



Redefining the MIS 3 climatic scenario for Neanderthals in northeastern Iberia: A multi-method approach

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ABSTRACT

One of the major challenges in scientific research is to understand past climate and the mechanisms of climate change. Small vertebrates, and especially rodents, are very sensitive to shifts in climate and habitat, and their variations over time in terms of taxa and abundance can be successfully used to reconstruct past environments. The vast array of approaches to palaeoclimatic reconstruction reflects the great effort that has gone into this line of investigation. Recently, the UDA-ODA discrimination technique has been postulated as a more reliable ecologically-based methodology compared to the classical MER method.

To provide biogeographical information to be analysed by the UDA-ODA discrimination technique, the distributions of four species (*Sorex minutus*, *Chionomys nivalis*, *Talpa europaea* and *Crocidura russula*) documented in levels O, N, E and D of the Abric Romaní site were processed. The results reveal a statistical difference between the climatic values for the occupied distribution areas (ODA) and those for the uncertain distribution areas (UDA). This technique was then applied to small-mammal assemblages from the above-mentioned levels of Abric Romaní, to test whether the use of the ODAs of the species improves the precision of the climatic reconstruction compared to the atlas distributions of the species used in MER procedures. Our results suggest an improvement in the discrimination analysis over the previous MER reconstructions when wider distributions for an assemblage are obtained. The coldest values obtained for level O of Abric Romaní seem to reinforce the pollen interpretation of the level as coetaneous with a cold period. For the whole MIS 3 climatic scenario for Neanderthals, a colder and wetter climate is derived from the small-mammal analysis. However, as different methods and analyses have inherent limitations, a standardization of the methods applied to the different levels and sites should be carried out in order to provide comparable results.

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Abbreviations: BM, bioclimatic model; m.a.s.l., meters above the sea level; MAP, mean annual precipitation; MAT, mean annual temperature; MER, mutual ecogeographic range; MTC, minimum temperature of the coldest month; MTW, maximum temperature of the warmest month; ODA, occupied distribution area; SD, standard deviation; Sig, significance; UDA, uncertain distribution area; UTM, universal transversal mercator.

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1. Introduction

One of the most researched topics in Quaternary palaeoecology is the reconstruction and interpretation of past atmospheric and ocean temperatures, which have been undertaken since the first half of the 20th century.

Environmental reconstructions are often qualitative and are presented as broad climate ranges (cold, wet, hot ...). However, palaeotemperature estimations have improved considerably in their accuracy and reliability over the past few decades (Lyman, 2017; Blain et al., 2016; Fernández-García et al., 2019; Royer et al., 2020, among others), and the demands for quantitative reconstructions of past climatic approaches have been met. The basic assumption of all climatic-environmental reconstructions in Quaternary palaeoecology is methodological uniformitarianism, that is the principle that the relationship between organism and environment has not changed over time and therefore current observations can be used as a model for past conditions (Gould, 1965; Birks et al., 2010).

In this work we carry out a methodological review of some of the most widely used methods of palaeoclimatic reconstruction based on small-mammal assemblages, focusing on levels D, E, N and O of the Abric Romaní site, where environmental estimations based on different proxies are available. The aim of this work is to shed light on the origins of the discrepancies in the different methods of palaeoclimatic reconstruction and to understand the climatic context of the well-established Neanderthals at this site, as well as the environmental evolution allowing for the subsistence of these populations. These hunter-gatherer groups, whose survival is strongly conditioned by their adaptation to the environment, would also be influenced by Quaternary climatic dynamics (Stewart, 2005).

2. Regional setting: Abric Romaní

Abric Romaní is a wide rock shelter in the Quaternary travertine cliff formation called *Cinglera del Capelló*, located in the town of Capellades (Barcelona, NE Iberia) (41° 31' 58" N, 1° 41' 17" E) at 265 m. a.s.l., in a narrow corridor through which the River Anoia runs. This position constitutes a strategic location, as the corridor connects the inland area with the coast, allowing access for past human groups to different ecotones (Fig. 1A).

The 20 m-deep stratigraphic sequence is mainly formed by well-stratified travertine sediments and includes 20 archaeological levels, 18 of which (from A to R) have been excavated to date. These all belong to the Middle Palaeolithic, except the uppermost level A, which is assigned to the Proto-Aurignacian (Carbonell et al., 1996; Vaquero et al., 2013). U-series and 14C-AMS dates indicate a chronological sequence ranging from ca. 40 ka (Level A) to ca. 60 ka (Bischoff et al., 1988; Vaquero et al., 2013). Drilling revealed an extension of the archaeological stratigraphy of 30 m below the levels excavated to date, reaching ~110 ka (U-series dating) 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, connecting regional aquifer springs with the River Anoia. Rock fragmentation and 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).

Capellades now falls within the continental sub-humid Mediterranean climate (Servei Meteorològic de Catalunya, 2018) and the mesomediterranean thermoclimatic stage (Rivas-Martínez, 1987). The climate is generally warm and temperate with a mean annual temperature of 13.9 °C, hot summers, and cool winters. The mean

annual precipitation is 628 mm, the wet seasons being spring and autumn, whereas winter and summer are relatively dry (Fick and Hijmans, 2017; Servei Meteorològic de Catalunya, 2018) (Fig. 1B).

Different environmental proxies have been addressed along the Abric Romaní stratigraphic sequence. Palaeobotanical proxies such as pollen and charcoal indicate the predominance of the genus *Pinus* around the site along the entire sequence. The expansions and contractions in these pine trees, related thermophilous taxa, and minor secondary vegetation formations have been correlated with the succession of wet and warm or cold and arid climatic episodes (Burjachs et al., 2012; Allué et al., 2017). Faunal proxies reveal formations of open forests and humid environments around the site (Burjachs et al., 2012; López-García et al., 2014; Fernández-García et al., 2016). Among the faunal remains, the amphibians and squamates, which are scarce at the site, are associated with cold and wet forest environments. The combination of these biological proxies has led to changes in the relative abundances of specific species with certain requirements being linked with stadial phases and resulted in different climatic correlations (levels D, E with Greenland Interstadial 12 (GI); levels Ja to H with Heinrich Event E5 (HE); level N with GI 16; level O with Greenland Stadial 17 (GS)) (Burjachs et al., 2012; López-García et al., 2014; Fernández-García et al., 2018).

As regards the large mammals at the site, a total of thirteen taxa have been recovered and identified as being a result of the activity of Neanderthals, who had primary access to the animal carcasses. Large and medium ungulates are predominant, red deer and equids being the most abundant species. Carnivores such as bears (*Ursus arctos*), wolves (*Canis lupus*), foxes (*Vulpes*), hyenas (*Crocuta spelaea*), lions (*Panthera spelaea*), panthers (*Panthera pardus*), lynx (*Lynx spelaea*), and wild cats (*Felis sylvestris*) are documented, although their presence is very scarce (Fernández-Laso et al., 2010; Chacón et al., 2014; Rosell et al., 2012, 2019; Gabucio et al., 2016; Modolo and Rosell, 2017; Marín et al., 2017). The lithic materials, typical of Middle Palaeolithic sites, mainly consists of chert, quartz, and limestone made with local and semi-local raw materials (Gómez de Soler et al., 2020; Gómez de Soler, 2009).

3. Material and methods

To determine the palaeoclimatic conditions at the Abric Romaní site (levels O, N, E, D), several methods have been applied: the mutual ecogeographic range (MER) method, the bioclimatic model (BM), and the UDA-ODA discrimination technique (Blain et al., 2009, 2016; Fagoaga et al., 2019b; Royer et al., 2020). Additionally, a variation on this latter method has also been applied, which consists of obtaining past climatic values from the mean temperatures and precipitation of the whole occupied distribution areas calculated for each species in the different levels (here called the mean ODAs method). The criterion for the selection of the levels was the possibility of conducting several palaeoclimatic estimations. The faunal list used here stems from Fernández-García (2020) and is set out in Table 1.

The MER method consists in identifying the geographic regions where all the species from the same assemblage live nowadays and extrapolating the current mean values of the climatic parameters to the past (Blain et al., 2009). An assumption that must be borne in mind is that the fossil representatives of the extant species have the same climatic tolerances and preferences as their living counterparts (Lyman, 2017). For both methods, the current distributions of species in the Iberian Peninsula were obtained from Palomo et al. (2007) and Bencatel et al. (2017), recording the presence/absence of each mammal taxon in 10 × 10 km square grids.

The UDA-ODA discrimination technique was used to identify species distributions within the 10 × 10 km square grid with

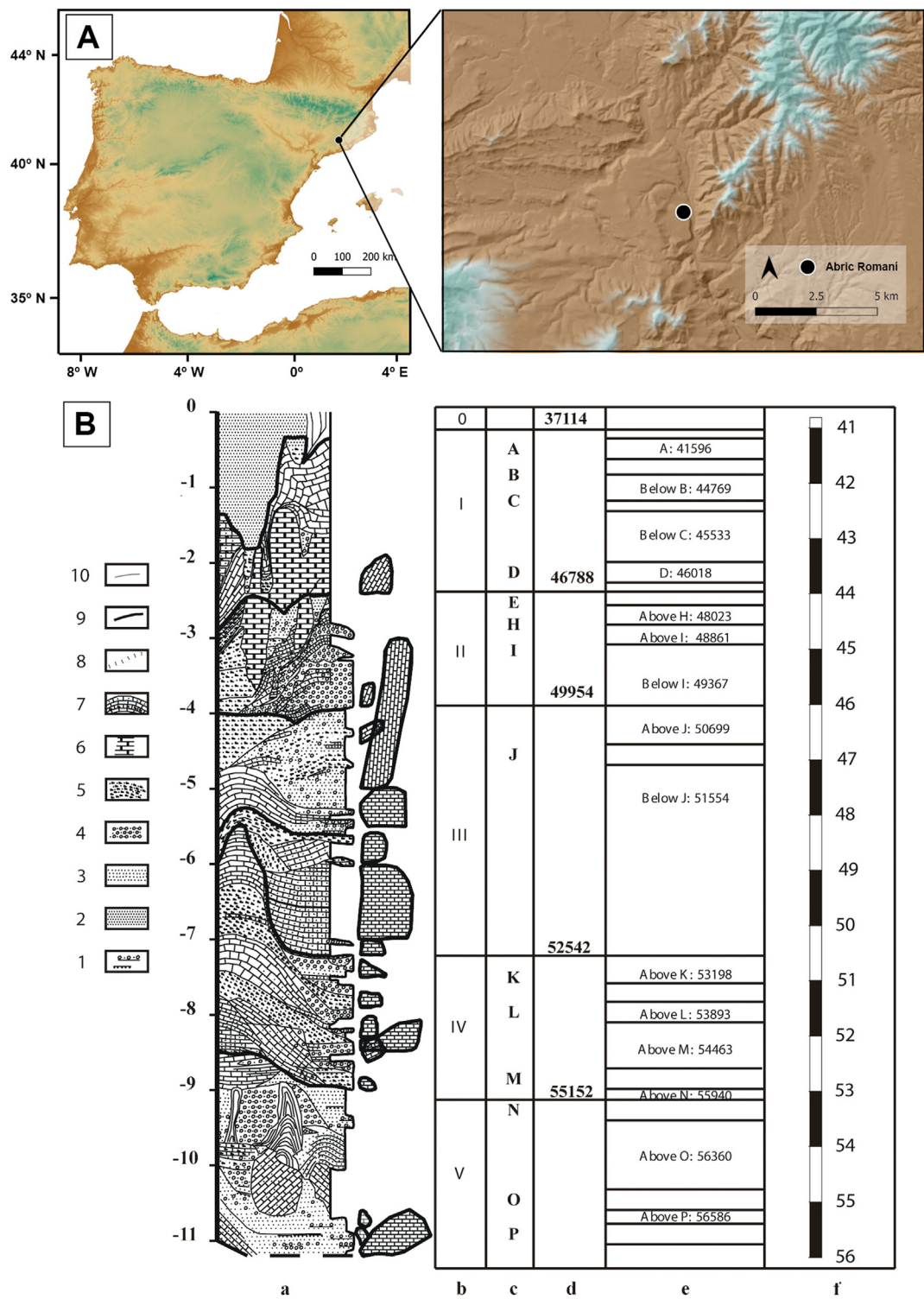


Fig. 1. A) Geographic location of the Abric Romaní site in the Iberian Peninsula and its position in the Anoia region. B) Stratigraphy and dating of the Coveta Nord sequence from the Abric Romaní rock shelter (modified from Vallverdú i Poch, 2018). Lithofacies legend: 1, bedded calcitic sands and travertine gravels; 2, siliciclastic and calcitic muddy sands; 3, calcitic sands; 4, travertine gravels and calcitic sands; 5, crystalline gravels and sands; 6, crystalline lamination; 7, microbreccia, calcarenite and stromatolithic lamination; 8, archaeological level; 9, boundary sequence; 10, diastem. Commentaries table: a, lithostratigraphy; b, sequence number; c, letters of archaeological levels; d, Bayesian dates for the start of the Abric Romaní sequences; e, Bayesian dates for Abric Romaní archaeological levels; f, U-series, radiocarbon, and luminescence dates of the Abric Romaní sedimentary samples (modified from Vallverdú i Poch, 2018).

greater precision. A distinction was drawn between the occupied distribution area (ODA), which calculates the real occupied areas where the species may be present using the species' environmental requirements as described in the literature, and the UDA (uncertain distribution area), which determines the areas within the species distribution where the species may be absent in accordance with

Table 1

Species identified in levels O, N, E, and D of the Abric Romaní site, as derived from Fernández-García (2020). 1 indicates presence, 0 absence. (*) denotes taxa not included in the palaeoclimatic reconstruction because their determination does not achieve species level, or their distribution is too perturbed.

Species	Level			
	O	N	E	D
<i>Crociodura russula</i>	1	0	1	1
<i>Sorex</i> gr. <i>Araneus/coronatus</i> *	1	0	1	0
<i>Sorex minutus</i>	1	0	0	0
<i>Neomys</i> gr. <i>Fodiens/anomalus</i> *	1	0	0	0
<i>Talpa europaea</i>	1	1	0	0
<i>Arvicola sapidus</i>	1	1	1	1
<i>Microtus arvalis</i>	1	0	1	1
<i>Microtus agrestis</i>	1	1	1	1
<i>Microtus cabreræ</i> *	1	1	1	1
<i>Chionomys nivalis</i>	1	1	1	0
<i>Microtus duodecimcostatus</i>	1	1	1	1
<i>Apodemus sylvaticus</i>	1	1	1	1
<i>Eliomys quercinus</i>	1	1	1	1
<i>Sciurus vulgaris</i>	1	0	0	0
Total	14	8	10	8

their ecological requirements (Palomo et al., 2007; Bencatel et al., 2017; Fagoaga et al., 2019b). Accordingly, our methodology considers elevation as the primary factor for discriminating ODA areas for each species (Table 2). In the case of *Chionomys nivalis* and *Sorex minutus* we also considered habitat preferences. From these more precisely defined regions, we extracted the current mean values of the climatic parameters for each species' ODA and UDA distribution, as well as using the MER method (atlas distributions) on the WorldClim 2 (Fick and Hijmans, 2017) climatic datasets: MAT, mean annual temperature; MTW, maximum temperature of the warmest month; MTC, minimum temperature of the coldest month; MAP, mean annual precipitation. For each species, we searched for their habitat preferences and elevation range (Table 2). Once each species' ODA and UDA distributions were obtained, ODA of the species were overlapped to find the mutual distribution for each assemblage studied (as MER method does with the whole assemblage). Climatic data codified in raster format (pixels) with 30 s of spatial resolution ($0.93 \times 0.93 = 0.86 \text{ km}^2$) were extrapolated to the time period of formation for each assemblage.

The MER method, and consequently the UDA-ODA discrimination technique as well, suggests avoiding species whose distribution is strongly affected by perturbing parameters such as human pressure. *Microtus cabreræ* has thus been removed from this study because it has undergone a contraction in range (Laplana and Sevilla, 2013), and many subpopulations are small, fragmented,

and subject to major interannual fluctuations (Palomo, 1999; Palomo and Gisbert, 2002). Only taxa determined to species level have been included in the analyses. Bats were removed from the overlapping analysis, as their distribution in the Iberian Peninsula is still not clear with the accuracy of other mammals. The occupied distribution areas for the species *Arvicola sapidus*, *Microtus agrestis*, *Microtus arvalis*, *Microtus duodecimcostatus*, *Apodemus sylvaticus*, and *Eliomys quercinus* were already calculated by Fagoaga et al. (2019b). The occupied distributions of *Crociodura russula*, *Chionomys nivalis*, *Sorex minutus*, and *Talpa europaea* are processed here. The MER method and the UDA-ODA discrimination technique were performed with QGIS 3.22 Białowieża.

The results established by the MER method cannot be compared directly with those based on ODA and UDA distributions, as these are a subsample of MER (Sokal and Rohlf, 2009). Therefore, mean statistical comparisons were performed between ODA and UDA for each species and level (variable and species; variable and assemblage). Significant differences between mean climatic values from ODA and UDA are taken to point to an improvement in the discrimination analysis over the MER method. If ODA and UDA are different, the areas corresponding to the absence of species will have a strong influence on the MER results. These areas must thus be excluded to obtain better estimates of past environments. These statistical analyses were performed using IBM® SPSS® Statistics software.

The refined bioclimatic method (Royer et al., 2020), developed from Hernández Fernández (2008) and Hernández Fernández and Peláez-Campomanes (2005), is based on a climatic restriction index for each small-mammal species ($\text{CRI}_i = 1/n$, where i is the climatic zone inhabited by the species and n is the number of climatic zones inhabited by the species). Based on each species' CRI, the bioclimatic component can be calculated ($\text{BC}_i = (\sum \text{CRI}_i)100/S$, where S is the number of species), constituting the representation of the species in a specific locality for each of the existing climates. From the BC it is then possible to calculate different climatic parameters by multiple linear regression, developed specifically for rodents and insectivores. Species weightings were deduced from the original species matrix for bioclimatic ascriptions provided by Hernández Fernández (2008) and Hernández Fernández et al. (2007), taking into account the update by Royer et al. (2020), who provide an R script (R v3.3.2; R Core Team, 2016) for the application of the bioclimatic model. The climatic parameters estimated are the mean annual temperature (MAT) and mean annual precipitation (MAP).

Current climatic values were extracted for the whole of Capel-lades using climate layers from WorldClim 2 with QGIS (Fick and Hijmans, 2017).

Table 2

Synthetic notes on the current distribution, elevation range, and habitat preferences for the species identified in the studied levels of Abric Romaní that were processed by the UDA-ODA discrimination technique. m.a.s.l.: metres above sea level. Data obtained from Palomo et al. (2007) and Bencatel et al. (2017).

Taxon	Distribution in Portugal	Distribution in Spain	Elevation range (m.a.s.l.)	Habitat preferences
<i>C. russula</i>	All continental Portugal	All the Iberian Peninsula including Gran Canaria	0–1500 (Catalan Pyrenees) 0–2000 (Mediterranean region)	Mediterranean requirements
<i>C. nivalis</i>	Northern Portugal. Recent presence confirmed in the Serra do Montesinho	Mountain areas in Lugo and the Sierra de los Ancares, the Sierra de la Demanda, the Sierra Cebollera, the Sierra de Gredos, Guadarrama, the Sierra Nevada, the Pyrenees, and most of the Cantabrian region.	More than 2000 in the Sierra Nevada More than 1800 in Guadarrama More than 1400 in the Pyrenees	Screes, rocky outcrops, and boulders.
<i>S. minutus</i>	Northeastern Portugal	From Galicia to Catalonia, northern end of the Iberian System	0–2000	Areas with more than 600 mm of annual precipitation
<i>T. europaea</i>	Absent	The Pyrenees and the Pre-Pyrenees, the Iberian System, the Cantabrian Mountain Range, mountains in Navarra, Euskal Herria and Burgos.	0–2000	Soft soils

Table 3

Mean values and standard deviation (SD) for MAT (mean annual temperature) and MAP (mean annual precipitation) for each species according to the atlas distribution (complete distributions from atlases) (Palomo et al., 2007; Bencatel et al., 2017), ODA, and UDA. The significance level of the Mann–Whitney *U* test is calculated from the values of ODA and UDA. In bold is the highest value from the comparison of ODA and UDA.

	Atlas distributions		ODA		UDA		Mann–Whitney <i>U</i> test
	Mean	SD	Mean	SD	Mean	SD	
<i>C. nivalis</i>							
MAT	8.41	2.72	7	3.18	10.07	2.3	0.000
MAP	943	281	1087	297	853	219	0.000
<i>T. europaea</i>							
MAT	10.41	2.82	10.81	2.15	2.65	1.28	0.000
MAP	871	270	845	242	1407	99	0.000
<i>S. minutus</i>							
MAT	10.33	2.53	12.60	0.93	7.83	3.9	0.000
MAP	971	280	1060	143	881	405	0.000
<i>C. russula</i>							
MAT	13.16	2.61	13.30	1.9	4.97	1.89	0.000
MAP	647	288	694	120	1213	194	0.000

4. Results

4.1. UDA-ODA discrimination technique: method comparison by variable and species

The non-parametric Mann–Whitney *U* test was applied to two independent samples for each climatic parameter for each species identified from the analysed levels at Abric Romaní (Table 1). A non-parametric test was conducted because neither normality nor homogeneity of variance is met. The Mann–Whitney *U* test shows significant differences between UDA and ODA for all the species and variables analysed. The non-parametric test was carried out after the normality test had rejected the null hypothesis. ODA had higher mean temperature values than UDA in all species except *C. nivalis*. As regards precipitation, *C. nivalis* and *S. minutus* had higher mean precipitation values for ODA than for UDA, whereas higher values were obtained for UDA for *T. europaea* and *C. russula* (Table 3).

4.2. UDA-ODA discrimination technique: method comparison by variable and assemblage

Bearing in mind that the distribution values were not normal, a non-parametric test was conducted. Only in level D were ODA and UDA significantly different for both climatic parameters (temperature and precipitation). In levels E, N, and O, they were different neither for temperature nor for precipitation (Table 4). Level D resulted in the least restricted distribution with eight species, although the species *M. cabreræ* was not included in the intersection process (seven species were overlapping).

UDA had higher mean temperature and precipitation values than ODA in all levels, apart from the temperature values in levels D and O (Table 4).

4.3. Bioclimatic model and the mean ODAs method

The climatic results obtained by these two methods for the studied levels of the site are listed in Table 5. The mean climatic values (temperature and precipitation) are also provided for each of the species identified in the studied levels of Abric Romaní (Table 6).

4.4. Palaeotemperature reconstruction: combining methods

The temperatures obtained by applying the different palaeoclimatic methods to the studied levels of the site are lower than the MATs currently recorded in Capellades (13.90 °C), the difference ranging from –6.32 to –1.62 °C, level O being the most different level (Tables 4 and 5).

The UDA-ODA discrimination technique and MER are the methods that show the most similar results (Tables 4 and 7). The greatest differences among methods in the results for temperature pertain to level O, where most species were recorded (Table 1) (MER = 7.58 °C, mean ODAs = 11.66 °C). The method that shows the most different temperature values between levels is the MER method (3.03 °C), whereas the mean ODAs method produces the most similar values (0.72 °C). Temperature estimations across the sequence analysed show a similar tendency between methods (Fig. 2).

As regards precipitation, the results obtained by the different palaeoclimatic reconstruction methods are higher than the MAP currently recorded in Capellades (628 mm), with the exception of the BM results and the results for level O by the mean ODAs method (Table 8). As for temperature, the level that is most different from current values is level O (13.9 °C).

For precipitation, the MER values are the highest, whereas the mean ODAs method recorded the lowest values. The UDA-ODA discrimination technique and MER are the methods with the most similar results (Tables 4 and 8). The greatest differences among methods in the results for precipitation pertain to level O (MER = 873 mm, BM = 613 mm), as with temperature estimations. The method that shows the greatest difference in precipitation values between levels is the mean ODAs method (342 mm), whereas the BM method produces the most similar values (9 mm).

The precipitation estimations across the part of the sequence analysed shows a similar tendency between methods, as occurs with temperature values (Fig. 2).

Table 4

Mean values and standard deviation (SD) for MAT (mean annual temperature) and MAP (mean annual precipitation) for each assemblage (D, E, N, and O) according to atlas distributions (MER method), ODA, and UDA. The significance level of the Mann–Whitney *U* test is calculated from the values of ODA and UDA. In bold is the highest value from the comparison of ODA and UDA.

	Atlas distributions		ODA		UDA		Mann–Whitney <i>U</i> test
	Mean	SD	Mean	SD	Mean	SD	
Level D							
MAT	10.61	1.21	10	0.60	7.22	2.24	0.000
MTC	3	1.19	2.43	0.95	0.1	2.04	0.000
MTW	19.39	1.32	18.81	0.98	16.02	2.2	0.000
MAP	642	217	645	202	1040	265	0.000
Level E							
MAT	9.53	1.94	8.98	1.05	9.56	1.92	0.349
MTC	2.18	1.8	1.58	1.07	2.21	1.77	0.26
MTW	18.27	1.92	17.63	0.79	18.3	1.92	0.495
MAP	776	171	713	89	773	170	0.689
Level N							
MAT	9.53	1.94	8.99	1.18	9.57	1.9	0.349
MTC	2.18	1.8	1.62	1.16	2.22	1.76	0.26
MTW	18.27	1.92	17.61	0.95	18.31	1.91	0.482
MAP	776	171	731	104	771	107	0.941
Level O							
MAT	7.58	1.19	7.86	0.51	7.59	0.35	0.383
MTC	0.38	1.12	0.42	0.53	0.38	0	0.811
MTW	16.41	1.14	18.86	0.49	16.41	0.59	0.228
MAP	873	282	708	111	873	282	0.348

Table 5

Mean annual temperature (MAT) in degrees Celsius and mean annual precipitation (MAP) estimations in millimetres for levels D, E, N, and O of the Abric Romani site obtained by the BM and mean ODAs methods. SD = standard deviation.

Level	BM				Mean ODAs			
	MAT		MAP		MAT		MAP	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
D	10.3	3.36	617	310	12.28	1.39	383	107
E	9.5	3.21	609	297	11.69	2.26	483	165
N	11.2	3.48	608	321	11.56	2.21	455	194
O	10.6	3.36	613	310	11.66	1.94	724	181

Table 6

Mean annual temperature (MAT) in degrees Celsius and mean annual precipitation (MAP) in millimetres for the occupied distribution area (ODA) of the species identified in levels D, E, N, and O of Abric Romani. *Denotes taxa not included in the palaeoclimatic reconstructions because their determination does not achieve species level or their distribution is too perturbed.

Species	MAT		MAP	
	Mean	SD	Mean	SD
<i>Crociodura russula</i>	13.3	1.9	694	120
<i>Sorex gr. Araneus/coronatus*</i>	—	—	—	—
<i>Sorex minutus</i>	12.6	0.93	1060	143
<i>Neomys gr. Fodiens/anomalus*</i>	—	—	—	—
<i>Talpa europaea</i>	10.81	2.15	845	242
<i>Arvicola sapidus</i>	12.49	2.65	655	246
<i>Microtus arvalis</i>	9.53	1.77	675	215
<i>Microtus agrestis</i>	11.34	1.99	892	247
<i>Microtus cabrerai*</i>	—	—	—	—
<i>Chionomys nivalis</i>	7	3.18	1087	297
<i>Microtus duodecimcostatus</i>	13.14	2.62	563	159
<i>Apodemus sylvaticus</i>	12.99	2.65	633	236
<i>Eliomys quercinus</i>	13.15	2.59	593	216
<i>Sciurus vulgaris</i>	11.93	2.53	757	293

Table 7

Temperature estimations (°C) obtained by means of the bioclimatic model (BM), the UDA-ODA discrimination technique, the mutual ecogeographic range (MER) method, and the mean ODAs method for levels D, E, N, and O of the Abric Romani site. SD = standard deviation.

Level	BM		UDA-ODA		MER		Mean ODAs	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
D	10.34	3.36	10.00	0.60	10.61	1.21	12.28	1.39
E	9.54	3.21	8.98	1.05	9.53	1.94	11.69	1.26
N	11.19	3.48	8.99	1.18	9.53	1.94	11.56	2.21
O	10.56	3.36	7.86	0.51	7.58	1.19	11.66	1.94

5. Discussion

5.1. UDA-ODA discrimination technique: discussion of the methods by variable and species

During the process of configuring the ODAs of the different species, some of the UTM squares in the atlas distribution of a species were completely removed and identified as part of the UDA. The reason for this was that those squares did not meet the conditions theoretically required by the species according to the bibliography. The exclusion from an ODA of at least a small area from a complete UTM square could be interpreted at first as a mistaken result. However, part of the information constituting the atlas database comes from pellet analysis. This implies that the species could actually come from the adjacent square, having been caught by a predator and regurgitated several kilometres away from its potential area. The loss of complete squares from the atlas

distribution could be due to lack of awareness of the species' ecological requirements, although in the unit of analysis of this work, the Iberian Peninsula, there is a high level of knowledge of the biology of the species. The complete squares here removed from the atlas distribution, which amount to a few squares for *S. minutus* and *C. russula*, are interpreted in terms of their origin as pellets, as occupied areas appear very close to the squares that were removed (Fig. 3).

As we already pointed out in Fagoaga et al. (2019b), ODAs include only areas where species are currently present, reflecting the values associated with each species more accurately. Thus, ODAs provide a better representation of species distributions than atlases. If ODAs and UDAs are different, then the ODA (whose climatic results are extrapolated to the past in palaeoclimatic reconstructions) is also different from the resulting MER value. The new ODA configurations established in the present work (for *C. nivalis*, *T. europaea*, *S. minutus* and *C. russula* (Tables 2 and 3)), as well as all the other ODA configurations for species developed to date (*E. europaeus*, *M. agrestis*, *M. arvalis*, *M. duodecimcostatus*, *E. quercinus*, *O. cuniculus*, *A. sapidus*, *S. vulgaris*, *A. sylvaticus* and *T. occidentalis*) have proved to be statistically different from their UDAs. Accordingly, ODAs constitute an optimal way of overcoming inaccuracy in the estimation of areas occupied by species based on atlases and in the association of climate values with species. This means that climatic reconstructions performed with ODAs are less prone to misestimation.

It is likely to be the species whose distribution includes the greatest topographic heterogeneity, incorporating ranges such as the Pyrenees, the Cantabrian Range, the Central System, the Baetic and Penibaetic Systems and the Iberian System, that introduce the greatest bias into climatic reconstructions (Fagoaga et al., 2019b). Of the species analysed by the UDA-ODA discrimination technique in the present work, as well as those already studied in Fagoaga et al. (2019b), it is *C. nivalis*, *T. europaea*, *S. minutus*, *M. agrestis* and *S. vulgaris* that occupy areas with the greatest topographic heterogeneity (Table 9).

5.2. UDA-ODA discrimination technique: discussion of the methods by variable and assemblage

Only in level D did ODAs provide more accurate palaeoclimatic information than atlases in overlapping distributions. When applying atlas distributions, ODAs and UDAs are considered together as part of the species distribution. However, as previously explained, the extrapolation of just the values from areas more similar to the areas occupied by all the species leads to climatic parameters that are more representative of the assemblage identified, resulting in more accurate palaeoclimatic reconstructions. By contrast with level D, ODAs did not result in an improvement with respect to MER for levels E, N, and O.

Level D, the only level with a significant difference, had the widest common distribution from a total of seven species after the overlapping process. Although level N had an equal number of species to level D, it had a smaller common distribution area due to the presence of *T. europaea*, with a distribution shifted northwards (Fig. 4).

Various factors can result in ODAs not producing an improvement over the whole area used from atlases. Apart from the number of species involved in an assemblage, and the level of heterogeneity of the resulting common area, both previously discussed, another factor that may limit the improvement is the degree of stenotopy of the species involved. The more generalist the species in an assemblage are, the greater the probability of an improvement. These three points are strongly related and influence the extent of the covered area in the mutual distribution: the more

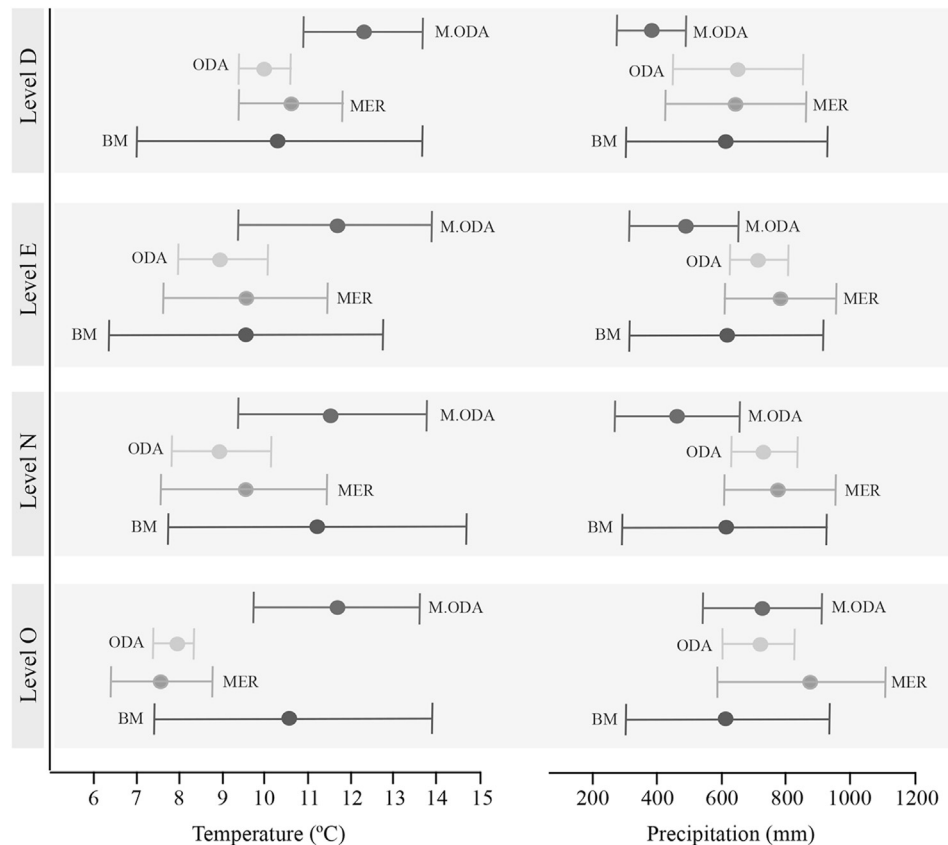


Fig. 2. Evolution of mean annual temperature (°C) and mean annual precipitation (mm) from level O to level D according to the bioclimatic model, the mutual ecogeographic range method, the UDA-ODA discrimination technique, and the mean ODAs method.

Table 8

Precipitation estimations (mm) obtained by means of the bioclimatic model (BM), the UDA-ODA discrimination technique, the mutual ecogeographic range (MER) method, and the mean ODAs method for levels D, E, N, and O of the Abric Romaní site. SD = standard deviation.

Level	BM		UDA-ODA		MER		Mean ODAs	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
D	617	311	645	201	642	217	383	108
E	609	297	713	89	776	171	484	165
N	608	321	731	104	776	171	456	194
O	613	311	708	111	873	282	725	181

restricted an area is, the more likely it is to be less heterogeneous, making the UDA-ODA discrimination technique no more accurate than the MER method.

5.3. Methodological aspects

Of the several methods that can be employed to estimate past climatic parameters, those conducted here have been applied to most of the small-vertebrate associations of the different Late Pleistocene sequences (Fagoaga et al., 2019b; Fernández-García et al., 2020; López-García et al., 2022a,b; Marquina-Blasco et al., 2022; Rey-Rodríguez et al., 2022, among others).

The discrepancies between the climatic estimations yielded by the MER method, the UDA-ODA discrimination technique, the BM method, and the mean ODAs method, both for the levels here analysed (Table 8), which reach a difference of 4.08 °C in the most extreme case (level O: MER = 7.58 °C; mean ODAs = 11.66 °C), and

for other Pleistocene sequences, can be explained by several factors (Fernández-García, 2019).

One of the factors is that all the methods are based on and influenced by the principle of actualism. All of them assume that the ecological requirements of present-day species are equivalent to those of past species (Lyman, 2017). The MER, UDA-ODA, and mean ODAs methods relate to the current distribution of species (Blain et al., 2016; Fagoaga et al., 2019b), although it is not easy to quantify and calibrate the effect that human pressure has on their distributions. The BM method uses the current climatic zone inhabited by the species and the number of climatic zones inhabited by them (Royer et al., 2020).

Discrepancies also may result from sampling issues. The selected methods depend on the occurrence of species regardless of their relative abundance, and the presence or absence of a single species can greatly alter the final palaeotemperature estimation (Birks et al., 2010). This risk increases when faunal assemblages are poor in remains. A related issue is that taphonomy may also alter palaeoclimatic estimations. For such methods based on the occurrence of species, a possible bias in the composition of the assemblage may exist as a consequence of the hunting preferences of predators. Taphonomic analyses focusing on the identification of the predator thus become important in order to ascertain whether a generalist or a specialized hunter was involved, and therefore whether the prey spectrum corresponds to what existed in the surrounding environment or to what was included in the predator diet (Andrews, 1990; Fernández-Jalvo et al., 2016).

Moreover, palimpsests, very common in archaeo-palaeontological levels, might also be the cause of discrepancies, as species that lived at different times and in different

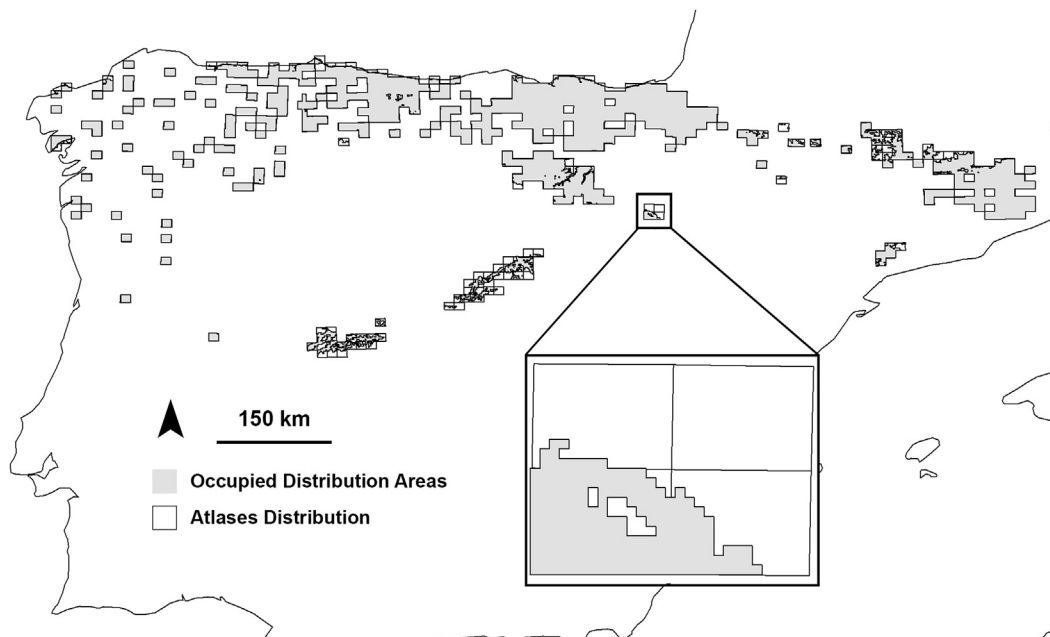


Fig. 3. ODA (occupied distribution area) for *Sorex minutus* in grey and atlas distribution in white, in the Iberian Peninsula (Palomo et al., 2007; Bencatel et al., 2017). The exclusion from the ODA of the species in the distribution square located in the upper right part of the amplification is justified by the presence of adjacent squares where the Eurasian pygmy shrew has been cited and is present.

Table 9

Percentage representation of areas classified by degree of topographic heterogeneity (low, intermediate, and high) for each of the species identified in the studied levels of Abric Romaní (0–90.11 = low heterogeneity; 90.12–207.37 = intermediate heterogeneity; 207.38–533.73 = high heterogeneity). In bold is the greatest degree of heterogeneity for each species.

Species	% Heterogeneity		
	Low	Intermediate	High
<i>Erinaceus europaeus</i>	63.71	28.74	7.55
<i>Sorex minutus</i>	30.65	46.46	22.89
<i>Crocidura russula</i>	63.00	29.02	7.98
<i>Talpa europaea</i>	29.14	48.98	21.89
<i>Talpa occidentalis</i>	54.64	30.88	14.48
<i>Oryctolagus cuniculus</i>	65.07	28.43	6.50
<i>Sciurus vulgaris</i>	36.76	44.75	18.49
<i>Arvicola sapidus</i>	59.16	29.55	11.29
<i>Microtus agrestis</i>	40.63	44.95	14.42
<i>Microtus arvalis</i>	68.23	21.93	9.84
<i>Microtus cabreræ</i>	60.86	29.67	9.47
<i>Microtus duodecimcostatus</i>	67.96	26.61	5.43
<i>Apodemus sylvaticus</i>	60.28	30.17	9.56
<i>Chionomys nivalis</i>	25.21	34.61	40.17
<i>Eliomys quercinus</i>	61.47	28.29	10.24

environmental conditions may be recovered together (Lyman, 1994). This is especially critical at a time of high climatic fluctuation, as in MIS 3.

In addition to the methods addressed here, oxygen isotope analyses also provide relevant palaeoenvironmental estimations, but these are not exempt from assumptions either. Such analyses are also based on the principle of actualism, as they assume that the present-day relationship between stable oxygen isotopes of phosphatic tissues, the oxygen isotope composition of meteoric water, and mean annual temperature was the same in the past. Taphonomy may also alter the resulting palaeoclimatic estimations. Diagenetic processes or chemical alterations during predator digestion can affect the conservation of $\delta^{18}\text{O}$ in the analysed enamel of rodent teeth (Barham et al., 2017). Moreover, the season in which

the predator hunted and regurgitated the remains and even the altitudes at which the predator may have been hunting can affect the final interpretation of isotope amplitudes in a fossil assemblage (Royer et al., 2013; Jeffrey et al., 2015; Fernández-García et al., 2019). The exact point where the samples are taken, the number of samples, and the taxa selected will influence the results too (Fernández-García, 2020).

The fact that the MER method and the UDA-ODA discrimination technique yielded the most similar results is due to the shared procedure of overlapping distributions. The latter method was initially named UDA-ODA discrimination analysis, but was later renamed the UDA-ODA discrimination technique, as it in fact constitutes the same methodology but involves the use of geographic information systems to achieve more accurate results (Fagoaga et al., 2019b). The temperature results attained by the mean ODAs method, despite its similar procedure to the aforementioned methods, are quite a lot higher and are more similar to the isotopic values obtained in Fernández-García et al. (2020). The precipitation results for the mean ODAs method, despite the fact that they also coincide in tendency with most of the other methods, differ most markedly from the others. Both the MER method and the UDA-ODA discrimination technique are determined by the narrowest species distribution. This could be a problem if the current distribution of the species occupies only a part of the range that it used to occupy in the past. The mean ODAs method solves this question by using the mean values of the occupied distribution of each species. It should be noted that the UDA-ODA discrimination technique obtains the narrowest standard deviation values between the methods here analysed in almost all cases (seven out of eight).

To sum up, all these methods and analyses have inherent limitations that should be taken into account in the final interpretation. Frequently, global trends along the sequence and the differences between levels are more informative than the absolute values obtained. Multidisciplinary climatic approaches, that is, the application of different disciplines in the field of palaeoclimatic reconstruction, as well as a combination of different methods applied even to the same proxy, are fully recommended and

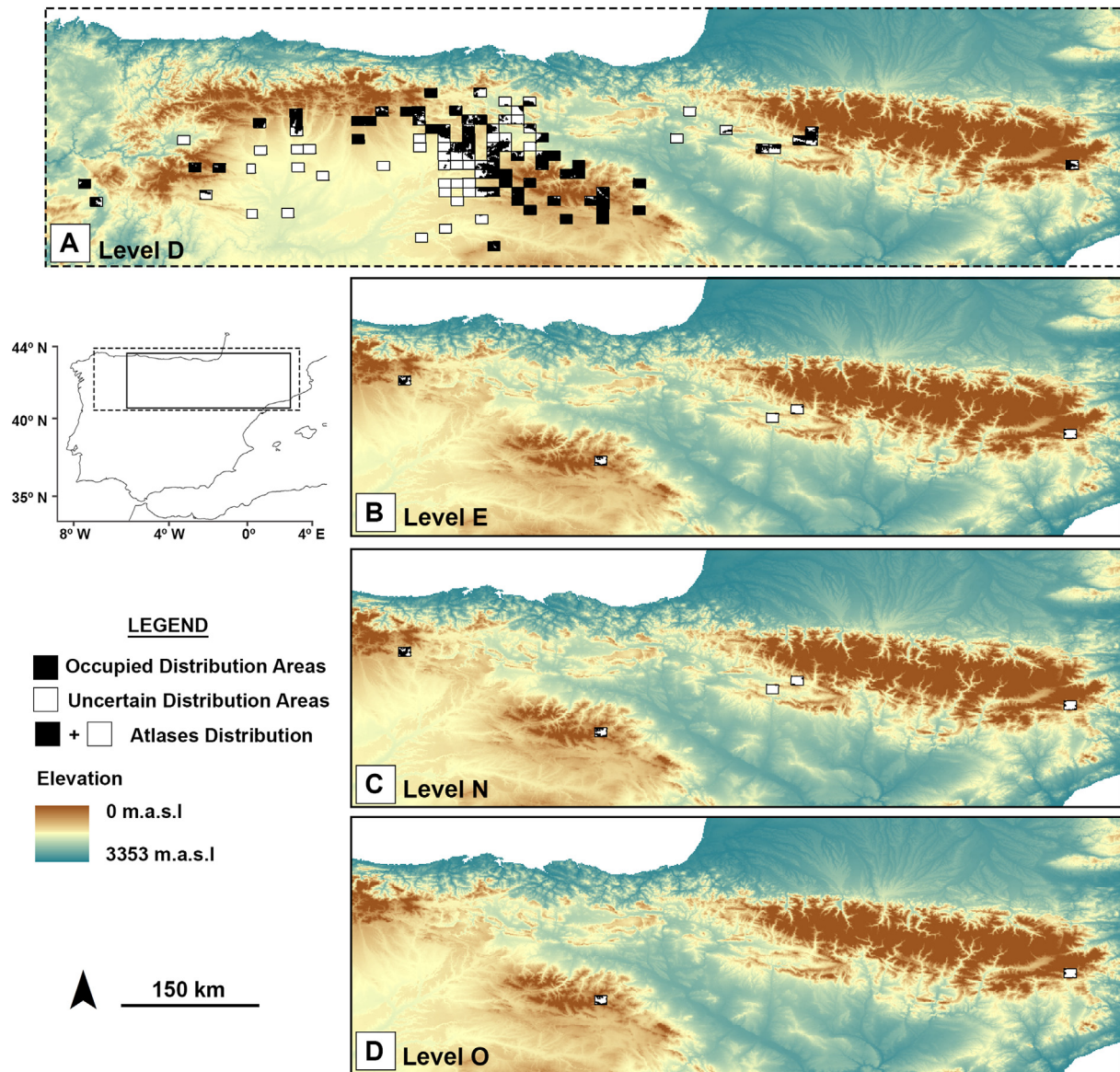


Fig. 4. Occupied distribution areas (black areas) and uncertain distribution areas (white areas) of the common species distribution for level D (A), level E (B), level N (C), and level O (D) of Abric Romaní (Capellades, Barcelona). Km: kilometres.

probably the best way of faithfully approaching past climatic conditions. Actualist comparisons, with known species and climate conditions, of the different methods will clarify the workings of the procedures and reveal the situations in which the application of one method rather than another will be preferable, in order to obtain more precise palaeoclimatic reconstructions.

5.4. Environmental context of a long-term neanderthal settlement in NE iberia

The fact that several studies have focused on the environmental and climatic features along the Abric Romaní sequence, including small-vertebrate, pollen and anthracological analyses together with high-resolution stratigraphy, allow us to juxtaposed them with the different climatic results derived from this work and relate the levels with global climatic oscillations (Burjachs and Julià, 1994; Burjachs et al., 2012; Vaquero et al., 2013; Allué et al., 2017).

Regarding the values obtained in the present work, all the

methods point to a colder scenario for the past than nowadays, which is in accordance with other smallmammal studies for the second third of the Late Pleistocene (López-García and Cuenca-Bescós, 2010; López-García, 2011; López-García et al., 2011a, 2011b, 2012a, 2012b, 2013, 2014, 2015; Rey-Rodríguez et al., 2016; Fernández-García et al., 2018). Moreover, in general, wetter conditions than today are indicated, which is also in accordance with the above-cited works.

Both for temperature and precipitation, level O showed the most different values compared to current conditions (Table 7). This level also showed the most different temperature and precipitation values between methods. López-García et al. (2014) and Fernández-García et al. (2018) already pointed to cold conditions for this level, suggesting a probable link to a cold episode between interstadial 14 and 17. This correspondence was based on low values for MAT and MTW and on the presence in this level of taxa with mid-European requirements, such as *Rana temporaria*, *M. arvalis*, and *M. agrestis*. In these previous works, level O was not the level with the lowest

temperature values, contrary to what is seen here (UDA-ODA). The level that showed the lowest values in previous works was level E, characterized by the high presence of *R. temporaria*, *M. arvalis*, and *M. agrestis*. This level was assigned to HE5. HEs are associated with very cold episodes, as indicated by the arrival of icebergs around the coastlines of the Iberian Peninsula (Heinrich, 1988; Cacho et al., 1999). To ascertain whether the values here obtained for level O are indeed related to a colder period or whether they are a result of the method applied and its assumptions will require further studies to test the different methods with different associations and in distinct contexts with known climatic conditions. What seems clear is that levels E and O were both formed during a cold period.

The dates obtained for levels O and N suggest that they were deposited during D-O 14 (ca. 54–49 ka b2K) or more likely during D-O 15 (ca. 54–55 ka b2K) (Svensson et al., 2008). In the case of level O, different indicators derived from microvertebrate studies point to its deposition during Greenland Stadial 15: the high difference between winter (MTC) and summer (MTW) temperatures, high mean annual precipitation, the presence of species currently typical of the north of the Iberian Peninsula, and equal proportions of species belonging to Mediterranean and Mid-European regions (characteristic feature of Mediterranean-influenced regions during cold episodes). The environment would have been dominated by forest formations with a notable presence of open meadows. Archaeobotanical studies of the level in question also reveal a generally cool and wet period, dominated by taxa such as *Artemisia*, *Poaceae*, and *Pinus* (Table 10) (Burjachs et al., 2012).

Level N seems to be less cold than level O since most of the palaeoclimatic reconstructions point to higher temperatures (Table 7). Moreover, an increase in *Pinus* forest and warm temperate taxa is recorded, which is in accordance with the increase in typical Mediterranean microvertebrate species and a reduction in mid-European ones (Table 10).

Higher up in the stratigraphy, levels E and D may have occurred during D-O 12 (ca. 46–43 ka b2k) or D-O 11 (ca. 43–41 ka b2k). Initially, these levels were considered by Burjachs et al. (2012) to belong to the coolest interstadial in the sequence, and subsequently Vaquero et al. (2013) and López-García et al. (2014) linked level E to HE5. This correlation was based on aeolian sedimentary facies, previous climatic estimations, and the abundance of mid-European species, especially *Epidalea calamita* and *R. temporaria* (Table 10) (Burjachs et al., 2012). The recovery of a fossil belonging to *Mammuthus primigenius* in this level (Rosell et al., 2012) is also relevant to this interpretation. Accordingly, the MER values obtained here and the BM results also indicate colder conditions with respect to level D. This younger level registered a predominance of the genus *Pinus* (74%), but also greater botanical diversity, an increase in

Mediterranean species such as *M. cabreræ*, and a significant decrease in mid-European taxa, indicating a milder climate for this level (Table 10).

5.5. MIS 3 climatic scenario for neanderthals in iberia

As set forth in numerous works, the late Middle Pleistocene to Late Pleistocene of Iberia is characterized by a wetter and colder climate than at present in the areas around the sites under study, the subsistence of Neanderthals being linked mainly to open woodland formations (López-García and Cuenca-Bescós, 2010; López-García et al., 2011a, 2011b, 2012a, 2012b, 2013, 2014, 2015; Rey-Rodríguez et al., 2016; Fernández-García et al., 2018) (Table 11).

For the Mediterranean area during the cold Heinrich events HE5, HE4 and HE3, the annual rainfall and the minimum temperatures of the coldest month would have been 400 mm and between 6 and 13 °C lower than at present, respectively (Sánchez-Goni and d'Errico, 2005). The change from a cold to a warm phase would imply changes of up to 10 °C in temperature in the Greenland atmosphere (Johnsen et al., 1992; d'Errico and Sánchez-Goni, 2003). As has been shown for the Cantabrian region in the marine core in the Bay of Biscay (Sánchez-Goni et al., 2008; Fourcade et al., 2022), moreover, abrupt shifts between stadial and interstadial episodes would have also taken place in this region (Fernández-García et al., 2023). The values obtained by small-mammal analyses for the different Mousterian levels range from 6 to 12.49 °C and 599.40–1827 mm (Table 11), which definitively constitutes a highly variable climatic scenario for Neanderthals in the Iberian Peninsula where they were able to survive. As was already pointed out by Marquina-Blasco et al. (2021), a progressive positive trend in the MAT and a negative trend in the MAP running from north to south is seen in small-vertebrate analyses, Abric del Pastor and El Salt (southeastern Iberia) being the sites with the highest temperature values and the lowest precipitation values, respectively, and Arbreda and Cova Eirós (northeastern and northwestern Iberia) being the sites with the lowest temperature values and the highest precipitation values, respectively (Table 11).

The sites with the greatest difference between current temperatures and palaeotemperature values are level O of Abric Romaní (−6.04 °C), levels G, H, and I of Arbreda (−6.4, −6.7 and −9.1 °C respectively), and levels II and III of Teixoneres (−7.7 and −8.3 °C) (Table 11). All of these levels have been associated with cold stages: level O of Abric Romaní has been linked with a stadial, level II of Teixoneres with a HE (3 or 4), level I of Arbreda with a cold stage between interstadials 12 and 10, and levels III of Teixoneres and H of Arbreda with interstadials with thermal improvement but within a glacial stage (Table 11). However, as has

Table 10

Synthesis of the results derived from the different proxies analysed at the Abric Romaní site. The information for small-mammals comes from López-García et al. (2014), Fernández-García et al. (2020) and this work; the information on the herpetofauna, pollen and anthracology is from Burjachs et al. (2012) and Allué et al. (2017). L = Level.

L. Small-mammals	Herpetofauna	Pollen	Anthracology
D Colder and wetter than today. Predominance of forest formations but with a high relevance of open meadows	Prevalence of humid meadows with the presence of moist-cold wooded areas. Presence of <i>Rana temporaria</i> (6) and <i>Vipera aspis</i> (1)	Extension of pioneer trees (Cupressaceae and <i>Pinus</i>), followed by an increase in <i>Quercus</i> spp. And <i>Olea-Phillyrea</i>	<i>Pinus</i> type <i>sylvestris</i> dominates. Greatest variability with the presence of mesothermophilous taxa
E Colder and wetter than today. Noticeable forest environment. Increase in mid-European species and decrease in Mediterranean ones	Prevalence of humid meadows with the presence of moist-cold wooded areas. Greater abundance of <i>B. calamita</i> (12). Presence of <i>Rana temporaria</i> (9)	Extension of pioneer trees (Cupressaceae and <i>Pinus</i>), followed by an increase in <i>Quercus</i> spp. And <i>Olea-Phillyrea</i>	<i>Pinus</i> type <i>sylvestris</i> dominates
N Colder and wetter than today. Abundance of open forest environment species	Prevalence of humid meadows with the presence of moist-cold wooded areas	Dominance of <i>Artemisia</i> , <i>Poaceae</i> , and <i>Pinus</i> . Occurrence of mesothermophilous taxa	<i>Pinus</i> type <i>sylvestris</i> dominates
O Colder and wetter than today. Balanced relative abundance between mid-European and Mediterranean species	Prevalence of humid meadows with the presence of moist-cold wooded areas. Presence of <i>Rana temporaria</i> (1)	Dominance of <i>Artemisia</i> , <i>Poaceae</i> and <i>Pinus</i> . Occurrence of mesothermophilous taxa	<i>Pinus</i> type <i>sylvestris</i> dominates

Table 11

Values for MAT (°C) and MAP (mm) for the sites Abric del Pastor, Abric Romaní (this work), Arbreda, Canyars, Cova Eirós, Cueva del Conde, El Salt, Galls Carboners, Teixoneres, and Cova dels Xaragalls (López-García et al., 2012a, 2012b, 2013, 2014, 2015, 2022a; Fagoaga et al., 2018, 2019a, 2019b; Fagoaga, 2020; Rey-Rodríguez et al., 2016). Δ MAT and Δ MAP show the differences between values from the different layers and the current values for the area where the site is located. The values given here for Abric Romaní were obtained by the UDA-ODA discrimination technique.

Site	Location	Level	MAT	Δ MAT	MAP	Δ MAP
Abric del Pastor	Comunitat Valenciana	IVd	12.49	−1.15	63	+88
Abric Romaní	Catalunya	D	10.00	−3.9	1040	+412
		E	8.98	−4.92	773	+144
		N	8.99	−4.91	771	+143
		O	7.86	−6.04	873	+245
Arbreda	Catalunya	G	8.70	−6.4	966	+159
		H	8.40	−6.7	154	+142
		I	6.00	−9.1	1500	+692
		—	10.11	−5.49	758	+99
Canyars	Catalunya	—	10.11	−5.49	758	+99
Cova Eirós	Galicia	3	8.18	−2.92	1827	794
Cueva del Conde	Asturias	N10b	8.40	−4.4	1441	+468
		N20a	10.50	−2.3	1500	+527
		N20b	11.70	−1.1	1438	+465
		N104	10.10	−2.7	1100	+127
		N103	10.00	−2.8	1000	+27
El Salt	Comunitat Valenciana	Xb F11 S3	9.82	−3.82	671	+127
		Vsup F24 S7	10.02	−3.62	619	+75
		Vsup F24 S8	10.08	−3.56	630	+86
		Vsup F24 S9	10.02	−3.62	619	+75
		Vsup F25	10.17	−3.47	599	+56
Galls Carboners	Catalunya	—	7.78	−3.72	1187	437
Teixoneres	Catalunya	II	7.60	−7.7	1008	+349
		IIb	10.00	−5.3	981	+322
		III	7.00	−8.3	840	+181
Xaragalls	Catalunya	C3	7.92	−5.48	1092	+463
		C4	8.00	−5.4	925	+296
		C5	10.36	−3.04	664	+35
		C6	8.00	−5.4	950	+321
		C7	8.67	−4.73	900	+271
		C8	10.48	−2.92	729	+100

been shown here, the method selected for the reconstruction could affect whether the level is considered more or less cold and wet. In fact, level O of Abric Romaní would show 2.34 °C less compared to current conditions if we had selected the results of the mean ODAs method (Table 7) instead of the UDA-ODA discrimination technique (Table 4), which shows a difference of 6.04 °C (Table 11). For this reason, actualist comparisons are needed in order to ascertain which method reconstructs the climate most accurately in each condition (see the Methodological aspects section in the Discussion) together with a standardization of the methods to allow comparisons to be drawn between climatic values from distinct levels.

6. Conclusions

The occupied distribution areas of the species here analysed, *C. russula*, *C. nivalis*, *S. minutus*, and *T. europaea*, reflect the values associated with each species more accurately than the atlas distributions. Reconstructions performed with the ODA of these species are thus expected to be less subject to misestimation. In the process of configuring the ODAs of the different species, some complete UTM squares may be assigned entirely to UDAs if adjacent areas have been assigned to ODAs. The identification of these species may have been based on pellet analysis, in which case these areas may not in fact fulfil the ecological requirements of the species in question.

Taking into account the assemblage as a whole, the number of species involved, the level of heterogeneity of the resulting common area, and the degree of stenotopy of the species in the fossil assemblage, are some of the main factors that can explain why the ODA need not always entail an improvement over the whole area used from atlases. Among the analysed levels of Abric Romaní, the

only level with a significant difference was level D, which obtained the widest common distribution after applying the UDA-ODA discrimination technique.

The discrepancies among the absolute values obtained by the different methods may be due to differences in the nature of the data. However, all the methods applied show a similar tendency as regards the evolution of temperature and precipitation along the sequence. Multidisciplinary environmental approaches that incorporate different methods and disciplines are fully recommended and probably the best way of faithfully approaching past climatic conditions.

The general environment and climate deduced from the combination of the different proxies and methods applied to the levels of Abric Romaní is a wetter and colder scenario, where forest formations of *Pinus* type *sylvestris* would have dominated the surrounding environment, with a high proportion of humid meadows as well.

The climatic scenario faced by Neanderthals during the second third of the Late Pleistocene of Iberia was wetter and colder than the current conditions at the different locations where the sites are located, as has been revealed by various small-mammal analyses. However, a standardization of the methods applied for the different sites is needed in order to provide comparable results.

CRediT authorship contribution statement

Ana Fagoaga: Conceptualization, Methodology, Formal analysis, Writing – original draft. **Mónica Fernández-García:** Formal analysis, Writing – review & editing. **Juan Manuel López-García:** Writing – review & editing. **M. Gema Chacón:** Writing – review & editing, Funding acquisition. **Palmira Saladié:** Writing – review & editing, Funding acquisition. **Josep Vallverdú:** Writing – review &

editing, Funding acquisition. **Francisco Javier Ruiz-Sánchez:** Conceptualization, Writing – review & editing. **Hugues-Alexandre Blain:** Conceptualization, Writing – review & editing, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

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