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

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ABSTRACT

Understanding ecosystem resilience requires long data series provided by palaeoecological studies, the best tool for reconstructing vegetation dynamics. Here, we analyzed a continuous and well-dated record of pollen, non-pollen palynomorphs, macrocharcoal remains, loss-on-ignition and magnetic susceptibility from one of the most singular peatlands in the Toledo Mountains (central Spain), in order to delineate the anthropogenic and/or climate impact on the peatland and the ecosystem's response. La Ventilla mire is an isolated site of birch woodland dominated by *Betula pubescens* subsp. *celtiberica* (Rothm. & Vasc.) Rivas Mart. This mire, acting as a refugium for this species, is located in Cabañeros National Park and is recognized as 'Special Area of Conservation' according to Habitats Directive of the Natura 2000 network. We describe major patterns and trends in the development of this palaeorefugium since the mid-Holocene (~6145 cal BP) and provide historical context for some natural and/or human-induced dynamics. Around 1500 cal BP, the lotic depositional environment with slow moving backwaters developed into a minerotrophic mire. Until the Middle Ages, macroclimate and autogenic succession appear to have been the main drivers of both local and regional development of vegetation. Between 1500 and 500 cal BP, an abrupt decline in birch cover started, coincident with the Visigothic period. The pronounced peaks in the coprophilous fungi record *ca.* 1000 and 150 cal BP reflect extensive pastoral activities in the area. This study shows how palaeoecological knowledge helps to explain present patterns in the composition of a valuable protected site, which may be used in prioritizing conservation.

1. Introduction

Marginal plant populations are usually located at the edge of the species' range and/or compose, isolated communities thriving in reduced favorable microhabitats within an overall environmentally unsuitable matrix (Lesica and Allendorf, 1995). These assemblages

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usually bear valuable genetic resources resulting from the adaptation to the 'unusual' (considering the entire distribution range of the species) local ecological conditions (Ellstrand and Elam, 1993; Petit et al., 1998; Hewitt, 2000). For instance, Mediterranean relict populations of temperate and boreal tree species often harbor unique genotypes (Hampe and Petit, 2005). The 'marginality' of these populations may be due to past environmental changes and anthropogenic impacts causing repeated shifts in species composition and habitat distributions, and eventually leading to the formation of island-like habitats (Web III, 1986; Benito-Garzón et al., 2008; Birks and Willis, 2008; Giesecke et al., 2017). Current marginal plant populations and communities may represent remnants of once more widespread distributions affected by fragmentation processes or, on the contrary, habitats or populations established recently in an area where they were previously absent, i.e. 'palaeorefugia' or 'neorefugia', respectively (Comes and Kadereit, 1998; Hewitt, 1999; Nekola, 1999). The unique features of such communities due to their fragmentation and isolation usually imply adopting specific management measures to ensure their conservation (Pulido et al., 2008; Sanz et al., 2009, 2011).

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

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

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

Land-use history has been a major driver of forest dynamics, composition and diversity in many Mediterranean mountain regions of southwestern Europe during the Holocene (Carrión, 2002; López-Merino et al., 2008; Carrión et al., 2010, 2013, 2015, 2018; González-Sampériz et al., 2010; Morales-Molino et al., 2017, 2021; Aranbarri et al., 2014; López-Sáez et al., 2014a; Camuera et al., 2018, 2019; Mesa-Fernández et al., 2018). Therefore, ecosystem 'authenticity' (Larsen, 1995), that is proximity to a 'pristine state' (Bradshaw, 2005), or otherwise, continuity, the absence of direct anthropogenic intervention in forest dynamics for long periods, is usually considered of high conservation value (Birks, 2012). On the other hand, disturbance regimes, particularly the frequency and type of disturbance are also relevant to forest diversity (Crandall et al., 2000). Thus, approaching local forest history under the light of palaeoecology is essential to assess which ecological factors are responsible for the current conservation status. The few long-term stand-scale studies that have been conducted in the Toledo Mountains so far suggest that fire history and, in recent times, the overabundance of wild ungulates after human disturbance have altered their population dynamics entailing major impacts on present forest attributes (Morales-Molino et al., 2018, 2019; Luelmo-Lautenschlaeger et al., 2019a). In this regard, the case of birch stands (*Betula* spp.) growing on peatlands and water streams in the Toledo Mountains is paradigmatic. These wetland ecosystems are currently under heavy grazing pressure, as abundant wild ungulates roam mostly uncontrolled (Acebedo et al., 2008; Muñoz et al., 2009; Perea and Gil, 2014). In fact, this is a major threat to several ecosystems worldwide, including many areas of the Toledo Mountains (Perea et al., 2014). While the response of forest vegetation to high density of herbivores has been well studied, responses of peatland vegetation are far less known (Pellerin et al., 2006; Balbo et al., 2017). Another major human impact on the birch populations of Toledo Mountains is groundwater exploitation for irrigation of the adjacent fields, which is lowering the water table in the peatlands (Rodríguez-Rodríguez and Martínez-Vega, 2017).

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

Ventilla', Cabañeros National Park) is the southernmost known Iberian population known (Sánchez del Álamo et al., 2010; Perea et al., 2015).

Birches have played a fundamental role in the Late Pleistocene and Holocene vegetation of northern Iberia (Carrión et al., 2010; Ochando et al., 2020a, 2020b). However, their importance in the landscape decreases southwards in the Mediterranean mountains (but see e.g. Franco et al., 1998; Morales-Molino et al., 2013). For example, birch forests dominated during the Lateglacial and the early Holocene in the Northern Iberian Range and the western Iberian Central System thanks to their pioneer and heliophilous character, forming mixed woodlands with pines or oaks, becoming rarer from the mid-Holocene onwards when they were restricted to mountain streams (López-Merino et al., 2008; Morales-Molino et al., 2013; Abel-Schaad et al., 2014; López-Sáez et al., 2014a). In contrast, birches expanded to some extent during the mid-Holocene, disappearing during the late Holocene (Carrión et al., 2013, 2015, 2018). In the Toledo Mountains, currently available palaeobotanical evidence demonstrates the past importance of birch groves (Morales-Molino et al., 2018, 2019; Luelmo-Lautenschlaeger et al., 2018a, 2018d, 2019a, 2019b, 2020). These were generally associated to peatland ecosystems, which were much more extensive than today as they have declined in recent millennia due to both climate change and human impact.

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

2. Regional settings

The study was conducted in the Cabañeros National Park, a protected area of 40,856 ha located on the southern slopes of the Toledo Mountains (Castilla-La Mancha, central-southern Spain; Fig. 1). The Cabañeros National Park is structured into two large units (Jiménez, 2004): i) the lowland area or 'raña' is a great plain of ~8000 ha located in the southeast where the current landscape of wooded grasslands originated after forests were cleared to grow cereal crops in the 1960s; ii) the mountainous area (650–1448 m a.s.l.) covers the rest of Cabañeros, and its vegetation is characterized by fragmented Mediterranean oak forests, shrublands (*Cistus ladanifer* L., *Genista hirsuta* Vahl, *Phillyrea angustifolia* L. and *Erica* spp.), pastures, crops, scree slopes and, to a lesser extent, pine afforestation (Perea and Perea, 2008). The National Park has a remarkably diverse vegetation that includes mainly Mediterranean oak woodlands with the evergreen *Q. ilex* L. subsp.

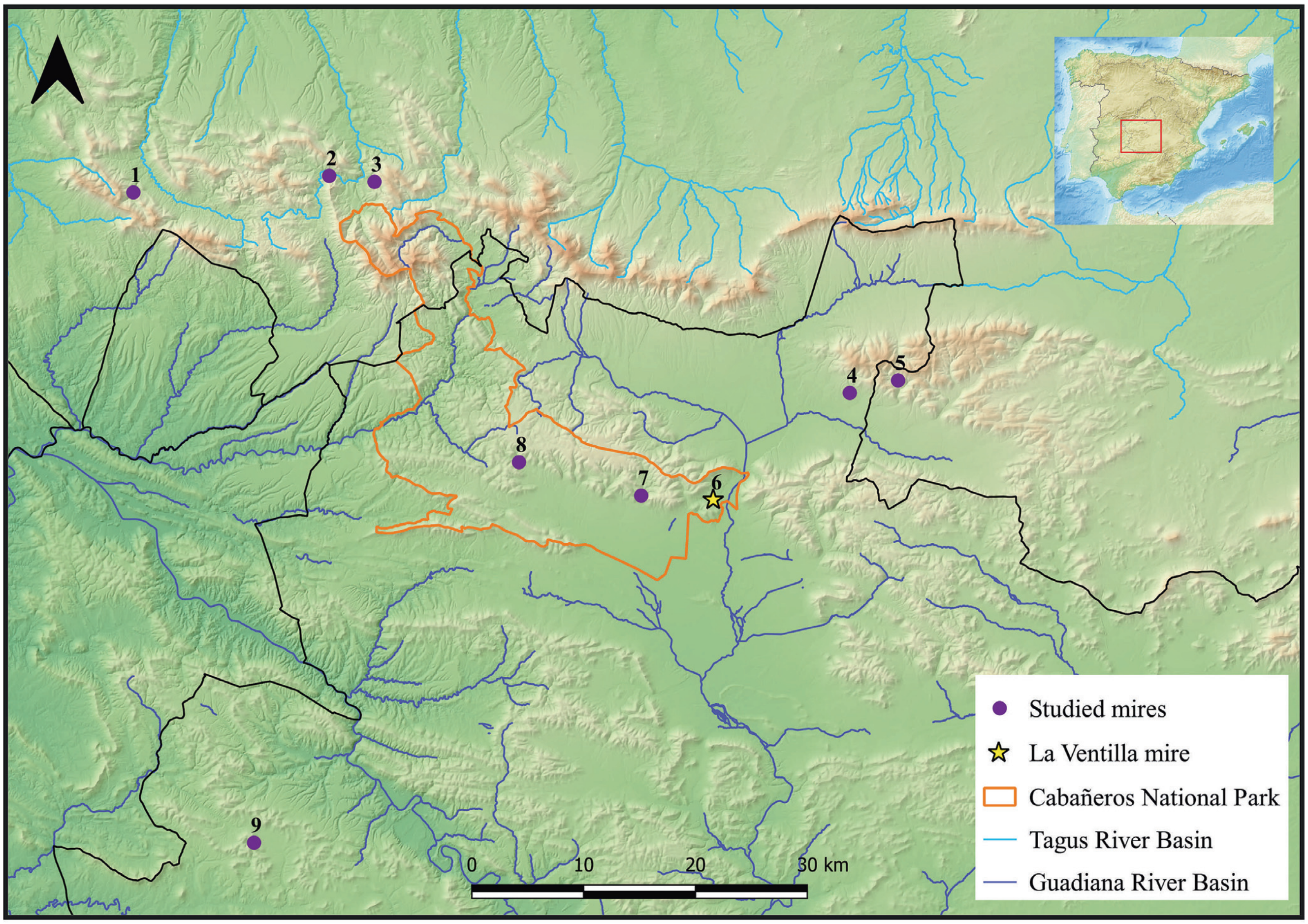

Fig. 1. Location of the study site (yellow star) and other pollen records (purple circles) from the Toledo Mountains mentioned in the text: 1, Las Lanchas; 2, Botija; 3, Patateros; 4, Bermú; 5, Valdeyernos; 6, La Ventilla; 7, El Brezoso; 8, Las Viñuelas; 9, El Perro.

ballota (Desf.) Samp. and *Q. suber* L., and the deciduous *Q. faginea* Lam. subsp. *broteroi* (Cout.) A. Camus, as dominant tree species (Vaquero, 1993; Perea et al., 2015). Additionally, stands of the deciduous *Quercus pyrenaica* Willd. cover some meso-Mediterranean valleys on deep and moist soils and dominate at higher elevation in the supra-Mediterranean belt. The climate is sub-humid continental Mediterranean, with mean annual temperature and precipitation of 13.7 °C and 699 mm, respectively (Sánchez-Palomares et al., 1999) with dry/hot summers and wet/mild winters. The main human impacts in this area were livestock grazing, farming, logging, and charcoal production (Perea and Perea, 2008; López-Sáez et al., 2014c). Today, there is no domestic ungulate (livestock) grazing in this National Park. Red deer (*Cervus elaphus* L.) and wild boar (*Sus scrofa* L.) are the main wild ungulates, whereas roe deer (*Capreolus capreolus* L.) are scarce. Current densities of wild ungulates in the eastern area of the National Park are high (red deer 12–78.5 individuals/km^2, wild boar ~10 individuals/km^2; Linares and Urivelarrea, 2021). Browsing, trampling, and wild boar uprooting are considered important limiting factors for the regeneration of many palatable woody plants (Perea and Gil, 2014; Perea et al., 2014).

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

3. Material and methods

3.1. Core sampling, lithology and chronology

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

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

Loss-on-ignition (LOI) analysis, based on heating of the dry samples at 550 °C in a muffle furnace for 4 h (Heiri et al., 2001), was carried out for 1-cm^3 volumetric samples taken contiguously at 2-cm resolution along the profile. The values of LOI for each sample were calculated according to the formula: $LOI_{550} = ((DW_{105}–DW_{550})/DW105)$ x 100%, where LOI_{550} represents LOI at 550 °C (as a percentage), DW_{105} is the dry weight of the sample (wet samples were dried at 105 °C during 12 h before combustion), and DW_{550} is the dry weight of the sample after heating to 550 °C (Heiri et al., 2001). LOI_{550} is thus expressed as a percentage of weight loss in dried sediment (Fig. 2). Magnetic susceptibility (MS) was measured at 1-cm resolution using a Bartington sensor MS2E (Bartington Instruments, Ltd, Whitney, UK) following standard procedures (Walden et al., 1999).

To reconstruct fire history, 1-cm thick sediment samples of 1 cm^3 were taken contiguously throughout the core according to the recommendations of Whitlock and Larsen (2001). Macroscopic charcoal particles were then counted assuming they have local origin (<10 km) (Carcaillet et al., 2001; Finsinger et al., 2014). Charcoal samples were soaked in a 10% KOH solution during 24 h and then in 15% H_2O_2 for 24 h more, to remove and bleach uncharred organic matter. The sediment was then sieved using a 125-μm mesh and the number of charcoal particles in each sample was counted under the stereomicroscope. Peak detection analysis to identify macroscopic charcoal spikes related to local to extra-local fire episodes was conducted using CharAnalysis (Long et al., 1998; Higuera et al., 2009, 2010) and the package 'Paleofire' (Blarquez et al., 2013) running in R (R Core Team, 2021). This method is based on a three-step decomposition of the charcoal accumulation rate (CHAR) series, and, in this case, we followed the recommendations of Blarquez et al. (2013). Pre-treatment involved interpolating the CHAR series to the median time resolution of the record to account for the variability in sedimentation rates that could introduce bias. To obtain the charcoal peak (C_{peak}) and the charcoal background (C_{back}) series, we first applied the five smoothing methods available in CharAnalysis, with smoothing windows ranging from 250 to 500 years in 25-year steps (Blarquez et al., 2013), then C_{back} was subtracted from the interpolated CHAR series (C_i-C_{back}) to get C_{peak} (Higuera et al., 2009). C_{peak} still embraces C_{noise}, the statistical noise produced in the previous steps and remaining C_{back}, and C_{fire}, which in principle represents the fire signal (Higuera et al., 2010). C_{fire} separated from C_{noise} using a Gaussian mixture model (Gavin et al., 2006), with the 99th-percentile threshold in each reconstruction and applying a local threshold in 500-year time windows (Higuera et al., 2009). A signal-to-noise index (SNI; Kelly et al., 2011) has been used to select all members (i.e., analysis iterations), choosing manually those reconstructions with the highest SNI. Fire events or groups of events were considered statistically robust and thus selected when a minimum agreement of 50% among the selected members was met (López-Sáez et al., 2018b). Fire frequency was calculated using a kernel density estimation with a width of 250 years, while the 95% confidence intervals of the fire frequency were obtained by means of bootstrap resampling of the kernel density estimation using the R package 'Paleofire' (Blaauw, 2010; Blarquez et al., 2013, 2014).

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

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

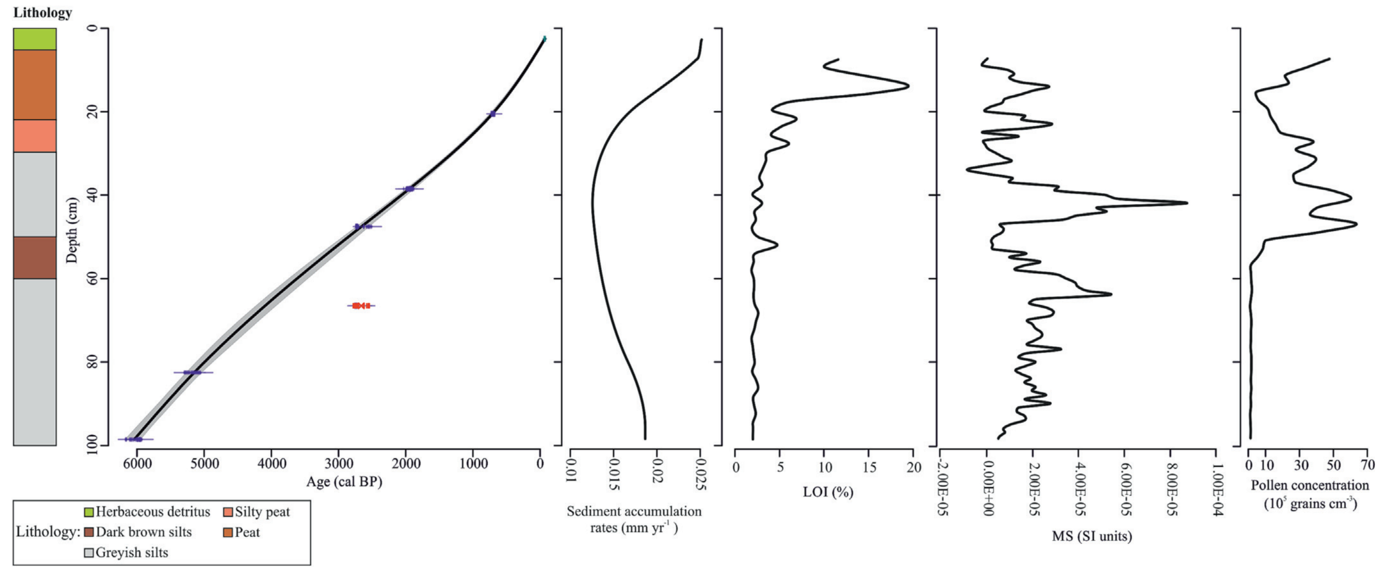

Fig. 2. From left to right. Lithostratigraphy and age–depth relationship for the La Ventilla sequence. Details of the AMS ^{14}C dates (blue distributions in the graph) are listed in Table 1. The model (smooth spline 0.2, black line) takes into account the 2σ confidence range of calibrated ages (grey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

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

Pollen analysis was carried out on 47 sub-samples of 1 cm^3 taken at ~2 cm intervals following the standard method of Moore et al. (1991). Palynomorphs were identified at 400× and 1000× magnifications to the lowest possible taxonomic level. Pollen identifications were based on photographic atlases (Reille, 1999), and the reference collection at the Institute of History-CSIC (Madrid, Spain). Ericaceae pollen differentiation followed Mateus (1989). Non-pollen palynomorphs (NPPs) were identified according to van Geel (2001) and (Cugny et al., 2010), and their nomenclature follows Miola (2012) with the abbreviations ‘HdV-’ corresponding to the Hugo de Vries Laboratory (University of Amsterdam, The Netherlands) where they were described. We identified and counted more than 400 pollen grains of terrestrial plants (trees, shrubs, herbs) per sample. Pollen of aquatic and wetland plants as well as spores and non-pollen palynomorphs (NPPs) were excluded from the pollen sum and their percentages calculated relative to the terrestrial pollen sum. *Betula* was also considered associated to the wetland and thus excluded of the terrestrial pollen sum (Janssen, 1984; Janssen et al., 1996). A *Lycopodium* tablet was added to each sample before the laboratory preparation to estimate pollen concentration (grains cm^{-3}: Stockmarr, 1971). Spores of obligate coprophilous fungi (dung fungal spores) represent a proxy for local grazing activities of both domestic and wild ungulates (López-Sáez and López Merino, 2007; Cugny et al., 2010), of particular relevance in the study area given the densities and impacts of ungulates in these mountains (see Introduction). We will mostly discuss total dung fungal spore influxes (no. spores cm^{-2} yr^{-1}) because these are independent from changes in vegetation and show a highly significant correlation with local herbivore densities (Morales-Molino et al., 2019). To establish the zonation of the pollen sequence, we tested several divisive and agglomerative methods with the program IBM SPSS Statistics 21. Based on the ecological meaning of the obtained zones, four local pollen assemblage zones (LPAZ-1 to LPAZ-4) were delimited using stratigraphically constrained cluster analysis by incremental sum-of-squares (CONISS) on square-root-transformed percentage pollen data (Grimm, 1987). The number of statistically significant zones was determined using the broken-stick model (Bennett, 1996). Pollen diagrams have been plotted against age using Tilia for Windows (Grimm, 2004). The terms ‘local’ (0–20 m), ‘extra-local’ (20 m–2 km), and ‘regional’ (>2 km) used in the text refer to different pollen source areas according to Prentice (1985).

4. Results

‘La Ventilla’ record spans the past *c.* 6145 years (Fig. 2), and the radiocarbon dates and age-depth model suggest that sediment accumulation was continuous over this period. We considered the 65-cm sample (D-AMS-036913) as an outlier probably related to the presence of reworked organic carbon as suggested by a MS peak (Fig. 2). The sequence shows low sediment accumulation rates (~0.013–0.020 mm yr^{-1}) between the bottom (99 cm) and 15-cm depth, and then a progressive increase to 0.025 mm yr^{-1} at the top of the sequence (Fig. 2). The lithostratigraphy of La Ventilla can be divided into two main sections (Fig. 2). The bottom (99–30 cm) corresponds to greyish silts typical of a lotic system, except for a more organic level of dark brown silts intercalated between 60 and 50 cm. The sediments became progressively peat-enriched towards the top, first as silty peat (30–22 cm) with the development of a mire ecosystem ~1400 cal BP, and then becoming peat at the top of the sequence (22–7 cm). Total organic matter content (LOI) in La Ventilla core (Fig. 2) shows great stability between 99 and 30 cm with values below 3%, except for a peak (5%) at 53 cm (3200 cal BP), corresponding to the organic matter enrichment of the silts (dark brown silts). Subsequently, their values increase slightly between 30 and 22 cm (4–7%), while at the top of the sequence (22–7 cm) there is a noticeable increase (>10%) with a maximum (20%) at 15 cm (~500 cal BP). Two high positive MS peaks (Fig. 2) are documented at 65 cm (5.36 x 10^5 SI units) and 41 cm (8.73 x 10^5 SI units).

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

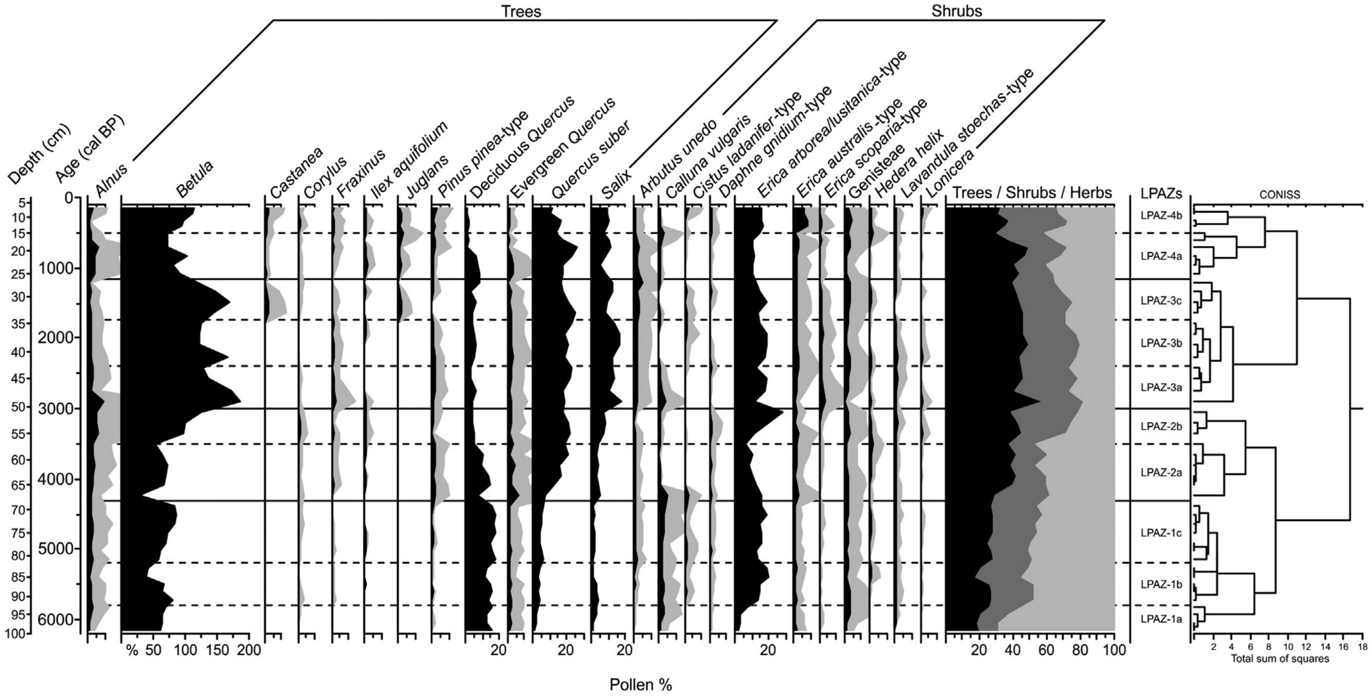

Fig. 3. Percentage pollen diagram of the La Ventilla sequence (woody taxa) plotted against age (cal BP). The black silhouettes show the percentage curves of the taxa, the grey silhouettes show the 5× exaggeration curves.

5. Discussion

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

The basal pollen subzone (LPAZ-1a; 99–93 cm; ~6145–5800 cal BP) shows the highest percentages of herb pollen (55–68%), mainly Poaceae, anthropogenic-nitrophilous and anthropozoogenic herbs (Figs. 4 and 7; Table 2). Through LPAZ-1b (93–82 cm; ~5800–5200 cal BP) herbaceous pollen values decrease (47–54%) although Poaceae still dominate and *Erica arborea/lusitanica*-type shows a noticeable increase (>20%). Low percentages of Cerealia-type are also recorded (1.2–1.4%) at ~5400–5300 cal BP (Figs. 4 and 7). These pollen assemblages point to a great development of open vegetation in the

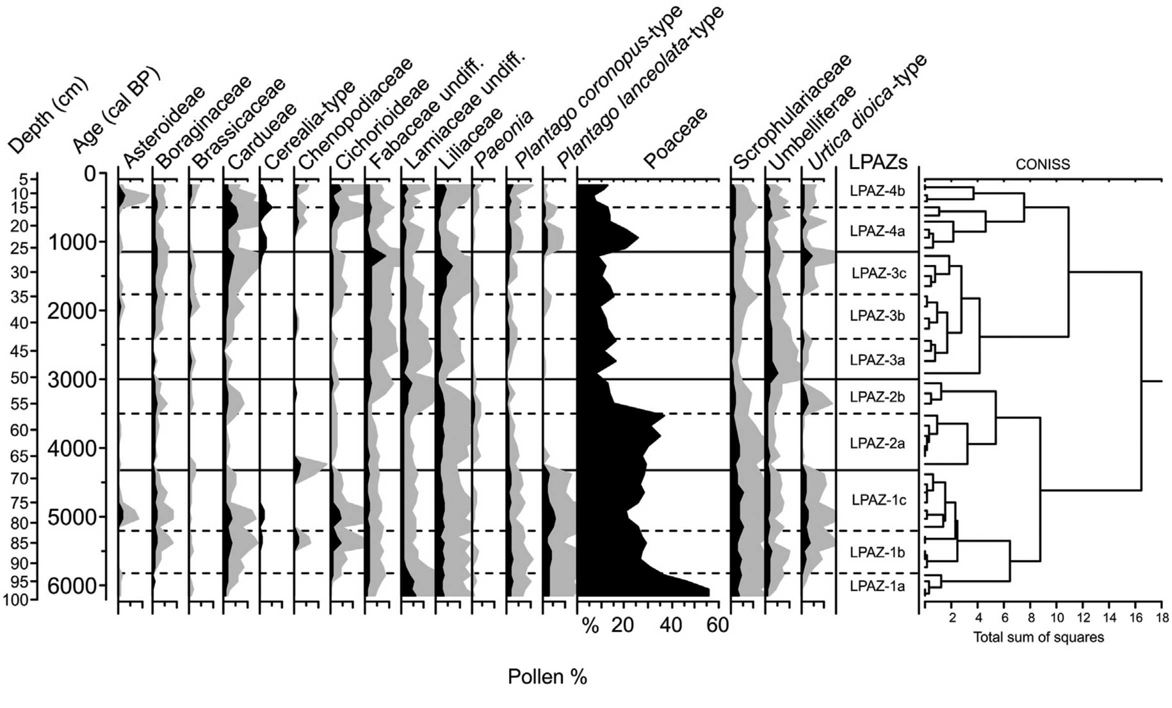

Fig. 4. Percentage pollen diagram of the La Ventilla sequence (upland herbs) plotted against age (cal BP). The black silhouettes show the percentage curves of the taxa, the grey silhouettes show the 5× exaggeration curves.

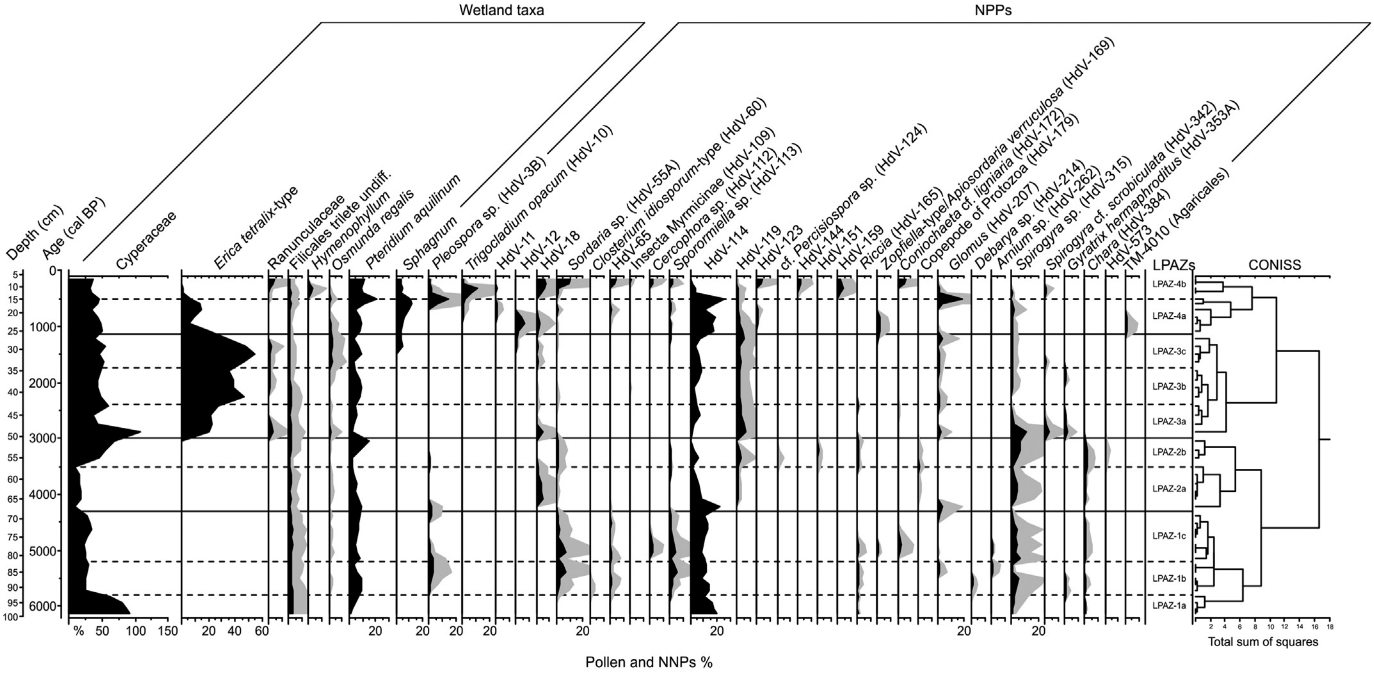

Fig. 5. Percentage pollen diagram of the La Ventilla sequence (hydro-hygrophytic taxa, ferns and non-pollen palynomorphs) plotted against age (cal BP). The black silhouettes show the percentage curves of the taxa, the grey silhouettes show the 5× exaggeration curves.

surrounding landscape, including the earliest evidence of human impact associated with local agricultural activities found in the Toledo Mountains (López-Sáez and López-Merino, 2005). Late Neolithic pastoral activities are also evidenced by the increase of coprophilous fungi influx and percentage at ~5400 cal BP (Figs. 5 and 7). The arboreal pollen sum (18–27.3%) during the Neolithic consists mainly of deciduous *Quercus* (11–16%) (Fig. 3), thus indicating that deciduous oak open woodlands (*Quercus pyrenaica*/*Q. faginea*) were dominant along La Ventilla valley during LPAZ-1a and LPAZ-1b (López-Sáez et al., 2015; Morales-Molino et al., 2020). Evergreen oaks (*Quercus ilex*, *Q. suber*) were also widespread (Fig. 3), but their low percentages suggest a regional origin (López-Sáez et al., 2010). During the Neolithic, La Ventilla showed a significant number of local fire events, at ~6150, 5510 and 5310 cal BP, although CHAR values are not very high and without major fluctuations (Figs. 6, 7). According to the local pollen evidence, these fires could have been related to farming activities around the study site (Fig. 7) and their spread favoured by prevalent dry conditions during this period (Fig. 7). This would mean that, despite the potential role played by humans in the landscape and the possible use of fire close to the mire, climate was probably the main driver of fire dynamics during the Neolithic.

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

Betula (38–80%), *Salix* and *Corylus* are also represented in both pollen subzones (Fig. 3), indicating the presence of birch-dominated riparian woodlands at La Ventilla mire during the mid-Holocene. The decline in birch pollen abundances during LPAZ-1b (<40%) can be correlated with the human impact noted above. The origin of the *Betula pubescens* subsp. *celtiberica* birch stand of La Ventilla mire has been debated among foresters, botanists and biogeographers in central Spain. Traditionally regarded as a floristic rarity, latest research considers this birch stand an impoverished relict of mesophilous forests of the glacial period (Sánchez del Álamo et al., 2010). Our data unambiguously demonstrate that birches thrived on the peatland ecosystem of La Ventilla for more than 6000 years (Fig. 7). This finding extends back in time the record of birch pollen in the Toledo Mountains, where it had so far been regularly documented only from ~5000 cal BP onwards (Morales-Molino et al., 2018, 2019; Luelmo-Lautenschlaeger et al., 2019a, 2019b), and allows to suggest the long-term persistence of *Betula* in the Toledo Mountains on suitable refuge areas. Available information on stand structure shows that marginal populations of downy birch, such as the one at La Ventilla, tend to be isolated and small (Kinnaird, 1974; Sanz et al., 2011). HdV-114, which corresponds to fragments of scalariform perforation plates occurring in vessels of hardwood, is also present in LPAZ-1a and LPAZ-1b (Figs. 6 and 7). In this case, the finding of some *Betula* woody fragments in this section suggests that the record of this NPP can be indicative of the presence of birch *in situ* (Prager et al., 2006).

Very low percentages of NPPs indicators of oligo-mesotrophic open water conditions, as well as very high (63–92% in LPAZ-1a) to moderate values (26–29.4% in LPAZ-1b) of Cyperaceae and NPPs indicators of eu-mesotrophic shallow and stagnant water conditions suggest temperate and humid settings (Fig. 7). The increase in NPPs indicators of dry conditions in LPAZ-1b suggests that a dry phase occurred at ~5800–5200 cal BP, which may also have contributed to the observed decline in birch along with human impact. The chronology of LPAZ-1a is synchronous with a temperate interval recorded in Greenland ice cores (Fig. 7) by high δ18OO values, while that of LPAZ-1b corresponds to an irregular period (Rasmussen et al., 2008). Between ~6145 and 5200 cal BP the sediment consists of greyish silts with minimal sediment accumulation rate (Fig. 2), characteristic of a lotic depositional environment with slow moving backwaters. This is in accordance with low MS units, LOI percentage and pollen concentration (Fig. 2).

Table 2
Description of pollen zones, and ecological groups from La Ventilla mire (see Figs. 2–5) according to Cugny et al. (2010), Perea et al. (2015), Luelmo-Lautenschlaeger et al. (2019b) and Morales-Molino et al. (2019, 2020).

SUBZONE Depth (cm)/ Age cal BP	Trees/Shrubs	Herbs /Wetland taxa	NPPs	Pollen concentration
LPAZ-1a, 99–93 cm 6145–5800 cal BP	AP 20–26%, SP 12–19%, deciduous *Quercus* 12–16%, evergreen *Quercus* 2%, *Quercus suber* 1–3.5%, RW 1–5%, *Betula* 60–70%, *Erica spp.*3.6–8.2%, Genisteae 1–3%, *Calluna vulgaris* 1–2.7%, Sporadic occurrences of *Arbutus unedo*, *Corylus*, *Daphne gnidium*, *Lavandula stoechas*, *Lonicera*, and *Pinus pinea*	HP 55–68%, Poaceae 37–56% ANH 0.4–2.4% AZH 2.7–3.7% Cyperaceae 63–92%	CF < 1% EUME < 2.5% OLME < 0.5% HdV-114 11–20%	Very low values (<2 x 10^5 grains cm^{-3})
LPAZ-1b, 93–82 cm 5800–5200 cal BP	AP 18–27.3%, SP 25–29%, deciduous *Quercus* 11–16%, evergreen *Quercus* 1–2%, *Quercus suber* 3.5–4.5%, RW 2–6%, *Betula* 38–80%, *Erica spp.* 15–21%, Genisteae 1–3–4%, *Calluna vulgaris* 1.3–2.4%, Sporadic occurrences of *Arbutus unedo*, *Cistus ladanifer*, *Corylus*, *Daphne gnidium*, *Hedera helix*, *Ilex aquifolium*, *Lavandula stoechas*, *Lonicera*, and *Pinus pinea*	HP 47–54%, Poaceae 26–30.5% Cerealia 0–1.4% ANH 2.7–8.8% AZH 3.8–6.3% Cyperaceae 26–29.4%	CF 2.5–13% DRY 0.5–3.3% EUME 1–7.5% OLME <1% ERO 0–1.3% HdV-114 8.5–14%	Very low values (<2 x 10^5 grains cm^{-3})
LPAZ-1c, 82–68 cm 5200–4250 cal BP	AP 25–29%, SP 22–29.3%, deciduous *Quercus* 15.5–18%, evergreen *Quercus* < 2%, *Quercus suber* 4–6.7%, RW 3.3–4%, *Betula* 57–86%, *Erica spp.* 14–20%, Genisteae 2%, *Calluna vulgaris* 1.3–4%, Low values (< 2%) of *Arbutus unedo*, *Cistus ladanifer*, *Corylus*, *Daphne gnidium*, *Hedera helix*, *Ilex aquifolium*, *Lavandula stoechas*, *Lonicera*, and *Pinus pinea*	HP 42–51%, Poaceae 21–28% Cerealia 0–1.7% ANH 2.5–10.6% AZH 4–8.3% Cyperaceae 23.5–35.5%	CF 2.2–15% DRY 0–2.5% EUME 1–7.5% OLME < 1% ERO 0–1.6% HdV-114 9–13.5%	Very low values (<2 x 10^5 grains cm^{-3})
LPAZ-2a, 68–57 cm 4250–3500 cal BP	AP 29.6–42%, SP 15–32%, deciduous *Quercus* 5.5–15%, evergreen *Quercus* 2–6%, *Quercus suber* 7–21.5%, RW 6.3–8%, *Betula* 26–72%, *Erica spp.* 8.5–19.5%, Genisteae 1.5–2.7%, *Calluna vulgaris* 0.2–5%, Low values (<2%) of *Arbutus unedo*, *Cistus ladanifer*, *Corylus*, *Daphne gnidium*, *Hedera helix*, *Ilex aquifolium*, *Lavandula stoechas*, *Lonicera*, and *Pinus pinea*	HP 38–46%, Poaceae 28–37% ANH < 2% AZH < 3% Cyperaceae 9–20% *Erica tetralix* 0–0.3%	CF <2% DRY 0–2% WET 0–4.4% EUME 0.3–5% OLME < 2% ERO 0–3.6% HdV-114 1.7–22.6%	Very low values (<2 x 10^5 grains cm^{-3})
LPAZ-2b, 57–51 cm 3500–3000 cal BP	AP 38.7–45.5%, SP 25.7–40.3%, deciduous *Quercus* 4–5.5%, evergreen *Quercus* 1.5–2.5%, *Quercus suber* 18–22.5%, RW 14%, *Betula* 98–127%, *Erica spp.* 14.5–30.5%, Genisteae 3%, *Calluna vulgaris* < 1%, Low values (< 2%) of *Arbutus unedo*, *Cistus ladanifer*, *Corylus*, *Daphne gnidium*, *Hedera helix*, *Ilex aquifolium*, *Lavandula stoechas*, *Lonicera*, and *Pinus pinea*	HP 21–29%, Poaceae 13–15.5% ANH 2–3% AZH < 3% Cyperaceae 46–70% *Erica tetralix* 0–0.4%	CF < 3% DRY 0–0.2% EUME 6.5–8.5% OLME 0.2–4.4% HdV-114 1–6%	Low but increasing values (5–10 x 10^5 grains cm^{-3})
LPAZ-3a, 51–42 cm 3000–2400 cal BP	AP 42–57.6%, SP 24.5–33%, deciduous *Quercus* 3–6%, evergreen *Quercus* 1.6–2.4%, *Quercus suber* 18–23%, RW 13.5–29.5%, *Betula* 129–189%, *Erica spp.* 15–23%, Genisteae 0.5–3.5%, *Calluna vulgaris* 1–3.5%, Low values (<2%) of *Arbutus unedo*, *Cistus ladanifer*, *Corylus*, *Daphne gnidium*, *Hedera helix*, *Ilex aquifolium*, *Lavandula stoechas*, *Lonicera*, and *Pinus pinea*	HP 18–26.6%, Poaceae 7.7–16.6% ANH 1% AZH < 1% Cyperaceae 38–107% *Erica tetralix* 20–28% Ranunculaceae 0–3.5%	CF < 1% WET < 1% EUME 1–16% OLME 2.5–6.5% ERO 0–2% HdV-114 2–7%	Very high values (>30 x 10^5 grains cm^{-3}) Maximum (64 x 10^5 grains cm^{-3}) ~2750 cal BP (47 cm)
LPAZ-3b, 42–34 cm 2400–1750 cal BP	AP 44–50%, SP 25.5–33.2%, deciduous *Quercus* 3.7–6%, evergreen *Quercus* 2–3%, *Quercus suber* 18.5–23%, RW 16–19.7%, *Betula* 122–167%, *Erica spp.* 17–23.3%, Low values (<3%) of *Arbutus unedo*, *Calluna vulgaris*, *Cistus ladanifer*, *Daphne gnidium*, Genisteae, *Hedera helix*, *Ilex aquifolium*, *Lavandula stoechas*, *Lonicera*, and *Pinus pinea*	HP 20–28.2%, Poaceae 9.5–15% ANH 1.5–4% AZH < 1% Cyperaceae 44–49% *Erica tetralix* 36–47% Ranunculaceae 0–1%	CF < 1% WET < 1% EUME < 2% OLME 2% ERO < 1% HdV-114 3–8%	Very high values (>25 x 10^5 grains cm^{-3}) Maximum (60 x 10^5 grains cm^{-3}) ~2250 cal BP (41 cm)
LPAZ-3c, 34–26 cm 1750–1150 cal BP	AP 40–46.3%, SP 25.6–31.7%, TC 0.2–4.3%, deciduous *Quercus* 4–8.5%, *Quercus suber* 17–25%, RW 10.5–14%, *Betula* 119–172%, *Erica spp.* 14–22%, *Arbutus unedo* 2–5.5%, Genisteae 3–4%, Low values (<2%) of *Calluna vulgaris*, *Cistus ladanifer*, *Corylus*, *Daphne gnidium*, evergreen *Quercus*, *Hedera helix*, *Ilex aquifolium*, *Lavandula stoechas*, *Lonicera*, and *Pinus pinea*	HP 24–34.7%, Poaceae 9–14% Cerealia 0–0.6% ANH 4–6.5% AZH 1–5% Cyperaceae 41–55% *Erica tetralix* 33.6–54.5% Ranunculaceae 0–2.2% *Sphagnum* 0.4.6%	CF < 1% WET < 1% EUME < 2% OLME 2–5% ERO 0.5–3.3% HdV-114 3.5–7%	High values (28–40 x 10^5 grains cm^{-3})
LPAZ-4a, 26–15 cm 1150–500 cal BP	AP 31–50%, SP 19–28.5%, TC 1–4%, deciduous *Quercus* 1–8.5%, *Quercus suber* 14–25.7%, RW 9–18.5%, *Betula* 72–104%, *Erica spp.* 13–16%, *Arbutus unedo* 1–3.4%, Genisteae 1–4%, Low values (<3%) of *Calluna vulgaris*, *Cistus ladanifer*, *Corylus*, *Daphne gnidium*, evergreen *Quercus*, *Hedera helix*, *Ilex aquifolium*, *Lavandula stoechas*, *Lonicera*, and *Pinus pinea*	HP 28–40.5%, Poaceae 13–26% Cerealia 0–5.6% ANH 3–10% AZH 2–3.5% Cyperaceae 35–52% *Erica tetralix* 5–21% *Sphagnum* 4.5–12%	CF 1–4% DRY 0–15.5% WET < 3% EUME 1–7.6% OLME 0.5–4% ERO 0–19% HdV-114 11–25%	Decreasing values (5–20 x 10^5 grains cm^{-3})

Table 2 (*continued*)

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

AP: Arboreal Pollen; SP: Shrubland Pollen; RW: Riparian Woods (*Alnus*, *Fraxinus*, *Salix*); TC: Tree Crops (*Castanea*, *Juglans*); HP: Herbaceous Pollen; ANH: Anthropogenic-Nitrophilous Herbs (Asterioideae, Boraginaceae, Carduoideae, Cichorioideae); AZH: Anthropozoogenic Herbs (Chenopodiaceae, *Plantago lanceolata*-type, *Urtica dioica*-type); CF: Coprophilous Fungi (HdV-55A, HdV-112, HdV-113, HdV-144, HdV-169, HdV-172, HdV-262, HdV-573, TM-4010); DRY: NPPs dry conditions (HdV-3B, HdV-10); WET: NPPs humid conditions (HdV-18); EUME: NPPs eu-mesotrophic shallow and stagnant water conditions (HdV-12, HdV-65, HdV-123, HdV-124, HdV-151, HdV-159, HdV-179, HdV-315, HdV-342, HdV-353A); OLME: NPPs oligo-mesotrophic open water conditions (HdV-119, HdV-384); ERO: NPPs soil erosion (HdV-207).

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

LPAZ-1c pollen subzone (82–68 cm; ~5200–4250 cal BP) is marked by progressive increases in *Betula* (57–86%), *Ilex aquifolium*, deciduous *Quercus* (15.5–18%), *Q. suber* (4–6.7%), *Arbutus unedo* L. and *Calluna vulgaris* (L.) Hull, abundances, while *Salix* reaches its lowest values and *Erica arborea*/*lusitanica* remain constant (Figs. 3 and 7; Table 2). These data suggest the persistence of deciduous oak woodlands and the increasing local dominance of birch in the riparian forest at La Ventilla at the expense of willow. As during the late Neolithic, cereal pollen (1.5–1.7%) and significant amounts of both anthropogenic-nitrophilous and anthropozoogenic herbs, and coprophilous fungi are recorded (Figs. 4, 5 and 7; Table 2), suggesting continued farming activities and human impact during the early Chalcolithic. Local fire episodes are reconstructed at ~5100, 4840 and 4570 cal BP, while CHAR values show an increasing trend (Figs. 6, 7). In short, the landscape remained largely unchanged from the previous period. A similar pattern has been documented in other Toledo Mountains pollen records (Fig. 1) such as El Perro mire (Luelmo-Lautenschlaeger et al., 2019a, 2019b). The dominance of NPPs indicators of eu-mesotrophic shallow and stagnant water conditions and dry conditions, as well as a constant lithology of greyish silts, low sediment accumulation rates and LOI percentages (Figs. 2 and 7), would probably indicate that a lotic depositional environment with slow moving back waters still existed.

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

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

The lower part of LPAZ-2a (68–66 cm; ~4200–4000 cal BP) is characterized by noticeable changes in the abundance of several trees, herbaceous taxa and NPPs (Figs. 3–5). *Betula* (26%), deciduous *Quercus* (7%), Cyperaceae (9%) and HdV-315 decrease. *Fraxinus* and *Ilex aquifolium* disappear, while evergreen *Quercus* (6%), *Salix*, *Calluna vulgaris*, *Cistus ladanifer*, *Erica arborea*/*lusitanica*, *E. australis*, Chenopodiaceae, *Pteridium aquilinum*, HdV-3B, HdV-114 and HdV-207 increase. These pollen assemblages suggest the advent of a markedly arid phase, during which riparian -particularly the birch-dominated-

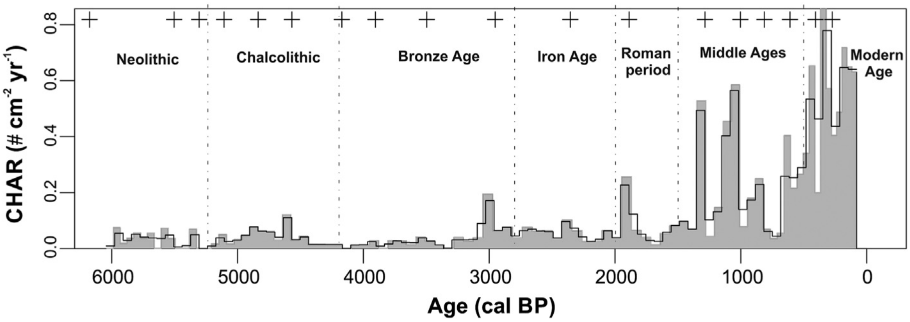

Fig. 6. Interpolated macroscopic charcoal accumulation rates (CHAR) and robust fire episodes (+) at La Ventilla mire. The grey areas correspond to raw charcoal data while the black lines correspond to CHAR interpolated to the median resolution of the record.

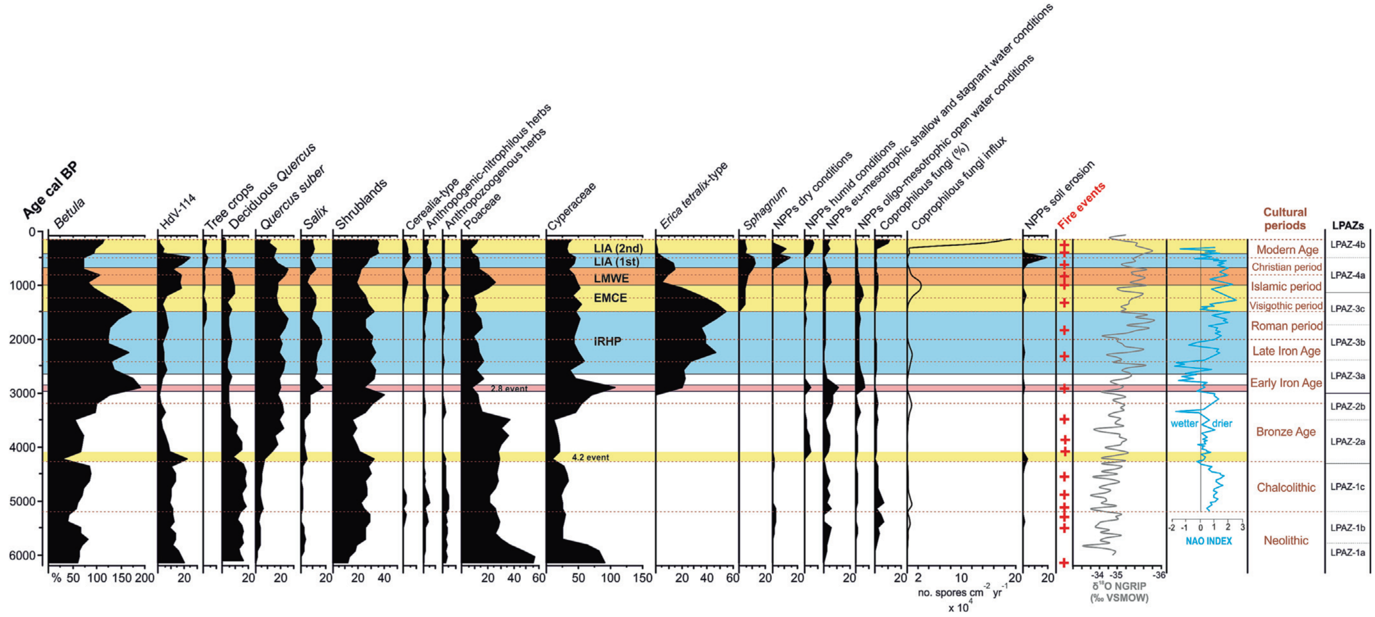

Fig. 7. Selected pollen taxa and ecological groups (see Table 2), and robust fire episodes (+) of La Ventilla sequence plotted against age (cal BP); δ18OO record from NGRIP record (Rasmussen et al., 2008); NAO Index from Olsen et al. (2012). LIA: Little Ice Age; LMWE: Late Medieval Warm Episode; EMCE: Early Medieval Cold Episode; IRHP: Ibero-Roman Humid Period.

and deciduous oak woodlands would have been greatly reduced, while elements associated with drier conditions, such as heathlands or holm oak woodlands (*Quercus ilex*) would have expanded. The joint occurrence (Fig. 5) of low percentages of *Spirogyra* (HdV-315) and higher values of *Pleospora* spp. (HdV-3B) suggest dry and eutrophic conditions in the wetland during a dry phase, while higher percentages of *Glomus* (HdV-207) can be correlated with erosive processes, also slightly visible in the magnetic susceptibility record (van Geel et al., 1989; van Geel and Aptroot, 2006). Similarly, the HdV-114 maximum can be correlated with the retreat of the birch forest (Pals et al., 1980).

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

From a palynological point of view, almost no trace of human impact on the vegetation can be found in the La Ventilla sequence, neither in the charcoal (Fig. 6) nor in the pollen records (Fig. 7). Coprophilous fungi show a strong downward trend, while anthropogenic-nitrophilous and anthropozoogenic herbs sharply decrease (Fig. 7), suggesting a very low or null human impact. There is only a fire episode or group of events detected in the analysis during this time (~4170 cal BP). Thus, the Copper Age-Early Bronze Age transition ~4200–4000 cal BP was abrupt in the Cabañeros National Park, with the collapse of the agro-pastoral Chalcolithic landscape and the abandonment of many archaeological sites as the most remarkable feature from an archaeological point of view (Muñoz, 1993; Lillios et al., 2016; Blanco-González et al., 2018).

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

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

Nevertheless, at ~3500 cal BP *Betula* (54%), Cyperaceae (10.8%), HdV-18 and HdV-315 show a marked decline (Figs. 3 and 5), concomitant with an abrupt increase in δ18O values documented in the NGRIP Greenland core (Rasmussen et al., 2008), as well as with higher NAO+ conditions (Fig. 7), suggesting lower rainfall and warmer temperatures (Olsen et al., 2012). At La Ventilla, a remarkable change from greyish silts to more organic dark brown silts occurred at this time, simultaneously to a maximum in LOI values (Fig. 2). Other Toledo

Mountains pollen records such as El Perro, Las Viñuelas and El Brezoso documented a similar pattern ~3500 cal BP (Fig. 1), with the development of Mediterranean woodlands and xerophytic taxa at the expense of hygrophilous communities (Morales-Molino et al., 2018, 2019; Luelmo-Lautenschlaeger et al., 2019a, 2019b).

In the lower part of the LPAZ-2b (57–53 cm; ~3500–3200 cal BP) subzone, the percentages of deciduous *Quercus* (4.5–5%), Poaceae (13–15.6%) and NPPs indicators of humid conditions slightly decrease, whereas those of *Betula* (98–127%), *Ilex aquifolium*, *Salix*, *Erica arborea/lusitanica*, Genisteae, Cyperaceae (46.3–70%), anthropogenic-nitrophilous and anthropozoogenic herbs increase (Figs. 3–5 and 7; Table 2). Similarly, regarding the NPPs (Figs. 5 and 7) this subzone is characterized by higher values of *Sordaria* spp. (HdV-55A), *Sporormiella* spp. (HdV-113), *Riccia* (HdV-165) and HdV-573, as well as NPPs indicators of eu-mesotrophic shallow and stagnant water conditions. These data suggest: (i) increased pastoral pressure, most significantly during the late Bronze Age (higher influx of dung fungal spores at ~3400–3200 cal BP; Fig. 7), which probably did not affect the riparian vegetation including birch woodlands but rather focused on deciduous oak woodlands; (ii) the development of heath and broom shrublands as a consequence of increased human impact; and (iii) drier and eu-mesotrophic conditions in the wetland, also attested by NAO + conditions, although a wet pulse with NAO- conditions is documented ~3350 cal BP (Fig. 7). During the Bronze Age, CHAR showed its lowest values with only two significant local fire episodes detected at ~3900 and 3500 cal BP (Figs. 6, 7).

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

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

A noticeable increase in tree pollen percentages (39–58%) is documented in the upper part of LPAZ-2b and the lower part of LPAZ-3a (53–49 cm; ~3200–2800 cal BP) pollen sub-zones (Fig. 3). In this period, *Betula* (100–189%), *Fraxinus*, *Ilex aquifolium* and *Salix* spread, while evergreen *Quercus* decreased. *Erica arborea /lusitanica*, Genisteae, Poaceae (7.7–16.6%), anthropogenic-nitrophilous and anthropozoogenic taxa, and coprophilous fungi also reduce their percentages. Hygrophytic taxa such as *Erica tetralix* (20%), Ranunculaceae, Cyperaceae and *Osmunda regalis* increased significantly, as well as NPPs indicators of humid conditions. At the same time, the eu-mesotrophic shallow and stagnant water conditions NPPs seem reduced, while oligo-mesotrophic water conditions NPPs increased (Figs. 4, 5 and 7; Table 2). The slight increase observed in CHAR values may reflect enhanced regional fire activity, and only two fire episodes have been detected (~2950–2360 cal BP) without significant landscape change afterwards (Fig. 6). These data suggest progressively wetter climatic conditions and reduced human impact, which according to the age-depth model (Fig. 2) could correspond to the so-called 2800 cal BP event (Fig. 7), an abrupt and short climatic oscillation detected at global scale (van Geel et al., 1998). This event was contemporary with the late Bronze Age-early Iron Age transition in the Toledo Mountains (López-Sáez et al., 2019), and represents a shift from the previous warm and dry conditions into wetter and colder ones. This event is documented in the NGRIP Greenland core by a decrease in δ18O values (Rasmussen et al., 2008), as well as by low NAO + conditions (Fig. 7). The lithology of La Ventilla record (greyish silts) alongside the low sediment accumulation rates and LOI values still indicate the existence of a lotic system. A similar pattern, including birch expansion, has been documented in previously studied sites not only on both the northern and southern slopes of the Toledo Mountains (El Perro, Botija, Valdeyernos, Patateros, El Brezoso and Las Viñuelas; Fig. 1) but also in the Iberian Central System (Dorado et al., 2014a, 2014b; López-Sáez et al., 2014a; Morales-Molino et al., 2018, 2019; Luelmo-Lautenschlaeger et al., 2018b, 2019a, 2019b). These data agree with the regional archaeological record, which shows remarkable changes in the settlement patterns and socio-economic dynamics, with continuity of the upland settlements established by the late Bronze Age communities into the early Iron Age (~3200–2400 cal BP) but showing abandonment of the lowland settlements (Muñoz, 1993; Barroso-Bermejo et al., 2003).

In contrast to the previous period, the upper part of LPAZ-3a (49–42 cm; ~2800–2400 cal BP) pollen subzone is characterized by decreasing values of *Betula* (128–175%), *Fraxinus*, deciduous *Quercus* (3–6%), *Salix*, Cyperaceae, *Osmunda regalis*, HdV-18, and the disappearance of *Ilex aquifolium* and Ranunculaceae (Figs. 3–5). Meanwhile, *Quercus suber* (18–23%), *Erica arborea/lusitanica*, Genisteae and HdV-114 increase (Figs. 3–5). Anthropogenic-nitrophilous and anthropozoogenic herbs, and coprophilous fungi are virtually absent at the end of the early Bronze Age (Fig. 7). CHAR values show a decreasing trend (Fig. 6), as in other pollen records from the Toledo Mountains (Luelmo-Lautenschlaeger et al., 2019a). These vegetational patterns could be related to the onset of the Iberian-Roman Humid Period (~2640–1500 cal BP; IRHP), a warm and humid period well documented in central and southern Iberia (Gil-García et al., 2006; Martín-Puertas et al., 2008, 2009). The onset of the IRHP is linked to a first dry pulse with NAO + conditions ~2640–2500 cal BP (Fig. 7; Olsen et al., 2012), which would have affected negatively the wetland vegetation, chiefly birch forest and other hygrophytic taxa, while xerophytic elements and cork oak woodlands would have developed in the immediate surroundings, followed by subsequent wet pulse with NAO- conditions ~2500–2400 cal BP. However, other pollen records in the Toledo Mountains (Fig. 1), such as El Brezoso and Las Viñuelas in the Cabañeros National Park (Morales-Molino et al., 2018, 2019), and El Perro, Botija, Patateros and Valdeyernos (Dorado et al., 2014a, 2014b; Luelmo-Lautenschlaeger et al., 2018b, 2019a, 2019b) recorded an expansion of birch during this period coinciding with very low human impact. This climatic irregularity would have affected La Ventilla birch forest to a greater extent than others in the Toledo Mountains, probably because *Betula pubescens* is not so tolerant as *B. pendula* –which is today more widespread in these mountains and we assume that this was also the case in the past– to drier soils (Sánchez del Álamo et al., 2010; Jonczak et al., 2020).

The late Iron Age (~2400–2000 cal BP; bottom of LPAZ 3b; 42–40 cm) was a phase of relative woodland stability around La Ventilla mire. *Betula* (122.5%), *Erica tetralix* (47%), *Pteridium aquilinum* and Cyperaceae (49.3%) increase, *Corylus*, *Ilex aquifolium* and *Calluna vulgaris* disappear, anthropogenic-nitrophilous and anthropozoogenic herbs decline significantly and coprophilous fungi are present but scarce (Figs. 3–5 and 7; Table 2). The humid and warm climate of the Iberian-Roman Humid Period might have favoured these dynamics, although conditions were notably variable at ~2400–2000 cal BP

(Fig. 7), with a first dry pulse (NAO+ conditions) and a late wet one (NAO- conditions). Finding of NPPs indicative of soil erosion (HdV-207; Figs. 5 and 7) and a very high positive MS peak (Fig. 2) at ~2260 cal BP (8.73 x 10^5 SI units), may be related to the increment of anthropic activities around the mire during the late Iron Age, and the dry pulse in the IRHP, which drove to major pollen concentration values (van Geel et al., 1989). An increase of birch woodlands has been also documented in the Cabañeros National Park during the late Iron Age (Morales-Molino et al., 2018, 2019), as well as in El Perro mire, located on the southern fringe of the Toledo Mountains (Luelmo-Lautenschlaeger et al., 2019a, 2019b). Meanwhile, other pollen records from the northern Toledo Mountains such as Valdeyernos and Pataterος (Fig. 1) show a slight decrease in birch cover despite the almost absence of human impact (Dorado et al., 2014a, 2014b). The Botija pollen record, also placed in the northern Toledo Mountains (Fig. 1), is a paradigmatic case in this regard because the strong human impact during the late Iron Age caused a very meaningful decline in the deciduous and evergreen oak woodlands and the definitive disappearance of birch and hazel around the mire, with the consequent development of xerophytic heathlands (Luelmo-Lautenschlaeger et al., 2018b). No archaeological site from the late Iron Age has so far been documented in the Toledo Mountains, but the nearest ones known to date are very close to their northern edge (López-Sáez et al., 2019), thus agreeing with the patterns described above. In general, these are small, walled settlements, with a marked sedentary character and located in strategic places of territorial control (Hurtado, 2000).

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

The upper part of LPAZ-3b (40–34 cm; ~2000–1750 cal BP) and the lower part of LPAZ-3c (34–30 cm; ~1750–1500 cal BP) pollen subzones are characterized by a progressive rise in *Betula* values (122.5–172%), the reappearance of *Ilex aquifolium*, Ranunculaceae and *Osmunda regalis*, a slight increase of *Cistus ladanifer*, *Calluna vulgaris* and Genisteae, the decrease of *Erica arborea/lusitanica*, and the first appearance in the pollen diagram of *Castanea* and *Juglans* at ~1750 cal BP (Figs. 3–5 and 7; Table 2). *Quercus suber* (18.5–25%), *Erica tetralix* (36–54.5%) and Cyperaceae (44–53%) still maintain very high values. Thus, the Roman period (~2000–1500 cal BP) was a rather stable phase in the mid-mountain woodlands in the Cabañeros National Park, with the progressive expansion of birch stands. This spread could have been favoured by decreasing temperature (decrease δ18O values in the NGRIP Greenland core) during a distinctively drier pulse (NAO+ conditions) at the end of the Iberian-Roman Humid Period (Fig. 7). The Roman domain brought higher CHAR values at La Ventilla, including a fire episode at ~1890 cal BP (Figs. 6, 7) that did not leave a trace in the MS curve (Fig. 2). A similar landscape and dynamics have been documented in other Toledo Mountains pollen records (Morales-Molino et al., 2018, 2019; Luelmo-Lautenschlaeger et al., 2019a, 2019b).

In any case, it is likelier that forest development was a consequence of the more discrete Roman use of mid-mountain environments, as attested by low values of both anthropogenic-nitrophilous and anthropozoogenic herbs as well as coprophilous fungi (Fig. 7). The presence of tree crops (chestnut and walnut) in La Ventilla pollen record is probably due to their regional cultivation during Roman period (Morales-Molino et al., 2020). Therefore, the fire activity detected in the southern Toledo Mountains records was probably more related to climate than to a virtually non-existent human impact. In fact, human pressure around the Toledo Mountains during the Roman period focused on the lowlands, away from these mountains, which were not settled and became a refuge for bandits (Carrasco, 2003; Hernández-Maroto, 2018; López-Sáez et al., 2019). This is the reason why, as it happened during the late Iron Age, those pollen records located in the northern Toledo Mountains (Botija, Pataterος, Valdeyernos; Fig. 1) closer to large Roman population centres such as *Consabura*, *Caesarobriga* or *Toletum* (Carrasco, 2012; Mangas, 2012), document larger human impact (Dorado et al., 2014a, 2014b; Luelmo-Lautenschlaeger et al., 2018b).

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

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

Therefore, a substantial growth in human impact and the progressive decline of the birch forest began in the Visigothic period (~1500–1240 cal BP), also affecting the cork oak woodland, although it was much more intense during the Islamic period (~1240–850 cal BP), when a maximum in coprophilous fungi influx and high values of cereal pollen (2.3–2.8%) are documented (Fig. 7). This increment could be related to Alhover-El Milagro mountain pass, through where transhumant livestock flocks were conducted, and to the Abraham defensive tower which was placed really close to the mire (Ruibal, 1985). During the Christian period (~850–500 cal BP), cereal pollen percentage increases notably (5.6%) -particularly from 700 cal BP (top of LPAZ-4a)-, coupled with rising abundances of anthropogenic-nitrophilous herbs and of NPPs indicators of erosion processes, and decreasing shares of deciduous *Quercus* and *Q. suber* (Fig. 7). This increase in farming can be linked to the establishment of new cultivated land from the 13th to 19th century AD in the Cabañeros National Park, when the mountainous complex was owned by the Toledo city Council, as its main resource asset (Perea et al., 2015). Other pollen records from the Toledo Mountains (Fig. 1), both in the northern (Botija, Valdeyernos, Pataterος, Bermú) and southern (El Brezoso, Las Viñuelas, El Perro) territories, show similar patterns of land use during this period, including increasing agricultural and livestock activities as well as the cultivation of olive trees (Dorado et al., 2014a, 2014b; Luelmo-Lautenschlaeger et al., 2018a, 2018b, 2018d, 2019a, 2019b; Morales-Molino et al., 2018, 2019). Taken together, medieval vegetation dynamics in the Toledo Mountains can be understood considering the following: (i) the Visigothic urban elites stayed in Toledo city, while most people settled in small villages in the rural areas; (ii) the constant and increasing occupation and exploitation of these mid-elevation mountains during the Islamic period, despite it was a border territory with the Christian kingdoms of the north of the Iberian Peninsula; and (iii) the subsequent Christian repopulation of the Toledo Mountains, especially after Toledo city Council bought these lands (Izquierdo, 1983; Ladero, 1984; Jiménez de Gregorio, 2001; Da Cunha, 2007; Barroso et al., 2012; Hernando, 2020).

Sphagnum appears for the first time in the sequence in LPAZ-3c (Fig. 5) and increases progressively in LPAZ-4a (4.5–12%), whereas *Erica tetralix* follows an opposite trend. The upper part of LPAZ-3c (30–26 cm) and the lower part of LPAZ-4a (26–22 cm) are composed of silty peat. Peat formation started during the upper part of LPAZ-4a (22–15 cm) at ~1500 cal BP, which is supported by maximum (20%) LOI values and growing sediment accumulation rates (Fig. 2). A correlative comparison suggests that a wet pulse linked to low NAO+

conditions at ~1500–1300 cal BP allowed *Sphagnum* to spread (Fig. 7; Olsen et al., 2012). Our results from La Ventilla agree with previous research suggesting that low NAO+ mediated climatic variability has been a major driver of peat inception in the Cabañeros National Park and southern Iberia (Fletcher et al., 2013; Ramos-Román et al., 2016; Camuera et al., 2018, 2019; Carrión et al., 2018; Morales-Molino et al., 2019; Alba-Sánchez et al., 2021).

The beginning of the Visigothic period matches the onset of the Early Medieval Cold Episode (Fig. 7), spanning from 1500 to 1000 cal BP, with greater aridity and lower temperatures (Martín-Puertas et al., 2010; López-Sáez et al., 2014a), as attested by low δ18O values and higher NAO+ conditions at ~1300–1000 cal BP (Fig. 7). This cold episode is also reflected in La Ventilla pollen record by a slight increase of NPPs indicative of oligo-mesotrophic open water conditions (Fig. 7) and may also have had some influence on the decline of the birch forest. The increase of CHAR values during the Islamic and Christian periods (Fig. 6) can also be correlated with the onset of the Late Medieval Warm Episode (~1000–600 cal BP; Fig. 7), whose more moderate thermal and rainfall conditions would probably have favoured the exploitation of mid-elevation mountain environments (López-Sáez et al., 2014a) and a slight recovery of the birch forest. Finally, the onset of the Little Ice Age ~600–400 cal BP (Manrique and Fernández-Cancio, 2000), with cooler and drier conditions (lower δ18O values and higher NAO+ conditions; Fig. 7), could explain the increase in the values of Cyperaceae, *Erica tetralix*, *Sphagnum* and NPPs indicators of dry conditions, and probably also influenced the further decline in birch cover documented at La Ventilla (Fig. 7).

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

LPAZ-4b pollen subzone (15–7 cm; ~500–150 cal BP) is characterized by the progressive expansion of *Betula* (94–113%), *Castanea*, *Cistus ladanifer*, *Erica arborea/lusitanica* (16%), *E. australis* and Genisteae, while deciduous *Quercus* (< 2%), *Q. suber* (11–17%), *Calluna vulgaris* and *Sphagnum* (3.5–5.3%) decline and *Erica tetralix* disappears (Figs. 3 and 5; Table 2). Anthropogenic-nitrophilous and anthropozoogenic herbs grow slightly (Fig. 7). Cerealia is still recorded (<1–3%), whereas coprophilous fungi show their maximum percentage and influx values of the sequence. CHAR values are also at their maximum (Figs. 6, 7), but only two fire episode or group of events were identified using peak detection analysis (~420 and 280 cal BP), suggesting that most of the fires were regional (Whitlock and Larsen, 2001). Therefore, the Modern Age (~500–150 cal BP) in La Ventilla pollen record shows the existence of a rather deforested landscape with declining cork and deciduous oak woodlands while the local birch forest expanded. This makes sense considering that during this period agriculture and livestock husbandry expanded and this affected Mediterranean woodlands rather than wetlands, as the population settled down and there was even some population growth (Jiménez de Gregorio, 2001; López-Sáez et al., 2019). The rise in coprophilous fungi matches higher livestock numbers according to historical archives (Perea et al., 2015). Overall, vegetation and fire dynamics during the Modern Age in La Ventilla pollen record follow the same trends as in the rest of pollen sequences of the Toledo Mountains so far mentioned. In the pollen record of Las Lanchas mire (Luelmo-Lautenschlaeger et al., 2018c; Fig. 1), for example, the low human impact on the wetland even allowed the survival of a relict element such as the yew (*Taxus baccata*).

High herbivore densities usually had a highly negative impact on Mediterranean *Sphagnum* bogs, probably because of trampling and increasing nutrient loads (López-Sáez et al., 2014c). However, ungulates indeed make an intensive use of mires in summer, when water availability is limited (Acebedo et al., 2008; Perea et al., 2015). Nevertheless, the Modern Age in La Ventilla pollen record was characterized by a humid climate, as attested by high NAO- conditions (Olsen et al., 2012) and increasing values of NPPs indicators of humid environment (Fig. 7), probably related to the second, still colder (decreasing δ18O values; Fig. 7) but wetter phase of the Little Ice Age ~400–100 cal BP (Manrique and Fernández-Cancio, 2000). These wet conditions would have implied a very low impact of herbivory at La Ventilla mire, which would have directly allowed the development of the birch forest and the disappearance of *Erica tetralix*.

5.9. Conservation of southernmost Iberian birch populations

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

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

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

In this scenario, the conservation of this endangered population will most probably require an active management aimed at preserving existing water sources and allowing the foundation of new populations through assisted seed dispersal and seedling protection. Nevertheless, the population of *Betula pubescens* in La Ventilla is a unique case in the whole Iberian Peninsula due to its marginal or extreme nature with respect to the distribution area of this species, so it must be considered as an 'evolutionarily significant unit' (ESU) *sensu* Crandall et al. (2000) due to its geographical isolation from the nearest populations (100–150 km from those of the Iberian Central System) but also genetically (Martín et al., 2008; Sánchez del Álamo et al., 2010). In this sense, one of the priority conservation measures must be to preserve their genetic identity, so any possible reinforcement should be made with materials from the same population. Clearly, the biggest problem facing the downy birch in the Toledo Mountains is the fragmentation of its habitat due to unfavourable climatic periods during the Holocene as well as the human impact over time (Morales-Molino et al., 2019), since in these mid-mountain territories there are many peatland ecosystems without birch trees but where this species could have thrived in the past (Luelmo-Lautenschlaeger et al., 2019b, 2020).

6. Conclusions

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

During the late Neolithic (~6145–5200 cal BP), La Ventilla wetland would correspond to a lotic system with slow moving backwaters. Its most characteristic vegetation would be open birch woodlands, related to temperate and humid ~6145–5800 cal BP and later ~5800–5200 cal BP arid climatic conditions. This period documents the earliest evidence of human impact, including agricultural activities and increasing pastoral pressure from ~5400 cal BP. During the Chalcolithic (~5200–4200 cal BP) the birch forest increases progressively, despite a low human impact and a documented dry pulse ~5200–4800 cal BP, developing further with the wet pulse ~4800–4200 cal BP related to NAO- conditions. By contrast, during the Chalcolithic-early Bronze Age transition (~4200–4000 cal BP) the birch forest suffered a sharp decline as a consequence of the abrupt climatic event 4200 cal BP, characterised by extremely arid climatic conditions. During the Bronze Age (~4000–3200 cal BP), the wetland ecosystem quickly recovered to conditions prior to the abrupt climatic event. The birch forest developed under humid and mesotrophic conditions. However, by ~3500–3200 cal BP La Ventilla birch forest would spread again as human impact shifted away from the wetland and focused on the deciduous oak woodlands. Subsequently, progressively wetter conditions related to the 2800 cal BP event and lower human impact with the abandonment of lowland settlements ~3200–2800 cal BP, allowed for further development of the birch forest and hygrophytic vegetation in the transition between the late Bronze Age and the early Iron Age. However, the birch forest receded again ~2800–2400 cal BP at the end of the early Iron Age, in connection with the climatic irregularity associated with the onset of the Ibero-Roman Humid Period, characterized by a first dry pulse with NAO+ conditions ~2640–2500 cal BP, and a subsequent wet pulse with NAO- conditions ~2500–2400 cal BP. The late Iron Age (~2400–2000 cal BP) and the Roman period (~2000–1500 cal BP) would correspond to a phase of relative stability of woodlands in La Ventilla mire, with a new development of birch forest under wetter and warmer climatic conditions at the beginning and drier and colder later on, and low human impact, despite irregular climate conditions. Tree crops (*Castanea*, *Juglans*) are documented ~1750–1500 cal BP. Agricultural and livestock activities, probably mediated by the anthropogenic use of fire, replaced climate as the critical driver of La Ventilla downy birch population dynamics during the Middle Ages, causing an abrupt birch decline ~1500–500 cal BP. Finally, during the Modern Age (~500–150 cal BP) the birch forest recovers again thanks to the humid climatic conditions of the second phase of the Little Ice Age ~400–100 cal BP, although agricultural activities and livestock pressure increase enormously in the cork and deciduous oak woodlands of the study area.

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

Data availability

Data will be made available on request.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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