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

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26 **Abstract**

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

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

48 **1. Introduction**

49 The end of the Middle Pleistocene is marked by the penultimate glacial period,
50 Marine Isotope Stage 6 (MIS 6 - ca. 185-135 ka), which corresponds with the Saalian

51 glaciation in Europe (e.g. Roucoux et al. 2011; Magari et al. 2014; Railsback et al. 2015).
52 MIS 6 was a glacial period where generally drier and cooler conditions have been detected
53 in the Mediterranean region of Europe as compared to interglacial periods (e.g. Hodge et
54 al. 2008; Wainer et al. 2013). During the second half of MIS 6 (from 150 ka) the global
55 sea level was 100 m below that of today and the sea surface temperatures (STT) reached
56 5 °C lower with respect to current ones (e.g. Elderfield et al. 2012; Margari et al. 2014).
57 Speleothem data (in Italy, France and Spain) and long pollen sequences (in Greece,
58 France and from a marine core off the Portuguese coast) are available for western Europe
59 (Fig. 1) showing the climatic and environmental conditions during the entirety of MIS 6
60 (e.g. Margari et al. 2014; Tzedakis et al. 2003; Roucoux et al. 2011; Wilson et al. 2013;
61 Bard et al. 2002; Hodge et al. 2008; Guiot et al. 1993; Ponel, 1995). For the early part of
62 this glacial period, long pollen sequence data suggest a fluctuating tree abundance in
63 Europe, while extreme conditions with tree loss have been detected for the latest part of
64 MIS 6 (e.g. Roucoux et al. 2011), with a high amplitude climatic oscillations detected in
65 the diatom species record (e.g. Wilson et al. 2021). In contrast, archaeological sites in
66 western Europe dated to MIS 6 with small vertebrate studies are scarce. Existing ones
67 include three Spanish sites, Sala de los Huesos in Maltravieso cave (Hanquet, 2011),
68 Estanque de Tormentas de Butarque H-02 (Blain et al. 2017; Laplana et al. 2015) and
69 Lezetxiki II (García-Ibaibarriaga et al. 2018), four sites in France, Baume Moula-Guercy
70 (Desclaux and Defleur, 1997), Grotte des Cèdres (Defleur and Crégut-Bonnoure, 1995),
71 Romain-la-Roche (Guérin et al. 2010) and Coudoulous 1 (Jaubert et al. 2003) and one
72 site in Italy Poggetti Vecchi (Benvenuti et al. 2017) (Fig. 1). The aim of the present study
73 is to characterize the environment and climate of the MIS 6 archeological sequence of
74 Lazaret cave (Nice, France) using small mammals (mainly rodents) and herpetofaunal
75 assemblages. Applying several paleoclimatic and paleoenvironmental tools to obtain a

76 multi-method approach, which it is hoped allows a better understanding of conditions in
77 Western Europe during the penultimate glacial.

78 **2. Lazaret Cave**

79 Lazaret Cave is located in southern France on the Mediterranean coast of the city
80 of Nice (43° 41' 25'' N, 7° 17'42'' E) (Fig. 1). Lazaret cave is formed in lower Jurassic
81 dolomite limestone and is 40 m long and 15 m wide with a ceiling of ca. 15 m high. The
82 current entrance faces the southwest at 26 m a.s.l. and is ca. 100 m from the coast. The
83 lower part of the cave sequence (Fig. 2) is composed by two marine transgressive phases.
84 The first phase, Complex A or the Lower Marine Beach, is without fossils and is ascribed
85 to Marine Isotope Stage 9 (MIS 9) (Lumley et al. 2004). The second phase, Complex B
86 or the Upper Marine Beach, is rich in coral and marine mollusks dating to around ca. 230
87 ka, corresponding to Marine Isotope Stage 7 (MIS 7) (Bahain, 1993; Michel and
88 Yokoyama 2001). These marine deposits rest under a continental fill (Complex C) 6-
89 meters in thickness (Fig. 2), mainly composed of clays and gravels, which are capped by
90 a stalagmitic layer (Complex E) dated between ca. 108-45 Ka (Shen 1985; Michel et al.
91 2009). Complex C is divided into three stratigraphic sub complexes, CI, CII and CIII,
92 which correspond to archaeological levels and date between 220-130 Ka (Michel, 1995;
93 Michel et al. 2009). The bottom of the continental deposits, sub complex CI, is not well
94 known as yet, but the CII and CIII sub complexes contain at least 29 archaeostratigraphic
95 units (UA), CIIinf. (UA 29-26), CIIsup. (UA 25-13) and CIII (UA 12-1). These
96 subcomplexes show a succession of hominin occupations, where humans and numerous
97 faunal (vertebrates and invertebrates) remains have been recovered, together with
98 abundant lithic bifacial tools attributed to the final Acheulean (e.g. Lumley et al. 2004;
99 Hanquet et al. 2010; Valensi et al. 2007, among others).

100 **3. Material and methods**

101 3.1. *Small vertebrate sorting, taxonomic and taphonomic study*

102 The small-vertebrate fossil remains used for this study come from the sub-complex
103 CII inf., CII sup. and CIII from Lazaret cave, in which 29 archaeo-stratigraphic units
104 (UA) of anthropic occupation have been identified (Fig. 2). Most of the small vertebrate
105 remains have been recovered by water-screening from the excavation sediments, using
106 two superimposed screens of 5 mm and 0.8 mm mesh sizes. The fossils were processed,
107 sorted and classified at the “Laboratoire de Préhistoire du Lazaret” (Nice, France). The
108 rodents from the sub-complexes CII sup. and CIII have been identified and partially
109 published by Hanquet et al. (2010), Desclaux (2013) and Lumley et al. (2019), while the
110 association of CII inf. is presented here for the first time. The amphibians and reptiles
111 from sub-complexes CII inf, CII sup and CIII have been published by Bailon
112 (1991), Lumley (2004), Hanquet et al. (2010), Manzano (2015) and Lumley et al. (2019).

113 The rodent assemblages used for this study correspond to minimum number of
114 5428 individuals, representing at least 16 taxa (Table 1: Fig. 3). The rodent remains were
115 identified using systematic paleontological methods. Specific identification of this
116 material rests principally on the best diagnostic elements: first lower molars for the
117 subfamily Arvicolinae; and isolated teeth for the subfamilies Cricetinae, Murinae and
118 Glirinae. The fossils were quantified using the minimum number of individuals (MNI)
119 method for each sample (i.e. from each level) and determined by counting the diagnostic
120 elements. A previous preliminary taphonomic study of sub-complex CII (UA25-27) has
121 been published by in Hanquet (2011) and Desclaux et al. (2011) using the criteria
122 proposed by Andrews (1990) and subsequently updated with the work of Fernández-Jalvo
123 et al. (2016) for alterations caused by digestion present in rodent incisors and molars.

124 *Marmota marmota* is not included in the environmental and climatic data analysis
125 for the following reasons: 1) is not possible to use with all the methods because

126 the climatic distributions data is not available for the species (e.g. Royer et al. 2020); 2)
127 Due to its large size, the accumulation of *M. marmota* is not commonly caused by small
128 birds of prey or small carnivore predatory activities (e.g. Armitage, 2003), like the other
129 rodent species (e.g. Fernández-Jalvo et al. 2016). In addition, its presence in
130 archaeological sites may also be the result of anthropic activities (e.g. Romandini et al.
131 2012). In order to complement rodent reconstructions, the faunal lists of amphibians and
132 reptiles published by Manzano (2015) have been used. The amphibian and reptile
133 assemblages used for this study correspond to at least 20 taxa (Table 2). As no detailed
134 taphonomical study of the remains has been done for sub-complexes CII sup and CIII and
135 we used only the presence-absence of taxa for the amphibians and reptiles and no
136 quantification has been included.

137 3.2. *Palaeoenvironmental reconstruction*

138 In order to reconstruct the environment, we used two main methods to analyse the
139 rodent assemblages, the Taxonomic Habitat Index (THI) and the Climatogram methods.
140 The THI was developed by Andrews and Evans (1983), a method that considers the
141 assemblage of rodent species identified, taking into account the diversity of the habitats
142 where these species live, and regardless of their relative proportions. The representation
143 of species by habitat has been done for Lazaret cave (Table 3) according to the current
144 distribution of the rodent species in France (Le Louran and Quéré, 2003), as well as the
145 distribution of the fossil rodent species in Pleistocene of France and western Europe,
146 according to Andrews (1990), Chaline (1977, 1983), Marquet (1993) and Desclaux et al.
147 (2008). The Climatogram quantitative method applied to rodent assemblages was
148 developed by Chaline (1977) and applied to numerous case studies (e.g. Marquet, 1993;
149 Desclaux and Defleur, 1997; Hanquet and Desclaux, 2011; Foury et al. 2016; Leberton et
150 al. 2016 or Crégut-Bonnoure et al. 2018). This method allows the climatic and

151 environmental variation represented by a stratigraphic sequence to be revealed. In this
152 way the rodent associations of Lazaret cave have been grouped into six climate-ecology
153 categories (Table 4).

154 3.3. *Palaeodiversity reconstruction*

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

170 3.4. *Palaeoclimatic reconstructions*

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

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

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

200 The MER method (Blain et al., 2009, 2016) has been used to estimate the
201 temperature and precipitation, for which we used the current geographical ranges of the
202 herpetofaunal species present in the Lazaret cave assemblages. To determine the current
203 spatial distributions of European amphibians and reptiles, we used the data from Sillero
204 et al. (2014), represented in a geographic coordinate system (datum WGS 84) with a 50
205 × 50 km grid. Once the common overlapping area of the species from the assemblage was
206 identified, approaching a more precise common species distribution area, the UDA-ODA
207 discrimination methodology (Fagoaga et al., 2019) was applied. This procedure, partially
208 derived from the MER method, sharpens each species distribution creating the real
209 Occupied Distribution Areas (ODA) that will be used as current analogue associations
210 from where climatic parameters will be extrapolated to past fossil assemblages. For
211 example, the upper elevation limits of *Pelobates cultripes* (1770 meters) and *Pelodytes*
212 *punctatus* (2000 meters) (Cejudo, 1990; Guixé et al., 2009) were used to obtain more
213 precise areas within the overlapping area in which all the species could coincide.

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

220 The same climatic parameters were calculated for Lazaret today (1970-2000),
221 choosing an area of 3,5 km² surrounding the site (i.e, in a radius of 1 km). MAT have
222 been estimated to be 15.0 ± 0.17°C and MAP to be 811.70 ± 3.8 mm.

223 **4. Results**

224 *4.1. Taphonomic remarks*

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

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

244 4.2. *Small vertebrate assemblages*

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

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

264 Among the herpetofauna, five taxa are the most abundant in the Lazaret assemblage,
265 including *Bufo bufo*, *Rana temporaria*, *Angis fragilis*, *Coronella austriaca* and *Vipera*
266 spp. Their presence in the Mediterranean region usually indicates a colder climate with a
267 humid environment in a landscape composed of mountain and valley habitats (Valensi et
268 al. 2007). The distribution of herpetofaunal species among the sub-complexes is relatively
269 homogeneous. However, urodeles (*Ichtyosauria alpestris* and Salamandridae indet.) and
270 *Hyla* sp. are only recorded from CII sup. and *Pelobates cultripes* is absent from CIII. For
271 squamate reptiles, CII inf. is the least diverse assemblage with an absence of *Timon*
272 *lepidus*, *Malpolon monspessulanus*, *Natrix gr. natrix*, *Coronella cf. girondica* and
273 *Zamenis scalaris* which are present in the other sub-complexes. The absence of such
274 Mediterranean species may suggest that CII inf. would be colder than the other sub-

275 complexes. However, *Podarcis* is absent from CII sup. and the snakes *Hierophis*
276 *viridiflavus* and cf. *Zamenis longissimus* are not recorded in CIII (Table 2).

277 4.3. Palaeoenvironmental and Paleoclimatic approach

278 In comparison with current climatic data (Table 7), the bioclimatic model and the
279 quantified ecology methods applied to the small mammals of the Lazaret cave sub
280 complexes suggested a generally colder climate ($\Delta\text{MAT}_{\text{CII}} = -6.7\text{ }^{\circ}\text{C}$ and $-6.2\text{ }^{\circ}\text{C}$;
281 $\Delta\text{MAT}_{\text{CIII}} = -6.35\text{ }^{\circ}\text{C}$ and $-6.2\text{ }^{\circ}\text{C}$) and with relatively lower rainfall ($\Delta\text{MAP}_{\text{CII}} = -294\text{ mm}$
282 and -201 mm ; $\Delta\text{MAP}_{\text{CIII}} = -243\text{ mm}$ and -210 mm). The herpetofaunal assemblages also
283 suggest cold climate conditions with somewhat less harsh temperatures than
284 reconstructed by the rodents ($\Delta\text{MAT}_{\text{CIIsup}} = -4.4^{\circ}\text{C}$ and -3.8°C ; $\Delta\text{MAT}_{\text{CIIinf}} = -3.8^{\circ}\text{C}$ and
285 -4.5°C ; $\Delta\text{MAT}_{\text{CIII}} = -4.0^{\circ}\text{C}$ and -4.1°C). They also indicated different results for rainfall.
286 The MER reconstructed MAP suggests slightly more humid conditions ($\Delta\text{MAP}_{\text{CIIsup}} =$
287 $+70.4\text{ mm}$; $\Delta\text{MAP}_{\text{CIIinf}} = +15.9\text{ mm}$; $\Delta\text{MAP}_{\text{CIII}} = +18\text{ mm}$), whereas the QE reconstructed
288 rainfall suggests a dryer climate ($\Delta\text{MAP}_{\text{CIIsup}} = -123.7\text{ mm}$; $\Delta\text{MAP}_{\text{CIIinf}} = -104.6\text{ mm}$;
289 $\Delta\text{MAP}_{\text{CIII}} = -149.2\text{ mm}$) than reconstructed using the small mammals. Taking into
290 account the chronological placement of these sub complexes, CII and CIII (between ca.
291 175-130 Kya), these could correspond to MIS 6 substages 6d to 6a (Fig. 4). These data
292 are also concordant with the percentage representation in both sub complexes, CII and
293 CIII, of the species associated with climate categories VI (typical temperate, related with
294 a temperate deciduous forest), VII (Arid temperate, related with a steppe and cold desert),
295 VIII (Cold-temperate, related to a boreal coniferous forest-taiga) and IX (Polar, related
296 with Tundra) which represents more than 70% of the Bioclimatic Component of the
297 bioclimatic model (Table 8). It is also consistent with the relatively high representation
298 (10 of 17) of small mammal species that require mean temperatures below 10°C (Table
299 5), according to the Quantified Ecology method.

300 On the other hand, both methods (THI and Climatograms) used in the
301 environmental reconstruction at Lazaret cave with rodent assemblages indicate a
302 landscape dominated by deciduous temperate forest and humid meadows with a
303 significant representation of shrublands (Fig. 4). The percentage of deciduous forest
304 obtained with the THI has values around ca. 35% in all the sub-complexes (Table 9),
305 mainly represented by the most abundant species *M. (A.) agrestis* and *A. (S.) sylvaticus*
306 and to a lesser extent by *Eliomys querciuns*, *Muscardinus avellanarius*, *Glis glis* and
307 *Clethrionomys glareolus*. These five last species are also those indicative of a temperate
308 forest using the Climatogram method, with percentages ranging between ca. 21-35% (Fig.
309 4; Table 10). Following the environmental category Mediterranean, Shrubland and
310 Humid habitats are the most abundant, between 16-21 %, according to the THI method
311 (Fig. 4; Table 9). The Mediterranean category is mainly represented by the species *E.*
312 *querciuns*, *G. glis*, *M. avellanarius*, *Microtus (Iberomys) brecciensis*, *A. mosbachensis*
313 and *Pliomys* sp. nov.. The Shrubland category is mainly represented by *G. glis*, *Cricetus*
314 *cricetus*, *Microtus (M.) arvalis*, *M. (I.) brecciensis* and *Pliomys* sp. nov.. Finally, the
315 humid habitat is mainly represented by *C. cricetus* and *M. (A.) agrestis*. *M. (A.) agrestis*
316 is responsible for the percentage representation of humid meadows, between 48-58%,
317 obtained with the Climatogram method (Fig. 4; Table 10).

318 Finally, the Simpson index (1-D) indicates a relatively high diversity (>0.5) with
319 similar values in the three studied sub complexes ($1-D_{\text{CIII-CIIsup.}} = 0.6$ and 0.67) from
320 Lazaret cave (Fig. 5). This is a signal of a relatively heterogeneous vegetation (mainly
321 related to deciduous forest, shrubland and mountain habitats) and rodent community
322 (relation between number of species and individual's distribution in each sub complex)
323 (Fig. 5). These most abundant rodents are one mouse (*A. (S.) sylvaticus*) and five vole

324 species (*M. (A.) agrestis*, *M. (T.) multiplex*, *A. mosbachensis* and *Pliomys* sp. nov.) which
325 represent more than 50 individuals in each sub complex (Fig. 5).

326 **5. Discussion**

327 *5.1. Comparison with other Lazaret environmental proxies*

328 The environmental studies done using other proxies from Lazaret cave include the
329 published works on herpetofauna (amphibians and reptiles), birds, marine gastropods, and
330 large mammals from subcomplexes CIII and CII sup (Hanquet et al., 2010 and Valensi et
331 al., 2007). In general, all the studied proxies from complex C of Lazaret cave indicate a
332 cooler climate and a more humid environment than today (Hanquet et al. 2010; Valensi
333 et al. 2007; Valensi and Abbassi, 1998). Former quantification of climate based on
334 herpetofauna at the level of the UAs (Manzano, 2015) using the MER method at a
335 regional level (200 km around the site) and QE for the sequence of Lazaret suggested an
336 alternance of temperate and cold phases during a globally colder than present MIS 6. Cold
337 periods (CII inf. and CIII) were characterized by MAT as being between 12 and 9.6°C
338 (i.e. -5.4°C to -3°C in relation to the present climate). CII sup., however, shows a general
339 improvement in climatic conditions with MAT indicating temperatures between 12 and
340 14°C (i.e. -3°C to -1°C). Reconstructed MAP suggested somewhat lower levels of rainfall
341 than today for temperate periods (around 700 mm; i.e. 100 mm lower than present level)
342 in opposition to much higher values obtained for cold periods with MAT reaching peaks
343 above 1000 mm (i.e. +200 mm in comparison with the present amount) (Manzano, 2015).
344 Some of the UAs (UA27, 18, 15 and 3) were said to correspond to non-analogue
345 herpetofaunal communities (Manzano, 2015), but even with a larger stratigraphical
346 consideration (i.e., at level of complexes) we found no non-analogue assemblages when
347 MER was used at a European scale. If climate reconstructions are quite similar concerning
348 anomalies (Δ) between Manzano (2015) and the present reconstructions, some differences

349 can be seen according to the methods applied. According to the MER, CII sup. would be
350 slightly warmer than the two other complexes, whereas, according to QE, CII sup. is
351 slightly warmer than CIII and CII inf. (Table 7). However, the differences fall within one
352 standard deviation and are therefore not significant. The same issue is observed
353 concerning precipitation. MER suggests a globally more humid climate whereas QE a
354 slightly dryer climate, but again most of the differences observed falls within the standard
355 deviation. In conclusion, climate indications obtained from the QE method on
356 herpetofauna is more in accordance with the occurrence of thermophilus, typically
357 Mediterranean, species (*T. lepidus*, *M. monspessulanus* and *Z. scalaris*) in the different
358 sub-complexes and in line with the results obtained by Manzano (2015) at a regional
359 level.

360 The large mammal assemblage has a faunal composition dominated by *Cervus*
361 *elaphus* and *Capra ibex*. More specifically the sub-complex CII sup. is composed of more
362 temperate species, with the abundance of *C. elaphus*, the presence of *Bos primigenius* and
363 *Capreolus capreolus* and a lower representation of *C. ibex*, than sub complex CIII, where
364 *Rangifer tarandus* and *Bison priscus* are well represented and *C. ibex* is more abundant
365 (Valensi et al. 2007). The avifaunal assemblage of sub-complexes CII sup. and CIII has
366 sedentary species associated with cold climates such as *Aegolius funereus*, *Bubo*
367 *scandiaca* and *Tetrao tetrix* (Hanquet et al. 2010). In general, the avifaunal assemblage
368 shows a predominance of species from cold climates and open environments, together
369 with species related to temperate climates and open environments as well as rock and
370 mountain habitats, with a remarkable closing of the vegetational landscape between
371 CII sup. and CIII sub complexes (Hanquet et al. 2010). Finally, the marine gastropods
372 assemblage highlights the presence of *Melarhaphe neritoides*, a Mediterranean
373 Littornidae species, together with Nordic Littornidae, *Littorina saxatilis* and *Littorina*

374 *fabalis*. The association of these gasteropods indicates a cooling of the sea in sub complex
375 CIII respect to CII (Valensi et al. 2007). In general, the data obtained from the different
376 methods applied to the rodent assemblages are in concordance with the trend shown by
377 the other proxies, with a relatively cold climate and a humid environment in relation to
378 today (Fig. 4). When considered according to sub-complexes within the cave sequence,
379 the results obtained from the rodent assemblages agree with the herpetofaunal data in that
380 there is a similar association in sub-complexes CII sup. and CIII (Table 1). However, the
381 cooling and/or closure detected in the other proxies from CII sup. to CIII are not observed
382 with the rodent results (Fig. 4). Nevertheless, relative colder conditions have been
383 detected with the rodent assemblage in sub complex CII inf., in relation to the overlying
384 complexes (Fig. 4). This is mainly indicated by the presence of *Lasipodomys gregalis*
385 (narrow-headed vole) in sub complex CII inf., a species that currently inhabits tundra and
386 forest tundra from the White Sea to the Kolyma River in Russia and in the steppes of
387 Kazakhstan, Kyrgyzia, SW Siberia, Yakutia, Mongolia and Northern China (Batsaikhan
388 et al. 2016).

389 5.2. Comparison with other MIS 6 sites

390 As noted above, there are few archaeological sites in western Europe dating to MIS
391 6 with small vertebrate studies. Together with Lazaret cave, four sites have been studied
392 in France, Baume Moula-Guercy (Desclaux and Defleur, 1997, Defleur et al., 1998; 2001,
393 Defleur and Desclaux, 2019; Defleur et al., 2020), Grotte des Cèdres (Defleur and Crégut-
394 Bonnoure, 1995), Romain-la-Roche (Guérin et al. 2010) and Coudoulous 1 (Jaubert et al.
395 2003), three in the Iberian Peninsula, Sala de los Huesos in Maltravieso cave (Hanquet,
396 2011), Estanque de Tormentas de Butarque H-02 (Blain et al. 2017; Laplana et al. 2015)
397 and Lezetxiki II (García-Ibaibarriaga et al. 2018) and one in Italy, Poggetti Vecchi
398 (Benvenuti et al. 2017). Regarding the expansion of the continental glaciers in western

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

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

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

424 *duodecimcostatus*, *Allocricetus bursae* and *A. (Sylvaemus) sylvaticus* (Hanquet, 2011). In
425 the lower layers Lezetxiki II, the more abundant rodent species are *A. amphibius*, *M.*
426 (*Agricola*) *agrestis* and *M. (Terricola)* sp. (García-Ibaibarriaga et al. 2018). During MIS
427 6 Lazaret combines, the presence of strictly Mediterranean species, such as *M. (I.)*
428 *brecciensis* and *M. (T.) savii* with strictly cold species, such as *L. gregalis*. This
429 phenomenon could be related to the position of the site, as previously suggested by
430 Valensi et al. (2007) and Desclaux (2013), showing that the glacial expansion in the
431 Maritime-Alps during MIS 6, caused changes in ecology and the area forms a transitional
432 zone between the steppe identified in the southern limits of permafrost in France and the
433 forest and grass identified in in the Italian peninsula (Fig. 6). The area therefore may have
434 acted as a refugial leading edge for some more temperate species.

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

446 5.3. Comparison with other environmental and climatic proxies in western Europe

447 Studies of marine cores, terrestrial pollen sequences and speleothems have been
448 done in western Europe containing the MIS 6 fluctuations (Margari et al. 2010; 2014,

449 Roucoux et al. 2011, Wilson et al. 2013, Tzedakis et al. 2003, Guiot et al. 1989; 1993,
450 Ponel, 1995, Bard et al. 2002, Hodge et al. 2008, Wainer et al. 2013).

451 The analysis of pollen from the marine core MD01-2444 off the Portuguese coast
452 divided the penultimate glacial, on basis of the amplitude of the millennial-scale
453 variability in two main periods (one between 185 to 160 Kya and the other one between
454 150-135 Kya), with a transitional period (between 160-150 Kya). The early period is
455 mainly characterized by a prominent oscillation in foraminiferal isotopes and tree pollen
456 values while the last period is mainly characterized by mild temperature swings in the
457 Antarctic and minimum tree pollen values. This suggests that MIS 6 is characterized by
458 cool climatic conditions with an open forest environment (Margari et al. 2010; 2014).

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

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

469 These data are consistent with the results obtained here where different methods
470 were applied to the rodent assemblages of Lazaret cave. On one side, the methods applied
471 to estimate climatic parameters show a generally cold conditions with relatively low
472 rainfall for all subcomplexes analyzed. On the other hand, the methods applied to
473 investigate the vegetational landscape show a habitat dominated by deciduous temperate

474 forest with humid meadows including relatively high proportions of scrublands (Fig. 4;
475 5).

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

481 **6. Conclusions**

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

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

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

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

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517

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812 Figure 1. Location of the Lazaret cave and the other MIS 6 sites mentioned in the
813 manuscript. Archaeological sites: MTV-SH (Hanquet, 2011), H-02 (ETB) (Blain et al.
814 2017; Laplana et al. 2015), Lezetxiki II (García-Ibaibarriaga et al. 2018), Moula-Guercy
815 (Desclaux and Defleur, 1997), Cèdres (Defleur and Crégut-Bonnoure, 1995), Romain-la-
816 Roche (Guérin et al. 2010), Codoulous (Jaubert et al. 2003), Poggetti Vecchi (Benvenuti
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820 (Wainer et al. 2013), Argentola cave (Bard et al. 2002).

821

822 Figure 2. Stratigraphic section of Lazaret cave. ESR ages taken from Michel et al.
823 (2009).

824

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

830

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

838

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

841

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

847

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

851

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

854

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

857

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

859

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

863

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

866

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

872

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

877

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

880

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