Rapid climatic changes and resilient vegetation during the Lateglacial and Holocene in a continental region of south-western Europe

Josu Aranbarri (1, 2, 3*), Penélope González-Sampériz (1), Blas Valero-Garcés (1), Ana Moreno (1), Graciela Gil-Romera (1), Miguel Sevilla-Callejo (1), Eduardo García-Prieto (1); Federico Di Rita (2), M. Pilar Mata (4), Mario Morellón (5), Donatella Magri (2), Julio Rodríguez-Lázaro (3), José S. Carrión (6)

(1) Instituto Pirenaico de Ecología-CSIC Avda. Montañana 1005, 50059 Zaragoza, Spain

josu.aran@ipe.csic.es; pgonzal@ipe.csic.es; blas@ipe.csic.es; amoreno@ipe.csic.es; graciela.gil@ipe.csic.es; msevilla@ipe.csic.es; eduardogpf@ipe.csic.es

(2) Dipartimento di Biologia Ambientale, Sapienza Università di Roma, Piazzale Aldo Moro, 5, 00185 Rome, Italy josu.aranbarri@uniroma1.it; federico.dirita@uniroma1.it; donatella.magri@uniroma1.it

(3) Departmento de Estratigrafía y Paleontología, Universidad del Pais Vasco-Euskal Herriko Unibertsitatea, B. Sarriena s/n, Ap. 644, 48080 Bilbao, Spain

julio.rodriguez@ehu.es

(4) Instituto Geológico y Minero de España, C. La Calera, 1, 28760 Tres Cantos, Spain

p.mata@igme.es

(5) Instituto de Geociencias-CSIC, UCM, Universidad Complutense de Madrid, C. José Antonio Nováis, 2, 28040, Madrid, Spain mario.morellon@igeo.ucm-csic.es

(6) Departmento de Biología Vegetal, Universidad de Murcia, 30100 Murcia, Spain

carrion@um.es

* Author for correspondence: josu.aran@ipe.csic.es

Abstract

Palynological, sedimentological and geochemical analyses performed on the Villarquemado paleolake sequence (987 m a.s.l, 40º30’N; 1º18’W) reveal the vegetation dynamics and climate variability in continental Iberia over the last 13500 cal yr BP. The Lateglacial and early Holocene periods are characterized by arid conditions with a stable landscape dominated by pinewoods and steppe until ca. 7780 cal yr BP, despite sedimentological evidence for large paleohydrological fluctuations in the paleolake. The most humid phase occurred between ca. 7780-5000 cal yr BP and was characterized by the maximum spread of mesophytes (e.g., *Betula*, *Corylus*, *Quercus faginea* type), the expansion of a mixed Mediterranean oak woodland with evergreen *Quercus* as dominant forest communities and more frequent higher lake level periods. The return of a dense pinewood synchronous with the depletion of mesophytes characterizes the mid-late Holocene transition (ca. 5000 cal yr BP) most likely as a consequence of an increasing aridity that coincides with the reappearance of a shallow, carbonate wetland environment. The paleohydrological and vegetation evolution shows similarities with other continental Mediterranean areas of Iberia and demonstrates a marked resilience of terrestrial vegetation and gradual responses to millennial-scale climate fluctuations. Human impact is negligible until the Ibero-Roman period (ca. 2500 cal yr BP) when a major deforestation occurred in the nearby pine forest. The last 1500 years are characterized by increasing landscape management, mainly associated with grazing practices shaping the current landscape.

Key words: Holocene, Multiproxy reconstruction, Vegetation resilience, Pinewoods, Aridity, Continental Iberia

1. Introduction

The progressive increase in the number of well-dated, high-resolution Holocene climate records in both marine and continental areas (Hoek et al., 2008; Lowe et al., 2008) has demonstrated the existence of complex millennial-scale oscillations and rapid climate changes in response to both extraterrestrial forcings (e.g., orbital parameters, insolation, etc.) and internal mechanisms (e.g., changes in deep-ocean circulation, internal climate system variability) (Bond et al., 1997; Alley et al., 2003; Mayewski et al., 2004; Denton and Broecker, 2008; Wanner et al., 2008; Renssen et al., 2009). In particular, the western Mediterranean Basin, strategically located under the incursion of North-Atlantic storm tracks and the influence of a high pressure system in summer-months, is a fundamental region to understand the climate evolution and the vegetation response to abrupt changes and perturbations originated at high (Fletcher and Sánchez Goñi, 2008) and lower latitudes (Peyron et al., 2011). Indeed, several marine cores from the western Iberian margin demonstrate the impact of short-lived Holocene climatic events (e.g., Preboreal Oscillation, 8200 cal yr BP event, 4200 cal yr BP aridity crisis) on vegetation firstly identified in North Atlantic cores (Alley et al., 1997; Björck et al., 1997; Rasmussen et al., 2007) and then recorded in the Iberian Peninsula as dry spells and probably cool conditions (Cacho et al., 2001; Frigola et al., 2007; Combourieu Nebout et al., 2009; Fletcher et al., 2010). Iberian sedimentary sequences have reported similar Holocene oscillations, clearly documented by prominent peaks of xerophytes in pollen records (Muñoz Sobrino et al., 2005; González-Sampériz et al., 2006; Fletcher et al., 2007; Moreno et al., 2011; Pérez-Sánz et al., 2013), by abrupt drops in lake water-levels (Carrión, 2002; González-Sampériz et al., 2008; Martín-Puertas et al., 2008; Morellón et al., 2009), and complex patterns of human adaptations (González-Sampériz et al., 2009; Cortés-Sánchez et al., 2012).

Regarding ecosystem responses to climate change, recent reviews have highlighted the unidirectional response of the Iberian phytodiversity throughout the late Quaternary (Carrión et al., 2010a; González-Sampériz et al., 2010), where regional ecological dissimilarities, enhanced by particular orographic and edaphic features, have prevented the unraveling of common climatic patterns. Ecosystem inertia to Lateglacial and Holocene climate changes has been a clear example of the mentioned unidirectional trend (e.g., Carrión and van Geel, 1999; Franco-Múgica et al., 2001, 2005; García-Antón et al. 2011; Morales-Molino et al., 2012), being long-term pinewood resilience the main distinctive aspect of wide areas of continental Iberia (Rubiales et al., 2010, and references therein).

Despite the number of Lateglacial and Holocene palaeoenvironmental sequences in the Iberian Peninsula increased during the last decades (Carrión et al., 2010a and references therein), the continental lowlands of Iberia have hardly been investigated, leaving a palaeobiogeographical gap between inner continental mountains and coastal areas. Climatically located near the Ebro Basin, the Iberian Range borders the northernmost area of truly semi-arid climate in Europe, whose patchy and fragile steppe-like vegetation is strongly conditioned by an arid climate regime and edaphic constraints (Vicente-Serrano et al., 2012; Pueyo et al., 2013). Permanent lakes are absent in the region and therefore, most of the regional paleorecords have been obtained from large ephemeral or hypersaline lakes (Valero-Garcés et al., 2000a,b, 2004; Davis and Stevenson. 2007; Luzón et al., 2007; González-Sampériz et al., 2008; Sancho et al., 2011; Gutiérrez et al., 2013), where recurrent hiatuses and complex geochemical processes often hamper chronological control and pollen preservation, preventing continuous high-resolution environmental reconstructions (González-Sampériz et al., 2008). Further southwest from the Ebro Basin, studies providing detailed climatic oscillations are available. These are derived mainly from lake level fluctuations and paleoflood frequency records, although they cover relatively short timescales spanning only the last three millennia (Moreno et al., 2008; Romero-Viana et al., 2011; López-Blanco et al., 2012; Barreiro-Lostres et al., 2013). Additional paleoenvironmental information, somewhat fragmentary and influenced by local peculiarities, is provided by geomorphological (Valero-Garcés et al., 2008; Constante et al., 2011) and archaeological studies (González-Sampériz et al., 2009; Aura et al., 2011; Utrilla et al., 2012).

Based on a multiproxy approach, the well-dated and continuous sedimentary sequence obtained from the Villarquemado paleolake offers the possibility to reconstruct the postglacial palaeoenvironmental history of a poorly-studied, ecotonal and continental, Mediterranean area. The main goals of the current study are to:

1) Understand both regional and local vegetation dynamics and hydrological response to the last ca. 13500 cal yr BP climate variability.

2) Place the Villarquemado vegetation development in regional context through correlation with other well-dated pollen records.

3) Explore the sensitivity of this and other ecotonal regions to detect Holocene abrupt climate changes, especially in areas where pinewoods have been the dominant communities.

2. Regional Setting

Villarquemado paleolake (40º30'N; 1º18'W, Figure 1) is located at about 1000 m a.s.l., in the Jiloca Basin (Iberian Range, NE Spain). This is a 60 km long, 6-10 km wide, N-S half-graben, bounded by NW-SE trending normal faults. The depression belongs to a series of intramontane basins developed in the Iberian Range during the second extensional episode that started in the Upper Pliocene (Simón-Gómez, 1989; Casas-

Sainz and De Vicente, 2009). The change from endorheic to exorheic conditions in these depressions occurred during the Neogene and Plio-Quaternary through the capture of the basins by the external drainage network and headwater erosion (Gutiérrez and Gracia, 1997). The Jiloca river captured the Daroca half-graben and subsequently the next depression to the south, the Jiloca Depression (Gracia et al., 2003). However the south-central sector of this depression remained an endorheic basin until it was artificially drained in the 18th century, when the maximum flooded area was 11.3 km^2 and the water depth up to 2.8 m (Rubio, 2004).

The current climate of the region is continental Mediterranean, characterized by severe summer droughts, strong seasonal and diurnal temperature oscillations and by relatively low precipitation values (Figure 2B). The maximum absolute temperature is about 40 ºC in summer and the winter minimum can reach -15 ºC with frequent freezing days in the region. The mean annual precipitation in the area is about 380 mm (Figure 2B: Cella station, 1023 m a.s.l.), with large interannual variability and irregular distribution through the year, while higher elevations are influenced by more regular orographic precipitations (Figure 2C: Griegos station, 1604 m a.s.l.). Regional-scale rainfall dynamics is principally controlled by the westerly winds, associated with cold fronts in spring and high-intensity convective storms in autumn. During the summer, the subtropical Azores anticyclone blocks the moisture from the west and brings warm and dry air masses from the south, being the negative water balance associated to high evapotranspiration values (Figure 2C).

The Villarquemado paleolake is located in the mesomediterranean bioclimatic belt, with *Quercus ilex* and *Quercus faginea* as principal tree species, along with other Mediterranean xerophytic shrubs (*Rhamnus alaternus*, *Genista scorpius*, *Ephedra fragilis*, *Thymus* spp.) and herbs (*Artemisia assoana*, *A .campestris*, *Atriplex prostata*, *Salicornia ramosissima*) (Figure 2D). The calcareous soils in the area support *Juniperus phoenicea* and *J. thurifera*. The supramediterranean belt is characterized by *Pinus sylvestris* communities with *Buxus sempervirens* and *Juniperus sabina*. In red sandstones areas, *Pinus pinaster* woodlands, with dense Cistaceae and Ericaceae shrubs, prevail. The hydroseral community is dense, well developed and linked to seasonal water level fluctuations. The dominant species here are *Phragmites australis*, *Juncus acutus*, *J. inflexus*, *J. maritimus* and *Scirpus holoschoenus*; scattered trees of *Salix fragilis* and *S. atrocinerea* with a scrubland of *Crataegus monogyna* and some *Populus canadensis* cultivars. The natural wetland vegetation has been substantially modified by agriculture and grazing (Figure 2D).

3. Material and methods

A 74 m long sediment core (core VIL-05-1B) was retrieved in 2005 from the deepest area of the Villarquemado wetland, using a truck-mounted drilling system (Moreno et al., 2012a; Gónzalez-Sampériz et al., 2013). The extracted material was extruded, transported to IPE-CSIC laboratory and stored at 4ºC until required for analysis. The top 61 cm were disturbed due to the coring system and were not considered for analysis. To complete the 0-61 cm gap, a parallel 247 cm long core (core VIL-05-1A) was taken with a modified 5 cm-diameter Livingstone piston corer, a coring system that allows recovering unaltered the uppermost part of the sequence.

Correlation between cores VIL-05-1A and VIL-05-1B was achieved using sedimentary facies, radiocarbon dating and pollen stratigraphy (Figure 3A). Therefore, the composite sequence of the Villarquemado paleolake was built using the uppermost 40 cm of the shorter core VIL-05-1A and the core VIL-05-1B, excluding the first 61cm (Figure 3B).

The cores were longitudinally opened and the sedimentary facies described according to Schnurrenberger et al. (2003). Geochemical data were obtained at 0.5 cm intervals by means of an XRF ITRAX Core scanner at the Large Lakes Observatory (University of Minnesota, USA). Total inorganic carbon (TIC) was analyzed every 2 cm with a LECO SC 144 DR elemental analyzer at the IPE-CSIC laboratory, after the organic matter had been removed. In addition, selected samples were analyzed by X-ray diffraction with a Philips PW1820 diffractometer and relative mineral abundance was determined using peak intensity to characterize the sedimentological facies. All the geochemical and elementary analyses were performed exclusively in core VIL-05-1B.

Samples for pollen analysis were taken every 2-3 cm intervals in the core VIL-05-1B while in the core VIL-05-1A only 15 samples were retrieved to complete the uppermost part of the sequence. Pollen extraction followed the standard chemical procedure (Moore et al., 1991).

Pollen identification was supported by the reference collection from IPE-CSIC, determination keys and photo atlases (Reille, 1992). Results are expressed as percentages, excluding hygrophytes, hydrophytes, Pteridophyta spores and other non pollen palynomorphs (NPP) from the pollen sum. The Psimpoll 4.27 software (Bennett, 2009) was used to draw the pollen diagram. Major palynological changes in pollen composition as well as cluster analysis, CONISS (Grimm, 1987), were used as criteria to subdivide the results into pollen assemblage zones.

The chronology of the core VIL-05-1B was established on the basis of five AMS ^{14}C dates, obtained from bulk sediment samples. In addition, other three AMS ^{14}C dates were retrieved from core VIL-05-1A. ^{14}C data were calibrated using Calib 6.11 (Stuiver and Reimer, 1993) with IntCal09 calibration datasets (Reimer et al., 2009) (Table 1) and the composite age-depth model (lineal interpolation) was obtained using the *Clam* software package for age-depth modeling (Blaauw, 2010) (Figure 3B). The chronological model shows a fairly constant accumulation rate, ca. 0.049 cm yr^{-1}, which spans from ca. 13500 to ca. 470 cal yr BP (Figure 3B).

4. Results

4.1. The sedimentological sequence

Visual description, smear slides microscopic observation, geochemical and mineralogical analyses allowed seven main sedimentary facies to be determined in Villarquemado paleolake sequence, later organized in three well-defined sedimentological units (Figure 4).

The base of the sequence corresponds to **UNIT-3** (311-233 cm depth, 13540-11240 cal yr BP), which is composed of medium, massive light grey carbonate silts (*facies 1*) grading upwards to coarser, dark grey carbonate silts (*facies 2*). *Facies 1* and *2* are characterized by relatively high siliciclastic content, as shown by mineral composition (significant quartz content) and by the maximum values of Si, Ti and Fe (Figure 4). In particular, silicates (quartz and feldspars) in *facies 2* range between 25-50 % *versus* 50-75% calcite. Subunit **SUB-3B** (311-256 cm, 13540-12170 cal yr BP), is relatively more carbonate-rich, with TIC (total inorganic carbon) up to 6%, and subunit **SUB-3A** (256-233 cm, 12170-11240 cal yr BP) has the highest silicate content of the whole sequence (only 3% TIC). The top of UNIT-3 is a sharp depositional surface in both Villarquemado cores (VIL-05-1A and VIL-05-1B) and it is located at approximately the same depth (ca. 230 cm). This transition from siliciclastic-rich to carbonate-rich sediments at the boundary between UNIT-3 and 2 is used as a correlation horizon (tie-point 1, TP-1) (Figure 3A).

UNIT-2 (233-61 cm depth, 11240-1940 cal yr BP) is an alternation of fine to medium, banded, creamy carbonate silts organized in dm-thick intervals (*facies 3*) and dark grey, mottled, massive, carbonate and organic-rich silts as cm-thick layers (*facies 4*). *Facies 3* is made of endogenic carbonates precipitated in the palustrine and littoral lake subenvironments (e.g., Charophyceae, carbonate coatings) with maximum Ca values. *Facies 4* has about 5% silicate content (clay minerals and quartz) marked by slight increases in the chemical elements associated to the siliciclastic fraction (Si, Fe, Ti). Both facies contain mm to cm-sized plant remains, suggesting a shallow depositional environment (littoral area). Mottled and soil textures (roots, bioturbation) are especially abundant in the grey silts indicating more frequent subaerial exposition.

UNIT-2 has been divided into three subunits depending on sedimentary facies and geochemical composition: SUB-2C (233-192 cm) is composed by *facies 3* creamy carbonate silts. SUB-2B (192-140 cm) is characterized by the predominance of *facies 4* with intercalations of more organic-rich facies (*facies 6*) and cm-thick coarse silt-fine sand carbonate-rich layers (*facies 5*). The presence of these organic-rich sediments in both sediment cores represents another correlation marker (TP-3) (Figure 3A). Finally SUB-2A (140-61 cm) represents the association of *facies 3* and *4*, with relatively higher carbonate content.

UNIT-1 (61-0 cm depth, post 1940 cal yr BP) is composed of dark brown to dark grey, massive, coarse peaty silt, with abundant plant fragments (*facies 7*) in VIL-05-1B and *facies 4* with two cm-thick intercalations of *facies 3* in core VIL-05-1A. UNIT-1 is composed of unconsolidated material; therefore geochemical properties were not analysed. As a result, correlation between the uppermost sections of the two cores (VIL-05-1A and VIL-05-1B) (TP-4) is based on the pollen composition (Figure 3A), as explained below.

4.2. The pollen sequence

The preservation of pollen grains was generally good. Composite pollen diagrams are presented in the Figures 5 and 6 showing the analytic results of 99 samples. Six Villarquemado pollen assemblage zones (VIL) have been established.

VIL-6 (311-233 cm depth; ca. 13540-11240 cal yr BP), Sedimentary UNIT-3

Based on the variation of Cyperaceae, *Typha/Sparganium* type, hydrophyte-group and Pteridophytes, two subzones have been defined:

VIL-6B (311-256 cm depth; ca. 13540-12170 cal yr BP) is characterized by relatively low, fluctuating arboreal pollen (AP). *Pinus nigra/sylvestris* type is dominant (Figure 5). Other trees are less important, such as *Juniperus* amongst the conifers; both *Quercus faginea* type and evergreen *Quercus* are rare, as well as *Betula*, *Salix*, *Ulmus* and *Fraxinus*. Shrubs such as *Tamarix*, *Ephedra fragilis* and *Ephedra distachya* type show minor occurrences. Xerophytes are well represented, with *Artemisia*, Chenopodiaceae and Compositae as main contributors (Figures 6). Poaceae is relatively abundant and within the hygrophytic community, Cyperaceae show the highest percentages of the sequence, accompanied by high frequencies of *Ranunculus*, Juncaceae, *Typha/Sparganium* type and a significant presence of *Myriophyllum* and *Potamogeton*.

VIL-6A (256-233 cm depth; ca. 12170-11240 cal yr BP) is defined by a drastic change in the hygrophyte community (Figure 6). Particularly, the transition from sedimentary subunit SUB-3B to SUB-3A corresponds to the replacement of the previous Cyperaceae-dominated environment (with abundant Juncaceae and *Ranunculus*) with a *Typha/Sparganium* type community. This hydrological change is also marked by the highest development of submerged aquatic plants (*Myriophyllum* and *Potamogeton*) and the maximum frequencies of Pteridophyta spores (Figure 6).

VIL-5 (233-164 cm depth; ca. 11240-7780 cal yr BP), Sedimentary UNIT-2; SUB-2C, SUB-2B

Oscillations in AP frequencies allow two subzones to be defined:

During the **VIL-5B** (233-192 cm depth; ca. 11240-9140 cal yr BP) xerophytes, mainly *Artemisia* and Chenopodiaceae, rise considerably (Figure 6). AP values are still low. *Pinus nigra/sylvestris* type frequencies decrease, although *Juniperus* increases significantly (Figure 5). Broadleaved trees like *Betula*, and both *Quercus* types are recorded. *Tamarix* development is noticeable.

VIL-5A (192-162 cm depth; ca. 9140-7780 cal yr BP) is defined by progressive increases of *Betula, Corylus,* and both *Quercus* (Figure 5). A progressive coeval decrease in *Artemisia,* Chenopodiaceae, hygrophytes and hydrophytes is noticed (Figure 6).

VIL-4 (164-112 cm depth; ca. 7780-5000 cal yr BP), Sedimentary UNIT-2; SUB-2B, SUB-2A

This zone is characterized by the maximum abundance of deciduous trees (*Corylus, Quercus faginea* type*, Alnus, Salix, Ulmus, Fraxinus, Fagus* and *Tilia*), a decline of the *Pinus nigra/sylvestris* type frequencies, and a decrease in xerophyte values. This is synchronous with an increase in thermophilous elements; evergreen *Quercus* is the most important arboreal element and its expansion parallels the maximum frequencies of Mediterranean shrubs (*Pistacia*, *Rhamnus*, *Phillyrea*, *Buxus*, *Thymelaea*) and the continuous presence of Ericaceae, Rosaceae, Fabaceae and Lamiaceae (Figures 5 and 6). Continuous values of *Juniperus* and a significant presence of *Artemisia* are recorded. Poaceae diminishes significantly, while the hygro-hydrophytic component falls to its sequence minimum (Figure 6).

VIL-3 (112-71 cm depth; ca. 5000-2530 cal yr BP), Sedimentary UNIT-2; SUB-2A

During VIL-3, both *Pinus nigra/sylvestris* type and *Pinus pinaster/hapensis* type show important increases. Overall, mesophytes are decreasing, which affects especially to

Corylus, while *Betula* and *Tilia* disappears. This zone also shows fluctuating evergreen *Quercus*. Although scant along previous zones, *Olea* occurs continuously showing a gradual increasing trend (Figure 5). During this period, pollen grains of *Cedrus* are recorded at 116, 103 and 99 cm depth (ca. 5230, 4490 and 4260 cal yr BP respectively). Hygrophyte and hydrophyte pollen grains occur in low abundances, similarly to the previous zone (Figure 6).

VIL-2 (71-62 cm depth; ca. 2530-1940 cal yr BP), Sedimentary UNIT-2; SUB-2A

A major change in forest structure is the main feature of this zone. *Pinus* reaches a minimum, and *Quercus faginea* and evergreen *Quercus* show significant expansions (Figure 5 and 6).

VIL-1 (61-32 cm depth; ca. 1940-470 cal yr BP), Sedimentary UNIT-1

Pinus nigra/sylvestris type values partially rise while both *Quercus faginea* type and evergreen *Quercus* decline. AP is low (Figure 5) while the herb component (Compositae, Chenopodiaceae, *Artemisia,* Lamiaceae and Fabaceae) exhibits a large increase. Coprophilous fungal spores, dominated by Sordariales peak while a maximum in *Glomus* chlamydospores is seen (Figure 6).

5. Discussion

5.1. Climate, vegetation and hydrological variability during the last 13500 cal yr BP

5.1.1. The Last Glacial-Interglacial transition (LGIT): resilient vegetation and hydrological variability (13540-11270 cal yr BP)

Last Glacial-Interglacial transition (LGIT) at Villarquemado was characterized by deposition of sediments with high siliciclastic content compared with the Holocene interval (Figure 4). The vegetation cover was composed by a relatively high amount of xerophytes (Figures 5 and 6) and the dominance of *Pinus nigra/sylvestris* type among the AP, with values around 40%. These percentages suggest the presence of some tree patches in an open landscape around the lake or a montane pinewood at higher altitudes, similarly to the present-day situation. Deciduous elements were poorly represented and probably were confined to riverbanks (e.g., *Ulmus*, *Salix*, *Fraxinus*) or in particular humid shelters of the Albarracín Range (Figure 5). The lack of a mesophyte vegetation expansion in response to the Allerød interstadial (GI-1a) period (Björck et al., 1997), corresponding to VIL-6B pollen zone according to our chronological model, differs from other Iberian areas where a broadleaf forest expansion has been recognized (Pons and Reille, 1988; Peñalba, 1994; Pérez-Obiol and Julià, 1994; Gil-García et al. 2002; González-Sampériz et al. 2006; Muñoz Sobrino et al., 2013). The lagged vegetation response to the GI-1a climate signal is attributable to the resilience of the continental ecosystems to increased moisture availability, although vegetation dynamics may be partly masked by the low sample resolution of this interval (Figures 7 and 8). The resilient behaviour of the vegetation continues during the Younger Dryas (GS-1) chronozone (Björck et al., 1997) when no major changes in the forest physiognomy are recorded (Figures 5 and 8). Nevertheless, the increase in *Pinus* between 13200 and 12200 cal yr BP (VIL-6B) may partially reflect an altitudinal migration of the of the pinewood treeline associated with the onset of cooler conditions at higher elevations. Unfortunately, this hypothesis cannot be tested through correlation due to the lack of Lateglacial paleoecological records at higher altitudes in our study area. In addition, the Younger Dryas is not always clearly documented in the eastern Iberian sequences (Carrión et al., 2010a and references therein), suggesting a low impact of this event in pine woodlands.

Therefore, although no important changes in the regional vegetation during the LGIT are clearly recorded, local aquatic taxa and sedimentological indicators point to relatively high water levels and sediment delivery. In fact, hydrophytes reach their maximum values during this period, especially in the VIL-6A interval (12170-11230 cal yr BP), showing a remarkable shift from Cyperaceae-rich to a Typha-rich ecosystem with large amounts of *Myriophyllum* and *Potamogeton* (Figures 6 and 8). These coincide with the high proportions of Ti and the siliciclastic composition of UNIT-3, particularly in SUB-3A, which indicate a lacustrine environment dominated by detrital supply to the basin (Figure 4). Such a situation would be related to an increase in the creeks/local rivers activity in the catchment as a response of (1) more intense rainfall events and/or (2) colder conditions in an open landscape. Both situations would favor erosion and the accumulation of detrital particles in the lake. The synchronous increase in aquatic pollen during the LGIT, indicating higher lake level, supports this hypothesis. The high lake level postulated for GS-1 would probably benefit from the decrease of evaporation rates as a consequence of the reduced annual temperatures in a global-scale cold period (Cacho et al., 2001; Moreno et al., 2010; Shakun and Carlson, 2010).

5.1.2. The early Holocene: vegetation and hydrological response to marked seasonality (11270-7780 cal yr BP)

The early phase of the Holocene in the region was still dominated by a steppe landscape (VIL-5B), although a progressive development of more water-demanding temperate taxa (e.g., *Betula*, *Corylus* and *Quercus faginea* type) occurred from ca. 9140 cal yr BP (VIL-5A), suggesting increased temperature and humidity (Figure 5). In agreement with other Mediterranean sequences from the north-eastern sector of the Iberian Peninsula, inner continental regions like the Villarquemado paleolake area were characterized by the prevalence of cool and arid conditions at the beginning of the Holocene (e.g., Lake Estanya, Morellón et al., 2009; Vegas-Vilarrúbia et al., 2013) with a remarkable persistence of Lateglacial xeric communities and pinewoods in the vegetation cover (González-Sampériz et al., 2005, and references therein). In particular, at Las Pardillas

Lake (Figure 1), steppe-like vegetation composed by *Juniperus*, *Artemisia* and Poaceae was well represented prior to ca. 10500 cal yr BP (Sánchez Goñi and Hannon, 1999) while at the nearby Ojos del Tremedal, situated in the Albarracín Range (Figure 1), a treeless environment persisted until ca. 9600 cal yr BP (Stevenson, 2000). The limited spread of mesic and thermophilous vegetation in Fuentillejo Maar (Vegas et al., 2010), inner continental Iberia (Figure 1), was also associated with a dry and probably cold climate regime during the first stages of the Holocene.

In southern and south-eastern Iberian intra-montane valleys and mid-altitude elevations, the same environmental conditions of the inner continental areas are clearly visible during this period. Thus, Navarrés (Carrión and van Geel, 1999), Villaverde (Carrión et al., 2001) and Siles (Carrión, 2002) exhibit a similar pattern of conifer prevalence during the first millennium of the Holocene as these communities are highly resilient and their fluctuations present a more inertial character (Figure 7). In a recent review, Rubiales et al. (2010) proposed that pinewoods spread in the Iberian mountains since the LGM until ca. 8000 yr BP, suggesting that empty ecological niches available after full-glacial climate conditions may have favoured the early colonization of *Pinus* in a still dry climatic scenario. Consequently, not only during Lateglacial times but also during the early Holocene, pinewoods would have been better adapted, climatically favoured and easily dispersed from multiple stands with respect to broadleaved species in medium altitude continental areas. Our data are coherent with the hypothesis by Rubiales et al. (2010) which points to a regional dominance of *Pinus* until 7780 cal yr BP in the lowlands of the Albarracín Range (Figures 5 and 7).

Model simulations for Eurasia confirmed that increased summertime insolation in the Northern Hemisphere at the Holocene onset caused an increase in summer temperatures (Rimbu et al., 2003; Kim et al., 2004). Paleoecological data in central and northern

Europe have showed an almost immediate response of terrestrial ecosystems to the rise in temperature during the early Holocene, visible by major fluctuations in the alpine timberline (Ali et al., 2003; Tinner and Kaltenrieder, 2005) and by the expansion of broadleaved trees reaching northern areas, even above the modern distributional range limit (Kullman, 2013, and references therein). Reduced winter insolation also implied minimum winter temperatures and extreme continentality due to the maximum amplitude of solar forcing. Thus, the persistence of steppe communities in the inner continental areas of Iberia may be associated with a reduced effective humidity, keeping moisture levels below the tolerance threshold for tree growth (Tzedakis, 2007). Further evidence comes from North-African palaeonvironmental studies (Lamb et al., 1989), where a strengthened monsoonal circulation has been considered as the main triggering factor promoting the persistence of a regional high pressure circulation mode (Cheddadi et al., 1998). In this mode, atmospheric stability and high summer temperatures may have led to higher evaporation rates and a consequent reduction of water tables in many continental Mediterranean areas. This mechanism may explain the prevalence of reduced water levels in Iberian lakes during the early Holocene, i.e., in Lake Estanya (ca. 11600-9400 cal yr BP) (Figure 8), (Morellón et al., 2009; Vegas-Vilarrúbia et al., 2013). In continental Iberian sites like Salines (Roca and Julià, 1997) or Laguna de Medina (Reed et al., 2001), in south-eastern Spain (Figure 1), recurrent water level oscillations are revelaed suggesting alternating permanent and ephemeral lake environments. In Villarquemado the reduction in Pteridophytes and aquatic plants (Figure 5), and the sharp decrease in siliciclastic elements (Ti, Si, Fe) contemporaneous to the substantial increase in freshwater gastropoda and charophyceae-rich facies, suggest an oscillation towards a shallower, carbonate-rich wetland, around 11240 cal yr BP (Figure 4 and 8). The increase in Mn with respect to the LGIT values also supports the existence of shallow environments where oxidation processes were more frequent. The extent of the wetland was drastically reduced, as indicated by the progressive decline in hygrophyte communities (Figure 6). Nevertheless, the continuous record of *Tamarix*, along with the scattered presence of *Myriophyllum* and *Potamogeton*, indicate the persistence of some unstable and seasonal ponds, probably in the lowest areas of the basin. At the same time, the increase in Chenopodiaceae and *Artemisia* pollen may reflect their local presence near the core site, in a climatic scenario with cold winter temperatures hindering the development of regional meso-thermophilous vegetation (Figure 6).

5.1.3. Mixed oak woodland expansion during the mid Holocene (7780-5000 cal yr BP)

The mid Holocene in Villarquemado was characterized by the expansion of mesophytes and Mediterranean taxa whereas *Pinus nigra/sylvestris* forests and the herbaceous understory decreased (VIL-4), indicating both higher temperatures and moister conditions than in the previous phase (Figure 5). Favorable conditions for forest development are indicated by the dominance of *Quercus faginea* type and evergreen *Quercus*, followed by the spread of broadleaved taxa, reaching their maximum values in this period (Figures 5 and 8). From a regional perspective, sequences located in both north (Peñalba, 1994; Sánchez Goñi and Hannon, 1999; Gil-García et al., 2002) and southern slopes of the Iberian Range (Stevenson, 2000) reported similar vegetation successions, where *Betula*, and to a lesser extent deciduous *Quercus*, were the most widespread deciduous elements. This pattern was also found in other north-eastern high-altitude localities (e.g., González-Sampériz et al. 2006; Pérez-Obiol et al. 2012; Pérez-Sanz et al., 2013), reflecting an upland tree colonization associated with the upward shift of the supramediterranean vegetation belt. The continuous record of *Betula* pollen in Villarquemado between 10200 and 8460 cal yr BP, a taxon currently absent in the area, may reflect the progressive birch colonization in the Albarracín Range as highlighted by Stevenson (2000). *Corylus*, whose modern distribution in the Iberian Peninsula is mainly related to the humid Eurosiberian region (Blanco-Castro et al., 1997), was continuously recorded from ca. 9540 cal yr BP in Villarquemado, although its maximum spread took place ca. 7450 cal yr BP (Figure 5), similarly to other continental Iberian locations (e.g., Siles, Carrión, 2002 ca. 7270 cal yr BP; Ojos del Tremedal, Stevenson, 2000 ca. 7500 cal yr BP).

The Villarquemado paleolake lowlands were most likely characterized by open evergreen oak formations accompanied by scattered juniper communities in dry slopes, with monospecific *Pinus pinaster* stands in redstones and an ericaceous understory (Figure 5). Maximum frequencies of riparian taxa (*Alnus*, *Salix*, *Ulmus*, *Fraxinus*, *Tilia*) reflect increased fluvial activity.

Significant *Artemisia* proportions, reaching ca. 20% despite the moister conditions, could be associated with the particular geomorphological features of the basin, mainly characterized by a massive spread of alluvial fans (Figure 2A), where an unstable substrate might be colonized by *Artemisia* as this taxon does nowadays (Figure 2D).

Beyond local peculiarities, the present study matches the general hydrological model established for Mediterranean Iberia, suggesting the highest lake levels ocurred in the 8000-5500 cal yr BP period (Carrión, 2002; Morellón et al., 2009; García-Alix et al., 2012) (Figure 8). Although a carbonate-producing wetland-shallow lake was established in Villarquemado through most of the Holocene sequence, dark, organic-rich silt facies with slight increases in Ti and Si occurred during the mid Holocene. Sedimentological and geochemical proxies underline increased water availability during this time (Figure 4). Furthermore, regional-scale evidence for this wet-phase comes from tufa deposits development at the Mijares River Canyon between 10000 and 5000 yr BP (Peña et al., 2000), from the Guadalaviar River Basin at 7300-6800 yr BP (Sancho et al., 1997) and from the headwaters of Las Parras River since 10100 cal yr BP (Rico et al., 2013) (Figure 1). The increase in temperature and moisture availability recorded during this period (7780-5000 cal yr BP) may be related to increased prevalence of westerlies in the continental areas of the Iberian Peninsula (Benito et al., 2003), probably linked to a weaker influence of the Hadley circulation system in the western Mediterranean Basin (Tzedakis, 2007; Vannière et al., 2011).

A secondary change in the forest composition was observed at ca. 6800-5800 cal yr BP, (VIL-4) (Figure 5). Although competition between *Quercus faginea* and evergreen *Quercus* cannot be ruled out as a factor for vegetation change, the general decline of mesophytes and the following increase in evergreen elements (evergreen *Quercus*, *Olea*, Ericaceae) as well as the significant presence of *Pinus*, suggest a reduction of summer precipitation and/or an increase of temperatures. In fact, estimates of $\delta^{13}C$ in mid Holocene archaeobotanical remains located in the nearby Valencia Region confirm a progressive reduction in July precipitation between 6000 and 5000 yr BP (Aguilera et al., 2012). On the other hand, the reduced seasonal thermal contrast of the mid Holocene caused warmer winters and milder summers, and consequently an increase in mean annual temperatures allowing the spread of more thermophilous, frost-sensitive elements (e.g., *Olea*, *Pistacia*, *Thymelaea*) (Figures 5 and 7) even in the inner areas of the Iberian Peninsula (Badal et al., 1994; Carrión et al., 2010).

Regionally, the same vegetation shift from deciduous to evergreen vegetation formations is reported from different continental sequences (Figure 7). At Siles, the maximum expansion of the Mediterranean forest-scrub was recorded at ca. 5900 cal yr BP (Carrión, 2002). At Navarrés, the colonization of sclerophyllous *Quercus* in pinewoods took place around 6000 cal yr BP, possibly triggered by human-induced fires under dry climate conditions (Carrión and van Geel, 1999). At Villaverde, the main change towards a dominance of evergreen *Quercus* is recorded ca. 5300 cal yr BP, several centuries later than other discussed records (Carrión et al., 2001) (Figure 7). Anthracological data published by Allué et al., (2009) from Cova de la Guineu confirm this regional-scale pattern, reporting a change from humid to sub-humid Mediterranean climate, suggested by increasing abundance of evergreen *Quercus*, *Erica* and *Rhamnus/Phillyrea* in the charcoal record. Although a steady increase in summer dry conditions is recorded, the relatively high amount of deciduous elements especially between 5800 and 5000 cal yr BP, suggests a favourable mean annual precipitation, although with a more pronounced seasonality.

Sedimentological indicators reflect a slight decrease in lake levels with a dominance of more ephemeral depositional environment that persisted through the remaining UNIT-2. The change from carbonate-lake environment (SUB-2B) into shallower carbonate wetland (SUB-2A) is also shown by the inverse relationship between siliciclastic elements and Ca (Figure 4). This pattern towards drier conditions in continental Iberia (Carrión et al., 2010a) and elsewhere in the Mediterranean Basin (Jalut et al., 2009), likely represents the hydrological and vegetational response to the end of the orbitally-driven African Humid Period (deMenocal et al., 2000).

5.1.4. Increase in the aridity trend from the mid to late Holocene (5000-2530 cal yr BP)

Between 5000 and 2530 cal yr BP a mixed evergreen *Quercus-Pinus* forest developed while *Corylus* and other mesic trees (e.g., *Fraxinus*, *Salix*, *Ulmus*), which were probably confined in riverbanks and humid gorges, reduced significantly (VIL-3) (Figure 5). More contrasted continental and drier climate conditions could have favoured the expansion of a *Pinus*-dominated landscape at the expense of mesophytes (Carrión et al., 2010a, and references therein) (Figure 5). Palynological data from areas within the thermo- and mesomediterranean areas reported woodland cover reductions after ca. 5200 cal yr BP (Jalut et al., 2000; Pantaleón-Cano et al., 2003; Carrión, 2002; Carrión et al., 2001, 2004; Fletcher et al., 2007) (Figure 8). During this period, an increase in fire activity, probably enhanced by arid climate conditions, may have played a crucial role in favoring the spread of sclerophyte and fire-prone communities (Carrión and van Geel, 1999; Carrión et al., 2003; Gil-Romera et al., 2010a), even at high elevations (Carrión et al., 2007; Anderson et al., 2011; Jiménez-Moreno and Anderson, 2012; Jiménez-Moreno et al., 2013). In addition, marked changes in several lake sequences took place approximately at 5100 cal yr BP. (Carrión et al., 2003; Anderson et al., 2011; García-Alix et al., 2012) (Figure 8). In Villarquemado, deposition in ephemeral lake conditions continued without major changes in the geochemical signature (SUB 2-A), except for a significant increase in Mn that might reflect higher occurrence of oxidation processes in a shallow environment (Figure 4).

Other pollen-independent studies reach similar conclusions: at Laguna de Medina, Reed et al. (2001) suggest a clear decrease in lake levels after 5530 cal yr BP, while at Siles phases of dramatic lake dessication around 5200 and 4100 cal yr BP are identified (Carrión, 2002) (Figure 8). An arid interval was recorded in Lake Estanya between 4800-4000 cal yr BP (Morellón et al., 2009), while the sequences at Lake Zoñar (Martín-Puertas et al., 2008) and Laguna de la Mula sequences (Jiménez-Moreno et al., 2013) start with low lake levels at ca. 4000 cal yr BP (Figure 8). Further evidence towards dry environments in continental areas of Iberia are confirmed by enhanced erosive phases in the Trabaque Canyon tufa deposits (Domínguez-Villar et al., 2012), and by the reduced water availability along with the consequent decline in the tufa deposition in the Añavieja River system (Luzón et al., 2011). At a broader scale, the spread of aridity in the southern Peninsula has been correlated with millennial and submillennial-scale arid intervals in North Africa as recorded in Tigalmamine Lake between 5010-4860 cal yr BP (Lamb and van der Kaars, 1995), Lake Sidi Ali at 6000-5000 cal yr BP (Lamb et al., 1999) and Dar Fatma (Ben Tiba and Reille, 1982). Single grains of *Cedrus* recorded in Villarquemado at the 5160-4240 cal yr BP interval suggest an enhanced influence of air masses reaching northern Mediterranean areas from North Africa (Magri and Parra, 2002; Di Rita and Magri, 2009).

5.1.5. Clearance of pine woodlands during Iberian-Roman times (2530-1940 cal yr BP)

The continuous *Pinus* frequencies (both *Pinus sylvestris/nigra* and *Pinus pinaster/halepensis* types) recorded in Villarquemado during the Lateglacial and the Holocene until 1950 cal yr BP (Figure 5) confirm the native character of pinewoods in the inner continental areas of Iberia, as shown by numerous studies (Franco-Múgica et al., 2001, 2005; Carrión et al., 2004; Figueiral and Carcaillet, 2005; Rubiales et al., 2009, 2011; López-Sáez et al., 2010; García-Antón et al., 2011; Morales-Molino et al., 2012). *Pinus pinaster/halepensis* type is recorded throughout the record without major changes, probably reflecting a long-term persistence of Mediterranean pinewoods in sandy substrates of the southern Iberian Range, a region already defined by Carrión et al., (2000) and recently confirmed by chloroplast microsatellite markers (Gómez et al., 2005; Bucci et al., 2007), as an important source area for cluster pine during pre- and postglacial times.

Despite the persistence of *Pinus* in our sequence, an abrupt pinewood decrease occurred about ca. 2530-1940 cal yr BP, suggesting an anthropogenic disturbance (Figure 5). Archaeological data and historical sources reveal that both the Celtiberian (Lorrio and

Ruiz-Zapatero, 2005) and Roman civilizations (Vicente-Redón, 2002) were present locally, significantly altering the environment by grazing practices and building structures for water management and river regulation (Rubio, 2004; Arenillas, 2007). In fact, during Roman times, the Albarracín-Cella aqueduct was constructed, a magnificent 25 km long hydraulic infrastructure built to transfer water from the Guadalaviar River to the Cella village (Almagro Gorbea, 2002) (Figure 1). Although some authors consider that the aqueduct was designed by Muslim engineers (Sebastián López, 1989), the discovery of high density of *terra sigillata hispanica* pottery fragments, indicates that at least some parts of the infrastructure were completed before I-II A.D and therefore Roman culture was present (Almagro Gorbea, 2002; Rubio, 2004). Calibrated radiocarbon dates in this part of the Villarquemado sequence confirm that a major change in the forest composition occurred during the Iberian-Roman Period (Figure 5). Pollen evidences that the deforestation was particularly intense in the pine forest, in contrast to the oak woodland (both *Quercus faginea* type and evergreen *Quercus*) that surprisingly reached the highest values of the whole sequence (Figure 5). Although, chronologically well-constrained, multiproxy studies have recognized the existence of a moister phase between 2600 and 1600 cal yr BP, named as the Iberian-Roman Humid Period (Gil-García et al., 2007; Martín-Puertas et al., 2009; Jiménez-Moreno et al., 2013), the abrupt change recorded in the *Pinus* values in just 3 cm (<130 years) is unlikely to be explained by climate change only. Problems linked to taphonomical processes might not be relevant since the same trend is repeated in different cores from Villarquemado paleolake (Figure 3A).

Deforestation has often been related to the intensification of agro-pastoral activities (Carrión et al., 2007; López-Merino et al., 2010; Pèlachs et al., 2009a; Bal et al., 2011), or mineral extraction and metallurgy (Pèlachs et al., 2009b). However, in the

Villarquemado sequence no agricultural intensification has been recorded during this period (Figures 5 and 6) since only isolated presence of *Cerealia* type is recorded, without any noticeable proportions of ruderals (e.g., *Plantago*, *Rumex*, Polygonaceae) or cultivated trees (e.g., *Olea*, *Castanea*, *Juglans* and *Vitis*).

In addition, a preference of conifers for construction purposes compared to *Quercus* and other mesophyte species has been postulated in many ethnobotanical studies (Rubiales et al., 2011; Ntinou et al., 2012). *Pinus nigra* and *Pinus sylvestris* are more suitable for construction as they produce straighter trunks in comparison with *Quercus ilex* which is more suitable for fuelwood (Rubiales et al., 2011). Therefore, we propose that the pinewood clearance recorded in Villarquemado was to obtain building material to construct the Albarracín-Cella aqueduct, following the Roman economic and social expansion in the area.

At a European scale, the climate during the Roman period (2600-1600 cal yr BP) was characterized by increased humidity (van Geel et al., 1996), affecting particularly the southern latitudes (Zanchetta et al., 2007). Pollen-based studies across the Iberian Peninsula, especially in those regions where the human impact was substaintially negligible, revealed noticeable changes in the vegetation composition, with the spread of deciduous elements, as recorded in Basa de la Mora (Pérez-Sanz et al., 2013), in Estany de Burg (Bal et al., 2011) and Laguna de la Mula (Jiménez-Moreno et al., 2013) among others. High lake productivity and the maximum diversity of the aquatic pollen characterizes the Tablas de Daimiel sequence during this period (Gil-García et al., 2007) coeval to the deposition of varves related to higher lake levels in Zoñar Lake (Martín-Puertas et al., 2009). Although the possible forcings and the detailed chronological delimitation of the mentioned period remain still unclear, the atmospheric circulation pattern has been pressumably related to a persistent negative NAO mode, with North

Atlantic origin storm tracks affecting with particular intensity south-western Mediterranean areas (Martín-Puertas et al., 2012).

Deposition in Lake Villarquemado during the late Holocene is characterized by the co-existence of carbonate wetland environments with peatbog areas. Sedimentological proxies reveal a sharp change from a carbonate wetland (SUB-2A) to a peat (UNIT-1) at ca. 1940 cal yr BP (Figure 4) in core VIL05-1B. However, it does not appear clearly in VIL05-1A (Figure 3A), underlying the depositional spatial variability in a shallow lacustrine system such as the Villarquemado paleolake.

5.1.6. Increased landscape management during the last 1500 years (1940-470 cal yr BP)

The time period between 1940-470 cal yr BP was characterized by the increase in anthropogenic pressure shaping the current patched landscape in the Jiloca Basin. Pinewoods partially recovered at high altitudes, while in the lowlands, covered by evergreen and deciduous oak communities, pine reduced noticeably (VIL-1) (Figure 5). Slash and burn practices were probably frequent (Figure 6) and during this period livestock became an important economic activity in the area, evidenced by an exponential increase in coprophilous fungi of Sordariales-group. Also, nitrophilous elements like Compositae, Chenopodiaceae, *Rumex* or Apiaceae increased substantially, reflecting a major change towards an open and degraded environment. Similarly, *Glomus* chlamydospores increased (Figure 6) suggesting enhanced soil erosion due to grazing practices.

The relatively poor pollen resolution for this period together with the lack of detailed geochemical analyses from the core VIL-05-1A do not allow a detailed definition of climate evolution from our proxies, although it is well-known that the last two millennia in the Iberian Peninsula were characterized by a marked climate variability with the alternation of warm/dry and cool/moist periods (Morellón et al., 2012; Moreno et al., 2012b). In general terms, deforestation ceased and pines spread in the highlands after the decline of the Roman Empire (Figure 5), possibly in a drier climate context. Similarly, in the nearby Albarracín Range, pinewood colonized the previous deciduous woodland at 1840 cal yr BP and remained dominant until ca. 440 cal yr BP (Stevenson, 2000). Nevertheless, water levels seem to have remained low in the Villarquemado paleolake with a patchy distribution of shallow carbonate lakes and wetlands since, no major evidence of recovery is inferred from the sedimentological sequence (Figure 4) or from the expansion of hygro- and hydrophyte communities (Figure 6).

In the 18th century, Villarquemado paleolake was artificially desiccated in order to achieve new land for cultivation and/or to reduce malarial-ridden swampy areas (Rubio, 2004). This transition has been dated in the sedimentary sequence of Villarquemado paleolake at 430±30 (470 cal yr BP) radiocarbon data.

5.2. Vegetation resilience to abrupt climate changes

It is now well-established that the Lateglacial and Holocene periods have been characterized by sharp climate changes occurring at millennial-scale (Bond et al., 1997). Pollen data from central Europe have revealed an immediate response of terrestrial ecosystems showing a widespread decline of drought-sensitive species such *Corylus* that retreated in response to increased cool, dry and windy conditions (Tinner and Lotter, 2001; Kofler et al., 2005). Similarly, the sensitivity of the Iberian vegetation to global-scale climate changes has been widely reported, although it was mainly found in Atlantic-influenced sequences where the vegetation succesion was characterized by a broadleaved vegetation expansion at the Holocene onset, shaped by short-lived peaks of xerophytes, and by the progressive increase in drought tolerant taxa in reponse to more-seasonal conditions from the mid-Holocene onwards (Carrión et al., 2010a and references therein). Examples of this vegetation succession have been well-defined in the Pyrenees by records such as El Portalet (González-Sampériz et al., 2006), Tramacastilla (Montserrat-Martí, 1992) or by the recently published Basa de La Mora (Pérez-Sánz et al., 2013), recording marked climate shifts towards arid conditions at ca. 9300 and 8300 cal yr BP. Similarly, pollen data obtained from sequences located in the Cantabrian Mountains (Moreno et al., 2011), in north-western Iberia (Muñoz-Sobrino et al., 2005; López-Merino et al., 2012) or from coastal areas of Portugal (Fletcher et al., 2007) have reported a similar vegetation succession characterized by forest opening and coeval increase in steppe elements.

In contrast, based on a palynological approach, continental areas of the Iberian Peninsula do not clearly reflect these centennial-scale climate events, even when the chronological models are well-established, without apparent hiatuses and abrupt changes in the sedimentation rates (e.g, Carrión and van Geel, 1999; Sánchez Goñi and Hannon, 1999; Stevenson, 2000; Carrión, 2002; Carrión et al., 2007; García-Antón et al., 2011) while resolution in most these cases is high enough to detect those oscillations (e.g. Sánchez Goñi and Hannon, 1999; Franco-Múgica et al., 2001; Carrión, 2002; Carrión et al., 2007). In Villarquemado paleolake, the depth-age model reflects a lineal, continuous and relatively high sediment accumulation rate for the Lateglacial (0.030 cm yr^{-1}), decreasing slightly to 0.049 cm yr^{-1} during the early Holocene (Figure 3B). Global-scale abrupt climate reversals such as the Preboreal Oscillation (Fisher et al., 2002), the 8200 cal yr BP event (Alley et al., 2003), and the 4200 cal yr BP aridity crisis (Cullen et al., 2000) have been chronologically well-constrained by means of radiocarbon dates reporting results centered at 9820±50 (11250 cal yr BP), 7460±50 (8280 cal yr BP) and 3750±40 (4110 cal yr BP) respectively (Table 1). Nevertheless, no major changes in the pollen sequence have been observed compared to the previous trend (Figure 8). In addition, pollen analysis performed for comparison in Core VIL-05-1A (not shown in this work) around the radiocarbon date 7460±40 (8275 cal yr BP) (Table 1) show a vegetation landscape similar to VIL-05-1B sequence, without a clear evidence of forest opening around 8200 cal yr BP.

Considering that peculiarities related to depth-age model or sampling resolution are not the main factors explaining the lack of vegetation response to abrupt events in the Villarquemado paleolake, the stable character of the continental forest communities could be partially explained by its optimal ecological niche, including the lack of successional competitors during harsh climatic periods. Modern ecophysiological studies have demonstrated that conifers are better adapted to water-stress induced by drought in comparison to broadleaved trees (Lloret et al., 2007). Then, the ecosystem's inertia would also play a role on buffering climate perturbations. This persistence is supported by the complex interactions of the postglacial pinewoods with the newly established junipers and oak forests during the recorded period. These interactions are usually difficult to establish but once they are created, they hamper perturbations in well-developed and mature communities (Gil-Romera et al., 2009, 2010b; Carrión et al, 2010b). Moreover, since aridity is an intrinsic driver of the Villarquemado landscape without any clear marker of regional forest contractions during the Lateglacial and early Holocene, short-lived arid spells in a drought-tolerant environment are likely to be substantially negligible. This model may be extrapolated to many Iberian records that see similar signals of vegetation inertia (e.g., Carrión and van Geel, 1999; Sánchez Goñi and Hannon, 1999; Stevenson, 2000; Franco-Mugica et al., 2001, 2005; Carrión, 2002; García-Antón et al., 2011). Instead, in Atlantic-influenced sequences the well-established deciduous vegetation seems more vulnerable to arid events as the forest responds showing a sharp opening or treeline experiences major shifts at high altitudes that result easier to detect than in continental sequences (e.g., Muñoz-Sobrino et al., 2005; González-Sampériz et al., 2006; Moreno et al., 2011; López-Merino et al., 2012; Pérez-Sánz et al., 2013). In many cases, these abrupt forest depletions are evidenced by increased *Pinus* pollen frequencies indicating its xeric behaviour (e.g., González-Sampériz et al., 2006; Pérez-Sánz et al., 2013).

6.- Conclusions

High-resolution multiproxy analyses of the Villarquemado paleolake allow the reconstruction of both meso- and supramediterranean vegetation dynamics, climate and hydrological changes in the southeastern Iberian Range during the last ca. 13500 cal yr BP. Most of the studied period has been characterized by a marked resilience of terrestrial vegetation and gradual responses to millennial-scale climate fluctuations. The main vegetation and hydrological responses to global climate variability have been identified using palynological, sedimentological and geochemical indicators, enabling correlations with other continental Iberian paleoenvironmental sequences. In general terms, six phases occurred between ca. 13500 and 450 cal yr BP as follows:

1) Regional cool conditions are inferred for the LGIT (13540-11270 cal yr BP) with conifers and steppe elements as main landscape elements. In addition, the well-developed hygro-hydrophyte pollen assemblages and the sedimentary facies associations reveal high water levels, probably as a consequence of reduced evapotranspiration rates and/or higher intensity of precipitation events.
2) Prevalence of dry conditions in response to increased seasonality is the main feature for the early Holocene (11270-7780 cal yr BP), when conifer forests and xerophytes spread regionally. Hydrologically, this phase corresponds with an abrupt change towards a shallow carbonate-wetland with both littoral and aquatic communities experiencing a marked decrease.

3) Moister conditions characterize the beginning of the mid Holocene (7780-5000 cal yr BP) in coherence with the regional pattern, showing the expansion of meso-thermophilous taxa with both *Quercus faginea* and evergreen *Quercus* as main woodland components. Local hydrological conditions suggest increased water availability in a carbonate-wetland system.
4) The progressive increase in arid conditions during the late Holocene (5000-2530 cal yr BP) enabled the expansion of a mixed *Pinus*-evergreen *Quercus* forest. The carbonate-lake environment persisted during this period.
5) During Ibero-Roman times, pinewood forest clearance (2530-1940 cal yr BP) represents the most important deforestation phase as a consequence of anthropogenic disturbance. Carbonate shallow lakes and wetlands dominated during this period and peat formation could have been favored during some intervals.
6) Between 1940 and 470 cal yr BP increased landscape management associated to grazing pressure shaped a patchy forest landscape without clear evidence of agricultural intensification.

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Figures and tables caption

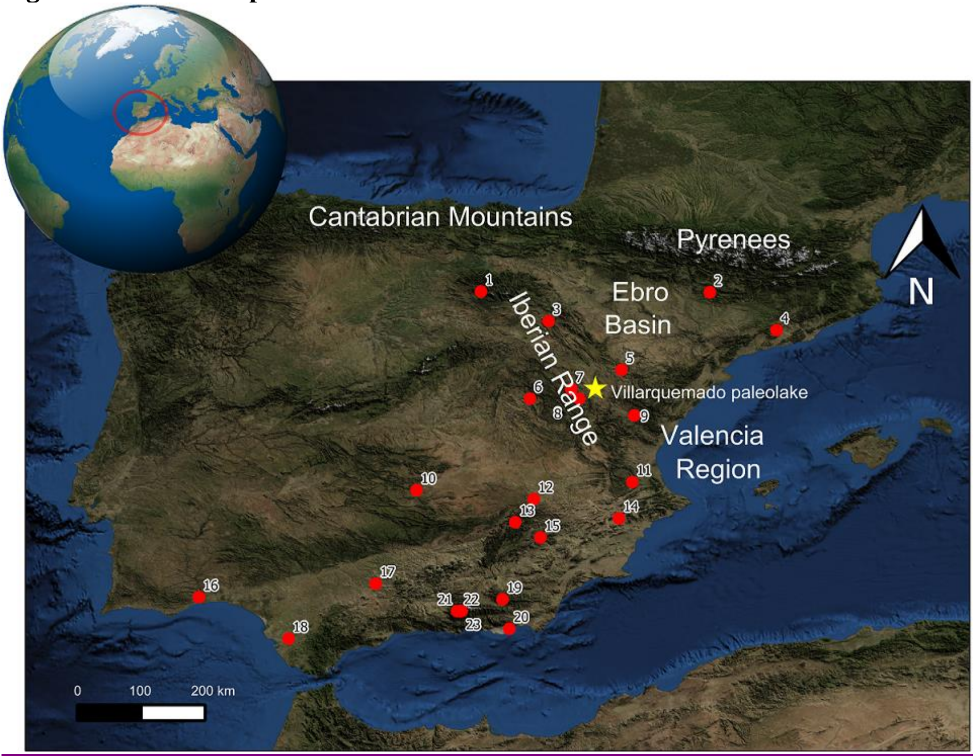

Figure 1. Location of the Villarquemado paleolake in the Iberian Peninsula. The sites cited in the discussion and in Figures 7 and 8 are also included; 1) Las Pardillas Lake (Sánchez-Goñi and Hannon, 1999); 2) Lake Estanya (Morellón et al., 2009; Vegas-Vilarrúbia et al., 2013); 3) Añavieja River system (Luzón et al., 2011); 4) Cova de la

Guineu (Allué et al., 2009); 5) Las Parras River system (Rico et al., 2013); 6) Trabaque Canyon (Domínguez-Villar et al., 2012); 7) Ojos del Tremedal (Stevenson, 2000); 8) Guadalaviar River system (Sáncho et al., 1997); 9) Mijares River system (Peña et al., 2000); 10) Fuentillejo Maar (Vegas et al., 2010); 11) Navarrés (Carrión and van Geel, 1999); 12) Villaverde (Carrión et al., 2001); 13) Siles (Carrión, 2002); 14) Salines (Roca and Julià, 1997); 15) El Sabinar (Carrión et al., 2004); 16) Guadiana Estuary, Core CM5 (Fletcher et al., 2007); 17) Lake Zoñar (Martín-Puertas et al., 2008); 18) Laguna de Medina (Reed et al., 2001); 19) Baza (Carrión et al., 2007); 20) San Rafael (Pantaleón-Cano et al., 2003); 21) Laguna de la Mula (Jiménez-Moreno et al., 2013); 22) Borreguiles de la Virgen (Jiménez-Moreno and Anderson, 2012; García-Alix et al., 2012); 23) Laguna del Río Seco (Andersón et al., 2011).

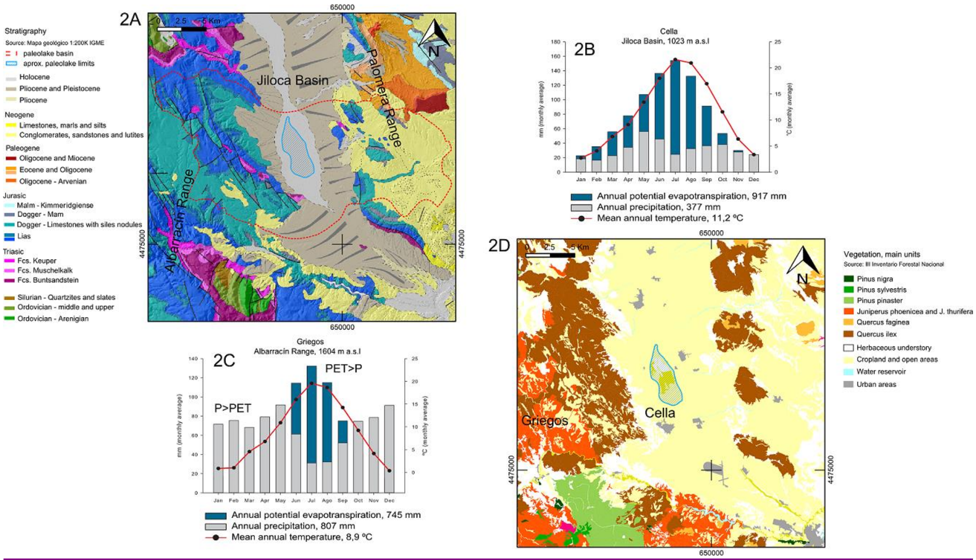

Figure 2. (A) Main geological, (B and C) climatic and (D) vegetational features of the Jiloca Basin.

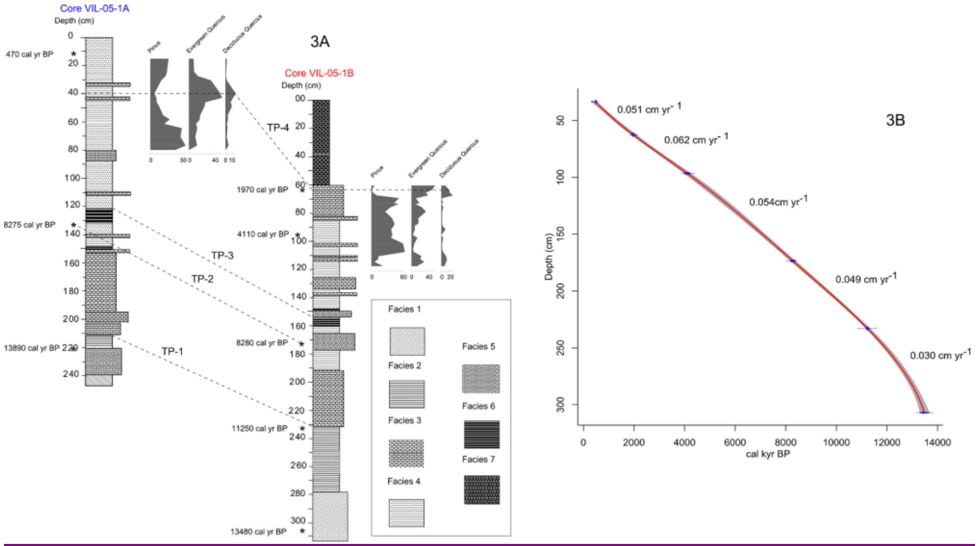

Figure 3. (A) Correlation of VIL-05-1A and VIL-05-1B cores based on sedimentological markers, ^{14}C dates and main palynological changes. (B) Composite depth-age model for the Villarquemado paleolake based on lineal interpolation of ^{14}C data (Table 1), obtained using the *Clam* software (Blaauw, 2010). The grey envelope shows the 95% confidence interval.

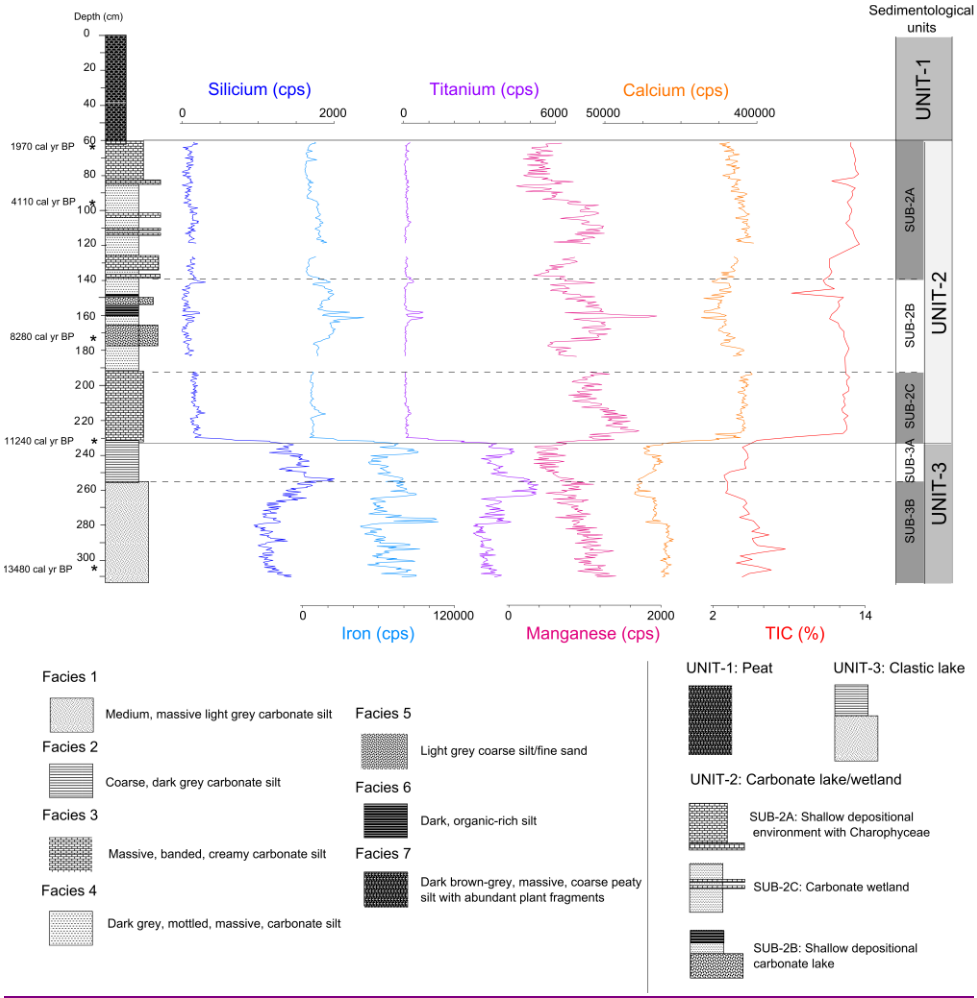

Figure 4. Sedimentary facies and sedimentological units, XRF analyses and TIC results for the Villarquemado sequence. XRF intensities are expressed in counts per second (cps) and TIC values in percentages. The facies description is supported by X-ray diffraction and visual inspection of relative mineral abundances on smear slides.

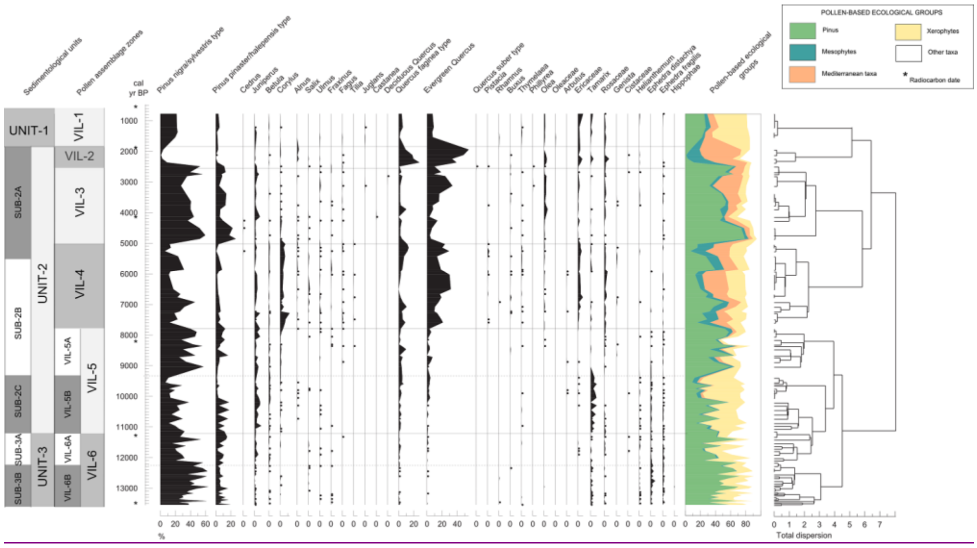

Figure 5. Pollen diagram from Villarquemado sequence for trees and shrubs. Mesophytes-group comprises *Betula*, *Corylus*, *Alnus*, *Salix*, *Ulmus*, *Fraxinus*, *Fagus*, *Tilia*, *Juglans*, *Castanea*, deciduous *Quercus* and *Quercus faginea* type; Mediterranean taxa-group is composed by Evergreen *Quercus*, *Quercus suber* type, *Pistacia*, *Rhamnus*, *Buxus*, *Thymelaea*, *Phillyrea*, *Olea*, Oleaceae and *Arbutus*; Xerophytes-group is formed by *Juniperus*, *Helianthemum*, *Ephedra distachya*, *E. fragilis*, *Hippophae*, *Artemisia*, Compositae and Chenopodiaceae; Other herbs-group includes Rubiaceae, *Gentiana*, Boraginaceae, Plumbaginaceae, *Armeria*, Primulaceae, *Papaver*, Geraniaceae, Malvaceae, Violaceae, Polygonaceae, *Crocus*, *Cytisus*, *Asphodelus*, *Galium*, Valerianaceae, Dipsacaceae, *Aristolochia* and *Cannabis/Humulus* type. Dots represent percentages <0.5%. Sedimentological units defined in Figure 4 are also reported to facilitate readability.

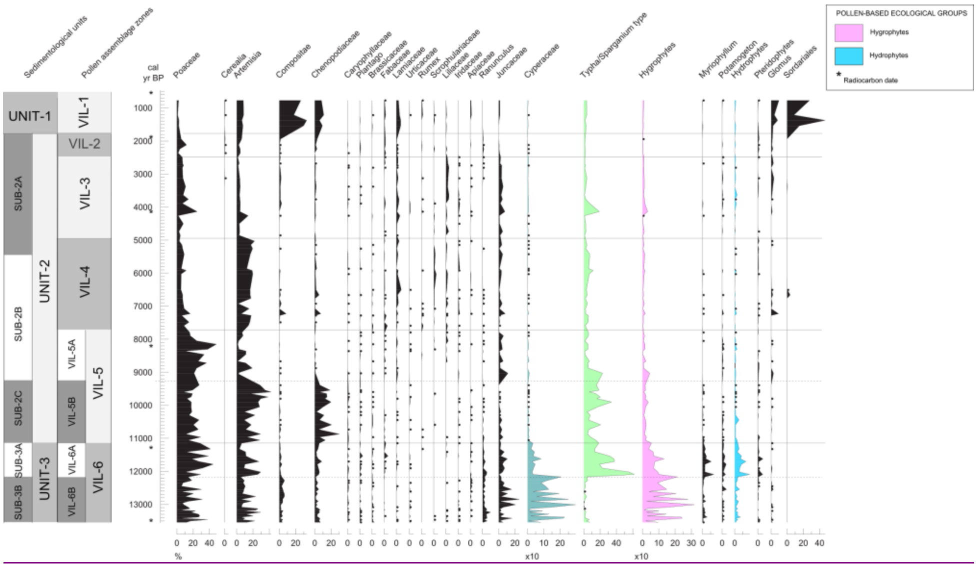

Figure 6. Pollen diagram from Villarquemado sequence for herbs, hygrophytes, hydrophytes, Pteridophytes and NPPs. Hygrophytes-group is composed by *Ranunculus*, Juncaceae, Cyperaceae, *Typha/Sparganium* type and *Thalictrum*. Hydrophytes-group includes *Myriophyllum*, *Potamogeton*, *Utricularia*, *Nuphar*, *Nymphaea* and *Callitriche*. Dots represent percentages <0.5%. Sedimentological units defined in Figure 4 are also reported to facilitate

readability.

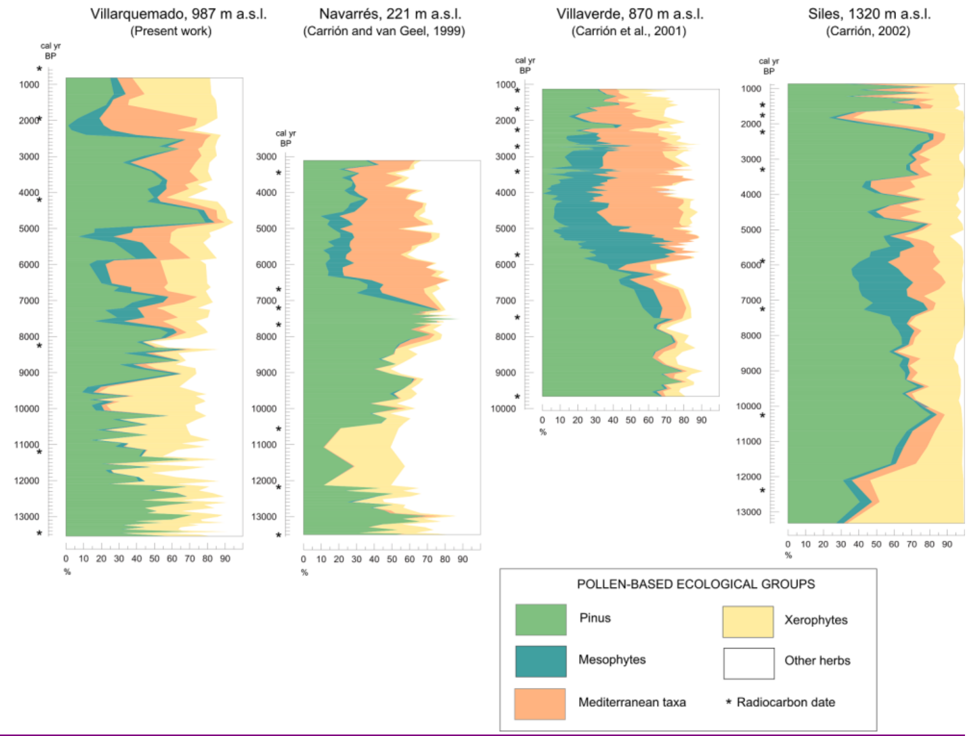

Figure 7. Main vegetation trends in the Villarquemado sequence and correlation with other Mediterranean continental records. Pollen-based ecological groups for Villarquemado are defined in Figure 5 caption. Pollen data for Navarrés, Villaverde and Siles have been obtained from Carrión and van Geel (1999), Carrión et al. (2001) and Carrión (2002), respectively.

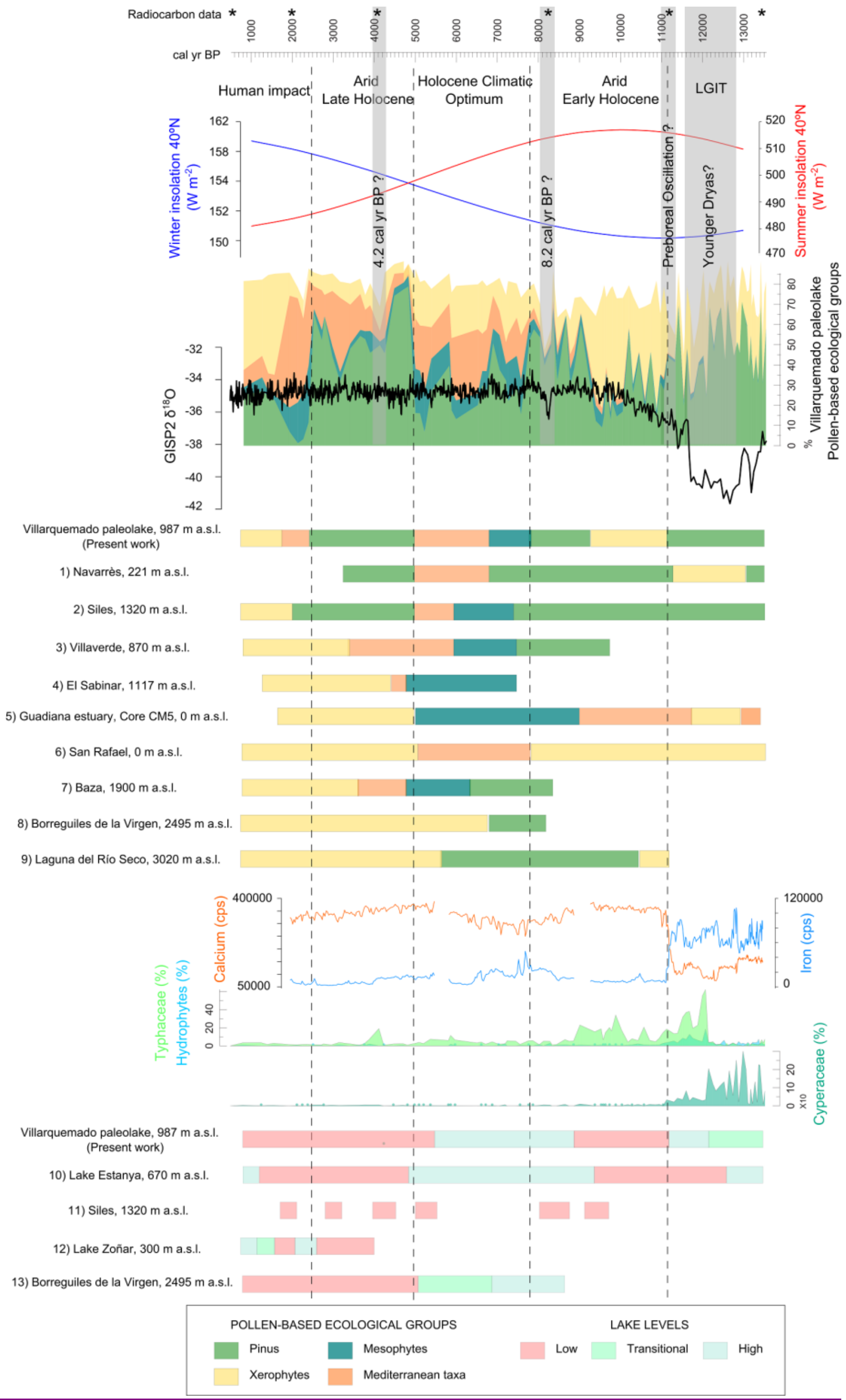

Figure 8. Comparison of the Villarquemado sequence (pollen-based ecological groups, top; aquatic taxa and geochemical composition, center) with selected records from

continental Iberia for the Lateglacial and Holocene derived from various approaches. Winter and summer insolation values for 40ºN are calculated by means of PAST software (Hammer et al., 2001) and GISP2 isotope values obtained from Stuiver et al., (1995). Pollen data have been acquired from 1) Navarrés (Carrión and van Geel, 1999); 2) Siles (Carrión, 2002); 3) Villaverde (Carrión et al., 2001); 4) El Sabinar (Carrión et al., 2004); 5) Core CM5 (Fletcher et al., 2007); 6) San Rafael (Pantaleón-Cano et al., 2003); 7) Baza (Carrión et al., 2007); 8) Borreguiles de la Virgen (Jiménez-Moreno and Anderson, 2012) and 9) Laguna del Río Seco (Anderson et al., 2011). The main lake level phases are derived from 10) Lake Estanya (Morellón et al., 2009); 11) Siles (Carrión, 2002); 12) Lake Zoñar (Martín-Puertas et al., 2008); and 13) Borreguiles de la Virgen (García-Alix et al., 2012). Pollen-based ecological groups for Villarquemado defined in the caption of Figures 5 and 6 and lake level reconstructions have been summarized by integrating sedimentological, geochemical and hygro-hydrophyte pollen assemblages.

Table 1. Radiocarbon dates (AMS) for the Villarquemado sequence obtained from bulk sediment.

Core	Lab. number	Depth (cm)	Radiocarbon date (^{14}C AMS yr BP)	Age error (yr BP)	Calibrated age (2σ) (cal. yr BP)
VIL-05-1A	Beta-332033	11	430	30	529-431
VIL-05-1A	Beta-332034	132	7460	40	8365-8190
VIL-05-1A	Poz-16073	220	11950	70	13997-13617
VIL-05-1B	Beta-319544	62.5	2020	30	2084-1898
VIL-05-1B	Poz-18451	96.5	3750	40	4232-3990
VIL-05-1B	Poz-18509	173.5	7460	50	8373-8185
VIL-05-1B	Poz-18453	233	9820	50	11339-11192
VIL-05-1B	Poz-15943	307	11620	60	13645-13306