1 **Quantified moorland vegetation and assessment of the role of burning over the past five millennia**

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10

11 **Abstract**

12 **Aims:** To apply the Landscape Reconstruction Algorithm (LRA) to pollen count data from multiple

13 sites to estimate local vegetation abundance and compare with charcoal-derived records of burning.

14 **Location:** Exmoor, southwest England, UK

15 **Methods:** Pollen count data from 16 sites were transformed to estimates of distance-weighted

16 vegetation abundance using the LRA (REVEALS and LOVE models), correcting for bias in pollen

17 production and dispersal. Charcoal concentration data from six sites were normalised using box-cox

18 transformation to produce z-scores. Moving-window correlation was undertaken to compare pollen

19 percentage values for key taxa (*Calluna*, Poaceae) and localised burning. Estimates of distance-

20 vegetation abundance (LRA output) and time-averaged charcoal z-scores were compared to assess

21 the role of burning as a driver for upland vegetation cover.

22 **Results:** Comparison of pollen percentage and normalised charcoal z-scores show little correlation

23 between vegetation cover and burning. Estimates of distance-weighted vegetation abundance and

24 normalised charcoal data show relationships between vegetation change and burning at four of the

25 six sites. The relationships are site-specific: three sites suggest burning promoted grass-dominated

26 vegetation, at one site burning promoted heather-dominated vegetation, and in two sites there is no

27 apparent relationship.

28 **Conclusions:** The patterning of vegetation within uplands is a crucial part of ecosystem service

29 delivery, and contemporary and future management benefits from understanding of 'long-term'

30 development i.e. patterns over millennia. The correction of biases within pollen production and

31 dispersal to produce local vegetation estimates has demonstrated spatial heterogeneity in

32 vegetation cover on Exmoor that is not otherwise evident in the pollen percentage data (which

33 retains a strong influence of the regional vegetation cover). The relationship between LRA-derived

34 vegetation cover and burning is not apparent in comparisons between pollen percentage data and

35 charcoal records. This implies that studies that use pollen proportional data alone can misrepresent

36 the relationship between vegetation cover and fire. This study demonstrates that fire has been an

37 important part of the development of this cultural landscape.

38

39 **Keywords**

40 Pollen; charcoal; Exmoor; Landscape Reconstruction Algorithm; REVEALS; LOVE; Holocene; *Calluna*

41

42 **Nomenclature**

43 Stace (2010) for plants; Bennett (2007) for pollen taxa

44

45 **Abbreviations**

46 *PPE*: pollen productivity estimate; *LRA*: Landscape Reconstruction Algorithm; *REVEALS*: Regional

47 vegetation estimates from large sites; *LOVE*: Local vegetation estimates; *subscript PP*: pollen

48 percentage; *subscript DWPA*: distance-weighted plant abundance; *cal. yr BP: c*alibrated years before

49 present (present = 1950)

50

51 **Running head**

52 Long-term upland moorland vegetation and burning

53

54

Introduction

55

56 Moorlands and uplands are highly valued landscapes as they deliver a wide range of ecosystem

57 services including: water supply to lowlands; locations for agricultural production (in particular

58 seasonal grazing); internationally-important sinks of greenhouse gases including carbon and

59 methane; and are locations favoured for recreational activities (Reed et al. 2009). They are also

60 areas that preserve and conserve nationally-important cultural heritage, including the traces of past

61 society (Riley and Wilson-North 2001). A significant component of this ecosystem service delivery is

62 the vegetation patterning of uplands, as many of the services are mediated through vegetation.

63 Ecological research has focussed on understanding what controls upland vegetation, and points

64 towards the importance of grazing, burning and climatic change (e.g. Yeo & Blackstock 2002). In the

65 case of burning in particular, debates have become polarised and there is now a narrative of burning

66 being predominantly damaging to upland moorlands (Davies et al. 2016). Datasets that look at

67 differences through time, as well as space, can help to develop an appropriate evidence basis. Re-

68 survey at known locations after 35-years on Scottish moorlands has been considered as a 'long-term'

69 dataset (Britton et al. 2016) and these data offer excellent ecological observations. Although the

70 temporal resolution of palaeo-ecological approaches cannot compare to ecological monitoring or

71 measurement, they make it possible to observe change and infer processes that control this change

72 over decadal to millennial timescales (Davies & Bunting 2010) and have the potential to identify

73 vegetation responses over lag times longer than those afforded by ecological monitoring (e.g. Tinner

74 et al. 1999).

75

76 A challenge to the application of palaeoecological datasets, and in particular pollen-based

77 reconstructions, is bridging the gap between highly-detailed records of change over time from a

78 small number of locations within a region and modern ecological survey data (e.g. many quadrats, or

79 remote-sensed data). There are also significant differences in the ways that vegetation is recorded,

80 and making pollen proportions from within a sedimentary basin commensurate with modern

81 vegetation data (from field survey or remote-sensed datasets) poses major translational challenges.

82 Various approaches to transformation of pollen into measures of land cover exist, although most are

83 at best semi-quantitative and do not always produce strong matches between land cover and

84 modern vegetation (Woodbridge et al. 2014). The relationship between pollen proportions and

85 vegetation cover is non-linear (Sugita et al. 1999), confounded by differential pollen production and

86 dispersal between taxa, and the nature of the regional (background) vegetation. Developments in

87 understanding the pollen-vegetation relationship have resulted in improved approaches to the

88 quantification of vegetation cover within the source area of pollen sites and resulted in the LRA

89   (Sugita 2007a, b). Much effort has gone into the parameterisation of this new approach (Broström

90   et al. 2008; Mazier et al. 2012), and it is now possible to estimate the relative abundance of key taxa

91   around pollen sites separate from the 'background' vegetation (e.g. Cui et al. 2013; Trondman et al.

92   2016). Where networks of pollen sites exist, it is possible to generate spatially-explicit, quantified

93   past vegetation abundances using pollen count data.

94

95   This paper applies the LRA to pollen data from Exmoor, southwest England, to address a long-

96   standing issue around a key driver of moorland vegetation, namely the importance of burning on

97   vegetation character over the past 5000 years. Understanding local-scale vegetation patterning is

98   important as 'standard' upland pollen sequences can include a significant background element

99   making is difficult to differentiate the local from the background (Bunting et al. 2008). Previous

100   work has indicated that Exmoor is a landscape with a long history of human land use spanning at

101   least the last 5000 years. The earliest indicators of human occupation are remains of a hunter-

102   gatherer camp site at Hawkcombe Head dating to around 7200 cal yrs BP; monuments dating to the

103   later Neolithic and Bronze Age (c. 5000-3500 cal yrs BP) include stone settings, circles and funerary

104   monuments (Riley & Wilson-North, 2001), and there are extensive remains of prehistoric field

105   systems thought to date broadly from the middle Bronze Age (from 3500 cal yrs BP). Pollen

106   stratigraphic studies have shown that the vegetation has been influenced by people throughout the

107   past 5000 years (Fyfe et al. 2003; Fyfe 2012). Whilst traditional pollen percentage diagrams can

108   indicate local-scale differences in vegetation (e.g. Davies & Tipping 2004), as stressed, these

109   comparisons are confounded by pollen from the wider region. Application of the LRA will allow this

110   background component to be removed, leaving a significantly clearer picture of local-scale

111   vegetation around each pollen site (Sugita et al. 2010). Comparison with charcoal records (as a

112   proxy for management using fire) will allow assessment of the role of burning in determining local

113   vegetation character.

114

115

116   **Materials and Methods**

117   Estimates of local vegetation abundance were made using the LRA (Sugita 2007a, b). The LRA is a

118   two-step model-based correction algorithm that can be applied to pollen count data to estimate

119   vegetation abundance. The first step is to estimate regional vegetation abundance using the

120   REVEALS model from pollen data that is thought to represent regional vegetation, such as large lakes

121   (>50 ha sensu Sugita 2007a). The second step is to estimate local vegetation abundance using the

122 LOVE model applied to pollen counts from target sites, taking in to account regional vegetation

123 cover (Sugita 2007b). The LRA requires pollen count data from chronologically-constrained

124 sequences, pollen productivity estimates (PPEs) that are expressed relative to a reference taxon and

125 estimates of the fall speed of the key pollen taxa for which estimates are required (Broström et al.

126 2008). PPEs have been measured across Europe by measuring modern pollen loading at networks of

127 sites, and comparing this against the surrounding vegetation cover. The LRA has a series of

128 important assumptions (Sugita et al. 2010), of which the key ones include: the main agent of pollen

129 transport and deposition to the site is through above-canopy winds; differences in height of release

130 of pollen between taxa do not matter; there is no inter-taxonomic preservation bias within the

131 pollen count data; regional vegetation is stationary; and PPEs are invariant through time.

132

133 Exmoor is an upland made of shales, siltstones and slates, and contains almost 20,000 ha of open

134 moorland, rising to 519 m above sea level. The upland has a maritime climate, with precipitation

135 between 800 in the east and up to 2000 mm per annum on the highest ground, and a temperature

136 range from 2 degrees in winter to 21 degrees in summer. Raw count data from 16 dated pollen

137 sequences from Exmoor was used as input to the LRA, although not all sites cover the same time

138 duration (Figure 1 and Table 1). In the absence of large lakes, Sugita et al (2010) and Trondman et al

139 (2016) have demonstrated it is possible to use a network of smaller sites to calculate the regional

140 vegetation abundance. Count data from each site were aggregated into 500-yr contiguous time

141 windows to facilitate correlation and comparison between sites. The PPEs used were those

142 established within the LANDCLIM project (Mazier et al 2012) and represent average PPEs from

143 multiple empirical studies within Europe (SI Table 1). The LRA was run separately for each site. The

144 data from the 'target' site in each run was used as input to the LOVE model, but excluded from the

145 estimate of regional vegetation. Resulting values are a distance-weighted plant abundance

146 (expressed as a percentage) within what is termed the necessary sources area of pollen *sensu* Sugita

147 (2007b), i.e. the distance at which all abundance estimates for all taxa lie between 0-100 % (to

148 within 1 standard error). The LOVE model produces local distance-weighted plant abundance for

149 each taxon (expressed as a percentage of total cover). LOVE output is differentiated from original

150 pollen percentage using the subscript DWPA (i.e. Poaceae$_{DWPA}$); pollen percentage results are

151 described using the subscript PP (i.e. Poaceae$_{PP}$). Taxon-specific output of the REVEALS model are

152 described using the subscript RV (i.e. Poaceae$_{RV}$)

153

154 Charcoal data is only available from six of the 16 sites. Charcoal counts exist in two size fractions:

155 10-50 µm and 50-180 µm. Charcoal counted from pollen slides is typically used to infer a regional

156 fire signal (Mooney and Tinner 2011). Charcoal in larger size fractions in thin section preparations

157 (>50 µm) is used to infer localised burning (Clark 1988). There is also support for the use of larger

158 charcoal fractions from pollen preparations to infer localised burning (e.g. Pitkanen et al. 1999;

159 Tinner et al. 2001). As a result, the coarse (50-180 µm) size fraction is used under the assumption

160 that this reflects more localised burning. Whilst the source area cannot be precisely determined, it

161 is expected to be closer to the source area of pollen than the smaller charcoal size fraction. The data

162 is expressed as concentrations of charcoal fragments cm^{-3} in the original publications. Charcoal

163 records are standardised using z-scores (using the mean and standard deviation over the record)

164 following a Box-Cox power transformation as described by Power et al (2010). Analysis of the

165 charcoal data was undertaken using the palaeofire R-package (Blarquez et al. 2014). Average z-

166 scores for each 500-yr time window have been calculated for comparison with $Calluna_{DWPA}$ and

167 $Poaceae_{DWPA}$.

168

169 Comparison of the original pollen proportion data for select taxa ($Poaceae_{PP}$, $Calluna_{PP}$) and charcoal

170 z-scores for the coarser charcoal fraction (50-180 µm) was undertaken by using a 10-sample moving-

171 window Pearson's product moment correlation coefficient. Use of a moving window allows changes

172 in the strength of relationships through time to be recognised (cf. Fyfe and Woodbridge 2012).

173

174 **Results**

175

176 ***Regional and local vegetation cover estimates***

177 The results of the estimates of regional vegetation cover are shown for each time window in Figure 2

178 and describe the general development of the upland landscape. In the oldest time window, at 5500-

179 6000 cal BP, regional woodland cover is estimated at around 60%, with half of this represented by

180 $Corylus_{RV}$, followed by $Quercus_{RV}$ and $Ulmus_{RV}$. Open-ground taxa at this time are a mix of $Calluna_{RV}$

181 and $Poaceae_{RV}$. Woodland cover declines over successive time windows and is halved by 4000-4500

182 cal BP (to 30 % regional vegetation cover). $Poaceae_{RV}$ becomes the dominant regional vegetation

183 cover at 5000-5500 cal BP, and generally increases. *Plantago lanceolata*$_{RV}$, which shows a continual

184 presence from 5000 cal BP implies some improved grassland. $Calluna_{RV}$ varies around an average of

185 20 % cover from 3500 cal BP onwards.

186

187   The general regional patterns that emerges from the results of the REVEALS model hides

188   considerable spatial variation that is shown when the LOVE model is applied to each pollen record

189   (Figure 3). For clarity, only the $Calluna_{DWPA}$, $Poaceae_{DWPA}$ and *Plantago lanceolata*$_{DWPA}$ results are

190   shown in detail, with 'other' largely representing woodland taxa. At 4000-4500 cal BP, when

191   regional vegetation cover is around 60 % $Poaceae_{RV}$, some sites are almost entirely surrounded by

192    $Poaceae_{DWPA}$ within the local vegetation (e.g. Long Breach at 95 % Poaceae cover) whilst others, even

193   in close proximity, have a more mixed local vegetation (e.g. Gourte Mires, adjacent to Long Breach,

194   has 48 % $Poaceae_{DWPA}$ and 35 % $Calluna_{DWPA}$). Other sites are pre-dominately $Calluna_{DWPA}$ (e.g.

195   Spooners with 64 %). This local-scale vegetation patterning continues through all time windows,

196   with sites close together supporting different local vegetation cover: in no time window is there a

197   'homogenous' signature. A second feature that is apparent both on Figure 3 and in examination of

198   individual site transformations (see Supplementary Information Figures 1-6) is the scale of change of

199   local vegetation between different time windows. The local vegetation estimates can show major

200   differences between adjacent time intervals, indicating major changes in the character of vegetation

201   at the temporal resolution of this study. .

202

203   ***Charcoal and pollen percentage/vegetation cover relationships***

204   Comparison of z-scores for the 50-180 μm charcoal data and the original (non-aggregated) pollen

205   percentage data from the six sites with charcoal data has been undertaken using moving-window

206   correlation analysis to identify time-specific relationships between the dominant open ground taxa

207   ($Poaceae_{PP}$ and $Calluna_{PP}$) and burning (Figure 4). Significant relationships between patterns of

208   micro-charcoal and the pollen percentage data are uncommon and show no temporal or spatial

209   relationship across sites. At Long Breach there is a strong positive relationship between charcoal

210   and $Poaceae_{PP}$ between 6000-4500 cal BP, and again a significant relationship (at the 0.1 level)

211   between 1500-1000 cal BP. Beckham and North Twitchen Springs has short-lived positive

212   relationships around 3000-3500 cal BP between $Poaceae_{PP}$ and micro-charcoal z-scores. Beckham

213   also shows a significant positive relationship between $Calluna_{PP}$ percentages and micro-charcoal z-

214   scores between 3500-2500 cal BP. Only two other sequences indicate a relationship between

215    $Calluna_{PP}$ and micro-charcoal, both negative correlations, at 4000-3500 cal BP for Gourte Mires and

216   1250-1000 cal BP for Long Breach.

217

7

218 Comparison of the z-scores for the 50-180 µm charcoal data at 500-yr time interval for $Calluna_{DWPA}$

219 and $Poaceae_{DWPA}$ are shown on Figure 5. Two sites show no apparent relationship between

220 $Calluna_{DWPA}$ or $Poaceae_{DWPA}$ (Larkbarrow and North Twitchen Springs). Two sites show a clear

221 positive relationship between $Poaceae_{DWPA}$ and charcoal z-scores through all time windows (Long

222 Breach and Beckham). Higher charcoal z-scores in these sites are strongly associated with higher

223 $Poaceae_{DWPA}$. A similar, but weaker, relationship can be observed at Gourte Mires. Relationships

224 between $Calluna_{DWPA}$ and charcoal z-scores are absent from all sites with the exception of Swap Hill,

225 where this is an apparent relationship from 5000-1500 cal BP: higher z-scores are associated with

226 higher $Calluna_{DWPA}$, although the relationship does not appear to persist to the more recent time

227 windows.

228

229 **Discussions**

230

231 ***Spatial heterogeneity in past upland vegetation and land cover***

232 The LRA is a major advance on examination of pollen percentages, as it explicitly attempts to

233 disentangle the regional pollen loading from the local vegetation signal (Sugita 2007a, b). Trondman

234 et al. (2016) identified issues with dealing with potential 'on-site' vegetation including *Calluna* and

235 Cyperaceae on bogs in southern Sweden. The Exmoor study has removed Cyperaceae from the

236 pollen records in recognition of the likely strong local signal; however, *Calluna* is widespread across

237 the upland in the present and not restricted to the small bogs that have been used here. It has thus

238 been included as an important component of the vegetation of the upland. Whilst pollen-analytical

239 methods do not allow the separation of grasses and it is assumed that the pollen originates from the

240 main acid grassland species *Molinia caerulea*, *Agrostis stolonifera*, *Agrostis canina*, *Festuca* spp. and

241 *Nardus stricta* (cf. Stevenson & Thompson, 1993; Stephenson & Rhodes, 2000). The size of the bogs

242 used on Exmoor is very small (Table 1) and thus even local pollen is likely recruited from well beyond

243 the extent of the bog.

244

245 The regional vegetation pattern for Exmoor shows a largely open landscape since 5500 cal BP, and

246 the archaeological record of the upland that demonstrates significant human presence from at least

247 3500 cal BP (Riley & Wilson-North 2001). The LOVE-based vegetation estimates demonstrate strong

248 differences between sites within the landscape that is not evident either from the REVEALS output

249 or from the original pollen percentage data. Many studies have demonstrated patterning and

250   differences using pollen percentage data (e.g. Davis et al. 1980; Fyfe et al. 2003; Davies & Tipping

251   2004; Fyfe & Woodbridge 2012). Application of the LRA separates the local and regional pollen

252   signals that exist in all pollen sequences, and this represents a major advance within pollen analysis.

253   Local estimates of vegetation abundance for individual sites demonstrates periods of time when

254   particular plants are not found in the local vegetation around the site, in spite of the significant

255   presence in the pollen percentage diagram (SI figures 1-6). This has been recognised elsewhere, for

256   example Cui et al. (2013) in southern Sweden have been able to successfully remove the impact of

257   large pollen producers such as *Pinus* that otherwise confound local vegetation reconstruction. Mehl

258   & Hjelle (2016) were also able to recognise plants that were common within the wider region but

259   not within the local vegetation of their sites in western Norway (particularly *Betula* and *Pinus*).

260

261   ***Burning as a driver of moorland vegetation cover***

262   Differences in the character of modern upland vegetation are normally explained through a

263   combination of climatic gradients and land use. At the macro-scale (e.g. national scale) gradients in

264   climate (oceanicity, temperature and rainfall) are strong determinants on moorland vegetation (Yeo

265   & Blackstock 2002); however, within an upland block such as Exmoor these climatic gradients are

266   marginal and are unlikely to be major determinants on vegetation composition. At the regional (e.g.

267   Exmoor) scale, anthropogenic controls are a significant determinant on modern moorland

268   vegetation, in particular burning frequency, grazing intensity and pollution (sulphur and nitrogen

269   deposition) (Stephenson & Rhodes 2000; Yeo & Blackstock 2002). Over millennial time scales

270   pollution can be discounted as this is elevated only in the post-industrial period. At the spatial scale

271   of this study, drawing on sites within the same region and on the same upland, long-term climatic

272   change may also be ruled out as an important control under the assumption that all sites will

273   experience the same climatic shifts. Shifts in regional climate to wetter conditions might have an

274   impact on raised bog vegetation (e.g. at 2800 cal BP: Pancost et al. 2004); the impact this may have

275   on moorland vegetation is unclear when vegetation composition is not tightly coupled to bog surface

276   wetness. Within the analysis presented here the temporal resolution (500 years) is insufficient to

277   identify the impact of decadal or centennial-scale climate shifts. More temporally-detailed work

278   would be necessary to identify such relationships, but there is currently no coherence between the

279   vegetation estimates to suggest climate as an important regional driver.

280

281   The transformation of charcoal count data to normalised z-scores here allows direct consideration of

282   the role of burning as an important driver of local moorland vegetation. Exploration of the

283   relationships between pollen percentages of key taxa and charcoal z-scores has shown few clear

284   relationships between burning and vegetation using moving window correlation (Figure 4). This is

285   similar to the findings of Fyfe & Woodbridge (2012), who also found few consistent relationships

286   between pollen proportions of key moorland taxa and fire, leading them to argue that fire alone was

287   not an important determinant of moorland vegetation. However, the results from application of the

288   LRA to the data from Exmoor show clear differences between pollen proportions and distance-

289   weighted vegetation abundances. When the LRA results are compared with the normalised charcoal

290   z-scores associations exist between grassland cover and burning at some sites throughout the

291   duration of the records (e.g. Long Breach and Beckham) and there is a weak relationship at Gourte

292   Mires. Modern ecological studies suggest that frequent or intense burning would promote grass-

293   dominance on moors, and this is frequently carried out as a management strategy to increase the

294   palatability of moorland vegetation for grazing animals (Hobbs & Gimingham 1987). Application of

295   the LRA allows this relationship to be extracted by considering only the local vegetation separate

296   from the regional background pollen rain. Palaeoecological studies by Chambers et al. (1999) and

297   Chambers et al. (2007), drawing on high-resolution (percentage-based) datasets have also noted

298   correlation between charcoal and increased Poaceae percentages over the past 500 years,

299   suggestive of more frequent or severe fires (Chambers et al. 1999). In this study, the results from

300   Swap Hill indicate a very different relationship between burning and local vegetation, with charcoal

301   z-scores correlating with $Calluna_{DWPA}$ cover, at least between 6000 and 1500 cal BP. Modern studies

302   demonstrate that low intensity rotational burning on a regular basis can promote heather

303   regeneration (Yeo & Blackstock 2002), although Davies et al. (2010) found through controlled

304   experimental burning regimes that the severity and frequency of the burning was less important

305   than the age structure of the *Calluna*: older stands have reduced capacity for vegetative

306   regeneration, and thus are reduced in extent. This points towards differentiated exploitation and

307   use of particular areas in relatively close proximity from prehistoric times on (Swap Hill and Beckham

308   are less than 1 km apart: Figure 1). At Swap Hill the weakening of the relationship between

309    $Calluna_{DWPA}$ and charcoal z-scores after 1500 cal BP suggests changes in land management practices

310   that ultimately break the link between burning and *Calluna* cover.

311

312   Two of the sites used in this study show no relationship between charcoal z-scores and either

313    $Poaceae_{DWPA}$ or $Calluna_{DWPA}$ (North Twitchen Springs and Larkbarrow). Chambers et al. (2007) also

314   recognise sites in south Wales that do not have this relationship (based on pollen percentage values

315   and macrofossil records), whilst others do. Other drivers of vegetation may thus have been

316   important, and Chambers et al. (2007) suggest that changes in grazing regimes (in particular changes

317   from cattle to sheep) could have been an important factor, although the evidence to support this is

318   limited. Archaeological evidence for grazing (field systems, enclosures) extends back to at least

319   4,000 years BP on Exmoor (Riley and Wilson-North, 2001), and grazing intensity is likely to have

320   varied both spatially and temporally. Coprophilious fungi can be used as indicators of grazing (Cugny

321   et al. 2010), and Davies (2016) has utilised this approach in the Pennines (UK) to assess the role of

322   grazing animals in recent moorland vegetation dynamics, finding associations between coprophilous

323   fungi, contraction of heather and increases in Poaceae (pollen percentage-based) over recent

324   centuries. The application of dung fungal spores on Exmoor is an avenue of research with high

325   potential for further elucidating moorland vegetation - grazer interactions, and high-resolution

326   coprophilous dung fungal records are in progress (Ombashi unpubl.). The relationship between

327   burning, grazing and vegetation is rarely clear, and in the current absence of indicators for grazing

328   such as coprophilous fungi, caution must be taken in attributing any one causal mechanism

329   (including burning), as even with high-resolution datasets, multiple causal factors may result in

330   similar palaeoecological signals (Chambers et al. 2007).

331

332   The main limitations on the application of the LRA in developing useful datasets to understand local-

333   scale patterns of vegetation change, and the drivers of those changes, are two-fold. First, there are

334   currently only a limited number of pollen taxa for which the key parameters (PPEs and fall speed) are

335   available. The application of networks of small bogs has overcome the need to use large lakes from

336   which regional vegetation estimates can be derived (this study; Sugita et al. 2010; Trondman et al.

337   2016), provided there are enough small bog records that can be used. Second, the necessity of

338   correlation between sequences limits the temporal resolution that can be achieved, as all sites need

339   to be reduced to time-equivalent samples. Within this study the limitations of the original age-depth

340   models (age uncertainty of each sample) and the temporal sampling resolution (years between

341   adjacent samples) necessitated a 500-yr time window. Moorland vegetation changes can occur on

342   considerably shorter time-scales, for example Davies (2016) details regime shifts from *Calluna*-

343   dominance to Poaceae dominance in the Pennines (UK) over periods of time as short as 25-85 years.

344   Where higher-resolution sampling and age-depth models supported by more radiocarbon dates or

345   other time-markers are available it may be possible to apply the LRA to shorter time windows (e.g.

346   Fredh et al. 2016). The LRA-based approach does not replace the highly detailed, high-temporal

347   resolution work from individual sites such as that of Chambers et al. (2007) and Davies (2016). This

348   is essential in exploring burning/vegetation relationships, and future and ongoing research on

349   Exmoor and other uplands which couples high-resolution pollen analyses with proxies for grazing

350   such as coprophilous fungi will provide powerful, conservation-management oriented insights.

351 What these studies cannot do is disentangle and quantify local vegetation cover from the regional

352 signal within the pollen datasets, although macrofossil analysis may go some way to qualitative

353 interpretation of the records.

354

355 **Conclusions**

356 The analytical approach to transformation of pollen count data into local vegetation abundance has

357 provided improved insights into the spatial patterning of vegetation. Within this particular region,

358 clear differences within the nature of the local vegetation have been identified, in particular the

359 relative importance of *Calluna* and Poaceae in moorland vegetation, that are not apparent from

360 pollen percentage data alone. Differences between sites within the region, which all have the same

361 geology and experience the same climate, are most likely to relate to human land use and

362 management approaches over the past 5000 years. Burning and/or changes in grazing intensity are

363 well-established controls on moorland vegetation in regions such as this. In the absence of data on

364 past grazing regimes, burning regimes have been explored through examination of micro-charcoal

365 records from six selected sites. At three sites, burning appears to promote and sustain grass-

366 dominated vegetation, at one site it promotes and sustains heather-dominated vegetation (at least

367 between 5500-1500 cal BP), and there is no clear signal from two others. Future research should

368 focus on testing the role of grazing as a driver of vegetation cover and change using appropriate

369 proxies for grazing such as coprophilous fungi.

370

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377

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493

494   Figure 1: Location of sites used for LRA analysis on Exmoor. Dashed lines on panels indicate 50 m

495   contour lines; roads and main drainage lines are given. Details of sites and site codes are given on

496   Table 1.
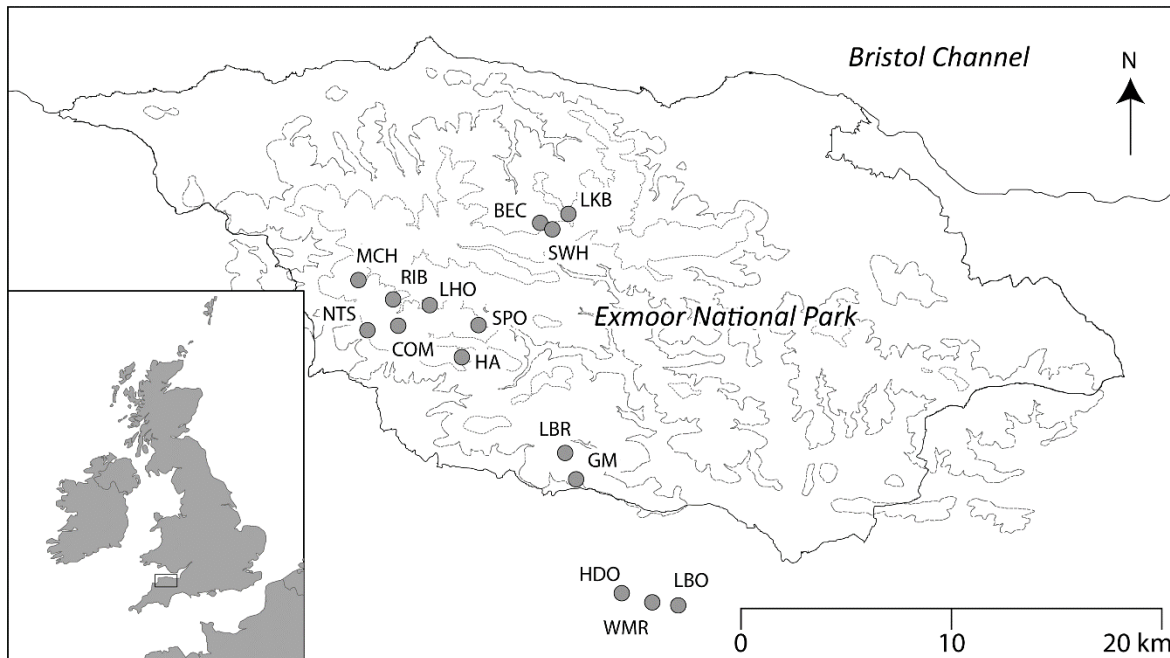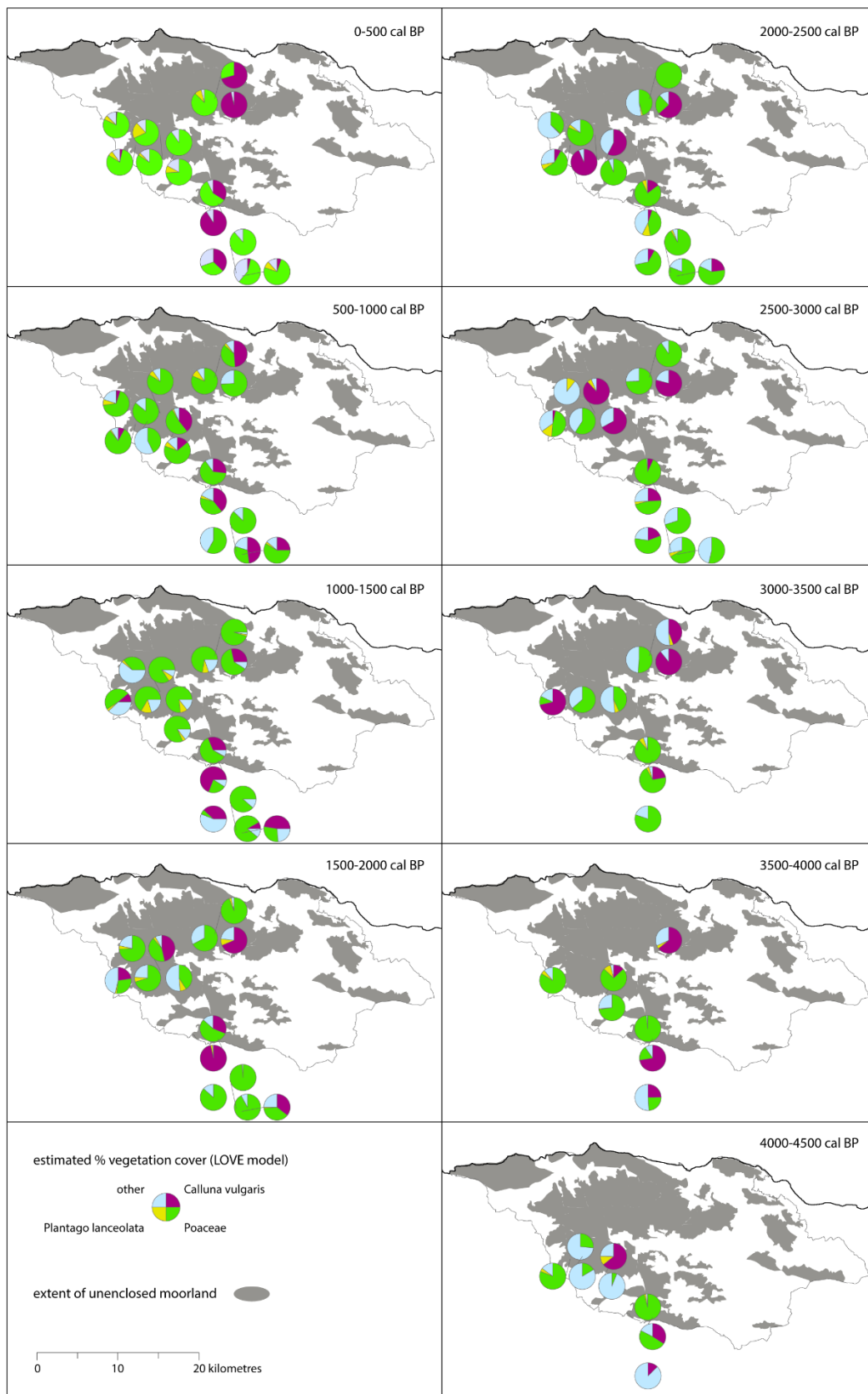
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499   Figure 2: REVEALS-based regional vegetation estimates for Exmoor for main taxa based on 16 pollen

500   sequences.
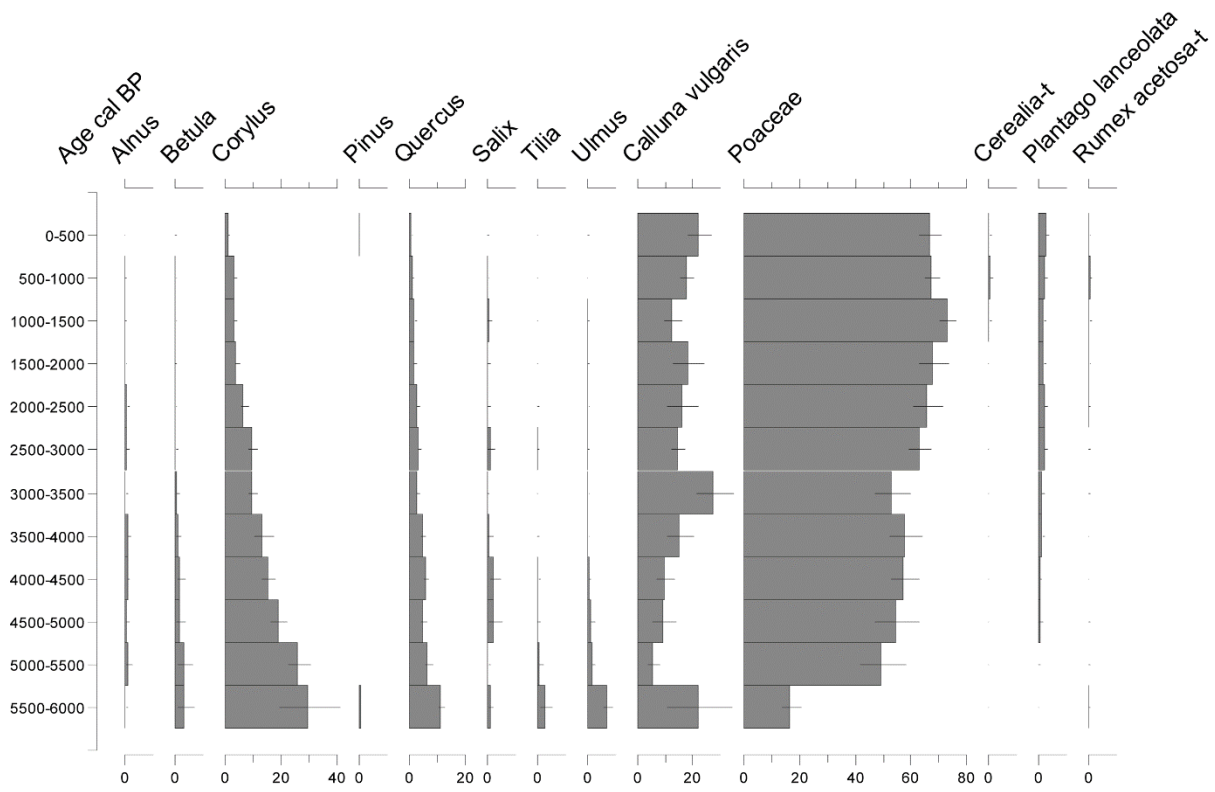
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503 Figure 3: LOVE estimates of percentage distance-weighed cover of key moorland taxa for all sites on

504 Exmoor.

505

506   Figure 4: Pearson's product moment correlation coefficient scores for 10-sample moving window

507   between pollen percentage data (top: *Calluna*, bottom: Poaceae) and charcoal z-scores (50-180 µm

508   fraction). Long vertical dashed lines indicate significance level at p<0.1. Short dashed vertical lines

509   indicate significance level at p<0.01. Grey boxes indicate periods of significant relationships at the

510   0.1 and 0.01 level.
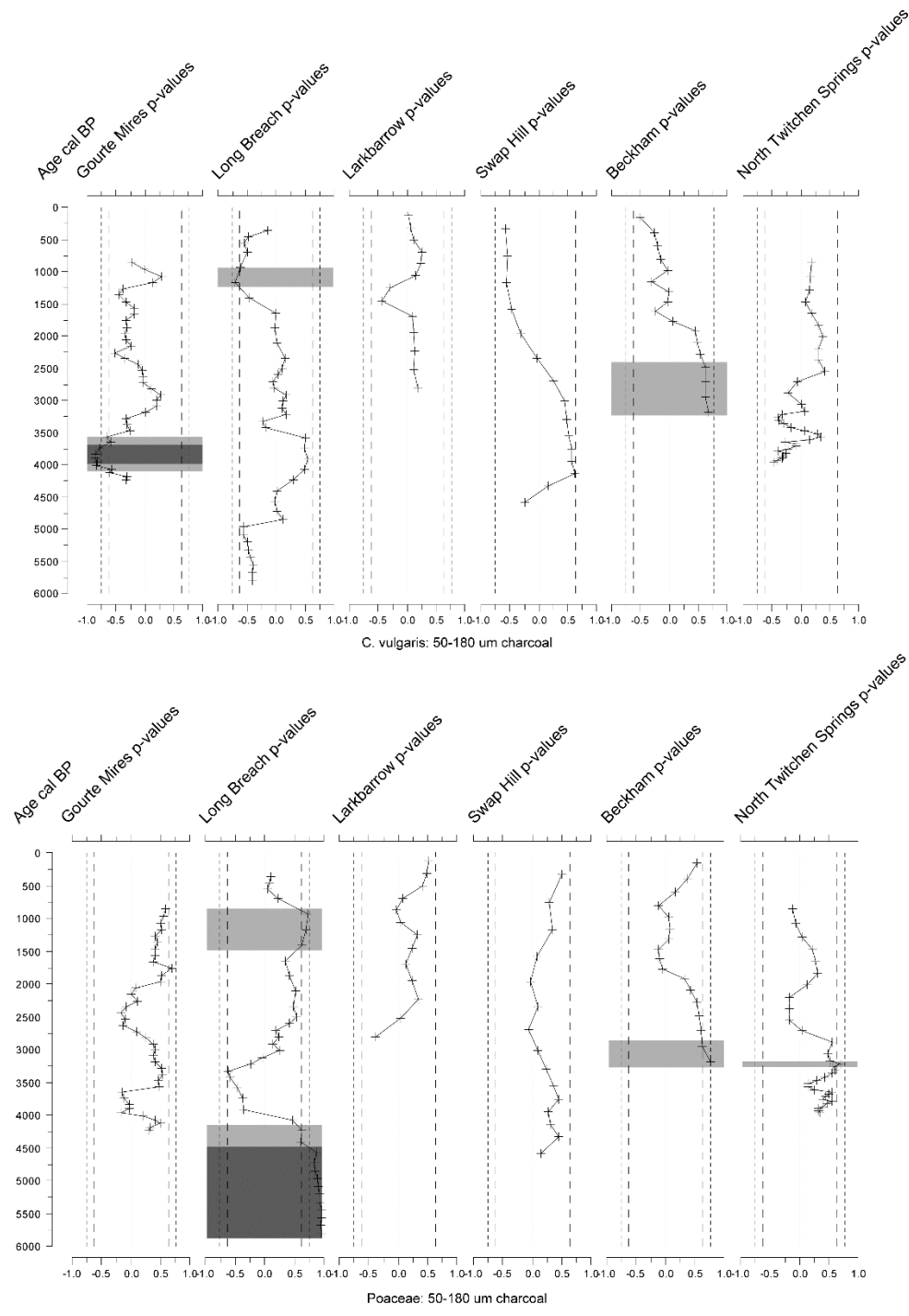
511

512   Figure 5: comparison between LRA estimates of distance weighted cover of *Calluna* and Poaceae,

513   and charcoal z-scores (50-180 µm fraction). + indicate charcoal z-scores; grey bars represent average

514   charcoal z-scores for each 500-yr time window for comparison with LOVE estimates.
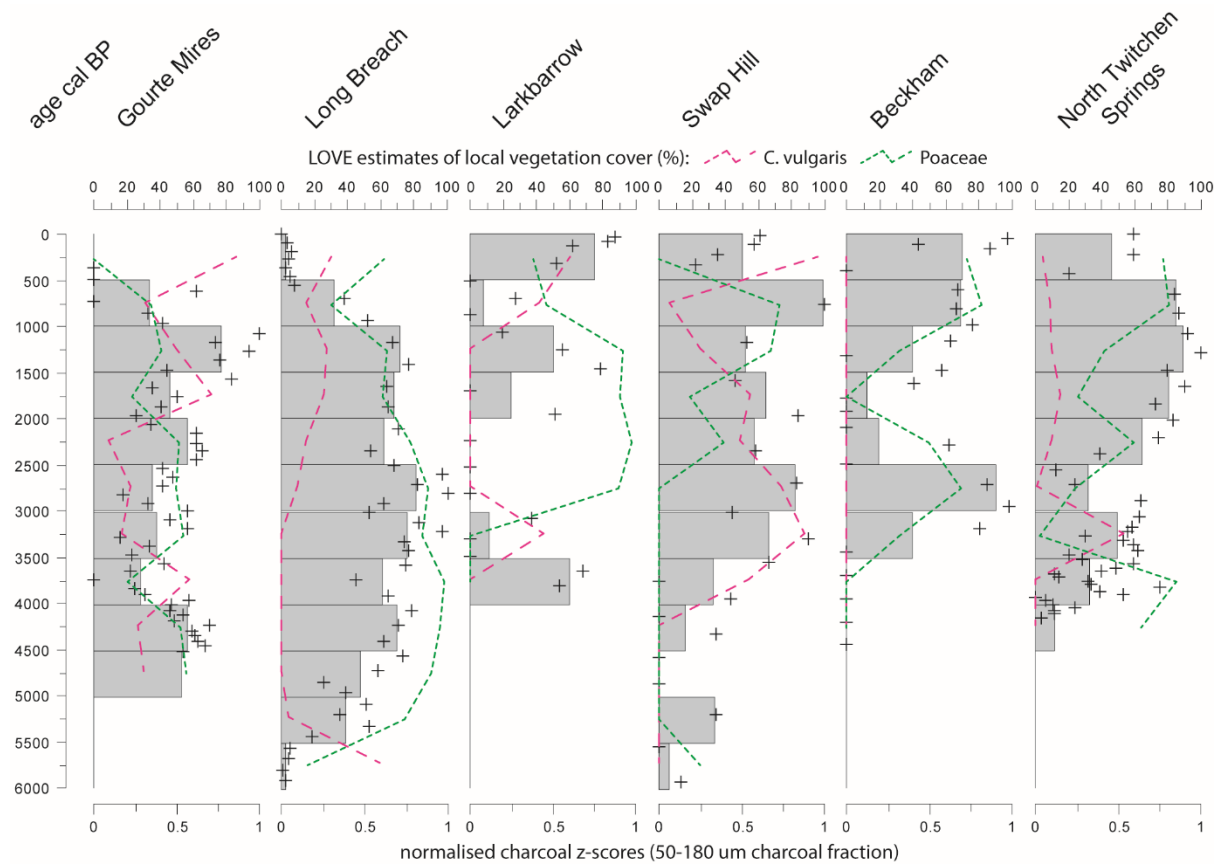
515

516   Table 1: Details of sites used for LRA on Exmoor. Sites marked with * include charcoal data. Codes

517   are those used on Figure 1. Locations are given as decimal degrees (WGS1984)

518

Site name (code)	Location	Elevation (m)	Site radius (m)	n 14C dates	Age range (cal BP)	Reference
Gourte Mires (GM)*	51.054, -3.678	291	20	4	4500-400	Fyfe et al (2003)
Long Breach (LBR)*	51.066, -3.687	339	30	5	6500-present	Fyfe et al (2003)
Long Holcombe (LHO)	51.107, -3.759	410	10	3	5300-present	Fyfe (unpublished)
Moles Chamber (MCH)	51.139, -3.833	421	15	6	3000-present	Fyfe (2012)
North Twitchen Spring (NTS)*	51.117, -3.826	352	15	5	4200-present	Fyfe (2012)
Roman Lode (RLO)	51.129, -3.783	442	50	2	2600-present	Fyfe (unpublished)
Comerslade (COM)	51.120, -3.805	447	100	6	8400-800	Fyfe (2012)
Larkbarrow (LKB)*	51.171, -3.688	378	50	4	3800-present	Davies et al (2015)
Swap Hill (SWH)*	51.164, -3.699	418	150	4	6400-present	Davies et al (2015)
Beckham (BEC)*	51.166, -3.706	392	30	4	4500-present	Davies et al (2015)
Ricksy Ball (RIB)	51.131, -3.809	430	10	8	6500-present	Fyfe (unpublished)
Spooners (SPO)	51.121, -3.750	412	60	3	8300-present	Fyfe (unpublished)
Windmill Rough (WMR)	50.975, -3.633	259	10	3	2600-present	Fyfe et al (2004)
Lobbs Bogg (LBO)	50.970, -3.624	242	15	5	2500-present	Fyfe et al (2004)
Hares Down (HDO)	50.978, -3.644	254	5	4	2600-present	Fyfe et al (2004)
Halscombe Allotment (HA)	50.989, -3.684	350	10	5	8800-200	Fyfe (unpublished)

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521 Supporting information to the paper

522 Fyfe, R.M., Ombashi, H., Davies, H. & Head, K. Moorland vegetation and burning over the past five millennia. *Journal of*

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524

525 **Appendix S1.** Pollen productivity estimates and fall-speed of pollen used within the Landscape Reconstruction Algorithm

526

527 Table 1: Pollen productivity estimates, standard errors and fall speeds of pollen used as input parameters for the LRA. PPEs and SEs are taken from

528 Mazier et al. (2012)

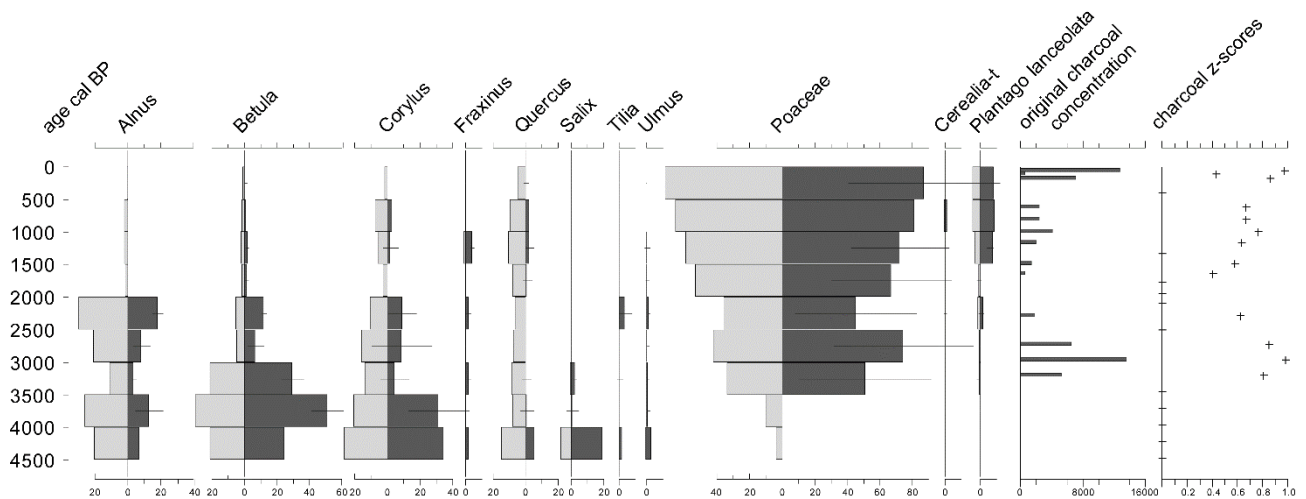| Taxon	PPE	Standard error	Fall speed (ms^{-1})
Abies	6.88	2.084	0.12
Alnus	9.07	0.011	0.021
Artemisia	3.48	0.039	0.025
Betula	3.09	0.072	0.024
Calluna vulgaris	0.82	0.001	0.038
Carpinus	3.55	0.181	0.042
Cerealia-t	1.85	0.146	0.06
Corylus	1.99	0.038	0.025
Fagus	2.35	0.012	0.057
Filipendula	2.81	0.185	0.006
Fraxinus	1.03	0.011	0.022
Poaceae	1	0.000	0.035
Juniperus	2.07	0.001	0.016
Picea	2.62	0.015	0.056
Pinus	6.38	0.200	0.031
Plantago lanceolata	1.04	0.009	0.029
Plantago media	1.27	0.033	0.024
Plantago montana	0.74	0.017	0.03
Quercus	5.83	0.023	0.035
Rumex acetosa-t	2.14	0.077	0.018
Salix	1.22	0.012	0.022
Secale-t	3.02	0.003	0.06
Tilia	0.8	0.001	0.032
Ulmus	1.27	0.003	0.032

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531 **Appendix S2.** Pollen and distance-weighted vegetation estimates for individual sites with charcoal records from Exmoor.
532
533 Figure S2-1: Pollen percentage (light grey bars) and distance-weighted vegetation estimates (dark grey bars) for key taxa from Swap Hill, Exmoor (original
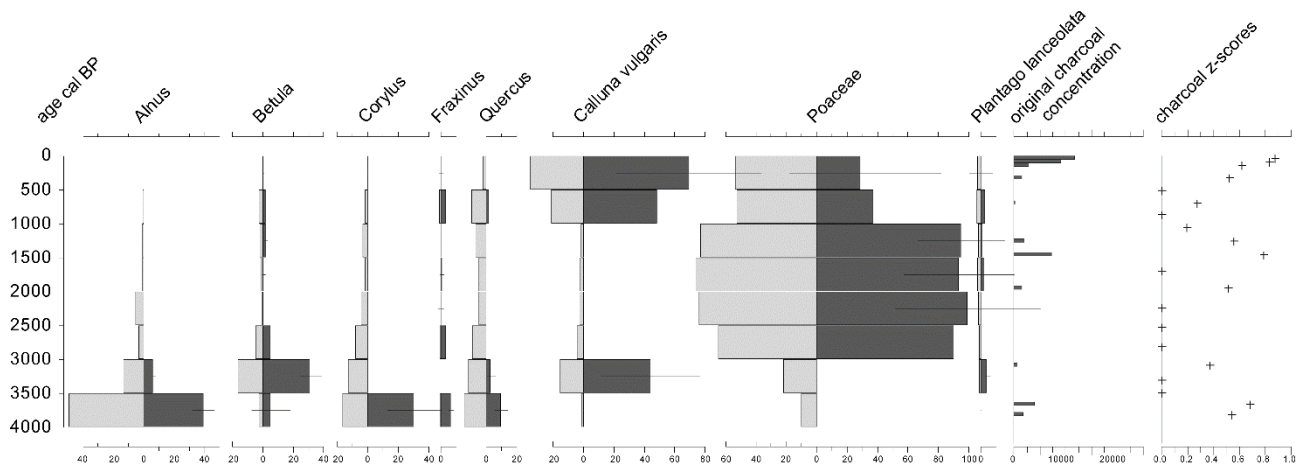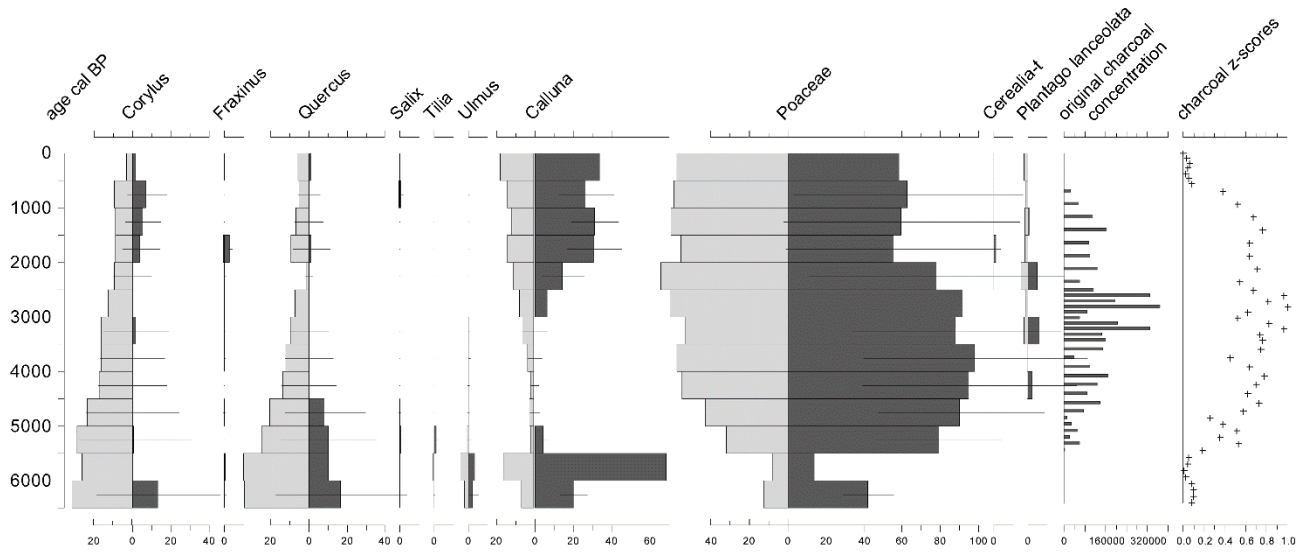534 data from Davies et al. 2015).

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538 Figure S2-2: Pollen percentage (light grey bars) and distance-weighted vegetation estimates (dark grey bars) for key taxa from Beckham, Exmoor (original
539 data from Davies et al. 2015).

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543 Figure S2-3: Pollen percentage (light grey bars) and distance-weighted vegetation estimates (dark grey bars) for key taxa from Larkbarrow, Exmoor
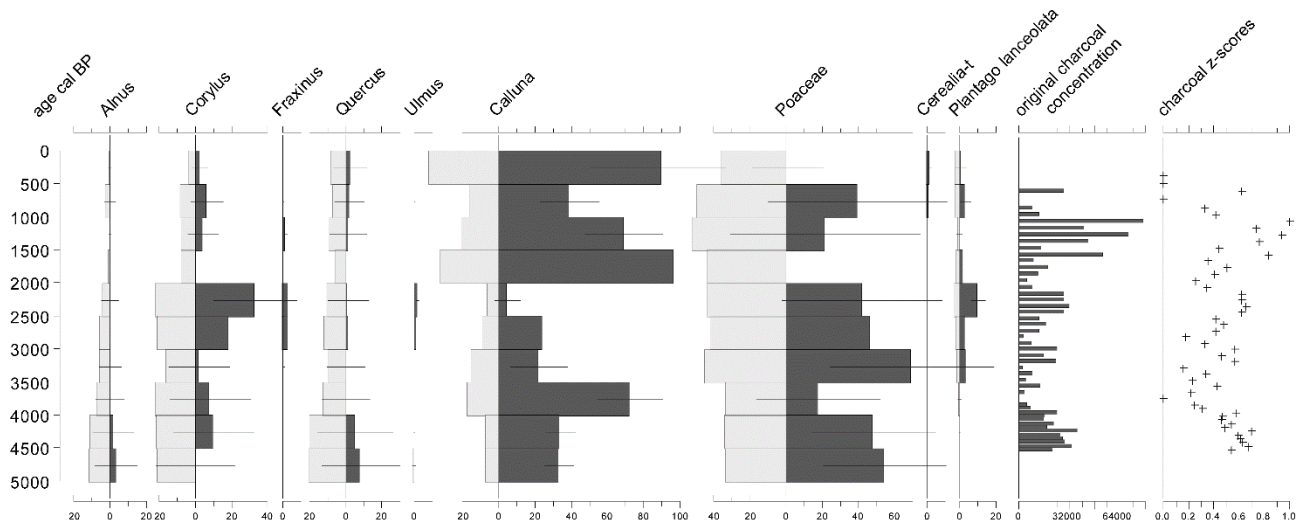544 (original data from Davies et al. 2015).

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Figure S2-4: Pollen percentage (light grey bars) and distance-weighted vegetation estimates (dark grey bars) for key taxa from Long Breach, Exmoor (original data from Fyfe et al. 2003).


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Figure S2-5: Pollen percentage (light grey bars) and distance-weighted vegetation estimates (dark grey bars) for key taxa from Gourte Mires, Exmoor (original data from Fyfe et al. 2003).

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Figure S2-6: Pollen percentage (light grey bars) and distance-weighted vegetation estimates (dark grey bars) for key taxa from North Twitchen Springs, Exmoor (original data from Fyfe 2012).
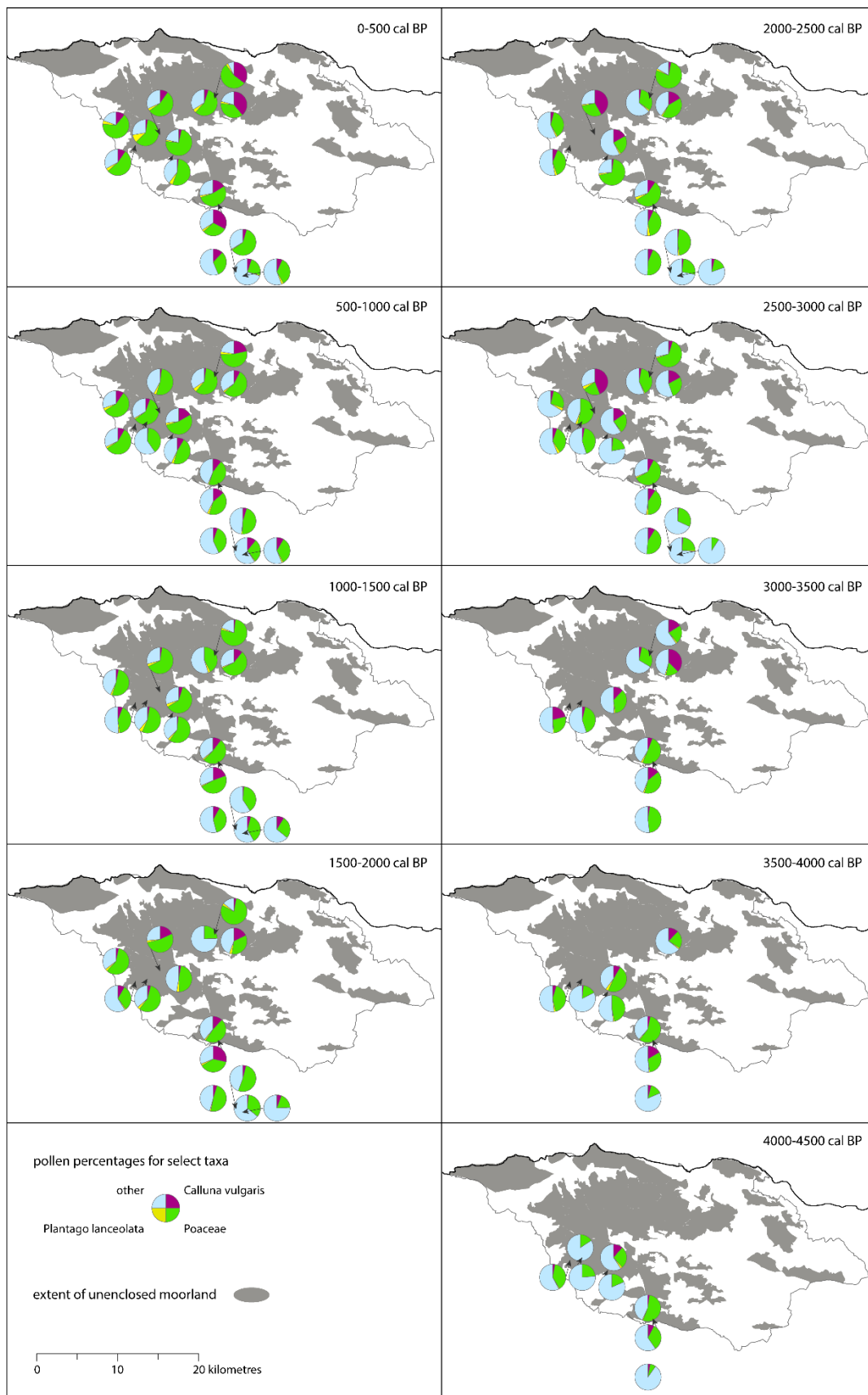

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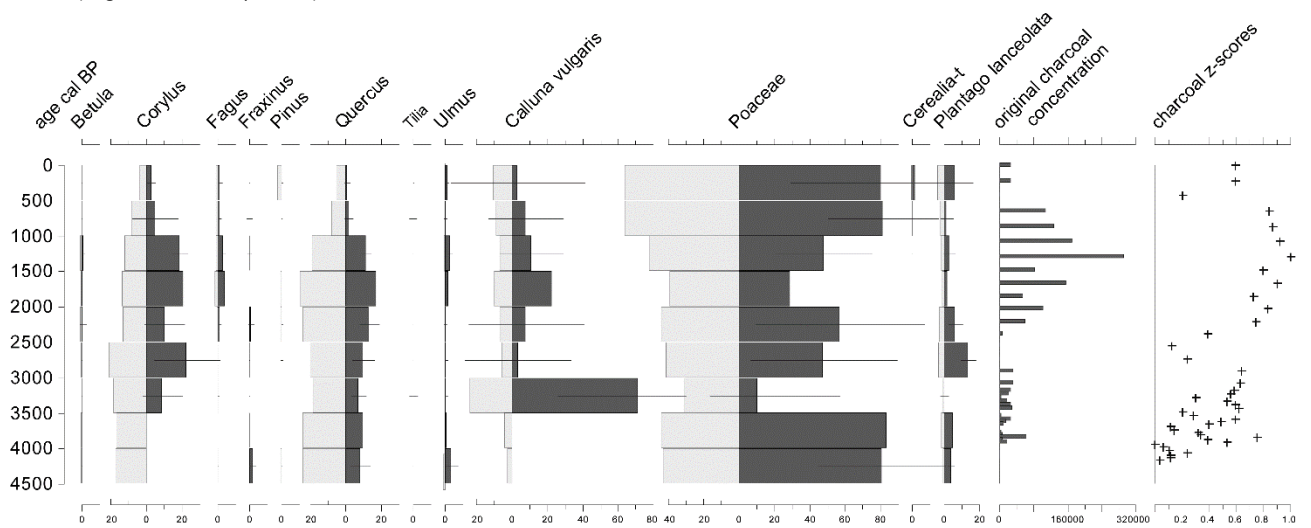
561 **Appendix S3.** Spatial pattern of pollen percentages data from sites on Exmoor.

562

563 Figure S3-1: Maps of pollen percentage data for sites on Exmoor in 500-year time windows. This figure should be compared with LOVE estimates
564 presented in Figure 3 (main article).

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