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JQS Journal of Quaternary Science QRA Quaternary Research Association

Iberian Neanderthals in forests and savannahs

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ABSTRACT: This article aims to delve into the reality of glacial refuges of forests and tree species (including conifers, mesothermophilous angiosperms and xerothermic scrub) during the cold dry phases of the Iberian Pleistocene in which there is evidence of occupation of Middle Palaeolithic people. The research framework focuses on the eastern sector of the Iberian Peninsula due to the physiographic, palaeobotanical and archaeological peculiarities, substantiated by recent studies. We contend that some Neanderthal occupations developed in the context of high geobiological complexity, high biological diversity and highly structured forest ecosystems. We highlight the importance of glacial refuges as local anomalies that, however, would be contingent on vegetational development, and on the survival of Palaeolithic groups in areas with a broad diversity of natural resources.
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KEYWORDS: Iberian Peninsula; Neanderthals; palaeoecology; palynology; Pleistocene

Introduction

In consonance with the long-standing prevalence of palaeoecological information from high latitudes, the traditional vision of cold-adapted Neanderthals (e.g. Trinkaus, 1981; Steegmann *et al.*, 2002) has been connected with 'mammoth steppes', involving denuded environments with a scarcity of trees (e.g. Markova *et al.*, 1995; Rudaya *et al.*, 2017). Although not without resistance, this interpretation has been modified over time, to accept open forested (savannah) as a biotope relevant to Neanderthals (Carrión *et al.*, 2008, 2019a,b), such as they were for *Sahelanthropus* (Brunet *et al.*, 2005), *Orrorin* (Roche *et al.*, 2013), *Ardipithecus* (Suwa and Ambrose, 2014), *Australopithecus* (Bonnefille *et al.*, 2004; Haile-Selassie *et al.*, 2010), *Kenyanthropus* (Leakey *et al.*, 2001), *Paranthropus* (de Ruiter *et al.*, 2009), and early *Homo* from Africa (deMenocal and Bloemendal, 1995; deMenocal, 2004; Wood and Strait, 2004) and Asia (Dennell and Roebroeks, 2005; Finlayson *et al.*, 2011).

Recent investigations have further diversified the landscape of occupation, by showing that Neanderthal populations survived for hundreds of millennia under relatively closed-forest habitat conditions which were not substantially stressed by climate during cold stadials. Three of these critical sites are the Iberian caves of Bolomor (Ochando *et al.*, 2019), Teixoneres (Ochando *et al.*, 2020a) and Toll (Ochando *et al.*, 2020b). Some independent studies support these data based on genetic and anatomical information deducing that Neanderthals were accomplished sprinters, ambushing and hunting prey over short distances (Stewart, 2005; Finlayson and Carrión, 2006; Rosas, 2016; Stewart *et al.*, 2019).

In this paper, we review palaeopalynological data for the Iberian Peninsula supporting the perspective of forested habitats for Neanderthal humans during glacial stadials. For practical purposes, we have adopted a wide temporal range reviewing the time span between Marine Isotope Stage (MIS) 12 to the Last Glacial Maximum MIS 2. We need to be aware that the taxonomic boundaries of *Homo neanderthalensis* are diffuse. The oldest confirmed Neanderthals are found in the Iberian Peninsula, dated to at least 430 000 years ago (Atapuerca Sima de los Huesos; Bischoff *et al.*, 2007; Meyer *et al.*, 2016). While their taxonomic connection with *H. heidelbergensis* is still open to debate (Roksandic *et al.*, 2018; Bermúdez de Castro *et al.*, 2019; Carrión and Walker, 2019; Rosas *et al.*, 2019), it does not affect the results of the present work, as Heidelbergs represent Neanderthals or at least an early part of the Neanderthal lineage.

With respect to their demise, it must be kept in mind that Neanderthals merged genetically with other archaic hominins that inhabited western Eurasia during the end of the last glacial

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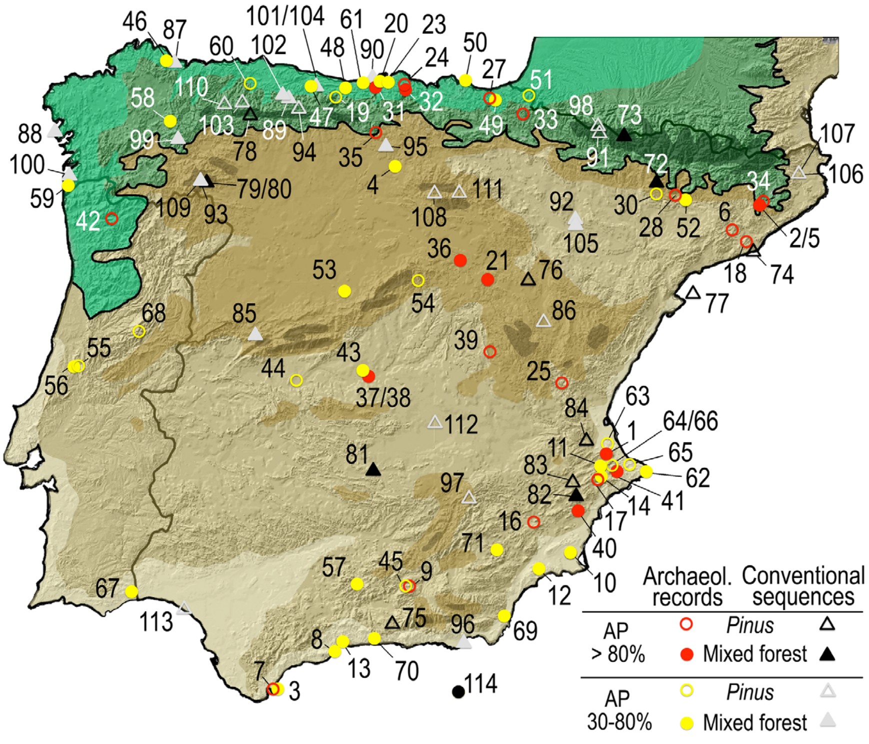

Figure 1. Location of Iberian sites with palaeobotanical data including stadials MIS 12 onwards (late Mid- and Upper Pleistocene). [Color figure can be viewed at wileyonlinelibrary.com]

stage (Krause *et al.*, 2010; Wall *et al.*, 2013; Bermúdez de Castro *et al.*, 2016; Kuhlwilm *et al.*, 2016; Lalueza-Fox, 2017; Slon *et al.*, 2018; Finlayson, 2019). The exact age of the last Neanderthal population is therefore far from clear, although it probably reached the end of MIS 3 in southern Iberia (Zilhão *et al.*, 2017; Carrión *et al.*, 2019c; Finlayson, 2019), while in the north of Iberia they disappeared as early as ca. 48–45 cal BP (Marín-Arroyo *et al.*, 2018). It must also be recognized that the connections between human species taxonomy and lithic technology are not straightforward (Finlayson, 2019; Greenbaum *et al.*, 2019; Haws *et al.*, 2020). While the Mousterian is most likely an exclusively Neanderthal industry in Western Europe (but not in Western Asia) and the post-Aurignacian Upper Palaeolithic seems clearly attributable to *Homo sapiens* (Finlayson, 2019), it is still not clear who manufactured industries such as the Szeletian, Uluzzian, Chatelperronian,

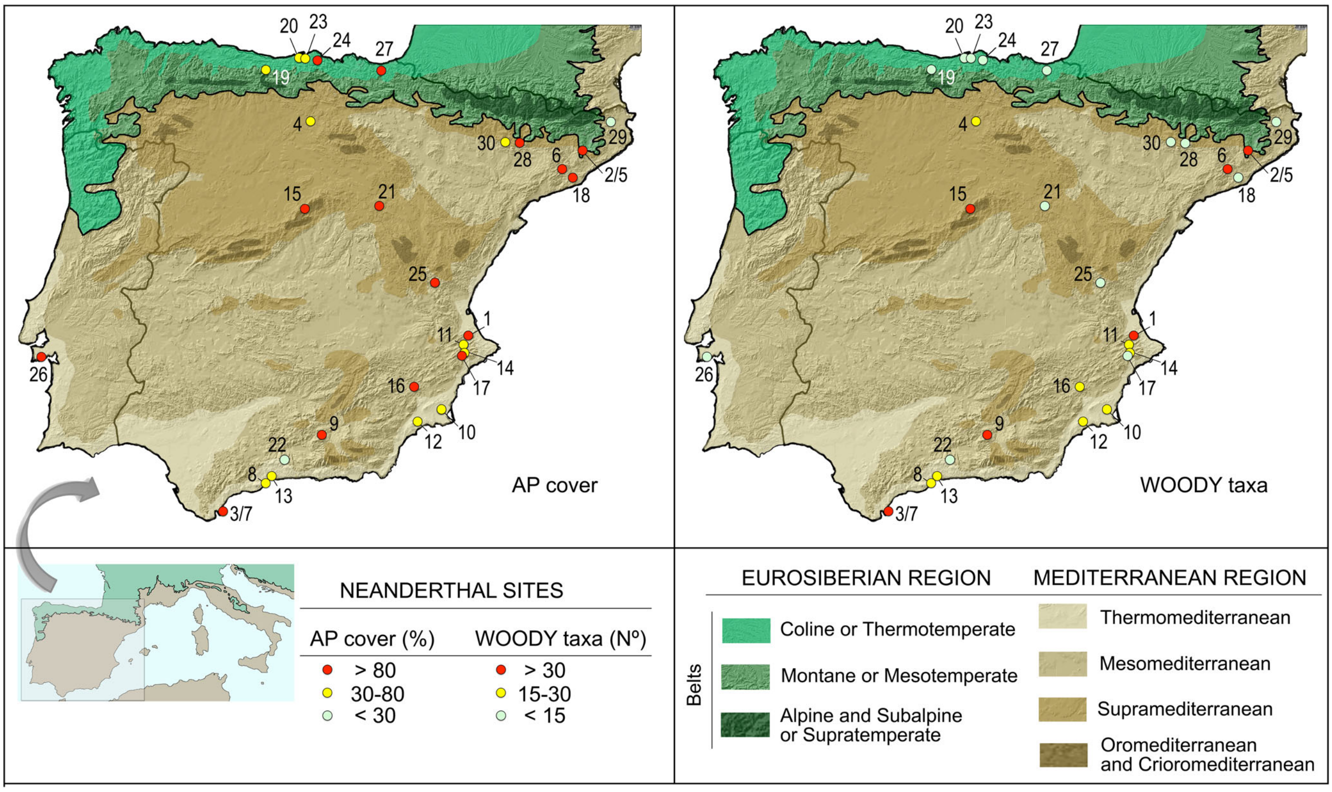

Figure 2. Distribution of Iberian Neanderthal pollen sites with respect to phytogeography and their arboreal pollen (AP) cover and number of woody taxa. [Color figure can be viewed at wileyonlinelibrary.com]

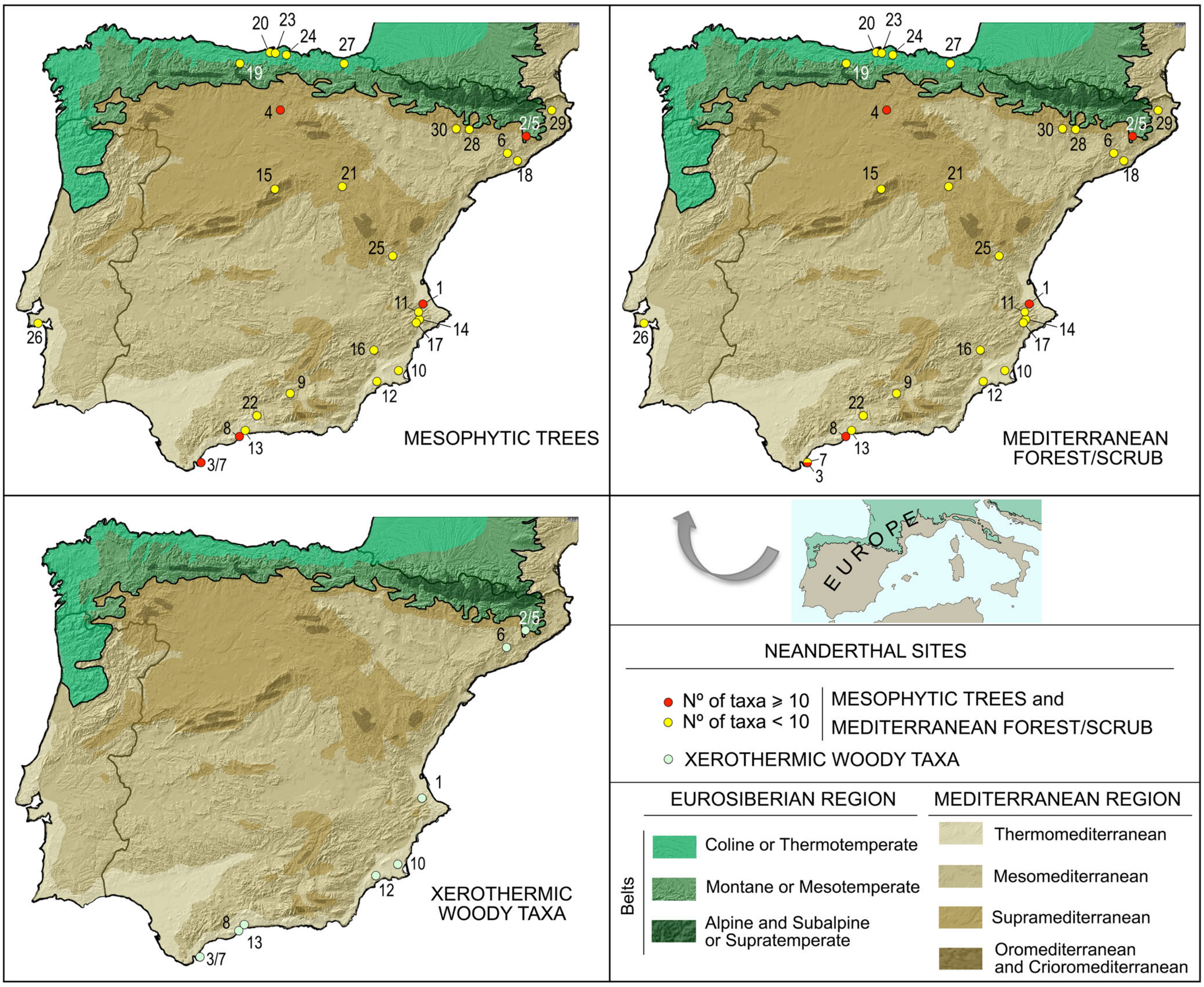

Figure 3. Distribution of Iberian Neanderthal pollen sites with respect to phytogeography and their number of mesophytic, Mediterranean and xerothermic woody taxa. [Color figure can be viewed at wileyonlinelibrary.com]

Ahmarian and Protoaurignacian, among others, including some regional Aurignacian such as the Levantine (Shea, 2016; de la Peña, 2019). In addition, under some circumstances, technological complexes may well be associated with different environmental conditions (Cascalheira and Bicho, 2018), rather than different hominin groups. By scrutinizing the Middle to Upper Palaeolithic transitional industries across Europe from 45 to 30 ka, Finlayson and Carrión (2007) found that their distribution was correlated with sharp physiographical boundaries, suggesting that these transitional industries were made either by Neanderthals or early modern humans as independent responses to the abrupt climatic changes occurring in ecotones. Environmental stress may therefore create templates for technological innovation, regardless of the purported differences in cognitive abilities of fossil hominins.

The Iberian Peninsula could represent the centre of origin and dispersal (Bermúdez de Castro *et al.*, 1997; Hublin, 2009; Meyer *et al.*, 2016; Rosas *et al.*, 2019), as well as one of the three most important glacial refugia (Bailey *et al.*, 2008; Carrión *et al.*, 2008). It was also very likely the last bastion of Neanderthal populations (Finlayson *et al.*, 2006, 2008; Jennings *et al.*, 2011; Zilhão *et al.*, 2017; Carrión *et al.*, 2019c), before they disappeared into our own species, leaving us multiple genetic traits that still persist (Sankararaman *et al.*, 2014; Kolodny and Feldman, 2017; Enard and Petrov, 2018; Slon *et al.*, 2018).

Our approach to reconstructing the landscape occupied by Neanderthals is to focus on palaeobotanical findings, mostly pollen sequences associated with excavation sites rather than conventional palynological basins (peat bogs, lake and marine environments), since we think that hominin adaptive processes are local/regional while the conventional pollen sequences lie frequently at a distance from sites (Figs. 1–3; Table 1). We acknowledge potential biases inherent in archaeological palynology (Dupré, 1988; Coles *et al.*, 1989; Bottema and Woldring, 1994; Sánchez-Goñi, 1994; Coles and Gilbertson, 1994; Carrión and Scott, 1999; McGarry and Caseldine, 2004), but, for the current analysis, most accepted pollen records have their own pitfalls. Admittedly, biases are implicit in pollen analyses of any kind, as well as in charcoal analysis (Badal García and Martínez Varea, 2018; Vidal-Matutano *et al.*, 2020). For example, it is well-known that *Pinus* is more often over-represented in all kinds of deposits, and Asteraceae including *Artemisia* pollen is in poorly preserved pollen assemblages of archaeological sites, while for instance *Quercus*, *Juniperus*, *Pistacia*, *Castanea*, *Rhamnus*, *Phillyrea*, *Juglans*, *Arbutus* and *Buxus*, among others, are most frequently under-represented in caves including minerogenic

Table 1. Location of Iberian sites with palaeobotanical data including for the late Mid- and Late Pleistocene (MIS 12–MIS 2)

Site number	Site	Coordinates	Type of site	Age/MIS	Pollen (P), charcoal (C), macrofossil (M), phytoliths (Ph)	Dominant (*Pinus*) or codominant taxa	References
1	Bolomor	(39°30′ N, 0°15′W, 100 m a.s.l.)	Archaeological site	MIS 9–5e	P, C	*Pinus, Quercus*	Ochando *et al.* (2019); Vidal-Matutano *et al.* (2019)
2	Teixoneres	(41°48′25″N, 02°09′02″E, 760 m a.s.l.)	Archaeological site	MIS 7–2	P	*Pinus, Quercus*	Ochando *et al.* (2020a)
3	Gorham's	(36°07′13″N, 05°20′31″W, 5 m a.s.l.)	Archaeological site	MIS 3–2	P, C	*Pinus, Quercus*	Carrión *et al.* (2008); Ward *et al.* (2012b)
4	Atapuerca	(42°21′N, 03°31′W, 1078 m a.s.l.)	Archaeological site	MIS 12–7	P	*Pinus, Quercus*	García-Antón (1989, 1992); García-Antón and Sainz-Ollero (1991); Rodríguez *et al.* (2011)
5	Toll	(41°48′25″N, 2°09′02″E, 760 m a.s.l.)	Archaeological site	Middle Pleistocene–Holocene	P	*Pinus, Quercus*	Serra *et al.* (1957); Bergadà and Serrat (2001); Ochando *et al.* (2020b)
6	Romaní	(41°31′43″N, 01°41′28″E, 300 m a.s.l.)	Archaeological site	MIS 5d–3	P, C	*Pinus*	Burjachs and Julià (1994); Allué *et al.* (2017); Biltekin *et al.* (2019); Val-Peón *et al.* (2019)
7	Vanguard	(36°07′17″N, 05°20′30″W, 0 m a.s.l.)	Archaeological site	MIS 3	P	*Pinus*	Ward *et al.* (2012a); Carrión *et al.* (2018)
8	Bajondillo	(36°37′02″N, 04°33′31″W, 0 m a.s.l.)	Archaeological site	MIS 3–2	P	*Pinus, Quercus*	López-Sáez *et al.* (2007); Cortes Sanchez *et al.* (2008)
9	Carihuela	(37°26′22″N, 03°26′12″W, 1020 m a.s.l.)	Archaeological site	MIS 5–2	P, C	*Pinus*	Carrión (1990, 1992b); Fernández *et al.* (2007); Carrión *et al.* (2019c)
10	Palomas	(37°47′54″N, 00°53′53″W, 120 m a.s.l.)	Archaeological site	MIS 4–3	P	*Pinus, Quercus*	Carrión *et al.* (2003a)
11	Beneito	(38°48′N, 00°28′W, 680 m a.s.l.)	Archaeological site	MIS 3–2	P, C	*Pinus, Quercus*	Carrión (1991, 1992a, 1994); Carrión and Munuera (1997)
12	Perneras	(37°32′13″N, 01°26′34″W, 100 m a.s.l.)	Archaeological site	MIS 3–2	P	*Pinus, Quercus*	Carrión *et al.* (1995)
13	Complejo del Humo (A3)	(36°42′52″N, 4°20′42″W, 5 m a.s.l.)	Archaeological site	Upper Pleistocene	P	Pinus, *Quercus*	Ochando *et al.* (2020c)
14	Pastor	(38°41′54″N, 00°28′25″W, 820 m a.s.l.)	Archaeological site	MIS 5–4	C	*Pinus, Quercus, Juniperus*	Vidal-Matutano *et al.* (2017); Vidal-Matutano and Pardo-Gordó (2020); Connolly *et al.* (2019)
15	Camino	(40°56′N, 03°46′W, 1114 m a.s.l.)	Archaeological site	MIS 4	C	*Pinus*	Arsuaga *et al.* (2010)
16	Antón	(38°03′51″N, 01°29′47″W, 356 m a.s.l.)	Archaeological site	MIS 5a–3	P	*Pinus*	Zilhão *et al.* (2016)
17	Salt	(38°41′14″N, 0°30′32″W, 680 m a.s.l.)	Archaeological site	MIS 3	C	*Pinus*	Vidal-Matutano and Pardo-Gordó (2020)
18	Coll Verdaguer	(41°23′35″N, 01°54′39″E, 448 m a.s.l.)	Archaeological site	MIS 3	P, C	*Pinus*	Daura *et al.* (2017)
19	Esquilleu	(43°12′05″N, 04°35′26″W, 350 m a.s.l.)	Archaeological site	MIS 3	C	*Pinus*	Baena *et al.* (2005)
20	Covalejos	(43°23′48″N, 03°55′58″W, 80 m a.s.l.)	Archaeological site	MIS 3	P, C	*Pinus, Betula, Corylus, Ulmus, Fraxinus, Salix*	Ruiz-Zapata and Gil-García (2005)
21	Casares	(40°56′22″N, 02°17′31″W, 1050 m a.s.l.)	Archaeological site	MIS 4–3	P, C	*Pinus, Quercus, Alnus*	Alcaraz-Castaño *et al.* (2017)

(*Continued*)

Table 1. (*Continued*)

Site number	Site	Coordinates	Type of site	Age/MIS	Pollen (P), charcoal (C), macrofossil (M), phytoliths (Ph)	Dominant (*Pinus*) or codominant taxa	References
22	Zafarraya	(36°57′04″N, 04°07′38″W, 1022 m a.s.l.)	Archaeological site	MIS 3	P, C	*Pinus*, Asteraceae, Poaceae, *Artemisia*, *Ephedra*	Lebreton *et al.* (2006); Vernet and Terral (2006)
23	Morín	(43°23′N, 03°50′W, 57 m a.s.l.)	Archaeological site	Upper Pleistocene	P	*Juniperus*, *Betula*, *Corylus*, *Alnus*, *Quercus*	Leroi-Gourhan (1971)
24	Otero	(43°21′10″N, 03°31′41″W, 60 m a.s.l.)	Archaeological site	MIS 2	P	*Pinus*	Leroi-Gourhan (1966)
25	Quebrada	(39°42′08″N, 00°58′20″W, 728 m a.s.l.)	Archaeological site	MIS 5–3	C	*Pinus*	Carrión Marco *et al.* (2019)
26	Figueira Brava	(38°28′23″N, 08°59′42″W, 0 m a.s.l.)	Archaeological site	MIS 5	C	*Pinus*	Zilhão *et al.* (2020)
27	Amalda	(43°14′06″N, 02°13′38″W, 205 m a.s.l.)	Archaeological site	MIS 3	P	*Pinus*	Dupré (1990)
28	Gran	(41°55′38″N, 00°48′46″E, 385 m a.s.l.)	Archaeological site	MIS 3–2	C	*Pinus*	Allué *et al.* (2018)
29	Arbreda	(42°09′36″N, 02°44′49″E, 200 m a.s.l.)	Archaeological site	MIS 5–2	P, C	*Pinus*, *Corylus*, Poaceae, *Artemisia*, Asteraceae	Burjachs (1987); Burjachs and Renault-Miskovsky (1992)
30	Gabasa	(42°00′N, 00°25′E, 780 m a.s.l.)	Archaeological site	MIS 3	P	*Pinus*	González-Sampériz *et al.* (2003)
31	Castillo	(43°17′30″N, 03°58′03″W, 170 m a.s.l.)	Archaeological site	Upper Pleistocene	C	*Pinus*, *Betula*	Uzquiano (1992c, 2007); Cabrera *et al.* (2005)
32	Cobrante	(43°19′10″N, 03°31′44″W, 80 m a.s.l.)	Archaeological site	MIS 2	P, C	*Pinus*, *Olea*, *Juniperus*	Ruiz-Zapata and Gil-García (2005); Uzquiano (2005)
33	Abauntz	(43°00′N, 01°38′W, 600 m a.s.l.)	Archaeological site	MIS 2-Holocene	P	*Pinus*	López-García (1982, 1986, 1987)
34	Balma del Gai	(41°49′00″N, 02°08′19″E, 760 m a.s.l.)	Archaeological site	MIS 2 to Holocene	C	*Pinus*	Allué *et al.* (2007)
35	Tubilla del Agua	(42°42′33″N, 03°48′14″W, 765 m a.s.l.)	Archaeological site	MIS 9 to Holocene	M	*Pinus*	García-Amorena *et al.* (2011)
36	Ambrona	(41°09′37″N, 02°29′54″W, 1130 m a.s.l.)	Archaeological site	MIS 9 to Holocene	P	*Pinus*, Cupressaceae	Ruiz-Zapata *et al.* (2005)
37	Pinedo (Tajo)	(39°51′N, 04°01′W, 500 m a.s.l.)	Archaeological site	Middle Pleistocene	P	*Salix*, *Olea*	Martín-Arroyo *et al.* (1996b, 2000); Martín-Arroyo (1998); Ruiz-Zapata *et al.* (2004)
38	Valdelobos	(39°51′N, 04°01′W, 500 m a.s.l.)	Archaeological site	Upper Pleistocene	P	*Quercus*, *Juniperus*	Martín-Arroyo *et al.* (1996a); Martín-Arroyo (1998)
39	Verdelpino	(40°09′N, 02°05′W, 990 m a.s.l.)	Archaeological site	MIS 2 to Holocene	P	*Pinus*	López-García (1977)
40	Ratlla del Buho	(38°16′45″N, 00°50′07″W, 400 m a.s.l.)	Archaeological site	Upper Pleistocene–Holocene	C	*Juniperus*	Badal (1995)
41	Santa Maira	(38°43′52″N, 00°12′52″W, 650 m a.s.l.)	Archaeological site	MIS 2 to Holocene	C	*Pinus*, *Quercus*, *Juniperus*	Carrión-Marco (2003); Aura *et al.* (2005)
42	Marinho	(41°45′38″N, 08°02′50″W, 1150 m a.s.l.)	Archaeological site	MIS 2 to Holocene	C	*Pinus*	Figueiral (1993)

(*Continued*)

Table 1. (*Continued*)

Site number	Site	Coordinates	Type of site	Age/MIS	Pollen (P), charcoal (C), macrofossil (M), phytoliths (Ph)	Dominant (*Pinus*) or codominant taxa	References
43	Salchicha (Tajo)	(39°51′N, 04°01′W, 490 m a.s.l.)	Archaeological site	Middle Pleistocene	P	*Olea, Quercus, Salix*	Martín-Arroyo *et al*. (1996b, 2000); Martín-Arroyo (1998); Ruiz-Zapata *et al*. (2004)
44	Puente Pino	(39°47′N, 5°08′W, 500 m a.s.l.)	Archaeological site	MIS 9–6	P	*Pinus*	Ruiz-Zapata *et al*. (2009)
45	Ventanas	(37°26′25″N, 03°26′00″W, 1056 m a.s.l.)	Archaeological site	MIS 3 to Holocene	P	*Pinus*	Carrión *et al*. (2001); Ochando *et al*. (2020d)
46	Moucide	(43°36′N, 07°21′W, 110 m a.s.l.)	Archaeological site	MIS 3 to Holocene	P	*Quercus, Betula*	Gómez-Orellana *et al*. (2001)
47	Sopeña	(43°19′N, 04°56′W, 450 m a.s.l.)	Archaeological site	MIS 3–2	C	*Juniperus*	Pinto *et al*. (2006)
48	Chufín	(43°17′33″N, 04°27′36″W, 130 m a.s.l.)	Archaeological site	MIS 2	P	*Pinus, Alnus*	Boyer-Klein (1984)
49	Erralla	(43°12′40″N, 02°10′57″W, 230 m a.s.l.)	Archaeological site	MIS 2	P	*Pinus, Alnus, Corylus*	Boyer-Klein (1985)
50	Santa Catalina	(43°22′38″N, 02°30′36″W, 35 m a.s.l.)	Archaeological site	MIS 2	C	*Pinus, Betula, Quercus*	Uzquiano (1992a, 1995)
51	Berroberría	(43°16′06″N, 01°30′30″W, 156 m a.s.l.)	Archaeological site	MIS 2 to Holocene	P	*Pinus*	Boyer-Klein (1984, 1988)
52	Parco	(41°54′48″N, 00°56′31″E, 420 m a.s.l.)	Archaeological site	MIS 2	P	*Pinus, Quercus*	Bergadà *et al*. (1999)
53	Villacastín	(40°47′52″N, 04°22′20″W, 1123 m a.s.l.)	Archaeological site	MIS 6–5e	P	*Pinus, Quercus*	Carrión *et al*. (2007)
54	Torrejones	(41°00′45″N, 03°15′10″W, 1100 m a.s.l.)	Archaeological site	MIS 4	P	*Pinus*	Carrión *et al*. (2007)
55	Buraca Escura	(39°55′N, 08°33′W, 270 m a.s.l.)	Archaeological site	MIS 3–2	C	*Pinus*	Aubry *et al*. (2001)
56	Buraca Grande	(39°55′9″N, 08°36′35″W, 350 m a.s.l.)	Archaeological site	MIS 2 to Holocene	C	*Pinus, Buxus*	Aubry *et al*. (1997); Figueiral and Terral (2002)
57	Pirulejo	(37°26′20″N, 04°11′13″W, 580 m a.s.l.)	Archaeological site	MIS 2	P	*Pinus, Quercus*	Díaz del Olmo *et al*. (1989)
58	Valiña	(42°46′57″N, 07°14′09″W, 620 m a.s.l.)	Archaeological site	MIS 3	C	*Pinus, Quercus*	Carrión-Marco (2005)
59	Oia	(42°00′N, 08°52′W, 0 m a.s.l.)	Archaeological site	MIS 2	P	*Quercus, Corylus*	Ramil-Rego and Gómez-Orellana (2002); Iriarte *et al*. (2005)
60	Conde	(43°17′23″N, 05°58′54″W, 180 m a.s.l.)	Archaeological site	MIS 3–2	C	*Pinus*	Uzquiano *et al*. (2008)
61	Altamira	(43°22′37″N, 04°07′12″W, 70 m a.s.l.)	Archaeological site	MIS 2	P, C	*Salix, Juniperus*	Uzquiano (1992b); Carrión and Dupré (2002)
62	Cendres	(38°41′10″N, 00°09′09″W, 45 m a.s.l.)	Archaeological site	MIS 3 to Holocene	C	*Pinus, Juniperus*	Badal and Carrión-Marco (2001); Badal García and Martínez Varea (2018); Villaverde *et al*. (2019)
63	Malladetes	(39°01′15″N, 00°17′57″W, 500 m a.s.l.)	Archaeological site	MIS 3–2	P	*Pinus*	Dupré (1980)

(*Continued*)

Table 1. (*Continued*)

Site number	Site	Coordinates	Type of site	Age/MIS	Pollen (P), charcoal (C), macrofossil (M), phytoliths (Ph)	Dominant (*Pinus*) or codominant taxa	References
64	Pardo	(38°48′57″N, 00°17′ 53″W, 650 m a.s.l.)	Archaeological site	MIS 2 to Holocene	P	*Pinus*	Soler *et al.* (2008)
65	Calaveres	(38°47′40″N, 00°00′ 59″W, 70 m a.s.l.)	Archaeological site	MIS 2	P	*Pinus*	Dupré (1988)
66	Tossal de la Roca	(38°47′26″N, 00°16′ 51″W, 691 m a.s.l.)	Archaeological site	MIS 2 to Holocene	P, C	*Pinus*	Cacho *et al.* (1995); Uzquiano and Arnanz (1997); Uzquiano (1988)
67	CM 5 Beliche	(37°16′N, 07°27′W, 25 m a.s.l.)	Archaeological site	MIS 2 to Holocene	P	*Pinus*, *Quercus*	Fletcher *et al.* (2007)
68	Candieira	(40°20′37″N, 07°34′ 40″W, 1400 m a.s.l.)	Archaeological site	MIS 2 to Holocene	P	*Pinus*	van der Knaap and van Leeuwen (1995, 1997)
69	Alfaix	(37°08′41″N, 01°56′ 39″W, 105 m a.s.l.)	Archaeological site	MIS 6–3	P	*Pinus*, *Quercus Olea*	Schulte *et al.* (2008)
70	Nerja	(36°45′43″N, 03°50′ 26″W, 158 m a.s.l.)	Archaeological site	MIS 3 to Holocene	C	*Pinus*, *Quercus*	Badal (1990)
71	Ambrosio	(37°49′57″N, 02°05′ 39″W, 1060 m a.s.l.)	Archaeological site	Upper Pleistocene to Holocene	P, C	*Pinus*, *Quercus*, *Juniperus*	López-García (1988); Rodríguez-Ariza (2006)
72	Estanya	(42°02′N, 00°32′E, 670 m a.s.l.)	Lake	MIS 2 to Holocene	P	*Pinus*, *Juniperus*	González-Sampériz *et al.* (2017)
73	Marboré	(42°41′44″N, 00°02′ 24″E, 3328 m a.s.l.)	Lake	MIS 2 to Holocene	P	*Pinus*, *Corylus*, deciduous forest	Leunda *et al.* (2017)
74	Riera del Canyars	(41°17′46″N, 01°58′ 47″E, 40 m a.s.l.)	Terraces	MIS 3	P, C, Ph	*Pinus*	Daura *et al.* (2013)
75	Padul	(37°00′21″N, 03°36′ 43″W, 723 m a.s.l.)	Peat bog	MIS 7 to Holocene	P	*Pinus*	Pons and Reille (1988); Camuera *et al.* (2019)
76	Gallocanta	(40°57′27″N, 01°29′ 22″W, 995 m a.s.l.)	Lagoon	MIS 2 to Holocene	P	*Pinus*	Burjachs *et al.* (1996)
77	KEB 25	(40°48′12″N, 00°59′ 30″E, 88 water depth m)	Delta	MIS 2 to Holocene	P	*Pinus*	Yll (1995)
78	Laguillín	(42°52′51″N, 06°02′ 25″W, 1850 m a.s.l.)	Lake	MIS 2 to Holocene	P	*Pinus*	García-Rovés (2007)
79	Sanabria	(42°07′21″N, 06°43′ 09″W, 1080 m a.s.l.)	Lake	MIS 2 to Holocene	P	*Pinus*, *Betula*	Hannon (1985)
80	Lleguna	(42°07′21″N, 06°43′ 09″W, 1050 m a.s.l.)	Peat bog	MIS 2 to Holocene	P	*Pinus*, *Quercus*, *Betula*	Muñoz-Sobrino *et al.* (2004)
81	Fuentillejo	(42°07′21″N, 06°43′ 09″W, 635 m a.s.l.)	Lagoon	MIS 2 to Holocene	P	*Pinus*, *Juniperus*	Ruiz-Zapata *et al.* (2008)
82	Salines	(38°30′02″N, 00°53′ 18″W, 470 m a.s.l.)	Lagoon	MIS 6 to Holocene	P	*Pinus*, Cupressaceae, *Quercus*	Burjachs *et al.* (2007); Burjachs (2009, 2012)
83	Villena	(38°36′49″N, 00°55′ 20″W, 502 m a.s.l.)	Lagoon	MIS 3 to Holocene	P	*Pinus*	Yll *et al.* (2003)
84	Navarrés	(39°04′N, 00°41′W, 225 m a.s.l.)	Peat bog	MIS 3 to Holocene	P	*Pinus*	Carrión and van Geel (1999)

(*Continued*)

Table 1. (*Continued*)

Site number	Site	Coordinates	Type of site	Age/MIS	Pollen (P), charcoal (C), macrofossil (M), phytoliths (Ph)	Dominant (*Pinus*) or codominant taxa	References
85	Navamuño	(40°19′16″N, 05°46′ 42″W, 1505 m a.s.l.)	Peat bog	MIS 2 to Holocene	P	*Pinus, Betula*	López-Sáez *et al.* (2020)
86	Villarquemado	(40°30′N, 01°18′W, 1000 m a.s.l.)	Lake	MIS 6 to Holocene	P	*Pinus*	González-Sampériz *et al.* (2013, 2020); Aranbarri *et al.* (2014)
87	Area Longa	(43°36′N, 07°18′W, 0 m a.s.l.)	Cliff	MIS 5c–3	P	*Quercus, Betula*	Gómez-Orellana *et al.* (2007)
88	Caamaño	(42°39′N, 09°02′W, 0 m a.s.l.)	Cliff	MIS 3–2	P	*Quercus, Alnus*	Ramil-Rego *et al.* (1996); Carrión *et al.* (2005)
89	Tarna	(43°07′N, 05°15′W, 1415 m a.s.l.)	Lagoon	MIS 2 to Holocene	P	*Pinus, Juniperus*	Ruiz-Zapata *et al.* (2000, 2002)
90	Pila	(43°25′40″N, 04°01′ 20″W, 25 m a.s.l.)	Archaeological site	MIS 2	C	*Juniperus*	Uzquiano (1992a, 1995, 1998)
91	Tramacastilla	(42°43′27″N, 00°22′ 07″W, 1668 m a.s.l.)	Lake	MIS 3 to Holocene	P	*Pinus*	Montserrat Martí (1992)
92	Mozarrifar	(41°42′55″N, 00°49′ 47″W, 220 m a.s.l.)	Peat bog	MIS 2	P	*Pinus, Juniperus*	González-Sampériz *et al.* (2005)
93	Sanguijuelas	(42°07′21″N, 06°43′ 09″W, 1080 m a.s.l.)	Lagoon	MIS 2 to Holocene	P	*Pinus, Quercus*	Muñoz-Sobrino *et al.* (2004)
94	Polvoredo	(43°03′N, 05°05′W, 1500 m a.s.l.)	Peat bog	MIS 2 to Holocene	P	*Pinus*	García-Rovés (2007)
95	Piedra	(42°38′00″N, 03°52′ 45″W, 950 m a.s.l.)	Peat bog	MIS 2 to Holocene	P	*Pinus, Betula*	Muñoz-Sobrino *et al.* (1996)
96	San Rafael	(36°46′25″N, 02°36′ 05″W, 8 m a.s.l.)	Peat bog	MIS 2 to Holocene	P	*Pinus, Quercus*	Pantaleón-Cano *et al.* (2003)
97	Siles	(38°23′21″N, 02°30′ 34″W, 1320 m a.s.l.)	Lagoon	MIS 2-Holocene	P	*Pinus*	Carrión (2002b)
98	Portalet	(42°48′N, 00°23′W, 1802 m a.s.l.)	Peat bog	MIS 2 to Holocene	P, C	*Pinus*	González-Sampériz *et al.* (2006); Gil-Romera *et al.* (2014)
99	Lucenza	(42°35′32″N, 07°06′ 47″W, 1375 m a.s.l.)	Lagoon	MIS 2 to Holocene	P	*Pinus, Quercus, Betula*	Muñoz Sobrino *et al.* (2001)
100	Mougás	(42°03′37″N, 08°53′ 29″W, 0 m a.s.l.)	Lagoon	MIS 2 to Holocene	P, C	*Pinus, Alnus*	Gómez-Orellana *et al.* (1998); Carrión-Marco (2005); Carrión *et al.* (2005)
101	Comella	(43°16′58″N, 04°59′ 22″W, 834 m a.s.l.)	Peat bog	MIS 3 to Holocene	P	*Pinus, Salix, Juniperus*	Ruiz-Zapata *et al.* (2002)
102	Brañagallones	(43°07′32″N, 05°17′ 56″W, 1230 m a.s.l.)	Peat bog	MIS 3–2	P	*Pinus, Juniperus*	Ruiz-Zapata *et al.* (2000, 2002)
103	Ajo	(43°02′36″N, 06°08′ 11″W, 1570 m a.s.l.)	Lake	MIS 2 to Holocene	P	*Pinus*	Allen *et al.* (1996)
104	Enol	(43°16′20″N, 04°59′ 32″W, 1070 m a.s.l.)	Lake	MIS 2 to Holocene	P	*Pinus, Quercus*	López-Merino (2009)
105	Salada de Mediana	(41°30′06″N, 00°44′ 00″W, 350 m a.s.l.)	Lagoon	MIS 2 to Holocene	P	*Pinus*, Juniperus, *Corylus*	González-Sampériz *et al.* (2004)
106	Estany	(42°11′18″N, 02°31′	Lagoon	MIS 3 to Holocene	P	*Pinus*	Burjachs (1994)

(*Continued*)

Table 1. (*Continued*)

Site number	Site	Coordinates	Type of site	Age/MIS	Pollen (P), charcoal (C), macrofossil (M), phytoliths (Ph)	Dominant (*Pinus*) or codominant taxa	References
		47″W, 520 m a.s.l.)					
107	Banyoles	(42°08′07″N, 02°45′23″E, 173 m a.s.l.)	Lake	MIS 2 to Holocene	P	*Pinus*	Pérez-Obiol and Julià (1994)
108	Quintanar de la Sierra	(42°01′49″N, 03°01′14″W, 1470 m a.s.l.)	Peat bog	MIS 2 to Holocene	P	*Pinus*	Peñalba *et al.* (1997)
109	Roya	(42°08′02″N, 06°47′28″W, 1608 m a.s.l.)	Lagoon	MIS 2 to Holocene	P	*Pinus, Betula*	Allen *et al.* (1996)
110	Leitariegos	(42°59′44″N, 06°24′44″W, 1700 m a.s.l.)	Peat bog	MIS 2 to Holocene	P	*Pinus*	García-Rovés (2007)
111	Iregua	(42°01′26″N, 02°45′00″W, 1780 m a.s.l.)	Peat bog	MIS 2 to Holocene	P	*Pinus*	Gil García *et al.* (2002)
112	San Gregorio	(39°18′N, 03°01′W, 640 m a.s.l.)	Dune	MIS 2	P	*Pinus*	Ruiz-Zapata *et al.* (2000)
113	Asperillo	(37°05′13″N, 06°41′51″W, 20–2 m a.s.l.)	Dune	MIS 2 to Holocene	P	*Pinus*	Stevenson (1984)
114	MD95-2043	(36°08′N, 02°37′W, 1841 m water depth)	Marine record	MIS 3–2	P	*Pinus, Cedrus, Quercus*	Sánchez-Goñi *et al.* (2002); Fletcher and Sánchez Goñi (2008)

sediments and fossil dung samples (Carrión *et al.*, 1999, 2009; Prieto and Carrión, 1999; Navarro *et al.*, 2000, 2001, 2002; Carrión, 2002a). Several strictly insect-pollinated taxa such as *Maytenus, Periploca, Withania, Calicotome* and *Lycium* are noticeably under-represented (Carrión, 2002a; Carrión *et al.*, 2003a). This means that, in dealing with cave sites, relatively high pollen percentages of arboreal taxa excluding pines, and zoophilous scrub species of the xerothermic belt may indicate high local cover of the species involved. This must be kept in mind here. In either case, pollen spectra are not particularly well suited to the spatial inference in the palaeoecosystem (Carrión, 2002a), so it seems practical to give the palaeofloristic contingent more weight than palaeoecological models based on pollen rain models from open depositional environments. Archaeological palynology is thus the fundamental evidence supporting the corollary of this work.

Palaeoecological records

Mixed forests in valleys of Eastern (Mediterranean) Iberia

Ochando *et al.* (2019) have produced palaeoenvironmental data for the Middle Pleistocene and early Late Pleistocene of Bolomor Cave, eastern Spain (Fig. 4). The excavations have uncovered Neanderthal remains (Arsuaga *et al.*, 2012) and some of the earliest evidence of controlled use of fire in Southern Europe (Fernández Peris *et al.*, 2012; Vidal-Matutano *et al.*, 2019). Mixed oak–pine forests persist throughout a long study period (MIS 9–5) and dominate the ecological scenario, which exhibits a variety of woody plants, including abundant *Castanea*, *Olea* and *Juniperus*, accompanied by broad-leaf trees such as *Alnus*, *Betula*, *Celtis*, *Corylus*, *Fraxinus*, *Populus*, *Salix* and *Ulmus*, as well as sclerophylls such as *Pistacia, Myrtus*, *Arbutus*, *Calicotome*, *Cistus*, *Ephedra fragilis*, *Ligustrum*, *Myrica*, *Rhamnus* and *Viburnum* (Fig. 4). With a few exceptions probably associated with cold spells, the xero-heliophytic cover with *Artemisia*, Amaranthaceae, *Erica* and Poaceae is relatively minor. Occurrences of some palynological types such as *Ceratonia*, *Castanea*, *Rhododendron* and *Celtis* are of note because they correspond to species that do not grow in the region at present.

Bolomor was characterized by a more forested habitat than has been reported from other sites during Pleistocene stadials (Carrión *et al.*, 2003a, 2013; González-Sampériz *et al.*, 2010). The human groups who inhabited Bolomor processed and consumed a diversity of animal species (ungulates, lagomorphs, tortoises, birds). Through the taphonomic study of faunal specimens, it was possible to demonstrate a broad-spectrum diet in the site (Sanchis-Serra and Fernández-Peris, 2008; Blasco and Fernández Peris, 2012a,b; Blasco *et al.*, 2013). To this, we can add a broad spectrum of edible plants such as hazelnut (*Corylus avellana*), chestnut (*Castanea sativa*), Mediterranean hackberry (*Celtis australis*), strawberry tree (*Arbutus unedo*), carob tree (*Ceratonia siliqua*), holly oak (*Quercus ilex*), olive (*Olea europaea*), elderberry (*Sambucus nigra*) and probably wild Rosaceae such as several species of *Prunus, Rubus*, *Rosa* and *Sorbus* (Ochando *et al.*, 2019).

The Neanderthals of Bolomor must have possessed highly adaptive subsistence strategies in forested environments (Blasco *et al.*, 2011, 2013). The low elevation of the site within an intramountainous valley, its proximity to marine resources and the large Pleistocene coastal platforms, as well as the availability of fresh water, make Bolomor a glacial refugium resembling the large phytodiversity reservoirs of the Balkans (Bennett *et al.*, 1991; Willis, 1994; Okuda *et al.*, 2001; Pross *et al.*, 2015; Sadori *et al.*, 2016;

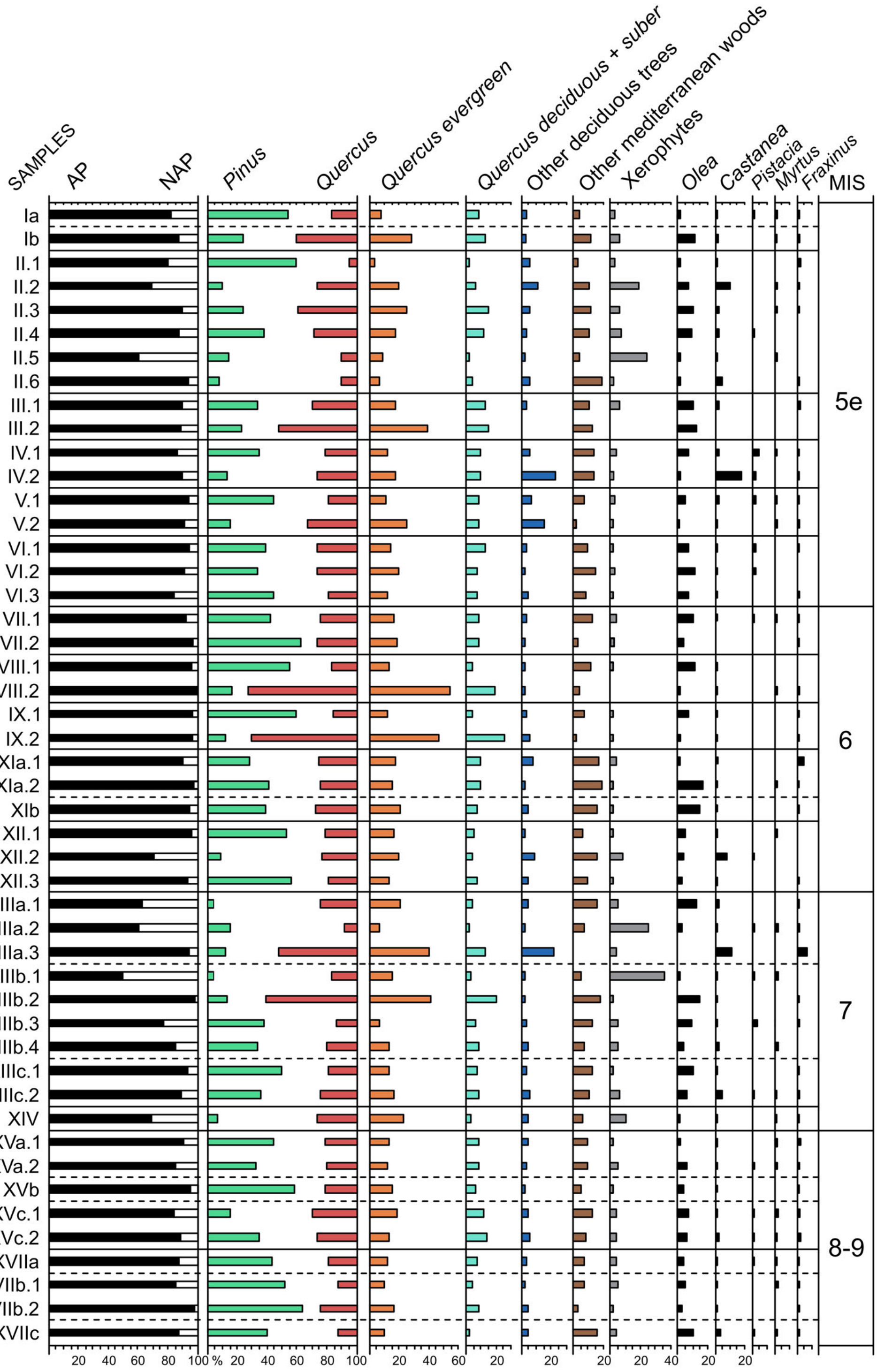

Figure 4. Synthetic pollen results from Bolomor Cave. Redrawn from Ochando *et al.* (2019). [Color figure can be viewed at wileyonlinelibrary.com]

Magri *et al.*, 2017). It should be noted that Neanderthals occupied this relatively stable biotope for more than 300 000 years, with that well-known forest resilience capable of cushioning the numerous climatic oscillations of such a long period (Carrión, 2001).

The existence of glacial forest refugia in the central eastern region of Iberia had already been inferred from lacustrine and peatbog pollen sequences, such as Navarrés in Valencia (Carrión and Dupré, 1996; Carrión and van Geel, 1999). The rapidity of the late MIS 3 colonization of steppe pinelands by Mediterranean mixed forests in this valley pointed to the proximity of Mediterranean forests in the nearby mountain ranges (Figs. 5 and 6). The pollen record of the Palaeolithic Cova Beneito, including during its Mousterian occupation, supports this view by showing late MIS 3 expansions of *Juniperus*, Oleaceae and *Quercus* at the expense of open pinelands and grasslands (Carrión, 1992a; Carrión and Munuera, 1997).

Pines, including Mediterranean and high-elevation species, were certainly an abundant component of these levantine woodlands. In line with former anthracological works (Badal, 2001; Esteban *et al.*, 2017), Real *et al.* (2021, this issue) have shown the widespread occurrence of cryophilous pines (*P. nigra*, *P. sylvestris*) in the forests of eastern Iberia during Neanderthal times, with Abrigo de la Quebrada (Carrión Marco *et al.*, 2019), El Salt (Vidal-Matutano and

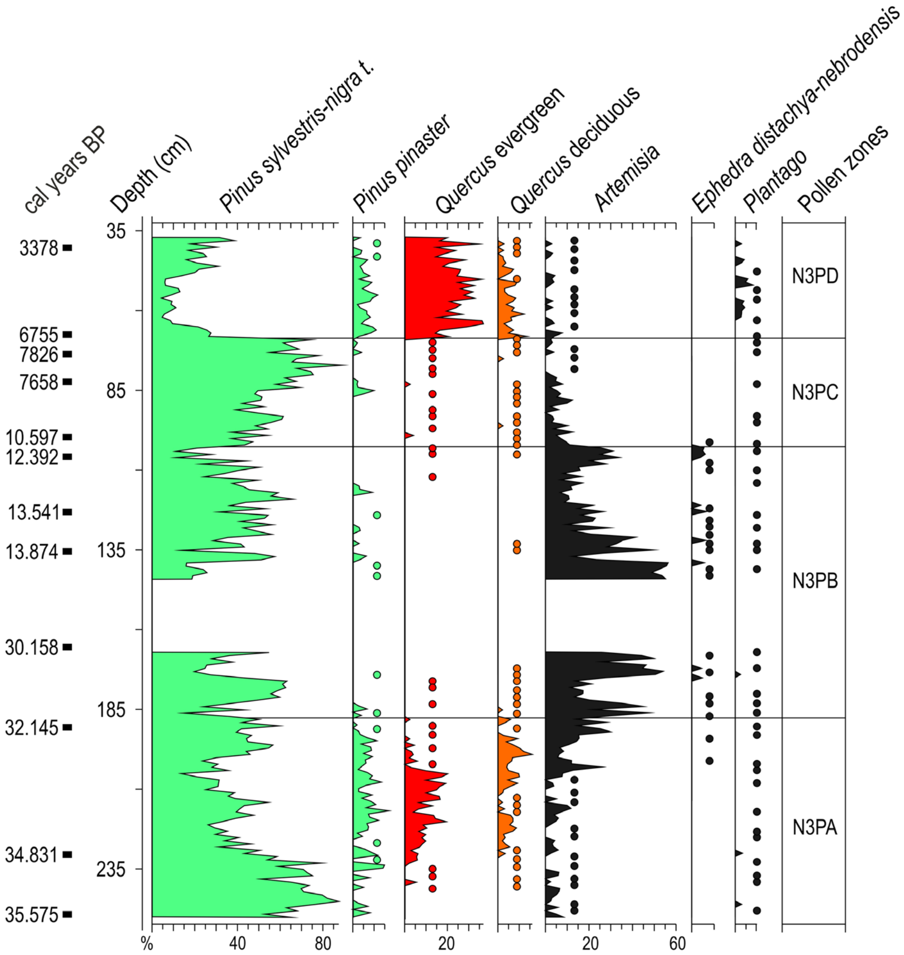

Figure 5. Synthetic pollen diagram of Canal de Navarrés peatbog, Valencia. Redrawn from Carrión and van Geel (1999). [Color figure can be viewed at wileyonlinelibrary.com]

Pardo-Gordó, 2020) and Abric del Pastor (Vidal-Matutano *et al.*, 2017; Connolly *et al.*, 2019; Vidal-Matutano and Pardo-Gordó, 2020) particularly relevant. Similarly, the appearance of xerophytic Mediterranean pines (*P. halepensis*, *P. pinea*) in Cueva Antón (Zilhão *et al.*, 2016), Figueira Brava (Zilhão *et al.*, 2020) and Gibraltar (Ward *et al.*, 2012a,b) is remarkable. In addition, these studies and other fieldwork in the region have provided further evidence of plant foods which would be accessible to Neanderthal and modern humans, as evidenced by carpological remains of *Celtis australis* and *Corema album* (Ward *et al.*, 2012a,b; Martínez-Varea *et al.*, 2019; Martínez-Varea, 2020; Zilhão *et al.*, 2020).

Farther north, at Bolomor in Barcelona, the pollen records of two adjacent Palaeolithic caves, Teixoneres and Toll, deserve attention. Although shorter than Bolomor, the pollen sequence of Teixoneres also shows the long-term permanence of a relatively dense forest ecosystem dominated by oaks and pines, accompanied by a variety of woody taxa such as *Juniperus, Corylus, Castanea, Abies, Taxus, Acer, Alnus, Betula, Celtis, Fraxinus, Juglans, Fagus, Buxus, Populus, Salix* and *Ulmus*, and several indicators of thermicity such as *Calicotome, Olea, Ceratonia, Cistus, Ephedra fragilis, Myrtus, Pistacia, Phillyrea, Rhamnus* and *Viburnum* (Fig. 7). The xero-heliophytic component (*Artemisia*, Poaceae, Amaranthaceae, *Erica*, *Ephedra fragilis*) spread episodically (IIb.1, IIb.2, IIIb.1, IV.1 and IV.3), but it was never dominant on the landscape. The vertebrate assemblages also suggest a forested environment with local meadows (López-García *et al.*, 2012).

Spanning from before MIS 4 up to MIS 1, Toll Cave is an important palaeontological and archaeological site near Teixoneres. Palynological investigations in Toll parallel those at Teixoneres and reinforce the idea that both Neanderthal settlements belonged to an important Quaternary forest refugium (Ochando *et al.*, 2020b). Again, the pollen record is characterized by the prevalence of pines and oaks with an important contribution of *Corylus*, *Juniperus* and *Castanea*, which were continuously accompanied by other trees such as *Abies, Taxus, Acer, Betula, Carpinus betulus, Tilia, Celtis, Fraxinus, Juglans, Buxus, Ilex, Populus, Salix* and *Ulmus*, as well as Mediterranean elements such as *Pistacia, Myrtus, Calicotome, Cistus, Ephedra fragilis, Ligustrum, Rhamnus* and *Viburnum* (Fig. 8). The heliophytic component (*Artemisia*, Poaceae, Amaranthaceae, *Erica, Ephedra*) would still have been relatively unimportant with the exception of in some phases (1.1, 2a.1, 2 c.2, crust 2 c.2-3a) (Fig. 8).

The pollen records of Teixoneres and Toll are particularly interesting in pointing to a high incidence of oak forests in a pleniglacial context and relatively high latitude within the Iberian Peninsula. These sequences must be therefore incorporated into the debates on glacial refugia for temperate trees in the Mediterranean Peninsulas (Bennett *et al.*, 1991; Willis, 1994; Carrión *et al.*, 1999, 2003a; Tzedakis *et al.*, 2003; Giardini, 2007; Bhagwat and Willis, 2008; Margari *et al.*, 2009; González-Sampériz *et al.*, 2010; Sadori *et al.*, 2016; Magri *et al.*, 2017; Manzano *et al.*, 2017; Sinopoli *et al.*, 2018). The evidence of evergreen *Quercus* (mainly *Quercus ilex*) during the Quaternary glacial stages had so far suggested limited cover in northern Iberia (Uzquiano *et al.*, 2016), as a result of stable isotope analyses of herbivore remains during MIS 3 (Jones *et al.*, 2018, 2019). A moderate presence of deciduous oaks has nevertheless been observed in the Mediterranean–Eurosiberian ecotonal territories of the north (Blanco-Castro *et al.*, 1997;

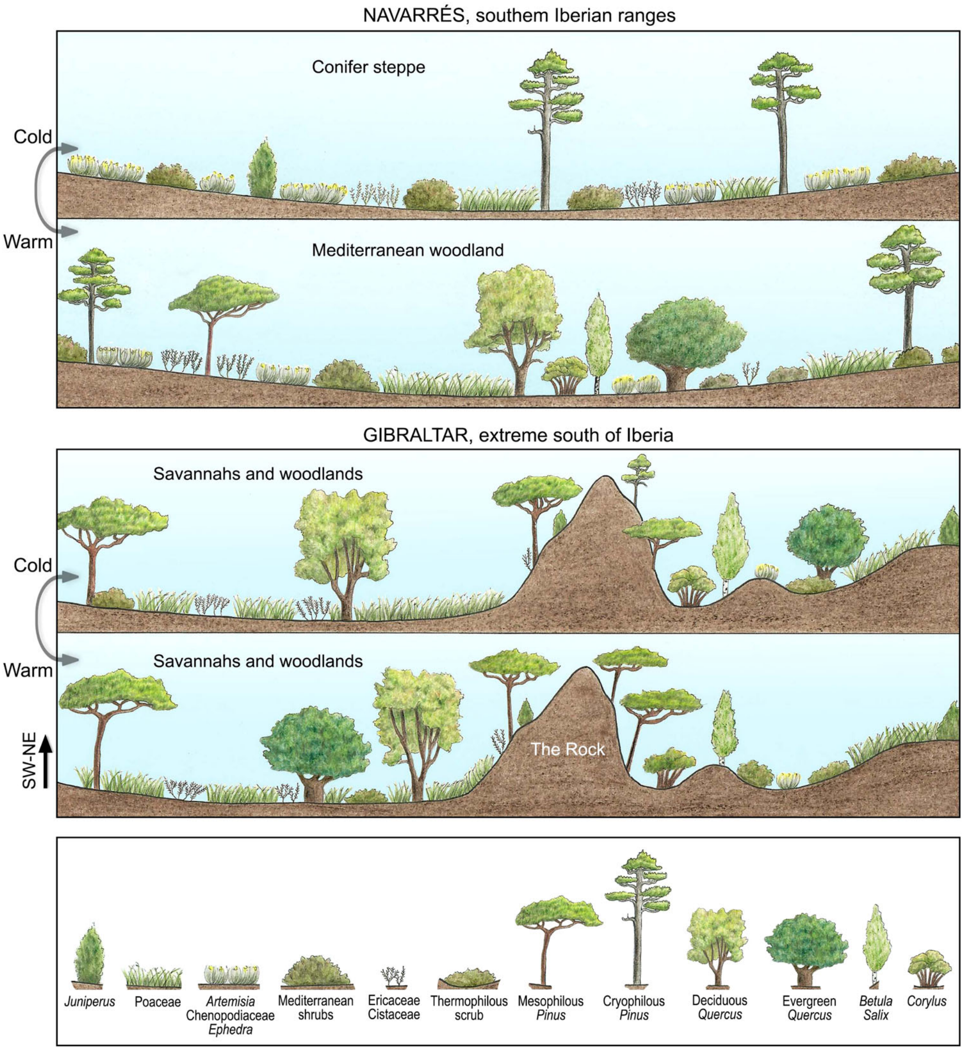

Figure 6. Latitudinal pattern in vegetation development across a part of Mediterranean Iberia. There is a lack of substantial vegetation and floristic changes between Pleistocene stadials and interstadials in a refugium context such as derived from palaeoecological data of Gorham's Cave (Carrión *et al*., 2008). In comparison, in the most continental site of Navarrés, climatic changes do affect the structure and composition of vegetation (Carrión and van Geel, 1999). Inspired by Finlayson and Carrión (2007). Artwork: Gabriela Amorós. [Color figure can be viewed at wileyonlinelibrary.com]

González-Sampériz, 2004; González-Sampériz *et al*., 2004, 2006, 2017; Gil-Romera *et al*., 2014; Morales-Molino and García-Antón, 2014; García-Mijangos *et al*., 2015; Aranbarri *et al*., 2016; Salomón *et al*., 2016).

Based on counts of of woody taxa of palaeobotanical sequences from the Iberian Pleistocene, Teixoneres and Toll rank at the top of a comparative abundance chart (Fig. 9), surpassing in number of trees and shrubs many sites in southern Iberia (Carrión *et al*., 2013). Apart from possible pollen-preservational biases, this high diversity might be because these caves are located in an ecotone between the Eurosiberian and Mediterranean regions.

Conifer forests and savannahs in continental territories

Pine forests, sometimes with junipers, were clearly abundant, and eventually dominant during cold stages of the peninsular Quaternary (Dupré, 1988; Burjachs and Renault-Miskovsky, 1992; Yll and Pérez-Obiol, 1992; Pérez-Obiol and Julià, 1994; González-Sampériz *et al*., 2003, 2010; Carrión *et al*., 2007, 2013; Val-Peón *et al*., 2019). Not far from the Mediterranean coast, under conditions of continentality, pines were the main constituents of wooded steppes and savannahs during cold dry phases, shown in sites such as in the Salines pollen record, inland Alicante (Julià *et al*., 1994; Giralt *et al*., 1999; Burjachs *et al*., 2007; Burjachs, 2009, 2012), which point to rapid developments of Mediterranean vegetation during the last glacial stage in the adjacent mountains (Giralt *et al*., 1999; Burjachs *et al*., 2007; Burjachs, 2009). *Pinus* and *Juniperus* are here the main components of cold-stage arboreal vegetation, but never indicating closed forests, rather open parklands. An open pine forest is also the main Pleistocene and Holocene vegetation type inferred from the Villena lake and Navarrés pollen sequences (Carrión and van Geel, 1999; Yll *et al*., 2003).

Abric Romaní, a Middle Palaeolithic cave (Capellades, Barcelona, 300 m asl, 35 km from the coast) contains a palynological sequence spanning MIS 5/4 to MIS 3 with a dominance of pines, although mesothermophilous plants (*Quercus, Rhamnus* cf. *alaternus, Pinus* cf. *halepensis, Olea, Hedera, Prunus*) are continuous between ca. 70 and 40 ka, with intermittent episodes characterized by increased steppic species (Burjachs and Julià, 1994, 1996; Burjachs, 2009; Allué *et al*., 2012) (Fig. 10). Charcoal analysis shows *Pinus sylvestris* as the main pine species (Allué, 2002).

The long pollen record of El Cañizar de Villarquemado palaeolake (40°30′N, 01° 18 ′W, 987 m asl), in the southern Iberian Range, covers the end of the Middle Pleistocene, the

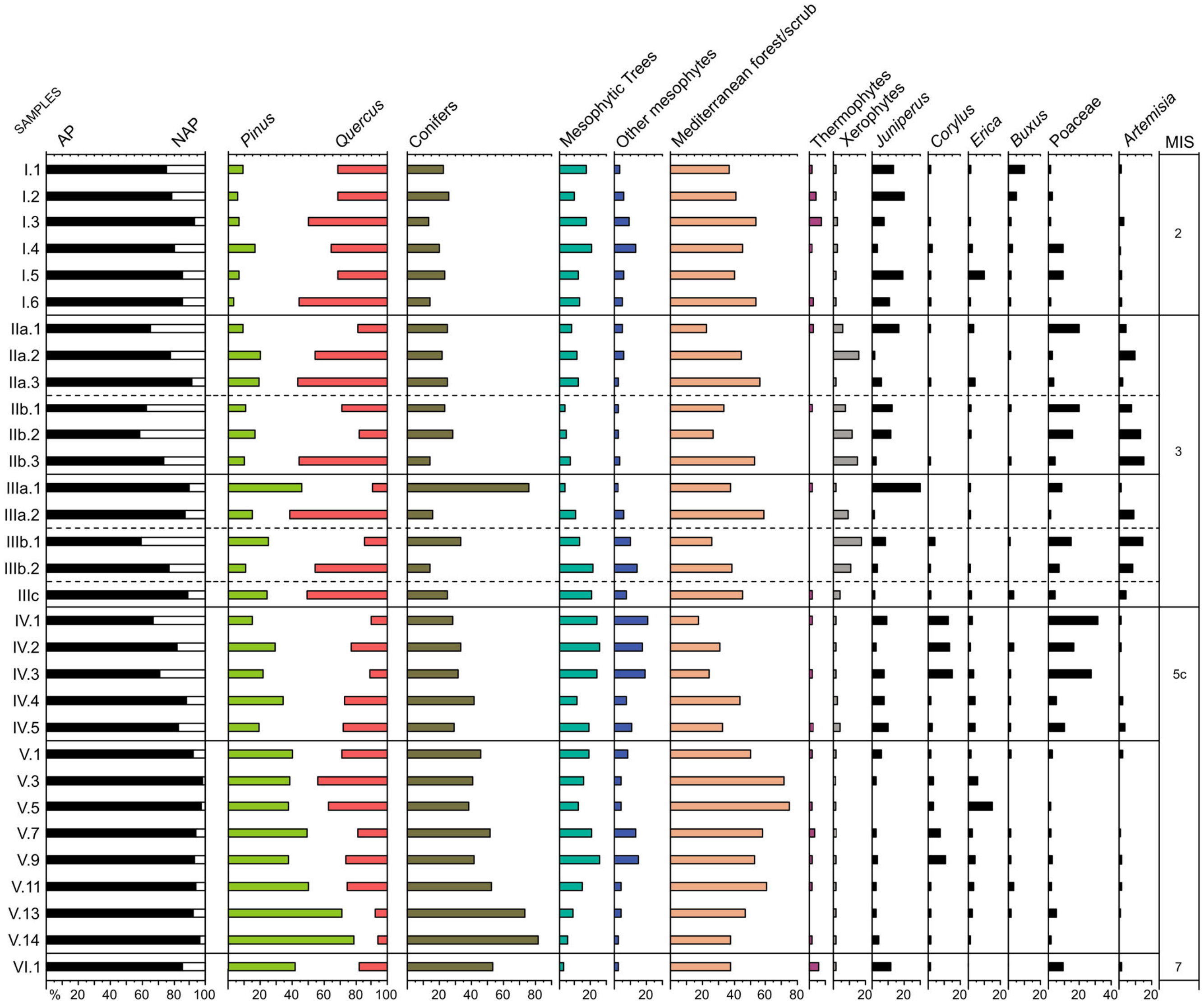

Figure 7. Synthetic pollen diagram of selected taxa from Teixoneres Cave. Redrawn from Ochando *et al.* (2020a). [Color figure can be viewed at wileyonlinelibrary.com]

whole Upper Pleistocene and most of the Holocene, and it is in one of the most continental locations where palynological studies have been carried out within the Iberian Peninsula (Fig. 11). This location, intensively influenced by climatic extremes, undoubtedly affects the composition of the pollen assemblages, which even during interglacials and interstadials show a complex patched vegetation landscape with high incidence of junipers and/or pines, relatively low mesophytic arboreal cover and high proportions of fluctuating xerophytic herbs (mainly *Artemisia*, Chenopodiaceae/Amaranthaceae, Asteraceae). Thus, vast steppes and a parkland mosaic do not only exist during cold stages (MIS 6, MIS 4, MIS 2). By contrast, pine, oak and especially juniper savannahs spread during the climate amelioration phases such as MIS 5e, MIS 5c, MIS 5a, some intervals of MIS 3 and the Holocene (González-Sampériz *et al.*, 2010, 2020; Aranbarri *et al.*, 2014). The inertial nature of conifer formations, surprisingly led by junipers during MIS 5 (as occurred in mid-Pleistocene inner Iberian palynological sequences) and later by pines, resisting competitive displacement by oaks (both evergreen and semi-deciduous), mesophytes or Mediterranean taxa, demonstrates the intense resilience of vegetation formations in Iberia, which is also seen in inner regions such as the Villarquemado area.

The Atapuerca hominin-bearing sites (42°21′N, 03°31′W; 980 m asl) are located at low elevation in an area with maximum altitude of 1078 m in the Sierra de Atapuerca and are made up of karstified Cretaceous limestones that include galleries and chasms filled with Quaternary sedimentary deposits. The construction of a railway route at the end of the 19th century uncovered some of these sedimentary fillings, such as those that comprise the so-called Trinchera del Ferrocarril and which include Gran Dolina, Galería and Sima del Elefante. They have all provided numerous archaeological and palaeontological remains including hominin fossils belonging to *Homo antecessor*, *H. heidelbergensis* and *H. neanderthalensis* covering from the Lower Pleistocene to the late Middle Pleistocene (e.g. Bermúdez de Castro *et al.*, 1997, 2011, 2016; Arsuaga *et al.*, 1999; Falguères *et al.*, 2013; Meyer *et al.*, 2016; Bógalo *et al.*, 2021).

By using habitat weighting methods on the record of vertebrates, charcoal and pollen, Rodríguez *et al.* (2011) inferred the past environmental conditions of Atapuerca between ca. 500 and 200 ka (Figs. 12 and 13). Of note is the coexistence of steppic species of vertebrates such as *Stenocranius gregaloides* and *Allocricetus bursae* with temperate and thermophilous taxa such as *Hystrix refossa* and *Crocidura*. Overall, the herpetofauna suggests a significant local woodland

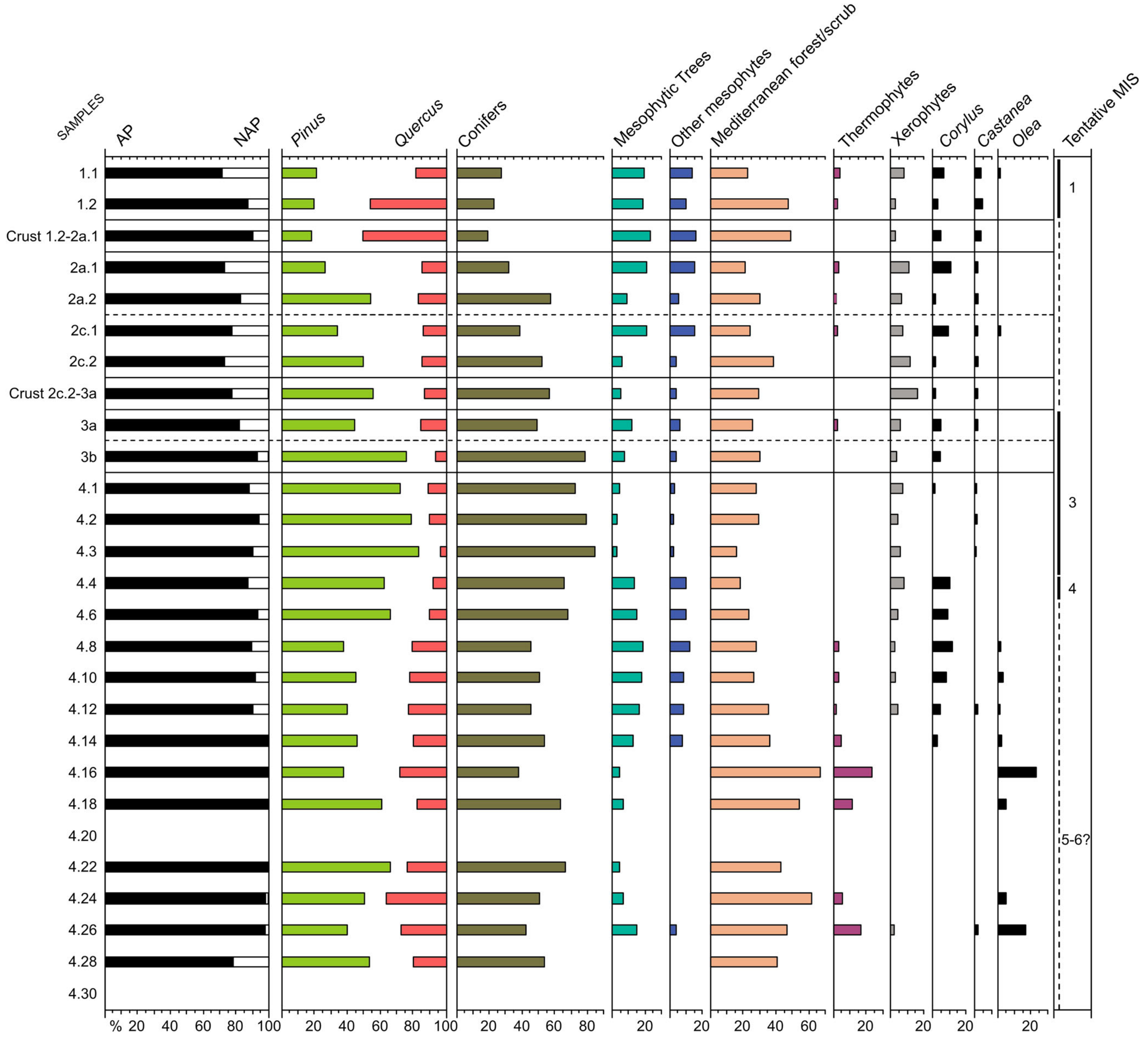

Figure 8. Synthetic pollen diagram of selected taxa from Toll Cave. Redrawn from Ochando *et al.* (2020b). [Color figure can be viewed at wileyonlinelibrary.com]

component, and the macrofauna indicates the coexistence of woodlands and open landscapes in the region. Palynological studies in the hominin-bearing levels of Atapuerca have been rather unrewarding (García-Antón and Sainz-Ollero, 1991; Burjachs, 2001) (Fig. 12), but the available data support Rodríguez *et al.*'s (2011) conclusion that Mediterranean and deciduous trees found refuge in the area, which embraced mosaic landscapes including woodlands, open-humid and open-dry meadows, watercourses, rocky habitats and steppes. The thermophilous component does not disappear from the assemblages, even when the whole sequence of up to 1 Myr is taken into account. The Galeria sequence shows peaks of *Quercus* and *Pinus* dominance together with *Fagus, Betula, Corylus, Juglans, Fraxinus, Olea, Pistacia, Phillyrea, Myrtus, Celtis, Carpinus, Ligustrum, Rhamnus, Salix* and the occasional presence of *Picea*. The herbaceous component is dominated by Ericaceae, Poaceae and Asteraceae (García-Antón and Sainz-Ollero, 1991) (Fig. 13).

For Sima de los Huesos, also in Atapuerca, García and Arsuaga (2011) reviewed the records of carnivores, ungulates and isotopes to construct a palaeoecological model, resolving that the dominant ecosystem was a savannah-like open woodland, in agreement with palynological data obtained from three clay-matrix samples (García-Antón, 1987), showing the abundance of pines together with oaks, *Betula* and *Fagus*. The carnivore assemblage (*Homotherium, Ursus, Panthera, Felis, Lynx, Vulpes, Canis, Cuon, Meles, Mustela, Martes*) was interpreted to represent a consequence of highly productive treelands.

Another important reference pollen sequence is Padul. This comes from a tectonic depression (37°00′21″N, 03°36′43″W) located about 22 km south of Granada, comprising a peaty area of about 2.5 × 3.5 km, at 700 m asl, east of Sierra Nevada. After the pioneering works of Menéndez-Amor and Florschütz (1962, 1964), the first systematic study was carried out by Florschütz *et al.* (1971), although there is no secure chronological control here. A subsequent study by Pons and Reille (1988) frames the sequence between isotopic stages 5 and 1. Another study on another core taken in the same area in the 1990s suggests that the deposition of peat begins about 400 000 years ago (Ortiz *et al.*, 2004). The changes in vegetation and climate of the last two glacial–interglacial

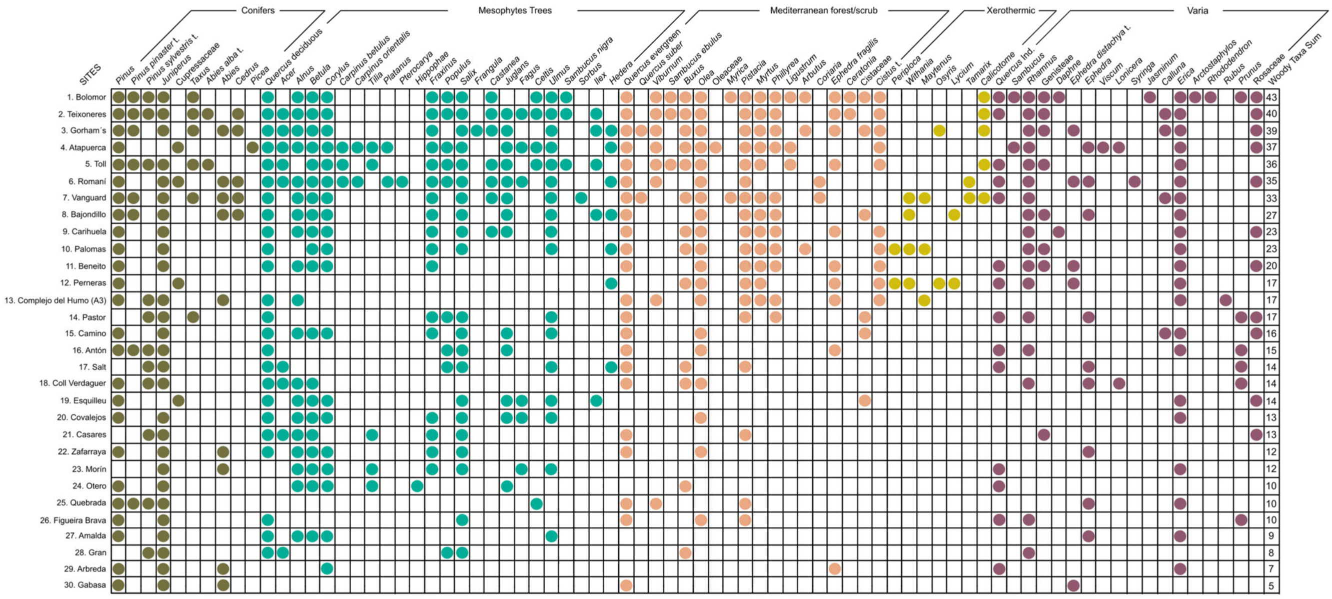

Figure 9. Woody taxa and their ecological categories in palynological sequences from Iberian Neanderthal sites. [Color figure can be viewed at wileyonlinelibrary.com]

cycles (~200 000 years) are described in the most recent work by Camuera *et al.* (2019).

In Padul, the end of the Middle Pleistocene (MIS 6) took place after a decline in Mediterranean forests and was characterized by the presence of a cold and arid climate indicated by high levels of xerophytes (*Artemisia*, Amaranthaceae, *Ephedra*) and the lowest PCI (Pollen Climate Index) values (Figs. 14 and 15). During MIS 6c and 6d the maximum peak of *Abies* occurred, in addition to an increase in Mediterranean and temperate-humid taxa (*Quercus, Fraxinus, Acer, Alnus* and *Betula*). Palaeoclimatic data support high rainfall conditions in the region. *Artemisia*, *Ephedra* and Amaranthaceae are

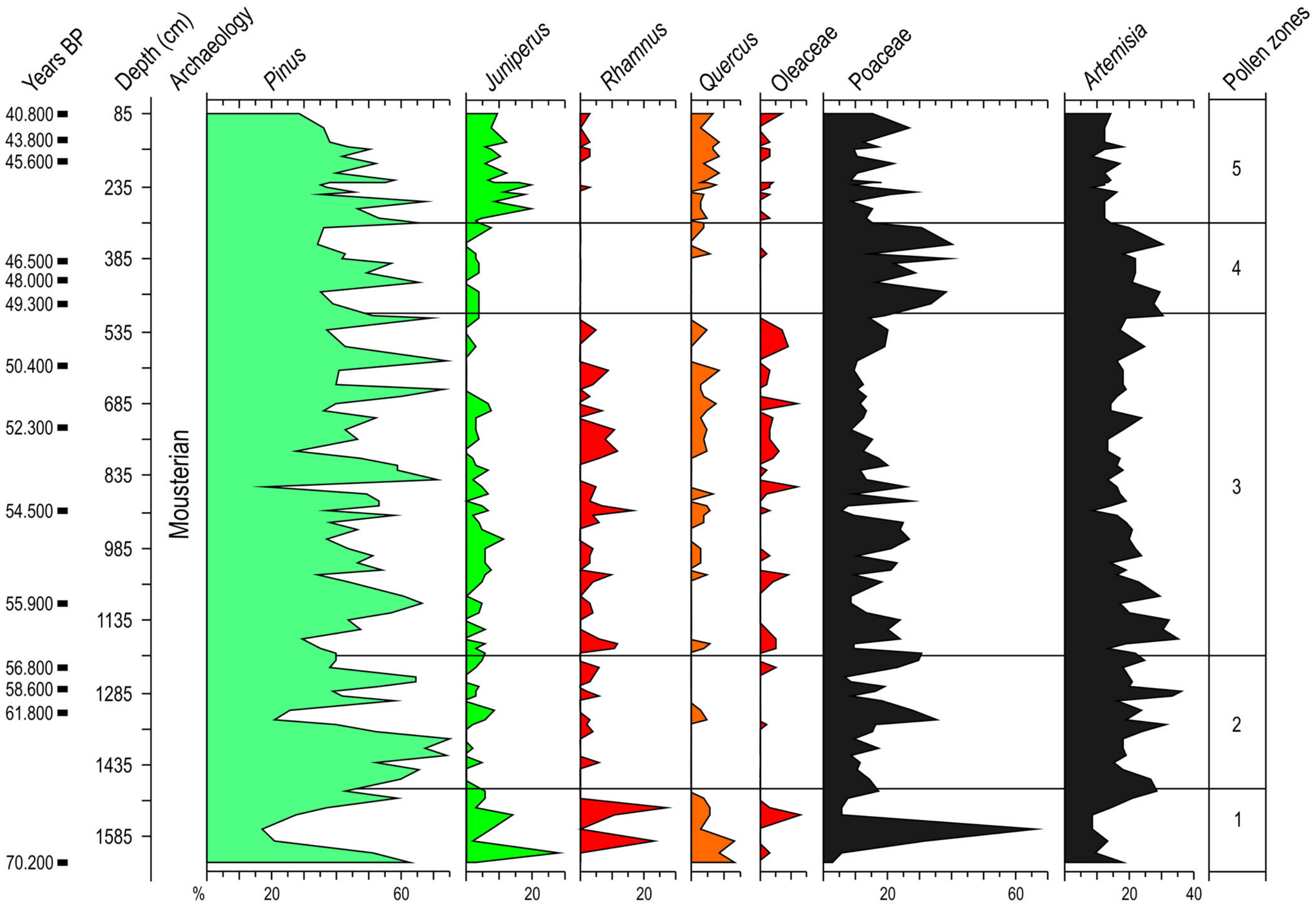

Figure 10. Main pollen curves and chronology of the Upper Pleistocene Romaní cave sequence (Burjachs and Julià, 1994). [Color figure can be viewed at wileyonlinelibrary.com]

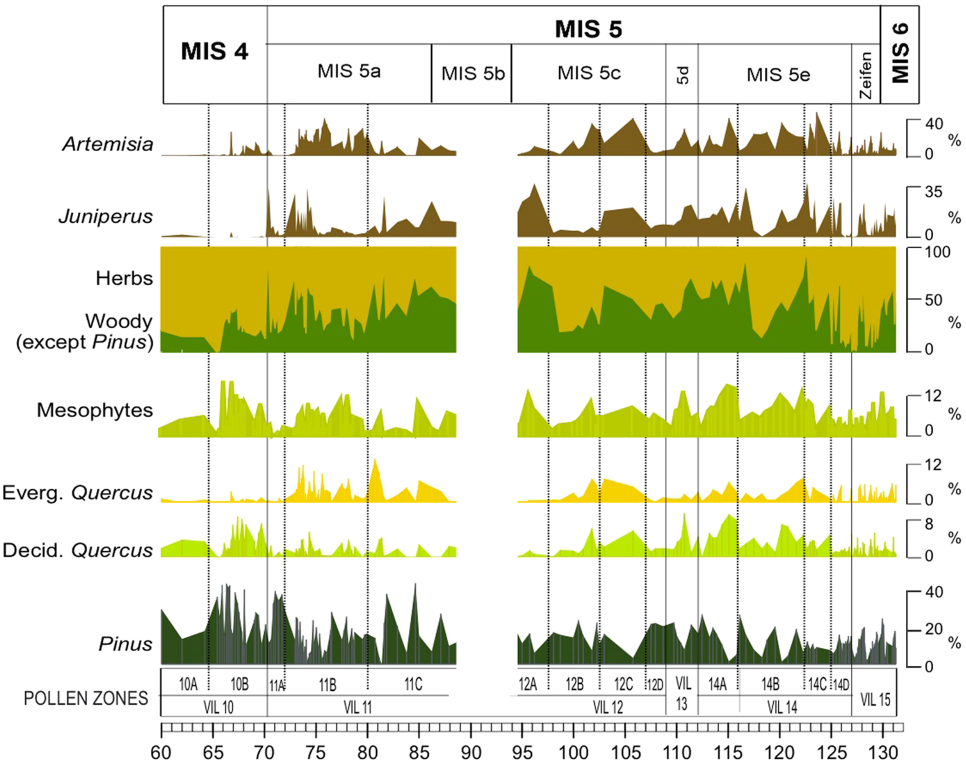

Figure 11. Synthetic pollen diagram of selected taxa (mainly woody component) in the sequence of El Cañizar de Villarquemado during the MIS 6–MIS 4 (135–60 ka BP) chronological interval. Redrawn from González-Sampériz *et al.* (2020). [Color figure can be viewed at wileyonlinelibrary.com]

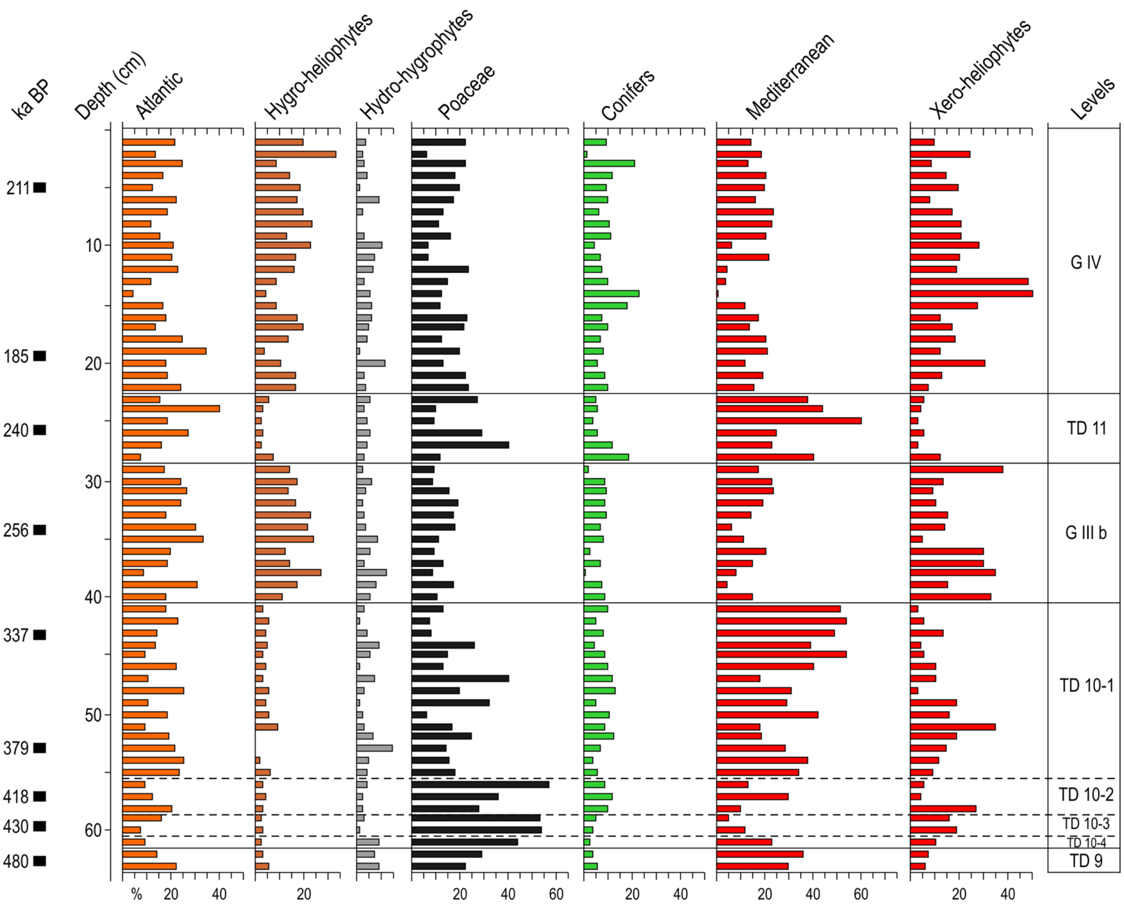

Figure 12. Combined pollen diagram for the sequences of Gran Dolina (TD) and Galería (G) in the Atapuerca hominin-bearing site. Taxa are grouped according to reported ecological types. Redrawn from Rodríguez *et al.* (2011) and Carrión *et al.* (2013). [Color figure can be viewed at wileyonlinelibrary.com]

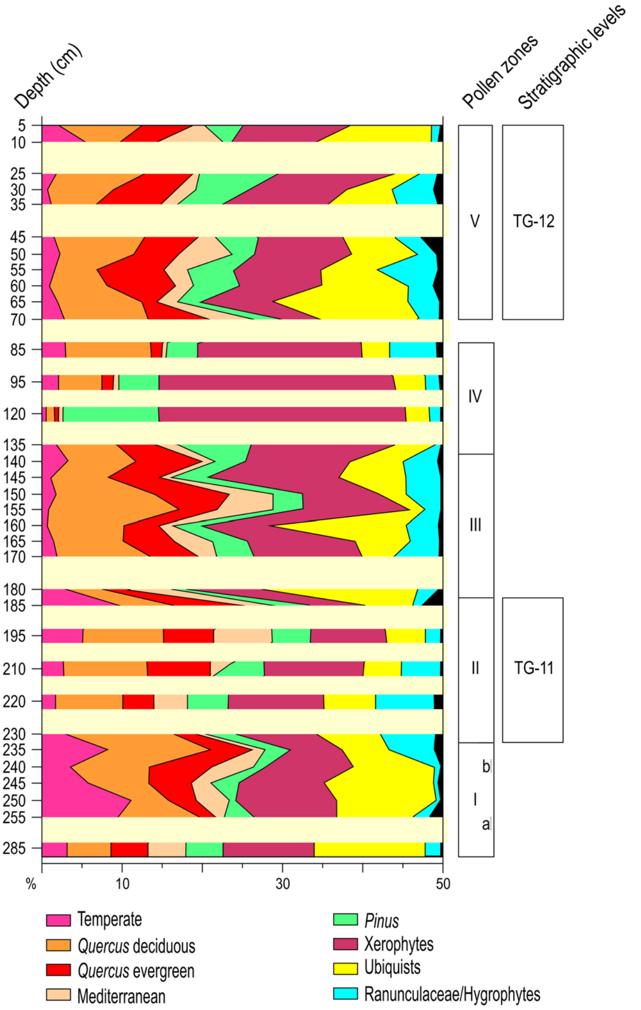

Figure 13. Summary of the most ecologically significant pollen curves in the sequence of Galería, Atapuerca. Redrawn from Rodríguez *et al.* (2011) and Carrión *et al.* (2013). [Color figure can be viewed at wileyonlinelibrary.com]

dominant for MIS 6b and 6a. From MIS 4 to MIS 2, the sequence is characterized by notable fluctuations within an increasing trend of *Pinus* and xerophytes, against the decrease of warm and humid Mediterranean forest taxa.

In general, vegetation changes in Padul are closely related to variations in the elevation of forest species in the bioclimatic vegetation belts in the Sierra Nevada linked to climatic oscillations (Camuera *et al.*, 2019). Additionally, there are orbital-scale vegetation oscillations that point to insolation as the main factor controlling vegetation changes in this record. Under harsher climatic conditions, the Late Pleistocene Carihuela pollen record (Carrión, 1992b; Carrión *et al.*, 1998, 1999; Carrión *et al.*, 2019c) parallels Padul showing similar dynamics of conifer savannahs and xerophytic grasslands during stadials. However, the long-distance pollen signal for Mediterranean sclerophylls is lower in Carihuela.

Mesothermic savannahs in coastal shelves

The Sima de las Palomas (Torre Pacheco, Murcia, 125 m. a.s.l., 5 km from the Mediterranean coast) includes a Neanderthal and Mousterian occupation dated from ca. 130 to 40 ka (Walker *et al.*, 2004, 2008). Pollen analyses in an interval implying a time ca. 44–40 ka include a mix of plant taxa with very different ecological affinities (Carrión *et al.*, 2003a, 2005; Yll and Carrión, 2003). In the context of the current climate of the southern coast of Murcia, with enclaves that do not exceed 200 mm of average annual rainfall, and high evapotranspiration values, the abundance of oaks is striking and, in particular, the presence of species that demand temperate-humid conditions such as hazel (*Corylus avellana*), ash (*Fraxinus*), strawberry tree (*Arbutus unedo*), box (*Buxus*) or birch (*Betula* cf. *celtiberica*) (Fig. 16). It is not easy to determine the exact area of origin of these tree populations, but there is no doubt that the oaks grew in the vicinity, since their pollen percentages range between 15 and 20% and, in a cave context, these cannot be due to long-distance dispersal (Prieto and Carrión, 1999; Navarro *et al.*, 2001, 2002). A local landscape can be conceived to have been made up of a much more diverse mosaic of plant formations than is currently observed. This would include a prevalence of xerophytic Mediterranean savannahs with pines (*Pinus nigra*, *P. halepensis*, *P. pinea*), oaks (*Quercus rotundifolia*, *Q. coccifera*, *Q. faginea*) and junipers, forest patches of pine and/or oaks with other deciduous trees, and an understorey of *Juniperus oxycedrus*, *Olea europaea*, *Phillyrea*, *Chamaerops humilis*, *Buxus*, *Rhamnus*, *Erica arborea*, *Maytenus europaeus*, *Smilax aspera* and *Pistacia*, as well as heliophilous formations with *Periploca angustifolia*, *Osyris quadripartita*, *Asphodelus*, Lamiaceae, Asteraceae, Cistaceae, *Thymelaea hirsuta*, *Calicotome intermedia*, and other Genisteae and, finally, marshes with chenopods, *Lycium* and *Whitania frutescens*. It is probable that many trees behaved like phreatophytes, growing on riverbanks and streams. Because the sequence is within a glacial period, the diversity and abundance of thermophytes can be considered relevant. It should be noted that some species such as *Periploca angustifolia* and *Maytenus senegalensis* can hardly bear frost, so it is evident that the local climate was not much colder than it is today.

The situation described for Sima de las Palomas may be extended to the coastal areas from Murcia to Gibraltar and beyond into the Atlantic coasts of Huelva. Similar vegetation records have been described in Perneras Cave, Mazarrón at Murcia province (Carrión *et al.*, 1995), Gorham's (Carrión *et al.*, 2008) and Vanguard Caves in Gibraltar (Carrión *et al.*, 2018), Mousterian Bajondillo (López-Sáez *et al.*, 2007) and Abrigo del Humo (Ochando *et al.*, 2020c) in Málaga. These records agree in suggesting the existence of a littoral location favourable for the survival of the greatest diversity of environments in the Iberian Peninsula during the last glacial in which the late survival and extinction of the Neanderthals took place (Finlayson *et al.*, 2006; Carrión *et al.*, 2018).

Gorham's Cave demands particular attention. The cave is one several located in the basal and south-easternmost level of the Gibraltar Peninsula, on the edge of the current sea level at 36°07′13″N and 05°20′31″W. The excavations, carried out intensively since 1997, have produced a four-level stratigraphy (Finlayson *et al.*, 1999, 2000, 2006), with level IV corresponding to a Mousterian occupation, dated between 32 560 and 23 780 a BP. However, there are three older basal dates of 44 090 a BP. Palaeobotanical studies at Gorham's Cave include anthracological and palynological analyses of sediment and coprolites (Carrión *et al.*, 2008; Ward *et al.*, 2012b). The anthracological sequence for level IV is dominated by *Pinus pinea-pinaster*, with a small contribution from *Pinus nigra-sylvestris*, *Juniperus*, Fabaceae, Cistaceae, *Olea* and *Erica*. The sediment palynology of level IV is characterized by high frequencies of *Juniperus*, *Pinus*, Ericaceae, Poaceae, Asteraceae, Cistaceae and, to a lesser extent, *Ilex aquifolium*, *Artemisia* and Chenopodiaceae. Among the components of arboreal pollen are *Olea*, *Pistacia*, *Betula*, *Corylus*, *Fraxinus*,

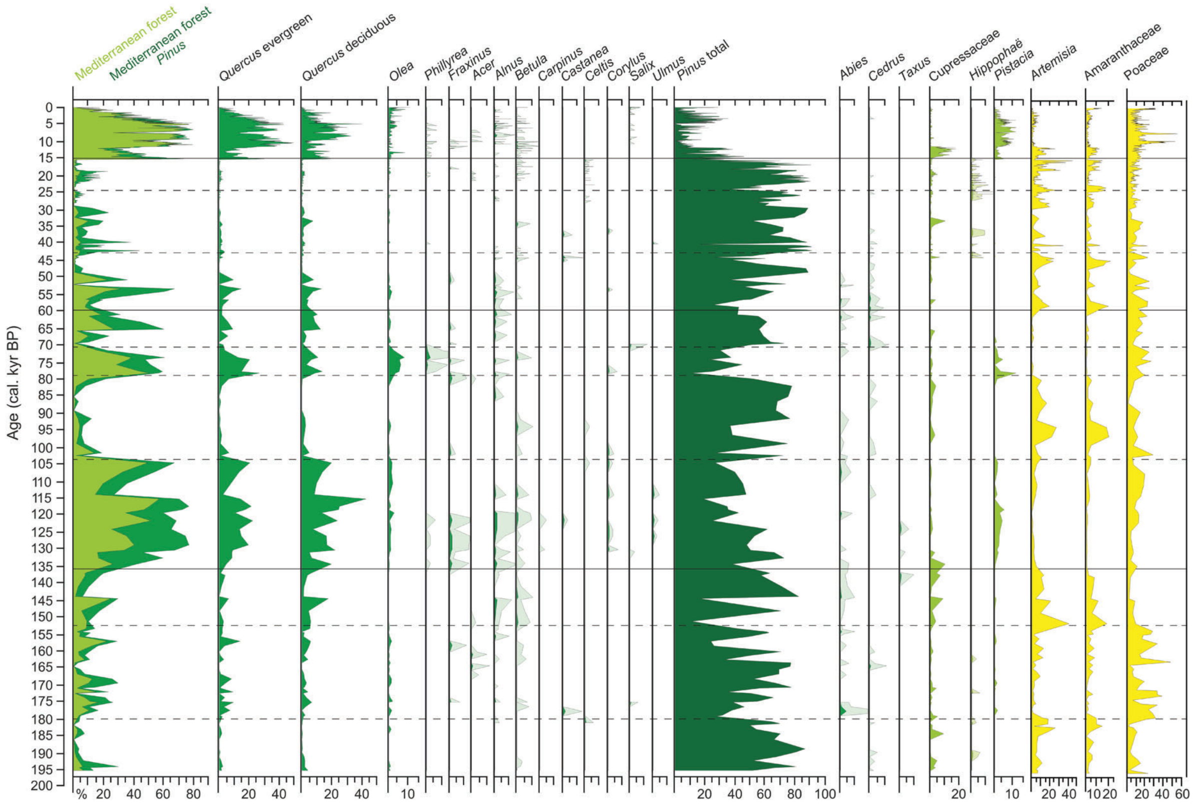

Figure 14. Synthetic pollen diagram of Padul-15-05 core, with percentages calculated with respect to the total terrestrial pollen sum. Silhouettes in lighter colour show 10× exaggeration percentages. The Mediterranean forest taxa category is composed by *Quercus* total, *Olea*, *Phillyrea* and *Pistacia*. Redrawn from Camuera *et al.* (2019). [Color figure can be viewed at wileyonlinelibrary.com]

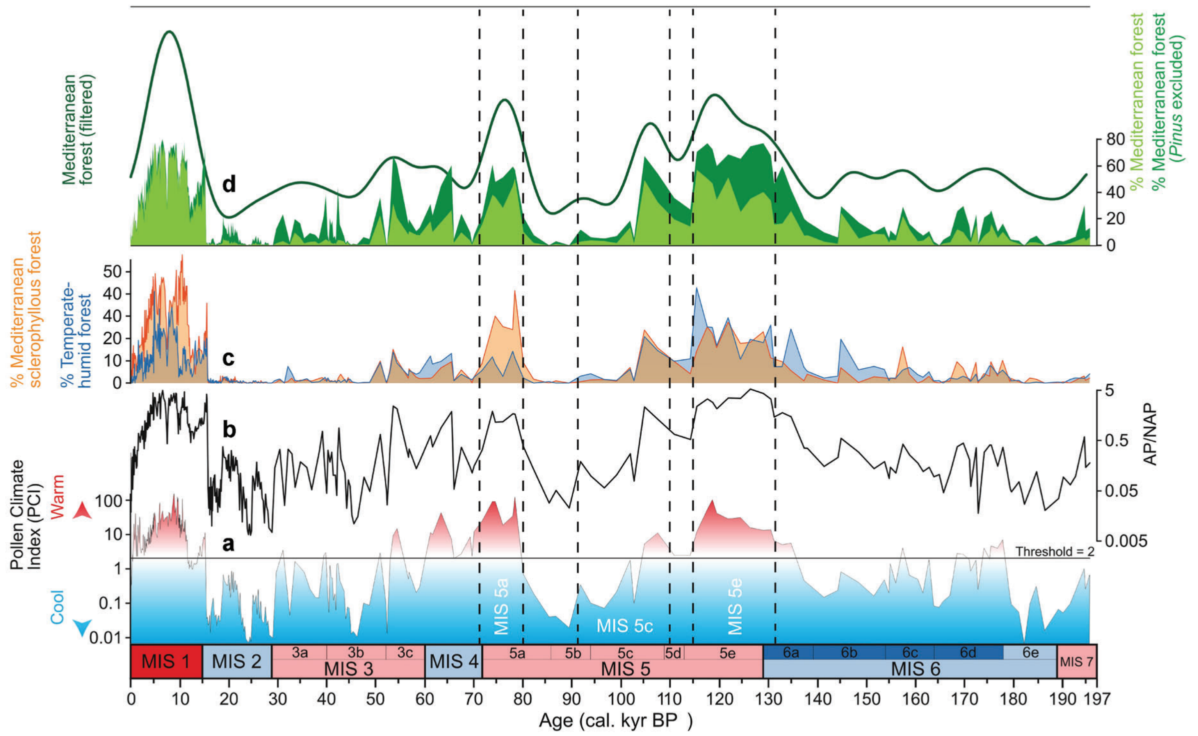

Figure 15. Illustration of plots showing, from bottom to top: (a) the Pollen Climate Index (PCI) with the horizontal black line (value ~2) indicating the boundary between glacial/stadial and interglacial/interstadial phases; (b) AP/NAP (arboreal pollen/non arboreal pollen) ratio (AP also includes *Pinus*), on a logarithmic scale; (c) percentages of Mediterranean sclerophyllous forest (orange) and temperate-humid forest (blue); (d) Mediterranean forest pollen percentages including *Pinus* (light green) and excluding *Pinus* (dark green) with respect to the total terrestrial pollen sum along with the filtered Mediterranean forest data (green line). Marine Isotope Stages (MIS) follow Sun and An (2005) and Fletcher *et al.* (2010). Redrawn from Camuera *et al.* (2019). [Color figure can be viewed at wileyonlinelibrary.com]

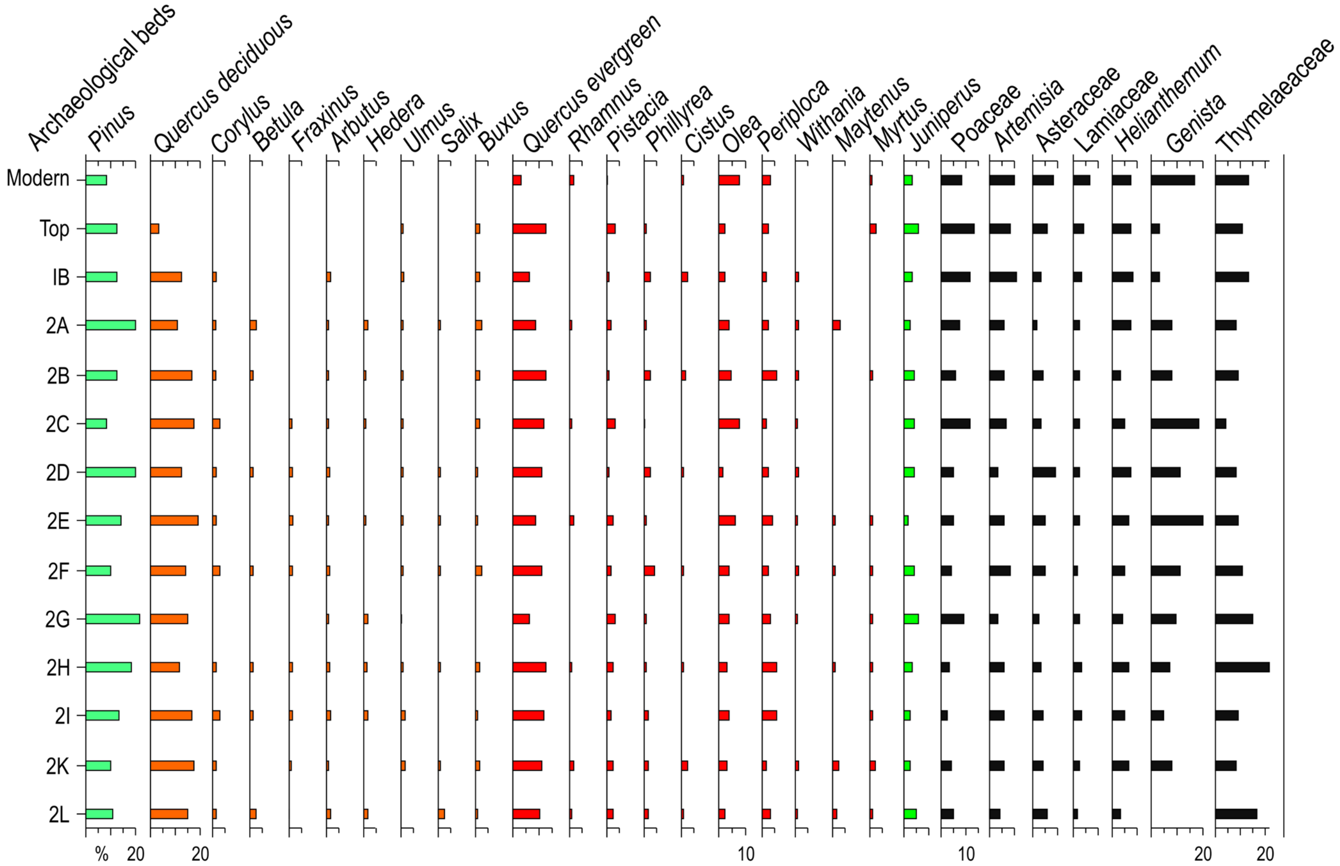

Figure 16. Main pollen taxa from the south-eastern Spain Neanderthal site of Sima de las Palomas (Carrión *et al.*, 2003a). Redrawn from Carrión *et al.* (2013). [Color figure can be viewed at wileyonlinelibrary.com]

Quercus and *Salix*. Coprolite palynology places the results in the context of a mosaic landscape and complements the previous data (Figs. 6 and 17). The dominant types of pollen spectra are *Pinus*, Poaceae, *Quercus* and *Juniperus*. Other taxa that eventually reach important percentages are *Artemisia*, Cyperaceae, Cistaceae, Ericaceae and Asteraceae. Apart from the above, of note are the presence of *Taxus, Pinus pinaster, Corylus, Alnus, Betula, Castanea, Ulmus, Fraxinus, Acer, Salix, Arbutus, Olea, Phillyrea, Buxus, Viburnum, Rhamnus, Maytenus, Myrtus*, *Calicotome*, Ericaceae, Genisteae, *Asphodelus*, *Artemisia* and *Plantago*, among others. Carrión *et al.* (2008) postulated the existence of savannahs, riparian forests, heliophytic and chaparral thickets with many chamaephytes and hemicryptophytes, grasslands and areas of steppe, and halophytic and littoral vegetation. Potentially, savannahs could include – in their arboreal layer – species such as *Pinus pinea*, *Juniperus phoenicea*, *Quercus ilex-rotundifolia*, *Quercus coccifera*, *Quercus suber*, *Erica arborea*, *Arbutus unedo* and *Pistacia terebinthus*. During the contemporary period of Gorham's Upper Palaeolithic, the vegetation did not change greatly, as expected in a coastal refuge (Finlayson *et al.*, 2006, 2008; Finlayson and Carrión, 2007; Bailey *et al.*, 2008).

Final remarks

The coastal shelves and mountains of southern Iberia where Neanderthals lived were certainly singular in floristic and ecostructural terms. Pine, oak and mixed savannahs may have been the dominant formation. Most interestingly, however, the coexistence of temperate, deciduous trees, cold-adapted pines currently growing in high altitudes, Mediterranean conifers, Mediterranean oaks and scrub, halophytic grasslands, and xerothermic North African matorral with palaeotropical elements represents a unique refugium ecosystem in the sense of a Noah's Ark for plant species. This coexistence is not exclusive to the Pleistocene. However, it reaches the middle Holocene in some mountains such as Sierra de Gádor, Almería, a local reservoir of edaphic water and forest patches in the heart of a semi-desertic region (Carrión *et al.*, 2003b).

Hominin refugia may have been preferentially distributed across regions with high levels of geological variability favouring the maintenance of mosaic habitats through time. This would include many coastlines (Carrión *et al.*, 2008; Finlayson *et al.*, 2008) which would have acted as corridors opening past expansion routes for humans (Bailey *et al.*, 2008). The progressive Neanderthal extinction ending in southern Iberia can be depicted within a continental to oceanic gradient, ending in the southernmost extreme (Finlayson, 2008).

Here we also show evidence of woodlands rich in species and depicting a palaeoecosystem with a tremendous structural complexity in which we find Neanderthals and/or their lithics during cold dry stages of the Iberian Pleistocene. It is likely that these forests were maintained by strong edaphic conditions added to the regional climatic humidity. This possibility has analogues in other geographically complex regions. Recently, Barboni *et al.* (2019), working on the Aramis Member (Awash Valley, Ethiopia), have emphasized the importance of springs for the palaeoecology of hominin-bearing sites. Springs would have favoured structurally complex vegetation representing, at the landscape scale, hydro-refugia favouring increased gathering of animals, allowing migrations during dry periods. Albert *et al.* (2018) concluded similarly: though their research was on phytoliths and plant macrofossils, plants from fluvial channels, levées and backswamp environments were of particular importance for human evolution in Africa.

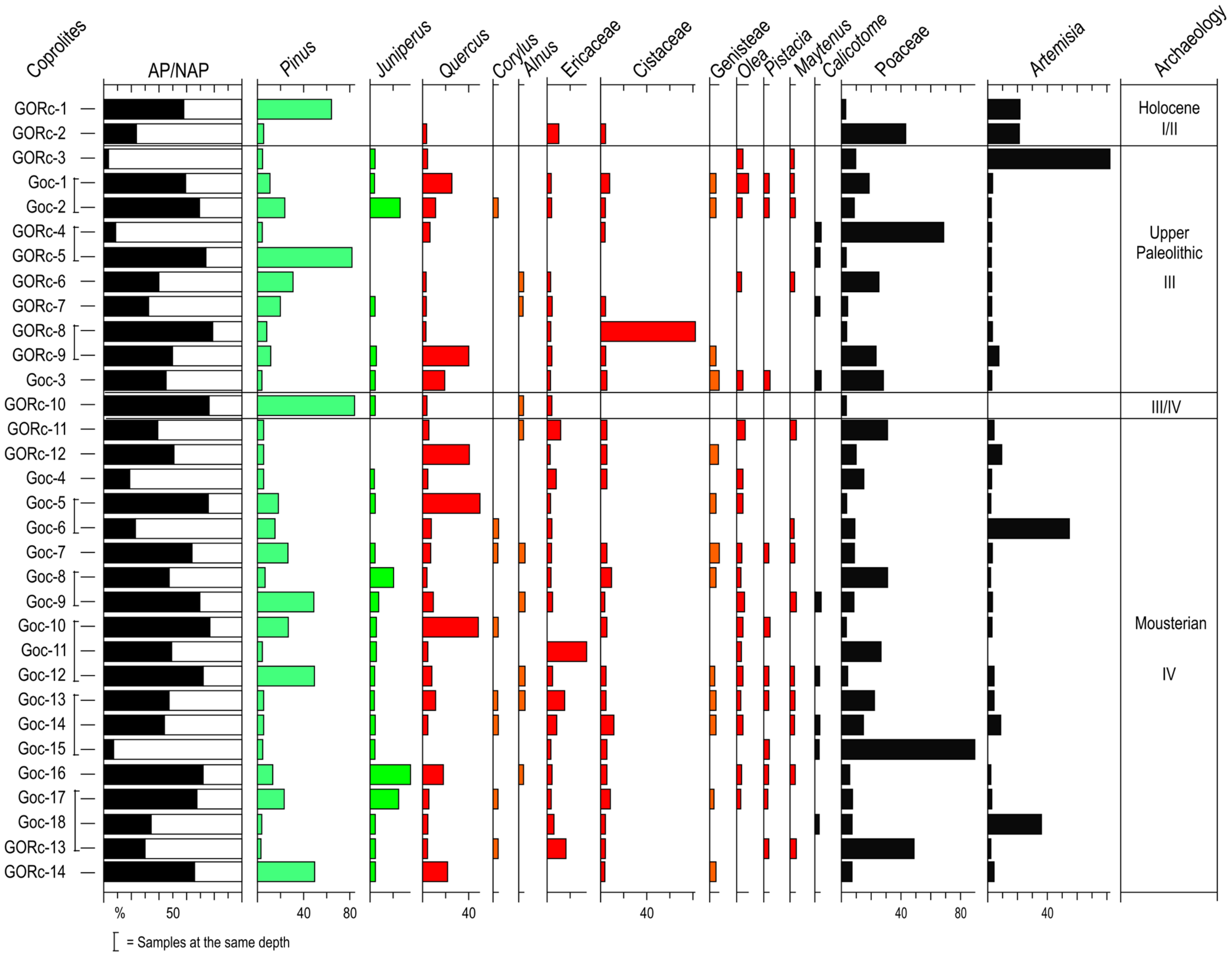

Figure 17. Synthetic pollen diagram from coprolites of Gorham's Cave, Gibraltar (Carrión *et al.*, 2008). Redrawn from Carrión *et al.* (2013). [Color figure can be viewed at wileyonlinelibrary.com]

In the southern European context, glacial refugia may be regarded as biodiversity reservoirs during cold phases (Hampe *et al.*, 2013). In other words, 'local anomalies' nevertheless have great relevance in terms of biological conservation and, with regard to the focus of this paper, multi-centennial and multi-millennial maintenance of hominin populations. Traditionally we have been highly dependent on palaeoenvironmental reconstructions that are actually based on 'average' pollen rain signals, reflecting the vegetation of broad continental environments (marine sequences) or very vast depositional basins (lakes) (e.g. Birks, 1986; see Carrión, 2004 for a discussion). These signals may be too coarse to facilitate reasonable speculation about the influences of plant ecology on the past ecology, biogeography or behaviour of human populations (Carrión *et al.*, 1999).

In a certain sense, the traditional perspective on the physical environment's influence on ecology and human evolution has been climaticist, in that most studies take as a general guideline the global data on astronomically induced climatic variation (Potts, 1998; Behrensmeyer, 2006). Not surprisingly, traditional deterministic views of vegetation–climate response are not satisfactory in explaining the observed patterns in the pollen diagrams of the Iberian Peninsula (Carrión, 2001; Carrión *et al.*, 2011; González-Sampériz *et al.*, 2020). We should consider a 'glacier refugium' as an entity endowed with spatial peculiarity and physiographical complexity, that is, plant mosaicity. Without a doubt, the Neanderthals of the Iberian Pleistocene were not everywhere. Here we see that some important occupations, otherwise permanent or quasi-permanent, suggest human preferences for the forest and tree savannah landscapes, probably because they presented environmental circumstances that favoured survival, including opportunities for hunting, gathering and shelter. The use of plant materials for food and technological items cannot be disregarded (Ward *et al.*, 2012a,b; Hardy, 2018; Zilhão *et al.*, 2020).

However, we should emphasize that Neanderthals adapted and responded properly to climatic changes, and the great diversity of palaeoenvironmental reconstructions show their occurrence from tundra to closed forests (Finlayson and Carrión, 2007). It is then clear that they were characterized by behavioural versatility, phenotypic plasticity and gene polymorphism (Antón *et al.*, 2014). Our goal here is to stress that the forested environments have been somewhat neglected among the broad diversity of habitats where Neanderthals subsisted not only during interglacials and interstadials, but also (in refugial stations) during cold and dry stages.

The role of Iberian glacial refugia in the radiation and selection of the Neanderthal lineage is still unknown. Although not as extensive and crucial for human evolution as eastern and southern Africa, the Mediterranean region is a biodiversity hotspot (Spathelf and Waite, 2007) with a high level of endemism, and probably a remnant of a larger and more fragmented territory that functioned like an engineer of plant and animal diversity over the Cenozoic (Carrión *et al.*, 2011). The Iberian Peninsula exhibits rugged and complex landscapes with a wide diversity of habitats, locally highly sensitive to climate change (Sechrest *et al.*, 2002), and containing large amounts of evolutionary history, ecological interaction and biotic complexity (Bascompte *et al.*, 2006). Perhaps these factors affect diversification by inducing speciation and reducing extinction rates.

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Abbreviations. MIS, Marine Isotope Stages; PCI, Pollen Climate Index.

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