



Reassessing palaeoenvironmental conditions during the Middle to Upper Palaeolithic transition in the Cantabrian region (Southwestern Europe)

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ABSTRACT

Climatic and environmental changes have been commonly proposed as driving factors behind the decline of Neanderthals in Europe. The Cantabrian region, in northern Iberia, is a key area for understanding the replacement of Neanderthals by Anatomically Modern Humans, where an early disappearance of Neanderthals in relation to other areas of Iberia has been proposed. To evaluate how climate might have influenced human behaviour during Marine Isotope Stage 3, an accurate review of palaeoecological conditions is required. For the first time, an assessment of the regional available terrestrial proxies linked to archaeo-palaeontological sites, including small vertebrate assemblages, pollen sequences, charcoal data and stable isotope studies on macromammals is undertaken in this region. In addition, records from macrofaunal assemblages and glacial records have also been considered. To standardise the information and allow inter-site comparison, data from pollen and small vertebrate sequences were transformed into quantitative climatic estimations of temperature and precipitation. Results show highly variable climatic shifts between archaeological levels, being consistent with the climatic fluctuations observed in the marine and ice core records. Small mammal assemblages reveal a mosaic landscape of open meadows followed by scattered forested areas. A progressive trend towards aridity from the end of the Mousterian to the early Aurignacian is reflected by changes in arboreal pollen, macromammal species and stable isotopes evidence on ungulates consumed by late Neanderthals and Anatomically Modern Humans in the region. This review suggests a decrease in temperatures and rainfall from 48,000 to 44,000 cal BP (after Heinrich Event 5) which coincides with the late Neanderthals in the region and followed by a populational hiatus until 43,000 cal BP. Despite the multiple intra-site environmental proxies available, this study challenges the fragmentary regional record during this key period for human evolution and reveals that further research is needed to obtain a complete regional high-resolution palaeoenvironmental and palaeoclimatic reconstruction.

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1. Introduction

The Middle to Upper Palaeolithic transition in Eurasia is dated approximately between 47,000 and 42,000 cal BP, corresponding with the earliest spread of Anatomically Modern Humans (AMH)

and the late disappearance of Neanderthals respectively (Davies et al., 2015; Higham et al., 2014; Hublin, 2015; Hublin et al., 2020), although recent research suggests pioneer AMH incursions in Europe earlier than 50,000 (Slimak et al., 2022). In the last two decades, advances in the archaeological evidence related to Neanderthal behaviour have provided a more detailed picture of who they were, their subsistence, technology, mobility, and treatment of death, among other aspects (see recent synthesis in Romagnoli et al., 2022). However, the causes behind their disappearance remains unsolved. Debates about the factors responsible for the

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decline of the Neanderthal have highlighted multiple possible explanations such as eco-cultural competition (Banks et al., 2008; Gilpin et al., 2016), demography and interbreeding (Zilhão et al., 2010; Cucart-Mora et al., 2018), volcanic activity (Lowe et al., 2012), or immunological diseases (Wolff and Greenwood, 2010). Climatic and environmental changes during MIS 3 have been also proposed as possible drivers leading towards their final decline, but the knowledge of their role is still diffuse (Vaesen et al., 2021). Several theories support the possibility that climate change was responsible for the human population crisis observed at this time, considering both an abrupt cooling event or gradual deterioration of the environment (D'Errico and Sánchez Goñi, 2003; Finlayson and Carrión, 2007; Sepulchre et al., 2007; Staubwasser et al., 2018; among others), such as in the case of Iberia, where the “Ebro Frontier” model was proposed (Zilhão, 2000, 2021). This model suggested a spatial division after the Heinrich Event 4 around the Ebro Basin between first AMH in the northern Ebro, and Neanderthals, in the south but today is not supported by the archaeological evidence (Cortés-Sánchez et al., 2019; Haws et al., 2020; Vidal-Cordasco et al., 2022).

The last Neanderthal populations inhabited Eurasia during Marine Isotope Stage 3 (MIS 3; ca. 60–30 ka BP), characterized by a millennial-scale climatic oscillations that alternated between environmental phases of forest development and the expansion of semi-arid areas, in accordance with warming and cooling sea-surface temperatures (Fletcher et al., 2010; Moreno et al., 2014; Roucoux et al., 2001; Sánchez Goñi et al., 2008). These fluctuations are well-recorded in the Greenland ice cores, such as the NGRIP (North Greenland Ice Core Project members, 2004; Rasmussen et al., 2014; Wolff et al., 2010), which reveals the succession of three Heinrich Events (HE) and fourteen Greenland Stadials (GS), alternated with Greenland Interstadial (GI) within this period (Fig. 1A). Abrupt and rapid warming episodes were followed by gradual cooling until reached stadial levels, known as Dansgaard–Oeschger cycles (D-O). During MIS 3, those climatic oscillations and D-O events have been observed in Iberia in high-resolution proxies, such as the marine sediments from the Atlantic Ocean (MD95-2039; MD95-2042; MD04-2845; MD99-2331) and the Alboran Sea, which recorded sea-level temperatures and pollen fluctuations (Fletcher and Sánchez-Goñi, 2008; Moreno et al., 2014; Naughton et al., 2007; Roucoux et al., 2001; Sánchez-Goñi et al., 1999; Sánchez Goñi et al., 2008) (Fig. 1B). Thus, climatic instability throughout MIS 3 is widely recorded in ice and marine records. However, the terrestrial data about the environment and ecologies directly exploited by both human species is still poorly understood. This information is critical to evaluate the degree of causality of the environmental changes during the Middle to the Upper Paleolithic transition.

The theory that global climate change, as the determining factor for Neanderthals disappearance, has declined in popularity since abrupt alternation in climatic cycles previously occurred over several millennia. It is well-known that Neanderthals coped with previous glacial phases (Davies et al., 2015; Sánchez Goñi, 2020) proving their resilience to unstable conditions, as well as their behavioural complexity, including their command of the use of fire (Roebroeks and Villa, 2011; Sorensen et al., 2018). The role of climatic and environmental change in the extinction of the Neanderthals cannot be assumed on a pan-Eurasian scale and must be evaluated on a regional scale, to determine the impact of these global abrupt climatic changes on regional populations. Characterising the local palaeoenvironmental conditions in archaeological sites occupied by late Neanderthals is crucial to characterise this human population replacement, especially in southern European peninsulas, which have traditionally been considering as refugium for humans during the Palaeolithic (Jones, 2022; Stewart et al.,

2010).

The Cantabrian region is extremely rich in archaeological sites and occupation levels dating to the late Middle and Early Upper Palaeolithic. This region extends between the Cantabrian Sea in the north and the Cantabrian Mountain Range in the south, terminating just before the Central Spanish Plateau. The region is approximately 350 km in length, spanning from the Nalón river in the east, to the Bidasoa river in the west and linked to eastern Iberia through the Ebro River Basin. Recent studies have demonstrated that the regional Mousterian, attributed to the classic Neanderthals, disappeared by 47.9–45.1 ka cal BP, followed by a brief Châtelperronian occupation, likely related to Neanderthals groups arriving from Southwestern France, that extend between 43.5 and 41.5 ka cal BP (Marín-Arroyo et al., 2018; Rios-Garaizar et al., 2022; Welker et al., 2016). The Mousterian and Châtelperronian cultures did not overlap producing a regional population gap. However, an overlapping between the Châtelperronian and the Aurignacian, the first technology attributed to AMH, appeared between 43.3 and 40.5 ka cal BP, is documented in the region. The Aurignacian technocomplex ended around 34.6 and 33.1 ka cal BP, after the Gravettian had already been established in that region (Marín-Arroyo et al., 2018; Rios-Garaizar et al., 2022) (Fig. 1). Today, the spatiotemporal disappearance of Neanderthals in Iberia has been proposed to be related to the different trends on ecosystem productivity within the Eurosiberian, Supramediterranean, Mesomediterranean and Thermomediterranean regions (Vidal-Cordasco et al., 2022). Whereas in Supramediterranean and Mesomediterranean regions the Mousterian technocomplex disappeared between 41 and 39 ka cal BP, in Thermomediterranean region the Mousterian disappeared between 35 and 32 ka cal BP.

Current research is providing an updated regional perspective of the Middle to Upper Palaeolithic transition in the Cantabrian region, in terms of chronology (Higham et al., 2014; Marín-Arroyo et al., 2018, 2020; Maroto et al., 2012; Wood et al., 2014, 2018), subsistence (Marín-Arroyo and Sanz-Royo, 2022) and environment, the latter obtained from stable isotope analysis of ungulate species exploited by human groups (Jones et al., 2018, 2019, 2020). Despite the abundance of intra-site environmental studies there is currently no general overview of the regional environmental terrestrial proxies directly related to human activities during MIS 3. This work compiles and assess the available proxies providing an updated state-of-the-art regarding the environmental and climatic conditions that occurred during this human and cultural transition between the Middle and the Upper Palaeolithic. By applying new and standardised analytical methods and by incorporating data compiled from pollen, charcoal, small vertebrate and the stable isotope studies, a general and regional view is presented for this key period of human evolution. This analysis allows the evaluation of how global climatic oscillations are reflected into local and regional scales, which is crucial to understand how human populations coped with climatic oscillations in the Cantabrian region.

2. Material and methods

2.1. Archaeo-palaeontological levels selected

After a chronological review of the regional sites attributed to the MIS 3, this study compiled data from 23 archaeo-palaeontological sites, located in the Cantabrian region (Asturias, Cantabria and the Basque Country), that yielded palaeoenvironmental evidence from small vertebrates, pollen, charcoal, macrofaunal, and stable isotopic studies on ungulates, related culturally to the end of the Middle Palaeolithic and the starting of the Upper Palaeolithic, ranging from 55,000 to 25,000 years BP, which corresponds to GS 15 to the GS 3 (SI1; SI2). A total of 111 archaeological levels were compiled in this

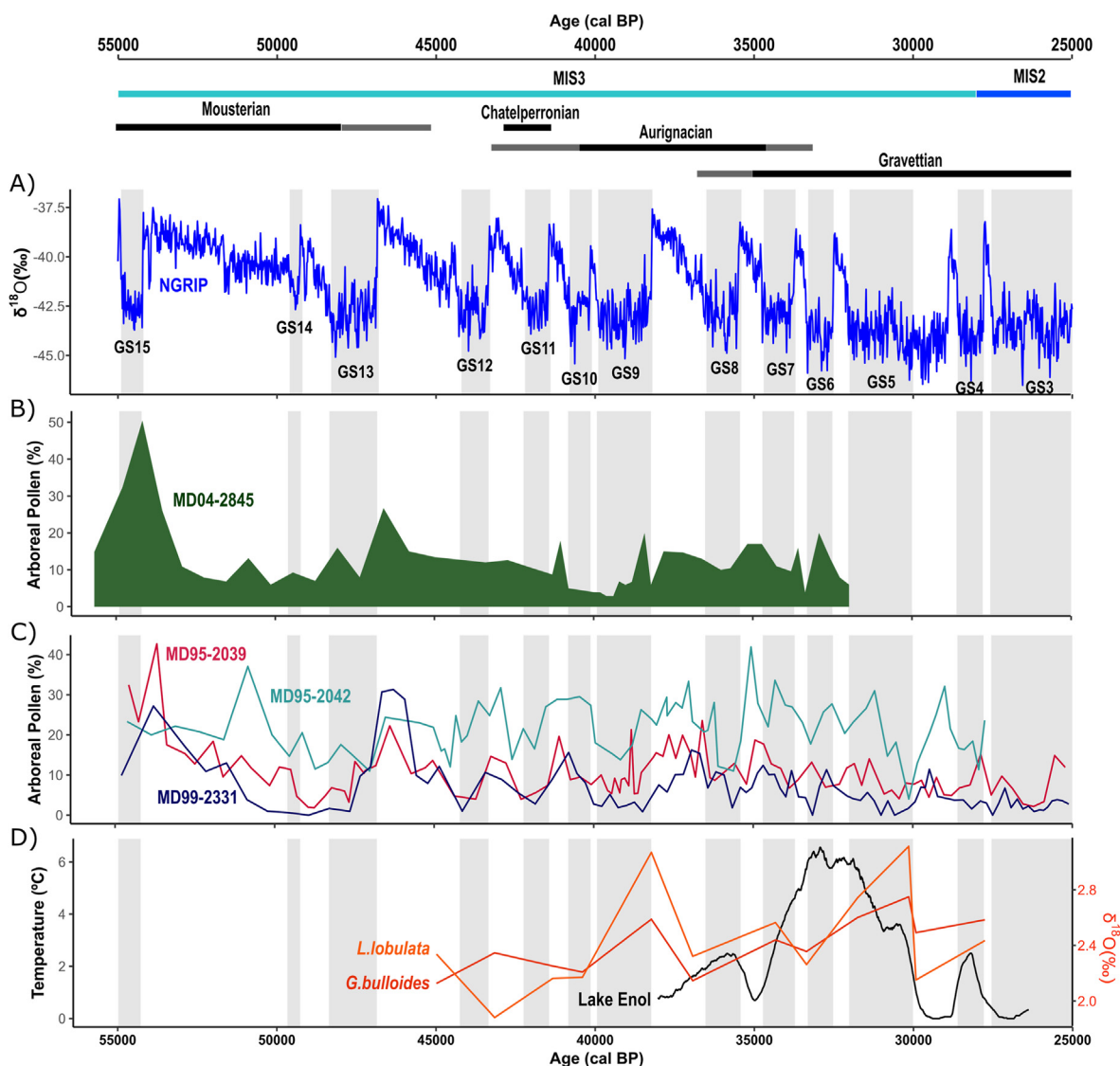


Fig. 1. Global and regional non-terrestrial climatic proxies from 55,000 to 25,000 cal PB. A) $\delta^{18}\text{O}$ record from the NGRIP ice core (North Greenland Ice Core Project members, 2004; Rasmussen et al., 2014); B) Arboreal pollen in marine core MD04-2845 from the Basque Shelf (Sánchez Goñi et al., 2008); C) Arboreal pollen in Atlantic marine cores MD95-2039, MD95-2042 and MD99-2331 (Naughton et al., 2007; Roucoux et al., 2001; Sánchez-Goñi et al., 1999; Sánchez Goñi et al., 2008); D) Temperature evolution of Enol Lake from 39 to 30 ka cal BP (Moreno et al., 2010) and $\delta^{18}\text{O}$ signals of *G. bulloides* (planktonic foraminifer) and *L. lobulata* (benthic foraminifer) from composite marine record of cores KS04-16 and KS05-05 from the Basque shelf (Rofes et al., 2015).

study, although not all proxies were consistently available for each of these levels. The selection of levels for inclusion was based on recent regional chronological reviews of these transitional sites and only levels with consistent stratigraphy and, when available, ultrafiltered radiocarbon dates were used (Higham et al., 2014; Marín-Arroyo et al., 2018; Marín-Arroyo and Sanz-Royo, 2022; Maroto et al., 2012; Wood et al., 2014). To ensure the quality of the data assessed, sites that were dated using old radiocarbon dating methodologies (e.g not processed using ultrafiltration), those with stratigraphic inconsistencies and those with highly fragmentary data (usually corresponding to ancient excavations or old environmental studies) were not compiled by this study. This resulted in the exclusion of some levels within archaeological sequences (Covalejos and Esquilleu) or in some instances entire sites (El Conde, El Pendo, Morín, Cibrante, El Otero, Lezetxiki, and Lezetxiki II) (SI2).

The archaeological levels were classified according to their cultural ascription and uncalibrated dates (absolute or relative) in

different chrono-cultural ranges with internal subdivisions within each culture (Table 1; Table 2), which were Mousterian (>45 to 42 ka uncal BP), Châtelperronian (40–36 ka uncal BP), Aurignacian (46–30 ka uncal BP) and Gravettian (31 to <26 ka uncal BP). From the selected sequences within this study, some levels were excluded from the analysis when they had an unclear chrono-cultural ascription or an inaccurate range of dates (“unknown range” levels in Table 2). In addition, each type of proxy required a different evaluation criterion in the selection of the levels to be analysed to guarantee the reliability of the results (see details in SI1). Although this stringent data selection resulted in large bodies of data being excluded, it ensured data quality in the general analyses performed. At the same time, it should be taken into account that each method of environmental reconstruction uses different types of data, varying the number of levels included in each case. Due to the nature of the archaeo-palaeontological levels, the precise temporal resolution of individual occupations remains unknown, thus the environmental data contained is the consequence

Table 1

Levels selected by the analysis of this work, classified by chrono-cultural ranges considering uncalibrated radiocarbon dates. Levels included contain records that correspond to one or more environmental proxies selected (small mammals, pollen, charcoals, and isotopes). In case of levels without radiocarbon dates, only those with clear chrono-stratigraphic context are included. Details on levels excluded in SI1.

Range	Mousterian			Châtelperronian		Aurignacian			Early Gravettian			
	>45	49-46	45-42	40-38	38-37	46-42	39-36	35-32	32-30	31-29	28-26	<26
Archaeological levels	Amllor: Amk	El Castillo: 20B, 20C, 20D, 20E	Llonin: VIII (CP)	La Güelga: 2 (D-Int)	Labeko Koba: IX inf	El Castillo: 18B, 18C	Labeko Koba: VII	Covalejos: A, B, C	La Viña (SO): XIII, XII, XI	Aitzbitarte III: IV, Va, Vb upper	Amalda: VI	Bolinkoba: 2sup
	Askondo: 13	El Mirón: 130	Esquilleu: VI		La Güelga (D-Int): 1		El Castillo: 16	El Cuco: III	Antoliñako: Lower Lmbk/Smk, Smb+sm, LsrB	Antoliñako: Upper Lmbk/Smk	Antoliñako: Lab/Sab	La Viña (SO): VII, VIII
	Bolinkoba: 3	El Cuco: Vb, VI, VII, IX, X, XII	Amalda: VII				El Cuco: IV	Aitzbitarte III: Vb central	Askondo: 9		El Mirón: 128	
	Covalejos: H, I, J, K	El Sidrón: III	Amllor: Lmc					Labeko Koba: VI, V, IV	Bolinkoba: 2inf		La Viña (SO): X, IX, VIc, VI	
	Axlor: IV, VI, VIII		Covalejos: D					La Güelga (D-Int): 5, 6				
		La Güelga (D-Int): 8, 9										
Total levels	10	12	7	1	2	2	3	10	8	4	7	3
Range	>45	49-46	45-42	40-38	38-37	46-42	39-36	35-32	32-30	31-29	28-26	<26
Archaeological & sterile levels	Amalda: X		El Castillo: 19	Reixidora: C-RXD-2	Torca de León		El Castillo: 16-17	La Güelga (D-Int): 3, 4	Reixidora: C-RXD-3	Askondo: 8		
	Amubate						La Güelga (D-Int): 7					
Total levels	3		1	1	1		2	3		1		

of an indeterminate amount of time, which may include different climatic phases, but still provides valuable information on global trends surrounding human occupation at each site.

2.2. Palaeoenvironmental proxies selected

2.2.1. Small vertebrate analyses

Small vertebrates and, specifically, rodents are well-known for their value in palaeoclimatic and palaeoenvironmental reconstructions, as they are highly sensitive to specific habitats (Chaline, 1974; López-García et al., 2014). Their origin within archaeological sites is usually related to diurnal and nocturnal raptors, that hunt nearby, providing a highly local signal (Andrews, 1990; Fernández-Jalvo et al., 2016). Nevertheless, these studies are not exempt from limitations that should be taken into consideration, such as small assemblages with a low MNI or biases derived from inaccurate recovering tasks in the field, especially in the old excavations. Taphonomic studies to detect possible ecological biases inflicted by predators are not always completed and most studies do not include any taphonomic information.

This study initially compiled data from 81 levels with potential small vertebrate records, including 61 found in levels with evidence of human occupation and 20 in archaeologically sterile levels, from a total of 18 sites, from west to east: La Viña, El Sidrón, La Güelga, Torca del León, Llonin, Esquilleu, Covalejos, El Castillo, El Mirón, Antoliñako, Askondo, Bolinkoba, Labeko Koba, Ekain, Amalda, Amutxake, Aitzbitarte III and Aitzbitarte IV (Altuna, 1972; Álvarez-Lao et al., 2020; Álvarez-Vena et al., 2021; Cuenca-Bescós et al., 2009; Garcia-Ibaibarriaga et al., 2015a, 2015b; Pemán, 1990, 2000, 2011; Rasilla et al., 2020; Rofes et al., 2015; Sesé, 2014, 2017, 2018, 2021; Uzquiano et al., 2012; Zabala, 1984) (Table 2; Fig. 1). Only levels with clear chrono-cultural adscription and with a minimal number of individuals (MNI>10) were finally included, restricting the available data to a total of 59 levels (Table 1). This criterion excludes Askondo (10, 11 and 12), Covalejos (F-G), La Viña (XIV from the Occidental Sector and IX from the Central Sector), Labeko Koba (IX inf, IV), Ekain (Xa, IXa, IXb), Amalda (VIII) and El Sidrón (IV) (details in SI1 and SI2). This means that the only two regional Châtelperronian levels from Ekain and Labeko Koba were excluded.

In this work, two methods are applied to suitable levels with small-mammal data: 1) the Habitat Weighting (HW) for palaeoenvironmental reconstruction, and 2) the Bioclimatic Model (BM) for palaeoclimatic reconstruction. The HW is a quantitative method that classifies the possible type of landscape by considering those currently present in the Iberian Peninsula, which are separated into five main groups: 1) open dry, meadows under seasonal change; 2)

open humid, evergreen meadows with dense pastures and suitable topsoil; 3) woodland, mature forest including woodland margins and forest patches, with moderate ground cover; 4) rocky, areas with suitable rocky or stony substratum, and 5) water, areas along streams, lakes, and ponds. Each species preference is distributed considering the probability to be found in each of those five groups (maxim score = 1), and the modern ecological species preferences (Palomo et al., 2007), in agreement with similar regional proposals of habitat weighting (Álvarez-Lao et al., 2020; Álvarez-Vena et al., 2021; Cuenca-Bescós et al., 2009; Fernández-García et al., 2020; López-García et al., 2012) (SI3). The HW method considers the relative abundance in each level, allowing to be applied just in levels with MNI data.

The BM is a qualitative method based on the adscription of small-mammal species to ten different climatic zones (Hernández Fernández, 2001; Hernández Fernández et al., 2007). This allows the initial calculation, of the Climatic Restriction Index (CRI_i = 1/n, where “i” is the climatic zone inhabited by the species and “n” is the number of climatic zones the species inhabit) and then, the Bioclimatic Component (BC_i=(ΣCRI_i)/100/S, where “S” is the number of species). From the BC, it is possible to then calculate several climatic parameters using multiple linear regression, developed specifically for rodents and insectivores. Species weighings were deduced from the original species matrix for bioclimatic adscriptions provided by Hernández Fernández (2001) and Hernández Fernández et al. (2007) and by considering the update by Royer et al. (2020), which provide a R script (R v3.3.2; R Core Team, 2016) for the application of the Bioclimatic Model (SI3). The main climatic parameters estimated are Mean Annual Temperature (MAT) and Mean Annual Precipitation (MAP).

Selected levels required in most cases a review to homogenise the data, such as a taxonomic terminological update in some sequences that still rely on old taxonomic terminologies (e.g., *Pytimis*). Today, the Cantabrian region is a confluence area inhabited by certain Eurosiberian-Mediterranean species of the same genus, with close morphological characteristics, which can be challenging to differentiate. This suggests that some published studies were not able to provide a species level identification and sometimes resulted in the grouping of species with different ecological signals, thus being less precise for environmental purposes. This affects the species groups categories of *A. amphibi-us-sapidus*, *M. arvalis-agrestis*, *A. sylvaticus-flavicollis*, *Talpa* sp. (*Talpa occidentalis-europaea*), *Neomys fodiens-anomalus* and *Sorex araneus-coronatus*.

The ecological implications that species grouping within studies might have for this assessment were carefully evaluated for the calculations of the Habitat Weighting and the Bioclimatic Model.

Table 2

Levels included this work compilation, classified by chrono-cultural ranges considering uncalibrated radiocarbon dates (when absent only those with clear chrono-stratigraphic context are included). "n" refers to levels non-analysed because do not reach the minimum proxy threshold; (*) refers to samples that merge different levels. More details in SI1.

	Archaeological levels	Microfauna	Pollen	Isotopes	Charcoals
Mousterian	>45	La Viña (SO) - xIV	n		x (*)
		Arrillor Amk		x	
		Askondo - 11	n		
		Askondo - 12	n		
		Askondo - 13	x		
		Bolinkoba - 3	x		
		Covalejos - F+G	n		
		Covalejos - H	x		
		Covalejos - I	x	x	
		Covalejos - J	x		x
		Covalejos - K	x	x	
		Axlor - IV			x
		Axlor - VI			x
		Axlor - VIII			x
		El Castillo - 20B	x		
		El Castillo - 20C	x	n	
		El Castillo - 20D	x		x
		El Castillo - 20E	x		
		El Miron - 130	x		x
		El Cuco - Vb		x	
		El Cuco - Vc		n	
		El Cuco - VI		x	
		El Cuco - VII		x	
		El Cuco - VIII		n	
		El Cuco - Ix		x	
		El Cuco - x		x	
		El Cuco - XI		n	
		El Cuco - XII		x	
	El Cuco - XIII		n		
	El Sidrón - III	x			
	Amalda - VII	x	n	x	
	Arrillor - Lmc		x		
	Covalejos - D	x	x	x	
	Esquilleu - VI	x	x	x (*)	
	La Güelga (D-Int) - 9	x			
	La Güelga (D-Int) - 8	x			
	Llonin VIII (CP)	x		x (*)	
Châtelperronian	40-38	La Güelga (D-Int) - 2	x		
	38-37	Labeko Koba - Ix inf	n	n	x
		La Güelga (D-Int) - 1	x		
	<36	Ekain - xa	x		
Aurignacian	46-42	El Castillo - 18B	x	n	x
		El Castillo - 18C	x	n	x
		Labeko Koba - VII	x	x	
	39-36	El Castillo - 16			x
		El Cuco - IV		x	
		El Cuco - Va		n	
		Covalejos - A	x		
		Covalejos - B	x	x	x
		Covalejos - C	x	x	x
		El Cuco - III		n	
	35-32	Aitzbitarte III - Vb central	x	x	x
		Labeko Koba - VI	x	x	x
		Labeko Koba - V	x	x	x
		Labeko Koba - IV	x		x
		Ekain - Ixa	n		
	La Güelga (D-Int) - 5	x			
	La Güelga (D-Int) - 6	x			

	Archaeological levels	Microfauna	Pollen	Isotopes	Charcoals
Aurignacian	32-30	Ekain - Ixb	n		x
		La Viña (SO) - XIII	x		
		La Viña (SO) - XII	x		
		La Viña (SO) - XI	x		
		La Viña (SC) - Ix	n		
		Antoliñako - Lower Lmbk/Smk	x		
		Askondo - 9	x		
		Askondo - 10	n		
		Bolinkoba - 2inf	x		
		Antoliñako - Smb+sm			x
		Antoliñako - LsrB			x
		Antoliñako - Sr-E			n
		Antoliñako - P+Sm-P			n
		Aitzbitarte III - IV	x	x	x
		Aitzbitarte III - Va	x	x	x
Early Gravettian	31-29	Aitzbitarte III - Vb upper		x	x
		Antoliñako - Upper Lmbk/Smk	x		x
		Amalda - VI	x	x	x
		Antoliñako - Lab/Sab	x		x
		El Miron - 128	x		x
	28-26	La Viña (SO) - x	x		
		La Viña (SO) - Ix	x		
		La Viña (SC) - Vic inf	x		
		La Viña (SC) - VI	x		
		Bolinkoba - 2sup	x		x
<26	La Viña (SO) - VII	x			
	La Viña (SO) - VIII	x			
Total		61	34	31	11

	Archaeological levels	Microfauna	Pollen	Isotopes	Charcoals
Archaeologically sterile levels	>45	Amalda - VIII	n	n	
		Amalda - x	x		
		Amutxate	x		
		Covalejos - E	x	x	
	45-42	El Castillo - 19	x	n	x
		Comella		n	
	40	Reixidora - C-RxD-2		x	
		Torca del León	x		
		El Castillo - 16-17			x
	39-36	El Castillo - 17C			x
		La Güelga (D-Int) - 7	x		
		La Güelga (D-Int) - 3	x		
	35-32	La Güelga (D-Int) - 4	x		
		Reixidora - C-RxD-3		x	
	<31	Askondo - 8	x		
	El Sidrón - IV	n			
Unknown range		Aitzbitarte III - VI	x	n	
		Aitzbitarte IV	x		
		Antoliñako - P	x		
		Antoliñako - Sj/P	n		
		Antoliñako - Sm-P	n		
		Antoliñako - Lsm-P	x		
		Antoliñako - Sm	x		
		El Mirón - 129	x		x
		El Sidrón - II	x		
		Reixidora - C-RxD-1		n	
Total		20	8	4	0

The optimal solution for Habitat Weighting was to estimate the average habitat weighing of the grouped species which can have a coincident distribution area in the Cantabrian region, then both species are possible. In relation to the *Neomys* and *Sorex* groups exclusively, the requirements of one species were favoured over another, giving preference to the species that is most likely to be found today in the Cantabrian region. In most cases these group of species are very anecdotal in relative abundances terms or have similar requirements, meaning that ecological implications will have little impact. But habitat differences are relevant for *M. arvalis* and *M. agrestis* considering their differing moisture preferences (Luzi et al., 2017; Palomo et al., 2007). Taking into account their abundances this can have implications in landscape reconstruction. For the BM method, as it only admits assignation to one species, the most commonly found species in the region nowadays was selected

in each case. It affects *Apodemus*, *Neomys* and *Talpa* pair-group of species. *A. sylvaticus*, *N. fodiens* and *T. europaea* were selected. This not affected *Arvicola amphibius/sapidus*, neither *Microtus arvalis/agrestis*, due to CRI is the same for both species (further details in SI3).

2.2.2. Pollen analyses

Pollen is the most common and traditional proxy used for palaeoecological reconstructions in archaeological research. Using continuous sediment sampling for pollen analysis, throughout a stratigraphic sequence, has great potential to inform on ecological settings from local to regional scales and to detect vegetation fluctuations. Some of the limitations inherent in palynology that are considered in the environmental interpretations, are the overrepresentation of some taxa (*Pinus*), underrepresentation of others

(*Quercus*, *Juniperus*, *Juglans*) or even poor preservation of some taxa (*Asteraceae* or *Artemisia*) (Carrión, 2012; Chevalier et al., 2020; Dupré, 1988; Ochando et al., 2021). Some pioneer palynological studies in Iberia were undertaken in the Cantabrian region (e.g., Dupré, 1988; Leroi-Gourhan, 1971, 1966; Sánchez-Goñi, 1991). However, the information reported in those studies is frequently not presented in the way modern studies do, lacking most of the quantitative data, which causes difficulties when compiling this information. In most cases, only pollen diagrams were available, rather than exact pollen counts (summarized in Carrión, 2012). Accordingly, the percentage of each pollen taxa was obtained from the species count whenever possible and from the published palynological diagrams, in most cases, with WebPlotDigitizer v.4.5 (SI2).

This study initially identified 10 potential archaeo-palaeontological sites with pollen analysis, from west to east: Raxidora, Comella, Esquilleu, Covalejos, El Castillo, El Cuco, Arrillor, Labeko Koba, Amalda, and Aitzbitarte III (Álvarez-Lao et al., 2015; Baena et al., 2005; Dupré, 1988, 1990; Iriarte-Chiapusso, 2000, 2011; Iriarte-Chiapusso et al., 2019; Ruiz-Zapata and Gil-García, 2005, 2007; Uzquiano et al., 2012) (Table 2; SI2). Two sets of analyses were performed from the pollen dataset: a vegetation cover analysis, and palaeoclimatic estimations. Regarding the vegetation cover analyses, the abundance of taxa related to arboreal pollen versus non-arboreal pollen presented in the palynological diagrams were used to assess the predominance of arboreal vegetation coverage (e.g., Burjachs et al., 2012; Carrión, 2012; Ochando et al., 2021). Furthermore, following previous studies (Ochando et al., 2020), the taxa were classified into four ecological categories: conifers, mesophyte trees, Mediterranean forest-shrubs and cold grasses. Three levels were excluded from Esquilleu and Covalejos because the total data were incoherent with abundance >100% (SI3).

For pollen-based palaeoclimatic reconstructions, we used Weighted Averaging (WA) regressions (Bartlein et al., 2011; Sun et al., 2020; Weitzel et al., 2019). Plant species are more abundant when they experience the climatic conditions to which they are best adapted, so WA regressions estimate the optimal climatic settings from a calibration dataset of modern pollen species (Chevalier et al., 2020; Ter Braak and Barendregt, 1986). In this study, to estimate the palaeoclimatic conditions from the palynological record, the predictive functions were obtained from a training set of modern pollen taxa obtained from the Eurasian Modern Pollen Database (EMPD) v.2 (Davis et al., 2020). The EMPD v.2. contains pollen taxa recovered from more than 2000 European and Asian localities and associated climatological measurements. This dataset was used to obtain temperature and precipitation predictive functions, based on pollen subsets, using WA regression techniques with the R package 'analogue' (Simpson and Oksanen, 2022). Prediction errors were simulated by bootstrap cross-validation (n of boot cycles: 500). After that, the transfer functions were applied to the fossil pollen from selected levels (see SI3).

Before estimating the palaeoclimate variables, several filter criteria were applied to the dataset. First, only the palynological assemblages obtained from sites with a clear stratigraphic sequence and well-dated archaeological levels were retained for analysis. Second, palynological assemblages with less than 100 pollen grains and species with representation lower than 5% were excluded from the WA regressions (Table 2; SI1; SI2). These filtering steps reduced the available record from 42 archaeo-palaeontological levels to 26. In addition, since terrestrial and aquatic taxa are unevenly affected by climatic conditions, all non-terrestrial pollen taxa, including ferns and non-pollen palynomorphs, were excluded (Chevalier et al., 2020). After these modifications, the percentages of each taxon were re-adjusted, and

the pollen taxa recovered from the archaeological record were included in the training dataset of extant pollen species.

2.2.3. Other environmental proxies

Another method for reconstructing the local environmental conditions with high-resolution potential is the recent approach of stable isotope analysis on mammal remains. Analyses of carbon ($\delta^{13}\text{C}$), nitrogen ($\delta^{15}\text{N}$) and sulphur ($\delta^{34}\text{S}$) have previously been undertaken on bone collagen from large ungulates, including equids, cervids and caprids. Those stable isotopic values represent the long-term average diet of the animal species and therefore, they reflect the environmental conditions experienced by the animals (Jones et al., 2021). The ungulates analysed are related to the hunting activities carried out by humans in the surroundings of the archaeological sites, meaning that their environmental signals can be directly linked to periods of human activity. In the Cantabrian region, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and $\delta^{34}\text{S}$ have been published covering the chronological period of the study, from 10 archaeological sites from west to east: Covalejos, El Castillo, El Mirón, Axlór, Antoliñako, Bolinkoba, Labeko Koba, Ekain, Amalda, and Aitzbitarte III (Jones et al., 2018, 2019; Rofes et al., 2015) (Table 1; Table 2). Data from all 32 of these levels are included in this work, as they provide clear chronological adscription, with data meeting required international quality standards (C:N ratio, %C, %N) (SI2; SI4).

Anthracological analyses based on charred plant and charcoal remains recovered in archaeo-palaeontological sites provide information on arboreal taxa present during the time that the levels were formed. The relative abundance of charcoal is mostly related to human activity, usually due to the transport of local arboreal species to be used as fuel or other activities. Thus, the significant limiting factor for this record as an environmental proxy is due to the anthropogenic origin of these remains. These analyses must be considered with their possible biases as the wood present reflects human selection which may overestimate or underrepresent species available in the nearby environment. As with pollen analysis, anthracological records can also be biased by differential preservation (Vidal-Matutano and Pardo-Gordó, 2020). Up to now, there are only four sites with reliable radiocarbon dates containing anthracological studies in the Cantabrian region during MIS 3, which are from west to east: La Viña, Llonín, Covalejos, and El Castillo (Rasilla et al., 2018, 2020; Uzquiano, 2006, 2021) (Table 2; SI1; SI2).

In addition to small mammals, pollen, anthracological remains, and stable isotope evidence, other proxies have been used to reconstruct the palaeoenvironment in the Cantabrian region. Sedimentological and soil micromorphology studies have been undertaken to identify climatic conditions (e.g., Areso et al., 1990; Areso and Uriz, 2013; Butzer, 1981; Pinto-Llona et al., 2012). However, climatic descriptions based on sedimentology were predominantly qualitative, resulting in inter-individual biases and they are not always consistently recorded and evidenced. Sedimentological studies are mostly focused on the fossiliferous microenvironment, such as water flows activation or cryogenic processes experienced during cold seasons, rather than local-to-regional climatic patterns. Moreover, the categories established are typically imprecise (e.g. cool, cold, temperate), based on qualitative descriptions without quantifiable data. Therefore, sedimentological descriptions were not included in this regional reassessment of environmental conditions during MIS 3.

2.3. Temperature and precipitations anomalies

Climatic estimations based on pollen and small-mammal records for each level took into account present-day climatic conditions surrounding each site, allowing an inter-site comparison and

expressed in relative terms. This helped to reduce the variability that might be a product of the particular orographic parameters of each site location (Fig. 2; SI3). Present-day temperatures and precipitation values were obtained from the WorldClim Dataset v2 (Fick and Hijmans, 2017). This dataset includes the average of bioclimatic variables between 1970 and 2000 in a set of raster files with a spatial resolution every 2.5 min. The exact location of the selected archeo-palaeontological sites was used, using geographical coordinates in the projection on modern climatic maps with QGIS software. We focused on MAT and MAP (SI3).

2.4. Bayesian age models

From the 19 archaeo-palaeontological sites with palaeoclimatic and palaeoenvironmental proxies used in this study, we compiled the published radiocarbon dates from the literature (Aguirre, 2001; Aguirre and González Sainz, 2011; Álvarez-Lao et al., 2015, 2020; Bargalló et al., 2012; González-Morales and Straus, 2012; Gutiérrez-Zugasti et al., 2018; Higham et al., 2014; Iriarte-Chiapusso et al., 2019; Iriarte-Chiapusso and Arrizabalaga, 2015; Kehl et al., 2018; Marín-Arroyo et al., 2020; Maroto et al., 2012; Menéndez et al., 2018; Rasilla et al., 2020; Sanchis et al., 2019; Torres et al., 2010; Wood et al., 2013, 2014, 2018). When only one radiocarbon date was available on a site, it was calibrated with the OxCal4.4 software (Ramsey, 2009) and the INTCAL20 calibration curve (Reimer et al., 2020). When more than one date was available for a level in a site, a Bayesian chronology model was built by using the same software (Ramsey, 2009). The radiocarbon dates obtained from a site were inserted into a “Sequence”. The chronometric determinations, associated with each level, were grouped within a single “Phase” with a start and end “boundary” to bracket each archaeological level. The codes used are available in SI4.

3. Results

3.1. Small vertebrate studies

After the specified selection criteria outlined above, this study has analysed 51 levels containing small-mammal remains from 15 sites: 18 levels were Mousterian, 2 Châtelperronian, 17 Aurignacian and 13 Gravettian (details in SI1; SI2). Moreover, archaeologically sterile levels within the archaeological sequence of sites such as Amalda (X), El Castillo (19), Covalejos (E), La Güelga (3, 4, 7), and Askondo (8) and the palaeontological sequences from Amutxake and Torca del León were also included, which accounted for 9 additional levels. Within the small vertebrate assemblages, the most commonly represented species have Euro-Siberian habitat preferences (*Microtus arvalis-agrestis*, *Talpa europaea*, *Arvicola terrestris*), whereas Mediterranean species (*Microtus duodecimcostatus*) are scarcely present and there is variability in the abundance of woodland dwellers (*Apodemus sylvaticus-flavicollis*, *Clethrionomys glareolus*, *Eliomys quercinus*) (SI3).

The Habitat Weighting method was exclusively applied to the 45 small mammal assemblages which provided data on the Minimal Number of Individuals (MNI) (SI2; SI3). Humid meadows were the main environmental zones represented (around 40–50%), in combination with open forest (around 20–30%), grassland and occasional dry shrubland (10–20%) (Fig. 3). This is a result of the high abundance of the species *Talpa europaea*, *Arvicola terrestris*, *Microtus lusitanicus* and *Microtus arvalis-agrestis*, which preferentially inhabit open-wet habitats or forest margins. The landscape remains homogeneous with neither abrupt nor progressive reduction in the forest composition between the end of the Mousterian and the Gravettian. There is no clear trend towards open dry meadows or rocky areas either.

The results of the modelled climatic data by applying the BM method show that absolute MATs are continuously oscillating between 3.5 and 13.8 °C, whereas MAPs are relatively stable around 600 mm, being between 30 and 40% lower than today (MAPs in the studied localities today range between 900 and 1300 mm) (SI3; Table 3). Occasional decreases in temperature, accompanied by a decrease in precipitation, are detected in some of the recent Mousterian assemblages or equivalent sterile levels (45–42 ka BP) and the early Aurignacian (35–32 ka BP), such as levels X and VII from Amalda or level Vb central, V and VI of Aitzbitarte which date to the Late Mousterian.

Observing relative changes in climatic conditions for each site, helps to provide a better inter-site comparison, avoiding particularities associated with each site (Fig. 4; Table 3). For the studied period between 50,000 and 25,000 years cal BP, MATs are generally lower than nowadays (mean: −3.3 °C; from 2 to −9 °C), with an average drop of −2.4 °C in the Mousterian, −4.4 °C in the Aurignacian and −4.1 °C in the Gravettian (SI4). By considering the levels individually, oscillations in climate are also observed. When applied to rainfall, moderate lower MAPs to nowadays ranges are observed (mean: −440 mm; from −825 to −175mm). The oscillations observed through MAP anomalies estimations should be taken with caution, because are highly dependent on the correction derived from raw MAPs estimations, which in most cases are similar (around 600 mm), using MAPs provided from each locality.

However, when classified by chrono-cultural ranges a progressive trend of temperature decrease started from the end of the Mousterian (49–42 ka BP) and continues with the early Aurignacian assemblages (35–32 ka BP), which is maintained throughout the Gravettian (SI3; Fig. 5). Aurignacian and Gravettian show higher temperature fluctuations than during the end of the Mousterian. The trends in MAPs are consistent with the MATs patterns, and reflect fluctuating conditions, with an average decrease from Mousterian to Aurignacian from around −300 to −500 mm. Therefore, a drop in temperatures and tentatively a progressive increase in aridity at the arrival of the Aurignacian is detected. Nevertheless, differences between periods do not show statistically significant differences (Mann-Whitney-Wilcoxon Test; p -value>0.05) (see SI3).

3.1.1. Palynological studies

To observe environmental trends, this study has used data from 9 sites containing pollen information, from 26 archaeo-palaeontological levels: 12 Mousterian, 7 Aurignacian, 4 Gravettian and 3 from archaeologically sterile levels (Table 1; Table 2). When considering the relative abundance of “Arboreal Pollen” (AP), there is a progressive reduction from an average 40% during the end of the Mousterian to 20% during the Aurignacian (39–36 ka uncal BP) (Fig. 3; SI3), although it is important to note that this is based on data from a reduced number of sites. The only data available was from the Mousterian levels of El Cuco, the early Aurignacian of Labeko Koba, and late Aurignacian of Aitzbitarte III. In the last two sites, a higher percentage of herbaceous plants is observed concerning the relative abundances previously observed in Mousterian levels.

Taxa relative abundances from each level are grouped considering the ecological categories frequently used in palynological studies (Fig. 3; SI3). Conifers and, especially *Pinus*, are the most represented taxa. In the Mousterian levels of Covalejos, *Pinus* is the most abundant species, with a minor presence of *Juniperus* (Ruiz-Zapata and Gil-García, 2005). Mesophyte trees are not rare, but are less frequent, with *Corylus* and *Salix* being the most common. Mediterranean taxa are rare, especially after the Mousterian, and are only present in sites close to the coast. *Quercus* is only detected in some Mousterian levels at Covalejos and El Cuco (Ruiz-Zapata

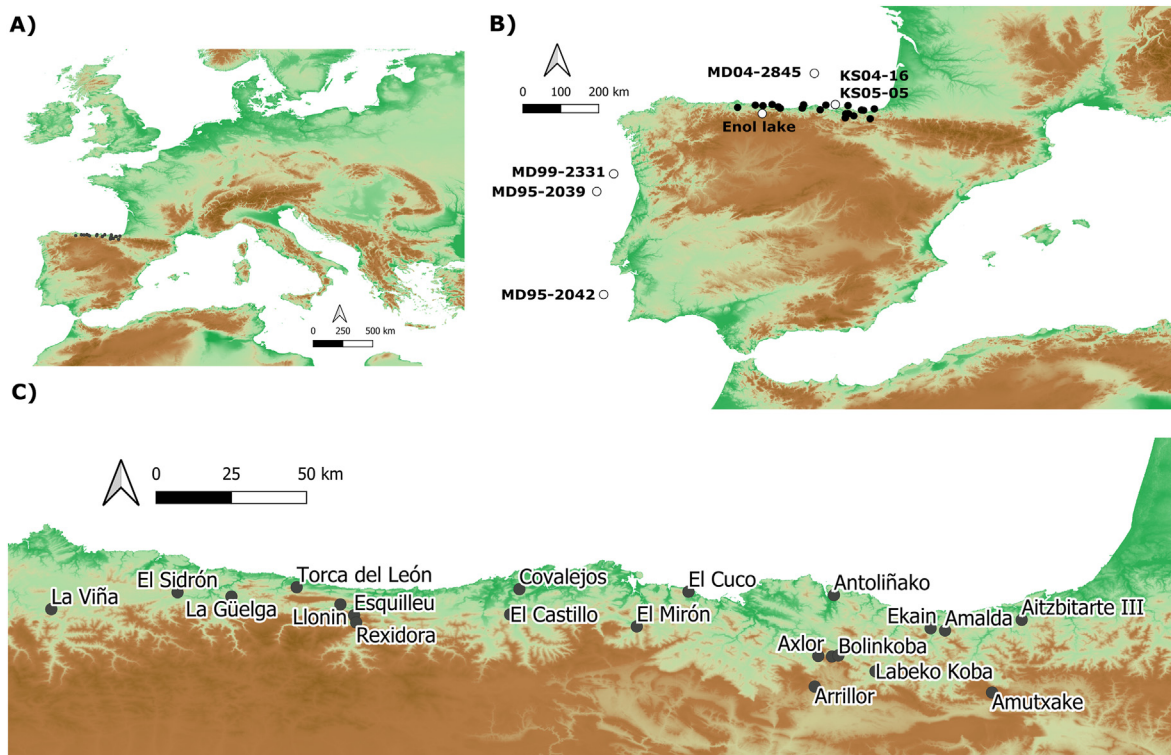


Fig. 2. Map with the selected records and sites included in this review: A) location in Eurasia; B) Iberian Peninsula map with marine and lake cores providing climatic information during the study period (white dots) and the archaeological and palaeontological sites (black dots) included in this review with pollen, small vertebrates, charcoal, and isotope records; C) detail and names of the sites.

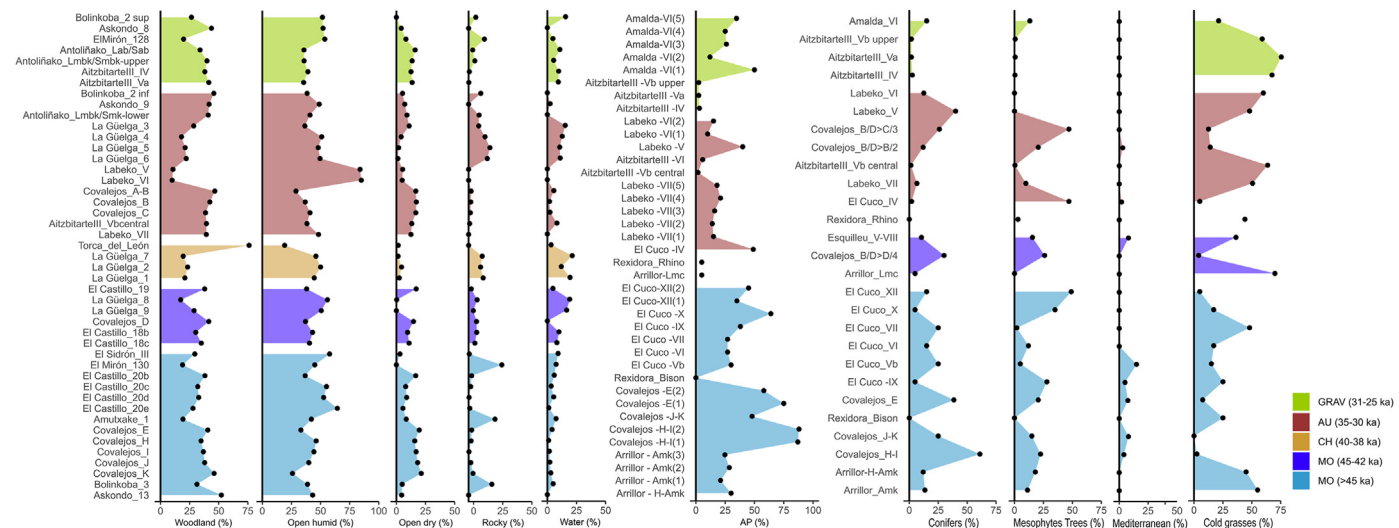


Fig. 3. Palaeoenvironmental evolution reconstructed from original data of the selected sites: A) Relative abundance of different types of landscape deduced by applying the Habitat Weighting method to small-mammal assemblages; B) Arboreal Pollen (AP) extracted from palynological analysis; C) Relative abundance of pollen taxa classified by ecological categories. Order by chrono-cultural ranges. MO, Mousterian; CH, Châtelperronian; AU, Aurignacian; GRAV, Gravettian.

and Gil-García, 2005, 2007). In summary, cold grasses are the most represented taxa in the pollen records of the selected sites, especially *Poaceae*. Those grasses start to increase at the end of the Mousterian, with further increases during the Aurignacian and Gravettian levels from Labeko Koba, Aitzbitarte and Amalda (Dupré, 1990; Iriarte-Chiapusso, 2000, 2011).

Some relevant information is extracted from the results of the WA regressions applied to the pollen frequencies. MATs estimations

are between 1 and 13 °C (mean: 8.1 °C; SD: 3.3) and MAPs between 300 and 1000 mm (mean: 530 mm; SD: 175), indicating that temperatures were usually cooler (mean ≈ -5 °C) and more arid (mean ≈ -600 mm) than nowadays in each analysed assemblage (Fig. 4; S13). Considering the limited quantity of pollen data for this period and the absence of other accurate environmental records between 45 and 39 ka uncal BP, deducing a climatic trend over time and obtaining a differentiation between periods is challenging.

Table 3

Summary test statistics (n, number of samples; mean; SD, Standard Deviations) comparing climatic parameters estimated for each archaeological cultures, considering results obtained from Bioclimatic Model (BM) for small-mammal studies and Weighted Averaging (WA) for pollen studies. It includes mean annual temperature (MAT) and mean annual precipitation (MAP) estimations, but also relative to current day records (RMAT and RMAP).

		Small-mammals (BM)			Pollen (WA)		
		n	mean	SD	n	mean	SD
MAT	Mousterian	18	10.43	2.43	12	8.53	3.53
	Châtelperronian	2	10.25	0.92	—	—	—
	Aurignacian	17	8.95	3.01	7	7.16	3.98
MAP	Gravettian	13	8.79	2.98	4	8.72	1.22
	Mousterian	18	604	26	12	585	181
	Châtelperronian	2	633	66	—	—	—
RMAT	Aurignacian	17	593	34	7	510	161
	Gravettian	13	591	42	4	415	184
	Mousterian	19	-2.47	2.63	12	-4.47	3.42
RMAP	Châtelperronian	2	-2.57	0.92	—	—	—
	Aurignacian	17	-4.03	2.87	7	-6.06	3.52
	Gravettian	13	-4.1	2.99	4	-4.45	1.18
	Mousterian	19	-428	138	12	-504	183
	Gravettian	17	-451	141	7	-614	180
	Gravettian	13	-506	195	4	-943	192

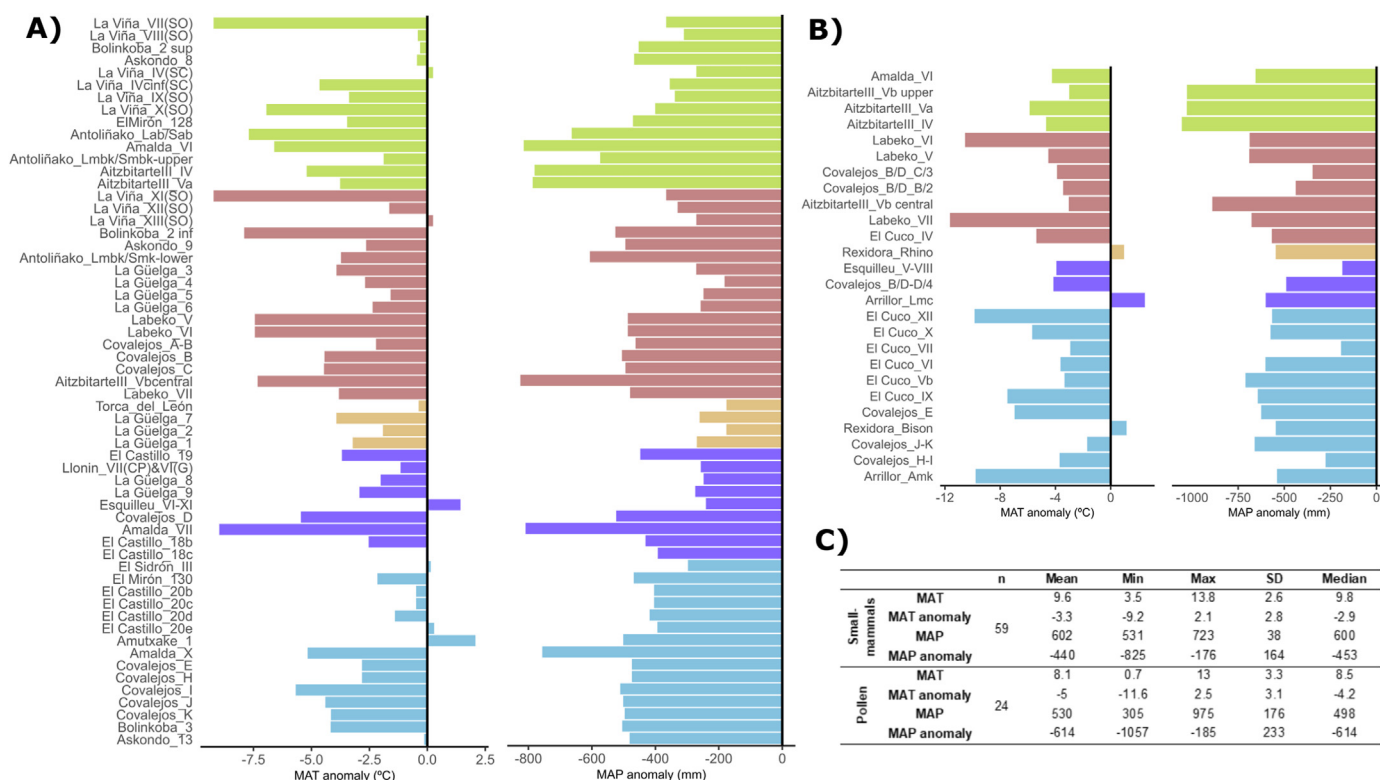


Fig. 4. Climatic estimations of mean annual temperature (MAT) and mean annual precipitation (MAP) with respect to nowadays from pollen (A) and small mammal (B) records in selected sites, order considering chronological ranges and cultures. C) Summary table of the estimations, including mean, minimum, maximum, standard deviation and median. Light blue for Mousterian (>45 ka); dark blue for Mousterian (45–42 ka uncal); orange for Châtelperronian (40–30 ka uncal); red for Aurignacian (40–30 ka uncal); green for Gravettian (31–25 ka uncal). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

However, when data is grouped by cultural periods (Fig. 5), a progressive trend towards aridity can be inferred by a decrease in the relative MAPs from the Mousterian (mean: -510 mm) to the Early Aurignacian (mean: -615 mm). Otherwise, palaeotemperature estimations do not follow a clear trend and show constant fluctuations. Differences by cultural groups considering both MATs and MAPs are not statistically significant (Mann-Whitney-Wilcoxon Test; p-value>0.05) (SI3).

3.1.2. Charcoal studies

This work has finally considered data from 4 sites containing charcoal studies, from 11 archaeological levels: 5 Mousterian, 5 Aurignacian, and 1 Gravettian. There is a high exploitation of *Betula* sp. during the Mousterian (represented by Covalejos H-E and El Castillo 20), which was also noted in the Transitional Aurignacian (represented by levels 18C and 18B at El Castillo) (Uzquiano, 2006). In the case of Covalejos, this exploitation is reduced in the Aurignacian levels C and especially in level B, in favour of *Pinus* and

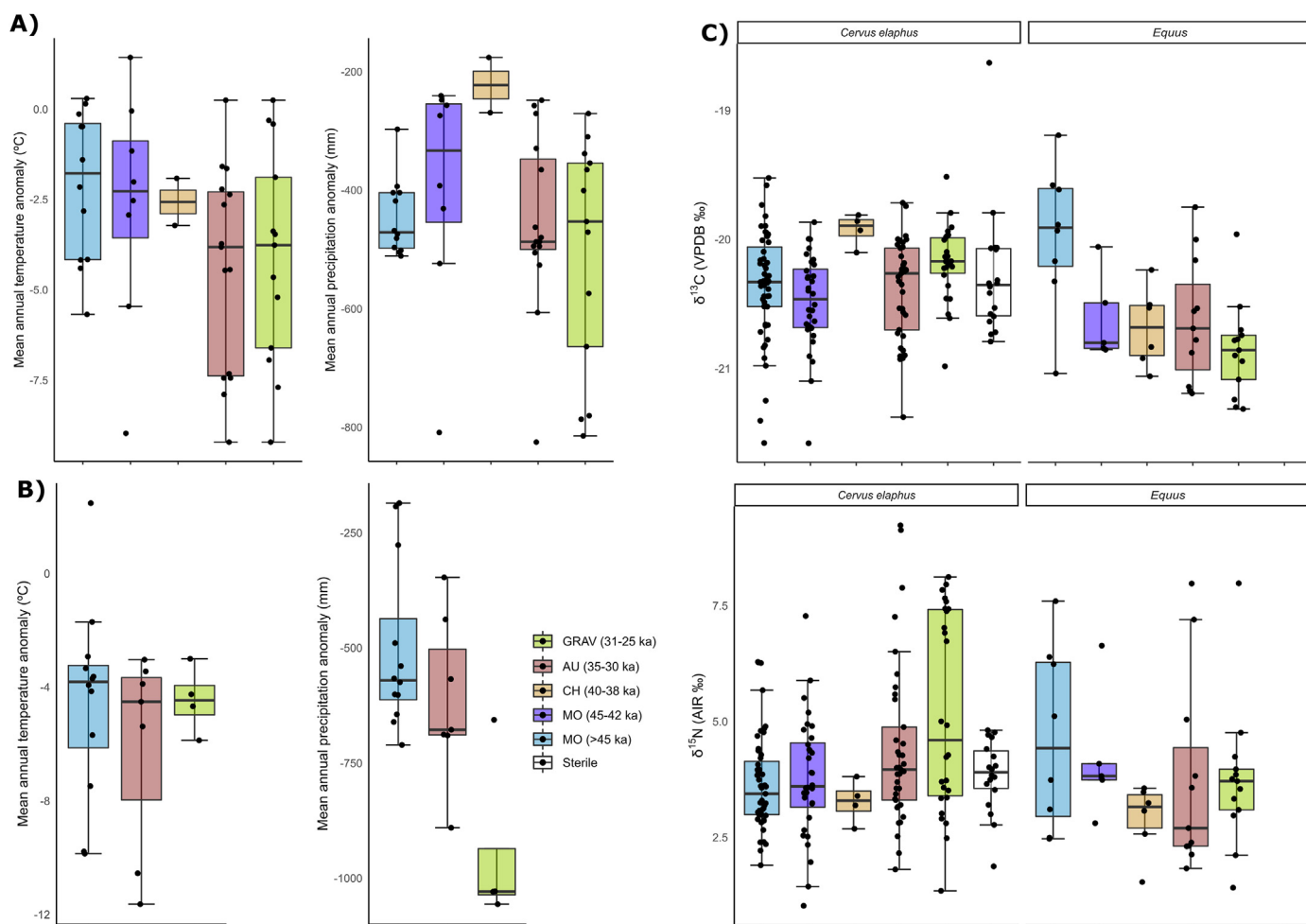


Fig. 5. Boxplots grouping data by chrono-cultural periods from the end of the Mousterian to the Gravettian: A) Small-mammal data; B) Pollen data; C) Stable isotopic data. In this graph any archaeologically sterile level within pollen and small-mammal records is included, and in case of stable isotopes analyses on *Cervus* is indicate in a different boxplot. In that graph El Castillo samples are included inside Mousterian range, even if their cultural adscription is officially “transitional Aurignacian”. MO, Mousterian; CH, Châtelperronian; AU, Aurignacian; GRAV, Gravettian.

Leguminosae/Fabaceae. Mousterian levels from Llonin and La Viña conversely presented the anecdotal presence of *Betula* but high abundances of *Rosaceae*, follow by Leguminosae/Fabaceae and Angiospermae (Rasilla et al., 2018, 2020). In the case of La Viña, a significant shift is noticed between Aurignacian levels with an increase in *Betula* acquisition, in contrast to the large increase in Leguminosae/Fabaceae abundance recorded in Gravettian levels.

3.1.3. Stable isotope analysis

This work included 265 values of stable isotopes on bone collagen (224 $\delta^{13}\text{C}/\delta^{15}\text{N}$ and 41 $\delta^{34}\text{S}$) achieved in ungulate remains, recovered at 31 levels from nine regional archaeological sites (Jones et al., 2018, 2019; Rofes et al., 2015). In total 168 values are from *Cervus elaphus*, 43 from *Equus* sp. and 6 from *Capra pyrenaica* (SI2; SI3). Most of the stable isotope analyses are focused on red deer, which is the most frequent ungulate species in archaeological sites from the Cantabrian region.

Grouped by cultural periods (Fig. 5), the $\delta^{13}\text{C}$ values in *Cervus elaphus* are highly stable with a mean between -20 and -20.5‰ , reflecting typical values of animals regularly inhabiting relatively open landscapes. The $\delta^{13}\text{C}$ values of red deer hardly change between the periods analysed. Red deer is a mixed feeder with a plastic dietary behaviour, switching from grazing to browsing. This changing feeding behaviour and habitat conditions may mask some

environmental signatures from being observable in the long-term bone collagen record. The $\delta^{15}\text{N}$ values have mean values between 3 and 5‰ with a high level of intra-species variation. Both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of cervids show a slight increase from the end of the Mousterian to Aurignacian-Gravettian periods, although this trend is subtle. Analysis performed on *Equus* sp. specimens shows a small and progressive decrease in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, with a marked change between Mousterian and Châtelperronian-Aurignacian occupations. Thus, both species follow contrary trends, which were previously interpreted as niche partitioning (Jones et al., 2019).

Inter-individual variability within the same archaeological levels with several high $\delta^{15}\text{N}$ values both in *Cervus elaphus* and *Equus* sp. remains is common. This trend may relate to human hunting dynamics and both Jones et al. (2019) and Rofes et al. (2015) suggest that these values could be related to non-local hunted animals or animals procured from very distinct micro-environments or isoscapes. This inter-individual variability occurred both during Mousterian and Aurignacian in the case of *Equus* sp., but for *Cervus elaphus* is more frequent during the Aurignacian and Gravettian levels. Remains from the archaeologically sterile levels of El Castillo (levels 16–17, 17C and 19) are consistent with the mean values from other levels analysed, which we can be interpreted as the “local” values, considering that those were not animals selected by humans.

The available regional $\delta^{34}\text{S}$ analyses for *Cervus elaphus* and *Equus* sp. were from Aitzbitarte III, Amalda, Labeko Koba in the Basque Country and Covalejos in Cantabria (Jones et al., 2018, 2019). These results also suggest variability in the hunting areas used by both Neanderthals and AMH in the vicinity of each site, resulting in high levels of inter-individual variability in the $\delta^{34}\text{S}$ observed (SI3). To date, there are still few $\delta^{34}\text{S}$ studies available that explore temporal changes which may be indicative of climatic and environmental changes (e.g. changing permafrost, in Reade et al., 2021). Further $\delta^{34}\text{S}$ analysis in the region is needed to explore this possibility.

4. Discussion

This research has compiled data from the available terrestrial environmental proxies in the Cantabrian region, which until now had never been unified to explore environmental trends on a regional level. Several challenges were overcome to produce a homogenous and reliable comparative dataset due to 1) the difficulty of processing the data provided in qualitative format (e.g. in pollen diagrams only graphic information without numerical values is generally presented); 2) low sample size that limited the interpretation of the data (e.g. low MNI or low pollen content); 3) sequences or levels with inadequate dating information, such as those without absolute or relative dates (which do not allow their interpretation in climatic or cultural terms); radiocarbon dated sequences but following old methodologies that require modern revision, or sequences showing stratigraphic inconsistencies. Additionally, some records were produced more than three decades ago and a review of the data and interpretations is recommended. In the case of small mammals, revisiting collections and refining certain taxonomic identifications would help in a better ecological characterisation, as an example: the ascription of several remains to the group *M.arvalis-agrestis* restricted the ecological resolution, considering that these species have different relationships with moisture (Luzi et al., 2017; Palomo et al., 2007). Despite these limitations, valuable information has been obtained in this study to characterise the environmental conditions from 55 to 25 ka BP. The rigorous selection of archaeological levels included in this analysis has contributed to ensure that only accurate datasets were used, facilitating a reliable environmental characterisation of the Middle to Upper Palaeolithic transition and facilitating the reconstruction of MATs and MAPs. Several methods have been proposed to homogenise and standardise ecological data, which has helped to offer some environmental clues and make them comparable to the global climate records of MIS 3.

This study proposes high-resolution modelling from the end of the Mousterian to Gravettian by combining data from levels with absolute dates, containing both pollen and small mammals (Fig. 6), which were standardised to allow diachronic palaeoecological trends to be correlated with global climatic proxies. It should be noted that only six levels had data of both proxies, but these did show consistent correlation results within one standard deviation. A highly variable climatic response is shown in the Cantabrian region during the Middle to Upper Palaeolithic transition. This variability is most likely linked to the abrupt shifts expected from the alternating stadial and interstadial episodes within each phase during the MIS 3, as has been recorded in the marine core in Biscay Bay (Fourcade et al., 2022; Sánchez Goñi et al., 2008). It was observed that both stadial and interstadial alternating phases occurred during the Mousterian, Aurignacian and Gravettian levels; showing that both Neanderthals and AMH were subsisting during both cold and temperate events in northern Iberia. These climatic oscillations are not statistically different between them (Table 3), suggesting that both human populations were equally experiencing these fluctuations. However other factors cannot be rejected as

being responsible for these anomalies, such as taphonomic causes, sampling bias or palimpsest limitations.

At the end of the Mousterian and during the Aurignacian, a progressive trend towards lower temperatures and greater aridity is visible from the environmental proxies explored in this work. But, when levels with calibrated values were considered (Fig. 6), a decrease in temperatures and rainfall is highlighted from 48 to 44 ka cal BP corresponding to the GS13 and GS12, after the HE5. This period coincides with the last Neanderthal settlements, followed by a populational hiatus until the 43 ka cal BP, when the Châtelperronian appears in the region quickly followed by the Aurignacian technocomplex (Marín-Arroyo et al., 2018). This moment is especially singular in the Cantabrian region compared to other parts of Iberia and Eurasia. The onset of GS12 corresponds to a decrease of 33.3% in net primary productivity (NPP) and a decrease of 45% in herbivore biomass coinciding when the frequency of Mousterian assemblages decline, around 45 ka cal BP (Vidal-Cordasco et al., 2022).

Local Last Glacial Maximum (LGM) events in Iberian Mountains where synchronous to global LGM (during MIS 2) and just a few systems present larger glacier extensions earlier, at ca. 50–40 ka cal BP (Oliva et al., 2022). In the Cantabrian region, the local LGM occurred thousands of years before the global LGM and the maximum glacial advance in Picos de Europa is established around 44 and 38 ka, considering both calibrated radiocarbon dating and OSL dating (Ruiz-Fernández et al., 2022). The glacier front at Lake Enol and Vega de Comeya reached its maximum extension from 44 to 38 ka (Ballesteros et al., 2020; Jiménez-Sánchez et al., 2013), when colder and drier conditions in the mountain areas dramatically affected the tree cover. Consistently, pollen data from the marine core MD04-2845 in the Cantabria Sea (Sánchez Goñi et al., 2008) show a low abundance of arboreal pollen with a saw-teeth pattern between 50 and 40 ka BP, suggesting a long-term forest opening from GI2 to GI8 in Atlantic forests (Fourcade et al., 2022). From ca. 47–40 ka is characterized by steppe expansion with associate cold grasses (*Artemisia*, Poaceae, Cyperaceae), but also punctual forest expansion, including *Betula*, *Quercus*, *Alnus*, *Corylus* or *Carpinus*.

Ungulates, as part of the human diet recovered from archaeological sites, are not an accurate climatic proxy, as the most exploited species such as red deer, ibex, horse or large bovids are eurytherms. Nevertheless, climatic, and environmental changes affected ungulate prey availability and subsequently the hunting strategies adopted by Neanderthals and AMH. Cold-adapted faunas such as *Mammuthus primigenius*, *Coelodonta antiquitatis* and *Rangifer tarandus*, although not abundant, are not rare in this region and usually related to occasional movements to the south of the continent during stadial moments (Álvarez-Lao et al., 2015; Álvarez-Lao and Méndez, 2016; Marín-Arroyo and Sanz-Royo, 2022). Mammoths are present during the latest phases of the Mousterian and occasionally during the Aurignacian. The woolly rhinoceros is only present during the Mousterian and in the Châtelperronian level of Labeko Koba. Whereas wooded-adapted animals tend to dominate in the Mousterian, during the Aurignacian species with a preference for open-landscape increased. This was the case for reindeer, which were notably more abundant during the Aurignacian and would reinforce the previous data of landscape opening at this time. In fact, different arrival episodes of cold-adapted faunas linked to cold and open landscapes are started around 45 ka cal BP, with subsequent episodes in 38, 36 and 30 ka cal BP. At around 45 ka cal BP, the presence of the woolly rhinoceros at the palaeontological site of Rexidora cave (Álvarez-Lao et al., 2015) provides supporting evidence for one of those migrations.

Recent chronological reassessment points to a discontinuity between the Mousterian and the Châtelperronian, based on the

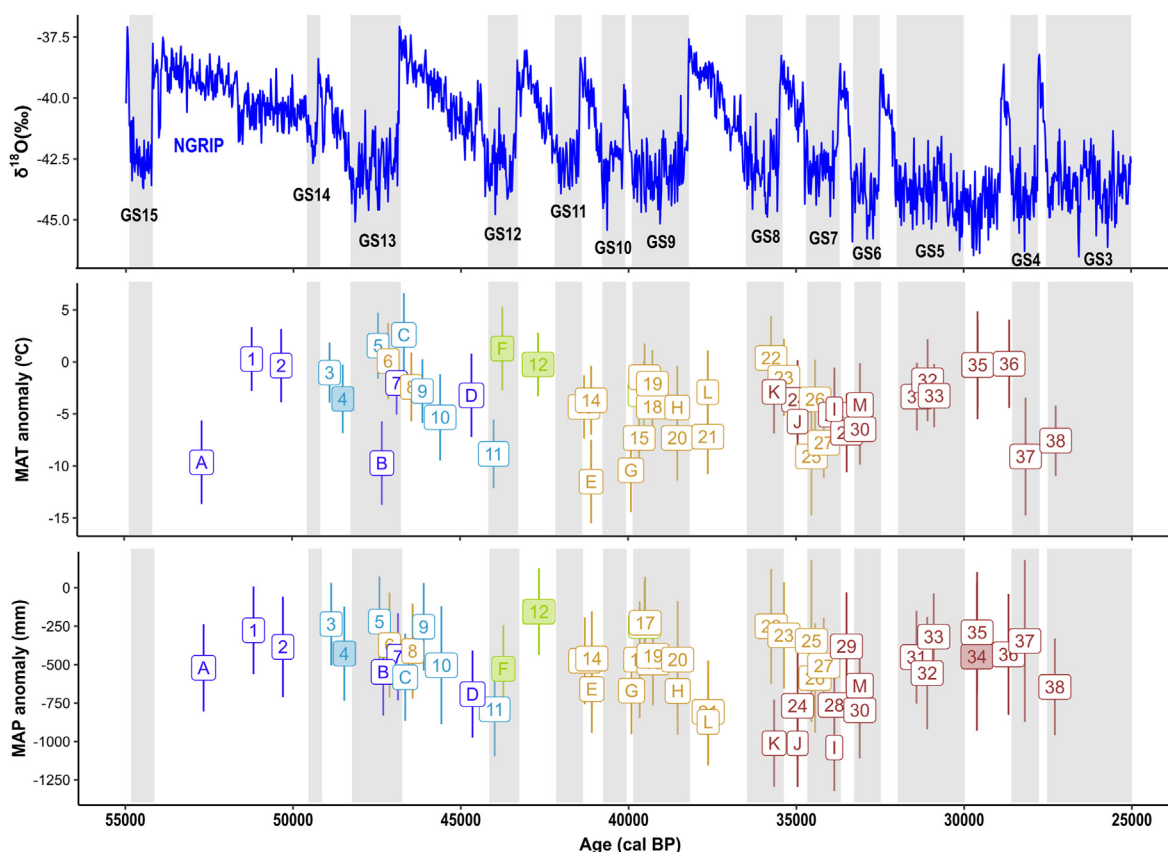


Fig. 6. Climatic correlation of Mean Annual Temperatures (MAT) and Mean Annual Precipitations (MAP) relative to the present day, from modelled pollen (A to L) and small mammal (1–38) records with associated radiocarbon dates, calibrated (calibration errors are not included in the figure, the summary table can be found in SI3 and Bayesian Models in SI4). 1.El Sidrón (III); 2. El Castillo (20C); 3. Llonín (VII-CP/VI-G); 4. El Castillo (19); 5. Esquilieu (VI-XI); 6. El Castillo (18C); 7. El Mirón (130); 8. El Castillo (18B); 9. La Güelga (9); 10. Covalejos (D); 11. Amalda (VII); 12. Torca del León; 13. Covalejos (C); 14. Labeko Koba (VII); 15. Labeko Koba (VI); 16. La Güelga (2); 17. La Güelga (5); 18. Covalejos (B); 19. Covalejos (A–B); 20. Labeko Koba (V); 21. Aitzbitarte III (Vb central); 22. La Viña (XIII-SO); 23. La Viña (XII-SO); 24. Aitzbitarte III (Va); 25. La Viña (XI-SO); 26. Antoliñako (Lmbk/Smk lower); 27. Bolinkoba (2inf); 28. Aitzbitarte III (IV); 29. La Viña (X–SO); 30. Amalda (VI); 31. El Mirón (128); 32. Antoliñako (Lmbk/Smk upper); 33. La Viña (IX-SO); 34. Askondo (8); 35. La Viña (VII–SO); 36. Bolinkoba (2 sup); 37. La Viña (VII–SO); 38. Antoliñako (Lab/Sab). A. Arrillor (H-Amk); B. El Cuco (XII); C. Arrillor (Lmc); D. El Cuco (Vb); E. Labeko Koba (VII); F. Rexidora (Rhino); G. Labeko Koba (VI); H. Labeko Koba (V); I. Aitzbitarte III (IV); J. Aitzbitarte III (Va); K. Aitzbitarte III (Vb upper); L. Aitzbitarte III (Vb central); M. Amalda (VI). In blue, Mousterian; in yellow, Aurignacian; in red, Gravettian. In dark, archaeologically sterile levels. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

chronological gap between both technocomplexes in the region without technological characteristics linking both. Those advances have proposed a local extinction of classical Neanderthals, followed by the arrival of new Neanderthals groups coming from southwestern France and crossing the Pyrenees, carrying with them the Châtelperronian technology (Marín-Arroyo et al., 2018; Rios-Garaizar et al., 2022; Wood et al., 2014). Similar phenomena may also be documented in north-eastern Iberia at 36–42 ka cal BP at Cova Foradada (Morales et al., 2019), the southernmost Châtelperronian episode within Iberia, maybe linked to a late Neanderthal arrival after the Mousterian technocomplex has already disappeared in that region. These human groups movements are key for understanding the population fragmentation that Neanderthals experienced (Staubwasser et al., 2018), that ultimately led to their spatio-temporal disappearance in Iberia (Vidal-Cordasco et al., 2022).

The present work reveals a climatic and likely environmental deterioration around 45 ka cal BP that was contemporaneous with a significant decrease in the available biomass for secondary consumers. This ecosystem disequilibrium might have accelerated the abandonment of northern Iberia by the Neanderthal groups, associated with the Mousterian technology, and their displacement to other areas of Iberia, first to the Iberian Plateau and later the

Mediterranean region. The limited data associated with the Châtelperronian levels does not allow the evaluation of the environmental conditions associated with that period. The only Châtelperronian levels of this period are La Güelga 1 and 2, which tentatively suggest an increase in rainfall and moderate temperatures (Álvarez-Vena et al., 2021). However, considering the secondary sedimentation at La Güelga, data must be viewed with caution. Just after the end of the populational hiatus, the sterile level of Rexidora cave (Rhino Area; 42 ka cal BP), as well as the archaeologically sterile level of Torca del León (43 ka cal BP), reveal an increase in temperatures, and the last show a rainfall increase and the maximum forest development (Fig. 3; 6) (Álvarez-Lao et al., 2020). Higher temperatures are also estimated for Rexidora (Rhino Area). These data suggest that the environment might have recovered relatively quickly since the GI11, at least in the western coastal zone, being coeval with the glacial retreat in Picos de Europa after their maximum reach at 45 ka (Jiménez-Sánchez et al., 2013) and rapid recovery of the herbivore biomass (Vidal-Cordasco et al., 2022). These new conditions may have favoured the arrival of new Neanderthal populations from southwestern France, carrying with them Châtelperronian technology. Nevertheless, the available regional environmental and climatic data from the terrestrial proxies analysed still do not provide enough resolution to build a

continuous sequence of the conditions that both human species had to face. Further environmental studies will help to unravel more detailed information.

There are a limited number of sites with environmental information available for the time when the first Anatomically Modern Humans occupied the region. Early Aurignacian levels in Labeko Koba (VII), El Cuco (IV) and La Güelga (7) provide some information about the environment during that time (Álvarez-Vena et al., 2021; Iriarte-Chiapusso, 2000; Pemán, 2000; Ruiz-Zapata and Gil-García, 2007). Data from those sites points over to arid and colder climatic conditions than the present day, and also concerning the analysed Mousterian levels (Fig. 4; 5; 6). The start of the Aurignacian reveals limited tree cover, lower temperatures, and higher aridity than during the Mousterian but coincided with an increase in herbivore carrying capacity motivated by smoother stadial-interstadial NPP fluctuations (Vidal-Cordasco et al., 2022). Thus, AMH might have arrived on the continent during harsh climatic conditions and more open environmental conditions. These are more severe conditions that when the late Neanderthal occupations took place in the region. Indeed, this cold climate has already been attested in other Eurasian sites such as Bacho Kiro (Pederzani et al., 2021).

Moreover, results reflect a highly unstable climate during the Aurignacian, with more intense oscillation in estimate MAT and MAP, which reach wider ranges. This is explained by more abrupt stadial-interstadial oscillations in the second half of MIS 3, but also shows that human occupation is evidenced throughout this time both in the stadial and interstadial periods. These harsh climatic conditions did not prevent the rapid expansion of the AMH into the continent, from east to west, in a few millennia, demonstrating their resilience. This shift to more arid and cooler climatic conditions from the end of the Mousterian to the Early Aurignacian, was accompanied by a reduction of forest masses. Conifers and, especially Pinus, are the most represented taxa, which is also common throughout the rest of Iberia (Allué et al., 2018; Carrión, 2012; Carrión et al., 2018; Daura et al., 2017). But the relative abundance of pollen data compiled by this work demonstrates a decrease in the arboreal pollen and an increase in cold grasses. However, considering the fragmentary pollen record, these data should be taken with caution. The marine core MD04-2845 in the northern margin of Iberia coincides in revealing a decrease in Atlantic forest and steppe expansion with cold indicators mainly from GS10 to GS9 (Fourcade et al., 2022).

The small mammal evidence suggests a heterogenous but stable landscape throughout all the periods. It reflects a mosaic landscape without significant changes along individual sequences or between cultural periods. However, it must be considered that it could be a consequence of the limitations related to dealing with faunal assemblages whose temporal resolution is unknown. A combination of different microhabitats within river valleys has been pinpointed by stable isotopic studies based on $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and $\delta^{34}\text{S}$ values (Jones et al., 2018, 2019). Indeed, the particular orography of the Cantabrian region with the mountain formations located inland, between 30 and 50 km to the current coast, and river valleys running perpendicular to it, favoured rather diverse ecosystems that change in a few kilometres of distance and make difficult environmental comparison between sites. These characteristics of the territory would facilitate success in survival, despite climatic instability.

The stable isotope analyses of hunted ungulates by humans also coincide in suggesting a climatic shift and aperture of the landscape from the Mousterian to the Aurignacian. Variations in $\delta^{13}\text{C}$ values can be related to changes in feeding behaviour from grassland to open forests, usually motivated by changes in habitat conditions. In Rofes et al. (2015), the increase in red deer $\delta^{13}\text{C}$ values at Antoliñako Koba (Bizkaia) from the Aurignacian to the Gravettian, is considered to reflect a decrease in forest cover in the site nearby. As this work

has observed (Fig. 5), whereas the $\delta^{13}\text{C}$ and the $\delta^{15}\text{N}$ values of *Equus* sp. increase from the Mousterian to the Upper Palaeolithic assemblages, *Cervus elaphus* isotopic values remain stable or even follow the contrary trend. That was previously interpreted as niche fractionation between equids and cervids, probably derived from a climatic shift (Jones et al., 2019). These results might support the interpretation of more open landscapes, that mainly affected horse niches with lower-quality pasture, whereas cervids as mix-feeders with a more plastic behaviour might have hidden this environmental effect.

In summary, this work proposes a regional perspective of the environmental conditions during MIS 3 in the Cantabrian region. Results indicate a predominance of open humid formations, with lower tree cover than seen in the Mediterranean environments during the entire study period, accompanied by lower temperatures and more arid conditions than the current day. The climatic reconstructions generated through this work reveal a progressive increase in aridity, and a temperature decrease from the Mousterian to Aurignacian, accompanied by a reduction of forest cover. Previous evidence from Iberia has suggested a preference of Neanderthal populations for inhabiting open forest and tree savannah environments, especially in the Mediterranean area during stadial periods, because this area might have offered favourable ecological conditions for hunting, gathering, shelter or fuel acquisition delaying their survival (Allué et al., 2018; Fernández-García et al., 2020; López-García et al., 2014; Ochando et al., 2021, 2020; Sánchez-Hernández et al., 2020). Thus, a progressive decline in woodland, as the preferred biome for Neanderthal groups, and a consequence decrease in the biomass of medium and medium-large herbivores, as the main elements of their subsistence, could have been crucial at the end of Mousterian for Neanderthals in the north to retreat to other areas of Iberia, where more stable biomes still were preserving biomass for secondary consumers (Vidal-Cordasco et al., 2022). Stadial conditions may had a higher impact in northern Iberia than in other Iberian regions and, the progressive worsening in climatic conditions after HE5 might have crucially compromised the persistence in the region.

5. Concluding remarks

The available terrestrial proxies selected for this study and their critical reassessment according to their chronology allow providing some clues about the climatic and environmental conditions experienced in the Cantabrian region during the Middle to Upper Palaeolithic transition. Using environmental modelling methods applied to pollen and small-mammal records, colder and drier conditions than the present day are detected from 55,000 to 25,000 uncal BP. The data show highly variable climatic shifts that correlate with the climatic fluctuations recorded in the marine and ice records, demonstrating that human populations subsisted in the region during both stadial and interstadial phases. A mosaic landscape with the predominance of humid meadows, in combination with open forest formations, is suggested as the predominant environment. This is linked to a high level of local ecological diversity characteristic of the Cantabrian range, which is influenced by valley and mountain configurations, as well as the proximity to the coast.

Relative mean annual temperatures and mean annual precipitation decreases from the Mousterian to the Aurignacian-Gravettian. The aperture of the landscape is suggested from Mousterian to Aurignacian based on pollen and stable isotope evidence, in combination with other local and regional proxies. Moreover, high-resolution modelling based on dated environmental records indicates a progressive trend towards lower

temperatures and aridity from the Mousterian to the Early Aurignacian, especially from 48,000 to 44,000 cal BP coinciding with the last Neanderthal regional settlements and followed by a populational hiatus until around 43,000 cal BP, when Châtelperronian and early Aurignacian sites appear in northern Iberia. The quality of the data associated with the few Châtelperronian assemblages available does not allow environmental conditions associated with that period to be assessed.

This review indicates that despite the multiple environmental studies available in the region, there is still a fragmentary environmental record during this key period of human evolution, restricting our knowledge about the effect of climate on human adaptations and survival. Considering the discontinuity of the archaeo-palaeontological deposits and the different sources of data, it is currently challenging to evaluate the impact of MIS 3 climate on a local and regional level, and a more accurate resolution is needed to understand human resilience. Further research focused on high-resolution proxies, associated with well-dated anthropic assemblages, will help to extend the conclusions reached by this work.

Author contribution

A.B.M.-A. and M.F.-G. designed the study; data collection and formal analysis were done by M.F.-G., A.B.M.-A., M.V.-C. and J.R.J.; all authors discussed the data and participated in writing and editing the original draft. The first draft of the manuscript was written by M.F.-G.; all authors commented on previous versions of the manuscript and, have read and approved the final manuscript.

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.

Data availability

All dataset is provided in the Supplementary Materials. R code and data files are available at <https://github.com/ERC-Subsilience/Data-and-code-associated-with-Reassessing-paleoenvironmental-conditions>.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.quascirev.2022.107928>.

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