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13 **A long-term perspective on biomass burning in the Serra da Estrela, Portugal**

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23 **Abstract**

24 Fire is currently perceived as a major threat to ecosystems and biodiversity in the
25 mountains of the Mediterranean region. Portugal's highest mountain range, the Serra da
26 Estrela, is one of the country's most important protected areas and also the most fire-
27 prone. We present a ~14000-year fire history based on microscopic charred particles in
28 an infilled glacial lake to better understand the antiquity of biomass burning and its
29 effects on Mediterranean vegetation at the Atlantic margin. Results indicate the
30 continuous occurrence of fire in the Serra da Estrela over the period of the record. Two
31 periods of increased fire activity – around 12000–11000 calendar years before the
32 present (cal. a BP) and 3500–2500 cal. a BP – were accompanied by major vegetation
33 changes and followed by long periods of vegetation stabilisation. Cross-correlation
34 analyses reveal that post-fire succession consistently began with herbaceous vegetation,
35 followed by forest and shrubland stages. Past successional trends were often markedly

36 different to those observed at present. Holocene climatic changes, including shifts in the
37 North Atlantic Oscillation, played a pivotal role in the vegetation development and fire
38 history of the Serra da Estrela. In the late Holocene, human use of fire became a major
39 agent of vegetation change, accelerating the Holocene decline of forests.

40 **Keywords**

41 Fire history; Iberian Peninsula; Late Quaternary; Mediterranean; palaeoecology

42

43 **1. Introduction**

44 Fire is intrinsically linked to Mediterranean-type ecosystems. Mediterranean plant
45 species present a variety of adaptations to frequent fire, having insulating bark, fire-
46 enhanced germination or the ability to resprout after burning (Grove and Rackham,
47 2001; Allen, 2008). At the same time, uncontrolled fires in Mediterranean vegetation
48 may have catastrophic consequences for human health, economies, natural resources
49 and life itself, constituting major challenges for management authorities in fire-prone
50 regions worldwide (Bowman et al., 2011).

51 Fire is currently a major management issue in Portugal, as the country has the highest
52 density of ignitions in Southern Europe (Moreira et al., 2010). Fires are especially
53 frequent and widespread in the country's protected areas and are therefore considered to
54 pose a major threat to nature conservation and biodiversity (ICN, 2006). The frequency
55 of large fires in these areas appears to have increased during the last few decades, a
56 trend linked, in part, to abandonment of rural land and subsequent accumulation of fuel
57 (Moreira et al., 2010; Jansen, 2011).

58 Although fire is undoubtedly one of humankind's most ancient tools, our collective fear
59 of wildfires and their capacity for destruction has promoted an attitude of repulsion
60 rather than of understanding. Bowman et al. (2011) argue that we need to know much
61 more about the human dimension of fire regimes, both now and in the past, to reduce
62 the damage caused by fires. The importance of a long-term perspective is particularly
63 great when it comes to fire and the conservation of biodiversity (Tinner and
64 Kaltenrieder, 2005; Colombaroli et al., 2007, 2009; Gil-Romera et al., 2010). High-
65 diversity ecosystems are the product of long periods of evolution and diversification in
66 response to climate, soils, disturbances and plant–animal interactions. The histories of
67 fire and biodiversity in fire-prone ecosystems may be strongly intertwined.

68 Europe's mountains have been identified as environments with an elevated risk of
69 losing biodiversity in the face of predicted climate change (Gitay et al., 2002). This risk
70 could be especially high in the Mediterranean region, which is considered a “hyper-hot”
71 hotspot for plant diversity (Myers et al., 2000; Sanz-Elorza et al., 2003). In this paper,
72 we present a record of microscopic charred particles from lake sediments from the Serra
73 da Estrela mountain range, Portugal. The Serra da Estrela is a Natural Park and is
74 currently the most fire-prone natural area in Portugal (ICN, 2006). Our aims are to: i)
75 determine the antiquity of fires in the ecosystems of the Serra da Estrela, ii) compare the
76 charcoal record to pollen data to gauge fire's effects on the vegetation, and iii) examine
77 how relationships between fire, climate and humans developed through time.

78

79 **2. Regional setting**

80 The Serra da Estrela is an isolated granitic massif of the Central Iberian Cordillera
81 located in the centre-north of Portugal. Its peak, Torre, is the highest point in continental

82 Portugal (1993 m). The range is formed of Hercynian granites which intruded through
83 the surrounding Precambrian–Cambrian schist/greywacke sedimentary complex.
84 Subsequent tectonic movements and erosion have shaped the range, which, broadly
85 speaking, consists of two NE–SW-oriented plateaux, separated by the U-shaped Zêzere
86 Valley and surrounded by deeply incised glacial and fluvial valleys (Fig. 1; ICNB,
87 2007). Soils on the granitic plateaux are lithosols (rankers), with more developed
88 cambisols occurring over schist bedrock at lower elevations.

89 The climate of the Serra da Estrela is Mediterranean, transitional between hot-summer
90 and warm-summer types (Csa and Csb in the Köppen classification: AEMet and IM,
91 2011). The height of the range, combined with its uninterrupted interception of westerly
92 airstreams, lend the Serra da Estrela's climate a distinctly Atlantic character. At Penhas
93 da Saúde (1383 m), annual precipitation averages 2900 mm (ICNB, 2007). Average
94 annual temperature at the same elevation is 9.2°C (AEMet and IM, 2011), dropping to
95 3–4°C at the highest elevations (Mora et al., 2001). Snow cover on the high plateaux
96 may persist for up to 90 days (ICNB, 2007).

97 The Serra da Estrela, on account of its unique physical and biological characteristics,
98 constitutes a distinct biogeographical area within the Mediterranean region – the *Sector*
99 *Estrelense* of Costa et al. (1998). Three bioclimatic belts are distinguished (Pinto da
100 Silva and Teles, 1999; ICNB, 2007): 1) a **meso-mediterranean** zone below 900 m
101 elevation, in which remnant forests of oak (*Quercus rotundifolia*, *Q. suber* and *Q.*
102 *pyrenaica*) and Portuguese laurel (*Prunus lusitanica*) exist alongside maquis vegetation,
103 agricultural fields, vineyards, olive groves and extensive plantations of *Pinus pinaster*; a
104 **supra-mediterranean** belt between 900 and 1600 m, with remnant woods of *Quercus*
105 *pyrenaica*, chestnut groves, shrublands and some rye cultivation; and 3) an **oro-**
106 **mediterranean** belt above 1600 m, in which juniper scrub, mat-grass lawns, heaths,

107 pastures and aquatic communities are found (for further details, see Costa et al., 1998;
108 Pinto da Silva and Teles, 1999). The vascular plant flora of the Serra da Estrela is
109 diverse and includes some 7 endemics, 27 protected species and 92 species of
110 conservation interest; of these, 8 species are considered to be at imminent risk of local
111 extinction (Costa et al., 1998; Pinto da Silva and Teles, 1999; ICNB, 2007).

112 The vegetation history of the Serra da Estrela during the Late-Glacial and Holocene has
113 been relatively well studied through pollen analysis (Romariz, 1950; Janssen and
114 Woldringh, 1981; van den Brink and Janssen, 1985; van der Knaap and van Leeuwen,
115 1995, 1997). The latter authors produced a detailed, 14800-year vegetation history from
116 the Charco da Candieira site, based on analysis of 301 pollen samples and 30
117 radiocarbon dates. Six phases of vegetation development were distinguished:

118 LG: 14800 to 11600 calendar years before the present (cal. a BP) – Alternation
119 between steppic vegetation and open forests in response to Late-Glacial climatic
120 oscillations;

121 A: 11600 to 9500 cal. a BP – Development of xerothermic oak-dominated forests
122 under warm, dry climates and in the absence of human influence;

123 B: 9500 to 6400 cal. a BP – Spread of mesothermic forests under a cooler, moister
124 climate, with little human influence;

125 C: 6400 to 3400 cal. a BP – Forest dynamics affected by grazing and deforestation;

126 D: 3400 to 970 cal. a BP – Large-scale deforestation, followed by partial forest
127 recovery;

128 E: 970 to -40 cal. a BP – Complete deforestation of the Serra da Estrela,
129 accompanied by soil erosion, grazing, burning, agriculture and silviculture.

130 Biomass burning is acknowledged as an important cause of Holocene vegetation
131 changes in the Serra da Estrela, as suggested by the presence of macroscopic charcoal
132 layers in soil profiles (Braun-Blanquet et al., 1952) and sediments from peatbogs around
133 Lagoa Comprida (van den Brink and Janssen, 1985). The latter were dated to
134 approximately 3500 cal. a BP, corresponding to the period of large-scale deforestation
135 (van den Brink and Janssen, 1985). However, the spatial scale of the fires represented
136 by the charcoal layers could be much smaller than the scale of the vegetation changes,
137 as macroscopic charcoal particles are considered to represent local fires (Clark and
138 Royall, 1995).

139

140 **3. Material and methods**

141 Charco da Candieira (or Lagoa da Candeeira) is an infilled lake situated in a hanging
142 valley on the western side of the Zêzere Valley (40°20'37"N, 7°34'41"W). At 1400 m
143 elevation, it is the lowest of the glacial lakes of the Serra da Estrela. The site covers
144 approximately 0.8 hectares and its surface dries completely in summer (Costa et al.,
145 2004). The lake basin is considered to have been degraded by rye cultivation and
146 grazing until recently (Costa et al., 2004) and is today surrounded by rocky slopes and
147 scrub vegetation (with a prevalence of *Genista*, *Cytisus*, and *Erica* species, *Calluna*
148 *vulgaris* and *Juniperus communis*). A complete list of plant species in and around the
149 site is given by van der Knaap and van Leeuwen (1995).

150 The samples analysed in the present paper were collected in 1985 and subjected to
151 detailed palynological analysis (van der Knaap and van Leeuwen, 1995, 1997).

152 Subsequently the sample residues (in silicone oil) were archived in glass vials at Utrecht
153 University, the Netherlands. In 2011, we re-mounted the residues of all 293 samples

154 from the central lake core and counted microscopic charred particles at 400×
155 magnification on a Leitz Dialux microscope (we were unable to find the 8 ‘*Molinia*
156 tussock’ samples analysed by van der Knaap and van Leeuwen, 1995). Particles were
157 identified according standard criteria and grouped into two size-classes: 5–50 µm and
158 50–250 µm (see Blackford, 2000).

159 In quantifying microscopic charcoal, Finsinger and Tinner (2005) demonstrated that
160 counting 200 items (charcoal particles and *Lycopodium* marker spores) is sufficient to
161 obtain a result with a <5% error if the ratio between charcoal and marker spores lies
162 between 0.1 and 0.91. Due to the enormous quantity of charred particles in the
163 Candieira material (ratio between 7 and 1460), we adapted this method by counting the
164 total number of charcoal particles in each field-of-view until a total of at least 200
165 particles was reached; thereafter only fields-of-view and *Lycopodium* marker spores
166 were counted to reach a minimum of 50 spores. The number of fields-of-view was then
167 used to correct the charcoal counts and calculate charcoal concentrations (particles cm⁻³).
168

169 Prior to further analysis, a new age–depth model was produced for the Candieira record
170 using a Bayesian approach implemented in OxCal 4.1.7 (Markov chain Monte-Carlo
171 analysis: Bronk Ramsey, 2009) and based on the previously published radiocarbon
172 dates (van der Knaap and van Leeuwen, 1995, 1997). Model acceptability was assessed
173 using A_{model} and A_{overall} statistics (Bronk Ramsey, 2009).

174 Temporal relationships between charcoal and pollen abundance were analysed using
175 time-series analysis (Green, 1981), implemented in the program PAST 2.11 (Hammer et
176 al., 2001). Pollen proportions, charcoal concentrations and pollen and charcoal
177 accumulation rates were re-sampled at 48-year intervals (median sample resolution),

178 detrended using a Lowess smoother and the residuals cross-correlated. Sixteen of the
179 most common and indicative pollen taxa were analysed during four periods of relatively
180 constant sediment accumulation: 1500–3500, 4500–6500, 7500–9500 and 11500–13500
181 cal. a BP.

182 Multivariate numerical analysis of the charcoal and pollen data was performed using
183 Principal Components Analysis (PCA) and Detrended Correspondence Analysis (DCA)
184 in the program PC-Ord (McCune and Mefford, 1999). Stratigraphic diagrams were
185 drawn in Tilia 1.7.16 (Grimm, 1992).

186

187 **4. Results**

188 The age–depth model for the Candieira sequence is shown in Fig. 2. This model has
189 acceptability indices of 63.5% (A_{model}) and 63.3% (A_{overall}). Estimated errors (1σ) range
190 from 36 to 119 years for individual interpolated samples, with an average of 75 years
191 for the entire sequence. The model is very similar to the previously published models
192 (van der Knaap and van Leeuwen, 1995, 1997) and places the pollen-derived
193 Pleistocene–Holocene boundary (950 cm depth) between 12067 and 11703 cal. a BP
194 (2σ). Age ranges for each of the pollen zones are given in Fig. 2.

195 Charcoal concentrations are very high throughout the Candieira record (Fig. 3),
196 averaging 11 million particles per cm^3 of sediment and reaching peaks of up to 59
197 million. Considering that all of the data included in the global charcoal analysis of
198 Power et al. (2008) had less than 10 million particles per cm^3 of sediment, the Candieira
199 values are exceptionally high. The highest total charcoal concentrations and
200 accumulation rates are found in the pollen zone representing large-scale deforestation
201 (D, Fig. 3), while the lowest values are associated with the Late-Glacial (LG, Fig. 3).

202 Pollen percentages most correlated with total charcoal concentrations over the entire
203 record include *Erica arborea* (r : 0.58), *E. australis*-type (0.56), Poaceae (0.56),
204 *Plantago lanceolata*-type (0.52) and *Genista*-type (0.48). *Pinus* pollen, which is most
205 abundant in Late-Glacial sediments, is negatively correlated with charcoal (r : -0.53). If
206 the Holocene section of the record is considered alone, the strongest positive correlates
207 with charcoal are taxa representing herbs and shrubs (e.g. Poaceae, Asteraceae, *Erica*,
208 *Genista*-type and *Plantago lanceolata*-type), while the strongest negative correlates are
209 arboreal taxa (e.g. *Quercus*, *Salix*, *Taxus* and *Pinus*).

210 Candieira's microcharcoal assemblages are clearly dominated by smaller charcoal
211 particles (5–50 μ m). Larger particles (50–250 μ m) constitute only a small proportion of
212 the assemblages (average 4%), but exhibit a slightly different temporal trend to the
213 smaller particles. Peak accumulations of larger charcoal particles, with more than 10^5
214 particles per cm³ per year, occur at approx. 11400, 11300, 8100, 7300, 4550, 4450,
215 1550, 1300 and 1100 cal. a BP.

216 Time-series analysis of pollen and charcoal accumulation rates produced similar results
217 for different taxa, suggesting interdependence between the variables. Fine-scale
218 variations in sedimentation rates could explain this pattern (Colombaroli et al., 2009).
219 Cross-correlations of pollen percentages and charcoal concentrations are less affected
220 by sedimentation rates and a selection of these is shown in Fig. 4.

221 During the earliest period analysed (13500–11500 cal. a BP), Poaceae is positively
222 correlated with charcoal at zero lags, indicative of an immediate response. Grasses are
223 then succeeded by *Genista*-type, *Calluna* and *Alnus* at 1 lag (approx. 50 years after a
224 charcoal peak). *Juniperus* and *Genista*-type exhibit positive responses at 5 lags (approx.
225 250 years). *Pinus* responds positively at 11 lags (approx. 550 years).

226 From 9500–7500 cal. a BP, upland herbs respond positively to charcoal at 1 lag,
227 followed by *Alnus* at 2–3 lags, with *Betula* (not shown) at 2 lags. *Quercus*, which
228 dominates the pollen spectra of this period, responds positively to charcoal at 5–6 lags
229 and Poaceae follows at 7–8 lags, accompanied by *Genista*-type. Herbs, *Erica*, *Calluna*
230 and *Alnus* respond collectively at 10–12 lags and *Quercus* exhibits a strong positive
231 response at 14–16 lags.

232 From 6500–4500 cal. a BP, upland herbs exhibit a strong positive response to charcoal
233 at zero lags, mirrored by the strong negative responses of *Quercus* and *Cerealia*-type.
234 *Erica* and Poaceae show significant negative responses at 1 lag, while *Pinus* and *Betula*
235 both produce significant positive responses at 1–3 lags. An inversion of this pattern is
236 observed after 6 lags (approx. 300 years), following a positive *Genista*-type response at
237 5 lags. A strong *Juniperus* response appears at 13 lags.

238 From 3500–1500 cal. a BP, *Pinus* and *Quercus* no longer exhibit significant responses
239 to charcoal over the first 10 lags, whereas upland herbs and *Cerealia*-type show a
240 significant positive response at 1–2 lags. As in the previous period, *Erica* and Poaceae
241 respond negatively to charcoal at 1 and 2 lags respectively. *Alnus* has a significant
242 positive response at 3–5 lags, followed by *Juniperus* and *Pteridium* at 6 lags (not
243 shown), *Calluna* and *Genista*-type at 7–8 lags and Poaceae at 8–9 lags.

244 Both PCA and DCA produced similar results on the first axis, as shown in Fig. 6. DCA
245 axis 1 is influenced by the relationship between negatively correlated taxa such as
246 *Erica*, *Alnus*, *Ranunculus*, *Plantago lanceolata*-type and *Pteridium* on the one hand, and
247 positively correlated taxa like *Pinus*, *Artemisia*, *Calluna*, *Juniperus* and
248 Chenopodiaceae on the other. PCA axis 1 is negatively correlated with *Quercus*,
249 *Pteridium* and *Taxus*, while positive correlates are almost identical to those of the DCA.

250

251 **5. Discussion**

252 *5.1. Problems of interpretation*

253 Despite the clear evidence for repeated fires in the Candieira record, some important
254 uncertainties must be taken into account. Firstly, the source-area of microscopic
255 charcoal is difficult to define and may amount to hundreds to thousands of metres,
256 depending on particle size, wind velocity and site characteristics (Whitlock and Larsen,
257 2001). It is difficult to say whether the fires recorded in the Candieira sediments
258 represent local fires in the lake catchment or more regional events. The prevalence of
259 small particles ($<50\mu\text{m}$) suggests that most of the charcoal derives from regional fires,
260 although over-representation of fine particles can also be caused by catchment processes
261 and sample preparation. Secondly, the transition from lake sediment to wetland
262 sediment at 175-cm depth adds further uncertainty to the source of the charcoal. Lake
263 sediments probably incorporate a greater regional component than wetland sediments
264 due to mixing processes in the water column. Wetland vegetation may directly
265 contribute charcoal to the sediment when the vegetation is burnt and may also trap
266 charred particles amongst its foliage (Tolonen, 1986; Whitlock and Larsen, 2001).
267 Increases in sediment bulk density (Fig. 3) could be an indication of erosion events,
268 which have the potential to introduce secondary charcoal into the sedimentary record.
269 Finally, some fire peaks may have been missed because sediment sampling was not
270 contiguous.

271

272 *5.2. Antiquity of biomass burning in the Serra da Estrela*

273 Braun-Blanquet et al. (1952, p. 319) speculated that soil charcoal in the Serra da Estrela
274 represented biomass burning from “hundreds, if not thousands, of years ago”. Our data
275 from Charco da Candieira confirm that fires have occurred with regularity since at least
276 14,000 cal. a BP. Indeed, even the name ‘Candieira’ is thought to relate to the deliberate
277 burning of the vegetation by pastoralists, hunters and charcoal producers (Batista,
278 1988).

279 Two major shifts in fire regime can be inferred from the charcoal record; the first at the
280 beginning of the Holocene (~12000–11000 cal. a BP) and the second in the mid-late
281 Holocene (~3500–2500 cal. a BP). During each of these periods, charcoal accumulation
282 in Candieira increased quite dramatically, followed by a slight decline and subsequent
283 establishment of a new equilibrium. Both shifts are accompanied by major changes in
284 the palaeovegetation, demonstrating a long-standing link between fire incidence and
285 vegetation change in the Serra da Estrela.

286 Low fire activity around the Serra da Estrela during the steppe vegetation phase of
287 the Younger Dryas is consistent with the interpretation of low fuel availability on the
288 Iberian Peninsula during stadial periods (Daniau et al., 2007). Holocene fire histories
289 from the SW Mediterranean region indicate that fire activity was relatively high during
290 the early Holocene, declined during the mid Holocene and increased again after ~5000
291 cal. a BP (Carrión, 2002; Tinner et al., 2009; Vannièrè et al., 2011; Carrión et al., 2012).
292 The Candieira fire history shares aspects of these trends and most closely resembles
293 records from sites in SE Spain and the west coast of Sicily, especially in relation to the
294 major increase in fire activity between ~3500–2500 cal. a BP (Carrión et al., 2007;
295 Tinner et al., 2009; Gil-Romera et al., 2010).

296 Unlike most fire histories from the Mediterranean region, the Candieira record gives no
297 indication of millennia-long periods in the mid Holocene when fire activity subsided.
298 Charcoal is constantly present in relatively high concentrations. There are, however,
299 shorter periods from which major charcoal peaks are lacking, i.e. approx. 10500–10000,
300 9000–8500, 7000–6500, 4500–4000, 2500–2000 cal. a BP. These may simply be
301 sections of the core in which charcoal peaks were missed, although the regular spacing
302 of these intervals could point to an underlying fire cycle. The 4500–4000 cal. a BP
303 reduction is recorded throughout the Mediterranean region (Vanni re et al., 2011).

304

305 ***5.3. Fire’s impact on the vegetation***

306 Given the antiquity and recurrence of biomass burning in the Serra da Estrela, it is
307 likely that fire has shaped the vegetation to a substantial degree. As noted above, the
308 two most important vegetation changes – early Holocene afforestation and mid-late
309 Holocene deforestation – are accompanied by major shifts in fire regime and arrival at
310 new metastable states (sensu Oldfield, 1983).

311 On millennial timescales, correlations between charcoal and pollen can reveal the
312 response of vegetation structure to fire activity (e.g. Tinner et al., 2009). Heathland taxa
313 are positively correlated with charcoal in the Candieira record overall, whereas
314 woodland taxa are negatively correlated, suggesting a strong link between Holocene fire
315 activity, forest decline and heathland development in the Serra da Estrela. Similar
316 relationships are observed in other mountain ranges of the Iberian Peninsula (Carri n et
317 al., 2007; Morales-Molino et al., 2011).

318 On shorter timescales of hundreds of years, the interactions between charcoal and pollen
319 abundances may hold a great deal of ecological information on plant species responses

320 to fire (Green, 1981; Walker, 1982; Colombaroli et al., 2007, 2009). The Candieira
321 pollen record is sufficiently detailed and well-dated to allow close examination of
322 population dynamics within discrete sections of the Late-Glacial and Holocene.

323 In interpreting the time-series results (Fig. 4), it is important to take into consideration
324 the potential source-area of the charcoal and pollen. *Pinus*, *Olea* and *Alnus* pollen in the
325 Candieira sediments probably derive mostly from lower elevations several kilometres
326 from the site, whereas *Quercus*, *Taxus* and *Cerealia*-type may come from somewhat
327 closer sources, and *Erica*, *Calluna*, *Genista*-type, *Pteridium* and the dominant upland
328 herbs are thought to come from an area ranging from tens of metres to a few kilometres
329 around the site (van der Knaap and van Leeuwen, 1995). The origin of the charcoal is
330 more difficult to define, though the prevalence of small particles suggests a
331 predominantly regional source.

332 In the four periods studied by time-series analysis, upland herbs appear to be the first
333 taxa to respond positively to a fire event, as indicated by positive correlations between
334 charcoal and pollen abundance at 0 or 1 lag (each lag representing a period of
335 approximately 50 years). The only exception to this is during the Late-Glacial, when the
336 correlation is positive but non-significant. The ‘upland herbs’ group includes non-
337 wetland taxa and is dominated by *Rumex acetosella*-type and various Apiaceae,
338 Asteraceae, Fabaceae and Liliaceae, which feature in post-fire vegetation succession in
339 the Serra da Estrela (Jansen, 2011). Poaceae were excluded from the group because
340 grasses occur in the wetland vegetation of Charco da Candieira (van der Knaap and van
341 Leeuwen, 1995).

342 *Betula* and *Alnus*, which are both pioneer taxa (van der Knaap and van Leeuwen, 1995),
343 feature prominently in Holocene post-fire successions, usually appearing shortly after

344 the initial appearance of herbfields. Fire is unlikely to be the main reason for the long-
345 term *Betula* decline in the Serra da Estrela (cf. van den Brink and Janssen, 1985). *Betula*
346 is thought to have occurred along mountain streamsides and near the margins of
347 mountain lakes (including Charco da Candieira), while *Alnus* probably occurred in
348 lower-elevation forests and riparian zones (van der Knaap and van Leeuwen, 1995).

349 In the Holocene periods analysed, *Erica* often responds negatively to fire over the first 4
350 lags (approx. 200 years). This response is unexpected, as heaths are important in post-
351 fire succession in the Serra da Estrela today (Jansen, 2011). Macrofossil evidence
352 demonstrates that *Erica arborea* was present near Charco da Candieira from as early as
353 8800 cal. a BP, despite low pollen representation at that time (van der Knaap and van
354 Leeuwen, 1995). Pollen filtration (Tauber, 1967) by dense *Salix* and *Betula* thickets that
355 developed around the site after fire could explain this phenomenon, as *Erica* species are
356 insect-pollinated and have poor pollen-dispersal capacity. It is also conceivable that
357 low-statured *Erica* shrubs were at a competitive disadvantage to taller deciduous species
358 (such as *Quercus* and *Betula*) and occupied marginal habitats until complete
359 deforestation took place in the late-Holocene (phase E).

360 Positive *Erica* and *Genista*-type responses at longer lag times (>6 lags) in some periods
361 could suggest that these taxa are favoured by repeated burning, considering that major
362 charcoal peaks occur approximately 300 years apart (a similar frequency of microscopic
363 charcoal peaks was observed during the mid-Holocene at 1530 m elevation in the Sierra
364 de Gádor in Almeria: Carrión et al., 2003, 2012). Alternatively, ecological succession to
365 treeless vegetation may occur after the senescence of oak forests.

366 Oaks (deciduous *Quercus*) generally respond negatively to fire in the short term, but
367 recover long after fire (approx. 250 years), exhibiting the classic ‘climax’ response (see

368 Green, 1981). However, oak behaviour differs from period to period. The significant
369 pre-fire increase at 11500–13500 and 1500–3500 cal. a BP could suggest that fire
370 occurrence was partly related to the accumulation of biomass. In the early-mid
371 Holocene, when *Quercus* was dominant, initial post-fire recovery is only significant in
372 the earlier phase (B: 7500–9500 cal. a BP) and post-fire decline is only significant in the
373 later period (C: 4500–6500 cal. a BP). A second phase of significant oak recovery is
374 observed after a much longer duration – approx. 700 years in phase B and 800 years in
375 phase C. No recovery is observed in phase D. Oak forests clearly had a greater capacity
376 for post-fire regeneration during the early Holocene. Fire and grazing pressure are major
377 factors inhibiting oak forest development in the Serra da Estrela today (Jansen, 2011).
378 Deciduous oaks tend to be more susceptible to post-fire mortality (Catry et al., 2010)
379 and less tolerant of grazing than evergreen oaks (Grove and Rackham, 2001). Under
380 these impacts, the Candieira area's late-successional vegetation may have switched
381 from climax oak forest to plagioclimax broom scrub (Fig. 4).

382 The role of *Pinus* in the Candieira record is poorly understood because much of its
383 pollen could have arrived from distant pine populations via long-distance pollen
384 transport (van der Knaap and van Leeuwen, 1995). Reduction of oak forest cover would
385 therefore increase the proportion of long-distance *Pinus* pollen, explaining why negative
386 oak responses to fire are synchronous with positive pine responses (Fig. 4) and vice
387 versa. The only definitive evidence for pine populations around Charco da Candieira
388 comes in the form of macrofossils and stomata of *Pinus* cf. *sylvestris*, which reached its
389 upper altitudinal limit in the middle of phase LG but died out completely after the Late-
390 Glacial (van der Knaap and van Leeuwen, 1997). The *Pinus sylvestris* decline
391 throughout Portugal is attributed to an unfavourable Holocene climate and the influence
392 of fire (Figueiral and Carcaillet, 2005). A few pines (possibly *P. pinaster*) entered into

393 forest dynamics in the period 4500–6500 cal. a BP, constituting an intermediate
394 successional stage between herbfields and scrub vegetation.

395 The post-fire response of grasses shows remarkable consistency through the Holocene.
396 Poaceae macrofossils were found throughout Candieira’s Holocene sediments,
397 suggesting that grasses were part of the wetland vegetation (van der Knaap and van
398 Leeuwen, 1995). Grasses may have been shaded out by the post-fire development of
399 deciduous vegetation, as indicated by the similarity between Poaceae and *Erica*
400 responses to fire through the Holocene (Fig. 4).

401 Cereal pollen, which appears sporadically before 6000 cal. a BP and frequently
402 thereafter, responded to fire in a similar fashion to the other Poaceae in the period 4500–
403 6500 cal. a BP, but exhibits a completely different behaviour in the period 1500–3500
404 cal. a BP (Fig. 4). The changing response of cereal pollen to fire in more recent
405 millennia is likely to relate to agricultural practices (see Section 5.4).

406 Post-fire vegetation succession in the present-day broom scrub communities of the Serra
407 da Estrela has been studied by Jansen (2011) using a botanical approach. His model,
408 which includes supra-mediterranean (middle elevation) and oro-mediterranean (higher
409 elevation) variants, is shown in Fig. 5 alongside the successional trends deduced from
410 time-series analysis of the Charco da Candieira pollen and charcoal data. It must be
411 remembered that these data are a palynologically biased picture of the vegetation in
412 which some taxa are over-represented (e.g. *Alnus*), while others are not represented at
413 all (e.g. *Prunus lusitanica*). Also, the pollen-to-charcoal comparison represents response
414 to fire, not necessarily the plant community that develops after fire. Nevertheless, there
415 is a striking similarity between the modelled post-fire trajectory for the oro-
416 mediterranean zone and the Late-Glacial pollen response.

417 The Holocene stages are influenced by the over-representation of wind-pollinated taxa
418 such as *Betula* and *Alnus*, as well as the under-representation of insect-pollinated *Erica*
419 and *Genista*. Uncertainty concerning the source of Poaceae pollen (wetland vs upland
420 vegetation) in the Candieira record means that Jansen's (2011) initial stage of 'open
421 grasslands' is represented palynologically by upland herbs. Pollen data from the early
422 and late Holocene indicate subsequent succession to a pioneer birch-woodland stage
423 that is not observed in the present day. *Betula alba* is associated with *Quercus*
424 *pyrenaica* forests (Pinto da Silva and Teles, 1999) and may have played a much more
425 important role in the supra-mediterranean zone prior to complete deforestation. The
426 subsequent *Alnus* stage is also not observed at present and reflects recovery of riparian
427 forest, probably at lower altitudes. In the early Holocene, this stage is followed by oak
428 forests, while in the late Holocene a succession to juniper scrub is observed (similar to
429 Late-Glacial dynamics). In both cases, scrub, grassland or heathland vegetation appears
430 as a final stage, either because of recurrent fire or because of the senescence of oak and
431 juniper communities. The mid-Holocene (4500–6500 cal. a BP) successional trend
432 deduced from pollen is quite different, involving a pine-woods stage not observed at
433 present. Subsequent succession to broom scrub and then heathland is in good agreement
434 with the Jansen (2011) model.

435 These observations indicate that grassland, scrub and heathland communities are
436 important in the long-term vegetation dynamics of the Serra da Estrela and are not
437 simply the product of recent deforestation. Moreover, oak forest requires hundreds of
438 years to recover after fire and it seems that its capacity for recovery has declined
439 through the Holocene. Oak was dominant in the early Holocene when vegetation
440 dynamics were largely governed by successional cycles. Changed climatic conditions
441 and disturbance regimes have favoured the expansion of treeless vegetation.

442 While the Candieira fire history does not extend into more recent times, vegetation
443 changes during the last thousand years (i.e. further expansion of heathland, felling of
444 oak woods, rye cultivation and establishment of pine, eucalypt and olive plantations; see
445 van der Knaap and van Leeuwen, 1995) have again altered the relationship between fire
446 and vegetation. While the response of individual taxa to fire appears to be quite
447 conservative, as indicated by similar responses in different Holocene periods, the
448 vegetation as a whole may respond to changed disturbance regimes in ways that are
449 difficult to predict.

450 The good news for plant biodiversity is that fire is not a new disturbance in the Serra da
451 Estrela and today's indigenous flora is relatively resilient to burning. Our observations
452 suggest that policies of total fire exclusion (e.g. ICNB, 2009) are unsustainable in the
453 Serra da Estrela and emphasis should instead be placed on reducing the damage caused
454 by large-scale wildfires, which have deleterious effects on habitats and biodiversity
455 (Jansen, 2011). Prescribed fire regimes can play a pivotal role in biodiversity
456 management, but must be supported by ecological knowledge and ecosystem
457 monitoring (Allen, 2008).

458

459 ***5.4. Interactions between fire, climate and humans***

460 The Holocene fire history of the Mediterranean region is regarded primarily as a
461 reflection of climatic changes (Carrion, 2002; Vanni re et al., 2011; Lionello, 2012; cf.
462 Tinner et al., 2009).

463 Interpretation of pollen records from Portugal has given rise to two opposing models for
464 the Holocene palaeoclimate. Based on numerous pollen profiles from lakes along the
465 west coast of Portugal, Queiroz (1999) proposed a wet early Holocene, dry mid

466 Holocene and hyper-wet late Holocene. Conversely, van der Knaap and van Leeuwen
467 (1995) interpreted the Candieira record as indicating a dry early Holocene and wet mid-
468 Holocene. Interpretation of palaeovegetation in strictly climatic terms is rendered
469 difficult by the influence of sea-level changes (‘inundation phases’) at the coastal sites
470 (Mateus, 1992; Queiroz, 1999; Queiroz and Mateus, 2004) and prehistoric human
471 impacts on the vegetation throughout the region (Mateus, 1992; van der Knaap and van
472 Leeuwen, 1995; Queiroz, 1999). In addition, Mediterranean climates are characterised
473 by their seasonality, an aspect which has not hitherto emerged from the Portuguese
474 palynological data.

475 Numerical analyses of the Candieira pollen data (Fig. 6) demonstrate that the vegetation
476 history reflects the major climatic fluctuations of the Late-Glacial – including the Older
477 Dryas (Heinrich event 1), Bølling–Allerød interstadial (Greenland interstadial 1) and
478 Younger Dryas – although the radiocarbon age model here appears too young (van der
479 Knaap and van Leeuwen, 1997). Holocene vegetation changes are more difficult to
480 interpret. The PCA result, which closely follows oak pollen percentages, bears some
481 resemblance to the reconstructed winter-temperature curve from Lake Tigalmamine in
482 Morocco (Cheddadi et al., 1998) and possibly reflects the sensitivity of *Quercus* species
483 to winter temperatures (Colombaroli et al., 2009). The DCA result takes a different
484 course that appears to track the overall trend in increasing warm-season sea-surface
485 temperatures off West Africa (deMenocal et al., 2000). This DCA axis is influenced by
486 the gradual increase in pollen from heathland species, such as *Erica* and *Genista*, which
487 have morphological adaptations to temperature variations, desiccating winds and
488 seasonal drought, as well as the ability to resprout after fire (Jansen, 2011). Temperature
489 might be expected to register palaeoecologically in a mountain area such as the Serra da
490 Estrela, although prehistoric human impacts on the vegetation may potentially override

491 the climatic signal. Gil-Romera et al. (2010) suggest that the early Holocene was
492 characterised by reduced temperature seasonality in SE Iberia, in agreement with the
493 trends reconstructed here.

494 Another climatic signal of interest is the increase in pollen accumulation rates from
495 approximately 13800 to 9700 cal. a BP (Fig. 6). High pollen concentrations during this
496 period are also observed in a marine record from the Alboran Sea (Fletcher and Sánchez
497 Goñi, 2008). These were interpreted as a reflection of increased biomass in response to
498 precession-driven changes in seasonality (Fletcher and Sánchez Goñi, 2008). The
499 development of the Serra da Estrela's xerothermic forests during the early Holocene
500 may be linked to this precession pattern, which has had a pervasive influence on the
501 Quaternary vegetation history of the Mediterranean region (Tzedakis, 2007; Gil-Romera
502 et al., 2010). Precession, however, has no discernable impact on the fire history from
503 Candieira.

504 Likewise, the Candieira pollen record provides no clear signal of Holocene aridity,
505 possibly because the Serra da Estrela rarely experiences drought in the usual
506 Mediterranean sense of the term. Independent evidence for aridity coincident with
507 increased late-Holocene fire activity in the Serra da Estrela comes from the multi-proxy
508 quantitative palaeoclimatic reconstructions from the Azores (Björck et al., 2006), pollen
509 data from southern Portugal (Fletcher et al., 2007), lowered lake levels in southern
510 Spain and Northern Africa (Lamb and van der Kaars, 1995; Reed et al., 2001; Carrión,
511 2002), as well as widespread sedimentation hiatuses in interdunal lakes in western
512 Portugal (Queiroz and Mateus, 2004). A drier climate may have initiated paludification
513 of Charco da Candieira itself, which switched from a lake to a seasonally dry pond
514 around 3400 cal. a BP (van der Knaap and van Leeuwen, 1995). Arid phases peaking at
515 the beginning of the Holocene (palaeovegetation phase A) and between ~3500–2500

516 cal. a BP (phase D) may have been the trigger for major fires in the region and the
517 subsequent reorganisation of the vegetation of the Serra da Estrela (Fig. 6). Major
518 increases in fire activity are registered across the Mediterranean zone of the Iberian
519 Peninsula between ~3500–2500 cal. a BP, indicating a coherent regional pattern
520 (Stevenson and Harrison, 1992; Carrión, 2002; Carrión et al., 2007, 2012; Gil-Romera
521 et al., 2010; Vannièrè et al., 2011; see also Rius et al., 2011).

522 Cyclic aridity phases in SW Europe are thought to be closely linked to variations in the
523 North Atlantic climate system (Reed et al., 2001; Davis and Stevenson, 2007; Fletcher
524 et al., 2007; Vannièrè et al., 2011), specifically the cooling events identified by Bond et
525 al. (1997). In the Candieira record, major peaks in large charcoal particles at approx.
526 11400–11300, 9700, 8100, 4500, 2700 and 1300 cal. a BP overlap temporally (2σ) with
527 ‘Bond events’ at approx. 11100, 9400, 8100, 4200, 2800 and 1400 cal. a BP,
528 respectively (Fig. 6). The reason that these events registered as local fires, rather than
529 the regional fires indicated by smaller charcoal particles, may be that North Atlantic
530 cooling events had a greater effect on the Serra da Estrela’s supra- and oro-
531 mediterranean belts than on the lower elevations due to orographic interception of
532 westerly air-streams.

533 While Holocene climatic changes may have been the driving force behind vegetation
534 change and fire incidence in the Serra da Estrela, human impacts cannot be disregarded,
535 especially in more recent millennia. Van der Knaap and van Leeuwen (1995) used
536 palynological indicators of anthropogenic activity and forest disturbance in the
537 Candieira record to place the earliest signs of human activity in phase B (9500–6400
538 cal. a BP). The first *Cerealia*-type pollen occurs in the Candieira record at ~10000 cal. a
539 BP and it is present almost continuously from 8500 to 7400 cal. a BP. Considering that
540 the earliest agricultural settlements in Portugal date to around 7400 cal. a BP (Zilhão,

541 2001; Zeder, 2008), these occurrences may reflect pollen of steppe grasses (van der
542 Knaap and van Leeuwen, 1995). Other traditional anthropogenic indicators, such as
543 *Rumex acetosella*-type and *Plantago lanceolata*-type (Behre, 1981), are not particularly
544 helpful in the Candieira record as they occur throughout the Late-Glacial and Holocene.

545 Sheep and goat herding is the traditional mainstay of the Serra da Estrela's economy.
546 Grazing's direct impact on the Serra da Estrela's vegetation and fire history is unknown;
547 along with fires lit by herders to promote pasture, it is probably quite significant (Braun-
548 Blanquet et al., 1952; van der Knaap and van Leeuwen, 1995). The regular occurrence
549 of spores from dung-inhabiting fungi (e.g. *Sporormiella* and *Podospora*: van Geel and
550 Aptroot, 2006) in the Candieira material demonstrates that grazing by wild or domestic
551 animals has a long history in the Serra da Estrela, extending back to the Late-Glacial.

552 The earliest archaeological site in the Serra da Estrela, Buraco da Moura de São Romão,
553 is located ~9km WNW of Charco da Candieira on the western flank of the mountains
554 and contains Neolithic, Chalcolithic, Bronze Age and Medieval levels (Senna-Martinez,
555 1993). Analysis of Bronze-Age faunal remains from the 2nd millennium BC provides
556 convincing evidence that pastoral activities, especially sheep and cattle herding, were
557 practised at this time (Cardoso et al., 1998), coincident with widespread deforestation in
558 the Serra da Estrela (van den Brink and Janssen, 1985; van der Knaap and van
559 Leeuwen, 1995). Regional aridity between ~3500–2500 cal. a BP may have intensified
560 occupation of better-watered mountain areas, leading to the clearance of forests for
561 pasture, or a population increase led to the same outcome.

562 Establishment of Roman roads and settlements in the Serra da Estrela is marked
563 palaeoecologically by the first appearance of *Castanea* pollen in the Candieira record
564 around 2000 cal. a BP. Roman-era activity was concentrated at the foot of the

565 mountains, far from the central plateaux (Alarcão, 1993), and no drastic changes are
566 evident in the pollen record from Charco da Candieira.

567 The same cannot be said of the Medieval, a period of rapid population growth that led to
568 the expansion of heathland and virtual disappearance of forests. Historical sources attest
569 to the importance of sheep grazing and rye cultivation at higher elevations (Batista,
570 1988), including in the surroundings of Charco da Candieira (Costa et al., 2004). Cereal
571 cultivation was often practised on common land during the Medieval, alongside animal
572 husbandry, charcoal production, firewood collection, timber harvesting and hunting;
573 deliberate agro-pastoral fires (*queimadas*, in Portuguese) were associated with many of
574 these activities (Batista, 1988).

575 Substantial amounts (>15%) of *Cerealia*-type pollen in the more recent Candieira
576 sediments are a clear testament to this local activity (Fig. 6). Fire and cereals are
577 strongly related in the period 1500–3500 cal. a BP, with a significant expansion of
578 cereal pollen 50–100 years after fire. This distinctive response is most likely to be a
579 reflection of prehistoric *queimadas*, possibly in the direct surroundings of Charco da
580 Candieira. Recent increases in pine and olive pollen, on the other hand, come from the
581 establishment of extensive plantations in the valleys and lowlands (van der Knaap and
582 van Leeuwen, 1995).

583 In summary, long-term trends in the fire history from Charco da Candieira can be
584 explained largely by Late-Glacial and Holocene climatic changes, particularly cycles of
585 aridity associated with shifts in the North Atlantic Oscillation. Fire was ever-present in
586 the Serra da Estrela, but, in the hands of prehistoric and historic human populations, it
587 became a major agent of vegetation change, accelerating the Holocene decline of
588 forests.

589 **6. Conclusions**

590 Ever since the ice cap and glaciers retreated, fire has always been an important
591 component of the ecosystems of the Serra da Estrela. Fire has directly shaped the
592 composition of the mountain's plant communities. Current trends toward increasing fire
593 incidence in the Serra da Estrela present immediate management difficulties, but are
594 nothing new when viewed from a long-term perspective. The Serra da Estrela has
595 witnessed several periods in the past in which fire incidence appears to have increased
596 dramatically due to climatic factors. In each case, the period of increasing fire activity
597 was followed by a much longer period of stabilisation. Although fire itself does not
598 seem to pose a threat to the region's plant biodiversity, the variety of vegetation
599 responses to fire in the past suggests that changes in climate, land-use and disturbance
600 regimes could have unpredictable outcomes in the future. For this reason it is important
601 to develop a better understanding of fire in the mountains of the Iberian Peninsula, both
602 now and in the historical past.

603

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610 **References**

611 Agencia Estatal de Meteorología (AEMet), Insitituto de Meteorologia (IM), 2011.
612 Iberian Climate Atlas: air temperature and precipitation (1971–2000). Ministerio
613 de Medio Ambiente y Medio Rural y Marino.

614 Alarcão, J., 1993. Arqueologia da Serra da Estrela. Instituto da Conservação da
615 Natureza, Parque Natural da Serra da Estrela, Manteigas.

616 Allen, H.D., 2008. Fire: plant functional types and patch mosaic burning in fire-prone
617 ecosystems. *Progress in Physical Geography* 32: 421–437.

618 Batista, J.D.L., 1988. O povoamento da Serra da Estrela de 1055 a 1223 e outros
619 estudos. Instituto de Cultura e Língua Portuguesa & Parque Natural da Serra da
620 Estrela, Lisboa/Manteigas.

621 Behre, K.-E., 1981. The interpretation of anthropogenic indicators in pollen diagrams.
622 *Pollen et Spores* 23: 225–245.

623 Berger, A.L., 1978. Long-term variations of caloric insolation resulting from the Earth's
624 orbital elements. *Quaternary Research* 9: 139–167.

625 Björck, S., Rittenour, T., Rosén, P., França, Z., Möller, P., Snowball, I., Wastegard, S.,
626 Bennike, O., Kromer, B., 2006. A Holocene lacustrine record in the central
627 North Atlantic: proxies for volcanic activity, short-term NAO mode variability,
628 and long-term precipitation changes. *Quaternary Science Reviews* 25: 9–32.

629 Blackford, J.J., 2000. Charcoal fragments in surface samples following a fire and the
630 implications for interpretation of subfossil charcoal data. *Palaeogeography,*
631 *Palaeoclimatology, Palaeoecology* 164: 33–42.

- 632 Bond, G., Showers, W., Cheseby, M., Lotti, R., Almasi, P., deMenocal, P., Priore, P.,
633 Cullen, H., Hajdas, I., Bonani, G., 1997. A pervasive millennial-scale cycle in
634 North Atlantic Holocene and Glacial climates. *Science* 278: 1257–1266.
- 635 Bowman, D.M.J.S., Balch, J., Artaxo, P., Bond, W.J., Cochrane, M.A., D'Antonio,
636 C.M., DeFries, R., Johnston, F.H., Keeley, J.A., Krawchuk, M.A., Kull, C.A.,
637 Mack, M., Moritz, M.A., Pyne, S., Roos, C.I., Scott, A.C., Sodhi, N.S.,
638 Swetnam, T.W., 2011. The human dimension of fire regimes on Earth. *Journal*
639 *of Biogeography* 38: 2223–2236.
- 640 Braun-Blanquet, J., Pinto da Silva, A.R., Rozeira, A., Fontes, F., 1952. Resultats de
641 deux excursions géobotaniques a travers le Portugal septentrional et moyen: 1
642 une incursion dans la Serra da Estrela. *Agronomia Lusitana* 14: 303–323.
- 643 Bronk Ramsey, C., 2009. Bayesian analysis of radiocarbon dates. *Radiocarbon* 51: 337–
644 360.
- 645 Carcaillet, C., Almquist, H., Asnong, H., Bradshaw, R.H.W., Carrión, J.S., Gaillard, M.-
646 J., Gajewski, K., Haas, J.N., Haberle, S.G., Hadorn, P., Müller, S.D., Richard,
647 P.J.H., Richoz, I., Rösch, M., Sánchez Goñi, M.F., von Stedingk, H., Stevenson,
648 A.C., Talon, B., Tardy, C., Tinner, W., Tryterud, E., Wick, L., Willis, K.J.,
649 2002. Holocene biomass burning and global dynamics of the carbon cycle.
650 *Chemosphere* 49: 845–863.
- 651 Cardoso, J.L., Senna-Martinez, J.C., Valera, A.C., 1998. Aspectos da economia
652 alimentar do Bronze Pleno da Beira Alta: a fauna de grandes mamíferos das
653 «Salas 2 e 20» do Buraco da Moura de S. Romão (Seia). *Trabalhos de*
654 *Arqueologia da EAM* 3: 253–261.

655 Carrión, J.S., 2002. Patterns and processes of Late Quaternary environmental change in
656 a montane region of southwestern Europe. *Quaternary Science Reviews* 21:
657 2047–2066.

658 Carrión, J.S., Fernández, S., González-Sampériz, P., López-Merino, L., Peña, L.,
659 Burjachs, F., López-Sáez, J.A., García-Antón, M., Carrión Marco, Y., Uzquiano,
660 P., Postigo, J.M., Barrón, E., Allué, E., Badal, E., Dupré, M., Fierro, E.,
661 Munuera, M., Rubiales, J.M., García Amorena, I., Jiménez Moreno, G., Gil
662 Romera, G., Leroy, S., García-Martínez, M.S., Montoya, E., Fletcher, W., Yll,
663 E., Vieira, M., Rodríguez-Ariza, M.O., Anderson, S., Peñalba, C., Gil García,
664 M.J., Pérez Sanz, A., Albert, R.M., Díez, M.J., Morales-Molino, C., Gómez
665 Manzanque, F., Parra, I., Ruiz Zapata, B., Riera, S., Zapata, L., Ejarque, A.,
666 Vegas, T., Rull, V., Scott, L., Abel Schaad, D., Andrade, A., Manzano, S.,
667 Navarro, C., Pérez Díaz, S., Moreno, E., Hernández-Mateo, L., Sánchez Baena,
668 J.J., Riquelme, J.A., Iglesias, R., Franco, F., Chaín, C., Figueiral, I., Grau, E.,
669 Matos, M., Jiménez Espejo, F., Valle-Hernández, M., Rivas-Carballo, R.,
670 Arribas, A., Garrido, G., Muñiz, F., Finlayson, G., Finlayson, C., Ruiz, M.,
671 Pérez Jordá, G., Miras, Y., 2012. *Paleoflora y Paleovegetación de la Península*
672 *Ibérica e Islas Baleares: Plioceno-Cuaternario*. Ministerio de Economía y
673 Competitividad, Madrid.

674 Carrión, J.S., Fuentes, N., González-Sampériz, P., Sánchez Quirante, L., Finlayson,
675 J.C., Fernández, S., Andrade, A., 2007. Holocene environmental change in a
676 montane region of southern Europe with a long history of human settlement.
677 *Quaternary Science Reviews* 26: 1455–1475.

- 678 Carrión, J.S., Sánchez-Gómez, P., Mota, J.F., Yll, R., Chaín, C., 2003. Holocene
679 vegetation dynamics, fire and grazing in the Sierra de Gádor, southern Spain.
680 *The Holocene* 13: 839–849.
- 681 Catry, F.X., Rego, F., Moreira, F., Fernandes, P.M., Pausas, J.G., 2010. Post-fire tree
682 mortality in mixed forests of central Portugal. *Forest Ecology and Management*
683 260: 1184–1192.
- 684 Cheddadi, R., Lamb, H.F., Guiot, J., van der Kaars, S., 1998. Holocene climatic change
685 in Morocco: a quantitative reconstruction from pollen data. *Climate Dynamics*
686 14: 883–890.
- 687 Clark, J.S., Royall, P.D., 1995. Particle-size evidence for source areas of charcoal
688 accumulation in late Holocene sediments of eastern North American lakes.
689 *Quaternary Research* 43: 80–89.
- 690 Colombaroli, D., Marchetto, A., Tinner, W., 2007. Long-term interactions between
691 Mediterranean climate, vegetation and fire regime at Lago di Massaciuccoli
692 (Tuscany, Italy). *Journal of Ecology* 95: 755–770.
- 693 Colombaroli, D., Tinner, W., van Leeuwen, J., Noti, R., Vescovi, E., Vannièrè, B.,
694 Magny, M., Schmidt, R., Bugmann, H., 2009. Response of broadleaved
695 evergreen Mediterranean forest vegetation to fire disturbance during the
696 Holocene: insights from the peri-Adriatic region. *Journal of Biogeography* 36:
697 314–326.
- 698 Costa, J.C., Aguiar, C., Capelo, J.H., Lousã, M., Neto, C., 1998. Biogeografia de
699 Portugal Continental. *Quercetea* 0: 5–56.

- 700 Costa, L.T., Fidalgo, J.P., Neves, R., Rufino, R., 2004. Lagoas do Planalto Superior da
701 Serra da Estrela. Instituto da Conservação da Natureza, Centro de Zonas
702 Húmidas.
- 703 Daniau, A.-L., Sánchez-Goñi, M.F., Beaufort, L., Laggoun-Défarge, F., Loutre, M.-F.,
704 Duprat, J., 2007. Dansgaard-Oeschger climatic variability revealed by fire
705 emissions in southwestern Iberia. *Quaternary Science Reviews* 26: 1369–1383.
- 706 Davis, B.A.S., Stevenson, A.C., 2007. The 8.2 ka event and early–mid Holocene
707 forests, fires and flooding in the Central Ebro Desert, NE Spain. *Quaternary
708 Science Reviews* 26: 1695–1712.
- 709 deMenocal, P.B., Ortiz, J., Guilderson, T., Sarnthein, M., 2000. Coherent high- and
710 low-latitude climate variability during the Holocene Warm Period. *Science* 288
711 (5474): 2198–2202.
- 712 Figueiral, I., Carcaillet, C., 2005. A review of Late Pleistocene and Holocene
713 biogeography of highland Mediterranean pines (*Pinus* type *sylvestris*) in
714 Portugal, based on wood charcoal. *Quaternary Science Reviews* 24: 2466–2476.
- 715 Finsinger, W., Tinner, W., 2005. Minimum count sums for charcoal concentration
716 estimates in pollen slides: accuracy and potential errors. *The Holocene* 15: 293–
717 297.
- 718 Fletcher, W.J., Boski, T., Moura, D., 2007. Palynological evidence for environmental
719 and climatic change in the lower Guadiana valley, Portugal, during the last
720 13000 years. *The Holocene* 17: 481–494.

721 Fletcher, W.J., Sánchez Goñi, M.F., 2008. Orbital- and sub-orbital-scale climate
722 impacts on vegetation of the western Mediterranean basin over the last 48,000
723 yr. *Quaternary Research* 70: 451–464.

724 Gil-Romera, G., Carrión, J.S., Pausas, J.G., Sevilla-Callejo, M., Lamb, H.F., Fernández,
725 S., Burjachs, F., 2010. Holocene fire activity and vegetation response in South-
726 Eastern Iberia. *Quaternary Science Reviews* 29: 1082–1092.

727 Gitay, H., Suárez, A., Watson, R.T., Dokken, D.J. (Eds.), 2002. *Climate Change and*
728 *Biodiversity: IPCC Technical Paper V. Intergovernmental Panel on Climate*
729 *Change*, Geneva.

730 Green, D.G., 1981. Time series in postglacial forest ecology. *Quaternary Research* 15:
731 265–277.

732 Grimm, E.C., 1992. Tilia and Tilia-graph: pollen spreadsheet and graphics programs.
733 Program and Abstracts, 8th International Palynological Congress, September 6–
734 12, Aix-en-Provence, p. 56.

735 Grove, A.T., Rackham, O., 2001. *The Nature of Mediterranean Europe: an Ecological*
736 *History*. Yale University Press, New Haven.

737 Hammer, Ø., Harper, D.A.T., Ryan, P.D., 2001. PAST: Paleontological Statistics
738 software package for education and data analysis. *Palaeontologia Electronica* 4:
739 1–9.

740 Instituto da Conservação da Natureza (ICN), 2006. Relatório sobre incêndios rurais na
741 Rede Nacional de Áreas Protegidas e na Rede Natura 2000. Ministério do
742 Ambiente, do Ordenamento do Território e do Desenvolvimento Regional,
743 Lisboa.

- 744 Instituto da Conservação da Natureza e da Biodiversidade (ICNB), 2007. Plano de
745 Ordenamento do Parque Natural da Serra da Estrela: II, Caracterização dos
746 Valores Naturais. Ministério do Ambiente, do Ordenamento do Território e do
747 Desenvolvimento Regional, Lisboa.
- 748 Instituto da Conservação da Natureza e Biodiversidade (ICNB), 2009. Plano Prévio de
749 Intervenção em Incêndios Rurais 2009, Parque Natural da Serra da Estrela.
750 Ministério do Ambiente, do Ordenamento do Território e do Desenvolvimento
751 Regional, Lisboa.
- 752 Jansen, J., 2011. Managing Natura 2000 in a changing world: the case of the Serra da
753 Estrela (Portugal). PhD thesis, Radboud University.
- 754 Janssen, C.R., Woldringh, R.E., 1981. A preliminary radiocarbon dated pollen sequence
755 from the Serra da Estrela, Portugal. *Finisterra* 16: 299–309.
- 756 Lamb, H.F., van der Kaars, S., 1995. Vegetational response to Holocene climatic
757 change: pollen and palaeolimnological data from the Middle Atlas, Morocco.
758 *The Holocene* 5: 400–408.
- 759 Lionello, P. (Ed.), 2012. *The Climate of the Mediterranean Region: from the Past to the*
760 *Future*. Elsevier, London.
- 761 Maher, L., 1972. Nomograms for computing 0.95 confidence limits of pollen data.
762 *Review of Palaeobotany and Palynology* 13: 85–93.
- 763 Mateus, J.E., 1992. Holocene and present-day ecosystems of the Carvalhal region,
764 Southwest Portugal. PhD thesis, Utrecht University.

- 765 McCune, B., Mefford, M.J., 1999. PC-ORD: Multivariate Analysis of Ecological Data.
766 MjM Software Design, Gleneden Beach, Oregon.
- 767 Mora, C., Vieira, G.T., Alcoforado, M.J., 2001. Daily minimum air temperatures in the
768 Serra da Estrela, Portugal. *Finisterra* 36(71): 49–60.
- 769 Morales-Molino, C., García Antón, M., Morla, C., 2011. Late Holocene vegetation
770 dynamics on an Atlantic–Mediterranean mountain in NW Iberia.
771 *Palaeogeography, Palaeoclimatology, Palaeoecology* 302: 323–337.
- 772 Moreira, F., Catry, F.X., Rego, F., Bacao, F., 2010. Size-dependent pattern of wildfire
773 ignitions in Portugal: when do ignitions turn into big fires? *Landscape Ecology*
774 25: 1405–1417.
- 775 Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., and Kent, J.,
776 2000. Biodiversity hotspots for conservation priorities. *Nature* 403: 853–858.
- 777 Oldfield, F., 1983. Man's impact on the environment: some recent perspectives.
778 *Geography* 68: 245–256.
- 779 Pinto da Silva, A.R., Teles, A.N., 1999. A flora e a vegetação da Serra da Estrela.
780 Parque Natural da Serra da Estrela, Manteigas.
- 781 Queiroz, P.F., 1999. *Ecologia Histórica da Paisagem do Noroeste Alentejano*.
782 Unpublished PhD thesis, Universidade de Lisboa.
- 783 Queiroz, P.F., Mateus, J.E., 2004. Paleoecologia litoral entre Lisboa e Sines do
784 Tardiglaciário aos tempos de hoje. In: Tavares, A.A., Tavares, M.J.F., Cardoso,
785 J.L. (Eds.) *Evolução Geohistórica do Litoral Português e Fenómenos*

786 Correlativos: Actas Geologia, História, Arqueologia e Climatologia.
787 Universidade Aberta.

788 Quézel, P., Médail, F., 2003. *Écologie et biogéographie des forêts du bassin*
789 *méditerranéen*. Elsevier, Paris.

790 Reed, J., Stevenson, A.C., Juggins, S., 2001. A multi-proxy record of Holocene climatic
791 change in southwestern Spain: the Laguna de Medina, Cádiz. *The Holocene* 11:
792 707–719.

793 Rius, D., Vannière, B., Galop, D., Richard, H., 2011. Holocene fire regime changes
794 from multiple-site sedimentary charcoal analyses in the Lourdes basin
795 (Pyrenees, France). *Quaternary Science Reviews* 30: 1696–1709.

796 Romariz, C., 1950. Contribuição da análise polínica no estudo da vegetação primitiva
797 da Serra da Estrela. *Compte rendu Congrès International Géographie Lisbonne*
798 2: 824–830.

799 Sanz-Elorza, M., Dana, E.D., González, A., Sobrino, E., 2003. Changes in the high-
800 mountain vegetation of the Central Iberian Peninsula as a probable sign of global
801 warming. *Annals of Botany* 92: 273–280.

802 Senna-Martinez, J.C., 1993. A ocupação do Bronze Pleno da 'Sala 20' do Buraco da
803 Moura de São Romão. *Trabalhos de Arqueologia da EAM* 1: 55–76.

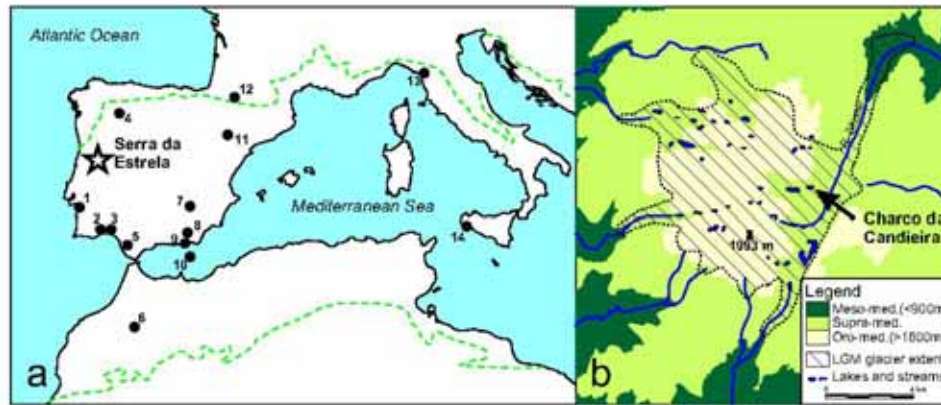
804 Stevenson, A.C., Harrison, R.J., 1992. Ancient forests in Spain: a model for land-use
805 and dry forest management in south-west Spain from 4000 BC to 1900 AD.
806 *Proceedings of the Prehistoric Society* 58: 227–247.

- 807 Tauber, H., 1967. Investigations of the mode of pollen transfer in forested areas.
808 Review of Palaeobotany and Palynology 3: 277–286.
- 809 Tinner, W., Kaltenrieder, P., 2005. Rapid responses of high-mountain vegetation to
810 early Holocene environmental changes in the Swiss Alps. *Journal of Ecology* 93:
811 936–947.
- 812 Tinner, W., van Leeuwen, J.F.N., Colombaroli, D., Vescovi, E., van der Knaap, W.O.,
813 Henne, P.D., Pasta, S., D'Angelo, S., and La Mantia, T., 2009. Holocene
814 environmental and climatic changes at Gorgo Basso, a coastal lake in southern
815 Sicily, Italy. *Quaternary Science Reviews* 28: 1498–1510.
- 816 Tolonen, K., 1986. Charred particle analysis. In: Berglund, B.E. (Ed.) *Handbook of*
817 *Holocene Palaeoecology and Palaeohydrology*. John Wiley & Sons, Chichester.
- 818 Tzedakis, P.C. 2007. Seven ambiguities in the Mediterranean palaeoenvironmental
819 narrative. *Quaternary Science Reviews* 26: 2042–2066.
- 820 Van den Brink, L.M., Janssen, C.R., 1985. The effect of human activities during
821 cultural phases on the development of montane vegetation in the Serra da
822 Estrela, Portugal. *Review of Palaeobotany and Palynology* 44: 193–215.
- 823 Van der Knaap, W.O., van Leeuwen, J.F.N., 1995. Holocene vegetation succession and
824 degradation as responses to climatic change and human activity in the Serra da
825 Estrela, Portugal. *Review of Palaeobotany and Palynology* 89: 153–211.
- 826 Van der Knaap, W.O., van Leeuwen, J.F.N., 1997. Late Glacial and early Holocene
827 vegetation succession, altitudinal vegetation zonation, and climatic change in the
828 Serra da Estrela, Portugal. *Review of Palaeobotany and Palynology* 97: 239–
829 285.

- 830 Van Geel, B., Aptroot, A., 2006. Fossil ascomycetes in Quaternary deposits. *Nova*
831 *Hedwigia* 82: 313–329.
- 832 Vanni re, B., Power, M.J., Roberts, N., Tinner, W., Carri n, J., Magny, M., Bartlein, P.,
833 Colombaroli, D., Daniau, A.L., Finsinger, W., Gil-Romera, G., Kaltenrieder, P.,
834 Pini, P., Sadori, L., Turner, R., Valsecchi, V., Vescovi, E., 2011. Circum-
835 Mediterranean fire activity and climate changes during the mid-Holocene
836 environmental transition (8500–2500 cal. a BP). *The Holocene* 21: 53–73.
- 837 Walker, D., 1982. Vegetation’s fourth dimension. *New Phytologist* 90: 419–429.
- 838 Whitlock, C., Larsen, C., 2001. Charcoal as a fire proxy. In: J.P. Smol, H.J.B. Birks,
839 W.M. Last (Eds.) *Tracking Environmental Changes using Lake Sediments –*
840 *Volume 3: Terrestrial, Algal, and Siliceous Indicators*. Kluwer Academic
841 Publishers, Netherlands, pp. 1–23.
- 842 Zeder, M., 2008. Domestication and early agriculture in the Mediterranean Basin:
843 origins, diffusion, and impact. *PNAS* 105: 11597–11604.
- 844 Zilh o, J., 2001. Radiocarbon evidence for maritime pioneer colonization at the origins
845 of farming in west Mediterranean Europe. *PNAS* 98: 14180–14185.

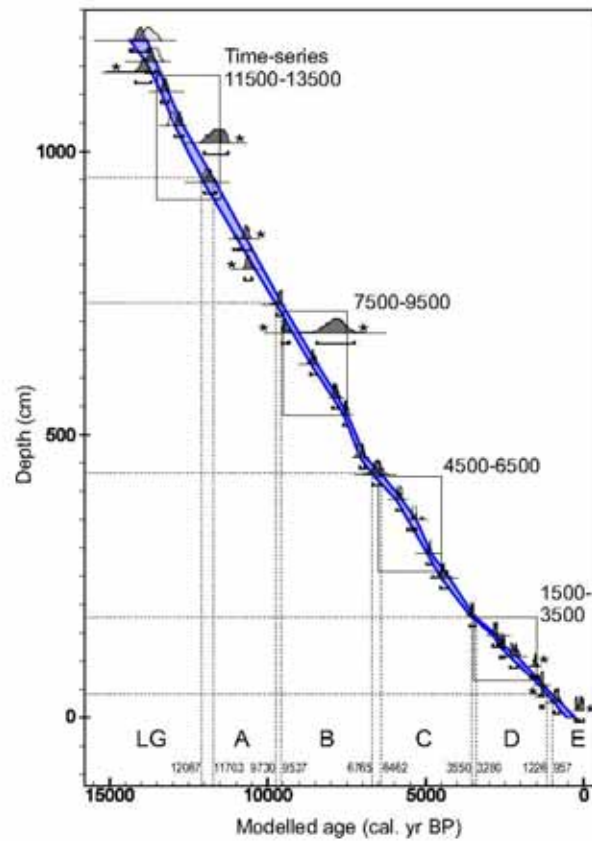
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847 **Figures**

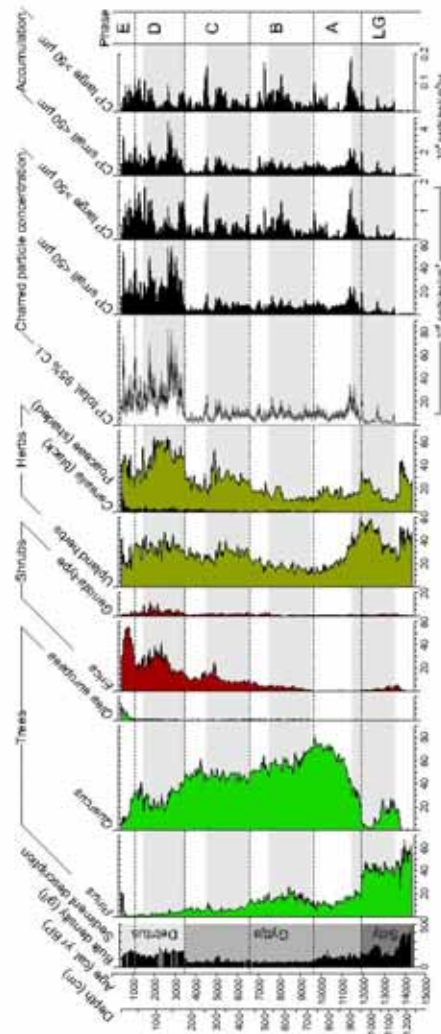


848
 849 Figure 1. Location of the Serra da Estrela, Portugal (a) and the study site, Charco da
 850 Candieira (b). The dashed line in Fig. 1a indicates the bioclimatic limit of the
 851 Mediterranean region (after Qu  zel and M  dail, 2003). Other sites mentioned in the text
 852 are shown: 1. NW Alentejo (Mateus, 1992; Queiroz, 1999; Queiroz and Mateus, 2004);
 853 2. Guadiana Estuary (Fletcher et al., 2007); 3. Laguna de las Madres (Stevenson and
 854 Harrison, 1992); 4. Vallefontido (Morales-Molino et al., 2011); 5. Laguna de Medina
 855 (Reed et al., 2001); 6. Lake Tigalmamine (Cheddadi et al., 1998; Lamb and van der
 856 Kaars, 1995); 7. Lake Siles (Carri  n, 2002; Gil-Romera et al., 2010); 8. Baza (Carri  n
 857 et al., 2007); 9. G  dor (Carri  n et al., 2003); 10. Alboran Sea (Fletcher and S  nchez
 858 Go  ni, 2008); 11. Central Ebro Desert (Davis and Stevenson, 2007); 12. Lourdes Basin
 859 (Rius et al., 2011); 13. Lago di Massaciuccoli (Colombaroli et al., 2007); 14. Gorgo
 860 Basso (Tinner et al., 2009). Fig. 1b shows the main bioclimatic zones of the Serra da
 861 Estrela (see Section 2), the extent of the most recent glaciation and the distribution of
 862 glacial lakes (after Daveau, 1971).

863



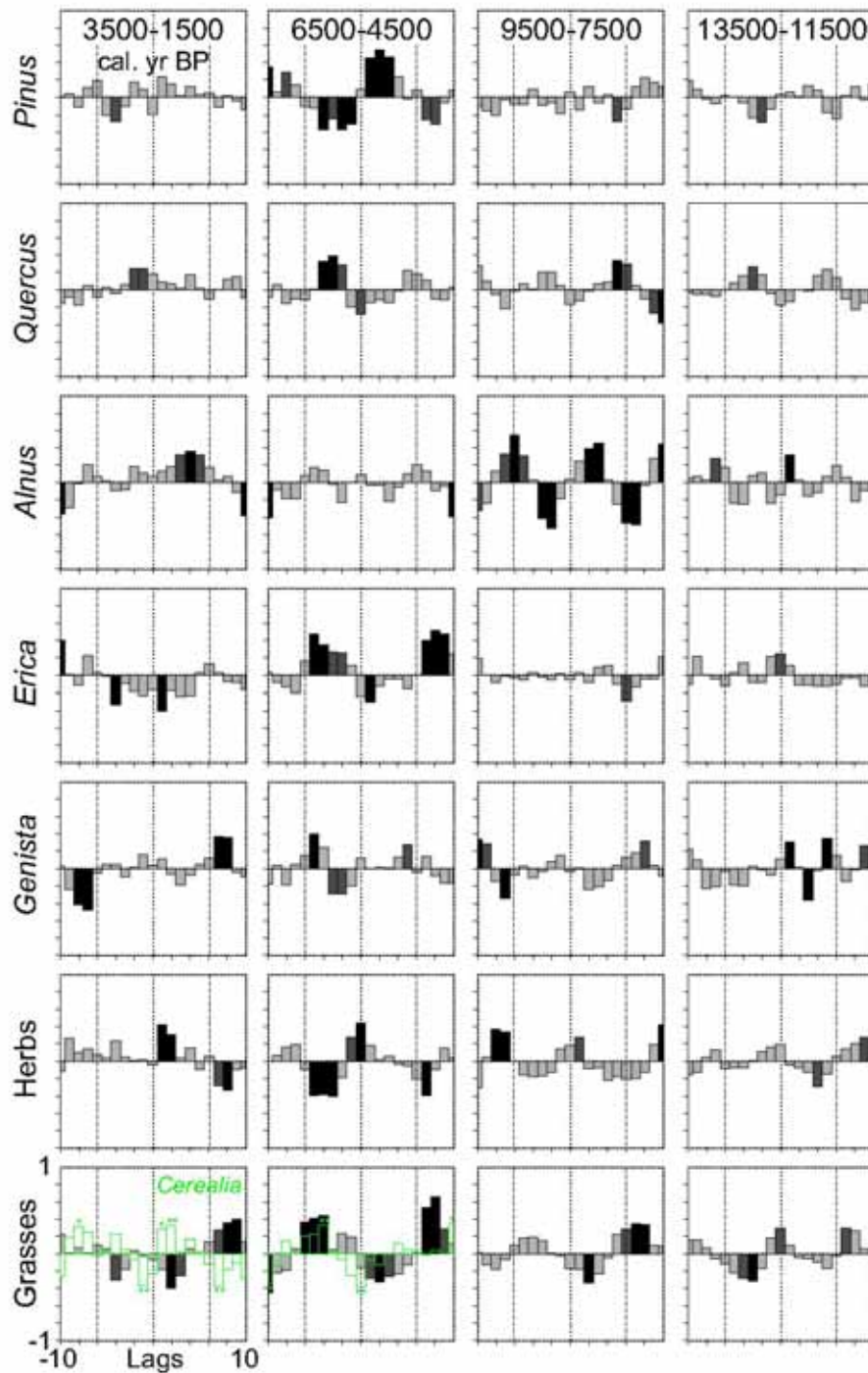
864
 865 Figure 2. Age–depth model for the Charco da Candieira sediment record showing
 866 probability distributions for each dated level, dates excluded from the model (*) and age
 867 ranges for each of the palaeovegetation phases (Section 2). Boxed periods were
 868 subjected to time-series analysis (Section 5.3; Fig. 4).



869

870 Figure 3. Stratigraphic diagram of proxies analysed in the Charco da Candieira sediment
 871 record. From left to right: depths, modelled ages, sediment bulk density (g/l dry weight),
 872 sediment description (details in der Knaap and van Leeuwen 1995, 1997), selected
 873 pollen percentages, total charred particle concentrations with 95% confidence intervals
 874 (estimated from Maher, 1972), concentrations of charred particles 5–50 and 50–250 μm
 875 in size, and accumulation rates of the same. Palaeovegetation phases (Section 2) shown
 876 at right; grey horizontal bands are time-series analysis periods (Fig. 4).

877



878
 879 Figure 4. Cross-correlograms of interpolated and detrended pollen percentages (selected
 880 taxa) and charred particle concentrations for four periods in the Charco da Candieira
 881 record. The vertical axis represents correlation coefficients and the horizontal axis
 882 represents lags (each equivalent to 48 years). Statistically significant correlations are

883 indicated by black columns ($p < 0.05$) and dark-grey columns ($p < 0.1$). *Cerealia* pollen is
 884 represented as hollow columns on the Poaceae graph (** $p < 0.05$ and * $p < 0.1$). When
 885 reading these graphs, a positive correlation at zero lags (centre of each graph) indicates
 886 a direct (immediate) correlation between charcoal and pollen abundance. A positive
 887 correlation to the right indicates that a charcoal increase leads a pollen increase. A
 888 positive correlation to the left indicates that the charcoal lags behind the pollen (see
 889 Green, 1981, for full explanation). Dashed vertical lines at 6 lags denote the average
 890 period between major charcoal peaks (approx. 300 years).

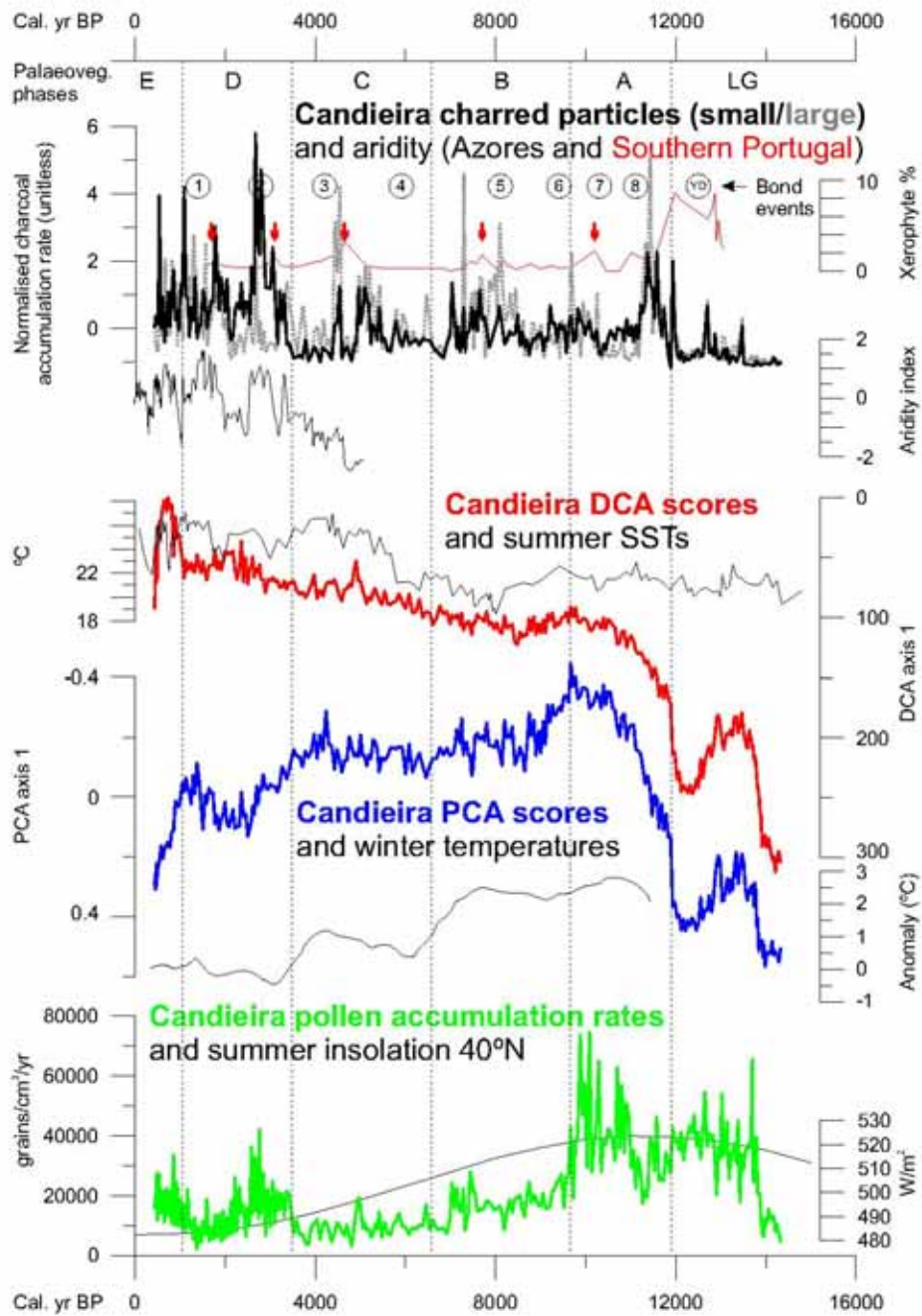


891

892 Figure 5. Comparison of a model of post-fire succession in the Serra da Estrela's oro-
 893 mediterranean and supra-mediterranean vegetation (Jansen, 2011) with successional
 894 trends deduced from time-series analysis of the Charco da Candieira pollen and charcoal
 895 record (Section 5.3). Significant post-fire pollen correlations have been translated into
 896 vegetation types to aid comparison. Numbers above the arrows indicate the approximate
 897 number of years since fire required to reach each stage. Taxa marked 1 are possibly

898 derived from long-distance pollen transport; taxa marked 2 may have occurred in the
899 local wetland vegetation; taxa in parentheses appear late in the successional stage in
900 which they are included.

901



902

903 Figure 6. Ordination results (PCA and DCA), normalised charred-particle accumulation

904 rates and dryland-pollen accumulation rates from the Charco da Candieira record (thick

905 lines) in relation to other palaeoclimatic records mentioned in the text (thin lines).
906 Charcoal data normalised to standard deviation (see Carcaillet et al., 2002). Azorean
907 aridity index redrawn from Björck et al. (2006); arid phases in Southern Portugal from
908 Fletcher et al. (2007); Bond events from Bond et al. (1997); summer sea surface
909 temperatures (SSTs) off West Africa from deMenocal et al. (2000); winter temperatures
910 in Morocco from Cheddadi et al. (1998); and summer insolation at 40°N from Berger
911 (1978).