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Abstract

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

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

Introduction

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

Exmoor is an upland region with a long history of pre- and post-1940s drainage (Riley and Wilson-North 2001). Landscape-scale drainage and management for agriculture on Exmoor began in the 1820s following the sale of the Royal Forest of Exmoor ($c.$ 60 km^2) to the Knight family in 1818 (Orwin and Sellick 1970; Riley and Wilson-North 2001; Hegarty and Wilson-North 2014), and further drainage took place during the mid-twentieth century. Restoration work aimed at reversing the effects of drainage on Exmoor (*e.g.* blocking nineteenth and twentieth century drainage ditches to raise local water tables: 're-wetting') has been on-going since 2010, with pre- and post-restoration monitoring to understand responses in hydrological and biological systems, and how these may relate to carbon flux (Grand-Clement et al. 2015; Gatis et al. 2016). The aim of the present research is to understand the ecological consequences of historic moorland 'improvement' by providing long-term context, and to assess the extent to which pre-drainage conditions can be used to evaluate the success of on-going restoration works.

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

Materials and Methods

Sampling Site

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

Chronology

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

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

The core was scanned for tephra horizons at 5 cm resolution, with precise depths established through shard counts from contiguous 1 cm thick samples where necessary. Tephra samples were prepared for chemical analysis following Dugmore, Larsen, & Newton (1995) and 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; Väliranta 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 yr^{-1} 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 (μm yr^{-1} cm-^{3}). Overall testate amoebae biovolume (μm^3 yr^{-1}) for each sample

189   was estimated by scaling the biovolume information by the influx of each taxon.

190

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

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

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

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.

Plant macrofossils

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

Testate amoebae

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

303 absent, and the assemblage becomes dominated by *Difflugia 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 *Difflugia pristis*-type, *Cyclopyxis arcelloides*-type and

313 *Pseudodifflugia 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

during this period suggests a change in local disturbance regimes. Fungal taxa like

Sporormiella and *Podospora* are specialist coprophiles (Baker et al. 2013; Perrotti and van

Asperen 2018), whereas *P. lanceolata* is an adaptable, ruderal generalist that may be

favoured by various disturbances, including moderate grazing (Mook et al. 1989; Reudler et

al. 2013). This suggests that local grazing pressure may have been reduced (*e.g.* fewer

grazing animals and/or modified annual grazing patterns), possibly associated with increasing

surface wetness. Around the eighteenth century (from 40.5 cm, ~210 cal BP / 1740 CE),

Sphagnum spores and overall testate amoeba biovolume both began general long-term

declines, suggesting a gradual decrease in *Sphagnum*-rich peatbog habitats, though these

habitats appear to have persisted locally, as indicated by *Sphagnum* macrofossils.

Ecological impacts of nineteenth century moorland 'improvement'

The most rapid ecological change recorded appears to have occurred during the late

nineteenth century (from ~10.5 cm, ~70 cal BP / 1880 CE, 95% confidence range: 1822-1931

CE). *Sphagnum* moss almost disappeared locally (indicated by plant macrofossils) and

declined substantially in the wider landscape (indicated by spores), with vegetation

communities becoming dominated by grasses. Testate amoeba assemblages became

dominated by *Difflugia pristis*-type, indicators of moderate surface wetness (but not standing

water) (Woodland et al. 1998; Charman et al. 2000; Swindles et al. 2009), largely replacing

species indicative of 'hummocky' bog surface conditions, suggesting a simplification of local

microtopography. These changes in floral and microbial communities indicate a rapid change

in the landscape, consistent with nineteenth century drainage on Exmoor (Hegarty and

Wilson-North 2014). A notable increase in influx rates of all coprophilous fungal spore types

(*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

Conclusions

459

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

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

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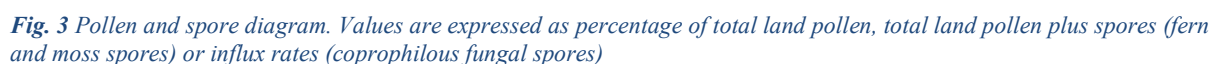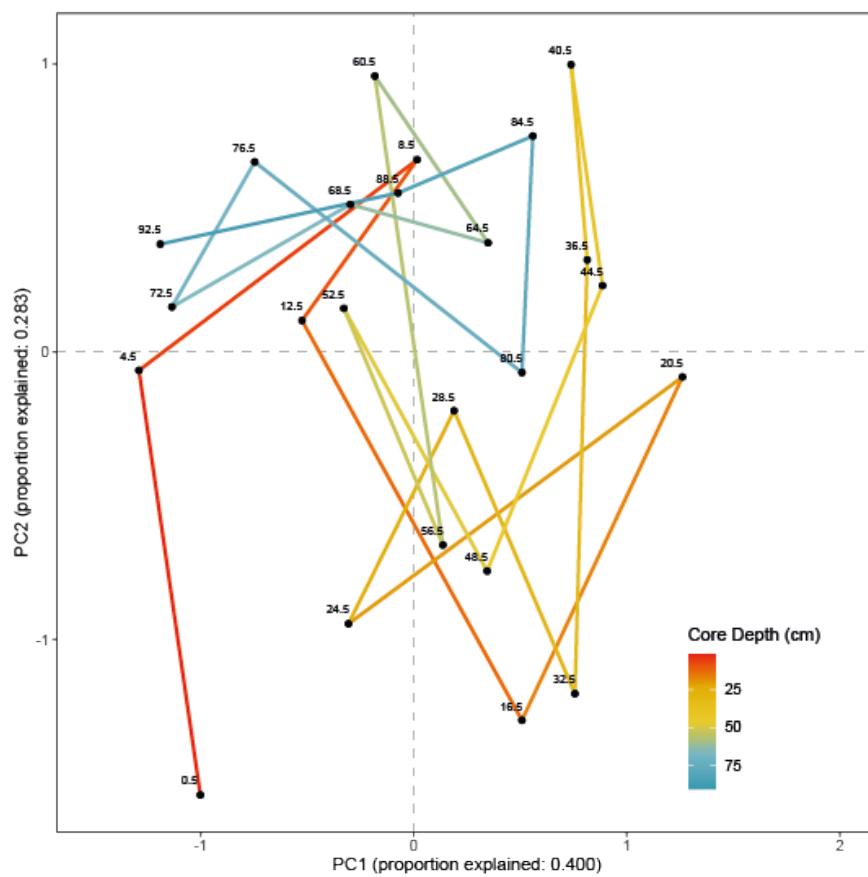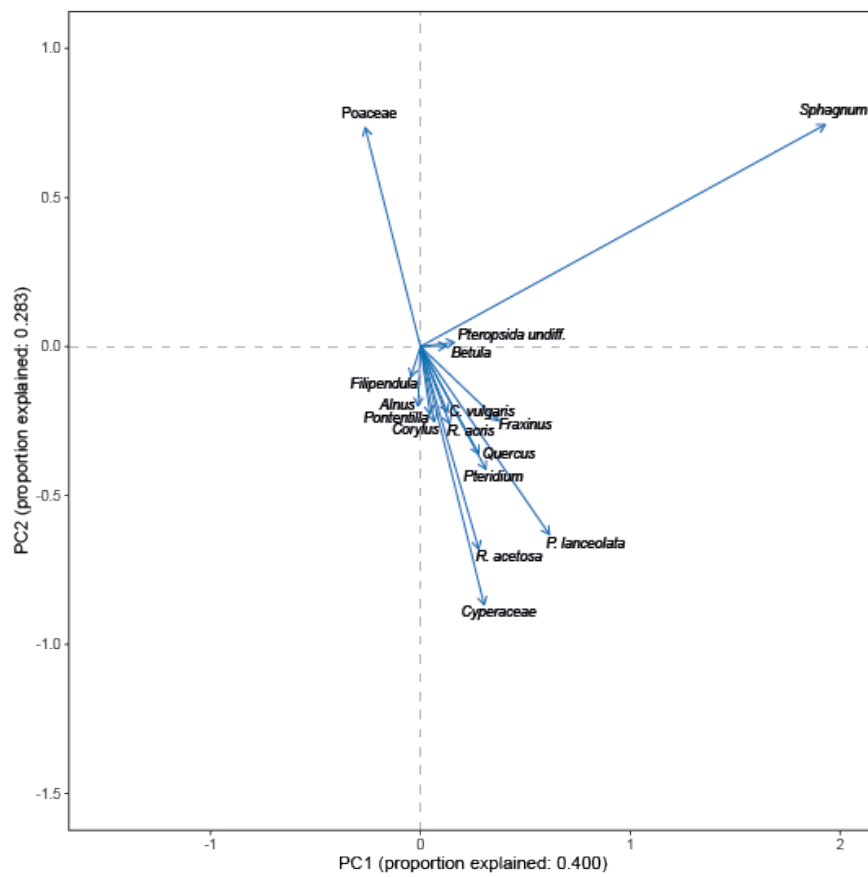685   https://doi.org/10.1191/095968398667004497

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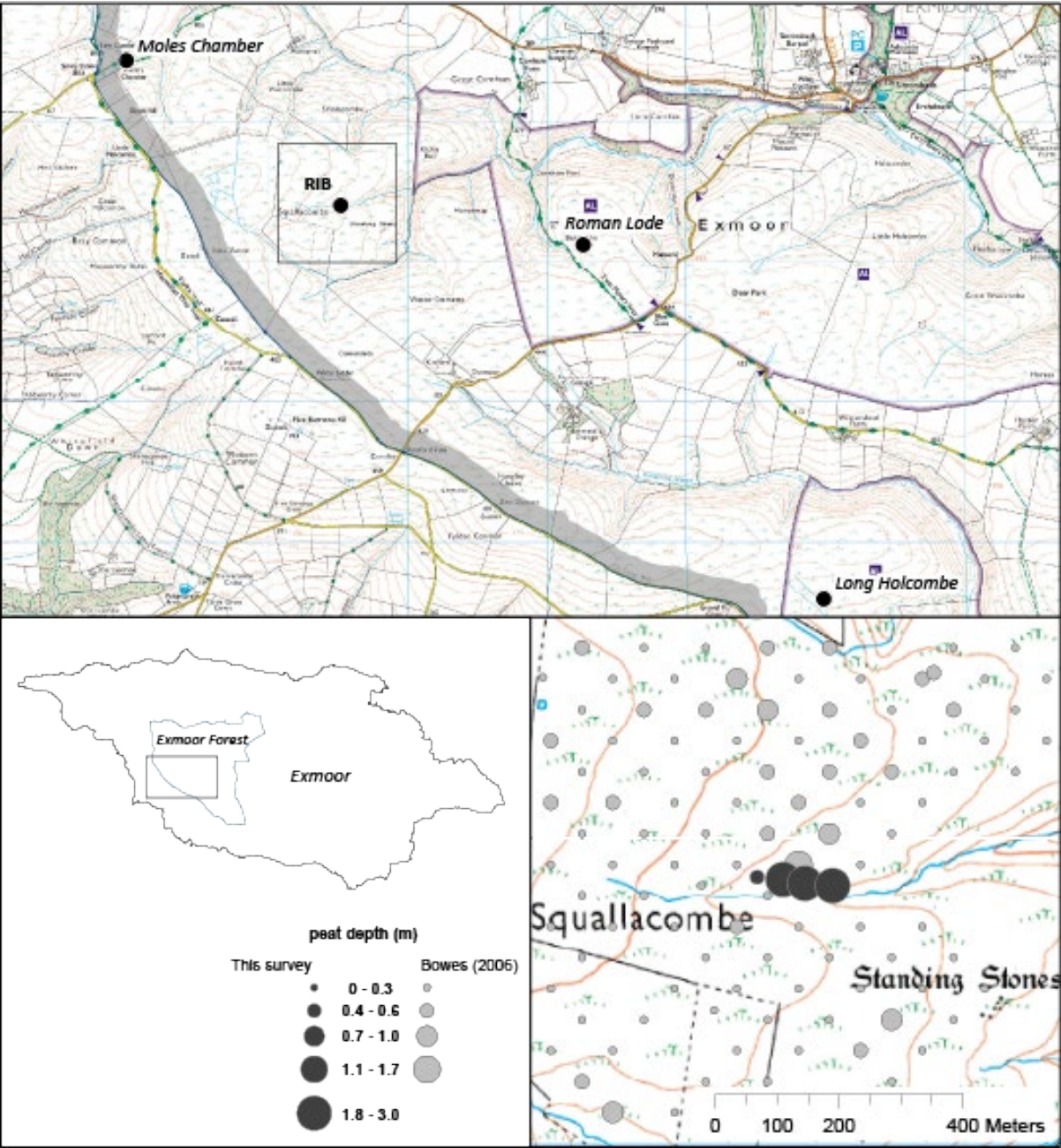
Fig. 1 *Location map showing Ricksy Ball and other notable sites nearby. Grey shading shows the boundary of the former Royal Forest. New and previously measured (Bowes 2006) peat depths.*

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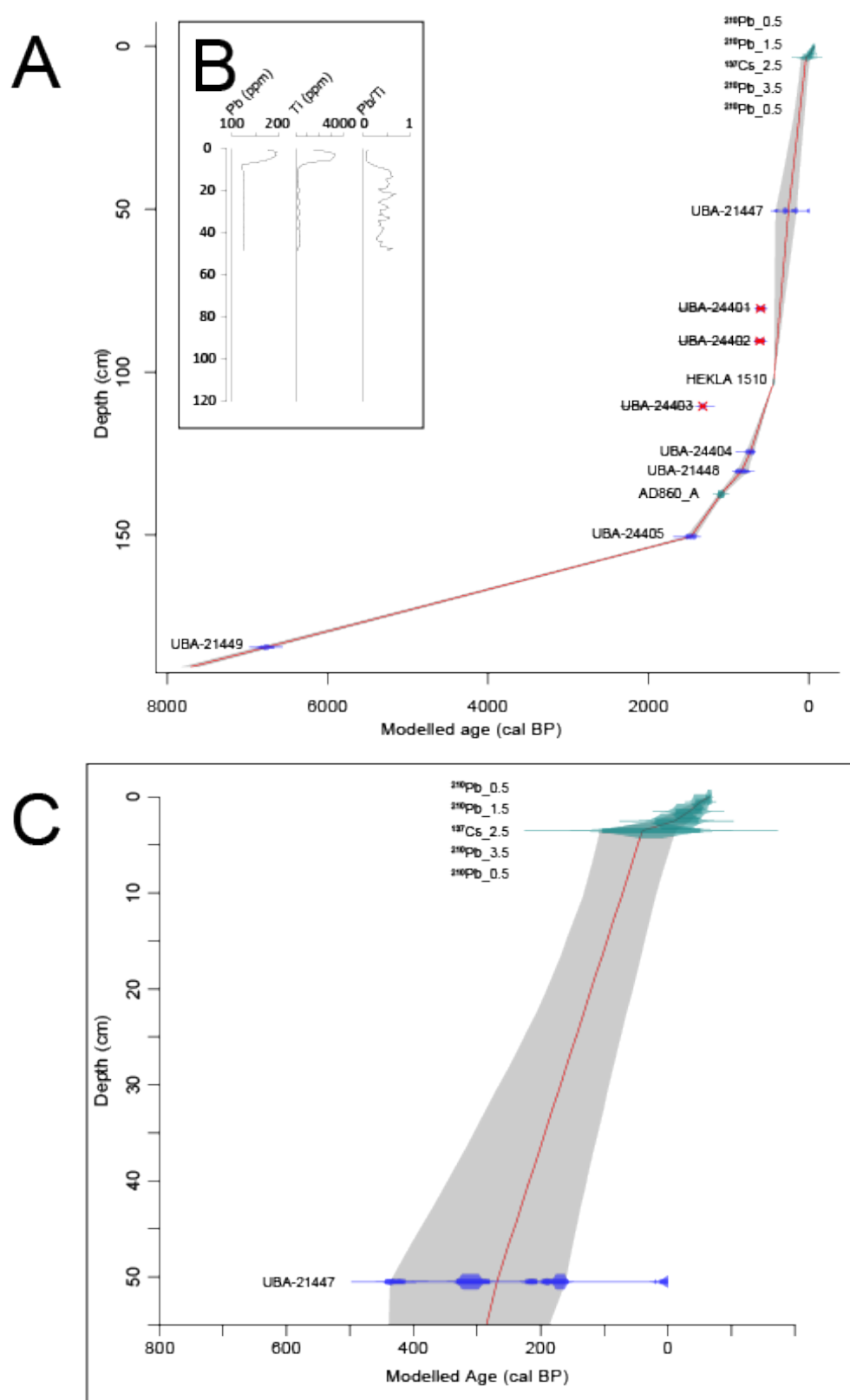
Fig. 2 *Chronological summary. A: Full age-depth model (with 95% confidence intervals); B: XRF results; C: Focussed view*
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of the upper 55cm of the age-depth model (with 95% confidence intervals). Dates with red crosses were not used in the
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model
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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*
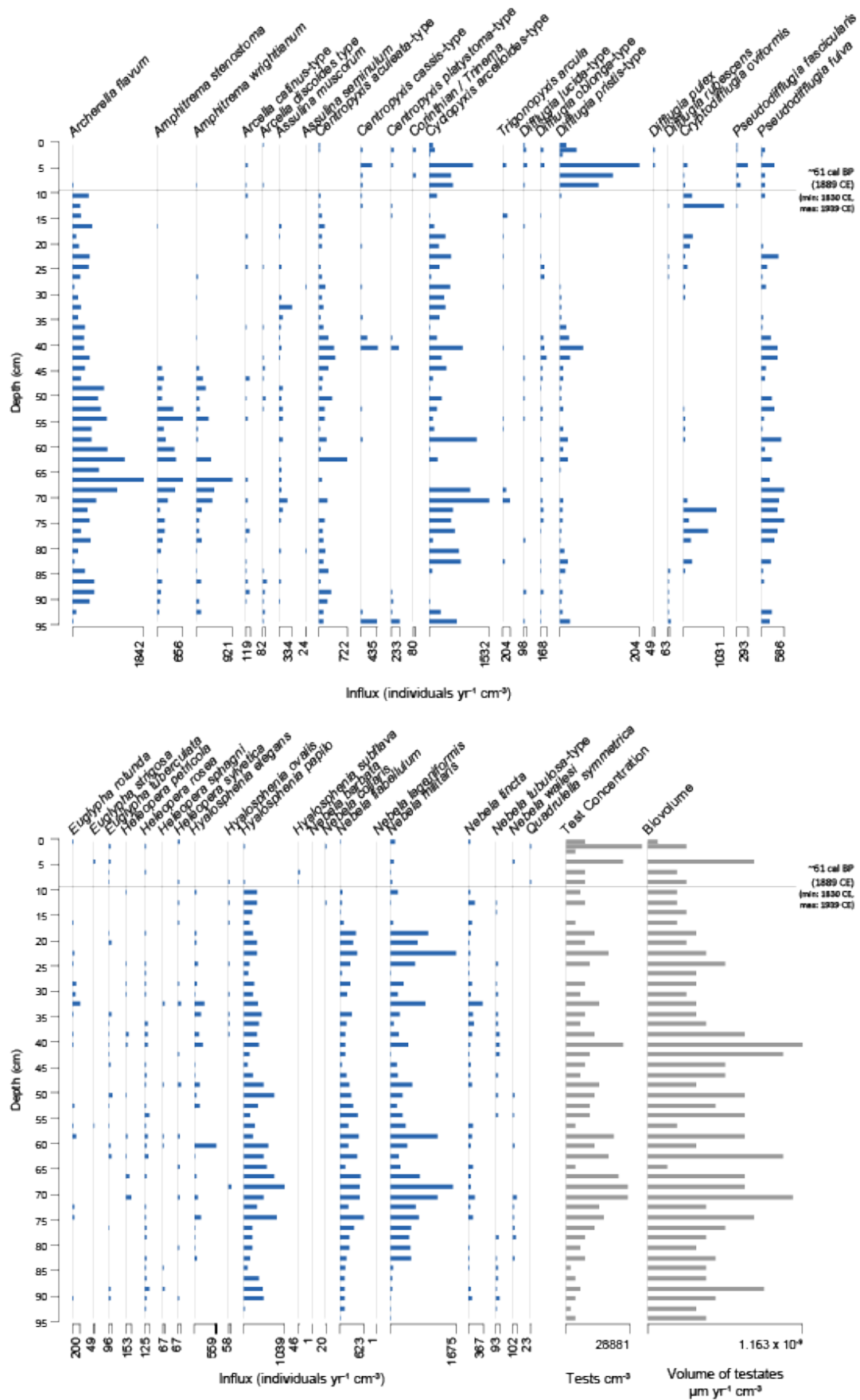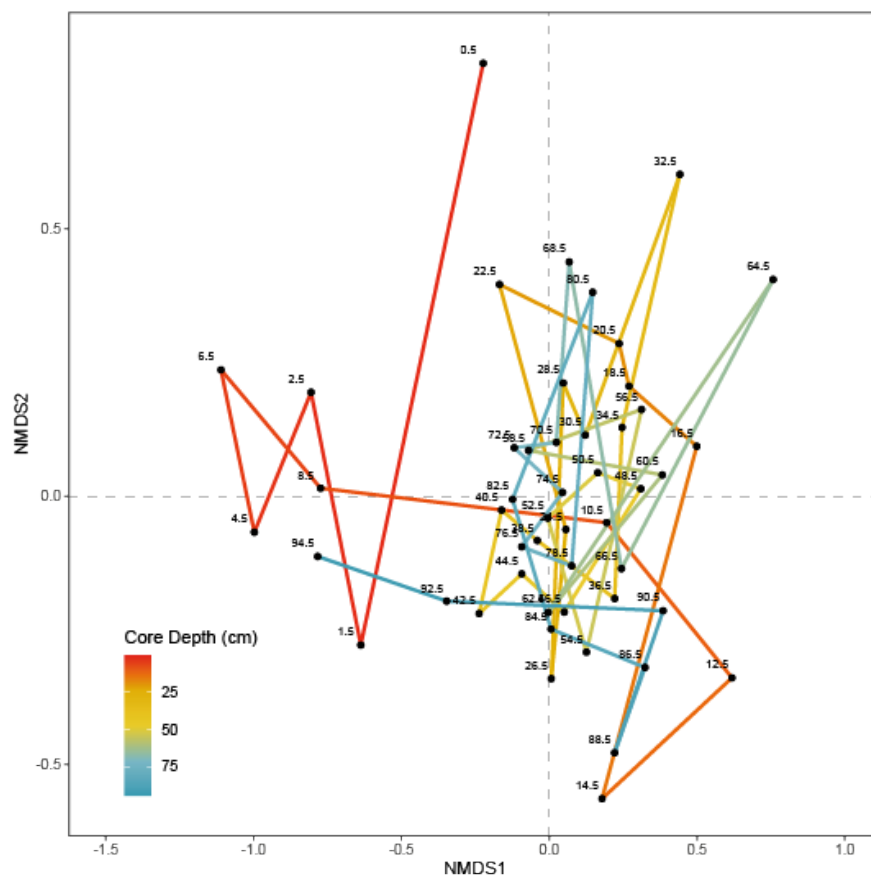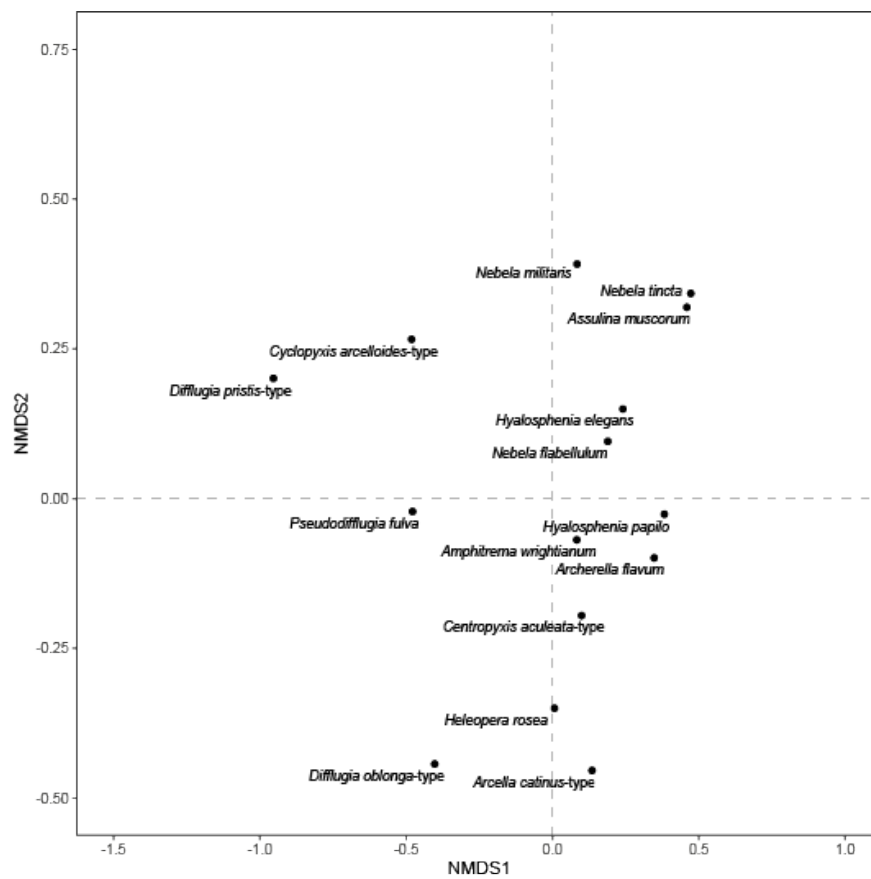
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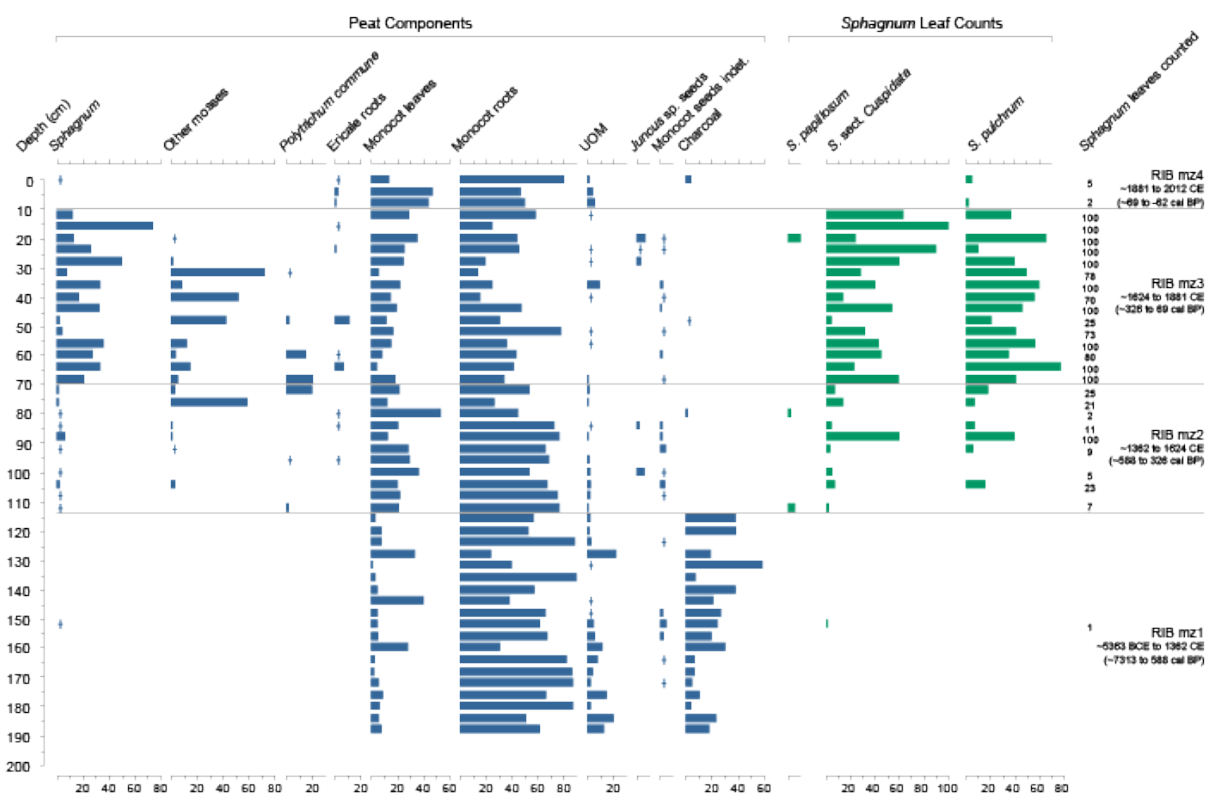
Fig. 5 *Plant macrofossil diagram. Values of peat components are percentage estimates of total composition for each sample.*
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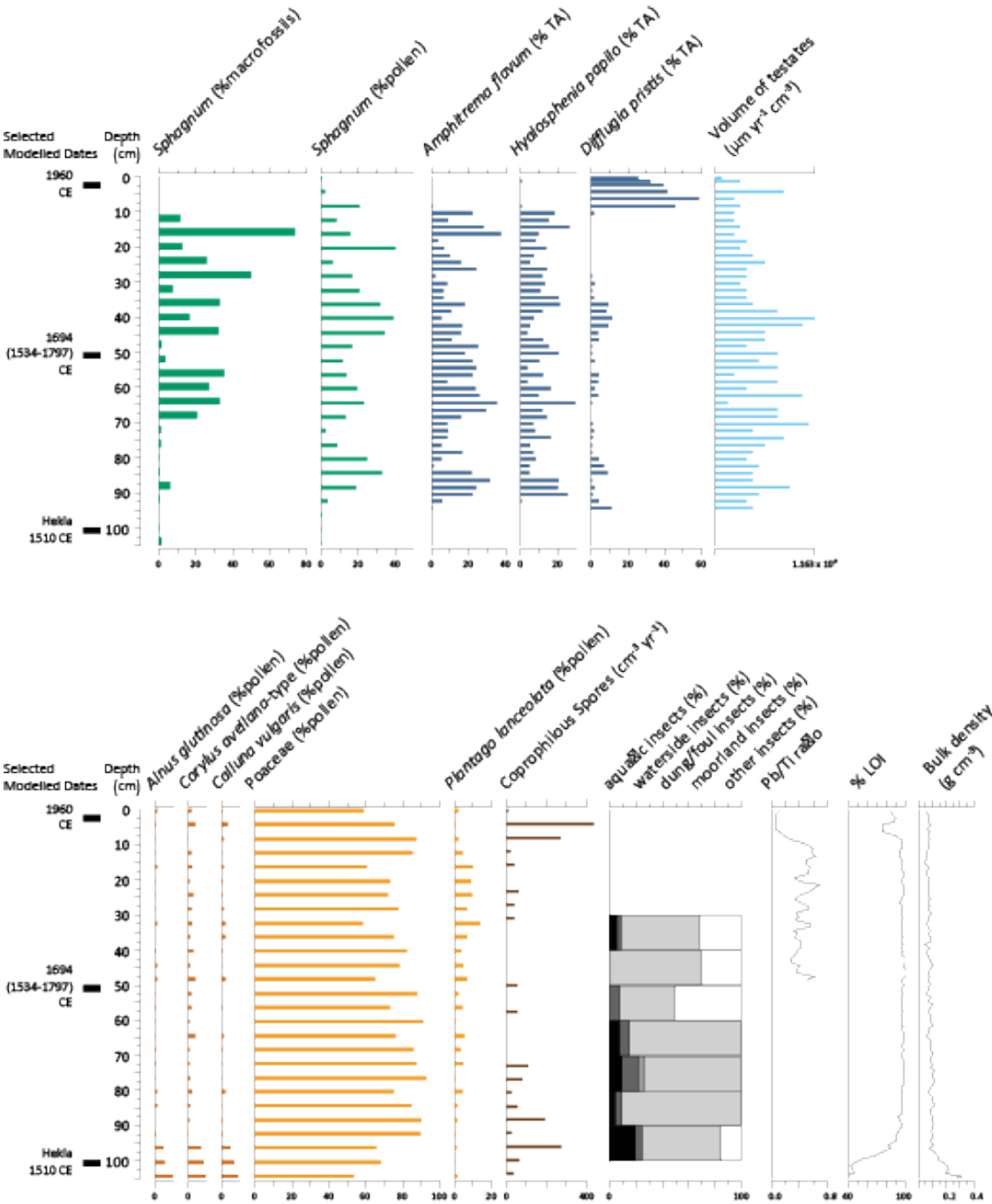707 *Sphagnum leaf counts as count data rather than proportional*

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710　*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*

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

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Table 1 Pollen assemblage zones

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 *Corlyus avellana*-type, *Betula*, *Quercus* and *Salix*. High levels of Pteropsida suggest a fern understory in open woodland. Various herbaceous taxa are recorded, including Poaceae, Cyperaceae, *Filipendula* and *Galium*.
RIB lpaz2	162.5 to 114.5 cm ~1390 BCE to 1355 CE (~3340 to 595 cal BP)	Decline in *Corylus avellane*-type and *Betula*, which are briefly replaced by *Alnus glutinosa*, followed by an increase (doubling) in Poaceae relative abundances. Most other woodland taxa (and Pteropsida) also decrease. Herbaceous grassland taxa increase, including *Potentilla*-type and *Plantago lanceolata* at low, but continuous levels. *Sporormiella*-type and *Sordaria*-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 *Calluna vulgaris*, *Alnus glutinosa* and *Corylus avellana*-type. Herbaceous grassland taxa (*Plantago lanceolata*, *Potentilla*-type) also decline slightly. Continued presence of coprophilous fungi: *Sporormiella*-type presence becomes less consistent, *Sordaria*-type becomes more consistent and there is a spike in *Podospora*-type.
RIB lpaz4	94.5 to 6.5 cm ~1540 to 1898 CE (~410 to 52 cal BP)	Poaceae dominates this zone, whilst *Corlyus avellana*-type, *Alnus glutinosa* and *Calluna vulgaris* relative abundances decline to <1%. Improved grassland taxa, notably *Plantago lanceolata*, increase to their highest levels. *Sphagnum* abundance increases substantially, peaking at around 40.5 cm (~210 cal BP / 1740 CE) before undergoing a general decreasing trend. *Sordaria*-type spores are present at low concentrations, and *Sporormiella*-type and *Podospora*-type spores are largely absent *Sordaria*-type increase substantially at 8.5 cm.
RIB lpaz5	6.5 to 0 cm ~1898 to 2012 CE	Poaceae and improved grassland taxa (*Plantago lanceolata*) 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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Table 2 Plant macrofossil assemblage zones

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 *Sphagnum*, 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 *Sphagnum* remains (~25% relative abundance). Leaf counts indicate two main *Sphagnum* types: *Sphagnum* section *Cuspidata* and *Sphagnum pulchrum*. Lower samples also include *Polytrichum commune*.
RIB mz4	10 to 0 cm ~1881 to 2012 CE (~69 to -62 cal BP)	Assemblages dominated by monocotyledon remains. *Sphagnum* almost absent. Slight increase in UOM.

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Table 3 Testate amoebae summary

Zone	Depth / Age	Description
Lower	94.5 to 8.5 cm ~1540 to 1889 CE (~410 to 61 cal BP)	Assemblage is largely dominated by *Archerella flavum*, *Hyalosphenia papilo*, *Nebela flabellelum* and *Nebela militaris*: 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.e.* 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).
Upper	8.5 to 0 cm ~1889 to 2012 CE (~61 to -62 cal BP)	Assemblage becomes dominated by *Difflugia pristis*-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 (*e.g. Archerella flavum* (Charman et al. 2000)). This suggests a simplification of the bog surface. *Cyclopyxis arcelloides*-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).

761