Global and Planetary Change 175 (2019) 238–250

Contents lists available at ScienceDirect

Global and Planetary Change

journal homepage: www.elsevier.com/locate/gloplacha

A palaeoecological approach to understanding the past and present of Sierra Nevada, a Southwestern European biodiversity hotspot

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ARTICLE INFO

Keywords:
Biogeography
Palaeoecology
Vegetation
Holocene
Submediterranean
Fire
Conservation
Environmental change

ABSTRACT

Mediterranean mountainous environments are biodiversity hotspots and priority areas in conservation agendas. Although they are fragile and threatened by forecasted global change scenarios, their sensitivity to long-term environmental variability is still understudied. The Sierra Nevada range, located in southern Spain on the northwestern European flanks of the Mediterranean basin, is a biodiversity hotspot. Consequently, Sierra Nevada provides an excellent model system to apply a palaeoecological approach to detect vegetation changes, explore the drivers triggering those changes, and how vegetation changes link to the present landscape in such a paradigmatic mountain system. A multi-proxy strategy (magnetic susceptibility, grain size, loss-on-ignition, macroremains, charcoal and palynological analyses) is applied to an 8400-year long lacustrine environmental archive from the Laguna de la Mosca (2889 masl). The long-term ecological data show how the Early Holocene pine forests transitioned towards mixed *Pinus-Quercus* submediterranean forests as a response to a decrease in seasonality at ~7.3 cal. kyr BP. The mixed *Pinus-Quercus* submediterranean forests collapsed drastically giving way to open evergreen *Quercus* formations at ~4.2 cal. kyr BP after a well-known aridity crisis. Under the forecasted northward expansion of the Mediterranean area due to global change-related aridity increase, mountain forests inhabiting territories adjacent to the Mediterranean Region could experience analogous responses to those detected in the Sierra Nevada forests to the Mid to Late Holocene aridification, moving from temperate to submediterranean and then Mediterranean formations.

1. Introduction

Regions under Mediterranean climate have been identified as biodiversity hotspots (Myers et al., 2000). The Mediterranean basin, in particular, is the most diverse and heterogeneous of these Mediterranean hotspots (Médail and Quézel, 1997, 1999; Myers et al., 2000). However, the spatial distribution of biodiversity within the Mediterranean basin is uneven, mountains having played a key role in the basin's biodiversity spread and survival through time (Manzano et al., 2017; Médail and Quézel, 1997, 1999). Furthermore, the importance of Mediterranean mountain areas is not only linked to their biodiversity, but also to the many critical ecosystem services they provide (Grêt-Regamey et al., 2012; Körner, 2003; Meybeck et al., 2001; Woodwell, 2004). Unfortunately, both the fragile mountain environments and the services they provide are threatened due to the present trends of unprecedented environmental change and the large anthropogenic pressure they experience (Diaz et al., 2003).

In Mediterranean mountains, climate-controlled vegetation belts provide niches for the coexistence of mediterranean, submediterranean and temperate taxa within a single massif (Blanca, 2000). However, belt boundaries are flexible to environmental change (Grabherr et al., 2010; Nagy and Grabherr, 2009) and, consequently, Mediterranean mountainous environments are fragile and their conservation a global concern (Diaz et al., 2003; Grêt-Regamey et al., 2010; Körner, 2004;

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https://doi.org/10.1016/j.gloplacha.2019.02.006
Received 30 August 2018; Received in revised form 28 December 2018; Accepted 14 February 2019
Available online 16 February 2019

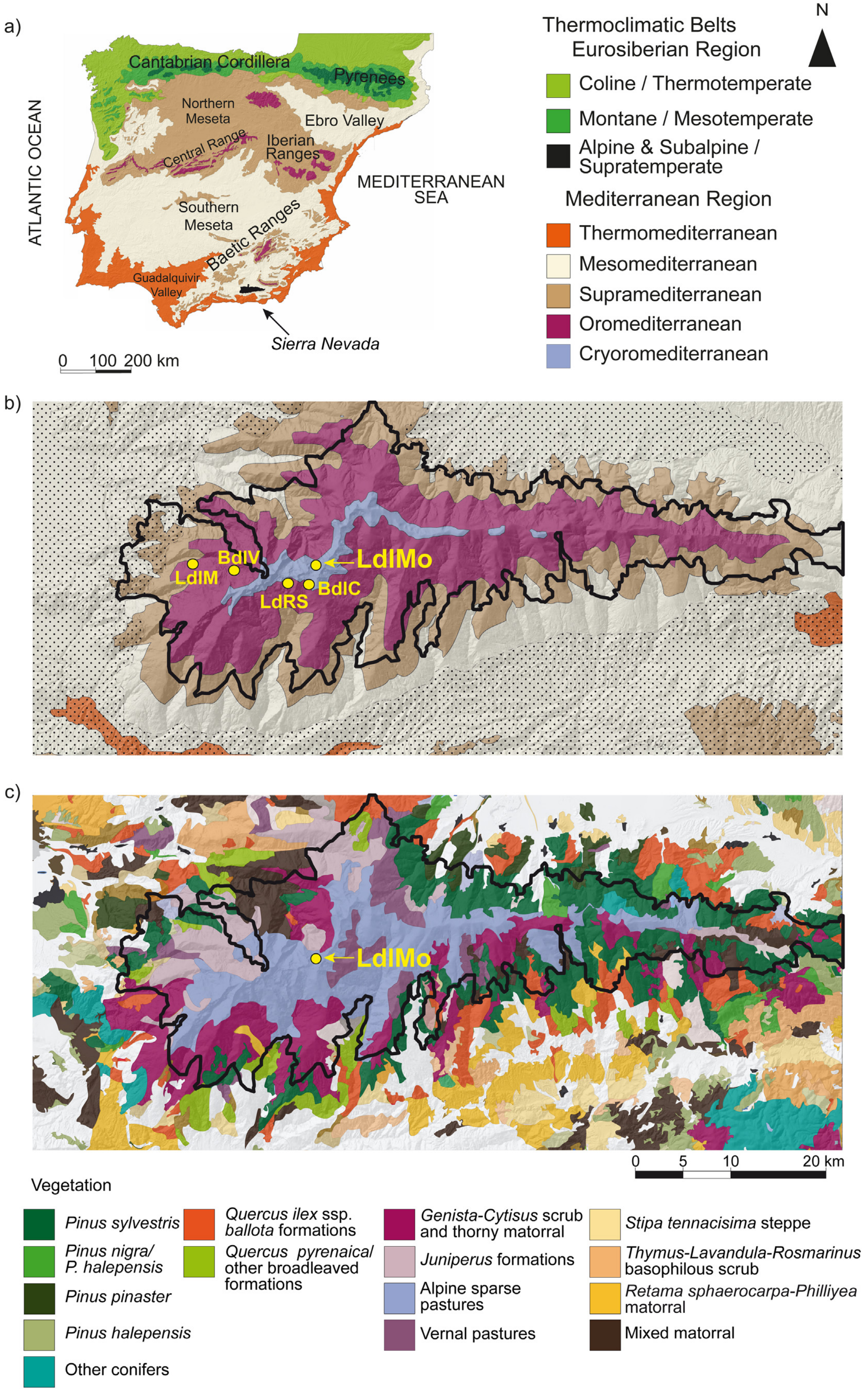

Fig. 1. Maps presenting biogeographical information of the study area. a) Iberian thermoclimatic belts (after Manzano et al., 2017). b) Sierra Nevada thermoclimatic belts and lithology (Rams Sánchez, 2007; Valle, 1985, 2003), shading indicates calcareous and dolomitic substrates, while blank areas indicate siliceous materials (Delgado Calvo-Flores et al., 2001; Rams Sánchez, 2007). The coring site (LdlMo) and other Sierra Nevada palaeoenvironmental records discussed in the text are indicated, as well as the Sierra Nevada National Park boundary. c) Vegetation units of the Sierra Nevada area (modified from REDIAM, Red de Información Ambiental de Andalucía, and own data). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Meybeck et al., 2001; Woodwell, 2004). Under the current global change scenario, mountain conservation issues should consider long-term ecological approaches that provide information on the responses that past vegetation belts had to environmental change (Willis and Baghwat, 2010; Willis et al., 2007). In this sense, Mediterranean mountain environments provide the ideal setting to explore complex biological interactions and vegetation trends through time (Carrión, 2002; Carrión et al., 2007, 2010; Vogiatziakis, 2012). However, the sensitivity of well-preserved Mediterranean mountain environments to long-term environmental variability is still understudied (Diaz et al., 2003).

The Sierra Nevada range (S Iberia) is one of the highest mountain ranges in Europe. Its heterogeneous geology, physiography and palaeoecological history are responsible for Sierra Nevada being the western Mediterranean's most important biodiversity hotspot (Blanca, 2000; Lorite, 2016). It was declared a UNESCO Biosphere Reserve in 1986, a Natural Park in 1989, and a National Park in 1999 (Gómez-Ortiz et al., 2005). Sierra Nevada houses ~30% of the Iberian and ~20% of the European flora, covering all European floristic elements and biotypes (Blanca, 2000; Blanco et al., 2005; Lorite, 2016). Therefore, Sierra Nevada is an ideal setting for understanding the effect that long-term environmental changes have on biodiverse Mediterranean mountain settings and how these environmental changes relate to the present structure and distribution of plant biodiversity.

Sierra Nevada's Holocene environmental and landscape changes are nested within the wider western Mediterranean Holocene climatic trends (Anderson et al., 2011; Carrión, 2002; Fletcher and Sánchez-Goñi, 2008; Jalut et al., 2009; Jiménez-Espejo et al., 2014; Jiménez-Moreno and Anderson, 2012; Jiménez-Moreno et al., 2013; Ramos-Román et al., 2016, 2018). Both astronomical forcing (i.e., changes in precession and solar irradiance; Bard et al., 2000; Laskar et al., 2004) and internal modes of climate variability (i.e., North Atlantic Oscillation; Trouet et al., 2009; Olsen et al., 2012) have been identified as the modellers of Sierra Nevada landscapes (Anderson et al., 2011; Ramos-Román et al., 2016). Briefly, the Early Holocene has been reconstructed as a humid phase (Anderson et al., 2011; Jiménez-Espejo et al., 2014; Jiménez-Moreno et al., 2015). This humid phase is followed by an increase in aridity related to a decrease in seasonality, with superimposed drier spells, since ~7 cal. kyr BP (Carrión, 2002; Fletcher and Sánchez-Goñi, 2008; Jiménez-Espejo et al., 2014). After the Mid-to-Late Holocene (~5–4.2 cal. kyr BP) more intense aridity pulses, it seems that the NAO variability is the main driver of vegetation change in Sierra Nevada, as it affected the winter-autumn storm tracks in S Iberia (Ramos-Román et al., 2016). Sierra Nevada current vegetation singularity is outstanding (Rivas Martínez, 1987, 2011; Valle, 1985, 2003). In addition, palaeoecological studies show the existence of a variety of vegetation responses to factors such as altitude and aspect (Anderson et al., 2011; Jiménez-Moreno and Anderson, 2012; Jiménez-Moreno et al., 2013; Ramos-Román et al., 2016, 2018) that could be behind the present Sierra Nevada singularity. However, the long-term ecological picture of Sierra Nevada is far from complete. New palaeoecological records are needed to fill the gaps in the available information of this unique Mediterranean mountain system in order to bridge Quaternary proxy data with contemporaneous information and merge them into useful, extrapolable models.

Here we present a high-resolution, multi-proxy palaeoecological record of the Sierra Nevada high-altitude Laguna de la Mosca lacustrine site (2889 masl) using palynological, charcoal, macroremains, magnetic susceptibility, loss-on-ignition, and grain size analyses. The aims of the environmental reconstruction of this paradigmatic western Mediterranean mountain setting are i) to detect landscape changes during the Holocene, ii) to explore the drivers triggering those past landscape changes, and iii) to link the detected past environmental changes to the present biodiversity of Sierra Nevada landscapes. This is of special interest in providing retrospective examination for events shaping the present-day diverse Sierra Nevada landscape. Furthermore, the palaeoecological reconstruction of the vegetation assembly and succession during the well-known S Iberian Holocene aridification trend (Anderson et al., 2011; Carrión, 2002; Carrión et al., 2003, 2010) could be used as an analogous for the future response of forest vegetation to the projected northwards expansion of the European Mediterranean climate area within the global change scenario.

2. Material and methods

2.1. Regional, physical and environmental setting

The Sierra Nevada mountains are in the Baetic Ranges at the south-eastern corner of the Iberian Peninsula (Fig. 1a). Covering 90 km in length, Sierra Nevada runs E-W, parallel to the coast, housing the highest Iberian peaks. Metamorphic siliceous rocks (mica schists) are dominant at the central part of the massif; to the south and west, the massif is framed by calcareous materials such as limestone and dolomite (Delgado Calvo-Flores et al., 2001; Fig. 1b). Sierra Nevada was extensively glaciated during the last glacial maximum (LGM). Evidence for LGM glaciers spanning over 2000–2200 masl and 2300–2400 masl is found on the north and south faces of the mountains, respectively (Palacios et al., 2016).

Sierra Nevada vegetation is distributed along an altitudinal gradient and affected by bedrock, determining the development of different soil types (Molero Mesa et al., 1992; Fig. 1c). On the detritic, alkaline materials surrounding the massif, open *Pinus halepensis* woodlands with *Pistacia lentiscus, Phillyrea angustifolia* and *Retama sphaerocarpa* dominate the thermomediterraean belt (< 700 masl; Valle, 1985, 2003). *Quercus rotundifolia* dominates the meso- and supramediterranean belts (700–1900 masl), with an understory of Cistaceae (i.e., *Cistus*, *Helianthemum*, *Fumana*) and woody Lamiaceae (i.e., *Rosmarinus officinalis, Salvia, Thymus, Teucrium*). Scattered stands of *Quercus faginea* appear in the supramediterranean belt, sometimes with *Acer opalus* ssp. *granatense*. In the oromediterranean belt (> 1800–1900 masl), sparse pinelands of *P. sylvestris* ssp. *nevadensis* and *P. nigra* ssp. *salzmanii* alternate with a creeping scrub of *Juniperus sabina* and *J. communis* ssp. *hemisphaerica,* frequently as part of a thorny matorral. On dolomites, important in the western areas, edaphic restrictions hamper the development of forests. *P. pinaster* ssp. *acutisquama-J. phoenicea/oxycedrus* assemblages dominate the landscape with *P. halepensis* replacing *P. pinaster* in the lower altitude, more thermic and xeric enclaves. Individuals of *P. nigra* ssp. *salzmannii* populate the higher elevation areas (Valle, 1985, 2003).

On siliceous substrates, the mesomediterranean belt (700–1500 masl) is dominated by *Q. rotundifolia* and *Q. coccifera* (on arid enclaves) with an understorey of *R. sphaerocarpa, Cytisus fontanesii*, *C. grandiflorus*, and Cistaceae (i.e., *Cistus monspeliensis, C. salviifolius*). In the supramediterranean (1500–1900 masl), the evergreen oak formations incorporate *Adenocarpus decorticans* in the understory. However, in altered sites a thorny matorral of *Cotoneaster granatensis, Berberis hispanica, Crataegus monogyna, Prunus ramburii,* and *Rosa* sp. become abundant. Scattered within this vegetation belt, *Q. pyrenaica* groves mark the timberline, sometimes enriched by *Sorbus aria, Acer opalus* ssp. *granatense* and *Fraxinus angustifolia*, and more rarely with *Betula pendula* ssp. *fontqueri* and *Salix caprea* (Valle, 1985, 2003). The treeless oromediterranean belt (2700–3000 masl) is covered by pastures as well as prostrated and cushion-like shrubs. It is noteworthy the *Genista versicolor-Juniperus communis* ssp. *nana* community, and the sparse scrub in altered and pronounced slopes dominated by woody Brassicaceae (*Hormatophylla spinosa, Vella spinosa), Arenaria pungens* ssp. *pungens*, *Reseda complicata* and *Sideritis glacialis* (Valle, 1985, 2003). Patchy waterlogged pastures (locally called *borreguiles*) develop in small depressions and over impermeable soils. They are dominated by mosses and sedges and incorporate many singular floristic elements like *Plantago nivalis, Aconitum nevadensis* or *Potentilla nevadensis* (Lorite et al., 2003). The highest altitudes comprised in the cryoromediterranean belt

(> 2700–3000 m), are vegetated by sparse pastures of great floristic endemicity dominated by *Festuca clementei, Nevadensia purpurea, Leontodon boryi, Viola crassiuscula, Herniaria boissieri, A. pungens* ssp. *pungens, A. tetraquetra* and *Linaria glacialis* (Fernández-Calzada, 2007; Fernández Calzado and Molero Mesa, 2011).

2.2. Sediment sampling

Linked to the past glacial history of Sierra Nevada, around 42 permanent lakes are found above 2600 masl. One of them is the Laguna de la Mosca (LdlMo, 2889 masl, 37° 3.58′ N, 3° 18.88′ W; Fig. 1), a small lake with a maximum depth of 3.4 m, a surface of 0.48 ha, and a drainage area of 39.7 ha. LdlMo is located in the foot of the north-facing Mulhacén cirque on metamorphic mica schists. The lake sits above the modern treeline, in the cryoromediterranean belt (Fig. 1). Two sediment cores were retrieved from the lake bottom using a floating platform in September 2013. A 190-cm long sediment core was collected using a Livingston corer. A short core of 20 cm was sampled using a universal corer (Aquatic Research Inc.). The latter core was extracted to avoid the potential mixing of the less compacted upper sediment layers from the former core.

2.3. Palaeoecological analyses and radiocarbon dating

Sixteen samples from the long sediment core were selected for AMS radiocarbon dating (Table 1). One date (1963 CE) was extracted from a ICP-MS Plutonium profile built on the top 15 cm of the short core (Table 1). Radiocarbon dates were calibrated with the IntCal13.14C calibration curve (Reimer et al., 2013), and used together with the Pu date and 2013 CE as the top of the sediment record in order to build an age-depth model (Blaaw, 2010; Fig. 2) This model was built to include the maximum number of radiocarbon dates possible, excluding the reversal dates (Telford et al., 2004). In total, six dates were identified as outliers (sensu Bronk Ramsey, 2009; Christen, 1994) and not included in the age-depth model (Table 1, Fig. 2). Classical, linear interpolation modelling was preferred to polynomic/logarithmic or Bayesian modelling acknowledging its limitations and favouring future improvement (Manzano et al., 2018). The composite sequence was built based on the coherence of the age-depth models of the short and long cores discarding an overlapping section of 3 cm from the top of the long core.

Magnetic susceptibility (MS; Sandgren and Snowball, 2001) was measured using a Bartington MS2E meter with readings every 5 mm in the long core. No MS measurements were obtained from the short core.

Loss-on-Ignition (LOI) and **grain size distribution** were analysed in 44 samples. LOI was measured after combustion at 450 °C for 4 h (Davies, 1974). Grain size distribution was obtained using a Coulter LS230 laser diffraction particle size analyser after the pre-treatment of the samples with sodium hexametaphosphate and water, as well as mixing in an ultrasonic bath.

Palynological analysis was performed every 2.5 cm on 0.5 cm-thick samples (75 samples) in the long core, and every 1 cm on 0.5 cm-thick samples in the short core (15 samples). Samples were processed according to Faegri and Iversen (1989), including density separation following Erdtman (1979). *Lycopodium* tablets were added to the samples at the onset of the process in order to calculate concentrations (Stockmarr, 1971). Palynological counting and identification (×400–1000 magnification) were assisted by the Universidad de Murcia's palynological reference collection, as well as keys and atlases (Díez et al., 1987; Faegri and Iversen, 1989; Moore et al., 1991; Reille, 1992, 1995; Sáenz, 1982; Ruiz del Castillo, 1988). Vascular plant taxonomy follows Flora Ibérica (www.floraiberica.es), if not possible, Flora Europaea or, when the author is indicated, the original species publication. Non-pollen palynomorphs (NPP) nomenclature follows van Geel (2001). The pollen sum consisted of an average of 285 upland pollen grains (trees, shrubs and herbs), and just in an exceptional case a minimum sum of 200 upland pollen grains was attained (25 cm depth). Due to the local presence of woody Brassicaceae (*Hormatophylla spinosa* and *Vella spinosa*), Brassicaceae taxa were considered shrubs rather than herbs. Percentages of all taxa were calculated on the basis of the upland pollen sum. **Microcharcoal** particles were counted on the palynological slides following Finsinger et al. (2004) and Mooney and Tinner (2011). The pollen diagram was zoned in four zones using Cavalli-Sforza chord distance based CONISS analysis. Only taxa with percentages > 5% were included in the analysis. Zonation analysis and diagram plotting were performed using Tilia (Grimm, 2011). Complete pollen diagrams plotted by age and by depth can be found in supplementary material.

Arthropod, seed and charcoal **macroremains** were extracted in 160 samples after deflocculating 1 cm^3 of sediment in tetrasodium pyrophosphate and sieving through 250 and 125 μm meshes. Counting and identification were performed at ×25–50 magnification. No macroremains were recovered in the top 5 cm.

Table 1
LdlMo Plutonium and radiocarbon dates.

Laboratory code[a]	Depth (cm)	Method	Material dated	Age (yr BP)	Calibrated age (cal. yr BP)	Median age (cal. yr BP)
	Surface	Present		−63 (2013 CE)		−63
	3,75	Plutonium	Bulk sediment	−13 (1963 CE)		−13
D-AMS 005126	25	14C	Bulk sediment	1700 ± 29	1545–1696	1602
D-AMS 005127	33	14C	Bulk sediment	2003 ± 21	1898–1994	1953
D-AMS 004807	40.5	14C	Plant Macrorremain	906 ± 28	745–913	842[b]
D-AMS 005128	44.5	14C	Bulk sediment	3747 ± 30	3986–4161	4109
D-AMS 005129	51	14C	Bulk sediment	2375 ± 34	2337–2605	2405[b]
D-AMS 005130	66	14C	Bulk sediment	4153 ± 31	4578–4826	4698
D-AMS 005131	77	14C	Bulk sediment	29,671 ± 245	28,506-29,247	28,876[b]
D-AMS 005132	82	14C	Bulk sediment	6275 ± 40	7027–7113	7211
D-AMS 005133	84	14C	Bulk sediment	5256 ± 36	5928–6178	6019[b]
D-AMS 005134	90.5	14C	Bulk sediment	6229 ± 42	7008–7255	7155[b]
D-AMS 004379	127.5	14C	Bulk sediment	6910 ± 34	7674–7825	7736
D-AMS 004380	136	14C	Bulk sediment	6785 ± 43	7576–7683	7632
D-AMS 004381	154	14C	Bulk sediment	6548 ± 31	7422–7551	7456
D-AMS 004382	165	14C	Bulk sediment	6791 ± 41	7579–7684	7635
D-AMS 004383	181	14C	Bulk sediment	7403 ± 36	8168–8332	8250
D-AMS 004384	182	14C	Bulk sediment	7334 ± 38	8023–8284	8125

[a] Reimer et al. (2013), 95% confidence intervals.

[b] Excluded from the age model.

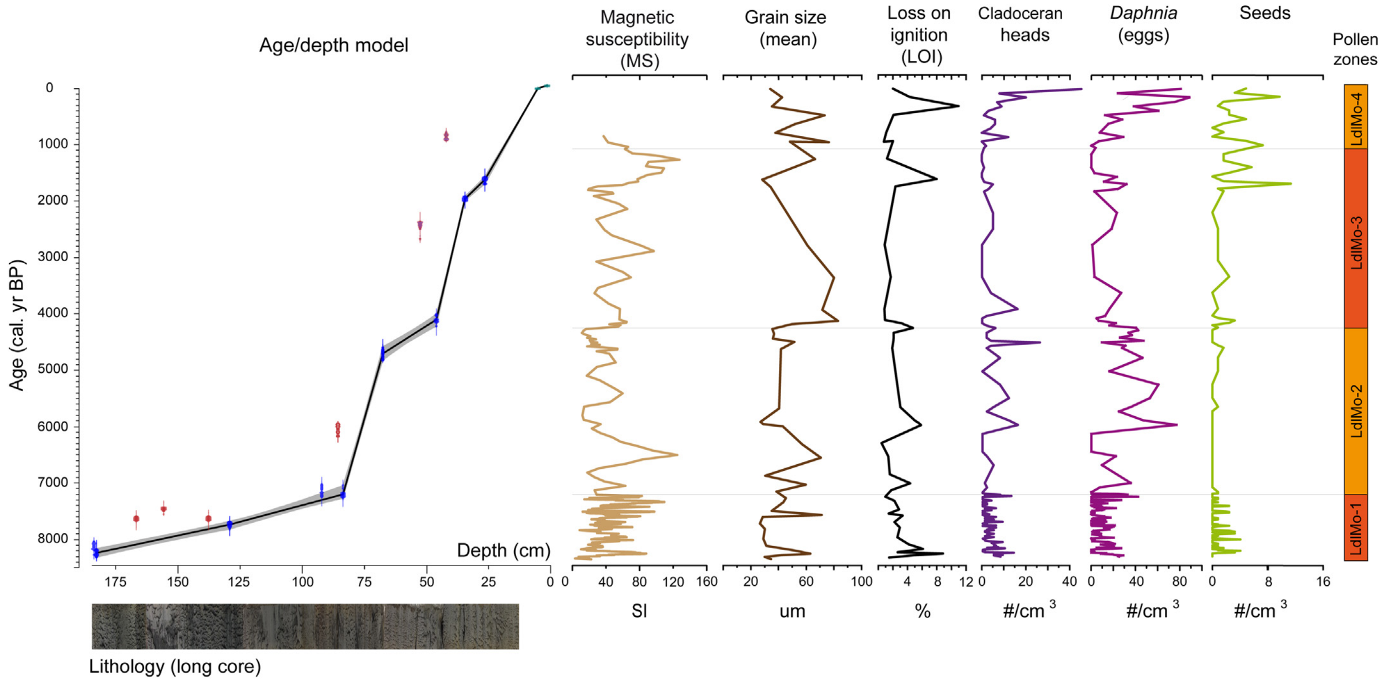

Fig. 2. Age-depth model and sedimentary log of the LdlMo lacustrine core. Records of magnetic susceptibility, grain size mean, loss-on-ignition (LOI), Cladoceran heads, *Daphnia* eggs and seed concentration are also included.

3. Results

3.1. Lithology, sediment accumulation rates, and records of grain size, LOI and magnetic susceptibility

According to the age-depth model, the LdlMo sediments, alternating clays and sandy clays, started to accumulate at ~8.4 cal. kyr BP (Fig. 2). Sediment accumulation rates (SAR) are highest before ~7.3 cal. kyr BP (82 cm), with an overall decreasing trend afterwards. The MS record shows high variability throughout the whole sequence (Fig. 2).

The onset of the LdlMo sedimentary sequence is characterised by a rise in mean grain size, reaching 65 μm. This is coeval to a peak in LOI that precedes a progressive decrease spanning to the top of the zone LdlMo-1 (Fig. 2). Values of LOI and grain size smoothly decrease until ~4.2 cal. kyr BP. Between ~4.2 and ~1.4 cal. kyr BP, grain size mean and LOI show two distinct episodes. Grain size increases from 71 to 85 μm, and LOI from 1 to 2%. Grain size, then, exhibits a gradual decrease followed by another steep rise at ~1.7 cal. kyr BP, when LOI rises from 1 to 8% (Fig. 2). During the last millennium, grain size displays a see-saw pattern while LOI displays a single maximum at 500 cal. yr BP and decreases towards the top of the sequence.

3.2. Palynological, charcoal and macroremains records

The **zone LdlMo-1** (~8.4–7.3 cal. kyr BP; 189–94 cm) shows the highest arboreal percentages for the whole record (Fig. 3). It registers the largest presence of *Pinus sylvestris/nigra* type (up to 60%), *P. halepensis/pinea* type, *P. pinaster* and *Betula*. Shrubs present low values, with *Juniperus* and *Cytisus/Genista* type as the most important shrubby types. Poaceae dominates the herbaceous assemblage, which also shows a significant presence of Caryophyllaceae, with recurring peaks in the percentages of *Herniaria* and *Spergularia* (Fig. 3). Cyperaceae and *Botrychium lunaria* are the most abundant types of the hygro-hydrophyte component, which is poorly developed (Fig. 3). The percentages of Zygnemataceae, and the concentrations of seeds and *Daphnia* eggs are fluctuant. The macro- and microcharcoal influx records show see-saw patterns (Fig. 3).

The **zone LdlMo-2** (~7.3–4.2 cal. kyr BP; 94–49 cm) is characterised by landscape stability. *Pinus* (~25%) and *Quercus* (5–10%) percentages remain constant, whereas *Quercus suber* displays the largest values in the whole record (Fig. 3). This zone shows the vanishing of the pollen signal of mesophytic taxa such as *Castanea* (at ~7 cal. kyr BP), *Corylus* (at ~5 cal. kyr BP) and *Betula* (at ~4.5 cal. kyr BP). *Cytisus/Genista* type percentages show decreasing values coeval to the increasing values of the *Juniperus*-Brassicaceae assemblage (Fig. 3). The herbaceous component shows increasing values, commanded by Poaceae, Caryophyllaceae and *Herniaria*, together with Chenopodiaceae, Ranunculaceae and *Artemisia* (Fig. 3). The microcharcoal influx record displays low, constant values contrasting with the oscillating values displayed by the macrocharcoal influx record. However, the top of the zone shows a peak in the microcharcoal influx (Fig. 3). Lacustrine vegetation is better represented in this zone than in the previous one, with larger values of Cyperaceae, Alismataceae and *Potamogeton* (Fig. 3). The upland vegetation stability contrasts with the algal fluctuations. Zygnemataceae peaks are coeval with those in Chrysophyceae, *Anabaena* and Cladoceran heads (Figs. 2 and 3).

The **zone LdlMo-3** (~4.2–1.1 cal. kyr BP; 49–18 cm) shows low arboreal percentages, with a significant decrease in the values of *P. sylvestris/nigra* type, *P. halepensis/pinea* type and deciduous *Quercus* (Fig. 3). However, evergreen *Quercus* shows similar values than in the previous zone. The *Q. suber* signal disappears at ~1.8 cal. kyr BP. *Juniperus, Cytisus/Genista* type and Brassicaceae are the most represented shrubby taxa. Mediterranean thermophytes and drought-tolerant taxa (i.e., *Phillyrea*, Lamiaceae, *Ephedra fragilis* type, *Daphne gnidium* type and Cistaceae) are more prevalent from ~3 cal. kyr BP onwards (Fig. 3). Poaceae dominates the herbaceous component, peaking at the onset of the zone and slowing decreasing its values towards the top of the zone while Caryophyllaceae percentages show increasing values. *Artemisia* becomes frequent, with average values of ~10%. Other herbaceous types such as Cichorioideae, *Aster* type, Chenopodiaceae and Ranunculaceae, are also more prevalent. The wetland assemblage (e.g., Cyperaceae, *Pteridium aquilinum* and scattered occurrences of *Potamogeton*, *Anabaena* and Zygnemataceae) lowers its importance (Fig. 3). Micro- and macrocharcoal influxes are low, the latter slightly increasing its values from ~2 cal. kyr BP, when a larger presence of seeds has also been detected (Fig. 3).

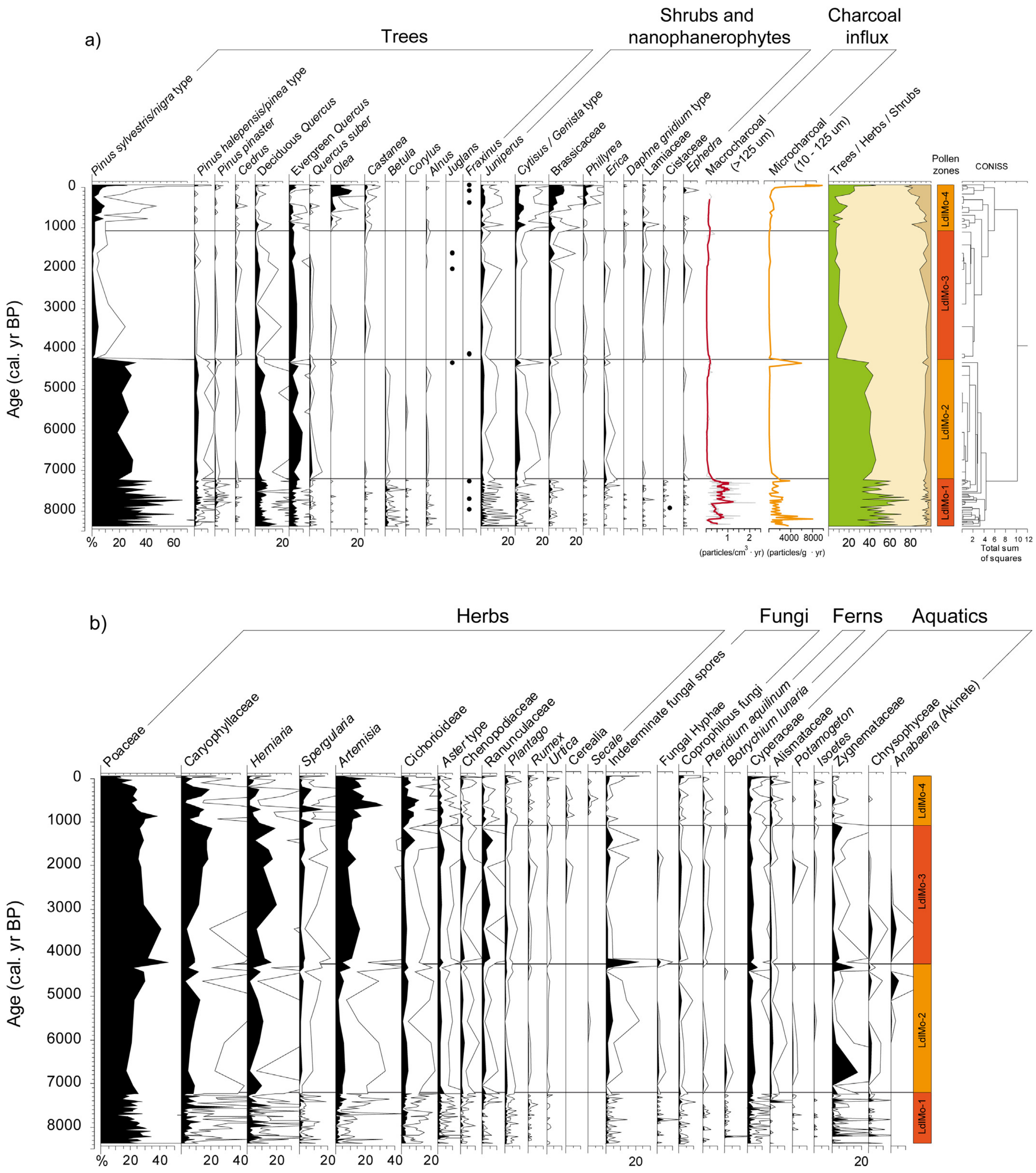

Fig. 3. Palynological (selected taxa) and charcoal diagram of the LdlMo lacustrine core plotted in age. a) Trees, shrubs, nanophanerophytes and charcoal influx. b) Herbs, fungi, ferns and aquatic taxa. Exaggeration curves (×5) are plotted in white. The complete palynological diagrams plotted by age and by depth are available in Supplementary Information 1 and 2.

The **zone LdlMo-4** (< ~1.1 cal. kyr BP; 18–0 cm) shows an increase in arboreal pollen, mainly due to *P. sylvestris/nigra* type, *Olea* and *Castanea* (Fig. 3). Alpine (*Juniperus, Cytisus/Genista* type and Brassicaceae) and thermophytic taxa (*Phillyrea*) also present increasing values. The most prominent feature of the herbaceous stratum in this zone is the see-saw pattern presented by the Caryophyllaceae-*Herniaria*-*Spergularia* assemblage, which is opposite to the pattern displayed by *Artemisia*. Deciduous *Quercus* vs. evergreen *Quercus/Quercus suber* also present alternating peak patterns (Fig. 3). Cerealia and *Secale* are recorded in this zone. Wetland taxa are represented by Cyperaceae, Alismataceae, *Isoetes* and the local presence of seeds (Figs. 2 and 3). Invertebrate remains show an increasing trend towards the top of the core, with coprophilous fungi following the same trend. Macro- and microcharcoal influx records show low values, the latter increasing abruptly in recent decades (Fig. 3).

4. Discussion

Lacustrine sedimentation and peat accumulation in Sierra Nevada started during the Holocene deglaciation. This is reflected in the oldest dates of available palaeoecological archives in the area, which follow three chronological patterns of sedimentary accretion and peat accumulation likely connected with climate events. The accumulation of lacustrine sediments in the south facing of the mountain massif, exemplified by the Laguna de Río Seco (LdRS) record (3020 masl, Fig. 1), started at ~11.5 cal. kyr BP, the Holocene onset (Anderson et al., 2011). Although lacustrine sedimentation also started during the late Holocene (~8.4–8.5 cal. kyr BP) in the north facing of Sierra Nevada, as shown by the BdlV record (2945 masl, Fig. 1), it was not after ~5.4 cal. kyr BP when peatlands became significant in this area (García-Alix et al., 2012, 2017; Jiménez-Moreno and Anderson, 2012). The LdlMo (this study, 2889 masl, Fig. 1) is in the northern slope of the massif, and the timing of the beginning of the lacustrine sediment accumulation agrees with the previously observed trend in peat accumulation in the BdlV, as the oldest sediments date back to ~8.4 cal. kyr BP. After the complete deglaciation during the Early Holocene and the retraction of the permanent snowline, high sediment accumulation rates show a large environmental dynamism. It is likely that, as reconstructed for the BdlV record, the LdlMo basin was formerly occupied by permanent snow, and it was just when the snow disappeared that environmental archives started to accumulate peat or sediments (Jiménez-Moreno and Anderson, 2012). A third common chronology for the onset of available deposits is detected in both northern and southern slopes of Sierra Nevada. The south facing Borreguiles de la Caldera (BdlC) record (2992 masl, Fig. 1) shows peat accumulation from ~4.5 cal. kyr BP (Ramos-Román et al., 2016), while the north facing Laguna de la Mula (LdlM) record (2497 masl, Fig. 1) presents lacustrine sedimentation from ~4.1 cal. kyr BP (Jiménez-Moreno et al., 2013).

4.1. Long-term vegetation response to environmental change

4.1.1. A wet Early Holocene with increased seasonality and aridity pulses (~8.4–7.3 cal. kyr BP): the importance of high-altitude Pinus forests

The maximum extension of pinewoods in the Sierra Nevada is documented by the notable presence of *P. sylvestris/nigra* type during the Early Holocene in the LdRS and BdlV records (Anderson et al., 2011; Jiménez-Moreno and Anderson, 2012), a picture also reconstructed in LdlMo (Figs. 3 and 4). The occurrence of the high-altitude pine forests evidences the Holocene highest elevation of the subalpine treeline in Sierra Nevada. This is supported by pollen rain studies in the Iberian peninsula (Andrade et al., 1994; Dorado and Ruiz-Zapata, 1994; Vázquez and Peinado, 1993) and an ongoing local pollen rain transect that shows the occurrence of *Pinus* pollen percentages of ~40–70% within pinelands (Ramos-Román *in prep*; preliminar results cited in: Ramos-Román et al., 2016). The treeline is sensitive to the length of the growing season, hence to temperature. It is likely that increased seasonality during the Early Holocene favoured the continuation of pine forests in many Southern Iberian landscapes (Anderson et al., 2011; Gil-Romera et al., 2010). However, the picture is far from stable. The palaeoecological reconstruction of the LdlMo evidences centennial-scale cold-aridity spells inferred by fluctuations in the *Pinus*-cryoxerophilous highland vegetation assemblage (Fig. 4). Centennial-scale altitudinal displacements of the treeline are observed by the contrasting patterns of *P. sylvestris/nigra* type and Caryophyllaceae (likely the cryoxerophilous *Arenaria tetraquetra* and *A. pungens*), *Herniaria* (likely the endemic *H. boissieri*) and *Spergularia* (Fig. 4). During arid pulses, decreasing winter snowpack would have allowed the upward availability of uncovered soils, as reflected by changes in the grain size distribution (Fig. 2), triggering the expansion of cryoxerophilous vegetation. Contrastingly, humid periods would have allowed the survival of the permanent snow cover for longer periods, hampering the upslope expansion of the cryoxerophilous pastures and cushion-like scrub.

Mediterranean pines (*P. pinea/halepensis* type and *P. pinaster*) occurred in the lowlands during the Early Holocene. The lowlands, however, were dominated by both evergreen and deciduous *Quercus,* as evidenced by the Padul record (Ramos-Román et al., 2018), *Quercus* occupying an ecotonal position bridging the lowland and mountain pinelands (Figs. 3 and 4). Mesophilous trees (e.g., *Betula*, *Alnus*, *Corylus* and *Castanea*) probably concentrated in riparian enclaves, and they show an important representation in zone LdlMo-1 (Fig. 3). These riparian trees seem to have tolerated the cold-aridity fluctuations within the overall warm-wet period. A significant part of the water source in the Sierra Nevada mid- and lowlands derives from groundwater discharges (Fernández Escalante et al., 2006). Summer melting and superficial runoff in the upper Sierra Nevada mountains infiltrate through the schist fractures, recharging the underlying aquifers. The resulting groundwater diffuses and forms springs, feeding watercourses and nurturing the lower-elevation vegetation. Therefore, it is likely that the persistence of mesophilous trees to the centennial-scale aridity pulses was mediated by groundwater storage.

4.1.2. Mid-Holocene decrease in seasonality and increase in aridity (~7.3–4.2 cal. kyr BP): the development of Pinus-Quercus submediterranean forests

The Mid-Holocene onset meant a progressive cooling trend due to a decrease in summer insolation (Laskar et al., 2004). A competitive readjustment between *P. sylvestris/nigra* type and evergreen/deciduous *Quercus* is observed in many SW European sites because of the decrease in seasonality (e.g., Carrión, 2002; Carrión et al., 2001, 2003, 2007; Fletcher and Sánchez-Goñi, 2008; Pantaleón-Cano et al., 2003). In Sierra Nevada, this is observed from ~7 to 4.5/4 cal. kyr BP in LdRS and BdlV (Anderson et al., 2011; Jiménez-Moreno and Anderson, 2012), and from ~7.3 to 4.2 cal. kyr BP in the LdlMo (Fig. 4). The three palaeoenvironmental sequences record the presence of pine together with a large importance of deciduous *Quercus,* most likely the marcescent *Q. pyrenaica* and *Q. faginea,* pointing to the development of submediterranean vegetation in Sierra Nevada (Figs. 4 and 5).

The *Pinus-Quercus* submediterranean forests persist during a period that experiences a decrease in humidity. The latter is evidenced by the virtual disappearance of some mesophytic taxa (*Alnus, Betula, Corylus*), the development of the Brassicaceae-*Juniperus* alpine scrub, and the rising trend in the values of Poaceae and Asteraceae (Figs. 3 and 4). The invasion of the submediterranean forests by evergreen *Quercus* (most likely *Quercus rotundifolia*) is also registered during the aridification trend. Very interestingly, the N and S aspects of Sierra Nevada seem to have responded differently to the generalised Mid-Holocene aridification trend identified for the southern Iberian Peninsula (e.g., Carrión, 2002; Carrión et al., 2001, 2003, 2007; Fletcher and Sánchez-Goñi, 2008; Pantaleón-Cano et al., 2003). The millennial-scale persistence of submediterranean *Quercus-Pinus* forests in the N aspect of Sierra Nevada contrasts with a gradual *Pinus* forest decline and *Quercus* forest increase in the S slopes (Anderson et al., 2011). The different vegetation responses to the aridification trend is attributed to the probable different species composition in the pinelands of the N and S slopes (see section 4.3.1).

4.1.3. Late Holocene aridity crisis (< ~4.2 cal. kyr BP) and forest collapse

The Late Holocene experienced an aridity crisis, as seen in many SW European environmental reconstructions (e.g., Carrión et al., 2003, 2010; Pantaleón Cano et al., 2003). In the specific case of Sierra Nevada, lower lake levels have been inferred in several records (Anderson

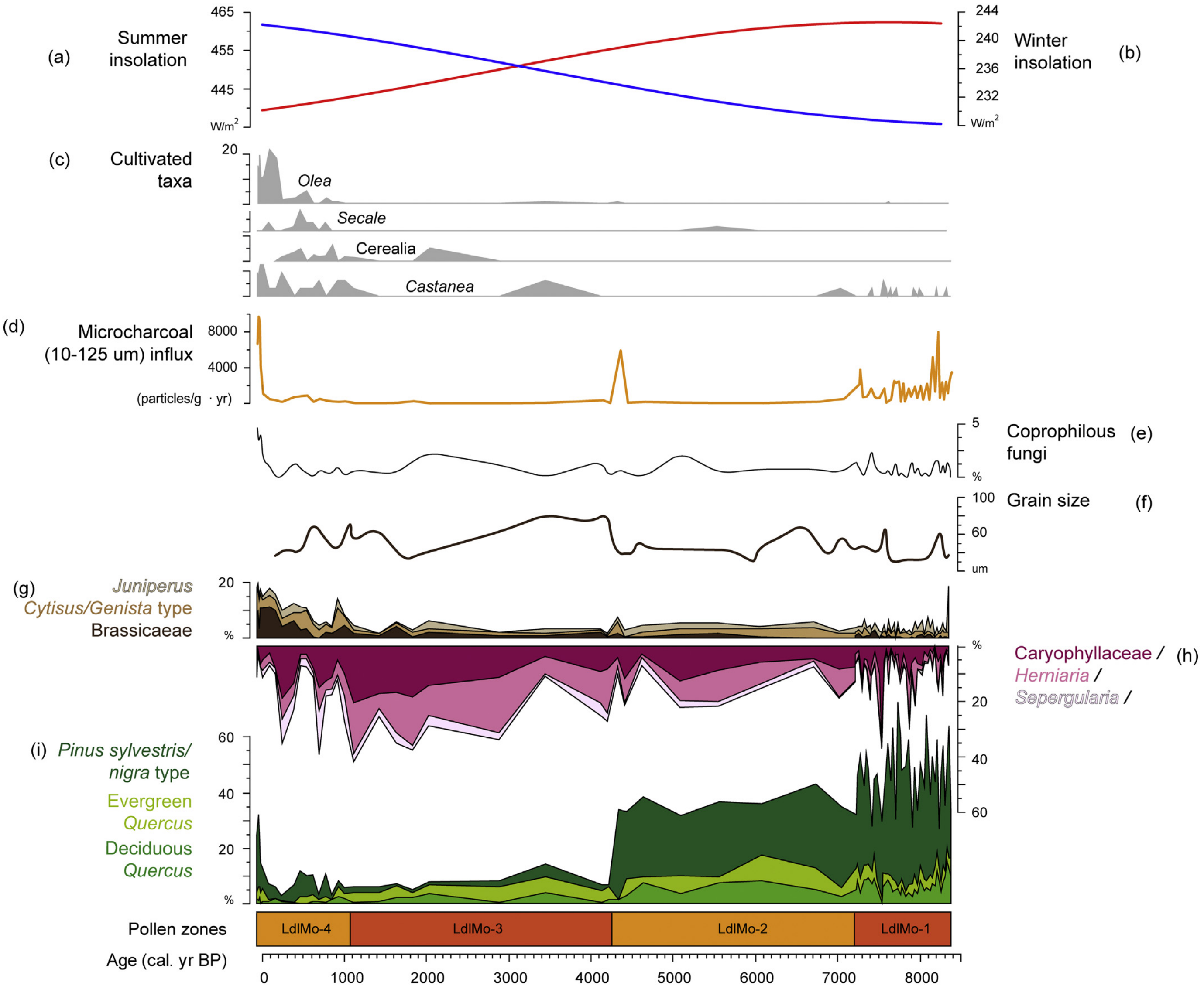

Fig. 4. Chronology of the Holocene landscape changes in Sierra Nevada after the LdlMo palaeoecological record. a) and b) Summer and winter insolation at 37°N (Laskar et al., 2004). c) Percentage curves of likely cultivated taxa. d) Microcharcoal (10–125 µm) influx. e) Percentage of coprophilous fungi. f) Grain size. g) Subalpine scrub abundance (Brassicaeae, *Cytisus/Genista* type and *Juniperus*). h) Cryoromediteranean pastures abundance (Caryophyllaceae, *Herniaria* and *Spergularia*). i) Percentages of deciduous *Quercus*, evergreen *Quercus* and *Pinus sylvestris/nigra* type.

et al., 2011; Jiménez-Moreno and Anderson, 2012; Jiménez-Moreno et al., 2013; Ramos-Román et al., 2016 and references therein). The LdlMo record shows the depletion of snow-favoured alpine and subalpine scrub (Brassicaceae, *Cytisus/Genista* type, *Juniperus*) in favour of Poaceae and *Artemisia* (Figs. 3 and 4), suggesting sparser vegetation in the summit areas (Valle, 1985, 2003). In addition, from ~4.2 cal. kyr BP onwards, the LdlMo record displays a drastic landscape opening manifested by abrupt drops in both arboreal pollen percentages (Fig. 4) and concentrations (Supplementary information 3). This drastic landscape opening happens just after a peak in the microcharcoal influx record (Fig. 4), suggesting higher fire activity triggered by the onset of the Late Holocene aridity crisis. The formerly extensive *Pinus-Quercus* submediterranean forest collapsed in Sierra Nevada about four millennia ago (Figs. 4 and 5).

After the ~4.2 cal. kyr BP forest collapse much of the thermic domain suitable for trees was probably deprived of soils due to the combination of steep slopes, deforestation and prevailing arid conditions. It is, therefore, expected that the Late Holocene vegetation of the Sierra Nevada highlands acquired a strong edaphophilous character. This is supported by the rising importance in subalpine scrub, alpine elements and xerophytes (Figs. 3 and 4). Late Holocene tree cover would have been restricted to the lowlands only, as well as likely dominated by open forests of the evergreen *Q. rotundifolia* (Figs. 4 and 5, Ramos-Román et al., 2018), with the secondary participation of other trees (i.e., *Quercus suber, Pinus halepensis*) that occupied favourable positions such as small basins and moister soils.

4.1.4. Late Holocene record of human activity

The importance of *Rumex*, *Plantago* and *Urtica* since four millennia ago frames the onset of human-favoured taxa. This is evidenced by land-use changes inferred by the larger occurrence of likely cultivated taxa such as *Castanea*, *Olea* and Cerealia, as well as of indicators of grazing activities such as coprophilous fungi (Fig. 4). Anthropogenic activities intensify in the last ten centuries, when crops (e.g., Cerealia, *Secale*, *Olea* and *Castanea*) are more abundant.

Interestingly, crops were not limited to the lowlands, as it has been documented that the cultivation of rye expanded up to 2300 masl (Boissier, 1839–1845). Further impact on the high-altitude landscapes during the last centuries is evidenced by the rise of coprophilous fungi not only in the LdlMo record (Fig. 4), but also in the LdRS and BdlC

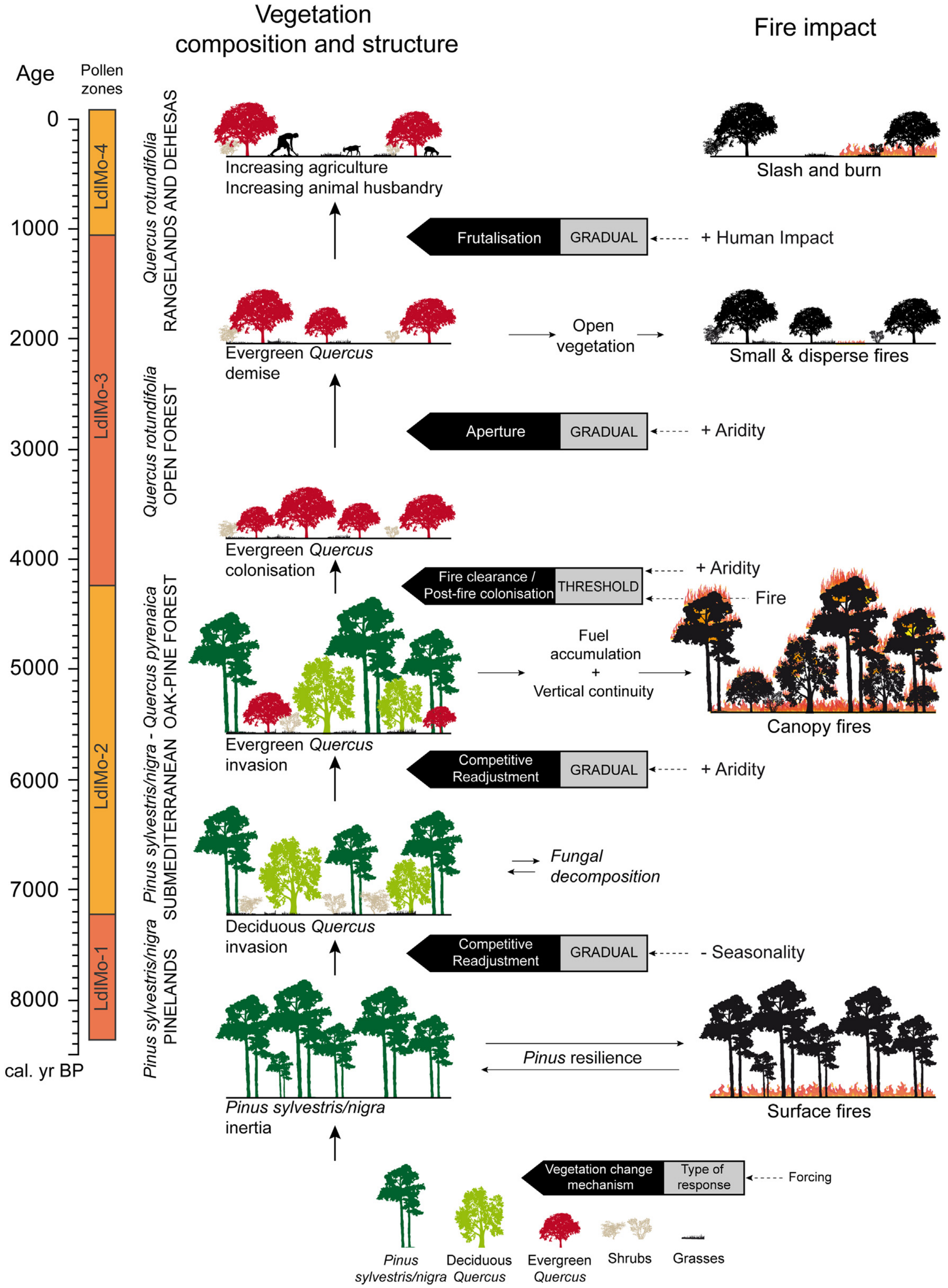

Fig. 5. Vegetation composition, structure and fire impact for the last ~8300 years in the Sierra Nevada mountains after the palaeoecological record obtained from the LdlMo lacustrine sequence. Inferred vegetation change mechanism, type of vegetation response, and climatic/anthropogenic forcings are outlined.

records (Anderson et al., 2011; Ramos-Román et al., 2016). The chronological frame of this grazing intensification agrees with the recorded evidence of animal husbandry in the late 18th century (Boissier, 1839–1845). However, coprophilous fungi from the onset of the LdlMo sequence (Fig. 4) may indicate that wild game, likely Spanish ibex (*Capra pyrenaica*), has inhabited the mountains and used the permanent water points of the Sierra Nevada highlands for the last eight millennia.

The landscape opening that started four millennia ago seems to have culminated during the 18th–19th centuries, when the lowest arboreal cover for the last eight millennia is registered (Figs. 3 and 4). In fact, a widely open landscape is pictured in *Voyage dans le midi de l'Espagne* (Boissier, 1839–1845). In this first comprehensive geobotanical study of

Sierra Nevada, trees are recorded in scattered patches up to ~1900 masl. According to Boissier (1839–1845), monospecific patches of *P. sylvestris, Q. pyrenaica* and *Q. rotundifolia* overlapped altitudinally, their distribution agreeing with edaphic rather than bioclimatic features. Finally, the 20th century *Pinus* pollen peak (Fig. 4) reflects the widespread afforestation with pines to prevent the soil erosion triggered by the open landscapes of the previous centuries (Arias-Abellán, 1981).

4.2. Forest composition and fire links

The LdlMo charcoal influx records show long-term fluctuations (Figs. 3 and 4). These fluctuations are related not only to the fuel load, as shown in Mediterranean landscapes (Gil-Romera et al., 2010), but also to its spatial distribution (Fig. 5). Thanks to the palaeoecological records recovered from the LdlMo, fire dynamics can be explained by the dominant forest-types that inhabited the mountainous landscape for the last eight millennia. In pine forests, such as the reconstructed at ~8.4–7.3 cal. kyr BP in Sierra Nevada (Fig. 5), the distribution of flammable materials is spatially segregated. Pine remains and resinous litter of difficult degradation accumulate on the ground, separated by ‘flameproof’ trunks from the fire-sensitive crowns (Fernandes et al., 2008; Ordoñez et al., 2013). Early Holocene pine forests' wildfires must have occurred most likely as surface fires (Fig. 5), with no major consequences for adult trees (Morales-Molino et al., 2017). Furthermore, surface fires reduce ground-level competition, and they have been observed to promote the establishment of the shade-tolerant *Pinus nigra* seedlings (Escudero et al., 1999; Ordoñez et al., 2004). Thus, recurrent surface fires probably contributed to the postglacial inertia of pinelands in Southern Iberia (Gil-Romera et al., 2010).

Mixed submediterranean *Pinus-Quercus* formations (Blanco et al., 2005; Sánchez de Dios, 2004; Sánchez de Dios et al., 2009), contrastingly, produce less flammable litter (Ganteaume et al., 2014). In addition, this less flammable litter is easily decomposed owing to enhanced fungal activity (Conn and Dighton, 2000). From ~7.3 to 4.2 cal. kyr BP, when mixed pine-oak forests are reconstructed in Sierra Nevada (Figs. 4 and 5), the presence of fungal spores is the highest for the entire LdlMo palaeoecological record (Fig. 4). In a context of attenuated seasonality, competition for litter between fungal decay and fire explains the low charcoal influx detected during the Mid-Holocene. Although fungal activity would have fuel-depleted the mixed *Pinus-Quercus* formations and, thus, repressed fire incidence, these formations constitute multistratified forests (Sánchez de Dios et al., 2009), hence providing vertical continuity for surface fires to spread into the canopy in case of punctual fires (Fig. 5). In fact, the ~4.2 cal. kyr BP arid spell, that would have likely repressed the fungal activity, must have triggered drastic fire episodes in the LdlMo-2 and LdlM-3 pollen zone boundary (Figs. 4 and 5). Fires, escalating to the canopy, likely triggered an abrupt shift from the mixed submediterranean *Pinus-Quercus* forests to evergreen *Quercus* sparse vegetation, as reconstructed by the forest collapse four thousand years ago (Figs. 4 and 5).

By the Late Holocene, the Sierra Nevada had few forests remaining (Figs. 4 and 5; Anderson et al., 2011; Jiménez-Moreno and Anderson, 2012; Jiménez-Moreno et al., 2013; Ramos-Román et al., 2016). Fire incidence, hence, would have been strongly limited by the sparsity of available fuel, as recorded with the low values in charcoal influx (Fig. 4). It is only very recently, in the last centuries, when an intensification of burning is recorded linked to the afforestation with pines and the increasing human impact in the Sierra Nevada mountains (Figs. 4 and 5).

4.3. A palaeoecological perspective to the understanding of the current Sierra Nevada landscape

The Baetic Ranges epitomises a geobotanical puzzle (Rivas Martínez, 1987; Valle, 1985, 2003). A holistic explanation for the extant vegetation of Sierra Nevada has challenged geobotanists for centuries, and several interpretations of its flora and vegetation have arisen from different neontological approaches (Blanca, 2000; Boissier 1839–1845; de Clemente, 1804; Losa Quintana et al., 1986; Quézel, 1953; Rivas Goday and Mayor, 1966; Rivas Martínez, 1987; Valle, 1985, 2003). Here, we attempt a geobotanical explanation integrating our new high-resolution, multi-proxy palaeoecological record in the context of the available floristic, biogeographical, cultural and palaeobotanical information for the area in order to shed light into the occurrence of some of the singular vegetation still thriving in Sierra Nevada.

4.3.1. Southern Baetic Pinus sylvestris ssp. nevadensis and Pinus nigra forests

Sierra Nevada, along with the nearby Sierra de Baza, hosts the world's southernmost *Pinus sylvestris* forests. The Quaternary history of migration and isolation has left morphological (Gaussen, 1960), ecological (Nicola and Gandullo, 1969) and genetic imprint (Prus-Głowacki et al., 2003; Sinclair et al., 1999; Soranzo et al., 2000) in such populations, supporting the classification of an endemic subspecies: *P. sylvestris* ssp. *nevadensis*. However, palaeobotanical micro and macroremains suggest that the most extended pine species during the Last Glacial in the Mediterranean was *P. nigra* (Desprat et al., 2015; Postigo-Mijarra et al., 2010a). The difficulty of identifying pollen grains beyond the *P. sylvestris/nigra* type hinders conclusions about the Holocene composition of Sierra Nevada pinelands. Nevertheless, the Sierra Nevada palaeobotanical data support widespread representation of mountain *Pinus* forests at the Early and Mid-Holocene (this study; Anderson et al., 2011; Jiménez-Moreno and Anderson, 2012).

It is unlikely, however, that Late Glacial conditions with a great proportion of the high-altitude zones under permanent snows or glaciers (Gómez-Ortiz et al., 2005), left altitudinal breadth for vegetation belt segregation along the steep slopes of Sierra Nevada mountains. Consequently, mixed *P. nigra* and *P. sylvestris* ssp. *nevadensis* would have likely occurred in the lowlands during the cold Late Pleistocene (Pons and Reille, 1988). Although rare, a modern analogue of these hypothetical mixed pinelands occurs at scattered locations, marking the treeline in some areas of the siliceous Iberian Central System. The small mixed patches of *P. sylvestris* and *P. nigra* that mark the timberline in some areas of the Sierra de Gredos are considered the last vestiges of more extended pinelands (Génova et al., 2009). Remarkably, these mixed groves, also display a more open structure with *Q. pyrenaica* taking over the gaps left by collapsing trees. A similar situation might have arisen along the Mid-Holocene in the Sierra Nevada highlands, and recorded in the LdlMo record and the other Holocene palaeoecological records (Fig. 5; Anderson et al., 2011; Jiménez-Moreno and Anderson, 2012; Jiménez-Moreno et al., 2013; Ramos-Román et al., 2016).

The moister conditions of the Early Holocene likely promoted the expansion of *P. sylvestris* ssp. *nevadensis* in areas where *P. nigra* was already living. Then, the Mid-Holocene decrease in seasonality and aridity intensification could have triggered a segregation of the mixed pinelands. *P. nigra* likely took over higher, colder and more xeric locations, while *P. sylvestris* ssp. *nevadensis* the lower and moister ones. At a landscape scale, it is probable that *P. sylvestris* dominated in the moister N aspect, and *P. nigra* in the S aspect of the mountains.

The Mid-Holocene progressive forest demise and invasion of the pinelands by deciduous *Quercus*, likely *Q. pyrenaica*, triggered a forest transition towards more open mixed *Pinus-Quercus* forests in the northern slope of the Sierra Nevada mountains. However, this invasion of the pinelands by deciduous *Quercus* was limited in the southern slopes, where effective humidity and insolation are more restrictive (Rams Sánchez, 2007). This feature is reflected in the magnitude of the deciduous *Quercus* pollen signal in LdlMo (N facing, this study) and LdRS (S facing, Anderson et al., 2011). The different forest composition in the two mountain slopes is also reflected in the different vegetation response to the ~4.2 cal. kyr BP arid event. While in the northern slope mixed, multi-stratified submediterranean *P. sylvestris-P. nigra-Q. pyrenaica* forests collapsed after a drastic fire event (this study, Figs. 4 and 5), the more xeric southern slope vegetated by *P. nigra* formations experienced a progressive decline (LdRS; Anderson et al., 2011).

Supporting the role of abrupt fire events in the shift from mixed *Pinus-Quercus* submediterranean forests to open *Quercus* formations, the extant *P. sylvestris* ssp. *nevadensis* woods found in Sierra Nevada survive only in locations where the calcifuge *Q. pyrenaica* is excluded, and thus where multi-stratified forests have never developed. The present-day Sierra Nevada pinelands are restricted to the calcareous enclaves in the western areas: the Monachil valley, the Barranco del Espinar and the Cerro del Tesoro between 1600 and 1900 masl (Blanca, 2000; Olmedo-Cobo et al., 2017). The pinelands in the Sierra de Baza, only ~40 km inland, are open forests on metamorphic, siliceous substrates, where deciduous *Quercus* are not lithology-restricted. However, the Baza pinelands are situated at higher altitudes (> 1800 masl) where the vegetative period is too short for the development of *Q. pyrenaica* or other broadleaved forests (Gómez Mercado and Valle, 1986). In both cases, *P. sylvestris* ssp. *nevadensis* occupies N facing, moister and cooler stations, while *P. nigra,* marking the timberline, grows in more xeric areas, in isolated, disperse stands.

4.3.2. *Quercus pyrenaica* at the treeline

The extant submediterranean *Q. pyrenaica* woods in Sierra Nevada are of great floristic and ecological singularity (Vilches de la Serna, 2014), as they include not only the typically submediterranean species such *as Acer opalus* ssp. *granatense, Daphne laureola or Lonicera arborea* (Sánchez de Dios, 2004) but also Mediterranean ones such as *Cytisus scoparius* ssp. *reverchoni*, *Daphne gnidium* or *Quercus rotundifolia* (Lorite et al., 2008). Under the prevailing and accentuated Mediterranean macroclimate, *Q. pyrenaica* forests represent a marginal formation (Blanca, 2000; Rams Sánchez, 2007). Their location at the timberline in Sierra Nevada is restricted to valleys, and it is explained by edaphic water compensation (Vilches de la Serna, 2014). Soil denudation elsewhere in the Sierra Nevada highlands together with the Late Holocene aridity crisis might have hampered the development of high-altitude forested belts in the N aspect of Sierra Nevada after the ~4.2 cal. kyr BP drastic fire event recorded in the LdlMo sequence (Fig. 4).

4.3.3. Broadleaved mesophytes and *Cedrus*

Betula, Corylus, Alnus, Castanea, Fraxinus, Ilex and *Populus* palaeobotanical microremains appear in Sierra Nevada during the Holocene (this study; Anderson et al., 2011; Jiménez-Moreno and Anderson, 2012; Ramos-Román et al., 2018) in agreement with the regional mesophytic maximum identified for S Iberia (Carrión, 2002). The presence of *Castanea* is noteworthy before any agricultural evidence in LdlMo, providing additional evidence to the naturalness of *Castanea* in S Iberia (Anderson et al., 2011; Carrión et al., 2008; García-Amorena et al., 2007; Morales-Molino et al., 2011; Pons and Reille, 1988). Evidence of the presence of *Juglans* in the nearby ranges can be traced back to the Upper Pleistocene (Carrión and Sánchez Gómez, 1992) albeit pollen evidence from Sierra Nevada only dates as far back as the Mid- to Late Holocene transition (this study, Fig. 3). Its origin, whether cultivated or not, is uncertain.

Cedrus is recorded in the LdlMo palaeoecological record (Fig. 3). The presence of *Cedrus* in Southern European Mediterranean palaeoenvironmental records has been much debated. Magri and Parra (2002) attribute the detection of *Cedrus* during arid and/or deforested periods to long-distance wind transport from N Africa. Under such circumstances, usually low pollen concentrations are found in the sediments, allowing for an overrepresentation of long-distant taxa (Magri and Parra, 2002). On the one hand, Sierra Nevada palaeoenvironmental data show *Cedrus* pollen after the Late Holocene forest collapse (this study; Anderson et al., 2011), a scenario compatible with Magri and Parra (2002). On the other hand, the presence of *Cedrus* is also detected before the aridity crisis, when forests where extensive (Fig. 3), a scenario not compatible with Magri and Parra (2002). Alternatively, it has been suggested that relict stands of cedars survived hidden in the Baetic Ranges during the Holocene (Postigo-Mijarra et al., 2010b). However, the lack of macroremains in the northern coast of the Mediterranean hampers a definitive conclusion on its Quaternary presence in Iberia (Magri and Parra, 2002).

5. Conclusions

The Holocene landscape history of Sierra Nevada has been influenced by climatic, edaphic and anthropogenic drivers. The pine forests that dominated the Sierra Nevada landscape during the Early Holocene were affected by a decrease in seasonality around seven millennia ago. This allowed the proliferation of deciduous and evergreen *Quercus* and the establishment of submediterranean mixed *Pinus-Quercus* forests that dominated the landscape for almost three millennia, between ~7.3 and 4.2 cal. kyr BP. Owing to the different structural complexity of the pine forest vs. the mixed pine-oak forests, the latter responded drastically to the fire activity detected at ~4.2 cal. kyr BP, triggering the collapse of the forest cover in Sierra Nevada. In addition, Late Holocene landscapes were also impacted by agricultural and grazing activities, that intensified in the last centuries. It is also in recent times when pine afforestation increased the forest cover in Sierra Nevada. The scattered forests that inhabit the landscape nowadays rely on soil moisture compensation to survive summer drought. This is the case of the *P. sylvestris* ssp. *nevadensis* pinelands or the *Q. pyrenaica* forests that mark the current timberline. Thus, forest cover in Sierra Nevada has not only climatic and anthropogenic imprints, but it is also marked by a strong edaphic and lithologic influence.

Under the current global change scenario, the projected increase of temperatures and subsequent aridification of the Mediterranean will notably affect European landscapes (IPCC, 2013). Forecasts include a northwards expansion of the summer-drought, meaning the spread of Mediterranean-like conditions to new areas (Barredo et al., 2016), including to forested mountains. This means that the mountainous forests inhabiting territories adjacent to the Mediterranean Region could experience analogous responses to those detected in the Sierra Nevada forests to the Late Holocene aridification, moving from temperate to submediterranean and then Mediterranean formations.

Author contributions

JSC and GJM obtained funding for the development of this work. GJM, AGA and RSA planned and conducted fieldwork, subsampled and described the sediments. JLT, HA and JLGP studied grain size, LOI and macroremains. SM performed palynological and charcoal analyses. SM wrote the first draft of this article, assisted by LLM. JSC, LLM and DSM, contributed with palaeoecological and geobotanical interpretations. All authors, especially LLM, have revised and contributed to the final version of this manuscript and agreed on its submission in the present form.

Acknowledgements

We thank the following funding bodies: Organismo Autónomo de Parques Nacionales (Ministerio de Medio Ambiente y Medio Rural y Marino; grant number 261-2011), Ministerio de Economía y Competitividad, (projects CGL-BOS-2012-34717 and CGL-BOS 2015-68604), Fondo Europeo de Desarrollo Regional FEDER and the research group RNM0190 (Junta de Andalucía; project CGL2013-47038-R), Consejería de Economía, Innovación, Ciencia y Empleo de la Junta de Andalucía (Project P11-RNM-7332), and Fundación Séneca (project 19434/PI/14). SM was supported by a FPI scholarship (BES-2013-064626). RSA thanks Northern Arizona University's College of Forestry, Engineering and Natural Sciences for travel funds. JLT is supported by a Small Carnegie Trust Grant. AGA was supported by a Ramón y Cajal fellowship (RYC-2015-18966) from the Spanish MINECO. Michael E. Ketterer (Metropolitan State University) is thanked for providing the Pu analysis.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gloplacha.2019.02.006.

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