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1 **Ecological consequences of historic moorland ‘improvement’**

2

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30 writing of the manuscript; Ralph M. Fyfe, Tim Daley, and David N. Smith collected samples
31 in the field; Ralph M. Fyfe, Francis M. Rowney, Philip Anderson, Robert Barnett, William
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40

41 **Abstract**

42 Upland peatlands are nationally and internationally important habitats that can provide a
43 range of ecosystem services, but many are considered degraded by human activities. On
44 Exmoor, (South West England, UK) restoration activities are often aimed at reversing the
45 effects of nineteenth century agricultural ‘improvement’ schemes, the effects of which are not
46 yet fully understood. To develop this understanding, long-term ecological context is essential.
47 We used sub-fossil pollen, plant macrofossils, testate amoebae, insects, coprophilous fungal
48 spores and charcoal to study ecological conditions and disturbance regimes over the last
49 ~7700 years at a site in Exmoor National Park (‘Ricksy Ball’). Multivariate analyses were
50 used to explore changes in ecological communities over time and a range of techniques were
51 used to establish the chronology. During the last ~7700 years, anthropogenic disturbance
52 regimes (burning, grazing, drainage) have varied through time, reflecting changing land use
53 and management, the effects of which are evident in vegetation (pollen, plant macrofossils)
54 and microbial (testate amoebae) communities. In particular, a combination of drainage and
55 high-intensity grazing appears to have substantially altered local ecology during the
56 nineteenth century, indicated by increases in coprophilous fungal spores and the loss of
57 *Sphagnum* and associated biota. This occurred in the context of more gradual, centennial-
58 scale declines in *Sphagnum* and microbial biovolumes. We provide a range of reference
59 conditions and show that the moorland has been influenced by land management changes for
60 millennia, and this may have been most pronounced during the nineteenth century. There is
61 no single, readily identifiable, ‘stable’ pre-drainage baseline.

62

63 **Keywords:** Peatlands, Palaeoecology; Pollen; Testate amoebae; Multi-proxy; Restoration

64

65 **Introduction**

66 Uplands provide nationally and internationally important habitats, particularly in areas with
67 spatially-extensive peatlands (Reed et al. 2009). Much recent attention has been placed on the
68 protection and restoration of upland peatlands, owing to their range of potential ecosystem
69 services, including regulatory services such as climate change mitigation (through
70 greenhouse gas sequestration), provisioning services (*e.g.* water supply) and cultural services
71 (*e.g.* recreation and preservation of heritage assets) (Grand-Clement et al. 2013). Peatland
72 vegetation and ecological function are important in the provision of these services (Belyea
73 and Malmer 2004; Ritson et al. 2016). Many peatlands in the UK and Ireland are considered
74 degraded as a result of anthropogenic activities including burning, peat cutting and drainage
75 (Holden et al. 2007; Bonn et al. 2016). In the UK, drainage has historically been used in
76 moorland ‘agricultural improvement’ schemes, particularly during the nineteenth century
77 following parliamentary enclosure acts (Whyte 2006) and in the post-war period (1940s to
78 late 1970s) in response to national food supply concerns (Dallimer et al. 2009; Loblely and
79 Winter 2009). Drainage ditches reduce vegetation diversity on blanket peat (Gatis et al.
80 2016), which may be exacerbated when drainage is used to facilitate increased grazing: long-
81 term data suggest this may have led to the expansion and dominance of purple moor-grass
82 (*Molinia caerulea*) across uplands (Chambers et al. 2007). Future climatic changes may also
83 have significant effects on peatland functioning, particularly in regions such as the southwest
84 of the UK where peatlands lie in climatically-marginal situations (Gallego-Sala et al. 2010).
85 Peatland restoration activities are often aimed at reversing the historical effects of drainage
86 (Bonn et al. 2016), and so understanding these effects, particularly from a long-term
87 perspective, is important. This includes understanding the extent of historical *Sphagnum*
88 losses, associated changes in broader ecological communities (vegetation, microbes, etc), and
89 the relative importance of other disturbance processes.

90 Exmoor is an upland region with a long history of pre- and post-1940s drainage (Riley and
91 Wilson-North 2001). Landscape-scale drainage and management for agriculture on Exmoor
92 began in the 1820s following the sale of the Royal Forest of Exmoor (*c.* 60 km²) to the
93 Knight family in 1818 (Orwin and Sellick 1970; Riley and Wilson-North 2001; Hegarty and
94 Wilson-North 2014), and further drainage took place during the mid-twentieth century.
95 Restoration work aimed at reversing the effects of drainage on Exmoor (*e.g.* blocking
96 nineteenth and twentieth century drainage ditches to raise local water tables: ‘re-wetting’) has
97 been on-going since 2010, with pre- and post-restoration monitoring to understand responses
98 in hydrological and biological systems, and how these may relate to carbon flux (Grand-
99 Clement et al. 2015; Gatis et al. 2016). The aim of the present research is to understand the
100 ecological consequences of historic moorland ‘improvement’ by providing long-term context,
101 and to assess the extent to which pre-drainage conditions can be used to evaluate the success
102 of on-going restoration works.

103 This paper presents a detailed multi-proxy palaeoecological study of an area of moorland that
104 is subject to on-going restoration (*e.g.* ditch-blocking) and monitoring on Exmoor, southwest
105 Britain (Fig. 1). Palaeoecological datasets offer unparalleled potential for understanding the
106 long-term dynamics of peatland systems (Davies and Bunting 2010; Gearey and Fyfe 2016;
107 Marcisz et al. 2022), and provide valuable insights to restoration projects (Chambers et al.
108 2007; Blundell and Holden 2015; McCarroll et al. 2016). In this case, palaeoecological study
109 provides the context of historical *Sphagnum* losses, how drainage may have influenced wider
110 ecologies, including the potential formation of novel communities, and the additional
111 importance of grazing and burning. We find that the moorland’s ecology has changed with
112 land use over millennia, and that nineteenth century ecological changes (probably related to
113 both drainage and high-intensity grazing) were particularly notable.

114

115 **Materials and Methods**

116 *Sampling Site*

117 Sampling was undertaken in 2012 in the Aclands catchment on Exmoor (0.179 km²), an area
118 subject to on-going restoration work (since 2014) and monitoring (Grand-Clement et al.
119 2015; Gatis et al. 2016). A key aim of this is to raise water tables, restoring hydrological
120 function and associated ecosystem services (*e.g.* carbon sequestration, enhanced water
121 quality, flood prevention) (Grand-Clement et al. 2015). Peat depths range from 0.33 to 2 m
122 and there are 7.5 km of drainage ditches arranged in a herring-bone pattern (Grand-Clement
123 et al. 2015) (Fig. 1). These drains direct water in the headwaters of the River Barle across an
124 area of deeper peat ('Ricksy Ball'), approximately 190 m long and up to 80 m wide. A 1.9 m
125 peat sequence was extracted from Ricksy Ball (-3.808° longitude, 51.131° latitude WGS84;
126 elevation: 421 m OD) using monolith tins (open section, upper 1.1 m) and a closed-chamber
127 corer (lower 0.8 m). The sampling site is located within the extensively drained area.

128

129 *Chronology*

130 Chronological control of the sequence was established using a suite of methods.

131 Samples of peat 1 cm thick were used for AMS (accelerator mass spectrometry) radiocarbon
132 analysis, with dating undertaken on the humic acid fraction to avoid contamination by
133 penetration of younger carbon from higher levels (Piotrowska et al. 2011).

134 The core was scanned for tephra horizons at 5 cm resolution, with precise depths established
135 through shard counts from contiguous 1 cm thick samples where necessary. Tephra samples
136 were prepared for chemical analysis following Dugmore, Larsen, & Newton (1995) and
137 Blockley et al. (2005). Further details are given in Supplementary Information.

138 Contiguous 1 cm samples were taken from the upper part of the section for fallout
139 radionuclide (unsupported ^{210}Pb , ^{137}Cs and ^{241}Am) based sediment dating techniques
140 (Appleby, 2001) at the University of Plymouth Consolidated Radioisotope Facility (CoRiF).
141 Further details are given in Supplementary Information. The Constant Rate of Supply (CRS)
142 model (Appleby and Oldfield 1978; Appleby 2001) was applied to construct core
143 chronologies from activity concentrations.

144 The analysis of major and trace elements within the upper 1.1 m of the core was undertaken
145 using a portable Niton X-Ray Fluorescence (XRF) elemental analyser. Major pollutants
146 (particularly lead (Pb)) and lithogenic elements (*e.g.* zirconium (Zr) and titanium (Ti)) were
147 measured (as parts per million: ppm). Ratios between pollutants (Pb) and lithogenic elements
148 (Ti) have been successful elsewhere in identifying increased atmospheric deposition
149 associated with known industrial pollution histories (Mighall et al. 2002), under the
150 assumption that increases in ratios indicate excess atmospheric Pb not otherwise visible in the
151 raw inventory.

152 Based on the results of the above analyses, an age-depth model was constructed for the
153 sequence. Radiocarbon dates were calibrated using the IntCal20 calibration curve (Reimer et
154 al. 2020). Using the R (R Core Team 2021) packages ‘rbacon’ (Blaauw and Christen 2011;
155 Blaauw 2021a) and ‘clam’ (Blaauw 2010, 2021b), a range of age-depth models were tested.
156 Three radiocarbon dates (UBA-24401, UBA-24402, UBA-24403) that gave age estimates
157 younger than underlying tephras were not used in estimating interpolated ages (automated in
158 ‘rbacon’). Whilst radiocarbon dates of peat are generally reliable, there are a number of
159 potential sources of error (Piotrowska et al. 2011; Väiliranta et al. 2014). Results were broadly
160 similar and the simplest model was chosen: ages between directly dated depths were
161 estimated by linear interpolation using ‘clam’ (Blaauw 2010, 2021b) and the following code:

162 clam(coredir="clam_runs", core="RicksyBall", cc=1, outliers=c(7,8,10),
163 depthseq=print(depths), type=1, its=10000)

164

165 *Palaeoecology*

166 *Plant macrofossils*

167 Material for plant macrofossil analysis was extracted following Mauquoy, Hughes, & van
168 Geel (2010) methods. Sub-samples of peat (2 cm contiguous intervals) were disaggregated
169 and wet sieved to 125 μm and examined using low-power (x10-50) microscopy. Where
170 epidermal material or *Sphagnum* leaves were present, an additional representative sample (50
171 *Sphagnum* leaves) was identified to sub-genus level using high-power microscopy (x100-
172 400).

173

174 *Testate amoebae*

175 Testate amoebae analysis followed Booth, Lamentowicz, & Charman (2010). Sub-samples of
176 sediment (1 cm^3) were disaggregated in potassium hydroxide, wet-sieved to isolate
177 particulate fractions (>15 to <300 μm), mounted in glycerol and identified using high-power
178 (x400-600) microscopy (using Charman, Hendon, & Woodland (2000)). A known amount of
179 an exotic spike (*Lycopodium* spores) (Stockmarr 1971)) was added to facilitate calculations
180 of test concentrations. One hundred tests were counted per sample, which is demonstrably
181 representative (Payne and Mitchell 2009). Count data were converted to influx (number of
182 individuals $\text{yr}^{-1} \text{cm}^{-3}$) using test concentrations and sediment accumulation rates from the age-
183 depth model. Testate amoeba biovolumes were estimated based on morphometric
184 measurements derived from the literature (see Supplementary Table 1) and test shape
185 ('hemispheric', 'ovoid', 'cylindrical' or 'saucer') according to equations in Mitchell (2004)

186 and Gilbert, Amblard, Bourdier, & Francez (1998). Total biovolume is the sum for all taxa,
187 which was then scaled by influx rates to give biovolume values per year per cubic centimetre
188 of sediment ($\mu\text{m yr}^{-1} \text{cm}^{-3}$). Overall testate amoebae biovolume ($\mu\text{m}^3 \text{yr}^{-1}$) for each sample
189 was estimated by scaling the biovolume information by the influx of each taxon.

190

191 *Pollen and coprophilous fungal spores*

192 Pollen and coprophilous fungal spore sample preparation followed Moore, Webb, &
193 Collinson (1991). One cm^3 sub-samples were disaggregated in potassium hydroxide, silicates
194 were removed using hydrofluoric acid, cellulose was digested using an acetolysis reaction
195 (acetic anhydride and sulphuric acid), samples were dehydrated with alcohols and mounted in
196 silicon oil for identification using high-power (x400-600) microscopy. Three hundred land
197 pollen grains were identified from each sub-sample, a sufficient number for characterising
198 assemblages (Djamali and Cilleros 2020). Coprophilous fungal spores (per 100 *Lycopodium*
199 spores) were counted on pollen slides to 168.5 cm core depth. *Sporormiella*-type spores may
200 occur as lone cells or chains of cells, and counts were based on the number of chains plus the
201 number of lone cells.

202

203 *Insects*

204 Contiguous 10 cm samples of ~10 litres were taken from the open peat section, adjacent to
205 the monolith tin samples. Samples were sieved (300 μm) before undergoing paraffin
206 (kerosene) flotation (Kenward et al. 1980). Insect remains were sorted and identified using
207 low-power (x15-45) microscopy. Where achievable, they were identified to species-level by
208 direct comparison to modern specimens (Gorham and Girling insect collections, University of

209 Birmingham). Identifiable insect remains are mostly from Coleoptera (beetles). Taxonomy
210 follows Lucht (1987). Coleoptera have been assigned to ecological groupings where possible,
211 following a simplified version of Robinson's (Robinson 1981, 1983) scheme. Dung, open
212 habitat and moorland ecological groupings are calculated as percentages of the total number
213 of terrestrial species, as opposed to the entire fauna.

214

215 *Multivariate analyses*

216 To explore the extent and directions of change in ecological communities over time, and the
217 taxa associated with these changes, unconstrained ordination techniques were used with both
218 testate amoeba (influx rates) and pollen assemblages (relative abundances), representing
219 more local and more regional ecological conditions, respectively (*n.b.* pollen and testate
220 abundances were treated as percentages and influx rates, respectively, in correspondence with
221 Figures 3 and 6, to aid understanding). Datasets were filtered prior to analysis to include only
222 common taxa (occurring in at least 50% of samples) and abundances were square root
223 transformed (to facilitate analyses based on the direction and relative magnitude of changes
224 in abundances). Testate amoebae were insufficiently preserved below 94 cm (~403 cal BP),
225 and so multivariate analyses of testate amoebae and pollen assemblages focus on the upper 94
226 cm to facilitate comparison.

227 Detrended correspondence analyses (DCA) were performed on each dataset to determine
228 environmental gradient lengths and all gradient lengths were <2.5 standard deviations. On
229 this basis (following Legendre & Birks (2012)), a linear method (principal components
230 analysis: PCA) was selected to explore trends in the composition of pollen assemblages, but
231 this was determined as inappropriate for testate amoebae assemblages. For these, non-metric
232 multidimensional scaling (NMDS) analysis was used instead. This uses rank-based

233 dissimilarity between samples, and is suitable for non-Gaussian data (Oksanen et al. 2019).
234 Analyses were performed using the R package ‘vegan’ (Oksanen et al. 2019).

235

236 **Results**

237 *Chronology*

238 A summary of the age-depth model is given in Fig. 2 and uncalibrated, calibrated and
239 modelled ages for dated depths are given in Supplementary Table 2. This model is used to
240 provide date estimates for key transitions in palaeoecological sequences, and to calculate
241 influx rates. Dates are given in calibrated years before present (cal BP), where 1950 CE is
242 ‘present’, and in some cases, calendar years (BCE/CE) are also given. Further details of
243 chronological results are given in Supplementary Information.

244

245 *Palaeoecology*

246 Assemblage changes and their implications for local environmental changes are summarised
247 here, and further details are given in Tables 1, 2 and 3, and in Supplementary Information.

248

249 *Pollen and coprophilous fungal spores*

250 The results of pollen and fungal spore analysis from 49 samples describe vegetation changes
251 in the local and wider area around Ricksy Ball, and grazing activity in the local area (Fig. 3).

252 As a general rule-of-thumb, herbaceous (and wetland) pollen types are likely to derived more
253 local sources (<100 m) than pollen from woody, dryland taxa (Binney et al. 2005; Blaus et al.
254 2020). The pollen has been visually divided into five local pollen assemblage zones (lpaz), to

255 aid the description of key periods of continuity and change (see Table 1 for detailed
256 descriptions). Mixed open woodland conditions are represented in the lowermost zone (zone
257 RIB lpaz1, 190.5-162.5 cm, from ~7703 to 3340 cal BP). At 162.5 cm (~3340 cal BP)
258 woodland taxa decline and are replaced by Poaceae and ‘improved’ grassland taxa.
259 Coprophilous fungal spores increase in concentration (Fig. 3), suggesting increased herbivore
260 density. The start of the third pollen zone at 114.5 cm (~595 cal BP / 1355 CE) is marked by
261 declining Poaceae and increases in woody heathland shrubs and some trees. Coprophilous
262 fungal spores are also present in this zone (Fig. 3). From 94.5 cm (~410 cal BP / 1540 CE)
263 the pollen assemblages are dominated by Poaceae and associated grassland taxa, with
264 *Calluna vulgaris* declining to trace levels. In this zone, *Sphagnum* is present in substantial
265 quantities for the first time. Coprophilous fungal spores are present at low levels, but with a
266 substantial increase in *Sordaria*-type at 8.5 cm (Fig. 3). In the uppermost samples (from 6.5 cm:
267 52 cal BP / 1898 CE) Poaceae and indicators of improved grassland decrease, replaced with
268 taxa more associated with ‘poorer’ moorland and levels of *Sphagnum* decline to very low
269 amounts. Coprophilous fungal spore concentrations increase during this period (Fig. 3).

270 Principal components analysis (PCA) of common pollen taxa in the upper parts of the
271 sequence (from 92.5 cm) (Fig. 4) supports this description of vegetation change. The first
272 axis represents 40.0% of variance, and the second axis represents 28.3% of variance. The
273 major assemblage change in this portion of the sequence is in the upper 8.5 cm (~61 cal BP /
274 1889 CE; min: 1830 CE, max: 1939 CE), where both Poaceae and *Sphagnum* decline relative
275 to a number of herbaceous taxa (e.g. *Plantago lanceolata*-type, *Rumex acetosa*-type,
276 Cyperaceae). Prior to this, there are continual fluctuations which appear to represent
277 relatively minor changes in Poaceae and *Sphagnum*, though there is some suggestion that
278 older samples (92.5 cm to 60.5cm, ~403 to 291 cal BP / 1547 to 1659 CE) may have a
279 tendency towards slightly higher Poaceae and lower *Sphagnum* relative abundances.

280

281 *Plant macrofossils*

282 Plant macrofossil analysis (48 samples) describes the character of local (*i.e.* on-site)
283 vegetation at Ricksy Ball (Fig. 5). There are four macrofossil zones (mz: see Table 2), which
284 are briefly described here. The earliest zone is dominated by monocotyledon remains.
285 Charcoal is abundant in every sample in this zone and increases around 160 cm (~2950 cal
286 BP). From 114 cm (~588 cal BP / 1362 CE), *Sphagnum* is recorded consistently, though at
287 low levels within an assemblage that continues to be dominated by monocotyledon remains.
288 From 70 cm (~ 325 cal BP / 1625 CE) *Sphagnum* remains increase significantly, but above
289 10 cm (~69 cal BP / 1881 CE) the samples are all dominated by monocotyledon remains,
290 with no *Sphagnum* present.

291

292 *Testate amoebae*

293 Testate amoebae were only preserved in concentrations sufficient for the development of
294 reliable counts in the upper 94 cm of the sampled section. Analysis therefore focussed on 49
295 samples from the upper section of the core (~ the last 500 years) (Fig. 6, Table 3). The most
296 notable assemblage change occurs at 8.5 cm depth (~61 cal BP / 1889 CE), and prior to this
297 the assemblage is largely dominated by species indicative of ‘hummocky’
298 (microtopographically complex) bog surface conditions. There is a general decrease in testate
299 biovolume (*i.e.* a shift to smaller species) from around 40.5 cm (~210 cal BP / 1740 CE),
300 suggesting decreasing community metabolic rates (reduced capacity in the food web to
301 process energy) (Koenig et al. 2018; Marcisz et al. 2020). Above 8.5 cm (~61 cal BP / 1889
302 CE), the taxa indicative of ‘hummocky’ conditions that were previously dominant are largely

303 absent, and the assemblage becomes dominated by *Diffflugia pristis*-type. These are small
304 testates that are indicators of moderate bog surface wetness, but generally not standing water
305 (Woodland et al. 1998; Charman et al. 2000; Swindles et al. 2009). The trend towards
306 decreasing biovolume is continued, asides from a brief peak at 4.5 cm (~43 cal BP / 1907
307 CE), indicating continued loss of larger species, which tend to be poorer colonisers and are
308 less able to overcome perturbations (Marcisz et al. 2020).

309 Non-metric multidimensional scaling (NMDS) analysis (based on testate amoeba influx
310 values) further illustrates the significance of the shift in testate amoeba assemblages from
311 10.5 cm (Fig. 7). This is shown on the first axis (NMDS1) and demonstrates a move towards
312 assemblages characterised by *Diffflugia pristis*-type, *Cyclopyxis arcelloides*-type and
313 *Pseudodiffflugia fulva*, possibly representing a novel stable state. This analysis indicates that
314 earlier in the sequence (below 8.5 cm, before ~61 cal BP / 1889 CE), abundances of
315 individual species fluctuated, but there were no similarly notable long-term changes in
316 assemblage characteristics, suggesting a previous state of dynamic equilibrium.

317

318 *Insects*

319 Seven insect samples were analysed, from peat taken in 10 cm thick spits between 100 and 30
320 cm depth (~429 to 162 cal BP / 1521 to 1788 CE) (Supplementary Table 3, Fig. 8). Relative
321 to pollen, palaeoentomological data typically represent more local conditions (Smith et al.
322 2010). Beetles (Coleoptera) represent the majority of insect remains recovered, with true bugs
323 (Hemiptera) and flies (Diptera) also present, but rare (see Supplementary Table 3,
324 nomenclature for Coleoptera follows Lucht 1987). Phytophagous beetle host plants
325 (predominantly from Koch (1989a, b, 1992)) are also presented on Supplementary Table 3
326 (plant taxonomy follows Stace (2010)).

327 There is little change in insect assemblages through the sequence (100 cm to 30 cm) and the
328 taxa present are characteristic of upland bogs (see Supplementary Table 3, Fig. 8), indicating
329 that this habitat has existed in the area for the entirety of the period represented.

330

331 **Discussion**

332 *Pre-nineteenth century ecological history*

333 The palaeoecological record presented here covers a substantial part of the Holocene, with
334 the lowest sections deposited earlier than 7000 cal BP (5000 BCE), during the Mesolithic.
335 Plant macrofossils indicate that local, peat-forming vegetation communities during this
336 period were dominated by monocots (grasses and sedges). *Alnus*, *Corylus*, *Betula*, *Quercus*
337 and *Salix* pollen indicates the presence of mixed woodlands nearby, and their absence in
338 macrofossil samples indicates that this was distal to the sampling site. Similar to previous
339 studies (Merryfield and Moore 1974; Fyfe 2012), from around 3000 cal BP (1000 BCE)
340 woodlands declined and there was a general increase in heathland (*e.g. Calluna vulgaris*) and
341 disturbed grassland (*e.g. Plantago lanceolata*, *Potentilla*) taxa. As at other sites across the
342 region, coincidently increasing quantities of charcoal suggests that increasing openness was
343 driven by enhanced burning regimes (Fyfe et al. 2003, 2018) and coprophilous fungal spores
344 suggest that grazing animals may have also played a role.

345 From the fourteenth century CE (112.5 cm: ~568 cal BP / 1382 CE), *Sphagnum* moss became
346 established locally (demonstrated by spores and plant macrofossils), increasing substantially
347 during the seventeenth century CE (68.5 cm: ~319 cal BP / 1631 CE). This was accompanied
348 by microbial (*e.g. Archerella flavum*) and faunal (*e.g. Plateumaris discolor*) wetland taxa.
349 Increasing *Plantago lanceolata* pollen and decreasing coprophilous fungal spore influx

350 during this period suggests a change in local disturbance regimes. Fungal taxa like
351 *Sporormiella* and *Podospora* are specialist coprophiles (Baker et al. 2013; Perrotti and van
352 Asperen 2018), whereas *P. lanceolata* is an adaptable, ruderal generalist that may be
353 favoured by various disturbances, including moderate grazing (Mook et al. 1989; Reudler et
354 al. 2013). This suggests that local grazing pressure may have been reduced (e.g. fewer
355 grazing animals and/or modified annual grazing patterns), possibly associated with increasing
356 surface wetness. Around the eighteenth century (from 40.5 cm, ~210 cal BP / 1740 CE),
357 *Sphagnum* spores and overall testate amoeba biovolume both began general long-term
358 declines, suggesting a gradual decrease in *Sphagnum*-rich peatbog habitats, though these
359 habitats appear to have persisted locally, as indicated by *Sphagnum* macrofossils.

360

361 ***Ecological impacts of nineteenth century moorland ‘improvement’***

362 The most rapid ecological change recorded appears to have occurred during the late
363 nineteenth century (from ~10.5 cm, ~70 cal BP / 1880 CE, 95% confidence range: 1822-1931
364 CE). *Sphagnum* moss almost disappeared locally (indicated by plant macrofossils) and
365 declined substantially in the wider landscape (indicated by spores), with vegetation
366 communities becoming dominated by grasses. Testate amoeba assemblages became
367 dominated by *Diffugia pristis*-type, indicators of moderate surface wetness (but not standing
368 water) (Woodland et al. 1998; Charman et al. 2000; Swindles et al. 2009), largely replacing
369 species indicative of ‘hummocky’ bog surface conditions, suggesting a simplification of local
370 microtopography. These changes in floral and microbial communities indicate a rapid change
371 in the landscape, consistent with nineteenth century drainage on Exmoor (Hegarty and
372 Wilson-North 2014). A notable increase in influx rates of all coprophilous fungal spore types
373 (*Sordaria*-type, *Sporormiella*-type and *Podospora*-type) and a decline in *Plantago lanceolata*

374 also occurred at the same time. Whilst *P. lanceolata* may be favoured by various
375 disturbances, including moderate grazing pressure (Mook et al. 1989), repeated defoliation
376 under heavy grazing pressure may conceivably reduce fitness (Reudler et al. 2013),
377 suggesting the initiation of a high-intensity grazing regime.

378 The precise timing of this ecological shift is difficult to determine on a decadal scale, due to
379 uncertainty inherent in age-depth modelling (e.g. 10.5 cm ~70 cal BP / 1880 CE, 95%
380 confidence range: 1822-1931 CE, see Fig. 2), but occurrence during Knight family ownership
381 of the Royal Forest of Exmoor (1818-1886) seems likely. This was a period of deliberate
382 social, economic and agricultural change (Orwin and Sellick 1970; Hegarty and Wilson-
383 North 2014), with relevance for modern Exmoor (e.g. Riley 2019). During the mid to late
384 nineteenth century thousands of Scottish Blackface and Northumbrian Cheviot sheep, which
385 could be pastured on Exmoor throughout the year, were introduced and areas of peat were
386 drained and managed to 'improve' the land for this purpose (Orwin and Sellick 1970;
387 Hegarty and Wilson-North 2014). Notably, a flock of Cheviot sheep were brought to
388 Cornham Farm (adjacent to Ricksy Ball, see Fig. 1), in 1873 (Orwin and Sellick 1970). This
389 is strikingly consistent with the palaeoecological evidence for the disappearance of
390 *Sphagnum*, intensification of grazing and associated changes in vegetation and microbial
391 communities in the upper 10.5 cm of the sequence and provides the most likely explanation.

392

393 ***Implications for modern landscape management***

394 The nature of local and regional ecology, and the functioning of the moorland, has been
395 influenced by successive changes in management practices, including different fire, grazing
396 and drainage regimes. Our palaeoecological analyses provide a range of reference conditions

397 from the past, as well as revealing the ecological consequences of these catchment
398 management practices.

399 Palaeoecological analyses demonstrate that the post-drainage ecology of Ricksy Ball is
400 characterised by novel communities that do not have past analogues. In vegetation
401 assemblages, the loss of *Sphagnum* is the most conspicuous difference pre- and post-
402 drainage, but more subtle changes in *Plantago lanceolata* (decline), monocots (increase) and
403 *Calluna vulgaris* (increase) are also evident. Microbial (testate amoebae) assemblages are
404 strikingly different post-drainage, shifting from a relatively diverse community of species
405 associated with ‘hummocky’ bog surfaces, to a community lacking in those species and
406 dominated by a small number of taxa. Sub-fossil insect assemblages were only recovered
407 from pre-drainage contexts, but these can be compared to a modern entomological survey
408 from Ricksy Ball (undertaken in 2009, prior to restoration works) (Boyce 2010): notably, the
409 most abundant taxon in sub-fossil samples, *Plateumaris discolor* (associated with a range of
410 marshland plants, often in acid conditions (Cox 2007)), was lacking from the modern survey.
411 Collectively, this evidence suggests that post-drainage Ricksy Ball was distinct from pre-
412 drainage in terms of both biota and microhabitat diversity. This is a common pattern amongst
413 UK uplands that underwent major disturbances (e.g. drainage, peat-cutting, high-intensity
414 grazing, nitrogen deposition) during the nineteenth and twentieth centuries, subsequently
415 becoming characterised by low *Sphagnum* abundance and mono-dominant surface vegetation
416 types (e.g. *Molinia caerulea* (Poaceae), *Calluna vulgaris*) (Chambers et al. 2013, 2017;
417 Davies 2016). As these periods of major disturbance typically occurred prior to the initiation
418 of long-term ecological monitoring studies (e.g. UK Countryside Survey (UK Centre for
419 Ecology & Hydrology 2022)), this highlights the utility of palaeoecological data in
420 understanding systems targeted for restoration (Davies and Bunting 2010; Chambers et al.
421 2017; Chambers 2022; Marcisz et al. 2022).

422 There is an opportunity for mutual learning between ecology and palaeoecology if organisms
423 studied as palaeoenvironmental proxies are incorporated into peatland restoration monitoring
424 programmes. In particular, these could be enhanced by the incorporation of testate amoebae
425 (Davis and Wilkinson 2004; Payne 2013; Swindles et al. 2016), which have been shown here
426 to be sensitive bioindicators of changing catchment conditions. They are important in
427 peatland microbial communities, often occupying high trophic levels (Jassey et al. 2013), and
428 they are a food source for invertebrates (*e.g.* chironomid larvae) (Mieczan et al. 2015),
429 providing a link between microbial and faunal food webs. The reduction in testate amoebae
430 biovolume over the last 500 years suggests decreasing community metabolic rates (reduced
431 capacity in the food web to process energy). Given the trophic position of testate amoebae,
432 this may be associated with changes in other parts of the trophic system (*e.g.* invertebrate
433 biomass), but more work is required to understand this aspect of peatland ecosystem function
434 (Swindles et al. 2016).

435 On Exmoor, there is considerable interest amongst certain stakeholder groups in ‘reversing’
436 the effects of nineteenth century land management practices, particularly peatland drainage
437 (Grand-Clement et al. 2015). A key aim of this is to raise water tables, restoring hydrological
438 function and associated ecosystem services (*e.g.* carbon sequestration, enhanced water
439 quality, flood prevention). This is achieved through practical interventions such as ditch-
440 blocking, which may promote the re-growth of *Sphagnum* and increase local biodiversity and
441 carbon storage (Grand-Clement et al. 2013, 2015). Whether the resultant ecological
442 communities are likely to be taxonomically comparable to past communities remains unclear,
443 though the relative importance of this may depend on different stakeholder interests, and
444 which points in time are compared to the present. For example, peatlands with a mixture of
445 surface vegetation functional types (*e.g.* ericaceous shrubs and grasses) are likely to be more

446 efficient for carbon sequestration than those with mono-dominant types (particularly grass)
447 (Ward et al. 2013), but both situations have existed in the past (see Figures 4 and 5).

448 There is no single, readily identifiable, ‘stable’ pre-drainage ecological baseline. The system
449 is inherently dynamic and successive changes in management practices over centuries and
450 millennia (including different fire, grazing and drainage regimes) have continually modified
451 the nature of local and regional ecology, and the functioning of the moorland. There is also
452 little evidence for post-drainage communities reverting to pre-drainage states within the
453 timescale of the record (*n.b.* sampling was undertaken prior to restoration works). In this
454 context, knowledge of the past derived from palaeoecological data acts as “a guide rather
455 than a template” (Higgs et al. 2014), providing a range of reference conditions and revealing
456 the consequences of past management practices, rather than specifying a single target for
457 restoration.

458

459 **Conclusions**

460 Palaeoecological analyses reveal varied management practices (burning, grazing, drainage)
461 and associated ecological responses over the last eight millennia at Ricksy Ball (Exmoor),
462 and major changes in vegetation and microbial communities have been broadly coincident
463 over the last five hundred years. During the nineteenth century, a combination of drainage
464 and increased grazing intensity appears to have substantially altered the local ecology,
465 resulting in the loss of *Sphagnum* and associated macro- and microbiota. This occurred in the
466 context of more gradual, centennial-scale declines in *Sphagnum* and microbial biovolumes.

467 There is no single, readily identifiable, ‘stable’ pre-drainage baseline. We provide a range of
468 reference conditions and reveal the consequences of past management practices, showing that

469 the moorland's character and ecological functioning have been influenced by changes in land
470 management for millennia, and this may have been most pronounced during the nineteenth
471 century.

472

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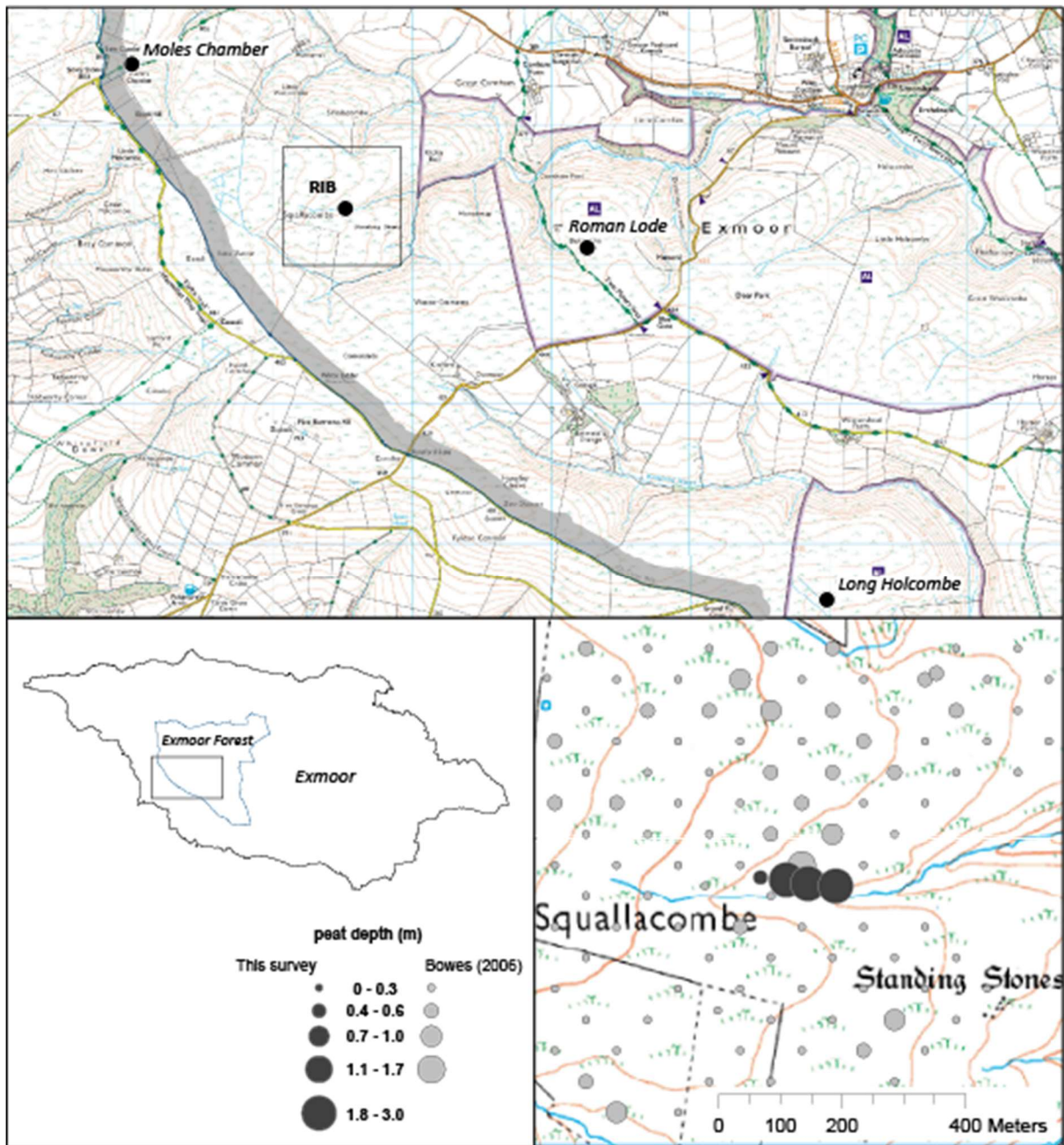
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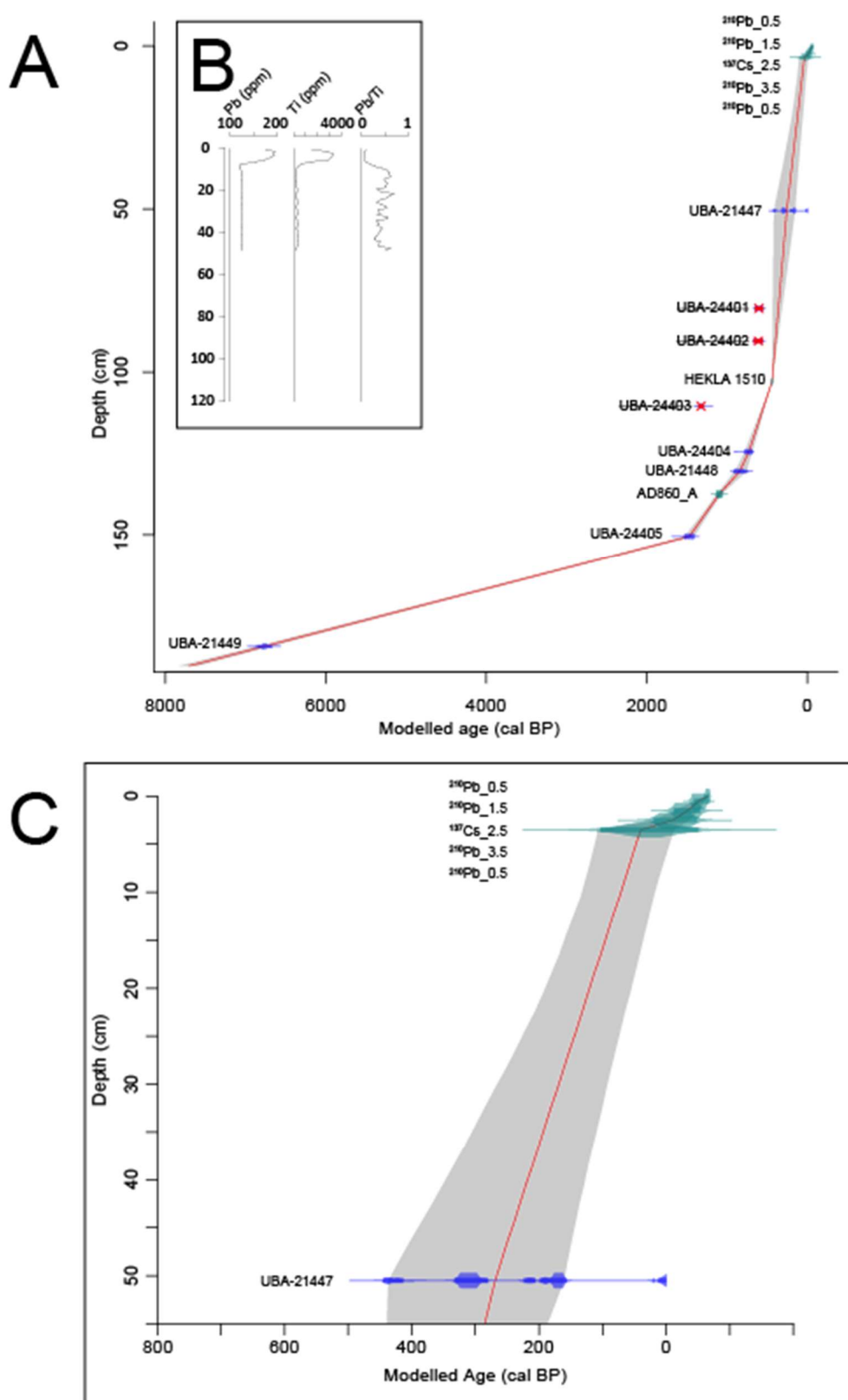
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690 *Fig. 1* Location map showing Ricksy Ball and other notable sites nearby. Grey shading shows the boundary of the former
691 Royal Forest. New and previously measured (Bowes 2006) peat depths.



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694 *Fig. 2 Chronological summary. A: Full age-depth model (with 95% confidence intervals); B: XRF results; C: Focussed view*
 695 *of the upper 55cm of the age-depth model (with 95% confidence intervals). Dates with red crosses were not used in the*
 696 *model*

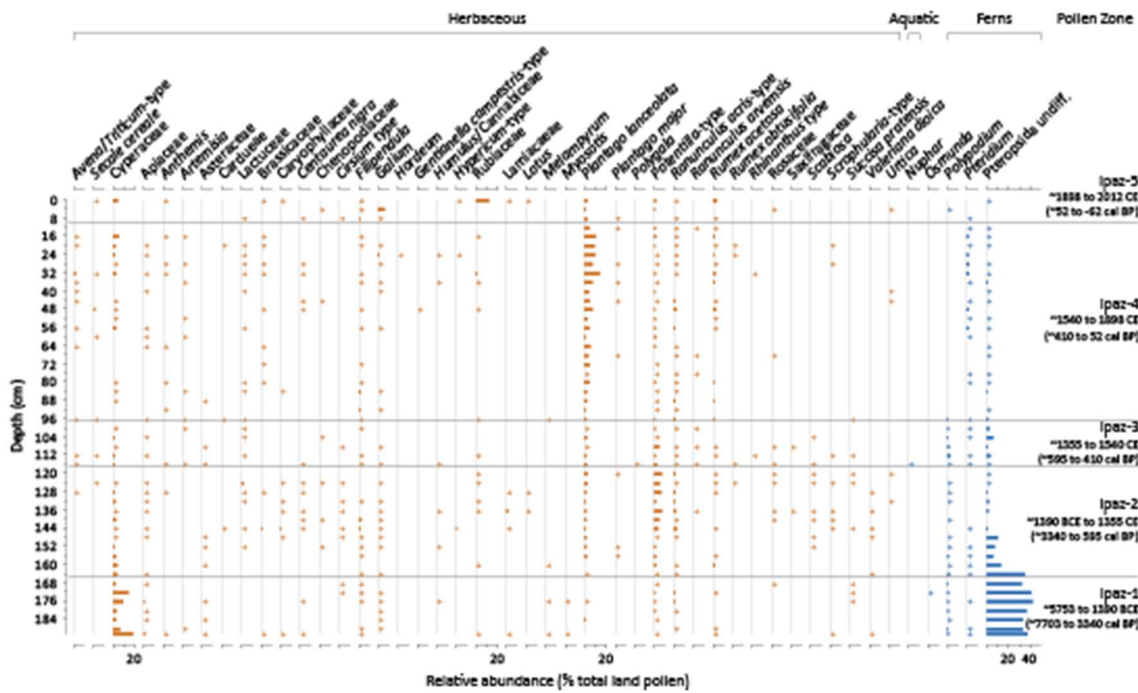
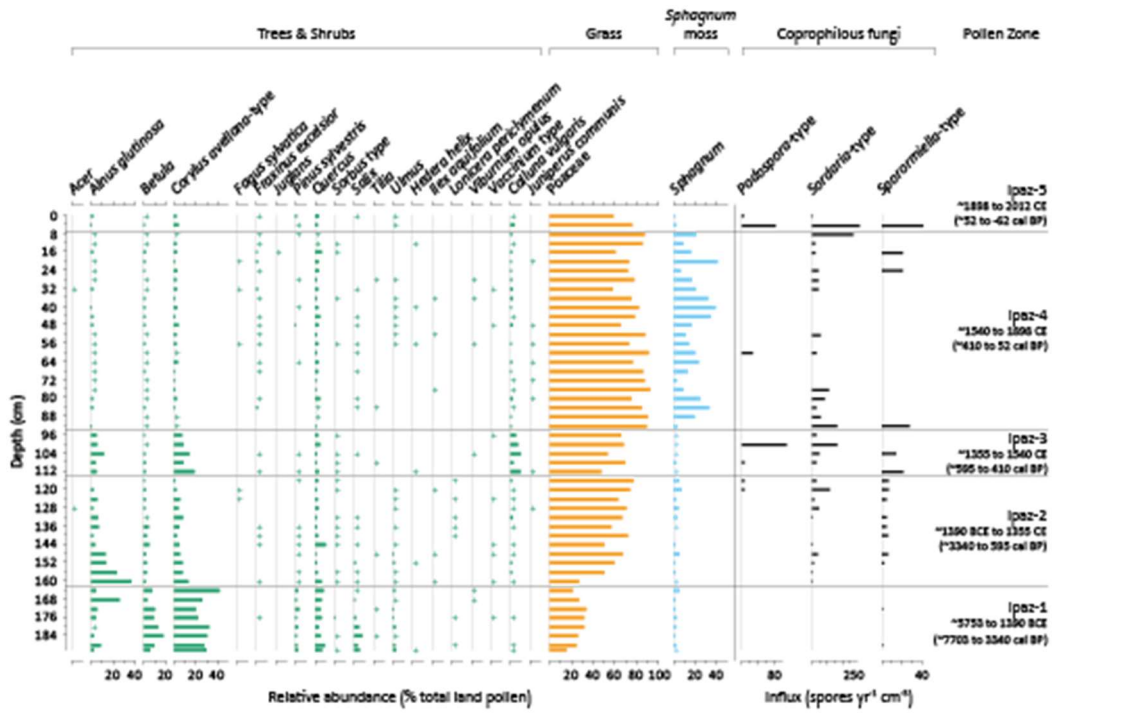
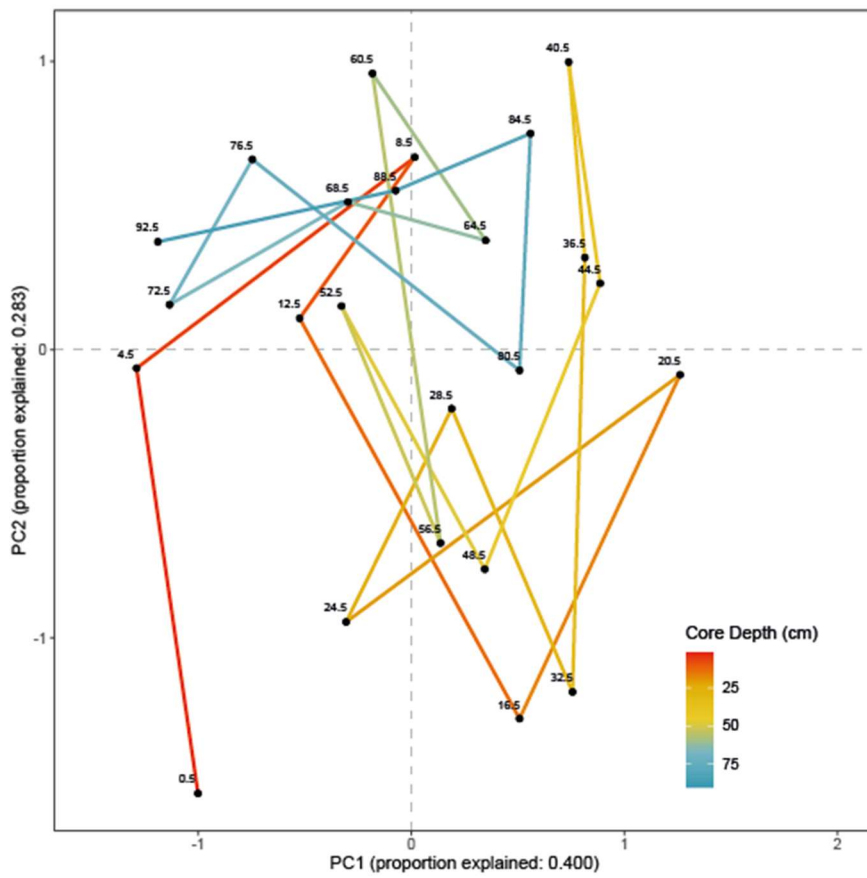
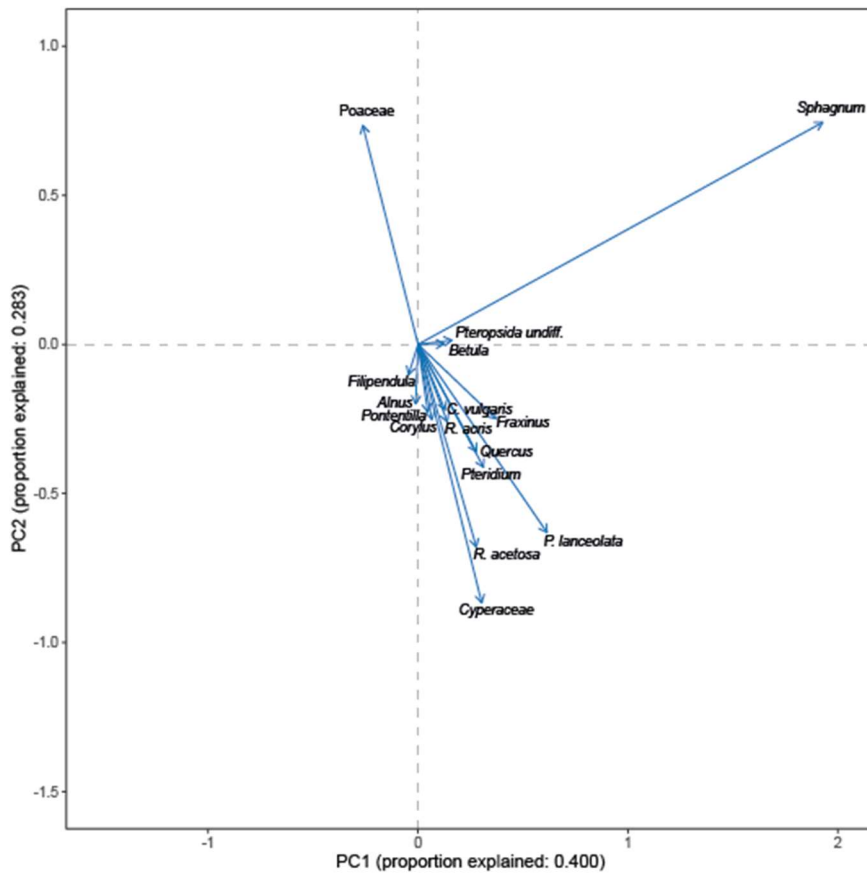


Fig. 3 Pollen and spore diagram. Values are expressed as percentage of total land pollen, total land pollen plus spores (fern and moss spores) or influx rates (coprophilous fungal spores)

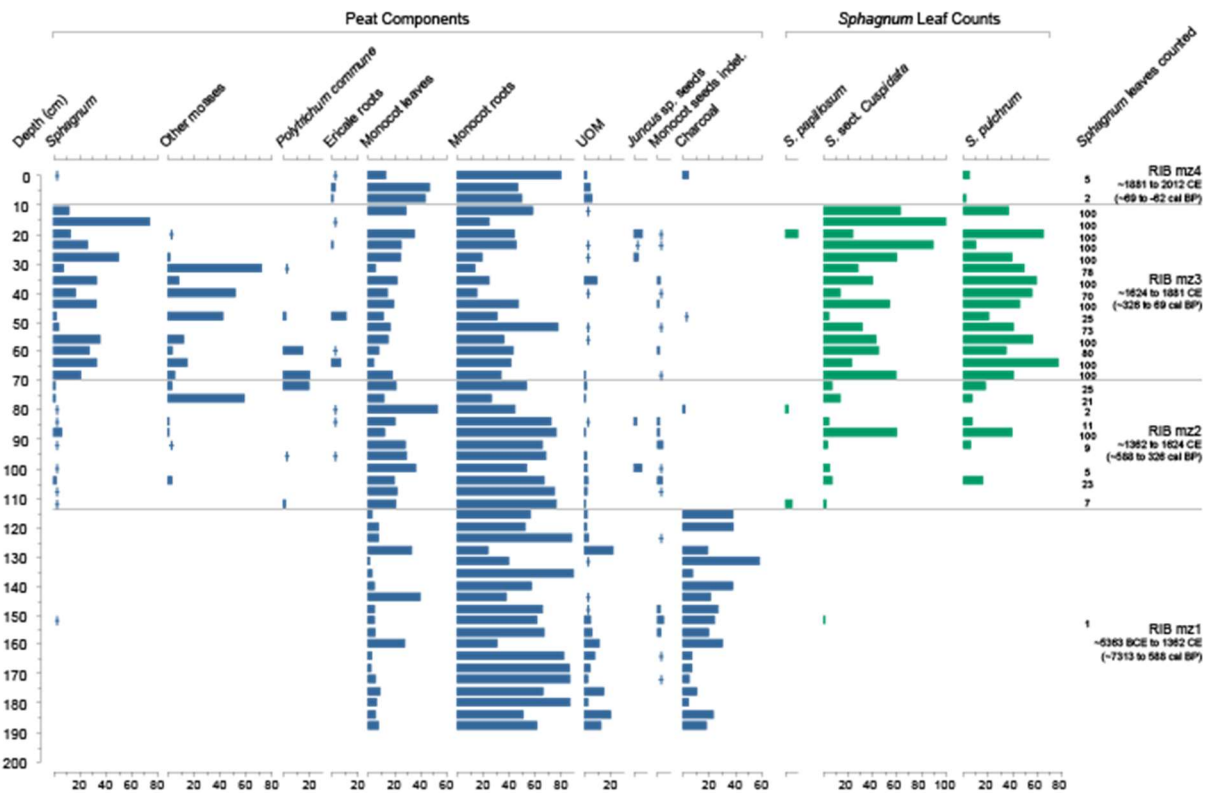


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Fig. 4 PCA of common (present in >50% samples) pollen and spore taxa. Upper diagram shows taxa, lower diagram shows samples

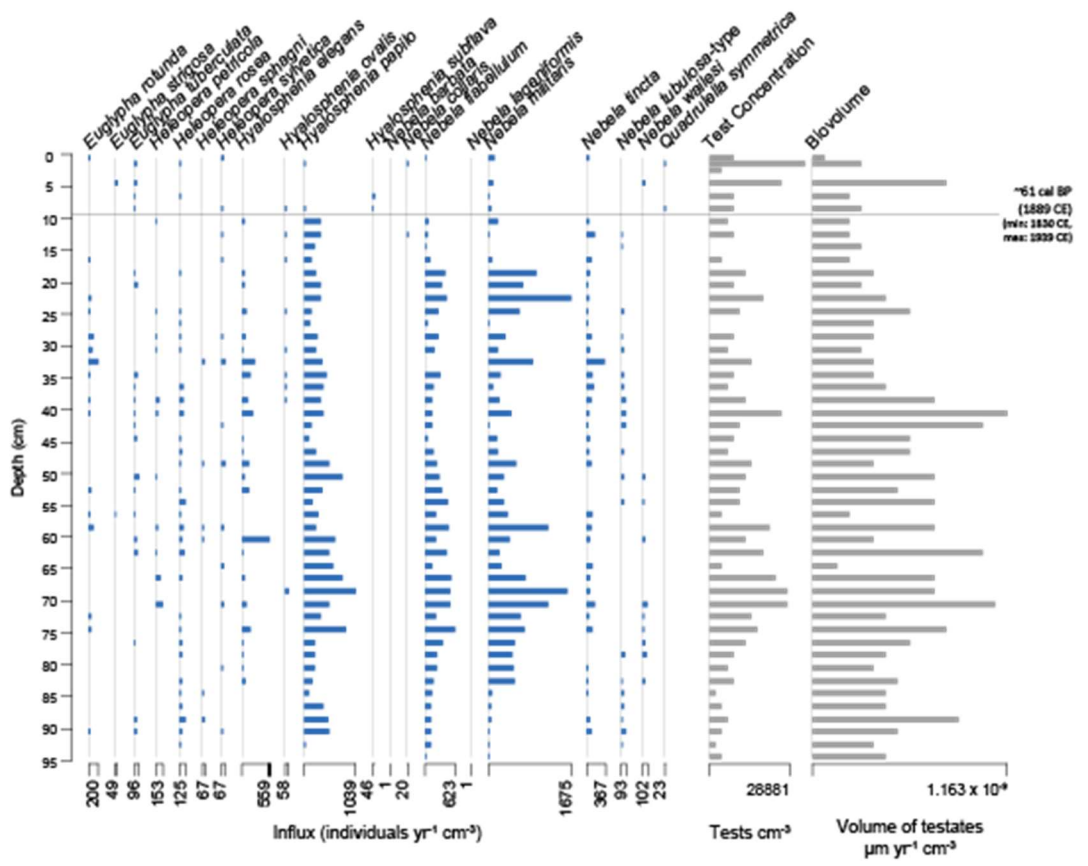
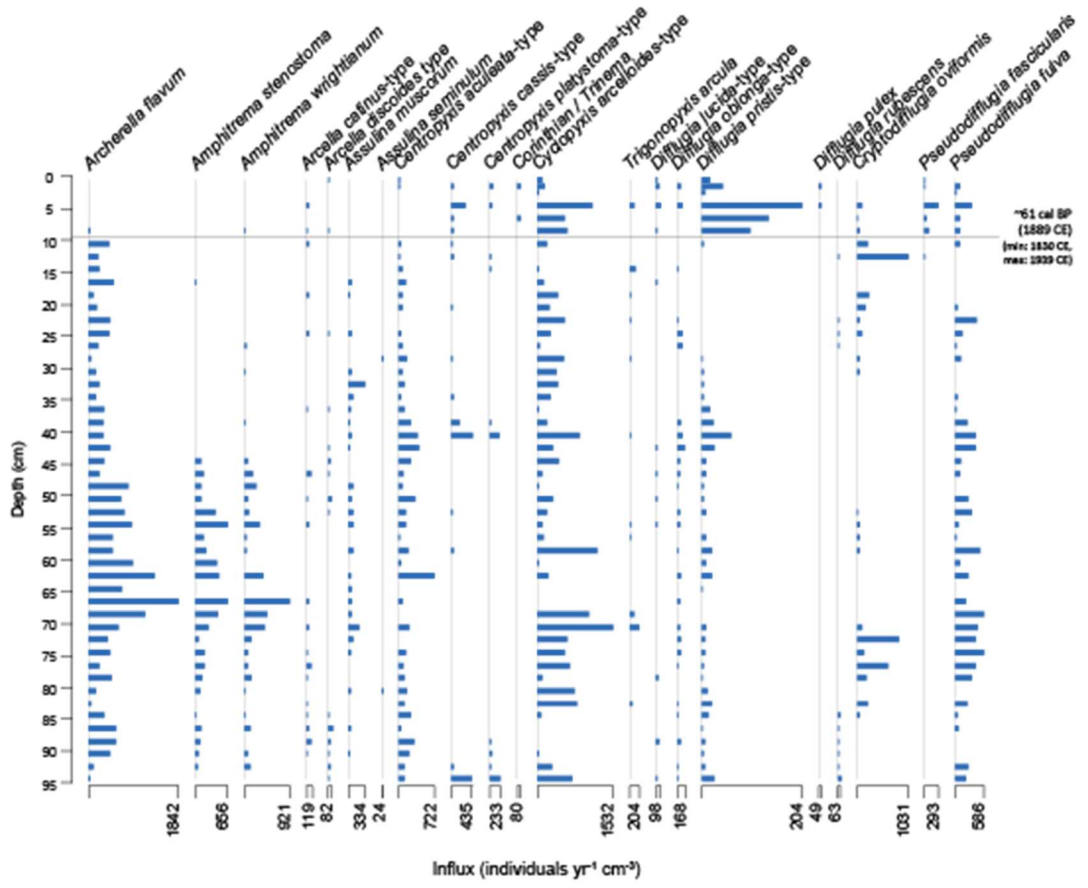
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706 *Fig. 5 Plant macrofossil diagram. Values of peat components are percentage estimates of total composition for each sample.*
707 *Sphagnum leaf counts as count data rather than proportional*

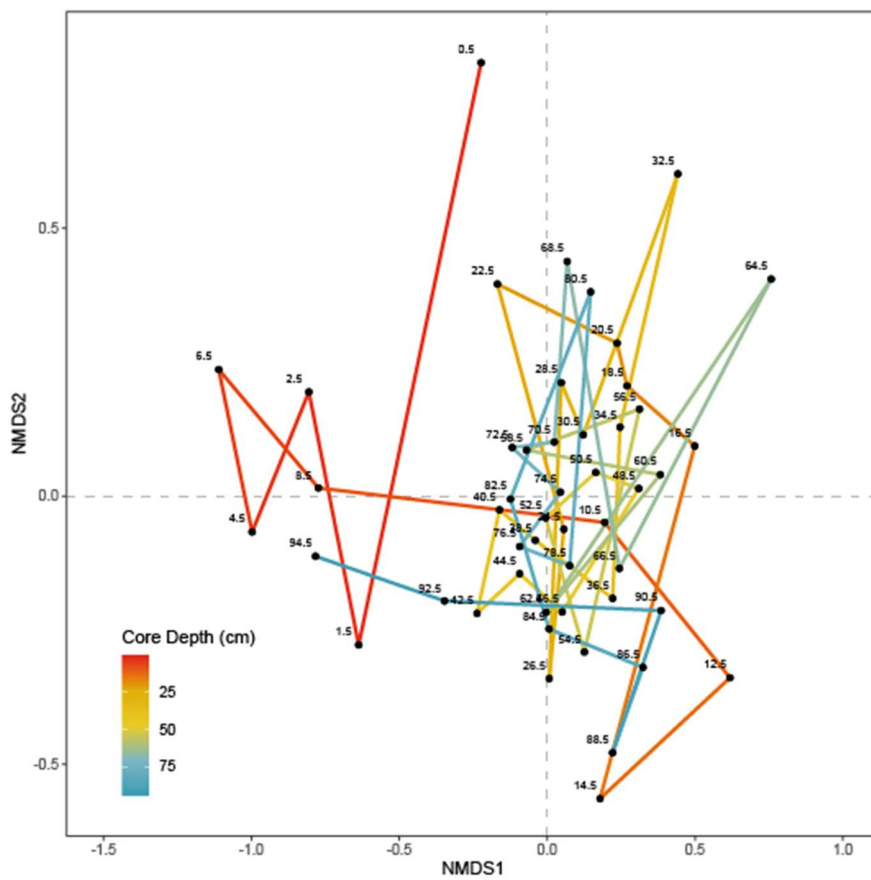
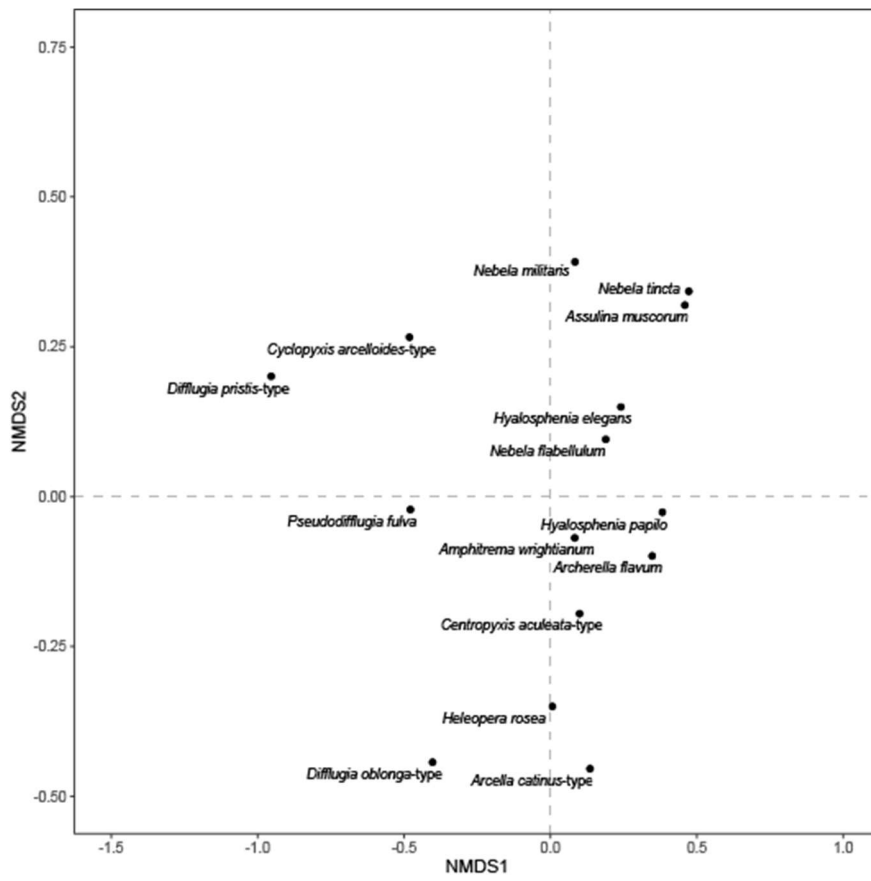
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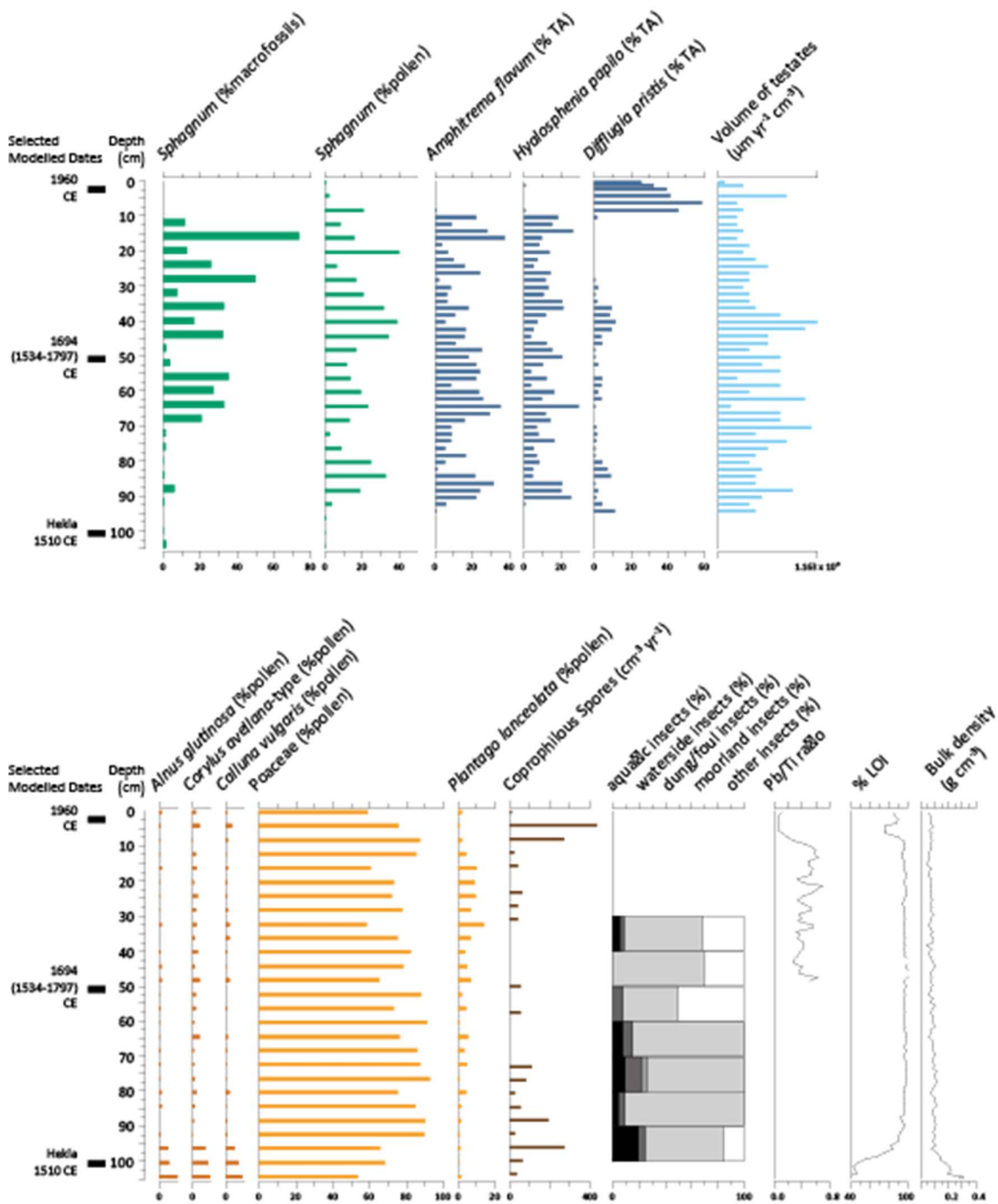
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Fig. 6 Testate amoebae diagram. Tests were not preserved below 94 cm at sufficient concentrations to be counted



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Fig. 7 NMDS of common (present in >50% samples) testate amoeba taxa. Upper diagram shows taxa, lower diagram shows samples



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715 Fig. 8 Summary of key proxy indicators for the top 1 m of the section

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Pollen Zone	Depth / Age	Description
RIB lpaz1	190.5 to 162.5 cm ~5753 to 1390 BCE (~7703 to 3340 cal BP)	The greatest relative abundances of arboreal taxa, including <i>Corylus avellana</i> -type, <i>Betula</i> , <i>Quercus</i> and <i>Salix</i> . High levels of Pteropsida suggest a fern understory in open woodland. Various herbaceous taxa are recorded, including Poaceae, Cyperaceae, <i>Filipendula</i> and <i>Galium</i> .
RIB lpaz2	162.5 to 114.5 cm ~1390 BCE to 1355 CE (~3340 to 595 cal BP)	Decline in <i>Corylus avellane</i> -type and <i>Betula</i> , which are briefly replaced by <i>Alnus glutinosa</i> , followed by an increase (doubling) in Poaceae relative abundances. Most other woodland taxa (and Pteropsida) also decrease. Herbaceous grassland taxa increase, including <i>Potentilla</i> -type and <i>Plantago lanceolata</i> at low, but continuous levels. <i>Sporormiella</i> -type and <i>Sordaria</i> -type spores increase in concentration at 152.5 cm (~1782 cal BP / 168 CE) (Fig. 3), suggesting increased herbivore density.
RIB lpaz3	114.5 to 94.5 cm ~1355 to 1540 CE (~595 to 410 cal BP)	Decrease in Poaceae and increases in <i>Calluna vulgaris</i> , <i>Alnus glutinosa</i> and <i>Corylus avellana</i> -type. Herbaceous grassland taxa (<i>Plantago lanceolata</i> , <i>Potentilla</i> -type) also decline slightly. Continued presence of coprophilous fungi: <i>Sporormiella</i> -type presence becomes less consistent, <i>Sordaria</i> -type becomes more consistent and there is a spike in <i>Podospora</i> -type.
RIB lpaz4	94.5 to 6.5 cm ~1540 to 1898 CE (~410 to 52 cal BP)	Poaceae dominates this zone, whilst <i>Corylus avellana</i> -type, <i>Alnus glutinosa</i> and <i>Calluna vulgaris</i> relative abundances decline to <1%. Improved grassland taxa, notably <i>Plantago lanceolata</i> , increase to their highest levels. <i>Sphagnum</i> abundance increases substantially, peaking at around 40.5 cm (~210 cal BP / 1740 CE) before undergoing a general decreasing trend. <i>Sordaria</i> -type spores are present at low concentrations, and <i>Sporormiella</i> -type and <i>Podospora</i> -type spores are largely absent <i>Sordaria</i> -type increase substantially at 8.5 cm.
RIB lpaz5	6.5 to 0 cm ~1898 to 2012 CE	Poaceae and improved grassland taxa (<i>Plantago lanceolata</i>) decrease and are replaced with taxa more associated with

(~52 to -62 cal BP)

‘poorer’ moorland (e.g. *Galium*, Rubiaceae). *Sphagnum* declines to very low abundances. *Sporormiella*-type, *Sordaria*-type and *Podospora*-type increase substantially, followed by near absence in the uppermost sample.

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Macro Zone	Depth / Age	Description
RIB mz1	188 to 114 cm ~5363 BCE to 1362 CE (~7313 to 588 cal BP)	Dominated by monocotyledon remains (some leaves, but mostly root material). Charred material is abundant. Some unidentified organic material (UOM) is present up to about 150 cm.
RIB mz2	114 to 70 cm ~1362 to 1624 CE (~588 to 326 cal BP)	An abrupt decline in charcoal, and the first consistent presence of <i>Sphagnum</i> , though at low abundances, and the monocotyledon remains continue to dominate.
RIB mz3	70 to 10 cm ~1624 to 1881 CE (~326 to 69 cal BP)	Marked by a substantial increase in <i>Sphagnum</i> remains (~25% relative abundance). Leaf counts indicate two main <i>Sphagnum</i> types: <i>Sphagnum</i> section <i>Cuspidata</i> and <i>Sphagnum pulchrum</i> . Lower samples also include <i>Polytrichum commune</i> .
RIB mz4	10 to 0 cm ~1881 to 2012 CE (~69 to -62 cal BP)	Assemblages dominated by monocotyledon remains. <i>Sphagnum</i> almost absent. Slight increase in UOM.

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Zone	Depth / Age	Description
Lower	94.5 to 8.5 cm	Assemblage is largely dominated by <i>Archerella flavum</i> , <i>Hyalosphenia papilo</i> , <i>Nebela flabellehum</i> and <i>Nebela militaris</i> : species indicative of ‘hummocky’ (microtopographically complex) bog surface conditions (Charman et al. 2000), alongside a wide range of other taxa. General decrease in testate biovolume (<i>i.e.</i> a shift to smaller species) from around 40.5 cm (~210 cal BP / 1740 CE). This suggests decreasing metabolic rates (reduced capacity in the food web to process energy) in microbial communities (Koenig et al. 2018; Marcisz et al. 2020).
	~1540 to 1889 CE (~410 to 61 cal BP)	
Upper	8.5 to 0 cm ~1889 to 2012 CE (~61 to -62 cal BP)	Assemblage becomes dominated by <i>Diffflugia pristis</i> -type: small testates that generally indicate moderate surface wetness (but not standing water) (Woodland et al. 1998; Charman et al. 2000; Swindles et al. 2009), and loses species indicative of ‘hummocky’ (microtopographically complex) surface conditions (<i>e.g.</i> <i>Archerella flavum</i> (Charman et al. 2000)). This suggests a simplification of the bog surface. <i>Cyclopyxis arcelloides</i> -type, a species complex that may indicate a range of relative wetness conditions (Charman et al. 2000), continues as a dominant part of the assemblage. The trend towards decreasing biovolume is continued, asides from a brief peak at 4.5 cm (~43 cal BP / 1907 CE), indicating continued loss of larger species, which tend to be poorer colonisers and are less able to overcome perturbations (Marcisz et al. 2020).