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# Vegetation and fire dynamics during the last 4000 years in the Cabañeros National Park (central Spain)

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## Abstract

The Holocene vegetation dynamics of low- and mid-altitude areas of 36 37 inland Iberia remain largely unknown, masking possible legacy effects of past land-use on current and future ecosystem trajectories. Here we present a 4000-38 year long palaeoecological record (pollen, spores, microscopic charcoal) from a 39 mire located in the Cabañeros National Park (Toledo Mountains, central Spain), 40 a region with key conservation challenges due to ongoing land-use changes. 41 42 We reconstruct late Holocene vegetation history and assess the extent to which climate, land-use and disturbances played a role in the observed changes. Our 43 results show that oak (Quercus) woodlands have been the main forested 44 45 community of the Toledo Mountains over millennia, with deciduous Quercus 46 pyrenaica and Quercus faginea more abundant than evergreen Quercus ilex 47 and Quercus suber, particularly on the humid soils of the valley bottoms. 48 Deciduous oak woodlands spread during drier periods replacing hygrophilous communities (Betula, Salix, hygrophilous Ericaceae) on the edges of the mire, 49 and could cope with fire disturbance variability under dry conditions (e.g. ca. 50 3800-3000 –1850-1050 BC- and 1300-100 cal BP –AD 650-1850-) as 51 52 suggested by regional palaeoclimatic reconstructions. Pollen and coprophilous 53 fungi data suggest that enhanced fire occurrence at ca. 1300-100 cal BP (AD 650-1850) was due to deliberate burning by local people to promote pastoral 54 and arable farming at the expense of woodlands/shrublands under dry 55 conditions. While historical archives date the onset of strong human impact on 56 the vegetation of Cabañeros to the period at and after the Ecclesiastical 57 Confiscation (ca. 150-100 cal BP, AD 1800-1850), our palaeoecological data 58 reveal that land-use was already intense during the Arab period (ca. 1250-900 59

cal BP, AD 700-1050) and particularly marked during the subsequent City of
Toledo's rule (ca. 700-150 cal BP, AD 1250-1800). Finally, we hypothesize that
persistent groundwater discharge allowed the mires of the Toledo Mountains to
act as interglacial hydrologic microrefugia for some hygrophilous woody plants
(*Betula, Myrica gale, Erica tetralix*) during pronounced dry spells over the past
millennia.

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## 67 Keywords

- 68 Pollen; charcoal; oak woodlands; hydrologic refugia; land-use; heathlands
- 69

## 1. Introduction

During the last decades, the publication of numerous local to regional 71 72 palaeobotanical records with high temporal and taxonomical resolution (e.g. Carrión et al., 2010a; Carrión, 2012; López-Sáez et al., 2014a; González-73 Sampériz et al., 2017) has increased our knowledge about the millennial-scale 74 drivers of ecosystem change (e.g. climate, human impact) in the Iberian 75 Peninsula. Nevertheless, several regions of the Iberian Peninsula with high 76 77 ecological and cultural value like the Southern Iberian Plateau and its internal mountains (Perea et al., 2015) remain under-investigated (see Carrión et al., 78 2010a; Carrión, 2012). The "Montes de Toledo" (Toledo Mountains) is one of 79 80 the mountain ranges that separate the Tagus and Guadiana river basins in the 81 Southern Iberian Plateau. These mountains host diverse and relatively wellpreserved Mediterranean vegetation (e.g. evergreen oak woodlands, maguis) 82 83 along with relict populations of Tertiary, Atlantic and Eurosiberian taxa (e.g. Prunus lusitanica, Betula spp., Myrica gale) that are rare in the Mediterranean 84 region (Vaguero, 1993; Perea and Perea, 2008). Despite the relative 85 abundance of mires potentially suitable for palaeoecological analyses in this 86 area (López-Sáez et al., 2014b), only five sites have been studied in the Las 87 88 Villuercas-Montes de Toledo mountain range: Garganta del Mesto (Gil-Romera et al., 2008), Patateros (Dorado-Valiño et al., 2014a), Valdeyernos (Dorado-89 Valiño et al., 2014b), Las Lanchas (Luelmo-Lautenschlaeger et al., 2017) and 90 Botija (Luelmo-Lautenschlaeger et al., 2018). Similarly, only few records are 91 currently available from La Mancha plain (e.g. García-Antón et al., 1986; 92 Dorado-Valiño et al., 2002; Gil-García et al., 2007). As a result, vegetation 93

94 dynamics and their ecological drivers at multi-decadal to millennial timescales
95 are poorly understood in this region of inland Spain.

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97 The landscape of the Toledo Mountains is mostly composed of lowland Mediterranean woody plant communities with dominance of broadleaved 98 sclerophyllous trees and shrubs. The diversity and relatively good conservation 99 of this vegetation in the Cabañeros area (central sector of the Toledo 100 Mountains: Figure 1) partly justified the establishment in 1995 of the first 101 102 Spanish National Park devoted to the protection of lowland Mediterranean ecosystems (Cabañeros NP, named Cabañeros onwards; Jiménez García-103 104 Herrera et al., 2011). Archaeological and historical records suggest that human 105 impact was low until the last centuries, and that such ecosystems remained relatively undisturbed over millennia (Jiménez García-Herrera et al., 2011). 106 107 Unfortunately, historical sources are scarce and often contradictory (e.g. 108 Jiménez García-Herrera et al., 2011; Perea et al., 2015). Human population was low and sparse in Cabañeros and most of the Toledo Mountains until the 109 19th-20th centuries AD (Gómez de Llarena, 1916; Jiménez García-Herrera et al., 110 2011). Historical land management limited woodland exploitation and burning in 111 the Toledo Mountains from mid-13<sup>th</sup> to mid-19<sup>th</sup> centuries AD (i.e. during the 112 City of Toledo's rule; Jiménez García-Herrera et al., 2011). Drastic woodland 113 exploitation and fragmentation started altering the landscape then by mid-19<sup>th</sup> 114 century AD and persisted until the protection of the Cabañeros area in AD 1988 115 (first as Natural Park). In contrast to this view of relatively "low impact", other 116 historical sources report that charcoal production, livestock raising and firewood 117 gathering caused marked landscape transformations since at least the 13<sup>th</sup> 118

century AD (Molénat, 1997; Jiménez de Gregorio, 2001; Perea et al., 2015). 119 Likewise, burning is documented since at least the 15<sup>th</sup> century AD in the 120 Toledo Mountains despite the existence of fire-ban bylaws (Redondo-García et 121 al., 2003; Perea et al., 2015). A more comprehensive and quantitative 122 assessment of land-use history in Cabañeros by means of proxy records is 123 urgently needed to better understand the past range of natural disturbance 124 125 variability and legacy effects and better guide forest management and conservation measures in the National Park. 126

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Land-use over millennia strongly affected the relative abundances of tree 128 129 and shrub species originally present in the native woodlands. For instance, in 130 oak woodlands, people have deliberately promoted species of economic interest such as Quercus ilex (wood, charcoal and acorn production) and 131 132 Quercus suber (cork extraction) at the expense of deciduous Quercus species 133 (Urbieta et al., 2008; Perea et al., 2015). Likewise, in many Mediterranean regions, human activities have also indirectly favoured the spread of shrubby 134 sclerophyllous communities (e.g. evergreen sclerophyllous oak woodlands, 135 maguis, garrigue) via soil degradation, vegetation burning and/or livestock 136 raising (e.g. Blondel, 2006; Colombaroli et al., 2007; Henne et al., 2013). 137 138 Climatic variability has also affected the balance between deciduous and evergreen sclerophyllous oaks, with drought-sensitive deciduous and drought-139 tolerant evergreen sclerophyllous oaks expanding during humid and dry 140 phases, respectively (e.g. Carrión et al., 2001, 2010b). Assessing the relative 141 142 importance of plant species through time, and their relative drivers (i.e. landuse, climate, disturbances) is relevant for management plans, particularly in 143

protected areas such as National Parks that aim at preserving or restoring
natural conditions (e.g. Stähli et al., 2006; Valsecchi et al., 2010).

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147 The Toledo Mountains host relict populations of several hygrophilous woody plants that are widespread and abundant in northern latitudes with more 148 149 humid climates (e.g. Betula pendula, Betula pubescens, Erica tetralix, Myrica gale), but with fragmented and reduced populations in the Mediterranean realm 150 (Vaguero, 1993; Perea and Perea, 2008). In Cabañeros, Betula stands and wet 151 152 heaths grow at relatively low altitudes in moist sites (600-800 m a.s.l.), usually mires (Sánchez-del-Álamo et al., 2010; Perea et al., 2015). Land-use and 153 154 overgrazing/trampling by wild ungulates threaten the persistence of mires in the 155 area (López-Sáez et al., 2014b). Mires located within Cabañeros are fenced and under protection, but under threat with drier conditions that may occur in 156 157 the future (Gao and Giorgi, 2008; Giorgi and Lionello, 2008). However, mires of 158 Cabañeros could have the potential to act as hydrologic refugia for the abovementioned species during dry periods in the future (McLaughlin et al., 159 2017). Spreading from these spatially restricted areas, hygrophilous species 160 might expand and colonize other suitable environments during humid intervals. 161 Assessing the past resilience and sensitivity of hygrophilous species to dry 162 163 episodes occurred in Mediterranean Iberia during the last millennia (e.g. Carrión, 2002; Martín-Puertas et al., 2008; Morellón et al., 2009) may therefore 164 contribute to assess the potential of Cabañeros peatlands. 165

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In this paper we present a 4000-year long pollen sequence from 167 168 Cabañeros to reconstruct vegetation history in the Toledo Mountains. We use spores of obligate coprophilous fungi and microscopic charcoal particles to track 169 170 changes in grazing pressure and regional fire activity through time. We complement our inferences from proxy records with published vegetation-171 independent climate reconstructions with the following aims: (i) to reconstruct 172 173 the changes occurred in upland vegetation (surrounding the mire) and fire 174 activity during the late Holocene in Cabañeros, identifying the drivers for these changes (climate variability, land-use); and (ii) to track the responses of the 175 176 Cabañeros hygrophilous vegetation (growing on the mire) to past climate and land-use changes, assessing the potential role of the mires of the Toledo 177 178 Mountains as hydrologic refugia.

## 2. Material and methods

## 181 *2.1 Study area*

Cabañeros is a 40,856 ha protected area especially renowned for its 182 183 large populations of wild ungulates (mainly *Cervus elaphus*) and birds of prev (notably the threatened Aegypius monachus and Aquila adalberti). The 184 185 landscape of Cabañeros is Appalachian-like, with mountains of moderate altitude (800-1449 m a.s.l.; highest summit: Peak Rocigalgo) locally known as 186 187 'sierras' and an extensive alluvial plain locally named 'raña' (600-700 m a.s.l.; 188 Jiménez García-Herrera et al., 2011). Ordovician quartzites and Cambrian siliceous slates are the dominant bedrocks in the 'sierras', where they often 189 190 outcrop at mountain tops and ridges. The 'raña' resulted from the infilling of 191 ancient valleys with clays and quartzitic pebbles transported from the 'sierras' in 192 massive events during the Cenozoic. The climate of Cabañeros is typically 193 Mediterranean, with the rainy season usually encompassing autumn, winter and 194 spring, relatively mild winters, and hot and dry summers. The Torre de Abraham weather station (697 m a.s.l.), representative of the widespread meso-195 mediterranean bioclimatic belt where the study site is located, registers a mean 196 annual temperature of 13.6°C (T<sub>Jan</sub>=4.9°C, T<sub>Jul</sub>=24.4°C), a mean annual 197 precipitation of 539.6 mm, and a marked and long summer drought (dry 198 199 period=3.5 months, P<sub>Jul-Sep</sub>=45.4 mm). Fire was in principle suppressed in Cabañeros with the creation of the Natural Park in 1988 (Jiménez García-200 Herrera et al., 2011), although some wildfires have anyway affected this 201 202 protected area during the last decades.

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In this study we have integrated the description of the Cabañeros 204 205 vegetation in Perea et al. (2015) with field observations. Most of the Cabañeros 206 surface (85%) lies within the meso-mediterranean vegetation belt, with the 207 supra-mediterranean restricted to the highest areas usually above 1000 m a.s.l. 208 Broadleaved evergreen sclerophyllous woodlands and shrublands dominate the meso-mediterranean vegetation. The evergreen sclerophyllous Quercus ilex 209 210 subsp. *ballota* is the most common oak species, especially in drier and more continental sites and/or on less developed soils. In Cabañeros, Quercus ilex 211 often forms mixed stands with the more frost-sensitive and moisture-demanding 212 213 Quercus suber (also evergreen sclerophyllous) at low- and mid-altitude sites (<1000 m a.s.l.), usually on south-facing and gentle slopes where soils are 214 215 more developed. In warmer sites thermophilous evergreen sclerophyllous 216 shrubs such as *Pistacia lentiscus* and *Myrtus communis* accompany *Quercus* ilex, whereas it is usually mixed with the deciduous and relatively drought-217 sensitive Quercus faginea subsp. broteroi on north-facing slopes where water 218 219 availability is higher. Almost pure Quercus faginea stands particularly develop in 220 (moister) north-facing slopes, seasonally waterlogged valley bottoms and areas 221 of groundwater discharge like the foothills of the 'sierras'. Similarly, some stands of the deciduous *Quercus pyrenaica* grow along the bottom of certain 222 223 valleys in the meso-mediterranean belt, where this relatively drought-sensitive 224 species finds sufficient moisture and deeper soils to cope with dry summers. Quercus pyrenaica is more common in the supra-mediterranean belt, above 225 226 900 and 1200 m a.s.l. on north-facing and south-facing slopes respectively, especially in moist and shady sites. Lastly, 'dehesas' (savanna-like oak 227

woodlands) extend over ca. 20% of Cabañeros and represent its most iconiclandscape.

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231 Riparian forest communities are also highly diverse in Cabañeros. Alnus glutinosa dominates along permanent rivers together with Salix spp., Fraxinus 232 233 angustifolia, Frangula alnus and Vitis vinifera, whereas Fraxinus angustifolia turns dominant where the water table oscillates. Some stands dominated by 234 Prunus lusitanica subsp. lusitanica grow on shady sites at the bottom of deep 235 236 and narrow valleys where subsurface water flow and groundwater discharge 237 provide sufficient moisture. There are two types of Betula-dominated stands in 238 the region (mostly Betula pendula subsp. fontqueri) according to site features: 239 (i) deep, shady and usually rocky gorges at the headwaters of permanent streams (>1000 m a.s.l.), along with Acer monspessulanum, Sorbus torminalis, 240 241 Ilex aquifolium and Taxus baccata; and (ii) mires on valley bottoms at mid-242 altitudes (600-800 m a.s.l.), usually with an understory of Erica tetralix and Myrica gale. 243

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245 Shrublands mostly originate from the degradation of former forests and 246 woodlands, with the sole exceptions of mountain scrubland (*Echinospartum* 247 *ibericum*, *Adenocarpus argyrophyllus*, *Genista cinerascens*) at the summit of 248 Peak Rocigalgo, and hygrophilous heathlands on mires (*Erica tetralix*, *Erica* 249 *lusitanica*, *Erica scoparia*, *Calluna vulgaris*, *Genista anglica*, *Genista tinctoria*, 250 *Myrica gale*). Maquis replaces evergreen Mediterranean forests, forming a 251 diverse evergreen community with *Arbutus unedo*, *Erica arborea*, *Erica* 

australis, Erica scoparia, Rhamnus alaternus, Phillyrea angustifolia, Pistacia 252 253 terebinthus, Ruscus aculeatus, Viburnum tinus, Cistus ladanifer and Cistus populifolius. Cytisus species are sometimes abundant in the plant communities 254 that first replace forests. As degradation progresses, highly flammable *Cistus* 255 spp. (Cistus ladanifer is the most common and dominant) and fire-resistant 256 257 *Erica* spp. become the dominant shrubs. The final stages of degradation are 258 Lamiaceae-dominated garrigues (dwarf shrublands with Rosmarinus officinalis, Lavandula pedunculata and Thymus mastichina among others) and grasslands. 259

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261 2.2 Study site

El Brezoso mire is a medium-sized mire (≈1.5 ha) located at the bottom 262 of El Brezoso valley in the Sierra del Chorito (Figure 1). The vegetation at the 263 264 coring site is a dense thicket of *Myrica gale* with *Carex paniculata*, *Erica tetralix* and Molinia caerulea (Vaguero, 2010). Nevertheless, the dominant plant 265 266 communities in the mire are hygrophilous heathlands dominated by *Erica* 267 tetralix, Molinia caerulea and Schoenus nigricans, with Carex spp., Juncus spp., Poaceae, Potentilla erecta, Dactylorhiza elata, Lotus pedunculatus, Narcissus 268 bulbocodium, Wahlenbergia hederacea, Galium palustre, Ranunculus bulbosus, 269 270 Calluna vulgaris and Genista anglica (for further details, see Vaquero, 2010). Dense Erica scoparia-dominated heathlands with Erica arborea, Calluna 271 vulgaris, Erica Iusitanica, Rubus ulmifolius, Cistus Iadanifer, Cistus salviifolius, 272 273 Daphne gnidium, Pteridium aguilinum and Asphodelus aestivus grow on drier soils bordering the mire (Vaguero, 2010). On the El Brezoso stream banks, 274 Erica scoparia-dominated heathland is also dominant, with some Betula 275 pendula subsp. fontqueri trees recently planted to restore the riparian 276

vegetation. Relatively open oak woodland (Quercus pyrenaica) extends all 277 278 along the bottom of El Brezoso valley outside the mires. On the adjacent slopes the vegetation is open woodland dominated by Quercus ilex subsp. ballota and 279 Quercus faginea subsp. broteroi with some Quercus suber, and a dense shrub 280 layer mostly composed of sclerophylls such as Arbutus unedo, Erica arborea, 281 Erica australis, Phillyrea angustifolia, Cistus ladanifer, Rosmarinus officinalis 282 283 and *Lavandula pedunculata*. Monitoring of this mire between 1990 and 2010 revealed an increase in *Erica scoparia*-dominated heathlands and an intense 284 impact by wild ungulates (Vaquero, 2010; Perea and Gil, 2014). 285

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287 [FIGURE 1]

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289 2.3 Coring and chronology

290 In April 2014, we retrieved a 175-cm long peat core at El Brezoso (39°20'55"N, 004°21'43"W, 730 m a.s.l.) using a Russian peat sampler. We 291 wrapped core sections with PVC guttering and cling film and stored them in a 292 cold (4°C) and dark room until sample processing for radiocarbon dating and 293 294 palynological analyses. To establish the chronology of the peat sequence, we 295 obtained ten AMS radiocarbon dates on terrestrial plant macrofossils and peat. As there was no indication of a recent interruption of peat formation, we 296 297 assigned the age of the coring to the core top. Radiocarbon ages were then converted to calendar years using the INTCAL13 calibration curve (Reimer et 298 al., 2013) with the program CALIB 7.1. We used the software CALIBomb and 299 300 the Northern Hemisphere Zone 2 calibration dataset for the most modern

sample (Hua et al., 2013). Finally, we modelled the age-depth relationship for
the whole sequence by fitting a smoothing spline function (smoothing
parameter=0.2) to the accepted radiocarbon dates with CLAM 2.2 (Blaauw,
2010). We chose this model after assessing its sensitivity to changing values of
the smoothing parameter and checking the strong similarities with the linear
interpolation model.

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## 2.4 Pollen, spore and microscopic charcoal analyses

In the laboratory, we prepared 68 peat samples of 0.5-1.0 cm<sup>3</sup> (1-cm 309 thick) for pollen analysis following a standard protocol (Moore et al., 1991) 310 consisting of chemical treatment with HCI, HF and KOH to remove carbonates, 311 silicates and organic matter respectively, as well as sieving through a 250 µm 312 313 mesh and decanting. Samples were spaced 2 or 4 cm depending on the time resolution of the particular section of the sequence, to reach comparable time 314 315 intervals between samples throughout the sequence. Lycopodium tablets were 316 added to the samples at the beginning of the treatment to estimate pollen concentration (grains cm<sup>-3</sup>; Stockmarr, 1971). Pollen grains were identified with 317 the aid of identification keys (Moore et al., 1991; Ramil-Rego et al., 1992; Beug, 318 319 2004), photographic atlases (Reille, 1992) and the reference collection at the Institute of Plant Science of the University of Bern. A minimum terrestrial pollen 320 321 sum of 300 pollen grains was in general achieved (mean  $\pm$  standard deviation =  $312 \pm 36$ ), excluding pollen from aquatic/wetland plants (see Figure 5) and 322 spores. Pollen percentages of wetland and aquatic plants were calculated with 323 respect to the terrestrial pollen sum. We used the program PSIMPOLL 4.27 324 325 (Bennett, 2009) to delimit local pollen assemblage zones (LPAZs) in the pollen

diagram using the optimal splitting by sums-of-squares method (Birks and 326 Gordon, 1985). Only terrestrial pollen types reaching values over 2% were 327 considered for the zonation. We then assessed the statistical significance of the 328 obtained LPAZs using the broken-stick model (Bennett, 1996). Spores of 329 obligate coprophilous fungi were also identified according to van Geel et al. 330 (2003) and their percentages calculated with respect to the terrestrial pollen 331 sum. Finally, we counted microscopic charcoal particles larger than 10 µm in 332 333 pollen slides to estimate charcoal concentrations (# cm<sup>-3</sup>) and accumulation rates (CHAR; # cm<sup>-2</sup> yr<sup>-1</sup>), following the indications by Tinner and Hu (2003) and 334 335 Finsinger and Tinner (2005).

## 3. Results and interpretation

### 338

## 3.1 Lithology and chronology

The El Brezoso sedimentary sequence is mainly composed of peat, with 339 340 only three silty peat layers at the bottom and the central section of the profile (Figure 2). They are likely related to the persistence of small temporary pools 341 342 when peat formation commenced (175-164 cm-deep) and the later occurrence of disturbance/erosive processes (86-81 and 75-69 cm-deep). Among the ten 343 radiocarbon dates (Table 1), we only rejected one (124-122 cm-deep, date 344 345 mostly on periderm) because the measured age is younger than expected (Figure 2). The dated periderm probably came from a root penetrating older 346 347 layers. Peat deposition time shows that peat formation was very fast at the beginning of the sequence (ca. 3.5 yr cm<sup>-1</sup>; 175-129 cm-deep), then slowed 348 quite sharply towards the middle section of the sequence (from 3.5 yr cm<sup>-1</sup> at 349 129 cm-deep to 87.1 yr cm<sup>-1</sup> at 91 cm-deep) and finally accelerated again until 350 the top of the profile, first quite abruptly (from 87.1 yr cm<sup>-1</sup> at 91 cm-deep to 351 25.7 yr cm<sup>-1</sup> at 66 cm-deep) and then more gently (from 25.7 yr cm<sup>-1</sup> at 66 cm-352 deep to 4.4 yr cm<sup>-1</sup> at the top of the profile). Maximum pollen concentration 353 354 occurs approximately at the same depth as the one in peat deposition time (98 cm-deep), therefore supporting a slowdown of peat formation in this section of 355 the sequence probably caused by a decrease in on-site peat production. 356

357

358 [FIGURE 2]

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360 3.2 Pollen, spores and microscopic charcoal records: vegetation and fire
 361 history

362 The El Brezoso pollen record consists of 135 terrestrial plant pollen types, 16 aquatic and wetland plant pollen types and six fern spore types 363 (Figures 3-5). The time resolution between samples is guite variable: less than 364 50 years at ca. 3950-3600 cal BP (2000-1650 BC) and ca. 500 cal BP-today 365 (AD 1450-2014), 50-100 years at ca. 3600-3300 and 1000-500 cal BP (1650-366 367 1350 BC and AD 950-1450), and 100-175 years at ca. 3300-1000 cal BP (1350 BC-AD 950). This is due to significant changes in peat accumulation rate along 368 369 the sequence (see Figure 2).

370

The assemblages mostly recorded vegetation dynamics at local to extra-371 372 local scales, given its relatively small size, and its location at the bottom of a relatively closed and narrow valley (Prentice, 1985; Sugita, 1994). Further, the 373 374 pollen content in the core top sample mostly reflects local to extra-local modern 375 vegetation. Previous empirical research has shown that microscopic charcoal is mostly related to extra-local to regional fire activity (0.01-100 km<sup>2</sup>; Tinner et al., 376 1998; Conedera et al., 2009), and dung fungal spores to local grazing activities 377 378 (e.g. Baker et al., 2016).

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380 [FIGURE 3]
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The El Brezoso pollen sequence is subdivided into ten statistically significant LPAZs (Figures 3-5). In addition, we have subdivided zone BRE-3 into two subzones to facilitate the interpretation of vegetation history. In general,

we will refer to *Q. ilex* when discussing the pollen curve of *Quercus* 385 386 ilex/coccifera-t. (t.=type), given that it is more widespread in the Toledo Mountains than Quercus coccifera and therefore more relevant for the 387 vegetation dynamics (see Perea et al., 2015). Vegetation reconstruction is 388 particularly challenging at El Brezoso because the same pollen type may be 389 produced by different plant species that may grow locally on the mire or. 390 391 conversely, on the drier soils of the adjacent slopes. Erica arborea/scoparia-t. and Poaceae are particularly relevant examples because of their abundance in 392 the pollen sequence and their importance in the landscapes of the Toledo 393 394 Mountains. We assume that *E. scoparia*, rather than *E. arborea*, produced most of the *E. arborea/scoparia*-t. pollen because it is wind-pollinated and usually 395 396 abundant in the hygrophilous plant communities of the Toledo Mountains 397 (Herrera, 1988; Vaguero, 2010; Perea et al., 2015). Nevertheless, a certain proportion of this pollen type has surely been produced by E. arborea and, to a 398 much lesser degree, E. lusitanica. In the Toledo Mountains, E. arborea is 399 currently more common and abundant in drier habitats such as Mediterranean 400 401 woodlands and maguis (Perea et al., 2015). Finally, E. lusitanica is a rare heath 402 typically growing in damp sites, like *E. scoparia*. Likewise, Poaceae pollen might have been produced by grass species growing on the mire like Molinia 403 caerulea, and/or in drier grasslands. 404

405

406 [FIGURE 4]

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At the beginning of the record (BRE-1, 3950-3800 cal BP, 2000-1850 408 409 BC), our pollen data indicate that hygrophilous heathlands (E. scoparia, E. tetralix, C. vulgaris) dominated local vegetation in the mire, along with Poaceae, 410 Cyperaceae, Sphagnum mats and some *M. gale* shrubs. Few *Betula* trees were 411 probably growing on the mire and/or along El Brezoso stream (see Jackson and 412 Kearsley, 1998) along with Salix. Finally, rather open Mediterranean woodland 413 414 or a mosaic-like landscape with small forest stands, shrublands and grasslands thrived on the adjacent slopes. Deciduous oaks (Q. pyrenaica, Q. faginea) 415 might have inhabited humid sites with well-developed soils such as valley 416 417 bottoms and north-facing slopes, whereas the sclerophyllous Q. ilex and Q. suber would have been more frequent on drier sites and/or where soils were 418 419 shallower. Low *Pinus* pollen percentages indicate that pines were not a relevant 420 component of the vegetation around El Brezoso. However, we cannot completely discard the regional presence of pines given that modern pine 421 422 representation is similar ( $\approx$ 5%) and there are extensive pine afforestations (several thousands of hectares) distant less than 5 km from El Brezoso. 423 424 Woodland understory and/or shrublands were rather species-rich but dominated 425 by sclerophyllous shrubs (Erica spp., Cistus, Phillyrea). Castanea sativa is sparsely and discontinuously recorded, pointing to a regional although not 426 relevant presence of sweet chestnut. During this period, there is a notable 427 428 mismatch in the microscopic charcoal record between charcoal concentration and CHAR suggestive of moderate fire activity in the surroundings of El 429 430 Brezoso.

431

432 [FIGURE 5]

Our pollen data suggest that Mediterranean woodland with deciduous 434 435 and, to a lesser degree, sclerophyllous Quercus as dominant trees expanded during BRE-2 (3800-3400 cal BP, 1850-1450 BC) at the expense of 436 hygrophilous communities with Betula, E. scoparia, Cyperaceae and 437 Sphagnum. Myrica gale shrubs might have spread over areas previously 438 covered with other mire vegetation. The charcoal record suggests two major 439 440 periods of fire activity at ca. 3800 and 3500 cal BP (1850 and 1550 BC), when fire activity over last 4000 years peaked. Pollen and spores indicative of human 441 activity (e.g. Plantago coronopus-t., Plantago lanceolata-t., Sordaria-t., 442 443 Sporormiella-t.) suggest that local grazing activities started to increase at ca. 444 3500 cal BP (1550 BC), together with increased burning. Subsequently they peaked during the next zone. 445

446

At the beginning of BRE-3a (3400-3050 cal BP, 1450-1100 BC) 447 448 Mediterranean evergreen sclerophyllous woodland (Q. ilex, Q. suber, Cistus, E. australis, Phillyrea) gradually replaced heathlands and grasslands. Erica tetralix 449 also moderately expanded within the local vegetation. Later, a remarkable 450 451 recovery of typical mire vegetation with *Betula* stands, hygrophilous heathlands (E. scoparia, C. vulgaris, E. tetralix), Sphagnum mats and sedge-dominated 452 meadows started at ca. 3300 cal BP (1350 BC), apparently replacing local 453 454 Mediterranean woodlands around the site. Hygrophilous communities persisted later throughout BRE-3b (3050-2150 cal BP, 1100-200 BC), with M. gale 455 peaking at ca. 2500 cal BP (550 BC) The charcoal record testifies that fire 456 activity was not particularly relevant during this period, with maximum burning 457

433

occurring at ca. 3000 cal BP (1050 BC) according to both microscopic charcoal
concentration and CHAR.. Instead, local grazing pressure as inferred from the
curves of the coprophilous fungi *Sporormiella*-t. and *Sordaria*-t. was significant
at the beginning of this period (ca. 3400 cal BP, 1450 BC) but notably
decreased after ca. 3200 cal BP (1250 BC), to remain low until ca. 2300 cal BP
(350 BC).

464

According to our pollen data the next vegetation stage, BRE-4 (2150-800 465 466 cal BP, 200 BC-AD 1150), was mainly characterized by the spread of pasturelands (Poaceae, Rumex acetosa/acetosella-t., Aster-t., Cichorioideae, P. 467 468 coronopus-t., P. lanceolata-t.) and hygrophilous meadows (Cyperaceae, 469 Potentilla-t.). These communities replaced Betula stands, M. gale thickets and, to some extent, hygrophilous heathlands (C. vulgaris decreases). Sphagnum 470 471 populations significantly oscillated during this period, with a major decline at ca. 472 800 cal BP (AD 1150). The first unambiguous evidence for cereal cultivation (continuous curve and percentages up to 1%) around the study site is dated at 473 ca. 1300-1050 cal BP (AD 650-900), while the regional introduction of sweet 474 chestnut (Castanea sativa) cultivation probably started at ca. 1700 cal BP (AD 475 250), when the Castanea pollen curve becomes nearly continuous. Cerealia-t. 476 is recorded earlier, during zones BRE-2 and BRE-3, but always as isolated 477 pollen grains discontinuous in time (Figure 4), suggesting limited arable farming 478 activities around the site. The regional presence of pines was markedly reduced 479 after ca. 1700 cal BP (AD 250). High values of dung fungal spores 480 (Sporormiella-t., Sordaria-t., Podospora-t.; Figure 5) suggest that pastoral 481 farming was particularly intense around 1900 cal BP (AD 50). Likewise, grazing 482

activities began to consistently increase around El Brezoso at ca. 850 cal BP 483 484 (AD 1100) according to the records of coprophilous fungal spores, in particular Sporormiella-t. (Figure 5). The establishment of a well-developed riparian forest 485 mostly composed of Betula, Salix and M. gale on the bottom of the valley (mire, 486 stream banks) was the most remarkable vegetation change during BRE-5 (800-487 600 cal BP, AD 1150-1350). Meanwhile, meadows retreated and the 488 surrounding Mediterranean woodland remained almost unchanged. Two 489 periods of higher fire activity occurred at ca. 1300 and 1000-900 cal BP (AD 650 490 and 950-1050), indicated by maxima in both charcoal concentration and CHAR. 491

492

493 The pollen record suggests that (humid) heathlands (mostly composed of 494 *E. arborea/scoparia* and *C. vulgaris*) were the dominant plant communities during BRE-6 (600-450 cal BP, AD 1350-1500), replacing Betula stands and 495 496 Mediterranean woodlands. The higher abundance of *Pteridium aguilinum* might 497 be indicative of disturbances nearby. Indeed fire occurrence increased along this period, reaching a maximum at ca. 500 cal BP (AD 1450). During BRE-7 498 (450-350 cal BP, AD 1500-1600) the palynological evidence indicates that 499 Mediterranean woodlands (Q. pyrenaica/faginea, Q. ilex, Q. suber) moderately 500 expanded. Mediterranean evergreen sclerophyllous shrubs (E. australis, 501 Phillyrea, Lamiaceae, Myrtus communis) also increased at the expense of 502 503 hygrophilous heathlands. Some Betula trees could have persisted in the El Brezoso valley until the end of this zone. The continuous curve of Cerealia-t. 504 and its relatively high percentages (≈1%) suggest the existence of agricultural 505 506 fields in relative proximity to the mire. The decreases in charcoal concentration

and CHAR along this zone indicate that fire activity notably diminished duringthis period.

509

510 Non-arboreal pollen increases (Poaceae, P. lanceolata-t., P. coronopust., R. acetosa/acetosella-t., Cardueae, Potentilla-t., Cichorioideae) during BRE-8 511 512 (350-250 cal BP, AD 1600-1700), showing that meadows re-expanded. This shift was associated to a temporary increase of grazing (Sporormiella-t., 513 Sordaria-t.). Meadows replaced wet heathlands and possibly also deciduous 514 515 oak woodlands previously growing at the valley bottom. A transient spread of Q. 516 ilex also occurred during this period, and fire activity was at its minimum of the 517 last 4000 years according to our microscopic charcoal data. Our pollen record 518 suggests that meadows remained abundant, deciduous and evergreen sclerophyllous oak woodlands were further cleared, and shrublands expanded 519 during BRE-9 (250-100 cal BP, AD 1700-1850). Disturbance-adapted Cistus, E. 520 521 australis and Lamiaceae became an important component of these shrublands, and several herbs indicative of disturbance and often linked to human activities 522 such as P. lanceolata-t., P. coronopus-t. and Cichorioideae also expanded. 523 Grazing additionally intensified during this phase as indicated by the increase in 524 dung fungal spores. The mire was almost depleted of Sphagnum while 525 hygrophilous heathlands with *E. scoparia* and *E. tetralix* spread. Olive 526 527 cultivation established at least 200 years ago (150 cal BP, AD 1800), as indicated by the steady increase in Olea europaea pollen percentages. All these 528 vegetation changes occurred under marked regional fire activity as indicated by 529 530 the moderate to high charcoal values.

531

Finally, a marked recovery of Mediterranean woodlands has taken place 532 533 during BRE-10 (100 cal BP-present, AD 1850-2014), especially during the last decades. Sclerophyllous (Q. ilex, Q. suber) and deciduous oaks (Q. pyrenaica, 534 Q. faginea) are the main tree species involved in the recent advance of forested 535 ecosystems, with pines playing a secondary role. Olive tree cultivation 536 537 continued its rise during this period. Shrubs were still very relevant in the local 538 and extra-local vegetation, forming the understory of the Quercus-dominated woodlands as well as shrublands. *Erica* species continued dominating but other 539 shrubs such as Cistus, Lamiaceae, A. unedo and Genista/Cytisus expanded. All 540 541 these woody plant communities replaced the formerly widespread pasturelands. On the mire, Cyperaceae and E. tetralix were dominant at the beginning of this 542 543 stage with a variable importance of *M. gale*, which seems to have largely 544 spread out during the last decades. The charcoal record shows that fire activity has been in general limited, despite several minor peaks. Lastly, grazing 545 pressure has been extremely high according to the curves of obligate 546 coprophilous fungi. 547

## 4. Discussion

550

## 4.1 Drivers of upland vegetation change and fire dynamics

Our data show that oaks were the most abundant trees in the woodlands 551 552 around El Brezoso during the last 4000 years, especially the deciduous Q. pyrenaica and Q. faginea. Although it is difficult to ascertain whether deciduous 553 554 or evergreen oaks prevailed (deciduous trees may have grown closer to the site due to higher water availability), the dominance of deciduous oaks is in 555 556 agreement with other pollen records from the Toledo Mountains (Dorado-Valiño 557 et al., 2014a, b). This mixed occurrence of evergreen and deciduous trees is also typical of today's meso-mediterranean environments (Costa et al., 2005). 558 559 Quercus ilex-t. pollen is more abundant in other sites from the Toledo 560 Mountains (Luelmo-Lautenschlaeger et al., 2017, 2018) as well as in the 561 relatively close Las Villuercas Mountains (Gil-Romera et al., 2008) over the last 562 millennia. Given that all sites are small mires with reduced pollen source areas, 563 the different vegetation patterns might be explained considering local factors such as topographical position (slope vs. valley bottom), slope grade and 564 aspect, or soil development. 565

Overall, Quercus percentages are rather low in El Brezoso (5-35%), suggesting 566 567 that vegetation was mainly composed of open woodlands or, alternatively, of shrublands and grasslands with sparse woodlands. However, landscape 568 openness must also be cautiously considered in El Brezoso because the 569 570 overrepresentation of wet heaths and meadows growing on the mire (mainly E. arborea/scoparia-t., Poaceae, E. tetralix-t. and C. vulgaris) might lower tree 571 pollen percentages. It is noteworthy that pines were not relevant in the 572 vegetation of Cabañeros during the last millennia, in contrast with other mid-573

altitude areas of inland Iberia located further east (e.g. Franco-Múgica et al.,
2001; Aranbarri et al., 2014; Morales-Molino et al., 2017a), where more
continental climatic conditions, lower soil development and, in some cases,
higher topographical complexity help increase pine competitiveness (e.g.
Rubiales et al., 2010).

579

580 [FIGURE 6]

581

582 Several coeval deciduous and evergreen Quercus woodland expansions occurred around El Brezoso at ca. 3800-3100 (1850-1150 BC), 1200-900 (AD 583 750-1050), 650-550 (AD 1300-1400), 450-350 (AD 1500-1600), 300-250 (AD 584 1650-1700) cal BP and finally from 100 cal BP to present (AD 1850-2014; 585 Figure 6). These oak woodland spreads occurred together with transient 586 587 retreats of hygrophilous communities (growing on the mire or its edges; Betula, Salix and hygrophilous Ericaceae in Figure 6). This vegetation pattern is 588 ecologically best explained by temporary shifts towards drier conditions in 589 Cabañeros during the Bronze Age, the Dark Ages (DA), the Medieval Climate 590 Anomaly (MCA), the Little Ice Age (LIA) and the Industrial Era (Figure 6), 591 considering the age uncertainties between the independently radiocarbon-dated 592 593 palaeoclimatic records (Martín-Puertas et al., 2008; Jiménez-Moreno et al., 2013; López-Blanco et al., 2016) and that we also account for climatic 594 reconstructions based on historical archives (Domínguez-Castro et al., 2008). 595 596 Contrarily, a major decline of Quercus began at ca. 3100 cal BP (1150 BC), when wet heaths and *Betula* stands replaced the deciduous oak woodlands 597

(Figure 6). A period of moderately increased fire activity commencing at ca.
3200 cal BP (1250 BC; Figure 6) apparently triggered this vegetation shift, but
the trend towards more humid conditions leading to the persistently wet Iberian
Roman Humid Period (IRHP; Martín-Puertas et al., 2008; Jiménez-Moreno et
al., 2013) may have been the true driver for the increasing competitiveness of
hygrophilous vegetation.

604

605 The expansions of evergreen/deciduous oak woodlands at ca. 3800-606 3100 (1850-1150 BC), 1200-900 (AD 750-1050), 650-550 (AD 1300-1400), 450-350 (AD 1500-1600) cal BP and 100 cal BP-present (AD 1850-2014) might 607 608 have been exacerbated by increased fire activity (Figure 6). Quercus 609 shrublands might have dominated these woodlands considering their higher post-disturbance resprouting ability compared to more developed evergreen 610 oak forests (Colombaroli et al., 2009). This long-term resistance and rate-of-611 612 recovery to fire disturbance of both evergreen (Q. ilex, Q. suber) and deciduous (Q. pyrenaica, Q. faginea) oaks may be related to their strong resprouting ability 613 and thick fire-resistant bark (Pausas, 1997; Calvo et al., 2003; Espelta et al., 614 615 2003). Further, evergreen Quercus shrublands exhibit a higher resprouting ability following disturbance than more developed evergreen oak forests 616 (Colombaroli et al., 2008, 2009). 617

618

The main periods of high fire activity at El Brezoso were centred at ca.
3800 (1850 BC), 3500 (1550 BC), 3000 (1050 BC), 1300 (AD 650), 850 (AD
1100), 500 (AD 1450) and 150 (AD 1800) cal BP (Figure 6). With the only

exception of the most recent minor one, i.e. ca. 250-100 cal BP (AD 17001850), all these fire episodes were synchronous with dry climatic phases from
other proxy records mostly occurring during dry episodes of the Bronze Age, the
DA, the MCA and the LIA (Figure 6), suggesting tight fire-climate linkages over
the centennial to millennial timescales.

627

Superimposed on the centennial changes in climate (Figure 6) are 628 alterations of the disturbance regimes by human activities. Our data suggest 629 630 that enhanced grazing followed fires at ca. 3500 cal BP (1550 BC; Figure 5), pointing to intentional burning during Bronze Age to promote pastures (and 631 probably also agriculture) and consequently increase landscape patchiness and 632 633 diversity (Colombaroli and Tinner, 2013). However, the impact of human 634 activities on vegetation seems to have been limited at the landscape scale, as 635 only a few disturbance-tolerant plants (mostly *Rumex* but also *Plantago*) 636 increased (Figure 6). Archaeological evidence also points to the presence of settlements during the Bronze Age in the Cabañeros area (Jiménez García-637 Herrera et al., 2011), whose economy was apparently based on livestock 638 raising (Ruiz-Taboada, 1997). Pastoral farming increased during Roman Times 639 (ca. 2000-1500 cal BP, 50 BC-AD 450), when pasturelands and disturbance-640 tolerant plants expanded (Poaceae, Rumex, Plantago; Figure 6) under high 641 grazing pressure (Sporormiella-t., Sordaria-t., Podospora-t. in Figure 5). 642 However, it was not until the Arab Period (ca. 1250-900 cal BP, AD 700-1050) 643 that cereal-based agriculture intensified in Cabañeros (Figures 4, 6). This 644 645 intensification might be consequence of the establishment of several important

roads crossing these mountains and the foundation of several small settlements
during the Arab period (Molénat, 1997; Jiménez García-Herrera et al., 2011).

648

649 Higher fire activity right before this land-use intensification at ca. 1300 cal BP (AD 650) might have been related to slash-and-burn activities at the end of 650 651 the Visigothic period (ca. 1500-1250 cal BP, AD 450-700) or more probably at the beginning of the Arab period. In sum, human activities replaced climate as 652 the main driver for fire regime only guite recently, ca. 1300 cal BP (AD 650), by 653 654 increasing the number of fire ignitions, under the dry conditions characteristic of the DA (Figure 6; Martín-Puertas et al., 2008) promoting its spread. 655 656 Palaeoecological records from the relatively close Cuenca Mountains and 657 Gredos Range also showed that human activities were the main driver of fire occurrence during the last millennium (López-Blanco et al., 2012; López-Sáez 658 et al., 2017). Nevertheless, it is likely that humans started to modify the natural 659 660 fire regime in Cabañeros several millennia earlier, as reported in other regions (e.g. Tinner et al., 2009; Carrión et al., 2003, 2007; Colombaroli et al., 2008; 661 Vannière et al., 2011; Morales-Molino and García-Antón, 2014), but more 662 evidence is needed in this area. 663

664

Later periods of enhanced fire activity were mainly related with intense land-use, including cereal cultivation and grazing that lead to the spread of disturbance-adapted vegetation, although dry conditions during the MCA (Moreno et al., 2012) might favour fire spread (at ca. 1000-750 -AD 950-1200and 250-100 cal BP -AD 1700-1850-; Figures 5, 6). When this area was the

border between Al-Andalus and Castile (ca. 900-700 cal BP, AD 1050-1250;
Jiménez García-Herrera, 2011), it is likely that fire was intentionally set to avoid
ambushes and/or destroy enemy's potential resources (Corella et al., 2013;
Morales-Molino et al., 2017a) as well as to promote pasturelands.

674

675 During the subsequent City of Toledo's rule (ca. 700-150 cal BP, AD 1250-1800), fire activity was particularly high at ca. 500 cal BP (AD 1450), 676 causing oak woodland retreat and the spread of pasturelands (Figure 6). This 677 678 increase in fire activity agrees with historical archives that registered a relevant incidence of fire in the Toledo Mountains during the 15<sup>th</sup> century AD to promote 679 pastoral and arable farming (Sánchez-Benito, 2005). Transhumance 680 681 undoubtedly played a role in the practice of using fire to promote pasturelands, as one major drove road crossed Cabañeros during City of Toledo's rule (Perea 682 et al., 2015). Human-set fires seem to have propagated despite the existence of 683 684 regulations trying to ban woodland clearance and burning and limiting livestock grazing (Redondo-García et al., 2003; Sánchez-Benito, 2005; Jiménez García-685 Herrera et al., 2011). Human impact further rose around El Brezoso at the end 686 of the City of Toledo's rule (from ca. 400 cal BP, AD 1550, onwards) after the 687 construction of a mill some hundred meters downstream (Perea et al., 2015). 688 689 Overall, our palaeoecological data show that diversified land-use activities (e.g. cereal cultivation, grazing) first intensified well before the Ecclesiastical 690 Confiscation (ca. 200-150 years ago, see Figure 6), and then further increased 691 after this period, resulting in increases of pastureland plants (Poaceae, Rumex, 692 693 Plantago, Cichorioideae), disturbance-adapted shrubs (Cistus, E. australis, Lamiaceae) and olive orchards (Figures 3, 6). The recent spread of olive 694

cultivation was a regionally widespread process in central and southern Iberia 695 696 (e.g. Gil-Romera et al., 2008; Anderson et al., 2011; Morales-Molino et al., 2013; Dorado-Valiño et al., 2014a; Ramos-Román et al., 2016), supported by 697 fire. The recent recovery of oak woodlands at the top of our sequence results 698 699 from the abandonment of charcoal production practices and goat raising in the 700 last century, and the later protection of Cabañeros (Perea et al., 2015). Soil 701 degradation during previous phases of high fire activity, grazing pressure and 702 charcoal production probably favoured the stronger expansion of Q. ilex coppices with respect to deciduous Quercus since ca. 300 cal BP (AD 1650) but 703 704 especially during the last century (see Figure 6). A similar Quercus expansion during the last centuries has been reported from the near Las Villuercas 705 706 Mountains (Gil-Romera et al., 2008).

707

708

## 4.2 Mire vegetation dynamics

709 Peat accumulation began when arid conditions prevailed in southern 710 Iberia according to available climate reconstructions (Carrión, 2002; Martín-Puertas et al., 2008; Jiménez-Moreno et al., 2013). Therefore, the start of peat 711 formation at El Brezoso might have been related to geomorphologic processes 712 713 such as small landslides. Deposition of coarse eroded material at the bottom of the valley during high-energy flooding events or after fire (see high CHAR 714 715 values at the base of the sequence) might have created an area of impeded 716 drainage fed with groundwater that resulted in the establishment of a pond/mire (see Figure 5). Fire might have increased erosion and thus possibly landslide 717 activity or alternatively soil hydrophobia (Pausas et al., 2008). 718

Our pollen record shows that most of the main hygrophilous plant taxa 720 721 were present in the El Brezoso mire for the last 4000 years, surviving drought phases, disturbances and land-use changes (see Figure 6). Even though wet 722 723 heathlands (E. scoparia, E. tetralix, C. vulgaris) and M. gale thickets experienced several expansions and contractions during the last millennia, they 724 725 always played a prominent role in mire vegetation (Figures 5, 6). The 726 persistence of these hygrophilous communities, although with oscillations related to dry periods (see Figure 6), suggests that groundwater discharge may 727 728 have buffered for millennia against reduced water availability as it is nowadays. 729 This highlights the possible role of the El Brezoso mire as an interglacial 'hydrologic microrefugium' (McLaughlin et al., 2017) from where relict 730 hygrophilous species could spread during more favourable conditions. 731 732 Decreases of *M. gale* seem to have been related to the impact of dryness but mostly human activities, as most demises coincided with the spread of 733 734 pasturelands and/or cereal cultivation (Figure 6). Local settlers might have cleared vegetation on the borders of the mire to grow cereals during dry periods 735 736 because of higher soil moisture availability. Particularly severe clearances of M. 737 gale thickets occurred during the Arab Period (ca. 1250-900 cal BP, AD 700-1050) and after the Ecclesiastical Confiscation (ca. 150-50 cal BP, AD 1800-738 1900). The continuous record of Cerealia-t. pollen during the Arab period 739 740 testifies for the intensification of cereal cultivation in close proximity to the mire, while high percentages of disturbance-tolerant herbs indicate pastureland 741 742 expansion at the time of Ecclesiastical Confiscation (Figure 6). Sphagnum bogs appear to have been even more responsive to climatic oscillations, tracking 743

719

humid and dry phases and particularly those comprised within the IRHP (ca.
2600-1600 cal BP –650 BC-AD 350-, Figure 6; Martín-Puertas et al., 2009).
However, more intense livestock grazing and trampling in the surroundings of
the mire might have caused their decline during the last millennium (Figures 5,
6).

749

Betula is a particularly interesting relict hygrophilous tree, since its 750 dynamics did not follow climate changes at all but fire disturbance. Thus, 751 birches established and/or expanded at El Brezoso valley during or following 752 the periods of increased fire activity centred at ca. 3800 (1850 BC), 3000 (1050 753 754 BC) and 850 (AD 1100) cal BP, mostly at the expense of oak woodlands and 755 meadows (Figure 6). Likewise, birches were also favoured by fire in the Las Villuercas pollen record (Gil-Romera et al., 2008). Betula are very light-756 757 demanding trees whose seedlings cannot tolerate any competition during their early life stages (Atkinson, 1992; Sánchez del Álamo et al., 2010) and could 758 have taken advantage of the reduced competition following wildfires to establish 759 and/or spread on suitable microsites (see previous subsection). Betula decline 760 at the Iron Age/Roman Times transition (ca. 2200-2100 cal BP, 250-150 BC) 761 might have been caused by human-driven spread of pasturelands and grazing 762 during a drier phase of the IRHP (Martín-Puertas et al., 2009), whereas the 763 764 major demise at the beginning of the City of Toledo's rule was probably related to cereal cultivation and pastoral farming (Figures 5, 6). This interpretation 765 agrees well with the sensitivity of birches to browsing (Atkinson, 1992; Sánchez 766 del Alamo et al., 2010). Also in the Toledo Mountains, the Valdeyernos mire 767 pollen record shows that Betula has been an important component of the local 768

vegetation over the last two thousand years accompanying the dominant 769 770 Corylus (Dorado-Valiño et al., 2014b). This represents a major difference with our record, where Corylus is very rare (Figure 3). Dorado-Valiño et al. (2014b) 771 772 might have included *M. gale* pollen in the *Corylus*-type pollen curve, given the similarities between both pollen types (Punt et al., 2002). The botanical surveys 773 774 conducted in the Valdevernos area during the last decades (e.g. Gómez 775 Manzaneque, 1988; Baonza Díaz et al., 2010) support this interpretation. First, Corylus avellana was not found in the surroundings of Valdevernos since at 776 least 30 years (see Gómez Manzaneque, 1988; Baonza Díaz et al., 2010). 777 778 Corylus avellana is a relatively tall shrub, thus it seems highly unlikely that botanists have overlooked it, if present. Such an identification blunder appears 779 780 extremely unlikely, particularly after the intensive sampling effort made by 781 Baonza Díaz et al. (2010). Contrarily, *M. gale* grew locally in the Valdeyernos mire until at least AD 1986 (Gómez Manzanegue, 1988). However, in their 782 783 pollen diagram, Dorado-Valiño et al. (2014b) show percentages of Corylus around 20% not only in the surface sample of their sequence but also in the 784 785 samples located immediately below, reflecting the period before and around AD 786 2006 and the previous decades, what is extremely unlikely according to the available vegetation surveys. In the near Las Villuercas Mountains, ca. 80 km to 787 the west of El Brezoso, Betula declined much earlier, i.e. at ca. 3500 cal BP 788 (1550 BC), probably because of the combined effect of climate warming and an 789 intensification of human activities (Gil-Romera et al., 2008). All these data show 790 791 that further research addressing in more detail the long-term impact of fire regimes and grazing on these southernmost populations of *Betula* is needed, 792 given their sensitivity to browsing (Atkinson, 1992; Sánchez del Álamo et al., 793

- 2010) and to high fire incidence (Tinner et al., 2000; Gil-Romera et al., 2014).
- 795 Overall, our data indicate that wetland vegetation of Cabañeros has
- experienced major changes during the last millennia as a result of both climatic
- and human causes. Although most hygrophilous communities have survived to
- dry periods and disturbances in the past, attention must be paid to their
- responses to the unprecedented events of high magnitude predicted for the
- near future in order to guarantee the preservation of this valuable ecosystem.

## 5. Conclusions

The current landscapes of Cabañeros mostly result from historical and 802 803 socio-economic processes during the last millennium, and are far from pristine conditions. However, climate variability continued playing a relevant role even 804 after human activities intensified in the Middle Ages. This new palaeoecological 805 806 record adds to the great heterogeneity of vegetation trajectories in space and time that characterizes the Iberian Peninsula. Spatio-temporal heterogeneity 807 808 makes it difficult, and possibly unpractical from a conservation perspective, predicting forthcoming vegetation successions. Our findings document land-use 809 810 changes in the area and highlight the ecological and biogeographical role of 811 mires as hydrologic microrefugia for several hygrophilous and temperate woody 812 plants in the Toledo Mountains (e.g. *M. gale*, *Betula*). Given that mires have the potential of preserving unique population adaptations (genetic resources) to 813 814 warmer/drier conditions, these mire habitats may result crucial for diversity conservation, particularly under the current context of anthropogenic climate 815 change. 816

817

818 Palaeoecological records are increasingly used to address ongoing 819 challenges in sustainability, forest management and biodiversity conservation (e.g. Willis and Birks, 2006; Colombaroli et al., 2013; Morales-Molino et al., 820 2017a, b; Whitlock et al., 2017). In key regions for nature conservation like the 821 Toledo Mountains, long-term changes in ecosystems in combination with 822 historical sources highlight the marked historical legacies on present 823 ecosystems. Likewise, specific measures are needed for forest conservation 824 825 and management when accounting for future scenarios of combined land-use

- abandonment and warmer temperatures that may endanger the persistence of
- 827 important microrefugia for hygrophilous woody plants.

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- perspective in biodiversity conservation. Science 314, 1261-1265.

- 1181 **Table 1.** Chronological setting, mostly based on AMS radiocarbon dates, for the
- 1182 El Brezoso peat sequence (Cabañeros National Park). The calibrated ages
- have been obtained using the programs CALIB 7.1 (Reimer et al., 2013) and
- 1184 CALIBomb (Hua et al., 2013).

| Laboratory<br>code | Depth<br>(cm) | Material   | Radiocarbon<br>age ( <sup>14</sup> C yr BP) | Calibrated age (cal<br>BP, 95.4%<br>confidence interval) | Calibrated age<br>(cal BP, median) |
|--------------------|---------------|--|---|--|------------------------------------|
| Surface            | 0             | Core top   |   | -64  | -64                                |
| BE-4641            | 12-16         | Angiosperm<br>twigs                                      | 20 ± 20                                     | -6-239   | 44                                 |
| BE-4640            | 34-36         | Charcoal   | 160 ± 20                                    | -5-283   | 187                                |
| BE-4639            | 56-58         | Charred <i>Erica</i><br>leaves,<br>charcoal              | 550 ± 20                                    | 524-630  | 549                                |
| BE-4638            | 80-82         | Charred <i>Erica</i><br>leaves and<br>flowers            | 1210 ± 20                                   | 1065-1224  | 1130                               |
| BE-5519            | 98-100        | Charred <i>Erica</i><br>leaves, fruits<br>and twigs      | 2840 ± 20                                   | 2873-3001  | 2943                               |
| BE-4637            | 110-112       | Charcoal   | 3340 ± 20                                   | 3484-3637  | 3582                               |
| BE-5520            | 122-124       | Periderm, leaf<br>fragments,<br><i>Carex</i> seeds       | 750 ± 20                                    | Rejected   | Rejected                           |
| UB-26709           | 130-132       | Charcoal, bark   | 3440 ± 45                                   | 3592-3831  | 3701                               |
| UB-26708           | 170-173       | Charcoal,<br>bark, other<br>terrestrial<br>plant remains | 3610 ± 35                                   | 3834-4068  | 3920                               |
| UB-26707           | 172-173       | Peat   | 3620 ± 35                                   | 3839-4074  | 3931                               |

## 1187FIGURE CAPTIONS

1188

Figure 1. (a) Location of the Cabañeros National Park (white contour) and El Brezoso mire (white star) in central Iberia. The Toledo Mountains are labelled using their Spanish name, *"Montes de Toledo"*. (b) Picture of the El Brezoso mire during early spring, with wet heaths and meadows in the foreground, *Erica scoparia* heath on the right bordering the mire, and some *Quercus pyrenaica* trees in the background.

1195

Figure 2. From left to right, lithology, age depth-model, peat deposition time and pollen concentration of the El Brezoso peat sequence. The age-depth model is a smoothing spline (smoothing parameter=0.2) fitted with the software CLAM 2.2 (Blaauw, 2010). The dashed lines delimit the 95% confidence interval of the age estimates.

1201

Figure 3. Pollen diagram of the El Brezoso mire showing percentages of the main tree and shrub pollen types calculated with respect to the terrestrial pollen sum (aquatics and spores excluded). Microscopic charcoal concentrations and accumulation rates (CHAR) are also shown. Empty curves represent 10x exaggerations. LPAZs: local pollen assemblage zones.

1207

Figure 4. Pollen diagram of the El Brezoso mire with the percentages of the main upland herb pollen types calculated with respect to the terrestrial pollen sum (aquatics and spores excluded). Microscopic charcoal

concentrations and accumulation rates (CHAR) are also shown. Empty curves
 represent 10x exaggerations. LPAZs: local pollen assemblage zones.

1213

Figure 5. Pollen diagram of the El Brezoso mire with the percentages of the main aquatic and wetland pollen types, and fern, moss and dung fungal spores calculated with respect to the terrestrial pollen sum (aquatics and spores excluded). Microscopic charcoal concentrations and accumulation rates (CHAR) of El Brezoso mire are also shown. Empty curves represent 10x exaggerations. LPAZs: local pollen assemblage zones.

1220

Figure 6. Summary vegetation dynamics and their main ecological 1221 drivers at the El Brezoso mire. Bands in red depict periods of increasing fire 1222 activity. Dashed lines indicate the boundaries of the main cultural periods and 1223 1224 dot-dashed lines show the dates of relevant historical events with consequences on land-use (according to Molénat, 1997; Jiménez de Gregorio, 1225 2001; Jiménez García-Herrera et al., 2011; Perea et al., 2015). Orangerange 1226 boxes represent the main dry periods identified in south-western Iberia from 1227 vegetation-independent proxies: (1) severe droughts identified from the analysis 1228 of the rogation ceremonies of the Cathedral of Toledo (Domínguez-Castro et al., 1229 1230 2008), (2) low lake-level phases at Lagunillo del Tejo lake (Iberian Range) based on the isotopic composition of authigenic carbonates (López-Blanco et 1231 al., 2016), (3) dry phases from the multi-proxy study of Lake Zóñar (Martín-1232 Puertas et al., 2008, 2009), (4) dry phases as reconstructed from the multi-1233 proxy study of Cimera Lake (Sánchez-López et al., 2016). Finally, red boxes 1234

- denote mostly dry regional periods whereas blue boxes represent
- 1236 predominantly humid regional phases. Abbreviations: t.: pollen type; CHAR:
- 1237 charcoal accumulation rate; LIA: Little Ice Age; MCA: Medieval Climate
- 1238 Anomaly; DA: Dark Ages; IRHP: Iberian Roman Humid Period.





## 1243 Figure 2



Figure 3











