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Ecological consequences of historic moorland 'improvement'

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1	Ecological consequences of historic moorland 'improvement'
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- 32 Blake, Katie Head, Alison Macleod, Ian Matthews and David N. Smith produced the proxy
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34

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41 Abstract

42 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 43 Exmoor, (South West England, UK) restoration activities are often aimed at reversing the 44 effects of nineteenth century agricultural 'improvement' schemes, the effects of which are not 45 vet fully understood. To develop this understanding, long-term ecological context is essential. 46 47 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 48 ~7700 years at a site in Exmoor National Park ('Ricksy Ball'). Multivariate analyses were 49 50 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 51 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) and microbial (testate amoebae) communities. In particular, a combination of drainage and 54 55 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 56 Sphagnum and associated biota. This occurred in the context of more gradual, centennial-57 58 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 59 millennia, and this may have been most pronounced during the nineteenth century. There is 60 no single, readily identifiable, 'stable' pre-drainage baseline. 61

62

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

65 Introduction

66 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 67 protection and restoration of upland peatlands, owing to their range of potential ecosystem 68 services, including regulatory services such as climate change mitigation (through 69 greenhouse gas sequestration), provisioning services (e.g. water supply) and cultural services 70 71 (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 72 and Malmer 2004; Ritson et al. 2016). Many peatlands in the UK and Ireland are considered 73 74 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 75 moorland 'agricultural improvement' schemes, particularly during the nineteenth century 76 77 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 78 79 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-80 term data suggest this may have led to the expansion and dominance of purple moor-grass 81 82 (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 83 of the UK where peatlands lie in climatically-marginal situations (Gallego-Sala et al. 2010). 84 85 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 86 87 perspective, is important. This includes understanding the extent of historical Sphagnum losses, associated changes in broader ecological communities (vegetation, microbes, etc), and 88 the relative importance of other disturbance processes. 89

90 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 91 began in the 1820s following the sale of the Royal Forest of Exmoor (c. 60 km²) to the 92 Knight family in 1818 (Orwin and Sellick 1970; Riley and Wilson-North 2001; Hegarty and 93 Wilson-North 2014), and further drainage took place during the mid-twentieth century. 94 Restoration work aimed at reversing the effects of drainage on Exmoor (e.g. blocking 95 96 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 97 98 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 99 ecological consequences of historic moorland 'improvement' by providing long-term context, 100 101 and to assess the extent to which pre-drainage conditions can be used to evaluate the success 102 of on-going restoration works.

This paper presents a detailed multi-proxy palaeoecological study of an area of moorland that 103 104 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 105 long-term dynamics of peatland systems (Davies and Bunting 2010; Gearey and Fyfe 2016; 106 107 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 108 provides the context of historical Sphagnum losses, how drainage may have influenced wider 109 ecologies, including the potential formation of novel communities, and the additional 110 importance of grazing and burning. We find that the moorland's ecology has changed with 111 land use over millennia, and that nineteenth century ecological changes (probably related to 112 both drainage and high-intensity grazing) were particularly notable. 113

114

115 Materials and Methods

116 Sampling Site

Sampling was undertaken in 2012 in the Aclands catchment on Exmoor (0.179 km²), an area 117 subject to on-going restoration work (since 2014) and monitoring (Grand-Clement et al. 118 119 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 120 quality, flood prevention) (Grand-Clement et al. 2015). Peat depths range from 0.33 to 2 m 121 122 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 123 area of deeper peat ('Ricksy Ball'), approximately 190 m long and up to 80 m wide. A 1.9 m 124 peat sequence was extracted from Ricksy Ball (-3.808° longitude, 51.131° latitude WGS84; 125 elevation: 421 m OD) using monolith tins (open section, upper 1.1 m) and a closed-chamber 126 corer (lower 0.8 m). The sampling site is located within the extensively drained area. 127

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

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.

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

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

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

```
162 clam(coredir="clam_runs", core="RicksyBall", cc=1, outliers=c(7,8,10),
163 depthseq=print(depths), type=1, its=10000)
164
```

Palaeoecology

Plant macrofossils

Material for plant macrofossil analysis was extracted following Mauquoy, Hughes, & van
Geel (2010) methods. Sub-samples of peat (2 cm contiguous intervals) were disaggregated
and wet sieved to 125 µm and examined using low-power (x10-50) microscopy. Where
epidermal material or *Sphagnum* leaves were present, an additional representative sample (50 *Sphagnum* leaves) was identified to sub-genus level using high-power microscopy (x100400).

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 μ m), 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)

and Gilbert, Amblard, Bourdier, & Francez (1998). Total biovolume is the sum for all taxa, which was then scaled by influx rates to give biovolume values per year per cubic centimetre of sediment (μ m yr⁻¹ cm⁻³). Overall testate amoebae biovolume (μ m³ yr⁻¹) for each sample was estimated by scaling the biovolume information by the influx of each taxon.

190

191 *Pollen and coprophilous fungal spores*

Pollen and coprophilous fungal spore sample preparation followed Moore, Webb, & 192 Collinson (1991). One cm³ sub-samples were disaggregated in potassium hydroxide, silicates 193 194 were removed using hydrofluoric acid, cellulose was digested using an acetolysis reaction (acetic anhydride and sulphuric acid), samples were dehydrated with alcohols and mounted in 195 silicon oil for identification using high-power (x400-600) microscopy. Three hundred land 196 197 pollen grains were identified from each sub-sample, a sufficient number for characterising assemblages (Djamali and Cilleros 2020). Coprophilous fungal spores (per 100 Lycopodium 198 spores) were counted on pollen slides to 168.5 cm core depth. Sporormiella-type spores may 199 occur as lone cells or chains of cells, and counts were based on the number of chains plus the 200 number of lone cells. 201

202

203 Insects

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

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

214

215 Multivariate analyses

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

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

dissimilarity between samples, and is suitable for non-Gaussian data (Oksanen et al. 2019).

Analyses were performed using the R package 'vegan' (Oksanen et al. 2019).

235

236 **Results**

237 Chronology

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

244

245 Palaeoecology

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

248

249 Pollen and coprophilous fungal spores

The results of pollen and fungal spore analysis from 49 samples describe vegetation changes in the local and wider area around Ricksy Ball, and grazing activity in the local area (Fig. 3). As a general rule-of-thumb, herbaceous (and wetland) pollen types are likely to derived more local sources (<100 m) than pollen from woody, dryland taxa (Binney et al. 2005; Blaus et al. 2020). The pollen has been visually divided into five local pollen assemblage zones (lpaz), to

aid the description of key periods of continuity and change (see Table 1 for detailed 255 descriptions). Mixed open woodland conditions are represented in the lowermost zone (zone 256 257 RIB lpaz1, 190.5-162.5 cm, from ~7703 to 3340 cal BP). At 162.5 cm (~3340 cal BP) woodland taxa decline and are replaced by Poaceae and 'improved' grassland taxa. 258 Coprophilous fungal spores increase in concentration (Fig. 3), suggesting increased herbivore 259 density. The start of the third pollen zone at 114.5 cm (~595 cal BP / 1355 CE) is marked by 260 261 declining Poaceae and increases in woody heathland shrubs and some trees. Coprophilous fungal spores are also present in this zone (Fig. 3). From 94.5 cm (~410 cal BP / 1540 CE) 262 263 the pollen assemblages are dominated by Poaceae and associated grassland taxa, with Calluna vulgaris declining to trace levels. In this zone, Sphagnum is present in substantial 264 quantities for the first time. Coprophilous fungal spores are present at low levels, but with a 265 substantial increase in Sordaria-type at 8.5 cm (Fig. 3). In the uppermost samples (from 6.5 cm: 266 52 cal BP / 1898 CE) Poaceae and indicators of improved grassland decrease, replaced with 267 taxa more associated with 'poorer' moorland and levels of Sphagnum decline to very low 268 amounts. Coprophilous fungal spore concentrations increase during this period (Fig. 3). 269 Principal components analysis (PCA) of common pollen taxa in the upper parts of the 270 271 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 major assemblage change in this portion of the sequence is in the upper 8.5 cm (~61 cal BP / 273 1889 CE; min: 1830 CE, max: 1939 CE), where both Poaceae and Sphagnum decline relative 274 275 to a number of herbaceous taxa (e.g. Plantago lanceolata-type, Rumex acetosa-type, Cyperaceae). Prior to this, there are continual fluctuations which appear to represent 276 277 relatively minor changes in Poaceae and *Sphagnum*, though there is some suggestion that older samples (92.5 cm to 60.5 cm, ~403 to 291 cal BP / 1547 to 1659 CE) may have a 278 tendency towards slightly higher Poaceae and lower Sphagnum relative abundances. 279

281 Plant macrofossils

Plant macrofossil analysis (48 samples) describes the character of local (*i.e.* on-site) 282 vegetation at Ricksy Ball (Fig. 5). There are four macrofossil zones (mz: see Table 2), which 283 284 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 285 BP). From 114 cm (~588 cal BP / 1362 CE), Sphagnum is recorded consistently, though at 286 287 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 288 10 cm (~69 cal BP / 1881 CE) the samples are all dominated by monocotyledon remains, 289 290 with no Sphagnum present.

291

292 *Testate amoebae*

293 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 49 294 295 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 296 the assemblage is largely dominated by species indicative of 'hummocky' 297 298 (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), 299 suggesting decreasing community metabolic rates (reduced capacity in the food web to 300 301 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 302

absent, and the assemblage becomes dominated by Difflugia pristis-type. These are small 303 testates that are indicators of moderate bog surface wetness, but generally not standing water 304 (Woodland et al. 1998; Charman et al. 2000; Swindles et al. 2009). The trend towards 305 decreasing biovolume is continued, asides from a brief peak at 4.5 cm (~43 cal BP / 1907 306 CE), indicating continued loss of larger species, which tend to be poorer colonisers and are 307 less able to overcome perturbations (Marcisz et al. 2020). 308 309 Non-metric multidimensional scaling (NMDS) analysis (based on testate amoeba influx values) further illustrates the significance of the shift in testate amoeba assemblages from 310 311 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 Pseudodifflugia fulva, possibly representing a novel stable state. This analysis indicates that 313 earlier in the sequence (below 8.5 cm, before ~61 cal BP / 1889 CE), abundances of 314 individual species fluctuated, but there were no similarly notable long-term changes in 315 assemblage characteristics, suggesting a previous state of dynamic equilibrium. 316

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

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,

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)).

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

330

331 Discussion

332 Pre-nineteenth century ecological history

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

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

- 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 Sporormiella and Podospora are specialist coprophiles (Baker et al. 2013; Perrotti and van 351 Asperen 2018), whereas *P. lanceolata* is an adaptable, ruderal generalist that may be 352 favoured by various disturbances, including moderate grazing (Mook et al. 1989; Reudler et 353 al. 2013). This suggests that local grazing pressure may have been reduced (e.g. fewer 354 grazing animals and/or modified annual grazing patterns), possibly associated with increasing 355 356 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 357 358 declines, suggesting a gradual decrease in Sphagnum-rich peatbog habitats, though these habitats appear to have persisted locally, as indicated by Sphagnum macrofossils. 359

360

361 *Ecological impacts of nineteenth century moorland 'improvement'*

The most rapid ecological change recorded appears to have occurred during the late 362 nineteenth century (from ~10.5 cm, ~70 cal BP / 1880 CE, 95% confidence range: 1822-1931 363 CE). Sphagnum moss almost disappeared locally (indicated by plant macrofossils) and 364 declined substantially in the wider landscape (indicated by spores), with vegetation 365 366 communities becoming dominated by grasses. Testate amoeba assemblages became 367 dominated by *Difflugia 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 (Sordaria-type, Sporormiella-type and Podospora-type) and a decline in Plantago lanceolata 373

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.

393 Implications for modern landscape management

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

from the past, as well as revealing the ecological consequences of these catchmentmanagement practices.

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

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

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

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

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

458

459 Conclusions

Palaeoecological analyses reveal varied management practices (burning, grazing, drainage) 460 and associated ecological responses over the last eight millennia at Ricksy Ball (Exmoor), 461 and major changes in vegetation and microbial communities have been broadly coincident 462 over the last five hundred years. During the nineteenth century, a combination of drainage 463 and increased grazing intensity appears to have substantially altered the local ecology, 464 resulting in the loss of Sphagnum and associated macro- and microbiota. This occurred in the 465 466 context of more gradual, centennial-scale declines in Sphagnum and microbial biovolumes. There is no single, readily identifiable, 'stable' pre-drainage baseline. We provide a range of 467 reference conditions and reveal the consequences of past management practices, showing that 468

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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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.



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)



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





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







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

 712
 Fig. 7 N

 713
 samples



721 Table 1 Pollen assemblage zones

Pollen Depth / Age Description Zone		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>Corlyus 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>Corlyus avellana</i> -type, <i>Alnus glutinosa</i> and <i>Calluna vulgaris</i> relative abundances decline to <1%. Improved grassland taxa, notably <i>Plantago</i> <i>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	6.5 to 0 cm	Poaceae and improved grassland taxa (<i>Plantago lanceolata</i>)
lpaz5	~1898 to 2012 CE	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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746 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 <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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760 Table 3 Testate amoebae summary

Zone	Depth / Age	Description
		Assemblage is largely dominated by Archerella flavum,
		Hyalosphenia papilo, Nebela flabellelum and Nebela
		militaris: species indicative of 'hummocky'
	94.5 to 8.5 cm ∼1540 to 1889 CE	(microtopographically complex) bog surface conditions
		(Charman et al. 2000), alongside a wide range of other
Lower		taxa. General decrease in testate biovolume (i.e. a shift
	(~410 to 61 cal BP)	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).
		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'
	8.5 to 0 cm ~1889 to 2012 CE (~61 to -62 cal BP)	(microtopographically complex) surface conditions
		(e.g. Archerella flavum (Charman et al. 2000)). This
Unnon		suggests a simplification of the bog surface. Cyclopyxis
Opper		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).