Multi-method approach using small vertebrate assemblages to reconstruct the Marine Isotope Stage 6 climate and environment of the Lazaret Cave sequence (Maritime Alps, Nice, France)

Juan Manuel López-García[1,2*], Hugues-Alexandre Blain[1,2], Christian Sánchez-Bandera[1,2], Jessica Cohen[3], Loïc Lebreton[4], Sophie Montuire[5,6], John R. Stewart[7], Emmanuel Desclaux[3,8]

[1]Institut Català de Paleoecologia Humana i Evolució Social (IPHES-CERCA), Zona Educacional 4, Campus Sescelades URV (Edifici W3), 43007 Tarragona, Spain. jmlopez@iphes.cat; hablain@iphes.cat; csanchezbandera@gmail.com.

[2]Universitat Rovira i Virgili, Departament d'Història i Història de l'Art, Avinguda de Catalunya 35, 43002 Tarragona, Spain.

[3]Laboratoire de préhistoire du Lazaret, Nice, France. jessica.co@outlook.fr; emmanuel.desclaux@gmail.com.

[4]Département Homme & Environnement, Muséum national d'Histoire naturelle, UMR 7194 HNHP, MNHN-CNRS-UPVD, Musée de l'Homme, Paris, France. loicLEB@hotmail.com.

[5]EPHE, PSL University, 6 Boulevard Gabriel, 21000 Dijon, France

[6]Biogéosciences, UMR 6282, CNRS, EPHE, Université Bourgogne Franche-Comté, 6 Boulevard Gabriel, 21000 Dijon, France. Sophie.Montuire@u-bourgogne.fr.

[7]Bournemouth University, Faculty of Science and Technology, Talbot Campus, Fern Barrow, Poole, BH12 5BB. jstewart@bournemouth.ac.uk.

[8]UMR CNRS 72 64 CEPAM, Université Côte d'Azur, Pôle Sant-Jean d'Angély, 25 avenue François Mitterrand 06300 Nice, France

*Corresponding author

Abstract

Marine Isotope Stage 6 (MIS 6; ca. 185-135 ka) is the penultimate glacial stage and constitutes the end of the Middle Pleistocene. This glacial period is typified by generally cold and dry conditions in the western Mediterranean region. Despite the relatively large number of pollen and speleothem studies of MIS 6 in this region, the number of MIS 6 archaeological sites is low. Lazaret cave, situated at 26 m a.s.l. in the city of Nice in southern France, contains an archeological sequence (layers CII inf. to CIII) dated to MIS 6. We present a multi-method approach using the small-vertebrate assemblages (mainly rodents and herpetofauna) from the entire sequence to characterize the climate and the environment of the site. The Mutual Ecogeographic Range, the Bioclimatic Model andthe Quantified Ecology methods, as well as the Taxonomic Habitat Index, Climatograms and the Simpson Diversity Index were used to reconstruct the palaeoenvironmental and palaeoclimatic conditions. The results suggest a generally cold climate with a relatively humid environment and a landscape dominated by deciduous temperate forests. The findings are consistent with the general trends reported from other proxies (large mammals, birds and marine gastropods) studied at Lazaret cave, other MIS 6 sites in the Mediterranean region with small vertebrate studies and the general trends shown by marine cores, terrestrial pollen sequences and speleothems from western Europe. Given the scarcity of data for MIS 6 archaeological sites, Lazaret cave constitutes an important site for our knowledge of the climate and the environment of this period.

Key words: Mutual Ecogeographic Range; Bioclimatic Model, Quantified Ecology; Taxonomic Habitat Index, Climatograms; Simpson Diversity Index

1. Introduction

The end of the Middle Pleistocene is marked by the penultimate glacial period, Marine Isotope Stage 6 (MIS 6 - ca. 185-135 ka), which corresponds with the Saalian glaciation in Europe (e.g. Roucoux et al. 2011; Magari et al. 2014; Railsback at al. 2015). MIS 6 was a glacial period where generally drier and cooler conditions have been detected in the Mediterranean region of Europe as compared to interglacial periods (e.g. Hodge et al. 2008; Wainer et al. 2013). During the second half of MIS 6 (from 150 ka) the global sea level was 100 m below that of today and the sea surface temperatures (STT) reached 5 ºC lower with respect to current ones (e.g. Elderfield et al. 2012; Margari et al. 2014). Speleothem data (in Italy, France and Spain) and long pollen sequences (in Greece, France and from a marine core off the Portuguese coast) are available for western Europe (Fig. 1) showing the climatic and environmental conditions during the entirety of MIS 6 (e.g. Margari et al. 2014; Tzedakis et al. 2003; Roucoux et al. 2011; Wilson et al. 2013; Bard et al. 2002; Hodge et al. 2008; Guiot el al. 1993; Ponel, 1995). For the early part of this glacial period, long pollen sequence data suggest a fluctuating tree abundance in Europe, while extreme conditions with tree loss have been detected for the latest part of MIS 6 (e.g. Roucoux et al. 2011), with a high amplitude climatic oscillations detected in the diatom species record (e.g. Wilson et al. 2021). In contrast, archaeological sites in western Europe dated to MIS 6 with small vertebrate studies are scarce. Existing ones include three Spanish sites, Sala de los Huesos in Maltravieso cave (Hanquet, 2011), Estanque de Tormentas de Butarque H-02 (Blain et al. 2017; Laplana et al. 2015) and Lezetxiki II (García-Ibaibarriaga et al. 2018), four sites in France, Baume Moula-Guercy (Desclaux and Defleur, 1997), Grotte des Cèdres (Defleur and Crégut-Bonnoure, 1995), Romain-la-Roche (Guérin et al. 2010) and Coudoulous 1 (Jaubert et al. 2003) and one site in Italy Poggetti Vecchi (Benvenuti et al. 2017) (Fig. 1). The aim of the present study is to characterize the environment and climate of the MIS 6 archeological sequence of Lazaret cave (Nice, France) using small mammals (mainly rodents) and herpetofaunal assemblages. Applying several paleoclimatic and paleoenvironmental tools to obtain a multi-method approach, which it is hoped allows a better understanding of conditions in Western Europe during the penultimate glacial.

2. Lazaret Cave

Lazaret Cave is located in southern France on the Mediterranean coast of the city of Nice (43º 41’ 25’’ N, 7º 17’42’’ E) (Fig. 1). Lazaret cave is formed in lower Jurassic dolomite limestone and is 40 m long and 15 m wide with a celling of ca. 15 m high. The current entrance faces the southwest at 26 m a.s.l. and is ca. 100 m from the coast. The lower part of the cave sequence (Fig. 2) is composed by two marine transgressive phases. The first phase, Complex A or the Lower Marine Beach, is without fossils and is ascribed to Marine Isotope Stage 9 (MIS 9) (Lumley et al. 2004). The second phase, Complex B or the Upper Marine Beach, is rich in coral and marine mollusks dating to around ca. 230 ka, corresponding to Marine Isotope Stage 7 (MIS 7) (Bahain, 1993; Michel and Yokoyama 2001). These marine deposits rest under a continental fill (Complex C) 6-meters in thickness (Fig. 2), mainly composed of clays and gravels, which are capped by a stalagmitic layer (Complex E) dated between ca. 108-45 Ka (Shen 1985; Michel et al. 2009). Complex C is divided into three stratigraphic sub complexes, CI, CII and CIII, which correspond to archaeological levels and date between 220-130 Ka (Michel, 1995; Michel et al. 2009). The bottom of the continental deposits, sub complex CI, is not well known as yet, but the CII and CIII sub complexes contain at least 29 archaeostratigraphic units (UA), CIIinf. (UA 29-26), CIIsup. (UA 25-13) and CIII (UA 12-1). These subcomplexes show a succession of hominin occupations, where humans and numerous faunal (vertebrates and invertebrates) remains have been recovered, together with abundant lithic bifacial tools attributed to the final Acheulean (e.g. Lumley et al. 2004; Hanquet et al. 2010; Valensi et al. 2007, among others).

3. Material and methods

3.1. Small vertebrate sorting, taxonomic and taphonomic study

The small-vertebrate fossil remains used for this study come from the sub-complex CII inf., CII sup. and CIII from Lazaret cave, in which 29 archaeo-stratigraphic units (UA) of anthropic occupation have been identified (Fig. 2). Most of the small vertebrate remains have been recovered by water-screening from the excavation sediments, using two superimposed screens of 5 mm and 0.8 mm mesh sizes. The fossils were processed, sorted and classified at the "Laboratoire de Préhistoire du Lazaret" (Nice, France). The rodents from the sub-complexes CII sup. and CIII have been identified and partially published by Hanquet et al. (2010), Desclaux (2013) and Lumley et al. (2019), while the association pf CII inf. is presented here for the first time. The amphibians and reptiles from sub-complexes CII inf, CII sup and CIII have been published by Bailon (1991), Lumley (2004), Hanquet et al. (2010), Manzano (2015) and Lumley et al. (2019).

The rodent assemblages used for this study correspond to minimum number of 5428 individuals, representing at least 16 taxa (Table 1: Fig. 3). The rodent remains were identified using systematic paleontological methods. Specific identification of this material rests principally on the best diagnostic elements: first lower molars for the subfamily Arvicolinae; and isolated teeth for the subfamilies Cricetinae, Murinae and Glirinae. The fossils were quantified using the minimum number of individuals (MNI) method for each sample (i.e. from each level) and determined by counting the diagnostic elements. A previous preliminary taphonomic study of sub-complex CII (UA25-27) has been published by in Hanquet (2011) and Desclaux et al. (2011) using the criteria proposed by Andrews (1990) and subsequently updated with the work of Fernández-Jalvo et al. (2016) for alterations caused by digestion present in rodent incisors and molars.

Marmota marmota is not included in the environmental and climatic data analysis for the following reasons: 1) is not possible to use with all the methods because theclimatic distributions data is not available for the species(e.g. Royer et al. 2020); 2) Due to it large size, the accumulation of *M. marmota* is not commonly caused by small bird of prey or small carnivore predatory activities (e.g. Armitage, 2003), like the other rodent species (e.g. Fernández-Jalvo et al. 2016). In addition, its presence in archaeological sites may also be the result of anthropic activities (e.g. Romandini et al. 2012). In order to complement rodent reconstructions, the faunal lists of amphibians and reptiles published by Manzano (2015) have been used. The amphibian and reptile assemblages used for this study correspond to at least 20 taxa (Table 2). As no detailed taphonomical study of the remains has been done for sub-complexes CII sup and CIII and we used only the presence-absence of taxa for the amphibians and reptiles and no quantificationhas been included.

3.2. Palaeonvironmental reconstruction

In order to reconstruct the environment, we used two main methods to analyse the rodent assemblages, the Taxonomic Habitat Index (THI) and the Climatogram methods. The THI was developed by Andrews and Evans (1983), a method that considers the assemblage of rodent species identified, taking into account the diversity of the habitats where these species live, and regardless of their relative proportions. The representation of species by habitat has been done for Lazaret cave (Table 3) according to the current distribution of the rodent species in France (Le Louran and Quéré, 2003), as well as the distribution of the fossil rodent species in Pleistocene of France and western Europe, according to Andrews (1990), Chaline (1977,1983), Marquet (1993) and Desclaux et al. (2008). The Climatogram quantitative method applied to rodent assemblages was developed by Chaline (1977) and applied to numerous case studies (e.g. Marquet, 1993; Desclaux and Defleur, 1997; Hanquet and Desclaux, 2011; Foury et al. 2016; Leberton et al. 2016 or Crégut-Bonnoure et al. 2018). This method allows the climatic and environmental variation represented by a stratigraphic sequence to be revealed. In this way the rodent associations of Lazaret cave have been grouped into six climate-ecology categories (Table 4).

3.3. Palaeodiversity reconstruction

Among the large number of indices proposed for evaluating the biodiversity of a sample, species evenness is fundamental for assessing the homogeneity of an environment (Magurran and McGill, 2011). Evenness is a diversity index that is used to quantify how equal the various communities are numerically. The evenness of a community can be represented by the Simpson index of diversity, which is also equivalent to the probability of interspecific encounter (Simpson, 1949; Blois et al., 2010; López-García et al., 2013): i.e., the Simpson index of diversity = $1 - \Sigma (pi^2)$, where pi is the proportion of total individual samples belonging to the ith species. The evenness index is constrained between 0 and 1. The lower the variation in species within a community, the higher the value of the evenness index. The index will be close to 0 if there is a single dominant species. To avoid the statistical problems of high sample-size dependence, we have standardized the absolute values by dividing them by the total sample abundances, expressed as percentages of the MNI. This standardization allows the taxon evenness to be compared in samples of different size. This index of evenness was obtained using the Paleontological Statistics Program (PAST) (Hammer et al., 2001).

3.4. Palaeoclimatic reconstructions

In order to assess the palaeoclimatic data from Lazaret cave, we used the Bioclimatic Model (BM) and the Quantified Ecology (QE) methods on small mammal assemblages and the Mutual Ecogeographic Range (MER) and the Quantified Ecology (QE) methods on the herpetofaunal assemblages.

The BM was established by Hernández-Fernández (2001a and b) and we use the recently updated R script PalBER published in Royer et al. (2020). This method is based on the hypothesis that a significant correlation exists between climate and mammal communities. According to Hernández-Fernández (2001a and b); Hernández-Fernández and Peláez-Campomanes (2005) and Hernández-Fernández et al. (2007), mammal assemblages can be assigned to ten climatic types, five of which are represented by the rodent assemblages of Lazaret cave. These assemblages were analyzed using the Climatic Restriction Index (CRIi = 1/n, where "n" is the number of climatic zones where the species are represented and "i" is the climatic zone where the species appears) (Table 5) and was assigned to the following zones: IV Subtropical with winter rains and summer droughts; VI Typical temperate; VII Arid temperate; VIII Cold-temperate (boreal) and IX Polar. After obtaining this distribution, the Bioclimatic Component (BC; representation by level of each of the three available climates) was calculated using the following formula: $BCi = (\Sigma \, CRIi) \times 100/S$, where S is the number of species per sub-complex at Lazaret cave. From the BC, a mathematical model was elaborated using a multiple linear regression (Hernández-Fernández and Peláez-Campomanes, 2005); by means of a series of functions, this allows the estimation of mean annual temperature (MAT) and mean annual precipitation (MAP).

The QE was developed by Jeannet (2010). This method is based on the combination of geographic and climatic distributions of small vertebrate species today, in this case we use the small mammal and herpetofaunal assemblages separately (Table 6), calculated from the sum of the climatic parameters (mean temperature and mean precipitation) by species divided by the total of species represented in each sub-complex of Lazaret cave. On the basis of these methods, two climatic factors are estimated: the mean annual temperature (MAT) and the mean annual precipitation (MAP).

The MER method (Blain et al., 2009, 2016) has been used to estimate the temperature and precipitation, for which we used the current geographical ranges of the herpetofaunal species present in the Lazaret cave assemblages. To determine the current spatial distributions of European amphibians and reptiles, we used the data from Sillero et al. (2014), represented in a geographic coordinate system (datum WGS 84) with a 50 × 50 km grid. Once the common overlapping area of the species from the assemblage was identified, approaching a more precise common species distribution area, the UDA-ODA discrimination methodology (Fagoaga et al., 2019) was applied. This procedure, partially derived from the MER method, sharpens each species distribution creating the real Occupied Distribution Areas (ODA) that will be used as current analogue associations from where climatic parameters will be extrapolated to past fossil assemblages. For example, the upper elevation limits of *Pelobates cultripes* (1770 meters) and *Pelodytes punctatus* (2000 meters) (Cejudo, 1990; Guixé et al., 2009) were used to obtain more precise areas within the overlapping area in which all the species could coincide.

The climate data are from WorldClim 2.0 (Ficks and Hijmans, 20176), also codified in a geographic coordinate system (datum WGS 84). Both data sets were processed using the ArcGIS 10.5 application (Redlands, 2011). The bioclimatic information used are the bioclimatic variables BIO1 (annual mean temperature) and BIO12 (mean annual precipitation) from Hijmans et al. (2005). The mean and standard deviations were calculated using the statistical program IBM SPSS Statistics 22.

The same climatic parameters were calculated for Lazaret today (1970-2000), choosing an area of 3,5 km^2 surrounding the site (i.e, in a radius of 1 km). MAT have been estimated to be 15.0 ± 0.17°C and MAP to be 811.70 ± 3.8 mm.

4. Results

4.1. Taphonomic remarks

The results obtained in the previous taphonomic studies by Hanquet (2011) and Desclaux et al. (2011) from units UA 27-25 (CII inf. and CII sup.) show that most of the small mammal accumulations were the result of predation by nocturnal birds of prey. The signs of digestion in the small mammal bones and teeth suggest that four nocturnal raptors (*Bubo bubo*, *Asio otus*, *Asio flammeus* and *Strix aluco*) may have been responsible for the accumulations at Lazaret cave (Hanquet, 2011; Desclaux et al. 2011). These kinds of predators do not generally display specific prey consumption patterns (Andrews, 1990). Therefore, palaeoecological interpretations based on the relative abundance of the rodent taxa from Lazaret cave are likely to be reliable indicators of the habitat in which the predators hunted.

In the case of the amphibians and reptiles, a taphonomic study has been carried out by Manzano (2015) for units UA 27-26 (CII inf.). It suggested that the bone accumulation is *in situ* because the bone surfaces lack polish and that no skeletal elements are missing. The skeletal remains show a high level of fragmentation, mostly with angular and irregular fractures attributable to diagenetic processes in the cave (Pinto-Llona and Andrews, 1999; Manzano,2015). The signs of digestion in amphibian and reptile bones are rare and can hardly be recognized. Traces of digestion have been observed in some bones of *Rana temporaria*, but the intensity of this digestion is very low (category 1, type *Tyto alba*; sensu Pinto-Llona and Andrews, 1999).

4.2. Small vertebrate assemblages

The rodent assemblage of complex C (including CII inf., CII sup. and CIII) of Lazaret cave is dominated by two species, the field vole (*Microtus* (*Agricola*) *agrestis*, more than 700 individuals) and the wood mouse (*Apodemus* (*Sylvaemus*) *sylvaticus*, more than 400 individuals). These two taxa represent more than 75% of the sub-complex (4209 individuals) in relation to the total number of individuals (5428 individuals) (Table 1).

Both species are also present in other MIS 6 sites with small mammal studies in France, such as Coudoulous I in Lot (Jaubert et al. 2003), Romain-la-Roche in Doubs (Guérin et al. 2010) and Moula Guercy in the Ardèche (Desclaux and Defleur, 1997) as well as sites in the Iberian Peninsula such as Lezetxki II in the Basque Country (Garcia-Ibaibarriaga et al. 2018). Both species are relatively abundant later on in western Europe during the late Pleistocene, with records in the Italian and Iberian Peninsula as well as in southern France (e.g. Royer et al. 2016; Berto et al. 2019; López-García 2011). On the other hand, while *A.* (*S.*) *sylvaticus* is currently present across the whole of France, *M.* (*A.*) *agrestis* is probably absent in the Maritime-Alps region (https://inpn.mnhn.fr). Moreover, while *A.* (*S.*) *sylvaticus* is an adaptable species, inhabiting a wide variety habitats including all types of woodland (Torre et al. 2002), *M.* (*A.*) *agrestis* mainly inhabits wet meadow areas and forests with dense herbaceous understories (Krystufek et al. 2016), suggesting that humid and open woodland landscapes dominated at the time the accumulation of rodents in sub-complexes CII inf., CII sup. and CIII of the Lazaret cave were being formed.

Among the herpetofauna, five taxa are the most abundant in the Lazaret assemblage, including *Bufo bufo*, *Rana temporaria*, *Angis fragilis*, *Coronella austriaca* and *Vipera* spp. Their presence in the Mediterranean region usually indicates a colder climate with a humid environment in a landscape composed of mountain and valley habitats (Valensi et al. 2007). The distribution of herpetofaunal species among the sub-complexes is relatively homogeneous. However, urodeles (*Ichtyosauria alpestris* and Salamandridae indet.) and *Hyla* sp. are only recorded from CII sup. and *Pelobates cultripes* is absent from CIII. For squamate reptiles, CII inf. is the least diverse assemblage with an absence of *Timon lepidus*, *Malpolon monspessulanus*, *Natrix* gr. *natrix*, *Coronella* cf. *girondica* and *Zamenis scalaris* which are present in the other sub-complexes. The absence of such Mediterranean species may suggest that CII inf. would be colder than the other sub-complexes. However, *Podarcis* is absent from CII sup. and the snakes *Hierophis viridiflavus* and cf. *Zamenis longissimus* are not recorded in CIII (Table 2).

4.3. Palaeoenvironmental and Paleoclimatic approach

In comparison with current climatic data (Table 7), the bioclimatic model and the quantified ecology methods applied to the small mammals of the Lazaret cave sub complexes suggested a generally colder climate (ΔMAT_{CII} = −6.7 °C and -6.2 ºC; ΔMAT_{CIII}= -6.35 ºC and -6.2 ºC) and with relatively lower rainfall (ΔMAP_{CII} = -294 mm and -201 mm; ΔMAP_{CIII} = -243 mm and -210 mm). The herpetofaunal assemblages also suggest cold climate conditions with somewhat less harsh temperatures than reconstructed by the rodents (ΔMAT_{CIIsup} = −4.4°C and -3.8ºC; ΔMAT_{CIIinf} = −3.8°C and -4.5ºC; ΔMAT_{CIII}= -4,0ºC and -4.1ºC). They also indicated different results for rainfall. The MER reconstructed MAP suggests slightly more humid conditions (ΔMAP_{CIIsup} = +70.4 mm; ΔMAP_{CIIinf} = +15.9 mm; ΔMAP_{CIII} = +18 mm), whereas the QE reconstructed rainfall suggests a dryer climate (ΔMAP_{CIIsup} = -123.7 mm; ΔMAP_{CIIinf} = -104.6 mm; ΔMAP_{CIII} = -149.2 mm) than reconstructed using the small mammals. Taking into account the chronological placement of these sub complexes, CII and CIII (between ca. 175-130 Kya), these could correspond to MIS 6 substages 6d to 6a (Fig. 4). These data are also concordant with the percentage representation in both sub complexes, CII and CIII, of the species associated with climate categories VI (typical temperate, related with a temperate deciduous forest), VII (Arid temperate, related with a steppe and cold desert), VIII (Cold-temperate, related to a boreal coniferous forest-taiga) and IX (Polar, related with Tundra) which represents more than 70% of the Bioclimatic Component of the bioclimatic model (Table 8). It is also consistent with the relatively high representation (10 of 17) of small mammal species that require mean temperatures below 10ºC (Table 5), according to the Quantified Ecology method.

On the other hand, both methods (THI and Climatograms) used in the environmental reconstruction at Lazaret cave with rodent assemblages indicate a landscape dominated by deciduous temperate forest and humid meadows with a significant representation of shrublands (Fig. 4). The percentage of deciduous forest obtained with the THI has values around ca. 35% in all the sub-complexes (Table 9), mainly represented by the most abundant species *M.* (*A.*) *agrestis* and *A.* (*S.*) *sylvaticus* and to a lesser extent by *Eliomys querciuns*, *Muscardinus avellanarius*, *Glis glis* and *Clethrionomys glareolus*. These five last species are also those indicative of a temperate forest using the Climatogram method, with percentages ranging between ca. 21-35% (Fig. 4; Table 10). Following the environmental category Mediterranean, Shrubland and Humid habitats are the most abundant, between 16-21 %, according to the THI method (Fig. 4; Table 9). The Mediterranean category is mainly represented by the species *E. querciuns*, *G. glis, M. avellanarius*, *Microtus* (*Iberomys*) *brecciencis*, *A. mosbachensis* and *Pliomys* sp. nov.. The Shrubland category is mainly represented by *G. glis*, *Cricetus cricetus*, *Microtus* (*M.*) *arvalis, M.* (*I.*) *brecciensis* and *Pliomys* sp. nov.. Finally, the humid habitat is mainly represented by *C. cricetus* and *M. (*A.*) agrestis*. *M. (*A.*) agrestis* is responsible for the percentage representation of humid meadows, between 48-58%, obtained with the Climatogram method (Fig. 4; Table 10).

Finally, the Simpson index (1-D) indicates a relatively high diversity (>0.5) with similar values in the three studied sub complexes ($1\text{-}D_{\text{CIII-CIIsup.}}$ = 0.6 and 0.67) from Lazaret cave (Fig. 5). This is a signal of a relatively heterogeneous vegetation (mainly related to deciduous forest, shrubland and mountain habitats) and rodent community (relation between number of species and individual's distribution in each sub complex) (Fig. 5). These most abundant rodents are one mouse (*A.* (*S.*) *sylvaticus*) and five vole species (*M.* (*A.*) *agrestis, M.* (*T.*) *multiplex, A. mosbachensis* and *Pliomys* sp. nov.) which represent more than 50 individuals in each sub complex (Fig. 5).

5. Discussion

5.1. Comparison with other Lazaret environmental proxies

The environmental studies done using other proxies from Lazaret cave include the published works on herpetofauna (amphibians and reptiles), birds, marine gastropods, and large mammals from subcomplexes CIII and CII sup (Hanquet et al., 2010 and Valensi et al., 2007). In general, all the studied proxies from complex C of Lazaret cave indicate a cooler climate and a more humid environment than today (Hanquet et al. 2010; Valensi et al. 2007; Valensi and Abbassi, 1998). Former quantification of climate based on herpetofauna at the level of the UAs (Manzano, 2015) using the MER method at a regional level (200 km around the site) and QE for the sequence of Lazaret suggested an alternance of temperate and cold phases during a globally colder than present MIS 6. Cold periods (CII inf. and CIII) were characterized by MAT as being between 12 and 9.6ºC (i.e. -5.4ºC to -3ºC in relation to the present climate). CII sup., however, shows a general improvement in climatic conditions with MAT indicating temperatures between 12 and 14ºC (i.e. -3ºC to -1ºC). Reconstructed MAP suggested somewhat lower levels of rainfall than today for temperate periods (around 700 mm; i.e. 100 mm lower than present level) in opposition to much higher values obtained for cold periods with MAT reaching peaks above 1000 mm (i.e. +200 mm in comparison with the present amount) (Manzano, 2015). Some of the UAs (UA27, 18, 15 and 3) were said to correspond to non-analogue herpetofaunal communities (Manzano, 2015), but even with a larger stratigraphical consideration (i.e., at level of complexes) we found no non-analogue assemblages when MER was used at a European scale. If climate reconstructions are quite similar concerning anomalies (Δ) between Manzano (2015) and the present reconstructions, some differences can be seen according to the methods applied. According to the MER, CII sup. would be slightly warmer than the two other complexes, whereas, according to QE, CII sup. is slightly warmer than CIII and CII inf. (Table 7). However, the differences fall within one standard deviation and are therefore not significant. The same issue is observed concerning precipitation. MER suggests a globally more humid climate whereas QE a slightly dryer climate, but again most of the differences observed falls within the standard deviation. In conclusion, climate indications obtained from the QE method on herpetofauna is more in accordance with the occurrence of thermophilus, typically Mediterranean, species (*T. lepidus, M. monspessulanus* and *Z. scalaris*) in the different sub-complexes and in line with the results obtained by Manzano (2015) at a regional level.

The large mammal assemblage has a faunal composition dominated by *Cervus elaphus* and *Capra ibex*. More specifically the sub-complex CIIsup. is composed of more temperate species, with the abundance of *C. elaphus*, the presence of *Bos primigenius* and *Capreolus capreolus* and a lower representation of *C. ibex*, than sub complex CIII, where *Rangifer tarandus* and *Bison priscus* are well represented and *C. ibex* is more abundant (Valensi et al. 2007). The avifaunal assemblage of sub-complexes CIIsup. and CIII has sedentary species associated with cold climates such as *Aegolius funereus*, *Bubo scandiaca* and *Tetrao tetrix* (Hanquet et al. 2010). In general, the avifaunal assemblage shows a predominance of species from cold climates and open environments, together with species related to temperate climates and open environments as well as rock and mountain habitats, with a remarkable closing of the vegetational landscape between CIIsup. and CIII sub complexes (Hanquet et al. 2010). Finally, the marine gastropods assemblage highlights the presence of *Melarhaphe neritoides*, a Mediterranean Littornidae species, together with Nordic Littornidae, *Littorina saxatilis* and *Littorina* *fabalis*. The association of these gasteropods indicates a cooling of the sea in sub complex CIII respect to CII (Valensi et al. 2007). In general, the data obtained from the different methods applied to the rodent assemblages are in concordance with the trend shown by the other proxies, with a relatively cold climate and a humid environment in relation to today (Fig. 4). When considered according to sub-complexes within the cave sequence, the results obtained from the rodent assemblages agree with the herpetofaunal data in that there is a similar association in sub-complexes CII sup. and CIII (Table 1). However, the cooling and/or closure detected in the other proxies from CII sup. to CIII are not observed with the rodent results (Fig. 4). Nevertheless, relative colder conditions have been detected with the rodent assemblage in sub complex CII inf., in relation to the overlying complexes (Fig. 4). This is mainly indicated by the presence of *Lasipodomys gregalis* (narrow-headed vole) in sub complex CII inf., a species that currently inhabits tundra and forest tundra from the White Sea to the Kolyma River in Russia and in the steppes of Kazakhstan, Kyrgizia, SW Siberia, Yakutia, Mongolia and Northern China (Batsaikhan et al. 2016).

5.2. Comparison with other MIS 6 sites

As noted above, there are few archaeological sites in western Europe dating to MIS 6 with small vertebrate studies. Together with Lazaret cave, four sites have been studied in France, Baume Moula-Guercy (Desclaux and Defleur, 1997, Defleur et al.,1998; 2001, Defleur and Desclaux, 2019; Defleur et al., 2020), Grotte des Cèdres (Defleur and Crégut-Bonnoure, 1995), Romain-la-Roche (Guérin et al. 2010) and Coudoulous 1 (Jaubert et al. 2003), three in the Iberian Peninsula, Sala de los Huesos in Maltravieso cave (Hanquet, 2011), Estanque de Tormentas de Butarque H-02 (Blain et al. 2017; Laplana et al. 2015) and Lezetxiki II (García-Ibaibarriaga et al. 2018) and one in Italy, Poggetti Vecchi (Benvenuti et al. 2017). Regarding the expansion of the continental glaciers in western

Europe during MIS 6 (Batchelor et al 2019), the composition of the rodent assemblages of the aforementioned sites may be influenced by the position of the localities (Fig. 6). Strictly cold species, such as *Dicrostonyx torquatus* (Artic lemming), *Lasiopodomys gregalis* and *Lemmus lemmus* (Norway lemming) are only represented in French sites, while in Iberian and Italian sites these species are not present, and the assemblages are composed mainly of temperate taxa.

Indeed, if we take the example of Baume Moula-Guercy, located in the Ardèche (France), along the Rhône corridor rodent species characteristic of open environments and cold climates, such as *Dicrostonyx torquatus*, *Allocricetus bursae*, *Lasiopodomys gregalis* and *Sicista betulina* (northern birch mice) are represented in levels assigned to MIS 6 (XIX to XVI). These small mammals are associated with large mammals such *Rangifer tarandus* (reindeer) and *Mammuthus primigenius* (woolly mammoth). Further south, in Provence, in the Grotte des Cèdres, these cold species are however absent in the levels dating from MIS 6 (Defleur and Crégut-Bonnoure, 1995). Rodent associations are present at the Grotte des Cèdres with a more temperate character (such as *M.* (*I.*) *brecciensis*, *M.* (*A.*) *agrestis*, *Eliomys quercinus*, *M.* (*T.*) *duodecimcostatus* and *A.* (*S.*) *sylvaticus*), similar to what is observed in the CIII and CII complexes of the Lazaret cave. It would therefore indicate that a latitudinal gradient was relatively well pronounced in south-eastern France during the late middle Pleistocene (MIS 6).

In Poggetti Vecchi Unit 2 the rodent assemblage is composed of *Arvicola amphibius*, *Microtus* (*Terricola*) sp. and *Microtus* cf. *M. arvalis* (Benvenuti et al. 2017). In H-02 the rodent assemblage is composed of *Allocricetus bursae*, *Arvicola* cf. *sapidus*. *Microtus* (*Microtus*) *arvalis*, *Microtus* (*Iberomys*) *brecciensis* and *A.*gr. *sylvaticus-flavicollis* (Laplana et al. 2015). In Maltravieso-SH the rodent assemblage is composed by *Eliomys quercinus*, *M.* (*Ibeormys*) *brecciensis*, *Micortus* (*Terricola*) cf.

duodecimcostatus, Allocricetus bursae and *A.*(*Sylvaemus*) *sylvaticus* (Hanquet, 2011). In the lower layers Lezetxiki II, the more abundant rodent species are *A. amphibius, M.* (*Agricola*) *agrestis* and *M.* (*Terricola*) sp. (García-Ibaibarriaga et al. 2018). During MIS 6 Lazaret combines, the presence of strictly Mediterranean species, such as *M.* (*I.*) *brecciensis* and *M.* (*T.*) *savii* with strictly cold species, such as *L. gregalis*. This phenomenon could be related to the position of the site, as previously suggested by Valensi et al. (2007) and Desclaux (2013), showing that the glacial expansion in the Maritime-Alps during MIS 6, caused changes in ecology and the area forms a transitional zone between the steppe identified in the southern limits of permafrost in France and the forest and grass identified in in the Italian peninsula (Fig. 6). The area therefore may have acted as a refugial leading edge for some more temperate species.

The nature of the Maritime-Alps coastal areas during MIS 6 was not the same during the cold stages of the Late Pleistocene. For example, during MIS 4, *Mammuthus primigenius* is observed in level 6 of Grotte du Prince and Foyer III of Grotte du Cavillon, in Ventimiglia, at the French-Italian border (Moussous et al., 2014). Furthermore, during MIS 2, the cold climate was also sufficiently marked to allow populations of Mammoths (*Mammuthus primigenius*) to reach the Mediterranean shores of Liguria, as evidenced for example by the observations of Braun and Palombo (2012) in the Arene Candide cave in Finale Ligure, Onoratini et al. (2011) in the Barma Grande, in Ventimiglia. It is possible that the occurrence of cold adapted taxa in Mediterranean coastal areas only took place during the Late Pleistocene and that during the Middle Pleistocene the glacial stadials

did not have the same intensity, at least in this region of Europe.

5.3. Comparison with other environmental and climatic proxies in western Europe

Studies of marine cores, terrestrial pollen sequences and speleothems have been done in western Europe containing the MIS 6 fluctuations (Margari et al. 2010; 2014, Roucoux et al. 2011, Wilson et al. 2013, Tzedakis et al. 2003, Guiot et al. 1989; 1993, Ponel, 1995, Bard et al. 2002, Hodge et al. 2008, Wainer et al. 2013).

The analysis of pollen from the marine core MD01-2444 off the Portuguese coast divided the penultimate glacial, on basis of the amplitude of the millennial-scale variability in two main periods (one between 185 to 160 Kya and the other one between 150-135 Kya), with a transitional period (between 160-150 Kya). The early period is mainly characterized by a prominent oscillation in foraminiferal isotopes and tree pollen values while the last period is mainly characterized by mild temperature swings in the Antarctic and minimum tree pollen values. This suggests that MIS 6 is characterized by cool climatic conditions with an open forest environment (Margari et al. 2010; 2014).

The terrestrial pollen sequences of Ioannina and Tenaghi Philippon in Greece suggest generally cool and wet conditions for the MIS 6 (Roucoux et al. 2011, Wilson et al. 2013, Tzedakis et al. 2003). Similarly, the French pollen sequences of Les Echets and Grande Pile, have mean temperatures and precipitation estimated suggesting MAT between 12 ºC and 4 ºC and MAP between 200 mm and 800 mm lower than at present (Guiot et al. 1989; 1993, Ponel, 1995).

The speleothem data coming from the Italian Argentarola cave, the Spanish Gitana cave and French Villara cave, show lower rainfall values during glacial periods and specifically characterize MIS 6 by cool and humid climatic conditions (Bard et al. 2002, Hodge et al. 2008, Wainer et al. 2013).

These data are consistent with the results obtained here where different methods were applied to the rodent assemblages of Lazaret cave. On one side, the methods applied to estimate climatic parameters show a generally cold conditions with relatively low rainfall for all subcomplexes analyzed. On the other hand, the methods applied to investigate the vegetational landscape show a habitat dominated by deciduous temperate forest with humid meadows including relatively high proportions of scrublands (Fig. 4; 5).

The apparent difference in results between the climatic parameter method and the landscape representation method could be due to a difference in rainfall regime predicted. Even if the rainfall is lower, however, the way in which precipitation is distributed throughout the years may have more impact on the vegetation. Unfortunately, it is currently not possible to reconstruct this variable.

6. Conclusions

On basis of a multi-method approach using the small-vertebrate assemblages of Lazaret cave MIS 6 sequence to reconstruct the past climate and environment, our analysis enables the following conclusions to be drawn:

1) The set of the used methods applied to the small-vertebrate associations (mainly rodents and herpetofauna) from the MIS 6 Lazaret cave sequence suggest a cold climate with a relatively humid environment dominated by deciduous temperate forest.
2) The comparison with other proxies (large mammals, birds and marine gastropods) identified at Lazaret cave shows, in general, the same environmental and climatic trend (cold climate and relatively humid environmental conditions) as identified using the small vertebrate assemblages.
3) The comparison with other MIS 6 sites in western Europe that include small vertebrate studies, shows that, although Lazaret cave is more similar to Mediterranean sites, than to sites in central France, it combines the presence of Mediterranean species, such as *M.* (*I.*) *brecciensis* or *M.* (*T.*) *savii* with strictly cold species, like *L. gregalis*. This could be related to the geographical position of the cave, that provides for this period, with the glacial expansion in the

Maritime-Alps, a transitional zone between the French cold steppe and the warmer Italian forest-grassland.

4) Finally, the comparison with other climatic and environmental proxies (marine cores, terrestrial pollen sequences and speleothems) in western Europe demonstrates similar environmental (open forest landscape) and climatic conditions (cool and relatively wet climate with a relatively low rainfall values) as those detected using the small-vertebrate assemblages from Lazaret cave during MIS 6.

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Figure 1. Location of the Lazaret cave and the other MIS 6 sites mentioned in the manuscript. Archaeological sites: MTV-SH (Hanquet, 2011), H-02 (ETB) (Blain et al. 2017; Laplana et al. 2015), Lezetxiki II (García-Ibaibarriaga et al. 2018), Moula-Guercy (Desclaux and Defleur, 1997), Cèdres (Defleur and Crégut-Bonnoure, 1995), Romain-la-Roche (Guérin et al. 2010), Codoulous (Jaubert et al. 2003), Poggetti Vecchi (Benvenuti et al. 2017). Pollen sequences: MD01-2444 (Margari et al. 2014), Les Echets (Guiot, 1993), La Grande Pile (Ponel, 1995), Ioannina (Roucoux et al. 2011), Tenaghi Philippon (Tzedakis et al. 2003). Speleothem data : Gitana cave (Hodge et al. 2008), Villars cave (Wainer et al. 2013), Argentola cave (Bard et al. 2002).

Figure 2. Stratigraphic section of Lazaret cave. ESR ages taken from Michel et al. (2009).

Figure 3. Some rodent’s teeth identified from Lazaret cave. 1-4. m1 left *Microtus* (*Agricola*) *agrestis*; 5-7 m1, two left-one right *Microtus* (*Terricola*) *multiplex*; 8-11. m1, two left-two right *Arvicola mosbachensis*; 12-13. M11, one right-one left *Pliomys*sp. nov.; 14-15. M1 and M2 right and M1 left *Apodemus* (*Sylvaemus*) *sylvaticus*; 16. m1 right *Cricetus cricetus*. All teeth are in occlusal view.

Figure 4. Comparison of the climate and landscape values obtained with the rodent's assemblages from the different complex and sub-complex of Lazaret Cave with the ^{18}O isotope curve values (modified from Railsback et al. 2015) for the MIS 6. BM: Bioclimatic Model; QE: Quantified Ecology; MAT: Mean Annual Temperature; MAP: Mean Annual Precipitation; TF: Temperate forest; RF: Riparian Forest; HM; Humid Meadow; DF: Deciduous Forest; HH: Humid Habitat; Sh: Shrubland; Med: Mediterranean; THI: Taxonomic Habitat Index.

Figure 5. Values obtained of the Simpson diversity index (1-D) for the sub-complexes of Lazaret cave. MNI: Minimum Number of Individuals

Figure 6. Location of the different archaeological sites with small vertebrate studies in relation with the MIS 6 glacial expansion (modified from Litt et al. 2007). 1. Lazaret cave; 2. Romain-la-Roche; 3. Moula-Guercy; 4. Codoulous; 5. Grotte des Cèndres ; 6. Poggetti Vecchi; 7. Lezetxiki II; 8. Maltravieso-Sala de los Huseos; 9. Estanque de Tormentas Butarque (H-02)

Table 1. Minimum number of individuals (MNI) and percentage of minimum number of individuals (% MNI) of the rodent's assemblage from the different sub-complexes of Lazaret cave.

Table 2. Herpetofaunal presence/absence faunal list from the different sub-complexes of Lazaret cave

Table 3. Repartition of the rodent species according to the Taxonomic Habitat Index (THI)

Table 4. Repartition of the rodent's species according to the Climatogram method

Table 5. Repartition of rodent's species in climates types according to the Bioclimatic Model. IV Subtropical with winter rains and summer droughts; VI Typical temperate; VII Arid temperate; VIII Cold-temperate (boreal) and IX Polar.

Table 6. Repartition of small-vertebrate species by mean temperature and mean precipitation according to the Quantified Ecology method.

Table 7. Comparison of the data obtained by means of the various climatic methods used applied to the small vertebrate assemblage's sub-complexes of Lazaret cave with the current mean temperature and precipitation. MAT: Mean Annual Temperature; MAP: Mean Annual Precipitation; SD: Standard deviation of the obtained values; Δ: difference with the nowadays values.

Table 8. Repartition of rodent's species by climate types to obtain the Bioclimatic component (BC) values. CRI: Climatic Restriction Index; S: total number of the species; IV Subtropical with winter rains and summer droughts; VI Typical temperate; VII Arid temperate; VIII Cold-temperate (boreal) and IX Polar.

Table 9. Repartition of the percentages obtained with the Taxonomic Habitat Index (THI) applied to the Lazaret cave rodent's assemblages

Table 10. Repartition of the percentages obtained with the Climatogram method applied to the Lazaret cave rodent's assemblages