

1 Long-term vegetation history of a relict birch forest (*Betula pubescens* subsp.
2 *celtiberica* (Rothm. & Vasc.) Rivas Mart.) in the Toledo Mountains (central Iberia).

3 Conservation implications

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25 ABSTRACT

26 Understanding ecosystem resilience requires long data series provided by palaeoecological studies, the best
27 tool for reconstructing vegetation dynamics. Here, we analyzed a continuous and well-dated record of pollen,
28 non-pollen palynomorphs, macrocharcoal remains, loss-on-ignition and magnetic susceptibility from one of
29 the most singular peatlands in the Toledo Mountains (central Spain), in order to delineate the anthropogenic
30 and/or climate impact on the peatland and the ecosystem's response. La Ventilla mire is an isolated site of
31 birch woodland dominated by *Betula pubescens* subsp. *celtiberica* (Rothm. & Vasc.) Rivas Mart. This mire,

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32 acting as a refugium for this species, is located in Cabañeros National Park and is recognized as ‘Special
33 Area of Conservation’ according to Habitats Directive of the Natura 2000 network. We describe major
34 patterns and trends in the development of this palaeorefugium since the mid-Holocene (~6145 cal BP) and
35 provide historical context for some natural and/or human-induced dynamics. Around 1500 cal BP, the lotic
36 depositional environment with slow moving backwaters developed into a minerotrophic mire. Until the
37 Middle Ages, macroclimate and autogenic succession appear to have been the main drivers of both local and
38 regional development of vegetation. Between 1500 and 500 cal BP, an abrupt decline in birch cover started,
39 coincident with the Visigothic period. The pronounced peaks in the coprophilous fungi record *ca.* 1000 and
40 150 cal BP reflect extensive pastoral activities in the area. This study shows how palaeoecological
41 knowledge helps to explain present patterns in the composition of a valuable protected site, which may be
42 used in prioritizing conservation.

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44 *Keywords:* Southwestern Europe, Mid-Mountains, Holocene, Human impact, Refugia.

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47 **1. Introduction**

48

49 Marginal plant populations are usually located at the edge of the species’ range and/or compose, isolated
50 communities thriving in reduced favorable microhabitats within an overall environmentally unsuitable matrix
51 (Lesica and Allendorf, 1995). These assemblages usually bear valuable genetic resources resulting from the
52 adaptation to the ‘unusual’ (considering the entire distribution range of the species) local ecological
53 conditions (Ellstrand and Elam, 1993; Petit et al., 1998; Hewitt, 2000). For instance, Mediterranean relict
54 populations of temperate and boreal tree species often harbor unique genotypes (Hampe and Petit, 2005).
55 The ‘marginality’ of these populations may be due to past environmental changes and anthropogenic impacts
56 causing repeated shifts in species composition and habitat distributions, and eventually leading to the
57 formation of island-like habitats (Webb III, 1986; Benito-Garzón et al., 2008; Birks and Willis, 2008;
58 Giesecke et al., 2017). Current marginal plant populations and communities may represent remnants of once
59 more widespread distributions affected by fragmentation processes or, on the contrary, habitats or
60 populations established recently in an area where they were previously absent, i.e. ‘palaeorefugia’ or

61 'neorefugia', respectively (Comes and Kadereit, 1998; Hewitt, 1999; Nekola, 1999). The unique features of
62 such communities due to their fragmentation and isolation usually imply adopting specific management
63 measures to ensure their conservation (Pulido et al., 2008; Sanz et al., 2009, 2011).

64 Understanding the impact of past disturbances (e.g. human impact, fire events) and climatic variability as
65 well as assessing long-term ecosystem resilience are essential to effectively preserve ecosystem properties
66 (e.g., biodiversity, soil features, primary productivity) and services (e.g., carbon sequestration, food
67 provisioning, natural hazard protection) and to eventually reverse their degradation (Chapin et al., 2009).
68 Such comprehensive assessments of ecosystem functioning, and particularly of resilience, require long-term
69 data series (López-Sáez et al., 2002, 2018a; Gil-Romera et al., 2010; Hennebelle et al., 2018), which are
70 often lacking (Cole et al., 2015). Palaeoecological research can contribute to fill this gap, and the study of
71 ecosystem responses to Holocene environmental and climatic change can actually provide a wealth of
72 information relevant to conservation and management purposes (Froyd and Willis, 2008; Birks, 2012; Page
73 and Baird, 2016; Giesecke et al., 2017). While it has been acknowledged that long-term ecological
74 information should be routinely incorporated in conservation planning (Willis et al., 2005, 2007; Willis and
75 Birks, 2006), successful examples of this practice remain quite rare in the Iberian Peninsula (Gil-Romera et
76 al., 2010; Carrión et al., 2013, 2015; Morales-Molino et al., 2017, 2019; López-Sáez et al., 2018a). Forest
77 species diversity and conservation value are both considerably influenced by site history (Svenning and
78 Skov, 2007), so historical and palaeoecological research provide valuable bases to develop management
79 strategies aimed at enhancing forest conservation (Honnay et al., 2004; Birks, 2012). Therefore, studying
80 palaeoenvironmental archives such as peatlands allows assessing the adaptability and vulnerability of
81 ecosystems to climate change and human impact (Petit et al., 2005; Balbo et al., 2017).

82 During the past few decades, long-term environmental change in southwestern Mediterranean mid-
83 mountain contexts have attracted increasing interest, not only because of their high sensitivity to climate
84 change but also because of their particular history of human settlement (McCarthy et al., 2001; Valladares et
85 al., 2004; Blondel, 2006; Carrión et al., 2010; González-Sampériz et al., 2010; Oliva et al., 2018). Usually
86 considered marginal and risky areas, humans settled in Mediterranean mid-elevation mountains quite late in
87 Prehistory, and only intermittently (Surmely et al., 2009; López-Sáez et al., 2014a). Besides, Mediterranean
88 mid-mountain ecosystems are more vulnerable to climate change than other European ecosystems. Predicted

89 climatic scenarios in Mediterranean mid-mountains show a very significant decrease in precipitation
90 concomitant with a considerable increase in temperature (McCarthy et al., 2001).

91 In the center of the Iberian Peninsula, the Toledo Mountains are a noteworthy example of south-western
92 Mediterranean mid-mountain range. Differences in morphology and elevation, as so their east-west
93 orientation create a mosaic of microclimatic environments while its location in the middle of the Southern
94 Iberian Plateau makes it behave as an island for biodiversity (Perea and Perea, 2008). Gorges and mires are
95 particularly important microhabitats, because high water availability and air moisture have allowed the
96 persistence of Eurosiberian and Tertiary woody species (e.g. *Betula* spp., *Corylus avellana* L., *Ilex*
97 *aquifolium* L., *Prunus lusitanica* L., *Taxus baccata* L.) until today, acting as hydrologic refugia (Perea and
98 Perea, 2008; Calleja et al., 2009; Sánchez del Álamo et al., 2010; López-Sáez et al., 2014c; Luengo-Nicolau
99 and Sánchez-Mata, 2015; Morales-Molino et al., 2018; López-Sáez et al., 2019; Luelmo-Lautenschlaeger et
100 al., 2020).

101 Land-use history has been a major driver of forest dynamics, composition and diversity in many
102 Mediterranean mountain regions of southwestern Europe during the Holocene (Carrión, 2002; López-Merino
103 et al., 2008; Carrión et al., 2010, 2013, 2015, 2018; González-Sampérez et al., 2010; Morales-Molino et al.,
104 2017, 2021; Aranbarri et al., 2014; López-Sáez et al., 2014a; Camuera et al., 2018, 2019; Mesa-Fernández et
105 al., 2018). Therefore, ecosystem ‘authenticity’ (Larsen, 1995), that is proximity to a ‘pristine state’
106 (Bradshaw, 2005), or otherwise, continuity, the absence of direct anthropogenic intervention in forest
107 dynamics for long periods, is usually considered of high conservation value (Birks, 2012). On the other hand,
108 disturbance regimes, particularly the frequency and type of disturbance are also relevant to forest diversity
109 (Crandall et al., 2000). Thus, approaching local forest history under the light of palaeoecology is essential to
110 assess which ecological factors are responsible for the current conservation status. The few long-term stand-
111 scale studies that have been conducted in the Toledo Mountains so far suggest that fire history and, in recent
112 times, the overabundance of wild ungulates after human disturbance have altered their population dynamics
113 entailing major impacts on present forest attributes (Morales-Molino et al., 2018, 2019; Luelmo-
114 Lautenschlaeger et al., 2019a). In this regard, the case of birch stands (*Betula* spp.) growing on peatlands and
115 water streams in the Toledo Mountains is paradigmatic. These wetland ecosystems are currently under heavy
116 grazing pressure, as abundant wild ungulates roam mostly uncontrolled (Acevedo et al., 2008; Muñoz et al.,
117 2009; Perea and Gil, 2014). In fact, this is a major threat to several ecosystems worldwide, including many

118 areas of the Toledo Mountains (Perea et al., 2014). While the response of forest vegetation to high density of
119 herbivores has been well studied, responses of peatland vegetation are far less known (Pellerin et al., 2006;
120 Balbo et al., 2017). Another major human impact on the birch populations of Toledo Mountains is
121 groundwater exploitation for irrigation of the adjacent fields, which is lowering the water table in the
122 peatlands (Rodríguez-Rodríguez and Martínez-Vega, 2017).

123 Two species of birch are native to the Iberian Peninsula (Moreno and Peinado, 1990; Beck et al., 2016):
124 silver birch (*Betula pendula* Roth) and downy birch (*B. pubescens* Ehrh.). Both are monoecious wind-
125 pollinated pioneer trees that have a wide climatic range (Beck et al., 2016). *Betula pendula* is diploid ($2n =$
126 28), it tolerates drier soils in Mediterranean contexts like the Toledo Mountains and reaches the mountains of
127 southern Eurasia and even north-western Africa, whereas *B. pubescens* is tetraploid ($4n = 56$), extends
128 further north and prefers wetter soils (Atkinson, 1992; Jonczak et al., 2020). *Betula pubescens* is represented
129 in the Iberian Peninsula by the subspecies *celtiberica*, which may grow up to 20 m tall with single or many
130 stems, and has distinctly hairy annual branches and sprouts. Downy birch is mainly present in the
131 Eurosiberian region of the Iberian Peninsula where it develops on peatlands, forested wetlands, riparian
132 forests, forest clearings, scree slopes and in montane and subalpine forests, where it even dominates defining
133 the forest line (Blanco et al., 1997). Downy birch is abundant in the Cantabrian Range, the Pyrenees and
134 northwestern Iberia, becoming rarer with fragmented populations in the central Iberian mountains such as the
135 Northern Iberian Range and the Iberian Central System (Castroviejo et al., 1990; Blanco et al., 1997). The
136 Mediterranean populations of this species represents fits southernmost range and are considered relict and
137 endangered due to the small size of their stands, the scarcity and fragmentation of suitable habitats, and a
138 significant number of anthropogenic threats (Devesa and Ortega, 2004; Sanz et al., 2011). The sole extant
139 population of downy birch in Toledo Mountains ('La Ventilla', Cabañeros National Park) is the
140 southernmost known Iberian population known (Sánchez del Álamo et al., 2010; Perea et al., 2015).

141 Birches have played a fundamental role in the Late Pleistocene and Holocene vegetation of northern
142 Iberia (Carrión et al., 2010; Ochando et al., 2020a, 2020b). However, their importance in the landscape
143 decreases southwards in the Mediterranean mountains (but see e.g. Franco et al., 1998; Morales-Molino et
144 al., 2013). For example, birch forests dominated during the Lateglacial and the early Holocene in the
145 Northern Iberian Range and the western Iberian Central System thanks to their pioneer and heliophilous
146 character, forming mixed woodlands with pines or oaks, becoming rarer from the mid-Holocene onwards

147 when they were restricted to mountain streams (López-Merino et al., 2008; Morales-Molino et al., 2013;
148 Abel-Shaad et al., 2014; López-Sáez et al., 2014a). In contrast, birches expanded to some extent during the
149 mid-Holocene, disappearing during the late Holocene (Carrión et al., 2013, 2015, 2018). In the Toledo
150 Mountains, currently available palaeobotanical evidence demonstrates the past importance of birch groves
151 (Morales-Molino et al., 2018, 2019; Luelmo-Lautenschlaeger et al., 2018a, 2018d, 2019a, 2019b, 2020).
152 These were generally associated to peatland ecosystems, which were much more extensive than today as
153 they have declined in recent millennia due to both climate change and human impact.

154 Within the framework of a research project focused on the resilience and vulnerability of the mountain
155 ecosystems in the Toledo Mountains, we have examined the natural and anthropogenic factors driving
156 vegetation dynamics and exploitation in the Cabañeros National Park. In this paper, we study the long-term
157 development of the only relict birch stand of *Betula pubescens* subsp. *celtiberica* currently documented in
158 the Toledo Mountains, with the aim of delineating guidelines for its future management that preserves and
159 enhances its biological and cultural values. This study is pertinent for various reasons, namely: i) the
160 available palaeobotanical data are insufficient to assess the naturalness of downy birch in this area of the
161 Iberian Peninsula; ii) this is the first Iberian pollen record, to our knowledge, from a peatland located within
162 a forest stand dominated by downy birch; and iii) the presented pollen record spans the past six millennia, for
163 which gaps in the palaeoecological record of the region are particularly significant.

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166 **2. Regional settings**

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168 The study was conducted in the Cabañeros National Park, a protected area of 40,856 ha located on the
169 southern slopes of the Toledo Mountains (Castilla-La Mancha, central-southern Spain; Fig. 1). The
170 Cabañeros National Park is structured into two large units (Jiménez, 2004): i) the lowland area or ‘raña’ is a
171 great plain of ~8000 ha located in the southeast where the current landscape of wooded grasslands originated
172 after forests were cleared to grow cereal crops in the 1960s; ii) the mountainous area (650-1448 m a.s.l.)
173 covers the rest of Cabañeros, and its vegetation is characterized by fragmented Mediterranean oak forests,
174 shrublands (*Cistus ladanifer* L., *Genista hirsuta* Vahl, *Phillyrea angustifolia* L. and *Erica* spp.), pastures,

175 crops, scree slopes and, to a lesser extent, pine afforestation (Perea and Perea, 2008). The National Park has a
176 remarkably diverse vegetation that includes mainly Mediterranean oak woodlands with the evergreen *Q. ilex*
177 L. subsp. *ballota* (Desf.) Samp. and *Q. suber* L., and the deciduous *Q. faginea* Lam. subsp. *broteroi* (Cout.)
178 A. Camus, as dominant tree species (Vaquero, 1993; Perea et al., 2015). Additionally, stands of the
179 deciduous *Quercus pyrenaica* Willd. cover some meso-Mediterranean valleys on deep and moist soils and
180 dominate at higher elevation in the supra-Mediterranean belt. The climate is sub-humid continental
181 Mediterranean, with mean annual temperature and precipitation of 13.7°C and 699 mm, respectively
182 (Sánchez-Palomares et al., 1999) with dry/hot summers and wet/mild winters. The main human impacts in
183 this area were livestock grazing, farming, logging, and charcoal production (Perea and Perea, 2008; López-
184 Sáez et al., 2014c). Today, there is no domestic ungulate (livestock) grazing in this National Park. Red deer
185 (*Cervus elaphus* L.) and wild boar (*Sus scrofa* L.) are the main wild ungulates, whereas roe deer (*Capreolus*
186 *capreolus* L.) are scarce. Current densities of wild ungulates in the eastern area of the National Park are high
187 (red deer 12–78.5 individuals/km², wild boar ~10 individuals/km²; Linares and Urivelarrea, 2021). Browsing,
188 trampling, and wild boar uprooting are considered important limiting factors for the regeneration of many
189 palatable woody plants (Perea and Gil, 2014, Perea et al., 2014).

190 La Ventilla mire (39° 20' 23.97" N, 4° 16' 41.45" W) is a medium-sized mire (~2 ha) located at the
191 confluence of the Bullaque River and Arroyo de las Bodeguillas valleys in El Chorito Range (Retuerta del
192 Bullaque, Ciudad Real province), within the meso-Mediterranean belt (636 m a.s.l.; Fig. 1). The mire is also
193 a Site of Community Importance because includes the only known population of *Betula pubescens* subsp.
194 *celtibérica* in the Toledo Mountains (Sánchez del Álamo et al., 2010), as well as numerous endangered plant
195 species such as *Athyrium filix-femina* (L.) Roth, *Drosera rotundifolia* L., *Erica lusitanica* Rudolphi, *E.*
196 *tetralix* L., *Ilex aquifolium* L., *Osmunda regalis* L., *Sphagnum denticulatum* Brid., *S. nemoreum* Scop. and *S.*
197 *palustre* L. (López-Sáez et al., 2014c). The main threats to this ecosystem are human-induced disruptions of
198 the hydrological regime (drainage and erosion) and overgrazing or rooting by wild ungulates, which have
199 caused peatland retraction in recent decades, despite the protective fence recently placed around the site.

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202 3. Material and methods

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204 3.1. Core sampling, lithology and chronology

205 A 99 cm-long sediment core was recovered from La Ventilla mire in 2019 (Fig. 1) with a Russian peat
206 sampler (GYK type, 50 cm length, 5 cm in diameter). The topmost 6 cm of the core were herbaceous detritus
207 and therefore discarded for pollen analysis. At the Environmental Archeology Research Group's facilities –
208 Institute of History-CSIC, Madrid, Spain–, the core was split lengthwise, photographed, lithologically
209 described, and then stored at 4°C. Six organic sediment (bulk peat) samples were selected for ¹⁴C dating in
210 the accelerator mass spectrometry (AMS) laboratory of DirectAMS Radiocarbon Dating Service (Bothell,
211 WA, USA). Their radiocarbon ages were calibrated to calendar years using CALIB 8.2 software with the
212 INTCAL20 curve (Reimer et al., 2020; Table 1). The age-depth relationship was modelled by fitting a
213 smoothing spline (smoothing parameter=0.2; iterations=10,000) to the radiocarbon dates using Clam 2.2
214 (Blaauw, 2010). Confidence intervals of the calibrations and the age-depth model were calculated at 95%
215 (2σ).

216

217 3.2. Loss-on-ignition, magnetic susceptibility and sedimentary macrocharcoal analysis

218 Loss-on-ignition (LOI) analysis, based on heating of the dry samples at 550°C in a muffle furnace for 4 h
219 (Heiri et al., 2001), was carried out for 1-cm³ volumetric samples taken contiguously at 2-cm resolution
220 along the profile. The values of LOI for each sample were calculated according to the formula: $LOI_{550} =$
221 $((DW_{105} - DW_{550}) / DW_{105}) \times 100\%$, where LOI_{550} represents LOI at 550°C (as a percentage), DW_{105} is the dry
222 weight of the sample (wet samples were dried at 105 °C during 12 h before combustion), and DW_{550} is the
223 dry weight of the sample after heating to 550°C (Heiri et al., 2001). LOI_{550} is thus expressed as a percentage
224 of weight loss in dried sediment (Fig. 2). Magnetic susceptibility (MS) was measured at 1-cm resolution
225 using a Bartington sensor MS2E (Bartington Instruments, Ltd, Whitney, UK) following standard procedures
226 (Walden et al., 1999).

227 To reconstruct fire history, 1-cm thick sediment samples of 1 cm³ were taken contiguously throughout the
228 core according to the recommendations of Whitlock and Larsen (2001). Macroscopic charcoal particles were
229 then counted assuming they have local origin (< 10 km) (Carcaillet et al., 2001; Finsinger et al., 2014).
230 Charcoal samples were soaked in a 10% KOH solution during 24 h and then in 15% H₂O₂ for 24 h more, to
231 remove and bleach uncharred organic matter. The sediment was then sieved using a 125-μm mesh and the
232 number of charcoal particles in each sample was counted under the stereomicroscope. Peak detection

233 analysis to identify macroscopic charcoal spikes related to local to extra-local fire episodes was conducted
234 using CharAnalysis (Long et al., 1998; Higuera et al., 2009, 2010) and the package ‘Paleofire’ (Blarquez et
235 al., 2013) running in R (R Core Team, 2021). This method is based on a three-step decomposition of the
236 charcoal accumulation rate (CHAR) series, and, in this case, we followed the recommendations of Blarquez
237 et al., (2013). Pre-treatment involved interpolating the CHAR series to the median time resolution of the
238 record to account for the variability in sedimentation rates that could introduce bias. To obtain the charcoal
239 peak (C_{peak}) and the charcoal background (C_{back}) series, we first applied the five smoothing methods available
240 in CharAnalysis, with smoothing windows ranging from 250 to 500 years in 25-year steps (Blarquez et al.,
241 2013), then C_{back} was subtracted from the interpolated CHAR series ($C_i - C_{\text{back}}$) to get C_{peak} (Higuera et al.,
242 2009). C_{peak} still embraces C_{noise} , the statistical noise produced in the previous steps and remaining C_{back} , and
243 C_{fire} , which in principle represents the fire signal (Higuera et al., 2010). C_{fire} separated from C_{noise} using a
244 Gaussian mixture model (Gavin et al., 2006), with the 99th-percentile threshold in each reconstruction and
245 applying a local threshold in 500-year time windows (Higuera et al., 2009). A signal-to-noise index (SNI;
246 Kelly et al., 2011) has been used to select all members (i.e., analysis iterations), choosing manually those
247 reconstructions with the highest SNI. Fire events or groups of events were considered statistically robust and
248 thus selected when a minimum agreement of 50% among the selected members was met (López-Sáez et al.,
249 2018b). Fire frequency was calculated using a kernel density estimation with a width of 250 years, while the
250 95% confidence intervals of the fire frequency were obtained by means of bootstrap resampling of the kernel
251 density estimation using the R package ‘Paleofire’ (Blaauw, 2010; Blarquez et al., 2013, 2014).

252

253 *3.3. Pollen and non-pollen palynomorphs (NPPs) analyses*

254 Pollen analysis was carried out on 47 sub-samples of 1 cm³ taken at ~2 cm intervals following the
255 standard method of Moore et al. (1991). Palynomorphs were identified at 400× and 1000× magnifications to
256 the lowest possible taxonomic level. Pollen identifications were based on photographic atlases (Reille, 1992,
257 1999), and the reference collection at the Institute of History-CSIC (Madrid, Spain). Ericaceae pollen
258 differentiation followed Mateus (1989). Non-pollen palynomorphs (NPPs) were identified according to van
259 Geel (2001) and (Cugny et al., 2010), and their nomenclature follows Miola (2012) with the abbreviations
260 ‘HdV-’ corresponding to the Hugo de Vries Laboratory (University of Amsterdam, The Netherlands) where
261 they were described. We identified and counted more than 400 pollen grains of terrestrial plants (trees,

262 shrubs, herbs) per sample. Pollen of aquatic and wetland plants as well as spores and non-pollen
263 palynomorphs (NPPs) were excluded from the pollen sum and their percentages calculated relative to the
264 terrestrial pollen sum. *Betula* was also considered associated to the wetland and thus excluded of the
265 terrestrial pollen sum (Janssen, 1984; Janssen et al., 1996). A *Lycopodium* tablet was added to each sample
266 before the laboratory preparation to estimate pollen concentration (grains cm⁻³: Stockmarr, 1971). Spores of
267 obligate coprophilous fungi (dung fungal spores) represent a proxy for local grazing activities of both
268 domestic and wild ungulates (López-Sáez and López-Merino, 2007; Cugny et al., 2010), of particular
269 relevance in the study area given the densities and impacts of ungulates in these mountains (see
270 Introduction). We will mostly discuss total dung fungal spore influxes (no. spores cm⁻² yr⁻¹) because these
271 are independent from changes in vegetation and show a highly significant correlation with local herbivore
272 densities (Morales-Molino et al., 2019). To establish the zonation of the pollen sequence, we tested several
273 divisive and agglomerative methods with the program IBM SPSS Statistics 21. Based on the ecological
274 meaning of the obtained zones, four local pollen assemblage zones (LPAZ-1 to LPAZ-4) were delimited
275 using stratigraphically constrained cluster analysis by incremental sum-of-squares (CONISS) on square-root-
276 transformed percentage pollen data (Grimm, 1987). The number of statistically significant zones was
277 determined using the broken-stick model (Bennett, 1996). Pollen diagrams have been plotted against age
278 using Tilia for Windows (Grimm, 2004). The terms ‘local’ (0-20 m), ‘extra-local’ (20 m-2 km), and
279 ‘regional’ (> 2 km) used in the text refer to different pollen source areas according to Prentice (1985).

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281

282 **4. Results**

283

284 ‘La Ventilla’ record spans the past *c.* 6145 years (Fig. 2), and the radiocarbon dates and age-depth model
285 suggest that sediment accumulation was continuous over this period. We considered the 65-cm sample (D-
286 AMS-036913) as an outlier probably related to the presence of reworked organic carbon as suggested by a
287 MS peak (Fig. 2). The sequence shows low sediment accumulation rates (~0.013-0.020 mm yr⁻¹) between the
288 bottom (99 cm) and 15-cm depth, and then a progressive increase to 0.025 mm yr⁻¹ at the top of the sequence
289 (Fig. 2). The lithostratigraphy of La Ventilla can be divided into two main sections (Fig. 2). The bottom (99-
290 30 cm) corresponds to greyish silts typical of a lotic system, except for a more organic level of dark brown

291 silts intercalated between 60 and 50 cm. The sediments became progressively peat-enriched towards the top,
292 first as silty peat (30-22 cm) with the development of a mire ecosystem ~1400 cal BP, and then becoming
293 peat at the top of the sequence (22-7 cm). Total organic matter content (LOI) in La Ventilla core (Fig. 2)
294 shows great stability between 99 and 30 cm with values below 3%, except for a peak (5%) at 53 cm (3200
295 cal BP), corresponding to the organic matter enrichment of the silts (dark brown silts). Subsequently, their
296 values increase slightly between 30 and 22 cm (4-7%), while at the top of the sequence (22-7 cm) there is a
297 noticeable increase (> 10%) with a maximum (20%) at 15 cm (~500 cal BP). Two high positive MS peaks
298 (Fig. 2) are documented at 65 cm (5.36×10^5 SI units) and 41 cm (8.73×10^5 SI units).

299 Considering its small size and position at the bottom of a narrow valley, La Ventilla mire has most
300 probably recorded local and extra-local vegetation. La Ventilla pollen record was divided into four local
301 pollen assemblage zones (Figs. 3-5; Table 2). Pollen concentration shows very low values between ~6145
302 and 3500 cal BP ($< 2 \times 10^5$ grains cm^{-3}) that later increase progressively until 1150 cal BP ($5-64 \times 10^5$ grains
303 cm^{-3}), then decrease ~1150-500 cal BP ($< 20 \times 10^5$ grains cm^{-3}), and finally increase again ~500-150 cal BP
304 (Fig. 2). Changes in pollen concentration through time are therefore in good agreement with the dynamics of
305 the lotic system.

306

307

308 5. Discussion

309 5.1. The earliest evidence of human impact in the Toledo Mountains: the Neolithic period (~6145-5200 cal 310 BP)

311 The basal pollen subzone (LPAZ-1a; 99-93 cm; ~6145-5800 cal BP) shows the highest percentages of
312 herb pollen (55-68%), mainly Poaceae, anthropogenic-nitrophilous and anthropozoogenic herbs (Figs. 4 and
313 7; Table 2). Through LPAZ-1b (93-82 cm; ~5800-5200 cal BP) herbaceous pollen values decrease (47-54%)
314 although Poaceae still dominate and *Erica arborea/lusitanica*-type shows a noticeable increase (> 20%).
315 Low percentages of Cerealia-type are also recorded (1.2-1.4%) at ~5400-5300 cal BP (Figs. 4 and 7). These
316 pollen assemblages point to a great development of open vegetation in the surrounding landscape, including
317 the earliest evidence of human impact associated with local agricultural activities found in the Toledo
318 Mountains (López-Sáez and López-Merino, 2005). Late Neolithic pastoral activities are also evidenced by
319 the increase of coprophilous fungi influx and percentage at ~5400 cal BP (Figs. 5 and 7). The arboreal pollen

320 sum (18-27.3%) during the Neolithic consists mainly of deciduous *Quercus* (11-16%) (Fig. 3), thus
321 indicating that deciduous oak open woodlands (*Quercus pyrenaica/Q. faginea*) were dominant along La
322 Ventilla valley during LPAZ-1a and LPAZ-1b (López-Sáez et al., 2015; Morales-Molino et al., 2020).
323 Evergreen oaks (*Quercus ilex, Q. suber*) were also widespread (Fig. 3), but their low percentages suggest a
324 regional origin (López-Sáez et al., 2010). During the Neolithic, La Ventilla showed a significant number of
325 local fire events, at ~6150, 5510 and 5310 cal BP, although CHAR values are not very high and without
326 major fluctuations (Figs. 6-7). According to the local pollen evidence, these fires could have been related to
327 farming activities around the study site (Fig. 7) and their spread favoured by prevalent dry conditions during
328 this period (Fig. 7). This would mean that, despite the potential role played by humans in the landscape and
329 the possible use of fire close to the mire, climate was probably the main driver of fire dynamics during the
330 Neolithic.

331 The Neolithic has been recorded very rarely in central-southern Spain (Rojo et al., 2012). The study area,
332 a vast territory today included in the Castilla-La Mancha region, has been usually considered a marginal area
333 for Neolithic agriculture. Although available data are still limited, detailed research suggests that this
334 assumption may be wrong as the earliest evidence of agriculture is documented ~6560-5270 cal BP between
335 the early and late Neolithic (Bueno et al., 2002; López-Sáez et al., 2019). At the moment, there is no
336 archaeological record from the Toledo Mountains dated to this period. Therefore, despite further research is
337 still needed, our multi-proxy analysis is the first attesting to this early human impact, demonstrating that the
338 palaeoecological study of natural deposits is useful to provide clues for the understanding of human impact
339 on the landscape.

340 *Betula* (38-80%), *Salix* and *Corylus* are also represented in both pollen subzones (Fig. 3), indicating the
341 presence of birch-dominated riparian woodlands at La Ventilla mire during the mid-Holocene. The decline in
342 birch pollen abundances during LPAZ-1b (< 40%) can be correlated with the human impact noted above.
343 The origin of the *Betula pubescens* subsp. *celtibérica* birch stand of La Ventilla mire has been debated
344 among foresters, botanists and biogeographers in central Spain. Traditionally regarded as a floristic rarity,
345 latest research considers this birch stand an impoverished relict of mesophilous forests of the glacial period
346 (Sánchez del Álamo et al., 2010). Our data unambiguously demonstrate that birches thrived on the peatland
347 ecosystem of La Ventilla for more than 6000 years (Fig. 7). This finding extends back in time the record of
348 birch pollen in the Toledo Mountains, where it had so far been regularly documented only from ~5000 cal

349 BP onwards (Morales-Molino et al., 2018, 2019; Luelmo-Lautenschlaeger et al., 2019a, 2019b), and allows
350 to suggest the long-term persistence of *Betula* in the Toledo Mountains on suitable refuge areas. Available
351 information on stand structure shows that marginal populations of downy birch, such as the one at La
352 Ventilla, tend to be isolated and small (Kinnaird, 1974; Sanz et al., 2011). HdV-114, which corresponds to
353 fragments of scalariform perforation plates occurring in vessels of hardwood, is also present in LPAZ-1a and
354 LPAZ-1b (Figs. 6 and 7). In this case, the finding of some *Betula* woody fragments in this section suggests
355 that the record of this NPP can be indicative of the presence of birch *in situ* (Prager et al., 2006).

356 Very low percentages of NPPs indicators of oligo-mesotrophic open water conditions, as well as very
357 high (63-92% in LPAZ-1a) to moderate values (26-29.4% in LPAZ-1b) of Cyperaceae and NPPs indicators
358 of eu-mesotrophic shallow and stagnant water conditions suggest temperate and humid settings (Fig. 7). The
359 increase in NPPs indicators of dry conditions in LPAZ-1b suggests that a dry phase occurred at ~5800-5200
360 cal BP, which may also have contributed to the observed decline in birch along with human impact. The
361 chronology of LPAZ-1a is synchronous with a temperate interval recorded in Greenland ice cores (Fig. 7) by
362 high $\delta^{18}O$ values, while that of LPAZ-1b corresponds to an irregular period (Rasmussen et al., 2008).
363 Between ~6145 and 5200 cal BP the sediment consists of greyish silts with minimal sediment accumulation
364 rate (Fig. 2), characteristic of a lotic depositional environment with slow moving backwaters. This is in
365 accordance with low MS units, LOI percentage and pollen concentration (Fig. 2).

366

367 5.2. Development of birch forest during the Chalcolithic period (~5200-4200 cal BP)

368 LPAZ-1c pollen subzone (82-68 cm; ~5200-4250 cal BP) is marked by progressive increases in *Betula*
369 (57-86%), *Ilex aquifolium*, deciduous *Quercus* (15.5-18%), *Q. suber* (4-6.7%), *Arbutus unedo* L. and
370 *Calluna vulgaris* (L.) Hull, abundances, while *Salix* reaches its lowest values and *Erica arborea/lusitanica*
371 remain constant (Figs. 3 and 7; Table 2). These data suggest the persistence of deciduous oak woodlands and
372 the increasing local dominance of birch in the riparian forest at La Ventilla at the expense of willow. As
373 during the late Neolithic, cereal pollen (1.5-1.7%) and significant amounts of both anthropogenic-
374 nitrophilous and anthropozoogenic herbs, and coprophilous fungi are recorded (Figs. 4-5 and 7; Table 2),
375 suggesting continued farming activities and human impact during the early Chalcolithic. Local fire episodes
376 are reconstructed at ~5100, 4840 and 4570 cal BP, while CHAR values show an increasing trend (Figs. 6-7).
377 In short, the landscape remained largely unchanged from the previous period. A similar pattern has been

378 documented in other Toledo Mountains pollen records (Fig. 1) such as El Perro mire (Luelmo-
379 Lautenschlaeger et al., 2019a, 2019b). The dominance of NPPs indicators of eu-mesotrophic shallow and
380 stagnant water conditions and dry conditions, as well as a constant lithology of greyish silts, low sediment
381 accumulation rates and LOI percentages (Figs. 2 and 7), would probably indicate that a lotic depositional
382 environment with slow moving back waters still existed.

383 During the Chalcolithic, the *Betula* curve shows an increasing trend (Figs. 3 and 7) despite the dry pulse
384 associated to NAO+ conditions (Olsen et al., 2012) and higher values of NPPs indicators of dry conditions
385 (Fig. 7). The inferred human impact, in contrast to the Neolithic (LPAZ-1b; ~5800-5200 cal BP), was
386 probably less intense around La Ventilla and did not affect birch cover. Even holly (*Ilex aquifolium*)
387 expanded slightly at this period (Fig. 3). This low human impact allowed birch pollen abundances to recover
388 the values they showed around ~6145-5800 cal BP (LPAZ-1a). Nevertheless, between ~4800 and 4200 cal
389 BP *Betula* widely spread (84-86%), as well as Cyperaceae (29-35.5%), during a wet pulse linked to
390 decreasing NAO values (Fig. 7). These facts suggest that: (i) episodes of intense winter rainfall, usually
391 associated to NAO- in the Iberian Peninsula (Madrigal-González et al., 2017), would have contributed to
392 recharge the aquifers that feed the mire and therefore attenuated summer drought (Morales-Molino et al.,
393 2019); and (ii) land use was reduced as a consequence of societal instability during this short humid episode
394 (Olsen et al., 2012). Our data corroborate previous research (Muñoz, 1993; Gil-García et al., 2006; López-
395 Sáez et al., 2019) that has also demonstrated the climatic and societal instability that existed in this
396 chronological framework in the Southern Iberian Plateau.

397

398 5.3. The Chalcolithic-early Bronze Age transition (~4200-4000 cal BP)

399 The lower part of LPAZ-2a (68-66 cm; ~4200-4000 cal BP) is characterized by noticeable changes in the
400 abundance of several trees, herbaceous taxa and NPPs (Figs. 3-5). *Betula* (26%), deciduous *Quercus* (7%),
401 Cyperaceae (9%) and HdV-315 decrease. *Fraxinus* and *Ilex aquifolium* disappear, while evergreen *Quercus*
402 (6%), *Salix*, *Calluna vulgaris*, *Cistus ladanifer*, *Erica arborea/lusitanica*, *E. australis*, Chenopodiaceae,
403 *Pteridium aquilinum*, HdV-3B, HdV-114 and HdV-207 increase. These pollen assemblages suggest the
404 advent of a markedly arid phase, during which riparian -particularly the birch-dominated- and deciduous oak
405 woodlands would have been greatly reduced, while elements associated with drier conditions, such as
406 heathlands or holm oak woodlands (*Quercus ilex*) would have expanded. The joint occurrence (Fig. 5) of low

407 percentages of *Spirogyra* (HdV-315) and higher values of *Pleospora* spp. (HdV-3B) suggest dry and
408 eutrophic conditions in the wetland during a dry phase, while higher percentages of *Glomus* (HdV-207) can
409 be correlated with erosive processes, also slightly visible in the magnetic susceptibility record (van Geel et
410 al., 1989; van Geel and Aptroot, 2006). Similarly, the HdV-114 maximum can be correlated with the retreat
411 of the birch forest (Pals et al., 1980).

412 Despite the striking uncertainty of the age-depth model in this section (Fig. 2), the lower part of LPAZ-2a
413 could be associated to the so-called 4200 cal BP event (Magny, 1993, 2004), an abrupt climate episode
414 characterized by marked aridification phase in the Mediterranean Iberian region (Jalut et al., 2009; Carrión et
415 al., 2010). This dry pulse would in turn be associated to NAO+ conditions (Fig. 7; Olsen et al., 2012). La
416 Ventilla pollen record strongly suggests that modern observations reporting particularly high birch seedling
417 mortality in Mediterranean Iberia during dry summers (Sánchez del Álamo et al., 2010; Sanz et al., 2011),
418 might well extend to multidecadal and centennial timescales. Similarly, evidence of this event has also been
419 documented in other pollen records from the Toledo Mountains (Fig. 1) such as El Perro (Luelmo-
420 Lautenschlaeger et al., 2019a, 2019b). Further, the palaeoenvironmental data of some archaeological sites in
421 La Mancha such as Motilla del Azuer or Castillejo del Bonete also detect this abrupt climatic event, which
422 had a significant impact on the settlement patterns, as it could be interpreted by the hiatus present in the first
423 mentioned archaeological site for this moment (López-Sáez et al., 2014b; Benítez et al., 2014, 2015, Nájera
424 et al. 2019). Interestingly, many archaeological sites belonging to the ‘Motillas culture’ in the eastern part of
425 the province, which corresponds to the Bronze Age in La Mancha and are characterized by featuring deep
426 wells excavated to capture groundwater (e.g. the Motilla del Azuer is the oldest well in Europe with a
427 masonry lining), were built precisely at ~4150-4000 cal BP (Mejías-Moreno et al., 2015, 2020, Nájera et al.
428 2019).

429 From a palynological point of view, almost no trace of human impact on the vegetation can be found in
430 the La Ventilla sequence, neither in the charcoal (Fig. 6) nor in the pollen records (Fig. 7). Coprophilous
431 fungi show a strong downward trend, while anthropogenic-nitrophilous and anthropozoogenic herbs sharply
432 decrease (Fig. 7), suggesting a very low or null human impact. There is only a fire episode or group of events
433 detected in the analysis during this time (~ 4170 cal BP). Thus, the Copper Age-Early Bronze Age transition
434 ~4200-4000 cal BP was abrupt in the Cabañeros National Park, with the collapse of the agro-pastoral

435 Chalcolithic landscape and the abandonment of many archaeological sites as the most remarkable feature
436 from an archaeological point of view (Muñoz, 1993; Lillios et al., 2016; Blanco-González et al., 2018).

437

438 5.4. Environmental and cultural dynamics during the Bronze Age (~4000-3200 cal BP)

439 During the upper part of LPAZ-2a (66-57 cm; ~4000-3500 cal BP), the vegetation recovers, reaching
440 conditions similar to those prior to the 4200 cal BP event (Figs. 3-5 and 7; Table 2). *Betula* (63-72%),
441 deciduous *Quercus* (9.5-13.8%), *Q. suber* (15.6-21.5%), *Fraxinus*, *Ilex aquifolium*, Cyperaceae and HdV-
442 315 progressively increased, whereas *Calluna vulgaris*, *Cistus ladanifer*, HdV-3B and HdV-114 sharply
443 decreased. In addition, NPPs indicators of humid conditions (HdV-18) and NPPs indicators of oligo-
444 mesotrophic open water conditions (HdV-119) appeared, suggesting humid and mesotrophic conditions (van
445 Geel et al., 1989; Mighall et al., 2006; van Geel and Aptroot, 2006). These data can be correlated with the
446 humid phase described by Magny (1993, 2004) in the western Mediterranean at ~4000-3500 cal BP,
447 characterized by low NAO+ conditions (Olsen et al., 2012). This stage would correspond to a period of
448 relative stability of the wetland ecosystem, with higher rainfall and low sediment accumulation rates, LOI
449 percentages and pollen concentration (Fig. 2).

450 Nevertheless, at ~3500 cal BP *Betula* (54%), Cyperaceae (10.8%), HdV-18 and HdV-315 show a marked
451 decline (Figs. 3 and 5), concomitant with an abrupt increase in $\delta^{18}\text{O}$ values documented in the NGRIP
452 Greenland core (Rasmussen et al., 2018), as well as with higher NAO+ conditions (Fig. 7), suggesting lower
453 rainfall and warmer temperatures (Olsen et al., 2012). At La Ventilla, a remarkable change from greyish silts
454 to more organic dark brown silts occurred at this time, simultaneously to a maximum in LOI values (Fig. 2).
455 Other Toledo Mountains pollen records such as El Perro, Las Viñuelas and El Brezoso documented a similar
456 pattern ~3500 cal BP (Fig. 1), with the development of Mediterranean woodlands and xerophytic taxa at the
457 expense of hygrophilous communities (Morales-Molino et al., 2018, 2019; Luelmo-Lautenschlaeger et al.,
458 2019a, 2019b).

459 In the lower part of the LPAZ-2b (57-53 cm; ~3500-3200 cal BP) subzone, the percentages of deciduous
460 *Quercus* (4.5-5%), Poaceae (13-15.6%) and NPPs indicators of humid conditions slightly decrease, whereas
461 those of *Betula* (98-127%), *Ilex aquifolium*, *Salix*, *Erica arborea/lusitanica*, Genisteae, Cyperaceae (46.3-
462 70%), anthropogenic-nitrophilous and anthropozoogenic herbs increase (Figs. 3-5 and 7; Table 2). Similarly,
463 regarding the NPPs (Figs. 5 and 7) this subzone is characterized by higher values of *Sordaria* spp. (HdV-

464 55A), *Sporormiella* spp. (HdV-113), *Riccia* (HdV-165) and HdV-573, as well as NPPs indicators of eu-
465 mesotrophic shallow and stagnant water conditions. These data suggest: (i) increased pastoral pressure, most
466 significantly during the late Bronze Age (higher influx of dung fungal spores at ~3400-3200 cal BP; Fig. 7),
467 which probably did not affect the riparian vegetation including birch woodlands but rather focused on
468 deciduous oak woodlands; (ii) the development of heath and broom shrublands as a consequence of
469 increased human impact; and (iii) drier and eu-mesotrophic conditions in the wetland, also attested by NAO+
470 conditions, although a wet pulse with NAO- conditions is documented ~3350 cal BP (Fig. 7). During the
471 Bronze Age, CHAR showed its lowest values with only two significant local fire episodes detected at ~3900
472 and 3500 cal BP (Figs. 6-7).

473 Greater human impact has also been documented in other pollen records of the Cabañeros National Park
474 (El Brezoso and Las Viñuelas) during the Bronze Age (~3500-3200 cal BP), associated with increased
475 pastoralism and fire activity and even cereal cultivation (Morales-Molino et al., 2018, 2019). At these sites,
476 unlike at La Ventilla, these human impacts affected the birch woodlands significantly (Morales-Molino et al.,
477 2018, 2019). El Perro pollen record (Fig. 1) also shows clear evidence of increased human impact during this
478 cultural period, through the development of anthropogenic-nitrophilous and anthrozoogenic communities
479 and the disappearance of birch (Luelmo-Lautenschlaeger et al., 2019a, 2019b). The greater extension of La
480 Ventilla birch-dominated riparian forests during the late Bronze Age compared to the three previous pollen
481 records mentioned above, is probably a consequence of human impact on the deciduous oak forests rather
482 than on the birch forest. This fact would have allowed *Betula pubescens* subsp. *celtibérica* to recover and
483 expand in La Ventilla mire. Although the Toledo Mountains is a territory where archaeological research is
484 largely lacking, currently available data confirm a noticeable demographic increase in these mid-elevation
485 mountains during the Bronze Age, normally defensive structures in hill summits in combination with
486 settlements in lowland areas, strongly associated with agricultural, pastoral and mining activities (Barroso-
487 Bermejo, 2015; Ruiz-Taboada, 2020).

488

489 5.5. Resilience, expansion, and retreat of birch forest during the Iron Age (~3200-2000 cal BP)

490 A noticeable increase in tree pollen percentages (39-58%) is documented in the upper part of LPAZ-2b
491 and the lower part of LPAZ-3a (53-49 cm; ~3200-2800 cal BP) pollen sub-zones (Fig. 3). In this period,

492 *Betula* (100-189%), *Fraxinus*, *Ilex aquifolium* and *Salix* spread, while evergreen *Quercus* decreased. *Erica*
493 *arborea/lusitanica*, Genisteae, Poaceae (7.7-16.6%), anthropogenic-nitrophilous and anthropozoogenic taxa,
494 and coprophilous fungi also reduce their percentages. Hygrophytic taxa such as *Erica tetralix* (20%),
495 Ranunculaceae, Cyperaceae and *Osmunda regalis* increased significantly, as well as NPPs indicators of
496 humid conditions. At the same time, the eu-mesotrophic shallow and stagnant water conditions NPPs seem
497 reduced, while oligo-mesotrophic water conditions NPPs increased (Figs. 4-5 and 7; Table 2). The slight
498 increase observed in CHAR values may reflect enhanced regional fire activity, and only two fire episodes
499 have been detected (~2950-2360 cal BP) without significant landscape change afterwards (Fig. 6). These
500 data suggest progressively wetter climatic conditions and reduced human impact, which according to the
501 age-depth model (Fig. 2) could correspond to the so-called 2800 cal BP event (Fig. 7), an abrupt and short
502 climatic oscillation detected at global scale (van Geel et al., 1998). This event was contemporary with the
503 late Bronze Age-early Iron Age transition in the Toledo Mountains (López-Sáez et al., 2019), and represents
504 a shift from the previous warm and dry conditions into wetter and colder ones. This event is documented in
505 the NGRIP Greenland core by a decrease in $\delta^{18}\text{O}$ values (Rasmussen et al., 2018), as well as by low NAO+
506 conditions (Fig. 7). The lithology of La Ventilla record (greyish silts) alongside the low sediment
507 accumulation rates and LOI values still indicate the existence of a lotic system. A similar pattern, including
508 birch expansion, has been documented in previously studied sites not only on both the northern and southern
509 slopes of the Toledo Mountains (El Perro, Botija, Valdeyernos, Patateros, El Brezoso and Las Viñuelas; Fig.
510 1) but also in the Iberian Central System (Dorado et al., 2014a, 2014b; López-Sáez et al., 2014a; Morales-
511 Molino et al., 2018, 2019; Luelmo-Lautenschlaeger et al., 2018b, 2019a, 2019b). These data agree with the
512 regional archaeological record, which shows remarkable changes in the settlement patterns and socio-
513 economic dynamics, with continuity of the upland settlements established by the late Bronze Age
514 communities into the early Iron Age (~3200-2400 cal BP) but showing abandonment of the lowland
515 settlements (Muñoz, 1993; Barroso-Bermejo et al., 2003).

516 In contrast to the previous period, the upper part of LPAZ-3a (49-42 cm; ~2800-2400 cal BP) pollen
517 subzone is characterized by decreasing values of *Betula* (128-175%), *Fraxinus*, deciduous *Quercus* (3-6%),
518 *Salix*, Cyperaceae, *Osmunda regalis*, HdV-18, and the disappearance of *Ilex aquifolium* and Ranunculaceae
519 (Figs. 3-5). Meanwhile, *Quercus suber* (18-23%), *Erica arborea/lusitanica*, Genisteae and HdV-114 increase
520 (Figs. 3-5). Anthropogenic-nitrophilous and anthropozoogenic herbs, and coprophilous fungi are virtually

521 absent at the end of the early Bronze Age (Fig. 7). CHAR values show a decreasing trend (Fig. 6), as in other
522 pollen records from the Toledo Mountains (Luelmo-Lautenschlaeger et al., 2019a). These vegetational
523 patterns could be related to the onset of the Iberian-Roman Humid Period (~2640-1500 cal BP; IRHP), a
524 warm and humid period well documented in central and southern Iberia (Gil-García et al., 2006; Martín-
525 Puertas et al., 2008, 2009). The onset of the IRHP is linked to a first dry pulse with NAO+ conditions ~2640-
526 2500 cal BP (Fig. 7; Olsen et al., 2012), which would have affected negatively the wetland vegetation,
527 chiefly birch forest and other hygrophytic taxa, while xerophytic elements and cork oak woodlands would
528 have developed in the immediate surroundings, followed by subsequent wet pulse with NAO- conditions
529 ~2500-2400 cal BP. However, other pollen records in the Toledo Mountains (Fig. 1), such as El Brezoso and
530 Las Viñuelas in the Cabañeros National Park (Morales-Molino et al., 2018, 2019), and El Perro, Botija,
531 Patateros and Valdeyernos (Dorado et al., 2014a, 2014b; Luelmo-Lautenschlaeger et al., 2018b, 2019a,
532 2019b) recorded an expansion of birch during this period coinciding with very low human impact. This
533 climatic irregularity would have affected La Ventilla birch forest to a greater extent than others in the Toledo
534 Mountains, probably because *Betula pubescens* is not so tolerant as *B. pendula* –which is today more
535 widespread in these mountains and we assume that this was also the case in the past– to drier soils (Sánchez
536 del Álamo et al., 2010; Jonczak et al., 2020).

537 The late Iron Age (~2400-2000 cal BP; bottom of LPAZ 3b; 42-40 cm) was a phase of relative woodland
538 stability around La Ventilla mire. *Betula* (122.5%), *Erica tetralix* (47%), *Pteridium aquilinum* and
539 Cyperaceae (49.3%) increase, *Corylus*, *Ilex aquifolium* and *Calluna vulgaris* disappear, anthropogenic-
540 nitrophilous and anthropozoogenic herbs decline significantly and coprophilous fungi are present but scarce
541 (Figs. 3-5 and 7; Table 2). The humid and warm climate of the Iberian-Roman Humid Period might have
542 favoured these dynamics, although conditions were notably variable at ~2400-2000 cal BP (Fig. 7), with a
543 first dry pulse (NAO+ conditions) and a late wet one (NAO- conditions). Finding of NPPs indicative of soil
544 erosion (HdV-207; Figs. 5 and 7) and a very high positive MS peak (Fig. 2) at ~2260 cal BP (8.73×10^5 SI
545 units), may be related to the increment of anthropic activities around the mire during the late Iron Age, and
546 the dry pulse in the IRHP, which drove to major pollen concentration values (van Geel et al., 1989). An
547 increase of birch woodlands has been also documented in the Cabañeros National Park during the late Iron
548 Age (Morales-Molino et al., 2018, 2019), as well as in El Perro mire, located on the southern fringe of the
549 Toledo Mountains (Luelmo-Lautenschlaeger et al., 2019a, 2019b). Meanwhile, other pollen records from the

550 northern Toledo Mountains such as Valdeyernos and Patateros (Fig. 1) show a slight decrease in birch cover
551 despite the almost absence of human impact (Dorado et al., 2014a, 2014b). The Botija pollen record, also
552 placed in the northern Toledo Mountains (Fig. 1), is a paradigmatic case in this regard because the strong
553 human impact during the late Iron Age caused a very meaningful decline in the deciduous and evergreen oak
554 woodlands and the definitive disappearance of birch and hazel around the mire, with the consequent
555 development of xerophytic heathlands (Luelmo-Lautenschlaeger et al., 2018b). No archaeological site from
556 the late Iron Age has so far been documented in the Toledo Mountains, but the nearest ones known to date
557 are very close to their northern edge (López-Sáez et al., 2019), thus agreeing with the patterns described
558 above. In general, these are small, walled settlements, with a marked sedentary character and located in
559 strategic places of territorial control (Hurtado, 2000).

560

561 5.6. Birch forest dynamics and human impact during the Roman period (~2000-1500 cal BP)

562 The upper part of LPAZ-3b (40-34 cm; ~2000-1750 cal BP) and the lower part of LPAZ-3c (34-30 cm;
563 ~1750-1500 cal BP) pollen subzones are characterized by a progressive rise in *Betula* values (122.5-172%),
564 the reappearance of *Ilex aquifolium*, Ranunculaceae and *Osmunda regalis*, a slight increase of *Cistus*
565 *ladanifer*, *Calluna vulgaris* and Genisteeae, the decrease of *Erica arborea/lusitanica*, and the first appearance
566 in the pollen diagram of *Castanea* and *Juglans* at ~1750 cal BP (Figs. 3-5 and 7; Table 2). *Quercus suber*
567 (18.5-25%), *Erica tetralix* (36-54.5%) and Cyperaceae (44-53%) still maintain very high values. Thus, the
568 Roman period (~2000-1500 cal BP) was a rather stable phase in the mid-mountain woodlands in the
569 Cabañeros National Park, with the progressive expansion of birch stands. This spread could have been
570 favoured by decreasing temperature (decrease $\delta^{18}O$ values in the NGRIP Greenland core) during a
571 distinctively drier pulse (NAO+ conditions) at the end of the Iberian-Roman Humid Period (Fig.7). The
572 Roman domain brought higher CHAR values at La Ventilla, including a fire episode at ~1890 cal BP (Figs.
573 6-7) that did not leave a trace in the MS curve (Fig. 2). A similar landscape and dynamics have been
574 documented in other Toledo Mountains pollen records (Morales-Molino et al., 2018, 2019; Luelmo-
575 Lautenschlaeger et al., 2019a, 2019b).

576 In any case, it is likelier that forest development was a consequence of the more discrete Roman use of
577 mid-mountain environments, as attested by low values of both anthropogenic-nitrophilous and
578 anthropozoogenic herbs as well as coprophilous fungi (Fig. 7). The presence of tree crops (chestnut and

579 walnut) in La Ventilla pollen record is probably due to their regional cultivation during Roman period
580 (Morales-Molino et al., 2020). Therefore, the fire activity detected in the southern Toledo Mountains records
581 was probably more related to climate than to a virtually non-existent human impact. In fact, human pressure
582 around the Toledo Mountains during the Roman period focused on the lowlands, away from these
583 mountains, which were not settled and became a refuge for bandits (Carrasco, 2003; Hernández-Marato,
584 2018; López-Sáez et al., 2019). This is the reason why, as it happened during the late Iron Age, those pollen
585 records located in the northern Toledo Mountains (Botija, Patateros, Valdeyernos; Fig. 1) closer to large
586 Roman population centres such as *Consabura*, *Caesarobriga* or *Toletum* (Carrasco, 2012; Mangas, 2012),
587 document larger human impact (Dorado et al., 2014a, 2014b; Luelmo-Lautenschlaeger et al., 2018b).

588

589 5.7. The progressive decline of birch forest during the Middle Ages (~1500-500 cal BP)

590 The upper part of LPAZ-3c (30-26 cm; ~1500-1150 cal BP) and LPAZ-4a (26-15 cm; ~1150-500 cal BP)
591 pollen subzones are characterized by an abrupt decline in *Betula* percentages (< 80%), while HdV-114
592 progressively increases (3.5-25%), and *Castanea* and *Juglans* stand stable (Figs. 3 and 5). *Ilex aquifolium*
593 and *Calluna vulgaris*, on the contrary, rose in LPAZ-4a, while *Cistus ladanifer*, *Erica arborea/lusitanica*, *E.*
594 *tetralix* and *Osmunda regalis* decreased (Figs. 3 and 5). Human impact indicators, such as anthropogenic-
595 nitrophilous and antropozoogenic herbs, Cerealia type, and coprophilous fungi, also increased their values
596 significantly during the Middle Ages (Figs. 4 and 7), suggesting higher human impact, which was probably
597 the cause of the abrupt retreat of the birch forest (Millet et al., 2006; Morales-Molino et al., 2019). CHAR
598 values showed an increasing trend during the whole period of Middle Age, with some fire episodes
599 documented in ~1290, 1020, 820 and 620 cal BP (Figs. 6-7) as so an interesting CHAR values increase ~750
600 cal BP.

601 Therefore, a substantial growth in human impact and the progressive decline of the birch forest began in
602 the Visigothic period (~1500-1240 cal BP), also affecting the cork oak woodland, although it was much more
603 intense during the Islamic period (~1240-850 cal BP), when a maximum in coprophilous fungi influx and
604 high values of cereal pollen (2.3-2.8%) are documented (Fig. 7). This increment could be related to Alhover-
605 El Milagro mountain pass, through where transhumant livestock flocks were conducted, and to the Abraham
606 defensive tower which was placed really close to the mire (Ruibal, 1985). During the Christian period (~850-
607 500 cal BP), cereal pollen percentage increases notably (5.6%) -particularly from 700 cal BP (top of LPAZ-

608 4a)-, coupled with rising abundances of anthropogenic-nitrophilous herbs and of NPPs indicators of erosion
609 processes, and decreasing shares of deciduous *Quercus* and *Q. suber* (Fig. 7). This increase in farming can be
610 linked to the establishment of new cultivated land from the 13th to 19th century AD in the Cabañeros National
611 Park, when the mountainous complex was owned by the Toledo city Council, as its main resource asset
612 (Perea et al., 2015). Other pollen records from the Toledo Mountains (Fig. 1), both in the northern (Botija,
613 Valdeyernos, Patateros, Bermú) and southern (El Brezoso, Las Viñuelas, El Perro) territories, show similar
614 patterns of land use during this period, including increasing agricultural and livestock activities as well as the
615 cultivation of olive trees (Dorado et al., 2014a, 2014b; Luelmo-Lautenschlaeger et al., 2018a, 2018b, 2018d,
616 2019a, 2019b; Morales-Molino et al., 2018, 2019). Taken together, medieval vegetation dynamics in the
617 Toledo Mountains can be understood considering the following: (i) the Visigothic urban elites stayed in
618 Toledo city, while most people settled in small villages in the rural areas; (ii) the constant and increasing
619 occupation and exploitation of these mid-elevation mountains during the Islamic period, despite it was a
620 border territory with the Christian kingdoms of the north of the Iberian Peninsula; and (iii) the subsequent
621 Christian repopulation of the Toledo Mountains, especially after Toledo city Council bought these lands
622 (Izquierdo, 1983; Ladero, 1984; Jiménez de Gregorio, 2001; Da Cunha, 2007; Barroso et al., 2012;
623 Hernando, 2020).

624 *Sphagnum* appears for the first time in the sequence in LPAZ-3c (Fig. 5) and increases progressively in
625 LPAZ-4a (4.5-12%), whereas *Erica tetralix* follows an opposite trend. The upper part of LPAZ-3c (30-26
626 cm) and the lower part of LPAZ-4a (26-22 cm) are composed of silty peat. Peat formation started during the
627 upper part of LPAZ-4a (22-15 cm) at ~1500 cal BP, which is supported by maximum (20%) LOI values and
628 growing sediment accumulation rates (Fig. 2). A correlative comparison suggests that a wet pulse linked to
629 low NAO+ conditions at ~1500-1300 cal BP allowed *Sphagnum* to spread (Fig. 7; Olsen et al., 2012). Our
630 results from La Ventilla agree with previous research suggesting that low NAO+ mediated climatic
631 variability has been a major driver of peat inception in the Cabañeros National Park and southern Iberia
632 (Fletcher et al., 2013, Ramos-Román et al., 2016; Camuera et al., 2018, 2019; Carrión et al., 2018; Morales-
633 Molino et al., 2019; Alba-Sánchez et al., 2021).

634 The beginning of the Visigothic period matches the onset of the Early Medieval Cold Episode (Fig. 7),
635 spanning from 1500 to 1000 cal BP, with greater aridity and lower temperatures (Martín-Puertas et al., 2010;
636 López-Sáez et al., 2014a), as attested by low $\delta^{18}O$ values and higher NAO+ conditions at ~1300-1000 cal

637 BP (Fig. 7). This cold episode is also reflected in La Ventilla pollen record by a slight increase of NPPs
638 indicative of oligo-mesotrophic open water conditions (Fig. 7) and may also have had some influence on the
639 decline of the birch forest. The increase of CHAR values during the Islamic and Christian periods (Fig. 6)
640 can also be correlated with the onset of the Late Medieval Warm Episode (~1000-600 cal BP; Fig. 7), whose
641 more moderate thermal and rainfall conditions would probably have favoured the exploitation of mid-
642 elevation mountain environments (López-Sáez et al., 2014a) and a slight recovery of the birch forest. Finally,
643 the onset of the Little Ice Age ~600-400 cal BP (Manrique and Fernández-Cancio, 2000), with cooler and
644 drier conditions (lower $\delta^{18}\text{O}$ values and higher NAO+ conditions; Fig. 7), could explain the increase in the
645 values of Cyperaceae, *Erica tetralix*, *Sphagnum* and NPPs indicators of dry conditions, and probably also
646 influenced the further decline in birch cover documented at La Ventilla (Fig. 7).

647

648 5.8. The recovery of birch forest during the Modern Age (~500-150 cal BP)

649 LPAZ-4b pollen subzone (15-7 cm; ~500-150 cal BP) is characterized by the progressive expansion of
650 *Betula* (94-113%), *Castanea*, *Cistus ladanifer*, *Erica arborea/lusitanica* (16%), *E. australis* and Genisteeae,
651 while deciduous *Quercus* (< 2%), *Q. suber* (11-17%), *Calluna vulgaris* and *Sphagnum* (3.5-5.3%) decline
652 and *Erica tetralix* disappears (Figs. 3 and 5; Table 2). Anthropogenic-nitrophilous and anthropozoogenic
653 herbs grow slightly (Fig. 7). Cerealia is still recorded (< 1-3%), whereas coprophilous fungi show their
654 maximum percentage and influx values of the sequence. CHAR values are also at their maximum (Figs. 6-7),
655 but only two fire episode or group of events were identified using peak detection analysis (~420 and 280 cal
656 BP), suggesting that most of the fires were regional (Whitlock and Larsen, 2001). Therefore, the Modern
657 Age (~500-150 cal BP) in La Ventilla pollen record shows the existence of a rather deforested landscape
658 with declining cork and deciduous oak woodlands while the local birch forest expanded. This makes sense
659 considering that during this period agriculture and livestock husbandry expanded and this affected
660 Mediterranean woodlands rather than wetlands, as the population settled down and there was even some
661 population growth (Jiménez de Gregorio, 2001; López-Sáez et al., 2019). The rise in coprophilous fungi
662 matches higher livestock numbers according to historical archives (Perea et al., 2015). Overall, vegetation
663 and fire dynamics during the Modern Age in La Ventilla pollen record follow the same trends as in the rest
664 of pollen sequences of the Toledo Mountains so far mentioned. In the pollen record of Las Lanchas mire

665 (Luelmo-Lautenschlaeger et al., 2018c; Fig. 1), for example, the low human impact on the wetland even
666 allowed the survival of a relict element such as the yew (*Taxus baccata*).

667 High herbivore densities usually had a highly negative impact on Mediterranean *Sphagnum* bogs,
668 probably because of trampling and increasing nutrient loads (López-Sáez et al., 2014c). However, ungulates
669 indeed make an intensive use of mires in summer, when water availability is limited (Acebedo et al., 2008;
670 Perea et al., 2015). Nevertheless, the Modern Age in La Ventilla pollen record was characterized by a humid
671 climate, as attested by high NAO- conditions (Olsen et al., 2012) and increasing values of NPPs indicators of
672 humid environment (Fig. 7), probably related to the second, still colder (decreasing $\delta^{18}O$ values; Fig. 7) but
673 wetter phase of the Little Ice Age ~400-100 cal BP (Manrique and Fernández-Cancio, 2000). These wet
674 conditions would have implied a very low impact of herbivory at La Ventilla mire, which would have
675 directly allowed the development of the birch forest and the disappearance of *Erica tetralix*.

676

677 5.9. Conservation of southernmost Iberian birch populations

678 Birches (*Betula pubescens* and *B. pendula*) are adapted to succeed on a wide range of soils and are the
679 commonest native trees in infertile regions (Patterson, 1993; Jonczak et al., 2020). Indeed, birch woodland
680 can increase the fertility of some mineral soils and supports a large number of specialist and generalist
681 phytophagous insects together with a wide variety of woodland plants, birds and mammals (Beck et al.,
682 2016). Downy birch (*Betula pubescens* subsp. *Celtiberica*) is legally protected as a species of ‘Special
683 Interest’ by the Castilla-La Mancha government and its relict stand in the Toledo Mountains is catalogued as
684 a ‘Special Protection Habitat’ (Martín-Herrero et al., 2003). Unfortunately, rare long-distance dispersal
685 capacity to suitable empty habitats combined with poor germination and unfavourable landscape
686 configuration might prevent the foundation of new downy birch populations (Perala and Alm, 1990; Sánchez
687 del Álamo et al., 2010), i.e. its current distribution is limited exclusively to the peaty habitat it occupies with
688 no possibility of further expansion. Furthermore, this short-distance seed dispersal is primarily a within-stand
689 phenomenon enhancing the likelihood of reaching safe (moist) microsites (peatlands) for seedling emergence
690 and survival (Perala, 1990; Sanz et al., 2011; Rousi et al., 2019). However, the size of the La Ventilla birch
691 population (806 adult stems in just 1.7 ha; Sánchez del Álamo et al., 2010) is large enough for this
692 population to be considered viable in the long term according to the criteria established for the categorization
693 of threatened species (Mace and Lande, 1991; Blanca and Marrero, 2003).

694 Obviously, the conservation of La Ventilla birch forest inevitably involves the conservation of the
695 peatland where it is located (López-Sáez et al., 2014c; Luelmo-Lautenschlaeger et al., 2020). Thus, mid-
696 elevation peat bogs can be considered as local refuges buffering distribution shifts such as those found in the
697 northern edge of the species' range (Kullman, 1986; Truong et al., 2007). The suitability of these habitats as
698 local refuges is predicted to decrease with the ongoing climate warming and subsequent changes in the
699 hydrological regime (Ohlemüller et al., 2006; Herranz et al., 2009), but also if human impact on these
700 habitats remains as high as it has been since recent decades, and even if herbivory pressure is maintained and
701 not regulated, which has already led to the disappearance of many birch forests in the Toledo Mountains
702 (Luelmo-Lautenschlaeger et al., 2019a, 2019b; Morales-Molino et al., 2018, 2019).

703 In the Toledo Mountains, several conservation and restoration efforts on peatlands are already underway
704 (García-Río, 2002; Vaquero, 2010; López-Sáez et al., 2014c). Understanding peatland resilience to human
705 and climate disturbances can assist in integrating local people and their socioeconomic needs into
706 conservation and management strategies (Gómez-Manzanaque, 1987; Fernández-González et al., 2009). The
707 combination of this insight with accurate palaeoecological knowledge is essential for successful conservation
708 programs (Muhumuza and Balkwill, 2013; Hennebelle et al., 2018). Thus, the palaeoecological record of La
709 Ventilla mire provides the first evidence of central Iberian peatland resilience to anthropogenic and climate
710 disturbance by revealing recovery of a relict downy birch forest during the past ~6145 years.

711 In this scenario, the conservation of this endangered population will most probably require an active
712 management aimed at preserving existing water sources and allowing the foundation of new populations
713 through assisted seed dispersal and seedling protection. Nevertheless, the population of *Betula pubescens* in
714 La Ventilla is a unique case in the whole Iberian Peninsula due to its marginal or extreme nature with respect
715 to the distribution area of this species, so it must be considered as an 'evolutionarily significant unit' (ESU)
716 *sensu* Crandall et al. (2000) due to its geographical isolation from the nearest populations (100-150 km from
717 those of the Iberian Central System) but also genetically (Martín et al., 2008; Sánchez del Álamo et al.,
718 2010). In this sense, one of the priority conservation measures must be to preserve their genetic identity, so
719 any possible reinforcement should be made with materials from the same population. Clearly, the biggest
720 problem facing the downy birch in the Toledo Mountains is the fragmentation of its habitat due to
721 unfavourable climatic periods during the Holocene as well as the human impact over time (Morales-Molino

722 et al., 2019), since in these mid-mountain territories there are many peatland ecosystems without birch trees
723 but where this species could have thrived in the past (Luelmo-Lautenschlaeger et al., 2019b, 2020).

724

725

726 **6. Conclusions**

727 High-resolution multiproxy analyses of La Ventilla record allow the reconstruction of vegetation, fire and
728 human dynamics in central-southern Iberian Peninsula during the mid-late Holocene (~6145-150 cal BP).
729 This core provides the first Iberian evidence of uninterrupted persistence of a dense and natural downy birch
730 (*Betula pubescens* subsp.) forest for at least six millennia in the Toledo Mountains, which can be considered
731 a palaeorefuge for this species. Most of the studied period has been characterized by the resilience of birch
732 woodlands to fire disturbances and anthropic dynamics, as well as by generally gradual responses to
733 millennial and centennial-scale climate fluctuations.

734 During the late Neolithic (~6145-5200 cal BP), La Ventilla wetland would correspond to a lotic system
735 with slow moving backwaters. Its most characteristic vegetation would be open birch woodlands, related to
736 temperate and humid ~6145-5800 cal BP and later ~5800-5200 cal BP arid climatic conditions. This period
737 documents the earliest evidence of human impact, including agricultural activities and increasing pastoral
738 pressure from ~5400 cal BP. During the Chalcolithic (~5200-4200 cal BP) the birch forest increases
739 progressively, despite a low human impact and a documented dry pulse ~5200-4800 cal BP, developing
740 further with the wet pulse ~4800-4200 cal BP related to NAO- conditions. By contrast, during the
741 Chalcolithic-early Bronze Age transition (~ 4200-4000 cal BP) the birch forest suffered a sharp decline as a
742 consequence of the abrupt climatic event 4200 cal BP, characterised by extremely arid climatic conditions.
743 During the Bronze Age (~4000-3200 cal BP), the wetland ecosystem quickly recovered to conditions prior to
744 the abrupt climatic event. The birch forest developed under humid and mesotrophic conditions. However, by
745 ~3500-3200 cal BP La Ventilla birch forest would spread again as human impact shifted away from the
746 wetland and focused on the deciduous oak woodlands. Subsequently, progressively wetter conditions related
747 to the 2800 cal BP event and lower human impact with the abandonment of lowland settlements ~3200-2800
748 cal BP, allowed for further development of the birch forest and hygrophytic vegetation in the transition
749 between the late Bronze Age and the early Iron Age. However, the birch forest receded again ~2800-2400
750 cal BP at the end of the early Iron Age, in connection with the climatic irregularity associated with the onset

751 of the Ibero-Roman Humid Period, characterized by a first dry pulse with NAO+ conditions ~2640-2500 cal
752 BP, and a subsequent wet pulse with NAO- conditions ~2500-2400 cal BP. The late Iron Age (~2400-2000
753 cal BP) and the Roman period (~2000-1500 cal BP) would correspond to a phase of relative stability of
754 woodlands in La Ventilla mire, with a new development of birch forest under wetter and warmer climatic
755 conditions at the beginning and drier and colder later on, and low human impact, despite irregular climate
756 conditions. Tree crops (*Castanea*, *Juglans*) are documented ~1750-1500 cal BP. Agricultural and livestock
757 activities, probably mediated by the anthropogenic use of fire, replaced climate as the critical driver of La
758 Ventilla downy birch population dynamics during the Middle Ages, causing an abrupt birch decline ~1500-
759 500 cal BP. Finally, during the Modern Age (~500-150 cal BP) the birch forest recovers again thanks to the
760 humid climatic conditions of the second phase of the Little Ice Age ~400-100 cal BP, although agricultural
761 activities and livestock pressure increase enormously in the cork and deciduous oak woodlands of the study
762 area.

763 Nowadays, the birch forest and mire of La Ventilla are currently undergoing a very significant regression
764 due to the exploitation of its aquifer to irrigate nearby maize and crop fields. Agricultural activities in the
765 immediate surroundings of peatland ecosystems and birch forests, as well as the sometimes very high
766 densities of wild and domestic ungulates, need to be controlled, as their impact on them may lead to their
767 extinction. It should not be forgotten that birches in the Toledo Mountains are almost always linked to
768 peatland ecosystems, especially in the case of the downy birch whose dispersal and expansion is very limited
769 in this respect, so that protection of birch trees must be closely associated with safeguarding the peatland
770 ecosystems in which they live. Restoration of birch stands is fully justified considering that land-use
771 intensification since prehistoric times has caused their decline and even disappearance in many places.

772

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774

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784

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786

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1282

1283 **FIGURE CAPTIONS**

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1286 **Fig. 1.** Location of the study site (yellow star) and other pollen records (purple circles) from the Toledo
1287 Mountains mentioned in the text: 1, Las Lanchas; 2, Botija; 3, Patateros; 4, Bermú; 5, Valdeyernos; 6, La
1288 Ventilla; 7, El Brezoso; 8, Las Viñuelas; 9, El Perro.

1289 **Fig. 2.** From left to right. Lithostratigraphy and age-depth relationship for the La Ventilla sequence. Details
1290 of the AMS ^{14}C dates (blue distributions in the graph) are listed in Table 1. The model (smooth spline 0.2,
1291 black line) takes into account the 2σ confidence range of calibrated ages (grey areas). Sediment accumulation
1292 rates (mm yr^{-1}), organic matter content (LOI), magnetic susceptibility (MS) and pollen concentration (10^5
1293 grains cm^{-1}) are also shown.

1294
1295 **Fig. 3.** Percentage pollen diagram of the La Ventilla sequence (woody taxa) plotted against age (cal BP). The
1296 black silhouettes show the percentage curves of the taxa, the grey silhouettes show the 5× exaggeration
1297 curves.

1298
1299 **Fig. 4.** Percentage pollen diagram of the La Ventilla sequence (upland herbs) plotted against age (cal BP).
1300 The black silhouettes show the percentage curves of the taxa, the grey silhouettes show the 5× exaggeration
1301 curves.

1302
1303 **Fig. 5.** Percentage pollen diagram of the La Ventilla sequence (hydro-hygrophytic taxa, ferns and non-pollen
1304 palynomorphs) plotted against age (cal BP). The black silhouettes show the percentage curves of the taxa,
1305 the grey silhouettes show the 5× exaggeration curves.

1306
1307 **Fig. 6.** Interpolated macroscopic charcoal accumulation rates (CHAR) and robust fire episodes (+) at La
1308 Ventilla mire. The grey areas correspond to raw charcoal data while the black lines correspond to CHAR
1309 interpolated to the median resolution of the record.

1310
1311 **Fig. 7.** Selected pollen taxa and ecological groups (see Table 2), and robust fire episodes (+) of La Ventilla
1312 sequence plotted against age (cal BP); $\delta^{18}\text{O}$ record from NGRIP record (Rasmussen et al., 2008); NAO
1313 Index from Olsen et al. (2012). LIA: Little Ice Age; LMWE: Late Medieval Warm Episode; EMCE: Early
1314 Medieval Cold Episode; IRHP: Ibero-Roman Humid Period.

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1316

1317 **Table 1.** AMS ^{14}C dates from La Ventilla mire, calibrated using the IntCal20 calibration curve (Reimer et
1318 al., 2020).
1319

Depth (cm)	Lab code	^{14}C Age BP	Calibrated age (cal BP; 95.4% confidence interval)	Median age (cal BP)
19	D-AMS-036910	770 ± 26	726-671	693
37	D-AMS-036911	1995 ± 35	2000-1830	1929
46	D-AMS-036912	2550 ± 32	2751-2497	2633
65	D-AMS-036913	2600 ± 36	2778-2522	2740
81	D-AMS-036914	4510 ± 37	5310-5042	5161
97	D-AMS-036915	5250 ± 40	6179-5924	6018

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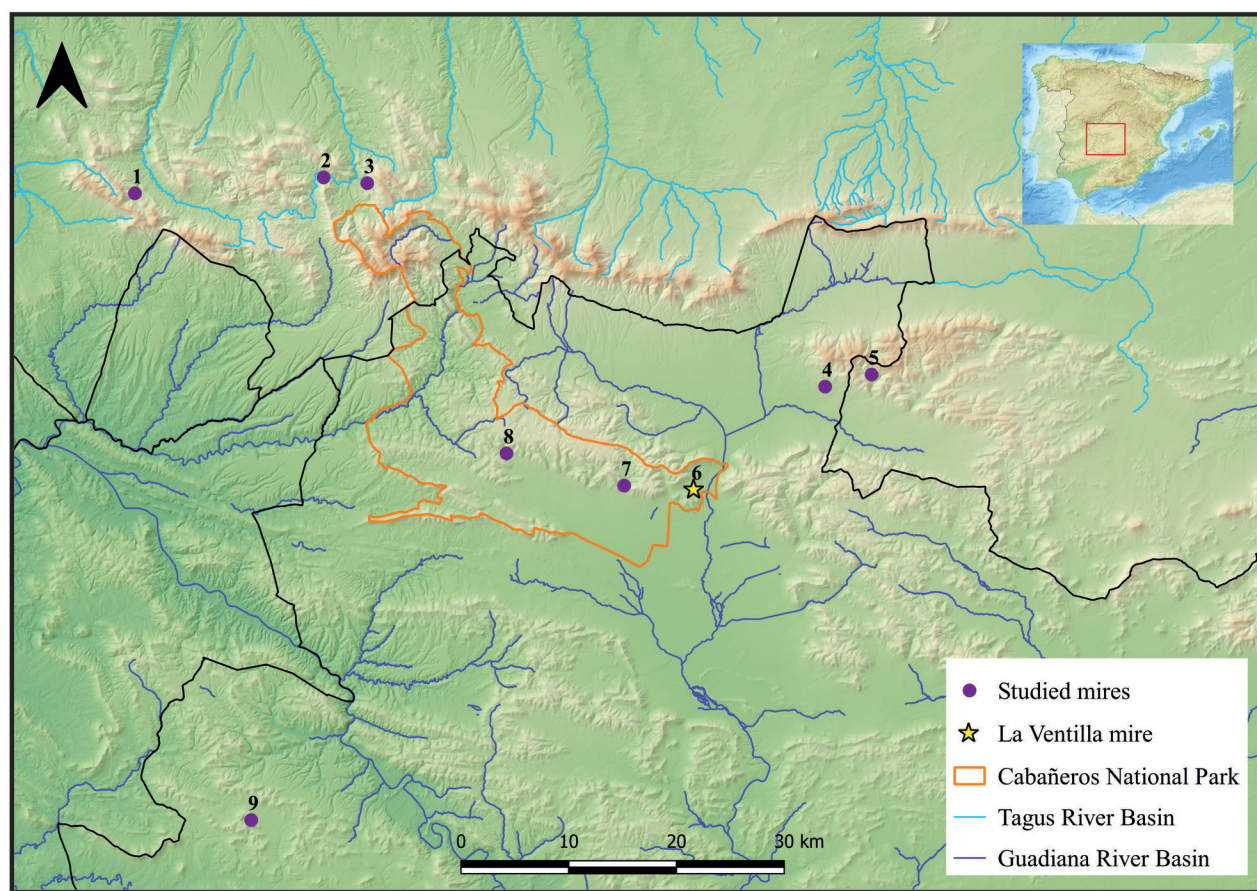
1323 **Table 2.** Description of pollen zones, and ecological groups from La Ventilla mire (see Figs. 2-5) according
 1324 to Cugny et al. (2010), Perea et al. (2015), Luelmo-Lautenschlaeger et al. (2019b) and Morales-Molino et al.
 1325 (2019, 2020). AP: Arboreal Pollen; SP: Shrubland Pollen; RW: Riparian Woods (*Alnus*, *Fraxinus*, *Salix*);
 1326 TC: Tree Crops (*Castanea*, *Juglans*); HP: Herbaceous Pollen; ANH: Anthropogenic-Nitrophilous Herbs
 1327 (Asterioideae, Boraginaceae, Carduoideae, Cichorioideae); AZH: Anthropozoogenic Herbs
 1328 (Chenopodiaceae, *Plantago lanceolata*-type, *Urtica dioica*-type); CF: Coprophilous Fungi (HdV-55A, HdV-
 1329 112, HdV-113, HdV-144, HdV-169, HdV-172, HdV-262, HdV-573, TM-4010); DRY: NPPs dry conditions
 1330 (HdV-3B, HdV-10); WET: NPPs humid conditions (HdV-18); EUME: NPPs eu-mesotrophic shallow and
 1331 stagnant water conditions (HdV-12, HdV-65, HdV-123, HdV-124, HdV-151, HdV-159, HdV-179, HdV-315,
 1332 HdV-342, HdV-353A); OLME: NPPs oligo-mesotrophic open water conditions (HdV-119, HdV-384); ERO:
 1333 NPPs soil erosion (HdV-207).
 1334

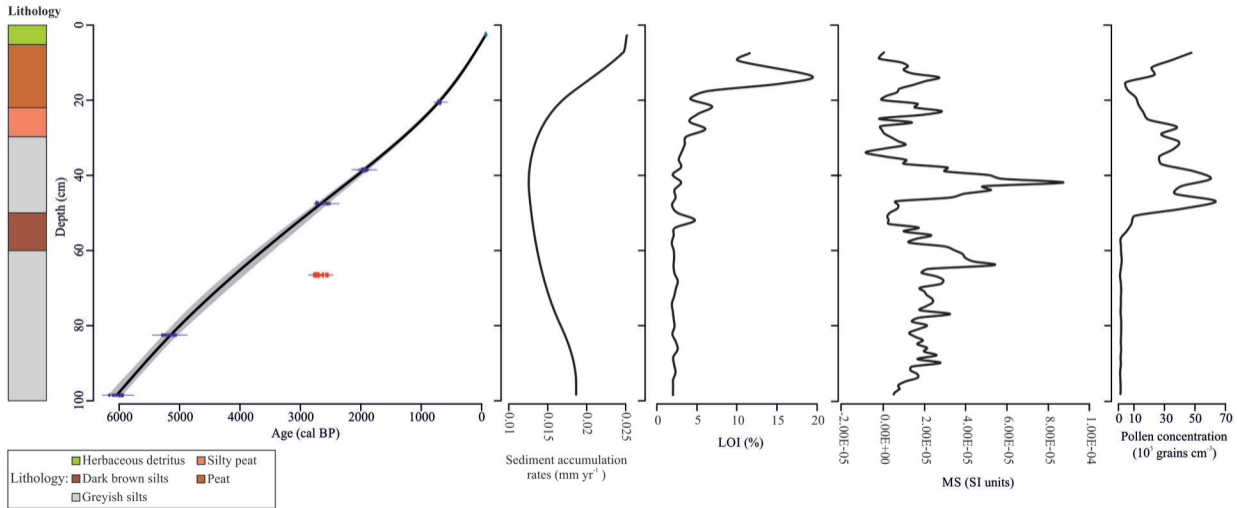
SUBZONE Depth (cm)/ Age cal BP	Trees/Shrubs	Herbs /Wetland taxa	NPPs	Pollen concentration
LPAZ-1a, 99-93 cm 6145-5800 cal BP	AP 20-26%, SP 12-19%, deciduous <i>Quercus</i> 12-16%, evergreen <i>Quercus</i> 2%, <i>Quercus suber</i> 1-3.5%, RW 1-5%, <i>Betula</i> 60-70%, <i>Erica spp.</i> 3.6-8.2%, Genisteae 1-3%, <i>Calluna vulgaris</i> 1-2.7%, Sporadic occurrences of <i>Arbutus unedo</i> , <i>Corylus</i> , <i>Daphne gnidium</i> , <i>Lavandula stoechas</i> , <i>Lonicera</i> , and <i>Pinus pinea</i>	HP 55-68%, Poaceae 37-56% ANH 0.4-2.4% AZH 2.7-3.7% Cyperaceae 63-92%	CF < 1% EUME < 2.5% OLME < 0.5% HdV-114 11-20%	Very low values ($< 2 \times 10^5$ grains cm ⁻³)
LPAZ-1b, 93-82 cm 5800-5200 cal BP	AP 18-27.3%, SP 25-29%, deciduous <i>Quercus</i> 11-16%, evergreen <i>Quercus</i> 1-2%, <i>Quercus suber</i> 3.5-4.5%, RW 2-6%, <i>Betula</i> 38-80%, <i>Erica spp.</i> 15-21%, Genisteae 1-3-4%, <i>Calluna vulgaris</i> 1.3-2.4%, Sporadic occurrences of <i>Arbutus unedo</i> , <i>Cistus ladanifer</i> , <i>Corylus</i> , <i>Daphne gnidium</i> , <i>Hedera helix</i> , <i>Ilex aquifolium</i> , <i>Lavandula stoechas</i> , <i>Lonicera</i> , and <i>Pinus pinea</i>	HP 47-54%, Poaceae 26-30.5% Cerealia 0-1.4% ANH 2.7-8.8% AZH 3.8-6.3% Cyperaceae 26-29.4%	CF 2.5-13% DRY 0.5-3.3% EUME 1-7.5% OLME < 1% ERO 0-1.3% HdV-114 8.5-14%	Very low values ($< 2 \times 10^5$ grains cm ⁻³)
LPAZ-1c, 82-68 cm 5200-4250 cal BP	AP 25-29%, SP 22-29.3%, deciduous <i>Quercus</i> 15.5-18%, evergreen <i>Quercus</i> < 2%, <i>Quercus suber</i> 4-6.7%, RW 3.3-4%, <i>Betula</i> 57-86%, <i>Erica spp.</i> 14-20%, Genisteae 2%, <i>Calluna vulgaris</i> 1.3-4%, Low values (< 2%) of <i>Arbutus unedo</i> , <i>Cistus ladanifer</i> , <i>Corylus</i> , <i>Daphne gnidium</i> , <i>Hedera helix</i> , <i>Ilex aquifolium</i> , <i>Lavandula stoechas</i> , <i>Lonicera</i> , and <i>Pinus pinea</i>	HP 42-51%, Poaceae 21-28% Cerealia 0-1.7% ANH 2.5-10.6% AZH 4-8.3% Cyperaceae 23.5-35.5%	CF 2.2-15% DRY 0-2.5% EUME 1-7.5% OLME < 1% ERO 0-1.6% HdV-114 9-13.5%	Very low values ($< 2 \times 10^5$ grains cm ⁻³)
LPAZ-2a, 68-57 cm 4250-3500 cal BP	AP 29.6-42%, SP 15-32%, deciduous <i>Quercus</i> 5.5-15%, evergreen <i>Quercus</i> 2-6%, <i>Quercus suber</i> 7-21.5%, RW 6.3-8%, <i>Betula</i> 26-72%, <i>Erica spp.</i> 8.5-19.5%, Genisteae 1.5-2.7%, <i>Calluna vulgaris</i> 0.2-5%, Low values (< 2%) of <i>Arbutus unedo</i> , <i>Cistus ladanifer</i> , <i>Corylus</i> , <i>Daphne gnidium</i> , <i>Hedera helix</i> , <i>Ilex aquifolium</i> , <i>Lavandula stoechas</i> , <i>Lonicera</i> , and <i>Pinus pinea</i>	HP 38-46%, Poaceae 28-37% ANH < 2% AZH < 3% Cyperaceae 9-20% <i>Erica tetralix</i> 0-0.3%	CF < 2% DRY 0-2% WET 0-4.4% EUME 0.3-5% OLME < 2% ERO 0-3.6% HdV-114 1.7-22.6%	Very low values ($< 2 \times 10^5$ grains cm ⁻³)
LPAZ-2b, 57-51- cm 3500-3000 cal BP	AP 38.7-45.5%, SP 25.7-40.3%, deciduous <i>Quercus</i> 4-5.5%, evergreen <i>Quercus</i> 1.5-2.5%, <i>Quercus suber</i> 18-22.5%, RW 14%, <i>Betula</i> 98-127%, <i>Erica spp.</i> 14.5-30.5%, Genisteae 3%, <i>Calluna vulgaris</i> < 1%, Low values (< 2%) of <i>Arbutus unedo</i> , <i>Cistus ladanifer</i> , <i>Corylus</i> , <i>Daphne gnidium</i> , <i>Hedera helix</i> , <i>Ilex aquifolium</i> , <i>Lavandula stoechas</i> , <i>Lonicera</i> , and <i>Pinus pinea</i>	HP 21-29%, Poaceae 13-15.5% ANH 2-3% AZH < 3% Cyperaceae 46-70% <i>Erica tetralix</i> 0-0.4%	CF < 3% DRY 0-0.2% EUME 6.5-8.5% OLME 0.2-4.4% HdV-114 1-6%	Low but increasing values ($5-10 \times 10^5$ grains cm ⁻³)
LPAZ-3a, 51-42 cm 3000-2400 cal BP	AP 42-57.6%, SP 24.5-33%, deciduous <i>Quercus</i> 3-6%, evergreen <i>Quercus</i> 1.6-2.4%, <i>Quercus suber</i> 18-23%, RW 13.5-29.5%, <i>Betula</i> 129-189%, <i>Erica spp.</i> 15-23%, Genisteae 0.5-3.5%, <i>Calluna vulgaris</i> 1-3.5%, Low values (< 2%) of <i>Arbutus unedo</i> , <i>Cistus ladanifer</i> , <i>Corylus</i> , <i>Daphne gnidium</i> , <i>Hedera helix</i> , <i>Ilex aquifolium</i> , <i>Lavandula stoechas</i> , <i>Lonicera</i> , and <i>Pinus pinea</i>	HP 18-26.6%, Poaceae 7.7-16.6% ANH 1% AZH < 1% Cyperaceae 38-107% <i>Erica tetralix</i> 20-28% Ranunculaceae 0-3.5%	CF < 1% WET < 1% EUME 1-16% OLME 2.5-6.5% ERO 0-2% HdV-114 2-7%	Very high values ($> 30 \times 10^5$ grains cm ⁻³) Maximum (64×10^5 grains cm ⁻³) ~2750 cal BP (47 cm)
LPAZ-3b, 42-34 cm 2400-1750 cal BP	AP 44-50%, SP 25.5-33.2%, deciduous <i>Quercus</i> 3.7-6%, evergreen <i>Quercus</i> 2-3%, <i>Quercus suber</i> 18.5-23%, RW 16-19.7%, <i>Betula</i> 122-167%, <i>Erica spp.</i> 17-23.3%, Low values (< 3%) of <i>Arbutus unedo</i> , <i>Calluna vulgaris</i> , <i>Cistus ladanifer</i> , <i>Daphne gnidium</i> , Genisteae, <i>Hedera helix</i> , <i>Ilex aquifolium</i> , <i>Lavandula stoechas</i> , <i>Lonicera</i> , and <i>Pinus pinea</i>	HP 20-28.2%, Poaceae 9.5-15% ANH 1.5-4% AZH < 1% Cyperaceae 44-49% <i>Erica tetralix</i> 36-47% Ranunculaceae 0-1%	CF < 1% WET < 1% EUME < 2% OLME 2% ERO < 1% HdV-114 3-8%	Very high values ($> 25 \times 10^5$ grains cm ⁻³) Maximum (60×10^5 grains cm ⁻³) ~2250 cal BP (41 cm)
LPAZ-3c, 34-26 cm 1750-1150 cal BP	AP 40-46.3%, SP 25.6-31.7%, TC 0.2-4.3%, deciduous <i>Quercus</i> 4-8.5%, <i>Quercus suber</i> 17-25%, RW 10.5-14%, <i>Betula</i> 119-172%, <i>Erica spp.</i> 14-22%, <i>Arbutus unedo</i> 2-5.5%, Genisteae 3-4%, Low values (< 2%) of <i>Calluna vulgaris</i> , <i>Cistus ladanifer</i> , <i>Corylus</i> , <i>Daphne gnidium</i> , evergreen <i>Quercus</i> , <i>Hedera helix</i> , <i>Ilex aquifolium</i> , <i>Lavandula stoechas</i> , <i>Lonicera</i> , and <i>Pinus pinea</i>	HP 24-34.7%, Poaceae 9-14% Cerealia 0-0.6% ANH 4-6.5% AZH 1-5% Cyperaceae 41-55% <i>Erica tetralix</i> 33.6-54.5% Ranunculaceae 0-2.2% <i>Sphagnum</i> 0.4.6%	CF < 1% WET < 1% EUME < 2% OLME 2-5% ERO 0.5-3.3% HdV-114 3.5-7%	High values ($28-40 \times 10^5$ grains cm ⁻³)
LPAZ-4a, 26-15 cm 1150-500 cal BP	AP 31-50%, SP 19-28.5%, TC 1-4%, deciduous <i>Quercus</i> 1-8.5%, <i>Quercus suber</i> 14-25.7%, RW	HP 28-40.5%, Poaceae 13-26%	CF 1-4% DRY 0-15.5%	Decreasing values ($5-20 \times 10^5$ grains cm ⁻³)

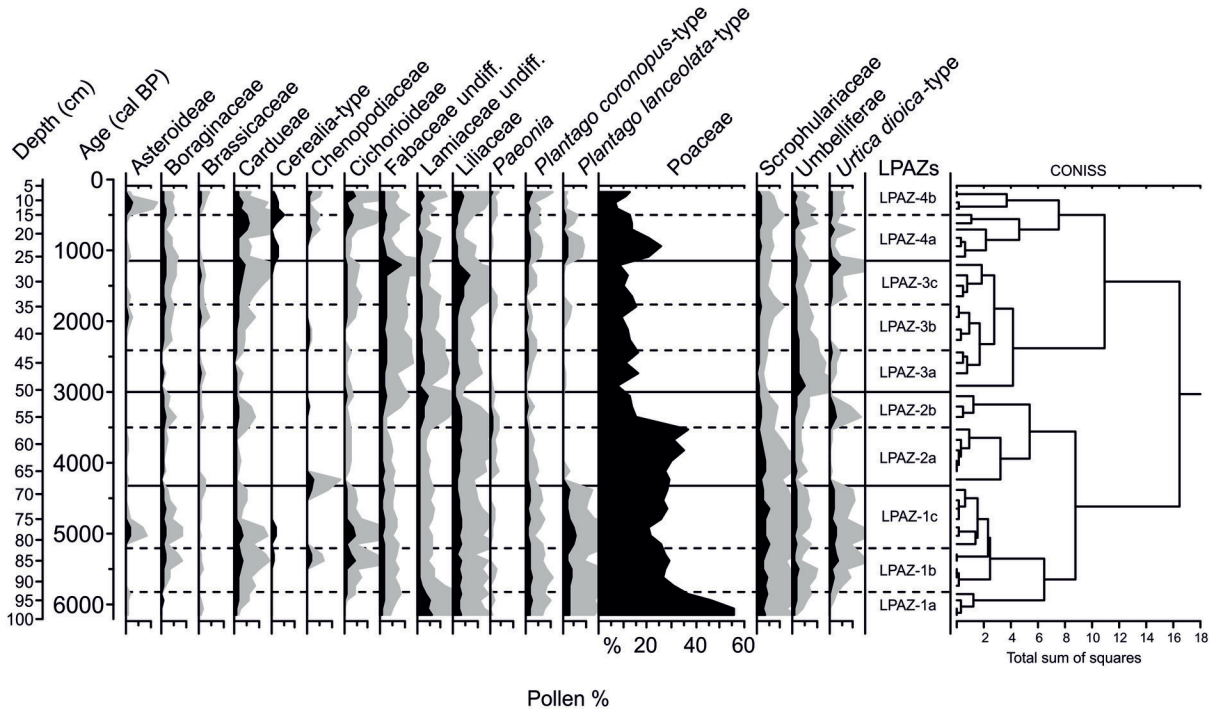
	9-18.5%, <i>Betula</i> 72-104%, <i>Erica spp.</i> 13-16%, <i>Arbutus unedo</i> 1-3.4%, Genisteae 1-4%, Low values (< 3%) of <i>Calluna vulgaris</i> , <i>Cistus ladanifer</i> , <i>Corylus</i> , <i>Daphne gnidium</i> , evergreen <i>Quercus</i> , <i>Hedera helix</i> , <i>Ilex aquifolium</i> , <i>Lavandula stoechas</i> , <i>Lonicera</i> , and <i>Pinus pinea</i>	Cerealia 0-5.6% ANH 3-10% AZH 2-3.5% Cyperaceae 35-52% <i>Erica tetralix</i> 5-21% <i>Sphagnum</i> 4.5-12%	WET < 3% EUME 1-7.6% OLME 0.5-4% ERO 0-19% HdV-114 11-25%	
LPAZ-4b, 15-7 cm 500-150 cal BP	AP 32-37.7%, SP 34-35.4%, TC 2-3.5%, <i>Quercus suber</i> 11-17%, RW 12-13%, <i>Betula</i> 94-113%, <i>Erica spp.</i> 22-23%, Low values (< 4%) of <i>Arbutus unedo</i> , <i>Calluna vulgaris</i> , <i>Cistus ladanifer</i> , <i>Corylus</i> , <i>Daphne gnidium</i> , deciduous <i>Quercus</i> , evergreen <i>Quercus</i> , Genisteae, <i>Hedera helix</i> , <i>Ilex aquifolium</i> , <i>Lavandula stoechas</i> , <i>Lonicera</i> , and <i>Pinus pinea</i>	HP 27.5-33%, Poaceae 7-12.6% Cerealia 1-3% ANH 6-7.6% AZH 2-3% Cyperaceae 32-38.3% Ranunculaceae 0.5-4.5% <i>Erica tetralix</i> 0-1.1% <i>Sphagnum</i> 3.5-5.3%	CF 2.5-22.5% DRY 1-12.5% WET 3-3-7% EUME 3.6-11% OLME 1% ERO 0-1.5% HdV-114 1-4.2%	Increasing values (21-47 x 10 ⁵ grains cm ⁻³)

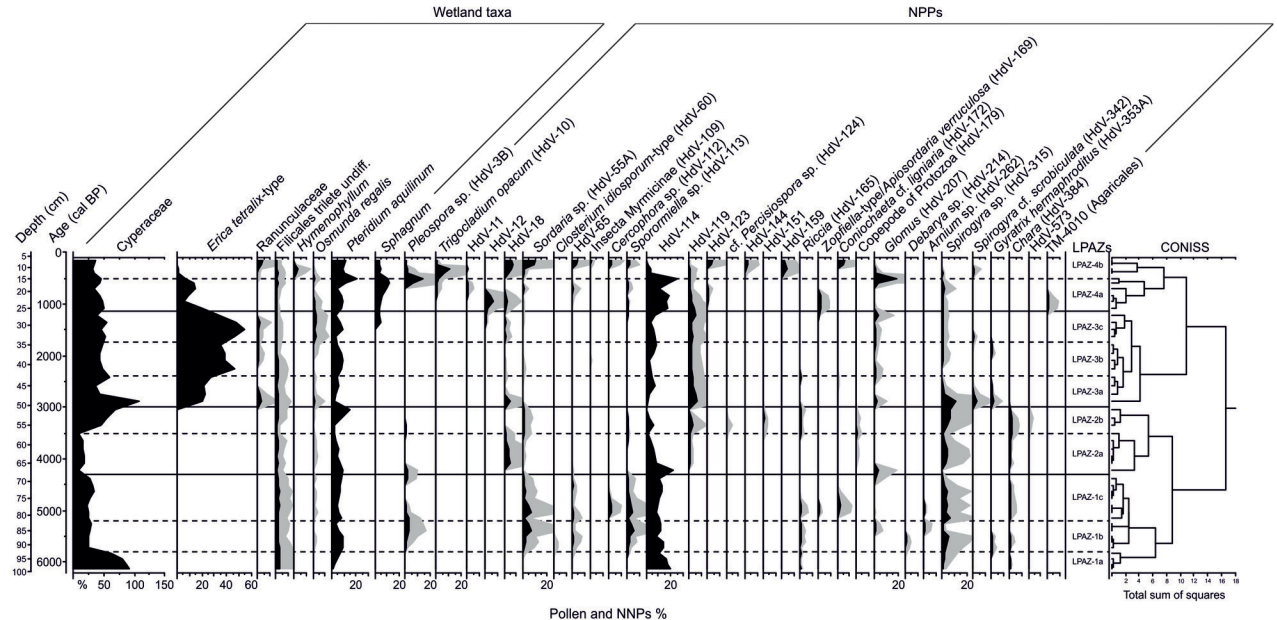
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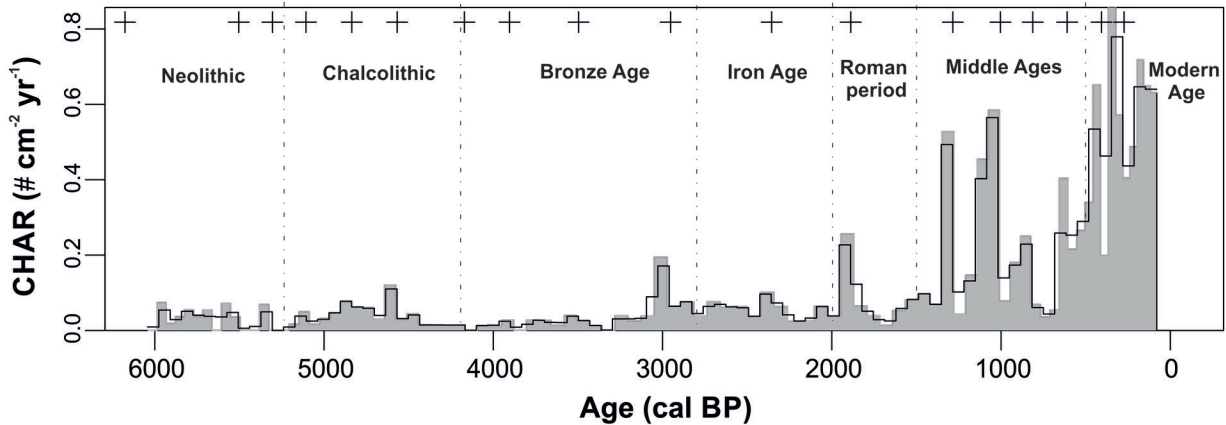


Table 1. AMS ^{14}C dates from La Ventilla mire, calibrated using the IntCal20 calibration curve (Reimer et al., 2020).

Depth (cm)	Lab code	^{14}C Age BP	Calibrated age (cal BP; 95.4% confidence interval)	Median age (cal BP)
19	D-AMS-036910	770 ± 26	726-671	693
37	D-AMS-036911	1995 ± 35	2000-1830	1929
46	D-AMS-036912	2550 ± 32	2751-2497	2633
65	D-AMS-036913	2600 ± 36	2778-2522	2740
81	D-AMS-036914	4510 ± 37	5310-5042	5161
97	D-AMS-036915	5250 ± 40	6179-5924	6018

1 **Table 2.** Description of pollen zones, and ecological groups from La Ventilla mire (see Figs. 2-5) according
2 to Cugny et al. (2010), Perea et al. (2015), Luelmo-Lautenschlaeger et al. (2019b) and Morales-Molino et al.
3 (2019, 2020). AP: Arboreal Pollen; SP: Shrubland Pollen; RW: Riparian Woods (*Alnus*, *Fraxinus*, *Salix*); TC:
4 Tree Crops (*Castanea*, *Juglans*); HP: Herbaceous Pollen; ANH: Anthropogenic-Nitrophilous Herbs
5 (Asterioideae, Boraginaceae, Carduoideae, Cichorioideae); AZH: Anthropozoogenic Herbs (Chenopodiaceae,
6 *Plantago lanceolata*-type, *Urtica dioica*-type); CF: Coprophilous Fungi (HdV-55A, HdV-112, HdV-113,
7 HdV-144, HdV-169, HdV-172, HdV-262, HdV-573, TM-4010); DRY: NPPs dry conditions (HdV-3B, HdV-
8 10); WET: NPPs humid conditions (HdV-18); EUME: NPPs eu-mesotrophic shallow and stagnant water
9 conditions (HdV-12, HdV-65, HdV-123, HdV-124, HdV-151, HdV-159, HdV-179, HdV-315, HdV-342,
10 HdV-353A); OLME: NPPs oligo-mesotrophic open water conditions (HdV-119, HdV-384); ERO: NPPs soil
11 erosion (HdV-207).
12

SUBZONE Depth (cm)/ Age cal BP	Trees/Shrubs	Herbs /Wetland taxa	NPPs	Pollen concentration
LPAZ-1a, 99-93 cm 6145-5800 cal BP	AP 20-26%, SP 12-19%, deciduous <i>Quercus</i> 12-16%, evergreen <i>Quercus</i> 2%, <i>Quercus suber</i> 1-3.5%, RW 1-5%, <i>Betula</i> 60-70%, <i>Erica spp.</i> 3.6-8.2%, Genisteae 1-3%, <i>Calluna vulgaris</i> 1-2.7%. Sporadic occurrences of <i>Arbutus unedo</i> , <i>Corylus</i> , <i>Daphne gnidium</i> , <i>Lavandula stoechas</i> , <i>Lonicera</i> , and <i>Pinus pinea</i>	HP 55-68%, Poaceae 37-56% ANH 0.4-2.4% AZH 2.7-3.7% Cyperaceae 63-92%	CF < 1% EUME < 2.5% OLME < 0.5% HdV-114 11-20%	Very low values ($< 2 \times 10^5$ grains cm ⁻³)
LPAZ-1b, 93-82 cm 5800-5200 cal BP	AP 18-27.3%, SP 25-29%, deciduous <i>Quercus</i> 11-16%, evergreen <i>Quercus</i> 1-2%, <i>Quercus suber</i> 3.5-4.5%, RW 2-6%, <i>Betula</i> 38-80%, <i>Erica spp.</i> 15-21%, Genisteae 1-3-4%, <i>Calluna vulgaris</i> 1.3-2.4%. Sporadic occurrences of <i>Arbutus unedo</i> , <i>Cistus ladanifer</i> , <i>Corylus</i> , <i>Daphne gnidium</i> , <i>Hedera helix</i> , <i>Ilex aquifolium</i> , <i>Lavandula stoechas</i> , <i>Lonicera</i> , and <i>Pinus pinea</i>	HP 47-54%, Poaceae 26-30.5% Cerealía 0-1.4% ANH 2.7-8.8% AZH 3.8-6.3% Cyperaceae 26-29.4%	CF 2.5-13% DRY 0.5-3.3% EUME 1-7.5% OLME < 1% ERO 0-1.3% HdV-114 8.5-14%	Very low values ($< 2 \times 10^5$ grains cm ⁻³)
LPAZ-1c, 82-68 cm 5200-4250 cal BP	AP 25-29%, SP 22-29.3%, deciduous <i>Quercus</i> 15.5-18%, evergreen <i>Quercus</i> < 2%, <i>Quercus suber</i> 4-6.7%, RW 3.3-4%, <i>Betula</i> 57-86%, <i>Erica spp.</i> 14-20%, Genisteae 2%, <i>Calluna vulgaris</i> 1.3-4%. Low values (< 2%) of <i>Arbutus unedo</i> , <i>Cistus ladanifer</i> , <i>Corylus</i> , <i>Daphne gnidium</i> , <i>Hedera helix</i> , <i>Ilex aquifolium</i> , <i>Lavandula stoechas</i> , <i>Lonicera</i> , and <i>Pinus pinea</i>	HP 42-51%, Poaceae 21-28% Cerealía 0-1.7% ANH 2.5-10.6% AZH 4-8.3% Cyperaceae 23.5-35.5%	CF 2.2-15% DRY 0-2.5% EUME 1-7.5% OLME < 1% ERO 0-1.6% HdV-114 9-13.5%	Very low values ($< 2 \times 10^5$ grains cm ⁻³)
LPAZ-2a, 68-57 cm 4250-3500 cal BP	AP 29.6-42%, SP 15-32%, deciduous <i>Quercus</i> 5.5-15%, evergreen <i>Quercus</i> 2-6%, <i>Quercus suber</i> 7-21.5%, RW 6.3-8%, <i>Betula</i> 26-72%, <i>Erica spp.</i> 8.5-19.5%, Genisteae 1.5-2.7%, <i>Calluna vulgaris</i> 0.2-5%. Low values (< 2%) of <i>Arbutus unedo</i> , <i>Cistus ladanifer</i> , <i>Corylus</i> , <i>Daphne gnidium</i> , <i>Hedera helix</i> , <i>Ilex aquifolium</i> , <i>Lavandula stoechas</i> , <i>Lonicera</i> , and <i>Pinus pinea</i>	HP 38-46%, Poaceae 28-37% ANH < 2% AZH < 3% Cyperaceae 9-20% <i>Erica tetralix</i> 0-0.3%	CF < 2% DRY 0-2% WET 0-4.4% EUME 0.3-5% OLME < 2% ERO 0-3.6% HdV-114 1.7-22.6%	Very low values ($< 2 \times 10^5$ grains cm ⁻³)
LPAZ-2b, 57-51- cm	AP 38.7-45.5%, SP 25.7-40.3%, deciduous <i>Quercus</i> 4-5.5%, evergreen <i>Quercus</i> 1.5-2.5%,	HP 21-29%,	CF < 3%	Low but increasing values

3500-3000 cal BP	<i>Quercus suber</i> 18-22.5%, <i>RW</i> 14%, <i>Betula</i> 98-127%, <i>Erica spp.</i> 14.5-30.5%, <i>Genisteae</i> 3%, <i>Calluna vulgaris</i> < 1%, Low values (< 2%) of <i>Arbutus unedo</i> , <i>Cistus ladanifer</i> , <i>Corylus</i> , <i>Daphne gnidium</i> , <i>Hedera helix</i> , <i>Ilex aquifolium</i> , <i>Lavandula stoechas</i> , <i>Lonicera</i> , and <i>Pinus pinea</i>	Poaceae 13-15.5% ANH 2-3% AZH < 3% Cyperaceae 46-70% <i>Erica tetralix</i> 0-0.4%	DRY 0-0.2% EUME 6.5-8.5% OLME 0.2-4.4% HdV-114 1-6%	(5-10 x 10 ⁵ grains cm ⁻³)
LPAZ-3a, 51-42 cm 3000-2400 cal BP	AP 42-57.6%, SP 24.5-33%, deciduous <i>Quercus</i> 3-6%, evergreen <i>Quercus</i> 1.6-2.4%, <i>Quercus suber</i> 18-23%, <i>RW</i> 13.5-29.5%, <i>Betula</i> 129-189%, <i>Erica spp.</i> 15-23%, <i>Genisteae</i> 0.5-3.5%, <i>Calluna vulgaris</i> 1-3.5%, Low values (< 2%) of <i>Arbutus unedo</i> , <i>Cistus ladanifer</i> , <i>Corylus</i> , <i>Daphne gnidium</i> , <i>Hedera helix</i> , <i>Ilex aquifolium</i> , <i>Lavandula stoechas</i> , <i>Lonicera</i> , and <i>Pinus pinea</i>	HP 18-26.6%, Poaceae 7.7-16.6% ANH 1% AZH < 1% Cyperaceae 38-107% <i>Erica tetralix</i> 20-28% Ranunculaceae 0-3.5%	CF < 1% WET < 1% EUME 1-16% OLME 2.5-6.5% ERO 0-2% HdV-114 2-7%	Very high values (> 30 x 10 ⁵ grains cm ⁻³) Maximum (64 x 10 ⁵ grains cm ⁻³) ~2750 cal BP (47 cm)
LPAZ-3b, 42-34 cm 2400-1750 cal BP	AP 44-50%, SP 25.5-33.2%, deciduous <i>Quercus</i> 3.7-6%, evergreen <i>Quercus</i> 2-3%, <i>Quercus suber</i> 18.5-23%, <i>RW</i> 16-19.7%, <i>Betula</i> 122-167%, <i>Erica spp.</i> 17-23.3%, Low values (< 3%) of <i>Arbutus unedo</i> , <i>Calluna vulgaris</i> , <i>Cistus ladanifer</i> , <i>Daphne gnidium</i> , <i>Genisteae</i> , <i>Hedera helix</i> , <i>Ilex aquifolium</i> , <i>Lavandula stoechas</i> , <i>Lonicera</i> , and <i>Pinus pinea</i>	HP 20-28.2%, Poaceae 9.5-15% ANH 1.5-4% AZH < 1% Cyperaceae 44-49% <i>Erica tetralix</i> 36-47% Ranunculaceae 0-1%	CF < 1% WET < 1% EUME < 2% OLME 2% ERO < 1% HdV-114 3-8%	Very high values (> 25 x 10 ⁵ grains cm ⁻³) Maximum (60 x 10 ⁵ grains cm ⁻³) ~2250 cal BP (41 cm)
LPAZ-3c, 34-26 cm 1750-1150 cal BP	AP 40-46.3%, SP 25.6-31.7%, TC 0.2-4.3%, deciduous <i>Quercus</i> 4-8.5%, <i>Quercus suber</i> 17-25%, <i>RW</i> 10.5-14%, <i>Betula</i> 119-172%, <i>Erica spp.</i> 14-22%, <i>Arbutus unedo</i> 2-5.5%, <i>Genisteae</i> 3-4%, Low values (< 2%) of <i>Calluna vulgaris</i> , <i>Cistus ladanifer</i> , <i>Corylus</i> , <i>Daphne gnidium</i> , evergreen <i>Quercus</i> , <i>Hedera helix</i> , <i>Ilex aquifolium</i> , <i>Lavandula stoechas</i> , <i>Lonicera</i> , and <i>Pinus pinea</i>	HP 24-34.7%, Poaceae 9-14% Cerealia 0-0.6% ANH 4-6.5% AZH 1-5% Cyperaceae 41-55% <i>Erica tetralix</i> 33.6-54.5% Ranunculaceae 0-2.2% <i>Sphagnum</i> 0.4.6%	CF < 1% WET < 1% EUME < 2% OLME 2-5% ERO 0.5-3.3% HdV-114 3.5-7%	High values (28-40 x 10 ⁵ grains cm ⁻³)
LPAZ-4a, 26-15 cm 1150-500 cal BP	AP 31-50%, SP 19-28.5%, TC 1-4%, deciduous <i>Quercus</i> 1-8.5%, <i>Quercus suber</i> 14-25.7%, <i>RW</i> 9-18.5%, <i>Betula</i> 72-104%, <i>Erica spp.</i> 13-16%, <i>Arbutus unedo</i> 1-3.4%, <i>Genisteae</i> 1-4%, Low values (< 3%) of <i>Calluna vulgaris</i> , <i>Cistus ladanifer</i> , <i>Corylus</i> , <i>Daphne gnidium</i> , evergreen <i>Quercus</i> , <i>Hedera helix</i> , <i>Ilex aquifolium</i> , <i>Lavandula stoechas</i> , <i>Lonicera</i> , and <i>Pinus pinea</i>	HP 28-40.5%, Poaceae 13-26% Cerealia 0-5.6% ANH 3-10% AZH 2-3.5%	CF 1-4% DRY 0-15.5% WET < 3% EUME 1-7.6% OLME 0.5-4%	Decreasing values (5-20 x 10 ⁵ grains cm ⁻³)

		Cyperaceae 35-52% <i>Erica tetralix</i> 5-21% <i>Sphagnum</i> 4.5-12%	ERO 0-19% HdV-114 11-25%	
LPAZ-4b, 15-7 cm 500-150 cal BP	AP 32-37.7%, SP 34-35.4%, TC 2-3.5%, <i>Quercus suber</i> 11-17%, RW 12-13%, <i>Betula</i> 94-113%, <i>Erica spp.</i> 22-23%, Low values (< 4%) of <i>Arbutus unedo</i> , <i>Calluna vulgaris</i> , <i>Cistus ladanifer</i> , <i>Corylus</i> , <i>Daphne gnidium</i> , deciduous <i>Quercus</i> , evergreen <i>Quercus</i> , Genisteae, <i>Hedera helix</i> , <i>Ilex aquifolium</i> , <i>Lavandula stoechas</i> , <i>Lonicera</i> , and <i>Pinus pinea</i>	HP 27.5-33%, Poaceae 7-12.6% Cerealia 1-3% ANH 6-7.6% AZH 2-3% Cyperaceae 32-38.3% Ranunculaceae 0.5-4.5% <i>Erica tetralix</i> 0-1.1% <i>Sphagnum</i> 3.5-5.3%	CF 2.5-22.5% DRY 1-12.5% WET 3-3-7% EUME 3.6-11% OLME 1% ERO 0-1.5% HdV-114 1-4.2%	Increasing values (21-47 x 10 ⁵ grains cm ⁻³)