



Landscape and subsistence in NW Iberia during the Middle Palaeolithic (MIS3): Faunal analysis of Cova Eirós (Triacastela, Galicia, Spain)[☆]

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ABSTRACT

Cova Eirós is a key reference site for understanding the life of the late Neanderthal groups in the northwest of the Iberian Peninsula, offering an extensive Mousterian sequence with level 3 standing out due to its late chronology (c. 41 ka cal BP). Its significant zooarchaeological record is a valuable source of information when attempting to reconstruct the environment in which these late Neanderthals lived. In this study, we propose a comprehensive analysis of the macrofaunal and small vertebrates record from the aforementioned level 3 to expand our knowledge of its faunal spectrum and how it was exploited by the various agents that occupied the cave. We also conducted a paleoclimatic and paleoenvironmental study employing the Bioclimatic Model and Habitat Weighting methods to reconstruct the conditions in which Neanderthal hunter-gatherers lived. The study has identified 31 taxa (NISF = 3746), with a particular emphasis on the exploitation of *Cervus elaphus* and *Ursus spelaeus*, as well as evidence of carnivores contributing smaller ungulates. The environmental reconstruction reflects a colder and slightly less humid climate, dominated by forests interspersed with open spaces. These data serve as an example of the tendency of Mousterian groups to occupy refuge areas along the Cantabrian Mountains, demonstrating that Neanderthal presence in the northwest of the Iberian Peninsula during the final phase of the Mousterian took place under favourable climatic conditions.

1. Introduction

The north of the Iberian Peninsula constitutes a key area for the study of the late Neanderthals, standing out for its abundance of archaeological sites covering a wide temporal spectrum. This area has more than 150 years of Palaeolithic research and contains one of the richest archaeological records on the presence of late Neanderthals and early Anatomically Modern Humans (AMH) (Gutiérrez-Zugasti et al., 2018;

Montes Barquín and Sanguino González, 2021; de la Rúa and Altuna, J., Hervella, M., Kinsley, L., Grün, R., 2016; Demuro et al., 2023; Estalrich and Marín-Arroyo, 2021; Gómez-Olivencia et al., 2020; Marín-Arroyo et al., 2018; Maroto et al., 2012; Garralda et al., 2023; López-Onaindia et al., 2023; Sala et al., 2024; Álvarez-Vena et al., 2021, among others). The abundance of shelters and caves in the region has allowed for the preservation of archaeological evidence of both species at some significant sites, framed between 45 – 30 ka cal BP, and containing layers

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ascribed to the Mousterian, Châtelperronian, Protoaurignacian, Early Aurignacian and Evolved Aurignacian technocomplexes.¹

This time frame roughly coincides with the terminal phase of MIS 3 (60 – 27 ka BP), a period marked by instability due to the rapid succession of cold and dry phases followed by temperate ones, known as the Dansgaard-Oeschger (DO) cycles (Dansgaard et al., 1984; 1993). Moreover, in recent years, paleoenvironmental studies have shown that during this period there was a progressive decline in the carrying capacity of the ecosystem in the northern Iberian Peninsula, along with a corresponding decrease in the available natural resources (Jones et al., 2018; Vidal-Cordasco et al., 2022, Vidal-Cordasco et al., 2023). This deterioration coincided with –but did not necessarily cause– the disappearance of Neanderthal groups in northern Iberia. This would add a new layer to the notion that Neanderthal extinction was determined by climate, which has been widely proposed in the past (Finlayson, 2004, 2009; Staubwasser et al., 2018). However, this theory has been contested by other popular hypothesis, namely that the arrival of AMH was the cause of this demise, either due to competition between the two species (Zilhão and d'Errico 1999; Slimak et al. 2022; Timmermann, 2020), or that neanderthals may have been assimilated through interbreeding (Stringer and Crété, 2022; Villa and Roebroeks, 2014). In this context, Level 3 of Cova Eirós, dated to 41,770–39,024 cal BP (de Lombera-Hermida et al., 2021; Rey-Rodríguez et al., 2016), offers a valuable opportunity to better understand the ecology of one of the late Neanderthal groups in the northern Iberia and to contribute to the debate on whether their extinction in the region may have been driven by adverse conditions or, on the contrary, whether they inhabited a favourable environment that could have supported these groups. To shed light on this matter, we conducted a study to reconstruct the paleoclimatic and paleoenvironmental conditions of the site using the Bioclimatic Model and Habitat Weighting methods combined with a comprehensive study of the faunal record.

1.1. Paleoclimatic investigations in NW Iberia

Research on the paleoenvironment of Palaeolithic sites in Galicia has been crucial in understanding the interaction between human populations and their environment. Early geomorphological and palynological studies on the southern coast of Galicia provided valuable insights into the climatic fluctuations of the last glacial cycle, aiding in estimating the paleotemperatures of the region (Cano Pan et al., 1997). A pioneering study in the 1960 s at the Palaeolithic site of Gándaras de Budiño employed paleoenvironmental methodology (Butzer, 1967). It was throughout the 1990 s that the palaeoecological methods began to become common in the research of the Galician Palaeolithic record; however, most of these studies were conducted at sites with much more recent chronologies, primarily located in the Upper Pleistocene – Holocene transition (Llana Rodríguez et al., 1993; Martínez Cortizas et al., 1994a, 1994b, 1996; Martínez Cortizas and Moares Domínguez, 1995, 1996; Ramil Rego, 1993; Ramil Rego et al., 1992).

Overall, pollen studies of marine, coastal and continental deposits of the NW Iberian Peninsula for this period show an alternation in the expansion of mixed forest during the interstadials (showing an abundance of deciduous *Quercus* pollen) with that of semi-desert vegetation for the stadials (*Artemisia*, *Chenopodiaceae* and *Ephedra distachya*) (Fletcher and Sánchez Goñi, 2008; Sánchez Goñi et al. et al., 2008; Harrison and Sanchez Goñi, 2010). For example, the deposits of Area Longa and Santa María de Oia show during MIS 3 a rapid alternation of warm pulses with an increase in shrub vegetation, interspersed with cooling phases in which herbaceous and shrub pollen prevail (Ramil Rego et al., 2005). It is of particular interest, that a phase of expansion of tree pollen –mainly from the genus *Fagus*– is detected beginning 35,850

ysrs ka BP (Gómez-Orellana, 2002).

At the regional level, the occupations of Level 3 of Cova Eirós would fall within the warm phase known as Fazouro II, defined by a predominantly arboreal predominance (Gómez Orellana et al., 2008, 2013). Studies of glacial and periglacial evolution in the NW peninsular stipulate that at the end of MIS 3, within a humid and cold phase, is when glaciers reach their maximum extent (Pérez Alberti et al., 2011).

A milestone in paleoecological study of Galicia is the research conducted at Cova da Valiña, an archaeopaleontological site within the final phase of MIS 3 (34,123–32,987 cal BP) (Llana Rodríguez et al., 1996) where paleoenvironmental and microfaunal analysis have been carried out revealing a cold but humid environment with a dominance of arboreal pollen over herbaceous and shrubs, with *Pinus sylvestris* as the main taxon accompanied by specimens of the genera *Abies* and *Juniperus*, indicating cold and humid conditions. However, there is also presence of mesophilic specimens such as *Castanea*, *Ulmus* and *Daphne*. The non-arboreal record consists of representatives of the genera *Poaceae*, *Daphne* and *Ericaceae*, which represents the importance –albeit secondary– of open spaces (Ramil Rego, 1993; Ramil Rego and Fernández Rodríguez, 1996). The faunal record also shows coexistence of cold-adapted fauna –mainly *Alexandromys oeconomicus* and *Chionomys nivalis*– with taxa associated with milder conditions: *Capreolus capreolus*, *Sus scrofa*, *Hystrix cristata* and *Marmota marmota* (Fernández Rodríguez et al., 1993; Peña and Rey, 1995).

2. Site description and archaeological background

Cova Eirós is situated in the northwest of the Iberian Peninsula, near the village of Canelo (Triacastela, Lugo, Galicia) (Fig. 1). The entrance of the cave is situated on the NNW slope of Monte Penedo, in the Serra do Ouribio, at an altitude of 785 m a.s.l. The current entrance is about 2 m high and 3.5 m wide. The site is in a strategic position, communicating the hydrographic headwaters of the rivers Navia (Cantabrian basin) and Oribio-Miño (Atlantic basin). Besides, its location in an ecotone is defined by the confluence of the mountainous region of the Western Ranges to the East (over 800–1,400 m a.s.l.) and the open valleys of the Galician hinterland Cenozoic basins to the West (Sarria-Monforte de Lemos, 400–290 m a.s.l.). These features explain the richness and diversity of the resources available in the area and its strategic position as a bridge connecting the Cantabrian coast and the Atlantic coast of northwestern Iberia.

The current archaeological research at the site started in 2008, confirming the presence of a Middle-Upper Palaeolithic sequence at the entrance (Rodríguez Álvarez et al., 2011; de Lombera-Hermida et al., 2020). The work carried out during this new phase, which continues today, revealed also some evidence from Holocene activities. So far, 6 archaeological levels have been identified, ascribed to the Middle Palaeolithic (levels 3, 4 and 5) and the Upper Palaeolithic (levels B, 1 and 2). Lithic tools and faunal remains have been recovered from these layers. Inside the cavity, there are panels with numerous engraved and painted motifs, most of them ascribed to the final Palaeolithic period (García-Díez et al., 2021; Mosquera Castro et al., 2023).

In level 3, three facies with Mousterian lithic industry and faunal remains were identified: 3C, 3B and 3A. Facies 3C contains small, very angular limestone pebbles and small micritic carbonate concretions and laminations (thickness: <12 cm); facies 3B contains very fine sand with scattered very angular pebbles and limestone pebbles (thickness: 8–10 cm); finally, facies 3A is composed of very fine sand with scattered very angular pebbles and limestone boulders (thickness: <25 cm). The available radiocarbon dating places the Level 3 (facies 3A) occupations at 41,770–39,024 yrs cal BP (OxA-30471) (de Lombera-Hermida et al., 2021), calibrated using the IntCal20 curve (Reimer et al., 2020), using the OxCal 4.4 online software (Bronk Ramsey, 2009). In early publications of the site, references were made to OSL datings suggesting an age of 84,807 ± 4,919 BP (MAD-5612BIN) and 87,540 ± 6,112 BP (MAD-5651BIN) (Rodríguez-Álvarez et al., 2011). However, these dates have

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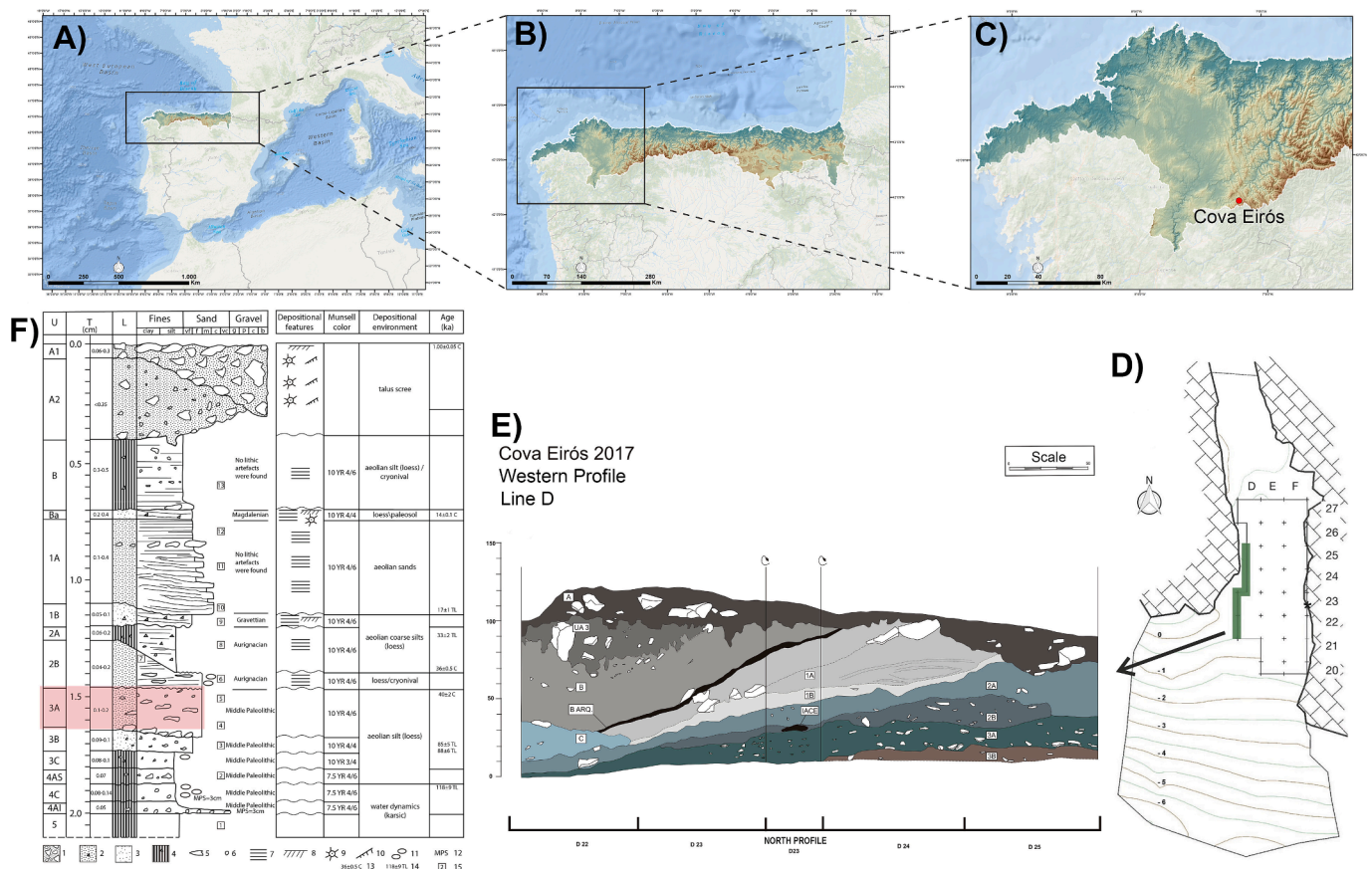


Fig. 1. Cova Eirós site. A-C) Location of the cave, highlighting the northern watershed of the Iberian Peninsula. D-F) Plan of the site, graphical representation of the western profile and detailed archaeostratigraphic description of the sequence (provenance of the sample dated by C14-AMS highlighted in red).

been dismissed as neither the paleoenvironmental context inferred from the micromammal / herpeto-fauna record and the sedimentological features, nor the industrial assemblage of the level are consistent with a late MIS 5 attribution. In any case, the discussion has already been addressed in previous studies (Rey-Rodríguez et al., 2016; de Lombera-Hermida et al., 2021) and will therefore not be dealt with here.

The lithic assemblage from Level 3 amounts to more than 3,400 artefacts. According to the technological analysis, the different facies of Level 3 display homogeneous features all along the sequence (de Lombera-Hermida et al., 2021). Interestingly, their artifact densities are lower than those from level 4 (>7,500 artifacts), interpreted as a campsite occupation (de Lombera-Hermida et al., 2014). Xenomorphic quartz clearly stands out as the most used raw material (91.1 %), followed by quartzite (7.9 %), along with other minority materials (rock crystal, sandstone, etc.). They usually come from local sources, mostly from secondary deposits in nearby riverbeds. The only allochthonous raw material is the fine-grained quartzite, with a higher metamorphism and knapping quality, possibly related to the Armorican formations, which are 10–20 km away (de Lombera-Hermida and Aldea Moreira, 2023).

The technological features of the lithic assemblage are defined by the predominance of immediate and local raw materials, and the preponderance of knapping products (87.7 %) over pieces related to percussion (2.5 %), or tool shaping (6.4 %). The reduction sequences among fine-grained quartzites and good quality xenomorphic quartz are fragmented, being only represented by medium-sized knapping products (flakes) and/or some retouched flakes (de Lombera-Hermida et al., 2021).

There is a differential management of the raw materials according to their local or allochthonous provenance and quality. A wide variety of knapping methods is reported at Level 3, with expedient reduction

methods (bipolar-on-anvil reduction, longitudinal, orthogonal and centripetal), mostly applied on local quartz, and structured and hierarchical methods implying a higher volumetric and morphological pre-determination (hierarchical centripetal/Levallois, discoidal and Kombewa) developed on the fine-grained quartzite and high-quality xenomorphic quartz. The shaping strategies are focused on the manufacturing of denticulates and notches, as well as side-scrapers (de Lombera-Hermida et al., 2021).

A remarkable feature of this lithic assemblage is the scarce retouching on fine-grained quartzites, which may indicate their use for specific and short activities, without major interest in extending the life of these artifacts. The use wear analysis of some artefacts identifies butchery activities related to the first processing of the animals such as dismemberment, carcass opening or butchering/defleshing, as well as skin processing and woodworking (Lazuén et al., 2011).

Summing up, the Level 3 lithic assemblage shows clear Middle Palaeolithic features such as the differential management of the raw materials, the obtention of small flakes, and the importance of the pre-determined and hierarchized methods (discoidal and Levallois), indistinctly applied on good quality xenomorphic quartz and quartzite. These features are observed in all the facies of level 3.

3. Methods

All faunal remains analysed in this study were obtained from archaeological excavations conducted at Cova Eirós between 2008 and 2021, corresponding to the years in which Level 3, the object of this study, was under excavation. This study includes, for the first time, the whole faunal assemblage of Level 3, updating the previous zooarchaeological studies (Valverde, 2019; de Lombera-Hermida et al., 2021; Rey-Rodríguez et al., 2016).

The dig follows a traditional methodology using 1 square metre grids. All bone fragments larger than 20 mm are recorded three-dimensionally at the site, while smaller finds are grouped by grid, following fixed intervals of 5 cm in depth. All the dental remains are individually recorded, regardless of their size. The extracted sediment is recovered and transported to the field lab for water screening using two superimposed metal sieves with mesh screens of 5 mm and 0.5 mm respectively. Then the sediment was sorted and classified at the Universidade de Santiago de Compostela (USC) in A Coruña, Spain; and at the Institut Català de Paleoecologia Humana i Evolució Social (IPHES-CERCA), in Tarragona, Spain.

For the study of the macrofaunal assemblage, the anatomical and taxonomical identifications were carried out using animal anatomy manuals (Davis, 1987; Hillson, 1992, 2005; Pales and Lambert, 1981b, Pales and Lambert, 1981a; Schmid, 1972; Varela and Rodríguez, 2004) and the reference collection from the Prehistory Laboratory at the Universidad de León (ULE), Spain. The remains were identified to the closest possible taxonomic unit, whether species, genus, family or size group. For each specimen, the laterality, bone portion, and degree of fusion for bone remains were recorded. Dental age estimation was done using the Individual Dental Age Stages (IDAS) system proposed by Anders et al. (2011). For specimens that could not be assigned to a taxon or family, weight groups were used following Brain (1981) model, modified by Marean et al. (2000): Size 1 (<20 kg), Size 2 (18–100 kg), Size 3 (70–300 kg), Size 4 (300–1,000 kg) and Size 5 (>1,000 kg), distinguishing between ungulates and carnivores when possible. To quantify the assemblage the Number of Identified Specimens (NISP), Minimum Number of Elements (MNE) and Minimum Number of Individuals (MNI) were used (Lyman, 2008).

The taphonomic study of these remains has been carried out using an Olympus SZ-51 and a ZEISS Stemi-508 stereomicroscopes with up to 50x magnification. The surface of these remains was examined for evidence of anthropic modifications (cutmarks, intentional fragmentation, thermal alteration), carnivore activity (tooth marks, digestion traces) (Andrés et al., 2012; Delaney-Rivera et al., 2009; Domínguez-Rodrigo et al., 2012; Domínguez-Rodrigo and Piqueras, 2003; Esteban-Nadal et al., 2010; Haynes, 1983), and fossil-diagenetic alterations (trampling, weathering, chemical dissolution, abrasion, manganese and iron coatings (Behrensmeyer, 1978; Courtenay et al., 2020; Fernández-Jalvo and Andrews, 2016; López-González et al., 2006).

The small vertebrate fossil assemblage was identified using established paleontological criteria: Furió (2007) for insectivores, Sevilla (1988) for Chiroptera, López-García et al. (2011a, 2011b) and Cuenca-Bescós et al. (2009) for rodents, and Blain (2005, 2009) for anurans and snakes. Species identification was based on diagnostic cranial and postcranial elements in accordance with systematic palaeontology. The material was examined using a binocular microscope, and images were captured with a Dino-lite AM7915MZTL.

The taphonomic analysis of rodent remains was carried out following a systematic descriptive method (Andrews, 1990; Fernández-Jalvo and Andrews, 2016). This approach focuses on identifying modifications to prey bones caused by predation, with particular emphasis on the degree of digestion observed on the teeth and broadly categorizing the types of modifications produced by predators. A previous taphonomic study by Rey-Rodríguez et al. (2016) was conducted, and this work incorporates an analysis of the new recovered material.

3.1. Paleoclimatic reconstruction

To reconstruct the paleoclimatic conditions at Cova Eirós, we applied the Bioclimatic Model (BM). This model enables the quantification of changes in palaeotemperature and palaeoprecipitation. The BM was originally developed by Hernández Fernández (2001) and Hernández-Fernández et al. (2007): small and large mammal species can be grouped into ten distinct climate zones. Based on the assemblage analysed all the ten zones are represented (Table 1).

To begin, the Climatic Restriction Index ($CRI_i = 1/n$, where i is the climatic zone and n is the number of zones where the species occurs) and the Bioclimatic Component ($BC_i = (\sum CRI_i) \times 100 / \sum S$, where i is the climatic zone and S is the number of species) were calculated. From these indices, a regression-based mathematical model was used to estimate climatic parameters.

Using the BM, we estimated the mean annual temperature (MAT), mean temperature of the coldest month (MTC), mean temperature of the warmest month (MTW), and mean annual precipitation (MAP). These values were then compared with data collected for the council of Triacastela by the European Centre for Medium-Range Weather Forecast (ECMWF) between 1991 and 2021 and retrieved from Climate-Data.org.

Table 1
Bioclimatic Model data for Cova Eirós Level 3 according to Hernández-Fernández (2001) and Hernández-Fernández et al. (2007). I) Equatorial; II) Tropical with summer rains; III) Transition tropical semi-arid; IV) Winter rain and summer drought; V) Warm-temperate; VI) Typical temperate; VII) Arid-temperate; VIII) Cold-temperate (boreal); IX) Arctic.

Taxa	I	II	II/III	III	IV	V	VI	VII	VIII	IX
<i>Rupicapra pyrenaica</i>	0	0	0	0	0.2	0.2	0.2	0.2	0.2	0
<i>Capra pyrenaica</i>	0	0	0	0	0.333	0	0.333	0.333	0	0
<i>Cervus elaphus</i>	0	0	0	0	0.333	0	0.333	0.333	0	0
<i>Capreolus capreolus</i>	0	0	0	0	0.5	0	0.5	0	0	0
<i>Sus scrofa</i>	0.143	0.143	0.143	0	0.143	0.143	0.143	0.143	0	0
<i>Equus ferus</i>	0	0	0	0.333	0.333	0	0	0.333	0	0
<i>Coelodonta antiquitatis</i>	0	0	0	0	0	0	0	0.333	0.333	0.333
<i>Canis lupus</i>	0	0.111	0.111	0.111	0.111	0.111	0.111	0.111	0.111	0.111
<i>Vulpes vulpes</i>	0	0	0	0.143	0.143	0.143	0.143	0.143	0.143	0.143
<i>Panthera pardus</i>	0.143	0.143	0.143	0.143	0.143	0.143	0.143	0	0	0
<i>Crocota crocuta</i>	0	0.2	0.2	0.2	0.2	0.2	0	0	0	0
<i>Ursus spelaeus</i>	0	0	0	0	0.25	0	0.25	0.25	0.25	0
<i>Oryctolagus cuniculus</i>	0	0	0	0	1	0	0	0	0	0
<i>Apodemus sylvaticus</i>	0	0	0	0	0.5	0	0.5	0	0	0
<i>Arvicola amphibius</i>	0	0	0	0	0.25	0	0.25	0.25	0.25	0
<i>Arvicola sapidus</i>	0	0	0	0	0.5	0	0.5	0	0	0
<i>Chionomys nivalis</i>	0	0	0	0	0.25	0	0.25	0	0.25	0.25
<i>Clethrionomys glareolus</i>	0	0	0	0	0	0	0.5	0	0.5	0
<i>Microtus (Terricola) lusitanicus</i>	0	0	0	0	0	1	0	0	0	0
<i>Microtus arvalis</i>	0	0	0	0	0	0	1	0	0	0
<i>Microtus agrestis</i>	0	0	0	0	0	0	0.5	0	0.5	0
<i>Alexandromys oeconomus</i>	0	0	0	0	0	0	0.33	0	0.33	0.33
<i>Pliomys coronensis</i>	0	0	0	0.2	0.2	0	0.2	0.2	0.2	0

3.2. Paleoenvironmental reconstruction

The paleoenvironmental reconstruction in this study utilizes the Habitat Weighting method (HW) (Evans et al. 1981; Andrews, 2006; modified by Blain et al. 2008; López-García et al., 2011a, b). This approach is based on the current habitat distribution of each taxon and averaged with the minimal number of individuals (MNI).

The habitats are categorized into five types (Blain et al. 2008; López-García et al. 2011a, López-García et al., 2010): Open Dry (OD) – meadows experiencing seasonal climatic variation; Open Humid (OH) – evergreen meadows with dense pastures and suitable topsoils; Woodland (Wo) – developed forests, including woodland margins and forest patches; Rocky (Ro) – rocky or stony areas with little to no vegetation; and Water (Wa) – regions near lakes, streams and ponds. A value of 1 is distributed among the habitats where the species are currently found (Table 2).

Special cases, such as *Alexandromys oeconomicus* and *Pliomys coronensis*, were considered, as these species are no longer present in the Iberian Peninsula. *Alexandromys oeconomicus* currently inhabits cold, open environments in northern and central Europe (Markova, 2006). However, during the Late Glacial, it was associated with both open humid and woodland habitats (interstadial types) (Cuenca-Bescós et al., 2009). This historical distribution has been incorporated into the Habitat Weighting method for this study. For *Pliomys coronensis*, its habitat preference for rocky substrates (Cuenca-Bescós et al., 2010) was taken into account. Values for *Pliomys coronensis* in the Habitat Weighting method were assigned based on the predominance of rocky environments, reflecting its ecological specificity. In the case of *Ursus spelaeus* and *Coelodonta antiquitatis*, two taxa extinct since the end of the Upper Pleistocene, their closest living taxonomic counterparts were used. As to the cave bear, we decided to use *Ursus arctos* due to its taxonomic affinity and because the species is native to the Iberian Peninsula. For *Coelodonta antiquitatis*, the closest living relative is *Dicerorhinus sumatrensis*, but it is an endemic species of Southeast Asia with a highly reduced habitat nowadays, so we consider that the potential ecological information provided by this taxon is not applicable to

Table 2

Habitat Weighting method applied to the faunal assemblage of Cova Eirós Level 3. OD) Open Dry; OH) Open Humid; Wo) Woodland; Ro) Rocky; Wa) Water.

Taxa	OD	OH	Wo	Ro	Wa
Rupicapra pyrenaica	0.25	0.25	0.25	0.25	
Capra pyrenaica		0.33	0.33	0.33	
Cervus elaphus	0.33	0.33	0.33		
Capreolus capreolus	0.33	0.33	0.33		
Sus scrofa	0.25	0.25	0.25		0.25
Equus ferus	0.5	0.5			
Coelodonta antiquitatis	0.5	0.5			
Canis lupus	0.25	0.25	0.25		0.25
Vulpes vulpes	0.33	0.33	0.33		
Panthera pardus	0.33	0.33	0.33		
Crocota crocuta	1				
Ursus spelaeus	0.25	0.25	0.25		0.25
Oryctolagus cuniculus	0.5	0.5			
Rana temporaria		0.4	0.4		0.2
Apodemus sylvaticus			1		
Arvicola amphibius		1			
Arvicola sapidus					1
Chionomys nivalis				1	
Clethrionomys glareolus			1		
Microtus (Terricola) lusitanicus		0.5	0.5		
Microtus arvalis		0.5	0.5		
Microtus agrestis	0.5		0.5		
Alexandromys oeconomicus		0.5	0.5		
Pliomys cf. coronensis				1	
Myotis sp.			0.5		0.5
Rhinolophus ferrumequinum			0.75	0.25	
Sorex minutus			0.5	0.5	
Sorex sp.		0.5	0.5		
Talpa cf. occidentalis		0.5	0.5		

our study case. For this reason, we have decided to rely on the historical distribution inferred from the bibliography (Álvarez-Lao and García, 2011b).

4. Results

4.1. Taxonomic and taphonomic study

The macrofaunal assemblage tallies a total of 3,353 specimens, a sample very marked by fragmentation, with 94.76 % of the bone remains being affected and with an average size of 28 x 12 mm. We were able to identify 787 specimens (23.47 %) anatomically and taxonomically (Table 3; Fig. 2), reaching both the element and species for all except for large bovines, where we lack elements that allow for the secure identification of aurochs (*Bos primigenius*) or bison (*Bison priscus*), and which we have grouped under the category *Bos/Bison*, as is commonly done in archaeological sites. In addition to these, 224 remains (6.6 %) have been identified anatomically reaching the element level and grouped by weight groups with the Size 2 being the best represented (n = 138), followed by size 4 (n = 40), size 3 (n = 37) and size 1 (n = 9), with no fragments being attributed to a size 5 animal. The best represented taxon is the cave bear, *Ursus spelaeus* (%NISP = 61.63 %, MNI = 52), followed by the red deer, *Cervus elaphus* (%NISP = 16.65 %, MNI = 9); the chamois, *Rupicapra pyrenaica* (%NISP = 7.24 %, MNI = 9); the roe deer, *Capreolus capreolus* (%NISP = 5.08 %, MNI = 6); and the red fox, *Vulpes vulpes* (%NISP = 2.67 %, MNI = 3). Among the indeterminate remains assigned to weight groups, remains identified as small-sized ungulates –those in which it is not possible to taxonomically distinguish between chamois and roe deer– stand out, representing 39.28 % of these remains. This is an important factor to consider because it would significantly increase the percentage of both taxa in terms of NISP and providing a more complete skeletal profile, as the vast majority of remains from small ungulates identified at the species level belong to dental remains, with postcranial elements being highly underrepresented, whereas in the small-sized ungulates category the situation is reversed. Ongoing ZooMS analysis will help in the resolution of this bias. A few leporid (*Oryctolagus cuniculus*), and unidentified bird and fish remains have been recovered too, but in very discrete numbers.

The total MNI for the level is 90, with more than half of these being *Ursus spelaeus*, representing 57.78 % of the total individuals. This taxon shows a typical pattern of non-violent attrition with an overrepresentation of immature individuals and a few senile individuals (Stiner, 1998; Weinstock, 2000). The remaining taxa, with a significantly lower number of individuals, provide less information, but there

Table 3

Cova Eirós Level 3 macrofaunal representation of the number of identified specimens (NISP), percentage of the number of identified specimens (%NISP), minimum number of elements (MNE) and minimum number of individuals (MNI), dividing between immature individuals (IDAS 1–2) on the left and adult individuals (IDAS 3–5) on the right.

Taxa	NISP	%NISP	MNE	MNI (imm/ad)
Bos/Bison sp.	6	0.76	3	1 (0/1)
Rupicapra pyrenaica	57	7.24	50	9 (2/7)
Capra pyrenaica	4	0.51	4	1 (0/1)
Cervus elaphus	131	16.65	56	9 (4/5)
Capreolus capreolus	40	5.08	37	6 (4/2)
Sus scrofa	4	0.51	4	1 (0/1)
Equus ferus	9	1.14	4	2 (1/1)
Coelodonta antiquitatis	7	0.89	2	1 (1/0)
Canis lupus	9	1.14	9	2 (1/1)
Vulpes vulpes	21	2.67	20	3 (2/1)
Panthera pardus	3	0.38	3	1 (0/1)
Crocota crocuta	5	0.64	5	1 (0/1)
Ursus spelaeus	485	61.63	455	52 (45/7)
Oryctolagus cuniculus	6	0.76	6	1 (0/1)
TOTAL	787	100	658	90 (60/30)



Fig. 2. Macrofaunal remains identified in Cova Eirós Level 3. A) *Cervus elaphus* metatarsal (sin); B) *Cervus elaphus* radius (sin); C) *Cervus elaphus* tibia; D) *Rupicapra pyrenaica* cranium (dex); E) *Rupicapra pyrenaica* mandible (dex); F) *Rupicapra pyrenaica* maxilar with upper first molar (dex); G) *Capreolus capreolus* axis; H) *Capreolus capreolus* unfused tibia (dex); I) *Ursus spelaeus* femur (sin); J) *Ursus spelaeus* metacarpal IV; K) *Ursus spelaeus* upper canine (dex); L) *Bos/Bison* sp. mandible (sin); M) *Bos/Bison* sp. lower first molar (dex); N) *Coelodonta antiquitatis* fourth decidual premolar (sin); O) *Crocota crocuta* mandible (dex); P) *Panthera pardus* metatarsal II; Q) *Vulpes vulpes* tibia (sin); R) *Vulpes vulpes* metacarpal IV; S) *Sus scrofa* scaphoides. Scale bar = 10 mm.

is a noticeable predominance of adults among chamois, a balance between adults and immature individuals among red deer, and a predominance of immature individuals among roe deer, which reflects different patterns for each taxon (Table 3).

Anthropic exploitation in the assemblage affects 5.5 % of the remains. This primarily consists of bones with evidence of intentional fracturing ($n = 69$), cutmarks ($n = 43$) and signs of thermal alteration ($n = 31$) (Fig. 3). Most of the marks are located on unidentified bone splinters, although exploitation of red deer ($n = 15$) and, to a lesser extent, cave bear ($n = 2$) has been confirmed. Additionally, bone tools have been identified, with two retouchers made from red deer metacarpals.

Carnivore activity is slightly higher in the assemblage, affecting 8 %

of the remains in the form of scores ($n = 131$), pitting ($n = 88$), crenulated edges ($n = 73$), digestion ($n = 48$) and furrowing ($n = 10$) (Fig. 3). Unlike the evidence of anthropic exploitation, this type of alteration seems to affect the entire faunal spectrum in proportions similar to the frequency of each taxon at the site. Thus, the species that shows the highest number of evidence of predatory action are the cave bear (8.6 %) and the red deer (5.6 %); when considering broader categories, small-sized ungulates show the highest percentage, with 9.1 % of the total modified assemblage, reaching 13.1 % when adding the percentages of chamois and roe deer. At last, although in a limited number of remains ($n = 6$), carnivore marks have been found overlapping cutmarks and percussion strikes, indicating that at least part of the assemblage altered by carnivores is associated with secondary scavenging after the

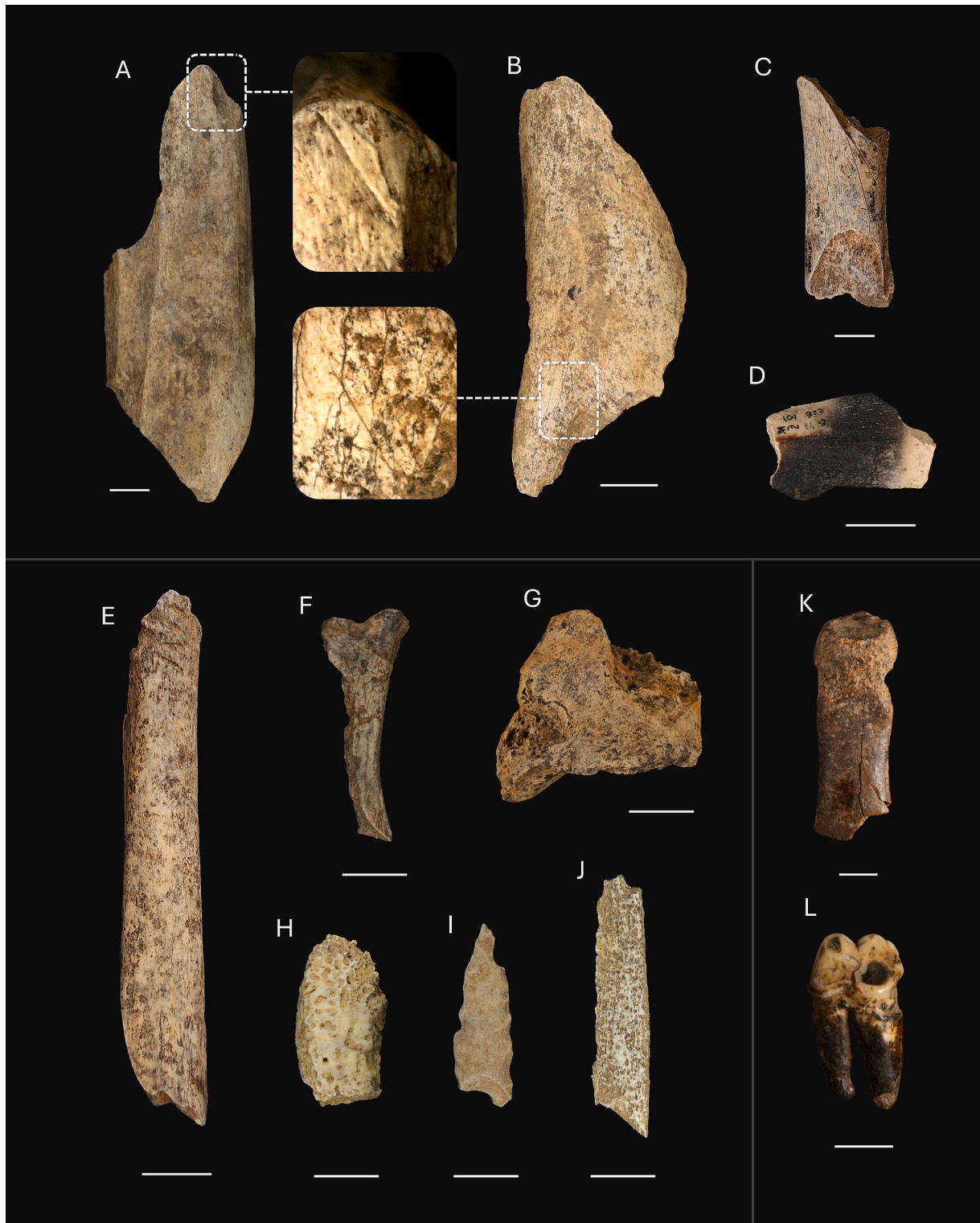


Fig. 3. Taphonomical alterations identified in Cova Eirós Level 3. A-B) Cutmarks; C) Percussion marks; D) Termoalteration; E-G) Carnivore tooth marks; H-J) Digested remains; K-L) Remains affected by water. Scale bar = 10 mm.

neanderthal groups abandoned the cave.

The broad range of prey, the abundance of scores over pits (scores/pits ratio = 1.49), the high quantity of digested remains (39.7 % of the remains altered by carnivores), the high fragmentation of the remains and the size of the tooth marks, with a mean pit size of 2.17×1.82 mm, suggests that the primary agents of this accumulation were either hyenas (*Crocota crocuta*) or wolves (*Canis lupus*) (Delaney-Rivera et al., 2009;

Domínguez-Rodrigo et al., 2012; Domínguez-Rodrigo and Piqueras, 2003; Esteban-Nadal et al., 2010; Haynes, 1983), being both taxa present at the site. However, the probable secondary involvement of other agents such as red fox or cave bear should not be ruled out, as has been observed in other areas of the cave system (Pérez-Rama et al., 2010).

Aside from these two accumulation agents, the presence of water at the site seems evident given the high number of remains stained with

manganese oxides (81.79 %), rounded (59.55 %), polished (78.4 %) and with abundant striations resulting from abrasion (41.46 %) (Fig. 3). This suggests that the accumulation of small pools of water or the formation of low-intensity currents from inside the cave played a significant role in the formation of this assemblage and that during the accumulation and sedimentation of the level, the region must have maintained relatively high humidity levels in order to form this type of flooded soils.

The small-vertebrates assemblage comprises 393 identified specimens, corresponding to a minimum of 238 individuals (Table 4; Fig. 4). The sample includes 17 taxa, with two species, *Clethrionomys glareolus* and *Pliomys* cf. *coronensis*, being recorded for the first time at Cova Eirós. These additions expand on the diversity previously documented by Rey-Rodríguez et al. (2016). *Microtus agrestis* is the most abundant species, making up 24.79 % of the assemblage, followed by *Microtus (Terricola) lusitanicus* (20.59 %) and *Microtus arvalis* (18.07 %). Other notable contributors include *Arvicola amphibius* and *Arvicola sapidus*, with 24 (10.08 %) and 16 (6.72 %) individuals, respectively. While taxa such as *Chionomys nivalis*, *Sorex* sp. and various bat species (Chiroptera indet., *Myotis* sp., *Rhinolophus ferrumequinum*) are represented in smaller proportions, their presence highlights the diverse range of habitats reflected in the assemblage. Amphibians, like *Rana temporaria*, are also present in small numbers.

The taphonomic study conducted on the small-vertebrates assemblage revealed that 52.29 % of the sample shows signs of digestion (Table 5), with the majority exhibiting light digestion (67.76 %), followed by moderate (24.59 %) and heavy digestion (7.65 %). These findings suggest a moderate degree of bone modification, consistent with predator category 3, typically associated with nocturnal raptors.

4.2. Bioclimatic model and habitat weighting

When performing both the BM and the HW calculations, discrepancies have been observed depending on whether only microfauna data is used or if macrofauna data is also incorporated. Notable differences include a change of almost 3 °C in the mean annual temperature or more than 300 mm in the annual precipitation calculation (Table 6). This difference is caused by the small vertebrates having a greater discriminant capacity than macromammals, as they are more climatically specialized, while large mammals are more influenced by the habitat type than by climate itself (Hernández Fernández, 2001). Although in this type of reconstruction it is generally assumed that incorporating a greater variety of taxa into the model will yield a more accurate

Table 4
Cova Eirós Level 3 small vertebrate representation of the number of identified specimens (NISP), percentage of the number of identified specimens (%NISP) and minimum number of individuals (MNI).

Taxa	NISP	%NISP	MNI
<i>Rana temporaria</i>	2	0.84	2
Rodentia indet.	2	0.00	0
<i>Apodemus sylvaticus</i>	6	1.26	3
<i>Arvicola amphibius</i>	37	10.08	24
<i>Arvicola sapidus</i>	29	6.72	16
<i>Chionomys nivalis</i>	10	2.52	6
<i>Clethrionomys glareolus</i>	3	1.26	3
<i>Microtus (Terricola) lusitanicus</i>	86	20.59	49
<i>Microtus arvalis</i>	73	18.07	43
<i>Microtus agrestis</i>	95	24.79	59
<i>Microtus</i> gr. <i>arvalis-agrestis</i>	15	4.20	10
<i>Alexandromys oeconomus</i>	1	0.42	1
<i>Pliomys</i> cf. <i>coronensis</i>	1	0.42	1
<i>Myotis</i> sp.	1	0.42	1
Chiroptera indet.	8	2.10	5
<i>Rhinolophus ferrumequinum</i>	1	0.42	1
<i>Sorex minutus</i>	3	0.84	2
<i>Sorex</i> sp.	13	2.94	7
<i>Talpa</i> cf. <i>occidentalis</i>	7	2.10	5
TOTAL	393	100	238

reconstruction of the paleoclimatic context (Hernández Fernández, 2001), we have chosen to calculate the climatic variables (MAT, MTW, MTC and MAP) using only the small-vertebrate record for several reasons. Firstly, when making comparisons with other sites, studies of this kind typically use only small vertebrates (Fernández-García et al., 2023), so it allows for more precise comparisons. The second reason is that small-vertebrate accumulations usually originate from the immediate surroundings of the site, regardless of the agent causing the accumulation, providing a more precise reconstruction; whereas large mammals roam larger areas and, given that this is an archaeopaleontological site, could have been brought from locations kilometres away by human or non-human predators and reflecting different climatic conditions. In contrast, for habitat reconstruction, we have chosen to use the data from all taxa present in the site to obtain a more comprehensive view that better aligns with a regional perspective that goes beyond the immediate surroundings of the cave. Even if the large mammal assemblage is not an exact reflection of the faunal diversity of the area, as presence/absence of species may be conditioned by hunting choices of both human and non-human predators, it provides insights into the diversity of environments that could be found in the vicinity of the site, rather than solely focusing on the specific habitat in which the cave is located. This distinction is important because it can also offer clues about the type of catchment strategies followed by both hunter-gatherers and other predators.

Thus, the paleoclimatic analysis (Table 1; Fig. 5) reflects a dominance of climate zones VI and IV, which together represent 50.33 % of the bioclimatic component of the site, being both forested zonobiomes. Other relevant –though less significant– climates range from the warm-temperate of zone V to arid and boreal conditions of zones VII and VIII. This reflects a mosaic habitat where different biomes converge, following a trend observed in the Cantabrian region where within a predominantly cold and dry climate, small refuge areas survived in the valleys with a significant arboreal development, even during the coldest phases of MIS 3 (Rivals and Álvarez-Lao, 2018).

Following the same trend, the paleoenvironmental reconstruction (Table 2; Fig. 6) reflects a habitat slightly dominated by woodland (36.4 %), with a broad and balanced importance of open humid areas (32.7 %) and open dry areas (17.6 %). The significance of rocky areas and water habitats is considerably lower, but still well represented by some taxa with strong associations, such as *Chionomys nivalis* with rocky areas or *Arvicola sapidus* with riverine formations.

We observed a significant decrease in the MAT and in the MTC compared to the current values, by −3 °C and −6.39 °C respectively, while the MTW remains almost unchanged, with a difference of only + 0.12 °C. The precipitation regime is relatively high, with figures similar to the current situation, with only about 150 mm less annually. This reflects a notably colder climate, with significantly harsher winters and mild summers, while retaining a relatively high precipitation regime.

5. Discussion

The evidence from both the traditional zooarchaeological study and the paleoenvironmental methods employed reflects a predominance of forest as the main habitat near the site. The application of the BM has shown that the main climatic zones, with a BCI of around 25 % each, are zones VI and IV. The former is characterized by a typical temperate climate, with cold winters and cool summers and high precipitations, being dominated by deciduous forests and rich herbaceous and shrub components. This aligns perfectly with the temperature and precipitation estimates inferred from the paleoclimate reconstruction (Table 1), indicating much colder winters than nowadays, mild summers and high precipitation levels. Meanwhile, zone IV is a transitional climate with abundant seasonal rains and summer droughts but reduced winter cold. We can also point out that, compared to the first BM carried out at the site (Rey-Rodríguez et al., 2016), the represented biomes have expanded from just six (IV, V, VI, VII, VIII and IX) to the ten zones considered by

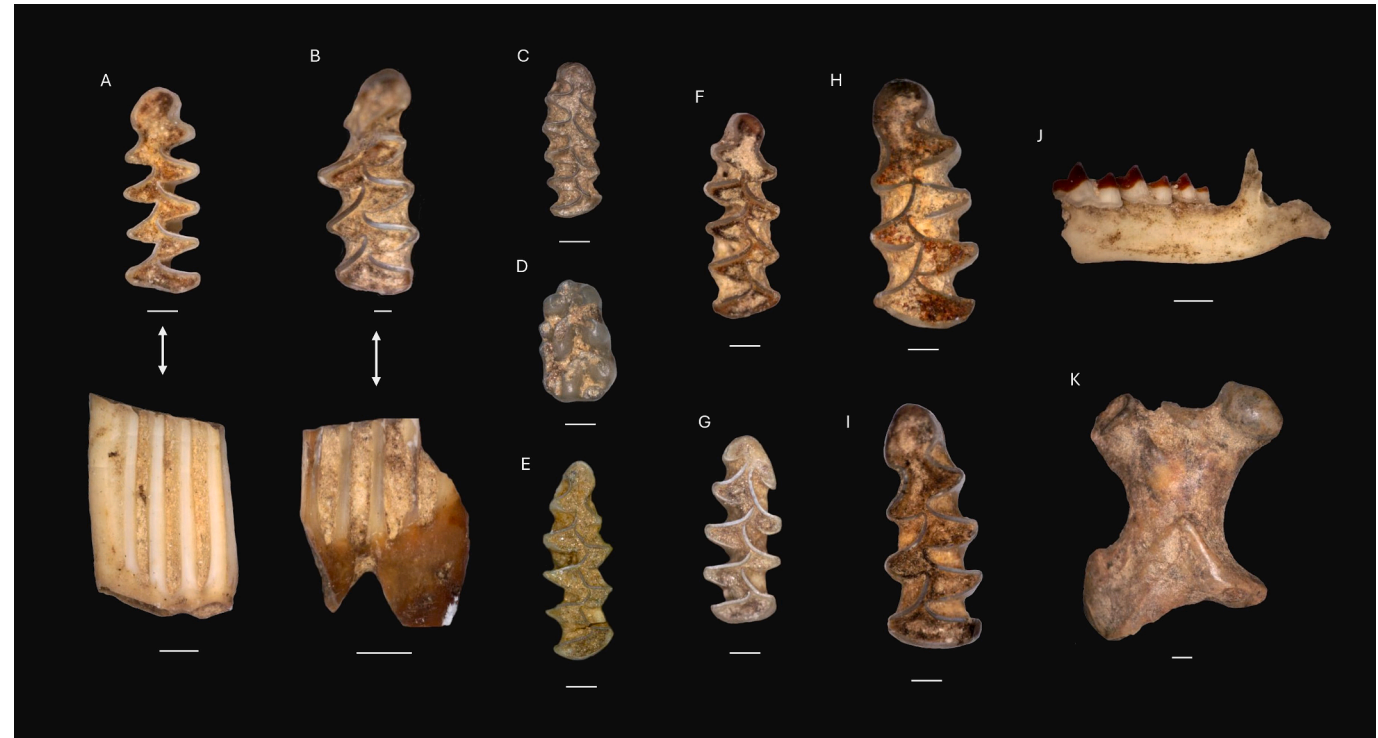


Fig. 4. Small vertebrates identified in Cova Eirós Level 3. A) *Pliomys* cf. *coronensis* M₁ (sin); B) *Clethrionomys glareolus* M₁ (sin); C) *Microtus* (*Terricola*) *lusitanicus* M₁ (dex); D) *Apodemus* cf. *sylvaticus* M₁ (sin); E) *Microtus agrestis* M₁ (dex); F) *Microtus arvalis* M₁ (dex); G) *Chionomys nivalis* M₁ (dex); H) *Arvicola sapidus* M₁ (sin); I) *Arvicola amphibius* M₁ (sin); J) *Sorex* sp. mandible (sin); K) *Talpa* cf. *occidentalis* humerus (dex). M₁ = First lower molar. Scale bar = 1 mm.

Table 5
Intensity of digestion on the small vertebrate remains from Cova Eirós Level 3. Relative percentage of the total digested remains between brackets.

	N	%
Absent	167	47.71
Light	124	35.43 (67.76)
Moderate	45	12.86 (24.59)
Heavy	14	4 (7.65)
TOTAL DIGESTED	183	52.29
TOTAL	350	100

Table 6
Comparison between the current values of Triacastela and those inferred from the Bioclimatic Model. Both the global data and those obtained by using only the microfauna are presented for comparison. MAT) Mean Annual Temperature; MTW) Mean Temperature of warmest month; MTC) Mean Temperature of Coldest Month; MAP) Mean Annual Precipitation. Standard deviation shown in parentheses. Data from Triacastela retrieved from [Climate-Data.org](https://climate-data.org).

	Triacastela	BM – Total	BM – Micro
MAT (°C)	10.3	10.35 (3.39)	7.32 (3.39)
MTW (°C)	17.5	20.48 (4.77)	17.62 (4.77)
MTC (°C)	4	0.52 (4.66)	–2.39 (4.66)
MAP (mm)	1293	833.40 (533.24)	1,135.14 (533.24)

the model, reflecting the broader environmental spectrum covered by the large mammals present at the site.

The habitat reconstruction obtained from the HW method also reflects a dominant role for the forest, covering 32.7 % of the habitat represented by the fauna. This picture aligns with the information obtained from the preliminary anthracological study, in which trees –particularly *Pinus sylvestris*– predominates (Martín Seijo, 2013). In summary, these results fully align with the reconstruction of the temperature and precipitation at the site, indicating cold winters, mild

summers and abundant rainfall.

The reconstruction of the temperature and precipitation regime for this period at the site reflects significant changes when compared to the current climate (Table 6) and with the results from the previous reconstruction (Rey-Rodríguez et al., 2016) and by using the climate data from the council where the site is located, we provide a more accurate comparison than that offered in 2016, which used data from the Lugo weather station, over 50 km away.

Based on criteria such as the comparison of the micromammal assemblages from sites in the Cantabrian region during this period, such as El Sidrón (Sesé, 2011), La Viña (de la Rasilla et al., 2020), Llonín (Sanchis et al., 2019) or El Esquilieu (Baena et al., 2005), we observe that they consistently reflect the same conditions inferred in this study: assemblages dominated by taxa typical of forested areas with abundant vegetation, high humidity, and interspersed open spaces. Cold-adapted taxa are not abundant in these assemblages, and as in the case of Cova Eirós, *A. oeconomus* is the taxon that represents the harshest conditions, being represented by few individuals or absent altogether. This indicates that the climatic bonanza observed in Cova Eirós is not an isolated occurrence, but rather a shared with the rest of the northern Iberian Peninsula. But if we focus on the palaeoecological reconstruction provided by these assemblages, we see that there are differences compared to the Cantabrian region (Fernández-García et al., 2023). The temperature decline aligns with the trend of the region, with an average loss of –3.3 °C compared to –3 °C at Cova Eirós, which is situated at an intermediate point between the –2.4 °C loss in the Mousterian (>45 – 42 ka BP) and the –4.4 °C in the Aurignacian (35–30 ka BP). On the other hand, MAP reconstruction shows a completely different situation, with Cova Eirós receiving almost twice the annual rainfall (1,135 mm) than rest of the sites and experiencing a decline of only 12.2 % compared to the current values, versus the 30–40 % decline observed in the region. The authors of the cited paper also pointed out the differences between the eastern and western sectors of the Cantabrian region, with the latter having a relatively more benign climate and greater precipitation, with

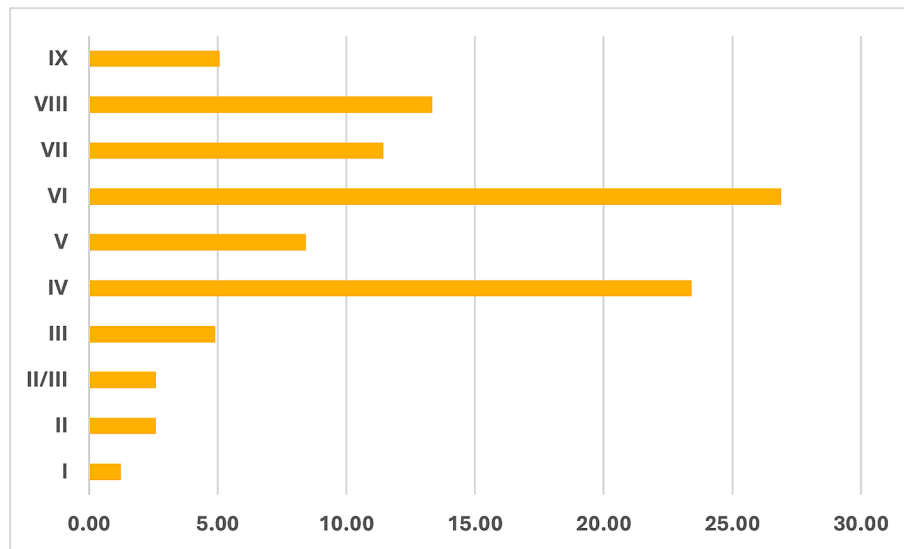


Fig. 5. Percentage of each climate zone represented by the faunal assemblage of Cova Eirós Level 3. I) Equatorial; II) Tropical with summer rains; III) Transition tropical semi-arid; IV) Winter rain and summer drought; V) Warm-temperate; VI) Typical temperate; VII) Arid-temperate; VIII) Cold-temperate (boreal); IX) Arctic.

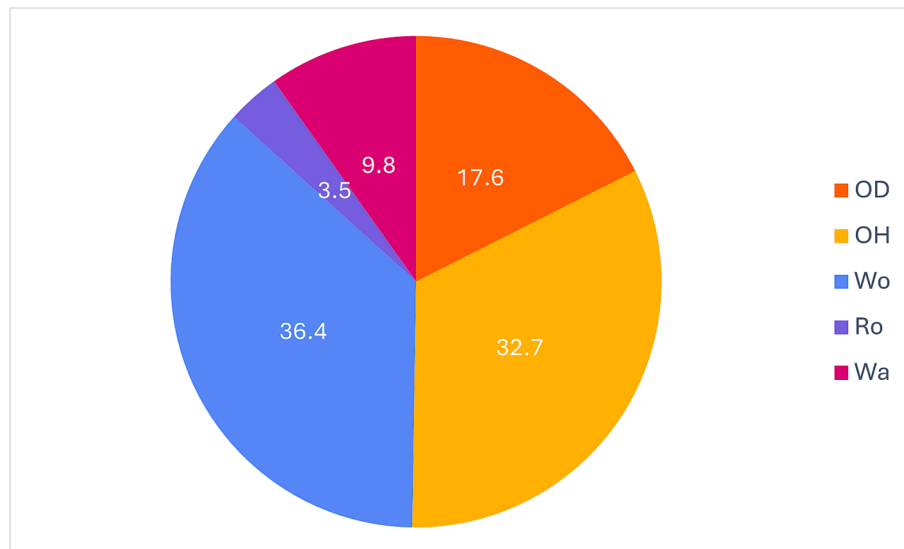


Fig. 6. Percentage of each habitat represented by the faunal assemblage of Cova Eirós Level 3. OD) Open Dry; OH) Open Humid; Wo) Woodland; Ro) Rocky; Wa) Water.

the highest MAP values recorded at La Güelga and Torca del León, both sites located in Asturias. If we consider the results obtained here for Cova Eirós this trend seems to increase drastically as we move further into the western extreme of the region, although we must be cautious with this interpretation considering two important factors. Firstly, we are analysing a single occupation level, and although the results from Level 2 (Rey-Rodríguez et al., 2016) also point in this same direction, they still reflect a single site. Secondly, there is both significant geographical separation between Cova Eirós and the rest of the sites in the Cantabrian region (>100 km in straight line), as well as differences in the location of the caves themselves, both in altitude (with Eirós at over 700 m a.s.l. compared to less than 300 m a.s.l. for the others) and in distance from the current coastline (over 80 km for Eirós versus less than 10–20 km in most cases in the Cantabrian region). In any case, the reconstruction carried out at Eirós reveals climatic characteristics that have not been observed at any other site in the northern part of the Iberian Peninsula, and further work in the future will help better understand this situation.

The faunal assemblage from level 3 shows that the subsistence

strategy of these Neanderthal hunter-gatherers was based on the exploitation of red deer, with other taxa –except for occasional exploitation of cave bear and size 4 ungulates– being outside the range of Neanderthal exploitation. The role of small ungulates –i.e. *Rupicapra pyrenaica* or *Capreolus capreolus*– does not show evidence of direct anthropic exploitation, but rather from carnivore activity during periods when human groups abandoned the cave. The absence of cutmarks on these taxa, along with the significant presence of carnivore tooth marks seems to confirm this interpretation. This pattern, in which red deer and large ungulates are brought into the site by hunter-gatherers and small ungulates by carnivores is common across other Middle Palaeolithic sites in the Iberian Peninsula (Sanchis et al., 2019; Yravedra and Cobo-Sánchez, 2015). In the Cantabrian region, for example, this pattern is observed at sites such as Amalda (Yravedra, 2006a, Yravedra, 2010a), Hornos de la Peña (Yravedra, 2010b) or El Ruso (Yravedra et al., 2010). However, there are occasional cases where these taxa were indeed hunted, such as El Esquilleu (Yravedra et al., 2014; Yravedra, 2006a, 2006b) or Valdegoba (Diez Fernández-Lomana, 2006), outside the

Cantabrian range.

The technological and zooarcheological analyses point to recurrent short-termed occupations at the site alternating with the use of the cavity by bears and other carnivores. The non-residential nature of those occupations, the relative low density of artefacts and the spatial fragmentation of the *chaînes opératoires* are indicative of the high mobility of these communities (de Lombera-Hermida et al., 2021; Valverde, 2019). These features, pointing to high logistic mobility, are consistent with other final Middle Palaeolithic neanderthal occupations across the Cantabrian region, like El Esquilieu or La Viña (Ríos-Garázar, 2012; Sanchis et al., 2019; Baena et al., 2012; Baena-Preysler and Carrión-Santafé, 2013; de la Rasilla et al., 2020).

The presence of cold-adapted species at the site, limited in this case to a single individual of both *Coelodonta antiquitatis* and *Alexandromys oeconomicus*, reflects a trend seen throughout the Cantabrian region, where these taxa along with *Rangifer tarandus*, *Mammuthus primigenius* and other rarer taxa such as *Ovibos moschatus*, *Saiga tatarica* or *Alopex lagopus* conform the so-called “glacial fauna” and consistently appears in MIS 3 assemblages, though always in very limited proportions within assemblages dominated by more mesophilic taxa like *Cervus elaphus*, *Rupicapra pyrenaica*, *Capra pyrenaica*, large bovids, etc. (Altuna, 1992; Álvarez-Lao and García, 2011a).

Within its immediate context, the limited number of identified faunal assemblages in NW Iberia determines the comparisons at a regional level. The assemblages from Cova Eirós Level 2 (36,136–35,032 cal BP) (de Lombera-Hermida et al., 2021; Rey-Rodríguez et al., 2016) and A Valiña (34,123–32,987 cal BP) (Llana Rodríguez et al., 1996), while slightly more recent and already attributed to Early Upper Palaeolithic, still fall within MIS 3. Paleoenvironmental evidence at these sites also points towards a pivotal importance of the forest and to relatively high precipitation regimes (Fernández Rodríguez et al., 1993; Llana Rodríguez et al., 1996; Rey-Rodríguez et al., 2016). In the small vertebrate record from A Valiña we find again the presence of *A. oeconomicus* and *P. coronensis* (Fernández Rodríguez et al., 1993; Peña and Rey, 1995). Therefore, these favourable conditions within a cold environment in the lower valleys of northwestern Iberia appear to have been relatively stable until –at least- the beginning of the Last Glacial Maximum (LGM). Evidence from Cova Eirós level 1 indicates that climatic deterioration caused a significant increase in aridity, leading to the formation of loess deposits at the site (Rodríguez Álvarez et al., 2011).

The taphonomic study revealed an abundance of evidence for water alteration of the faunal remains (i.e. manganese staining, rounding and polishing of surfaces, abrasion, etc.). This is interesting as it seems to confirm the formation of small pools and water flows in the cave during the formation of the level. This aligns with the results obtained from the BM, which indicate a high precipitation regime that likely led to the reactivation or rise of the groundwater level there.

It is worth noting the widespread presence of *Capreolus capreolus* in the record, a taxon that, while not considered rare in the Cantabrian Mousterian record, rarely appears in large quantities both in archaeological and paleontological sites before the Upper Pleistocene – Holocene transition amelioration (Marín-Arroyo and Sanz-Royo, 2022). The other identified taxa, while not closely linked to the habitat, also fit within a landscape dominated by forests, especially in the case of the small vertebrates (i.e. *Clethrionomys glareolus*, *Apodemus sylvaticus*, *Rhinolophus ferrumequinum*, etc.). The taxa strictly typical of open habitats, such as *Equus ferus* or *Coelodonta antiquitatis* are present in much smaller quantities, being limited to just one individual each. In the case of the woolly rhinoceros it is not surprising, as this taxon rarely appears in large quantities in the Cantabrian archaeopaleontological sites (Álvarez-Lao and García, 2011b). However, the horse is an animal that can reach high frequencies in MIS 3 sites such as El Castillo (Cabrera, 1984; Luret et al., 2020). This probably indicates that, while present, open habitats –both dry and humid- are less representative than forests in the surroundings of the site, which we interpret as evidence of the formation of a refuge area in the valley where the site is located. Another alternative

explanation would be that these species were indeed present in the immediate environment, but their absence could be attributed to hunting strategies focused on other taxa, both by humans and carnivores. However, we consider this hypothesis less likely, as the degree of anthropic intervention on the assemblage is not substantial enough to regard them as the sole accumulators, and the carnivores likely to contribute carcasses to the cave –*Crocota crocuta* and/or *Canis lupus*– regularly target equids as prey. For example, at the nearby site of A Valiña, a typical hyena den, equids represent 21.15 % of the ungulates (Fernández Rodríguez et al., 2018), while studies on wolves address their role as hunters of horses, even today, in the northwestern Iberian Peninsula (Yravedra et al., 2011).

Although the presence of these refuge areas corresponds to local anomalies from a climatic perspective (Hampe et al., 2013), the importance of these habitats was central to the Neanderthal groups that inhabited the Iberian Peninsula, favouring the occupation of these forested valleys over open and dry areas with much more limited resources (Ochando et al., 2022). In the valleys of the Cantabrian region, this is a constant trend we observe throughout the entire Palaeolithic sequence. These areas would serve as refuges for both tree species and the associated animal communities during the cold and dry stadial phases and served as a reservoir from which the recolonization of the surrounding steppe took place during interstadials. Such habitats would also be sought by Neanderthal hunter-gatherer groups in search of both refuge and fauna to exploit during the Late Middle Palaeolithic, as the recurrent neanderthal occupations at Cova Eirós point out (de Lombera-Hermida et al., 2021).

6. Conclusions

The analysis carried out at the late Mousterian level 3 of Cova Eirós has served to taxonomically and anatomically identifying a total of 1,180 specimens (NISP), with an MNI of 328 from at least 31 different taxa. This faunal record reflects a typical palimpsest in which remains from different accumulation episodes, with various agents involved, are interwoven. Firstly, there are short episodes of human occupation by hunter-gatherer groups with Mousterian technology, focusing their subsistence mainly on red deer. Secondly, some remains have been contributed by the activity of carnivores (either wolves or hyenas), which show a more diversified subsistence but with a significant contribution of small-sized ungulates. Their activity also involves the modification of remains associated with human presence, likely scavenged following the abandonment of the site, thus highlighting the rapid succession of different occupation episodes. The remains of cave bears, linked to the use of the cave as a hibernation den by these animals, constitute a substantial portion of the assemblage, as indicated by the high frequency of immature individuals (MNI = 45). Additionally, small-vertebrates are represented through contributions from nocturnal raptors, as demonstrated by the digestion patterns observed in their remains.

This varied assemblage reflects the presence of various habitats nearby, which have been confirmed by the paleoclimatic and paleoenvironmental reconstruction carried out. Both the reconstruction and the faunal assemblage show an environment typical of a glacial-period refuge area, with a predominantly wooded habitat interspersed with open spaces. Notably, the high Mean Annual Precipitation (MAP) is nearly the same as the current precipitation regime and doubles the precipitation regime inferred for other Cantabrian sites, which likely contributed significantly to the maintenance of these forested areas. Additionally, this region experienced a temperature significantly lower than today, a condition especially evident during the winter months, with a drop of over 6 °C on average.

The persistence of small Neanderthal groups in the mountain areas of the Cantabrian region has been interpreted as a result of territorial fragmentation caused by the climatic deterioration at the end of MIS 3. This would have led to much more mobile groups with shorter

occupations, which explains these final deposits being materially poorer as compared to earlier occupations at the same sites (Baena Preysler and Carrión Santafé, 2006). In recent years, this highly debated theory has regained relevance, as it has been shown that there was indeed a decline in the productivity of ecosystems in the northern Iberian Peninsula, matching the alleged beginning of the demographic decline around GS-12 (Vidal-Cordasco et al., 2022, Vidal-Cordasco et al., 2023). Our study demonstrates that there were Neanderthal communities in an environment favourable for occupation after this purported impoverishment of the habitats and that the environments occupied by these late Neanderthals do not differ significantly from those occupied by the first AMH during the Early Upper Palaeolithic in the region (de Lombera-Hermida et al., 2021; Rey-Rodríguez et al., 2016). Anyway, in the future it will be interesting to expand this study to the older Mousterian levels at the cave (levels 4 and 5), which represent a more intense and prolonged occupation, to see if the aforementioned climatic deterioration at the mid-late MIS 3 is reflected on the Cova Eirós sequence.

CRedit authorship contribution statement

Hugo Bal-García: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Iván Rey-Rodríguez:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Arturo de Lombera-Hermida:** Writing – review & editing, Writing – original draft, Project administration, Investigation, Funding acquisition. **Mikel Díaz-Rodríguez:** Writing – review & editing, Writing – original draft, Visualization, Investigation. **Carlos Fernández-Rodríguez:** Writing – review & editing, Investigation. **Xosé Pedro Rodríguez-Álvarez:** Writing – review & editing, Writing – original draft, Project administration, Investigation, Funding acquisition. **Ramón Fábregas Valcarce:** Writing – review & editing, Project administration, Funding acquisition.

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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.

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Appendix A. Supplementary data

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Data availability

Data will be made available on request.

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