



HAL
open science

New bioclimatic models for the quaternary palaeartic based on insectivore and rodent communities.

Aurélien Royer, Blanca A. García Yelo, Rémi Laffont, Manuel Hernández Fernández

► To cite this version:

Aurélien Royer, Blanca A. García Yelo, Rémi Laffont, Manuel Hernández Fernández. New bioclimatic models for the quaternary palaeartic based on insectivore and rodent communities.. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 2020, 560, pp.110040. 10.1016/j.palaeo.2020.110040 . hal-02969659

HAL Id: hal-02969659

<https://hal.science/hal-02969659>

Submitted on 9 Nov 2020

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

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

3

4 Aurélien Royer^{1,*}, Blanca A. García Yelo², Rémi Laffont¹, Manuel Hernández Fernández^{3,4}

5

6 ¹Biogéosciences, UMR 6282 CNRS, Université Bourgogne Franche-Comté, 6 Boulevard Gabriel,
7 21000 Dijon, France.

8 ² *Departamento de Didáctica de las Ciencias Experimentales, Sociales y Matemáticas, Facultad*
9 *de Educación. Universidad Complutense de Madrid. Rector Royo Villanova s/n. 28040 Madrid,*
10 *Spain.*

11 ³ *Departamento de Geodinámica, Estratigrafía y Paleontología, Facultad de Ciencias*
12 *Geológicas. Universidad Complutense de Madrid. José Antonio Nováis 12, 28040 Madrid, Spain.*

13 ⁴ *Departamento de Cambio Medioambiental, Instituto de Geociencias (UCM, CSIC). Severo*
14 *Ochoa 7, 28040 Madrid, Spain*

15 * Corresponding author e-mail: aurelien.royer@u-bourgogne.fr

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 Palaeartic 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 Palaeartic 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^{th} climate zone, j for the j^{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 2σ (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 Palaeartic 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

454 **Acknowledgments**

455 This research was conducted by the PMMV Team (Palaeoecology, Macroecology and
456 Macroevolution of Vertebrates (<http://pmmv.com.es>), as part of Evolution of Cenozoic Mammals
457 and Continental Palaeoenvironments research group (UCM-910607). This research was supported

458 by projects of the Spanish Ministries of Education, Science and Innovation (PGC2018-094122-B-
459 I00; PGC2018-094955-A-I00) and the Biogéosciences Laboratory of the University of Burgundy.

460

461 **References:**

462 Álvarez Sierra, M.A., Díaz Molina, M., Lacomba, J.L., & López Martínez, N. (1990). *Taphonomic*
463 *and sedimentary factors in the fossil record of mammals. European neogene mammal chronology.*
464 In: European Neogene Mammal Chronology (eds. by E.H. Lindsay, V. Fahlbusch and P. Mein),
465 pp. 461-474.

466 Andrews, P. (1990). *Owls, Caves and Fossils*. University of Chicago Press, Chicago.

467 Andrews, P. (1996). Palaeoecology and hominoid palaeoenvironments. *Biological Reviews*, 71(2),
468 257-300.

469 Andrews, P. (2006). Taphonomic effects of faunal impoverishment and faunal mixing.
470 *Palaeogeography, Palaeoclimatology, Palaeoecology*, 241(3-4), 572-589.

471 Araújo, M.B., Nogués-Bravo, D., Diniz-Filho, J. A.F., Haywood, A.M., Valdes, P.J., & Rahbek,
472 C. (2008). Quaternary climate changes explain diversity among reptiles and amphibians.
473 *Ecography*, 31(1), 8-15.

474 Artemiou, C. (1984). Mammalian community palaeoecology: a review of recent methods with
475 special reference to Miocene mammalian faunas of Europe. *Paléobiologie continentale*, 14, 91-
476 109.

477 Avery, D.M. (1987). Late pleistocene coastal environment of the Southern Cape province of South
478 Africa: Micromammals from Klasies river Mouth. *Journal of Archaeological Science*, 14(4), 405-
479 421.

480 Atkinson, T.C., Briffa, K.R., & Coope, G.R. (1987). Seasonal temperatures in Britain during the
481 past 22,000 years, reconstructed using beetle remains. *Nature*, 325(6105), 587-592.

482 Bañuls-Cardona, S., López-García, J. M., Blain, H. A., Lozano-Fernández, I., & Cuenca-Bescós,
483 G. (2014). The end of the Last Glacial Maximum in the Iberian Peninsula characterized by the
484 small-mammal assemblages. *Journal of Iberian Geology*, 40(1), 19-27.

485 Bartolomé, M., Moreno, A., Sancho, C., Stoll, H.M., Cacho, I., Spötl, C.,... Hellstrom, J.C. (2015).
486 Hydrological change in Southern Europe responding to increasing North Atlantic overturning
487 during Greenland Stadial 1. *Proceedings of the National Academy of Sciences*, 112(21), 6568-
488 6572.

489 Behrensmeier, A.K. (1991). Terrestrial vertebrate accumulations. *Taphonomy: releasing the data*
490 *locked in the fossil record*, 9, 291-335.

491 Berto, C., Boscato, P., Boschini, F., Luzi, E., & Ronchitelli, A. (2017). Palaeoenvironmental and
492 palaeoclimatic context during the Upper Palaeolithic (late Upper Pleistocene) in the Italian
493 Peninsula. The small mammal record from Grotta Paglicci (Rignano Garganico, Foggia, Southern
494 Italy). *Quaternary Science Reviews*, 168, 30-41.

495 Berto, C., Santaniello, F., & Grimaldi, S. (2019). Palaeoenvironment and palaeoclimate in the
496 western Liguria region (northwestern Italy) during the Last Glacial. The small mammal sequence
497 of Riparo Mochi (Balzi Rossi, Ventimiglia). *Comptes Rendus Palevol*, 18(1), 13-23.

498 Blanco, F., Gómez Cano, A.R., Cantalapiedra, J.L., Soledad Domingo, M.S., Domingo, L.,
499 Menéndez, I., Flynn, L.J., & Hernández Fernández, M. (2018). Differential responses of Miocene
500 rodent metacommunities to global climatic changes were mediated by environmental context.
501 *Scientific Reports*, 8, 2502.

502 Britton, K., Pederzani, S., Kindler, L., Roebroeks, W., Gaudzinski-Windheuser, S., Richards, M.
503 P., & Tütken, T. (2019). Oxygen isotope analyses of *Equus* teeth evidences early Eemian and early
504 Weichselian palaeotemperatures at the Middle Palaeolithic site of Neumark-Nord 2, Saxony-
505 Anhalt, Germany. *Quaternary Science Reviews*, 226, 106029.

506 Bronk Ramsey, C. (2017). OxCal Program, version 4.3; University of Oxford, Radiocarbon
507 Accelerator Unit: Oxford, UK.

508 Brunet-Lecomte, P. (1988). *Les Campagnols souterrains, Terricola, Arvicolidae, Rodentia,*
509 *actuels et fossiles d'Europe occidentale* (Doctoral dissertation, Dijon).

510 Carrasco, A., Sacristán, S., Benítez-López, G., Romero-Nieto, D., Fesharaki, O., & López
511 Martínez, N. (2008). Aplicaciones paleoclimáticas y paleoambientales de los estudios
512 mineralógicos al yacimiento de vertebrados miocenos de Somosaguas. *Publicaciones del*
513 *Seminario de Paleontología de Zaragoza*, 8, 135-149.

514 Chaline, J. (1977). Les rongeurs au pilori? Analyse critique des reconstitutions paléoécologiques
515 en microthériodontologie. *Bulletin de l'AFEQ*, 47, 75-81.

516 Chaline, J., & Brochet, G. (1989). Les Rongeurs: leurs significations paléoécologiques et
517 paléoclimatiques in La Baume de Gigny (Jura). *Supplément à Gallia Préhistoire*, 27, 97-109.

518 Chernick, M.R. (1999). *Bootstrap Methods: A Practitioner's Guide* - Wiley, 264p.

519 Clark, J., Beerbower, J.R., & Kietzke, K.K. (1967). *Oligocene sedimentation, stratigraphy,*
520 *paleoecology and paleoclimatology: in the Big Badlands of South Dakota* (Vol. 5). Field Museum
521 of Natural History.

522 Cuenca-Bescós, G., Straus, L.G., & Morales, M.R.G. (2008). Paleoclima y paisaje del final del
523 Cuaternario en Cantabria: los pequeños mamíferos de la Cueva del Mirón (Ramales de la victoria).
524 *Revista Española de Paleontología*, 23(1), 91-126.

525 Cuenca-Bescós, G., Straus, L.G., Morales, M.R.G., & Pimienta, J.C.G. (2009). The reconstruction
526 of past environments through small mammals: from the Mousterian to the Bronze Age in El Mirón
527 Cave (Cantabria, Spain). *Journal of Archaeological Science*, 36(4), 947-955.

528 Cuenca-Bescós, G., Melero-Rubio, M., Rofes, J., Martínez, I., Arsuaga, J.L., Blain, H.A.,... de
529 Castro, J.B. (2011). The Early–Middle Pleistocene environmental and climatic change and the
530 human expansion in Western Europe: a case study with small vertebrates (Gran Dolina, Atapuerca,
531 Spain). *Journal of Human Evolution*, 60(4), 481-491.

532 Daams, R., Van der Meulen, A.J., Alvarez Sierra, M.D.L.A., Peláez-Campomanes, P., Calvo, J.P.,
533 Alonso Zarza, M.A., & Krijgsman, W. (1999). Stratigraphy and sedimentology of the Aragonian
534 (Early to Middle Miocene) in its type area (North-Central Spain). *Newsletters on stratigraphy*,
535 37(3), 103-139.

536 Daams, R., & van der Meulen, A.J. (1984). Paleoenvironmental and paleoclimatic interpretation
537 of micromammal faunal successions in the Upper Oligocene and Miocene of North Central Spain.
538 *Paléobiologie Continentale*, 14, 241-257.

539 de Bonis, L., Bouvrain, G., Geraads, D., & Koufos, G. (1992). Multivariate study of late Cenozoic
540 mammalian faunal compositions and paleoecology. *Paleontologia i Evolució*, 24-25, 93-101.

541 Denys, C. (1985). Nouveaux critères de reconnaissance des concentrations de microvertébrés
542 d'après l'étude des pelotes de chouettes du Botswana (Afrique australe). *Bulletin du Muséum
543 national d'histoire naturelle. Section A, Zoologie, biologie et écologie animales*, 7 (4), 879-933.

544 Discamps, E., & Royer, A. (2017). Reconstructing palaeoenvironmental conditions faced by
545 Mousterian hunters during MIS 5 to 3 in southwestern France: A multi-scale approach using data
546 from large and small mammal communities. *Quaternary International*, 433, 64-87.

547 Domingo, L., Pérez-Dios, P., Hernández Fernández, M., Martín-Chivelet, J., Ortiz, J.E., & Torres,
548 T. (2015). Late Quaternary climatic and environmental conditions of northern Spain: An isotopic
549 approach based on the mammalian record from La Paloma cave. *Palaeogeography,
550 Palaeoclimatology, Palaeoecology*, 440, 417-430.

551 Efron, B. (1982). The Jackknife, the Bootstrap and Other Resampling Plans - Society for Industrial
552 and Applied Mathematics, 92p.

553 Escarguel, G., Legendre, S., & Sigé, B. (2008). Unearthing deep-time biodiversity changes: the
554 Palaeogene mammalian metacommunity of the Quercy and Limagne area (Massif Central,
555 France). *Comptes Rendus Geoscience*, 340(9-10), 602-614.

556 Fagoaga, A., Blain, H.A., Marquina-Blasco, R., Laplana, C., Sillero, N., Hernández, C.M., ...
557 Ruiz-Sánchez, F.J. (2019). Improving the accuracy of small vertebrate-based palaeoclimatic
558 reconstructions derived from the Mutual Ecogeographic Range. A case study using geographic

559 information systems and UDA-ODA discrimination methodology. *Quaternary Science Reviews*,
560 223, 105969.

561 FAUNMAP Working Group (1996). Spatial response of mammals to Late Quaternary
562 environmental fluctuations. *Science*, 272, 1601-1606.

563 Fernández-García, M., López-García, J. M., & Lorenzo, C. (2016). Palaeoecological implications
564 of rodents as proxies for the Late Pleistocene–Holocene environmental and climatic changes in
565 northeastern Iberia. *Comptes Rendus Palevol*, 15(6), 707-719

566 Fernández-García, M., López-García, J. M., Royer, A., Lécuyer, C., Allué, E., Burjachs, F., ...
567 Carbonell, E. (2020). Combined palaeoecological methods using small-mammal assemblages to
568 decipher environmental context of a long-term Neanderthal settlement in northeastern Iberia.
569 *Quaternary Science Reviews*, 228, 106072.

570 Fernández-Jalvo, Y., Scott, L., & Andrews, P. (2011). Taphonomy in palaeoecological
571 interpretations. *Quaternary Science Reviews*, 30(11-12), 1296-1302.

572 Fernández-López, S.R. (2000). *Temas de Tafonomía*. Departamento de Paleontología, Universidad
573 Complutense de Madrid, Madrid.

574 Fletcher, W.J., & Sánchez Goñi, M.F. (2008). Orbital-and sub-orbital-scale climate impacts on
575 vegetation of the western Mediterranean basin over the last 48,000 yr. *Quaternary Research*, 70(3),
576 451-464.

577 Frouin, M., Ploquin, F., Soressi, M., Rendu, W., Macchiarelli, R., El Albani, A., & Meunier, A.
578 (2013). Clay minerals of late Pleistocene sites (Jonzac and Les Cottés, SW France): Applications

579 of X-ray diffraction analyses to local paleoclimatic and paleoenvironmental reconstructions.
580 *Quaternary international*, 302, 184-198.

581 Furió, M., Casanovas-Vilar, I., & van den Hoek Ostende, L.W. (2011). Predictable structure of
582 Miocene insectivore (Lipotyphla) faunas in Western Europe along a latitudinal gradient.
583 *Palaeogeography, Palaeoclimatology, Palaeoecology*, 304(3-4), 219-229.

584 García-Alix, A., Minwer-Barakat, R., Martín Suárez, E., Freudenthal, M., & Martín, J.M. (2008).
585 Late Miocene–Early Pliocene climatic evolution of the Granada Basin (southern Spain) deduced
586 from the paleoecology of the micromammal associations. *Palaeogeography, Palaeoclimatology,*
587 *Palaeoecology*, 265, 214-225.

588 García Yelo, B.A., Gómez Cano, A.R., Cantalapiedra, J.L., Alcalde, G.M., Sanisidro, O., Oliver,
589 A., ... Hernández Fernández, M. (2014). Palaeoenvironmental analysis of the Aragonian (middle
590 Miocene) mammalian faunas from the Madrid Basin based on body-size structure. *Journal of*
591 *Iberian Geology*, 40, 129-140.

592 Genty, D., Blamart, D., Ghaleb, B., Plagnes, V., Causse, C., Bakalowicz, M., ... Bourges, F.
593 (2006). Timing and dynamics of the last deglaciation from European and North African $\delta^{13}\text{C}$
594 stalagmite profiles—comparison with Chinese and South Hemisphere stalagmites. *Quaternary*
595 *Science Reviews*, 25(17-18), 2118-2142.

596 Girard, V., Fauquette, S., Adroit, B., Suc, J.P., Leroy, S.A.G., Ahmed, A., ... Roiron, P. (2019).
597 Fossil mega and micro-flora from Bernasso (Early Pleistocene, southern France): A multimethod
598 comparative approach for paleoclimatic reconstruction. *Review of Palaeobotany and Palynology*,
599 267, 54-61.

600 Gómez Cano, A.R., García Yelo, B.A., & Hernández Fernández, M. (2006). Cenogramas, análisis
601 bioclimático y muestreo en faunas de mamíferos: implicaciones para la aplicación de métodos de
602 análisis paleoecológico. *Estudios Geológicos*, 62, 135-144.

603 Griggo, C. (1996). Etablissement de courbes climatiques quantifiées à partir des communautés
604 animales pléistocènes suivi d'une application aux gisements de l'abri Suard (Charente) et de la
605 grotte du Bois-Ragot (Vienne). *Paléo* 8, 81–97.

606 Heinz, C., Ruas, M.P., & Vaquer, J. (1992). La grotte de l'Abeurador (Félines-Minervois, Hérault):
607 paléoécologie d'après l'anthracologie et la carpologie. *Bulletin de la Société Botanique de France.*
608 *Actualités Botaniques*, 139(2-4), 465-482.

609 Héran, M.A. (2006). *Mammifères et climat : reconstitutions paléoclimatiques du Cénozoïque*
610 *d'Europe occidentale sur la base des faunes fossiles*. Doctoral dissertation, Lyon 1.

611 Hernández Fernández, M. (2001). Bioclimatic discriminant capacity of terrestrial mammal faunas.
612 *Global Ecology and Biogeography*, 10 (2), 189-204.

613 Hernández Fernández, M., Álvarez Sierra, M.Á., & Peláez-Campomanes, P. (2007). Bioclimatic
614 analysis of rodent palaeofaunas reveals severe climatic changes in Southwestern Europe during
615 the Plio-Pleistocene. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 251(3-4), 500-526.

616 Hernández Fernández, M., Cantalapiedra, J.L., & Gómez Cano, A.R. (2015). Plio-Pleistocene
617 climatic change had a major impact on the assembly and disassembly processes of Iberian rodent
618 communities. *Palaeobiodiversity and Palaeoenvironments*, 95, 387-404.

619 Hernández Fernández, M., & Peláez-Campomanes, P. (2003). The bioclimatic model: a method of
620 palaeoclimatic qualitative inference based on mammal associations. *Global Ecology and*
621 *Biogeography*, 12 (6), 507-517.

622 Hernández Fernández, M., & Peláez-Campomanes, P. (2005). Quantitative palaeoclimatic
623 inference based on terrestrial mammal faunas. *Global Ecology and Biogeography*, 14(1), 39-56.

624 Hernández Fernández, M., & Vrba, E.S. (2006). Plio-Pleistocene climatic change in the Turkana
625 Basin (East Africa): evidence from large mammal faunas. *Journal of Human Evolution*, 50, 595-
626 626.

627 Hinton, M.A. (1926). *Monograph of the voles and lemmings*. British Museum (Natural History),
628 London.

629 Holdridge, L. R. 1967. «Life Zone Ecology». Tropical Science Center. San José, Costa Rica.
630

631 Hokr, Z. (1951). A method of the quantitative determination of the climate in the Quaternary period
632 by means of mammal associations. *Sbornik of the geological Survey of Czechslovakia*, 18, 209-
633 219.

634 IUCN (2019). *The IUCN Red List of Threatened Species. Version 2019-2*.
635 <http://www.iucnredlist.org>. Downloaded on june 2019.

636 Jalut, G., & Turu, V. (2009). La végétation des Pyrénées françaises lors du dernier épisode
637 glaciaire et durant la transition Glaciaire-Interglaciaire (Last Termination). *Els Pirineus i les àrees*
638 *circumdants durant el Tardiglaciàr. Mutacions i filiacions tecnoculturals, evolució*

- 639 *paleoambiental (16 000–10 000 BP)*, XIV Col· loqui internacional d'Arqueologia de Puigcerdà.
640 *Institut d'Estudis Ceretans, Puigcerdà*, 129-150.
- 641 Jeannet, M. (2010). L'écologie quantifiée. Essai de description de l'environnement continental à
642 l'aide des microvertébrés. *Préhistoires méditerranéennes*, (1).
- 643 Kay, R.F., Madden, & R.H. (1997). Mammals and rainfall: paleoecology of the middle Miocene
644 at La Venta (Colombia, South America). *Journal of Human Evolution*, 32(2-3), 161-199.
- 645 Kolbek, J., Srutek, M., & Box, E.E. (2013). *Forest Vegetation of Northeast Asia* (Vol. 28).
646 Springer Science & Business Media.
- 647 Köppen, W., 1918: Klassifikation der Klimate nach Temperatur, Niederschlag und Jahresablauf.
648 Petermanns Geogr. Mitt., 64, 193-203, 243-248.
- 649
- 650 Kowalski, K. (1990). Some problems of the taphonomy of small mammals. In: *International*
651 *Symposium Evolution, Phylogeny and Biostratigraphy of Arvicolids Rohanov* (Eds. Fejfar, O.,
652 Heinrich, W.-D.), May 1987, pp. 285-296.
- 653 Laplana, C., Muñoz Jiménez, A., Pueyo Morer, E.L., & Sevilla, P. (2016). Los micromamíferos y
654 la interpretación ambiental de los yacimientos de la Cuenca de Villarroya. In: *Villarroya:*
655 *yacimiento clave de la paleontología riojana* (Coord. M.T. Alberdi, B. Azanza & E. Cervantes),
656 Instituto de Estudios Riojanos, Logroño, 281-296.
- 657 Legendre, P. & Legendre, L. (2012). *Numerical Ecology* - 3rd edition, Elsevier, 990p.

658 Legendre, S. (1986). Analysis of mammalian communities from the late Eocene and Oligocene of
659 southern France. *Palaeovertebrata*, 16(4), 191-212.

660 Legendre, S. (1989). *Les communautés de mammifères du Paléogène (Eocène supérieur et*
661 *Oligocène) d'Europe occidentale: structures, milieux et évolution*. F. Pfeil, München, Allemagne.

662 Legendre, S., Montuire, S., Maridet, O., & Escarguel, G. (2005). Rodents and climate: a new model
663 for estimating past temperatures. *Earth and Planetary Science Letters*, 235(1-2), 408-420.

664 López-García, J.M., Blain, H.A., Cuenca-Bescós, G., Ruiz-Zapata, M.B., Dorado-Valiño, M., Gil-
665 García, M.J., ... Carbonell, E. (2010). Palaeoenvironmental and palaeoclimatic reconstruction of
666 the Latest Pleistocene of El Portalón Site, Sierra de Atapuerca, northwestern Spain.
667 *Palaeogeography, Palaeoclimatology, Palaeoecology*, 292, 453-464.

668 López-García, J. M., Luzi, E., & Peresani, M. (2017). Middle to Late Pleistocene environmental
669 and climatic reconstruction of the human occurrence at Grotta Maggiore di San Bernardino
670 (Vicenza, Italy) through the small-mammal assemblage. *Quaternary Science Reviews*, 168, 42-54.

671 López García, J.M. (2008). *Evolución de la diversidad taxonómica de los micromamíferos en la*
672 *península ibérica y cambios paleoambientales durante el Pleistoceno Superior*. Doctoral
673 dissertation, Universitat Rovira i Virgili.

674 Lyons, S.K. (2003). A Quantitative Assessment of the Range Shifts of Pleistocene Mammals.
675 *Journal of Mammalogy*, 84, 385-402.

676 Lyman, R.L. (1994). *Vertebrate taphonomy*. Cambridge University Press.

677 Lyman, R.L. (2017). Paleoenvironmental reconstruction from faunal remains: ecological basics
678 and analytical assumptions. *Journal of Archaeological Research*, 25(4), 315-371.

679 Marquet, J.C. (1987). Les modifications de l'environnement Postglaciaire en France
680 méditerranéenne d'après les rongeurs de l'Abeurador et de Font-Juvenal. *Premières communautés*
681 *paysannes en méditerranée occidentale*. Paris: Comité National de la Recherche Scientifique, 155-
682 163.

683 Martínez Pillado, V., Aramburu Artano, A., Arsuaga, J.L., Ruiz-Zapata, B., Gil García, M.J., Stoll,
684 H., ... Cheng, H. (2014). Upper Pleistocene and Holocene palaeoenvironmental records in Cueva
685 Mayor karst (Atapuerca, Spain) from different proxies: speleothem crystal fabrics, palynology,
686 and archaeology. *International Journal of Speleology*, 43(1), 1-14.

687 Menéndez, I., Gómez Cano, A.R., García Yelo, B.A., Domingo, L., Domingo, M.S.,
688 Cantalapiedra, J.L., ... Hernández Fernández, M. (2017). Body-size structure of Central Iberian
689 mammal fauna reveals semidesertic conditions during the middle Miocene Global Cooling Event.
690 *PLoS ONE*, 12(10), e0186762.

691 Mistrot V. (2001). *Contribution des micromammifères de la Balma de l'Abeurador à la*
692 *connaissance de l'évolution des paysages tardiglaciaires et holocènes en Languedoc-Roussillon*.
693 Doctoral dissertation, Université Paris 1 Panthéon-Sorbonne.

694 Montuire, S., & Desclaux, E. (1997). Palaeoecological analysis of mammalian faunas and
695 environmental evolution in the South of France during the Pleistocene. *Boreas*, 26(4), 355-365.

696 Montuire, S., Michaux, J., Legendre, S., & Aguilar, J.P. (1997). Rodents and climate. 1. A model
697 for estimating past temperatures using arvicolidids (Mammalia: Rodentia). *Palaeogeography,*
698 *Palaeoclimatology, Palaeoecology, 128*(1-4), 187-206.

699 Morellón, M., Aranbarri, J., Moreno, A., González-Sampériz, P., & Valero-Garcés, B.L. (2018).
700 Early Holocene humidity patterns in the Iberian Peninsula reconstructed from lake, pollen and
701 speleothem records. *Quaternary Science Reviews, 181*, 1-18.

702 Moreno, A., Stoll, H., Jiménez-Sánchez, M., Cacho, I., Valero-Garcés, B., Ito, E., & Edwards, R.
703 L. (2010). A speleothem record of glacial (25-11.6 kyr BP) rapid climatic changes from northern
704 Iberian Peninsula. *Global and Planetary Change, 71*(3-4), 218-231.

705 Moreno, A., González-Sampériz, P., Morellón, M., Valero-Garcés, B.L., & Fletcher, W.J. (2012).
706 Northern Iberian abrupt climate change dynamics during the last glacial cycle: a view from
707 lacustrine sediments. *Quaternary Science Reviews, 36*, 139-153.

708 Moritz, C., Patton, J.L., Conroy, C.J., Parra, J.L., White, G.C., & Beissinger, S.R. (2008). Impact
709 of a century of climate change on small-mammal communities in Yosemite National Park, USA.
710 *Science, 322*, 261-264.

711 Muñoz-Sobrino, C. M., Heiri, O., Hazekamp, M., Van der Velden, D., Kirilova, E.P., García-
712 Moreiras, I., & Lotter, A. F. (2013). New data on the Lateglacial period of SW Europe: a high
713 resolution multiproxy record from Laguna de la Roya (NW Iberia). *Quaternary Science Reviews,*
714 *80*, 58-77.

715 Nieto, M., & Rodríguez, J. (2003). Inferencia paleoecológica en mamíferos cenozoicos:
716 limitaciones metodológicas. *Coloquios de Paleontología Vol. Extra. 1*, 459-474.

717 Piñero, P., Agustí, J., Blain, H.-A., & Laplana, C. (2016). Paleoenvironmental reconstruction of
718 the Early Pleistocene site of Quibas (SE Spain) using a rodent assemblage reconstruction. *Comptes*
719 *Rendus Palevol*, 15, 659-668.

720 Puzachenko, A.Y., & Markova, A.K. (2019). Evolution of mammal species composition and
721 species richness during the Late Pleistocene-Holocene transition in Europe: A general view at the
722 regional scale. *Quaternary International*, 530-531, 88-106.

723 Quéré, J.P., & Le Louarn, H. (2011). *Les rongeurs de France: Faunistique et biologie*. 3e édition
724 revue et augmentée. Editions Quae.

725 R Core Team (2019). R: A Language and Environment for Statistical Computing. R Foundation
726 for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.

727 Reed, D.N. (2007). Serengeti micromammals and their implications for Olduvai
728 paleoenvironments. In: *Hominin environments in the East African Pliocene: An assessment of the*
729 *faunal evidence* (pp. 217-255). Springer, Dordrecht.

730 Reimer, P.J., Bard, E., Bayliss, A., Beck, J.W., Blackwell, P.G., Bronk Ramsey, C., ... van der
731 Plicht, J. (2013). IntCal13 and Marine13 radiocarbon age calibration curves 0-50,000 Years cal
732 BP. *Radiocarbon*, 55, 1869-1887.

733 Rencher, A.C. (2002). *Methods of Multivariate Analysis* - 2nd edition, Wiley, 708p.

734 Reumer, J.W. (1995). The evolution of shrews (Mammalia, Soricidae): a key role for humidity.
735 *Geobios*, 28, 367-372.

736 Řičánková, V.P., Robovský, J. Riegert, J., & Zrzavý, J. (2015). Regional patterns of postglacial
737 changes in the Palearctic mammalian diversity indicate retreat to Siberian steppes rather than
738 extinction. *Scientific Reports*, 5, 12682.

739 Rivas-Martínez, S. (1994). Clasificación bioclimática de la Tierra. *Folia Botanica Matritensis* 13,
740 1-27.

741 Rivas-Martínez, S. (2008). Global bioclimatics. *Internet: [http://www. globalbioclimatics. org](http://www.globalbioclimatics.org)*, 2008.

742 Rofes, J., García-Ibaibarriaga, N., Aguirre, M., Martínez-García, B., Ortega, L., Zuluaga, M.C.,
743 ...Murelaga, X. (2015). Combining small-vertebrate, marine and stable-isotope data to reconstruct
744 past environments. *Scientific Reports*, 5, 14219.

745 Royer, A., Lécuyer, C., Montuire, S., Escarguel, G., Fourel, F., Mann, A., & Maureille, B. (2013).
746 Late Pleistocene (MIS 3–4) climate inferred from micromammal communities and $\delta^{18}\text{O}$ of rodents
747 from Les Pradelles, France. *Quaternary research*, 80(1), 113-124.

748 Royer, A., Lécuyer, C., Montuire, S., Primault, J., Fourel, F., & Jeannet, M. (2014). Summer air
749 temperature, reconstructions from the last glacial stage based on rodents from the site Taillis-des-
750 Coteaux (Vienne), Western France. *Quaternary research*, 82(2), 420-429.

751 Royer, A., Montuire, S., Legendre, S., Discamps, E., Jeannet, M., & Lécuyer, C. (2016).
752 Investigating the influence of climate changes on rodent communities at a regional-scale (MIS 1-
753 3, Southwestern France). *PloS one*, 11(1), e0145600.

754 Rutilevskiy, G. L. (1979). The zoogeography of the Yamal-Gydan area, Western Siberia. *Polar*
755 *Geography*, 3(2), 88-117.

756 Sesé, C. (1991). Interpretación paleoclimática de las faunas de micromamíferos del Mioceno,
757 Plioceno y Pleistoceno de la Cuenca de Guadix-Baza (Granada, España). *Estudios Geológicos*,
758 47, 73 – 83.

759 Sneath, P.H.A. & Sokal, R.R. (1973). *Numerical Taxonomy* - Freeman and Company, 573p.

760 Sokal, R.R. & Rohlf, F.J. (1995). *Biometry* - 3rd edition, Freeman and Company, 887p.

761 Stahl, P.W. (1996). The recovery and interpretation of microvertebrate bone assemblages from
762 archaeological contexts. *Journal of archaeological method and theory*, 3(1), 31-75.

763 Stoetzel, E., Lalis, A., Nicolas, V., Aulagnier, S., Benazzou, T., Dauphin, Y., ... Denys C. (2019).
764 Quaternary terrestrial microvertebrates from mediterranean northwestern Africa: State-of-the-art
765 focused on recent multidisciplinary studies. *Quaternary Science Reviews*, 224, 105966.

766 Straus, L.G., & Morales, M.R.G. (2003). El Mirón Cave and the C¹⁴ chronology of Cantabrian
767 Spain. *Radiocarbon*, 45, 41-58.

768 Straus, L.G., & Morales, M.R.G. (2007). Further radiocarbon dates for the Upper Paleolithic of El
769 Mirón Cave (Ramales de la Victoria, Cantabria, Spain). *Radiocarbon*, 49, 1205-1214.

770 Straus, L.G., & Morales, M.R.G. (2012). The Magdalenian settlement of the Cantabrian region
771 (northern Spain): the view from El Mirón Cave. *Quaternary International*, 272, 111-124.

772 Straus, L. G., & Morales, M. R. G. (2019). The Upper Paleolithic sequence in el Miron Cave
773 (Ramales de la Victoria, Cantabria, Spain): An overview. *Journal of Archaeological Science:*
774 *Reports*, 27, 101998.

775 Tchernov, E. (1975). Rodent faunas and environmental changes in the Pleistocene of Israel. In:
776 *Rodents in desert environments* (eds: I. Prakash et al.). Springer, Dordrecht, pp. 331-362.

777 Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., ...
778 Hughes, L., (2004). Extinction risk from climate change. *Nature*, 427, 145-148.
779 <https://doi.org/10.1038/nature02121>.

780 Turvey, S.T., & Cooper, J.H. (2009). The past is another country: is evidence for prehistoric,
781 historical and present-day extinction really comparable. *Holocene extinctions*, 193-212.

782 van Dam, J.A. (2006). Geographic and temporal patterns in the late Neogene (12–3 Ma)
783 aridification of Europe: the use of small mammals as paleoprecipitation proxies. *Palaeogeography,*
784 *Palaeoclimatology, Palaeoecology*, 238(1-4), 190-218.

785 van de Weerd, A., & Daams, R. (1978). Quantitative composition of rodent faunas in the Spanish
786 Neogene and paleoecological implications (I and II). *Proceedings of the Koninklijke Nederlandse*
787 *Akademie Van Wetenschappen Series B*, 81, 448-473.

788 van der Meulen, A. J., & Daams, R. (1992). Evolution of Early-Middle Miocene rodent faunas in
789 relation to long-term palaeoenvironmental changes. *Palaeogeography, Palaeoclimatology,*
790 *Palaeoecology*, 93 (3-4), 227-253.

791 Valverde, J.-A. (1964). Remarques sur la structure et l'évolution des communautés de Vertébrés
792 terrestres I. structure d'une communauté II. Rapports entre prédateurs et proies. *La Terre et la Vie,*
793 121-154.

794 Vaquer, J., Geddes, D., Barbaza, M., & Erroux, J. (1986). Mesolithic plant exploitation at the
795 Balma Abeurador (France). *Oxford Journal of Archaeology*, 5(1), 1-18.

796 Vaquer, J., & Ruas, M.P. (2009). La grotte de l'Abeurador Félines-Minervois (Hérault) :
797 occupations humaines et environnement du Tardiglaciaire à l'Holocène. *De Méditerranée et*
798 *d'ailleurs...*, *Mélanges offerts à Jean Guilaine. Archives d'Ecologie Préhistorique, Toulouse*, 761-
799 792.

800 Venables, W.N., & Ripley, B.D. (2002). *Modern Applied Statistics with S-PLUS*. Fourth Edition.
801 Springer, New York.

802 Villa, A., Blain, H. A., & Delfino, M. (2018). The Early Pleistocene herpetofauna of Rivoli
803 Veronese (Northern Italy) as evidence for humid and forested glacial phases in the Gelasian of
804 Southern Alps. *Palaeogeography, palaeoclimatology, palaeoecology*, 490, 393-403.

805 Walter, H. (1970) *Vegetationszonen und Klima*. Eugen Ulmer, Stuttgart.

806 Wilson, D.E., Lacher, T.E., & Jr. Mittermeier, R.A. (eds.) 2017: *The Mammals of the World-Vol.*
807 *7, Rodents II*. Lynx Edicions, Barcelona, 1008 pp.

808 Wilson, D.E., & Jr. Mittermeier, R.A. (eds.) 2018: *The Mammals of the World-Vol. 8, Insectivores,*
809 *Sloths and Colugos*. Lynx Edicions, Barcelona, 709 pp.

810 Zar, J.H. (1999). *Biostatistical Analysis* - 4th edition, Prentice Hall, 929p.

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