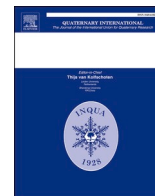


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Changes in pollen and small mammal spectrum compositions and in human-landscape relationships during the last 40,000 years of the Pleistocene in El Mirón Cave, Cantabrian Spain

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ABSTRACT

The important albeit discontinuous pollen and more complete small mammal microrecords from the long, Late Upper Pleistocene stratigraphic deposit in El Mirón Cave (Cantabria, Spain, >47,000–12,000 cal BP) are presented and compared in detail. They describe a sequence of environmental conditions varying from cold and relatively dry to somewhat more temperate and more humid throughout the course of late MIS 3 and MIS 2, and into the early Holocene conditions of MIS 1, with variable intensity and function of human occupation of the cave during late Mousterian, Gravettian, Solutrean, Magdalenian and Azilian cultural periods. In general, the discontinuous palynological record is concordant with the more continuous small mammal sequence in tracing the changes in local climate and landscape within the broader context of the high relief and coastal setting of the Cantabrian region of northern Atlantic Iberia. Shifts in the extent and composition of open versus wooded vegetation in the montane and low valley surroundings of the cave are documented by the analyses detailed here. Some of the environmental fluctuations, namely the Last Glacial Maximum, the Late Glacial and the at the beginning of the Holocene, seem to have had significant effects on the nature of human uses of this cave with short, ephemeral, special/limited-function visits, while Oldest Dryas, despite its still-rigorous conditions but abundant pasture for game species (red deer and ibex), did not prevent the cave from being used as a major, repetitive, long-term base camp for foraging bands, notably during the Cantabrian Lower Magdalenian.

1. Introduction

The aim of this work is to analyse the interaction between landscapes and humans in Cantabria (northern Atlantic Spain) during the last 50,000 years based on pollen and small mammals. To this end, we present a comparative study of the small mammal and micro-floral remains sampled from the sedimentary deposits of El Mirón Cave in Ramales de la Victoria. The cave, while situated in the first range of the Cantabrian Cordillera, is not very far from the shore of the Bay of Biscay, thus in an area of steep relief. We show correlations in compositional shifts and taxonomic turnovers among the fossils of pollen and small mammals throughout the long stratigraphic sequence of El Mirón Cave.

1.1. Review of climatic reconstruction using past floral and faunal proxies

There are many studies to reconstruct past climates and environments through the fossil record, mainly from pollen and other floral remains, birds, large mammals, and small vertebrates (e.g., Dietl and Flessa, 2017; Alfaro-Ibañez et al., 2023; Blanco-Lapaz et al., 2021, 2023; Núñez-Lahuerta et al., 2021; López-García et al., 2021; Martínez-Monzón et al., 2021). Climate variability is generally based on external forcing and internal dynamics ranging from sub-daily weather to multi-centennial trends and beyond (Huybers and Curry, 2006). State-of-the-art paleoclimatic methods routinely use historical documents and instrumental techniques, as well as natural archives.

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Human-induced climate change in recent centuries is one of the most concerning issues in current European and global policy-making, as highlighted in the European Working Group II of Climate Change (2022).

One of the most interesting possible applications of studies that reconstruct Pleistocene climate changes would be to try to predict future developments, but this is a difficult endeavour. Nonetheless, in long, well-dated stratigraphic sequences in caves, we have a unique window on the past with which to address the problem through the search for patterns, namely the record of the deep past. The study of pollen grains and bones of small vertebrates, among other fossil remains, can be used to understand how changing climates and environments have affected flora, fauna, people, and/or how humans have influenced the landscape. Palaeontology shows that humans have long affected the populations of small mammals even in pre-agricultural times (Bañuls-Cardona et al., 2017; Galán et al., 2019; Cuenca-Bescós et al., 2021).

The decade of the 1960s in the Cantabrian region witnessed an inflection point in Pleistocene paleoclimate studies through the analysis of small mammal remains, pollen grains and spores. In 1965, Jean Chaline published the first study of small mammals from the region in the Sima del Mortero, Peña Rocías, in the Asón basin (Cantabria), which is also the location of El Mirón Cave (Chaline, 1965). Similarly, Arlette Leroy-Gourhan (1966) established the initial basis for the palynological analysis of archaeological sites in the region to reconstruct the landscapes in which Paleolithic peoples lived, beginning with her study of El Otero Cave, also in the Asón basin.

From that time on, the number of studies has grown, although there were often discrepancies between the two kinds of records. Nonetheless, planned interdisciplinarity in archaeological projects, improvements in the methodologies of the two kinds of analyses (e.g., systematic sampling techniques, fine-mesh water-screening, flotation), and increased and higher accuracy and precision in radiometric dating are some of the main factors that have contributed considerably to reduce the initial discrepancies (Cuenca-Bescós et al., 2007, 2008, 2009, 2010, 2012; Higham et al., 2014; Iriarte-Chiapusso and Murelaga, 2013; Wood et al., 2014). The methodological changes during the present century have led to the availability of not only greater knowledge of paleoclimatic and paleoenvironmental conditions under which the hominins have evolved but also a better understanding of the development of animals and plants, as well as their capacities for adaptation to changing landscapes (e.g., Rofes et al., 2012). An important conditioning factor must not be forgotten when trying to correlate between different kinds of paleoenvironmental records, namely depositional hiatuses.

The correlation of faunal and floral shifts in El Mirón Cave, during the last c.50,000 years is a potential source of data for climate modelling in Cantabria and, more broadly, along the Atlantic coast of northern Spain. Certain limitations of the fossil record, however, have to be kept in mind. It is temporally discontinuous and limited to those events that had a significant impact on the faunal and floral remains that are fossilized in the cave. The species of small mammals and flora present in the sediments are taxonomically identified using classical methods as well new ones, such as analysis of ancient DNA extracted from certain bones that will permit correlation of morphology with genetic evidence in vole species (Alfaro-Ibáñez et al., 2023).

1.2. Geographical location of El Mirón Cave

El Mirón is a large cave (mouth 20 m high x 16 m wide) that faces West from the very steep slope of the highly karstic Pando-Moro limestone massif, part of a foothill range of the Cantabrian Cordillera on the border between the Spanish provinces of Cantabria and Bizkaia, in Rames de la Victoria (Fig. 1). Its geographical coordinates are 43°14'44" N x 3°27'09" W. In a straight line, it is c. 20 km from the Holocene shore (c. 25 km from the Last Glacial littoral) of the Bay of Biscay and is surrounded by summits of c. 1000 m a.s.l. At 260 m a.s.l., it strategically overlooks a broad, intermontane segment of the Asón River

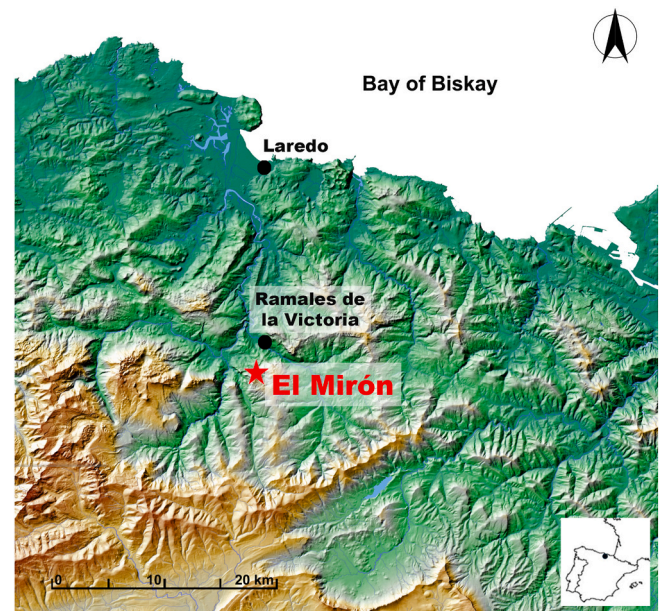


Fig. 1. (in colour).- Location of El Mirón Cave.

valley, whose floor is c. 150 below the cave, near the confluence of this major river with two tributary streams at the foot of the cliff in which the cave is located. The site is c. 10 straight-line km from one of the lowest (920 m a.s.l.) mountain passes over the central sector of the Cordillera that leads up to the high tablelands and canyons of the upper Ebro River in Burgos Province (Straus and González Morales, 2012a).

The cave vestibule is 30 m deep x 16-8 m wide x 13 m high and is generally very dry and sunlit (albeit darker at its rear). The cave continues straight back (eastward) for c. 100 m, with a higher, narrower, totally dark inner gallery, filled (ultimately to its ceiling) with alluvial sediments (Fig. 2).

1.3. The chronology and stratigraphic record of El Mirón cave

The site, excavated under the direction of L.G. Straus and M. González Morales (2012a, 2019) between 1996 and 2013, has yielded a sequence of archaeological levels attributed to the Mousterian, Gravettian, Solutrean, Magdalenian, Azilian, Mesolithic, Neolithic, Chalcolithic and Bronze Age cultural periods, corresponding to the timespan between Greenland Interstadial G-12 and the recent Holocene. The principal excavations were conducted in the vestibule: a 9.25 m² area in the outer vestibule ("the Cabin"), a 15.5 m² area in the vestibule rear ("the Corral" + "the Deep Sondage" [the only area where pre-Magdalenian layers were excavated] + "the Red Lady Burial" [locus of the c.19 ka cal BP Lower Magdalenian human female interment adjacent to the "Corral" area in the SE rear corner of the vestibule]), and a 9 x 0.5-1 m connecting trench between the "Cabin" and "Corral" (Fig. 2) (Straus et al., 2015).

The sources of the sediments in the vestibule (silty loams with varying amounts of sand, clay and limestone debris content) in general are the alluvial deposit that fills the inner cave washed downslope into the vestibule by running water, clasts (*éboulis*) fallen from the cave ceiling, fine aeolian sediments blown into the cave from the exterior, human activity notably the deposition of faunal remains, lithic artifacts/debris, fuel wood/charcoal, ochres, vegetal bedding, faeces, etc., and animal activity (roosting birds, occasional occupation by a variety of carnivores during periods of human absence) (Farrand, 2012; Straus et al., 2001). Humans also reworked the sediments in prehistory by trampling, scuffing, cleaning, and especially the digging of pits, construction of hearths, one human burial in a small pit, and a possible wall in the Lower Magdalenian (Straus and González Morales, 2007, 2012c,

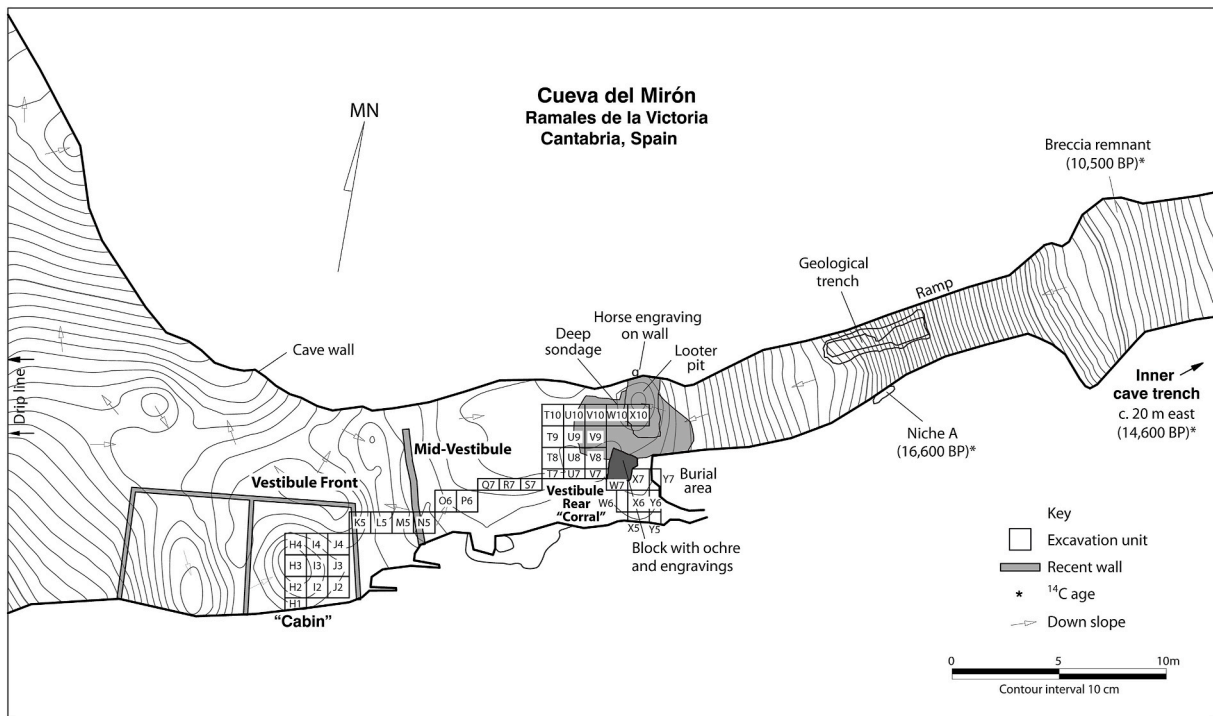


Fig. 2. Plan of El Mirón Cave showing excavation areas (L.G. Straus & R.L. Stauber, topography by E. Torres).

2018; Nakazawa et al., 2009). Such disturbance was especially significant in the Lower Magdalenian and Chalcolithic/Early Bronze Age deposits. Among the Paleolithic levels, those of the Initial and Lower Magdalenian are the most intensively anthropogenic, generally dark, “chocolate” brown in colour, very rich in lithic and osseous artifacts, fire-cracked rocks, faunal remains, charcoal and hearths. The abundance of fire evidence could signal reasons for the frequent poor preservation of pollen grains. These levels clearly suggest repeated, long-term, multi-functional, relatively large-scale human occupations of the cave (very much like the extremely rich Lower Magdalenian horizons in such regional cave sites as Altamira, El Castillo and El Juyo) (e.g., Straus, 1992, 2013; Marín-Arroyo et al., 2023). In contrast, the later (Middle, Upper, Final) Magdalenian and Azilian layers are often poorer in finds and less organic in contact, indicating less intensive human occupations. Even poorer in anthropogenic evidence are the Solutrean and especially

the Gravettian, (virtually sterile) Early Upper Paleolithic and Mousterian levels, which are lighter (yellowish, light brown-beige) in colour, indicating only brief, ephemeral, probably special-purpose human visits to the cave (Straus et al., 2001; Farrand, 2012; Marín-Arroyo et al., 2023).

There are hiatuses in the cultural and sedimentary sequence, notably between the Mousterian (Level 130) and Gravettian (128), early Gravettian (128) and Solutrean (127), and (briefly) between the Solutrean (121) and Initial Magdalenian (119.2). The levels corresponding to the Mesolithic time range (10.1, 101–102, 304) are almost culturally sterile, with clear evidence of gentle water flow in the vestibule rear. The density of cultural and macro-mammalian materials varies considerably throughout the whole stratigraphic sequence in El Mirón, notably between the extraordinarily rich Initial and Lower Magdalenian levels on one hand and, on the other hand, the poorer underlying Solutrean and

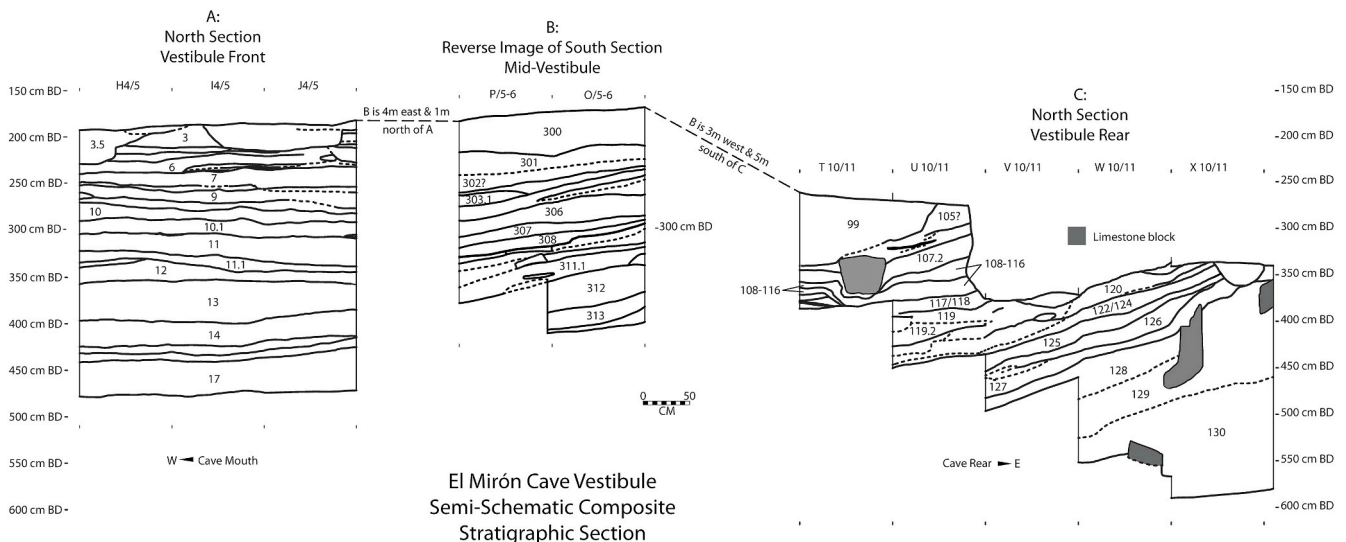


Fig. 3. Semi-schematic, simplified, W-E composite profile: A. Outer Vestibule; B. Middle Vestibule and C. Vestibule Rear (L. G. Straus & R. L. Stauber).

especially Gravettian, EUP and Mousterian levels and the overlying Middle and Upper Magdalenian and Azilian levels (Fig. 3). Most of the levels from all or some of these excavation areas were systematically sampled for sedimentological, micromorphological, magnetic susceptibility, palynological and small mammal analyses (Farrand, 2012; Ellwood et al., 2001; Courty and Vallverdú, 2001; Iriarte-Chiapusso, 2012; Iriarte-Chiapusso et al., 2015; Straus et al., 2011, 2013; Cuenca-Bescós et al., 2008, 2009, 2012).

The stratigraphic sequence is now dated by 101 radiocarbon assays ranging from >47,000 cal BP for the Mousterian (level 130) to c. 4000 cal BP for the Bronze Age (level 3) and 580 cal BP for sub-modern surface charcoal. Methodologies, date lists, critical analyses and Bayesian modelling of the assays are presented in Hopkins et al. (2021). Levels 1–21 are in the Outer Vestibule (“Cabin”), levels 301–313 in the Mid-Vestibule Trench, levels 101–130 in the Vestibule Rear (“Corral”+ Deep Sondage), and levels 500–506 in the Human Burial Area of the Vestibule Rear (Straus et al., 2015). In general terms, besides the Mousterian and Bronze Age levels, the composite chrono-stratigraphic sequence from the vestibule is as follows with approximate, but non-modeled, calibrated (IntCal 20) dates (e.g., Straus and González Morales, 2012a, 2012b, 2019; Straus et al., 2001; Hopkins et al., 2021 with references). Specific radiocarbon dates are given with the sample descriptions.

Mousterian	>47,000	130
Early Upper Paleolithic		129 (culturally nearly sterile)
Gravettian-age	c. 31,000	128
Solutrean	c.	127 to 121
	24,500–22,000	
Initial Magdalenian	c.	119.3 to 117, 21 to 18 (?), 313 (?)
	21,500–20,500	
Lower Magdalenian	c.	116 to 109, 506 to 503.1, 312, 17 to 15
	20,500–18,500	
Middle Magdalenian	c.	108 to 104, 311 to 309, 14, 13
	18,500–16,500	
Upper Magdalenian	c.	103, 308–307, 12
	16,500–14,000	
Final Magdalenian/ Azilian	14,000–12,000	102.1, 306 to 305, 11.2 to 11
Mesolithic-age	12,000–7500	102, 101, 304, 10.1
Neolithic	7500–5000	303.3 to 302, 10 to 8
Chalcolithic	5000–4000	7 to 4
Bronze Age	4000–3400	3, 1

2. Methodology

The archaeological and/or palaeontological methods of excavation are extensively described elsewhere (Straus and González Morales, 2012b).

It is necessary to recall that the joint goal for both types of analyses of fossil remains studied and compared here (pollen and small mammals) is to obtain a reliable and meaningful representation of the paleoenvironmental sequence of the El Mirón site. Both studies sampled the same three excavation areas: Outer Vestibule (OV); Mid-Vestibule Trench (MV) and Vestibule Rear (VR). Thus, the analyses of the small mammal remains include samples from 54 of the 65 stratigraphic units defined by Straus and González Morales in earlier publications (e.g., Straus and González Morales, 2012a; Straus et al., 2001), while the palynological study is derived from the following 9 pollen columns.

- Outer Vestibule: 2 columns (profile H2/G2)
- Mid-Vestibule Trench: 2 columns (profiles K5/L5 and P6/Q6)
- Vestibule Rear: 5 columns (square X10, profiles W10/X10, V8/U8, U9/T9 and X6/W6)

There are few analyses from the Iberian Peninsula with both pollen and small mammals as climatic proxies in human-context localities; among the examples are the classic study of Cueva del Toll in Catalonia

(Donner and Kurten, 1958; Iriarte-Chiapusso et al., 2015). Here we introduce an innovative synthetic methodology by correlating the floral and faunal composition turnovers throughout the long, well-dated and stratigraphically-studied sequence of El Mirón Cave using pollen and small mammals. The correlation is based on the chronology of the layers as well as on the shifts of the fossils of the fauna and pollen.

3. Results

3.1. Palynological study

A common characteristic of the El Mirón sequence is the uneven degree of preservation of pollens and spores among the different stratigraphic units, independent of their location in the front, middle or rear of the cave vestibule (Figs. 7–12). Although all the pollen columns include samples that yielded satisfactory pollen and spore counts, in quite a number of them, the quantity of pollen and spores is insufficient to be considered statistically valid (number of remains minor than 90. Supplementary material: Tables S1–S6). Thus, the palynological hiatuses interrupt the evolutionary dynamics of the vegetation landscape surrounding the cave and we lack information for several levels.

The results obtained from the various analysed columns are internally coherent and reflect changes in the landscape that occurred as a result of the adaptation of vegetation communities to the succession of climatic events during the Late Upper Pleistocene and Early Holocene. In general terms, stadial phases are marked by very open landscapes with few trees that were mostly pines and birches (*Betula*). The grass-shrub stratum at these times displayed the maximum representation of composites (Compositae liguliflora and tubuliflora), which in turn decreased in importance vis à vis grasses (the clearly dominant taxon) and heaths in periods of climatic amelioration. During interstadials, the arboreal diversity was greater with the addition of such species as hazel (*Corylus*), oak (*Quercus robur* tp.) willow (*Salix*) or chestnut (*Castanea*) (which nonetheless appear in small numbers, and especially the latter two only rarely). A notable aspect of the El Mirón sequence is the absence (except in two samples) of plants characteristic of steppe such as *Artemisia* or *Ephedra*. This fact shows that even during periods of greatest cold the decrease in humidity was not sufficiently great to permit the development of this kind of vegetation in the area around the cave.

3.2. Small mammals

The fossil remains of small mammals of El Mirón cave have been widely studied in several scientific publications in which detailed systematic studies have been carried out (e.g., Cuenca-Bescós et al., 2008, 2009, 2010; Alfaro-Ibáñez et al., 2023). They are generally well preserved and complete. The cranial skeleton is composed of loose teeth and mandibles with partial dentition. The postcranial is composed of long bones. The taphonomic analysis allows us to deduce that the small mammal remains in El Mirón Cave were fundamentally deposited by small-medium size predators, i.e., small carnivores and nocturnal raptors of categories I and II in the terminology of Andrews (1990; Cuenca-Bescós et al., 2008). The ecology, environmental adaptations, habitat distribution and geographic distribution of rodents is based on the study of the Quaternary rodents from the Iberian Peninsula (Cuenca-Bescós and Morcillo-Amo, 2022). The study of the biostratigraphic distribution, the composition of the species associations in each level and the taphonomy of small mammals allow us to conclude that the small mammal associations in the Late Pleistocene and Holocene levels reflect the composition and evolution of the faunas in the area around the cave and thus useful for reconstructing both of the paleoclimates and environments of the local area in Cantabria.

The description of the results is done following the chrono-cultural sequence of El Mirón as established by Straus and González Morales and summarised together with the full radiocarbon record analysed by Hopkins et al. (2021) (Table 1).

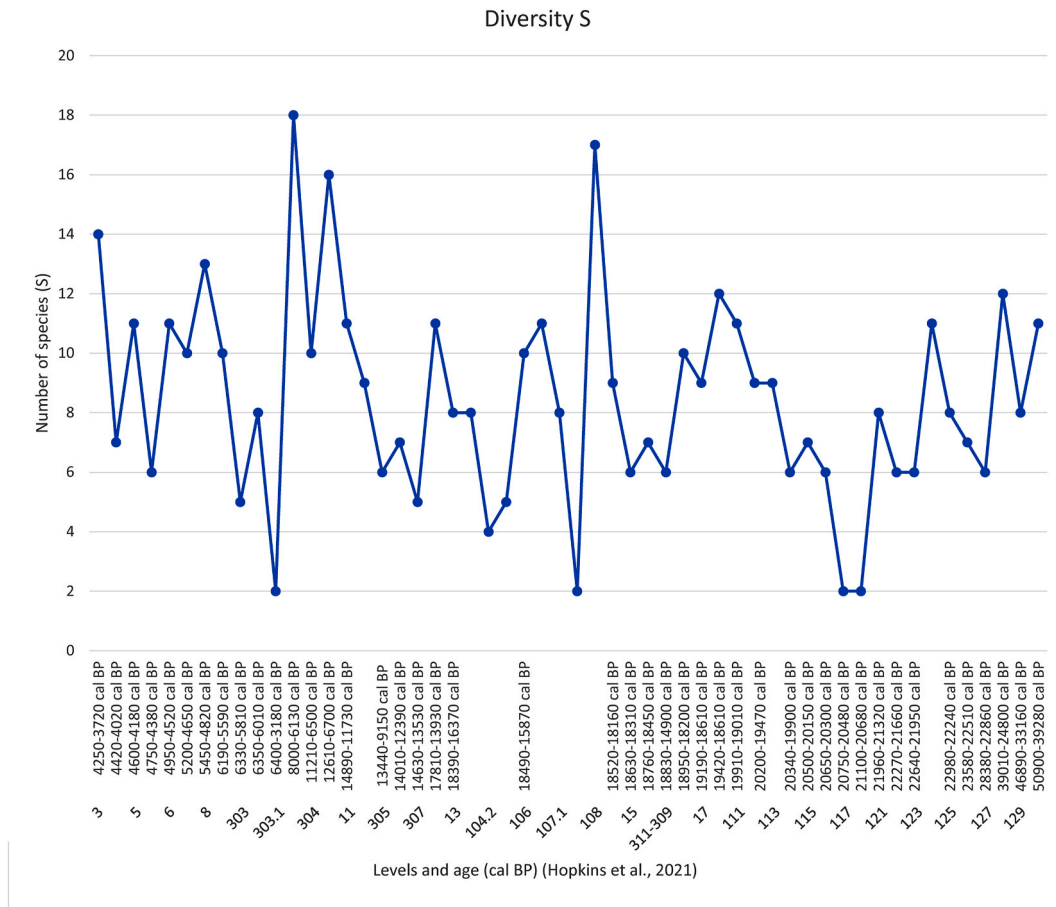


Fig. 4. (in colour).- Variation of the diversity (S) of the small mammals in the sequence of El Mirón cave.

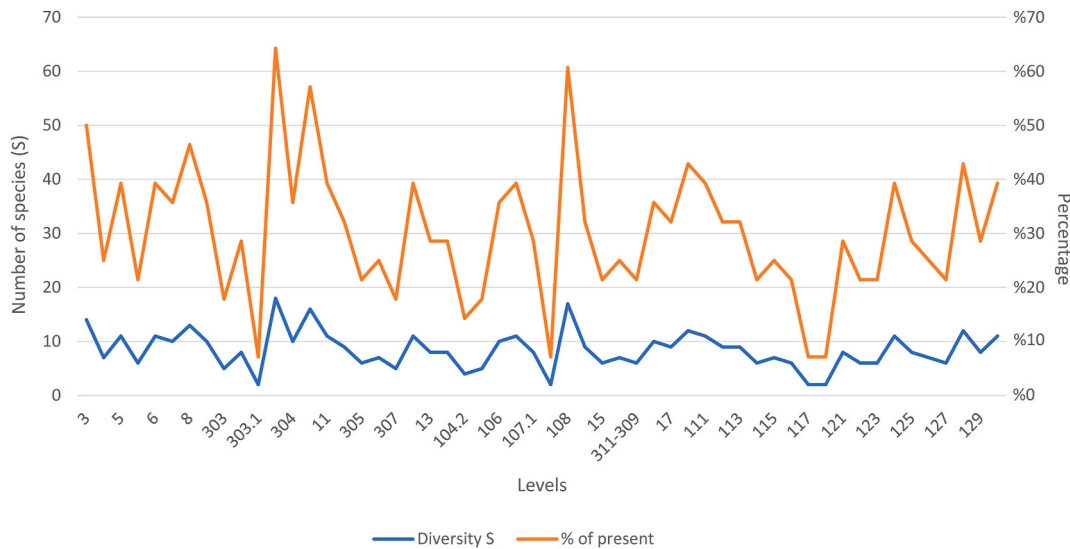


Fig. 5. (in colour).- Variation of the diversity (S) of the small mammals in El Mirón cave, compared to percentage (%) of actual diversity of Cantabria.

In the case of the small mammal remains, we merge them in a single culture-stratigraphic sequence (Table 2) while we keep the pollen and spore results separated by sampling columns.

3.2.1. Biodiversity of small mammals

First, we have analysed the small mammal diversity from El Mirón (Fig. 4) and compared it with the number of species that are living in

Cantabria today (Fig. 5), following the work of Cuenca-Bescós et al. (2008, 2009) and Alfaro-Ibáñez et al. (2023). We measure the biodiversity of small mammals using the species richness (S) or the number of species that occur in a given area. The Minimum Number of Individuals per Species (MNIS) was calculated by counting the parts of the skeleton that are taxonomically diagnostic: lower first molars in the majority of voles or diagnostic molars or some equally identifiable post-cranial

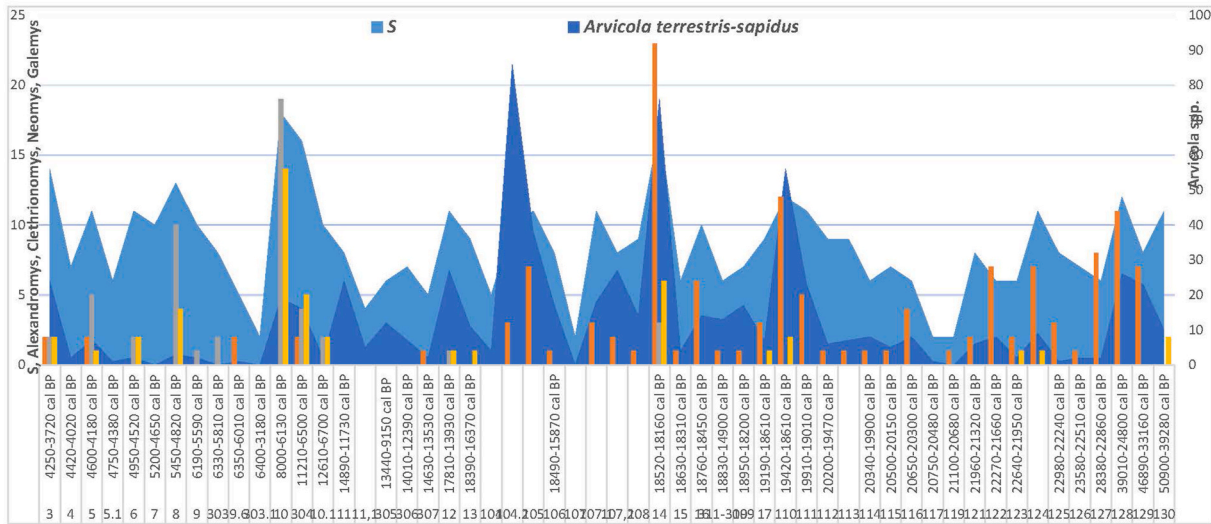


Fig. 6. (in colour).- Distribution graph of the water body and riverbank-dwelling small mammal species, organized by levels.

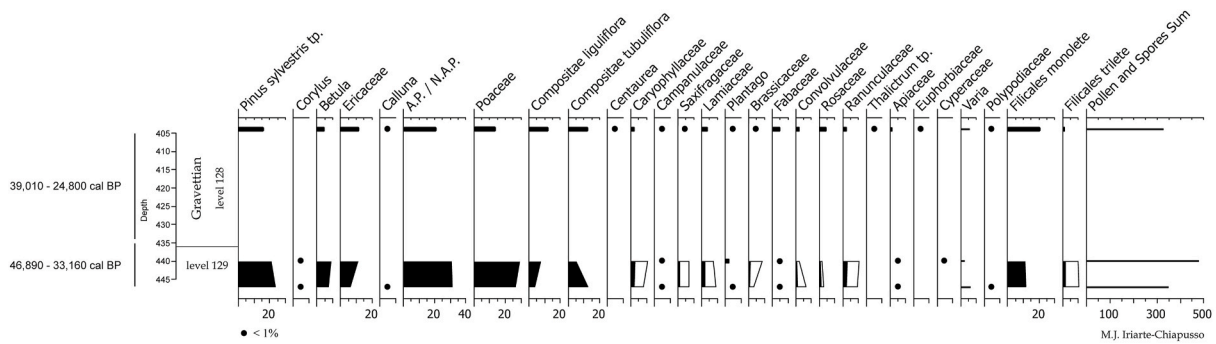


Fig. 7. Pollen diagram column X10 (Vestibule Rear, "Deep Sondage").

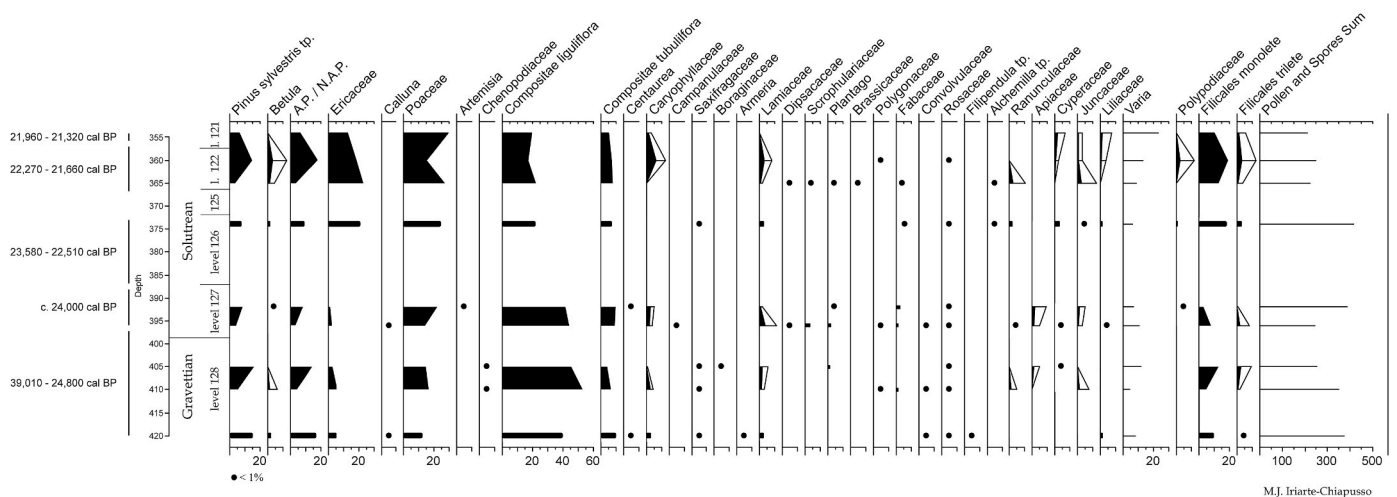


Fig. 8. Pollen diagram column W10/X10 (Vestibule Rear, "Deep Sondage").

elements for the rest of the rodents. Diversity is based on the number of species per layer, summing together all the squares excavated in each archaeological layer.

When comparing the small mammal species diversity of Cantabria today with that of the past 50,000 years, we observe that there is no single layer in the cave's sequence that contains more than 65% of the diversity found in Cantabria today.

3.2.2. Systematic palaeontology: Order rodentia, family cricetidae, subfamily arvicolinae

Arvicolinae rodents are represented at El Mirón by the genera *Microtus*, *Terricola*, *Chionomys*, *Alexandromys*, *Lassiopodomys*, *Pliomys* and *Arvicola* (Cuenca-Bescós et al., 2009, 2012; Alfaro-Ibáñez et al., 2021, 2023). We followed the nomenclature proposed by Abramson et al. (2021), except in the case of *Agricola agrestis* where we used the

Table 1
Chrono-cultural sequence of El Mirón (Hopkins et al., 2021)

Level	Radiocarbon dates cal BP (Hopkins et al., 2021)	<i>Arvicola terrestris</i>	<i>Arvicola sapidus</i>	<i>Terricola lusitanicus</i>	<i>Terricola pyrenaicus</i>	<i>Alexandromys oeconomus</i>	<i>Microtus agrestis</i>	<i>Microtus arvalis</i>	<i>Chionomys nivalis</i>	<i>Clethrionomys glareolus</i>	<i>Pliomys sp</i>	<i>Lasiopodomys gregalis</i>	<i>Apodemus sylvaticus-flavicolis</i>	<i>Eliomys quercinus</i>
3	4250–3720	24	0	6	0	2	7	10	14	2	0	0	33	0
4	4420–4020	2	0	0	0	0	0	1	0	0	0	0	17	0
5	4600–4180	7	0	0	0	2	0	2	0	5	0	0	21	0
5.1	4750–4380	1	0	1	0	0	1	2	0	0	0	0	8	0
6	4950–4520	2	0	0	0	0	3	0	1	2	0	0	27	1
7	5200–4650	0	0	1	0	0	1	0	2	0	0	0	17	1
8	5450–4820	3	0	1	0	0	1	2	1	10	0	0	31	1
9	6190–5590	2	0	2	0	0	1	0	1	1	0	0	14	1
303	6330–5810	1	0	0	0	2	0	0	0	0	0	0	3	0
9.6	6350–6010	0	0	2	0	0	3	1	2	2	0	0	23	0
303.1	6400–3180	0	0	0	0	0	0	0	0	0	0	0	2	0
10	8000–6130	18	1	33	0	0	21	2	18	19	0	0	337	12
304	11210–6500	2	0	1	0	0	0	0	2	2	0	0	23	0
10.1	12610–6700	16	0	20	2	2	15	0	6	4	0	0	100	1
11	14890–11730	27	0	6	0	0	3	0	4	1	0	0	8	0
11.1		11	0	3	0	0	6	4	4	0	0	0	12	0
305	13440–9150	12	0	0	0	0	0	0	1	0	0	0	3	1
306	14010–12390	7	0	0	0	0	3	1	1	0	0	0	1	0
307	14630–13530	2	0	0	0	1	2	1	2	0	0	0	0	0
12	17810–13930	18	0	2	0	3	4	2	5	0	0	0	3	1
13	18390–16370	27	0	4	0	2	13	13	5	0	0	0	0	0
104	18490–15870	24	0	0	0	0	0	3	2	0	0	0	2	0
104.2		5	0	0	0	0	0	1	0	0	0	0	1	0
105		4	0	1	0	0	6	4	3	0	0	0	0	0
106		86	0	4	1	3	15	12	9	0	2	0	14	0
107		38	0	5	0	7	21	17	2	0	0	0	9	0
107.1		17	0	0	0	1	9	3	7	0	0	0	4	0
107.2		0	0	0	1	0	1	0	1	0	0	0	0	0
108		76	0	26	0	23	38	22	23	3	1	0	57	2
14	18520–18160	14	0	4	0	1	7	15	2	0	0	0	0	0
15	18630–18310	13	0	0	0	1	0	6	3	0	0	0	0	0
16	18760–18450	17	0	3	0	1	1	8	3	0	0	0	0	0
311–309	18830–14900	4	0	2	1	1	1	5	4	0	0	0	0	0
109	18950–18200	14	0	3	0	6	6	2	2	0	2	0	2	0
17	19190–18610	7	0	6	2	3	4	4	4	0	0	0	0	0
110	19420–18610	56	0	9	1	12	4	10	8	0	3	0	0	0
111	19910–19010	23	0	4	0	5	2	6	9	0	0	0	4	0
112	20200–19470	6	0	2	0	1	1	3	4	0	0	0	1	0
113		7	0	1	0	1	0	2	1	0	0	1	0	0
114	20340–19900	8	0	1	0	1	0	2	0	0	0	0	0	0
115	20500–20150	5	0	1	0	1	0	3	1	0	0	0	0	0
116	20650–20300	8	0	2	0	4	1	2	2	0	0	0	0	0
117	20750–20480	1	0	0	0	0	0	1	0	0	0	0	0	0
119	21100–20680	0	0	1	0	0	0	0	0	0	0	0	0	0
121	21960–21320	6	0	3	1	2	2	3	2	0	1	0	0	0
122	22270–21660	8	0	7	0	7	11	6	5	0	0	0	0	0
123	22640–21950	2	0	1	0	2	0	1	0	0	0	0	0	0
124		9	0	4	0	7	5	6	5	0	1	0	0	0
125	22980–22240	1	0	3	0	3	4	1	3	0	0	0	0	0
126	23580–22510	2	0	0	0	1	2	6	1	0	0	0	0	0
127	28380–22860	2	0	10	0	2	6	2	3	0	0	0	0	0
128	39010–24800	26	0	4	4	11	15	23	18	0	0	0	1	0
129	46890–33160	23	0	8	3	7	7	4	6	0	1	0	0	0
130	50900–39280	10	0	9	4	0	25	0	4	0	20	0	0	0

most widely accepted nomenclature of *Microtus agrestis*. For the climatic interpretations of species found nowadays in the Iberian Peninsula, we have followed the work of Palomo et al. (2007).

3.2.2.1. *Microtus Schrank, 1798*. *Microtus arvalis*, and *M. agrestis*, today on the Iberian Peninsula occur in open landscapes with humid climate and grass or shrub cover that was stable across time. Today these species are found in a wide variety of habitats, from the edges of rivers, lakes and marshes, woods, mountain areas, and humid to arid meadows (Palomo et al., 2007).

The short-tailed vole, *M. agrestis*, is also found on the edges of young woods and occasionally in heaths and dunes. It is generally characteristic of Atlantic European climate and environments. The common vole,

M. arvalis, is characterized by opportunistic behaviour and is found in open landscapes and even in wooded areas and in climatic zones drier than those inhabited by *M. agrestis* (Palomo et al., 2007).

3.2.2.2. *Terricola Fatio, 1867*. *Terricola lusitanicus* and *T. pyrenaicus* are characterized as living in Mediterranean-type climatic zones with hot temperatures. In addition, the two species identified in the site, *T. lusitanicus* and *T. pyrenaicus*, live in habitats characterized by open landscapes with soft, humid soils and stable vegetation cover (Palomo et al., 2007).

The presence of Pyrenean pine vole (*T. pyrenaicus*) in El Mirón was proven for the first time by Alfaro-Ibáñez et al. (2023). This species, in contrast to the Lusitanian vole (*T. lusitanicus*), is found in subalpine areas

<i>Glis glis</i>	<i>Sciurus vulgaris</i>	<i>Sorex minutus</i>	<i>Sorex araneus</i>	<i>Neomys fodiens</i>	<i>Crocidura sp.</i>	<i>Galemys pyrenaicus</i>	<i>Talpa sp.</i>	<i>Erinaceus sp.</i>	<i>Lagomorpha indet.</i>	<i>Mustela sp.</i>	<i>Miniopterus schreibersii</i>	<i>Myotis sp.</i>	<i>Quiroptera indet.</i>	Diversity S	number of samples
8	0	0	4	2	1	0	6	0	0	0	0	0	1	14	33
8	0	0	2	0	0	0	1	0	0	1	0	0	0	7	19
14	0	0	2	1	0	0	1	0	3	1	0	0	0	11	30
4	0	0	0	0	0	0	0	0	0	0	0	0	0	6	7
20	0	0	3	2	0	0	9	0	1	0	0	0	0	11	29
13	0	0	2	0	1	0	4	1	0	0	0	0	0	10	29
27	0	0	0	4	5	0	7	0	0	0	0	0	1	13	17
14	0	0	2	0	0	0	10	0	0	0	0	0	0	10	19
13	0	0	0	0	0	0	1	0	0	0	0	0	0	5	5
9	0	0	0	0	0	0	7	0	0	0	0	0	0	8	17
1	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2
97	0	1	31	14	2	0	19	0	0	1	1	4	0	18	31
10	0	0	1	2	2	0	3	0	0	0	0	0	0	10	4
25	1	1	7	5	1	0	8	0	0	1	0	0	0	16	15
2	0	0	6	1	0	0	18	0	0	2	0	0	0	11	15
0	0	0	1	1	0	0	6	0	0	0	0	0	0	9	8
1	0	0	0	0	0	0	2	0	0	0	0	0	0	6	6
0	0	0	1	0	0	0	1	0	0	0	0	0	0	7	7
0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	5
0	0	0	0	0	0	0	6	0	0	2	0	0	2	11	16
0	0	0	2	0	0	0	2	0	0	0	0	0	0	8	42
0	0	0	1	0	0	0	13	0	0	1	0	0	1	8	16
0	0	0	0	0	0	0	0	0	0	0	0	0	1	4	2
0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	4
0	0	0	3	0	0	0	24	0	0	0	0	0	0	10	37
0	0	0	7	0	0	0	16	0	0	1	0	0	1	11	21
0	0	0	0	0	0	0	6	0	0	2	0	0	0	8	6
0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2
4	0	0	15	6	2	0	57	0	0	0	2	0	1	17	48
0	0	1	3	0	0	0	5	0	0	0	0	0	0	9	22
0	0	0	1	0	0	0	9	0	0	0	0	0	0	6	17
0	0	0	0	0	0	0	16	0	0	0	0	0	0	7	26
0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	9
0	0	0	0	0	0	0	10	0	0	0	0	0	0	10	11
0	0	4	0	0	0	0	1	0	0	1	0	0	0	9	23
0	0	0	0	1	0	0	0	0	0	0	0	0	0	9	7
0	0	0	4	2	0	0	39	0	0	3	0	0	1	12	37
0	0	0	4	0	0	0	22	0	1	1	0	0	0	11	27
0	0	0	1	0	0	0	8	0	0	0	0	0	0	9	7
0	0	2	0	0	0	0	4	0	0	1	0	0	0	9	3
0	0	0	1	0	0	0	6	0	0	0	0	0	0	6	6
0	0	0	2	0	0	0	6	0	0	0	0	0	0	7	4
0	0	0	0	0	0	0	5	0	0	0	0	0	0	6	13
0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2
0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2
0	0	0	0	0	0	0	0	0	0	1	0	0	0	8	7
0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	10
0	0	0	0	1	0	0	2	0	0	0	0	0	0	6	3
0	0	0	0	1	0	0	6	0	0	1	0	0	1	11	14
0	0	2	0	0	0	0	4	0	0	0	0	0	0	8	8
0	0	1	0	0	0	0	4	0	0	0	0	0	0	7	1
0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	9
0	0	1	0	0	0	0	15	0	3	3	0	0	0	12	12
0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	11
0	0	0	4	1	0	1	7	0	0	1	0	0	0	11	7

with lower average temperatures (15-16 °C) than the rest of the species of *Terricola* (Palomo et al., 2007).

3.2.2.3. *Chionomys* Miller, 1908 - *Chionomys nivalis* (Martins, 1842). *Chionomys nivalis*, also known as snow vole, is native to cold climates and high montane zones, particularly in the mountains of Europe and Asia. It prefers to live in stable, rocky areas such as scree or fields of pebbles, where it can dig its burrows and find shelter from the cold (Cuenca-Bescós and Morcillo-Amo, 2022; Palomo et al., 2007). Due to their specialized habitat requirements, snow voles are of conservation concern. Habitat loss and degradation, as well as the impacts of climate change, pose a threat to their survival.

3.2.2.4. *Alexandromys* Ognev, 1914 - *Alexandromys oeconomicus* (Pallas, 1776). Generally, this species, known as the root vole, had been

included in the genus *Microtus*, but due to recent analyses done on genetic material from modern specimens (e.g., Abramson et al., 2021), it has been possible to differentiate the genus *Alexandromys*. *A. oeconomicus* is now extinct on the Iberian Peninsula but surviving today in NW Europe in tundra and taiga with abundant vegetation cover (Linzey et al., 2016). *Alexandromys oeconomicus* is found in northern regions of Eurasia and North America, where it is well adapted to living in cold, snowy environments. They are important prey for many predators in their ecosystem, including owls, hawks, and foxes, thus, due to their role in the food web and their adaptability to harsh environments, root voles are the subject of ongoing research in fields such as ecology and conservation biology.

3.2.2.5. *Lasiopodomys* Lataste, 1887 - *Lasiopodomys gregalis* (Pallas, 1778). Similar to the case of *A. oeconomicus*, this species also had been

3.2.3. Waterbody and riverbank-dwelling small mammal species

Some observations made with the analyses of the diversity statistics throughout the stratigraphic sequence include the following: aquatic and riverbank dwellers are considered here to be the *Arvicola* species, *Alexandromys oeconomus*, *Clethrionomys glareolus*, the *Neomys*, and the *Talpa* species (Palomo et al., 2007). We decided to include *C. glareolus* as a river bank-dwelling small mammal because of its presence along river courses in the Iberian Peninsula (Palomo et al., 2007; Spitzenberger, 1999). It is interesting to observe that there is a strong correlation between the higher scores of diversity, as measured in numbers of species, such as in layers 10 and 108 (respectively with 18 and 17 species) with the highest number of water and river bank dwellers. These points are related to a relatively humid climate and a landscape around El Mirón probably rich in water bodies and wetlands. Layer 10 is dated to 5000–6000 BP and layer 108 to 13,000–14,000 BP. In general, Fig. 6 shows that wetland species were more abundant in times when there was also greater species diversity, indicating a richer, more mature landscape under humid, temperate climatic conditions.

3.2.4. Open landscape small mammal species

The small mammals that live in open landscapes or open meadows are *Microtus arvalis*. *Pliomys* and *Chionomys* species are inhabitants of open landscapes though in mountain terrains (Cuenca-Bescós et al., 2010; Palomo et al., 2007; Kryštufek, 2018).

3.2.5. Species of small sylvan mammals

Species of small mammals that live under abundant vegetation cover are *Eliomys quercinus*, *Glis glis*, *Clethrionomys glareolus*, *Microtus agrestis* and *Alexandromys oeconomus* (Palomo et al., 2007; Spitzenberger, 1999).

4. The paleoenvironmental dynamics of El Mirón Cave

Despite having planned the palynological sampling to obtain information on the whole sedimentary sequence of the El Mirón archaeological site, this objective was not achieved due to a large number of pollen hiatuses. The samples that did not contain the minimum counts of pollen and spores to be considered statistically valid corresponded mainly to areas where there were hearths. These samples are ones with large amounts of micro-charcoal fragments together with poor preservation of pollen and spores. As noted, in contrast, small mammals are present in all the archeostratigraphic levels of El Mirón, though the number of remains and species varies. Nevertheless, the combined information recovered from both types of records does permit a definition of the paleoenvironmental dynamics under which the Pleistocene human occupations of the site took place in this cave.

4.2. Level 129 (VR) (modeled age range: 46,890 - 33,160 cal BP)

The paleoenvironmental information on this sedimentary deposit, which is virtually lacking in evidence of human occupation, is limited to the two highest samples from the pollen column in square X10 (Fig. 7). The dynamic of both is similar and reflects a period of somewhat warmer climate which supported tree growth with arboreal pollen values of 30% and the minor presence of *Corylus* in the landscape. The benign character of the climate is a bit more marked in the uppermost sample (24), a fact which is reflected in the increased presence of *Betula*, Ericaceae, Poaceae, Brassicaceae, Fabaceae and Ranunculaceae and in the opposite trend for pine and Compositae. However, in no instance are these percentage differences really great.

Regarding the small mammals, we observe the appearance of the species *A. oeconomus*, which indicates the presence of bodies of fresh-water (ponds or rivers, with abundant vegetation cover), as well as *M. arvalis*, characteristic of open meadows. We also note a drastic decrease in representatives of the species *M. agrestis* and *P. lenki*, which can be an indication of greater development of woods.

4.3. Gravettian (modeled age 39,010–24,800 cal BP): level 128 (VR)

The pollen record for this level comes from samples in square X10 and in the W10/X10 section of the Vestibule rear. The pollen column from W10/X10 begins the sequence for this level which is of Gravettian-age, but lacks culturally diagnostic artifacts. Attempts to obtain more precise C14 dates failed. The data from the lowest samples indicate the existence of adverse climatic conditions which reach their worst point in the most recent of the samples for this period (Fig. 8). The landscape was characterized by a very reduced forest cover in which pine was the main component. Birch (with a pollen representation of less than 3%) accompanied it at first but disappeared at the top of the level. The herbaceous-shrub layer was clearly dominated by Compositae, whose increasing trend (contrary to that of the grasses and heathers) reflects a progressive decrease in humidity (Straus et al., 2011).

The information from sample 28 in square X10 is coherent with the above (Fig. 7) and reflects a worsening of climatic conditions relative to those of underlying Level 129. Both records show that the Gravettian-age visits to the cave took place under cold, but not very dry conditions, which worsened through time.

We identified a total of 12 small mammal species in the Gravettian level, the most abundant of which belong to the species *A. terrestris* and *M. arvalis*. The high representation of these two species would indicate a landscape near the cave dominated by open meadows with the presence of water (presumably the Calera stream). The presence of fresh water would also explain the increased representation of *A. oeconomus*. Another species that clearly increased is *C. nivalis*, which, together with *T. pyrenaicus* is an indicator of colder climatic conditions.

4.4. Solutrean (modeled age range: 28,380–21,320 cal BP, but Intcal20 age range: 24,820/24,270–22,980/21,470 BP): levels 127 to 121 (VR)

We have palynological information from Solutrean levels 127, 126, 122 and 121 (Fig. 8 – Straus et al., 2013).

The samples from the oldest Solutrean level (127: 2 dates with a combined range between 24,820–22,960 cal BP) and the oldest sample from the next level (126: 1 date of 23,770–22,280 cal BP) are characterized by colder and drier climatic conditions than those of the preceding level 128. The arboreal cover was less (AP: <5%) and was composed solely of pine. The Compositae maintained their percentages, and although the Poaceae increased their representation on the open landscape, the dynamic of the heathers and ferns together with the sporadic presence of *Artemisia* and *Centaurea*, indicated a decrease in humidity.

Despite the hiatuses in the pollen record, which are a constant in the entire palynological study of El Mirón, we can see a clear change in the paleoclimatic dynamic from the upper part of level 126. Humidity increased as evidenced by the continued and significant increase in the heathers, hygrophile taxa and ferns versus the decrease in Compositae and the disappearance of the rare steppic taxa. The forest cover recovered (AP maximum: 20% in level 122), with the return of birch. In the case of the only fertile sample from the most recent Solutrean level (121, with one date: 22,980–21,470 cal BP), the same dynamic continued, but the deterioration suffered by the pollen does not permit greater precision (Straus et al., 2011, 2013).

In terms of the small mammals, during the Solutrean species that live in open meadows dominate in a cold, Atlantic climate. There is a significant decrease in biodiversity in levels 127 and 126 compared to level 128, indicating a worsening of climatic conditions, with less humidity. From level 127 to 124 the number of small mammal species increases, with the last of these levels having almost the same biodiversity as seen in the Gravettian level (128), although with fewer individuals of species characteristic of open meadows. There is a slight increase in humidity, with more individuals pertaining to *A. terrestris* and *A. oeconomus*, however not reaching the percentages found in the Gravettian.

The uppermost Solutrean levels (123–121), again see a decrease in

biodiversity. In level 122 there is a significant increase in individuals of *M. agrestis* compared to levels 123 and 121, a fact which could indicate an increase in local vegetation. In level 121 small mammal biodiversity increases slightly, with clear dominance by open meadow-dwelling species, including *P. lenki*.

It is worth noting the presence of *Talpa* sp. in levels 126-123, with its highest representation in level 124. This coincides with a progressive recuperation of biodiversity in these levels and could represent some increase in wooded areas.

4.5. Initial Magdalenian (modeled age range: 21,960–20,480 cal BP): levels 119.3 to 117 (VR); (modeled age range: 20,370–18,890 cal BP): 21 to 18 (OV)

The small mammal samples from the Initial Magdalenian are scarce. Only four species were identified in these levels in the Vestibule rear: *T. lusitanicus* and *A. oecnomus* in level 119, *A. terrestris* and *M. arvalis* in level 117. In both cases, the species present indicate a landscape dominated by open meadows with the presence of water near the cave under conditions of an Atlantic climatic regime.

4.6. Lower Magdalenian (modeled age range: 20,650–18,610 cal BP): levels 115 to 110 (VR); levels 505 to 503.1 (BA); level 312 (MV); (modeled age range: 19,190–18,320 cal BP): levels 17 to 15 (OV)

We have pollen information for this Lower Magdalenian cultural horizon from the residential areas of both the outer and inner vestibule (stratigraphic sections V8/U8 and H2/G2) and from the area of the human burial in the SE corner of the vestibule rear (but not from the Mid-Vestibule trench). From all the many samples taken from the Lower Magdalenian, the only palynologically fertile ones were those from levels 115 (1 credible date of 20,720–20,100 cal BP) in the Vestibule Rear, 17 in the Outer Vestibule (5 dates ranging between 19,280 – 18,240 cal BP), and 504 in the Burial Area (2 dates ranging between 19,110–18,240 cal BP).

The oldest reference corresponds to sample 1B from V8/U8. In it (Fig. 8), the arboreal cover displays its greatest extension in the whole Pleistocene sequence of the cave (AP: 57%). The deciduous taxa are clearly dominant: *Tilia* (11%), *Corylus* (7%), *Quercus robur* sp. (5%) and *Betula* (3%). Among the riparian taxa, alder is the most relevant (*Alnus*: 11%), accompanied by *Salix* (2%), while the conifers are only represented by pine (*Pinus sylvestris* sp.: 16%).

The greater occupation of the environment by trees in this period meant a grass-shrub component was reduced in importance on the landscape. The grasses continued to be the most relevant non-arboreal group (Poaceae: 17%), followed in importance by the Caryophyllaceae (6%) and Compositae liguliflora (3%). In the low shrub stratum, heathers and Cistaceae only appear as traces.

The proportion of the fern spores (64% of the pollen-spore total) is another of the notable aspects of this sample and confirms the considerable degree of humidity which existed at the base of level 115.

These paleoclimatic characteristics are completely different from the pollen spectrum of level 17. In this level of the Outer Vestibule, we have a continuous record (profile H2/G2) that indicates environmental conditions of stadial character, although there is a slight improvement in sample 3 (Fig. 10). The two oldest samples are those with the lowest percentages of arboreal pollen (AP: 2–3%, respectively), the second being the one with the most markedly stadial character (juniper accompanied pine and birch, and there was a decrease in humidity). In both samples, the dominant grass-shrub stratum is composed fundamentally of Compositae liguliflora (35 and 47%) and Poaceae (27 and 22%), while Compositae tubuliflora, Ericaceae, Fabaceae and Cyperaceae present values under 10%. *Cistus*, *Centaurea*, Lamiaceae, *Plantago*, Brassicaceae, Ranunculaceae and Apiaceae appear only discontinuously.

The pollen spectrum of level 504 came from the Red Lady

Magdalenian burial and corresponds to a stadial episode of intense cold like that of the lower part of the H2/G2 column (samples 1 and 2). In this instance, however, there is evidence of less humidity than in the sample from level 505 (with a low representation of fern spores –3%, presence of cryoxeric taxa like *Artemisia* –4%, lower percentages of heathers and grasses, etc.) (Fig. 11). Nonetheless, the most significant difference between the two approximately contemporaneous spectra is the overwhelming predominance of Chenopodiaceae in the burial context that could be due to the deposition of this kind of plants in the grave (Iriarte-Chiapusso et al., 2015).

The small mammal record of the Lower Magdalenian comes from levels 115-110 in the Vestibule Rear and 17-15 in the Outer Vestibule. From levels 115 to 112, we generally see the same level of biodiversity with few individuals per species, dominated by those that inhabit open meadows, notably *M. agrestis* in levels 115-113. This fact, together with the low numbers of individuals per species, could be explained by a worsening of climatic conditions.

Starting with level 113, there is an increase in the number of individuals of *C. nivalis* up to level 110, caused by a progressive lowering of mean temperature, as also suggested by the reappearance of *T. pyrenaicus* in level 110.

In the whole Lower Magdalenian sequence, except in level 17, the taxa *A. terrestris* and *Talpa* sp. dominate, indicating environmental conditions that included water bodies with wooded copses. The drastic decrease in these taxa in level 17 indicates that there was a significant environmental change at that time, with greater ambient dryness and dominance of open grasslands. In addition, the co-presence of *C. nivalis* and *T. pyrenaicus* indicates colder climatic conditions.

Levels 15 and 16 witness small mammals that indicate a decrease in open meadows and an increase in humidity compared to level 17.

4.1. Mousterian (modeled age range: 50,900–39,280 cal BP): level 130 (VR)

The small mammals observed in the Mousterian of El Mirón (*M. agrestis* and *P. lenki*) indicate a paleoenvironment dominated by open meadows. There are also species that are typical of areas near waterbodies and in humid zones (*A. terrestris* and *Galemys pyrenaicus*). The climate during the Mousterian was of Atlantic type (as shown by *T. lusitanicus*), with temperate-cold temperatures, as indicated by the presence of *T. pyrenaicus* and *C. nivalis*.

4.7. Middle Magdalenian (modeled age range: 18,950–16,370 cal BP): levels 109, 108 (VR); 311, 310 (MV); 14, 13 (OV)

The available palynological information comes from levels 311 and 310 (Mid-Vestibule Trench: profile P6/Q6) which are not directly dated. (level 312 -19,530–18,830 cal BP- and level 309 between 15,140 and 13,850 cal BP). The oldest sample (10: level 311) reflects stadial climatic conditions (Fig. 12). In this open landscape (NAP: 96%), only pines made up the (scanty) forest cover (AP: 3%). The fern spore values (7%), the dominance of Compositae (especially Compositae liguliflora: 52%), the absence of Ericaceae and the scarce taxonomic diversity of the herbaceous stratum (Caryophyllaceae, Lamiaceae, Scrophulariaceae, Fabaceae, Rosaceae) reaffirm the cold, dry character of this climatic episode.

After a pollen hiatus, sample 14 (level 310) maintained the same stadial characteristics in the composition of the vegetation, although a few little hints suggest a very slight recuperation in the degree of humidity: arboreal pollen rises to 5%, and birch reappears; fern spores increase by 1% in their representation, and Liliaceae appear in the record (Fig. 12).

The following sample in the diagram (sample 15: level 309) displays no significant climatic changes with respect to the earlier ones, although its archaeological characteristics do not allow us to securely assign it to the Middle Magdalenian.

The small mammal record is more abundant in levels 108, 109, 14 and 13 than in levels 311–310, with levels 108 and 13 having the largest numbers of samples. During the Middle Magdalenian open meadow taxa and wetland species predominate (*A. terrestris* and *A. oeconomus*). In addition, we see the presence of *C. nivalis*, which indicates cold temperatures. In level 108, there is an increase in biodiversity, with the presence of species characteristics of woods: *Crociodura* sp., *E. quercinus*, *G. glis* and *C. glareolus*; this would indicate some improvement in environmental conditions, although the climate continued to be rather cold, as suggested by *C. nivalis*.

There is a drastic decrease in biodiversity measured by the reduction in the number of species between levels 108 and 13, with the disappearance of those taxa characteristic of woods and the notable presence of *A. terrestris*, *M. arvalis* and *M. agrestis*, the latter two of which are opportunistic species in open meadows as well as forest-edges. The snow vole, *C. nivalis* decreases significantly in terms of the number of identified individuals, a fact that indicates a rise in average temperature. Thus, we observe an improvement in the environment from level 109 to level 108, with slightly worse conditions in level 13, when woodland again decreased in the cave's vicinity despite a slight increase in temperature.

4.8. Upper Magdalenian (modeled age range: 17,810–13,530 cal BP; but IntCal20 age range: 15,740–13,280 BP): levels 308, 307 (MV); 12 (OV)

Throughout the occupation of level 307 (not directly dated; level 308 has 1 assay between 15,140–13,850 cal BP and level 306 has 1 assay between 13,610–13,360 cal BP), the surroundings of the cave continued to have an open vegetation with few trees (pines and birches). Nonetheless, in contrast to the previous samples from this profile (P6/Q6) in the two samples from this level have twice as many arboreal pollen values (AP: 11 and 9%, respectively), and the more recent of them, *Pinus sylvestris* sp. and *Betula* are equally represented in the landscape. There are also significant changes in the grass-shrub stratum, the most relevant of which is the new dominance of the grasses (Poaceae: 30 and 39%) vis à vis the Compositae and the reappearance of heathers. These circumstances, together with the notable rise in fern spores (52 and 31%, respectively), indicate that the stadial conditions were less intense, especially in terms of aridity (Fig. 11).

The Upper Magdalenian displays small mammal spectra similar to those of the end of the Middle Magdalenian, with a slight increase in biodiversity. The environment was characterized by the presence of freshwater bodies and a temperate-cold climate, with the presence of the species *A. terrestris*, *A. oeconomus* and *C. nivalis*. The surroundings of El Mirón Cave were dominated by open meadows but with some woods, as shown by *E. quercinus*. The grassland species that dominate the record are *Lagomorpha indet.*, *M. agrestis*, *M. arvalis*, and *A. sylvaticus-flavicolis*.

4.9. Azilian/Final Magdalenian (modeled age range: 14,010–12,390 cal BP): levels 103 (VR); 306 (MV)

The two samples corresponding to level 306 (13,610–13,360 cal BP) indicate significant changes in the landscape (Fig. 12). The oldest sample shows a notable improvement in climatic conditions relative to the earlier level that facilitated a major expansion in forest cover (AP: 30%). Although pines and birches continue to be the principal arboreal components (14.5 and 13%, respectively), deciduous species appear in the record (*Quercus robur* sp., *Corylus* and *Castanea*) and willow shows up along water courses (such as the Calera, Gándara, and Asón rivers below the cave). The dynamic of the grass-shrub stratum maintains its principal characteristics. The representation of fern spores continues to make up 50%, and Cyperaceae and Liliaceae reappear.

The situation changes in the next sample and there is a new paleoclimatic downturn evidenced by a decrease in arboreal pollen (AP: 11%) and the disappearance of deciduous taxa. Again, pine is the principal tree in the landscape (10%). Grasses descend slightly (Poaceae: 30%), while Compositae, Ericaceae, Lamiaceae, Rosaceae and Fabaceae

increase. Although Cyperaceae, Ranunculaceae and Liliaceae disappear, the ferns maintain their values (52%).

During the Final Magdalenian/Azilian there are only small mammal data from level 306. In this level, there is a notable decrease in the number of individuals that inhabited open meadows, as well as in the overall number of represented species as compared with the Upper Magdalenian levels. The presence of *C. nivalis* also decreases, indicating an average temperature higher than in the Upper Magdalenian.

4.10. Azilian: levels 305 (MV); 11.2 to 11 (OV)

The last pollen spectrum in profile P6/Q6 belongs to level 305 (12,460–11,810 cal BP; modeled age range: 13,440–9150 cal BP). It is characterized by a new climatic improvement reflected by recuperation in arboreal pollen (AP: 25%) and the reappearance of hazels, oaks and willows. Compared to the co-dominance by pines and birches during the initial improvement in level 306, this time it is birch alone that is the most important taxon (*Betula*: 15%). In the grass-shrub stratum there are no significant changes except for a decrease in Compositae and an increase in Poaceae. Despite the important percentage declines in fern spores (22%), Ranunculaceae, Cyperaceae, Liliaceae and Juncaceae all increase (Fig. 12).

Most of the studied small mammal samples come from levels 11.1 and 11. In these levels, we observe species that are favoured by humid environments and abundantly vegetated fields: *A. terrestris*, *M. arvalis*, *M. agrestis*, *T. lusitanicus*, *A. sylvaticus-flavicolis*, *Lagomorpha indet.* and *Talpa* sp.

In both levels 11 and 305, we find species whose habitat is woodland: *E. quercinus*, *G. glis* and *C. glareolus*. These taxa indicate a greater presence of woods near El Mirón than in the Upper Magdalenian.

5. The paleoenvironmental sequence of El Mirón Cave in the context of the Cantabrian Region of northern Atlantic Iberia

To obtain a robust chronostratigraphic sequence, a rigorous analytical critique of the dates and Bayesian modelling were conducted (Hopkins et al., 2021), whose results are largely utilized in this article. The Paleolithic sequence in El Mirón formed during the second half of the Last Glacial: late MIS 3 and MIS2 (The interdisciplinary study of the Holocene sequence is included in the monograph edited by Straus and González Morales, 2012a).

The maximum chronological range for the oldest levels in El Mirón (levels 130 and 129) covers some 20,000 years. In level 130 (50,900–39,280 cal BP), hominin (Neanderthal) occupation was very sporadic and ephemeral. It was probably formed during part of the first half of Marine Isotope Stage 3. The small mammal assemblage displays a predominance of an open landscape under stadial conditions that were not very intense and with a degree of humidity sufficient for the existence of aquatic biotopes required for such species as *Arvicola terrestris* and *Galemys pyrenaicus*. The following level (129: 46,890–33,160 cal BP) lacks almost any indication of human presence in the cave. The data from both records confirm an amelioration of climatic conditions which permitted increased development of trees in the area of the cave (arboreal pollen: 30%) with even the presence of deciduous species such as hazel. This change is also seen in the communities of small mammals, in which, for example, there was a decrease in such notable species of open landscapes as *Microtus agrestis* and *Pliomys lenki*. Both records are a reflection of the climate variability that characterizes this phase of MIS 3.

In the Cantabrian Region, paleoenvironmental information for this period comes from the non-anthropogenic (bog) source of Area Longa (Lugo, Galicia), some 350 km to the west. The various facies of peat and clayey sediments that have been studied are located on a coastal cliff on the uplifted shore at the west end of the region and constitute the most continuous palynological sequence currently available (Gómez-Orellana et al., 2007). At this location, it is observed that the stadial and

interstadial phases of MIS 3 were neither as cold nor as warm, respectively, as those of earlier periods (MIS 4 and MIS 5c). This paleoclimatic variability is also detected within MIS 3 itself where, for example, the increase in temperatures during interstadial phases (AREL-12, AREL-14 and AREL-16) were also not homogeneous, for which reason there were differences in the composition of the vegetation landscape.

The level of environmental humidity constitutes a notable aspect of all the available records in the Cantabrian Region. In contrast to other Iberian and Continental European pollen sequences, in Northern Atlantic Spain a higher degree of humidity is evidenced even during stadial phases. This is reflected in the lower representation of steppe species, even during the periods of greatest cold. Taxa such as *Artemisia* or *Ephedra* only appear during brief episodes and were never very common in the landscape, as opposed to the case of other taxa such as heathers.

The records for levels 130 and 129 de El Mirón are coherent with those from other archaeological sites in the region such as Covalejos Cave (Ruiz-Zapata and Gil-García, 2005), El Cuco Rockshelter (Ruiz-Zapata and Gil-García, 2007), Esquilleu Cave (Baena et al., 2005), Arrillor Cave (Iriarte-Chiapusso et al., 2019) or Labeko Cave (Iriarte-Chiapusso, 2000).

Humans occasionally visited the cave during the Gravettian period (level 128: 39,010–24,800 cal BP). These took place under stadial conditions that were cold but not particularly dry. The landscape was once again dominated by open areas with some pines and even fewer birches. In the middle of this level, these conditions worsened, with a decrease in arboreal pollen from 16 to 6%, and the fern spores decreased by half to 5%. In the upper part of the level, there was a return to the percentages of the base of level 128. Likewise, this climatic situation saw an increase in small mammal species associated with open fields with the presence of waterbodies (*Arvicola terrestris* and *Microtus arvalis*) and colder conditions (*Chionomys nivalis* and *Terricola pyrenaicus*).

This dynamic is observed in other Gravettian-age records in the Cantabrian Region, in which open landscapes with few trees (with pine being the main taxon, accompanied by *Juniperus* and/or *Betula*), although there are phases during which some deciduous arboreal taxa (e.g., *Corylus* and *Quercus robur* tp.) reappear in the records (Iriarte-Chiapusso and Murelaga, 2013) reflecting some degree of episodic climate amelioration.

The totality of the information in the Cantabrian region for this period comes from archaeological sites in caves. However, this class of data is different from those obtained in open-air loci (the kind of deposits that are clearly under-represented because of poor preservation). There is no doubt about the wide range of potential habitats that this region provided and that human groups chose among them based on their particular interests/needs at various times and on the benefits that could be obtained from such choices that in part could depend on the environmental conditions at each time. It is in this last aspect that the data from open-air sites differ notably from those from caves. We have two examples, one from the Cantabrian region itself near the present coast and another from the Mediterranean (Ebro River) drainage on the south side of the Cantabrian Cordillera at more than 900 m of altitude: Ametzagaina (in San Sebastián, Gipuzkoa) and Mugarduia Sur (Sierra de Urbasa, Navarra). Both of these Gravettian sites confirm that during certain interstadials the climatic amelioration was sufficiently great to permit dominantly deciduous woodlands to dominate the landscape (Iriarte-Chiapusso et al., 2016).

Before discussing the Solutrean sequence of El Mirón and the region, it is important to make reference to the glacial dynamic observed in the nearby Pas Mountain range, about 25 km from the site. In these mountains, the geographical location, orography and altitude (up to 1718 m a.s.l.) determined relevant glacier formation with major differences between the southern and northern slopes. As in other mountain ranges of the Cantabrian Region and Pyrenees, and in contrast to other areas of the north and northwest of Europe, the maximum expansion of glacial ice took place before the Last Glacial Maximum

(Turu et al., 2007; Moreno et al., 2010; Serrano et al., 2012; Rico, 2012; Rodríguez-Rodríguez et al., 2016). In the Pas Mountains the maximum expansion took place during MIS 3, between about 44,000 and 29,000 cal BP, although it is still necessary to establish an adequate chronological seriation to situate which periods of successive glacier advance and stability could have occurred during the LGM and end of the Late Glacial (Serrano et al., 2013).

Taking into consideration this information, the Solutrean occupations of El Mirón did not coincide with the maximum extension of the cordilleran glaciers in the Pas Mountains. At the beginning of the Solutrean sequence (level 127: c. 24,000 cal BP), the climatic deterioration intensified, especially at the base, where the arboreal pollen values do not even reach 4% and are composed of only *Pinus sylvestris* tp. In addition, *Artemisia*, a taxon typical of relatively dry steppes, appears in the spectrum. Precisely it is in the degree of humidity that exists the difference between levels 126 (23,580–22,510 cal BP) and 127 (this level could be related to GS 2.2). Beginning at this time, the values of fern spores and pollen of such taxa as Cyperaceae, Juncaceae or Ranunculaceae recover, especially the first of these (from 3 to 22%).

From levels 127 to 124, the number of small mammal species increases, with the last of these levels presenting practically the same degree of biodiversity observed during the Gravettian, although with a lesser quantity of individuals of the species characteristic of open fields. One detects a slight increase in humidity, with individuals of *Arvicola terrestris* and *A. oecconomus*, but without reaching the numbers seen during the Gravettian.

In the uppermost Solutrean levels (123–121), one observes another decrease in biodiversity. During the formation of level 122 there was a significant increase in individuals of *Microtus agrestis* with respect to levels 123 and 121, which could indicate an increase in vegetation cover. It is worthwhile mentioning the presence of *Talpa* sp. in levels 126 to 123, with its highest numbers in level 124. This coincided with the progressive recuperation of biodiversity during these Last Glacial Maximum times and could represent some increase in wooded areas.

In level 122, the same characteristics of the landscape as seen in the one pollen sample from level 126 were maintained (i.e., increase in heathers, grasses, hygrophile taxa and ferns; decrease in Compositae and disappearance of rare steppic taxa), although in its base forest cover decreased (AP: 4%). However, in the upper zone of this level, one detects an amelioration in climatic conditions that (while still predominantly an open landscape) made possible a notable recuperation in trees (AP: 17.5%).

The biodiversity of species of small mammals increases in level 121 (the uppermost Solutrean occupation), including the presence of the later extinct *Pliomys lenki* (Table 3).

This dominance of open landscape species with very few trees observed in El Mirón also characterizes the rest of the sequences from the Cantabrian region during stadial phases, with detection of climatic fluctuations in respect to the intensity of cold and degree of humidity. Although we lack records from contemporary open-air sites, it is unlikely that the modest improvement in climatic conditions during the interstadials of this period would have been sufficient to permit as significant an expansion of woodlands as during the preceding Gravettian as noted above. In that case, during the times of climatic improvement there had been moderate expansions of deciduous trees, together with increases in Poaceae, Ericaceae and species related to humidity in the grass-shrub stratum (García-Ibaibarriaga et al., 2019).

At the limit between GS3 and GS2, the glaciers in the uppermost zones of the nearby mountains retreated again, permitting the deposition of organic materials in montane lakes, ponds and bogs (Serrano et al., 2013). For this reason, we have more information from non-anthropogenic loci at this time and, although not in the Cantabrian region per se (while still in northern Atlantic Spain), the pollen sequence from Lagoa de Lucenza (Lugo, Galicia) attests how the altitudinal gradient and the barrier effect of the mountain ranges reduced environmental humidity, thereby allowing for a greater presence of steppe

Table 3

Comparison of the species of small mammals present today in Cantabria, with the fossil species identified in El Mirón.

El Mirón Late Pleistocene	Cantabria today
<i>Erinaceus europaeus</i>	<i>Erinaceus europaeus</i>
<i>Familia Soricidae</i>	
<i>Crocidura russula</i>	<i>Crocidura russula</i>
<i>Crocidura suaveolens</i>	<i>Crocidura suaveolens</i>
<i>Neomys fodiens</i>	<i>Neomys fodiens</i>
<i>Sorex minutus</i>	<i>Sorex minutus</i>
<i>Sorex gr. Coronatus-araneus</i>	
	<i>Sorex araneus</i>
	<i>Sorex coronatus</i>
	<i>Suncus etruscus</i>
<i>Galemys pyrenaicus</i>	<i>Galemys pyrenaicus</i>
<i>Talpa europaea</i>	<i>Talpa europaea</i>
<i>Myotis</i>	<i>Myotis</i>
<i>Miniopterus schreibersii</i>	<i>Miniopterus schreibersii</i>
<i>Mustela nivalis</i>	<i>Mustela nivalis</i>
<i>Sciurus vulgaris</i>	<i>Sciurus vulgaris</i>
<i>Arvicola terrestres</i>	<i>Arvicola terrestris cantabrae</i>
<i>Arvicola sapidus</i>	<i>Arvicola sapidus</i>
<i>Chionomys nivalis</i>	<i>Chionomys nivalis</i>
<i>Clethrionomys glareolus</i>	<i>Clethrionomys glareolus</i>
<i>Microtus agrestis</i>	<i>Microtus agrestis</i>
<i>Microtus arvalis</i>	<i>Microtus arvalis asturianus</i>
<i>Microtus oeconomus</i>	
<i>Microtus gregalis</i>	
<i>Terricola pyrenaicus-gerbei</i>	<i>Terricola pyrenaicus-gerbei</i>
<i>Terricola lusitanicus</i>	<i>Terricola lusitanicus</i>
<i>Pliomys lenki</i>	

plants in the landscape at this time (Muñoz-Sobrino et al., 2001).

The paleoenvironmental information for the Initial Magdalenian of El Mirón cave (21,900–21,100 cal BP) is conditioned by the lack of palynological data and the scant record of small mammals, which are limited to four species (level 119: *Terricola lusitanicus* and *Alexandromys oeconomus*; level 117: *Arvicola terrestris* and *Microtus arvalis*). Faced with this unfavourable situation, all we can note is that these species inhabit open fields and wetlands along bodies of water.

In the Vestibule Rear, the oldest pollen record for the Lower Magdalenian (level 115: 20,500–20,150 cal BP) is totally different from all the earlier ones. The climatic conditions at this time were the best of the whole Upper Pleistocene record, with a considerable degree of humidity (*Filicales*: 65%) and a significant expansion of woods (AP: 57%). In addition, the woods became taxonomically more diverse, so that although pine continued to be the dominant type of tree (16%), linden (11%), hazel (7%) and oaks (5%) appear on the landscape, and birch increased its representation (3%). Furthermore, riparian woods became more important in the local environment (*Alnus*: 11%; *Salix*: 2%). The species of small mammals, *A. terrestris*, *T. lusitanicus*, *A. oeconomus*, *M. arvalis*, *C. nivalis*, *S. araneus*, and *Talpa* sp., from level 115 indicate a diverse landscape with an Atlantic climate like today.

Beginning with level 113 (20,200–19,470 cal BP), the dynamic of *Chionomys nivalis* suggests a progressive decrease in average temperature, culminating in level 110 (19,420–18,610 cal BP).

A new change in landscape defines massive Lower Magdalenian level 17 (19,190–18,160 cal BP). In this unit excavated in the Outer Vestibule, the environmental conditions returned to ones of stadial character. It is the period of the least arboreal cover in the whole sequence, with pollen values rising only from 2.5 to 5%, although water courses (i.e., the rivers directly below the cave) still flowed. Among small mammals, the co-presence of *C. nivalis* and *T. pyrenaicus* indicates colder climatic conditions.

In the record pertaining to the Human Burial Area at the rear of the cave Vestibule (level 504: 18,790–18,670 cal BP) the open landscape was also dominant. Nevertheless, although the arboreal pollen values are almost double those of level 17, the reappearance of *Artemisia*, together with the development of the herbaceous-shrub stratum,

suggests that the degree of humidity was less (Iriarte-Chiapusso et al., 2015).

In levels 16 and 15, the observed small mammals are indicators of a decrease in open fields and an increase in humidity as compared to level 17.

The (presumptive) Middle Magdalenian (defined by the stratigraphic position of levels above the classic Cantabrian Lower Magdalenian and -only unambiguously in the Outer Vestibule excavation area-under the antler harpoon-bearing Upper Magdalenian) poses serious chronostratigraphic problems: the lack of radiocarbon dates in levels 109, 311, 310 and 14, major contradictions among the five dates from artifact-rich level 108, the lack of any temporally diagnostic artifacts, and the absence of pollen in most of the relevant levels except 310 and 311 in the Mid-Vestibule Trench.

Levels 311 and 310 of the Middle Magdalenian developed under stadial (i.e., cold) conditions, although in the older of these levels, the degree of humidity was lower. In both, however, the presence of trees in the landscape was slight (AP: 4 and 5%, respectively).

In the small mammal spectrum for levels 109 and 108 can be detected an increase in biodiversity which would indicate an improvement in environmental conditions, although the climate continued to be cold with the presence of *Chionomys nivalis*. At levels 14 and 13, there is a drastic decrease in the biodiversity measured in the reduction in the number of species, with the disappearance of those taxa characteristic of woods and the notable presence of opportunistic species in open meadows as well as forest-edges.

Of the levels attributed to the Upper Magdalenian, level 307 provides the best information. The most significant change in level 307 (14,630–13,530 cal BP) with respect to the Middle Magdalenian is the increment in arboreal cover. Although open areas continue to dominate the landscape, the pollen values double and ultimately in the most recent Upper Magdalenian level, *Pinus sylvestris* tp. and *Betula* have the same percentage representations. The dynamic of *Apodemus sylvaticus-flavicolis*, *Eliomys quercinus* and *Glis glis* is coherent with this change in environment, while *Microtus agrestis*, *M. arvalis* are the dominant open-field species. Despite this relative improvement, species including *Arvicola terrestris*, *A. oeconomus* and *Chionomys nivalis* persisted.

The climatic improvement is clearly recorded at the base of level 306 (14,010–12,390 cal BP), attributed to the Final Magdalenian/Azilian. The arboreal cover triplicated (AP: 30%) and although pine and birch continued to be the dominant taxa, deciduous trees now appear in the record (*Quercus robur* tp., *Corylus* and *Castanea*), while *Salix* reappears along nearby watercourses. Among the communities of small mammals this meant the regression of species associated with open spaces, an increase in biodiversity, and the presence of *Apodemus*, *Eliomys*, *Glis* and *Talpa* species.

However, in the most recent pollen sample, the tendency is inverted, with indications of another climate downturn. This change meant a reduction of arboreal cover by more than half, with the disappearance of deciduous trees and the return of pine to its dominant role. In addition, the composition of the herbaceous-shrub stratum reflects a decrease in environmental humidity. These characteristics coincide with a reduction in biodiversity among small mammals.

These records indicate that the groups that inhabited El Mirón during the Lower Magdalenian were living under a variety of environmental conditions during the second half of Greenland Stadial-2.1. The oldest of these occupations took place under one of the most favourable environments of the Pleistocene sequence in the site while beginning with level 113 there was a marked climatic downturn which reached its worst in major palimpsest level 17. This is a clear example of the adaptive capacity of these groups of hunter-gatherers (all of whom pertain to the same archeo-cultural period) to weather environmental changes that would have seen differences in the availability of certain resources in the territory surrounding the site. In Level 15, for example, woods may have occupied roughly half of the site catchment area, while in level 17 they would have made up no more than about 31%. These overall stadial

conditions, with fluctuations, continued during the following Middle Magdalenian.

This paleoenvironmental dynamic is coherent with what is observed in other records from the period which are enriched with studies from lakes, ponds and bogs, whose formation was made possible by the retreat of the mountain glaciers. This greater information confirms what was intuited for earlier periods in the sequence: such factors as greater or lesser oceanic influence at different times, orography or orientation of the different biogeographical zones of the Cantabrian region all had to do with especially the degree of environmental humidity even during stadial periods (Iriarte-Chiapusso et al., 2016)

The sequence of the Upper Magdalenian fits well with the climatic amelioration that characterized Greenland Interstadial-1 (with its various fluctuations), with the base of level 306 having the sample in which this is best evidenced. This improvement permitted a clear advance of the meso-thermophile taxa of wooded cover, even in high zones of the Cantabrian Cordillera (Iriarte-Chiapusso et al., 2016). The animal and vegetation communities underwent different dynamics and pulses of change depending on each taxon's location within its biogeographic zone.

Because of the range of dates for the Upper Magdalenian occupations of El Mirón (although an age of around 15,500 cal BP for at least harpoon-yielding Level 12 is most reasonable), we cannot confirm whether the deterioration of climatic conditions observed at the end of this cultural period can be attributed to one of the subevents of Greenland Interstadial-1 (e.g., GI-1c2 or GI-1b) or to Greenland Stadial-1. In other Cantabrian sequences, the same cultural period has been shown to have taken place during this time of rapid climatic fluctuations near the end of the Last Glacial and Pleistocene (Iriarte-Chiapusso et al., 2016; Iriarte-Chiapusso, 2017).

The environmental characterisation of the Azilian levels attests the end of the Last Glacial. At this time (level 305: c. 12,000 cal BP), in contrast to the usual dynamic of the Pleistocene sequence, the recuperation of the arboreal cover (AP: 25%) is not based on pine, but rather on birch (15%). Hazel and oaks reappear on the landscape and, from now on, are always present in the record. Both in this level, as in level 11, the greater presence of woods made possible the development of such species as *Eliomys quercinus*, *Glis glis* and *Clethrionomys glareolus*, together with other taxa associated with humid habitats and lushly vegetated fields.

The Pleistocene sequence in El Mirón Cave ends with the onset of the great change in landscapes that came at the beginning of the Holocene (Straus and González Morales, 2012a).

6. Final observations

The paleoenvironmental information provided in this article has as its objective the explication of the changing lifeways of successive hunter-gatherer groups that inhabited El Mirón Cave over a long period of time in the late Upper Pleistocene. The succession of climatic events that affected the landscapes around the site and the resources (particularly food and fuel) that were available to the cave's inhabitants ever since Neanderthals first utilized it.

The coldest period during the whole sequence took place at the beginning of the Solutrean (base of level 127), although, as in other parts of the Cantabrian region, most of the stadial phases display a higher than expected level of humidity, due to the oceanic character of the region. Indeed, the El Mirón Solutrean-age levels are among the highest and farthest inland of any LGM occupations in the northern Atlantic strip of Iberia and it is not surprising, therefore, that they seem to have been short-term, limited-function episodes, such as hunting camps, whose base camps may have been in the coastal zone or on the narrow, now-inundated continental shelf off eastern Cantabria Province (Straus, 1983; Straus et al., 2013). The predominance of open landscapes in the environs of El Mirón Cave, was reduced during interstadial phases, although there were differences in the intensity of these episodes of

climatic improvement. In this context, the most (relatively) temperate paleoenvironmental conditions in the Pleistocene sequence of the cave are recorded in level 115 (20.500–20.150 cal BP). In this specific moment of the Lower Cantabrian Magdalenian the inhabitants of El Mirón inhabited a rather wooded landscape (arboreal pollen >50%) and surroundings that included a greater diversity of animal and vegetal taxa than in earlier times and, thus, more available resources for the humans. The later Magdalenian groups lived under a succession of different landscapes created by the short, rapidly fluctuating climatic of the Lateglacial events (some again moderately cold, such as at the time of the human burial) that culminated in the great environmental changes that came at the outset of the Holocene. The post-LGM fluctuations do not seem to have put a damper on significant, repeated, long-term human occupations of the cave during the early (Initial + Lower) Magdalenian, although the intensity and/or frequency of stays in the cave decreased notably during Middle and Upper Magdalenian and Azilian times, despite the continued climatic oscillations (some moderately cold, others relatively temperate) during the last six millennia of the Pleistocene. Humans were clearly able successfully to deal with the variety of climatic conditions in the period immediately after the LGM, while unknown factors seemingly other than climatic may have been at play in leading to a lessened human presence in El Mirón, while at the same time (Upper/Final Magdalenian and Azilian) there is significant evidence of human occupation of the mid-upper Asón basin at the cave sites of El Horno and especially El Valle. On the other hand, the near-total abandonment of the interior during earliest Holocene times, with human settlement concentrated around the newly-formed estuary of the Asón at sites such as La Fragua, La Chora, El Perro and La Trecha could be explained by the abundance of marine food resources (mollusks, fish) on the one hand, and the dense Preboreal-age mixed pine-deciduous forests (e.g., van der Horst et al., 2024), unconducive to large-scale hunting (and even human mobility) in the montane hinterland (Straus et al., 2002). El Mirón once again became an important human settlement with the early (for northern Atlantic Spain) arrival of agricultural and pastoralism in the Neolithic and continued to be a significant site of Chalcolithic and Bronze Age habitation (and burial) as humans increasingly shaped the regional landscape through deforestation, tilling and livestock grazing.

CRedit authorship contribution statement

María-José Iriarte-Chiapusso: Writing – original draft, Investigation. **María-Pilar Alfaro-Ibañez:** Writing – original draft, Investigation. **Gloria Cuenca-Bescós:** Writing – original draft, Investigation. **Manuel Ramón González-Morales:** Investigation. **Lawrence Guy Straus:** Investigation, Writing – review & editing, Investigation.

Data availability

Data used for the present research will be available on request.

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 ASupplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.quaint.2024.10.001>.

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