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1 **Holocene fire and vegetation dynamics in the Central Pyrenees**
2 **(Spain)**

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15

16 **Abstract**

17 Fire-vegetation relationships are critical to understand transient mountain ecosystems and
18 their long-term landscape dynamics, which is essential for alpine forest conservation. In this
19 paper we aim to 1) reconstruct the Holocene fire history at high altitudes of the southern
20 Central Pyrenees, 2) add evidence to the debate on fire origin, naturally or anthropogenically
21 produced, 3) determine the importance of fire as a disturbance agent for sub-alpine and alpine
22 vegetation, in comparison with the plant community internal dynamics applying conditional

23 inference trees. We present and compare microcharcoal and pollen data series, from two
24 lacustrine sedimentary sequences in the Central Pyrenees: Basa de la Mora (BSM), within the
25 treeline ecotone at the sub-alpine belt (1914 m a.s.l.) and Marboré Lake, above the treeline at
26 the alpine belt (2612 m a.s.l.).

27 We evidence that, fire activity was not the most important factor in driving vegetation
28 dynamics regionally. Our results suggest that spatially, the fire signal might be site-dependent
29 while over time, climate exerted a strong influence on fire activity during the early-to-mid
30 Holocene, showing more fires during the Holocene Thermal Maximum (HTM) (ca. 7000-6000
31 cal yr BP) whereas fire activity decreased with the cold Neoglacial period. At ca. 3700 cal yr BP,
32 fire activity increased coinciding with a regional landscape opening, suggesting that human
33 activities may have strengthened the importance of fire. Fire activity remained low over the
34 last two millennia but a remarkable Holocene maximum for the last centuries in both
35 sequences is observed, likely related to increasing human pressure.

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37 **Key words:** Microcharcoal, pollen, lake sediments, palaeoclimate, human impact, fire-history

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45 **1. Introduction**

46 Fire is a relevant disturbance of the Earth system, driving significant changes in ecosystem
47 structure and function, species evolution, biomass dynamics or global carbon cycling (Bond
48 and Midgley, 1995; Bowman et al., 2009; Pausas and Schwilk, 2012; Archibald et al., 2013). Fire
49 regimes are driven by factors such as climate (e.g. Daniau et al., 2012), vegetation through fuel
50 load, connectivity or flammability, soil types, ignition sources-natural or anthropogenic-, and
51 topographical features (Whitlock et al., 2010; Krawchuk and Moritz, 2011). Thus, the sensitivity
52 of any ecosystem to fire depends on its own characteristics.

53 Sub-alpine and alpine plant communities are formed by alpine pastures and weakly flammable
54 conifer woodlands like *Pinus sylvestris* L., *Pinus uncinata* Ramond ex DC, *Juniperus communis* L.
55 and *Abies alba* Mill, which hold no post-fire strategy, especially after crown fires (Keeley et al.,
56 2012). Fire in mountains is associated with the occurrence of woody species (Leys et al., 2014),
57 and is therefore infrequent above the treeline due to the lack of arboreal biomass. Under
58 natural conditions, fire occurrence will generally be controlled by the fuel moisture degree, in
59 turn driven by precipitation and temperature.

60 The high landscape heterogeneity in mountain areas often implies different fire behaviour
61 (Leys and Carcaillet, 2016; Fréjaville et al., 2018) at the sub-regional or local scales. Mountain
62 environments are in addition very sensitive to climate, fire, and land use changes, because of
63 their narrow tolerance capabilities, especially at the boundaries of the treeline (Theurillat
64 and Guisan, 2001; Pauli et al., 2012).

65 Fire occurrence is generally low in alpine ecosystems under present climatic conditions and
66 land use patterns in the Pyrenees. However, fire activity has changed over time (Jiménez-
67 Ruano et al., 2019) and may have been a more frequent disturbance over the last millennia,
68 with different climatic settings and more intense human activities. In fact, human activities
69 have been modifying natural fire regimes through changing land use (Pausas and Keeley, 2014)

70 since centuries or even millennia (Carracedo et al., 2017; Morales-Molino et al., 2017), using
71 fire as a tool in land management. For instance, during the mid-19th century humans used fire
72 as a common tool to maintain opened mountain landscapes in the Pyrenees (García-Ruiz et al.,
73 2015; García-Ruiz and Lasanta, 2018), modifying the structure of sub-alpine systems. However,
74 due to the abandonment of traditional land uses, the extension of opened areas has been
75 reduced, increasing forest connectivity and the accumulation of standing fuel loads.
76 Consequently, the increase in drought conditions and temperature due to global warming
77 (IPPC, 2014), together with the increase in the amount of standing fuel may enhance the risk of
78 wildfires in southern European mountains (Ryan, 2000; Wastl et al., 2013). This may reduce
79 forest resilience to wildfires (Stevens-Rumann et al., 2018), while it can also provide an
80 opportunity for ecosystem restoration under particular circumstances (Leverkus et al., 2019).

81 Understanding to what extent changing fire regimes at longer temporal scales have
82 contributed to the current mountain landscapes is paramount for designing sustainability
83 policies for socio-ecological systems. In this context, long-term ecology research emerges as a
84 critical tool to obtain the needed time series to address environmental changes at centennial
85 to millennial time-scales. Sedimentary microcharcoal analysis improves our understanding
86 on the long-term role of fire as a key ecological factor (Whitlock and Larsen, 2001; Power et al.,
87 2008; Colombaroli et al., 2010; Feurdean et al., 2012), whereas pollen analysis in sediments
88 has been widely used for the study of vegetation changes (Carrión et al., 2010; and references
89 therein Birks and Björn, 2018). Both proxies have facilitated and strengthened our
90 understanding of past disturbances in the landscape.

91 The comparison of different charcoal records at global scale has revealed significant regional
92 differences in fire activity during the Holocene, probably caused by the complex interplay
93 between climate, vegetation and human impact (Power et al., 2008; Vannièrè et al., 2011,
94 2016; Marlon et al., 2013). Thus, despite climate seems to be the main fire driving force at

95 large spatial scales in fire-prone areas, regional studies evidence that other local factors would
96 be also determining the high temporal variability in biomass burning (e.g. Gavin et al., 2006;
97 Feurdean et al., 2012, 2017; Leys and Carcaillet, 2016). Given this spatial and temporal
98 heterogeneity in variables controlling fire, site-specific histories are needed to show how fire
99 activity has been modulated by microclimate, vegetation, topography and land-use (Gavin et
100 al., 2006; Whitlock et al., 2010; Rius et al., 2011).

101 Apart from fire, climate and other external disturbances, plant population dynamics are also
102 determined by the ecological memory of a community, defined as the capacity of past states of
103 the system to influence present or future responses (Padisak, 1992; Ogle et al., 2015). In this
104 regard, antecedent taxa dynamics and fire activity may also be relevant explaining the
105 abundance of a taxa at a given time. Therefore, understanding ecological memory may help to
106 assess long-term ecosystem resilience.

107 Contrary to other European mountain ranges, where long-term fire activity has been widely
108 studied in mountain sites (e.g. Tinner et al., 1998, 2015; Blarquez and Carcaillet, 2010;
109 Colombaroli et al., 2010; Feurdean et al., 2012; Leys et al., 2014; Florescu et al., 2018), we
110 know little about the long-term fire history of the Iberian Peninsula mountain ranges (Pérez-
111 Obiol et al., 2012; Carracedo et al., 2017; Morales-Molino et al., 2017) and, in particular, of the
112 Pyrenean mountains. While most studies focus on the eastern part (Ejarque et al., 2010; Bal et
113 al., 2011; Pérez-Obiol et al., 2012; Cunill et al., 2013; Garcés-Pastor et al., 2017) presenting the
114 evolution of fire activity during the Lateglacial and Holocene periods very few have been
115 developed at the central part (Gil-Romera et al., 2014), and little is known about the role of
116 fire transforming alpine ecosystems.

117 In the current research we aim to 1) reconstruct the long-term fire history in the southern
118 Central Pyrenees, 2) add evidence to the debate on fire origin, naturally or anthropogenically
119 driven, comparing our Holocene fire series with other local and regional evidence, and 3)

120 compare the relative influence of antecedent values of pollen abundance and fire activity
121 versus concurrent fire activity on the dynamics of several taxa. We present an encompassing
122 comparison of well-dated Holocene sedimentary charcoal records and their fossil pollen
123 assemblages from the sub-alpine, Basa de la Mora Lake (BSM) (at the treeline) and alpine
124 Marboré Lake (MAR) (above the treeline).

125 **2. Regional setting**

126 The Pyrenees are a mountain range located in north eastern Iberian Peninsula (Fig. 1a),
127 between the Atlantic Ocean and the Mediterranean Sea. Water availability in the Pyrenees is
128 controlled by an important west-east rainfall gradient (2000 to 1000 mm) driven by the
129 North Atlantic Oscillations (Araguas-Araguas and Díaz Teijeiro, 2005). The western Pyrenees
130 have a direct Atlantic influence with a humid climate, while the eastern Pyrenees have a
131 stronger Mediterranean influence, with a drier and warmer season. Beyond these general
132 features, there is also a high-climatic variability controlled by topography and elevation, with
133 highest mean annual precipitation (MAP) values occurring at the highest elevations (2000-
134 2500 mm), and a temperature lapse rate of ca. $-0.6^{\circ}/100$ m (García-Ruiz et al., 2015) with a
135 mean annual temperature gradient that goes from 5-10 °C, in the valleys to below 0 °C in the
136 high massifs (Ninyerola et al., 2005) (Fig. 1b).

137 The altitudinal gradient defines the main vegetation belts in the Pyrenees (Fig. 2). The low
138 montane community (ca. 1200-1400 m a.s.l.) is characterized by mosaics of croplands and
139 open mixed areas of *Quercus ilex* L., *Quercus faginea* Lam. /*cerrroides* Willk. & Costa, *P.*
140 *sylvestris* with a dense shrub land of different juniper species, *Buxus sempervirens* L. and
141 *Genista scorpius* (L.) DC. among others. The upper montane community (ca. 1400-1600 m
142 a.s.l.) features well-developed broadleaf forests mainly composed by *Corylus avellana* L.,
143 *Betula pendula* Roth, *Fraxinus excelsior* L., *Acer campestre* L., *Sorbus aria* (L.) Crantz, *Sorbus*
144 *aucuparia* L. mixed with *P. sylvestris*, *P. uncinata* or *A. alba*. The sub-alpine belt (ca. 1600-2000

145 m a.s.l.) is dominated by coniferous forests of *P. uncinata* with sparse shrubs like *J. communis*
146 or *Rhododendron ferrugineum* L. Although slope orientation, soil formation, microclimate and
147 past human activities interact to determine the upper limit of the closed forest, the timberline
148 is located at ca. 1800-1900 m a.s.l. Both timberline and treeline (up to ca. 2000-2200 m a.s.l.)
149 are communities where the dominant tree is *P. uncinata* (Fig. 2). Alpine and sub-nival
150 communities (higher than ca. 2000 m a.s.l.) are formed by alpine herbs and dwarf shrubs.

151 Fires in the Pyrenees occur mostly in forested areas (Cubo et al., 2012; Vázquez de la Cueva,
152 2016) and they are mostly naturally produced, triggered by lightning as the main ignition
153 source in high altitude locations (Amatulli et al., 2007; Cubo et al., 2012; Vázquez de la Cueva,
154 2016), during summer storms (Font, 1983; Vázquez de la Cueva, 2016). Despite human-caused
155 fires do happen as well, these take place in the more fragmented areas in the montane zone
156 (Amatulli et al., 2007).

157 MAR is an alpine glacial lake located at 2612 m a.s.l. at the base of the Monte Perdido Glacier
158 (Fig. 1c). BSM (1914 m a.s.l.) is a shallow glacial lake located on the north-facing slope of the
159 Cotiella Peak (Fig. 1d). Although both lakes in this study lay at the Central Pyrenees and are ca.
160 30 km from each other, each lake presents quite different geographical and ecological
161 characteristics summarized in Table 1. MAR does not present woody vegetation around the
162 lake, as it is placed in the alpine belt. The treeline is located 600 m below, thus, fires are less
163 likely locally. However, BSM is currently located in the sub-alpine belt, and thus, within the
164 treeline ecotone dominated by *P. uncinata* communities. Fires can potentially occur in the
165 vicinity of the lake, although fire activity is nowadays low in this place. Furthermore, the
166 modern fire activity at a regional scale in both areas is weak, with ca. 1 to 2 fire events
167 occurring every 30 years, invariably set by natural causes (mostly summer storms) that,
168 however, often create mid-to-large fires with a burnt area between 10-100 Ha (Vázquez de la
169 Cueva, 2016).

170

171 **3. Materials and Methods**

172 **3.1 Lake-coring, chronology and pollen analysis**

173 Previous multiproxy analyses of both sedimentary records have already been published, Pérez-
174 Sanz et al. (2013) for BSM Lake and Leunda et al. (2017) and Oliva-Urcia et al. (2018) for MAR
175 Lake. In the present study we focus on the Holocene section of both sequences. BSM depth-
176 age model is based on 13 ^{14}C terrestrial plant macrofossil ages along 11 m depth (mean
177 sedimentation rate: 0,149 cm/yr), and MAR depth-age model is based on 9 ^{14}C bulk sediment
178 dates along 6 m depth (mean sedimentation rate: 0,061 cm/yr). In both cases, the most recent
179 part has been dated with $^{210}\text{Pb}/^{137}\text{Cs}$. Depth-age models were carried out with Clam 2.2
180 software (Blaauw, 2010) using linear interpolation between dated levels (Fig. 3). Pollen
181 analysis for both sequences was conducted in Pérez-Sanz et al. (2013) and Leunda et al. (2017)
182 following the standard chemical procedure (Moore et al., 1991) but including Thoulet solution
183 (2.0 g/cm^3) for separation and *Lycopodium clavatum* spores to calculate concentration
184 (Stockmarr, 1971). Pollen has been identified under a light microscope, and using the
185 reference collection from the Pyrenean Institute of Ecology (IPE-CSIC), determination keys and
186 photo atlases (Moore et al., 1991; Reille, 1992). Results have been calculated both in
187 percentages and pollen accumulation rates; (PAR $\#/\text{cm}^2\text{yr}$). More details about the
188 chronological framework and pollen analysis are provided in Pérez-Sanz et al. (2013) and
189 Leunda et al. (2017).

190 **3.2 Microcharcoal analysis**

191 We present here microcharcoal series for BSM and MAR as fire proxy, aiming to achieve our
192 first objective, i.e. to reconstruct the long-term regional fire activity. The term microcharcoal
193 refers to small carbonized particles (Fig. S1) produced during vegetation fires (Jones et al.,

194 1997) and transported by aeolian and fluvial agents from the combustion site to the
195 sedimentation basin. In lakes charcoal preserves well due to its relatively high resistance to
196 chemical and microbial decomposition (Habib et al., 1994; Hart et al., 1994; Verardo, 1997;
197 Hockaday et al., 2006; Quénéa et al., 2006).

198 Microcharcoal analyses were carried out in a total of 108 samples for MAR and 130 samples
199 for BSM. We sampled microcharcoal at the same depths of the pollen samples previously
200 analysed. In BSM sample resolution was every 5 cm with a mean temporal resolution between
201 samples ca. 70 years, while MAR sampling was performed every 5-10 cm with a mean
202 temporal resolution between samples ca. 109 years, except for the upper part, where
203 sampling was every 2 cm. Sediment samples were processed using the chemical procedure
204 following Daniau et al. (2009, 2013) at the UMR-EPOC laboratory (CNRS-Université de
205 Bordeaux). The microcharcoal extraction technique consisted of a chemical treatment of 37%
206 HCl, 68% HNO₃ and 33% H₂O₂ performed over 24 h on 0,3 g of dried sediment, followed by a
207 dilution of 0,1 applied to the residue. The suspension was then filtered onto a cellulose acetate
208 membrane containing nitrocellulose of 0,45 µm porosity and 47 mm in diameter. A portion of
209 this membrane was mounted onto a slide.

210 The identification and quantification of microcharcoal was performed using automated image
211 analysis with an automated Leica DM6000M microscope at x500 magnification in transmitted
212 light and following the criteria proposed by Boulter (1994), identifying charcoal as being black,
213 opaque and angular with sharp edges. This technique, allows identifying microcharcoal
214 particles automatically, once colour and lightning settings are established for identifying them,
215 reducing considerably the counting task. Identification of unburned particles, characterized by
216 the absence of plant structures and distinct level of reflectance, was used to set the best-fit
217 threshold level to secure identification of microcharcoal by image analysis. Critical particles
218 were distinguished from dark minerals by reflected light (Clark, 1984) and in order to have a

219 good statistical representation of each sample, 200 view fields (200 images) of 0.0614 mm^2
220 were taken in colour with a 1044×772 pixels digitizing camera (1 pixel = $0.276 \mu\text{m}$). The
221 surface scanned by the microscope represented a surface area of 12.279 mm^2 . Although this
222 technique has primarily been applied in marine sediments (Daniau et al., 2009, 2013) it has
223 also been successfully used for lake sediments (e.g. Tinner et al., 1999; Leys et al., 2014; Remy
224 et al., 2018). Microcharcoal particles below $10 \mu\text{m}$ have not been considered, as theoretical
225 considerations showed that particles smaller than $5\text{-}10 \mu\text{m}$ in diameter are difficult to identify
226 (Clark, 1988).

227 From the microcharcoal measurements, three parameters were calculated for each sample: (i)
228 the concentration of microcharcoal (CCnb: #/g); (ii) the concentration of microcharcoal surface
229 (CCs), which is the sum of all surfaces of microcharcoal in one sample per gram ($\mu\text{m}^2/\text{g}$) and (iii)
230 microcharcoal accumulation rate (CHAR: #/cm²yr), in order to have a time-fitted value of
231 charcoal. 1cm^3 of sediment was sampled with a syringe and weighted (g) in order to calculate
232 sediment density (g/cm^3) and multiply it with charcoal concentration (#/g) and sedimentation
233 rate (cm/yr) to obtain microcharcoal accumulation rate (#/cm²yr).

234 Several replicate analyses were done (7 for MAR and 10 for BSM) randomly analysing 10 times
235 each. For this replicate samples, the mean value and standard deviation was calculated. For
236 the comparison of both sequences, microcharcoal influx data was normalized with Z-scores
237 (Glantz et al., 2016).

238 **3.3 Numerical analyses: conditional inference trees**

239 Accomplishing the third objective of our research implied estimating to what extent long-term
240 fire dynamics is a relevant variable shaping the sub-alpine and alpine Pyrenees landscape. We
241 thus calculated the effect that antecedent and concurrent fires (CHAR), have on the
242 abundance of certain taxa (PAR). On the other hand, we intend to quantify to what extent PAR
243 itself is determined by its own antecedent values. In doing so, we incorporate a quantitative

244 approach to the ecological memory concept (Ogle et al., 2015). In order to analyse the effect
245 of past and concurrent CHAR and past PAR on each PAR value, we aligned the samples of each
246 site with their antecedent ones, generating a data structure with a lag of order 1, following the
247 model expressed in Equation 1:

248 Equation 1: $PAR \sim CHAR + CHAR.ancestor + PAR.ancestor$

249 PAR is the response, with the same age and depth as CHAR which represents concurrent fire,
250 while CHAR.ancestor and PAR.ancestor have the age and depth of the previous sample,
251 and represent the effect of past states on the dynamics of the system.

252 PAR values of *Pinus*, *Abies*, *Betula*, *Corylus*, and Herbs were used as response variable for both
253 sites. Deciduous *Quercus* was only modelled in BSM because MAR records very low and sparse
254 *Quercus* PAR values.

255 The models were fitted with conditional inference trees (Hothorn et al., 2006) through the
256 `ctree` function of the R package `partykit` (Hothorn and Zeileis, 2015). Conditional inference
257 trees are recursive partition models that use a permutation test to find on each iteration the
258 threshold of any predictive variable that better splits the data into two homogeneous
259 partitions. The process is repeated on each data partition until further data splitting is not
260 possible, or the terminal nodes of the recursive partition tree reach a minimum sample size.

261 The resulting model is a regression tree, in which variables located higher up in the tree
262 hierarchy are more important to explain patterns in the data than variables located in lower
263 nodes. Regression trees are easy to interpret, represent partial interactions among predictive
264 variables, and do not rely on assumptions about the properties of the data in the way linear
265 models do. Despite the fact that they are generally underused in ecology, conditional inference
266 trees have proved to be extremely useful in conservation biology (Johnstone et al., 2014).

267 **4. Results**

268 **4.1 Temporal trends in microcharcoal records**

269 Variations in microcharcoal concentrations (CCnb and CCs) in each lake show very similar
270 fluctuations (Fig. S2). This confirms that both CCnb and CCs record the same pattern of
271 microcharcoal concentration variability, suggesting that there is no microcharcoal
272 overrepresentation as the result of potential fragmentation during particle production or
273 transport and thus, both units could be used to interpret the fire record (Daniau et al., 2012).
274 CHAR values (microcharcoal influx) also follow similar concentration variability in both
275 sequences (Fig. S2).

276 **4.1.1 MAR Lake microcharcoal sequence**

277 The beginning of the sequence shows a low microcharcoal influx between ca. 9500-7000 cal yr
278 BP (mean influx of 9×10^4 particles/cm²yr; ^{SD} 2.3×10^4 #/cm²yr). Microcharcoal increases from
279 7000-6500 and 6200-5700 cal yr BP (mean influx of 1.7×10^5 particles/cm²yr; ^{SD} 3.9×10^4
280 particles/cm²yr). A significant decrease is appreciated from 5700-3600 cal yr BP (mean influx of
281 1×10^5 particles/cm²yr; ^{SD} 2.8×10^4 particles/cm²yr). Fluctuating CHAR values are found between
282 3600 and 1600 with several local maxima (up to an influx value of 2.6×10^5 particles/cm²yr). The
283 signal becomes weak between 1600-1000 cal yr BP but an abrupt and consistent charcoal
284 increase is observed afterwards until present day, reaching maximum values (maximum influx
285 value 3.1×10^5 particles/cm²yr) (Fig. S2 and Fig. 4a).

286 **4.1.2 BSM Lake microcharcoal sequence**

287 At BSM, low but fluctuating values are present during 9500-6600 cal yr BP (mean influx 1.6×10^5
288 particles/cm²yr; ^{SD} 2×10^5 particles/cm²yr) with a significant microcharcoal peak at ca. 6700 cal
289 yr BP (microcharcoal influx of 2.2×10^5 particles/cm²yr). Subsequently, the signal is weakened
290 with sustained low microcharcoal values until ca. 3700 cal yr BP (mean influx 5.4×10^4
291 particles/cm²yr; ^{SD} 2.4×10^4 particles/cm²yr), where it increases showing a marked isolated

292 maximum (microcharcoal influx of 2.2×10^5 particles/cm²yr). Microcharcoal signal maintains low
293 afterwards, until almost recent times (mean influx 4.4×10^4 particles/cm²yr; ^{SD} 2.3×10^4
294 particles/cm²yr) with the exception of a minor fire peak ca. 1200 cal yr BP. The maximum
295 microcharcoal signal is found for the last decades (up to an influx value of 2.4×10^5
296 particles/cm²yr) (Fig. S2 and Fig. 4g).

297 **4.2 Conditional inference trees**

298 Conditional inference trees (Fig. 5 and Fig. S3 for all taxa and sites) found significant patterns
299 of influence of the explanatory variables we have used (antecedent PAR, antecedent CHAR and
300 CHAR) on PAR, except in the case of *Pinus* and *Betula* in MAR (Fig. S3a,b). For most taxa,
301 PAR.antecedent, which represents the endogenous dynamics of the taxa, is the best
302 explanatory variable (Fig. 5a,c,d,e,f and Fig. S3c,d,e). Hence, larger values of antecedent PAR
303 seem to have a positive effect on the taxa's abundance, at any given time, especially in BSM.
304 Antecedent CHAR had a significant and positive effect on *Quercus* PAR in BSM (Fig. 5f), while
305 concurrent CHAR influenced positively the pollen abundance of *Abies* and *Corylus* in MAR (Fig.
306 5a,b). The boxplots represent mean values of each PAR series classified according to the
307 explanatory variables. For instance, looking at *Abies* MAR (Fig. 5a), abies.antecedent is the best
308 explanatory variable determining large *Abies* values (right boxplot), only when
309 abies.antecedent is low, concurrent CHAR succeeds predicting *Abies* PAR to a certain
310 threshold, producing the next classified group (central boxplot).

311 **5. Discussion**

312 **5.1 Pollen and microcharcoal source: considerations for the studied sequences**

313 Comparing these two sequences brings forward the need to look at site-specific settings, as
314 these might be determining different fire behaviour and, what it is most important, source
315 area for biological proxies and transport pathways (Corella et al., 2018). The study sites are

316 defined by both catchment dimensions and altitude, thus, several studies have evidenced that
317 higher elevations may record best regional rather than local environmental variations
318 (Escudero et al., 2016; Corella et al., 2018).

319 MAR (2612 m a.s.l.) is placed ca. 600 m higher than the current treeline (Figs. 1c and 2), and
320 we infer that due to the absence of tree macrofossils along the sedimentary sequence (Leunda
321 et al., 2017), the treeline would have not reached the Marboré cirque during the Holocene.
322 Moreover, MAR lies in an open cirque wind-exposed supporting that the source area of both
323 arboreal pollen and microcharcoal particles would come from large areas both from northern
324 and southern slopes of the Pyrenees, having a wide catchment area and thus registering fires
325 and vegetation dynamics from far. Indeed, regional tropospheric circulation becomes a more
326 important factor in particle transport and deposition above ca. 2100 m a.s.l., whereas below
327 this altitude horizontal regional transport is less patent (Escudero et al., 2016).

328 On the other hand, BSM is currently located in the sub-alpine belt (1914 m a.s.l.) at the
329 treeline ecotone (Figs. 1d and 2). During the Holocene the lake would have been likely
330 colonized by different forest communities (Pérez-Sanz et al., 2013), enabling fires to also occur
331 locally. Thus, the source area of both tree pollen and microcharcoal could be partially a
332 background signal but still more local than in MAR, with an important input from nearby forest
333 communities.

334 **5.2 Fire history through the Holocene in the Central Pyrenees**

335 *5.2.1 Low fire activity during the early Holocene (ca. 9500-7000 cal yr BP)*

336 Fire activity was relatively low during the early Holocene, as inferred from both BSM and MAR
337 sequences, although they show differing patterns; MAR holds a lower variability compared to
338 BSM which evidences a fluctuating fire activity (Fig. 4a,g). A rather low fire activity is also
339 detected in other Pyrenean sequences (Cunill et al., 2013; Gil-Romera et al., 2014; Garcés-

340 Pastor et al., 2017). Pine communities dominated both lakes at a regional scale (ca. 70% of
341 pine pollen; Fig. 4b,h), and despite the lack of treeline reconstructions for the early Holocene
342 in the Pyrenees, Cunill et al. (2013) demonstrated the existence of pine biomass at 2200 m
343 a.s.l. in the eastern Pyrenees, which could mean that BSM could already be surrounded by
344 pines. On the other hand, the importance of mesophytes (mainly *Corylus* and *Betula*) is clear in
345 the MAR sequence, similar to more Atlantic sites like El Portalet (González-Sampéris et al.,
346 2006; Gil-Romera et al., 2014). In this regard, significant differences in vegetation composition
347 have been recorded along the Pyrenees during the early Holocene related to the more Atlantic
348 (González-Sampéris et al., 2006; Gil-Romera et al., 2014; Leunda et al., 2017) vs. more
349 Mediterranean influence (e.g. Miras et al., 2007; Pérez-Obiol et al., 2012; Pérez-Sanz et al.,
350 2013; Connor et al., 2019).

351 Thus, the different patterns between BSM and MAR in terms of fire activity could be related to
352 the differences in biomass type and availability and to the lake's geographical settings, which
353 today is characterized by different amounts of rainfall (Fig. 1b). Especially, the rainfall gradient
354 has a critical effect on the landscape flammability as, if biomass is available, dry settings will
355 more easily become flammable. This would have been the case in BSM, located at a denser
356 vegetated, drier and more continental lower altitude (Pérez-Sanz et al., 2013) compared to the
357 alpine, locally wetter MAR site.

358 Even if fire severity and extent is difficult to infer from microscopic charcoal data alone, pollen
359 assemblages variation (e.g. an increase in herbaceous pollen taxa) can be used as indirect
360 evidence for high severity fires (Minckley and Shriver, 2011). As there are no evidences of
361 landscape opening in terms of herb expansion, it is likely that these fires did not play a
362 significant role in vegetation dynamics. In addition to this, no human occupation signs have
363 been detected for the Central Pyrenees at this period. The livelihood of Mesolithic (11700-
364 7800 cal yr BP) people was hunting-gathering in small nomadic groups (Valdeyron et al., 2008;

365 Ejarque et al., 2010), which implies weak environmental imprints (Montes et al., 2016; Rojo-
366 Guerra et al., 2018).

367 5.2.2 Increasing fire activity at HTM (ca. 7000-5500 cal yr BP)

368 Fire activity increased over the mid-Holocene in both sequences. MAR records an earlier
369 increase starting at ca. 7000 cal yr BP and, although fluctuating, lasting until ca. 5500 cal yr BP
370 (Fig. 4a), whereas the increase in fire activity in BSM occurs at ca. 6700 cal yr BP (Fig. 4g).
371 Other eastern Pyrenean sequences such as in Estanilles peatbog also show a fire increase
372 (Pérez-Obiol et al., 2012).

373 The expansion of mesophytes (especially *Betula*, deciduous *Quercus* and *Corylus*) in BSM
374 occurred during the mid-Holocene (8200-5500 cal yr BP; Fig. 4 j,k), when *Betula* could have
375 reached the sub-alpine belt (Pérez-Sanz et al., 2013; Leunda et al., 2019). The treeline, mainly
376 composed by *Pinus*, would have reached the highest levels during this period (Cunill et al.,
377 2013; Leunda et al., 2019). This biomass expansion has been closely related to a summer
378 temperature increase. In fact, the chironomid based July temperature reconstruction for the
379 Holocene in BSM, shows that the maximum summer temperatures occurred between 8000-
380 6500 cal yr BP (Fig. 4n) which is in agreement with other European summer temperature
381 reconstructions defining the HTM (Renssen et al., 2009; Samartin et al., 2017). Thereby,
382 favourable climate conditions for burning established supported by the constant and
383 increasing biomass availability. Nevertheless, fires were probably neither intense nor virulent,
384 since vegetation does not show important changes.

385 In addition to this, scatter Neolithic archaeological sites have been found at lower elevations in
386 the Central Pyrenees where sparse *fumier* levels (succession of animal manure, soil and plant
387 remains, which besides being naturally fermented, were sometimes burned to sanitize the
388 enclosure (Alday et al., 2012; Montes and Alday, 2012) were identified (Figs. 1a and 6o).
389 However, no pollen evidence for agro-pastoral activities are detected in MAR and BSM nor in

390 the nearby palaeoenvironmental sequences at this time (González-Sampéris et al., 2017).
391 Nevertheless, a rather early human impact with punctual presence of cereal pollen grains since
392 the Neolithic onset (ca. 7000 cal yr BP) or even earlier (Ejarque et al., 2010; Pérez-Obiol et al.,
393 2012) has been detected in the eastern Pyrenean palaeoenvironmental sequences, where
394 sparse sub-alpine Neolithic settlements were found (Gassiot Ballbè et al., 2014; Gassiot Ballbè,
395 2016).

396 Thus, even if it is not possible to discard punctual anthropogenic burning practices during the
397 Neolithic period, it is not likely that they would leave a large imprint at high altitude sites as
398 evidences for human presence occur locally at lower altitudes (González-Sampéris et al., 2019).
399 Thus, the driving mechanism for the increase in fire activity at both sites at ca. 7000 cal yr BP
400 might be related to both biomass availability and increasing summer temperatures.

401 *5.2.3 Fire activity decline during the Neoglacial period (ca. 5500-3700 cal yr BP)*

402 Both in BSM and MAR there's a general fire activity decline concurrent at regional (Rius et al.,
403 2011; Garcés-Pastor et al., 2017) and subcontinental scales (Vannière et al., 2011) at ca. 5700
404 cal yr BP (Fig. 4a,g). Wildfire weakening coincides with the beginning of the Neoglacial period
405 (Davis et al., 2009; Kumar, 2011) where a glacier expansion occurred at ca. 5100 ± 100 cal yr
406 BP, in both southern (García-Ruiz et al., 2014) and the northern (Gellatly et al., 1992) slopes of
407 the Central Pyrenees. We lack an independent temperature reconstruction for 6000-4200 cal
408 yr BP period due to low chironomid contents in BSM. However, during the late-Holocene
409 (4200-2000 cal yr BP) inferred temperatures were the lowest through the Holocene (Fig. 4n;
410 Tarrats et al., 2018).

411 A lower proportion of archaeological settlements were present in Central Pyrenees at this time
412 (Fig. 4o), as societies may have also been affected by the wetter/cooler oscillations of the
413 Neoglacial period. Rius et al. (2011) also indicated fewer signs of human activities at the

414 northern slope of the Pyrenees. This scenario suggests that climatic control is still dominant in
415 promoting fire occurrence during the mid-to-late-Holocene transition.

416 Simultaneously, *Abies* spread from ca. 6000 cal yr BP in both BSM and MAR (Fig. 4c,i) and in
417 other Pyrenean records (Miras et al., 2007; Pérez-Sanz et al., 2013; Garcés-Pastor et al., 2017).
418 *Abies* is a mesophilous, late-successional tree species very shade tolerant and considered to
419 prefer cool and moist sites (Villar et al., 1997). Different studies have also demonstrated that
420 *Abies* is a fire sensitive taxon, being negatively affected by fire activity (Tinner et al., 1999;
421 Schwörer et al., 2015). So, we argue that the fir spread could be favoured by both the
422 temperature descent and a weaker fire activity until ca. 3500 cal yr BP (Fig. 4a,g).

423 Deciduous trees progressively declined during this period in our study sites following the same
424 pattern as other Pyrenean sequences (González-Sampériz et al., 2006; Miras et al., 2007;
425 Pèlachs et al., 2007; Pérez-Sanz et al., 2013; Garcés-Pastor et al., 2017; Leunda et al., 2017),
426 very likely related to these changing climatic conditions.

427 *5.2.4. High variability of fire activity over the last 3700 years*

428 A great increase in fire activity is appreciated in both sequences; at ca. 3700 cal yr BP in BSM,
429 followed by the rise in MAR between 3500-3000 cal yr BP. In regard to the eastern Pyrenean
430 palaeoenvironmental sequences, a general intensification of fire occurrence is observed for
431 the last ca. 4000 years, with an alternation of higher and lower periods of fire activity,
432 denoting spatial and temporal disparities in fire activity (Bal et al., 2011; Rius et al., 2011;
433 Garcés-Pastor et al., 2017). Dated palaeofire layers also appear more frequently from ca. 3000
434 cal yr BP onwards, indicating the occurrence of fires.

435 Herbs increase significantly both in MAR and BSM (reaching values >30%) (Fig. 4f,m), indicating
436 a regional opening of the landscape where fire may have played an important role. Previous
437 fires were probably not as severe as those occurred over the last four millennia. Hence, fire did

438 not provoke important biomass losses, contrarily to what may have occurred over the last ca.
439 3700 years. *Abies* decreased (Fig. 4c,i), suggesting again that fir's populations may have been
440 negatively affected by fires.

441 Regarding climatic factors, reconstructed summer temperatures in the area are the lowest for
442 the whole Holocene (Fig. 4n; Tarrats et al., 2018), which apparently may have not favoured fire
443 occurrence. A decoupling of fire and climatic control has been attributed to human impact,
444 overriding the effect of natural ignition in alpine ecosystems (Colombaroli et al., 2010).
445 However, there is a significant gap of archaeological settlements during the Bronze-Iron Age,
446 from 4000 cal yr BP onwards both in the Central (Fig. 4o; González-Sampéris et al., 2019) and
447 in the eastern Pyrenees (Gassiot Ballbè et al., 2014), despite an intensification of agricultural
448 and grazing indicators has been detected in the eastern Pyrenean sequences (Miras et al.,
449 2007; Pèlachs et al., 2007; Bal et al., 2011; Pérez-Obiol et al., 2012; Garcés-Pastor et al., 2017).

450 This heterogeneous pattern in fire activity, during an arguable period of anthropogenic fire
451 dynamics, could be associated with a steady but non-permanent human impact in mountain
452 areas during the Bronze Age and onwards in a complex landscape scenario. Human-induced
453 fires, would have locally maintained more open landscapes in specific areas (González-
454 Sampéris et al., 2019).

455 A great spatial variability in terms of fire activity has also been observed in other European
456 mountain ranges such as the Alps (Colombaroli et al., 2010; Leys et al., 2014) and in the
457 Carpathians (Feurdean et al., 2012; Florescu et al., 2018) but generally indicating increasing
458 human related landscape transformations during the last 4000 years.

459 The slight increase of fire activity in BSM during the Medieval Period (Fig. 4g) could be related
460 to the intensification of the landscape opening over the last 1000 years, (increase in *Artemisia*,
461 *Poaceae*, *Cichorioideae*, *Chenopodiaceae*) (Fig. 4f,m) as well as the high presence of human
462 settlements in the eastern Pyrenees (Gassiot Ballbè, 2016). Simultaneously, and perhaps with a

463 synergistic effect to human activity, drier conditions during the Medieval Climate Anomaly
464 (MCA), a period of aridity recognized in most of south-western Europe (Seager et al., 2007;
465 Moreno et al., 2012), could have also favoured fire occurrence.

466 In addition to this, historical documents record mining activities to exploit iron, silver and lead
467 at least since Medieval times (Bielza de Ory et al., 1986) in the Bielsa-Parzán area (Fig. 1a) as
468 well as in other Pyrenean areas (Pèlachs et al., 2009). The increase in herbs at this time, could
469 be very likely related to the land-use intensification that occurred, as miners were given lands
470 in order to ensure their permanence in the valley (Bielza de Ory et al., 1986). Both mining and
471 smelting activities very likely affected forests through deforestation and burning due to
472 increasing energy demand (Bielza de Ory et al., 1986; Jouffroy et al., 2005; Pèlachs et al.,
473 2009). However, no signs of contamination in terms of trace metal deposition increase is
474 detected in MAR and BSM lakes at this time (Corella et al., 2018; Oliva-Urcia et al., 2018),
475 probably related to the low intensity of the mining activities to cause a regional imprint.

476 MAR shows a prominent charcoal peak at the end of the 19th century, which stays relatively
477 high until ca. 1930 AD (Fig. 6). This tendency concurs with the Pb enrichment in MAR Lake
478 sediments (Fig. 6) (Corella et al., 2018; Oliva-Urcia et al., 2018) likely related to the onset of
479 large-scale Pb production in the Parzán area which started by the end of the 19th century
480 lasting until 1930, when the closure of the mines occurred due to the decrease in Pb prices
481 (Nieto-Callén, 1996; Fanlo et al., 1998). The historical metal mining in this area ended at this
482 time. This Pb enrichment is not detected in BSM, probably related to the lake characteristics
483 and its lower altitude, that greatly reduce the lake sensitiveness to record historical pollution
484 of trace metals as suggested by Corella et al. (2018).

485 For more recent times, the significant increase in fire activity registered in BSM at 1980 AD
486 (being the maximum microcharcoal peak) (Fig. 4g) could be related to the large fires that
487 occurred in summers of 1980 AD, 1981 AD, 1986 AD and 1991 AD in the Central Pyrenees

488 where 2200 to 6500 Ha of woodlands were burnt in each fire (El País, 1980; Vázquez de la
489 Cueva, 2016).

490

491 **5.3 How determinant was fire modifying alpine landscapes in the Pyrenees during the** 492 **Holocene?**

493 Regardless the site-to-site variations that seem to determine fire activity most, an interesting
494 finding is that fire at these altitudes has not generally played a critical role in vegetation
495 dynamics. This finding suggests that, as occurs in the present, past alpine and sub-alpine
496 vegetation communities were not, broadly speaking, fire-prone neither fire-driven ecosystems
497 (Leys et al., 2014). Thus, fire regimes may have not been the most relevant factor on forest
498 dynamics, unlike Mediterranean ecosystems, which are composed of highly flammable
499 sclerophilous vegetation (Keeley et al., 2012). This situation has also been observed in other
500 studies in mountain areas e.g. in the Dolomites (Leys et al., 2014).

501 According to our data, the selected forest taxa in BSM and MAR are best characterised by their
502 own endogenous effect, i.e., a higher antecedent presence of a particular taxa has a positive
503 effect on its abundance (Fig. 5a,c,d,e,f). In other words, a larger population will cope better
504 with environmental change and disturbances, and remain large until a certain threshold in a
505 specific forcing is reached. While in MAR fire may have played a more important role for
506 *Corylus* and *Abies* (Fig. 5a,b), we interpret inter-site differences as a consequence of the proxy
507 potential source area, as several studies have evidenced that higher elevations may record
508 best regional rather than local environmental variation (Escudero et al., 2016; Corella et al.,
509 2018).

510 Fire at BSM might be indeed reflecting local but scattered events that, according to our data,
511 do not imply any response for most taxa, except for deciduous *Quercus* (Fig. 5f) (likely *Quercus*

512 *pubescens* or *Q. humilis*). This taxon, unlike all the others, may not have been locally present
513 nearby the lake (Pérez-Sanz et al., 2013). However, it successfully sprouts after fire generally
514 out-competing non-serotinous pines like the ones present in the sub-alpine belt (Sánchez-
515 Pinillos et al., 2018) as the ones present in BSM. MAR, more exposed to tropospheric
516 circulation due to its higher altitude, is possibly reflecting an even more regional picture of
517 both vegetation and fire variability. This fact implies, on the one hand, that proxies might be
518 recorded with larger lags than expected. On the other hand, it indicates that environmental
519 variability from different locations might be harmonized by sedimentary processes at these
520 altitudes that prevents evidencing spatial co-occurrent effects of disturbance on vegetation
521 response. Such might be the case of the positive effect that CHAR has on *Abies* if antecedent
522 PAR values are under the threshold (Fig. 5a). This would be one example of a, probable, lack of
523 spatial simultaneity on fire occurrence and vegetation response where charcoal and pollen
524 might be arriving from different areas. While this might be the case for all other taxa in MAR
525 too, concurrent CHAR is the only variable with a positive influence on *Corylus* PAR in this site
526 (Fig. 5b). In this particular case hazel is indeed a clear case of a temperate tree where both
527 neo- and palaeoecology studies (Tinner et al., 1999; Finsinger et al., 2006) have evidenced a
528 fast and positive fire response given its resprouting ability after burning (Delarze et al., 1992).
529 Besides the post-fire strategy, hazel pollen production is enhanced when vegetation is opened
530 by disturbance (Aaby, 1986; Bégeot, 1998). This fact is likely explaining why the concurrent
531 rather than the antecedent fire is more critical in affecting *Corylus* presence, as resprouting
532 and pollination would happen very soon after fire.

533 Finding that fire might not be the most critical factor shaping the long-term dynamics of the
534 analysed tree taxa has important consequences for conservation practices as fire occurrence
535 has been predominantly low in these sub-alpine areas and thus future scenarios with more
536 active fires might threaten the treeline ecosystems. In fact, the abandonment of agro-pastoral
537 activities in mountain areas during the past decades in the Pyrenees has provoked bush

538 encroachment, which concurring with the rise in average temperatures, may increase fire risk
539 during the next decades forced by the synergistic effect of both climate conditions and human
540 impact

541

542 **6. Conclusion**

543 Here we present the comparison of two long-term fire activity records from different altitudes
544 in the Central Pyrenees providing a better understanding of the Holocene fire-vegetation
545 dynamics in this mountain range. Our results highlight that caution should be taken when
546 comparing the results of different lacustrine sequences, even if they are in the same mountain
547 range, and just few km away, as site-specific settings may determine different fire behaviour
548 and source areas. We argue that fire activity during the early-to-mid-Holocene was relatively
549 low and mostly controlled by climate. High summer temperatures together with high biomass
550 accumulation led to a prolonged period of high fire activity during ca. 7000-6000 cal yr BP as
551 recorded in MAR with a coeval increase in fire activity, but shorter in duration, in BSM at ca.
552 6700 cal yr BP. Burning decreased, concurring with the Neoglacial period, which suggests that
553 climatic control was still dominant in promoting fire occurrence until 3700 cal yr BP, when fire
554 activity increased coevally to the opening of the landscape and decoupled from climate as the
555 only fire driver. Although from ca. 3000 cal yr BP onwards, fire activity decreases the increasing
556 human pressure over the last centuries, lead to a remarkable rise in fire activity. Our results
557 highlight that, overall fire activity does not seem to be a critical factor shaping alpine
558 ecosystem through the Holocene. However, the increase in arboreal biomass due to
559 abandonment of traditional land uses in mountain areas together with the rise in average
560 temperatures during the last decades, may increase fire risk in the nearby future, as occurred
561 in the HTM.

562

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1004 pp. 75–97.
1005
- 1006 **Data and code availability**

1007 The code and data are available in this GitHub link: <https://github.com/BlasBenito/PyreFire>,
1008 and are deposited in Zenodo under the DOI 10.5281/zenodo.3266002.

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1011 Figures

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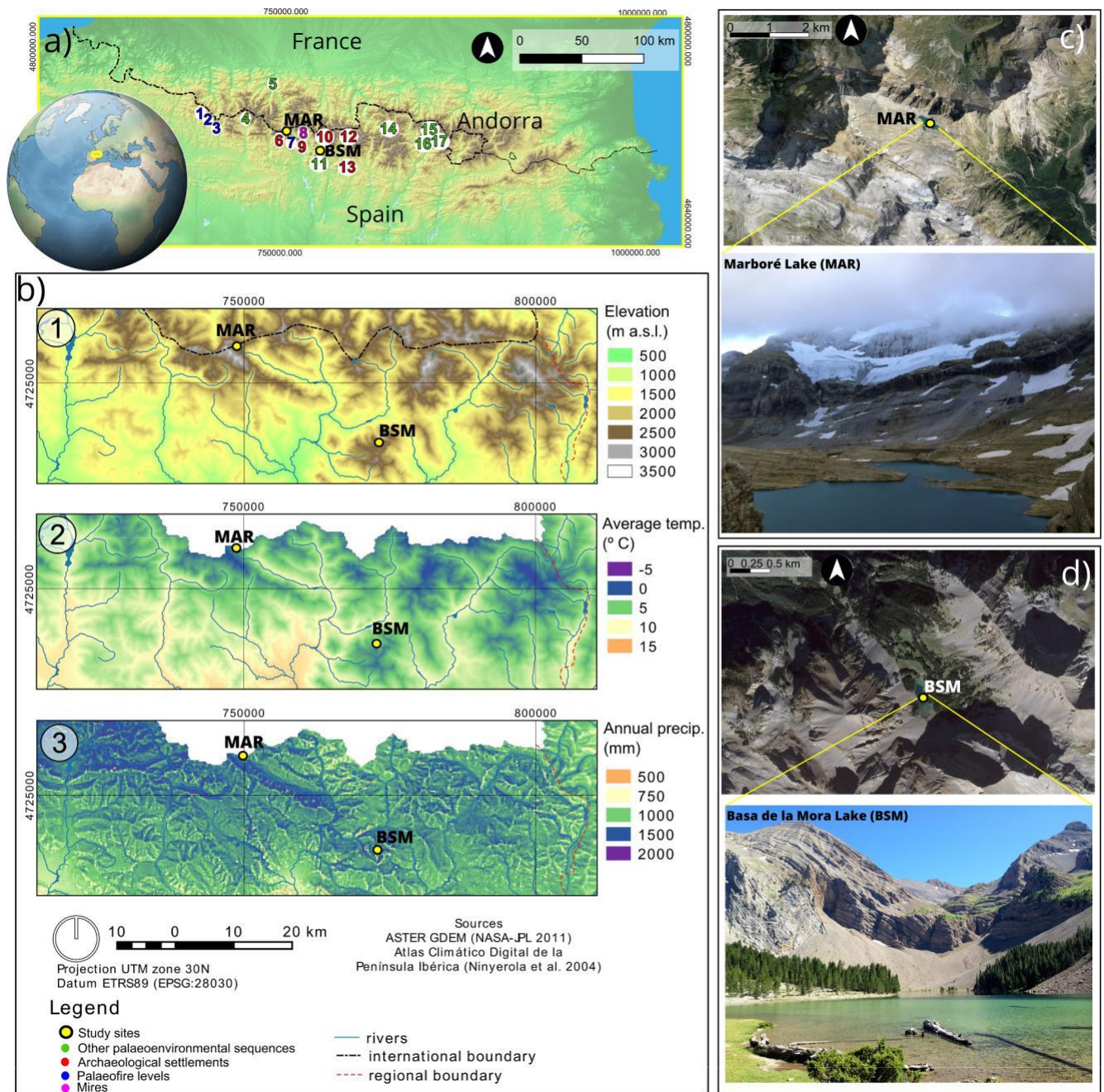
1013 Holocene fire and vegetation dynamics in the Central

1014 Pyrenees (Spain)

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1016 Maria Leunda, Graciela Gil-Romera, Anne-Laure

1017 Daniau, Blas M. Benito, Penélope González-Sampéiz



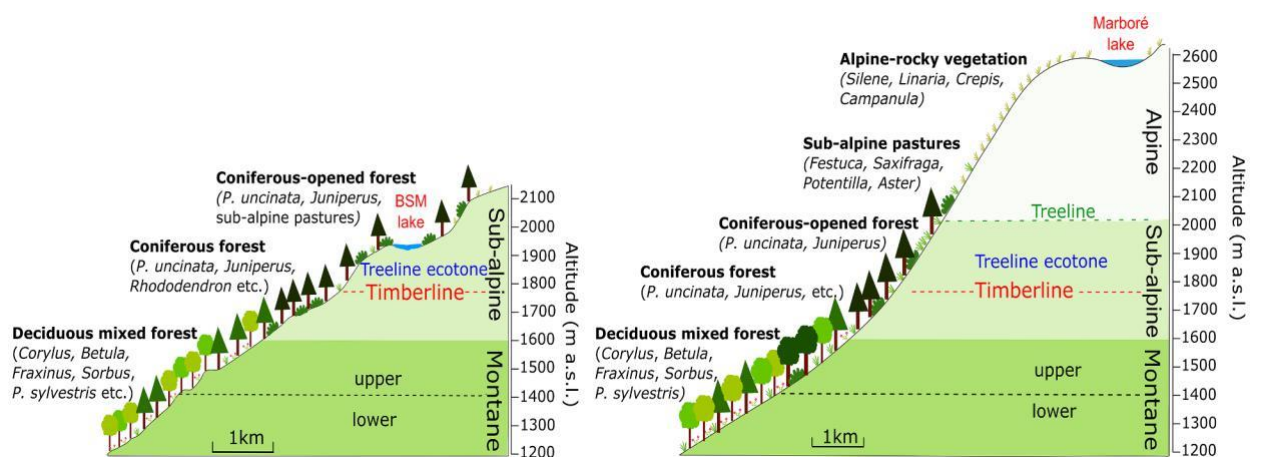
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1019 **Figure 1.** (a) Location map of the study lakes Marboré (MAR) and Basa da la Mora
 1020 (BSM) in the Pyrenees together with other existing records; in blue: dated palaeofire
 1021 levels; in red: archaeological settlements; in green: other existing fire and pollen
 1022 records; in pink: mires. 1: Plandaniz (González-Sampéris et al., 2019); 2: Aragiüés
 1023 (González-Sampéris et al., 2019); 3: Las Blancas (González-Sampéris et al., 2019), 4:
 1024 Portalet peatbog (González-Sampéris et al., 2006; Gil-Romera et al., 2014); 5: Lourdes

1026 Lake (Rius et al., 2011); 6: Barranco Pardina (Laborda et al., 2017); 7: Valle Pardina
 1027 (González-Sampéris et al., 2019); 8: Parzán mires; 9: Corotrasito (Clemente et al.,
 1028 2016); 10: Puyascada (Baldellou, 1987); 11: Armeña-A294 Ice Cave (Leunda et al.,
 1029 2019); 12: Hospital de Benasque (Ona and Calastrenc, 2009); 13: Els Trocs (Rojo et al.,
 1030 2013); 14: Bassa Nera (Garcés-Pastor et al., 2017); 15: Estanilles peatbog (Pérez-Obiol
 1031 et al., 2012); 16: Plaus de Bodis-Montarenyo (Cunill et al., 2013); 17: Burg (Pèlachs et
 1032 al., 2011). (b) Topographic (1), Temperature (2) and Precipitation (3) maps of the study
 1033 areas. c) Ortophoto and photography of the MAR Lake and surrounding area. d)
 1034 Ortophoto and photography of BSM and surrounding area (Google, Imagery 2019.
 1035 CNES. Institut Cartografic de Catalunya, Landsat. Copernicus, Maxar Technologies,
 1036 Map data 2019).

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1040 **Figure 2.** Simplified vegetation transects for Basa de la Mora (left) and Marboré (right)

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1048 **Table 1**

1049 Summary of main features of Marboré and Basa de la Mora Lakes. MAP: mean annual
 1050 precipitation; SP: summer precipitation; WP: winter precipitation; MAT: mean annual
 1051 temperature; SMMT: summer mean maximum temperature. Climatic data have been
 1052 extracted from Ninyerola et al. (2005) and Batalla et al. (2018).

	Basa de la Mora (BSM)	Marboré (MAR)
Coordinates	42°32'N, 0°19'E	42°41'N, 0°2'E
Altitude (m a. s. l.)	1914	2612
Lake type and dimensions	· Holomictic lake	· Cold Dimictic lake
	· ~300 m length	· ~500 m length
	· ~100 m across	· ~200 m across
Lake basin characteristics	· Maximum water depth of 4.5 m	· Maximum water depth of 30 m
	· Shallow glacial lake	· Alpine glacial lake
	· Glacial over-deepened basin enclosed by a frontal moraine, surrounded by steep limestone walls	· Glacial over-deepened basin within a glacial cirque at the border between the northern and the southern slopes of the Pyrenees
	· Catchment consists of Mesozoic limestones and sandy limestones	· Sandy limestones and fine-grain sandstones cemented by a carbonatic matrix
MAP	1500 mm	2000 mm

SP	ca. 180 mm	ca. 230 mm
WP	ca. 150 mm	ca. 200 mm
MAT	5 °C	0 °C
SMMT	15 °C	10 °C
Vegetation belt	Sub-alpine	Alpine
Treeline altitude in the valley (m a.s.l.)	2000–2200	2000–2100
Timberline altitude in the valley (m a.s.l.)	1700–1900	1700–1900
Local vegetation	Treeline ecotone: <i>P. uncinata</i> together with <i>J. communis</i> , <i>R. ferrugineum</i> and sub-alpine pastures	Patches of annual and perennial herbs such as <i>Silene acaulis</i> , <i>Linaria alpina</i> and <i>Crepis pygmaea</i>

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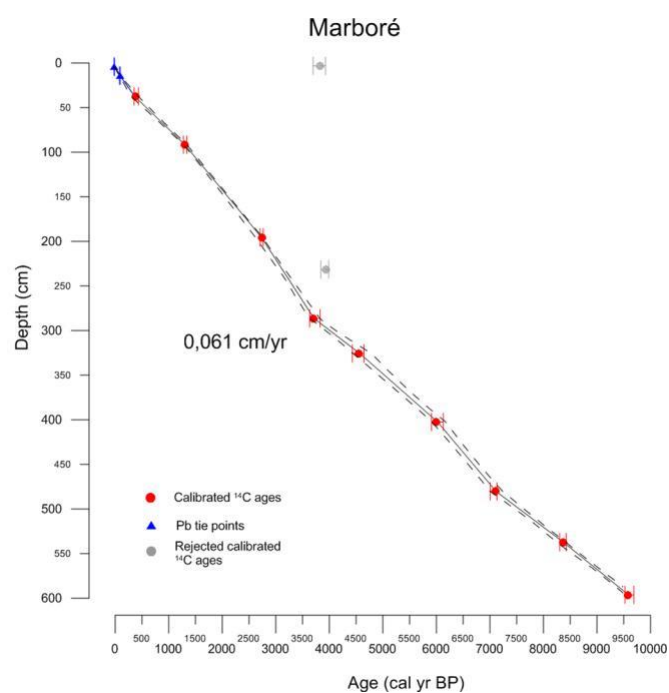
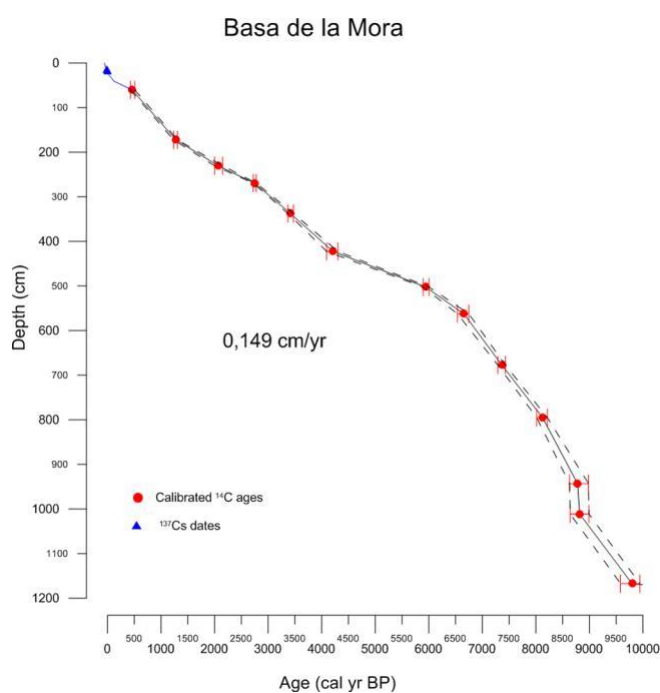
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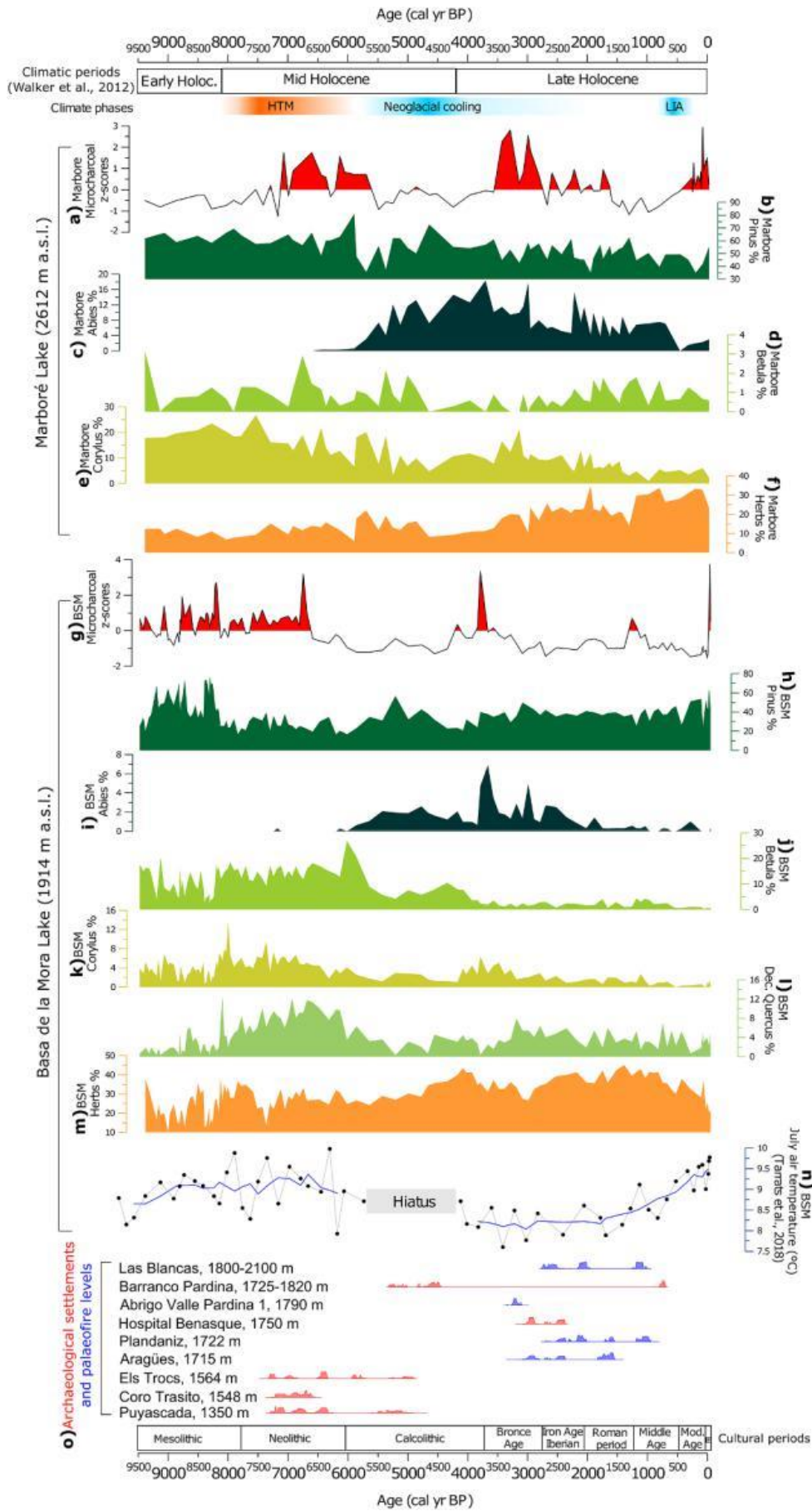
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1066 **Figure 3.** Holocene depth-age models for both sequences based on Pérez-Sanz et al.
1067 (2013) and Leunda et al. (2017).

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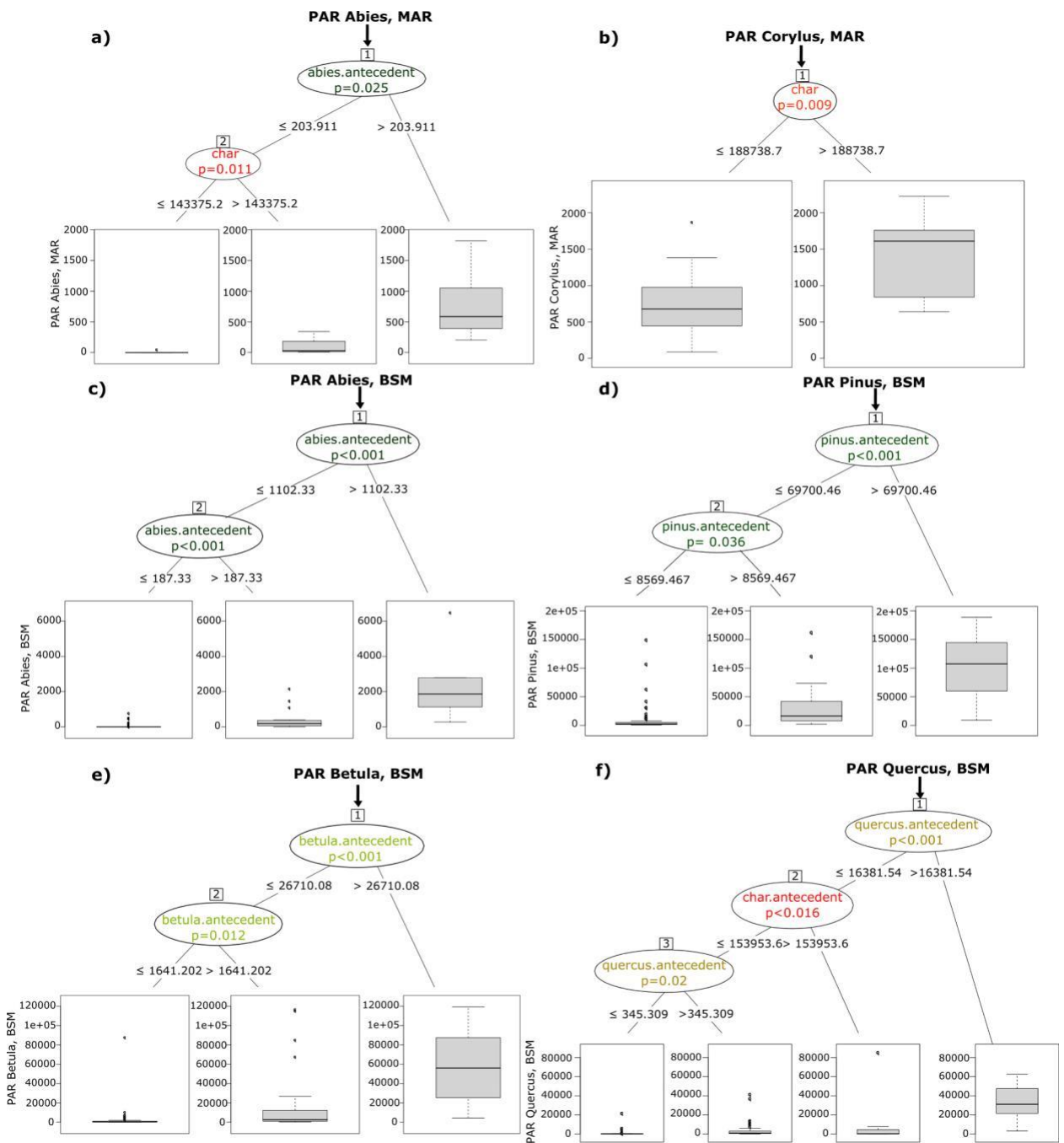
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1071 **Figure 4.** Comparison of different indicators from both MAR and BSM lake se-
1072 quences: (a) and (g) Microcharcoal z-scores from MAR and BSM sequences (the red
1073 shade indicate values above 0 in the z-scores standardized values), selected pollen taxa
1074 from MAR: (b) *Pinus*, (c) *Abies*, (d) *Betula*, (e) *Corylus*, and (f) Herbs (Leunda et al.,
1075 2017), selected pollen taxa from BSM: (h) *Pinus*, (i) *Abies*, (j) *Betula*, (k) *Corylus*, (l)
1076 Deciduous *Quercus* and (m) Herbs (Pérez-Sanz et al., 2013), (n) Chironomid-based
1077 Holocene summer temperature reconstruction from BSM (Tarrats et al., 2018) and (o)
1078 distribution and probability sum of calibrated radiocarbon dates of archaeological
1079 settlements (in red) and palaeofire layers, referring to layers in a soil, paleosoil,
1080 stratified scree or ravine which contain abundant charcoal particles of past fires (in blue)
1081 in the Central Pyrenees. Palaeofires: Las Blancas, Abrigo Valle Pardina; Plandániz,
1082 Aragüés (González-Sampéris et al., 2019). Archaeological settlements: Hospital de Be-
1083 nasque (Ona and Calastrenc, 2009), Barranco Pardina (Laborda et al., 2017), Coro
1084 Trasito (Clemente et al., 2016), Puyascada (Baldellou, 1987) Els Trocs (Rojo et al.,
1085 2013). HTM: Holocene Thermal Maximum. LIA: Little Ice Age. (See above-mentioned
1086 references for further information.)

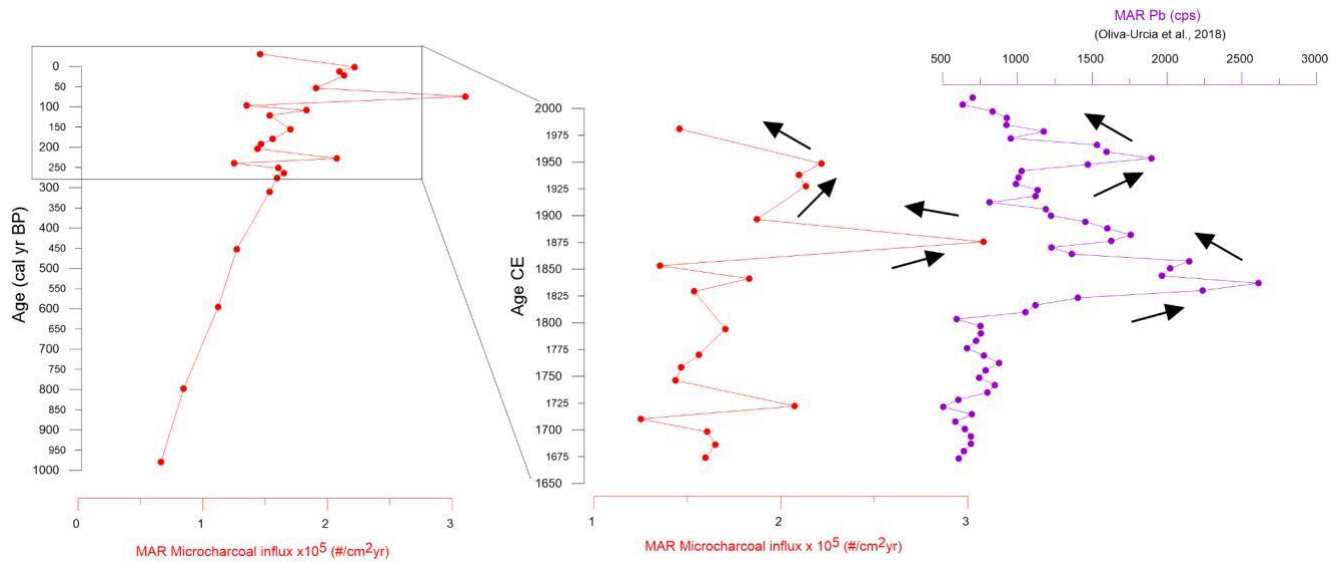
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1089 **Figure 5.** Conditional inference trees for selected taxa in both MAR and BSM
 1090 sequences: (a) PAR *Abies* in MAR, (b) PAR *Corylus* in MAR, (c) PAR *Abies* in BSM,
 1091 (d) PAR *Pinus* in BSM, (e) PAR *Betula* in BSM and (f) PAR *Quercus* in BSM. At the
 1092 top of each regression tree, the initial PAR values for each taxa are indicated. Each of
 1093 the circles (with a number e.g. 1,2,3) show the best explanatory variable (with the
 1094 corresponding p value) from all the considered variables (CHAR, CHAR.antecedent or

1095 PAR.antecedent) for the initial PAR values for each taxa. The boxplots, represent mean
1096 values of each PAR series classified according to the explanatory variables.
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1099 **Figure 6.** Microcharcoal influx in MAR for the last 1000 years (left side) with a zoom
1100 over the last 300 years and compared it with Pb element profile (Oliva-Urcia et al.,
1101 2018) in MAR (right side).

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