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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.

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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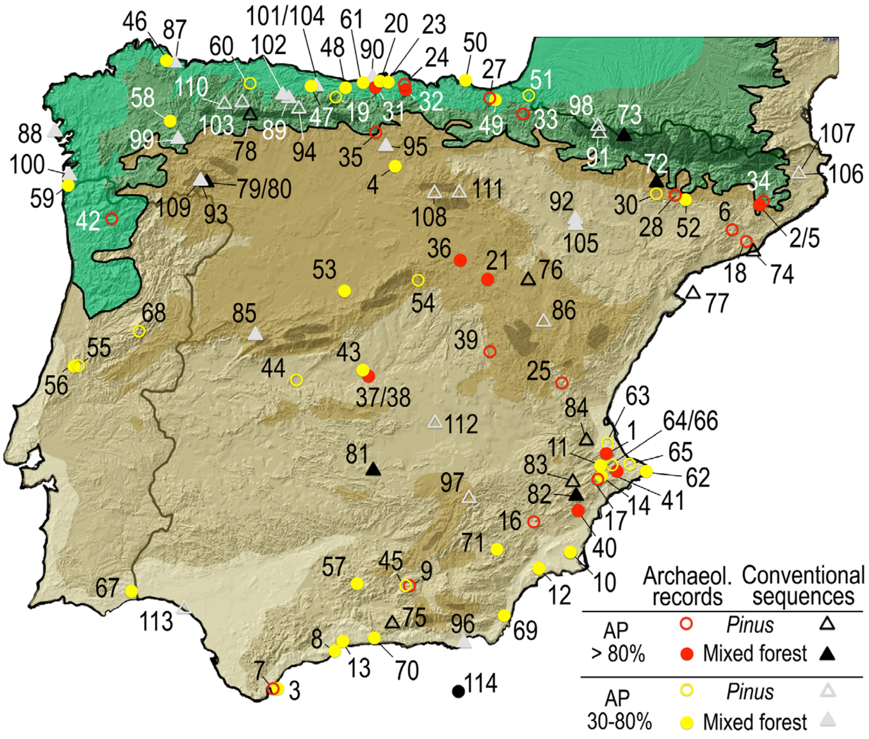

Figure 1. Location of Iberian sites with palaeobotanical data including stadials MIS 12 onwards (late Mid- and Upper Pleistocene). [Color figure can be viewed at wileyonlinelibrary.com]

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,

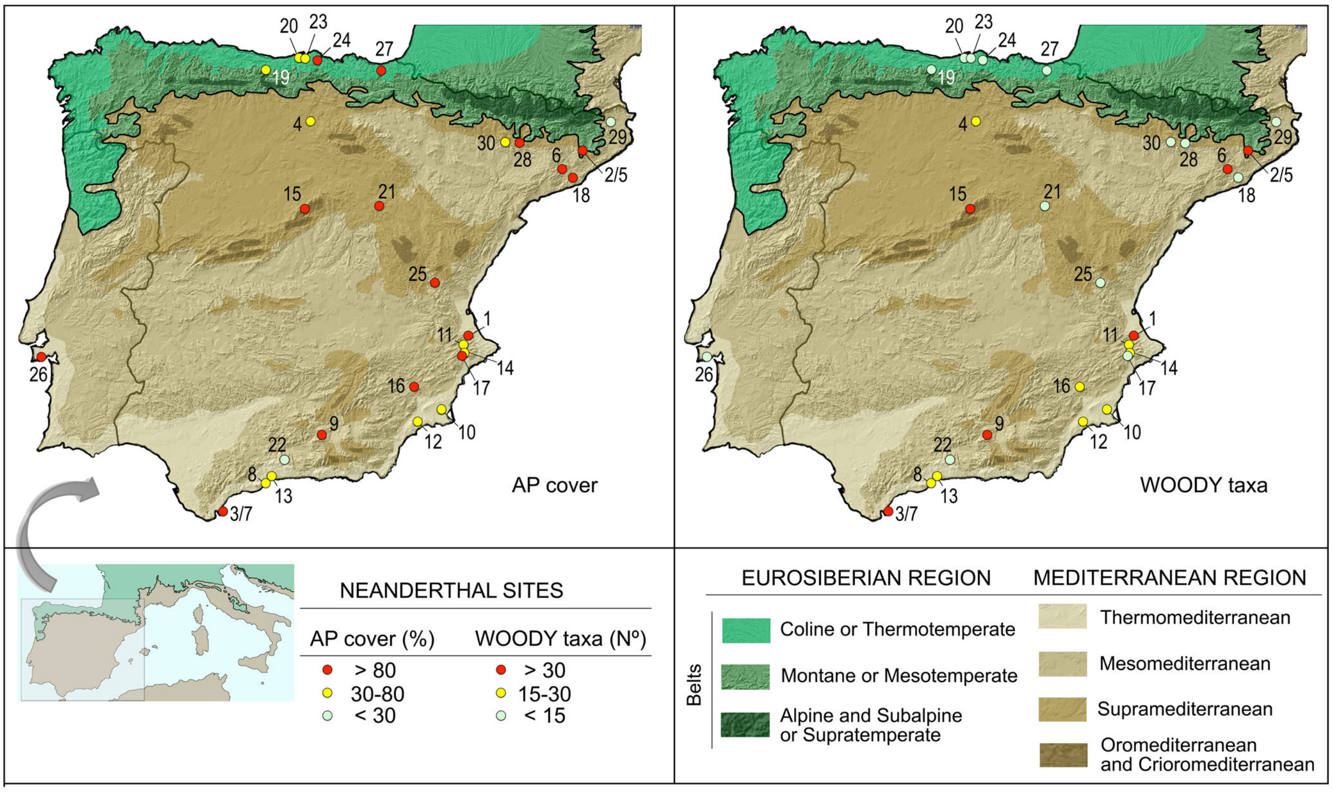

Figure 2. Distribution of Iberian Neanderthal pollen sites with respect to phytogeography and their arboreal pollen (AP) cover and number of woody taxa. [Color figure can be viewed at wileyonlinelibrary.com]

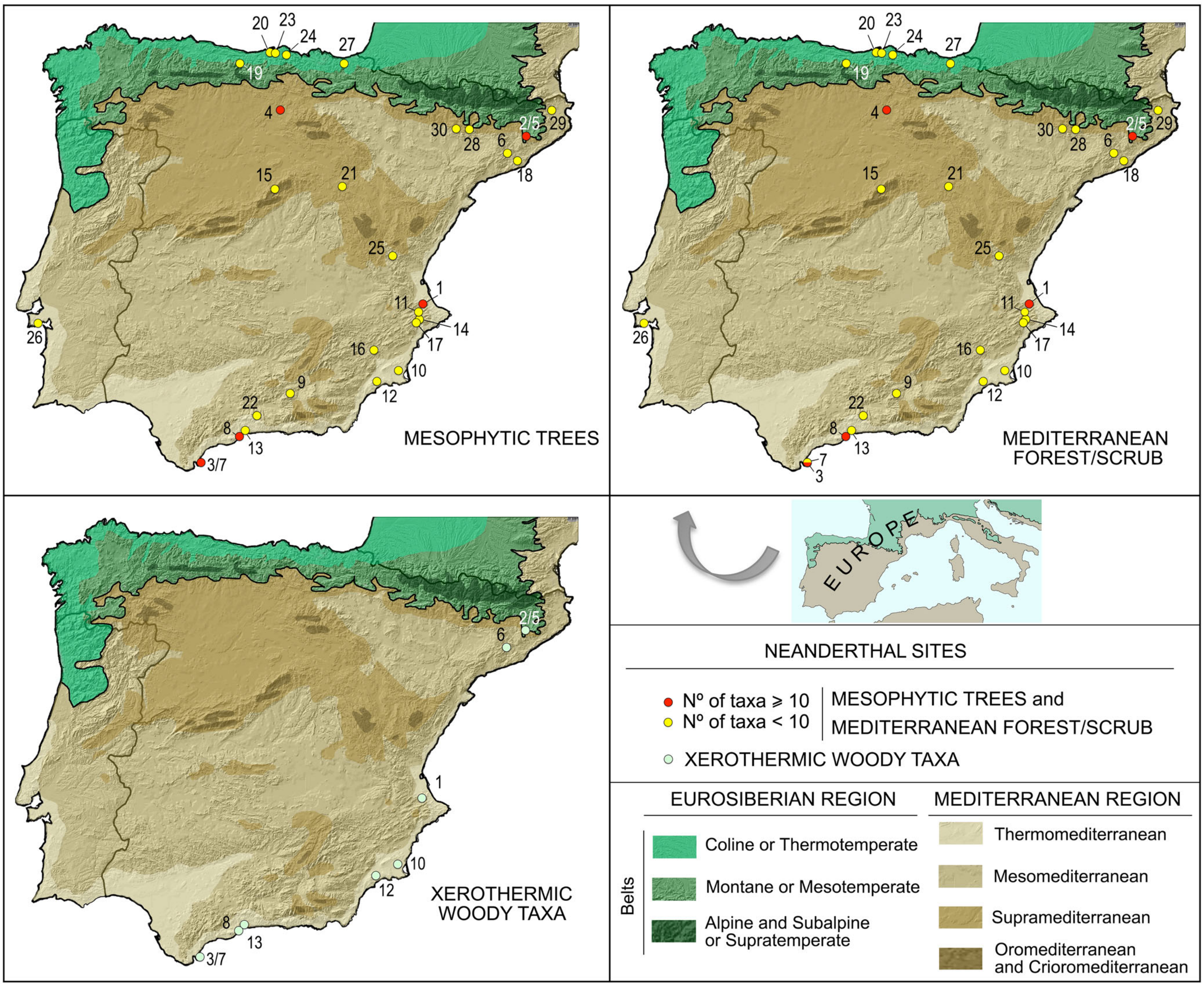

Figure 3. Distribution of Iberian Neanderthal pollen sites with respect to phytogeography and their number of mesophytic, Mediterranean and xerothermic woody taxa. [Color figure can be viewed at wileyonlinelibrary.com]

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;

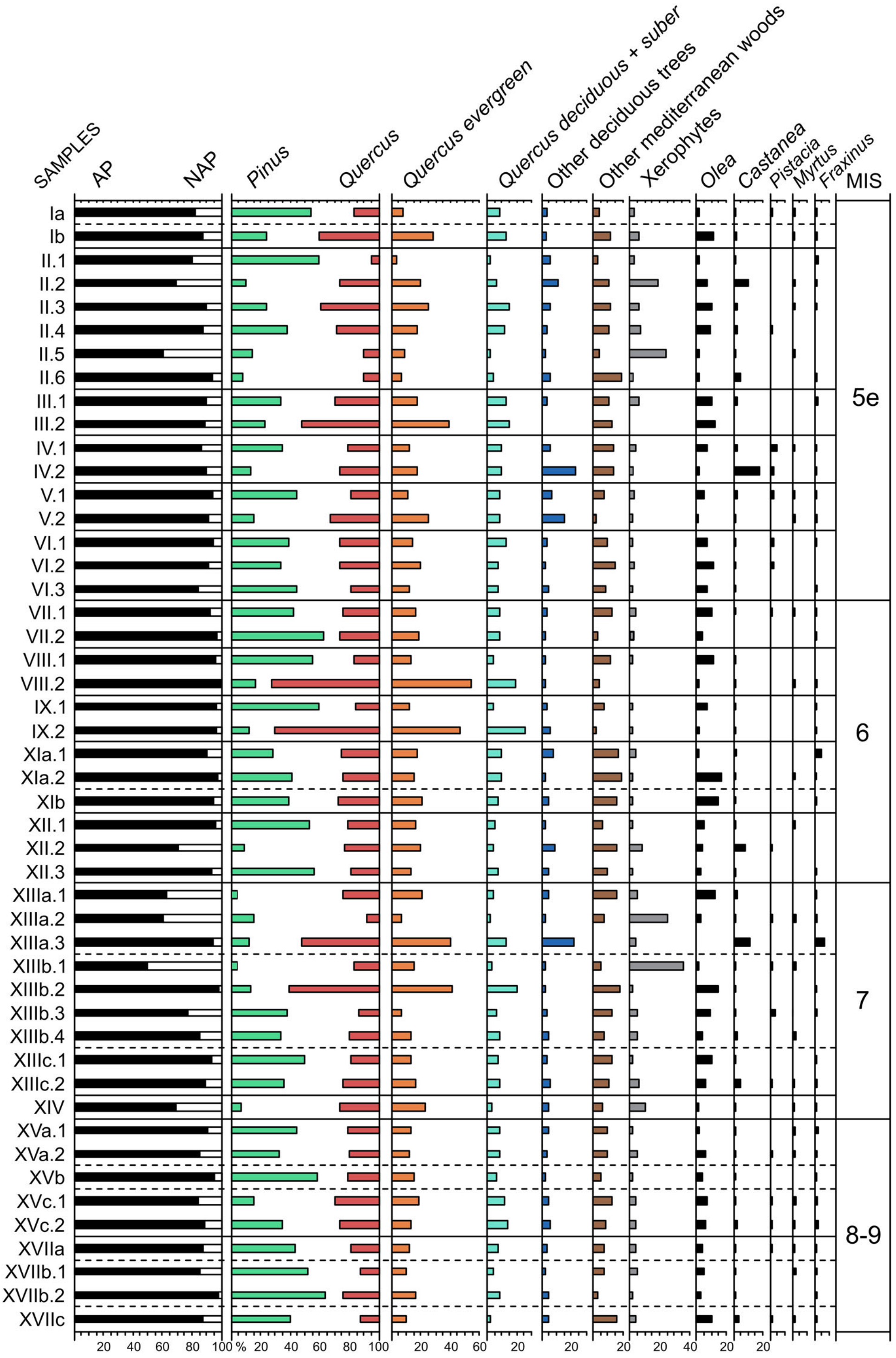

Figure 4. Synthetic pollen results from Bolomor Cave. Redrawn from Ochando *et al.* (2019). [Color figure can be viewed at wileyonlinelibrary.com]

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

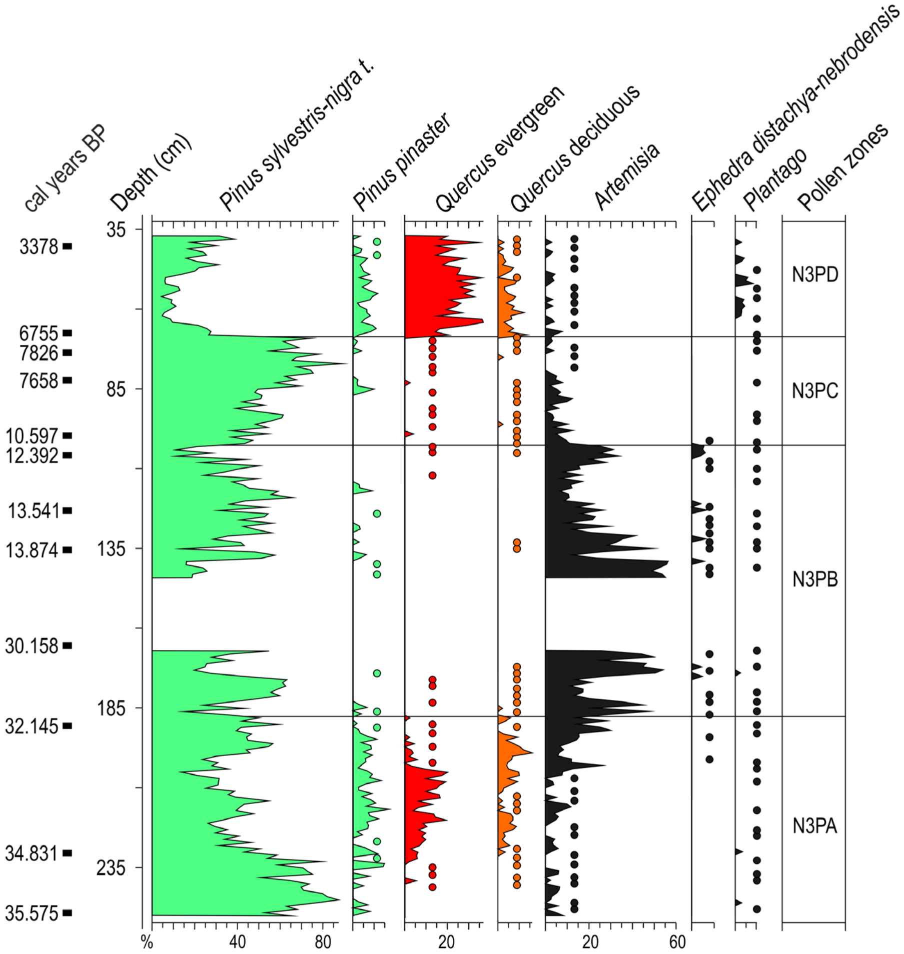

Figure 5. Synthetic pollen diagram of Canal de Navarrés peatbog, Valencia. Redrawn from Carrión and van Geel (1999). [Color figure can be viewed at wileyonlinelibrary.com]

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;

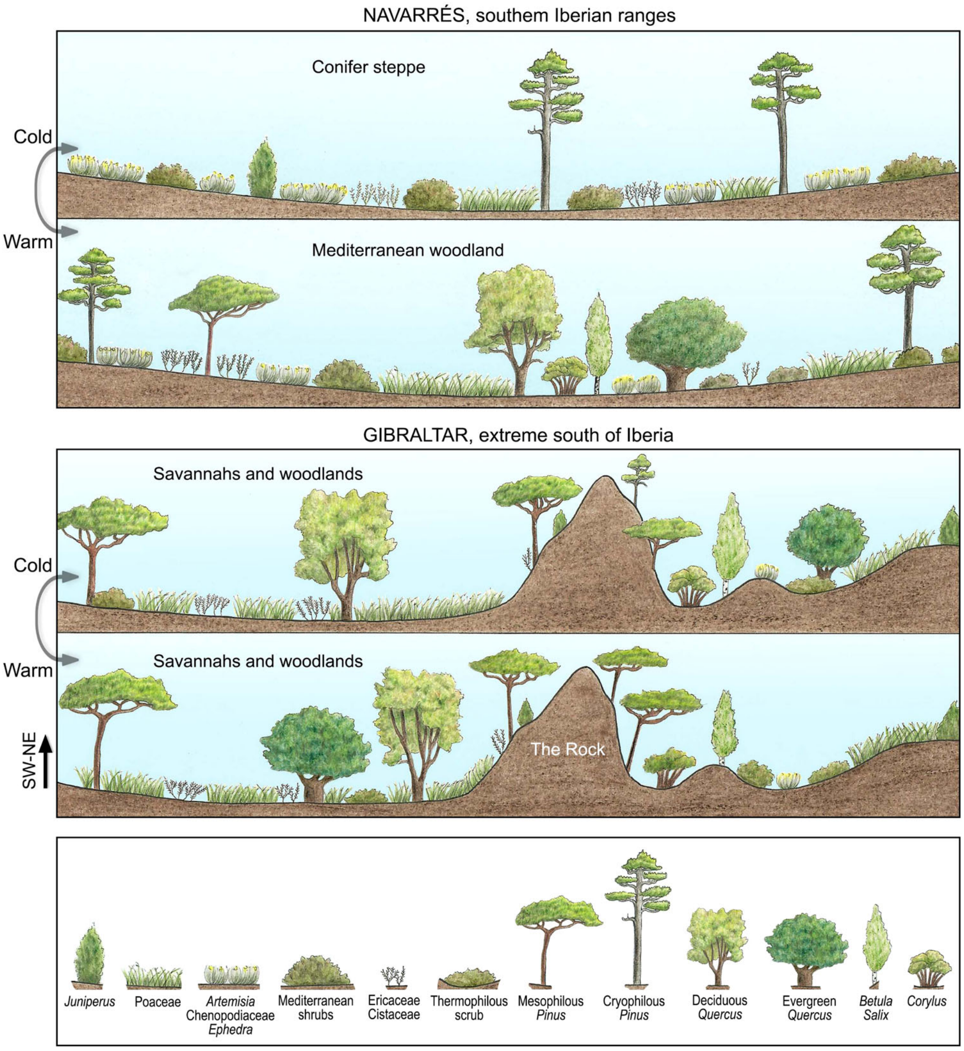

Figure 6. Latitudinal pattern in vegetation development across a part of Mediterranean Iberia. There is a lack of substantial vegetation and floristic changes between Pleistocene stadials and interstadials in a refugium context such as derived from palaeoecological data of Gorham's Cave (Carrión *et 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

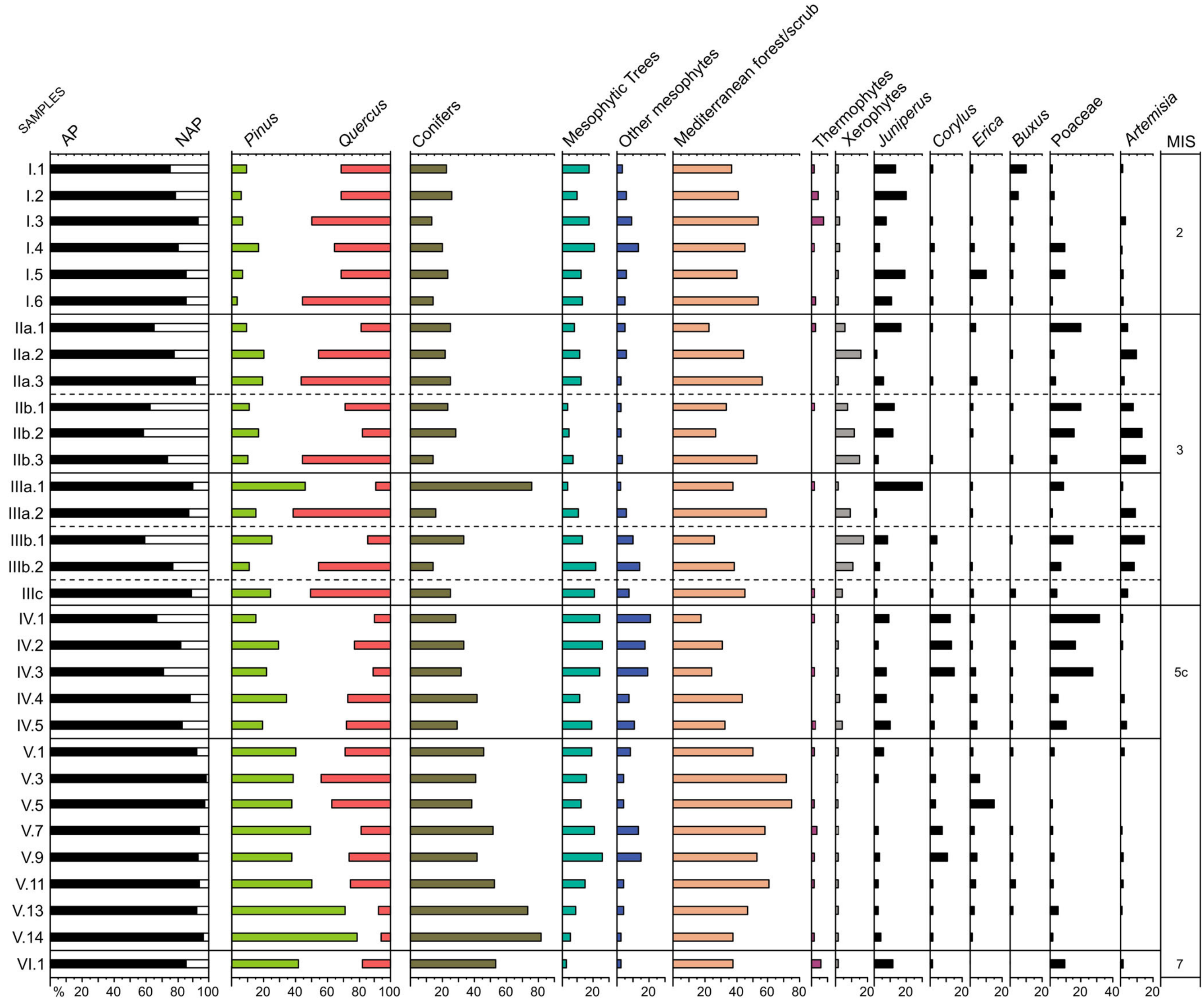

Figure 7. Synthetic pollen diagram of selected taxa from Teixoneres Cave. Redrawn from Ochando *et al.* (2020a). [Color figure can be viewed at wileyonlinelibrary.com]

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

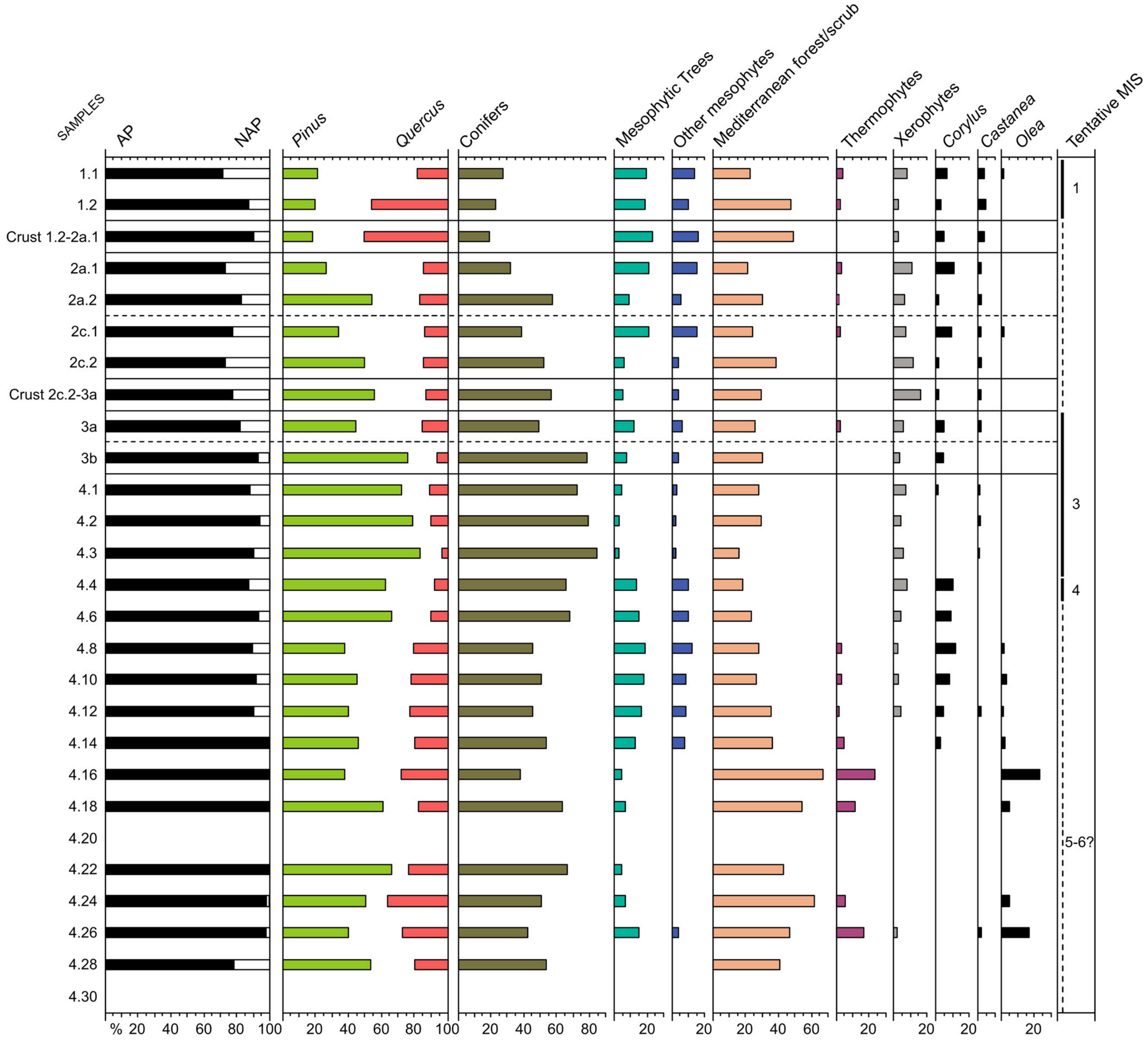

Figure 8. Synthetic pollen diagram of selected taxa from Toll Cave. Redrawn from Ochando *et al.* (2020b). [Color figure can be viewed at wileyonlinelibrary.com]

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

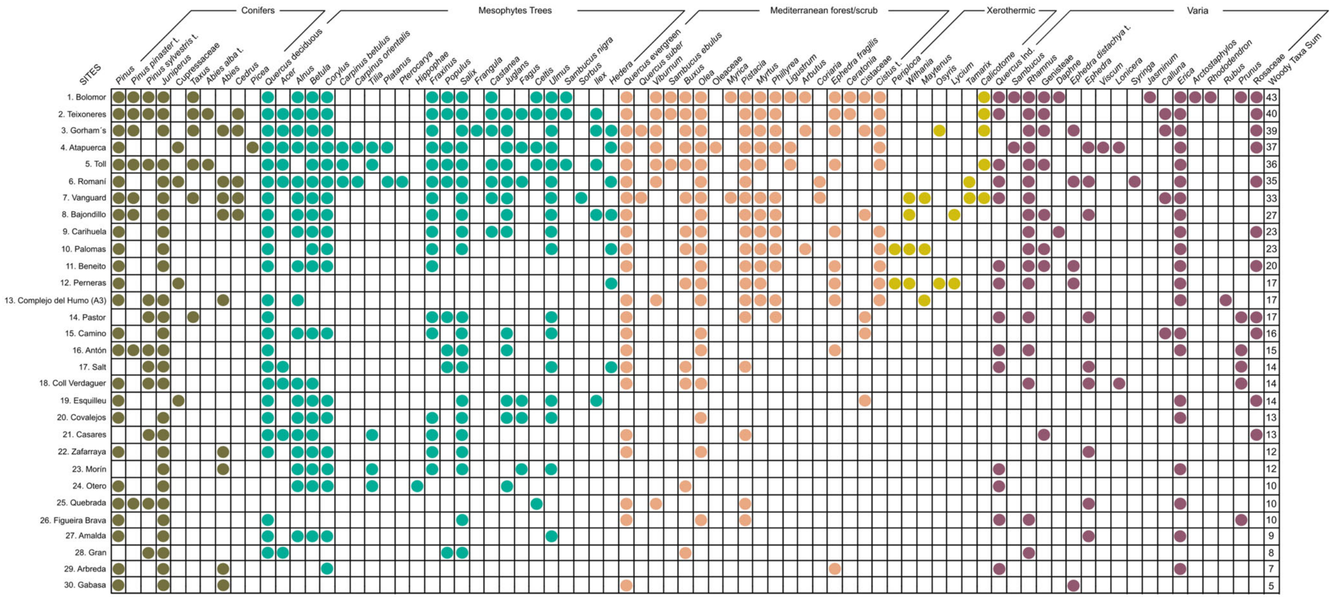

Figure 9. Woody taxa and their ecological categories in palynological sequences from Iberian Neanderthal sites. [Color figure can be viewed at wileyonlinelibrary.com]

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

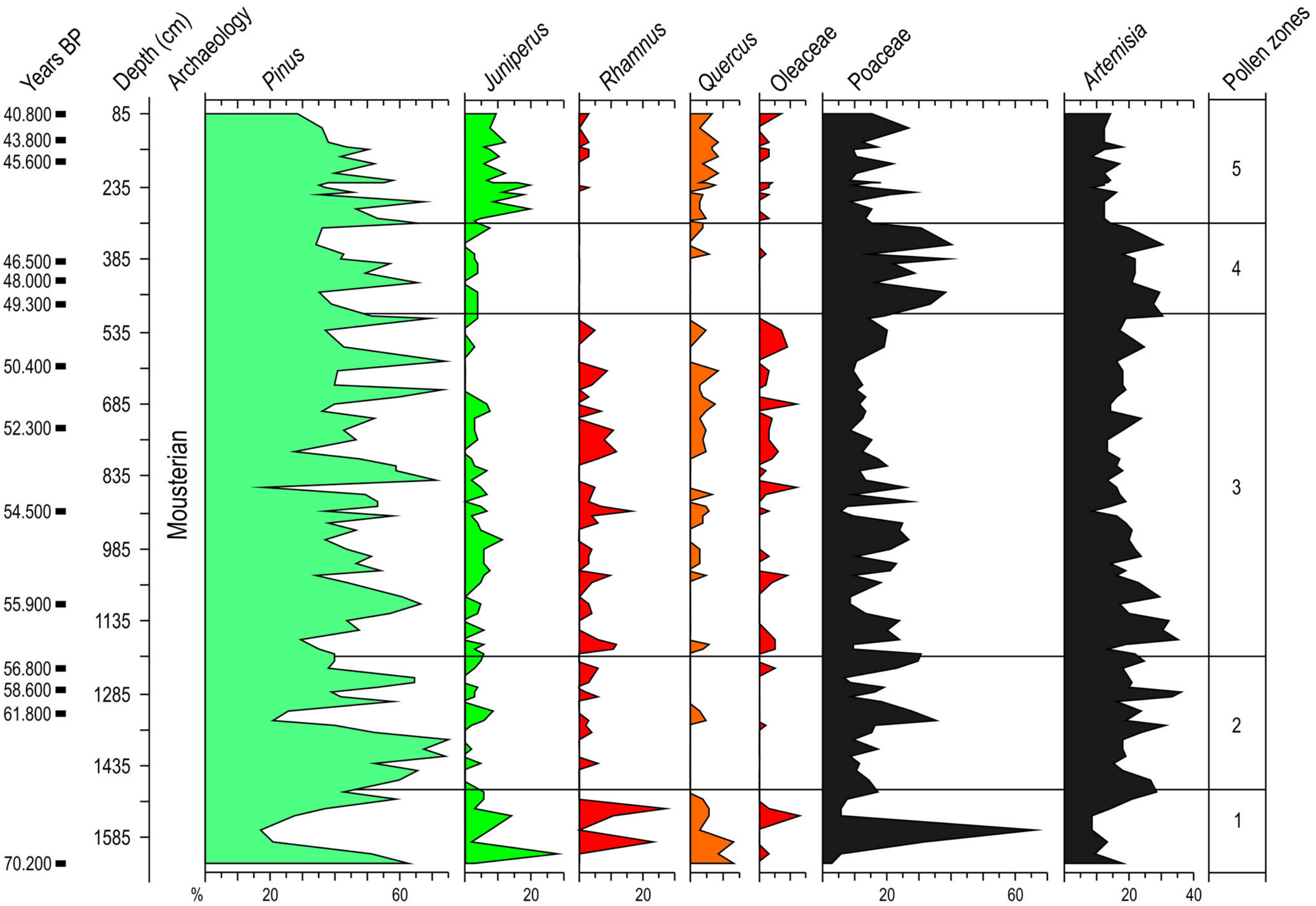

Figure 10. Main pollen curves and chronology of the Upper Pleistocene Romaní cave sequence (Burjachs and Julià, 1994). [Color figure can be viewed at wileyonlinelibrary.com]

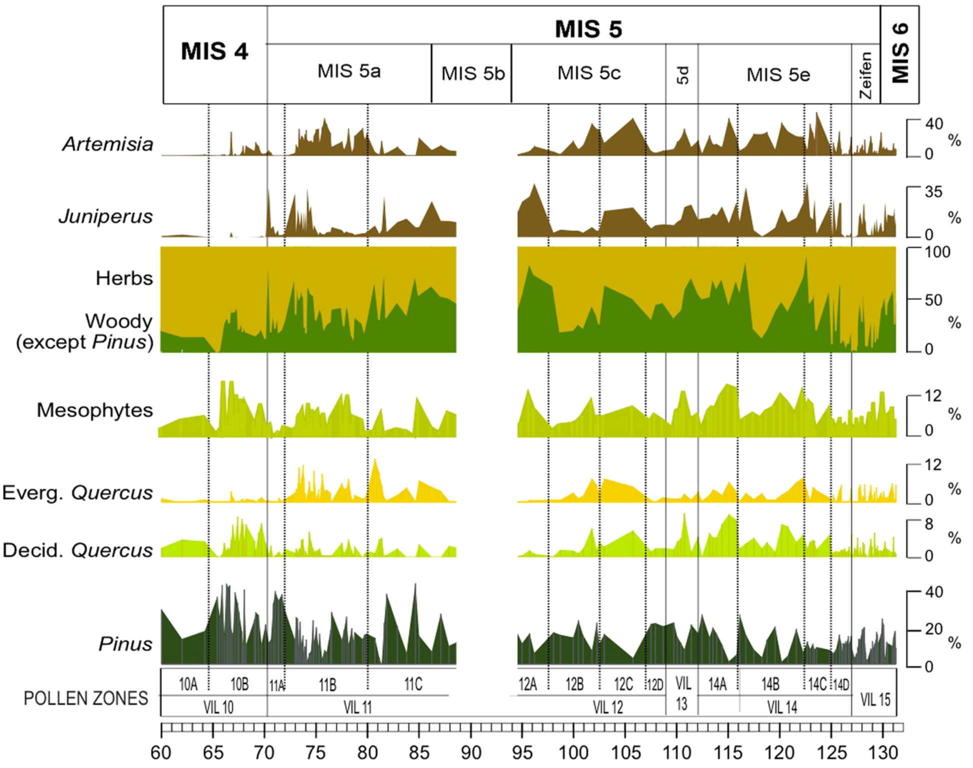

Figure 11. Synthetic pollen diagram of selected taxa (mainly woody component) in the sequence of El Cañizar de Villarquemado during the MIS 6–MIS 4 (135–60 ka BP) chronological interval. Redrawn from González-Sampériz *et al.* (2020). [Color figure can be viewed at wileyonlinelibrary.com]

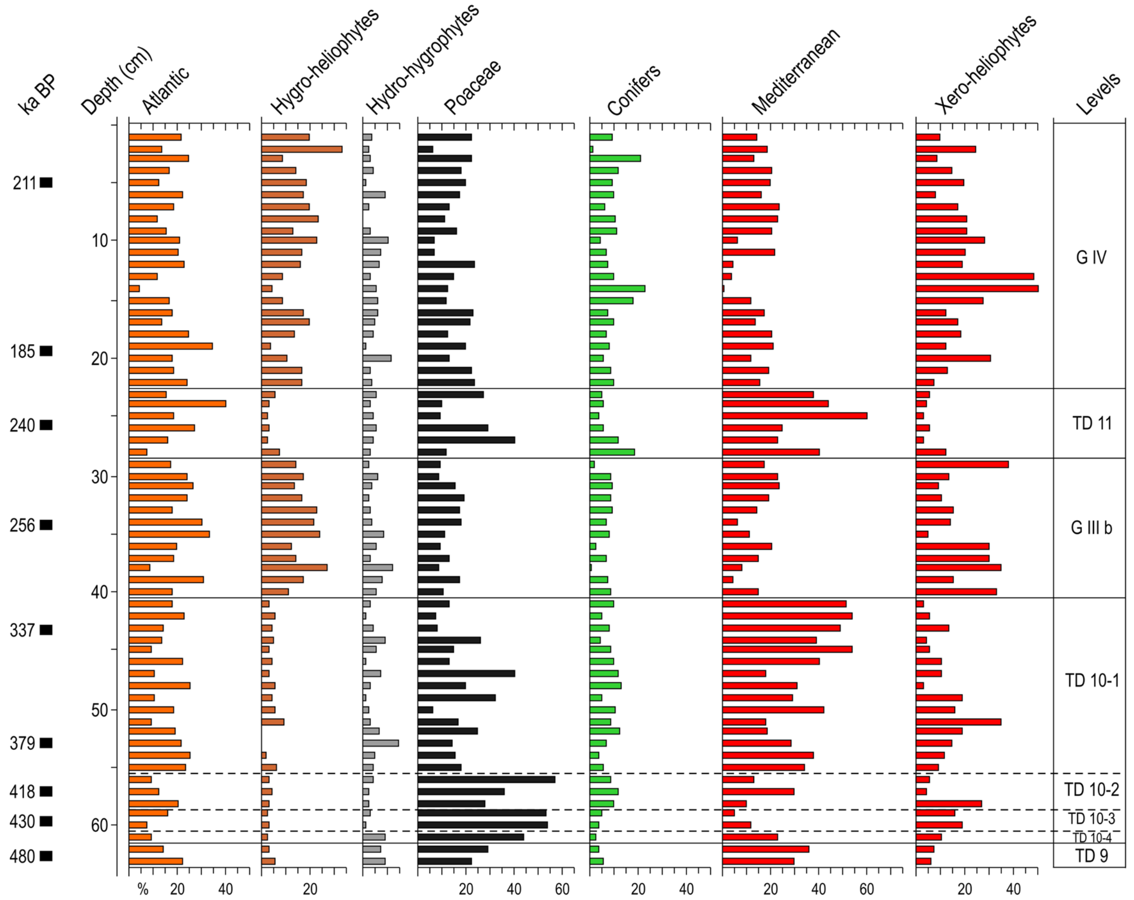

Figure 12. Combined pollen diagram for the sequences of Gran Dolina (TD) and Galería (G) in the Atapuerca hominin-bearing site. Taxa are grouped according to reported ecological types. Redrawn from Rodríguez *et al.* (2011) and Carrión *et al.* (2013). [Color figure can be viewed at wileyonlinelibrary.com]

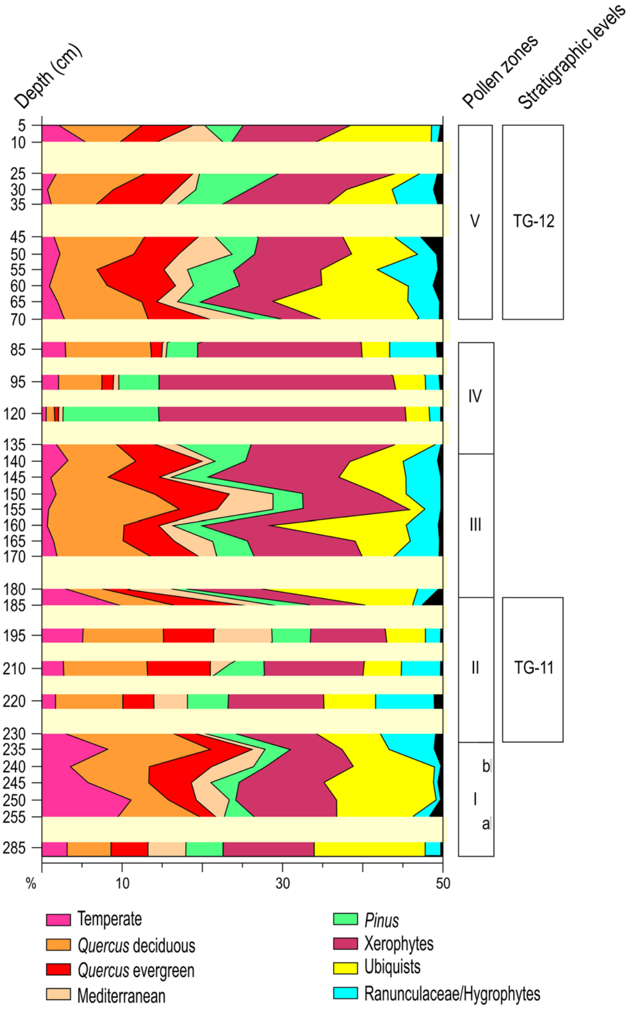

Figure 13. Summary of the most ecologically significant pollen curves in the sequence of Galería, Atapuerca. Redrawn from Rodríguez *et al.* (2011) and Carrión *et al.* (2013). [Color figure can be viewed at wileyonlinelibrary.com]

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*,

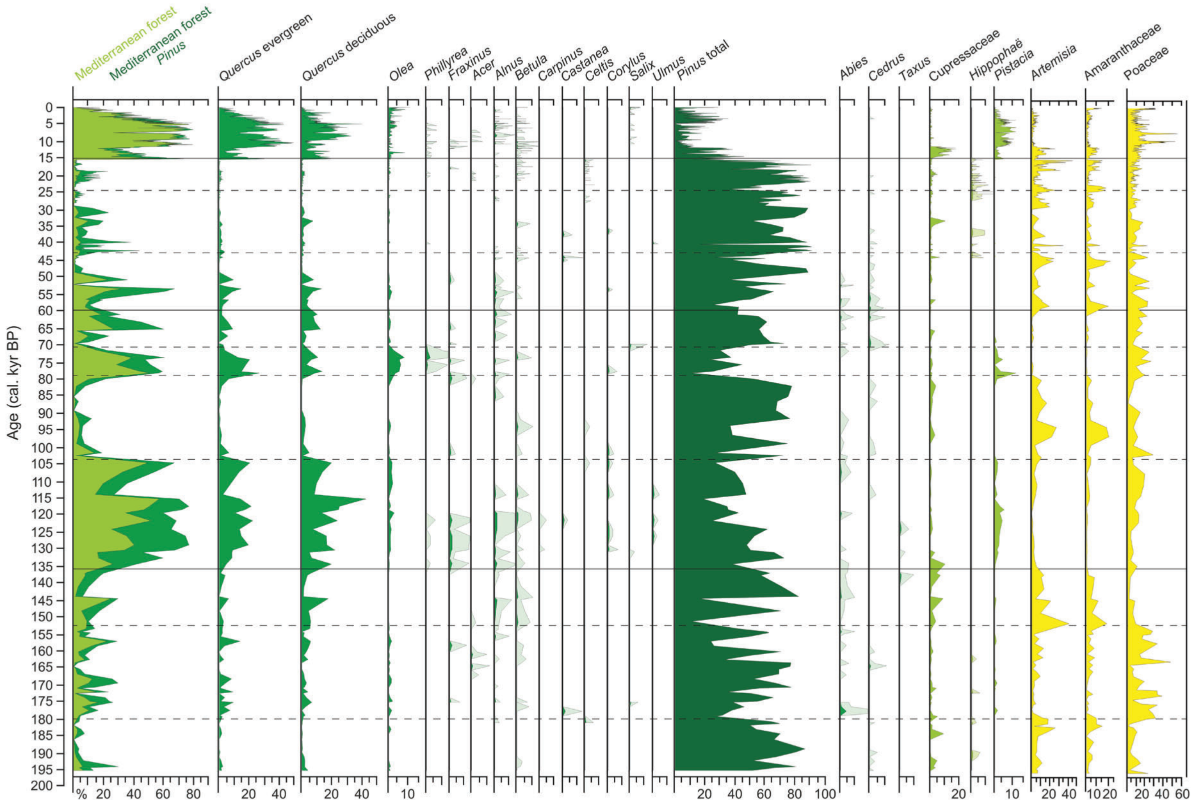

Figure 14. Synthetic pollen diagram of Padul-15-05 core, with percentages calculated with respect to the total terrestrial pollen sum. Silhouettes in lighter colour show 10× exaggeration percentages. The Mediterranean forest taxa category is composed by *Quercus* total, *Olea*, *Phillyrea* and *Pistacia*.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

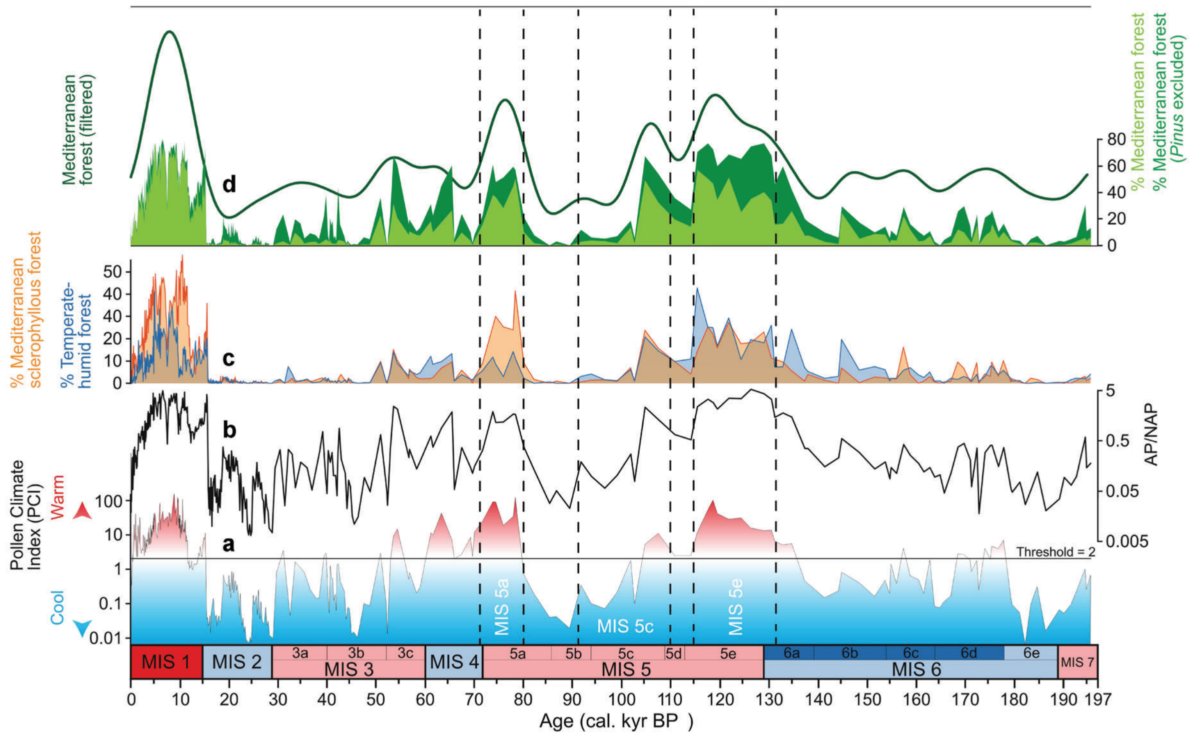

Figure 15. Illustration of plots showing, from bottom to top: (a) the Pollen Climate Index (PCI) with the horizontal black line (value ~2) indicating the boundary between glacial/stadial and interglacial/interstadial phases; (b) AP/NAP (arboreal pollen/non arboreal pollen) ratio (AP also includes *Pinus*), 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]

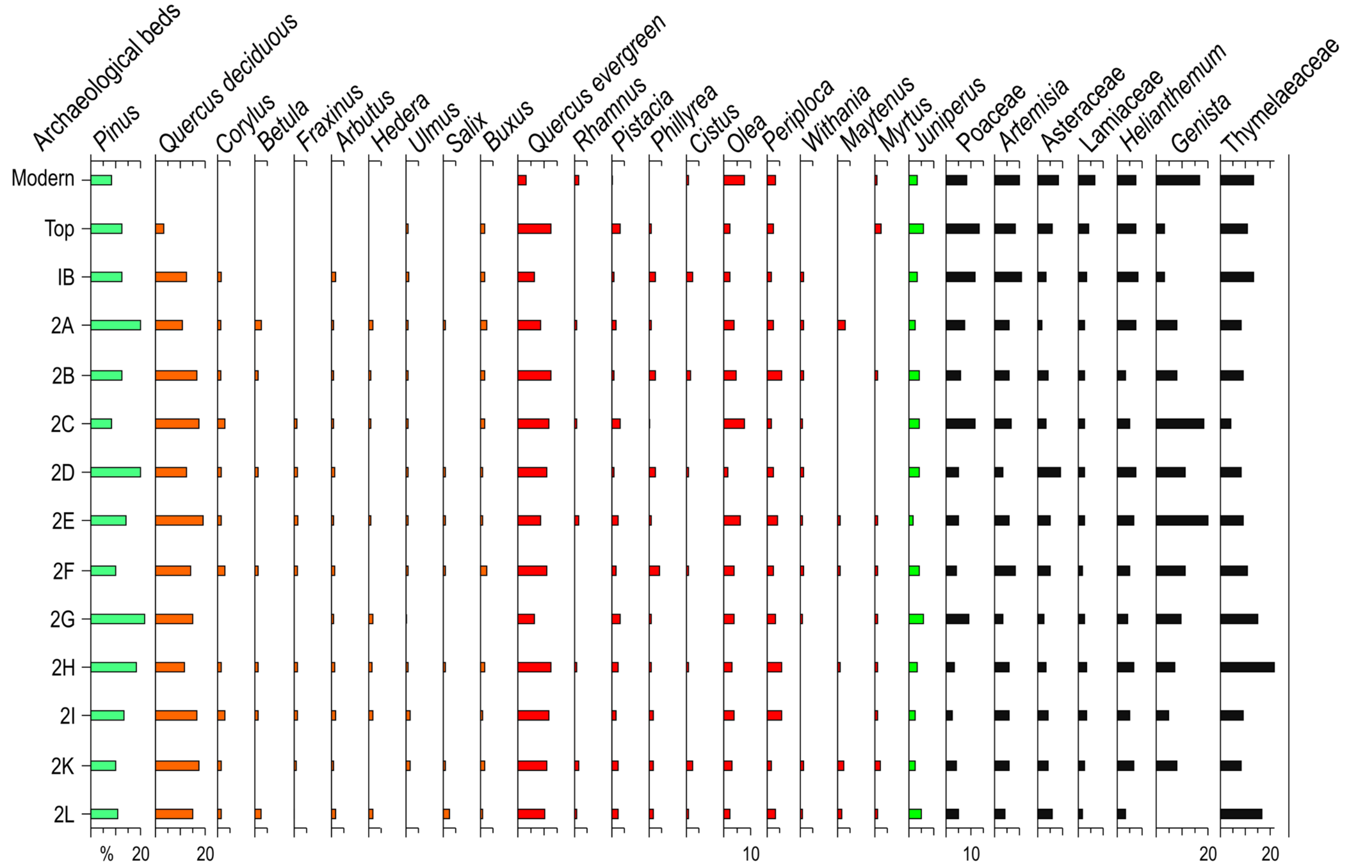

Figure 16. Main pollen taxa from the south-eastern Spain Neanderthal site of Sima de las Palomas (Carrión *et al*., 2003a). Redrawn from Carrión *et al*. (2013). [Color figure can be viewed at wileyonlinelibrary.com]

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 eco-structural 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.

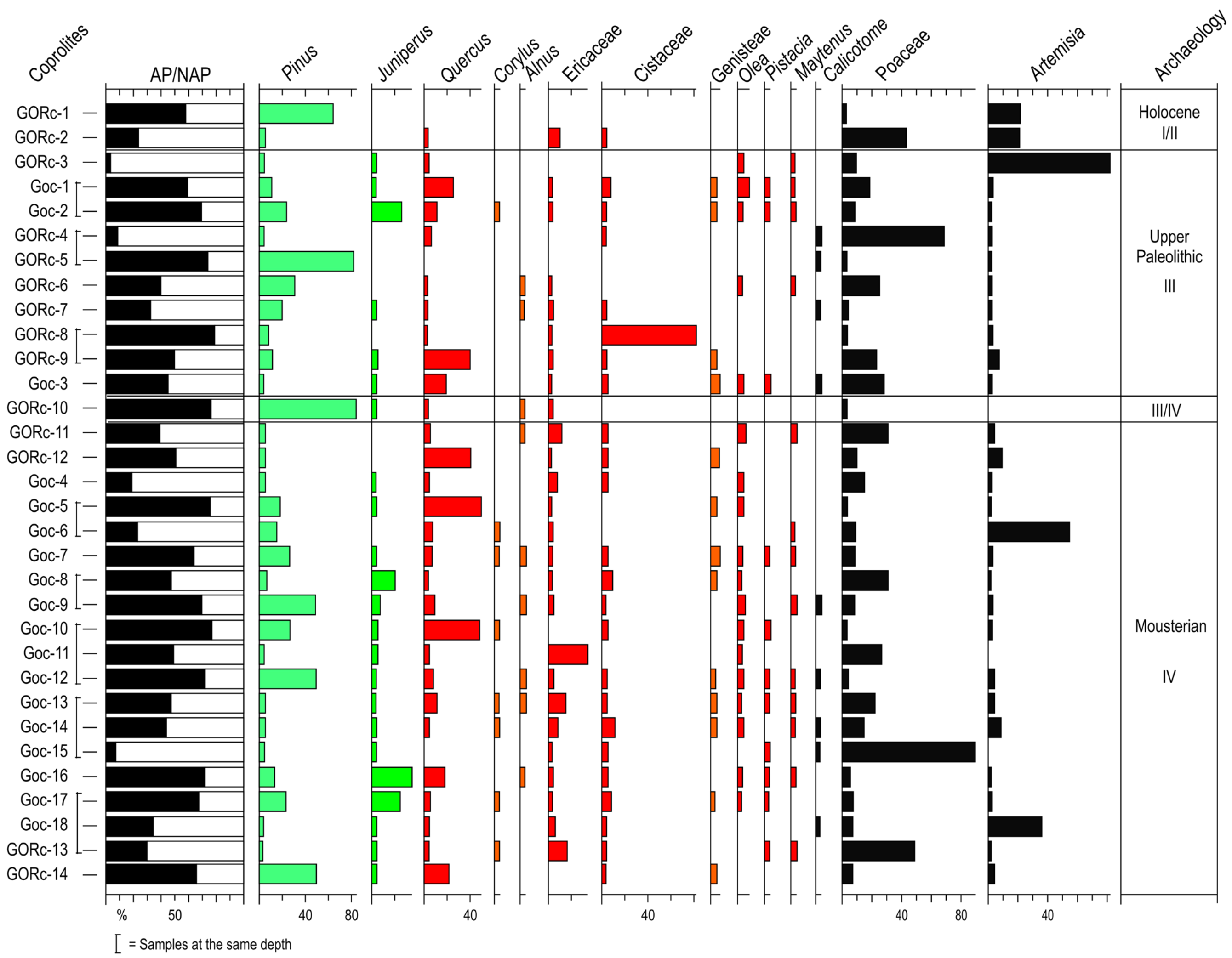

Figure 17. Synthetic pollen diagram from coprolites of Gorham's Cave, Gibraltar (Carrión *et al.*, 2008). Redrawn from Carrión *et al.* (2013). [Color figure can be viewed at wileyonlinelibrary.com]

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.

References

Albert RM, Bamford MK, Stanistreet IG *et al.* 2018. River-fed wetland palaeovegetation and palaeoecology at the HWK W site, Bed I, Olduvai Gorge. *Review of Palaeobotany and Palynology* **259**: 223–241.

Alcaraz-Castaño M, Alcolea-González J, Kehl M *et al.* 2017. A context for the last Neandertals of interior Iberia: Los Casares cave revisited. *PLoS ONE* **12** e0180823.

Allen JRM, Huntley B, Watts WA. 1996. The vegetation and climate of northwest Iberia over the last 14,000 years. *Journal of Quaternary Science* **11**: 125–147.

Allué E. 2002. *Dinámica de la vegetación y explotación del combustible leñoso durante el Pleistoceno Superior y el Holoceno del Noreste de la Península Ibérica a partir del análisis antracológico*. Tesis Doctoral, Universitat Rovira i Virgili, Tarragona.

Allué E, Angelucci DE, Cáceres I *et al.* 2007. La Cativera (el Catllar, Tarragonès). Noves dades sobre el límit pleistocè-holocè al sud de Catalunya. *Jornades d'Arqueologia. Comarques de Tarragona. Tortosa 1999*. Departament de Cultura i Mitjans de Comunicació, Generalitat de Catalunya: Barcelona; 29–45.

Allué E, Martínez-Moreno J, Alonso N *et al.* 2012. Changes in the vegetation and human management of forest resources in mountain ecosystems at the beginning of MIS 1 (14.7–8 ka cal BP) in Balma Guilanyà (Southeastern Pre-Pyrenees, Spain). *Comptes Rendus Palevol* **11**: 507–518.

Allué E, Martínez-Moreno J, Roy M *et al.* 2018. Montane pine forests in NE Iberia during MIS 3 and MIS 2. A study based on new anthracological evidence from Cova Gran (Santa Linya, Iberian pre-Pyrenees). *Review of Palaeobotany and Palynology* **258**: 62–72.

Allué E, Solé A, Burguet-Coca A. 2017. Fuel exploitation among Neanderthals based on the anthracological record from Abric Romaní (Capellades, NE Spain). *Quaternary International* **431**: 6–15.

Antón SC, Potts R, Aiello LC. 2014. Human evolution. Evolution of early *Homo*: an integrated biological perspective. *Science* **345**: 1236828.

Aranbarri J, Bartolomé M, Alcolea M *et al.* 2016. Palaeobotanical insights from Early-Mid Holocene fluvial tufas in the Moncayo Natural Park (Iberian Range, NE Spain): regional correlations and biogeographic implications. *Review of Palaeobotany and Palynology* **234**: 31–43.

Aranbarri J, González-Sampériz P, Valero-Garcés B *et al.* 2014. Rapid climatic changes and resilient vegetation during the Lateglacial and Holocene in a continental region of south-western Europe. *Global and Planetary Change* **114**: 50–65.

Arsuaga JL, Baquedano E, Pérez-González A *et al.* 2010. *El yacimiento kárstico del Pleistoceno Superior de la Cueva del Camino en el Calvero de la Higuera (Pinilla del Valle, Madrid).* 1ª Reunión de cientoficos sobre cubiles de hiena (y otros grandes carnívoros) en los yacimientos arqueológicos de la Península Ibérica; 349–368.

Arsuaga JL, Fernández Peris J, Gracia-Téllez A *et al.* 2012. Fossil human remains from Bolomor Cave (Valencia, Spain). *Journal of Human Evolution* **62**: 629–639.

Arsuaga JL, Martínez I, Lorenzo C *et al.* 1999. The human cranial remains from Gran Dolina Lower Pleistocene site (Sierra de Atapuerca, Spain). *Journal of Human Evolution* **37**: 431–457.

Aubry T, Brugal JP, Chauvière FX *et al.* 2001. Modalités d'occupations au Paléolithique supérieur dans la grotte de Buraca Escura (Redinha, Pombal, Portugal). *Revista Portuguesa de Arqueologia* **4**: 19–46.

Aubry T, Fontugne M, Moura M. 1997. Les occupations de la grotte de Buraca Grande depuis le Paléolithique supérieur et les apports de la séquence holocène à l. *Bulletin de la Société Préhistorique Française* **94**: 182–190.

Aura JE, Carrión Y, Estrelles E *et al.* 2005. Plant economy of hunter-gatherer groups at the end of the last Ice Age: plant macroremains from the cave of Santa Maira (Alacant, Spain) ca. 12000–9000 b.p. *Vegetation History and Archaeobotany* **14**: 542–550.

Badal E. 1990. *Aportaciones de la antracología al estudio del paisaje vegetal y su evolución en el Cuaternario reciente, en la costa mediterránea del País Valenciano y Andalucía (18.000–3.000 bp).* Tesis Doctoral, Universitat de València.

Badal E. 1995. *La vegetación carbonizada. Resultados antracológicos del País Valenciano. El cuaternario en el País Valenciano.* Universitat de València: Valencia; 217–226.

Badal E. 2001. La recolección de piñas durante la prehistoria de la Cueva de Nerja (Málaga). In *De Neandertales a Cromañones. El inicio del poblamiento humano en tierras valencianas*, Villaverde V (ed.). Universitat de València: Valencia; 21–40.

Badal E, Carrión-Marco Y. 2001. Del Glaciar al Interglaciar: los paisajes vegetales a partir de los restos carbonizados hallados en las cuevas de Alicante. In *De Neandertales a Cromañones. El inicio del poblamiento humano en tierras valencianas*, Villaverde V (ed.). Universidad de Valencia: Valencia; 21–40.

Baena J, Carrión E, Ruiz-Zapata MB *et al.* 2005. Paleoecología y comportamiento humano durante el Pleistoceno superior en la comarca de la Liébana: la secuencia de la cueva de el Esquilleu (Occidente de Cantabria, España). In *Neandertales cantábricos, estado de la cuestión*, Montes R, Las Heras JA (eds). Monografías Museo de Altamira 20: Santander; 461–487.

Badal García E, Martínez, Varea CM. 2018. Different parts of the same plants. Charcoals and seeds from Cova de les Cendres (Alicante, Spain). *Quaternary International* **463**: 391–400.

Bailey G, Carrión JS, Fa D *et al.* 2008. The coastal shelf of the Mediterranean and beyond: corridor and refugium for human populations in the Pleistocene. *Quaternary Science Reviews* **27**: 2095–2099.

Barboni D, Ashley GM, Bourel B *et al.* 2019. Springs, palm groves, and the record of early hominins in Africa. *Review of Palaeobotany and Palynology* **266**: 23–41.

Bascompte J, Jordano P, Olesen JM. 2006. Asymmetric coevolutionary networks facilitate biodiversity maintenance. *Science* **312**: 431–433.

Behrensmeyer AK. 2006. Atmosphere. Climate change and human evolution. *Science* **311**: 476–478.

Bennett KD, Tzedakis PC, Willis KJ. 1991. Quaternary refugia of north European trees. *Journal of Biogeography* **18**: 103–115.

Bergadà M, Burjachs F, Fullola JM. 1999. Évolution paléoenvironnementale du 14.500 au 10.000 BP dans le Prépyrénées catalans: La Grotte du Parco (Alòs de Balaguer, Lleida, Espagne). *Anthropologie* **103**: 249–264.

Bergadà MM, Serrat D. 2001. Seqüència sedimentària i paleoambiental de la Cova del Toll (Moià): darreres aportacions. Modilianum. *Revista d'Estudis del Moianès* **24**: 8–22.

Bermúdez de Castro JM, Arsuaga JL, Carbonell E *et al.* 1997. A hominid from the Lower Pleistocene of Atapuerca, Spain: possible ancestor to Neandertals and modern humans. *Science* **276**: 1392–1395.

Bermúdez de Castro JM, Martinón-Torres M, Gómez-Robles A *et al.* 2011. Early Pleistocene human mandible from Sima del Elefante (TE) cave site in Sierra de Atapuerca (Spain): a comparative morphological study. *Journal of Human Evolution* **61**: 12–25.

Bermúdez de Castro JM, Martinón-Torres M, Martínez de Pinillos M *et al*. 2019. Metric and morphological comparison between the Arago (France) and Atapuerca-Sima de los Huesos (Spain) dental samples, and the origin of Neanderthals. *Quaternary Science Reviews* **217**: 45–61.

Bermúdez de Castro JM, Martinón-Torres M, Rosell J *et al*. 2016. Continuity versus discontinuity of the human settlement of Europe between the late Early Pleistocene and the early Middle Pleistocene. The mandibular evidence. *Quaternary Science Reviews* **153**: 51–62.

Bhagwat SA, Willis KJ. 2008. Species persistence in Northerly glacial refugia of Europe: a matter of chance or biogeographical traits? *Journal of Biogeography* **35**: 464–482.

Biltekin D, Burjachs F, Vallverdú J *et al*. 2019. Vegetation and climate record from Abric Romaní (Capellades, northeast Iberia) during the Upper Pleistocene (MIS 5d–3). *Quaternary Science Reviews* **220**: 154–164.

Birks JHB. 1986. Late Quaternary biotic changes in terrestrial and lacustrine environments, with particular reference to north-west Europe. In *In Handbook of Holocene Palaeoecology and Palaeohydrology*, Berglund BE (ed.). Wiley: Chichester; 3–65.

Bischoff JL, Williams RW, Rosenbauer RJ *et al*. 2007. High-resolution U-series dates from the Sima de los Huesos hominids yields: implications for the evolution of the early Neanderthal lineage. *Journal of Archaeological Science* **34**: 763–770.

Blanco-Castro E, Casado-González MA, Costa-Tenorio M *et al*. 1997. *Los bosques ibéricos. Una interpretación geobotánica*. Planeta, S.A.

Blasco R, Blain HA, Rosell J *et al*. 2011. Earliest evidence for human consumption of tortoises in the European Early Pleistocene from Sima del Elefante, Sierra de Atapuerca, Spain. *Journal of Human Evolution* **61**: 503–509.

Blasco R, Fernández, Peris J. 2012a. A uniquely broad spectrum diet during the Middle Pleistocene at Bolomor Cave (Valencia, Spain). *Quaternary International* **252**: 16–31.

Blasco R, Fernández, Peris J. 2012b. Small and large game: human use of diverse faunal resources at Level IV of Bolomor Cave (Valencia, Spain). *Comptes Rendus Palevol* **11**: 265–282.

Blasco R, Rosell J, Fernández Peris J *et al*. 2013. Environmental availability, behavioural diversity and diet: a zooarchaeological approach from the TD10-1 sublevel of Gran Dolina (Sierra de Atapuerca, Burgos, Spain) and Bolomor Cave (Valencia, Spain). *Quaternary Science Reviews* **70**: 124–144.

Bógalo MF, Bradák B, Villalaín JJ *et al*. 2021. High-resolution late Middle Pleistocene paleoclimatic record from the Galería Complex, Atapuerca archaeological site, Spain – an environmental magnetic approach. *Quaternary Science Reviews* **251**.

Bonnefille R, Potts R, Chalié F *et al*. 2004. High-resolution vegetation and climate change associated with Pliocene *Australopithecus afarensis*. *Proceedings of the National Academy of Sciences of the United States of America* **101**: 12125–12129.

Bottema S, Woldring H. 1994. Bronze Age and Byzantine pollen of the Kestel tin-mine (Turkey) and its possible origin, practical and experimental pollen analysis in archaeological context. In *Aspects of Archaeological Palynology, Methodology and Applications, AASP Contribution Series n°. 29*, Davis OK (ed.); 7–15.

Boyer-Klein A. 1984. Analyses polliniques cantabriques au Tardiglaciare. *Revue de Paléobiologie* vol. spécial: 33–39.

Boyer-Klein A. 1985. Nouveaux résultats palynologiques dans les Cantabres au Tardiglaciare. Palynologie archéologique. Actes des journées du 25-26-27 jan. 1984. Sophia Antipolis: Paris; 397–399.

Boyer-Klein A. 1988. Analyses polliniques au Tardiglaciaire dans le nord de L'Espagne: au sujet des Dryas I, II, III. In *Actas del VI Simposio de Palinología (APLE)*, Civis J, Valle MF (eds). Salamanca; 277–283.

Brunet M, Guy F, Pilbeam D *et al*. 2005. New material of the earliest hominid from the Upper Miocene of Chad. *Nature* **434**: 752–755.

Burjachs F. 1987. Palinología de los niveles Gravetiense, Solutrense y Postsolutrense de la Cova de L'Arbreda (Serinyà, Girona). Actas de la VII Reunión sobre Cuaternario. Universidad de Santander, AEQUA: Santander; 19–21.

Burjachs F. 1994. Palynology of the upper Pleistocene and Holocene of the North-East Iberian Peninsula: pla de l'Estany (Catalonia). *Historical Biology* **9**: 17–33.

Burjachs F. 2001. Paleoecología del *Homo antecesor*: palinología de las unidades TD5, 6 y 7 de la Gran Dolina de Atapuerca (Burgos, Spain). *XXII Jornadas de la Sociedad Española de Paleontología* 365–372.

Burjachs F. 2009. Paleoambient del Tardiglacial al sud dels Pirineus vist a través de la Palinologia. In *Els Pirineus i les àrees circumdants durant el Tardiglacial. Mutacions i filiacions tecnoculturals, evolució paleoam- biental (16.000-10.000 bp)*, Mercadal O (coord.). Museu Cerdà: Puigcerdà; 151–162.

Burjachs F. 2012. Salines. Alto Vinalopó, Salines, Alicante. Pleistoceno superior-Holoceno (~115.000–2960 años Cal. BP). In *Paleoflora y Paleovegetación de la Península Ibérica e Islas Baleares: Plioceno-Cuaternario. Madrid (e-book)*, Carrión JS (coord.). Ministerio de Economía y Competitividad, 607–609.

Burjachs F, Expósito I, Yll IE. 2007. Tendencias, crisis y desfases de la vegetación y el clima en el litoral mediterráneo de La Península Ibérica durante el Holoceno. I Congreso Nacional sobre Cambio Global. Universidad Carlos III de Madrid. Getafe, 25–27 April. Póster.

Burjachs F, Julià R. 1994. Abrupt climatic changes during the Last Glaciation based on pollen analysis of the Abric Romaní, Catalonia, Spain. *Quaternary Research* **42**: 308–315.

Burjachs F, Julià R. 1996. Palaeoenvironmental evolution during the Middle-Upper Palaeolithic transition in the NE of the Iberian Peninsula. In *The Last Neandertals, the First Anatomically Modern Humans*, Carbonell E (coord.). URV: Tarragona; 377–383.

Burjachs F, Renault-Miskovsky J. 1992. Paléoenvironnement et paléoclimatologie de la Catalogne durant près de 30 000 ans (du Würmien ancien au début de l'Holocène) d'après la palynologie du site de l'Arbreda (Gérone, Catalogne). *Quaternaire* **3**: 75–85.

Burjachs F, Rodó X, Comín FA. 1996. Gallocanta: ejemplo de secuencia palinológica en una laguna efímera. In *Estudios Palinológicos. Servicio de Publicaciones de la Universidad de Alcalá, Alcalá de Henares*, Ruiz-Zapata MB (ed.); 25–29.

Cabrera V, Bernaldo de Quirós F, Maíllo JM. 2005. *Neandertales cantábricos. Estado de la cuestión.*Excavaciones en el Castillo: veinte años de reflexiones. In, Lasheras Corruchaga JA, Montes Barquín R (eds). *Monografías Museo de Altamira* 20: 505–526.

Cacho C, Fumanal MP, López-García P *et al*. 1995. El Tossal de la Roca (Vall d'Alcalá, Alicante). Reconstrucción paleoambiental y cultural de la transición del Tardiglaciar al Holoceno inicial. *Recerques del Museu d'Alcoi* **4**: 11–101.

Camacho CN, Carrión JS, Navarro J *et al*. 2000. An experimental approach to the palynology of cave deposits. *Journal of Quaternary Science* **15**: 603–619.

Camuera J, Jiménez-Moreno G, Ramos-Román MJ *et al*. 2019. Vegetation and climate changes during the last two glacial-interglacial cycles in the western Mediterranean: A new long pollen record from Padul (southern Iberian Peninsula). *Quaternary Science Reviews* **205**: 86–105.

Carrión JS. 1990. *Evolución paleoambiental durante el Pleistoceno superior en el sureste de España. Las secuencias polínicas de las Cuevas de la Carihuela (Granada) y Beneito (Alicante).* Tesis Doctoral, Universidad de MurciaL Murcia.

Carrión JS. 1991. Desarrollo de vegetaciones mediterráneas durante el Pleistoceno Superior en el Sureste Ibérico. Nuevos datos polínicos. *Anales de Biología* **17**: 109–131.

Carrión JS. 1992a. A palaeoecological study in the western Mediterranean area. The Upper Pleistocene pollen record from Cova Beneito (Alicante, Spain). *Palaeogeography, Palaeoclimatology, Palaeoecology* **92**: 1–14.

Carrión JS. 1992b. Late Quaternary pollen sequence from Carihuela Cave, southern Spain. *Review of Palaeobotany and Palynology* **71**: 37–77.

Carrión JS. 1994. *Análisis polínico de los depósitos turbosos de la Canal de Navarrés. X Simposio de Palinología*. APLE: Valencia.

Carrión JS. 2001. Dialectic with climatic interpretations of Late-Quaternary vegetation history in Mediterranean Spain. *Journal of Mediterranean Ecology* **2**: 145–156.

Carrión JS. 2002a. A taphonomic study of modern pollen assemblages from dung and surface sediments in arid environments of Spain. *Review of Palaeobotany and Palynology* **120**: 217–232.

Carrión JS. 2002b. Patterns and processes of Late Quaternary environmental change in a montane region of southwestern Europe. *Quaternary Science Reviews* **21**: 2047–2066.

Carrión JS. 2004. The use of two pollen records from deep sea cores to frame adaptive evolutionary change for humans: a comment on "Neanderthal extinction and the millennial scale climate variability of OIS 3" by F. d'Errico and M.F. Sánchez Goñi. *Quaternary Science Reviews* **23**: 1217–1219.

Carrión JS, Dupré M. 1996. Late Quaternary vegetational history at Navarrés, Eastern Spain. A two core approach. *New Phytologist* **134**: 177–191.

Carrión JS, Dupré M. 2002. Los paisajes vegetales de Altamira en el Paleolítico Superior. Redescubrir Altamira. Turner: Madrid; 141–150.

Carrión JS, Dupré M, Fumanal MP *et al*. 1995. A palaeoenvironmental study in semi-arid southeastern Spain: the palynological and sedimentological sequence at Perneras Cave (Lorca, Murcia). *Journal of Archaeological Science* **22**: 355–367.

Carrión JS, Fernández S, González-Sampériz P *et al*. 2009. Sterility cases and causes in Quaternary pollen analysis in the Iberian Peninsula: the advantages of reporting bad luck. *Internet Archaeology*.

Carrión JS, Fernández S, González-Sampériz P *et al*. 2013. *Paleoflora Ibérica: Plioceno-Cuaternario, 2 vols*. Ministerio de Economía y Competitividad: Madrid. Universidad de Murcia y Fundación Séneca.

Carrión JS, Fernández S, Jiménez-Arenas JM *et al*. 2019c. The sequence at Carihuela Cave and its potential for research into Neanderthal ecology and the Mousterian in southern Spain. *Quaternary Science Reviews* **217**: 194–216.

Carrión JS, Finlayson C, Fernández S *et al*. 2008. A coastal reservoir of biodiversity for Upper Pleistocene human populations: palaeoecological investigations in Gorham's Cave (Gibraltar) in the context of the Iberian Peninsula. *Quaternary Science Reviews* **27**: 2118–2135.

Carrión JS, Lalueza-Fox C, Stewart J. 2019a. Neanderthals: ecology and evolution. *Quaternary Science Reviews* **217**: 1–6.

Carrión JS, Munuera M. 1997. Upper Pleistocene palaeoenvironmental change in Eastern Spain: new pollen-analytical data from Cova Beneito (Alicante). *Palaeogeography, Palaeoclimatology, Palaeoecology* **128**: 287–299.

Carrión JS, Munuera M, Navarro C. 1998. The palaeoenvironment of Carihuela Cave (Granada, Spain): a reconstruction on the basis of palynological investigations of cave sediments. *Review of Palaeobotany and Palynology* **99**: 317–340.

Carrión JS, Munuera M, Navarro C *et al*. 1999. The palaeoecoloical potential of pollen records in caves: the case of Mediterranean Spain. *Quaternary Science Reviews* **18**: 1061–1073.

Carrión JS, Ochando J, Fernández S *et al*. 2018. Last Neanderthals in the warmest refugium of Europe: palynological data from Vanguard Cave. *Review of Palaeobotany and Palynology* **259**: 63–80.

Carrión JS, Riquelme JA, Navarro C *et al*. 2001. Pollen in hyaena coprolites reflects late glacial landscape in southern Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology* **176**: 193–205.

Carrión JS, Rose J, Stringer C. 2011. Early human evolution in the western Palaearctic: ecological scenarios. *Quaternary Science Reviews* **30**: 1281–1295.

Carrión JS, Sánchez-Gómez P, Mota JF *et al*. 2003b. Holocene vegetation dynamics, fire and grazing in the Sierra de Gádor, Southern Spain. *Holocene* **13**: 839–849.

Carrión JS, Scott L. 1999. The challenge of pollen analysis in palaeoenvironmental studies of hominid beds: the record from Sterkfontein caves. *Journal of Human Evolution* **36**: 401–408.

Carrión JS, Scott L, Arribas A *et al*. 2007. Pleistocene landscapes in central Iberia inferred from pollen analysis of hyena coprolites. *Journal of Quaternary Science* **22**: 191–202.

Carrión JS, Scott L, deMenocal P. 2019b. Paleofloras, paleovegetation and human evolution. *Review of Palaeobotany and Palynology* **267**: 32–38.

Carrión JS, van Geel B. 1999. Fine-resolution Upper Weichselian and Holocene palynological record from Navarrés (Valencia, Spain) and a discussion about factors of Mediterranean forest succession. *Review of Palaeobotany and Palynology* **106**: 209–236.

Carrión JS, Walker MJ. 2019. Background to Neanderthal presence in western Mediterranean Europe. *Quaternary Science Reviews* **217**: 7–44.

Carrión JS, Yll EI, Chaín C *et al*. 2005. Fitodiversidad arbórea en el litoral del sureste español durante el Pleistoceno Superior. In *Geomorfología litoral i Quaternari. Homenatge al profesor Vicenç Roselló i Verger*, Sanjaume E, Mateu JF (eds); 103–112.

Carrión JS, Yll EI, Walker MJ *et al*. 2003a. Glacial refugia of temperate, Mediterranean and Ibero-North African flora in south-eastern Spain: new evidence from cave pollen at two Neanderthal man sites. *Global Ecology and Biogeography* **12**: 119–129.

Carrión Marco Y, Guillem Calatayud P, Eixea A *et al*. 2019. Climate, environment and human behaviour in the Middle Palaeolithic of Abrigo de la Quebrada (Valencia, Spain): the evidence from charred plant and micromammal remains. *Quaternary Science Reviews* **217**: 152–168.

Carrión-Marco Y. 2003, *Afinidades y diferencias en las secuencias antracológicas en las vertientes mediterránea y atlántica de la Península Ibérica*. Tesis Doctoral, Universidad de Valencia: Valencia.

Carrión-Marco Y. 2005. La vegetación mediterránea y atlántica de la península Ibérica. Nuevas secuencias antracológicas. *Trabajos Varios de S.I.P. (Servicio de Investigación Prehistórica)* **104**.

Cascalheira J, Bicho N. 2018. Testing the impact of environmental change on hunter-gatherer settlement organization during the Upper Paleolithic in western Iberia. *Journal of Quaternary Science* **33**: 323–334.

Coles GM, Gilbertson DD. 1994. The Airfall-pollen Budget of Archaeologically Important Caves: Creswell Crags, England. *Journal of Archaeological Science* **21**: 735–755.

Coles GM, Gilbertson DD, Hunt CO *et al*. 1989. Taphonomy and the palynology of cave sediments. *Cave Science* **16**: 83–89.

Connolly R, Jambrina-Enríquez M, Herrera-Herrera AV *et al*. 2019. A multiproxy record of palaeoenvironmental conditions at the Middle Palaeolithic site of Abric del Pastor (eastern Iberia). *Quaternary Science Reviews* **225**.

Cortes Sanchez M, Morales Muniz A, Simon, Vallejo M *et al*. 2008. Palaeoenvironmental and cultural dynamics of the coast of Málaga (Andalusia, Spain) during the Upper Pleistocene and early Holocene. *Quaternary Science Reviews* **27**: 2176–2193.

Daura J, Sanz M, Allué E *et al*. 2017. Palaeoenvironments of the last Neanderthals in SW Europe (MIS 3): cova del Coll Verdaguer (Barcelona, NE of Iberian Peninsula). *Quaternary Science Reviews* **177**: 34–56.

Daura J, Sanz M, García N *et al*. 2013. Terrasses de la Riera dels Canyars (Gavà, Barcelona): the landscape of Heinrich stadial 4 north of the 'Ebro frontier' and implications for modern human dispersal into Iberia. *Quaternary Science Reviews* **60**: 26–48.

de la Peña P. 2019. Dating on its own cannot resolve hominin occupation patterns. *Nature Ecology and Evolution* **3**: 712.

de Ruiter DJ, Pickering R, Steininger CM *et al*. 2009. *New Australopithecus robustus fossils. In The Palaeolithic Settlement of Asia*. Cambridge University Press: Cambridge.

deMenocal PB. 2004. African climate change and faunal evolution during the Pliocene–Pleistocene. *Earth and Planetary Science Letters* **220**: 3–24.

deMenocal PB, Bloemendal J. 1995. Plio-Pleistocene subtropical African climate variability and the paleoenvironment of hominid evolution: A combined data-model approachIn *Paleoclimate and Evolution with Emphasis on Human.* In *Origins*, Vrba E, Denton G, Burckle L, Partridge T (eds). Yale University Press: New Haven; 262–288.

Dennell RW, Roebroeks W. 2005. An Asian perspective on early human dispersal from Africa. *Nature* **438**: 1099–1104.

Díaz del Olmo F, Vallespi E, Baena R *et al*. 1989. Terrazas Pleistocenas del Guadalquivir Occidental: geomorfologia, suelos, paleosuelos y secuencia cultural. In *El Cuaternario en Anda luciae Occidental*, Díaz del Olmo F, Rodríguez Vidal J (eds). Monografias 1, AEQUA; 27–31.

Dupré M. 1980. Análisis polínico de sedimentos arqueológicos de la cueva de les Malladetes (Barx, Valencia). *Cuadernos de Geografía* **26**: 1–22.

Dupré M. 1990. Análisis polínico de la Cueva de Amalda. In: *La Cueva de Amalda (Zestoa, País Vasco): ocupaciones paleolíticas y postpaleolíticas*, Altuna J, Baldeón A, Mariezkurrena K (Dir.). Fundación José Miguel de Barandiarán, Colecc. Barandiarán 4: San Sebastián; 49–51.

Dupré M. 1988. *Palinología y Paleoambiente. Nuevos datos españoles*. Referencias. Trabajos Varios 84, Servicio de Investigación Prehistórica: Valencia.

Enard D, Petrov DA. 2018. Evidence that RNA viruses drove adaptive introgression between Neanderthals and modern humans. *Cell* **175**: 360–371.e13.

Esteban I, Albert RM, Eixea A *et al*. 2017. Neanderthal use of plants and past vegetation reconstruction at the Middle Paleolithic site of Abrigo de la Quebrada (Chelva, Valencia, Spain). *Archaeological and Anthropological Sciences* **9**: 265–278.

Falguères C, Bahain JJ, Bischoff JL *et al*. 2013. Combined ESR/U-series chronology of Acheulian hominid-bearing layers at Trinchera Galería site, Atapuerca, Spain. *Journal of Human Evolution* **65**: 168–184.

Fernández Peris J, González VB, Blasco R *et al*. 2012. The earliest evidence of hearths in southern Europe: the case of Bolomor Cave (Valencia, Spain). *Quaternary International* **247**: 267–277.

Fernández S, Fuentes N, Carrión JS *et al*. 2007. The Holocene and Upper Pleistocene pollen sequence of Carihuela Cave, southern Spain. *Geobios* **40**: 75–90.

Figueiral I. 1993. Cabeço de Porto Marinho: une approche paléoécologique. Premiers résultats. In *Estudios sobre Cuaternario: medios sedimentarios, cambios ambientales, hábitat*, Fumanal MP, Bernabeu J (eds). Asociación Española para el Estudio del Cuaternario, 167–172.

Figueiral I, Terral J-F. 2002. Late Quaternary refugia of Mediterranean taxa in the Portuguese Estremadura: charcoal based palaeovegetation and climatic reconstruction. *Quaternary Science Reviews* **21**: 549–558.

Finlayson C. 2008. On the importance of coastal areas in the survival of Neanderthal populations during the Late Pleistocene. *Quaternary Science Reviews* **27**: 2246–2252.

Finlayson C. 2019. *The Smart Neanderthal. Bird Catching, Cave Art and the Cognitive Revolution*. Oxford University Press: Oxford.

Finlayson C, Carrión JS. 2006. Neandertales y humanos modernos en ecosistemas mediterráneos. In *Paleoambientes y Cambio Climático. Quaderna*, Carrión JS, Fernández S, Fuentes N (eds). Fundación Séneca, Agencia Regional de Ciência y Tecnología: Murcia.

Finlayson C, Carrión JS. 2007. Rapid ecological turnover and its impact on Neanderthal and other human populations. *Trends in Ecology and Evolution* **22**: 213–222.

Finlayson C, Carrión JS, Brown K *et al*. 2011. The Homo habitat niche: using the avian fossil record to depict ecological characteristics of Palaeolithic Eurasian hominins. *Quaternary Science Reviews* **30**: 1525–1532.

Finlayson C, Fa DA, Jiménez Espejo F *et al*. 2008. Gorham's Cave, Gibraltar—the persistence of a Neanderthal population. *Quaternary International* **181**: 64–71.

Finlayson C, Finlayson G, Fa D(eds). 2000. Gibraltar During the Quaternary. The Southermost Part of Europe in the Last Two Million Years. Gibraltar.

Finlayson C, Giles Pacheco F, Gutiérrez, López JM *et al*. 1999. Recientes excavaciones en el nivel neolítico de la Cueva de Gorham (Gibraltar. Extremo sur de Europa). *Saguntum-Plav Extra* **2**: 213–221.

Finlayson C, Pacheco FG, Rodríguez-Vidal J *et al*. 2006. Late survival of Neanderthals at the southernmost extreme of Europe. *Nature* **443**: 850–853.

Fletcher WJ, Boski T, Moura D. 2007. Palynological evidence for environmental and climatic change in the lower Guadiana valley, Portugal, during the last 13 000 years. *Holocene* **17**: 481–494.

Fletcher WJ, Sánchez Goñi MF. 2008. Orbital- and sub-orbital-scale climate impacts on vegetation of the western Mediterranean basin over the last 48,000 yr. *Quaternary Research* **70**: 451–464.

Fletcher, WJ, Sánchez Goñi, MF & Allen, JRM (2010) Millennial-scale variability during the last glacial in vegetation records from Europe. *Quaternary Science Reviews*, **29**: 2839–2864.

Florschütz F, Menéndez-Amor J, Wijmstra T. 1971. Palynology of a thick Quaternary succession in S. Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology* **10**: 233–264.

García N, Arsuaga JL. 2011. The Sima de los Huesos (Burgos, northern Spain): palaeoenvironment and habitats of Homo heidelbergensis during the Middle Pleistocene. *Quaternary Science Reviews* **30**: 1413–1419.

García-Amorena I, Rubiales JM, Moreno Amat E *et al*. 2011. New macrofossil evidence of *Pinus nigra* Arnold on the northern Iberian Meseta during the Holocene. *Review of Palaeobotany and Palynology* **163**: 281–288.

García-Antón M. 1987. Estudio polínico preliminar de los yacimientos de la sierra de Atapuerca (Burgos). In *El hombre fósil de Ibeas y el Pleistoceno de la sierra de Atapuerca*, Aguirre E, Carbonell E, Bermúdez de Castro JM (eds). Junta de Castilla y León: Soria; 55–59.

García-Antón M. 1989. Estudio palinológico de los yacimientos mesopleistocenos de Atapuerca (Burgos): reconstrucción paisajística y paleoclimática. PhD Thesis, Universidad Autónoma de Madrid.

García-Antón M, Sainz-Ollero H. 1991. Pollen records from Middle Pleistocene Atapuerca site (Burgos, Spain). *Palaeogeography, Palaeoclimatology, Palaeoecology* **85**: 199–206.

García-Antón M. 1992. Paleovegetación del Pleistoceno medio de Atapuerca a través del análisis polínico. In: *Actas: Evolución humana en Europa y los yacimientos de la sierra de Atapuerca 1*, Carbonell E, Arsuaga JL (eds); 147–165.

García-Mijangos I, Campos JA, Biurrun I *et al*. 2015. Marcescent forests of the Iberian Peninsula: floristic and climatic characterization, *Geobotany Studies*. Springer: Berlin; 119–138.

García-Rovés E. 2007. *Dinámica de la Paleovegetación y cambios climáticos durante el Tardiglaciar y Holoceno en secuencias sedimentarias de la provincia de León*. Tesis Doctoral, Universidad de León: Léon.

Giardini M. 2007. Late Quaternary vegetation history at Stracciacappa (Rome, central Italy). *Vegetation History and Archaeobotany* **16**: 301–316.

Gil García MJ, Valiño MD, Rodríguez AV *et al*. 2002. Late-glacial and Holocene paleoclimatic record from Sierra de Cebollera (northern Iberian range, Spain). *Quaternary International* **93–94**: 13–18.

Gil-Romera G, González-Sampériz P, Lasheras-Álvarez L *et al*. 2014. Biomass-modulated fire dynamics during the Last Glacial–Interglacial Transition at the Central Pyrenees (Spain). *Palaeogeography, Palaeoclimatology, Palaeoecology* **402**: 113–124.

Giralt S, Burjachs F, Roca JR *et al*. 1999. Late Glacial to Early Holocene environmental adjustmente in the Mediterranean semi-arid zone of the Salines playa-lakes (Alacante, Spain). *Journal of Paleolimnology* **21**: 449–460.

Gómez-Orellana L, Ramil-Rego P, Muñoz, Sobrino C. 2007. The Würm in NW Iberia, a pollen record from Area Longa (Galicia). *Quaternary Research* **67**: 438–452.

Gómez-Orellana L, Ramil-Rego P, Muñoz-Sobrino C. 1998. Una nueva secuencia polínica y cronológica para el depósito pleistoceno de Mougás (NW de la Península Ibérica). *Revue de Paléobiologie* **17**: 35–47.

Gómez-Orellana L, Ramil-Rego P, Muñoz-Sobrino C *et al*. 2001. Análisis polínico y cronológico de los depósitos pleistocenos de Moucide (Cangas de Foz, Lugo) y Río Boó (Muras, Lugo). In *Palinología: Diversidad y Aplicaciones*, Fombella-Blanco MA, Fernández González D, Valencia Barrera RM (eds). Secretariado de Publicaciones, Universidad de León: León; 153–160.

Goñi MS, C I, T J *et al*. 2002. Synchroneity between marine and terrestrial responses to millennial scale climatic variability during the last glacial period in the Mediterranean region. *Climate Dynamics* **19**: 95–105.

González-Sampériz P. 2004. *Evolución paleoambiental del sector central de la cuenca del Ebro durante el Pleistoceno superior y Holoceno*. Instituto Pirenaico de Ecología-CSIC: Zaragoza.

González-Sampériz P, Aranbarri J, Pérez-Sanz A *et al*. 2017. Environmental and climate change in the Southern Central Pyrenees since the Last Glacial Maximum: A view from the lake records. *CATENA* **149**: 668–688.

González-Sampériz P, García-Prieto E, Aranbarri J *et al*. 2013. Reconstrucción paleoambiental del último ciclo glacial-interglacial en la Iberia continental: la secuencia del Cañizar de Villarquemado (Teruel). *Cuadernos de Investigación Geográfica* **39**: 49–76.

González-Sampériz P, Gil-Romera G, García-Prieto E *et al*. 2020. Strong continentality and effective moisture drove unforeseen vegetation dynamics since the last interglacial at inland Mediterranean areas: the Villarquemado sequence in NE Iberia. *Quaternary Science Reviews* **242**.

González-Sampériz P, Leroy SAG, Carrión JS *et al.* 2010. Steppes, savannahs, forests and phytodiversity reservoirs during the Pleistocene in the Iberian Peninsula. *Review of Palaeobotany and Palynology* **162**: 427–457.

González-Sampériz P, Montes L, Utrilla P. 2003. Pollen in hyena coprolites from Gabasa Cave (northern Spain). *Review of Palaeobotany and Palynology* **126**: 7–15.

González-Sampériz P, Valero-Garcés B, Carrión JS. 2004. Was the Ebro valley a glacial refugium for temperate trees? *Anales de Biología* **26**: 13–20.

González-Sampériz P, Valero-Garcés BL, Carrión JS *et al.* 2005. Glacial and Lateglacial vegetation in Northeastern Spain: new data and a review. *Quaternary International* **140–141**: 4–20.

González-Sampériz P, Valero-Garcés BL, Moreno A *et al.* 2006. Climate variability in the Spanish Pyrenees during the last 30,000 yr revealed by the El Portalet sequence. *Quaternary Research* **66**: 38–52.

Greenbaum G, Friesem DE, Hovers E *et al.* 2019. Was inter-population connectivity of Neanderthals and modern humans the driver of the Upper Palaeolithic transition rather than its product? *Quaternary Science Reviews* **2017**: 316–329.

Haile-Selassie Y, Latimer BM, Alene M *et al.* 2010. An early *Australopithecus afarensis* postcranium from Woranso-Mille, Ethiopia. *Proceedings of the National Academy of Sciences of the United States of America* **107**: 12121–12126.

Hampe A, Rodríguez-Sánchez F, Dobrowski S *et al.* 2013. Climate refugia: from the Last Glacial Maximum to the twenty-first century. *New Phytologist* **197**: 16–18.

Hannon GE. 1985. *Late Quaternary vegetation of Sanabria Marsh, North West, Spain.* MSc Thesis, Trinity College: Dublin.

Hardy K. 2018. Plant use in the Lower and Middle Palaeolithic: food, medicine and raw materials. *Quaternary Science Reviews* **191**: 393–405.

Haws JA, Benedetti MM, Talamo S *et al.* 2020. The Early Aurignacian dispersal of modern humans into westernmost Eurasia. *Proceedings of the National Academy of Sciences of the United States of America* **117**: 25414–25422.

Hublin JJ. 2009. Out of Africa: modern human origins special feature: The origin of Neandertals. *Proceedings of the National Academy of Sciences of the United States of America* **106**: 16022–16027.

Iriarte MJ, Gómez-Orellana L, Muñoz-Sobrino C *et al.* 2005. La dinámica de la vegetación en el NW peninsular durante la transición del Paleolítico medio al Paleolítico Superior. *Monografías del Museo de Altamira* **20**: 231–253.

Jennings R, Finlayson C, Fa D *et al.* 2011. Southern Iberia as a refuge for the last Neanderthal populations. *Journal of Biogeography* **38**: 1873–1885.

Jones JR, Richards MP, Reade H *et al.* 2019. Multi-Isotope investigations of ungulate bones and teeth from el Castillo and Covalejos caves (Cantabria, Spain): implications for paleoenvironment reconstructions across the Middle-Upper Palaeolithic transition. *Journal of Archaeological Science: Reports* **23**: 1029–1042.

Jones JR, Richards MP, Straus LG *et al.* 2018. Changing environments during the Middle-Upper Palaeolithic transition in the eastern Cantabrian Region (Spain): direct evidence from stable isotope studies on ungulate bones. *Scientific Reports* **8**: 14842.

Julià R, Negendank JFW, Seret G *et al.* 1994. Origin and evolution of desertification in the Mediterranean environment in Spain. *Informe Final del Proyecto Europeo EV5V*-CT91- 0037. Bruselas.

Kolodny O, Feldman MW. 2017. A parsimonious neutral model suggests Neanderthal replacement was determined by migration and random species drift. *Nature Communications* **8**: 1040.

Krause J, Fu Q, Good JM *et al.* 2010. The complete mitochondrial DNA genome of an unknown hominin from southern Siberia. *Nature* **464**: 894–897.

Kuhlwilm M, Gronau I, Hubisz MJ *et al.* 2016. Ancient gene flow from early modern humans into eastern Neanderthals. *Nature* **530**: 429–433.

Lalueza-Fox C. 2017. A brief history of palaeogenomics: how a young discipline revolutionised the study of the past. *Mètode Revista De Difusió de La Investigació* **8**: 91–97.

Leakey MG, Spoor F, Brown FH *et al.* 2001. New hominin genus from eastern Africa shows diverse Middle Pliocene lineages. *Nature* **410**: 433–440.

Lebreton V, Renault-Miskovksy J, Carrión JS *et al.* 2006. Etude palynologique du remplissage de la grotte du Boquete de Zafarraya. In *La Grotte du Boquete de Zafarraya*, Barroso C, de Lumley H (eds). Monographies Institut de Paléontologie Humaine, Junta de Andalucía, Consejería de Cultura: Málaga; 629–660.

Leroi-Gourhan A. 1966. Análisis polínico de la cueva de el Otero. In *Excavaciones en la cueva del Otero (Santander). Excavaciones arqueológicas en España 53*, González Echegaray J, García Guinea MA, Begines Ramínez A (eds). Ministerio de Educación: Madrid; 83–85.

Leroi-Gourhan A. 1971. Análisis polínico de la cueva Morín. In *Cueva Morín: excavaciones 1966–1968. Publicaciones del Patronato de las cuevas prehistóricas de la provincia de*, González Echegaray J, Freeman LG (eds). Santander: Santander; 359–365.

Leunda M, González-Sampériz P, Gil-Romera G *et al.* 2017. The Late-Glacial and Holocene Marboré Lake sequence (2612 m asl, Central Pyrenees, Spain): testing high altitude sites sensitivity to millennial scale vegetation and climate variability. *Global and Planetary Change* **157**: 214–231.

López-García JM, Blain H-A, Burjachs F *et al.* 2012. A multidisciplinary approach to reconstructing the chronology and environment of southwestern European Neanderthals: the contribution of Teixoneres cave (Moià, Barcelona, Spain). *Quaternary Science Reviews* **43**: 33–44.

López-García P. 1977. Análisis polínico de Verdelpino (Cuenca). *Trabajos de Prehistoria* **34**: 82–84.

López-García P. 1982. Abauntz: análisis polínico. *Trabajos de Arqueología Navarra* **3**: 355–358.

López-García P. 1986. Estudio palinológico del Holoceno español a través del análisis de yacimientos arqueológicos. *Trabajos de Prehistoria* **43**: 143–158.

López-García P. 1987. Datos polínicos del Holoceno de Navarra y Aragón. In *Actas del VI Simposio de Palinología APLE, septiembre de 1986. Acta Salmanticensia 65*, Civis Llovera J, Valle Hernández MF (eds). Universidad de Salamanca: Salamanca; 315–320.

López-García P. 1988. Análisis palinológico. La cueva de Ambrosio (Vélez Blanco, Almería) y su posición cronoestratigráfica en el Mediterráneo Occidental. *British Archaeological Reports* **462**: 127–134.

López-Merino L. 2009. *Paleoambiente y antropización en Asturias durante el Holoceno*. Tesis Doctoral, Universidad Autónoma de Madrid.

López-Sáez JA, Carrasco RM, Turu V *et al.* 2020. Late Glacial-Early Holocene vegetation and environmental changes in the western Iberian Central System inferred from a key site: the Navamuño record, Béjar range (Spain). *Quaternary Science Reviews* **230**.

López-Sáez JA, López-García P, Cortés, Sánchez M. 2007. Paleovegetación del Cuaternario reciente: estudio arqueopalinológico. In *Cueva Bajondillo (Torremolinos). Secuencia cronocultural y paleoambiental del Cuaternario reciente en la Bahía de Málaga*, Cortés Sánchez M (ed.). Centro de Ediciones de la Diputación de Málaga, Junta de Andalucía, Universidad de Málaga, Fundación Cueva de Nerja y Fundación Obra Social de Unicaja: Málaga, 139–156.

Magri D, Di Rita F, Aranbarri J *et al.* 2017. Quaternary disappearance of tree taxa from Southern Europe: timing and trends. *Quaternary Science Reviews* **163**: 23–55.

Manzano S, Carrión JS, López-Merino L *et al.* 2017. Mountain strongholds for woody angiosperms during the Late Pleistocene in SE Iberia. *CATENA* **149**: 701–712.

Margari V, Gibbard PL, Bryant CL *et al.* 2009. Character of vegetational and environmental changes in Southern Europe during the last glacial period; evidence from Lesvos Island, Greece. *Quaternary Science Reviews* **28**: 1317–1339.

Marín-Arroyo AB, Rios-Garaizar J, Straus LG *et al.* 2018. Chronological reassessment of the Middle to Upper Paleolithic transition and early Upper Paleolithic cultures in Cantabrian Spain. *PLoS ONE* **13**: e0194708.

Markova AK, Smirnov NG, Kozharinov AV *et al.* 1995. Late Pleistocene distribution and diversity of mammals in northern Eurasia. *Paleontologia I Evolucio* **28–29**: 5–143.

Martín Arroyo T. 1998. *Paleoclimatología y Paleoambiente durante el Pleistoceno medio y Superior en el valle del Tajo.* Tesis Doctoral, Universidad de Alcalá de Henares.

Martín-Arroyo T, Ruiz-Zapata B, Pérez-González A. 1996b. Paleoambiente en el valle del río Tajo durante el Pleistoceno superior: primeros datos polínicos. In *Biogeografía Pleistocena-Holocena de la Península Ibérica. Xunta de Galicia. Conselleria de Cultura*, Ramil-Rego P, Fernández Rodríguez C, Rodríguez Guitián M (coords.). Santiago de Compostela; 73–83.

Martín-Arroyo T, Ruiz-Zapata B, Pérez-González A *et al*. 2000. Registro paleoclimático del Pleistoceno medio en el valle del Tajo. *Geotemas* **1**: 259–262.

Martín-Arroyo T, Ruiz-Zapata MB, Pérez, González A. 1996a. Reconstrucción de la vegetación durante el cuaternario reciente en el Puente del Arzobispo (Toledo, España): primeros datos polínicos. *Estudios Palinologicos* **1**: 91–94.

Martínez-Varea CM. 2020. Gathering in the dunes. Seeds and fruits from the Gravettian levels of Cova de les Cendres (Teulada-Moraira, Alicante, Spain). *Journal of Archaeological Science: Reports* **33**.

Martínez-Varea CM, Ferrer-Gallego PP, Raigón MD *et al*. 2019. Corema álbum archaeobotanical remains in western Mediterranean basin. Assessing fruit consumption during Upper Palaeolithic in Cova de les Cendres (Alicante, Spain). *Quaternary Science Reviews* **207**: 1–12.

McGarry S, Caseldine CJ. 2004. Speleopalynology, a neglected tool in British Quaternary studies. *Quaternary Science Reviews* **23**: 2389–2404.

Menéndez-Amor J, Florschütz F. 1962. Un aspect de la végétation en Espagne méridionale durant la derniere glaciation et l'holocène. *Geologie en Mijnbouw* 131–134.

Menéndez-Amor J, Florschütz F. 1964. Results of the preliminary palynological investigation of samples from a 50 m boring in southern Spain. *Bol. R. Soc. Española His. Nat.* **62**: 251–255.

Meyer M, Arsuaga JL, de Filippo C *et al*. 2016. Nuclear DNA sequences from the Middle Pleistocene Sima de los Huesos hominins. *Nature* **531**: 504–507.

Montserrat Martí J. 1992 *Evolución glaciar y postglaciar del clima y la vegetación en la vertiente sur del Pirineo: estudio palinológico*. Monografías del Instituto Pirenaico de Ecología-CSIC: Zaragoza.

Morales-Molino C, García-Antón M. 2014. Vegetation and fire history since the Last Glacial Maximum in an inland area of the western Mediterranean Basin (northern Iberian Plateau, NW Spain). *Quaternary Research* **81**: 63–77.

Muñoz Sobrino C, Ramil-Rego P, Rodríguez, Guitián MA. 2001. Vegetation in the mountains of northwest Iberia during the last glacial-interglacial transition. *Vegetation History and Archaeobotany* **10**: 7–21.

Muñoz-Sobrino C, Ramil-Rego P, Delibes de Castro G *et al*. 1996. Datos paleobotánicos sobre la turbera de la Piedra (Paramo de Tozo, Burgos). In *Biogeografía Pleistocena-Holocena de la Península Ibérica. Consellería de Cultura de Santiago de Compostela, Santiago de Compostela*, Ramil-Rego P, Fernández Rodríguez C, Rodríguez-Guitián M (coord.); 149–163.

Muñoz-Sobrino C, Ramil-Rego P, Gómez-Orellana L. 2004. Vegetation of the Lago de Sanabria area (NW Iberia) since the end of the Pleistocene: a palaeoecological reconstruction on the basis of two new pollen sequences. *Vegetation History and Archaeobotany* **13**: 1–22.

Navarro C, Carrión JS, Munuera M *et al*. 2001. Cave surface pollen and the palynological potential of karstic cave sediments in palaeoecology. *Review of Palaeobotany and Palynology* **117**: 245–265.

Navarro C, Carrión JS, Prieto AR *et al*. 2002. Modern cave pollen and its application to describe the palaeorecords in an arid environment. *Complutum* **13**: 7–18.

Ochando J, Carrión JS, Blasco R *et al*. 2019. Silvicolous Neanderthals in the Far West: the Mid-Pleistocene palaeoecological sequence of Bolomor Cave (Valencia, Spain). *Quaternary Science Reviews* **217**: 247–267.

Ochando J, Carrión JS, Blasco R *et al*. 2020a. Neanderthals in a highly diverse, Mediterranean-Eurosiberian forest ecotone: the Pleistocene pollen record of Teixoneres Cave, Northeastern Spain. *Quaternary Science Reviews* **241**.

Ochando J, Carrión JS, Blasco R *et al*. 2020b. The Late Quaternary pollen sequence of Toll Cave, a palaeontological site with evidence of human activities in Northeastern Spain. *Quaternary International* **554**: 1–14.

Ochando J, Carrión JS, Rodríguez-Vidal J *et al*. 2020d. Palynology and chronology of hyaena coprolites from the Piñar karstic Caves Las Ventanas and Carihuela, southern Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology* **552**.

Ochando J, López-Sáez JA, Pérez-Díaz S *et al*. 2020c. A new pollen sequence from southern Iberia suggesting coastal Pleistocene phytodiversity hotspot. *Review of Palaeobotany and Palynology* **281**.

Okuda M, Yasuda Y, Setoguchi T. 2001. Middle to Late Pleistocene vegetation history and climatic changes at Lake Kopais, Southeast Greece. *Boreas* **30**: 73–82.

Ortiz JE, Torres T, Delgado A *et al*. 2004. The palaeoenvironmental and palaeohydrological evolution of Padul Peat Bog (Granada, Spain) over one million years, from elemental, isotopic and molecular organic geochemical proxies. *Organic Geochemistry* **35**: 1243–1260.

Pantaleón-Cano J, Yll EI, Pérez-Obiol R *et al*. 2003. Palynological evidence for vegetational history in semi-arid areas of the western Mediterranean (Almería, Spain). *Holocene* **13**: 109–119.

Peñalba MC, Arnold M, Guiot J *et al*. 1997. Termination of the last glaciation in the Iberian Peninsula inferred from the pollen sequence of Quintanar de la Sierra. *Quaternary Research* **48**: 205–214.

Pérez-Obiol R, Julià R. 1994. Climatic change on the Iberian Peninsula recorded in a 30,000 yr pollen record from Lake Banyoles. *Quaternary Research* **41**: 91–98.

Pinto AC, Clark G, Miller A. 2006. Sopeña, un nuevo yacimiento de Paleolítico Medio y Superior Inicial en el norte de la Península Ibérica. *Actas del IV Congreso de Arqueología Peninsular: Faro* 407–418.

Pons A, Reille M. 1988. The Holocene and Upper Pleistocene pollen record from Padul (Granada, Spain): a new study. *Palaeogeography, Palaeoclimatology, Palaeoecology* **66**: 243–263.

Potts R. 1998. Environmental hypotheses of hominin evolution. *American Journal of Physical Anthropology* **27**: 93–136.

Prieto A, Carrión JA. 1999. Tafonomía polínica: sesgos abióticos y bióticos del registro polínico en cuevas. *Archivos de la Asociación Paleontológica Argentina* **6**: 59–64.

Pross J, Koutsodendris A, Christanis K *et al*. 2015. The 1.35-Ma-long terrestrial climate archive of Tenaghi Philippon, northeastern Greece: evolution, exploration, and perspectives for future research. *Newsletters on Stratigraphy* **48**: 253–276.

Ramil-Rego P, Gómez-Orellana L. 2002. Nuevos planteamientos para la periodización climática de los territorios Cántabro-Atlánticos de la península Ibérica durante el Pleistoceno Superior. *XV Congreso de Estudios Vascos, Ciencia y Cultura vasca y redes telemáticas*, Donostia; 69–91.

Ramil-Rego P, Gómez-Orellana L, Muñoz-Sobrino C. 1996. Valoración de las secuencias polínicas del noroccidente ibérico para el último ciclo glaciar- interglaciar. In: *Arqueometría y Paleoecología del Norte de la Península Ibérica. Cambios naturales y perturbaciones antrópicas Férvedes, Número Monográfico*, Ramil-Rego P, Fernández Rodríguez C (coords). **3**: 33–116.

Real C, Martínez-Varea CM, Carrión-Marco Y *et al*. 2021. Could the central-eastern Iberian Mediterranean region be defined as a refugium? Fauna and flora in MIS 5–3 and their implications for Palaeolithic human behaviour. *Journal of Quaternary Science*. (this issue).

Roche D, Ségalen L, Senut B *et al*. 2013. Stable isotope analyses of tooth enamel carbonate of large herbivores from the Tugen Hills deposits: palaeoenvironmental context of the earliest Kenyan hominids. *Earth and Planetary Science Letters* **381**: 39–51.

Rodríguez J, Allué E, Burjachs F *et al*. 2011. One million years of environmental changes and cultural evolution at Atapuerca (Burgos, Spain). *Quaternary Science Reviews* **30**: 1396–1412.

Rodríguez-Ariza MO. 2006. Análisis antracológico del yacimiento solutrense de la Cueva de Ambrosio (Vélez Blanco, Almería). In *Simposio de Prehistoria Cueva de Nerja. La Cuenca Mediterránea durante l Paleolítico superior (38.000–10.000 años)*, Sanchidrián JL, Márquez AM, Fullola JM (eds). Málaga; 226–233.

Roksandic M, Radović P, Lindal J. 2018. Revising the hypodigm of *Homo heidelbergensis*, a view from the eastern Mediterranean. *Quaternary International* **466**: 66–81.

Rosas A 2016. *La evolución del género 'Homo'*. Los Libros de la Catarata-CSIC: Madrid.

Rosas A, Bastir M, Alarcón JA. 2019. *Tempo* and mode in the Neandertal evolutionary lineage: A structuralist approach to mandible variation. *Quaternary Science Reviews* **217**: 62–75.

Rudaya N, Vasiliev S, Viola B *et al*. 2017. Palaeoenvironments during the period of the Neanderthals settlement in Chagyrskaya cave (Altai Mountains, Russia). *Palaeogeography, Palaeoclimatology, Palaeoecology* **467**: 265–276.

Ruiz-Zapata MB, Dorado-Valiño M, Valdeolmillos Rodríguez A *et al*. 2004. Registro paleoambiental y paleoclimático del Pleistoceno medio y Superior en depósitos fluviales del valle del río Tajo (Toledo). Zona Arqueológica 4: Miscelánea en homenaje a Emiliano Aguirre II, Alcalá de Henares: 506–517.

Ruiz-Zapata MB, Gil-García MJ. 2005. Los Neandertales cantábricos: su paisaje vegetal. *Monografias Museo de Altamira* **20**: 275–284.

Ruiz-Zapata MB, Gil-García MJ, Dorado-Valiño M *et al*. 2005. El Paisaje vegetal durante el Pleistoceno medio en el interior de la península. Zona arqueológica: yacimientos paleolíticos de Ambrona y Torralba (Soria). *Un Siglo de Investigaciones Arqueológicas* **5**: 214–221.

Ruiz-Zapata MB, Jiménez M, Farias Arquer P *et al*. 2002. Registro palinológico de un depósito holoceno del Parque Natural de redes (Cordillera Cantábrica). In *Libro de Textos Completos*, Moreno Grau S, Elvira Rendueles B, Moreno Angosto JM (eds). Universidad Politécnica de Cartagena; 391–400.

Ruiz-Zapata MB, Jiménez M, Gil-García MJ *et al*. 2000. Registro palinológico de un depósito postglaciar en el Parque Natural de redes (Cordillera Cantábrica, Noroeste de España): implicaciones climáticas. *Geotemas* **1**: 279–283.

Ruiz-Zapata MB, Rodríguez de Tembleque JM, Pérez-González A *et al*. 2009. Paleovegetación en el yacimiento achelense de Puente Pino y su entorno (Toledo, España). *Revista Cuaternario y Geomorfología* **23**: 113–126.

Ruiz-Zapata MB, Vegas J, García-Cortés A *et al*. 2008. Comportamiento de la vegetación durante el último máximo glaciar en la secuencia FU-1 (Laguna del maar de Fuentillejo, Campo de Calatrava, Ciudad Real). *Polen* **18**: 37–459.

Sadori L, Koutsodendris A, Panagiotopoulos K *et al*. 2016. Pollen-based paleoenvironmental and paleoclimatic change at Lake Ohrid (South-Eastern Europe) during the past 500 ka. *Biogeosciences* **13**: 1423–1437.

Salomón R, Rodríguez-Calcerrada J, Zafra E *et al*. 2016. Unearthing the roots of degradation of *Quercus pirenaica* coppices: a root-to-shoot imbalance caused by historical management? *Forest Ecology and Management* **363**: 200–211.

Sánchez-Goñi MF. 1994. The identification of European upper palaeolithic interstadials from cave sequences. Aspects of archaeological palynology, methodology and applications. In, AASP Contribution Series Vol. 29, Davis OK (ed.); 161–182.

Sanchis-Serra A, Fernández-Peris J. 2008. Procesado y consumo antrópico de conejo en la Cova del Bolomor (Tavernes de la Valldigna, Valencia). El Nivel XVIIc (ca 350 Ka). *Complutum* **18**: 25–46.

Sankararaman S, Mallick S, Dannemann M *et al*. 2014. The genomic landscape of Neanderthal ancestry in present-day humans. *Nature* **507**: 354–357.

Schulte L, Julià R, Burjachs F *et al*. 2008. Middle Pleistocene to Holocene geochronology of the River Aguas terrace sequence (Iberian Peninsula): fluvial response to Mediterranean environmental change. *Geomorphology* **98**: 13–33.

Sechrest W, Brooks TM, da Fonseca GAB *et al*. 2002. Hotspots and the conservation of evolutionary history. *Proceedings of the National Academy of Sciences of the United States of America* **99**: 2067–2071.

Serra JC, Villalta JF, Thomas J *et al*. 1957. *Livret Guide Des Excursions B2-B3. Alentours de Barcelona et Moià*. V Congrés International del INQUA: Madrid, Barcelona; 3.

Shea J. 2016. *Stone Tools in Human Evolution. Behavioral Differences Among Technological Primates*. Cambridge University Press: Cambridge.

Sinopoli G, Masi A, Regattieri E *et al*. 2018. Palynology of the last interglacial complex at Lake Ohrid: palaeoenvironmental and palaeoclimatic inferences. *Quaternary Science Reviews* **180**: 177–192.

Slon V, Mafessoni F, Vernot B *et al*. 2018. The genome of the offspring of a Neanderthal mother and a Denisovan father. *Nature* **561**: 113–116.

Soler JA, Ferrer C, Roca de Togores C *et al*. 2008. Cova d'en Pardo (Planes, Alicante). [Un avance sobre la secuencia cultural]. In *Congreso del Neolítico peninsular (Alicante 27–30 de noviembre de 2006)*. Hernández Pérez MS, Soler Díaz JA, López, Padilla JA (eds).Museo Arqueológico de Alicante: Alicante; 79–89.

Spathelf M, Waite TA. 2007. Will hotspots conserve extra primate and carnivore evolu- tionary history? *Diversity and Distributions* **13**: 746–751.

Steegmann AT, Cerny FJ, Holliday TW. 2002. Neandertal cold adaptation: physiological and energetic factors. *American Journal of Human Biology* **14**: 566–583.

Stevenson AC. 1984. Studies on the vegetational history of S.W. Spain. III. Palynological investigations at El Asperillo, Huelva. *Journal of Biogeography* **11**: 527–551.

Stewart JR. 2005. The ecology and adaptation of Neanderthals during the non-analogue environment of Oxygen Isotope Stage 3: Armageddon or entente? The demise of the European Neanderthals in Isotope Stage 3. *Quaternary International* **137**: 35–46.

Stewart JR, García-Rodríguez O, Knul MV *et al*. 2019. Palaeoecological and genetic evidence for Neanderthal power locomotion as an adaptation to a woodland environment. *Quaternary Science Reviews* **217**: 310–315.

Sun Y & An Z. 2005. Late Pliocene-Pleistocene changes in mass accumulation rates of eolian deposits on the central Chinese Loess Plateau. *Journal of Geophysical Research*, **110**: 1–8.

Suwa G, Ambrose SH. 2014. Reply to Cerling *et al*. *Current Anthropology* **55**: 473–474.

Trinkaus E. 1981. Neanderthal limb proportions and cold adaption. In *Aspects of Human Evolution*, Stringer CB (ed.). Taylor & Francis: London; 187–224.

Tzedakis PC, McManus JF, Hooghiemstra H *et al*. 2003. Comparison of changes in vegetation in Northeast Greece with records of climate variability on orbital and suborbital frequencies over the last 450,000 years. *Earth and Planetary Science Letters* **212**: 197–212.

Uzquiano P. 1988. Analyse anthracologique du Tossal de la Roca (Paléolithique Superieur-final/Epipaléolithique, province d'Alicante, Espagne). In: *Révue PACT, 22.IV.1, Proceedings of "Wood and Archaeology". Congress. Louvain-la-Neuve*, Hackens T, Munaut A, Till C (eds); 209–217.

Uzquiano P. 1992a. *Recherches anthracologiques dans le sécteur Pyréneo-Cantabrique (Pays Basque, Cantabria et Asturias): environnements et rélations homme-milieu au Pléistocène supérieur et début de l'holocène*. Tesis Doctoral, Environnements et Archéologie, Universidad de Montpellier II.

Uzquiano P. 1992b. L'homme et le bois au Paléolithique en Region Cantabrique, Espagne. Les exemples d'Altamira et El Buxu. In: *Les charbons de bois, les anciens écosystèmes et le rôle de l'homme Bull. Soc. Bot. Fr. Actualités Botaniques*, Vernet JL (ed.). **2/3/4**: 361–372.

Uzquiano P. 1992c. The Lateglacial-Postglacial transition in the Cantabrian Cordillera (Asturias and Cantabria, Spain) based on charcoal analysis. *Palaios* **7**: 540–547.

Uzquiano P. 1995. L'évolution de la végétation à l'holocène initial dans le nord de l'Espagne à partir de trois sites archéologiques. *Quaternaire* **6**: 77–83.

Uzquiano P. 1998. La végétation cantabrique de 13000 à 9000 bp d'après l'analyse anthracologique. Habitats et ramassages de bois dans un milieu changeant. *Proceedings of the XIIIth UISPP Congress, vol. I ABACO*, Forli, Italia; 477–482.

Uzquiano P. 2005. El Registro antracológico durante la transición Musteriense-Pale- olítico Superior Inicial en la Región Cantábrica: vegetación, paleoambiente y modos de vida en torno al fuego. In *Neandertales cantábricos, estado de la cuestión*, Montes R, Lasheras JA (eds). Monografías Museo de Altamira **20**: 255–274.

Uzquiano P. 2007. La Antracología de las unidades musterienses y del Auriñaciense de Transición de la cueva de el Castillo (1984–2001). In *Dinámica de la vegetación y de gestión del combustible. Miscelánea en homenaje a Victoria Cabrera vol. 1*, Maíllo JM, Baquedano E (eds). Museo Arqueológico Regional: Alcalá de Henares; 132–143.

Uzquiano P, Arbizu M, Arsuaga JL *et al.* 2008. Datos paleoflorísticos en la cuenca media del Nalón entre 40-32 Ka. bp: antracoanálisis de la cueva del Conde (Santo Adriano, Asturias). In: *Actas XII Reunión Nacional de Cuaternario AEQUA, Ávila, 21-23 Junio 2007 Cuaternario y Geomorfología*, Baena J, Lario J (eds). **22**: 121–133.

Uzquiano P, Arnanz AM. 1997. Consideraciones paleoambientales del Tardiglaciar y Holoceno inicial en el Levante español: macrorrestos vegetales de el Tossal de la Roca (Vall d'Alcalà, Alicante). *Anales del Jardín Botánico de Madrid* **55**: 125–133.

Uzquiano P, Ruiz-Zapata M, Gil-Garcia M *et al.* 2016. Late Quaternary developments of Mediterranean oaks in the Atlantic domain of the Iberian Peninsula: the case of the Cantabrian region (N Spain). *Quaternary Science Reviews* **153**: 63–77.

Val-Peón C, Expósito I, Soto M *et al.* 2019. A taphonomic approach to the pollen assemblage from layer M of the Abric Romaní archaeological site (NE Iberian Peninsula). *Review of Palaeobotany and Palynology* **270**: 19–39.

van der Knaap WO, van Leeuwen JFN. 1995. Holocene vegetation succession and degradation as responses to climatic change and human activity in the Serra da Estrela, Portugal. *Review of Palaeobotany and Palynology* **89**: 153–211.

van der Knaap WO, van Leeuwen JFN. 1997. Late Glacial and Early Holocene vegetation succession, altitudinal vegetation zonation, and climatic change in the Serra da Estrela, Portugal. *Review of Palaeobotany and Palynology* **97**: 239–285.

Vernet JL, Terral JF. 2006. Les charbons de Bois des niveux mousteriens et protoaurignaciens de la Grotte du Boquete de Zafarraya. In *La Grotte du Boquete de Zafarraya-tome-II. Junta de Andalucía, Consejería de Cultura*, Barroso C, de Lumley H (eds); 661–673.

Vidal-Matutano P, Blasco R, Sañudo P *et al.* 2019. The anthropogenic use of firewood during the European Middle Pleistocene: charcoal evidence from Levels XIII and XI of Bolomor Cave, Eastern Iberia (230–160 ka). *Environmental Archaeology* **24**: 269–284.

Vidal-Matutano P, Henry A, Carrión-Marco Y *et al.* 2020. Disentangling human from natural factors: taphonomical value of micro-anatomical features on Wood and charcoal assemblages. *Journal of Archaeological Sciences* **31**.

Vidal-Matutano P, Henry A, Théry-Parisot I. 2017. Dead wood gathering among Neanderthal groups: charcoal evidence from Abric del Pastor and El Salt (eastern Iberia). *Journal of Archaeological Science* **80**: 109–121.

Vidal-Matutano P, Pardo-Gordó S. 2020. Predictive Middle Palaeolithic climatic conditions from eastern Iberia: a methodological approach based on charcoal analysis and modelling. *Archaeological and Anthropological Sciences* **12**: 36.

Villaverde V, Real C, Roman D *et al.* 2019. The early Upper Palaeolithic of Cova de les Cendres (Alicante, Spain). *Quaternary International* **515**: 92–124.

Villaverde V, Sanchis A, Badal E *et al.* 2021. Cova de les Malladetes (Valencia, Spain): New Insights About the Early Upper Palaeolithic in the Mediterranean Basin of the Iberian Peninsula. *Journal of Paleolithic Archaeology* 4.

Walker MJ, Gibert J, López MV *et al.* 2008. Late Neanderthals in southeastern Iberia: Sima de las Palomas del Cabezo Gordo, Murcia, Spain. *Proceedings of the National Academy of Sciences of the United States of America* **105**: 20631–20636.

Walker MJ, Gibert J, Rodríguez-Estrella T *et al.* 2004. Neanderthals and their landscapes: middle Palaeolithic land use in the Segura Basin and adjacent areas of south- eastern Spain. In *Settlement Dynamics of the Middle Paleolithic and Middle Stone Age. Tübingen Publications in Archaeology* Vol. II, Conard N (ed.); 461–512.

Wall JD, Yang MA, Jay F *et al.* 2013. Higher levels of Neanderthal ancestry in East Asians than in Europeans. *Genetics* **194**: 199–209.

Ward S, Gale R, Carruthers W. 2012a. Late Pleistocene vegetation reconstruction at Vanguard Cave. In *Neanderthals in Context. A Report of the 1995–1998 Excavations at Gorham's and Vanguard Caves, Gibraltar*, Barton RNE, Stringer CB, Finlayson C (eds). Institute of Archaeology, University of Oxford: Oxford; 218–223.

Ward S, Gale R, Carruthers W. 2012b. Late Pleistocene vegetation reconstruction at Gorham's Cave. In *Neanderthals in Context: A Report of the 1995–1998 Excavations at Gorham's and Vanguard Caves, Gibraltar*, Barton RNE, Stringer CB, Finlayson C (eds). Institute of Archaeology, University of Oxford: Oxford, Oxford, 89–101.

Willis KJ. 1994. The vegetational history of the Balkans. *Quaternary Science Reviews* **13**: 769–788.

Wood B, Strait D. 2004. Patterns of resource use in early *Homo* and *Paranthropus*. *Journal of Human Evolution* **46**: 119–162.

Yll EI. 1995. *Estudi de l´evolució de la vegetació I el clima durant el Tardiglacial I el Postglacial a partir d´análisis pollíniques del Delta de l´Ebre I de Menorca*. Publications de la Universitat Autònoma de Barcelona. Edición Microfotográfica. ETD Micropublicaciones, SL.

Yll EI, Carrión JS, Pantaleón J *et al.* 2003. Palinología del Cuaternario reciente en la Laguna de Villena (Alicante). *Anales de Biología* **25**: 65–72.

Yll EI, Pérez-Obiol R. 1992. Instalación de los bosques deducida a partir del análisis po- línico de un sondeo marino del Delta del Ebro (Tarragona, España). *Orsis* **7**: 21–30.

Yll R, Carrión JS. 2003. Refugios glaciares de vegetación mediterránea y su relación con la ocupación humana en el Ibérico. *Polen* **13**: 1–12.

Zilhão J, Ajas A, Badal E *et al.* 2016. Cueva Antón: a multi-proxy MIS 3 to MIS 5a paleoenvironmental record for SE Iberia. *Quaternary Science Reviews* **146**: 251–273.

Zilhão J, Anesin D, Aubry T *et al.* 2017. Precise dating of the Middle-to-Upper transition in Murcia (Spain) supports late Neanderthal persistence in Iberia. *Heliyon* **3**: e00435.

Zilhão J, Angelucci DE, Igreja MA *et al.* 2020. Last Interglacial Iberian Neandertals as fisher-hunter-gatherers. *Science* **367**: 6485.