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Neanderthals in a highly diverse, mediterranean-Eurosiberian forest ecotone: The pleistocene pollen record of Teixoneres Cave, northeastern Spain

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ABSTRACT

A palynological study of the archaeological layers from the Neanderthal site of Teixoneres Cave, located in Northeastern Spain, is presented. Vegetation dynamics for the MIS 7-MIS 2 period are described, revealing the long-term resilience of mixed oak-pine forests throughout cold phases and a high diversity of woody taxa, including conifers, mesophytes, Mediterranean, and xerothermics. Unexpected features of the Teixoneres sequence include the relative abundances of evergreen *Quercus*, deciduous *Quercus* + *suber* and *Juniperus*, the continuous occurrences of *Corylus*, *Castanea*, *Betula*, *Fraxinus*, *Buxus*, *Olea*, *Populus, and Salix*, and the presence of *Abies*, *Taxus*, *Cedrus*, *Acer*, *Alnus*, *Celtis*, *Juglans*, *Fagus*, *Ulmus*, *Calicotome*, *Ceratonia*, *Cistus*, *Ephedra fragilis*, *Myrtus*, *Pistacia*, *Phillyrea*, *Rhamnus* and *Viburnum*. To our knowledge, the existence of a forest refugium during the coldest and most arid stages of the upper Pleistocene has not previously been documented across this region. The high values of oak pollen during depositional episodes III, II and I of Teixoneres do not have an equivalent in any pollen sequence of the northern Iberian Peninsula during the MIS 4-MIS 2 interval. Our palynological analyses reveals a specific forest environment within the Mediterranean-Eurosiberian ecotone for the human occupation of Teixoneres Cave. These forested environments would have undoubtedly required highly adaptive subsistence strategies and expertise to ensure the long-term survival of Neanderthal groups in the region.

1. Introduction

Although conventional pollen sequences (e.g. lake bottoms, peat bogs) are most frequently used to reconstruct past vegetation (Bennett and Willis, 2001; Birks, 2005; Ritchie, 1995), there are relatively few suitable sequences in Europe that extend back to the Pleistocene and have the capacity to decipher local vegetation contexts of Neanderthals occupation sites. The composition and structure of vegetation surrounding Neanderthal habitat sites represent critical sources of information for understanding the paleoecological context of this human species. In this context, archaeological palynology may be crucial while the old disputes about its usefulness (e.g. discontinuities gaps in sedimentary sequences, differential preservation of palynomorphs, pollen transport by animals leading to over-representation of some taxa, and vertical movement or reworking leading to contamination by younger or modern pollen: Bottema, 1975; Bottema and Woldring, 1993; Coles et al., 1989; Coûteaux, 1977; Sánchez-Goñi, 1991, 1994;

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Turner and Hannon, 1988) can be left behind. Certainly, caves and rockshelters have traditionally suffered from a dearth of experimental data capable of determining the effectiveness of pollen spectra in representing source vegetation. However, after taking due precautions, the usefulness of depending upon cave sediments in areas where conventional pollen-rich deposits are rare must not be overlooked, as shown by Carrión et al. (2009), Hunt and Fiacconi (2018), Navarro et al. (2000, 2001), among others.

The karst complex of Toll Caves, located within the Northeastern Mediterranean Region of Spain and near the present-day limit with the Eurosiberian Region, represents a sensitive ecotone for investigating environmental changes associated with the Neanderthal occupations of the Iberian Peninsula. Here we present a palynological study developed at Teixoneres Cave, within this karstic system. Interestingly, the results provide new insights into the commonly accepted notion that glacial refugia for trees were restricted to more southern positions within the European peninsulas. In this context, the complexity and fluctuations of Neanderthal occupation and subsistence strategies acquire an important ecological dimension which, from a modern multidisciplinary research perspective, necessitates joint consideration of archaeological, geochemical and palaeontological records.

2. Physical setting and archaeological overview

Teixoneres Cave (2° 09′ 02’ ‘E, 41° 48′ 25″ N, 760 m a.s.l.) is an archaeological site lying within the karstic system known as Toll Caves, 4 km East of Moià (Barcelona province, Northeastern Spain) (Fig. 1). This karstic system is related to the drainage of the Mal Torrent, which has carved through autochthonous limestone of Neogene origin (the Collsuspina Formation). The region is located between the Llobregat River to the south and the Ter River to the North, which connect the inner area of Northern Catalonia with the Mediterranean Sea. Teixoneres Cave is U-shaped, displays a North-South orientation and has three main chambers, all of which contain archaeological remains (Fig. 2). Chamber X, towards the South, is the largest (30 m long, 5–6 m wide) (Rosell et al., 2017). Chamber Y, North facing, is a short West-East gallery. In the Eastern zone, the cavern heads South and, from a small corridor, it connects with another small entrance to the South (chamber Z).

The cave is infilled by an ~8 m-thick sedimentary sequence, which formed by two main depositional regimes (Rosell et al., 2010, 2016; Talamo et al., 2016) (Fig. 2). The lower assemblage (Unit VIII and IX) consists of silts and sands related to fluvial processes occurring inside the cave. The middle and upper assemblages

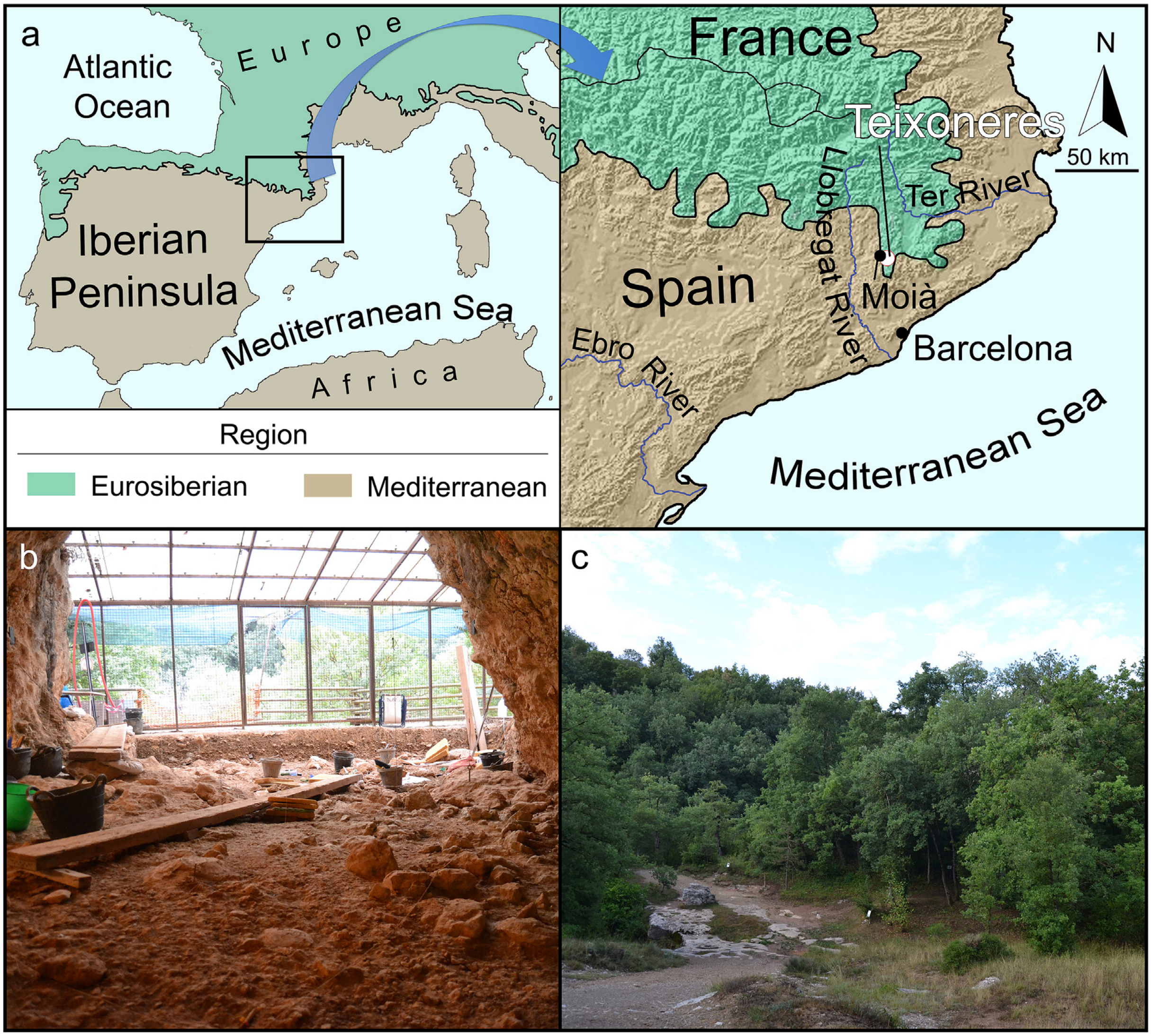

Fig. 1. Teixoneres Cave. a) Location in Mediterranean northeastern Spain near the Eurosiberian region, b) cave entrance, c) area of access to the cave.

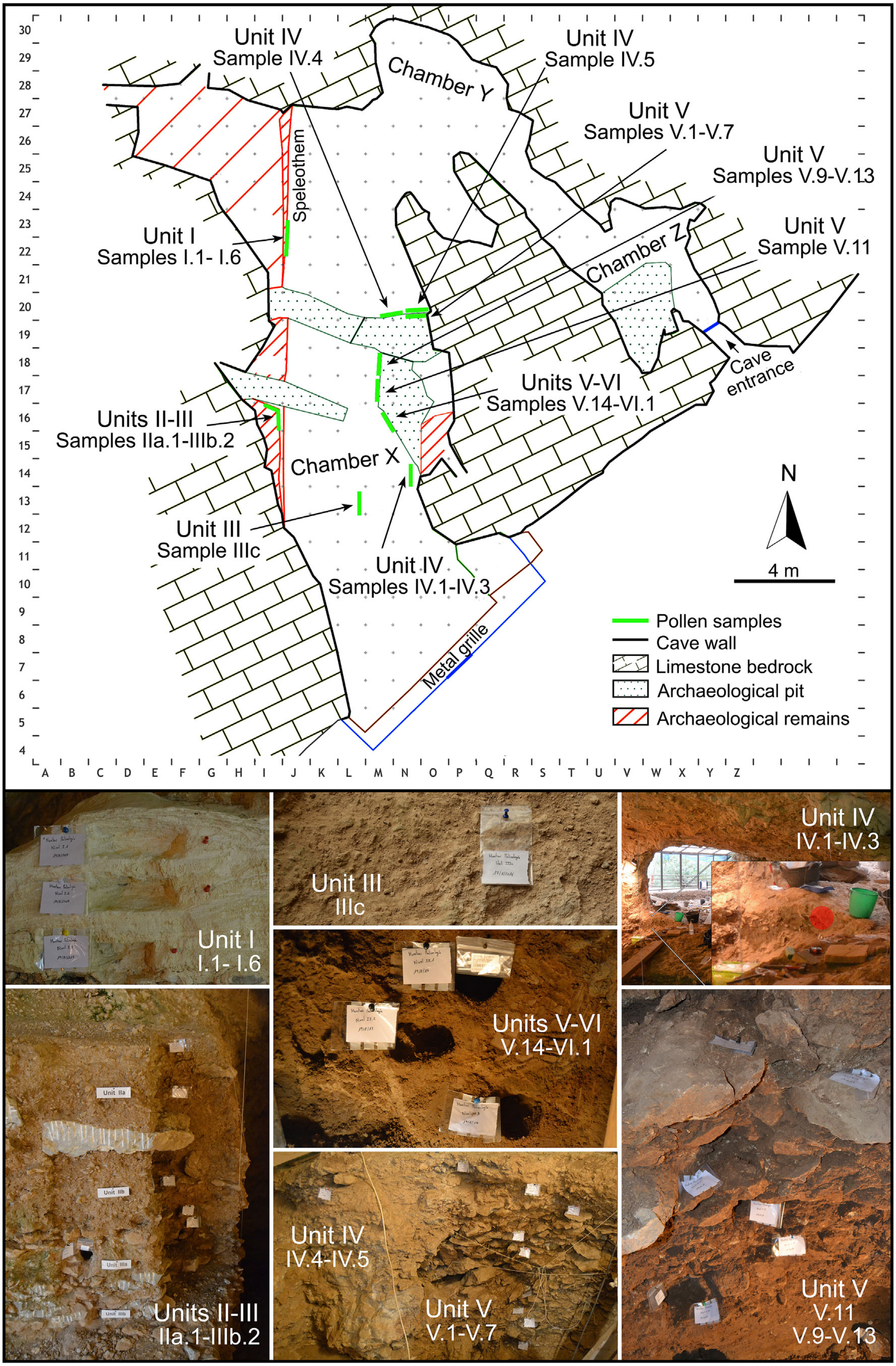

Fig. 2. Lithostratigrafical units and sections sampled for pollen analysis in Teixoneres Cave. Redrawn from Rufà et al. (2016).

Table 1
Geochronological data for Teixoneres Cave. Further details of the ^{14}C and U-series ages can be found in Talamo et al. (2016) and Tissoux et al. (2006). The pIR-IRSL age has been obtained as part of the present study.

Unit	Composition	Sample type	^{14}C Ultrafiltration (cal kyr BP 95.4% C.I.)	U-series (ka ± 1σ)	pIR-IRSL (ka ± 1σ)
I	Speleothem	Speleothem	–	16.0 ± 1.1	
		Speleothem	–	14.9 ± 1.2	
		Speleothem	–	14.7 ± 2.2	
		Speleothem	–	14.4 ± 1.3	
II	Brown-reddish sandy lutite with subangular and heterometric limestone clasts	Bone	41.0–41.9	–	
		Bone	39.0–40.0	–	
		Bone	42.4–43.3	–	
		Bone	43.7–45.0	–	
		Bone	34.4–35.0	–	
		Bone	42.6–43.6	–	
		Bone	38.9–39.9	–	
III	Brown-reddish sandy lutite with subangular and heterometric limestone clasts	Bone	46.0–48.7	–	
		Bone	44.7–46.1	–	
		Bone	43.4–44.9	–	
		Bone	44.9–46.3	–	
		Bone	44.1–45.4	–	
		Bone	44.4–45.7	–	
		Bone	>51.0	–	
IV	Speleothem	Speleothem	–	94.6 ± 3.2	
		Speleothem	–	100.7 ± 6.5	
		Speleothem	–	100.3 ± 6.1	
V	Limestone clasts in a poor reddish lutite matrix	–	–	–	
VI	Brown-yellowish sand and silt	Sediment	–	–	198 ± 11

(Units II, III, V VI and VII) were formed by debris flows, and are characterized by a lutitic matrix with limestone blocks from the walls and roof. There are two stalagmitic beds (Units I and IV) that cover much of the cave surface, representing specific periods with very low (or non-existent) entry rates of detrital sediment into the cave.

The archaeological excavations carried out so far have focused on the detrital units between the stalagmitic beds. Unit IV is a speleothem developed along the East wall of the cave and decreases in thickness towards the central area. It consists mainly of columnar calcite and includes limestone clast of varied sizes. U-series dating of this unit has provided an average age of c. 100 ka (Table 1) (Tissoux et al., 2006). Unit III (subunits IIIc, IIIb and IIIa) is formed by lutites of allochthonous colluvial origin, which were incorporated into the cave through the main entrance and through a chimney located in the Northeast area. The unit also includes limestone blocks of autochthonous origin from the walls and roof of the cave. Radiocarbon (^{14}C ultrafiltration) age obtained on bones from Unit III indicate a coherent chronology from beyond 51 ka at the bottom of the sequence to 44 ka at the top (Table 1) (Talamo et al., 2016). Unit II (subunits IIb and IIa) consists of lutites and small scattered limestone blocks. ^{14}C dating of bones from Unit II provides a chronology of c. 44 ka for the bottom for this deposit and 34 ka for the top (Table 1) (Talamo et al., 2016). Unit I consists of speleothems (flow stones, columns and stalagmites) that developed from different points of water entry to the cave, partially covering the upper part of Unit IIa. U-series dating has provided a chronology of c. 14–16 ka for this unit (Table 1) (Tissoux et al., 2006).

The sedimentary deposits located below the Unit IV speleothem have not been dated previously. As part of the present study, therefore, we have undertaken a preliminary geochronological examination of the Unit VI sand and silt deposits using luminescence dating. Given the expected antiquity of Unit VI (i.e., marine isotope stage (MIS) 5c or earlier; as indicated by U-series dating of Unit IV; Tissoux et al., 2006), we have used post-infrared infrared stimulated luminescence of K-feldspars (pIR-IRSL; e.g., Buylaert et al., 2009), which exhibits considerably higher dose saturation properties than conventional optically stimulated luminescence of quartz (OSL) (e.g., Arnold et al., 2015) and has been used to establish reliable depositional chronologies over Middle Pleistocene timescales for a number of Iberian sites (e.g., Arnold et al., 2014; Demuro et al., 2014, 2015; 2019; Méndez-Quintas et al., 2018). Additional luminescence dating of the entire Teixoneres infill sequence is ongoing and will be the subject of a dedicated future publication; here we aim to provide initial luminescence age constraint on the lowermost deposits that have been sampled for palynological analyses.

The lithic finds from Units II and III are concordant with the most common Middle Palaeolithic techno-complexes in the region (Bustos-Pérez et al., 2017; Picin et al., 2020). The lithic reduction sequences usually appear fragmented, with an abundance of flakes, final products and exhausted cores. Nevertheless, discoid and Levallois methods are recognized. Some retouched tools have also been recovered, among which points and scrapers are the most common. The abundance of lithics decreases significantly in Unit II, probably due to the loss of materials from previous excavations. Anthropogenic evidence on faunal remains is identified in the form of cut-marks, intentional breakage and thermo-alteration. These modified faunal remains have mainly been discovered at the entrance of the cave (chamber X), which was the most used area by past human groups (Rosell et al., 2010). In contrast, carnivore damage is common on bones recovered from the inner areas (chambers Y and Z).

Early interpretations of the cave from the 1950's onwards suggested it was a hyaena den experiencing sporadic visits by Middle Palaeolithic human groups. The current data, based on extensive excavations, confirm this idea but suggest some variations regarding the intensity (and probably the purpose) of these human occupations (Rosell et al., 2017). Thus, the units located at the top of the stratigraphic sequence (IIa, IIb and IIIa) show occupations characterized by isolated hearths and few spatial organisation which has been interpreted as a succession of short-term human occupations by small groups (Sánchez-Hernández et al., 2014; Sánchez-Hernández et al.,in press; Rosell et al., 2017). Moreover, the lithics of these assemblages are mainly made on allochthonous raw material, indicating the strong relationships of these groups with areas far from their territory. However, Unit IIIb displays the largest use of the space and a significant reversal in the proportions of local and allochthonous raw materials, which is interpreted as indicating greater territorial integrity of the groups and longer duration occupations of the site. The diversity of past human occupational patterns is currently one of the main subjects of archaeological research being undertaken at the cave.

3. Modern-day vegetation and climate

Teixoneres is located in a temperate, oceanic bioclimate, within the upper limits of the Mediterranean Region (Sub-Mediterranean climate) and near the Eurosiberian Region of Northern Iberia (Fig. 1). The nearby meteorological station in Moià shows an annual average temperature of 13.7 °C (9 °C in the coldest months and 18,5 °C in the warmest months) and annual precipitation of 749 mm. The area is located in the supramediterranean belt with subhumid ombroclimate and, biogeographically, it belongs to the Pyrenean Province of the Eastern Pyrenean Sector (Rivas-Martínez, 1987; Rivas-Martínez et al., 2007). The vegetation of the area is dominated by forests adapted to mild summers and cold winters, patchily altered by disturbances such as overgrazing, fires, and extreme weather events (unusually cold periods, droughts, windstorms, snowfall). The surroundings of the cave are dominated by *Buxus sempervirens*, *Pinus halepensis* and *Quercus pubescens/humilis*, accompanied by other trees such *Acer campestre/monspessulanum*, *Fraxinus angustifolia, Corylus avellana*, *Pinus nigra* subsp. *salzmannii*, *Pinus sylvestris*, *Quercus ilex, Quercus suber,* and *Quercus petraea* (Fig. 1). These forests also contain a rich, woody stratum, with *Cornus sanguinea*, *Crataegus monogyna*, *Daphne laureola*, *Hedera helix*, *Hippocrepis emerus*, *Ilex aquifolium*, *Juniperus communis*, *Juniperus oxycedrus*, *Laurus nobilis*, *Lonicera xylosteum*, *Pistacia lentiscus*, *Pistacia terebinthus*, *Prunus spinosa*, *Quercus coccifera*, *Rhamnus alaternus*, *Rhamnus saxatilis*, *Rubus ulmifolius*, *Ruscus aculeatus*, *Sorbus aria*, *Sorbus torminalis* and *Viburnum lantana*, among other species.

4. Material and methods, and palynological potential

As recommended for archaeological beds (Girard, 1975), palynology sampling was conducted on several vertical stratigraphic profiles (Fig. 2) within chamber X (units I-VI), assuming that the whole sequence is not necessarily represented in a single section. Preliminarily, one sample per unit was processed to evaluate the palyno-analytical potential of the cave sediment. Once it was known that the sedimentary sequence is well suited for palynology (e.g. good preservation, counts above 100 per sample, low number of indeterminable palynomorphs, pollen taxa diversity), more exhaustive sampling was carried out, focusing on the middle and inner parts of the cave in chamber X, approximately 14–23 m from the main entrance. Unit I was sampled in squares I-22 and I-23, Units II and III in I-16 and L-13, Unit IV in N-14, M-20 and N-20, Unit V in N-19, M-18, M-17 and M-16, and Unit VI in square M-16 (Fig. 2). 33 samples were analysed and 31 were found to be polleniferous (Table 2). The two sterile samples came from Unit VI (VI.2, VI.3). Exposed surface layers of sediment were cleaned back and discarded to a depth of 45–50 cm in Units II and III, and 5–10 cm in the rest of the units, in order to avoid potential sources of contamination and recent bioturbation (Fig. 2). The mass of sediment treated for each sample was the net weight (Table 2).

Extraction of palynomorphs in the laboratory followed the classical chemical method (Dimbleby, 1985), with the modifications proposed by Girard and Renault-Miskovsky (1969) for archaeological sediments. In order to evaluate the quality of the laboratory preparation procedures, we added to each sample three tablets of *Lycopodium* spores of a known concentration. Palynological identification and counting were performed with conventional light microscopy (400x and 1000x), and the help of the pollen reference collection of the Department of Plant Biology at the University of Murcia. The pollen counts were treated with Tilia Graph 1.7.16 to depict the results through pollen diagrams (Figs. 3–5; S.I. Fig. I). A total of 15,158 palynomorphs were identified; 10,319 pollen grains and 4839 spores were counted, excluding those not identified. Spores, non-pollen microfossils, and the pollen grains of Compositae (Asteroideae, Cichorioideae, *Anthemis* t., *Centaurea montana* t., *Centaurea nigra* t. and *Echinops*) were excluded from the pollen sum. The number of pollen taxa is between 15 and 37 per sample, with a total of 78 taxa being recognized. The percentage of indeterminable is lower than 8% (Table 2), and the preservation was generally good. The lowest pollen concentrations were recorded in the Unit I speleothem, and the maxima were found in the most anthropogenic subunit IIIb, perhaps due to compactation. Interestingly the highest number of taxa are recorded in the speleothems (Units I and IV).

The pollen groups established for certain taxa should be clarified. Pine pollen grains >50 μm were collected within the *Pinus halepensis - pinea* type, except those >50 μm with thickenings in the distal exine, which belong to *Pinus pinaster*. Those pine pollen grains larger than 50 μm were included in the *Pinus nigra - sylvestris* type. As regards *Quercus*, two taxa are established. *Quercus* deciduous + *suber*, which would comprise brevicolpate pollen grains larger than 20 μm with large apocolpia. *Quercus* evergreen type includes grains <20 μm with long colpi and small apocolpia (concerning principally *Quercus coccifera* and *Quercus ilex* agg.).

A pIR-IRSL sediment sample (TEX17-1) was collected from Unit VI in square M16 to provide an estimate of when sedimentary K-feldspar grains were last exposed to light prior to burial. Equivalent dose (D_e) values were determined for 6 aliquots (each aliquot containing ~350 grains) using the preparation steps, instrumentation, single-aliquot regenerative dose (SAR) procedure and quality assurance criteria outlined in Méndez-Quintas et al. (2018). The SAR protocol used for sample TEX17-1 involves raised temperature pIR-IR stimulation at 225 °C after a preheat of 250 °C for 60 s (pIR-IRSL$_{225}$ signals). The suitability of these D_e measurement conditions was confirmed by undertaking 600 Gy dose recovery tests using the approach described in Méndez-Quintas et al. (2018) (pIR-IRSL$_{225}$ dose recovery ratio $= 0.95 \pm 0.03$ at 1σ). Anomalous fading assessments were performed on a subset of 3 aliquots by undertaking repeated regenerative dose measurements after delayed storage times of 0.2–30 h, following the procedures of Auclair et al. (2003) and Huntley and Lamothe (2001). The environmental dose rate for TEX17-1 was estimated using a combination of *in situ* field gamma spectrometry and low level beta counting, taking into account cosmic ray contributions, an assumed internal alpha dose rate, beta-dose attenuation and long-term water content (Table 3).

5. Pollen stratigraphy

Overall, the pollen record of Teixoneres is characterized by the prevalence and continuity of a *Quercus-Pinus* forest, which is almost continuously accompanied by *Juniperus, Corylus* and to a lesser extent, *Castanea, Buxus, Betula* and *Erica* (Figs. 3–6). The woody component has high cover and relatively high diversity, and includes a combination of mesophytes, such as deciduous trees that feature in Eurosiberian temperate forests (*Acer*, *Alnus*, *Celtis*,

Table 2
Summary of palynological features of the Teixoneres samples.

Sample	Level	Nº	Coordinates	Depth (cm)	Gross Weight (g)	Net Weight (g)	Concentration (grains/g)	Indeterminable (%)	Pollen sum	Pollen sum including the Compositae	Number of taxa (Pollen)	Spores sum
I.1	I	1	I22 x900 y2125	72	87.3	87.3	22.90	4.47	201	204	27	67
I.2	I	2	I22 x900 y2125	80	83.7	83.7	24.05	7.46	201	206	27	98
I.3	I	3	I23 x930 y2540	83	95.1	95.1	62.12	6	200	213	33	131
I.4	I	4	I23 x930 y2540	86	71	71	52.72	0.60	498	510	37	417
I.5	I	5	I23 x930 y2540	89	71.9	71.9	35.55	7.50	200	212	23	186
I.6	I	6	I22 x900 y2123	92	87.2	87.2	87.13	6.90	217	222	31	100
IIa.1	IIa	7	I16 x860 y1570	137	88.2	65.1	1077.12	7.50	200	244	28	487
IIa.2	IIa	8	I16 x870 y1530	148	73.2	31.9	635.53	0.22	438	508	23	324
IIa.3	IIa	9	I16 x900 y1813	156	84.9	61.5	1052.22	3.86	207	260	17	12
IIb.1	IIb	10	I16 x847 y1575	174	87.2	53.5	1911.78	3.50	200	499	23	47
IIb.2	IIb	11	I16 x881 y1555	195	90.6	56.9	1242.58	5.50	200	506	18	103
IIb.3	IIb	12	I16 x860 y1555	205	73.8	52.5	1189.09	0.51	387	505	26	292
IIIa.1	IIIa	13	I16 x900 y1518	223	86.4	53.4	120.48	3	200	287	16	278
IIIa.2	IIIa	14	I16 x850 y1580	232	74.7	46.5	1117.11	0.68	292	505	23	365
IIIb.1	IIIb	15	I16 x850 y1582	236	88.1	56.1	3665.43	1.46	205	852	21	1
IIIb.2	IIIb	16	I16 x845 y1685	242	73.4	50.8	4279.32	0.79	253	503	26	250
IIIc	IIIc	17	L13 x1135 y1240	269	72.9	72.9	567.55	0.22	435	518	29	1218
IV.1	IV	18	N14 x1340 y1330	221	117.1	117.1	649.79	3.57	308	318	28	78
IV.2	IV	19	N14 x1340 y1332	224	60.1	60.1	1946.55	0.60	496	512	32	46
IV.3	IV	20	N14 x1340 y1330	227	100.6	100.6	1398.19	2.94	272	275	29	31
IV.4	IV	21	M20 x1230 y1985	230	72.1	72.1	962.27	6.50	200	280	25	85
IV.5	IV	22	N20 x1314 y1902	235	72.4	72.4	1766.59	7.50	200	351	25	27
V.1	V	23	N19 x1370 y1881	246	94.3	67.3	101.34	4.76	210	218	22	15
V.3	V	24	N19 x1358 y1885	275	96.9	75.4	152.42	4.24	212	215	16	5
V.5	V	25	N19 x1376 y1900	323	99	75	1332.92	1.44	208	208	16	4
V.7	V	26	N19 x1398 y1900	352	96.4	65.2	268.46	3.80	210	216	29	16
V.9	V	27	M18 x1200 y1700	383	95.6	64.1	579.84	3.52	227	228	21	22
V.11	V	28	M17 x1217 y1686	407	81.1	63.3	294.04	3.84	208	213	18	19
V.13	V	29	M18 x1200 y1709	433	80.7	59.5	330.25	2.84	211	215	20	17
V.14	V	30	M16 x1295 y1595	453	80.2	35	479.48	3.84	208	208	15	22
VI.1	VI	31	M16 x1300 y1515	466	81.1	58.9	59.33	4.76	105	108	18	76
								TOTAL 7809		10319		4839

*Pollen sum column without Asteroideae, Cichorioideae, *Anthemis* type, *Centaurea montana* type, *Centaurea nigra* type and *Echinops*.

Fraxinus, *Juglans*, *Fagus*, *Populus*, *Salix, Ulmus*), and Mediterranean taxa in addition to evergreen oaks and pines (*Viburnum, Pistacia, Myrtus, Calicotome*, *Cistus*, *Ephedra fragilis*, *Phillyrea*, *Rhamnus*). The xero-heliophytic component (Poaceae, *Artemisia*, Amaranthaceae, *Ephedra fragilis*) is relatively unimportant, with the exception of samples IIb.1, IIb.2, IIIb.1, IV.1 and IV.3 (Figs. 3–6).

5.1. Unit VI

This unit only includes sample VI.1 (Figs. 3–6), which is dominated by arboreous pollen (AP), accounting for more than 85% of the total counts. Coverage of *Pinus nigra-sylvestris* is above 26%, evergreen *Quercus* is 17%, *Pinus halepensis-pinea* is higher than 15%, *Juniperus* reaches 11%, deciduous *Quercus* + *suber* is below 1%, and *Olea* is above 3%. Other lesser contributors to AP include *Alnus*, *Corylus*, *Phillyrea* and Rosaceae. In the non-arboreous pollen (NAP) category, Poaceae attains relative abundances close to 10%, and Urticaceae, Cichorioideae, *Artemisia*, Asteroideae and *Plantago lanceolata,* are frequent. Fungal spores abound, especially *Inapertisporites* (43%), *Glomus*, *Hypoxylonites*, *Microsporonites*, *Pluricellaesporites*, *Polycellaesporonites* and *Scleroderma* (SI Fig. I).

5.2. Unit V

This unit includes pollen samples V.1, V.3, V.5, V.7, V.9, V.11, V.13 and V.14 (Figs. 3–6) and is also clearly dominated by trees, with AP higher than 92%. The abundance of pines is noteworthy, with a decreasing trend for *Pinus nigra-sylvestris* throughout the zone. *Pinus halepensis-pinea* is consistently high, fluctuating between 27 and 40%, while *Pinus pinaster* does not exceed 2%. *Quercus* shows an increasing trend from 6% (V.14) up to 37% (V.5), 44% (V.3) and 29% (V.1). Evergreen *Quercus* ranges from 3 to 33% and deciduous *Quercus* + *suber* between 3 and 11%. *Corylus* (2–11%), *Castanea* (1–5%), *Erica* (peak of 15%) and *Juniperus* (5%) are noteworthy, as are the occurrence of *Acer*, *Alnus*, *Betula*, *Fraxinus*, *Salix*, *Buxus*, *Olea*, *Myrtus*, *Rhamnus*, *Juglans*, *Viburnum*, *Sambucus nigra*, *Pistacia* and Genisteae. Poaceae (1–6%) and Fabaceae (1–3%) are not abundant, nor are *Artemisia*, Amaranthaceae, Asteroideae, Cichorioideae and

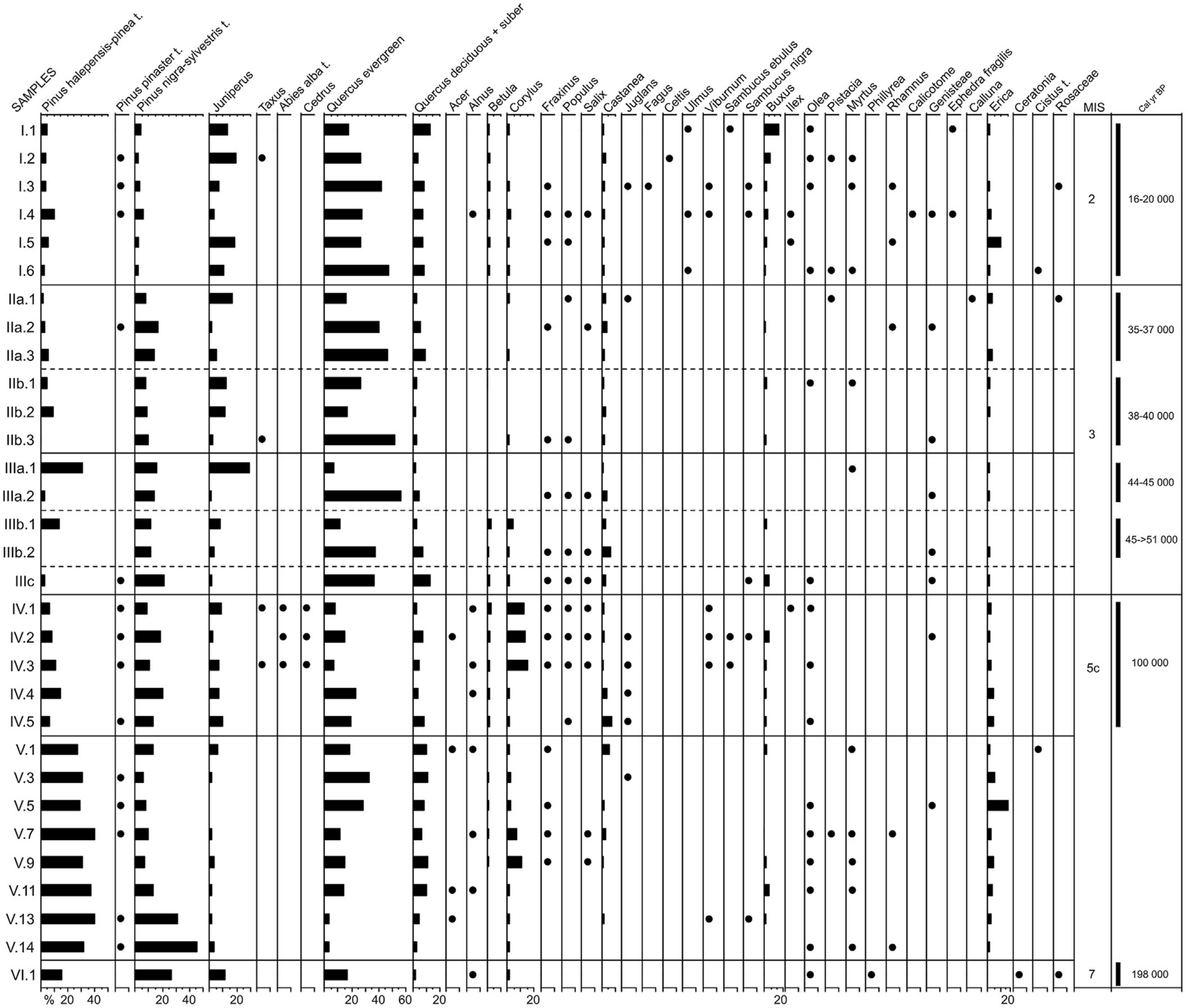

Fig. 3. Pollen diagram of Teixoneres including principally the woody component. Black dots for percentages below 3%. Dashed lines for subdivisions within archaeological levels.

Centaurea montana. The abundance of *Glomus* is outstanding (S.I. Fig. I). *Hypoxylonites*, *Inapertisporites*, *Quilonia* and Type 209 are frequent. Fern spores are represented by *Polypodium* (19%) in sample V.7, while bryophyte spores abound in V.7 (S.I. Fig. I).

5.3. Unit IV

This unit includes samples IV.1, IV.2, IV.3, IV.4 and IV.5 (Figs. 3–6). AP surpasses 67% including relatively high percentages of *Corylus* (2–15%), and evergreen *Quercus* (7–23%). *Pinus halepensis-pinea* declines down to 6%, while *Pinus nigra-sylvestris* varies between 9 and 20%, and *Pinus pinaster* does not exceed 3%. Deciduous *Quercus* + *suber* (3–9%) is continuously present, as are *Juniperus* (2–10%), *Erica* (c. 5%), *Betula* (1–4%), and *Castanea* (1–7%); the latter reaching its sequence maximum. Other palaeoecologically meaningful taxa occurring in this zone are *Taxus*, *Abies*, *Cedrus*, *Alnus*, *Fraxinus*, *Populus*, *Salix*, *Juglans*, *Viburnum*, *Buxus*, *Olea*, *Acer*, *Fraxinus*, *Sambucus ebulus*, *Sambucus nigra*, *Ilex* and Genisteae. Poaceae, the major herbaceous taxon in this zone, increases (5–31%). Other less frequent NAP includes *Artemisia*, Amaranthaceae, Caryophyllaceae, Asteroideae, Cichorioideae, Dipsacaceae, *Anthemis*, and *Centaurea montana*. *Glomus* and *Microsporonites* are very frequent, and *Diporisporites*, *Hypoxylonites*, *Inapertisporites*, *Monoporisporites*, *Multicellites*, *Polycellaesporonites* and *Scleroderma* occur continuously (S.I. Fig. I).

5.4. Unit IIIc

This unit was studied using a single sample (Figs. 3–6). AP is again dominant, surpassing 88%. Evergreen *Quercus* (37%), *Pinus nigra-sylvestris* (21%) and deciduous *Quercus* + *suber* (13%) are noticeable. *Castanea* is 3% and *Corylus* less than 2%. Other AP contributors are *Juniperus*, *Fraxinus*, *Sambucus nigra*, *Olea* and Genisteae. Poaceae declines abruptly down to 5%, while *Artemisia* is more frequent than in Unit IV, exceeding 4%. Among the fungal spores, *Dictyosporonites* stands out as being above 93%, and *Monoporisporites*, *Diporisporites*, *Dyadosporites* and *Hypoxylonites* are frequent (S.I. Fig. I).

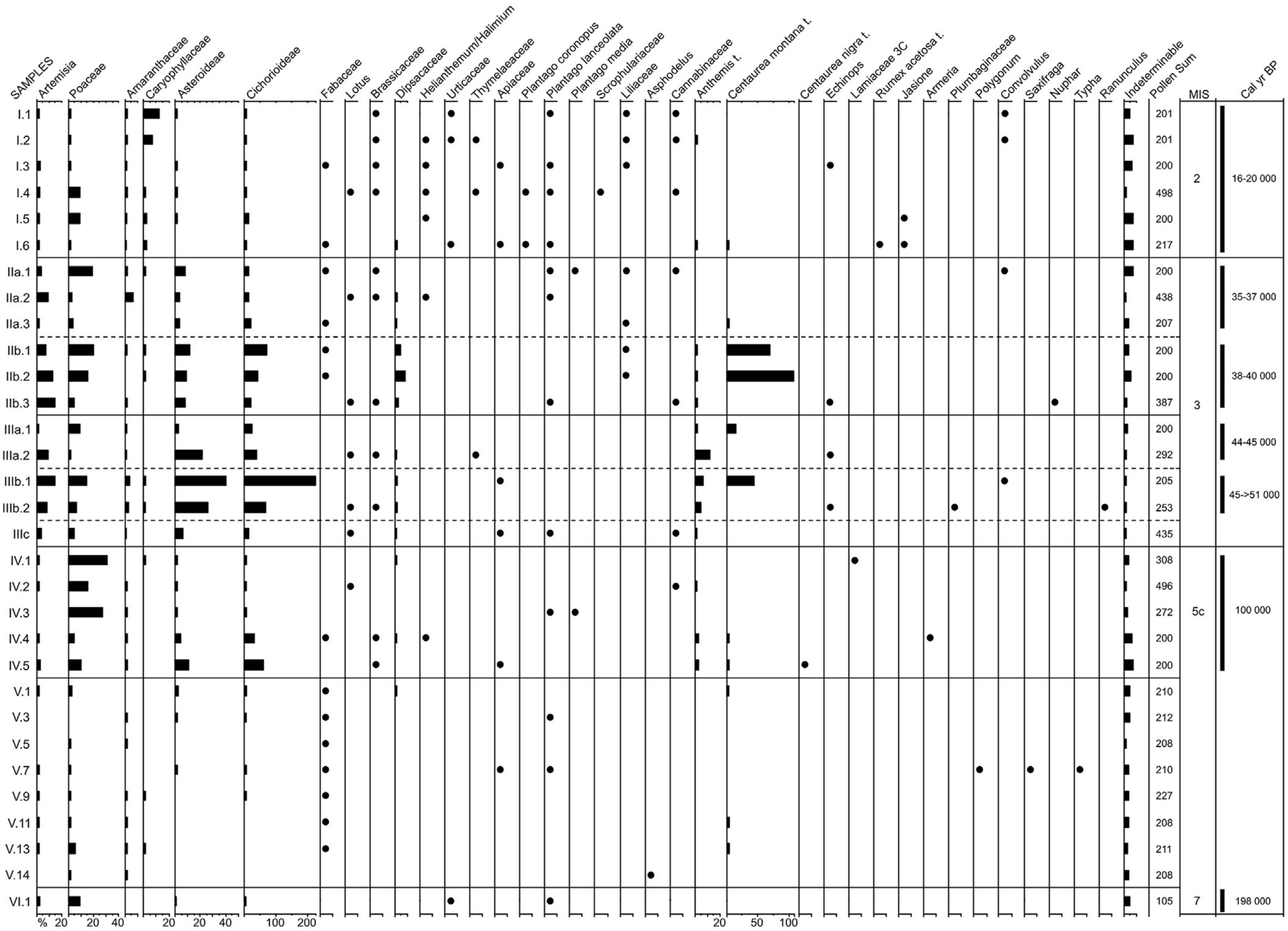

Fig. 4. Pollen diagram of Teixoneres including mainly non arboreal elements. Asteroideae, Cichorioideae, *Anthemis* type, *Centaurea montana* type, *Centaurea nigra* type and *Echinops* are out from the total pollen sum. Black dots for percentages below 3%. Dashed lines for subdivisions within archaeological levels.

5.5. Unit IIIb

In samples IIIb.1 and IIIb.2 (Figs. 3–6), AP attains relative abundances of c. 60%. *Pinus* varies from 11 to 26%, *Quercus* from 46 to 14%, with evergreen type (11–38%) prevailing, and deciduous taxa being less important (3–8%). *Juniperus* is 3–8%, *Castanea* 3–6%, *Betula* peaks at 3% and *Corylus* exceeds 4%. The common occurrence of *Fraxinus*, *Populus*, *Salix*, Genisteae and *Erica* at the base of this unit is worth mentioning. Poaceae (7–15%), *Artemisia* (8–14%) and Amaranthaceae (3–4%) are the main herbs. *Glomus* is again abundant (S.I. Fig. I).

5.6. Unit IIIa

This unit includes samples IIIa.1 and IIIa.2 (Figs. 3–6). AP exceeds 87%. Evergreen *Quercus* is outstanding (7–56%), as are *Pinus halepensis-pinea* (2–31%), *Juniperus* (1–30%) and *Pinus nigra-sylvestris* (14–16%). *Castanea* 4%, and deciduous *Quercus* + *suber* (5%) are also frequent. Other minor arboreal types include *Fraxinus*, *Populus*, *Salix*, *Myrtus*, Genisteae and *Erica*. Several fungal spore types are particularly abundant, such as *Monoporisporites* (5–52%), *Hypoxylonites* (21–38%), and *Gelasinospora* (1–28%) (S.I. Fig. I).

5.7. Unit IIb

This unit includes samples IIb.1, IIb.2 and IIb.3 (Figs. 3–6). AP is continuously higher than 58%, with a peak above 74%, and is dominated by evergreen *Quercus* (17–52%), with a visible representation of *Juniperus* (2–13%), *Pinus nigra-sylvestris* (8–10%), *Pinus halepensis-pinea* (1–10%), *Castanea* (1–3%), and deciduous *Quercus* + *suber* (<4%). *Taxus*, *Betula*, *Fraxinus*, *Buxus*, Genisteae and *Erica* are well represented. Poaceae (5–20%), *Artemisia* (8–15%) and Dipsacaceae (3–8%) are the main herbaceous taxa.

5.8. Unit IIa

This unit includes samples IIa.1, IIa.2 and IIa.3 (Figs. 3–6). AP is above 65%, with evergreen *Quercus* (16–47%), *Pinus nigra-sylvestris* (8–17%) and *Juniperus* (1–17%), *Pinus halepensis-pinea* (2–5%), deciduous *Quercus* + *suber* (3–10%), *Castanea* (>2%), and *Erica* (4%) as principal taxa, accompanied by *Corylus*, *Fraxinus*, *Salix*, *Buxus*, *Pistacia*, Genisteae, Rosaceae, *Pinus pinaster*, *Rhamnus*, *Calluna*, *Populus* and *Juglans*. Poaceae (3–20%) and *Artemisia* (2–10%) are dominant within NAP. *Glomus* (2–100%), *Diporisporites* (3–20%), *Hypoxylonites* (5–50%) and *Monoporisporites* (3–60%) are abundant, and *Ctenosporites*, *Dicellaesporites*, *Fractisporonites*, *Gelasinospora*,

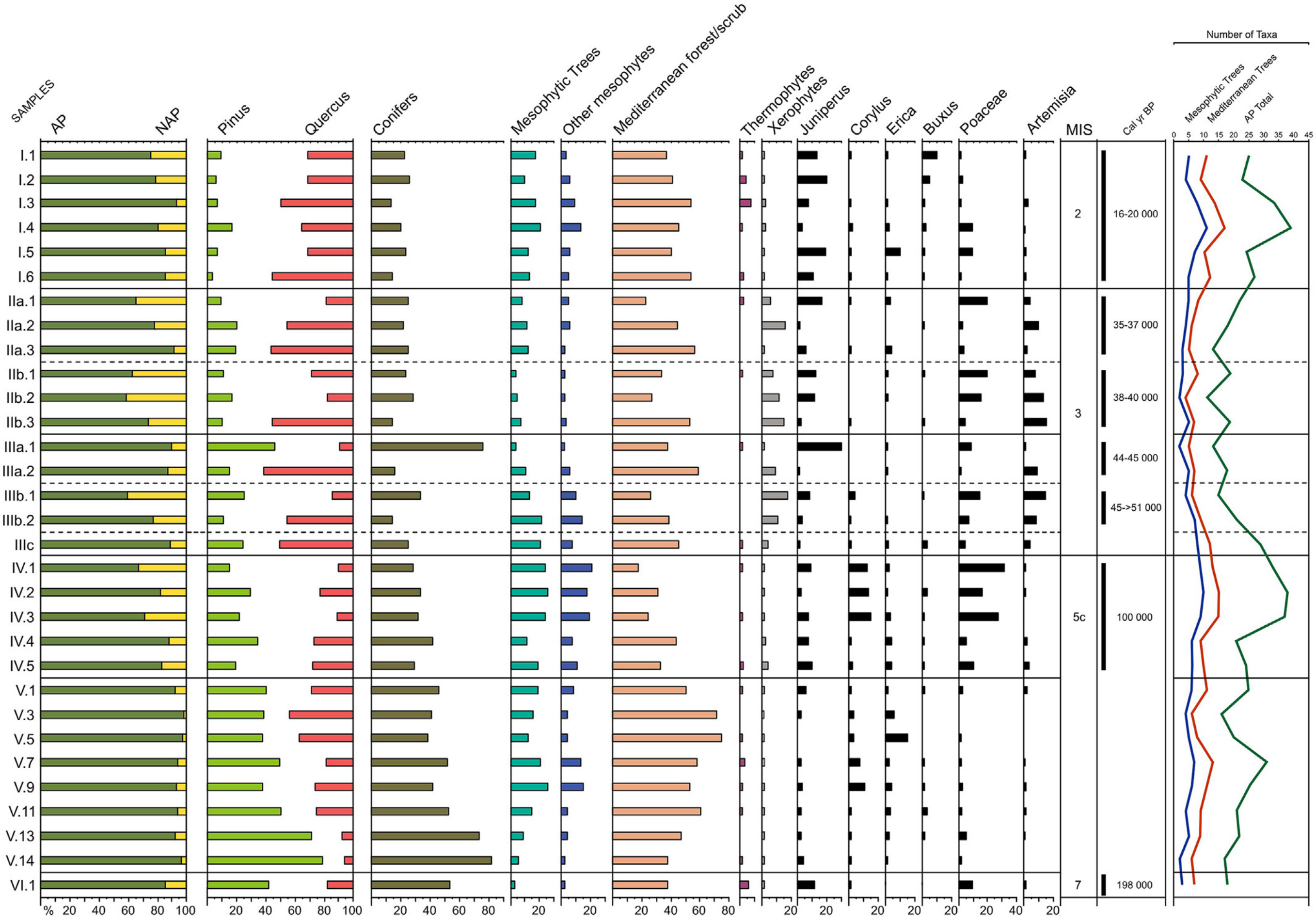

Fig. 5. Synthetic pollen diagram of Teixoneres including ecological groups and the main pollen contributors. Conifers include *Pinus*, *Juniperus*, *Taxus*, *Abies* and *Cedrus*. Mesophytic trees include deciduous *Quercus* + *suber*, *Acer*, *Alnus*, *Betula*, *Corylus*, *Fraxinus*, *Populus*, *Salix*, *Castanea*, *Juglans*, *Fagus*, *Celtis*, *Ulmus*, *Sambucus nigra* and *Ilex*. Other Mesophytes comprise mesophytes trees minus deciduous *Quercus* + *suber*. Mediterranean forest/scrub include evergreen *Quercus*, *Pinus halepensis*, *Pinus pinaster*, *Viburnum*, *Sambucus ebulus*, *Buxus*, *Olea*, *Pistacia*, *Myrtus*, *Phillyrea*, *Calicotome*, *Ephedra fragilis*, *Erica*, *Cistus* and *Ceratonia*. Thermophytes include *Olea*, *Pistacia*, *Myrtus*, *Phillyrea*, *Calicotome*, *Ephedra fragilis*, *Ceratonia*, *Cistus* and *Asphodelus*. Xerophytes include *Artemisia*, Amaranthaceae, *Asphodelus*, Lamiaceae and *Ephedra fragilis*. The dashed lines indicate subdivisions within an archaeological level.

Table 3
pIR-IRSL dose rate data, equivalent doses and final age for sample TEX17-1.

Sample	Layer	Grain size (μm)	Water content (%)[a]	Environmental dose rate (Gy/ka)					Equivalent dose (D_e) data				
				Beta dose rate[b,c]	Gamma dose rate[c,d]	Cosmic dose rate[e]	Internal dose rate[f]	Total dose rate[g]	No. of aliquots[h]	Overdispersion (%)[i]	Age model[m]	D_e (Gy)[i]	Age (ka)[g,k]
TEX17-1	VI	90–125	21 ± 4	2.00 ± 0.10	0.92 ± 0.03	0.05 ± 0.01	0.49 ± 0.04	3.46 ± 0.18	6/6	4 ± 1	CAM	687 ± 13	198.4 ± 11.0

j Age model used to calculate the sample-averaged D_e value for each sample. CAM = central age model (Galbraith et al., 1999).

[a] Long-term estimated water content, expressed as % of dry mass of mineral fraction, with an assigned relative uncertainty of ±20%. The long-term water content of these samples is taken as 50% of the saturated water content estimate on the basis of proportional saturation assessments made on sediment samples collected from fresh exposures in Teixoneres Cave.

[b] Beta dose rates were calculated using a Risø GM-25-5 low-level beta counter, after making allowance for beta dose attenuation due to grain-size effects and HF etching (Mejdahl, 1979; Brennan, 2003).

[c] Radionuclide concentrations and specific activities have been converted to dose rates using the conversion factors given in Guérin et al. (2011) and Readhead (2002).

[d] Gamma dose rates were calculated from *in situ* measurements made at each sample position with a NaI:Tl detector using the 'energy windows' method detailed in Arnold et al. (2012).

[e] Cosmic-ray dose rates were calculated according to Prescott and Hutton (1994) and assigned a relative uncertainty of ±10%.

[f] Assumed internal feldspar dose rate based on internal^{4} K and^{87}Rb concentrations of 12.5 ± 0.5% (Huntley and Baril, 1997) and 400 ± 100 ppm (Huntley and Hancock, 2001), respectively, yielding an internal beta dose rate of 0.43 ± 0.03 Gy/ka for the 90–125 μm K-feldspar grains measured in this study. An additional internal alpha + beta dose rate of 0.06 ± 0.03 Gy/ka has been calculated for the K-feldspar fractions using assumed intrinsic^{238}U and^{232}Th concentrations of 0.15 ± 0.03 ppm and 0.35 ± 0.07 ppm, respectively (following Mejdahl, 1987; Huntley and Clague, 1996; Huntley and Lian, 1999; and Alappat et al., 2010), and an a-value of 0.09 ± 0.03 (following Rees-Jones, 1995; Lang and Wagner, 1997; Banerjee et al., 2001; Lang et al., 2003; Berger et al., 2008; Feathers et al., 2012).

[g] Mean ± total uncertainty (68% confidence interval), calculated as the quadratic sum of the random and systematic uncertainties.

[h] Number of D_e measurements that passed the SAR rejection criteria and were used for D_e determination/total number of D_e values analysed.

[i] The relative spread in the D_e dataset beyond that associated with the measurement uncertainties for individual D_e values.

[k] Total uncertainty includes a systematic component of ±2% associated with laboratory beta-source calibration.

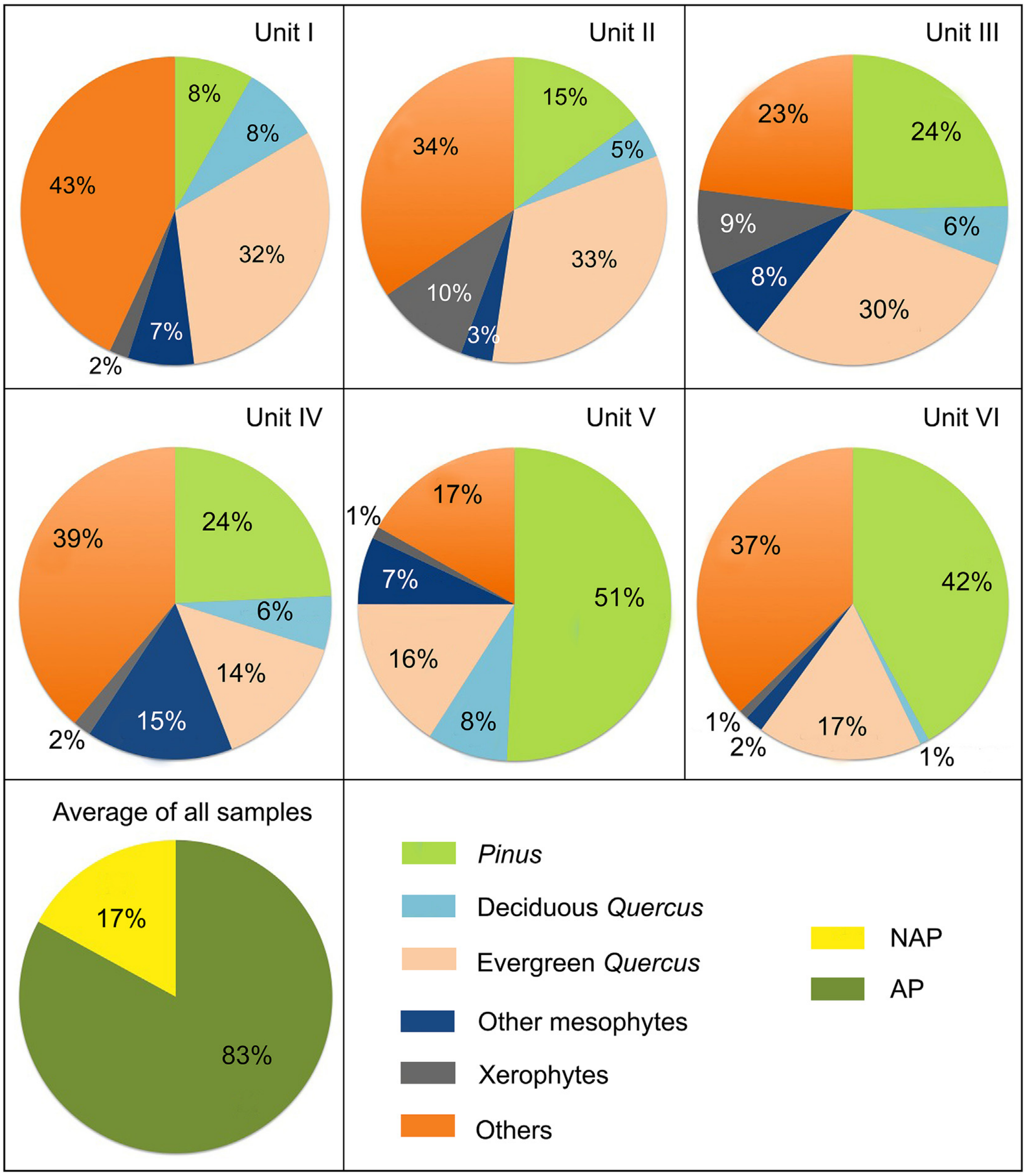

Fig. 6. Sum of pollen frequencies for selected taxa and pollen groups, including arboreal (AP) and non-arboreal (NAP) components in the sequence of Teixoneres.

Inapertisporites, *Pluricellaesporites*, and fern spores, including *Polypodium*, occur in this zone. The abundance of moss spores (5%) in sample IIa.1 is additionally noteworthy (S.I. Fig. I).

5.9. Unit I

This unit includes samples I.1, I.2, I.3, I.4, I.5 and I.6 (Figs. 3–6). The predominant pollen type continues to be arboreal, with total values higher than 75%. The abundance of *Quercus* (31–55%) is remarkable, with evergreen *Quercus* ranging between 18 and 47%, and deciduous *Quercus* + *suber* between 4 and 13%. *Pinus halepensis-pinea* (3–10%) increases with respect to the previous levels, while *Pinus nigra-sylvestris* (1–6%) declines. The relatively high frequencies of *Juniperus* (7–19%), *Buxus* (1–10%) and *Erica* (1–10%), together with the maximum of *Olea* (7%) are noticeable. *Castanea* does not exceed 3%, while *Betula* and *Corylus* are close to 3%. *Pinus pinaster*, *Fraxinus*, *Populus*, *Salix*, *Ulmus*, *Myrtus* and *Rhamnus* are well represented, and it is also worth noting the presence of *Taxus*, *Alnus*, *Juglans*, *Fagus*, *Celtis*, *Viburnum*, *Sambucus ebulus*, *Sambucus nigra*, *Ilex*, *Pistacia*, Genisteae, *Ephedra fragilis* and Rosaceae.

6. pIR-IRSL dating results

Table 3 and Fig. 7 summarise the pIR-IRSL$_{225}$ dating results for Unit VI. The D$_e$ distribution for sample TEX17-1 is characterized by low overdispersion of 4 ± 1% and is normally distributed according to the log skewness test outlined by Arnold and Roberts (2011). The final burial dose has therefore been calculated using the central age model of Galbraith et al. (1999), assuming that these favourable D$_e$ distribution characteristics reflect sufficient optical resetting of grain populations prior to burial (e.g., Bailey and Arnold, 2006; Arnold and Roberts, 2009). However, given that the Unit VI fluvial silts and sands may have been transported through the deeper karst system prior to deposition, it is worth noting that potential

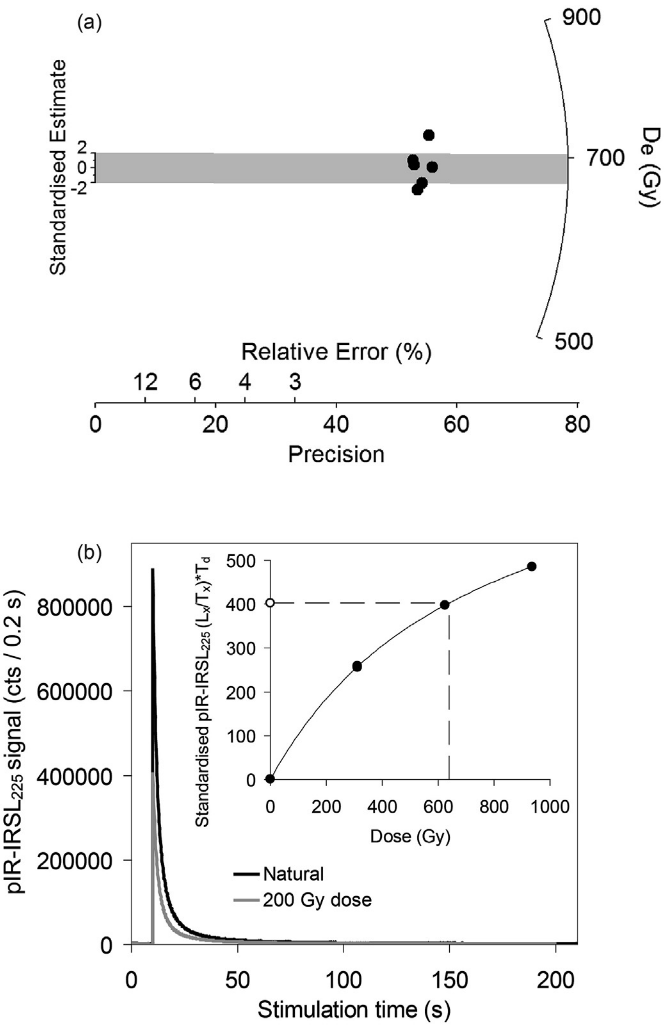

Fig. 7. (a) pIR-IRSL equivalent dose (D_e) distribution for sample TEX17-1, shown as a radial plot. The grey band is centred on the D_e values used for the final age calculation. (b) Representative pIR-IRSL$_{225}$ decay and dose response curves for a ~350-grain K-feldspar aliquot used for dating. The pIR-IRSL$_{225}$ decay curves typically decrease by >95% within the first 30 s of stimulation and are optimally fitted with a single saturating exponential plus linear function.

remains for heterogeneous bleaching of the TEX17-1 K-feldspar grains; specifically, there could have been syn-depositional mixing of externally derived sediments with pre-existing cave deposits during transportation through the closed cave system. Such complications are not necessarily discernible from multi-grain D_e analyses alone, hence efforts are ongoing to validate the bleaching characteristics of the Unit VI infill deposits using complementary single-grain analyses.

The anomalous fading assessments undertaken on TEX17-1 yielded a weighted-mean g-value (normalised to 2 days) of 1.39 ± 0.12%/decade. This low empirical fading rate is consistent with published g-values for higher temperature pIR-IRSL signals (e.g., pIR-IRSL$_{290}$ signals involving pIR-IR stimulation at 290 °C following a preheat of 320 °C for 60 s; see summary in Arnold et al., 2015) and athermally stable quartz samples (e.g., Buylaert et al., 2012). Consequently, we have not applied an additional fading correction to the pIR-IRSL$_{225}$ age estimate for sample TEX17-1. The final age for Unit VI is 198 ± 11 thousand years ago (ka) (1σ uncertainty range), indicating that the lowermost deposits included in the palynological study most likely accumulated during MIS 7 or early MIS 6.

7. Palaeobotanical and palaeobiogeographical interpretations

At present, the species of evergreen *Quercus* growing in the region are *Quercus ilex* subsp. *ilex* in the tree stratum, and *Quercus coccifera* in shrub formations. *Q. ilex* subsp. *ilex* is found between 700 and 1200 m, within an intermediate belt between the coastal holm oak typical of the lowlands and the mid-elevation marcescent/deciduous oak groves. The mountain formations of this subspecies are established exclusively on decarbonated siliceous or calcareous substrates (Blanco-Castro et al., 1997). Although the Northerly evidence of *Quercus ilex* during the Quaternary glacial stages indicates limited abundance (Uzquiano et al., 2016), anthracological records have postulated the occurrence of local stands in the mountains of the East (Badal et al., 2012). The latter interpretation is confirmed by the present study.

Deciduous oak species growing in the present-day surroundings include *Quercus humilis* and *Quercus petraea*. Communities of *Quercus humilis* with *Buxus sempervirens* understory are frequent in numerous Western Catalonian mountains. In addition, *Quercus humilis* is mixed with other hardwoods (*Quercus petraea*) to form mixed oak woodlands in the interior, mainly on acidic soils. The most typical pubescent oak structure and composition is found around the Pyrenean axis, from the Cap de Creus in the East to the Central Pyrenees. These communities are indicative of the transition from Mediterranean to Eurosiberian communities (Aranbarri et al., 2016; Blanco-Castro et al., 1997; García-Mijangos et al., 2015; Gil-Romera et al., 2014; González-Sampériz et al., 2004, 2017; Loidi, 2017; Morales-Molino and García-Antón, 2014; Sáez et al., 1998; Salomón et al., 2016).

Taking into consideration the present-day ecology and biogeography of these species, and the own palynological features of the pollen spectra, the cork oak (*Quercus suber*) must also have been present around Teixoneres during the Pleistocene, although we have not been able to discriminate its palynotype (Magri et al., 2007). In fact, *Quercus suber* pollen is frequently underrepresented in regional pollen diagrams. The Catalan cork oak tree is presented in two clearly differentiated nuclei, located between altitudes of 500 and 800 m: namely, the Alberes mountains and the regions close to the sea (La Selva and Baix Empordà) (Allué Andrade, 1990, Caritat et al., 2006; Jiménez et al., 1999; Pons and Pausas, 2006; Salis et al., 2019). In the Holocene, it seems that cork oaks recovered quickly, so that they were already of great importance by 10 ka (Carrión et al., 2000a; Villar et al., 1989). Considering the broader Iberian Peninsula, in addition to the well-known site of Navarrés (Carrión and van Geel, 1999), other Late Quaternary pollen sequences such as Sobrestany (Parra et al., 2005), Casablanca-Almenara (Parra, 1993), Padul (Camuera et al., 2019; Pons and Reille, 1988), SU 8103 (Parra, 1994), SU 8113 (Parra, 1994), 8057B (Hooghiemstra et al., 1992), Gádor (Carrión et al., 2003a) and Gorham's Cave (Carrión et al., 2008), there is abundant evidence for last glacial survival of the cork oak in Southern and coastal areas. Later, cork oak developments occur from the Lateglacial to the middle Holocene in non-monospecific forests, sharing the arboreal stratum both with other sclerophyllous and deciduous *Quercus*, as well as with *Pinus* species (Carrión et al., 2000a).

The Aleppo pine (*Pinus halepensis*), and to a lesser extent the black pine (*Pinus nigra* subsp. *salzmannii*) and the Scots pine (*Pinus sylvestris*), are currently the dominant trees in the forest masses of the studied region. Palaeobotanical evidence from numerous Upper Pleistocene sites across Northeastern Iberia, similarly confirms *Pinus* as one of the main forests, especially during stadials (Allué et al., 2007; Bergadà et al., 1999; Burjachs, 1987, 1994; 2009; Burjachs and Julià, 1994; Burjachs and Renault-Miskovsky, 1992; González-Sampériz, 2004; González-Sampériz et al., 2003; Pérez-Obiol and Julià, 1994; Val-Peón et al., 2019; Yll, 1995). Fossil charcoal from Teixoneres shows *Pinus pinea/pinaster* and *Pinus sylvestris* types are abundant in hearths within units II, IIb and III (López-García et al., 2012).

The presence of cluster pine (*Pinus pinaster*) in Catalonia is reduced today to small isolated formations, but it was clearly present during the Pleistocene, probably being part of mixed forests with deciduous and evergreen oaks (Carrión et al., 2000b). *Pinus pinaster* forests exhibit great ecological plasticity, tolerating the cold and temperate climates of inland winter near the coast. Additionally, we do not rule out the presence of *Pinus pinea* in the past due to the proximity of the site to the Mediterranean coastal platforms (50–60 km away). Currently, this species can be found in the coastal mountains North of Barcelona, on mainly granite substrates (Blanco-Castro et al., 1997; González et al., 2007; González-Sampériz et al., 2017; Loidi, 2017; Rodrigo et al., 2007; Sáez et al., 1998; Tapias et al., 2004).

Considering their current distribution, it is worth mentioning the possible past local existence of some typically Eurosiberian tree species such as *Abies alba* and *Fagus sylvatica*. Debate persists about whether pollen occurrences of other taxa (e.g., *Cedrus*) in the Iberian upper Pleistocene and Holocene records are due to long-distance transport from North Africa, or if the species survived naturally until a few millennia ago (Magri and Parra, 2002; Magri et al., 2017; Postigo-Mijarra et al., 2009, 2010).

The presence of walnut (*Juglans regia*) at Teixoneres reinforces previous palynological data (Carrión and Sánchez-Gómez, 1992; Postigo-Mijarra et al., 2008) that indicates the naturalness of the species in Western Europe. The walnut inhabited mixed Mediterranean forests, possibly along with *Acer, Castanea, Celtis, Corylus, Betula, Quercus* and *Ulmus*. *Juglans regia* shows fossil record continuity from the Early Miocene to the Holocene (Carrión et al., 2010, 2013; García-Antón et al., 1990; Gómez-Orellana et al., 2007). More abundant and continuous is the local presence of the chestnut (*Castanea sativa*), whose native character in Europe has been discussed by Huntley and Birks (1983), Ochando et al. (2019) and Postigo-Mijarra et al. (2008, 2010). The virtually uninterrupted appearance of *Castanea* through the Teixoneres sequence confirms its persistence in the Mediterranean and especially in the North of the Iberian Peninsula (Carrión et al., 2003b, 2013; García-Antón et al., 1990; Huntley and Birks, 1983; Morla-Juaristi, 1996; Postigo-Mijarra et al., 2008, 2010). Similarly, the presence of *Celtis* in Unit I of Teixoneres reinforces the native character of the hackberry (Ruiz de la Torre, 2006; Shillito and Almond, 2010; Simchoni and Kislev, 2011).

The current distribution of *Ceratonia siliqua* is not limited to the Iberian Peninsula and Western North Africa (Viruel et al., 2020). Although the appearance of *Ceratonia* in the Teixoneres sequence is limited to the lowest stratigraphic unit (unit VI), a greater and prolonged abundance in the past should not be excluded, since it has been proven that its low frequencies in Southwestern Europe sequences could be due to the low dispersion potential of this pollen (Jahns, 2003). The first fossil records of the carob tree in the Iberian Peninsula are from the Middle Miocene, although this record is discontinuous until the Lower Pleistocene (García-Antón et al., 1992; González-Sampériz et al., 2004; Jiménez-Moreno and Suc, 2007). However, the presence of *Ceratonia* pollen has been confirmed in the TD-6 level of Gran Dolina (Atapuerca), and is accompanied by other Mediterranean elements such as *Celtis, Olea, Pistacia* and *Phillyrea* (García-Antón, 1989, García-Antón et al., 1992). *Ceratonia* pollen is also continuously present from MIS 9 to MIS 5e at the Bolomor site in Eastern Spain (Ochando et al., 2019).

8. Teixoneres: an extraordinary forest resilience history during the cold pleistocene

There are sections of the Teixoneres chronological framework that still need to be improved, and efforts are now being focused on strengthening the existing age estimate for the lower units via additional sampling and use of complementary extended-range luminescence dating signals (particularly single-grain thermally transferred OSL; e.g., Arnold and Demuro, 2015; Demuro et al., 2019). Regardless, this sequence demonstrates the long-term permanence of a relatively dense forest ecosystem dominated by oaks and pines, with important implications for a large number of trees including *Juniperus, Corylus*, *Castanea*, *Abies, Taxus*, *Acer, Alnus, Betula, Celtis, Fraxinus, Juglans, Fagus, Buxus, Populus, Salix*, and *Ulmus*, as well as indicators of thermicity such as *Calicotome, Olea, Ceratonia, Cistus, Ephedra fragilis, Myrtus, Pistacia, Phillyrea, Rhamnus* and *Viburnum* (Figs. 3–5). The xero-heliophytic component (*Artemisia*, Poaceae, Amaranthaceae, *Erica*, *Ephedra fragilis*) increases in some episodes (IIb.1, IIb.2, IIIb.1, IV.1 and IV.3), but is never dominant in the landscape. The small vertebrate assemblages studied for units III and II also suggest a temperate, forested environment with local meadows (López-García et al., 2012).

Given that the studied pollen sequence covers numerous climatic fluctuations, as well as related changes in vertebrate biota, an open question remains regarding whether forest resilience at Teixoneres could be linked to the diversity of woody taxa, as suggested by Carrión (2003) and Thompson et al. (2009). Two similar cases of forest inertia, albeit with somewhat different taxonomic compositions, have been reported south of Teixoneres: namely, the Middle Pleistocene Neanderthal pollen sequence of Bolomor (Ochando et al., 2019), and the Upper Pleistocene to middle Holocene sequence of Navarrés (Carrión and Dupré, 1996; Carrión and van Geel, 1999; Carrión et al., 1999). The case of Teixoneres is nevertheless, outstanding: by counting the woody taxa of palaeobotanical sequences from the Iberian Pleistocene, this sequence emerges as highly diverse and ranks at the top of a comparative abundance chart (Figs. 8–9, S.I. Figs. II-V), surpassing in number of trees and shrubs other sites such as Gorham's Cave, Vanguard Cave, Navarrés, Bajondillo, Padul, and Sima de las Palomas, all located in Southern Iberia (Carrión et al., 2013). Biases related to microscope discrimination efforts might play some role in these patterns, but this cannot obscure the relevance of the Teixoneres palynological findings, which may well be linked to the pollen catchment area in the Eurosiberian-Mediterranean ecotone and its shifting range throughout the Pleistocene.

Doubtless, the cave is located in an ecologically sensitive region that is well-suited to recording latitudinal and altitudinal plant species migrations and competitive displacements, but with enough resilience to retain the woodland structure and composition through time. Bearing in mind the former, the existence of a forest refugium during the coldest and most arid stages of the upper Pleistocene is remarkable, as is the extraordinary abundance of *Quercus* at such a high latitude in the Iberian Peninsula. The high values of oak pollen, for example, during Teixoneres Units III, II and I, do not have an equivalent in any pollen sequence from the northern Iberian Peninsula during the MIS 4-MIS 2 interval (Carrión et al., 2015; González-Sampériz et al., 2010; Manzano et al., 2017), except during shorter intervals and with a more fluctuating pattern in the Area Longa, coastal Galicia (Gómez-Orellana et al., 2007), and Abric Romaní, sub-coastal Catalunya (Burjachs and Julià, 1994). Other Northern Iberia pollen sites with oak occurrence show considerably lower frequencies, such as Cova de L'Arbreda (Girona)

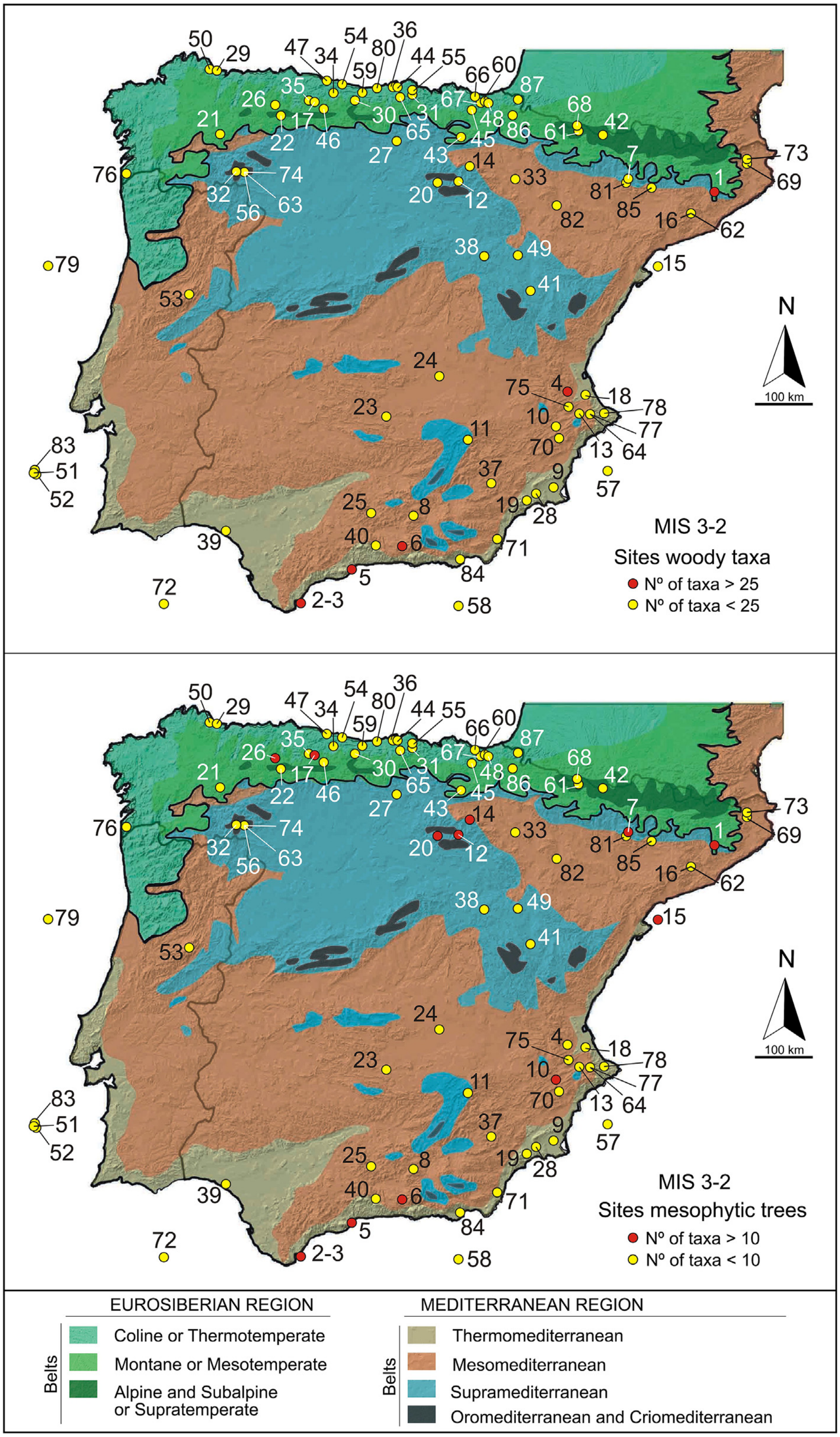

Fig. 8. Quaternary palaeoecological sequences of the Iberian Peninsula for the MIS 3 to MIS 2 interval. Sites with woody taxa are listed on the top map and sites with mesophytic trees appear listed on the map below. Teixoneres arises as the site with highest woody taxa and mesophytic trees diversity. Data obtained from Carrión et al. (2013).

(Burjachs, 1987; Burjachs and Renault-Miskovsky, 1992), Abric Romaní (Barcelona) (Burjachs and Julià, 1994), Pla de L'Estany (Girona) (Burjachs, 1994), Banyoles (Girona) (Pérez-Obiol and Julià, 1994), KEB 25 Delta del Ebro (Tarragona) (Yll, 1995), Cova del Parco (Lleida) (Bergadà et al., 1999), and Gabasa (Huesca) (González-Sampériz, 2004; González-Sampériz et al., 2003). Undoubtedly, there are similarly high oak values in late Pleistocene sequences from the southern Iberian Peninsula, such as Sima de las Palomas

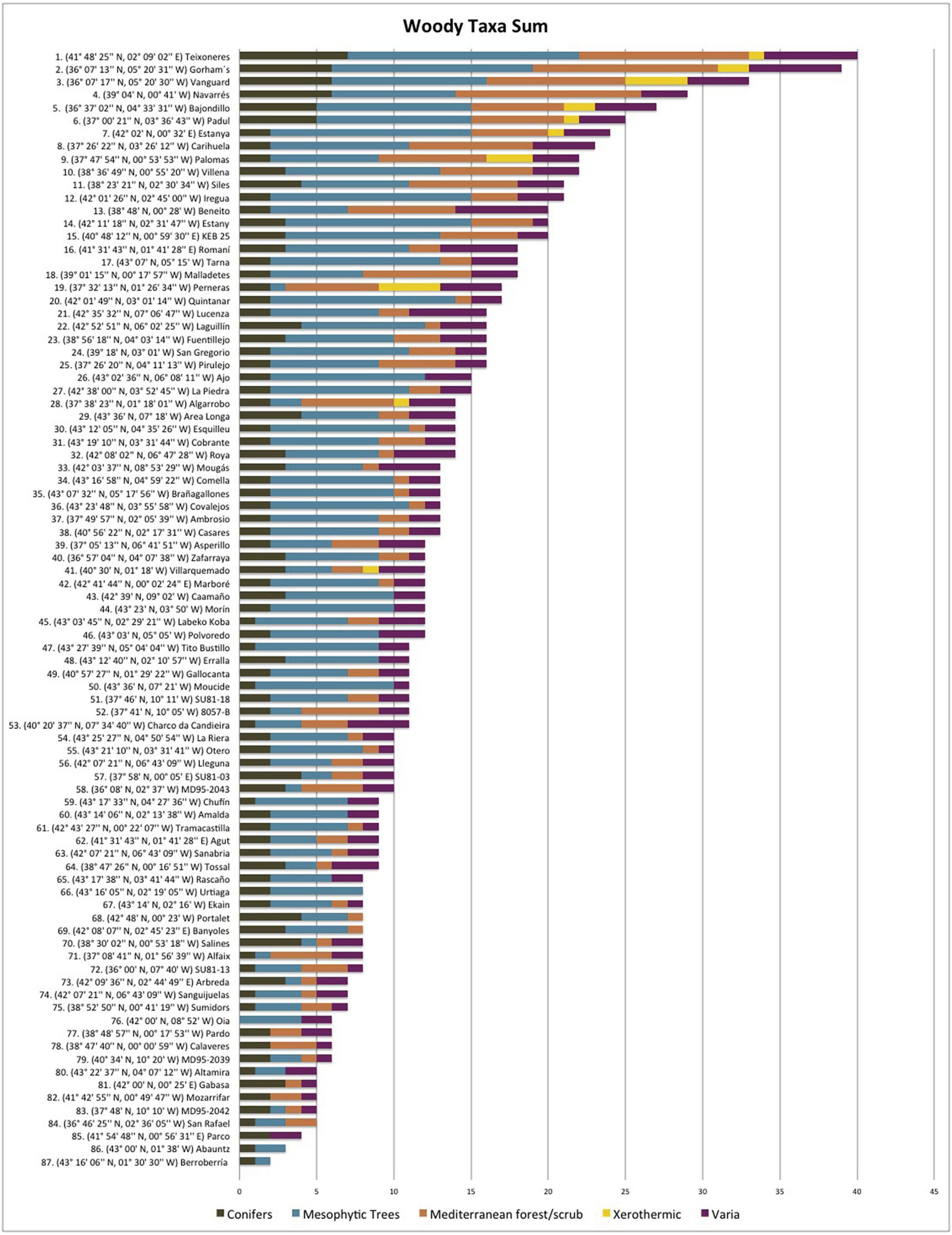

Fig. 9. Number of woody taxa, conifers, mesophytes, Mediterranean and xerothermics in Quaternary palaeoecological sequences of the Iberian Peninsula for the MIS 3-2 interval. Teixoneres arises as the site with highest woody taxa diversity. Data obtained from Carrión et al. (2013).

(Carrión et al., 2003b) and Cueva Perneras (Carrión and Dupré, 1994; Carrión et al., 1995) in the littoral zone of Murcia, San Rafael in the Almería littoral zone (Pantaleón-Cano et al., 2003), Bajondillo in coastal Málaga (López-Sáez et al., 2007), the Gibraltar Gorham's (Carrión et al., 2008) and Vanguard Caves (Carrión et al., 2018), some marine pollen sequence such as MD95-2043 (Fletcher and Sánchez-Goñi, 2008), and to a lesser extent Siles lake in the Segura Mountains of Southern Spain (Carrión, 2002). But definitively, the findings from Teixoneres confirm the hypothesis that scattered glacial strongholds existed within montane areas near the Pyrenees in Northern Spain (Manzano et al., 2017). This palaeoecological scenario is not much different to that of other European peninsulas (Bhagwat and Willis, 2008; Giardini, 2007; Lawson et al., 2004; Magri and Sadori, 1999; Magri et al., 2017; Margari et al., 2009; Pini et al., 2010; Sadori et al., 2008, 2016; Tzedakis, 1994, 1999; Tzedakis et al., 2002, 2003; Wagner et al., 2009, 2014; Willis, 1994), and Teixoneres may well be now regarded as an unique angiosperm forest reservoir during the last glacial stage in Northern Iberia.

9. Neanderthals persistence in Mediterranean-Eurosiberian forest ecotone

Interestingly, the studied pollen sequence site can be directly compared with Neanderthal occupation histories at Teixoneres, and the important connections between these past human groups and their ecosystem should not to be overlooked. Excavations in Teixoneres have shown a high faunal diversity with more than 20 species belonging to Carnivora, Proboscidea, Ungulata and small vertebrates, such as Leporidae, Aves, Amphibia and Squamate reptiles (Álvarez-Lao et al., 2018; López-García et al., 2012; Rufà et al., 2014, 2016). Among the large mammals, significant taxa include bear (*Ursus spelaeus*), hyaena (*Crocuta crocuta*), wolf (*Canis lupus*), fox (*Vulpes vulpes*), lynx (*Lynx spelaea*), badger (*Meles meles*), woolly mammoth (*Mammuthus primigenius*), woolly rhinoceros (*Coelodonta antiquitatis*), horse (*Equus ferus*), wild ass (*Equus hydruntinus*), red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), auroch (*Bos primigenius*), ibex (*Capra pyrenaica*), chamois (*Rupicapra pyrenaica*), and wild boar (*Sus scrofa*). It is also worth considering the added possibility of a broad spectrum of edible plants that likely grew in the vicinity, such as walnut (*Juglans regia*), hazelnut (*Corylus avellana*), chestnut (*Castanea sativa*), Mediterranean hackberry (*Celtis australis*), carob tree (*Ceratonia siliqua*), holly oak (*Quercus ilex*), olive (*Olea europaea*), elderberry (*Sambucus nigra*), and probably wild Rosaceae.

Climate has always been considered as an influential factor involved in biogeographical reordering. Thus, several authors consider that climate must have played a role in Neanderthal extinction (Burjachs and Julià, 1996; Djindjian, 1993; Mellars, 1992; Zilhão, 1993). In this context, d'Errico and Sánchez-Goñi (2003) designed a climate driven model for the extinction of Iberian Neanderthals based on millennial-scale palaeovegetation data and palaeoclimatic models that play down the influence of anatomically modern humans. Elsewhere, Finlayson et al. (2004) point out that the whole issue of Neanderthal extinction may be addressed from an ecological and palaeoclimatic perspective. Climatic and ecological challenges at sub-millennial scales had a substantial impact on Neanderthal communities during MIS 3, affecting the availability of food resources, changing distributions of plant and animal communities, and forcing costly and repeated mobility and changes in dietary habits (El Zaatari et al., 2016; Hodgkins et al., 2016).

The recent work of Stewart et al. (2019) puts into question whether Neanderthals were specialised hunters of woodlands that necessitated a rapid turn of speed. These authors postulate that North European Neanderthals were particularly adapted to the conditions of temperate episodes, such as MIS 5e or the warmer MIS 3 interstadials (e.g., GI12), during which a wooded landscape and rich faunal diversity existed. Stewart et al. (2019) contend that Neanderthal hunting strategies were more likely to have been an encounter or ambush style than pursuit hunting, which involves a power mode of locomotion, such as sprinting, rather than an endurance-based long distance running pursuit mode. The idea that Neanderthals were woodland hunters has also been suggested by earlier authors (Stewart, 2005; Finlayson and Carrión, 2006, 2007) and more recently by Rosas (2016), Carrión et al. (2018) and Carrión and Walker (2019). This closed forest environment could have favored Neanderthal hunting strategies, as evident at Bolomor cave (Ochando et al., 2019). Similarly, Neanderthal hunter-gatherers adopted complex and variegated settlement strategies, showing good adaptations to a wide range of environments, but also different cultural expressions (Spagnolo et al., 2019). Likewise, there is evidence that Neanderthals were highly knowledgeable of their environment, including in their diet, which incorporated both small prey, such as turtles (Nabais and Zilhao, 2019), and large raptors, such as the Golden Eagle (Stewart et al., 2019). That said, Spikins et al. (2019) suggests that pressures from predation and hunting in difficult terrain will also have led to risks of injury and mortality in even the most favourable environments.

At Vanguard cave, the geological, floristic and faunal repertoire is of outstanding richness and suggests coastal platforms occupied by a vegetation mosaic with an extensive biome of "Mediterranean savannah" (Carrión et al., 2018; Finlayson et al., 2011). The Neanderthals who occupied this coastal environment were omnivorous, ambush hunters, including among their prey marine animals and numerous birds (Finlayson and Carrión, 2006, 2007). Together the regional paleovegetation picture has important implications for existing arguments about the long survival of Neanderthals in the Iberian Peninsula (Carrión, 2004; Finlayson and Carrión, 2007; Higham, 2014; Jiménez-Espejo et al., 2007; Stewart, 2005; Wood et al., 2013; Zilhão et al., 2017).

One of the possible reasons for the disappearance of Neanderthals in the south of the Iberian Peninsula might be the loss and fragmentation of forests, which were mainly composed of oaks and coniferous woodlands, as documented at Carihuela cave (Carrión, 1992; Carrión et al., 1998, 2019). In eastern Spain, a climatic deterioration from temperate and wet conditions to more arid climate has been documented at El Salt site, Alcoi (Fagoaga et al., 2019). In this region, it is hypothesized that the end of the Middle Palaeolithic corresponded to serious climatic deterioration, which lead to sparse vegetation cover that would have affected the availability of key resources for Neanderthals. That said, mediterranean influences could have played an important role in softening the extent of this climate deterioration compared to other regions of the Iberian Peninsula. Pollen studies carried out at Abric Romaní (Biltekin et al., 2019) reveal the continuous occurrences of *Olea* with *Quercus ilex/coccifera* during MIS 5, which is related to mediterranean wood refugia that may have survived in the surrounding mountain valleys of the study region. Similarly, during MIS 3, taxonomic and taphonomic studies suggest that the charcoal assemblage mainly belongs to the *Pinus sylvestris* type, providing insights into Neanderthal fuel acquisition strategies, mobility and occupation patterns in the region (Allué et al., 2017a). Though not related to a closed forest setting, charcoal studies carried out at Abrigo de la Quebrada (Carrión-Marco et al., 2019) show the dominance of *Pinus sylvestris*, and to a lesser extent *Pinus nigra*, together with other thermophilous and xeric bio-indicators such as *Pinus halepensis*, *Pinus pinea*, *Ephedra*, *Juniperus*, Fabaceae and *Olea* *europaea*, which would have found refuge in the southernmost parts of the peninsula only. The charcoal study from Abric del Pastor (Connolly et al., 2019) reveals mixed forest taxa in units that exhibit decreasing values of juniper. The presence of these taxa, with different ecological requirements to juniper, point to the existence of a local vegetation refugium, composed of several biotopes, providing sufficient tree and shrub cover for Neanderthal groups to thrive, as well as an abundant and diverse source of woody biomass that could have been exploited as fuel. Defleur and Desclaux (2019), describe a deciduous forest environment at Baume Moula-Guercy, Ardèche, France. The vegetation is characteristic of a temperate climate similar to that of the present, although it includes wired broadleaf, which is typically a Mediterranean species. Rapid climate warming at the end of MIS 6 led to the development of a thick deciduous forest throughout the continent, including the northern areas previously occupied by glaciers and permafrost (Gaudzinski-Windheuser et al., 2014). The palaeoenvironmental reconstruction reported by Daura et al. (2017) for Cova del Coll Verdaguer indicates that floristic and faunal elements were initially related to open meadows at the base of the sequence. Subsequently, the arboreal component increased from the base to the top of the sequence, signalling the development of closed forest or woodland conditions. The results of this multi-proxy analysis are an important source of information for gaining a better understanding of the environmental conditions at the beginning of MIS 3 and, hence, of their relationship with the last Neanderthal populations on the peninsula.

Overall, the vegetation record for northeastern Iberian Peninsula during MIS 3 (Allué et al., 2017b; Carrión, 2002; Daura et al., 2013; González-Sampériz et al., 2010) points to a landscape dominated by conifers (*Pinus sylvestris* type and *Juniperus*) in association with components of evergreen and deciduous species (*Quercus*, *Corylus*, *Betula*, *Castanea*, *Juglans*, *Alnus*, *Tilia*, *Buxus*, *Acer*, *Sorbus domestica*, *Rhamnus*, *Prunus*, *Fagus*, *Fraxinus*, *Populus*, *Salix*). The results from Teixoneres cave match the records of other Pleistocene sites (e.g. Abric Romaní, Cova de l'Arbreda, Cova Gran, Terrasses de la Riera dels Canyars, Cova del Coll Verdaguer), for which charcoal and pollen data indicate the predominance of arboreal vegetation coverage (Allué et al., 2017a; Burjachs et al., 2012; Daura et al., 2017). The new palynological study of Teixoneres cave therefore reinforces the ongoing shift towards a better understanding of the adaptation and persistence of Neanderthals in forested environments within Mediterranean-Eurosiberian forest ecotones.

The Teixoneres record reveals a landscape that offered a broad and constant spectrum of possibilities for past human populations occupying the cave during its sedimentary infilling history (198-35 ka). The diversity of animal remains that exhibit evidence of anthropogenic processing suggests varied subsistence strategies, which probably would have also included an important component of plant community resources. The archaeological evidence also indicates significant changes in occupational strategies over time, not only regarding the presence of human groups in the cave, but also in the surrounding territory. Unit IIIb (50-45 ka), for example, shows a certain territorial stability characterized mainly by the exploitation of local raw materials. In contrast, the lithic assemblage from the upper units (45-35 ka) is made mainly on allochthonous raw materials, suggesting significant mobility of groups among territories (Bustos-Pérez et al., 2017; Picin et al., 2020). From this perspective, the changes in human behaviour do not seem to be influenced in a significant way by the ecologic characteristics of the region and, therefore, may be related to cultural or genetic factors. Teixoneres Cave could fit with the hypotheses suggested by some researchers that the decline of Neanderthal populations in the Iberian Peninsula was not directly related to environmental changes or contact (or acculturation) with the first populations of anatomically modern humans (Mallol et al., 2012). However, more research is necessary at a range of sites to advance this debate further. This study has revealed, from a palynological perspective, the specific environments inhabited by the Neanderthal groups of Teixoneres Cave. These Neanderthal populations were undoubtedly experts of forested ecosystems, possessing highly adaptive subsistence strategies that enabled them to exploit the benefits offered by a diverse and rich environment.

CRediT authorship contribution statement

Juan Ochando: Methodology, Software, Formal analysis, Investigation, Writing - original draft, Visualization. **José S. Carrión:** Conceptualization, Methodology, Validation, Investigation, Resources, Writing - original draft, Visualization, Supervision. **Ruth Blasco:** Conceptualization, Resources, Writing - review & editing, Supervision. **Florent Rivals:** Resources, Writing - review & editing. **Anna Rufà:** Resources, Writing - review & editing. **Martina Demuro:** Formal analysis. **Lee J. Arnold:** Formal analysis. **Gabriela Amorós:** Data curation, Visualization. **Manuel Munuera:** Software, Visualization. **Santiago Fernández:** Software, Data curation, Writing - original draft, Visualization. **Jordi Rosell:** Conceptualization, Resources, Writing - review & editing, Supervision.

Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.quascirev.2020.106429.

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