

2018-05

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

Fyfe, R

<http://hdl.handle.net/10026.1/11084>

10.1111/jvs.12594

Journal of Vegetation Science

Wiley

All content in PEARL is protected by copyright law. Author manuscripts are made available in accordance with publisher policies. Please cite only the published version using the details provided on the item record or document. In the absence of an open licence (e.g. Creative Commons), permissions for further reuse of content should be sought from the publisher or author.

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

2

3 Ralph M. Fyfe¹, Havananda Ombashi¹, Heather J. Davies² & Katie Head¹

4

5 Fyfe, R.M. (corresponding author, ralph.fyfe@plymouth.ac.uk)¹

6 ¹ School of Geography, Earth and Environmental Sciences, University of Plymouth, Plymouth, PL4

7 8AA, UK

8 ² School of Geography Earth and Environmental Sciences, University of Birmingham, Birmingham B15

9 2TT, UK.

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**: calibrated years before
49 present (present = 1950)

50

51 **Running head**

52 Long-term upland moorland vegetation and burning

53

54

55 **Introduction**

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 it 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

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. Coprophilous 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

371 **Acknowledgements**

372 This work has been supported by Exmoor National Park Authority and Rob Wilson-North and Lee
373 Bray are thanked in particular. The paper is a contribution to the Past Global Changes (PAGES)
374 LANDCOVER6K project coordinated by Marie-José Gaillard. We thank Shinya Sugita for use of his
375 LRA models.

376

377

378 **References**

- 379 Bennett, K.D. 2007. *Annotated Catalogue of Pollen and Pteridophyte Spore Types*. University of
380 Belfast, Belfast.
- 381 Blarquez, O., Vanniere, B., Marlon, J.R., Daniau, A.L., Power, M.J., Brewer, S. & Bartlein, P.J. 2014.
382 Paleofire: an R package to analyse sedimentary charcoal records from the Global Charcoal Database
383 to reconstruct past biomass burning. *Computers & Geosciences* 72: 255-261.
- 384 Britton, A.J., Hester, A.J., Hewison, R.L., Potts, J.M. & Ross, L.C. 2016. Climate, pollution and grazing
385 drive long-term change in moorland habitats. *Applied Vegetation Science* 20: 194-203.
- 386 Broström, A., Nielsen, A.B., Gaillard, M.-J., Hjelle, K., Mazier, F., Binney, H., Bunting, M.-J., Fyfe, R.M.,
387 Meltsov, V., (...) & Sugita, S. 2008. Pollen productivity estimates – the key to landscape
388 reconstructions. *Vegetation History and Archaeobotany* 17: 461-478.
- 389 Bunting, M.J., Twiddle, C.L. & Middleton, R. 2008. Using models of pollen dispersal and deposition in
390 hilly landscapes: Some possible approaches. *Palaeogeography, Palaeoclimatology, Palaeoecology*
391 259: 77-91.
- 392 Chambers, F.M., Mauquoy, D. & Todd, P.A. 1999. Recent rise to dominance of *Molinia caerulea* in
393 environmentally sensitive areas: new perspectives from palaeoecological data. *Journal of Applied*
394 *Ecology* 36: 719-733.
- 395 Chambers, F.M., Mauquoy, D., Gent, A., Pearson, F., Daniell, J.R. & Jones, P.S. 2007. Palaeoecology of
396 degraded blanket mire in South Wales: data to inform conservation management. *Biological*
397 *Conservation* 137: 197-209.
- 398 Clark, J.S. 1988. Particle motion and the theory of charcoal analysis: source area, transport,
399 deposition, and sampling. *Quaternary Research* 30: 67-80.
- 400 Cugny, C., Mazier, F. & Galop, D. 2010. Modern and fossil non-pollen palynomorphs from the Basque
401 mountains (western Pyrenees, France): the use of coprophilous fungi to reconstruct pastoral activity.
402 *Vegetation history and Archaeobotany* 19, 391-408.
- 403 Cui, Q.Y., Gaillard, M.J., Lemdahl, G., Sugita, S., Greisman, A., Jacobson, G. L. & Olsson, F. 2013. The
404 role of tree composition in Holocene fire history of the hemiboreal and southern boreal zones of
405 southern Sweden, as revealed by the application of the Landscape Reconstruction Algorithm:
406 implications for biodiversity and climate-change issues. *The Holocene* 23: 1747-1763.
- 407 Davies, A.L. 2016. Late Holocene regime shifts in moorland ecosystems: high resolution data from
408 the Pennines, UK. *Vegetation History and Archaeobotany* 25: 207-219.

- 409 Davies, A.L. & Bunting, M.J. 2010. Applications of palaeoecology in conservation. *Open Ecology*
410 *Journal* 3: 54–67.
- 411 Davies, A.L. & Tipping, R. 2004. Sensing small-scale human activity in the pollen palaeoecological
412 record: fine spatial resolution pollen analyses from Glen Affric, northern Scotland. *The Holocene* 14:
413 233–245.
- 414 Davies, G.M., Kettridge, N., Stoof, C.R., Gray, A., Ascoli, D., Fernandes, P.M., Marrs, R., Allen, K.A.,
415 Doerr, S.H., (...) & McMorrow, J. 2016. The role of fire in UK peatland and moorland management:
416 the need for informed, unbiased debate. *Philosophical Transactions of the Royal Society series B* 371:
417 20150342.
- 418 Davies, G.M., Smith, A.A., MacDonald, A.J., Bakker, J.D. & Legg, C. 2010. Fire intensity, fire severity
419 and ecosystem response in heathlands: factors affecting the regeneration of *Calluna vulgaris*. *Journal*
420 *of Applied Ecology* 47: 356–365.
- 421 Davies, H., Fyfe, R.M. & Charman, D. 2015. Does peatland drainage damage the palaeoecological
422 record? *Review of Palaeobotany and Palynology* 221: 92–105.
- 423 Davis, M.B., Spear, R.W., Shane, L.C.K. 1980. Holocene climate of New England. *Quaternary Research*
424 14: 240–250.
- 425 Fredh, D., Broström, A., Zillén, L., Mazier, F., Rundgren, M., & Lagerås, P. 2012. Floristic diversity in
426 the transition from traditional to modern land-use in southern Sweden AD 1800–2008. *Vegetation*
427 *History and Archaeobotany* 21, 439–452.
- 428 Fyfe, R.M. 2012. Bronze Age landscape dynamics: spatially detailed pollen analysis from a
429 ceremonial complex. *Journal of Archaeological Science* 39: 2764–2773.
- 430 Fyfe, R.M. & Woodbridge, J. 2012. Differences in time and space in upland vegetation patterning:
431 analysis of pollen data from Dartmoor, UK. *Landscape Ecology* 27: 745–760.
- 432 Fyfe, R.M., Brown, A.G. & Rippon, S.J. 2003. Mid- to late-Holocene vegetation history of Greater
433 Exmoor, UK: estimating the spatial extent of human-induced vegetation change. *Vegetation History*
434 *and Archaeobotany* 12: 215–232.
- 435 Fyfe, R.M., Brown, A.G. & Rippon, S.J. 2004. Characterising the late prehistoric, “Romano-British”
436 and medieval landscape, and dating the emergence of a regionally distinct agricultural system in
437 South West Britain. *Journal of Archaeological Science* 31: 1699–1714.

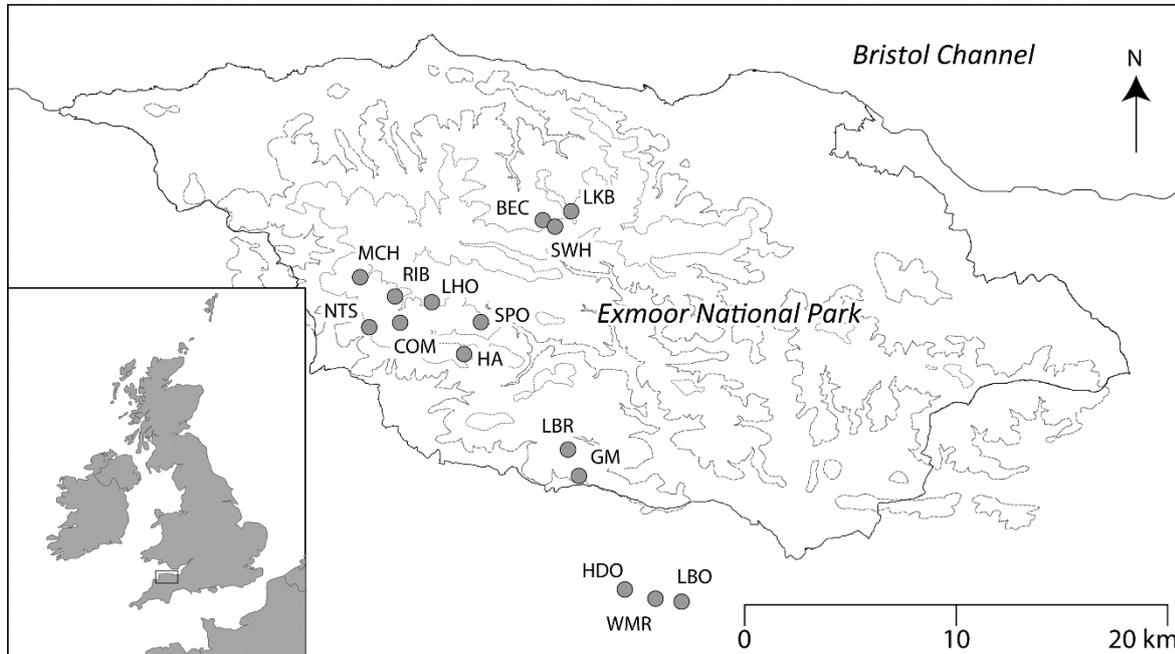
- 438 Hjelle, K.L., Mehl, I.K., Sugita, S. & Andersen, G.L. 2015. From pollen percentage to vegetation cover:
439 evaluation of the Landscape Reconstruction Algorithm in western Norway. *Journal of Quaternary*
440 *Science* 30: 312-324.
- 441 Hobbs, R.J. & Gimingham, C.H. 1987. Vegetation, fire and herbivore interactions in heathland.
442 *Advances in Ecological Research* 16: 87-173.
- 443 Mazier, F., Gaillard, M.J., Kuneš, P., Sugita, S., Trondman, A.K. & Broström, A. 2012. Testing the effect
444 of site selection and parameter setting on REVEALS-model estimates of plant abundance using the
445 Czech Quaternary Palynological Database. *Review of Palaeobotany and Palynology* 187: 38-49.
- 446 Mehl, I.K. & Hjelle, K.L. 2016. From deciduous forest to open landscape: application of new
447 approaches to help understand cultural landscape development in western Norway. *Vegetation*
448 *History and Archaeobotany* 25: 153-176.
- 449 Mooney, S.D. & Tinner, W. 2011. The analysis of charcoal in peat and organic sediments. *Mires and*
450 *Peat* 7: 1-18.
- 451 Pancost, R.D., Baas, M., van Geel, B., Sinninghe Damste, J.S. 2003. Response of an ombrotrophic bog
452 to a regional climate event revealed by macrofossil, molecular and carbon isotope data. *The*
453 *Holocene* 13: 921-932.
- 454 Pitkanen, A., Lehtonen, H. & Huttunen P. 1990. Comparison of sedimentary microscopic charcoal
455 particle records in a small lake with dendrochronological data: evidence for the local origin of
456 microscopic charcoal produced by forest fires of low intensity in eastern Finland. *The Holocene* 9:
457 559-567.
- 458 Power, M.J., Marlon, J.R., Bartlein, P.J. & Harrison, S.P. 2010. Fire history and the Global Charcoal
459 Database: a new tool for hypothesis testing and data exploration. *Palaeogeography,*
460 *Palaeoclimatology, Palaeoecology* 291: 52-59.
- 461 Reed, M.S., Bonn, A., Slee, W., Beharry-Borg, N., Birch, J., Brown, I., Burt, T.P., Chapman, D.,
462 Chapman, P.J., (...) & Worrall, F. 2009. The future of the uplands. *Land Use Policy* 265: S204–S216.
- 463 Riley, H. & Wilson-North, R. 2001. *The field archaeology of Exmoor*. English Heritage, London
- 464 Stevenson, A.C. & Rhodes, A.N. 2000. Palaeoenvironmental evaluation of the importance of fire as a
465 cause for *Calluna* loss in the British Isles. *Palaeogeography, Palaeoclimatology, Palaeoecology* 164:
466 195-206.

- 467 Stevenson, A.C. & Thompson, D.B.A. 1993. Long-term changes in the extent of heather moorland in
468 upland Britain and Ireland: palaeoecological evidence for the importance of grazing. *The Holocene* 3:
469 70-76.
- 470 Sugita, S. 2007a. Theory of quantitative reconstruction of vegetation I: pollen from large sites
471 REVEALS regional vegetation composition. *The Holocene* 17: 229-241.
- 472 Sugita, S. 2007b. Theory of quantitative reconstruction of vegetation II: all you need is LOVE. *The*
473 *Holocene* 17: 243-257.
- 474 Sugita, S., Gaillard, M. J. & Broström, A. 1999. Landscape openness and pollen records: a simulation
475 approach. *The Holocene* 9: 409-421.
- 476 Sugita, S., Parshall, T., Calcote, R. & Walker, K. 2010. Testing the Landscape Reconstruction Algorithm
477 for spatially explicit reconstruction of vegetation in northern Michigan and Wisconsin. *Quaternary*
478 *Research* 74: 289-300.
- 479 Tinner, W., Conedera, M., Ammann, B., Gaggeler, H.W., Gedye, S., Jones, R. & Sagesser, B. 1998.
480 Pollen and charcoal in lake sediments compared with historically documented forest fires in
481 southern Switzerland since AD 1920. *The Holocene* 8: 31-42.
- 482 Tinner, W., Hubschmid, P., Wehrli, M., Ammann, B. & Conedera, M. 1999. Long-term forest fire
483 ecology and dynamics in southern Switzerland. *Journal of Ecology* 87: 273-289.
- 484 Trondman, A.-K., Gaillard, M.J., Sugita, S., Bjorkman, L., Greisman, A., Hultberg, T., Lageras, P.,
485 Lindbladh, M. & Mazier, F. 2016. Are pollen records from small sites appropriate for REVEALS model-
486 based quantitative reconstructions of past regional vegetation? An empirical test in southern
487 Sweden. *Vegetation History and Archaeobotany* 25: 131-151.
- 488 Woodbridge, J., Fyfe, R.M. & Roberts, N. 2014. A comparison of remotely-sensed and pollen-based
489 approaches to mapping Europe's land cover. *Journal of Biogeography* 41: 2080-2092.
- 490 Yeo, M.J.M. & Blackstock, T.H. 2002. A vegetation analysis of the pastoral landscapes of upland
491 Wales, UK. *Journal of Vegetation Science* 13, 803-816.

492

493

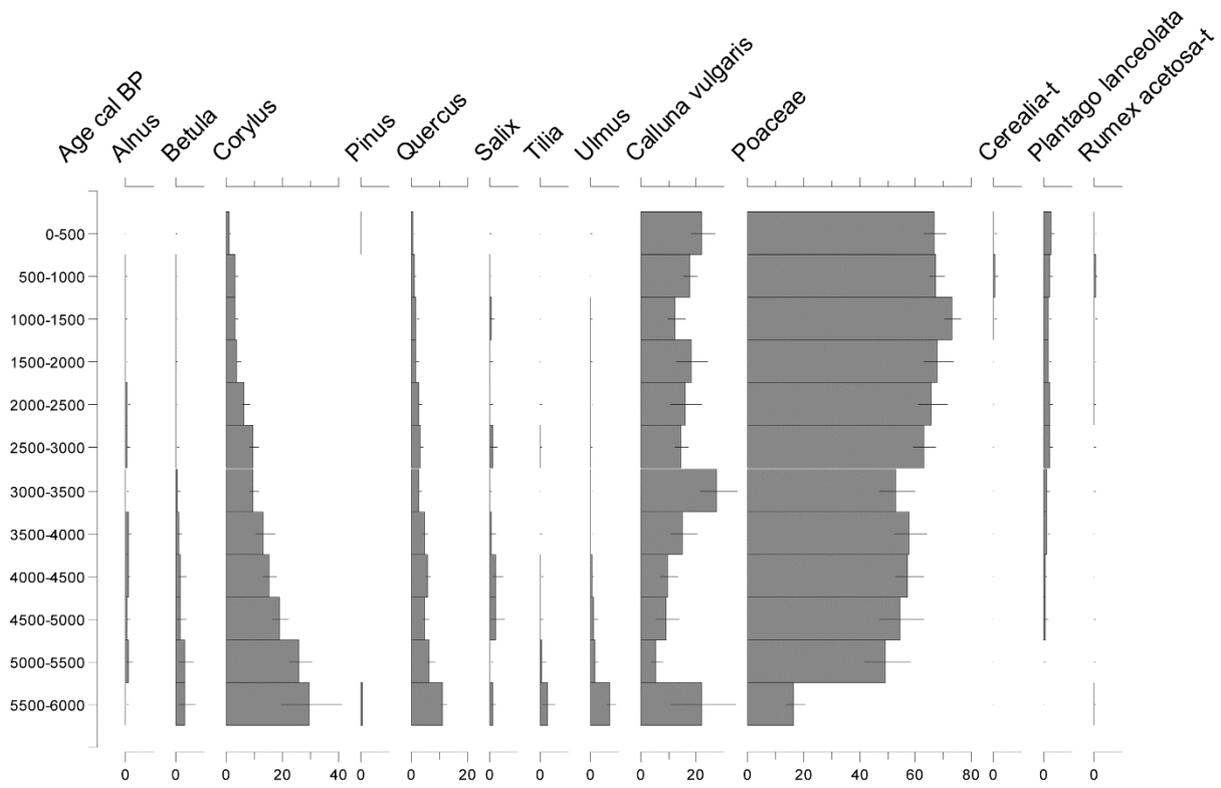
494 Figure 1: Location of sites used for LRA analysis on Exmoor. Dashed lines on panels indicate 50 m
495 contour lines; roads and main drainage lines are given. Details of sites and site codes are given on
496 Table 1.



497

498

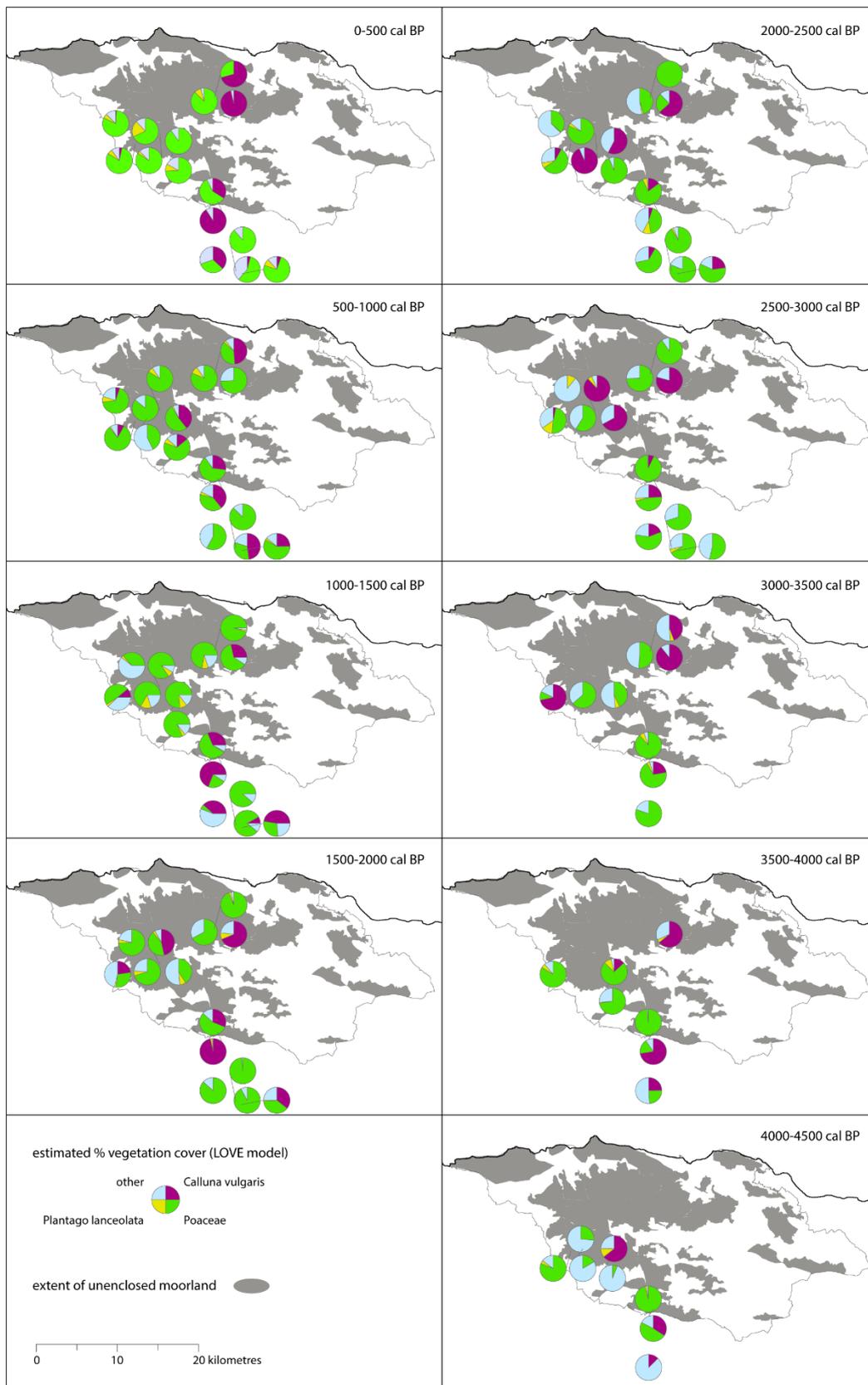
499 Figure 2: REVEALS-based regional vegetation estimates for Exmoor for main taxa based on 16 pollen
500 sequences.



501

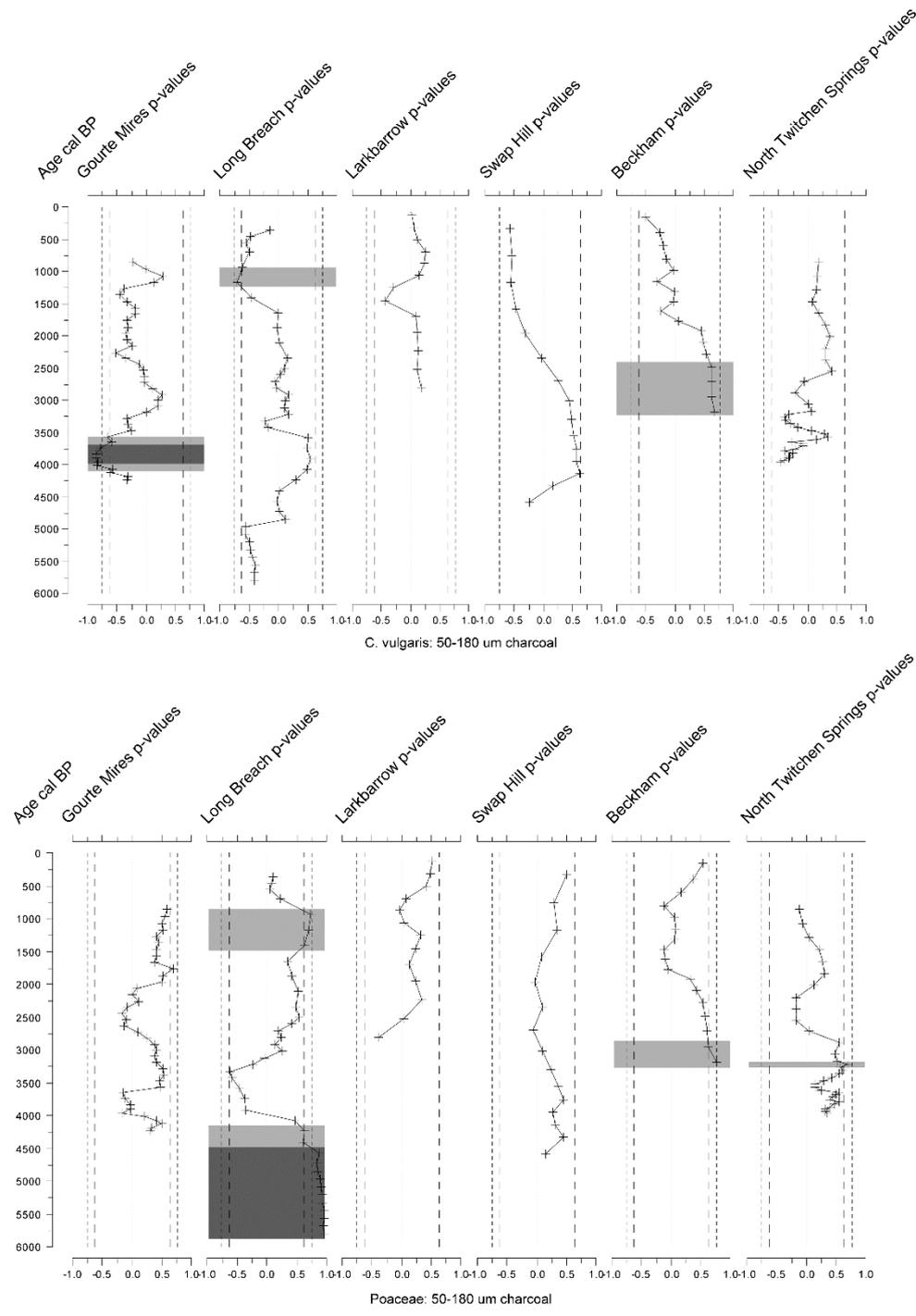
502

503 Figure 3: LOVE estimates of percentage distance-weighted cover of key moorland taxa for all sites on
504 Exmoor.



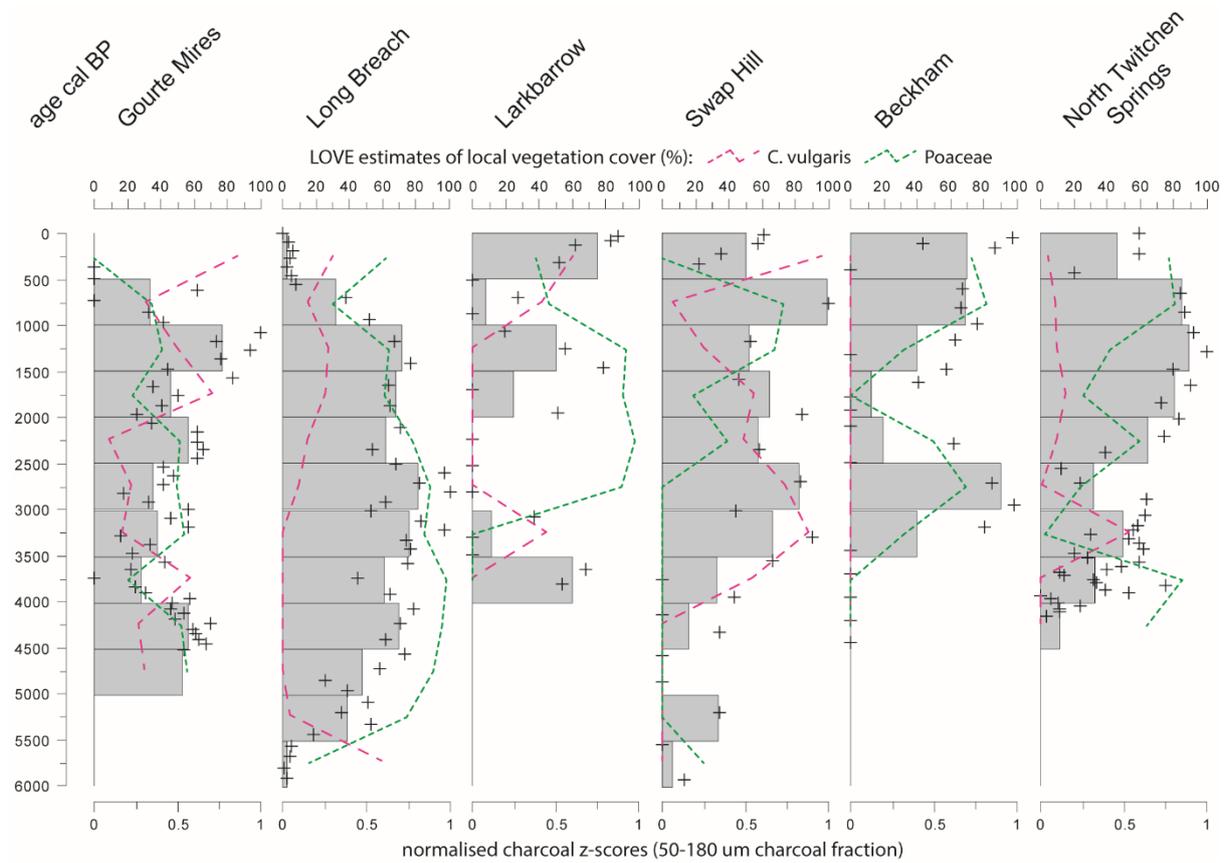
505

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 μ m
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 μ m 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)

519

520

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*
 523 *Vegetation Science*.

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)

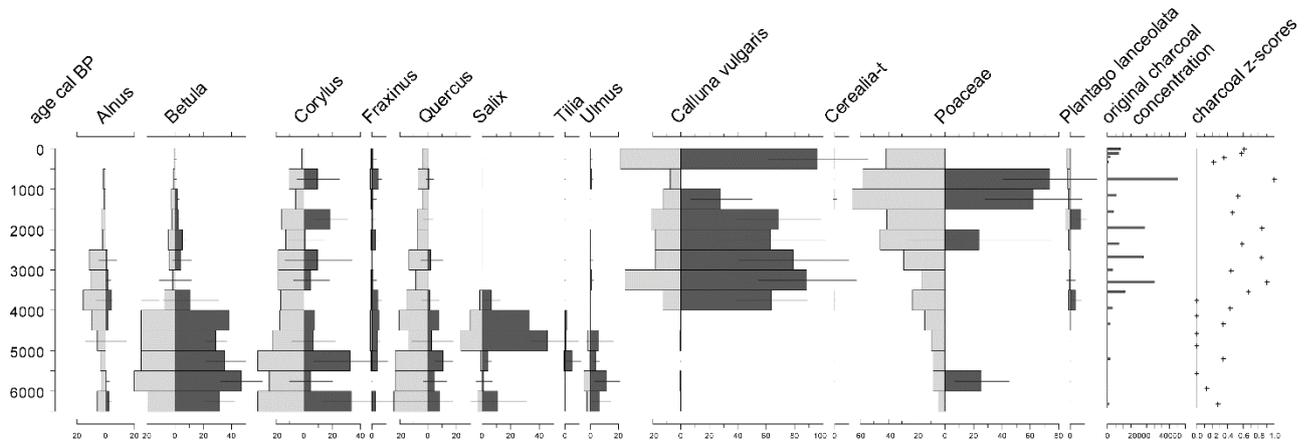
Taxon	PPE	Standard error	Fall speed (ms ⁻¹)
<i>Abies</i>	6.88	2.084	0.12
<i>Alnus</i>	9.07	0.011	0.021
<i>Artemisia</i>	3.48	0.039	0.025
<i>Betula</i>	3.09	0.072	0.024
<i>Calluna vulgaris</i>	0.82	0.001	0.038
<i>Carpinus</i>	3.55	0.181	0.042
Cerealia-t	1.85	0.146	0.06
<i>Corylus</i>	1.99	0.038	0.025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

529
 530

531
532
533
534

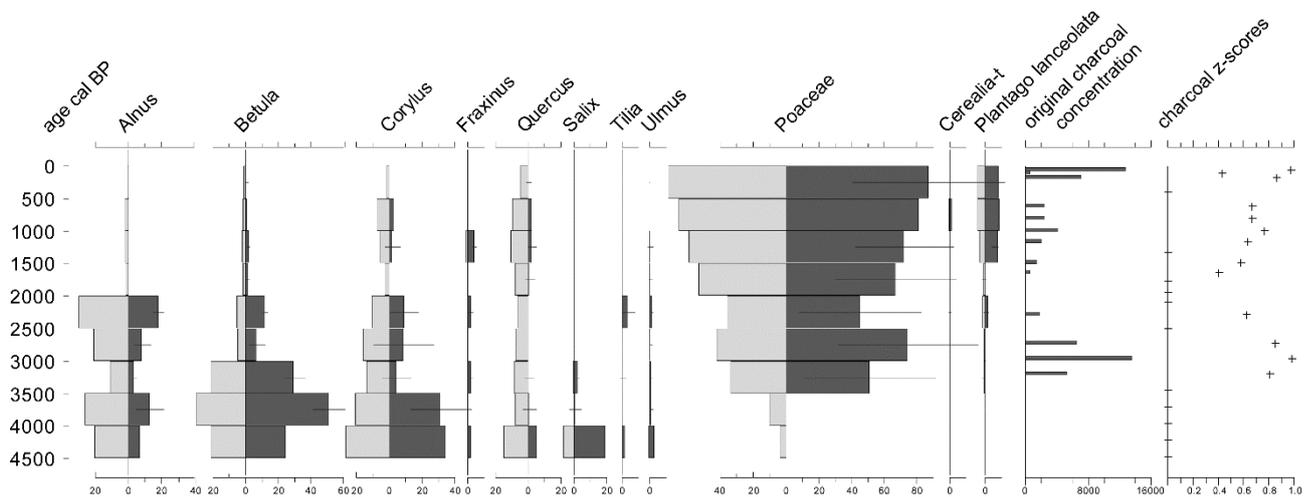
Appendix S2. Pollen and distance-weighted vegetation estimates for individual sites with charcoal records from Exmoor.

Figure S2-1: Pollen percentage (light grey bars) and distance-weighted vegetation estimates (dark grey bars) for key taxa from Swap Hill, Exmoor (original data from Davies et al. 2015).



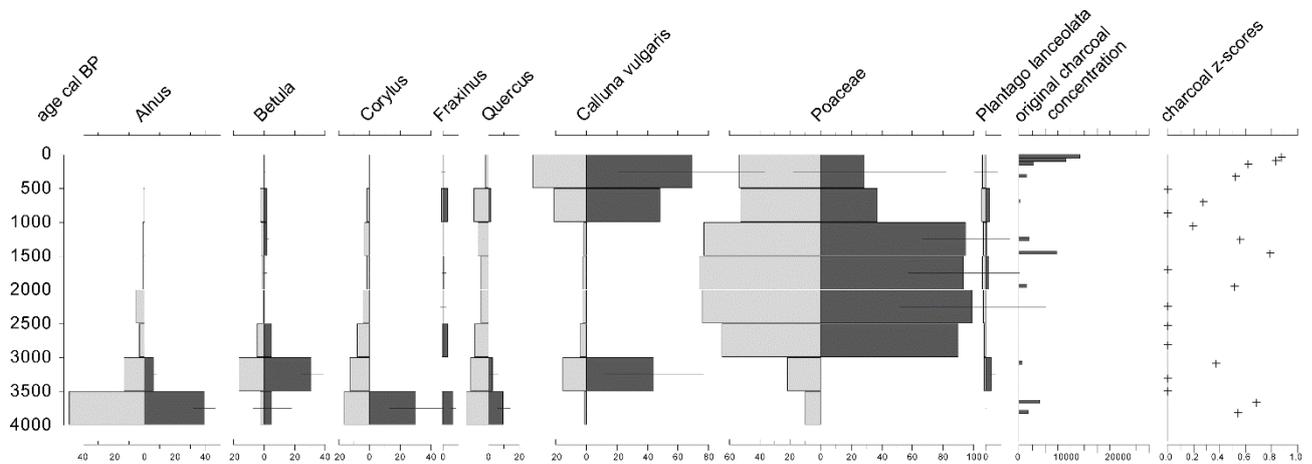
535
536
537
538
539

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



540
541
542
543
544

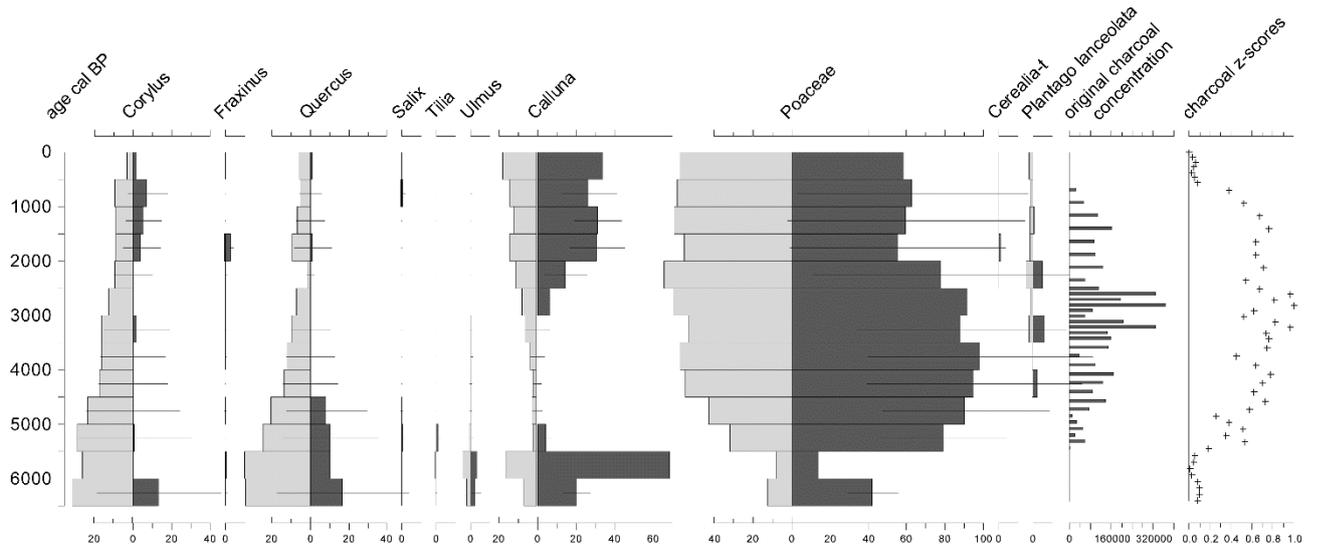
Figure S2-3: Pollen percentage (light grey bars) and distance-weighted vegetation estimates (dark grey bars) for key taxa from Larkbarrow, Exmoor (original data from Davies et al. 2015).



545
546
547
548

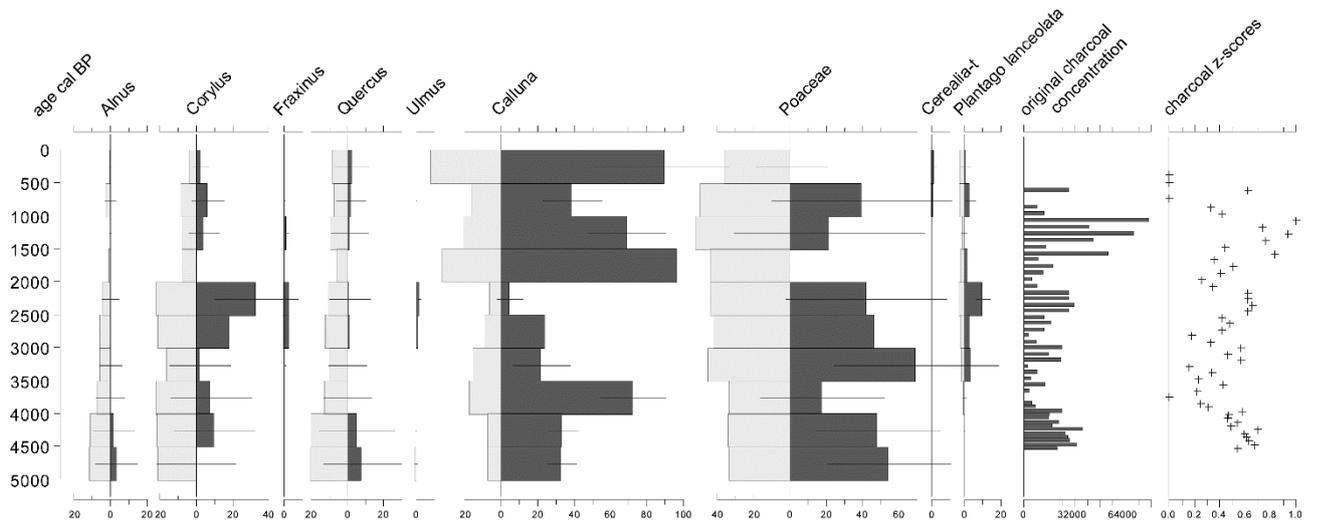
549
550

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).



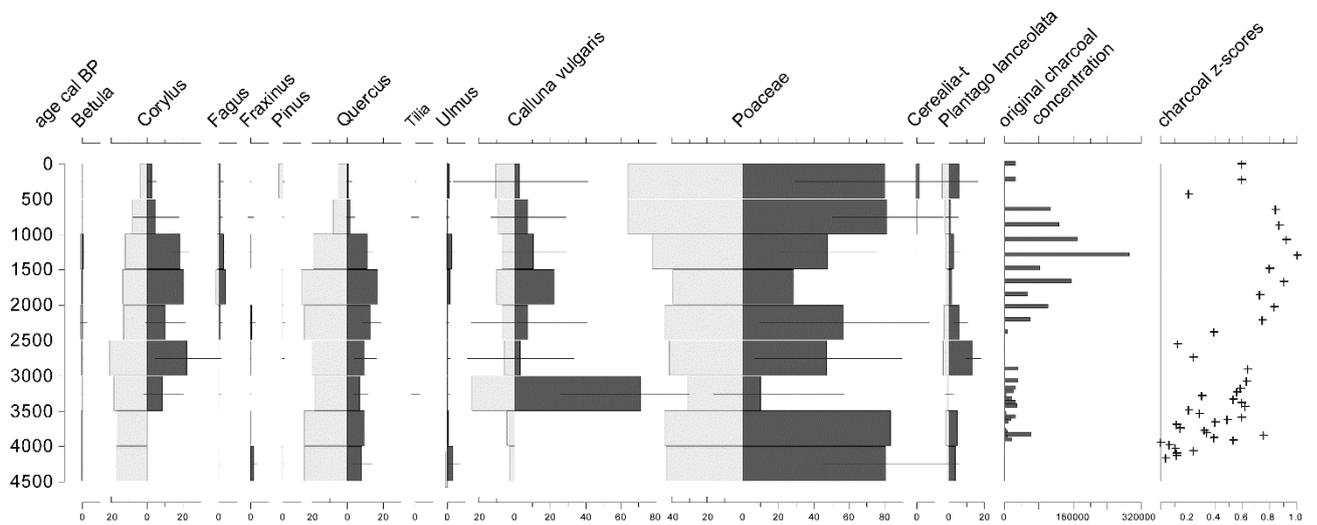
551
552
553
554

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).



555
556
557
558

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).

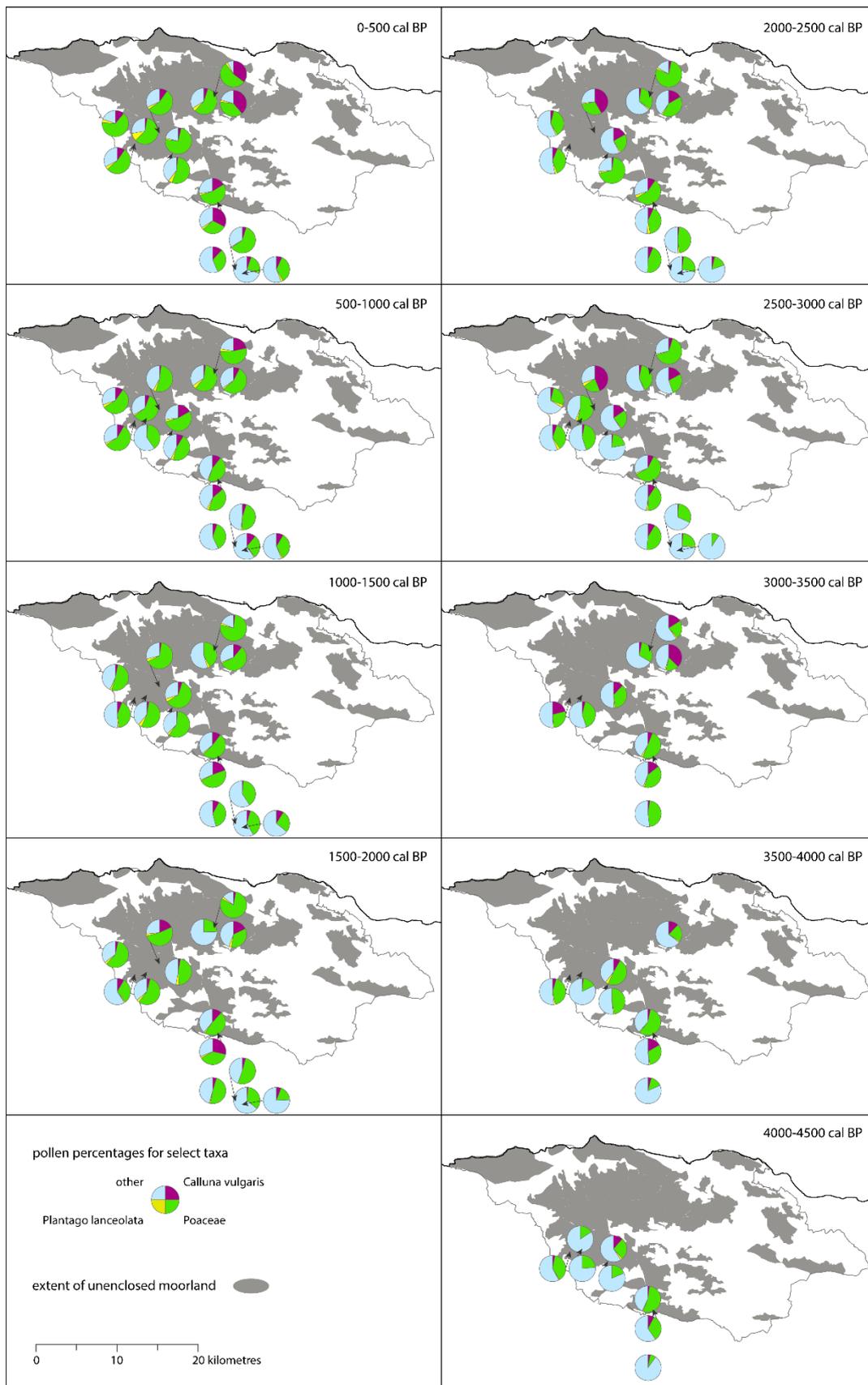


559
560

561
562
563
564
565

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

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 presented in Figure 3 (main article).



566