Quaternary Science Advances 19 (2025) 100293

Contents lists available at ScienceDirect

Quaternary Science Advances

journal homepage: www.sciencedirect.com/journal/quaternary-science-advances

Cueva del Arco: Paleoecological insights into Paleolithic landscapes

José S. Carrión [a,*], Yolanda Carrión-Marco [b], Carmen M. Martínez-Varea [b], Juan Ochando [a,c], Cristina Real-Margalef [b], Manuel Munuera [d], Gloria Martínez-Sagarra [e], Gabriela Amorós [a], Aldara Girona [a], Diego Angelucci [f], Jacopo Armellini [g], Noelia Sánchez-Martínez [h], Dídac Román [g], Ignacio Martín-Lerma [h]

[a] Department of Plant Biology (Botany Area), Faculty of Biology, University of Murcia, Campus de Espinardo, 30100, Murcia, Spain
[b] Universidad de Valencia, Departamento de Prehistoria, Arqueología e Historia Antigua, Avda Blasco Ibáñez 28, 46010, Spain
[c] Sapienza University of Rome, Department of Environmental Biology, Piazzale Aldo Moro 5, 00185, Rome, Italy
[d] Universidad Politécnica de Cartagena, Departamento de Ingeniería Agronómica, Plaza Cronista Isidoro Valverde, 30202, Cartagena, Spain
[e] Departamento de Botánica, Ecología y Fisiología Vegetal, Facultad de Ciencias, Universidad de Córdoba, Campus de Rabanales, 14071, Córdoba, Spain
[f] Dipartimento di Lettere e Filosofia, Università di Trento, Via Tommaso Gar, 14, 38122, Trento, Italy
[g] Departament d'Història, Geografia i Art, Universitat Jaume I, Av. Sos Baynat, s/n, 12071 Castelló de la Plana, Spain
[h] Área de Prehistoria, Faculty of Letters, University of Murcia, Campus de Espinardo, 30100, Murcia, Spain

ARTICLE INFO

Keywords:
Palaeoecology
Archaeobotany
Palynology
Anthracology
Vertebrate paleontology
Neanderthal
Pleistocene
Spain
Arco cave

ABSTRACT

This article presents new data from Cueva del Arco and offers a comprehensive perspective on the palaeoenvironments inhabited by Neanderthals and *Homo sapiens* in the interior of Murcia, southeastern Spain, during the Mousterian and Gravettian periods. We focus on the ecological structure and floristic composition of prehistoric landscapes, drawing on pollen records from coprolites and cave sediments, as well as charcoal and plant macroremains, particularly seeds. Vertebrate assemblages are discussed through taphonomic and paleoecological lenses. Our results show that the landscapes surrounding Cueva del Arco during MIS 3 underwent only limited changes despite climatic fluctuations, likely buffered by nearby glacial strongholds, such as immediate riverine hydrorefugia and biodiversity reservoirs in the Segura-Cazorla-Alcaraz Mountains. We highlight the coexistence of plant species with currently disparate bioclimatic affinities, suggesting a compression of vegetation belts. Locally, under the edaphic influence of lithosols overlying karstic bedrock, the landscape remained open, with scattered trees or small groves on deeper soils. Notably, Cupressaceae were a dominant feature of the local vegetation and constituted a critical resource for firewood, supporting human adaptation to the environment. In this resilient and ecologically diverse setting, Paleolithic populations had access to a wide variety of plant and animal resources essential for their survival.

1. Introduction

The southeastern region of the Iberian Peninsula presents a unique physiographic mosaic that likely played a crucial role in the survival strategies and lifeways of its early human populations since the Paleolithic (Finlayson and Carrión, 2006; Bailey et al., 2008; Carrión, 2009; Walker et al., 2013; Carrión et al., 2011, 2018a, 2019a, 2019b, 2019c, 2024a; Zilhão et al., 2017; Altolaguirre et al., 2019; Carrión and Walker, 2019; Fyfe et al., 2019; Vidal-Cordasco et al., 2022; Finlayson et al., 2023; Sánchez-Bandera et al., 2023; Berlioz et al., 2025). This territory is notable for its geomorphological and, consequently, edaphic diversity. Mountain ranges, valleys, and broad coastal platforms are intricately connected by a network of river corridors, all within relatively short distances from the sea (Romero and Belmonte, 2002; Rodríguez-Estrella et al., 2011). The coastline itself is equally varied, spanning kilometers of beaches, cliffs, and continental shelves of differing depths. In some areas, shallow waters have created a landscape especially sensitive to long-term sea-level fluctuations (Silva Barroso et al., 2021; Bardaji et al., 2024). Floristically, the region harbors high biodiversity and striking variation in structural and functional vegetation types (Alcaraz et al., 1991, 2008)—an ecological richness shaped by a complex bioclimatic mosaic and a tumultuous geological history since the Tertiary (Carrión et al., 2010b, 2024a; Romagny et al., 2020; Verdú et al., 2020). Episodes of insularization and periodic connections with North Africa and

* Corresponding author.
E-mail address: carrion@um.es (J.S. Carrión).

https://doi.org/10.1016/j.qsa.2025.100293
Received 10 June 2025; Received in revised form 2 August 2025; Accepted 11 August 2025
Available online 12 August 2025

western Asia further enhanced its ecological heterogeneity (Peinado Lorca et al., 1992; Pugnaire et al., 2024). The region also includes one of the most arid areas in Europe, and although much of the desertification is anthropogenic, there is evidence of xerophytism and sub-desertic communities at least since the Miocene (Postigo-Mijarra et al., 2009; Barrón et al., 2010; Jiménez-Moreno et al., 2013; Carrión et al., 2024a).

Ecological research into the Pleistocene of southeastern Iberia has produced numerous paleobotanical studies. Yet, the vegetation dynamics vary considerably across time and space (Munuera and Carrión, 1991; Carrión, 1992; Badal et al., 1994; Carrión and Dupré, 1994; Rodríguez-Ariza et al., 1996; Araus et al., 1997; Carrión and Munuera, 1997; Giralt et al., 1999; Pantaleón-Cano et al., 2003; Yll et al., 2003; Fuentes et al., 2006; Jiménez-Moreno et al., 2015; Ramos-Román et al., 2016, 2018; Zilhão et al., 2016; Manzano et al., 2017; Azuara et al., 2020; Carrión et al., 1995, 2003a,b, 2004, 2006, 2010a,b, 2018a, 2018b, 2024a,b,c; Carrión and van Geel, 1999; Ochando et al., 2022a; Martínez-Sánchez et al., 2024; Sánchez-García et al., 2024, Casas-Gallego et al., 2025). This highlights the need for new paleoecological sequences in underexplored areas. One such area is the mid-altitude interior of Murcia, home to Cueva del Arco—a site that could prove pivotal for understanding both the Middle and Upper Paleolithic in western Europe. Excavations carried out since 2015 have yielded valuable insights into the landscape and subsistence strategies of the human groups who once inhabited the site. While recent research has primarily focused on the Upper Paleolithic (Román et al., 2024), this study expands the paleoecological framework to include the Mousterian period and a broader array of paleoenvironmental proxies, such as vertebrate remains, archaeological charcoal, seeds, and pollen grains derived from coprolites and cave sediments.

2. Physical setting, archaeology, and chronology

Cueva del Arco is a rockshelter located in the municipality of Cieza (Murcia province, southeastern Spain) at an altitude of 335–350 m a.s.l. It is situated within a small ravine (Barranco de la Tabaquera), which flows into the Segura River, near Los Almadenes Canyon and the Quípar River Canyon (Figs. 1 and 2). The site comprises several cavities (A-E) surrounding a large natural arch, from which the complex derives its name. Excavations since 2015 have primarily focused on cavities A and D, with cavity A providing the data for this study (Fig. 3). In addition to the archaeological work conducted in these two cavities, the chamber E and a small cavity adjacent to Cueva del Arco, known as Arco II, contain evidence of Palaeolithic rock art (Salmerón et al., 1997). More recently, a large cavity accessible from chamber D has been cleared and is now designated as Arco III. This newly discovered cavern extends approximately 1500 m and is currently under study and exploration (Gázquez et al., 2024).

Cave A yielded the most complete and best-preserved archaeological deposit, where four cultural units were identified and attributed to the Middle and Upper Palaeolithic (Aurignacian, Gravettian, and Solutrean), with Early Neolithic material found in the uppermost layers. In Cave D, Neolithic occupation has been documented, while the Palaeolithic remains recovered so far—primarily lithic and faunal—do not allow for a clear cultural attribution. The test-pit in Cave E has not yet

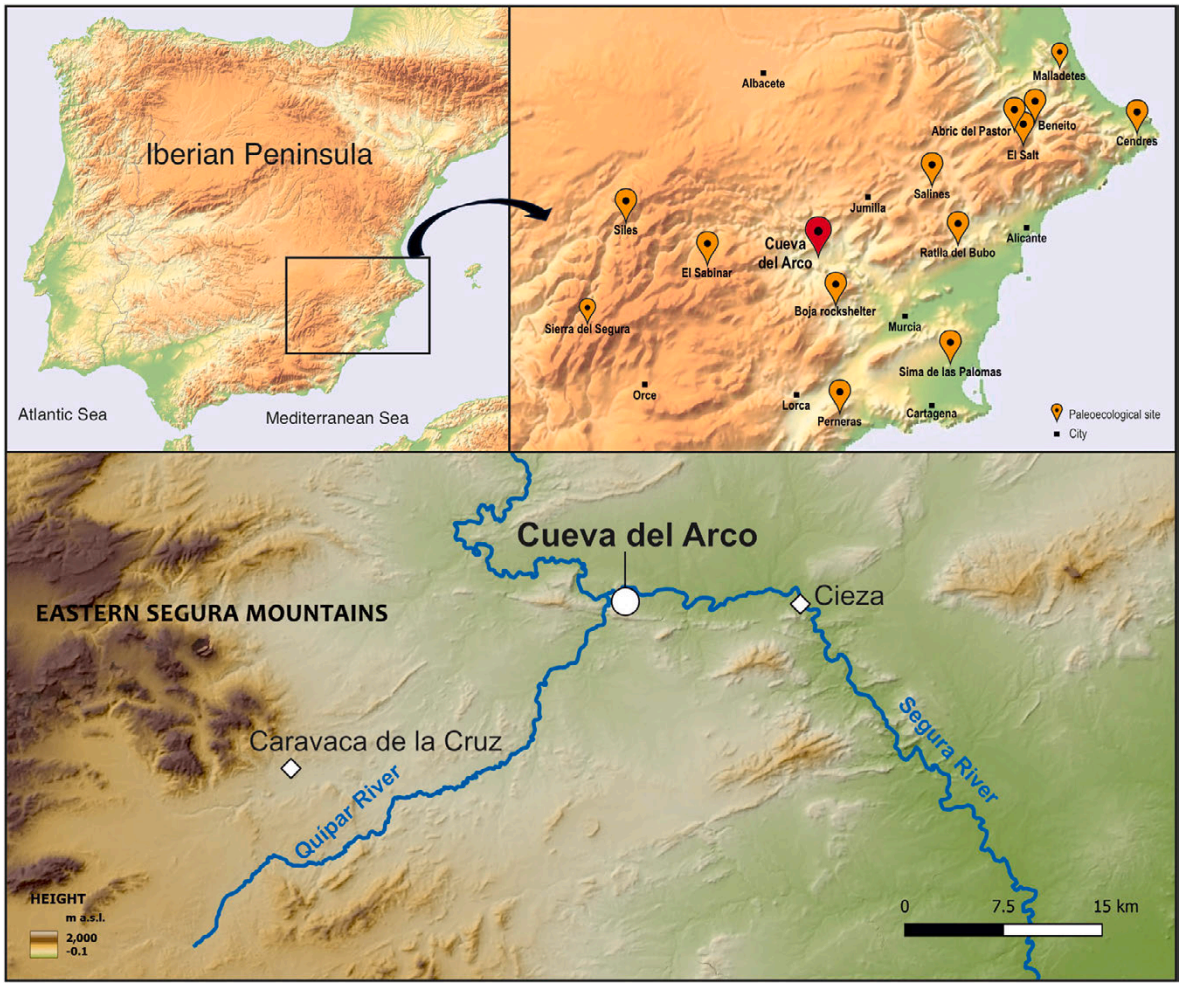

Fig. 1. (a) Location of Cueva del Arco in the southern Iberian Peninsula, and (b) other paleoecological sites mentioned in this paper.

Fig. 2. (a) Physical setting of Cueva del Arco within the context of Almadenes Canyon, the Segura River, the Quípar River Canyon, and Sierra del Almorchón. Location map generated with Google Earth (38.2274°N, 1.6124°W; image captured on April 22, 2025; source: Google Earth. © 2025). (b) Almadenes Canyon (photo by Fran Ramírez). (c, d) Access areas to the cave.

provided evidence of human occupation.

The stratigraphy of Cave A reveals a sequence of geoarchaeological field units (GFUs) that, during excavation, were consolidated into three principal excavation units (I, II, III) (Martín-Lerma et al., 2023) (Fig. 3). These excavation units are characterized by a high presence of angular limestone debris originating from the cave's own roof and walls. The uppermost stratum, labelled as Unit I sup. (GFU A1), belongs to the Holocene period. It is composed of dark, organic-rich sediments containing traces of combustion and only sparse stone material. Underlying this, Units I inf. and II correspond to the upper Pleistocene sequence. In the interior of the cave, these layers lie nearly horizontal, gradually tilting outward near the dripline. The sediments consist mainly of limestone clasts mixed with finer materials, varying in color from yellowish to brown.

At the base of Unit I lies a fine-grained layer (GFU A3), dominated by silts and fine sands, interspersed with horizontally oriented stones. This transitions into A4, a clast-supported breccia composed of angular, plate-like stones—some likely frost-derived—embedded in minimal fine sediment. Below that, A5, the thickest layer, mirrors the composition of A3 but includes slightly larger stones and weak calcium carbonate cementation, sometimes forming small nodules. This unit overlies a concave ash- and charcoal-rich lens, marking the top of Unit III (A6). Overall, the sedimentary sequence of Units II and III reflect the typical characteristics of Mediterranean rock shelters in southern Europe: loosely organized stratification, a dominance of angular limestone clasts, poor sorting, localized calcite cementation, and limited biogenic disturbance. The prevalence of frost-fractured slabs suggests episodes of freeze-thaw activity under cold and humid climatic conditions. The thinness of the deposit points to a low rate of sediment accumulation, likely due to the location of the excavated area, which received minimal

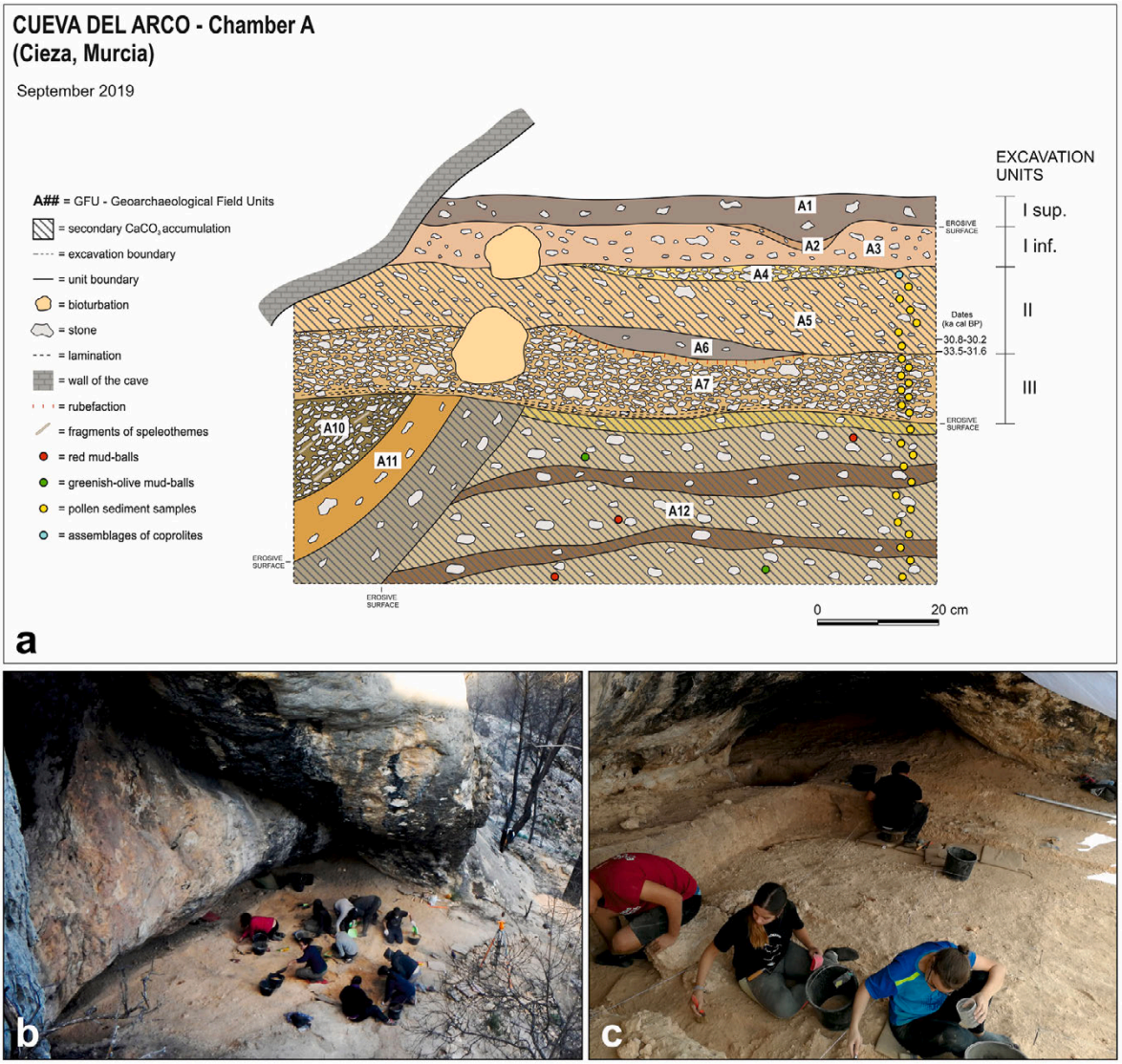

Fig. 3. (a) Stratigraphic profile of Cueva del Arco showing archaeological units and the position of pollen samples (section of Cave A). Redrawn from Román et al. (2024). (b, c) Excavation area (Cave A).

input beyond wall and roof detritus (Román et al., 2024).

In the lower section of Unit I, evidence points to an Evolved Solutrean presence. This is primarily indicated by the discovery of two shouldered points. Based on the broader regional sequence, this occupation likely dates to around 23,000–20,500 cal BP (Villaverde, 1994). Its significance lies in the stylistic connection to the nearby rock art in Cave E. However, no direct radiometric dates are currently available for this stratigraphic level. The subsequent occupation, attributed to the Gravettian period and located in Unit II, is notably better preserved than earlier phases. This is evidenced by the presence of multiple hearths in their original context. The material remains associated with these hearths include a notable assemblage of Gravette and Micrograveette points, along with backed tools characteristic of the Gravettian cultural tradition. This attribution is supported by three radiocarbon dates ranging around 30 and 31 ka (Table 1).

At certain points within the site, a thin gravel layer has been

Table 1
Dating of charcoal samples in Cueva del Arco according to Martín-Lerma et al. (2023).

Sample	Lab. ref	Unit	GFU	Charcoal sample	Date (BP)	$\delta^{13}C$ (‰)	Cal BP (2σ)
Arco D17	ETH-67833	II	A5	*Juniperus*	26193 ± 104	−20.5 ± 1.0	30801–30148
Arco D17	ETH-67834	II	A5	*Juniperus*	26279 ± 106	−21.0 ± 1.0	30870–30233
Arco C18	VERA-7068	II	A4+A5	*Juniperus*	26151 ± 172	−21.4 ± 1.4	30846–30068
Arco D17	VERA-7063	IIb	A5-A6	*Juniperus*	28617 ± 287	−27.8 ± 1.1	33780–31948
Arco B17	Beta-627630	IIb	A6+A7	Seed *Celtis australis*	31190 ± 190	−6.5 ??	36091–35203
Arco C18	VERA-7064	III	A6+A7	*Pinus nigra- sylvestris*	>50368	−27.3 ± 0.6	Out of range
Arco C17	VERA-7065	III	A6+A7	*Juniperus*	45699 ± 1931	−14.1 ± 4.2	Out of range
Arco D18	VERA-7066	III	A6+A7	*Pinus nigra- sylvestris*	54594 ± 8522	−29.6 ± 0.8	Out of range
Arco B15	VERA-7067	III	?	Bract of pine cone	7101 ± 35	−23.5 ± 0.7	8010–7845

identified just beneath the documented occupations. While its origin remains uncertain, it may correspond to an earlier Upper Palaeolithic phase, as it marks the interface between archaeological units II and III. Notably, beneath Hearth H1, a few subtle indicators of possible Aurignacian activity have emerged—among them, a finely retouched bladelet that might tentatively resemble a Dufour type, though its classification remains inconclusive. Supporting this hypothesis, a radiocarbon date of 33,780–31,948 cal BP (Table 1) has been obtained, suggesting the potential existence of an undetected Aurignacian presence. Beneath these levels, a Middle Palaeolithic deposit forms the core of archaeological unit III. This is lithologically distinct from the overlying sediments and it is clearly associated with the Mousterian due to both its sedimentary characteristics and lithic content. The tool assemblage stands out for the high frequency of retouched pieces, including a significant number of scrapers (lateral, transverse, and convergent), various Mousterian points, as well as notched and denticulated tools (Román et al., 2024). Radiocarbon dates obtained from this layer indicate a minimum age of approximately 45–50 ka (Table 1). In summary, there is no available chronological control for the potential Aurignacian phase or for the Solutrean. The Mousterian could be associated with MIS 3, MIS 4, or—though much less likely—with a cold stadial within MIS 5, considering, as will be discussed, the pollen sequence. Given the similarity between the anthracological assemblages of El Arco and Abric del Pastor (Vidal-Matutano, 2016), it is plausible to hypothesize that the Mousterian occupation at El Arco corresponds to MIS 4. The Gravettian appears to be present around 30–31 ka, and the transition between the Middle and Upper Paleolithic is tentatively placed at approximately 35–36 ka (see Table 1).

3. Modern climate and vegetation

Cueva del Arco is within the Murciano-Almeriense biogeographical Province (Rivas-Martínez et al., 1977; Rivas-Martínez, 1987) with a present-day climate characterised by warm and dry summers. The annual average precipitation is 250–350 mm and the average annual temperature exceeds 15 °C. Positioned above the Quípar and Almadenes gorges, the rocky promontories and flat uplands in this area are dominated by xerophytic shrublands. The vegetation around the cave site consists mainly of drought-adapted Mediterranean species such as *Salvia rosmarinus*, *Thymus vulgaris*, *Cistus clusii*, and *Macrochloa tenacissima*, interspersed with small shrubs such as *Rhamnus lycioides*. Scattered individuals of *Pinus halepensis* appear on more stable soils, along with occasional *Quercus coccifera* on rocky shelves. These plant communities are typical of the thermo-to meso-Mediterranean belt under semi-arid to dry Mediterranean climates, and reflect a strong edaphic control.

The vegetation of the Region of Murcia is structured along an altitudinal gradient into distinct bioclimatic belts, each characterized by specific floristic assemblages (Alcaraz et al., 1991, 2008). In the inframediterranean zone, restricted to coastal sectors and some inner slopes exposed to marine influence, the flora is shaped by arid conditions and frost-free winters, supporting open shrublands dominated by *Periploca angustifolia, Gymnosporia senegalensis* subsp. *europaea, Launaea arborescens*, and *Lycium intricatum*, with sparse occurrences of *Pinus halepensis* limited to shaded enclaves. Moving inland and upward into the thermomediterranean zone, mild winters with occasional frosts permit the persistence of thermophilous taxa, including *Chamaerops humilis*, *Osyris lanceolata*, *Asparagus albus*, *Withania frutescens*, and relic populations of *Tetraclinis articulata* in the Sierra de Cartagena; esparto grasslands and diverse thyme-dominated communities are widespread. The mesomediterranean zone, the most extensive altitudinal band, spans from approximately 400 to 1300 m and is characterized by colder winters and the retreat of thermophiles; vegetation is composed of *Macrochloa tenacissima* steppes, scattered *Pinus halepensis* woodlands, and sclerophyllous shrublands with *Quercus coccifera* and *Pistacia lentiscus*, while in moister sectors, *Quercus rotundifolia*, *Arbutus unedo*, *Viburnum tinus*, and *Quercus faginea* may occur. The supramediterranean zone, occupying high-elevation slopes and summits in the northwest and central mountains, experiences harsh winters that exclude many lowland species; vegetation is dominated by cushion-forming shrubs such as *Erinacea anthyllis* and *Genista longipes*, along with tree species like *Juniperus thurifera* and *Pinus nigra* subsp. *salzmannii*, and shrubs including *Berberis vulgaris*, *Rhamnus saxatilis*, and *Lonicera splendida*. Finally, the oromediterranean zone is confined to exposed, rocky crests above 1700 m in the Sierra Seca and Sierra de Taibilla, where tree cover becomes sparse and is restricted to *Juniperus communis* subsp. *hemisphaerica* and *Pinus nigra* subsp. *salzmannii*, interspersed with alpine grasslands and specialized shrubs such as *Genista longipes*, *Satureja intricata*, and *Thymelaea granatensis*, many of which are rare or endemic to this high-elevation context.

The riparian corridors of the Almadenes Canyon and the Quípar River, situated within the mesomediterranean bioclimatic belt near Cueva del Arco, support a remarkably diverse set of plant communities adapted to narrow valleys and frequently entrenched streambeds. The outer riparian zone hosts mature stands of *Populus alba, P. nigra,* and *Ulmus minor*, often associated with *Fraxinus angustifolia*, *Rubus ulmifolius* and *Coriaria myrtifolia*, as well as tamarisk groves (*Tamarix gallica*). Evergreen grasslands dominated by *Brachypodium phoenicoides* and open formations with *Imperata cylindrica* and *Saccharum* are also present. In the more hydrologically active inner zones, shrubby willows such as *Salix neotricha* occur alongside tall helophytes including *Typha domingensis* and *Schoenoplectus glaucescens.*

4. Materials and methods

4.1. Vertebrate fauna

A sample of macro- and mesofaunal remains was analysed (Table 2, Fig. 4). Taxonomic and anatomical identification of the assemblage was conducted using the comparative osteological collection from the University of Valencia. Indeterminate remains were initially classified based on bone type and weight, following established criteria (Blasco, 2011; Cáceres, 2002). Weight categories were defined as follows: very small (<5 kg), small (5–100 kg), medium (100–300 kg), and large (>300 kg), based on the average adult weight of each taxon represented.

To assess the overall composition of the assemblage, the Number of Identified Specimens (NISP), the Minimum Number of Individuals (MNI) and the Minimum Number of Elements (MNE) were calculated (Lyman, 1994, 2008) (Table 2). In this study, age-at-death determinations were carried out only for *Capra pyrenaica* (Pérez Ripoll, 1988; Serrano et al., 2004) and leporids. The age of *Oryctolagus cuniculus* was assessed based on epiphyseal fusion, following the methods proposed by Sanchis (2012) and Cochard (2004). Specimens were categorized into three age classes: neonatal, juvenile (up to five months), and adult (>9 months).

All bones were examined under a stereomicroscope (Nikon SMZ-10A) to identify taphonomic modifications. Diagnostic surface alterations were recorded to determine the origin of the assemblage. Non-anthropogenic modifications included tooth marks, fracture patterns, and digestive corrosion (e.g., Andrews, 1990; Binford, 1981; Domínguez-Rodrigo and Piqueras, 2003; Sala et al., 2012). Anthropogenic modifications included percussion marks (Vettese et al., 2020), cut marks (Binford, 1981; Pérez Ripoll, 1992; Shipman and Rose, 1983; Soulier and Costamagno, 2017), and burning (Stiner et al., 1995; Théry-Parisot et al., 2004). Fractures were analysed following Villa and Mahieu's (1991) criteria to distinguish between fresh and dry breakage, while morphotype classification was based on Real et al. (2022a).

Given the predominance of leporids in the assemblage, specific references were employed for their taphonomic analysis (Cochard et al., 2012; Hockett and Haws, 2002; Lloveras and Nadal, 2015; Lloveras et al., 2009, 2011; Rosado-Méndez et al., 2016; Pérez Ripoll, 1993).

Table 2
Taxonomic composition based on NISP (Number of Identified Specimens), MNI (Minimum Number of Individuals), and taphonomic data including cut-marks (CM), fracture marks (FM), burnt bones (BB), tooth marks (TM), digestions (D) and notches (N).

	Mousterian							Gravettian								
	NISP	% NISP	MNI	Anthropogenic		Non-anthropogenic		NISP	% NISP	MNI	Anthropogenic			Non-anthropogenic		
				CM	BB	TM	D				CM	FM	BB	TM	D	N
DETERMINATE	**300**	**41.8**	**12**					**516**	**49.7**	**22**						
Perissodactyla								**4**	**0.4**	**1**						
Equus ferus								4	0.4	1			1 (25 %)			
Artiodactyla	**16**	**2.2**	**4**					**36**	**3.5**	**4**						
Bos primigenius	1	0.1	1					1	0.1	1						
Cervus elaphus	2	0.3	1		1 (50 %)			3	0.3	1						
Capra pyrenaica	9	1.3	2	1 (11.1 %)			1 (11.1 %)	32	3.1	2	2 (6.2 %)	1 (3.1 %)		1 (3.1 %)		
Small size	3	0.4					2 (66.7 %)									
Small/medium size	1	0.1														
Carnivora	**1**	**0.1**	**1**					**3**	**0.3**	**1**						
Canidae	1	0.1	1													
Felis silvestris								3	0.3	1				1 (33.3 %)		
Lagomorpha	**283**	**39.4**	**7**					**473**	**45.6**	**16**						
Oryctolagus cuniculus	283	39.4	7		3 (1.1 %)	2 (0.7 %)	13 (4.6 %)	473	45.6	16			8 (1.7 %)		30 (6.3 %)	2 (0.4 %)
BY SIZE	**71**	**9.9**						**206**	**19.8**							
Very small size	3	0.4				1 (33.3 %)	1 (33.3 %)	7	0.7						1 (14.3 %)	
Small size	8	1.1		1 (12.5 %)	1 (12.5 %)		2 (25 %)	5	0.5							1 (20 %)
Small/medium size	53	7.4			7/ 13.2 %)		1 (1.9 %)	177	17.1		1 (0.6 %)		16 (04 %)		11 (6.2 %)	
Medium size	5	0.7			1 (20 %)			9	0.9			8 (88.9 %)	3 (33.3 %)	1 (11.1 %)		
Medium-large size								3	0.3							
Large size	2	0.3						5	0.5							
INDETERMINATE	**347**	**48.3**			**19 (5.5 %)**			**316**	**30.4**				**25 (8 %)**			
TOTAL	**718**		**12**	**2**	**32**	**3**	**20**	**1038**		**22**	**3**	**9**	**53**	**3**	**42**	**3**
%				**0.3**	**4.5**	**0.4**	**2.8**				**0.3**	**0.9**	**5.1**	**0.3**	**4.0**	**0.3**

4.2. Charcoal and seeds

Archaeobotanical remains, including wood charcoal and seeds, were manually recovered during excavation as well as through dry sieving of sediment. In addition, 14 sediment samples from Unit III—amounting to 56.5 L and primarily originating from Hearth 4 in spit 4—were processed using a flotation system equipped with 1 mm and 0.25 mm mesh screens to recover the heavy and light fractions, respectively. The taxonomic diversity and richness of the archaeological assemblage, particularly of the carpological component, may be underestimated due to the absence of samples from certain sub-units of Unit III. Sediment flotation was also conducted on Unit II; however, the analysis of these samples is still ongoing and is not addressed in this study. All manually recovered remains, along with both flotation fractions, were examined under a Leica M165C low-power stereomicroscope to identify wood charcoal fragments and non-woody elements such as seeds, fruits, scale bracts, stems, and leaves.

Charcoal analysis was based on the taxonomic identification of fragments to determine their botanical origin (Table 3, Figs. 5 and 6). Each specimen was manually fractured to produce diagnostic transverse, radial, and tangential sections, which were examined under a Leica DM6000 M optical microscope using brightfield, darkfield, and polarized light modes. No chemical treatment was applied, allowing for potential subsequent radiocarbon dating (Vernet et al., 1979). Anatomical features were compared with modern charred wood samples from the reference collection of the *Laboratori d'Arqueologia* at the University of Valencia and with specialized anatomical literature (Greguss, 1955, 1959; Schweingruber, 1990). Depending on the degree of anatomical resolution, identifications were made at the species, genus, family, or higher taxonomic levels (Table 3). Specific identifications and microphotographs (Figs. 5 and 6) were obtained using a Hitachi S-4800 scanning electron microscope (SEM) with a field emission gun (FEG) and a resolution of 1.4 nm at 1 kV, located at the Central Service for Experimental Research Support (SCSIE), University of Valencia. Taxon frequency was calculated as a percentage of the total number of identified fragments. These results provide insights into the woody taxa

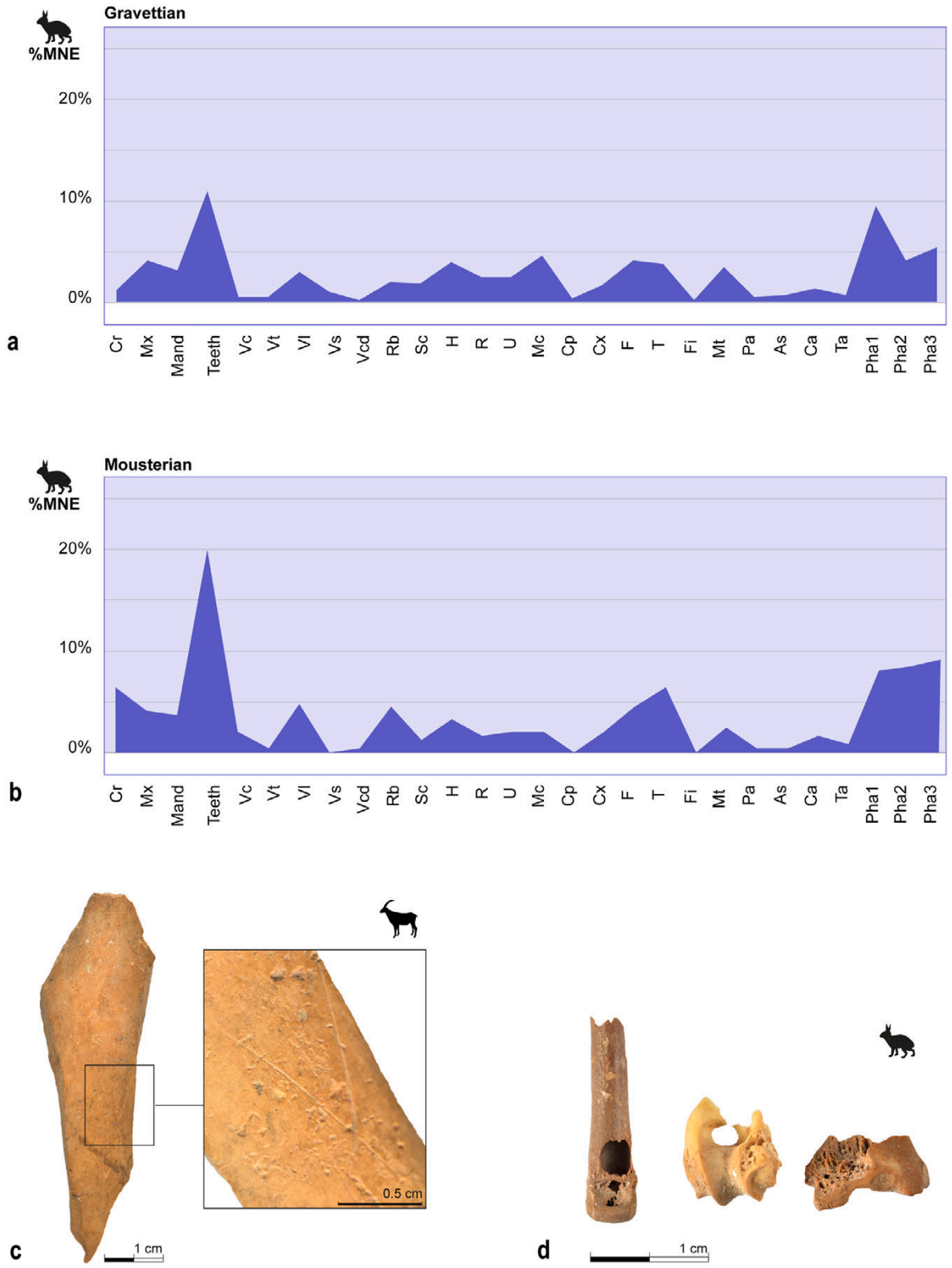

Fig. 4. Anatomical representation of leporid remains based on %MNE (Minimum Number of Elements) from the Gravettian (a) and the Mousterian (b). Example of anthropogenic modification (cut-mark) on a *Capra pyrenaica* humerus (c), and non-anthropogenic modification (digestion marks) on *Oryctolagus cuniculus* remains (d), both from the Mousterian. Abbreviations: Cr (cranium), Mx (maxilla), Mand (mandible), Vc (cervical vertebra), Vt (thoracic vertebra), Vl (lumbar vertebra), Vs (sacrum vertebra), Vcd (caudal vertebra), Rb (rib), Sc (scapula), H (humerus), R (radius), U (ulna), Mc (metacarpal), Cp (carpal), Cx (coxal), F (femur), T (tibia), Fi (fibula), Mt (metatarsal), Pa (patella), As (astragalus), Ca (calcaneus), Ta (tarsal), Mtp (metapodia), Pha (phalanx).

Table 3
Frequencies of the carpological remains from Mousterian Unit III. Cueva del Arco (fr. = fragment)

	Spit	1		2		3		4		Hearth 4		7		9		10		11		
	Volume (L)	–	–	–	–	0.5		16		40		–	–	–	–	–	–	–	–	
	Vol Flot (mL)	–	–	–	–	46		30.7		199		–	–	–	–	–	–	–	–	
Taxa	**Remain type**	**N**	**%**	**N**	**%**	**N**	**%**	**N**	**%**	**N**	**%**	**N**	**%**	**N**	**%**	**N**	**%**	**N**	**%**	**TOTAL**
Juniperus phoenicea type	Leaf					5	36	3	5.6	2	0.6									10
	Leafy Stem					3	21	3	5.6	3	0.9									9
Juniperus	Endocarp fr.									1	0.3			1	25					2
Pinus	Cone scale fr.	5	71.4	5	83.3	1	7.1	4	7.4	5	1.5	1	50							21
Pinus nigra type	Cone scale fr.	1	14.3	1	16.7															2
Pinus halepensis type	Cone scale fr.	1	14.3					1	1.9											2
Macrochloa tenacissima	Rhizome									25	7.4	1	50							26
	Leaf									1	0.3									1
cf. *Macrochloa tenacissima*	Rhizome															1	16.7			1
Celtis	Uncharred endocarp fr.							7	13	159	46.9			3	75	5	83.3	2	100	176
	Charred endocarp fr.							1	1.9	75	22.1									76
Buglossoides arvensis	Uncharred nutlet					1	7.1	22	40.7	9	2.7									32
	Uncharred nutlet fr.					2	14	2	3.7	5	1.5									9
	Charred nutlet							1	1.9											1
cf. *Neatostema apulum*	Uncharred nutlet							1	1.9	3	0.9									4
	Uncharred nutlet fr.									1	0.3									1
Boraginaceae	Uncharred nutlet							3	5.6											3
cf. Asteraceae	Seed					1	7.1													1
Galium	Seed									1	0.3									1
Monocotyledon	Stem							2	3.7	11	3.2									13
Dicotyledon	Leaf fr.							1	1.9											1
Indeterminable	Seed					1	7.1	2	3.7	1	0.3									4
	Seed fr.							1	1.9	6	1.8									7
	Endocarp fr.									26	7.7									26
	Parenchyme									3	0.9									3
	Bark									1	0.3									1
	Indeterminate									1	0.3									1
	TOTAL	7		6		14		54		339		2		4		6		2		434

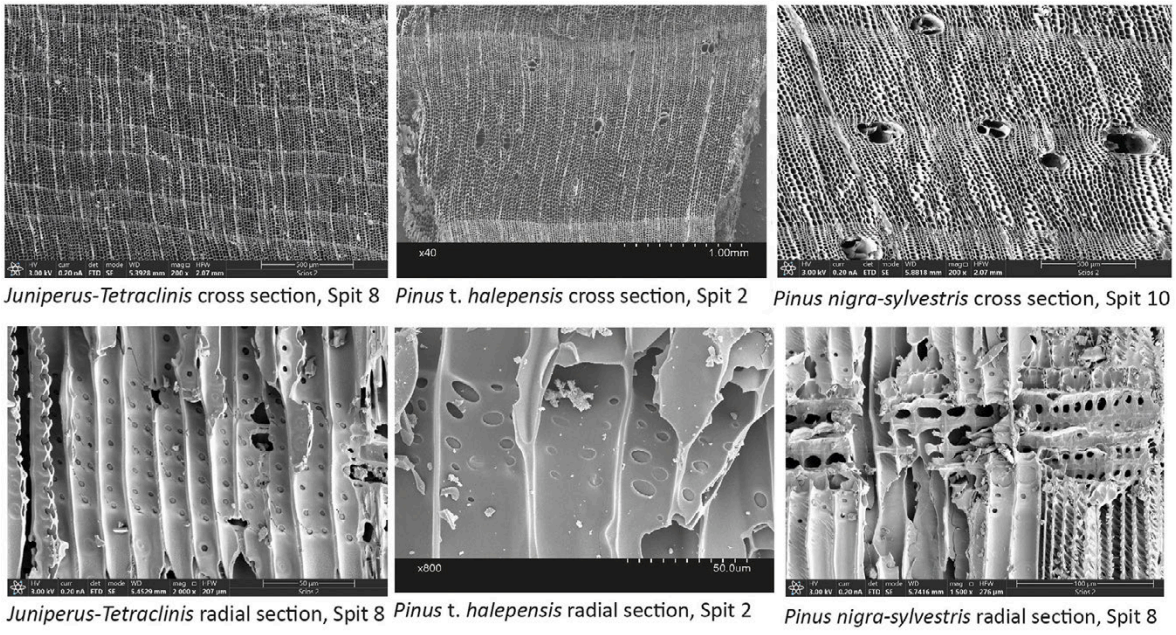

Fig. 5. SEM photographs of gymnosperm taxa identified in charcoal samples from Cueva del Arco.

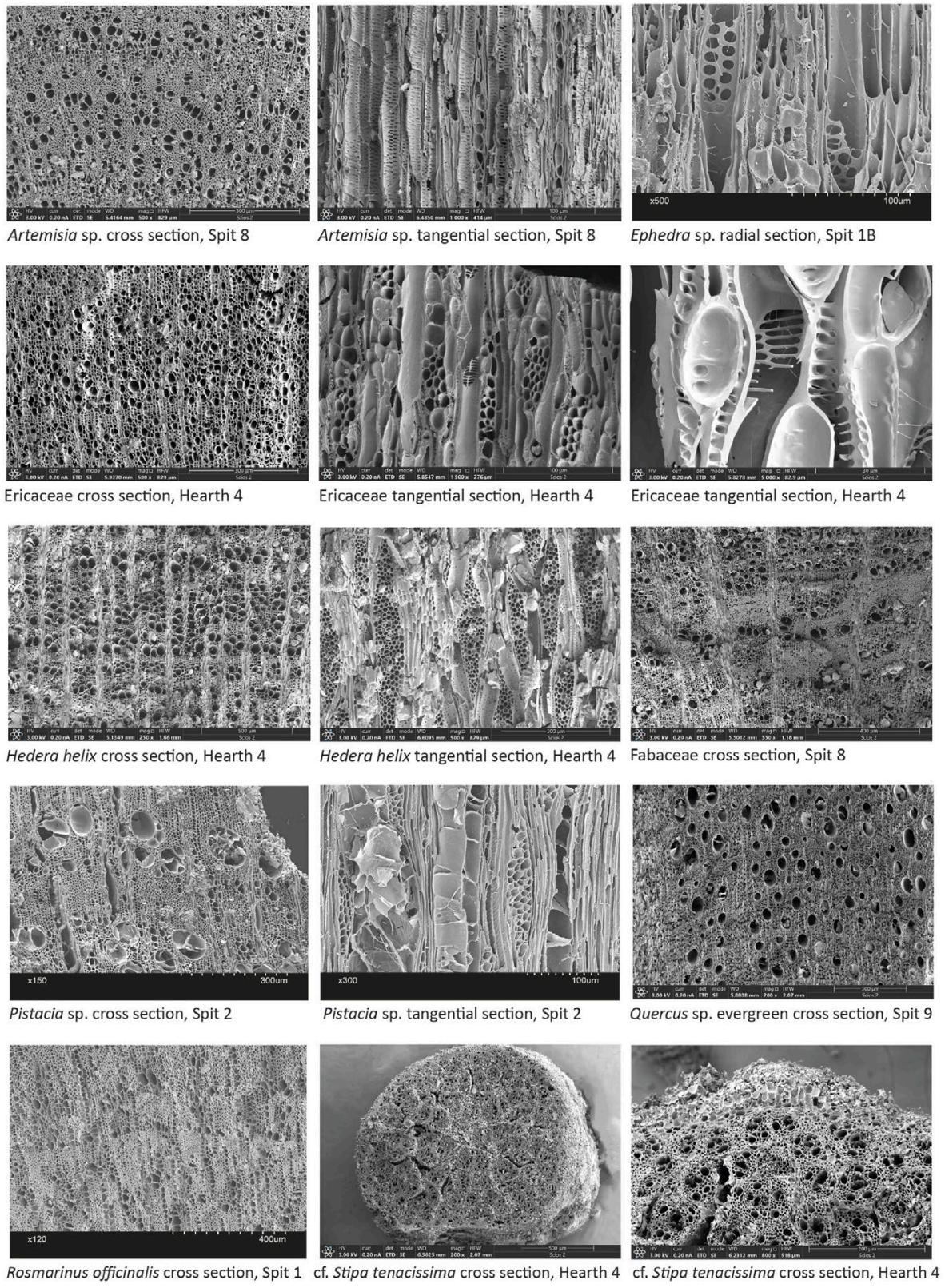

Fig. 6. SEM photographs of angiosperm taxa identified in charcoal samples from Cueva del Arco.

exploited for fuel and serve as a reliable proxy for reconstructing past vegetation (Chabal, 1997) (Fig. 7).

In Unit II, 360 charcoal fragments from three Gravettian spits (1, 1B, and 2), including Hearth H2, were analysed (Román et al., 2024). In Unit III, 1123 charcoal fragments of Mousterian chronology were studied, with 250 concentrated in the large combustion structure H4 and 827 distributed across various spits. Five spits (3, 4, 8, 9, and 10) yielded statistically representative samples, whereas spits 5, 6, and 7 produced fewer remains; data from the latter were thus treated qualitatively in terms of taxon presence/absence.

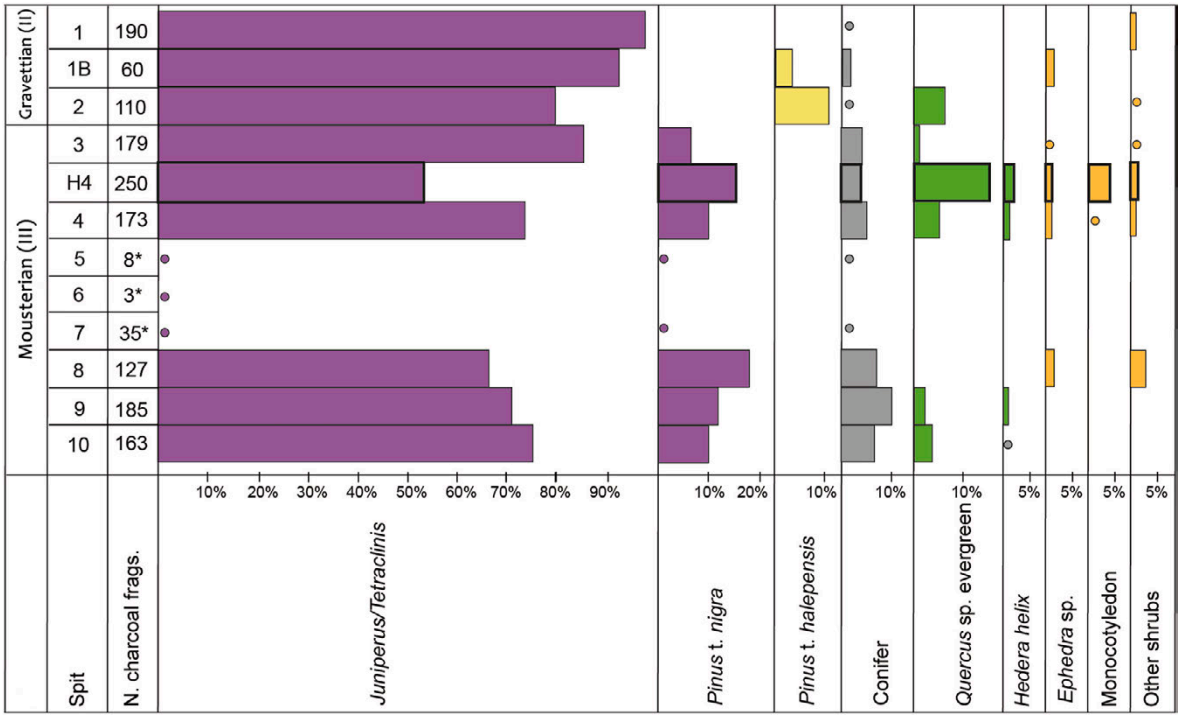

Fig. 7. Charcoal diagram from Cueva del Arco (*spits with a statistically non-significant number of charcoal fragments are indicated with *; only presence was considered*). "Other Shrubs" include *Artemisia*, *Ephedra*, Fabaceae, and Ericaceae.

Carpological remains were taxonomically identified using the modern seed and fruit collection of the *Laboratori d'Arqueologia* at the University of Valencia, supplemented by relevant bibliographic references (Cappers et al., 2006; Sabato and Peña-Chocarro, 2021; Torroba Balmori et al., 2013) (Fig. 8). Photographs were taken using Leica Application Suite V3 and Helicon Focus 3.10.3 software. In Unit III, 434 carpological remains—including seeds, scale bracts, leaves, and rhizomes—were recovered from nine spits (1, 2, 3, 4, 7, 9, 10, and 11), with 339

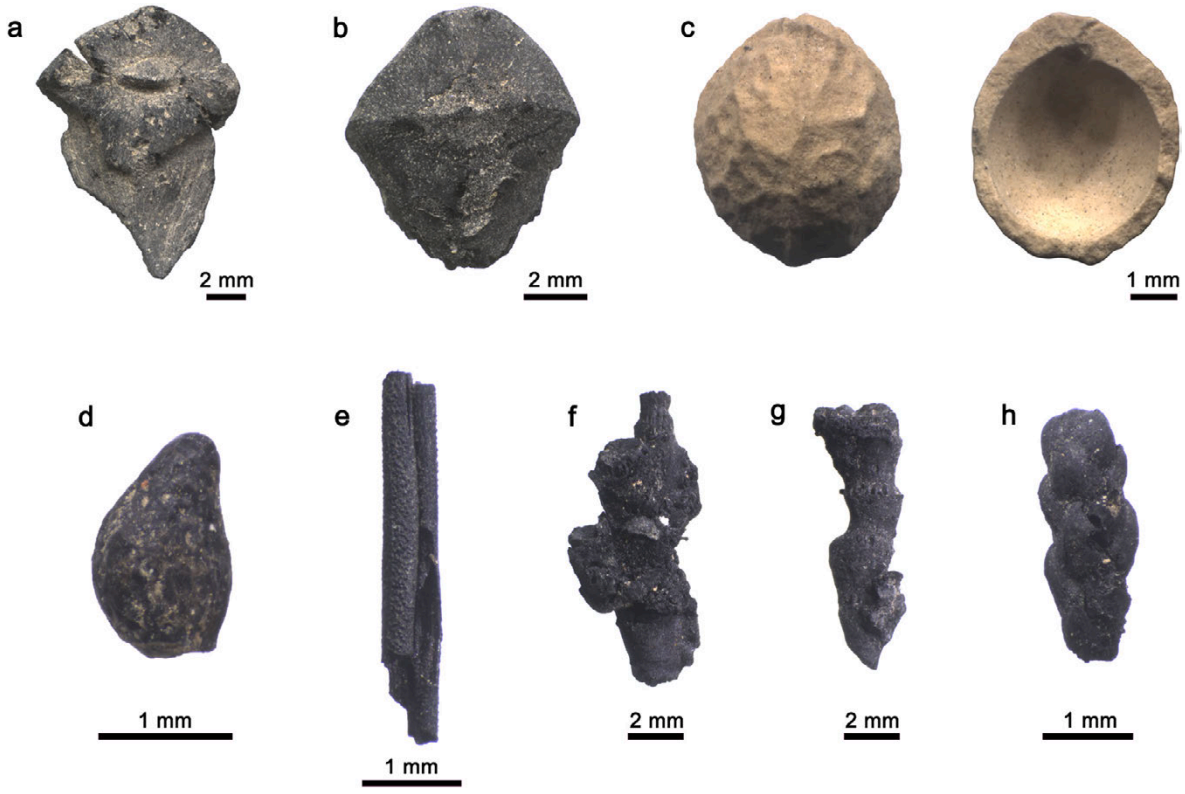

Fig. 8. Plant macroremains from Mousterian layers of Cueva del Arco: (a) *Pinus cf. halepensis* cone bract, (b) *Pinus tp. nigra* cone bract, (c) *Celtis* sp., (d) *Buglossoides arvensis*, (e) *Macrochloa tenacissima* leaf, (f, g) rhizomes, and (h) *Juniperus phoenicea*-type leaves.

concentrated in Hearth 4 (Table 3). In Unit II, 43 carpological remains had previously been recovered and analysed (Román et al., 2024), although the overall assemblage is larger and currently under study.

4.3. Pollen analysis

Pollen sampling was conducted on a vertical stratigraphic profile during the 2017 and 2021 fieldwork seasons, following established protocols for archaeological contexts (Girard, 1975). Sediment samples (Arc-Sed) were obtained from a single archaeological section located in the northeastern sector of the site, specifically in excavation square E−18 (Angelucci, 2002). To reduce the risk of contamination or recent bioturbation, the exposed surface layer was removed to a depth of 10–15 cm prior to sampling.

A set of coprolite samples (Arc-Cop), recovered during the 2017 field season, was also analysed for pollen, and formerly published (Román et al., 2024). These samples originate from Unit II (squares C-18 and C-19; Fig. 3). Based on their morphological characteristics, the coprolites are likely to derive from medium- and/or small-sized mammals, consistent with the faunal assemblage identified in this level (Román et al., 2024). Coprolites of hyena origin were excluded due to morphological discrepancies, following the criteria proposed by Carrión et al. (2001, 2007, 2008, 2018a, 2019c) and Ochando et al. (2020a, 2024).

Following weighing of the sediment and coprolite samples (Table 4), palynomorphs were extracted using the Classical Chemical Method (Erdtman, 1969; Dimbleby, 1985), incorporating modifications introduced by Girard and Renault-Miskovsky (1969). To ensure quality control during laboratory processing, three *Lycopodium* spore tablets (batch No. 177745.500) were added to each sediment sample and one tablet (batch No. 710961.500) to each coprolite sample. After chemical treatment, samples were mounted in liquid paraffin for microscopic analysis. Palynological identifications were carried out under a light microscope at 400 × and 1000 × magnification using reference collections from the Department of Plant Biology (University of Murcia) and the Department of Environmental Biology (Sapienza University of Rome). Pollen types belonging to Asteroideae, Cichorioideae, *Centaurea*, and Lamiaceae, as well as spores and non-pollen palynomorphs (NPPs), were excluded from the total pollen sum due to potential overrepresentation related to differential preservation and taphonomic biases (Havinga, 1984; Carrión et al., 2009). Pollen diagrams were generated using Tilia Graph software (version 1.7.16) and subsequently redrawn with CorelDRAW (versión 24.0.0.301) (Figs. 9–11).

5. Faunal assemblages

A total of 718 faunal remains were analysed from Mousterian Unit

Table 4
Summary of palynological features of Arco Cave samples

Sample	Unit	Square	Material bag	Gross Weight (g)	Net Weight (g)	Concentration (grains/g)	Indeterminable (%)	[a]Pollen sum	Pollen sum	Number of taxa (Pollen)	Spores sum
Sediment Samples											
Arc-Sed1	II	E−18	6	80.80	40.50	1753	2.60	269	275	16	13
Arc-Sed2	II	E−18	24	35.30	13.80	84,289	8.10	408	459	25	13
Arc-Sed3	II	E−18	23	35.20	18.10	29,584	7.71	350	413	24	16
Arc-Sed4	II	E−18	22	40.00	17.90	22,977	12.13	404	450	28	62
Arc-Sed5	II	E−18	21	35.50	17.50	15,713	13.75	269	291	21	22
Arc-Sed6	II	E−18	20	40.10	21.60	5998	8.39	298	330	16	24
Arc-Sed7	III	E−18	19	35.40	18.80	12,775	20.00	210	224	13	20
Arc-Sed8	III	E−18	18	35.70	18.00	16,234	10.99	273	304	17	15
Arc-Sed9	III	E−18	15	41.20	20.10	8164	20.60	214	259	22	43
Arc-Sed10	III	E−18	14	35.00	16.20	9277	21.88	224	248	21	5
Arc-Sed11	III	E−18	13	39.90	18.00	3473	27.81	187	194	14	30
Arc-Sed12	GFU	E−18	2	70.30	30.20	4460	5.58	269	302	23	7
Arc-Sed13	GFU	E−18	10	30.70	12.50	9873	20.41	245	259	15	4
Arc-Sed14	GFU	E−18	3	35.20	20.00	5926	15.92	201	270	23	16
Arc-Sed15	GFU	E−18	0	77.40	39.70	22,937	1.08	279	294	15	6
							TOTAL	**4100**	**4572**		**296**
Coprolites											
Arc-Cop1	II	C-19	129		2.02	7020	1.47	201	211	21	12
Arc-Cop2	II	C-19	130		10.74	2914	0.48	201	207	10	11
Arc-Cop3	II	C-19	134		0.84	23,843	1.49	201	203	9	1
Arc-Cop4	II	C-18	135		3.83	4137	0.99	191	205	15	18
Arc-Cop5	II	C-18	136		0.41	20,075	2.81	142	142	17	4
							TOTAL	**936**	**968**		**46**

[a] Asteroideae, Cichorioideae, Centaurea, and Lamiaceae excluded.

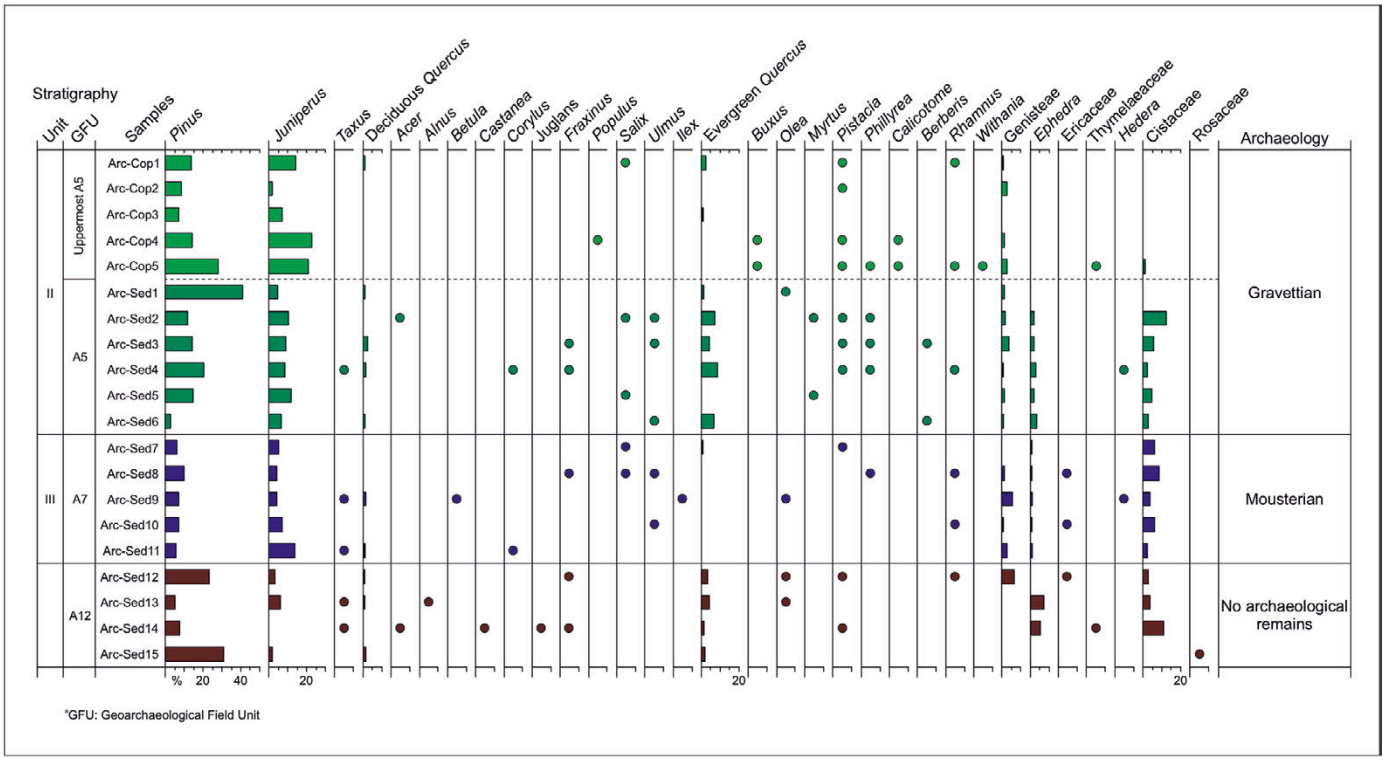

Fig. 9. Percentage pollen diagram of woody taxa from sediment and coprolite samples from Cueva del Arco. Dots represent values < 3 %.

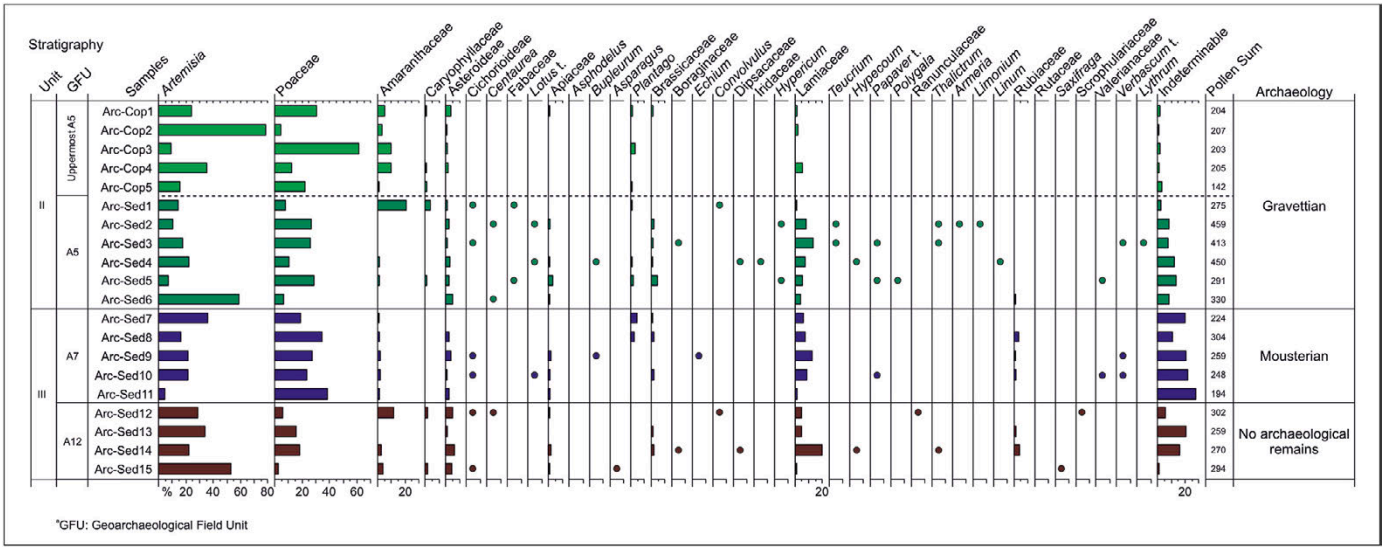

Fig. 10. Percentage pollen diagram of non-arboreal taxa from sediment and coprolite samples from Cueva del Arco. Dots represent values < 3 %.

III, of which 41.8 % were taxonomically and anatomically identified, and 9.9 % were assigned to anatomical groups only. The remaining 48.3 % were indeterminate (Table 2). Among the identified remains, Leporidae are the most abundant, followed by ungulates and carnivores. Additionally, 71 specimens were classified based solely on size. Leporids account for 283 remains (39.4 % of the total), representing a minimum of seven individuals: one neonate, three individuals under five months, and three adults. All major anatomical regions are represented, with particular abundance of cranial elements, long bones (femur, tibia), and extremities (Fig. 4). Ungulates are mainly represented by *Capra pyrenaica* (n = 9), with most remains corresponding to the postcranial limb: phalanges (2), metapodials (2), femur (1), tibia (1), carpus (1), sesamoid (1), and one deciduous incisor. At least two individuals are present—one juvenile and one probable adult. *Bos primigenius* and *Cervus elaphus* are represented by isolated dental and postcranial fragments. *Cervus* includes two poorly preserved molar fragments, and *Bos* is represented by a proximal metacarpal fragment. Carnivores are minimally present, with a single canid patella recorded, complete and unmodified.

The assemblage exhibits significant diagenetic alteration, including root etching, manganese staining, concretions, and surface erosion. Fragmentation is high (85.1 %), with complete bones representing 14.9 % of the assemblage—96.2 % of them from leporids. These complete remains consist mainly of isolated teeth, phalanges, metapodials, and vertebrae, along with two *Capra* bones (phalanx and sesamoid) and the

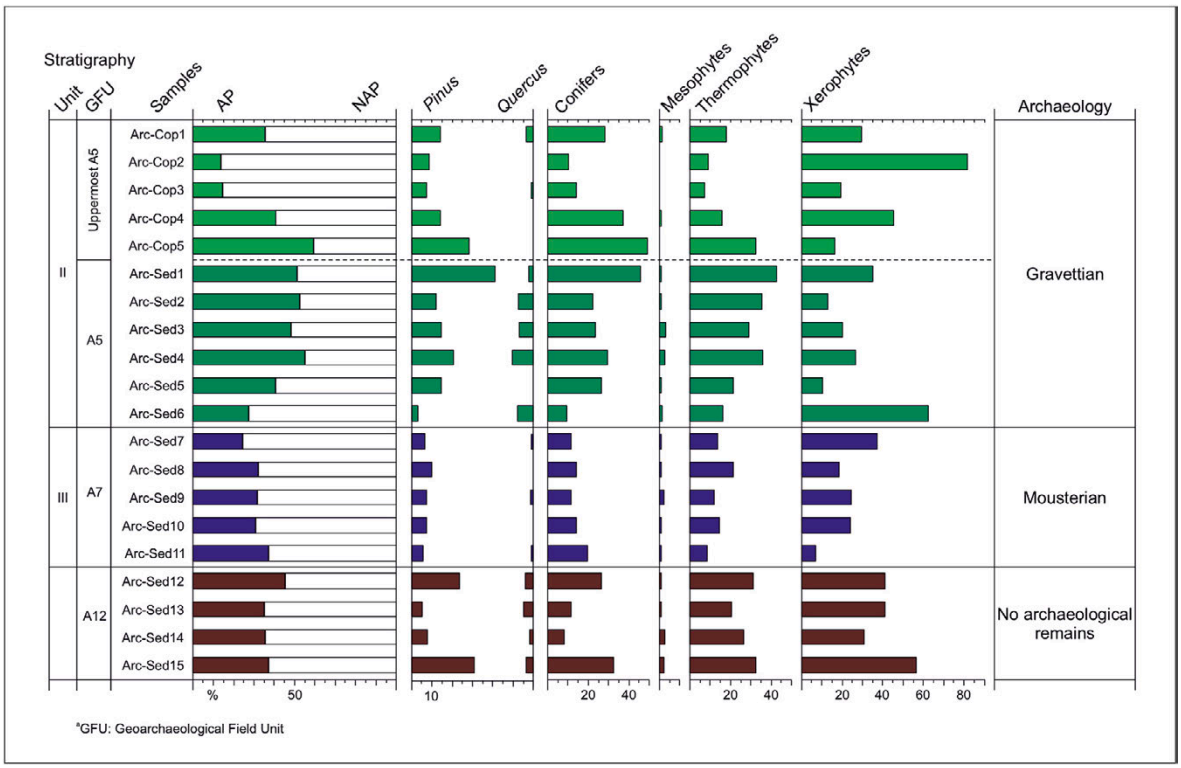

Fig. 11. Composite pollen diagram showing ecological groups and the main pollen contributors from sediment and coprolite samples from Cueva del Arco.

canid patella. Excluding indeterminate specimens, fracture types include fresh (13.2 %), dry (26.5 %), mixed (3.6 %), and indeterminate (56.6 %). A total of 56 modifications were recorded (4.7 % anthropogenic; 3.1 % non-anthropogenic, based on total number of bones) (Table 2). Human modifications include 32 burnt remains and two with cut-marks: one incision on a *Capra* humerus fragment and one incision/scraping on a small rib fragment (Fig. 4c). Non-anthropogenic alterations include three notches attributed to carnivore tooth action and moderate digestive corrosion on ten *Oryctolagus cuniculus* bones (Fig. 4d) and several *Capra* fragments of various sizes.

A total of 1038 faunal remains were recorded from the Gravettian Unit II, of which 49.7 % were identified to taxonomic or anatomical level (Table 2). Leporids dominate the assemblage, comprising 91.7 % of the identified remains. Leporid skeletal representation is broad (Fig. 4), with cranial and long bones (maxilla, femur, humerus, tibia) exceeding 50 %, followed by mandible, cranium, radius, and ulna (30–40 %), and scapula, coxal, and sacrum (~20 %). Axial bones, carpals, tarsals, and phalanges are underrepresented (<20 %). A minimum of 16 individuals was identified: one juvenile, five subadults, and ten adults. Among ungulates, *Capra pyrenaica* is the most frequent (6.2 % of identified remains), represented by cranial elements, long bones, calcaneus, and astragalus. Axial and pelvic elements are absent. *Equus ferus* is represented by a molar, coxal, tibia fragment, and a metapodial; *Cervus elaphus* by a hemimandible and radius; and *Bos primigenius* by a tooth fragment. The only carnivore is *Felis silvestris*, represented by a humerus fragment, an ulna epiphysis, and a third phalanx. One adult individual is estimated for each of the large mammals and carnivore taxa; *Capra* includes one infant (1–2 years) and one adult.

Only 17.1 % of bones are complete. For medium-sized animals, only a few teeth and one phalanx are complete. Fresh or indeterminate fractures predominate, particularly on *Capra*-sized specimens, with frequent diaphyseal and articular breakage on mandibles, calcanei, astragali, and phalanges. Leporid remains are 42.6 % complete; complete elements include phalanges, metapodials, cranial and axial bones, and non-fused long bone epiphyses. Fractures were classified as indeterminate (42.2 %), fresh (28.9 %), dry (28 %), and mixed (0.9 %), with fresh breaks especially common on long bones, metapodials, and phalanges. Thermal alteration is the most frequent modification (5.1 %), affecting up to 33.3 % of medium-sized fauna. Charring accounts for 79.2 % of these cases, and often affects the entire bone surface (75.5 %). Anthropogenic modifications are rare (1.2 %) and include nine percussion marks (eight flakes and one notch on a *Capra* tibia) and three cut-marks: one on an unidentified long bone (defleshing) and two on *Capra* bones (skinning and disarticulation). Non-anthropogenic alterations (4 %) are mainly digestive corrosion, primarily affecting leporid bones <20 mm. These are characterized by polished surfaces, rounded edges, and porous trabecular tissue. Rare modifications (0.3 %) include scoring on long bones and a *Capra* calcaneus, as well as partial epiphyseal consumption and corrosion on a *Felis silvestris* humerus. Indeterminate notches were found on long and pelvic bones of small to medium-sized animals, possibly due to non-human predator activity.

6. Paleobotanical record

6.1. Charcoal and carpological remains

The charcoal assemblage is dominated by coniferous taxa, particularly *Juniperus/Tetraclinis* and *Pinus*. In the Mousterian levels (Unit III), *Pinus nigra*-type is present, while in the Upper Palaeolithic (Unit II), only *P. halepensis*-type has been identified. Together, conifers account for between 67 % and 97 % of the assemblage (Fig. 7). Notably, Hearth 2 (Unit II), which is not included in the charcoal diagram, yielded 100 % juniper wood. Due to their highly similar anatomical structure, it is not possible to distinguish between juniper and *Tetraclinis* wood in the Cupressaceae family. However, the identification of squamiform leaf fragments is more consistent with juniper species, likely *J. phoenicea*-type, although the potential coexistence of both genera cannot be ruled out, as they share similar ecological niches. Shrub taxa occur at low frequencies but are consistent with a steppe-like landscape. Identified taxa include *Artemisia*, *Ephedra*, Fabaceae, Ericaceae, and

Monocotyledons, including both stems and rhizomes. These shrubs are slightly more abundant in the upper part of the sequence and in Hearth 4.

Anatomical characteristics of pine charcoal from Unit III (Mousterian)—including fenestriform pits in the cross-fields—indicate a mountainous origin, corresponding to species adapted to cold conditions. These taxa currently thrive under supramediterranean to oromediterranean climates (8–4 °C annual mean temperature, 400–1000 mm rainfall) (Blanco-Castro et al., 1997). In contrast, pine remains from Unit II (Gravettian) display features such as multiple small pinoid-like pits per cross-field, typical of thermophilous species like *Pinus halepensis*. Although species like *P. pinea* or *P. pinaster* cannot be excluded, the presence of pine cone bracts strongly suggests *P. halepensis*. Indeed, low but consistent presence of mesophilic elements, such as *Quercus*, *Pistacia*, and *Hedera helix*, suggest locally milder and more humid conditions, possibly related to riparian zones nearby (Fig. 2). The ivy, being a climbing species, may reflect incidental gathering along with wood from supporting trees. The sporadic presence of *P. halepensis* also points to the function of this locality as a climatic refuge.

Spit 4 revealed a well-preserved combustion structure (Hearth 4) with a dense concentration of fragile plant remains, many with preserved external morphology. This hearth contains nearly all taxa identified throughout the sequence, indicating broad exploitation of available plant resources. Monocotyledon stems and esparto (*Macrochloa tenacissima*) rhizomes are particularly noteworthy—not for their frequency (Fig. 7)—but for their near-exclusive presence in this context. This pattern suggests either (i) specific processing of these plants or (ii) the use of mixed fuel types, both of which imply advanced fire control and resource management. These remains are also present in Unit II.

In total, 14 carpological taxa were identified in Unit III (Table 3; Fig. 8), including a minimum of six species: Boraginaceae, *Buglossoides arvensis*, Dicotyledons, *Celtis*, Asteraceae, *Neatostema apulum*, *Galium*, *Juniperus*, *Juniperus phoenicea*, Monocotyledons, *Pinus halepensis*, *Pinus*, *Pinus nigra*, and *Macrochloa tenacissima*. Taxonomic diversity is highest in spit 4 and Hearth 4, as observed in the charcoal assemblage. *Celtis* endocarps—both carbonized and uncharred—dominate the carpological assemblage, with a total of 252 fragments, most of which are concentrated in Hearth 4. Both preservation types have been identified; however, charred remains are primarily associated with the hearth, while uncharred remains are more dispersed and also present within the combustion structure. The presence of uncharred remains could be explained by their falling among the ashes or at the margins of the hearth, preventing full combustion, or by their deposition after the fire had extinguished. Lastly, we cannot entirely rule out the misidentification of the preservation state of some remains, as *Celtis* endocarps do not blacken when charred but instead turn grey or white (Miller, 2003), although this color-based criterion has been applied in their classification.

Buglossoides arvensis nutlets are the second most abundant (42 specimens). The mineral composition of these diaspores likely favoured their preservation (Cowan et al., 1997; Pustovoytov and Riehl, 2006), although both taxa are also represented by charred remains. Twenty-five fragments of pine cone bracts were recovered, attributed to *Pinus halepensis* and *P. nigra*, mostly from the upper spits of Unit III (Table 3). Additional bracts, including *P. halepensis*, were recorded in Unit II. Among non-woody vegetative remains, *Macrochloa tenacissima* rhizomes (26 fragments) are most notable and mainly associated with Hearth 4 (Table 3). Leaves attributed to *Juniperus phoenicea* are also present.

6.2. Pollen and spores

6.2.1. Sediment samples

A total of 26 sediment samples from Units I, II, III, and GFU-A12 were analysed, of which 15 yielded palynological content (Arc-Sed1 to Arc-Sed15), while the remaining eleven were sterile, with this sterility affecting samples from Level I and some from Level III. A total of 4868 palynomorphs were identified. The percentage of indeterminable grains remained below 28 % (Table 4), and overall preservation was considered good. The number of pollen types per sample ranged from 13 to 28, with a total of 68 taxa identified across the assemblage. Pollen concentration values varied from 1753 to 84,289 grains per gram of sediment. Pollen diagrams were constructed, distinguishing between arboreal pollen (AP) and non-arboreal pollen (NAP), and are presented in Figs. 9 and 10. A synthetic diagram summarising the main taxa and their corresponding ecological groups is also provided (Fig. 11). The conifer group includes *Pinus*, *Juniperus*, and *Taxus*. Mesophilous taxa are represented by deciduous *Quercus*, *Acer*, *Alnus*, *Betula*, *Corylus*, *Castanea*, *Juglans*, *Fraxinus*, *Salix*, *Ulmus*, *Ilex*, and Rosaceae. Thermophilous taxa include *Pinus*, evergreen *Quercus*, *Buxus*, *Olea*, *Pistacia*, *Myrtus*, *Phillyrea*, *Ephedra fragilis*, Ericaceae, and Cistaceae. Xerophytes are represented by *Artemisia*, Amaranthaceae, *Ephedra*, and *Teucrium*.

In the basal GFU-A12 (Arc-Sed15 to Arc-Sed12: Figs. 9–11) the pollen spectra show a clear dominance of non-arboreal pollen (NAP), comprising 55–65 % of the assemblage. This is mainly due to high percentages of *Artemisia* (22–53 %), *Poaceae* (3–18 %), and Amaranthaceae (3–12 %). Notably, this interval also contains the highest frequencies of Lamiaceae in the sequence. Other frequently represented herbaceous taxa include Asteroideae, Rubiaceae, Apiaceae, Brassicaceae, and Caryophyllaceae. Additional NAP elements such as Cichorioideae, *Centaurea*, *Asparagus*, Boraginaceae, *Convolvulus*, Dipsacaceae, *Hypecoum*, Ranunculaceae, *Thalictrum*, Saxifragaceae, and Scrophulariaceae also appear. Arboreal pollen (AP) includes *Pinus* (5–31 %) and evergreen *Quercus* (1–4 %). *Ephedra* reaches its maximum concentration in sample Arc-Sed13 (>7 %). Other AP elements with notable values include Cistaceae (<11 %), Genisteae (7 %), and *Juniperus* (>6 %). Additional AP taxa include *Taxus*, deciduous *Quercus*, *Acer*, *Alnus*, *Castanea*, *Juglans*, *Fraxinus*, *Olea*, *Pistacia*, *Rhamnus*, Ericaceae, Thymelaeaceae, and Rosaceae.

Mousterian Unit III (Arc-Sed11 to Arc-Sed7: Figs. 9–11) is characterised by high NAP percentages, reaching up to 76 %, with notable abundances of *Poaceae* (19–39 %) and *Artemisia* (4–36 %). These are accompanied by Amaranthaceae, Asteroideae, Apiaceae, *Plantago*, Brassicaceae, Lamiaceae, and Rubiaceae. Other herbaceous components include Cichorioideae, *Lotus*, *Bupleurum*, *Echium*, Valerianaceae, and *Verbascum*. Among AP taxa, *Juniperus* (4–14 %), *Pinus* (5–10 %), Cistaceae (2–9 %), and Genisteae (1–6 %) are particularly well represented. Deciduous *Quercus* and *Ephedra* are consistently present throughout this sequence. Additional arboreal taxa such as evergreen *Quercus, Taxus*, *Betula*, *Corylus*, *Fraxinus*, *Salix*, *Ulmus*, *Ilex*, *Olea*, *Pistacia*, *Phillyrea*, *Rhamnus*, Ericaceae, and *Hedera* appear sporadically.

In the lower half of Upper Paleolithic Unit II (Arc-Sed6 to Arc-Sed5 Figs. 9–11), NAP dominates (59–73 %), except in Arc-Sed4 where it decreases to 45 %. In contrast, the upper half (Arc-Sed4 to Arc-Sed1) shows a notable increase in AP values (51–53 %), except for Arc-Sed3, where AP accounts for 48 %. *Artemisia* (7–59 %), *Poaceae* (7–29 %), and Brassicaceae (1–5 %) are dominant within NAP, along with Amaranthaceae, Caryophyllaceae, Asteroideae, *Centaurea*, Fabaceae, *Lotus*, Apiaceae, *Bupleurum*, *Plantago*, Dipsacaceae, Iridaceae, *Hypericum*, *Hypecoum*, *Papaver*, *Polygala*, *Linum*, Rubiaceae, and Valerianaceae. In AP, the most abundant taxa are *Pinus* (3–21 %), *Juniperus* (7–12 %), evergreen *Quercus* (7–9 %), and Cistaceae (2–5 %). Other frequent elements include *Taxus*, deciduous *Quercus*, *Corylus*, *Fraxinus*, *Salix*, *Ulmus*, *Myrtus*, *Pistacia*, *Phillyrea*, *Berberis*, *Rhamnus*, Genisteae, *Ephedra*, and *Hedera*.

In the upper half of Unit II, Cistaceae reaches its highest representation (12 %, Arc-Sed2). The most distinctive pattern is the dominance of *Pinus* (12–41 %), *Juniperus* (5–10 %), and evergreen *Quercus* (up to 7 %), while Genisteae does not exceed 4 %. AP also includes deciduous *Quercus*, *Acer*, *Fraxinus*, *Salix*, *Ulmus*, *Olea*, *Myrtus*, *Pistacia*, *Phillyrea*, *Berberis*, and *Ephedra*. NAP in this phase remains rich, with *Poaceae* (8–27 %) and *Artemisia* (11–18 %) being most frequent. Amaranthaceae reaches its peak here (21 %, Arc-Sed1). Other common herbaceous taxa

include Caryophyllaceae, Asteroideae, Cichorioideae, *Centaurea*, Fabaceae, *Lotus*, Apiaceae, *Plantago*, Brassicaceae, Boraginaceae, *Convolvulus*, *Hypericum*, Lamiaceae, *Teucrium*, *Papaver*, *Thalictrum*, *Armeria*, *Limonium*, *Verbascum*, and *Lythrum*.

6.2.2. Coprolite samples

A total of five coprolite samples from Unit II were studied for pollen (Arc-Cop1 to Arc-Cop5: Figs. 9–11) (Román et al., 2024). In total, 1014 palynomorphs were identified, with less than 3 % classified as indeterminable (Table 4). The number of pollen types per sample ranges from 9 to 21, with a cumulative total of 28 taxa identified. Pollen concentration values vary between 2914 and 23,843 grains/g (Table 4). Pollen diagrams include arboreal pollen (AP), non-arboreal pollen (NAP), and a synthetic summary of major taxa and ecological groups. The conifer component includes *Pinus* and *Juniperus* (Fig. 9). Mesophilous taxa are represented by deciduous *Quercus*, *Populus*, and *Salix*. Thermophilous taxa include *Pinus*, evergreen *Quercus*, *Buxus*, *Pistacia*, *Phillyrea*, *Calicotome*, *Withania*, and Cistaceae. Xerophytes include *Artemisia* and Amaranthaceae. NAP is predominant in most coprolites, exceeding 86 %, except in Arc-Cop5, where it decreases to 41 %. The most distinctive features of the assemblage include the high proportions of *Artemisia* (9–76 %), *Poaceae* (4–61 %), and Amaranthaceae (1–10 %), while *Plantago* remains below 4 % (Fig. 10). Additional NAP elements include Asteroideae, Caryophyllaceae, Apiaceae, Brassicaceae, *Coris*, and Lamiaceae. Among AP, *Pinus* (7–28 %) and *Juniperus* (2–23 %) are the most abundant. Ecologically relevant occurrences also include evergreen *Quercus*, *Pistacia*, and Genisteae, along with lower but consistent frequencies of deciduous *Quercus*, *Populus*, *Salix*, *Buxus*, *Phillyrea*, *Calicotome*, *Withania*, *Rhamnus*, Thymelaeaceae, and *Cistus*. Fungal spores, algae, bryophytes, pteridophytes, and other non-pollen palynomorphs (NPPs) are scarce throughout the assemblage.

7. Discussion

7.1. Paleolithic vegetation landscapes

The pollen spectra are generally co-dominated by several of the main pollen contributors—*Pinus*, *Juniperus*, *Artemisia*, and Poaceae (Figs. 9–11). Exceptions include Arc-Cop2 and Arc-Cop3 (dominated exclusively by *Artemisia* and Poaceae, respectively), Arc-Sed1 (*Pinus*, Amaranthaceae), and Arc-Sed6 (*Pinus*). Overall, the pollen spectra reflect the occurrence of a diverse assemblage of trees, shrubs, and herbs, including broad-leaved and Mediterranean species, conifers, and xerothermophytes (Fig. 12). The main heliophytic component (Poaceae, *Artemisia*, Amaranthaceae) exhibits high coverage. However, despite their relatively low pollen frequencies, woody taxa are highly diverse. These include a mixture of deciduous trees (*Quercus*, *Acer*, *Alnus*, *Betula*, *Castanea*, *Corylus*, *Juglans*, *Fraxinus*, *Populus*, *Salix*, *Ulmus*), and Mediterranean taxa, alongside evergreen oaks and pines (*Olea*, *Myrtus*, *Pistacia*, *Phillyrea*, *Calicotome*, *Cistus*, *Withania*, *Rhamnus*).

According to this evidence, the Palaeolithic vegetation surrounding Arco Cave likely comprised grasslands, pine and oak woodlands, juniper stands, *Pistacia* and wormwood-dominated steppes, heliophytic matorrals, rocky scrub with hemicryptophytes, shrubby grasslands, and—undoubtedly—extensive patches of riparian forest (Fig. 12). For the Gravettian, this pattern is comparable to that seen at other Iberian pollen sites such as Lagar Velho (Ochando et al., 2022b), Bajondillo (Cortés-Sánchez et al., 2008; López-Sáez et al., 2007), Beneito (Carrión, 1991, 1992; Carrión and Dupré, 1994; Carrión and Munuera, 1997), Cendres (Badal and Carrión-Marco, 2001; Badal and Martínez-Varea, 2018; Villaverde et al., 2019), Malladetes (Dupré, 1980), Morín (Leroi-Gourhan, 1971), and Amalda (Dupré, 1990). The consistent presence of riparian species near these sites provides strong evidence for the availability of freshwater resources for both humans and the animals they hunted. This hydrorefugium scenario extends to other periods of the peninsular Pleistocene (Carrión et al., 2024b).

The occurrence of *Withania frutescens* and *Calicotome* cf. *intermedia* is key for characterizing the local floristic composition during the Upper

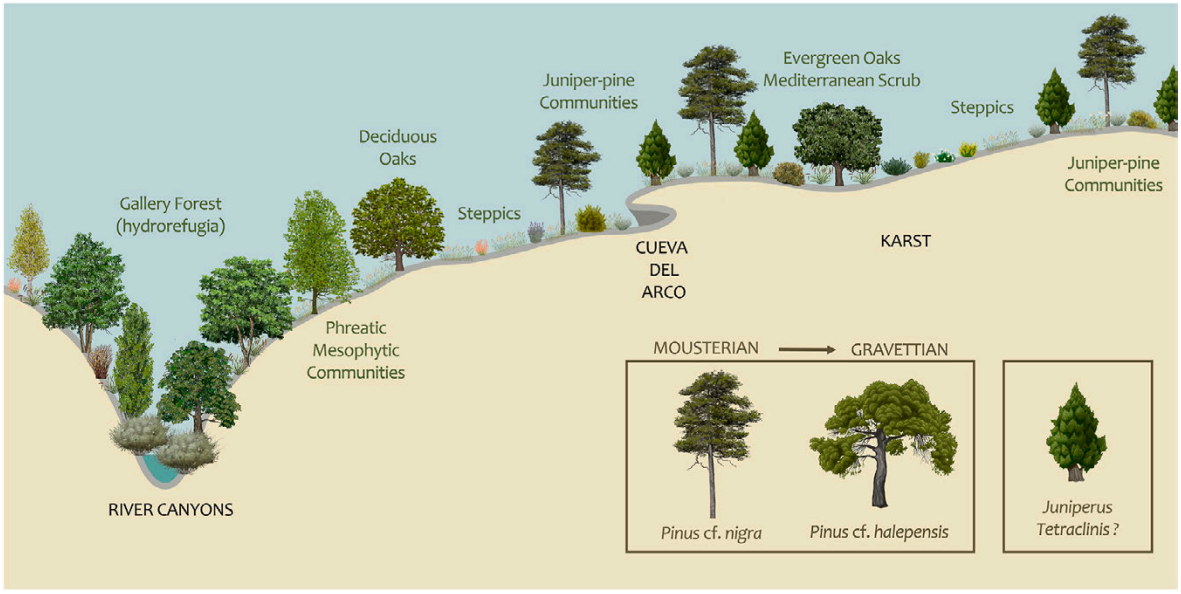

Fig. 12. Schematic representation of a "paleocatena" illustrating the Palaeolithic vegetation of Cueva del Arco, including the karstic zone in which the cave is located and the rugged valley floors traversed by the Segura and Quípar rivers. Juniper woodlands and steppe vegetation (*Artemisia*, *Poaceae*, *Asteraceae*, *Amaranthaceae*, *Ephedra*, *Cistaceae*, *Lamiaceae*) would have primarily occupied lithosols, while deeper soils would have supported Mediterranean-type *Quercus*-dominated communities, including *Olea*, *Pistacia*, *Myrtus*, and *Phyllirea*, among others. Riparian gallery forests (*Salix*, *Ulmus*, *Populus*, *Fraxinus*, and occasionally *Alnus* in more leached soils) would have developed in river canyons and surrounding areas. Sites with greater edaphic moisture and deeper soils would have hosted various broad-leaved tree species (*Juglans regia*, *Castanea sativa*, *Acer* spp., *Betula celtiberica*, and even *Quercus faginea* and *Q. suber*). The key to arboreal survival during the coldest stadials likely lay in sheltered mountain microenvironments and river valleys, acting as hydrorefugia. Artwork: G Amorós.

Pleistocene. These taxa, along with *Gymnosporia senegalensis* subsp. *europaea*, *Periploca angustifolia*, *Osyris lanceolata*, *Lycium intricatum*, and *Myrtus communis*, have also been documented in Bajondillo (López-Sáez et al., 2007), Gorham's Cave (Carrión et al., 2008), Vanguard Cave (Carrión et al., 2018a), Sima de las Palomas (Carrión et al., 2003a) (Fig. 16), Cueva Perneras (Carrión et al., 1995), and Abrigo 3 of the Complejo del Humo (Ochando et al., 2020b) during the cold phases of the Late Pleistocene, indicating frost-free conditions—at least in certain microhabitats near Arco Cave. This clearly aligns with the strong thermophilous component observed in the pollen record (Fig. 11) and the presence of evergreen oaks in the charcoal record (Fig. 7).

This new palaeobotanical record reinforces previous evidence for the native status of certain tree species in southeastern Spain, such as walnut (*Juglans regia*), hackberry (*Celtis australis*), and sweet chestnut (*Castanea sativa*) (Carrión and Sánchez-Gómez, 1992; Carrión et al., 2024b, *2024c*). The presence of some taxa—nowadays extremely rare in the region—such as *Ilex aquifolium*, *Corylus avellana*, and *Taxus baccata* is also remarkable. The lacustrine pollen sequence from Gádor, near the present-day Tabernas Desert in Almería, suggests that many of these mesic species experienced population extinctions during the recent Holocene due to the combined effects of progressive aridification and forest degradation associated with metallurgical activities since the Argaric Bronze Age (Carrión et al., 2003b, 2010a).

7.2. Wood resources for human use and the palaeoecological context

The Mousterian human groups occupying Cueva del Arco exploited woody resources primarily from coniferous formations, especially pines and Cupressaceae, likely represented by *Juniperus* and/or *Tetraclinis*. Among these, Cupressaceae are notably more abundant across the analysed sequence, suggesting the predominance of an open woodland landscape under conditions of moderate aridity and/or continental climate. This environmental interpretation is further supported by the presence of steppe-adapted taxa such as *Artemisia*, *Ephedra*, and *Macrochloa tenacissima*—the latter known to thrive in nutrient-poor soils and under annual precipitation levels between 200 and 400 mm (Maestre et al., 2007).

Studies of plant macroremains in the region are indeed scarce for the Middle Palaeolithic. At Cueva Antón, whose sequence is dated to MIS 5, the presence of cryophilic species (mountain pines) and steppe species (*Juniperus*, *Artemisia*, *Ephedra*) is noteworthy. However, the presence of thermophilic taxa at the base of the sequence (AS5) is also significant, indicating climatic conditions similar to those of the present (Zilhão et al., 2016). The pollen record from this site, nevertheless, shows a dominance of pollen from cryophilic pines, suggesting that their ecological importance persisted at the regional scale.

The tendency to exploit cryophilic and/or steppe woody species can be observed at several Middle Palaeolithic sites across the region. This is the case at Abric del Pastor (Alcoi), where *Juniperus* is also identified as the main source of fuel, accompanied by cryophilic elements (such as pines) and, sporadically, other mesophilic taxa—likely available due to the proximity of a watercourse (Vidal-Matutano et al., 2015). Thus, despite the existence of thermophilic refugia, widespread aridity appears to have been a dominant environmental feature.

The occurrence of mesophilic taxa—such as Aleppo pine (*Pinus halepensis*), *Quercus*, *Hedera helix*, and *Celtis*—supports previous palynological interpretations that propose the existence of microrefugia within the area, likely associated with fluvial corridors. These zones may have provided a broader array of ecological niches and exploitable resources. Such taxa are more frequent in the upper part of Unit III and in Unit II, indicating a more diverse and possibly locally wetter environment during those periods.

Despite these ecological variations, a degree of continuity is observed between the Mousterian Unit III and the overlying Unit II, attributed to the Gravettian. In both levels, Cupressaceae-dominated assemblages remain prevalent, although mesophilic taxa are also present (Román et al., 2024). Interestingly, shrub taxa are underrepresented in both contexts. This is somewhat unexpected, given that coniferous woodlands with open canopies often support diverse understorey vegetation. The scarcity of such shrubs in the anthracological record may reflect selective wood collection practices, favouring larger and more durable species for fuel or other utilitarian purposes. Dendrological observations indicate the use of wood derived from long-lived trees, as suggested by the presence of growth rings with low curvature, implying slow growth over time. However, due to the fragmentary nature of the charcoal samples, it was not possible to reconstruct the original calibre of the firewood used.

7.3. The cupressoid conundrum: Juniperus, Tetraclinis, or both?

The abundance of Cupressaceae throughout the palaeobotanical record warrants particular attention (Figs. 7, 9 and 13). Today, non-coastal sectors of the southeastern Iberian Peninsula—including inland areas of Murcia, Albacete, and parts of Jaén and Granada—host substantial woodland formations dominated or codominated by *Juniperus* species, especially in degraded woodlands or dry montane landscapes (Table 5). *Juniperus phoenicea* and *J. oxycedrus* are widespread on shallow, calcareous soils, forming dense thickets or mixed shrublands with *Pistacia lentiscus*, *Rhamnus lycioides*, and *Ephedra fragilis*. On some arid upper slopes and plateaus, *Juniperus* may become the primary arboreal component, occasionally replacing pine-dominated forests in areas affected by fire or past anthropogenic clearance (Fig. 13).

Anthracological evidence suggests that although conifers are well represented in most Upper Pleistocene sequences in the region, *Juniperus* tends to dominate in more arid contexts—such as sites in the southeastern peninsula and the Ebro Valley. Clear examples include Abrigo de La Boja (Mula, Murcia), where *Juniperus* accounts for nearly 100 % of the anthracological assemblage during the Solutrean, and around 90 % during the Gravettian (Badal et al., 2019), or Ratlla del Bubo (Crevillent, Alicante), where *Juniperus* charcoal exceeds 90 % (Martínez-Alfaro et al., 2022) (Fig. 14). In other cases, multiple *Juniperus* species are documented as coexisting during the Pleistocene. At the Upper Palaeolithic site of Cova de les Cendres, for instance, up to three different species—*J. sabina*, *J. communis*, and *J. oxycedrus*—have been identified through seed remains (Badal and Martínez-Varea, 2018). This assemblage reflects vegetation types now found above 1000 m a.s.l. in Iberian Mediterranean mountain environments under strong continental influence, implying a significant altitudinal shift in bioclimatic zones. Unfortunately, the fragmented state of juniper endocarps from Cueva del Arco prevents species-level identification, while the few recovered leaves only indicate the presence of squamiform-leaved taxa, such as *J. phoenicea*.

Of particular ecological and palaeoecological interest are the relict woodlands of *Juniperus thurifera* (commonly known as *sabina albar*) in the highlands of Moratalla, especially around El Sabinar, extending into the Nerpio area (Albacete province). These open woodlands, or *sabinares*, occur between 1200 and 1600 m a.s.l. on cold, exposed plateaus and slopes with stony soils, where *J. thurifera* grows in isolation or in association with *Quercus rotundifolia*, forming a characteristic supra-Mediterranean vegetation type with strong biogeographic ties to the Iberian interior, where its distribution is more continuous (Table 5, Fig. 13). Notably, these formations, which have been studied from a palaeoecological perspective in the Holocene, have expanded in recent millennia, often at the expense of denser pine forests, largely due to human impact (Carrión et al., 2004).

The biogeographical status of *Tetraclinis articulata* in southeastern Iberia—particularly within the coastal mountain ranges of the Murcia region—has long been a subject of scientific debate and interest (Esteve et al., 2017) (Fig. 13). While its primary native range is situated in North Africa (including Morocco, Algeria, and Tunisia), small, disjunct populations have been documented in southern Europe. This distribution raises questions about whether these Iberian occurrences represent

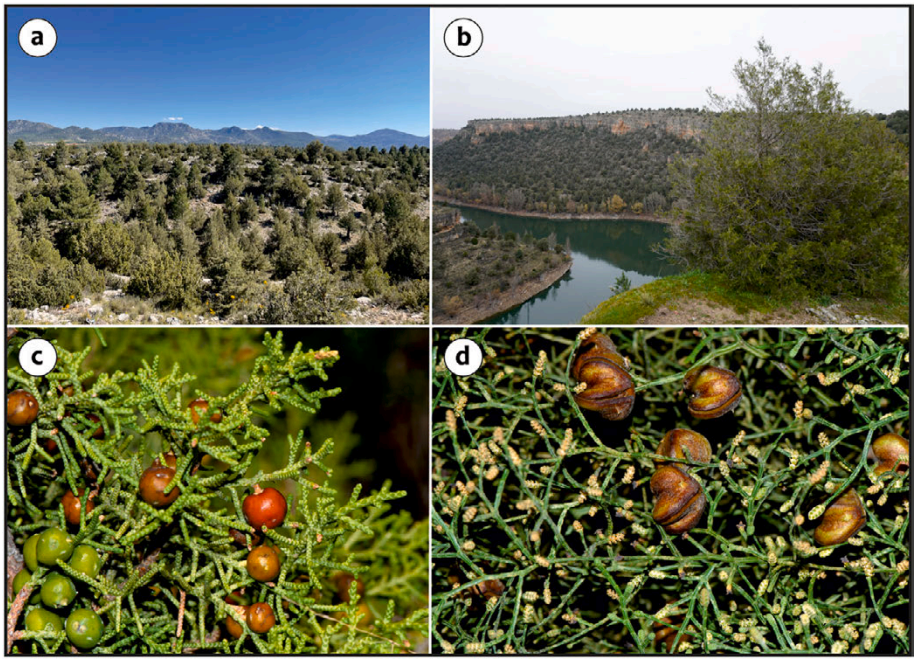

Fig. 13. (a) Mixed formations on karstic substrate under a continental Mediterranean climate, with *Juniperus thurifera*, *Juniperus phoenicea*, *J. oxycedrus*, *Quercus rotundifolia* (on deeper soils), and *Pinus nigra* near Nerpio, Albacete, in the western part of the Arc in the eastern Sierras de Segura (photos: Gabriela Amorós); (b) Formations dominated by *Juniperus thurifera* and *Juniperus oxycedrus*, with scattered *Quercus rotundifolia*, on limestone plateaus in the Hoces del Río Duratón, Segovia, central Spain (photos: Gloria Martínez-Sagarra); (c) *Juniperus phoenicea* (photo: J.A. Devesa); (d) *Tetraclinis articulata* (photo: J.A. Devesa).

Table 5
Distribution and Ecology of *Juniperus* and *Tetraclinis* species in the Iberian Peninsula and Balearic Islands. For species distribution and ecology: Amaral Franco and Juniperus (1986), López González (2001), Anthos (2025), GBIF.org (2025)

Species	Distribution	Ecology	Bioclimatic zone	Altitudinal range (m a.s.l.)
Juniperus communis L. (incl. *J. communis* subsp. *hemisphaerica*)	Almost the entire Iberian Peninsula, more common in the north, centre, and east	Sclerophyllous shrublands and forests, high-elevation shrublands	(Thermo-) mesomediterranean to oromediterranean	(100)450–3100
Juniperus oxycedrus L.	Central, eastern, and southern Iberian Peninsula and Balearic Islands	Mediterranean sclerophyllous shrublands and forests	Thermomediterranean to supramediterranean	0–1400
Juniperus macrocarpa Sm.	SW and E of the Iberian Peninsula and Balearic Islands	Coastal dunes and sandy areas	Thermomediterranean	0–50
Juniperus badia (H. Gay) Rivas Mart. et al.	Inland regions of Spain, NE and CE Portugal	Interior forests and shrublands	Mesomediterranean and supramediterranean	200–1200
Juniperus navicularis Gand.	SW Iberian Peninsula; endemic	Inland maritime sands, coastal sands and dunes	Thermomediterranean	0–225
Juniperus phoenicea L.	Southern and eastern half of the Iberian Peninsula and Balearic Islands	Xerophytic forests and shrublands, rocky ridges and crevices	Thermomediterranean to supramediterranean	0–1850
Juniperus turbinata Guss.	W, SW, S and E of the Iberian Peninsula and Balearic Islands	Coastal sands, dunes, and cliffs	Thermomediterranean and mesomediterranean	0–800
Juniperus thurifera L. subsp. *thurifera*	Central, north-central, eastern and southern Spain	Plateaus and valleys, preferably on calcareous substrates	Meso- and supramediterranean	(250)800–1650 (2000)
Juniperus sabina L.	N, E and S of the Iberian Peninsula; absent in Balearic Islands and Portugal	Mountain pine forests and shrublands, ridges and rocky outcrops	Supramediterranean and oromediterranean	(900)1100–2750
Tetraclinis articulata (Vahl) Mast.	Sierra de Cartagena (Murcia); naturalized in Ronda and Málaga	Sunny, rocky sublittoral slopes	Thermomediterranean	0–300

(*) *Juniperus communis* is a highly polymorphic species, and the delimitation between its infraspecific taxa remains uncertain due to the absence of clear morphological discontinuities. Moreover, molecular data do not adequately support the morphological distinctions (Adams and Schwarzbach, 2012). For this reason, *Juniperus communis* is treated here broadly, including under its synonymy the infraspecific taxa [subsp. *hemisphaerica* (J. Presl & C. Presl) Nyman and subsp. *alpina* (Suter) Čelak., nom. illeg.].

natural relict populations or anthropogenically introduced stands (Table 5). In the Iberian Peninsula, the populations located in the Sierra de la Muela, Cabo Tiñoso, and the broader Cartagena–La Unión massif are especially noteworthy. Multiple lines of evidence support a natural, autochthonous origin for these populations (Esteve et al., 2017). The species typically grows in steep, xeric limestone habitats that are difficult to access and unlikely to have been subject to ornamental planting or reforestation. These stands are frequently embedded within well-preserved Mediterranean shrubland communities—including *Pistacia lentiscus*, *Juniperus phoenicea*, and *Salvia rosmarinus*—suggesting long-term ecological integration and continuity rather than recent establishment.

Moreover, the fragmented distribution of *Tetraclinis* in southern Europe resembles that of other thermophilous relict taxa, which are

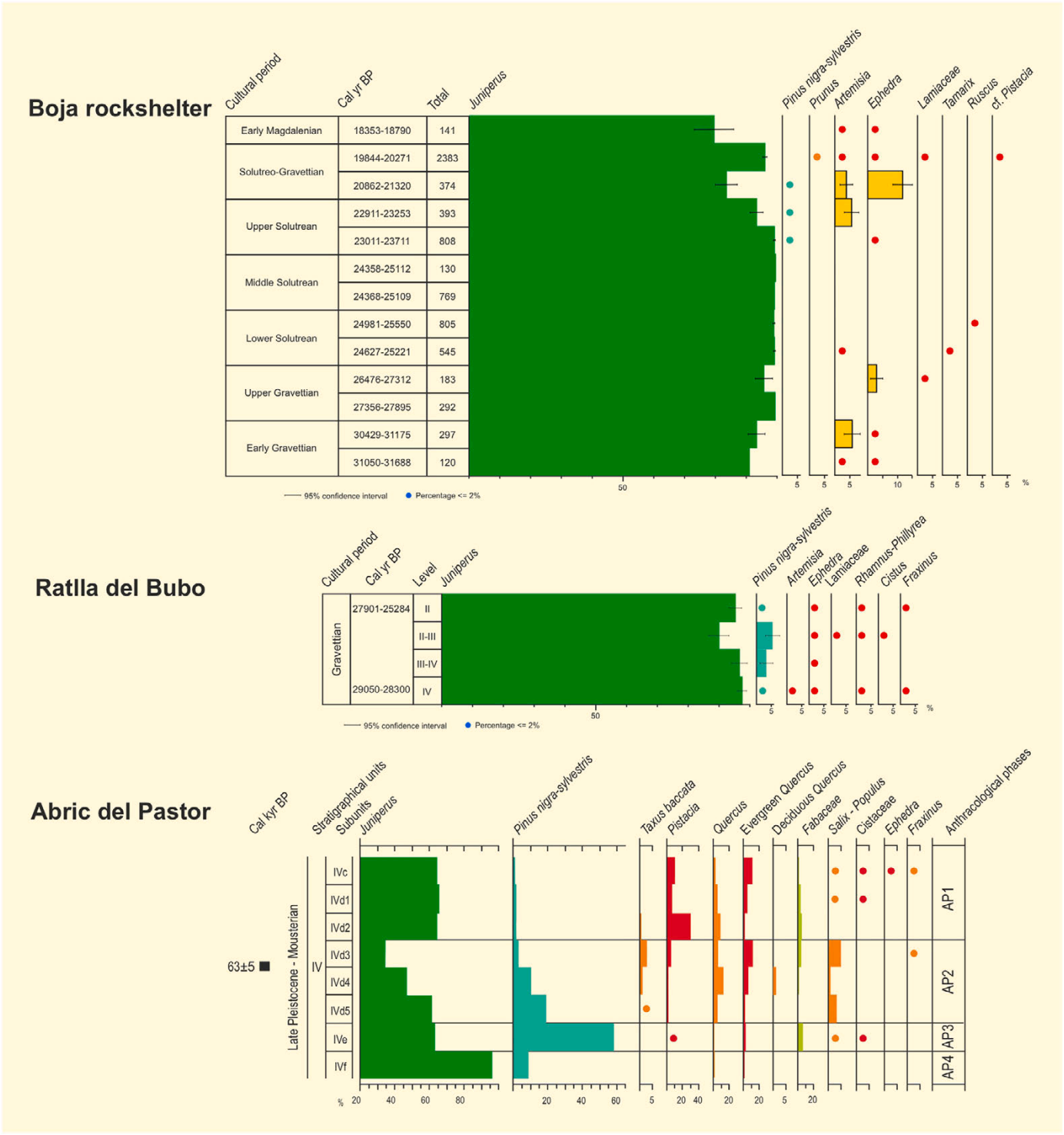

Fig. 14. Selection of the most relevant taxa from the charcoal analysis in: (a) Upper Palaeolithic Abrigo de la Boja (Mula, Murcia), redrawn from Carrión et al. (2024b) based on data and original diagram from Badal et al. (2019); (b) Ratlla del Bubo, redrawn from Carrión et al. (2024b) based on data and original diagram from Martínez Alfaro et al. (2022); (c) Abric del Pastor, redrawn from Carrión et al. (2024b) based on data and original diagram from Vidal Matutano (2016) and Vidal Matutano and Pardo-Gordó (2020). See Fig. 1 for site location.

hypothesized to have persisted through Pleistocene climatic fluctuations within microrefugia (Kvaček et al., 2000). Palaeobotanical data suggest that *Tetraclinis*, or closely related taxa, were once more widespread throughout the western Mediterranean basin during earlier geological periods (Suc et al., 2025), although macrofossil and palynological evidence specific to the Iberian Peninsula remains limited (Carrión et al., 2024a).

At Cueva del Arco, anthracological analysis has not definitively distinguished *Tetraclinis* from *Juniperus*, likely due to anatomical overlap in their charcoal structure. However, previous anthracological studies conducted at Holocene archaeological sites in southeastern Spain have offered more conclusive identifications of *Tetraclinis*. These include Bronze Age contexts at Punta de los Gavilanes (García-Martínez et al., 2008) and Cerro de las Viñas (Grau, 1990), as well as Chalcolithic and

Bronze Age assemblages at Los Millares (Rodríguez-Ariza, 1992) and Fuente Álamo (Carrión et al., 2004, 2005) in neighboring Almería province.

Nevertheless, the possibility of human-mediated introduction cannot be definitively ruled out. The southeastern Iberian region has a long and well-documented history of human occupation and maritime connectivity, particularly during the Phoenician, Roman, and Islamic periods. It is plausible that *Tetraclinis* may have been intentionally or inadvertently introduced, given its value as a source of aromatic resin (sandarac) and durable timber (Esteve et al., 2017). Genetic studies reveal low divergence between Iberian and North African populations, which could indicate a recent founder effect. However, such genetic similarity may also result from historical geographic isolation and limited gene flow across the Mediterranean (Sánchez-Gómez et al., 2013).

7.4. Taphonomic and palaeoecological considerations of the vertebrate assemblage

The faunal assemblage from Cueva del Arco offers support for the palaeoenvironmental context outlined above. However, as an independent dataset, faunal evidence provides only limited palaeoecological resolution. The macro- and mesofaunal remains exhibit clear signs of taphonomic alteration, including extensive fragmentation and notable diagenetic modification. The taxonomic composition of the Mousterian assemblage mirrors that observed in the Gravettian levels (Román et al., 2024), with a marked paucity of ungulate and carnivore remains and a significant predominance of Leporidae. These leporid remains are notable not only for their abundance but also for their complex taphonomic profile, suggesting multiple accumulation agents. While human exploitation of rabbits is well attested for the Upper Palaeolithic (Real, 2020)—particularly in later phases—evidence from earlier periods such as the Aurignacian and Gravettian reveals more variable levels of human involvement (Sanchis et al., 2016).

At Cueva del Arco, available evidence suggests that humans were not the primary agents responsible for leporid accumulation. Although certain fracture patterns and burnt elements may indicate processing, the absence of cut-marks or tooth impressions renders a definitive interpretation elusive. Comparable assemblages elsewhere show that leporid exploitation by humans can occur even in the absence of direct anthropogenic modifications. In the Mousterian sample, anatomical distribution, age profiles, and surface alterations—including gnawing and digestion traces—align with non-human accumulation, consistent with patterns documented at regional sites such as Cueva Antón (Sanchis, 2012; Lloveras and Nadal, 2015). The presence of Iberian ibex (*Capra pyrenaica*) supports palaeovegetation reconstructions suggesting a rocky, mountainous landscape in the site's vicinity. In contrast, the rare occurrence of aurochs (*Bos primigenius*) and red deer (*Cervus elaphus*) may reflect the patchy availability of open and wooded environments, respectively. However, the small number of remains for these taxa limits any robust interpretations regarding landscape use by Neanderthal or anatomically modern human groups.

Skeletal representation of Iberian ibex is biased, with axial elements particularly underrepresented—although some unidentified fragments may derive from this species. Due to the limited sample size, transport strategies remain unclear. Nevertheless, the possibility of whole carcass transport cannot be excluded, a pattern documented at other Mediterranean sites such as Cova del Comte and Cova de les Cendres (Casabó et al., 2017; Villaverde et al., 2019). The highly fragmented state of the bones, together with cut-marks, burning, and evidence of marrow extraction, indicates anthropogenic processing. Non-human predation indicators are minimal and primarily consist of digestive etching and isolated coprolites, likely attributable to small carnivores. This taphonomic profile aligns with that of other Gravettian contexts, where human processing of medium and large mammals predominates, though brief incursions by carnivores or birds of prey are also attested (Sanchis et al., 2023.

Regarding palaeoenvironmental conditions, the identified taxa are largely eurythermic and therefore provide limited climatic specificity. While diversity indices and mammal-based bioclimatic models have been successfully applied in other contexts (Real et al., 2022b), the scarcity of remains at Cueva del Arco precludes such quantitative approaches. In sum, the ungulate assemblage primarily reflects anthropogenic activity, whereas leporid remains are the product of multiple accumulating agents. The low density of faunal material, together with its taphonomic signature, suggests ephemeral and possibly sporadic human occupations at the site, with additional contributions from natural agents such as nocturnal raptors.

8. Final remarks

A broad examination of the palynological and anthracological sequences from Cueva del Arco, based on the relative abundances of plant taxa, reveals a palaeovegetation landscape dominated by shrub and herbaceous elements, interspersed with scattered pines and junipers in an open setting. However, several contextual factors must be taken into account. First, the cave is located in a karstic environment, marked by scarce deep soils and exposed to thermal contrasts and prevailing winds due to its hilltop position. In this setting, the local vegetation around the cave would have exerted a dominant influence on the pollen rain, shaping the resulting spectra. This is especially relevant given the particular taphonomic conditions of pollen in cave and rockshelter contexts, where input can include not only ambient deposition but also material transported by animals (including humans), water flow, and stochastic intra-cave sedimentary processes. Experimental studies of modern pollen rain inside and outside caves support this interpretation (Hunt and Coles, 1988; Prieto and Carrión, 1999; Navarro et al., 2000, 2001; Hunt and Rushworth, 2005; Hunt and Fiacconi, 2018).

As a result, the frequencies of minor arboreal angiosperm taxa should be interpreted as evidence of the local and extra-local presence of the corresponding plant communities. These likely persisted in nearby mountain ranges and valleys—particularly along the adjacent river canyons of the Segura and Quípar—favoured by microclimatic conditions and groundwater-regulated water availability (Figs. 1, 2 and 12). Further west, in the highlands of the Segura Mountains, evidence for glacial refugia during the Late Pleistocene is clearly documented in the Siles record (Carrión, 2002) (Fig. 1). Since at least the Early Pleistocene, southeastern Iberia has emerged as a major stronghold of plant biodiversity (López-Sáez et al., 2007; Carrión et al., 2024b, 2024d) (Figs. 15 and 16). Despite fluctuating climatic conditions, Palaeolithic humans in inland Murcia likely had consistent access to a rich mosaic of ecosystems and plant and animal resources, which would have supported their survival.

The general climate of the region was not particularly favorable, which underscores the importance of local refugia associated with favorable topographic settings. During MIS 4, paleoceanographic records from the Alboran Sea indicate a marked decline in sea surface temperatures, with values estimated to be 4–6 °C lower than at present, reflecting the full onset of glacial conditions (Martrat et al., 2004). This period was characterized by a cold and arid climatic regime, with enhanced latitudinal temperature gradients and reduced oceanic circulation, suggesting a continental environment dominated by widespread dryness and likely limited hydrological activity. In contrast, MIS 3 was marked by strong climatic variability, driven by abrupt millennial-scale oscillations. These alternated between cold, arid stadials and relatively milder interstadials, during which sea surface temperatures in the western Mediterranean approached modern values. Despite these temporary warmings, the overall continental climate remained unstable, with frequent shifts between dry and semi-humid phases, consistent with the oceanographic evidence of recurrent water mass destabilization and regional climatic fluctuations (Martrat et al., 2007).

The paleoecological findings may be extrapolated to other regions, particularly mid-altitude intramontane valleys. Specifically, they

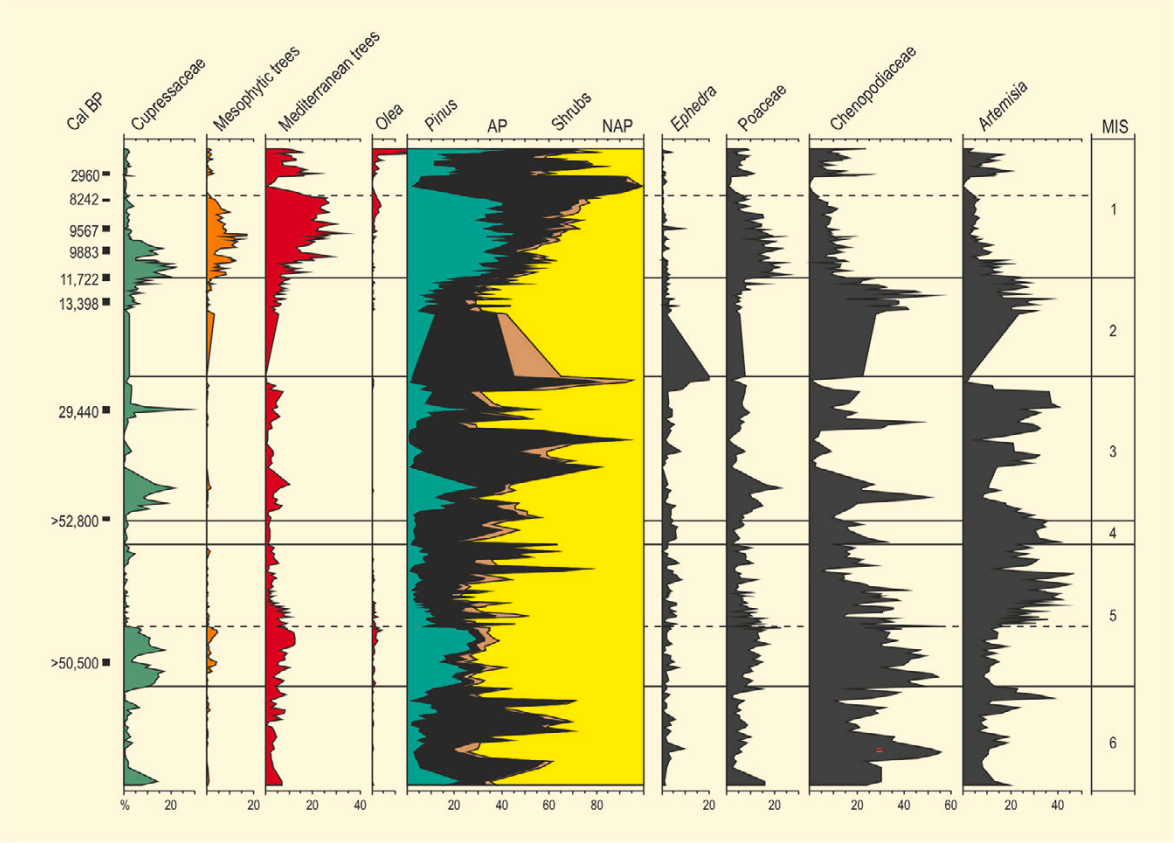

Fig. 15. Pollen diagram of selected taxa from Salines Lake, inland Alicante, near the Arco region (Fig. 1). Redrawn from Carrión et al. (2024b), based on the original data from Burjachs (2009).

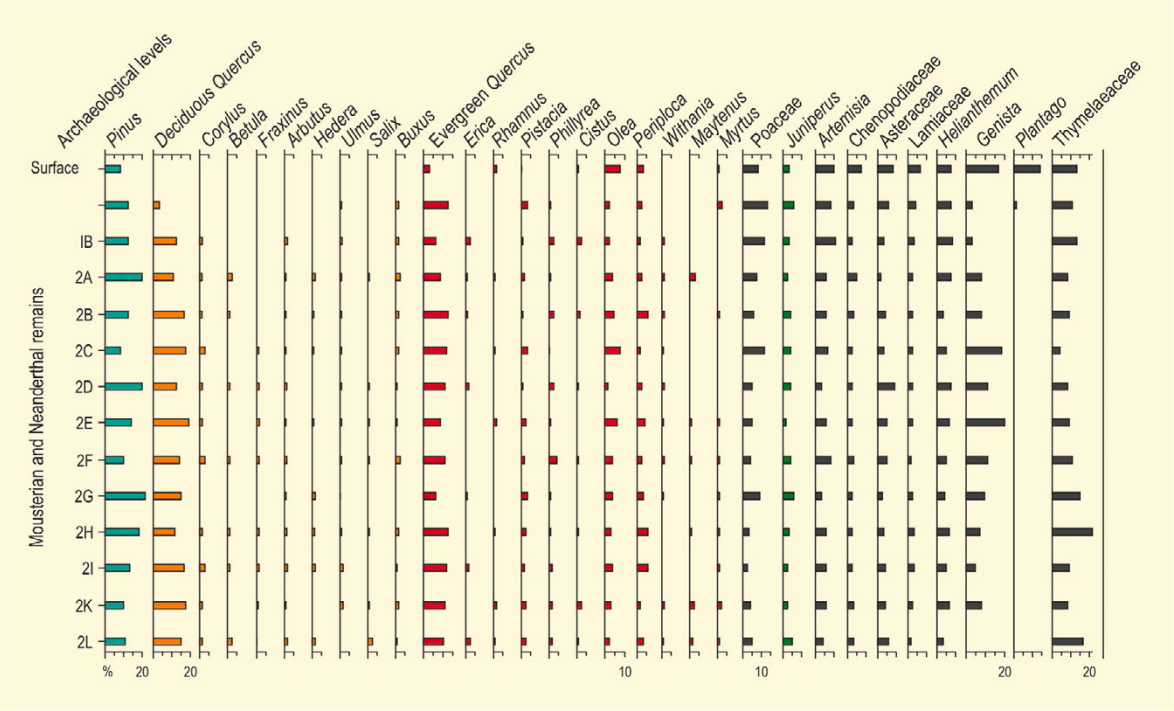

Fig. 16. Synthetic pollen diagram of selected taxa of Sima de las Palomas in Cabezo Gordo, Murcia. Redrawn from Carrión et al. (2003c).

pertain to continental and relatively arid Mediterranean environments of the southeastern interior, such as the fossil pollen site of Salines (Alicante). The record spanning MIS 4 to MIS 2 indicates a persistent presence of Mediterranean taxa, including *Pinus* and Cupressaceae, within a relatively open landscape dominated by grasses, *Ephedra*, and *Artemisia* (Burjachs et al., 2016) (Fig. 15). Notably, mesophytic elements are also present, albeit in low proportions—similar to patterns observed in the Arco region. Closer to the Mediterranean coast, within the same region of Murcia, arboreal population reservoirs exhibited greater woody phytodiversity, as evidenced at the Neanderthal site of Sima de las Palomas (Carrión et al., 2003b). In addition to the dominance of *Pinus* and *Juniperus*, the site reveals a higher degree of forest cover, including mixed woodlands composed of both evergreen and deciduous *Quercus*, alongside other broadleaved taxa such as *Corylus*, *Fraxinus*, *Arbutus*, *Ulmus*, and *Betula*. Thermophilous elements are also more abundant at this site, particularly *Pistacia*, *Olea*, *Periploca*, *Gymnosporia*, and *Myrtus* (Fig. 16). From a floristic standpoint, these vegetation formations lack direct modern analogues, highlighting their unique ecological composition.

It is also important to note that cave pollen spectra, whether derived from sediments or coprolites, provide insights into the past vegetation of a territory whose geographical boundaries are difficult to delineate, and within which long-distance transport of pollen is invariably present to varying extents (Navarro et al., 2000). This can lead to biogeographical paradoxes, such as the coexistence of *Berberis* (currently supramediterranean) alongside *Myrtus* and *Withania* (currently thermomediterranean), which may be explained by differences in the distances of their source populations. This issue forms part of a more complex, longstanding and unresolved debate (Horowitz, 1992; Carrión, 2001; Carrión et al., 2003a; Cheddadi et al., 2006; Svenning et al., 2008; Stewart et al., 2010; Nieto Feliner, 2011), although some hypotheses propose that, under glacial refugia conditions, species with diverse bioclimatic affinities could have coexisted—and even formed associations—within confined landscapes such as intramontane valleys, river gorges, or coastal platforms (Bailey et al., 2008; Rodríguez-Sánchez et al., 2008; Carrión-Marco et al., 2010; Magri et al., 2017; Behre and van der Knaap, 2023; Tzedakis et al., 1997; Carrión et al., 2024d, 2024e).

Ultimately, the paleoecological record from Cueva del Arco transcends the interpretative limitations of pollen, charcoal and faunal assemblages by offering a compelling snapshot of biotic resilience under extreme climatic stress (Fig. 12). Within a chronostratigraphic framework that likely spans from the end of MIS 4 through much of MIS 3 and into early MIS 2, the site captures a dynamic window in which human groups endured major climatic oscillations—including the progressive cooling of MIS 3, the episodic severity of Heinrich Events H5 (~50 ka), H4 (~39 ka), H3 (~31 ka), and the onset of the Last Glacial Maximum (~26.5–19.0 ka) (Rasmussen et al., 2014; Camuera et al., 2018; Carrión et al., 2024d). These large-scale events, marked by dramatic iceberg discharges and shifts in oceanic circulation, left clear imprints on southern European ecosystems. It is within this volatile climatic backdrop that the Arco record stands out: as a testament to the persistence of plant populations, the complexity of ecological responses, and the capacity of human and non-human communities alike to navigate periods of profound environmental upheaval.

CRediT authorship contribution statement

José S. Carrión: Writing – original draft, Visualization, Validation, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Yolanda Carrión-Marco:** Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Carmen M. Martínez-Varea:** Writing – original draft, Methodology, Investigation, Data curation, Conceptualization. **Juan Ochando:** Writing – original draft, Methodology, Investigation. **Cristina Real-Margalef:** Writing – original draft, Software, Methodology, Investigation, Conceptualization. **Manuel Munuera:** Writing – original draft, Visualization, Software, Methodology, Investigation, Formal analysis, Conceptualization. **Gloria Martínez-Sagarra:** Writing – original draft, Visualization, Investigation, Formal analysis, Conceptualization. **Gabriela Amorós:** Writing – original draft, Visualization, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Aldara Girona:** Software, Resources, Methodology, Data curation. **Diego Angelucci:** Methodology, Investigation. **Jacopo Armellini:** Methodology, Investigation. **Noelia Sánchez-Martínez:** Methodology, Investigation. **Dídac Román:** Writing – original draft, Project administration, Methodology, Investigation, Conceptualization. **Ignacio Martín-Lerma:** Writing – original draft, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization.

Declaration of competing interest

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

Acknowledgements

This research has been primarily funded by the project HOMEDSCAPE Agencia Estatal de Investigación, and PID2022-136832NB-100 Fundacion Seneca Region de Murcia, project 22525/PI/24. C Real thanks CIGE/2023/5 project of Conselleria de Educación, Cultura, Universidades y Empleo, Generalitat Valenciana. Other funding come from ARQ105/2018, PID2021-128349NB-I00 by MCIN/AEI and FEDER CIDEGENT/2018/043 of Generalitat Valenciana), and Cieza City Council.

Data availability

Data will be made available on request.

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