeds are analysed by counts. Calluna vulgaris, wood, bark and insect remains are analysed with a three-part scale (+=rare, ++=occasional, +++=abundant).

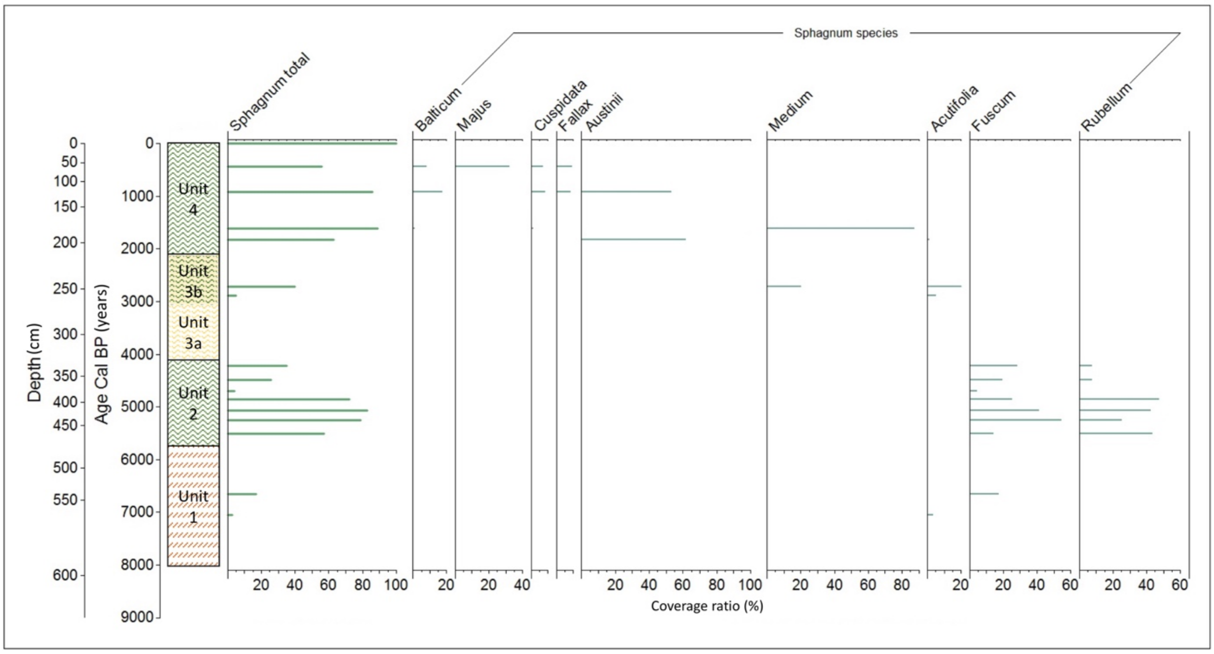

Figure 5: Data from SM B (from left to right): lithology and unit division, Sphagnum total following the different Sphagnum species. All of the macrofossils are analysed with coverage percentages. The Sphagnum species add up to total Sphagnum.

Discussion

Interpretation of SM B:

Macrofossils provide an important means of identifying the fen-bog transition, particularly when paired with bulk density data. The SM B sequence begins with a fen stage (unit 1, figure 3) dominated by *Eriophorum spp.* (e.g. *Eriophorum vaginatum*), *Carex spp*. and *Ericaceae.* This stage carries on until around 5800 cal years BP when the bulk density and the PAR abruptly drops. At the same time the dominant vegetation type changes drastically from fen-like vegetation to *Sphagnum spp.* (*S. fuscum* and *S. rubellum*). This marks the fen-bog transition and the SM B sequence has now moved into the first bog stage (unit 2, figure 3). This bog stage is rather stable with the exception of a rapid decline in *Sphagnum spp.* accompanied by an increase in sedges and *Ericaceae* around 4780 cal years BP. This event can also be observed in the bulk density and PAR as sharp increases. Sphagnum recovers quickly to begin with but then something noteworthy happens. At about 4100 cal years BP there is a shift in the bulk density, PAR and macrofossil signal indicating a change towards more fen-like conditions in the sequence (unit 3a, figure 3). Fluctuations in the bulk density are stronger and the general trend suggests drier conditions. *Sphagnum spp.* disappears while *Ericaceae*, *Eriophorum vaginatum*, *Carex spp.* and UOM increase significantly. This period is considered a form of retrogression due to the change in the macrofossil signal together with the shift in the bulk density.

The transition period (unit 3b, figure 3) from the retrogression (unit 3a, figure 3) towards the final stage (unit 4), or the second “fen-bog transition”, is rather diffuse and it is hard to set a specific date to this change. The bulk density gradually decreases implying a trend towards lower bulk density values. There are data gaps in the macrofossil record during this period, but *Sphagnum spp.* are appearing in the sequence again. This transition period is interpreted as a prolonged unstable period where the peatland is slowly recovering from the preceding retrogression period. At around 2100 cal years BP the bulk density and PAR change in character suggesting more certainly that the transition period (unit 3b, figure 3) is over. With the last period (unit 4, figure 3) comes an increase in *Sphagnum spp.* while *Ericaceae, Eriophorum spp., Carex spp.* and UOM decrease. The bulk density is generally lower and the fluctuations are not as strong, suggesting moister conditions, with the exception of some sharp peaks. Considering the changes in the dominating *Sphagnum* species throughout the section and the sudden peaks in bulk density and PAR, this bog stage is not as stable as the first one (unit 2, figure 3).

Published data from SM A and SM O in context with SM B:

SM A begins with a pre-fen stage and around 9000 cal years BP rapid change in the vegetation and a shift in the bulk density indicate the beginning of the fen stage around 6050 cal years BP (figure 6), which is earlier than when the fen-bog transition takes place in SM B (5800 cal years BP). During this first bog stage the dominating *Sphagnum* species are *S. fuscum* and *S. rubellum*. The same pattern is seen in both SM A and SM B with a rapid decline of *Sphagnum spp.* accompanied with an increase in sedges and *Ericaceae* around 4780 cal years BP. This event can also be observed in the bulk density and PAR as sharp increases (figure 6). In both SM B and SM A *Sphagnum spp.* recovers quickly to begin with but is then abruptly stopped at different times (at ~ 4100 cal year BP in SM B and ~ 4500 cal years BP in SM A). This is quite interesting considering that SM B and SM A were taken around 10 meters apart from each other. These offsets could possibly be due to uncertainties in the age dating (from for example, a different number of ^{14}C dates), but considering the agreement in timing of the event at 4780 cal years BP in both cores, this seems less likely. In SM A the first bog stage lasts until around 4500 cal years BP when there is a rapid change in the dominant vegetation type as well as a visible increase in the bulk density (figure 6). This period, lasting from around 4500 to 2900 cal years BP, is considered a retrogression period due to the rapid decline of *Sphagnum spp.* that occurs simultaneously to a substantial increase in *Eriophorum spp*., *Carex spp*., *Ericaceae* (roots) and UOM (figure 7) together with the change in bulk density and PAR (figure 6). The period has reoccurring layers of charcoal at roughly every 500 years. Around 2900 cal years BP there’s a swift change towards generally lower bulk densities, which indicates the beginning of the end of the retrogression period.

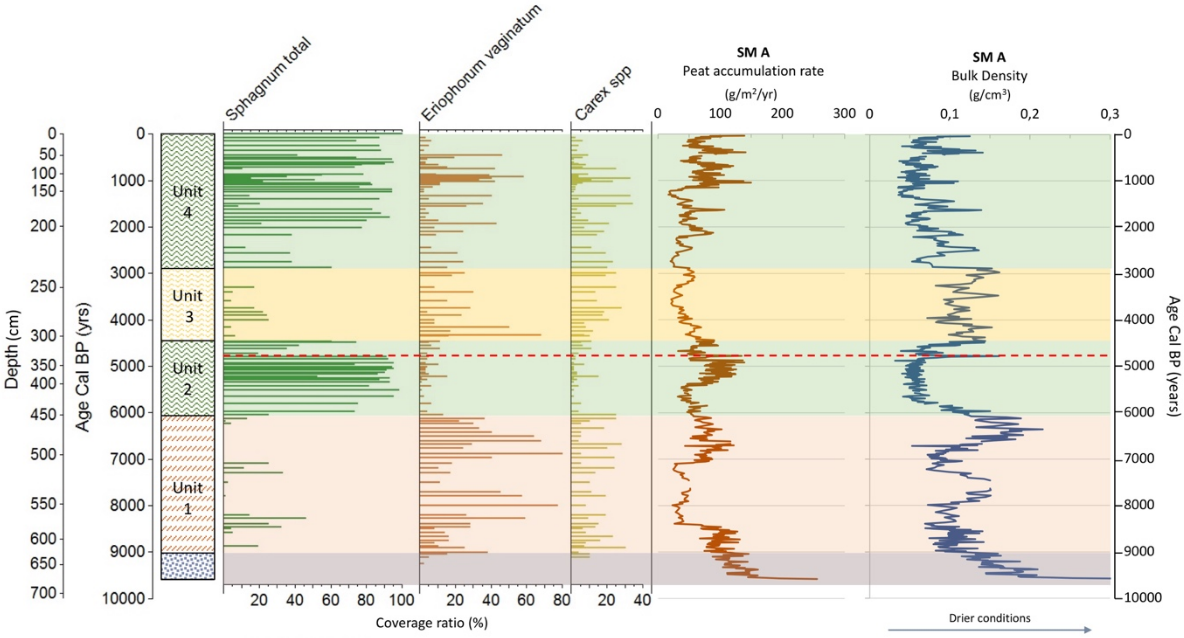

Figure 6: Data from SM A (from left to right): lithology of interpreted peatland development, the three main macrofossil indicators; Sphagnum spp., Eriophorum spp. (mainly Eriophorum vaginatum) & Carex spp., PAR and bulk density. The background colours indicate the different sections in the interpreted development lithology. The dashed red line indicates possible disturbance.

The same general retrogression period is found in SM B and SM A but there is a difference in both the longevity and termination of the period. Here it is important to have in mind that the SM B macrofossil record is very low resolution and to be able to get an idea of what is happening during the data gaps SM A can be indicative. When the *Sphagnum spp.* are disappearing in SM B during the retrogression the reality of the scenario is probably more like what is occurring in SM A, *Sphagnum spp.* are still present but in a much lower extent than before. In SM A, the last bog stage (circa 2900 cal years BP to present time), begins a little bit shaky with fluctuations in the dominant vegetation type and throughout the period the sedges are present to a greater extent than during the bog period before the retrogression (figure 7). It seems like the final bog stage has a different balance among species, compared with the first bog stage, where *Sphagnum spp.* are not as strongly dominant throughout the period. Among *Sphagnum spp.* the dominating species seems to be *S. medium* and from about 1300 cal years BP, *S. medium* and *S. Balticum*. Here and there, there are some peaks of a few other *Sphagnum* species during this period, but they don't seem to gain a larger foothold. The bulk density is rather inconsistent and fluctuates a lot compared to the first stable bog period, ~ 6050 to 4500 cal years BP.

The geochemical data from SM O indicate a significant change in the La mass accumulation rates beginning around 7000 cal years BP and peaking around 5800 cal years BP (figure 8). A peak can also be seen in the Sc mass accumulation rates around the same time as the fen-bog transition in SM B (figure 8). The humification gradually declines starting around 6850 cal years BP (figure 8). A small peak is seen in the Al mass accumulation rates at around the same time as the fen-bog transition in the SM B (figure 8). Al mass accumulation rates seems to fluctuate a lot during the first stable bog period established in SM B (figure 8). The C/N ratio is peaking during a period corresponding to the bog stage dominated by *S. fuscum* and *S. rubellum* in SM B (figure 8).

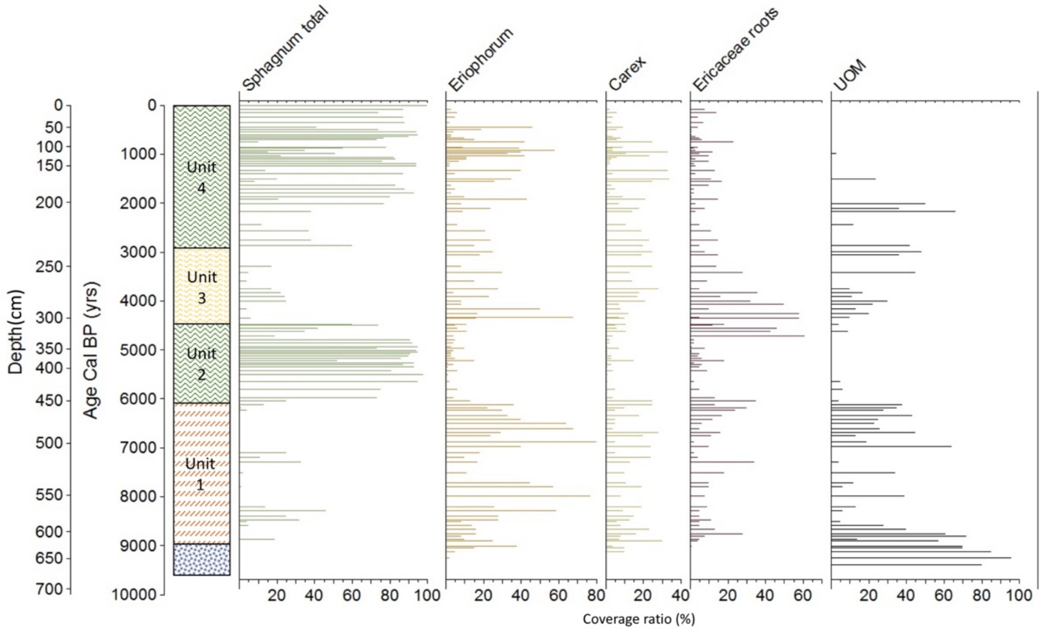

Figure 7: Data from SM A (from left to right): lithology of interpreted peatland development and following that the five main categories of macrofossils. Sphagnum spp., Eriophorum spp. (e.g. Eriophorum vaginatum), Carex spp., Ericaceae (roots) and UOM (unidentified organic matter) are analysed as coverage percentages.

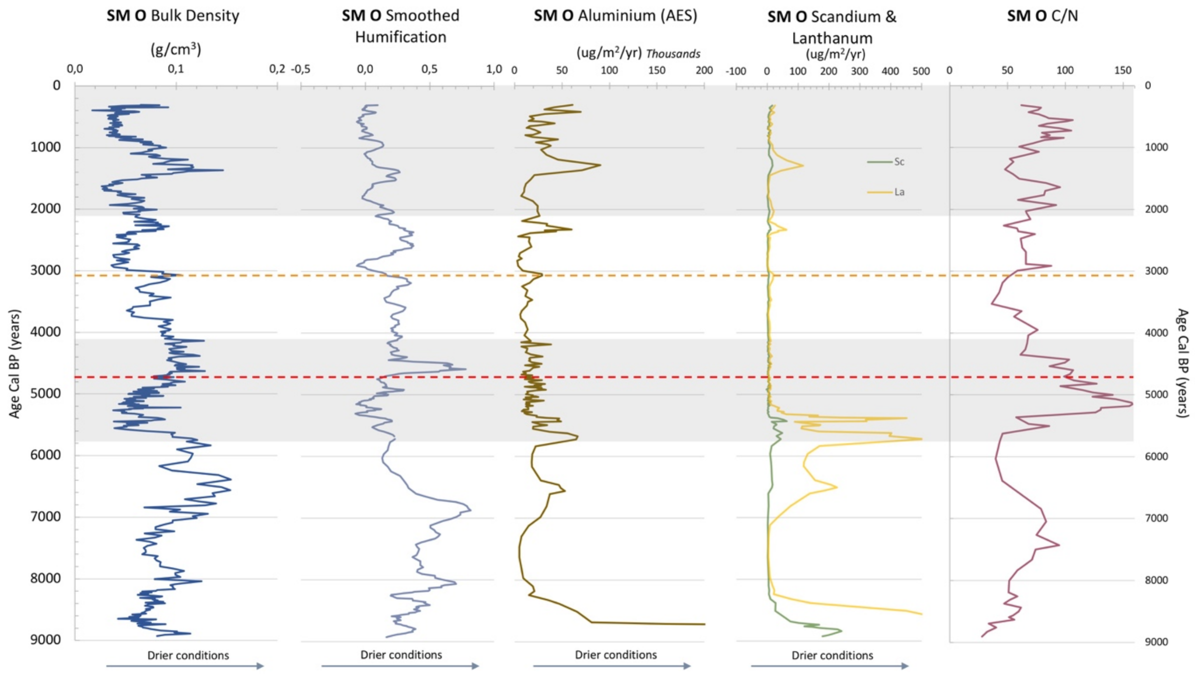

Figure 8: Data from SM O (from left to right): bulk density, humification (smoothed), Al, Sc and La mass accumulation rates and C/N ratio. The grey boxes represent the two relatively stable bog stages from the interpretation from SM B while the dashed yellow and red lines indicates the start of the diffuse transition period (3b) which follows the retrogression period and the possible disturbance, respectively (as seen in figure 3).

When comparing the bulk densities of SM B, SM A and SM O the best agreement, not surprisingly, is seen between SM B and SM A (figure 9). The bulk density of SM O is in general more stable throughout the sequence and does not fluctuate as much as in SM B and SM A cores (figure 9). The initiation of the fen-bog transition based on bulk density is not coherent in the three cores with again, SM B and SM A being more similar. When it comes to PAR the three sequences are more comparable although SM O has lower PAR during the fen stage than the other two sequences (figure 10). After the fen-bog transition SM B stands out with a seemingly more fluctuating PAR (figure 10). In all three sequences PAR increases significantly around 5400 cal years BP (figure 10).

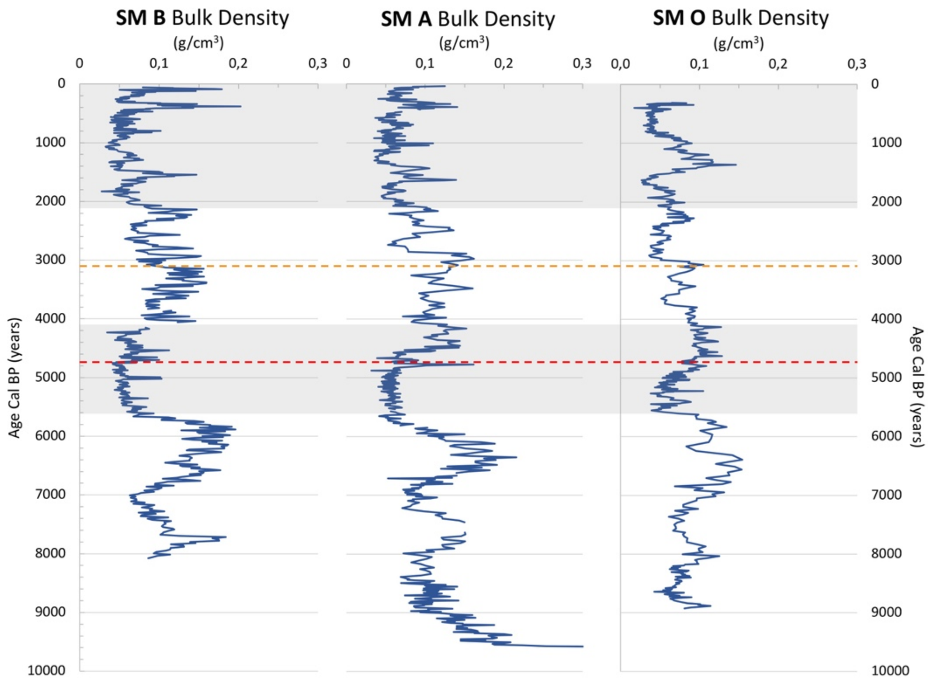

Figure 9: The bulk density from SM B, SM A and SM O. The grey boxes represent the two relatively stable bog stages from the interpretation from SM B (figure 3). The dashed yellow line indicates the start of the diffuse transition period (3b) which follows the retrogression period (figure 3). The dashed red line indicates possible disturbance.

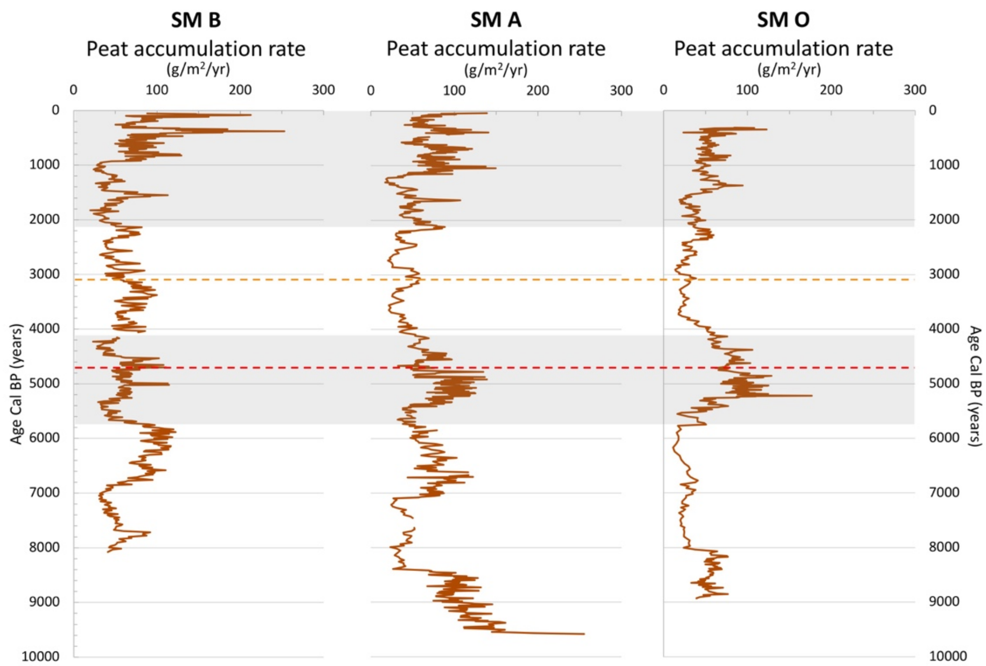

Figure 10: The peat accumulation rate from all three cores, SM B, SM A and SM O. The grey boxes represent the two relatively stable bog stages from the interpretation from SM B core (figure 3). The dashed yellow line indicates the start of the diffuse transition period (3b) which follows the retrogression period (figure 3). The dashed red line indicates possible disturbance.

The fen-bog transition (Unit 1, 8000 - 5800 cal years BP):

In 1988 it was suggested Store Mosse had gone through four main development stages; it began with a lake and fen stage and this was then followed by three different bog stages characterized by the dominant *Sphagnum* species. The transition from the fen stage into the first bog stage, dominated by *Sphagnum fuscum*, was established to have started as early as around 7000 cal years BP ago in the southern parts of the bog. Based on a series of core transects across Store Mosse it was found that the fen-bog transition took place rather synchronously around 5000 cal years BP ago. The *S. fuscum* bog stage lasted until 2400 cal years BP where the bog moved into a *S. rubellum-fuscum* bog stage which lasted until approximately 1000 cal years BP where the bog moved into a *S. magellanicum* bog stage (Svensson, 1988). But this accepted stratigraphy of the bog is simplified and only dated with a total of 4 age dates for the whole sequence (circa 10 000 years). Species distribution and dominance together with microtopography, different heights above the water table and the size of the bog makes the whole ecosystem very complex with a lot of internal variation.

The succession of peatlands can be complex and many factors, both allogenic and autogenic, influence their development. The development of the peatland seen in both SM B and SM A is complex and the possible explanation to why and when significant changes happens is equally as complex. The timing of the fen-bog transition mentioned previously, which occur in the cores at about 250 years apart, follows a similar vegetation development with *Eriophorum vaginatum* dominating together with *Carex spp.* and *Ericaceae* (roots). Especially in SM A (due to low resolution in SM B) one can see high percentages of *Eriophorum vaginatum* and a peaking trend in *Ericaceae* just before the fen-bog transition. *Eriophorum vaginatum* is a species that is well adapted to tolerate low water tables and flooding and it has been suggested that the species can be dominant at the fen-bog transition due to unstable water tables in newly formed bog peats (Hughes et al., 2000).

The fen-bog transition occurs during the Atlantic period (8000-5000 cal years BP), which is a moister period compared to the previous warm and dry boreal period (9000-8000 cal years BP). Even though the Holocene thermal optimum happens during the Atlantic period, the wetter climate makes Sphagnum bogs appear more frequently in contrast to the boreal period which saw drying of peatlands (Rydin & Jeglum, 2013). The changes in the climate during the Holocene are of interest when explaining the timing of the development in Store Mosse. It seems like the first initiation towards ombrotrophic conditions transpires during a period of wetter and warmer conditions suggesting that ombrotrophication and Sphagnum are more responsive to changes in precipitation than in temperature. But even this is complex given that effective precipitation (precipitation minus evapotranspiration) is directly linked with temperature.

One study comparing 14 Holocene fen-bog transitions in raised bogs in the British isles and Ireland found that there was two routes towards ombrotrophication, one “wet-pioneer” (autogenic succession = rapid accumulation of peat in moist climate) and one “dry-pioneer” (periods of reduced effective precipitation, only possible when the conditions are marginal for bog development), suggesting that the fen-bog transition should not always be used as an indicator for wetter climate conditions (Hughes & Barber, 2003). In SM B, PAR peaks prior to dropping in connection with the fen-bog transition at 5800 cal years BP. Considering the fen-bog transition occurring during an overall moister climate period and the pattern of a peaking PAR right before the transition, ombrotrophication at Store Mosse should be one of “wet-pioneers”, in other words predominantly driven by autogenic succession. Several factors point towards the fen-bog transition being driven by autogenic succession, but a contradictory signal comes from the elemental mass accumulation rates of Al and La in SM O. Especially La which indicates drier conditions during a period before the fen-bog transition. This is an indication though and singlehandedly it might not be of huge significance determining the system succession since the La dust could originate from a source far away, not necessarily indicating local conditions. For example, the smoothed humification indicating a shift towards less dry conditions during a period before the fen-bog transition.

The first bog stage (Unit 2, 5800 – 4100 cal years BP):

This bog stage is initiated during the end of the Atlantic period which is followed by the Subboreal period (5000-2600 cal years BP) which saw drier conditions with continuing warmth but a slow trend towards cooler climate (Rydin & Jeglum, 2013). At around 5400 cal years BP, during the first bog stage after the fen-bog transition, a significant increase in the PAR can be seen in all three of the cores (figure 10). Around the same time as this increase in PAR occurs the general deposition of dust on the bog changes in character from clayey minerals to minerals of feldspar and phosphate suggesting that the PAR could have been affected by an increase in nutrients which spiked the productivity of the bog (Kylander et al., 2018). This change in nutrient characteristics could also be a factor influencing the change in the vegetation and dominant species. In the SM O core, the C/N ratio peaks at 160 during the first bog stage in SM B while, during the retrogression, it declines to 36 at the lowest point.

In SM B there is an abrupt change in vegetation at 4780 cal years BP that can also be found in SM A. *Sphagnum spp.* suddenly decrease while *Ericaceae* increases rapidly followed by an increase in the sedges. *Sphagnum* then recovers (better in SM A than SM B) until a major shift and a retrogression is initiated. The timing of the initial shift is the same in both cores, 4780 cal years BP, while the retrogression seems to initiate around 400 years apart (at 4100 cal years BP in SM B and at 4500 cal years BP in SM A). The timing of this is during the drier Subboreal climatic period. One study found that *Ericaceae* shrubs, with their tolerance of drier surface conditions, have a significant advantage over both mosses and sedges when conditions are drier with less frequent precipitation (Radu & Duval, 2018). In SM B charcoal is found at 4780 cal years BP which could suggest that the sudden change in vegetation could be following a fire disturbance. Another study from Finland found that *Eriophorum vaginatum* was dominating and almost entirely replacing *Sphagnum spp.* after disturbance events (e.g. fires) especially in low hummocks (Swindles et al., 2019). There is a possibility that the disturbance could be a consequence of for example, flooding and not fire. This could also have significant effect on the *Sphagnum* community dominated by *S. fuscum* and *S. rubellum*. One study found that *Sphagnum fuscum*, when transplanted to a brown moss carpet at a very low height above the water table, almost stopped photosynthesising but also that *S. fuscum* was still doing well at an intermediate height above the water table (Granath et al., 2010). The same study also found that *S. fuscum* was critically harmed when subjected to seasonal flooding (Granath et al., 2010). This suggests that S. fuscum are very sensitive to changes in the water table. In general *Sphagnum* mosses are often sensitive to changes in the water table and hydrological system, especially when it comes to changes is the moisture dynamics near the bog surface (Radu & Duval, 2018). It could also be that the change happening 4780 cal years BP is the first indication of a larger change in the ecosystem leading up to the retrogression period.

The retrogression period (Unit 3a, 4100 - 3100 cal years BP) and the transition period (Unit 3b, 3100 – 2100 cal years BP):

This leads us in on the most intriguing period in the sequence, the retrogression. The start of this period is indicated in both the bulk density and macrofossil signal and it transpires as suddenly as the first fen-bog transition. Even here there is slight difference between the SM B and SM A, where it begins in the former at 4100 cal years BP and in the latter at 4500 cal years BP, respectively. The *Sphagnum spp.* rapidly decline while *Eriophorum vaginatum, Carex spp.*, *Ericaceae* and UOM all increase. The vegetation composition is very similar to the vegetation dominating before the fen-bog transition. The increasing amounts of UOM suggest that the level of decomposition is higher but when comparing this with the smoothed humification in SM O the rates of humification are quite stable during the same time period, with an exception of a low point at around 2900 cal years BP. Without macrofossil records from SM O it is hard to completely determine but just by analysing the different bulk densities and the data available, but it can be suggested that this retrogression found in SM B and SM A is not transpiring over the whole of Store Mosse to the same extent. This could also be an explanation as to why the two sequences are not in sync with each other. In SM A the retrogression period coincides with layers of charcoal suggesting that the area has been burned repeatedly which would further favour species such as *Eriophorum vaginatum* over *Sphagnum spp.*.

Store Mosse is a huge bog complex and likely has the capability to buffer against allogenic changes. One study from a large raised bog in Canada found that plant community species could vary greatly within the bog depending on if the local area had been left undisturbed or been subjected to drainage and consequently a lowering of the water table (Howie et al., 2020). It could be that different parts of Store Mosse are more or less sensitive to changes after earlier smaller disturbances and therefore the changes in allogenic factors can be expressed differently within the bog. The study also concluded that a significant lowering of the water table which effected the moisture gradient would have a plant community where *Sphagnum* was scarce (Howie et al., 2020). The retrogression period at Store Mosse occurrs slightly after the transition to the Subboreal, a drier period compared with the previous Atlantic period. The ending of the retrogression is gradual in SM B but at 2100 cal years BP the macrofossil signal and the bulk density seem to stabilize. This roughly coincides with the beginning of the Subatlantic at 2600 cal years BP, a period of cooler and wetter climate which saw widespread growth and expansion of *Sphagnum* (Rydin & Jeglum, 2013).

The final bog stage (Unit 4, 2100 cal years BP – present):

This stage is initiated shortly after climate conditions change to cooler and wetter. *Sphagnum spp*. rapidly increase, but different *Sphagnum* species dominate during this period compared with the first bog stage. The dominating *Sphagnum* species changes throughout the period, indicating less stability. Another interesting aspect is that the sedges does not seem to decrease as prominently as during the first bog stage. This final bog stage appears to be less stable than the first bog stage both regarding bulk density and macrofossil signal (this is more apparent in SM A, probably due to the low resolution of SM B). In SM O a peak in bulk density, Al mass accumulation rate and La mass accumulation rate can be seen at around 1400 cal years BP. This peak is, interestingly, not found at 1400 cal years BP in either SM B or SM A. In the SM B and SM A sequences peaks in bulk density appears slightly before 1400 cal years BP at around 1600 cal years BP. Again, suggesting that the size and complex nature (e.g. different microtopography) of the bog could buffer the internal ecosystem from different driving factors.

Drivers of change and succession:

The duration of the retrogression is seemingly different in SM B and SM A and the ending of the period is vaguer in SM B. But for both cores the change back to an increasingly *Sphagnum* dominated vegetation happens around the same time as the climate shift from Subboreal to Subatlantic, moving from drier conditions into wetter and cooler conditions. Suggesting that once again, the moisture gradient and effective precipitation are important factors for the growth and spreading of bog-like vegetation (e.g. *Sphagnum spp*.). It seems like the small local differences within a bog (e.g. microtopography and variations in the water table associated with that) could have an influence on how allogenic changes are received. The microtopography within a bog ecosystem could be playing a significant part of the bog being able to buffer against allogenic changes. It is likely that autogenic factors are dominant when it comes to the initiation of the fen-bog transition, but that for autogenic succession to happen certain climatic conditions must be meet. In other words, when wetter conditions are favourable the autogenic process can take over and rapid change can occur within the peatland ecosystem moving from fen to bog. Allogenic and autogenic factors appear to always be working together and the dominance between the two varies depending on the state of the peatland. The typical fen-bog succession with the bog stage being final is not always applicable. Even though the bog stage is generally more influenced by autogenic factors it is not always a stable state and retrogression to fen-like conditions do occur. Peatlands are sensitive ecosystems that depending on different attributes (e.g. size, local geology and geomorphology, surrounding vegetation etc.) can be more or less sensitive to lager changes in for example climate conditions.

It is quite plausible that the retrogression period is the consequence of changes in the amount of precipitation due to a drier climate in the broad sense. With *Sphagnum spp.* being very sensitive to changes in the moisture gradient and the height above the water table this is a reasonable explanation. It could also be a period of unstable and fluctuating water tables causing the more fen-like species to have a competitive advantage over *Sphagnum.* With the changing climate we are facing today we are already experiencing more extreme variations with drought and precipitation and these variations will only increase if insufficient actions are taken to change the future we are heading towards. A recent study, already warning about wide spread drying of European peatlands, found that over the last 300 years 69% of the studied peatlands had shifted to drier conditions while only 7% had shifted to wetter conditions (Swindles et al., 2019). This is alarming considering bogs, which are highly dependent on the moisture gradient and effective precipitation, being a CO_2 sink and storing more carbon compared to fens. The drying of peatlands and declining of bog dominated vegetation could be a positive feedback of the already warming climate. For example, the increase of dominance of *Ericaceae* shrubs would further increase the CO_2 fluxes to the atmosphere as the storage of carbon in the peatland would decrease due to higher decomposition rates (Radu & Duval, 2018). *Ericaceae*, as mentioned before, being a drought tolerant species that have the upper hand over *Sphagnum* in a drier and more unstable climate.

Conclusion

It is clear that the peatland development and changes in vegetation in the SM B core at Store Mosse are complex. Moving from a dominance of fen vegetation to bog vegetation during the fen-bog transition taking place at 5800 cal years BP, then moving back to fen-like vegetation dominance during a period of retrogression at around 4100 cal years BP, to gradually shift back to bog-like vegetation dominance starting at 3100 cal years BP. It is likely that the shifts towards bog-like vegetation dominance are driven by autogenic factors being enhanced with the support of allogenic factors (major shifts towards wetter climate conditions) influencing the height above the water table and the moisture gradient. The retrogression period on the other hand, is more likely to a greater extent be influenced by allogenic factors (major shifts towards drier climate conditions) influencing the precipitation and thereby the water table and moisture gradient. This conclusion is drawn based on the typical autogenic succession for peatland being from fen to bog and not vice versa. For a bog to reverse in development allogenic factors are needed to influence such changes. One should be careful to think of bogs as stable and final stages of peatland development. With climate change already happening and increasing in the future causing more extreme drought and precipitation we can have high implications for the peatland ecosystems. Especially worrying given that bogs are CO_2 sinks and peatlands are a part of the positive feedback cycle of climate warming. More research is needed on the dynamics of peatland and their buffering capacity against allogenic changes influencing their development.

Acknowledgement

First of all, a would like to thank my supervisor Malin Kylander, not only for quickly coming up with this project when the initially thought-out project was hindered due to the corona pandemic, but also for helpful feedback and being so supportive and motivating during these strange times of zoom-meetings and working from home. I would also like to thank my supervisor Eleonor Ryberg for all of the zoom-meetings we’ve had, supporting and advising, especially regarding the macrofossils. I would also like to thank Elsa Björnehult Korning for all of the support throughout this project, discussing problems and helping me sustain my motivation during these special circumstances. Lastly, I also want to thank Darius Pakarinen for being always being my mental support, especially during these weeks.

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