

# Vegetation History and Archaeobotany

## Late Holocene regime shifts in moorland ecosystems: high resolution data from the Pennines, UK --Manuscript Draft--

<b>Manuscript Number:</b>	VHAA-D-15-00015R3	
<b>Full Title:</b>	Late Holocene regime shifts in moorland ecosystems: high resolution data from the Pennines, UK	
<b>Article Type:</b>	Original Article	
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<b>Order of Authors Secondary Information:</b>		
<b>Funding Information:</b>	Economic and Social Research Council (RES-229-27-0003)	Dr Althea L Davies
<b>Abstract:</b>	<p>Identifying critical shifts in ecosystems caused by human impacts has become a priority for understanding resilience to change and setting realistic management goals. Previous work suggests that many British blanket peats have suffered a loss of functional integrity over recent centuries, but it is unclear whether all moorland habitats are equally vulnerable. This study examines the relative sensitivity of four contrasting moorland communities to historic land-use changes and assesses whether these management pressures are pushing some moorlands beyond their Holocene range of variability. Late Holocene dynamics in the Peak District, northern England, were investigated using high-resolution pollen, fungal spore and charcoal data, and multivariate analyses. All sites show high <i>Calluna</i> values during the nineteenth century and converge on local <i>Poaceae</i>-dominance during the twentieth century. This involved a shift from gradual or cyclical variability and moderate changes in pollen abundance during preceding centuries, to rapid transitions between mono-dominant pollen assemblages and a functional shift to taxa with competitive traits; these are interpreted as a regime shift. Evidence for the recent recovery of dwarf-shrubs and <i>Sphagnum</i> is strong at one site, with slight evidence from two others, but disturbance could push the system back to grass-dominance. The deep blanket peat site may have crossed a threshold, leading to a persistent grass-dominated state. Studying regime shifts on decadal to centennial scales can help bridge the gap between ecology and palaeoecology by providing a robust basis for assessing vulnerability, setting restoration priorities and managing novel peatland states.</p>	
<b>Response to Reviewers:</b>	<p>Revisions made to this submission:</p> <p>Updated Bennett reference - with current School name (the pollen catalogue gives the older Archaeology and Palaeoecology departmental name)</p> <p>Attached all figures in EPS format.</p> <p>Checked image resolution in Online resource 1: sufficient for viewing at &gt;100% size. I have uploaded an amended file without 'track changes' which were inadvertently left in revision r2.</p>	

Accepted minor text amendments

## Late Holocene regime shifts in moorland ecosystems: high-resolution data from the Pennines, UK

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### ABSTRACT

Identifying critical shifts in ecosystems caused by human impacts has become a priority for understanding resilience to change and setting realistic management goals. Previous work suggests that many British blanket peats have suffered a loss of functional integrity over recent centuries, but it is unclear whether all moorland habitats are equally vulnerable. This study examines the relative sensitivity of four contrasting moorland communities to historic land-use changes and assesses whether these management pressures are pushing some moorlands beyond their Holocene range of variability. Late Holocene dynamics in the Peak District, northern England, were investigated using high-resolution pollen, fungal spore and charcoal data, and multivariate analyses. All sites show high *Calluna* values during the nineteenth century and converge on local Poaceae-dominance during the twentieth century. This involved a shift from gradual or cyclical variability and moderate changes in pollen abundance during preceding centuries, to rapid transitions between mono-dominant pollen assemblages and a functional shift to taxa with competitive traits; these are interpreted as a regime shift. Evidence for the recent recovery of dwarf-shrubs and *Sphagnum* is strong at one site, with slight evidence from two others, but disturbance could push the system back to grass-dominance. The deep blanket peat site may have crossed a threshold, leading to a persistent grass-dominated state. Studying regime shifts on decadal to centennial scales can help bridge the gap between ecology and palaeoecology by providing a robust basis for assessing vulnerability, setting restoration priorities and managing novel peatland states.

**Keywords** Conservation • Dung fungi • Heathland • Peak District • Peatland • Pollen analysis

# Late Holocene regime shifts in moorland ecosystems: high-resolution data from the Pennines, UK

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## Introduction

Long time-series are essential for understanding the variability that underpins ecosystem function and for detecting when a system is moving outside its 'normal' response range (Jackson 2006; Wolkovich et al. 2014). This is particularly relevant for peatlands because they contribute substantially to biodiversity, biogeochemical processes and ecosystem services, and are also at high risk of degradation from climate change and inappropriate management (Gallego-Sala et al. 2013; Holden et al. 2007; Parish et al. 2008). The United Kingdom (UK) is amongst the top ten countries in terms of peatland area, supporting around 9-15% of Europe's peatland, but only ca. 20% of UK peatlands are considered undamaged (Bain et al. 2011; Tallis 1998). Numerous changes over the last ca. 200–800 years have contributed to a loss of functional integrity in some UK peatlands, including regional evidence for the contraction of heather (*Calluna vulgaris*) moorland and spread of unpalatable grasses (Poaceae: mainly *Molinia caerulea* and *Nardus stricta*), the local extinction of key peat-forming *Sphagnum* species and onset of extensive blanket peat erosion (Chambers et al. 2007a; Hughes et al. 2008; Stevenson and Thompson 1993; Tallis 1998; Tipping 2000; higher plant nomenclature follows Stace 2010). It is therefore unsurprising that several authors have advocated the use of palaeoecology to inform peatland conservation and restoration (Chambers et al. 2007a; Davies and Bunting 2010).

Most existing analyses, however, either derive from lakes with a regional pollen source area reflecting catchment-scale trends rather than community-level patterns, or focus on 'degraded' communities, such as eroding blanket peat or grass-dominated moors. As a result, it is unclear whether all moorland habitats should be considered equally vulnerable or if they exhibit differential sensitivity to stress which could help prioritise sites for conservation and restoration. In particular, there is a lack of data on the dynamics of non-eroding communities during recent centuries, when severe impacts have emerged. This creates uncertainty about the extent of moorland turnover (Dallimer et al. 2009) and the role of burning in sustainable management (Lee et al. 2013). Extrapolating across heterogeneous upland terrain may underestimate the extent of past spatial heterogeneity and temporal variability (Davies and Tipping 2004; Fyfe and Woodbridge 2012), so high spatial-resolution pollen analyses from different peatland habitats can usefully be employed to address these issues. This is also the scale at which palaeoecology can contribute to management (Davies and Bunting 2010).

This paper examines changes in the late Holocene (historic) range of variability across a network of four non-eroding sites, i.e. with continuous vegetation cover, and representing a gradient from degraded grass-dominated moor (grassmoor) to heather moorland with high conservation-value. It assesses whether changes in the relative abundance of the main moorland taxa (*Calluna* and Poaceae) are comparable with previous findings, indicating regional homogenisation (Chambers et al. 1999, 2013; Smart et al. 2006; Stevenson and Thompson 1993), or whether they show heterogeneous patch-scale dynamics indicative of differential sensitivity to late Holocene land-use pressures. The paper then considers whether cumulative pressures during the late Holocene have caused some moorland communities to move beyond their previous range of variability, and assesses the implications for conservation management, particularly the restoration of heterogeneity on grass-dominated moors.

## Study area

1 The study sites are located in the Peak District, South Pennines, northern England (Fig. 1). The Pennine  
2 uplands contain the main area of deep blanket peat in England (Joint Nature Conservation Committee  
3 2011). South Pennine moors lie on the south-eastern range limits for extensive, deep blanket peat in  
4 Britain, and so are at risk from climate change (House et al. 2010). Historic and twentieth-century  
5 grazing densities were high, and the moorlands inherited a heavy pollution burden from adjacent,  
6 formerly industrial, cities and towns (Dallimer et al. 2009; Lee 1998; Shimwell 1974). These accumulated  
7 pressures contributed to extensive erosion which may challenge ecosystem capacity for recovery and  
8 have costly implications for biodiversity conservation, managing carbon budgets and water quality  
9 (Anderson et al. 2009; Worrall et al. 2006).

## Materials and methods

### Site selection

14 Four sites were selected along a gradient from 'degraded' grassmoor on deep blanket peat (Withens  
15 Moor), where drainage may enhance decomposition and reinforce *Molinia* dominance (cf. Tallis 1985),  
16 to a *Calluna*-rich moor (Emlin Dike) which represents an internationally-distinctive community and  
17 restoration target (Thompson et al. 1995) (Table 1, Online resource 1). These are complemented by two  
18 grass/dwarf-shrub moors with heterogeneous hydrology and vegetation, including some *Vaccinium*  
19 *oxycoccus*, *V. myrtillus* and *Erica tetralix* (Bar Brook; Cranberry Bed). All sites are grazed, and heather  
20 cover on Emlin Dike has been managed by rotational patch burning for grouse production since AD 1950  
21 (Estate manager, 2010, personal communication). The topography and small diameter of the sampling  
22 sites suggest that vegetation growing within ca. 2–50 m dominates the pollen signal (particularly for  
23 herbaceous and heath taxa), with smaller contributions from the surrounding 400–1000 m (Broström et  
24 al. 2005; Bunting 2003). The sites thus record community variability on a spatial scale comparable with  
25 ecological monitoring, albeit with differing taxonomic resolution. High-resolution analyses focus on  
26 recent centuries. As Peak District moors have been monitored since 1913, this provides a century of  
27 overlap between ecology and palaeoecology (Online resource 2).

### Sampling and analysis

28 A 50 cm peat core was extracted at each site using a golf-hole corer, which allows an undisturbed  
29 sediment core to be obtained from poorly-humified, near-surface peat deposits. Cores were analysed  
30 for pollen, non-pollen palynomorphs (NPP) and microscopic charcoal. Analysis of 0.5 cm<sup>3</sup> samples  
31 followed standard pollen processing techniques (Moore et al. 1991). Pollen identification was based on  
32 standard keys (Moore et al. 1991) and the University of Stirling reference collection. Pollen  
33 nomenclature follows Bennett (1994). *Vaccinium*-type follows Bennett (1994). Grains were identified as  
34 *Erica* where colpus margins were sufficiently clear to permit distinction (cf. Oldfield 1959). Ericales  
35 includes all ericoid tetrads that could not be identified to a higher taxonomic unit. Selected NPP were  
36 identified and counted on pollen slides to provide additional proxies for grazing (coprophilous fungal  
37 spores: *Sporormiella* HdV-113, *Sordaria*-type HdV-55A, *Podospora*-type HdV-368), burning  
38 (*Gelasinospora* HdV-1, *Gelasinospora cf. reticulispota* HdV-2, *Coniochaeta xylariispora* HdV-6,  
39 *Neurospora* HdV-55C), and particular moorland taxa or hydrological conditions (*Meliola ellisii* HdV-14,  
40 *Triglocladium opacum* HdV-10, HdV-18) (van Geel 1978; van Geel and Aptroot 2006; Yeloff et al. 2007).  
41 Microscopic charcoal fragments >10 µm were counted on pollen slides in different size classes as a  
42 proxy for burning. Charcoal quantities were overwhelmingly high in a few samples (primarily dated to  
43 the 20<sup>th</sup> century), so only fragments >75µm were tallied in these. A minimum of 300 total land pollen  
44 (TLP, including bog taxa as important components of moorland vegetation, but excluding aquatic taxa  
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and spores) was counted for each sample (mean count: 352 TLP). Percentage values for taxa outside the TLP sum were calculated as TLP + taxon. Non-pollen sums (charcoal fragments, NPP) were calculated as a percentage of TLP.

Pollen diagrams were constructed using TILIA and TILIA\*GRAPH, with local pollen assemblage zones defined at each site using constrained sum of squares analysis (Grimm 1987) to identify periods of similar pollen composition. Changes in pollen diversity are estimated using rarefaction (Birks and Line 1992) implemented in Psimpoll 4.27 (written by K.D. Bennett) with a standardised pollen sum of 300 TLP. Using small sites maximises the local pollen signal (alpha-diversity) over landscape and regional pollen contributions (gamma-diversity). Rarefaction results are interpreted as an indication of species richness and vegetation evenness, since changes in local population size are likely to influence palynological richness values at sites with a small pollen source area (Birks and Line 1992; Odgaard 2013).

The combined pollen dataset from the four sequences was analysed using principal components analysis (PCA) to compare compositional differences and trajectories between sites. Gradient length in an initial detrended correspondence analysis was <2 SD, indicating that a linear response model was appropriate. Only taxa with a value of  $\geq 2\%$  in at least one site were included to avoid rare types biasing the analysis. To compare the extent of compositional change among sites, each sequence was also analysed using detrended canonical correspondence analysis (DCCA). Gradient length on the first DCCA axis provides an estimate of the amount of compositional turnover (beta-diversity) over time (Birks 2007). Sample age was used as the external constraint (canonical variable). DCCA was implemented for each full sequence and also for the period since ca. AD 1860 to summarise the amount of turnover for the longest common timespan represented in all four profiles. Percentage data were square-root transformed prior to PCA and DCCA analysis to stabilise variance, and were detrended by segments. Ordinations were carried out in Canoco 4.5 (ter Braak and Smilauer 2002).

The sequences were dated using radiocarbon (AMS  $^{14}\text{C}$ ) ages, calibrated using Calib 7.1 and INTCAL13 (Reimer et al. 2013), combined with lead-210 ( $^{210}\text{Pb}$ ) and spheroidal carbonaceous particle data (SCPs: soot particles from fossil fuel combustion; Yang et al. 2001, method modified by R. McCulloch, unpubl.).  $^{210}\text{Pb}$  and SCP records provide generally more precise age estimates than  $^{14}\text{C}$  after AD 1850 (Oldfield et al. 1995; Rose and Appleby 2005).  $^{210}\text{Pb}$  dates were obtained from the Environmental Radioactivity Laboratory, University of Stirling, and ages were calculated using the Constant Rate of Supply model (Oldfield and Appleby 1984). Calendar ages were assigned to the earliest appearance of SCPs (AD  $1850 \pm 25$ ), rapid rise (AD  $1955 \pm 15$ ) and peak concentration (AD  $1974 \pm 4$ ) using data from UK lake profiles that have been dated using radiometric methods (Rose and Appleby 2005). The study area lies on the boundary between three UK SCP regions (Rose and Appleby 2005), and age estimates were based on an average of two of these (the south and central, and north-western England regions), excluding the third (north-east England region), where sites are fewer in number and more distant from the study area. A composite chronology was constructed for each site using the probability-weighted average of the calibrated  $^{14}\text{C}$  dates to provide basal age estimates, with  $^{210}\text{Pb}$  and SCP ages to constrain the chronology from ca. AD 1850 to the present, assuming a linear rate of accumulation between dated samples.

## Results

### *Chronology and basis for vegetation interpretation*

1 The chronological data and time-depth curve constructed for each sequence are shown in Fig. 2. All  
2 dates are presented in calibrated years AD. The three key SCP dating horizons compare well (within  
3 error margins) with the  $^{210}\text{Pb}$  results for three of the sites and the more highly-resolved  $^{210}\text{Pb}$  dates were  
4 used to construct the chronologies at all sites. Divergence between  $^{210}\text{Pb}$  and SCP results at Cranberry  
5 Bed occurs mainly near the limits of the  $^{210}\text{Pb}$  method, which could suggest that the chronology is  
6 subject to a higher uncertainty. The SCP estimate for AD 1850 was therefore included in this chronology.  
7  $^{14}\text{C}$  dating is omitted from the Emlin Dike chronology because the discrepancy between the basal  $^{14}\text{C}$   
8 date (cal. AD 1580 at 49 cm) and  $^{210}\text{Pb}$  and SCP dates (nineteenth century AD ages below 46 cm)  
9 indicates a potential hiatus or contamination by older carbon at the base. The SCP estimate for AD 1850  
10 was also used at Withens Moor due to an incomplete  $^{210}\text{Pb}$  inventory.

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13 Peat accumulation rates were much higher at the fen sites (Cranberry Bed, Emlin Dike) than the blanket  
14 peats (Bar Brook, Withens Moor). The sequences span the last 200–1200 years (Figs. 3–6), with longer  
15 records available from the blanket peat sites. Sampling intervals of 2–4 cm (occasionally less during key  
16 transitions) at all sites produced histories with differing temporal resolution. There is an average of ca.  
17 10–60 years between samples (mean sampling resolution ca. 10–15 years after AD 1850 in less  
18 humified, acrotelm peat at all sites) and each sample represents ca. 3–7 years of pollen accumulation.

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23 Pollen data are interpreted as a reflection of changing vegetation community composition based on  
24 comparisons between pollen assemblages from plant growth at the top of the cores and current  
25 vegetation (Table 1), and general pollen productivity patterns (Broström et al. 2008; Bunting 2003).  
26 *Calluna* and Poaceae pollen dominate the top of core samples, as reflected in their positions across PCA  
27 Axis 1 (Online resource 3): heather-dominant moorland at Emlin Dike contributes 60% *Calluna* pollen,  
28 while substantial areas of grass dominance (primarily *M. caerulea*) at Withens Moor contribute 60%  
29 Poaceae pollen. Cranberry Bed and Bar Brook show intermediate *Calluna* and Poaceae values. Co-  
30 dominant pollen taxa at Cranberry Bed (32% Poaceae, 23% *Erica* and *Vaccinium*-type, 15% *Calluna*)  
31 reflect the approximately equivalent pollen contribution of heath, grass and fen communities. On this  
32 basis, 60–70% *Calluna* and Poaceae pollen values are considered to indicate that ling and grasses were  
33 the dominant contributors to the vegetation within the pollen source area. Herbaceous taxa such as  
34 *Potentilla*-type (cf. *P. erecta*) and *Rumex* spp. are indicative of acidic conditions, and, with *Plantago*  
35 *lanceolata* and coprophilic fungal spores (CFS), reflect the sheep grazing observed around all sites  
36 during sampling. *Sphagnum* spores are only recorded in any abundance in the topmost core sample  
37 from Bar Brook.

#### 44 45 *Vegetation dynamics*

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48 *Bar Brook*. From ca. AD 670–1690 (zone BB1) the assemblage is characterised by Poaceae with *Calluna*  
49 *vulgaris*, trees and shrubs, primarily *Betula*, *Quercus* and *Corylus avellana*-type (Fig. 3). In subzone BB1b  
50 (AD 890–1690), temporary increases in heather and then grass coincide with higher frequencies for  
51 Cyperaceae, *Potentilla*-type, *Sphagnum* and HdV-18, a NPP associated with wetter conditions and  
52 Cyperaceae pollen (van Geel 1978). Charcoal values are variable but remain comparatively high  
53 throughout zone BB1 and fungal spore types associated with charred material are also recorded  
54 (*Gelasinospora* HdV-1 and HdV-2, *Coniochaeta* HdV-6). Zone BB2 (AD 1690–1920) is characterised by a  
55 shift towards *Calluna* dominance, with increased values for *P. lanceolata* and reduced occurrence of  
56 many herb pollen taxa. This coincides with a reduction in arboreal pollen (AP) values. Charcoal values  
57 are also lower and HdV-18 disappears. Rarefaction values rise through subzone BB1b, before declining  
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1 as *Calluna* frequencies increase. Poaceae pollen dominates the assemblage in zone BB3 (AD 1920-2008),  
2 with reductions in *Calluna* and the two most common herb taxa, *P. lanceolata* and *Potentilla*-type. CFS  
3 (*Sporormiella* HdV-113, *Sordaria* HdV-55A and *Podospora* HdV-368) are recorded at higher levels, as is  
4 *Coniochaeta xylariispora* (HdV-6), a non-obligate dung fungus. Rarefaction values rise with the transition  
5 towards a more mixed pollen assemblage (AD 1060-1550), before declining as *Calluna* and then  
6 Poaceae frequencies increase. AP values, including coniferous and deciduous taxa, rise after ca. AD  
7 1930, with a slight increase in *Calluna* values.

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9 *Withens Moor*. Subzones WM1a and WM1b (AD 830–1880) are characterised by rising *Calluna*  
10 frequencies and decreasing tree and shrub values, particularly after ca. AD 1620 when Poaceae levels  
11 increase (Fig. 4). Charcoal frequencies are comparatively high. *P. lanceolata* and CFS values rise at ca. AD  
12 1410 and increase further at ca. AD 1720, when *Sphagnum* disappears from the record. *Calluna*  
13 representation declines and Poaceae values increase in subzones WM1c and 2a (AD 1880–1930).  
14 Plantain and CFS frequencies peak during this transition and AP values rise. A high abundance of  
15 charcoal fragments is present from ca. AD 1890–1940 and at ca. AD 1970, but no pyrophilic NPP are  
16 recorded, with the possible exception of *C. xylariispora* (HdV-6) which may be responding to grazing  
17 and/or burning (Yeloff et al. 2007). Grass pollen remains dominant up to AD 2008 and input from all  
18 Ericaceae types is low after ca. AD 1910 (subzone WM2b). There are no strong rarefaction trends.

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24 *Cranberry Bed*. *Calluna* is the main pollen producer in zone CB1 (AD 1800–1870), with continuous curves  
25 for *Meliola ellisii* (HdV-14) and *Triglocladium opacum* (HdV-10), which are associated with Ericaceae  
26 roots and relatively dry peat, respectively (van Geel 1978; Yeloff et al. 2007) (Fig. 5). *P. lanceolata* values  
27 rise through the zone, with peak levels of CFS and *C. xylariispora* (HdV-6) at the end of zone CB1 and in  
28 subzone CB2a (AD 1870–1880). Temporary increases in *Empetrum nigrum* and then Poaceae occur in  
29 subzone CB2a. *Calluna* values recover in subzone CB2b (AD 1880–1960), but *Meliola* (HdV-14) and  
30 *Triglocladium* (HdV-10) spores are largely absent, suggesting localised heather loss. *Sphagnum* declines  
31 markedly around AD 1880. Plantain remains the most abundant herb pollen type in subzone CB2b,  
32 although CFS values are lower and discontinuous. Heather is replaced by Poaceae with rising tree pollen  
33 values, particularly *Pinus sylvestris*, in zone CB3 (AD 1960–2008). Samples were black with charcoal  
34 during rising and peak grass values at ca. AD 1910 and 1970, respectively. The plantain curve declines  
35 and consistent, low levels of CFS are recorded during zone CB3. Palynological richness fluctuates around  
36 the mean, with higher values associated with mixed pollen assemblages.

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43 *Emlin Dike*. *Calluna* is the main pollen producer in zone ED1 (Fig. 6). A stepped rise in Poaceae around  
44 AD 1950 coincides with increased charcoal values. *P. lanceolata* and *Sordaria* (HdV-55A) are the most  
45 consistent herb and CFS types, respectively. Zone ED2 (AD 1960–1980) is characterised by a switch from  
46 heather to grass pollen abundance and comparatively high charcoal values. *Calluna* values exceed  
47 Poaceae in zone ED3 (AD 1980–2008), in which palynological richness is also higher. *Empetrum* is  
48 present at low frequencies from ca. AD 1980 and *Sphagnum* values become continuous from ca. AD  
49 2000, when plantain frequencies decline but *Sporormiella* (HdV-113) is consistently recorded. AP values,  
50 including *Betula*, *P. sylvestris* and *Quercus*, are higher from ca. AD 1990.

#### 51 52 53 54 55 56 *Ordination*

57 In the PCA (Online resource 3), Axis 1 (explaining 52% of variation) differentiates between the relative  
58 abundance of Poaceae (positive values) and *Calluna* (negative), and Axis 2 (17% variation) separates the  
59 pre-eighteenth century AD landscape, with relict native tree and shrub growth (positive), from more  
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1 recent moorland with plantation trees (negative values). The sites are locally treeless, so 10–26% tree  
2 pollen at the top of the cores reflects trees in the surrounding landscape and long-distance transport,  
3 especially at Cranberry Bed and Withens Moor, which lie in catchments with extensive conifer  
4 plantations. Extralocal and regional AP values thus exaggerate the separation of the four sites on PCA  
5 Axis 2. Sample scores for the two shorter sequences (Cranberry Bed and Emlin Dike) align with Axis 1,  
6 shifting between *Calluna* (negative) to Poaceae (positive) values. Emlin Dike shows the strongest shift  
7 back towards the quadrant dominated by dwarf-shrubs (negative values on Axes 1 and 2) over recent  
8 decades. Bar Brook displays a near circular trajectory, transitioning from a grass/dwarf-shrub/tree  
9 assemblage towards *Calluna* and then Poaceae scores, before fluctuating between high grass and more  
10 mixed species scores during the late twentieth century. Withens Moor displays the strongest directional  
11 trend, reflecting the loss of trees and shrubs during the transition to high *Calluna* scores, before the  
12 twentieth century shift to Poaceae dominance. This site also exhibits the highest amount of  
13 compositional change in the DCCA summary statistics (Online resource 3). Sample scores for Cranberry  
14 Bed show relative stability around the dwarf-shrub quadrant prior to ca. AD 1950 and this sequence has  
15 the least compositional change from AD 1860–2008, the time period represented at all sites. All  
16 sequences exhibit higher compositional change (turnover) near the base of the profile and a slight rise  
17 in turnover approaching AD 2008 (Figs. 3-6). For Bar Brook and Withens Moor, the extent of  
18 compositional change is greatest post-AD 1860 than for the full profile. Lower rarefaction values and  
19 reduced or stabilised turnover are common during phases of increased grass and heather pollen  
20 abundance (Figs. 3-6).

## 27 Discussion

28 The vegetation histories of the four study sites are compared and set in the context of previous  
29 palaeoecological evidence from the Pennines and the UK before discussing the evidence for regime  
30 change and implications for conservation.

### 34 *Late Holocene moorland dynamics*

35 Open moorland has dominated the Pennines for over 2000 years (Hicks 1971; Tallis 1991), although the  
36 two older records from Bar Brook and Withens Moor, spanning the last ca. 1200–1340 years, indicate  
37 that fragmented tree and shrub cover persisted until the seventeenth century AD (Scurfield 1999). At  
38 Withens Moor, an increase in *P. lanceolata* and coprophilic fungal spore (CFS) levels at ca. AD 1400 and  
39 1700 suggests that grazing intensification allowed *Calluna* moorland to replace tree cover. There are no  
40 marked changes in grazing indicators or CFS at Bar Brook, suggesting that prolonged grazing led to  
41 gradual woodland attrition and the expansion of a mixed grass-heather community. Consistent charcoal  
42 values and associated pyrophilic NPP suggest that fire was also used in management and may have  
43 contributed to the contraction of trees and shrubs. The economic importance of livestock, particularly  
44 sheep, is likely to have encouraged pastoral expansion (Anderson and Shimwell 1981; Shimwell 1974).  
45 These sequences indicate that *Calluna* dominance emerged via different trajectories. At Bar Brook,  
46 heather values increased following cyclical changes heather and grass; a similar relationship is evident  
47 on other British moors over the last ca. 1200–2000 years (Chambers et al. 1999, 2007b). The stepped  
48 rise in *Calluna* values at Withen Moor indicates that some heathland formed via a more direct process  
49 of tree replacement and moorland expansion.

50 *Calluna* pollen values of 60–80% are recorded in all four sequences during the nineteenth century,  
51 suggesting that heather-dominated moorlands were regionally widespread. This compares well with  
52 extensive heather moorlands mapped in the South Pennines during the early twentieth century

1 (Anderson and Yalden 1981; see Online resource 2). When these first developed in the region is less  
2 clear: *Calluna* pollen values rise above 60% from ca. AD 1460 at Withens Moor, but not until nearly four  
3 centuries later at Bar Brook (ca. AD 1820). High *Calluna* values are present at the base of the sequences  
4 from Cranberry Bed (ca. AD 1770) and Emlin Dike (ca. AD 1870), so it is not possible to establish when  
5 heather dominance first emerged there. Some existing pollen records from the south, central and north  
6 Pennines show a mid–late nineteenth century rise in *Calluna* abundance (Hicks 1971; Livett et al. 1979)  
7 and a similar pattern is evident in moorland sequences from northern England and south Wales, dated  
8 to the nineteenth and twentieth centuries (Atherden 2004; Chambers et al. 2007a; Livett et al. 1979;  
9 Turner et al. 2014). This may indicate a widespread shift in moorland composition between the mid-  
10 nineteenth and twentieth centuries, with some sites, like Withens Moor, showing long-standing heather  
11 dominance.  
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14 The subsequent rapid replacement of *Calluna* by high Poaceae values at all four sites is also comparable  
15 with previous evidence for the loss of heather and spread of grasses in the Pennines and on many  
16 British blanket moors over the last ca. 100–500 years, particularly in England and Wales (Chambers et al.  
17 1999, 2007b; Conway 1947; Eyre 1966; Hicks 1971; Stevenson and Thompson 1993; Tallis 1964, 1985).  
18 The range of dates for reductions in *Calluna* pollen (from ca. 1900 at Withens Moor to 1960 at Emlin  
19 Dike) indicates that heather contraction was asynchronous not only between but also within regions  
20 (Stevenson and Thompson 1993).  
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26 In common with previous studies, changing grazing and burning regimes are likely to be the main  
27 mechanisms for heather and grass expansion in this study, possibly interacting with drainage and the  
28 deposition of atmospheric pollution (Chambers et al. 2007a; Davies and Dixon 2007; Stevenson and  
29 Rhodes 2000; Yeloff et al. 2006). However, interpretation of grazing proxies is by no means  
30 straightforward since pollen indicators (Behre 1981) and CFS values show similar trends at some sites  
31 and times, but contrasting relationships at others. For instance, at Withens Moor, there is similarity in  
32 subzone WM1b (with *Calluna* expansion), but a reciprocal pattern (lower *P. lanceolata* and higher CFS  
33 values) in subzones WM2a and WM2b (with grass expansion). Reciprocal trends are a feature of  
34 twentieth century grass-dominated assemblages (e.g. zones BB3 and CB3, late in zone ED3), and were  
35 also recorded during the preceding temporary grass increase at Cranberry Bed (subzone CB2a). Stocking  
36 densities were high during the second half of the twentieth century (Dallimer et al. 2009). Intense  
37 herbivory, disturbance and competition could have increased the abundance of dung (and hence CFS)  
38 while reducing the flowering or abundance of grazing-resistant herbs (cf. Gill et al. 2013; Hjelle 1998).  
39 This inference would benefit from further testing, including the potential influence of increased extra-  
40 local tree pollen on local pollen representation.  
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48 The complexity of the grazing signal highlights the difficulty of identifying causal factors, many of which  
49 are likely to have had interacting and cumulative impacts. This is evident from palynological and NPP  
50 dynamics during grass expansion. The tussock-forming habit of coarse grasses, such as *Molinia*, can  
51 enable them to resist burning and grazing, particularly if heather is checked by winter grazing (Hulme et  
52 al. 2002; Taylor et al. 2001). For example, at both Withens Moor and Emlin Dike, the transition to  
53 Poaceae abundance coincides with higher grazing indicators (*P. lanceolata*, CFS) and high charcoal  
54 abundance. A continuous curve for *C. xylariispora* (HdV-6) at Emlin Dike indicates local burning (Yeloff et  
55 al. 2007). The spread of grasses at Withens Moor and Bar Brook may have been reinforced by moorland  
56 drainage, inferred from reduced *Sphagnum* values at Bar Brook around AD 1880, and from increases in  
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*Empetrum* and Cyperaceae representation at Withens Moor around AD 1900–1960. Similar responses have been recorded on eroding blanket peats due to gullyng (Tallis 1994, 1997).

Proximity to former industrial centres led to high atmospheric pollution deposition in the Pennines and the disappearance of *Sphagnum* has been attributed to sulphate deposition (Lee 1998; Tallis 1964). However, the range of dates for *Sphagnum* disappearance (from AD 1770 at Withens Moor, to AD 1900 at Cranberry Bed, and AD 1920 at Bar Brook) suggests that sulphate pollution compounded other pressures, rather than being the main cause of decline (Hughes et al. 2008; Yeloff et al. 2006). The twentieth century increase in nitrogen deposition may have reinforced grass dominance due to fertilisation and acidification effects, especially when combined with disturbance (Lee 1998; Maskell et al. 2010; Taylor et al. 2001). This could be a contributory factor at Withens Moor (cf. Chambers et al. 2007a), but the reappearance of *Sphagnum* at the other three sites between 1960 and 1990 suggests that N-deposition has not exceeded critical levels in recent decades.

#### *Moorland regime shift and conservation implications*

The widespread emergence of common trends suggests that Pennine and other British moorlands exhibit regime change, that is, a shift beyond the bounds of recent ‘normality’ in terms of the patterns of turnover and the range of variability (Wolkovich et al. 2014). This is inferred from the shift from gradual or cyclical variability and moderate changes in species abundance before ca. AD 1800, to ecosystems characterised by more rapid transitions between mono-dominant pollen assemblages, and from the ‘atypically’ high historic *Calluna* and Poaceae values when viewed in a broader Holocene context (Chambers et al. 1999, 2007a, b; Hicks 1971). These features indicate an increase in the range of variability, extent and pace of turnover. The shifts occurred across a range of communities, from ‘degraded’ grassmoor on eroding and uneroded blanket peat (Bar Brook, Withens Moor; Chambers et al. 1999, 2007a, 2013; Hicks 1971; Yeloff et al. 2006), to fen peats (Cranberry Bed), drier moors (Davies and Dixon 2007; Tipping 2000), and ‘high conservation value’ heather moorland (Emlin Dike; Stevenson and Thompson 1993).

In addition to converging on local heather and then grass dominance, the pollen data suggest significant functional shifts in moorland floras. Intensified management since ca. AD 1800 (Berglund et al. 2008; Davies and Dixon 2007; Hanley et al. 2008) and within the last century (Jiang et al. 2013) has contributed to biodiversity loss in many ecosystems. No overall diversity trend emerges in this study, possibly due to comparatively low pollen counts and/or the characteristic low diversity of moorland vegetation. However, the palynological ‘winners’ and ‘losers’ indicate that competitive traits are required for survival during the late Holocene. Rising heather representation at Bar Brook is characterised by a prolonged decline in rarefaction which may reflect shifts in vegetation composition and/or the swamping effect of *Calluna* pollen on the probability of encountering other taxa (Fig. 3). Reductions in grazing-sensitive (e.g. *Melampyrum*, Pteropsida) and more grazing-tolerant taxa (e.g. *Rumex*, Rubiaceae), followed around AD 1950 by the disappearance of *Potentilla*-type (cf. *P. erecta*, which is considered unpalatable to livestock), suggest significant growth stress and homogenisation within the pollen source area. At Withens Moor, the taxa persisting after ca. AD 1900 are those that benefit from nutrient enrichment and have morphological and/or chemical defences that allow them to resist grazing pressure (e.g. *P. lanceolata*, *Rumex*, *Urtica*, *Artemisia*-type) (cf. Smart et al. 2005). These changes are in addition to the documented decline or regional extinction of distinctive moorland taxa, like *Drosera rotundifolia* and *Andromeda polifolia* (Anderson and Shimwell 1981; Chambers et al. 2007a). These functional shifts are comparable with survey evidence for biotic homogenisation during

the late twentieth century (Smart et al. 2006), and emphasise the scale of the challenge facing conservation.

Evidence of late Holocene regime shift in a range of moorland settings raises significant questions about the feasibility of restoration. Practical experience demonstrates that restoration of grassmoors is a costly, time-consuming and uncertain process (Marrs et al. 2004). The present findings are therefore used to assess the opportunities and difficulties likely to face conservation managers, based on longer-term knowledge of changes in composition and dynamics. Some moorland communities have alternated between heather and grass over the last ca. 1200–1500 years (e.g. Bar Brook; Chambers et al. 1999, 2007b), but it is unclear whether the systems can revert to this dynamic given the unprecedented extent of change during recent centuries. Recent evidence is equivocal. Positive indicators include ecological evidence that the study sites are in ‘recovering’ conservation condition, based on dwarf-shrub diversity and structure (Table 1). This is partially supported by the palynological data. The vegetation and pollen data are in agreement at Emlin Dike, which shows a strong reversal of grass pollen dominance and corresponding recovery in *Calluna* and other dwarf-shrub values since ca. AD 1970 (Table 1, Fig. 6). There is a more modest rise in *Calluna* at Bar Brook around AD 1980 (Fig. 3) and in Ericales within the topmost core sample at Cranberry Bed (Fig. 5), but no dwarf-shrub recovery is recorded at Withens Moor (Fig. 4). In part, differences between the vegetation and pollen evidence may be due to vegetative changes that are not yet evident in pollen production. The influx of extra-local plantation pollen may also influence local representation, particularly of comparatively low pollen producers like Ericales other than *Calluna* and *Vaccinium* (Broström et al. 2008).

Increased dwarf-shrub representation (most notably in the pollen record at Emlin Dike) and rising diversity (such as the rarefaction trends at Emlin Dike and Cranberry Bed) are common early successional characteristics (Hobbs and Gimingham 1987). These could provide a favourable stage for increasing species richness and structural diversity through managed disturbance (Mitchell et al. 2008). The reappearance of *Sphagnum* at Cranberry Bed, Emlin Dike and Bar Brook since ca. AD 1960–1990, post-dating the AD 1956 Clean Air Act, also suggests local-level recovery from disturbance and sulphur deposition (Lee 1998). However, higher pollen values for Ericales other than *Calluna* were also recorded at all sites during the transition to Poaceae dominance, so recent mixed grass/dwarf-shrub assemblages represent a delicate balance that could switch back to grass dominance if burning, grazing or drainage stress occur. This illustrates the importance of using long time-series to identify potential turning points and vulnerabilities associated with them.

In contrast, at Withens Moor, heather dominance begins earlier and the declines in *Calluna* and *Sphagnum* are more persistent than at the other study sites. This could reflect more intensive local land-use, but may also indicate the sensitivity of deep, extensive blanket peats to disturbance (Ellis 2008; Tallis 1998). ‘Recovering’ conservation status relates mainly to steeper slopes with *Nardus* and bilberry/crowberry mix, than to wet areas with substantial *Molinia*. The failure of dwarf-shrubs to recover on deep peat at Withens Moor could suggest that the grassmoor represents a persistent state, rather than a temporarily ‘unfavourable’ phase in conservation management (Grime et al. 2008; Hobbs et al. 2009). Although the time-depth curve suggests that peat is continuing to accumulate (Fig. 2b), grass abundance can have negative impacts on peatland carbon balance under warmer conditions (Ward et al. 2013). This could lead to a switch from carbon sequestration to emission, particularly where peatlands are already showing signs of historical climate-induced drying or may face increased drought stress in the near future (House et al. 2010; Swindles et al. 2010; Worrall et al. 2006).

## Conclusions

1 Palaeoecological research on regime shifts often considers regional responses over millennial  
2 timescales, in recognition that these can unfold slowly and that non-equilibrium conditions may persist  
3 for millennia (Hughes et al. 2012; Jackson 2006; Wolkovich et al. 2014). The present data show how  
4 studying regime shifts on decadal to centennial scales using a multi-site approach can capitalise on the  
5 temporal overlap between palaeoecology and ecology. Moorland transitions appear abrupt on  
6 palaeoecological timescales, with the shift from peak heather to high grass values taking ca. 25–80 years  
7 ( $\pm <1-26$  years), but from an ecological monitoring perspective, this trend would only become evident  
8 after multi-decadal surveys. This study indicates that even 100 years of intermittent ecological  
9 monitoring does not reveal the extent of moorland variability (Online resource 2). Without  
10 palaeoecological input, the slow unfolding of regime change and survey intervals which do not capture  
11 vegetation variability could lead to over-optimistic assessments of the ability of peatlands to tolerate  
12 environmental or management pressures.  
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19 Quantitative approaches are increasingly used to assess regime shifts (Scheffer et al. 2009) and are also  
20 being applied to palaeoenvironmental data (Seddon et al. 2014; Streeter and Dugmore 2014). However,  
21 rigorous data demands mean that a statistical approach will not be applicable to all datasets. In this  
22 case, high-resolution data for the period predating the expansion of *Calluna* are needed to assess  
23 whether these systems show statistical signs of increasing sensitivity to perturbations or impending  
24 state change (e.g. critical slowing or increased variance). These may provide an empirical basis for  
25 assessing whether late nineteenth and twentieth-century communities represent a novel state in the  
26 history of the ecosystem. However, independent records of the management changes that may be  
27 causal will be difficult to obtain on appropriate spatial or temporal scales. In the absence of 'ideal' data,  
28 the results indicate the ability of multi-site, semi-quantitative approaches to identify regime shifts  
29 predating recent ecological records. Future work would benefit from cross-scale approaches to  
30 diagnose and monitor vulnerability. For example, combining high-resolution palaeoecology as an  
31 indicator of temporal mosaic dynamics (Williams et al. 2011) with spatial changes from monitoring and  
32 remotely sensed data (e.g. patch-size distribution as a measure of degradation; Kéfi et al. 2014) could  
33 provide a more robust method of assessing contemporary and long-term dimensions of ecosystem  
34 dynamics and contribute a more integrated temporal and spatial framework for managing  
35 environmental change (Wolkovich et al. 2014).  
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43 **Acknowledgements** I thank landowners and managers for site access and management information,  
44 Richard Streeter and Ian Lawson for useful discussions about resilience, and two anonymous reviewers  
45 for their helpful comments. This research was funded by the Economic and Social Research Council  
46 through the Rural Economy and Land-Use Programme (RES-229-27-0003). All raw data have been  
47 archived in Davies, A., *Foundations for the Future: Learning from the Past, 2007-2010*. Colchester, Essex:  
48 UK Data Archive, February 2012. <http://dx.doi.org/10.5255/UKDA-SN-6791-1>  
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## References

- 1 Anderson P, Buckler M, Walker J (2009) Moorland restoration: potential and progress. In: Bonn A, Allott  
2 T, Hubacek H, Stewart J (eds) Drivers of environmental change in uplands. Routledge, Abingdon, pp 432-  
3 447  
4
- 5 Anderson P, Shimwell D (1981) Wild flowers and other plants of the Peak District: an ecological study.  
6 Moorland Publishing, Ashbourne (Derbyshire)  
7
- 8 Anderson P, Yalden DW (1981) Increased sheep numbers and the loss of heather moorland in the Peak  
9 District, England. *Biol Conserv* 20:195-213  
10
- 11 Atherden M (2004) Ecological changes on the North York Moors during the last millennium and their  
12 impact on the landscape. In: Whyte ID, Winchester AJL (eds) Society, landscape and environment in  
13 upland Britain. Society for Landscape Studies, supplementary series 2: 1-9  
14
- 15 Bain CG, Bonn A, Stoneman R, Chapman S, Coupar A, Evans M, Gearey B, Howat M, Joosten H,  
16 Keenleyside C, Labadz J, Lindsay R, Littlewood N, Lunt P, Miller C.J, Moxey A, Orr H, Reed M, Smith P,  
17 Swales V, Thompson DBA, Thompson, PS, Van de Noort R, Wilson JD, Worrall F (2011) IUCN UK  
18 commission of inquiry on peatlands. IUCN UK Peatland Programme, Edinburgh  
19
- 20 Behre K-E (1981) The interpretation of anthropogenic indicators in pollen diagrams. *Pollen Spores*  
21 23:225–245  
22
- 23 Bennett KD (1994) Annotated catalogue of pollen and pteridophyte spore types of the British Isles.  
24 School of Geography, Archaeology and Palaeoecology, Queen’s University Belfast  
25 <http://www.chrono.qub.ac.uk/pollen/pc-intro.html>. Accessed 1 June 2015  
26
- 27 Berglund BE, Gaillard MJ, Bjorkman L, Persson T (2008) Long-term changes in floristic diversity in  
28 southern Sweden: palynological richness, vegetation dynamics and land-use. *Veget Hist Archaeobot*  
29 17:573-583  
30
- 31 Birks HJB (2007) Estimating the amount of compositional change in late-Quaternary pollen-  
32 stratigraphical data. *Veget Hist Archaeobot* 16:197-202  
33
- 34 Birks HJB, Line JM (1992) The use of rarefaction analysis for estimating palynological richness from  
35 Quaternary pollen-analytical data. *Holocene* 2:1-10  
36
- 37 Briggs DJ, Gilbertson DD, Jenkinson RDS (eds) (1985) Peak District and Northern Dukeries field guide.  
38 Quaternary Research Association, Cambridge  
39
- 40 Broström A, Sugita S, Gaillard MJ, Pilesjö P (2005) Estimating the spatial scale of pollen dispersal in the  
41 cultural landscape of southern Sweden. *Holocene* 15:252-262  
42
- 43 Broström A, Nielsen A, Gaillard MJ, Hjelle K, Mazier F, Binney H, Bunting J, Fyfe R, Meltsov V, Poska A,  
44 Rasanen S, Soepboer W, Stedingk H, Suutari H, Sugita S (2008) Pollen productivity estimates of key  
45 European plant taxa for quantitative reconstruction of past vegetation: a review. *Veget Hist Archaeobot*  
46 17:461-478  
47
- 48 Bunting MJ (2003) Pollen-vegetation relationships in non-arboreal moorland taxa. *Rev Palaeobot*  
49 *Palynol* 125:285-298  
50
- 51 Chambers FM, Mauquoy D, Todd PA (1999) Recent rise to dominance of *Molinia caerulea* in  
52 environmentally sensitive areas: new perspectives from palaeoecological data. *J Appl Ecol* 36:719-733  
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62  
63  
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65
- Chambers FM, Mauquoy D, Gent A, Pearson F, Daniell JRG, Jones PS (2007a) Palaeoecology of degraded blanket mire in South Wales: data to inform conservation management. *Biol Conserv* 137:197-209
- Chambers FM, Mauquoy D, Cloutman EW, Daniell JRG, Jones PS (2007b) Recent vegetation history of Drygarn Fawr (Elenydd SSSI), Cambrian Mountains, Wales: implications for conservation management of degraded blanket mires. *Biodivers Conserv* 16:2821-2846
- Chambers FM, Cloutman EW, Daniell JRG, Mauquoy D, Jones PS (2013) Long-term ecological study (palaeoecology) to chronicle habitat degradation and inform conservation ecology: an exemplar from the Brecon Beacons, South Wales. *Biodivers Conserv* 22:719-736
- Conway VM (1947) Ringinglow Bog, near Sheffield. Part I. Historical. *J Ecol* 34:149-181
- Dallimer M, Tinch D, Acs S, Hanley N, Southall HR, Gaston KJ, Armsworth PR (2009) 100 years of change: examining agricultural trends, habitat change and stakeholder perceptions through the 20th century. *J Appl Ecol* 46:334-343
- Davies AL, Bunting MJ (2010) Applications of palaeoecology in conservation. *Open Ecol J* 3:54-67
- Davies AL, Dixon PJ (2007) Reading the pastoral landscape: palynological and historical evidence for the impacts of long-term grazing on Wether Hill, Cheviot foothills, Northumberland. *Landscape Hist* 29:35-45
- Davies AL, Tipping R (2004) Sensing small-scale human activity in the palaeoecological record: fine spatial resolution pollen analyses from West Glen Affric, northern Scotland. *Holocene* 14:233-245
- Ellis CJ (2008) Interactions between hydrology, burning and contrasting plant groups during the millennial-scale development of sub-montane wet heath. *J Veget Sci* 19:693-704
- Eyre SR (1966) The vegetation of a south Pennine upland In: SR Eyre and GRJ Jones (eds) *Geography as human ecology methodology by example*. Arnold, London, pp 147-173
- Fyfe RM, Woodbridge J (2012) Differences in time and space in vegetation patterning: analysis of pollen data from Dartmoor, UK. *Landscape Ecol* 27:745-760
- Gallego-Sala AV, Prentice CI (2013) Blanket peat biome endangered by climate change. *Nature Clim Change* 3:152-155
- Gill JL, McLauchlan KK, Skibbe AM, Goring S, Zirbel CR, Williams JW (2013) Linking abundances of the dung fungus *Sporormiella* to the density of bison: implications for assessing grazing by megaherbivores in palaeorecords. *J Ecol* 101:1125-1136
- Grime JP, Fridley JD, Askew AP, Thompson K, Hodgson JG, Bennett CR (2008) Long-term resistance to simulated climate change in an infertile grassland. *Proc Nat Acad Sci USA* 105:10028-10032
- Grimm EC (1987) CONISS: a FORTRAN 77 program for stratigraphically constrained cluster analysis by the method of incremental sum of squares. *Computers Geosci* 13:13-35
- Hanley N, Davies A, Angelopoulos K, Hamilton A, Ross A, Tinch D, Watson F (2008) Economic determinants of biodiversity change over a 400 year period in the Scottish uplands. *J Appl Ecol* 45:1557-1565
- Hicks SP (1971) Pollen analytical evidence for the effect of prehistoric agriculture on the vegetation of North Derbyshire. *New Phytol* 70:647-667
- Hjelle KL (1998) Herb pollen representation in surface moss samples from mown meadows and pastures in western Norway. *Veget Hist Archaeobot* 7:79-96

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53  
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55  
56  
57  
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60  
61  
62  
63  
64  
65
- Hobbs RJ, Gimingham CH (1987) Vegetation, fire and herbivore Interactions in heathland. In: Macfadyen A, Ford ED (eds), Advances in ecological research. Academic Press, London, pp 87-173
- Hobbs RJ, Higgs E, Harris JA (2009) Novel ecosystems: implications for conservation and restoration. Trends Ecol Evol 24:599-605
- Holden, J, Shotbolt, L, Bonn, A, Burt, TP, Chapman, PJ, Dougill, AJ, Fraser, EDG, Hubacek, K, Irvine, B, Kirkby MJ, Reed MS, Prell C, Stagl S, Stringer LC, Turner A, Worrall F (2007) Environmental change in moorland landscapes. Earth Sci Rev 82:75-100
- House JI, Orr HG, Clark JM, Gallego-Sala AV, Freeman C, Prentice IC, Smith P (2010) Climate change and the British uplands: evidence for decision-making. Clim Res 45:3-12
- Hughes PDM, Lomas-Clarke SH, Schulz J, Barber KE (2008) Decline and localized extinction of a major raised bog species across the British Isles: evidence for associated land-use intensification. Holocene 18:1033-1043
- Hughes TP, Linares C, Dakos V, van de Leemput IA, van Nes EH (2012) Living dangerously on borrowed time during slow, unrecognized regime shifts. Trends Ecol Evol 28:149-155
- Hulme PD, Merrell BG, Torvell L, Fisher JM, Small JL, Pakeman RJ (2002) Rehabilitation of degraded *Calluna vulgaris* (L.) Hull-dominated wet heath by controlled sheep grazing. Biol Conserv 107:351-363
- Jackson, ST (2006) Vegetation, environment, and time: the origination and termination of ecosystems. J Veget Sci 15:549-557
- Jiang M, Bullock JM, Hooftman DAP (2013) Mapping ecosystem service and biodiversity changes over 70 years in a rural English county. J Appl Ecol 50:841-850
- Joint Nature Conservation Committee (2011) Towards an assessment of the state of UK Peatlands. JNCC report no. 445, Peterborough
- Kéfi S, Guttal V, Brock WA, Carpenter SR, Ellison AM, Livina VN, Seekell DA, Scheffer M, van Nes EH, Dakos V (2014) Early warning signals of ecological transitions: methods for spatial patterns. PLoS ONE 9:e92097
- Lee H, Alday JG, Rose RJ, O'Reilly J, Marrs RH (2013) Long-term effects of rotational prescribed burning and low-intensity sheep grazing on blanket-bog plant communities. J Appl Ecol 50:625-635
- Lee JA (1998) Unintentional experiments with terrestrial ecosystems: ecological effects of sulphur and nitrogen pollutants. J Ecol 86:1-12
- Livett EA, Lee JA, Tallis JH (1979) Lead, zinc and copper analyses of British blanket peats. J Ecol 67:865-891
- Marrs RH, Phillips JDP, Todd PA, Ghorbani J, Le Duc MG (2004) Control of *Molinia caerulea* on upland moors. J Appl Ecol 41:398-411
- Maskell LC, Smart SM, Bullock JM, Thompson K, Stevens CJ (2010) Nitrogen deposition causes widespread loss of species richness in British habitats. Global Change Biol 16:671-679
- Mitchell RJ, Rose RJ, Palmer SCF (2008) Restoration of *Calluna vulgaris* on grass-dominated moorlands: The importance of disturbance, grazing and seeding. Biol Conserv 141:2100-2111
- Moore PD, Webb JA, Collinson ME (1991) Pollen analysis (2nd edn). Blackwell, Oxford

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2  
3  
4  
5  
6  
7  
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- Odgaard BV (2013) Reconstructing past biodiversity development. In: Elias SAM, Cary J (eds) Encyclopedia of Quaternary Science (2nd edn). Elsevier, Amsterdam, pp 816-820
- Oldfield F, Appleby PG (1984) Empirical testing of  $^{210}\text{Pb}$ -dating models for lake sediments. In: Haworth EY, Lund JWG (eds) Lake sediments and environmental history. University of Minnesota Press, Minneapolis, pp 93-124
- Oldfield F (1959) The pollen morphology of some of the west European Ericales. Pollen Spores 1:19–48
- Oldfield F, Richardson N, Appleby PG (1995) Radiometric dating ( $^{210}\text{Pb}$ ,  $^{137}\text{Cs}$ ,  $^{241}\text{Am}$ ) of recent ombrotrophic peat accumulation and evidence for changes in mass-balance. Holocene 5:141-148
- Parish F, Sirin A, Charman D, Joosten H, Minayeva T, Silvius M, Stringer L (eds) (2008) Assessment on peatlands, biodiversity and climate change: main report. Global Environment Centre and Wetlands International, Kuala Lumpur and Wageningen
- Reimer PJ, Bard E, Bayliss A, Beck JW, Blackwell PG, Bronk Ramsey C, Buck CE, Cheng H, Edwards RL, Friedrich M, Grootes PM, Guilderson TP, Hafliadason H, Hajdas I, Hatté C, Heaton TJ, Hogg AG, Hughen KA, Kaiser KF, Kromer B, Manning SW, Niu M, Reimer RW, Richards DA, Scott EM, Southon JR, Turney CSM, van der Plicht J (2013) IntCal13 and MARINE13 radiocarbon age calibration curves 0-50000 years cal BP. Radiocarbon 55: 1869-1887
- Rose NL and Appleby PG (2005) Regional applications of lake sediment dating by spheroidal carbonaceous particle analysis I: United Kingdom. J Paleolimn 34:349-361
- Scheffer M, Bascompte J, Brock WA, Brovkin V, Carpenter SR, Dakos V, Held H, van Nes EH, Rietkerk M, Sugihara G (2009) Early-warning signals for critical transitions. Nature 461:53-59
- Scurfield G (1999) The Peak District in the early seventeenth century: 1: (Hope) woodlands and lands adjacent. Peak District J Nat Hist Archaeol 1:1-11
- Seddon AWR, Froyd CA, Witkowski A, Willis KJ (2014) A quantitative framework for analysis of regime shifts in a Galápagos coastal lagoon. Ecol 95:3046-3055
- Shimwell D (1974) Sheep grazing intensity in Edale, 1692-1747 and its effect on blanket peat erosion. Derbyshire Archaeol J 94:35-40
- Smart SM, Bunce RGH, Marrs R, Leduc M, Firbank LG, Maskell LC, Scott WA, Thompson K, Walker KJ (2005) Large-scale changes in the abundance of common higher plant species across Britain between 1978, 1990 and 1998 as a consequence of human activity: tests of hypothesised changes in trait representation. Biol Conserv 124:355-371
- Smart SM, Thompson K, Marrs RH, Le Duc MG, Maskell LC, Firbank LG (2006) Biotic homogenization and changes in species diversity across human-modified ecosystems. Proc R Soc Lond B 273:2659-2665
- Stace C (2010) New flora of the British Isles, 3rd edn. Cambridge University Press, Cambridge
- Stevenson AC, Thompson DBA (1993) Long-term changes in the extent of heather moorland in upland Britain and Ireland: palaeoecological evidence for the importance of grazing. Holocene 3:70-76
- Stevenson AC, Rhodes AN (2000) Palaeoenvironmental evaluation of the importance of fire as a cause for *Calluna* loss in the British Isles. Palaeogeogr Palaeoclimatol Palaeoecol 164:211-222
- Streeter R, Dugmore A (2014) Late-Holocene land surface change in a coupled social–ecological system, southern Iceland: a cross-scale teprochronology approach. Quat Sci Rev 86:99-114

1 Swindles GT, Blundell A, Roe HM, Hall VA (2010) A 4500-year proxy climate record from peatlands in the  
2 north of Ireland: the identification of widespread summer ‘drought phases’? *Quat Sci Rev* 29:1577-1589  
3  
4 Tallis JH (1964) Studies on Southern Pennine peats. III. The behaviour of *Sphagnum*. *J Ecol* 52:345-353  
5  
6 Tallis JH (1985) Mass movement and erosion of a southern Pennine blanket peat. *J Ecol* 73:283-315  
7  
8 Tallis JH (1991) Forest and moorland in the south Pennine uplands in the mid-Flandrian period. III. The  
9 spread of moorland, local regional and national. *J Ecol* 79:401-415  
10  
11 Tallis JH (1994) Pool-and-hummock patterning in a southern Pennine blanket mire. II. The formation and  
12 erosion of the pool system. *J Ecol* 82:789-803  
13  
14 Tallis JH (1997) The pollen record of *Empetrum nigrum* in southern Pennine peats: implications for  
15 erosion and climate change. *J Ecol* 85:455-465  
16  
17 Tallis JH (1998) Growth and degradation of British and Irish blanket mires. *Environ Rev* 6:81-122  
18  
19 Taylor K, Rowland AP, Jones HE (2001) *Molinia caerulea* (L.) Moench. *J Ecol* 89:126-144  
20  
21 ter Braak CJF, Smilauer P (2002) CANOCO Reference manual and CanoDraw for Windows user’s guide:  
22 software for canonical community ordination (version 4.5). Ithaca, New York  
23  
24 Thompson DBA, MacDonald AJ, Marsden JH, Galbraith CA (1995) Upland heather moorland in Great  
25 Britain: a review of international importance, vegetation change and some objectives for nature  
26 conservation. *Biol Conserv* 71:163-178  
27  
28 Tipping R (2000) Palaeoecological approaches to historical problems: a comparison of sheep-grazing  
29 intensities in the Cheviot hills in the medieval and later periods. In: Atkinson J, Banks I, MacGregor G  
30 (eds) Townships to farmsteads: rural settlement studies in Scotland, England and Wales. BAR, British  
31 Series, pp 130-143  
32  
33 Turner TE, Swindles GT, Roucoux KH (2014) Late Holocene ecohydrological and carbon dynamics of a UK  
34 raised bog: impact of human activity and climate change. *Quat Sci Rev* 84:65-85  
35  
36 van Geel B (1978) A palaeoecological study of Holocene peat bog sections in Germany and the  
37 Netherlands, based on the analysis of pollen, spores and macro- and microscopic remains of fungi,  
38 algae, cormophytes and animals. *Rev Palaeobot Palynol* 25:1-120  
39  
40 van Geel B, Aptroot A (2006) Fossil ascomycetes in Quaternary deposits. *Nova Hedwigia* 82:313-329  
41  
42 Ward SE, Ostle NJ, Oakley S, Quirk H, Henrys PA, Bardgett RD (2013) Warming effects on greenhouse gas  
43 fluxes in peatlands are modulated by vegetation composition. *Ecol Letters* 16:1285-1293  
44  
45 Williams JW, Blois JL, Shuman BN (2011) Extrinsic and intrinsic forcing of abrupt ecological change: case  
46 studies from the late Quaternary. *J Ecol* 99:664-677  
47  
48 Wolkovich EM, Cook BI, McLauchlan KK, Davies TJ (2014) Temporal ecology in the Anthropocene. *Ecol*  
49 *Letters* 17:1365–1379  
50  
51 Worrall F, Burt TP, Adamson JK (2006) Trends in drought frequency — the fate of DOC export from  
52 British peatlands. *Clim Change* 76:339-359  
53  
54 Yang H, Rose NL, Battarbee RW (2001) Dating of recent catchment peats using spheroidal carbonaceous  
55 particle (SCP) concentration profiles with particular reference to Lochnagar, Scotland. *Holocene* 11:593-  
56 597  
57  
58  
59  
60  
61  
62  
63  
64  
65

Yeloff D, Charman D, Van Geel B, Mauquoy D (2007) Reconstruction of hydrology, vegetation and past climate change in bogs using fungal microfossils. *Rev Palaeobot Palynol* 146:102-145

Yeloff DE, Labadz JC, Hunt CO (2006) Causes of degradation and erosion of a blanket mire in the southern Pennines, UK. *Mires Peat* 1:1-18

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## LIST OF FIGURE LEGENDS

1 **Fig. 1** Map of the study area showing the location of the four sampling sites and other geographical  
2 features. Inset shows the location of the study area (rectangle) in a British/Irish context and distribution  
3 of blanket peat (UK only)  
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7 **Fig. 2** Age-depth curves for study sites, showing  $^{210}\text{Pb}$ , spheroidal carbonaceous particle (SCP) and AMS  
8  $^{14}\text{C}$  age estimates with 95% confidence intervals, and the time-depth curve (TDC) constructed for each  
9 sequence. Basis for chronologies: (a) Bar Brook:  $^{14}\text{C}$  and  $^{210}\text{Pb}$ , omitting oldest  $^{210}\text{Pb}$  result because of  
10 large error range; (b) Withens Moor:  $^{14}\text{C}$ ,  $^{210}\text{Pb}$  and SCP estimate for AD 1850 at 19 cm; (c) Cranberry  
11 Bed:  $^{14}\text{C}$ , SCP estimate for AD 1850 at 40 cm and  $^{210}\text{Pb}$ , omitting the two oldest  $^{210}\text{Pb}$  dates with high  
12 errors at the limits of detection for this method; (d) Emlin Dike:  $^{210}\text{Pb}$  only, omitting radiocarbon dates  
13 (see text for explanation)  
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19 **Fig. 3** Selected percentage pollen, NPP and charcoal data for Bar Brook, with palynological richness  
20 (rarefaction values and mean) and compositional change (DCCA, axis 1). Charcoal histogram represents  
21 all size classes, except where plus symbols (+) indicate samples with extremely high charcoal abundance  
22 when only fragments  $>75\ \mu\text{m}$  (shown as line) were counted. Exaggeration  $\times 10$  is indicated by a  
23 silhouette on selected curves. CFS = Coprophilic fungal spores  
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28 **Fig. 4** Selected percentage pollen, spore, charcoal and statistical data for Withens Moor. See Fig. 3 for  
29 details  
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33 **Fig. 5** Selected percentage pollen, spore, charcoal and statistical data for Cranberry Bed. See Fig. 3 for  
34 details  
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38 **Fig. 6** Selected percentage pollen, spore, charcoal and statistical data for Emlin Dike. See Fig. 3 for  
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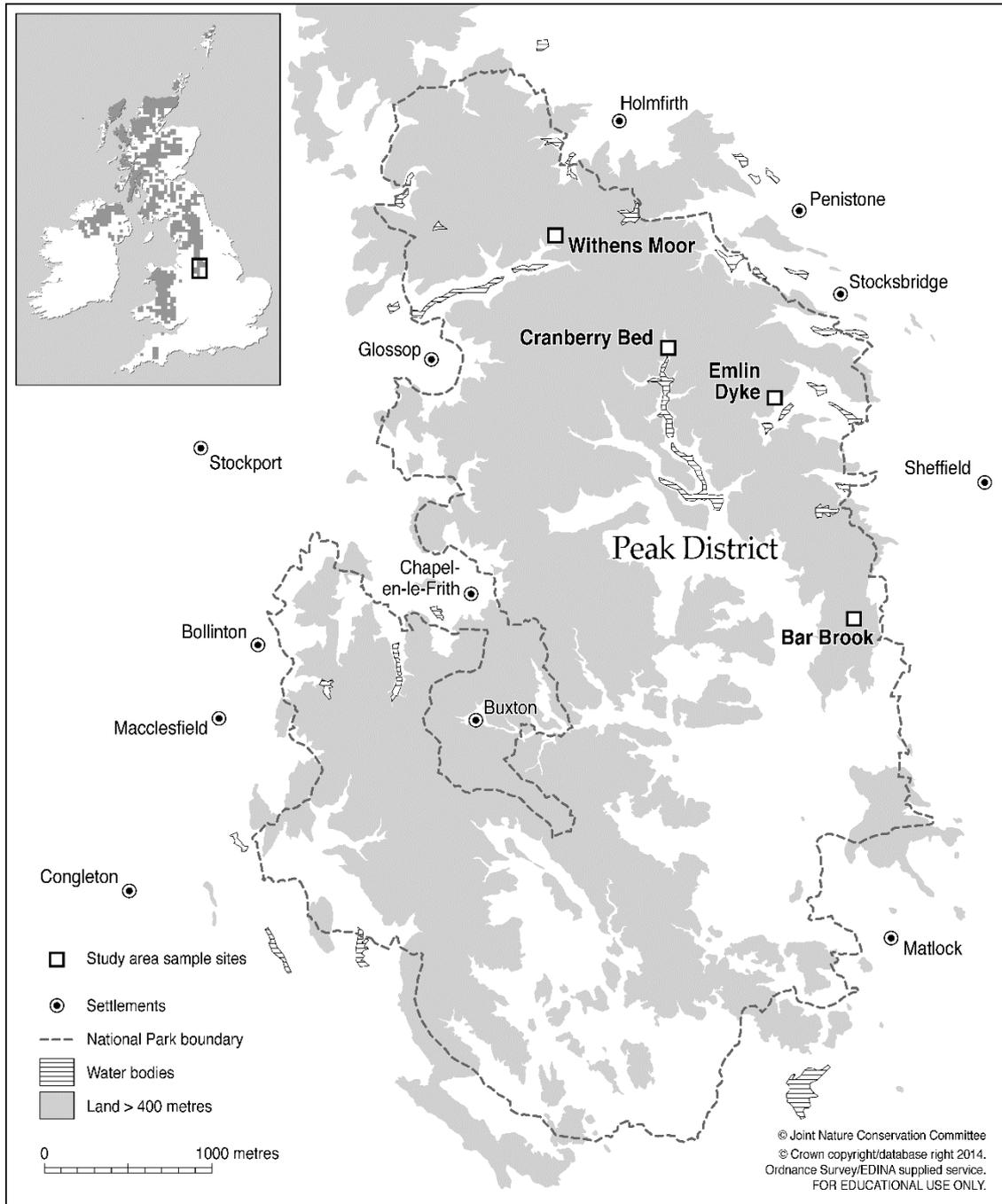


Fig. 1

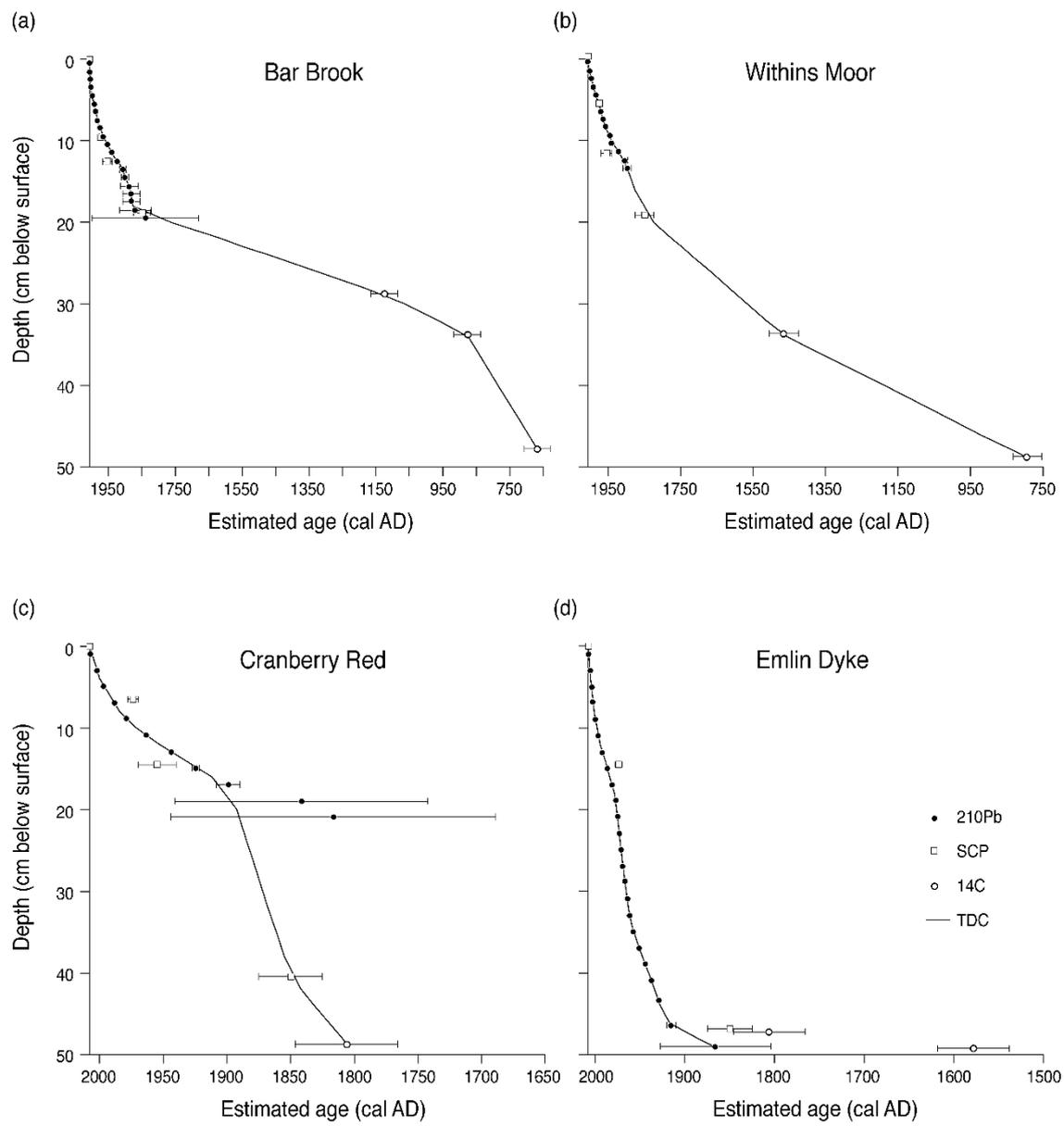


Fig. 2



Withens Moor

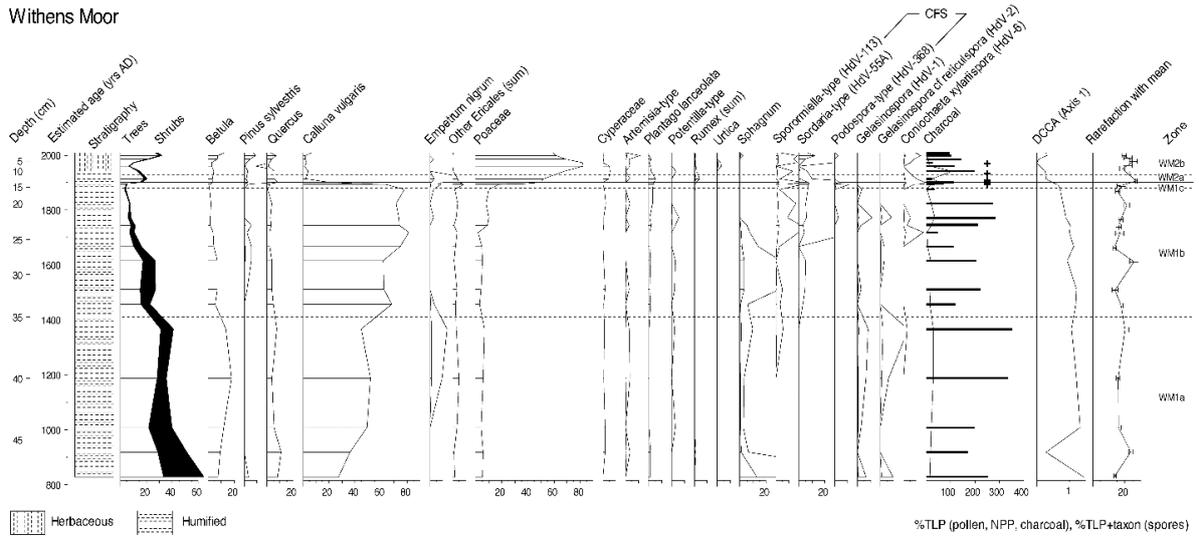


Fig. 4

Cranberry Bed

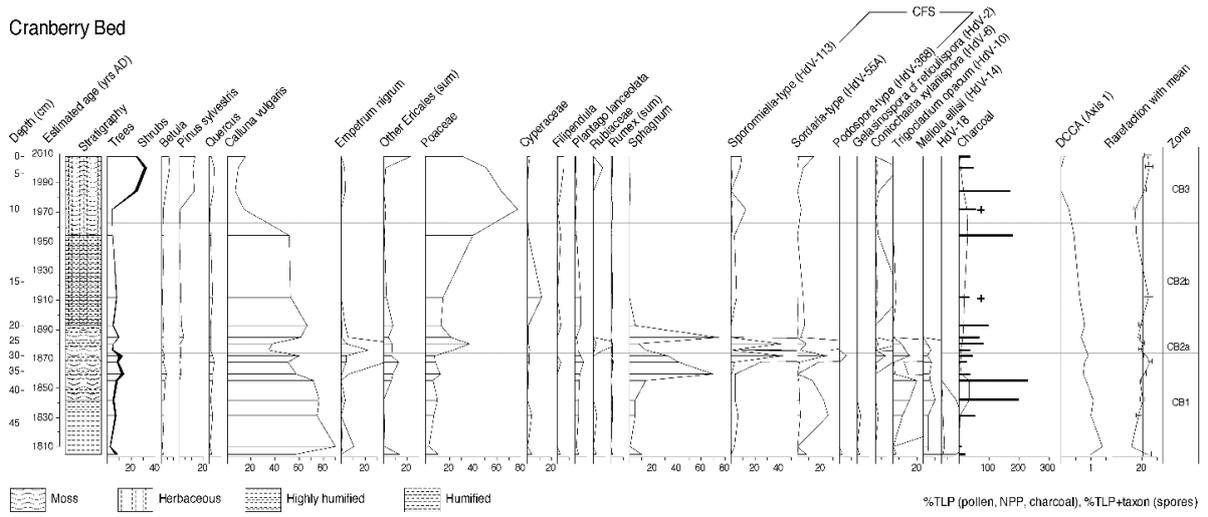


Fig. 5

Emlin Dike

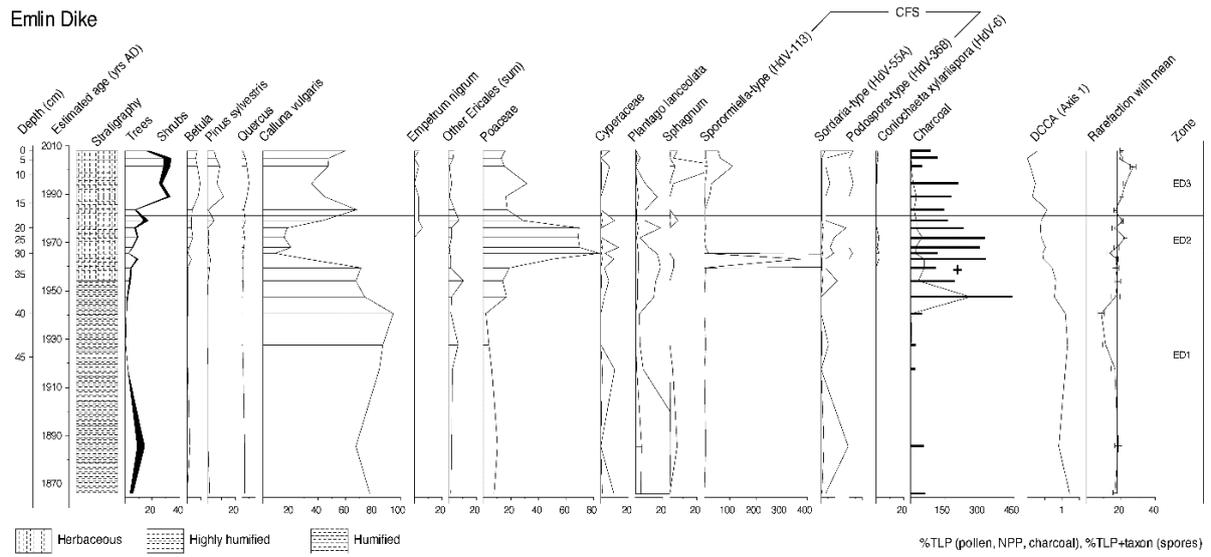
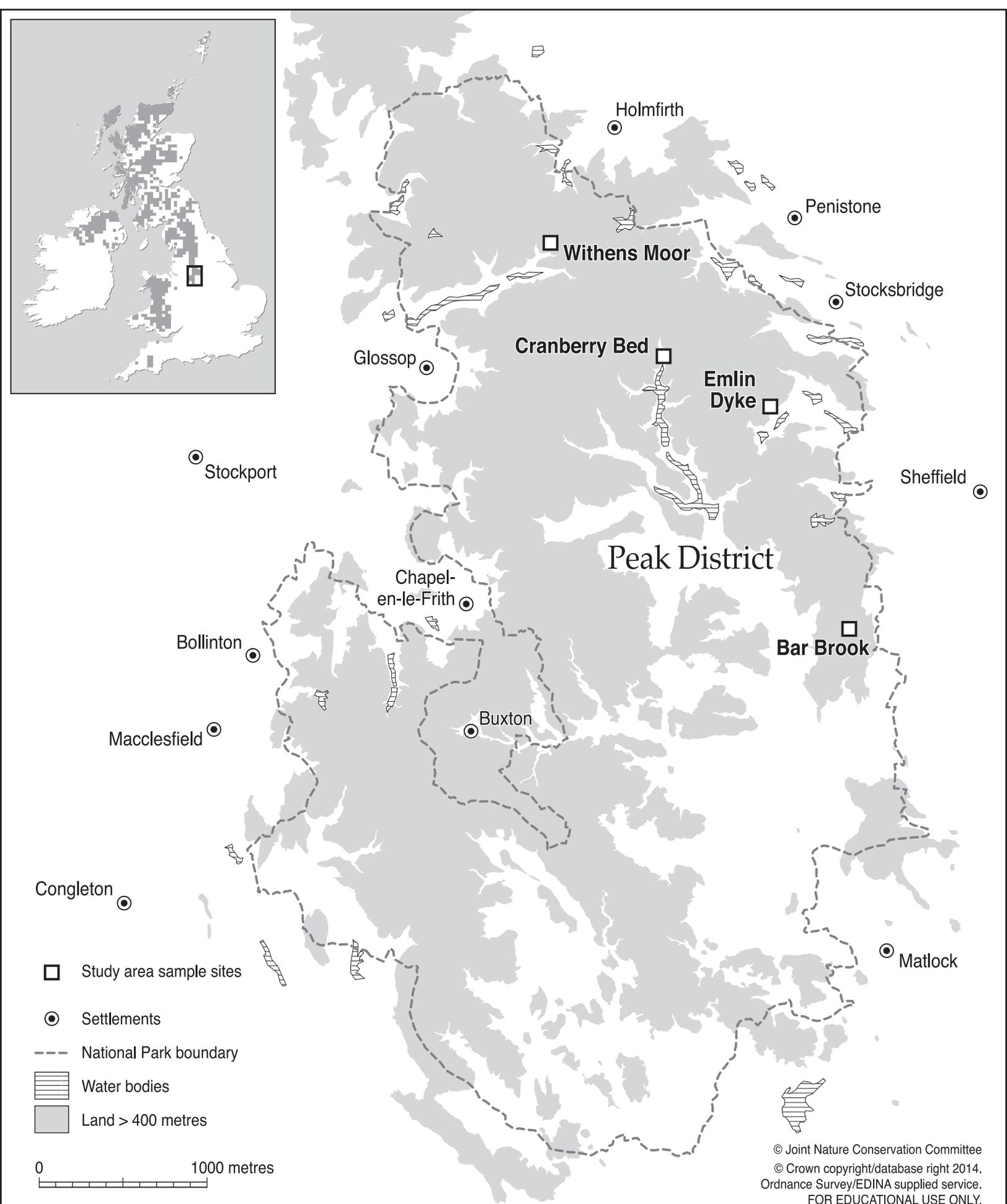


Fig. 6

Figure 1



- Study area sample sites
- Settlements
- - - National Park boundary
- ▨ Water bodies
- Land > 400 metres

0 1000 metres

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Figure 2

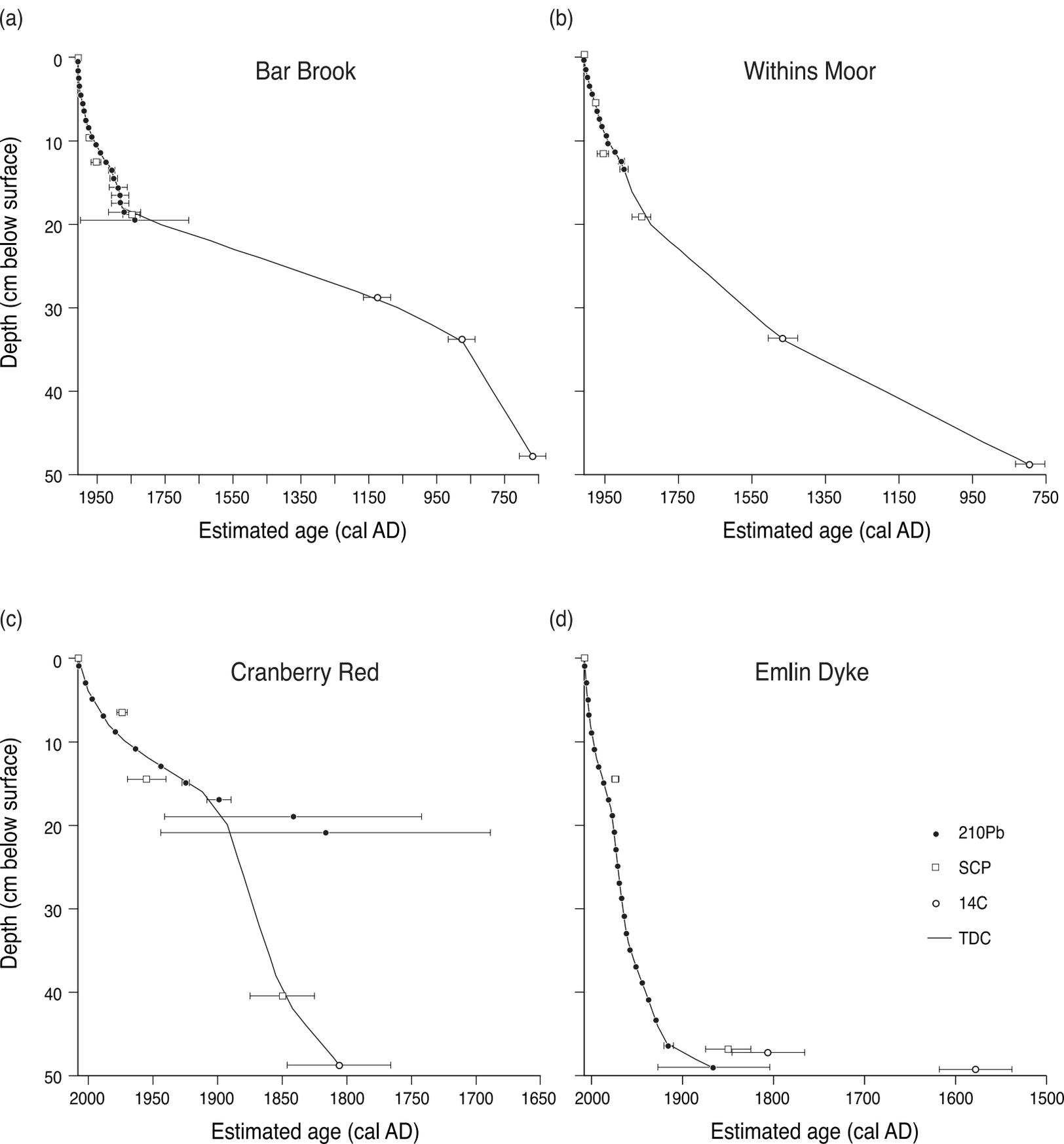


Figure 3

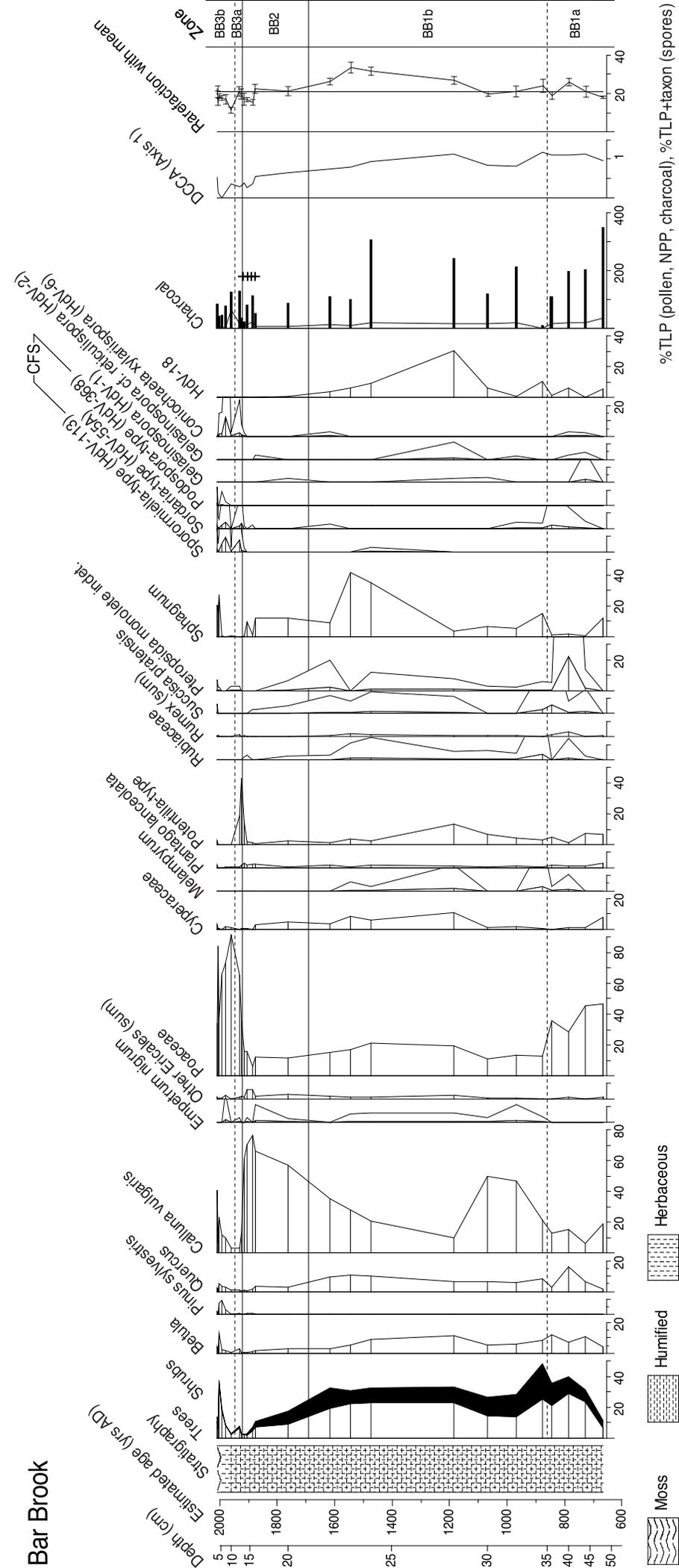


Figure 4

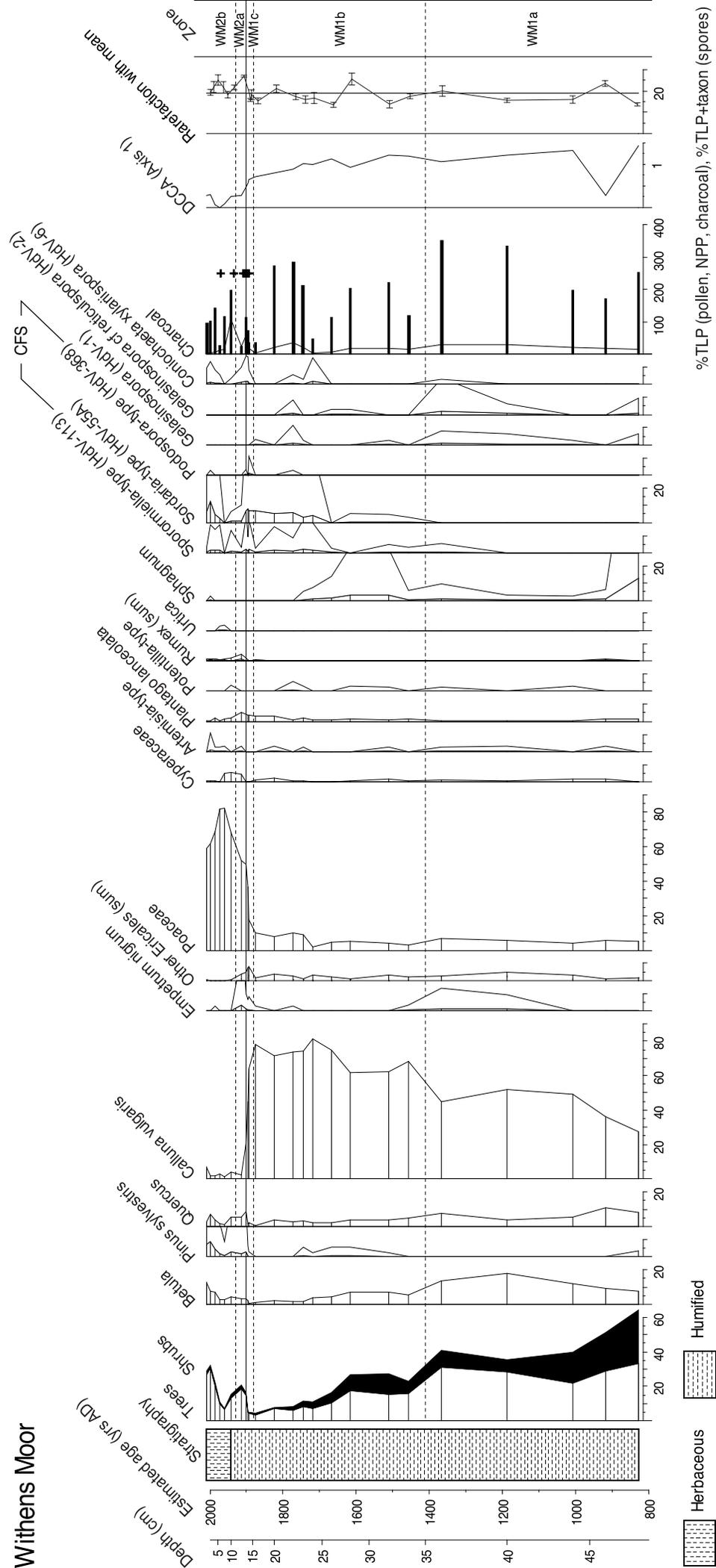
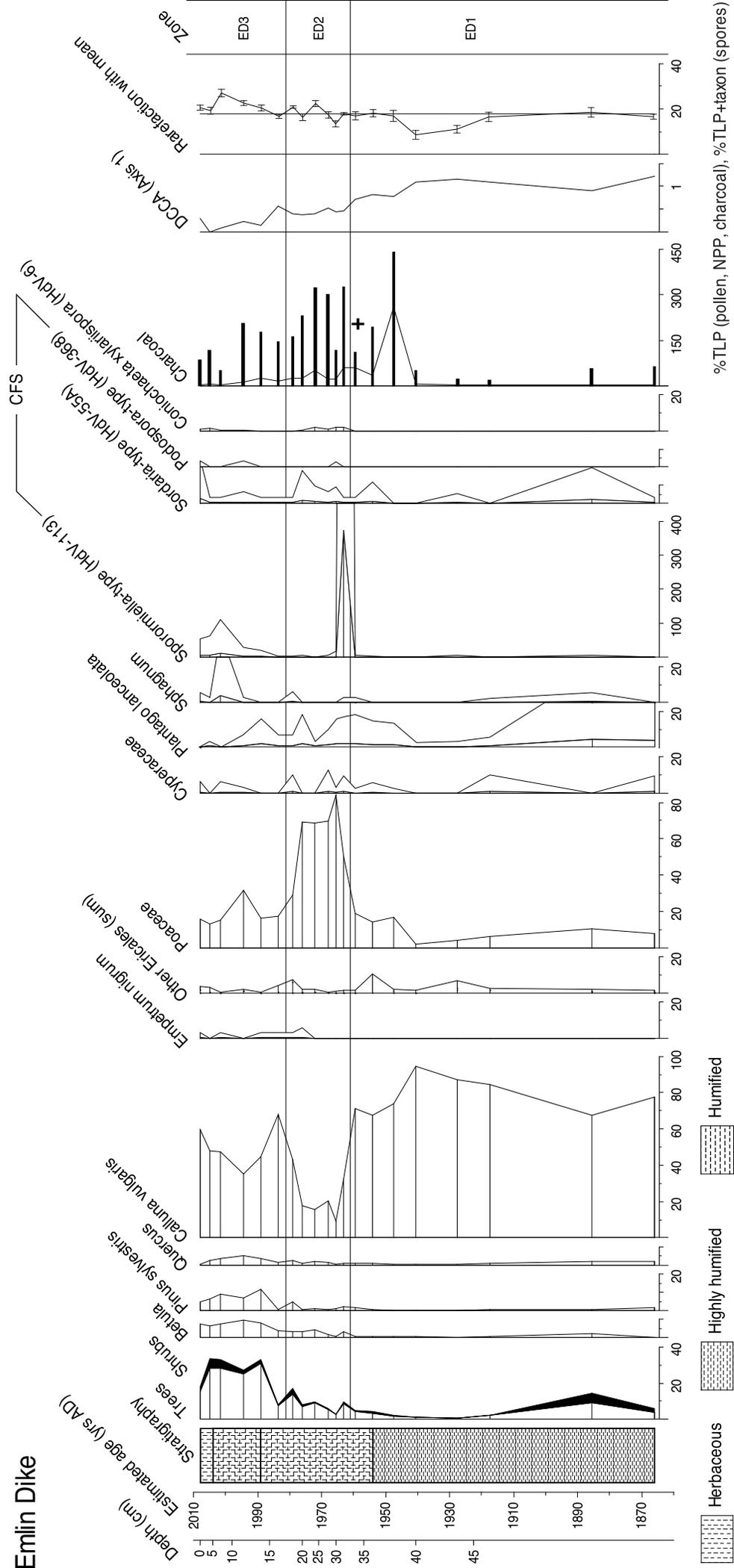




Figure 6



Supplementary Material 1

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Supplementary Material 2

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Supplementary Material 3

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**Table 1.** Sampling site descriptions

Site and location	Description
Bar Brook (BB) 53°18'05''N 1°34'49''W, 360 m OD	Channel mire on southern edge of blanket bog with wet heath, <i>Molinia</i> and dry heath, and adjacent dry acid grassland (all Biodiversity Action Plan [BAP] priority habitats). Many channels on this moor have been modified by drainage. Selected as a relatively rare intact deep peat; sampled previously to study prehistoric vegetation history (Hicks 1971). Main habitat: bog. Conservation status: 'unfavourable recovering' (March 2010)
Withens Moor (WM) 53°31'08''N 1°50'53''W, 440 m OD	Peat shelf on west-sloping extensive deep blanket peat (>1.5-2.0 m), adjacent to <i>Molinia</i> and rush pasture (BAP priority habitats) with substantial areas of grass dominance, including <i>Molinia</i> and <i>Nardus</i> . Selected to assess timing and drivers of grass expansion on deep peat. Main habitat: acid grassland. Conservation status: 'unfavourable recovering' (March 2013)
Cranberry Bed (CB) 53°27'19''N 1°44'38''W, 290 m OD	Fen showing acidic tendency, formed behind landslip at base of valley slope (Briggs et al. 1985), within <i>Molinia</i> and rush pasture, with upland heath and blanket bog on surrounding slopes and tops (all BAP priority habitats). Underlain by up to 4.1 m peat (University of Sheffield, 2004, unpublished). Selected to assess long-term ecology of valley-bottom community with relatively species-rich mosaic. Main habitat: acid grassland. Conservation status: 'unfavourable recovering' (March 2009)
Emlin Dike (ED) 53°25'54''N 1°39'21''W, 390 m OD	Fen containing one of few deeper peat deposits on eastern heather-rich moors, located in heather-dominant upland heath with diverse dwarf-shrub heath and blanket bog (BAP priority habitats). Selected to examine heathland dynamics near the moorland-edge, in an area with a history of grouse management. Peat overlies sandy clay. Main habitat: dwarf-shrub heath. Conservation status: 'favourable', with localised bracken encroachment (September 2012)