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Resilience of peatland ecosystem services over millennial timescales: evidence from a degraded British bog

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Summary

[1] Many peatland ecosystems in Europe have become degraded in the last century owing to the effects of drainage, burning, pollution, and climate change. There is a need to understand the drivers of peatland degradation because management and restoration interventions can affect the natural ecohydrological dynamics of such sensitive environments, and are expensive. However, if given enough time peatlands may have the ability to recover spontaneously without deliberate action.

[2] We use a detailed multiproxy palaeoecological dataset from a degraded raised bog in Northern England to examine its ecosystem stability and long-term dynamics in response to anthropogenic disturbance over a variety of timescales. One feature of many degraded peatlands (including our study site) is the local dominance of *Molinia caerulea* (purple moor-grass), which has expanded at the expense of characteristic peatland plants, including sedges and *Sphagnum* mosses.

[3] Our data show that there has been a long history of human impacts at the site which have culminated in its current unfavourable condition. Several distinct episodes of past peat cutting are evident as hiatuses in peat accumulation; however, peat accumulation and plant community structure have subsequently recovered spontaneously. The appearance of *M. caerulea* occurs coevally with an unprecedented variety of recent anthropogenic impacts, all of which have arguably contributed to providing a suitable environment for its rise to dominance. We have dated the appearance of *M. caerulea* to the latter half of the twentieth century which corresponds to a number of anthropogenic press disturbances, including: dust loading from post-war expansion of the adjacent quarry; burning; drainage; airborne pollution; and contamination from soil dust and agrochemicals.

[4] [*Synthesis*] Our study demonstrates the importance of palaeoecology for understanding the trajectories of peatland development and ecosystem dynamics, including their resilience and resistance to pulse and press disturbances. We show that peatlands have the capability to recover spontaneously from severe disturbances such as peat cutting, albeit on timescales much longer than those applied to monitoring of restoration efforts. The implications are relevant for determining whether it is better to manage and restore peatlands, or to allow them to recover naturally without human intervention.

Introduction

Northern peatlands provide globally-valuable ecosystem services, including soil carbon storage (Gorham, 1991; Turunen *et al.* 2002), water-quality moderation (Holden, 2005) and habitat provision for endemic plants, particularly the *Sphagnum* moss genus (Rydin and Jeglum, 2013). In some northern European nations the combustion of peat also accounts for an important component of domestic energy budgets (e.g., Turunen, 2008), making peatlands a valuable natural resource. However, many peatlands face increasing impacts from changes in climate (Ise *et al.* 2008), land-use (e.g., Brown *et al.* 2015) and disturbance regimes (e.g., wildfire) (e.g., Kettridge *et al.* 2015), as well as direct damage from drainage and peat harvesting (Turunen, 2008). Relatively modest disruptions to peatland ecohydrology can set into motion a number of positive feedbacks between ecological, hydrological and biogeochemical processes at the ecosystem-scale that could potentially lead to the rapid degradation of peatlands and the catastrophic loss of their soil carbon stocks over short timescales (Ise *et al.* 2008). On the other hand, it is also possible to identify a number of negative feedbacks that can provide both resistance and resilience in the face of disturbance (e.g. Belyea, 2009; Waddington *et al.* 2015). As such, it is difficult to judge the overall vulnerability of peatlands to disturbances, and to determine the most appropriate conservation techniques and land management policies to preserve their valuable ecosystem services.

Efforts to restore damaged (usually drained and harvested) peatlands have focussed on rewetting in order to promote *Sphagnum* re-colonisation, enhance peat accumulation and subdue carbon dioxide emissions – albeit often at the expense of elevated methane emissions and greater global warming potential (e.g., Wilhelm *et al.* 2015) – on timescales of years to decades. Plant community structure and carbon sequestration in harvested peatlands can sometimes recover spontaneously in the decades that follow intensive harvesting without deliberate restoration efforts (Lavoie *et al.* 2003; Graf *et al.* 2008); while others continue to degrade rapidly, sometimes despite heavy investment in restoration and conservation (González & Rochefort, 2014). Compound disturbances, such as drought followed by wildfire (e.g., Sherwood *et al.* 2013) or repeated harvesting in the same peatland (Cooper *et al.* 2001), can alter peat hydraulic properties sufficiently to surpass the ecosystem's threshold for resistance or resilience. The result can be runaway degradation, including loss of biodiversity and soil carbon (Waddington & McNeil, 2002; González *et al.* 2013). Studies that document peatland ecosystem dynamics after harvesting shed some light on the resilience of peatland ecosystem services, although the study periods are typically no longer than 50 to 70 years (e.g., Yli-Petäys *et al.* 2007), and are often much shorter. Observations over longer timescales are required in order to gain a fuller appreciation of post-disturbance recovery or degradation and the effects of restorative interventions. Palaeoenvironmental reconstructions of ancient disturbances in peatlands offer the possibility to fill the gap until longer-term studies become available.

The aim of our study is to use a multiproxy palaeoecological dataset from a degraded British raised bog (Swarth Moor) to assess its resilience to ancient pulse disturbances and its resistance to contemporary compound press disturbances. We use the terms 'pulse' and 'press' to mean disturbances that occur quasi-instantaneously or more gradually, respectively (after Bender *et al.* 1984). In reference to peatland ecosystem services we also distinguish between resistance (the insensitivity of a system to disturbances) and resilience (the ability of a system to recover after a disturbance), according to Grimm and Wissel (1997). Various strands of evidence suggest that the bog has undergone extreme disturbance in the past. The site provides a unique opportunity to study long-term ecosystem trajectories in response to disturbance events over timescales far beyond those of contemporary monitoring studies. The site and its ecosystem services are also currently threatened by multiple factors, including climatic change, inputs of dust from nearby quarries, relatively high levels of background nitrogen deposition, and changes in land management. We recognise the importance of climate in influencing peatland development (e.g. Barber, 1981). However, climatic interpretations of peat records, even from pristine bogs, requires caution (see Swindles *et al.* 2012, 2013; Morris *et al.* 2015 - in press). Given the highly disturbed nature of our site, we are not confident that it would be possible to identify responses to Holocene climate change in the palaeoecological dataset, so here we focus solely on non-climatic factors.

Study Site

Swarth Moor (Figures 1 and 2) (54.1215°N, 2.2985°E) is a lowland ombrotrophic raised bog with a classic dome profile (cf. Ingram, 1982) that runs into surrounding lagg fen and grassland communities (Turner *et al*. 2013). There is evidence that edges of the bog have been cut in the past for peat: a series of peat cutting cliffs and baulks are clearly visible on the historic aerial photographs and Google Earth images (Figures 1 and 2). However, the age of these features is unknown owing to a lack of historical record. Vegetation is characterised by *Molinia caerulea*, *Eriophorum vaginatum*, *Erica tetralix* and *Calluna vulgaris*, with localised *Vaccinium oxycoccus*, *Andromeda polifolia*, *Rhynchospora alba* and *Narthecium ossifragum*. Bryophyte cover is predominantly comprised of *Sphagna* including *S. capillifolium*, *S. papillosum*, *S. palustre*, and *S. cuspidatum* (Turner *et al*. 2013). In Europe, *M. caerulea* (purple moor-grass) is a common indicator of peatland degradation or disturbance (Chambers *et al*. 2013) and can smother other plants including *Sphagnum* (Taylor *et al*. 2001; Chambers *et al*. 2013). Its rise to dominance in peatlands has been attributed to a wide variety of causes, including: nutrient enhancement (e.g. Tomassen *et al.* 2003), peat cutting (e.g. Chambers *et al*. 2013), drainage (Tomassen *et al*. 2004), burning (Taylor *et al*. 2001), and changes in land-use (Marrs *et al*. 2004).

Formerly known as Helwith Moss - prior to its classification as a Site of Special Scientific Interest (SSSI) in 1958 - the bog and its adjacent lagg fen have been monitored for over half a century to assess the likely causes of change to the peatland and its flora (Meade *et al*. 2007). Observations since the 1950s include a loss of plant biodiversity, drying of the bog surface, nutrient enrichment in areas affected by agriculture, and the encroachment of Dry Rigg Quarry onto the south-western border of the SSSI. Other current drivers of change include the cessation of grazing in 2001 due to the UK outbreak of Foot and Mouth Disease and increased nitrogen (N) input from atmospheric pollution and terrestrial contamination from agrochemicals, manure and slurry dust/spray. Furthermore, outflows from the quarry and the construction of a bund on the peatland's south-west margin may have affected the hydrology of the site. As a result the bog is now considered to be in an "unfavourable recovering" nature conservation condition (Natural England, 2010) due to the dominance of *M. caerulea*, and also the lack of certain species of *Sphagnum* moss (Labadz *et al*. 2000, Meade *et al*. 2007, Headley, 2010).

Materials and methods

We collected eight surface monoliths in February/March 2014 from the highest points along parallel transect lines (Figure 1). We used these surface samples to perform preliminary tests for the presence or absence of spheroidal carbonaceous particles (SCPs) to determine if the top 20 cm of the contemporary bog surface was intact. Particles of elemental carbon (SCPs) that form during high temperature combustion of coal and oil can provide an unambiguous indicator of atmospheric pollution from industrial sources over the last ~150 years (Swindles, 2010). We subsampled our surface monoliths in 5 cm contiguous blocks. We then processed each subsample using nitric acid (HNO_3) extraction after Swindles (2010), and mounted the precipitate on microscope slides using Histomount. Further fieldwork was then undertaken to collect a series of longer peat cores from strategic sample points across the site to provide adequate material for multiproxy analysis from the upper 1 m of the bog's surface.

Three peat cores were extracted from small hollows constrained within the baulks between obvious peat cuttings on the Swarth Moor site using a wide-capacity Russian D-section corer with a 100 cm long chamber (Jowsey, 1966, De Vleeschouwer *et al*. 2010). Core locations are: Core SM1: 54.1218°N, 2.2962°W; Core SM2: 54.1220°N, 2.2984°W; Core SM3: 54.1221°N, 2.3009°W (see Figure 1). Each core-set was taken from three overlapping sample points, the horizontal distances between which were no more than 100 cm, to provide sufficient and stratigraphically comparable material for multiproxy analysis. The cores were sealed in plastic wrap, returned to the laboratory and stored in refrigeration at 4°C prior to sub-sampling.

Testate amoebae were extracted from the core samples using a modified version of the method described by Hendon and Charman (1997), using deionised water as a storage medium and mountant rather than glycerol.

Testate amoebae were identified using Charman *et al*. (2000) and Turner (2009). Peatland water-table reconstructions were performed using the transfer function for the Yorkshire Dales of Turner *et al*. (2013). Quadrat and leaf count plant macrofossil analysis was undertaken following Barber *et al*. (1994). Plant macrofossils were identified using Grosse-Brauckmann (1972, 1974, 1992) and Katz *et al*. (1977). Pollen extraction was carried out using standard potassium hydroxide (KOH 10%) digestion following Moore *et al*. (1999). A pollen sum of 500 total land pollen (TLP) grains was counted, excluding spores. Rare pollen types were quantified at ≤ 2. A 'spike' of *Lycopodium* spores was added to the samples to provide an indication of pollen concentration (cf. Stockmarr, 1971). Microscopic charcoal in fractions of ≤ 20 µm, 21-50 µm, > 50 µm and combined summary micro-charcoal counts were counted in addition to TLP, but not included in the pollen sum. Pollen was identified in accordance with keys in Moore *et al*. (1999), Beug (2004), supported by Reille (1999) and a modern pollen type-slide reference collection (University of Leeds). Nomenclature follows Stace (2010). Non-pollen palynomorphs (NPPs) were identified to provide additional palaeoenvironmental data (cf. Pals & van Geel (1980); and van Geel *et al*. (1982/1983, 1986, 2003)). These data are presented as percentages (n = 350). All data were plotted using C2 (v.1.7.6; Juggins, 2014).

Loss-on-ignition (LOI) analysis was carried out following Schulte and Hopkins (1996) to evaluate mineral inputs to the peatland. Determination of bulk density, following Jones *et al*. (2000), was conducted to assess relative proportions of mineral and organic constituents. C/N ratios were examined to illustrate recent peat accumulation and decomposition trends and to identify signs of nutrient enrichment from nitrogen deposition. C/N samples were ground using an MM301 mixer mill at a frequency of 25 Hz for six minutes, weighed (~4 mg) into tin capsules, and analysed using a Elementar Vario Max Cube Combustion Analyser calibrated using sulphanilic acid. Calibration was checked using Energy Peat (*Sphagnum*) NJV942 and B2150 High Organic Sediment standards. Geochemical analysis (ICP-MS) was undertaken on 110 peat sub-samples to determine the impact and chronology of dust and heavy metal deposition, i.e. natural background and quarry source, and airborne and terrestrial pollutants. The analytical process was carried out by Chemtech Environmental Ltd. Samples were digested on a hot block with Aqua regia at 120°C. Samples were analysed for calcium and silicon by Thermo ICAP 7400 and all other extracts by Agilent 7700x, and calibrated against ISO guide 34 standards.

Macrofossil sub-sampling was undertaken at 4 cm intervals and then fine-tuned at 1 cm intervals to constrain the first appearance of *M. caerulea*. Sub-samples were taken at 4 cm intervals for pollen and testate amoeba analysis. Analysis of testate amoebae was carried out down to 50 cm in each core, as hiatuses were present in the records and test preservation was poor in the lower levels. The Swarth Moor core chronologies are based on AMS ^{14}C dating (25 cm and below) (Table 2) provided by the DirectAMS laboratory, and SCP stratigraphic markers (20 cm and above) as described in Rose & Appleby (2005) and Swindles *et al*. (2010, 2012, 2015a, b). Above-ground macrofossils >125 µm (*Sphagnum* leaves and stems, *Calluna vulgaris* wood and seeds) were extracted for ^{14}C dating at intervals of 10 cm from 25 cm and below, because SCP analysis at 1 cm intervals had provided a modern date range for the top 20 cm of peat. Calibrated ages were calculated using IntCal13 (Reimer *et al*. 2013) in Clam v.2.2 (Blauuw, 2010). Age-depth models were generated using linear interpolation, which was deemed the only appropriate model due to the hiatuses in the record. Any ^{14}C dates that caused an age reversal were removed from the model.

Results

Analysis revealed that SCPs were present in the eight surface monoliths and the three deep cores (n = 11), indicating that there has been at least some degree of recent peat accumulation across Swarth Moor (Figure 3). All three cores (SM1, SM2 and SM3) were stratigraphically and compositionally similar (Table 1). However, AMS ^{14}C determinations reveal that the bog stratigraphy is not continuous. There is a series of hiatuses revealed by the age-depth models (Figure 4) that, on account of the temporal length of the gaps, appears to indicate at least two episodes of peat cutting. SM1 indicates peat was cut in (or before) the nineteenth century AD down into peats of the twelfth century AD (744-679 cal. BP), and an earlier cutting from the twelfth century AD or before down into Bronze Age peats (4287-4008 cal. BP). SM2 shows peat cutting occurred during the Late Iron Age (1922-1741 cal. BP) into Bronze Age peats (3700-3573 cal. BP), with later peat-cutting activity most probably occurring before the ~1850s AD, which cut down into the peats dating from the Dark Ages (1335-1279 cal. BP).

In core SM3 the early industrial rise of SCPs is not present in the record, suggesting that the peatland was cut after the ~1850s. This recent cutting extends down into Bronze Age peats (4147-3934 cal. BP) (see Figure 5 – SM3). The maximum and minimum accumulation rates calculated from the age-depth models were used to approximate the thicknesses of peat removed at each core location (Table 3). These peat cuttings appear to have been spatially extensive because they are identifiable between multiple cores; and intensive in nature because each has removed several thousand years' worth of accumulated peat (Figures 4-7). This likely represents cuttings of several decimetres in depth (Table 3). After hiatus 1a *M. caerulea* and *S. papillosum* dominate. Immediately after hiatus 1b *E. vaginatum* and Ericaceae dominate, followed by an increase in *S. austinii*. After hiatus 2a *S.* section *Cuspidata* dominates indicating locally wet conditions. After hiatuses 2b and 3a there is an increase in *E. vaginatum*, prior to an increase in *Sphagnum* abundance (Figure 7).

The upper ~10 cm of all cores displayed a distinctive black-brown coloured top. The presence of SCPs in this section at 13.5 cm (SM1 and SM2) and 8.5 cm (SM3) (Figure 5 and 6) signifies peats of the last ~150 years (Rose & Appleby, 2005; Swindles *et al*. 2010; Swindles *et al*. 2015b). The first appearance of *M. caerulea* leaf epidermis macrofossils (Figure 7) is coincident with raised counts of *Poaceae* pollen in all three deep cores and with the rapid increase in the SCP curves which begin in the 1950s. A horizon based on the influx of *M. caerulea* macrofossils is used to provide a cross-diagram marker to stratigraphically define the appearance of this taxon in conjunction with the other proxy data (see Figures 5-11). The beginning of the rise to local dominance of *M. caerulea* at Swarth Moor has been calculated from the maximum and minimum determinations in the age-depth models of SM1 and SM2 and constrained to ~1950-1975.

All three cores (Figure 5) demonstrate similar trends at ~10 cm in physical and chemical properties, including bulk density, LOI, and C/N ratios. Decreases in LOI and concomitant decrease in C content indicate greater proportions of minerogenic material being deposited on the peatland through aeolian transport (dust-loading). Geochemical data also demonstrate marked changes in the top ~10 cm of the peat profiles reflecting input of dust from local quarrying and soil erosion, as well as atmospheric pollution (Figure 6).

Macrofossil data reveal the first occurrence of *M. caerulea* epidermis and the subsequent spread of *M. caerulea* at Swarth Moor in the top ~10 cm of each core (Figure 7) is coeval with the large shift in the geochemical signatures. The rise to dominance of *M. caerulea* in all three cores corresponds with a general decline in dwarf shrubs (*Ericaceae*, *C. vulgaris* and *E. tetralix*) and sedges (*Carex* sp., *Eriophorum* sp., *Scirpus cespitosus*), the disappearance of *S. austinii* and its replacement by *S. papillosum*. Coincident and contemporary burning activity is revealed by increased micro-charcoal (Figure 9), which also corresponds with the rise of *M. caerulea* (Figure 7). The data from core SM3 (Figure 10) indicate heightened burning activity prior to the influx of *M. caerulea*, which is evidence of a differential burning pattern in the western sector of the bog that optimised ground conditions for the spread of *M. caerulea* across the site.

Poaceae pollen counts illustrate a general rise in grasses that correspond with a reduction in tree and shrub species, a decline in dwarf shrubs and increased burning activity coeval with the rise in *M. caerulea* leaf epidermis (see Figures 8-10). There is a small increase in *Sphagnum* spores in the top ~10 cm of all three cores, which correlates with increases in *S. papillosum* leaf counts apparent in the macrofossil data (see Figure 8). NPP data show subtle cross-site similarities in the top ~10 cm (Figures 8-10). Notably, Type 71 (a marker for presence of spiders) responds negatively to burning phases and habitat clearance, whereas Type 10 (a marker for dry conditions in raised bog peat) is coincident with heightened micro-charcoal counts and the shift to drier conditions that are also indicated by testate amoebae data (Figure 11). Types 55A (mostly coprophilous) and 55B (a coprophilous marker) shows similar fluctuations at all three core sites, suggesting intermittent grazing cycles associated with vegetation management by fire.

The testate amoeba results (Figure 11), including reconstructed water-table depths, indicate a high degree of within-site variability. SM1 suggests a shift to slightly wetter conditions at the point when *M. caerulea* rises as signified by the decline of *Hyalosphenia subflava* and *Trigonopyxis arcula* type (xerophilous markers), and the rise of hygrophilous taxa, i.e. *Archerella flavum*, *Arcella discoides* type, and *Centropyxis aculeata* type. Conditions at SM2 are more ambiguous as hygrophilous taxa decrease (e.g. *Archerella flavum* and *Arcella discoides*) and the xerophilous taxon *Heleopera rosea* peaks. SM3 also indicates a similarly variable environment, but with a swing to drier conditions indicated by the decline of *Arcella discoides* type and the rise of *Heleopera rosea*.

Patterns of vegetation response to disturbance and subsequent recovery are observed throughout the cores. For example, SM1 shows a clear increase in charcoal abundance at ~25cm that is coincident with a sharp decline in *Corylus* pollen and a rise in Poaceae pollen. This is reflective of the pattern observed in the top ~10 cm of all three cores, where evidence for *M. caerulea* becoming locally dominant throughout Swarth Moor is clear from the presence and abundance of epidermis remains. The rise in Poaceae pollen and charcoal abundance at ~25cm may suggest that *M. caerulea*, or another fast-growing, disturbance-resistant grass, became dominate in the area during a period of cutting in or before the nineteenth century (Figures 4 and 8). These spikes are less clearly obvious in SM2 and SM3, possibly suggesting less extensive disruption to the peatland than in more recent times. However, it does highlight that the area has experienced previous ecological disturbance and recovered in the relatively recent past.

Discussion

The ancient peat harvesting at Swarth Moor may reflect the need for fuel in the Yorkshire Dales, which has had limited tree cover since the Bronze Age (Rushworth, 2010). The example of Tollund Man, an Iron Age bog body from Denmark who was found beside ancient peat cutting tools, provides a precedent for prehistoric peat cutting in Europe (Glob, 1969). There is also evidence for Bronze Age deep-peat cutting from the Outer Hebrides of Scotland (Branigan *et al.* 2002). It is unclear how long peat accumulation took to re-establish on the cut surfaces, but these severe pulse disturbances have evidently been insufficient to overcome the ecosystem's capacity for resilience in the long term. The repeated re-initiation of peat accumulation was almost certainly spontaneous (*i.e.*, without deliberate restoration efforts by humans), suggesting that peat C accumulation and plant community structure at our site have been highly resilient to harvesting. However, the plant macrofossil data suggest that re-establishment of plant communities has taken different pathways after each disturbance event (Figure 7). After past periods of cutting, the ecosystem underwent limited further disturbance (e.g. lower levels of charcoal, low levels of elemental pollutants), and clearly had sufficient time for vegetation communities to re-establish and peat formation to resume. The early success of *E. vaginatum* after hiatuses 2b and 3a is consistent with contemporary observations of re-colonisation on restored peat surfaces (e.g. Lavoie and Rochefort, 1996).

The distinctive black-brown coloured uppermost peats have been attributed to recent drier and warmer climate leading to more humified peats as well as raised levels of soil dust from intensified agriculture identified at other sites in the Yorkshire Dales (Rushworth, 2010; Turner *et al*. 2014; Swindles *et al.* 2015b). Synchronous peaks in chemical elements in the top ~10 cm of the cores, such as aluminium, calcium, iron, magnesium, silicon, titanium and yttrium, are attributed to a sudden and heightened influx of minerogenic dust-loading from localised quarrying (Harrison *et al*. 2002, Nieminen *et al*. 2002) and anthropogenically-triggered soil erosion (Hölzer & Hölzer, 1998). Near-surface peaks in calcium, copper, arsenic, cadmium, lead, phosphorous, potassium, and uranium may reflect dust-loading, or agrochemical/agricultural slurry-rich dust/spray, soil-erosion, atmospheric pollution, natural trace lithogenic and marine aerosol deposition (Chalmers *et al.* 1990; Shotyk, 1996, 1997, 2002; Shotyk *et al.* 2002; Shotyk & Krachler, 2010; Denaix *et al.* 2011). Calcium (in the form of field lime) is also still used as a fertiliser and to neutralise acidification in surface soils (Olson, 1987). The notable cross-element correlation in the geochemical data in the top ~10 cm of peat corresponds not only with the expansion of the adjacent quarry in the post-war period, but also the intensification of agrochemical use in Britain after the passage of the 1946 Agricultural Act (Holderness, 1985; Robinson & Sutherland, 2002; Ogaji, 2005). Modern atmospheric pollutants also appear to be an additional contributory factor and may explain the presence of cadmium, copper, lead, zinc and uranium, with these peaks coincident with changes in post-war industry and energy-generation.

The most recent testate amoeba communities may have been affected by dust deposition and these results need to be treated with caution (e.g. Ireland and Booth, 2012). Nevertheless, the water-table reconstructions do support what is known about recent hydrological change at Swarth Moor. SM1 might have been affected by the hydrological impacts of quarry outflows (which increased significantly in the 1940s), and the construction of a bund on the south-west margin which has effectively dammed the peatland in this area (Labadz *et al*. 2000, Meade *et al*. 2007). The rise in water table in SM1 is supported by monitoring data from dipwells near these core locations (Labadz *et al*. 2000). SM3 is probably responding to drainage in the western part of the bog, as it is in an area of marked peat-cutting cliffs and baulks, and has a steep hydrological gradient down to a large drain (Comb Dyke).

The increase in abundance of *M. caerulea* in the top ~10 cm of the three cores as a result of severe disturbance is not surprising. Grasses typically have fast growth rates, low leaf mass per areas (Poorter *et al.* 2009) and efficient use of resources that make them ideal to colonise and dominate disturbed environments, providing them with an advantage in the early successional stages after a disturbance (Suter & Edwards, 2013). It is clear that the recent spread of *M. caerulea* across the site is coincident with the intensification of human impacts. It is interesting to note that this species appears to be absent from plant communities after recovery from ancient disturbances, illustrating the unprecedented intensity of recent impacts on the bog. Our multiproxy evidence suggests that *M. caerulea* dominance in recent years has been sustained in part due to continued disturbance of the environment (Figures 8-12), and also perhaps due to insufficient time having passed for recovery to take place. It is unlikely that *M. caerulea* is a new addition to the environment –

Poaceae pollen is found throughout the core records, and it is possible that some of this pollen may have been produced by *M. caerulea*. It is likely that *M. caerulea* was recruited from the local plant population and exploited the disturbed environment to become locally dominant. *M. caerulea* is known to thrive in nutrient poor conditions (e.g. Tomassen *et al*. (2003)), when it is not over-shadowed during early growth by other plants (Nurjaya & Tow, 2001) and is also capable of rapidly exploiting disturbed environments (e.g. Jacquemyn, Brys & Neubert, 2005) and becoming dominant in an area due to rapid growth and efficient use of resources that help it to out-compete other species.

Many species that do not tolerate exposure to dust or other particulate pollution well (e.g. *Sphagnum*; Farmer, 1993), express a range of negative physiological and/or morphological responses, including cell damage and reduced photosynthetic efficiency (Farmer, 1993; van Heerden, Kruger & Kilbourn Louw, 2007; Rai *et al*. 2010). Such responses slow growth (Farmer, 1993) and can provide faster growing species, such as *M. caerulea,* with a competitive advantage (Taylor *et al.* 2001). *M. caerulea* may continue to have a competitive advantage because it retains the vast majority of nutrients, particularly nitrogen, within its biomass through efficient recycling of nitrogen into its bulbous stem base at the end of each growing season (Taylor *et al.* 2001). Additionally, while *M. caerulea* has been shown to thrive in disturbed and nutrient-enriched environments (Byrs *et al.* 2005; Heil & Bruggink, 1987), *Sphagnum* species have been shown to decline with exposure to dust particulates and be replaced by faster growing, more competitive species (Farmer, 1993; Ireland *et al.* 2014). In particular, the decline of *S. austinii* in many British and Irish peatlands has been attributed to human-environment impacts, specifically dust-loading and burning (Swindles *et al*. 2015a).

Our findings indicate that there was no single trigger for the significant and sudden rise in abundance of *M. caerulea* in Swarth Moor. There is a clear correlation between the rise to dominance of the species and contemporaneous rises in micro-charcoal, the reduction of organic matter (LOI), and nutrient (e.g. P) deposition and dust-loading (e.g. Al, Ti) within a hydrologically variable and heterogeneous site (Figure 12).

The rise of *M. caerulea* can be constrained to within a *c*. 25 year window that coincides with the first major expansion of the adjacent quarry ~1946-1973 (see Figure 2). This also coincides with increased inputs of nitrogen deposition and increased burning. Increased deposition of nitrogen is likely to have come from from the intensification of agriculture locally as well as regional increases from vehicular and industrial sources. However, the decline of Type 112 (a coprophilous marker) in the uppermost part of the cores may correspond to the reduction and eventual cessation of animal grazing within the peatland in recent years (Labadz *et al*. 2000, Meade *et al*. 2007, Headley, 2010).

Increased deposition of dust from the expansion of the quarries will have increased the inputs of nutrients and base minerals to the bog surface. Additionally, burning likely favoured *M. caerulea* by removing the dwarf-shrub cover as well as increasing mineral concentrations in the surface layers. Other factors may have also been important, including changes in grazing regime; the absence of any recent management strategy to remove or reduce *M. caerulea*; and hydrological changes in the site due to drainage and recent climatic variability. We surmise that these various factors have combined to form a compound press disturbance, sufficient to cause major and ongoing changes to ecosystem structure and functioning.

Our study illustrates how peatlands can recover naturally over long timescales from anthropogenic pulse disturbances, such as major peat cutting. Although spontaneous recovery of vegetation on peat surfaces following peat cutting has been recorded previously (Campeau and Rochefort, 1996; Cooper *et al.* 2001; Lavoie *et al.* 2003), and evidence of peat cutting has been found in the palaeoecological record (Buttler *et al.* 1996; Magyari *et al.* 2001), our research shows spontaneous recovery after several episodes of damage. In comparison, the magnitude of the anthropogenic compound press disturbances in the last ~50 years appears to be sufficient to overcome the ecosystem's capacity for resistance in the short term. Our study site represents an example of a peatland subjected to extreme local impacts from human activity, but may provide explanations for events observed on other peatlands. Our work may also serve as a model for the future of peatlands if land-use intensity and impacts continue to increase into the Anthropocene.

Conclusions

1. We developed a comprehensive multiproxy palaeoecological dataset from a degraded raised bog in Northern England to examine its ecosystem stability and long-term dynamics in response to anthropogenic disturbance over a variety of timescales.
2. A combination of recent factors set against a background of severe impacts in the past has led to the bog's current condition. Peat cutting during the Iron Age, medieval period and post-medieval periods, including more recent peat cutting in the late-eighteenth/nineteenth-century, has removed several metres of peat. However, following past peat cutting, peat accumulation spontaneously resumed without active restoration illustrating the long-term resilience of the ecosystem to this kind of pulse disturbance.
3. A major influx of *Molinia caerulea* between ~1950 and 1975 is coincident with anthropogenic impacts, including increased dust-loading from localised quarrying, nutrient-loading and heavy metal deposition from agricultural fertilizers and airborne pollutants, and localised within-site burning. It is most likely that there was no single trigger for the invasion and subsequent dominance of *M. caerulea*. Instead many factors have acted in concert in the last ~50 years to create the right conditions for its recent dominance across the site.
4. Our unique study illustrates the importance of palaeoecology for understanding resilience and resistance in peatland ecosystems. The long timescales involved in spontaneous recovery of peatlands are beyond those of direct human observation or monitoring schemes following contemporary restoration efforts. The ability of peatlands to recover spontaneously over long timescales is perhaps instructive in shaping contemporary restoration efforts and policy.

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Data Accessibility

All data are available in the Dryad Digital Repository (Swindles et al. 2015): http://dx.doi.org/10.5061/dryad.762b8.

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Figure captions

Fig. 1. Map of Swarth Moor overlying Google Earth image (see Fig. 2) showing SM1-3 core locations and positions of short monolith samples (A-H). Each square represents an area of 100 × 100 metres.

Fig. 2. Aerial photographs of Swarth Moor: (A) RAF/106G/UK/1514 (318) (16 May 1946) English Heritage (RAF photography). (B) MAL/52022 (1022) (Apr. 1952) Historic England. (C) MAL/68048 (136) (14 Jun. 1968) © North Yorkshire County Council. (D) OS/71346 (27) (11 Jul. 1971) © Crown copyright, Ordnance Survey, All rights reserved. (E) OS/73387 (266) (28 Jul. 1973) © Crown copyright, Ordnance Survey, All rights reserved. (F) ADA/BKS/2951 (259) (12 May 1980) © Crown copyright, Historic England. (G) OS/95535 (58) (1 May 1995) © Crown copyright, Ordnance Survey, All rights reserved. (H) OS/991017 (3) (9 Nov. 1999) © Crown copyright, Ordnance Survey, All rights reserved. (I) OS/00578 (113) (16 Jun. 2000) Crown copyright, Ordnance Survey. Google Earth 7.0.2. 2015, 54° 07’ 12.54’’N, 2° 18’ 05.89’’W, elevation 216 m: (J) and (K) Google Earth 2015 (Infoterra Ltd. and Bluesky) (viewed 20 April 2015). (A) and (B) are reproduced by permission of Historic England.

Fig. 3. Spheroidal carbonaceous particle profiles from eight monolith samples.

Fig. 4. Age-depth models based on linear interpolation of maximum probabilities for cores SM1-3. The probable hiatuses are illustrated.

Fig. 5. Physical properties of cores SM1-3. The orange line denotes the depth of the first appearance of *M. caerulea* leaf epidermis in each core. The sections containing probable hiatuses are illustrated (blue shading). The precise locations of the hiatuses were determined from the palaeoenvironmental data (major shifts in bulk density, geochemistry and/or macrofossil content) and marked on subsequent diagrams.

Fig. 6. Geochemical data for cores SM1-3. The orange line denotes the depth of the first appearance of *M. caerulea* leaf epidermis in each core. The location of the hiatuses are illustrated.

Fig. 7. Percentage macrofossil data from cores SM1-3. Circles indicate the presence/absence of some minor components. Leaf counts are expressed as a percentage of the total identifiable *Sphagnum*. The orange line denotes the depth of the first appearance of *M. caerulea* leaf epidermis in each core. The probable hiatuses are illustrated.

Fig. 8. Percentage pollen diagram for SM1 including micro-charcoal and the *Lycopodium* spike. Non-pollen palynomorphs (NPPs) are shown juxtaposed with Poaceae (grass pollen) percentages to the left, and micro-charcoal and the *Lycopodium* spike to the right. The orange line denotes the depth of the first appearance of *M. caerulea* leaf epidermis in each core. The probable hiatuses are illustrated.

Fig. 9. Percentage pollen diagram for SM2 including micro-charcoal and the *Lycopodium* spike. Non-pollen palynomorphs (NPPs) are shown juxtaposed with Poaceae (grass pollen) percentages to the left, and micro-charcoal and the *Lycopodium* spike to the right. The orange line denotes the depth of the first appearance of *M. caerulea* leaf epidermis in each core. The probable hiatuses are illustrated.

Fig. 10. Percentage pollen diagram for SM3 including micro-charcoal and the *Lycopodium* spike. Non-pollen palynomorphs (NPPs) are shown juxtaposed with Poaceae (grass pollen) percentages to the left, and micro-charcoal and the *Lycopodium* spike to the right. The orange line denotes the depth of the first appearance of *M. caerulea* leaf epidermis in each core. The probable hiatuses are illustrated.

Fig. 11. Percentage testate amoebae data from cores SM1-3. The water table reconstruction is shown with errors generated from bootstrapping. The orange line denotes the depth of the first appearance of *M. caerulea* leaf epidermis in each core. The probable hiatuses are illustrated.

Fig. 12. Key data from each sequence plotted against age (the data are interpolated across the hiatuses).

Core	Depth (cm)	Troels-Smith (1955)	Humification	Description	Additional observations
SM1					
	0 - 3	*Th2 Tb(Sphag)2*	*none*	Contemporary *Molinia*/*Sphagnum* surface vegetation	
	3 - 15	*Sh2 Th2*	*very*	Very dark brown well-humified peat with little discernable plant matter and *Molinia* roots	Black coloured top
	15 - 34	*Tb(Sphag)2 Th2*	*moderate*	Brown moderately humified *Sphagnum* and sedge peat	
	34 - 80	*Tb(Sphag)2 Th2*	*poorly*	Brown less humified *Sphagnum* and sedge peat with more *Sphagnum*	
	80 - 92	*Tb(Sphag)2 Th2*	*moderate-well*	Moderately to well-humified orange-brown *Sphagnum*/sedge peat	
SM2					
	0 - 3	*Th2 Tb(Sphag)2*	*none*	Contemporary *Molinia*/*Sphagnum* surface vegetation	
	3 - 16	*Sh2 Th2*	*very*	Very dark brown well-humified peat with little discernable plant matter and *Molinia* roots	Black coloured top
	16 - 48	*Tb(Sphag)2 Th2*	*moderate*	Brown moderately humified *Sphagnum* and sedge peat with *Molinia* roots	
	48 - 64	*Tb(Sphag)2 Th2*	*poorly*	Brown less humified *Sphagnum* and sedge peat	
	64 - 84	*Tb(Sphag)2 Th2*	*Well*	Well-humified orange-brown *Sphagnum*/sedge peat	
	84 - 100	*Tb(Sphag)2 Th2*	*moderate*	Moderately humified dark brown *Sphagnum* peat with sedges	
SM3					
	0 - 3	*Th2 Tb(Sphag)2*	*none*	Contemporary *Molinia*/*Sphagnum* surface vegetation	
	3 - 20	*Sh2 Th2*	*very*	Very dark brown well-humified peat with little discernable plant matter and *Molinia* roots	Black coloured top
	20 -39	*Tb(Sphag)2 Th2*	*moderate*	Brown moderately humified *Sphagnum* and sedge peat	
	39 -61	*Tb(Sphag)2 Th2*	*moderate-well*	More humified orange-brown *Sphagnum*/sedge peat (*Eriophorum vaginatum*)	
	61 - 100	*Tb(Sphag)2 Th2*	*moderate-well*	Moderately to well-humified orange-brown *Sphagnum*/sedge peat	As 39 - 61 cm but more humified

Table 1. Lithostratigraphy of three cores from Swarth Moor (SM1-3).

Lab code	Depth (cm)	$\delta^{13}C$ (per mil)	Fraction of modern (pMC)	1σ error	^{14}C age (BP)	1σ error
SM1						
D-AMS 009188	25	-22.5	90.50	0.25	802	22
D-AMS 009189	35	-25.9	62.41	0.27	3787	35
D-AMS 009190	45	-23.5	62.47	0.23	3779	30
D-AMS 009191	55	-36.5	62.26	0.21	3806	27
D-AMS 009192	65	-28.2	62.16	0.23	3819	30
D-AMS 009193	75	-28.8	61.35	0.20	3925	26
D-AMS 009194	85	-29.1	61.32	0.20	3929	26
SM2						
D-AMS 009195	25	-23.9	84.18	0.26	1383	25
D-AMS 009196	35	-29.9	81.49	0.27	1644	27
D-AMS 009197	45	-28.4	78.90	0.27	1903	27
D-AMS 009198	55	-20.5	65.52	0.24	3396	29
D-AMS 009199	65	-35.7	64.08	0.22	3576	28
D-AMS 009200	75	-39.6	63.48	0.22	3651	28
D-AMS 009201	85	-28.9	64.13	0.26	3569	33
D-AMS 009202	95	-21.9	62.88	0.22	3727	28
SM3						
D-AMS 009203	25	-26.6	63.06	0.23	3704	29
D-AMS 009204	35	-33.2	62.57	0.20	3767	26
D-AMS 009205	45	-29.9	61.89	0.24	3854	31
D-AMS 009206	55	-34.8	61.43	0.22	3915	29
D-AMS 009207	65	-20.6	61.17	0.22	3948	29
D-AMS 009208	75	-33.9	60.49	0.22	4038	29
D-AMS 009209	85	-38.6	60.47	0.23	4040	31
D-AMS 009210	95	-17.5	59.27	0.23	4202	32

Table 2. ^{14}C determinations from Swarth Moor cores SM1-3.

Accumulation rates
SM1: 53.2 yr cm^{-1} (min), 14.5 yr cm^{-1} (max), **32.1 yr cm^{-1} (mean)**
SM1: 30.6 yr cm^{-1} (min), 9.5 yr cm^{-1} (max), **21.2 yr cm^{-1} (mean)**
SM3: 22.9 yr cm^{-1} (min), 9.1 yr cm^{-1} (max), **14.1 yr cm^{-1} (mean)**

Estimates of peat removed
SM1 Upper: 11 cm (min), 41 cm (max), **19 cm (mean)**
SM1 Lower: 65 cm (min), 238 cm (max), **108 cm (mean)**
SM2 Upper: 39 cm (min), 127 cm (max), **57 cm (mean)**
SM2 Lower: 58 cm (min), 188 cm (max), **84 cm (mean)**
SM3: 177 cm (min), 443 cm (max), **286 cm (mean)**

Table 3. Peat accumulation rates and estimates of peat removed (as represented by the hiatuses in the age models).

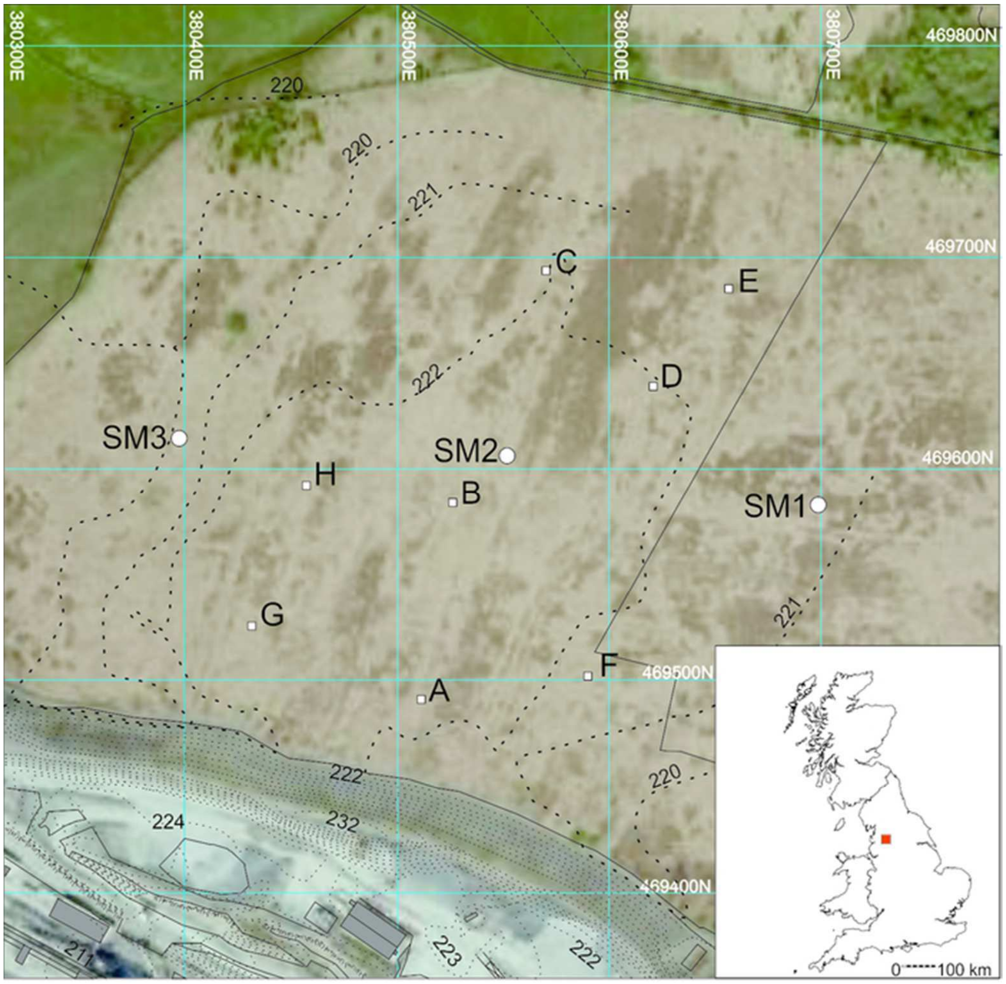
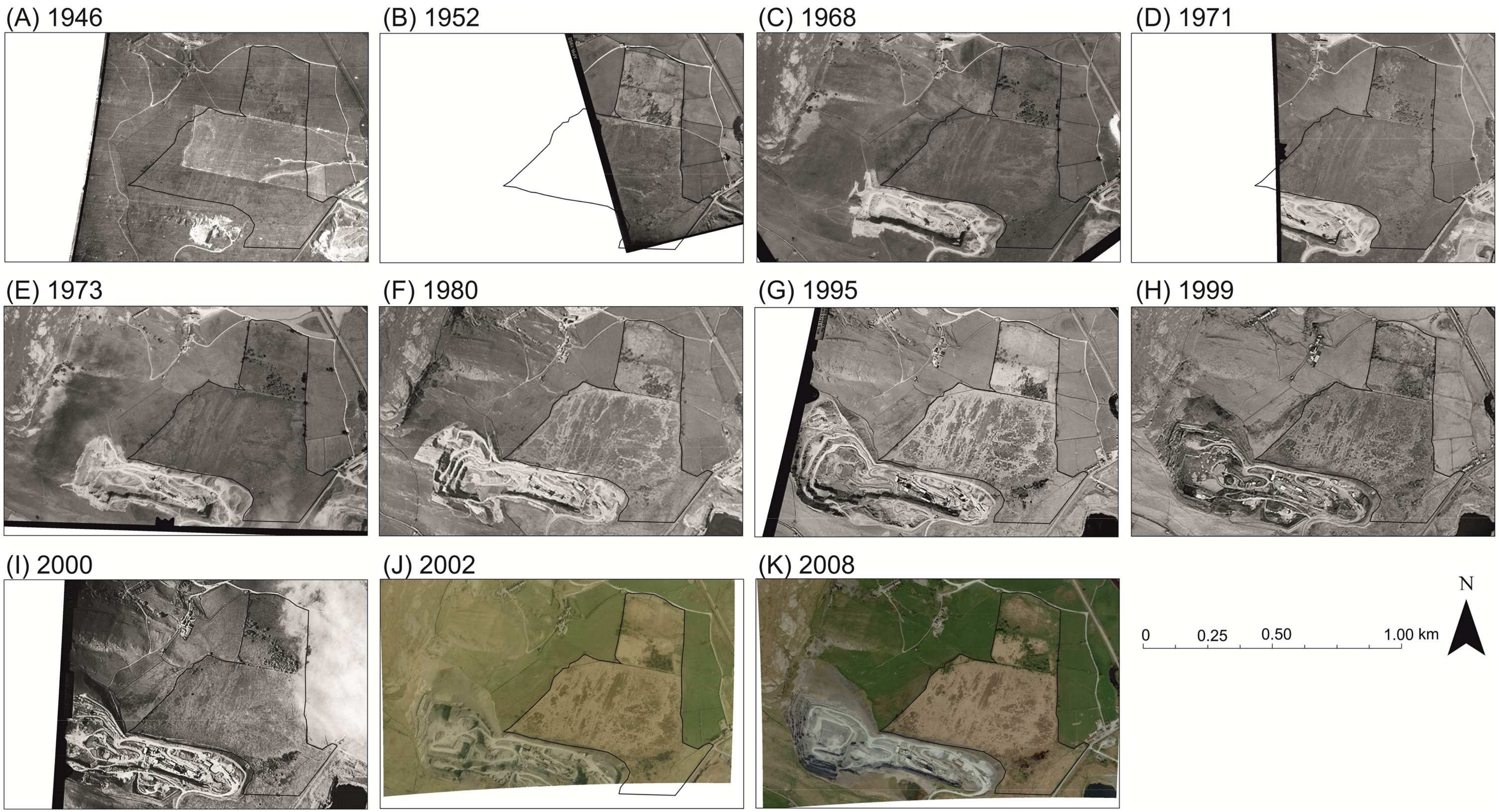
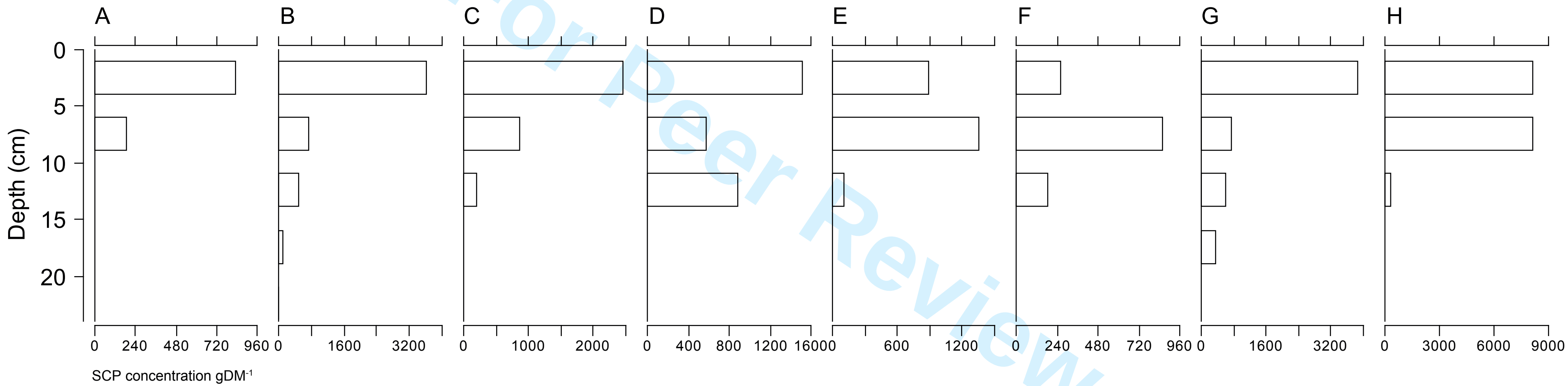
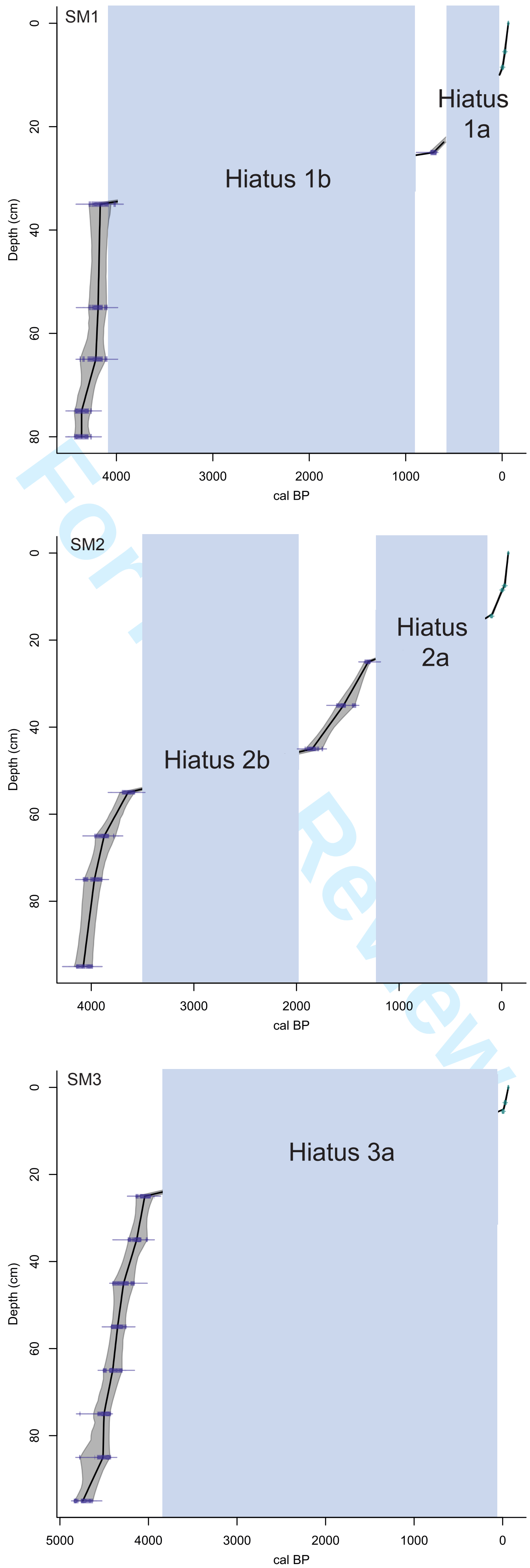
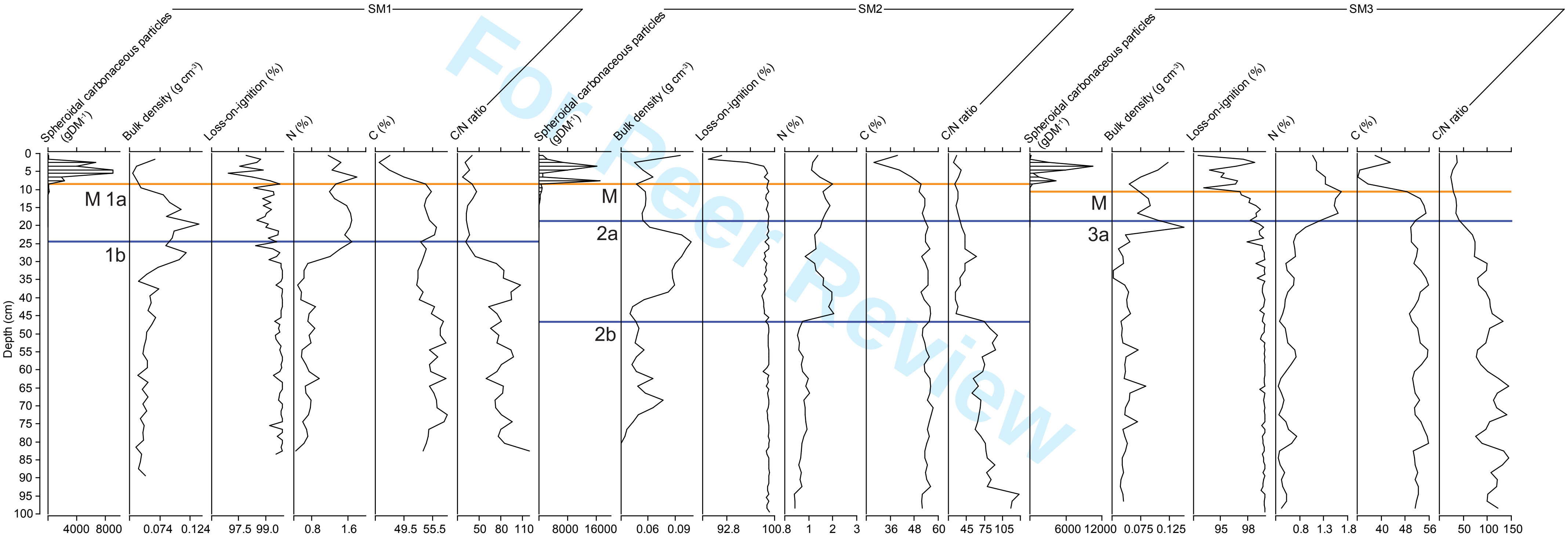


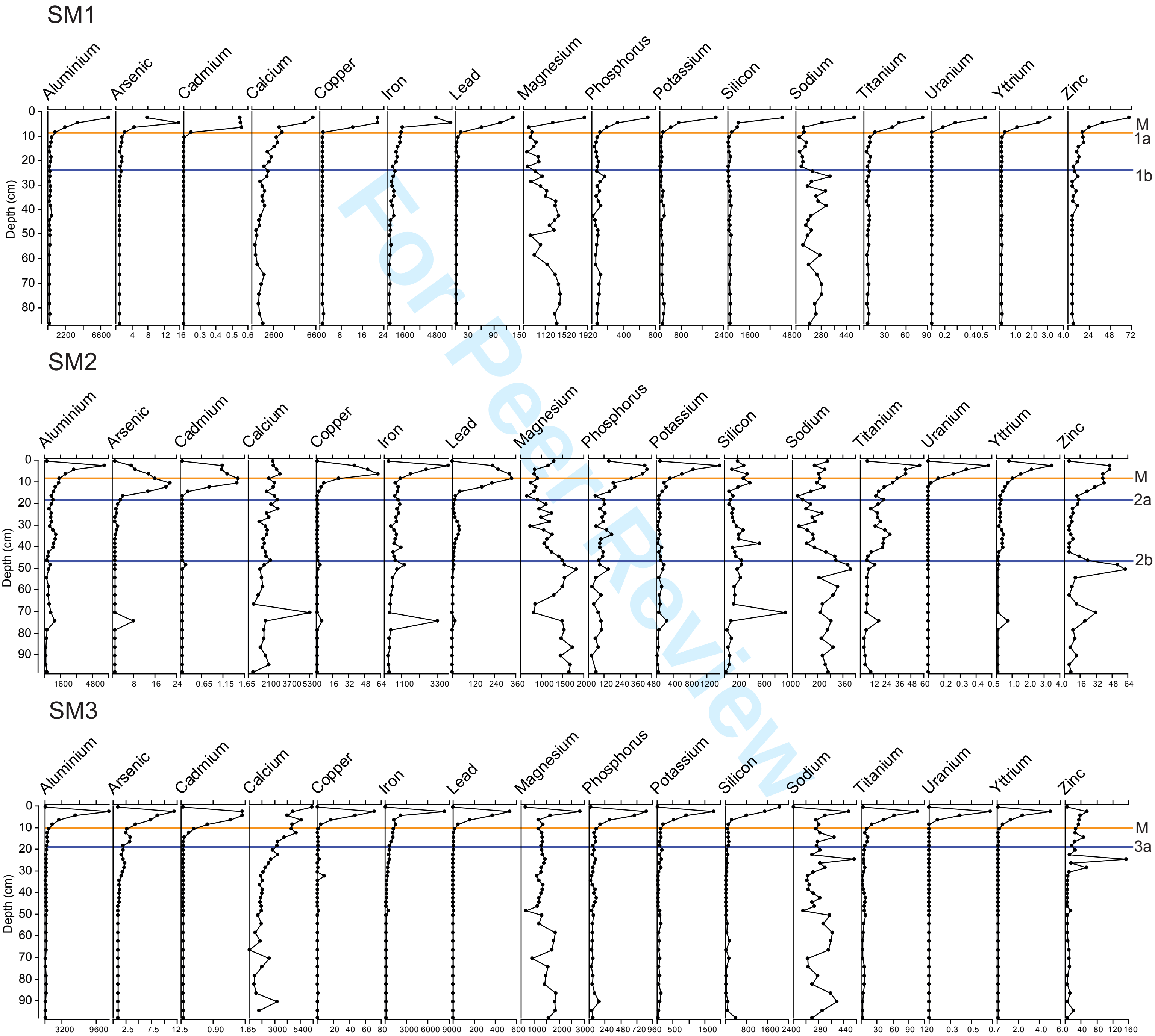
Fig. 1. Map of Swarth Moor overlying Google Earth image (see Fig. 2) showing SM1-3 core locations and positions of short monolith samples (A-H). Each square represents an area of 100 × 100 metres.
59x57mm (300 x 300 DPI)

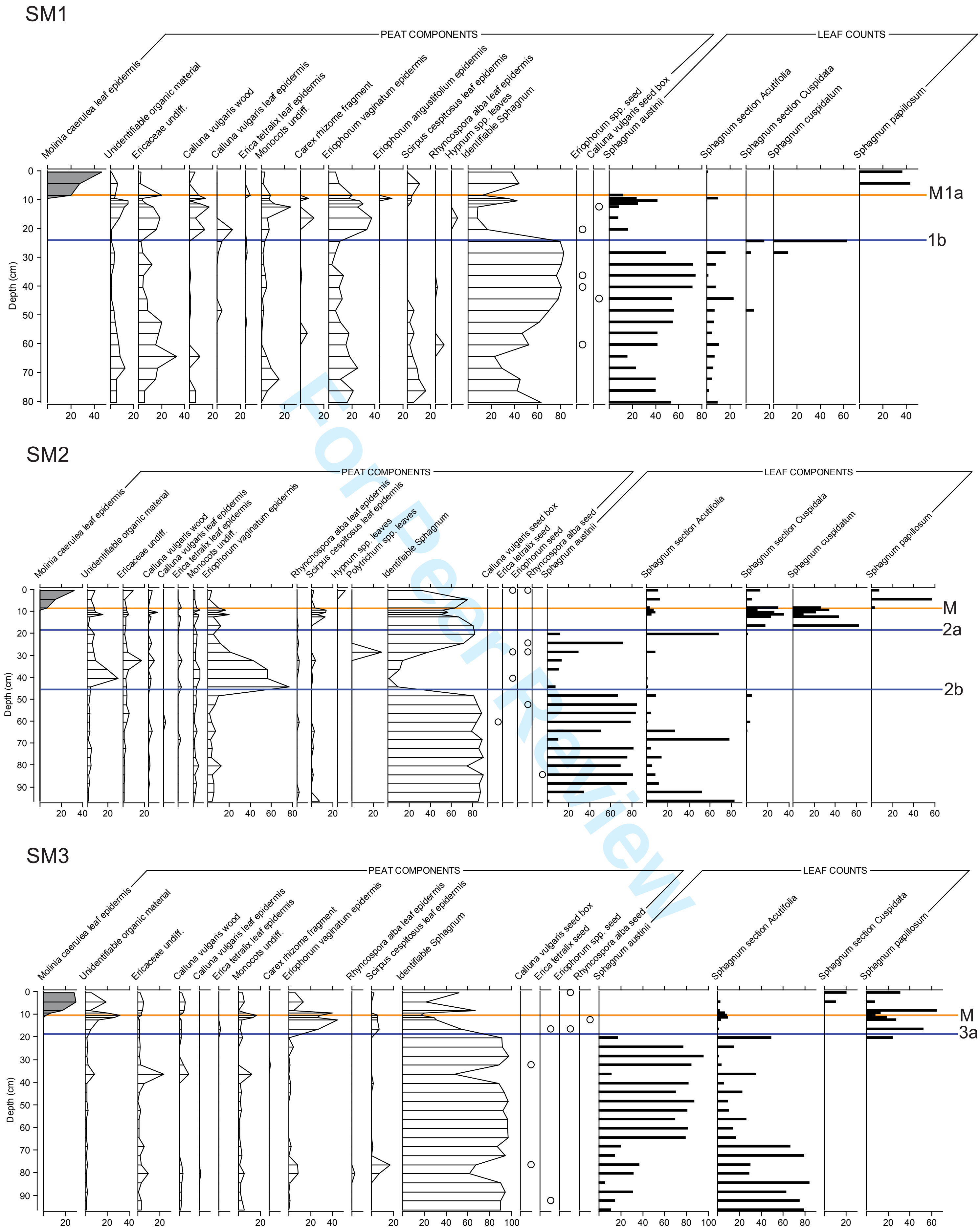

(A) 1946
(B) 1952
(C) 1968
(D) 1971
(E) 1973
(F) 1980
(G) 1995
(H) 1999
(I) 2000
(J) 2002
(K) 2008
0
0.25
0.50
1.00 km
N

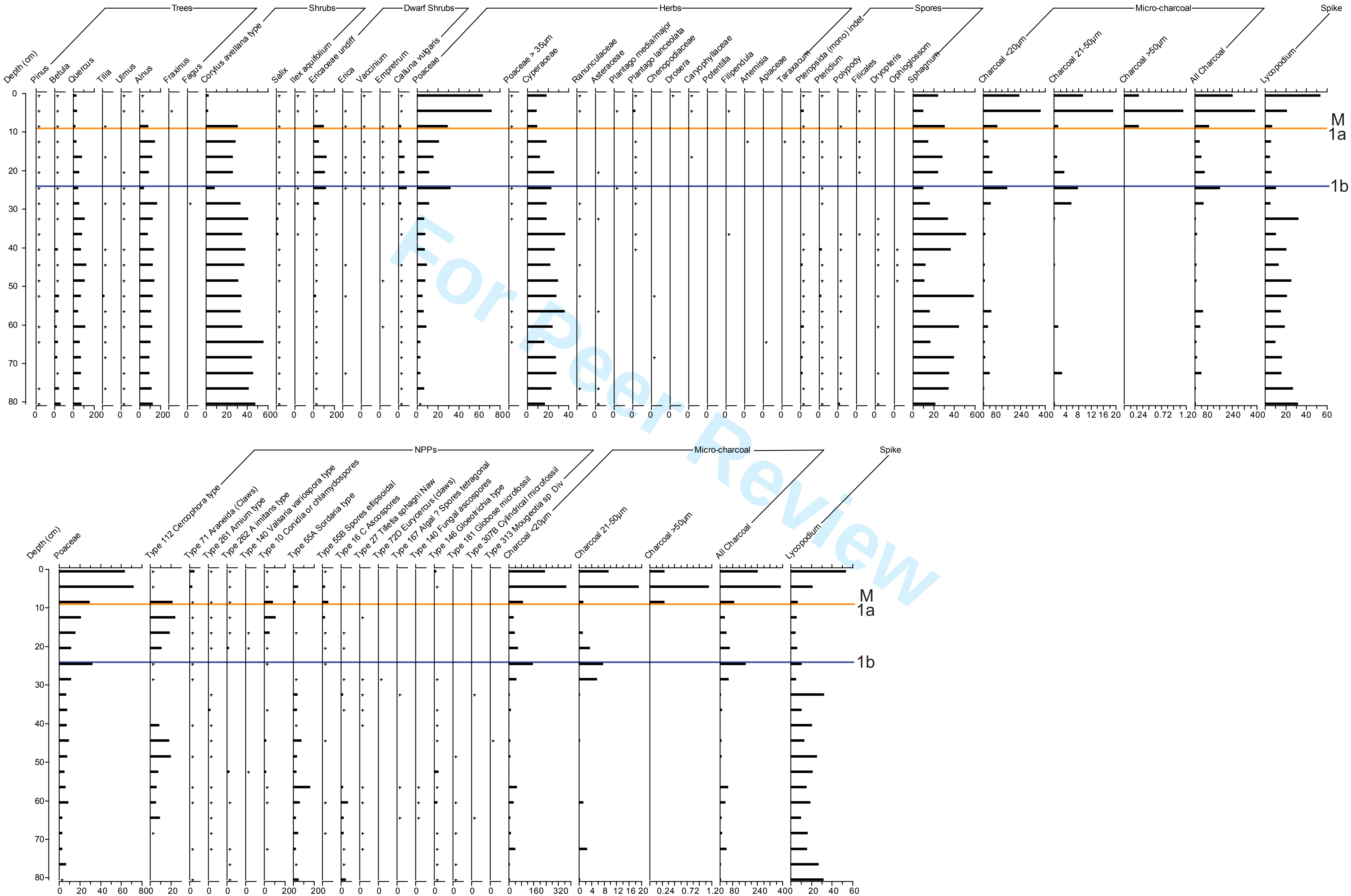

A
B
C
D
E
F
G
H
Depth (cm)
0
5
10
15
20
0 240 480 720 960
0 1600 3200
0 1000 2000
0 400 800 1200 1600
0 600 1200
0 240 480 720 960
0 1600 3200
0 3000 6000 9000
SCP concentration gDM-1

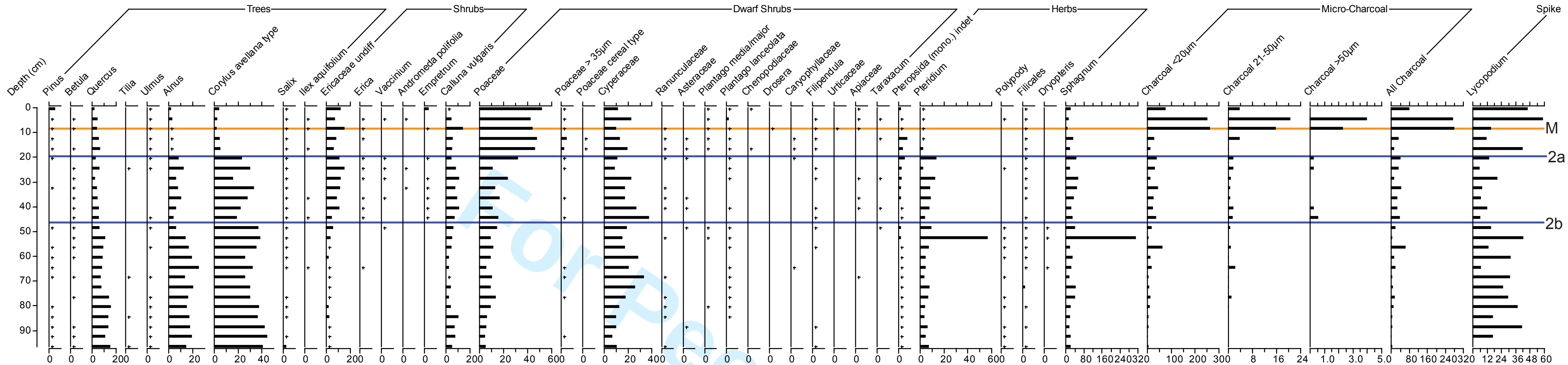

SM1
Hiatus 1b
Hiatus 1a
Depth (cm)
cal BP
SM2
Hiatus 2b
Hiatus 2a
Depth (cm)
cal BP
SM3
Hiatus 3a
Depth (cm)
cal BP

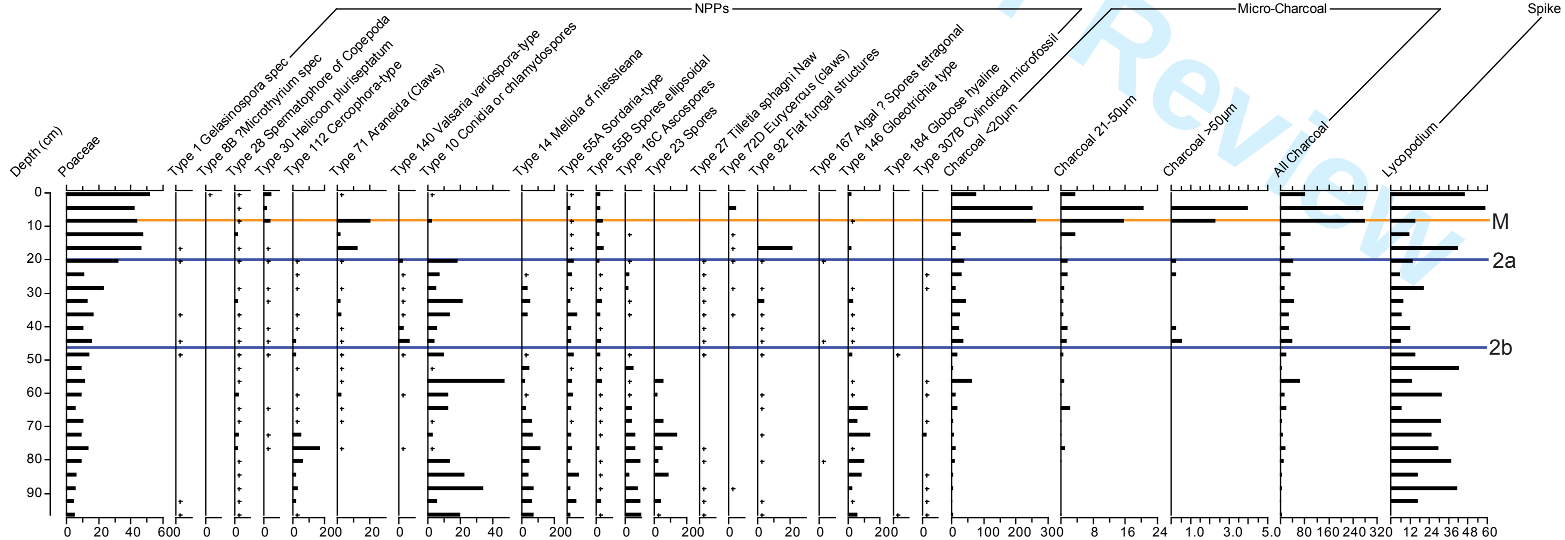

SM1
SM2
SM3
Spheroidal carbonaceous particles (gDM-1)
Bulk density (g cm-3)
Loss-on-ignition (%)
N (%)
C (%)
C/N ratio
Depth (cm)
M 1a
1b
M
2a
2b
3a
For Peer Review


SM1
Aluminium
Arsenic
Cadmium
Calcium
Copper
Iron
Lead
Magnesium
Phosphorus
Potassium
Silicon
Sodium
Titanium
Uranium
Yttrium
Zinc
Depth (cm)
M
1a
1b
SM2
M
2a
2b
SM3
M
3a

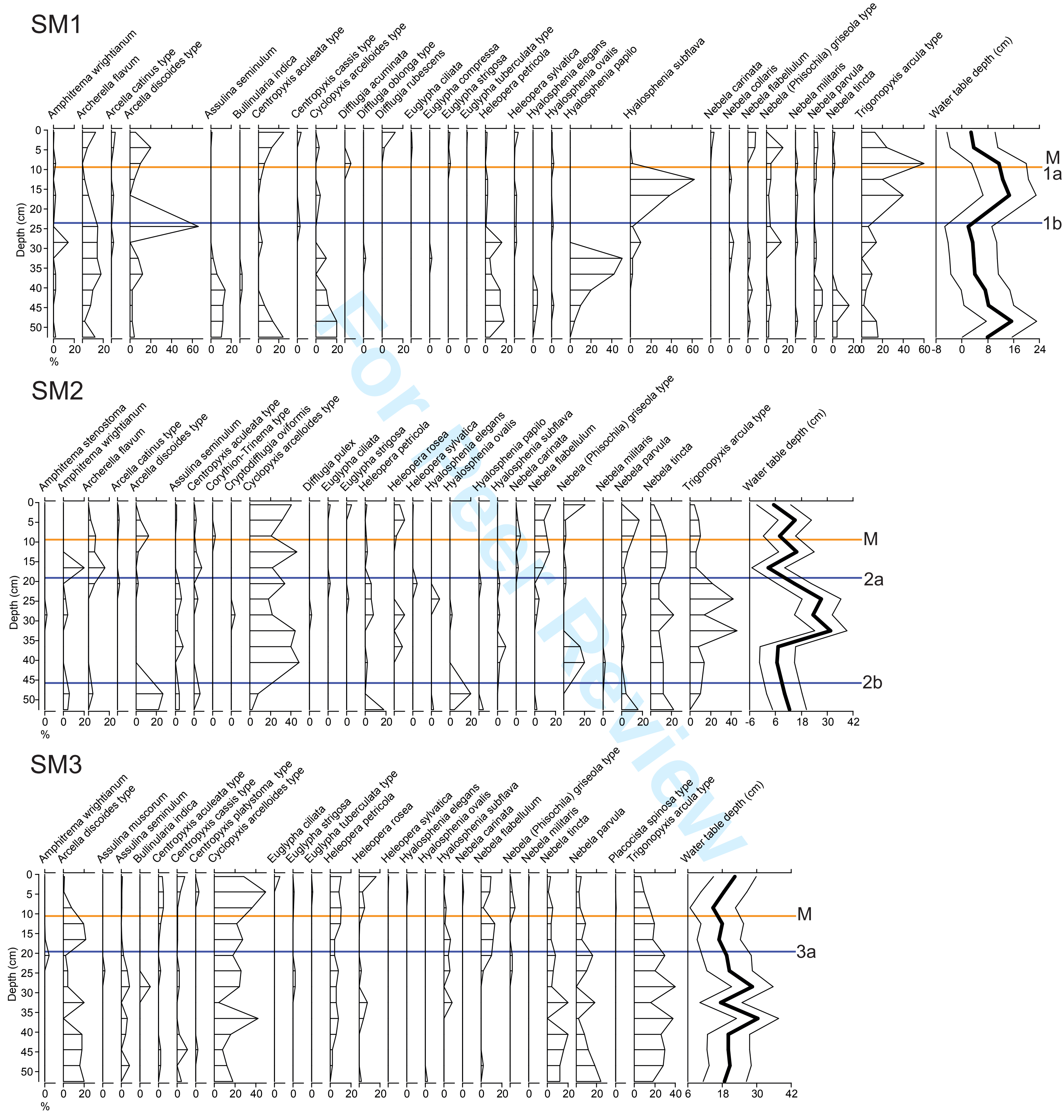

SM1
PEAT COMPONENTS
LEAF COUNTS
Molinia caerulea leaf epidermis
Unidentifiable organic material
Ericaceae undiff.
Calluna vulgaris wood
Calluna vulgaris leaf epidermis
Erica tetralix leaf epidermis
Monocots undiff.
Carex rhizome fragment
Eriophorum vaginatum epidermis
Eriophorum angustifolium epidermis
Scirpus cespitosus leaf epidermis
Rhyncospora alba leaf epidermis
Hypnum spp. leaves
Identifiable Sphagnum
Eriophorum spp. seed
Calluna vulgaris seed box
Sphagnum austinii
Sphagnum section Acutifolia
Sphagnum section Cuspidata
Sphagnum cuspidatum
Sphagnum papillosum
Depth (cm)
M1a
1b
SM2
PEAT COMPONENTS
LEAF COMPONENTS
Molinia caerulea leaf epidermis
Unidentifiable organic material
Ericaceae undiff.
Calluna vulgaris wood
Calluna vulgaris leaf epidermis
Erica tetralix leaf epidermis
Monocots undiff.
Eriophorum vaginatum epidermis
Rhynchospora alba leaf epidermis
Scirpus cespitosus leaf epidermis
Hypnum spp. leaves
Polytrichum spp. leaves
Identifiable Sphagnum
Calluna vulgaris seed box
Erica tetralix seed
Eriophorum seed
Rhyncospora alba seed
Sphagnum austinii
Sphagnum section Acutifolia
Sphagnum section Cuspidata
Sphagnum cuspidatum
Sphagnum papillosum
Depth (cm)
M
2a
2b
SM3
PEAT COMPONENTS
LEAF COUNTS
Molinia caerulea leaf epidermis
Unidentifiable organic material
Ericaceae undiff.
Calluna vulgaris wood
Calluna vulgaris leaf epidermis
Erica tetralix leaf epidermis
Monocots undiff.
Carex rhizome fragment
Eriophorum vaginatum epidermis
Rhyncospora alba leaf epidermis
Scirpus cespitosus leaf epidermis
Identifiable Sphagnum
Calluna vulgaris seed box
Erica tetralix seed
Eriophorum spp. seed
Rhyncospora alba seed
Sphagnum austinii
Sphagnum section Acutifolia
Sphagnum section Cuspidata
Sphagnum papillosum
Depth (cm)
M
3a

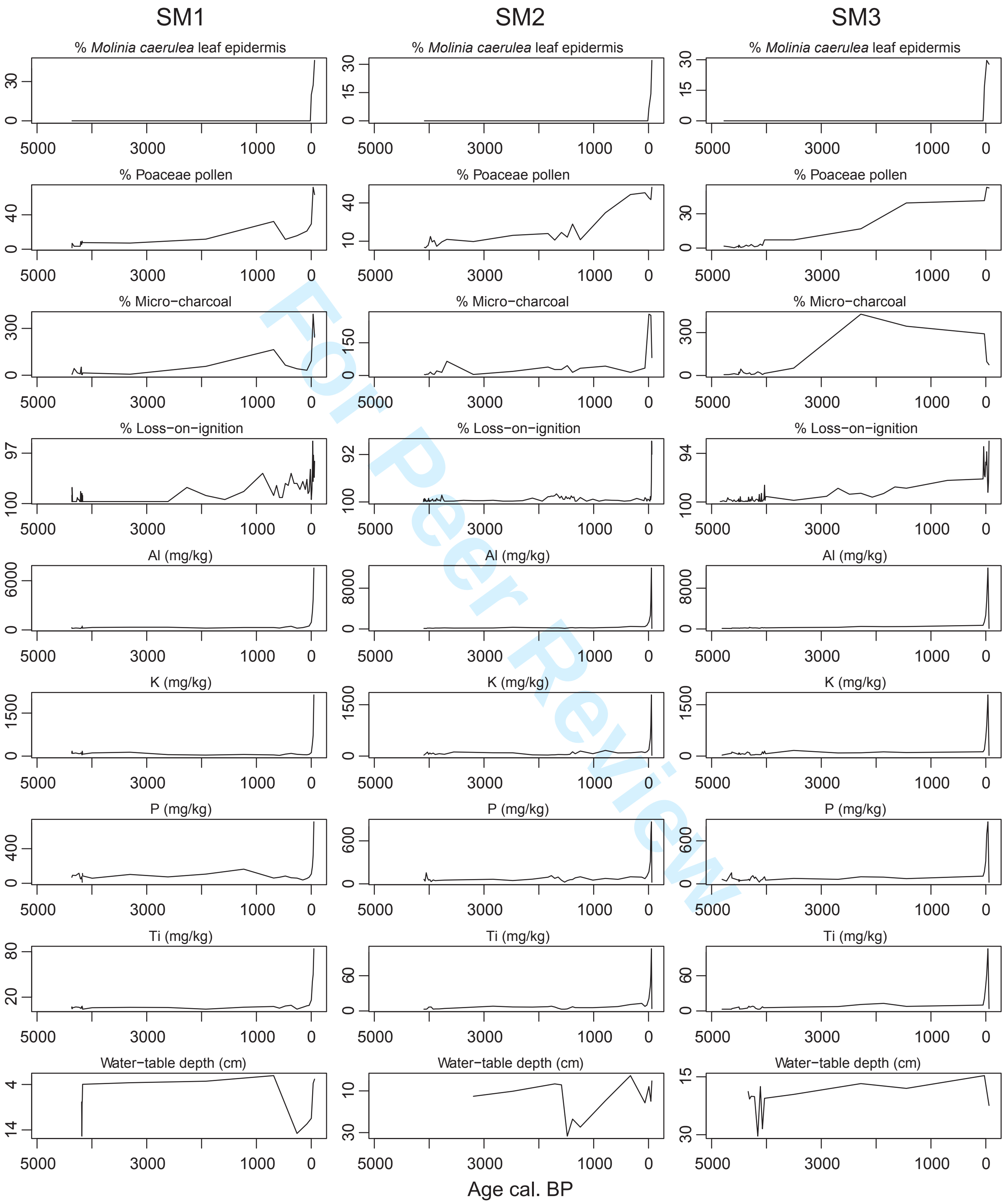

Trees
Shrubs
Dwarf Shrubs
Herbs
Spores
Micro-charcoal
Spike
Depth (cm)
Pinus
Betula
Quercus
Tilia
Ulmus
Alnus
Fraxinus
Fagus
Corylus avellana type
Salix
Ilex aquifolium
Ericaceae undiff
Erica
Vaccinium
Empetrum
Calluna vulgaris
Poaceae
Poaceae > 35µm
Cyperaceae
Ranunculaceae
Asteraceae
Plantago media/major
Plantago lanceolata
Chenopodiaceae
Drosera
Caryophyllaceae
Potentilla
Filipendula
Artemisia
Apiaceae
Taraxacum
Pteropsida (mono) indet
Pteridium
Polypody
Filicales
Dryopteris
Ophioglossom
Sphagnum
Charcoal <20µm
Charcoal 21-50µm
Charcoal >50µm
All Charcoal
Lycopodium
M
1a
1b
NPPs
Micro-charcoal
Spike
Depth (cm)
Poaceae
Type 112 Cercophora type
Type 71 Araneida (Claws)
Type 261 Arnium type
Type 262 A imitans type
Type 140 Valsaria variospora type
Type 10 Conidia or chlamydospores
Type 55A Sordaria type
Type 55B Spores ellipsoidal
Type 16 C Ascospores
Type 27 Tilletia sphagni Naw
Type 72D Eurycercus (claws)
Type 167 Algal ? Spores tetragonal
Type 140 Fungal ascospores
Type 146 Gloeotrichia type
Type 181 Globose microfossil
Type 307B Cylindrical microfossil
Type 313 Mougeotia sp. Div
Charcoal <20µm
Charcoal 21-50µm
Charcoal >50µm
All Charcoal
Lycopodium
M
1a
1b


Trees
Shrubs
Dwarf Shrubs
Herbs
Micro-Charcoal
Spike
Depth (cm)
Pinus
Betula
Quercus
Tilia
Ulmus
Alnus
Corylus avellana type
Salix
Ilex aquifolium
Ericaceae undiff
Erica
Vaccinium
Andromeda polifolia
Empetrum
Calluna vulgaris
Poaceae
Poaceae > 35µm
Poaceae cereal type
Cyperaceae
Ranunculaceae
Asteraceae
Plantago media/major
Plantago lanceolata
Chenopodiaceae
Drosera
Caryophyllaceae
Filipendula
Urticaceae
Apiaceae
Taraxacum
Pteropsida (mono.) indet
Pteridium
Polypody
Filicales
Dryopteris
Sphagnum
Charcoal <20µm
Charcoal 21-50µm
Charcoal >50µm
All Charcoal
Lycopodium
M
2a
2b


NPPs
Micro-Charcoal
Spike
Depth (cm)
Poaceae
Type 1 Gelasinospora spec
Type 8B ?Microthyrium spec
Type 28 Spermatophore of Copepoda
Type 30 Helicoon pluriseptatum
Type 112 Cercophora-type
Type 71 Araneida (Claws)
Type 140 Valsaria variospora-type
Type 10 Conidia or chlamydospores
Type 14 Meliola cf niessleana
Type 55A Sordaria-type
Type 55B Spores ellipsoidal
Type 16C Ascospores
Type 23 Spores
Type 27 Tilletia sphagni Naw
Type 72D Eurycercus (claws)
Type 92 Flat fungal structures
Type 167 Algal ? Spores tetragonal
Type 146 Gloeotrichia type
Type 184 Globose hyaline
Type 307B Cylindrical microfossil
Charcoal <20µm
Charcoal 21-50µm
Charcoal >50µm
All Charcoal
Lycopodium
M
2a
2b


Trees
Shrubs
Dwarf Shrubs
Herbs
Spores
Micro-Charcoal
Spike
Depth (cm)
Pinus
Betula
Quercus
Tilia
Ulmus
Alnus
Fagus
Corylus avellana type
Salix
Ilex aquifolium
Ericaceae undiff
Erica
Vaccinium
Andromeda polifolia
Empetrum
Calluna vulgaris
Poaceae
Poaceae > 35µm
Cyperaceae
Ranunculaceae
Asteraceae
Plantago lanceolata
Caryophyllaceae
Filipendula
Apiaceae
Taraxacum
Pteropsida (mono.) indet
Pteridium
Polypody
Filicales
Sphagnum
Charcoal <20µm
Charcoal 21-50µm
Charcoal >50µm
All Charcoal
Lycopodium
M
3a
NPPs
Type 1 Gelasinospora spec
Type 3B Pleospora spec
Type 8B ?Microthyrium spec
Type 28 Spermatophore of Copepoda
Type 30 Helicoon pluriseptatum
Type 63 Mites
Type 112 Cercophora-type
Type 71 Araneida (Claws)
Type 140 Valsaria variospora-type
Type 10 Conidia or chlamydospores
Type 14 Meliola cf niessleana
Type 55A Sordaria-type
Type 55B Spores ellipsoidal
Type 16C Ascospores
Type 23 Spores
Type 27 Tilletia sphagni Naw
Type 72D Eurycercus (claws)
Type 92 Flat fungal structures
Type 146 Gloeotrichia type
Type 184 Globose hyaline
Type 307B Cylindrical microfossil


SM1
Amphitrema wrightianum
Archerella flavum
Arcella catinus type
Arcella discoides type
Assulina seminulum
Bullinularia indica
Centropyxis aculeata type
Centropyxis cassis type
Cyclopyxis arcelloides type
Difflugia acuminata
Difflugia oblonga type
Difflugia rubescens
Euglypha ciliata
Euglypha compressa
Euglypha strigosa
Euglypha tuberculata type
Heleopera petricola
Heleopera sylvatica
Hyalosphenia elegans
Hyalosphenia ovalis
Hyalosphenia papilo
Hyalosphenia subflava
Nebela carinata
Nebela collaris
Nebela flabellulum
Nebela (Phisochila) griseola type
Nebela militaris
Nebela parvula
Nebela tincta
Trigonopyxis arcula type
Water table depth (cm)
Depth (cm)
%
M
1a
1b
SM2
Amphitrema stenostoma
Amphitrema wrightianum
Archerella flavum
Arcella catinus type
Arcella discoides type
Assulina seminulum
Centropyxis aculeata type
Corythion-Trinema type
Cryptodifflugia oviformis
Cyclopyxis arcelloides type
Difflugia pulex
Euglypha ciliata
Euglypha strigosa
Heleopera petricola
Heleopera rosea
Heleopera sylvatica
Hyalosphenia elegans
Hyalosphenia ovalis
Hyalosphenia papilo
Hyalosphenia subflava
Nebela carinata
Nebela flabellulum
Nebela (Phisochila) griseola type
Nebela militaris
Nebela parvula
Nebela tincta
Trigonopyxis arcula type
Water table depth (cm)
Depth (cm)
%
M
2a
2b
SM3
Amphitrema wrightianum
Arcella discoides type
Assulina muscorum
Assulina seminulum
Bullinularia indica
Centropyxis aculeata type
Centropyxis cassis type
Centropyxis platystoma type
Cyclopyxis arcelloides type
Euglypha ciliata
Euglypha strigosa
Euglypha tuberculata type
Heleopera petricola
Heleopera rosea
Heleopera sylvatica
Hyalosphenia elegans
Hyalosphenia ovalis
Hyalosphenia subflava
Nebela carinata
Nebela flabellulum
Nebela (Phisochila) griseola type
Nebela militaris
Nebela tincta
Nebela parvula
Placocista spinosa type
Trigonopyxis arcula type
Water table depth (cm)
Depth (cm)
%
M
3a


SM1
SM2
SM3
% Molinia caerulea leaf epidermis
% Poaceae pollen
% Micro−charcoal
% Loss−on−ignition
Al (mg/kg)
K (mg/kg)
P (mg/kg)
Ti (mg/kg)
Water−table depth (cm)
Age cal. BP