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2022-07

Postglacial peatland vegetation succession in Store Mosse bog, south-central Sweden: An exploration of factors driving species change

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Boreal peatlands are facing significant changes in response to a warming climate. *Sphagnum* mosses are key species in these ecosystems and contribute substantially to carbon sequestration. Understanding the factors driving vegetation changes on longer time scales is therefore of high importance, yet challenging since species changes are typically affected by a range of internal and external processes acting simultaneously within the system. This study presents a high-resolution macrofossil analysis of a peat core from Store Mosse bog (south-central Sweden), dating back to nearly 10 000 cal. a BP. The aim is to identify factors driving species changes on multidecadal to millennial timescales considering internal autogenic, internal biotic and external allogenic processes. A set of independent proxy data was used as a comparison framework to estimate changes in the bog and regional effective humidity, nutrient input and cold periods. We found that Store Mosse largely follows the expected successional pathway for a boreal peatland (i.e. lake → fen → bog). However, the system has also been affected by other interlinked factors. Of interest, we note that external nutrient input (originating from dust deposition and climate processes) has had a negative effect on *Sphagnum* while favouring vascular plants, and increased fire activity (driven by allogenic and autogenic factors) typically caused post-fire, floristic wet shifts. These effects interactively caused a floristic reversal and near disappearance of a once-established *Sphagnum* community, during which climate acted as an indirect driver. Overall, this study highlights that the factors driving vegetation change within the peatland are multiple and complex. Consideration of the role of interlinked factors on *Sphagnum* is crucial for an improved understanding of the drivers of species change on short- and long-term scales.

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Peatlands are waterlogged terrestrial ecosystems in which plant and biomass production exceeds the rate of decomposition, resulting in the accumulation of organic-rich material called peat. Peat is made up of partially decomposed plant remains representing the vegetation that was once living on the surface. By accumulating plant remains and capturing surface and groundwater inputs from the surrounding catchment as well as atmospheric deposition, peat archives are rich sources of information of past environmental change (Rydin & Jeglum 2013) often spanning the Holocene in previously glaciated landscapes. Given the abundance of organic material, these archives can be easily dated and are particularly suitable for macrofossil analysis – a well-established palaeoecological method commonly used in palaeoclimatic and environmental reconstructions (e.g. Birks & Birks 1980; Mauquoy *et al.* 2002; Mauquoy & van Geel 2007; Birks 2013; Väliranta *et al.* 2007, 2015, 2017).

Northern peatlands store approximately one-third of the global soil carbon (Bubier *et al.* 2007; Beilman *et al.* 2008; Oke & Hager 2017). Divided into two main types based on hydrological, chemical and botanical differ-ences, these ecosystems often start as minerotrophic fens which undergo a transition into ombrotrophic bogs, where fens tend to accumulate less carbon and have higher decomposition rates compared with bogs (Vitt & Wieder 2008; Väliranta *et al.* 2017; Loisel & Bunsen 2020). These so-called fen–bog transitions (FBTs) influence vegetation composition and biomass growth within the system, and their geographical distribution is largely considered to be driven by climatic parameters (e.g. temperature and precipitation gradients; Väliranta *et al.* 2017; Loisel & Bunsen 2020).

Sphagnum mosses are abundant species in ombrotrophic peatlands (bogs) and are often described as ecosystem engineers, as they make their surrounding environments wet, acidic and anoxic, while promoting peat accumulation through their decomposition-resistant qualities (Robroek *et al.* 2007a, b; de Jong *et al.* 2010; Rydin & Jeglum 2013; Johnson *et al.* 2014). As a result, *Sphagnum* mosses contribute substantially to the accumulation of organic matter and play a key role in carbon sequestration (Bubier *et al.* 2007; Robroek *et al.* 2007a, b). Since *Sphagnum* species differ in growth, decomposition rates and water retention

capacity, changes in species composition are likely to affect ecosystem functioning (e.g. peat formation and carbon sequestration; Robroek *et al.* 2007b; Chaudhary *et al.* 2018).

High-latitude ecosystems are expected to be strongly affected by climate change in the future with higher temperatures and changes in precipitation and evapotranspiration (e.g. increased winter precipitation and summer evapotranspiration; Robroek *et al.* 2007b; Väliranta *et al.* 2017; Chaudhary *et al.* 2018). Studies have suggested that certain *Sphagnum* species may struggle to adapt, particularly wetter hollow species when subjected to drier habitat conditions since they are more sensitive to desiccation (Rydin 1993; Robroek *et al.* 2007a; Vitt & Wieder 2008), potentially resulting in species loss (e.g. through bog microtopography changes and diminished taxonomic biodiversity; Robroek *et al.* 2007a). The underlying assumption is, however, that effective humidity (precipitation minus evapotranspiration), and hence climate, is the most important driver explaining the abundance and distribution of *Sphagnum* species in northern peatlands (e.g. species abundance and changes over time). In fact, hydrology is just one of several factors controlling peatland vegetation. Both internal (autogenic) and external (allogenic) factors can control peatland species distribution. Broadly speaking such factors include: (i) internal autogenic successional processes, e.g. peatland initiation, vertical peat growth, shift to ombrotrophy and water table changes (i.e. hydrological changes; Tuittila *et al.* 2007; Ruppel *et al.* 2013; Väliranta *et al.* 2017); (ii) internal biotic processes (e.g. interspecific competition and competitive balance in terms of positioning above water table, space, and nutrients availability; Rydin 1993; Bubier *et al.* 2007; Robroek *et al.* 2007a, b; Laine *et al.* 2014; Vicherova *et al.* 2015); and (iii) external allogenic climatic processes, e.g. temperature, effective precipitation, and hydrology (Mauquoy *et al.* 2002; Robroek *et al.* 2007a, b; Tuittila *et al.* 2007; Tahvanainen 2011; Chaudhary *et al.* 2018).

Some factors are not readily classified into just one of these categories, however. For example, peatland hydrological changes are affected by internal autogenic processes in terms of vertical peat growth as a successional process and local microtopographic relationships affecting the position of the water table directly (Väliranta *et al.* 2007, 2017; Ruppel *et al.* 2013; Chaudhary *et al.* 2018), as well as climate as an allogenic driver (Hilbert *et al.* 2000; Tahvanainen 2011). Likewise, many factors are interlinked, which makes it difficult to isolate a single driving factor. For example, internal autogenic processes can be triggered by allogenic effects (e.g. changes in moisture level may influence the shift from fen to bog; Loisel & Bunsen 2020). Fire activity is also driven by allogenic processes in that the climate creates dry conditions, promoting potential ignition, as well as autogenic processes in terms of litter production and fuel availability (Tuittila *et al.* 2007; Sillasoo *et al.* 2011;

Väliranta *et al.* 2017). Thus, differentiating between several factors, many of which operated simultaneously, in order to constrain the allogenic or autogenic effects within the peatland is challenging (see Payette 1988; Magyari *et al.* 2001; Hughes & Dumayne-Peaty 2002; Ellis & Rochefort 2006; Tuittila *et al.* 2007) and few studies have attempted to do this at the species level.

Store Mosse ("The Great Bog") in south-central Sweden represents an extensive (77 km^2) and well-studied peatland, first mentioned in scientific texts as early as 1932 (Granlund 1932). A number of studies looking at recent processes have been carried out at this site (e.g. Hansson *et al.* 2014; Robroek *et al.* 2016), but most focus has been on longer-term changes. This is because material in the southern bog complex began accumulating as early as ~10 000 cal. a BP, providing a sequence that covers nearly the entire Holocene (Svensson 1988a; Malmer *et al.* 1997; Kylander *et al.* 2013, 2016, 2018). Much of what we know about different phases of the peatland development comes from the macrofossil work of Svensson (1988a, b), but these data are not well constrained temporally, with just six ^{14}C dates available on a 5.5-m-long sequence, and four ^{14}C dates available on a 4.0-m-long sequence from the area. In 2008 a sequence (SM$_{2008}$) was collected in order to examine the palaeoenvironmental changes over the last ~9000 years. This work focused in particular on the inorganic fraction of the peat to reconstruct past changes in atmospheric dust deposition (Kylander *et al.* 2013, 2016, 2018). A remarkable high peat accumulation event (HPAE, between ~5420 and ~4550 cal. a BP; Kylander *et al.* 2013, 2016, 2018), which occurred in parallel with a humid period and the input of minerals richer in K, Ca and P, all important plant nutrients, was identified (Kylander *et al.* 2013, 2016). Low-resolution molecular analyses across the HPAE suggested the presence of *Sphagnum* but this has not yet been confirmed by detailed macrofossil analyses (Kylander *et al.* 2018). More recent work on the same sequence examined the molecular composition (i.e. polysaccharides, aromatics and lignin, aliphatics, nitrogen-rich compounds and organic acids) of the peat organic matter fraction using infrared spectroscopic techniques. Peat decomposition, strongly controlled by bog hydrology, showed two main patterns. The first was a long-term trend highly correlated to peat age (Martinez-Cortizas *et al.* 2021). The second, short-term changes showed periods of increased decomposition that largely corresponded to drier climate periods and subsequent effects on bog hydrology (Martinez-Cortizas *et al.* 2021).

This paper aims to identify factors driving species changes on multidecadal to millennial timescales through high-resolution macrofossil analysis of a new peat sequence collected from Store Mosse in 2018 (SM-A$_{2018}$), extending previous work by ~1000 years. The specific objectives were: (i) to establish a high-resolution plant macrofossil analysis record of the peatland development; and (ii) to identify and assess the factors driving

species changes within the record in terms of internal (autogenic and biotic) and external (allogenic) drivers, in order to disentangle the most important factors controlling the species change on longer timescales, moving beyond those used in contemporary studies. Previous work on the SM_{2008} sequence provides within-site proxies that allow us to constrain allogenic factors and evaluate the assumption that climate is the main driver of changes in peatland species composition. Specifically, local changes in effective humidity are described by decomposition proxies (bulk density, humification, and spectroscopic data) while regional shifts in the hydrological climate are described by changes in atmospheric mineral dust fluxes (Kylander *et al.* 2016; Martinez-Cortizas *et al.* 2021). From the same sequence, we can also compare the changes in nutrient input as described by key indicator elemental ratios (Kylander *et al.* 2018). Finally, past shifts in temperature, being spatially less heterogeneous than effective humidity, can be gleaned using a Holocene temperature compilation (Wanner *et al.* 2011).

Study setting

Store Mosse is an ombrotrophic bog located in south-central Sweden (Fig. 1; 57°13′38.22′′N, 13° 55′10.86′′E, ~160–170 m a.s.l.; Svensson 1988a, b; Malmer *et al.* 1997; Kylander *et al.* 2013, 2016, 2018). The area, which was deglaciated by ~13 900 cal. a BP, is characterized by granitic bedrock overlain by sediments of the former ice lake Fornbolmen (Lundqvist & Wolfharth, 2001; Kylander *et al.* 2013, 2016, 2018). Isostatic rebound caused Fornbolmen to drain by tipping it to the south, leaving an oligotrophic lake which was eventually overgrown by fen vegetation (Svensson 1988b; Kylander *et al.* 2013). Peat formation began around ~9000 cal. a BP (Svensson 1988a; Malmer *et al.* 1997; Kylander *et al.* 2018).

Material and methods

General postglacial development of Store Mosse

Early macrofossil research at Store Mosse established three successional phases within the peatland: oligotrophic lake, minerotrophic rich fen and ombrotrophic bog (Svensson 1988a, b). The introduction of minerotrophic *Sphagna* occurred ~9000 cal. a BP and eventually led to ombrotrophy between ~6000 and ~5000 cal. a BP (Svensson 1988b; Malmer *et al.* 1997; Kylander *et al.* 2013). The ombrotrophic bog includes three main *Sphagnum* stages: *fuscum*, *rubellum/fuscum* and *magellanicum* stages, separated by two highly humified peat layers (Svensson 1988a, b; Malmer *et al.* 1997). Today, Store Mosse is a relatively open, raised bog with few trees (*Pinus* sp.). It has a maritime climate (Länsstyrelsen i Jönköpings län 2012) and is dominated by *Sphagnum* hummock, hollow and lawn microtopography, including

ericaceous dwarf shrubs (*Andromeda* sp., *Vaccinium* spp., *Calluna vulgaris*, *Erica tetralix*), sedges *sensu lato* (*s.l.*) (*Rhynchospora alba*, *Eriophorum* spp.) and lichens (*Cladonia* spp.). There are numerous fossil sand dunes in the area with the string of dunes that bisect Store Mosse emplaced between 8 and 6 ka (Svensson 1988a; Kylander *et al.* 2013, 2018; Bjermo 2019). Previous research has reported no fires, hiatuses or other disturbances in the successional development (Svensson 1988a, b; Malmer *et al.* 1997; Kylander *et al.* 2013).

Previously published elemental and spectroscopic data from Store Mosse

In order to constrain allogenic factors with the potential to control changes in species distribution, we turned to previously published bulk density, humification, and elemental and molecular (infrared spectroscopy) data from the SM_{2008} peat sequence (Kylander *et al.* 2013, 2016, 2018; Martinez-Cortizas *et al.* 2021), presented in this study with an improved age model made using the R_Bacon package (Blaauw & Christen 2011), which utilizes the IntCa13.14C calibration curve (Reimer *et al.* 2013). Peat sequence SM_{2008} (Figs 2A, 3A) was subsampled at 1-cm resolution and the bulk density (Fig. 2B) for each sample was established using a tracing method. Humification was measured using a colorimetric method modified from Blackford & Chambers (1993) (Fig. 2C). Spectroscopic data were obtained using an FTIR-ATR in the mid-infrared region (4000–400 cm^{-1}). Principal component analysis was performed on selected absorbances and change-point modelling was applied to the records of scores to determine a precise chronology of the changes. We use the detrended principal component 1 (dCP1) to represent changes not associated with long-term age related changes in decomposition (Fig. 2D). Eight time intervals of within bog wet periods have been identified that are associated with allogenic signalling: 8.7–8.5, 8.3–8.1, 7.9–7.0, 5.6–4.7, 3.9–3.5, 3.0–2.4, 2.1–1.4 and 0.8–0.4 ka (Fig. 2, shaded boxes). While humification and decomposition may be affected by the composition of the vegetation, bulk density, humification and dCP1 are all different expressions of these processes (physical compaction of material; chemical extraction of humic acids; and the amount of decomposition-resistant organic matter moieties such as lignin, aliphatics and organic acids, respectively). In previous publications, each of the proxy records has been linked to the local and regional hydrology through the interpretation of proxies from the same record as well as through comparison with other records (Kylander *et al.* 2013; Martinez-Cortizas *et al.* 2021). By combining the three proxies to make a local effective humidity stack, we are able to cope with the limitations (i.e. the possible confounding effects of allogenic and autogenic factors) of the individual proxies – agreement across all three of these proxies provides confidence in the defined low decomposition intervals.
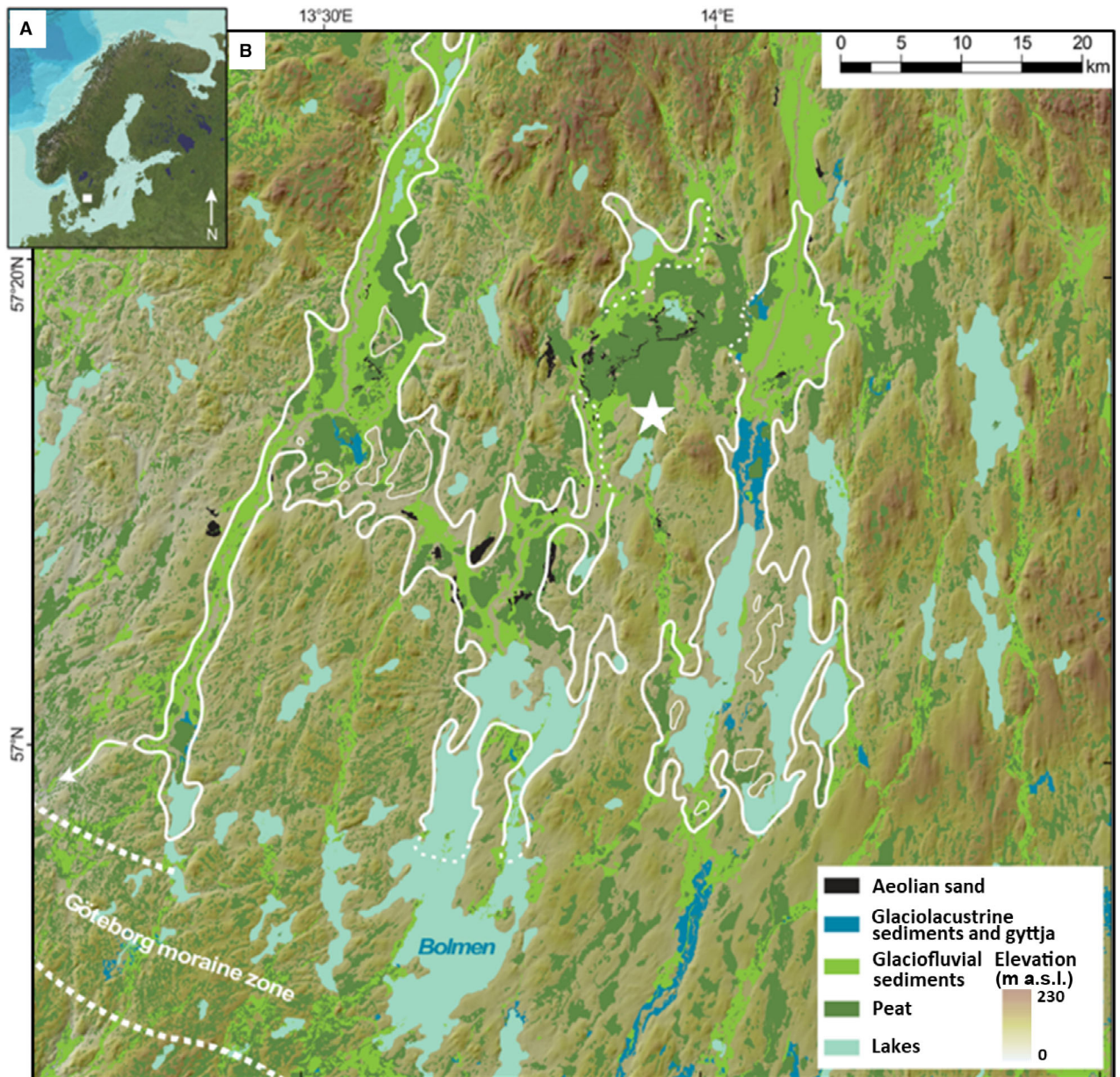
Fig. 1. Store Mosse in south-central Sweden (sampling location indicated by the star), in the southern portion of Scandinavia (inset map). The white lines represent the modelled extent of the former ice lake Fornbolmen (solid lines indicating greater degree of certainty than the dashed lines).

Changes in regional effective humidity at Store Mosse are reconstructed using Al and Sc elemental mass accumulation rates from the SM_{2008} peat sequence, which were calculated using elemental concentration data measured by Inductively Coupled Plasma-Mass Spectrometry/Atomic Emission Spectrometry (ICP-MS/AES) and the peat accumulation rates (peat-AR). Mineral dust deposition increased during regionally dry periods which have been dated to: 7.0–5.3, 3.6–3.4, 3.2–3.0, 2.4–2.2, 2.1–1.8 and 1.4–1.1 ka (Fig. 3B, C, shaded boxes). Based on the same elemental dataset, changes in key rare earth element ratios signal a change in the character of the mineral dust being deposited at Store Mosse. Three intervals of increased nutrient input have been inferred based on $[Eu/Eu]_{UCC}$ (inferring K and Ca input) and La/Lu (inferring P input), and are thus interpreted as signalling fertilization events: 5.7–4.2, 1.9–1.3 and 1.0–0.3 ka (Fig. 3D, E, shaded boxes).

Sampling

The sampling site for this study is located in the southern part of the bog complex at one of the deepest points of the
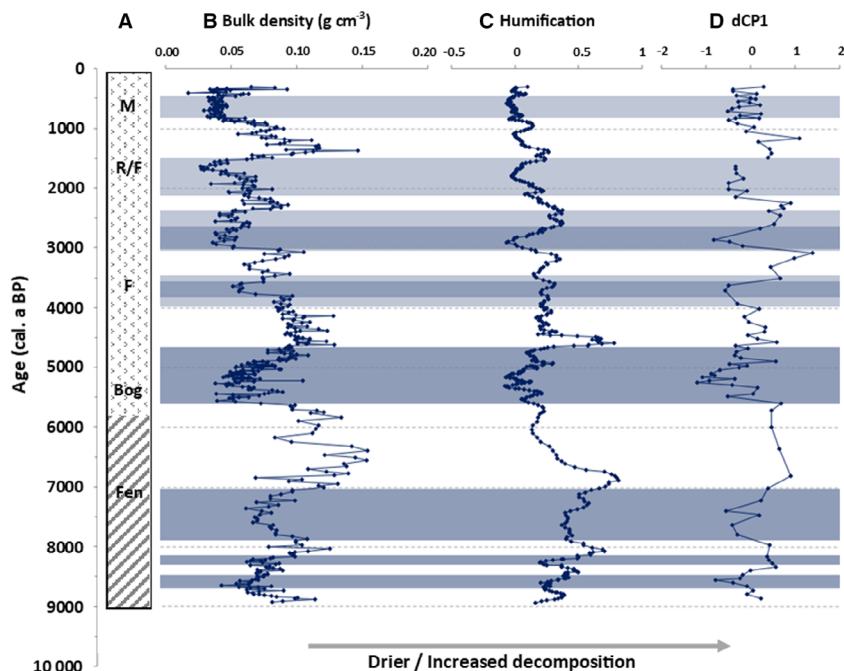
Fig. 2. A–D. Using an improved age model, the bog wetness periods in Store Mosse (peat sequence SM_{2008}) are represented by eight time intervals (shaded blue) after Martinez-Cortizas *et al.* (2021). Darker shades indicate greater agreement across the proxies. F = *Sphagnum fuscum*; R/F = *Sphagnum rubellum*/*Sphagnum fuscum*; M = *Sphagnum medium*.

deposit (57°13′38.22″N, 13°55′10.86″E), in close proximity (less than 100 m) to SM_{2008}. Three new sequences were collected during fieldwork in November 2018 (denoted SM-A, SM-B and SM-C) using a Russian corer (1-m-long, 10-cm-wide barrel). The work presented here focuses exclusively on the master core $SM\text{-}A_{2018}$. $SM\text{-}A_{2018}$ comprises nine consecutive 1-m cores with 25-cm overlap, from two alternating bore holes in a lawn habitat dominated by *Sphagnum medium* and *Sphagnum balticum*. The cores were then subsampled into 1-cm slices and stored in a cold room.

Core alignment and chronology

From each subsampled slice, a cube of peat (~1 cm³) was freeze-dried and weighed for bulk density at 1-cm resolution. The bulk density was obtained by measuring each side of the cube using a calliper to calculate the volume more precisely, then dividing the mass of each sample by this volume. The bulk density was then used to align the cores and for a composite depth of 678 cm.

Sixteen samples of macrofossil remains were sent for radiocarbon dating at the Tandem Laboratory, Uppsala University (Ua), Sweden (Table 1). An age–depth model was created using R_Bacon (Blauuw & Christen 2011), which utilizes the IntCa13.14C calibration curve (Reimer *et al.* 2013) (Fig. 4). Using the bulk density data and the 14C dates from the age model, peat-ARs were calculated at 1-cm resolution throughout the

sequence by dividing the total mass (g m^{-2}) by time between each sample, presented as g m^{-2} a^{-1}.

Plant macrofossil analysis

A total of 119 samples were analysed for plant macrofossils at intervals of ~5 cm throughout the peat sequence. A 5 cm³ sample of fresh peat was gently cleaned using a 120-µm mesh sieve under running water (no pre-analysis treatment was required). The samples were examined for species coverage percentages in a Petri dish under a stereomicroscope (magnification ranging between 10 and 40×), using graph paper with a 10 × 10 mm grid as scale, according to methods described by Mauquoy & van Geel (2007), Väliranta *et al.* (2007, 2017) and Birks (2013). High-power microscope analyses were employed using a modified Quadrat Leaf Count protocol for *Sphagnum* species identification based on branch and stem leaves examined under microscope, using Laine *et al.* (2018) as the key, where the *Sphagnum* coverage percentage was higher than 15% (Mauquoy & van Geel, 2007; Väliranta *et al.* 2017).

The samples were examined for coverage percentages in the most common plant groups, such as *Cyperaceae, Ericaceae* (roots), *Sphagnum* and brown moss remains, along with other vascular plants when present. The unidentifiable organic matter (UOM) coverage percentage, also called amorphous organic matter, was used as an indicator for degree of peat
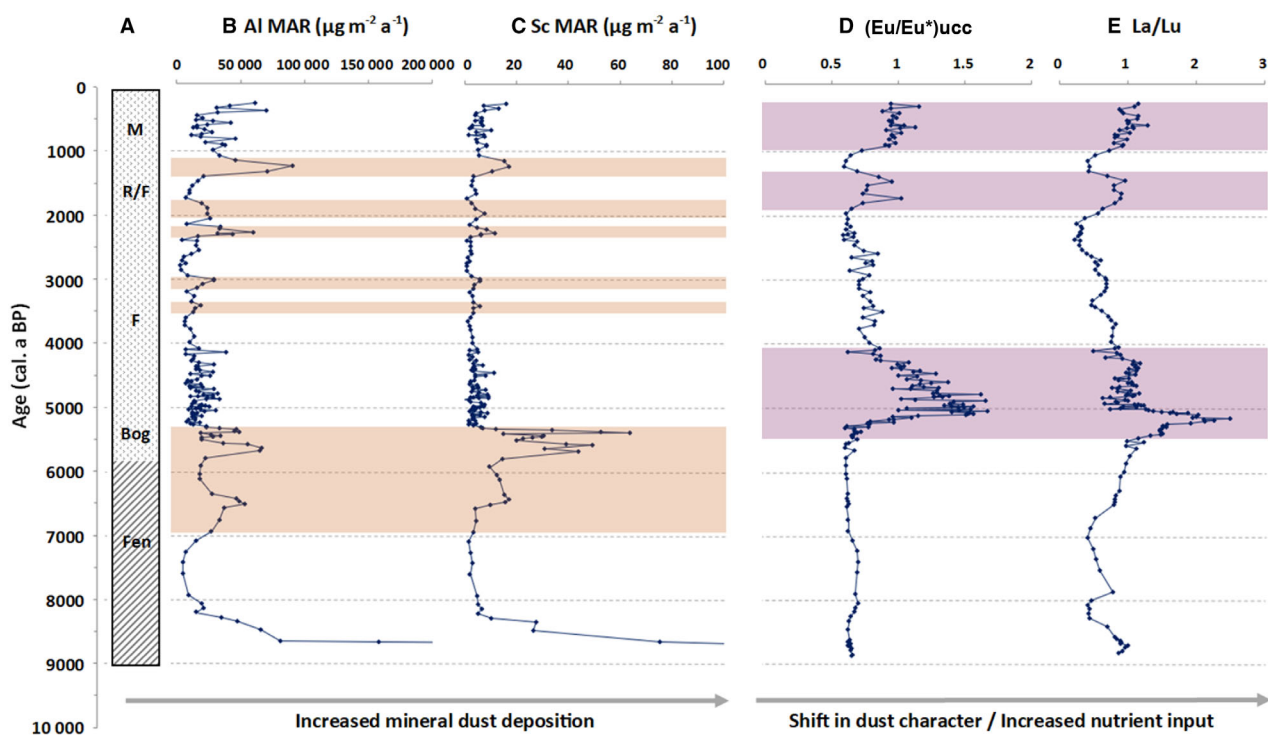
Fig. 3. A–E. Using an improved age model, the regionally dry period signals within Store Mosse (peat sequence SM$_{2008}$) are represented by six time intervals (B, C; orange shaded boxes) of increased mineral dust deposition, and periods of increased nutrient input represented by three time intervals (D, E; purple shaded boxes) of increased mineral dust deposition, based on previously published data from Kylander *et al.* (2013, 2016, 2018). F = S. *fuscum*; R/F = S. *rubellum/s. fuscum*; M = S. *medium*.

decomposition as described in Gałka *et al.* (2013, 2018). *Ericaceae* seeds and leaves were counted in absolute numbers. Pieces of charcoal were categorized according to size – (i) larger than 1 mm or (ii) smaller than 1 mm – and counted in absolute numbers. The presence of wood and bark remains was noted on a tripartite scale of rare (+), occasional (++) and

abundant (+++). The phase names within the palaeobotanical record are based on microhabitat preferences and/or major shifts in vegetation (e.g. dry denotes hummock species, wet denotes hollow and lawn species and floristic reversal denotes a major shift in vegetation composition specifically referring to vegetation associated with typical bog development

Table 1. Accelerator Mass Spectrometry (AMS) ^{14}C measurements from SM-A$_{2018}$, Store Mosse. The calibrated age ranges were obtained using the IntCal[13–14]C calibration curve (Reimer *et al.* 2013) and the age–depth model was created using the software R_Bacon (Blauuw & Christen 2011).

| Sample depth (cm)	Laboratory ID	Dated material	Age ([14]C a BP ±1 SD)	Calibrated age range (cal. a BP)
65	Ua-61463	*Sphagnum* stems and leaves, wood remains	683±30	635–682
141	Ua-61464	*Sphagnum* stems and leaves	1093±30	936–1060
176	Ua-63973	*Sphagnum papillosum* stems and leaves, wood remains	1717±28	1559–1700
212	Ua-61466	*Eriophorum vaginatum* remains, *Sphagnum* stems, wood and bark remains	2111±31	1995–2153
254	Ua-63974	*Eriophorum vaginatum* remains, wood remains	3114±29	3240–3390
265	Ua-61468	*Equisetum* remains, wood and bark remains	3515±32	3698–3876
295	Ua-63975	*Eriophorum vaginatum* remains, wood remains, charcoal	4039±30	4423–4580
329	Ua-61469	*Sphagnum* stems, wood remains	4389±32	4864–5044
390	Ua-63976	*Sphagnum* stems and leaves	4496±31	5042–5298
416	Ua-61470	*Sphagnum* stems	4521±33	5049–5195
450	Ua-63977	Terrestrial mix (*Vaccinium* spp. leaves, wood remains)	4490±31	5038–5297
489	Ua-61472	Terrestrial mix (*Betula nana* bark and wood), charred plant remains	5860±34	6603–6752
514	Ua-63978	Bryophyte and *Eriophorum vaginatum* remains	6000±35	6748–6935
573	Ua-61473	Wood and bark (conifer), *Equisetum* spp. and Bryophyte remains	7658±37	8393–8539
632	Ua-61475	*Betula* seeds, *Equisetum* spp. remains	8067±38	8858–9092
677	Ua-61476	*Equisetum* spp. remains	8641±47	9530–9700
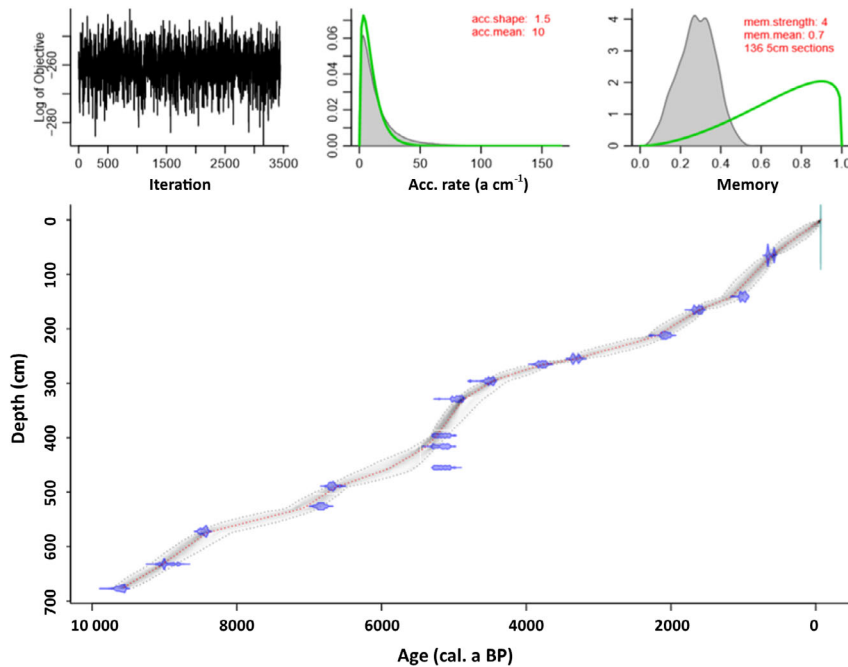
Fig. 4. SM-A$_{2018}$ age-depth model created using R_Bacon, based on 16 age dates of macrofossil material outlined in Table 1. The calculated average peat growth is relatively constant at ~14 a cm^{-1}, with the exception for the distinct increase (indicated by the steep curve) in peat thickness between ~5500 and ~5000 cal. a BP.

and autogenic succession, although not necessarily representing a reversed autogenic successional development).

Results

Age–depth model

Plant macrofossil remains were picked from 16 samples and analysed for Accelerator Mass Spectrometry (AMS) radiocarbon dating (Table 1) with the resultant dates used in the age–depth model (Fig. 4). The model shows a relatively constant average peat growth (~14 a cm^{-1}); however, it includes a notable period of extremely rapid growth between ~5500 and ~5000 cal. a BP (~7 a cm^{-1}) indicated by the steep section of the curve at that time.

Peat properties

The bulk density ranges between 0.03 and 0.37 g cm^{-3} with an average of 0.09±0.82 g cm^{-3} (n = 668, 2σ; Fig. 6). The values are highest in the bottom part of the sequence (678 cm; 9595 cal. a BP) and drop sharply at ~9500 cal. a BP followed by a gradual decrease until ~8000 cal. a BP. Two peaks are visible between ~8000 and ~7200 cal. a BP and ~6800 to ~5800 cal. a BP with the latter reaching 0.22 g cm^{-3}. A relatively stable period of low values follows until ~4500 cal. a BP (with the exception of a peak at ~4800 cal. a BP). A sharp increase at ~4400 cal. a BP marks the start of a ~1700-year period

characterized by highly fluctuating values which eventually drop at ~2800 cal. a BP. From here on towards the present, the values are mainly low but include distinct, repeating peaks (some reaching values of 0.14 g cm^{-3}). Note that the top 10 cm of the sequence were excluded in this analysis.

The peat-ARs range from 17 to 149 g m^{-2} a^{-1} with an average of 72±59 g m^{-2} a^{-1} (n = 660, 2σ, excluding the bottommost samples which are composed of highly compacted minerogenic material; Fig. 6). The high values at the base of the sequence decrease gradually from ~9500 cal. a BP before dropping sharply at ~8400 cal. a BP. Low values remain until ~7100 cal. a BP when a sharp increase occurs (from 27 to 87 g m^{-2} a^{-1}), after which the values gradually increase until ~6700 cal. a BP. The values then decrease over the next ~1000 years. After stabilizing at around 40–50 g m^{-2} a^{-1} at ~5700 cal. a BP a significant increase in peat-AR occurs, reaching values of 140 g m^{-2} a^{-1}. This increase occurs between ~5400 and ~4750 cal. a BP and is followed by a brief drop to 32 g m^{-2} a^{-1}. A small peak is visible between ~4700 and ~4500 cal. a BP. From here until ~3100 cal. a BP the values fluctuate between 25 and 94 g m^{-2} a^{-1}, although during this period overall the peat-AR values decrease. A small peak is visible between ~3100 and ~2800 cal. a BP, after which several distinct, repeating peaks of increased peat-AR are visible towards the present (some reaching values of 149 g m^{-2} a^{-1}). Note that the top 10 cm of the sequence were excluded in this analysis.
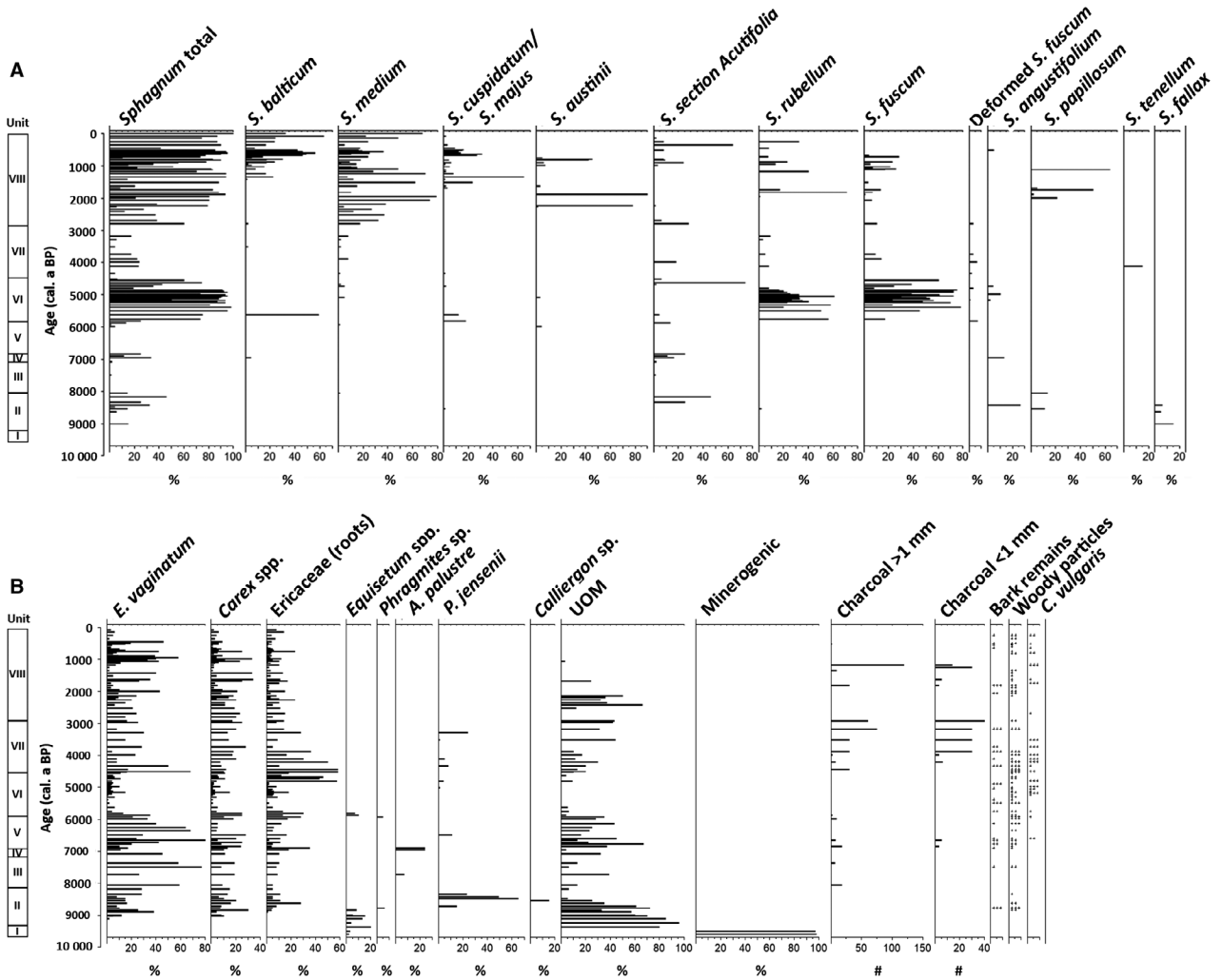
Fig. 5. Store Mosse-A$_{2018}$ macrofossil diagram showing (A) the total Sphagnum proportion percentages and individual species identified, followed by (B) vascular plants, other bryophytes as proportion percentages and macroscopic charcoal remains as counts (along with abundance/presence of bark, wood particles and *Calluna vulgaris*). Stratigraphic units (I–VIII) are based on visual zonation of dominant plant groups and changes in peat properties throughout the peat sequence.

Vegetation changes throughout SM-A$_{2018}$

Based on visual zonation of dominant plant groups, aided by the peat properties and vegetation transitions, the palaeobotanical record was divided into five vegetation phases and eight stratigraphic units (see Material and Methods for description of phase names). These are from the bottom towards the current surface and top of the peat sequence: the Minerogenic Phase (Unit I), the Herbaceous Phase (Units II–V), the Dry Sphagna Phase (Unit VI), the Floristic Reversal Phase (Unit VII) and the Wet Sphagna Phase (Unit VIII) (Figs 5, 6).

The Minerogenic Phase (Unit I; 678–648 cm; ~9595 to 9225 cal. a BP) consists of lake sediments and *Equisetum* spp. remains. This is followed by the Herbaceous Phase (Units II–V; 648–454 cm; ~9925 to 5865 cal. a BP), which is dominated by sedge remains (up to 80% in some sections) occurring together with spells of true mosses

(up to 60% in some sections; *Polytrichum jensenii* and *Calliergon* sp.) and small amounts of *Sphagnum* spp. (cf. *Sphagnum angustifolium*, *Sphagnum fallax* and *Sphagnum papillosum*, as well as *Sphagnum* section *Acutifolia*, up to 40% in some sections). The section between 648 and 565 cm (Unit II; ~9225 to 8145 cal. a BP) represents a transition from gyttja with *Equisetum* spp. remains into sedges (*s.l.*). The presence of macroscopic charcoal at ~8100 cal. a BP (Fig. 6, represented by black lines) precedes a section dominated by *Eriophorum vaginatum* remains (Unit III; 565–532 cm; ~8145 to 7155 cal. a BP) which includes an additional presence of macroscopic charcoal at ~7400 cal. a BP. The section between 532 and 514 cm (Unit IV; ~7155 to 6905 cal. a BP) is characterized by an increase in bryophyte remains (*Aulacomnium palustre*, *S. angustifolium* and *S.* section *Acutifolia*) and the presence of macroscopic charcoal at ~6900 cal. a BP. This is followed by a section that contains little to no
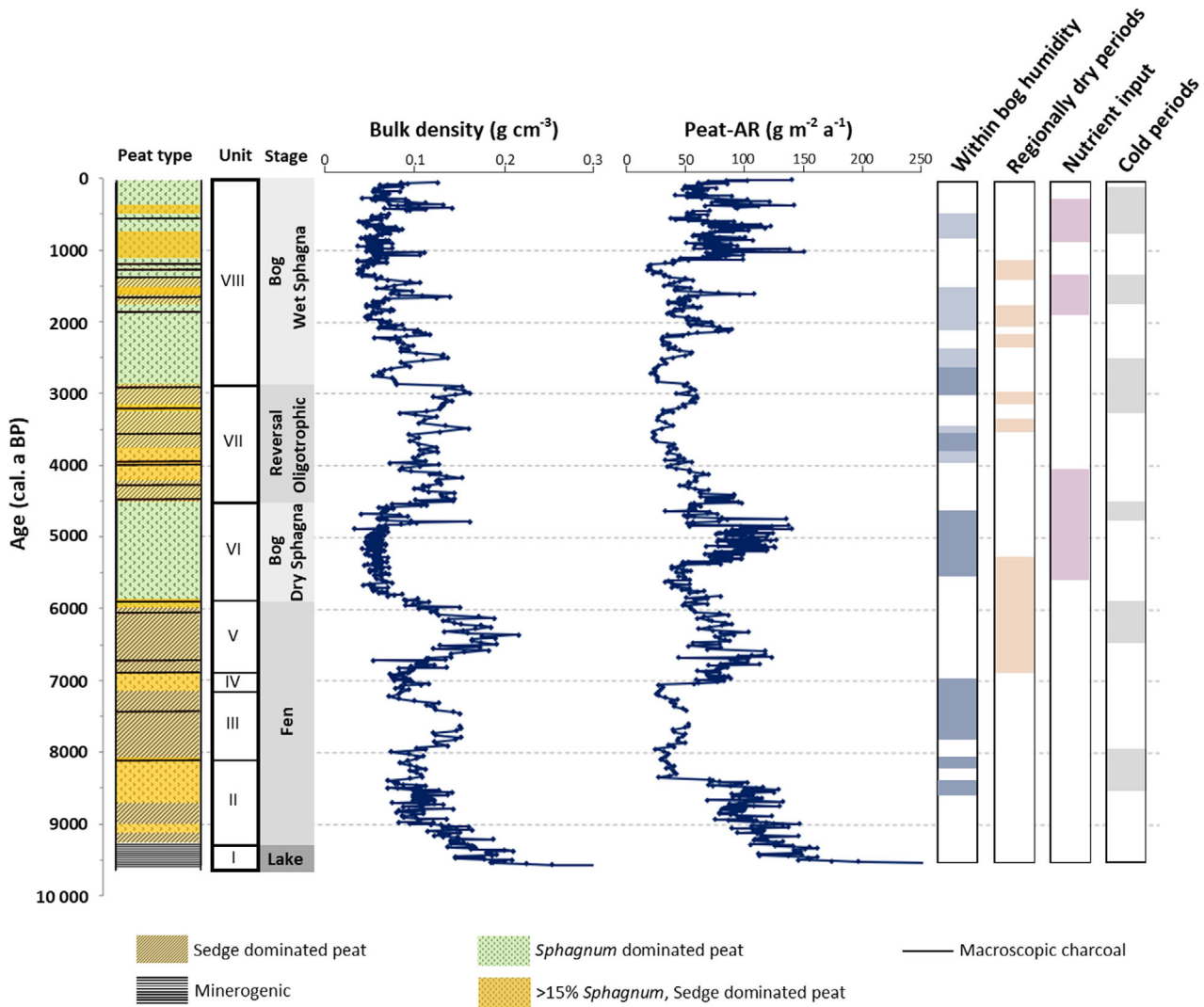
Fig. 6. Summary figure of the Store Mosse-A$_{2018}$ results (macrofossil analysis and peat properties). The parameters used for assessing the controlling factors on species change within Store Mosse from SM$_{2008}$ include within bog humidity (represented in blue, based on Fig. 2), regionally dry periods (represented in orange, based on Fig. 3B, C), nutrient input (represented in purple, based on Fig. 3D, E), and cold periods from the Holocene (represented in grey; Wanner *et al.* 2011). The macrofossil data was acquired from the SM-A$_{2018}$ core and while the charcoal data is also from SM-A$_{2018}$, we consider this to represent within bog and local effective humidity.

Sphagnum but rather is dominated by remains of *E. vaginatum* and *P. jensenii* (Unit V; 514–454 cm; ~6905 to 5865 cal. a BP). Additional macroscopic charcoal is visible at ~6800 and ~6000 cal. a BP. After that, a short section including *Phragmites* and *Equisetum* spp. occurs, concluding the Herbaceous Phase.

The Dry Sphagna Phase (Unit VI; 454–301 cm; ~5865 to 4530 cal. a BP) is dominated almost exclusively by *Sphagnum fuscum* and *Sphagnum rubellum* until ~4700 cal. a BP. The amount of *C. vulgaris* and dwarf shrubs (*s.l.*) remains increases significantly between ~4800 and ~4400 cal. a BP and stays high across the transition into the Reversal Phase (Unit VII; 301–238 cm; ~4530 to 2855 cal. a BP). In the Floristic Reversal Phase *S. fuscum* and *S. rubellum* are replaced by *E. vaginatum* and sedges (*s.l.*), together with *S. angustifolium* and *S. tenellum*. *Polytrichum jensenii* was observed at some depths (Fig. 5). Several occurrences of macroscopic charcoal occur between ~4400 and ~2900 cal. a BP. The Wet Sphagna Phase II (Unit VIII; 238–0 cm, ~2855 cal. a BP to present) includes bog *Sphagna* dominated by *S. medium*, *S. balticum* and *Sphagnum cuspidatum/majus*, alternating with *Sphagnum austinii* and *S. Acutifolia*. Between ~1900 and ~300 cal. a BP macroscopic charcoal particles are found at several depths, most of which are followed by brief sections dominated by *E. vaginatum* and sedges (*s.l.*) and in some cases *S. papillosum* is also present. From ~300 cal. a BP to the present, the assemblages are dominated by lawn bog taxa *S. medium* and *S. balticum*.

Discussion

Our results indicate that multiple factors have affected species change interactively throughout the sequence. We first discuss the peatland development from this study (SM-A$_{2018}$). Then we review the results of previous studies with specific reference to the allogenic proxies (i.e. the combined local effective humidity stack (Fig. 2), atmospheric dust deposition and external nutrient input (Fig. 3) from SM$_{2008}$), as well as Holocene cold periods (from Wanner *et al.* 2011). Using these proxies as a comparison framework (Fig. 6, columns on the right), we then assess the drivers of species changes within the peatland in terms of (i) internal autogenic (successional) factors, (ii) internal biotic factors and (iii) external climatic factors.

Peatland development

The peat properties and the palaeobotanical characteristics in sequence SM-A$_{2018}$ represent five stages of peatland development (based on the five vegetation phases): Lake Stage (Unit I), Fen Stage (Units II–V), Bog Stage – Dry Sphagna (Unit VI), Oligotrophic Reversal (Unit VII) and Bog Stage – Wet Sphagna (Unit VIII) (Fig. 6).

Lake Stage (Minerogenic Phase); Unit I (678–648 cm; ~9595 to 9225 cal. a BP). – The high bulk density at the bottom of the sequence results from the denser, abundant mineral material, which also explains the high peat-AR values in this part of the sequence. This unit represents the end of an *Equisetum* lake stage with accumulation of peat starting from ~9300 cal. a BP, and corresponds to the end of an oligotrophic lake stage previously defined in Svensson (1988a, b). This most likely reflects an autogenic (succession) via infilling processes (Ruppel *et al.* 2013; Väliranta *et al.* 2017) linked to basin topography and drainage during Early Holocene warming (Wanner *et al.* 2011; Väliranta *et al.* 2015) (Fig. 6). Note that Unit I is not present in the previously published data from SM$_{2008}$ owing to different basal depths.

Fen Stage (Herbaceous Phase); Unit II (648–565 cm; ~9225 to 8145 cal. a BP). – The bulk density and peat-AR show relatively constant and generally low values during Unit II except for a distinct drop in peat-AR before the transition into Unit III. This unit initially reflects a sedge-rich habitat and a higher percentage of UOM and gradually incorporates greater amounts of oligotrophic to mesotrophic *Sphagna* (*S. fallax*, *S. angustifolium* and *S. papillosum*) along with *Polytrichum* sp. This increase in recalcitrant *Sphagna* (*S. angustifolium*, *S. fallax* and *S. papillosum*) between ~8800 and ~8000 cal. a BP explains the lower bulk density values (Malmer *et al.* 2003; Rydin & Jeglum 2013) and can be linked with a cold period (8.2 ka cold event; Wanner *et al.*

2011; Fig. 6). The 8.2 ka cold event is associated with both dry and wet climate conditions depending on geographic location (Alley & Agustdottir, 2005; Seppä *et al.* 2005; Wanner *et al.* 2011). The 8.2 ka cold event appears to be locally dry at Store Mosse which potentially promoted a small increase in ombrotrophic *Sphagna* (*S. Acutifolia*) at the end of this period (Unit II), although the lower rates of atmospheric dust deposition at this time also suggests relatively higher effective humidity regionally. The appearance of *Sphagna* at this time represents typical postglacial successional processes with alternating assemblages of *Sphagna* and other pioneering taxa (Ruppel *et al.* 2013; Piilo *et al.* 2020 and references therein). This study (SM-A$_{2018}$) suggests that the paludification process was initially triggered by generally wetter conditions of the Early Holocene (Seppä *et al.* 2005), which led to establishment of minerotrophic *Sphagna*, in which the recalcitrant *Sphagnum* litter and initially warmer climate enhanced peat growth (Yu 2012) (Fig. 6).

Fen Stage (Herbaceous Phase); Unit III (565–532 cm; ~8145 to 7155 cal. a BP). – The bulk density values increase during Unit III while peat-AR remain low. The vegetation represents a shift to sedge-rich habitat with higher UOM content and increased decomposition as a result of the vascular plant-rich vegetation assemblage (Vitt & Wieder 2008; Gałka *et al.* 2013). Abundant *E. vaginatum* remains (peaking ~7400 cal. a BP) suggest oligotrophic conditions at the time (Hughes & Dumayne-Peaty 2002; Väliranta *et al.* 2017). The lower input of atmospheric dust deposition suggests generally wet conditions, which aligns with the increased bog wetness in SM$_{2008}$. However, SM-A$_{2018}$ (this study) shows increased bulk density and therefore, decreased local effective humidity during this same period (Fig. 6). The discrepancy between SM-A$_{2018}$ and SM$_{2008}$ records could relate to local microtopographic differences or potential time lags owing to age uncertainties and differences in the chronologies associated with using different age models. The increase in the amount of vascular plants and sedges (*s.l.*) at this time appears to be driven by allogenic factors, regulated by wetter and warmer climate conditions (Fig. 6).

Fen Stage (Herbaceous Phase); Unit IV (532–514 cm; ~7155 to 6905 cal. a BP). – Bulk densities and peat-AR are lower in Unit IV as the system re-introduces recalcitrant *Sphagna* along with *Aulacomnium* sp., although peat-ARs distinctly increase halfway through this unit. Similar to the previous increase in *Sphagna* in Unit II, this increase appears to be controlled by successional processes (Laine *et al.* 2014) and potentially represents a change of conditions towards ombrotrophication. The comparison data (SM$_{2008}$) suggest that this was triggered by allogenic factors regulated by wet

conditions until a shift towards drier conditions occurred at the end of Unit IV, when atmospheric dust deposition rates increased ~7000 cal. a BP (Fig. 6). The controlling factors on vegetation in this unit therefore appear to be successional (autogenic), however, possibly triggered by allogenic factors (regulated by wetter climate conditions).

Fen Stage (Herbaceous Phase); Unit V (514–454 cm; ~6905 to 5865 cal. a BP). – Overall bulk densities and peat-AR increase in Unit V until a gradual decrease towards the transition into Unit VI. The system suggests mesotrophic to oligotrophic, poor fen conditions indicated by higher abundance of *Carex* sp. (Mauquoy & van Geel, 2007) and *E. vaginatum* remains (Hughes & Dumayne-Peaty 2002; Väliranta *et al*. 2017). A brief interval of *Phragmites* sp. and *Equisetum* sp. occurs between ~6000 and ~5900 cal. a BP, suggesting higher levels of nutrients in the system, indicated by increased vascular plant remains (Mauquoy & van Geel, 2007), potentially triggered by dry conditions in a period of increased atmospheric dust deposition at the end of the unit, as reflected in the comparison data (SM$_{2008}$; Fig. 6). The comparison data (SM$_{2008}$) suggest initially dry and warm conditions with increased atmospheric dust deposition that gradually shifted to dry but cool climate conditions, represented by a cold period between ~6500 and ~5900 cal. a BP (Fig. 6). Thus, the controlling factors on the vegetation in this unit appear to be mainly allogenic, regulated by the dry and cold climate conditions.

Bog Stage – Dry Sphagna (Dry Sphagna Phase); Unit VI (454–301 cm; ~5865 to 4530 cal. a BP). – Bulk densities initially decrease from the lower boundary of Unit VI and then remain low while peat-ARs are unchanged. The vegetation here is dominated by dry hummock *Sphagna*, in particular ombrotrophic bog species *S. fuscum* and *S. rubellum* (Väliranta *et al*. 2017 and references therein; Fig. 5). The expansion of *Sphagna* is rapid and appears to be controlled by successional (autogenic) processes triggered by dry climate conditions, in which increased productivity, peat accumulation and peat thickness eventually led to bog development and the FBT when the peatland surface vegetation became disconnected from the groundwater (Granath *et al*. 2010; Ruppel *et al*. 2013; Väliranta *et al*. 2017 and references therein; Loisel & Bunsen 2020). Thus, the expansion of *Sphagna* at this time was promoted by increased productivity and accumulation through relatively dry conditions, during which the lowering of the water table benefitted the establishment of dry hummock species such as *S. fuscum* and *S. rubellum* (Väliranta *et al*. 2017), and corresponds to the previously defined *Fuscum* bog stage in Svensson (1988a, b).

Halfway through the unit, however, we see an increase in bog wetness and higher nutrient input through a fertilization event ~5600 and ~4200 cal. a BP (Fig. 6), which appears to generate an increase in peat-AR (the HPAE; Kylander *et al*. 2013, 2016; Martinez-Cortizas *et al*. 2021). The vegetation remains dominated by dry hummock *Sphagna* until a shift occurs between ~4800 and 4400 cal. a BP (Fig. 6), after which a decline in *Sphagna* and peat-AR and a distinct increase in ericaceous dwarf shrubs are observed. The comparison data (SM$_{2008}$) suggest that the nutrient input (fertilization event) controlled the vegetation change at this time, while being indirectly driven by allogenic factors, regulated by the dry and cool climate conditions (Fig. 6).

Oligotrophic Reversal (Floristic Reversal Phase); Unit VII (301–238 cm; ~4530 to 2855 cal. a BP). – Unit VII shows highly fluctuating bulk density and peat-AR values, although there is an overall decrease in the peat-AR. A distinct shift in the vegetation composition occurs in which *Sphagnum* nearly disappears and is replaced by oligotrophic fen vegetation. The unit mostly reflects warmer climate conditions which shift to generally colder climate conditions towards the end of the unit, including the transition into Unit VIII (cold event; Fig. 6), and is especially characterized by disturbance. Several depths containing macroscopic charcoal suggest the system underwent recurring fire disturbance, which promoted post-fire establishment of vascular plants – sedges (*s.l.*) in particular – which tend to be the first colonizers after severe fire activity (Tuittila *et al*. 2007; Sillasoo *et al*. 2011). These assemblages include abundant *E. vaginatum* remains, which is said to benefit from disturbance (Väliranta *et al*. 2017 and references therein), along with *S. tenellum* remains, i.e. a taxon that is often associated with bare or burned peat surface (Daniels & Eddy 1990). Furthermore, it overlaps with a period of very low peat-AR reported from the nearby Draftinge Mosse bog (Sjöström *et al*. 2020), which coincides with the end of HPAE and lasts until ~2500 cal. a BP. However, comprehensive macrofossil and macroscopic charcoal data are not yet available for Draftinge Mosse to confirm any further correlation (see modified macrofossil analysis in Sjöström *et al*. 2020). This study (SM-A$_{2018}$) and the comparison data (SM$_{2008}$) suggest that the vegetation here is controlled directly by fire activity and indirectly by a combination of autogenic factors (litter availability for fuel) and external allogenic factors, such as dry climate or weather conditions which promote combustion (e.g. dry seasons and lowering of the water table; Sillasoo *et al*. 2011).

Bog Stage – Wet Sphagna (Wet Sphagna Phase); Unit VIII (238–0 cm; ~2855 cal. a BP to the present). – The bulk density and peat-AR values are generally low throughout Unit VIII but include distinct repeating peaks of higher values from about two-thirds into the unit towards the present. A pronounced and relatively constant increase in lawn *Sphagna*, dominated by

S. medium and *S. austinii* (Laine *et al.* 2018), occurs between ~2900 and ~1900 cal. a BP as a response to increased bog wetness (Fig. 6) during which time expansion of *Sphagna* slowed decomposition which in turn promoted peat accumulation (Väliranta *et al.* 2017). This first part of this unit (~2900 to ~1900 cal. a BP) aligns with the previously defined *rubellum/fuscum* bog stage in Svensson (1988a, b). However, our data show that here the vegetation is dominated by *S. medium*, not *S. rubellum* and *S. fuscum*, although brief dry hummock *Sphagna* spells do occur.

Halfway through the unit, *Sphagna* starts to alternate with brief wet sections of sedges (*s.l.*) and hollow habitat vegetation, especially abundant *E. vaginatum* remains, that are preceded by small amounts of *S.* Section *Acutifolia* and macroscopic charcoal episodes, producing a pattern of sedge-rich disturbance successions triggered by fire activity (Tuittila *et al.* 2007; Sillasoo *et al.* 2011). In between fire activity, periods of increased bog wetness and cold events overlap with external nutrient input, causing fertilization events between ~1900 and ~300 cal. a BP. This part of the unit (~1900 cal. a BP to the present) corresponds to the *magellanicum* (former name of *S. medium;* Laine *et al.* 2018) bog stage in Svensson (1988a, b) and is dominated by *S. medium*, *S. balticum* and *S. cuspidatum/majus*. This study (SM-A$_{2018}$) and the comparison data (SM$_{2008}$) suggest that the vegetation changes at this time are controlled in particular by fire disturbance, and potentially also by external nutrient input in which climate acts as an indirect driver.

Factors driving species changes in Store Mosse

Previous macrofossil work on Store Mosse did not report any signs of disturbance, perhaps owing to lower sampling resolution or different methods, apart from two highly humidified peat layers separating the *Sphagnum* stages which were attributed to allogenic factors, such as drier climate conditions and lower water levels in the area (Svensson 1988a, b; Malmer *et al.* 1997). Our study identified several interlinked environmental factors affecting the peatland. Of interest, we identified the external nutrient input and fire disturbance as direct factors affecting SM-A$_{2018}$ species assemblages, for which climate acts as an indirect (underlying) driver (Fig. 7).

The autogenic processes and associated vegetation changes within Store Mosse largely follow the well-established successional pathways for peatland development (Granlund 1932; Hughes & Dumayne-Peaty 2002; Väliranta *et al.* 2017 and references therein; Loisel & Bunsen 2020): lake → fen → bog. The initial peat accumulation shifts relatively quickly from the *lake* stage assemblages to peat dominated by sedges (*s.l.*), after which increased *E. vaginatum* remains precede the FBT resembling several cases in Finnish peatlands and elsewhere (Väliranta *et al.* 2017 and references therein).
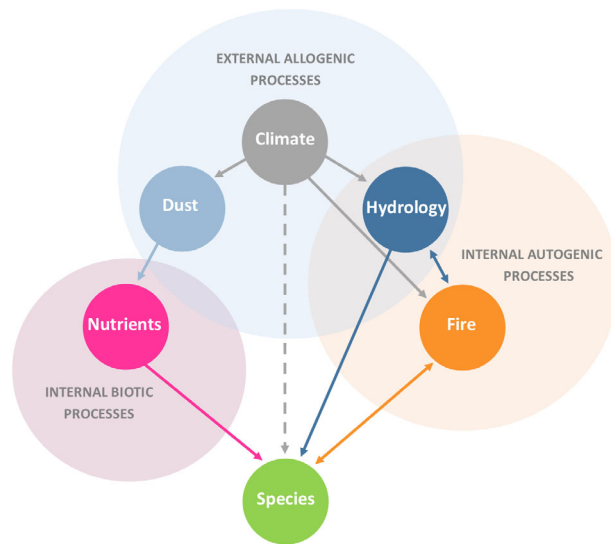

Fig. 7. A simplified scheme of the relationships between the driving factors of species change within Store Mosse core SM-A$_{2018}$, including external allogenic processes, internal autogenic processes and internal biotic processes. Arrows denote direction of the relationship between the factors, dashed line represents an indirect driver and solid lines represent directional relationship. The overlapping circles represent the interlinked nature of the processes involved in the species changes within SM-A$_{2018}$.

The emergence of bog *Sphagna* (*S. fuscum* and *S. rubellum*) occurs rapidly and represents a well-established community that has shifted the peatland from a groundwater-fed fen to atmospherically fed bog system.

Assessing the exact role of different biotic interactions within this study would require further analysis involving macrofossil analyses on additional cores and species distribution modelling. The biotic interactions identified within this study mostly relate to the external nutrient input and associated effects on the competitive balance between *Sphagnum* mosses and vascular plants. However, we note that a decline in *S. austinii*, representing one of the two species formerly known as *S. imbricatum* (Laine *et al.* 2018), occurs ~700 to 800 cal. a BP which aligns with previous research investigating the decline of *S. austinii* across NW European bogs (McClymont *et al.* 2008; Swindles *et al.* 2015). Its habitat preferences for interpretation purposes are somewhat complicated owing to its ability to thrive in both hummocks and lawns (Mauquoy & Barber 1999; McClymont *et al.* 2008; Swindles *et al.* 2015; Laine *et al.* 2018). The increasing abundance of *S. medium* within the sequence suggests that it previously represented a lawn habitat and was potentially outcompeted by *S. medium* (McClymont *et al.* 2008), possibly influenced by increased bog wetness (Mauquoy & Barber 1999) inferred by larger amounts of wetter *Sphagna* (*S. balticum* and *S. cuspidatum/majus*) ~800 to 500 cal. a BP (Laine *et al.* 2018).

The allogenic processes are complex and more difficult to detangle as they involve several interplaying factors which in turn create direct and indirect effects on species change (Fig. 7). Firstly, hydrological changes, which are linked with autogenic successional changes influenced by peat thickness and FBT as well as allogenic factors, such as local basin morphology and effective humidity (Hilbert *et al.* 2000; Tahvanainen 2011; Ruppel *et al.* 2013; Chaudhary *et al.* 2018), also potentially influence biotic interactions. For example, changes in water table levels may affect the performance of different *Sphagnum* species since the microtopographic positions of different *Sphagnum* species including their rates of productivity and decomposition are closely linked with the hydrology along the hummock–hollow gradient (Robroek *et al.* 2007a; Chaudhary *et al.* 2018). Secondly, peatland fires are promoted by allogenic (e.g. dry climate) and autogenic (e.g. fuel and availability of litter; Sillasoo *et al.* 2011; Ronkainen *et al.* 2013) factors, while also impacting the local hydrology by influencing the microtopography (Kuhry 1994; Tuittila *et al.* 2007; Sillasoo *et al.* 2011; Howie *et al.* 2020). Local hydrology also affects fire activity, since dry bog microhabitats tend to be more vulnerable to fires than wetter hollow microhabitats (Ronkainen *et al.* 2013). In fact, hummock habitats often act as a starting point and dispersal paths for the episodic disturbance successions (i.e. episodic wet shifts occurring after the fire activity has burnt away the dry layers of the peat and reached the water table, leading to establishment of sedges (*s.l.*); Tuittila *et al.* 2007; Sillasoo *et al.* 2011; Ronkainen *et al.* 2013; Väliranta *et al.* 2017). Thirdly, changes in the amount and the character of atmospheric dust deposition are driven by shifts in climate and can influence the nutrient balance within the system (Kylander *et al.* 2013, 2016, 2018), which in turn affects biotic interactions and productivity.

Fire events are common features on boreal bogs and can cause damage to various degrees (Kuhry 1994; Tuittila *et al.* 2007; Vitt & Wieder 2008; Sillasoo *et al.* 2011; Väliranta *et al.* 2017). While surface fires tend to be less damaging to the vegetation in terms of recovery (Magnan *et al.* 2012), higher frequencies or more severe fire episodes can have a much greater impact on peatland hydrology, vegetation and peat properties (Vitt & Wieder 2008; Sillasoo *et al.* 2011). Severe burning could lead to changes in peat-AR and, ultimately, carbon loss – directly through the burning of surface peat and indirectly through decreased production and increased decomposition immediately following the fire episodes (Kuhry 1994; Vitt & Wieder 2008). Locally, the combustion of surficial peat layers can also influence microtopography by changing the distance between the water table and the vegetation, which in turn affects the species distribution along the hummock–hollow gradient (Benscoter *et al.* 2005; Tuittila *et al.* 2007; Sillasoo *et al.* 2011).

Nutrient availability also has a particularly important role in the competitive balance between *Sphagnum* and vascular plants within peatlands (Limpens *et al.* 2004). Since ombrotrophic peatlands are disconnected from the groundwater system and only receive input from the atmosphere, mineral dust deposition is the most important pathway for nutrient input (McClymont *et al.* 2008). These nutrients are usually used up by *Sphagnum* before they reach the roots of vascular plants whose nutrient input remains restricted by the decomposition-resistant *Sphagnum* litter, as they rely on release of nutrients via decomposition of organic matter (Limpens *et al.* 2004; Rydin & Jeglum 2013) and mineral weathering. Therefore, despite nutrient addition typically benefitting vascular plants more than mosses in general (Bubier *et al.* 2007; Juutinen *et al.* 2010; Larmola *et al.* 2013), within these systems *Sphagnum* will have a competitive advantage over vascular plants (Limpens *et al.* 2004). However, an increase in nutrients which *Sphagnum* is unable to retain may shift the advantage in favour of vascular plants, allowing them to potentially outcompete *Sphagnum* (Limpens *et al.* 2004).

While the first fertilization event (~5500 to ~4200 cal. a BP; Figs 3, 6) was interpreted to boost productivity within the system (linked to the HPAE in Kylander *et al.* 2018; Martinez-Cortizas *et al.* 2021), it is possible that the long-term P, K and Ca nutrient input triggered the notable decline in *Sphagnum*. This may have caused a shift in the competitive interactions to favour vascular plants, as reflected in the increased abundance of ericaceous dwarf shrub remains between ~4800 and ~4400 cal. a BP, a behaviour that follows the results described in previous fertilization experiments involving N, K and P input (Bubier *et al.* 2007; Larmola *et al.* 2013). These studies noted a negative fertilization effect on *Sphagnum* especially linked to the K and P nutrient loads, which resulted in a decline. The decline was strengthened by increasing amounts of shrub biomass, which in turn slowed *Sphagnum* growth further by shading and changing litter composition (Bubier *et al.* 2007).

The increase in ericaceous dwarf shrubs (~4800 to ~4400 cal. a BP) led to increased amounts of litter susceptible to ignition and thus increased the system's vulnerability to fires (Sillasoo *et al.* 2011). Dry climate conditions enabled more frequent fires, which is reflected in the macroscopic charcoal record during the Oligotrophic Reversal (Unit VII). Since higher fire frequency or more severe fires can cause major shifts in vegetation and peat properties (Vitt & Wieder 2008; Sillasoo *et al.* 2011), the repeated fire disturbance in the Oligotrophic Reversal probably furthered the *Sphagnum* decline, impacted post-fire recovery, and as a result, produced prolonged disturbance successions dominated by vascular plants, which in turn also affected decomposition rates and slowed down peat accumulation in the system.

While a near disappearance of a once-established *Sphagnum* community is unexpected and diverges from the typical successional pathways (Granlund 1932; Hughes & Dumayne-Peaty 2002; Väliranta *et al.* 2017 and references therein), it is important to note that the system here remains ombrotrophic despite oligotrophic fen vegetation prevailing. The significant size (e.g. area covered and peat depth) of the Store Mosse peatland system gives it a large buffering capacity against disturbance coming from changes in peatland hydrology and ground water flows (Sjöström *et al.* 2020). The reversal effect is more likely to be related to the external disturbance caused by interlinked processes of the episodic nutrient input and repeated fire disturbance, with allogenic factors (e.g. climatically driven nutrient input through atmospheric dust deposition, dry climate conditions and lowered water tables enhancing fire susceptibility) as underlying drivers.

Conclusions

This study reconstructed postglacial vegetation succession of Store Mosse bog using macrofossil analysis and reviewing results from previous work (humification, elemental and spectral data) at the site in order to identify the internal autogenic, internal biotic and external allogenic factors that drive species change. The results show that Store Mosse largely follows the expected autogenic (successional) pathways for boreal peatlands. However, the system has also been affected by other interlinked autogenic, allogenic and biotic factors. These other factors affected species as direct drivers of change, in which climate and hydrology acted as indirect drivers. Of interest, we note that external nutrient input (originating from dust deposition associated with climate and allogenic drivers) potentially altered the competitive interactions and had a negative effect on *Sphagnum* while favouring establishment of vascular plants, and that increased fire activity on the peatland (driven by allogenic and autogenic factors) caused vegetation shifts, typically brief post-fire wet shifts dominated by sedges (*s.l.*) as the fire burns away the dry layers and reaches the water table. These effects interactively led to changes in the outcomes of competitive interactions between *Sphagnum* and vascular plants (i.e. the fertilization event allowed vascular plants to access more nutrients, leading to the decline in *Sphagnum* which previously had a competitive advantage, using up most of the available nutrients in the system), increased the fire vulnerability of the system (owing to litter change and drier climate conditions) and triggered a floristic reversal (e.g. a shift from ombrotrophic bog communities to oligotrophic fen vegetation; the Oligotrophic Reversal) as the ombrotrophic system underwent a prolonged period of disturbance and drastic species changes. This study highlights that controlling factors and processes of species changes

on the peatland are manifold, complex and interlinked, and that it is crucial to consider the role of the interactive processes when assessing the drivers of species change and their implications on both short- and long-term time scales.

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