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RESEARCH PAPER

800 ka of Palaeoenvironmental changes in the Southwestern Mediterranean realm

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Abstract

We provided valuable information about the palaeoenvironmental evolution of Southwestern Europe during the last 800 ka through the palynological study of the longest continuous continental Quaternary record in the Iberian Peninsula and in the Southwestern Mediterranean region. The SPD core studied here constituted the longest sequence recovered at the Padul Basin and we improved the chronological precision with respect to previous research. Furthermore, the high sampling resolution provided interesting insights into the main vegetation changes occurred at long-term timescales in the region and allowed correlating these variations with other long continental records of Europe. Dating using palaeomagnetism, amino acid racemisation, U/Th and ^{14}C allowed us to construct a robust Bayesian age-depth function, thereby making it possible to determine the chronological framework for the Padul record. From the palynological content of the samples, which were grouped in 11 clusters, we obtained a large variable number of minor pollen variations totalling 21 palynozones identified along the record. From the statistical analysis of the pollen data, some pollen environmental indexes were defined, allowing the reconstruction of palaeotemperature and palaeohumidity conditions. Five climatic scenarios were established: cold/arid, cold/semi-arid, cold/wet, temperate/wet (Mediterranean-climate), and warm/wet (Mediterranean-climate with higher moisture). Of note, the vegetation in the Padul Basin differed from that of other European basins with long pollen records due to regional characteristics, but main palaeoenvironmental trends were in agreement. *Pinus*, Steppic, Xerophilous, and Mediterranean taxa in the Padul Basin showed a continuous and dominant presence along the whole record, while only in certain periods did humidity increase, reflected by the expansion of Spores, Deciduous and Mediterranean taxa (especially in Pz 2, 7 and 13), but without any large expansion of deciduous forest. Comparison with other European records revealed the singular bioclimatic position of the Padul Basin in the Southwestern Mediterranean realm, and this part of Iberia can be considered a Quaternary vegetation refuge, mainly for mesophillous taxa and sclerophyllous oak. Although the biomes of the Padul basin and other European basins could not be compared directly, the main palaeoenvironmental trends were coincident (interstadials were marked by warmer periods and greater humidity, whereas stadials were cooler and more arid). These observations suggest that environmental changes in the Padul Basin were in tune with variations in global palaeoclimatic conditions.

Keywords Palynology · Palaeoclimatology · Padul · Quaternary · Southwestern Mediterranean

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Evolución paleoambiental de la región suroccidental de Europa durante los últimos 800 ka

Resumen

En este trabajo proporcionamos información valiosa sobre la evolución paleoambiental de la zona suroccidental de Europa durante los últimos ca. 800 ka, a través del estudio palinológico del registro cuaternario continental más largo de la Península Ibérica y del suroeste del Mediterráneo. El sondeo SPD representa la secuencia más larga de la cuenca de Padul en el que se realizó una mejora del modelo cronológico publicado anteriormente. Asimismo, el muestreo de alta resolución proporcionó información importante sobre los principales cambios de vegetación ocurridos en la zona y permitió correlacionar estas variaciones con las de otros registros continentales europeos largos. La datación mediante paleomagnetismo, racemización de aminoácidos, U/Th y ^{14}C permitió construir un modelo cronológico bayesiano robusto del registro de Padul. A partir del contenido de polen de las muestras, que se agruparon en 11 asociaciones, se interpretaron numerosas variaciones menores, pudiéndose identificar 21 palinozonas. A partir del análisis estadístico de los datos de polen se definieron diversos índices paleambientales que permitieron la reconstrucción de las condiciones de paleotemperatura y paleohumedad. Se establecieron 5 escenarios climáticos: frío/árido, frío/semiárido, frío/húmedo, templado/húmedo (clima mediterráneo) y cálido/húmedo (clima mediterráneo con mayor humedad). Cabe destacar que la vegetación en la cuenca de Padul difería de la de otras cuencas europeas debido a sus características locales y regionales, aunque con una buena correspondencia con las tendencias paleoambientales principales a nivel global. Los taxones de pino, plantas esteparias, xerófilos y mediterráneos mostraron una presencia continua y dominante a lo largo de todo el registro, mientras que solamente en ciertos períodos se produjo un incremento de la humedad, reflejada en la expansión de esporas y polen de taxones de árboles caducifolios y mediterráneos (especialmente en Pz2, 7 y 13), pero sin ninguna gran expansión del bosque caducifolio. La comparación con otros registros europeos reveló la posición bioclimática singular de la cuenca de Padul en el Mediterráneo suroccidental, pudiendo considerarse esta zona de la Península Ibérica como un refugio de vegetación durante el Cuaternario, principalmente de taxones mesófilos y *Quercus* esclerófilos. Aunque los biomas de la cuenca de Padul y otras cuencas europeas no pudieron compararse directamente, las principales tendencias paleoambientales mostraron una coincidencia clara (los períodos interestadiales estuvieron marcados por condiciones más cálidas y de mayor humedad, mientras que los períodos estadiales fueron más fríos y áridos). Estas observaciones sugieren que los cambios en la cuenca de Padul estaban en sintonía con las variaciones paleoclimáticas a nivel mundial.

Plalabras clave Palinología · Palaeoclimatología · Padul · Cuaternario · Mediterráneo Suroccidental

1 Introduction

The study of past climate variations is important to better understand current climate change and its impact on terrestrial ecosystems, particularly at the mid-latitudes (Tegart et al., 1990, 1993). Among different proxies, the pollen content in sedimentary records contribute to the reconstruction of palaeoenvironmental changes and provides accurate representations of vegetation changes. Specifically, the study of pollen in continental sequences fundamentally contributes to the reconstruction of terrestrial palaeoclimatic changes, and constitutes a quantitative proxy that can provide continuous and valuable information of vegetation variations (Sadori et al., 2016).

Knowledge of the vegetation history of Europe during the Pleistocene derives from a long history of investigations of records along the continental and marine cores. Our understanding of Pleistocene vegetation changes within and between glacial and interglacial periods has been historically dominated by the northern European pollen record. In fact, the biostratigraphy of those records has frequently served as the basis for correlation and the development of chronostratigraphical schemes (Florschütz et al. 1971; Follieri et al. 1988; Tzedakis 1994; Allen et al. 2000, among others).

In this regard, long lacustrine pollen sequences from Southern Europe are particularly important as at such latitudes glaciations have not caused stratigraphic gaps in lacustrine sediments, unlike in northern European records. Thus, lacustrine pollen sequences from Southern Europe provide long and continuous paleoclimate records. However, long Pleistocene European continental series ranging some hundreds of thousand years are scarce, as there are only few lacustrine records spanning more than 300 ka: Velay (Southern France), with ca. 450 ka (Reille et al. 2000; de Beaulieu et al. 2001), Valle di Castiglione (central Italy), with ca. 300 ka (Follieri et al. 1988), Lake Ohrid (Albania-Macedonia), with ca. 500 ka (Sadori et al. 2016), Ioannina (Western Greece), with ca. 480 ka (Tzedakis 1994), Kopais (Southeastern Greece), with ca. 500 ka (Tzedakis 1999; Okuda et al. 2001), and Tenaghi Philippon (Northeastern Greece), with 1.35 Ma (Tzedakis et al. 2003, 2006; Pross et al. 2015), most of them located in Southeastern Europe.

Moreover, plant taxa variations along time can differ in records located in distinct climatic regions (Follieri et al. 1988). In this regard, some sites, such as Ioannina (Greece), acted as refuge, with relative ecological stability, and did not experience the extreme effects of Quaternary climate variability during glacial times recorded in Norther European sites (Tzedakis et al. 2002). Thus, pollen data revealed divergence between populations of many arboreal species in Southern Europe refugial areas, and different migration paths (Carrión et al. 2003; González-Sampériz et al. 2010; Magri and Palombo 2013; Tzedakis 2009; Orain et al. 2013 Magri et al. 2017; Tzedakis et al. 2002, 2013). However, most mechanisms still have to be understood and therefore, it is essential to compare palynological records.

Furthermore, in most cases, there has been a lack of independent chronologies. In this regard, Tzedakis et al. (1997, 2001) established a terrestrial chronological framework for long and continuous pollen records in Europe (Velay, Valle di Castiglione, Ioannina and Tenaghi Philippon). This framework allowed a complete stratigraphical scheme of major vegetation events for the last 430 ka and facilitated differentiation of the palynological characteristics within MISs. Likewise, correlation between European pollen records of distinct climatic regions, including marine cores, has been attempted, especially for MIS5 (Sánchez-Goñi et al. 1999, 2005; Brewer et al. 2008), MIS7 (Desprat et al. 2006; Roucaux et al. 2008), and MIS9 (Fletcher et al. 2013).

However, the knowledge about the vegetation and climate variations during the past glacial-interglacial cycles in the Southwestern Mediterranean based on continental pollen sequences is poor, with the exception of the studies of the continental sequences of Fuentillejo, covering > 220 ka (Vegas et al., 2009, 2013; Ruiz-Zapata et al., 2012; Ortiz et al., 2013) and Villarquemado, with ca. 135 ka (González-Sampériz et al., 2013; Valero-Garcés et al., 2019; Wei et al., 2019), and the marine cores covering the last ca.140 ka (Sánchez-Goñi et al. 1999, 2000, 2005, 2008, 2016; Fletcher et al. 2010; Oliveira et al. 2016). In the southwestern Mediterranean realm an exceptional combination of subsidence and sedimentation resulted in one of the few examples of long palustrine/lacustrine sequences with a unique palaeoclimatological record. The Padul Basin (PB) contains one of the longest terrestrial records in the world, with more than 100 m covering ca. 800 ka (Ortiz et al. 2006, 2010). The relevance of the PB record was first recognised in the seminal pollen studies of Menéndez Amor and Florschütz (1962, 1964) and Florschütz et al. (1971) performed in a ca. 100-m deep borehole core (MF), and in a palynological reconstruction of a composite record of 22.8 m (PR) by Pons and Reille (1988). Also, Valle et al. (2003) reported the palaeoecological reconstruction of the uppermost 8 m (from 30 to 4.5 cal ka BP) on the basis of the pollen content of this basin. Recently, Ramos-Román et al. (2018) provided a detailed climate reconstruction of the PB for the last 4700 cal yr BP based of the pollen record of a borehole core (RR) drilled at the western part of the basin. Also Camuera et al. (2019) provided the pollen record of the last 200 ka. However, the chronological model used by these authors must be taken with caution, as it was constructed using only 2 ages older than 50 ka (ca. 65 ka and ca. 120 ka, after the rejection of 3 ages), and using linear extrapolation with two different sediment rates beyond ca. 120 ka (Camuera et al., 2018).

In the present study we re-examined the PB palaeoclimatological record, with shorter sampling intervals from a 107 m-long borehole core (SPD)-financed by an European Union Project-drilled where the basin reaches its maximum depth near its western edge (Nestares and Torres 1998).

Thus, the importance of this study lies on this record is the longest, continuous, available pollen sequence extending back to the last 800 ka in the Iberian Peninsula (indeed, the temporal extent of the PB record is significantly larger than other records in the Iberian Peninsula) and it is one of the longest in Southern Europe and the Mediterranean realm, where this type of sequences is scarce. Moreover, the data obtained here constitutes the last chance to study the palaeoenvironmental evolution of this long terrestrial Quaternary record because the former pit was flooded and the possibility to drill a similar sequence is out of reach (Camuera et al., 2018).

Specific objectives of this study are (1) to present the results of a more detailed and complete palaeoclimatological reconstruction of the southern Iberian Peninsula within Marine Isotope Stages (MISs) 20 to 1 on the basis of the pollen content at higher sampling resolution, and to check if the PB acted as a refugee area for tree populations; (2) to enhance our understanding of the palaeoclimatological characteristics of the Southwestern Mediterranean realm, by comparing the PB record with other long continental and marine European pollen records (Fig. 1). For this purpose, we improved the chronological model of Ortiz et al. (2004) by the dating of new 13 ages and using the previously ones obtained through consistent numerical datings (^{14}C, U/Th, amino acid racemisation and palaeomagnetism).

2 Study area

The PB catchment has a total area of 44 km^2, while the present peat bog sensu stricto covers 4.6 km^2 and is located 720 m a.s.l. (Fig. 2). The basin is a closed flat depression 12 km south of Granada. The western boundary is formed by the elevations of the Albuñuelas range (1000 m a.s.l), while the eastern one is the craggy Sierra Nevada, which reaches its highest point at the Mulhacén peak (3482 m a.s.l.), only 20 km east of Padul. The northern boundary is a

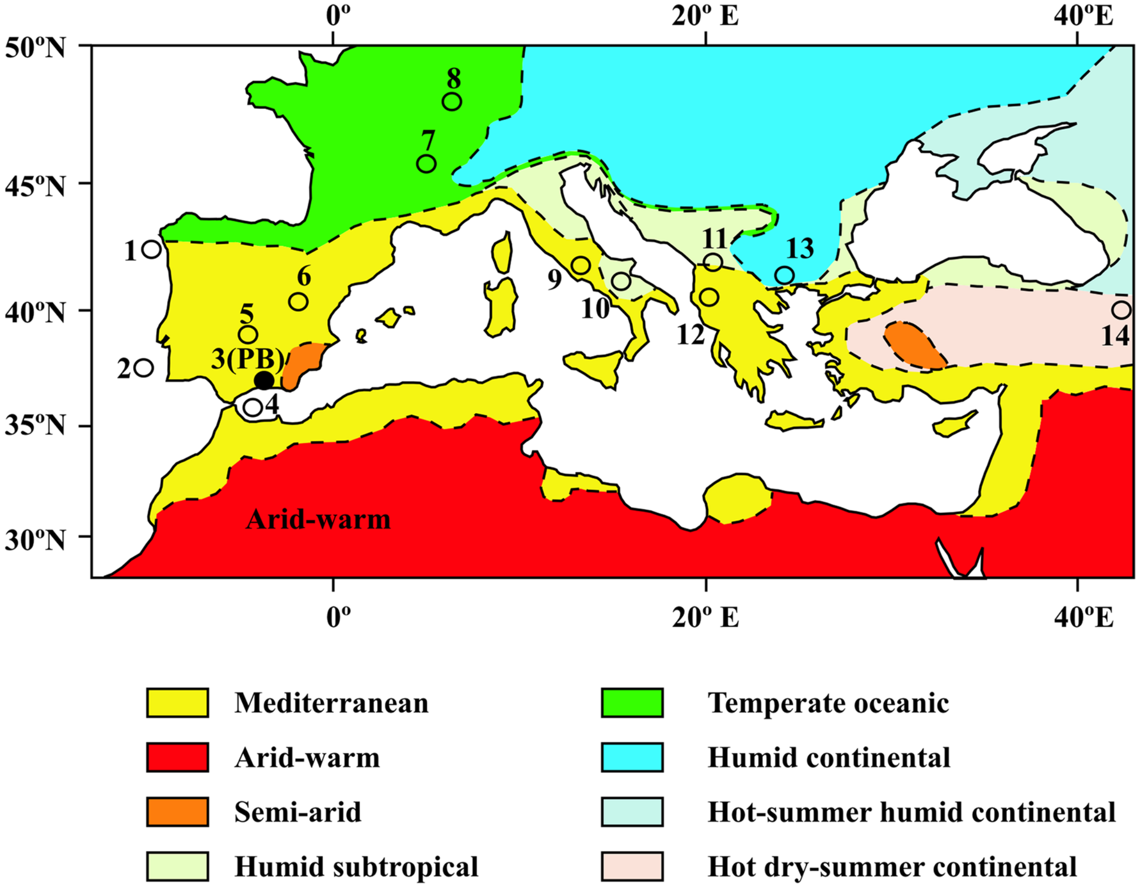

Fig. 1 Geographical location of the Padul Basin and other European records, including the areas of the Köppen climate classification (Rubel and Kottek 2010; Chen and Chen 2013). 1: MD99-2331; 2: MD95-2042; 3: Padul; 4: ODP-976; 5: Fuentillejo; 6: Villarquemado; 7: Velay; 8: La Grande Pile; 9: Valle di Castiglione; 10: Lago Grande di Monticchio; 11: Lake Ohrid; 12: Ioannina; 13: Tenaghi Phillipon; 14: Lake Van

small elevation (Suspiro del Moro, 830 m a.s.l.) that divides the PB and the Granada depression. The southern boundary is defined by the Dúrcal river gorge.

The PB resembles a typical endorheic basin which is tectonic-controlled (Viseras et al. 2001): an alluvial fan system developed along its eastern border, grading into the lacustrine-palustrine environment. The still active Padul fault provides continuous subsidence at the western boundary of the basin, and the alluvial fan apices are aligned along the fault trace at 800–900 m a.s.l. (García et al. 1998; Alfaro et al. 2001a, b) (Fig. 2). The PB is an asymmetric graben (Enadimsa-Endesa 1981), with its maximum thickness near the Padul fault. The maximum thickness of ca. 110 m is reached towards the eastern boundary of the basin, with Pleistocene sediments overlying Miocene marine sediments.

A dominant groundwater regime controls the hydrology of the basin (Cañada 1984), with a hydrogeological connection between the karst rock of Sierra Nevada and the PB itself.

The climate in the basin is Mediterranean with a continental influence. Winters are cold and dry, while summers are extremely hot, with maximum temperatures over 40 °C (Fig. 3a). The average annual rainfall ranges from 400 to 450 mm (July and August are the driest months and December the most humid), evapotranspiration is 700–900 mm/yr, and the mean annual temperature is between 15 and 16 °C, being July and August the warmest months (ca. 24 °C), and January the coldest, with ca. 9 °C (Rivas-Martínez and Rivas-Sáenz 2009).

The present day accumulation of organic matter in the PB is not linked to ferns or mosses but to litter from semi-aquatic plants like *Phragmites australis*, helophytic species (*Typha angustifolia, Scirpus lacustris, Ranunculus repens, Lythrum junceum, Apium nodiflorum, Veronica anagallis-aquatica*) and other hygrophilous plants (*Cyperus longus, Juncus articulatus, Ranunculus trilobus, Scrophularia auriculata*) that drop pollen grains directly onto the bog (Sánchez-Castillo and Morales-Torres 1981). Riparian representatives, such as *Populus* sp., *Salix* sp. and *Fraxinus* sp.,

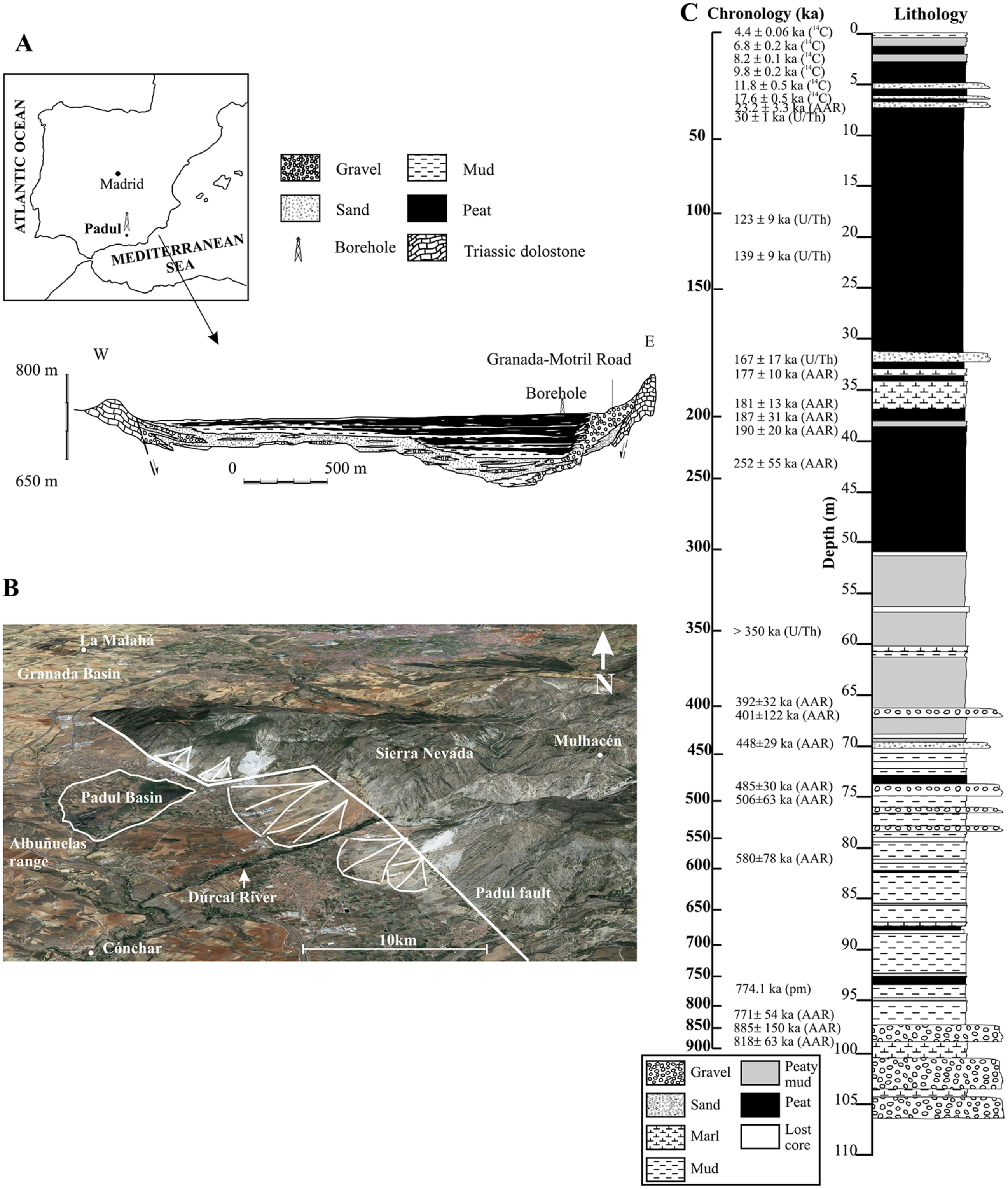

Fig. 2 Modified from Ortiz et al. (2004a) **a** Geographical setting and cross-section of the Padul Basin. **b** A composite aerial photograph is included in which the Padul normal fault is shown. **c** Stratigraphy and chronology of the Padul Basin record. Datings are followed by the method used for their calculation: ^{14}C, U/Th, AAR (amino acid racemization), pm (palaeomagnetism); owing to drawing limitations, some ^{14}C results have not been represented (SPD-0213: 7285 ± 127 ka; SPD-0335: 9013 ± 234; SPD-0345: 9017 ± 239, SPD-0407: 11,253 ± 144)

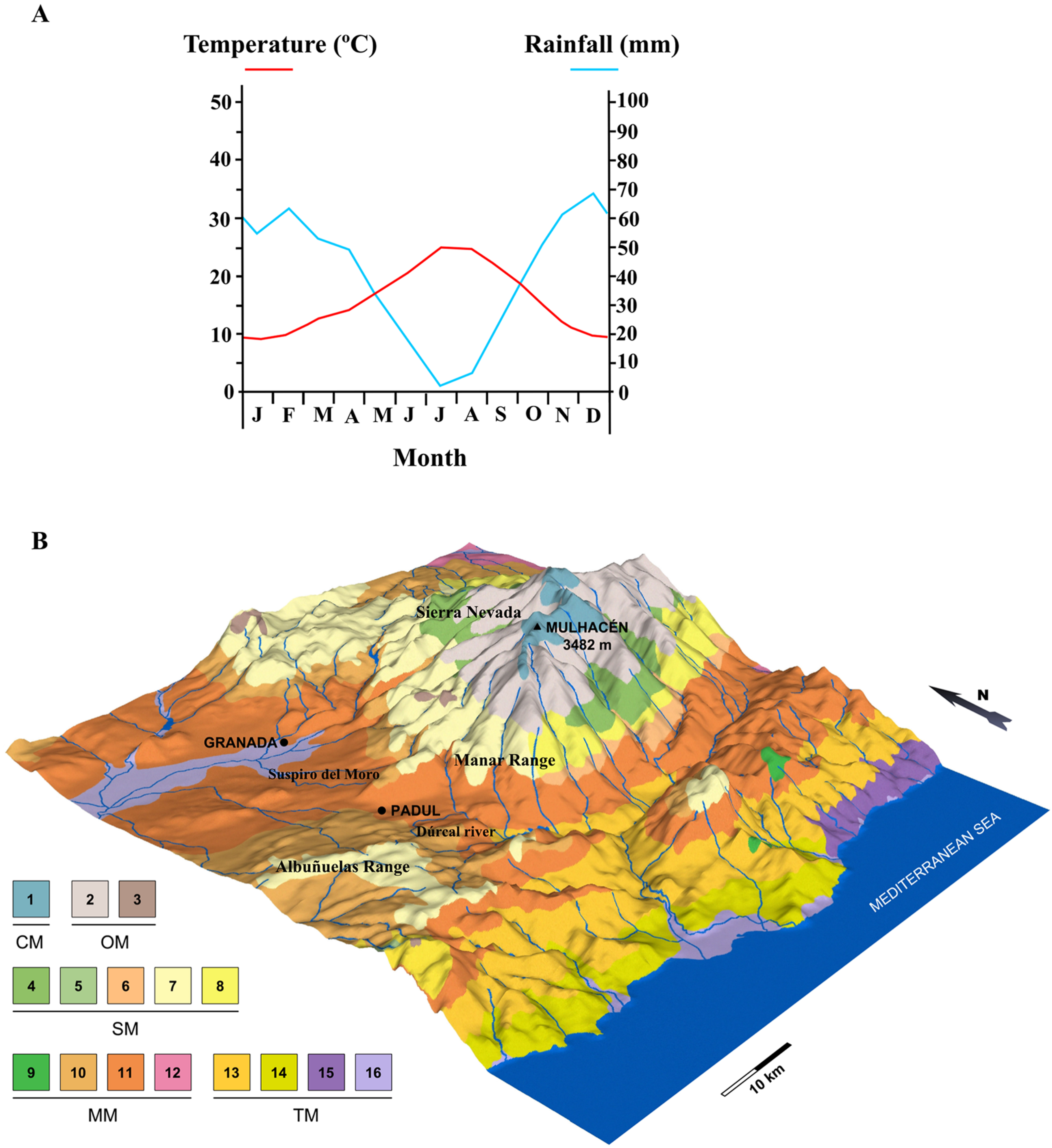

Fig. 3 **a** Ombrothermic diagram of Padul (Rivas-Martínez and Rivas-Sáenz 2009); **b** 3D view of the Padul Basin and surroundings showing the vegetation associations (Rivas-Martínez 1987). The altitudinal boundaries change slightly depending on the slope orientation. Nomenclature appears in detail in Table 1. CM: Cryo-mediterranean (1: silicean); OM: Oro-mediterranean (2: silicean; 3: basophyllous); SM: Supra-mediterranean (4: silicean; 5: Supra-mediterranean basophilous of *Quercus faginea*; 6: Typical meso-mediterranean faciation of *Retama sphaerocarpa;* 7: Supra-mediterranean basophilous; 8: Supra-meso-mediterranean silicean); MM: Meso-mediterranean (9: Meso-thermo-mediterranean and Betic humid-hyperhumid; 10 Betic meso-mediterranean; 11 Betic thermophilous faciation; 12 Betic faciation); TM: Thermo-mediterranean (13: Betic thermo-mediterranean; 14: Thermophilous faciation; 15: Typical semi-arid faciation; 16: Riparian mediterranean geomegaseries and orchards)

Table 1 The Mediterranean vegetation belts (Rivas-Martínez 1987) shown in Fig. 3

N	Vegetation belt
1	Cryo-mediterranean (CM) silicean (*Erigeronto frigidi-Festuceto clementei sigmetum*). VP psicroxerophyllous pastures
2	Oro-mediterranean (OM) silicean (*Genisto baeticae-Junipereto nanae sigmetum*). VP creeping *Juniperus* and creeping *Genista*. Creeping juniper and broom
3	Oro-mediterranean (OM) basophyllous (*Daphno oleidi-Pineto sylvestris sigmetum*). VP Pine groves and creeping sabines
4	Supra-mediterranean (SM) silicean (*Adenocarpo decorticantis-Querceto pyrenaicae sigmetum*)
5	Supra-mediterranean (SM) basophilous of *Quercus faginea*
6	Typical meso-mediterranean (MM) faciation of *Retama sphaerocarpa*
7	Supra-mediterranean (SM) basophilous (*Berberidi hispanicae-Querceto rotundifoliae sigmetum*). Evergreen oak groves
8	Supra-meso-mediterranean (S-MM) silicean (*Adenocarpo decorticantis-Querceto rotundifoliae sigmetum*). Evergreen oak groves
9	Meso-thermo-mediterranean (M-TM) and Betic humid-hyperhumid (*Teucrio baetici-Querceto suberis sigmetum*). Blockhead grove
10	Betic meso-mediterranean (MM) (*Paeonio coriaciae*-Querceto *rotundifoliae sigmetum*). Evergreen oak groves
11	Betic thermophilous faciation with *Pistacia lentiscus* (meso-mediterranean)
12	Betic faciation with *Ephedra fragilis* (meso-mediterranean)
13	Betic thermo-mediterranean (TM) Series (*Smilaci mauritanicae-Querceto rotundifoliae sigmetum*). Evergreen oak groves
14	Thermophilous faciation with *Maitenus europaeus*
15	Typical semi-arid faciation (*Chamaerops-Rhamneto lycioides sigmetum*). Mastic-tree forest (thermo-mediterranean).
16	Riparian mediterranean geomegaseries and orchards (thermo-mediterranean)

Table 2 Areal distribution of the present-day vegetation belts according to 100 m elevation intervals at the Padul catchment (based on Rivas-Martínez 1987)

Elevation (m a.s.l.)	Surface (km^2)	Surface (%)	Vegetation belts	Plant species	Common name
> 1300	2.086	5	OM & SM	*Pinus sylvestris* *Quercus faginea* *Taxus baccata* *Quercus pyrenaica* *Acer granatense*	Scotch pine Portuguese oak European yew Pyrenean oak Maple
1200-1300	1.743	4	MM	*Pinus pinaster*	Maritime pine
1200-1100	2.686	6	MM	*Quercus suber*	Cork oak
1100-1000	10.029	22	MM	*Quercus faginea*	Portuguese oak
1000-900	2.829	6	MM	*Ceratonia siliqua*	Carob, St. John's bread
900-800	14.657	33	MM	*Juniperus phoenicea*	Sabina
800-700	10.743 (4.6 corresponds to the peat bog)	24	MM	*Juniperus oxycedrus* *Cistus clusii* *Ephedra fragilis* *Quercus rotundifolia* *Pistacia lentiscus* *Artemisia sp.*	Prickly juniper Rockrose Joint-pine Holm oak Mastic tree Mugwort
<700		0	TM	*Pistacia lentiscus* *Genista spartioides* *Buxus balearica* *Pinus halepensis* *Ceratonia siliqua* *Quercus suber* *Erica terminalis*	Mastic tree Bolina Balearic boxwood Aleppo pine Carob, St. John´s bread Cork oak Heather

OM oro-mediterranean, *SM* supra-mediterranean, *MM* meso-mediterranean, *TM* thermo-mediterranean

among others, also appear on the banks of the bog. Furthermore, the PB (720 m a.s.l.) receives pollen not only from the water body but from the Sierra Nevada Range, which holds a series of vegetation belts (Table 1) (Rivas-Martínez 1987) (Fig. 3b), the main contribution belonging to the meso-Mediterranean belt below 900 m (57% of current vegetation). There is a noticeable pollen source comprised between

1100 and 1000 m a.s.l. (22% of current vegetation), which also belongs to the meso-Mediterranean belt. In contrast, the contribution of supra-Mediterranean-oro-Mediterranean vegetation is almost negligible (Table 2). Thus, the pollen rain on the PB surface is a complex integration of several types of plants.

3 Materials and methods

The drilling operations were performed by the Geological Service of Spain, using a drilling rig with a conventional drill pipe and direct flow of bentonite-water mud.

The stratigraphy of the SPD Padul borehole (latitude: 37° 01′ 01″ N; Longitude: 3° 36′ 07″ W; Elevation: 714.20 m) is described in Ortiz et al. (2004a) and Ortiz et al. (2010) (Fig. 2c): coarse detrital material was predominant in the lower part of the core (from 107 to 70 m) with some scarce peaty intervals (fibric peat), whereas between 70 and 50 m peaty mud was dominant. In the uppermost 50 m, peat (fibric peat) was abundant, with some marly and sandy interbeds at 37–33 m and 7–5 m, respectively.

After the field description and sampling at 20-cm intervals, the borehole core was wrapped in aluminium foil and refrigerated. We refer the sampled horizons of the borehole by their depth, in cm, from top to bottom (e.g. sampled level SPD-1280 is at 1280 cm).

3.1 Chronology

The chronology of the PB record presented here was improved respect to the previous one Ortiz et al. (2004a), obtained through consistent numerical datings (^{14}C, U/Th, amino acid racemisation-AAR- and palaeomagnetism). The age-depth model was improved here by the dating of new 13 levels mainly of the intermediate part of the PB sequence (between 67.25 and 97.50 m) through AAR. In four horizons (SPD-6790, SPD-6905, SPD-7450, SPD-8080) gastropods belonging to the genus *Radix* were selected, whereas in the rest (SPD-6725, SPD-7430, SPD-9670 and SPD-9750), *Bythinia* opercula were recovered. We also selected ostracodes in 5 horizons for AAR dating (SPD-140, SPD-539, SPD-710, SPD-3700, and SPD-3830).

The original datings obtained in SPD core are described in Ortiz et al. (2004a), and briefly summarised here. Radiocarbon dating was undertaken on peat of nine samples (Supplementary Material Table 1). The ages were calibrated (cal yr) were converted using the Radiocarbon Calibration Program 7.1 (CALIB 7.1) (Stuiver et al. 2018) with the calibration dataset IntCal13 (Reimer et al. 2013). For U/Th dating we selected and prepared peat of five horizons (Supplementary Material Table 2). For AAR dating, we were able to recover ostracode shells mainly constituted by representatives of the *Herpetocypris reptans* (Baird) species in horizons SPD-3200, SPD-3600, and SPD-4135 (Supplementary Material Table 3). We also analyse 5 gastropods belonging to the genus *Bythinia* in horizon SPD-9710 (Supplementary Material Table 4). Palaeomagnetism was determined in samples from 15 beds (Supplementary Material Table 5).

3.1.1 Amino acid racemization dating

For amino acid racemization dating purposes, we reject the first centimetre of the borehole to avoid surface contamination. We selected 24 valves of *H. reptans* valves in five new horizons SPD-140, SPD-539, SPD-710, SPD-3700, and SPD-3830, which were not previously analysed. In other horizons (SPD-6725, SPD-6790, SPD-6905, SPD-7430, SPD-7450, SPD-8080, SPD-9670, and SPD-9750) 19 gastropods belonging to the genera *Radix* and *Bythinia* were selected.

Samples were sieved under running water, dried at room temperature, and studied under a binocular microscope to determine the faunal assemblages. Ostracods and gastropods were carefully sonicated and cleaned with water to remove the sediment. Afterwards, at least 4–7 ostracode valves and 15–20 mg of gastropod shells were picked.

Amino acid concentrations and ratios of ostracode valves from some the new sampled horizons were quantified using high performance liquid chromatography (HPLC) following the sample preparation protocol described by Kaufman and Manley (1998) and Kaufman (2000). Only translucent specimens were selected for the analysis, and a single valve of *H. reptans* specimens was used for each analytical sample. The procedure involves hydrolysis, which was performed under N_2 atmosphere in 7 µL of 6 M HCl for 20 h at 100 °C. The hydrolysates were evaporated to dryness in vacuo, and then rehydrated in 7 µL 0.01 M HCl with 1.5 mM sodium azide and 0.03 mM L-*homo*-arginine (internal standard). Samples were injected into an Agilent-1100 HPLC equipped with a fluorescence detector. Excitation and emission wavelengths were programmed at 335 nm and 445, respectively. A Hypersil BDS C18 reverse-phase column (5 µm; 250 × 4 mm i.d.) was used for the analysis.

The sample preparation protocol for gastropods is described in Goodfriend (1991) and involves hydrolysis under N_2 atmosphere in HCl (2.9 µl/mg of 12 N HCl and 100 µl of 6 N HCl) for 20 h at 100 °C, and derivatization in two steps: first esterification with thionyl chloride in isopropanol and acylation with trifluoroacetic acid anhydride in dichloromethane. 1–4 µl aliquots were injected into a Hewlett-Packard 5890 gas chromatograph with a Chirasil-L-Val fused silica column (0.39 mm × 0.25 µm × 25 m) from Chrompack and a nitrogen-phosphorous detector.

Table 3 Aspartic acid (Asp) and glutamic acid (Glu) *D*/*L* values in ostracode valves with their corresponding ages

Sample	Depth (cm)	Ostracode	*N*	*D*/*L* Asp	*D*/*L* Glu	Age (ka)
SPD-140	140	*Herpetocypris reptans*	4	0.183 ± 0.002	0.052 ± 0.007	6.777 ± 0.216
SPD-539	539	*Herpetocypris reptans*	7	0.256 ± 0.015	0.062 ± 0.009	17.962 ± 2.373
SPD-710	710	*Herpetocypris reptans*	7	0.281 ± 0.013	0.076 ± 0.007	23.250 ± 3.320
SPD-3700	3700	*Herpetocypris reptans*	6	0.404 ± 0.020	0.142 ± 0.019	187 ± 31
SPD-3830	3830	*Herpetocypris reptans*	4	0.407 ± 0.021	0.146 ± 0.029	190 ± 20

Table 4 Isoleucine (Ile), leucine (Leu), aspartic acid (Asp), phenylalanine (Phe) and glutamic acid (Glu) *D*/*L* values in gastropod shells with their corresponding ages

Sample	Depth (cm)	Gastropod	*N*	Dallo/L-Ile	*D*/*L* Leu	*D*/*L* Asp	*D*/*L* Phe	*D*/*L* Glu	Age (ka)
SPD-6725	6725	*Bithynia*	1	0.734	0.694	0.808	0.748	0.586	392 ± 32
SPD-6790	6790	*Radix*	4	0.543 ± 0.014	0.587 ± 0.070	0.654 ± 0.058	0.587 ± 0.049	0.447 ± 0.052	401 ± 122
SPD-6905	6905	*Radix*	1	0.561	0.670	0.755	0.585	0.442	448 ± 29
SPD-7430	7430	*Bithynia*	1	0.779	0.733	0.826	0.756	0.680	485 ± 30
SPD-7450	7450	*Radix*	1	0.612	0.682	0.768	0.604	0.479	506 ± 63
SPD-8080	8080	*Radix*	1	0.647	0.762	0.772	0.655	0.470	580 ± 78
SPD-9670	9670	*Bithynia*	3	0.910 ± 0.016	0.821 ± 0.006	0.902 ± 0.054	0.879 ± 0.009	0.756 ± 0.008	771 ± 54
SPD-9710	9750	*Bithynia*	2	0.939 ± 0.010	0.823 ± 0.011	0.902 ± 0.001	0.869 ± 0.011	0.805 ± 0.020	818 ± 63

Mean amino acid racemisation ratios (*D*/*L* values) and standard deviations of each horizon are shown in Tables 3 and 4. In gastropod samples (*Radix* and *Bithynia)* *D*/*L* values of diverse amino acids (Asp, Glu, Leu, Ile, and Phe *D*/*L*) were introduced into the age calculation algorithms of Torres et al. (1997) for central and southern Iberian Peninsula. In ostracode valves, aspartic acid and glutamic acid *D*/*L* values were selected for the age calculation because in most of them they account for over ca 50% of the amino acid content (Kaufman 2000; Bright and Kaufman 2011). The numerical age of each bed was determined by introducing the aspartic acid and glutamic acid *D*/*L* values obtained in *H. reptans* valves collected at each level into the age calculation algorithms established by Ortiz et al. (2004b).

The age of a single bed is the average of the numerical dates obtained for each amino acid *D*/*L* value measured in gastropods or ostracodes from that level, and the age uncertainty is the standard deviation of the numerical ages calculated in each level.

3.2 Palynology

A total of 389 samples from between 0 and 98 m were taken for palynological analyses. Basal gravel deposits were not sampled. The sampling density was higher in the upper 8 m of the core record (10–15 cm) than in the lower part (20–25 cm). Because of the lack of lamination, samples were taken on the basis of their lithology and/or colour change. In this regard, beds made of gravels and sands were not sampled with the same resolution that peaty and muddy horizons.

For each sample 1–1.5 g of dry sediment was treated following the standard procedure following Moore et al. (1991) and Phipps and Playford (1984) using the classical chemical treatment by HF, HCl and KOH with mineral separation with Thoulet dense liquid. Residues were mounted in glycerine jelly. The final concentration of palynomorphs was obtained using sieves of 150, 75 and 10 µm mesh. A database and graphs were made using Tilia 1.0.1 ® (Grimm 2008), Excel and Corel Draw software. Pollen percentages for all palynomorphs were based on the sum of at least 300 terrestrial pollen taxa by sample (Maher 1972; Rull 1987).

3.3 Screening

A total of 126 plant taxa were identified. A number of representative taxa was selected (Figs. 4, 5, 6), allowing the discrimination of 11 groups according to their environmental significance, some of them formed by a single genus. Apart from Aquatic taxa and Spores, these main groups were as follows (Table 5): *Pinus*, Mediterranean, Steppic, Xerophilous, Poaceae, Mesophilous, Montane, Cupressaceae, Hygrophilous, Riparian and Exotic. We used Hygrophilous for the high mountain hygrophilous meadows.

Of note, *Artemisia* and *Ephedra* were included within the Steppic group. Given that Amaranthaceae showed high percentages along the PB record (Fig. 6) we considered that it was important to individualized it within the Xerophilous

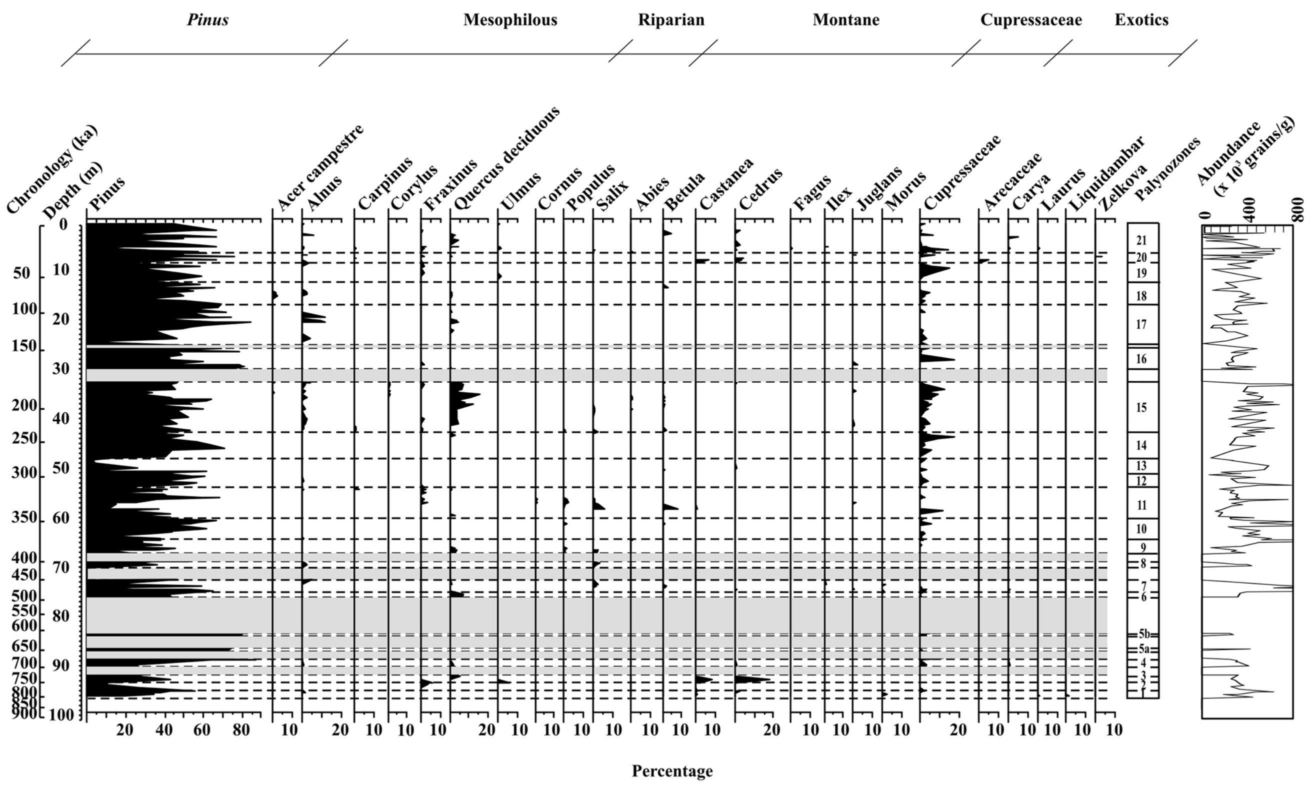

Fig. 4 Pollen diagram percentage of the main pollen taxa plotted against depth (m) and age (ka)

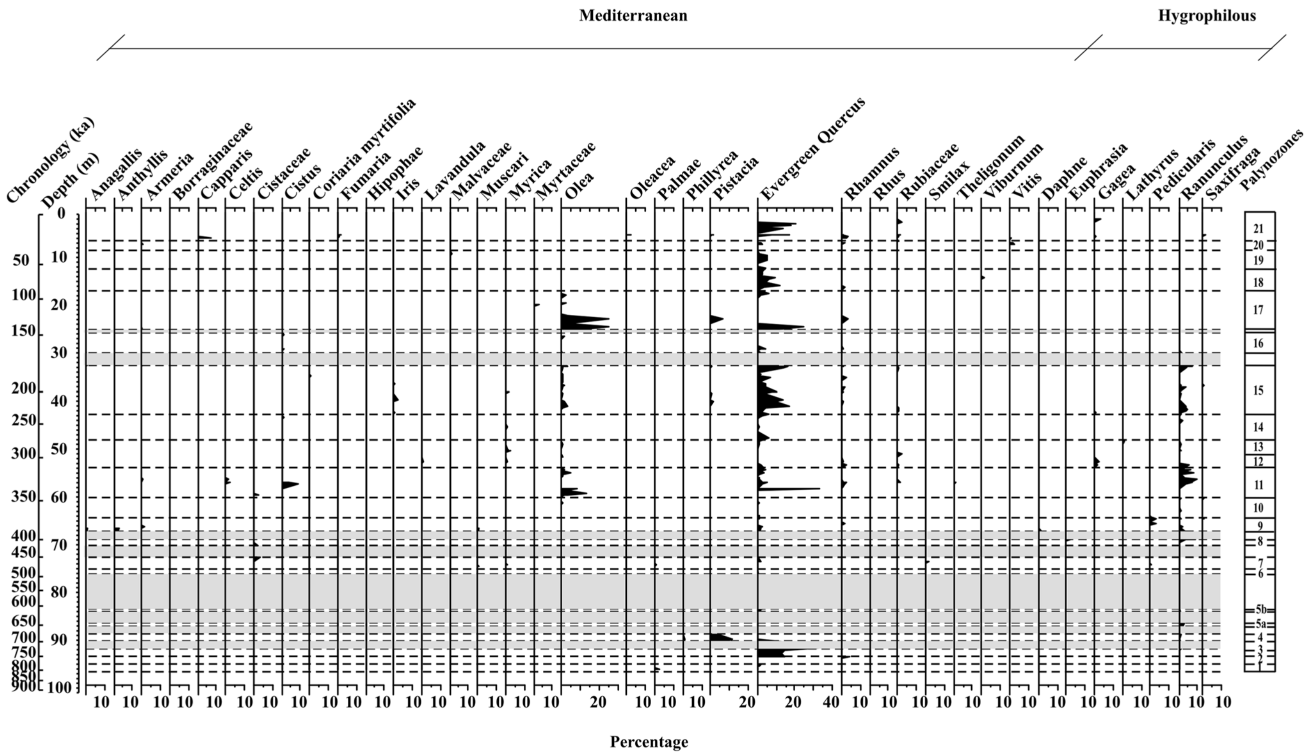

Fig. 5 Pollen diagram percentage of the main pollen taxa plotted against depth (m) and age (ka)

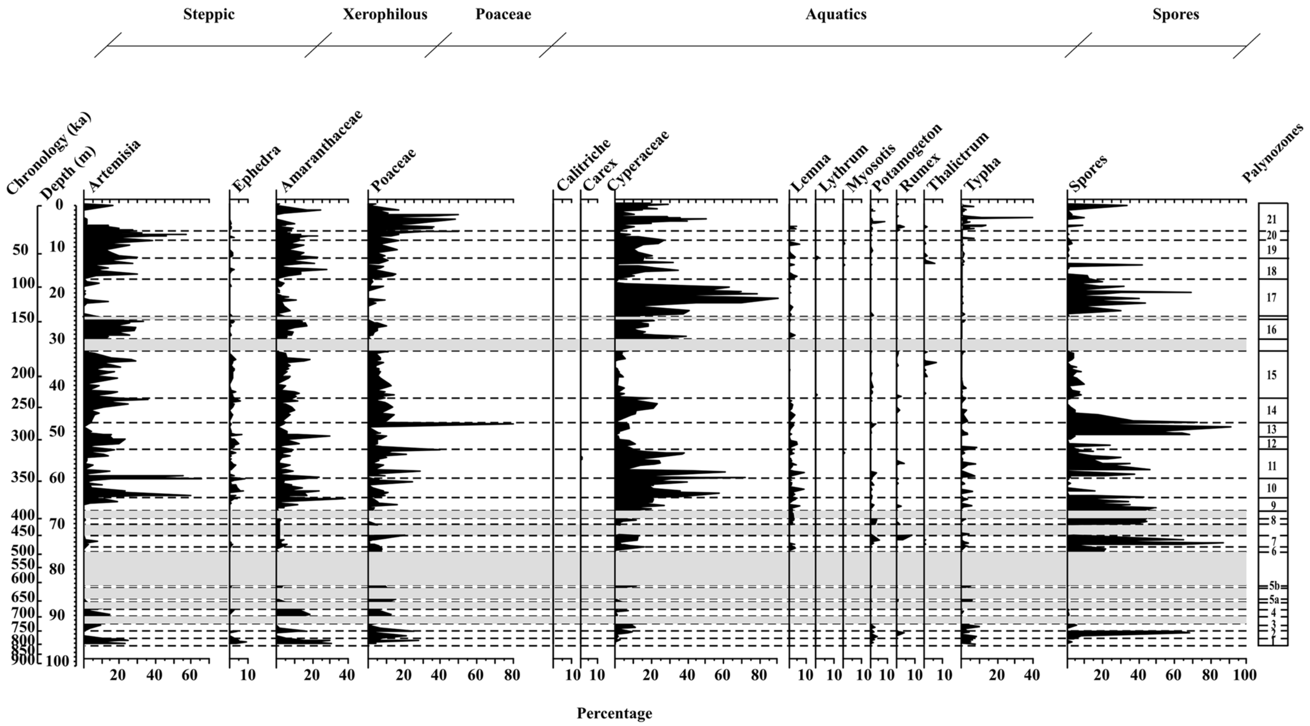

Fig. 6 Pollen diagram percentage of the main pollen taxa plotted against depth (m) and age (ka)

Table 5 Main taxa included in the palynological groups identified in the Padul record

Palynological Groups	Taxa
Pinus	*Pinus*
Poaceae	Poaceae
Hygrophilous	*Daphne, Euphrasia, Gagea, Lathyrus, Pedicularis, Ranunculus, Saxifraga*
Mesophilous	*Acer, Acer campestre, Alnus, deciduous Quercus*, Corylus, *Carpinus, Fraxinus, Ulmus*
Montane	*Abies, Betula, Castanea, Cedrus, Fagus, Ilex, Juglans, Morus*
Mediterranean	*Anagallis, Anthyllis, Armeria,* Boraginaceae*, Capparis, Celtis,* Cistaceae*, Cistus, Coriaria, Fumaria, Hippophae, Iris, Lavandula,* Malvaceae*, Muscari, Myrica,* Myrtaceae*, Olea,* Oleaceae*, Phillyrea, Pistacia, evergreen Quercus, Rhamnus, Rhus,* Rubiaceae*, Smilax, Theligonum, Viburnum, Vitis*
Cupressaceae	Cupressaceae
Exotics	Arecaceae*, Carya, Laurus, Liquidambar, Zelkova*
Steppic	*Artemisia*, *Ephedra*
Xerophilous	Amaranthaceae
Aquatics	*Callitriche, Carex,* Cyperaceae, *Lemna*, *Lythrum, Myosotis, Potamogeton, Rumex, Thalictrum Typha*
Riparian	*Cornus, Populus, Salix*
Spores	Monolete and trilete spores

taxa following Ramos et al. (2014), although it is commonly found in steppe environments together with *Artemisia* and *Ephedra*.

As the Padul peat bog is almost entirely covered by a dense carpet of the helophytic species and other aquatic macrophytes, we therefore separated the pollen from Aquatic taxa into a single log.

Pollen zones were established with the help of CONISS (Grimm 1987) together with the visual inspection based on changes in the main taxa groups. We also performed statistical analysis (Principal Component Analysis, unconstrained Cluster analysis) on the main groups of pollen assemblages with the software STATISTICA in order to clarify the identification of climate oscillations.

4 Results and discussion

4.1 Age model

For the construction of the new age–depth model we considered the ages from several levels obtained with diverse methods (Ortiz et al., 2004a) and those obtained here. Of note, samples recovered from the bottom of the stratigraphic section showed a paleomagnetic polarity change from normal to reverse in meter 93 and 97 (Fig. 2c) which was interpreted as the end of the Matuyama/Brunhes magnetozone boundary established at ca. 774.1 ka (Cohen and Gibbard 2019, based on Channel et al. 2010 and Singer 2014). These results corroborated the AAR datings of horizons SPD-9670 (771 ± 54 ka), SPD-9710 (885 ± 150 ka) and SPD-9750 (818 ± 63 ka).

It must be highlighted that in levels dated using AAR of gastropods, the age was calculated by introducing the Asp, Glu, Leu, Ile, and Phe *D*/*L* values determined in the shells (1 to 5 specimens analyzed in each level) into the age-calculation algorithms established by Torres et al. (1997). Thus, the uncertainties associated with AAR ages were higher than those usually obtained with other dating methods such as radiocarbon dating or U/Th. Generally, ages obtained by other methods are performed using a single sample, and the uncertainties are attributed only to the analytical error. However, when a number of analytical samples from the same horizon are dated, the differences are larger. Thus, ages with a relatively high standard deviation can be explained because we used different amino acids (Asp, Glu, Leu, Ile, and Phe) and diverse samples (1–5) for the age calculation of a particular level.

In general, numerical datings obtained with different methods were consistent (Fig. 2c). The chronological model for the Padul record (Fig. 7) was created with the Bayesian R-code package "Bacon 2.3.7" (Blaauw and Christen 2011), as Bayesian age–depth modelling is considered more robust and flexible than other types. This age model enabled the estimation of the age of undated intermediate horizons and improves that of Ortiz et al. (2004a) using a polynomial relationship.

4.2 Pollen zonation

We identified 21 pollen assemblage zones (Table 6; Fig. 8), which corresponded to major shifts in glacial-interglacial vegetation, these reflecting distinct palaeoenvironmental conditions. This interpretation took into account the peculiar bioclimatic position of the PB, which is summarised below.

As observed along the PB record, *Pinus* accounted for the bulk of tree forest in this part of Iberia during Lower Pleistocene-Holocene times. In this regard, some authors interpret *Pinus* overrepresentation to be caused by river transportation, which is common in marine environments (Sánchez-Goñi et al. 2000). We cannot totally discard a similar process in the PB area, where seasonal or storm-linked run-off may have transported pine pollen from the surrounding mountains. However, pines dominated and have prevailed from the Pleistocene to the present in the Iberian Peninsula (Sánchez Goñi et al. 2000).

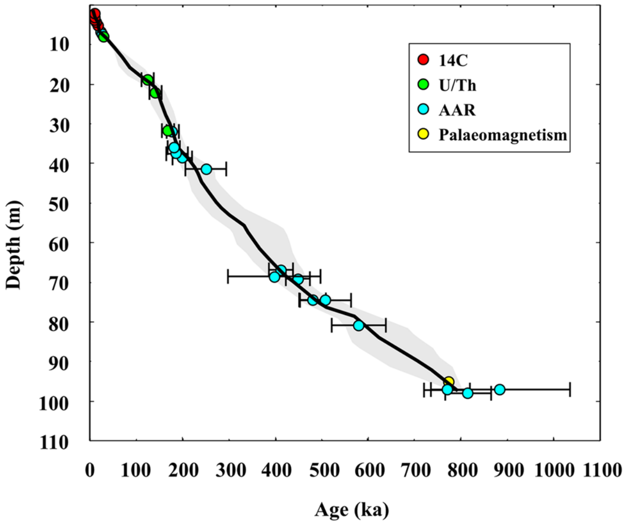

Fig. 7 Bayesian age-depth model established for the PB record constructed using the software R-code package "Bacon 2.3.7" (Blaauw and Christen 2011), after 300 Markov Chain Monte Carlo iterations. The black line indicates the single best model based on the weighted mean age for each depth, and the grey area shows 95% confidence intervals. Dates were obtained through radiocarbon, U/Th, amino acid racemization and palaeomagnetism

The presence of Mesophilous representatives, accompanied by a growth in the Mediterranean and Hygrophilous group, must be interpreted in terms of climate amelioration, reflected in a decrease in evapotranspiration, temperature rise and a drop in the snow line. In this regard, the increase in evaporation rates plays a fundamental role in increasing water-stress, mostly in the summer months. The review of Hughes et al. (2006) of the Quaternary glacial history of the Mediterranean mountains reinforces this interpretation, in accordance with palaeobotanical evidence (Tzedakis 1999; Allen et al. 2000; Joannin et al. 2011).

According to palaeoenvironmental studies, the presence/absence and frequency of *Artemisia* are crucial for the development of cold steppe environments (Pons and Reille 1988). Of note, according to Díaz de la Guardia and Alba (1998), between 1996 and 1997 in the city of Granada, 20 km north of the PB, high daily rain of *Artemisia* pollen was registered in a Hirst pollen trap (112–880 pollen grains/day). In Almería, 120 km east of the PB, Sabariego et al. (2002) counted a mean of 975 *Artemisia* grains/day between 2000 and

Table 6 Main vegetational characteristics of the Padul Basin core pollen assemblage zones (Pz)

Pz	Depth (m)	Age (ka)	Main palynological characteristics	Environment	MIS
PD-1	95.60–94.00	800–790	Growing *Pinus* towards the top together with a descent of aridity indicators: Steppic, and Xerophilous. Appearance of small amounts of Mesophilous and Cupressaceae at the top	From steppe to Mediterranean	20
PD-2	94.00–92.80	790–760	Presence of *Pinus* and Poaceae. Significant amounts of Mediterranean and Riparian. Maximum in the Spore frequency	Temperate-humid	19
PD-3	92.80–91.25	760–730	High frequency of *Pinus* accompanied by Mediterranean, Mesophilous, and Montane; Steppic is present	Mediterranean-dry	18
PD-4	89.30–88.00	710–675	*Pinus* dominates, especially at the end. Mediterranean, Steppic, and Xerophilous are present. Hygrophilous and Cupressaceae appear at the lower half. Abundance of Spores is low	Mediterranean	17
PD-5	86.00–82.80	660–610	Only 3 samples. *Pinus* largely dominate. Poaceae appears together with Mediterranean. Steppic is absent, and there is a visible presence of Cupressaceae. Spores are absent	Mediterranean-dry	16, 15
PD-6	75.40–74.00	500–480	*Pinus* largely dominates. Presence of Mediterranean and Mesophilous. Low abundance of Steppic, Xerophilous, and Poaceae. Spores appear	Mediterranean	13
PD-7	74.00–69.05	480–425	Rise of Spores. *Pinus* diminishes as well as Mediterranean, Steppic, Xerophilous and Poaceae. Significant presence of Mesophilous, Cupressaceae and Riparian	Temperate-humid	12
PD-8	69.05–68.10	425–400	*Pinus* is abundant. There are Riparian and Hygrophilous and traces of Steppic, and Xerophilous. Spores are well represented. At the end, *Pinus* decreases, while Mediterranean progressively dominates	Mediterranean	11
PD-9	66.35–63.40	385–365	*Pinus* dominates and Steppic is absent at the beginning. There are three peaks linked to higher contents of Riparian, Mesophilous and Hygrophilous (in the uppermost one Riparian is substituted by *Ephedra*). The frequency of Mediterranean decreases towards the top while there is a clear augmentation of Steppic and Xerophilous and a decrease of Mesophilous. Spores appear well represented	From Mediterranean to Steppe	11
PD-10	63.40–59.20	365–340	Low frequency of *Pinus* at the beginning and at the end. Episode with a marked rise of Steppic and Xerophilous. Presence of Mediterranean, Poaceae and Cupressaceae. Spores and Mesophilous are very scarce	Steppe	10
PD-11	59.20–53.00	340–310	Almost all pollen groups are represented. There is a marked rise of Mediterranean, Riparian, Hygrophilous, Mesophilous, and Spores. In contrast, *Pinus* decreases, and there are low frequencies of Steppic, Xerophilous, Poaceae, and Cupressaceae	Mediterranean	9
PD-12	53.00–49.50	310–295	There is a marked rise of *Pinus*. The most striking characteristic is the high frequency of Steppic, that, in general, negatively covariates with Mediterranean. Xerophilous also grow, while Hygrophilous and Cupressaceae disappear. Poaceae remains constant but there are low frequencies of Spores	Steppe	9
PD-13	49.50–47.20	295–280	Spores predominate. Arboreal pollen is dominated by *Pinus*, followed by Hygrophilous and Mediterranean. Poaceae are also represented, especially at the end, where dominates. There is a marked decrease of Steppic, and Xerophilous	Mediterranean	9
PD-14	47.20–42.20	280–240	*Pinus* shows high frequency. Spores and Mediterranean are frequent at the beginning and later descend. There is a growing presence of Cupressaceae. The episode is characterised by the increase of Steppic, Xerophilous and Poaceae	Steppe	8
PD-15	42.20–32.00	240–180	It is characterised by a high taxa diversity. *Pinus* frequency remains, as well as Steppic, Xerophilous and Poaceae. Mediterranean, Mesophilous, Riparian, Cupressaceae, Hygrophilous increase significantly (the frequency of Mediterranean groups seems to be fairly equivalent to the sum of Steppic, Xerophilous, and Poaceae). Spores frequency remains low	Mediterranean	7

Table 6 (continued)

Pz	Depth (m)	Age (ka)	Main palynological characteristics	Environment	MIS
PD-16	29.10–24.50	180–130	Diversity decreases. *Pinus* pollen frequency is never below 50%. Mediterranean is very low, while Herbaceous.-steppic clearly dominates along the whole palynozone being followed by Xerophilous and Poaceae. There is a noteworthy presence of Cupressaceae and Hygrophilous in two episodes. Spores show very low abundance	Steppe	6
PD-17	23.90–17.50	130–73	Important presence of Aquatics, followed by *Pinus* and Spores. At the beginning, Mediterranean rises. Low presence of Steppic, Xerophilous and Poaceae, with slight increases in some episodes. In some phases Mesophilous, Riparian and Cupressaceae rise	Mediterranean	5
PD-18	17.50–11.65	73–60	There is a decrease of Spores. *Pinus* frequency accounts for ca. 50%. Steppic, Xerophilous, Poaceae and Mediterranean markedly rise. With an exception at the beginning, Spores fall, and disappear	Steppe	4
PD-19	11.65–7.50	60–28	This palynozone reflects an expansion of Aquatics and Riparian. *Pinus* is dominant. There is a visible reduction of Mediterranean. Mesophilous is represented at the bottom and at the top	Mediterranean-steppe	3
PD-20	7.50–5.20	28–14	Spores are lacking. High presence of *Pinus*. Mediterranean decreases towards the top as well as Mesophilous while there is a marked rise of Steppic, Xerophilous and Poaceae. Riparian, Mediterranean and Mesophilous appears in some short phases, especially at the top	Steppe	2
PD-21	5.20–0.00	14–0	Palynozone with high variability of pollen frequencies, with episodes in which there is a high diversity. *Pinus*, Poaceae and Mediterraenan is abundant along the whole period. In some episodes, Riparian and Mesophilous increase, while in others, Steppic and Xerophilous rise. Mediterranean shows marked increases	Mediterranean	1

2001, and in 1998 Ruiz et al. (1999) registered 120 *Artemisia* grains/day in Jaén (100 km north of the PB). Therefore, *Artemisia*, considered an indicator of cold/arid or semi-arid conditions, could also be found during warm/arid episodes in central and southern Iberian Peninsula, although with less percentages.

The same considerations can be made with respect to Amaranthaceae pollen, which appears in the areas described above (Díaz de la Guardia and Alba 1998; Sabariego et al. 2002; Ruiz et al. 1999). Likewise, Amaranthaceae representatives are linked to saline soils (dominant in the north of the PB), a substrate on which other plants rarely thrive.

Thus, the interpretation of a steppe in the Iberian Peninsula with *Artemisia* and Amaranthaceae was adopted by Fletcher and Sánchez Goñi (2008), who considered the Mediterranean steppe a semi-arid environment in which *Ephedra* was also frequent.

Therefore, in some episodes in which *Pinus* retracted, the relative frequency of Steppic (*Artemisia*, *Ephedra*) and Xerophilous (Amaranthaceae) increased, thereby indicating a shift towards arid to semi-arid colder conditions. In contrast, the presence of Mediterranean, Mesophilous, Hygrophilous and Cupressaceae (mainly represented by *Juniperus*) marked main climatic changes, as a result of increased water availability and temperature and less evaporation. Of note, the presence of Cupressaceae must be considered with care because of its xerophily, vitality, resistance, ecological amplitude and tolerance to extreme continentalisation.

The presence of Poaceae has also been considered to indicate a steppe in some studies, although Tzedakis et al. (2003) rejected its use for the calculation of vascular plant percentages because *P. australis* grows in semi-aquatic environments, as is now found in the PB, thus obscuring regional vegetation trends.

In this regard, to better ascertain the climate oscillations interpreted from the pollen content recorded in the PB, we performed a Principal Component Analysis (PCA) following Joannin et al. (2011) on the main ecological groups of pollen assemblages.

4.2.1 Principal component analysis

PCA provides a scaled pollen index roughly corresponding to palaeoclimate variations and used to confirm the pollen assemblage zones. The aim was to identify and group samples along the PB record with similar palaeoenvironmental characteristics. We did not consider Aquatics as, in our opinion, their presence was not directly related to climatic oscillations, as a water mass was always present and they could be influenced by a bias caused by local factors.

Results of PCA were assembled in four main groups (Fig. 9). Group 1 (G1) was separated with respect to the

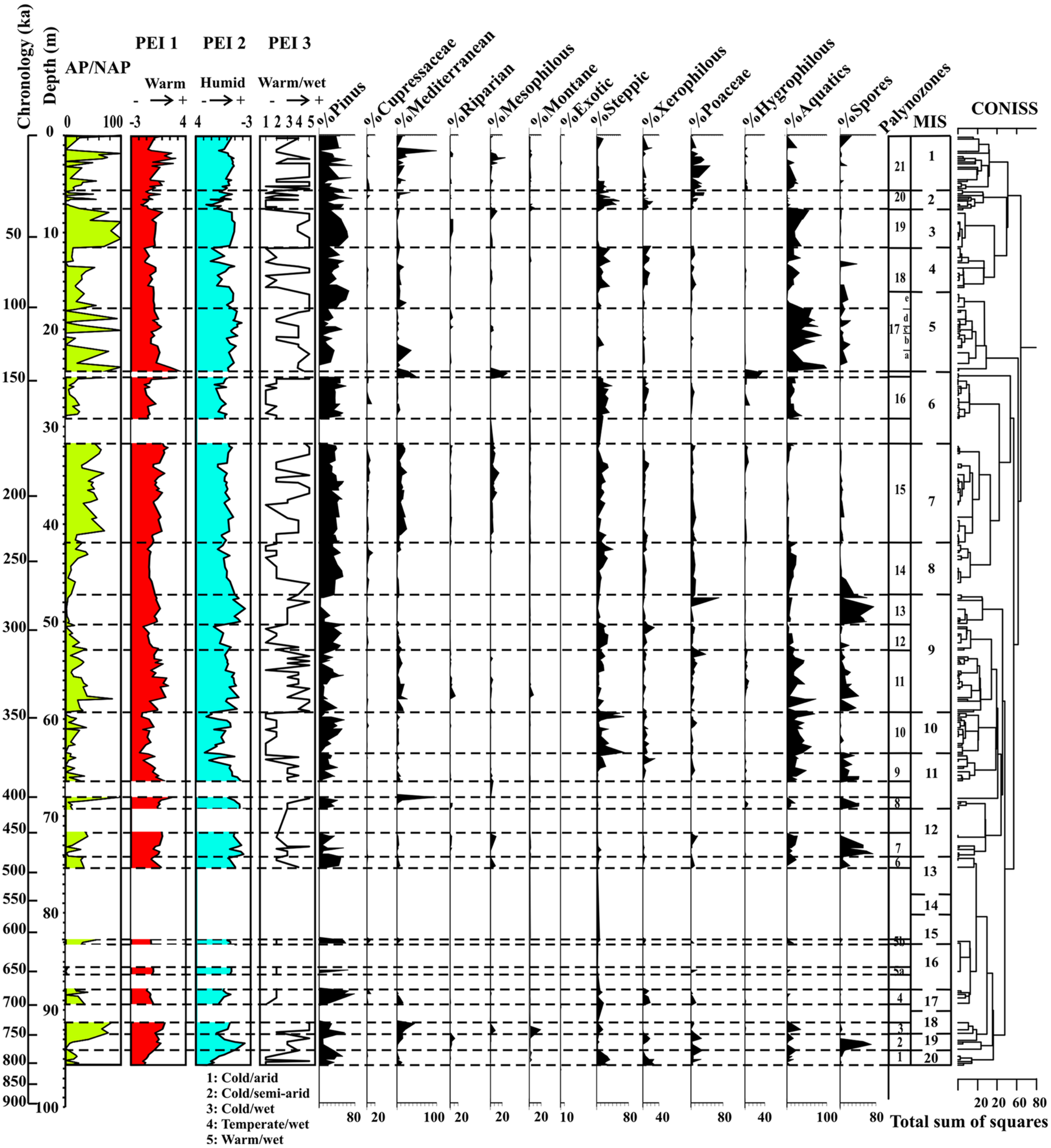

Fig. 8 Pollen diagram inferred from Padul Basin sediments with the percentages of the main pollen assemblages plotted against depth (m) and age (ka). Pollen assemblage zones, defined from CONISS cluster analysis are indicated on the right and described in Table 6. The AP/NAP (Arboreal Pollen/Non Arboreal Pollen) ratio (the AP excludes *Pinus*), Pollen Environmental Indexes PEI 1 (used to discriminate between cold and warm episodes), PEI 2 (used to discriminate between wetter and dryer phases), and PEI 3 (with 5 scenarios defined from the cluster analysis) are included. Marine isotope stages (MIS) after Lisiecki and Raymo (2005) are shown on the right

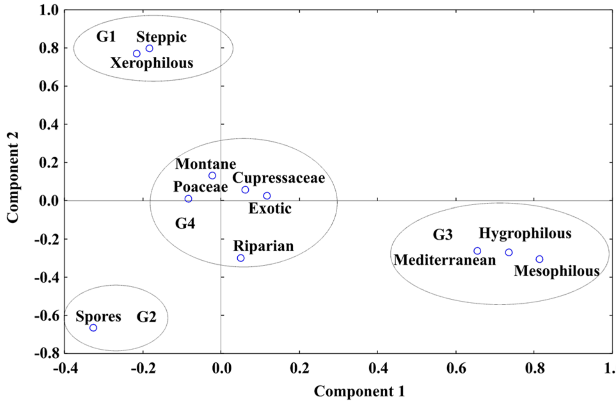

Fig. 9 Principal Component Analysis (PCA) from different pollen taxa showing the scatter plot with PC1 and PC2 axis

others because of its positive loading to the Principal Component 2 (PC2) and negative loading to the Principal Component (PC1), and included Steppic and Xerophilous, whereas Spores belong to G2, characterised by negative loading to both PC1 and PC2. G3 was composed by Mesophilous, Mediterranean and Hygrophilous taxa, and was separated due to its positive loading to PC1. The other ecological groups were included in G4.

PCA performed on the pollen dataset showed that 40% of the variance could be explained by the principal component PC1, which was characterised by marked positive loadings for group G3 and by negative loadings for groups G1 and G2. PC1 thus appeared to discriminate between warmer/temperate-wetter taxa (Mediterranean and Mesophilous) and colder taxa. Therefore, the scores of PC1 were used to discriminate between cold and warm/humid phases, and defined the Pollen Environmental Index 1 (PEI 1), which gives information about palaeotemperature conditions (Fig. 8), in coincidence with the Pollen Climate Index (PCI) proposed by Joannin et al. (2011), based on the mesothermic/steppic taxa ratio from Combourieu Nebout et al. (1999). In this regard, Joannin et al. (2008, 2011), Bertini et al. (2015) and Toti (2018) used this pollen derived climate index for a relative palaeotemperature reconstruction.

PC2 explained 20% of the variance. Loadings of PC2 were markedly positive for the Steppic and Xerophilous taxa (G1), typical of arid conditions, while were negative for Spores, typical in wet environments, with Riparian, Mesophilous, Mediterranean and Hygrophilous taxa also with negative values. PC2 thus appeared to discriminate between herbaceous taxa (*Artemisia*, Amaranthaceae, *Ephedra*) adapted to low values of atmospheric moisture (arid to semi-arid conditions) and a plant community requiring adequate rainfalls. Thus, the scores of PC2, which provided the Pollen Environmental Index 2 (PEI 2), allowed to discriminate between humid vs. arid conditions (Fig. 8).

Of note, there was a good correspondence between episodes in which temperature increased with those showing greater humidity (Mediterranean-like conditions). In contrast, colder phases coincided with arid to semi-arid conditions.

We also performed an unconstrained cluster analysis (using the Ward method and Euclidean distance), which complemented the PCA analysis and the information provided by PEI 1 and PEI 2 (Fig. 8).

From the dendrogram (Supplementary Material Fig. 1), five clusters could be differentiated, which represented various climatic scenarios whose characteristics are shown in Supplementary Material Table 6 and Supplementary Material Fig. 2: Cluster 1, Steppic, Xerophilous, and Poaceae were dominant indicating a cold and arid scenario; Cluster 2, *Pinus* was abundant followed by Steppic, and Xerophilous (cold and semi-arid scenario); Cluster 3, Spores predominated (cold and more humid scenario); Cluster 4, Spores, Mesophilous and Mediterranean taxa were abundant (temperate/wetter scenario: Mediterranean-like climate) and Cluster 5, dominated by Mediterranean, Mesophilous and Poaceae (warm/wetter scenario: Mediterranean-like climate with higher moisture).

Thus, we used these clusters to construct the Pollen Environmental Index 3 (PEI 3) ranging from 1 to 5 (Fig. 8) in which values closer to 1 represent colder and dryer conditions. In contrast, higher values (5) represented warmer and wetter episodes. It is worth noting that the interpretation of the cluster analysis had a good correspondence with the information provided by the PEI 1 (temperature) and PEI 2 (humidity) (Fig. 8).

Of note, glacial/stadial (even-numbered MIS) phases were characterized by a rise in steppic taxa (*Artemisia*, *Ephedra*, Amaranthaceae), whereas interglacial/interstadial (odd-numbered MIS) periods Mediterranean and Mesophilous taxa increased, indicating warmer and wetter conditions.

Taking these considerations into account, we described the changes in the palynozones and the PEIs in terms of palaeoclimatological variations, clustering them into the diverse MISs following Lisiecki and Raymo (2005). This approach differs from other methodological principles in which the pollen record is correlated to MISs on the basis of predetermined European scenarios or correlations between $\delta^{18}O$ signals (Tzedakis 1993, 1994; Tzedakis et al., 2001; de Abreu et al. 2003; Sánchez-Goñi et al. 2002, 2005, 2008; Roucoux et al. 2005, 2006).

MIS20 815–790 ka, 95.6–94.0 m (Pz1)

At the beginning of Pz1 there were scattered *Pinus* in a semi-arid environment dominated by aridity indicators (Steppic, and Xerophilous). At the top of the record, there was a recovery of *Pinus* accompanied by Cupressaceae and Mesophilous assemblages, thereby indicating higher moisture availability than at the beginning. Similarly, the presence of Aquatics indicate that there was moderate water input into the basin.

MIS19 790–760 ka, 94.0–92.8 (Pz2)

Although the abundance of *Pinus* was similar to that registered at the top of Pz1, Poaceace markedly increased at the beginning of Pz2. Afterwards, there was greater water availability, as reflected by an increase in Riparian and Mesophilous representatives, whereas semi-arid indicators decreased. Riparian plant growth in the middle of this palynozone was clearly linked to the dominance of Spores, thereby suggesting that the PB became a fern field, with more humid conditions, whereas at the end of this period drier conditions predominated.

MIS18 760–710 ka, 92.8–90.2 m (Pz3)

Pz3 was characterised by an increase of *Pinus*, with some presence of Mesophilous vegetation, and a progressive increase in Mediterranean plants, which are linked to wetter conditions, reflecting a Mediterranean-like climatic phase. Towards the top of Pz3, the presence of Hygrophilous indicated a change to slightly colder conditions.

The lack of pollen between 91.0 and 90.0 m was interpreted in terms of the influence of taphonomical factors, since the presence of gravelly mud indicated a sudden input of coarse sediments.

MIS 17 710–675 ka, 90.2–88.0 m (Pz4)

After barren samples at the beginning (between 90.0 and 89.5 m), Pz4 was characterised by impoverished vegetation cover, in which *Pinus* was abundant and accompanied by Steppic and Xerophilous.

MIS16 675–620 ka, 88.0–83.2 m (Pz5a)

Only one sample contained pollen, with an overwhelming presence of *Pinus*, followed by Xerophilous and Poaceae, thus indicating low water availability. The absence of pollen was probably linked to the presence of gravelly mud, indicating debris flows.

MIS15 620–565 ka, 83.2–81.0 m (Pz5b)

As occurred in some previous episodes, the presence of coarse-grain sediments (gravels and sands) indicated the re-activation of the alluvial fan system, and no pollen was observed.

Pz6 was characterised by a high percentage of *Pinus*, which oscillated between 80 and 90%, together with the presence of Poaceae, Xerophilous and Cupressaceae. The abundance of Aquatics was low and Spores were negligible. Thus, dry conditions were interpreted.

MIS14 565–535 ka, 81.0–79.0 m

There was an absence of pollen in the samples belonging to this stage. See MIS18 for a possible explanation.

MIS13 535–480 ka, 79.0–74.1 m (Pz6,)

At the end of this stage (Pz6) There was a predominance of *Pinus*, and some *Cedrus* grains were found, together with high plant diversity, including Mediterranean and Mesophilous pollen indicating more humid conditions. This is reinforced by the high frequency of Spores.

MIS12 480–425 ka, 74.1–69.2 m (Pz7)

Although Steppic, Xerophilous and Poaceae were present, they were less abundant than in other palynozones. The plant diversity and the presence of Mesophilous, Cupressaceae, Riparian and Hygrophilous pollen indicated more humid and colder conditions. This is reinforced by the high frequency of spores. Thus, the fern field scenario described in Pz2 reappeared twice in MIS12. Nevertheless, dry phases, with a dominance of semi-arid indicators were observed. Mediterranean pollen frequency did not change significantly.

At the end of this stage, pollen grains were absent, which was interpreted to be the result of alluvial progradation and the presence of debris flows, as reflected by the predominance of gravels and sands.

MIS11 425–365 ka, 69.2–63.4 m (Pz8, Pz9)

Pinus largely dominated in Pz8, with the presence of Riparian and Hygrophilous taxa and traces of Steppic and Xerophilous, indicating increasing moisture. Attention is drawn to the absence of *Pinus* at the end of Pz8 and its replacement by Mediterranean plants, which was an unusual phenomenon in the PB record and interpreted as the occurrence of Mediterranean-like climatic conditions.

Between Pz8 and Pz9, pollen grains were absent. This observation is interpreted to be the result of alluvial progradation, probably linked to humid conditions.

Pz9 was characterised by an almost continuous presence of relatively moister climatic conditions, as inferred from the high pollen diversity, including representatives of Mesophilous, Cupressaceae, and Hygrophilous taxa, together with a fairly constant presence of Spores, in which Mediterranean-humid conditions were interpreted.

Riparian plants were absent at the end of Pz9, in which Steppic and Xerophilous increased, paralleled by a decrease in Aquatic taxa and Spores, thereby indicating increasing aridity.

MIS10 365–340 ka, 63.4–59.2 m (Pz10)

This stage was characterised by a large presence of *Pinus*, together with Steppic and Xerophilous, and some Mediterranean taxa, thereby indicating dry conditions. The absence of Aquatic taxa was noticeable.

MIS9 340–280 ka, 59.2–47.2 m (Pz11, Pz12, Pz13)

It must be highlighted that, following Tzedakis et al. (1997), we considered the isotopic event 8.5 was included within the MIS9 complex (event 8.5 corresponding to MIS9a), with the MIS9/8 boundary placed at ca. 280 ka, which will be useful for the correlation with other long European records.

Increasing moisture occurred in Pz11, with a relative decrease in *Pinus*, an increase in Mediterranean vegetation and significant presence of Riparian, Cupressaceae, Mesophilous, Montane (*Juglans* among others) and Hygrophilous representatives. It is noteworthy that the Spore frequency reached high values. Nevertheless, there were short pulses with drier conditions in which *Pinus* decreased, paralleled by an important increase in Steppic, Xerophilous and Poaceae.

In Pz12 there was a marked recovery of *Pinus* with respect to Pz11 and an important growth of semi-arid indicators (Steppic, Xerophilous). Although there was a decline of Hygrophilous and Cupressaceae, their presence was vestigial. These observations, together with the low frequencies of Spores, and the absence of Riparian pollen suggested low water/moisture availability in the PB area. The end of this stage was characterised by a notable increase in Hygrophilous and Spores (Pz13), indicating higher humidity.

MIS8 280–240 ka, 47.2–42.2 m (Pz14)

Mediterranean-like climatic conditions prevailed in Pz14, with low presence of Spores and Cupressaceae, and existence of Mediterranean taxa. The ever-present Aquatics indicated water availability in the basin.

The end of MIS8 showed colder/arid conditions, though there was a decrease in the frequency of *Pinus*, while the abundance of pollen from semi-arid plants (Steppic, Xerophilous) was high and a progressive increase in Cupressaceae occurred.

MIS7 240–180 ka, 42.2–32.0 m (Pz15)

This stage was characterised by high taxa diversity, with a decrease in the percentage of *Pinus*, while the increase in Mediterranean, Riparian, Hygrophilous and Mesophilous taxa was significant, especially for the latter, thus indicating Mediterranean-like conditions with increasing moisture. In contrast, Aquatic taxa and Spores were rare. In some samples, the presence of Steppic and Xerophilous increased, indicating phases of drier conditions.

MIS6 180–130 ka, 32.0–24.5 m (Pz16)

After a pollinic-hiatus, which was interpreted as an arid period (Holloway 1989; Campbell and Campbell 1994), there was a noticeable peak of *Pinus* (Pz30), which remained at high percentages along the whole MIS6, together with a low presence of Mediterranean pollen. Steppic and Xerophilous were frequent, and a very low Spore content was detected, indicating increased aridity. However, three episodes of slightly less arid conditions were interpreted, where higher frequencies of Cupressaceae, Hygrophilous, and Riparian pollen appeared.

The MIS6/5e transition in the PB was characterised by the absence of pollen, thereby suggesting arid conditions, probably linked to saline characteristics (Holloway 1989; Campbell and Campbell 1994).

MIS5 130–73 ka, 24.5–17.0 m (Pz17)

The beginning of this stage was reliably dated and began with a singular event with the total dominance of Mediterranean, though few pollen grains were counted, indicating warmer conditions. This was followed by a sharp decrease in *Pinus*, paralleled by an increase in Cupressaceae, Hygrophilous and Riparian representatives, together with the Spore content, indicating relatively humid Mediterranean conditions. The beginning of this palynozone (17a) was correlated with MIS5e (130–119 ka) (Fig. 8). In this regard, it must be considered that the direct correlation between terrestrial and marine proxies shows that the Eemian in Iberia does not match the entire MIS5e, which began ca. 6 ka earlier (Sánchez-Goñi et al. 1999; Shackleton et al. 2002, 2003). Of note, coinciding with Sánchez-Goñi et al. (2005) who proposed a Younger Dryas-like event in the Iberian Peninsula at the MIS6/5e transition, and also observed in Fuentillejo sequence (Ruiz-Zapata et al. 2012), this period was characterised in the PB by the absence of pollen, thereby pointing to arid conditions or saline characteristics. Similarly in Villarquemado record there were low percentages of Mediterranean taxa and aquatics, and increasing steppe taxa at the MIS 6/5 boundary pointing to relatively cooler and drier climate conditions (Valero-Garcés et al. 2019; Wei et al., 2019).

In general, MIS5e was characterised by a Mediterranean climate, also observed in sites from central Spain: Madrid (Gil-García et al. 2018), Fuentillejo (Ruiz-Zapata et al., 2012), and Villarquemado (González-Sampériz et al., 2013; Valero-Garcés et al. 2019; Wei et al., 2019), with the increase of pollen taxa diversity together with Mediterranean and Mesophillous forest components, typical of warmer and more humid conditions.

Pz17b was characterised by increasing aridity, with an important presence of *Pinus*, Steppic and Xerophilous, as well as some Mediterranean plants. This episode was correlated with MIS5d (119–107 ka). According to Prado-Pérez et al. (2013) $\delta^{18}O$ values of tufa deposits from Alicún (ca. 50 km eastwards to PB) were less negative during this substage, indicating dryer conditions.

Towards the end of this stage, three events showing more moisture (Pz17c, which was correlated with MIS5c, and Pz17e, which could correspond to MIS5a) were distinguished, in which Mesophilous and Riparian taxa increased, these alternating with a drier period (Pz17b) with an important rise of Poaceae, correlating with MIS5b.

Of note, Pz17e, which would represent the end of MIS5a, recorded Mediterranean climatic conditions, as indicated by the high frequency of *Pinus*, and Mediterranean pollen, with some Spores.

MIS4 73–60 ka, 17.0–11.7 m (Pz18)

MIS4 was characterised by the high frequency of *Pinus*, Steppic and Xerophilous, while Mediterranean pollen decreased, thus indicating colder/arid conditions. Spores were scarce, with the exception of a peak that correlated with an increase in *Pinus* frequency, linked to an increase in moisture. However, a short phase with benign conditions, as reflected by the presence of Cupressaceae, Mesophilous and Riparian pollen, was observed.

MIS3 60–28 ka, 11.7–7.5 m (Pz19)

The beginning of MIS3 revealed low plant diversity, *Pinus* dominating. However, the presence of Riparian and Mesophilous pollen and the absence of semi-arid representatives indicated Mediterranean-like conditions. Notwithstanding, two especially dry episodes occurred, in which the frequency of *Pinus* diminished and was paralleled by a sharp growth of semi-arid plants (Steppic and to a lesser extent Xerophilous), which according to Valle et al. (2003), corresponded to Heinrich Event 3 (HE-3) (Heinrich 1988; Broecker 1994).

MIS2 28–14 ka, 7.5–5.2 m (Pz20)

MIS2 was characterised by scarce pollen diversity, high percentage of Steppic and Xerophilous decrease in the frequency of *Pinus* and low presence of Mediterranean representatives, indicating colder/arid conditions. In this regard, according to Valle et al. (2003), the beginning and the end of Pz20 corresponded to HE-2 and HE-1, respectively.

Of note, in the middle of Pz20 was characterised by a decrease in the frequency of *Pinus*, an increase in Steppic, the presence of Mesophilous, Hygrophilous and Cupressaceae, and the low presence of Mediterranean representatives, indicating cold conditions with low precipitation.

Nevertheless there were short phases in which climate changed towards much more benign conditions (decrease of Steppic, Xerophilous and Poaceae fall to minimum values and Mesophilous appear) and this could reflect rapid deglaciation (Valle et al. 2003).

MIS1 14–0 ka, 5.2–0.0 m (Pz21)

Pz21 marked a general amelioration of the climate after MIS2, characterised by a Mediterranean-like climate, although there were short episodes reflecting changing conditions. The presence of Mediterranean and Poaceae was significant, while steppe plants decreased. In some cases, Mesophilous and Hygrophilous, together with Cupressaceae were considerable.

The beginning of this stage was characterised by the decline of *Pinus*, accompanied by a progressive reduction in steppe plants followed by an increase in Mesophilous, and a slightly recovery of Mediterranean, which could be correlated with the Bølling–Allerød (Valle et al. 2003). A strong increase in the diversity of the vegetation was observed, with the first appearance of *Betula,* together with an increase in Spores. These samples contained the first marked maxima of Riparian.

After this episode there was a sharp decline of Mesophilous, together with a maximum of steppe plants, which would correspond to the Younger Dryas (Valle et al. 2003). Another episode linked to increasing aridity occurred at ca. 7.5–8 ka BP.

4.3 Comparison with long European pollen records

We compared the palaeoenvironmental characteristics of the PB inferred from the pollen assemblages and those of other long European pollen records (Table 7, Fig. 10) from distinct climatic regions (Rubel and Kottek 2010; Chen and Chen 2013) (Fig. 1). La Grande Pile (Woillard 1978; de Beaulieu and Reille 1992), and the composite sequence of Velay (de Beaulieu et al. 2001) are located in the temperate oceanic region, whereas Lago Grande di Monticchio (Allen et al. 2000; Brauer et al. 2007) belongs to the temperate humid subtropical climatic region; Tenaghi Philippon (Tzedakis et al. 2003, 2006; Pross et al. 2015), Lake Ohrid (Sadori et al. 2016; Sinopoli et al. 2018), and the marine core MD99-2331 (Sánchez-Goñi et al. 2005, 2008) are located in the border area of the Mediterranean and humid continental climatic regions. Valle di Castiglione (Follieri et al. 1988) and Ioannina (Wijmstra 1969, 1976; Tzedakis 1994), together with the marine cores ODP-976 and MD-95-2042 (Sánchez-Goñi et al. 1999, 2000, 2008), are included in the Mediterranean climatic region. In contrast, Lake Van (Litt et al. 2014; Pickarski and Litt 2017) is characterised by a continental climate.

Of note, the characteristics of the flora and vegetation in the PB differed from those of other long European pollen records due to regional characteristics, but main palaeoenvironmental trends were coincident. In the PB, *Pinus*, Steppic, Xerophilous, and Poaceae showed an overwhelming presence along the whole record, while in certain periods did humidity and temperature increase significantly. During these times Mediterranean and Mesophilous taxa increased, but without any large expansion of the latter, like in central Spain (Gil-García et al. 2018). In contrast, in other European records, main states characterised by forest, wooded steppe and steppe are typically identified (Wijmstra 1969; Wijmstra et al. 1976; Woillard 1978; Follieri et al. 1988; Tzedakis

Table 7 Tentative correlation between the palynozones established in the Padul record (3) and those identified in other European records: La Grande Pile (Woillard 1978; de Beaulieu and Reille 1992), Velay (de Beaulieu et al. 2001), Ioannina (Wijmstra 1969, 1976; Tzedakis 1994), Tenaghi Phillipon (Tzedakis et al. 2006; Pross et al. 2015), Lake Ohrid (Sadori et al. 2016, Sinopoli et al. 2018), Lake Van (Litt et al. 2014, Pickarski and Litt 2017), Valle di Castiglione (Follieri et al. 1988), Lago Grande di Monticchio (Allen et al. 2000), MD95-2042 (Sánchez-Goñi et al. 1999, 2000, 2008), and ODP-976 (Combourieu-Nebout et al. 2009)

MIS	La Grande Pile	Velay	Ioannina-249	Tenaghi Phillipon	Lake Ohrid	Lake Van	Valle di Castiglione	Monticchio	MD95-2042 & ODP-976	Padul (1)	Padul (2)	Padul (3)
1	Post-glaciaire	Holocene	Holocene G	Holocene Z-Y Xanthi	OD-1	I	VdC-18	1-4	6 5 (YD) 4 (B/A)	Z Y3 (YD) Y2(B/A)	P3: m-t P3: l (YD) P3: k (B/A)	21
2	Lantern 3	Würm	IN-41	X Philippi Photolivos	OD-2	II	VdC-17	4-5a	3 (H1) 2 (LGM) 1 (H2)	Y1 (H1) X (6-8)	P3:g-i (H1) P3:f (LGM) P3: d (H2)	20
3	Lantern 2	Würm	IN-40	P Krinides I, II Kalabaki I, II Heraklitsa I, II	OD-2	II	VdC-16	13c-5b	42-16 to 27	X(1-5)	P3: a-c P2:l-o	19
4	Lantern 1	Würm	IN-39	V	OD-2	II	VdC-15	17a-14	42-13 to 15	V	P2:k	18
5a	Saint Germain II	St-Geneys 2	Vikos	Elevtheroupolis U	OD-3G to 3 M	II	VdC-14	18-17b	42-12	U	P2:i-j	17
5b	Melisey II	St-Haon	IN-37	T	OD-3F	II	VdC-13	19a-18	42-11	T	P2:h	17
5c	Saint Germain I	St-Geneys 1	Perama IN-35 Thyamis	Dramas (S) R1 Doxaton (R2)	OD-3C to 3E	IIIa	VdC-12	19b	42-8 to 10	S	P2:f-g	17
5d	Melisey I	St-Nicolas	IN-33	R1	OD-3B	IIIb	VdC-11		42-7	R	P2:c-e	17
5e	Eemien	Ribains	Metsovon F	Pangaion M–O-Q	OD-3A	IIIc	VdC-10		42-2 to 6	Q	P2: a-b	17
6	Linexert	Costaros	IN-28	Neakaterini (K-L)	OD-4,5	IV	VdC-9 VdC-8		42-1	L-M		16
7		Bouchet 3 Bonnefond Bouchet 2 Belvezet Bouchet 1	IN-27 IN-26 Zitsa-E IN-23b IN-23a	Symvdon (H2-3) Symvdon (H1) Stymon (F)	OD-6	V	VdC-7/Roma III VdC-6 VdC-5/Roma II VdC-4 VdC-3/Roma I VdC-2			K-J		15
8		Charbonnniers	IN-21 to 22	D Axios (E)	OD-7	VI	VdC-1			I		14
9		Amargiers Monteils Ussel Cayres Landos	Katára-D IN-18 IN-17 IN-15,16 Pamvótis	Kavalla (C) B Krimenes (A) ZZ Litochoris (YY)	OD-8	VII				G-H		11, 12, 13
10		Bargette	IN-12	XX	OD-10	VIII						10

Table 7 (continued)

MIS	La Grande Pile	Velay	Ioannina-249	Tenaghi Phillipon	Lake Ohrid	Lake Van	Valle di Castiglione	Monticchio	MD95-2042 & ODP-976	Padul (1)	Padul (2)	Padul (3)
11		Jagonas 2 Coucouron Jagonas 1 Chaconac Praclaux	Dodóni II IN-9 Dódoni I IN-5	PP Lekanis 1 to 5	OD-11,12	IX						8, 9
12		Barges	IN-1 to 4	W		X						7

Palynozones identified in the Padul Basin by Florschütz et al. (1971) (1) and Pons and Reille (1988) (2) were also included. The location of these sites and the climatological region to which they belong are in Fig. 1. *YD* Younger Dryas, *B/A* Bolling–Allerod, *LGM* last glacial maximum, *H* Heinrich event

1994; Allen et al. 2000; Sadori et al. 2016; Sinopoli et al. 2018). In Padul, *Abies*, *Picea*, *Fagus* and *Taxus* are negligible, and *Carpinus*, *Betula* and *Corylus* grains appear only in short intervals. In contrast, in the Velay and La Grande Pile records, pollen from Mediterranean taxa is absent (Woillard 1978; de Beaulieu and Reille 1992; Reille et al. 2000; de Beaulieu et al. 2001). Thus, the biomes represented in the PB cannot be directly compared with those included in other European records. However, closer palaeoenvironmental similarities were found between PB and the records from the Mediterranean climatic region, especially with the records of ODP-976 and MD95-2042 (Sánchez-Goñi et al. 1999, 2000, 2008).

The hypothesis of viable refuge areas in southern Spain (Carrión et al. 2003, Tzedakis 2009; González-Sampériz et al. 2010; Tzedakis et al. 2013) is greatly reinforced by our findings. The persistence of Mesophilous representatives (especially in palynozones 3, 6, 7, 9, 11, 15, 17–21), as well as sclerophyllous oak in the Mediterranean pollen group (present in almost all palynozones) implies that this part of Iberia can be considered a Quaternary vegetation refuge. For many years, vegetation refugia were considered to lie mainly on the SW of Europe (Carrión et al. 2003; Krebs et al. 2004). In this regard, in a review of the pollen signal from between the last interglacial period (MIS5) to Holocene times, Carrión et al. (2000) and Tzedakis et al. (2013), concluded that a wide number of scattered refugia provided rapid recovery of Mesophilous taxa and sclerophyllous oak in the Iberian Peninsula. In fact, tree survival is critical in mountain ranges as it allows altitudinal displacement of tree populations (Bennett et al. 1991; Tzedakis 2009; Tzedakis et al. 2013), and according to our data this occurred throughout the Pleistocene.

Similarly, pollen from exotic trees, a relic of tropical Miocene-Pliocene flora, such as *Carya*, was recorded in the PB record within MIS13 and *Liquidambar* up to 95.60 m (MIS21), in coincidence with Magri and Palombo (2013), Orain et al. (2013), and Magri et al. (2017), i.e., these taxa were recorded locally in southern Europe up to MIS9 and the end of Early Pleistocene, respectively, serving for identification of refuge areas. Moreover, according to Virgili and Pérez-González (1970), *Carya* leaf imprints appear in the Priego tufa deposits belonging to MIS11 (Torres et al. 2005), implying that even in this area of Central Iberia, far from milder Mediterranean influence, this refuge-like character persisted, at least, until Middle Pleistocene times.

Likewise, there was a subtle presence of “African” pollen, with Arecaceae and *Cedrus* at very low frequencies, with the exception of the bottom and top of the record. We consider that these pollen grains were carried on the wind from a distant source, adopting the conclusions drawn by Magri and Parra (2002), Joannin et al. (2011) and Magri and Palombo (2013), namely that the presence of *Cedrus* pollen

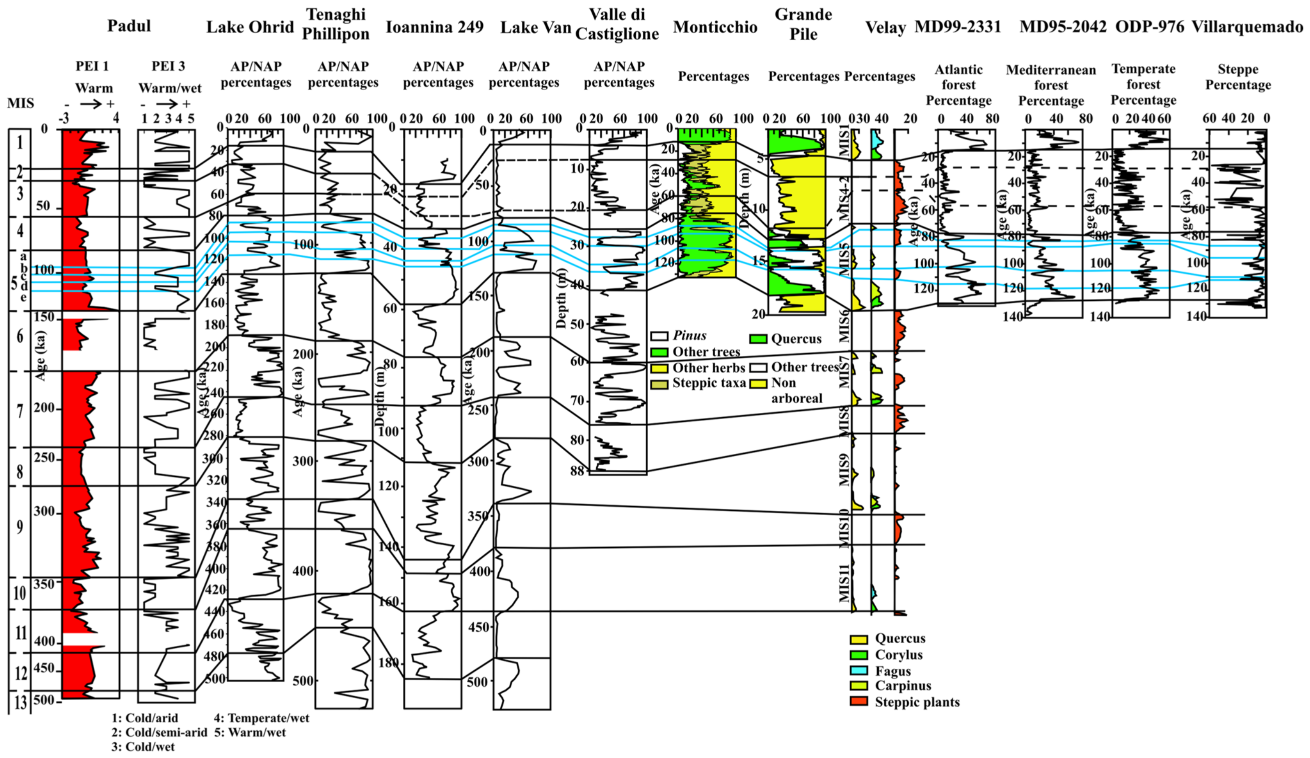

Fig. 10 Correlation between the palaeoenvironmental conditions during MIS interpreted the Padul Basin based on the pollen content (PEI 1 and PEI 3) and those in the following long European records: La Grande Pile (Woillard 1978; de Beaulieu and Reille 1992); Velay (de Beaulieu et al. 2001); Ioannina (Wijmstra 1969, 1976; Tzedakis 1994); Tenaghi Philipon (Tzedakis et al. 2003, 2006); Valle di Castiglione (Follieri et al. 1988); Lago Grande di Monticchio (Allen et al. 2000); Lake Ohrid (Sadori et al. 2016, Sinopoli et al. 2018), Lake Van (Litt et al. 2014, Pickarski and Litt 2017), MD99-2331 (Sánchez-Goñi et al. 2005, 2008, 2008); MD95-2042 (Sánchez-Goñi et al. 1999, 2000, 2008, 2000, 2008); ODP-976 (Sánchez Goñi et al. 2008), and Villarquemado (Valero-Garcés et al., 2019). AP: arboreal pollen, NAP: non-arboreal pollen. The location of these sites and the climatological region to which they belong are in Fig. 1. Of note, following Tzedakis et al. (1997), the isotopic event 8.5 was included within the MIS9 complex (event 8.5 corresponding to MIS9a), with MIS8 commencing at ca. 280 ka. The pollen records were plotted in age or depth according to their original published source, and the correlation was performed according to the description of environmental episodes and MIS found in the original papers

in eastern European records is the result of wind blowing in from Africa, and Arecaceae can be carried on the wind from the coast. Of note, appreciable amounts of *Cedrus* pollen occurred at the bottom of PB record (palynozones 1–7), in coincidence with the continuous presence of this taxon observed in the Lower Pleistocene of core ODP-976 (Joannin et al. 2011), and in the upper part of PB record, coinciding with its presence during the Late Pleistocene and Holocene in cores MD95-2042 (Sánchez-Goñi et al. 1999), MD95-2043 (Fletcher and Sánchez-Goñi 2008) and ODP-976 (Combourieu-Nebout et al. 2009).

Some similarities can be observed between the PB and Ioannina record, as according to Tzedakis et al. (2002) the latter was considered an area of relative ecological stability that was immune to the extreme effects of Quaternary climate variability. In particular, during glacial stages, this area was a refuge for many tree populations, including Mediterranenan taxa.

Therefore, the detailed comparison between the palynozones of the PB and the coeval ones of other sites is sometimes complex. According to Tzedakis et al. (2001, 2013), palynological variability arising from local factors can hinder definite assignments at individual sites. In fact, Fletcher et al. (2010) observed that high resolution pollen sequences from Europe reveal contrasts between vegetation response at southernmost latitudes and at those above 40º N during MIS4-2. Nevertheless, the PB pollen diagram seemed to fit satisfactorily into the framework of European pollen stratigraphy, as the main palaeoenvironmental trends were also recorded here, but with different characteristics (Table 7, Fig. 10).

In this regard, in the European reference records, interstadials (MIS 13, 11, 9, 7, 5 and 1) were characterised by a marked expansion of deciduous forest (Sánchez-Goñi et al. 1999; Tzedakis et al. 2001; Desprat et al. 2006; Brewer et al. 2008; Fletcher et al. 2013; Sadori et al. 2016; Gil-García et al. 2018; Sinopoli et al. 2018) (Fig. 10), although some short phases of increasing aridity were also identified within these stages. In the PB, phases with increasing humidity also occurred during interstadials, but the replacement of Mediterranean taxa by Eurosiberian forests, such as in Tenaghi Pillipon (Tzedakis et al. 2006), Valle di Castiglione (Follieri et al. 1988) or Lake Ohrid (Sadori et al. 2016; Sinopoli et al. 2018), did not occur in Padul. In fact, some periods with semi-arid and Mediterranean climatic conditions were also registered within MIS13, 11, 9, 7 and 5 in the PB.

Of note, good correspondence was observed between the palaeoenvironmental characteristics of MIS9 between the PB and Tenaghi Phillipon (Fletcher et al. 2013). Moreover, changes between Mediterranean and semi-arid conditions during MIS7 in the PB could be correlated with coeval oscillations observed in other European pollen records (Desprat et al. 2006; Roucaux et al. 2008).

It is note worthing that aridity conditions interpreted during some short events of MIS11 in PB, were also documented in marine cores off the coast of the Iberian Peninsula by Oliveira et al. (2016) and Sánchez-Goñi et al. (2016), and in central Spain (Gil-García et al. 2018) who observe periods of contraction of Mediterranean taxa and expansion of dry-grasslands (Steppic, Xerophilous and Poaceae). This fact was attributed to the disruption of the Atlantic Meridional Overturning Circulation and intensification of Mediterranean Outfow Water, pointing to differences in the palaeoenvironmental characteristics in Southwestern and Southeastern Europe.

During stadials, the forests retreated in Europe, with the exception of *Pinus*, and steppe plants were abundant. Likewise, in the PB, episodes dominated by Steppic, Xerophilous and Poaceae occurred, reflecting increasing aridity.

Moreover, there was good correspondence between the palaeoenvironmental characteristics of MIS5 substages in the PB record and those of other European records: palynozones within MIS5e, 5c, and 5a reflected less arid conditions, whereas the pollen zones of MIS5d and 5b were characterised by the expansion of steppe taxa, coinciding with Woillard (1978), Follieri et al. (1988), de Beaulieu and Reille (1992), Tzedakis (1994), Allen et al. (2000), de Beaulieu et al. (2001), Tzedakis et al. (2001), Sánchez-Goñi et al. (2005), Tzedakis et al. (2006), and Brauer et al. (2007).

MIS5e was characterised by a Mediterranean climate in Southwestern Europe, also observed in central Spain (Ruiz-Zapata et al. 2012; González-Sampériz et al., 2013; Gil-García et al. 2018; Valero-Garcés et al., 2019; Wei et al., 2019) which was gradually replaced by oceanic conditions (Sánchez-Goñi et al. 1999; 2005), as also occurred in the PB.

Palaeoenvironmental conditions from MIS 4 to MIS 1 had good correspondence with those of other European records, being able to identify Heinrich Events HE-3, HE-2, and HE-1, LGM, and the Younger Dryas which defined a highly impoverished biome. In this regard, the high sampling density in the uppermost part of the core record allowed the discrimination of these events. Afterwards, a Mediterranean climate dominated in the PB.

5 Conclusions

The palynology and lithology of a 107-m long core drilled in the PB (the longest sequence recovered at this basin) were successfully used to reconstruct the palaeoclimatological evolution of the southwestern part of Europe from the Lower Pleistocene (ca. 800 ka) to the mid-Holocene (ca. 4.5 ka). In this regard, the PB record is the longest continuous continental Quaternary record in the Iberian Peninsula and in the Southwestern Mediterranean realm. With the aid of new 13 ages obtained through AAR we improved the chronological precision with respect to previous research by constructing a new robust Bayesian age-depth model.

A number of palynozones (21) were distinguished on the basis of clear differences in the frequencies of distinct representative pollen groups. The high sampling resolution provided valuable information about the main vegetation changes occurred at long-term timescales in the region. Thus, Southern Iberia was dominated by *Pinus* throughout Quaternary times and was not a simple refuge. This scenario differs from that of Northern Iberia, with a Eurosiberian climate, where the development of deciduous (broad leafed trees) forests could have displaced *Pinus* to refuge areas. The role of *Pinus* as shadow canopy (lowering insolation) cannot be discarded. Another important observation was that the PB acted as a viable refuge area during the Pleistocene, especially for Mesophilous representatives (especially in palynozones 3, 6, 7, 9, 11, 15, 17–21), and sclerophyllous oak (present in almost all palynozones). Furthermore, we found pollen from exotic trees, such as *Carya* and *Liquidambar*, relics of tropical Miocene-Pliocene flora, during MIS13, and MIS21, respectively.

If we consider the Mediterranean-Mesophilous pollen assemblage as an indicator of the Mediterranean climate (setting up of the seasonality of the precipitation and summer drought), it appears reasonable to accept that this assemblage reflects a long adaptation to very low water availability, and without large expansion of forest vegetation.

Comparison with other European pollen records revealed that biomes could not be directly compared, although the main palaeoenvironmental trends coincided. From the pollen data, interstadials showed warmer and more humid conditions, Mediterranean and Mesophilous taxa increased, whereas the stadials were cooler and more arid, characterized by a rise in steppic taxa (*Artemisia*, *Ephedra*, Amaranthaceae). In this regard, the general arid conditions produced during Heinrich events, mainly HE-3, HE-2 and HE-1, and climate amelioration during alternating periods, were also recorded in the PB. Therefore, these results suggest that climate changes in the PB were in tune with global climatic variations in the Southern Mediterranean realm, although the palaeoclimatological evolution of the Padul area shows some peculiarities as a result of its geographical location.

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