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An environmental scenario for the earliest hominins in the Iberian Peninsula: Early Pleistocene palaeovegetation and palaeoclimate

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ABSTRACT

The Early Pleistocene deposits of the Iberian Peninsula provided some of the oldest hominin fossil sites of Western Europe. Evidence also shows that early *Homo* thrived in the Mediterranean peninsulas during the Early Pleistocene 'interglacial' phases. To assess the role of climatic conditions on early human environments, the present work features a quantitative palaeoclimatic analysis for a number of Early Pleistocene macroflora and pollen assemblages located at different geographical locations where hominin activity has been recorded. The results picture a cyclic climate with a possible latitudinal aridity gradient. Warm and humid ('interglacial') phases would have been wetter and slightly warmer than the modern climate. During cooler and drier ('glacial') phases, temperature and precipitation were comparatively milder and more similar to modern ones. The favourable conditions during the humid phases may have allowed for the earliest hominin communities arriving in Europe to rapidly thrive during 'interglacial' periods. The present climatic quantification suggests that hominins in Iberia may have survived these mild 'glacial' Early Pleistocene stages.

1. Introduction

In the Early Pleistocene, about 42 global climatic cycles have been recorded as marine isotope stages (MIS 104–MIS 19; Lisiecki and Raymo, 2005). In Europe, these cycles forced subsequent vegetation successions, generally from open vegetation to dense forests and back (Leroy and Ravazzi, 1997; Leroy et al., 2011). Overall, in the Iberian Peninsula, forests developed during the warm and humid 'interglacial' phases, whereas, during the cold and dry 'glacial' phases, open landscapes and open-forests became widespread (González-Sampériz et al., 2010; Postigo-Mijarra and Barrón, 2017). Because the Early Pleistocene did not experience true, eccentricity-driven glacial phases like the later Pleistocene, but weaker and shorter cold periods which generally did not allow large-scale ice-sheet development outside the polar regions (Ehlers and Gibbard, 2008), it is strongly suggested to use the terms glacial and interglacial with caution for Early Pleistocene obliquity driven climatic cycles. Putting the terms in quotation marks stresses this caution, following Klotz et al. (2006).

Palaeobotanical data of the Iberian Early Pleistocene are mainly provided by palynological studies (e.g. Diniz, 1972; Geurts, 1977, 1979; Suc, 1980; Antunes et al., 1986; García-Antón and Sainz-Ollero, 1991; Leroy, 1988, 1997, 2008; Leroy et al., 2001; García-Antón et al., 2002; Rodríguez et al., 2011), and to a lesser extent, macrobotanical research, like the sites of Crespià (De Villalta and Vicente, 1972; Roiron, 1983, 1992), Caranceja (Alcalde-Olivares et al., 2004) and Cal Guardiola (Postigo-Mijarra et al., 2007; 2008). All these studies are an important source of knowledge to understand the oldest Quaternary history of vegetation and climate in the Iberian Peninsula (see Carrión et al., 2013 for compilation). For instance, they provide dates for the last occurrence of a significant number of plant taxa from the Iberian fossil record including *Aesculus*, Araliaceae (non-*Hedera*), *Cathaya*, *Elaeagnus*, *Engelhardia*, *Eucommia*, *Liquidambar*, *Keeteleria*, *Nyssa*, *Sciadopitys*, *Parrotia*, *Parthenocissus*, *Pterocarya* and *Tsuga* (Postigo-Mijarra et al., 2010). Even during the Last Glacial Maximum, the Iberian Peninsula was also a refuge for warmth-loving deciduous trees (Leroy and Arpe, 2007; Arpe et al., 2011).

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The hominin fossil record across the western Palaearctic during the Early Pleistocene (2.6–0.78 Ma; MIS 103–MIS 19) is very scant (Carrión et al., 2011). The oldest evidences are traced to *Homo erectus* and can be traced back to 1.4 Ma (Agustí and Lordkipanidze, 2011; Duval et al., 2011a, 2012; Toro-Moyano et al., 2011, 2013). However, the relationship between early *Homo* and the Early Pleistocene climate is still not clear (Agustí et al., 2009; Cuenca-Bescós et al., 2011; Dennell et al., 2011; Leroy et al., 2011; Bermúdez de Castro and Martinón-Torres, 2013), Kahlke et al. (2011) and Carrión et al. (2008, 2011), among others, indicate that human fossil and archaeological sites occur preferentially in situations with high diversity of habitats and resources. Leroy et al. (2011) have suggested a climatic envelope including all Early Pleistocene hominin sites. According to their model, all sites are situated in a confined climatic range. Temperatures show very few days of frost, but distinctively cold winters, with especially narrow limits of the minimum temperature of the coldest month between 0 and 6 °C. Precipitation data reveal no summer drought and summer precipitation between 30 and 60 mm/month. This climatic envelope places the presence of hominins in 'interglacials' periods. Their arrival in Iberia would probably occur only at the beginning of 'interglacials', when the vegetation was still sufficiently open to allow the grazing of large herbivore herds, i.e. their source of food, and when the climate was already warm enough for these African mammals (Leroy et al., 2011).

The Iberian Peninsula is an important region in the contexts of hominin evolution, adaptation and dispersal taking into account the presence of very significant sites like Orce (in the Baza Basin) and Atapuerca, where some of the oldest and most complete records of their presence can be found. For this reason, a detailed knowledge of climatic trends and patterns in the Early Pleistocene is crucial for the understanding of the appearance and migration of hominin populations in the Iberian Peninsula. Quantitative data have already suggested mild climatic requirements for hominins in Iberia (Leroy et al., 2011; Agustí et al., 2018). However, quantitative climate data for the Early Pleistocene are rare, except a limited number of studies based on a range of methodologies such as the Coexistence Approach (Alcalde-Olivares et al., 2004), the Mutual Climatic Range (Blain et al., 2009, 2010, 2011 and 2016) and the Climatic Amplitude Method (Leroy et al., 2011). The sites that provide botanical data are often not dated accurately nor are they contemporaneous for the most part. Because of this, a correlation of the climate between different geographical points at any given point in time has not been conducted so far. Therefore, the aims of the present paper are: (1) to reconstruct and quantify the Iberian Early Pleistocene palaeoclimate using the Coexistence Approach (CA) method, (2) to infer palaeoenvironments along this period and, (3) to evaluate the possible relationships between these palaeoenvironments and the first hominin communities in the Iberian Peninsula.

2. Material and methods

An exhaustive palaeobotanical review of the literature, published from the seventies to present, referring to the Early Pleistocene of the Iberian Peninsula was undertaken. The sites considered for this study correspond to drill cores and surface outcrops located in three regions of Spain (Fig. 1, A and B). In northeastern Spain, the site and core sections of Banyoles-Besalú Basin (drill cores of Tres Pins II, Bòvila Ordis IV and open quarry of Crespiá) (42° 07′N, 2°45′E) and the section of the Cal Guardiola site (41°34′N, 2°00′W). In north-central Spain, Sierra de Atapuerca, which contains the section of Gran Dolina (42°21′N, 3°32′W). Finally, in southeastern Spain, the Baza Basin contains the drill section of Palominas (37° 29′ 20″N, 2° 46′ 16″W).

Data from the upper part of the marine borehole Garraf 1 (MIS 109–MIS 98; Suc and Cravatte, 1982) has been discarded because of the high possibility of reworked pollen in its assemblages. The Caranceja site (Alcalde-Olivares et al., 2004) is excluded due to its uncertain stratigraphy. Data from Molí Vell I section (Geurts, 1977, 1979) are not included due to their low taxonomic resolution. The Portuguese sites of Pampilhosa do Botão, Morgadinho and Algoz (Diniz, 1972; Antunes et al., 1986) were also disregarded because they provide low numbers of taxa and have an uncertain stratigraphy. Pollen sections from marine boreholes (Combourieu Nebout et al., 1999; Oliveira et al., 2017) have been left out to avoid the problem of long-distance transport and the mixture of pollen from widely different geographical sources. The time scale used for the Early Pleistocene follows the proposals of the International Commission on Stratigraphy, ICS (Cohen and Gibbard 2016).

Palaeoclimatic conditions were determined by using the CA method for a quantitative estimation of various climatic parameters. The CA is based on the assumption that since the Neogene the climatic requirements of fossil plant taxa are similar to those of their nearest living relatives (NLRs). For each climatic parameter separately, the CA defines the climatic ranges in which a maximal number of NLRs of a given fossil flora can coexist. Those climatic ranges, the 'coexistence intervals', are considered the best description of the palaeoclimatic situation under which the given fossil flora lived (Mosbrugger and Utescher, 1997; Utescher et al., 2000, 2014). While the justification of using modern climatic requirements of NLRs of Neogene plants to infer quantitative

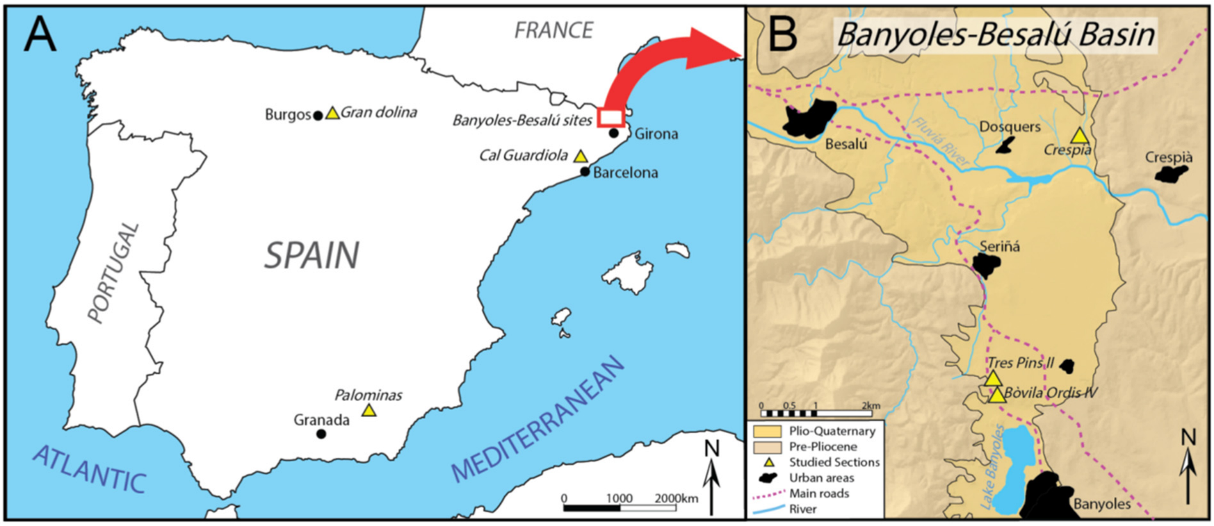

Fig. 1. (A) Locations of the studied sites and within the Iberian Peninsula. (B) Simplified map of the Banyoles-Besalù Basin with the specific locations of the studied sites, simplified geology and urban areas (modified from Barnolas et al., 1994).

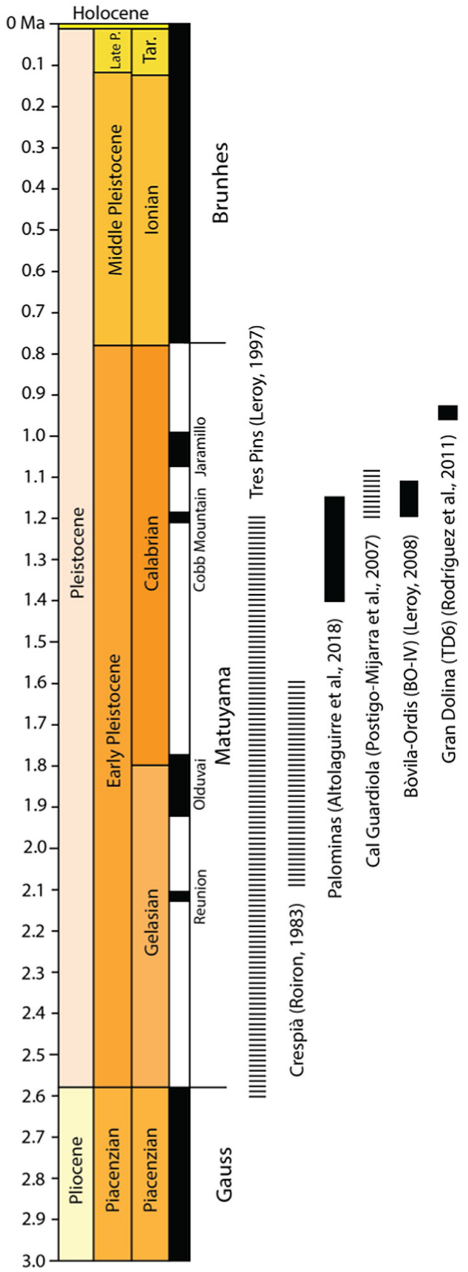

Fig. 2. Age ranges for the Early Pleistocene sites studied in this work. Stratigraphic scheme and chronological frame after Cohen and Gibbard (2016). The reference for each age model is given in the figure. Well-dated sections are represented by black solid marks; uncertainly dated sections are presented by discontinuous black marks.

palaeoclimatic values has been questioned by some authors and for specific environmental conditions (see discussion and defence of the method in Grimm and Denk, 2012; Utescher et al., 2014; Grimm and Potts, 2016), the application of the method on Quaternary assemblages is robust since changes of environmental requirements between modern plants and their Quaternary counterparts are regarded minimal (Utescher et al., 2014; Grimm and Potts, 2016). The CA takes the presence–absence information of a taxon into account. The advantage of this is its applicability to all types of plant fossils, like pollen and leaf assemblages in this study, and the comparability of results. On the other hand, climatic changes that are merely expressed in variations of taxon abundances cannot be detected and are encompassed by the coexistence intervals. The application of the CA is facilitated by the computer program ClimStat and the database PALAEOFLORA, which contains climatic requirements of more than 1800 extant plant taxa. The climatic data used in the present study is collected in the supplementary material. The data are derived from meteorological stations located within the distribution area of the respective taxon and comprise seven climatic parameters; mean annual temperature (MAT), mean temperature of the coldest month (MTCold), mean temperature of the warmest month (MTWarm), mean annual precipitation (MAP), mean precipitation of the wettest month (MPWet), mean precipitation of the driest month (MPDry), and mean precipitation of the warmest month (MPWarm) (for details see www.palaeoflora.de and supplementary information).

In all datasets compiled for analysis here, palynomorphs were usually identified at genus level and, when possible, at species level. Some of them were identified only at family level, as is common practice in palynology (e.g. Pinaceae, Poaceae, Cyperaceae). Macroremains are usually identified at species level. For the application of the CA, some taxa had to be excluded from the analysis, i.e. those for which no climatic data were available (e.g. *Equisetum*, Caryophyllaceae, Poaceae, Asteraceae), monotypic genera such as *Cathaya*, and *Sciadopitys* considered as outliers (see Utescher et al., 2014), and azonal hygrophytes such as *Potamogeton* or *Thelypteris*. For pollen assemblages, also single grain occurrences were excluded from the climatic calculations due to the possibility of long-distance transport or contamination. For all assemblages analysed applies that no climatic inferences have been made if the number of taxa is below 10. If the number of taxa available for analysis is lower than 10–15, the coexistence interval obtained can be very wide, and consequently the climatic information that can be extracted is limited (Mosbrugger and Utescher, 1997).

In total, 385 palynological samples and two macrofloristic assemblages (level D2 of Cal Guardiola site and the calcarenites of Crespià) were considered for the CA analysis. More than 10 taxa with climate information are available for both macrofloras and 216 pollen samples (3 from Gran Dolina, 32 from Palominas, 1 from Cal Guardiola, 63 from Tres Pins, 115 from Bòvila Ordis and 2 samples from Crespià). Only those have been considered for further analyses.

3. Geographic and geological settings

Six Early–Middle Pleistocene sites, located in three different areas of the Iberian Peninsula (Fig. 1, A and B), have been analysed in this work. In order to construct a comprehensive and integrative analysis, the general setting and dating for each section is presented. A compilation of age models for each site can be found in Fig. 2. Modern measurements for temperature and precipitation parameters are compiled in Table 1. These values were obtained from the meteorological stations closest to the fossil sites (MAPAMA, 2017).

Table 1
Modern values of climatic parameters for the different study regions; obtained from the database of the Agrarian Geographic Information System (SIGA) (MAPAMA, 2017).

Section	Meteorological station	MAT (°C)	MTWarm (°C)	MTCold (°C)	MAP (mm)	MPWet (mm)	MPDry (mm)	MPWarm (mm)
Gran Dolina	Burgos “Villafría”	10.2	18.9	2.8	537.4	57.2	23.8	23.8
Palominas	Baza “Instituto técnico”	13.2	24.0	4.9	366.4	44.4	6.8	6.8
Cal Guardiola	Tarrasa “Plaza de la Cruz”	15.2	24.0	8.4	623.0	73.9	25.5	25.5
Banyoles-Besalù	Foncoberta “L'Angada”	15.0	24.0	7.3	783.9	95.6	38.9	51.4

3.1. *The Gran Dolina site*

The Gran Dolina fossil site is an 18 m thick cave infill, at an altitude of about 1000 m a.s.l., found at the Trinchera del Ferrocarril (Sierra de Atapuerca) (Fig. 1, A). These karstic deposits, located 15 km east of Burgos, have a stratigraphic succession divided into 11 units: TD1-TD11 from bottom to top (Gil et al., 1987; Parés and Pérez-González, 1999). The discovery of the Matuyama-Brunhes boundary, detected between TD7 and TD8, allows for the division of the cave record into Early Pleistocene (TD1–2 to TD7) and Middle Pleistocene (TD8 to TD11) (Parés and Pérez-González, 1999). Gran Dolina is one of the most important sections of Atapuerca owing to the discovery of *Homo antecessor* in the TD6-2 subunit (Bermúdez de Castro et al., 1997, 2008). TD6 level has been dated as 0.936 Ma (Falguères et al., 1999; Parés et al., 2013).

3.2. *The Palominas section*

The section of Palominas (Baza Basin) was obtained from the Palominas drill core (Gibert et al., 2015), at an altitude of about 780 m a.s.l., located 15 km northeast of the town of Baza (Granada) (Fig. 1, A). Baza Basin, part of the bigger Guadix-Baza Basin, was endorheic during the Pliocene and Early Pleistocene and developed a lacustrine system that led to the deposition of evaporites and fine sediments (Gibert et al., 2007). Pollen data for the CA calculation come from the upper 60 m of the original core. The lower levels of the section were correlated to MIS 43 (1.4 Ma) by magnetostratigraphy and correlation of palynological, geophysical and geochemical data to the LR04 oxygen stack (Gibert et al., 2015). The lower boundary of the Jaramillo reversal (1.1 Ma) was found in the outcropping layers immediately next to the drilling site (Gibert et al., 2015). These dates give the Palominas section a time span of approximately 0.3 million years (Fig. 2), during which, several climatic cycles can be recorded. Baza Basin harbours several sites with evidence of human activity, most importantly: Barranco León, Fuente Nueva-3 and Venta Micena, all of them located in the northeastern border of the basin, near the locality of Orce. These sites have provided mostly lithic industry and few bone remains (Gibert et al., 1983; Martínez-Navarro et al., 1997; Toro-Moyano et al., 2011). Both, Barranco León and Venta Micena have been dated around 1.4 Ma (Duval et al., 2011a), while Fuente Nueva-3 has been dated as 1.2 Ma (Duval et al., 2012). One of the most exceptional finds comes from Barranco León, where a deciduous molar associated with *Homo erectus* was found. It would represent one of the earliest proofs of human presence in Western Europe (Toro-Moyano et al., 2013). The age constrains of the Palominas drill core and the dating of the hominin sites do not allow for a direct correlation. Nevertheless, the Palominas section covers the time of deposition of the hominin-bearing layers; hence the climatic data obtained from the core material can provide evidence for the environmental dynamics during the time span of hominin presence.

3.3. *The Cal Guardiola site*

The Cal Guardiola site is situated in the tectonic trough of the Vallés-Penedés region (Barcelona province, Catalan Ranges, c. 310 m a.s.l.) (Postigo-Mijarra et al., 2007) (Fig. 1, A). Its stratigraphic section is composed of several strata with a total thickness of 5.5 m. These were formed as the result of successive alluvial fans alternating with different sedimentary units (Berástegui et al., 1997). Magnetostratigraphic analysis and micromammal remains suggest an age for the Cal Guardiola site between 1.2 and 0.8 Ma (Fig. 2) (Postigo-Mijarra et al., 2007). Fossilised wood, pollen, coprolites and bones were extracted from the D2 level, a sedimentary unit 0.4–1.2 m thick. The sedimentary body that contains Cal Guardiola also accommodates the fossil site of Vallparadís (Madurell-Malapeira et al., 2010), both situated less than 100 m from each other. The site of Vallparadís contains an extensive record of faunal remains and lithic industry. The lithic assemblage is accompanied with bones bearing human-generated cut marks and fractures. The archaeological material was found in layer 10, which has been dated by ESR to 0.8 Ma (Martínez et al., 2010; Duval et al., 2011b). Magnetostratigraphic correlation suggests an age for the D2 layer of Cal Guardiola older than the base of Jaramillo (1.07 Ma) (Madurell-Malapeira et al., 2010).

3.4. *The Banyoles-Besalú sites*

The Plio-Pleistocene basin of Banyoles-Besalú is located 10 km north of Girona (Northern Spain) (Fig. 1) at an altitude of about 100–200 m a.s.l. This satellite basin is separated from the greater Empordà Basin to the West by tectonically elevated deposits of Neogene age. Both basins were generated during extensional faulting of the eastern Pyrenees during the Neogene (Barnolas et al., 1994). Being surrounded by pre-Quaternary geomorphological units, the Banyoles-Besalù developed an endorheic lacustrine complex. This complex reached northward as far as the localities of Besalú and Crespià and southwards as far as the present Lake Banyoles. It comprised several lakes originated due to karstic activity and the dissolution of Eocene gypsum layers below the Pliocene deposits (Julià, 1980). The sections of Tres Pins II, Bóvila Ordis IV and

Table 2
Coexistence intervals for each site, number of taxa used in brackets. For the sections of Baza, Tres Pins and BO-IV the number of taxa used (in brackets) is an average. Intervals for Baza, Tres Pins and BO-IV were selected to exemplify the differences between climate phases. Intervals composed of two competing intervals are marked by asterisks; the climatic implications of these intervals are discussed in the text. Intervals in red are above the modern value for that climatic parameter. Intervals in blue are below the modern value.

Section	MAT (°C)	MTWarm (°C)	MTCold (°C)	MAP (mm)	MPWet (mm)	MPDry (mm)	MPWarm (mm)
Gran Dolina (20)	10.0–22.1	19.9–28.3	0.4–13.3	373–1741	48/68 –293	3–71	5/15–178
Palominas humid phase (14.5)	10–21.4	19.3–28.3	0.4–10.9	473–1958	81–336	3–72	72–214
Palominas dry phase (11.0)	11.6–18.3	18.8–28.1	0.4–13.3	224–1096	48–220	1–45	5–122
Cal Guardiola pollen (44)	13.9–19.2*	22.5–23.8	9–9.1	473–854	80–122	8–29	20–54*
Cal Guardiola macro (12)	7.4–16.4	17.8–26.4	-4.4–9.2	550–1333	78–170	9–47	9–86
TP-II humid phase (12.0)	10.6–19.4	20.2–28.3	-5.6–9.6	705–1724	108–358	8–64	108–258
TP-II dry phase (11.3)	4.4–21.3	19.3–28.1	-11.5–13.6	373–1724	68–293	8–45	45–221
BO-IV humid phase (10.9)	10.6–21.7	20.2–28.3	-5.6–15.1	641-1724	108-424	8-93	108-258
BO-IV dry phase (10.8)	10.6–20.5	19.3–28.3	-5.6–13.6	453–1724	68–293	8–64	45–221
Crespià pollen middle (17)	11.7–17.4	19.9–26.1	0.4–5	473–1217	71–159	3–8	15–116
Crespià pollen lower (13)	11.7–19.5	19.9–26.1	1–13.3	399–1356	71–159	-2–41	5–92
Crespià macroflora (29)	13.7–15.2	23.8–25.5	4.9–8.9*	563–741*	77–111	23–24	23–70*

Table 3
List of taxa responsible for the coexistence intervals of temperature parameters shown in Table 1. (E) = evergreen, (D) = deciduous, (i-c) = ilex-coccifera type.

Section	MAT Min.	MAT Max.	MTWarm Min.	MTWarm Max.	MTCold Min.	MTCold Max.
Gran Dolina (20)	*Olea*	*Quercus*(E)	*Olea*	*Quercus*(D)	*Quercus*(E)	*Quercus*(E)
Palominas humid phase (14.5)	*Olea*	*Sanguisorba*	*Olea*	*Quercus*(D)	*Quercus*(i-c)	*Carpinus orientalis*
Palominas dry phase (11.0)	*Cedrus*	*Carpinus orientalis*	*Quercus*(i-c)	*Centaurea*	*Quercus*(i-c)	*Quercus*(i-c)
Cal Guardiola pollen (44)	*Lygeum*	*Polygonum persicaria*	*Chamaerops*	*Filipendula*	*Chamaerops*	*Polygonum persicaria*
Cal Guardiola macro (12)	*Acer pseudoplatanus*	*Acer pseudoplatanus*	*Aesculus hippocastanum*	*Acer campestre*	*Acer pseudoplatanus*	*Aesculus hippocastanum*
TP-II humid phase (12.0)	*Eucommia ulmoides*	*Eucommia ulmoides*	*Eucommia ulmoides*	*Quercus*	*Hedera*	*Eucommia ulmoides*
TP-II dry phase (11.3)	*Carya*	*Populus*	*Carya*	*Centaurea*	*Carya*	*Populus*
BO-IV humid phase (10.9)	*Eucommia ulmoides*	*Picea*	*Eucommia ulmoides*	*Quercus*	*Hedera*	*Tsuga*
BO-IV dry phase (10.8)	*Eucommia ulmoides*	*Hedera*	*Carya*	*Quercus*	*Hedera*	*Hedera*
Crespià pollen middle (17)	*Cedrus*	*Quercus*(i-c)	*Olea*	*Quercus*(i-c)	*Quercus*(i-c)	*Parrotiopsis jacquemontiana*
Crespià pollen lower (13)	*Cedrus*	*Quercus*(i-c)	*Olea*	*Quercus*(i-c)	*Phillyrea*	*Quercus*(i-c)
Crespià macroflora (29)	*Quercus faginea*	*Tilia tomentosa*	*Laurus nobilis*	*Tilia tomentosa*	*Quercus faginea*	*Quercus cerris*

Crespià, included in the present study, come from the lower Pleistocene deposits of the Banyoles-Besalú Basin.

3.4.1. Tres Pins II

The Tres Pins II (TP-II) section (Leroy, 1997) comes from a drill core, 27 m long, located 3 km northwest of the city of Banyoles (c. 210 m a.s.l.) (Fig. 1, B). The Tres Pins II sequence shows short hiatuses in the sedimentary record, probably due to karstic activity, faulting or erosion of the lake floor during episodes of low water level. The presence of hiatuses created abrupt changes between some of the pollen zones. Although no precise dating of the section can be proposed so far, its palynological association is typical of the Early Pleistocene (2.6–1.2 Ma). The time interval represented by the sediment is likely to be of c. 30 kyr.

3.4.2. Bòvila Ordis IV

The Bòvila Ordis sections are composed of three different sections each one representing independent lake environments separated by normal faults and karstic activity. The section lies near Banyoles (c. 190 m a.s.l.) (Fig. 1, B). Lake 1 is the oldest one and is represented by the BO-IV sequence, dated at the Cobb-Mountain subchron (1.2 Ma) (Leroy, 2008). Lake 2 is younger and represented by the BOC-III and BOC-IV sequences (Leroy, 1988, 1990) while the third and youngest lake system is represented by the BO-III sequence (Leroy 1987, 1990). The present study includes sequences from the first two lakes represented in BO-IV. The BO-IV section was obtained by drilling into a limestone hill near the drilling site of Tres Pins II and near the Ordis clay quarry. This sedimentary record is 52 m long and it is interrupted by two hiatuses linked to bank collapse due to bioturbation or tectonic activity. The Cobb-Mountain subchron of normal polarity has been recorded in the BO-IV sequence between 16.7 and 4.05 m. This places the BO-IV section around an age of 1.2 Ma (Løvlie and Leroy, 1995; Leroy, 2008).

3.4.3. The Crespià site

Finally, the Crespià site (c. 150 m a.s.l.) is located at the northeastern margin of the Banyoles-Besalù depression, in a quarry that cuts through lacustrine carbonate sediments composed of resedimented travertine levels (Fig. 1, B). Apart from a rich mammal fauna the site has provided well-preserved leaf imprints studied by De Villalta and Vicente (1972) and Roiron (1983, 1992). The site is estimated to have been formed somewhere between 2.1 and 1.6 Ma (Roiron, 1983).

4. Results

Detailed results with values of coexistence intervals for each climatic parameter and each section, as well as the limiting taxa responsible for each value are given in Tables 2–4. The results for the long sections of Palominas, Tres Pins II and Bòvila Ordis IV are also visualised

Table 4
List of taxa responsible for the coexistence intervals of precipitation parameters shown in Table 1. (E) = evergreen, (D) = deciduous, (i-c) = *ilex-coccifera* type.

Section	MAP Min.	MAP Max.	MPWet Min.	MPWet Max.	MPDry Min.	MPDry Max.	MPWarm Min.	MPWarm Max.
Gran Dolina (20)	*Tilia*	*Pinus haploxylon*	*Quercus*(E)/*Tilia*	*Pinus haploxylon*	*Tilia*	*Olea*	*Quercus* (D)/*Tilia*	*Pistacia*
Palominas humid phase (14.5)	*Castanea*	*Chenopo-dioideae*	*Nyssa*	*Sanguisorba*	*Cedrus*	*Quercus*(i-c)	*Nyssa*	*Ephedra*
Palominas dry phase (11.0)	*Quercus*(i-c)	*Ephedra*	*Quercus*(i-c)	*Ephedra*	*Sanguisorba*	*Ephedra*	*Quercus*(D)	*Carpinus orientalis*
Cal Guardiola pollen (44)	*Castanea*	*Chamaerops*	*Buxus*	*Chamaerops*	*Carya*	*Chamaerops*	*Filipendula*	*Cistus*
Cal Guardiola macro (12)	*Acer pseudopla-tanus*	*Aesculus hippocasta-num*	*Acer pseudoplata-nus*	*Acer campestre*	*Aesculus hippocasta-num*	*Acer pseudoplatanus*	*Ligustrum*	*Aesculus hippocasta-num*
TP-II humid phase (12.0)	*Pteris*	*Carya*	*Eucommia ulmoides*	*Populus*	*Carya*	*Pterocarya*	*Eucommia ulmoides*	*Carya*
TP-II dry phase (11.3)	*Carya*	*Carya*	*Carya*	*Pinus haploxylon*	*Carya*	*Ephedra*	*Carya*	*Centaurea*
BO-IV humid phase (10.9)	*Ilex*	*Carya*	*Eucommia ulmoides*	*Pterocarya*	*Carya*	*Eucommia ulmoides*	*Eucommia ulmoides*	*Carya*
BO-IV dry phase (10.8)	*Hedera*	*Carya*	*Carya*	*Pinus haploxylon*	*Carya*	*Pterocarya*	*Carya*	*Amarantha-ceae*
Crespià pollen middle (17)	*Castanea*	*Mercurialis*	*Platanus*	*Quercus*(i-c)	*Tilia*	*Parrotiopsis jacquemontiana*	*Tilia*	*Quercus*(i-c)
Crespià pollen lower (13)	*Platanus*	*Phillyrea*	*Platanus*	*Quercus*(i-c)	*Picea*	*Cedrus*	*Quercus*(D)	*Phillyrea*
Crespià macroflora (29)	*Ilex aquifolium*	*Sorbus domestica*	*Hedera helix*	*Acer sem-pervirens*	*Tilia tomentosa*	*Laurus nobilis*	*Tilia tomentosa*	*Quercus cerris*

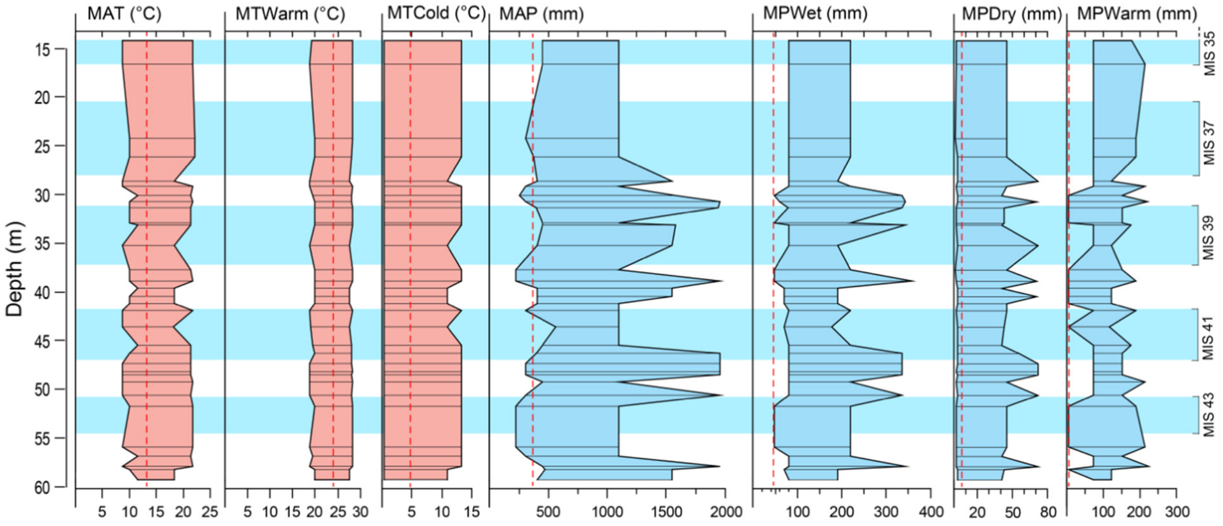

Fig. 3. Compilation of coexistence intervals for temperature (red) and precipitation (blue) parameters from Palominas section. Each coexistence interval is represented by a horizontal line. Modern values for each parameter are represented by dashed red lines. Exact values are: 13.2 °C MAT, 24 °C MTWarm, 4.9 °C MTCold, 366.4 mm MAP, 44.4 mm MPWet, 6.8 mm MPDry, 6.8 mm MPWarm (Table 2). Correlation with MIS stages as described by Gibert et al. (2015).

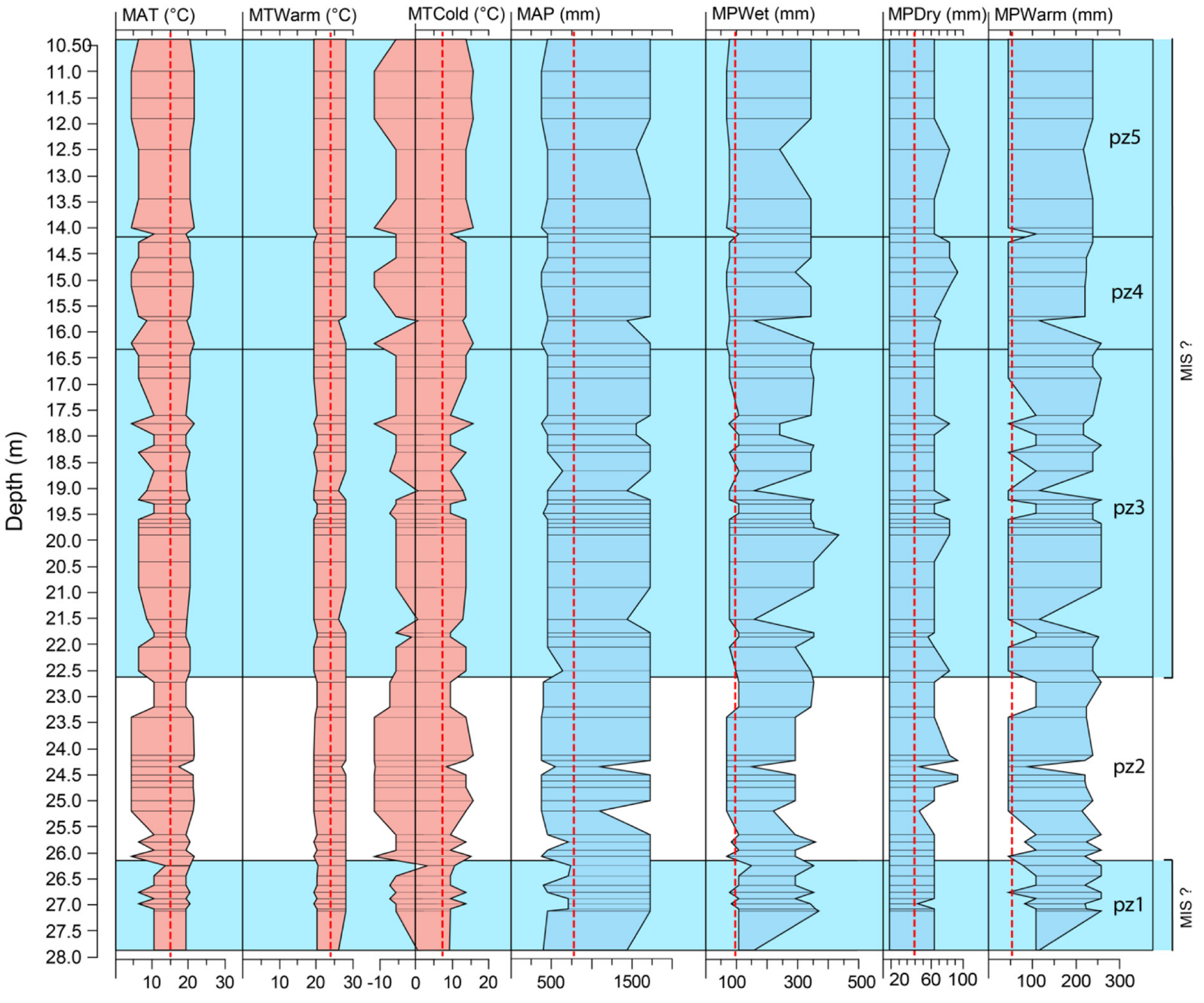

Fig. 4. Compilation of coexistence intervals for temperature (red) and precipitation (blue) parameters from Tres Pins II section. Each coexistence interval is represented by a horizontal line. Modern values for each parameter are represented by dashed red lines. Exact values are: 15.0 °C MAT, 24 °C MTWarm, 7.3 °C MTCold, 783.9 mm MAP, 95.6 mm MPWet, 38.9 mm MPDry, 38.9 mm MPWarm (Table 2). Pollen zones (pz) are grouped and correlated with MIS stages as described by Leroy (1997).

(Figs. 3–5). Only the main characteristics and patterns of the climatic reconstructions are described here for each section.

For the Gran Dolina section, only three samples from the palynological record (Rodríguez et al., 2011) contained enough taxa with climatic information to apply the CA analysis (samples between 1030 and 1045 cm in the original diagram, placed in the upper part of the TD6 level). The taxa composition among these levels is similar, and due to that, the results of the CA analysis are the same, with the exception of the presence of *Tilia* in one of the samples, which provides narrower intervals for the precipitation parameters (Tables 2–4).

The analysis of the Palominas section resulted in 33 samples providing coexistence intervals (Tables 2–4; Fig. 3). Values for temperature related parameters do not show any trends throughout the section. But, coexistence intervals for MAP display shifts between higher and lower precipitation values; however, the intervals remain generally wide. Similar changes can be seen for coexistence intervals of other precipitation parameters, although these changes are expressed in broadening and narrowing of the intervals instead of directional displacements.

In Cal Guardiola (Tables 2–4), the CA calculations provide intervals for a single pollen sample and for the macroflora assemblage. The pollen assemblage sets a broad interval of 13.9 to 19.2 °C for MAT. This interval comprises two MAT coexistence intervals for one single sample, 13.9–16.2 °C and 16.4–19.2 °C. These two coexistence intervals are the result of a disagreement between the individual MAT requirements of two taxa which are co-occurring in same sample. *Filipendula* sets the maximum value for one interval at 16.2 °C while *Chamaerops* sets the minimum range for the other, 16.4 °C. A similar case occurs for MPWarm calculation, which results in two different intervals, 20.0–29.0 mm (set by *Filipendula* and *Chamaerops*, respectively) and 45.0–54.0 mm (set by *Carya* and *Cistus*). This inconsistency is originated by the coexistence of *Chamaerops* and *Carya* in the fossil record.

The analysis of the Tres Pins II section provides coexistence intervals for 63 pollen samples (Fig. 4). The section shows temperature intervals with clear broadening and narrowing between the different pollen zones, except for MTWarm, which presents intervals from 20 to 28 °C throughout the section with little change. Precipitation parameters show more variability between the pollen zones (Fig. 4, Tables 2–4).

In Bòvila Ordis 113 samples provided coexistence intervals (Fig. 5). Much like the TP-II sequence, the temperature intervals for BO-IV are wide, while the precipitation intervals depict climatic changes more clearly (Fig. 5, Tables 2–4).

The analysis of the Crespià pollen sample revealed the coexistence intervals for two pollen samples and for the macroflora assemblage. The analysis of the macroflora provides narrow coexistence intervals. For MTCold and MAP, the intervals are divided in two competing coexistence intervals. This situation is created by the occurrence of taxa with

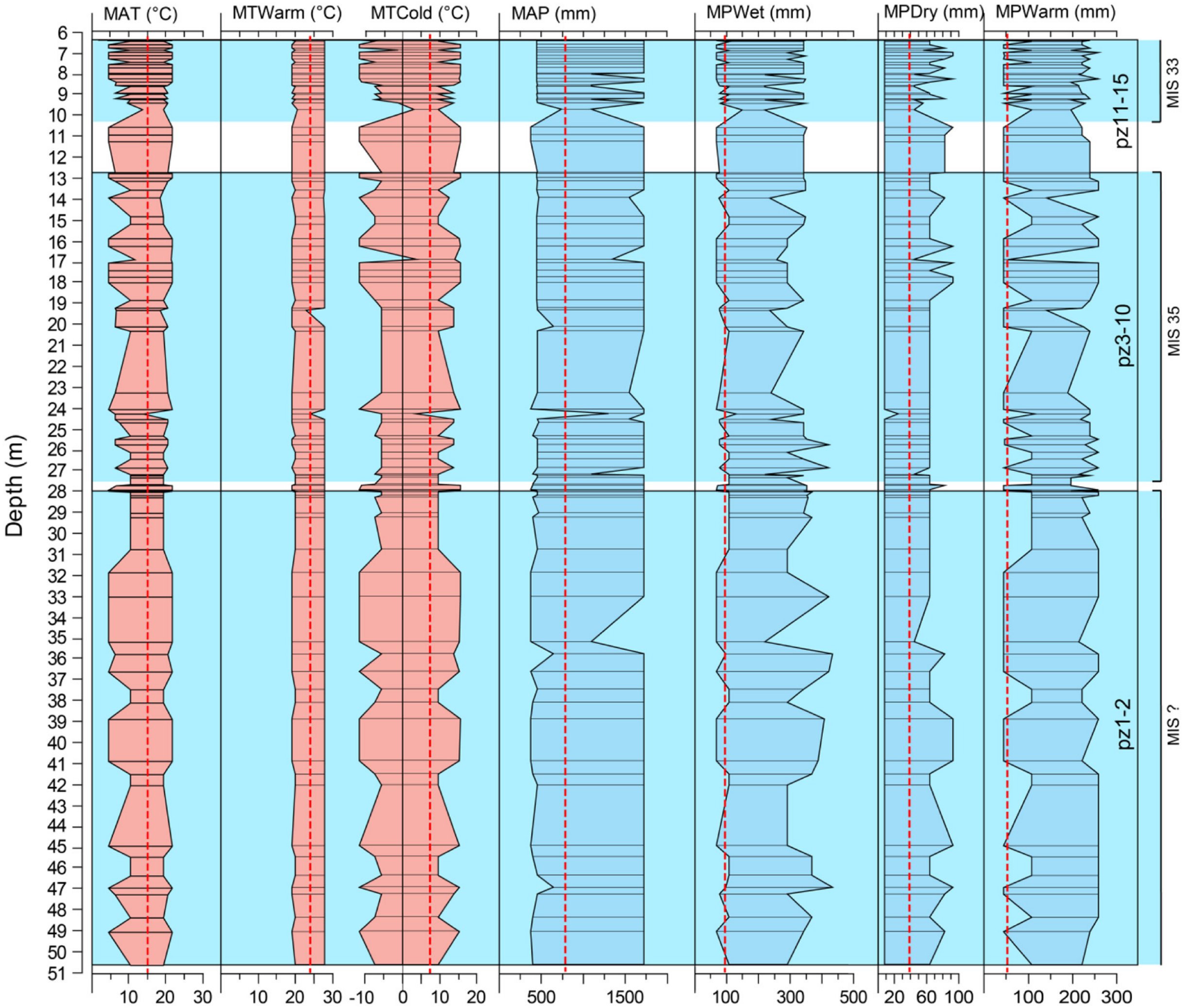

Fig. 5. Compilation of coexistence intervals for temperature (red) and precipitation (blue) parameters from Bòvila Ordis IV. Each coexistence interval is represented by a horizontal line. Modern values for each parameter are represented by dashed red lines. Exact values are: 15.0 °C MAT, 24 °C MTWarm, 7.3 °C MTCold, 783.9 mm MAP, 95.6 mm MPWet, 38.9 mm MPDry, 38.9 mm MPWarm (Table 2). Pollen zones (pz) are grouped and correlated with MIS stages as described by Leroy (2008).

climatic requirements that exclude each other, in this way impeding the creation of a single coexistence interval. In the case of MTCold, one interval is set by *Quercus faginea* (>4.9 °C) and *Tilia tomentosa* (<5.4 °C) and the second interval is set by *Laurus nobilis* (>5.6 °C) and *Quercus cerris* (<8.9 °C). For MAP, one interval is set by *Ilex aquifolium* (>563 mm) and *Acer sempervirens* (syn. *Acer creticum*) (<604 mm), the other interval is set by *Quercus cerris* (>619 mm) and *Sorbus domestica* (<740 mm). The coexistence intervals obtained from the pollen assemblage of Crespià are more precise and narrower in the lower part of the section than the middle part.

5. Discussion

The quality of coexistence intervals, resulting from the application of the CA method to the fossil plant assemblages from the six selected sites, range from narrow and accurate to wide and difficult to examine. Those obtained from the sections of Cal Guardiola and Crespià are narrow enough to outline accurately the values of temperature and precipitation during the Lower Pleistocene of northern Spain (Table 2). However, the resulting intervals for other sections are often wide, which hampers the possibility of discerning accurate climatic values. Nonetheless, these wide intervals often fall below or stay above the modern climatic measurements (Table 1). This is common for the sections of Palominas, Tres Pins and Bòvila Ordis (Figs. 3, 5–6, respectively). In these cases, the climatic information given by these intervals is still insightful in comparison with modern measurements, even though precise Pleistocene reconstructed values are not possible to deduce.

5.1. Vegetation and climate at the Early Pleistocene sites

The Early Pleistocene vegetation of the Iberian Peninsula was controlled by cyclic climatic changes, which resulted in corresponding vegetation successions (Leroy, 2007). The climate was driven by obliquity forces, which caused c. 41 kyr long cycles, until since c. 1.2 Ma. The Mid Pleistocene Transition let eccentricity cycles (with c. 100 kyr cyclicity) become increasingly dominant causing long and severe glacial phases since the Middle Pleistocene (Lisiecki and Raymo, 2005, 2007; Clark et al., 2006; Tzedakis et al., 2009; Leroy et al., 2011). Over the Early Pleistocene forests thrived during warm and humid phases, while during cold and dry phases, the landscape was dominated by steppes, savannas and open forests (González-Sampériz et al., 2010). In the NE region, forests would develop during the ‘interglacial’ phases, while during the ‘glacial’ phases the low precipitations would cause the development of more open environments (Suc and Popescu, 2005; Leroy, 1997, 2008; González-Sampériz et al., 2010). These areas would still receive enough precipitation for the development of forested steppes or cool-temperate open forests (Leroy 1997; González-Sampériz et al., 2010). However, with the plausible exception of some mountain strongholds (Manzano et al., 2017), the southern regions would see the development of steppes with few arboreal components during the ‘glacial’ phases (González-Sampériz et al., 2010). These areas record steppic vegetation dominated mainly by *Artemisia.*

During warm and humid ‘interglacial’ periods, Iberian forests were far more diverse than modern ones. Forested palaeoenvironments were mainly composed by species currently found in the floras from the Iberian Peninsula such as *Pinus*, *Quercus,* mesophilous taxa (e.g. *Acer*, *Corylus, Ulmus*) and a well-diversified Mediterranean flora (González-Sampériz et al., 2010). In addition to these groups, the Early Pleistocene forests contained Arctotertiary taxa that will disappear from the Peninsula over the Middle Pleistocene (Postigo-Mijarra et al., 2009, 2010; Magri et al., 2017). Taxa like *Zelkova, Carya, Ostrya, Eucommia, Elaeagnus, Engelhardia, Liquidambar, Parthenocissus, Symplocos, Parrotia, Cathaya, Nyssa, Pterocarya* or *Tsuga*, among others, were a common component of Iberian forests during warm and humid stages. No modern analog exists for these forests; however, similarities with the modern warm and humid Hyrcanian forests of the Southern Caspian and the Colchis region in the Caucasus, have been highlighted (Leroy, 1997).

5.1.1. Gran Dolina

The palynological analysis suggests the occurrence of different climatic cycles showing a landscape alternating between a dry and open stage and one humid and more forested. According to Rodríguez et al. (2011), Mediterranean conditions prevailed during the sedimentation of the TD6 level. This period would have seen the development of a mosaic environment with significant presence of *Pinus* and *Quercus* (deciduous and evergreen), mesophilous trees (e.g. *Carpinus* or *Acer*) and Mediterranean taxa (e.g. *Olea-Phyllirea* or *Pistacia*). The occurrence of *Taxodium*-type and *Pinus haploxylon* occur in TD-6 as Tertiary relict species (Rodríguez et al., 2011). Expósito et al. (2015) analysis of non-pollen palynomorphs attributed to TD6 a context of local humidity within the cave area, but regionally located in a dry environment. The data pictures an alternating landscape between a dry and open stage and one wet and more forested.

Comparison of the Early Pleistocene and present-day climates of Atapuerca reveals coincident precipitation values (Tables 1 and 2). Thus, all modern values for MAP, MPDry and MPWarm lie within the intervals inferred for the Early Pleistocene. The coexistence intervals for MPWet could signal a humid season with precipitations slightly higher than modern (Tables 1 and 2). The main differences between the present-day climate and the palaeoclimate lie in their temperature values. The Early Pleistocene climate was warmer, as documented by the interval for MTWarm 19.9–28.3 °C and the current value for this parameter 18.9 °C. Agustí et al. (2009) and Blain et al. (2009, 2013 and 2018) analysed palaeoclimatic parameters by applying the Mutual Climatic Range (MCR) method for squamata and amphibian assemblages found in TD6. Their results put TD6 in the context of a wetter and warmer climate when compared with modern measurements. The MCR results agree with the ones obtained by the CA method. The analysis of Blain et al. (2009) provides for the mid-upper levels of TD6 the intervals for MAT (7.5/10.5–14.5 °C), MTCold (−1/0.5–6 °C), MTWarm (18–22 °C) and MAP 900–1100 mm. Thus, both results based on herpetofauna and on pollen as presented here, show a warmer climate for the Early Pleistocene. The CA reconstruction also fits the MCR results for the TD6.2 subunit (Blain et al., 2013) of MAT values around 12.3 °C and MAP around 962 mm. Moreover, the analysis of the structure of small-vertebrate assemblages proves the existence of a warmer and relatively wooded landscape during the formation of level TD6 (Cuenca-Bescós et al., 2011).

In the context of global climatic cycles these features suggest an ‘interglacial’ context for the analysed samples of TD6 (Rodríguez et al., 2011). The higher temperatures would carry an increase of Mediterranean influence in the local flora. Despite the increase of arboreal taxa, the herbaceous group is still a relevant part of the pollen profiles described for TD6, which means that, instead of a fully forested landscape, these conditions would create a mosaic landscape. This landscape would be composed of patches of both forest and open vegetation, and a high diversity of flora and plant communities.

5.1.2. The Palominas section

First palynological analysis of the Palominas core (Gibert et al., 2015; Altolaguirre et al., In preparation) depict several vegetation cycles, deeply controlled by humidity. During dry stages, vegetation was composed mainly of herbaceous elements (e.g. *Artemisia* and Poaceae), while over humid stages the arboreal component increases, creating a wooded steppe or open forests represented mostly by deciduous and evergreen *Quercus*. These wooded environments also hosted taxa that will disappear from Iberia during the mid-Pleistocene transition, such as *Eucommia*, *Parrotia*, *Cathaya*, *Tsuga* or *Nyssa* (Postigo-Mijarra et al., 2009, 2010).

Temperature intervals for the Palominas section are relatively wide and all parameters include the modern measurements within their intervals. Precipitation intervals, especially those for MAP, show a clear climatic cyclicity (Fig. 3). At least six humid to dry cycles can be seen in the Palominas section. During dry phases, the intervals are usually broad and enclose the modern climatic values. During the humid phases, the intervals become narrower and stay above the modern MAP. During humid stages, the minimum MAP values of the intervals are around 100 to 200 mm higher than modern precipitation (366 mm). These values are set by the presence of taxa typical of relatively humid environments such as *Carpinus*, *Castanea*, *Fagus* or *Buxus*. Gibert et al. (2015) found a climatic cyclicity in the sediments of the Palominas section by comparing magnetic susceptibility and geochemical data. Correlating these phases to the MAP intervals reveals an overall high level of coincidence between the humid phases identified by Gibert et al. (2015) and the ones drawn by the MAP intervals (Fig. 3).

The results of CA analysis for the Palominas section match the climatic data reported by Blain et al. (2011 and 2016) and Agustí et al. (2009) for the sites of Barranco León and Fuente Nueva 3, in Orce. The climatic intervals obtained by the authors from the analysis of herpetofaunas reveal a warmer (MAT: 12/15 to 18.5 °C; MTCold: 5 to 11.5 °C) and wetter climate (MAP: 400/500–1000 mm) (Blain et al., 2011, 2016). This precipitation interval matches the ones presented here, especially the ones linked with humid phases. Both studies relate Barranco León and Fuente Nueva 3 to 'interglacial' stages. Unlike CA results, the temperature values presented by Blain et al. (2011) allow for further environmental reconstruction of the environment at Baza with temperatures above modern ones.

5.1.3. *Cal Guardiola site*

The palynological assemblage at Cal Guardiola (Postigo-Mijarra et al., 2007) depicts a forested environment, where *Pinus* and evergreen *Quercus* show the highest abundances. Thermophilous, mesohygrothermophilous and riparian forest species were present in both pollen and macroflora assemblages (e.g. *Quercus* subgen. *Quercus, Juglans, Carya, Salix, Acer* aff. *Pseudoplatanus, Carpinus, Platanus* or *Aesculus*) (Postigo-Mijarra et al., 2007). In this forest, several remarkable gymnosperms have been recorded, such as *Pinus haploxylon*-type and Taxodiaceae (sensu Taxodioideae and Sequoioideae). Mediterranean species like *Cistus, Ligustrum vulgare, Vitis* or *Chamaerops* were also present (Postigo-Mijarra et al., 2007).

The coexistence intervals for the Cal Guardiola site reconstruct a climate warmer than the current one, with slightly less seasonality and higher precipitations (Tables 1 and 2). The climatic intervals for the palynoflora are substantially more narrow, and point to warmer winters and colder summers, MTCold was at least 0.6 °C warmer and MTWarm was at least 0.7 °C lower than today (Tables 1 and 2). The coexistence of *Filipendula* (maximum MAT of 16.2 °C) and *Chamaerops* (minimum MAT of 16.0 °C) suggests that MAT value for Cal Guardiola was probably around 16 °C, slightly above the modern one of 15.2 °C. The disagreement of the two MAT intervals most probably refers to slight differences in the climatic requirements of modern and fossil taxa. Similarly, the inconsistency between the MPWarm ranges of *Chamaerops* and *Carya* creates two different intervals. The coexistence of these taxa suggests a value of MPWarm between 29 and 45 mm, which would have been above the modern value (25.5 mm). MPWet was at least 6 mm higher due to the presence of *Platanus* (Tables 1 and 2). Agustí et al. (2009) obtained climatic data from the amphibian and squamate assemblage of Cal Guardiola using the Mutual Climatic Range (MCR) method. Their results are in agreement with the calculations presented here, and comparison between both provides even more accurate climatic results. Consolidating the results of the CA and the MCR method, the MAT for Cal Guardiola shows a minimum value of 13.9 °C (CA) and a maximum of 14.5 °C (MCR). MTCold, MTWarm and MAP values obtained by the MCR method agree with the CA results (MTCold between −0.5 and 9.0 °C (Agustí et al., 2009)). However, the correlation between the herpetofauna assemblage and the hominin-bearing layers should be taken with caution due to possible stratigraphic uncertainties (Blain et al., 2018).

5.1.4. *The Banyoles-Besalú sites*

5.1.4.1. Tres Pins II. The palynoflora from Tres Pins shows a high arboreal diversity. The arboreal pollen assemblages are dominated by *Quercus* and *Carpinus*, but pollen from Mediterranean species are present along with taxa absent in modern Iberian vegetation, such as *Cathaya*, *Eucommia, Carya* or more tropical trees such as *Nyssa* or *Symplocos* (Leroy, 1997). The section is divided into five zones (Leroy, 1997). Zone 1 represents a dense and diversified deciduous forest, set by a humid and warm climate that matches the climatic configuration of an 'interglacial' phase. Zone 2 assemblage pictures a steppe or forested steppe, indicating low rainfall. Zone 3 sees the recovery of tree pollen with overall wetter conditions but with fluctuations between cool and warm temperatures. Zone 4 depicts a significant retreat of deciduous trees in favour of conifers of cool and humid environments. Finally, Zone 5 represents a less diversified forest environment due to the loss of arboreal taxa like *Eucommia*.

Temperature intervals for the TP-II section comprise the modern values in all instances and not much climatic information can be inferred. Nevertheless, intervals for MPWet and MPWarm often rise above modern values (Fig. 4). Pollen zones 1 and 3 show increased humidity when compared with other zones and higher MPWet compared to modern values, matching their interpretation as humid 'interglacial' stages (Fig. 4) (Leroy, 1997). This is caused by the predominance of *Eucommia* (>108 mm), which sets the intervals above the modern values (95.6 mm). Zone 2 results also fit with its original interpretation as a 'glacial' stage (Leroy, 1997), showing drier conditions when compared to zones 1 and 3. Temperature intervals of zone 2 show broadening towards colder values, due to the disappearance of taxa like *Hedera* or *Eucommia.* This could be linked to a cooling of climatic conditions. However, the coexistence intervals are not narrow enough to assert if the climate was colder or drier in comparison with the modern climatic measurements for the region (see Fig. 4). In contrast with zones 1 to 3, the results for zones 4 and 5 do not seem to match previous interpretations as warmer and humid environments, which is confirmed by high arboreal pollen counts (Leroy, 1997). These intervals are more similar to the ones from zone 2, with precipitation intervals lower than the ones for zones 1 and 3. This is caused by the disappearance of certain taxa, like *Eucommia*, that is predominant in zones 1 and 3. The climatic differences between zones 4–5 and 2 are qualitatively described due to the changes in pollen abundances rather than different taxa assemblages. Because the CA method accounts only for presence-absence information, the resulting intervals remain the same in zones with the same floristic composition, encompassing the different climatic settings in one coexistence interval.

5.1.4.2. Bòvila Ordis IV. The Bòvila Ordis IV sequence provides pollen assemblages defined by high proportions of arboreal taxa, represented mainly by *Quercus*, *Carya*, *Picea* and Pinaceae pollen. Together with these arboreal types, the forests were also composed of taxa typical of the Early Pleistocene, such as *Cathaya*, *Eucommia* or *Parthenocissus* (Leroy, 2008). The 15 pollen zones described for the BO-IV section are grouped according to climatic cycles (Leroy, 2008). Pollen zones 1–2 would represent an 'interglacial' stage, while zones 3–10 record a full climate cycle, from 'glacial' to 'interglacial' stage and from wooded steppe to coniferous forest. The last zones, 11–15, show the beginning of the next cycle with the development of a wooded steppe.

The coexistence intervals show very little change between the different zones, with intervals usually encompassing the modern climatic values. Only some precipitation intervals show variations from the modern values. MPWet and MPWarm intervals often show minimum values higher than the modern precipitation values (Fig. 5). The higher

MPWet and MPWarm values is due to the occurrence of *Pterocarya* and *Eucommia*, which set MPWet values at least 15 mm higher than the modern value and 60 mm higher for MPWarm (Fig. 5 and Table 2). During the dry 'glacial' phases these taxa are absent and the intervals encompass the modern precipitation values. In general, the coexistence intervals do not show great differences between the dry and the humid phases as described by Leroy (2008). This is the result of a relatively similar taxonomic composition during both phases (Leroy, 2008).

5.1.4.3. Crespià. The macroflora of Crespià is dominated by dicotyledonous leaves attributed to *Quercus cerris* and *Carpinus* (e.g. *C. suborientalis, C. betulus*) (Roiron, 1983). The palynological record of the Crespià site (Suc, 1980) describes an environment dominated by conifers but also composed of both mesophilous and Mediterranean trees. The palynoflora found at Crespià points to a warm-temperate and humid climate with development of a drier and cool phase (Suc and Cravatte, 1982).

The coexistence intervals for the macroflora of Crespià suggest an environment drier than modern (Tables 1 and 2) while the microflora reflects a change from conditions similar to the modern climate to colder and drier conditions; this would match the transition from an 'interglacial' into a 'glacial' stage (Suc and Cravatte, 1982).

The coexistence intervals obtained from the two pollen assemblages of Crespià show different ranges. However, the intervals from the lower part of the section are generally broader than the ones for the middle part. The intervals for the lower part of the section reveal colder winter temperatures, with a difference of at least 2 °C, and drier summers, with a difference of almost 30 mm from the modern values. The intervals for the middle part are shifted to higher temperature and precipitation values, yet the intervals encompass the modern measurements and no comparison with the modern climate can be made. The colder and drier conditions inferred from the climatic range of *Parrotiopsis jacquemontiana* must be taken with caution since the species is currently found at mid-altitudes in the Himalayas and had a wider climatic range during the Pleistocene (Weaver, 1976).

Looking at the intervals for the macroflora from Crespià, three cases of disagreeing climatic ranges occur, whose detailed analysis can lead to further climatic information. For MTCold, the coexistence of *Tilia tomentosa* (which endures a maximum of 5.4 °C MTCold) and *Laurus nobilis* (minimum 5.6 °C) means that winter temperature was around 2 °C lower than modern (7.3 °C). The next case of disagreement between intervals arises in the MAP results, between *Acer sempervirens* (syn. *Acer creticum*) (maximum 604 mm) and *Quercus cerris* (minimum 619 mm). The coexistence of these species would set the MAP for Crespià around 600 mm, significantly lower than the modern one (783.9 mm). MPWarm values present the third event of disagreeing intervals: *Laurus nobilis* (maximum 27 mm) coexists with *Carya* (minimum 45 mm). A narrower MPWarm value for Crespià could be set between 27 and 45 mm being lower than the modern value of 51.5 mm. The MPDry interval establishes a summer precipitation around 24 mm, 15 mm lower than the modern one.

5.2. Latitudinal climate patterns on the Iberian Peninsula during the Early Pleistocene

Italian Early Pleistocene palaeofloras register a latitudinal climatic gradient between North and South, showing increasing aridity towards the southern regions (Suc and Popescu, 2005; Fusco, 2007; Bertini, 2010; Combourieu-Nebout et al., 2015). For the Iberian Peninsula, a Pliocene climatic gradient is described by Fauquette et al. (1999). During the Pliocene, the difference between the Spanish NE and S regions with respect to MAT and MAP was around 4.5 °C and 800 mm, with the southern region experiencing higher temperatures and aridity (Fauquette et al., 1999).

The Palominas and BO-IV sections have been dated precisely enough (Gibert et al., 2007; Leroy, 2008) and therefore it allows for a comparison of contemporaneous palaeoclimatic conditions across two different biogeographical areas of Spain (Fig. 1). The upper part of the Palominas

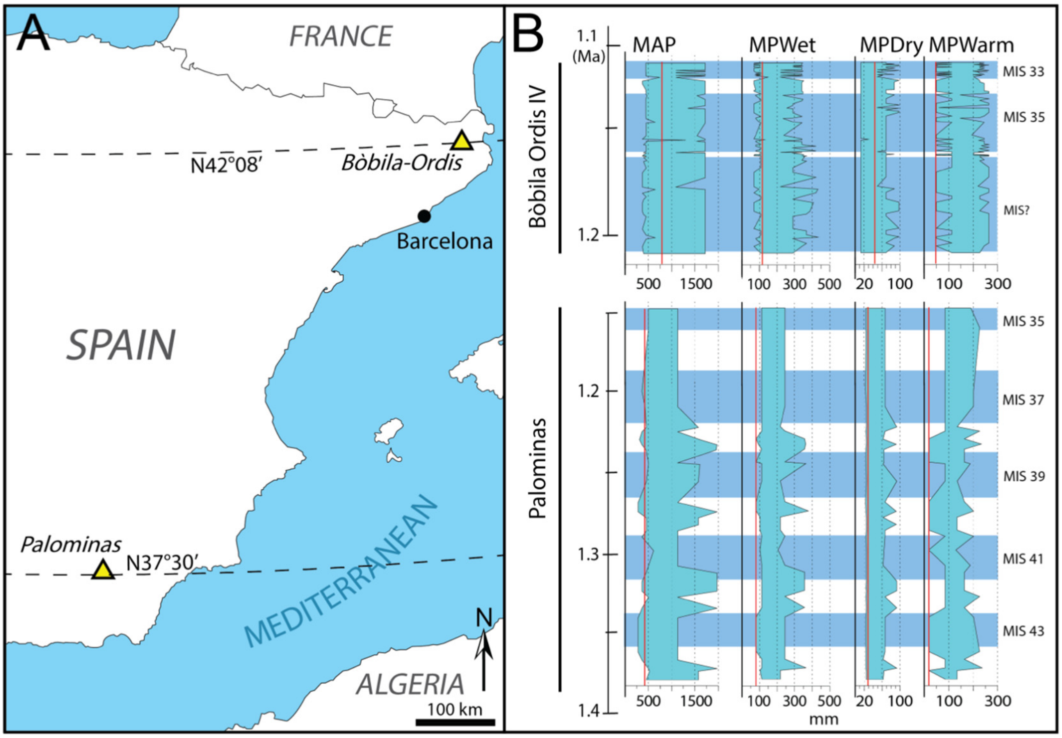

Fig. 6. (A) Map of the eastern part of the Iberian Peninsula showing the latitudinal values for the sites of Bòvila Ordis and Palominas. (B) Coexistence intervals for the main precipitation parameters of the sections of Bòvila-Ordis IV (top) and Palominas (bottom). Blue bands represent humid phases associated with MIS stages (Leroy, 2008; Gibert et al., 2015).

section, located in southeastern Spain, and the BO-IV section in northeastern Spain represent a similar time interval from c. 1.2 to 1.1 Ma (around MIS 35), 690 km apart (Fig. 2). The precipitation intervals from Palominas are significantly lower than the ones resulting from BO-IV palynoflora. The humid phase recorded in the lower part of BO-IV (Leroy, 2008) displays MAP intervals with average values of c. 1000 mm while the MAP intervals for the humid phases at Palominas have a lower average, c. 750 mm. Since Palominas and BO-IV are respectively located in the south and northeastern parts of the peninsula (Fig. 1), a N-S gradient of decreasing humidity can be postulated (Fig. 6). The existence of such gradients during the Early Pleistocene has been suggested by Blain et al. (2013).

Due to the basins of Baza and Banyoles-Besalú being located relatively near great mountain ranges, the vegetation in these areas may be influenced by local climatic conditions rather than representing supraregional trends in Mediterranean climate. Additional data from different latitudes of the Iberian Peninsula is required to confirm the hypothesis of a climatic gradient. Nevertheless, the differences in precipitation between the two basins in the north and in the south of Spain are obvious. Such climatic patterns may have played a crucial role for hominin environments.

5.3. Relationships between climate and the occurrence of hominins on the Iberian Peninsula during Early Pleistocene

The Early Pleistocene records the first appearance of early *Homo* in Europe (Gabunia and Vekua, 1995; Toro-Moyano et al., 2013). Early hominin populations could have started to colonise Southern Europe during times of favourable climatic conditions (Agustí et al., 2009; Leroy et al., 2011, Agustí et al., 2018). A low climatic variability favoured a high floral, vegetational, and faunal diversity of more or less open habitats, e.g. Palominas, Gran Dolina or Tres Pins II sections. Such open or semi-open landscapes harboured a diverse megafauna, carnivores and mega-herbivores, well documented in several sites studied in this investigation, e.g. Baza Basin, Gran Dolina or Cal Guardiola, which could be one of the main resources exploited by *Homo* over some periods (Kahlke et al., 2011; Carrión et al., 2011). Other regional, palaeontological studies support this view (Arribas et al., 2009; Saladié et al., 2014). It is clear that these kinds of open or semi-open landscapes, such as grasslands or forested steppes, were also dominant in other hominin sites in Europe (Leroy et al., 2011). However, the exact mechanics and patterns of dispersal from Africa into Europe and the influence of climate are still under discussion (Agustí et al., 2009; Blain et al., 2009; Cuenca-Bescós et al., 2011; Dennell et al., 2011; Leroy et al., 2011; Bermúdez de Castro and Martinón-Torres, 2013). Climatic oscillations during the Early Pleistocene, prior to the mid-Pleistocene transition, were not extremely severe when compared with the oscillations during the Middle and Late Pleistocene (Ehlers and Gibbard, 2008). The limited number of sites does not allow determining when the first entry in Europe occurred and how many pulses of population out of Africa (across how many climatic cycles) where necessary before hominins could survive a full ‘glacial–interglacial’ cycle in southern Europe.

For the first moments of hominin colonisation from Africa to Europe, it has been proposed that the climate was still too harsh for early hominins since they might have not been able to endure low winter temperatures (Leroy et al., 2011). During the early stages of the colonisation of Europe, hominin communities could have disappeared from Western Europe during ‘glacial’ stages as well as during the fully forested ‘interglacial’ stages. Hominins would have been only able to recolonise the continent at the beginning of the ‘interglacial’ phases, when the temperatures were warmer but the landscape still preserved a certain degree of openness (Leroy et al., 2011; Agustí et al., 2018). Once these early populations were able to survive the first full climatic cycles in southern Europe, favoured by the milder ‘glacial’ phases of the Early Pleistocene, they would then start spreading northwards. This led to the creation of a ‘sources and sinks’ model, in which after the initial colonisation of Europe, early hominin populations would endure ‘glacial’ periods in the southern latitudes while disappearing from northern Europe. In this way the peninsulas in southern Europe would act as glacial refuge and allow these communities to repopulate northern latitudes during the following warm phases (Pross and Klotz, 2002; Eller et al., 2004; Dennell et al., 2011; Garcia et al., 2011; Kahlke et al., 2011). Perhaps Iberia could have acted as a pseudo-sink (Watkinson and Sutherland, 1995). Thus, small populations of hominins could resist in specific ‘glacial’ refugia, but Iberia was also able to accommodate incoming populations from Levant and North of Europe. In this manner, the Iberian Peninsula could have contained a potential source population for the earliest hominins in Britain (MacDonald et al., 2012).

The palaeoclimatic analysis carried out via the CA method (Fig. 3–5, Tables 1 and 2) allows drawing a reasonable reconstruction of the precipitation parameters and the cyclicity between dry and wet phases. Specifically, the results from multi-cyclical sequences of BO-IV and Palominas reveal that these precipitation oscillations were not extremely severe. ‘Interglacial’ precipitations would be, at least, slightly higher than modern precipitations, while the ones during ‘glacial’ phases were probably more similar to modern ones. This would have allowed for the development of mosaic environments during ‘glacial’ phases in the Iberian Peninsula, where the early hominin communities would have benefited from both open environments and access to a higher variety of plant and animal resources. The weak difference between ‘glacials’ and ‘interglacials’, in terms of reconstructed precipitation values, supports the ‘sources and sinks’ model and the idea that the Iberian Peninsula could be one of the main refuge areas in Europe already from the Early Pleistocene (Hewitt, 1999; Carrión et al., 2003, 2008; Dennell et al., 2011). Nevertheless, for other areas of Central and Northern Europe, a model of “colonisation and recolonization” has to be considered since these ‘glacial’ phases could have been harsher (Leroy et al., 2011). Comparing the envelope of tolerance of summer precipitation (30–60 mm) for the presence of early hominins in Europe (Leroy et al., 2011) with the reconstructed values of MPDry and MPWarm reveals that the coexistence intervals of most sections either encompass or fit into the envelope (Table 2). However, the NE sections of TP-II and BO-IV (Table 2 and Figs. 4 and 5) provide MPWarm values higher than 60 mm during the humid phases. As suggested by the identified latitudinal gradient of increased dryness towards the southern regions (Fig. 6), early humans during ‘interglacial’ phases could have preferred the SE region of Iberia, with more dry and open landscapes than the more humid and forested NE region.

While the present analysis draws a clear picture of the cyclical precipitation changes, temperature changes are harder to discern given the current data. Sections such as Gran Dolina, Cal Guardiola and Crespià give punctual insight into milder or slightly warmer temperatures, but such information is unattainable from the long multi-cyclical sequences. The climatic tolerance of early hominins, as inferred by modelling (Leroy et al., 2011) sets the presence of hominin sites in areas with reconstructed MTCold not lower than 0 °C (Leroy et al., 2011). Higher than 0 °C MTCold values are calculated for the sections of Gran Dolina, Cal Guardiola, Crespià and Palominas (Table 2). While no hominin activity is recorded in Crespià, these results agree with the presence of hominin remains and artefacts in the areas of Atapuerca, Baza Basin and the site of Vallparadís, stratigraphically correlated with Cal Guardiola. Moreover, the results from the Palominas section (Table 2; Fig. 3) provide MTCold values never lower than 0.4 °C both during the ‘glacial’ and ‘interglacial’ phases. This way, the SE Iberian region and the Baza Basin, could have acted as glacial refuge for early hominins.

These results confirm previous studies that claim that, in Iberia, warm conditions prevailed during the interval between 1.2 and 0.9 Ma (Dennell et al., 2011; Kahlke et al., 2011). Thus, it would be possible that hominin populations in the Iberian Peninsula persisted during ‘glacial’ periods (Dennell et al., 2011; Kahlke et al., 2011); these periods had a mild climate similar to the modern one during ‘glacial’ stages and slightly wetter during ‘interglacials’. The occurrence of mild climates in the three areas of Iberia studied here is related to a lack of strong climatic fluctuations. Such a climate would have supported the development of mosaic landscapes in the Iberian Peninsula, supporting hominin survival and dispersal (Kahlke et al. 2011; Carrión et al. 2011). However, the calculations presented here do not account for the absolute minimum winter temperatures and number of days of frost during the year. These parameters could have hindered hominin survival (Leroy et al., 2011) since there was no recorded use of fire by early *Homo* in the Early Pleistocene (Gowlett, 2006; Blain et al., 2009) and could have impeded its survival during 'glacial' phases (Leroy et al., 2011; MacDonald et al., 2012).

6. Conclusions

The CA method allows for quantification of temperature and precipitation values based on pollen and macroflora assemblages from six Early Pleistocene sites from different latitudes of the Iberian Peninsula. The palaeoclimatic analysis provides these fundamental conclusions:

1. Temperature reconstructions are represented as wide intervals that usually encompass the modern temperature. These temperatures might be similar to the ones found today in the Iberian Peninsula, although some sites record less seasonal differences. In several cases, climate was clearly warmer. Thus, the Gran Dolina vegetation would have developed during a climate that experienced slightly warmer summer temperatures and Cal Guardiola vegetation provide evidence of warmer annual and winter temperatures, as well as slightly colder summer temperatures. Overall, the CA method depicts a climate similar to the one found currently in the Iberian Peninsula. The shifts of coexistence intervals in the long pollen sequences of Palominas, Tres Pins, and Bòvila Ordis might show the existence of slight temperature changes during the deposition of these sections, pointing to warmer periods during 'interglacials' and colder during 'glacial' stages. The seasonality of temperature during the Early Pleistocene was weaker than today.
2. The coexistence intervals for precipitation parameters provide more insightful results. They are often wide, at times offering values above the modern measurements (e.g. Cal Guardiola). The precipitation values for the long pollen sequences of Palominas, Tres Pins, and Bòvila Ordis display cyclic changes of precipitation. Zones with precipitation intervals above the modern values correspond with zones associated with 'interglacial' stages, while zones where the intervals include the modern values are generally linked to 'glacial' phases. During 'glacial' phases, precipitation values would have been closer to the ones found today in each region. At the Palominas section, the minimum difference between the Early Pleistocene annual precipitation during an 'interglacial' phase and the modern one is 200 mm. The difference between modern and 'interglacial' precipitations during the wet and dry season was at least 100 and 50 mm, respectively. For the sections of Tres Pins and Bòvila Ordis, the minimum difference in precipitation between 'interglacial' phases and the modern climate is significant and of c. 350 mm annually, 40 mm during the wet season and 50 mm during the dry one.
3. Differences in precipitation between sites located in northern and southern Iberia latitudes may evidence the existence of a latitudinal precipitation gradient. This may account for regional climatic patterns that discouraged the spread of closed forests throughout the Iberian Peninsula, but provided habitable niches for hominin presence also during less favourable times.
4. The Iberian climate during 'interglacial' periods of the Early Pleistocene was wetter and slightly warmer than the modern climate. During the 'glacial' phases the climate would be more similar to the modern Iberian climate. These climatic conditions during both phases could have been favourable for the survival and dispersal of hominins in the Iberian Peninsula. Especially in southern Spain, these conditions favoured the development of mosaic landscapes with open or semi-open environments, which might have granted human populations the access to a variety of plant and animal resources.
5. The climatic data obtained by the CA method for the sections of Gran Dolina, Cal Guardiola and Palominas agrees with the climatic data revealed by the Mutual Climatic Range method applied to amphibian and squamate fossil assemblages from the sites of Gran Dolina, Cal Guardiola and the sites located in Baza Basin.

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Appendix A. Supplementary data

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