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General Palaeontology, Systematics and Evolution (Vertebrate Palaeontology)

Palaeoecological implications of rodents as proxies for the Late Pleistocene–Holocene environmental and climatic changes in northeastern Iberia



Implications paléoécologiques des rongeurs comme indicateurs des changements environnementaux et climatiques du Pléistocène supérieur à l'Holocène dans le Nord-Est de la péninsule Ibérique

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ABSTRACT

Rodents are among the most useful proxies for reconstructing the ecology and environment of the Quaternary. The present paper focuses on a series of fossil rodent assemblages from northeastern Iberia of the Late Pleistocene (ca. 128–11.7 ka BP) and the beginning of the Holocene (< 11.7 ka BP). Descriptive and multivariate statistical methods have been applied to expand what is known about the species involved and their palaeoecological implications. The results show the importance of the three predominant species: *Microtus arvalis*, *Microtus agrestis* and *Apodemus sylvaticus*. A transition in the ecological conditions is shown in the studied area during the course of this interval: from open environments and cooler climatic conditions to more forested landscapes and temperate conditions. The beginning of the Late Pleistocene and the Holocene share similarities, and both differ clearly from the end of the Late Pleistocene, showing the singular nature of the environmental conditions of Marine Isotope Stage 2 in the northeastern sector of the Iberian Peninsula.

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R É S U M É

Les rongeurs sont parmi les marqueurs les plus significatifs pour la reconstruction de l'écologie et de l'environnement du Quaternaire. Ce travail prend en compte une série d'assemblages de rongeurs fossiles du Pléistocène supérieur (environ 128 à 11,7 ka BP) et du début de l'Holocène (< 11,7 ka BP), provenant du Nord-Est de la péninsule Ibérique. Des méthodes statistiques descriptives et multivariées ont été appliquées, afin d'obtenir une meilleure connaissance des espèces concernées et de leurs implications paléoécologiques. Les résultats obtenus indiquent l'importance de trois espèces dominantes : *Microtus arvalis*, *Microtus agrestis* et *Apodemus sylvaticus*. Une transition des conditions écologiques est mise en évidence dans la région étudiée pendant cet intervalle : depuis des environnements

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ouverts avec un climat plutôt frais vers des paysages plus boisés traduisant un climat tempéré. Les ressemblances mises en évidence parmi les sites datant du début du Pléistocène supérieur et de l'Holocène se démarquent nettement de ceux de la fin du Pléistocène supérieur, soulignant la singularité des conditions environnementales pendant le stade isotopique marin 2 dans le Nord-Est de la péninsule Ibérique.

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1. Introduction

The Late Pleistocene (128–11.7 ka BP) is an interval characterized by high climate instability, which alternates cold and warm phases and isolated climatic episodes (such as Heinrich Events or Dansgaard-Oeschger events) (Sánchez-Goñi and D'Errico, 2005). These fluctuations are likely to have had impacts on flora, fauna and human societies. The transition from the Latest Pleistocene to the Holocene, characterized by a sharp increase in temperatures occurring around 11,700 years ago, also constituted an environmental break with major consequences (Bradley and England, 2008).

Different proxies (such as Greenland ice cores, marine pollen cores or continental records) have increased what is known of the Quaternary environment. In the continental domain, the temporal discontinuity of sedimentary records limits the reconstruction of reliable climatic parameters. Many proxies have been developed in order to quantify climatic parameters, on the basis either of palaeobiological approaches or geochemical methods. Over the last two decades, multidisciplinary approaches have been developed in order to improve the reconstruction of continental climate models and understand the responses of living organisms to climatic changes (Sánchez-Goñi and D'Errico, 2005; Sánchez-Goñi et al., 2008). For the Iberian Peninsula, climatic particularities have been discussed that differed from the dynamics of the rest of Europe on account of geographical situation and as a consequence of the condition of southern Europe as particularities that can also be found in the Italian Peninsula and the Balkans (Fletcher et al., 2010; Harrison and Sánchez-Goñi, 2010).

Rodents are one of the most noteworthy groups of mammals in the European Quaternary, and they have become one of the most useful tools for reconstructing the ecology and environment of the Quaternary. Species from this order tend to undergo an accelerated evolution and are generally characterized by short life spans (Van Dam et al., 2006), a close relationship with their environment and strict ecological requirements. These factors make them extremely good markers for studies that focus on evolution, biochronology and particularly for inferring a record of their local living environments. Moreover, their widely ranging geographical distribution and the high presence of their remains in Quaternary sedimentary deposits makes it possible to apply multiple statistical approaches and quantitative methods (Alcalde and Galobart, 2002; Chaline, 1988; López-García, 2011). In the present study, the statistical analysis of rodent assemblages from Late Pleistocene (128–11.7 ka BP) and Holocene (< 11.7 ka BP) sites from the northeastern Iberian Peninsula increases what is known

of the species in question during this time frame, taking into account the specific palaeoecological implications of the assemblages with the aim of understanding the environmental evolution of this region. On the basis of this methodology, our aim is to ascertain the differences and similarities between these sites/levels depending on the occurrence of species and also establish which species assemblages are the most common and which are the dominant ones.

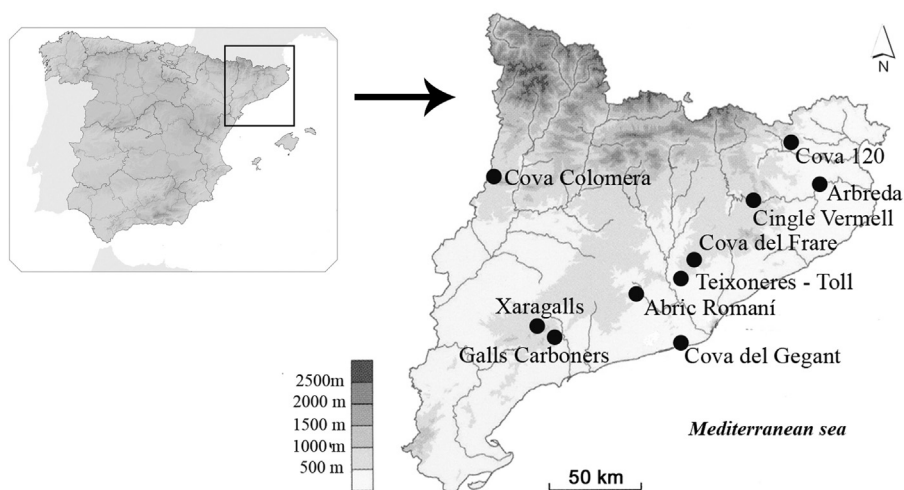
2. Materials and methods

2.1. Data matrix

The data matrix employed corresponds to specimens recovered from 37 levels from 12 archaeological sites from the Northeast of the Iberian Peninsula, chronologically located in the Late Pleistocene and the beginning of the Holocene. For each species, the minimum number of individuals (MNI) has been taken into account. Only levels with an MNI greater than or equal to 15 have been included in these analyses. This MNI limit has been decided as the optimal point to remove the assemblages with low individuals but not loss to many levels from this region (Fig. 1; Table 1) (Appendix A1).

Corrections have been applied to the data matrix in order to simplify the interpretation and reduce the dispersion of the results. Firstly, the specimens of *Microtus arvalis* and *Microtus agrestis* are integrated into a single group because it is common, especially in older publications, not to differentiate between these two species (identified as *Microtus arvalis-agrestis*). In order not to overlook the importance of the presence of these two species, the adopted solution is to put these categories into a single group. As regards the ecological restrictions on the two species, both are mid-European species associated with cool climates, high altitudes and open landscapes; they only differ in their preference for moisture (Palomo et al., 2007; Sans-Fuentes and Ventura, 2000).

Secondly, all specimens identified as *Arvicola* sp. in previous publications (Alcalde, 1986) have been interpreted as belonging to the species *Arvicola sapidus*, because this is the only species from this genus present during this interval in the Northeast of Iberia (López-García, 2011). The only example of *Arvicola terrestris*, the other extant species from this genus, is located in Cova d'Olopte B (Villalta, 1972), and this is probably misidentified, also corresponding to *A. sapidus*, a species widely extended in Catalonia during the Late Pleistocene–Holocene. Finally, the specimens identified as *Terricola* sp. have been considered to be *Microtus* (*Terricola*) *duodecimcostatus*. The other known species of



Sites	Levels	Chronology
Teixoneres cave	III, II	90–30 ka BP
Abric Romani rockshelter	O, N, E	55–49 ka BP
Cova del Gegant (old levels)	I	128–40 ka BP
Cova del Gegant (new levels)	V, III	55.7–49.3 ka cal BP
Xaragalls cave	C8, C7, C6, C4	45–13 ka BP
Arbreda cave	I, H, G, F, E, D, C, B, A	40–18.8 ka BP
Galls Carboners cave	Capa 100	31.17–31.38 ka cal BP
Toll cave	3, 2	<35 - >13
Cova Colomera	CE15, CE13–14, CE12, EE1, A. sup	13–3.5 ka BP
Cingle Vermell		9.76 ± 0.16 ka BP
Cova del Frare	6, 5, 4, 3	6.3–3.9 ka BP
Cova 120	III, II, I	4.27–3.1 ka BP

Fig. 1. Location of Late Pleistocene–Holocene archaeological sites included from the northeast of the Iberian Peninsula, and table showing the site and the corresponding levels, with their general chronology.

Fig. 1. Localisation des sites archéologiques du Pléistocène supérieur–Holocène dans le Nord-Est de la péninsule Ibérique, et tableau montrant les noms des sites, leurs niveaux correspondants et leurs chronologies.

this genus that is close morphologically, *Microtus (T.) gerbei*, is not an abundant species in the region and is commonly associated with cooling temperatures (Palomo et al., 2007). The reason for this grouping is not to lose sight of the importance of *M. (T.) duodecimcostatus* as a result of fragmentation of the information associated with this species, which is dominant in some assemblages.

2.2. Classification of levels

The 37 studied levels have been grouped, in accordance with their chronology, in three time intervals:

- Early Late Pleistocene (ELP). This includes all archaeological levels from ca. 128 to 40 ka BP, generally related to the Middle Palaeolithic and consequently to *Homo neanderthalensis* activity. Since in the Northeast of Iberia there are only a few Middle Palaeolithic sites with chronologies older than 60 ka BP, the greater part of the assemblages belong to MIS 3 (ca. 60–30 ka BP). Thirteen levels of five different fossil sites are included: Levels III and II from Teixoneres cave (López-García et al., 2012b); Levels O, N and E from Abric Romani (López-García, 2011; Fernández-García, 2014); Levels I, V and III from Cova del

Gegant (López-García et al., 2012c); Levels C8, C7, C6 and C4 from Xaragalls Cave (López-García et al., 2012a) and Level I from Arbreda cave (Alcalde, 1986; López-García, 2011). This group represents a total of 946 individuals.

- Latest Late Pleistocene (LLP). This comprises all archaeological levels from ca. 40 to 11.7 ka BP, commonly related to the Upper Palaeolithic and the presence of Anatomically Modern Humans. This time interval is equivalent to end of MIS 3 and the complete MIS 2 (ca. 30–14 ka BP). Twelve levels from four different fossil sites are included: Levels I, H, G, F, E, D, C, B and A from Arbreda cave (Alcalde, 1986; López-García, 2011); the assemblage from Galls Carboners cave (López-García et al., 2014b); Levels 3 and 2 from Toll cave (Fernández-García and López-García, 2013) and Level CE15 from Cova Colomera (López-García et al., 2010). This group represents a total of 1455 individuals.
- Holocene (HOL). Groups all archaeological sites recent than 11.7 ka BP, including Epipalaeolithic, Neolithic, Chalcolithic and Bronze Age sites. All these levels belong to MIS 1. Twelve levels from four different fossil sites are included: Level CE13–14, CE12, EE1 and A. sup. from Cova Colomera (López-García et al., 2010); the assemblage from Cingle Vermell (Alcalde, 1986); Level 6, 5, 4

Table 1

Data matrix for the occurrence of species in Late Pleistocene–Holocene archaeological levels in the northeastern of Iberia. The occurrence of the species is expressed as the minimum number of individuals (MNI).

Tableau 1

Matrice de données pour la présence d'espèces dans les niveaux archéologiques du Pléistocène supérieur–Holocène dans le Nord-Est de l'Ibérie. La présence de l'espèce est exprimée en nombre minimum d'individus (NMI).

	<i>Arvicola sapidus</i>	<i>Chionomys nivalis</i>	<i>Microtus arvalis- agrestis</i>	<i>M. (Terricola) duodecim- costatus</i>	<i>Microtus (Terricola) gerbei</i>	<i>Microtus oeconomus</i>	<i>Iberomys cabreræ</i>	<i>Clethrionomys glareolus</i>	<i>Pliomys lenki</i>	<i>Apodemus sylvaticus</i>	<i>Mus musculus</i>	<i>Eliomys quercinus</i>	<i>Glis glis</i>	<i>Hystrix sp.</i>	<i>Spermophilus cf. citellus</i>	<i>Sciurus vulgaris</i>	Total MNI
<i>Early Late Pleistocene (128–40 ka BP)</i>																	
Teixoneres – Level III	3	1	35	35	1	0	2	0	1	75	0	11	7	0	0	0	171
Teixoneres – Level II	2	8	100	9	0	0	0	0	1	19	0	8	0	0	0	0	147
Abric Romaní – Level O	55	0	55	25	0	0	45	0	0	69	0	8	0	0	0	1	258
Abric Romaní – Level N	3	0	0	1	0	0	8	0	0	3	0	0	0	0	0	0	15
Abric Romaní – Level E	3	0	3	4	1	0	0	0	0	5	0	1	0	0	0	0	17
Cova del Gegant – Level I	0	0	5	5	2	0	4	0	0	24	0	4	0	2	0	0	46
Cova del Gegant – Level V	0	0	0	1	0	0	5	0	0	1	0	17	0	0	0	0	24
Cova del Gegant – Level III	0	0	1	0	0	0	3	0	0	3	0	11	0	0	0	0	18
Xaragalls – C8	0	0	1	4	0	0	2	0	0	18	0	2	0	0	0	0	27
Xaragalls – C7	0	0	2	0	0	0	1	0	0	33	0	3	0	0	0	0	39
Xaragalls – C6	1	1	4	7	0	0	3	0	0	69	0	6	0	0	0	0	91
Xaragalls – C4	0	2	6	2	0	0	1	0	0	14	0	3	0	0	0	0	28
Arbreda – Level I	5	7	30	4	0	0	0	0	0	12	0	7	0	0	0	0	65
<i>Latest Late Pleistocene (40–11 ka BP)</i>																	
Arbreda – Level H	4	0	95	12	0	0	0	0	0	3	0	2	0	0	0	0	116
Arbreda – Level G	0	0	41	7	0	1	0	0	0	3	0	3	1	0	0	0	56
Arbreda – Level F	2	0	89	2	0	0	0	0	0	7	0	6	0	0	0	0	106
Arbreda – Level E	6	0	98	1	0	1	0	0	0	6	0	4	0	0	0	0	116
Arbreda – Level D	16	0	192	4	0	0	0	0	0	7	0	9	0	0	0	0	228
Arbreda – Level C	13	0	248	0	0	2	0	0	0	5	0	8	0	0	2	0	278
Arbreda – Level B	2	0	61	0	0	0	0	0	0	3	0	3	0	0	1	0	70
Arbreda – Level A	6	0	125	60	0	0	2	0	0	22	0	15	0	0	1	0	231
Galls Carboners	0	9	3	0	0	0	0	0	0	9	0	33	0	0	0	0	54
Toll – Level 3	0	1	16	19	0	0	1	0	0	1	0	2	1	0	0	0	41
Toll – Level 2	0	0	3	61	2	0	3	0	0	2	0	0	0	0	0	0	71
Colomera – Level CE15	0	34	33	4	0	0	0	0	0	12	0	5	0	0	0	0	88
<i>Holocene (< 11 ka BP)</i>																	
Colomera – Level CE13–14	0	24	11	5	0	0	1	0	0	36	0	4	0	0	0	0	81
Colomera – Level CE12	0	11	11	4	0	0	2	0	0	32	0	6	0	0	0	0	66
Colomera – Level EE1	0	6	8	1	0	0	1	0	0	22	0	4	0	0	0	0	42
Colomera – Level A sup.	0	0	0	6	0	0	1	0	0	32	0	9	0	0	0	0	48
Cingle Vermell	3	0	6	2	0	0	1	1	0	37	0	3	0	0	0	0	53
Cova del Frare – Level 6	0	0	0	16	0	0	0	0	0	8	0	0	0	0	0	0	24
Cova del Frare – Level 5	0	0	0	33	0	0	8	0	0	29	0	2	0	0	0	0	72
Cova del Frare – Level 4	0	0	0	25	0	0	9	1	0	19	0	3	1	0	0	0	58
Cova del Frare – Level 3	0	0	0	5	0	0	2	0	0	8	0	1	1	0	0	0	17
Cova 120 – Level III	0	0	3	6	0	0	0	0	0	49	0	2	0	0	0	0	60
Cova 120 – Level II	0	3	4	11	0	0	11	0	0	70	2	6	7	0	0	0	114
Cova 120 – Level I	1	0	1	0	0	0	1	0	0	18	6	3	1	0	0	0	31
<i>Early Late Pleistocene</i>	72	19	242	97	4	0	74	0	2	345	0	81	7	2	0	1	946
<i>Latest Late Pleistocene</i>	49	44	1004	170	2	4	6	0	0	80	0	90	2	0	4	0	1455
<i>Holocene</i>	4	44	44	114	0	0	37	2	0	360	8	43	10	0	0	0	666
<i>Total MNI</i>	125	107	1290	381	6	4	117	2	2	785	8	214	19	2	4	1	3067

and 3 from Cova del Frare (Alcalde, 1986) and Level III, II and I from Cova 120 (Alcalde, 1986). This group represents a total of 666 individuals.

2.3. Multivariable statistical methodology

To provide a better understanding of such a large corpus of data, multivariate statistical methods have been applied, allowing us to reduce the number of variables involved in order to facilitate our ecological interpretations. Methods of multivariate analysis without previous assumptions of dependence and independence have been selected, with the aim of defining coherent patterns in space and time (Shennan, 1997). The original data correspond to absolute frequency variables, so the most recommended multivariate statistics proxy is correspondence analysis (López-Roldán and Lozares-Colina, 2000). However, this method has been shown to have limitations for the studied data, such as its low representativeness and the low explanatory capacity of its results. Consequently, other methods have been applied.

On the one hand, a principal component analysis (PCA) has been applied. This analysis has been performed after the transformation of the data from absolute frequency variables to ratio variables, replacing the original values by percentages. This data for which the sum over the variables is 100% is equivalent to compositional data (Baxter, 2003). The PCA makes it possible to analyse the sample in standardized form and yields advantages in interpretation by placing the different variables on a coordinate axis, distinguishing different components (the resulting variables) that indicate the weight of each original variable in the graphical representation obtained (Jolliffe, 2002). The covariance matrix has been used, because it proves to be the most appropriate to increase the total variance obtained in the first, second and third components (López-Roldán and Lozares-Colina, 2000; Shennan, 1997).

On the other hand, for a better and more visual compression of the data, a cluster analysis has been applied. Behind this method lies the idea that objects can be similar to one another at different levels; accordingly, the results can be represented in the form of a dendrogram, where the hierarchical relationships can be detected (Shennan, 1997). In the both cluster analyses presented, the original values have also been transformed into ratio variables. The first one have included the same data than the PCA; whereas in the second, the levels have been group in the three time intervals distinguished, including totals. A Euclidean Index is selected for grouping the data in both; this index is recommended for quantitative measures and ratio variables. The “paired group linkage” has been applied in all cases. For all the statistical approaches, the Paleontological Statistics program has been used (PAST3) (Hammer et al., 2001).

3. Results

3.1. Previous data

A preliminary view of the occurrence of species in different levels from the Late Pleistocene–Holocene epoch clearly shows the dominance of some taxa over other, more

poorly represented taxa. The most abundant taxa, listed in increasing order, are: the group of the common vole and the field vole (*Microtus arvalis-agrestis*), the wood mouse (*Apodemus sylvaticus*), the Mediterranean pine vole (*M. (T.) duodecimcostatus*), Cabrera's vole (*Iberomys cabreræ*), the garden dormouse (*Eliomys quercinus*), the European snow vole (*Chionomys nivalis*) and the southwestern water vole (*Arvicola sapidus*). However, in many cases their dominance do not extend for long intervals of time and are restricted to the singularities of certain sites (Table 1). The important presence of *M. arvalis-agrestis* is clear, but it combines an abundant presence in some levels with being very scarce in others. Meanwhile, *A. sylvaticus* is dominant in some levels but always at lower rates than in intervals of *M. arvalis-agrestis* dominance (Table 1; Fig. 2).

Leaving aside the peculiarities of each site and taking into account the species representativeness during the different time intervals, various trends have been observed (Fig. 3). Notable changes in species abundance are observed for certain intervals, particularly regarding the presence of these two domain species. During the early Late Pleistocene, both species show a roughly equal representation: *A. sylvaticus* (36.5%) and *M. arvalis-agrestis* (25.6%). However, with the arrival of the latest Late Pleistocene, a significant shift is detected, involving a remarkable decrease in *A. sylvaticus* (5.5%) and the almost complete dominance of *M. arvalis-agrestis* (69%). In the Holocene, by contrast, the opposite situation occurs: *A. sylvaticus* undergoes a revival (54%) and *M. arvalis-agrestis* loses in importance (6.6%). The other species barely exceed 1% in any of the intervals considered, except for *M. (T.) duodecimcostatus*, *E. quercinus*, *C. nivalis*, *A. sapidus* and *I. cabreræ*, which are better represented but remain more or less constant in the different intervals.

3.2. Multivariate statistics

3.2.1. Principal component analysis

Interesting results were obtained when principal component analysis was applied (Fig. 4). Considering the eigenvalues attributed to each of the components (Appendix A2), the first three should be included. The scree plot clearly shows that Component 4 is not relevant (PC4, less than 5% of variance). In contrast, the first three principal components present high representativeness, summarizing more than 90% of the variance of the studied sample (PC1, 55.6%; PC2, 19.4%; PC3, 15.5%; Appendix A2).

PC1 arranges the archaeological levels in relation to high values of MNI of two main groups of species (Fig. 4A): *M. arvalis-agrestis* for positive values of this axis and *A. sylvaticus* for negative values. The *M. arvalis-agrestis* group of species can be related with open environments, low humidity rates and cold temperatures, whereas the second is adapted to forest environments in a temperate climate without major climatic constraints (Palomo et al., 2007). Nevertheless, it is also remarkable the importance of *M. (T.) duodecimcostatus*, *E. quercinus* and *I. cabreræ* for negative values. *M. (T.) duodecimcostatus* and *I. cabreræ* are species typical of Mediterranean areas, while *E. quercinus* is a generalist species but usually related to forest cover

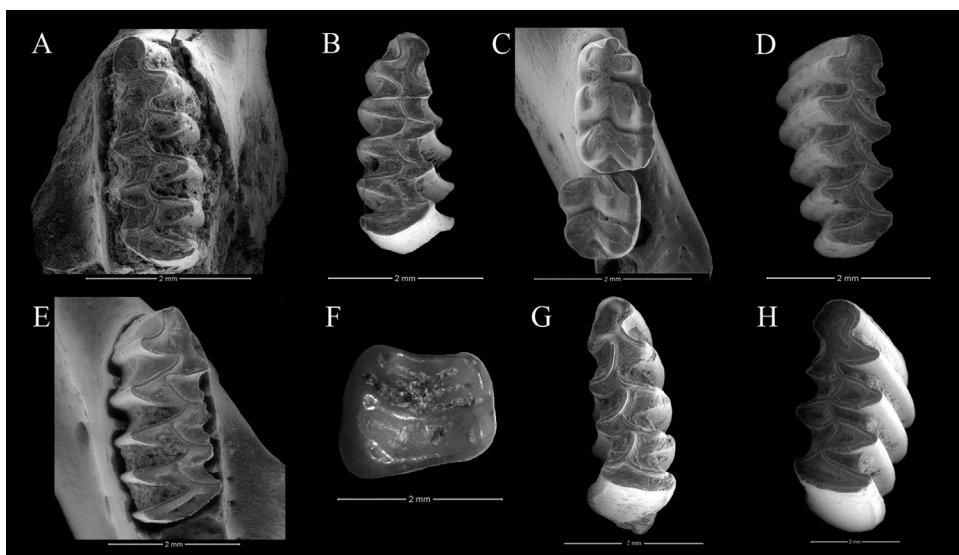


Fig. 2. Most common rodent species from northeastern Iberia during the Late Pleistocene–Holocene. A. Left m1 of *Microtus arvalis* (Toll cave). B. Right m1 of *Microtus agrestis* (Cova del Gegant). C. Right m1 and m2 of *Apodemus sylvaticus* (Toll cave). D. Right m1 of *Microtus (Terricola) duodecimcostatus* (Cova del Gegant). E. Right m1 of *Iberomys cabrerai* (Abric Romani). F. Right m2 of *Eliomys quercinus* (Toll cave). G. Left m1 of *Chionomys nivalis* (Toll cave). H. Left m1 of *Arvicola sapidus* (Toll cave). Occlusal view: scale 2 mm.

Fig. 2. Espèces de rongeurs les plus communes du Nord-Est de la péninsule Ibérique au cours du Pléistocène supérieur–Holocène. A. m1 gauche de *Microtus arvalis* (grotte du Toll). B. m1 droite de *Microtus agrestis* (Cova del Gegant). C. m1 et m2 droites de *Apodemus sylvaticus* (grotte du Toll). D. m1 droite de *Microtus (Terricola) duodecimcostatus* (Cova del Gegant). E. m1 droite de *Iberomys cabrerai* (Abric Romani). F. m2 droite de *Eliomys quercinus* (grotte du Toll). G. m1 gauche de *Chionomys nivalis* (grotte du Toll). H. m1 gauche de *Arvicola sapidus* (grotte du Toll). Vues occlusales : échelle = 2 mm.

(Palomo et al., 2007; Purroy and Varela, 2003; Sans-Fuentes and Ventura, 2000). From a palaeoenvironmental point of view, a distribution of sites along the PC1 can be inferred between a more open and possibly colder climate, represented by “the *M. agrestis-arvalis* tendency”, to forested areas and more temperate weather, represented by “the *A. sylvaticus* tendency”. Accordingly, the simplest interpretation for the distribution of levels on the graph would be a gradient from more closed environments (negative values on PC1 axis) to more open environments (positive values of PC1 axis), with the climatic implications that this might entail.

In addition, positive PC2 values are determined by the occurrence of *M. (T.) duodecimcostatus* and secondly by *I. cabrerai*. Both are commonly associated with Mediterranean conditions and related forest or wet grassland habitats (Palomo et al., 2007; Sans-Fuentes and Ventura, 2000). On the other hand, negative values depend on *A. sylvaticus* and *M. arvalis-agrestis* and in lesser proportion on *C. nivalis*. The latter three are mid-European species nowadays living in areas at notable altitudes, with cold temperatures and lower rainfall; by contrast, *A. sylvaticus* is a generalist species, related to the forest and not restricted by altitudinal factors (Palomo et al., 2007; Purroy and Varela, 2003; Sans-Fuentes and Ventura, 2000). In this sense, it proves difficult to develop a palaeoecological interpretation for PC2. Nevertheless, the contrast between PC1 and PC2 suggests a classification of assemblages in terms of the three most dominant species (*M. arvalis-agrestis*, *A. sylvaticus* and *M. (T.) duodecimcostatus*) in the Northeast of the Iberian Peninsula during the Late Pleistocene and Early Holocene.

As regards the three above-defined time intervals, it can be observed that the closest associations over time within each time interval tend to appear together on the graph. Specifically, LLP levels appear separated from the rest of the associations and concentrated together in relation to *M. arvalis-agrestis*. Moreover, ELP and HOL levels are grouped together, their distribution depends on the dominance of *A. sylvaticus* or *T. duodecimcostatus*, showing no particularly distinctive patterns between these two time intervals. In complementary form, the ELP and HOL samples tend to appear far away from *M. arvalis-agrestis*, and the LLP ones from *A. sylvaticus*, showing the respective low presence of these species. This demonstrates the great similarity of these two climatic phases (ELP and HOL), or rather the high particularity of LLP.

On the one hand, all the LLP levels from Arbreda cave and Level CE15 from Cova Colomera are grouped together in the “*M. arvalis-agrestis* tendency”. The location of some LLP levels shows that, in spite of the above-noted clear bipolarization between the two main groups of species, there are other determinant taxa during this interval, such as the Mediterranean pine vole (*M. (T.) duodecimcostatus*). The high presence of this taxon is evident in levels from Toll cave and is the reason about its position in the graph. The only incoherent level is Galls Carboners cave assemblage, which appears somewhat distant, because is the oldest site from the LLP samples and is affected by the Mediterranean influence on its location.

On the other hand, among the ELP and HOL levels, two levels appear closer to the LLP group: Level I from Arbreda cave and Level II from Teixoneres cave. These correspond to the latest and earliest levels, respectively, among the ELP

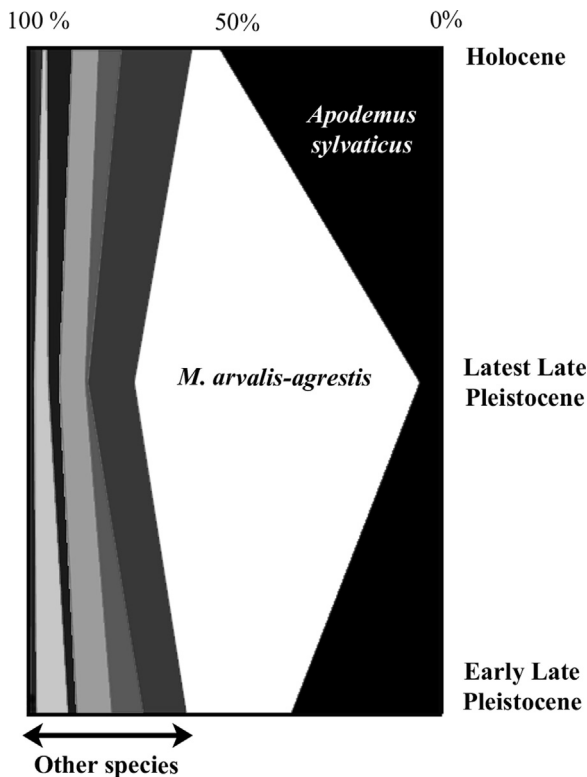


Fig. 3. Relative frequency of Late Pleistocene–Holocene rodent species in northeastern Iberia throughout the three chronological periods differentiated. From left to right: non-significant species (*Microtus (Terricola) gerbei*, *Microtus oeconomus*, *Clethrionomys glareolus*, *Pliomys lenki*, *Mus musculus*, *Glis glis*, *Hystrix* sp., *Spermophilus citellus*, *Sciurus vulgaris*); *Arvicola sapidus*; *Chionomys nivalis*; *Eliomys quercinus*; *Iberomys cabreræ*; *Microtus (Terricola) duodecimcostatus*; *Microtus arvalis-agrestis*; *Apodemus sylvaticus*.

Fig. 3. Fréquence relative des espèces de rongeurs au cours du Pléistocène supérieur–Holocène dans le Nord-Est de la péninsule Ibérique à travers les trois périodes chronologiques différenciées. De gauche à droite : espèces non significatives (*Microtus (Terricola) gerbei*, *Microtus oeconomus*, *Clethrionomys glareolus*, *Pliomys lenki*, *Mus musculus*, *Glis glis*, *Hystrix* sp., *Spermophilus citellus*, *Sciurus vulgaris*); *Arvicola sapidus*; *Chionomys nivalis*; *Eliomys quercinus*; *Iberomys cabreræ*; *Microtus (Terricola) duodecimcostatus*; *Microtus arvalis-agrestis*; *Apodemus sylvaticus*.

assemblages. The reasons could be related both to chronological and geographical influences. The former could be interpreted as a marker for a progressive trend on decrease of temperatures and changing conditions associated with the beginning of the LLP and the resulting glacial acceleration. Level II from Teixoneres cave has been linked in previous publications (López-García et al., 2014c) with Heinrich Event 2 or 3, a cooling episode that led to a high presence of mid-European species such as *M. arvalis* and *M. agrestis*. This phenomenon is also found in Levels O and E of the Abric Romaní rock-shelter, previously associated with cold episodes: Stadial 17–15 and Heinrich Event 5, respectively (Fernández-García, 2014; López-García, 2011).

By combining PC1 and PC3, we can observe small differences in the association of levels (Fig. 4B). Positive values for PC3 are related with the occurrence of *E. quercinus* and, less importantly, with *C. nivalis* and *I. cabreræ*, while negative values are defined by the proportionally greater occurrence of *M. (T.) duodecimcostatus*, *A. sylvaticus* and

M. arvalis-agrestis. As occurred in the PC2, this makes an ecological interpretation somewhat more complex, but a chronological trend is conserved, clustering LLP closer to *M. arvalis-agrestis* and the rest (ELP and HOL) closer to *A. sylvaticus*. The only exceptions are the Galls Carboners assemblage and levels III and V from Cova del Gegant, a result of a tendency established by the predominance of *E. quercinus* in these samples, which is a particularity of these locations. However, the chronological distribution detected by the combination of PC1 and PC2 is in general terms maintained in the combination of PC1 and PC3, revealing the great influence of the *M. arvalis-agrestis* and *A. sylvaticus* bipolarization shown by PC1.

3.2.2. Cluster analysis

The results obtained by the cluster analysis of the total occurrences of species by time intervals are congruent with those obtained through the PCA (Fig. 5). Certainly, the divergence of the assemblages from the LLP from the other two time intervals can be appreciated, with the ELP and the HOL assemblages appearing closer to each other (Fig. 5B). This phenomenon can be observed clearly if the relative presence of the species by interval is tested, but also if we cluster their occurrence by isolated levels (Fig. 5A). The clustering level analysis shows only three possible outliers. The possible reasons for this anomaly have already been explained for the PCA. In the case of Level 2 from Toll cave (LLP), the high presence of *M. (T.) duodecimcostatus* would be determinant in its association.

Once again, the trend showed is probably related to the high occurrence of mid-European species during the LLP, while in the other two time intervals the dominant species are those common in forest environments and more temperate environments or climates with a Mediterranean influence. If we pay attention to how the graph shows the association of species (Fig. 5B), *M. arvalis-agrestis* is clearly far from the rest, as is *A. sylvaticus*. *M. (T.) duodecimcostatus* is also somewhat further away from the rest but to a lower degree. These relations demonstrate the singular character of these three species, which are commonly more abundant in northeastern assemblages, as has been observed by means of the PCA. The rest of the species appear much more clustered, with only *E. quercinus*, *A. sapidus*, *I. cabreræ* and *C. nivalis* showing a certain distance from the rest (but always within this group of unrepresentative species).

4. Discussion

There are some species that dominate in specific archaeological records as a result of the precise conditions of each site, including parameters such as the altitude, the proximity to the coast or to river courses. In the light of the results obtained in this study, however, it seems consistent to interpret an ecological trend reflected in the rodent associations, a trend that is relatively independent of the precise conditions of the archaeological sites in the Northeast of Iberia. In short, one can observe a gradient in the environmental conditions running from open spaces such as meadows or grasslands and linked to the presence of *M. arvalis-agrestis*, to more wooded areas or areas with greater vegetation cover associated with *A. sylvaticus*.

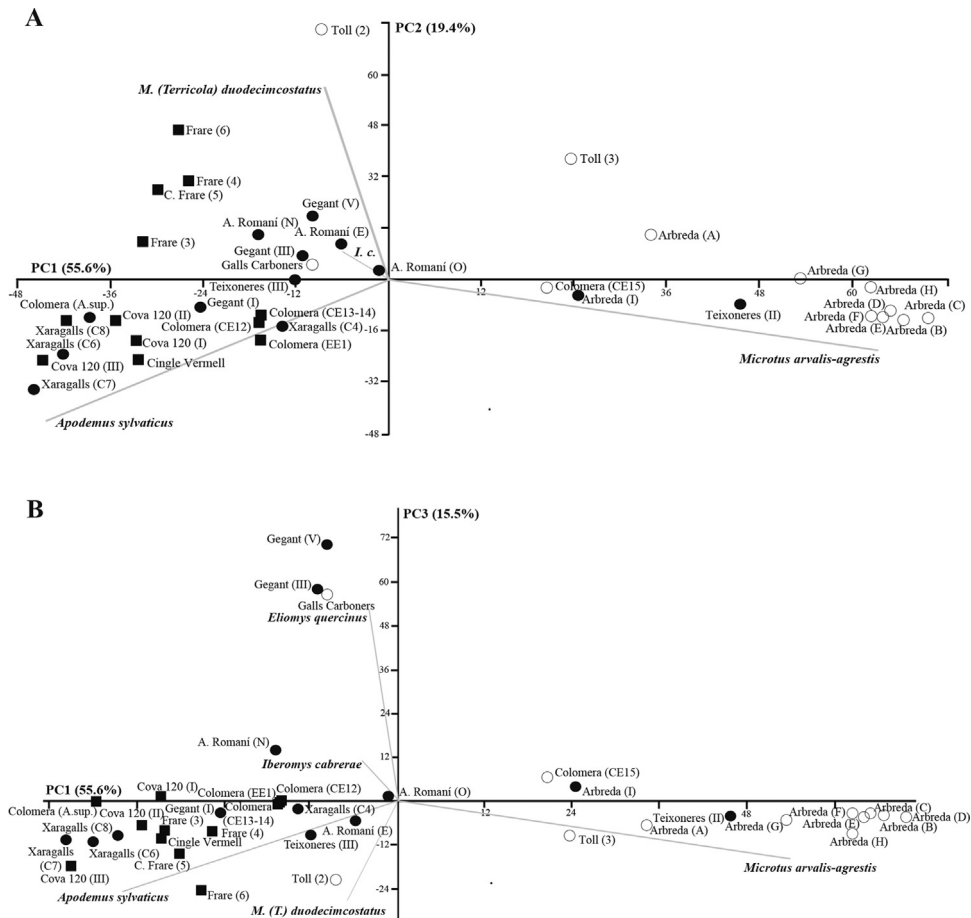


Fig. 4. Principal component analysis of Late Pleistocene–Holocene levels from northeastern Iberia according to rodent species occurrence. A. Graphical representation of components 1 (x) and 2 (y). B. Graphical representation of components 1 (x) and 3 (y). Early Late Pleistocene levels in black dots, Latest Late Pleistocene levels in white dots, and Holocene levels in squares.

Fig. 4. Analyse en composantes principales des niveaux du Pléistocène supérieur–Holocène des sites du Nord-Est de la péninsule Ibérique, selon la présence des espèces de rongeurs. A. Représentation graphique des composantes 1 (x) et 2 (y). B. Représentation graphique des composantes 1 (x) et 3 (y). Niveaux du début du Pléistocène supérieur en points noirs, derniers niveaux du Pléistocène supérieur tardif en points blancs, et niveaux de l’Holocène en carrés.

Nonetheless, the particularities of the Iberian Peninsula make some Mediterranean species (such as *M. (T.) duodecimcostatus* and *I. cabreræ*) or woodland species (such as *E. quercinus*) crucial in the interpretation of the environment (Palomo et al., 2007; Purroy and Varela, 2003). The continuous transitions in the ecological conditions between open and cooling environments and more forested and temperate ones constitute a common tendency in the western Mediterranean during the Late Pleistocene cycles (Harrison and Sánchez-Goñi, 2010). Overall, the Late Pleistocene is in general terms considered colder than the Holocene because of the alternation of glacial and interglacial cycles, whereas the Holocene constitutes an interval of climatic recovery, identified as the last interglacial before the present (Uriate, 2003). However, we can see a greater proximity in the overall association of species during the HOL and ELP than during the LLP. The singularity of the LLP can be observed in its fauna composition characterized by species related with mid-European requirements and open environments (*M. arvalis*, *M. agrestis* and *C. nivalis*). By contrast, the ELP (Middle Palaeolithic) assemblages are not as

different from the HOL ones as might have been expected, presenting similar proportions of woodland species (*A. sylvaticus*) and Mediterranean species (*M. (T.) duodecimcostatus* and *I. cabreræ*). This can be understood in terms of climate issues related with MIS 2 and the Last Glacial Maximum (LGM), which testifies to the largest drop in temperature experienced during this time interval and the subsequent reduction of wood cover (Sánchez-Goñi and D’Errico, 2005). However, it should be borne in mind that this phenomenon occurs in lower intensity in Iberia than in the rest of Europe, where the conditions of aridity in cold moments are more pronounced, as reflected in faunal communities and other proxies (Fletcher and Sánchez-Goñi, 2008; Sommer and Nadachowski, 2006). The maintenance of woodland cover remains a constant in Iberia in spite of the intervals of instability.

4.1. Early Late Pleistocene environment (128–40 ka BP)

During MIS 4, solar insolation was minimal, initiating a global cold period. Long-term pollen records obtained

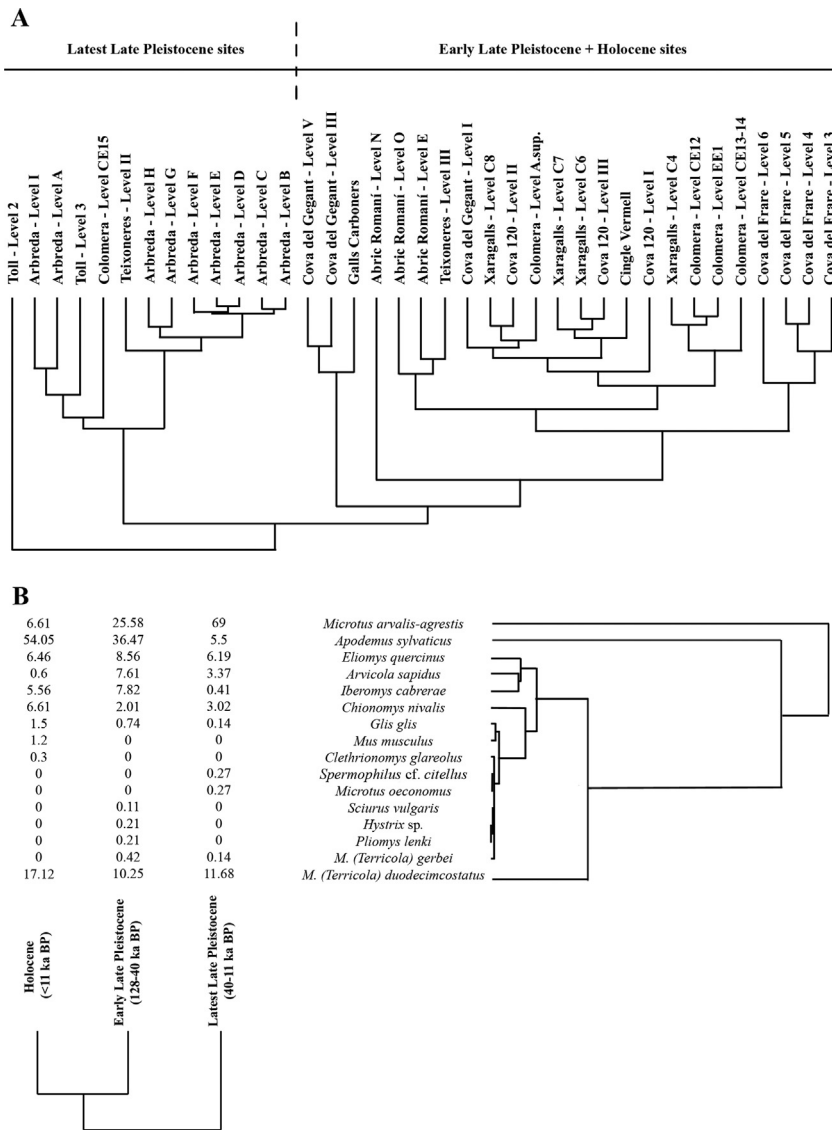


Fig. 5. Late Pleistocene–Holocene species occurrence in northeastern Iberia by cluster analysis in different levels (A) and associated by chronological periods (B) (on the top right, the species groups and, on the lower left margin, the periods grouped).

Fig. 5. Analyse de groupes montrant la présence des espèces dans les différents niveaux des sites du Nord-Est de la péninsule Ibérique au Pléistocène supérieur–Holocène (A) et associées par périodes chronologiques (B) (en haut à droite, les groupes d'espèces et, sur la marge inférieure gauche, les périodes regroupées).

from French lacustrine deposits, such as La Grande Pile and the Velay Maars, indicate the predominance of boreal forests during MIS 4, declining at the end of MIS 4 with the expansion of steppe–tundra vegetation (Fletcher et al., 2010; Sánchez-Goñi et al., 2008). According to pollen analysis, MIS 3 is characterized in southern Europe by a dynamic that alternates between phases of forest development and the expansion of semi-arid areas in accordance with the warming and cooling, respectively, of the sea-surface temperatures (Fletcher et al., 2010; Harrison and Sánchez-Goñi, 2010). However, various proxies, including pollen and small mammals, have shown that this alternation of dryness and wetness and the consequent reduction–extension of forest are not straightforward.

There are many Middle Palaeolithic sites located in the Northeast of Iberia during MIS 3. Some of them present interesting climatic reconstructions based on small mammals, such as Level II from Teixoneres cave (60–30 ka BP), Level IV from Cova del Gegant (60 ± 3.8 ka BP), Level O from Abric Romaní (54.24 ± 0.42 ka BP), Level C8 from Xaragalls cave (> 43.5 ka BP), Level I from Arbreda cave (40–32 ka BP) and Galls Carboners (31.38–31.17 ka BP) (Fernández-García, 2014; López-García, 2011; López-García et al., 2012a,b,c, 2014b). As has previously been reported by López-García et al. (2014c), small-mammal proxies show lower mean annual temperatures and higher precipitation levels throughout this period in this region (Fernández-García, 2014). Coexistence is also

observed between temperate and cold rodent species, which underwent changes in proportion depending on the stadial-interstadial fluctuations. Moreover, Mediterranean species (*M. (T.) duodecimcostatus* or *I. cabreræ*) are always present in the assemblages. However, the predominance of typical woodland species (*A. sylvaticus* and *E. quercinus*) in MIS 3 assemblages becomes a defining characteristic of the environment conditions, independent of whether it was a stadial or interstadial phase. These two latter trends are probably related with the clustering of the ELP sites with HOL assemblages in the statistical proxy in this paper.

This is coherent with palynological studies that have suggested that southern Europe (below 40°N) never underwent a complete loss of woodland, even in stadials or Heinrich Events (Fletcher et al., 2010). During interstadials the forest recovered extremely quickly, though depending on regional climatic conditions (Fletcher et al., 2010; Sánchez-Goñi and D'Errico, 2005). The Mediterranean coast was where the forest development was most pronounced, as a result of the influence of the Mediterranean climate and the smaller effect of North Atlantic fluctuations (Fletcher et al., 2010; Harrison and Sánchez-Goñi, 2010). In fact, important differences from the rodent communities of southwestern France can be noted. The typical rodent species in sedimentary sequences from MIS 4 and MIS 3 in these areas are *M. arvalis*, *Microtus gregalis* and *Dicrostonyx torquatus* (Chaline, 1972; Marquet, 1993; Royer et al., 2013). These three species today live in open habitats (tundras, forested tundras or steppes) and have a distribution that is latitude-dependent (MacDonald and Barrett, 2008). Their presence thus argues in favour of a very cold and arid environment, different from that detected for the Northeast of Iberia during this interval.

4.2. Latest Late Pleistocene (40–14.7 ka BP)

The LLP is basically represented by the end of MIS 3, the complete MIS 2 and the beginning of MIS 1 (ca. 14.7 ka BP) (Lisiecki and Raymo, 2005). These stages are highlighted in all geological sources as the most intense glacial phases, characterized by rapid and major climatic changes (Vermeersch, 2005), and ranging chronologically from ca. 27 to 11.7 ka BP. MIS 2 contains two Heinrich Events (H2 and H1), dated respectively to ca. 24 ka BP (H2) and to 16 ka BP (Oldest Dryas or H1), and also the Last Glacial Maximum (LGM) (ca. 22–19 ka BP), the moment of maximum cold in the Northern Hemisphere which represents the time of maximum extension of ice sheets at the polar caps (Fletcher and Sánchez-Goñi, 2008). This singularity of the LLP (Upper Palaeolithic) can be observed beyond the changes in the fauna composition and is clear in our statistical proxy, associated with an important increase in the species related with mid-European requirements and open environments (*M. arvalis*, *M. agrestis* and *C. nivalis*) and a lower representation of woodland species (*A. sylvaticus*).

According to the available data, the rodent species present in the northeastern Iberian Peninsula during the LLP were predominantly mid-European taxa with an ecological preference for cold environmental conditions (*M. arvalis* and *M. agrestis*), humid meadows (*M. agrestis* and *M. (T.) gerbei*) and, to a lesser extent, open forests

(*A. sylvaticus* and *E. quercinus*) (Alcalde, 1986; López-García, 2011). Assemblages with such characteristics have been described in Levels C4–C1 of Cova dels Xaragalls (48.2–13.7 ka BP) (López-García et al., 2012a), Level III of Balma de la Griera (21.2 ka BP) (Nadal, 2000) and the oldest levels of Arbreda cave (39.9–17.3 ka BP) (Alcalde, 1986; López-García, 2011). LLP levels from Arbreda cave (39.9–17.32 ka BP) present a clear predominance of rodent species associated with open humid conditions (*M. arvalis*, *M. agrestis* and *M. (T.) duodecimcostatus*), whereas species associated with forest conditions are present in much lower proportions (*A. sylvaticus*, *G. glis* and *E. quercinus*). The association is also characterized by a strong representation of mid-European species (*M. arvalis* and *M. agrestis*), meaning cold conditions and open landscapes (Alcalde, 1986; Alcalde and Brunet-Lecomte, 1985). This great relative abundance of *M. arvalis* and *M. agrestis* is a common trend in other sites in Iberia (López-García, 2011). Additionally, it has been detected in some southern French sequences, accompanied by a high presence of *Microtus gregalis*, as at Tailles-des-Coteaux (Jeannet, 2011; Royer et al., 2014), and is also common in the LLP sites of the Italian Peninsula, such as Grotta della Serratura, Cava Filo, Grotta de la Ferrovia, Grotta Paglicci, Riparo Tagliente and Grotta del Romito (Berto, 2013; Bertolini et al., 1996; López-García et al., 2014a).

However, mention should be made of the Galls Carboners (López-García et al., 2014b) assemblage, which is located somewhat further away from the rest of the LLP levels in our PCA proxy. Associated with Heinrich Event 3, this level is at a distance from the rest of the sites as a result of the high presence of *E. quercinus*, a generalist species that is nonetheless linked with woodland cover, and the scarce representation of *M. arvalis-agrestis* group. This site provides an example of the particularities of small-mammal proxies in the Iberian Peninsula. Firstly, it warns us that there are other species, generally less abundant than *A. sylvaticus*, which should also be taken into account in the definition of open vs. closed landscape changes; in other words, that we cannot reduce the north-eastern Iberian scenario to the bipolarization between *M. arvalis-agrestis* and *A. sylvaticus*. In this case, *E. quercinus* is the predominant species, indicating the importance of woodland cover, as well as *C. nivalis*, a species that is scarcely present in the northeastern Iberian Peninsula but is extremely indicative of cool periods (nowadays being restricted to the Pyrenean region) (Palomo et al., 2007; Pérez-Aranda, 2009). Secondly, it warns us that, within the cool and open environmental tendency of the LLP, some Iberian sites were exceptions to the global European pattern, showing the importance of a Mediterranean influence, also influenced by their geographical location. This finds expression in the maintenance of woodland cover even in the coldest episodes, such as Heinrich Event 3 or the LGM.

In fact, the Iberian Peninsula enjoyed a milder climate than the rest of Europe and served as a refugium for certain mid-European species (Sommer and Nadachowski, 2006), such as *C. nivalis* or *M. oeconomicus*. Marine cores close to the coast of Iberia Peninsula reveal that during the LGM the Iberian Peninsula was characterized by

conditions that were slightly more humid than in the rest of Europe (Fletcher and Sánchez-Goñi, 2008; Kageyama et al., 2005; Sánchez-Goñi and D'Errico, 2005). The study of pollen fluctuations has established that the climate was cold and wet during the LGM (Kageyama et al., 2005), while the analysis of lakes has shown a greater degree of humidity than in other areas of Europe during the same interval. The study of small-mammal faunas from Iberia has also suggested a predominance of woodland during this time interval, with small-mammal species indicating an environment with a high level of humidity. This has been shown by small-mammal studies from four Iberian sites dated to the LGM: El Mirón Cave (Ramales de Victoria, Cantabria), Valdavara-1 (Becerreá, Lugo), El Portalón (Sierra de Atapuerca, Burgos) and Sala de las Chimeneas (Maltravieso, Cáceres) (Bañuls-Cardona et al., 2014; Cuenca-Bescós et al., 2009; López-García et al., 2011, 2012b). In general, these sites show a combination of species associated with mid-European requirements (*M. arvalis*, *M. agrestis*, *M. oeconomus* and *C. nivalis*) and species associated with Mediterranean climatic conditions (*I. cabreræ* and *M. (T.) duodecimcostatus*). As regards the landscape, there is a high presence of species associated with open woodland areas and wet environments. In short, it is suggested that the climate was harsher than nowadays during the LLP, though not as rigorous as elsewhere in Europe, with mean annual temperatures lower than at present and an environment dominated by wet open meadows (with species associated with humidity: *A. terrestris* and *M. agrestis*). However, it is also considered a more humid period than in the rest of Europe with higher precipitation levels than nowadays.

4.3. Pleistocene–Holocene transition (< 14.7 ka BP)

This glacial maximum phase is followed by the Late Glacial (corresponding to the beginning of MIS 1), which precedes the Holocene and ranges chronologically from ca. 14.7 to 11.7 ka BP (Bradley and England, 2008; Lisiecki and Raymo, 2005; Walker et al., 2009). The Younger Dryas–Holocene transition is dated to ca. 10–11 ka BP, and is characterized by a sharp increase in temperatures and precipitation, constituting a definitive break from Pleistocene climatic dynamics and leading to the climatic improvement related to the Holocene, an overall stable period from the thermal point of view (Bradley and England, 2008; Walker et al., 2009). Many studies demonstrate a clear change in the landscape composition of the Iberian Peninsula during this period, which culminated in the current composition of the flora and fauna. In the Iberian Peninsula a variety of pollen and anthracological sequences reveal this sudden rupture, with the majority agreeing that there was a change in landscape composition marked in most places by the substitution of certain taxa by others (Carrión et al., 2010; Fernández et al., 2007; Gil García et al., 2002). There is clear increase in thermophilous plant species indicative of a warm climate and in species associated with vegetation cover, with a greater expansion of forests to the detriment of open spaces (Burjachs and Renault-Miskovsky, 1992; Carrión et al., 2010).

This change is also manifest in the small-vertebrate associations from the Northeast of the Iberian Peninsula. The general pattern observed throughout rodent communities is a sharp increase in taxa with warmer requirements or a Mediterranean character (*M. (T.) duodecimcostatus* and *I. cabreræ*) and others linked to forest habitats (*A. sylvaticus* and *E. quercinus*), together with a decrease in mid-European species with cold requirements and open habitat preferences (*M. arvalis*, *M. agrestis* and *C. nivalis*). This transition is detected in several localities, such as Toll Cave (35–13 ka BP), Balma de la Griera (21.25 ± 0.35 ka BP), Cova Colomera (13–3 ka BP), Cingle Vermell (9.76 ± 0.16 ka BP) and Cova de la Guineu (9.8 ± 0.8 ka BP) (Alcalde, 1986; Alcalde and Brunet-Lecomte, 1985; Fernández-García and López-García, 2013; López-García, 2011; López-García et al., 2010). The greater or lesser descent in mid-European species depends on the particular characteristics of the sites in question (latitude, altitude, proximity to coast); sites of mid-European influence and at high altitude will preserve adequate conditions for the preservation of some of these specimens, as at Cova Colomera (López-García et al., 2010).

The Pleistocene–Holocene faunal transition can also be detected in other small-mammal associations from Iberia. There is a break in the faunal assemblage at the cave of El Mirador in Burgos (López-García et al., 2008), where this transition is marked by the disappearance of micro-mammal species with mid-European requirements such as *C. nivalis* and *M. oeconomus*, taxa with mid-European requirements and nowadays only found at higher altitudes. It is also in evidence at El Mirón in Cantabria (Cuenca-Bescós et al., 2009). This transition is also present in other southern European localities; a turning point is detected in faunal assemblages from this period in southern Italy. There, the general trend is the replacement of *M. arvalis* and *M. agrestis* by a strictly Mediterranean species, *M. (T.) savii*. This phenomenon is observed in Grotta de la Seratura, Riparo Salvini, Grotta Paglicci, Caballo Cave and Grotta delle Mura (Berto, 2013; Bertolini et al., 1996). However, in Grotta del Romito (Calabria) this substitution is related with the dominance of a glirid species, *Glis glis*, associated with woodland formations (López-García et al., 2014a). However, both species indicate a climatic improvement, with an increase in forest cover.

5. Conclusions

Both descriptive statistical methods and more complex statistical methods bring to light that there are three dominant species during the studied chronology: *Microtus arvalis*, *Microtus agrestis* and *Apodemus sylvaticus*. *M. arvalis* and *M. agrestis* are species associated with mid-European requirements that were especially dominant at the end of the Late Pleistocene (ca. 40–11.7 ka BP), whereas *A. sylvaticus*, a generalist species but mainly associated with wooded areas and temperate environments, was dominant at the beginning of the Late Pleistocene (ca. 128–30 ka BP) and regained its importance with the arrival of the Holocene (< 11.7 ka BP). Accordingly, this bipolarization between *M. arvalis-agrestis* and *A. sylvaticus* could be interpreted as a transition in the ecological conditions at the different sites

between open, cooling environments and more forested and temperate ones. Nevertheless, there are other species that seem determinant to evaluate the faunal dynamics of this time interval (*M. (T.) duodecimcostatus*, *E. quercinus* and *I. cabreræ*). The results also show that the beginning of the Late Pleistocene and the Holocene have similarities in common and differ clearly from the end of the Late Pleistocene, demonstrating the singular nature of the environment associated with the extreme environmental conditions of MIS 2 and the Late Glacial Maximum in the Northeast of the Iberian Peninsula. Other palaeoenvironmental proxies and small-mammal studies from Iberia and southern Europe confirm the singular nature of the latest Late Pleistocene and the general increase in woodland cover with the arrival of the Holocene period.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.crpv.2015.08.005>.

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