The end of Late Glacial in north-eastern Iberia: the small mammal assemblage from Cudó cave (Mont-Ral, Tarragona)

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ABSTRACT: One of the markers of the Late Pleistocene is highly fluctuating climatic conditions, with the Last Glacial Maximum (LGM, 26.5–19 ka cal before present (BP)) known to be one of the coldest periods. This work explores how the environment of north-eastern Iberia changed in relation to global climatic changes experienced during the Late Pleistocene, specifically around the LGM. Small mammal assemblages from Cudó cave (Tarragona, Spain) were used considering their well-known reliability for palaeoenvironmental reconstructions. Based on the taxonomic identification and the taphonomic analysis, several methodologies covering both qualitative and quantitative approaches were used to obtain the palaeoenvironmental information corresponding to level 107 and level 105 of Cudó cave (31.2–24.4 and 15.5–10.2 ka cal BP, respectively). The taphonomic results obtained point out owls (category 3) as the main accumulator of the small mammals. The palaeoenvironmental reconstruction shows that both levels experienced colder (−7.2°C/–4.4 °C) and wetter (+848 mm/ + 586 mm) climatic conditions than nowadays. However, in level 107 the environment was dominated by mid-European species and rocky landscape, while in level 105 it was dominated by Mediterranean species and woodland habitat. These conditions are consistent with the trend in north-eastern Iberia following several climatic events before and after the LGM coinciding with the period of Cudó cave assemblages.

KEY WORDS: Last Glacial Maximum, palaeoclimate, palaeoecology, small mammal taphonomy, Southwestern Europe

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1. Introduction

Marine records have provided high-resolution palaeoenvironmental information regarding the climatic changes during the Pleistocene in regional-to-global spatial scale. However, some terrestrial areas have their own ecological peculiarities that prevent the use of marine proxies to infer the environmental condition. The Iberian Peninsula is one of the examples of an area with high ecological diversity, considering the mountainous region and the strong effects of the Mediterranean Sea and Atlantic Ocean (e.g., Sanchez Goñi *et al.* 2000; Roucoux *et al.* 2005; Fletcher & Sánchez Goñi 2008; Álvarez-Lao *et al.* 2020; Álvarez-Vena *et al.* 2021). Particular to the Mediterranean Basin, the effects of global climatic fluctuations during the last glacial period were milder and less contrasting compared to the records from north-western Iberia or northern latitudes, as previous palynological (e.g., Carrión *et al.* 2003; Finlayson *et al.* 2008; Burjachs *et al.* 2012) and small vertebrate studies (e.g., López-García *et al.* 2014b; Fernández-García *et al.* 2016, 2019, 2020) have suggested.

Despite becoming one of the crucial periods during human history, the Last Glacial Maximum (LGM) is still highly discussed, regarding the chronology, for instance. There is no a single agreement among scholars about when this event took place. It is highly dependent on the definition and the geographical context discussed. However, the period from 26.5 to 19 ka cal before present (BP) (Clark *et al.* 2009) is commonly used as a timeframe when discussing about the Iberian Peninsula; at least it is consistent for the mountainous region (Cascalheira *et al.* 2021). From the cultural development perspective, this period coincides with the Upper Palaeolithic occupations, consisting of the Gravettian, Proto-Solutrean, and Magdalenian cultures. According to Cascalheira *et al.* (2021), the development of those cultures could be linked to the ecogeographical diversity of the region with a pronounced inter-regional variability. However, these authors noted that it is still necessary to do further studies with updated methods to understand and to fill the gaps in the knowledge about the archaeological and palaeoenvironmental diversity in the Iberian Peninsula.

North-eastern Iberia is one of the areas with limited information about archaeological and palaeoenvironmental condition

around or during the LGM. Some already known sites from this period are an open-air site of Montlleó in the southern slope of Pyrenees (Lleida), dated to 22.7–22.4 ka cal BP with Solutrean–Badegoulian lithic culture (Fullola *et al*. 2019); and, the Banyoles Lake (Girona), covering the period of the last 30 ka cal BP. Considering this limited record, the small-mammal assemblage from Cudó cave (Tarragona) adds clues to environmental information to fill the gap in this singular spatial and temporal context.

2. Site description

Cudó cave, also known as Aixàviga cave is a natural cavity located in the Prades Mountains (*Muntanyes de Prades*), a large calcareous mountain massif which belongs to the Catalan Pre-Coastal Range. It is situated at the southern face of Motllats cliff on the elevation of 987 metres above sea level (m.a.s.l.), directly facing the Aixàviga valley where the Glorieta river flows on its base. Specifically, it is located at 41°17′01.5″N 1°04′13.1″E, within the municipality of Mont-ral, in Alt Camp County (Tarragona, Spain). In a straight line, it is roughly 24 km from the modern coastline of Tarragona (Fig. 1) (Vergès 2017).

The surrounding landscape today shows high variability as a consequence of the abrupt relief changes from high mountain ranges to low plain and by significant hydrological changes, from water springs and streams on the low land to the arid plateau (Fig. 1). These hydrological differences lead to the widely diverse vegetation found within this area, producing a mosaic landscape. The plateau is currently covered with semi-open woodland consisting of *Quercus ilex* ssp. *rotundifolia* (holm oak), *Pinus sylvestris* (Scot's pine), *Juniperus communis* (common juniper), *Buxus sempervirens* (common box) as well as shrubs. The slope where Cudó cave is located is covered by a closed woodland which consists of holm oak and Scot's pine on the upper parts and *Pinus halepensis* (Aleppo pine) on the lower parts. The brushwood consists mainly of boxwood, *Viburnum tinus* (laurustinus), *Rhamnus alaternus* (Mediterranean buckthorn) and *Arbutus unedo* (strawberry tree) also found within this level. The plain at the bottom of the mountains is currently used as a cultivation area (Fig. 1) (López-García *et al*. 2014a). With those types of vegetation cover, small mammal species with woodland habitat preferences such as *Apodemus sylvaticus*, *Eliomys quercinus*, *Sciurus vulgaris*, *Myotis myotis*, *Myotis blythii*, *Rhinolophus* ferrumequinum and *Pipistrellus pipistrellus* can be expected to be found; as well as semi-open habitat preferences, such as *Crocidura russula*. With an agriculture area and water stream in the bottom of the valley, it is also possible to find *Arvicola sapidus*. On the raptorial birds, it some nocturnal and diurnal raptors such as *Athene noctua, Strix aluco, Bubo bubo, Circus cyaneus, Falco tinnunculus* and *Falco peregrinus* (Palomo *et al*. 2007) have been reported. *Chionomys nivalis* is currently absent from this region as it is exclusively found in several isolated areas of the Iberian Peninsula such as in the mountainous region (Palomo *et al*. 2007).

Archaeological interventions are unknown prior to 2016, and since then, an archaeological excavation has been conducted on this site (Vergès 2017). Two different sectors have been excavated, sector 100 and sector 200, which are situated in the inner and outer part of the cave gallery. From these recent interventions, nine and three stratigraphic levels have been exposed in sector 100 and sector 200, respectively. Among them, levels 107 and 105 of sector 100 are the richest undisturbed levels with archaeological and palaeontological remains, including the small mammal remains.

Radiocarbon dates placed level 107 from 24 to 31 ka cal BP and level 105 from ca. 10 to 15 ka cal BP (Vergès 2017). These dates were obtained from a marine shell of *Bittium reticulatum* and bone from an unidentified species from level 107 and from charcoal and unidentified bone fragment from level 105 (Table 1). The analysis was conducted using the carbon-14 accelerator mass spectrometry method.

3. Materials and methods

This work studies the small mammal assemblages from Cudó cave, recovered from excavation campaigns in 2016 and 2017. The remains were identified taxonomically following several published guidelines, among them are: Wilson & Reeder (2005) for the systematics taxonomy; Reumer (1984) and Furió (2007) for insectivores; Dupuis (1986), Sevilla (1988), and Galán (2019) for chiropters; Nadachowski (1982) and Gosàlbez (1987) for Arvicolinae; as well as Chaline (1972), Chaline *et al*. (1974) and Gosàlbez (1987) for Muridae, Gliridae, and Sciuridae. For practical reasons in recording and analysing, abbreviation of dental remains was used, including incisor (i), canine (c), antemolar (a), premolar (p) and molar (m). Lowercase letter indicates mandibular dentary and uppercase letter indicates maxillar dentary. Numbers are assigned after the letter to indicate the position of the specific tooth. The number starts from the mesial side or anterior side of the mandible or maxilla. The identified remains were all quantified as the number of identified specimens present (NISP). The NISP were grouped into the minimum number of individuals by counting the most represented diagnostic element for each species, considering laterality.

Before performing further analysis, taphonomic alteration were assessed to determine the cause of accumulation. To identify these processes of accumulation, analyses that account for the chemical-induced alterations, which are related to the digestion processes of the predators, were performed following Andrews (1990) and the last review Fernández-Jalvo *et al*. (2016). These previous approaches established four grades of digestion marks for the small mammal remains: light; moderate; heavy; and extreme. Digestion marks on the dental remains are usually easy to identify and distinguished with respect to other taphonomic alterations. The taphonomic analysis on Cudó cave materials was carried out on the taxonomically identified molars from all taxa and also the incisors in the case of rodents. The observation was conducted on the occlusal and lateral surfaces of the molars and incisors. Apart from those four grades, the specimens also were assigned to an 'absent' classification for one with no visible digestion traces, and for the teeth with unclear digestion marks due to its preservation state they were classified as 'null'.

In order to obtain palaeoenvironment information in the vicinity of Cudó cave, several methods were combined in this work. First, the Simpson's index was used to evaluate the evenness of the small mammal community of Cudó cave (Whittaker, 1972). This analysis was performed in the Paleontological Statistics (PAST) software (version 4.0) (Hammer *et al*. 2001). Then, it was applied to the habitat weighting method, a quantitative method used for landscape reconstruction based on the habitat preferences of each taxon (Rowe 1956; Evans *et al*. 1981; Gauch 1989), considering a modern atlas of Iberian mammals (Palomo *et al*. 2007). In this method, a fractioned value between 0 and 1 is assigned to each species according to its preferred habitat, where 0 means not preferred and 1 means strongly preferred habitat. The third method was the chorotype classification, a quantitative analysis which aims to climatically characterise the biotic region based on the concept of chorotypes, which considers groups of species with overlapping climatic requirements that determine their current geographical distribution and association (Fattorini 2015). In this study, four chorotypes were used to infer the past environmental condition within the vicinity of Cudó cave (Sans-Fuentes & Ventura 2000). The relative
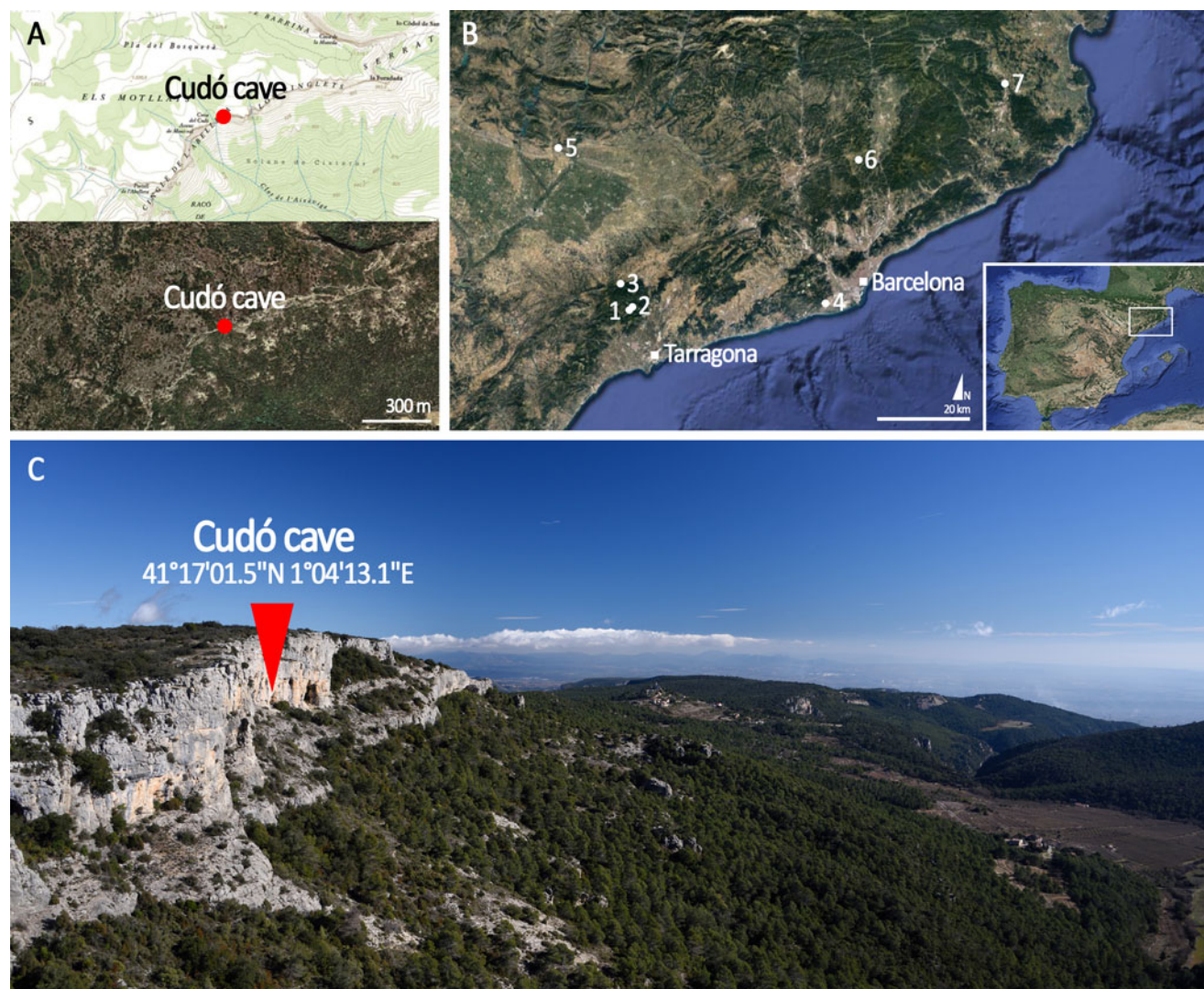
Figure 1 (A) The location of Cudó cave; (B) the location of Cudó cave in relation to the sites mentioned in this work: (1) Cudó cave; (2) Galls Carboners; (3) Xaragalls cave; (4) Canyars; (5) Colomera cave; (6) Toll cave; (7) Arbreda cave; and (c) current situation in the vicinity of Cudó cave.

abundance of species within each chorotype was considered to quantify the importance of each chorotype in the site area in the past.

In addition, to evaluate the palaeoclimatic conditions, the bioclimatic model (BM) (Hernández Fernández 2001; Hernández Fernández & Peláez-Campomanes 2003) and mutual ecogeographical range (MER) methods (Blain *et al*. 2009; López-García *et al*. 2010; Lyman 2016) were used. The first method uses faunal population, specifically on rodents, which represents climatic zones over the world to infer the climatic condition of the area. In the case of Cudó cave, four climatic zones were considered following the species presented on the assemblages. Those are zone IV, winter rain and summer drought; zone VI, typical temperate; zone VIII, cold temperate; and zone IX, Arctic. From the representation of each climatic typology and using multiple

linear regression (Hernández Fernández *et al*. 2007), the palaeoclimatic information including mean annual temperature (MAT), mean annual precipitation (MAP), mean temperature for the coldest month and mean temperature of the warmest month could be obtained. Furthermore, on the MER analysis, modern climatic condition (30-years average) of the intersecting area of the species identified from a stratigraphic unit (obtained considering each species' current distribution in 10 × 10 Universal Transverse Mercator grid) became the basis of palaeoclimatic inferences. Careful consideration was paid on the taxa selection for these two methods. In this analysis, insectivores were included, otherwise, chiropters were not included because of their scarcity and their seasonal migration behaviour. Species with a strong distribution relationship with anthropic activity, in this case *Microtus (Iberomys) cabrerae*, were also discarded.

Table 1 Date analysis result on the seven samples from Cudó cave (Vergès 2017).

Material	Species	Level	Laboratory reference	Radiocarbon age (years before present (BP))	Calibrated (years BP; 2 sigma)
Charcoal	*Pinus sylvestris*	105	Beta-455058	12,900 ± 50	15,585–15,245
Bone	Rib indeterminate	105	Beta-455059	11,250 ± 30	13,140–13,070
Bone	*Pyrrhocorax pyrrhocorax*	105	Beta-489614	9090 ± 30	10,273–10,199
Marine shell	*Bittium reticulatum*	107	Beta-484788	27,510 ± 120	31,245–30,842
Bone	Indeterminate	107	Beta-489615	20,510 ± 60	24,991–24,404

Sets of recent information were used for modern species' geographical distributions (Palomo *et al.* 2007), for climatic information (Rivas Martínez 1987; Agencia Estatal de Meteorología (España) & Instituto de Meteorologia (Portugal) 2011) for the vegetation zone of the Iberian Peninsula, as well as the online sources from the climate-data.org.

4. Results and discussion

4.1. Small mammals of Cudó cave

Small mammals are considered a reliable palaeoenvironmental proxy to reconstruct the climatic and landscape dynamics through time (e.g., López-García *et al.* 2011b; Hadler *et al.* 2013; Fernández-García *et al.* 2016, 2018; Fernández & Pardiñas 2018; Baca *et al.* 2020; Avery 2022). This is possible because the small mammal species are commonly adapted to a specific habitat, restricted to a relatively small geographical area, sensitive to habitat changes; moreover, they have a short lifespan, high reproduction and evolutionary rate, and can be quickly dispersed over the area (e.g., Chaline *et al.* 1974; Andrews 1990; Barnosky 1994; Repenning 2001; Van Dam *et al.* 2006).

In total, 1178 remains have been identified in this work, which correspond to a minimum of 502 individuals (Table 2). Those numbers are distributed into 528 taxonomically identified specimens in level 107, which corresponds to a minimum of 264 individuals, and 658 in level 105, which corresponds to a minimum of 238 individuals. From the taxonomic analysis, 14 different taxa have been identified (Table 2; Fig. 2). However, some specimens were unable to be identified into species level, therefore they were grouped at the genus level (cf. *Myotis* and cf. *Pipistrellus*) and order level (Chiroptera gen. et sp. indet). These groups, with addition of *Microtus* gr. *arvalis-agrestis* are not considered for the environmental reconstruction since they provide little ecological information.

Considering relative abundance of the taxa, in level 107, *C. nivalis* which appears to be dominating the assemblage, is significantly higher than the other taxa. The taxonomic relative abundances in level 105 are notably different from those in level 107. The species *C. nivalis* is still highly represented, but it is not dominating the assemblage due to a significant increase of the abundance of *A. sylvaticus*. Other taxa are relatively well represented in level 105.

All species recovered from Cudó cave correspond to extant species in the Iberian Peninsula. However, in the comparison to the species currently present in the vicinity of the site, not all recovered species can be found today, such as *Sorex araneus*, *Sorex coronatus*, *Microtus arvalis*, *Microtus agrestis*, *M.* (*I.*) *cabrerae* and *C. nivalis*. This absence is mainly linked to the open habitat preferences and mid-European environmental requirements of those species which recently cannot be supported by the environment around Cudó cave. The diminishing *C. nivalis* particularly in the north-eastern Iberian Peninsula is evident after the LGM, with the earliest remains from Colomera cave dated younger than 17 ka BP (López-García & Cuenca-Bescós 2010; Fernández-García & López-García 2013). In addition, anthropic environmental changes could also be linked to the missing species from the Cudó cave vicinity. The increase of agriculture during the Neolithic period in the mid-Holocene leads to decreasing wet soils, the preferred habitat of *M.* (*I.*) *cabrerae* in this region (López-García *et al.* 2012).

4.2. The origin of the assemblages

Up to 1131 molars and 349 isolated incisors have been included from both levels in the taphonomic analysis. A wide range of digestion marks are detected on the remains from both levels, covering the digestion degree from light to heavy (Table 3; Fig. 3).

The high abundance of digested remains indicates that predation is the main cause of accumulation in both levels. This is consistent with the common pattern of small mammal remains' accumulation with predatory activity becoming the most common agent of accumulation (Fernández-Jalvo *et al.* 2016). This general pattern of digested remains with the domination of light digested remains with notable proportion of moderate and high digested remains could point to nocturnal raptors as the main producer group of the assemblages. The probable species contributing, and capable to produce such percentage, are classified as the category 3 predators, including *S. aluco*, *B. bubo*, *A. noctua* and *Bubo africanus* (Fernández-Jalvo *et al.* 2016).

Associating the accumulation of small mammal remains in Cudó cave with those species of category 3 predators, with the exception of *B. africanus*, is possible considering their current geographical distribution in the Iberian Peninsula (Sociedad Española de Ornitología/Birdlife 2021). All mentioned species also have similar habitat preferences for dwelling on cliffs, natural crevices or woodland. For the hunting environment, they tend to hunt in open landscapes, such as grassland or woodland margins (Scott *et al.* 1996). However, their hunting range will vary depending on the landscape and the abundance of their preys.

Among those predators, *S. aluco* is the most probable species considering the digestion pattern. Compared to *B. bubo*, *S. aluco* induces a higher frequency of digested molars and isolated incisors with moderate to high digestion marks. Otherwise, the frequency and intensity of digestion marks are not as high as *A. noctua* (Andrews 1990; Fernandez-Jalvo & Andrews 1992; Fernández-Jalvo *et al.* 2016). This high proportion of digested remains are observed in both level 107 and 105 of Cudó cave. However, the shifting pattern of digestion marks the degree between these two levels being present. There is an increase of non-digested molars (level 107, 57.8%; level 105 67.5%) and a decrease of heavy-digested molars (level 107, 18.2%; level 105 10.7%). It cannot be barely interpreted as a change of predators involved in the accumulation. Instead, it is linked to the increase of *A. sylvaticus* remains in the level 105 (Table 4), as it known to have more resistant molar enamel to digestive corrosion (Fernández-Jalvo *et al.* 2016; Avery 2022). Therefore, the change of contributing predator can be omitted from the discussion as it implies that the same predators contribute to the accumulation of small mammal remains in both levels.

Strix aluco is considered as an opportunist nocturnal predator that will get pretty much any species present within its hunting range. This predator is known to hunt a relatively equal proportion of rodents or the other prey (Fernández-Jalvo *et al.* 2016). It indicates that the predatory selection is minimum and the prey species represent the environmental condition within their hunting range, which in average is around $0.7\,km^2$ (Andrews 1990; Fernández-Jalvo *et al.* 2016).

4.3. Palaeoenvironment of Cudó cave

There are clear differences between level 107 and level 105 results considering the palaeoenvironmental methods of analysis. From the Simpson's diversity index analysis, level 107 shows a lower index compared to level 105 (Fig. 4). It indicates that level 105 has lower richness and evenness of taxonomic composition than level 105. This signal is consistent with the quantification results, which show *C. nivalis* dominating the assemblage in level 107, whereas in level 105 *A. sylvaticus* appears in a considerable proportion (Fig. 4). The increasing diversity index and the change of domination pattern from level 107 to level 105 become a signal of ecosystem improvement, from a less to more

Table 2 Quantification table of the small mammal remains recovered from levels 107 and 105 at Cudó cave and their distributions based on the chorotype and habitat.

	Level 107			Level 105			Chorotype				Habitat weightings			
	NISP	MNI	%	NISP	MNI	%	Ch1	Ch2	Ch3	Ch4	OD	OH	WO	R
Crocidura russula	19	5	1.9	38	10	4.2			x		0.5	–	0.5	–
Sorex gr. *araneus-coronatus*	1	1	0.4	0	0	0	x				–	0.5	0.5	–
Rhinolophus cf. *ferrumequinum*	0	0	0	2	1	0.4				x	–	0.5	0.5	–
Myotis gr. *myotis-blythii*	1	1	0.4	14	4	1.7				x	–	–	0.75	0.25
Pipistrellus cf. *pipistrellus*	1	1	0.4	9	3	1.3				x	–	–	0.5	0.5
Microtus arvalis	30	23	8.7	19	11	4.6		x			0.5	–	0.5	–
Microtus agrestis	30	17	6.4	16	13	5.5		x			–	0.5	0.5	–
Microtus gr. *arvalis-agrestis*	1	1	0.4	0	0	0					–	–	–	–
Microtus (*Tericola*) *duodecimcostatus*	15	8	3	35	18	7.6			x		–	0.5	0.5	–
Microtus (*Iberomys*) *cabrerae*	1	1	0.4	32	17	7.1			x		–	0.5	0.5	–
Chionomys nivalis	321	175	66.3	124	64	26.9	x				–	–	–	1
Apodemus sylvaticus	100	28	10.6	306	88	37				x	–	–	1	–
Eliomys quercinus	7	3	1.1	55	8	3.4				x	–	–	0.5	0.5
Sciurus vulgaris	0	0	0	1	1	0.4				x	–	–	1	–
Total	527	264	100	651	238	100	–	–	–	–	–	–	–	–

NISP, number of identified specimens present; MNI, minimum number of individuals; Ch, chorotype; OD, open dry; OH, open humid; WO, woodland; R, rocky.

favourable ecosystem. The ecosystem could have increased its capacity to support more species linked to an increase on vegetation complexity of arboreal ecosystems (e.g., Williams *et al.* 2002).

The signal of landscape change is supported with the data obtained from the habitat weighting method. In level 107 a habitat with rocky substrate prevails (67.1%) with only a small proportion of woodland habitat (22.1%) (Fig. 4). In contrast, in level 105 there is a predominance of woodland habitat (55.7%) and a smaller proportion of rocky substrate-habitat (29.6%). The increasing proportion of woodland and decreasing rocky substrate in level 105 could be an indicator that there was a climatic amelioration that increased the possibilities of closed vegetation cover to develop. The positive shift is also visible on the proportion of open humid landscape relative to the other types of landscape in level 105. It signals the increase of humidity or
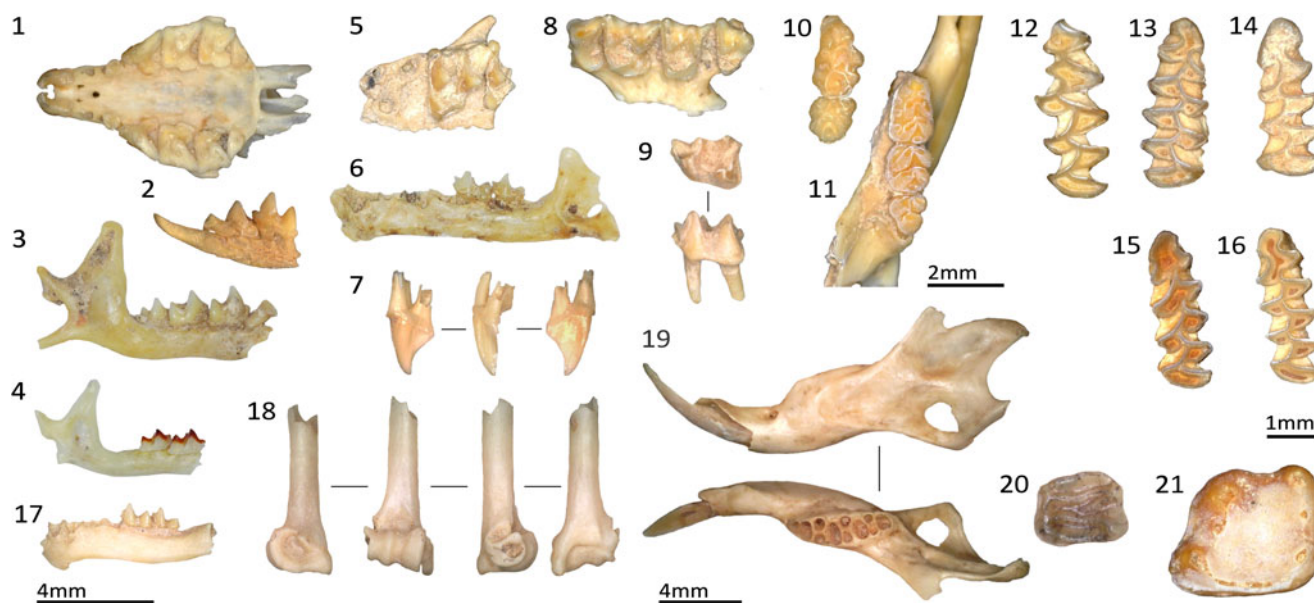

Figure 2 Selected specimens from each taxon recovered from Cudó cave. (1–3) *Crocidura russula*: (1) anterior fragment of cranium from level 105 in palatal view; (2) anterior fragment of left hemimandible with i–m1 from level 105 in labial view; (3) right hemimandible with a4–m3 from level 105 in labial view; (4) *Sorex* gr. *areneus-coronatus* posterior fragment of right hemimandible with m2–m3 from level 107 in labial view. (5–7) *Myotis* gr. *myotis-blythii*: 5, fragment of left hemimaxilla with M2–M3 from level 105 in palatal view; (6) left hemimandible with m2–m3 from level 105 in labial view; (7) isolated left P4 in mesial, lingual, and distal view. (8–9) *Rhinolophus* cf. *ferrumequinum*: (8) fragment of left hemimaxilla with P4 – M3 from level 105 in palatal view; (9) isolated left m1 from level 105 in occlusal and labial view. (10–11) *Apodemus sylvaticus*: (10) right M1 and M2 from level 105 in occlusal view; (11) left hemimandible with m1–m3 from level 105 in occlusal view; (12) *Microtus* (*Iberomys*) *cabrerae* left m1 from level 105 in occlusal view; (13) *Microtus agrestis* right m1 from level 105 in occlusal view; (14) *Chionomys nivalis* left m1 from level 105 in occlusal view; (15) *Microtus* (*Tericola*) *duodecimcostatus* left m1 from level 105 in occlusal view; (16) *Microtus arvalis* left m1 from level 105 in occlusal view; (17–18) *Pipistrellus* cf. *pipistrellus*: 17, left hemimandible with m2–m3 from level 105 in labial view; (18,) right humerus with epiphysis distal from level 105 in anterior, external, posterior and interior views: (19–20) *Eliomys quercinus*: (19) left hemimandible from level 105 in labial and dorsal views; (20) left M1 from level 105 in occlusal view; (21) *Sciurus vulgaris* left m1 from level 105 in occlusal view. Scale in 4 mm for insectivores, chiropters and the mandible of *Eliomys quercinus*, 2 mm for *A. sylvaticus* and 1 mm for Arvicolinae, molar of *Eliomys quercinus*, and *Sciurus vulgaris*. Terminological abbreviations: I = incisor; c = canine; a = antemolar; p = premolar; m = lower molar. Lowercase letter indicates mandibular dentition and uppercase letter indicates maxillary dentition. Numbers situated after the letters constitute the position of the teeth, starting from mesial or anterior side of the mandible or maxilla.

Table 3 Digestion marks of analysed remains from Cudó cave, differentiating digestion categories reached.

	Isolated incisor				Molars			
	Level 107		Level 105		Level 107		Level 105	
Digestion category	*n*	%	*n*	%	*n*	%	*n*	%
Null	1	–	16	–	6	.	7	.
Absent	70	41.7	105	58.0	286	57.8	429	67.5
Light	73	43.5	59	32.6	43	8.7	43	6.8
Moderate	14	8.3	9	5.0	76	15.4	96	15.1
Heavy	11	6.5	8	4.4	90	18.2	68	10.7
Total	168	100	181	100	495	100	636	100

Remains with unclear digestion marks due to poor preservation are considered as 'null' and not included in the quantification.

precipitation in this area during 15.5–10.2 ka cal BP, consistent with the palynological data extracted from the Banyoles Lake which shows increases on the trees' taxa after 15 ka BP compared to the period between 31 and 24 ka BP (Pèrez-Obiol & Julià 1994). However, despite this decreasing proportion, the presence of rocky substrate cannot be ignored as it still has a considerable portion in the landscape (29.6%). It is possible, considering the habitat preference of *C. nivalis* currently inhabiting the Iberian Peninsula, that they could also live in the bushes or wooded area with stable rocky substrate (Palomo *et al.* 2007).

Moreover, the result displayed from chorotype analysis indicates a consistent trend for this environmental change. The chorotype 1, which corresponds to mid-European faunal taxa, including *Sorex* gr. *araneus-coronatus* and *C. nivalis*, notably dominates the assemblage of level 107 (81.9%). This condition also provides a suitable habitat for chorotype 2 species such as *M. arvalis* and *M. agrestis*. Otherwise, in level 105 this domination is shifted to the Mediterranean and generalist species (chorotypes 3 and 4: 63%) (Fig. 4). The increases of chorotypes 3 and 4 taxa and decrease of chorotypes 1 and 2 taxa signal the increase of temperature and humidity (Sans-Fuentes & Ventura 2000). This could provide better conditions for the flourishing of the woodland habitat and increasing small mammal diversity in level 105.

On the climatic aspect, the BM and MER analysis show detailed information regarding past climatic parameters' estimations around Cudó cave during the deposition of the remains. In both levels, the results suggest lower mean temperature (level 107, MER $-7.2\,°C$ BM $-3.3\,°C$; level 105, MER $-4.1\,°C$ BM $-3.8\,°C$) and higher precipitation rates (level 107, MER $+848$ mm BM 657.3 mm; level 105, MER $+273$ BM $+856.3$) compared to the current condition on the area (Fig. 4). However, several differences could be observed when comparing the results of the BM and MER in detail. Both methods follow a qualitative approach based on the presence or absence of the taxa without consideration on the relative abundance. It leads to a significant difference by only a subtle change on the assemblage. By this means, using a different set of data, in case of this work by involving insectivores on the mutual ecogeographical range analysis, can significantly affect the result. Moreover, as both methods were performed using current small mammal distribution, it securely will be affected by the anthropic activities. Even though the distribution of some species (e.g., *M.* (*I.*) *cabrerae*) is already known to be strongly affected by anthropic activities, the impacts on the other species distribution are still difficult to be assessed (López-García *et al.* 2012; Fernández-García 2019).

In spite of that, when the results are compared to other results of this work, such as those derived from the habitat weighting and chorotype analysis, the MER results fit better than those
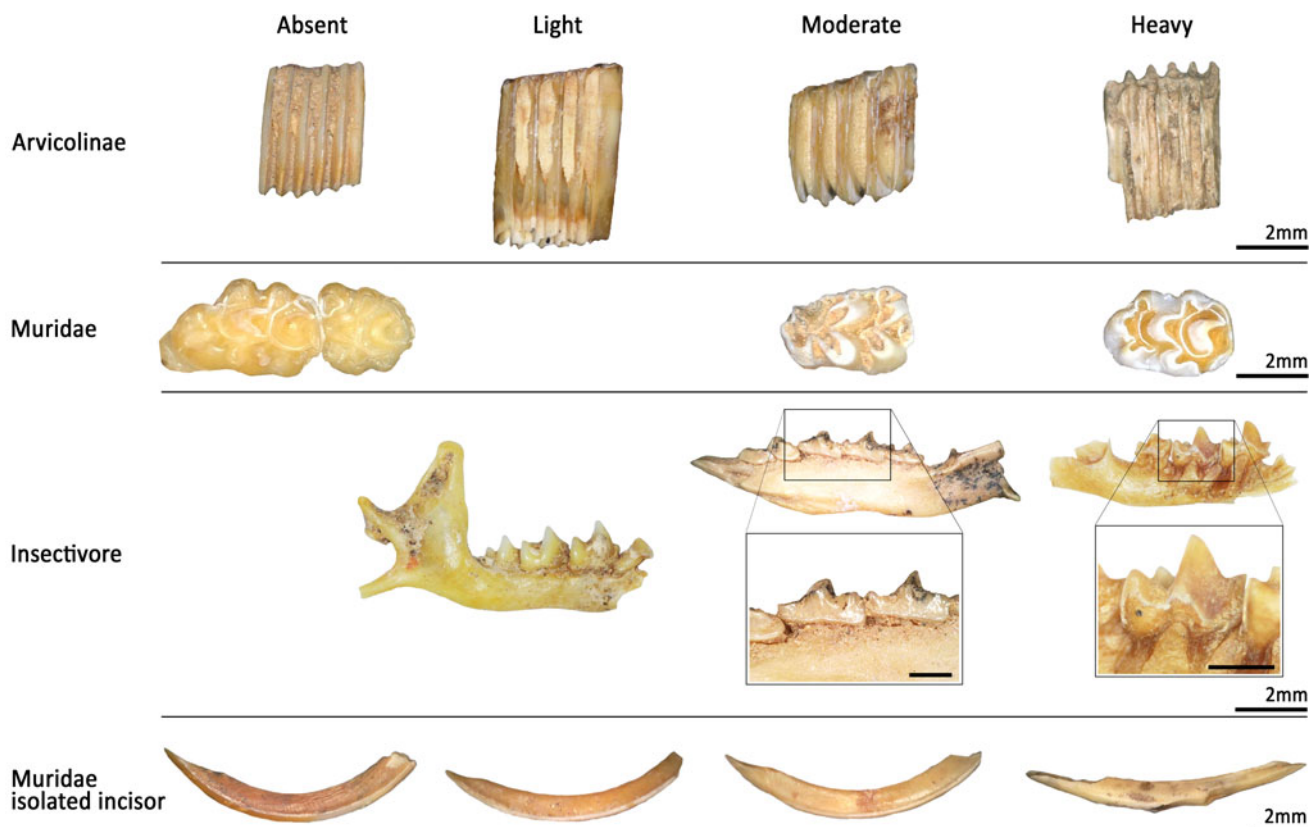

Figure 3 Digestion marks on the Arvicolinae m1 (top row), Muridae molars (second row), insectivores and chiropters (third and fourth row) and isolated incisors of rodents (bottom row). (A) absent; (B) light digestion; (C) moderate digestion; (D) heavy digestion. Scale in 2 mm and 1 mm for detailed view of insectivore digestion marks. Light digested remains are not shown here as they are difficult to distinguish from the non-digested molars.

Table 4 Proportion of digested isolated molars by taxonomic groups of the Cudó cave assemblages.

Level 107 Taxonomic group	Total remains	Absent	%	Light	%	Moderate	%	Heavy	%
Arvicolinae	366	174	47.5	43	11.7	71	19.4	78	21
Muridae, Gliridae and Sciuridae	107	91	85	0	0	4	3.7	12	11
Soricidae	20	19	95	0	0	1	5	0	0
Chiroptera	2	2	100	0	0	0	0	0	0
Level 105									
Arvicolinae	216	106	49.1	42	19.4	46	21.3	22	10
Muridae, Gliridae and Sciuridae	358	275	76.8	1	0.3	46	12.8	36	10
Soricidae	38	25	65.8	0	0	4	10.5	9	24
Chiroptera	24	23	95.8	0	0	0	0	1	4.2

of the BM. In addition, by the comparison to palynological data from the Banyoles Lake where there were increases on the tree taxa after 15 ka BP (Pèrez-Obiol & Julià 1994), the result from MER analysis also shows better consistency.

4.4. Palaeoenvironment of north-eastern Iberia and the Prades Mountains during the end of Late Glacial

Cudó cave is not the only site providing small mammal assemblage for the palaeoenvironment inference in north-eastern Iberia dated under 35,000 years. There are two other sites situated in very close proximity that could add complementary information about the palaeoenvironment of this region, which are Xaragalls cave and Galls Carboners. In spite of these sites not being exactly contemporaneous to Cudó cave, they provide clue contextual ecological information from the era just before the Cudó cave assemblage formation.

Two important layers from Xaragalls cave, for its chronological proximity to Cudó cave, are C4-dated to 48.2–45.1 ka BP and C3, situated just above layer C4 (López-García et al. 2011a; Vallverdú et al. 2012). Palaeoenvironmental inferences from these two layers show domination of woodland covers and mid-European climatic conditions (chorotypes 1 and 2) (López-García et al. 2011a). From the small mammal analysis, this is indicated by a considerable amount of *M. agrestis* and also a notably high abundance of *A. sylvaticus*. Compared to the Cudó cave assemblages, both layer C4 and C3 show a higher proportion of woodland landscape than level 107 and are roughly similar to 105 at Cudó cave. Otherwise, the climatic inference shows that the proportion of species from chorotypes 1 and 2 of Xaragalls cave is lower than in Cudó cave level 107 (Fig. 5). In addition, by the MAT, Xaragalls cave layer C4 was likely warmer than Cudó cave level 107 but still colder than Cudó cave level 105, while Xaragalls cave layer C3 was warmer than Cudó cave level 105 (Fig. 6).

Moreover, the assemblage from Galls Carboners, dated to ca. 31.3–31.1 ka cal BP (López-García et al. 2014a) could be even more interesting as it is contemporaneous to the early stage of Cudó cave level 107 and they have close geographical proximity. However, the palaeoenvironment inferences show a different pattern than what it is inferred in level 107 from Cudó cave. This level represents an exceptional cold and wet event with the lowest woodland habitat representation and highest proportion of rocky habitat, in contrast to the condition in Galls Carboners which is dominated by woodland. In the species composition, level 107 shows strong dominance of mid-European species (81.9%) with the lowest Mediterranean taxa (17.8%), while in Galls Carboners only 55% of the assemblage composed of mid-European species and 45% of the assemblage are Mediterranean taxa. The big difference also can be seen in the MAT and MAP estimations – level 107 at Cudó cave has lower temperature (−3.5 °C) and significantly higher precipitation (+411 mm) than Galls

Carboners (Fig. 6). Furthermore, the signal from Simpson's diversity index shows that Galls Carboners have more diverse and equally represented small mammal species (1–D = 0.83) compared to Cudó cave level 107 (1–D = 0.54). These results indicate that the Galls Carboners palaeoenvironmental condition was more favourable to support diverse small mammal communities.

The difference between the MAT and MAP of Cudó cave level 107 and Galls Carboners is important to be noted since these two sites are located in very close proximity, in similar elevation (around 1000 m.a.s.l.), and chronologically overlapping. Taphonomic biases cannot be rejected as the cause of these differences, although *S. aluco* is considered the main accumulator of the assemblages from both sites, with a well-known opportunistic hunting behaviour. Further research is recommended to evaluate the real influence. Nevertheless, even if the predatory selection played a major role during the accumulation, the significant difference of mid-European taxa in both assemblages, including the domination of *C. nivalis* in Cudó cave, become clear evidence of different environmental conditions. Also, the ecological changes between levels 107 and 105 are not accompanied by the change of taphonomic pattern, thus these changes can be significant.

The possible reason is that the Galls Carboners assemblage only correspond to a short chronological period, coincident with the beginning of the Heinrich Event 3 (HE3). Despite that the Heinrich Events are known to have severe climatic conditions, most of these events could be divided into three stages based on the different climatic conditions, which are the early, main, and late stages. The sea surface temperature and palynological records suggest that the climatic condition during the early stage of HE3 was not so severe (see Cacho et al. 2001, 2006; Fletcher & Sánchez Goñi 2008). The less harsh climate maintains the higher proportion of Mediterranean taxa with woodland habitat preferences compared to a colder and dryer climate.
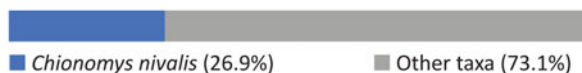
In contrast, level 107 of Cudó cave, which represent the coldest and most humid period, has a chronological range that spans over a longer period, including the whole HE3 and the beginning of Heinrich Event 2 (HE2) and LGM (Fig. 7). The later stage of level 107 might be coincident with the early stage of glaciers' expansion in the southern latitude (Lewis et al. 2009; Moreno et al. 2012; Lécuyer et al. 2021). With this expansion and considering the high altitude of the Cudó cave, snow covers were possibly present in the vicinity of Cudó cave during a major part of the year. This consequently increased the abundance of mid-European taxa with rocky habitat preferences, such as *C. nivalis* species, and demonstrate the importance of glacial deposit extension in high altitudes even in Mediterranean-affected environments that generally were experiencing milder conditions.

The exceptionally cold and wet conditions of level 107 are probably related to HE3 or HE2 when the cold summer and humid winter conditions were experienced. It suggests that
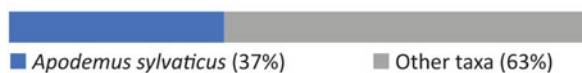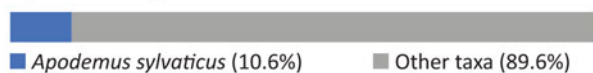
Level 107
(31.2 - 24.4 ka cal BP)

Chionomys nivalis

■ *Chionomys nivalis* (66.3%)   ■ Other taxa (33.7%)

Apodemus sylvaticus

■ *Apodemus sylvaticus* (10.6%)   ■ Other taxa (89.6%)

Diversity index

0 ———————— 0.54 ———————— 1.0

Habitat weighting

■ Open dry   ■ Open humid   ■ Woodland   ■ Rocky

Chorotype

■ Chorotype 1   ■ Chorotype 2   ■ Chorotype 3   ■ Chorotype 4

Mean annual temperature (°C)

0 —— 7.5 —— 11.4 —— 14.7 —— 20

Mean temperature of the coldest month (°C)

0 —— 5.1 —— 10.0 ———————— 20

Mean temperature of the warmest month (°C)

0 ———————— 17.5 — 20 / 18.8

Mean annual precipitation (mm)

0 —— 552.0 —— 1209.3 — 1400

Level 105
(15.5 - 10.2 ka cal BP)

Chionomys nivalis

■ *Chionomys nivalis* (26.9%)   ■ Other taxa (73.1%)

Apodemus sylvaticus

■ *Apodemus sylvaticus* (37%)   ■ Other taxa (63%)

0 ———————— 0.78 ———— 1.0

0 —— 10.6 —— 14.7 —— 20 / 10.8

0 —— 2.5 —— 10.0 ———————— 20 / 3.7

0 ———————— 16.9 — 20 / 18.9

0 —— 552.0 —— 825.0 —— 1138.3 — 1400
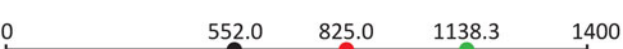
● Mutual ecogeographic range   ● Bioclimatic model   ● Current data

Figure 4 Comparison of some ecological indicators extracted from the assemblages of levels 107 and 105 of Cudó cave, including comparison between *Chionomys nivalis* and *Apodemus sylvaticus* abundances, Simpson's diversity index score, chorotypes classification, habitat distribution and climatic estimations, expressly with respect to the current climatic conditions surrounding Cudó cave.

these events have different climatic conditions with the previous Heinrich Event 4 (HE4) event conditions. As Xaragalls cave C4 is recorded also in Terrasses de la Riera dels Canyars (López-García *et al.* 2013), HE4 is distinctively warmer and drier than what is recorded in Cudó cave level 107. Furthermore, if Cudó cave level 107 is compared to level C from Arbreda cave (23.5–22.9 ka cal BP), the Cudó cave level 107 is still colder and significantly wetter (López-García *et al.* 2015). These discrepancies could be linked to the geographical condition where Cudó cave is situated. The mountainous relief with elevation reaching 1000 m.a.s.l. and the presence of cliffs could give this colder

condition. Even so, the domination of mid-European taxa in level C of Arbreda cave could be evidence of the cold and humid climate after the HE2 and during the LGM.

From the taphonomic aspect, the same predator also has been identified from Galls Carboners assemblages (López-García *et al.* 2014a). The quantification of digested marks on the incisors is comparable with Cudó cave level 107. The percentage of digested incisors from Galls Carboners, particularly from levels 106–108, ranges from 45.7% to 55.9%, while in Cudó cave level 107 it is 58.3%. These values fit to category 3 predator, including also *B. africanus*, *B. bubo* and *A. noctua* (Fernández-Jalvo *et al.*
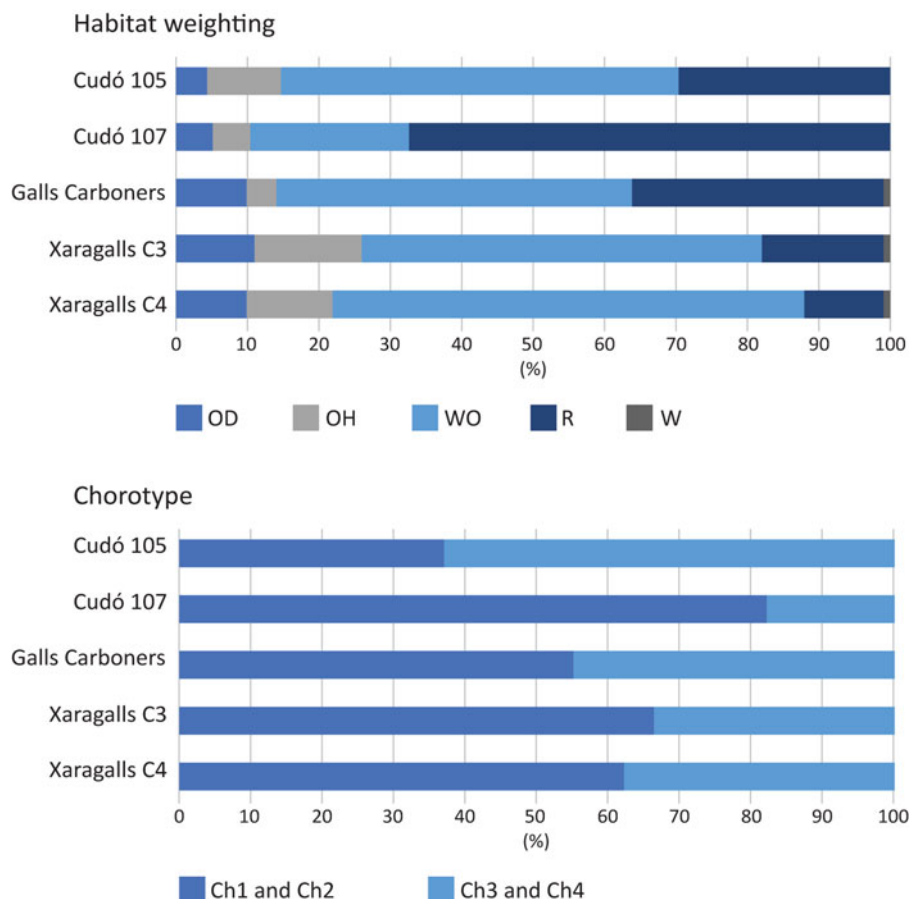
Figure 5 Chorotype and habitat comparison between Cudó levels 107 and 105 with Galls Carboners (López-García *et al.* 2014a, b) and Xaragalls cave levels C4 and C3 (López-García *et al.* 2011a).

2016). Further studies point out that *S. aluco* was the main accumulator of small mammal remains in Galls Carboners (López-García *et al.* 2014a). Thus, it can be demonstrated that the different analysis results between Cudó cave and Galls Carboners are not a result of hunting preferences of the predators.

Otherwise, the Cudó cave level 105 is in line with contemporaneous sites in north-eastern Iberia. It is roughly similar to level CE15 of Colomera cave (ca. 13 ka BP) (López-García *et al.* 2010), where the mid-European taxa become the most abundant group of the assemblage. The inferred habitat is also dominated with woodland (54%) and a quite high proportion of rocky habitat (24%). The climatic improvement also observed in Toll cave (Fernández-García & López-García 2013), from a roughly equal proportion of mid-European and Mediterranean taxa in level 3 (ca. 47.1–45.5 ka cal BP) become dominated by Mediterranean taxa in level 2. Unfortunately, there is no absolute date assigned to this level to build a better correlation.

Thus, the small mammal assemblage of level 105 clearly indicates a climatic improvement compared to level 107. This is particularly shown by the decreasing mid-European taxa and the
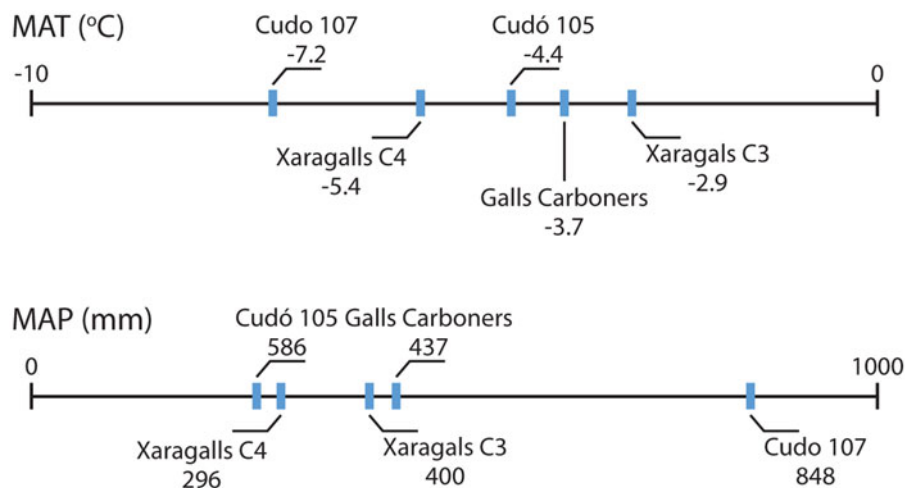

Figure 6 Comparison of the difference of mean annual temperature and mean annual precipitation between Cudó cave levels 107 and 105 with Galls Carboners (López-García *et al.* 2014a, b) and Xaragalls cave levels C4 and C3 (López-García *et al.* 2011a, b). The data are based on mutual ecogeographical range analysis result and in respect to current data from the nearest climatic station of each site.
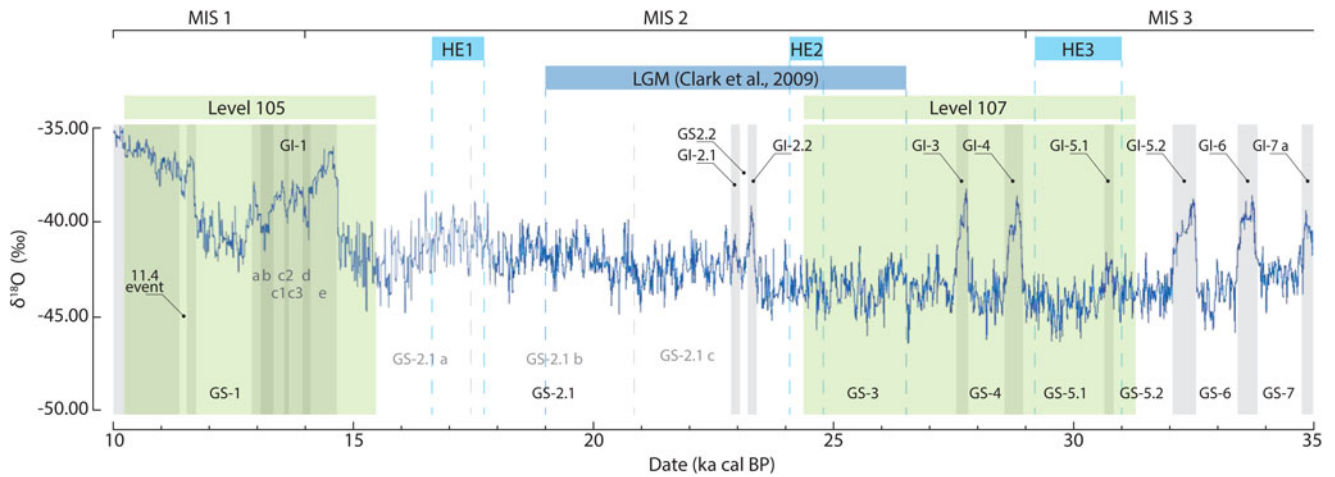
Figure 7 Chronological position of level 107 and 105 of Cudó cave among the global climatic events (Rasmussen *et al*. 2014; Maier *et al*. 2021).

increasing woodland habitat. However, this improvement is not exceptional if the older assemblages from the Prades Mountains are considered. The increasing Mediterranean taxa is not so much different from the Xaragalls cave C4, C3, and particularly the Galls Carboners assemblage. The woodland and open humid habitat composition even shows more similarities. Interestingly, the rocky habitat appears with a bigger proportion in Cudó cave level 105 than the Xaragalls cave C4 and C3 assemblages. This pattern could be related to several abrupt climatic events such as Older Dryas (GI-1d) and Inter-Allerød Cold Period (GI-1b) (Fig. 7).

5. Conclusions

Cudó cave that belongs to the Prades Mountains system yielded two archaeo-palaeontological stratigraphic levels, which are levels 107 and 105, dated between 31.2–24.4 ka cal BP and 15.5–10.2 ka cal BP, respectively. These two levels contain archaeological remains associated with the Upper Palaeolithic period, including lithic and faunal artefacts. Moreover, levels 107 and 105 of Cudó cave are rich in small mammal remains, with 1185 specimens being identified in this work corresponding to a minimum of 502 individuals. From this assemblage, 14 species have been identified.

Predatory activity has been identified as the main factor determining the accumulation of this assemblage, based on the high number of elements digested. Considering the digestion marks, *S. aluco* which belongs to the category 3 predators is the most possible accumulator of the assemblage. It is considered as an opportunistic hunter. It dwells on the cliffs, natural crevices, or woodland and preferentially hunts in an open landscape. However, from the inspection on the digestion pattern in relation to the predator's categories of both levels, it is deduced that the climatic factors indicate that the taphonomic explanation prevails. Apparently, the same type of predators was involved in the small mammal remains' accumulation in both levels.

On the palaeoenvironmental aspect, it has been inferred that level 107 shows a moderate level of diversity comprising the predominance of *C. nivalis*, a mid-European species. The high abundance of this species also links to the predominance of rocky habitat as well as the estimated cool mean annual temperatures and high precipitation rates with respect to current conditions. Such an environmental pattern, together with the chronology proposed for this level, suggested this level could be correlated to the HE3 or HE2 as well as the beginning of LGM. This contrasts with level 105, where the environment was more diverse with a relatively low proportion of required mid-European taxa compared to Mediterranean taxa. The habitat also seems

to be improved with a significant increase of woodland habitat and a decrease of rocky habitat. Furthermore, the mean annual temperatures and the precipitation rates also differ from the current condition. It could be an indicator of an environmental improvement in respect to level 107.

Despite of the climatic improvement, level 105 shows that the environmental conditions were not exceptionally different compared to the other sites such as Colomera cave level CE-15, the upper level of Toll cave, as well to the older levels of Xaragalls cave C4 and C3. It is indicated by the remarkable proportion of rocky habitat, the low temperature and the high precipitation rates that are still maintained in this level. This pattern might correspond to several abrupt climatic events during the period of 15.5–10.2 ka cal BP, such as Older Dryas (GI-1d) and Inter-Allerød Cold Period (GI-1b).

Finally, those patterns observed in the Cudó cave small mammal assemblages provide some global-to-regional climatic insights. First, consistent with previously published works, the HE3 and HE2 were cold and humid periods in north-eastern Iberia, with more severe climatic conditions than the HE4. Second, the environmental conditions in this area could have been more diverse despite the similar Mediterranean affected climate. Moreover, the environmental improvement after 15 ka as it seen in many studies does not appear so significant in all areas and within all proxies. Instead, the climatic changes were responded to differently depending on the proxies and the geographical area.

To sum up, this work advises to enlarge the taphonomic study in order to complete the taphonomic characterisation on the small mammal assemblages from this site and finally evaluate the ecological biases. With a similar goal, studies on other environmental proxies of Cudó cave, such as pollen, charcoal or phytoliths analysis, large vertebrate studies and the sedimentological analysis will be helpful to characterise the site. A better understanding of this site will be useful in a larger geographical scope than local studies, considering the scarcity of environmental data linked to the LGM context in north-eastern Iberia.

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8. Conflicts of interest

None.

9. Authors' contributions

Conceptualisation, investigation, data collection and formal analysis were mainly performed by D.Q. Arjanto. M. Fernández-García and J.M. López-García were actively involved in the conceptualisation, formal analysis, investigation, resources and writing and editing of the original draft. J.M. Vergès provided guidance in the conceptualisation, resources and reviewing–editing the manuscript. The first draft of the manuscript was written by D.Q. Arjanto and all authors commented on previous versions and approved the final manuscript.

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