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1 <New bioclimatic models for the Quaternary Palaeartic based on insectivore and rodent  
2 communities

3

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5

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16

17 **Abstract**

18 Mammal remains, preserved in archaeological and palaeontological deposits, are commonly used  
19 to reconstruct past terrestrial climates and environments. Here we propose new species-specific  
20 models for Bioclimatic Analysis, a palaeoclimatic method based on a climatic restriction index for  
21 each mammal species, discriminant analysis, and multiple linear regressions. Our new models are  
22 based on small mammal associations, particularly insectivores and rodents, from Quaternary  
23 paleoarctic contexts. A dataset including new localities and an updated taxonomy was constructed  
24 in order to develop two approaches, the first using only Rodentia, the second based on associations  
25 including both Rodentia and Eulipotyphla. Both approaches proved to be reliable for inferring both  
26 climate zone and quantifying temperature, precipitation, and seasonality. Rarefaction analysis  
27 revealed these new models to be reliable even when a substantial percentage of species from the  
28 original palaeocommunity was absent from the fossil site. Application of these new models to  
29 small mammal associations from two sequences (Balma de l'Abeurador, France and El Mirón,  
30 Spain) spanning from the Last Glacial Maximum to the Holocene are consistent with the primary  
31 climatic changes recorded by regional Pyrenean proxies and showed an increase in mean annual  
32 temperature of between 3 and 5°C.

33 **Key-words**

34 Small mammalian communities; Paleoclimatology; Paleoecology; Pleistocene; Climate  
35 reconstructions

36

37 **1. Introduction**

38           Understanding past climatic and environmental changes and their impact on continental  
39 ecosystems remains a major challenge, particularly in terms of human biological and social  
40 evolution. Currently, environmental reconstructions are built from mineralogical, geochemical,  
41 floral, and faunal data recovered from palaeontological or archaeological sites (e.g. Carrasco et al.,  
42 2008; Frouin et al., 2013; Domingo et al., 2015; Menéndez et al., 2017; Villa et al., 2018; Britton  
43 et al., 2019; Girard et al., 2019). Vertebrates are particularly sensitive to changes in climate and  
44 habitat (e.g., Faunmap, 1996; Thomas et al., 2004), and it is generally assumed that these changes  
45 induce new biotic conditions, which, in turn, constrain vertebrate species distributions, biotic  
46 interactions and, ultimately, community organization (Lyons, 2003; Moritz et al., 2008; Hernández  
47 Fernández et al., 2015; Řičánková et al., 2015; Royer et al., 2016; Blanco et al., 2018). Based on  
48 this assumption, numerous methods have been developed to reconstruct environmental conditions  
49 and quantify past climate parameters from mammalian fossil remains (for syntheses see Artemiou,  
50 1984; Andrews, 1996; Lyman, 2017; Nieto & Rodríguez, 2003). Several such models are based  
51 on modern species distributions and ecological niches (e.g., Atkinson et al., 1987; López García,  
52 2008; Jeannet, 2010; Fagoaga et al., 2019), while others employ species richness (Montuire et al.,  
53 1997; Legendre et al., 2005; Araújo et al., 2008). Relatively few, however, utilize whole mammal  
54 communities (Valverde, 1964; Legendre, 1986, 1989; Kay and Madden, 1997; García Yelo et al.,  
55 2014; Escarguel et al., 2008) or large mammal species associations (de Bonis et al., 1992; Griggo,  
56 1996; Hernández Fernández and Vrba, 2006). Most environmental reconstructions are, in fact,  
57 based on small mammals or uniquely rodents (Hokr, 1951; van de Weerd and Daams, 1978; Daams  
58 and van der Meulen, 1984; Chaline and Brochet, 1989; Sesé, 1991; van der Meulen and Daams,  
59 1992; van Dam, 2006), as these species present several unique particularities. First, they are  
60 frequently preserved in archaeological and palaeontological deposits in caves and rock shelters,

61 sometimes in association with human remains and artifacts and, unlike larger mammals, are less  
62 susceptible to human-induced biases (e.g., Chaline, 1977; Discamps and Royer, 2017). Second,  
63 small mammals are key prey for numerous predators and inhabit a wide variety of ecological  
64 habitats (e.g., Quéré and Le Louarn, 2011; Wilson et al., 2017, 2018). Finally, due to their small  
65 size and large taxonomic diversity, rodent communities reflect local environments and are highly  
66 sensitive to environmental parameters and climatic changes, leading to their being considered one  
67 of the most reliable proxies for inferring past environmental and climatic conditions (e.g., Hinton,  
68 1926; Tchernov, 1975; Avery, 1987; Montuire and Desclaux, 1997; Hernández Fernández et al.,  
69 2007; García-Alix et al., 2008; Cuenca-Bescós et al., 2009; López García et al., 2010; Cuenca-  
70 Bescós et al., 2011; Royer et al., 2013, 2014; Rofes et al., 2015; Royer et al., 2016; Fernández-  
71 García et al., 2016; Laplana et al., 2016; Piñero et al., 2016; Berto et al., 2017; López García et al.,  
72 2017; Berto et al., 2019; Stoetzel et al., 2019; Fernández-García et al., 2020).

73         Among the many methods for reconstructing palaeoenvironments, Bioclimatic Analysis  
74 (Hernández Fernández, 2001) produces both qualitative and quantitative climatic reconstructions  
75 built from the structure of mammal communities, including multiple taxonomic orders, and their  
76 global distribution along broad climatic gradients and biozones. One of its main advantages is that  
77 entire mammal communities are taken into consideration, giving equal value to all species as  
78 climatic indicators related to their ecological tolerance. Here we further refine this approach by  
79 using Eulipotyphla (moles, shrews and hedgehogs, commonly referred to simply as insectivores)  
80 combined with Rodentia (rodents), or uniquely Rodentia recovered from Pleistocene to Late  
81 Holocene Palaeartic faunal assemblages. Although recent research has begun to combine rodents  
82 and insectivores in analyzes, these small mammals had almost always been previously considered  
83 separately by specialists. Fossil material from palaeontological and archaeological sites commonly

84 result from the same accumulation agent and are recovered using similar excavation methods.  
85 Moreover, Eulipotyphla are regularly preserved in European fossil sites and are highly sensitive  
86 to several climatic parameters, such as rainfall, (e.g., Reumer, 1995; Hernández Fernández, 2001;  
87 Hérán, 2006; van Dam, 2006; Furio et al., 2011), making them considerably more robust proxies  
88 for inferring past climates. Furthermore, integrating these taxa is equally essential for generating  
89 a broader, more holistic vision of the past ecology of small mammal communities. Quaternary  
90 sites in the Palaearctic realm frequently yield both human and mammalian fossil remains (e.g.,  
91 Puzachenko and Markova, 2019) and provide essential evidence for reconstructing the influence  
92 of climate changes on human biological and cultural evolution. Developing new palaeoclimatic  
93 modelling techniques focused on this realms's rich fossil record potentially offers a means to  
94 increase both the precision and spatiotemporal resolution of palaeoclimatic inferences. To test  
95 these new models, we mobilized data from Balma de l'Abeurador (Languedoc-Roussillon, France)  
96 and El Mirón (Cantabria, Spain), two archaeological sequences that cover the period from the Last  
97 Glacial Maximum to the beginning of the Holocene.

98

## 99 **2. Material and methods**

100 The Bioclimatic Analysis technique originally described by Hernández Fernández (2001)  
101 and Hernández Fernández and Peláez-Campomanes (2003, 2005) consists of two sets of analyses.  
102 The first uses linear discriminant functions deduced from the bioclimatic structure of modern  
103 mammalian communities in a specific climate zone (defined following Walter's typology, 1970),  
104 which are subsequently used to classify additional observations (extinct communities in our case)  
105 in each climatic zones. The second is built from transfer functions by means of multiple linear

106 regression analyses of climatic parameters and modern bioclimatic mammalian community  
107 structures. These models are ultimately used to infer climatic variables for additional data (i.e.  
108 extinct communities). These two sets of analyses use a single global dataset of localities for which  
109 the composition of mammalian communities and climatic variables are known.

110

### 111 *2.1 - Localities, faunal lists, and climate variables*

112 While multiple global bioclimatic classification systems (e.g. Rivas-Martinez, 2008) are  
113 available, we employed the climate typology defined by Walter (1970), which is based in the  
114 interaction between monthly precipitation and average temperatures. This typology was originally  
115 used in the original qualitative Bioclimatic Analysis (Hernández Fernández, 2001), due to its  
116 simplicity and correlations with major terrestrial biomes. We collated faunal data from 49 modern  
117 localities from across the Palearctic (Table 1, Fig. 1), seven for each of the climate zones present  
118 in this biogeographic realm (see Hernández Fernández, 2001 for more details). Localities were  
119 selected to be representative of the average climatic conditions of each climate zone and to be as  
120 widely distributed as possible (see Table 1 for details). Our sample includes 18 localities from  
121 Hernández Fernández (2001), 13 from García Yelo et al. (2014), to which we added an additional  
122 18 new localities (Table 1), for a total of 49 data points. Localities in climate zones I (equatorial  
123 climate), II (tropical climate with summer rains), and II/III (transitional tropical to semi-arid  
124 climate) are not present in the Palearctic realm and, therefore, contrary to the methodology used  
125 by Hernandez Fernandez (2001), were excluded in the development of the new models.

126 In order to compare results from the two approaches, we built two faunal lists from  
127 published data (Rutilevskiy, 1979; Hernández Fernández, 2001; Héran, 2006; García Yelo et al.,

128 2014) for each locality: one comprising only rodent species, the other including both rodents and  
129 insectivores. Species taxonomies were revised for each list, integrating the most recent species  
130 distribution data (Wilson et al., 2017; Wilson and Mittermeier, 2018; IUCN red list, 2019).

131 Nine climatic variables were collected for each locality (Table 1): mean annual temperature  
132 (MAT); annual positive temperature (TP), calculated as the sum of monthly mean temperature for  
133 months with average temperatures above 0 °C; mean temperature of the warmest month (Tmax);  
134 mean temperature of the coldest month (Tmin); mean annual thermal amplitude (MTA), calculated  
135 as the difference between Tmax and Tmin; thermicity index (It), which reflects the intensity of  
136 winter cold (eq .1);

$$137 \quad It = 10*(MAT + 2xTmin) \quad (eq.1)$$

138 compensated thermicity index (Itc), which was designed to balance the harsh winter in the  
139 continental climates and the extremely mild winter in the oceanic regions in order to make this  
140 index comparable worldwide (see Rivas Martínez, 1994); annual total precipitation (P); drought  
141 length (D), which is the period when P values are lower than 2\*MAT.

142

## 143 *2.2-Calculation of bioclimatic spectra*

144 A climate zone vs species presence matrix was constructed for each locality. When a  
145 species is absent from a given climate zone, it is encoded as 0. When the species is present in that  
146 climate zone, a value of 1/n (referred to as the Climatic Restriction Index, CRI; Hernández  
147 Fernández, 2001), where n is the number of climates in which the species is present (the division  
148 by n ensures that the sum of CRI values for a given species equals 1). The more climatically



149 restricted a species is, the higher its CRI values it has. As species with higher CRI imply more  
150 specific environmental requirements, they offer more reliable indications of climatic conditions.  
151 CRI values for Rodentia and Eulipotyphla species were reexamined (Supplementary material 1)  
152 and modified following updated taxonomic and geographical range information (Wilson et al.,  
153 2017; Wilson and Mittermeier, 2018). Although localities from the three tropical climatic zones  
154 were not included, the large range distributions of some small mammal species extend into these  
155 zones. Consequently, all ten global climate zones were used to calculate the different Bioclimatic  
156 Components (BC) per locality (see below).

157 For a given locality, the Bioclimatic Component (BC) is the representation of each of the  
158 10 existing climates. All 10 BC values for each locality were calculated according to the formula  
159 (eq. 2):

$$160 \quad BC_i = (100 \sum_{j=1}^k CRI_{ij}) / S \quad (\text{eq. 2})$$

161 where  $i$  stands for the  $i^{\text{th}}$  climate zone,  $j$  for the  $j^{\text{th}}$  species present in the locality, with  $S$  being the  
162 number of species in the locality. The 10 BC values for a given locality constitute its bioclimatic  
163 spectrum. The bioclimatic spectrum of each locality was calculated using both datasets: one  
164 comprised uniquely of rodents (Supplementary material 2), the other including both Rodentia and  
165 Eulipotyphla species (Supplementary material 3).

166

### 167 *2.3-Palaeoclimatic inferences*

168 All statistical analyses were performed using the R software package (R core team, 2019).  
169 Linear Discriminant Analysis (LDA - Sneath and Sokal, 1973; Rencher, 2002; Legendre and

170 Legendre, 2012) with the LDA function from the R package MASS (Venables and Ripley, 2002)  
171 was used to classify localities into different climate zones. We subsequently used a Leave-One-  
172 Out Cross Validation (LOOCV – Efron, 1982; Chernick, 1999) to evaluate classification quality.  
173 Predictive equations for each of climatic variable were obtained from multiple linear regressions  
174 (Sokal and Rohlf, 1995; Zar, 1999; Rencher, 2002; Legendre and Legendre, 2012) using the lm()  
175 function, with the ten bioclimatic components as independent variables and the climatic variable  
176 as the dependent ones. We generated a script to easily calculate the bioclimatic spectra and inferred  
177 climatic zone, which is available as supplementary material (Supplementary material 4 and  
178 available at <https://github.com/AurelienRoyer/PalBER>).

179

#### 180 *2.4-Testing sampling biases on palaeoclimatic inference through randomization*

181 Small mammal associations from fossil sites potentially present biased representations of  
182 past community structure due the nature of the accumulation and subsequent taphonomic  
183 alterations (Clark, Beerbower and Kietzke, 1967; Denys, 1985; Andrews, 1990; Kowalski, 1990;  
184 Stahl, 1996; Reed, 2007), which may, in turn, impact climatic inferences drawn from Bioclimatic  
185 Analysis. For instance, many fossil assemblages of small mammals are accumulated by predators,  
186 especially nocturnal raptors, who are relatively selective in their choice of prey (e.g., Andrews,  
187 1990). Bioclimatic Analysis has the advantage of dampening this potential bias by taking into  
188 account the general representativeness of the taxonomic composition of micromammal death  
189 assemblages (i.e. the presence or absence of particular taxa) rather than their relative abundance.  
190 This method does not differentially weight taxa, and the occurrence of a single fossil of a unique  
191 species could theoretically alter a locality's bioclimatic spectrum and, therefore, its climate

192 reconstruction. However, although high levels of ecological redundancy in mammalian  
193 communities (Gómez Cano et al., 2006) somewhat minimize this problem, it can be better  
194 overcome with adequate sample size. Although the fragile nature of small mammal fossils means  
195 they are unlikely to be redistributed (Álvarez-Sierra et al., 1990, Fernández-López, 2000), potential  
196 species loss associated with different processes of accumulation, fossilization, and sampling bias  
197 cannot be ruled out (Andrews, 1990 Behrensmeyer, 1991; Lyman, 1994; Andrews, 2006; Gómez  
198 Cano et al., 2006; Turvey and Cooper, 2009; Fernández-Jalvo, Scott and Andrews, 2011), raising  
199 questions as to how these potential biases affect Bioclimatic Analysis (Gómez Cano et al., 2006).

200 To investigate the potential impact of species loss, we randomly removed species in the  
201 modern localities in order to replicate impoverished faunal associations. Multiple LDA and  
202 multiple linear regressions were performed for each locality by randomly removing  $k$  taxa ( $k$   
203 varying from 1 to  $n-2$ , with  $n$  being number of species in the locality). For a given locality and a  
204 given  $k$ , 100 impoverished samples were generated. A total of 69,000 randomized samples were  
205 produced, for which simulated climatic inferences were calculated using the new rodents and  
206 rodents plus insectivores models. Three locations in the arctic climate zone (IX) were left  
207 unchanged, as they contain less than three species. We used logistic regressions (Sokal and Rohlf,  
208 1995; Legendre and Legendre, 2012) to explore the coherence of simulated climatic inferences for  
209 each climate zone. Quantitative inferences of climatic variables were evaluated using standard  
210 deviations of predicted values calculated for a given locality and a given  $k$  taxa removed.  
211 ANCOVAs (Zar, 1999; Sokal and Rohlf, 1995) were performed for each climate parameter using  
212 log-transformed standard deviations of predicted values, with the percentage of taxon removed  
213 and climate zones used as independent variables.

214 *2.5-Application of the new models to palaeoclimatic reconstruction*

215           The two new approaches for Bioclimatic Analysis allow us to analyze small mammal  
216 associations from the Palaeartic Quaternary and reconstruct climatic conditions. We used small  
217 mammal associations from La Balma de l'Abeurador (Languedoc-Roussillon, Hérault, France)  
218 and El Mirón (Cantabria, Spain), two sites located in typical temperate climate areas and that  
219 yielded sequences spanning from the end of the Late Pleistocene to the beginning of the Holocene  
220 (Fig. 2). All radiocarbon dates were calibrated at  $2\sigma$  (95%) using Oxcal v4.3 (Bronk Ramsey,  
221 2017) and the IntCal13 calibration curve (Reimer et al., 2013).

222           The site of Balma de l'Abeurador is located in southern France and currently has a mean  
223 annual temperature of 13.6°C and annual precipitation around 700 mm. The central sector of the  
224 cave produced six multi-level deposits (Heinz et al., 1992; Vaquer et al., 1986; Vaquer and Ruas,  
225 2009), whose chronology was determined by the nature of the lithic assemblage, palynology, and  
226 radiocarbon dates (Vaquer and Ruas, 2009). Small mammals from Balma de l'Abeurador were  
227 first studied by Marquet (1987) and then by Mistrot (2001), who identified at least 19 taxa in an  
228 assemblage comprising at least 2000 individuals (Table 2). We used Mistrot's (2001) data, as it  
229 benefits from a taphonomical analysis demonstrating no bias in the representativity of the small  
230 mammal assemblage. This detailed taphonomical approach, together with the high number of  
231 remains (more than 100 first and second upper and lower rodent molars for each level) and an  
232 adequate minimum fossil sample size of fossils, allows for reliable palaeoclimatic inferences (van  
233 de Weerd and Daams, 1978; Daams et al., 1999). Several differences do exist between Mistrot's  
234 (2001) and Marquet's (1987) analyses in terms of species identification, with the latter employing  
235 extreme caution when identifying fossils to species. For *Apodemus*, *Arvicola*, and *Microtus*  
236 (*Terricola*), Mistrot (2001) made no specific identifications, whereas Marquet (1987) and Brunet-  
237 Lecomte (1988) identified almost exclusively *Ap. sylvaticus*, *Ar. Amphibius*, and *M. (T.)*

238 *duodecimcostatus* throughout the sequence. For the insectivore genus *Sorex*, *Neomys*, and  
239 *Crocidura*, no distinction was made between *Sorex araneus* and *Sorex coronatus*, between *Neomys*  
240 *anomalous* and *Neomys fodiens*, or between *Crocidura leucodon* and *Crocidura russula*.

241

242 Table 2: Faunal lists of identified Rodentia and Eulipotyphla per level at Balma de l’Abeurador.  
243 Crosses indicate species present, circles represent absence species. Data are from Mistrot (2001).

244

245 The site of El Mirón is located in northern Spain, and enjoys relatively similar climate  
246 conditions to Balma de l’Abeurador, but with slightly higher annual precipitation (reaching 1,000  
247 mm) and smaller seasonal differences in rainfall (Fig. 2). The site yielded a long stratigraphic  
248 sequence (Strauss and Morales, 2019) and numerous radiocarbon dates (e.g., Strauss and Morales,  
249 2003, 2007, 2012, 2019). Twenty-one insectivore and rodent taxa were identified from throughout  
250 the 44 studied levels of the stratigraphy (Cuenca-Bescós et al., 2008, 2009). Although over 3,000  
251 individuals were identified, they are highly unevenly distributed among the different levels. To  
252 ensure the reliability of palaeoclimatic inferences, we selected only deposits with more than 50  
253 individuals, or grouped together several successive levels (i.e. the Solutrean levels 120 to 126 from  
254 the Last Glacial Maximum). For *Apodemus* and *Sorex*, no distinctions were made between *Ap.*  
255 *sylvaticus* and *Ap. flavicollis* or between *S. araneus* and *S. coronatus*.

256 When reliable criteria for confidently distinguishing between species are unavailable, two  
257 approaches can be taken: either building bioclimatic spectra from all the potentially present species  
258 and calculating a palaeoclimate inferences for each; or using an average species, sometimes

259 referred to as “quimeric” species. When a taxon is only identified to genus, the biome occupation  
260 of all the potential species can be used. For instance, if one species inhabits biomes VI and VII,  
261 and the other inhabits IV and VI; the genus can be considered to inhabit IV, VI, and VII. Even if  
262 relatively little uncertainty is introduced, "quimeric" species have a lower discriminatory power  
263 than any of the potential original species while still providing useful information for community  
264 structure. Consequently, both approaches were used and their results compared.

265 Extinct species potentially present an additional limitation, as no past climate data is  
266 available for their geographic distribution. Following Hernández Fernández et al. (2007), we  
267 assigned extinct taxa to different BCs according to the distribution of their extant relatives. As  
268 “quimeric” species, they provide reduced discriminatory power. The El Mirón sequence has the  
269 particularity of yielding remains of the now-extinct rodent *Pliomys coronensis* (= *Pliomys lenki*),  
270 for which we used the bioclimate characterization proposed by Hernández Fernández et al. (2007).

271

## 272 **3-Results and discussion**

### 273 *3.1-Qualitative climatic classification and quantitative climatic inferences*

274 The number of species in modern localities from the different climate zones ranges on  
275 average between 17 and 24, except for bioclimate zones III and IX (Supplementary material 6).  
276 Localities in these two climate zones yielded a maximum of 15 species, with some containing less  
277 than 5 species. Eulipotyphla produced around 25 % of all faunal lists on average, but faunal lists  
278 from bioclimate zones IV, VI and VIII included 30 % or more of Eulipotyphla.

279           The two linear discriminant analyses based on the bioclimatic spectra correctly classified  
280 nearly all localities, inducing a very low rate of error. When only Rodentia was used, incorrectly  
281 classified localities rose to 6 % (Table 3), a similar figure to the one calculated by Hernández  
282 Fernández (2001). When the combined Rodentia and Eulipotyphla dataset is used, only  
283 Blagoveshchensk was incorrectly classified in climate zone VIII instead of VI. However, the cool-  
284 temperate and boreal forests throughout the region of Blagoveshchensk (Kolbek, Srutek and Box,  
285 2013) are home to numerous species typical of colder climates, including *Lemmus amurensis*,  
286 *Clethrionomys rufocanus*, *Myopus schisticolor*, *Pteromys volans*, or *Sorex tundrensis*), which  
287 likely goes some way in explaining the incorrect climate zone attribution.

288 Table 3: Apparent error rate, prediction error, and prediction quality (proportion of observations  
289 with a posterior probability > 0.9) for each approach (Rodentia, Rodentia plus Eulipotyphla) for  
290 LDA. The prediction error is based on LOOCV.

291

292           The Leave-One-Out Cross Validation (LOOCV) indicated very low prediction error; the  
293 rodent-only dataset produced approximately 12 % misclassifications, while the dataset including  
294 both sets of mammals had both a lower level of error (Table 3) and predictions associated with a  
295 high posterior probability (Table 3). This would indicate climate inferences based on the  
296 combination of rodents and insectivores to be slightly more reliable. The high predictive power of  
297 both models reveals a close relationship between small mammal communities and climate, which  
298 makes them suitable to infer past climate conditions (Hernández Fernández, 2001).

299           Most predictive equations generated by the multiple linear regressions for each climatic  
300 factor, as a function of the bioclimatic components of either Rodentia or Rodentia and

301 Eulipotyphla, produced highly significant determination coefficients (Table 4). The different  
302 transfer functions for each climatic variable had similar coefficients of determination for both  
303 datasets, with minor trends towards slightly higher values for the combined Rodentia and  
304 Eulipotyphla dataset. Values were also relatively similar to those obtained by Hernández  
305 Fernández and Peláez-Campomanes (2005). Only MTA showed very low coefficients of  
306 determination ( $<0.6$ ). Precipitation shows a slightly better coefficient of determination than the  
307 one obtained by Hernández Fernández and Peláez-Campomanes (2005), although it is still lower  
308 than 0.8 (Table 4), which resulted in calculated prediction with large intervals.

309

### 310 *3.2-Loss of species and bias in climate inferences*

311 Overall, few incorrect qualitative inferences were generated when species were removed  
312 from the faunal lists (usually below 15 % per climate zone – fig. 3, supplementary material 7). The  
313 S-shaped curves of logistic regressions are skewed upwards (Fig. 3; Supplementary material 7),  
314 meaning there is no “turning point” when climatic inferences become erroneous and that reliable  
315 classifications can nevertheless be obtained using relatively few species, although they may have  
316 a high probability of error (Fig. 4). The two approaches behaved differently according to climate  
317 zone when species are randomly removed; inferences drawn from rodent communities are more  
318 robust for climate zones III, V, and IX, while the second approach (Rodentia plus Eulipotyphla) is  
319 more robust for climate zones IV, VI, and VIII. Incorrect inferences for communities in the polar  
320 climate zone (IX) are low with the rodent-only dataset (4.2%) and much higher with the Rodentia  
321 plus Eulipotyphla, with incorrect inferences mainly classified into the boreal climate zone (VIII).  
322 The percentage of incorrect classifications increased for all climate zones when more taxa are



323 removed (Figs. 3 and 4, supplementary material 7). Although classification error generally  
324 increased after the removal of 30-40 % of taxa from the localities (Fig. 4), most reached the 25 %  
325 incorrect classifications threshold when more than 50 % of taxa were removed. Nevertheless, the  
326 warm temperate (climate zone V; except for the Batumi locality) and arid temperate climate (VII)  
327 zones appeared to be much more resistant to species loss independent of the dataset used (Fig. 3,  
328 supplementary material 7). Substantial variability is evident between localities in the same climate  
329 zone, demonstrating faunal communities from the same climate zone to be highly variable. This  
330 variability reflects varying responses of different taxa inhabiting the same climate zone.

331         Quantification of climatic parameters follows similar trends. Differences between  
332 theoretical and calculated values in impoverished communities for each climatic parameter are  
333 highly dependent on the percentage of remaining taxa (Supplementary material 8). These  
334 differences vary as a function of the climate zone considered and the dataset used. For instance, in  
335 the case of precipitation estimates from climate zones III and VIII (subtropical arid and boreal),  
336 less impoverished communities produced larger differences when the rodent-only dataset was  
337 used. Figures 5 and 6 show standard deviations of predicted values obtained for impoverished  
338 faunal associations computed for each climatic parameters. These standard deviations follow  
339 exponential variations, which increase with the percentage of taxa removed. Overall, standard  
340 deviations of predicted values become important when half of the faunal list is removed (Fig. 5  
341 and 6). ANCOVAs for each climate parameter show no significant difference between climate  
342 zones ( $F = (6, 676)$ ,  $p > 0.7$ ). The approach based on rodent communities generated steeper  
343 regression curves than those based on Rodentia plus Eulipotyphla, which suggests the former to  
344 be more sensitive to species loss. This is probably related to the fact that faunal lists comprised  
345 exclusively of rodents contain less species than those combining both orders of small mammals.

346 When confronted with species loss, the combined dataset therefore appears better adapted to  
347 producing robust climate quantifications.

348 As expected, our results indicate that palaeoclimatic inferences obtained by Bioclimatic  
349 Analysis depend significantly on the integrity of the past faunal communities used. Satisfactory  
350 levels of confidence can be obtained only when species loss is below 50 %, which is similar to the  
351 initial estimates produced by Gómez Cano et al. (2006). When quantifying climatic parameters,  
352 the approach combining Rodentia and Eulipotyphla proved less sensitive to faunal  
353 impoverishment, and should be preferred when species loss is suspected.

354

#### 355 **4-Palaeoclimatic inferences from past small mammal communities**

356 Climate zone classifications and mean annual temperature predictions generated by the two  
357 approaches were applied to multiple faunal lists from El Mirón and Abeurador (Figure 7). All  
358 possibilities related to uncertainties in species identifications (see above) were tested. Climate  
359 prediction remained the same for both datasets, except for the case of Abeurador level 5b, for  
360 which two different climate zones (IV and VI) were predicted depending on the Eulipotyphla  
361 species used. When uncertainties concern only two species, variations in mean annual temperature  
362 values remain minimal (Fig. 7, Supplementary material 5). For instance, temperature variation was  
363 less than 0.5°C between communities in which *Apodemus* specimens were identified as *A.*  
364 *sylvaticus* instead of *A. flavicollis*, and vice versa. In the case of *N. anomalus* and *N. fodiens*,  
365 variation reached almost 2°C. Observed variations can reach up to 4°C (e.g. Abeurador level 8)  
366 when all possibilities are run using either of the two approaches. The highest degree of variation  
367 primarily concerns uncertain species inhabiting only a few climate zone that are different between

368 them, such as *S. araneus* and *S. coronatus*. As a consequence, faunal lists employed in bioclimatic  
369 modelling should only include reliably identified species. Finally, small variations could also be  
370 observed according to the approach used, the one based on rodents tending to estimate mean annual  
371 temperature two degrees lower.

372 Figure 8 depicts the mean annual temperature obtained from small mammal lists of  
373 Abeurador and El Mirón. For levels with uncertainties in species classification, we used  
374 “quimeric” species for climatic inferences. Overall, the two approaches show similar trends in both  
375 sequences; an attribution to climate zone IV during the Holocene and a progressive warming with  
376 the onset of the Bølling interstadial. While the same trend can be observed for predictions based  
377 on Rodentia and Eulipotyphla and only Rodentia, the latter tended to produce lower mean annual  
378 temperature estimates. Mean annual temperatures obtained for the Abeurador sequence using the  
379 rodent dataset ranges from 3.8°C to 9.2°C, whereas the approach based on Rodentia and  
380 Eulipotyphla ranges from 6.3 to 11.6°C. Similarly, mean annual temperature varied throughout the  
381 El Mirón sequence, averaging around 1.2°C for both approaches, which is included in the  
382 confidence intervals (and so in the prediction intervals). The lowest mean annual estimations were  
383 for the LGM levels 112-114. Temperatures rose around 3.0°C between Heinrich stadial 1 and the  
384 beginning of the Holocene at El Mirón, which is slightly lower than was calculated for Abeurador.  
385 No major differences are observed between the two approaches for precipitation and thermal index  
386 conditions (Fig. 9, Supplementary material 5). Throughout the Abeurador sequence, the  
387 Eulipotyphla approach showed an increase of precipitation between Heinrich Stadial 1 and the  
388 Boreal interstadial, suggesting wetter climate conditions to have prevailed during the Holocene at  
389 Abeurador. Nevertheless, no differences were inferred with the rodent approach, suggesting that  
390 if changes in precipitation did occur, they were not important enough to have a significant impact

391 on rodent communities. A progressive increase in the Thermicity index can be observed  
392 throughout the sequence, confirming milder conditions associated with the Holocene deposits.  
393 Apart from a slight decrease at the end of the sequence, no abrupt changes in precipitation were  
394 recorded anywhere in the El Mirón record, and no differences are evident between predictions for  
395 both approaches. Several variations in the Thermicity index are evident across the sequence, with  
396 several notable decreases in levels 112-114 and 107-106, whereas a slight increasing trends  
397 emerges at the end of the Late Glacial. These variations were recorded for a level where low mean  
398 annual temperature were predicted, suggesting these changes were associated with modifications  
399 in seasonality and the intensity of winter colds. Climate parameters from levels 110 and 111 of El  
400 Mirón were previously explored using the Mutual Climatic Range of the rodents (Bañuls-Cardona  
401 et al., 2014). Mean annual temperatures were estimated to be 3 to 4 °C higher, averaging around  
402 10.6°C, whereas the mean temperature of the coldest months diverge by 6°C. The Bioclimatic  
403 approach suggests colder climatic conditions for the LGM levels of El Mirón.

404 Our analysis of the Balma de l'Abeurador and El Mirón sequences primarily focused on  
405 three climate variables (mean annual temperature, precipitation, and thermicity index) considered  
406 susceptible to changes during this time period. These two terrestrial sequences are in relative  
407 agreement with evidence from regional climate evidence recorded in speleothems as well as lake  
408 and marine core records (Jalut and Turu, 2009; Moreno et al., 2012). The LGM appears as a cold,  
409 relatively dry period (but not as dry as Heinrich Stadial 1), inducing a hiatus in speleothem and  
410 lake records. Bioclimatic models built from LGM deposits tend to estimate lower mean annual  
411 temperature and a lower Thermicity index, as is the case in El Mirón level 112.114. With that said,  
412 our models revealed no major change in precipitation coincident with the LGM, with all variations  
413 falling within the large confidence intervals. Speleothems from northern Spain and southern

414 France (Chauvet Cave) have suggested an increase in temperature and humidity just before the  
415 Bølling interstadial (15.4 kyr), which reached their maximum during the Allerød (Genty et al.,  
416 2006; Moreno et al., 2010; Martínez Pillado et al., 2014). Mean annual temperature based on small  
417 mammals closely mirror the mean annual temperature model built from speleothems. The  
418 Younger-Dryas at El Mirón is represented by two levels with radiocarbon dates compatible with  
419 this period. Overall, speleothem and pollen records suggest the Younger-Dryas to be characterized  
420 by an abrupt cold event associated with a reduction in arboreal communities (Fletcher and Sánchez  
421 Goñi, 2008; Morellón et al., 2018). There is currently little evidence supporting this event to  
422 comprise two phases; an initial dry phase followed by a progressive increase in humidity and  
423 warmer conditions (e.g. Muñoz-Sobrino et al., 2013; Bartolomé et al., 2015; Morellón et al., 2018).  
424 Two hypotheses could explain the pattern observed for the Younger-Dryas at El Mirón; low  
425 archaeological resolution or the relatively insignificant impact of this event on small mammal  
426 communities.

427         Despite being located on different sides of the Pyrenees, these two sequences are relatively  
428 close geographically and today lie in typical temperate climates. Our results suggest that warming  
429 during the Holocene differed slightly of either side of this natural barrier, being less marked in  
430 northern Spain compared to southern France.

431

## 432 **5. Conclusions**

433         By focusing on Palaearctic small mammal communities, our work refines the Bioclimatic  
434 Analysis first developed by Hernández Fernández two decades ago and extends its use to rich  
435 fossil record of the Eurasian Quaternary. Although rodent communities alone generate informative

436 qualitative and quantitative climatic reconstructions, combining rodents and insectivores increases  
437 precision for several climatic parameters, particularly precipitation. As previously indicated by  
438 Hernández Fernández and Peláez-Campomanes (2005), due to the statistical uncertainty present  
439 in every climate transference function, the inferences drawn should not be taken as absolutes but  
440 as indicators of general trends. Although it is robust against sampling bias, this method  
441 nevertheless requires data from secure contexts with proper sampling efforts and adequate  
442 taphonomical control in order to ensure accurate taxonomic identification and the representativity  
443 of faunal assemblages. Although imprecisions in taxonomic identification do not impact general  
444 trends, they could engender variations in climatic estimations, which highlights the importance of  
445 confidence intervals. The R script developed for this analysis (and available as supplementary  
446 material 4) provides a simple means for using Bioclimatic Analysis for past climate  
447 reconstructions.

448         The application of these new models to the Quaternary sequences of Balma de l'Abeurador  
449 and El Mirón to reconstruct paleoclimate revealed relatively similar changes with those built from  
450 other proxies, such as speleothems. The bioclimatic inferences from these two archaeological  
451 sequences suggest that, depending on the side of Pyrenees, mean annual temperatures warmed  
452 from 3 to 5°C between the Late Glacial and the Holocene.

453

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460

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811

812 **Figure captions:**



813 Figure 1: Maps of the 10 climate zones and 49 selected localities. See Table 1 for the list of  
814 localities.

815 Figure 2: A) location of Abeurador and El Mirón, B) Walter and Lieth climate diagrams  
816 (calculated between 1985 and 2015) and, C) available radiocarbon dates for levels from both  
817 sequence with associated cultural attributions. Radiocarbon dates calibrated using OxCal v4.3 and  
818 IntCal13.

819 Figure 3: Fitted curves (red) for logistic regressions of the correctness of the LDA classification  
820 for each climatic zone (vertical axes: above, correct predictions, below, incorrect predictions)  
821 against the percentage of remaining taxon (horizontal axes). This percentage was calculated from  
822 the randomization procedure of 49 rodent and Eulipotyphla faunal associations (seven for each  
823 climate zone), which were impoverished by randomly removing species. Histograms illustrate  
824 frequencies of classification as a function of the percentage of species remaining in the association  
825 (number of impoverished localities is shown on the right axis). Boxplots illustrate median, quartile,  
826 and range of incorrect inferences for all the randomly impoverished communities in each climate  
827 zone. A detailed indication of the percentage for each climate zone estimated by incorrect  
828 classifications is provided in the middle of each graph (numbers as in Table 1).

829 Figure 4: Evolution (colored curves) of the percentage of incorrectly classified localities (vertical  
830 axes) depending on the percentages of remaining taxa (horizontal axes) obtained with randomly  
831 impoverished communities for each locality (numbers as in Table 1) and per climate zone.  
832 Numbers of localities are reported in table 1. Blagoveshchensk was excluded from climate zone  
833 IV. Three localities (44, 45 and 46) were not randomly impoverished for climate zone IX due to  
834 very low species numbers.

835 Figure 5: Fitted curves (black) and associated confidence intervals (blue) for the exponential  
836 regressions of the standard deviations of the predicted values against the percentage of remaining  
837 taxon from impoverished faunal list for the approach based on Rodentia. Point color codes for the  
838 climate zones are the same as in Fig. 1

839 Figure 6: Fitted curves (black) for each climatic parameter and associated confidence intervals (in  
840 blue) for the exponential regressions of the standard deviations of predicted values against the  
841 percentage of remaining taxon from the impoverished faunal list for Rodentia and Rodentia plus  
842 Eulipotyphla. Point colors codes for the climate zones are the same as in Fig. 1.

843 Figure 7: Influence of the species identification uncertainty on Mean Annual Temperature  
844 estimates for deposits from El Mirón and Abeurador (squares indicated rodents and circles and  
845 rodents plus Eulipotyphla). The symbol colors represent inferred climate zone. Confidence  
846 intervals for the estimated MAT values shown as vertical lines.

847 Figure 8: Evolution of the estimated Mean Annual Temperature along the El Mirón (bottom) and  
848 Abeurador (top) chronozone by means of multiple regression. Squares represent estimated MAT  
849 values obtained from the Rodentia approach, circles for the Rodentia plus Eulipotyphla approach.  
850 Symbol colors indicate inferred climatic zone. Vertical lines represent confidence intervals for  
851 estimated MAT values. Horizontal lines delimit levels associated with chronozones.

852 Figure 9: Evolution of estimated precipitation and thermicity index (TI) along the El Mirón  
853 (bottom) and Abeurador (top) chronozone by means of multiple regression. Squares represent  
854 estimated MAT values from the Rodentia approach, circles for the Rodentia plus Eulipotyphla  
855 approach. Symbol colors indicate inferred climatic zone. Vertical lines represent confidence  
856 intervals for estimated MAT values. Horizontal lines delimit levels associated with chronozones.

857

858 **Table captions:**

859 Table 1: Coordinates, climate zone, and climatic parameters values for the 49 localities. New  
860 localities added for this study are indicated with asterisks. Abbreviations: MAT = mean annual  
861 temperature; TP = annual positive temperature; Tmax = mean temperature of the warmest month;  
862 Tmin = mean temperature of the coldest month; MTA = mean annual thermal amplitude; It =  
863 thermicity index; Itc = compensated thermicity index; P = annual total precipitation; D= drought  
864 length.

865 Table 2: Faunal lists of identified Rodentia and Eulipotyphla per level at Balma de l'Abeurador.  
866 Crosses stand for species presence, circles for species absence. Data are from Mistrot (2001).

867 Table 3: Apparent error rate, prediction error, and prediction quality (proportion of observations  
868 with a posterior probability  $> 0.9$ ) for each approach (Rodentia, Rodentia plus Eulipotyphla) for  
869 LDA. The prediction error is based on LOOCV.

870 Table 4: Coefficient of determination values obtained for multiple linear regressions for each  
871 climatic variable according to the two approaches (Rodentia, Rodentia plus Eulipotyphla).

872

873

874

875 **Supplementary captions:**

876 Supplementary material 1: Climatic restriction index of Rodentia and Eulipotyphla. The last  
877 column provides details for each locality (numbers as in Table 1), from which these taxa were  
878 found.

879 Supplementary material 2: Bioclimatic spectra of Rodentia for each locality.

880 Supplementary material 3: Bioclimatic spectra of Rodentia and Eulipotyphla for each locality.

881 Supplementary material 4: Palber.R Script applied to bioclimatic method and bioclimatic spectra  
882 files (.csv) necessary to run it.

883 Supplementary material 5: Predictions calculated for each level of Abeurador and El Mirón,  
884 obtained from the two approaches.

885 Supplementary material 6: Number of rodents and Eulipotyphla per modern locality.

886 Supplementary material 7: For each climatic zone, S-shape curves (red) for logistic regressions of  
887 the correctness of the LDA classification for each climate zone (vertical axes: above, correct  
888 predictions, below, wrong predictions) against the percentage of the remaining taxon (horizontal  
889 axes). This percentage was calculated from the randomization procedure of 49 rodent faunal  
890 associations (seven for each climate zone), which were impoverished by randomly removing  
891 species. Histograms illustrate frequencies of classification as a function of the percentage of  
892 species remaining in the association (number of impoverished localities is shown on the right  
893 axes). Boxplots illustrate median, quartile, and range of incorrect inferences for all the randomly  
894 impoverished communities in each climate zone. A detailed of incorrect classifications (%) are  
895 provided in the middle of each graph (numbers as in Table 1), with the average details of the  
896 climate zones into which they are classified.

897

898 Supplementary material 8: Evolution of differences between estimated climate values by means of  
899 multiple regression for each climate variable and both approaches (Rodentia or Rodentia +  
900 Eulipotyphla) according to the percentage of remaining taxa and values calculated when the faunal  
901 list is complete. Each figure corresponds to a combination of a given climate variable and a given  
902 approach.

903