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Combined palaeoecological methods using small-mammal assemblages to decipher environmental context of a long-term Neanderthal settlement in northeastern Iberia

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a b s t r a c t

Recurrent long- and short-term Neanderthal occupations occurred in the Abric Romaní rock shelter (Capellades, Barcelona, Spain) for more than 20,000 years. This provides an opportunity to enhance our understanding of the evolution of behavioral strategies of these human groups. The site has a long and high-resolution sequence with 17 levels completely excavated, 13 of which are presented in this work, from D to Q; ca. 40e60 ka. These levels have generated extensive research concerning Neanderthal hunting strategies, lithic production, and fire technology. Here is presented the evolution of palaeoenvironment under which these populations lived applying different methods of palaeoecological reconstruction based on small-mammal remains along the entire sequence. The study is completed with taphonomic analyses that locate the primary origin of their accumulation under the action of owls and describe a past humid fossiliferous microenvironment where intense human occupation occurred. Oxygen isotope analyses were performed on rodent incisors from the richest levels (D, E, N and O), in order to reconstruct the past air temperatures. The medium to low intra-level ranges of oxygen isotopic values indicate a period of preferential accumulation moment of small mammals, which is likely related to spring-summer predator activity. Throughout the sequence, the landscape evolution is marked by an extended forest cover and abundant water resources, both integrated in a patchy landscape. Climatic conditions were globally cooler and slightly wetter than present, but rather stable across the sequence. The greater relative presence of mid-European small-mammal species and the estimated lower palaeotemperatures correspond to relatively cooler episodes, such as stadial events, in levels E and O. However, certain discrepancies in palaeotemperature estimations are detected between oxygen isotopic analyses and other methods based on species occurrence. Northeastern Iberia environmental conditions related to Mediterranean climate provide a favorable MIS 3 scenario compared to European higher latitudes. Indeed, the milder glacial fluctuations detected within the Abric Romaní site are coeval to other

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1. Introduction

Neanderthal settlements in Iberia took place between the end of the Marine Isotope Stage 5 (MIS 5) and the MIS 3 (Arsuaga et al., 2012b, 2012a; Finlayson et al., 2006; Higham et al., 2014; Lorenzo et al., 2012; Maroto et al., 2012). Some Iberian archaeological sites show evidence of short- and long-term occupations of these human groups, allowing us to understand their livelihood strategies (e.g., Daura et al., 2010; Maroto et al., 2012; Rosell et al., 2010; Soler et al., 2014; Vallverdú et al., 2014; Zilhão, 2006). The ecological framework in which these populations established repeated occupations is essential to understand their adaptive behaviour. Indeed, a causality between millennial-scale climate cycles and the replacement of Neanderthals by modern humans in Eurasia was tentatively suggested (e.g., D'Errico and Sánchez Goni, 2003; Sepulchre et al., 2007; Staubwasser et al., 2018; Wolf et al., 2018). There were three Heinrich Stadials (HS5-HS3) and fourteen interstadials (GI17-GI4) during MIS 3 (North Greenland Ice Core Project members, 2004; Rasmussen et al., 2014; Svensson et al., 2008; Wolff et al., 2010). Globally, cool and dry climates were identified in Western European sequences during stadials (GS) while the climate was warmer and more humid during GI (Fletcher et al., 2010; Moreno et al., 2014). These environmental shifts modify the vegetation structure, the faunal composition and the availability of specific resources and then conditionate the mobility patterns and the feeding strategies of each hunter-gatherer group (Butzer, 1989; Lyman, 2017; Wilson et al., 1999). Rapid climate changes could weaken Neanderthals population if these regional groups were not able to quickly modify their adaptive strategies and adapt them to new ecological contexts.

Marine climate records are the main source of high-resolution climatic information in southwestern Europe and provide important insights into rapid glacial changes (Fletcher et al., 2010; Fletcher and Sánchez Goni, 2008; Moreno et al., 2014; Rasmussen et al., 2014; Roucoux et al., 2001; Staubwasser et al., 2018), in response to Dansgaard-Oeschger (D-O) cycles (Dansgaard et al., 1982; Johnsen et al., 1992; Rasmussen et al., 2014). However, the expressions of D-O scale changes differ from region to region and climatic changes had different repercussions on marine and continental domains (Fletcher et al., 2010). Moreover, there is a lack of quantitative data from the marine domain during the last stages of MIS 3 in the Mediterranean region (Moreno et al., 2014), with cores fairly located from northeastern Iberia, representing a major limitation for understanding abrupt climate variability associated with D-O cycles and their correlation with archaeological contexts inland. Some good testimonies of the continental domain are the small mammals collected in archaeological sites, which are strongly dependent of its environment, and can improve our knowledge of inland environments at local and regional scales (e.g., Chaline, 1972; Cuenca-Bescòs et al., 2011; López-García, 2011; Royer et al., 2016). Furthermore, geochemical approaches based on stable oxygen isotope compositions of phosphate ($d^{18}O_p$) obtained from vertebrate teeth have been recently developed for rodent remains, which allow some climatic parameters to be quantified (García-Alix, 2015; Jeffrey et al., 2015; Longinelli and Nuti, 1973; Navarro et al., 2004; Royer et al., 2013a). Combining palaeoecological data inferred from small-mammal assemblage methods with geochemical approaches offers the opportunity to reconstruct both environmental and climatic conditions (Royer et al., 2013b;

Fernández-García et al., 2019).

The high-resolution stratigraphy from the Abric Romaní rock-shelter, complemented with different dating methods, along with the exceptional preservation of materials at this site, provide detailed knowledge of subsistence strategies of groups of Neanderthals well-settled in this region. The aim of this paper is to evaluate the environmental evolution that framed the subsistence of these populations based on all available small-mammal assemblage data (historical and new). A taphonomic analysis was performed in order to detect and quantify the variations in composition of small vertebrate communities, and the potential impacts of depositional and post-depositional processes. Oxygen isotope analyses were performed on murid teeth to quantify past temperature changes. Furthermore, the Abric Romaní sequence constitutes a methodological challenge for testing and comparing different environmental proxies, not only because several studies have focused on the environmental features of this rock-shelter, including charcoal, pollen or dental wear analyses (e.g., Allué et al., 2017; Biltekin et al., 2019; Burjachs et al., 2012; Burjachs and Julià, 1996, 1994; Rivals et al., 2009; Vaquero et al., 2013), but also because the different aspects of human behaviour have been studied in each of its levels through analyses of lithic and large mammal assemblages or combustion structures (e.g., Allué et al., 2017; Bargallo et al., 2016; Fernández-Laso et al., 2010; Gabucio et al., 2017; Gómez de Soler, 2016; Marín et al., 2017a; Romagnoli et al., 2018; Vallverdú et al., 2012; Vaquero et al., 2012).

2. The Abric Romaní sequence

The Abric Romaní archaeological site is a rock-shelter in the Quaternary travertine cliff formation known as "Cinglera del Capelló", near the town of Capellades (Barcelona, Spain). The coordinates are $41^{\circ}32'N$ and $1^{\circ}41'03''E$ and the altitude is 280 m a.s.l. (Fig. 1A). The site is located 70 m above a narrow gorge of the Anoia river, which constitutes a strategic passage between inland mountains and the coastal plain (Carbonell et al., 1996; Fernández-Laso et al., 2010; Vallverdú et al., 2012). Capellades is located in an area currently included into the continental sub-humid Mediterranean climate (Servei Meteorològic de Catalunya, 2018). The climate is generally warm and temperate with mean annual temperatures around 14 °C, hot summers (21e23 °C), cool winters (7e8 °C) and a large thermic annual oscillation of 15 °C. The amount of mean annual precipitation ranges from 550 to 650 mm. The wet seasons are spring and autumn, while winter and summer are relatively dry (Climate-Data.org, 2018; Servei Meteorològic de Catalunya, 2018) (Fig. 1B).

Ongoing excavations at the Abric Romaní started in 1983, since then the full extent of the rock-shelter surface (around 250e300 m²) has been excavated (Bartrolí et al., 1995; Carbonell et al., 1996, 1994; Chacón et al., 2013). The excavated stratigraphy is made up of 20 m of well-stratified travertine sediments, including seventeen sedimentary levels (labeled from A to Q) (Fig. 1C). These levels belong to the Middle Palaeolithic, except the uppermost Level A which is assigned to the Proto-Aurignacian (Carbonell et al., 1996; Giralt and Julià, 1996; Vaquero and Carbonell, 2012; Vaquero et al., 2013). Dates obtained by U-series and ¹⁴C AMS provide a chronological sequence ranging from ca. 40 ka (Level A) to ca. 60 ka (on the current base of excavation) (Bischoff

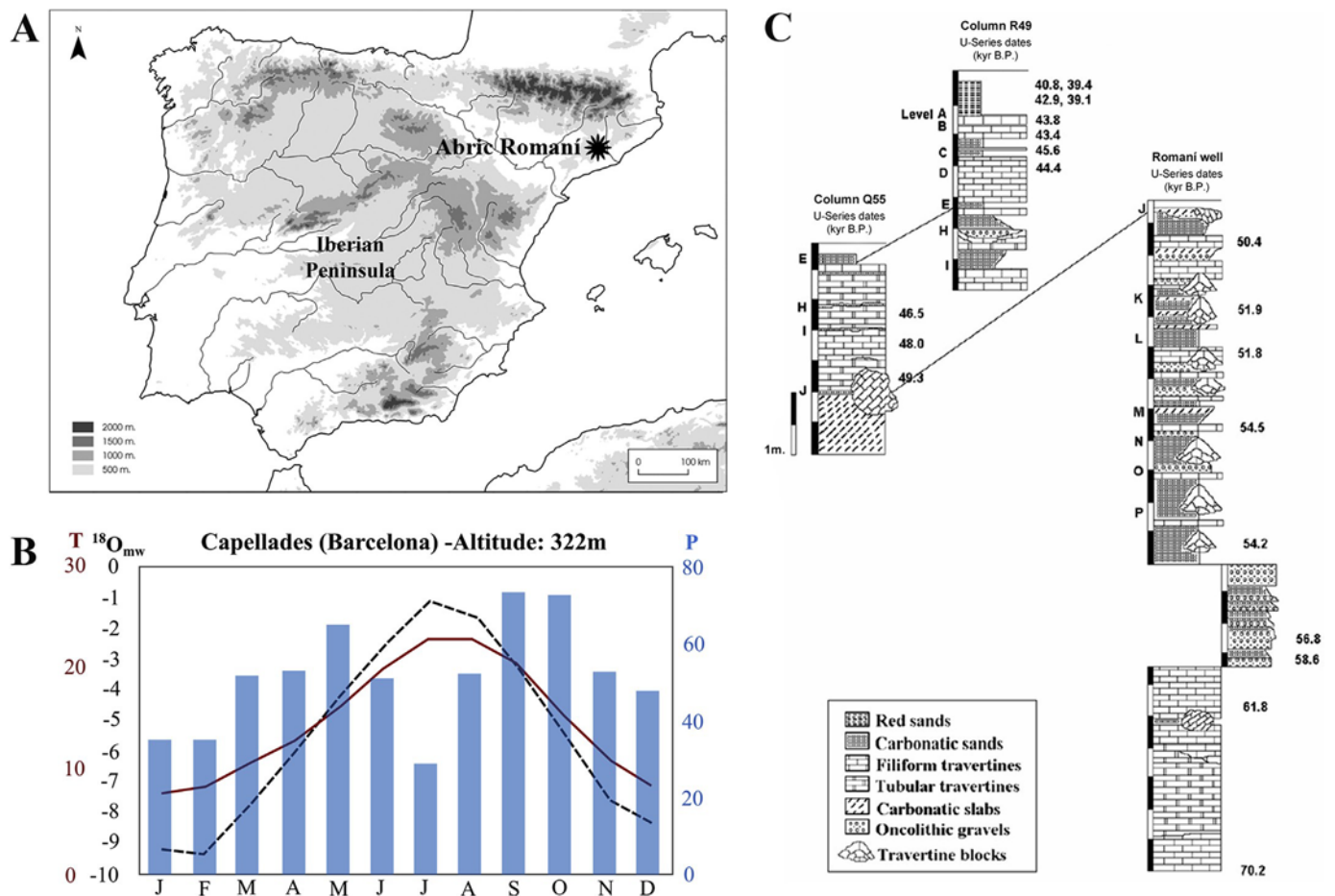


Fig. 1. (A) Location of the Abric Romaní site in Iberia; (B) Current monthly temperatures (red line; T; in °C) and precipitations (bars; P; in mm)(Climate-data.org) and present-day oxygen isotope composition of meteoric waters (dash black; $d^{18}O_{mw}$; in ‰ V-SMOW) (Bowen, 2017) of Capellades; (C) Stratigraphy of Abric Romaní with U/Th dates (Bischoff et al., 1988). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

et al., 1994, 1988; Vaquero et al., 2013). An exploratory drilling has suggested that the archaeological stratigraphy extend at least 30 m below levels excavated to date, reaching ~110 ka (U-series dates) at the base of the core (Sharp et al., 2016). The travertine formation is associated with a waterfall system that was intermittently active during the Pleistocene, which connected regional aquifer springs with the Anoia river. Rock fragmentation as well as alluvial and biochemical sedimentary processes have generated beds of consolidated stones, gravels, calcarenites and calcilutites interleaved with sandy and well-delimited thin archaeological levels (Bischoff et al., 1988; Vaquero et al., 2013).

The different archaeological levels of the Abric Romaní sequence are the result of the accumulation of an unknown number of occupational events, distinguishing between long-term and short-term (and/or non-residential) occupations events (Chaçon et al., 2013; Picin and Carbonell, 2016; Vallverdú et al., 2005a, 2010; Vaquero et al., 2012). Lithic assemblages are typical of Middle Palaeolithic sites and are mainly composed of flakes, whereas cores and retouched flakes are scarce (Bargalló, 2014; Chaçon et al., 2007; Chaçon and Fernández-Laso, 2007; Picin et al., 2014; Vaquero, 2008; Vaquero et al., 2001). The predominant raw material is flint from regional areas (10e30 km), but other common raw materials (such as quartz and limestone) derive from a local source (Gómez de Soler, 2016, 2007; Morant and García-Antón, 2000; Picin and Carbonell, 2016; Vaquero et al., 2012). Faunal remains are abundant in all levels and a total of thirteen taxa have been identified

(Cáceres et al., 1998; Chaçon and Fernández-Laso, 2007; Fernández-Laso et al., 2010; Gabucio et al., 2018, 2017, 2014; Marín et al., 2017a, 2017b; Rosell et al., 2012b, 2012a). Large and medium ungulates are predominant, with red deers (*Cervus elaphus/hydruntinus*) and equids (*Equus ferus*) being the most abundant species. Remains of aurochs (*Bos primigenius*) are also common. In addition, scarce remains of chamois (*Rupicapra pyrenaica*) and rhinoceros (*Stephanorhinus cf. hemitoechus*) and one element of proboscidean have been documented. The faunal record is the result of Neanderthal activities, who had primary access to animal carcasses, while carnivore's presence and activity is rare. Hearths and wood imprints have been documented at all archaeological levels. Hearths are normally reused, especially during long-term occupations (Allué et al., 2017, 2012; Carbonell et al., 1996; Carbonell and Castro-Curel, 1992; Carrancho et al., 2016; Castro-Curel and Carbonell, 1995; Solé et al., 2013; Vallverdú et al., 2012, 2010; Vaquero and Pasto, 2001).

Abric Romaní sequence has provided several environmental proxy-data through floral and faunal records with different temporal resolution. Initial pollen analyses differentiated five palynological phases throughout the sequence (Burjachs and Julià, 1996, 1994). Pollen analyses and anthracological record obtained from the site confirm the importance of the montane pine forest growing near the site and indicate that *Pinus* dominated throughout the entire sequence. Variations in minor secondary vegetation formations of Mediterranean and mid-European character have been

observed with expansions and contractions of pine trees and related thermophilous taxa (such as *Quercus* spp. or *Olea*). These fluctuations have been correlated with the succession in wet and warm or cold and arid climatic episodes (Burjachs et al., 2012). Dental wear analyses on ungulates have confirmed the presence of various biotopes near the site, in both closed and open habitats, where these animals were hunted (Burjachs et al., 2012; Rivals et al., 2009). Previous studies, both on large and small mammals, point to assemblages dominated by open forest dwellers and species requiring relative humid environments (Burjachs et al., 2012; Fernández-García et al., 2016; López-García, 2011; López-García et al., 2014). The remains of amphibians and squamate reptiles are scarce at the site (e.g., *Bufo bufo* sensu lato, *Epidalea calamita*, *Rana temporaria*), and their presence is related to a wet and cold forest environment. According to pollen analysis, periods when open-landscapes species occurred are related to stadial phases, which complemented with previous past temperatures estimations based on small-vertebrate studies, has led to climatic correlations

by Burjachs et al. (2012), Fernández-García et al. (2018), López-García (2011) and López-García et al. (2014) (Table 1).

3. Material and methods

3.1. Recovering, sampling and identification

The small-mammal remains included in this study were recovered from sediment samplings during excavation seasons between 1990 and 2017. Remains were collected by hand-picking from the sediment after water-sieved using two superimposed meshes of 5 mm and 0.5 mm. The sampling strategy consists in a random selection of 1x1 m squares dispersed over the excavated surface in each level. From a total of 7333 remains, a minimum of 500 individuals were identified, including 20 taxa identified at the species level (Fig. 2; Table 2). The taxonomic identification is based on various reference criteria (Bab et al., 2007; Chaline, 1972; Cuenca-Bescós et al., 2014; Gosálbez, 1987; López-García, 2011;

Table 1
Summary of palaeoenvironmental studies performed on the Abric Romaní sequence through different proxies. Dating information comes from Bischoff et al. (1988), Carbonell et al. (1994) and Sharp et al. (2016). Mean Annual Temperature Anomalies (MATA); Mean Annual Precipitation Anomalies (MAPA).

Level	Age (ka BP)	Pollen (Burjachs and Juliá, 1994, 1996)	Multidisciplinary approach: pollen, charcoals, dental wear and small vertebrates (Burjachs et al., 2012)	Sedimentary analyses (Vaquero et al., 2013)	Small vertebrates (López-García et al., 2014)	Charcoals (Allué et al., 2017)
Level D	Plat. Sup.: 44.4 (U-series)/Plat. Inf.: 44.9 ± 2.5 (U-series)/40.6 ± 0.9 (¹⁴ C AMS)	Palynological Phase 5 (G-A): Warm with arboreal taxa increment. Expansion of pioneer taxa (<i>Juniperus</i> , <i>Pinus</i>) and mesotermophilous taxa (<i>Quercus</i> , <i>Olea-Phillyrea</i>). Decrease of	Correlation with GI 12. Cool interstadial. Extension of pioneer trees (<i>Cupressaceae</i> and <i>Pinus</i>) and increase of termophilous taxa (<i>Quercus</i> spp. and <i>Olea-Phillyrea</i>). Small-mammal estimations (MATA ¼ -5.7/-5.4 °C; MAP ¼ β150/β60 mm)	Capelló V sequence - Romaní sedimentary unit 1 (D-B): Thick tufas and speleothems in the base indicate a warm and wet period, correlated with an ending Bond cycle.	Cool and less wet interstadial.	Dominance of <i>Pinus sylvestris</i> type. Most taxadiverse level, with mesotermophilous taxa (<i>Acer</i> , <i>Vitis</i> , <i>Quercus</i> spp., <i>Olea</i> , <i>Hedera</i>)
Level E	43.2 ± 1.1 (¹⁴ C AMS)	Asteraceae and <i>Artemisia</i>	Correlation with H55 (Ja-H). Cold phase with aridity peaks, intermediate phase of pine forest spreading. Forest steppe with grassland and xerophytic steppe elements (Asteraceae, Poaceae, <i>Artemisia</i>). Abundance of <i>Bufo calamita</i> .	Capelló VI sequence - Romaní sedimentary unit 2 (E-J): Sedimentary facies indicate interstadial conditions were dominant. Harsh conditions only in top of unit 2, irregular bed of red sands related to aeolian activity, absence of dripping and abrupt lithological change. The end of this stage is correlated with H55.	Correlation with H55. Mid-European species present.	Dominance of <i>Pinus sylvestris</i> type. Presence of <i>Rhamnus cathartica/saxatilis</i>
Level J	Plat. Sup.: 49.3 ± 1.6 (U-series)/Plat. Inf.: 50.4 ± 1.6 (U-series)/47 ± 2.1 (¹⁴ C AMS)	Palynological Phase 3 (O-J): Cold phase interrupted by warm and humid events. Dominance of <i>Artemisia</i> , Asteraceae, Poaceae and <i>Pinus</i> . Considerable oscillations in pollen curves and occurrence of mesotermophilous taxa (<i>Quercus</i> spp., <i>Olea-Phillyrea</i> , <i>Rhamnus</i>).	Correlation with D-O14 (M-J). Pine forest development and warm temperate taxa. Dental wear analysis on ungulates indicate patchy landscape. Small-mammal estimations (MATA ¼ -5.4 °C; MAP ¼ β60 mm)	Capelló VII- Romaní sedimentary unit 4 and 3 (K-O): abrupt changes from Mediterranean-type temperate groves to arid steppe. Tufa points a transition from the base of unit 3, a interstadial stage with low seasonality in dripping activities, to the higher seasonality in rainfall in top of the unit. Correlation D-O17 to D-O14.	Cool and less wet period with lower summer temperatures.	Dominance of <i>Pinus sylvestris</i> type. Presence of <i>Populus/Salix</i>
Level K	Plat. Sup.: 50 ± 1.6/Plat. Inf.: 51.9 ± 9 (U-series)				No data.	Dominance of <i>Pinus sylvestris</i> type
Level N	54.9 ± 0.1/55.1 ± 0.1 (U-series)		Correlation with GI16. Pollen records maintenance of pine forest with warm temperate taxa. Anthracology confirms predominance of pine grooves as firewoods. Small-mammal estimations (MATA ¼ -4.6 °C; MAP ¼ β75 mm)			Dominance of <i>Pinus sylvestris</i> type. Presence of <i>Populus/Salix</i>
Level O	Plat. Sup.: 54.2 ± 0.4/Plat. Inf.: 54.6 ± 0.4 (U-series)		Correlation with GS17. Open forest, grassland and xerophytic steppe elements. Small-mammal estimations (MATA ¼ -7.5 °C; MAP ¼ β350 mm)		Cold and wet period between GI14 and GI17. Mid-European taxa.	Dominance of <i>Pinus sylvestris</i> type. Presence of <i>Juniperus</i> , <i>Prunus</i> and <i>Sambucus</i> .

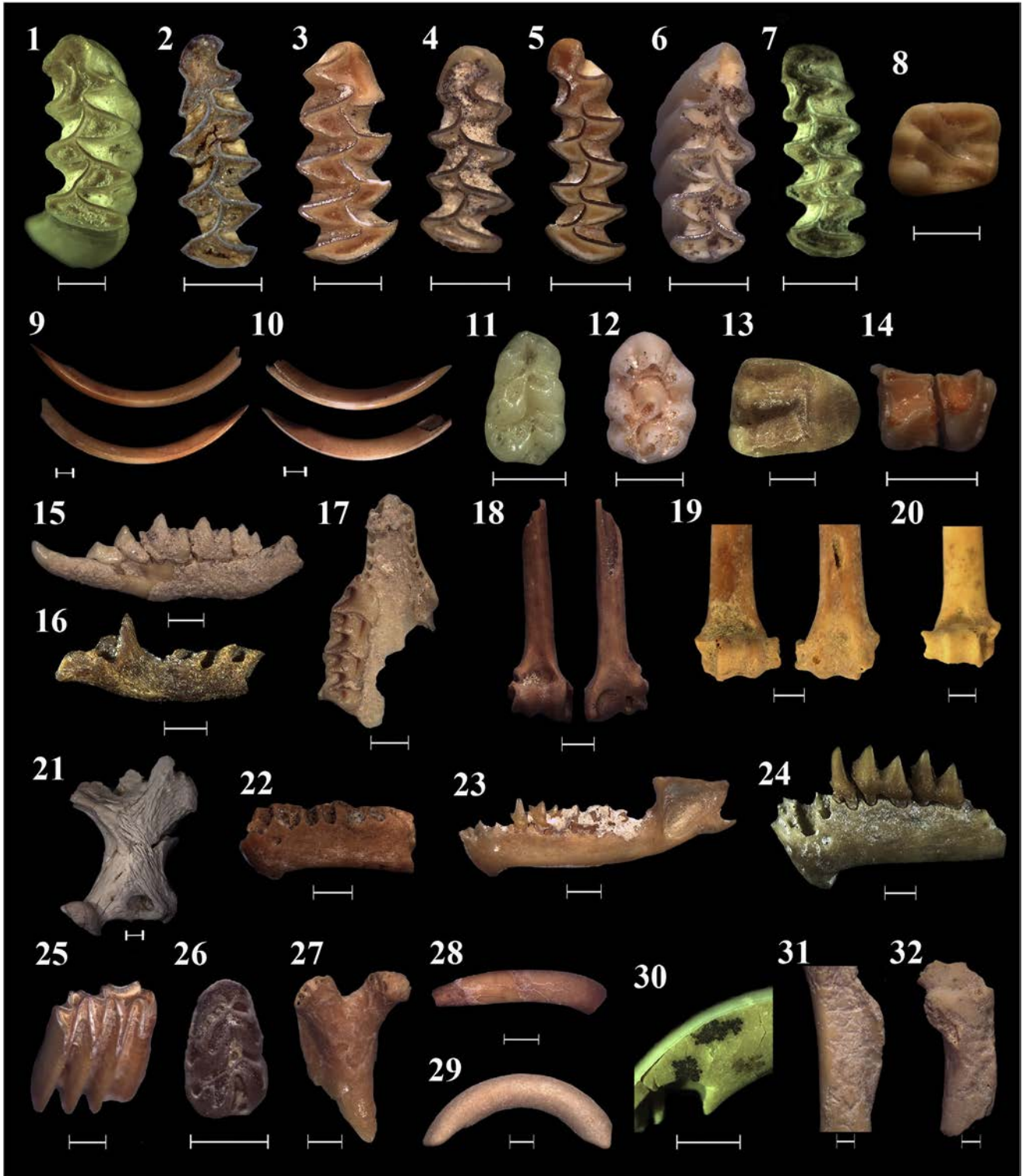


Fig. 2. Small mammals of the Abric Romani sequence and some associated taphonomic features. 1) left m1 of *Arvicola sapidus* from level O, occlusal view; 2) left m1 of *Microtus (Terricola) gerbei* from level Q, occlusal view; 3) right m1 of *Iberomys Cabrerae* from level Q, occlusal view; 4) left m1 of *Chionomys nivalis* from level E, occlusal view; 5) left m1 of *Microtus arvalis* of level H, occlusal view; 6) right m1 of *M. (T.) duodecimcostatus* from level N, occlusal view, with manganese oxide pigmentation; 7) left m1 of *M. agrestis* from level O, occlusal view; 8) left m2 of *Eliomys quercinus* from level N, occlusal view; 9) left lower incisor of Arvicolinae from level D, in labial and lingual view, used in geochemical analysis; 10) right lower incisor of *Apodemus* cf. *sylvaticus* from level D, in labial and lingual, used in geochemical analysis; 11) left m1 of *A. sylvaticus* from level O, occlusal view; 12) right M1 of *A. sylvaticus* of level N, occlusal view; 13) right M1 of *Sciurus vulgaris* from level O, occlusal view; 14) right m2 of *Myotis* sp. from level N, occlusal view; 15) left mandible of *Crociodura russula* from level E, labial view, with travertine cementation; 16) right mandible of *Sorex minutus* from level O, labial view, burned; 17) maxilla of *Sorex* gr. *araneus-coronatus* from level E, occlusal view; 18) right humerus of *Pipistrellus pipistrellus* burned from level N; 19) left humerus of *Myotis* gr. *myotis-blythii* from level D; 20) right humerus of *Plecotus* gr. *auritus-austriacus* from level E; 21) right humerus of *Talpa europaea* calcinated from level N; 22) left mandible of *Miniopterus* cf. *schreibersii* from level N, in labial view; 23) left mandible of *P. pipistrellus* from level N, in labial view; 24) left mandible of *Nyctalus lasiopterus* from level O, in labial view; 25) Arvicolinae molar with moderate digestion, level N; 26) left m1 of *A. sylvaticus* burned and with heavy digestion, level E; 27) right rodent femur with heavy digestion, level N; 28) rodent incisor with intra-mandibular digestion, level E; 29) rodent incisor completely covered by travertine patina and rounded, level E; 30) detail of dispersed manganese oxide pigmentation in a rodent incisor, level O; 31) rodent femur with generalized root corrosion, level J; 32) rodent femur with root corrosion, after round, level P. Scale 1 mm.

Table 2
Number of remains (NR) and minimum number of individuals (MNI) as a percentage of the total for the small-mammal assemblage in Abric Romaní sequence. The extended information of species occurrence can be found in Appendix B.

Recount	D		E		F		H		I		J		K		L		M		N		O		P		Q		
	NR (n)	MNI (%)	NR (n)	MNI (%)	NR (n)	MNI (%)	NR (n)	MNI (%)	NR (n)	MNI (%)	NR (n)	MNI (%)	NR (n)	MNI (%)	NR (n)	MNI (%)	NR (n)	MNI (%)	NR (n)	MNI (%)	NR (n)	MNI (%)	NR (n)	MNI (%)	NR (n)	MNI (%)	
<i>Crociodura russula</i>	3	4	2	2.1					1	14.3											9	1.1					
<i>Sorex gr. araneus-</i> <i>coronatus</i>			1	2.1																	3	0.7					
<i>Sorex minutus</i>																					1	0.4					
<i>Neomys gr. fodiens-</i> <i>anomalus</i>																					10	0.7					
<i>Talpa europaea</i>											2	5.6					21	40	7	7.7	31	2.5			4	7.1	
Soricidae indet.	2		4						1		6		1							5	12		2		4		
Myotis sp.																				1	2.6						
<i>Myotis gr. myotis-blythii</i>	3	4																									
<i>Miniopterus cf.</i> <i>schreibersii</i>																					1	2.6					
<i>Plecotus gr. auritus-</i> <i>austriacus</i>			4	8	4.3																						
<i>Pipistrellus sp.</i>				1	2.1																						
<i>Pipistrellus pipistrellus</i>																					7	5.1	1	0.4			
<i>Nyctalus lasiopterus</i>																					2	0.4					
Chiroptera indet.	7		5																		4	1				1	
<i>Arvicola sapidus</i>	35	21	19	6.4	2	100	11	40	15	42.9	74	38.9	210	61.1	26	57.1	21	40	54	15.4	266	19.9	59	72.7	12	14.3	
<i>Microtus arvalis</i>	3	2	7	12.8			2	40	1	14.3	4	16.7	2	5.6							54	10.9					
<i>Microtus agrestis</i>	4	4	4	8.5			1	20	2	14.3	2	5.6	1	5.6						1	2.6	45	9.1				
<i>Iberomys cabreræ</i>	14	21	1	2.1							5	16.7	3	11.1	1	14.3	1	20	11	15.4	87	16.3			12	42.9	
<i>Chionomys nivalis</i>				2.1																							
<i>M. (Terricola)</i> <i>duodecimcostatus</i>	6	8	16	2.1									4	16.7	2	14.3				10	23.1	46	9.1	1	9.1	1	7.1
<i>M. (Terricola) gerbei</i>																										2	7.1
<i>Apodemus sylvaticus</i>	74	29	75	48.9					2	14.3	6	11.1			2	14.3				41	20.5	310	25.0	7	18.2	2	14.3
<i>Eliomys quercinus</i>	14	4	17	6.4							2	5.6								12	5.1	55	2.9				
<i>Sciurus vulgaris</i>																					10	0.7				1	7.1
Rodentia indet.	410		744		4		57		21		309		110		22		19			543		1193		91		126	
Taxonomically indet.	344		385		8		4		26		175		81		2		17			126		481		26		44	
Total	919	100	1290	100	14	100	75	100	69	100	585	100	412	100	55	100	79	100	823	100	2617	100	186	100	209	100	

Menu and Popelard, 1987; Nadachowski, 1982; Sevilla, 1988; among others). Specific identifications were mainly based on the best diagnostic elements: isolated teeth for Murinae, Glirinae and Sciuridae; first lower molars for Arvicolinae; mandibles, maxilla, isolated teeth and postcranial elements for Chiroptera and Soricomorpha. All recovered remains were counted (NR), differentiating the number of identified specimens (NISP) then grouped using the minimum number of individuals (MNI) method, which involves counting the most highly represented diagnostic element while considering laterality for each species.

3.2. Taphonomic analysis

The taphonomic study is based on the observation and description of the superficial modifications of skeletal elements (Andrews, 1990; Fernández-Jalvo et al., 2016), including the differentiation between predation and post-depositional modifications. All recovered small-mammal remains from each level were included in the analysis, except in levels O and D. These levels present a high amount of small-mammal material available, thus, samples dispersed over the complete level surface were randomly selected. This study considers three main aspects to detect predation effects (Andrews, 1990; Fernández-Jalvo et al., 2016; Fernández-Jalvo and Andrews, 1992): anatomical representation, breakage, and corrosion by digestion. All the elements of a given sample were considered to determine the anatomical representation and the relative abundance index (Dodson and Wexlar, 1979). Indices that compare proportions of skeletal elements (Andrews, 1990) have been slightly modified as suggested by Royer et al. (2019), in order to standardized results, which would be comprise between 0 and 100. The main indices performed are:

- $PC/CR \frac{1}{4} [(humeri \ \& \ radii \ \& \ ulnae \ \& \ femora \ \& \ tibiae) *16] / [(humeri \ \& \ radii \ \& \ ulnae \ \& \ femora \ \& \ tibiae) *16] \ \& \ ((mandibles \ \& \ maxillae \ \& \ isolated \ molars) *10) *100$
- $F \ \& \ H/Mx \ \& \ Md \ \frac{1}{4} (femora \ \& \ humeri) / (femora \ \& \ humeri \ \& \ mandibles \ \& \ maxillae) *100$
- $R \ \& \ T/H \ \& \ F \ \frac{1}{4} (radii \ \& \ tibiae) / (radii \ \& \ tibiae \ \& \ humeri \ \& \ femora) *100$
- $Ts/Av \ \frac{1}{4} \text{ isolated teeth} / (\text{isolated teeth} \ \& \ \text{empty alveoli}) *100$

Incisors, molars, and femora of rodents, talpids, soricids, and chiropters were inspected for markers of breakage and digestion; however, only rodents were included in final analyses due to low sample sizes for other groups. Post-depositional processes were also evaluated in molars, incisors, and femora of all orders, including effects associated with roots etching, water abrasion, cementation, combustion, manganese oxide pigmentation and weathering. To identify and characterize these modifications, we used the criteria published by Shipman et al. (1984), Andrews and Cook (1985), Andrews (1990), Fernández-Jalvo (1992), Lyman (1994), Bennàsar (2010), Fernández-López (2000) and Cáceres (2002), Denys and Patou-Mathis (2004), among others.

3.3. Palaeoenvironmental and palaeoclimatic reconstruction

Several methodologies were used for reconstructing the ecological conditions during the deposition of Abric Romani. First, the species evenness and diversity were evaluated using Simpson's Diversity Index $[1 \ e \ S(ni/n)^2]$, where ni is the number of individuals of taxon i (Simpson, 1949), via Paleontological Statistics (PAST) software (Hammer et al., 2001). Secondly, landscape reconstructions were based on the Habitat Weighting Method (Andrews, 2006; Evans et al., 1981). This quantitative method is

based on the distribution of each taxon in the habitat(s) in which it is currently present on the Iberian Peninsula (Palomo et al., 2007), considering five main types: open dry, open humid, woodland, rocky, and, water. Finally, species occurrence is evaluated under chorotype classification previously established for present-day small-mammal faunas in Catalonia (López et al., 2006; Sans-Fuentes and Ventura, 2000), differentiating species with mid-European requirements (chorotype 1; C1), mid-European species tolerant to Mediterranean conditions (C2); Mediterranean species (C3) and species which in general provide limited climatic information (C4) (Appendix B).

Past temperatures and precipitations were estimated by two independent qualitative palaeoenvironmental methods: the Mutual Ecogeographic Range (MER) method (Blain et al., 2009, 2016; López-García, 2011) and the Bioclimatic Model (BM) method (Hernández Fernández, 2001; Hernández Fernández, 2007). Using MER, current species distributions (Palomo et al., 2007) are employed to locate the geographical area of intersection of fossil species assemblages; present-day climatic conditions (AEMET and IMP, 2011) of the intersecting area were used to infer mean annual temperature (MAT) and mean annual precipitation (MAP). *Iberomys cabreræ* and bat species were excluded from this analysis due to their modern distribution subordinated by anthropic factors and their little known and fragmentary distribution, respectively (Palomo et al., 2007). From the BM method, the MAT and MAP are calculated from a multiple linear regression specifically developed for the order Rodentia, based on the adscription of small-mammal species to ten different climatic zones (Hernández Fernández, 2001; Hernández Fernández, 2007).

3.4. Oxygen isotope analysis on rodent teeth: sampling and analytical techniques

Oxygen isotope compositions of 38 rodent teeth phosphate were measured. They come from levels O, N, E and D, from which eight to ten samples were selected from each layer in order to gather a representative range of samples (Lindars et al., 2001; Navarro et al., 2004; Penycad et al., 2019; Royer et al., 2013a). To avoid potential issues of interspecific variability, *Apodemus sylvaticus* remains were preferentially selected, with 34 incisors from at least 21 individuals (Table 3). Four incisors from the subfamily Arvicolinae, belonging to a minimum of four individuals, were also included. Unbroken and well-preserved lower incisors from adult rodents were preferentially selected (Barham et al., 2017; Fernández-García et al., 2019; Royer et al., 2014). The phosphate component constitutes the major source of oxygen in biogenic apatite and is less prone to mechanisms of geochemical and biological alteration (Clementz, 2012; Grimes et al., 2008; Lécuyer et al., 1999; Lindars et al., 2001), favouring the preservation of the original oxygen isotope composition at geological timescales. Nevertheless, diagenetic modification cannot be excluded in some cases, such as the processes of dissolution and recrystallization induced by microbial activity (Blake et al., 1997; Zazzo et al., 2004). On the basis of the phosphate chemical yields measured during this work wet chemistry procedure, clustered phosphorus pentoxide (P_2O_5) contents close to 35 wt% indicate that the original stoichiometry of analyzed rodent teeth was most likely preserved (Héran et al., 2010; Navarro et al., 2004; Royer et al., 2013b) (Appendix A). The absence of a significant relationship ($p > 0.05$) between the oxygen isotope composition of rodent samples and the P_2O_5 yields supports the assumption that the analyzed samples did not suffer major processes of diagenetic alteration, although it is not possible to definitively reject the possibility that unidentified factors could have altered the original isotopic signal.

Table 3
Oxygen isotope compositions of tooth enamel phosphate ($d^{18}O_p$; ‰ V-SMOW) from rodent lower incisors sampled from Abric Romani. The table includes the stratigraphic layer, identified taxa, obtained yield after the wet chemistry procedure and the conversion to the oxygen isotope composition of meteoric waters ($d^{18}O_{mw}$; ‰ V-SMOW) according to Royer et al. (2013a) oxygen isotope fractionation equation. SD, Standard Deviation.

Sample	Level	Taxon	Remain	Laterality	Location	$d^{18}O_p$ (‰ V-SMOW)	SD	$d^{18}O_{mw}$ (‰ V-SMOW)
ARD20	D	<i>Apodemus cf. sylvaticus</i>	Lower incisor	right	<i>in situ</i>	21.1	0.2	±3.0
ARD544	D	<i>Apodemus cf. sylvaticus</i>	Lower incisor	left	isolated	19.2	0.5	±4.6
ARD519	D	<i>Apodemus cf. sylvaticus</i>	Lower incisor	left	<i>in situ</i>	18.8	0.1	±4.9
ARD7	D	<i>Apodemus cf. sylvaticus</i>	Lower incisor	right	isolated	18.8	0.4	±5.0
ARD12	D	Arvicolinae	Lower incisor	right	<i>in situ</i>	18.7	0.3	±5.0
ARD6	D	Arvicolinae	Lower incisor	left	isolated	18.0	0.5	±5.6
ARD8	D	<i>Apodemus cf. sylvaticus</i>	Lower incisor	left	isolated	18.0	0.3	±5.6
ARD1	D	<i>Apodemus cf. sylvaticus</i>	Lower incisor	left	isolated	17.4	0.1	±6.0
ARD877	D	<i>Apodemus cf. sylvaticus</i>	Lower incisor	left	isolated	17.3	0.3	±6.1
ARD4	D	<i>Apodemus cf. sylvaticus</i>	Lower incisor	right	isolated	17.1	0.8	±6.3
ARE120	E	<i>Apodemus cf. sylvaticus</i>	Lower incisor	left	isolated	23.5	0.1	±1.0
ARE454	E	<i>Apodemus cf. sylvaticus</i>	Lower incisor	left	isolated	20.2	0.5	±3.8
ARE522	E	<i>Apodemus cf. sylvaticus</i>	Lower incisor	right	isolated	19.8	0.3	±4.1
ARE517	E	<i>Apodemus sylvaticus</i>	Lower incisor	left	<i>in situ</i>	19.2	0.4	±4.6
ARE2067	E	<i>Apodemus sylvaticus</i>	Lower incisor	right	<i>in situ</i>	19.0	0.4	±4.7
ARE830	E	<i>Apodemus sylvaticus</i>	Lower incisor	left	<i>in situ</i>	18.8	0.7	±4.9
ARE2060	E	Arvicolinae	Lower incisor	right	<i>in situ</i>	18.2	0.2	±5.4
ARE452	E	Arvicolinae	Lower incisor	right	isolated	17.9	0.1	±5.7
ARE2022	E	<i>Apodemus sylvaticus</i>	Lower incisor	left	<i>in situ</i>	17.8	0.2	±5.8
ARE2039	E	<i>Apodemus sylvaticus</i>	Lower incisor	right	<i>in situ</i>	16.8	0.3	±6.6
ARN36	N	<i>Apodemus cf. sylvaticus</i>	Lower incisor	left	isolated	21.4	0.5	±2.8
ARN700c	N	<i>Apodemus cf. sylvaticus</i>	Lower incisor	left	isolated	20.7	0.6	±3.4
ARN536	N	<i>Apodemus cf. sylvaticus</i>	Lower incisor	right	isolated	20.1	0.7	±3.9
ARN479	N	<i>Apodemus cf. sylvaticus</i>	Lower incisor	right	isolated	18.9	0.1	±4.8
ARN540	N	<i>Apodemus cf. sylvaticus</i>	Lower incisor	right	isolated	17.5	0.3	±6.0
ARN733	N	<i>Apodemus cf. sylvaticus</i>	Lower incisor	right	isolated	17.2	0.8	±6.3
ARN391	N	<i>Apodemus cf. sylvaticus</i>	Lower incisor	right	isolated	17.0	0.7	±6.4
ARN700b	N	<i>Apodemus cf. sylvaticus</i>	Lower incisor	left	isolated	15.7	0.3	±7.5
ARO1875	O	<i>Apodemus cf. sylvaticus</i>	Upper incisor	left	isolated	21.4	0.6	±2.8
ARO983	O	<i>Apodemus cf. sylvaticus</i>	Lower incisor	right	isolated	20.9	0.6	±3.2
ARO1049	O	<i>Apodemus cf. sylvaticus</i>	Lower incisor	left	isolated	20.5	0.2	±3.5
ARO1538	O	<i>Apodemus cf. sylvaticus</i>	Lower incisor	right	isolated	19.7	0.4	±4.2
ARO1859	O	<i>Apodemus cf. sylvaticus</i>	Lower incisor	left	isolated	19.1	0.1	±4.7
ARO1317	O	<i>Apodemus cf. sylvaticus</i>	Upper incisor	left	isolated	18.8	0.3	±4.9
ARO974	O	<i>Apodemus cf. sylvaticus</i>	Lower incisor	left	isolated	18.8	0.6	±4.9
ARO2033	O	<i>Apodemus cf. sylvaticus</i>	Lower incisor	right	isolated	18.4	0.1	±5.2
ARO2028	O	<i>Apodemus sylvaticus</i>	Lower incisor	left	<i>in situ</i>	18.2	0.3	±5.4
ARO551	O	<i>Apodemus cf. sylvaticus</i>	Lower incisor	right	isolated	16.7	0.2	±6.7

The rodent teeth were cleaned with double-deionized water in an ultrasonic bath. Then, the basal part of the enamel was discarded while the remaining part was gently crushed in an agate mortar. Enamel fragments were separated from dentine by hand-picking under a binocular microscope. The enamel tooth samples were treated following the wet chemistry procedure described by Crowson et al. (1991) and Lécuyer et al. (1993), adapted for small-sample weights (Bernard et al., 2009). This protocol is based on the isolation of phosphate ions (PO_4^{3-}) from apatite as silver phosphate (Ag_3PO_4) crystals using acid dissolution and anion-exchange resin. For each sample, around 1e3 mg of enamel powder was dissolved in 1 ml of hydrofluoric acid (2M HF) overnight. Calcium fluoride (CaF_2) residue was separated by centrifugation and the solution was neutralized by adding 1 ml of potassium hydroxide (2M KOH); then 1.5 ml of Amberlite™ anion-exchange resin was added to the solution to separate the PO_4^{3-} ions. After 24 h, the solution was removed, and the resin was eluted with 6 ml of ammonium nitrate (0.1M NH_4NO_3). After 4 h, 0.1 ml of ammonium hydroxide (NH_4OH) and 3 ml of an ammoniacal solution of silver nitrate ($AgNO_3$) were added to the solution and the samples were placed in a thermostated bath at 70 °C for 6 h, enabling the precipitation of Ag_3PO_4 crystals. Four standard samples of natural phosphorite (NBS120c) were included during each batch of wet chemistry. Oxygen isotope compositions were measured using a varioPYROcube™ elemental analyser interfaced in continuous flow

mode with an isotopic ratio mass spectrometer Isoprime™ (EA-Py-CF-IRMS technique performed at UMR5276 LGL; Fourel et al., 2011; Lécuyer et al., 2007). For each sample, five aliquots of 300 mg of Ag_3PO_4 were mixed with 300 mg of pure powder graphite loaded in silver foil capsules. Measurements were calibrated with the standard samples of NBS120c phosphorite (21.7‰; V-SMOW; Lécuyer et al., 1993), and NBS127 barium sulfate (9.3‰; V-SMOW; Hut, 1987). The average standard deviation for the Abric Romani sequence samples is $0.36 \pm 0.07\text{‰}$ (n = 48) (Table 3).

3.5. The $d^{18}O$ interpretation and palaeotemperature estimation

Oxygen stable isotope compositions in precipitation ($d^{18}O_{mw}$) are mainly the result of the combined effects of temperature and rainfall (Dansgaard, 1964; Rozanski et al., 1993). Usually, when the rainfall density is small, there is a positive correlation between temperature and $d^{18}O_{mw}$ (so-called “temperature effect”). According to Dansgaard (1964), the temperature effect occurs mainly in high and mid-high latitude continents. Considering current IAEA data-sets from Iberia, there is a strong positive relationship between $d^{18}O_{mw}$ and temperatures, both annually or monthly. On the contrary, it is observed a negative relationship between $d^{18}O_{mw}$ and the amount of precipitation, but usually weaker compare to temperature. In this approach, we assumed that the temperature effect is the dominant pattern in the $d^{18}O_{mw}$ values recorded in

northeastern Iberia during MIS3. By this reason, as general rule, we related high values of $\delta^{18}\text{O}_{\text{mw}}$ with warm and dry conditions and low $\delta^{18}\text{O}_{\text{mw}}$ values with cool and humid climate. Nevertheless, complex regional climate patterns, based primarily on air mass circulation, have been attested through recent work based on oxygen isotopes on speleothems, lake cores and loess deposits across the Mediterranean Basin during the Late Pleistocene and early Holocene (Martrat et al., 2004; Moreno et al., 2014; Raicich et al., 2003; Zanchetta et al., 2014). These movements of air masses condition the origin of the moisture source ("source effect") and the subsequent rainfall, being able to have important repercussions in the isotopic composition registered inland at regional and local scale. Past changes in rainfall density can affect local and regional isotope composition of precipitation, since when the rainfall density is very large, the temperature effect is masked and $\delta^{18}\text{O}_{\text{mw}}$ are inversely related to temperatures (so-called "amount effect"). Moreover, associated secondary factors, as "latitude effect", "continental effect" and "altitude effect" should also be considered (Dansgaard, 1964; Rozanski et al., 1993).

In parallel, rodents acquire great part of the oxygen isotope composition of their body water from various water sources, mostly of meteoric origin. The $\delta^{18}\text{O}$ of the ingested water precipitates in equilibrium (kinetic fractionation) in the phosphatic tissues of rodent teeth ($\delta^{18}\text{O}_{\text{p}}$) (Longinelli, 1984; Luz et al., 1984; Luz and Kolodny, 1985), which allows to develop quantitative approaches to past environmental conditions. Several studies point to metabolic and physiological factors (such as diet, body temperature, body mass or basal metabolic rate) and complex relationships with the environment (such as source of drinking water, seasonality, altitude or humidity levels) that have influence on the $\delta^{18}\text{O}_{\text{p}}$ preserved in rodent body tissues (Barham et al., 2017; D'Angela and Longinelli, 1990; Kolodny et al., 1983; Luz et al., 1984; Podlesak et al., 2008; Royer et al., 2013a). $\delta^{18}\text{O}_{\text{p}}$ of rodent teeth record a $\delta^{18}\text{O}_{\text{mw}}$ value that corresponds to a short time interval, in the case of murid lower incisors most likely the last two months of the individual life (Royer et al., 2013a), due to their small body size, rapid water turnover (Podlesak et al., 2008), continuous incisor growth (Klevezal, 2010), and rapid tooth mineralization (Hillson, 2005). In case of predation, the $\delta^{18}\text{O}_{\text{p}}$ should reflect the $\delta^{18}\text{O}_{\text{mw}}$ at the time and space each rodent was captured (Fernández-García et al., 2019; Peneycad et al., 2019; Royer et al., 2013a, 2013b).

This work follows the three-step strategy proposed for $\delta^{18}\text{O}_{\text{p}}$ from rodent tooth accumulated in Iberia (Fernández-García et al., 2019) for estimating mean annual temperatures (MAT):

- 1) calculation of $\delta^{18}\text{O}_{\text{mw}}$ from $\delta^{18}\text{O}_{\text{p}}$ throughout the linear oxygen isotope fractionation equation determined by Royer et al. (2013a) [$\delta^{18}\text{O}_{\text{p}} \approx 1.21 (\pm 0.20) \times \delta^{18}\text{O}_{\text{mw}} \mp 24.76 (\pm 2.70)$];
- 2) application of seasonality correction from a linear regression, when occurred predatory bias of rodent assemblages towards air temperatures of the spring-early summer months [$\delta^{18}\text{O}_{\text{mw}} (\text{annual mean}) \approx 1.04 (\pm 0.05) \times \delta^{18}\text{O}_{\text{mw}} (\text{March-June mean}) - 0.86 (\pm 0.28)$];
- 3) calculation of air temperatures from $\delta^{18}\text{O}_{\text{mw}}$ using a linear regression model specific to Iberia [MAT (°C) $\approx 2.388 (\pm 0.10) \times \delta^{18}\text{O}_{\text{mw}} \mp 28.19 (\pm 0.58)$].

One additional correction should be performed before $\delta^{18}\text{O}_{\text{mw}}$ values can be quantitatively estimated related to sea level fluctuations, ice masses extent and the influence that these oscillations have in the oxygen isotope compositions of the oceans (Shackleton, 1987; Zachos et al., 2001). During the Last Glacial Maximum, the sea level was 120 m below present-day sea level, which involved an increase in the global $\delta^{18}\text{O}$ of seawater around 1‰ (Schrag

et al., 2002). During MIS 3 sea level was around 25e75 m lower than present-day (Chappell and Shackleton, 1986) and Catalan Coast was estimated roughly 4e12 km further away (López-García et al., 2008). If the estimation established by Schrag et al. (2002) holds for past chronologies, the MIS3 sea level descent may have contributed to an increase in the global $\delta^{18}\text{O}_{\text{mw}}$ not above 0.6‰. Present-day $\delta^{18}\text{O}_{\text{mw}}$ values were obtained using the Online Isotopes in Precipitation Calculator (OIPC; Bowen, 2017) based on datasets collected by the Global Network for Isotopes in Precipitation (IAEA/WMO, 2018).

4. Results and discussion

4.1. Origin of small-mammal accumulation in the Abric Romaní

A total of 7333 small-mammal remains have been analyzed while 6517 of them have been analyzed for taphonomic approach. In each subunit, between 80% and 85% of total remains was anatomically identified. Fragmentary and uneven representation of remains was detected along the sequence. Some levels contained a low number of remains (Table 2). Only levels O, N, K, J, E, and D, present NR (>400) and MNI (>15) high enough to perform reliable taphonomic interpretations. The most abundant small-mammal assemblages were found at levels O, D and E, whereas low sample sizes at levels K and J preclude any robust interpretations. Rodents are the most represented order, with abundance varying between 82% (level N) and 96% (level O). Among these rodents, remains comprise mostly arvicolins and murins and, occasionally, glirids and sciurids. A minimum of 27 individuals from the Soricidae and Talpidae families were recovered in total, with relative abundances ranging from 2.5% (level O) to 7.7% (level N). Similarly, remains from the order Chiroptera were only recovered from levels O, N, E and D, with a total minimum number of 13 individuals and with a relative abundance comprised between 0.8% (level O) and 10.3% (level N) (Table 2).

The levels with better relative presence of skeleton elements are J and E, with a total relative abundance of elements up to 60%; on the contrary, level O presents the major disequilibrium between identified individuals and preserved remains of these individuals (29.6%) (Table 4; Appendix C). Indices comparing cranial and postcranial elements indicate equivalent proportions, only except by level K, which show a higher representation of cranial elements. Proximal elements are more abundant than distal ones (<44%). Indeed, humeri and femora are better preserved than mandibles and maxillae, except in level K. The proportion between isolated teeth and empty alveoli highlights the destruction of mandibles and maxillae in level O, N and K. In addition, a disproportion between incisors and molars is detected in all levels, with the former clearly overrepresented, indicating a significant loss of molars. Molars of arvicolids are more easily detached from their alveoli than the incisors, and breakage of lost teeth is usually greater than molars preserved *in situ* (Bennasar et al., 2016; Fernández-Jalvo, 1992). Most recovered teeth in these assemblages are isolated, especially in levels O and N, where less than 6% of molars and 2% of incisors were found in their alveolar place. The molars preserved *in situ* were most commonly those of murids, which have rhizodont teeth. At all studied levels, total breakage was 45% for incisors and >90% for femora. Molar breakage was more variable, with the highest rates being present at levels O and N (>40%) to the lowest rates at <13% in levels K, E, and D. Breakage and anatomical representation rates are not coincident with any predator profile (Andrews, 1990, Fig. 3). However, such discrepancy with modern collections is common in archaeological contexts where palimpsests and long-term post-depositional processes have occurred.

Table 4
Summary of analyzed taphonomic variables, including recounts (NR, number of remains; NISP, number of identified specimens; MNI, minimum number of individuals of order Rodentia considered in skeletal representation), modifications caused by predation (skeletal representation, proportional representation indices, breakage and digestion) and post-depositional modifications. Discrepancies with [Table 2](#) are explained due to elements in NR and NISP here are considered independent regardless of whether they are *in situ* or isolated (e.g. each tooth on a mandible is counted here as a single remain).

	O		N		K		J		E		D	
	n	%	n	%	n	%	n	%	n	%	n	%
Recount												
NR (n)	2268		827		419		667		1390		946	
NISP (n)	1874		712		363		589		1131		781	
Rodentia NISP (n)	1676		629		279		366		825		483	
Rodentia MNI (n)	149		32		18		17		42		33	
Skeletal representation												
Relative Abundance Index (%)	29.6		54.6		38.3		67.7		61.9		42.8	
SD of Relative Abundance Index	26.6		64.8		27.2		31		29.1		19	
Proportional representation indices												
PC/CR Index	41		47		33		56		56		48	
FpH/MxpMd Index	55		67		36		61		56		48	
RpT/HpF Index	44		39		43		42		43		35	
Ts/Av Index	67		65		58		51		50		48	
Breakage												
Incisors fracture (%)	67.3		68.2		47.8		62.5		48.7		59.4	
Molars fracture (%)	41.3		50.5		9.2		23.7		12.6		12.9	
Femora fracture (%)	98.2		100		100		90.9		93.3		100	
Digestion												
Total of digested elements	399	39.6	152	37.5	14	8.4	60	31.9	113	25.9	46	17
Light	275	27.3	121	29.9	8	4.8	33	17.6	64	14.6	32	11.8
Moderate	101	10	27	7	5	3	17	9	28	6	8	3
Heavy	23	2.3	4	1	1	0.6	10	5.3	21	4.8	6	2.2
Extreme	0	0	0	0	0	0	0	0	0	0	0	0
Digested incisors	151	40.5	109	50.2	4	8.3	18	35.3	45	28.3	11	13.8
Light	115	30.8	93	42.9	1	2.1	11	21.6	29	18.2	9	11.3
Moderate	30	8	14	6.5	2	4.2	4	7.8	10	6.3	2	2.5
Heavy	6	1.6	2	0.9	1	2.1	3	5.9	6	3.8	0	0
Extreme	0	0	0	0	0	0	0	0	0	0	0	0
Digested molars	191	33.4	33	19.6	9	8.1	29	26.4	51	22.1	23	14.4
Light	119	20.8	20	11.9	7	6.3	12	10.9	22	9.5	12	7.5
Moderate	55	9.6	12	7.1	2	1.8	10	9.1	14	6.1	6	3.8
Heavy	17	3	1	1	0	0	7	6	15	6	5	3
Extreme	0	0	0	0	0	0	0	0	0	0	0	0
Digested femora	57	90.5	10	50	1	12.5	13	48.1	17	36.2	12	38.7
Light	41	65.1	8	40	0	0.0	10	37	13	27.7	11	35.5
Moderate	16	25.4	1	5	1	12.5	3	11.1	4	8.5	0	0
Heavy	0	0	1	5	0	0	0	0	0	0	1	3
Extreme	0	0	0	0	0	0	0	0	0	0	0	0
Post-depositional agents												
Cracking for humidity and temperature changes	910	68.6	238	46.5	28	14.4	64	27.5	114	21.8	50	15.3
Desquamation	92	6.9	3	0.6	0	0	0	0	0	0	0	0
Cementation	175	13.2	15	2.9	26	13.3	13	5.6	49	9.4	11	3.4
Manganese oxide pigmentation	621	46.8	159	31.1	21	10.8	70	30	233	44.6	61	18.7
Plant Activity	600	45.2	138	27.0	44	22.6	130	55.8	134	25.7	126	38.5
Water abrasion	73	5.5	8	1.6	1	0.5	4	1.7	8	1.5	2	0.6
Burned	192	14.5	32	6.3	0	0	6	2.6	60	11.5	9	2.8
Weathering	3	0.2	0	0	0	0	0	0	0	0	0	0

Digestion observed in these levels ranges between 8.4% at level J to 39.6% at level O ([Table 4](#)). Different degrees of digestion from light to heavy were observed. Remains without digestion marks predominate the sample collection, while light degree of digestion is the most frequent pattern and extreme digestion was not detected. Based on these observations, and despite the breakage rates at some levels, the potential presence of predators in Category 4e5, such as diurnal raptors or small carnivores ([Andrews, 1990](#); [Fernández-Jalvo and Andrews, 1992](#); [Terry, 2007](#)) can be excluded ([Fig. 3](#)). Two different trends can be distinguished. In levels O and N, at least 35% of the elements exhibit digestion marks: 40e50% of incisors, 19e33% of molars and 50e90% of femora. The predominant digestion marks are light in degree (27e30%), but a significant presence of moderate (7e10%) and some heavy digestion marks (1e2%) are also observed. Otherwise, in levels E and D digestion affects less than 25% of remains: 14e22% of incisors, 14e28% of molars and 36e38% of femora. With respect to levels O and N, we

observed a decrease in remains with evidence of light digestion (12e15%). Level J is characterized by an intermediate position between these two types of assemblages (32% of total elements with digestion). Some digestion was detected in soricids from levels N and O and in chiropters from level N. Though their presence is scarce, it is most likely that soricids, talpids and bats were occasionally preyed by same rodent predators ([Fernández-Jalvo and Andrews, 1992](#); [Kowalski, 1995](#)).

The origin of the small-mammal assemblages is most likely related to predator activity as suggested by the alteration patterns caused by digestion. Level O small-mammal remains were already related by [Fernández-García et al. \(2018\)](#) to the action of nocturnal raptors in the intermediate category of modification (Category 3 considering digestion; [Andrews, 1990](#)), most likely the tawny owl (*Strix aluco*). The high rates of breakages, the proportion of digested dental elements and the presence of some strongly digested teeth in level N point to the same kind of predator, and fit with the

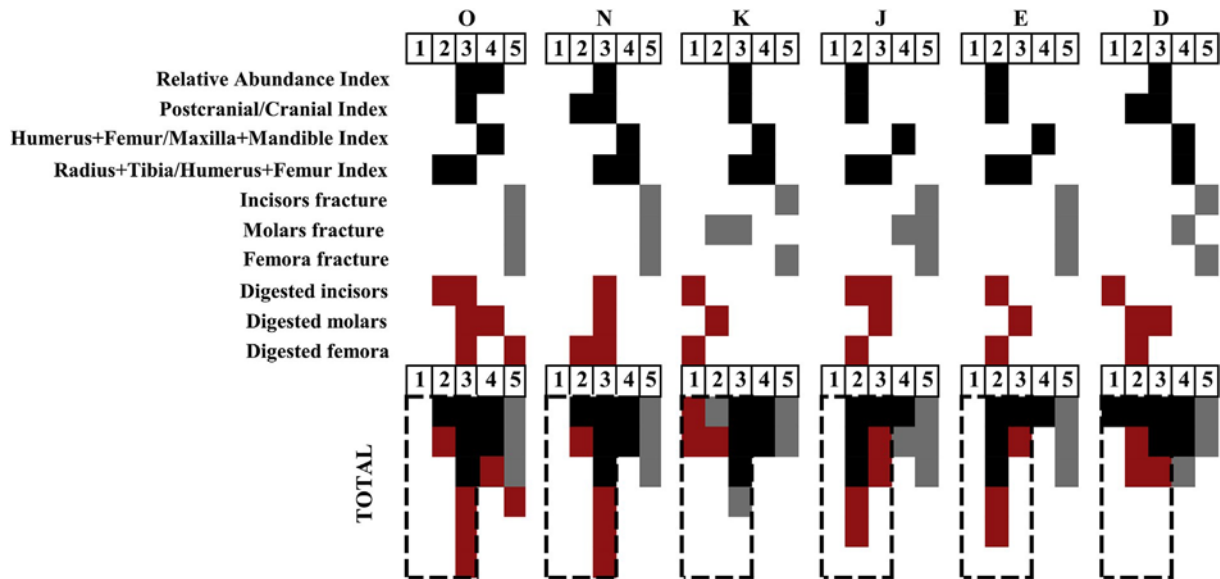


Fig. 3. Predator categories obtained for the different taphonomic variables considered in analyzed levels. Each taphonomic variable is assigned to a category (from 1 to 5) according to Andrews (1990) classification and Fernández-Jalvo et al. (2016) revision. Black squares, postcranial representation indices; grey squares, breakage; red squares, digestion. Each level total is the sum of each category. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

expected values for the tawny owl (Andrews, 1990; Andrews and Fernández-Jalvo, 2018; Comay and Dayan, 2018; Fernández-Jalvo et al., 2016; Fernández-Jalvo and Andrews, 1992). The progressive proportion of digestion degrees and the coherence between the proportion and degrees of digestion observed in small-mammals remains from levels O and N, indicates that these modifications are most likely due to a single kind predator (Bennasar, 2010; Bennasar et al., 2016). This pattern is not evident in upper levels (K, J, E and D) where the quantity of digested remains is incompatible with the heavy degrees of digestion reached. Indeed, equal ratios of digested molars and incisors observed in these levels are rare considering modern collections (Andrews, 1990; Fernández-Jalvo et al., 2016). Whereas some indices of anatomical representation, proportions of digested incisors and the detection of some incisors retained during digestion point to a Category 2 predator (such as *Asio otus*), the proportion of digested molars and the degrees of digestion attained suggest a Category 3 predator (such as *Bubo bubo* or *Strix aluco*). These discrepancies suggest that these small-mammal assemblages are the result of a mixture of light and intermediate modification predators. It is possible that the actions of *Strix aluco*, detected in levels O and N, continue in upper levels, but the intervention of another predator type that inflicts less damage on bones obscures the proportion of digested elements. *Asio otus* is a good candidate, as it tends to inflict light modification on dental remains, but higher than other owls of this category. It is also characteristic the retention of incisors inside mandibles during digestion, detected in some incisors of level E (Andrews, 1990). The large sample presented in this work provides enough evidence to rule out the preliminary attribution to Category 1 predators (such as *Asio otus* or *Tyto alba*) as the main small-mammal accumulators in some levels of the Abric Romaní sequence (Allué et al., 2012; Burjachs et al., 2012; López-García et al., 2014), at least in exclusivity; but confirms the frequentation of nocturnal birds of prey to the rock-shelter.

The tawny owl (*Strix aluco*) is a sedentary predator that is strongly territorial. It usually places its nest in tree holes, cliffs, or rocky walls, which are reused year after year. It is a typical generalist and opportunistic hunter, including in its diet whatever is available in its hunting territory, which usually comprises an area

between 1 and 3 km². Its prey assemblages are highly diverse and reflect the local ecological variability of its nesting area. Forest and semi-open forest are its preferential habitats, but it can also be found in riversides and open landscapes located near forests or in rocky areas (Andrews and Fernández-Jalvo, 2018; Arribas, 2004; Manzanares, 2012; Mikkola, 1983; Obuch, 2011; Svensson, 2010; Yalden, 1985). The presence of this species has been confirmed in Iberia since the Early Pleistocene (Arribas, 2004) and it is currently present in the Anoia region (Jiménez, 2003). Alternatively, the action of a light modification predator (Category 2 considering digestion; Andrews, 1990), could distort the original ecological signal of its local environment through a bias in its prey assemblages. Caution should be taken in ecological interpretations deduced from prey assemblages produced by the long-eared owl (*Asio otus*), since it is considered as a selective hunter of voles and other small mammals in open country habitats, and thus does not provide a complete picture of its ecological niche (Andrews, 1990; Yalden, 1985). This owl has been present in Iberia since the Middle Pleistocene, most likely with a similar, or perhaps more southern distribution than today (Arribas, 2004; Manzanares, 2012). Moreover, this species inhabits boreal and temperate forests as well as Mediterranean and steppe areas of Eurasia (Mikkola, 1983; IUCN, 2018).

4.2. Taphonomy history of small-mammal remains in Abric Romaní

Post-depositional agents have also been evaluated (Table 4; Appendix C). Chemical corrosion related to plant activity is usually the main agent in all levels, often with a scattered distribution over the remains, affecting between 22.6% (level K) and 37.3% (level D), with an exceptional rate of 55.8% in level J. Cracking and manganese oxide stains are also common (14.4e68.6% and 10.8e46.8%, respectively). Cracking is related to fissures in the small-mammal remains, although we can detect slight striations in most of them. Precipitation of manganese oxides is common, but it appears in an isolated way, except in levels O, J, and E. Remains affected by cementation, sometimes occurring as a fine carbonated patina, extends from 2.9% (level N) to 13.3% (level K). Abrasion is present in all analyzed levels, but in a low percentage (from 0.5% to 5.5%) and

never exceeding mild degrees of polishing and rounding (P1 and R1, according to the classification of Cáceres (2002)). Some burning remains related to indirect human activity were also found (from 2.6% to 14.5%), except in level K. The degree of burning extends from weak color modifications to carbonization (levels O, N, E and D) and calcination (levels O and N) states. Other modifications such as dissolution, desquamation, or weathering are absent. None of the modifications shows a taxonomic or anatomical preference. No particular spatial distribution of modifications is detected across level surfaces, however in levels N, E, and D most of the small-mammal accumulation occurs next to shelter walls or even in rock fissures.

A homogenous pattern is identified through the post-depositional modifications observed in all studied levels. All levels show grooves and chemical corrosions produced by roots and mosses related to an open microenvironment, modifications caused by water (manganese oxide coatings) and changes in humidity and dryness (cementation and cracking). In some cases, as in level J, manganese oxide occurs inside fissures and below chemical corrosions produced by roots, indicating the order of post-depositional processes: humidity changes for water activation, followed by subsequent flooding and organic matter decomposition and posterior mosses activity. These processes are consistent with a fossiliferous rock-shelter context (Fernández-Jalvo, 1992) and the depositional fossiliferous microenvironment previously described for level O from Abric Romaní (Fernández-García et al., 2018). Such microenvironment is indeed characterized by wet conditions and weak water flows and flooding, which is expected for this kind of travertine formation (Cáceres et al., 2012; Fernández-García et al., 2018; Gabucio et al., 2012; Vallverdú et al., 2012). A different pattern for small-mammal assemblages from levels E and D was not detected, despite their different sedimentary conditions that are closer to a cave environment (Vallverdú et al., 2005b; Vaquero et al., 2013). Otherwise, levels K and D contains a lower abundance of remains with manganese oxide coating (10±18%; mainly with isolated distribution), and fewer remains affected by cracking (14±15.3%) and water abrasion (0.5±0.6%). This could indicate less humidity and stagnant water during their deposition, and consequently fewer humidity and temperature change effects. However, manganese oxide has also been related to intense human activity due to the abundant presence of organic matter (Marín-Arroyo et al., 2014). Indeed, these levels are related to short-term human occupation (Marín et al., 2017a).

The absence of notable abrasion modifications, desquamation, and weathering, and the consistence of taphonomic patterns with large mammal remains, mainly accumulated by hominins in all levels (Cáceres et al., 2012; Fernández-Laso et al., 2010; Gabucio et al., 2017, 2014; Marín et al., 2017a, 2017b; Modolo and Rosell, 2017), do not support the presence of re-sedimentation processes and fixed *in situ* production and rapid burial of the remains (Fernández-García et al., 2018). It is probable that the nocturnal raptors, identified as small-mammal accumulators, established their roosts or nests directly on rock outcrops or crevices that were part of the Abric Romaní rock-shelter (Andrews, 1990; Mikkola, 1983). The high breakage rates, cracking, molar and maxillary losses, and the predominance of isolated teeth point to high-destructive post-depositional agents, especially for levels O and N. Frequently, manganese oxide precipitation coexists with cracking and covers bone fissures, indicating that some fragmentation took place previously. One of the most common causes of high breakage is trampling by other animals, including birds of prey at their nesting sites (Andrews, 1990; Andrews et al., 2016; Lloveras and Moreno-García, 2009). Moreover, taphonomic data obtained from large-mammal remains point to a good state of bone

preservation and no differential conservation with regards to bone density, therefore suggesting that bone fragmentation can be explained by intensive human occupations and the processing of large-mammal carcasses (Fernández-Laso et al., 2010; Gabucio et al., 2012). Thus, the fragmentation and the subsequent isolated teeth recovered in small-mammal remains are probably the consequence of a combination of predator activity and post-depositional agents such as humidity changes, weak water streams or sediment compaction, but also intense human activities (such as trampling or even undirected burning).

4.3. Palaeoecological reconstruction: species occurrence, chorotypes and landscape

Along the sequence of Abric Romaní, 22 different taxa have been identified, consisting of shrews, moles, bats, voles, mice, dormice and squirrels (Table 2; Fig. 2). With respect to previous studies (Burjachs et al., 2012; López-García, 2011; López-García et al., 2014), the current research has incorporated 7199 remains and at least 427 individuals. The enlarged sample allows for the identification of species not previously recorded in some levels, and even species not previously detected in the sequence, such as *Chionomys nivalis*, *Myotis* gr. *myotis-blythii* and *Plecotus auritus-austriacus*. Nevertheless, given the fragmentary representation of remains along the sequence, only levels O, N, K, J, E and D are considered reliable for palaeoecological reconstructions. The species with a major relative abundance in the sequence are *Arvicola sapidus*, *Iberomys cabreræ* and *Apodemus sylvaticus*. In some levels there is also a moderate abundance of *Microtus (Terricola) duodecimcostatus*, *Microtus arvalis*, *Microtus agrestis* and *Talpa europaea* (Table 2). The presence of *A. sapidus*, a species commonly found near water courses, is continuous throughout the sequence, even in more impoverished levels. *A. sylvaticus*, mainly a generalist species, although with some preference for forested covertures (Blanco, 1998; Palomo et al., 2007), is present in all studied levels, except level K, with variations in its relative presence. Co-occurrence between *I. cabreræ* and *M. (T.) duodecimcostatus*, which are typical Mediterranean species, with *M. arvalis* and *M. agrestis*, which are mid-European species that preferred open environments and wetter and cooler climate, is frequent (Blanco, 1998; Palomo et al., 2007; Sans-Fuentes and Ventura, 2000). The occasional occurrences of *T. europaea* indicate the presence of moist soils, which are necessary for burrowing (Blanco, 1998; Palomo et al., 2007). None of the mid-European species found along the sequence it is nowadays recorded in the surroundings of the site but are commonly found in Iberia, mainly in higher altitudes, inland territories or areas of Atlantic influence (Gosalbez, 1987; Jiménez and Tomás, 2009; Palomo et al., 2007).

The richest levels in small-mammal remains, which are D, E, N and O, and J and K as well, scored >0.6 beyond the Simpson's Diversity Index, indicating that the species are approximately numerically equal and that no single species dominates the assemblage (Appendix D). Level O, the richest level of the sequence, presents the highest level of species evenness (15 small-mammal species) and diversity (Simpson's Diversity Index record 0.84). This level characterized by high diversity of species is consistent with an opportunistic-type predator, such as the tawny owl (Obuch, 2011), as suggested by the taphonomic analyses of some levels. Level K presents the lowest species diversity, due to the notable dominance of the water vole (>60%) and the low number of individuals recovered. Regarding chorotype classification, generalist species are predominant (>45%) in all studied levels (Fig. 4). Unfortunately, these species provide little information about climate evolution. However, slight fluctuations between Mediterranean and mid-

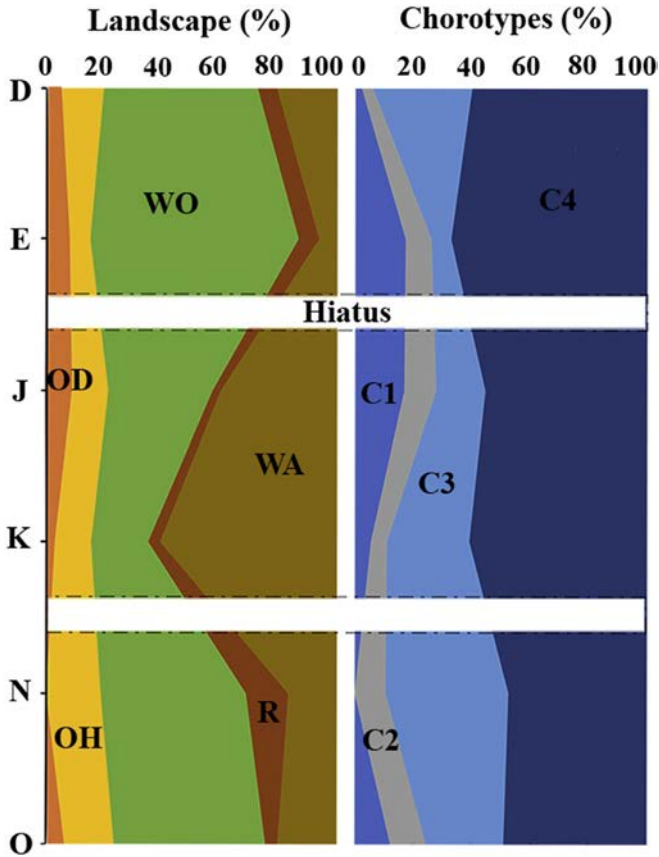


Fig. 4. Palaeoenvironmental reconstruction based on small-mammal assemblages of Abric Romani, considering chorotypes classification and landscape components. C, chorotype (1e4); OD, open dry; OH, open humid; WO, woodland; R, rocky; WA, water.

European species occur throughout the sequence. A notable increase of mid-European species and concomitant decrease of Mediterranean ones was detected in levels E and J; whereas level O has a balanced relative abundance between both groups. According to landscape evolution, the woodland component is the most notable, supporting the hypothesis of a stable open forest at Abric

Romani. Only levels J and K point some forest retreatment (<40%), however this phenomenon is only related to an increase of the open field component in level J. Otherwise, the forest environment is noticeable in level E (>70%). The water component is also constant, and its fluctuations are closely related to the abundance of the water vole, indicating the existence of water courses next to the site throughout the sequence. Finally, the open humid component points to humid meadows surrounding the site and enclosing the patchy landscape previously described (Burjachs et al., 2012); this area was mainly composed of open woodlands, grasslands, and water sources, which are optimal for human subsistence. In addition to earlier reported small-mammal data, the existence of open forest in the areas surrounding the rock-shelter is further supported by the identification of the tawny owl in the lower levels, and its possible contribution to upper ones (Arribas, 2004; Domingo de Pedro, 2011; Manzanares, 2012). The possible contribution of *Asio otus* to upper levels is expected to overrepresent open landscape species (Andrews, 1990; Mikkola, 1983).

4.4. Climatic reconstruction and palaeotemperature estimations from Abric Romani

Only the richest levels in small-mammal remains (O, N, E, and D) were used for palaeoclimatic reconstructions (MNI>35; NISP>800). The oxygen isotope compositions of the rodent incisor enamel sampled from the different studied levels of Abric Romani range from 15.7‰ to 23.5‰, representing a variation of 7.8‰ (Fig. 5; Table 3; Table 5). Both mean and median $d^{18}O_p$ values are very similar between different levels ($D < 0.4$), and no sizable differences have been observed between them (ANOVA sample test; $p > 0.01$), with values varying between 19.3‰ and 18.2‰. The oxygen isotope compositions of Arvicolinae remains included in level D and E are within the general range obtained from *A. sylvaticus* measurements and have no influence on either the mean or median values. All sedimentary layers show a normal distribution of data (Shapiro-Wilk test, p -value>0.01). Little intra-level variations are observed, ranging from 4‰ (level D) to 6.7‰ (level E). The ranges observed in levels D and E are highly skewed by one value each (21.1‰ and 23.5‰, respectively). When these values are excluded, the major amplitude is consistent with that of level N (5.7‰; SD: 2).

The low to medium $d^{18}O_{mw}$ amplitudes recorded at all levels are lower than the current seasonal amplitude for $d^{18}O_{mw}$ values at

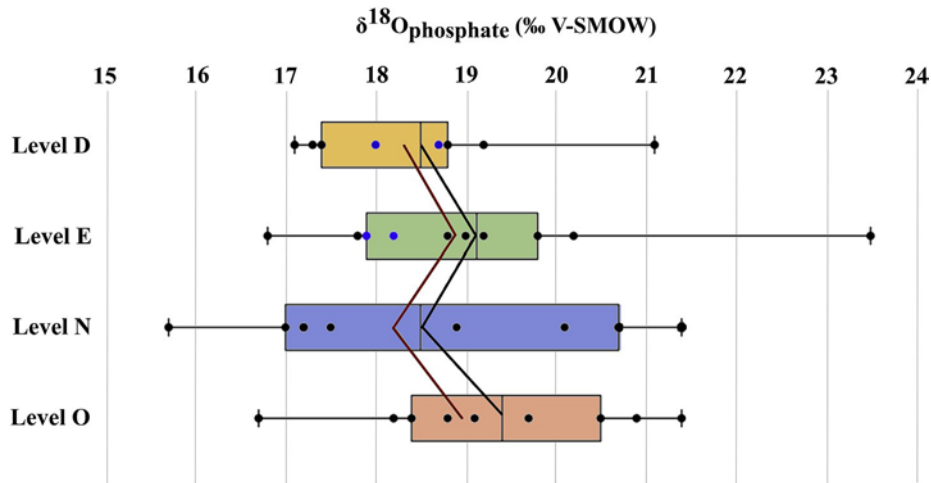


Fig. 5. Oxygen isotope compositions (‰ V-SMOW) of rodent incisor enamel from the Abric Romani samples. Box plots and distribution of $d^{18}O_p$ values per layer, with median (red line) and mean (black line) curves. Box plot bars cover the full extension of the values; the boxes extend from the 1st to 3rd quartile. Black points illustrate *Apodemus sylvaticus* and blue points Arvicolinae samples. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Table 5

Minimum, maximum, mean, median, standard deviation, and range of oxygen isotope composition of incisor enamel phosphate ($d^{18}O_p$; ‰ V-SMOW) from fossil rodents recovered from Abric Romaní sequence; conversion to the oxygen isotope composition of meteoric waters ($d^{18}O_{mw}$; ‰ V-SMOW), including minimum, maximum, mean, median and range; and, mean annual temperature estimations (MAT; °C), including seasonality and sea-level corrections of $d^{18}O_{mw}$. SD, standard deviation. MAT and Mean Annual Precipitation (MAP) estimates based on the mutual ecogeographical range (MER) and the bioclimatic model (BM) methods are also included.

	Levels	D	E	N	O
	n	10	10	8	10
$d^{18}O_p$	Min	17.1	16.8	15.7	16.7
	Max	21.1	23.5	21.4	21.4
	Mean	18.4	19.1	18.6	19.3
	Median	18.4	18.9	18.2	19.0
	Range	4.0	6.7	5.7	4.7
	SD	1.2	1.8	2.0	1.4
$d^{18}O_{mw}$	Min	-6.3	-6.6	-7.5	-6.7
	Max	-3.0	-1.0	-2.8	-2.8
	Mean	-5.2	-4.7	-5.1	-4.6
	Median	-5.3	-4.8	-5.4	-4.8
	Range	3.3	5.5	4.7	3.9
	MAT	$d^{18}O_{mw}$ - seasonality correction	-6.4	-5.9	-6.5
$d^{18}O_{mw}$ - sea level correction		-7.0	-6.5	-7.1	-6.5
MAT (°C)		11.6	12.7	11.3	12.8
SD		1.3	1.4	1.5	1.4
Error margin		2.6	2.7	2.9	2.7
MER	MAT (°C)	11.6	9.7	12.2	11.1
	MAP (mm)	981	950	925	840
BM	MAT (°C)	14.3	12.7	14.5	13.3
	MAP (mm)	1431	927	793	1286

Capellades (7.8‰; OIPC data; Bowen, 2017) (Fig. 1B; Table 5) and the average seasonal amplitude of $d^{18}O_{mw}$ values for Iberia (8‰; (Fernández-García et al., 2019). Although several spatial and temporal factors can influence oxygen isotope compositions as well as unknown diagenetic processes (Barham et al., 2017; Gehler et al., 2012; Jeffrey et al., 2015; Peneycad et al., 2019; Royer et al., 2014), these isotopic patterns suggest that only moderate variability is recorded on sampled remains and that rodent accumulation most likely occurred in similar conditions. The most parsimonious hypothesis is that analyzed rodent remains were introduced into the site during a preferential period of the year. Given the higher number of murid specimens and the observed oxygen isotope compositions of contemporaneous Iberian rodent tooth samples, spring-early summer months may have resulted in a higher probability of prey capture by owls (Fernández-García et al., 2019; Lagos, 2019; Manzanares, 2012; Norrdahl and Korpima, 2002; Royer et al., 2013a, 2013b; Salamolard et al., 2000). Past $d^{18}O_{mw}$ values interpolated have mean (from -4.5‰ to -5.2‰) and median (from -4.8‰ to -5.4‰) values that are higher than the modern mean $d^{18}O_{mw}$ values of -5.9‰ recorded at Capellades. Over-estimated mean $d^{18}O_{mw}$ values may be explained by the amount effect that operates in northeastern Iberia during spring months (Moreno et al., 2014), since intense or prolonged precipitations can produce an enrichment of $d^{18}O_{mw}$ values respect those expected only considering air temperatures. The $d^{18}O_p$ values recorded in all levels most likely do not reflect predation during the cold season because of the absence of low $d^{18}O_p$ values (<15‰) that will equiva to the low $d^{18}O_{mw}$ values (<-8‰) reach on winter months in the study region.

Taphonomic analyses suggest that the predator *Strix aluco* is most likely responsible for the rodent accumulation in levels N and O, whereas in upper levels the observed accumulation of small-mammal remains is due to the combined effect of the same kind

of predator and a light modification predator. Today, the tawny owl breeds between February and April in the Iberian Peninsula. Incubation lasts about a month, and offspring can fly after about five weeks (Manzanares, 2012). This may support the hypothesis of preferential accumulation in the warmest months. Although this species hunts small mammals throughout the year, some studies show an intensification of this activity in the breeding season (Andrews and Fernández-Jalvo, 2018; Chaline, 1974; Southern, 1954; Yalden, 1985). Southern (1954) and Andrews and Fernández-Jalvo (2018) note that small-mammal accumulation in pellets decreases in early summer in England forests, when the incorporation of high rates of insects is documented. Southern (1954) suggested that this is mainly related to the ground vegetation growth, which can hinder hunting of small mammals by their predators. However, both studies specified that the weather of each season would be determinant in terms of temperature and rainfall. Thus, the seasonal evolution of the landscape is expected to be quite different in Mediterranean areas, which tend to dryness in summer months.

The estimated MATs obtained from median $d^{18}O_p$ vary between 12.8 ± 2.7 °C (level O) and 11.3 ± 2.9 °C (level N) (Table 5; Fig. 6). These temperatures are lower than the current MAT recorded at Capellades (14.8 °C; Climate-Data.org, 2008), with mean annual temperature anomalies (MATA) ranging from -3.5 °C to -2.0 °C. Interlevel MAT differences are small (± 1.5 °C). Therefore, from the perspective of oxygen isotope compositions, a homogenous and temperate climate without notable changes is suggested. The two other methods of palaeoclimatic reconstruction, based on small-mammal assemblages (the BM and the MER methods; Appendix E and F), support negative MATAs. Magnitude of changes depends nonetheless on the method, with differences ranging from 2.2 °C to 3.0 °C between methods when applied to each of the studied levels. The BM method yields the highest air temperatures (MATAs from -0.5 °C to -2.1 °C), whereas MER estimations provide the lowest temperatures (MATAs from -2.6 to -5.1 °C). The $d^{18}O$ proxy yields intermediate temperature estimations position between both methods (Fig. 6). Oxygen isotope data are in accordance with BM temperatures for levels O and E (~13 °C and 12.7 °C, respectively), whereas MER temperatures are lower (11.1 °C and 9.2 °C, respectively). Nevertheless, these offsets remain small enough to fall within the error margin of temperatures inferred from the $d^{18}O$ of tooth enamel phosphate. Mean annual precipitation anomalies (MAPA) are globally reduced respect to present-day MAP (619 mm; Climate-Data.org, 2008). By the BM method are slightly higher (between p172/p205 mm), except for level E (-69 mm); whereas MER method no reports MAPAs for levels N (-4 mm) and D (-13 mm), but positive MAPAs for levels O (p252 mm) and E (p141 mm) (see Fig. 6).

4.5. Environmental evolution and Neanderthals subsistence during MIS 3 in northeastern Iberia

• Combined palaeoecological approaches to reconstructing the palaeoenvironmental conditions of the Abric Romaní sequence

Besides extensive dating, the high-resolution stratigraphy of Abric Romaní gives us the opportunity to evaluate the local environmental evolution conditions around the site and their variations forced by the global climatic oscillations as recorded in the Northern Hemisphere (Fig. 5; 6; Table 5). The deposition of levels O and N, regarding its chronology, occurred during D-O 14 (ca. 54-49 ka b2K) or, most likely, during D-O 15 (ca. 54e55 b2K). Both levels were included in the defined Palynological Phase 3 (ca. 57-50 ka) of the site, characterized by cyclic variations of arboreal pollen and mesothermophilous species, although interstadial conditions

prevailed (Burjachs et al., 2012; Burjachs and Julià, 1996, 1994; Vaquero et al., 2013). Level O has been confirmed as a cool phase tentatively related to GS15, for its negative MATAs (between -1.5 and -3.7°C), seasonal temperature variation and equal proportions of mid-European and Mediterranean species (Fernández-García et al., 2018). Compared to level O, the upper level N presents an increase in Mediterranean species with a concomitant reduction in mid-European ones. This level was related to an interstadial phase based on increments in *Pinus* forest associated with warm temperate taxa (Burjachs et al., 2012; López-García et al., 2014). Consistently qualitative methods estimate a climatic improvement between levels O and N (BM $\frac{1}{4}$ $\pm 1.2^{\circ}\text{C}$; MER $\frac{1}{4}$ $\pm 1.1^{\circ}\text{C}$), but oxygen isotope compositions point to the opposite situation (-1.5°C).

Otherwise, no notable differences in the landscape component between levels O and N are observed, due to species with preference for open forest environments always remained abundant (*A. sylvaticus*, *E. quercinus*, *Sciurus vulgaris*, *N. lasiopterus* and *P. pipistrellus*). The predator identified as the main agent of small-mammal remain accumulation in the lower levels, *Strix aluco*, is a good indication that forests surrounded the site. It is higher up in the stratigraphy, in levels K-J, when a decrease in species with preferences for the forest is documented, along with an increase in species of mid-European requirements (C1 and C2) from level K to level J (Fig. 4; 6). The deposition of these levels took place between D-O 14 (ca. 54-49 ka b2k) and D-O 13 (ca. 49-46 ka b2k). Both levels correspond to the end of the previously mentioned Palynological Phase 3, characterized by continuous oscillations between cool-dry and warm-humid episodes (Burjachs and Julià, 1996, 1994) (Table 1; Fig. 6). Environmental deterioration recorded in level J pointed by small-mammal assemblages is consistent with a

decrease in thermophilous taxa and arboreal pollens detected by palynological studies, as well as an increase in dry pollen taxa (Burjachs et al., 2012), also detected by phytolith studies (Cabanes et al., 2007). This can tentatively agree with previous correlation of sublevel Ja with the HS5 or, most likely, with the beginning of the GS13. However, in the light of the scarce small-mammal remains and the possible contribution of *Asio otus* to this level, cautious interpretation is recommended.

At the top of the sequence, levels E-D may be contemporaneous with D-O 12 (ca. 46-43 ka b2k) or with D-O 11 (ca. 43-41 ka b2k). Climate fluctuations documented during this period have been highlighted in some studies, which have linked GS12 and GS11 to the initial fragmentation of Neanderthal populations resulting from the cooling and arid conditions of these stadials (e.g., Staubwasser et al., 2018; Wolf et al., 2018). Nevertheless, D-O 12 is characterized by strong forest development with temperate elements in southernmost European latitudes, based on marine pollen records (Fletcher et al., 2010; Fletcher and Sánchez Goñi, 2008). Levels E and D were initially identified inside the Palynological Phase 5 (46-41 ka BP), which was a warm phase with forest expansion (Burjachs and Julià, 1996, 1994), but these levels were correlated to a cool period (Burjachs et al., 2012; López-García et al., 2014; Vaquero et al., 2013). This research supports a significant proportion of forestall component in both levels, especially in level E, where the highest relative presence of *A. sylvaticus* is observed ($\sim 50\%$) (Table 2; Fig. 4; 6) and a slight climatic deterioration recorded in level E, based on an increase of mid-European species (C1 and C2; such as *M. arvalis*, *M. agrestis* and *C. nivalis*), related to an aridity event, expressed by the highest oxygen isotope compositions from the sequence inside level E (Fig. 5). This is further supported by the

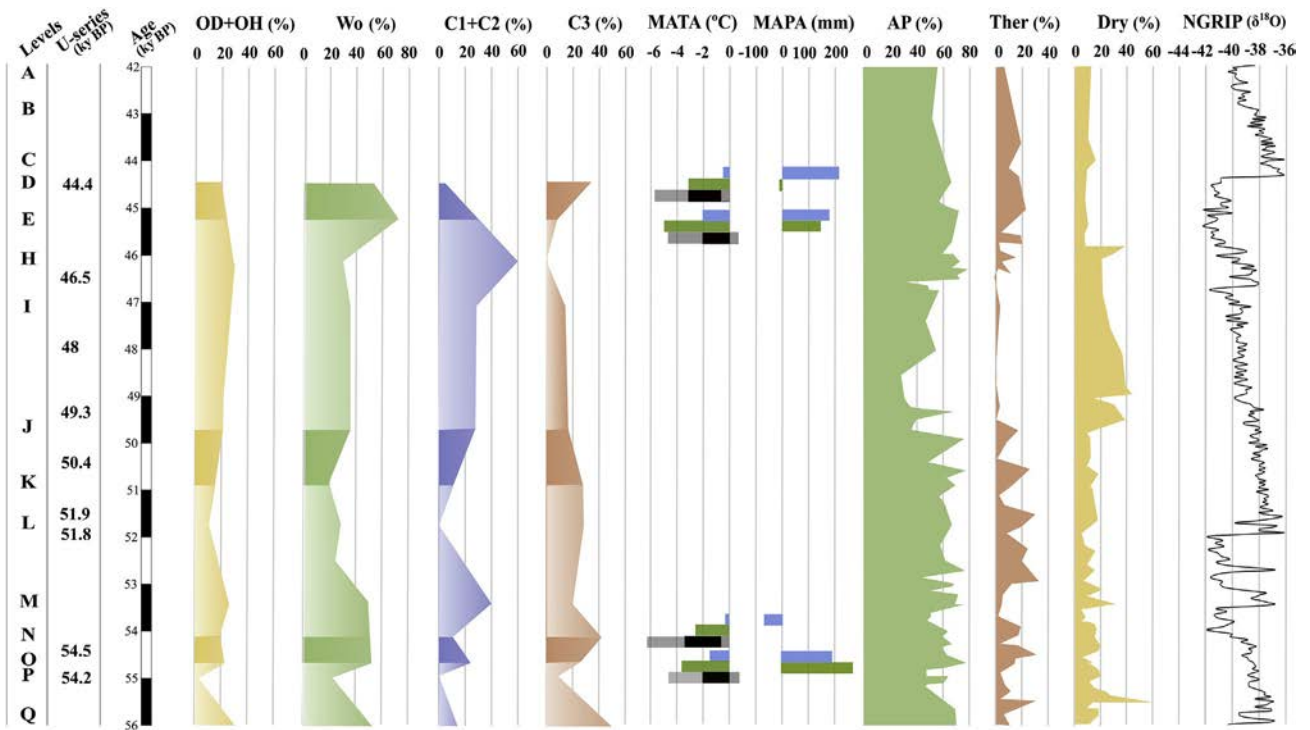


Fig. 6. Comparison of ecological methods apply to Abric Romani sequence. Species abundances obtained through small-mammal studies: OD \neq OH, open dry and open humid; Wo, woodland; C1+C2, chorotypes 1 and 2 (mid-European species); C3, chorotype 3 (Mediterranean species). Light areas are related to levels with poor small-mammal remains and, hence considered as dubious. Mean Annual Temperature Anomalies (MATA) and Mean Annual Precipitation Anomalies (MAPA) estimations for levels O, N, E and D, considering the oxygen isotope compositions ($\delta^{18}\text{O}_p$; black) of rodent phosphate samples (associated error in grey), the Bioclimatic Model (blue) and Mutual Ecogeographical Range (green) methods. Present-day MAT is 14.8°C and MAP is 619 mm (Climate-data.org). Pollen curves from Burjachs et al. (2012): AP, Arboreal pollen, including *Pinus*; Ther, Thermophilous pollen taxa; Dry, dry pollen taxa. Isotopic curve from the NGRIP ice core (North Greenland Ice Core Project members, 2004; Svensson et al., 2008). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

prevalence of *Epidalea calamita*, aeolic sedimentary facies, and a major development of steppic vegetation (Burjachs et al., 2012; López-García et al., 2014; Vaquero et al., 2013). It can also explain the recovery of a *Mammuthus primigenius* remain in this level (Rosell et al., 2012b). Based on the present results, level D reports an increase of Mediterranean species (C3, highest presence of *I. cabreræ*) and higher MATAs (BM $\frac{1}{4}$ ± 1.6 °C; MER $\frac{1}{4}$ ± 1.9 °C) (Fig. 4; 6). However, oxygen isotope compositions do not suggest an important change in mean air temperatures between these two levels (~ 1 °C).

- *Discrepancies between methods of palaeotemperatures estimation*

Discrepancies in palaeotemperatures estimates between oxygen isotope compositions of tooth phosphate and BM and MER approaches can be explained by several methodological aspects. BM and MER qualitative methods rely on the occurrence of species, with independence of their relative abundance (Blain et al., 2009, 2016; Hernández Fernández, 2001; Hernández Fernández, 2007). These methods rely on present-day biogeography species data, that could have suffered of anthropic pressure effect or other non-environmental factors on their current distributions (Blain et al., 2016; López-García et al., 2012a; Lyman, 2017). The presence or absence of a single species can highly alter the final palaeotemperature estimate. The species composition is highly dependent on the preservation and taphonomic history of recovered remains, as the hunting preferences of the main accumulator (Andrews, 1990; Fernández-Jalvo et al., 2016; Lyman, 2017; Scott et al., 1996). This risk increases when faunal assemblages are fragmentary or poor in remains, as in Abric Romaní assemblages. The relatively lower MATs recorded by BM and MER methods in levels O and E on this site are mainly affected by the presence of the vole species *Chionomys nivalis* and *Microtus arvalis*, respectively. For instance, removing these species with the MER method induces an increase in MAT by ± 1.2 °C in level O and ± 1.9 °C in level E. Nonetheless, climatic factors are not the unique limiting parameter that determined the distribution area of species (Lyman, 2017). Discrepancy between methods could show us that the presence/absence of some species mostly rely in local environmental conditions than in precise climatic conditions. The presence of *Chionomys nivalis* at level E could be more related to the rocky microhabitat need for this species than to harsh climatic conditions associated with its current area of distribution. This species still inhabits the Iberian Peninsula and it is mainly found in the Pyrenees (1000e2600 m a.s.l.), but it is preferentially link to mountainous areas by the availability of scree on mountain slopes or forest clearings more than to the low temperatures that these region provides (Blanco, 1998; Laplana et al., 2016; MacDonald and Barret, 2008; Perez-Aranda, 2009).

Moreover, the palimpsest conditions inherent to archaeological levels, and stadial and interstadial fluctuations experienced during MIS 3, could imply mixing faunal assemblages produce during different environmental conditions or even conditionate by exactly point of sampling (e.g., Royer et al., 2013b). These mixed assemblages can lead to contradictory results either to BM and MER methods due to mixed faunal assemblages coming from different environmental or climatic conditions (Andrews, 2006; Lyman, 1994). But it also can potentially biased isotopic results, when oxygen isotopes compositions of selected samples are conditionate by different variations in temporal and spatial factors both on an intra- or inter-annual scale (Fernández-García et al., 2019; Peneycad et al., 2019; Royer et al., 2013b). Moreover, interpretation of oxygen stable isotopes preserved in vertebrate body tissues in terms of past temperatures requires a comprehensive understanding of the

climate factors and processes that influence the $d^{18}O$ signal through the atmosphere to the body water finally acquire. In this approach, we assumed that the temperature effect is the dominant factor in $d^{18}O_{mw}$ record in Northeastern Iberia during the MIS3. But not only temperatures are modulating the oxygen isotope compositions in rainfall, which after are recorded in rodent teeth. Stable isotopes of oxygen are an integrated product of both history of an air mass and specific meteorological conditions (temperature and amount of precipitation) at the time of condensation (Craig, 1961; Dansgaard, 1964; Moreno et al., 2014; Zanchetta et al., 2014). Either reduced levels of moisture during stadial events or the amount effect derived from prolonged rainfall in spring season can supposed $d^{18}O_{mw}$ enrichment. Previous works on small mammals highlighted a complex relationship between $d^{18}O$ and moisture, which may have potential influence in the palaeoclimatic interpretation. In northwestern Africa, the $d^{18}O$ of gerbil tooth apatite is strongly correlated with mean annual precipitation (MAP) below 600 mm (Jeffrey et al., 2015); whereas in the MIS3 site of Les Pradelles (Western France), $d^{18}O_p$ enrichments are related to aridity events (Royer et al., 2014).

- *The Abric Romaní sequence inside Iberian environmental trend*

Marine records underline abrupt climatic changes for MIS3 period, more common at warming than at cooling, synchronic with D/O cycles in Greenland ice cores records (Fletcher et al., 2010; Martrat et al., 2004). Thus, cold stadials were periods of limited duration, immediately follow by warm recovering, with estimated variations of >6 °C on sea surface from the Alboran Sea (Martrat et al., 2004). These climatic fluctuations are expected to produce changes inland, mainly in temperatures or vegetation cover. However, lake sequences recording D/O fluctuations are not frequent in Iberia, probably by an insufficient sampling resolution (Moreno et al., 2012). For the Abric Romaní sequence, cooler and more or less wetter conditions than present-day are reported. Despite previously described oscillations, comparison between lower (O-N, ca. 54e55 ka) and upper (E-D, ca.43e45 ka) levels suggests equivalent climatic conditions, reflecting only slight climatic fluctuations primarily detected on the basis of the faunal composition. The climatic changes recorded between levels are estimated lower than 2.5 °C, independently of the method used. Dramatic climatic worsening is not observed along this sequence, except for some aridity indicators on level E. This level was most likely related to HS5, which in agreement with Fuentillejo maar (Vegas et al., 2010), is considered relatively warm compared to posterior arid HSs identified in this lake sequence.

Under geochemical perspective, homogenous sequence and low variability in MATs were also observed in a contemporaneous palaeontological site of northeastern Iberia, Xaragalls cave (Vimbodí-Poblet) (Fernández-García et al., 2019; López-García et al., 2012a). Medium to small $d^{18}O_p$ ranges, which are always associated with high means and relatively constant throughout these sequences, differ from a contemporaneous archaeological site in southern France, Les Pradelles (Royer et al., 2013b). At the site of Les Pradelles (Charente, ca. 65-55 ka BP) the total range of $d^{18}O_p$ values is 12.2‰, with inter-level variations comprised between 2‰ and 11.4‰. The same kind of isotopic pattern can be observed at Taillades-Coteaux (Vienne, 35-17 ka cal. BP), where the total range of $d^{18}O_p$ values is 13.1‰, with inter-level variations between 3.6‰ and 12.7‰ (Royer et al., 2014). In the MIS 3 levels from these sites, species with steppe-tundra preferences are usually predominant along the sequences (*Dicrostonyx torquatus*, *Microtus gregalis*, *Microtus oeconomus*, *Spermophilus* sp.), while *M. arvalis* and *M. agrestis* are common and *A. sylvaticus* is usually anecdotal.

Thereby demonstrating a remarkably different faunal composition in association with severe climatic conditions in opposition to northeastern Iberia.

The climatic pattern associated with Neanderthal occupations in northeastern Iberia considering small-mammal communities from MIS 3 always show an important presence of the forest biotope integrated into mosaic environments with high levels of humidity (Fernández-García et al., 2016; López-García et al., 2014). This is confirmed for the Abric Romaní site, where open forest dominated the entire sequence, with only punctuated periods of opening, and active water courses next to the rock-shelter. Anthracological and palynological studies reported widespread *Pinus sylvestris* type throughout the territory (Allué et al., 2017; Burjachs et al., 2012; Burjachs and Allué, 2003; Burjachs and Julià, 1994). The maintenance and, usually predominance, of the forest biotope, together with wetter and cooler conditions, is a trend recurrently observed in MIS 3 Iberian archaeo-palaeontological sites. This is also supported by small-vertebrate compositions, especially for the Mediterranean area (Fernández-García et al., 2016; López-García et al., 2014), as it is recorded in Gorham cave (Blain et al., 2013; López-García et al., 2011b), El Salt (Fagoaga et al., 2018; Marquina et al., 2017), Cova del Coll Verdaguer (Daura et al., 2017), Texioneres cave (López-García et al., 2012b) or Cova del Gegant (López-García et al., 2012c). Small-mammal assemblages from these sites include Mediterranean species (*M. (T.) duodecimcostatus* or *I. cabreræ*) and typical woodland species (*A. sylvaticus* and *E. quercinus*), independently of stadial-interstadial cycles. This pattern is also noted for northern and northwestern Iberia, in Lezetxiki II, Askondo, Cueva del Conde, and Cova Eiròs (García-Ibaibarriaga, 2015; López-García et al., 2011a; Murelaga et al., 2012; Rey-Rodríguez et al., 2016); in central Iberia, Los Casares (Alcaraz-Castaño et al., 2017) and even in the Atlantic coast, in Figueira Brava cave (Jeannet, 2000) and Caldeirão cave (Povoas et al., 1992).

Marine records reveal that the preservation of extended woodland masses is a regional trend characteristic of both Iberia and the Mediterranean Basin (Fletcher et al., 2010; Fletcher and Sanchez Goñi, 2008; Harrison and Sanchez Goñi, 2010). Anthracological and palynological records inland reveal well-established montane pine forest covertures, associated with components of evergreen and deciduous species, from the southern Iberian coasts to the Pyrenees during Late Pleistocene, until their decline with the beginning of the Holocene (Allué et al., 2018; Camuera et al., 2019; Carrión, 2012; Carrión et al., 2018; Daura et al., 2017). Even if Mediterranean forest experienced some expansion-contraction cycles during this period, coniferous woodlands were constant all along the last glacial period (MIS 4 e MIS 2), pointing to oromediterranean/supramediterranean stages dominating during the MIS 3 in the northeast. The maintenance of woodland covertures, steady climatic conditions, along with the absence of any large change in rodent communities confirm altogether the peculiarities of northeastern Iberia during MIS 3, when globally climatic deterioration and subsequent forestall reduction took place in northern Europe. Moreover, the detection of these forest covertures next to Mediterranean archaeological sites associated with Neanderthals may suggest an ecological preference for arboreal covertures by these populations when establishing their occupation in this region. These forest areas possibly provided the necessary resources for the survival of Neanderthal groups, where they were able to develop gathering and hunting activities, along with obtaining the necessary fuel to develop their pyrotechnic activities, widely documented in the occupations of the rock-shelter. Charcoal analysis, wood imprints and combustion structures recovered in Abric Romaní reveal that wood exploitation, as fuel or even as raw material for tools, was an organized activity related to the daily

requirements of the occupations at the site, probably gathered from the areas surrounding the shelter (Allué et al., 2017; Solé et al., 2013; Vallverdú et al., 2012).

5. Conclusions

The small-mammal remains preserved in some of the levels of the Abric Romaní sequence provides extensive information for reliable palaeoecological reconstructions for the MIS 3 period, through a combination of approaches that relies on small-mammal analyses and other environmental proxies. Taphonomic studies related the small-mammal origin to owl predation activities. Remains sampled from lower levels (O-N) are most likely the result of an intermediate modification predator (probably *Strix aluco*), whereas those found in upper levels (J-E) are prey assemblages deposited by a mixture of light and intermediate modification predators. Species diversity and richness point to an opportunistic predator, that draws a complete ecological picture of the past; although caution in the interpretation of upper levels is recommended. The low intra-level ranges of oxygen isotope ratios tooth enamel phosphate suggest that rodent accumulations are mainly related to spring-early summer months when predators are more actively hunting. Among post-depositional agents, plant activity, cracking, and manganese oxide precipitations are common, describing a humid fossiliferous microenvironment where human occupation was intense.

The results presented in this study considered together with those previously obtained using pollen and anthracological analyses support minor changes of the landscape with continuous presence of relative humid open forest, punctuated by expansions of grassland, and active watercourses next to the rock shelter. Lower temperatures and slightly higher or equal amounts of precipitation levels than present-day are estimated for levels O, N, D and E. Slight fluctuations in the relative presence of Mediterranean versus mid-European species, seems to be in agreement with palynological analyses and other environmental proxies applied to the site, indicating that levels O, J and E were cooler and could be related to stadial periods. Despite these fluctuations, this work reports weak climatic changes between the studied archaeological levels (<2.5 °C), independently of the method applied. Oxygen isotope compositions of analyzed rodent teeth indicate steady and equal climatic conditions recorded across the lower and upper levels, in agreement with other MIS 3 sequences of northeastern Iberia. By the complementation of different types of ecological analyses, we propose more temperate, wetter and steady climatic conditions for northeastern Iberia during Neanderthal settlements than previously expected. A significant woodland cover is underline; which indicates: 1) the preservation of this kind of landscape even during periods of climatic deterioration in Europe and/or, 2) the ecological preference of Neanderthal populations for arboreal covertures available next to their settlements, as woodlands provide the basic resources for their daily subsistence.

Declaration of competing interest

The authors have no conflict of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.quascirev.2019.106072>.

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