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EARLY PLEISTOCENE ENVIRONMENTS BEFORE, DURING AND AFTER THE FIRST EXPANSION OF EARLY *HOMO* INTO SOUTHERN SPAIN

Dissertation zur Erlangung des Doktorgrades der Naturwissenschaften

GOETHE
UNIVERSITÄT
FRANKFURT AM MAIN

Vorgelegt beim Fachbereich 11
Geowissenschaften / Geographie der
Johann Wolfgang Goethe-Universität
in Frankfurt am Main

Frankfurt am Main, 2021
(D 30)

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aus Madrid

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(D 30)

vom Fachbereich 11 der
Johann Wolfgang Goethe – Universität als Dissertation angenommen.

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Datum der Disputation:

Die Doktorarbeit wurde finanziert über eine Projektförderung der Forschungsstelle ROCEEH 'The role of culture in early expansions of humans' am Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt am Main, durch die **Heidelberger Akademie der Wissenschaften.**

HEIDELBERGER AKADEMIE DER WISSENSCHAFTEN
Akademie der Wissenschaften des Landes Baden-Württemberg

THE ROLE OF CULTURE IN EARLY EXPANSIONS OF HUMANS

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Abbreviations

AP	Arboreal pollen
BL5	Barranco León 5
CA	Coexistence Approach
CMIX	Cool mixed evergreen needleleaf and deciduous broadleaf forest
DBWD	Deciduous broadleaf woodland
EMPT	Early-Middle Pleistocene Transition
EPP	Edible plant part
ESR	Electron spin resonance
FN3	Fuente Nueva 3
Fm	Formation
GDGT	Glycerol dialkyl glycerol tetraethers
GRAM	Graminoids with forbs
ka	Thousand years ago
kyr	Thousand years
Ma	Million years ago
MAP	Mean annual precipitation
MARP	Mean annual range of precipitation
MART	Mean annual range of temperature
MAT	Mean annual temperature
MCR	Mutual climatic range
MIS	Marine isotopic stage
MPDry	Mean precipitation of the driest month
MPWet	Mean precipitation of the wettest month
MPWarm	Mean precipitation of the warmest month
MTCold	Mean temperature of the coldest month
MTWarm	Mean temperature of the warmest month
Myr	Million years
NAP	Non-arboreal pollen
NLR	Nearest living relative
PC	Principal component
PCA	Principal component analysis

PCI	Pollen climate index
PFT	Plant functional type
PTI	Pollen temperature index
VM	Venta Micena
VU	Vegetation unit
WTSHB	Warm-temperate evergreen sclerophyll broadleaf shrubland
XSBH	Xeric shrubland

Abstract

One of the most important events in human history occurred during the Early Pleistocene: the dispersal of early hominins out of Africa and into Europe and Asia. In Western Europe, the earliest evidences of the genus *Homo* have been found in the Baza Basin, at the sites of Orce in the SE of the Iberian Peninsula. These sites contain fossils and lithic industry dated approximately as 1.4–1.3 Ma. While hominin remains and artifacts at Orce, as well as the accompanying fauna, have been extensively studied, the properties and evolution of the Early Pleistocene vegetation in the basin remain unknown. The general effect of climate change on the expansion of early hominins from Africa into Eurasia still remains unclear. It is not known if the Early Pleistocene climate changes and the development of glacials periods led to the extirpation of European communities, or if those communities were able to endure and persist through such adverse climatic periods. This open question highlights the need for climate and environmental analyses for the time before, during and after the first presence of *Homo* in Europe. This PhD thesis contributes to that need by the presentation of the first long pollen record of the Baza Basin, where the oldest hominin sites in Western Europe are found.

The novel pollen material was obtained from the Palominas drill core, a 142 m long core which cuts through Early Pleistocene lacustrine deposits found at the depocenter of the Baza Basin. The pollen assemblages are used to reconstruct past biomes and climate parameters. The core samples are also subjected to biomarker analysis in order to reconstruct temperature changes Finally, the palaeoclimatic measurements and the reconstructed vegetation are used in an effort to map the different vegetation types in the area, thus recreating the changing habitat of early hominins and the different plant resources available.

The Palominas core records the majority of the Calabrian period, it covers an age approximately between ca. 1.5 to 1.1 Ma, comprising around 400 ka. The pollen assemblages depict alternations between dry and humid phases. Dry phases are characterized by the dominance of herbaceous and steppe plants, while humid phases feature an increase in arboreal pollen. The arboreal pollen is abundantly represented by multiple tree groups, especially conifers and both evergreen and deciduous *Quercus*, but it also includes other trees typical of temperate and Mediterranean climates. Conifer pollen is overwhelmingly represented by *Pinus,* although *Picea* pollen also appears, often in the form of peaks of great abundance. The pollen assemblages also include taxa typical of the Early Pleistocene European floras, such as *Tsuga*, *Carya*, *Parrotia*, *Cathaya* or *Eucommia*, which were extirpated during the Middle Pleistocene. Overall, the reconstructed vegetation displays a relatively dry climate where herbs and steppe plants were common, even during humid periods. This landscape is strikingly different from the ones depicted by coeval records from localities in the north of the Iberian Peninsula, which generally represent intensely forested environments. Instead, the pollen assemblages found in the Palominas core are more similar to those reported from Early Pleistocene deposits of Southern Italy and Greece, which also represent relatively dry vegetation and open environments.

Climate data for the Early Pleistocene was obtained by the application of the Coexistence Approach method to the pollen assemblages, which revealed significant changes in annual precipitation. During humid phases the basin experienced annual precipitation values significantly higher than the modern ones, while during dry phases precipitation values were more similar to those experienced today. The Coexistence Approach method was also applied to pollen and macroflora fossil assemblages from northern Spanish locations also associated with early hominin presence: Sierra de Atapuerca (Burgos), Cal Guardiola and multiple sites from the Banyoles-Besalú Basin (Catalonia). Northern sites revealed higher precipitation values and an overall warm and humid climate. These results suggest the presence of a N-S gradient of decreasing precipitation in the Iberian Peninsula during the Early Pleistocene, similar to the one seen in the modern climate.

Additionally, biomarkers (glycerol dialkyl glycerol tetraethers or GDGTs) obtained from the core were useful at reconstructing relative changes in annual temperature. In the context of a saline lacustrine environment, like the Baza Palaeolake, the values suggest that dry phases were generally colder while humid phases were warmer. Such configuration is in agreement with the general understanding of the Early Pleistocene climate in the Iberian Peninsula.

Lastly, the development of novel methodologies for vegetation mapping and for quantification of the seasonal availability of edible plant parts revealed key features of the hominin habitat in the Baza Basin. Vegetation maps for the Early Pleistocene reveal that during dry phases, the predominant vegetation type was the steppe, while during humid phases the vegetation was mostly composed of Mediterranean woodlands, deciduous forests and conifer forests. As shown in the pollen record, the lake system allowed for the development of a permanent body of marshland vegetation, which would contract and expand in tune with the climate cycles. Mediterranean woodlands and deciduous forests provided a high amount of plant resources, except during winter. However, riparian and marshland vegetation would have been a reliable source of plant food for hominin communities through the whole year.

In conclusion, the results presented by this PhD thesis reveal that the vegetation of the hominin habitat at Orce, and in the Baza Basin, was severely constrained by climate, specifically, by humidity. The Early Pleistocene glacial-interglacial cyclicity forced drastic environmental changes as the forested environments of the interglacial periods were replaced by steppes during glacial ones. Nonetheless, temperature changes were relatively mild during the Early Pleistocene, especially when compared with those of northern latitudes, and average winter temperatures were high enough to allow the survivability of *Homo* even during glacial periods. The successive vegetation changes were translated into significant changes of the availability of plant-based resources useful to hominins, decreasing the diversity and accessibility of edible plant foods at Orce. And yet, the presence of plant foods in the steppe vegetation and in the permanent marshland vegetation could have supplied hominins with basic dietary components, even during cold and dry climatic periods.

All these results offer a new perspective to the distribution of early *Homo* at the Iberian Peninsula and Europe: the climatic and environmental conditions at the Baza Basin would have created a refugium environment, able to support permanent hominin populations through the Early Pleistocene. Thus, the European continent had the potential to be continuously populated since the time of the first arrival of *Homo* out of Africa.

Chapter 1

Introduction

1.1. The first Europeans

The earliest known evidences of species of the genus *Homo* out of Africa are found in Shangchen, China, in the form of lithic artifacts dated to approximately 2.1 Ma (Zhu et al., 2018). In Eastern Europe, the oldest proof of hominin presence is found as well-preserved fossils at Dmanisi cave (Georgia) (Gabunia and Vekua, 1995; García et al., 2010), around 1.8 Ma according to ^{40}Ar/^{39}Ar dates (Gabunia et al., 2000). In Europe several sites contain early hominin fossils or artifacts dated as older than 1.1 Ma (pre-Jaramillo magnetic reversal (Fig. 1.1). Among European sites, some of the oldest hominin sites are found in Southern Spain, providing lithic artifacts and sparse fossil material dated as old as 1.4 Ma by means of U-series/electron spin resonance (ESR) (Toro-Moyano et al., 2013). All these age results designate the Early Pleistocene (2.58 to 0.774 Ma; Gibbard and Cohen, 2019) as the period which saw the first event of expansion of *Homo* out of its native continent, Africa, and the colonization of Eurasia.

Despite the existence of these sites, the fossil record of early hominins outside of Africa is sparse and fragmentary. Because of this, key factors surrounding the expansion of *Homo* during the Early Pleistocene are largely unknown. Some of the major open

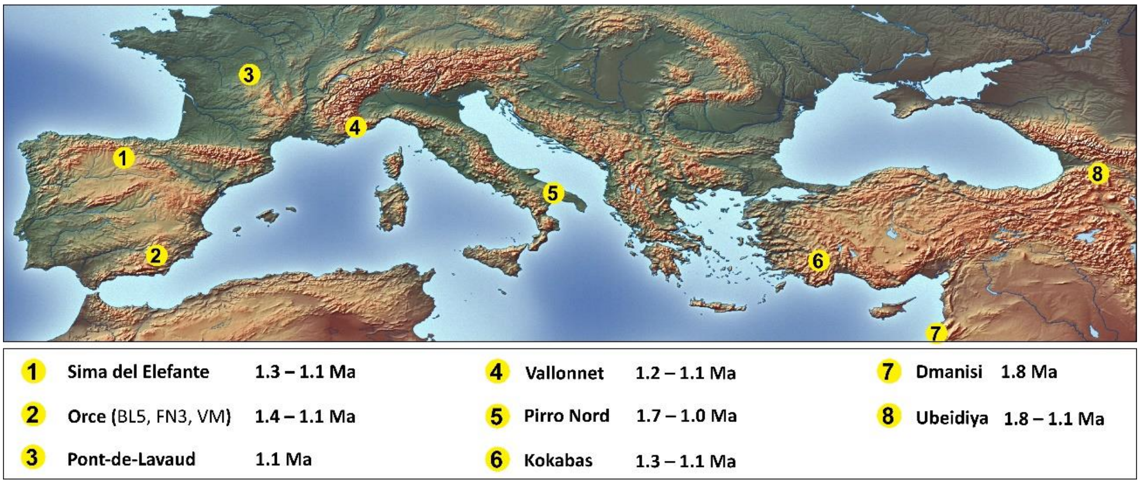


Fig. 1.1: Map of hominin sites older or potentially older than the Jaramillo magnetic reversal (1.071 to 0.99 Ma; Gibbard and Cohen, 2018). Dating methods and references in Table 1. The sites of Orce are abbreviated as BL5 (Barranco León 5), FN3 (Fuente Nueva 3).

Table 1.1: List of European hominin sites depicted in Fig. 1.1

Site	**Age (Ma)**	**Methods**	**Material**	**References**
Dmanisi	1.8 Ma	^{40}Ar/^{39}Ar	Fossil & lithics	Gabunia and Vekua, 1995; García et al., 2010
Ubeidiya	1.8–1.1 Ma	-	Fossil & lithics	Belmaker et al., 2002;
Kocabas	1.3–1.1 Ma	^{26}Al/^{10}Be	Fossil	Lebatard et al., 2014
Pirro Nord	1.7–1.3 Ma	-	Lithics	Arzarello et al., 2007, 2016
Vallonnet	1.2–1.1 Ma	U–Pb, ESR	Lithics	Michel et al., 2017; Yokoyama et al., 1988
Pont-de-Lavaud	1.1 Ma	ESR	Lithics	Despriée et al., 2018
Barranco Leon 5	1.4–1.1 Ma	ESR	Fossil & lithics	Toro Moyano et al., 2013
Fuente Nueva-3	1.3–1.1 Ma	ESR	Lithics	Duval et al., 2012
Venta Micena	1.4–1.1 Ma	ESR	Fossil	Duval et al., 2011
Sima del Elefante	1.3–1.1 Ma	^{26}Al/^{10}Be	Fossil & lithics	Carbonell et al., 2008

questions seek to answer why *Homo* left Africa at this time, or how such geographical expansion impacted hominin evolution, or how many ‘waves’ of hominins penetrated into Eurasia from Africa. However, the present PhD thesis will inquire and contribute to a different open question: what role played the changing climate of the Early Pleistocene and how did it affect the process of hominin expansion? In order to contribute to this question, this thesis will combine the fields of palynology with palaeoclimate and palaeovegetation mapping.

1.2. The unknown environments of the first hominins in Western Europe

This PhD thesis focuses on some of the few described early hominin sites in Europe: the sites of Orce, in Southeastern Spain. These have provided multiple artifact assemblages (Gibert and Martínez, 1992; Gibert et al., 1992; 1998a; 2006a; Gibert et al., 2006b; Toro-Moyano et al., 2009; 2011) and sparse fossil material (Toro-Moyano et al., 2013) pertaining to the genus *Homo*. The preservation of rich vertebrate fossil assemblages at Orce (e.g., Martínez Navarro et al., 2003), the sedimentological analysis (e.g., Oms et al., 2011) and the invertebrate assemblages preserved at different layers (e.g., Anadón et al., 1986; 2015) furthers the knowledge of the environment in which these hominins lived. And yet, there was a glaring absence of fossil flora at the Orce sites until recently.

Despite the great amount of works and surveys carried out at the Orce sites and other Pleistocene fossils sites and outcrops at both the Guadix and Baza Basins, there was no comprehensive description of palaeobotanical material. No classification of macroflora has ever been presented and attempts at recovering pollen from surface samples and coprolites have been unsuccessful (Carrión et al., 2009). Pollen was initially reported from the Orce sites (Jiménez-Moreno, 2003) but later revealed to represent the effects of modern contamination (Jiménez-Moreno, personal communication). Ortiz et al. (2003) were successful at retrieving small amounts of pollen grains from the Venta Micena site, only describing the presence of Pine and grass pollen, without accompanying pollen counts.

With such lack of palaeobotanical information, the reconstruction of the hominin habitat has been restricted mainly to palaeofaunal and geochemical analyses (e.g., Palmqvist et al., 2008; Agustí et al., 2010, 2015a; Blain et al., 2011; Rodríguez-Gómez et al., 2016). These analyses are able to hint at the existence and succession of different environments through the Early Pleistocene, with the presence of presumably open and forested areas near the Orce sites. Nonetheless, the specifics of these Early Pleistocene environments and their relationship with climate remained concealed. Most palaeoclimate analyses performed often target the relatively short time intervals recorded by the strata at the hominin sites (e.g, Agustí et al., 2010; Blain et al., 2011; 2016) and those which target longer sections (Ortiz et al., 2006) employ a sampling resolution too broad to allow for direct correlation with the Early Pleistocene glacial-interglacial cycles. These analyses employ resolutions too short or too high to properly highlight the environmental changes that might have affected the distribution of *Homo*. Consequently, there is a lack of palaeoenvironmental information regarding the frequency and amplitude of the climatic and vegetational shifts and cycles which could have affected the presence of early hominins at Southern Spain.

Therefore, the knowledge gaps regarding the hominin occupation of the Baza Basin during the Early Pleistocene are clear: Although different palaeoclimate analyses have been conducted targeting specific time intervals of the Early Pleistocene, there is no large-scale climate analysis which allows to identify the glacial-interglacial cyclicity of the climate of the Baza Basin. Furthermore, the types of vegetation present at the Orce sites and in the whole basin, as well as their taxonomic composition are unknown. Finally, the lack of palaeobotanical data also obstructs the full understanding of the hominin environment and its resources.

All these knowledge gaps prevent the complete reconstruction of the habitat that some of the first hominins out of Africa found in the European continent. By closing those gaps, it will be possible to obtain a better understanding of why early *Homo* is found in Southern Spain and whether or not it could have inhabited the region consistently through the Early Pleistocene. Additionally, by defining the early hominin habitat at Baza, the present research contributes to the characterization of the Eurasian hominin habitat. In the future, the identification of similar potentially habitable environments along the Afro-Eurasian border regions could allow for the locating of hominin migration routes which allowed *Homo* to colonize Eurasia.

1.3. Objectives

The present PhD thesis aims at reconstructing the changing hominin environment present at the Baza Basin during the Early Pleistocene and at understanding how such environmental dynamics might have affected the expansion of *Homo* into Europe. To this aim, three specific objectives are defined:

1- To identify the climatic dynamics of the Early Pleistocene in the Iberian Peninsula and, specifically, to identify the dynamics of climate change which affected the Baza Basin, where the Orce hominin sites are found. In this way, it would be possible to understand how climate change could have influenced the habitat and the distribution of early *Homo*.

2- Reconstructing and mapping the vegetation composition and organization during the time when *Homo* was present in the area of Baza and identifying the major vegetation shifts and cycles which transitioned during the Early Pleistocene. Completing this task allows for the understanding of the nature and severity of climate-driven shifts in vegetation composition and structure, and allows estimating the intensity of the climate changes which might have affected early hominin communities.

3- Assessing the number of plant foods available at each vegetation unit and their seasonal availability. By achieving this, it would be possible to identify the 'richest' types of vegetation and at what seasons these sources of food were accessible to early *Homo*. Together with the identification of long-term vegetation changes it will be possible to identify how the Early Pleistocene climate changes impacted the availability of plant resources and survivability of hominins at Orce.

Together, all these three main objectives will reveal the climate dynamics in Southern Spain, how these dynamics created shifts in the vegetation of Baza and, finally, how these shifts of vegetation affected the distribution of potential plant resources. With these questions answered, new insights may be gained regarding the relationship between early hominins and their environment, how climate may have affected hominin expansion into Europe and what made Orce an area susceptible of hosting *Homo* communities.

1.4. Early Pleistocene climate and vegetation

The climate during the Quaternary period is characterized by an alternation of glacial and interglacial climate cycles. These cycles have been recorded by geochemical, sedimentological and fossil archives, which describe periodical changes in the Earth's surface temperatures, which oscillate between warm (interglacial) and cold (glacial) periods. A comparison between the global $\delta^{18}O$ record from benthic and planktonic foraminifera, which describes the alternation between different climate periods, and past changes in the Earth's orbital forces suggests that these same forces are behind the Quaternary periodic climate oscillations (Lisiecki and Raymo, 2005, 2007; Fig. 1.2). These forces are: eccentricity (the shape of Earth's orbit), obliquity (axial tilt with respect to the orbital plane) and precession (the direction of Earth's axis of rotation).

At the beginning of the Quaternary, during the Early Pleistocene, the glacial and interglacial alternation rates seem to be in tune with the cyclicity described by obliquity forces, with a periodicity of ca. 41 kyr (Huybers, 2006; Lisiecki and Raymo, 2005, 2007;

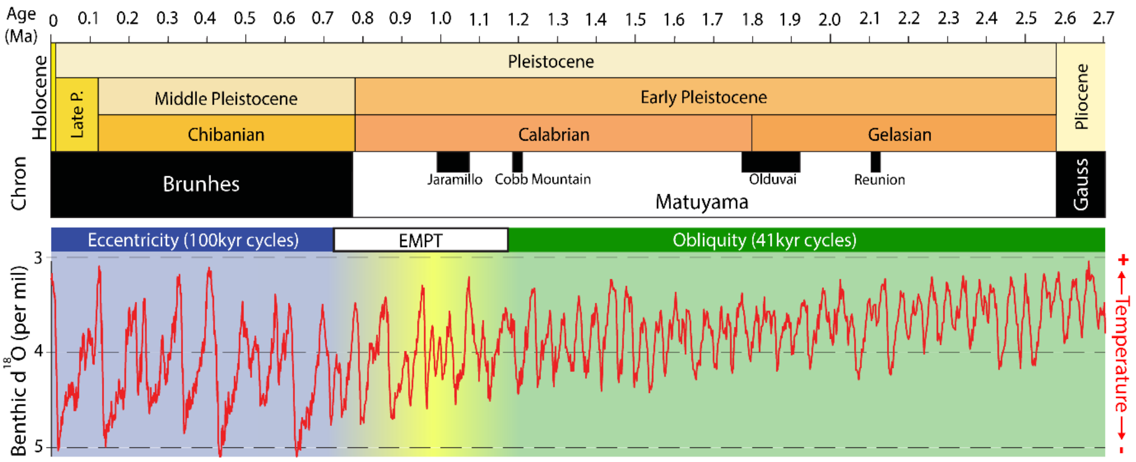


Fig. 1.2: Subdivisions of the Quaternary period into chronostratigraphical periods and polarity chrons (geomagnetic reversals) according to Gibbard and Cohen (2019). Bethic d^{18}O curve from Lisiecki and Raymo (2005) indicating the alternation between periods of global warming (interglacials) and cooling (glacials).

Fig 1.2). These interglacial periods experienced overall warming and an increase in precipitations, while glacial periods were generally colder, dryer and saw the advance of polar ice sheets towards lower latitudes. However, when compared with the glacial periods of the Middle and Late Pleistocene, the glacials of the Early Pleistocene underwent a relatively mild global cooling (Lisiecki and Raymo, 2005; Shakun, 2017), showing moderately low ice volumes and developing relatively thin glacial ice sheets (Rea et al., 2018). At the end of the Early Pleistocene and during the Middle Pleistocene, this climatic configuration changes, as the climatic cycles increase in amplitude and decrease in frequency. The new cycles seem to match the variation of orbital eccentricity, which has a periodicity of ca. 100 kyr (Lisiecki and Raymo, 2005, 2007). This progression from obliquity-driven to eccentricity-driven climate is named the Early-Middle Pleistocene Transition (EMPT), developing between 1.2 and 0.6 Ma (Head and Gibbard, 2005). The glacial periods of the Middle and Late Pleistocene involved a more intense global cooling than the ones experienced prior, causing the glacial sheets to advance into lower latitudes, creating extreme environmental changes (e. g., Siegert and Dowdeswell, 2004).

With respect to the Mediterranean Basin and the Iberian Peninsula, the Early Pleistocene climate is known from several continental and marine sequences. These describe warm and humid interglacial periods and cold and dry glacials (e.g., Suc and Popescu, 2005; Bertini, 2010; Fusco, 2010; Combourieu-Nebout et al., 2015). The global climatic cyclicity carried severe environmental changes in the Mediterranean area. Usually, the warm and humid conditions of the interglacial periods allowed the development of warm-temperate forests, while the dry and cold climate of glacial periods was accompanied by the expansion of steppe plants such as *Artemisia* or *Ephedra* (Suc, 1984; Pons et al., 1995; Suc and Popescu, 2005; Klotz et al., 2006; Bertini, 2010, 2013). These climatic and environmental patterns were also experienced in the Iberian Peninsula (González-Sampériz et al., 2010), where a similar climatic cyclicity is reported from Early Pleistocene continental and marine sequences containing long pollen records (Combourieu-Nebout, 1993; Combourieu-Nebout et al., 1999; Leroy, 2008; Camuera et al., 2019; Torres et al., 2020; Toti et al., 2020).

Furthermore, and regardless of the climatic cyclicity, a humidity gradient seems to have existed in the Mediterranean realm during the Early Pleistocene. Northern latitudes often developed lush humid broadleaf and needleleaf forests, as recorded by the palynological records from the coast of France (Leroy et al., 1994), Northern Italy (Ravazzi and Strick, 1995; Ravazzi, 2003) and the central part of the Balkan Peninsula (Panagiotopoulos et al., 2020). In contrast, southern latitudes of these same regions show a greater abundance of herbaceous and xerophytic plants, pointing to the presence of much more open environments, such as woodlands, open forests or even steppes. (e. g. Joannin et al., 2008; Tzedakis et al., 2006). At the Iberian Peninsula, the northern latitudes also contain pollen assemblages describing forested environments (e. g., Leroy, 1997; 2008), but the lack of pollen records from the Southern Iberian Peninsula did not allow identifying similar aridity gradients.

The Early Pleistocene flora in the Mediterranean realm was partly composed of the same taxa which can be found in the modern environments of the region, with the exception of several Arctotertiary taxa. Those taxa were remnants of the widespread subtropical Neogene floras which persisted up to the Early and Middle Pleistocene. Tree genera, such as *Taxodium*, *Sciadopitys*, *Cathaya*, *Tsuga*, *Eucommia*, *Engelhardia*, *Carya*, *Pterocarya*, *Parrotia*, *Liquidambar* and *Zelkova*, were common in the Early Pleistocene floras of Southern Europe (Magri et al., 2017), including the Iberian Peninsula (Postigo-Mijarra et al., 2010). Progressively and through the Early and Middle Pleistocene, these taxa were extirpated from the European floras, with one likely cause being the general aridification and cooling associated with the EMPT (Head and Gibbard, 2015; Magri et al., 2017). An eastward direction of extirpation can be identified, with the majority of these taxa disappearing first from the Western Mediterranean regions and subsequently from the Eastern regions (Magri et al., 2017). In modern environments, these genera are completely absent from Western Europe natural environments and can generally be found only in modern subtropical climates of North America and East Asia.

1.5. Relationship between the expansion of *Homo* and climate

1.5.1. State of the art and open debates

The role of climate in the expansion of early hominins into Europe is yet to be fully understood, mainly due to the lack of a common chronological framework between the extensive climatic archives and the scarcity of hominin sites (Moncel et al., 2018). Nonetheless, it is believed that climate played a critical role in the first hominin dispersal outside of Africa. Climate changes at the beginning of the Pleistocene may have led to the displacement of herbivores from Africa into Eurasia, which in turn caused *Homo* to follow these herds and to encounter new warm and habitable environments with comparatively low carnivore density (Carotenuto et al., 2016). Such environments were found in the Southern European regions, where Early Pleistocene carnivore density is thought to have been significantly lower than that of African environments (Rodríguez and Mateos, 2018).

After the first hominin colonization of Europe, the glacial-interglacial cyclicity of the Early Pleistocene climate would have affected the distribution of *Homo* in the continent. Climate could have played a constraining effect since it is believed that early hominins did not achieve control of fire until ca. 1 Ma in Africa (Berna et al. 2012) and 0.9/0.7 Ma in Eurasia (Rhodes et al., 2016). It is also believed that *Homo* did not have access to advanced clothing during the Early Pleistocene due to the lack of both direct and indirect evidence of clothing or cloth-making tools (Hosfield et al., 2020, pp. 97–107, and references therein). This left early *Homo* unprotected from severe climate changes and especially susceptible to the cold climate associated with the development of glacial periods.

Despite most authors favouring a hominin preference for warm and humid climates (e.g., Agustí et al., 2009; 2015a; Dennell et al., 2011; Falguères, 2020), no consensus exists regarding the effect of cold glacial climate on European hominin populations. Leroy et al. (2011) cross-referenced hominin sites in Europe against climate models and found that early *Homo* might not have been able to withstand average winter temperatures below 0ºC. These measurements lead to the suggestion that glacial periods, glacial winters specifically, would have caused the extirpation of *Homo* populations from Europe. Then, subsequent African hominins would have re-entered Europe at the onset of the following interglacial period and the warming of the climate.

Furthermore, Leroy et al. (2011) suggest *Homo* entered Europe only during the transition between glacial and interglacial periods, when the incipient interglacial warm climate overlapped with the declining glacial open landscapes, before open environments were replaced by lush forests. The authors consider *Homo* strictly as an African mammal restricted by a set of environmental requirements such as a combination of warm climate and open landscapes or dry meadows. These requirements would have been met during periods of environmental transition, creating windows of opportunity for early *Homo* to disperse into Europe. This hypothesis relies on the relative lack of hominin sites formed in a context of cold climate.

Thus, the presence of *Homo* in Europe would have been intermittent and driven by climate forcing (Bermúdez de Castro et al., 2003; Agustí et al., 2009, 2015a; Leroy et al., 2011; Bermúdez de Castro and Martinón-Torres, 2013). This hypothesis can be summarized in a ‘sources and sinks’ model of hominin colonization (Dennell et al., 2011). The model assumes the existence of ‘source’ populations, or areas, situated outside of Europe which act as launching pad for migrant waves into the continent when the environmental conditions are favourable. These new European ‘sink’ populations would disappear during harsher climatic periods, and the cycle would be repeated following the Early Pleistocene climate cyclicity (e.g., MacDonald et al., 2012).

Alternative views claim that the hominin record is not complete enough to rule out the possibility of *Homo* being present during glacial periods and their uninterrupted occupation of Europe since the time of first arrival (Moncel et al., 2018). Some authors doubt that the potential habitat of early hominins was delimited by a strict set of environmental parameters, such as specific temperature values or the availability of dry meadows, and propose that *Homo*, as early as 2 Ma, had the capacity to adapt and survive in a great array of environmental scenarios, from xeric open steppes to woodlands and lush humid forests, both in Africa (Mercader et al., 2021) and in Europe (Messager et al., 2010). In this way, alternative hypotheses suggest that, while northern European populations were likely to be displaced by lower temperatures and the advance of ice sheets (MacDonald et al., 2012), southern populations could survive in glacial refugia in the Mediterranean peninsulas (Pross and Klotz, 2002; Carrión et al., 2003; 2011). These populations would endure the harsher climatic phases and act as 'source' populations, expanding northward during the following warmer period (Cuenca-Bescós et al., 2011; Orain et al., 2013; Bermúdez de Castro et al., 2016).

Generally, the EMPT is seen as a favourable event regarding the distribution of *Homo* in Europe, as the general aridification and disappearance of heavily forested environments in favour of semi-open woodlands, steppes and dry meadows, is seen as an improvement to hominin habitats (Cuenca-Bescos et al., 2011; Leroy et al., 2011). Nonetheless, the EMPT could have also represented a challenge for the survival of *Homo* in Europe due to the intensification of the glacial periods, making them longer and colder, which could have pushed hominin communities to seek refuge areas (Orain et al., 2013). However, by the Middle Pleistocene early *Homo* likely had developed the use of fire and clothing (Hosfield et al., 2020, pp. 87–107, and references therein), in this way increasing its adaptability to glacial climate and ensuring a permanent presence in Europe.

An indirect way in which climate could have influenced the dispersal of early hominins is its effect on the environmental resources available to hominins. Resource availability has been identified as a strong driver of *Homo* presence (e.g., Orain et al., 2013; Huguet et al., 2017), including food, raw materials and water. Changes in climate carry changes in vegetation, which in turn also lead to faunal changes. These environmental changes bear the decrease or increase in resources potentially used by *Homo*, mainly animal and plant foods. In this way, some authors indicate that hominin presence could be linked with high environmental diversity (Kahlke et al., 2011; Carrión et al., 2008; 2011; Orain et al., 2013). Highly diversified environments would grant access to equally diverse animal and plant-based resources. Thus, climate changes which increase or reduce the diversity of vegetation types and faunas could have great repercussion regarding hominin occupation.

1.5.2. Was *Homo* in the Iberian Peninsula constrained by climate?

The Iberian Peninsula contains one of the richest records of Early Pleistocene hominin occupation in Europe. Specifically, the southeastern part of the Peninsula contains several sites. The sites of Orce, in the province of Granada, provide lithic artifacts and scarce fossil material dated around 1.4 and 1.2 Ma (Toro-Moyano et al., 2013). Additionally, the cave sites of Cueva Victoria and Estrecho del Quıpar (Cueva Negra de Estrecho del Río Quípar), in the region of Murcia, yielded a hominin phalanx, lithic tools and hominin teeth, dated approximately to ca. 0.9 to 0.8 Ma according to palaeomagnetic and biochronological data (Scott and Gibert, 2009; Gibert et al., 2008; Gibert et al., 2015; 2016).

At Northern Spain, in the province of Burgos, the sites of Sierra de Atapuerca provide an exceptionally unique record of hominin habitation through the Pleistocene. These sites represent multiple fill sequences of a complex karstic system which have yielded thousands of fossils and lithic artifacts. Two sequences in Atapuerca contain Early Pleistocene hominin records: Sima del Elefante and Gran Dolina. A hominin mandibular fragment was uncovered at the TE9 stratigraphic level of Sima del Elefante, dated approximately as 1.2 to 1.1 Ma based on a combination of magnetostratigraphy, cosmogenic nuclides and biostratigraphy (Carbonell et al., 2008). At the sequence of Gran Dolina, level TD6 contains well preserved hominin remains which allowed the discovery of *Homo antecessor* (Bermúdez de Castro et al., 1997, 2008), dated to 0.936 Ma by combining magnetostratigraphy, radiometry (U-Pb) and ESR (Parés et al., 2013).

At North-eastern Spain, in Catalonia, the sites of Vallparadís and Barranc de la Boella both reveal Early Pleistocene hominin presence. The site of Vallparadís revealed lithic assemblages and cut marks on ungulate bones in layer 10 of the site, which has been dated by ESR to approximately 0.85 Ma (Martínez et al., 2010; Duval et al., 2015). The Barranc de la Boella site contains lithic artifacts in unit II, where average cosmogenic nucleid dates give an age of ca. 1 Ma (Vallverdú et al., 2014).

Although largely fragmentary, the exceptional hominin record of the Iberian Peninsula offers a unique examination of the relationship between early *Homo* and their environments, as well as the repercussions of climate changes in hominin distribution. The habitat of early *Homo* at the Iberian Peninsula has been partially reconstructed using mostly the faunal record at the hominin sites. Faunal analyses were performed at Atapuerca (Blain et al., 2010, 2013), Vallparadís (using the fossil material from the stratigraphically adjacent site of Cal Guardiola; Agustí et al., 2009) and Orce (Agustí et al., 2009, 2015a; Blain et al., 2011, 2016). The results describe the predominance of a warm and humid climate at the time of hominin occupation of these sites.

The remarkable palaeoanthropological and archaeological yield of the Atapuerca hominin sites has attracted scientific attention in the form of multidisciplinary analyses aimed to reconstruct every aspect of the hominin environment. The Early Pleistocene climate at the site of Atapuerca had the features of a slightly humid Mediterranean climate, with mild winters and dry summers (Blain et al., 2013). Specifically, the climate was mainly warm and humid at the time of the formation of the different hominin- and lithic-bearing strata, like level TE9 at Sima del Elefante (Huguet et al., 2017) or level TD6 at Gran Dolina (Antoñanzas and Bescós, 2002; Rodríguez et al., 2011). The Early Pleistocene environment at Atapuerca is described as a mosaic environment, characterized by the coexistence of fauna typical of open environments, grasslands, woodlands and humid forests (Rodríguez et al., 2011; Huguet et al., 2017).

In conclusion, the available evidence at different early hominin sites suggests that the presence of *Homo* at the Iberian Peninsula was linked with the existence of relatively warm and humid climate and local environments with a high diversity of vegetation types.

1.6. Background

1.6.1. Geology of the Baza Basin

The Guadix-Baza Basin, where the Orce sites are located, is an intramontane basin within the Betic Ranges in SE Spain, in the province of Granada (Fig. 1.3). The basin has a mean altitude of 1,000 m a. s. l., with the surrounding mountains reaching heights above 2,000 m. The tallest of these mountains chains is Sierra Nevada, with a maximum altitude of 3,478 m, the tallest point in the Iberian Peninsula. The Baza Basin is found between the two main geological complexes of the Betic Ranges, the Internal and the External Zones (Vera et al., 2004; Fig. 1.4). Technically, the Baza Basin is a sub-basin of the greater Guadix-Baza Basin, since it shares the same hydrographical network with the Guadix sub-Basin (to the southwest of Baza). This PhD Thesis will often use the term ‘Baza Basin’ to refer to the Baza Sub-basin, which has a highly distinct tectonic and sedimentological evolution from the Guadix sub-Basin.

The Baza Basin presents a semi-graben structure controlled by the Baza Fault, a normal fault with N-S strike and NE dip situated at the western border of the area. The semi-graben structure led to an asymmetric filling of the basin, where sediment thickness increases westward to a maximum of ca. 2,200 m in the depocenter of the basin, near the Baza Fault (Haberland et al., 2017). The oldest deposits in the basin accumulated during the Late Tortonian (ca, 7.3 Ma), when the region was part of the Betic Seaway connecting the Atlantic with the Mediterranean. The uplift of the Betic Cordillera by the end of the Tortonian caused the transition of the seaway into continental depositional environments and its separation into multiple sub-basins with different depocenters (Haberland et al.,

Fig. 1.3: Landscape of Baza with the mountains of the western Sierra de las Estancias at the background. The vegetation is composed mostly of grasses and brushes. The soil has clear coloration due to the high amount of gypsum from the lacustrine deposits. Photograph by Yul Altolaguirre.

2017). By the end of the Miocene the Baza Basin had developed an endorheic saline lake, being fed primarily by the fluvial systems present in the Guadix Basin (Vera, 1970). The lacustrine depositional environment occupied the centre of Baza Basin until the Middle Pleistocene (ca. 0.6 Ma), when the Guadix-Baza Basin was captured by the hydrographical network of the Guadalquivir River, which drains into the Atlantic Ocean (Gibert et al., 2007b). The capture of the basin led to the disappearance of the lacustrine sedimentation environment in the basin, which was replaced by an erosional configuration. The lacustrine deposits were partially dismantled by erosion which led to the creation of most of the Pleistocene to Miocene outcrops and the modern badlands landscape seen today in parts of the area. During the Holocene the basin continues to experience tectonic activity (Alfaro et al., 2008).

The Early Pleistocene materials of Baza are organized into the Baza Formation (Vera, 1970), which describes palustrine and lacustrine deposits dated from Late Miocene/Pliocene to Middle Pleistocene. The lacustrine facies distribution in the basin shows three concentric facies belts correlated to zones of increasing salinity towards the

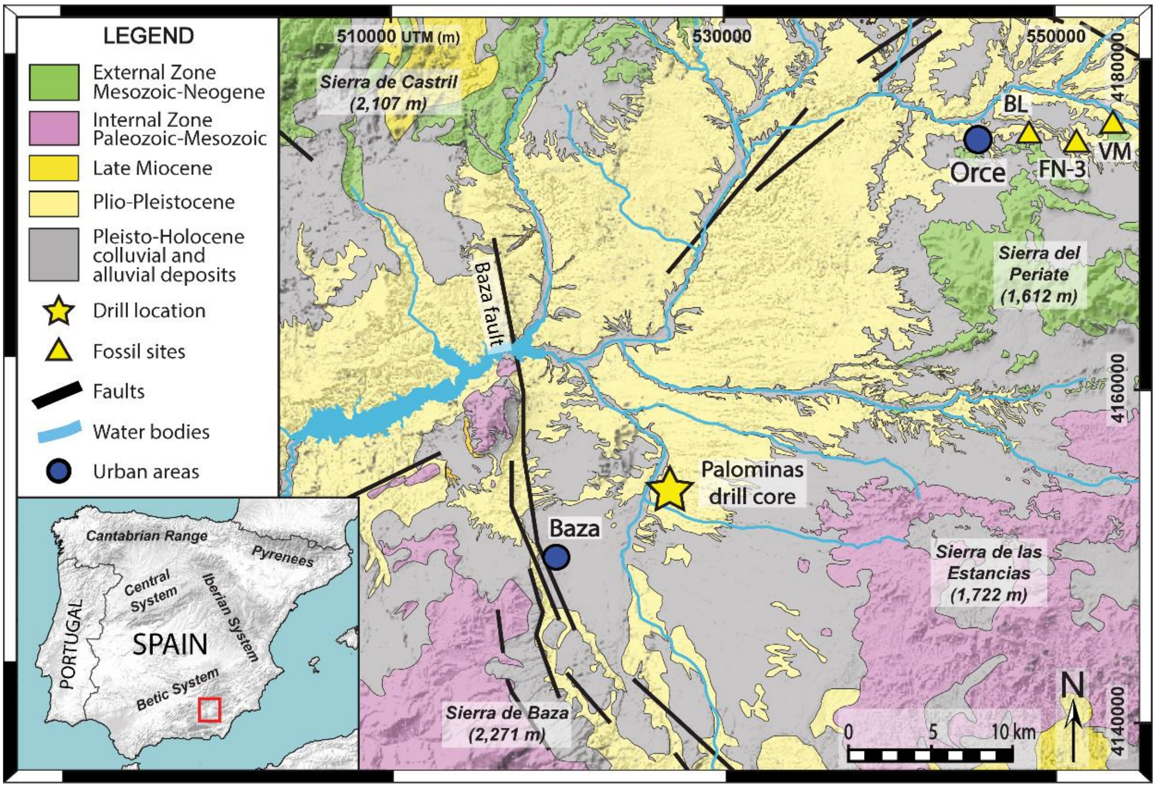


Fig. 1.4: Simplified geological map of the Guadix-Baza Basin. On the right lower corner: the position of the Guadix-Baza area in the Iberian Peninsula. Geological data from Roldán et al. (2012). Main faults from Sanz de Galdeano et al. (2012).

Inner zone of the lake (Gibert et al., 2007a). The Marginal zone includes sediments deposited in the more proximal area, close to the mountains, where alluvial and palustrine deposits alternate. The Intermediate zone contains gypsiferous-calcareous facies, and is interpreted as a mosaic of shallow ponds surrounding the main lake body. The Inner zone represents the most distal part of the lacustrine environment occupied by a shallow saline lake. The deposits in this Inner zone consist generally of an alternation of laminated gypsum and fine-grained carbonates (Fig. 1.5; Gibert et al., 2007a).

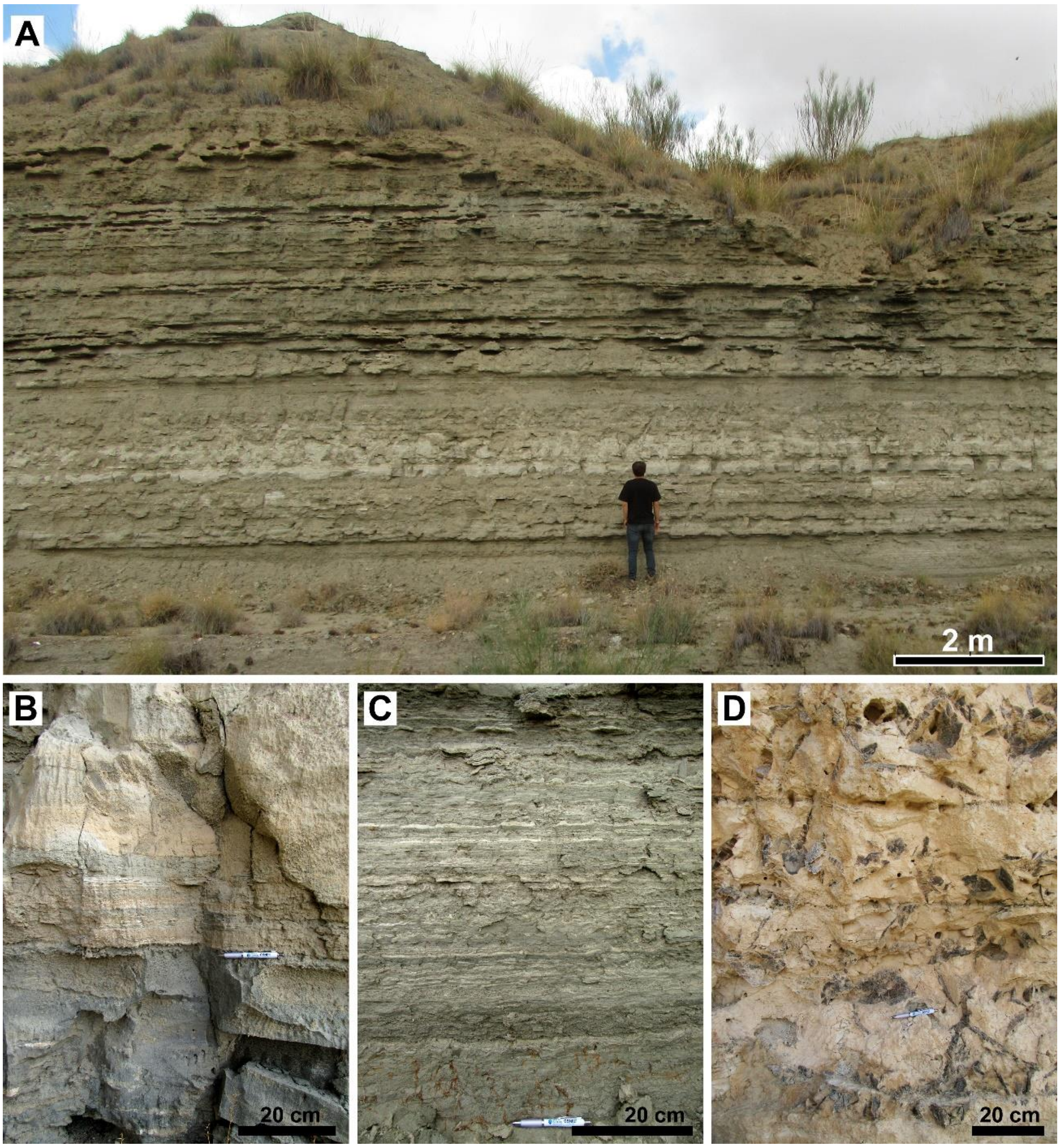


Fig. 1.5: Photographs of lacustrine materials from different lithofacies of the Inner Zone (as defined by Gibert et al., 2007a), taken at outcrops located near the locality of Río de Baza. A) Lacustrine deposits of white and grey carbonates (marls) and evaporites. B) Gray and white lutite/clay levels with intercalations of gypsum laminae. C) Alternation between gypsum laminae (dark) and carbonate laminae (clear). D) Lutite level with macrocrystalline gypsum lenses. Photographs by Yul Altolaguirre.

The interpretation of the lacustrine deposits describes the Baza Palaeolake system as formed by a shallow but large and presumably permanent water body surrounded by smaller ponds. Fresh to slightly saline waters probably characterized the satellite ponds, while higher-salinity conditions predominated in the central body (Gibert et al., 2007a; El Hamouti and Gibert, 2012; Anadón et al., 2015).

1.6.2. The Orce sites

The sites of Orce are found in the NE part of the Baza Basin, near the small locality of Orce (Fig. 1.4). The sites are found within marginal lacustrine deposits belonging to the Baza Fm. (Oms et al., 2011). In this PhD thesis, the term ‘Orce sites’ will be used in reference to the three hominin fossil sites found in close geographical proximity. These the are sites of Venta Micena (VM), Barranco León 5 (BL5) and Fuente Nueva 3 (FN3), listed from stratigraphically lower to higher (Fig. 1.6). Sedimentological evidence (Oms et al., 2011) suggest that BL5 was formed by a high energy current entering a lacustrine/palustrine environment, transporting clasts, gravel, bones and lithic artifacts

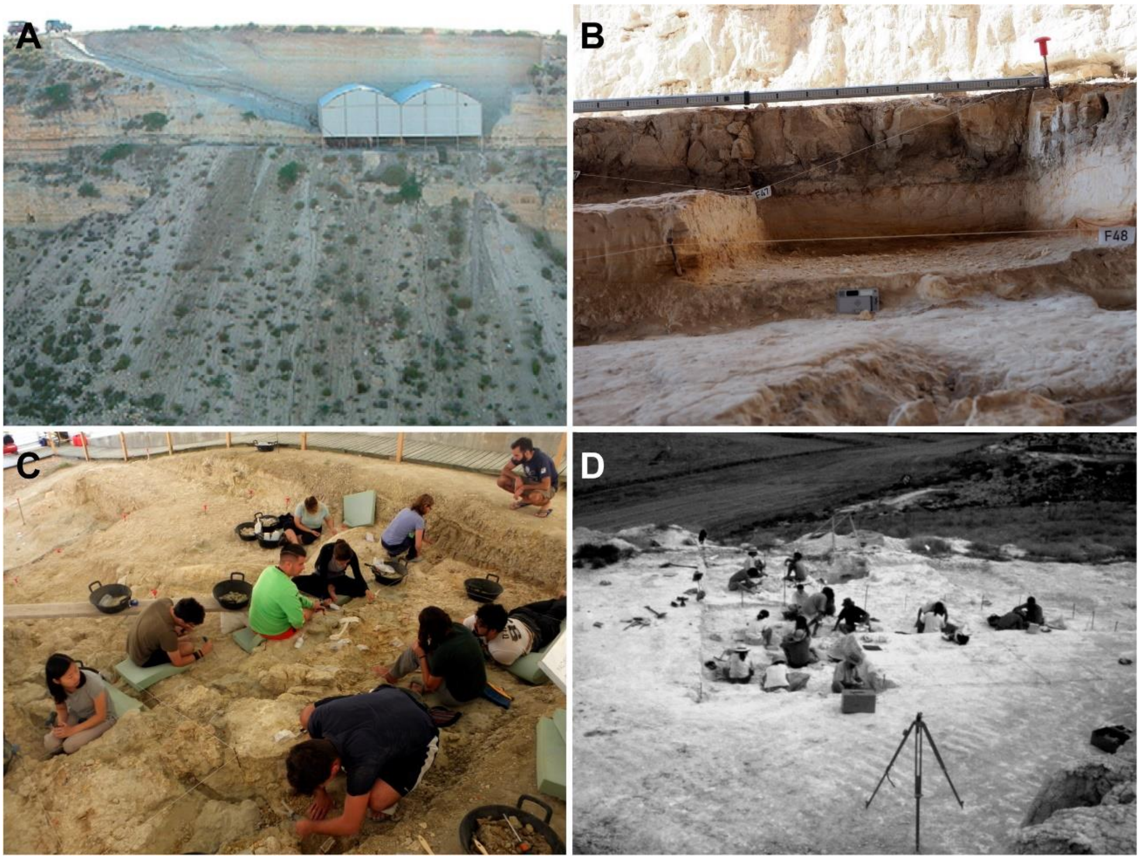


Fig. 1.6: Photographs of the hominin sites of Orce. A) General view of the Barranco León site; B) Excavation at BL5; C) Excavations at Fuente Nueva 3; D) Excavations at Venta Micena. Photograph A from Toro-Moyano et al. (2011), B and D by Juan Manuel Jiménez Arenas and D by Luis Gibert.

from a short distance. On the contrary, FN3 could have been formed in a low energy palustrine environment, by slow sediment accumulation rates (Oms et al., 2011). The site of VM is interpreted according to taphonomical evidence as a biogenic accumulation by the giant short-faced hyena *Pachycrocuta brevirostris* near the entrance of their dens, those having been excavated near shallow ponds (Arribas and Palmqvist, 1997).

Both BL5 and FN3 have yielded ample assemblages of Oldowan lithic artifacts (Gibert and Martinez, 1992; Gibert et al., 2006a; Gibert et al., 1992, 1998a, 2006b; Toro-Moyano et al., 2009, 2011). Despite of the abundance of lithic tools, fossil material is scarce. The only uncontested hominin fossil material from Orce is a deciduous lower molar, found at the BL5 site (Toro-Moyano et al., 2013). Tooth fragments tentatively classified as *Homo* are also reported from the BL5 site (Gibert et al., 1999; Ribot et al., 2015), although Toro-Moyano et al. (2013) argue against that classification due to morphology and their stratigraphic position.

The site of VM contains one of the most important vertebrate assemblages of the European Early Pleistocene, with more than 10,000 bones representing at least 214 individual animals (Gibert et al., 1992). However, its status as a hominin site has been surrounded in controversy. It was the first fossil site at Orce where hominin fossil material was reported, consisting of cranium and humerus fragments (Gibert et al., 1983). Although no lithic industry is found at VM, cut marks on mammal bones were described as the product of hominin activity (Gibert and Martinez, 1992; Gibert et al., 1992). These discoveries were followed by scepticism regarding the validity of the findings, triggering a back and forth of scientific publications arguing for and against the hominin nature of the fossil material from Venta Micena (Gibert et al., 1989; Moyà-Solà and Köhler 1997; Palmqvist 1997; Gibert et al, 1998b, 2002; Borja et al., 1997; Martínez-Navarro, 2002; Palmqvist et al, 2005). Although still not formally resolved, the last publication on the topic argues that the unique morphology of the cranium fragment justifies its classification as *Homo* (Campillo et al., 2006).

With respect to the age of the sites, the lack of volcanic material complicates the accurate dating of the Orce sites. Despite of multiple attempts at dating the sites, results are often in conflict with other age estimations and no consensus on an accurate age model exists (Fig. 1.7). The faunal assemblages of the sites clearly reflect Early Pleistocene faunas and the rodent assemblages from VM are older than the ones from BL5 and FN3 (Oms et al., 2011; Agustí et al., 2015b). The site of VM would belong to the biozone of the rodent *Allophaiomys ruffoi*, dated approximately between 1.6 and 1.4 Ma, while BL5 and FN3 belong to the *A. lovocati* biozone, tentatively dated as 1.4 to 1.07 Ma (Agustí et al., 2015b). Rodent biostratigraphy has also been employed in other dating attempts. Since

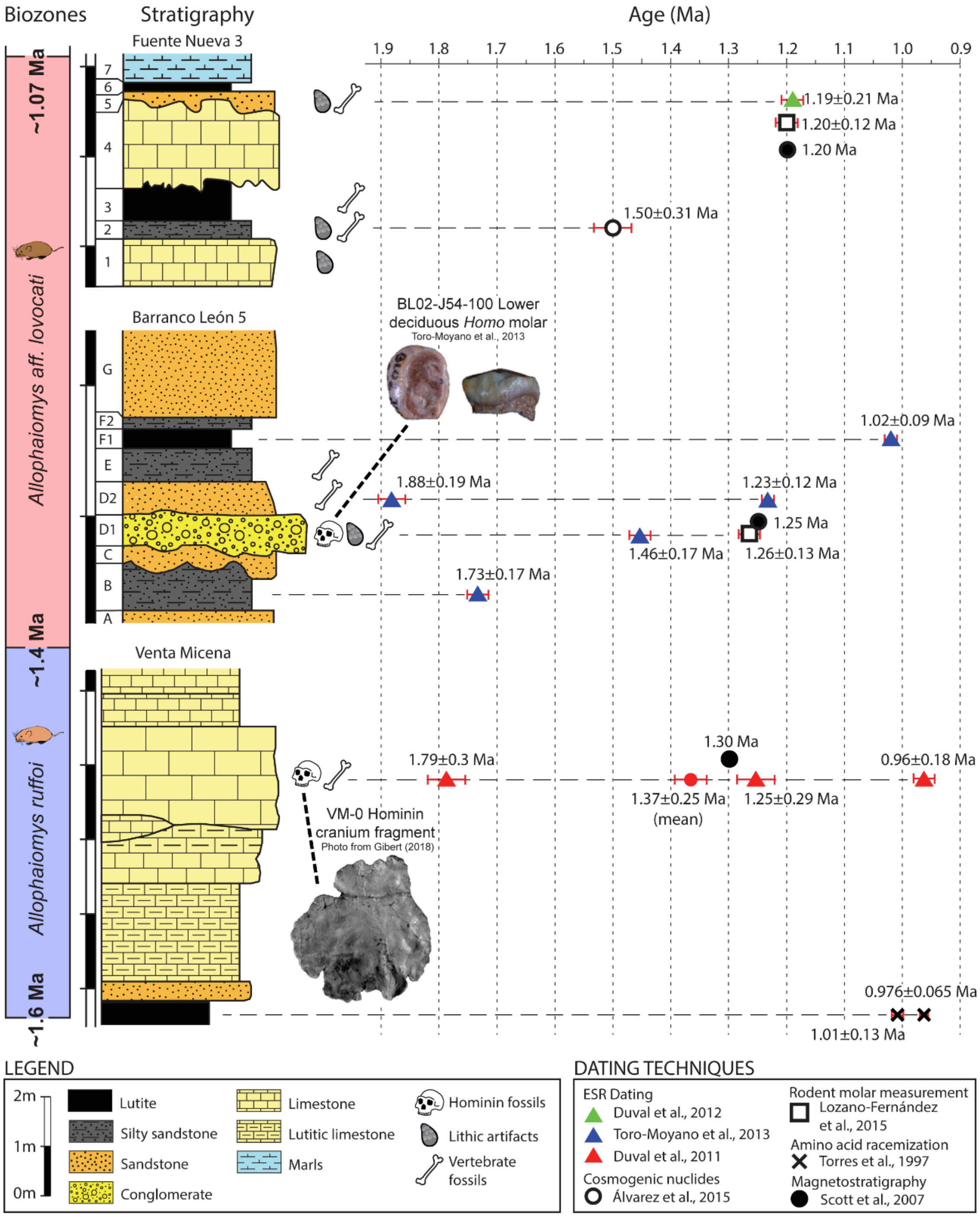


Fig. 1.7: Stratigraphical column of the sites of FN3, BL5 (from Oms et al., 2011) and VM (from Anadón et al., 1987). Biozones from Agustí et al. (2015b) and several age estimates at the different stratigraphic levels of each site.

rodent dental evolutionary trends through time are well known, dental measurements have been used as a dating method. In this way, the dimensions of molars of the vole *Mimomys savini* fount at BL5 were extrapolated to an age of 1.26 Ma, the molars found at FN3 were dated as 1.20 Ma (Lozano-Fernández et al., 2015). Nevertheless, the validity of this dating technique is contested (Palmqvist et al., 2015).

Multiple magnetostratigraphic studies were conducted revealing reverse polarities at the Orce sites (Oms et al., 2000; Scott et al., 2007; Toro-Moyano et al., 2013), associated with the Matuyama chron (0.773-2.595 Ma; Gibbard and Cohen, 2018). An approach based on the interpolation of palaeomagnetic data and stratigraphic vertical distances allowed to date the hominin sites with minimum ages of 1.3 Ma for VM, 1.25 Ma for BL5 and 1.2 Ma for FN3 (Scott et al. 2007), although Oms et al. (2011) claim that employing such method might produce problematic dates.

Dating by amino acid racemization was also applied to the lower strata of VM, generating ages around 1.0 Ma (Torres et al., 1997) although the method might have produced underestimated values (Gibert, 2018). Additionally, the FN3 site was dated to 1.5 Ma, using ^{26}Al and ^{10}Be cosmogenic nuclides present in quartz to date sediment burial (Álvarez et al., 2015).

More attempts at dating all three of the Orce sites were carried out using the U-series/electron spin resonance (ESR) method. ESR was first applied to mammal teeth from VM, where the mean value of all age measurements was 1.37±0.25 Ma, a value deemed realistic by the authors (Duval et al., 2011). The same methodology was applied to FN3 and BL5 (Duval et al., 2012), which allowed the authors to place the Orce sites between the Olduvai and Jaramillo subchrons (1.78–1.07 Ma). The ESR methodology was also applied to quartz grains from BL5 (Toro-Moyano et al., 2013), where the authors present a weighted mean age of 1.4±0.38 Ma. Although the ESR method has been applied to all three of the sites, the measurements for each individual site present a considerable spread. In some cases, ESR measurements from the same layer can report a difference of over 0.5 Myr (such as level D1 at BL5; Toro-Moyano et al., 2013; Fig. 1.7). These and other problems with the method (Muttoni et al., 2013) introduce uncertainty regarding the age of the sites and difficult the task of placing the Orce sites within the dynamics of the Early Pleistocene climate.

This disparity of age measurements, by different methodologies, prevents finding a consensus regarding the exact time when *Homo* was present at Orce. Thus, the age of the first hominin occupation cannot be narrowed down to specific climatic cycles or MIS stages. Any palaeoenvironmental analysis with the objective of reconstructing the hominin environment must observe a broad time interval of the Early Pleistocene.

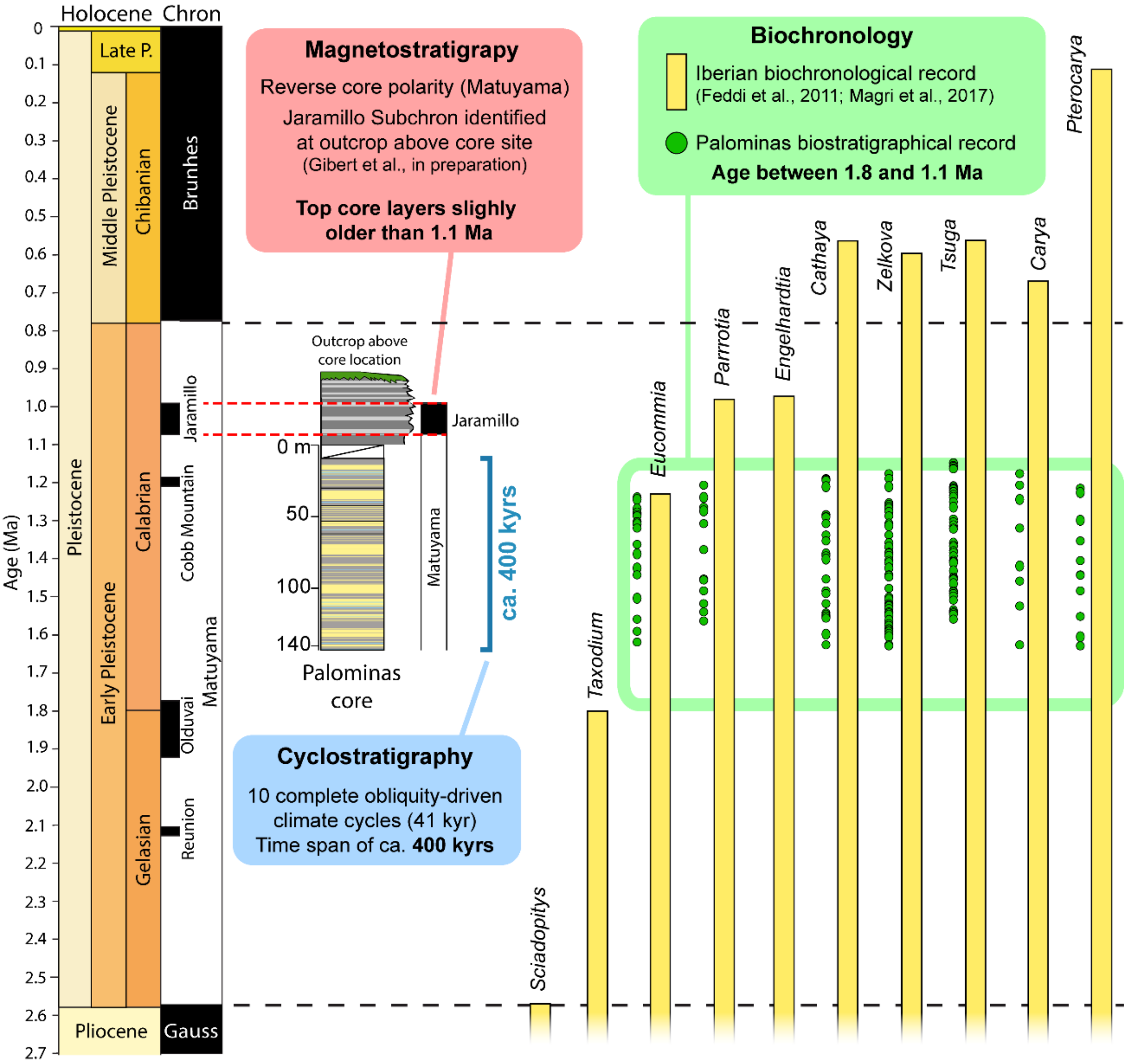
1.6.3. The Palominas drill core

The Palominas drill core was performed by the Centro Tecnológico del Mármol in 2011, at the Pleistocene lacustrine deposits situated 7 km NE of the town of Baza (37º31’03”N; 2º42’39”W; 750 m a.s.l.), near the locality of Río de Baza and the Palominas cave. According to the classification of the lacustrine materials of the Baza Fm. by Gibert et al. (2007a), the drilled material belongs to the Inner zone, which comprises over 500 m of laminated lacustrine deposits (Haberland et al 2017; Fig. 1.5). Drilling operations stopped at a depth of 107.5 m. During the operations, the material expanded vertically due to decompression. After drilling, the total length of the core was measured at 142.32 m, as it is now stored in core boxes.

The upper 10.1 m of the core are described as conglomerates and gravels overlaying uncomfortably the lacustrine. The initial 10.1 m are interpreted as recent alluvial materials. The lacustrine materials materials (10.1 to 142.32 m) consist of fine endogenic carbonates of grey to dark coloration. Gypsum appears as laminated beds and also as large lenticular crystals of post-sedimentary interstitial growth. Layers of cemented dolomite (< 20 cm thickness) and of grey-dark clays are found occasionally through the record. The core material is currently stored at the Faculty of Earth Sciences of the University of Barcelona, where it was split into two halves.

The core and the lacustrine material of the Baza Fm. contain a high concentration of pollen grains. The pollen appears in good state of preservation, which may be directly related to the evaporitic nature of the deposits. The evaporites might have protected the pollen grains from weathering, as seen in Badenian evaporitic deposits of the Polish Miocene (Durska, 2016, 2018). The preservation of the pollen grains and their features allow for the determination of 107 distinct pollen types identified to genus or family level, as well as multiple cryptogam, algal and fungal spores. The pollen assemblages from the Palominas core are typical of Early Pleistocene palynofloras.

According to the regional biostratigraphical data, the core should comprise an age older than 1,1/1.2 Ma but younger than 1.8 Ma, placing the time interval recorded in the core within the Calabrian stage (1.8 to 0.774 Ma; Gibbard and Cohen, 2018). This age model may be further constrained by correlating the cycles described by the pollen record to obliquity cyclicity, the predominant climate force of the Early Pleistocene. In this way, the Palominas core represents a period of 400 kyr, tentatively dated to between 1.1 to 1.5



Magnetostratigrapy
Reverse core polarity (Matuyama)
Jaramillo Subchron identified at outcrop above core site
(Gibert et al., in preparation)
Top core layers slighly older than 1.1 Ma

Biochronology
Iberian biochronological record (Feddi et al., 2011; Magri et al., 2017)
Palominas biostratigraphical record
Age between 1.8 and 1.1 Ma

Cyclostratigraphy
10 complete obliquity-driven climate cycles (41 kyr)
Time span of ca. **400 kyrs**

Fig. 1.8: Diagram illustrating the three components of the age model for the Palominas core: Palaeomagnetical data suggests the presence of the Jaramillo subchron in the outcrop of the sequence drilled by the Palominas core. Biochronological data indicates a deposition age between 1.8 and 1.1 Ma, due to the presence of taxa such as Eucommia and the absence of older taxa (*Sciadopitys* and *Taxodium*). Cyclostratigraphical data points to the core comprising a time period of at least 400 kyrs according to the identification of 10 complete climatic cycles driven by obliquity forcing (41 kyr cycles).

Ma (Altolaguirre et al., 2020/Chapter 3). This age model could be supported by unpublished preliminary palaeomagnetic data (Gibert et al., 2015; Gibert et al., in preparation) which reveal the entirety of the core to be of normal polarity, associated with the Matuyama Chron (0.773–2.595 Ma; Gibbard and Cohen, 2018). Additionally, layers of normal polarity at an outcrop immediately above the drilling site could indicate the presence of the Jaramillo reversal (1.071 to 0.99 Ma; Gibbard and Cohen, 2018) directly above the layers recorded at the core (Fig. 1.8).

There are no erosive surfaces or evidence of bioturbation recorded through the core which, together with the sedimentological interpretation of the Inner zone facies of the Baza Fm. (Gibert et al., 2007a), suggest an uninterrupted sedimentation rate. Therefore, the Palominas core potentially comprises the uninterrupted time interval between 1.5 to 1.1 Ma.

1.7. Introduction to employed methodologies

Multiple methodologies are applied in order to achieve the outlined objectives and aims of this PhD thesis. These methods can be grouped into palaeoclimate reconstruction methods, palaebotanical methods and the methodology for quantifying plant food availability.

1.7.1. Methodologies focused on palaeoclimate reconstruction

Coexistence Approach

The Coexistence Approach (CA) (Mosbrugger and Utescher, 1997; Utescher et al., 2000, 2014) is used in order to infer palaeoclimate data from pollen and other palaeobotanical assemblages. Employing this method allows to recreate past temperatures and precipitation values. The CA method assigns nearest living relatives (NLRs) to the fossil taxa. In this way, the climate range (precipitation and temperature) of the NLRs are extrapolated to those fossil taxa. Then, all the climatic ranges assigned to fossil taxa for one pollen sample, or stratigraphical level in the case of macroflora, are overlapped. The interval where all the climatic ranges coincide is defined as a ‘coexistence interval’, these intervals are the description of the palaeoclimatic context under which the selected fossil fora existed. While a broader interval (e.g., a mean annual temperature interval of 5 to 25ºC) does not reveal accurate information, these intervals can be quite narrow, allowing for the collection of realistic palaeoclimate measurements.

The CA allows the calculation of several climatic parameters: mean annual temperature (MAT), mean temperature of the coldest month (MTCold), mean temperature of the warmest month (MTWarm), MART (temperature difference between of MTWarm and MTCold), mean annual precipitation (MAP), mean precipitation of the wettest month (MPWet), mean precipitation of the driest month (MPDry), mean precipitation of the warmest month (MPWarm), and MARP (precipitation difference between MPWet and MPDry).

The CA method relies on presence and absence of taxa, while ignoring abundance. Therefore, any hypothetic climate changes expressed in variations of taxa abundance between assemblages, while conserving similar taxonomic composition, would be undetected by the CA. This challenge can be alleviated by the inclusion of additional methodologies such as biomarker analysis and other pollen-based methods, and compare those with the coexistence intervals. These pollen-based methods, such as the pollen temperature index (PTI) or the pollen climate index (PCI), correlate taxa abundance to relative environmental changes.

The application of the CA to the pollen assemblages from the Palominas core and other pollen records associated to early hominin presence is presented in Chapter 2 (Altolaguirre et al., 2019) and Chapter 3 (Altolaguirre et al., 2020). Results allow for the differentiation of humid phases and dry phases, which alternate through the Palominas record.

Pollen indexes (PTI and PCI).

The pollen temperature index (PTI; Suc et al., 2010) describes the ratio of pollen produced by tree taxa typical of warm and temperate climates, against the pollen from plants typical of steppe environments. The later (*Artemisia* and *Ephedra*) are the main representatives of the steppe environments which developed over the European continent during glacial periods. In this way, the ratio between pollen from plants typical of warm and cold climates describes relative temperature changes. The PTI has been successful at describing such temperature changes at different Pleistocene records of the Mediterranean basin, where the PTI matches other temperature proxies such as isotope records (e. g., Suc et al., 2010; Bertini et al., 2015; Toti and Bertini et al., 2018).

The pollen climate index (PCI; Joannin et al., 2011) does not track temperature directly, but the main climatic shifts represented in any given pollen record. The PCI tracks the main principal component (PC-1) resulting from a principal component analysis (PCA) of all studied pollen assemblages. The PC-1 represents the main source of variance affecting the pollen assemblages, being generally linked with environmental shifts. The use of the PCI in several Pleistocene records from Southern Spain has revealed a direct correlation with the glacial-interglacial cyclicity (Camuera et al., 2019; Carrión et al., 2019; Torres et al., 2020).

The application of the PTI and PCI is presented in Chapter 4, where it is compared with other temperature proxies, the CA and GDGT analysis.

Analysis of GDGTs biomarkers

Glycerol dialkyl glycerol tetraethers (GDGTs) are lipids found on the membranes of bacteria and archaea inhabiting soil and aquatic environments. Although their exact origin is still unknown, their degree of cyclization (number of cyclopentane rings) is correlated with environmental temperature (Schouten et al., 2013 and references therein). In this way, GDGTs retrieved from sediment samples have been successfully used as temperature proxy (MAT) in multiple palaeoenvironmental reconstructions. Specifically, GDGTs have been used to reconstruct temperature changes in Quaternary lacustrine records of the Eastern Mediterranean region (Ardenghi et al., 2019; Panagiotopoulos et al., 2020).

The temperature reconstructions are conditioned by the GDGT calibration employed in each case. These empirical calibrations are synthesized from sediment archives with different distribution of GDGTs. Some of these calibrations originate from the analysis of global sedimentary archives from a great array of environments, while others were created from the study of specific and regional environmental scenarios, such as hypersaline lakes (e. g., Günther et al., 2014.). Although ‘global’ calibrations are generally found to be applicable to most environments, environments with a unique set of environmental parameters could require the application of ‘environment-specific’ GDGT calibrations (Naeher et al., 2014).

GDGT analysis of the Palominas core is presented in Chapter 4. The results, in conjunction with the PTI and PCI indexes, reveal that the humid phases of the Early Pleistocene of Baza were warm, while dry phases were generally cooler. These results allow for the correlation of humid phases to interglacial periods.

1.7.2. Methodologies focused on palaeoflora reconstruction

Pollen analysis

A total of 196 sediment samples from the Palominas core were processed for palynomorphs and counted. Samples had an average mass of ca. 30 to 50 g of sediment which was treated with 30% HCl and 30% HF to dissolve carbonate and siliceous material. The material was then centrifuged, sifted and mounted into slides for their observation under transmitted light microscope. The excellent pollen preservation allowed pollen counts averaging on 885 pollen grains identified per slide. Most of these grains were identified as *Pinus*, which is greatly overrepresented in the samples. Excluding *Pinus*, counts average to 334 grains per slide.

Changes in taxonomic composition and relative abundances between pollen assemblages from successive core depths mark significant environmental shifts, describing the alternation between different landscapes of the Baza Basin. The application of statistical methods allows for a more in-depth analysis of the pollen assemblages. The application of PCA and spectral analysis conducted for the study in Chapter 3 (Altolaguirre et al., 2020) revealed which pollen groups underwent intense cyclical shifts through the record and the exact periodicity of these cycles. The latter results allowed the comparison of the cyclicity seen in the Palominas record of Baza with orbital forces (Chapter 3/Altolaguirre et al., 2020).

Biomization

Following the biomization technique (Prentice et al., 1996; Prentice and Webb, 1998) permitted reconstructing the biomes most likely to have existed in the Baza Basin according to qualitative and quantitative pollen data. The biomization method uses plant functional types (PFTs) characterized according on leaf morphology and phytogeographic distribution. Each pollen taxa are assigned one or more PFTs according to the properties of the producing plant, in this way creating a 'taxa – PFT' data matrix. The different biomes are defined as associations of PFTs, this relationship constitutes the 'PFT – biome' matrix. Multiplying both matrices creates a 'taxa – biome' matrix which allows assigning different affinity scores to each biome according to the taxonomic composition and relative abundances of any give pollen assemblage. The higher the biome's affinity score, the higher the likelihood of it having occurred at the time of deposition. The application of the biomization method is featured in Chapter 3 (Altolaguirre et al., 2020), where it allows the distinction of three dominant forested biomes during humid periods and two herbaceous biomes during dry ones. These results also played a major role in the reconstruction of the Early Pleistocene vegetation units of the Guadix-Baza Basin in Chapter 5 (Altolaguirre et al., 2021).

1.7.3. Methodology focused in the assessment of plant resources

Vegetation unit mapping

A new methodology was developed in order to study the hominin environment at Orce and its resources. This method aimed at spatially structuring the Early Pleistocene vegetation of Baza into different vegetation units (VUs) and mapping them into a palaeogeographic reconstruction. The methodology was laid out conceptually and applied in Chapter 5 (Altolaguirre et al., 2021), using existing palaeogeographic data and the new climate data obtained in previous analysis.

The pollen data and the biomes reconstructed with the biomization method were the basis for defining different VUs. These being: steppes, Mediterranean woodlands, deciduous forests, conifer forests, marshlands, riparian vegetation and alpine vegetation. Then, a modern analogue is assigned to each of these Early Pleistocene vegetation types. These modern analogues are found among the modern vegetation of Southern Spain, on the basis of taxonomic similarity and geographic proximity to Baza. Then, each analogue is defined according to the environmental parameters which constrain their extent in their respective geographic area. In the case of Baza, these parameters were found to be precipitation, presence of bodies of water and altitude. Thus, each modern analogue was defined by the precipitation/altitude intervals in which they occur, or by their association of water bodies. In the following step, these intervals of precipitation/altitude are extrapolated from the analogue VU into the Early Pleistocene vegetation that each analogue represents. In this way, the mapping units are created, each representing the Early Pleistocene vegetation and defined on the basis of constrained environmental parameters.

Palaeogeographic data was employed to recreate the elevations of the Guadix-Baza region during the Early Pleistocene. Precipitation data obtained by using the CA method was employed to recreate mean annual precipitation maps, both for dry periods (glacials) and humid periods (interglacials). Once these environmental parameters were mapped, the mapping units were drawn, according to their previously defined environmental constrains. In this way, two vegetation maps were created, one for dry phases and another for humid phases.

This method is conceptually developed and applied in Chapter 5 (Altolaguirre et al., 2021), where it is described in detail. The resulting vegetation maps illustrate the great diversity of vegetation types present at the region of Guadix and Baza, at the time when hominin communities were present in the region. During humid periods, the dominant vegetation type were Mediterranean woodlands. During dry periods, the dominant vegetation was the steppe. The sites of Orce were in close distance to several vegetation types, including the marshland vegetation which existed on the shores of the lake system.

Assessment of potential plant foods

Ethnobotanical data was compiled with the aim of studying potential plant-based resources available to hominins at Orce. The number of edible plant parts (EPPs) potentially useful to *Homo* was calculated on the basis of the previously defined VUs and their analogue vegetation.

Taxa lists were created for each of the different Early Pleistocene vegetation units at the Guadix-Baza Basin that were defined during the application of the method for vegetation unit mapping. These lists represent the dominant taxa at each vegetation unit, being constituted by the dominant vegetation of the modern analogue and the pollen taxa identified from the Palominas core.

With these taxonomic lists, ethnobotanical data was assigned to each of the taxa in each VU. With regards to potential source of food for early *Homo*, EPPs were defined as plant parts which would occur in significant amounts, digestible in large quantities and could be consumed without the need of sophisticated processing or the use of fire. Furthermore, the collection of data regarding the phenology of edible plants led to the creation of calendars displaying the number and type of plant food that early *Homo* could have collected per month in each of the different VUs.

The results are presented in Chapter 5 (Altolaguirre et al., 2021). These describe a high number of EPPs in the Mediterranean woodland VU, during the months of summer and autumn, and in the marshland and riparian VUs, available through the year. During glacial periods, the development of the steppe as the dominant vegetation type in the region carried a reduction of the diversity and number of EPPs available to early hominins.

1.8. Structure and overview of this PhD thesis

Three main objectives have been outlined in order to answer the questions regarding early hominin expansion into the Iberian Peninsula and Western Europe: ‘how did the climate change?’, ‘how did vegetation shape the environment of early *Homo*?’ and ‘what kind of plant resources were available?’. This PhD thesis comprises three published studies and currently unpublished additional material. These aim to answer these specific questions and further advance the knowledge of Early Pleistocene environments and the journey of *Homo* out of Africa.

Chapter 2 features the study entitled ‘An environmental scenario for the earliest hominins in the Iberian Peninsula: Early Pleistocene palaeovegetation and palaeoclimate’ by Yul Altolaguirre, José M. Postigo-Mijarra, Eduardo Barrón, José S. Carrión, Suzanne A.G.

Leroy and Angela A. Bruch., published in the journal *Review of Palaeobotany and Palynology* (2019, 260, 51–64, doi:10.1016/j.revpalbo.2018.10.008). This paper presents the application of the CA method to both macro- and microbotanical fossil assemblages from the Early Pleistocene sites and sections which are associated to early hominin sites. These being the sites of Orce, Atapuerca and Vallparadís. The new climate data reveals generally warm and humid conditions at the hominin sites. Nonetheless, at Orce, winter temperatures during glacial times do not seem to have been prohibitively low, allowing hominins to inhabit Southern Spain continuously through the glacial-interglacial cycles. These results help to better understand the broader climatic context of the hominin colonization of the Iberian Peninsula.

Chapter 3 introduces the publication ‘A long Early Pleistocene pollen record from Baza Basin (SE Spain): Major contributions to the palaeoclimate and palaeovegetation of Southern Europe’ by Yul Altolaguirre, Angela A. Bruch and Luis Gibert. The article was published in the journal *Quaternary Science Reviews* (2020, 231, 106199, doi:10.1016/j.quascirev.2020.106199). It tackles the reconstruction of the Early Pleistocene palaeoflora of Baza and its organization into different vegetation types by the means of pollen analysis and biomization. Statistical analysis and the CA allow to reconstruct the Early Pleistocene climate and its relationship with the global orbital cyclicity. The new pollen record describes the alternation of at least 11 cycles, during which the predominant vegetation of the basin alternates between that of xeric steppes and open forests or woodlands. The study identifies an association of these cyclical vegetation changes to obliquity forcing and establishes similitudes of the pollen record at Baza with pollen assemblages of Southern Italy and Greece.

Chapter 4 contributes to the characterization of the Early Pleistocene climate changes by presenting the result from biomarker analysis, at present unpublished. This analysis was employed in order to reconstruct relative temperature changes, since the previous pollen-based analysis did not provide a comprehensive reconstruction of temperature changes over time. The biomarker results were studied in cooperation with Iuliana Vasiliev, Manuel Casas-Gallego, Luis Gibert, Adele Bertini, Andreas Mulch and Angela A. Bruch.

Chapter 5 presents the study entitled ‘Mapping Early Pleistocene environments and the availability of plant food as a potential driver of early *Homo* presence in the Guadix-Baza

Basin (Spain)' by Yul Altolaguirre, Meike Schulz, Luis Gibert and Angela A. Bruch, published in *Journal of Human Evolution* (2021, 155, 102986, doi:10.1016/j.jhevol.2021.102986). This study introduces the conceptual basis for two novel methodologies and their application to produce maps of the Early Pleistocene vegetation of Guadix and Baza Basins and to calculate the number of edible plant parts available to early hominins. The resulting maps indicate that hominins from the sites at Orce had access to multiple vegetation types within a small radius, allowing hominins to forage different environments in close proximity. The assessment of EPPs highlight the importance of the marshland vegetation at the lake system as source of plant food, especially during the winter months when other food sources diminish. These results point to the EMPT as a potentially severe disturbing force for the hominin habitat, leading to the loss of multiple food sources.

Finally, Chapters 6 (in English) and 7 (in German) summarize the major findings of the research done during the PhD Thesis. These chapters present the ways in which the research has advanced the knowledge about the Early Pleistocene flora and climate and, most importantly, how environmental factors influenced the first expansions of *Homo* into Europe.

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Chapter 2

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

Yul Altolaguirre, José Maria Postigo-Mijarra, Eduardo Barrón, José S. Carrión, Suzanne A.G. Leroy and Angela A. Bruch.

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ARTICLE INFO

Article history:
Received 4 September 2018
Received in revised form 19 October 2018
Accepted 21 October 2018
Available online 16 November 2018

Keywords:
Early Pleistocene
Hominin dispersal
Iberian Peninsula
Palaeoclimate
Coexistence Approach
Palaeoenvironments

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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https://doi.org/10.1016/j.revpalbo.2018.10.008
0034-6667/

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

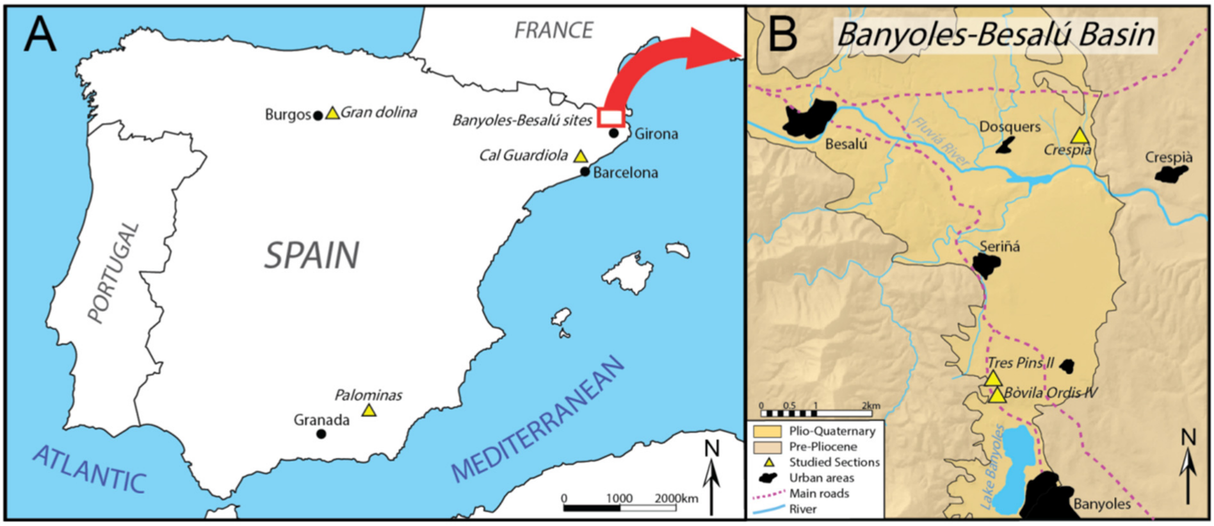

Fig. 1. (A) Locations of the studied sites and within the Iberian Peninsula. (B) Simplified map of the Banyoles-Besalù Basin with the specific locations of the studied sites, simplified geology and urban areas (modified from Barnolas et al., 1994).

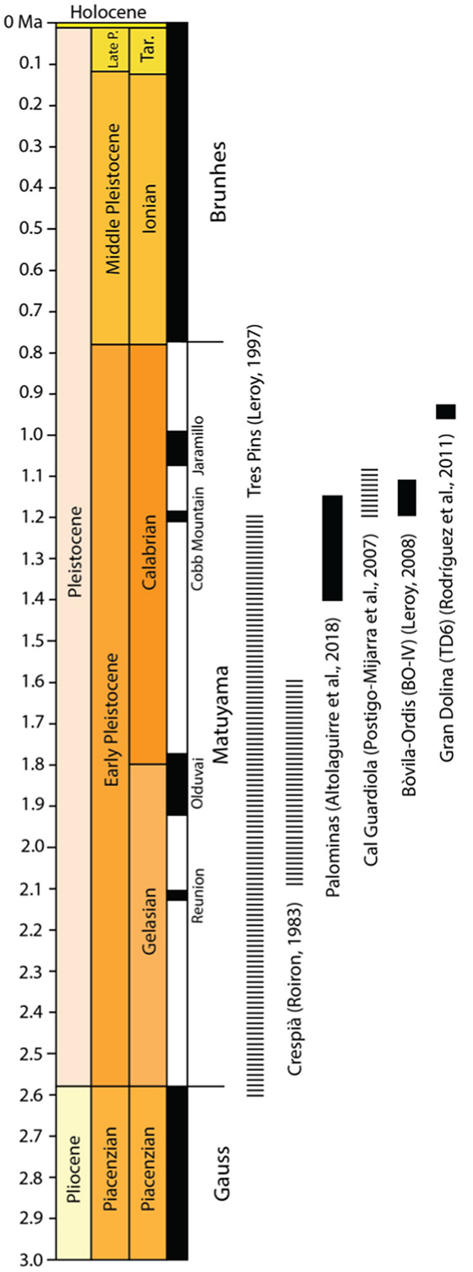

Fig. 2. Age ranges for the Early Pleistocene sites studied in this work. Stratigraphic scheme and chronological frame after Cohen and Gibbard (2016). The reference for each age model is given in the figure. Well-dated sections are represented by black solid marks; uncertainly dated sections are presented 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 (Julìà, 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 pseudoplatanus*	*Aesculus hippocastanum*	*Acer pseudoplatanus*	*Acer campestre*	*Aesculus hippocastanum*	*Acer pseudoplatanus*	*Ligustrum*	*Aesculus hippocastanum*
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*	*Amaranthaceae*
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 sempervirens*	*Tilia tomentosa*	*Laurus nobilis*	*Tilia tomentosa*	*Quercus cerris*

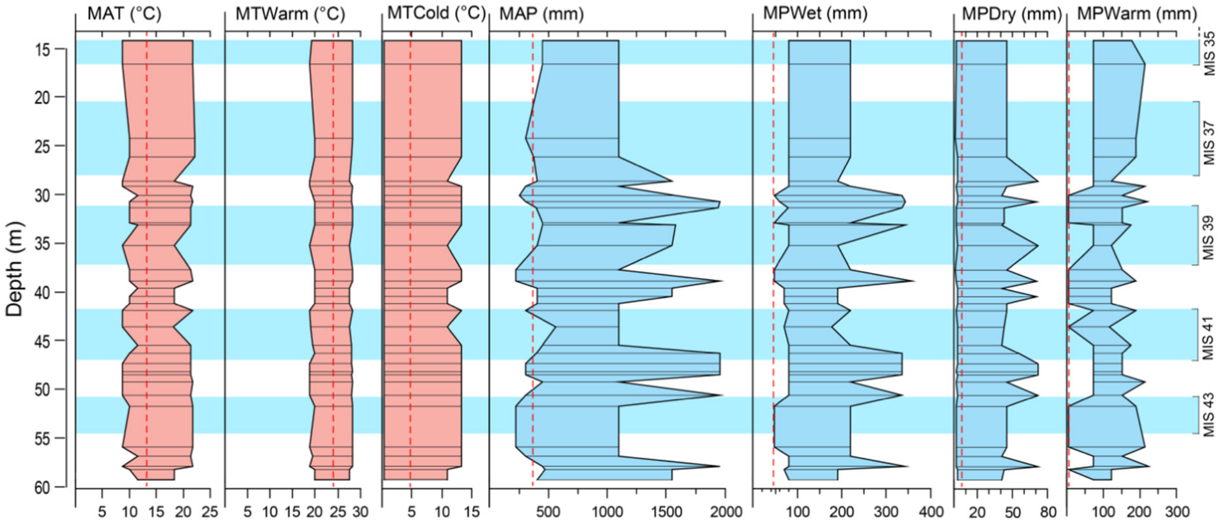

Fig. 3. Compilation of coexistence intervals for temperature (red) and precipitation (blue) parameters from Palominas section. Each coexistence interval is represented by a horizontal line. Modern values for each parameter are represented by dashed red lines. Exact values are: 13.2 °C MAT, 24 °C MTWarm, 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).

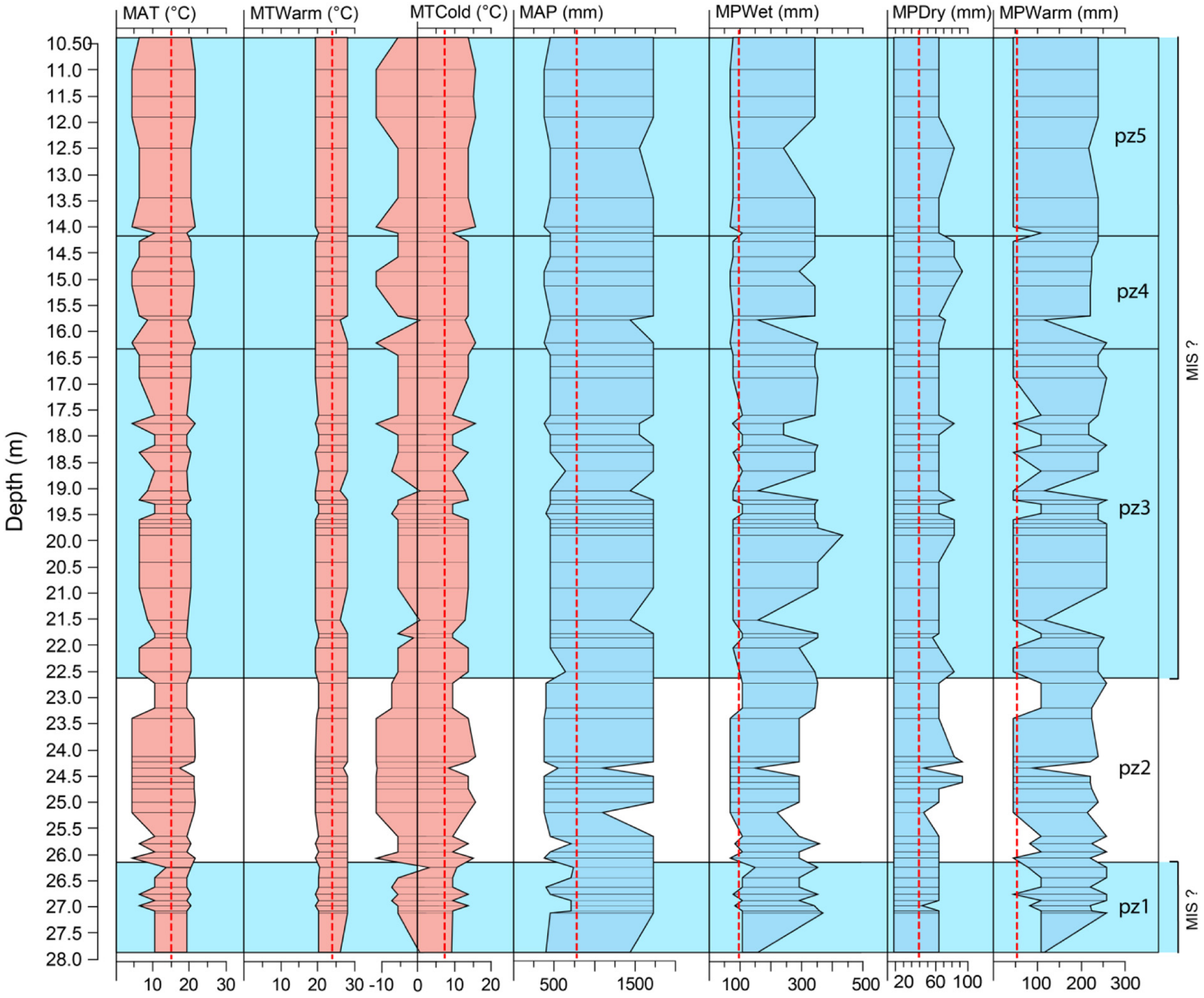

Fig. 4. Compilation of coexistence intervals for temperature (red) and precipitation (blue) parameters from Tres Pins II section. Each coexistence interval is represented by a horizontal line. Modern values for each parameter are represented by dashed red lines. Exact values are: 15.0 °C MAT, 24 °C MTWarm, 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

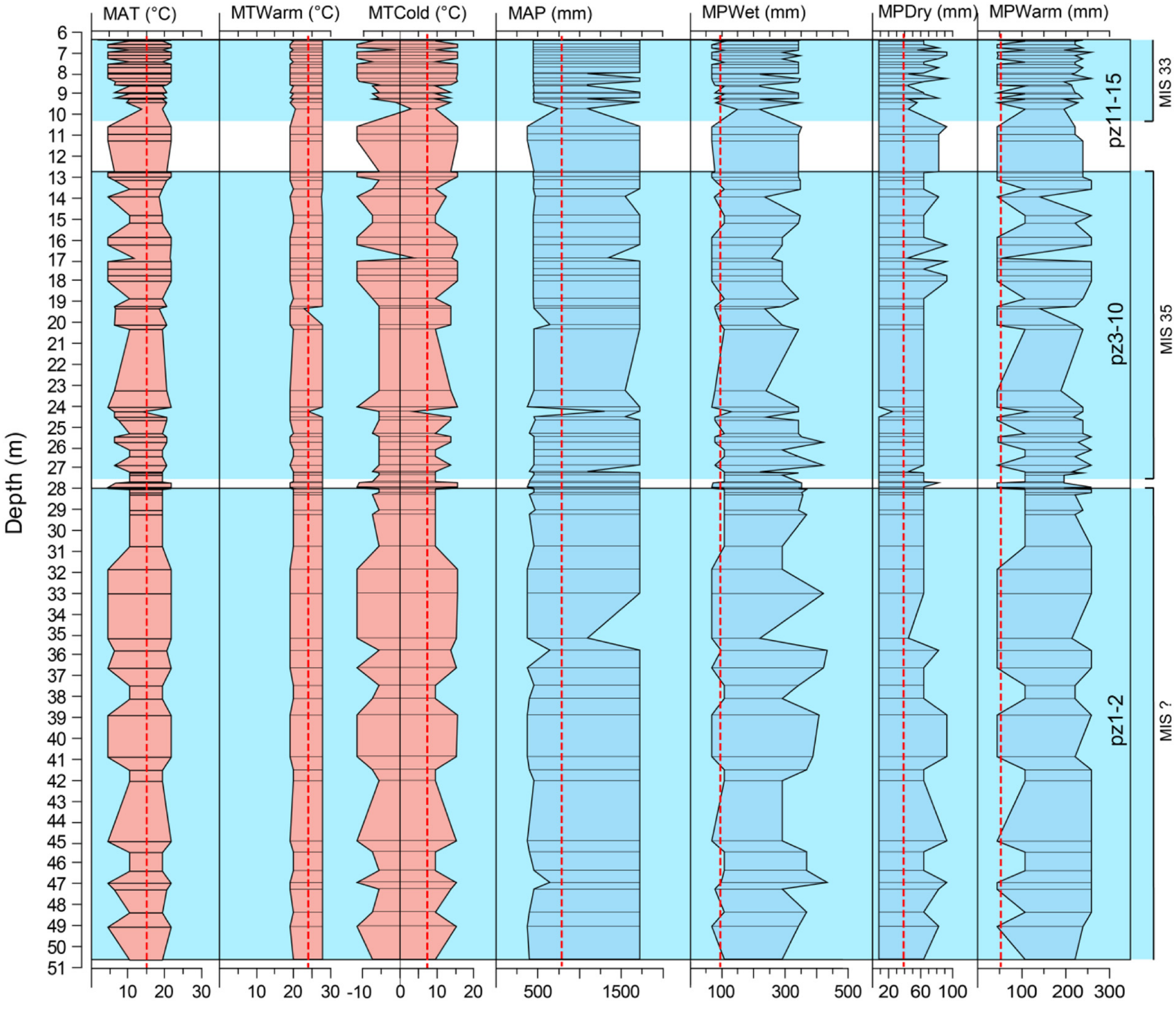

Fig. 5. Compilation of coexistence intervals for temperature (red) and precipitation (blue) parameters from Bòvila Ordis IV. Each coexistence interval is represented by a horizontal line. Modern values for each parameter are represented by dashed red lines. Exact values are: 15.0 °C MAT, 24 °C MTWarm, 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

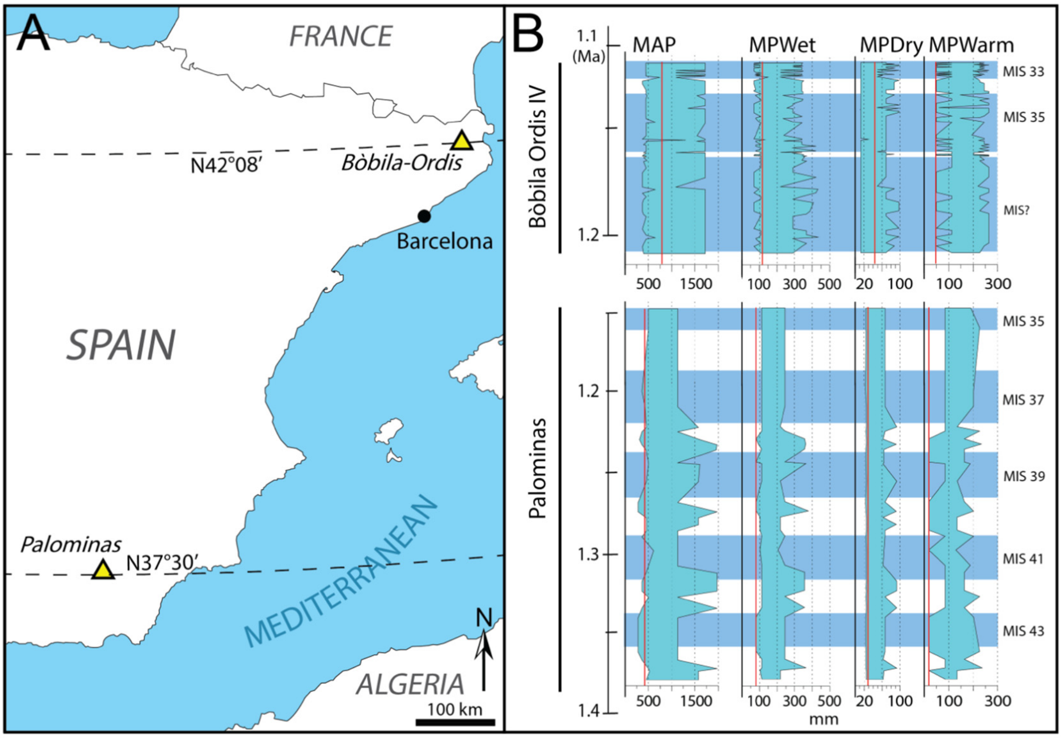

Fig. 6. (A) Map of the eastern part of the Iberian Peninsula showing the latitudinal values for the sites of Bòvila Ordis and Palominas. (B) Coexistence intervals for the main precipitation parameters of the sections of Bòvila-Ordis IV (top) and Palominas (bottom). Blue bands represent humid phases associated 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.

Acknowledgements

This work was jointly performed and founded by ROCEEH Research Centre 'The role of culture in early expansions of humans' of the Heidelberg Academy of Sciences and Humanities (www.roceeh.net), and the research projects CGL2015-68604-P, CSO2015-65216-C2-2-P, CGL2012-34717, founded by the Spanish Government, and the project Fundación Séneca grant numbers 19434/PI/14. This work is a contribution to NECLIME (Neogene Climate Evolution in Eurasia, www.neclime.de). The authors thank Alfonso Arribas (IGME, Madrid) for his invaluable assistance. The authors also thank Hugues-Alexandre Blain and an anonymous reviewer for their insightful comments and suggestions.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.revpalbo.2018.10.008.

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Chapter 3

A long Early Pleistocene pollen record from Baza Basin (SE Spain): Major contributions to the palaeoclimate and palaeovegetation of Southern Europe

Yul Altolaguirre, Angela A. Bruch and Luis Gibert.

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A long Early Pleistocene pollen record from Baza Basin (SE Spain): Major contributions to the palaeoclimate and palaeovegetation of Southern Europe

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ARTICLE INFO

Article history:
Received 9 November 2019
Received in revised form
27 January 2020
Accepted 27 January 2020
Available online xxx

ABSTRACT

The basin of Baza is located in the central area of the Betic Range (SE Spain) with a catchment area of over 4000 km^2. It contains a continuous and well preserved lacustrine sedimentary record from the Late Miocene to the Middle Pleistocene. The basin encloses numerous Miocene to Pleistocene mammal fossil sites that include some of the oldest hominin occurrences in Western Europe, found at the Orce sites. The present work features the palynological analysis of sediment samples obtained from the Palominas drill core. The Palominas core cuts thorough fine grained sedimentary units located in the depocenter of the basin, which contain well preserved pollen grains. The palynoflora found in the core is rich in herbaceous pollen, as well as *Quercus* and *Pinus*, with other tree taxa appearing in lesser quantities. Spectral analysis reveals strong climatically controlled vegetation successions. The application of the Biomization method on these assemblages allows for a reconstruction of the biome succession. The Early Pleistocene landscape was dominated by a sequence of steppe, evergreen-bushland and mixed-forest biomes. The Coexistence Approach method shows that SE Spain experienced humid periods, during which precipitations were significantly higher than during the modern climate. These humid phases are correlated with warm interglacial periods which featured the development of open forests. Dryer phases and fully open environments are correlated with colder glacial periods. Based on the palynoflora a Calabrian age is suggested for the Palominas core. The flora and climatic patterns identified in Baza are similar to the ones identified in Calabrian records of Southern Italy and Greece.

1. Introduction

The Guadix-Baza Basin is an intramontane depression situated in Southeastern Spain (Fig. 1) with a mean elevation of 900–1000 m a.s.l. and surrounded by mountains up to 3.478 m (Mulhacén Mt.). The Early Pleistocene deposits of the Guadix-Baza Basin contain 37 vertebrate sites, some of which are of great importance in understanding the faunas and ecosystems of Western Europe during the Pleistocene (Maldonado-Garrido et al., 2017). Among these, the sites of Orce are of exceptional importance due to their remarkable record of Early Pleistocene faunas and the presence of early hominins. These are the sites of Venta Micena (VM), Fuente Nueva-3 (FN-3) and Barranco León-5 (BL-5), found in the Baza sub-basin (eastern part of the larger Guadix-Baza Basin) (Fig. 1B). These sites have yielded Oldowan lithic industry assemblages (Gibert et al., 1989, 1992, 1998a, 2006a, b; Toro-Moyano et al., 2009) and evidence of anthropic use of tools on large mammal bones (Jiménez and Gibert, 1992; Gibert et al., 2006a, b; Espigares, 2010; Espigares et al., 2013; Gibert, 2018). The site of Venta Micena contains fragmentary material linked to early *Homo* (Gibert et al., 1983, 1998a, 1998b, 1999, 2002; Borja et al., 1997; Campillo et al., 2006; Ribot et al., 2015). The Barranco León-5 site has supplied abundant lithic artifacts and two deciduous molars attributed to hominins, one complete and a second one fragmented (Gibert et al., 1999; Toro-Moyano et al., 2013; Ribot et al., 2015). The dating of

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https://doi.org/10.1016/j.quascirev.2020.106199
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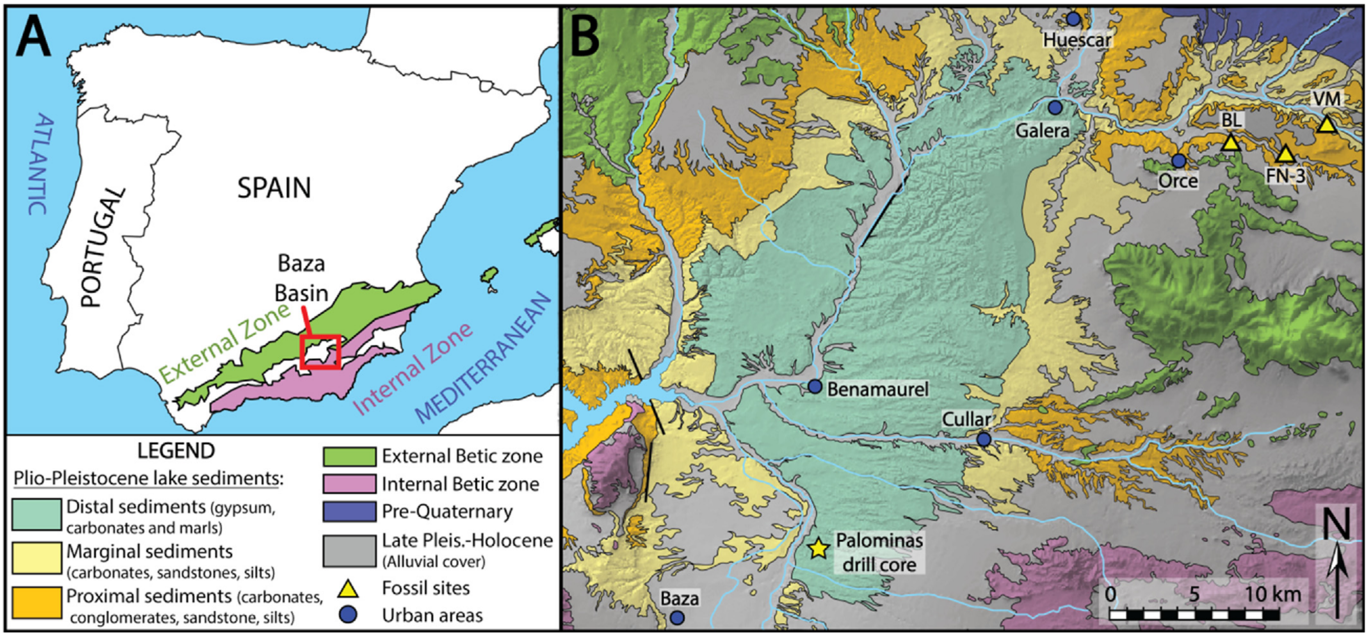

Fig. 1. (A) Location of Baza Basin in the Iberian Peninsula. The map highlights the two more relevant geological units, the External and Internal Betic zones. (B) Simplified geological map of Baza Basin. Fossil sites are: BL: Barranco León, FN-3: Fuente Nueva 3, VM: Venta Micena. Geological data from Baena et al. (1979, 2006), García et al. (2006) and Lupiani et al. (2006).

these three sites was accomplished through a detailed palaeomagnetic study (Scott et al., 2007) and minimum ages of 1.3, 1.25 and 1.2 Ma were stablished for the VM, BL-5 and FN-3 sites, respectively. Other studies suggest ages of around 1.4 Ma based on a combined U-series/electron spin resonance (ESR) (Duval et al., 2011; Toro-Moyano et al., 2013), however due to the lack of reproducibility on fossils from the same site, the results of this method should be taken with care (Gibert, 2018). In any case, the findings at these sites consist of some of the oldest evidences of hominin presence in Western Europe and the oldest in the Iberian Peninsula. Hominin presence at the Orce sites has been linked to humid phases due to accompanying fauna (Agustí et al., 2010; Blain et al., 2011, 2016).

Despite the importance and high number of vertebrate fossil sites, very little is known about the paleoflora of the region during the Early Pleistocene. No macroflora is reported for any of the Early Pleistocene fossils sites in the area of Guadix-Baza. Attempts at obtaining a palynological record of the Pleistocene of Baza Basin (Jiménez-Moreno, 2003; Carrión et al., 2009) led to negative results (barren samples) or were affected by external contamination (Jiménez-Moreno, personal communication). Ortiz et al. (2003) succeeded at retrieving pollen grains from the lower layers of the Venta Micena site. They report the presence of mainly fresh water algae spores with the occasional occurrence of Pinaceae and Poaceae pollen grains. Although interesting from a sedimentological point of view, these reports do not allow for a full understanding of the Early Pleistocene vegetation of the region.

In recent years multiple studies have outlined the general features, development and trends of the Early Pleistocene climate in the Mediterranean Basin using palynological records (Suc, 1984; Suc and Popescu, 2005; Joannin et al., 2007b; Combourieu-Nebout et al., 2015; Altolaguirre et al., 2019). The Pleistocene climate was characterized by the alternation of glacial and interglacial periods, during which the continental ice sheets in the northern hemisphere expanded and retreated (Ruddiman et al., 1989). This alternation was driven by the orbital forces of eccentricity, obliquity and precession (Lisieky and Raymo, 2005, 2007). Unlike for the rest of the Pleistocene, eccentricity was not the main orbital force responsible for climate cyclicity during the Early Pleistocene. During this time, the main climatic force was obliquity (Huybers, 2006). This caused glacial periods to be relatively short and not as cold when compared to the glacial periods of the Middle and Late Pleistocene (Ehlers and Gibbard, 2008).

In the Mediterranean Basin, the Early Pleistocene glacial periods have been traditionally correlated with cool and dry climate, which led to the development of open environments dominated by herbs and steppic plants such as *Artemisia* and *Ephedra*. Similarly, the interglacial warm and humid climate would allow for the spread of *Quercus* forests and other warm-temperate taxa (Suc, 1984; Pons et al., 1995; Suc and Popescu, 2005; Klotz et al., 2006; Bertini, 2010, 2013). This is especially true in the Mediterranean littoral, although exceptions can exist (Bertini, 2010). While most of the modern flora of the Mediterranean Basin was already present during the Early Pleistocene, this period was characterized by the presence of Arctotertiary taxa that, over the Middle Pleistocene, disappeared from the Iberian Peninsula and much of the Mediterranean region. Taxa like *Zelkova*, *Carya*, *Ostrya*, *Eucommia*, *Elaeagnus*, *Engelhardia*, *Liquidambar*, *Parthenocissus*, *Symplocos*, *Parrotia*, *Cathaya*, *Nyssa*, *Pterocarya* or *Tsuga*, among others, were a common component of forests during warm and humid stages of the Early Pleistocene (Postigo-Mijarra et al., 2010; Postigo-Mijarra; Barrón, 2017; Magri et al., 2017).

The main aim of the present study is to analyze the pollen material from the Palominas drill core in order to reconstruct climatic and vegetation changes in the area of Baza (SE Spain). This also includes establishing the most likely period in which the pollen assemblages were formed. An additional aim is to identify over regional climatic patterns by comparing the new data with other pollen assemblages from the Mediterranean Basin.

The pollen record of the Palominas core, presented here, could represent the longest terrestrial pollen archive for the Iberian Early Pleistocene, spaning multiple climatic cycles. It could complete the relatively poor pollen record from the Calabrian in the Iberian Peninsula, which is only known from the marine core ODP 976 (ca.

0.9–1.1 Ma) (Combourieu-Nebout et al., 1999; Toti and Bertini, 2018) from the Alborán Sea and the shorter pollen records of Bòvila Ordis-IV (ca. 1.1–1.2 Ma) (Leroy, 2008), TresPins (Gelasian/ early Calabrian) (Leroy, 1997), Gran Dolina (ca. 0.9 Ma) (Rodríguez et al., 2011), Cal Guardiola (0.8/1.0 Ma) (Postigo-Mijarra et al., 2007), Molí Vell (late Early Pleistocene) (Geurts, 1977, 1979), Crespià (late Gelasian or early Calabrian) (Suc, 1980), located in the North and NE parts of the Peninsula.

2. Modern climate and vegetation

According to the Köppen's classification, the areas of lower elevation in the Guadix-Baza region fall under cold semi-arid climate (BSk). The areas where altitude starts to increase, in the foothills of the surrounding mountains, experience a Hot-summer Mediterranean climate (Csa) and the high-altitude mountain areas are under Warm-summer Mediterranean climate (Csb) (AEMET and IM, 2011). Annual rainfall in low altitudes of SE Spain is recorded between 250 and 300 mm on average, with autumn and winter as humid seasons (Lázaro et al., 2001). Meteorological stations for the locality of Baza (7 km away from the drilling site) record annual average rainfall values of 366 mm, average annual temperature of 13.2 °C, with average summer and winter temperatures around 22 °C and 5 °C, respectively (MAPAMA, 2017).

Regarding potential vegetation and ecoregions, the basin of Baza is located within the "Mediterranean Forests, Woodlands, and Scrub" Biome inside the Palearctic biogeographic realm (Olson et al., 2001). The lower altitude parts of the basin are located within the "Iberian sclerophyllous and semi-deciduous forests" ecoregion. The mountain ranges situated immediately to the north, east and south of the basin fall into the "Iberian conifer forest" ecoregion (Olson et al., 2001).

The dominant plant association in the basin is typical for a Mesomediterranean bioclimatic region (Rivas-Martínez, 1987; Mercado and Tendero, 1988; Valle et al., 2004), and is primarily represented by *Quercus coccifera* and *Q. ilex* subsp. *rotundifolia* (Bohn et al., 2004) associated with other Mediterranean taxa such as *Rhamnus lycioides*, *Pinus halepensis*, *Juniperus phoenicea*, *J. oxycedrus*, *J. thurifera, Daphne gnidium* and *Ephedra nebrodensis* (Rivas-Martínez, 1987; Rodriguez-Ariza, 1992). The steppic landscape of the basin is composed mainly of Poaceae and Lamiaceae. *Garrigue* type shrublands are common near carbonatic outcrops and soils (Blanca et al., 2009). It also features heliophilic plants like *Pistacia lentiscus*, *Ephedra fragilis* and *Asparagus stipularis* among others (Rivas-Martínez, 1987; Rodriguez-Ariza, 1992; Bohn et al., 2004). Halophytes, such as *Pinus halepensis*, can be found in evaporitic soils (Rivas-Martínez, 1987; Rodriguez-Ariza, 1992). At the bordering foothills, increased humidity allows for the formation of oak groves (*Quercus faginea*) (Bohn et al., 2004). The mountains surrounding the basing fall into the oromediterranean region (Rivas-Martínez, 1987; Valle et al., 2004) and contain pine forests (*Pinus sylvestris, P. uncinata)* and juniper scrub (*Juniperus communis, Genista*) (Bohn et al., 2004). Riparian environments are mainly composed of *Populus*, *Salix* and *Ulmus* (Mercado and Tendero, 1988; Bohn et al., 2004). Agricultural activity in the area focuses on cerealia and almond tree (*Prunus dulcis*) (Blanca et al., 2009).

The extant vegetation in the basin of Baza, and in other intramontane regions in SE Spain, reflects the effects of human activity, which started having an important impact on the landscape since the start of Roman colonization (2000 BC). From that point onwards the forest cover in SE Spain experienced heavy deforestation by overgrazing, human-set fires, war effort, agriculture and the support of the metallurgic industry of the region (Mercado and Tendero, 1988). These activities pushed and degraded the mountain forests and helped the spread of grassland, thorny scrub, junipers and nitrophilous plant communities (Carrión et al., 2010). Currently, the area is experiencing widespread desertification (Rodriguez-Ariza, 1992).

3. Geological setting

The drilling site of the Palominas core is located in the municipality of Baza, in Southeastern Spain, about 90 km northeast of Granada and to the west of the Baza River. Geographically, the study area is within the Guadix-Baza Basin (>4.000 km^2), in the Betic Range (SE Iberian Peninsula) (Fig. 1A). The Betic Range is divided into two main geological domains: the External and the Internal Zones. The External Zone consists of deformed sedimentary material of Triassic to early Miocene age deposited in the southern margin of the Iberian Massif. The Internal Zone is more deformed and divided into several overlaying tectonic subunits, composed mainly of Palaeozoic and Mesozoic metamorphic rocks (Vera et al., 2004).

The depression of Guadix-Baza is located between the External and the Internal Zones (Vera, 1970) (Fig. 1). It can be divided in two sub-basins separated by the Jabalcon inselberg, the Guadix subbasin to the West, mainly filled with fluvio-alluvial sediments, and the Baza sub-basin to the East, which represents the main depocenter of the Guadix-Baza complex and was dominated by lacustrine sediments during the Late Pliocene to Middle Pleistocene (Gibert et al., 2007a; Haberland et al., 2017). Since these two basins shared the same hydrographical network they are often regarded in the literature as Guadix-Baza Basin. The term "Baza Basin" will be used through this work to refer also to the western sector of the Guadix-Baza depression. Baza Basin has an approximate altitude of between 900 and 1000 m a.s.l, while the highest altitude of the immediate area can be found in the Sierra de Baza Range, to the SW, at 2269 m a.s.l. The basin has experienced severe seismic activity in the past (Gibert et al., 2005; Alfaro et al., 2010) and is still tectonically active (Alfaro et al., 2008). Baza Basin saw greater tectonic subsidence than the Guadix Basin, which caused important sedimentological differences (Alfaro et al., 2008). The Guadix Basin developed a fluvial system flowing east into the basin of Baza, were an endorheic lake system developed (Viseras et al., 2004, 2006). The different depositional environments caused a vast contrast in layer thickness between the two sub-basins. Recent seismic survey shows a depocenter in Baza Basin, with more than 2200 m of marine to continental sediments in a semi-graben structure (Haberland et al., 2017).

The sedimentary filling of the basin started around 8 Ma, with the deposition of Late Miocene marine sediments (Haberland et al., 2017 and references therein). At this point the basin was part of the Guadix Seaway connecting the Atlantic Ocean with the Mediterranean. Subsequent tectonic uplift caused the segmentation of the seaway into disconnected depressions which became progressively isolated from the marine environments and evolved into a continental basin. During the Latest Miocene, Pliocene and Early Pleistocene the formation of the lake system in Baza favored the deposition of lacustrine sediments in a shallow and extensive lake system (Gibert et al., 2007a; Haberland et al., 2017). Sedimentation in the basin stopped during the Middle Pleistocene (0.6 Ma) after the capture of the basin by the topographically lower Guadalquivir Basin (Gibert et al., 2007b). This event prompted an episode of differential erosion that, together with active tectonics, created the modern badlands landscape and most of the current Miocene to Pleistocene outcrops. These outcrops include Early Pleistocene sections which propitiated the elaboration of several sedimentological and stratigraphic works. However, the centre of the depression remained relatively unstudied due to the lack of vertebrate fauna and age control.

3.1. Sedimentology and lithology of the Palominas core

The material studied here is part of the informally defined Baza formation (Vera, 1970) which contains all Late Miocene to Middle Pleistocene lacustrine deposits found in the area. The Baza Basin shows three concentric facies belts or zones related to different parts of the lacustrine system: Inner, Intermediate and Marginal (Gibert et al., 2007a). The Marginal Zone consists of alternations of detrital sediments and carbonates, it also includes minor amounts of gypsum. This zone is characterized by the presence of mammal fossil sites associated to carbonates which developed in an ephemeral palustrine environment. The Intermediate Zone is composed of gypsiferous and carbonatic facies, including native sulfur nodules. This area is interpreted as a mosaic of shallow lakes located between the Marginal and the Inner zones. The Inner Zone corresponds with an internal and permanent lake system. It is composed of alternations of laminated gypsum layers, endogenic carbonates (mainly aragonite and dolomite) and lutite beds with macrolenticular gypsum crystals (intersticial growth). The Intermediate and Inner Zones are bundled together into the "Benamaurel Gypsum unit" (Gibert et al., 2007a) (Fig. 2). The cyclic nature of the sedimentation in the Inner Zone and Intermediate Zone is believed to be driven by wet/arid cyclic periods (Gibert et al., 2000, 2007a).

The layers drilled by the Palominas core belong to the uppermost part of the sediments that fill the Inner Zone. The deposition of this zone started at the end of the Pliocene, continued through the Early Pleistocene and ended during the Middle Pleistocene (Gibert et al., 2007a; Haberland et al., 2017). The lacustrine materials located in the depocenter of the basin appear in seismic profiles as structurally unaltered, laterally continuous and at least 700–500 m thick (Haberland et al., 2017).

4. Material and methods

4.1. Drilling and sampling of the Palominas core

Drilling of the Palominas core (drilling site ca. 7 km NE of the city of Baza) was performed by the Instituto Tecnológico del Marmol in 2011. Recovered material represents lacustrine sediments of the inner zone of the Baza Basin. Drilling stopped at 107.5 m depth. During drilling the core quickly expanded vertically due to decompression. The core material was put in core boxes with a total measured length of 142.32 m. This is the core length which will be used in the present study. The core material is currently stored at the Faculty of Earth Sciences of the University of Barcelona. It was split into two halves and examined for lithology. A total of 392 samples were taken for palynological analysis. Approximately, 3 samples were taken for each meter of core. The upper 10 m of core contain gravels and conglomerates which sit discomformably over the lacustrine sediments (not sampled for pollen). The upper and lowermost samples were taken at the 10.1 m and 142.48 m depths respectively. Out of the total of pollen samples, 177 samples have been counted for palynomorphs and included in the present analysis. Pollen samples, as well as the resulting palynological slides, remain stored at the ROCEEH palynological laboratory, at Senckenberg Research Institute in Frankfurt/Main, Germany.

4.2. Pollen analysis

Sediment samples taken for pollen analysis were processed with 30% HCl and 30% HF. *Lycopodium* tablets were added allowing for calculation of pollen concentration. Sodium polytungstate (SPT) was used to separate particle fractions by gravity. The samples were sieved with a 6 μm filter and mixed with glycerol, then mounted on glass slides, topped with a cover slip and sealed with lacquer. All but 6 samples exhibited high concentrations of pollen grains and other palynomorphs. Over 300 pollen grains were counted per sample, not including *Pinus* grains which were overrepresented in all slides and were counted separately. Spores from cryptogams, fungi and algae and other non pollen palynomorphs (NPPs) were counted separately for the purpose of obtaining further environmental information. The pollen profiles and diagrams were constructed using Tilia 2.0.41 software (Grimm, 2011).

4.3. Statistical methods

Principal Component Analysis (PCA) was employed in order to observe the underlying trends in the matrix of pollen data (Davis, 1986). The PCA converted the matrix of pollen data into linearly uncorrelated variables or Principal Components (PC) which may account with real-world variables such as climatic or environmental parameters. PCA was applied first to the pollen matrix of proportional (%) data. *Pinus* was excluded from this first analysis since the high proportions greatly skewed the results. In order to observe the relationship of *Pinus* with other taxa the pollen matrix was normalized and subjected to a second PCA. Normalization of data adjusted the *Pinus* signal and the rest of the taxa to a similar scale. Data was normalized following formula $X = (x - mean)/standard\ deviation$. Principal Components Analysis (PCA) was carried out using Past 3.17 (Hammer et al., 2001). Spectral analysis was applied to the components of the first PCA (PC1 and PC2). These two PCs were the most representative of the total variance of the pollen matrix. The spectral analysis consisted of a simple periodogram which represented the periodicity and frequency of the variables (PC) portrayed by the pollen matrix.

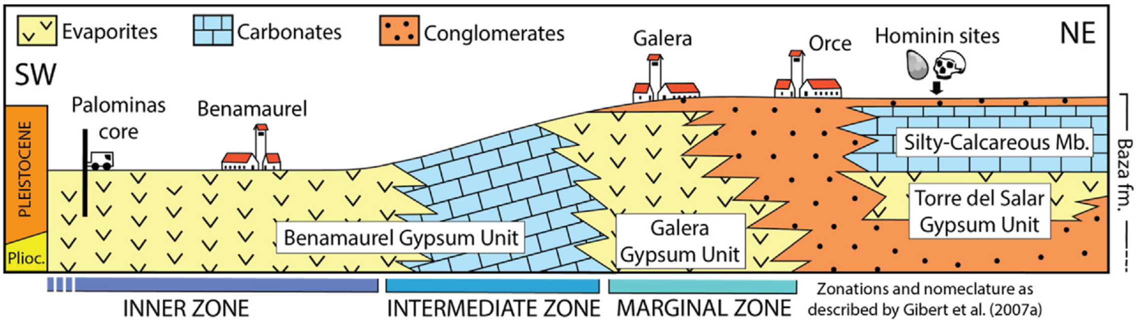

Fig. 2. Simplified stratigraphic diagram and zonation of the Benamaurel evaporites from the Baza fm. (Pliocene-Middle Pleistocene). The Torre del Salar Gypsum is a local unit of that grows inside alluvial sediments of Early Pleistocene age, below the Orce sites. Modified after Gibert et al. (2007a).

4.4. Biomization

Biome reconstruction was obtained employing the Biomization method (Prentice et al., 1996; Prentice and Webb, 1998). This method assigns the most likely biome produced by the pollen assemblage found in any given sample. For this, each pollen taxa is assigned one or more Plant Functional Types (PFTs) on the basis of leaf morphology and phytogeographic distribution ('taxa – PFT' matrix). In turn, a certain aggrupation of PFTs defines each biome ('PFT– biome' matrix). Multiplying both matrices produces a 'taxa – biome' matrix. Therefore, the pollen assemblage for each sample is used to calculate affinity scores for each possible biome. The biome with the highest affinity score is assumed to be the biome most likely to have occurred at the time of sedimentation. Matrix calculation was carried out using the software Biomise3 (Ben Smith, Lund University) (Prentice et al., 1996; Prentice and Webb, 1998), and using the PFTs association of Marinova et al. (2018), with small modifications (the complete 'biome – PFT – taxa' association is collected in Supplementary material 1). This association has been proven useful at reconstructing biomes from pollen data in the Eastern Mediterranean region (Marinova et al., 2018). Taxa proportionally lower than 0.5% are excluded from the calculation. Additional environmental information could be extracted by observing the second and third most likely biomes, as well as the distance between these and the most likely biome.

4.5. Coexistence approach

The Coexistence Approach (CA) method was employed in order to obtain quantitative estimations of temperature and precipitation parameters. This method requires the assumption that the climatic requirements for Pleistocene plant taxa are similar to those of their Nearest Living Relative (NLR). Each pollen taxa is assigned to a NLR, then the CA calculates the climatic values in which all of the NLRs could have coexisted. These values are represented as a coexistence interval (Mosbrugger and Utescher, 1997; Utescher et al., 2000, 2014). The nature of this assumption also requires the exclusion of taxa from the analysis which had remarkable differences in distribution and habitats between the Pleistocene and the present. In this case, the taxa *Cathaya* and *Parrotia* were excluded from the CA calculations. These genera are currently found in relict communities with very narrow climatic ranges; however, they had multicontinental distribution and a wide climatic range during the Pleistocene. Additionally, taxa with single occurrences are not counted towards CA calculations for that assemblage. This reduces this possibility of accidental introduction into the CA analysis of transported taxa foreign to the climatic region. The analysis was carried out using the ClimStat software and the PALEOFLORA database. This database gathers the climatic requirements of more than 1800 extant plant taxa, which are derived from meteorological stations located within their distribution areas (for details see www.paleoflora.de and Supplementary material 2). Nine climatic parameters were calculated: mean annual temperature (MAT), mean temperature of the coldest month (MTCold), mean temperature of the warmest month (MTWarm), MART (temperature difference between of MTWarm and MTCold), mean annual precipitation (MAP), mean precipitation of the wettest month (MPWet), mean precipitation of the driest month (MPDry), mean precipitation of the warmest month (MPWarm), and MARP (precipitation difference between MPWet and MPDry). The present CA analysis represents an expansion of the analysis performed in Altolaguirre et al. (2019) where the method was used to obtain preliminary climatic data from 31 pollen samples from the upper half of the Palominas core.

5. Palynological analysis

5.1. The pollen record

The light microscopic analysis of 177 samples from the Palominas core reveals good preservation of pollen grains and rich taxa diversity with 104 different pollen taxa. 6 samples, including the three uppermost samples, were found barren of pollen grains and are excluded from the pollen analysis. The average pollen count per sample was 332.8 and the total sum of counted pollen grains was 56,902. These numbers do not include *Pinus* which accounts for a total of 151,550 grains, with an average of 886.2 grains per sample. The average pollen concentration, not including *Pinus*, is 11,645.76 pollen grains per gram. Including *Pinus* the concentration is 31,011.03 pollen grains per gram.

The majority of pollen grains are found well preserved and unbroken, displaying yellowish coloration (Plate 1). A small proportion of pollen grains contain sub-angular or rounded dark-yellow structures that resemble fossilized and plasmolyzed cytoplasm alike to the structures reported in pollen assemblages from gypsum-rich materials from the Polish Miocene (Durska, 2016, 2018). These structures are unequivocally different from the unfossilized cytoplasm of modern pollen contamination.

The most abundant taxa recorded in the pollen assemblages from Palominas are herbaceous taxa (Fig. 3). According to the average proportional abundance per sample the most abundant taxa are: Poaceae (9.6% including *Pinus*/19.2% not including *Pinus*), *Artemisia* (9.8%/17.9%), Chenopodioideae (6.11%/11.76%) and Asteraceae (4.8%/9.6%). *Euphorbia*, Plumbaginaceae, *Plantago* and Ranunculaceae are also common components of the palynoflora. The most abundant arboreal plants (Fig. 3) are *Pinus* (50.5%) and evergreen *Quercus* (5.1%/10.3%) with the deciduous variety following closely (3.9%/7.9%). Multiple other tree taxa appear through the core in lower proportions (Fig. 3). A selection of pollen grains from arboreal and herbaceous taxa is displayed in Plate 1. Pollen from aquatic and wetlands plants (Fig. 3) appear in proportions usually below 10% of the total pollen sum. The aquatic plants are mostly portrayed by Cyperaceae and *Typha* or *Sparganium* pollen. A selection of environmentally relevant taxa, pollen group proportions and concentration is depicted in Fig. 4.

Associations with higher proportion of arboreal pollen are interpreted as humid periods. Therefore, eleven humid phases are defined (labeled in roman numerals). These phases are drawn by the proportional curves for warm-temperate taxa plotted against stepe taxa, and by the curve for arboreal pollen against non-arboreal pollen (AP-NAP curve) (Fig. 4). The use of these pollen signals for climatic correlation has been proved useful in Early Pleistocene sections (Joannin et al., 2008 and references therein). Two additional humid phases could be partially recorded in the uppermost and lowermost parts of the core.

The pollen profile has been divided in three different sections according to differences in the proportion of the main pollen groups. The Lower Section (142–102 m) and Upper Section (142–102 m) feature alternation periods dominated by *Quercus* and periods dominated by herbaceous taxa. This patter is interrupted during the Middle Section (102–55 m), which features periods of high proportion of *Picea* (Fig. 4).

5.2. Other palynomorphs

Cryptogam spores were identified as *Anthoceros*, *Riccia*, *Sphagnum* and indeterminate Lycopodiaceae and Osmundaceae, appearing in very low proportion (<1%). Algae spores (Fig. 4) appear regularly though the core in low to moderate quantities (10 – 20%), occasionally appearing in spikes of extremely high

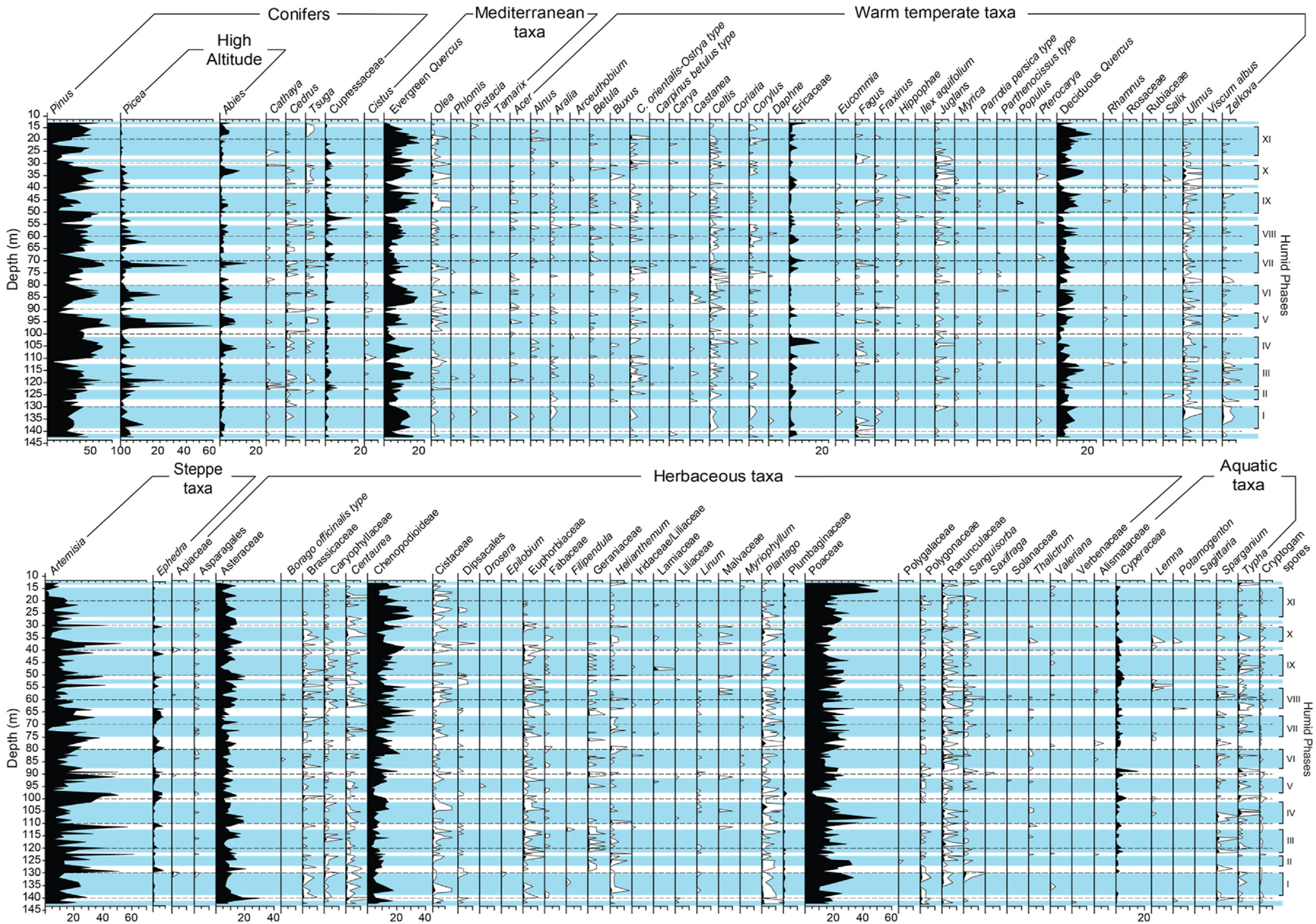

Fig. 3. Detailed pollen diagrams of the Palominas core including cryptogam spores. All taxa percentages have been calculated using pollen counts that exclude *Pinus* grains due to overrepresentation. Black curves represent true percentages; white curves show a 10x exaggeration. Humid Phases I to XI in light blue. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

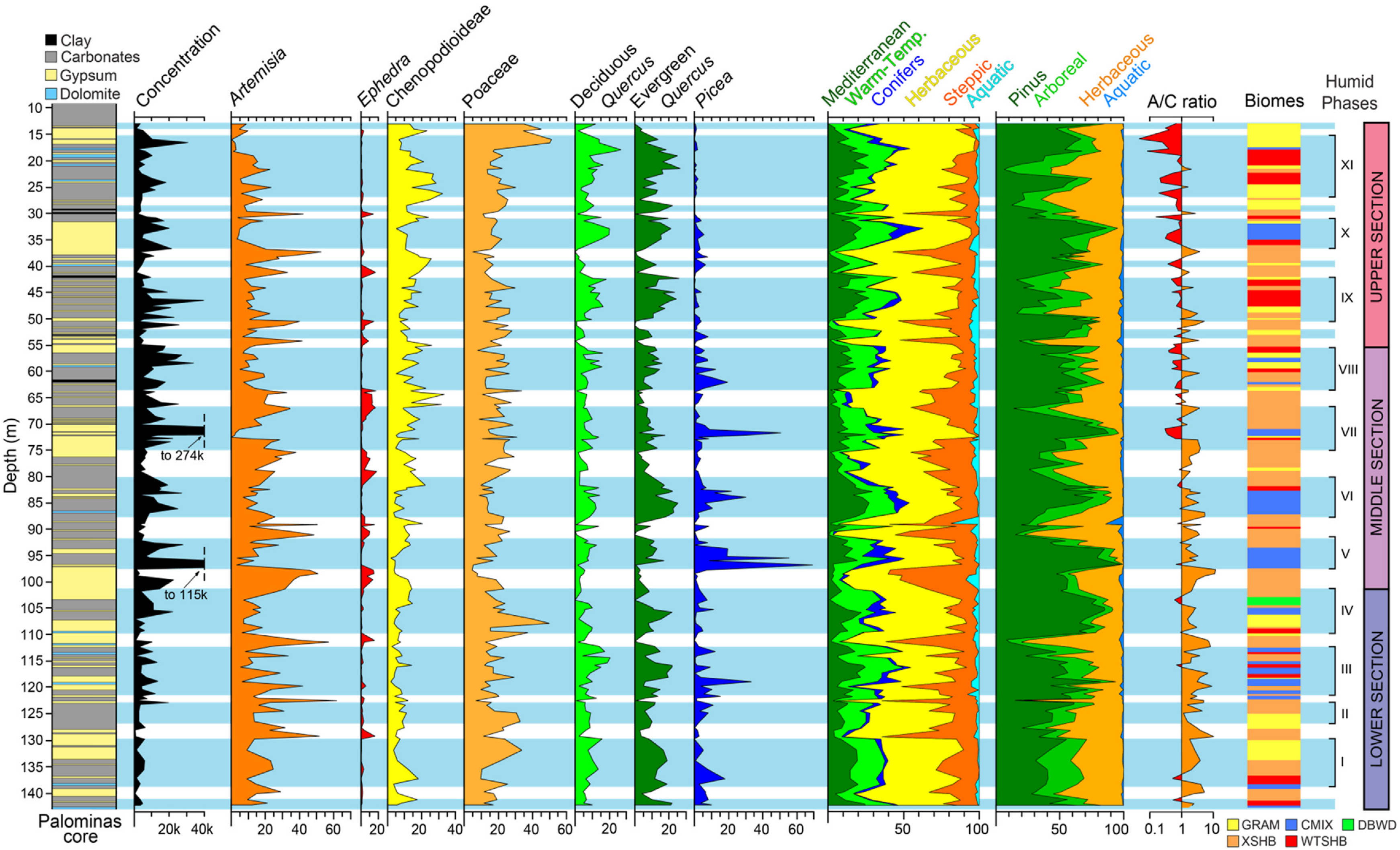

Fig. 4. Simplified pollen diagram featuring different aspects of the pollen record from the Palominas core. From left to right: Lithology of the Palominas drill core, pollen concentration (number of grains per gram of sediment, without *Pinus*); relative abundances (%) of a selection of 7 environmentally relevant pollen taxa; staked percentages of pollen combined to eco-groups (*Picea* and *Pinus* excluded due to overrepresentation); pollen grouped according to botanical affinity including *Pinus* (dark green); *Artemisia* to Chenopodioideae (A/C) ratio; Biome affinity scores, XSBH (Xeric shrubland) in orange, GRAM (Graminoids with forbs) in yellow, WTSHB (Warm-temperate evergreen sclerophyll broadleaf shrubland) in red, CMIX (Cool mixed evergreen needleleaf and deciduous broadleaf forest) in blue and DBWD (Deciduous broadleaf woodland) in green. Humid Phases I to XI in light blue. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

proportions (>60%). The most abundant algae are identified as *Botryococcus* and *Sigmopollis* (classification relates to the "HdV 128" type described by Pals et al., 1980). These two taxa usually occur as spikes of high proportion at different depths. During the algae spikes these taxa can account for 20 to 50 or even above 90% of the total palynomorph sum (Fig. 4). Supplementary material 3 contains the palynogram of the main palynomorphs types identified in the core.

5.3. Statistical analysis

The Principal Component Analysis (PCA) of the pollen matrix (without *Pinus*) found that PC1 represents 40.8% of the total variance of the matrix, while PC2 represents 21.6%. Additional PCs were found to represent too small percentages of variance (PC3 = 12%, PC4 = 10%, PC5 = 4% ...). The biplot diagram of PC1 against PC2 clusters the samples into an arc shape (Fig. 5A). Most taxa are assigned very low loading (Table 1), creating a cluster of noise in the origin of coordinates of the biplot diagram. Only *Artemisia*, Poaceae and *Picea* reach loadings above 0.04 and only Chenopodiaceae, *Ephedra*, and *Quercus* reach loading values above 0.1. PC1 separates the steppic pollen groups (*Artemisia* and *Ephedra*), with negative values, from both *Quercus* groups, *Picea* and Poaceae, which score in positive values. Chenopodioideae is assigned low statistical significance by PC1. Alternatively, PC2 gives high positive values to Chenopodioideae and Poaceae, while *Picea* reaches high negative values. *Artemisia* and *Quercus* get low negative and positive values, respectively. Since PC1 separates the steppic taxa from *Quercus* and *Picea*, it is likely that positive values of PC1 are related to higher precipitations, while negative values are related to dry climatic conditions. PC2 could also be linked with differences in precipitation due to the anti-correlation of *Picea* (humid environments) with the herbaceous groups.

The PCA of the normalized pollen matrix, including *Pinus*, clusters the samples in a triangular shape (Fig. 5B). Due to normalization of the data matrix, all PCs represent very low percentages of the variance and all taxa groups achieve only low loading values. PC1 represents 6.1% while PC2 represents 4.3%. *Quercus*, *Artemisia*, *Ephedra* and Cyperaceae, among most of the herbaceous, arboreal and warm-temperate taxa score positive values in PC1, while *Pinus* and other conifers score negative values. PC2 separates conifers, *Quercus* and most of the arboreal taxa in positive values, while the negative values are assigned to *Ephedra*, *Artemisia*, Cyperaceae, *Cedrus* and most herbaceous groups. Most likely, PC1 represents an altitudinal signal while PC2 represents a humid/dry signal.

Table 1
Loadings resulted from the PCA of the data matrix including all pollen groups as % of the total pollen sum per sample (minus *Pinus*). Scores over ±0.4 in any of the PC marked in bold. Taxa with scores below ±0.01 in all 4 PC are omitted.

Pollen taxa	PC1 (40.8%)	PC2 (21.6%)
Evergreen *Quercus*	0.272	0.054
Picea	0.235	**−0.799**
Deciduous *Quercus*	0.214	0.055
Poaceae	0.152	**0.558**
Abies	0.086	−0.041
Ericaceae	0.026	0.012
Chenopodioideae	−0.005	0.176
Asteraceae	−0.030	0.021
Cyperaceae	−0.034	0.023
Ephedra	−0.107	0.001
Artemisia	**−0.883**	−0.093
Other pollen taxa	<0.01	<0.01

The PCA for both pollen matrices support the interpretation of the pollen diagrams with respect to a clear cyclic signal of humid and dry phases. The PC1 and PC2, resulting of the PCA of the matrix of proportional pollen data (Fig. 5A), are subjected to a spectral analysis in order to identify the frequency of this cyclicity. The results identify a clear periodicity in the data with a frequency of 0.08226 (12.1 m) (Fig. 6).

5.4. Biome reconstruction from pollen assemblages

The Biomization results allow for the reconstruction of biome successions through time using the calculated affinity scores for each biome. When including counts for *Pinus*, the analysis concludes that ENDW (evergreen needleleaf woodland) is dominant for every pollen association. This is not deemed realistic, as *Pinus* is

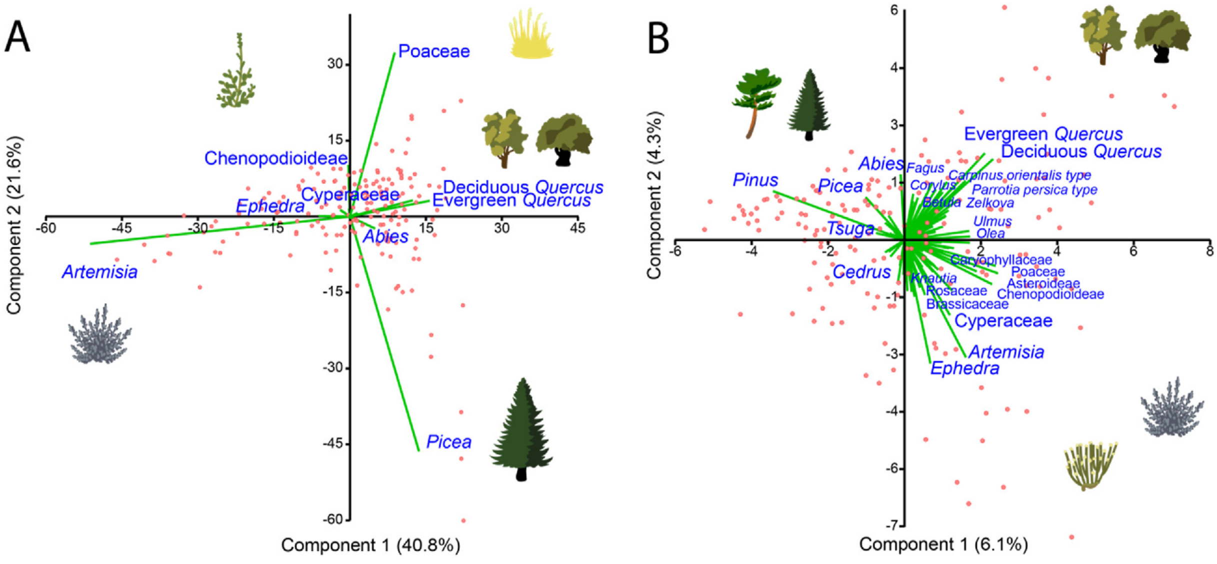

Fig. 5. PCA results plotted. The percentage of variance accounted by each PC is given in brackets. Dots represent single pollen samples. Variables (taxa) plotted as green lines and illustrated. (A) PCA of the pollen matrix (proportional data) (*Pinus* not included). (B) PCA of the normalized pollen matrix (proportional data) (*Pinus* included). Taxa names of low loading were removed in order to enhance readability. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

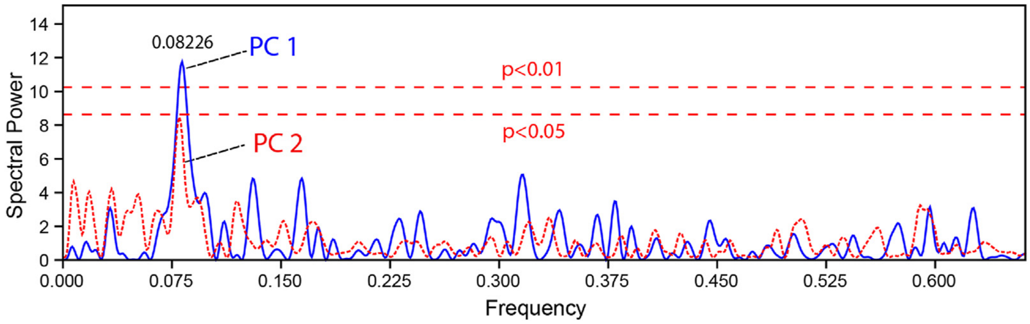

Fig. 6. Periodograms for Principal Components (PC) 1 and 2 resulted from the PCA of the matrix of proportional pollen data (Fig. 5A). The periodicity of both PC 1 and PC 2 reaches the highest intensity with a frequency of 0.08226 (12.1 m).

overrepresented in the samples. The results portrayed in Fig. 4 represent associations which exclude *Pinus*. Out of all 13 biomes, 5 of them achieve the highest affinity score for different pollen samples. These are XSBH (xeric shrubland), GRAM (graminoids with forbs), WTSHB (Warm-temperate evergreen sclerophyll broadleaf shrubland), CMIX (cool mixed evergreen needleleaf and deciduous broadleaf forest) and DBWD (deciduous broadleaf woodland).

The xeric biome (XSBH) is the predominant biome throughout the core (44%), followed by the grassy biome (GRAM, 17%). Forested biomes are less common, mixed forest (CMIX, 20%) is followed closely by the evergreen shrubland (WTSHB, 18%), while the deciduous biome (DBWD) appears only once (at 104 m depth, 0.6%). XSBH appears most commonly through the Middle Section of the core, while GRAM is more common in the Upper and Lower Section. CMIX appears more commonly in the Lower and Middle Sections, while WTSHB appears more consistently in the Upper one. XDBH is more frequent in the Middle Section.

6. Palaeovegetation reconstruction

The environment present in the basin of Baza during the interval recorded in the Palominas core can be reconstructed by combining the resulting pollen data, statistical analysis and Biomization. All these point to a strong response of the vegetation to humidity changes. In the Iberian Early Pleistocene these humid stages have been traditionally linked with warm or interglacial periods, while the dry stages are associated with cold glacial periods (Agustí et al., 2010; González-Sampériz et al., 2010; Postigo-Mijarra and Barrón, 2017). These dry and humid periods, as represented in the pollen record of the Palominas core, show marked differences in vegetation, climate and landscape of the Baza Basin during these cycles.

6.1. Vegetation during dry periods

During dry periods the pollen associations suggest that the landscape was dominated by grasses and herbaceous plants, while most of the arboreal communities were considerably reduced (Fig. 7B). According to the Biomization analysis, the main biomes present in the area during these periods were “xeric shrubland” (*Artemisia*-rich pllen assemblages, more common during the Middle Section of the core) and “graminoids with forbs” (Poaceae-rich assemblages, frequent during the Upper and Lower Sections) (Fig. 4). The xeric shrubland (steppe vegetation) is characterized mainly by high proportions of *Artemisia* and *Ephedra*. In the Pleistocene record of the Mediterranean basin, these taxa usually indicate arid conditions and the stablishment of glacial stages (Suc, 1984; Pons et al., 1995; Subally and Quézel, 2002; Bertini, 2010, 2013; Combourieu-Nebout et al., 2015). Although Poaceae pollen increase during dry phases, the group is likely to also contain semi aquatic taxa such as *Phragmites*, or taxa growing in relatively humid grasslands. High abundance of Poaceae should not be used alone as an indicator of dry climatic conditions.

Chenopodioideae pollen contains a substantial number of halophytic plants (Djamali et al., 2008) and thus, its abundance in Baza during dry periods could be linked to the development of saline environments like those described by Gibert et al. (2007a). This idea is also supported by the identification of several clusters of Chenopodioideae pollen embryos in the associations from dry environments. These “clusters” lack means of long distance transportat, so their presence in samples indicative of dry periods points to the existence of Chenopodioideae communities growing directly next to the lacustrine environments, in soils rich in salts and evaporites. Although the decreasing A/C (*Artemisia* - Chenopodioideae) pollen ratio in the upper half of the core (Fig. 4) could suggest a development towards higher environmental aridity, in this case it is likely to reflect edaphic conditions. The increase in Chenopodiaceae in the Upper Section could represent an overall increase in soil salinity over multiple vegetation cycles.

During dry periods the warm-temperate forest possibly disappeared from most of the lower altitudes of the basin, only surviving in micro-climates such as humid and somber valleys or close to mountain creeks. The Mediterranean flora was reduced as well, occupying only the more humid areas. This pattern is valid for most dry phases. Nonetheless, the dry episodes between Humid Phases II to VI saw an increment of *Olea* (Figs. 3 and 4), raising the possibility that some of these dry phases could allow the development of xerophytic arboreal communities. Since *Pinus* is relatively drought-tolerant (Novenko et al., 2018) its high pollen proportion during dry phases could point to the existence of pine communities in the basin. On the other hand, *Pinus* pollen could also represent communities from other regions of Souther Spain, due to its long-distance transportation (Dunwiddie, 1987). Cupressaceae pollen is also relatively common in the herbaceous-dominated assemblages (Fig. 3). These pollen grains lack enough features to allow for genus identification, but could be mostly related to *Juniperus*. This is due to morphological similarities and it being the most abundant and diversified Cupressaceae in the modern dry vegetation of the region (Blanca et al., 2009). *Juniperus* in Quaternary pollen assemblages has been linked with dry stages and open environments (Carrión, 1992a, 1992b; Yu, 1997).

6.2. Vegetation during humid periods

During humid periods the pollen associations depict a forested landscape in which herbs are still relatively abundant (Fig. 7A). Mediterranean vegetation was probably widespread along the plains and dryer parts of the basin, while warm-temperate forests

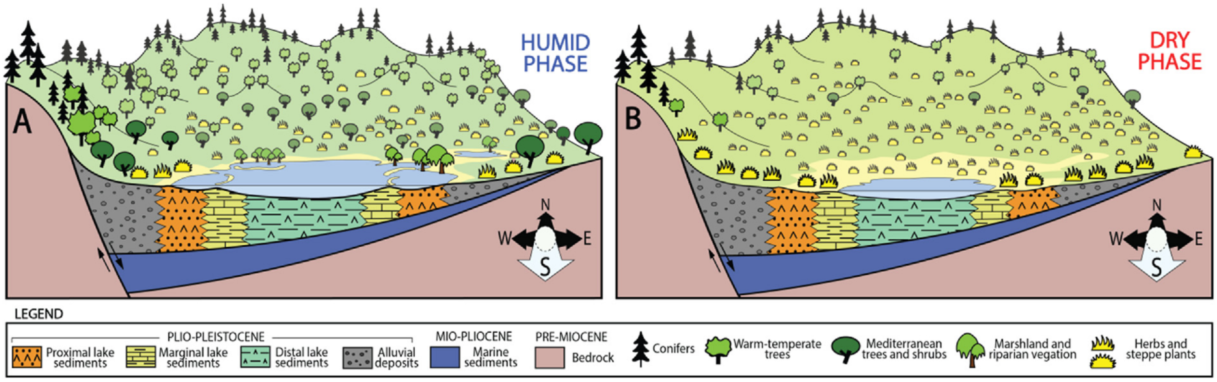

Fig. 7. Landscape diagram for Baza Basin with simplified geologic and sedimentological information. A) Landscape reconstruction of a humid phase, possibly related to an interglacial period. Forests are well distributed among herbs and steppe plants, creating a mosaic landscape. B) Landscape reconstruction during a dry phase, possibly related to a glacial period. Steppe or savannah-like environments prevail, with arboreal components significantly reduced.

would grow in areas of higher humidity such as hills, mountains and river valleys. Mixed forests of conifers and deciduous trees would develop in high altitude areas and mountain tops. The Biomization analysis represents the Mediterranean biome (WTSHB) and the mixed forest (CMIX) as the two more predominant biomes. The true warm-temperate forest (DBWD) obtains the highest affinity score only once though the core, during Humid Phase VI (Fig. 4). These three biomes most likely coexisted at the same time in the basin as different vegetation units or belts based on local geography and precipitation patterns.

The Mediterranean vegetation was mostly represented by the evergreen *Quercus* pollen type. This group probably contains species such as *Q. ilex* and *Q. coccifera*, which were common in SE Spain during the Pleistocene (Carrión et al., 2003). Evergreen *Quercus* was accompanied, in minor proportion, by taxa such as *Olea*, *Cistus* and *Pistacia* (Fig. 3). These trees and shrubs would create low-density woodlands or scrublands of low canopy; dispersed enough to allow the existence of open spaces colonized by herbs and grasses. Towards the lowest altitudes and the driest parts of the basin, the Mediterranean forest would disperse into patches of woodland creating a forested-savannah landscape. These environments were common in the southern part of the Iberian Peninsula throughout the Pleistocene (González-Sampériz et al., 2010).

The warm-temperate vegetation is mostly represented in the pollen associations by the deciduous variety of *Quercus.* This pollen type likely groups species found in the Iberian SE during the Pleistocene such as *Q. faguinea* and *Q. pyrenaica* (Carrión et al., 2003) and could even include *Q. suber* due to morphological similarities. These forests were also composed to a lesser extent by *Acer*, members of Ericaceae, *Betula*, *Carpinus*, *Castanea*, *Fagus*, *Ilex*, *Corylus* and *Ulmus*, among others. *Ilex aquifolium* is found in modern day in the area of Sierra Nevada (~40 km from Baza) in relict communities (Blanca et al., 1998). The low pollen count of *Ilex* in the Palominas record could suggest that it was already a relict in the area during the Early Pleistocene. In areas of higher altitude, the deciduous trees were accompanied by *Picea* and *Abies*, creating mixed forests. During Humid Phases V to VII, these mixed humid forests could have been even dominated by conifers, as evidenced by the spikes of *Picea* pollen abundance (Figs. 3 and 4).

Even if *Pinus* pollen could represent communities growing outside of the basin (Dunwiddie, 1987), it was probably an important component of the vegetation of Baza during humid periods. Although, not as prominent as its pollen abundance might suggest. Ortiz et al. (2003) report high concentration of dehydroabietic acid in the lower levels of the lake-shore site of Venta Micena. This acid is found in conifer resin and suggests that a great part of vascular plant matter transported into to the lake system could have originated from *Pinus*. Additionally, *Arceuthobium* pollen (parasite of *Pinus*) has been identified in the assemblages (Plate 1.6–7). Its pollen grains have low wind transportation (Gregor et al., 1974) and thus its presence suggests the existence of *Pinus* communities growing relatively proximal to the lake system. The existence of halophytic species, such as *Pinus halepensis*, within the modern Iberian flora (Rivas-Martínez, 1987; Rodriguez-Ariza, 1992) suggests that part of the pine communities in the Early Pleistocene of Baza may have benefited from the saline soils that developed in the margins of the lacustrine system (Gibert et al., 2007a). Additionally, the PCA (Fig. 5B) associates *Pinus* with the rest of the altitudinal conifers, indicating the presence of high altitude *Pinus* species, possibly *P. sylvestris* or *P. nigra*.

Cedrus pollen appears intermittently through the entire section, often linked with high proportions of arboreal pollen. It is yet not clear if the occurrence of *Cedrus* pollen in the Early Pleistocene deposits of Southern Europe represent European communities or are the result of long distance transport from Northern African populations (Postigo-Mijarra et al., 2010; Magri and Palombo, 2013).

Picea and *Abies*, the latter to a lesser extent, appear through the section in the form of spikes of high proportional value. Unlike *Pinus* pollen, grains from *Picea* and *Abies* are comparatively heavy and do not experience such long-range transportation (Bezrukova et al., 2005). The producing plant communities in Baza could not have been too far away from the depositional area. These spikes point to the presence of conifer forests in the mountain ranges surrounding the basin, like Sierra de Baza to the south, Sierra de Cazorla, to the north, and Sierra Nevada to the southwest.

This reconstruction of the palaeovegetation for humid phases fits with the environments described for the vertebrate fossil sites of the Early Pleistocene of Baza Basin, indicating that some of these sites could habe been formed during humid periods. The abundance of grazers, like *Equus*, *Bison*, *Mammuthus meridionalis* and *Hemitragus*, among others, would point to the existence of savannah-like open environments. However, mixed feeders and browsers such as *Praemegaceros* or *Stephanorhinus* are also found in the sites, indicating the existence of closed canopies and forests (Mendoza et al., 2005; Palmqvist et al., 2008; Agustí et al., 2009, 2015, 2010; Blain et al., 2011; Rodríguez-Gómez et al., 2016).

6.3. *The riparian and lacustrine environments of Baza*

Small river system must have flowed from the surrounding mountains into the lacustrine system. The main fluvial influx was generated by the Palaeo-Fardes River, which flowed from the neighboring basin of Guadix, into the NW part of the basin of Baza (Viseras et al., 2004, 2006). Other two important rivers feeding into the lake were the Palaeo-Castril River and the Palaeo-Guardal River, which collected water from the N and NE drainage areas of the basin. These rivers would have developed riparian vegetation composed mainly of Cyperaceae and *Salix*. In the lacustrine system of Baza, the existence of marginal freshwater bodies (Anadón et al., 1986, 2015; Anadón and Gabàs, 2009; Gibert et al., 2007a) would have supported the development of wetland environments (Anadón et al., 2015) composed of banks of Cyperaceae. Additionally, parts of this wetland must have supported the growth of trees, creating riparian forests constituted of *Salix* and *Alnus*. The relatively low proportion of these pollen taxa in the Palominas core (Fig. 3) can be explained in two ways: On one hand, these environments could have occupied a relatively small area and developed only in small communities. On the other hand, the marginal lacustrine areas where these vegetation types grew are described to cover considerable areas but could have been separated from the central body of water, as suggested by Ortiz et al. (2003) and Gibert et al. (2007a). They rather may have been isolated and shallow satellite ponds, impeding pollen transportation and deposition in the central lake. These satellite ponds would be composed of fresh to slightly saline water (Anadón et al., 1986, 2015; Anadón and Gabàs, 2009; Ortiz et al., 2003; El Hamouti and Gibert, 2012). During dry periods, as the base level lowered and the main lake shrunk, the wetland vegetation would have moved towards the depocenter of the basin. Therefore, the vegetation would have developed closer to the depositional environment represented in the Palominas core, thus explaining the occasional increase of pollen groups such as Cyperaceae during dry phases (Fig. 3). In this context, it should be noted that the dry phases cannot be correlated straightforwardly with the occurrence of gypsum in the lithological log. Most likely, this is due to the presence of gypsum of interstícial growth (post-sedimentary) (Gibert et al., 2007a). This gypsum is not contemporaneous with the fine-grained lacustrine carbonate matrix. It forms during the early diagenesis, when the chemical conditions of the water change, so it is temporally correlated to layers located stratigraphically higher.

The presence of moss and liverwort spores, such as *Riccia,* indicates that the lake experienced changes of water level relatively frequently (Van Geel et al., 1983). Some of the more common fungal spores in the record, type 200 and 201 according to Van Geel et al. (1989), are assumed to colonize dry soils after an aquatic phase, pointing to lowering of the water table (Van Geel et al., 1989). Also, the spikes in *Botryococcus* could point to abrupt changes in lake salinity of the waters (Guy-Ohlson, 1992), similar to those observed by different proxies for other parts of the Baza fm. (Anadón et al., 1986, 2015; Anadón and Gabàs, 2009; Ortiz et al., 2003; El Hamouti and Gibert, 2012). The abundance of *Sigmopollis* suggests the presence of shallow mesotrophic to eutrophic waters in some levels (Van der Wiel, 1982; Van Geel et al., 1983).

6.4. Flora endemic of the Early Pleistocene

The forests of Baza were accompanied by 'rare' taxa typical of the Early Pleistocene that would end up being extirpated from the Iberian Peninsula before or during the Middle Pleistocene (Postigo-Mijarra et al., 2007; 2009, 2010; Postigo-Mijarra and Barrón, 2017; Magri et al., 2017). This includes warm-temperate taxa such as *Carya*, *Parrotia persica, Zelkova*, *Eucommia* and *Pterocarya.* Tropical taxa not found in modern Europe, such as *Aralia,* are also present in the pollen assemblages. The conifers *Tsuga* and *Cathaya* also disappear before the Middle Pleistocene but are still found in Baza. The taxa that remained after the Middle Pleistocene are the main components of the modern Iberian vegetation (González-Sampériz et al., 2010; Postigo-Mijarra and Barrón, 2017).

Parrotia is in modern day restricted to few geographical locations in Hyrcanian region (Northern Iran), and Eastern China. In both regions, *Parrotia* is found as a component of mesophilous and humid forests (Yue et al., 2006; Sefidi et al., 2011). *Carya* is found in modern environments as part of mesophitic forests in Asia and North America (Orain et al., 2013). In the Iberian Peninsula *Carya* would grow as part of the interglacial warm-temperate forest (Leroy, 1997; González-Sampériz et al., 2010) and its presence in Baza could point to the existence of an ecological refuge (Orain et al., 2013). *Tsuga* grows in upland areas as part of mixed forests (Rogers, 1978). Modern *Cathaya* is a palaeo-endemism located only in small populations in high-altitude areas of China (Wang and Ge, 2006). In Baza, these conifers probably grew together with *Picea* and *Abies* in the moist and cool areas of the surrounding mountain ranges, forming high-altitude conifer forests. The presence of small proportions of warm-temperate taxa such as *Olea*, *Ulmus* or *Zelkova* during the dry phases, linked with glacial periods (Fig. 3), raises the possibility of the basin of Baza acting as glacial refuge for some tree taxa.

7. Correlation and age model

The intense cyclical control of the vegetation changes recorded in the Palominas pollen profile is related to the cyclical climate of the Quaternary period. In the majority of the Quaternary pollen records of the Mediterranean, arboreal pollen increases during interglacial stages due to humid conditions. Similarly, glacial stages see a rise in steppic taxa, indicating dry conditions (Suc and Popescu, 2005; Bertini, 2010). Therefore, the 11 humid phases (Fig. 4) recorded in the Palominas record are most likely correlated with interglacial periods, while the dry phases are correlated with the 'moderate' glacial periods of the Early Pleistocene (Klotz et al., 2006). The main force behind climate cyclicity during the Early Pleistocene was obliquity (Huybers, 2006), which is most likely the force driving the cycles recorded in the Palominas record with a frequency of 12.1 m. It is likely that changes in precession are also featured in the pollen curves, represented by one of the smaller peaks of frequency in the spectral diagraman (Fig. 6). The periodicity of the pollen signal, when plotted (Fig. 8), indicates that Phases II and III could belong to the same cycle. Therefore, the Palominas core would record 10 complete climate cycles.

The taxonomic composition of the Palominas pollen assemblages resembles Pleistocene pollen associations from other sites of the Iberian Peninsula. Specifically, the ocurrence of rare taxa such as *Aralia*, *Cathaya*, *Tsuga*, *Eucommia*, *Perocarya*, *Parrotia* and *Zelkova* evidences an Early Pleistocene age, since these taxa disappeared from the Peninsula before the Middle Pleistocene (Postigo-Mijarra et al., 2010; Magri et al., 2017). An age older than Early Pleistocene is unlikely due to the prevalence of steppes of *Artemisia* and *Ephedra,* as well as the lack of taxa typical of arid and semi-arid regions in the South of the Peninsula during the Pliocene, such as *Lygeum*, *Neurada*, *Nitraria* and *Calligonum* (Jiménez-Moreno et al., 2010; Feddi et al., 2011).

Taking into account the established timeline for the disappearance of the Early Pleistocene rare arboreal taxa from the Iberian Peninsula (Postigo-Mijarra et al., 2010; Magri et al., 2017) the age of the Palominas pollen associations can be further constrained. The presence of *Eucommia* (Plate 1.15–16), which disappeared from the Iberian Peninsula around 1.2 Ma (Leroy, 2008; Magri et al., 2017), and the absence of older taxa such as *Taxodium* and *Sciadopitys*, whose last record in the south of the Peninsula is during the Gelasian (Feddi et al., 2011; Magri et al., 2017), date the Palominas associations as older than 1.2 but younger than 1.8 Ma. Since the

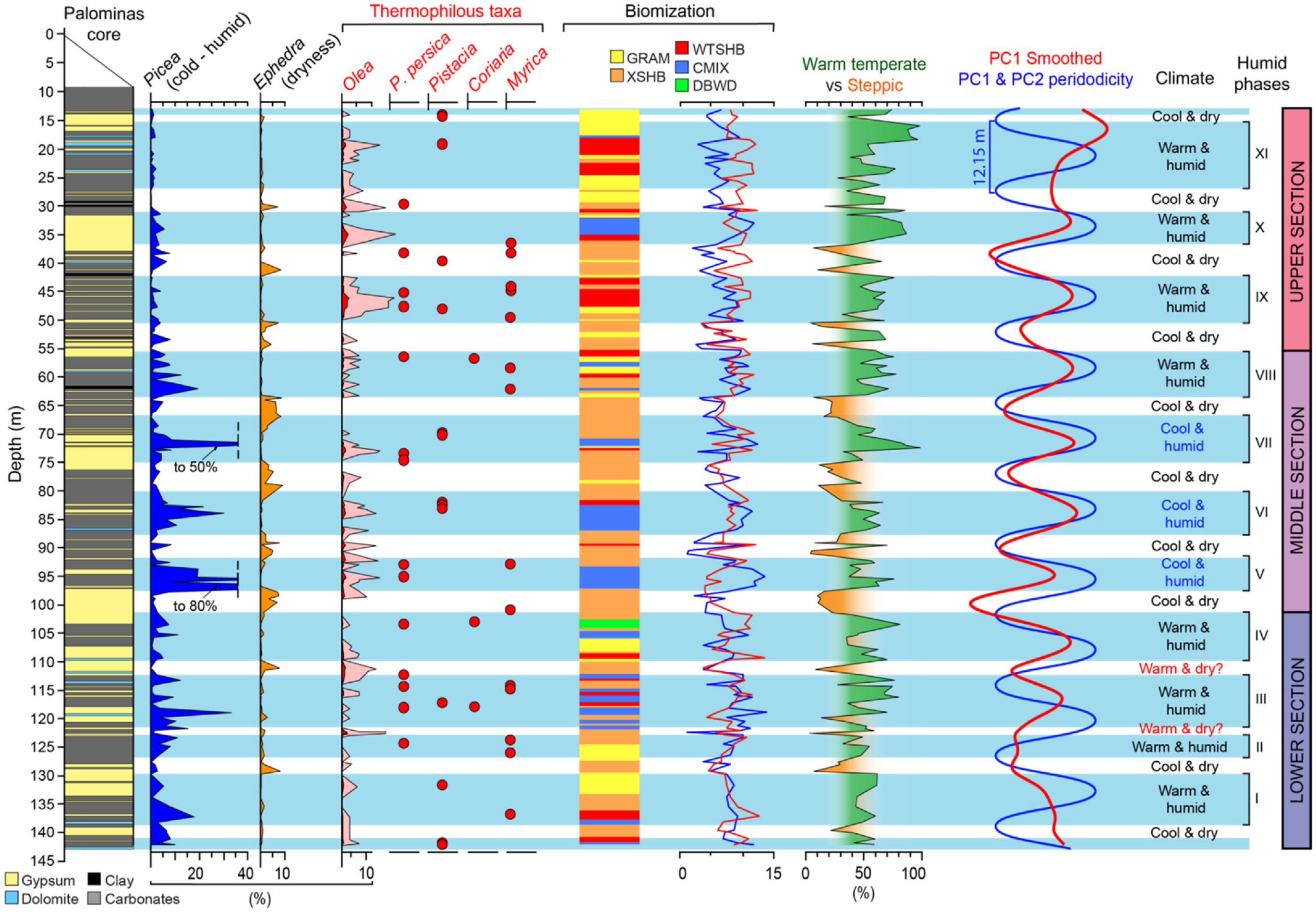

Fig. 8. Correlation between different climate-indicative variables of the Palominas core. Light blue bands represent Humid Phases I to XI. Regarding the pollen data, from left to right: lithology of the core, pollen abundances for *Picea*, *Ephedra*, *Olea*, *Parrotia persica*, *Pistacia*, *Coriaria* and *Myrica*, relative to the total pollen sum (excluding *Pinus*); Biomization affinity scores, described in Fig. 4; warm-temperate arboreal pollen vs. steppe taxa pollen ratio; Smoothed Spline of PC1 values (in red) and periodicity of the PC1 and PC2 values (in blue). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

last appearance of *Eucommia* in the Palominas record occurs at 40 m, the upper meters of the section could be slightly younger than 1.2 Ma. This age model, if accurate, would indicate that the Palominas core records the Calabrian stage. As previously discussed, the pollen record depicts 10 complete climatic cycles, most likely driven by obliquity (41 kyr cycles). Therefore, the age comprised in the Palominas core would be of ca. 400 kyr.

This pollen-based age model represents an interpretative hypothesis based on a palynostratigraphic approach. However, this hypothesis is not without challenges. First, the record of the aforementioned pollen taxa in the South of the Iberian Peninsula during the Early Pleistocene is sparse. Second, it is unsure if the last appearances of indicative taxa, such as *Eucommia* represent, the Last Appearance Datum. Therefore, the pollen associations of the Palominas core can be identified as typical of the Early Pleistocene, but further constrains of the age model as the one proposed here should be taken with care until independent dating methods are used.

8. Early Pleistocene climate dynamics in the baza basin

8.1. Climate quantification

The Coexistence Approach has already been proven successful in outlining the changing palaeoclimatic conditions recorded in the upper part of the Palominas core (Altolaguirre et al., 2019). The application of the CA to the entire Palominas record offers new information on the climatic patterns during the Calabrian (Fig. 9).

A total of 122 pollen samples, out of the original 177, were found to have more than 10 taxa with quantitative climatic information stored in the PALEOFLORA database and thus are suited for the CA analysis. The average number of taxa with climatic information per sample is 12.6, and the maximum is 21. Fig. 7 offers a visual representation of the coexistence intervals for the parameters: MAT, MTCold, MTWarm, MART, MAP, MPWet, MPDry, MPWarm and MARP, plotted against depth.

The coexistence intervals for temperature parameters (MAT, MTCold, MTWarm and MART) are broad and stay mostly within a similar temperature range. In the case of MAT, the minimum border of the intervals is usually set by either evergreen *Quercus* (>8.7 °C) or *Olea* (>10 °C) while the maximum value is mostly set between 18–21 °C by a variety of taxa. MTWarm provides narrower intervals, the minimum end alternates between averages of >19.4 °C and <27.9 °C, with the minimum values set by evergreen *Quercus* and *Olea* and the maximum set mostly by deciduous *Quercus* and different herbaceous taxa. Intervals for MTCold are also broad, with the lowest possible value of the intervals being set by evergreen *Quercus* (>0.4 °C), in almost each case. The maximum values of the intervals offer more variability (10–13 °C) with punctual low values on the occasional appearance of *Hippophae* (<8.3 °C). As result of

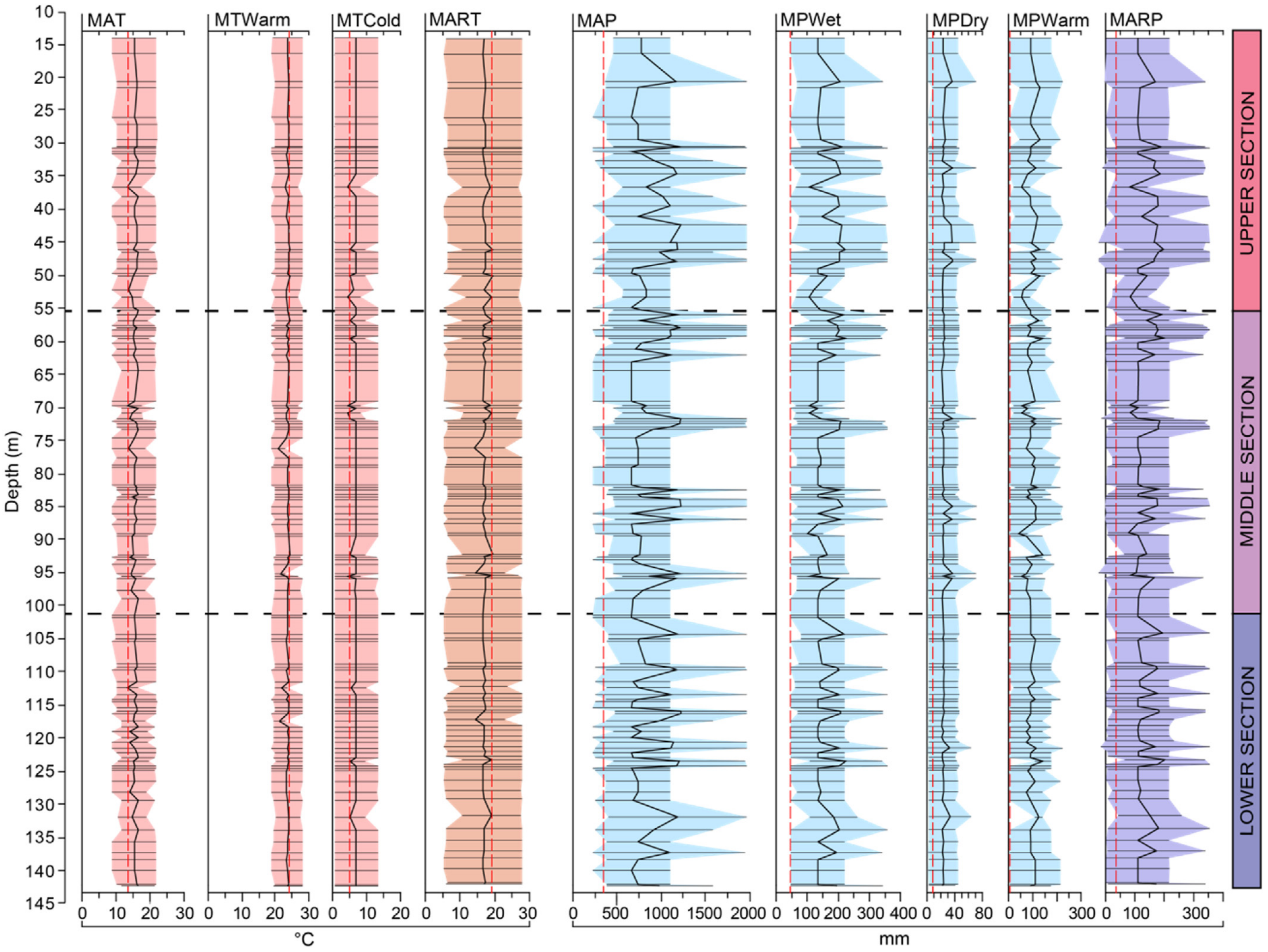

Fig. 9. Compilation of coexistence intervals for temperature (red) and precipitation (blue) parameters. Horizontal stripes comprise the coexistence intervals for each pollen sample. Modern values for each parameter are represented by dashed red lines. Exact values are: 13.2 °C MAT, 24 °C MTWarm, 4.9 °C MTCold, 19.1 C° MART, MAP 366.4 mm, 44.4 mm MPWet, 6.8 mm MPDry, 6.8 mm MPWarm, 37,6 mm MARP. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

the low variability of the MTWarm and MTCold intervals, the intervals for MART also display little variability and overall broad values.

Although it is difficult to find insightful climatic information on the wide intervals for temperature parameters, the mean interval value of MAT (15 °C) and MTCold (6.3 °C) are above the modern values of the area of Baza (13.2 and 4.9 °C respectively). Interval averages for MTWarm (23.6 °C) are similar to the modern measurement (24 °C), only the appearance of *Hippophae* in the pollen record pushes the maximum MTWarm value down (<27 °C), pointing to lower temperatures. With summer temperatures similar to modern and winter temperatures warmer than today, the seasonally differences in temperature (MART) should have been slightly lower during the Calabrian. The scarcity of information regarding temperatures in the CA results could point to the absence of significant temperature changes during this time period. But it could also be accredited to the low taxonomic resolution of the pollen record.

The coexistence intervals for precipitation parameters display more variability within the core than temperature parameters and offer more insightful climatic information. For MAP, the minimum values alternate through the record between 200 and 500 mm, implying the alternation between dry and more humid periods respectively. The change between these values is generally observed to occur in a progressive manner due to changes in the taxa composition of the samples. This pattern cannot be found in the changes between the maximum values of the MAP intervals, where the changes are sharp, between values set by *Ephedra* (<1096 mm), *Helianthemum* (<1171.5 mm) or Chenopodioideae (<1958 mm).

Intervals for MPWet, MPDry and MPWarm also show great changes of minimum and maximum values through the depth of the core. Intervals for MPWet display minimum values set mostly by *Eucommia* (>108 mm) and evergreen *Quercus* (>48 mm). The maximum values are set mostly by *Ephedra* (<220 mm) and Chenopodioideae (<203 mm). The MPDry intervals display minimum values between 2–5 mm set by various warm-temperate arboreal groups, while the maximum values are set usually by *Olea* (<71 mm), evergreen *Quercus* (<72 mm) and *Ephedra* (<45 mm). The intervals for MPWarm are mostly set by deciduous *Quercus* (>5 mm) and *Eucommia* (>108 mm) for minimum values, and *Ephedra* (<214 mm) and Cistaceae (<177 mm) for maximum values. Changes on the intervals for the parameters of MPWet and MPDry through depth also translate into the MARP intervals.

The precipitation parameters clearly show the existence of phases or stages of different precipitation levels. The dry phases are represented by intervals which comprise the modern precipitation values, although the mean value of the interval is usually above the modern value. Humid phases are represented by precipitation intervals in which the minimum value of the interval is higher than the modern precipitation values. The progression between different humidity phases results from the progressive change in pollen taxa. As an example of this progression, between the depths 64 to 60 m, the lowest possible MAP value is given by evergreen *Quercus* (>224 mm), then, upwards, the next interval has a minimum set by *Corylus* (>305 mm) and then *Tsuga* (>450 mm). This floristic progression fits the vegetation cyclicity during the Early Pleistocene (Combourieu-Nebout, 1993; Tzedakis et al., 2009). Overall, the CA results reconstruct the climate of Baza as a changing climate with distinct humid and dry phases. During humid phases the precipitations were significantly higher than modern ones, while during dry phases the precipitation would have been relatively low and more similar to the modern ones.

8.2. *Climatic cyclicity and long-term trends*

In the Mediterranean pollen record of the Pleistocene, arboreal pollen increase is linked to interglacial stages (humid) while increase of steppic taxa is linked with glacial periods (dry) (Suc and Popescu, 2005; Bertini, 2010). This was also true for Southern Spain (Camuera et al., 2019). This cyclical succession carries specific changes in the vegetation which have can be summarized into an idealized glacial-interglacial vegetation cycle (Combourieu-Nebout, 1993; Tzedakis, 2007; Bertini, 2010). This idealized cycle describes the evolution of steppe environment (cool and dry) into Mediterranean forest/scrub environment (warm and dry), then into deciduous forest (warm and humid), then into coniferous forest (cool but still humid) and again into the development of steppe. A similar pattern, albeit not exemplary, can be identified during Humid Phases IV, VI, VII, X and XI. However, several humid phases do not display the idealized pattern clearly. Phases I, II + III, V, IX and VIII seem to record the succession from steppe into conifer forest (spikes of proportion of *Picea* pollen), then, in last, an increase of the Mediterranean groups and the warm-temperate forest.

Picea spikes of abundance during Humid Phases I, III and VIII occur during the first stages of the forested period. Only during Phase VI *Picea* unmistakably appears during the later phase of the forested period. Contrarily, *Abies* is more abundant at the later stages of the forested periods (Figs. 3 and 5) fitting the idealized cycle (Fig. 3). The spread of *Picea* at the beginning of a humid period could carry two possible scenarions in relation to temperature changes. On one hand, if the temperature rises first while precipitation remains low, then *Picea* extends to higher altitudes where it can find more humidity. In this case, *Picea* spikes represent the initial warming of an interglacial period. Second: if the temperature remains low and precipitation increases, then *Picea* expands towards lower altitudes. In this case, *Picea* communities would be situated closer to the depositional environment, causing the spikes in concentration and abundance of their pollen. These spikes then would represent the later stages of glacial periods.

Similar periods of high abundance of *Picea* pollen have been identified in the Northern Italian section of Stirone, during the Pliocene-Pleistocene transition, associated with different glacial periods (Bertini, 2001). These examples are not limited to northern regions; in Crotone, Southern Italy, glacials MIS 20 and 18 also feature alpine forest conditions (Capraro et al., 2005). Similarly to these examples, the increase of *Picea* in Baza could respond to the development of cool and humid condition during the later stages of cool and dry glacial periods.

A different explanation for the *Picea* spikes could be that their origin is not climatic, but taphonomic. These spikes coincide with great values of total pollen concentration, up to more than 100.000 grains per gram (Fig. 4), indicating an increase pollen transport into the lake. During the transition between dry to humid phase, the lack of developed forest cover could have boosted the transport of pollen from the higher altitudes into the depositional environment. Furthermore, fluvial transport is known to lead to overrepresentation of *Picea* in lacustrine and arid environments (Wu et al., 2013). Still, even accounting for an increase in the rate of pollen transport, the deposition of such quantities of pollen grains would require the existence of *Picea* communities in the area or in the regions adjacent to Baza, probably in the higher altitudes of the Sierra Nevada mountain range.

Long term trends in the evolution of climate and vegetation in the Baza Basin are reflected in alternating proportions of climate-indicative taxa and biome scores (Fig. 8). During the Lower Section of the core, *Picea* reaches 20–40%, out of the total pollen assemblage during humid phases, while *Ephedra* reaches proportions of 10% during the dry ones. In comparison with other sections of the core, these low abundances could indicate that climatic changes between dry and humid periods were relatively milder. Regarding temperature, in the Lower Section the thermophilous taxon *Olea* reaches higher proportions during dry phases than during humid ones. *Olea* can survive in extremely dry and warm climates, granted sufficient winter precipitation (Anthelme et al., 2008). Therefore, this pattern suggests that these specific dry phases could have been warmer than other dry phases recorded in the core. Nonetheless, other termophilous taxa appear during the humid phases, not the dry ones (Fig. 8), pointing to the warm nature of these periods as well. The biome curves suggest the establishment of both cool and warm-temperate forested biomes during the humid periods of the Lower Section of the core. All indicates that the climate during the Lower Section of the core underwent moderate changes between dry and humid periods. Temperatures fluctuated, but could have remained relatively warm throughout the Lower Section.

The Middle Section of the core records a different climatic pattern (Fig. 8). *Picea* sees an increment to 50–80% during humid periods. *Ephedra* stays at 10% during dry periods, although it now covers longer parts of the core than previously. The high proportion of *Picea* pollen results in the prevalence of cool mixed forest (CMIX) as the dominant forested biome during humid phases. This change suggests that during Humid Phases V to VIII the climate of the humid phases could have been more humid but cooler than during the Lower Section, while the dry glacial phases were more prolonged than the ones in the Lower Section (although longer core intervals may not be necessarily related with longer time intervals). The Middle Section of the core could represent a generally cooler period spaning several climatic cycles. According to the age model proposed above, the Middle Section would record an age approximately between 1.4 and 1.3 Ma. A similar cold period is described by Ortiz et al. (2006) for Baza, based on isotopic analysis and assigned to and age of ca. 1.4–1.1 Ma. This climatic trend could be similar to the one described for Italy during the same period (1.4–1.3 Ma). There, pollen profiles also record climatic cooling and intensification of dry conditions (Combourieu-Nebout et al., 2015).

The Upper Section of the core sees an improvement of the climate and a return to conditions similar to those of the Lower Section. In general, dry phases are shorter again, while humid phases are now warmer than during the Middle Section, with warm-temperate shrubland (WTSHB) being the dominant biome. *Picea* reaches only 5–10% out of the entire assemblage in the Upper Section, much lower than in the two previous sections, and shows a steady decline during each successive humid phase (Fig. 4). This decline in *Picea* could relate to a long term increase in summer aridity in the upper parts of the core, which is thought to be the cause of the decline of *Picea* in the Italian Peninsula during the Pleistocene (see Magri and Palombo, 2013, and references therein).

Besides a clear cyclicity of climate and vegetation successions, most probably driven by obliquity, the Palominas pollen assemblages also record several long term trends in vegetation and climate change. From the Lower to the Middle Section of the core the increase of abundances of pollen of *Picea* and *Ephedra* suggests a general cooling, with longer dry phases. From the Middle to the Upper sections, the proportions of steppe plants and *Picea* decrease in favour of warn-temperate trees, depicting an evolution towards warmer conditions and less severe dry periods.

9. Comparison with other Mediterranean pollen profiles

The Palominas core provides a long pollen record of the Early Pleistocene (most probably Calabrian) which spans multiple climatic cycles. According to the age model discussed in this work, the Palominas record would cover the majority of the Calabrian. Since the Calabrian is only known in the Ibertian Peninsula from short and fragmentary records, this new pollen profile contributes to shed light on the continental dynamics of the Mediterranean realm when compared with previously described pollen records of the region (Fig. 10) (Table 2).

9.1. Comparison with pollen records from southern Spain

Early Pleistocene vegetation data was reported by palynological analysis of offshore drill cores ODP 976 (0–1.12 Ma) (Combourieu-Nebout et al., 1999; Von Grafenstein et al., 1999; Joannin et al., 2011; Toti and Bertini, 2018), and both the Andalucía G1 (Gelasian to Zanclean) and Nador 1 cores (Calabrian (1.7 Ma) to Zanclean) (Feddi et al., 2011), performed in the Alborán Sea approximately 200–300 km away from the Palominas drill site. These cores cut through Early Pleistocene marine sediments and provide pollen assemblages dominated by *Pinus*, herbs and steppe plants. In these records, *Quercus* appears in low quantities but still as the predominant tree type (apart from *Pinus*), while Mediterranean taxa are being represented mostly by *Olea/Phillyrea* and evergreen *Quercus* (Combourieu-Nebout et al., 1999). Assemblages with abundant deciduous taxa alternate with those dominated by steppe and semi-desert taxa (Toti and Bertini, 2018). This alternation of dry steppes and *Quercus* forests (forested savannahs) matches the dynamics seen in the Palominas record. The drill core of Site U1385 or “Shackleton Site” also provides pollen data for the SW region off the coast of the Iberian Peninsula (MIS 30–32) (Oliveira et al., 2017). This pollen record depicts obliquity-controlled climate and vegetation, rich in *Quercus* during the MIS 31 period, while glacial phases were dominated by *Artemisia* and other herbs. These pollen assemblages match the ones found in Baza, with the difference that the proportion of evergreen *Quercus* is significantly lower than in Baza and the proportion of *Cedrus* is higher. These differences may reflect taphonomic bias due to transportation of pollen grains into a marine sedimentary environment. Although *Cedrus* pollen is relatively common in the Pleistocene record of the Iberian Peninsula (González-Sampériz et al., 2010; Postigo-Mijarra et al., 2010), it is still under discussion whether this pollen represents Iberian or African communities (Combourieu-Nebout et al., 1999). The intramontane condition of the Baza Basin should limit the influence of long-distance transported pollen from Africa. Nonetheless, the low abundance of *Cedrus* in the Palominas record cannot by itself rule out the influence of African communities.

9.2. Comparison with pollen records from northern Spain and southern France

The palynofloras from Baza can be compared with pollen data from Early Pleistocene continental sites of Northern Spain which have been dated with relative accuracy, such as Bóbila Ordis-IV (MIS 35–33) (Leroy, 2008) and Cal Guardiola (between 1.2 and 0.8 Ma) (Postigo-Mijarra et al., 2007). Additionally, it can also be compared with continental palynofloras from older or younger parts of the Early Pleistocene or from dubiously dated sites. These are the palynofloras from Tres Pins (Gelasian or early Calabrian) (Leroy, 1997), Molí Vell (late Early Pleistocene) (Geurts, 1977, 1979), Crespià (late Gelasian or early Calabrian) (Suc, 1980; Roiron, 1983, 1992) and Gran Dolina in Atapuerca (0.9 Ma) (Rodríguez et al., 2011). The Palominas palynoflora shows a higher percentage of herbs compared to the northern sites, which have higher proportion of arboreal pollen. Only the site of Cal Guardiola (Postigo-Mijarra et al., 2007) also presents high proportion of pollen from grasses (Poaceae). However, the pollen at Cal Guardiola most likely represent the local signal from grasslands associated to a fluvial environment, not necessarily reflecting the broader vegetation. Warm-temperate trees seem to be more abundant and diversified in the northern sites than in Baza. Leroy (1997, 2008) describes high proportion of *Carpinus*, *Quercus*, *Carya* and *Ulmus-Zelkova* in NE Spain. Whereas in the Palominas record, all these warm-temperate trees show low pollen abundances except for deciduous *Quercus*. Similarly, pollen assemblages from the Early Pleistocene of Southern France at Saint-Macaire (ca. 1.4 to 0.7 Ma) describe alternations between dry floras (dominated by *Artemisia* and *Pinus*) and humid floras with higher arboreal proportion than those of Baza during humid periods (Leroy et al., 1994).

The sequence of Bòvila Ordis-IV, in Catalonia, records MIS 36 to 33 (Leroy, 2008) which may correspond to the Palominas section according to the proposed age model. The climatic comparison between these localities is described in Altolaguirre et al. (2019), showing higher precipitations in the northern location of Bòvila Ordis-IV than in Baza, to the south. The humid periods (described as interglacials) recorded in Bòvila Ordis-IV start as a wooded steppe rich in warm-temperate taxa such as *Quercus*, *Ulmus-Zelkova*, *Carya* and *Carpinus*. This is followed by a decrease of warm-temperate trees and an increase of conifers, probably linked to cooler temperatures. In Baza, some of the humid periods follow a similar trend, especially in the Upper Section. However, the foresed steppes are dominated almost entirely by *Quercus*, with *Ulmus-Zelkova*, *Carya* and *Carpinus* only appearing in low proportions.

Picea is virtually ever-present in the pollen records of Bòvila Ordis-IV and Tres Pins (Leroy, 1997, 2008). In contrast, the proportion of *Picea* in Baza is generally low, except during the brief periods of high abundance (Fig. 4). The absence of *Picea* in other northern Early Pleistocene sites of Spain (Postigo-Mijarra et al., 2007; Rodríguez et al., 2011) suggest that its presence in the Bòvila Ordis-IV and Tres Pins records must be linked to high-altitude populations growing in the neighboring Pyrenees (max. alt. 3.404 m a.s.l.). In Baza, such populations could grow in the surrounding mountains located around the core locality. Within a radius of 25 km there are, Sierra de Baza (2.271 m a.s.l.), Sierra de las Estancias (>1.500 m), Sierra del Periate (1.612 m), Sierra de Cástril (2.107 m). Also, in a radius of 50 km there are, Sierra de María (2.045 m), Sierra de la Sagra (2.383 m) Sierra Magina (2.164 m), Sierra de Arana (2.027 m), and even Sierra Nevada, being the highest massif of continental Spain (3.482 m). Thus, *Picea* populations in Spain during the Early Pleistocene would have been restricted to areas of high altitude.

9.3. Comparison with pollen records from Italy, the Balkans and Greece

Pollen data from Italy show a clear N–S gradient; northern profiles contain more arboreal pollen than the southern ones, where steppe plants are more predominant (Combourieu-Nebout

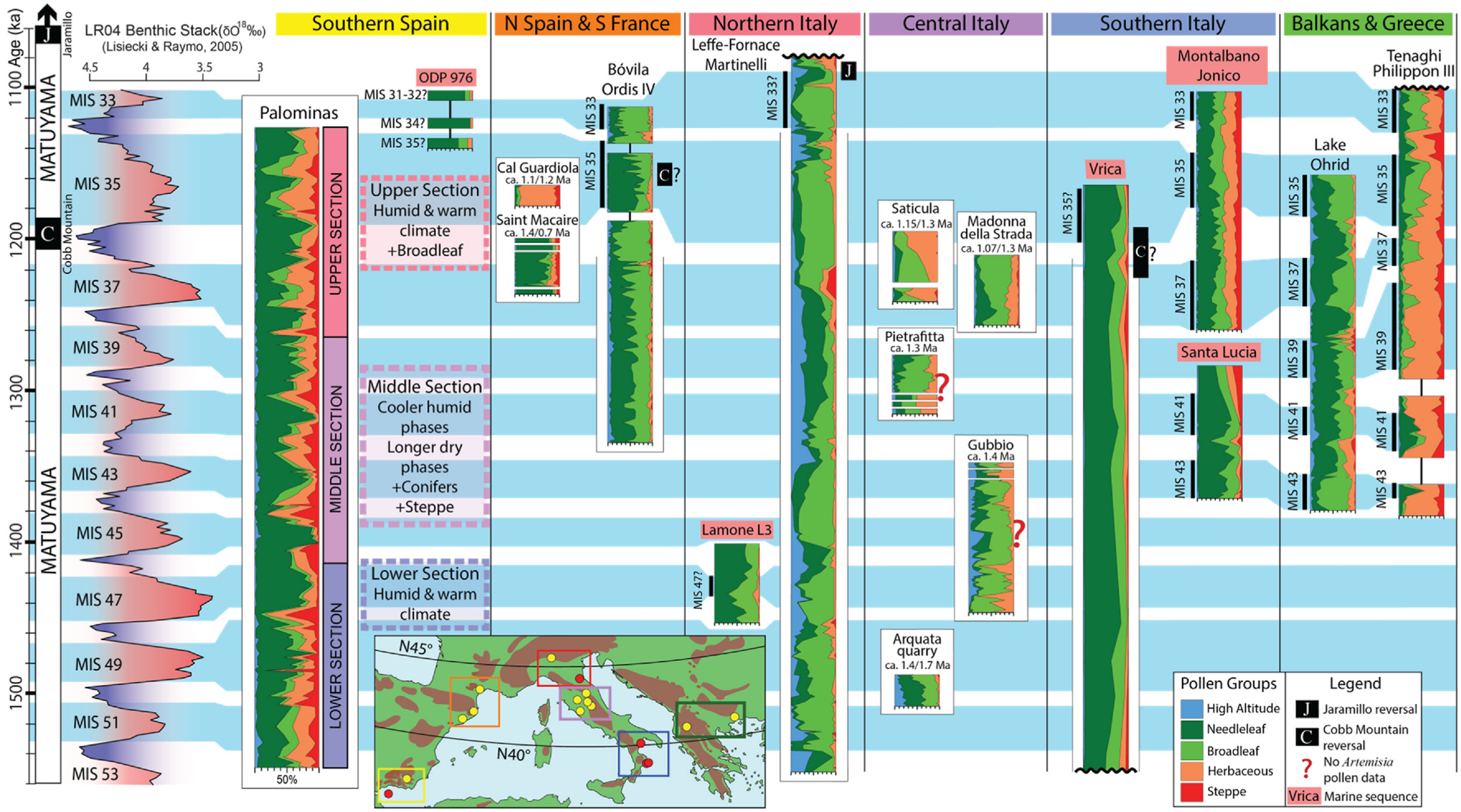

Fig. 10. Pollen diagrams of selected pollen profiles of the Mediterranean Basin which could record a time interval similar to the age model proposed for the Palominas core. Pollen data for all profiles has been grouped into five main groups: High altitude (*Picea* + *Abies*), Needleleaf (including *Pinus*, no *Picea/Abies*), Broadleaf, Herbaceous and Steppe (*Artemisia* + *Ephedra*). Blue bands represent the correlation of interglacial MIS stages. The original height of each profile has been proportionally preserved except in the case of Vrica, in which the uppermost part has been comprised to accommodate the magnetic reversal into the figure. Further information regarding the featured profiles can be found in Table 2. Profiles of uncertain dating appear featured inside white boxes, separated from the blue bands. Climatic sections of the Palominas core refer to general climatic trends, not to specific glacial-interglacial stages. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

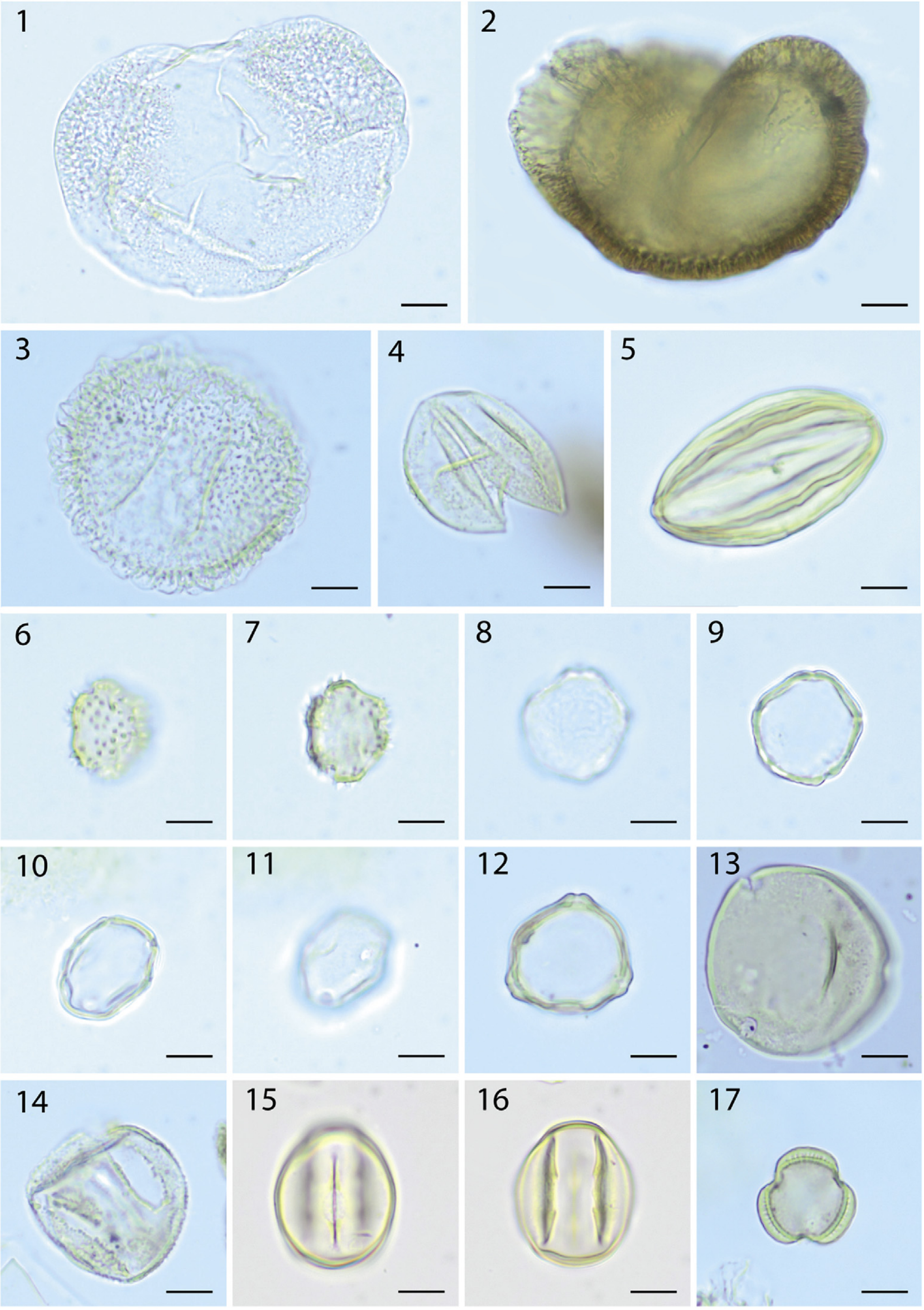

Plate 1. Selection of pollen grains from the Palominas core. 1: *Picea*; 2: *Cedrus*; 3: *Tsuga*; 4: Cupressaceae indet. 5: Type *Ephedra fragilis*; 6–7: *Arceuthobium*, different focal depths; 8–9: *Ulmus*, different focal depths; 10–11: *Pterocarya*, different focal depths; 12: *Betula*; 13: *Carya*; 14: Type *Parrotia persica*; 15–16: *Eucommia*, different focal depths; 17: *Artemisia*. The scale in all pictures equals to 10 µm.

et al., 2015). The Northern Italian sections which could share a similar time interval with the record from Baza are: Lamone (marine, MIS 64 to 46) (Fusco, 2007), Leffe - Fornace Martinetti (continental, 1.94/1.78 to 0.87 Ma) (Ravazzi, 2003; Ravazzi and Strick, 1995; Muttoni et al., 2007) and Fornaci di Ranica (Late Calabrian) (Ravazzi et al., 2005). These palynofloras are dominated by pollen from warm-temperate trees and conifers (mostly *Pinus*, *Picea* and *Tsuga*), with taxa from colder climates such as *Larix*. These are drastically different from the herbaceous-rich assemblage found at Baza, and are more similar to those of Northern Spain. The proximity to the Alps explains the high proportion of high altitude conifers (mainly *Abies* and *Picea*) in those continental profiles.

At Central Italy several continental pollen profiles, although short and not accurately dated, could share a similar age with the Palominas record. These are the profiles of Madonna della Strada (ca. 1.3/1.1 Ma) (Magri et al., 2010), Saticula (ca. 1.3/1.1 Ma) (Russo-Ermolli et al., 2010), Pietrafitta (ca. 1.3 Ma) (Ricciardi, 1961; Martinetto et al., 2014), and Gubbio (dated as Early Pleistocene,

Table 2
List of pollen profiles featured in Fig. 10.

Site/Drill Core	Age	Vegetation cycles	Chronological control	References
Palominas	Calabrian	Multiple vegetation cycles	Palynostratigraphy	Present study
ODP 976	Present – MIS 34?	Multiple vegetation cycles	Oxygen isotope stratigraphy	Combourieu-Nebout et al. (1999); Von Grafenstein et al. (1999).
Bóvila Ordis IV	1.2 Ma (MIS 35–33)	Complete and partial vegetation cycles	Mammal biostratigraphy, magnetostratigraphy	Leroy (2008)
Cal Guardiola	Ca. 1.2/1.1 Ma	Interglacial period?	Mammal biostratigraphy, magnetostratigraphy	Postigo-Mijarra et al., 2007
Saint Macaire	1.4–0.7 Ma	Glacial period	Magnetostratigraphy	Leroy et al. (1994)
Leffe - Fornace Martinelli	Ca 1.5–1.0 Ma	~8 cycles (MIS 31–47?)	Mammal biostratigraphy, Magnetostratigraphy	Ravazzi and Rossignol Strick, 1995; Ravazzi (2003); Muttoni et al. (2007)
Lamone L3	MIS 48–46	Complete interglacial and partial glacial periods	Correlation of vegetation cycles	Fusco (2007).
Saticula	Between 1.3 and 1.15 Ma	Transition into glacial period	Mammal biostratigraphy	Russo-Ermolli et al. (2010)
Madonna della Strada	Between 1.3 and 1.07 Ma	Interglacial (MIS 37 or 35)	Mammal biostratigraphy	Magri et al. (2010)
Pietrafitta	Middle Calabrian (ca. 1.3 Ma?)	Glacial period?	Mammal biostratigraphy	Ricciardi (1961); Martinetto et al. (2014)
Gubbio	Ca. 1.4?	Multiple vegetation clyces?	Palynostratigraphy	Lona and Ricciardi (1961)
Arquata quarry	Between 1.7 and 1.4 Ma	Interglacial to glacial transition?	Pollen, carpological remains, mollusk & ostracod biostratigraphy	Bizzarri et al. (2018)
Montalbano Jonico	1.25–0.9 Ma	Multiple vegetation cycles	Oxygen isotope & vegetation correlation	Joannin et al. (2008)
Santa Lucia	1.36–1.28 Ma	One complete and one partial vegetation cycles	Oxygen isotope & vegetation correlation	Joannin et al., 2007a, b
Vrica	Ca. 2.3 – ca. 1.2 Ma	Multiple vegetation cycles (low resolution)	Magnetostratigraphy, marine biostratigraphy	Combourieu-Nebout et al. (1990); Lourens et al. (1996)
Tenaghi Philippon III	1.35–0.66 Ma (TF III)	Multiple vegetation cycles	Astronomic calibration	Van der Wiel and Wijminstra, 1987; Tzedakis et al. (2006).
Lake Ohrid	1.36–1.16 Ma	Multiple vegetation cycles	Astronomic tuning	Panagiotopoulos et al. (2020)

possibly around 1.6/1.3 Ma) (Lona and Ricciardi, 1961). These depict palynofloras similar to the ones from Baza in the sense that much of the arboreal pollen is represented by *Quercus*, with high representation of *Picea*. Nonetheless, these Italian records differ in the high amount of arboreal pollen, especially from broadleaf trees. Arboreal pollen dominates these pollen associations during humid periods and only diminishes slightly during dry phases. Also, *Carya* and *Tsuga* represent a fair share of the arboreal pollen in Central Italy, while in Baza they appear in smaller quantities. However, the record of Saticula resembles the one from Baza in the sense that herbaceous pollen often represents more than half of the association (Russo-Ermolli et al., 2010). Although the record at Saticula could describe arid conditions, the authors also suggest that the high herbaceous and grass pollen content represents grasslands in association with fluvial environments. The scarcity of steppe taxa and the abundance of *Carya* reinforce this interpretation and emphasize the difference to the pollen assamblages from Baza, which records a more broad pollen signal.

The continental pollen profile from Arquata quarry, near Bevagna (Bizzarri et al., 2018) describes a transition from humid to dry phase around 1.4/1.7 Ma. Similar to other profiles from Central Italy, the high proportion of trees (especially rich in *Cedrus* and *Carya*) makes these assemblages radically different from the ones in Palominas. Although Arquata quarry might record local conditions there is an interesting similarity; the transition into a dry phase is accompanied by a decrease of conifers and an increase of Mediterranean taxa. This is similar to the sequences of some of the vegetation cycles from Palominas such as the ones described for Humid Phases II + III, V or IX, in which the Mediterranean taxa increase at the end of the interglacial periods while conifers decrease.

Certain marine pollen assemblages from Southern Italy could coincide with the time period recorded in the Palominas core, such as Santa Lucia (1.36–1.28 Ma) (Joannin et al., 2007b), Montalbano Jonico (1.25–0.9 Ma) (Joannin et al., 2008), Vrica (ca. 2.2 to 1.3 Ma) (Combourieu-Nebout et al., 1990), or Camerota (ca. 1.7/1.6 Ma) (Russo-Ermolli, 1999). The pollen associations from these profiles present more similarities with the ones from Baza than those from Central or Northern Italy. These assemblages record humid stages in which *Quercus* pollen dominates above all other warm-temperate taxa and dry stages are rich in *Artemisia*, *Ephedra* and other herbs. Nonetheless, some differences remain. The pollen signal of Mediterranean taxa is weaker in Southern Italy than in Baza, with remarkable lower proportion of evergreen *Quercus*. Additionally, Southern Italian assemblages present high proportion of *Tsuga* and *Cedrus*, like the other Italian records, while both taxa are sparse in the Palominas assemblages. Even if Southern Italy and Southern Spain shared a similar climate during the Calabrian, *Tsuga* and *Cedrus* communities seem to have had a wider distribution at the Italian Peninsula.

Further East, the continental pollen associations of Tenaghi Philippon (Greece, 1.35 Ma to Holocene) (Van der Wiel and Wijmstra, 1987; Tzedakis et al., 2006) and part of the Lake Ohrid drill core (Albania and North Macedonia, 1.36–1.16 Ma) (Panagiotopoulos et al., 2020) could partially share a similar time interval as Palominas. This could also be the case for the continental pollen association from Bezhan (Albania, Calabrian age) (Denk et al., 2019) and the marine sequence of Tsampika (1.16–0.96 Ma) (Joannin et al., 2007a). Tenaghi Philippon and Tsampika depict palynofloras which are remarkably similar to the ones from Baza, with high proportion of *Artemisia*, Poaceae and Chenopodioideae during dry phases, while *Quercus* dominates humid periods. Furthermore, an increase of broadleaf forest, like the one recorded in Baza during the Upper Section, is identifiable also in the Tenaghi Philippon record (MIS 39 and onwards) (Fig. 10). According to the proposed age model for the Palominas core, these two events could be synchronous. The only significant differences are the abundance of *Tsuga* and *Cedrus* in the Greek records, which are similar to the ones from Southern Italy, but do not occur in Baza in such high proportions. Pollen assemblages from Lake Ohrid for the Early Pleistocene (Panagiotopoulos et al., 2020) are much richer in pollen from altitudinal conifers than the assemblages from Baza and Greece, and with a highly diversified and abundant presence of pollen from extirpated arboreal taxa, especially *Cedrus*, *Tsuga* and *Cathaya*. The single pollen assemblage of Bezahn is also dissimilar to those of Palominas in that arboreal pollen and pollen from extirpated taxa appear in higher proportions (Denk et al., 2019). Both these records contain a higher amount of conifer pollen than Tenaghi Phillipon and Palominas and likely record a much more intense alpine signal.

In essence, the herb-rich Palominas pollen associations are most similar to the pollen floras reported from Southern Italy and Greece (especially similar to the Tenaghi Philippon record). On the other hand, they are sharply different from associations of more northern latitudes from the Iberian and Italian peninsulas, which are richer in warm-temperate woody plants and conifers (non-*Pinus*). Such discrepancies are likely to be caused by latitudinal differences in precipitation, known to exist during modern day and during the Early Pleistocene in these regions (Suc and Popescu, 2005; Fusco, 2007; Bertini, 2010; Combourieu-Nebout et al., 2015; Altolaguirre et al., 2019). Longitudinally, Mediterranean vegetation, mainly evergreen *Quercus*, was more developed in SE Spain than in Southern Italy. This may suggest the existence of a more developed Mediterranean climate in SE of the Iberian Peninsula. The *Tsuga* record is scarce in SE Spain in comparison with the richer Italian and Greek records. Since *Tsuga* prefers humid and cool conditions, this difference implies that the climate in Baza could have been generally dryer than the ones in Southern Italy and Greece.

10. Conclusions

The palynological analysis of the Palominas sedimentary record retrieved pollen grains with excellent preservation. The pollen record depicts the vegetation developed in the Baza Basin with strong cyclical components. Two main vegetation phases can be identified. First, phases where the pollen associations are composed mostly of herbs, predominantly *Artemisia*, Chenopodioideae, Asteraceae and Poaceae. Secondly, phases with an increase in the proportion of arboreal pollen, although the pollen from herbaceous plants and grasses still constitutes a considerable portion of the tkjotal assemblage. The arboreal pollen assemblages represent environments of higher humidity, traditionally linked with warmer ‘nterglacial stages. Herbaceous assemblages formed during dry periods and are associated with colder glacial periods.

The pollen flora of the Palominas core is typical for those of the Early Pleistocene. A Calabrian age could be proposed on the basis of the presence and absence of key pollen taxa such as *Eucommia*. At least 10 complete vegetation cycles are recorded, possibly driven by obliquity forcing. Thus, the Palominas core could comprise more than 400 kyr. Beside these cycles, three phases of regional climatic trends are found throughout the core. The Lower Section records dry phases that may have been relatively warm. The Middle Section of the core archives a climatic change to cooler humid phases and longer dry periods. During the Upper Section of the core, the climate became warmer, with shorter dry periods. These regional climatic trends are similar to those identified in the Italian Peninsula.

In the higher latitudes of the Iberian and Italian Peninsula, the increased precipitations during both glacial and interglacial stages must have allowed for the development of fully forested environments throughout the Early Pleistocene. The pollen associations found in Baza, rich in herbaceous and steppe pollen and with overrepresentation of *Pinus*, are similar to those of Southern Italy and Greece for Calabrian. During that time, southern latitudes in both the Western and Eastern Mediterranean developed open and dry vegetation communities during glacial periods. The landscapes would be similar to steppes or, if climatic conditions were humid enough, forested steppes. During interglacial periods, the improvement of the climate would allow these southern regions to develop forested environments, still preserving a certain degree of openness nonetheless.

Acknowledgements

This work was performed with the financial support by ROCEEH Research Centre ‘The role of culture in early expansions of humans’ of the Heidelberg Academy of Sciences and Humanities (www.roceeh.net). We thank the support (LG) from the projects of the Spanish Government CGL2016-79458-P and Catalan Government 2017-SGR-824. Funding for Palominas drilling was provided to Dr. Dieter F. Mertz (Mainz) via an internal funding program of the Johannes Gutenberg University of Mainz, Germany. The authors highly appreciate the opportunity to sample the Palominas core. The authors also appreciate the help of Claudia Groth (ROCEEH Frankfurt) with laboratory and technical assistance. This work is a contribution to NECLIME (Neogene Climate Evolution in Eurasia, www.neclime.de).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.quascirev.2020.106199.

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Chapter 4

Early Pleistocene temperature changes in the Baza Basin (SE Spain)

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4.1. Introduction

This chapter contains as of yet unpublished additional data which contributes to the palaeoenvironmental reconstruction of the hominin environment at the Baza Basin during the Early Pleistocene.

The Quaternary climate is strongly marked by the cyclical alternation between glacial and interglacial phases. In the Mediterranean Basin, Pleistocene glacials have been mainly linked to dry and cold conditions, contrasting the warm and humid interglacial periods (e.g., Suc and Popescu, 2005; Bertini, 2010). Such conditions are also documented by southern Spanish pollen records (e.g., Combourieu-Nebout et al., 1999; Camuera et al., 2019; Altolaguirre et al., 2020; Torres et al., 2020; Toti et al., 2020).

The Palominas core in the depocenter of the Baza Basin allows studying climate and vegetation during several glacial-interglacial cycles of the Calabrian stage (Early Pleistocene). The pollen record from the Palominas core depicts a palaeoenvironment heavily influenced by changes in precipitation (Altolaguirre et al., 2019; 2020). However, temperature reconstructions based on pollen did not allow a solid assessment of the characteristics of temperature change. Ortiz et al. (2006) used a long (360 m) $\delta^{18}O$ isotope record from Pleistocene ostracod shells from the Cortes de Baza section to interpret large-scale temperature changes, but the quantification of changes within single glacial-interglacial climatic cycles was limited due to low sampling resolution. Other approaches for climatic reconstructions in the area include the mutual ecogeographic range (MER) method (Blain et al., 2016), which provided measurements for the temperature and precipitation intervals which could support the presence of the reptile and amphibian fossil species found at the hominin sites of Orce (Agustí et al., 2009; Blain et al., 2011, 2016). These results describe the prevalence of warm and humid phases related to interglacial periods, and of dry and cooler phases linked to glacials. However, the MER method was only applied on punctual strata from the short stratigraphic interval that includes the Orce sites. Therefore, magnitude and rate of temperature changes over series of glacial-interglacial cycles during the Early Pleistocene of Baza remain largely unknown.

The present work features the application of organic geochemistry palaeo-thermometers in the Baza Basin in conjunction with detailed palynological analyses carried out from the same core samples. Collectively, these data aim at revealing information on the relative temperature changes in the region and their relation to the alternation between humid and dry periods inferred from the pollen record (Altolaguirre et al., 2020). Branched glycerol dialkyl glycerol tetraethers (brGDGTs) are membrane lipids found in aquatic and soil bacteria frequently used in palaeoclimate studies as a proxy for mean annual air temperature (MAT) (e.g., Weijers et al., 2007; Schouten et al., 2013; Berke, 2018). BrGDGTs have been successfully used to reconstruct relative temperature changes throughout selected climatic cycles of continental Quaternary records in the eastern Mediterranean region (Ardenghi et al., 2019; Panagiotopoulos et al., 2020). In a similar way, these biomarkers could be able to successfully reconstruct temperature changes at the time of the first hominin occupation of the Iberian Peninsula.

4.2. Geological setting

The Baza Basin is located in the province of Granada, in SW Spain. It is the largest intramontane basin (>4,000 km^2) in the Betic Ranges (Fig. 4.1). At present, low altitude areas experience sparse rainfall, with mean annual precipitation (MAP) values of 250 to 350 mm and temperatures (MAT) of 16 to 14 °C (MAPAMA, 2020).

The sedimentary fill of the Baza Basin covers around 8 Myr, from the late Tortonian (ca. 7.3 Ma) to the Middle Pleistocene (ca. 0.6 Ma). During the late Tortonian the uplift of the Betic ranges isolated the region from the marine realm, leading to a transition from marine to continental sedimentation (Soria et al., 1998). An endorheic lacustrine system was established in the Baza Basin while alluvial sedimentation dominated in the Guadix Basin (Gibert et al., 2007a).

The palaeo-Lake Baza consisted of a shallow but large and presumably permanent water body surrounded by smaller ponds (Fig. 4.2). Fresh to slightly saline waters characterized the satellite ponds, while higher-salinity conditions predominated in the central body (Gibert et al., 2007b; El Hamouti and Gibert, 2012; Anadón et al., 2015). Relatively frequent changes in salinity have been inferred in the marginal areas of the lake system based on ostracod assemblages (Anadón et al., 1986, 2015; Anadón and Gabas, 2009; Ortiz et al., 2003), diatoms (El Hamouti and Gibert, 2012) and foraminifers (Anadón et al., 1986).

The lacustrine facies distribution in the basin shows three concentric belts or zones of increasing salinity towards the Inner zone (Gibert et al., 2007b) (Fig. 4.2). The Marginal and Intermediate zones represent palustrine and ephemeral lacustrine environments respectively. The Inner zone represents the most distal part of the lacustrine environment

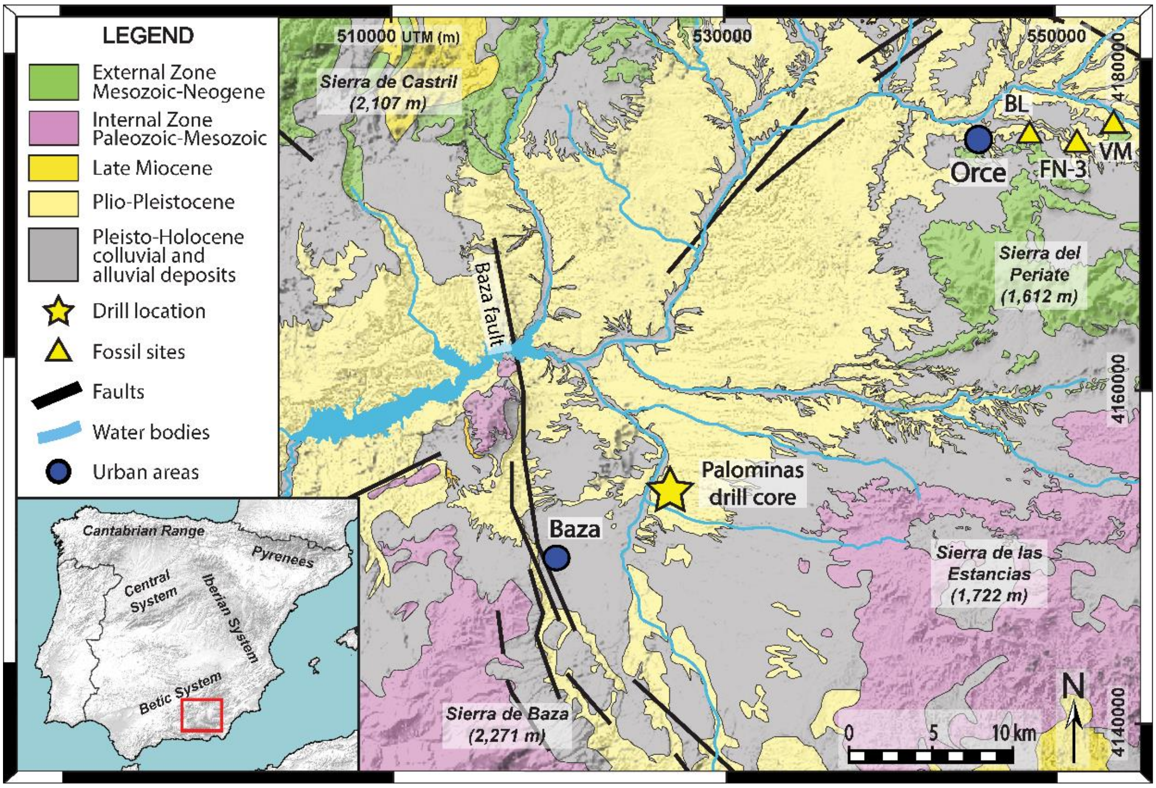

Fig. 4.1: Simplified geological map of the Guadix-Baza Basin. Orce fossil sites are: BL: Barranco León, FN-3: Fuente Nueva 3, VM: Venta Micena. On the right lower corner: the position of the Guadix-Baza area in the Iberian Peninsula. Geological data from Roldán et al. (2012). Main faults from Sanz de Galdeano et al. (2012).

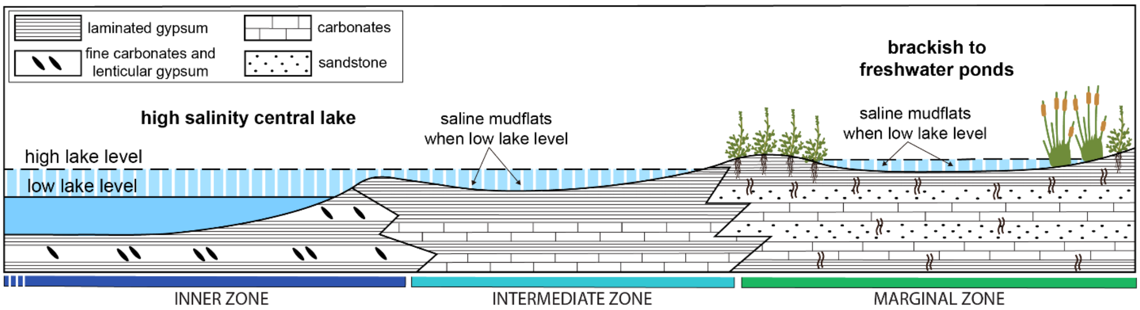

Fig. 4.2: Simplified depositional model of Lake Baza (modified from Gibert et al., 2007b).

occupied by a shallow saline lake. The deposits in the Inner zone consist of an alternation of laminated gypsum and fine-grained carbonates (Gibert et al., 2007b). The Palominas core was drilled in the Inner zone of the basin, where > 500 m of laminated lacustrine deposits occur (Haberland et al., 2017).

4.3. Material and methods

4.3.1. Pollen-based climatic analyses

A total of 64 samples were selected and analysed for GDGTs biomarkers in parallel. A higher sampling resolution was employed between 100 – 82 m and 53 – 40 m in order to study changes through entire climatic cycles. Palynological analyses were carried out on 18 samples from the Palominas core in addition to the 177 pollen samples already studied previously (Altolaguirre et al., 2020).

The coexistence approach (CA) method (Mosbrugger and Utescher, 1997; Utescher et al., 2014) was applied as described in Altolaguirre et al. (2020) with the purpose of calculating mean annual temperatures on the basis of the taxonomic composition of the pollen assemblages. The CA method relies on the assumption that fossil taxa share a similar climatic distribution with their nearest living relative (NLR).

The present study employs two pollen indexes, with the purpose of understanding relative temperature changes: Firstly, the pollen temperature index (PTI) (Suc et al., 2010), which describes the ratio between pollen from warm-temperate trees (deciduous *Quercus*, *Carya*, *Pterocarya*, *Carpinus*, *Acer*, etc.) and the pollen from ‘steppe’ plants (*Artemisia*, *Ephedra*). The PTI has been employed successfully in Early Pleistocene records from the

Mediterranean basin, where it accurately describes relative temperature changes which match regional and global isotope records (e. g., Suc et al., 2010; Bertini et al., 2015; Toti and Bertini et al., 2018). Secondly, the pollen climate index (PCI) (Joannin et al., 2011), which accounts for the main variance of the pollen record, identified as representing main climatic shifts. Recent studies of Pleistocene pollen records from southern Spain, in conjunction with isotopic dating methods, have found the PCI to accurately represent the glacial-interglacial climate cyclicity (Camuera et al., 2019; Carrión et al., 2019; Torres et al., 2020). As described by Joannin et al. (2011), the PCI should be identified as the main component from a principal component analysis (PCA) of the pollen assemblage. Altolaguirre et al. (2020) found that the main component (PC-1) from the PCA of the Palominas pollen assemblage accounts for 42 % of the variance and is mainly related it to shifts in humidity. Thus, in the present work, PC-1 was interpreted as the PCI.

4.3.2. Lipid extraction and analysis

The samples were weighed, ground in an agate mortar and dried using a Christ Alpha 1−2 LD freeze dryer (sample weight was averaging 6.405 g). The total lipid extracts (TLE) were isolated from the sediment using accelerated solvent extraction in a Büchi E-916 Speed Extractor, with 4 cycles at 100 bar, 75 °C, dichloromethane (DCM)/methanol 9:1. Elemental sulphur was removed from the TLE dissolved in DCM by adding previously activated copper turnings (using HCl 10 %) and left stirring on a magnetic rotary plate for 24 h. The TLE were then dried over an anhydrous Na2SO4 column. This process was repeated until no reaction with the activated copper was observed. An aliquot of the TLE was archived while the rest was separated by column chromatography using activated Al2O3 as stationary phase. The separation was achieved by elution with n-hexane/DCM (9:1), DCM and DCM/methanol (1:1) to obtain, respectively, the apolar (n-alkanes), ketone and aromatics, and polar fractions containing the GDGTs, biomarkers of interest for this study.

The polar fraction containing the GDGTs was dissolved in 1 ml of n-hexane:isopropanol (n-Hex:IPA) mixture (99:1) and gently pushed over a 0.4 µm PTFE filter using a plastic syringe. The samples were analysed on a HPLC Shimadzu, ultra-high performance liquid chromatography (UFLC) system using an Alltech Prevail© Cyano 3 mm, 150 x 2.1 mm column; n-Hex (A) and IPA (B) eluents and coupled to an ABSciex 3200 QTrap chemical ionization mass spectrometer (HPLC/APCI-MS). Injection volume was in general 5 µl. Exceptionally, at lower signal, a 10 µl volume was also injected. The GDGT's were eluted isocratically from 0 to 5 min with 1% (B); then a gradient to 1.8% (B) from 5 to 32.5 min, ramped to 30% (B) to min 33.5, held 10 min, back to 1% (B) in 1 min. Detection was achieved through single ion monitoring (m/z: 1018, 1020, 1022, 1032, 1034, 1036, 1046, 1048, 1050, 1292, 1296, 1298, 1300, 1302).

The methylation of branched tetraethers (MBT) and cyclization of branched tetraethers (CBT) indices relate to the number of methyl branches and cyclopentane structures present in the brGDGTs. Mean annual air temperatures (MAT) were calculated using the MBT (1) and CBT (2) proxies according to Weijers et al. (2007), using the following formulas, where Roman numerals correspond to branched GDGT structures.

$$MBT = \frac{[Ia]+[Ib]+[Ic]}{[Ia]+[Ib]+[Ic]+[IIa]+[IIb]+[IIc]+[IIIa]+[IIIb]+[IIIc]} \quad (1)$$

$$CBT = -\log\frac{[GDGTIb]+[GDGTIIb]}{[GDGTIa]+[GDGTIIa]} \quad (2)$$

Peterse et al. (2012) revised the MBT index as MBT' (3).

$$MBT' = \frac{[Ia]+[Ib]+[Ic]}{[Ia]+[Ib]+[Ic]+[IIa]+[IIb]+[IIc]+[IIIa]} \quad (3)$$

The calibration of Günther et al. (2014) (4) was used to reconstruct annual temperatures. This calibration is unique in that it was exclusively elaborated from the GDGT content of surface sediments from a set of modern saline lakes from the Tibetan Plateau, representing a salinity gradient from 0.31 to 153 psu. This calibration is useful when working with the GDGT distribution of an ancient saline lake environment such as the Palaeolake Baza.

$$MAT = -3.84 + 9.84 * CBT + 5.92 * MBT' \quad (4)$$

4.4. Results

The 18 pollen samples analysed in this study yield similar results to those presented in Altolaguirre et al. (2020). The palynological data describe an alternation of dry and humid phases (Fig. 4.3B). Dry phases are dominated by pollen from herbs, including steppe plants, whereas humid phases are characterised by an increase in arboreal pollen mostly represented by deciduous and evergreen *Quercus*. Besides *Pinus,* arboreal pollen includes a significant abundance of other conifers such as *Picea* and *Abies*. The CA-based coexistence intervals for MAT calculated from the pollen assemblages of the Palominas core are generally broad, with the average interval ranging from 9.8 to 21 °C and a mean value of 15.3 °C. In some samples, the presence of taxa such as *Cedrus* and *Olea* results in higher minimum values (11.6 °C and 10 °C, respectively) while the lowest maximum values are usually set by *Hippophae* (17.4 °C) and *Carpinus betulus* (17.6 °C).

The PTI curve (Fig. 4.3C) describes a clear cyclicity of relative temperature changes, where humid phases coincide with relative warming (PTI > 1) and dry phases with relative cooling (PTI < 1). The PTI describes a progressive warming through the three sections of the core, with an average value of 1.1 in the Lower Section, 1.9 in the Middle Section and 2.8 in the Upper Section. The PCI curve (Fig. 4.3D) describes the main climate shifts in the record, related mainly to changes in humidity (Altolaguirre et al.,2020). Positive PCI values are associated with forested taxa and thus, interglacial climate, while negative values indicate a lack of arboreal pollen and a higher influence of steppe plants, typical of the glacial climate. The parallel shifts between PTI and PCI point to the oscillation of warm-humid (interglacial) and cool-dry (glacial) cycles.

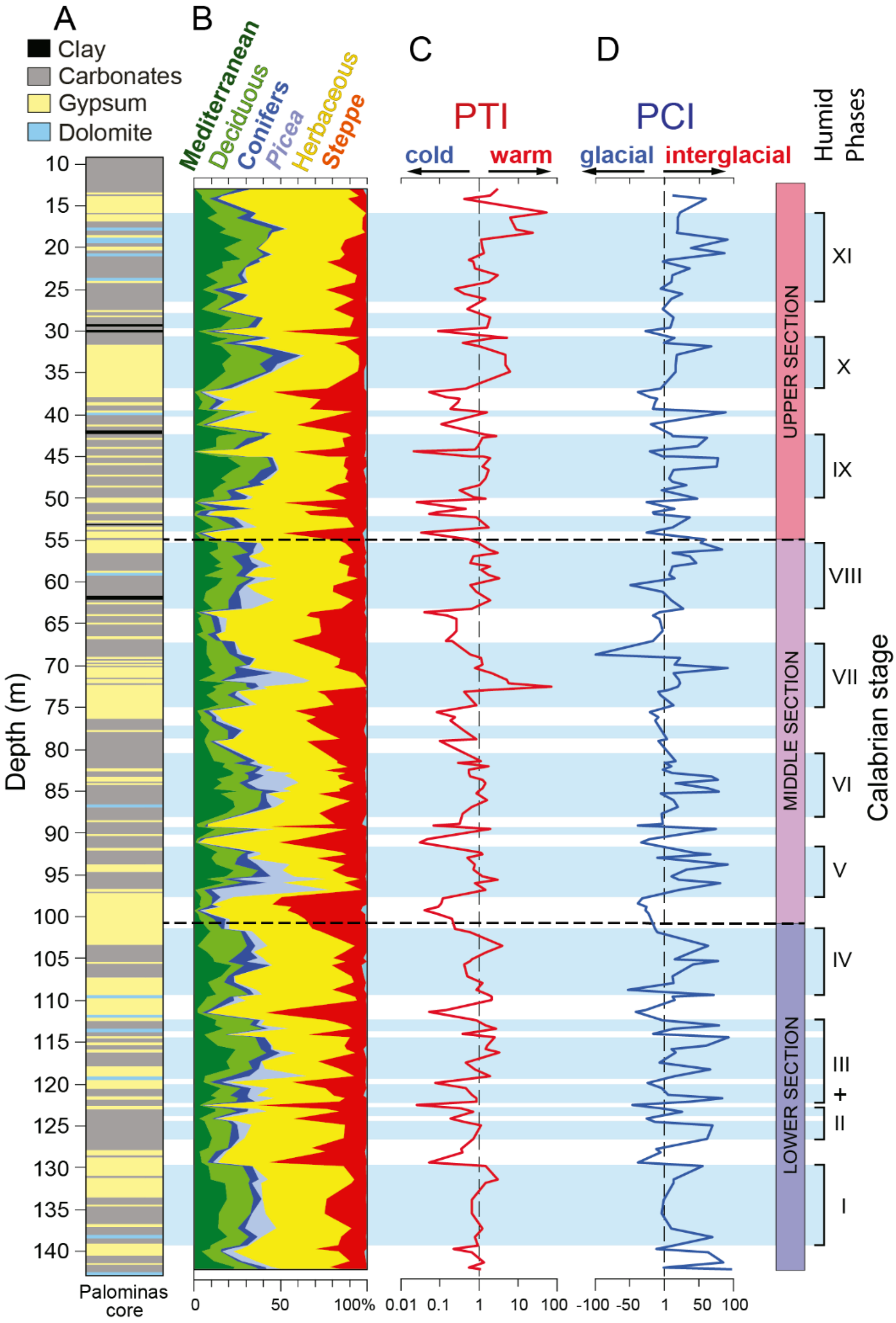

Fig. 4.3: A) Simplified lithological column of the Palominas core. B) Variation of the main pollen taxa grouped according to their ecological preference (*Picea* is separated from other conifers due to its high proportion. *Pinus* is not included in the pollen sum due to its overrepresentation. Among the herbaceous (yellow), steppe taxa have been distinguished (red). C) Pollen Temperature Index (PTI) as indicator of relative temperature changes (After Suc et al., 2010). D) Pollen Climate Index (PCI), used to identify different climatic periods (After Joannin et al., 2011). Humid phases (represented by blue bands and numerated in roman numerals), core sections and dating are described in Altolaguirre et al. (2020).

Isoprenoid GDGTs are the most abundant GDGT types in the Palominas core, with a relative abundance of 54 % against branched GDGTs (46 %) (Fig. 4.4 and Fig. 4.5A). GDGT-0 is the most abundant GDGT type, while the rest of the isoGDGTs appear in extremely low quantities. Complete GDGT values can be found in Appendix Table A4.1. Applying the brGDGT calibration by Günther et al. (2014) for saline lakes shows MAT temperature values which range between 0 to 13 °C, with a mean value of 6.4 ºC. The curve of MAT values seems to indicate that, overall, humid phases experience higher MAT values, while dry phases experience lower MAT. This is especially noticeable during Humid Phases V, VI and IX (and their associated dry phases), subjected to higher sampling resolution (Fig. 4.5C).

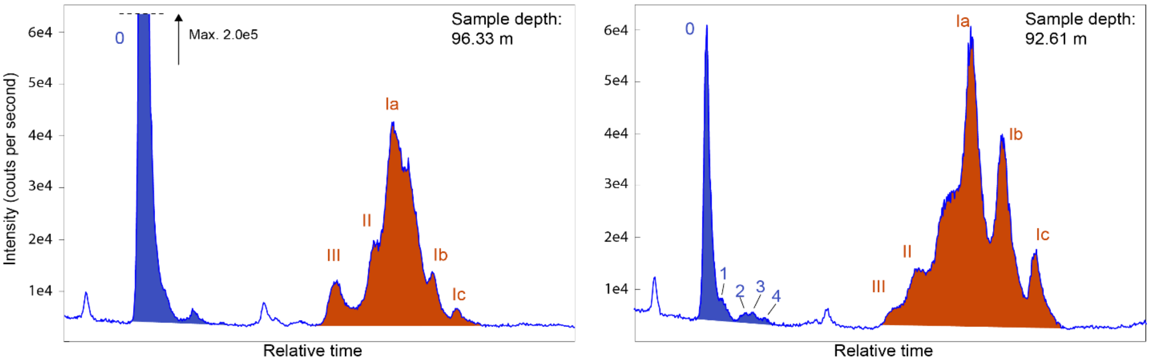

Fig. 4.4: Base peak chromatogram of GDGTs from two selected samples. Arabic numerals correspond to isoprenoid GDGTs (blue) while roman numerals correspond with branched GDGTs (orange).

4.5. Discussion

4.5.1. Temperature reconstruction from GDGTs and comparison with pollen

Overall, the Baza GDGT data provide an important contribution to determining glacial-interglacial cyclicity. The GDGT-based MAT results reveal an absolute MAT difference of ~10 ºC between climatic periods. This is within the range of estimated temperature change between glacial and interglacial periods in the Alboran Sea (SE of the Iberian Peninsula) during the Early Pleistocene (González-Donoso et al., 2000). Also, the widths of pollen-based coexistence intervals for MAT are in this ~10 °C range. Furthermore, these coexistence intervals provide a confidence interval in which the ‘real’ MAT values are expected to be found. In this way, the coexistence intervals can be used as a validation tool for the GDGT calibrations by direct comparison of both proxies. The MAT values obtained by applying the calibration of Günther et al. (2014) underestimate temperature values when compared with the CA results (as much as 10 ºC difference compared to the coexistence intervals).

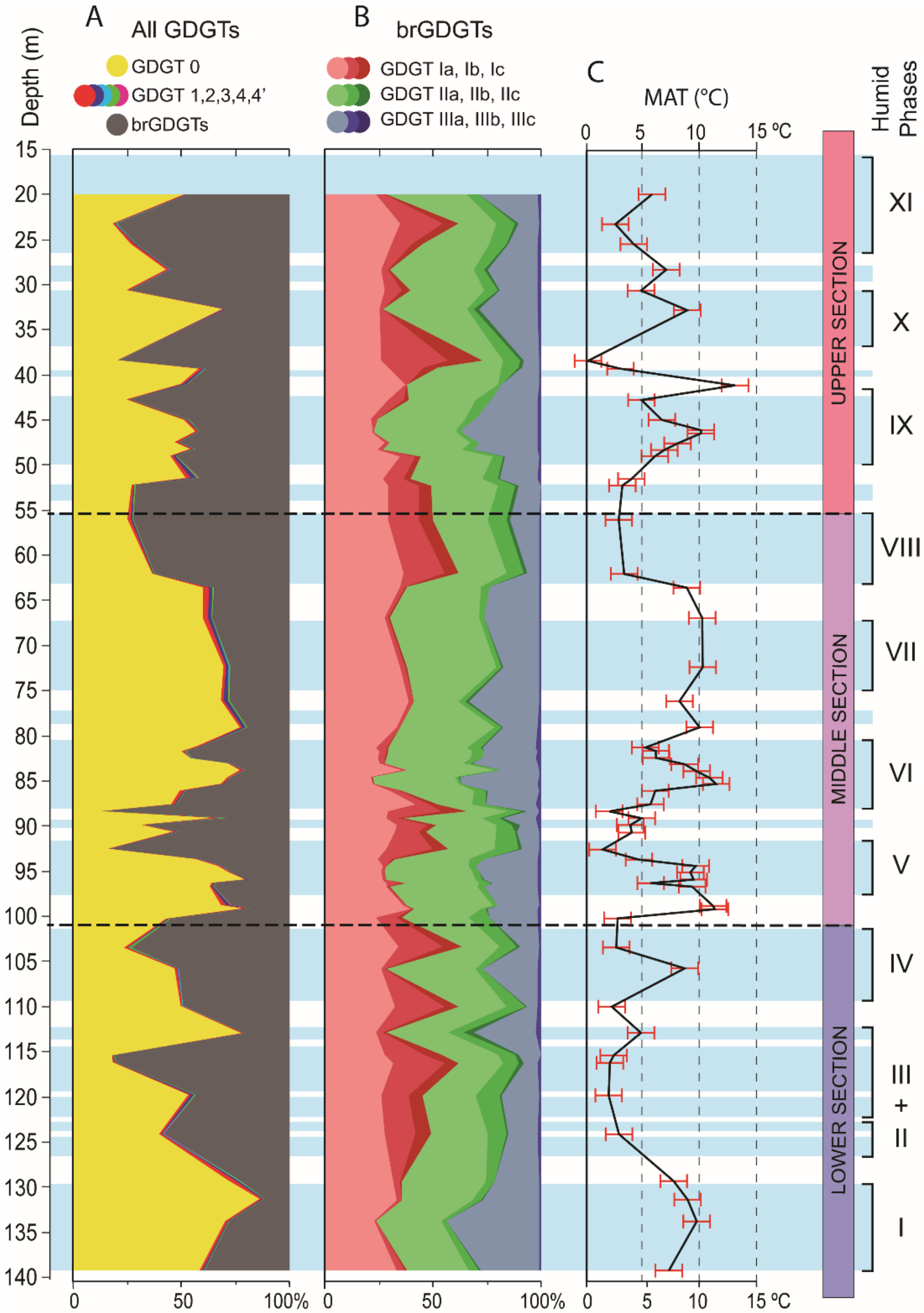

Fig. 4.5: A) Relative abundances of all GDGTs. B) Relative abundances of brGDGTs. C) Curve of mean annual air temperature (MAT) values obtained applying the calibration by Günther et al. (2014). Horizontal blue bands represent humid phases.

With respect to relative changes in temperature, the GDGT-based MAT reconstruction describes the alternation between warmer and cooler periods (Fig. 4.5). The cyclicity is most clearly observable during Humid Phases V, VI and IX, which were sampled at a higher resolution and, thus, allow identifying progressive change between high and low temperature values. The GDGT-based MAT curve mostly assigns warmer values to humid phases and colder values to dry phases.

These relative temperature changes are in accordance with previous climatic reconstructions of the Early Pleistocene of the Baza Basin, which describe a climate composed of the alternation of warm-humid and cold-dry periods, according to the micro-vertebrate fossil record (Agustí et al., 2010; Blain et al., 2011, 2016) (Fig. 4.5C). This configuration is also in agreement with Mediterranean palaeoclimatic archives which describe cold periods (glacials) correlated with dry conditions, while warm periods (interglacials) are correlated with humid conditions (e.g., Suc, 1984; Combourieu-Nebout et al., 1999; Suc and Popescu, 2005; Bertini, 2010; 2013; González-Sampériz et al., 2010; Camuera et al., 2019; Torres et al., 2020; Toti et al., 2020).

The GDGT-based MAT curve seems to match the pollen-based PTI and PCI curves, especially during Humid Phases V, VI and IX, which were sampled to higher resolution (Fig. 4.6). During these humid phases, PTI and MAT values describe warm climate and the PCI index assigns them to an interglacial climate (warm and humid). Contrarily, during the dry periods in between these humid phases, the PTI and MAT values describe a relative lowering of the temperatures, while the PCI assigns these periods to glacial climate (dry and cool). The match between pollen-based and GDGT-based temperature proxies indicates that the calibration of Günther et al. (2014) successfully reconstructs relative temperature changes from the GDGT distribution of a saline palaeo-lake. Nonetheless, the absolute GDGT-based MAT systematically underestimate MAT when compared with the coexistence intervals (Fig. 4.6E). Moreover, there are parts of the core where there is no clear match between the MAT values by the calibration of Günther et al. (2014) and the PTI and PCI curves, such as in Humid Phases II+III and VIII. This could be attributed to the Palominas core recording intervals of different salinity levels.

The relative temperature changes described by the MAT curve of Günther et al. (2014) can be pictured within the coexistence intervals (~ 10 to 20 °C) (Fig. 4.6E), which act as a sort of confidence interval. In this way, the MAT curve could describe relatively realistic temperature values, where warm periods in Baza could have reached maximum MAT values between 20 and 21 ºC and cold periods reached minimums of 10 to 11º C.

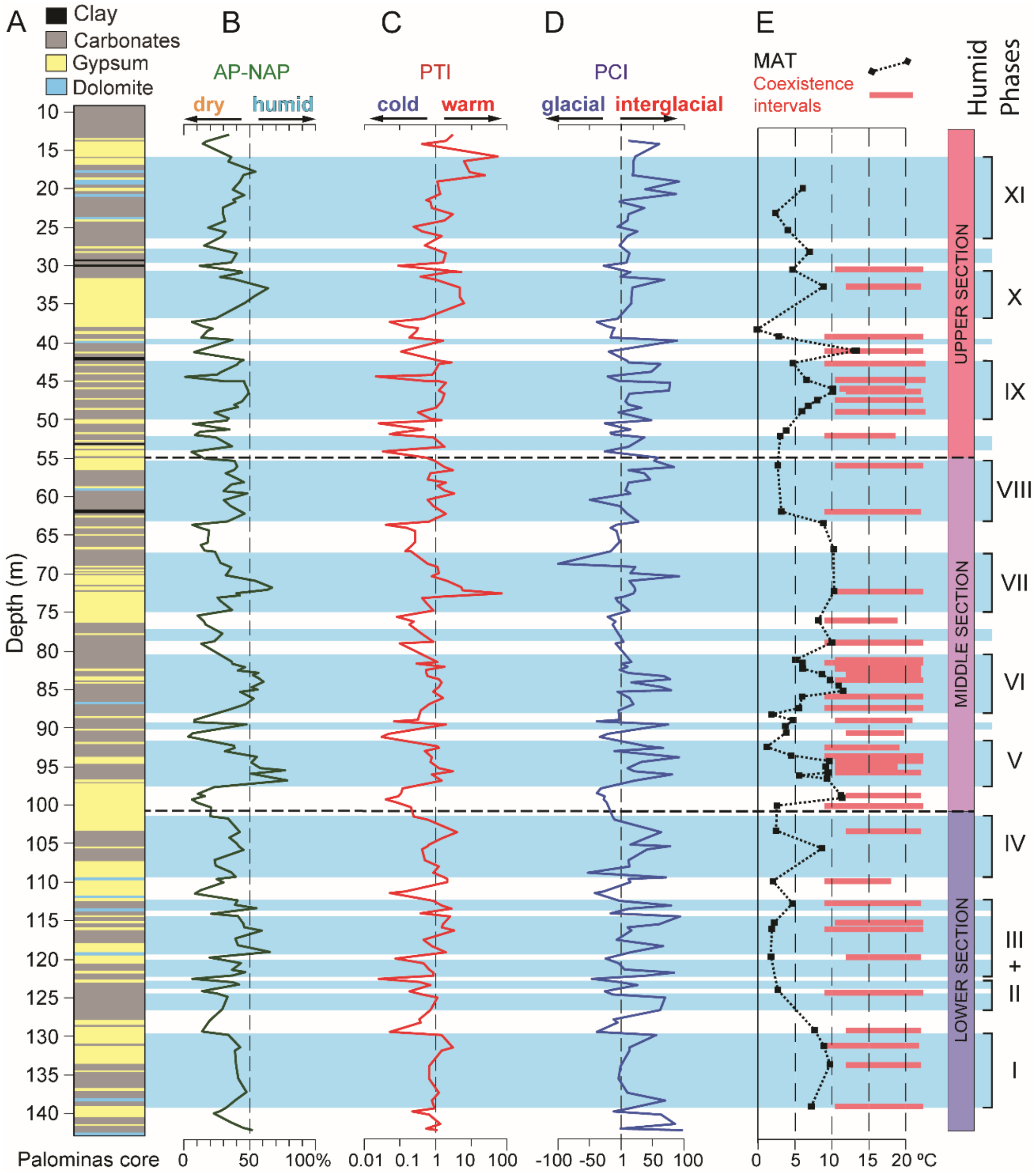

Fig. 4.6: A) Lithology of the Palominas core, B) arboreal pollen against non arboreal pollen (AP-NAP), C) pollen temperature index (PCI) indicating alternations between warmer and cooler climatic periods, D) pollen climate index (PCI) indicating alternation between glacial and interglacial periods, E) MAT values obtained applying the Günther et al. (2014) calibration (black) and MAT coexistence intervals (red). Horizontal blue bands represent humid phases.

4.5.2. Environmental impacts on the GDGT distribution and the effect of salinity

The underestimation of brGDGT-based MAT values, when compared with the MAT measures obtained using the CA method (Fig. 4.6E) could reflect a known phenomenon affecting GDGT analyses. Multiple authors have identified an underrepresentation of GDGT-based temperature results against other proxies, considering it a result of the multiple potential sources of GDGTs and the coexistence of both autochthonous and allochthonous GDGTs in the same depositional environment (Blaga et al., 2009; Tierney and Russell, 2009; Tierney et al., 2010; Tyler et al., 2010; Zink et al., 2010; Woltering et al., 2014; Buckles et al., 2014; Huguet et al., 2015; Watson et al., 2018). Initially, it was assumed that brGDGTs were exclusively produced in soils (Hopmans et al., 2004). It was only later revealed that parts of the brGDGTs in lakes were produced in situ (e.g., Tierney and Russell, 2009; Tierney et al., 2010; Bechtel et al., 2010). Autochthonous and allochthonous brGDGTs can be produced under different environmental parameters and possibly even by different bacterial organisms, leading to errors in temperature calculations. Weijers et al. (2007) and Peterse et al. (2012) recognize also another explanation for the underestimation of GDGT-based temperature values: arid and semi-arid regions (MAP < 500 mm) are subject of substantial underestimations by up to 20 °C, probably due to decreased metabolic activity of soil bacteria. Accordingly, the off-set seen in the temperature results from the Palominas core when applying the calibration of Günther et al. (2014) could be a feature of the semi-arid nature of the Basin during the dry periods of the Early Pleistocene.

Nonetheless, the most important potential source for bias in the GDGT data originates from changes in lake salinity, since the palaeo-Lake Baza has been described as a high-salinity environment (El Hamouti and Gibert, 2012; Anadón et al., 2015). The existence of saline mudflats (Gibert et al., 2007b) and halophitic vegetation close to the lake shore (Altolaguirre et al., 2020) suggests that the distribution of GDGTs in the Palominas core is more than likely to be influenced by salinity, even if part of the GDGTs were produced in nearby soils and later transported into the lake. Additionally, the dominance of GDGT-0 over all other isoprenoid GDGTs in the Palominas core (Fig. 4.5A) might also be related to salinity. Similar high GDGT-0 content has been reported from soils in dry environments (Wang et al., 2016; Zang et al., 2018), which has been explained by the presence of halophilic archaea (Zang et al., 2018). Thus, in Baza, the high GDGT-0 content might be explained by the transport of soil matter from nearby saline mudflats.

Analysis of the GDGT distribution in different saline lakes reveals in-situ production of brGDGTs (Huguet et al., 2015; Li et al., 2016), proving the existence of producing organism in saline lakes. However, some saline lakes report significantly different GDGT proportions than those from freshwater lakes (Tierney et al., 2010). The exact nature of the relationship between salinity and GDGT distribution is currently not well understood.

As any GDGT calibration, the calibration by Günther et al. (2014) is strictly empirical, but it is unique in having been produced exclusively from the analysis of the GDGT distribution in saline lake environments. Importantly, this calibration provides a curve of relative MAT changes which matches the PTI and PCI curves, also matching the results of different studies of Early Pleistocene climate in the Mediterranean realm and in southern Spain. Thus, this calibration might be able to account for the distorting effects of salinity in the GDGT distribution in an ancient saline lake like palaeo-lake Baza. In this way, the present study indicates that the universal application of global GDGT calibrations in ancient lake sediments may be affected due to the extreme effects of environmental parameters other than temperature, such as salinity. In such cases, environment-specific GDGT calibrations may provide a more appropriate approach to successfully reconstruct temperature changes.

Although the relative MAT changes generally describe warm and humid climatic phases when applying the Günther et al. (2014) calibration, there are exceptions in certain parts of the core. Humid Phases II+III and VIII seem to present relatively low MAT values, which do not fit the pollen-based reconstruction. These specific humid phases could have experienced periods of relatively low salinity due to a higher influx of freshwater. These changes in salinity would lead to shifts in the composition of assemblages of GDGT-producing organisms. Additionally, the incongruent values could also represent an increased influx of allochthonous GDGTs transported from non-saline soils, probably increased by precipitation runoff.

4.6. Conclusions

The GDGT distribution of Early Pleistocene lacustrine materials of the Baza Basin is analysed in order to establish a record of mean annual temperature (MAT) and its evolution. The results obtained from the calibration of Günther et al. (2014), specifically synthetised from saline lacustrine environments, provides MAT values lower than the ones indicated by the CA method. Nonetheless, the values describe relative temperature changes which match the Early Pleistocene climatic configurations described from Mediterranean and southern Spanish pollen records. The present work represents a unique application of a GDGT calibration as palaeo-thermometer in an ancient saline environment. These results stress the need for environment-specific calibrations in order to successfully apply GDGT analysis in ancient extreme environments.

According to the GDGT-based MAT values, the Early Pleistocene dry phases experienced mostly lower temperatures (glacial) and featured vegetation composed of herbs and steppe plants, while humid phases were characterised by higher temperatures (interglacial) and the development of arboreal communities. Although this general trend might vary between different climatic cycles, it was identified in the three climatic cycles where a higher sampling resolution was employed (Humid Phases V, VI and IX).

Acknowledgements

This work was performed with the financial support of the ROCEEH Research Centre ‘The role of culture in early expansions of humans’ of the Heidelberg Academy of Sciences and Humanities (www. roceeh.net). We thank the support (LG) from the projects of the Spanish Government CGL2016-79458-P and Catalan Government 2017-SGR-824. Funding for Palominas drilling was provided to Dr. D. Mertz (Mainz) via an internal funding program of the Johannes Gutenberg University of Mainz, Germany. The authors highly appreciate the opportunity to sample the Palominas core. The authors thank U. Treffert (Senckenberg Biodiversity and Climate Research Centre) for laboratory assistance. This work is a contribution to NECLIME (Neogene Climate Evolution in Eurasia, www.neclime.de).

4.7. References

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Chapter 5

Mapping Early Pleistocene environments and the availability of plant food as a potential driver of early *Homo* presence in the Guadix-Baza Basin (Spain)

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Mapping Early Pleistocene environments and the availability of plant food as a potential driver of early *Homo* presence in the Guadix-Baza Basin (Spain)

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ARTICLE INFO

Article history:
Received 21 October 2020
Accepted 4 March 2021
Available online xxx

Keywords:
Orce
Vegetation maps
Hominin
Diet
Edible plants
Habitat

ABSTRACT

The Guadix-Baza Basin, in SE Spain, harbors hominin fossils and lithic artifacts dated to ca. 1.4—1.3 Ma, representing the first hominin habitat in the Iberian Peninsula and possibly in Western Europe. Recent palynological studies have described a high diversity of plant taxa and biomes existing in the basin at the time of hominin presence. However, the relationship between these hominins and their environment has not been fully explored. Two novel methodologies are developed. The first method maps the distribution of the Early Pleistocene vegetation units based on paleobotanical and paleogeographic data. The second method assesses the availability of edible plant parts using a combination of Early Pleistocene and modern taxa lists. The resulting vegetation maps reveal a great diversity of vegetation types. During dry (glacial) periods, the vegetation of the basin was represented mostly by steppes, with the appearance of forested vegetation only in the mountainous regions. During humid (interglacial) periods, Mediterranean woodlands represented the dominant vegetation, accompanied by deciduous and conifer forests in the areas of higher altitude. The lake system present in the basin also allowed for the presence of marshland vegetation. The assessment of the availability of edible plant parts reveals that early *Homo* could have found a high number of resources in marshland and riparian environments throughout the year. Mediterranean woodlands and deciduous forests also provided numerous edible plant parts. During dry periods, the availability of plant resources decreased heavily, but the prevalence of marshland and riparian vegetation and of forested vegetation in the areas of higher altitude could have sustained hominin communities during harsher climatic periods. However, the disappearance of the lake system and an increase of aridity after the Mid-Pleistocene Transition and during the Middle Pleistocene probably led to an impoverishment of plant resources available to early *Homo* in the Guadix-Baza Basin.

1. Introduction

1.1. Background

Given the scarcity of the early hominin record in Western Europe, some authors have raised the debate regarding whether hominin presence was continuous or intermittent. It has been proposed that early hominin expansion and presence was heavily constrained by climate and that Western Europe was 'recolonized' by outsider populations at multiple times (Agustí et al., 2009; Leroy et al., 2011; Bermúdez de Castro and Martinón-Torres, 2013; Bermúdez de Castro et al., 2016). The Iberian Peninsula could have hosted 'sink' populations of hominins residing in glacial refugia, where they would have endured the harsher climate of the Early Pleistocene glacial periods (Dennell et al., 2011). These sink populations were still sensible to decreases in temperatures, and harsher glacial periods might have extirpated them completely (MacDonald et al., 2012).

The Guadix-Baza Basin, in SE Spain, has provided the oldest evidence of early *Homo* presence in the Iberian Peninsula and possibly in Western Europe and plays a critical role in the debate surrounding hominin expansion. There, the oldest proof of hominin

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https://doi.org/10.1016/j.jhevol.2021.102986

activity is found at the Orce sites and dated to ca. 1.3 Ma by magnetostratigraphy (Scott et al., 2007) or to ca. 1.4 Ma by means of U-series/electron spin resonance (Toro-Moyano et al., 2013). Findings include fragmentary fossil material (Gibert et al., 1989; Toro-Moyano et al., 2013), Oldowan lithic assemblages (Gibert et al.,1998, 2006; Toro-Moyano et al., 2009), and cutmarks found on ungulate long bones (Gibert and Martínez, 1992; Jiménez and Gibert, 1992; Gibert et al., 2006; Espigares, 2010; Espigares et al., 2013; Gibert, 2018). The Basin was also home to a diversified fauna of grazers and browsers (Rodríguez-Gómez et al., 2016) and probably experienced a relatively low density of carnivores (Rodríguez and Mateos, 2018). During the Early Pleistocene, the area of Guadix-Baza was an endorheic basin, featuring a saline lake system surrounded by mountains >2000 m high (Gibert et al., 2007). Recent pollen analysis (Altolaguirre et al., 2020) revealed that, throughout the Early Pleistocene, the vegetation of the area alternated between dry steppes and open forests or woodlands. This alternation was controlled by changes in precipitation and the Early Pleistocene orbital forcing (Altolaguirre et al., 2019, 2020). Even during glacial periods, the temperatures were relatively mild thorough the Early Pleistocene, with mean winter temperatures steadily higher than 0 °C (Altolaguirre et al., 2019), indicating that hominins could have survived the glacial periods in the southernmost latitudes of the Iberian Peninsula and expanded during the onset of the following interglacial periods.

However, climate is not only directly affecting hominin survival but also, and probably even more importantly, the distribution and the availability of food resources. While the paleofauna of Orce is well known and cutmarks evidence meat consumption, the use of plant food is usually very difficult to confirm for early *Homo*. Trace element distribution of the fossil material from Orce suggests a mostly vegetarian diet, although the authors warned of possible diagenetic contamination (Malgosa et al., 1999). Still, it is widely accepted that early *Homo* generally did consume a mixed diet consisting of meat and plant food (e.g., Ungar et al., 2006; Hardy, 2018 and references therein) and that plant foods are crucial for providing essential macronutrients and micronutrients (Hardy et al., 2015). As there is little direct evidence for early plant use in general and no evidence from the Guadix-Baza Basin, the reconstruction of vegetation units (VUs) and their dominant constituents provides an indirect way to assess the availability of potential plant foods.

The aim of this work is to develop and apply a new approach of reconstructing paleovegetation maps in a reproducible and quantitative way and to provide objective means to compare vegetation maps from different time intervals with respect to their implications for early human dispersal and changes in their resource space. With the focus on Early Pleistocene *Homo* in southern Spain, the spatial extent of paleovegetation units from the Guadix-Baza Basin during the Early Pleistocene is reconstructed for (idealized) glacial and interglacial climatic periods. Furthermore, the variety of edible plant parts (EPPs) per VU is estimated. Together, this analysis allows for an interpretation of resource availability and its shift between glacial and interglacial climatic periods. This analysis will contribute to the discussion regarding the potential of the Iberian Peninsula, and the Guadix-Baza Basin specifically, as a glacial refugium. It will also highlight some aspects of the hominin resource space, providing novel insight into the specific characteristics of an early *Homo* habitat outside of Africa.

In addition, Quaternary vegetation and resource availability reconstructions, such as the one presented here, represent a step forward in attempts to model the dynamic relationship between early hominins and their environment (Rodríguez et al., 2016). The resulting maps offer the opportunity to use them as a paleobotanically accurate setting for simulating early human communities by methods such as agent-based modeling (Hölzchen et al., 2016).

1.2. Geography and geology

The intramontane Basin of Guadix-Baza is located in the Betic Ranges in SE Spain, in the province of Granada. The basin has a mean altitude of ca. 1000 m a.s.l., and it is surrounded by several mountain chains, with altitudes between 1500 and 2200 m (Fig. 1). The highest mountain range is Sierra Nevada, to the NW of the basin, with a maximum altitude of 3478 m.

The Guadix-Baza Basin occurs between the two main geological complexes of the Betic System, the Internal and the External Zones (Vera et al., 2004). The basin is composed of the two sub-basins of Guadix and Baza, separated by the Jabalcón inselberg. The sedimentary record of the Guadix-Baza Basin began in the late Tortonian, when the basin was part of the Betic Seaway connecting the Atlantic with the Mediterranean (Haberland et al., 2017 and references therein). Subsequent tectonic forces caused the uplift of the seaway, evolving into a continental setting at around the latest Tortonian. During the latest Miocene, the Guadix Sub-basin developed a fluvial system that supplied water to the Baza Sub-basin, where a saline lake system was present. This fluvial and lacustrine configuration continued through the Pliocene and Early Pleistocene until the Middle Pleistocene (until ca. 0.6 Ma), when sedimentation ended owing to the capture of the Guadix-Baza Basin by the hydrographic network of the topographically lower Guadalquivir Basin (García-Aguilar and Martín, 2000; Gibert et al., 2007; Haberland et al., 2017). This event led to the initiation of a strong erosional regime that dismantled previous deposits and produced deep canyons and a badland landscape.

1.3. Modern climate and vegetation

As per the Köppen-Geiger climate classification of the Iberian Peninsula (AEMET-IM, 2011), the Guadix-Baza Basin represents one of the areas of greater diversity of climate types in the Peninsula. The areas of lower altitude fall within the winter-cold semiarid steppe climate (Bsk). As altitude increases, the foothill areas experience hot-summer Mediterranean climate (Csa), while the surrounding mountainous areas are found within the fully humid warm-temperate climate (Cfa). Finally, the Sierra Nevada range experiences both hemiboreal (Dsb) and subarctic (Dsc) cold climates in its higher altitudes.

Modern vegetation in the region is influenced by thermal and precipitation gradients that organize the vegetation of the area in different bioclimatic belts (Rivas-Martínez, 1987). The areas of lower altitude, located in the inner parts of each sub-basin, experience low rainfall, with mean annual precipitation (MAP) values of 250–500 mm and a mean annual temperature (MAT) of 14–12 °C (SIGA, 2020). These areas are covered by the 'mesomediterranean' vegetation belt, characterized by herbaceous flora and *Quercus coccifera* scrub. Sparse woodlands of *Quercus ilex* can be found, accompanied by *Rhamnus lycioides* and *Juniperus phoenicea*. The evaporitic nature of the Pleistocene lacustrine deposits outcropping in the Baza Sub-basin allows for the presence of halophytes such as *Pinus halepensis* (Rivas-Martínez, 1987; Rodriguez-Ariza, 1992). The mountainous areas surrounding the basin fall within the ranges of the 'supramediterranean' bioclimatic zone (MAP = 500–700 mm; MAT = 12–10 °C). There, increased precipitation determines greater vegetation density, featuring arboreal communities mostly represented by *Quercus faginea*, *Q. ilex*, *Juniperus oxycedrus*, and *Adenocarpus decorticans*. The 'oromediterranean' vegetation occurs only at the highest altitudes surrounding the basin

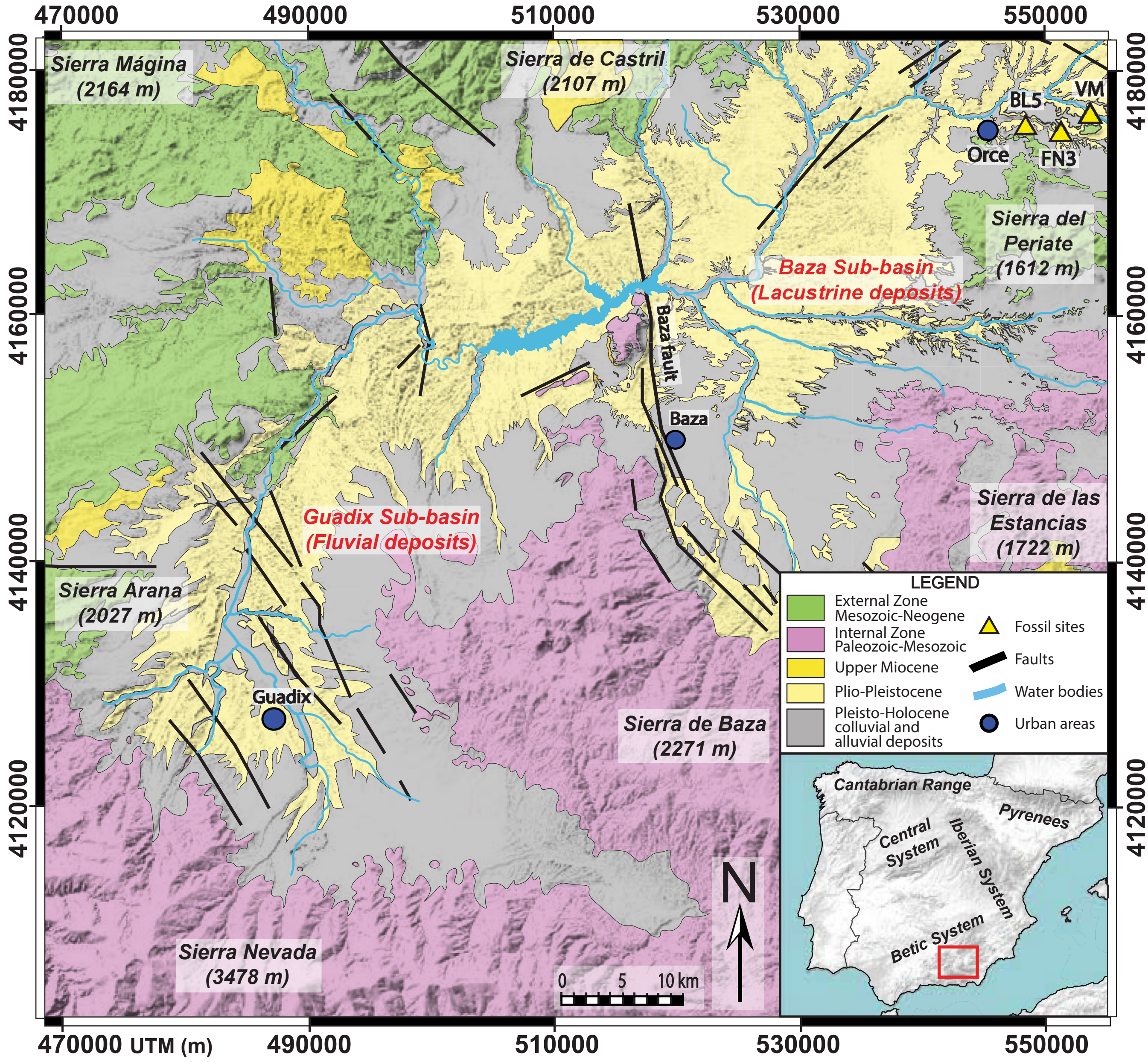

Figure 1. Simplified geological map of the Guadix-Baza Basin. Fossil site abbreviations: BL5 = Barranco León 5; FN3 = Fuente Nueva 3; VM = Venta Micena. On the right lower corner: the position of the Guadix-Baza area in the Iberian Peninsula. Geological data from Roldán et al. (2012). Main faults from Sanz de Galdeano et al. (2012).

(MAP = 700–1400 mm; MAT = 8–6 °C). Vegetation there is often composed of open forests of *Pinus sylvestris* and communities of *Genista versicolor* and *Juniperus communis*, among others (Rivas-Martínez, 1987). Riparian environments feature *Populus*, *Salix*, and *Ulmus* (Mercado and Tendero, 1988). The modern vegetation is heavily impacted by deforestation and agriculture, which reduced forest cover and promoted widespread desertification (Rodriguez-Ariza, 1992; Carrión et al., 2010).

1.4. Early Pleistocene climate and vegetation

Pollen-based climate reconstructions using the Coexistence Approach method (Altolaguirre et al., 2019, 2020) report that MAP values during dry (glacial) periods were relatively similar to modern ones, whereas values during humid periods (interglacial) were higher than the modern average precipitation of the area. The Coexistence Approach method indicates that MAT values in the Baza Sub-basin remained within a range between 10 and 20 °C through the Early Pleistocene, only slightly increasing during humid periods (interglacials) and decreasing during dry periods (glacials; Altolaguirre et al., 2019, 2020). The mutual climatic range method applied to fossil herpetofauna from the Orce sites (Agustí et al., 2009; Blain et al., 2011, 2016) indicates that the interglacial MAT averages could have been around 15 and 16 °C, slightly warmer than modern values (14–12 °C), while MAP results averaged to around 700 mm.

Pollen analysis of Early Pleistocene material from Baza (Altolaguirre et al., 2020) reveals that vegetation during this period was characterized by the alternation of dry and humid climatic phases. During the dry phases, the predominant pollen types were herbs, grasses and xerophilous plants such as *Artemisia* or *Ephedra*, and members of Chenopodioideae and Asteraceae. The dry phases created open spaces such as steppes and grasslands, where the few arboreal taxa would be relegated to small communities growing inside humid valleys or in the mountainous areas. During humid phases, arboreal pollen was more abundant, especially pollen of *Quercus* and conifers such as *Pinus*, *Picea*, and *Abies*. These trees would create deciduous and conifer forests in the mountain areas that surround the Guadix-Baza Basin. However, precipitation in the lower altitudes probably was not high enough to allow for the presence of fully developed forests; therefore, the plains of the basin would host a semiopen landscape with open Mediterranean woodlands of evergreen *Quercus* species.

2. Methods

2.1. Paleovegetation mapping

Conceptual approach A new approach for reconstructing Quaternary vegetation maps was developed (Fig. 2) with the purpose of creating maps of the distribution of the Early Pleistocene VUs in the Guadix-Baza Basin. Such an approach is heavily reliant on the presence of similarities between the Quaternary and the modern vegetation structures and organization. It is reliant as well on the assumption that the relationship between vegetation and environmental parameters during the Quaternary was similar to the one seen in modern environments. Because these similarities can never be completely exact, such extrapolations would induce unavoidable inaccuracies in the reconstruction. However, the method introduced here has the potential to produce relatively accurate maps and allows for an approximation to the 'real' Quaternary vegetation distribution.

For a reconstruction of Quaternary vegetation maps, two factors must be known:

(a) The qualitative and quantitative aspects of the Quaternary vegetation: These should be available through macrofloristic and/or microfloristic studies that reveal not only the taxonomic composition of the vegetation but also allow for an approximated interpretation of the organization of the vegetation as per geographical and climatic parameters such as elevation, temperature, precipitation, and proximity to water bodies.
(b) Paleogeographic data regarding the altitude of the area during the Quaternary, as well as the approximate extent and distribution of water bodies, and any other geographic or geomorphological particularities that might affect the distribution of the vegetation in the area.

If paleobotanical and paleogeographic data are available, the methodology can be applied in five steps (Fig. 2). In the first step, the Quaternary vegetation of the area, its composition, and its structure must be reconstructed on the basis of the available fossil content. This includes classical interpretation of pollen assemblages and statistical evaluation of the taxonomic composition. In this step, trait-based methodologies, such as biomization (Prentice et al., 1996; Prentice and Webb, 1998), allow the identification of predominant biomes. The organization of the Quaternary vegetation into biomes is especially useful as it allows identifying suitable analogs in the next step.

In the second step, modern VUs must be identified as analogs to the Quaternary vegetation known from the fossil record. The analog vegetation must match the biomes identified in the first step. If possible, these analog units should be selected from the modern VUs in relative geographical proximity to the area of study. Doing so introduces the possibility that the selected analog vegetation could be in fact the direct genetic descendent from the Quaternary vegetation (Magri and Palombo, 2013). Modern vegetation from different regions should only be chosen as an analog when no modern VU in the area matches the properties of the Quaternary vegetation. In such cases, the analog vegetation should reasonably resemble the taxonomic composition of the fossil assemblages. The relationship between the analog VUs and the environmental parameters that constrain them must also be defined and quantified. In real-life ecosystems, multiple climatic and geographic parameters are simultaneously responsible for the distribution of the vegetation. However, a spatial correlation of the analog vegetation and environmental parameters helps to identify the major influencing factors (e.g., precipitation and/or temperature, altitude, or the presence of water bodies) for the purpose of an approximate reconstruction of the spatial distribution of Quaternary VUs. Ultimately, the identification of analog VUs requires a form of 'informed subjectivity' since researchers must be familiar with the taxonomic composition and structure of both the Quaternary and analog vegetation.

The third step is to define the Quaternary VUs to be featured in the reconstruction, which will be named here as 'mapping units.' These units should be characterized on the basis of the paleoecological methodology applied in the first step and mirroring the properties of the analog VUs. In this way, the previously defined relationship 'environment-analog VUs' (step 2) is extrapolated to the mapping units. During this step, modifications can be made to accommodate particular properties of the Quaternary VUs (e.g., the mapping units may contain plant species of specific climatic requirements not found in the analog VUs). The fourth step is to use quantitative paleoenvironmental methods to estimate the Quaternary values of those environmental parameters that define the

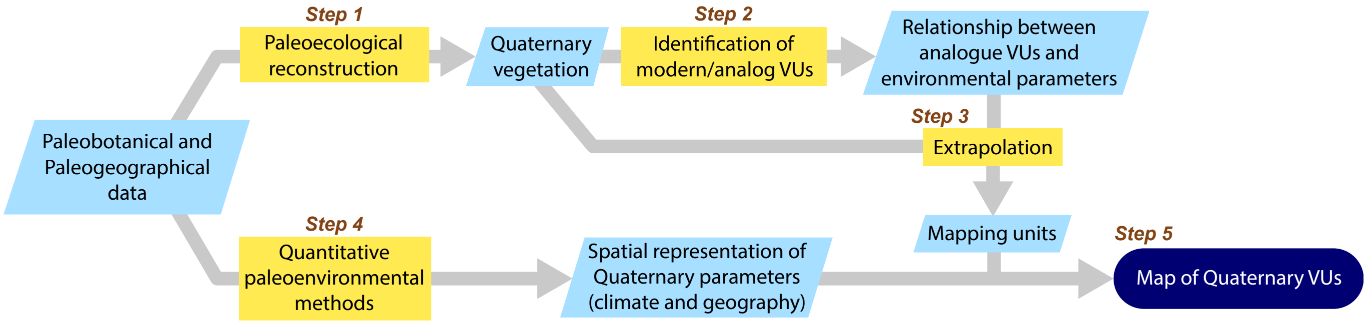

Figure 2. Conceptual diagram of the methodology developed to create maps of Quaternary vegetation units. Light blue parallelograms represent data and yellow rectangles represent processes based on and resulting to those data which are connected by gray arrows. The dark blue stadium represents the final result. Abbreviation: VU = vegetation unit. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

mapping units and represent them spatially for the study area. Finally, in a fifth step, a map of the Quaternary VUs can be created based on the defined relationship of environmental parameters with the mapping units (steps 1 to 3) and the spatial representation of the Quaternary values for those same parameters (step 4).

Step 1: Reconstructing Early Pleistocene vegetation The reconstruction of Early Pleistocene VUs of Guadix-Baza was based on the available pollen assemblages and biome reconstructions from the Palominas drill core in the center of the Baza Sub-basin (Altolaguirre et al., 2020). The biomization analysis, based on plant traits (plant functional types), revealed that during dry periods, the basin was dominated by biomes featuring mostly herbaceous vegetation. During humid periods, three forested biomes coexisted in the basin, which will be discussed in the next step.

Step 2: Identifying analog VUs and their relationship with environmental factors Analogs for the Quaternary vegetation were chosen to fit each of the different biomes identified during the trait-based biomization analysis presented by Altolaguirre et al. (2020). These modern analogs were chosen preferably from the modern vegetation of the Guadix-Baza Basin. In the absence of suitable analogs, these were chosen from other geographical areas, based on their proximity to southern Spain and on recommendations of published works. To this aim, the European Vegetation Map (EuroVegMap) by Bohn et al. (2004) was consulted. This map was deemed useful because it allows the selection of analog VUs from the wide range of vegetation formations found on the European continent. Locally, EuroVegMap is based on the phytogeographical classification of the vegetation in the south of the Iberian Peninsula by Rivas-Martínez (1987). The VUs in the EuroVegMap are defined on the basis of floristic-phytogeographical criteria, with ecological and geographical features being used as aids for characterization and localization (Bohn et al., 2004).

The Early Pleistocene lowland vegetation, which was composed mainly of plants typical of Mediterranean climates, was defined as the 'Mediterranean woodlands VU.' This unit belongs to the 'warm-temperate evergreen sclerophyll broadleaf shrubland' biome identified from the Pleistocene pollen record (Altolaguirre et al., 2020) and was mostly represented by evergreen *Quercus*. Analogs for a similar *Q. ilex*-*Q. coccifera* woodland/shrubland VU can be found in the modern vegetation of the Guadix-Baza Basin. Thus, VUs J3, J10, and J31 (Bohn et al., 2004; Table 1) are identified as potential analogs for the Early Pleistocene Mediterranean vegetation of Guadix-Baza.

The deciduous forests in the Early Pleistocene were represented mostly by pollen of deciduous oaks, accompanied less predominantly by other deciduous taxa. These compose the 'deciduous broadleaf woodland' biome (Altolaguirre et al., 2020). In the modern-day Guadix-Baza Basin, two VUs that resemble this biome can be found: units G69 and G74 (Bohn et al., 2004; Table 1). These modern VUs are dominated by *Quercus faginea* and *Quercus pyrenaica*, which grow in mountainous areas of high precipitation. These VUs were chosen as analogs for the *Quercus*-dominated 'deciduous forests VU' of the Early Pleistocene. During the Early Pleistocene, the deciduous forests represented by this unit contained arboreal taxa that were extirpated from the Iberian floras during and after the Middle Pleistocene—taxa such as *Carya*, *Tsuga*, *Eucommia*, *Pterocarya*, and *Zelkova* (Altolaguirre et al., 2020). However, despite these taxa being an important part of Early Pleistocene European floras (Postigo-Mijarra et al., 2010; Magri et al., 2017 and references therein), including those from Northern Spain (Leroy, 2008), in Guadix-Baza, their sparse stratigraphical record and low abundance in the Palominas core (generally <1% of the total pollen sum) suggest these were relict taxa and not important components. Only *Carpinus orientalis* appeared consistently and in significant amounts to be considered a common element of the paleoflora.

Conifer pollen from the Early Pleistocene is represented mostly by *Pinus*, *Abies*, and *Picea*. These taxa most likely formed high-altitude conifer forests, represented by the 'cool mixed evergreen needleleaf and deciduous broadleaf forest' biome (Altolaguirre et al., 2020). Among the modern VUs of the area, high-altitude conifer forests are represented mostly by VUs C30 and C34 (Bohn et al., 2004; Table 1). Modern conifer forests of the basin (C30 and C34) were considered a suitable analog for the mapping unit 'conifer forests VU,' although the prominence of *Abies* and *Picea* in the pollen record seems to indicate that the 'conifer forests VU' had a higher humidity requirement than the analog VUs. The pollen record also shows the occurrence of the conifers *Tsuga* and *Cathaya*, which also suggests higher humidity. However, these two taxa appear sparsely in the pollen record and in very low amounts (<1%) and therefore could have been relict elements, not representative of the conifer forests of the region.

The Quaternary 'steppes VU' of the Guadix-Baza Basin is identified by pollen analysis and biome reconstruction, which describe grassland and xeric shrubland biomes, dominated by *Artemisia* (Altolaguirre et al., 2020). For such a vegetation type, the Iberian Peninsula lacks any suitable modern analog. However, Prentice et al. (1992) proposed the modern Ukrainian steppes as a suitable

Table 1
List of the modern vegetation units (VUs; Bohn et al., 2004) chosen as analogs for the Early Pleistocene vegetation.

VU	Description
M15	Transvolgian halophytic grass steppes
M14	Central Pontic-Transvolgian grass steppes
M13	Central Pontic grass steppes
M12	West Pontic grass steppes with *Allium guttatum*
J31	Inner Baetic meso-Mediterranean kermes oak forests with *Bupleurum gibraltarium*
J3	Baetic meso-Mediterranean basiphilous *Quercus ilex* subsp. *rotundifolia*-forests with *Paeonia coriacea*
J10	Baetic supra-Mediterranean basiphilous *Quercus ilex* subsp. *rotundifolia*-forests with *Berberis vulgaris* subsp. *Australis*
G74	South Iberian supra-Mediterranean *Quercus faginea*-forests with *Daphne laureola* subsp. *latifolia*
G69	Baetic supra-Mediterranean *Quercus pyrenaica*-forests with *Adenocarpus decorticans*
C30	Southeast Iberian oro-Mediterranean pine forests with *Juniperus sabina*, *Pinus nigra* subsp. *salzmannii*, *Daphne oleoides*, *Berberis vulgaris* subsp. *australis* on carbonate rocks
C34	Baetic oro-Mediterranean scrub with *Genista versicolor* on siliceous rocks
U30	Iberian meso- to thermo-Mediterranean hardwood alluvial forests in combination with willow and poplar alluvial forests
U32	Southeast Iberian (meso-)thermo-Mediterranean willow and poplar alluvial forests and scrub in valleys of periodically flowing streams and rivers
B50	Baetic crioro-Mediterranean xerophytic grasslands on siliceous rocks

analog for the *Artemisia* steppes characteristic of the Quaternary. Therefore, the VUs M12 to M15 (Bohn et al., 2004; Table 1) from SE Ukraine and SW Russia were chosen as modern analogs for the grasslands and *Artemisia* shrubland biomes that occupied the driest areas of the Guadix-Baza Basin during the Early Pleistocene.

Two azonal VUs were described for the Early Pleistocene Guadix-Baza Basin: the 'marshland' and 'riparian.' The 'marshland VU' is based on the constant presence of pollen from *Typha* and Cyperaceae (Altolaguirre et al., 2020), whereas the 'riparian VU' is represented by the occurrence of *Alnus*, *Ulmus*, and *Salix*. The modern riparian vegetation of Guadix-Baza is described in the EuroVegMap under unit U32 (Bohn et al., 2004; Table 1), which describes vegetation associated with periodically flowing rivers. As there is no modern marshland vegetation in the area, analogs were found in the more proximal areas of the Guadalquivir Marshes and Tablas de Daimiel National Park (in Southern and Central Spain, respectively). These are identified in the EuroVegMap as unit U30 (Bohn et al., 2004), which describes vegetation associated with permanent water bodies.

In addition, one extrazonal VU is used, the 'alpine VU.' This is the only mapping unit that is not represented in the fossil record, but it is assumed to have existed at the highest altitudes. The modern alpine vegetation in the Betic Ranges is found in the crioromediterranean belt, above 2700 m (Rivas-Martínez, 1987). In the surroundings of the Guadix-Baza Basin, only the Sierra Nevada massif surpasses such altitudes and allows for the presence of alpine vegetation, in unit B50 (Bohn et al., 2004; Table 1). This unit was chosen as an analog for the Early Pleistocene 'alpine VU.'

Finally, the environmental factors that regulate the distribution of the analog vegetation must be identified. Precipitation has been identified as the main driving force for the distribution of the Early Pleistocene vegetation and the cyclic vegetation changes caused by the glacial-interglacial climatic cycles in the Guadix-Baza Basin (Altolaguirre et al., 2020). On the contrary, temperature changes in the region were relatively moderate between glacial and interglacial periods (Altolaguirre et al., 2019). Therefore, MAP was used in the present work as the main parameter for the spatial reconstruction of the Early Pleistocene zonal vegetation.

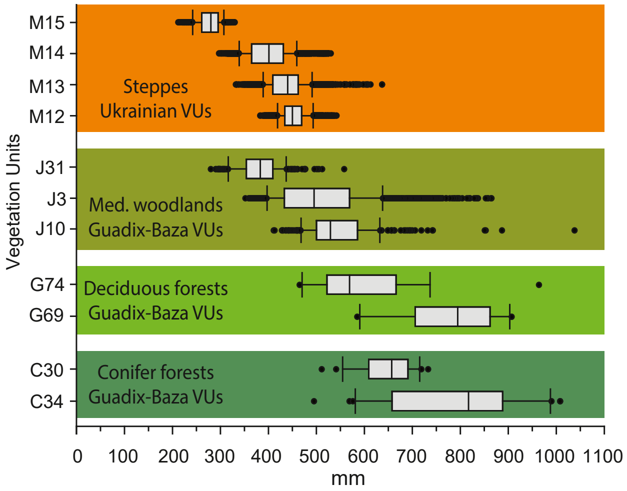

Figure 4. Box and whisker plots of mean annual precipitation values in the distribution areas of the vegetation units used as analogs for Early Pleistocene vegetation in the Guadix-Baza Basin. Azonal and extrazonal vegetation units (VUs) are not included. Precipitation values are derived from WorldClim 2.0 (Fick and Hijmans 2017). Boxes extend from the first to third quartile, and the middle line represents the median. Whiskers extend to maximum and minimum values, excluding outliers, which are represented by dots.

To quantify the relationship between precipitation and the analog VUs, the area of each VU (Bohn et al., 2004) was overlaid on a map of modern MAP of the Iberian Peninsula (Fick and Hijmans, 2017). Figure 3 represents an example applied only to the Guadix-

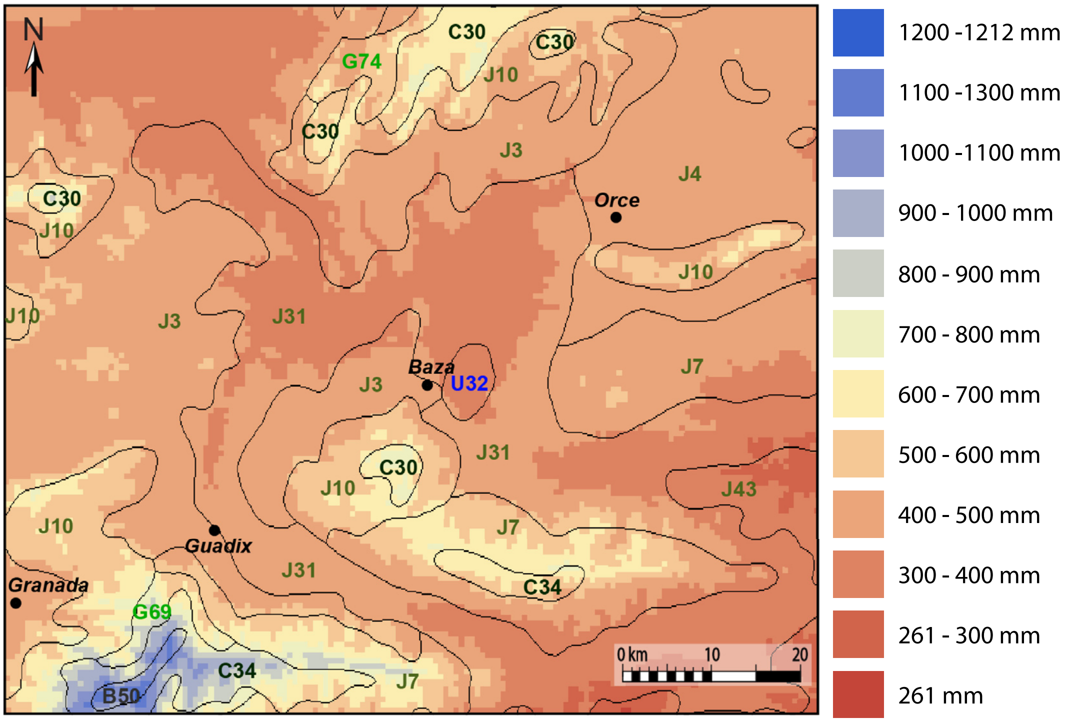

Figure 3. Map of modern mean annual precipitation (Fick and Hijmans, 2017). Limits of the modern vegetation units are outlined in black (Bohn et al., 2004), showing the general accordance of vegetation with precipitation patterns in the region.

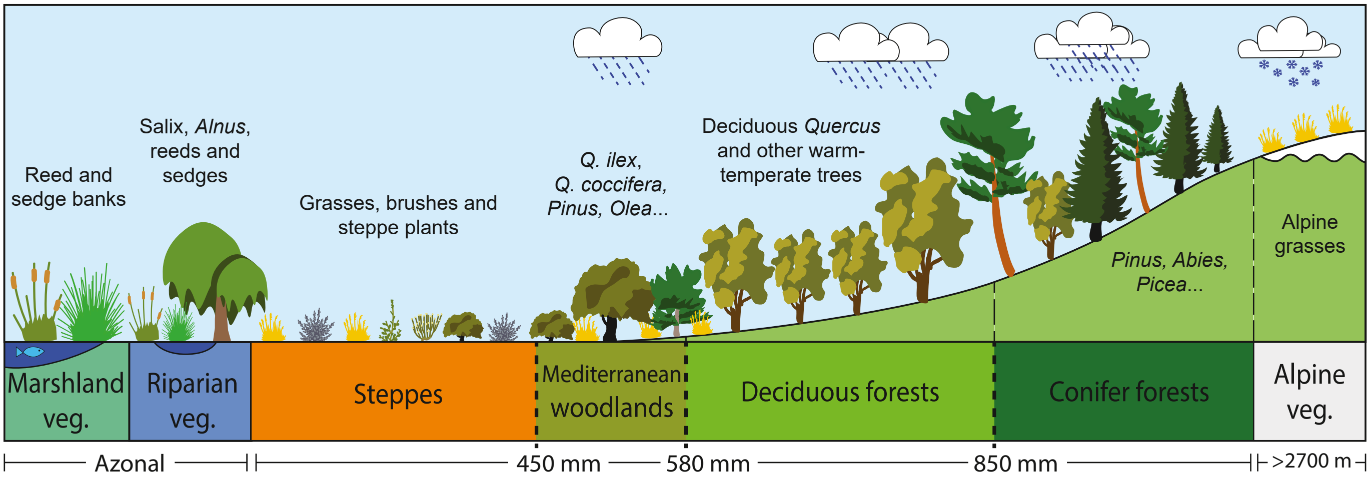

Figure 5. Diagram of the Early Pleistocene vegetation units (VUs) in the Guadix-Baza Basin used as mapping units. Below, intervals of mean annual precipitation or altitude are indicated, which are used to define the Early Pleistocene VUs (except azonal VUs). Abbreviations: veg = vegetation; VU = vegetation unit.

Baza Basin. Then, precipitation values for each pixel within each VU were extracted using ArcGIS and the 'Spatial Analyst' tool (Fig. 4).

Step 3: Definition of mapping units based on environmental parameters The interquartile annual precipitation ranges of the analog VUs, obtained in the previous step, were extrapolated as the precipitation range for the Quaternary vegetation. In this way, the mapping units as Early Pleistocene vegetation are defined by the rainfall requirements of their modern analog VUs. Thus, for the Ukrainian steppes/grasslands VU, the MAP interval is set from the lowest MAP values up to 450 mm (Fig. 4). This is the precipitation interval assigned to the Early Pleistocene 'steppes VU' mapping unit (Fig. 5). Regarding the units representing the Mediterranean vegetation, the interquartile range of units J3 and J10 is 450–580 mm (Fig. 4), these thresholds were used to define the Early Pleistocene 'Mediterranean woodlands VU' (Fig. 5). Unit J31 however gives lower values more similar to steppe-type vegetation rather than to typical woodland vegetation, and therefore, its data were excluded here. Consistently, this unit describes shrub vegetation, growing in the driest areas of the Basin (Bohn et al., 2004). The modern units that encompass the deciduous *Quercus* forests in Guadix-Baza (G69 and G74) show an interquartile range of 520–860 mm (Fig. 4). Owing to slight overlap with the 'Mediterranean woodlands VU,' the lower boundary of the precipitation range for the Early Pleistocene unit 'deciduous forests VU' was slightly shifted to 580 mm (Fig. 5). The precipitation intervals of the modern conifer forests units (C30 and C34) show overlap with the deciduous units (Fig. 4), although the conifer units have a preference for higher precipitation values. This overlap indicates that precipitation is not the only discriminating factor between these modern units, with altitude/temperature likely playing an important role. Furthermore, Early Pleistocene conifer forests were different from the modern ones (C30 and C34 are composed of mostly *Pinus* and *Juniperus*) in the sense that they included *Abies* and *Picea*, which have a preference for high altitudes where the climate is cooler and wetter (Ravazzi, 2002). To represent this, a higher precipitation interval (850–1200 mm) was assigned to the Early Pleistocene 'conifer forests VU' mapping unit (Fig. 5).

Regarding the distribution of azonal wetland vegetation types, edaphic factors such as soil moisture and soil texture play a key role. Marshland environments are characterized by a very shallow groundwater table and still water. Thus, the environmental parameter that determines the area of the marshland vegetation is the water level of the lake system. Riparian environments are rather linked to river courses that provide somewhat running, fresh water and a slightly lower groundwater table than the marshland. Another environmental parameter to take into account is altitude. The modern alpine vegetation, unit B50, appears in the region on areas above 2700 m. This altitude was extrapolated to the mapping unit 'alpine VU.'

Table 2
Average values of minimum (min), maximum (max), and average (avrg) mean annual precipitation (MAP) for the humid and dry phases identified in the pollen assemblages of the Palominas core, in the sub-basin of Baza (data from Altolaguirre et al., 2020). The lower row features the percentage difference between the dry phase and humid phase. On average, precipitations during humid phases are 21% higher than during dry phases.

Climatic phases	MAP, min	MAP, avrg	MAP, max
Palominas, humid phase	401	920	1439
Palominas, dry phase	313	759	1205
MAP increment from dry to humid	28%	21%	19%

Step 4: Mapping Quaternary environmental parameters Precipitation during the Early Pleistocene is acquired from climate analysis based on the pollen flora found in the basin (Altolaguirre et al., 2019, 2020). These analyses used the coexistence approach method to estimate temperature and precipitation on the basis of the taxonomic composition of the pollen assemblages. During the Early Pleistocene, fluctuations in precipitation led to the appearance of two main climatic periods: dry phases, wherein MAP was relatively similar to that recorded today, and humid phases, wherein annual precipitation was higher. To reconstruct precipitation values during the dry phases of the Early Pleistocene, modern values were used, on account of the similarities between the vegetation distribution of these phases and the modern one (Altolaguirre et al., 2019). On average, humid phases had annual precipitation values 21% higher than dry phases (Table 2). For a geographical representation of modern precipitation, the WorldClim MAP map was used (Fick and Hijmans, 2017). Annual values were increased by 21% to reconstruct precipitation values during humid phases.

Regarding altitude, the average uplift rates for the Betic Ranges have been estimated to around 200 m/Myr for the late Neogene to present (Braga et al., 2003). Therefore, at the time of early hominin occupations, the Sierra Nevada range could have been around 200 m lower than present. To recreate the alpine VU during the Early Pleistocene, the values of an elevation map of the area (CNIG,

2004) were reduced by 200 m. Apart from altitudinal changes, the modern elevation map depicts a network of valleys and canyons in areas that were relatively flat during the Early Pleistocene, as per terrain reconstruction models (Pérez-Peña et al., 2009). These valleys can cause 'artificial' precipitation patterns on the maps for Early Pleistocene, reflecting the modern topography rather than the paleoprecipitation patterns. Consequently, the precipitation map was adjusted accordingly, to represent the Early Pleistocene terrain and precipitation.

In the Baza Sub-basin, marshes would have been present surrounding the marginal area of the lake system (Gibert et al., 2007). While the main lake body would have contained saline water, a series of freshwater or slightly saline satellite occurred in some of the margins of the Baza Sub-basin, like in the Orce area where hominid sites occur (Anadón et al., 1986; Gibert et al., 2007). These shallow satellite lakes would have allowed for the development of marshland vegetation. To accurately place the extent of the central body of the lake system of Baza during periods of low and high water level, the stratigraphical and mapping work of Gibert et al. (2007) was consulted. During dry periods, the constrained lake would have sat in the depocenter of the Baza Sub-basin, near the Baza Fault (Fig. 1), which is responsible for the semigraben configuration of the basin (Haberland et al., 2017). In addition, the extent of the satellite lake of Orce was based on the paleogeographic reconstruction of El Hamouti and Gibert (2012).

The riparian VU would have appeared in association with the system of rivers and springs in the Basin. During the Early Pleistocene, the biggest fluvial system in the area of Guadix-Baza was the Fardes Paleoriver (Viseras et al., 2004), which flowed from the southern areas of the Guadix Sub-basin into the lacustrine system of the Baza Sub-basin, to the northeast (Fig. 1). The course of the Fardes Paleoriver, the main fluvial course in the basin, was featured in the map reconstructions. Additional riparian vegetation associated with smaller river courses was represented in the maps and inferred from the modern rivers present in the area. Not featured in the maps is vegetation associated with any other minor rivers and streams, which must have occurred as well.

Step 5: Translating the environmental maps into vegetation maps The Early Pleistocene MAP was reconstructed in the form of two precipitation maps, one for humid and one for dry periods. These precipitation maps were then translated into vegetation maps by applying the thresholds assigned to each of the mapping units in the previous step (Fig. 5). Thus, areas of both maps where the annual precipitation is below 450 mm were assigned as 'steppes VU,' while areas where the precipitation is between 450 and 580 mm were assigned as 'Mediterranean woodlands VU' and so on. The VUs not bound by precipitation levels are reconstructed in accordance with the Early Pleistocene elevation model and in accordance with the extent of the lake and fluvial systems. The 'riparian VU' follows the approximate course of the Fardes Paleoriver. Riparian vegetation associated with smaller streams and rivers were not represented because it would occupy only slim and small areas.

2.2. Quantifying plant resources

The reconstruction of Early Pleistocene VUs of the Guadix-Baza Basin allows for the elaboration of 'potential' taxa lists for these units. These lists consist of a combination of the dominant taxa in the modern VUs, chosen as analogs (as described in Section 2.1) from the EuroVegMap (Bohn et al., 2004), and additional taxa documented in the fossil record (Altolaguirre et al., 2020; see Supplementary Online Material [SOM] Table S1). The latter consists of relatively abundant pollen types that are assumed to have been dominant in the respective VU. Only spermatophytes (seed plants) are included here (i.e., no ferns, mosses, and lichens). Those lists provide the basis for a comprehensive compilation of data on the edibility and availability for each species.

Sources for information on edibility are found in databases such as Plants For A Future (Fern, 1997), Useful Temperate Plants (Fern, 2019), and others, as well as in botanical and ethnobotanical publications (e.g., Tardío et al., 2006). Full references are given in SOM References. The retrieved information is organized and stored in the PlantBITES database. Additional information from gray sources (such as culinary and gardening literature) was at times necessary to be considered. Occasionally, general information about one species of a genus was extrapolated to another species. These 'gray' and extrapolated entries are given as 'derived data' and were kept separate from the database proper, being marked in the SOM accordingly. In cases wherein no information regarding edibility was available or listed, the taxon was considered as being probably not edible in relevant amounts. Because the PlantBITES database is not yet available online, all data used in this study are given in SOM Tables S1–S3, which contain a full list of taxa with the information compiled with respect to their edibility, seasonality, and processing.

The PlantBITES database comprises information on edibility and other uses of plants that occur in natural environments. The information stored in this database is most detailed with respect to edibility, nutrition, and seasonal availability of plant parts. In addition, toxicity, 'other uses' (e.g., as dye, fiber, tool, and so on), and the relevance as animal food are also considered. In the vast field of medicinal plants, only basic information that may serve future studies is gathered. In PlantBITES, the availability of plant resources is considered taking not only natural aspects into account but also the different levels of cultural capacities necessary for the utilization of plants as it is usually not included in ethnobotany. Cultural capacities of different hominin groups, regarding the exploitation of plant resources, change considerably through time with respect to the use of fire, and especially the capability to process and store plant materials. Therefore, besides botanical and ethnobotanical information, the database also keeps data on necessary practices for harvesting, processing, and storage.

To consider the plant food items available for early *Homo*, four assumptions are necessary to be made:

(a) Dominant taxa represent easy targets as a food resource if edible. They should occur in amounts high enough to be found easily and should be widely distributed in the respective VU. Thus, the analysis is confined to taxa that are listed in Bohn et al. (2004) to be dominant in the respective VU.

(b) Only food items that are digestible in larger quantities are a considerable food resource for early *Homo*. Plant parts that provide spices, condiments, edible decoration, and so on are not included in this analysis (e.g., fruits of *J. communis* and *Fraxinus angustifolia*).

(c) Early Pleistocene *Homo* in Southern Spain (1.4/1.3 Ma) did not use fire to process their food. The oldest evidence of fire use is dated to 1 Ma from Wonderwerk Cave in South Africa (Berna et al., 2012); in Eurasia, the earliest potential evidence is dated to 0.980–0.780 Ma from Cueva Negra del Estrecho del Rio Quípar, around 100 km away from Orce (Rhodes et al., 2016). Furthermore, there is no evidence for the use of fire at 1.2 Ma at Sima del Elefante, Spain (Hardy et al., 2017). Therefore, only food items that can be eaten raw are considered here.

(d) Still, early *Homo* can be assumed to having been capable of simple methods of food processing. Plant parts that require such kind of processing, such as peeling, cracking (e.g.,

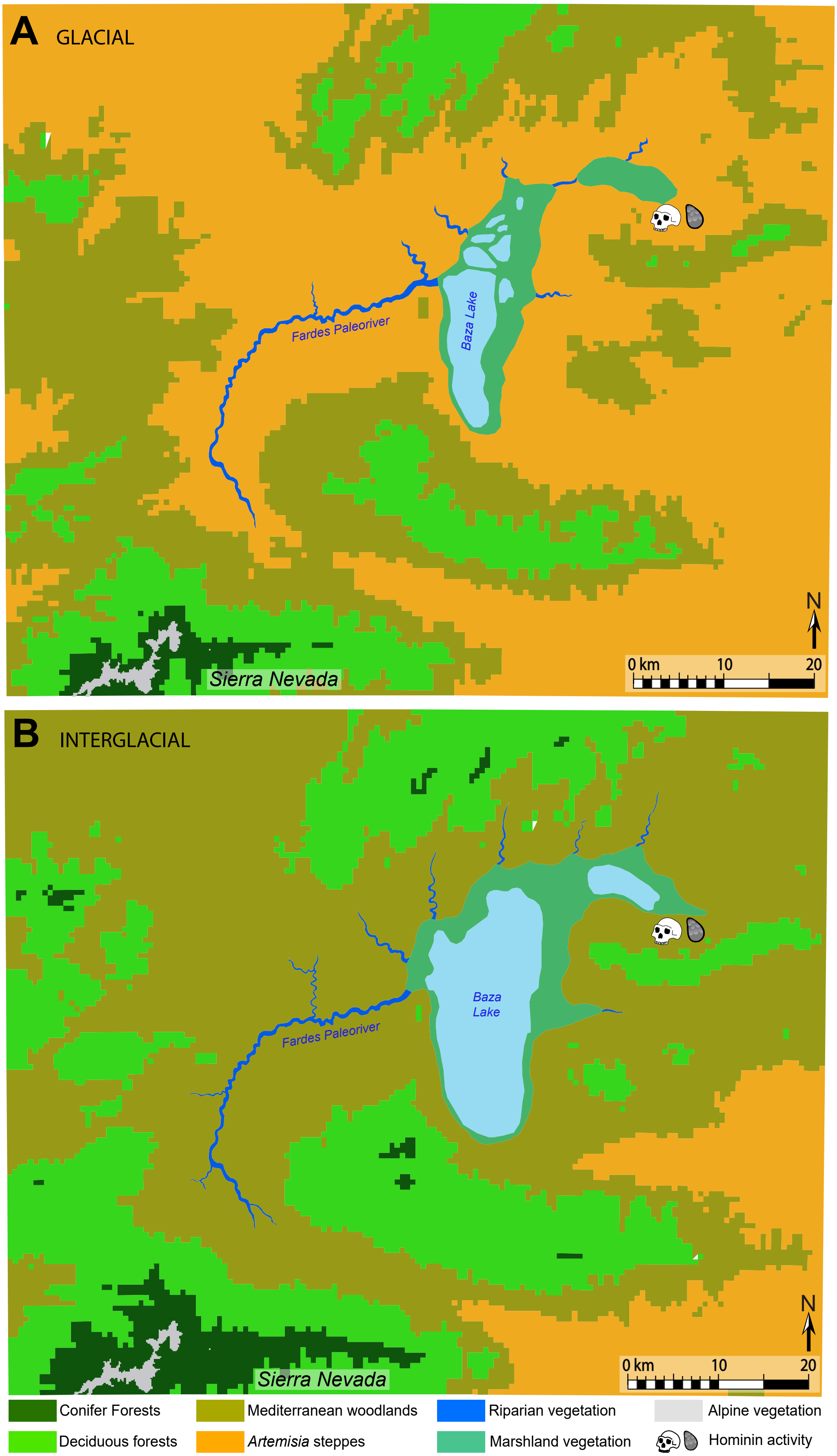

Figure 6. Map of the Early Pleistocene vegetation units of Guadix-Baza during: A) dry periods, associated with glacial climate; B) humid periods, associated with interglacial climate.

Q. ilex), or digging for underground storage organs (USOs; e.g., *Typha latifolia*), are included in the analysis. Nevertheless, plants parts that necessitate the use of sophisticated processing methods before being edible were not considered (e.g., *Olea europaea*).

3. Results

3.1. Vegetation maps

Following the approach described previously (Fig. 2), two maps of the distribution of vegetation formations for the Early Pleistocene are produced: a vegetation map exemplifying the climatic situation of dry periods (glacials; Fig. 6A) and a vegetation map for humid periods (interglacials; Fig. 6B). The vegetation maps are digitally stored at the ROCEEH Metadata Catalogue (ROCEEH, 2020).

The glacial/dry phase map features the 'steppes VU' as the predominant vegetation in areas of lower altitudes in the basin. There, the steppe vegetation is only interrupted by the azonal units of 'riparian' and 'marshland VUs.' In areas of higher altitude and precipitation, the 'steppes VU' leaves ground to the woodland and forested units. The 'Mediterranean woodlands VU' appears only in the foothills surrounding the main mountain ranges of the area, whereas the 'deciduous forests VU' is present at higher altitudes, in the mountains. The 'conifer forests VU' appears only at highest altitudes of the Sierra Nevada range, to the SW, and is replaced by the 'alpine VU' above 2700 m. Owing to low rainfall, the lake system and its bordering 'marshland VU' are contracted and only present in the central areas of the lacustrine facies (Gibert et al., 2007). The riparian vegetation associated with the fluvial system of the Guadix Sub-basin occupies the approximate channel of the river.

The vegetation map for the interglacial/humid periods presents the 'Mediterranean woodlands VU' as the most widespread unit in the areas of lower altitude. The 'steppes VU' is pushed out of the Guadix-Baza Basin and is only present in the southeastern part of the map. The 'deciduous forests VU' is most widespread on the hills and mountains. The higher precipitation allows the 'conifer forests VU' to colonize areas of lower altitude, but it is still restricted to the top of the mountain ranges bordering the Basin and again replaced by the 'alpine VU' above 2700 m. During humid periods, the lake level rises, allowing the lake system to occupy a larger area and to develop satellite lakes, such as the one near Orce. Owing to the expansion of the lake system, the 'marshland VU' occupies a large part of the Baza Sub-basin.

3.2. Plant food availability in the Early Pleistocene Guadix-Baza Basin

The information on edibility gained from the compilation of EPPs in the PlantBITES database is analyzed with respect to the availability of plant food resources for early *Homo* for each of the seven VUs defined as part of the Early Pleistocene environment in the Guadix-Baza Basin. In total, these VUs comprise 178 taxa, of which 61 are edible. Considering only those EPPs that can be eaten raw without sophisticated processing and could have been consumed in larger quantities, 25 taxa can be further assessed as a potential food source with substantial nutrient supply for early *Homo*.

Those 25 edible taxa are not distributed equally in the basin. The highest number of taxa with EPPs occur in the 'Mediterranean woodlands VU' (10 species) and in the 'marshland VU' (9 species). However, 'riparian' and 'marshland VUs' reveal the highest relative abundance of edible taxa, both VUs contain a 30% of edible taxa against the complete list of dominant taxa (SOM Table S1). Therefore, it is likely that the 'riparian' and 'marshland VUs' had a higher density of edible plants and EPPs per area. Then, these two VUs could represent the richest source of plant food in the basin.

Besides the abundance of edible plant species, the type of their EPPs provides further information on the nutritional potential of each VU (SOM Table S2). Although the nutrient content of the plant parts listed in this study is not yet compiled in detail, fruits, seeds, and USOs (i.e., bulbs, rhizomes, roots) can be assumed to generally contain high amounts of carbohydrates (sugars and starch), protein, and fats. These plant parts are storage organs and therefore to have higher (macro)nutritional value than leaves and other plant parts (e.g., González et al., 2011). Such high-quality food items occur in higher amounts in the 'Mediterranean woodland VU' (six fruit-EPPs and two seed-EPPs) and in the 'marshland VU' (five fruit-EPPs and one USO-EPP). The cattail reed *T. latifolia*, assigned to the 'riparian' and 'marshland VUs' and documented frequently in the pollen record of the Baza Sub-basin (Altolaguirre et al., 2020), is a specifically important taxon because almost all plant parts are edible to some extent. Especially, the rhizome (an USO) provides high protein and starch content and is reliably available around the year, being richest in starch in winter (Launert, 1981).

On the other hand, dietary fibers also are crucial for a healthy diet. Fiber content can be assumed to be higher in the EPP category 'greens.' This category encompasses leaves, shoots, flowers, buds, petals, tendrils, and stems, which are eaten today as salad or vegetables. For example, Pinela et al. (2017) reported high contents of dietary fibers and vitamin C in the shoots of wild asparagus (*Asparagus acutifolius*), which in our study is assigned to the 'Mediterranean woodland VU.' Generally, 'greens'-EPPs occur in largest amounts (10 EPPs) in the 'marshland VU,' adding further importance to the potential of this VU as a plant food supply.

The category 'others' represents manna of the tamarisk *Tamarix gallica*, which can be a substantial source of sugar. Manna of the tamarisk *T. gallica* is not a plant part sensu stricto, but most probably honeydew secreted by insects and accumulated at the stems of tamarisks and other plants; its sugar content exceeds 74% (Grami, 1998).

The phenology of EPPs in each VU displays the differences in their seasonal availability (Fig. 7; SOM Table S3). During winter, plant food availability is generally scarce. Only USOs provide substantial energy in the 'marshland,' 'riparian,' and 'steppes VUs.' Spring is characterized by the availability of young leaves and shoots and early fruits, whereas summer and autumn offer the richest diversity of EPPs. The 'deciduous forests' and 'conifer forests' VUs have peaks in EPP numbers in autumn with the ripening of most of the fruits, whereas in the 'Mediterranean woodlands VU,' EPPs are more equally distributed through spring to autumn. Azonal and 'steppes' units show highest EPP values in spring and summer. The seasonal distribution of EPPs in the 'marshland VU' displays a peculiar pattern combining an increase of 'greens' in spring and summer, with a peak of fruits in autumn and the permanent availability of USOs. This stresses the importance of the 'marshland' vegetation as a reliable and nutrient rich source of plant foods for early *Homo*.

4. Discussion

The vegetation maps presented here (Fig. 6) represent an approximation to the structure of the vegetation in the Guadix-Baza Basin during the Early Pleistocene. The maps reveal a relatively high diversity of vegetation types, with the description of seven different VUs. This diversity of vegetation types within a relatively small area could have created an ideal environment for the first hominin communities in the Iberian Peninsula.

Despite the scarcity of Early Pleistocene hominin records, early *Homo* is considered a moderately common element in European

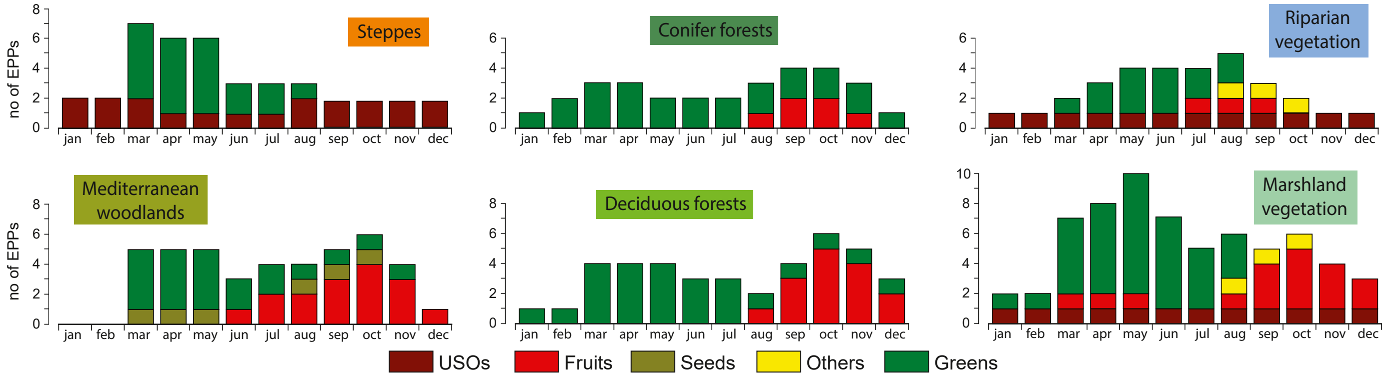

Figure 7. Bar graphs representing the number of edible plant parts (EPPs) available to hominins per month. Each graph represents a different vegetation unit. The Alpine vegetation unit is not included here owing to the lack of EPPs. In the present study, underground storage organs (USOs) comprise rhizomes, bulbs, and roots; 'greens' are leaves, shoots, stems, flowers, buds, tendrils, and petals; 'others' represents manna from *Tamarix gallica.*

faunas (Rodríguez et al., 2015). It is also assumed to have been common in the Guadix-Baza Basin during interglacial periods, when the climate was warm and humid (Rodríguez-Gómez et al., 2016). Furthermore, recent pollen-based climatic analyses provide evidence that glacial temperatures in Guadix-Baza were not prohibitively low as to impede the presence of hominins during dry and cold periods (Altolaguirre et al., 2019). Recent studies of the herpetofauna fossil assemblages from the sites of Orce revealed that the hominin-bearing layer of Barranco León 5 could represent a humid period, whereas some of the artifact-bearing strata of Fuente Nueva 3 could represent a dry period (Sánchez-Bandera et al., 2020). Together, pollen and herpetofauna studies allow to contemplate the possibility of the Guadix-Baza Basin having been occupied by early *Homo* during both interglacial (humid) and glacial (dry) periods. The vegetation maps presented here visualize the range of environmental diversity that early hominins may have faced through the cyclical environmental changes of the Early Pleistocene.

During humid (interglacial) periods, hominins would have had access to a great variety of different vegetation types, which may have also granted them access to a variety of plant and animal resources. This could have made the Guadix-Baza Basin an ideal hominin habitat because a high environmental diversity is regarded a key factor in hominin colonization (Kahlke et al., 2011; Carrión et al., 2011). The areas of lower altitude were occupied by a Mediterranean woodland and shrubland of holm oak trees and kermes oak scrubs (*Q. ilex* and *Q. coccifera*). The great amount of herbaceous pollen still being reported during these periods (Altolaguirre et al., 2020) indicates that these woodlands were relatively open, probably allowing for the movement of herds of grazers, such as *Equus*, *Bison*, *Mammuthus meridionalis*, and *Hemitragus,* found also at the Orce sites (Martínez Navarro et al., 2003). These herds would have been a potential source of meat for early *Homo*. In the mountains, the deciduous and conifer forests probably had a much higher arboreal density, where forest-dweller species could have been found, such as *Praemegaceros*. In addition, early hominins could have used forested areas as protection from predators and competitors (Huguet, 2007). This would have been an important factor since competition between *Homo* and the giant hyena *Pachycrocuta brevirostris* has been recorded at Fuente Nueva 3 (Espigares et al., 2013). Based on the location of the sites of Orce, early *Homo* was present in an area where they could find several different environments within a radius of less than 10 km (Fig. 6). Hominins in Orce, during a humid period, would find themselves in an open Mediterranean woodland, where they had access to a small freshwater, or slightly brackish, satellite lake (El Hamouti and Gibert, 2012; Anadón et al., 2015) and the surrounding marshland vegetation. To the south, they were also close to the deciduous oak forests growing on the Sierra del Periate. These three VUs might have provided a high number of EPPs from spring to autumn. During winter, still, multiple EPPs could have been found in the marshland vegetation, securing survival independently from meat supply (Fig. 7).

During dry (glacial) periods, the Guadix-Baza Basin experienced a generalized loss of arboreal cover as steppes became the predominant vegetation type. This limited the diversity of vegetation types and plant resources available. Still, the arboreal vegetation preserved in the mountainous regions of the area could have granted early *Homo* enough access to plant resources. The steppe vegetation contains a relatively low number of EPPs (Fig. 7), but multiple steppe USOs were a reliable food source through the year. Furthermore, steppes could have been exploited by hominins during dry periods for meat as these would be the preferred habitat of large grazers. Therefore, early *Homo* could have managed to survive in dry and open areas, evidencing a certain degree of adaptability to changing environments as advocated earlier for Africa (Ungar et al., 2006) and Europe (Messager et al., 2011) in general, and the Iberian Peninsula in particular (Huguet et al., 2013). The hominins in Guadix-Baza could have been able to obtain enough resources in glacial environments dominated by herbs and grasses, as they did in African savannah environments (Ungar et al., 2006). Hence, the Guadix-Baza Basin could have acted as a refugium for early *Homo*. This observation does not rule out a scenario wherein the hominin communities were abandoning the basin, temporally or seasonally, and seeking areas of more temperate climatic conditions such as the nearby Mediterranean coast.

The marshland and riparian vegetation most probably played an important role as a reliable source of plant food for early *Homo* because it contains relatively high numbers of EPPs throughout the year. Early hominins could have relied on these areas for their plant diet, especially during the months of winter, when the number of EPPs presented by other VUs was heavily reduced or nonexistent (Fig. 7). However, it is possible that the marshland vegetation, despite plentiful, presented a challenge for hominins with respect to foraging because it was probably divided into muddy banks separated by ponds of water. These areas could have been difficult to traverse and populated by bloats of *Hippopotamus antiquus* (Martínez-Navarro et al., 2003), which were bigger than their modern relatives. Still, the location of the Orce sites near the edge of the reconstructed marshland vegetation (Fig. 6) could suggest that hominins were keeping relative proximity to the marshland as it was an important source of plant food and fresh water. The riparian and marshland VUs were reduced during dry periods (glacials), creating additional environmental stress over the hominin communities. However, the permanence of the lake system and its associated marshland vegetation, although diminished, could have provided early *Homo* with a reliable source of plant food during these harsher climatic periods. Such permanent wetlands in dry environments could have played an important role in the early expansion of hominins into Eurasia (Ashley et al., 2009; Joordens et al., 2009; Barboni et al., 2019).

The vegetation maps show that, during the Early Pleistocene, early *Homo* in southern Spain had access to a great variety of environments. However, in the course of the Mid-Pleistocene Transition (MPT), this situation changed. The MPT led to an increased aridification and significant loss of arboreal cover in the Mediterranean region (Magri and Palombo, 2013) and the Iberian Peninsula (Postigo-Mijarra et al., 2010; Cuenca-Bescós et al., 2011; Kahlke et al., 2011), causing the substitution of humid and forested environments with dry and open ones. The intensification of dry periods and the loss of even more forest cover associated with the MPT could have reduced the number of vegetation types and plant resources available to early hominins in Orce. Moreover, during and after the MPT, the Iberian floras experienced the extirpation of several arboreal taxa (Postigo-Mijarra et al., 2010), further reducing plant food diversity. Together with the hydrographical catchment of the basin and the transition of the lake system of Baza to a fluvial system during the Middle Pleistocene (ca. 600 ka), the marshland vegetation strongly retracted or may even have completely disappeared. After the MPT and during the Middle Pleistocene, the Guadix-Baza Basin probably became a more hostile environment to early *Homo*, especially during glacial periods.

5. Conclusions

Following a methodology based on fossil material, paleogeographic data and paleoclimate calculations allows generating maps of the Early Pleistocene VUs of the Guadix-Baza Basin for both glacial and interglacial scenarios. A second methodology is presented to assess the availability of EPPs in each of the Early Pleistocene VUs. The compilation of phenological information for EPPs useful to Early Pleistocene hominins allows creating a calendar of plant food availability.

The resulting vegetation maps represent a great diversity of vegetation types in the Guadix-Baza Basin, with seven different units that change their distribution based on climatic changes, i.e., dry (glacial) and humid (interglacial) periods. During dry periods, the dominant vegetation type is the steppe, with Mediterranean woodlands and deciduous and conifer forests largely reduced and restricted to valleys or mountainous areas. During humid periods, the steppes are replaced by open Mediterranean woodlands, whereas deciduous and conifer forests occupy larger areas in the mountain ranges. Of these units, the Mediterranean woodlands and the deciduous forests show a high number of diverse EPPs, especially fruits and ‘greens,’ but these numbers decrease considerably during winter.

The distribution of marshland vegetation has been reconstructed based on the extent of the lacustrine sedimentary facies. This vegetation occupied a large area during humid periods, when the lake reached its maximum extent. During dry periods, the marshlands must have been severely constrained, although they remained present owing to the permanence of a reduced lake body. Together with riparian vegetation, the marshlands presented a high number of EPPs. Unlike other VUs, these two vegetation types could have been a reliable source of EPPs for hominins during the months of winter. These units, especially the marshland, owing to its larger area, could also have been a critical source of plant food for early *Homo* during dry (glacial) periods. Therefore, the disappearance of the lake system during the Middle Pleistocene, and increasing aridity after the MPT, caused a severe degradation of the hominin habitat in the Guadix-Baza Basin.

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.

Acknowledgments

This work was performed with the financial support by ROCEEH Research Centre ‘The role of culture in early expansions of humans’ of the Heidelberg Academy of Sciences and Humanities (http://www.roceeh.net). This work is a contribution to NECLIME (http://www.neclime.de) and to the METHOD International Focus Group (1604F) (http://www.method-ifg.com) funded by the INQUA Humans and Biosphere Commission. We are grateful to Christine Hertler (ROCEEH), Jesús Rodríguez (CENIEH), and Ana Mateos (CENIEH) for the encouraging discussion at the METHOD IFG meetings. We are also grateful to Karen Hahn (Frankfurt University) and Astghik Paikyan (Botanical Institute of the Armenian Academy of Sciences) for inspiring discussions on edible plants and appreciate helpful comments by Friedemann Schrenk (Frankfurt University) on an earlier version of the manuscript. We also thank the editors and two anonymous reviewers for their supportive remarks.

Supplementary Online Material

Supplementary Online Material to this article can be found online at https://doi.org/10.1016/j.jhevol.2021.102986.

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Chapter 6

Conclusions and Outlook

How climate dynamics may have affected hominins

The palynological assemblages retrieved from the Palominas core (Baza Basin, SE Spain) have allowed the application of quantitative and qualitative palaeoclimate methods leading to the reconstruction of the climate dynamics of the south of the Iberian Peninsula during the Early Pleistocene (Chapter 2/Altolaguirre et al., 2019; Chapter 3/Altolaguirre et al., 2020 and Chapter 4). Furthermore, by extending the application of the CA method to macro- and micro-palaebotanical Early Pleistocene records from the north of the Iberian Peninsula, these climate dynamics can be analysed at a broader regional scale and in the context of the first expansion of early *Homo* into Western Europe (Altolaguirre et al., 2019/ Chapter 2).

The palaeoclimate results, from the application of the Coexistence Approach at the hominin sites in the north of the Iberian Peninsula, describe a climate generally warm and humid. In the South, at Baza Basin, the results describe the alternation of climate periods of significantly different precipitation. The CA reveals the existence of humid phases, during which MAP and MPWet values were higher than the modern ones for the area of Baza. These humid phases were in alternation with dry phases, during which precipitation values could have more closely resembled the relatively low values created by the modern climate of Southern Spain. On average, precipitation values during humid phases were 21% higher than during dry phases. The CA did not provide definitive temperature measurements for the area of Baza, as the resulting temperature intervals are too broad. Nonetheless, the coexistence intervals for MTCold were consistently above 0ºC due to the virtually persistence of pollen from evergreen *Quercus*, likely belonging to species of holm and kermes oaks (*Q. ilex* and *Q. coccifera*) whose saplings cannot tolerate excessive winter stress (Terradas and Savé, 1992). Palaeaoclimate measurements from the North of the Iberian Peninsula, on average, show higher precipitation values than those of the South, at Baza. This latitudinal contrast might suggest the existence of an Early Pleistocene North-South gradient of aridity, as seen in the modern climate.

The application of the Pollen Climate Index (PCI) also reveals the oscillation of humid and dry phases, as identified by the CA. Together with the results from the Pollen Temperature Index (PTI) and biomarker analysis, it is possible to characterize humid phases as relatively warm, while dry phases were generally cooler (Chapter 4). In this way, the humid and warm phases are associated with interglacial periods, while dry and cold phases would represent glacial periods. This characterization of the glacial and interglacial climates is in agreement with Quaternary paleoclimate reconstructions of the Mediterranean region (e.g., Suc, 1984; Suc and Popescu, 2005; Bertini, 2010) and of the Iberian Peninsula (Combourieu-Nebout et al., 1999; Camuera et al., 2019; Torres et al., 2020).

Overall, the palaeoclimate data obtained from the analysis of pollen and macrofloral assemblages from hominin sites in Northern Spain (Altolaguirre et al., 2019/ Chapter 2) reveal that hominin occupation was associated with the existence of a climate warmer and more humid than the modern one.

At Southern Spain, hominin occupation cannot be securely placed in the context of the glacial-interglacial cyclicity due to the lack of an accurate age model. Thus, it is not clear whether the hominin occupation evidenced at Orce took place during a glacial or interglacial period. Still, faunal analyses from the sites suggests hominin presence was associated with interglacial climate (Agustí et al., 2009; Blain et al., 2011, 2016). The new palaeoclimate data presented here indicates that during interglacial periods the climate was significantly wetter than the modern one. During glacial periods, precipitations were more similar to the relatively low modern ones, while temperatures were lower in comparison with the interglacial periods. MAT difference between interglacial and glacial periods was around 10º C. Still, mean winter temperatures were not too low as to impede the survivability of early *Homo*.

The palaeoflora of Baza Basin and how vegetation shifts impacted *Homo*

The pollen analysis from the Palominas core has revealed well preserved palynomorph assemblages, allowing the identification of a total of 100 different angiosperm pollen taxa and 7 conifer pollen taxa. Additionally, 10 cryptogam taxa and multiple fungal and algal spore types were identified.

The pollen assemblages of the Palominas record are consistently dominated by pine pollen grains (Chapter 3/Altolaguirre et al., 2020). The prevalence of pine trees in the Baza Basin during the Early Pleistocene is not too dissimilar from modern day environments of Southern Spain, where different species of pine are common elements of multiple vegetation types, from alpine forests to lowland Mediterranean woodlands (Pérez-Latorre and Cabezudo, 2009). Nonetheless, pine pollen is overrepresented in the pollen record due to the exceptionally high pollen production reported in pines, combined with the high buoyancy and long-distance transport of the pollen grains (Dunwiddie, 1987). Excluding pine pollen, the pollen assemblages of the Palominas core alternate between two main states: First, pollen assemblages where the arboreal pollen represents ca. 40–50% of the pollen sum, the rest being constituted mainly by pollen from herbs and grasses. These assemblages are related to humid phases. Second, assemblages dominated by herbaceous groups while arboreal pollen represents only 10–20% of the pollen sum, associated with dry phases. The application of PCA highlights this duality, indicating that precipitation was likely to be the main environmental parameter forcing the succession of Early Pleistocene vegetation cycles. The cycles represented in the pollen record seem to be associated with obliquity cyclicity (41 kyr).

Dry phases, associated with glacial climate, led to the development of steppes in the majority of the Baza and Guadix Basins. These steppes were mainly composed of *Artemisia*, *Ephedra*, grasses and other herbs. The abundance of *Artemisia* is a staple of glacial environments in the Pleistocene of Southern Europe. The few trees present during dry periods would have retreated into the humid valleys and mountainous areas of the Betic Mountains, surrounding the Baza Basin. During humid phases, the arboreal cover increased, although with the permanence of reduced open spaces. In the lowlands Mediterranean woodlands of evergreen oaks would create forested steppes, combining the presence of trees with fields of herbs. Arboreal density probably increased with altitude, with the highlands and mountains hosting lush forests mainly composed of deciduous oaks and, in lesser abundance, other warm and temperate taxa such as *Fagus*, *Carpinus* or members of Ericaceae. At higher altitudes, the broadleaf trees would be progressively replaced by *Picea* and *Abies*, creating cool conifer forests. The lake system at Baza Basin is represented in the pollen record with the presence during both dry and humid phases of pollen from reeds and sedges (Cyperaceae, *Typha*, *Sparganium*) and trees typical of moist soils like *Alnus* and *Salix*. These plant groups would create marshlands surrounding the borders of the lake system such as the area where the Orce sites are found.

Additionally, the pollen record from the Palominas core provides new insights regarding the biostratrigraphy and biogeography of the arctotertiary taxa which became extirpated from European floras during the Pleistocene. The pollen record shows the presence of *Aralia*, *Cathaya*, *Tsuga*, *Carya*, *Parthenocissus*, *Eucommia*, *Perocarya*, *Parrotia* and *Zelkova*. These taxa represent the remnants of the tropical and subtropical floras which were common in Europe during the Paleogene and Neogene (Postigo-Mijarra et al., 2010).

The palaeoclimate and palynological data obtained from the Palominas core were employed, in conjunction with palaeogeographic data, in the creation of maps of the different vegetation units (VUs) (Chapter 5/Altolaguirre et al., 2021). The resulting vegetation maps depict the VUs of the regions of Guadix and Baza during both dry and humid periods of the Early Pleistocene. The map representing dry phases shows a predominance of the ‘steppes VU’, which is present in the areas of lower altitude of both basins, with the forested VUs being present only in the mountainous regions. During humid phases, the map represents the forested VUs extending to lower altitudes, while the steppes are replaced by the ‘Mediterranean woodlands VU'. The extension of the ‘marshland VU’ changes accordingly to lake level changes due to lower or higher precipitation rates.

The climate-driven succession of these two vegetation configurations, dry and humid, must have altered the behaviour and survivability of the hominin communities from Orce. During humid periods, the great vegetation diversity led to an equally great diversity of faunas. Such environmental diversity could have been a key factor in the context of early hominin expansion (Kahlke et al., 2011; Carrión et al., 2011), thus establishing Orce as an ideal hominin habitat. During dry periods, the loss of vegetation diversity and the expansion of the steppes likely led to environmental stress over the hominin populations in the area of Baza. Still, early hominins were able to adapt to different environments

(Ungar et al., 2006; Messager et al., 2011; Huguet et al., 2013; Mercader et al., 2021). Similarly, early *Homo* could have adapted to the cyclical vegetation changes at Southern Spain and to the steppe environments which developed during dry and cooler climatic periods.

Resource availability at Orce and how it was affected by climate changes

The methodology for the assessment of edible plant parts (EPPs) (Chapter 5/Altolaguirre et al., 2021) relies on the same analogue modern vegetation employed in the VU mapping. The lists of dominant taxa of the analogue VUs are combined with the dominant pollen groups seen in the record, thus creating an approximated taxonomic list of the dominant vegetation in each of the Early Pleistocene VU.

A database of plant edibility is created using the taxa lists in conjunction with ethnobotanical and phenological literature. This database records information on plant parts which are edible, whether or not the EPP can be consumed with or without processing and in which amount. Furthermore, phenological data allowed the creation of a calendar, indicating during which months each EPP is available for collection.

The results indicate that the high diversity of vegetation types reconstructed for the vicinity of the hominin sites of Orce was translated into a high variety of plant food sources. Most of the forested VUs contain a high amount of EPPs, with ‘greens’ being most abundant during spring and fruits being more prevalent during autumn. Although ‘greens’ represent an important source of plant fibres, fruits contain higher amounts of carbohydrates, proteins and fats and could be considered as ‘high quality’ foods (González et al., 2011).

The ‘Mediterranean woodlands VU’ would have been the forested VU with the highest number of fruits and seeds available, especially during spring. Even the steppe vegetation would have granted hominins access to some EPPs in the form of roots and rhizomes present through the year. Furthermore, the riparian and the marshland vegetation contained a high number of EPPs, including USOs and fruits. The persistent nature of these two VUs through the successive glacial-interglacial climatic changes would have represented a consistent food source for the hominins at Orce during the Early Pleistocene.

The EPPs identified must have represented sizable part of the hominin diet at Orce, as it is known that early hominins consumed mixed diets (e.g., Ungar et al. 2006, Hardy, 2018 and references therein). It can be assumed from cut marks on ungulate and elephant bones that hominins at Orce also consumed meat as part of their diet (Espigares, 2010; Espigares et al., 2013; Gibert, 2018). Their prey were most likely carcasses of grazers such as bovids and horses, elephants (*Mammuthus meridionalis*) or wild goats, all these being found also at the Orce sites (Martínez Navarro et al., 2003; Espigares et al., 2013). Grazers moved through open vegetation and would have been most commonly found in the steppes and in the Mediterranean woodlands, owing to the open spaces and clearings present there. Browsers present in the forested environments, such as the giant deer *Praemegaceros*, could have been a potential source of food present at higher altitudes. Fish, which are also found to be fossilized in Orce (Blanco et al., 2015), would have been found in the rivers and in the marginal areas of Lake Baza itself, and could have been a food source for hominins. Hypothetically, early *Homo* at Orce could have been capable of collecting freshwater fish, similar to Early Pleistocene African populations (Braun et al., 2010).

Regarding changes in meat consumption over time, faunal shifts over the glacial-interglacial cyclicity have not been explored. Still, the characterization of major vegetation changes allows gaining new insights into hypothetical faunal changes. During interglacial periods the expansion of forests and woodlands would have invited an increase in browser fauna and in faunal diversity. However, the total animal density in the basin might have been relatively low, as the forested vegetation hampered the movement of large herds of browser through the basin. During glacial periods, the widespread steppe vegetation must have allowed the movement of herds of grazers, which provided animal food and other resources to the hominins at Orce, either as live prey or as carcasses. Thus, during glacial periods plant resource diversity was lower, but hominins had easier access to meat and other animal resources.

Distribution of *Homo* and their potential continuous presence in the South of the Iberian Peninsula

The idea of a continuous occupation of the Iberian Peninsula by *Homo* (Cuenca-Bescós et al., 2011; Orain et al., 2013; Bermúdez de Castro et al., 2016) goes against other models of early hominin expansions for the Early Pleistocene. Such models suggest an 'intermittent' occupation, where hominins entered Europe during warm periods, migrating from 'source' populations in areas at lower latitudes such as the Levant, and were extirpated at the beginning of the following glacial period (e. g., Agustí et al., 2009; Dennell et al., 2011; Leroy et al., 2011; Bermúdez de Castro and Martinón-Torres, 2013). The new data presented in this PhD Thesis contributes to this on-going discussion.

The climate data obtained through the application of the Coexistence Approach (Chapter 2/Altolaguirre et al., 2019) indicates that glacial periods in the south of the Iberian Peninsula were relatively mild, with MTCold values at Baza never below 0º C. This mark of 0º C has been proposed as the limit for *Homo* habitability by Leroy et al. (2011). Areas with mean winter temperatures below 0º C might not have been able to sustain hominin populations. The new palaeoclimate results presented by this PhD thesis indicate that winter temperatures might have not gone below 0º C, thus not being a limiting factor regarding the continuous habitation of the southern latitudes of the Iberian Peninsula through complete glacial-interglacial periods of the Early Pleistocene.

The new climate data and the suggestion of the continuous presence of *Homo* in the Baza Basin presented by this PhD Thesis (Chapter 2/Altolaguirre et al., 2019) would seem to be confirmed by the independent analysis of Sánchez-Bandera et al. (2020). Their study shows climate changes within the sediment sequence in one of the Orce sites (Fuente Nueva 3). One of the layers carrying stone tools contains a fossil herpetofauna assemblage which is typical of humid climates, while a different overlaying layer, also with stone tools, contains a faunal assemblage typical of dry environments. As indicated by the authors, the new results could suggest the presence of *Homo* during glacial periods. Furthermore, the assessment of the number of EPPs (Chapter 5/Altolaguirre et al., 2021) reveals that hominins had access to multiple food sources and to a high number of edible plants, even during dry-glacial periods. Also, the persistence of the marshland vegetation during these periods meant that *Homo* might have been able to survive glacial climate in the Baza Basin, since the environmental changes would not have drastically reduced the availability of plant resources.

In conclusion, the results presented by this PhD thesis support the hypothesis of the continuous habitation of the Iberian Peninsula and the European continent since the first hominin expansion event. The Baza Basin might have acted as a glacial refugium for hominin populations during the cold and dry periods of the Early Pleistocene climate. The uninterrupted presence of *Homo* in Southern Spain could be compatible with the 'sources and sinks' model for hominin expansion, where the south of the Iberian Peninsula would host 'source' populations during harsher climatic periods (Dennell et al., 2011). These populations would then disperse northwards at the onset of warmer climatic periods. In this way, the distribution area of Western European hominin populations would shift following the climate cycles of the Early Pleistocene.

The new data also contributes to the characterization of the potential early *Homo* habitat and to the task of identifying when and where such potential habitats might have occurred. Early Pleistocene environments capable of supporting *Homo* in Eurasia were highly diversified environments, enhanced by proximity to coastal or lacustrine areas. The existence of such environments alongside migration corridors between Africa and Eurasia might have been a key factor for supporting the transit of hominins (Derricourt, 2005; Martínez-Navarro, 2010). Therefore, identification of such palaeoenvironments among these potential corridors could answer another long-standing open question in palaeoanthropology: which path took early *Homo* on their route out of Africa?

Despite the favourable environment that early *Homo* found at Baza, their habitat might have experienced severe degradation at the end of the Early Pleistocene. Some authors see the Early-Middle Pleistocene Transition (EMPT) as a climatic process with overall favourable repercussions for the expansion of *Homo* into Europe due to the opening of the vegetation and the reduction of lush forests (e. g., Cuenca-Bescós et al., 2011; Kahlke et al., 2011; Leroy et al., 2011). However, at Baza, the EMPT caused the aridification and intensification of the cyclic climate changes and could have led to a significant loss of vegetation diversity. Together with the disappearance of the lacustrine system and its associated marshland vegetation, the Baza Basin would have seen its plant resources severely diminished by the end of the Early Pleistocene. New data regarding hominin occupation and palaeoenvironmental reconstructions during the Middle Pleistocene would be needed in order to assess the specific impact of the EMPT regarding the continued occupation of Orce and Southern Spain during this period.

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Chapter 7

Schlussfolgerungen und Ausblick

Frühpleistozäne Klimadynamik in Südspanien und wie sie sich auf Frühmenschen ausgewirkt haben könnte

Die aus dem Palominas-Bohrkern (Baza-Becken, Südost Spanien) gewonnenen Palynofloren haben die Anwendung quantitativer und qualitativer paläoklimatischer Methoden ermöglicht, die zur Rekonstruktion der Klimadynamik im Süden der Iberischen Halbinsel während des frühen Pleistozäns führten (Altolaguirre et al., 2019/ Kapitel 2; Altolaguirre et al., 2020/Kapitel 3 und Kapitel 4). Durch die Ausweitung der Anwendung der Methode des Koexistenzansatzes (CA) auf makro- und mikropaläobotanische Archive des frühen Pleistozäns aus dem Norden der Iberischen Halbinsel konnte diese Klimadynamik außerdem auf einer breiteren regionalen Ebene und im Kontext der ersten Ausbreitung des frühen *Homo* nach Westeuropa analysiert werden (Altolaguirre et al., 2019/Kapitel 2).

Die Klimaergebnisse von Homininen-Fossilfundstellen im Norden der Iberischen Halbinsel deuten auf ein allgemein warmes und feuchtes Klima. Im Süden, im Baza-Becken, beschreiben die Daten einen Wechsel von Klimaperioden mit deutlich unterschiedlichen Niederschlägen. Der CA zeigt die Existenz von feuchten Phasen, in denen die MAP- und MPWet-Werte höher waren als die heutigen im Gebiet von Baza. Diese Feuchtphasen wechselten mit Trockenphasen, in denen die Niederschlagswerte eher den relativ niedrigen Werten des modernen Klimas Südspaniens entsprachen. Im Durchschnitt lagen die Niederschlagswerte in Feuchtphasen um 21 % höher als in Trockenphasen. Der CA lieferte keine definitiven Temperaturmessungen für das Gebiet von Baza, da die resultierenden Temperaturintervalle sehr breit sind. Nichtsdestotrotz lagen die Koexistenzintervalle für die mittlere Temperatur des kältesten Moants (MTCold) durchweg über 0°C. Dieser Wert ergibt sich aus dem fast durchgehenden Auftreten von Pollen des immergrünen *Quercus*, die wahrscheinlich zu den Arten der Stein- und Kermeseiche (*Q. ilex* und *Q. coccifera*) gehören, deren Sämlinge kein Übermaß an Winterstress vertragen (Terradas and Savé, 1992). Paläoklima-Abschätzungen aus dem Norden der Iberischen Halbinsel zeigen im Durchschnitt höhere

Niederschlagswerte als diejenigen aus dem Süden bei Baza. Dieser Unterschied könnte auf die Existenz eines Nord-Süd-Gradienten der Trockenheit im frühen Pleistozän hinweisen, wie er auch im modernen Klima zu sehen ist.

Die Anwendung des Pollen-Klima-Index (PCI) zeigt auch das von dervom CA identifizierte Oszillieren von Feucht- und Trockenphasen. Zusammen mit den Ergebnissen von Pollen-Temperatur-Index (PTI) und Biomarkeranalyse erlauben die Daten, Feuchtphasen als relativ warm zu charakterisieren, während Trockenphasen generell kühler waren (Kapitel 4). Auf diese Weise werden die Feucht- und Warmphasen mit Zwischeneiszeiten assoziiert, während Trocken- und Kaltphasen Eiszeiten darstellen würden. Diese Charakterisierung des glazialen und interglazialen Klimas stimmt mit anderen paläoklimatischen Rekonstruktionen für das Quartär des Mittelmeerraums (z. B. Suc und Popescu, 2005; Bertini, 2010) und der Iberischen Halbinsel (Combourieu-Nebout et al., 1999; Camuera et al., 2019; Torres et al., 2020) überein.

Generell zeigen die Ergebnisse der Analyse von Pollen- und Makrofloren aus Homininen-Fossilfundstellen in Nordspanien (Altolaguirre et al., 2019/Kapitel 2), dass das Vorkommen von Frühmenschen mit einem Klima assoziiert war, das wärmer und feuchter war als das moderne.

In Südspanien kann das Auftreten von Frühmenschen aufgrund des Fehlens eines genauen Altersmodells nicht sicher in den Kontext der glazial-interglazialen Zyklizität eingeordnet werden. Daher ist nicht klar, ob die Homininen von Orce während einer Eiszeit oder einer Zwischeneiszeit lebten. Dennoch deuten Faunenanalysen an den Fundstellen darauf hin, dass die Anwesenheit von Homininen mit einem interglazialen Klima in Verbindung gebracht wurde (Agustí et al., 2009; Blain et al., 2011, 2016). Die hier präsentierten neuen Paläoklimadaten weisen darauf hin, dass das Klima während der Zwischeneiszeiten deutlich feuchter und etwas wärmer war als heute. Während der Eiszeiten entsprach die jährliche Niederschlagsmenge eher den relativ niedrigen modernen. Die Temperaturen während der Eiszeiten waren niedriger als in den Zwischeneiszeiten. Der Unterschied in der mittleren Jahrestemperatur (MAT) zwischen Eis- und Zwischeneiszeit betrug etwa 10°C. Dennoch waren die mittleren Wintertemperaturen nicht zu niedrig, um die Überlebensfähigkeit des frühen *Homo* zu beeinträchtigen.

Die Paläoflora des Baza-Beckens und wie sich Vegetationsverschiebungen auf *Homo* auswirkten

Die Pollenanalyse aus dem Palominas-Kern hat gut erhaltene palynomorphe Floren ergeben, die die Identifizierung von insgesamt 100 verschiedenen Angiospermenpollentaxa und 7 Nadelbaumpollentaxa ermöglicht. Darüber hinaus wurden 10 Kryptogamtaxa und mehrere Pilz- und Algensporentypen identifiziert.

Die Pollenfloren des Palominas-Datensatzes werden durchweg von Pollenkörnern dominiert, die der Kifer (*Pinus*) zugeordnet werden können (Altolaguirre et al., 2020/Kapitel 3). Die Prävalenz von Kiefern im Baza-Becken während des frühen Pleistozäns ist der heutigen Umgebung Südspaniens nicht allzu unähnlich, wo verschiedene Kiefernarten gemeinsame Elemente mehrerer Vegetationstypen sind, von alpinen Wäldern bis hin zu mediterranen Tieflandwäldern (Pérez-Latorre und Cabezudo, 2009). Nichtsdestotrotz ist Kiefernpollen aufgrund der außergewöhnlich hohen Pollenproduktion bei Kiefern in Kombination mit hohem Auftrieb und Ferntransport der Pollenkörner in Pollenarchiven meist überrepräsentiert (Dunwiddie, 1987). Abgesehen von Kiefernpollen wechseln die Pollenfloren des Palominas-Bohrkern zwischen zwei Hauptzuständen: Einerseits Pollenfloren, bei denen Baumpollen ca. 40–50% der Pollensumme ausmachen, während der Rest hauptsächlich aus Pollen von Kräutern und Gräsern besteht. Diese Floren kennzeichnen feuchte Phasen. Andererseits, die von krautigen Gruppen dominierten Floren, in denen Baumpollen nur 10–20 % der Pollensumme ausmachen. Diese sind assoziiert mit Trockenphasen. Die Ergebnisse der statistische Hauptkomponentenanalyse (PCA) unterstreichen diese Dualität, was darauf hindeutet, dass Niederschlag wahrscheinlich der wichtigste Umweltparameter war, der die Abfolge der Vegetationszyklen des frühen Pleistozäns erzwang. Die sich in den Pollendaten zeigenden Zyklen scheinen mit Änderungen der Obliquität (41 kyr Zyklizität) in Zusammenhang zu stehen.

Trockenphasen, in Verbindung mit dem eiszeitlichen Klima, führten zur Entwicklung von Steppen in den größten Teilen der Baza- und Guadix-Becken. Diese wurden hauptsächlich von *Artemisia*, *Ephedra*, Gräsern und anderen Kräutern. Die Dominanz von *Artemisia* ist ein Grundcharakteristikum der glazialen Umwelt im Pleistozän Südeuropas (Suc, 1984; Suc und Popescu, 2005; Bertini, 2010). Die wenigen Bäume, die während Trockenperioden vorhanden waren, zogen sich in feuchtere Täler und Bergregionen der Betischen Kordillere zurück, die das Baza-Becken umgeben. In feuchten Phasen nahm die Baumbedeckung zu, allerdings mit immernoch vorhandenen, jedoch reduzierten Offenlandschaften. Im Tiefland würden mediterrane Wälder mit immergrünen Eichen mehr oder weniger dichte Baumbestände mit krautiger Bodenbedeckung schaffen. Die Baumdichte nahm wahrscheinlich mit der Höhe zu, wobei Hochland und Berge mit üppigen Wäldern bedeckt waren, die hauptsächlich von Laubeichen und in geringerem Umfang von anderen warmen und gemäßigten Gattungen wie *Fagus* (Buche), *Carpinus* (Hainbuche) oder Arten der Ericaceae-Familie gebildet wurden. In höheren Lagen würden die Laubbäume nach und nach durch *Picea* (Fichte) und *Abies* (Tanne) ersetzt und Nadelwälder entstehen. Das Seensystem des Baza-Beckens ist in der Pollenflora mit dem Vorhandensein von Pollen von Schilf und Seggen (Cyperaceae, *Typha*, *Sparganium*) und Bäumen, die für feuchte Böden typisch sind wie *Alnus* (Erle) und *Salix* (Weide), sowohl in trockenen als auch in feuchten Phasen belegt. Diese Pflanzengruppen schufen ein Marschland, das das Seensystem umgab, wie zum Beispiel das Gebiet, in dem sich die archäologischen Fundstätten von Orce befinden.

Über die detaillierte Rekonstruktion der regionalen Vegetation des Baza-Beckens hinausliefert die Pollenflora des Palominas-Bohrkerns außerdem neue Erkenntnisse über die Biostratrigraphie und Biogeographie der arktotertiären Taxa, die im Pleistozän aus europäischen Floren verschwanden. Der Pollendaten zeigen das Vorkommen von *Aralia, Cathaya, Tsuga, Carya, Parthenocissus, Eucommia, Perocarya, Parrotia* und *Zelkova*. Diese Taxa stellen die Überreste der tropischen und subtropischen Flora dar, die in Europa während des Paläogens und Neogens verbreitet waren (Postigo-Mijarra et al., 2010).

Für eine räumliche Interpretation der erzielten Ergebnisse, wurden die paläoklimatischen und palynologischen Daten aus dem Palominas-Bohrkern in Verbindung mit paläogeographischen Daten zur Erstellung von Karten der verschiedenen Vegetationseinheiten (VUs) verwendet (Altolaguirre et al., 2021/Kapitel 5). Die resultierenden Vegetationskarten zeigen die VUs der Regionen Guadix und Baza sowohl während trockener als auch feuchter Perioden des frühen Pleistozäns. Die Karte der Trockenphasen zeigt ein Überwiegen der “Steppen-VU”, die in den tiefer gelegenen Gebieten beider Becken vorhanden ist, wobei die waldreicheren VUs nur in den

Bergregionen vorkommen. Für feuchte Phasen stellt die Karte überwiegend die bewaldeten VUs dar, die sich bis in tiefere Lagen erstrecken, während die Steppen durch die “Mediterrane Offenwälderoffene Wälder VU” ersetzt werden. Die Ausdehnung der “Sumpfland VU” ändert sich entsprechend den Veränderungen des Seespiegels aufgrund geringerer oder höherer Niederschlagsraten.

Die klimabedingte Abfolge dieser beiden Vegetationskonfigurationen, trocken und feucht, muss das Verhalten und die Überlebensfähigkeit der Homininen von Orce verändert haben. In feuchten Perioden führte die große Vegetationsvielfalt zu einer ebenso großen Vielfalt an Faunen. Eine solche Umweltvielfalt könnte ein Schlüsselfaktor im Zusammenhang mit der frühen Ausbreitung der Homininen gewesen sein (Kahlke et al., 2011; Carrión et al., 2011), wodurch Orce zu einem idealen Lebensraum für Frühmenschen wurde. Während Trockenperioden führten der Verlust der Vegetationsvielfalt und die Ausdehnung der Steppen wahrscheinlich zu Umweltstress für die Homininen-Populationen im Gebiet von Baza. Dennoch konnten sich frühe Hominine an verschiedene Umgebungen anpassen (Ungar et al., 2006; Messager et al., 2011; Huguet et al., 2013; Mercader et al., 2021). In ähnlicher Weise könnte sich der frühe *Homo* auch an die zyklischen Vegetationsänderungen in Südspanien und an die Steppenumgebung angepasst haben, die sich während trockener und kühlerer Klimaperioden entwickelte.

Ressourcenverfügbarkeit für die frühen *Homo* von Orce und wie diese durch den Klimawandel beeinflusst wurde

Die Methodik zur Bewertung der Verfügbarkeit pflanzlicher Ressourcen (Altolaguirre et al., 2021/Kapitel 5) basiert auf der gleichen analogen modernen Vegetation, die bei der VU-Kartierung verwendet wird. Die Listen der dominanten Taxa der analogen VUs werden mit den im Pollenprofil dominanten Pollengruppen kombiniert, wodurch eine angenäherte taxonomische Liste der dominanten Pflanzen für jede der frühpleistozänen VUs erstellt wird. Anhand dieser Taxalisten wird in Verbindung mit ethnobotanischer und phänologischer Literatur eine Datenbank zur erstellt. Diese erfasst Informationen über essbare Pflanzenteile (EPPs), wie das EPP konsumiert werden kann, ob mit oder ohne Verarbeitung, und in welchen Mengen. Darüber hinaus ermöglichten phänologische

Daten die Erstellung eines Kalenders, der angibt, in welchen Monaten jedes EPP zur Verfügung steht.

Die Ergebnisse dieser Analyse deuten darauf hin, dass sich die große Vielfalt an Vegetationstypen, die für das Gebiet der archäologischen Fundstätten von Orce rekonstruiert wurden, in eine große Vielfalt pflanzlicher Nahrungsquellen übersetzt. Die meisten Gehölz-Vegetationen enthalten einen hohen Anteil an EPPs, wobei “Grünes” (Blätter, Stängel, Knospen etc.) im Frühjahr am häufigsten und Früchte im Herbst häufiger anzutreffen sind. Obwohl “Grünes” eine wichtige Quelle für Pflanzenfasern darstellt, enthalten Früchte höhere Mengen an Kohlenhydraten, Proteinen und Fetten (González et al., 2011) und können als hochwertigere Lebensmittel angesehen werden. Die “Mediterranen Offenwälder VU” wäre die Gehölz-Vegetation mit der höchsten Anzahl an verfügbaren Früchten und Samen, insbesondere im Frühjahr. Sogar die Steppenvegetation hätte den Homininen Zugang zu hochwertigen EPPs in Form von unterirdischen Speicherorganen (USOs) wie Wurzeln und Rhizomen ermöglicht, die das ganze Jahr über vorhanden sind. Darüber hinaus enthielt die Ufer- und Marschlandvegetation eine hohe Anzahl von EPPs, einschließlich USOs und Früchten. Die Beständigkeit gerade dieser beiden beiden Vegetationstypen während der glazialen und interglazialen Klimaänderungen hätte eine konstante Nahrungsquelle für die Homininen in Orce während des frühen Pleistozäns dargestellt.

Die identifizierten EPPs müssen einen beträchtlichen Teil der Hominin-Diät bei Orce ausgemacht haben, da bekannt ist, dass frühe Homininen gemischte Diäten konsumierten (z. B. Ungar et al. 2006, Hardy, 2018 und weitere Referenzen darin). Aus Schnittspuren an Huftier- und Elefantenknochen lässt sich vermuten, dass die Homininen von Orce auch Fleisch als Teil ihrer Ernährung verzehrten (Espigares, 2010; Espigares et al., 2013; Gibert, 2018). Ihre Beute waren höchstwahrscheinlich Kadaver von Weidetieren wie Rindern und Pferden, Elefanten (*Mammuthus meridionalis*) oder Wildziegen, die alle auch an den Orce-Fundstellen nachgewiesen sind (Martínez Navarro et al., 2003; Espigares et al., 2013). bevorzugt grasfressende Herbivoren (grazer) bewegten sich durch die offene Vegetation und waren aufgrund der dort vorhandenen Freiflächen und Lichtungen am häufigsten in den Steppen und in den mediterranen offenen Wäldern anzutreffen. In den bewaldeten Umgebungen vorkommende Blattfresser (browser), wie der Riesenhirsch *Praemegaceros*, könnten eine potenzielle Nahrungsquelle in höheren

Lagen gewesen sein. Fische, die ebenfalls fossil in Orce belegt sind (Blanco et al., 2015), stammen sicherlich aus den Flüssen der Umgebung oder dem Baza-See selbst, und könnten auch als menschliche Nahrung genutzt worden sein. Hypothetisch könnte der frühe *Homo* von Orce durchaus in der Lage gewesen sein, Süßwasserfische zu sammeln, ähnlich wie afrikanische Populationen des frühen Pleistozäns (Braun et al., 2010).

Hinsichtlich der Veränderungen des Fleischkonsums im Laufe der Zeit wurden die Veränderungen der Fauna während des glazialen-interglazialen Zyklus nicht untersucht. Dennoch erlaubt die Charakterisierung großer Vegetationsveränderungen neue Einblicke in hypothetische Faunenveränderungen. Während der Zwischeneiszeiten hätte die Ausdehnung von Wäldern und offenen Wäldern zu einer Zunahme der Browserfauna und der Faunavielfalt generell geführt. Insgesamt könnte die Tierdichte im Becken jedoch relativ gering gewesen sein, da die bewaldete Vegetation die Bewegung großer Browserherden durch das Becken behinderte. Während der Eiszeiten muss die weit verbreitete Steppenvegetation die Bewegung größerer Herden von Weidetieren ermöglicht haben, die den Homininen von Orce entweder als lebende Beute oder als Kadaver fleischliche Nahrung und andere Ressourcen lieferten. Während der Eiszeiten war die Vielfalt an Pflanzenressourcen geringer, aber die Frühmenschen hatten leichteren Zugang zu tierischen Ressourcen.

Verbreitung von *Homo* und ihr möglicherweise kontinuierliches Vorkommen im Süden der Iberischen Halbinsel

Die Vorstellung einer kontinuierlichen Besiedlung der Iberischen Halbinsel durch *Homo* (Cuenca-Bescós et al., 2011; Orain et al., 2013; Bermúdez de Castro et al., 2016) widerspricht anderen Modellen früher Hominin-Expansionen für das frühe Pleistozän. Solche Modelle legen eine “zeitweilige” Besiedlung nahe, bei der Hominінen in warmen Perioden von “Ursprungs”-Populationen in Gebieten niedrigerer Breiten wie der Levante nach Europa gelangten, und zu Beginn der folgenden Eiszeit wieder ausstarben (z. B. Agustí et al., 2009; Dennell et al., 2011; Leroy et al., 2011; Bermúdez de Castro und Martinón-Torres, 2013). Die in dieser Dissertation präsentierten neuen Daten tragen zu dieser laufenden Diskussion bei.

Die durch Anwendung des Koexistenzansatzes gewonnenen Klimadaten (Altolaguirre et al., 2019/Kapitel 2) zeigen, dass die Temperaturen während der Eiszeiten im Süden der Iberischen Halbinsel relativ mild waren, mit MTCold-Werten in Baza nie unter 0°C. Diese Marke von 0°C wurde von Leroy et al. (2011) als Grenzwert für den von *Homo* nutzbaren Lebensraum vorgeschlagen. In Gebieten mit durchschnittlichen Wintertemperaturen unter 0°C waren Hominiden möglicherweise nicht in der Lage, ihre Populationen aufrechtzuerhalten. Demzufolge zeigen die neuen paläoklimatischen Ergebnisse dieser Dissertation, dass die Wintertemperaturen kein limitierender Faktor für die kontinuierliche Besiedlung der südlichen Breiten der Iberischen Halbinsel während vollständiger glazial-interglazialer Perioden des frühen Pleistozäns.gewesen seien müssen.

Die in dieser Dissertation (Altolaguirre et al., 2019/Kapitel 2) präsentierten neuen Klimadaten und der Hinweis auf die kontinuierliche Präsenz von *Homo* im Baza-Becken werden durch die unabhängige Analyse von Sánchez-Bandera et al. (2020) bestätigt. Deren Studie weist Klimaänderungen innerhalb der Sedimentabfolge in einer der Orce-Fundstellen (Fuente Nueva 3) nach. Eine der Steinwerkzeug-führenden Schichten enthält fossile Herpetofauna, die typisch für feuchtes Klima ist, während eine andere, ebenfalls mit Steinwerkzeugen, eine für trockene Umgebungen typische Faunenvergesellschaftung enthält. Wie von den Autoren angegeben, könnten diese neuen Ergebnisse auf die Anwesenheit von *Homo* auch während der Eiszeiten hinweisen. Darüber hinaus zeigt die Bewertung der Zahl der EPPs (Altolaguirre et al., 2021/Kapitel 5), dass Homininen auch in Trockenperioden Zugang zu diversen Nahrungsquellen und zu einer hohen Zahl essbarer Pflanzen hatten. Vor allem die beobachtete Persistenz der Sumpfvegetation während der Trockenphasen deutet darauf hin, dass *Homo* auch während der trockenen Glazialphasen im Baza-Becken überleben konnte, da diese Umweltveränderungen keine schwerwiegenden Beeinträchtigungen in der Verfügbarkeit pflanzlicher Ressourcen mit sich gebracht hätten.

Zusammenfassend stützen die in dieser Dissertation präsentierten Ergebnisse die Hypothese der kontinuierlichen frühmenschlichen Besiedlung der Iberischen Halbinsel und des europäischen Kontinents seit dem ersten Expansionsereignis. Das Baza-Becken könnte durchaus während der kalten und trockenen Perioden des frühen Pleistozäns als eiszeitliches Refugium für Hominin-Populationen gedient haben. Die ununterbrochene

Präsenz von *Homo* in Südspanien könnte mit dem “Quellen und Senken” Modell für die Ausbreitung der Hominininen vereinbar sein, wobei der Süden der Iberischen Halbinsel während harscherer Klimaperioden „Quellen“-Populationen beherbergen würde (Dennell et al., 2011). Diese Populationen würden sich mit Beginn wärmerer Klimaphasen nach Norden zerstreuen und dem Zyklus folgen, der die Klimaveränderungen des frühen Pleistozäns kennzeichnet.

Die neuen Daten tragen auch zur Charakterisierung des potentiellen frühmenschlichen Lebensraums bei und können helfen zu identifizieren, wann und wo solche potentiellen Habitate aufgetreten sein könnten. Eine frühpleistozäne Umwelt, die *Homo* in Eurasien einen Lebenraum bieten konnten, sollte stark diversifiziert sein, was durch Nähe zu Küsten- oder Seegebieten zusätzlich unterstützt würde. Die Existenz solcher Umweltbedingungen entlang von Migrationskorridore zwischen Afrika und Eurasien könnte die Ausbreitung von Hominininen essentiell unterstützt haben (Derricourt, 2005; Martínez-Navarro, 2010). Daher könnte die Identifizierung solcher Paläoumweltbedingungen in potenziellen Korridoren eine weitere seit langem offene Frage in der Paläoanthropologie beantworten: Welchen Weg nahmen die frühen *Homo* auf ihrer Expansion aus Afrika?

Der für den frühen *Homo* günstige Lebensraum in Baza könnte zum Ende des frühen Pleistozäns stark beeinträchtigt worden sein. Einige Autoren sehen diese *Early-Middle-Pleistocene-Transition* (EMPT) als eine klimatische Phase mit insgesamt günstigen Auswirkungen auf die Ausbreitung von *Homo* nach Europa aufgrund der Öffnung der Vegetation und des Rückgangs dichter Wälder (z. B. Cuenca-Bescós et al., 2011; Kahlke et al., 2011; Leroy et al., 2011). In Baza könnte die Aridifizierung und die generelle Intensivierung der mit dem EMPT verbundenen Klimaveränderungen jedoch zu einem erheblichen Verlust der Vegetationsvielfalt geführt haben. Zusammen mit dem Verschwinden des Seesystems und der damit verbundenen Marschlandvegetation wären die Pflanzenressourcen des Baza-Beckens bis zum Ende des frühen Pleistozäns stark zurückgegangen. Neue Daten über die frühmenschliche Besiedlung und paläoökologische Rekonstruktionen während des mittleren Pleistozäns wären erforderlich, um die spezifischen Auswirkungen der EMPT auf eine möglicherweise fortgesetzte Besiedlung des Baza-Beckens und Südspaniens während dieser Zeit zu bewerten.

Acknowledgements

This dissertation has been possible thanks to the initiative of Dr. Angela Bruch (ROCEEH Research Centre, Heidelberg Academy of Sciences, Senckenberg Research Institute) which granted me the wonderful opportunity to conduct the research presented in this PhD Thesis at Frankfurt, Germany. Salary, analytical and travel costs were covered by the ROCEEH project (The Role of Culture in Early Expansions of Humans) of the Heidelberg Academy of Sciences.

The guidance of Dr. Angela Bruch and Prof. Dr. Andreas Mulch (Senckenberg Biodiversity and Climate Research Centre Frankfurt (BiK-F), Goethe University Frankfurt), both advisors to this PhD Thesis, has been of vital importance and I am grateful to both of them for their tireless scientific counsel and advise.

Many colleagues have contributed and added incalculable value to this PhD Thesis through collaboration, consultation and instruction. I wish to give my earnest thanks to, Friedemann Schrenk and Ottmar Kullmer (Senckenberg Research Institute, Goethe University Frankfurt) for their advice and encouragement during the initial presentations of my project. I owe thanks to Torsten Utescher (Senckenberg Research Institute, Bonn University), Eduardo Barron (Geological and Mining Institute of Spain), Edoardo Martinetto (University of Turin), Marianna Kováčová (Comenius University in Bratislava) and Gonzalo Jiménez-Moreno (Granada University) for their advice regarding palynology, climate and environmental sciences. I am also thankful to Christine Hertler (ROCEEH) and Ana Mateos and Jesus Rodríguez (National Research Centre on Human Evolution, CENIEH) for inviting me as part of the METHOD working group and for their help when planning of new lines of research.

I also wish to thank the many colleagues with whom I have had the chance to collaborate on different projects: Luis Gibert (Barcelona University), José Sebastián Carrion (University of Murcia), José María Postigo-Mijarra (IES Clara Campoamor), Manuel Casas-Gallego (CGG Robertson), Suzanne Leroy (Aix-Marseille University, University of Liverpool), Adele Bertini (University of Florence), and Juan Manuel Jiménez-Arenas

(Granada University). I am especially thankful to Iuliana Vasiliev (Bik-F) for introducing me and guiding me through the world of biomarker analysis.

I would also like to thank my friends from ROCEEH and Germany for their friendship and support: Meike Schulz, Claudia Groth, Ericson Hölzchen, Susanne Krüger, Quy Thi Kim Tran, Julia Heß, Johan Jarl, Almudena Estalrrich, Christine and Hermann Tries, and Geanina Adriana Butiseaca. And also, to my Spanish friends going through their own PhDs at the time: Sonia Campos Soto and Andrea Herrero, thank you for your encouragement.

Above all, I wish to thank my advisor, Angela Bruch, for introducing me to a new country and to the fascinating world of Quaternary palynology, which has awakened in me a deep love for nature, plants and forests.

Finally, I wish to thank all my family, my parents, my aunt, my sisters, my friends and Alejandra, for their everlasting support and encouragement. I could not have done it without you all.

Appendices

Appendix to Chapter 1

Table A.1: Complete pollen counts from the Palominas core.

Depth (m)	Sum with *Pinus*	Sum w/o *Pinus*	*Acer*	*Adonis*	Alismataceae	*Alnus*	*Althaea officinalis*	Apiaceae	Araliaceae	*Arceuthobium*	*Armeria*	*Artemisia*	Asparagales	Asteraceae	*Betula*	Boraginaceae	Brassicaceae	*Buxus*	*C. orientalis/ Ostrya*	*Carpinus betulus*	*Carya*	Caryophyllaceae	*Castanea*	*Celtis*	*Centaurea*	*Centranthus*	Chenopodioideae	*Cistaceae*	*Coriaria*	*Corylus*	*Cyperaceae*	*Daphne*
10.1	30	13																									3					
11.06	46	41																														
12.04	113	78							10					14											1		4					
13.01	1148	249										20		7													32	1				
13.9	596	316										15		44								1		1			49					
14.21	614	311										29		34								1		1	1		72	2		1	11	
14.95	0	0																														
15.9	994	332										1		13								1					22			2	4	
16.54	887	347				2						7		17								1					28	6				
17.8	739	344										10		46								1			2		25				2	
18.24	1102	362										4		51	1							1			11		49	4			7	
19.07	362	223										27		14					5					1			29	3			2	
20.08	358	226				4						33		15										1			48	1		3	4	
20.8	385	318										40	1	21										2	1		43	1		2	6	
21.43	415	378										60		30													45	1		1	6	
21.68	369	346										77		24	2				2		2	1		2	3		37			2	4	
22.47	400	331										46		34					1			2					89	2			3	
23.38	886	318										17	1	43								1		2			82	5			2	
24.22	567	250				1						16		24					1								71	3			5	
25.05	668	318						1			1	74		23			1							3			45				9	
25.6	536	327				1						46		20			1										80	1		1	6	
26.2	419	332										20		29					2			1		2			105	3			3	
27.33	357	278										50		36								1		2	3		68	2				
28.42	432	379				1						28		52	1		1								1		42					
29.58	550	328							2			30		48			1		9		2	1		3	2	1	38	1		2	8	
30.07	482	335										139		33								1		1	1		50	2			2	
30.73	539	328			1						1	12		31				2	1			1		4			78	2		2	4	
30.9	449	338	1						1		1	17		35					2			1		2			55	3		1	4	
31.44	886	330										60		42								1		3	1		61	4			4	
31.74	934	344										39		32	4		1		2			1		1	2		48	4		2	8	
32.91	2427	322										15		12			2								3		17	1		1		
33.98	943	302				1						13	1	30			1								5		36	1		2		
34.83	721	361										12		27			4	4						1	1		39	1			6	
36.23	3	3												1																		
36.8	830	321								1	1	65		57								2					33	1			16	
37.33	1175	333	1									174		53								2			1		45				7	
37.9	654	329										123		35			3					1		1	1		59	6			3	
38.2	966	381						1				100		36			1					1		4			71	3			10	
38.51	494	279						1	1			78		32					1								71	2			6	
39.38	684	367										120		44								2	1	3			76	2			2	
39.69	1284	331	1					3				28	2	15			1		1		1	4					76	6			8	
41.23	558	318										103		35			2					4		1	3		57				9	
42.26	472	360	1						1			36		25					1			2	1	2			44			1	14	
42.55	424	358				2						29		35	2		1		3			1	2	2	1		59				7	
42.84	453	351										46		28					1			1		4			62	2		1	7	
43.82	480	337										39		46								2		1	1		52	1		1	9	
44.11	401	315										63		31	1							3		2			26				9	
44.47	514	337										108		29			3					3		2	1		87				36	
45.04	632	349	2								1	72		42			2							4			47	3		1	3	
45.07	633	365							1			36		30					1			1			1		73	1			3	

45.16	649	351	2					1			41		25	2		1		2			2		2	3		49	9		2	2	
46.19	829	398	2				1	1			54		20			1	2	4	1		2		2			55	2		1	2	
46.54	612	412		1							36		11					2			4			2		39				11	
47.65	564	343						1			42		18	2		1		3			3					61				2	
48.01	491	389						1			37		34			6		2			1		3			39			1	10	
48.38	397	310									50		18	1		1					3		1	1		33	3		1	9	
49.08	366	308									69		32			1		2			2			2		21				14	
49.84	1116	315									42	1	55			2		1						1		22	3		1	16	
50.14	819	330	2			2		1			35	2	41	2		1		3	1				2			39				18	
50.53	1449	312									124		62								2			1		23				12	
51.24	705	298						1	1		45		15			1					2			2		23				12	
51.6	580	332						1			101	1	36			2		1					2			27	1			32	
51.97	1081	351								1	107		49			1								1		38				22	
52.31	936	312									29		60					2			10		3	1	1	42				18	
53.43	769	364	2					1			23	1	39					2			12		1	4	2	40	3		1	14	
54.19	455	373									153		46			6					3		1			42				13	
54.98	512	363									52	1	51								2		2			93				5	
55.32	1148	357						1	3	1	39		40				1				2		1	2		57	6		2	5	
56.1	842	327	1		1	2	1	3		1	26		35	1			3				3			1		67	2		1	4	
56.49	676	305				2		1			21		43					4	1		3		2	1		51	3		2	6	
56.9	697	454	2		1						58		45	2		6		3			1		5	1		52		2	2	10	
57.67	837	337									53		16			1					1		2	2		29	5		2	3	
58.07	881	336						1			27		15		1	2					1		1	1		50	3			4	
58.45	673	323									31		17										2			59	2			3	2
59.21	738	378									39	3	46			3								2		51	3		1	6	
59.59	999	381									19		60		1			2		2	1		1	4		39	6			8	
60.41	653	321						1			60		41	3							4	1	2	1		16	6		3	5	
61.14	795	320				1		1			61		33					3			4		2	3		48	2		3	3	
62.1	1257	360									26	1	48								3		1	6		34	2		1	8	
63.23	620	324						1			44		28	1			1				5		2			71			1	6	
63.62	809	314								1	70	1	14			1					4		1			42				12	
64.01	492	267									86		17								2		2			52			1	12	
64.41	691	308									66		14								2		2			102	1			7	
65.9	713	303									58		27			1					1					42				6	
66.24	527	303									62		12	1							1					96	1			15	
66.97	513	367									125		23			1					1		1	1		34			1	6	
67.04	407	351	2								120		11			5							1			32				2	
68.61	598	319						1			60		18	1		2					1		1			49	1		1	3	
69.14	821	316				1					40		47	2							1		1			59				8	
69.81	1413	340								1	53		20	3							1		2	1		50	3			11	
70.21	1065	332				2					59		16			2		1			1		2			38	3			2	
70.96	2464	370									18		15										1			60	4			6	
71.72	2846	341									8	1	14					2	2					4		24				5	
72.11	1378	311									6		22											1		16	2			1	
72.43	1173	358				1						1	58					3				2	1	10		21	1		1	1	
72.84	703	379									46	1	31					5						1		70	1			11	
73.07	654	339									96		23			1		1					4			29	2			1	
73.46	740	343									79	1	23			1		2			1					23	2			17	
74.65	694	316									59		29			1		4			1		4	2		15	4		4	7	
75.45	489	322	1								121		27	1		1										34	1			10	
76.19	516	340	1				1	2			87		27										3	1		47				5	1
76.58	492	327									97		18			2					2		7			55			1	12	
77.67	642	302	2	1	2						63		42					1			2		1			29				10	
78.71	458	340									46		37								2		5			56	1			10	
79.08	592	415					1				105	1	34								3		2			55	2			6	
81.32	663	333				2					51		21								1	2	4	1		66	4		2	8	
81.7	750	325									53	1	32								1		2			72	2			2	
82.09	1510	342	2								34		38			2	2				1		4	3		37	1		3	2	
82.47	773	370									84		22	1		2	2					1		2		43	2				
82.82	1255	355									40		17								1		2	1		22				3	
83.17	1626	338									52		17			2		1			1	1	1	1		13	1		1	5	

83.54	795	308	2						1			44	1	14					2					1	3		27	1			3
83.95	1412	341			1	1			1			23		31		1	1					1	1				17	2			1
84.67	749	287										45	1	17								1		1			25			1	2
85.01	1048	348										53		25					2				3	3			15	1			1
85.35	452	340		1					2			92	1	28					2			1		1			25	1			
86.11	514	310										27		29			1		1		1	1	1				31	1			
86.88	507	316										60		39			4						4				11			2	1
87.6	482	326	1					1				83		19										1			15	2			1
88.99	408	304	2									46		35										3			63	1			48
89.15	401	322							1			162		21			1								2		39	2			3
89.53	552	330	2						1			36	1	30			1		3			2		4	1		32	7			8
89.9	5	5																				2									
90.74	450	349										122		21					1					2	1		39	3		1	17
91.09	425	361							2			174		19			3					1		1			47	2			8
92.24	693	316				2						45		36	2							2					32	3		2	1
92.61	569	329									2	36		40					1			1		2			41	2		1	3
93.01	613	329										91		32								1			1		44	3			
93.73	2085	312										39		12								1		1	2		29				4
94.44	1027	309							1			61		15			1						1	3	1		10	2			3
95.14	1248	328	2						1			37		24			1		3						1		11				3
95.51	2281	476	2			1			2		1	16		26	2		1		2			1			4		9	1			1
95.94	2242	339					1					44		23			1					1					15	1			8
96.72	13732	328										10		13					2		1				1		15			1	
97.7	858	342									2	156	1	36	1				1						1		13				6
98.09	4	4												1																	
98.49	640	337									1	170		49								2		3	1		15	1			7
98.85	702	330									1	132		45			5					4			2		23				14
99.25	699	370										149		41			1					2					29				22
99.63	762	335	1									121		18			1					1		1			40	1			26
100.24	754	319	2							2	1	105		27			1					2			2		36	1		2	15
101.41	731	328								1		102		21								1		1			46	2			3
101.79	707	347										93		35	1				3			3					45	3			1
103.46	1484	318				2					1	23		31					1			3		5	1		38	6	2	2	9
104.2	1222	308										40		26			1	2				1			1		45	8			1
105	2321	345							1		1	60		30				2				2		2	2		21	1			6
105.35	2095	306										38	1	26								1		2	3		15	1			7
105.77	1780	305				2						52		17									1				22				4
107.08	995	302										22		58										2	1		14				1
107.86	1021	353	1									25		41				1						1	1		14				1
108.66	1490	338										62		63								1		2	2		20	4			3
109.36	1037	365				2						38		74	2				4			1		3	3		31	5			2
109.6	1130	325							2		1	21		55								1			1		23	3			7
110.01	4004	264							1		2	14	3	18					2	2		1			9		8	5		2	2
111.11	371	341									1	140		32			3		1						1		21				13
111.44	355	318							1			180		19			1					1			2		24	1			8
112.35	502	365	2									83		30					5			2		2	2		10	1			5
112.91	561	333				2						37		48								2			1		23	4		3	9
113.31	601	316						1	1			26		29								1		1			22	5			
114.07	470	361							2			120		62					1		1			4	1	1	31				3
114.42	469	308										30		41					2			3					15	2			8
115.4	742	327									1	41		54					1			3		3			21	3			6
115.81	663	336							1			33	1	42			1		2			1	2	1	1		48	6		2	1
116.23	663	313										17		25								5	2	1			17	3		2	1
117.36	726	320							2			90		19	1				4			4		2	1		13	1		2	3
118.17	627	353				1						54		18	1				2					1	1		14	1	1	1	3
118.98	1708	313	3								1	21		22			1		3						2		6	2			8
119.83	587	339										139		29													15				13
120.52	1203	339										80		37	1				1	1				1	1		26	2		2	
121.33	687	337										58		28	1									2	1		29			1	17
121.73	754	319										41		37					1						1		13				5
122.14	772	318										50	2	45											1		27	2		1	7

122.53	363	309		1			1			189		27						1		1		1	37	2		1	
122.93	906	351								80		44	2	1				1			2		16			5	
123.32	788	312								50		37						3			2		33	3		2	
124.13	466	339								142		38			1	1		5		6	1		33	4		2	
124.48	565	352						1		106		50	1		4			3	1	2	1		23	2		1	
124.88	601	337								43		20						2		3	2		37	1		4	
126.48	641	360						2	1	48		35						2		1			31			6	
127.68	410	327						1		101		32	3	2				1	2		3		32			1	
128.08	526	276							2	62		58						1			3	1	16			1	
129.32	528	350								181		21						1			2		17	1		11	
129.77	667	302					3	1	1	39	1	41						3			1		22	1	1	1	
131.37	1610	326	1			1				23		24		1	2			5	2	3	5		26	3		1	
131.78	651	377						2	2	34		30	3		1			3		2	4		13	1	2	1	
133.78	499	345	2		1			1		79		24	1		2			1		1			20		1	1	
135.51	508	306							1	74		20						1		1	3		36	3			1
137.16	622	369								34		39	2					1		2	1		66	8		1	
138.22	518	316							1	45		34	1					1		2	2		11	1	1	5	
139.23	515	333						1		55		55						1		1	3		29	4		3	
139.75	561	389						1		113		73	4		1			2		1	1		21			2	
140.05	444	322								47		97						2			8	1	20			2	
141.2	784	345							1	32		43					2	1			1		60	3		3	
141.87	595	347							1	73		26			2			1			1		29	1	1	3	1
142.18	807	297								37		25			1						2		17	2	2	1	

Depth (m)	**Dipsacales**	***Drosera***	***Ephedra fragilis***	***Ephedra distachya***	***Epilobium***	**Ericaceae**	***Erodium***	***Eucommia***	***Euphrasia***	**Euphorbiaceae**	**Fabaceae**	***Fagus***	***Filipendula***	***Fraxinus***	***Geranium***	**Hamamelidaceae**	***Helianthemum***	***Hippophae***	***Ilex aquifolium***	**Iridaceae/ Liliaceae**	**Ixieae**	***Juglans***	***Knautia***	**Lamiaceae**	***Lemna***	**Liliaceae**	***Linum***	***Lythrum***	**Malvaceae**	***Myrica***	***Olea***	***Parrotia***
10.1						1																									2	
11.06						1																										
12.04						6																										
13.01				1		31						1					3					1										
13.9						13						1																			1	
14.21				5		6																										
14.95																																
15.9						7																1										
16.54			1	1		8																									1	
17.8						1											1														1	
18.24						17						2																				
19.07			1			5								1																	3	
20.08			1			8																									1	
20.8						1				1														1							2	
21.43																						2				1					1	
21.68				2					3	1							1									1					2	
22.47			1	1		7											1															
23.38				2		19											1						1									
24.22				2		6																2	1								1	
25.05				1		2										1															1	
25.6						2				1												2									1	
26.2				4		2						1					1														1	
27.33				3		2						3										3									2	
28.42						4						2					1					5										
29.58				3		9				3		2															1				3	1
30.07			4	20		3																4							1		5	
30.73	1			1		5				2							4					2	1				1		2		2	
30.9				1		1				3	1			1																		
31.44			1	2		2				2								1				1									1	
31.74			3	1		1				1																						
32.91			1																			5							1			
33.98						2																					1		2		2	
34.83				1		1					2			3			2					8		2	1						8	
36.23																																
36.8				3		19											2	2							3					1	1	
37.33	1			6		8	1																2				1		2			
37.9			2	1		13																										
38.2				1		16				4							1								1					1	2	1
38.51						14		1		1															1							
39.38			1			5	1			3					1																	
39.69						11		1		5												4				1	1					
41.23				26						2				1			1															
42.26						1				1					1		1					4										
42.55				1		5				3	1																				2	
42.84				2		4						2					1														1	
43.82			1	2		5	1			2								4				1									1	
44.11				2		5								2			1					1								1	2	
44.47			3	27						1							2											1				
45.04				3		7						4		1			1														2	
45.07			1			6				2												3								1	2	
45.16			1			5				1		6		2		1															2	1
46.19						3	1	2			1	2		1			1														10	
46.54			1			3						2		1				1		1											7	

47.65						1	1		11		1						1														6	1
48.01						1																									3	
48.38			1	1		1				1		1		2																	2	
49.08			1	4		3		1			1							1													2	
49.84			2			7				2												2	1							1		
50.14				3		6		2		1					1		4															
50.53				23		1																	1						2			
51.24				1			1	1		1												2			1							
51.6				19		1	1																1				1					
51.97				8		2				1				1																		
52.31			1	5		11				4				1			2	1	2							1	1					
53.43				4		15				3								3													2	
54.19			1	15																		1			8							
54.98				4		17		1		5																						
55.32				2		8		1										1				1			3						1	
56.1				1		5				5		1						1				4			1				3		2	
56.49				2		5	1					1															1					2
56.9			1	4		2	2	2		4	1	2		2			1														3	
57.67			1			4	1			2												1							2		1	
58.07				1		1	1			1		1					1														2	
58.45										1								1				2		1					1	1	1	
59.21						4																2					1					
59.59						14		2		1							5	1													1	
60.41			1	1		15					1											1		3			1					
61.14			1	1		22	1		2	2		1																			2	
62.1						16				5										1		4					1		1	1		
63.23				2						1								1				2									2	
63.62				27			1										3															
64.01				5		1				1																						
64.41			1	18			1			1																						
65.9				20		3	2			1	1																1					
66.24				19						1																						
66.97			1	30		1				3																						
67.04			1	25		1											2	1														
68.61				9		6											1					1							1			
69.14				9		16				1				1			1															
69.81			1	1		37				1		3					1	2									1				1	
70.21				3		20						2					1	2									1					
70.96			1	2		14		1		3							2	2				1										
71.72						3						5					1	2						1							2	
72.11						2				2																			1		1	
72.43	1		1			10								1			4					1		1							3	
72.84			1			24						1					1					3					1				5	
73.07			1			20				2		1			1		1			1											4	
73.46				1		14				2	1											1		2	1						2	
74.65				2		4				4														1								1
75.45				11		1																1			1				1			
76.19				11		2				1		1			2			1				2			1							
76.58				18								1																				
77.67				10				1		1																					2	
78.71			1	6		1				1				1								4	1								1	
79.08			5	33		1					2						5														1	
81.32				6		8																									2	
81.7				3		5				1		1					1															
82.09				2		6				1																					2	
82.47			1											2						3											3	
82.82			1			2	1			1																	1				2	
83.17				2		3						2										1					1				3	
83.54				2		4	2			2		2					1										1				3	
83.95						4				2												1							1		4	

84.67						2								2																	1	
85.01				1		1											1	1						1								
85.35			1			7	1				1	1																			3	
86.11			1	1		3	1			2	1											1							1			
86.88						1					1											1		1					1		3	
87.6			2	5		1		1		3				1															1		1	
88.99				7		4																	1									
89.15			1	24		3	1							5								1					2		1		2	
89.53				2		14	2			1		2	1		1		2							1							4	
89.9																																
90.74			2	16		2	2																				1					
91.09				17						1																1			2		2	
92.24				2		14		2		3																					4	
92.61				6		19				5							1	1				1										
93.01			3	2		4																1		2						1	2	
93.73				2		1				1												2										
94.44						2	1				2																				4	
95.14		1				1				1		3		1	2		1														3	1
95.51						2				1								2						1					2		3	
95.94						1					1			1								1		1							2	1
96.72				1		5				1	1											1					1				1	
97.7				25						1													2								2	
98.09																																
98.49			2	23										1									1				1				3	
98.85			3	8						3												3										
99.25				17			1			1																						
99.63			1	22						1															1							
100.24	1		2	15		5	1										1															
101.41				4		10				3												2					1			1		
101.79			1	5		40				2												1										
103.46						71				2		2					1										1				1	1
104.2						26				5												6										
105			3	1		2					1						2					1							2			
105.35			1	3		2				1		2										1					1					
105.77						2																			1							
107.08			1			2				1		2																			1	
107.86			1			2				1	1	3						1						1		1					1	
108.66			1	1		11	1	1				3		1		2													1		2	
109.36						23				3							7														2	
109.6						8				1							1					3										
110.01						4	2			1		1						1														
111.11			2	25										1																	4	
111.44				6											1						1	1							2		3	
112.35			1	3		7	1			1		4	2				1														3	2
112.91			1	4		3				1		3																				
113.31						14				4					1																2	
114.07				2		21	1			3					1							1										
114.42			1	1		11				4	1						1					1								1		
115.4				5		6					1	1																		1	2	
115.81						2	1			1																					2	
116.23				1		8				2							1															
117.36						3				1					2		2															
118.17			2			5																4									1	1
118.98				2		5	2			1	1						1										1					
119.83				10						4												2					1				1	
120.52			1			5	2			1																	1					
121.33						10				5																						
121.73				1		9																					1					
122.14				6		9				2							6														2	
122.53				5		2																									6	

122.93				5		8				2																					1	
123.32				1		17		2		6							2															
124.13				1		9	1			3		2					1															
124.48				3		13				1					1			1											1	1		1
124.88				2		12											4					1										
126.48			1	5		2	1			1							1	1												1	1	
127.68			1												1																	
128.08				5		4	1			1		1																			1	
129.32				29		3											1															
129.77			1		1	6											1					3					1					
131.37	1					3																										
131.78			1			4		2						2			1														2	
133.78						4							1				1															
135.51			3	2		5			1	2		3		1			1															
137.16						15											5										1			1	1	
138.22			1	1		2				1	1	7																			1	
139.23			1	3		4	1	1				1										2							1		3	
139.75			4			2				4	1	1					1					1							1		1	
140.05	1			3		14				1												1				1			1		1	
141.2				2		20						1												1					1		1	
141.87	1		1	1		7				1		8				1						1		1		1					2	
142.18				1		2						6				1	1															

Depth (m)	***Parthenocissus***	***Phlomis***	***Pistacia***	***Plantago***	**Plumbaginaceae**	**Poaceae**	**Polygalaceae**	**Polygonaceae**	***Polygonum***	***Populus***	***Potamogenton***	***Pterocarya***	**Deciduous *Quercus***	**Evergreen *Quercus***	**Ranunculaceae**	***Rhamnus***	**Rosaceae**	**Rubiaceae**	***Rumex***	***Sagittaria***	***Salix***	***Sanguisorba***	***Saxifraga***	***Scabiosa***	***Scrofularia***	***Sideritis***	**Solanaceae**	**Sparganium**	***Tamarix***	***Thalictrum***	***Turgenia***	***Typha***
10.1					1	5		1																								
11.06					3	37																										
12.04					3	42		1						1	3																	
13.01				1	5	86							29									2										6
13.9			1		6	142							14	13	4																1	
14.21			2		2	107							6	10	1																	
14.95																																
15.9				1		169							47	45																		1
16.54					5	169							48	20																		
17.8					8	59							91	62	1																	
18.24					3	61		1					81	49	7							1										
19.07			1		1	50							19	55	1							2										
20.08					1	35							25	37	1				1			1										
20.8				1	3	48							51	68	2				3									1				
21.43				1	3	85							29	100	1				3			1										
21.68				3	5	46							44	54	1							1										1
22.47					6	46							32	54	2													1				
23.38				1	1	68			1				36	17	1																	
24.22					1	50							24	31								1										
25.05				2	2	96							12	15	2																	1
25.6				2	1	62							11	43	1													1				
26.2				4		65							26	40	1							1										2
27.33					3	70							16	8																		
28.42				2	6	91			1				41	83	1																	1
29.58				1	3	65							21	46					1			1										
30.07				2	2	37							5	1	2																	
30.73				2	3	40							50	42							1									1		
30.9				2	2	60							36	65	4													1				
31.44					1	64							17	26																		
31.74				4		64						1	33	50	3				3			1										
32.91				8	2	52							64	68								3										
33.98				1	2	47							60	46																		1
34.83				4		78						3	54	55					1			4						2				3
36.23					2																											
36.8				1	2	50					2		5	17	3						2									2		
37.33						16			1					2																		
37.9				1	2	49							5	4								1										
38.2					2	67							9	9	1																	
38.51					1	33							5	12	1		1					1										
39.38					4	61			2				13	7								1										
39.69			1		4	55							19	41	3	1		1	2													
41.23	2			1	7	37			1				9	4	1		1					1									1	
42.26					6	55			2				36	91	3																	3
42.55				3	1	57							64	49	1				2			1						1				1
42.84						53							48	42	5							1						1				1
43.82				1	1	83							26	41														2				
44.11				1		94							38	19	3																	2
44.47				1		26							1		1																	3
45.04				2		61							27	44								1						3		1		2
45.07						44							32	85	4																	
45.16				1		57							51	58		2			2			1						1				1

46.19				4		58				2			47	96	1							2										
46.54						90							56	85	4				1													8
47.65				4		42							55	48														2				
48.01			2	3	1	103							38	68	1																	4
48.38				1	1	59							44	42		1												1				
49.08				2	2	80							16	32	4																	1
49.84					2	60							19	34	1																	
50.14				2	2	63							31	13	1				1			3						1				
50.53					3	34							3	2												1						
51.24					1	82							14	22	3		1							1								1
51.6				1		66							5	3								1										
51.97				1	1	90							3		1																	
52.31				1	2	57							12	8					1													1
53.43					2	84							20	36								1		1								
54.19					1	57	1					2	1	3	1																	2
54.98					3	79							11	19	1				1			3						3				1
55.32				2	5	51	1						19	41	5				1													2
56.1				3	2	26	1						25	42	9							1										1
56.49				3	1	53							48	24																		1
56.9				1	2	106							21	47	3				2			2						3				1
57.67				1	1	78							21	47	3				1			2						1				
58.07				3		63							47	33	1													4	1		2	2
58.45				1	2	85							28	52								1					1	4				
59.21				3	4	89							59	20	1							9								1		5
59.59		2		4	3	46			1				39	54	3							1						1				
60.41					1	84							11	36	1				1													
61.14				4	1	40							20	18	1							2										
62.1				1	2	43							27	18	4				2			2										4
63.23				3	4	41							21	33	6				1													2
63.62				3	3	104					3		3	4										1								2
64.01				1		51							9	12					1											1		2
64.41				1		33							21	7								2		1								
65.9				3		83							17	16														2				
66.24				1		53							18	4								1										3
66.97	1			1		78							17	25	3													2				
67.04					1	66							24	26	1															1		1
68.61				5	2	75			1			2	29	22																		1
69.14				2	2	27							31	27	2							1										
69.81			2	1	1	79							20	29	1							1										1
70.21			1	3	2	94							17	24								3										2
70.96					2	52							22	42	2	1						1						2				2
71.72					2	50							29	8	1							1										
72.11					3	60							31	54	2																	
72.43				2	1	110			1				49	34	1				1								1					
72.84				4		40							43	43	7																	4
73.07				2	1	90							13	33	2						1	1										
73.46				4	1	81							22	21	4							1										1
74.65	1	1		3	3	71							32	41								1	1									
75.45					4	76		1					6	5	1																	
76.19	1			1	1	99							10	14	1													1				
76.58				2	1	66							11	12																		
77.67				8	2	36							21	25	4													3				
78.71				3	2	92			1				26	20	1				1													
79.08					1	107			1				11	22																		1
81.32			2	7	1	50							44	30																		
81.7					1	32							8	56	3				1			1								1		
82.09	3		1	3		56							46	52														2		1		
82.47			2	4		40						1	38	72	9							2								1		5
82.82		1		2		59							18	78	1													3				
83.17			3	1		59							24	65	3									1				3				

83.54					1	27				45	37										2			1
83.95				1	1	44				25	48	5									1			
84.67				2	2	43				51	31													1
85.01				2	4	49				40	87			1										
85.35					3	34				69	48	1			1									3
86.11				1	1	42				38	69	4			1						1			
86.88						44				34	71	4				1								
87.6				1		75				27	58	4			3							1		
88.99				1		67				5	4						3							9
89.15						39				2	2		1											
89.53				1		47				44	30						2	2						
89.9					3																			
90.74					5	93	1	2		1	3												2	2
91.09				1	2	71				3														
92.24				2		70			2	24	36	2			1						1			
92.61					1	60			1	17	35	3		1						1	2			
93.01				2	3	38				41	28	1			2		2					1		2
93.73				1	2	45		1		26	40		1								1			
94.44				6		47				35	64													
95.14					3	44	1			33	57	2					1							2
95.51				3	3	34		1		32	30										1			2
95.94				4	1	57				26	57	3					3							1
96.72				3	7	17				5	2	1												
97.7					6	16				19	11	2			1									
98.09					3																			
98.49					4	26	1			17	6													
98.85				4	1	25	1			10	12										1			7
99.25				1	1	66				3	1	1		1							11			1
99.63				1	1	61				8	7	2												2
100.24	1			3	1	39				13	9	1		1							3			
101.41				1	4	75		1		11	23													
101.79				1	3	43				12	29	1												
103.46				13		59			2															
104.2				5		73				24	15	1		1								1		
105				2	1	58				34	36	7					1					1		7
105.35				4	1	73				17	34	3										1		
105.77					2	59				16	66	1									1			8
107.08				2	2	120				6	46	4									5			
107.86				2		174				21	27										2			
108.66				2	1	52				34	30	1									3			2
109.36				4	1	55				34	40	1					1							
109.6				3		120	1			26	21	4					1							1
110.01			1			120		1		15	10													2
111.11						57				18	2								2			2	1	
111.44	1					40				6	3	2		1										
112.35				1		69				51	42	1	3				1		2					1
112.91				1	4	64		1		55	35	1			1		2		2					1
113.31				4	4	40		2		54	47	4			1						1			
114.07				3		55				16	22													1
114.42						72				63	21	5												
115.4				1		43	2			61	39	1										1		1
115.81				2		40				38	73	1			1						6			1
116.23						53				47	67						1				4		1	
117.36			1			53		1		28	58	2					1							
118.17		2		3		103				23	69	9									1			1
118.98				1		37				31	18										1			1
119.83				1	6	51				7	17	2												3
120.52					7	33				26	50	1					2				1			
121.33				1	1	62			2	20	33	3							1		7			
121.73				1	3	65		1		27	43	1					1							

122.14			2	3	45							39	20				1		1					
122.53				1	21							2	2				1		1				1	
122.93			2	1	56							21	42	6										1
123.32			2		41		1					18	35	1										
124.13			4	1	57							5	6		1				1	1	1	1		
124.48				3	62							21	19	5		1								
124.88			3	4	102	1						30	22					3	2					
126.48			3	2	117							29	36	1										
127.68			3	2	71		1					28	27									2		
128.08			2	3	64			1				17	8									3		
129.32				1	40		1					8	13	1										
129.77			1	1	69		1					46	24	2					5	2				2
131.37			14	3	76				2			56	29	2					4			1		
131.78		2	3	2	126		3					28	62	1					2					
133.78	1		1		73							36	65	3										2
135.51			2	4	31						1	41	40											
137.16			3	4	36		1					23	43											
138.22			3	1	80							27	59				2					1		1
139.23			2	4	65			2				46	25			1								
139.75			4	3	45			2				18	35									1		
140.05					55			3				18	13									4		1
141.2			6	1	66			1		1		23	35	1					1					1
141.87	1	1	4	1	40						2	17	75	3										
142.18		2	6		50			2				30	62					1						

Depth (m)	***Ulmus***	***Valeriana***	**Verbenaceae**	***Viscum albus***	***Zelkova***	**Pollen indet**	***Abies***	***Cathaya***	***Cedrus***	**Cupressaceae**	***Picea***	***Pinus***	***Tsuga***
10.1												17	
11.06												5	
12.04						2						35	
13.01	2					1	19				1	899	
13.9	1						2			3	3	280	1
14.21		1				3	8			4	2	303	2
14.95													
15.9							15					662	2
16.54							25				4	540	2
17.8		1					23		1		6	395	1
18.24						3	8					740	1
19.07							1					139	
20.08						3				3		132	
20.8						1	13			2	3	67	
21.43	2					1	2			3		37	
21.68	2				2		5			13	3	23	
22.47										3		69	
23.38	1					2	7			1	6	568	
24.22						1	3			5	1	317	
25.05					1	1	5	3	1	10	5	350	
25.6	2					2	9	2		25	3	209	
26.2	2						8	1		4	4	87	
27.33						1	4			1		79	
28.42							7			7	1	53	
29.58	2						3			13	1	222	
30.07	2					1	1			15	1	147	
30.73	2				2		5	6		4	6	211	2
30.9	1						6			21	9	111	
31.44	1						14		1	6	13	556	1
31.74	2					1	11			17	2	590	2
32.91	8					1	48		2		7	2105	1
33.98	1						29				17	641	1
34.83	10					4	9				6	360	1
36.23													
36.8	1					2	1		1	13	10	509	2
37.33	1									3	5	842	
37.9										4	15	325	
38.2	2					1			3	2	29	585	2
38.51						1	1			13	1	215	
39.38							5			3	9	317	
39.69	5					1	5			2	21	953	
41.23		1					4			1	2	240	1
42.26	1					2	2			19		112	
42.55	4				3	4	3			5	2	66	
42.84	2						6			28	1	102	
43.82					1	2	6			5		143	
44.11						1				8		86	
44.47						1	1					177	
45.04	1				1	2	1			6	1	283	1
45.07	4	1					16			2	14	268	
45.16	2	1				1	5		1	3	2	298	
46.19					1		7			3	5	431	
46.54	2					2	25		3	10	4	200	
47.65	1						21			4	9	221	
48.01	1				1	1	14			13	1	102	

48.38	1					2	2			23	1	87	
49.08	1						2			12		58	
49.84							15		1	14	9	801	
50.14	3	1				2	2	1		26	10	489	
50.53								1	1	2	12	1137	
51.24	1				1					61		407	
51.6						1		1		17	10	248	
51.97							4	1		13	5	730	
52.31							2			29	4	624	
53.43	2						2		3	11	28	405	2
54.19	1						4		1	4	4	82	
54.98							3			5		149	
55.32	1						21		5	16	7	791	2
56.1	3						14			6	19	515	
56.49					1		8	1		1	12	371	
56.9	2				1	4	3		1	41		243	
57.67	3						16			10	25	500	
58.07	2	1			2		23			8	26	545	2
58.45							11			10	4	350	
59.21	2						15		1	4	2	360	
59.59	1					1	8			1	47	618	2
60.41	2						8			3	4	332	2
61.14	1						6			2	29	475	
62.1	1					1	12		1	12	69	897	
63.23						1	5			20	18	296	
63.62						2	2		1	3	6	495	
64.01	1					1	2			7		225	
64.41					1		9	1	2		15	383	
65.9	1						9		2		6	410	
66.24							11			3	1	224	
66.97	1						2		1	7	1	146	
67.04	1						1			25	1	56	
68.61	1					2	2	1		11	9	279	
69.14	2					4	7			21	3	505	
69.81					1	2	2			2	3	1073	2
70.21	3						4		3		19	733	2
70.96	2					1	74		3		32	2094	
71.72							6				169	2505	
72.11	3						10		1	1	86	1067	5
72.43	2						20			3	9	815	2
72.84	1				1	1				1	32	324	
73.07	1					1	1			3	2	315	
73.46	1					4	5		3	7	14	397	
74.65	2						1			3	13	378	
75.45	1					1	2		3	5	5	167	1
76.19							1		1	6	7	176	
76.58					1		1			6	12	165	2
77.67	4				2		20	2		2	5	340	
78.71	5	1			3	1	5			4	2	118	
79.08							3	1		3	8	177	1
81.32	1					1	2	1		14	2	330	
81.7	1						23			6	16	425	
82.09					2	2	5			3	23	1168	2
82.47	3						9			2	14	403	
82.82						1	15			5	76	900	1
83.17							23		4	3	40	1288	
83.54							13				64	487	2
83.95					1	3	7		1	4	100	1071	3
84.67	2						10			5	41	462	
85.01							33			2	21	700	

85.35							8			1	4	112	
86.11	4					1	9			2	33	204	
86.88						1	3			23	6	191	
87.6	1				1	2	2		1	3	9	156	
88.99	3						1			1		104	
89.15						1	4			1		79	
89.53	2						1		1	11	28	222	2
89.9													
90.74							2		6		1	101	
91.09											3	64	
92.24	2				2		12			5	7	377	
92.61	4				4	2	5			6	25	240	
93.01	1						11			8	1	284	
93.73					2		32			4	60	1773	3
94.44	2	1				1	6			3	33	718	1
95.14	3					1	27	1		7	44	920	2
95.51	3					1	17		2	2	259	1805	2
95.94	5					1	40		1	7	29	1903	
96.72	1						12			2	224	13404	
97.7							2			13	24	516	
98.09													
98.49											1	303	1
98.85							6		6	8	6	372	
99.25	3					2	1		2	2	9	329	
99.63	2					2	4		1	4	3	427	
100.24							2			18	7	435	
101.41	1								1	3	9	403	
101.79	2				1		3			6	13	360	
103.46	2						6	1	2	4	23	1166	2
104.2	3					1	13		1	2	5	914	1
105							37		1	10	10	1976	
105.35				1			21	2		8	34	1789	1
105.77	1						39		2	6	3	1475	
107.08						1	8			1	1	693	1
107.86	1				2	1	10			10	3	668	
108.66	1						16			1	13	1152	
109.36							10		1		18	672	
109.6	4				1		3			5	7	805	
110.01	2						15				18	3740	1
111.11	4					1	1			8		30	
111.44						2	2			6	3	37	
112.35					2	2	10	1		2	9	137	
112.91							5			7	9	228	
113.31	1				3		3			6	38	285	
114.07							4				5	109	
114.42	2				5	1	6			10	1	161	
115.4	4					1	7		1	14	2	415	
115.81					2		4			15	5	327	
116.23						1	14			10	29	350	
117.36						1	12		2	8	1	406	1
118.17	4				1		7		3	2	13	274	1
118.98					4	1	28	1		1	102	1395	2
119.83	3						8		2	11	12	248	1
120.52					2		13	4		3	35	864	
121.33	2						6		1	26	19	350	
121.73	1						7	6		6	48	435	
122.14	1	1				3	6			30	4	454	
122.53								1			3	54	
122.93							10		4	22	19	555	
123.32	2					1	10			7	34	476	2

124.13					1		5				5	127
124.48	2					2	5		1	4	10	213
124.88	1						6		1	4	27	264
126.48	2				1		8			10	11	281
127.68	1				4	2	3		1	1	1	83
128.08	3						10			3	5	250
129.32							3		3	4	9	178
129.77	1				2		12			5		365
131.37	2				2		17				17	1284
131.78	8				2		6			1	20	274
133.78	2				3		4	1	2	9	2	154
135.51		1			2		1			2	23	202
137.16							14			2	66	253
138.22							11			5	8	202
139.23						1	9		1	4	4	182
139.75	2						14			5	25	172
140.05	2					3	2				21	122
141.2					1		7	1			28	439
141.87			1		1	3	10			10	13	248
142.18	2					1	3		2	8	30	510

Table A1.2: Non-pollen palynomorph counts from the Palominas core.

Depth (m)	***Lycopodium***	**Osmundaceae**	***Polypodium***	***Asplenium***	***Anthoreceros***	***Anagramma***	***Dryopteris***	***Riccia***	***Selaginella***	***Sphagnum***	**Other Spores**	**Fungi**	**Zygnemataceae**	***Pseudoschizaea***	**Other Algae**	***Botryococcus***	**"*Sigmopollis*"**
10.1												3			4	1	
11'.06												15			11	4	
12.04	1											25			6	11	
13.01												1			13	3	10
13.9												27			21	27	15
14.21												37			2	40	20
14.95																	
15.9			1													2	16
16.54			1		1											2	30
17.8	1									1		3			1	1	24
18.24												4			9	4	17
19.07		1				1						7			49		147
20.08												6			6		103
20.8											1						25
21.43															60		17
21.68															2	1	19
22.47												7				1	8
23.38												1			1	3	7
24.22												10					49
25.05												10	1		8		30
25.6											1	32	2	1	6		89
26.2												2			2		42
27.33												5		2	3		80
28.42												1			3	1	33
29.58								1				1			7	5	4
30.07												6	1		3	6	45
30.73											2	4			5	1	35
30.9											3	3	1		1	1	5
31.44												8					6
31.74											3	3			19	1	24
32.91													1	1	2	1	4
33.98												2				1	8
34.83											4	3				5	17
36.23																	
36.8												2	1		1	16	8
37.33	1														26	244	177
37.9												5				2	6
38.2											1	12		1	17	3	2
38.51											2	7			4	4	7
39.38								1				8				544	3
39.69											1	19			3	9	30
41.23												3				5	3
42.26											4	247	2		2		5
42.55								1				5			1	1	8
42.84								1				5			4	3	10
43.82												3	1		4	10	5
44.11												2			1	68	7
44.47												102	3		28	2	43
45.04												3			43	186	
45.07											3	4		3	3	2	75
45.16												4			2	2	217
46.19											1	4			1		95
46.54												3	1		1		36
47.65											2	9					87
48.01												5	2	1	3		122
48.38											2	7	3		3	2	64
49.08											1	4			2	6	
49.84											1	7	1		2	4	7
50.14											2	7			6	40	
50.53								1			1	1			32	223	65
51.24											1	9	1		2	362	14
51.6											1	4	3		6	80	9
51.97											1	5			5	938	74
52.31												40	1		5	1562	33
53.43															1	5	8
54.19											2	9				131	27

54.98									1	6			23	638	15
55.32									1	15	4	1	9	1	5
56.1										9		1	2	1	14
56.49										1					1
56.9										3			1	1	55
57.67									3	6				92	1
58.07				1		1				4			1		12
58.45										6					583
59.21									2	3				3	60
59.59										6	3		3	3	8
60.41									3	6					14
61.14										9			1	2	
62.1									2	5	1		1	8	2
63.23									3	15	2	1	7		9
63.62										8	4		5		9
64.01									1	12			4	3	26
64.41										9			1	6	54
65.9									1	3			19	1	13
66.24										9	9		11	1	196
66.97										3				1	9
67.04															5
68.61										3			1	1	34
69.14										1					36
69.81										2	1		3	11	5
70.21										1				2	
70.96									3	10	2		3	6	25
71.72									1	4			3	20	3
72.11									2	7					7
72.43										5	1		2		9
72.84										1			1		2
73.07										4				1	20
73.46									2	1	2		2	2	6
74.65									1	4			5	3	7
75.45										5			1	3	10
76.19										4				2	8
76.58										7			6		29
77.67										25	15		29	1	23
78.71										15			38	1	16
79.08										10	1	2	4		4
81.32										8	1		1		1116
81.7										5	3	1	4	1	161
82.09		1								1					
82.47										3				4	328
82.82									1	1				1	25
83.17									1	3					190
83.54										2					
83.95									4	3				1	56
84.67					1				1	3					130
85.01									1	2			3		40
85.35										4					12
86.11										6			1	1	6
86.88										8		1	2		2
87.6										5			1	2	
88.99										49	2		34	13	39
89.15									2	5			1	46	3
89.53						1				12			2	2	4
89.9															
90.74							1		2	11	4		5	375	
91.09										5	1		2	3	3
92.24										1				12	
92.61										15				666	5
93.01									1	7			2	4	10
93.73										1			3		30
94.44						1			2		1		1	3	20
95.14						1			2	3	1		16		35
95.51		3							3	1				2	8
95.94									2	10			4	3	212
96.72										1					6
97.7									1	4	1		2	2	14
98.09															
98.49	1									9	1		4	2	6
98.85										16	2		5	2	26
99.25						2				6	4		5	3	3
99.63									4	4	2		3	1	7
100.24										5	2		2	5	20
101.41						1				3					1

101.79			2				3	
103.46		2	7			2	6	3
104.2			2				2	3
105			5	1		2	2	98
105.35		2	4					
105.77			1	1		1	4	32
107.08		1	1				15	100
107.86		3	3					58
108.66		2	2			3	71	15
109.36		1	1				6	2
109.6		1	5	4		5	1	
110.01		3	1	1	1	2	5	
111.11	1		3	1		2	1	30
111.44		1	8				1	4
112.35	1		3	1		1	2	
112.91	2	2	17	1		5	9	5
113.31	1		12	5		7	22	35
114.07			9	2		5	120	8
114.42			15			1	322	52
115.4			20			8	1	15
115.81			12				2	3
116.23		1	8			1	7	35
117.36		2					1	54
118.17		1				2	16	27
118.98		3	1			6	8	4
119.83		2	2			1	1116	17
120.52			6			4	617	70
121.33		3	19	1		6	8167	60
121.73			10			1	268	77
122.14		3	23	6		6	10933	8
122.53	2		11			1	24	1
122.93			23	2		4	115	35
123.32		1	10				3570	13
124.13			2	1		1	78	17
124.48		1	13			1	865	357
124.88			14			11	4752	365
126.48			5	3		5		143
127.68			5			2	47	140
128.08		1					145	30
129.32		1	10	1		2	20	20
129.77		1	2				4	7
131.37			3				2	3
131.78		1	2	1		1	9	14
133.78		1	2					660
135.51			6				9	45
137.16			8				12	60
138.22		1	4					41
139.23		1	7	2		3	12	44
139.75		2	5				24	20
140.05			6			2	11	2
141.2		2	3				3	49
141.87		1	18	2		3	5	29
142.18		1	5	2		3		47

Appendix to Chapter 2

Table A2.1: Supplementary data

Taxa	**MAT min**	**MAT max**	**MTCold min**	**MTCold max**	**MTWarm min**	**MTWarm max**	**MAP min**	**MAP max**	**MPwet min**	**MPwet max**	**MPdry min**	**MPdry max**	**MPwarm min**	**MPwarm max**
Abies sp.	-6.7	27.4	-32.4	25.6	7.1	29.5	201	3000	33	700	0	135	0	700
Acer campestre	3.9	17.6	-12	10.2	14.7	26.4	512	1475	64	170	1	85	6	125
Acer sempervirens	5.1	18.6	-15.6	12.3	22.8	26.8	115	906	19	207	0	4	0	11
Acer monspessulanum	9.6	20.5	0.2	13.6	18.4	27.5	399	1333	77	191	0	85	0	100
Acer opalus	9.7	18.5	0.4	12.5	18.2	25.6	470	1742	66	214	1	85	3	185
Acer pseudoplatanus	7.4	16.4	-4.4	9.4	17.5	27	550	1741	78	262	8	47	8	93
Acer sp.	-1.1	24	-25.8	20.6	9.5	29.3	115	10798	19	2446	0	135	0	1100
Aesculus hippocastanum	4.2	16.9	-12.2	9.2	17.8	27	519	1333	71	170	9	85	9	86
Alnus sp.	-13.3	27.4	-40.9	25.6	4.9	38.6	160	2730	25	353	0	135	0	533
Amaranthaceae	-1.1	27.7	-25.8	27	14.4	30.9	279	3151	60	389	0	165	0	221
Anthocerotales	4.8	27.7	-6.1	27	15.1	28.1	252	3151	44	389	3	165	3	221
Aralia sp.	-5.5	27.7	-24.4	27	13.5	28.1	373	10798	36	2446	3	165	5	1100
Araliaceae	-5.5	27.7	-24.4	27	13.5	28.1	373	10798	36	2446	3	165	5	1100
Arceuthobium sp.	-5.5	27.7	-27.8	27	15.4	28.8	250	3151	36	389	0	165	0	221
Armeria sp.	-8.9	18.8	-26.5	13.1	7.9	27.7	264	1958	55	262	0	83	2	141
Berberis sp.	-4.9	18	-32.4	10	15	27.1	304	2336	45	454	0	75	1	220
Betula sp.	-15	25.8	-41	21.1	1.3	28.7	110	10798	23	2446	0	135	2	1100
Boraginaceae	3.4	27.7	-12.9	27	9.2	35.6	170	3151	51	389	2	165	2	221
Buxus sp.	9.7	25.3	-1.2	20	17.3	29.4	399	2540	80	566	0	56	0	252
Calluna/Vaccinium	-12.4	20.8	-27.9	13.3	3.9	31.6	110	10798	23	2446	1	83	2	1100
Caprifoliaceae	-4.9	28.5	-32	27	16.3	33.4	224	3151	43	450	0	165	0	221
Carpinus betulus	5.3	17.6	-7.5	9.7	17.4	26.4	471	1958	56	236	1	85	6	219
Carpinus orientalis	7.7	18.3	-5.3	10.9	18.6	27.6	402	1548	71	191	3	82	3	122
Carpinus sp.	0	25.8	-22.7	21.1	16.8	29.5	164	10798	20	2446	0	130	2	1100
Carya sp.	4.4	26.6	-11.5	22.2	19.3	30.6	373	1724	68	434	8	93	45	258
Castanea sp.	7.6	24.2	-8.2	18	14.5	29.4	473	2336	70	454	2	93	1	304
Cedrus sp.	11.6	21.4	-0.3	13.9	19.4	31.8	164	1577	43	434	0	41	0	175
Celtis sp.	2.5	25.8	-17.7	23	18.7	28.8	116	2730	25	597	0	88	2	533
Centaurea sp.	-0.3	27.7	-13.2	27	14.7	28.1	252	3151	44	389	3	165	3	221
Chamaerops sp.	16.4	21.7	9	13.8	22.5	28.3	24	854	8	122	0	29	0	29
Chenopodiaceae	-11	27.7	-29.5	23.6	12	36.1	193	1958	46	358	0	83	0	224
Cistaceae	-7.2	26.6	-27.5	26.1	12	28.3	24	3285	8	569	0	47	0	177
Cistus sp.	11.6	21.4	3.5	13.9	18.9	29.7	160	1352	20	259	2	44	2	54
Coriaria sp.	8.8	27	-7.3	26.3	16.7	29.4	396	1930	108	358	0	103	64	224
Corylus sp.	-4.9	24	-32.4	16.7	12.9	29.4	305	1958	45	343	0	83	3	239
Cupressaceae	-15.6	26.5	-48.9	26.1	11.2	32.9	184	4486	22	409	0	326	0	378
Dipsacaceae	-1.7	24.6	-25.4	23.6	16.2	29.4	24	1828	8	343	0	85	0	239
Dryopteris sp.	3.1	27.7	-9.5	27	17.8	29.5	777	3151	92	322	29	165	92	312
Elaeagnus sp.	-0.4	27.7	-24.2	27	18.2	28.5	84	3151	28	389	2	165	13	221
Engelhardtia sp.	13.8	27	3.1	25	20.6	33.6	740	10798	150	2446	5	152	79	1100
Ephedra sp.	3.1	28.8	-12	25	16.4	32.9	33	1096	5	220	0	45	2	214
Epilobium sp.	-6.7	24.2	-24.4	18.3	13.8	29.8	227	1958	26	236	0	83	0	141
Erodium sp.	0.1	19.2	-18.3	16.7	15	29.7	160	1958	20	236	2	83	2	141
Eucommia ulmoides	10.6	19.4	-7.3	9.6	20.2	29.3	396	1967	108	370	3	64	108	304
Euphorbiaceae	-0.3	27.7	-17.7	27	14.7	28.3	24	10798	8	2446	0	165	0	1100
Fabaceae	-7.7	27.7	-22.7	25.9	10.5	31.2	224	3905	46	610	0	196	1	221
Fagus sp.	4.4	23.1	-18.6	17	17.3	31.7	376	2648	46	448	3	94	5	431
Filipendula sp.	-3.8	18	-25.6	10.1	9.8	23.8	213	1958	45	236	1	83	1	141
Fraxinus sp.	0	24	-25.8	16.7	14.9	33.9	148	10798	28	2446	2	95	0	1100
Geranium sp.	-7.7	18.5	-22.7	13.8	9.8	23.1	224	1958	46	236	0	83	1	141
Hamamelidaceae	0.2	27.7	-16.6	27	16.3	29.5	529	3151	74	610	0	165	6	221
Hedera helix	7.6	18.3	-4.2	12.3	13.1	25.6	482	1958	77	236	0	83	1	141

Hedera sp.	6.2	20.5	-5.6	13.6	13.1	28.3	453	10798	77	2466	0	83	1	1100
Helianthemum sp.	3.4	24.8	-12.9	19	18.9	33.1	37	1944	8	342	0	43	0	244
Hippophae sp.	1.6	17.4	-11.1	8.3	13.4	27	552	1151	64	149	5	57	20	89
Ilex aquifolium	7.2	18.2	-0.4	12.2	14.1	27.6	563	1451	67	178	2	72	4	116
Ilex sp.	-0.4	27.7	-12.9	27	10.4	33.6	641	10798	98	2446	2	165	4	1100
Juglans sp.	0	27.5	-22.7	25	9.5	31.2	210	2617	28	582	1	114	2	189
Knautia sp.	0.1	18.5	-18.3	12.5	14.2	28	470	1958	66	236	1	83	3	141
Laurus nobilis	12.5	19.2	5.6	11.7	19.3	29.7	160	1352	20	259	0	59	0	84
Ligustrum sp.	0	27.7	-22.7	27	14.8	29.3	422	3151	58	389	7	165	9	221
Linum sp.	4.6	20.5	-7.9	17.8	14.2	28.4	233	1167	53	151	0	62	0	79
Liquidambar sp.	11.5	25.5	-1	23.8	23	29.3	578	1823	109	448	2	93	5	431
Lonicera sp.	-10.7	26.6	-29.5	25.6	12	28.3	206	10798	34	2446	1	91	2	1100
Lycopodium clavatum	-11.9	27.7	-27.8	27	4.9	28.1	184	3151	30	389	5	165	10	221
Lygeum sp.	13.9	19.9	6.1	12.3	19.3	28.8	241	1198	32	155	0	59	1	84
Lythraceae	9.1	28.5	-2.7	27	19.3	35.3	609	3151	79	450	8	165	20	221
Malvaceae	-3.2	27.7	-26	27	16.1	30.9	213	3151	60	389	2	165	3	221
Mercurialis sp.	6.1	25.8	-9.9	21.1	13	28.7	187	1217	40	270	0	67	0	169
Myrica sp.	-8.9	28.1	-29	27	8.9	33.9	233	3151	34	508	0	165	0	368
Myrtus sp.	11.3	27.7	0.1	27	18.8	28.1	520	3151	68	389	2	165	2	221
Nuphar sp.	-12	24.3	-38.8	19.2	9.8	28.2	115	1958	19	281	4	83	11	177
Nymphaea sp.	-3.4	26.9	-25.8	24.8	12.8	33.6	287	2399	56	467	0	108	47	269
Nyssa sp.	4.4	23.9	-10.4	15	15	29.4	305	2645	81	343	0	122	72	246
Olea sp.	10	27.5	-7.3	26	19.9	29.7	160	3293	20	985	0	71	0	304
Oleaceae	-1.1	27.7	-25.8	27	19.6	33.1	37	3293	8	985	0	165	0	320
Osmunda sp.	0.2	27.4	-16.6	25.6	13.9	30.6	206	4150	34	914	0	89	2	228
Osmundaceae	-11.9	27.7	-27.8	27	4.9	30.6	184	4150	30	914	0	165	2	228
Parrotia persica	11.6	15.8	-4	1.7	25.1	29.5	235	340	48	56	0	9	0	41
Parrotiopsis jacquemontiana	5.6	17.4	-7.2	5	16.7	31.4	87	3037	15	798	0	8	0	798
Parthenocissus sp.	2.5	23.9	-17.7	19.4	13.9	28.9	373	1551	76	241	3	89	26	217
Phillyrea sp.	9.3	20.5	1	17.8	17.9	29.7	160	1356	20	170	2	71	2	92
Picea sp.	-8.9	21.7	-31.2	15.6	7.3	31.6	142	6000	36	700	2	400	2	400
Pinaceae	-14.5	27.4	-41.4	25.6	7.1	32.9	122	2648	28	434	0	94	0	344
Pinus haploxylon	-9.2	25.5	-36.8	21.4	7.1	32.9	180	1741	28	293	0	94	0	304
Pinus sp.	-9.2	25.5	-36.8	21.4	7.1	32.9	180	10798	28	2446	0	94	0	1100
Pistacia sp.	5.9	27	-9.4	25.7	19.3	28.6	187	3370	40	479	0	158	0	178
Platanus sp.	6.6	27.4	-10.9	25.6	13.7	29.5	399	2540	71	566	0	83	0	196
Polygonum persicaria	-2.2	19.2	-22	9.1	14.7	29.7	160	1958	20	262	2	83	2	141
Polygonum sp.	-0.6	21.7	-12.8	14.8	15.6	28.2	453	10798	63	2446	1	135	1	1100
Polypodium sp.	-4.9	27.7	-32.4	27	18.2	28.5	224	3151	43	454	0	165	0	269
Polypodium vulgare	-4.9	18.8	-32.4	12.5	15.4	27.9	224	1551	43	205	0	89	0	165
Populus alba	2.5	18.5	-14.6	12.5	17.9	26.4	419	1741	57	254	1	109	3	80
Populus sp.	-16	21.3	-49	13.6	9.8	28.9	25	2559	8	358	0	93	0	224
Populus tremula	-16	19	-49	12.2	9.8	28.3	155	1958	33	236	2	83	2	141
Pteris sp.	2	27.7	-12.8	27	13.5	28.2	705	3151	84	454	6	165	82	269
Pterocarya sp.	3.9	24.2	-12.8	17	15.3	31.6	246	2648	46	424	1	64	2	424
Quercus (deciduous)	-1.4	27	-25.1	25.9	8.4	28.3	201	10798	33	2446	0	180	5	1100
Quercus (evergreen)	8.7	22.1	0.4	13.3	18.8	28.6	224	1967	48	370	0	72	0	236
Quercus cerris	9.6	19	-1.6	8.9	20.1	28.3	619	1179	69	178	5	65	5	70
Quercus faginea	13.7	18.5	4.9	12.5	19.8	25.6	438	1475	53	170	1	85	3	125
Quercus ilex/coccifera	8.7	19.5	0.4	13.3	18.8	26.1	224	1437	48	159	0	72	0	116
Quercus ilex	8.7	19.5	0.4	13.3	18.8	26.1	224	1437	48	159	0	72	0	116
Quercus sp.	-1.4	27	-25.1	25.9	8.4	28.3	201	10798	33	2446	0	180	5	1100
Rhamnaceae	1.6	27.7	-14.1	27	16.3	33.1	37	3151	8	389	0	165	0	221
Salix sp.	-17	27.7	-50.1	26.5	7.6	32.9	122	2399	22	448	0	108	0	252
Sambucus sp.	-9.2	27.7	-38.2	27	12.2	28.1	226	10798	43	2446	0	165	15	1100
Sanguisorba sp.	-15	21.4	-41	13.9	10.8	28.3	122	2399	43	336	1	108	2	152
Sapotaceae	12.9	27.7	0.9	27	23.6	29.7	359	3293	106	988	2	165	38	236
Sciadopityaceae	3.7	14	-8.4	3.7	15.8	24.3	1300	2648	130	369	25	75	115	344
Sorbus domestica	8.6	19	-4.2	12.2	17.9	28.3	482	741	70	117	2	45	4	70
Symplocos sp.	13.6	27.7	1.8	27	23.6	32.2	505	10798	109	2446	3	208	43	1100
Tamarix sp.	9.6	24.8	1.3	15.6	16	33.1	37	1150	8	131	0	61	0	90

Taxodioideae	3.8	25	-9.4	19.8	13.7	31.2	290	2615	60	448	0	114	3	431
Taxus sp.	3.1	18.5	-16.8	12.5	13.7	26.3	470	2648	55	369	1	108	3	344
Thymelaeaceae	-0.6	28.5	-12.6	27	15.6	33.4	37	3151	8	450	0	165	0	221
Tilia sp.	1.3	22.2	-17.7	15.1	15	29.4	373	2336	68	454	3	95	15	258
Tilia tomentosa	9.9	15.2	-2.3	5.4	20.8	25.5	413	1455	49	226	23	47	23	79
Tsuga sp.	-5	21.9	-15.6	15.6	8	29.5	450	2648	48	350	0	108	0	344
Ulmus sp.	-4.9	26.6	-25.8	26.1	16	29.4	201	3285	33	569	0	100	0	239
Ulmus/Zelkova	-4.9	26.6	-25.8	26.1	16	29.4	201	3285	33	569	0	100	0	344
Valeriana sp.	0.3	18.8	-15	8.7	9.8	29.4	285	1741	56	262	0	75	0	95
Viburnum sp.	-1.1	27.7	-25.8	27	12.9	36.1	193	10798	46	2446	0	165	0	1100
Viscum sp.	4.7	27.7	-7.1	27	13.8	33.1	344	3151	61	389	0	165	1	221
Vitis sp.	0	27.4	-22.7	25.6	17.2	31.2	210	2100	44	322	0	94	2	269
Zelkova sp.	6.2	21.9	-12.8	13.6	19.4	29.7	246	2648	46	370	3	67	3	344

Appendix to Chapter 3

Table A3.1: Supplementary Material 1. Complete matrix of Plant Functional Types (PFT) and associated taxa used in the Biomization analysis.

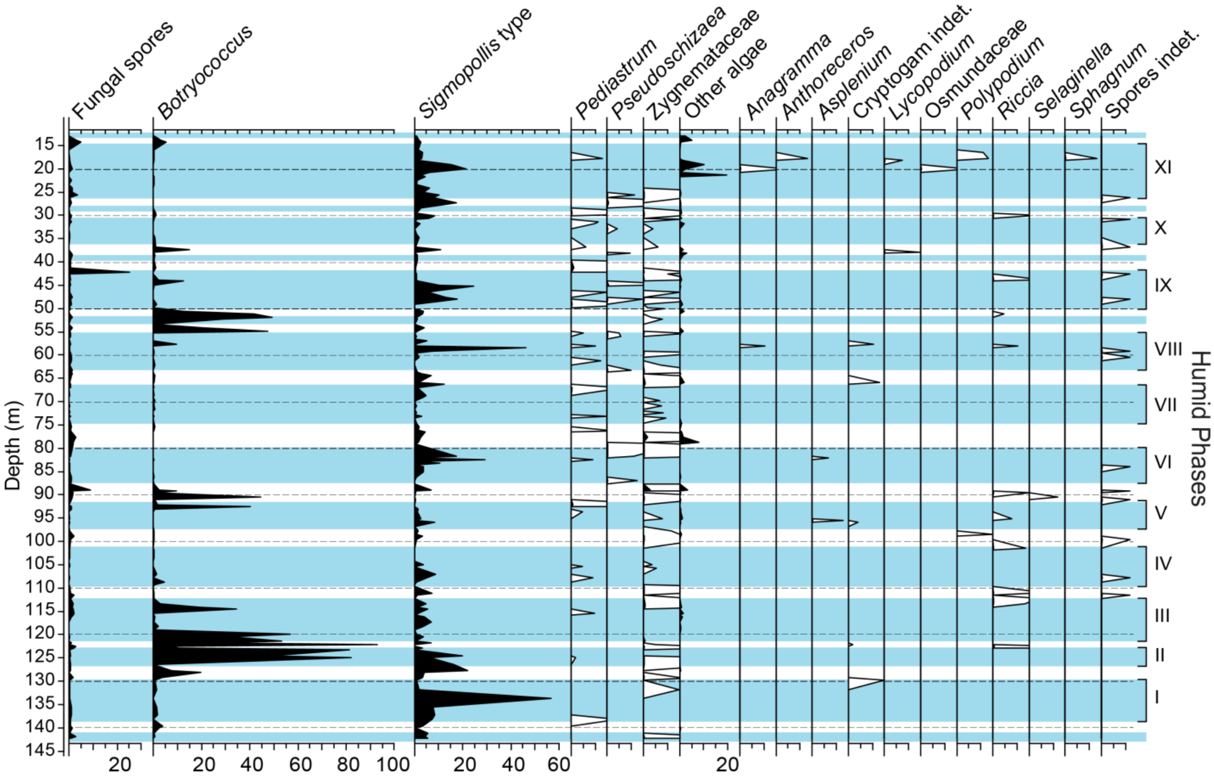
PFT code	Plant Functional Type	Constituent taxa from the Palominas associations
arc.f	Arctic forb	Lamiaceae, Polygonaceae, *Polygonum*, Ranunculaceae, *Salix, Saxifraga*, *Valeriana*, *Drosera.*
ross.cush.f	Rosette or cushion forb	*Artemisia*, Asteraceae, Euphorbiaceae, *Phlomis*, *Scabiosa*
drou.tol.f	Drought-tolerant forb	*Adonis*, *Armeria*, *Artemisia*, Asteraceae, Caryophyllaceae, *Centaurea*, Chenopodioideae, Dipsacales, Euphorbiaceae, *Knautia*, Lamiaceae, *Scabiosa*.
other.f	Other forbs	Apiaceae, Malvaceae, Asparagales, Asteraceae, Boraginaceae, Brassicaceae, Caryophyllaceae, *Centaurea*, *Centranthus*, Chenopodioideae, Dipsacales, *Drosera*, *Epilobium*, *Erodium*, *Euphrasia*, Fabaceae, *Filipendula*, *Geranium*, Lamiaceae, *Linum*, *Plantago*, Plumbaginaceae, Polygalaceae, Polygonaceae, *Polygonum*, Ranunculaceae, Rosaceae, *Rumex*, *Sanguisorba*, Solanaceae, *Valeriana*, Verbenaceae.
halo	Halophyte	Chenopodioideae, *Tamarix.*
geo	Geophyte	Asparagales, *Asphodelus*, Iridaceae/Liliaceae.
succ	Succulent	Chenopodioideae, Euphorbiaceae.
grss.gran	Grass graminoid	Poaceae.
sedg.gram	Sedge graminoid	Alismataceae, Cyperaceae.
arc.dw.shrb	Arctic dwarf shrub	*Betula*, Ericaceae.
sw.pl	Switch plants	*Ephedra*.
liana	Climber/liana/vine	*Parthenocissus*, Ranunculaceae, Solanaceae.
bor.lth.shrb	Boreal low-to-high shrub	Ericaceae, *Myrica*.
t.lth.shrb	Temperate low-to-high shrub	Chenopodioideae, *Cistus*, *Daphne*, Ericaceae, Fabaceae, *Hippophae*, Lamiaceae, *Rhamnus*, Rosaceae.
wt.lth.shrb	Warm-temperate low-to high shrub/small tree	*Carpinus orientalis-Ostrya* type, Chenopodioideae, *Cistus*, *Coriaria*, *Daphne*, Ericaceae, *Helianthemum*, Lamiaceae, *Olea*, *Pistacia*, *Rhamnus*, Rosaceae, Solanaceae.
xero.shrb	Xerophytic shrub	*Artemisia*, Chenopodioideae, *Cistus*, Ericaceae, Euphorbiaceae, *Rhamnus*.
bor.cd.m.b.t	Boreal cold-deciduous malacophyll broadleaved tree	*Alnus*, *Betula*, *Populus*, *Salix*.
bor.ev.nl.t	Boreal evergreen need-leleaved tree	*Picea*, *Abies*.
bor.nl.cd.t	Boreal needle-leaved deciduous tree	(No taxa from the Palominas pollen associations is assigned to this PFT)
ct.ev.nl.t	Cool-temperate evergreen needle-leaved tree	*Picea*.
eut.ev.nl.t	Eurythermic evergreen needle-leaved tree	Cupressaceae.
t.b.cd.m.b.t	Temperate (frost-induced late budburst) cold deciduous malacophyll broadleaved tree	*Acer*, *Corylus*, *Fraxinus*, *Populus*, *Quercus* (deciduous), *Salix*.
t.t.cd.m.b.t	Temperate (spring frost tolerant) cold-deciduous malacophyll broadleaved tree	*Carpinus betulus*-type, *Eucommia*, Fabaceae, *Fagus*, *Parrotia persica*-type, *Rhamnus*, *Ulmus*.
t.i.cd.m.b.t	Temperate (spring frost intolerant) cold-deciduous malacophyll broadleaved tree	Araliaceae, *Carpinus orientalis-Ostrya* type, *Carya*, *Pterocarya*, *Castanea*, *Celtis*, *Coriaria*, Fabaceae, *Fagus*, Hamamelidaceae, *Juglans*, *Rhamnus*, *Zelkova*.
t.ev.nl.t	Temperate evergreen needle-leaved tree	*Abies*, *Cathaya*, *Podocarpus*.
wt.ev.m.b.t	Warm-temperate evergreen malacophyll broadleaved tree	*Ilex*.
wt.scl.t	Warm-temperate sclerophyll tree	*Buxus*, Fabaceae, *Olea*, *Quercus* (evergreen).
wt.nl.ev.t	Warm-temperate needle-leaved evergreen tree	*Cathaya*, Cupressaceae, *Podocarpus*.
tuft.t	Tuft tree	(No taxa from the Palominas pollen association is assigned to this PFT)

Table A3.1: Supplementary Material 2. Minimum and maximum values of the climatic intervals for the taxa used in the calculation of the coexistence intervals for the pollen assemblages of the Palominas associations. Featured parameters are: 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). Precipitation values in mm. Temperature values in °C. Source: www.paleoflora.de

Taxa	**MAT min**	**MAT max**	**MTCold min**	**MTCold max**	**MTWarm min**	**MTWarm max**	**MAP min**	**MAP max**	**MPwet min**	**MPwet max**	**MPdry min**	**MPdry max**	**MPwarm min**	**MPwarm max**
Abies sp.	-6.7	27.4	-32.4	25.6	7.1	29.5	201	3000	33	700	0	135	0	700
Alnus sp.	-13.3	27.4	-40.9	25.6	4.9	38.6	160	2730	25	353	0	135	0	533
Aralia sp.	-5.5	27.7	-24.4	27	13.5	28.1	373	10798	36	2446	3	165	5	1100
Arceuthobium sp.	-5.5	27.7	-27.8	27	15.4	28.8	250	3151	36	389	0	165	0	221
Armeria sp.	-8.9	18.8	-26.5	13.1	7.9	27.7	264	1958	55	262	0	83	2	141
Betula sp.	-15	25.8	-41	21.1	1.3	28.7	110	10798	23	2446	0	135	2	1100
Boraginaceae	3.4	27.7	-12.9	27	9.2	35.6	170	3151	51	389	2	165	2	221
Buxus sp.	9.7	25.3	-1.2	20	17.3	29.4	399	2540	80	566	0	56	0	252
Carpinus betulus	5.3	17.6	-7.5	9.7	17.4	26.4	471	1958	56	236	1	85	6	219
Carpinus - Ostrya	0	25.8	-22.7	21.1	16.8	28.7	164	10798	20	2446	0	130	0	1100
Carya sp.	4.4	26.6	-11.5	22.2	19.3	30.6	373	1724	68	434	8	93	45	258
Castanea sp.	7.6	24.2	-8.2	18	14.5	29.4	473	2336	70	454	2	93	1	304
Cedrus sp.	11.6	21.4	-0.3	13.9	19.4	31.8	164	1577	43	434	0	41	0	175
Celtis sp.	2.5	25.8	-17.7	23	18.7	28.8	116	2730	25	597	0	88	2	533
Centaurea sp.	-0.3	27.7	-13.2	27	14.7	28.1	252	3151	44	389	3	165	3	221
Chenopodiaceae	-11	27.7	-29.5	23.6	12	36.1	193	1958	46	358	0	83	0	224
Cistaceae	-7.2	26.6	-27.5	26.1	12	28.3	24	3285	8	569	0	47	0	177
Cistus sp.	11.6	21.4	3.5	13.9	18.9	29.7	160	1352	20	259	2	44	2	54
Coriaria sp.	8.8	27	-7.3	26.3	16.7	29.4	396	1930	108	358	0	103	64	224
Corylus sp.	-4.9	24	-32.4	16.7	12.9	29.4	305	1958	45	343	0	83	3	239
Cupressaceae	-15.6	26.5	-48.9	26.1	11.2	32.9	184	4486	22	409	0	326	0	378
Dipsacaceae	-1.7	24.6	-25.4	23.6	16.2	29.4	24	1828	8	343	0	85	0	239
Ephedra sp.	3.1	28.8	-12	25	16.4	32.9	33	1096	5	220	0	45	2	214
Epilobium sp.	-6.7	24.2	-24.4	18.3	13.8	29.8	227	1958	26	236	0	83	0	141
Erodium sp.	0.1	19.2	-18.3	16.7	15	29.7	160	1958	20	236	2	83	2	141
Eucommia ulmoides	10.6	19.4	-7.3	9.6	20.2	29.3	396	1967	108	370	3	64	108	304
Euphorbiaceae	-0.3	27.7	-17.7	27	14.7	28.3	24	10798	8	2446	0	165	0	1100
Fabaceae	-7.7	27.7	-22.7	25.9	10.5	31.2	224	3905	46	610	0	196	1	221
Fagus sp.	4.4	23.1	-18.6	17	17.3	31.7	376	2648	46	448	3	94	5	431
Filipendula sp.	-3.8	18	-25.6	10.1	9.8	23.8	213	1958	45	236	1	83	1	141
Fraxinus sp.	0	24	-25.8	16.7	14.9	33.9	148	10798	28	2446	2	95	0	1100
Geranium sp.	-7.7	18.5	-22.7	13.8	9.8	23.1	224	1958	46	236	0	83	1	141
Hamamelidaceae	0.2	27.7	-16.6	27	16.3	29.5	529	3151	74	610	0	165	6	221
Helianthemum sp.	3.4	24.8	-12.9	19	18.9	33.1	37	1944	8	342	0	43	0	244
Hippophae sp.	1.6	17.4	-11.1	8.3	13.4	27	552	1151	64	149	5	57	20	89
Ilex aquifolium	7.2	18.2	-0.4	12.2	14.1	27.6	563	1451	67	178	2	72	4	116

Juglans sp.	0	27.5	-22.7	25	9.5	31.2	210	2617	28	582	1	114	2	189
Knautia sp.	0.1	18.5	-18.3	12.5	14.2	28	470	1958	66	236	1	83	3	141
Ligustrum sp.	0	27.7	-22.7	27	14.8	29.3	422	3151	58	389	7	165	9	221
Linum sp.	4.6	20.5	-7.9	17.8	14.2	28.4	233	1167	53	151	0	62	0	79
Malvaceae	-3.2	27.7	-26	27	16.1	30.9	213	3151	60	389	2	165	3	221
Myrica sp.	-8.9	28.1	-29	27	8.9	33.9	233	3151	34	508	0	165	0	368
Olea sp.	10	27.5	-7.3	26	19.9	29.7	160	3293	20	985	0	71	0	304
Oleaceae	-1.1	27.7	-25.8	27	19.6	33.1	37	3293	8	985	0	165	0	320
Parthenocissus sp.	2.5	23.9	-17.7	19.4	13.9	28.9	373	1551	76	241	3	89	26	217
Picea sp.	-8.9	21.7	-31.2	15.6	7.3	31.6	142	6000	36	700	2	400	2	400
Pinus sp.	-9.2	25.5	-36.8	21.4	7.1	32.9	180	10798	28	2446	0	94	0	1100
Pistacia sp.	5.9	27	-9.4	25.7	19.3	28.6	187	3370	40	479	0	158	0	178
Podocarpus sp.	4.9	27.7	-0.6	27	10.6	28.8	652	10798	68	2446	13	165	26	1100
Polygonum sp.	-0.6	21.7	-12.8	14.8	15.6	28.2	453	10798	63	2446	1	135	1	1100
Polypodium sp.	-4.9	27.7	-32.4	27	18.2	28.5	224	3151	43	454	0	165	0	269
Populus sp.	-16	21.3	-49	13.6	9.8	28.9	25	2559	8	358	0	93	0	224
Pterocarya sp.	3.9	24.2	-12.8	17	15.3	31.6	246	2648	46	424	1	64	2	424
Quercus (deciduous)	-1.4	27	-25.1	25.9	8.4	28.3	201	10798	33	2446	0	180	5	1100
Quercus (evergreen)	8.7	22.1	0.4	13.3	18.8	28.6	224	1967	48	370	0	72	0	236
Rhamnaceae	1.6	27.7	-14.1	27	16.3	33.1	37	3151	8	389	0	165	0	221
Salix sp.	-17	27.7	-50.1	26.5	7.6	32.9	122	2399	22	448	0	108	0	252
Sanguisorba sp.	-15	21.4	-41	13.9	10.8	28.3	122	2399	43	336	1	108	2	152
Tamarix sp.	9.6	24.8	1.3	15.6	16	33.1	37	1150	8	131	0	61	0	90
Tsuga sp.	-5	21.9	-15.6	15.6	8	29.5	450	2648	48	350	0	108	0	344
Ulmus sp.	-4.9	26.6	-25.8	26.1	16	29.4	201	3285	33	569	0	100	0	239
Valeriana sp.	0.3	18.8	-15	8.7	9.8	29.4	285	1741	56	262	0	75	0	95
Viscum sp.	4.7	27.7	-7.1	27	13.8	33.1	344	3151	61	389	0	165	1	221
Zelkova sp.	6.2	21.9	-12.8	13.6	19.4	29.7	246	2648	46	370	3	67	3	344

Figure A3.1: Supplementary Material 3. Detailed diagram of Non-Pollen Palynomorphs (NPP) of the Palominas core. Cryptogam proportions calculated against the sum of pollen and spores (excluding *Pinus*). All other taxa proportions have been calculated against the total palynomorphs sum. Black curves represent true percentages; white curves show a 10x exaggeration. Humid Phases I to XI in light blue.



Appendix to Chapter 4

Table A4.1: Complete GDGT values (peak area) from the Palominas core.

Depth (m)	Weight (g)	GDGT-0	GDGT-1	GDGT-2	GDGT-3	GDGT-4	GDGT-4'
20.08	2.28	6.28E+06	1.38E+05	1.01E+05	1.35E+04	5.07E+04	8.24E+03
23.38	4.95	8.17E+06	3.71E+05	1.69E+05	5.58E+04	1.40E+05	1.15E+04
25.6	11.28	4.19E+06	2.44E+05	9.72E+04	1.31E+04	5.97E+04	7.19E+03
28.42	4.30	3.25E+06	9.96E+04	4.51E+04	6.12E+03	2.31E+04	1.55E+03
30.73	3.19	6.39E+06	3.58E+05	1.06E+05	2.01E+04	7.84E+04	3.77E+03
32.91	5.22	7.98E+06	5.81E+04	6.71E+04	5.66E+03	3.10E+04	4.62E+03
38.51	4.67	2.27E+06	6.52E+04	1.95E+04	6.33E+03	2.99E+04	2.87E+03
39.38	1.79	1.33E+07	3.84E+05	2.51E+05	3.38E+04	6.87E+04	1.08E+04
41.23	2.00	1.10E+07	2.94E+05	2.74E+05	2.92E+04	1.19E+05	1.11E+04
42.84	1.48	1.30E+07	5.05E+05	2.51E+05	2.43E+04	1.52E+05	1.89E+04
43.82	2.31	1.20E+06	2.65E+04	1.67E+04	2.25E+03	9.61E+03	1.23E+03
44.47	1.14	4.90E+05	1.79E+04	9.98E+03	2.60E+03	1.12E+04	1.11E+03
45.04	7.19	2.67E+07	6.82E+05	3.42E+05	4.87E+04	3.80E+05	4.69E+04
46.19	1.85	1.16E+07	2.43E+05	1.06E+05	1.66E+04	9.17E+04	1.14E+04
46.54	6.95	1.16E+07	2.43E+05	1.06E+05	1.66E+04	9.17E+04	1.14E+04
47.65	1.24	1.08E+07	2.82E+05	1.36E+05	2.05E+04	5.98E+04	5.78E+03
48.38	1.34	9.07E+06	2.30E+05	9.70E+04	1.49E+04	1.14E+05	8.29E+03
49.08	2.53	2.44E+07	7.81E+05	5.36E+05	5.90E+04	2.18E+05	1.96E+04
49.84	3.82	2.78E+05	9.83E+03	4.79E+03	7.32E+02	1.96E+03	2.04E+02
51.6	3.70	8.63E+06	4.37E+05	4.25E+05	3.43E+04	1.82E+05	2.32E+04
52.31	10.80	3.16E+06	1.11E+05	4.49E+04	1.38E+04	6.99E+04	3.32E+03
56.1	7.60	3.63E+06	2.26E+05	1.16E+05	1.93E+04	5.35E+04	6.55E+03
62.1	3.17	7.58E+06	1.44E+05	6.77E+04	1.11E+04	2.61E+04	3.14E+03
63.62	8.61	1.20E+08	5.52E+06	3.39E+06	2.73E+05	1.10E+06	1.40E+05
66.97	30.34	9.62E+07	3.68E+06	2.19E+06	1.71E+05	4.97E+05	6.72E+04
71.72	2.68	5.56E+06	1.20E+05	6.75E+04	3.13E+03	2.12E+04	4.37E+03
72.43	47.88	3.82E+07	7.19E+05	6.62E+05	3.36E+04	2.26E+05	2.19E+04
75.45	1.35	7.22E+06	2.68E+05	1.57E+05	1.05E+04	8.48E+04	1.01E+04
76.19	6.24	6.61E+07	1.13E+06	1.90E+06	1.54E+05	5.06E+05	5.57E+04
79.08	2.81	2.98E+07	5.07E+05	5.10E+05	3.86E+04	3.53E+05	4.50E+04
81.32	7.58	6.75E+07	2.16E+06	6.30E+05	7.98E+04	4.88E+05	7.46E+04
81.7	10.81	1.61E+07	3.72E+05	1.47E+05	1.62E+04	1.85E+05	2.54E+04
82.47	9.59	5.43E+06	3.30E+04	4.20E+04	6.12E+03	2.94E+04	4.17E+03
83.17	2.32	2.09E+07	1.42E+05	1.39E+05	1.87E+04	6.65E+04	4.27E+03
83.95	9.48	1.93E+07	3.33E+05	2.38E+05	1.96E+04	1.15E+05	2.06E+04
84.67	5.70	6.55E+07	1.02E+06	1.88E+05	3.97E+04	1.94E+05	2.22E+04
85.35	5.63	9.15E+06	1.79E+05	2.27E+04	4.55E+03	2.74E+04	3.88E+03
86.11	5.31	1.10E+07	3.95E+05	5.98E+04	1.51E+04	8.70E+04	7.67E+03
87.6	21.73	1.39E+07	5.13E+05	1.45E+05	2.38E+04	9.58E+04	1.06E+04
88.39	6.12	1.34E+06	8.08E+04	2.91E+04	6.70E+03	2.56E+04	1.09E+03
89.15	1.13	6.21E+06	3.25E+05	1.29E+05	2.49E+04	2.37E+05	3.76E+04
89.9	0.16	1.83E+06	7.10E+04	1.10E+04	6.41E+03	1.51E+04	1.48E+03
90.74	6.30	1.19E+07	4.20E+05	3.74E+05	2.07E+04	1.89E+05	1.36E+04
92.61	1.06	1.18E+06	5.86E+04	1.37E+04	4.33E+03	1.20E+04	9.04E+02
93.73	2.61	9.52E+06	2.18E+05	6.64E+04	6.81E+03	4.61E+04	4.64E+03
94.44	2.41	1.17E+07	2.12E+05	1.26E+05	1.46E+04	2.85E+04	6.70E+03
95.14	2.87	1.17E+07	1.20E+05	7.62E+04	7.60E+03	2.55E+04	3.60E+03
95.94	3.43	1.41E+07	1.16E+05	1.21E+05	9.66E+03	2.08E+04	2.26E+03
96.33	4.35	4.78E+06	7.06E+04	4.07E+04	4.44E+03	1.13E+04	2.06E+03
96.72	17.30	7.02E+07	1.12E+06	7.40E+05	4.78E+04	1.52E+05	1.22E+04
97.7	0.25	3.31E+05	7.95E+03	6.04E+03	3.79E+03	1.19E+04	7.04E+03
98.09	1.10	1.03E+06	4.64E+04	1.54E+04	3.74E+04	5.24E+04	5.82E+03
98.85	1.58	1.36E+07	4.75E+05	3.77E+05	2.40E+04	1.09E+05	1.53E+04
99.22	3.49	1.04E+07	3.32E+05	1.73E+05	1.32E+04	6.00E+04	6.56E+03
100.24	2.42	1.26E+06	3.06E+04	1.83E+04	3.31E+03	1.95E+04	2.17E+03
103.46	2.31	2.94E+06	1.83E+05	5.03E+04	1.13E+04	1.69E+05	9.02E+03
105.77	13.41	2.52E+07	6.16E+05	3.64E+05	4.48E+04	1.72E+05	1.46E+04
110.01	5.83	8.63E+06	1.65E+05	1.94E+04	7.71E+03	4.80E+04	5.01E+03
112.91	2.03	8.99E+06	1.54E+05	6.30E+04	3.92E+03	2.69E+04	2.44E+03
115.4	8.91	1.32E+07	5.24E+05	1.46E+05	3.12E+04	1.90E+05	2.18E+04
116.23	5.89	1.52E+06	7.66E+04	3.08E+04	4.81E+03	2.50E+04	2.93E+03
119.83	11.85	3.02E+06	7.95E+04	7.96E+04	7.81E+03	3.57E+04	2.66E+03
124.13	17.30	2.20E+07	5.53E+05	3.20E+05	5.84E+04	1.99E+05	2.00E+04
129.32	4.71	1.17E+07	4.89E+05	2.18E+05	1.12E+04	1.34E+05	1.40E+04
131.37	5.62	1.53E+07	1.45E+05	1.57E+05	5.91E+03	4.86E+04	3.65E+03
133.78	14.91	1.10E+07	1.80E+05	7.98E+04	9.10E+03	4.57E+04	6.22E+03
139.23	4.34	8.67E+06	2.13E+05	9.83E+04	1.52E+04	4.57E+04	1.15E+04

Depth (m)	**GDGT-Ia**	**GDGT-Ib**	**GDGT-Ic**	**GDGT-IIa**	**GDGT-IIb**	**GDGT-IIc**	**GDGT-IIIa**	**GDGT-IIIb**	**GDGT-IIIc**
20.08	1.35E+06	2.20E+05	5.01E+04	2.08E+06	3.18E+05	3.48E+04	1.50E+06	1.01E+05	9.11E+03
23.38	1.23E+07	6.92E+06	2.62E+06	6.11E+06	3.02E+06	5.99E+05	3.25E+06	3.89E+05	3.98E+04
25.6	3.42E+06	1.07E+06	4.70E+05	3.42E+06	9.04E+05	9.00E+04	1.52E+06	1.40E+05	1.37E+04
28.42	1.06E+06	1.41E+05	4.24E+04	1.60E+06	1.75E+05	8.72E+04	9.33E+05	6.54E+04	6.29E+03
30.73	5.19E+06	1.61E+06	7.05E+05	6.56E+06	1.09E+06	2.03E+05	3.36E+06	2.53E+05	3.55E+04
32.91	8.64E+05	4.03E+04	1.60E+04	1.31E+06	1.18E+05	8.90E+04	9.07E+05	6.01E+04	3.87E+03
38.51	2.24E+06	2.65E+06	1.35E+06	8.09E+05	7.47E+05	9.03E+04	6.26E+05	6.62E+04	1.24E+04
39.38	2.56E+06	1.45E+06	6.08E+05	2.58E+06	7.28E+05	9.03E+04	6.89E+05	9.69E+04	9.49E+03
41.23	3.84E+06	7.71E+04	1.93E+04	4.39E+06	1.77E+05	1.86E+04	1.81E+06	5.57E+04	9.88E+03
42.84	1.12E+07	2.60E+06	8.80E+05	1.20E+07	2.60E+06	2.61E+05	8.16E+06	5.25E+05	6.34E+04
43.82	4.27E+05	4.96E+04	1.56E+04	4.59E+05	6.67E+04	4.79E+03	3.43E+05	2.59E+04	3.73E+03
44.47	6.57E+04	1.24E+04	3.90E+03	6.91E+04	1.37E+04	3.22E+03	4.71E+04	3.54E+03	2.02E+03
45.04	5.17E+06	6.02E+05	1.38E+05	9.62E+06	1.18E+06	8.09E+04	6.72E+06	4.56E+05	1.58E+04
46.19	1.90E+06	5.62E+04	1.59E+04	3.32E+06	2.12E+05	2.05E+04	3.03E+06	1.02E+05	1.54E+04
46.54	1.90E+06	5.62E+04	1.59E+04	3.32E+06	2.12E+05	2.05E+04	3.03E+06	1.02E+05	1.54E+04
47.65	3.24E+06	2.31E+05	2.50E+04	4.31E+06	4.72E+05	4.14E+04	3.15E+06	1.50E+05	1.99E+04
48.38	1.75E+06	1.71E+05	3.56E+04	2.68E+06	3.52E+05	2.38E+04	2.13E+06	1.21E+05	1.47E+04
49.08	9.86E+06	2.06E+06	5.52E+05	9.54E+06	1.47E+06	1.36E+05	4.52E+06	2.17E+05	6.97E+04
49.84	6.70E+04	2.39E+04	8.21E+03	5.77E+04	1.35E+04	1.58E+03	3.20E+04	2.41E+03	5.46E+02
51.6	1.83E+06	6.37E+05	2.33E+05	2.28E+06	5.16E+05	5.60E+04	1.22E+06	7.28E+04	2.03E+04
52.31	2.42E+06	1.20E+06	4.66E+05	2.57E+06	7.23E+05	8.51E+04	8.69E+05	1.39E+04	5.17E+02
56.1	2.99E+06	1.50E+06	6.72E+05	2.70E+06	9.04E+05	9.54E+04	1.42E+06	9.98E+04	1.23E+04
62.1	4.74E+06	2.41E+06	8.20E+05	2.93E+06	1.00E+06	2.75E+05	6.62E+05	1.23E+05	2.05E+04
63.62	2.43E+07	1.54E+06	4.00E+05	2.44E+07	2.60E+06	2.35E+05	1.57E+07	7.20E+05	4.19E+04
66.97	1.59E+07	7.57E+05	1.92E+05	2.37E+07	1.42E+06	1.19E+05	1.44E+07	5.01E+05	5.57E+04
71.72	2.78E+05	1.80E+04	8.78E+03	1.61E+05	1.85E+04	5.99E+03	1.09E+05	8.40E+03	3.41E+03
72.43	5.28E+06	3.01E+05	7.13E+04	6.26E+06	4.01E+05	3.77E+04	2.52E+06	1.59E+05	1.82E+04
75.45	5.90E+05	4.12E+04	9.73E+03	6.26E+05	8.90E+04	1.83E+04	3.80E+05	2.09E+04	4.63E+03
76.19	1.03E+07	6.80E+05	1.20E+05	5.47E+06	9.69E+05	4.13E+05	8.70E+06	2.21E+05	1.31E+03
79.08	2.47E+06	1.02E+05	2.13E+04	3.23E+06	2.55E+05	2.07E+04	1.23E+06	9.00E+04	1.06E+04
81.32	1.12E+07	2.17E+06	3.46E+05	1.73E+07	3.01E+06	1.79E+05	1.19E+07	1.05E+06	9.55E+03
81.7	3.80E+06	5.58E+05	1.55E+05	5.89E+06	8.62E+05	4.03E+04	3.73E+06	2.71E+05	4.81E+03
82.47	1.07E+06	1.72E+05	2.92E+04	1.74E+06	2.32E+05	1.54E+04	1.11E+06	9.24E+04	3.27E+03
83.17	2.03E+06	1.34E+05	3.94E+04	2.92E+06	2.50E+05	6.35E+04	2.41E+06	1.14E+05	1.15E+04
83.95	1.78E+06	1.05E+05	5.70E+03	2.03E+06	1.58E+05	1.03E+04	8.69E+05	3.16E+04	6.99E+02
84.67	5.16E+06	1.40E+05	4.69E+04	9.49E+06	4.80E+05	2.64E+04	9.00E+06	3.01E+05	5.98E+03
85.35	8.89E+05	2.51E+04	5.25E+03	1.57E+06	6.67E+04	2.18E+03	1.40E+06	5.60E+04	2.83E+03
86.11	3.22E+06	5.08E+05	6.14E+04	3.60E+06	5.86E+05	5.85E+04	2.55E+06	9.20E+04	6.12E+03
87.6	6.61E+06	1.08E+06	5.83E+05	2.55E+06	9.79E+05	6.84E+04	3.72E+06	3.06E+05	2.50E+04
88.39	2.54E+06	2.13E+06	9.84E+05	1.66E+06	5.64E+05	2.41E+05	4.50E+05	6.70E+04	7.23E+03
89.15	7.42E+05	1.61E+05	4.76E+04	9.72E+05	2.11E+05	4.04E+04	3.92E+05	6.35E+04	9.65E+03
89.9	1.31E+06	5.42E+05	1.46E+05	1.11E+06	2.77E+05	1.45E+05	3.30E+05	4.94E+04	7.61E+03
90.74	4.24E+06	1.44E+06	3.79E+05	4.23E+06	1.17E+06	1.22E+05	1.27E+06	1.15E+05	2.60E+04
92.61	1.66E+06	1.28E+06	4.06E+05	1.28E+06	6.48E+05	8.75E+04	4.74E+05	5.26E+04	8.21E+03
93.73	1.72E+06	4.09E+05	1.18E+05	2.40E+06	4.84E+05	3.97E+04	1.70E+06	1.11E+05	8.80E+03
94.44	1.45E+06	5.99E+04	1.80E+04	2.06E+06	1.58E+05	1.22E+04	1.55E+06	7.59E+04	1.35E+04
95.14	1.11E+06	4.56E+04	1.10E+04	1.71E+06	1.48E+05	1.36E+04	1.14E+06	5.50E+04	6.66E+03
95.94	8.97E+05	4.27E+04	1.04E+04	1.40E+06	1.06E+05	7.13E+03	8.54E+05	3.88E+04	4.11E+03
96.33	7.29E+05	1.49E+05	7.68E+04	8.72E+05	1.43E+05	1.03E+04	5.24E+05	4.61E+04	4.63E+03
96.72	1.09E+07	5.20E+05	9.18E+04	1.58E+07	1.30E+06	8.33E+04	9.62E+06	5.69E+05	2.74E+04
97.7	6.93E+04	1.86E+04	3.23E+04	1.15E+05	4.24E+04	5.74E+03	1.00E+05	2.22E+04	5.64E+03
98.09	3.21E+05	3.64E+04	5.63E+04	1.95E+05	3.22E+04	1.71E+04	1.44E+05	1.89E+04	9.23E+03
98.85	1.94E+06	6.97E+04	2.11E+04	2.08E+06	1.29E+05	1.86E+04	9.93E+05	4.87E+04	1.08E+04
99.22	9.22E+05	2.59E+04	8.44E+03	7.33E+05	5.59E+04	9.16E+03	5.54E+05	2.53E+04	3.93E+03
100.24	3.76E+05	1.60E+05	4.04E+04	4.93E+05	1.51E+05	1.19E+04	3.48E+05	2.76E+04	3.71E+03
103.46	3.09E+06	1.83E+06	8.26E+05	1.58E+06	6.94E+05	1.40E+05	7.92E+05	7.76E+04	1.95E+04
105.77	7.00E+06	5.70E+05	1.88E+05	1.13E+07	8.61E+05	7.20E+04	7.04E+06	3.45E+05	2.15E+04
110.01	2.73E+06	1.98E+06	5.60E+05	1.90E+06	7.15E+05	1.24E+05	4.02E+05	1.08E+05	1.45E+04
112.91	5.52E+05	7.86E+04	3.56E+04	6.71E+05	1.63E+05	1.14E+05	6.74E+05	4.52E+04	3.32E+03
115.4	1.64E+07	1.11E+07	4.82E+06	1.57E+07	4.84E+06	7.71E+05	6.12E+06	2.13E+05	0.00E+00
116.23	2.10E+06	1.57E+06	4.18E+05	1.38E+06	5.24E+05	1.44E+05	4.37E+05	7.14E+04	1.55E+04
119.83	6.37E+05	3.22E+05	1.41E+05	6.09E+05	2.85E+05	1.71E+04	4.26E+05	1.78E+04	2.09E+03
124.13	8.85E+06	4.49E+06	2.38E+06	8.44E+06	2.75E+06	2.33E+05	4.37E+06	4.57E+05	5.47E+04
129.32	1.17E+06	1.27E+05	3.16E+04	1.46E+06	1.59E+05	1.35E+04	7.60E+05	3.27E+04	6.37E+03
131.37	6.87E+05	3.55E+04	1.24E+04	6.68E+05	7.49E+04	2.33E+04	5.36E+05	1.62E+04	4.87E+03
133.78	9.90E+05	4.11E+04	8.19E+03	1.32E+06	9.05E+04	1.02E+04	1.85E+06	4.15E+04	5.61E+03
139.23	1.94E+06	2.10E+05	6.36E+04	1.69E+06	2.42E+05	7.07E+04	1.58E+06	2.99E+04	1.26E+04

Appendix to Chapter 5

Table A5.1: SOM Table S1. Lists of taxa per vegetation unit (VU); each list is a combination of dominant taxa from analogue vegetation units based on EuroVegMap (Bohn et al. 2003) and taxa identified in the fossil pollen record.

VU Code	Veg. Unit	Source	Taxa	Edibility
C	**‘ Conifer forests VU’**	fossil record	*Abies* sp.	no info
		C34	*Arenaria pungens* ec Lag.	no info
		C30	*Berberis vulgaris* subsp. *australis* (Boiss.) Heywood	yes
		C30	*Cerastium boissierianum* Greuter & Burdet	no info
		C34	*Chamaespartium undulatum* (Ern) Talavera & L. Sáez	no info
		C30	*Crataegus monogyna* Jacq.	yes
		C34	*Cytisus oromediterraneus* (G. López & C.E. Jarvis) Rivas Mart. & al.	no info
		C30	*Daphne oleoides* Schreb.	no
		C34	*Deschampsia flexuosa* subsp. *iberica* Rivas Mart.	no info
		C34	*Dianthus subacaulis* subsp. *brachyanthus* (Boiss.) P.Fourn.	no info
		C34	*Erinacea anthyllis* Link	no info
		C34	*Genista versicolor* Boiss.	no info
		C30	*Geum heterocarpum* Boiss.	no info
		C30	*Helictotrichon filifolium* (Lag.) Henrard	no info
		C30, C34	*Juniperus communis* subsp. *hemisphaerica* (C. Presl) Nyman	yes
		C30	*Juniperus sabina* L.	no
		C30	*Lonicera splendida* Boiss.	no info
		C30	*Luzula caespitosa* (J.Gay ex E.Mey.) Steud.	no info
		fossil record	*Picea abies* (L.) H.Karst.	yes
		C30	*Pinus nigra* subsp. *salzmannii* (Dunal) Franco	no info
		C30	*Pinus sylvestris* var. *nevadensis* Christ	no info
		C30	*Polygala boissieri* Coss.	no info
		C30	*Rosa micrantha* Borrer ex Sm.	yes
		C30, C34	*Senecio boissieri* DC.	no info
		C34	*Thlaspi nevadense* Boiss. & Reut.	no info
		C30	*Vella spinosa* Boiss.	no info
		C30	*Viola hirta* L.	yes
G	**‘ Deciduous forests VU’**	G69, G74	*Acer granatense* Boiss.	no info
		G74	*Acer monspessulanum* L.	no
		G69	*Adenocarpus decorticans* Boiss.	no info
		G69	*Alliaria petiolata* (M.Bieb.) Cavara & Grande	yes
		G69	*Anthoxanthum odoratum* L.	yes
		G69	*Aristolochia paucinervis* Pomel	no
		G69, G74	*Berberis vulgaris* subsp. *australis* (Boiss.) Heywood	yes
		G74	*Bromus erectus* Huds.	no info
		fossil record	*Carpinus orientalis* Mill.	no
		G69	*Clinopodium vulgare* L.	yes
		G74	*Crataegus monogyna* Jacq.	yes
		G69	*Cytisus scoparius* (L.) Link	yes
		G74	*Daphne laureola* subsp. *latifolia* (Coss.) Rivas Mart.	not known
		G74	*Dictamnus albus* L.	yes
		fossil record	*Erica* sp.	no info
		G69	*Festuca elegans* Boiss.	no info
		G69	*Fraxinus angustifolia* Vahl subsp. *angustifolia*	yes
		G69, G74	*Helleborus foetidus* L.	not known
		G74	*Juniperus communis* subsp. *hemisphaerica* (C. Presl) Nyman	yes
		G74	*Lonicera arborea* Boiss.	no info
		G69	*Luzula forsteri* (Sm.) DC.	no info
		G69	*Paeonia coriacea* Boiss.	no info
		G74	*Paeonia officinalis* subsp. *microcarpa* Nyman	not known
		G74	*Polygkala boissieri* Coss.	no info
		G74	*Polygonatum odoratum* (Mill.) Druce	yes
		G74	*Primula acaulis* (L.) Hill	yes
		G74	*Prunus mahaleb* L.	yes

		G74	*Quercus faginea* Lam.	yes
		G69	*Quercus pyrenaica* Willd.	yes
		G74	*Rosa canina* L.	yes
		G69	*Rosa pouzinii* Tratt.	yes
		G74	*Saponaria ocymoides* L.	not known
		G69	*Sorbus aria* (L.) Crantz	yes

J	**‘Mediterranean woodlands VU’**	J10	*Acer granatense* Boiss.	no info
		J10	*Amelanchier ovalis* Medik.	yes
		J03	*Asparagus acutifolius* L.	yes
		J31	*Asparagus horridus* L.	yes
		J10	*Berberis vulgaris* subsp. *australis* (Boiss.) Heywood	yes
		J31	*Brachypodium* retusum (Pers.) P.Beauv.	no info
		fossil record	*Cistus* sp.	yes
		J03, J31	*Clematis flammula* L.	yes
		J10	*Crataegus monogyna* Jacq.	yes
		J03	*Cytisus scoparius* subsp. *reverchonii* (Degen & Hervier) Rivas Goday & Rivas Mart.	no
		J10, J31	*Daphne gnidium* L.	not known
		J31	*Ephedra fragilis* Desf.	yes
		J03	*Festuca gigantea* (L.) Vill.	no info
		J03, J10	*Genista cinerea* (Vill.) DC.	no
		J03	*Geum sylvaticum* Pourr.	no info
		J03	*Hedera helix* L.	no
		J31	*Jasminum fruticans* L.	no info
		J10, J31	*Juniperus oxycedrus* L.	yes
		J31	*Juniperus phoenicea* L.	yes
		J03	*Lonicera etrusca* Santi	no info
		J03	*Lonicera periclymenum* subsp. *hispanica* (Boiss. & Reut.) Nyman	no info
		J31	*Lygeum spartum* Loefl. ex L.	not known
		J03	*Olea europaea* subsp. *oleaster* (Hoffmanns. & Link) Negodi	yes
		J03	*Paeonia broteroi* Boiss. & Reut.	no info
		J03	*Paeonia coriacea* Boiss.	no info
		J31	*Pinus halepensis* Mill.	yes
		J03, J31	*Pistacia lentiscus* L.	yes
		J10	*Prunus ramburii* Boiss.	no info
		J03	*Ptilostemon hispanicus* (Lam.) Greuter	no info
		J03, J31	*Quercus coccifera* L.	yes
		J10	*Quercus faginea* Lam.	yes
		J03	*Quercus faginea* subsp. *faginea*	yes
		J03, J10	*Quercus ilex* subsp. *rotundifolia* (Lam.) O.Schwarz ex Tab.Morais	yes
		J03	*Retama sphaerocarpa* (L.) Boiss.	not known
		J03	*Rhamnus alaternus* L.	yes
		J31	*Rhamnus lycioides* L.	not known
		J10	*Rosa canina* L.	yes
		J31	*Rubia peregrina* L.	not known
		J10	*Ruscus aculeatus* L.	yes
		J10	*Sorbus aria* (L.) Crantz	yes
		J03	*Stipa bromoides* (L.) Dörfl.	no info
		J31	*Stipa tenacissima* L.	not known

M	**‘Steppe VU’**	M13	*Agropyron cristatum* subsp. *pectinatum* (M.Bieb.) Tzvelev	no info
		M14, M15	*Agropyron desertorum* (Fisch. ex Link) Schult.	no info
		M12	*Allium carinatum* subsp. *pulchellum* (G.Don) Bonnier & Layens	yes
		M12	*Allium guttatum* Steven	no info
		M12	*Allium sphaerocephalon* L.	yes
		M14	*Alyssum desertorum* Stapf	no info
		M14	*Androsace maxima* L.	no info
		M14	*Arenaria procera* Spreng. subsp. *procera*	no info
		M12	*Armeria elongata* Hoffm.	no info
		M14	*Artemisia austriaca* Jacq.	yes
		M14, M15	*Artemisia lerchiana* Weber	no info
		M13, M14, M15	*Artemisia pauciflora* Weber ex Stechm.	no info
		M12, M13	*Artemisia santonicum* L.	no info
		M15	*Aster oleifolius* (Lam.) Wagenitz	no info
		M13	*Aster sedifolius* subsp. *angustissimus* (Tausch) Merxm.	no info

M	**‘Steppe VU’**	M13	*Aster tarbagatensis* (K.Koch) Merxm.	no info
		M12	*Astragalus henningii* (Steven) Boriss.	no info
		M14	*Carex supina* Willd. ex Wahlenb.	no info
		M12	*Cerastium ucrainicum* (Kleopow) Klokov	no info
		M12	*Dianthus guttatus* M.Bieb.	no info
		M12	*Dianthus lanceolatus* Steven ex Rchb.	no info
		M13	*Dianthus leptopetalus* Willd.	no info
		M12	*Erophila verna* (L.) DC.	yes
		M12	*Falcaria vulgaris* Bernh.	yes
		M12	*Ferula caspica* M.Bieb.	not known
		M12, M13, M14, M15	*Festuca valesiaca* Schleich. ex Gaudin	no info
		M12	*Gagea bulbifera* (Pall.) Salisb.	no info
		M14	*Galium ruthenicum* Willd.	yes
		M13	*Goniolimon tataricum* (L.) Boiss.	no info
		M12	*Holosteum umbellatum* L.	yes
		M12, M13	*Kochia prostrata* (L.) Schrad	no info
		M12, M13, M14	*Koeleria macrantha* (Ledeb.) Schult.	yes
		M14	*Leymus ramosus* (C.Richt.) Tzvelev	no info
		M12	*Limonium bungei* (Claus) Gamajun	no info
		M13	*Limonium sareptanum* (A.K.Becker) Gams	no info
		M13	*Onosma simplicissima* L.	no info
		M14	*Phlomoides puberula* (Krylov & Serg.) Adylov, Kamelin & Makhm.	
		M12	*Salvia tesquicola* Klok. & Pobed.	no info
		M13	*Seseli campestre* Besser	no info
		M13, M15	*Stipa capillata* L.	no info
		M12, M13, M14, M15	*Stipa lessingiana* Trin. & Rupr.	no info
		M12	*Stipa ucrainica* P.A.Smirn.	no info
		M13, M14, M15	*Tanacetum achilleifolium* (M.Bieb.) Sch.Bip.	no info
		M12	*Tanacetum millefolium* (L.) Tzvelev	no info
		M14	*Taraxacum serotinum* (Waldst. & Kit.) Fisch.	no info
		M12	*Tulipa schrenkii* Regel	no info
		M12	*Tulipa sylvestris* subsp. *australis* (Link) Pamp.	no info

U30	**‘ Marshland VU’**	U30	*Fraxinus excelsior* L.	yes
		U30	*Acanthus mollis* L.	not known
		U30	*Alnus glutinosa* (L.) Gaertn.	not known
		U30	*Arum italicum* Mill.	yes
		U30	*Brachypodium sylvaticum* (Huds.) P.Beauv.	no info
		U30	*Bryonia dioica* Jacq.	yes
		U30	*Crataegus monogyna* Jacq.	yes
		U30	*Frangula alnus* Mill.	not known
		U30	*Fraxinus angustifolia* Vahl subsp. *angustifolia*	yes
		U30	*Hedera helix* L.	no
		U30	*Iris foetidissima* L.	not known
		U30	*Lithospermum purpurocaeruleum* L.	no info
		U30	*Lonicera periclymenum* subsp. *hispanica* (Boiss. & Reut.) Nyman	yes
		U30	*Populus alba* L.	yes
		U30	*Ranunculus ficaria* L.	yes
		U30	*Rosa canina* L.	yes
		U30	*Rosa sempervirens* L.	no info
		U30	*Rubia tinctorum* L.	not known
		U30	*Salix* × *rubens* Schrank	yes
		U30	*Salix atrocinerea* Brot.	not known
		U30	*Salix salviifolia* Brot.	no info
		U30	*Sambucus nigra* L.	yes
		U30	*Tamarix africana* Poir.	not known
		U30	*Tamarix gallica* L.	yes
		U30	*Tamus communis* L.	yes
		fossil record	*Typha latifolia* L.	yes

		U30	*Ulmus minor* Mill.	yes
		U30	*Vinca difformis* Pourr.	no
		U30	*Vitis vinifera* subsp. *sylvestris* (C.C.Gmel.) Hegi	yes

U32	**’ Riparian VU’**	U32	*Limbarda crithmoides* (L.) Dumort.	yes
		U32	*Lonicera biflora* Desf.	no
		U32	*Nerium oleander* L.	not known
		U32	*Rubus ulmifolius* Schott	yes
		fossil record	*Salix* sp.	no info
		U32	*Tamarix gallica* L.	yes
		fossil record	*Typha latifolia* L.	yes
		U32	*Vinca difformis* Pourr.	no
		U32	*Vitex agnus-castus* L.	yes
		U32	*Populus alba*	yes

B	**‘ Alpine VU’**	B50	*Agrostis nevadensis* Boiss.	no info
		B50	*Artemisia granatensis* Boiss.	no info
		B50	*Biscutella glacialis* (Boiss. & Reut.) Jord.	no info
		B50	*Chaenorhinum glareosum* (Boiss.) Willk	no info
		B50	*Erigeron frigidus* Boiss. ex DC.	no info
		B50	*Festuca clementei* Boiss.	no info
		B50	*Festuca frigida* (Hack.) K.Richt.	no info
		B50	*Jasione crispa* subsp. *amethystina* (Lag. & Rodr.) Tutin	no info
		B50	*Trisetum glaciale* Boiss.	no info

Table A5.2: SOM Table S2. List of edible plant species with details on the edibility and processing of the respective edible plant parts.

VU Code	Species*	PlantpartID *	Edibility *	Large quantity	Comments on quantity	Processing RAW mandatory*	RAW processing*	Sources*
C	*Berberis vulgaris* subsp. *australis* (Boiss.) Heywood	berbvulg_fruits	raw, cooked	yes	as chutney, fruit soups, snack, seasoning, dried, tea; acid flavour mainly used in preserves, though some eat it raw when fully ripe	no		Rivera et al 2012; Essbare Wildpflanzen 2016
C	*Berberis vulgaris* subsp. *australis* (Boiss.) Heywood	berbvulg_leaves	raw, cooked	yes	as vegetable, seasoning/flavoring, condiment; as an acid nibble	no		Essbare Wildpflanzen 2016; Plants For A Future
C	*Crataegus monogyna* Jacq.	cratmono_fruits	raw, cooked	yes	normally used for making jams and preserves; mixed with flour and used for making bread	no		Rivera et al 2012; Plants For A Future; Essbare Wildpflanzen 2016
C	*Crataegus monogyna* Jacq.	cratmono_leaves	raw, cooked	no	as flavour, as tea	no		Essbare Wildpflanzen 2016
C	*Crataegus monogyna* Jacq.	cratmono_shoots	raw	no	they are a good addition to the salad bowl	no		Chevalier et al 2014
C	*Juniperus communis* subsp. *hemisphaerica* (C. Presl) Nyman	junicomm_fruits	raw, cooked	no	used as a flavouring in sauerkraut, stuffing, vegetable pates etc.,	no		Plants For A Future
C	*Picea abies* (L.) H.Karst.	piceabie_bark	raw, cooked	no		yes	dried	Plants For A Future
C	*Picea abies* (L.) H.Karst.	piceabie_catkins	raw, cooked	no	used as a flavouring	no		Plants For A Future
C	*Picea abies* (L.) H.Karst.	piceabie_seeds	raw	no		yes	removing from cone	Plants For A Future
C	*Picea abies* (L.) H.Karst.	piceabie_shoots	raw, cooked	no		no		Plants For A Future
C	*Rosa micrantha* Borrer ex Sm.	rosamicr_shoots	raw	no	as a snack	yes	peeled	Tardío et al 2006
C	*Viola hirta* L.	violhirt_buds	raw, cooked	yes	based on info for leaves	no	based on info for leaves	Plants For A Future
C	*Viola hirta* L.	violhirt_flowers	raw	no	used to decorate salads and desserts	no		Plants For A Future
C	*Viola hirta* L.	violhirt_leaves	raw, cooked	yes	salad, used in bulk	no		Plants For A Future
G	*Alliaria petiolata* (M.Bieb.) Cavara & Grande	allipeti_ inflorescences	raw	no	used as aromatic decoration for dishes	no		Essbare Wildpflanzen 2016
G	*Alliaria petiolata* (M.Bieb.) Cavara & Grande	allipeti_leaves	raw, cooked	no	as a potherb or as a flavouring in cooked foods, they can be finely chopped and added to salads	no		Plants For A Future; Essbare Wildpflanzen 2016
G	*Alliaria petiolata* (M.Bieb.) Cavara & Grande	allipeti_roots	raw, cooked	no	used as condiment horse radish like, spicy flavor	no		Essbare Wildpflanzen 2016
G	*Alliaria petiolata* (M.Bieb.) Cavara & Grande	allipeti_seeds	raw, cooked	no		no info		Essbare Wildpflanzen 2016
G	*Alliaria petiolata* (M.Bieb.) Cavara & Grande	allipeti_shoots	raw, cooked	no		no info		Essbare Wildpflanzen 2016
G	*Anthoxanthum odoratum* L.	anthodor_leaves	raw, cooked	no	used to prepare tea	no info		Plants For A Future

G	*Berberis vulgaris* subsp. *australis* (Boiss.) Heywood	berbvulg_fruits	raw, cooked	yes	as chutney, fruit soups, snack, seasoning, dried, tea; acid flavour mainly used in preserves, though some eat it raw when fully ripe	no		Rivera et al 2012; Essbare Wildpflanzen 2016;
G	*Berberis vulgaris* subsp. *australis* (Boiss.) Heywood	berbvulg_leaves	raw, cooked	yes	as vegetable, seasoning/flavoring, condiment; as an acid nibble	no		Essbare Wildpflanzen 2016; Plants For A Future
G	*Clinopodium vulgare* L.	clinvulg_flowers	raw, cooked	no	flavouring decoration for salads and raw vegetables	no		Essbare Wildpflanzen 2016
G	*Clinopodium vulgare* L.	clinvulg_leaves	raw, cooked	no	flavouring in cooked foods or fresh as a flavouring in salads	no		Plants For A Future; Essbare Wildpflanzen 2016
G	*Clinopodium vulgare* L.	clinvulg_ shootingtips	raw, cooked	no		no		Essbare Wildpflanzen 2016
G	*Clinopodium vulgare* L.	clinvulg_ wholeplant	raw	no	used as a condiment or additive in salads	no		Essbare Wildpflanzen 2016
G	*Crataegus monogyna* Jacq.	cratmono_fruits	raw, cooked	yes	normally used for making jams and preserves; mixed with flour and used for making bread etc.	no	no	Rivera et al 2012; Plants For A Future; Essbare Wildpflanzen 2016
G	*Crataegus monogyna* Jacq.	cratmono_leaves	raw, cooked	no	as flavour, as tea	no	no	Essbare Wildpflanzen 2016
G	*Crataegus monogyna* Jacq.	cratmono_shoots	raw	no	they are a good addition to the salad bowl	no	no	Chevalier et al 2014
G	Cytisus scoparius (L.) Link	cytiscop_ flowerbuds	raw, cooked	no	used as a substitute for capers, they can also be added to salads. used as a caper substitute	yes	pickeld	Plants For A Future
G	*Fraxinus angustifolia* Vahl subsp. *angustifolia*	fraxangu_seeds	raw	no	used as a condiment	yes	peeled	Plants For A Future
G	*Juniperus communis* subsp. *hemisphaerica* (C. Presl) Nyman	junicomm_fruits	raw, cooked	no	used as a flavouring in sauerkraut, stuffing, vegetable pates etc,	no		Plants For A Future
G	*Primula acaulis* (L.) Hill	primacau_flowers	raw, cooked	yes	can also be used as a cooked vegetable or in conserves etc, attractive garnish to salads	no		Plants For A Future
G	*Primula acaulis* (L.) Hill	primacau_leaves	raw, cooked	no	potherb, added to soups	no		Plants For A Future
G	*Prunus mahaleb* L.	prunmaha_seeds	raw, cooked	no	dried seed kernels are used as a flavouring in breads, sweet pastries, confectionery etc	yes	drying	Plants For A Future
G	*Quercus pyrenaica* Willd.	querpyre_seeds	raw, cooked	yes	used as a thickening in stews etc or mixed with cereals for making bread	yes	commonly dried	Useful Temperate Plants; Tardío et al 2006
G	*Rosa canina* L.	rosacani_fruits	raw, cooked	yes		yes		Plants For A Future; Tardío et al 2006
G	*Rosa canina* L.	rosacani_leaves	raw, cooked	yes	Young leaves in early spring are cut into small pieces and mixed into stews, soups or vegetable dishes	yes	drying	Plants For A Future; Kostbare Natur
G	*Rosa canina* L.	rosacani_petals	raw, cooked	yes	eaten as vegetable	yes	base best removed	Plants For A Future
G	*Rosa canina* L.	rosacani_shoots	raw	no	as a snack	yes	peeled	Tardío et al 2006

G	*Rosa pouzinii* Tratt.	rosapouz_petals	raw	yes	young ones in early spring are cut into small pieces and mixed into stews, soups or vegetable dishes	no info		Tardío et al 2006; Plants For A Future; Kostbare Natur
	Rosa pouzinii Tratt.	rosapouz_leaves						Kostbare Natur
G	*Rosa pouzinii* Tratt.	rosapouz_fruits	raw	yes		no info		Tardío et al 2006
G	*Rosa pouzinii* Tratt.	rosapouz_shoots	raw	no	eaten raw as a snack	yes	peeled	Tardío et al 2006
G	*Sorbus aria* (L.) Crantz	sorbaria_flowers	raw, cooked	no	are prepared as tea in early summer or used candied or in sweet dishes as a flower cream	no info		Essbare Wildpflanzen 2016
G	*Sorbus aria* (L.) Crantz	sorbaria_fruits	raw, cooked	yes		yes	stored in a cool dry place until ripe	Plants For A Future

J	Amelanchier ovalis Medik.	ameloval_fruits	raw, cooked	yes		no		Plants For A Future; Tardío et al 2006
J	*Asparagus acutifolius* L.	aspaacut_shoots	raw, cooked	yes	as vegetable, rarely raw as a snack, as seasoning	no		Plants For A Future; Tardío et al 2006
J	*Berberis vulgaris* subsp. *australis* (Boiss.) Heywood	berbvulg_fruits	raw, cooked	yes	as chutney, fruit soups, snack, seasoning, dried, tea; acid flavour mainly used in preserves, though some eat it raw when fully ripe	no		Rivera et al 2012; Essbare Wildpflanzen 2016;
J	*Berberis vulgaris* subsp. *australis* (Boiss.) Heywood	berbvulg_leaves	raw, cooked	yes	as vegetable, seasoning/flavouring, condiment; as an acid nibble	no		Essbare Wildpflanzen 2016; Plants For A Future
J	*Crataegus monogyna* Jacq.	cratmono_fruits	raw, cooked	yes	normally used for making jams and preserves; mixed with flour and used for making bread etc.	no	no	Rivera et al 2012; Plants For A Future; Essbare Wildpflanzen 2016
J	*Crataegus monogyna* Jacq.	cratmono_leaves	raw, cooked	no	as flavour, as tea	no	no	Essbare Wildpflanzen 2016
J	*Crataegus monogyna* Jacq.	cratmono_shoots	raw	no	they are a good addition to the salad bowl	no	no	Chevalier et al 2014
J	*Ephedra fragilis* Desf.	ephefrag_fruits	raw, cooked	no info		no info		Plants For A Future
J	*Juniperus phoenicea* L.	juniphoe_fruits	raw, cooked	no	used as a strong flavouring for wine, mead, and other alcoholic beverages, as well as a spice for meats, stews, sauerkraut and other dishes	no info		Gardening know how
J	*Pinus halepensis* Mill.	pinuhale_resin	raw, cooked	no	used for chewing	yes	from the trunk	Plants For A Future
J	*Pinus halepensis* Mill.	pinuhale_seeds	raw, cooked	yes	eaten as a snack either raw or roasted. also added to porridge, and used in the production of quzmat bread	yes	removing from cone	Tardío et al 2006; Tukan et al 2013
J	*Pistacia lentiscus* L.	pistlent_resin	raw, cooked	no	used as a flavouring in puddings, sweets (including 'Turkish delight') cakes etc, it is chewed to strengthen the gums and as a breath sweetener	yes	obtained from bark incisions	Plants For A Future
J	*Pistacia lentiscus* L.	pistlent_seeds	raw, cooked	no	used as oil	yes	oil obtained	Plants For A Future

							from seeds	
J	*Quercus coccifera* L.	quercocc_galls	raw	no	green galls are eaten as a snack	no info		Tardío et al 2006
J	*Quercus coccifera* L.	quercocc_seeds	raw, cooked	yes	used as a thickening in stews etc. or mixed with cereals for making bread, or as coffee	yes	dried, grounded, watering	Tardío et al 2006; Plants For A Future
J	*Quercus ilex* subsp. *rotundifolia* (Lam.) O.Schwarz ex Tab.Morais	querilex_seeds	raw, cooked	yes	sweet and low tannin content	yes	needs to be cracked	Tardío et al 2006; Rosengarten 2004
J	*Rhamnus alaternus* L.	rhamalat_fruits	raw	no info		no info		Tardío et al 2006
J	*Rosa canina* L.	rosacani_fruits	raw, cooked	yes		yes	hairs should be removed	Plants For A Future; Tardío et al 2006
J	*Rosa canina* L.	rosacani_leaves	raw, cooked	yes		yes	drying	Plants For A Future
J	*Rosa canina* L.	rosacani_petals	raw, cooked	yes	eaten as vegetable	yes	base best removed	Plants For A Future
J	*Rosa* canina L.	rosacani_shoots	raw	no	as a snack	yes	peeled	Tardío et al 2006
J	*Ruscus aculeatus* L.	ruscacul_shoots	raw, cooked	yes	used as asparagus substitute (vegetable use), used in salads	no		Plants For A Future; Tardío et al 2006; Tardío et al 2016
J	*Sorbus aria* (L.) Crantz	sorbaria_flowers	raw, cooked	no	are prepared as tea in early summer or used candied or in sweet dishes as a flower cream	no info		Essbare Wildpflanzen 2016
J	*Sorbus aria* (L.) Crantz	sorbaria_fruits	raw, cooked	yes		yes		Plants For A Future

M	*Erophila verna* (L.) DC.	eropvern_leaves	raw	no	minute plant	no		Plants For A Future; Düll Kutzelnigg 2011
M	*Allium sphaerocephalon* L.	allispha_bulbs	raw, cooked	yes	large plant, mild flavor	no		Plants For A Future
M	*Allium sphaerocephalon* L.	allispha_flowers	raw	yes	used as a garnish on salads	no		Plants For A Future
M	*Allium sphaerocephalon* L.	allispha_leaves	raw, cooked	yes	large plant, mild flavour	no		Plants For A Future
M	*Artemisia austriaca* Jacq.	arteaust_ aerialpart	raw, cooked	no	can be used as a spice, either dried or raw	no		Essbare Wildpflanzen 2016
M	*Falcaria vulgaris* Bernh.	falcvulg_roots	raw, cooked	yes	eaten as vegetable	no		Essbare Wildpflanzen 2016; Gala search
M	*Galium ruthenicum* Willd.	galiruth_flowers	raw, cooked	no	used in salads. A sweet pudding can be made from the juice of the boiled flowers. used as an aroma, e.g., for herbal limos and other beverages	no		Essbare Wildpflanzen 2016
M	*Galium ruthenicum* Willd.	galiruth_ floweringstems	raw, cooked	no	a yellow dye from the flowering stems is used as a food colouring	no info		Plants For A Future & Essbare Wildpflanzen 2016
M	*Galium ruthenicum* Willd.	galiruth_seeds	raw, cooked	no	kept in dark containers, used in winter as fresh seed or roasted as a coffee substitute	no		Essbare Wildpflanzen 2016

M	*Galium ruthenicum* Willd.	galiruth_shoots	raw, cooked	yes	the thick, juicy, very mild shoots that sprout in spring can be used as the main ingredient and as an addition to any leafy vegetable dish or as spinach	no		Essbare Wildpflanzen 2016
M	*Galium ruthenicum* Willd.	galiruth_shootingtips	raw, cooked	no	shooting tips can be prepared as salad. can be used in mixtures of minced herbs. can be used as pesto and added in juices.	no		Essbare Wildpflanzen 2016
M	*Holosteum umbellatum* L.	holoumbe_flowers	raw, cooked	no	additive for a lot of cooked dishes, as well as salads, pesto and as edible decoration for sweet and salty dishes	no		Essbare Wildpflanzen 2016
M	*Holosteum umbellatum* L.	holoumbe_ influorescences	raw, cooked	yes	additive for a lot of cooked dishes, as well as salads, pesto	no		Essbare Wildpflanzen 2016
M	*Holosteum umbellatum* L.	holoumbe_leaves	raw, cooked	yes	additive for a lot of cooked dishes, as well as salads, pesto	no		Essbare Wildpflanzen 2016
M	*Holosteum umbellatum* L.	holoumbe_stems	raw, cooked	yes	additive for a lot of cooked dishes, as well as salads, pesto	no		Essbare Wildpflanzen 2016

U30	*Crataegus monogyna* Jacq.	cratmono_fruits	raw, cooked	yes	normally used for making jams and preserves; mixed with flour and used for making bread	no	no	Rivera et al 2012; Plants For A Future; Essbare Wildpflanzen 2016
U30	*Crataegus monogyna* Jacq.	cratmono_leaves	raw, cooked	no	as flavour, as tea	no	no	Essbare Wildpflanzen 2016
U30	*Crataegus monogyna* Jacq.	cratmono_shoots	raw	no	they are a good addition to the salad bowl	no	no	Chevalier et al 2014
U30	*Fraxinus angustifolia* Vahl subsp. *angustifolia*	fraxangu_seeds	raw	no	used as a condiment	yes	peeled	Plants For A Future
U30	*Fraxinus excelsior* L.	fraxexce_seeds	raw	no	for seasoning; used as a condiment for other foods	yes	peeled, pickled; salted	Feed plants 3; Essbare Wildpflanzen 2016; Plants For A Future
U30	*Fraxinus excelsior* L.	fraxexce_shoots	raw	yes		no	no	Essbare Wildpflanzen 2016
U30	*Lonicera periclymenum* subsp. *hispanica* (Boiss. & Reut.) Nyman	loniperi_sap	raw	no	The nectar is extracted from the flowers, poisonous in large doses.			Plants For A Future
U30	*Ranunculus ficaria* L.	ranufica_ flowerbuds	raw	no	make a good substitute for capers	yes	pickled	Plants For A Future
U30	*Ranunculus ficaria* L.	ranufica_leaves	raw, cooked	yes	the first leaves in spring make an excellent salad, made like spinach, as potherb	no		Plants For A Future
U30	*Rosa canina* L.	rosacani_fruits	raw, cooked	yes		yes	hairs should be removed	Plants For A Future; Tardío et al 2006
U30	*Rosa canina* L.	rosacani_leaves	raw, cooked	yes		yes	drying	Plants For A Future
U30	*Rosa canina* L.	rosacani_petals	raw, cooked	yes	eaten as vegetable	yes	base best removed	Plants For A Future
U30	*Rosa canina* L.	rosacani_shoots	raw	no	as a snack	yes	peeled	Tardío et al 2006
U30	*Salix × rubens* Schrank	salirube_bark	raw, cooked	no	probably not edible in large quantities, very	no info		Plants For A Future

					bitter and high medicinal use			
U30	*Salix × rubens* Schrank	salirube_shoots	raw, cooked	no	probably not edible in large quantities, very bitter and high medicinal use	no info		Plants For A Future
U30	*Sambucus nigra* L.	sambnigr_flowers	raw, cooked	no	raw as a refreshing snack. Flowers provide muscatel flavor to stewed fruits and jams.	no	no	Plants For A Future
U30	*Sambucus nigra* L.	sambnigr_fruits	raw, cooked	yes	the raw fruit is not acceptable to many tastes, when cooked it makes jams, preserves, pies and so forth. Can be used fresh or dried, it is also often used to make wine	no	tastes better, if cooked or dried	Plants For A Future
U30	*Tamarix gallica* L.	tamagall_manna	raw, cooked	yes	"the manna of Persia"	no	sieving	Plants For A Future; Grami 1998
U30	*Typha latifolia* L.	typhlati_ floweringspikes	raw, cooked	yes	young flowering stems can be used to prepare soup	no	cooked	Plants For A Future
U30	*Typha latifolia* L.	typhlati_pollen	raw, cooked	no		no		Plants For A Future
U30	*Typha latifolia* L.	typhlati_rhizomes	raw, cooked	yes		yes	macerated	Grossheim 1952; Plants For A Future
U30	*Typha latifolia* L.	typhlati_shoots	raw	yes	an asparagus substitute	yes	peeled	Plants For A Future
U30	*Typha latifolia* L.	typhlati_stems	raw, cooked	yes		yes	remove outer layer	Plants For A Future
U30	*Ulmus minor* Mill.	ulmumino_leaves	raw, cooked	yes	young ones eaten as vegetable (mild flavour) or addition to salads; tea also made from leaves	no		Useful Temperate Plants
U30	*Ulmus minor* Mill.	ulmumino_seeds	raw	yes	immature ones are used after they have formed	yes	peeled	Useful Temperate Plants
U30	*Vitis vinifera* subsp. *sylvestris* (C.C.Gmel.) Hegi	vitivini_fruits	raw, cooked	yes	juicy, sweet fruits can be eaten raw, added to fruit salads, added to cheese platters, processed into dried fruit. Fruits can be pressed into juice or fermented further into wine	no		Plants For A Future; Essbare Wildpflanzen 2016
U30	*Vitis vinifera* subsp. *sylvestris* (C.C.Gmel.) Hegi	vitivini_sap	raw	no	used as a drink	no		Plants For A Future
U30	*Vitis vinifera* subsp. *sylvestris* (C.C.Gmel.) Hegi	vitivini_ flowerclusters	raw, cooked	yes	used as a vegetable; raw use as beverage flavoring; tart used as an aromatic	no	but only sophisticated use	Plants For A Future; Forum Ernährung; Essbare Wildpflanzen 2016
U30	*Vitis vinifera* subsp. *sylvestris* (C.C.Gmel.) Hegi	vitivini_seeds	raw, cooked	no	can be eaten with the fruits, and are said to be very healthy,	yes	raosted, the oil has to be obtained from the seeds	Plants For A Future
U30	Vitis vinifera subsp. sylvestris (C.C.Gmel.) Hegi	vitivini_tendrils	raw, cooked	yes	tendrils are used for leaf roulades or cut into strips as sauerkraut.	no		Plants For A Future;Essbare Wildpflanzen 2016
U30	*Vitis vinifera* subsp. *sylvestris* (C.C.Gmel.) Hegi	vitivini_leaves	raw, cooked	yes	young leaves are used for leaf roulades or cut into strips as sauerkraut.	no	tender young ones	Essbare Wildpflanzen 2016

U32	*Rubus ulmifolius* Schott	rubuulmi_flowers	raw	no		no info		Tardío et al 2006
U32	*Rubus ulmifolius* Schott	rubuulmi_fruits	raw, cooked	yes	cooked in jams, and for making liqueur	no	smashed with sugar	Plants For A Future; Tardío et al 2006; Tardío et al 2016
U32	*Rubus ulmifolius* Schott	rubuulmi_shoots	raw, cooked	yes	as vegetable, in salads; as a snack	yes	peeled	Tardío et al 2006; Tardío et al 2016
U32	*Tamarix gallica* L.	tamagall_manna	raw, cooked	yes	"the manna of Persia"	no	sieving	Plants For A Future; Grami 1998
U32	*Typha latifolia* L.	typhlati_ floweringspikes	raw, cooked	yes	young flowering stems can be used to prepare soup	no	cooked	Plants For A Future
U32	*Typha latifolia* L.	typhlati_pollen	raw, cooked	no		no		Plants For A Future
U32	*Typha latifolia* L.	typhlati_rhizomes	raw, cooked	yes		yes	macerated	Grossheim 1952; Plants For A Future
U32	*Typha latifolia* L.	typhlati_shoots	raw	yes	an asparagus substitute	yes	peeled	Plants For A Future
U32	*Typha latifolia* L.	typhlati_stems	raw, cooked	yes		yes	remove outer layer	Plants For A Future
U32	*Vitex agnus-castus* L.	viteagnu_fruits	raw, cooked	no	used as a condiment, it is a pepper substitute	no info		Plants For A Future
U32	*Vitex agnus-castus* L.	viteagnu_leaves	raw, cooked	no	the aromatic leaves are also used as a spice	no info		Plants For A Future

Table A5.3: SOM Table S3. List of edible plant species that can be eaten raw and in larger quantities without sophisticated processing necessary. Seasonal availability is inferred from information on phenology and harvesting of the respective edible plant parts.

VU Code	Species*	plantpartID	Seasonal availability	Phenology	Comments on phenology	Harvesting	Sources*
			*derived info				
C	*Berberis vulgaris* subsp. *australis* (Boiss.) Heywood	berbvulg_fruits	*VIII-X	IX-X	seeds ripen from September to October	mature fruits are harvested from August to September	Plants For A Future; Essbare Wildpflanzen 2016
C	*Berberis vulgaris* subsp. *australis* (Boiss.) Heywood	berbvulg_leaves	III-XI	III-XI	it is in leaf then	young ones	Plants For A Future; Essbare Wildpflanzen 2016
C	*Crataegus monogyna* Jacq.	cratmono_fruits	IX-XI	IX-XI	seeds ripen then	September to October	Tardío et al 2016; Plants For A Future; Essbare Wildpflanzen 2016
C	*Viola hirta* L.	violhirt_buds	II-IV	II-IV	in flower from February to April, seeds ripen from April to June		Plants For A Future
C	*Viola hirta* L.	violhirt_leaves	I-XII	I-XII	is in leaf all year	available through winter	Plants For A Future
G	*Berberis vulgaris* subsp. *australis* (Boiss.) Heywood	berbvulg_fruits	*VIII-X	IX-X	seeds ripen from September to October	mature fruits are harvested from August to September	Plants For A Future; Essbare Wildpflanzen 2016
G	*Berberis vulgaris* subsp. *australis* (Boiss.) Heywood	berbvulg_leaves	III-XI	III-XI	it is in leaf then	young ones	Plants For A Future; Essbare Wildpflanzen 2016
G	*Crataegus monogyna* Jacq.	cratmono_fruits	IX-XI	IX-XI	seeds ripen then	September to October	Tardío et al 2016; Plants For A Future; Essbare Wildpflanzen 2016
G	*Primula acaulis* (L.) Hill	primacau_flowers	XII-V	XII-V			Plants For A Future
G	*Rosa canina* L.	rosacani_fruits	X-XII	X-XII	seeds ripen from October to December	frost softens and sweetens the flesh	Plants For A Future
G	*Rosa canina* L.	rosacani_leaves	*III-V			young leaves in early spring	Kostbare Natur
G	*Rosa canina* L.	rosacani_petals	VI-VII	VI-VII	is in flower from June to July		Plants For A Future
G	*Rosa pouzinii* Tratt.	rosapouz_petals	VI-VII	VI-VII	information taken from Rosa canina	information taken from Rosa canina	
G	*Rosa pouzinii* Tratt.	rosapouz_leaves	III-V		information taken from Rosa canina	information taken from Rosa canina	
G	*Rosa pouzinii* Tratt.	rosapouz_fruits	X-XII	X-XII	information taken from Rosa canina	information taken from Rosa canina	
G	*Sorbus aria* (L.) Crantz	sorbaria_fruits	IX-XI	IX-XI	seeds ripen	August until November, best to harvest after the first frost	Plants For A Future; Essbare Wildpflanzen 2016
J	*Amelanchier ovalis* Medik.	ameloval_fruits	VII	VII	seeds ripen in July		Plants For A Future
J	*Asparagus acutifolius* L.	aspaacut_shoots	*III-V		spring	young ones; the new shoots are rather thin and are not produced in abundance	Plants For A Future; Tardío et al 2006; Tardío et al 2016
J	*Berberis vulgaris* subsp. *australis* (Boiss.) Heywood	berbvulg_fruits	*VIII-X	IX-X	seeds ripen from September to October	mature fruits are harvested from August to September	Plants For A Future; Essbare Wildpflanzen 2016
J	*Berberis vulgaris* subsp. *australis* (Boiss.) Heywood	berbvulg_leaves	III-XI	III-XI	it is in leaf then	young ones	Essbare Wildpflanzen 2016; Plants For A Future
J	*Crataegus monogyna* Jacq.	cratmono_fruits	IX-XI	IX-XI	seeds ripen then	September to October	Tardío et al 2016; Plants For A Future; Essbare Wildpflanzen 2016
J	*Pinus halepensis* Mill.	pinuhale_seeds	*III-V		spring		Tardío et al 2006

J	*Quercus ilex* subsp. *rotundifolia* (Lam.) O.Schwarz ex Tab.Morais	querilex_seeds	VIII-X	VIII-X			Navarro et al 1998
J	*Rhamnus alaternus* L.	rhamalat_fruits	*VI-VIII		summer		Tardío et al 2006
J	*Rosa canina* L.	rosacani_fruits	X-XII	X-XII	seeds ripen from October to December	frost softens and sweetens the flesh	Plants For A Future
J	*Rosa canina* L.	rosacani_leaves	*III-V			young leaves in early spring	Kostbare Natur
J	*Rosa canina* L.	rosacani_petals	VI-VII	VI-VII	is in flower from June to July		Plants For A Future
J	*Ruscus aculeatus* L.	ruscacul_shoots	*III-V		spring	young and tender ones; harvested in spring as they grow through the soil	Plants For A Future; Tardío et al 2006
J	*Sorbus aria* (L.) Crantz	sorbaria_fruits	IX-XI	IX-XI	seeds ripen	August until November, best to harvest after the first frost, eat them then dried or raw	Plants For A Future; Essbare Wildpflanzen 2016

M	*Allium sphaerocephalon* L.	allispha_bulbs	*VIII-III		the bulb lasts until the next spring		Mein schöner Garten
M	*Allium sphaerocephalon* L.	allispha_flowers	VI-VII	VI-VII	Bloom Time: June to July		Missouri botanical garden
M	*Allium sphaerocephalon* L.	allispha_leaves	*III-VIII		in spring, the leaves and the flower stem sprout from the underground storage organ.		Mein schöner Garten
M	*Falcaria vulgaris* Bernh.	falcvulg_roots	I-XII	I-XII	the high drought resistance is due to a taproot that can be a meter or more deep.		Gala search
M	*Holosteum umbellatum* L.	holoumbe_ influorescences	III-V	III-V			Essbare Wildpflanzen 2016
M	*Holosteum umbellatum* L.	holoumbe_stems	III-V	III-V			Essbare Wildpflanzen 2016
M	*Holosteum umbellatum* L.	holoumbe_leaves	III-V	III-V			Essbare Wildpflanzen 2016
M	*Galium ruthenicum* Willd.	galiruth_shoots	III-V	III-V	spring		Essbare Wildpflanzen 2016

U30	*Crataegus monogyna* Jacq.	cratmono_fruits	IX-XI	IX-XI	seeds ripen then	September to October	Tardío et al 2016; Plants For A Future; Essbare Wildpflanzen 2016
U30	*Fraxinus excelsior* L.	fraxexce_shoots	IV			young ones in April	Essbare Wildpflanzen 2016
U30	*Ranunculus ficaria* L.	ranufica_leaves	I-VI	I-VI		young ones; the leaves turn poisonous as the fruit matures	Plants For A Future
U30	*Rosa canina* L.	rosacani_fruits	X-XII	X-XII	seeds ripen from October to December	frost softens and sweetens the flesh	Plants For A Future
U30	*Rosa canina* L.	rosacani_leaves	*III-V			young leaves in early spring	Kostbare Natur
U30	*Rosa canina* L.	rosacani_petals	VI-VII	VI-VII	in flower from June to July		Plants For A Future
U30	*Sambucus nigra* L.	sambnigr_fruits	*VIII-XII	VIII-X	the fruits remain on the branches even in winter		Feed plants 3; Plants For A Future
U30	*Tamarix gallica* L.	tamagall_manna	*VIII-X			gathering may begin in late August and continue until mid-October	Grami 1998
U30	*Typha latifolia* L.	typhlati_ floweringspikes	VI-VIII	VI-VIII	in flower from June to August		Plants For A Future
U30	*Typha latifolia* L.	typhlati_rhizomes	*I-XII		always available	best harvested from late autumn to early spring	Grossheim 1952; Plants For A Future
U30	*Typha latifolia* L.	typhlati_shoots	IV-VI	IV-VI		May to August; young ones in spring	Plants For A Future
U30	*Typha latifolia* L.	typhlati_stems	*V-VIII			May to August	Plants For A Future
U30	*Ulmus minor* Mill.	ulmumino_leaves	*III-V			young ones; the very young leaves of all	Useful Temperate Plants

						Ulmus species can be eaten	
U30	*Ulmus minor* Mill.	ulmumino_fruits	*III-V			immature fruits	Useful Temperate Plants
U30	*Vitis vinifera* subsp. *sylvestris* (C.C.Gmel.) Hegi	vitivini_fruits	IX-X	IX-X			Plants For A Future
U30	*Vitis vinifera* subsp. *sylvestris* (C.C.Gmel.) Hegi	vitivini_leaves	*III-V			tender young ones	Essbare Wildpflanzen 2016
U30	*Vitis vinifera* subsp. *sylvestris* (C.C.Gmel.) Hegi	vitivini_tendrils	*III-V			young ones	Plants For A Future, Essbare Wildpflanzen 2016

U32	*Rubus ulmifolius* Schott	rubuulmi_fruits	VII-IX	VII-IX			Herrera 1986
U32	*Rubus ulmifolius* Schott	rubuulmi_shoots	*III-V		spring	young ones	Tardío et al 2006; Tardío et al 2016
U32	*Tamarix gallica* L.	tamacana_manna	*VIII-X			gathering may begin in late August and continue until mid-October	Grami 1998
U32	*Typha latifolia* L.	typhlati_ floweringspikes	VI-VIII	VI-VIII	in flower from June to August		Plants For A Future
U32	*Typha latifolia* L.	typhlati_rhizomes	*I-XII		always available	best harvested from late autumn to early spring	Grossheim 1952; Plants For A Future
U32	*Typha latifolia* L.	typhlati_shoots	IV-VI	IV-VI		May to August; young ones in spring	Plants For A Future
U32	*Typha latifolia* L.	typhlati_stems	*V-VIII			May to August	Plants For A Future

Table A5.4: Table SOM References. Complete reference list of the sources for the EPP database.

Reference ID*	**Full reference**	**Access date**
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Gala search	https://galasearch.de/plants/13688-falcaria-vulgaris	July 2020
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Mein schöner Garten	https://www.mein-schoener-garten.de/pflanzen/zierlauch	July 2020
Missouri botanical garden	https://www.missouribotanicalgarden.org/PlantFinder/PlantFinderDetails.aspx?taxonid=282226&isprofile=0&	July 2020
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