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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 inland Iberia remain largely unknown, masking possible legacy effects of past land-use on current and future ecosystem trajectories. Here we present a 4000-year long palaeoecological record (pollen, spores, microscopic charcoal) from a mire located in the Cabañeros National Park (Toledo Mountains, central Spain), a region with key conservation challenges due to ongoing land-use changes. 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 results show that oak (*Quercus*) woodlands have been the main forested community of the Toledo Mountains over millennia, with deciduous *Quercus pyrenaica* and *Quercus faginea* more abundant than evergreen *Quercus ilex* and *Quercus suber*, particularly on the humid soils of the valley bottoms. Deciduous oak woodlands spread during drier periods replacing hygrophilous communities (*Betula*, *Salix*, hygrophilous Ericaceae) on the edges of the mire, and could cope with fire disturbance variability under dry conditions (e.g. ca. 3800–3000–1850–1050 BC- and 1300–100 cal BP–AD 650–1850-) as suggested by regional palaeoclimatic reconstructions. Pollen and coprophilous 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 and arable farming at the expense of woodlands/shrublands under dry conditions. While historical archives date the onset of strong human impact on the vegetation of Cabañeros to the period at and after the Ecclesiastical Confiscation (ca. 150–100 cal BP, AD 1800–1850), our palaeoecological data reveal that land-use was already intense during the Arab period (ca. 1250–900 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.

1. Introduction

During the last decades, the publication of numerous local to regional palaeobotanical records with high temporal and taxonomical resolution (e.g. Carrión et al., 2010a; Carrión, 2012; López-Sáez et al., 2014a; González-Sampériz et al., 2017) has increased our knowledge about the millennial-scale drivers of ecosystem change (e.g. climate, human impact) in the Iberian Peninsula. Nevertheless, several regions of the Iberian Peninsula with high ecological and cultural value like the Southern Iberian Plateau and its internal mountains (Perea et al., 2015) remain under-investigated (see Carrión et al., 2010a; Carrión, 2012). The "*Montes de Toledo*" (Toledo Mountains) is one of the mountain ranges that separate the Tagus and Guadiana river basins in the Southern Iberian Plateau. These mountains host diverse and relatively well-preserved Mediterranean vegetation (e.g. evergreen oak woodlands, maquis) along with relict populations of Tertiary, Atlantic and Eurosiberian taxa (e.g. *Prunus lusitanica*, *Betula* spp., *Myrica gale*) that

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are rare in the Mediterranean region (Vaquero, 1993; Perea and Perea, 2008). Despite the relative abundance of mires potentially suitable for palaeoecological analyses in this area (López-Sáez et al., 2014b), only five sites have been studied in the Las Villuercas-Montes de Toledo mountain range: Garganta del Mesto (Gil-Romera et al., 2008), Patateros (Dorado-Valiño et al., 2014a), Valdeyernos (Dorado-Valiño et al., 2014b), Las Lanchas (Luelmo-Lautenschlaeger et al., 2018a) and Botija (Luelmo-Lautenschlaeger et al., 2018b). Similarly, only few records are currently available from La Mancha plain (e.g. García-Antón et al., 1986; Dorado-Valiño et al., 2002; Gil-García et al., 2007). As a result, vegetation dynamics and their ecological drivers at multi-decadal to millennial timescales are poorly understood in this region of inland Spain.

The landscape of the Toledo Mountains is mostly composed of lowland Mediterranean woody plant communities with dominance of broadleaved sclerophyllous trees and shrubs. The diversity and relatively good conservation of this vegetation in the Cabañeros area (central sector of the Toledo Mountains; Fig. 1) partly justified the establishment in 1995 of the first Spanish National Park devoted to the protection of lowland Mediterranean ecosystems (Cabañeros NP, named Cabañeros onwards; Jiménez García-Herrera et al., 2011). Archaeological and historical records suggest that human impact was low until the last centuries, and that such ecosystems remained relatively undisturbed over millennia (Jiménez García-Herrera et al., 2011). Unfortunately, historical sources are scarce and often contradictory (e.g. Jiménez García-Herrera et al., 2011; Perea et al., 2015). Human

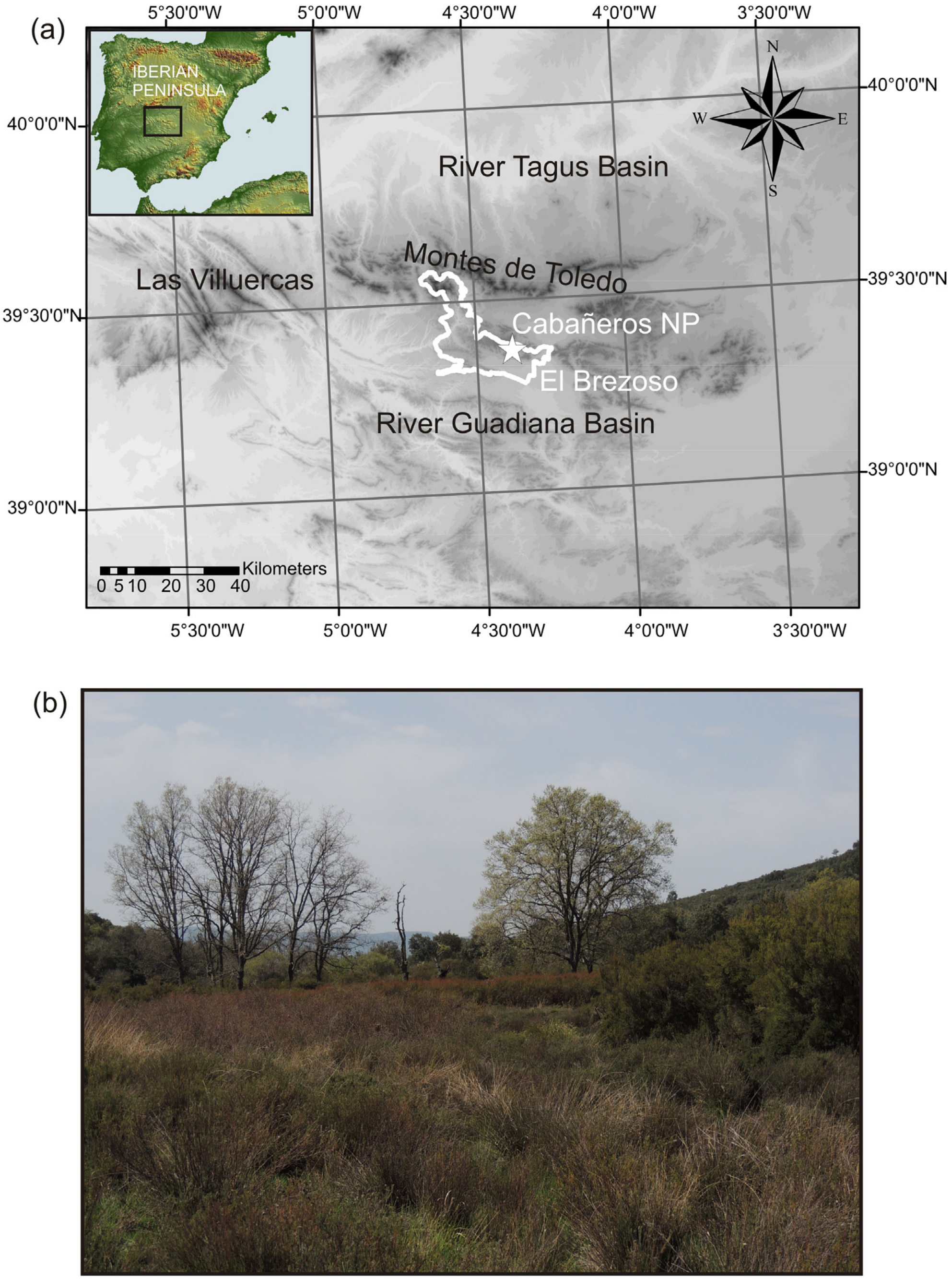

Fig. 1. (a) Location of the Cabañeros National Park (white contour) and El Brezoso mire (white star) in central Iberia. The Toledo Mountains are labelled using their Spanish name, "*Montes de Toledo*". (b) Picture of the El Brezoso mire during early spring, with wet heaths and meadows in the foreground,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

population was low and sparse in Cabañeros and most of the Toledo Mountains until the 19th–20th centuries AD (Gómez de Llarena, 1916; Jiménez García-Herrera et al., 2011). Historical land management limited woodland exploitation and burning in the Toledo Mountains from mid-13th to mid-19th centuries AD (i.e. during the City of Toledo's rule; Jiménez García-Herrera et al., 2011). Drastic woodland exploitation and fragmentation started altering the landscape then by mid-19th century AD and persisted until the protection of the Cabañeros area in AD 1988 (first as Natural Park). In contrast to this view of relatively "low impact", other historical sources report that charcoal production, livestock raising and firewood gathering caused marked landscape transformations since at least the 13th century AD (Molénat, 1997; Jiménez de Gregorio, 2001; Perea et al., 2015). Likewise, burning is documented since at least the 15th century AD in the Toledo Mountains despite the existence of fire-ban bylaws (Redondo-García et al., 2003; Perea et al., 2015). A more comprehensive and quantitative assessment of land-use history in Cabañeros by means of proxy records is urgently needed to better understand the past range of natural disturbance variability and legacy effects and better guide forest management and conservation measures in the National Park.

Land-use over millennia strongly affected the relative abundances of tree and shrub species originally present in the native woodlands of the Mediterranean Basin. For instance, in oak woodlands, people have deliberately promoted species of economic interest such as *Quercus ilex* (wood, charcoal and acorn production) and *Quercus suber* (cork extraction) at the expense of deciduous *Quercus* species (Urbieta et al., 2008; Perea et al., 2015). Likewise, in many Mediterranean regions, human activities have also indirectly favoured the spread of shrubby sclerophyllous communities (e.g. evergreen sclerophyllous oak woodlands, maquis, garrigue) via soil degradation, vegetation burning and/or livestock raising (e.g. Blondel, 2006; Colombaroli et al., 2007; Henne et al., 2013). Climatic variability has also affected the balance between deciduous and evergreen sclerophyllous oaks, with drought-sensitive deciduous and drought-tolerant evergreen sclerophyllous oaks expanding during humid and dry phases, respectively (e.g. Carrión et al., 2001, 2010b). Assessing the relative importance of plant species through time, and their relative drivers (i.e. land-use, climate, disturbances) is relevant for management plans, particularly in protected areas such as National Parks that aim at preserving or restoring natural conditions (e.g. Stähli et al., 2006; Valsecchi et al., 2010).

The Toledo Mountains host relict populations of several hygrophilous woody plants that are widespread and abundant in northern latitudes with more humid climates (e.g. *Betula pendula*, *Betula pubescens*, *Erica tetralix*, *Myrica gale*), but with fragmented and reduced populations in the Mediterranean realm (Vaquero, 1993; Perea and Perea, 2008). In Cabañeros, *Betula* stands and wet 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 overgrazing/trampling by wild ungulates threaten the future persistence of mires in the area (López-Sáez et al., 2014b). Mires located within Cabañeros represent an exception because they are fenced and under protection, but are still menaced by drier conditions that may occur in the future (Gao and Giorgi, 2008; Giorgi and Lionello, 2008). However, mires of Cabañeros could have the potential to act as hydrologic refugia for the abovementioned species during dry periods in the future (McLaughlin et al., 2017). Spreading from these spatially restricted areas, hygrophilous species might expand and colonize other suitable environments during humid intervals. Assessing the past resilience and sensitivity of hygrophilous species to dry episodes occurred in Mediterranean Iberia during the last millennia (e.g. Carrión, 2002; Martín-Puertas et al., 2008; Morellón et al., 2009) may therefore contribute to assess the potential of Cabañeros peatlands.

In this paper we present a 4000-year long pollen sequence from Cabañeros to reconstruct vegetation history in the Toledo Mountains. We use spores of obligate coprophilous fungi and microscopic charcoal particles to track changes in grazing pressure and regional fire activity through time. We complement our inferences from proxy records with published vegetation-independent climate reconstructions with the following aims: (i) to reconstruct the changes occurred in upland vegetation (surrounding the mire) and fire 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 Cabañeros hygrophilous vegetation (growing on the mire) to past climate and land-use changes, assessing the potential role of the mires of the Toledo Mountains as hydrologic refugia.

2. Material and methods

2.1. Study area

Cabañeros is a 40,856 ha protected area especially renowned for its large populations of wild ungulates (mainly *Cervus elaphus*) and birds of prey (notably the threatened *Aegypius monachus* and *Aquila adalberti*). The landscape of Cabañeros is Appalachian-like, with mountains of moderate altitude (800–1449 m a.s.l.; highest summit: Peak Rocigalgo) locally known as "*sierras*" and an extensive alluvial plain locally named "*raña*" (600–700 m a.s.l.; Jiménez García-Herrera et al., 2011). Ordovician quartzites and Cambrian siliceous slates are the dominant bedrock in the "*sierras*", where they often outcrop at mountain tops and ridges. The "*raña*" resulted from the infilling of ancient valleys with clays and quartzitic pebbles transported from the "*sierras*" in massive events during the Cenozoic. The climate of Cabañeros is typically Mediterranean, with the rainy season usually encompassing autumn, winter and 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-Mediterranean bioclimatic belt where the study site is located, registers a mean annual temperature of 13.6 °C ($T_{Jan} = 4.9$ °C, $T_{Jul} = 24.4$ °C), a mean annual precipitation of 539.6 mm, and a marked and long summer drought (dry period = 3.5 months, $P_{Jul-Sep} = 45.4$ mm). Fire was in principle suppressed in Cabañeros with the creation of the Natural Park in 1988 (Jiménez García-Herrera et al., 2011), although some wildfires have anyway affected this protected area during the last decades.

In this study we have integrated the description of the Cabañeros vegetation in Perea et al. (2015) with field observations. Most of the Cabañeros surface (85%) lies within the meso-Mediterranean vegetation belt, with the supra-Mediterranean restricted to the highest areas usually above 1000 m a.s.l. Broadleaved evergreen sclerophyllous woodlands and shrublands dominate the meso-Mediterranean vegetation. The evergreen sclerophyllous *Quercus ilex* subsp. *ballota* is the most common oak species, especially in drier and more continental sites and/or on less developed soils. In Cabañeros, *Q. ilex* often forms mixed stands with the more frost-sensitive and moisture-demanding *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 more developed. In warmer sites thermophilous evergreen sclerophyllous shrubs such as *Pistacia lentiscus* and *Myrtus communis* accompany *Q. ilex*, whereas it is usually mixed with the deciduous and relatively drought-sensitive *Quercus faginea* subsp. *broteroi* on north-facing slopes where water availability is higher. Almost pure *Q. faginea* stands particularly develop in (moister) north-facing slopes, seasonally waterlogged valley bottoms and areas of groundwater discharge like the foothills of the "*sierras*". Similarly, some stands of the deciduous *Quercus pyrenaica* grow along the bottom of certain valleys in the meso-Mediterranean belt, where this relatively drought-sensitive species finds sufficient moisture and deeper soils to cope with dry summers. *Quercus pyrenaica* is more common in the supra-Mediterranean belt, above 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 woodlands) extend over ca. 20% of Cabañeros and represent its most iconic landscape.

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

Shrublands mostly originate from the degradation of former forests and woodlands, with the sole exceptions of mountain scrubland (*Echinospartum ibericum*, *Adenocarpus argyrophyllus*, *Genista cinerascens*) at the summit of Peak Rocigalgo, and hygrophilous heathlands on mires (*Erica tetralix*, *Erica lusitanica*, *Erica scoparia*, *Calluna vulgaris*, *Genista anglica*, *Genista tinctoria*, *Myrica gale*). Maquis replaces evergreen Mediterranean forests, forming a diverse evergreen community with *Arbutus unedo*, *Erica arborea*, *Erica australis*, *E. scoparia*, *Rhamnus alaternus*, *Phillyrea angustifolia*, *Pistacia terebinthus*, *Ruscus aculeatus*, *Viburnum tinus*, *Cistus ladanifer* and *Cistus populifolius*. *Cytisus* species are sometimes abundant in the plant communities that first replace forests. As degradation progresses, highly flammable *Cistus* spp. (*C. ladanifer* is the most common and dominant) and fire-resistant *Erica* spp. become the dominant shrubs. The final stages of degradation are Lamiaceae-dominated garrigues (dwarf shrublands with *Rosmarinus officinalis*, *Lavandula pedunculata* and *Thymus mastichina* among others) and grasslands.

2.2. Study site

El Brezoso mire is a medium-sized mire (~1.5 ha) located at the bottom of El Brezoso valley in the Sierra del Chorito (Fig. 1). The vegetation at the coring site is a dense thicket of *Myrica gale* with *Carex paniculata*, *Erica tetralix* and *Molinia caerulea* (Vaquero, 2010). Nevertheless, the dominant plant communities in the mire are hygrophilous heathlands dominated by *E. tetralix*, *M. caerulea* and *Schoenus nigricans*, with *Carex* spp., *Juncus* spp., Poaceae, *Potentilla erecta*, *Dactylorhiza elata*, *Lotus pedunculatus*, *Narcissus bulbocodium*, *Wahlenbergia hederacea*, *Galium palustre*, *Ranunculus bulbosus*, *Calluna vulgaris* and *Genista anglica* (for further details, see Vaquero, 2010). Dense *Erica scoparia*-dominated heathlands with *Erica arborea*, *C. vulgaris*, *Erica lusitanica*, *Rubus ulmifolius*, *Cistus ladanifer*, *Cistus salviifolius*, *Daphne gnidium*, *Pteridium aquilinum* and *Asphodelus aestivus* grow on drier soils bordering the mire (Vaquero, 2010). On the El Brezoso stream banks, *E. scoparia*-dominated heathland is also dominant, with some *Betula pendula* subsp. *fontqueri* trees recently planted to restore the riparian vegetation. Relatively open oak woodland (*Quercus pyrenaica*) extends all 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 *Quercus faginea* subsp. *broteroi* with some *Quercus suber*, and a dense shrub layer mostly composed of sclerophylls such as *Arbutus unedo*, *E. arborea*, *Erica australis*, *Phillyrea angustifolia*, *C. ladanifer*, *Rosmarinus officinalis* and *Lavandula pedunculata*. Monitoring of this mire between 1990 and 2010 revealed an increase in *Erica scoparia*-dominated heathlands and an intense impact by wild ungulates (Vaquero, 2010; Perea and Gil, 2014).

2.3. Coring and chronology

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 wrapped core sections with PVC guttering and cling film and stored them in a cold (4 °C) and dark room until sample processing for radiocarbon dating and palynological analyses. To establish the chronology of the peat sequence, we obtained ten AMS radiocarbon dates on terrestrial plant macrofossils and peat. As there was no indication of a recent interruption of peat formation, we 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 al., 2013) with the program CALIB 7.1. We used the software CALIBomb and 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.

2.4. Pollen, spore and microscopic charcoal analyses

In the laboratory, we prepared 68 peat samples of 0.5–1.0 cm^3 (1-cm thick) for pollen analysis following a standard protocol (Moore et al., 1991) consisting of chemical treatment with HCl, HF and KOH to remove carbonates, silicates and organic matter respectively, as well as sieving through a 250 μm 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 intervals between samples throughout the sequence. *Lycopodium* tablets were added to the samples at the beginning of the treatment to estimate pollen concentration (grains cm^{-3}; Stockmarr, 1971). Pollen grains were identified with the aid of identification keys (Moore et al., 1991; Ramil-Rego et al., 1992; Beug, 2004), photographic atlases (Reille, 1992) and the reference collection at the Institute of Plant Science of the University of Bern. A minimum terrestrial pollen sum of 300 pollen grains was in general achieved (mean ± standard deviation = 312 ± 36), excluding pollen from aquatic/wetland plants (see Fig. 5) and spores. Pollen percentages of wetland and aquatic plants were calculated with respect to the terrestrial pollen sum. We used the program PSIMPOLL 4.27 (Bennett, 2009) to delimit local pollen assemblage zones (LPAZs) in the pollen diagram using the optimal splitting by sums-of-squares method (Birks and Gordon, 1985). Only terrestrial pollen types reaching values over 2% were considered for the zonation. We then assessed the statistical significance of the obtained LPAZs using the broken-stick model (Bennett, 1996). Spores of obligate coprophilous fungi were also identified according to Van Geel et al. (2003) and their percentages calculated with respect to the terrestrial pollen sum. Finally, we counted microscopic charcoal particles larger than 10 μm in pollen slides to estimate charcoal concentrations (# cm^{-3}) and accumulation rates (CHAR; # $\text{cm}^{-2}\ \text{yr}^{-1}$), following the indications by Tinner and Hu (2003) and Finsinger and Tinner (2005).

3. Results and interpretation

3.1. Lithology and chronology

The El Brezoso sedimentary sequence is mainly composed of peat, with only three silty peat layers at the bottom and the central section of the profile (Fig. 2). They are likely related to the persistence of small temporary pools 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 radiocarbon dates (Table 1), we only rejected one (124–122 cm-deep, date mostly on periderm) because the measured age is younger than expected (Fig. 2). The dated periderm probably came from a root penetrating older layers. Peat deposition time shows that peat formation was very fast at the beginning of the sequence (ca. 3.5 yr cm^{-1}; 175–129 cm-deep), then slowed quite sharply towards the middle section of the sequence (from 3.5 yr cm^{-1} at 129 cm-deep to 87.1 yr cm^{-1} at 91 cm-

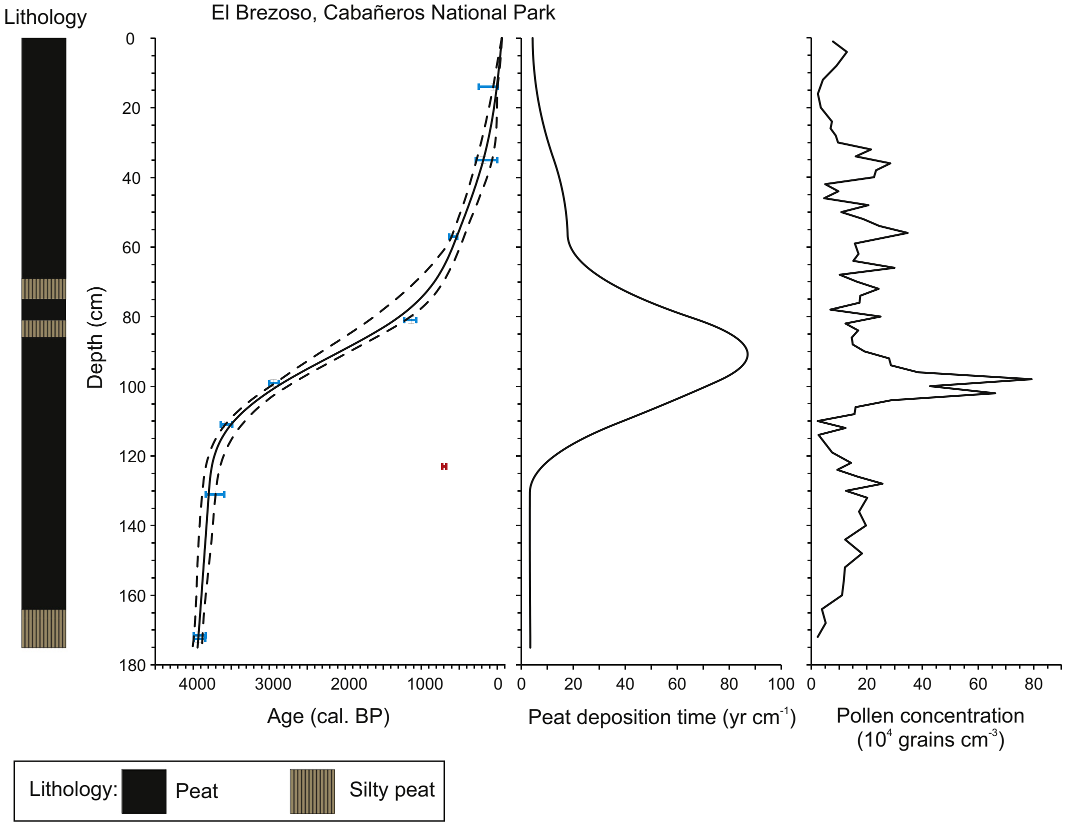

Fig. 2. From left to right, lithology, age depth-model, peat deposition time and pollen concentration of the El Brezoso peat sequence. The age-depth model is a smoothing spline (smoothing parameter = 0.2) fitted with the software CLAM 2.2 (Blaauw, 2010). The dashed lines delimit the 95% confidence interval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

deep) and finally accelerated again until the top of the profile, first quite abruptly (from 87.1 yr cm^{-1} at 91 cm-deep to 25.7 yr cm^{-1} at 66 cm-deep) and then more gently (from 25.7 yr cm^{-1} at 66 cm-deep to 4.4 yr cm^{-1} at the top of the profile). Maximum pollen concentration 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 the sequence probably caused by a decrease in on-site peat production.

3.2. Pollen, spores and microscopic charcoal records: Vegetation and fire history

The El Brezoso pollen record consists of 135 terrestrial plant pollen types, 16 aquatic and wetland plant pollen types and six fern spore types (Figs. 3–5).The time resolution between samples is quite variable: less than 50 years at ca. 3950–3600 cal BP (2000–1650 BC) and ca. 500 cal BP-today (AD 1450–2014), 50–100 years at ca. 3600–3300 and 1000–500 cal BP (1650–1350 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 the sequence (see Fig. 2).

The assemblages mostly recorded vegetation dynamics at local to extra-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 pollen content in the core top sample mostly reflects local to extra-local modern vegetation. Previous empirical research has shown that microscopic charcoal is mostly related to extra-local to regional fire activity (0.01–100 km^2; Tinner et al., 1998; Conedera et al., 2009), and dung fungal spores to local grazing activities (e.g. Baker et al., 2016).

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

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

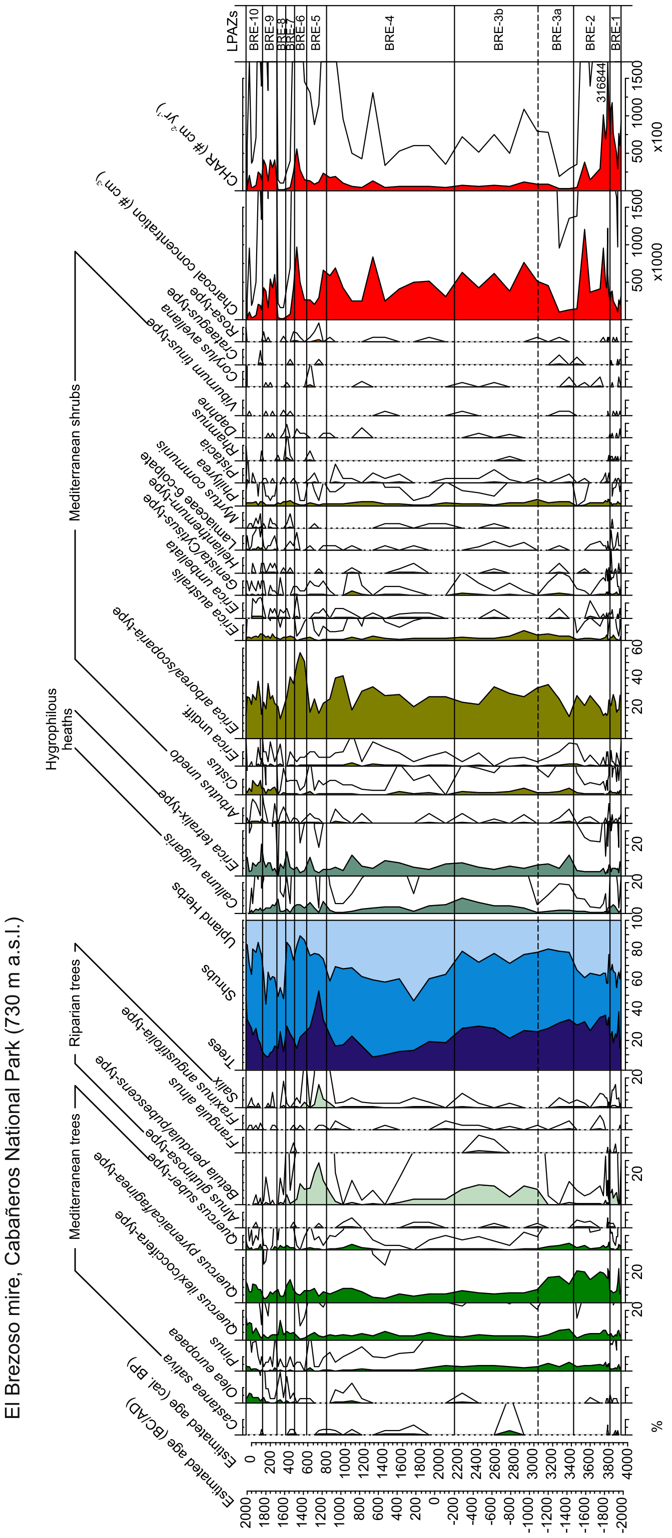

Fig. 3. Pollen diagram of the El Brezoso mire showing percentages of the main tree and shrub pollen types calculated with respect to the terrestrial pollen sum (aquatics and spores excluded). Microscopic charcoal concentrations and accumulation rates (CHAR) are also shown. Empty curves represent 10×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

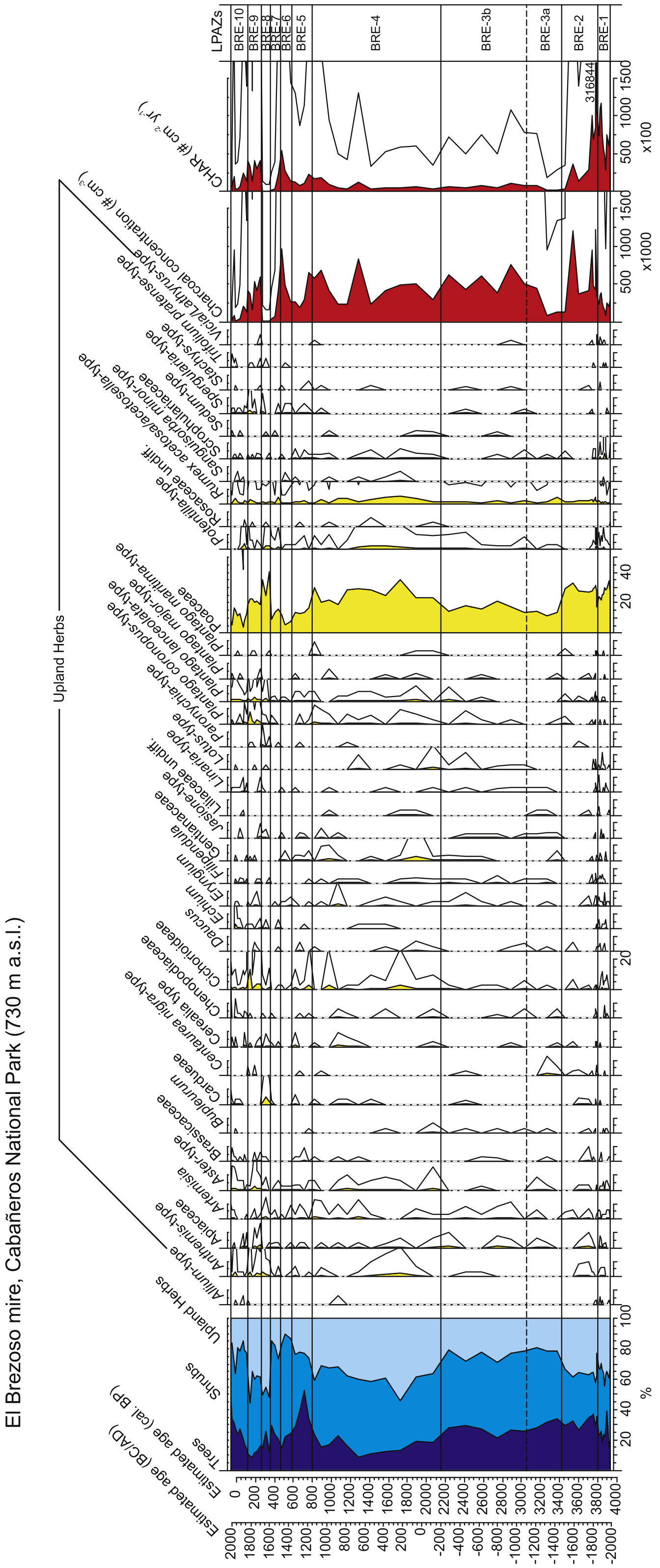

Fig. 4. Pollen diagram of the El Brezoso mire with the percentages of the main upland herb pollen types calculated with respect to the terrestrial pollen sum (aquatics and spores excluded). Microscopic charcoal concentrations and accumulation rates (CHAR) are also shown. Empty curves represent 10× exaggerations. LPAZs: local pollen assemblage zones.

The El Brezoso pollen sequence is subdivided into ten statistically significant LPAZs (Figs. 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 *Quercus ilex* when discussing the pollen curve of *Q. ilex/coccifera*-t. (t. = type), given that it is more widespread in the Toledo Mountains than *Quercus coccifera* and therefore more relevant for the vegetation dynamics (see Perea et al., 2015). Vegetation reconstruction is particularly challenging at El

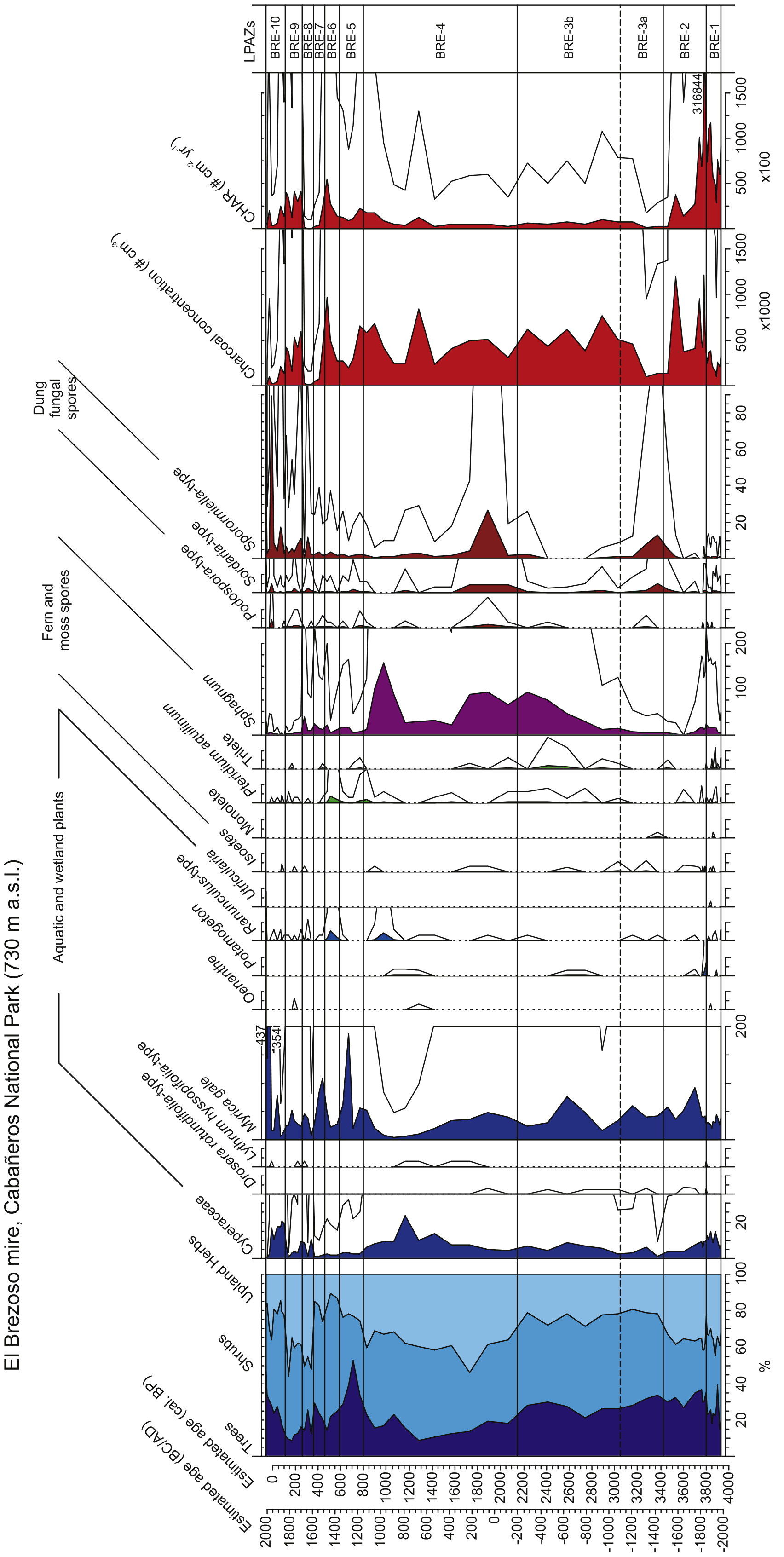

Fig. 5. Pollen diagram of the El Brezoso mire with the percentages of the main aquatic and wetland pollen types, and fern, moss and dung fungal spores calculated with respect to the terrestrial pollen sum (aquatics and spores excluded). Microscopic charcoal concentrations and accumulation rates (CHAR)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

Brezoso because the same pollen type may be produced by different plant species that may grow locally on the mire or, conversely, on the drier soils of the adjacent slopes. *Erica arborea*/*scoparia*-t. and Poaceae are particularly relevant examples because of their abundance in the pollen sequence and their importance in the landscapes of the Toledo 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 abundant in the hygrophilous plant communities of the Toledo Mountains (Herrera, 1988; Vaquero, 2010; Perea et al., 2015). Nevertheless, a certain proportion of this pollen type has surely been produced by *E. arborea* and, to a much lesser degree, *Erica lusitanica*. In the Toledo Mountains, *E. arborea* is currently more common and abundant in drier habitats such as Mediterranean woodlands and maquis (Perea et al., 2015). Finally, *E. lusitanica* is a rare heath typically growing in damp sites, like *E. scoparia*. Likewise, Poaceae pollen might have been produced by grass species growing on the mire like *Molinia caerulea*, and/or in drier grasslands.

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

Our pollen data suggest that Mediterranean woodland with deciduous 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 hygrophilous communities with *Betula*, *Erica scoparia*, Cyperaceae and *Sphagnum*. *Myrica gale* shrubs might have spread over areas previously covered with other mire vegetation. The charcoal record suggests two major 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 activity (e.g. *Plantago coronopus*-t., *Plantago lanceolata*-t., *Sordaria*-t., *Sporormiella*-t.) suggest that local grazing activities started to increase at ca. 3500 cal BP (1550 BC), together with increased burning. Subsequently they peaked during the next zone.

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

According to our pollen data the next vegetation stage, BRE-4 (2150–800 cal BP, 200 BC–AD 1150), was mainly characterized by the spread of pasturelands (Poaceae, *Rumex acetosa*/*acetosella*-t., *Aster*-t., Cichorioideae, *Plantago coronopus*-t., *Plantago lanceolata*-t.) and hygrophilous meadows (Cyperaceae, *Potentilla*-t.). These communities replaced *Betula* stands, *Myrica gale* thickets and, to some extent, hygrophilous heathlands (*Calluna vulgaris* decreases). *Sphagnum* populations significantly oscillated during this period, with a major decline at ca. 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 ca. 1300–1050 cal BP (AD 650–900), while the regional introduction of sweet chestnut (*Castanea sativa*) cultivation probably started at ca. 1700 cal BP (AD 250), when the *Castanea* pollen curve becomes nearly continuous. Cerealia-t. is recorded earlier, during zones BRE-2 and BRE-3, but always as isolated pollen grains discontinuous in time (Fig. 4), suggesting limited arable farming activities around the site. The regional presence of pines was markedly reduced after ca. 1700 cal BP (AD 250). High values of dung fungal spores (*Sporormiella*-t., *Sordaria*-t., *Podospora*-t.; Fig. 5) suggest that pastoral farming was particularly intense around 1900 cal BP (AD 50). Likewise, grazing activities began to consistently increase around El Brezoso at ca. 850 cal BP (AD 1100) according to the records of coprophilous fungal spores, in particular *Sporormiella*-t. (Fig. 5). The establishment of a well-developed riparian forest mostly composed of *Betula*, *Salix* and *M. gale* on the bottom of the valley (mire, stream banks) was the most remarkable vegetation change during BRE-5 (800–600 cal BP, AD 1150–1350). Meanwhile, meadows retreated and the surrounding Mediterranean woodland remained almost unchanged. Two periods of higher fire activity occurred at ca. 1300 and 1000–900 cal BP (AD 650 and 950–1050), indicated by maxima in both charcoal concentration and CHAR.

The pollen record suggests that (humid) heathlands (mostly composed of *Erica arborea*/*scoparia* and *Calluna vulgaris*) were the dominant plant communities during BRE-6 (600–450 cal BP, AD 1350–1500), replacing *Betula* stands and Mediterranean woodlands. The higher abundance of *Pteridium aquilinum* might 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 (450–350 cal BP, AD 1500–1600) the palynological evidence indicates that Mediterranean woodlands (*Quercus pyrenaica*/*faginea*, *Quercus ilex*, *Quercus suber*) moderately expanded. Mediterranean evergreen sclerophyllous shrubs (*Erica australis*, *Phillyrea*, Lamiaceae, *Myrtus communis*) also increased at the expense of 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. and its relatively high percentages (~1%) suggest the existence of agricultural fields in relative proximity to the mire. The decreases in charcoal concentration and CHAR along this zone indicate that fire activity notably diminished during this period.

Non-arboreal pollen increases (Poaceae, *Plantago lanceolata*-t., *Plantago coronopus*-t., *Rumex acetosa*/*acetosella*-t., Cardueae, *Potentilla*-t., Cichorioideae) during BRE-8 (350–250 cal BP, AD 1600–1700), showing that meadows re-expanded. This shift was associated with a temporary increase of grazing (*Sporormiella*-t., *Sordaria*-t.). Meadows replaced wet heathlands and possibly also deciduous oak woodlands previously growing at the valley bottom. A transient spread of *Quercus ilex* also occurred during this period, and fire activity was at its minimum of the last 4000 years according to our microscopic charcoal data. Our pollen record suggests that meadows remained abundant, deciduous and evergreen sclerophyllous oak woodlands were further cleared, and shrublands expanded during BRE-9 (250–100 cal BP, AD 1700–1850). Disturbance-adapted *Cistus*, *Erica australis* and Lamiaceae became important components of these shrublands, and several herbs indicative of disturbance and often linked to human activities such as *P. lanceolata*-t., *P. coronopus*-t. and Cichorioideae also expanded. Grazing additionally intensified during this phase as indicated by the increase in dung fungal spores. The mire was almost depleted of *Sphagnum* while hygrophilous heathlands with *Erica scoparia* and *Erica tetralix* spread. Olive 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 vegetation changes occurred under marked regional fire activity as indicated by the moderate to high charcoal values.

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

4. Discussion

4.1. Drivers of upland vegetation change and fire dynamics

Our data show that oaks were the most abundant trees in the woodlands around El Brezoso during the last 4000 years, especially the deciduous *Quercus pyrenaica* and *Quercus faginea*. Although it is difficult to ascertain whether deciduous 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 agreement with other pollen records from the Toledo Mountains (Dorado-Valiño et al., 2014a, 2014b). This mixed occurrence of evergreen and deciduous trees is also typical of today's meso-Mediterranean environments (Costa et al., 2005). *Quercus ilex*-t. pollen is more abundant in other sites from the Toledo Mountains (Luelmo-Lautenschlaeger et al., 2018a, 2018b) as well as in the relatively close Las Villuercas Mountains (Gil-Romera et al., 2008) over the last millennia. Given that all sites are small mires with reduced pollen source areas, the different vegetation patterns might be explained considering local factors such as topographical position (slope vs. valley bottom), slope grade and aspect, or soil development.

Overall, *Quercus* percentages are rather low in El Brezoso (5–35%), suggesting that vegetation was mainly composed of open woodlands or, alternatively, of shrublands and grasslands with sparse woodlands. However, landscape openness must also be cautiously considered in El Brezoso because the overrepresentation of wet heaths and meadows growing on the mire (mainly *Erica arborea*/*scoparia*-t., Poaceae, *Erica tetralix*-t. and *Calluna vulgaris*) might lower tree pollen percentages. It is noteworthy that pines were not relevant in the vegetation of Cabañeros during the last millennia, in contrast with other mid-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, limited soil development and, in some cases, higher topographical complexity help increase pine competitiveness (e.g. Rubiales et al., 2010).

Several coeval deciduous and evergreen *Quercus* woodland expansions occurred around El Brezoso at ca. 3800–3100 (1850–1150 BC), 1200–900 (AD 750–1050), 650–550 (AD 1300–1400), 450–350 (AD 1500–1600), 300–250 (AD 1650–1700) cal BP and finally from 100 cal BP to present (AD 1850–2014; Fig. 6). These oak woodland spreads occurred together with transient retreats of hygrophilous communities (growing on the mire or its edges; *Betula*, *Salix* and hygrophilous Ericaceae in Fig. 6). This vegetation pattern is ecologically best explained by temporary shifts towards drier conditions in Cabañeros during the Bronze Age, the Dark Ages (DA), the Medieval Climate Anomaly (MCA),the Little Ice Age (LIA) and the Industrial Era (Fig. 6), considering the age uncertainties between the independently radiocarbon-dated palaeoclimatic records (Martín-Puertas et al., 2008; Jiménez-Moreno et al., 2013; López-Blanco et al., 2016) and that we also account for climatic reconstructions based on historical archives (Domínguez-Castro et al., 2008). 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 (Fig. 6). A period of moderately increased fire activity commencing at ca. 3200 cal BP (1250 BC; Fig. 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.

The expansions of evergreen/deciduous oak woodlands at ca. 3800–3100 (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 have been exacerbated by increased fire activity (Fig. 6). This long-term resistance and rate-of-recovery to fire disturbance of both evergreen (*Quercus ilex*, *Quercus suber*) and deciduous (*Quercus pyrenaica*, *Quercus faginea*) oaks may be related to their strong resprouting ability and thick fire-resistant bark (Pausas, 1997; Calvo et al., 2003; Espelta et al., 2003). Post-fire expansions of *Q. ilex* in Cabañeros contrast with the negative response of evergreen oak forests in the peri-Adriatic region (Colombaroli et al., 2008, 2009). We hypothesize that *Q. ilex* subsp. *ballota* (growing in inland dry and continental areas of the western Mediterranean, like Cabañeros) might respond to fire disturbance quite differently to *Q. ilex* subsp. *ilex* (inhabiting milder and usually moister sites generally not far from the coast, like the study sites in Colombaroli et al., 2009). Nevertheless, this hypothesis should be tested by means of high-resolution pollen and charcoal records and cross-correlation analysis in inland sites of the Iberian Peninsula.

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 (Fig. 6). With the only exception of the most recent minor one, i.e. ca. 250–100 cal BP (AD 1700–1850), 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 (Fig. 6), suggesting tight fire-climate linkages over the centennial to millennial timescales.

Superimposed on the centennial changes in climate (Fig. 6) are alterations of the disturbance regimes by human activities. Our data suggest that enhanced grazing followed fires at ca. 3500 cal BP (1550 BC; Fig. 5), pointing to intentional burning during Bronze Age to promote pastures (and probably also agriculture) and consequently increase landscape patchiness and diversity (Colombaroli and Tinner, 2013). However, the impact of human activities on vegetation seems to have been limited at the landscape scale, as only a few disturbance-tolerant plants (mostly *Rumex* but also *Plantago*) increased (Fig. 6). Archaeological evidence also points to the presence of settlements during the Bronze Age in the Cabañeros area (Jiménez García-Herrera et al., 2011), whose economy was apparently based on livestock raising (Ruiz-Taboada, 1997). Pastoral farming increased during Roman Times (ca.

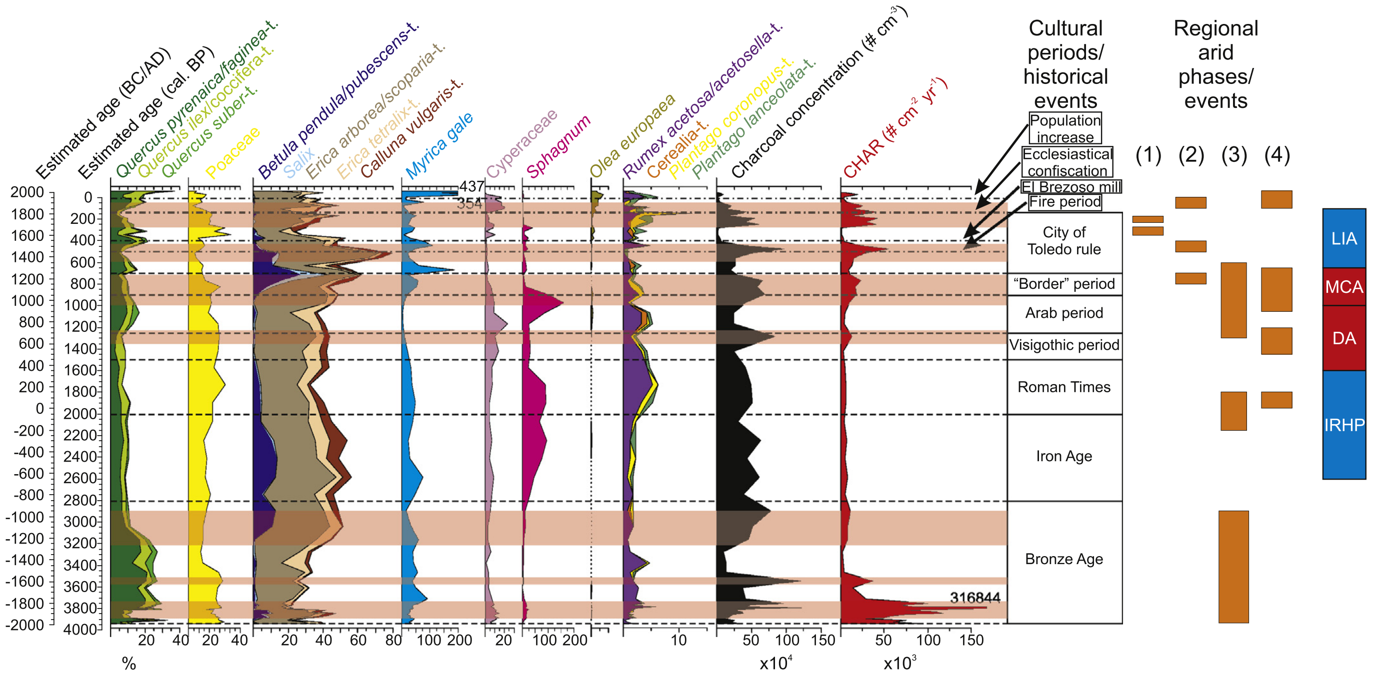

Fig. 6. Summary vegetation dynamics and their main ecological drivers at the El Brezoso mire. Bands in red depict periods of increasing fire activity. Dashed lines indicate the boundaries of the main cultural periods and dot-dashed lines show the dates of relevant historical events with consequences on land-use (according to Molénat, 1997; Jiménez de Gregorio, 2001; Jiménez García-Herrera et al., 2011; Perea et al., 2015). Orange boxes represent the main dry periods identified in south-western Iberia from vegetation-independent proxies: (1) severe droughts identified from the analysis of the rogation ceremonies of the Cathedral of Toledo (Domínguez-Castro et al., 2008), (2) low lake-level phases at Lagunillo del Tejo lake (Iberian Range) based on the isotopic composition of authigenic carbonates (López-Blanco et al., 2016), (3) dry phases from the multi-proxy study of Lake Zóñar (Martín-Puertas et al., 2008, 2009), (4) dry phases as reconstructed from the multi-proxy study of Cimera Lake (Sánchez-López et al., 2016). Finally, red boxes denote mostly dry regional periods whereas blue boxes represent predominantly humid regional phases. Abbreviations: t.: pollen type; CHAR: charcoal accumulation rate; LIA: Little Ice Age; MCA: Medieval Climate Anomaly; DA: Dark Ages; IRHP: Iberian Roman Humid Period

2000–1500 cal BP, 50 BC–AD 450), when pasturelands and disturbance-tolerant plants expanded (Poaceae, *Rumex*, *Plantago*; Fig. 6) under high grazing pressure (*Sporormiella*-t., *Sordaria*-t., *Podospora*-t. in Fig. 5). However, it was not until the Arab Period (ca. 1250–900 cal BP, AD 700–1050) that cereal-based agriculture intensified in Cabañeros (Figs. 4, 6). This 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).

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 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 the main driver for fire regime only quite recently, ca. 1300 cal BP (AD 650), by increasing the number of fire ignitions, under the dry conditions characteristic of the DA (Fig. 6; Martín-Puertas et al., 2008) promoting its spread. Palaeoecological records from the relatively close Cuenca Mountains and 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 et al., 2017). Nevertheless, it is likely that humans started to modify the natural 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; Vannière et al., 2011; Morales-Molino and García-Antón, 2014; Valbuena-Carabaña et al., 2010), but more evidence is needed.

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 950–1200- and 250–100 cal BP–AD 1700–1850-; Figs. 5, 6). When this area was the border between Al-Andalus and Castile (ca. 900–700 cal BP, AD 1050–1250; Jiménez García-Herrera et al., 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.

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), causing oak woodland retreat and the spread of pasturelands (Fig. 6). This increase in fire activity agrees with historical archives that registered a relevant incidence of fire in the Toledo Mountains during the 15th century AD to promote pastoral and arable farming (Sánchez-Benito, 2005). Transhumance 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 et al., 2015). Human-set fires seem to have propagated despite the existence of regulations trying to ban woodland clearance and burning and limiting livestock grazing (Redondo-García et al., 2003; Sánchez-Benito, 2005; Jiménez García-Herrera et al., 2011). Human impact further rose around El Brezoso at the end of the City of Toledo's rule (from ca. 400 cal BP, AD 1550, onwards) after the construction of a mill some hundred metres downstream (Perea et al., 2015). Overall, our palaeoecological data show that diversified land-use activities (e.g. cereal cultivation, grazing) first intensified well before the Ecclesiastical Confiscation (ca. 200–150 years ago, see Fig. 6), and then further increased after this period, resulting in increases of pastureland plants (Poaceae, *Rumex*, *Plantago*, Cichorioideae), disturbance-adapted shrubs (*Cistus*, *Erica australis*, Lamiaceae) and olive orchards (Figs. 3, 6). The recent spread of olive cultivation was a regionally widespread process in central and southern Iberia (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 fire. The recent recovery of oak woodlands at the top of our sequence results from the abandonment of charcoal production practices and goat raising in the last century, and the later protection of Cabañeros (Perea et al., 2015). Soil degradation during previous phases of high fire activity, grazing pressure and charcoal production probably favoured the stronger expansion of *Quercus ilex* coppices with respect to deciduous *Quercus* since ca. 300 cal BP (AD 1650) but especially during the last century (see Fig. 6). A similar *Quercus* expansion during the last centuries has been reported from the near Las Villuercas Mountains (Gil-Romera et al., 2008).

4.2. Mire vegetation dynamics

Peat accumulation began when arid conditions prevailed in southern Iberia according to available climate reconstructions (Carrión, 2002; Martín-Puertas et al., 2008; Jiménez-Moreno et al., 2013). Therefore, the start of peat formation at El Brezoso might have been related to geomorphologic processes 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 values at the base of the sequence) might have created an area of impeded drainage fed with groundwater that resulted in the establishment of a mire (see Fig. 5). Fire might have increased erosion and thus possibly landslide activity or alternatively soil hydrophobia (Pausas et al., 2008).

Our pollen record shows that most of the main hygrophilous plant taxa were present in the El Brezoso mire for the last 4000 years, surviving drought phases, disturbances and land-use changes (see Fig. 6). Even though wet heathlands (*Erica scoparia*, *Erica tetralix*, *Calluna vulgaris*) and *Myrica gale* thickets experienced several expansions and contractions during the last millennia, they always played a prominent role in mire vegetation (Figs. 5, 6). The persistence of these hygrophilous communities, although with oscillations related to dry periods (see Fig. 6), suggests that groundwater discharge may have buffered for millennia against reduced water availability as it is nowadays. This highlights the possible role of the El Brezoso mire as an interglacial "hydrologic microrefugium" (McLaughlin et al., 2017) from where relict hygrophilous species could spread during more favourable conditions. 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 pasturelands and/or cereal cultivation (Fig. 6). Local settlers might have cleared vegetation on the borders of the mire to grow cereals during dry periods because of higher soil moisture availability. Particularly severe clearances of *M. 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 1800–1900). The continuous record of Cerealia-t. pollen during the Arab period testifies for the intensification of cereal cultivation in close proximity to the mire, while high percentages of disturbance-tolerant herbs indicate pastureland expansion at the time of Ecclesiastical Confiscation (Fig. 6). *Sphagnum* bogs appear to have been even more responsive to climatic oscillations, tracking humid and dry phases and particularly those comprised within the IRHP (ca. 2600–1600 cal BP–650 BC–AD 350-, Fig. 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 (Figs. 5, 6).

Betula is a particularly interesting relict hygrophilous tree, since its dynamics did not follow climate changes at all but fire disturbance. Thus, birches established and/or expanded at El Brezoso valley during or following the periods of increased fire activity centred at ca. 3800 (1850 BC), 3000 (1050 BC) and 850 (AD 1100) cal BP, mostly at the expense of oak woodlands and meadows (Fig. 6). Likewise, birches were also favoured by fire in the Las Villuercas pollen record (Gil-Romera et al., 2008). *Betula* are very light-demanding trees whose seedlings cannot tolerate any competition during their early life stages (Atkinson, 1992; Sánchez del Álamo et al., 2010) and could have taken advantage of the reduced competition following wildfires to establish and/or spread on suitable microsites (see previous subsection). *Betula* decline at the Iron Age/Roman Times transition (ca. 2200–2100 cal BP, 250–150 BC) might have been caused by human-driven spread of pasturelands and grazing during a drier phase of the IRHP (Martín-Puertas et al., 2009), whereas the major demise at the beginning of the City of Toledo's rule was probably related to cereal cultivation and pastoral farming (Figs. 5, 6). This interpretation agrees well with the sensitivity of birches to browsing (Atkinson, 1992; Sánchez del Álamo et al., 2010). Also in the Toledo Mountains, the Valdeyernos mire pollen record shows that *Betula* has been an important component of the local vegetation over the last two thousand years accompanying the dominant *Corylus* (Dorado-Valiño et al., 2014b). This represents a major difference with our record, where *Corylus* is very rare (Fig. 3). Dorado-Valiño et al. (2014b) might have included *Myrica gale* pollen in the *Corylus*-type pollen curve, given the similarities between both pollen types (Punt et al., 2002). The botanical surveys conducted in the Valdeyernos area during the last decades (e.g. Gómez Manzaneque, 1988; Baonza Díaz et al., 2010) support this interpretation. First, *Corylus avellana* was not found in the surroundings of Valdeyernos since at least 30 years ago (see Gómez Manzaneque, 1988; Baonza Díaz et al., 2010). *Corylus avellana* is a relatively tall shrub, thus it seems highly unlikely that botanists have overlooked it, if present. Such an identification blunder appears extremely unlikely, particularly after the intensive sampling effort made by Baonza Díaz et al. (2010). Contrarily, *M. gale* grew locally in the Valdeyernos mire until at least AD 1986 (Gómez Manzaneque, 1988). However, in their 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 samples located immediately below, reflecting the period before and around AD 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 the west of El Brezoso, *Betula* declined much earlier, i.e. at ca. 3500 cal BP (1550 BC), probably because of the combined effect of climate warming and an intensification of human activities (Gil-Romera et al., 2008). All these data show that further research addressing in more detail the long-term impact of fire regimes and grazing on these southernmost populations of *Betula* is needed, given their sensitivity to browsing (Atkinson, 1992; Sánchez del Álamo et al., 2010) and to high fire incidence (Tinner et al., 2000; Gil-Romera et al., 2014). 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 socio-economic processes during the last millennium, and are far from pristine conditions. However, climate variability continued playing a relevant role even after human activities intensified in the Middle Ages. This new palaeoecological record adds to the great heterogeneity of vegetation trajectories in space and time that characterizes the Iberian Peninsula. Spatio-temporal heterogeneity makes it difficult, and possibly unpractical from a conservation perspective, predicting forthcoming vegetation successions. Our findings document land-use changes in the area and highlight the ecological and biogeographical role of mires as hydrologic microrefugia for several hygrophilous and temperate woody plants in the Toledo Mountains (e.g. *Myrica gale*, *Betula*). Given that mires have the potential of preserving unique population adaptations (genetic resources) to warmer/drier conditions, these mire habitats may result crucial for diversity conservation, particularly under the current context of anthropogenic climate change.

Palaeoecological records are increasingly used to address ongoing challenges in sustainability, forest management and biodiversity conservation (e.g. Willis and Birks, 2006; Colombaroli et al., 2013;

Morales-Molino et al., 2017a, 2017b; Whitlock et al., 2018). In key regions for nature conservation like the Toledo Mountains, long-term changes in ecosystems in combination with historical sources highlight the marked historical legacies on present ecosystems. Likewise, specific measures are needed for forest conservation and management when accounting for future scenarios of combined land-use abandonment and warmer temperatures that may endanger the persistence of important microrefugia for hygrophilous woody plants.

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References

Anderson, R.S., Jiménez-Moreno, G., Carrión, J.S., Pérez-Martínez, C., 2011. Postglacial history of alpine vegetation, fire, and climate from Laguna de Río Seco, Sierra Nevada, southern Spain. Quat. Sci. Rev. 30, 1615–1629.

Aranbarri, J., González-Sampériz, P., Valero-Garcés, B., Moreno, A., Gil-Romera, G., Sevilla-Callejo, M., García-Prieto, E., Di Rita, F., Mata, M.P., Morellón, M., Magri, D., Rodríguez-Lázaro, J., Carrión, J.S., 2014. Rapid climatic changes and resilient vegetation during the Lateglacial and Holocene in a continental region of south-western Europe. Glob. Planet. Chang. 114, 50–65.

Atkinson, M.D., 1992. Biological Flora of the British Isles. No. 175: *Betula pendula* Roth (*B. verrucosa* Ehrh.) and *B. pubescens*. J. Ecol. 80, 837–870.

Baker, A.G., Comelissen, P., Bhagwat, S.A., Vera, F.W.M., Willis, K.J., 2016. Quantification of population sizes of large herbivores and their long-term functional role in ecosystems using dung fungal spores. Methods Ecol. Evol. 7, 1273–1281.

Baonza Díaz, J., Caparrós Callejo, R., García Medina, N., Martínez García, F., Gómez Manzaneque, F., 2010. Flora vascular de los Quintos de Mora (Los Yébenes, Toledo). Ecología 23, 39–58.

Bennett, K.D., 1996. Determination of the number of zones in a biostratigraphical sequence. New Phytol. 132, 155–170.

Bennett, K.D., 2009. Documentation for PSIMPOLL 4.27 and PSCOMB 1.03. C Programs for Plotting and Analyzing Pollen Data. The 14 Chrono Centre, Archaeology and Palaeoecology. Queen's University of Belfast, Belfast, UK.

Beug, H., 2004. Leitfaden der Pollenbestimmung für Mitteleuropa un angrezende Gebiete. F. Pfeil Verlag, München.

Birks, H.J.B., Gordon, A.D., 1985. Numerical Methods in Quaternary Pollen Analysis. Academic Press, London.

Blaauw, M., 2010. Methods and code for 'classical' age-modelling of radiocarbon sequences. Quat. Geochronol. 5, 512–518.

Blondel, J., 2006. The 'design' of Mediterranean landscapes: a millennial story of humans and ecological systems during the historic period. Hum. Ecol. 34, 713–729.

Calvo, L., Santalla, S., Marcos, E., Valbuena, L., Tárrega, R., Luis, E., 2003. Regeneration after wildfire in communities dominated by *Pinus pinaster*, an obligate seeder, and in others dominated by *Quercus pyrenaica*, a typical resprouter. For. Ecol. Manag. 184, 209–223.

Carrión, J.S., 2002. Patterns and processes of Late Quaternary environmental change in a montane area of southwestern Europe. Quat. Sci. Rev. 21, 2047–2066.

Carrión, J.S. (Ed.), 2012. Paleoflora y paleovegetación de la península Ibérica e islas Baleares: Plioceno-Cuaternario. Ministerio de Economía y Competitividad, Murcia, Spain (coord.).

Carrión, J.S., Andrade, A., Bennett, K.D., Navarro, C., Munuera, M., 2001. Crossing forest thresholds: inertia and collapse in a Holocene sequence from south-central Spain. The Holocene 11, 635–653.

Carrión, J.S., Sánchez-Gómez, P., Mota, J.F., Yll, R., Chaín, C., 2003. Holocene vegetation dynamics, fire and grazing in the Sierra de Gádor, southern Spain. The Holocene 13, 839–849.

Carrión, J.S., Fuentes, N., González-Sampériz, P., Sánchez-Quirante, L., Finlayson, J.-C., Fernández, S., Andrade, A., 2007. Holocene environmental change in a montane region of southern Europe with a long history of human settlement. Quat. Sci. Rev. 26, 1455–1475.

Carrión, J.S., Fernández, S., González-Sampériz, P., Gil-Romera, G., Badal, E., Carrión-Marco, Y., López-Merino, L., López-Sáez, J.A., Fierro, E., Burjachs, F., 2010a. Expected trends and surprises in the Lateglacial and Holocene vegetation history of the Iberian Peninsula and Balearic Islands. Rev. Palaeobot. Palynol. 162, 458–475.

Carrión, J.S., Fernández, S., Jiménez-Moreno, G., Fauquette, S., Gil-Romera, G., González-Sampériz, P., Finlayson, C., 2010b. The historical origins of aridity and vegetation degradation in southeastern Spain. J. Arid Environ. 74, 731–736.

Colombaroli, D., Tinner, W., 2013. Determining the long-term changes in biodiversity and provisioning services along a transect from Central Europe to the Mediterranean. The Holocene 23, 1625–1634.

Colombaroli, D., Marchetto, A., Tinner, W., 2007. Long-term interactions between Mediterranean climate, vegetation, and fire regime at Lago di Massaciuccoli (Tuscany, Italy). J. Ecol. 95, 755–770.

Colombaroli, D., Vannière, B., Chapron, E., Magny, M., Tinner, W., 2008. Fire–vegetation interactions during the Mesolithic–Neolithic transition at Lago dell'Accesa, Tuscany, Italy. The Holocene 18, 679–692.

Colombaroli, D., Tinner, W., van Leeuwen, J., Noti, R., Vescovi, E., Vannière, B., Magny, M., Schmidt, R., Bugmann, H., 2009. Response of broadleaved evergreen Mediterranean forest vegetation to fire disturbance during the Holocene: insights from the peri-Adriatic region. J. Biogeogr. 36, 314–326.

Colombaroli, D., Beckmann, M., van der Knaap, W.O., Curdy, P., Tinner, W., 2013. Changes in biodiversity and vegetation composition in the central Swiss Alps during the transition from pristine forest to first farming. Divers. Distrib. 19, 157–170.

Conedera, M., Tinner, W., Neff, C., Meurer, M., Dickens, A.F., Krebs, P., 2009. Reconstructing past fire regimes: methods, applications, and relevance to fire management and conservation. Quat. Sci. Rev. 28, 435–456.

Corella, J.P., Stefanova, V., El Anjoumi, A., Rico, E., Giralt, S., Moreno, A., Plata-Montero, A., Valero-Garcés, B.L., 2013. A 2500-year multi-proxy reconstruction of climate and human activities in northern Spain: the Lake Arreo record. Palaeogeogr. Palaeoclimatol. Palaeoecol. 386, 555–568.

Costa, M., Morla, C., Sainz, H. (Eds.), 2005. Los bosques ibéricos. Una interpretación geobotánica. Ed. Planeta, Barcelona, Spain.

Domínguez-Castro, F., Santisteban, J.I., Barriendos, M., Mediavilla, R., 2008. Reconstruction of drought episodes for central Spain from rogation ceremonies recorded at the Toledo Cathedral from 1506 to 1900: a methodological approach. Glob. Planet. Chang. 63, 230–242.

Dorado-Valiño, M., Valdeolmillos, A., Ruiz-Zapata, M.B., Gil-García, M.J., de Bustamante, I., 2002. Climate changes since the La-Glacial/Holocene transition in La Mancha Plain (South-central Iberian Peninsula, Spain) and their incidence on Las Tablas de Daimiel marshlands. Quat. Int. 93-94, 73–84.

Dorado-Valiño, M., López-Sáez, J.A., García-Gómez, E., 2014a. Contributions to the European Pollen Database: 21. Patateros, Toledo Mountains (central Spain). Grana 53, 171–173.

Dorado-Valiño, M., López-Sáez, J.A., García-Gómez, E., 2014b. Contributions to the European Pollen Database: 26. Valdeyernos, Toledo Mountains (central Spain). Grana 53, 315–317.

Espelta, J.M., Retana, J., Habrouk, A., 2003. Resprouting patterns after fire and response to stool cleaning of two coexisting Mediterranean oaks with contrasting leaf habits on two different sites. For. Ecol. Manag. 179, 401–414.

Finsinger, W., Tinner, W., 2005. Minimum count sums for charcoal-concentration estimates in pollen slides: accuracy and potential errors. The Holocene 15, 293–297.

Franco-Múgica, F., García-Antón, M., Maldonado-Ruiz, J., Morla-Juaristi, C., Sainz-Ollero, H., 2001. The Holocene history of *Pinus* forests in the Spanish Northern Meseta. The Holocene 11, 343–358.

Gao, X., Giorgi, F., 2008. Increased aridity in the Mediterranean region under greenhouse gas forcing estimated from high resolution simulations with a regional climate model. Glob. Planet. Chang. 62, 195–209.

García-Antón, M., Morla, C., Ruiz-Zapata, B., Sainz Ollero, H., 1986. Contribución al conocimiento del paisaje vegetal holoceno en la submeseta sur ibérica: análisis polínico de sedimentos higroturbosos en el Campo de Calatrava (Ciudad Real, España). In: López Vera, F. (Ed.), Quaternary Climate in Western Mediterranean. Publicaciones de la Universidad Autónoma de Madrid, Madrid, pp. 189–204.

Gil-García, M.J., Ruiz-Zapata, M.B., Santisteban, J.I., Mediavilla, R., López-Pamo, E., Dabrio, C.J., 2007. Late Holocene environments in Las Tablas de Daimiel (south central Iberian Peninsula, Spain). Veg. Hist. Archaeobotany 16, 241–250.

Gil-Romera, G., García-Antón, M., Calleja, J.A., 2008. The late Holocene palaeoecological sequence of Serranía de las Villuercas (southern Meseta, western Spain). Veg. Hist. Archaeobotany 17, 653–666.

Gil-Romera, G., González-Sampériz, P., Lasheras-Álvarez, L., Sevilla-Callejo, M., Moreno, A., Valero-Garcés, B., López-Merino, L., Carrión, J.S., Pérez-Sanz, A., Aranbarri, J., García-Prieto Fronce, E., 2014. Biomass-modulated fire dynamics during the Last Glacial-Interglacial Transition at the Central Pyrenees (Spain). Palaeogeogr. Palaeoclimatol. Palaeoecol. 402, 113–124.

Giorgi, F., Lionello, P., 2008. Climate change projections for the Mediterranean region. Glob. Planet. Chang. 63, 90–104.

Gómez de Llarena, J., 1916. Bosquejo Geográfico-Geológico de los Montes de Toledo. Trabajos del Museo Nacional de Ciencias Naturales (Serie Geológica) vol. 15 (Madrid, 74 pp).

Gómez Manzaneque, F., 1988. La cubierta vegetal de los Montes de Mora (Los Yébenes, Toledo). Ecología 2, 111–130.

González-Sampériz, P., Aranbarri, J., Pérez-Sanz, A., Gil-Romera, G., Moreno, A., Leunda, M., Sevilla-Callejo, M., Corella, J.P., Morellón, M., Oliva, B., Valero-Garcés, B., 2017. Environmental and climate change in the southern Central Pyrenees since the Last Glacial Maximum: a view from the lake records. Catena 149, 668–688.

Henne, P.D., Elkin, C., Colombaroli, D., Samartin, S., Bugmann, H., Heiri, O., Tinner, W., 2013. Impacts of changing climate and land use on vegetation dynamics in a Mediterranean ecosystem: insights from paleoecology and dynamic modeling. Landsc. Ecol. 28, 819–833.

Herrera, J., 1988. Pollination relationships in southern Spanish Mediterranean shrublands. J. Ecol. 76, 274–287.

Hua, Q., Barbetti, M., Rakowski, A.Z., 2013. Atmospheric radiocarbon for the period 1950–2010. Radiocarbon 55, 2059–2072.

Jackson, S.T., Kearsley, J.B., 1998. Quantitative representation of local forest composition in forest-floor pollen assemblages. J. Ecol. 86, 474–490.

Jiménez de Gregorio, F., 2001. La comarca histórica de los Montes de Toledo. Publicaciones del Instituto Provincial de Investigación y Estudios Toledanos serie VI: Temas Toledanos vol. 100. Diputación de Toledo, Toledo, Spain.

Jiménez García-Herrera, J., Carrasco Redondo, M., Gómez Manzaneque, Á., Bonache López, J., Fernández Valero, E., 2011. Guía de visita del Parque Nacional de Cabañeros. Organismo Autónomo de Parques Nacionales, Madrid.

Jiménez-Moreno, G., García-Alix, A., Hernández-Corbalán, M.D., Anderson, R.S., Delgado-Huertas, A., 2013. Vegetation, fire, climate and human disturbance history in the southwestern Mediterranean area during the late Holocene. Quat. Res. 79, 110–122.

López-Blanco, C., Gaillard, M.-J., Miracle, M.R., Vicente, E., 2012. Lake-level changes and fire history at Lagunillo del Tejo (Spain) during the last millennium: climate or humans? The Holocene 22, 551–560.

López-Blanco, C., Andrews, J., Dennis, P., Miracle, M.R., Vicente, E., 2016. North Atlantic Oscillation recorded in carbonate δ^{18}O signature from Lagunillo del Tejo. Palaeogeogr. Palaeoclimatol. Palaeoecol. 441, 882–889.

López-Sáez, J.A., Abel-Schaad, D., Pérez-Díaz, S., Blanco-González, A., Alba-Sánchez, F., Dorado, M., Ruiz-Zapata, B., Gil-García, M.J., Gómez-González, C., Franco-Múgica, F., 2014a. Vegetation history, climate and human impact in the Spanish Central System over the last 9000 years. Quat. Int. 353, 98–122.

López-Sáez, J.A., García-Río, R., Alba-Sánchez, F., García-Gómez, E., Pérez-Díaz, S., 2014b. Peatlands in the Toledo Mountains (central Spain): characterisation and conservation status. Mires and Peat 15, 1–23 (Article 04).

López-Sáez, J.A., Vargas, G., Ruiz-Fernández, J., Blarquez, O., Alba-Sánchez, F., Oliva, M., Pérez-Díaz, S., Robles-López, S., Abel-Schaad, D., 2017. Paleofire dynamics in central Spain during the late Holocene: the role of climatic and anthropogenic forcing. Land Degrad. Dev. https://doi.org/10.1002/ldr.2751.

Luelmo-Lautenschlaeger, R., López-Sáez, J.A., Pérez-Díaz, S., 2018a. Contributions to the European Pollen Database 39. Las Lanchas, Toledo Mountains (Central Spain). Grana 57, 246–248.

Luelmo-Lautenschlaeger, R., López-Sáez, J.A., Pérez-Díaz, S., 2018b. Contributions to the European Pollen Database 40. Botija, Toledo Mountains (Central Spain), Grana. https://doi.org/10.1080/00173134.2017.1400587.

Martín-Puertas, C., Valero-Garcés, B.L., Mata, M.P., González-Sampériz, P., Bao, R., Moreno, A., Stefanova, V., 2008. Arid and humid phases in southern Spain during the last 4000 years: the Zoñar Lake record. The Holocene 18, 907–921.

Martín-Puertas, C., Valero-Garcés, B.L., Brauer, A., Mata, M.P., Delgado-Huertas, A., Dulski, P., 2009. The Iberian–Roman Humid Period (2600–1600 cal yr BP) in the Zoñar Lake varve record (Andalusia, southern Spain). Quat. Res. 71, 108–120.

McLaughlin, B.C., Ackerly, D.D., Klos, P.Z., Natali, J., Dawson, T.E., Thompson, S.E., 2017. Hydrologic refugia, plants, and climate change. Glob. Chang. Biol. 23, 2941–2961.

Molénat, J.-P., 1997. Campagnes et monts de Tolède du XII^{e} au XV^{e} siècle. Casa de Velázquez. vol. 63 (Madrid, Spain).

Moore, P.D., Webb, J.A., Collinson, M.E., 1991. Pollen Analysis. Blackwell Scientific Publications, Oxford, UK.

Morales-Molino, C., García-Antón, M., 2014. Vegetation and fire history since the last glacial maximum in an inland area of the western Mediterranean Basin (Northern Iberian Plateau, NW Spain). Quat. Res. 81, 63–77.

Morales-Molino, C., García-Antón, M., Postigo-Mijarra, J.M., Morla, C., 2013. Holocene vegetation, fire and climate interactions on the westernmost fringe of the Mediterranean Basin. Quat. Sci. Rev. 59, 5–17.

Morales-Molino, C., Tinner, W., García-Antón, M., Colombaroli, D., 2017a. The historical demise of *Pinus nigra* forests in the Northern Iberian Plateau (south-western Europe). J. Ecol. 105, 634–646.

Morales-Molino, C., Colombaroli, D., Valbuena-Carabaña, M., Tinner, W., Salomón, R.L., Carrión, J.S., Gil, L., 2017b. Land-use history as a major driver for long-term forest dynamics in the Sierra de Guadarrama National Park (central Spain) during the last millennia: implications for forest conservation and management. Glob. Planet. Chang. 152, 64–75.

Morellón, M., Valero-Garcés, B., Vegas-Vilarrúbia, T., González-Sampériz, P., Romero, Ó., Delgado-Huertas, A., Mata, P., Moreno, A., Rico, M., Corella, J.P., 2009. Lateglacial and Holocene palaeohydrology in the western Mediterranean region: the lake Estanya record (NE Spain). Quat. Sci. Rev. 28, 2582–2599.

Moreno, A., Pérez, A., Frigola, J., Nieto-Moreno, V., Rodrigo-Gámiz, M., Martrat, B., González-Sampériz, P., Morellón, M., Martín-Puertas, C., Corella, J.P., Belmonte, Á., Sancho, C., Herrera, G., Canals, M., Grimalt, J.O., Jiménez-Espejo, F., Martínez-Ruiz, F., Vegas-Vilarrúbia, T., Valero-Garcés, B.L., 2012. The Medieval Climate Anomaly in the Iberian Peninsula reconstructed from marine and lake records. Quat. Sci. Rev. 43, 16–32.

Pausas, J.G., 1997. Resprouting of *Quercus suber* in NE Spain after fire. J. Veg. Sci. 8, 703–706.

Pausas, J.G., Llovet, J., Rodrigo, A., Vallejo, R., 2008. Are wildfires a disaster in the Mediterranean basin? A review. Int. J. Wildland Fire 17, 713–723.

Perea, L., Gil, L., 2014. Shrubs facilitating seedling performance in ungulate-dominated systems: biotic versus abiotic mechanisms of plant facilitation. Eur. J. For. Res. 133, 525–534.

Perea, D.F., Perea, R., 2008. Vegetación y Flora de los Montes de Toledo. Ed. Covarrubias, Toledo, Spain.

Perea, R., Perea, D.F., Giménez, G.F., 2015. Vegetación y Flora del Parque Nacional de Cabañeros, vol. I. El paisaje vegetal: ecología, conservación y rutas de interés geobotánico. Organismo Autónomo de Parques Nacionales, Madrid.

Prentice, I.C., 1985. Pollen representation, source area, and basin size: towards a unified theory of pollen analysis. Quat. Res. 23, 76–86.

Punt, W., Marks, A., Hoen, P.P., 2002. The Northwest European pollen flora, 66: Myricaceae. Rev. Palaeobot. Palynol. 123, 99–105.

Ramil-Rego, P., Aira-Rodríguez, M.J., Saá-Otero, P., 1992. Clave polínica de las Ericaceae gallegas. Lazaroa 13, 33–40.

Ramos-Román, M.J., Jiménez-Moreno, G., Anderson, R.S., García-Alix, A., Torney, J.L., Jiménez-Espejo, F.J., Carrión, J.S., 2016. Centennial-scale vegetation and North Atlantic Oscillation changes during the Late Holocene in southern Iberia. Quat. Sci. Rev. 143, 84–95.

Redondo-García, M.M., Ferreras-Chasco, C., González-Baselga, I., 2003. Breve cronología histórica forestall de Hontanar y San Pablo de los Montes (Toledo, España). Cuadernos de la Sociedad Española de Ciencias Forestales 16, 179–184.

Reille, M., 1992. Pollen et spores d'Europe et d'Afrique du Nord. Laboratoire de botanique historique et palynologie, Marseille, France.

Reimer, P.J., Bard, E., Bayliss, A., Beck, J.W., Blackwell, P.G., Bronk Ramsey, C., Buck, C.E., Cheng, H., Edwards, R.L., Friedrich, M., Grootes, P.M., Guilderson, T.P., Haflidason, H., Hajdas, I., Hatté, C., Heaton, T.J., Hoffmann, D.L., Hogg, A.G., Hughen, K.A., Kaiser, K.F., Kromer, B., Manning, S.W., Niu, M., Reimer, R.W., Richards, D.A., Scott, E.M., Southon, J.R., Staff, R.A., Turney, C.S.M., van der Plicht, J., 2013. IntCal13 and Marine13 radiocarbon age calibration curves 0–50,000 years cal BP. Radiocarbon 55, 1869–1887.

Rubiales, J.M., García-Amorena, I., Hernández, L., Génova, M., Martínez, F., Gómez Manzaneque, F., Morla, C., 2010. Late Quaternary dynamics of pinewoods in the Iberian Mountains. Rev. Palaeobot. Palynol. 162, 476–491.

Ruiz-Taboada, A., 1997. Asentamiento y subsistencia en La Mancha durante la Edad del Bronce: el sector noroccidental como modelo. Complutum 8, 57–71.

Sánchez del Álamo, C., Sardinero, S., Bouso, V., Hernández Palacios, G., Pérez Badia, R., Fernández-González, F., 2010. Los abedulares del Parque Nacional de Cabañeros: sistemática, demografía, biología reproductiva y estrategias de conservación. Proyectos de Investigación en Parques Nacionales: 2006–2009, Organismo Autónomo de Parques Nacionales, Ministerio de Agricultura, Alimentación y Medio Ambiente, Madrid, pp. 275–309.

Sánchez-Benito, J.M., 2005. La Hermandad de los Montes de Toledo entre los siglos XIV y XV. Espacio, Tiempo y Forma, serie III, Historia Medieval, t. 18, pp. 209–229.

Sánchez-López, G., Hernández, A., Pla-Rabes, S., Trigo, R.M., Toro, M., Granados, I., Sáez, A., Masqué, P., Pueyo, J.J., Rubio-Inglés, M.J., Giralt, S., 2016. Climate reconstruction for the las two millennia in central Iberia: the role of East Atlantic (EA), North Atlantic Oscillation (NAO) and their interplay over the Iberian Peninsula. Quat. Sci. Rev. 149, 135–150.

Stähli, M., Finsinger, W., Tinner, W., Allgöwer, B., 2006. Wildfire history and fire ecology of the Swiss National Park (Central Alps): new evidence from charcoal, pollen and plant macrofossils. The Holocene 16, 805–817.

Stockmarr, J., 1971. Tablets with spores used in absolute pollen analysis. Pollen Spores 13, 615–621.

Sugita, S., 1994. Pollen representation of vegetation in Quaternary sediments: theory and method in patchy vegetation. J. Ecol. 82, 881–897.

Tinner, W., Hu, F.S., 2003. Size parameters, size-class distribution and area-number relationship of microscopic charcoal: relevance for fire reconstruction. The Holocene 13, 499–505.

Tinner, W., Conedera, M., Ammann, B., Gaggeler, H.W., Gedye, S., Jones, R., Sagesser, B., 1998. Pollen and charcoal in lake sediments compared with historically documented forest fires in southern Switzerland since AD 1920. The Holocene 8, 31–42.

Tinner, W., Conedera, M., Gobet, E., Hubschmid, P., Wehrli, M., Ammann, B., 2000. A palaeoecological attempt to classify fire sensitivity of trees in the southern Alps. The Holocene 10, 565–574.

Tinner, W., van Leeuwen, J.F.N., Colombaroli, D., Vescovi, E., van der Knaap, W.O., Henne, P.D., Pasta, S., D'Angelo, S., La Mantia, T., 2009. Holocene environmental and climatic changes at Gorgo Basso, a coastal lake in southern Sicily, Italy. Quat. Sci. Rev. 28, 1498–1510.

Urbieta, I.R., Zavala, M.Á., Marañón, T., 2008. Human and non-human determinants of forest composition in southern Spain: evidence of shifts towards cork oak dominance as a result of management over the last century. J. Biogeogr. 35, 1688–1700.

Valbuena-Carabaña, M., López de Heredia, U., Fuentes-Utrilla, P., González-Doncel, I., Gil, L., 2010. Historical and recent changes in the Spanish forests: A socio-economic process. Rev. Palaeobot. Palynol. 162, 492–506.

Valsecchi, V., Carraro, G., Conedera, M., Tinner, W., 2010. Late-Holocene vegetation and land-use dynamics in the Southern Alps (Switzerland) as a basis for nature protection and forest management. The Holocene 20, 483–495.

Van Geel, B., Buurman, J., Brinkkemper, O., Schelvis, J., Aptroot, A., van Reenen, G., Hakbijl, T., 2003. Environmental reconstruction of a Roman Period settlement site in Uitgeest (The Netherlands), with special reference to coprophilous fungi. J. Archaeol. Sci. 30, 873–883.

Vannière, B., Power, M.J., Roberts, N., Tinner, W., Carrión, J., Magny, M., Bartlein, P., Colombaroli, D., Daniau, A.L., Finsinger, W., Gil-Romera, G., Kaltenrieder, P., Pini, R., Sadori, L., Turner, R., Valsecchi, V., Vescovi, E., 2011. Circum-Mediterranean fire activity and climate changes during the mid-Holocene environmental transition (8500–2500 cal. BP). The Holocene 21, 53–73.

Vaquero, J., 1993. Flora del Parque Natural de Cabañeros (Montes de Toledo, Ciudad Real). Ecología 7, 79–111.

Vaquero, J., 2010. Situación actual y estudio comparativo de los trampales del Parque Nacional de Cabañeros. Ed. P.N. de Cabañeros, Pueblonuevo de Bullaque, Spain.

Whitlock, C., Colombaroli, D., Conedera, M., Tinner, W., 2018. Land-use history as a guide for forest conservation and management. Conserv. Biol. 32, 84–97.

Willis, K.J., Birks, H.J.B., 2006. What is natural? The need for a long-term perspective in biodiversity conservation. Science 314, 1261–1265.