



HAL
open science

Temperature and precipitation regime in LGM human refugia of southwestern Europe inferred from $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ of large mammal remains

Christophe Lécuyer, Claude Hillaire-Marcel, Ariane Burke, Marie-Anne Julien, Jean-François Hélié

► To cite this version:

Christophe Lécuyer, Claude Hillaire-Marcel, Ariane Burke, Marie-Anne Julien, Jean-François Hélié. Temperature and precipitation regime in LGM human refugia of southwestern Europe inferred from $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ of large mammal remains. *Quaternary Science Reviews*, 2021, 255, 10.1016/j.quascirev.2021.106796 . insu-03710147

HAL Id: insu-03710147

<https://insu.hal.science/insu-03710147v1>

Submitted on 22 Mar 2023

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.



Distributed under a Creative Commons Attribution - NonCommercial 4.0 International License

1 Temperature and precipitation regime in LGM human refugia of southwestern
2 Europe inferred from $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ of large mammal remains

3

4

5

6 Christophe Lécuyer^{1,*}, Claude Hillaire-Marcel², Ariane Burke³, Marie-Anne Julien⁴, Jean-
7 François Hélie²

8

9

10 ¹Univ Lyon, Univ Lyon 1, ENSL, CNRS, LGL-TPE, 69622 Villeurbanne, France

11 ²Geotop-UQAM, CP 8888, Montréal, QC, H3C 3P8, Canada

12 ³Université de Montréal, Département d'Anthropologie, C.P. 6128, Centre-Ville, Montréal,
13 QC, H3C 3J7, Canada

14 ⁴ Independent researcher.

15 *corresponding author: Christophe.lecuyer@univ-lyon1.fr

16

17

18 Abstract – The climate shift of the Last Glacial Maximum (LGM) strongly impacted the
19 vegetation cover and related trophic chains of western Europe. Harsh, cold and dry conditions
20 then prevailed in most regions, strongly impacting migrations and survival of human beings.
21 Nonetheless, environments suitable for mammalian fauna to survive persisted in SW Europe
22 thus providing refugia for hunters. Tooth enamel from large herbivorous mammal remains
23 from archeological sites located in southwest France and Spain were analyzed for their stable
24 carbon and oxygen isotope compositions for documenting paleotemperatures and
25 paleoprecipitations. These sites were occupied by humans between 25 ky and 16 ky. Skeletal
26 remains of Cervidae, Equidae and Caprinae suggest colder and drier conditions relative to
27 present-day. Paleoprecipitations were reconstructed from a modern-based transfer function
28 using $\delta^{13}\text{C}$ -values of apatite carbonate, then corrected for the low atmospheric pCO_2 value of
29 the LGM. They ranged from $\approx 250 \text{ mm yr}^{-1}$ on the Mediterranean façade, to $\approx 550 \text{ mm yr}^{-1}$ on
30 the Atlantic side. Setting the $\delta^{18}\text{O}$ -value of the northeastern North Atlantic LGM-surface
31 water to $+0.8\text{‰}$, based on Biscay Golf marine core studies, mean air temperatures inferred
32 from ^{18}O -data in apatite calcite were close to $14\text{--}15^\circ\text{C}$ (Mediterranean) and 6°C to 10°C
33 (Atlantic), i.e., about $4\text{--}5^\circ\text{C}$ and $5\text{--}8^\circ\text{C}$ higher than pre-industrial temperatures, respectively.
34 The two areas thus define distinct clusters of air temperatures and precipitation regimes with
35 strong negative offsets vs the Present. These isotopically-reconstructed climate conditions
36 indicate a strong control from proximal surface ocean/marine waters, in particular of mean
37 annual air temperatures.

38

39

40

41 Keywords: Last Glacial; temperature; precipitation; stable isotopes; apatite; mammals;

42 Western Europe

43

44

45 1. Introduction

46 The Last Glacial, also named Weichselian in Northwest Europe, covers a time period
47 from 115 ka to 11.7 ka. It was characterized by rapid, large amplitude climatic fluctuations
48 recorded in the Greenland ice cores (Dansgaard et al., 1993; Grootes et al., 1993; NGRIP
49 members, 2004; Rasmussen et al., 2014) and North Atlantic marine sediments (Heinrich,
50 1988; Bond et al., 1992; Sanchez Goñi et al., 2008). During this period, global climate
51 conditions oscillated between stadial and interstadial conditions, sometimes punctuated by
52 abrupt climate events known as Heinrich events. These highly contrasted climate regimes
53 influenced faunal communities, including humans, through the development of new migration
54 pathways, allopatric speciation in refugia, and enhanced rates of extinction during the coldest
55 and driest stages of the Last Glacial.

56 The Last Glacial Maximum (LGM), conventionally dated between 23 and 19 ka ago
57 (MARGO, 2009; Mix et al., 2001), is defined as the most recent period of maximum global
58 ice volume (Mix et al., 2001). It featured lowered greenhouse gas (CH₄, CO₂) concentrations,
59 a mean sea level ~120 m lower than today and generally cold and dry climatic conditions
60 resulting in significant modifications of both floral and faunal assemblages (Lister, 2004;
61 Sommer and Nadachowski, 2006; Clark et al., 2009; Binney et al., 2017; Cao et al., 2019).
62 During this interval, and in response to global tropospheric cooling, the Northern Hemisphere
63 experienced a southward expansion of continental ice sheets, which reached as far as 52°N in
64 western Europe. Various models suggest a decrease in global mean surface air temperatures
65 during the LGM ranging from 4°C to 10°C vs pre-industrial (PI) climatic conditions (Masson-
66 Delmotte et al., 2006; Schneider von Deimling et al., 2006; Annan and Hargreaves, 2013).
67 The main causes of this decrease are thought to be the combined effect of lower atmospheric

68 CO₂ values (with a partial pressure as low as 190 ppm; Bouttes et al., 2011) and ice-sheet
69 forcing, which would jointly account for about 75% of the total LGM cooling (Schneider von
70 Deimling et al., 2006). Additional cooling effects are related to changes in atmospheric dust
71 content and vegetation cover. In response to this maximal extent of continental ice (glaciers
72 and ice caps), mean global sea level dropped by 120±10 m (Lambeck et al., 2014).

73 Faunal associations described in the archaeological sites of southwestern Europe are
74 generally compatible with cold and dry, open environments, such as tundra and dry steppe,
75 but there are important regional differences as suggested by Yravedra and Brugal (2005) who
76 defined several biogeographic zones in southwest Europe. During the LGM, the vegetation in
77 Europe was characterized by an expansion of tundra and steppe. In Southwestern France and
78 in the northern part of the Iberian Peninsula, cold temperate fauna (horse, reindeer, ibex)
79 dominated vertebrate assemblages during the LGM, but co-existed with cold-adapted fauna
80 such as mammoth, woolly rhinoceros and reindeer (Yravedra and Brugal, 2005; Sommer and
81 Nadachowski, 2006; Álvarez-Lao and García, 2011; Álvarez-Lao and García, 2011). Recent
82 models suggest that the most suitable habitats for humans during the LGM were concentrated
83 in southwest France and the Iberian Peninsula, excluding the interiors, as also demonstrated
84 by the distribution of archaeological sites (e.g., Ludwig et al., 2018; Burke et al., 2017; Wren
85 and Burke, 2019). Modern humans who had arrived in Europe ≈ 45,000 years ago survived
86 the LGM in the SW Europe refugia (Fu et al., 2016). A post-ice age expansion followed, with
87 their descendants spreading out in Iberia, after ≈ 19,000 years ago, then defining the
88 Magdalenian culture (Fu et al., 2016).

89 The LGM in Southwest Europe illustrates a major faunal and vegetation partitioning in
90 biogeographic provinces, which constrained the human strategy of land occupation. Whether
91 Mean Annual Precipitation (MAP) or Mean Annual Air Temperature (MAAT) were limiting
92 factors in this strategy remains to be fully elucidated. In this study, special attention is paid to

93 sites from coastal areas under the influence of the Atlantic Ocean or the Mediterranean Sea.
94 They represent three distinct biogeographic zones, following the classification of Yravedra
95 and Brugal (2005) for southwestern Europe: southwest France (zone VI), Cantabria/Asturias
96 (zone IV) and the Mediterranean coast (zone IIIa).

97 MAAT and MAP may be reconstructed using oxygen and carbon isotope compositions of
98 the apatite carbonate from vertebrate skeletons. As highlighted by Pederzani and Britton
99 (2019), in particular the oxygen isotope analyses of skeletal remains ($\delta^{18}\text{O}$) are a powerful
100 tool for exploring past human-environment interactions as well as to reconstruct paleoclimatic
101 parameters. An approach not yet used for documenting the LGM refugia of SW Europe will
102 fill this gap using large mammal remains (teeth) from the above defined human occupation
103 areas. We also intend to demonstrate that carbon isotope ($\delta^{13}\text{C}$) from such remains may
104 inform specifically on paleoprecipitation.

105 The basic principles to interpret $\delta^{13}\text{C}$ as MAP and $\delta^{18}\text{O}$ as MAAT are summarized as
106 follows:

107 The most common strategy consists in estimating air temperature from the oxygen isotope
108 composition of the carbonate or the phosphate groups of the tooth enamel of the vertebrate
109 apatite. During tooth growth, the oxygen isotope composition of apatite carbonate ($\delta^{18}\text{O}_c$)
110 records body temperature (a near constant close to 37°C) and body water composition
111 ($\delta^{18}\text{O}_{\text{bw}}$) (Koch et al., 1989; Bryant et al., 1996; Chenery et al., 2012). The oxygen isotope
112 composition of body water reflects that of meteoric water (Bryant and Froelich, 1995; Kohn,
113 1996; Langlois et al., 2003) and depends principally on the composition of oceanic moisture
114 source(s), the length and precipitation history of humid air mass trajectories,
115 evapotranspirative processes along these trajectories, air temperature (MAAT) during
116 precipitation, the relative amount of precipitation and altitude relative to sea level (Dansgaard,
117 1964; Rozanski et al., 1992; Fricke and O'Neil, 1999). At mid- and high-latitudes (tropical

118 bands excluded), MAAT of areas close to oceanic moisture sources are linearly related to the
119 weighted mean annual $\delta^{18}\text{O}_{\text{mw}}$ (Dansgaard, 1964; Yurtsever, 1975; von Grafenstein et al.,
120 1996; Fricke and O'Neil, 1999; Skrzypek et al., 2011; Lécuyer, 2013). This property of the
121 water cycle has already been used for the reconstruction of past air temperatures from the
122 oxygen isotope composition of vertebrate tooth enamel from large mammals (e.g., Ayliffe et
123 al., 1992; Bryant et al., 1994; Tütken et al., 2007; Bernard et al., 2009; Fabre et al., 2011).

124 The reconstruction of MAP from the carbon isotope composition of apatite carbonate was
125 made in several steps. In the first step, the $\delta^{13}\text{C}$ values of plants ($\delta^{13}\text{C}_{\text{pl}}$) can be estimated from
126 tooth enamel carbonate ($\delta^{13}\text{C}_{\text{carb}}$) taking into account the isotopic fractionation that takes
127 place between diet-derived carbon ingested by the herbivores and the carbon mineralized as
128 carbonate present in the apatite crystal lattice of their teeth (Tejada-Lara et al., 2018). In a
129 second step, MAP values are calculated using $\delta^{13}\text{C}_{\text{pl}}$ and a transfer function based on plant
130 leaf discrimination factors (Kohn, 2010) that may be estimated in the case of animal diets
131 strictly based on Calvin Cycle (C3) plants. Atmospheric pCO_2 -changes and reduced biomass
132 production by plants during glacials (Gerhart and Ward, 2010) may have led to some global
133 relative increase in the abundance of C4 plants, thus to some possible dietary changes, but
134 C3/C4 plant ratios within given biomes remained broadly stable if biome distributions
135 differed (Ehleringer, 2005). Moreover, C4 plants amount to only about 1% in the European
136 vegetation (Collins and Jones 1985). They are slightly more abundant in herb-dominated
137 biomes (see their taxonomic distribution in Pyankov et al. (2010). Now, if such biomes
138 experienced a ~ 10% relative increase over other biomes during the LGM (Binney et al.,
139 2017), their content in C4 plants is unlikely to have increased as these plants are strongly
140 sensitive to temperatures (Pyankov et al., 2010), adding to the equivocal response of the
141 C4/C3 plant ratio of Poaceae, one of their major components, to pCO_2 changes (Wand et al.,

142 1999). One may thus assume a nearly exclusive C3-plant vegetation during the LGM interval
143 whatever the changes in biome distribution.

144 The goal of the present study is thus to build paleoclimate reconstructions for several
145 archaeological sites of the LGM (Figure 1) using the above isotopic approaches. The specific
146 sampled sites are Laugerie-Haute (Dordogne, France), El Cierro (Asturias Province), Hornos
147 de la Peña, El Pendo and El Ruso (Cantabria Province), Nerja (Málaga Province) and
148 Malladetes (Valencia Province). The present study provides the first quantitative information
149 about LGM-MAAT and -MAP ranges of these sites. They will be discussed in the light of
150 proxies based on pollen assemblages (continental climate) and foraminiferal- $\delta^{18}\text{O}$ data
151 (marine moisture sources), climatic model outputs, past topography, as well as in that of
152 reconstructed vegetation cover and faunal communities.

153

154 2. Archaeological sites and sample collection

155 2.1. Description of the sampled archaeological sites

156 *Laugerie Haute Est* (LHE) forms part of a much larger rock-shelter on the right bank of
157 the Vézère river in the Dordogne region of France (Fig. 1). The shelter, which is about 30 m
158 deep and 180 m long, is separated into two excavated sections (East and West) due to the
159 presence of a house occupying the centre of the shelter. First discovered at the end of the 19th
160 Century the site's stratigraphic integrity has come under close scrutiny (Texier, 2009;
161 Delpech, 2012; Verpoorte et al., 2019). The occupation sequence of the site spans the
162 Aurignacian and the Solutrean. For this study, level 4-8, attributed to Magdalenian II, level
163 10-16 (F. Bordes collection) attributed to Magdalenian I and level 18-20, attributed to
164 Magdalenian 0, were sampled. Biostratigraphically, levels attributed to Magdalenian I-III
165 form a unit, with faunal assemblages dominated by reindeer, while the Magdalenian 0 level,
166 which is dominated by horse, is distinct (Delpech, 2012). The Magdalenian levels are

167 bracketed by ages of ~ 23 and ~21 ¹⁴C cal. kyr (Delpech, 2012) and can thus be assigned to
168 the LGM. Four sites were sampled in northern Spain, including: El Ruso, Hornos de la Peña
169 and El Pendo in Cantabria, and El Cierro in Asturias (Fig. 1). El Ruso is a small cave located
170 about 6 km from the modern coastline, near El Pendo and El Juyo (unsampled). The cave
171 contains a sequence of occupation that spans from the Mousterian to the Solutrean Level 3,
172 the Upper Solutrean level sampled here overlies a Solutrean level (IV) dated 20–19 ¹⁴C cal.
173 kyr (Yravedra, 2010a).

174 At El Pendo level 4, the samples are labelled “level 4” and attributed to the Upper
175 Solutrean. If this corresponds to level IV (Eschegaray excavations) this level is attributed to
176 the Late Aurignacian, although it is intercalated between Gravettian and Magdalenian levels
177 (Hoyos Gómez and Laville, 1982). Unfortunately, the stratigraphic integrity of this site is in
178 some doubt (de los Terreros and Castanedo, 2010; Barquin, 2014). Consequently, results from
179 this site must be interpreted with caution.

180 At Hornos de la Peña, we sampled level B. This level is dated 23–21 ¹⁴C cal. kyr and is
181 attributed to the Aurignacian in its lower part, and the Solutrean in its upper part (Breuil and
182 Obermeier, 1912 cited in Tejero et al., 2008; Yravedra, 2010b). The faunal assemblage at
183 Hornos de la Peña is dominated by horse (Tejero et al., 2008). At El Cierro (Asturias),
184 another deeply stratified cave site excavated by several different teams over the years, a
185 revised chronostratigraphy and several AMS dates are available (Alvarez-Fernandez et al.,
186 2016). We sampled levels G (Magdalenian), G1 and H (Solutrean) which form part of the
187 earliest occupation sequence of the cave. AMS dates obtained for these levels indicate that the
188 site was occupied during the LGM (¹⁴C cal. ages of 20–19 kyr) (Alvarez-Fernandez et al.,
189 2016).

190 Two sites on the Mediterranean seaboard of Spain were sampled: Nerja and
191 Malladetes (aka Mallaetes) (Fig. 1). Nerja, the southernmost sample site, is a deeply stratified

192 cave located on the coastal plain of eastern Andalusia. The site contains one of the longest
193 occupation sequences in Mediterranean Spain, spanning the Gravettian to the Copper Age
194 (Aura Tortosa et al., 2006; Jordá Pardo and Aura Tortosa, 2008). Paleoclimate proxies and a
195 large number of recently reviewed radiocarbon dates provide a robust chronostratigraphic
196 frame for the sequence (Jordá Pardo and Aura Tortosa, 2008). Unit 8 (vestibule) was sampled
197 for this study. This unit contains Solutrean material and is generally considered to date to the
198 LGM, based on paleoclimate proxies and conventional and AMS radiocarbon dates yielding
199 ^{14}C cal. ages comprised between 23 and 21 kyr (Vallejo et al., 2005; Aura Tortosa et al.,
200 2006), although a much younger and possibly unrepresentative AMS date (≈ 14.4 ^{14}C cal.
201 kyr) has also been reported (Jordá Pardo and Aura Tortosa, 2008).

202 Malladetes (or Mallaetes) is located in the central Mediterranean region of Spain, in
203 Valencia. The levels sampled for this study include levels 7 (entrada D), 8 and 9 (entrada D)
204 which should be associated with the Gravettian (de la Peña Alonso, 2013). An AMS ^{14}C cal.
205 age of 30–26 kyr was obtained from modern human remains associated with unspecified
206 Gravettian levels in sector E, likely corresponding to levels VII to XI (Forteza Perez and Jorda
207 Cerda, 1976; Arsuaga et al., 2002), indicate that our samples probably predate the LGM and
208 level 8 at Nerja (Fumanal and Dupré, 1983; Aura Tortosa et al., 2006).

209

210 2.2. Sample collection

211 The samples recovered from the seven archaeological sites described above (Table 1)
212 include mammal remains assigned to Cervidae (*Cervus elaphus*, *Rangifer tarandus*), Equidae
213 (*Equus* sp.) and Caprinae (*Capra pyreneica*, *Rupicapra rupicapra*, *Saiga tatarica*). The
214 cervids (*Cervus elaphus*) and caprids (*Capra pyreneica*) were sampled as a priority, but
215 wherever these taxa were poorly represented, we sampled alternate species including smaller

216 cervids and small bovids. At Laugerie Haute Est and Hornos de la Peña we sampled horse
217 remains because of their abundance at both sites.

218

219 2.3. Habitat and diet of Cervidae, Equidae and Caprinae

220 *Cervus elaphus* (red deer) is a large mammal observed in semi-open habitats, often
221 found in forest margins and clearings, while it also occupied open environments such as
222 steppes during the Last Glacial (Straus, 1981; Bugalho and Milne, 2003). It tolerates a wide
223 range of temperature, as long as the habitat is not too dry. Its diet is highly eclectic and
224 seasonally variable, although it shows a 60-70% herbaceous source. *Cervus elaphus* mainly
225 browses leaves, conifer needles, twigs, nuts, shoots and bark of trees in winter, and grazes
226 more on grasses, herbs, ferns, mosses, mushrooms, sedges or even rushes, during the summer
227 and intermediate seasons.

228 *Rangifer tarandus* (reindeer) lives in subarctic and arctic regions (taiga and tundra),
229 however some sub-species such as *R. tarandus tarandus* (woodland caribou) occupy the
230 boreal forests (Ihl and Klein, 2001; Thompson et al., 2015) In winter, reindeers mainly feed
231 on lichens which they access by digging holes in the snow cover. In the mild seasons, their
232 diet is mainly based on grasses, green leaves of shrubs, tree bark and sedges as well as tree
233 shoots such as larch, willow and birch. Mushrooms are also consumed during the late summer
234 and early autumn.

235 *Equus caballus* (horse) was widely distributed in Eurasia and the Americas during the
236 late Pleistocene. Equids are adapted to open habitats and are found in steppe, tundra and taiga
237 habitats, as well as in more temperate grasslands. They are non-selective grazers and tolerate
238 a wide range of temperatures (Berger, 1986).

239 *Capra pyreneica* (ibex) is a montane species living exclusively in open environments
240 with high relief (cliffs and stone ravines; pastures in spring) at altitudes ranging from about

241 500 m to about 3500 m as observed in the Alps (Villaret et al., 1997). Its diet is essentially
242 composed of herbaceous plants.

243 *Rupicapra rupicapra* (chamois) feeds on herbs and lives in mountains meadows and
244 on the edge of forests. Chamois are well-adapted to rough terrain and tolerate a large range of
245 temperatures as low as -20°C in winter and up to 25°C in summer (Christie, 1967; La Morgia
246 and Bassano, 2009) although they are actually distributed in a wide range of temperate
247 conditions.

248 *Saiga tatarica* (Eurasian antelope) feeds on salt-coated herbs, some grasses (Poaceae),
249 Euphorbiaceae and Artemisia. This antelope lives in hilly areas and is considered an indicator
250 of a dry climate (steppe environment) with highly-seasonally contrasted temperatures
251 (Bekenov et al., 1998).

252 Among these large mammals, obligate to semi-obligate drinkers are horse (strict
253 obligate drinker), red deer (drinks large amounts of water during the warm season), reindeer
254 (free water in summer, snow during the cold season) whilst semi-obligate to non-obligate
255 drinkers are ibex, chamois and antelope that drink free water occasionally (Macdonald, 2006).

256

257 3. Sample preparation and isotopic analysis

258 The tooth samples were prepared and analyzed at the Stable Isotopes Laboratory of the
259 Geotop research center (Université du Québec à Montréal). Prior to any treatment, tooth
260 crowns were mechanically cleaned to remove any trace of remaining glue or altered hard
261 tissues. They were then immersed in an ultrasonic bath in order to eliminate potential remains
262 of sedimentary particles. From 10 mg to 20 mg of enamel powder samples were collected
263 using a micro-drill equipped with a diamond-studded drill bit. Grooves were drilled
264 perpendicularly to the tooth growth axis from the cervix to the apex of the tooth crown.

265 Following the protocol used by Vigeant et al. (2017), organic matter was removed from
266 tooth enamel apatite by soaking an aliquot of the untreated sample in a 2% sodium
267 hypochlorite (NaOCl) solution for 24 h. Then, the samples were rinsed with large amounts of
268 water, then dried before being treated with 1 M acetic acid-Ca acetate buffer (pH = 4.75) for
269 24h at 20°C to remove secondary carbonate phases (Bocherens et al., 1996), and finally
270 washed with distilled water and dried at ambient temperature. For each sample, about 1 mg of
271 enamel powder was analyzed for $\delta^{13}\text{C}$ -values (‰ VPDB) and $\delta^{18}\text{O}$ -values (‰VPDB) of the
272 carbonate using a Micromass Isoprime™ isotopic ratio mass spectrometer operated in dual
273 inlet mode and coupled to a Multicarb™ system. Overall analytical uncertainties ($\pm 1\sigma$) for
274 $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ were close to 0.05‰ and 0.1‰, respectively, based on statistics from replicate
275 measurement of samples, compared to ± 0.02 and ± 0.03 ‰, respectively, on reference
276 carbonate materials (e.g., NBS 19, IAEA-603 and the home reference carbonate), thus
277 suggesting some isotopic heterogeneity in the ground carbonate samples.

278 4. Results 279

280 The dataset is characterized by $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values ranging respectively from -12.89‰
281 to -8.93‰ (mean = -10.42 ± 0.76 ‰) and -8.65 to -0.14‰ (mean = -5.19 ± 1.99 ‰). An
282 examination of data compiled in Table 1 reveals that they form two distinct clusters
283 corresponding to sites located on the Atlantic side and along the Mediterranean coast (Figure
284 1). As a first approach, pooling the taxa in each geographic cluster reveals that the $\delta^{18}\text{O}$
285 values of mammal remains from Nerja and Malladetes have much higher $\delta^{18}\text{O}$ values (-
286 1.45 ± 0.74) than those (-6.03 ± 0.94) from the sites located on the Atlantic side (Table 1). The
287 difference is not so striking for $\delta^{13}\text{C}$ values which average -10.60 ± 0.70 ‰ in the Atlantic sites,
288 i.e., slightly but significantly lower than that the mean value of Mediterranean sites, which is -
289 9.65 ± 0.44 ‰ (Welch t-test: $p = 4.4 \times 10^{-7}$; $H_0 =$ means are equal).

290 Discrimination between the datasets increases further when distinguishing Cervidae from
291 Caprinae in the cluster of Atlantic sites, which removes a sampling bias as only Caprinae
292 were sampled in the Mediterranean sites. In the case of Cervidae, the distribution of data
293 satisfies the statistical criteria required by a normal distribution when using Shapiro-Wilk test
294 ($p = 0.30$ and $W = 0.963$ in the 95% critical range [0.937; 1.000] for $\delta^{13}\text{C}$ values; $p = 0.15$ and
295 $W = 0.953$ in the 95% critical range [0.937; 1.000] for $\delta^{18}\text{O}$ values). Similar conclusions are
296 obtained for the Caprinae when using Shapiro-Wilk test ($p = 0.50$ and $W = 0.964$ in the 95%
297 critical range [0.920; 1.000]) for $\delta^{13}\text{C}$ -values; $p = 0.37$ and $W = 0.957$ in the 95% critical
298 range [0.920; 1.000] for $\delta^{18}\text{O}$ -values).

299 Cervidae have $\delta^{13}\text{C}$ values ranging from -12.89‰ to -9.47‰ (mean = $-10.96 \pm 0.66\text{‰}$)
300 and $\delta^{18}\text{O}$ values ranging from -8.65‰ to -3.67‰ (mean = $-5.96 \pm 1.03\text{‰}$) in the Atlantic sites.
301 These data statistically differ for $\delta^{13}\text{C}$ values (Welch t-test: $p = 1.03 \times 10^{-6}$; $H_0 =$ mean are
302 equal), but not for $\delta^{18}\text{O}$ values (Welch t-test: $p = 0.71$; $H_0 =$ mean are equal) of Caprinae
303 coming from the same sites (mean $\delta^{13}\text{C} = -10.12 \pm 0.49\text{‰}$ and mean $\delta^{18}\text{O} = -6.06 \pm 0.88\text{‰}$).

304 Caprinae from the Atlantic sites have slightly lower $\delta^{13}\text{C}$ -values ($-10.12 \pm 0.49\text{‰}$ against -
305 $9.65 \pm 0.44\text{‰}$) and much lower $\delta^{18}\text{O}$ -values ($-6.06 \pm 0.88\text{‰}$ against $-1.45 \pm 0.74\text{‰}$), than those
306 originating from Mediterranean sites with $\delta^{13}\text{C}$ -values of $-9.65 \pm 0.44\text{‰}$ and $\delta^{18}\text{O}$ -values of -
307 $1.45 \pm 0.74\text{‰}$ (Welch t-test for $\delta^{13}\text{C}$: $p = 3.6 \times 10^{-3}$; $H_0 =$ mean are equal; Welch t-test for $\delta^{18}\text{O}$:
308 $p = 1.7 \times 10^{-16}$; $H_0 =$ mean are equal).

309 Few samples are available for Equidae: 2 samples from Hornos de la Peña and 2 from
310 Laugerie-Haute, have $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values in the range of values from other herbivorous
311 mammals at sites located on the Atlantic side. It is worth pointing out that no temporal trend
312 is observed for either $\delta^{13}\text{C}$ - or $\delta^{18}\text{O}$ -values of both Cervidae and Caprinae in the Atlantic sites
313 (Table 1). Nevertheless, whatever their age, Caprinae from this study are characterized by

314 lower $\delta^{18}\text{O}$ values and higher $\delta^{13}\text{C}$ values than Cervidae. In addition, statistics that show a
315 normal distribution with relatively small standard deviations are consistent with inter-annual
316 variations of considered climatic parameters.

317

318 5. Discussion

319 5.1. Preservation and meaning of the isotopic compositions

320 Assessing the potential blurring effect of diagenetic processes represents the greatest
321 challenge for geochemists hoping to reconstruct environmental parameters based on isotopic
322 proxies. Biogenic apatites have undergone diagenesis, at least during the first step of the
323 mineral transformation commonly referred to as “early diagenesis”, which follows the decay
324 of the organic matter. Changes in the content of major and trace elements of biogenic apatites
325 do not necessarily mean that their initial stable C- and O-isotope compositions have been
326 fully reset or even partly modified (Goedert et al., 2018). The acquisition of secondary
327 isotopic signatures mainly takes place during the first stages of burial, when processes of
328 mineral dissolution and recrystallization under microbially-mediated conditions may alter the
329 skeletal tissues (Kolodny et al., 1996; Trueman et al., 2003; Zazzo et al., 2004). Enamel is
330 considered a more suitable material for paleoenvironmental or paleoclimatic reconstructions
331 because its apatite carbonate fraction has been shown to be generally resistant to isotopic
332 alteration during early diagenesis due to its highly dense and packed crystallites (Zazzo et al.,
333 2004).

334 Nonetheless, the preservation of pristine isotopic records needs to be assessed before
335 attempting paleoenvironmental interpretations of the oxygen and carbon isotope compositions
336 of fossil apatites. Whereas there is no method for determining whether the original isotopic
337 compositions are preserved, several tests may help assess the preservation state of the initial
338 isotopic signatures. In the present study, three complementary approaches are used:

339 i) Although $\delta^{13}\text{C}$ - and $\delta^{18}\text{O}$ -values may covariate in the case of specific climate variations,
340 usually detected through geographic or temporal trends (e.g., a combination of higher
341 precipitation and lower temperatures), a linear correlation generally indicates a mixing
342 relationship between two endmembers: the original isotopic signature and a contaminant,
343 such as soil carbonate. Our data do not reveal any such mixing (Atlantic sites {2 outliers}: n =
344 61; $R^2 = 10^{-3}$; p = 0.76 for H_0 : no correlation; Mediterranean sites: n = 13; $R^2 = 3 \times 10^{-2}$; p =
345 0.57 for H_0 : no correlation).

346 ii) Loose clusters and scrambling of isotopic compositions should affect all tooth material
347 independently of the taxa. Here, the systematic differences in $\delta^{13}\text{C}$ - and $\delta^{18}\text{O}$ -values of
348 Cervidae vs Caprinae supports the hypothesis of a preserved isotopic imprint of their
349 respective diets and habitats.

350

351 5.2. Reconstitutions of MAP

352 5.2.1. Method: principles and limits

353 The $\delta^{13}\text{C}$ of consumed food by vertebrates mainly controls the $\delta^{13}\text{C}$ of their skeleton
354 (Ambrose, 1993; Ballasse et al., 1999; Szostek, 2009). Carbon isotope ratios of apatite
355 carbonate may be considered as a “dirty window” that opens on a combination of factors: the
356 diet, the degree of openness of the environment (exposure to light) and the amount of
357 precipitation. The reconstruction of MAP is thus done in two steps.

358 The first step consists in converting the $\delta^{13}\text{C}$ of carbonate ($\delta^{13}\text{C}_{\text{carb}}$) into the $\delta^{13}\text{C}$ of diet
359 ($\delta^{13}\text{C}_{\text{diet}}$), and the second one in converting the $\delta^{13}\text{C}_{\text{diet}}$ into MAP values (mm.yr^{-1}). As a MAP
360 proxy, $\delta^{13}\text{C}_{\text{carb}}$ is basically tarnished with several important sources of uncertainty. Therefore,
361 we consider that only broad estimates may be obtained. The commonly used isotopic $\delta^{13}\text{C}_{\text{carb}}$
362 $-\delta^{13}\text{C}_{\text{diet}}$ offset value ($\Delta^{13}\text{C}_{\text{PI}}$) of 14.1‰ (Cerling and Harris, 1999) cannot be used in this study
363 as it varies from one species to another. More recently, Tejada-Lara et al. (2018) proposed a

364 series of equations that consider the specificities in the digestive system as well as the body
 365 mass of different herbivorous mammals. Calculations of $\delta^{13}\text{C}_{\text{diet}}$ of the study taxa in Table 1
 366 follow this model. It must be kept in mind that animal diets do not necessarily reflect the
 367 composition of the vegetation cover; the stricter an animal's food preferences, the larger the
 368 bias between the isotopic composition of the diet and that of the vegetation cover.

369 The second step consists in estimating MAP from the $\delta^{13}\text{C}$ of vegetation, here
 370 assumed to be close to $\delta^{13}\text{C}_{\text{diet}}$. The empirical relationship proposed by Rey et al. (2013),
 371 which we will use below, is valid if the vegetation cover was composed of C3 plants. This is
 372 still an open debate, however, and conflicting reconstructions of the LGM paleovegetation of
 373 western Europe from models vs pollen data exist in the literature (e.g., Elenga et al., 2000;
 374 Leng, 2006; Woillez et al., 2011; Hatté et al., 2013; Binney et al., 2017; see a discussion and
 375 an explanatory hypothesis in Kaplan et al., 2016). Thus, our estimates of MAP from $\delta^{13}\text{C}$ -data
 376 must be seen as a first approximation that needs to be confronted with estimates from other
 377 approaches. The method established by Rey et al. (2013), using a least square regression from
 378 the dataset of Kohn (2010), is based on relationship (1) below, established between plant leaf
 379 discrimination ($\Delta^{13}\text{C}_{pl}$) as defined above and mean annual precipitations (MAP):

$$380 \quad \text{Log}_{10}(\text{MAP} + 300) = 0.092(\pm 0.004)\Delta^{13}\text{C}_{pl} + 1.148(\pm 0.074) \quad (1)$$

$$381 \quad \text{with } \Delta^{13}\text{C}_{pl} = \frac{\delta^{13}\text{C}_{atm} - \delta^{13}\text{C}_{pl}}{1 + \frac{\delta^{13}\text{C}_{pl}}{1000}} \quad \text{and MAP in mm yr}^{-1}$$

382 $\delta^{13}\text{C}_{atm}$ values of atmospheric CO_2 have been measured in air bubbles trapped within the
 383 Vostok ice cores between 20 and 43 ka (Leuenberger et al., 1992; Schmitt et al., 2012). For
 384 the LGM, this value has been estimated to be close to -7‰ (VPDB). Calculations of MAP are
 385 given in Table 1. However, this equation does not consider the pCO_2 effect on $\delta^{13}\text{C}$ values of
 386 the vegetation (Farquhar et al., 1982; Schubert and Jahren, 2012). Hare et al. (2018) related
 387 the $\delta^{13}\text{C}$ increase by $\approx 1\text{‰}$ of plants and faunal collagen to the low pCO_2 values (≈ 180 ppm)

388 of the LGM relatively to those (≈ 300 ppm) of the post deglacial rise that took place about 15
389 kyr ago (Peacock et al., 2006). Consequently, it is most likely that our calculated MAP values
390 according to equation (1) are underestimated by about 150 mm y^{-1} . Final estimates from the
391 model will thus be corrected using this offset.

392 The validity and robustness of this empirical approach were tested successfully in a study
393 (Prud'homme et al., 2018) devoted to the reconstruction of MAP in Germany (Nussloch)
394 during the Last Glacial, which was based on the $\delta^{13}\text{C}$ of earthworm granule calcite crystals. In
395 this study, the estimated MAP values range from ~ 270 to 460 mm with a mean value of \sim
396 370 mm for the Upper Pleniglacial (\sim LGM) and of ~ 300 mm, for the Middle Pleniglacial,
397 covering a time interval between 17 ka and 55 ka. Uncertainties associated with the estimated
398 MAP values are on the order of ± 100 to 200 mm. Based on $\delta^{13}\text{C}$ values of organic matter
399 preserved in the Nussloch loess deposits and using an inverse modelling approach (BIOME
400 4), Hatté and Guiot (2005) estimated MAP values ranging from 280_{-60}^{+120} to 460_{-160}^{+80} mm.
401 Considering the large uncertainties associated with the various methods of MAP
402 reconstructions, Prud'homme et al. (2018) concluded that the empirical method developed by
403 Kohn (2010) may be used for MAP estimates in the absence of other proxies or modelling
404 approaches.

405

406 5.2.2. Interpretation

407 The reconstructed $\delta^{13}\text{C}$ -values of animal diet ($\delta^{13}\text{C}_{\text{diet}}$) suggest that they mainly fed on
408 C_3 plants as revealed by a mean $\delta^{13}\text{C}_{\text{diet}}$ of $-23.5 \pm 1.0\text{‰}$ for the whole data base (Table 1),
409 thus supporting the scenario of a C_3 -plant dominated vegetational cover (compare with Hare
410 et al., 2018). The C_3 Calvin-Benson pathway (~ 75 wt% of the present-day vegetal biomass
411 including trees, temperate grasses, some forbs, shrubs) is the most discriminating regarding
412 the heavy carbon isotopes, thus leading to low $\delta^{13}\text{C}$ values ranging from -34‰ to -22‰ and

413 averaging -26‰ (Park and Epstein, 1960; 1961; Smith and Epstein, 1971; O’Leary, 1981).
414 Variations within this range of $\delta^{13}\text{C}$ values result from external factors such as air
415 temperature, water stress, exposure to light, $\delta^{13}\text{C}$ of atmospheric CO_2 , pCO_2 and rate of CO_2
416 recycling (O’Leary, 1981). Worth mentioning is the fact that a $\delta^{13}\text{C}_{\text{diet}}$ of $-23.5\pm 1.0\text{‰}$ could
417 as well be compatible with a diet of up to $\sim 20\%$ of C_4 plants, as illustrated for grazers from
418 modern steppe environments (Auerswald et al., 2009). Interestingly, this study also
419 demonstrates that despite a large overall variability of the relative abundance of C_4 - vs C_3 -
420 plants, no preferential grazing is observed.

421 Nevertheless, on the Atlantic side of the Iberian Peninsula, Caprinae have higher $\delta^{13}\text{C}_{\text{diet}}$
422 (mean = $-22.8\pm 0.5\text{‰}$) than Cervidae and Equidae (mean for both = $-24.3\pm 0.6\text{‰}$), all
423 populations being characterized by normal distributions (Caprinae: $p = 0.11$ and $W = 0.953$ in
424 the 95% critical range [0.944; 1.000]; Cervidae and Equidae: $p = 0.19$ and $W = 0.960$ in the
425 95% critical range [0.942; 1.000]). Such distinct carbon isotope compositions reflect diet
426 differences related to distinct habitats or grazing habits (Figure 2). This observation is in
427 agreement with Jones et al. (2020) who concluded that ibex adapted their niche during the
428 LGM.

429 Among Cervidae, *C. elaphus* have lower $\delta^{13}\text{C}_{\text{diet}}$ values (mean = $-24.4\pm 0.6\text{‰}$) than *T.*
430 *rangifer* (mean = $-23.2\pm 0.36\text{‰}$), even though only three samples were available of *C.*
431 *elaphus*. A higher $\delta^{13}\text{C}_{\text{diet}}$ for reindeers, relative to other animals, has been explained by their
432 specific diet mainly based on lichens, especially consumed during the cold season (Park and
433 Epstein, 1960; Máguas and Brugnoli, 1996; Ben-David et al., 2001)

434 Based on the estimated $\delta^{13}\text{C}_{\text{diet}}$ values, MAP values were calculated in the range ~ 100 to
435 $400 \text{ mm}\cdot\text{yr}^{-1}$ for Atlantic sites (100 to $200 \text{ mm}\cdot\text{yr}^{-1}$ recorded by Caprinae and 200 to 400

436 mm.yr⁻¹ recorded by Cervidae and Equidae), while they are close to 100 mm.yr⁻¹ for the two
437 Mediterranean sites (Table 2). The present-day reference values (Table 2) extracted from
438 meteorological records (IAEA/WMO database) correspond to cities in the vicinity of the
439 studied archaeological sites, specifically Almeria (202±66 mm.yr⁻¹), for the Nerja site,
440 Valencia (532±173 mm.yr⁻¹), for the Malladetes site , Santander (1050±140 mm.yr⁻¹), for the
441 sites located in Asturias and Cantabria (Spain), and Cestas-Pierroton (937±192 mm.yr⁻¹), for
442 the Laugerie-Haute site. The Caprinae record of drier environmental conditions than those
443 inferred from Cervidae and Equidae, suggests differences in diets and/or seasonal/altitudinal
444 grazing habitats between some of the representative herbivorous species sampled.

445 Diet preferences between C3 and C4 may cause δ¹³C differences by several ‰ between
446 sheep and goat, for example, as shown by Balasse and Ambrose (2005) for C4 grassland
447 environments of the Central Rift Valley of Kenya. However, C4 was most likely absent or
448 very scarce in the studied LGM-environments (Collins and Jones, 1985). δ¹³C differences
449 among C3-eating large mammals may result from differences in water stress and/or exposure
450 to light (O’Leary, 1981). It means that δ¹³C values of Caprinae should be higher than those of
451 Cervidae and Equidae if the Caprinae habitat was open (sparse vegetation cover in a rocky
452 environment) and characterized by a vegetation submitted to water stress (e.g. dry sides of
453 mountains).

454 Nevertheless, during the LGM, precipitation followed a pattern similar to the modern one
455 (Figure 3), with sites under Atlantic vs Mediterranean influence defining two distinct clusters.
456 The Mediterranean cluster is significantly drier than the Atlantic one, but both depict much
457 drier conditions than at present. LGM precipitation estimates obtained here broadly agree
458 with pollen-based reconstructions (e.g., Peyron et al., 1998), but disagree with the wetter
459 conditions reconstructed from climate model experiments (e.g., Ludwig et al., 2016; Arpe et
460 al., 2011).

461

462 5.3. Reconstitutions of MAAT

463 5.3.1. Method: principles and limits

464 Oxygen isotope ratios of apatite carbonate may be seen as a “frosted glass window” open
465 on the composition of dietary sources of water and local meteoric water, ultimately used as a
466 proxy for air temperatures (e.g. Fricke and O’Neil, 1998; Daux et al., 2005). The $\delta^{18}\text{O}$ of
467 consumed water by vertebrates mainly controls the $\delta^{18}\text{O}_c$ of their skeleton (Longinelli, 1984;
468 Kohn, 1996). The oxygen isotope composition of leaf water can somewhat blur the
469 relationship between the $\delta^{18}\text{O}_c$ of apatite carbonate and the $\delta^{18}\text{O}$ of drinking water (Ayliffe
470 and Chivas, 1990; Cormie et al., 1994; Luz et al., 1990; Pederzani and Britton, 2019). It
471 constitutes, however, a good indicator of aridity (Levin et al., 2016; Blumenthal et al., 2017).

472 In this approach, the reconstitution of MAAT is done in four steps.

473 First, oxygen isotope compositions of apatite carbonate ($\delta^{18}\text{O}_c$) measured on the VPDB
474 scale (Coplen et al., 1983) must be converted into those of their phosphate counterparts
475 ($\delta^{18}\text{O}_p$) before being used to estimate the composition of drinking water on the basis of the
476 equations available in the literature. This step is achieved by using equation (2) that was
477 determined by Iacumin et al. (1996) for modern herbivorous mammals. Unfortunately, this
478 step is a source of large uncertainties ($\delta^{18}\text{O}_p$: standard error of estimate = 0.73). We computed
479 Equation (2) using the original data set published in Iacumin et al. (1996) in order to tighten
480 uncertainties as follows:

$$481 \delta^{18}\text{O}_p = 0.975(\pm 0.031) \delta^{18}\text{O}_c - 8.43(\pm 0.81) \quad (n = 17; R^2 = 0.985) \quad (2)$$

482 The second step consists in calculating the oxygen isotope composition of water
483 consumed (free water and water derived from the food such as leaves and herbs) by the
484 animals. Several oxygen isotope fractionation equations between apatite phosphate ($\delta^{18}\text{O}_p$)
485 and water ($\delta^{18}\text{O}_w$) have been published for large herbivorous mammals, covering all taxa

486 investigated in the present study. It is worthy to note that animal physiology is integrated in
487 the oxygen isotope fractionation equations (Longinelli, 1984; Luz and Kolodny, 1985; Kohn,
488 1996; Langlois et al., 2003) that have been established on present-day fauna, either the same
489 species or close relatives. The relevant equations have also been recalculated to set the $\delta^{18}\text{O}_w$
490 variable as the estimator (Y-axis) in the regression line along with the associated statistics, as
491 follows:

492 - Deer (*Cervus elaphus*) (D'Angella and Longinelli, 1990):

$$493 \quad \delta^{18}\text{O}_w = 0.88(\pm 0.03)\delta^{18}\text{O}_p - 22.50(\pm 0.52) \quad (n = 7; R^2 = 0.99) \quad (3)$$

494 - Reindeer (*Rangifer tarandus*) (Iacumin and Longinelli, 2002):

$$495 \quad \delta^{18}\text{O}_w = 1.21(\pm 0.01)\delta^{18}\text{O}_p - 26.41(\pm 1.31) \quad (n = 34; R^2 = 0.74) \quad (4)$$

496 Note that 2 outliers were removed from the original database for the setting of equation 4, as
497 recommended by Iacumin and Longinelli (2002).

498 - Horse (*Equus burchelli*, *E. zebra*, *E. caballus*) (Bryant et al., 1994; Sanchez Chillon et al.,
499 1994; Delgado-Huertas et al., 1995):

$$500 \quad \delta^{18}\text{O}_w = 1.09(\pm 0.128)\delta^{18}\text{O}_p - 25.83(\pm 1.08) \quad (n = 25; R^2 = 0.77) \quad (5)$$

501 Note again that 2 outliers were removed from the original database deduced from linear
502 regression analysis

503 - Wild Goat (*Capra hircus* and *C. ibex*) (Delgado-Huertas et al., 1995)

$$504 \quad \delta^{18}\text{O}_w = 1.09(\pm 0.06)\delta^{18}\text{O}_p - 26.45(\pm 0.98) \quad (n = 21; R^2 = 0.95) \quad (6)$$

505 A major caveat here is the possibility of distinct $\delta^{18}\text{O}_w$ vs $\delta^{18}\text{O}_p$ relationships during
506 the cold LGM, due to reduced evapotranspiration (e.g., Kohn, 1996). Isotope enrichment from
507 precipitation to plant-water and finally to the animal body-water could have prevailed. Thus,
508 under LGM conditions, the $\delta^{18}\text{O}_w$ -value calculated with the above equations must be seen as a
509 maximum value.

510 The third step consists in correcting the $\delta^{18}\text{O}$ of seawater from the volume of
511 continental ice. Indeed, any change in the isotopic composition of oceanic sources will
512 propagate throughout the entire surface water cycle. Knowing that the mean depth of the
513 oceans is 3,700 m (Charette and Smith, 2010), a decrease in sea level by 120 ± 10 m (Lambeck
514 et al., 2014) results in a mean increase of the global ocean reservoir $\delta^{18}\text{O}$ -value by $+1.2\pm 0.1\text{‰}$
515 provided the mean $\delta^{18}\text{O}$ of the LGM ice-sheets is close to -40‰ (Blunier and Brook, 2001).
516 This isotopic offset is very close to that proposed by Schrag et al. (2002) and Steele et al.
517 (2009), but perhaps a little overestimated, based on isotopic composition for the Laurentide
518 Ice Sheet proposed by Hillaire-Marcel and Causse (1989) or Sima et al. (2006). Duplessy et
519 al. (2002) proposed an offset of $1.05\pm 0.20\text{‰}$ probably encompassing the effective overall
520 change in the ocean isotopic composition. However, moisture sources relate to ocean surface
521 water masses: their isotopic composition differs from that of the whole ocean, and may show
522 large regional offsets, especially in the present case, between the Bay of Biscay and the
523 western Mediterranean. The Bay of Biscay was likely the major moisture supplier for the
524 Atlantic sites, whereas a mixture of Atlantic and western Mediterranean moisture supplies
525 may be hypothesized for the Mediterranean sites. The two marine areas were of course
526 characterized by distinct MAAT, mean salinity and isotopic composition.

527 Based on Schrag et al. (2002), one may assume an isotopic composition of surface
528 waters from the northeast North Atlantic in the $+0.7\pm 0.1$ to $+0.8\pm 0.1\text{‰}$ range vs VSMOW, a
529 range compatible with model estimates from Paul et al. (2001). According to Loncaric et al.
530 (1998), MAAT depicted large amplitude oscillations between $<5^\circ\text{C}$ and up to 15°C , with a
531 mean value of about 7 to 9°C (e.g., Kuhlemann et al., 2008). Comparatively, surface waters
532 from the western Mediterranean were not only warmer but enriched in ^{18}O . Planktic
533 foraminifera (Hayes et al., 2005) and biomarkers (Rodrigo-Gámiz et al., 2014), both
534 suggesting a mean LGM sea-surface temperature (SST) of $\sim 13.5^\circ\text{C}$, whereas $\delta^{18}\text{O}_{\text{carb}}$ values

535 reported from this sector of the Mediterranean during the same interval range from
536 $+3.5\pm 0.5\text{‰}$ vs VPDB in planktic foraminifera (Thunell and Williams, 1989) to $+3.9\pm 0.2\text{‰}$ in
537 shallow mollusk shells (Fergusson et al., 2011). Combining these values, one may set the
538 LGM $\delta^{18}\text{O}_{\text{sw}}$ -value at about $+3\text{‰}$ vs VSMOW in the western Mediterranean, to be compared
539 with a modern value of $\sim +1.3\text{‰}$ (Goddard Institute data base; Schmidt et al., 1999; see also
540 Benetti et al., 2017). Potential moisture generated during the evaporation of the western
541 Mediterranean Sea, which had a $\delta^{18}\text{O}$ higher than the Atlantic Ocean by $\sim +2\text{‰}$, may thus
542 have played some role during the LGM. However, climate models suggest a southward shift
543 of the North Atlantic jet stream during the LGM, governing the relatively abundant winter
544 precipitation in comparison with summer rains which were somewhat controlled by local
545 processes (e.g., Beghin et al., 2016). Thus, the most likely LGM moisture source, for both the
546 Mediterranean and the Atlantic sites, would have been the northeastern North Atlantic Ocean,
547 leading to adopt the $\delta^{18}\text{O}_{\text{sw}} \sim +0.8\text{‰}$ value for the primary source water, and allowing for
548 some ^{18}O -enriched precipitation in summer, influenced by the high $\delta^{18}\text{O}_{\text{sw}}$ -values of the
549 western Mediterranean waters ($\sim +3\text{‰}$). Perhaps worth of mention here is the fact that under
550 the modern conditions, i.e., with a $\Delta\delta^{18}\text{O}$ offset of $\sim +0.8\text{‰}$ between surface waters of the
551 western Mediterranean ($\delta^{18}\text{O}_{\text{sw}} \sim 1.3\text{‰}$) and those of the northeastern North Atlantic ($\delta^{18}\text{O}_{\text{sw}}$
552 $\sim 0.5\text{‰}$; Benetti et al., 2017), the long-term isotopic composition of precipitation in both areas
553 is almost similar ($\sim -6\text{‰}$; Araguas-Araguas et al., 2005), thus pointing even today to a major
554 contribution of Atlantic moisture sources to precipitation on the Iberian Peninsula.

555 We used the $+0.8\text{‰}$ offset between modern vs LGM moisture sources as a base line
556 for both regions and subtracted it from the $\delta^{18}\text{O}_{\text{w}}$ -values derived from equations (3) to (6) (see
557 Table 1). Nevertheless, we also increased this offset to $+1.2\text{‰}$ for the Mediterranean sites, a
558 value that would account for about 20% of Mediterranean moisture source supplies on a
559 yearly basis, based on the $\sim 2\text{‰}$ offset in $\delta^{18}\text{O}_{\text{sw}}$ -values between the Bay of Biscay and the

560 Western Mediterranean. Again, this seems a reasonable estimate considering the regional
561 atmospheric circulation in SW Europe during the LGM (cf. Ludwig et al., 2016; see also
562 Kuhlemann et al., 2008; Beghin et al., 2016).

563 The fourth step aims at converting $\delta^{18}\text{O}_w$ to MAAT. Here again, one may question
564 whether or not present-day relationships fully apply to the LGM. Firstly, all of the sites of the
565 present study are close to coastlines, thus, they are not affected by continental Rayleigh-
566 evolution of humid air-masses or by major altitudinal effects (e.g., Gat et al., 2001), a process
567 well illustrated by Rozanski et al. (1982) for inland precipitation patterns in Europe. Isotopic
568 compositions of precipitation at the study sites should then follow a relatively linear
569 relationship with mean annual temperatures, as observed at global scale, despite some
570 latitudinal/regional variations in the slope and intercept of the local regression lines (e.g., Lee
571 et al., 2008). The slope of a MAT– $\delta^{18}\text{O}_{mw}$ linear relationship is mainly temperature–
572 dependent at mid- and high-latitudes. This point is firstly well illustrated by the existence of a
573 strongly positive linear correlation ($R^2 = 0.83$) between the dew point (T_d) and the oxygen
574 isotope composition of meteoric water (Figure 4). T_d , expressed in °C, represents the
575 temperature at which the actual water vapour pressure equals the saturated water vapour
576 pressure (RH = 100%). This climatic parameter plays a key role in the distribution of $\delta^{18}\text{O}_{mw}$
577 over the continental masses located in the mid-latitudes (Lécuyer et al., 2020). Secondly,
578 there is a unique MAT– $\delta^{18}\text{O}_{mw}$ linear relationship for present-day (Figure 5A) for latitudes >
579 32°, even if it samples various continental areas from both hemispheres, which are submitted
580 to various moisture-bearing prevailing winds.

581 The MAAT (in °C) vs $\delta^{18}\text{O}_w$ linear relationship from equation (7), established for
582 Europe (Skrzypek et al., 2011), is indistinguishable in terms of slope and intercept from
583 equation (8) obtained at a global scale (Figure 5A). For a reliable comparison, equation (8)

584 was computed by excluding data from the tropics as well as those corresponding to air
585 temperatures lower than 0°C (Figure 5B).

$$586 \quad \text{MAAT } (^\circ\text{C}) = 1.41 \delta^{18}\text{O}_{\text{w-MAP}} + 21.63 \quad (7)$$

587 where MAT represents the mean annual temperature and $\delta^{18}\text{O}_{\text{w-MAP}}$, the weighted mean
588 isotopic composition of annual precipitation.

$$589 \quad \text{MAAT } (^\circ\text{C}) = 1.40(\pm 0.08) \delta^{18}\text{O}_{\text{w-MAP}} + 21.86(\pm 0.64) \quad (8)$$

$$590 \quad (n = 90; R^2 = 0.81)$$

591 Equation (7) was thus used to calculate MAAT (reported in Table 1) during the LGM in
592 southwestern Europe. There are three caveats when using this method:

593 1) Altitude effect: in Spain, the rate of air-temperature decrease with altitude is close to 5°C
594 per 1000 m in mountain areas (Navarro-Serrano et al., 2018). In the Pyrenees, altitudinal
595 oxygen isotope gradients average -3‰ per 1000 m (Hughes et al., 2018), a value within
596 the range observed in southern Europe (e.g., Tazioli et al., 2019). Consequently,
597 differences between present-day reference stations (cities are close to sea-level) and
598 mammal ranges (between 0 and 1000 m) during the LGM may lead to overestimates of
599 temperature differences by about 2°C in northern Spain and up to 4°C in south and
600 southeast Spain.

601 2) Source effect: the source of drinking water may differ isotopically from local meteoric
602 waters, for example in rivers since their sources are located at altitudes. A comparison
603 between present-day river and precipitation $\delta^{18}\text{O}$ maps (Nan et al., 2019) reveals that
604 differences between those two parameters are close to 2‰ over Europe on a yearly
605 average. Once again, true air temperatures may be higher than those calculated following
606 the above method. Similarly, animals that seasonally migrate may have a $\delta^{18}\text{O}_{\text{w}}$ record
607 that is biased relative to their place of death.

608 3) Reservoir effect: water stored in ponds, lakes or in snow cover may suffer evaporation or
609 sublimation that tends to enrich the residual liquid–solid water in heavy isotopes. Such
610 processes may induce oxygen isotope biases in the order of a few per mil.

611 However, a sporadic influence of the above boundary conditions on the isotopic approach
612 should be detectable by altering the normal distribution of the studied population; which does
613 not seem to be the case here.

614

615 5.3.2. Interpretation

616 $\delta^{18}\text{O}_{\text{w-MAP}}$ have been calculated according either to ocean surface water having a $\delta^{18}\text{O}$ of
617 $+1.2$ or $+0.8\text{‰}$. Inferred temperatures using equation (7) are shifted by $\approx +0.6^\circ\text{C}$. In the case
618 of a prevailing oceanic surface source of moisture having a $\delta^{18}\text{O}$ of $+1.2\text{‰}$, calculated mean
619 $\delta^{18}\text{O}_{\text{w-MAP}}$ are $-10.1\pm 0.9\text{‰}$ ($n = 46$) and $-10.3\pm 1.0\text{‰}$ ($n = 17$) for northern Spain and
620 Laugerie-Haute, respectively (Table 1). Pooled data follow a normal distribution (Figure 6)
621 according to the Shapiro-Wilk test ($p = 0.26$ and $W = 0.976$ in the 95% critical range [0.9620;
622 1.000]). The range of $\delta^{18}\text{O}_{\text{w-MAP}}$ values comprised between $\sim -12\text{‰}$ and $\sim -8\text{‰}$ correspond to
623 present-day compositions of precipitation in south Scandinavia and Central Europe
624 (IAEA/WMO database and maps). Calculated mean $\delta^{18}\text{O}_{\text{w-MAP}}$ are $-5.4\pm 0.8\text{‰}$ ($n = 8$) and -
625 $5.8\pm 0.8\text{‰}$ ($n = 6$) for Malladetes and Nerja, respectively. Pooled data follow a normal
626 distribution (Figure 6) according to the Shapiro-Wilk test ($p = 0.93$ and $W = 0.975$ in the 95%
627 critical range [0.875; 1.000]). The range of $\delta^{18}\text{O}_{\text{mw}}$ values between $\sim -7\text{‰}$ and $\sim -4\text{‰}$
628 correspond to present-day compositions of precipitation along the Mediterranean rim
629 (IAEA/WMO database and maps).

630 The calculated $\delta^{18}\text{O}_{\text{w-MAP}}$ values based on a $\delta^{18}\text{O}_{\text{sw}}$ of $+0.8\text{‰}$ range from $\sim 6^\circ\text{C}$ to \sim
631 10°C for Atlantic sites. This range may be explained by altitudinal gradients recorded by the
632 faunal remains and/or by the large amplitude oscillations of LGM-SST and LGM- $\delta^{18}\text{O}_{\text{carb}}$

633 values in the Bay of Biscay reported by Loncaric et al. (1998). It is interesting that the range
634 of temperature inferred for the Atlantic sites in the present study is within the range proposed
635 by these authors for surface waters of the Bay of Biscay during the LGM. On the
636 Mediterranean side, the estimated LGM-MAAT values are close to 14–15°C for both sites
637 ($\delta^{18}\text{O}_{\text{sw}}$ of +0.8‰) or close to 13.5–14.5°C ($\delta^{18}\text{O}_{\text{sw}}$ of +1.2‰) when accounting for some
638 contribution of Mediterranean moisture to summer precipitations (Table 2). Here also, this
639 value is practically identical to LGM-SST values in the Western Mediterranean estimated by
640 Hayes et al. (2005) or by Rodrigo-Gámiz et al., (2014).

641 The air temperatures reconstructed during the LGM are lower than the present-day ranges
642 recorded in meteorological stations located either in the vicinity of the Atlantic sites
643 (Santander: $14.8 \pm 0.4^\circ\text{C}$ and Cestas-Pierroton: $13.1 \pm 0.6^\circ\text{C}$), or close to the Mediterranean
644 sites (Almeria: $19.2 \pm 0.4^\circ\text{C}$; Valencia: $18.5 \pm 0.6^\circ\text{C}$). As shown in Figure 7, MAAT decreased
645 during the LGM from South to North according to a trend roughly similar to the modern one.
646 As a whole, MAAT values in southern Spain were about 4–5°C below modern pre-industrial
647 temperatures, and by 5–8°C in northern Spain and southwest France (Figure 7).

648

649 5.4. LGM climate inferred from large mammal isotopes and biogeographic patterns.

650 Faunal associations described in the archaeological sites of southwestern Europe are
651 generally compatible with cold and dry, open environments, such as tundra and dry steppe,
652 but there are important regional differences. The sites sampled in this study are from three
653 distinct biogeographic zones, following the classification suggested by Yravedra and Brugal
654 (2005) for southwestern Europe. The zones sampled for this study are: southwest France
655 (zone VI), Cantabria/Asturias (zone IV) and the Mediterranean coast (zone IIIa). A general
656 reduction in faunal diversity is observable in Southwestern Europe during the LGM, signaling
657 the severity of the climate downturn, but the relative diversity of herbivores and carnivores

658 differs between zones. Diversity decreases in zone VI reaching minimum levels during the
659 LGM, in zone IV (Cantabria/Asturias) diversity also decreases but reaches a minimum after
660 the LGM, while carnivore diversity actually increases with time, whereas the opposite pattern
661 occurs in zone IIIa (e.g., Valencia) where a gradual increase in herbivore diversity is
662 observable over the course of the last Glacial (Yravedra and Brugal, 2005).

663 In SW France (zone VI), horse dominates sites such as Laugerie Haute Est at the
664 beginning of the LGM (e.g., in the Magdalenian 0 level; Table 1) but reindeer, a taxon
665 associated with tundra environments, increases dramatically in importance throughout the
666 sequence, eventually dominating during Magdalenian I and II (see: Delpech, 2012). In
667 northwest Spain (zone IV), on the other hand red deer, a taxon generally considered more
668 indicative of temperate, wooded contexts often dominates late Glacial faunal assemblages,
669 while the proximity of sites to the coastal ranges is signaled by the presence of ibex and
670 chamois (Straus, 2018). Our results are consistent with the biogeographic patterns described
671 above, indicating strong contrasts between Mediterranean sites (in Zone IIIa) and sites in
672 zones IV and VI in terms of MAAT and MAP.

673 During the LGM, tundra extended across northern Europe while steppes dominated
674 the Mediterranean areas, resulting in a geographic reduction and fragmentation of boreal
675 evergreen forests (taiga) and temperate deciduous forests (Tarasov et al., 2000). The mean
676 value of $350 \pm 100 \text{ mm.yr}^{-1}$ reconstructed for MAP from the $\delta^{13}\text{C}_{\text{carb}}$ of the dental apatite of
677 herbivorous mammals (above) is consistent with this observation. However, a few samples of
678 *Cervus elaphus* from zone IV, El Cierro and El Ruso, the closest to the Atlantic ocean depict
679 a $\delta^{13}\text{C}_{\text{carb}}$ -value low enough to suggest that some years or periods in the year were
680 characterized by $\text{MAP} \geq 500 \text{ mm.yr}^{-1}$. This could mean that the climate in northern Spain was
681 rather unstable at inter-decadal or inter-centennial scales towards the end of the LGM, or

682 simply that *C. elaphus* used a large seasonal altitudinal range, as observed in modern
683 specimens in the Alps (Luccarini et al., 2006) or from the Rockies (Morgantini et al., 1989).

684 Geochemical proxies similar to those used in this study were applied to faunal remains
685 (horse, deer and ibex) recovered from the archaeological site of Peña Capón (Yravedra et al.,
686 2016), a rock shelter located in central Iberia which contains sedimentary deposits assigned to
687 Marine Isotope Stage 2 (MIS 2). Yravedra et al. (2016) estimated MAAT for archaeological
688 levels with a ^{14}C cal. age of ~23.8 kyr, ranging from 9°C to 12°C, i.e. only slightly below the
689 present-day MAAT of 12°C–13°C recorded in the locality of Muriel. These estimates for the
690 central part of the Iberian Peninsula may reflect milder conditions prior to the onset of the
691 LGM. Nevertheless, it is interesting to note that they are bracketed by our results. It is also
692 worthy to note that ibex recorded higher $\delta^{13}\text{C}$ values and lower $\delta^{18}\text{O}$ values than the other co-
693 habitating mammals such as Cervidae and Equidae. These data point to a specific habitat for
694 Caprinae as recently suggested by Jones et al. (2020) who analyzed both carbon and nitrogen
695 isotope compositions of bone collagen. These authors concluded that the existence of refugia
696 in south Europe allowed most herbivores to adapt despite harsh and fluctuating climatic
697 conditions.

698 The LGM climate conditions have been reconstructed from palynological data (e.g.,
699 Peyron et al., 1998). In the north of Spain (Lago Ajo) and in the south (Padul), MAAT values
700 were estimated in the 10°C to 5°C range. Palynological estimates of MAP, range from 900-
701 600 mm in the north of Spain, to close to 200 mm in the south. The temperatures from
702 palynological records are congruent with the estimates of the present study. However,
703 whereas paleoprecipitation estimates from palynology or from the present isotopic approach
704 fit well in zone IIIa, on the Mediterranean side, the MAP estimates for Northern Spain from
705 pollen proxies are somewhat higher than those based on $\delta^{13}\text{C}_{\text{carb}}$ values. This leads us to
706 consider the possibility that isotopic reconstructions, such as used here, vs reconstructions

707 from transfer function using palynological assemblages, do not necessarily encompass the
708 same space-time dimensions. For example, differences in the seasonality of pollen production
709 and patterns of altitudinal grazing may result in distinct signals.

710 As mentioned above, the study sites are close to either the Bay of Biscay (in zones IV
711 and VI) or the western Mediterranean (zone IIIa). Hayes et al. (2005) and Rodrigo-Gámiz et
712 al. (2014) estimated LGM-SSTs of $\sim 13.5^{\circ}\text{C}$ off the Mediterranean coastline of Spain,
713 whereas Kucera et al. (2005) estimated LGM-SST of $\sim 8^{\circ}\text{C}$ for the Bay of Biscay on the basis
714 of foraminifera $\delta^{18}\text{O}$ values. Both values fit with the corresponding inland, but coastal
715 temperatures reconstructed here, highlighting the strong influence of adjacent marine basin
716 SSTs on proximal inland MAAT. Moreover, these temperature estimates based on marine as
717 well as on continental proxies, enforce the hypothesis of cold regional conditions as well as of
718 a marked difference between the Atlantic and Mediterranean zones; the latter being less
719 affected by global LGM cooling.

720 At odds with these results are the model outputs of paleo-glaciers (Allen et al., 2008),
721 which provided both large amounts of precipitation (1000 to 1400 $\text{mm}\cdot\text{yr}^{-1}$) and temperature
722 anomalies from -16°C to -11°C in northern and southern Spain, respectively. Such climatic
723 patterns cannot be easily reconciled with the present knowledge of the LGM vegetation cover
724 and faunal associations (Sommer and Nadachowski, 2006; Benito Garzón et al., 2007;
725 Morales-Molino and García-Antón, 2014; Binney et al., 2017; Quinzin et al., 2017).

726 Atmosphere-ocean global climate models (GCMs) computed global mean LGM-air
727 temperatures 4°C to 7°C lower than Present, when adding feedback effects due to changes in
728 the vegetation cover and the amount of atmospheric dust (Crucifix and Hewitt, 2005; Jansen
729 et al., 2007; Roche et al., 2007; Cao et al., 2019). In southwest Europe, the air temperature
730 anomaly was estimated between -8°C and -4°C based on a multi-model regression of proxy
731 data and PMIP2 model output (Annan and Hargreaves, 2013). Mean annual air temperatures

732 anomalies were also estimated in the range -10°C to -5°C for ice-free areas of Europe, based
733 on a regional climate model (Strandberg et al., 2011). Jost et al. (2005) emphasized the need
734 of high-resolution spatial climate models to solve discrepancies with reconstructions based on
735 proxies such as pollen assemblages. Models tend to underestimate the magnitude of cooling
736 (especially in winter) with the consequence of overestimating the amount of precipitation.
737 When applied to Europe, most simulated climates, such as the those of the *Paleoclimate*
738 *Modelling Intercomparison Project* (PMIP) or from refined General Climate Model (GCM),
739 generate warmer and wetter LGM-conditions than those inferred from palynological or
740 geochemical proxies (Kageyama et al., 2001; Latombe et al. 2018; present study). Latombe et
741 al. (2018) study indicates temperatures and precipitation were close to $5\text{-}6^{\circ}\text{C}$ and $200\text{-}250$
742 mm y^{-1} in northern Spain, close to 7°C and 160 mm y^{-1} at Laugerie-Haute, and close to 11°C
743 and 225 mm y^{-1} at Nerja, in southern Spain. Within uncertainties, such air temperatures are
744 coherent with those estimated from our isotopic proxy approach even though Latombe et al.
745 (2018) obtained slightly lower temperatures for Nerja. Our MAP estimates are generally
746 slightly higher than those modeled by Latombe et al. (2018), especially in the case of northern
747 Spain.

748 Spatial resolution is critical in areas either close to the ocean (e.g., Atlantic Ocean) or
749 along a mountain range (e.g., Pyrenees). Kageyama et al. (2006) performed a comparison of
750 PMIP models, SSTs from MARGO (*Multiproxy Approach for the Reconstruction of the*
751 *Glacial Ocean surface*) and pollen-based reconstructions over Europe. These authors
752 highlighted the main data-model discrepancy observed for western Europe, with winter
753 temperatures underestimated by all models that could be at least partly explained by a high
754 interannual variability in the temperatures of the coldest months. However, more recent high-
755 resolution climatic simulations tend to reduce the discrepancy vs geochemical proxy-derived
756 temperature estimates. This is for example the case of the central part of Iberia ($\sim 21 \text{ ka}$) with

757 a computed MAAT close to $7\pm 3^{\circ}\text{C}$ (Burke et al., 2014) that are comparable or only slightly
758 higher than those inferred from the oxygen isotope composition of large mammals (Yravedra
759 et al., 2016).

760 The geochemical data presented in our study do not provide a temporal resolution at
761 the seasonal scale, but large inter-annual variations in winter air temperatures should be
762 imprinted on the half-year or full year time record provided by mammal tooth enamel. For the
763 studied archaeological sites located on the Atlantic side, the range of $\delta^{18}\text{O}_{\text{w-MAP}}$ is 4‰ (Figure
764 6), which corresponds to a temperature variation of $\pm 5.5^{\circ}\text{C}$ around the mean, according to
765 equation (7). If interpreted as inter-decadal or inter-centennial variations in MAAT, such a
766 magnitude is higher than that observed ($2\pm 1^{\circ}\text{C}$) during periods of relative climate steadiness
767 (e.g., Corona et al., 2010; Ljungqvist et al., 2019). Whether this temperature variation of
768 $\pm 5.5^{\circ}\text{C}$ indicates high-frequency climate instabilities in western Europe during the LGM, in
769 agreement with Jones et al. (2020)'s or Loncaric et al. (1998), remains to be further
770 investigated.

771 Climate conditions on the Iberian Peninsula are driven by large-scale processes that
772 create strong regional contrasts in rainfall and temperature values. Our results demonstrate
773 that these contrasts are reliably recorded in hard tissues and that isotope analyses of vertebrate
774 remains can be used as proxies of mean annual temperature and precipitations on a regional
775 scale. We confirm that, during the LGM, populations living in Franco-Cantabria and on the
776 Mediterranean coast faced different environmental challenges. As the paleontological and
777 archaeozoological records demonstrate it (Brugal and Yravedra, 2005) this difference
778 impacted the relative availability of different prey species, which would have required
779 adjustments of human hunting strategies, potentially driving technological change. Indeed, the
780 LGM coincides with the appearance of the Solutrean technocomplex, which is geographically
781 limited to the Iberian Peninsula and France. Three Solutrean “culture areas” (Andalucia,

782 Portugal and Vasco-Cantabria) are described for the Iberian Peninsula (Straus, 2000) and
783 these differences in the material culture used by human groups could reflect regional
784 adaptations to contrasting environmental conditions such as those described here. These
785 results are also consistent with archaeological research using an agent-based model that
786 suggests that the population of Western Europe was spatially fragmented during the LGM as
787 a result of climate-driven differences in habitat suitability (Wren and Burke, 2018). In this
788 latter study, the SE region of the Iberian Peninsula was described as a “sink” during the LGM,
789 with human population numbers declining periodically and being replenished from a larger
790 “source” population, located in SE France and NE Spain.

791 Considering the uncertainties associated with our stable isotope proxy approach,
792 including the altitudinal effect that is not easy to constrain, the present MAAT estimates are
793 coherent with those inferred from other proxies (pollens, foraminifera) and some recent model
794 outputs. In the case of MAP reconstructions, the isotopic approach suggests dry environments
795 in agreement with our knowledge of LGM-flora and faunal associations. However, most
796 modeling approaches still generate divergent patterns with some of them suggesting
797 paleoenvironments as wet as those of today, or even more, along with similar MAAT.

798 Future research priorities may focus on the initial conditions required by the GCM
799 models to reproduce the dry and cold conditions of the LGM in southwestern Europe. In
800 addition, reconstructing the amplitude of precipitation and air temperature seasonality by
801 high-resolution incremental sampling of tooth enamel may be of great interest. Indeed,
802 mammals could have fed on resources (water, vegetation) mainly renewed during the winter
803 and intermediate seasons, not in summer, hence biasing the isotopic record at least toward too
804 negative mean air temperatures.

805

806 6. Conclusions

807 Our study documents the carbon and oxygen isotope composition of tooth enamel
808 carbonate of Cervidae, Equidae and Caprinae remains dated to the LGM in southwest Europe.
809 The $\delta^{13}\text{C}$ of tooth enamel carbonate was ultimately used to obtain semi-quantitative estimates
810 of MAP. Precipitation in the range of ~ 250 to 550 mm.yr^{-1} were obtained for Atlantic sites
811 and values close to 250 mm.yr^{-1} for the Mediterranean sites; both estimates are lower than
812 local precipitation today ($200\text{--}1000 \text{ mm.yr}^{-1}$). Despite the large uncertainties associated with
813 each step of the method, the reconstruction of a dry and cold LGM environment is consistent
814 with the faunal and floral associations documented for this period. The limitation of the $\delta^{13}\text{C}$
815 method for estimating paleo-precipitation is mainly related to the behavior of the studied
816 vertebrate species. The observed $\delta^{13}\text{C}$ differences between Caprinae and Cervidae or Equidae,
817 for example, most likely reflects habitat use, with Caprinae occupying possibly drier habitats.

818 The $\delta^{18}\text{O}$ of tooth enamel carbonate was used for estimating MAAT. In southern Spain,
819 temperatures during the LGM were lower by about $4\text{--}5^\circ\text{C}$ relative to modern times and lower
820 by $5\text{--}8^\circ\text{C}$ in northern Spain and southwest France. Several steps are necessary to calculate
821 MAAT, and each one potentially propagates sizable uncertainties due to the combined use of
822 empirical linear equations relating the isotopic compositions of the biomineral, the meteoric
823 water and the air temperature. Moreover, we identified additional sources of uncertainties.
824 The first two are related to an “altitude effect” and a “source effect” that lead to an
825 overestimate of the air temperature differences between the LGM and the present day on the
826 order of a few $^\circ\text{C}$. The third one, which we refer to as the “reservoir effect”, relates to the ^{18}O -
827 enrichment of meteoric waters stored in a natural reservoir (pond, lake, snow cover) open to
828 the atmosphere and subsequently exposed to evaporation. In this case, the lower the residence
829 time of water in the reservoir, the higher the increase in the $\delta^{18}\text{O}$ of stored water, hence
830 leading to a potential overestimation of air temperatures.

831 At first glance, our estimates of MAP and MAAT are compatible with the faunal
832 associations described in the archaeological sites of southwestern Europe with generally cold
833 and dry, open environments such as tundra and dry steppe. Sea surface temperatures inferred
834 from the oxygen isotope composition of planktonic foraminifera enforce the hypothesis of
835 cold regional conditions as well as a marked difference between the Atlantic and
836 Mediterranean sides; the latter being less impacted by the global cooling.

837 Close to montane areas, topography is highly variable with a juxtaposition of micro-
838 climates that makes a comparison of geochemical proxy results with model outputs risky and
839 potentially fruitless, considering the unresolved differences in temporal and spatial resolution
840 inherent in both scientific approaches. Nevertheless, there is room for improvement with, for
841 example, the reconstitution of the seasonal amplitude of precipitation and air temperature
842 performed by high-resolution incremental sampling of vertebrate tooth enamel. Precipitation
843 and air temperature for the coldest and warmest months could be directly compared to model
844 output with the aim to identify potential biases intrinsic to each method.

845

846 **Acknowledgements** – We are grateful to A. Álvarez-Fernández and J. Bécares (Universidad
847 de Salamanca), E. Aura Tortosa and E. Muñoz Fernández (Colectivo para la Ampliación de
848 Estudios de Arqueología Prehistórica), C. Cacho (Museo Arqueológico Nacional), A.
849 Chauvin and R. Ontañón (Museo de Prehistoria y Arqueología de Cantabria), J-J. Cleyet-
850 Merle and S. Madeleine (Musée national de Préhistoire), M. Pérez Ripoll (Universitat de
851 València) and J. Yravedra (Complutense University) for their great and kind help during the
852 first stages of this study, as well as for providing access to samples and allowing us to work in
853 their different laboratories. We warmly thank J. Lepage for her help in the data collection,
854 who was awarded an MEESR mobility grant. This study was possible thanks to an Early
855 Career Research grant to MAJ. This research was supported by the Fonds de Recherche du

856 Québec Société et Culture, grant #SE-179537 (to AB). A NSERC-Canada Discovery Grant to
857 chm and an infrastructure award from the Fonds de Recherche du Québec en Sciences
858 Naturelles et Technologie to Geotop supported the analytical work. Three anonymous
859 reviewers are thanked for their comments and suggestions that helped to improve our
860 interpretations.

861

862

864 **References**

865

866 Allen, R., Siegert, M. J., Payne, A. J., 2008. Reconstructing glacier-based climates of LGM
867 Europe and Russia–Part 2: A dataset of LGM precipitation/temperature relations derived
868 from degree-day modelling of palaeo glaciers. *Climate of the Past*, 4(4), 249–263.

869 Álvarez-Fernández, E., Álvarez-Alonso, D., Bécáres, J., Carral, P., Carriol, R.-P., Chauvin,
870 A., Cubas, M., Cueto, M., Domingo, R., Douka, K., Emorza, M., Jordá-Pardo, J.F.,
871 Murelaga, X., Portero, R., Rivero, O., Tapia, J., Tarrío, A., Teira, L.C., 2016. Nouvelles
872 données sur le Magdalénien inférieur de la Région Cantabrique: le Niveau F de la grotte de
873 El Cierro (Ribadesella, Asturias, Espagne). *L'Anthropologie* 120, 537–567.

874 Álvarez-Lao, D. J., and García, N., 2011a. Southern dispersal and Palaeoecological
875 implications of woolly rhinoceros (*Coelodonta antiquitatis*): review of the Iberian
876 occurrences. *Quaternary Science Reviews* 30, 2002–2017.

877 Álvarez-Lao, D. J., and García, N., 2011b. Geographical distribution of Pleistocene cold-
878 adapted large mammal faunas in the Iberian Peninsula. *Quaternary International* 233, 159–
879 170.

880 Ambrose, S. H., and Norr, L., 1993. Experimental evidence for the relationship of the carbon
881 isotope ratios of whole diet and dietary protein to those of bone collagen and carbonate.
882 In *Prehistoric human bone* (pp. 1–37). Springer, Berlin, Heidelberg.

883 Annan, J. D., and Hargreaves, J. C., 2013. A new global reconstruction of temperature
884 changes at the Last Glacial Maximum. *Climate of the Past* 9, 367–376.

885 Araguas-Araguas, L. J., Diaz Teijeiro, M. F., 2005. Isotope composition of precipitation and
886 water vapour in the Iberian Peninsula: first results of the Spanish network of isotopes in
887 precipitation. *International Atomic Energy Agency Technical Report* 1453, 173–190.

888 Arpe, K., Leroy, S.A.G., Mikolajewicz, K., 2011. A comparison of climate simulations for the
889 last glacial maximum with three different versions of the ECHAM model and implications
890 for summer-green tree refugia. *Climate of the Past* 7, 91–114. doi:10.5194/cp-7-91-2011

891 Arsuaga, J. L., Villaverde, V., Quam, R., Gracia, A., Lorenzo, C., Martínez, I., Carretero, J.
892 M., 2002. The Gravettian occipital bone from the site of Malladetes (Barx, Valencia,
893 Spain). *Journal of Human Evolution*, 43, 381–393.

894 Auerswald, K., Wittmer, M.H.O.M., Männel, T.T., Bai, Y.F., Schäufele, R., Schnyder, H.,
895 2009. Large regional-scale variation in C3/C4 distribution pattern of Inner Mongolia
896 steppe is revealed by grazer wool carbon isotope composition. *Biogeosciences* 6, 795–805.

897 Aura Tortosa, E.J., Jordá Pardo, J.F. and Fortea Perez, F.J., 2006. Cueva de Nerja (Málaga,
898 Espana) y los inicios del solutrense en Andalucía. *Zephyrus* 59, 67–88.

899 Ayliffe, L. K., and Chivas, A. R., 1990. Oxygen isotope composition of the bone phosphate of
900 Australian kangaroos: potential as a palaeoenvironmental recorder. *Geochimica et*
901 *Cosmochimica Acta* 54, 2603–2609.

902 Ayliffe, L. K., Lister, A. M., Chivas, A. R., 1992. The preservation of glacial-interglacial
903 climatic signatures in the oxygen isotopes of elephant skeletal
904 phosphate. *Palaeogeography, Palaeoclimatology, Palaeoecology* 99, 179–191.

905 Balasse, M., and Ambrose, S. H., 2005. Distinguishing sheep and goats using dental
906 morphology and stable carbon isotopes in C4 grassland environments. *Journal of*
907 *Archaeological Science* 32, 691–702.

908 Balasse, M., Bocherens, H., Mariotti, A., 1999. Intra-bone variability of collagen and apatite
909 isotopic composition used as evidence of a change of diet. *Journal of Archaeological*
910 *Science* 26, 593–598.

911 Barquín, R.M., 2014. La secuencia estratigráfica de la Cueva de El Pendo:(Escobedo de
912 Camargo, Cantabria). in Los cazadores recolectores del Pleistoceno y del Holoceno en
913 Iberia y el estrecho de Gibraltar: estado actual del conocimiento del registro arqueológico.
914 Universidad de Burgos.

915 Beghin, P., S. Charbit, S., M. Kageyama, M., Combourieu-Nebout, N., Hatté, C., C. Dumas,
916 C., Peterschmitt, J.-Y., 2016. What drives LGM precipitation over the western
917 Mediterranean? A study focused on the Iberian Peninsula and northern Morocco. *Climate*
918 *Dynamics* 46, 2611–2631. DOI 10.1007/s00382-015-2720-0

919 Bekenov, A. B., Grachev, I. A., Milner-Gulland, E. J., 1998. The ecology and management of
920 the saiga antelope in Kazakhstan. *Mammal Review* 28, 1–52.

921 Belmaker, M., Hovers, E., 2011. Ecological change and the extinction of the Levantine
922 Neanderthals: implications from a diachronic study of micromammals from Amud Cave,
923 Israel. *Quaternary Science Reviews* 30, 3196–3209.

924 Ben-David, M., Shochat, E., Adams, L. G., 2001. Utility of stable isotope analysis in studying
925 foraging ecology of herbivores: examples from moose and caribou. *Alces* 37, 421–435.

926 Benetti, M., Reverdin, G., Aloisi, G., Sveinbjörnsdóttir, Á., 2017. Stable isotopes in surface
927 waters of the Atlantic Ocean: Indicators of ocean-atmosphere water fluxes and oceanic
928 mixing processes. *Journal of Geophysical Research: Oceans* 122, 4723–4742.

929 Benito Garzón, M., Sánchez de Dios, R., Sáinz Ollero, H., 2007. Predictive modelling of tree
930 species distributions on the Iberian Peninsula during the Last Glacial Maximum and Mid-
931 Holocene. *Ecography* 30, 120–134.

932 Berger, J., 1986. *Wild horses of the Great Basin: Social Competition and Population Size.*
933 Chicago, University of Chicago Press.

934 Bernard, A., Daux, V., Lécuyer, C., Brugal, J. P., Genty, D., Wainer, K., Gardien, V., Fourel,
935 F., Jaubert, J., 2009. Pleistocene seasonal temperature variations recorded in the $\delta^{18}\text{O}$ of
936 *Bison priscus* teeth. *Earth and Planetary Science Letters* 283, 133–143.

937 Binney, H., Edwards, M., Macias-Fauria, M., Lozhkin, A., Anderson, P., Kaplan, J. O.,
938 Andreev, A., Bezrukova, E., Blyakharchuk, T., Jankovska, V., Khazina, I., Krivonogov,
939 S., Kremenetski, K., Nield, J., Novenko, E., Ryabogina, N., Solovieva, N., Willis, K.,
940 Zernitskaya, V., 2017. Vegetation of Eurasia from the last glacial maximum to present:
941 Key biogeographic patterns. *Quaternary Science Reviews* 157, 80–97.

942 Blumenthal, S.A., Levin, N.E., Brown, F.H., Brugal, J.-P., Chritz, K.L., Harris, J.M., Jehle,
943 G.E., Cerling, T.E., 2017. Aridity and hominin environments. *Proc. Natl. Acad. Sci.* 114,
944 7331–7336.

945 Blunier, T., and Brook, E. J., 2001. Timing of millennial-scale climate change in Antarctica
946 and Greenland during the last glacial period. *Science* 291, 109–112.

947 Bocherens, H., Koch, P. L., Mariotti, A., Geraads, D., Jaeger, J. J., 1996. Isotopic
948 biogeochemistry (^{13}C , ^{18}O) of mammalian enamel from African Pleistocene hominid
949 sites. *Palaios* 11, 306–318.

950 Bond, G., Heinrich, H., Broecker, W., Labeyrie, L., McManus, J., Andrews, J., Huon, S.,
951 Jantschik, R., Clasen, S., Simet, C., Tedesco, K., Klas, M., Bonani, G., Ivy, S., 1992.
952 Evidence for massive discharges of ice-bergs into the North Atlantic Ocean during the last
953 glacial period. *Letters to Nature* 360, 245–249.

954 Bouttes, N., Paillard, D., Roche, D. M., Brovkin, V., Bopp, L., 2011. Last Glacial Maximum
955 CO_2 and $\delta^{13}\text{C}$ successfully reconciled. *Geophysical Research Letters*, 38, L02705,
956 doi:10.1029/2010GL044499

957 Breuil, H., and Obermaier, H., 1912. *Les premiers travaux de l'Institut de Paléontologie*
958 *Humaine.* Masson et Cie.

959 Bryant, J. D., and Froelich, P. N., 1995. A model of oxygen isotope fractionation in body
960 water of large mammals. *Geochimica et Cosmochimica Acta* 59, 4523–4537.

- 961 Bryant, J. D., Koch, P. L., Froelich, P. N., Showers, W. J., Genna, B. J., 1996. Oxygen
 962 isotope partitioning between phosphate and carbonate in mammalian apatite. *Geochimica*
 963 *et Cosmochimica Acta* 60, 5145–5148.
- 964 Bryant, J. D., Luz, B., Froelich, P. N., 1994. Oxygen isotopic composition of fossil horse
 965 tooth phosphate as a record of continental paleoclimate. *Palaeogeography,*
 966 *Palaeoclimatology, Palaeoecology* 107, 303–316.
- 967 Bugalho, M. N., and Milne, J. A., 2003. The composition of the diet of red deer (*Cervus*
 968 *elaphus*) in a Mediterranean environment: a case of summer nutritional constraint? *Forest*
 969 *Ecology and Management* 181, 23–29.
- 970 Burke, A., Kageyama, M., Latombe, G., Fasel, M., Vrac, M., Ramstein, G., James, P. M.,
 971 2017. Risky business: The impact of climate and climate variability on human population
 972 dynamics in Western Europe during the Last Glacial Maximum. *Quaternary Science*
 973 *Reviews* 164, 217–229.
- 974 Burke, A., Levavasseur, G., James, P. M., Guiducci, D., Izquierdo, M. A., Bourgeon, L.,
 975 Kageyama, M., Ramstein, G., Vrac, M., 2014. Exploring the impact of climate variability
 976 during the Last Glacial Maximum on the pattern of human occupation of Iberia. *Journal of*
 977 *Human Evolution* 73, 35–46.
- 978 Cao, J., Wang, B., Liu, J., 2019. Attribution of the Last Glacial Maximum climate
 979 formation. *Climate Dynamics* 53, 1661–1679.
- 980 Cerling, T. E., and Harris, J. M., 1999. Carbon isotope fractionation between diet and
 981 bioapatite in ungulate mammals and implications for ecological and paleoecological
 982 studies. *Oecologia* 120, 347–363.
- 983 Charette, M. A., and Smith, W. H., 2010. The volume of Earth's ocean. *Oceanography* 23,
 984 112–114.
- 985 Chenery, C. A., Pashley, V., Lamb, A. L., Sloane, H. J., Evans, J. A., 2012. The oxygen
 986 isotope relationship between the phosphate and structural carbonate fractions of human
 987 bioapatite. *Rapid Communications in Mass Spectrometry* 26, 309–319.
- 988 Christie, A. H. C., 1967. The sensitivity of chamois and red deer to temperature fluctuations.
 989 In *Proceedings New Zealand Ecological Society* 14, 34–39.
- 990 Clark, P. U., Dyke, A. S., Shakun, J. D., Carlson, A. E., Clark, J., Wohlfarth, B., Mitrovica,
 991 J.X., Hostetler, S.W., McCabe, A. M., 2009. The last glacial maximum. *Science* 325, 710–
 992 714.
- 993 Collins, R.P. and Jones, M.B., 1986. The influence of climatic factors on the distribution of
 994 C4 species in Europe. *Vegetatio* 64, 121–129.
- 995 Coplen, T. B., Kendall, C., Hopple, J., 1983. Comparison of stable isotope reference
 996 samples. *Nature* 302, 236–238.
- 997 Cormie, A. B., Luz, B., Schwarcz, H. P., 1994. Relationship between the hydrogen and
 998 oxygen isotopes of deer bone and their use in the estimation of relative
 999 humidity. *Geochimica et Cosmochimica Acta* 58, 3439–3449.
- 1000 Corona, C., Guiot, J., Edouard, J. L., Chalié, F., Büntgen, U., Nola, P., Urbinati, C., 2010.
 1001 Millennium-long summer temperature variations in the European Alps as reconstructed
 1002 from tree rings. *Climate of the Past* 6, 379–400.
- 1003 Crucifix, M., and Hewitt, C. D., 2005. Impact of vegetation changes on the dynamics of the
 1004 atmosphere at the Last Glacial Maximum. *Climate Dynamics* 25, 447–459.
- 1005 Cuenca-Bescós, G., Melero-Rubio, M., Rofes, J., Martínez, I., Arsuaga, J.L., Blain, H.A.,
 1006 López-García, J.M., Carbonell, E., Bermúdez de Castro, J.M., 2011. The Early–Middle
 1007 Pleistocene environmental and climatic change and the human expansion in Western
 1008 Europe: A case study with small vertebrates (Gran Dolina, Atapuerca, Spain). *Journal of*
 1009 *Human Evolution* 60, 481–491.

- 1010 D'Angela, D., and Longinelli, A., 1990. Oxygen isotopes in living mammal's bone phosphate:
 1011 further results. *Chemical Geology: Isotope Geoscience section* 86, 75–82.
- 1012 Dansgaard, W., 1964. Stable isotopes in precipitation. *Tellus* 16, 436–468.
- 1013 Dansgaard, W., Johnsen, S., Clausen, H., Dahl-Jensen, D., Gundestrup, N., Hammer, C.,
 1014 Hvidberg, C., Steffensen, J., Sveinbjörnsdottir, A., Jouzel, J., Bond, G., 1993. Evidence for
 1015 general instability of past climate from a 250-ka ice-core record. *Nature* 364, 218–220.
- 1016 Daux, V., Lécuyer, C., Adam, F., Martineau, F., Vimeux, F., 2005. Oxygen isotope
 1017 composition of human teeth and the record of climate changes in France (Lorraine) during
 1018 the last 1700 years. *Climatic Change* 70, 445–464.
- 1019 De la Peña Alonso, P., 2013. Estudio estratigráfico y tecnotipológico de los niveles basales de
 1020 la cueva de Les Mallaetes (Barx, Valencia): nuevas claves para el Paleolítico superior
 1021 inicial mediterráneo. *Zephyrus* 71, 61–88.
- 1022 De los Terreros, J.Y.S. and Castanedo, A.G., 2010. Las estrategias de subsistencia en la
 1023 región central de la cornisa cantábrica ¿Continuidad o ruptura? Nivel cero: revista del
 1024 grupo arqueológico. *Attica* 12, 35–51.
- 1025 Delgado-Huertas, A., Iacumin, P., Stenni, B., Chillón, B. S., Longinelli, A., 1995). Oxygen
 1026 isotope variations of phosphate in mammalian bone and tooth enamel. *Geochimica et*
 1027 *Cosmochimica Acta* 59, 4299–4305.
- 1028 Delpech, F., 2012. Biostratigraphie des niveaux solutréens de Laugerie-Haute (Les Eyzies,
 1029 Dordogne, France). Implications archéologiques. *PALEO. Revue d'archéologie*
 1030 *préhistorique* 23, 105–116.
- 1031 Discamps, E., Jaubert, J., Bachellerie, F., 2011. Human choices and environmental
 1032 constraints: deciphering the variability of large game procurement from Mousterian to
 1033 Aurignacian times (MIS 5-3) in southwestern France. *Quaternary Science Reviews* 30,
 1034 2755–2775.
- 1035 Duplessy, J. C., Labeyrie, L., Waelbroeck, C., 2002. Constraints on the ocean oxygen isotopic
 1036 enrichment between the Last Glacial Maximum and the Holocene: Paleooceanographic
 1037 implications. *Quaternary Science Reviews* 21, 315–330.
- 1038 Ehleringer, J.R., 2005. On the influence of atmospheric CO₂, temperature, and water on the
 1039 abundances of C3/C4 taxa. In J.R. Ehleringer, T.E. Cerling, and M.D. Dearing (eds.), *A*
 1040 *history of atmospheric CO₂ and its effect on plants, animals, and ecosystems*. Springer
 1041 Verlag, New York.
- 1042 Ehleringer, J.R., 2005. On the influence of atmospheric CO₂, temperature, and water on the
 1043 abundances of C3/C4 taxa. In J.R. Ehleringer, T.E. Cerling, and M.D. Dearing (eds.), *A*
 1044 *history of atmospheric CO₂ and its effect on plants, animals, and ecosystems*. Springer
 1045 Verlag, New York
- 1046 Elenka, H., Peyron, O., Bonnefille, R., Jolly, D., Cheddadi, R., Guiot, J., Andrieu, V.,
 1047 Bottema, S., Buchet, G., de Beaulieu, J.-L., Hamilton, A.C., Maley, J., Marchant, R.,
 1048 Perez-Obiol, R., Reille, M., Riollet, G., Scott, L., Straka, H., Taylor, D., Van Campo, E.,
 1049 Vincens, A., Laarif, F. Johnson, H., 2000. Pollen-based biome reconstruction for southern
 1050 Europe and Africa 18,000 yr BP. *Journal of Biogeography* 27, 621–634.
- 1051 Fabre, M., Lécuyer, C., Brugal, J.-P., Amiot, R., Fourel, F., Martineau, F., 2011. Late
 1052 Pleistocene climatic change in the French Jura (Gigny) recorded in the δ¹⁸O of phosphate
 1053 from ungulate tooth enamel. *Quaternary Research* 75, 605–613.
- 1054 Farquhar, G. D., O'Leary, M. H., Berry, J. A., 1982. On the relationship between carbon
 1055 isotope discrimination and the intercellular carbon dioxide concentration in
 1056 leaves. *Functional Plant Biology* 9, 121–137.
- 1057 Ferguson, J. E., Henderson, G. M., Fa, D. A., Finlayson, J. C., Charnley, N. R., 2011.
 1058 Increased seasonality in the Western Mediterranean during the last glacial from limpet
 1059 shell geochemistry. *Earth and Planetary Science Letters* 308, 325–333.

- 1060 Fortea Perez, J. and Jorda Cerda, F., 1976. La Cueva de Les Mallaetes y los Problemas del
1061 Paleolítico Superior del Mediterráneo Español. *Zephyrus* XXVI-XXVII, 129–166.
- 1062 Fricke, H. C., Clyde, W. C., O’Neil, J. R., 1998. Intra-tooth variations in $\delta^{18}\text{O}$ (PO_4) of
1063 mammalian tooth enamel as a record of seasonal variations in continental climate
1064 variables. *Geochimica et Cosmochimica Acta* 62, 1839–1850.
- 1065 Fricke, H.C., O’Neil, J.R., 1999. The correlation between $^{18}\text{O}/^{16}\text{O}$ ratios of meteoric water and
1066 surface temperature: its use in investigating terrestrial climate change over geologic time.
1067 *Earth and Planetary Science Letters* 170, 181–196.
- 1068 Fu, Q. et al., 2016. The genetic history of ice age Europe. *Nature* 534, 200–205.
- 1069 Fumanal, M. and Dupré, M., 1983. Schéma paléoclimatique et chrono-stratigraphique d'une
1070 séquence du Paléolithique supérieur de la région de Valence (Espagne). *Quaternaire* 20,
1071 39–46.
- 1072 Gat, J.R., Mook, W.G. and Meijer, H.A.J., 2001. Observed isotope effects in precipitations. In
1073 *Environmental Isotopes in the Hydrological cycle*, G. Mook., ed., IHP-V ITechnical
1074 Documents in Hydrology I No. 39, Vol. II UNESCO, Paris.
- 1075 Gerhart, L.M. and Ward, J.K., 2010. Plant responses to low $[\text{CO}_2]$ of the past. *New*
1076 *Phytologist* 188, 674–695.
- 1077 Goedert, J., Lécuyer, C., Amiot, R., Arnaud-Godet, F., Wang, X., Cui, L., Cuny, G., Douay,
1078 G., Fourel, F., Panczer, G., Simon, L., Steyer, J.-S., Zhu, M., 2018. Euryhaline ecology of
1079 early tetrapods revealed by stable isotopes. *Nature* 558, 68–72.
- 1080 Grafenstein von, U., Erlenkeuser, H., Müller, J., Trimborn, P., Alefs, J., 1996. A 200-year
1081 mid-European air temperature record preserved in lake sediments: An extension of the
1082 $\delta^{18}\text{O}$ -air temperature relation into the past. *Geochimica et Cosmochimica Acta* 60, 4025–
1083 4036.
- 1084 Grootes, P.M., Stuiver, M., White, J.W.C., Johnsen, S., Jouzel, J., 1993. Comparison of
1085 oxygen isotope records from the GISP2 and GRIP Greenland ice cores. *Nature* 366, 552–
1086 554.
- 1087 Hammer, Ø., Harper, D.A.T., and P. D. Ryan, 2001. PAST: Paleontological Statistics
1088 Software Package for Education and Data Analysis. *Palaeontologia Electronica* 4(1), 9 spp.
- 1089 Hare, V. J., Loftus, E., Jeffrey, A., Ramsey, C. B., 2018. Atmospheric CO_2 effect on stable
1090 carbon isotope composition of terrestrial fossil archives. *Nature communications* 9, 1–8.
- 1091 Hatté, C., and Guiot, J., 2005. Palaeoprecipitation reconstruction by inverse modelling using
1092 the isotopic signal of loess organic matter: application to the Nußloch loess sequence
1093 (Rhine Valley, Germany). *Climate Dynamics* 25, 315. <https://doi.org/10.1007/s00382-005-0034-3>
- 1094
- 1095 Hatté, C., Gauthier, C., Rousseau, D. D., Antoine, P., Fuchs, M., Lacroix, F., Markovic, S.B.,
1096 Moine, O., Sima, A., 2013. Excursions to C-4 vegetation recorded in the Upper Pleistocene
1097 loess of Surduk (Northern Serbia): an organic isotope geochemistry study. *Climate of the*
1098 *Past* 9, 1001–1014.
- 1099 Hayes, A., Kucera, M., Kallel, N., Saffi, L., Rohling, E. J., 2005. Glacial Mediterranean sea
1100 surface temperatures based on planktonic foraminiferal assemblages. *Quaternary Science*
1101 *Reviews* 24, 999–1016.
- 1102 Heinrich, H., 1988. Origin and consequences of cyclic ice rafting in the Northeast Atlantic
1103 ocean during the past 130,000 years. *Quaternary Research* 29, 142–152.
- 1104 Hernández Fernández, M., Álvarez Sierra, M.Á., Peláez-Campomanes, P., 2007. Bioclimatic
1105 analysis of rodent palaeofaunas reveals severe climatic changes in Southwestern Europe
1106 during the Plio-Pleistocene. *Palaeogeography, Palaeoclimatology, Palaeoecology* 251,
1107 500–526.
- 1108 Hillaire-Marcel, C., Causse, C., 1989. The late Pleistocene Laurentide glacier: ThU dating of
1109 its major fluctuations and $\delta^{18}\text{O}$ range of the ice. *Quaternary Research* 32, 125–138.

- 1110 Hoyos Gómez, M., and Laville, H., 1982. Nuevas aportaciones sobre la estratigrafía y
 1111 sedimentología de los depósitos del Paleolítico Superior de la Cueva de El Pendo
 1112 (Santander): sus implicaciones. *Zephyrus* 34–35.
- 1113 Hughes, P. D., 2018. Little Ice Age glaciers and climate in the Mediterranean mountains: a
 1114 new analysis. *Cuadernos de investigación geográfica/Geographical Research Letters* 44,
 1115 15–45.
- 1116 Iacumin, P., Bocherens, H., Mariotti, A., Longinelli, A., 1996. Oxygen isotope analyses of co-
 1117 existing carbonate and phosphate in biogenic apatite: a way to monitor diagenetic
 1118 alteration of bone phosphate? *Earth and Planetary Science Letters* 142, 1–6.
- 1119 Iacumin, P., Longinelli, A., 2002. Relationship between $\delta^{18}\text{O}$ values for skeletal apatite from
 1120 reindeer and foxes and yearly mean $\delta^{18}\text{O}$ values of environmental water. *Earth and*
 1121 *Planetary Science Letters* 201, 213–219.
- 1122 Ihl, C., and Klein, D. R., 2001. Habitat and diet selection by muskoxen and reindeer in
 1123 western Alaska. *The Journal of Wildlife Management* 65, 964–972.
- 1124 Jansen, E., Overpeck, J., Briffa, K. R., Duplessy, J. C., Joos, F., Masson-Delmotte, V., and
 1125 others (2007). Paleoclimate. *Climate change 2007: the physical science basis; contribution*
 1126 *of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on*
 1127 *Climate Change*.
- 1128 Jones, J.R., Marín-Arroyo, A.B., Straus, L.G., Richards, M.P., 2020. Adaptability, resilience
 1129 and environmental buffering in European Refugia during the Late Pleistocene: Insights
 1130 from La Riera Cave (Asturias, Cantabria, Spain). *Scientific Reports* 10, 1217.
 1131 doi.org/10.1038/s41598-020-57715-2
- 1132 Jordá Pardo, J.F. and J.E. Aura Tortosa, 2008. 70 fechas para una cueva. revisión crítica de 70
 1133 dataciones c^{14} del Pleistoceno superior y Holoceno de la cueva de Nerja (Málaga,
 1134 Andalucía, España). *Espacio, Tiempo y Forma. Serie I, Nueva época. Prehistoria y*
 1135 *Arqueología* 1, 239–255.
- 1136 Jost, A., Lunt, D., Kageyama, M., Abe-Ouchi, A., Peyron, O., Valdes, P. J., Ramstein, G.,
 1137 2005. High-resolution simulations of the last glacial maximum climate over Europe: a
 1138 solution to discrepancies with continental palaeoclimatic reconstructions? *Climate*
 1139 *Dynamics* 24, 577–590.
- 1140 Kageyama, M., Laîné, A., Abe-Ouchi, A., Braconnot, P., Cortijo, E., Crucifix, M., de Vernal,
 1141 A., Guiot, J., Hewitt, C.D., Kitoh, A., Kucera, M., Marti, O., Ohgaito, R., Otto-Bliesner B.,
 1142 Peltier, W.R., Rosell-Melé, A., Vettoretti, G., Weber, S.L., Yu, Y., MARGO Project
 1143 members, 2006. Last Glacial Maximum temperatures over the North Atlantic, Europe and
 1144 western Siberia: a comparison between PMIP models, MARGO sea–surface temperatures
 1145 and pollen-based reconstructions. *Quaternary Science Reviews* 25, 2082–2102.
- 1146 Kageyama, M., Peyron, O., Pinot, S., Tarasov, P., Guiot, J., Jousaume, S., Ramstein, G.,
 1147 2001. The Last Glacial Maximum climate over Europe and western Siberia: a PMIP
 1148 comparison between models and data. *Climate Dynamics* 17, 23–43.
- 1149 Koch, P. L., Fisher, D. C., Dettman, D., 1989. Oxygen isotope variation in the tusks of extinct
 1150 proboscideans: a measure of season of death and seasonality. *Geology* 17, 515–519.
- 1151 Kohn, M. J. 2010. Carbon isotope compositions of terrestrial C_3 plants as indicators of
 1152 (paleo) ecology and (paleo) climate. *Proceedings of the National Academy of*
 1153 *Sciences* 107, 19691–19695.
- 1154 Kohn, M. J., 1996. Predicting animal $\delta^{18}\text{O}$: accounting for diet and physiological
 1155 adaptation. *Geochimica et Cosmochimica Acta*, 60(23), 4811–4829.
- 1156 Kolodny, Y., Luz, B., Sander, M., Clemens, W. A., 1996. Dinosaur bones: fossils or
 1157 pseudomorphs? The pitfalls of physiology reconstruction from apatitic
 1158 fossils. *Palaeogeography, Palaeoclimatology, Palaeoecology* 126, 161–171.

- 1159 Kucera, M., Weinelt, M., Kiefer, T., Pflaumann, U., Hayes, A., Weinelt, M., Chen, M.-T.,
 1160 Mix, A.C., Barrows, T.T., Cortijo, E., Duprat, J., Juggins, S., Waelbroeck, C., 2005.
 1161 Reconstruction of the glacial Atlantic and Pacific sea-surface temperatures from
 1162 assemblages of planktonic foraminifera: multi-technique approach based on geographically
 1163 constrained calibration datasets. *Quaternary Science Reviews* 24, 951-998.
- 1164 Kuhlemann, J., Rohling, E. J., Krumrei, I., Kubik, P., Ivy-Ochs, S., Kucera, M., 2008.
 1165 Regional synthesis of Mediterranean atmospheric circulation during the Last Glacial
 1166 Maximum. *Science*, 321, 1338–1340.
- 1167 La Morgia, V., and Bassano, B., 2009. Feeding habits, forage selection, and diet overlap in
 1168 Alpine chamois (*Rupicapra rupicapra* L.) and domestic sheep. *Ecological Research* 24,
 1169 1043–1050.
- 1170 Lambeck, K., Rouby, H., Purcell, A., Sun, Y., Sambridge, M., 2014. Sea level and global ice
 1171 volumes from the Last Glacial Maximum to the Holocene. *Proceedings of the National
 1172 Academy of Sciences* 111, 15296–15303.
- 1173 Langlois, C., Simon, L., Lécuyer, C. H. (2003). Box-modeling of bone and tooth phosphate
 1174 oxygen isotope compositions as a function of environmental and physiological
 1175 parameters. *Isotopes in Environmental and Health Studies* 39, 259–272.
- 1176 Latombe, G., Burke, A., Vrac, M., Levavasseur, G., Dumas, C., Kageyama, M., Ramstein, G.,
 1177 2018. Comparison of spatial downscaling methods of general circulation model results to
 1178 study climate variability during the Last Glacial Maximum. *Geoscientific Model
 1179 Development* 11, 2563–2579.
- 1180 Lécuyer, C., 2013. *Water on Earth*. John Wiley & Sons, 266 pp.
- 1181 Lécuyer, C., Bojar, A. V., Daux, V., Legendre, S. (2020). Geographic variations in the slope
 1182 of the $\delta^2\text{H}$ – $\delta^{18}\text{O}$ meteoric water line over Europe: A record of increasing
 1183 continentality. *Geological Society, London, Special Publications*, 507. doi:10.1144/SP507-
 1184 2020-68.
- 1185 Lee, J.-E., Fung, I., DePaolo, D.J., Otto-Bliesner, B., 2008. Water isotopes during the Last
 1186 Glacial Maximum: New general circulation model calculations. *Journal of Geophysical
 1187 Research* 113, D19109, doi:10.1029/2008JD009859.
- 1188 Leng, M. J., 2006. *Isotopes in Palaeoenvironmental Research*. Dordrecht, Springer.
- 1189 Leuenberger, M., Siegenthaler, U., Langway, C., 1992. Carbon isotope composition of
 1190 atmospheric CO₂ during the last ice age from an Antarctic ice core. *Nature* 357, 488–490.
- 1191 Levin, N. E., Cerling, T. E., Passey, B. H., Harris, J. M., Ehleringer, J. R., 2006. A stable
 1192 isotope aridity index for terrestrial environments. *Proceedings of the National Academy of
 1193 Sciences* 103, 11201-11205.
- 1194 Lister, A. M., 2004. The impact of Quaternary Ice Ages on mammalian
 1195 evolution. *Philosophical Transactions of the Royal Society of London. Series B: Biological
 1196 Sciences* 359, 221–241.
- 1197 Ljungqvist, F. C., Zhang, Q., Brattström, G., Krusic, P. J., Seim, A., Li, Q., Zhang, Q.,
 1198 Moberg, A., 2019. Centennial-scale temperature change in last millennium simulations and
 1199 proxy-based reconstructions. *Journal of Climate* 32, 2441–2482.
- 1200 Loncaric, N., Auffret, G.A., Abrantes, F., Baas, J.H., Gaspar, L., Pujol, C., 1998. Late
 1201 Quaternary sedimentation patterns on the Meriadzek Terrace, Bay of Biscay (ESSCAMP
 1202 02 core: 47°N 9°W). *Marine Geology* 152, 57–73.
- 1203 Longinelli, A., 1984. Oxygen isotopes in mammal bone phosphate: a new tool for
 1204 paleohydrological and paleoclimatological research? *Geochimica et cosmochimica
 1205 Acta* 48, 385–390.
- 1206 López-García, J.M., Blain, H.A., Cuenca-Bescós, G., Ruiz-Zapata, M.B., Dorado-Valiño, M.,
 1207 Gil-García, M.J., Valdeolmillos, A., Ortega, A.I., Carretero, J.M., Arsuaga, J.L., de
 1208 Castro, J.M.B., Carbonell, E., 2010. Palaeoenvironmental and palaeoclimatic

1209 reconstruction of the latest Pleistocene of El Portalón site, Sierra de Atapuerca,
1210 northwestern Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology* 292, 453–464.

1211 Luccarini, S., Mauri, L., Ciuti, S., Lamberti, P., Apollonio, M., 2006. Red deer (*Cervus*
1212 *elaphus*) spatial use in the Italian Alps: home range patterns, seasonal migrations, and
1213 effects of snow and winter feeding. *Ethology Ecology & Evolution* 18, 127–145.
1214 doi:10.1080/08927014.2006.9522718

1215 Ludwig, P., Schaffernicht, E.J., Shao, Y., Pinto, J.G., 2016. Regional atmospheric circulation
1216 over Europe during the Last Glacial Maximum and its links to precipitation, *Journal of*
1217 *Geophysical Research Atmosphere* 121, 2130–2145. doi:10.1002/2015JD024444.

1218 Ludwig, P., Shao, Y., Kehl, M., Weniger, G. C., 2018. The Last Glacial Maximum and
1219 Heinrich event I on the Iberian Peninsula: A regional climate modelling study for
1220 understanding human settlement patterns. *Global and Planetary Change* 170, 34–47.

1221 Luz, B., and Kolodny, Y., 1985. Oxygen isotope variations in phosphate of biogenic apatites,
1222 IV. Mammal teeth and bones. *Earth and Planetary Science Letters* 75, 29–36.

1223 Luz, B., Cormie, A. B., Schwarcz, H. P., 1990. Oxygen isotope variations in phosphate of
1224 deer bones. *Geochimica et Cosmochimica Acta* 54, 1723–1728.

1225 Macdonald, D. W., 2006. *The Encyclopedia of Mammals* (3 ed.), Oxford University Press,
1226 936 pp.

1227 Máguas, C., and Brugnoli, E., 1996. Spatial variation in carbon isotope discrimination across
1228 the thalli of several lichen species. *Plant, Cell & Environment* 19, 437–446.

1229 MARGO Project members, Waelbroeck, C., Paul, A., Kucera, M., Rosell-Melé, A., Weinelt,
1230 M., Schneider, R., Mix, A., 2009. Constraints on the magnitude and patterns of ocean
1231 cooling at the Last Glacial Maximum. *Nature Geoscience* 2, 127–132.

1232 Masson-Delmotte, V., Kageyama, M., Braconnot, P., Charbit, S., Krinner, G., Ritz, C.,
1233 Guilyardi, E., Jouzel, J., Abe-Ouchi, A., Crucifix, M., Gladstone, R. M., Hewitt, C.D.,
1234 Kitoh, A., LeGrande, A.N., Marti, O., Merkel, U., Motoi, T., Ohgaito, R., Otto-Bliesner,
1235 B., Pletier, W.R., Ross, I., Valdes, P.J., Vettoretti, G., Weber, S.L., Wolk, F., Yu, Y., 2006.
1236 Past and future polar amplification of climate change: climate model intercomparisons and
1237 ice-core constraints. *Climate Dynamics* 26, 513–529.

1238 Mix, A. C., Bard, E., Schneider, R., 2001. Environmental processes of the ice age: land,
1239 oceans, glaciers (EPILOG). *Quaternary Science Reviews* 20, 627–657.

1240 Morales-Molino, C., and García-Antón, M. (2014). Vegetation and fire history since the last
1241 glacial maximum in an inland area of the western Mediterranean Basin (Northern Iberian
1242 Plateau, NW Spain). *Quaternary Research* 81, 63–77.

1243 Morgantini, L.E., and Hudson, R. J., 1989. Nutritional Significance of Wapiti (*Cervus*
1244 *Elaphus*) Migrations to Alpine Ranges in Western Alberta, Canada. *Arctic and Alpine*
1245 *Research* 21, 288–295.

1246 Nan, Y., Tian, F., Hu, H., Wang, L., Zhao, S., 2019. Stable isotope composition of river
1247 waters across the world. *Water* 11, 1760. Doi:10.3390/w11091760

1248 Navarro-Serrano, F., López-Moreno, J. I., Azorin-Molina, C., Alonso-González, E., Tomás-
1249 Burguera, M., Sanmiguel-Valladolid, A., Revuelto, J., Vicente-Serrano, S. M., 2018.
1250 Estimation of near-surface air temperature lapse rates over continental Spain and its
1251 mountain areas. *International Journal of Climatology* 38, 3233–3249.

1252 NGRIP members, 2004. High-resolution record of Northern Hemisphere climate extending
1253 into the last interglacial period. *Nature* 431, 147–151.

1254 O'Leary, M. H., 1981. Carbon isotope fractionation in plants. *Phytochemistry* 20, 553–67.

1255 Park, R., and Epstein, S., 1961. Metabolic fractionation of C¹³ & C¹² in plants. *Plant*
1256 *Physiology* 36, 133–138.

1257 Park, R., Epstein, S., 1960. Carbon isotope fractionation during photosynthesis. *Geochimica*
1258 *et Cosmochimica Acta* 21, 110–26.

1259 Paul, H. A., Bernasconi, S. M., Schmid, D. W., McKenzie, J. A., 2001. Oxygen isotopic
1260 composition of the Mediterranean Sea since the Last Glacial Maximum: constraints from
1261 pore water analyses. *Earth and Planetary Science Letters* 192, 1–14.

1262 Peacock, S., Lane, E., Restrepo, J. M., 2006. A possible sequence of events for the
1263 generalized glacial-interglacial cycle. *Global Biogeochemical Cycles*, 20, GB2010,
1264 doi:10.1029/2005GB002448.

1265 Pederzani, S. and K. Britton, K. 2019. Oxygen isotopes in bioarchaeology: Principles and
1266 applications, challenges and opportunities. *Earth-Science Reviews* 188, 77–107.

1267 Peyron, O., Guiot, J., Cheddadi, R., Tarasov, P., Reille, M., de Beaulieu, J. L., Bottema, S.,
1268 Andrieu, V., 1998. Climatic reconstruction in Europe for 18,000 yr BP from pollen
1269 data. *Quaternary Research* 49, 183–196.

1270 Prud'Homme, C., Lécuyer, C., Antoine, P., Hatté, C., Moine, O., Fourel, F., Amiot, R.,
1271 Martineau, F., Rousseau, D. D. (2018). $\delta^{13}\text{C}$ signal of earthworm calcite granules: A new
1272 proxy for palaeoprecipitation reconstructions during the Last Glacial in western
1273 Europe. *Quaternary Science Reviews* 179, 158–166.

1274 Pyankov, V.I., Ziegler, H., Akhiani, H., Deigele, C. and Lüttge, U., 2010. European plants
1275 with C4 photosynthesis: geographical and taxonomic distribution and relations to climate
1276 parameters. *Botanical Journal of the Linnean Society* 163, 283–304.

1277 Quinzin, M. C., Normand, S., Dellicour, S., Svenning, J. C., Mardulyn, P., 2017. Glacial
1278 survival of trophically linked boreal species in northern Europe. *Proceedings of the Royal
1279 Society B: Biological Sciences* 284, 20162799. doi.org/10.1098/rspb.2016.2799

1280 Rasmussen, S.O., Bigler, M., Blockley, S.P., Blunier, T., Buchardt, S.L., Clausen, H.B.,
1281 Cvijanovic, I., Dahl-Jensen, D., Johnsen, S.J., Fischer, H., et al., 2014. A stratigraphic
1282 framework for abrupt climatic changes during the Last Glacial period based on three
1283 synchronized Greenland ice-core records: refining and extending the INTIMATE event
1284 stratigraphy. *Quaternary Science Reviews* 106, 14–28.

1285 Reimer, P., Austin, W. E. N., Bard, E., Bayliss, A., Blackwell, P. G., Bronk Ramsey, C.,
1286 Butzin, M., Cheng, H., Lawrence Edwards, R., Friedrich, M., Grootes, P. M., Guilderson,
1287 T. P., Hajdas, I., Heaton, T. J., Hogg, A. G., Hughen, K. A., Kromer, B., Manning, S. W.,
1288 Muscheler, R., Palmer, J. G., Pearson, C., van der Plicht, J., Reimer, R. W., Richards,
1289 D.A., Scott, E.M., Southon, J.R., Turney, C.S.M., Wacker, L., Adolphi, F., Büntgen, U.,
1290 Capano, M., Fahrni, S., Fogtmann-Schulz, A., Friedrich, R., Köhler, P., Kudsk, S., Miyake,
1291 F., Olsen, J., Reinig, F., Sakamoto, M., Sookdeo, A., Talamo, S., 2020. The IntCal20
1292 Northern Hemisphere radiocarbon age calibration curve (0-55 cal kBP). *Radiocarbon* 62,
1293 725–757.

1294 Rey, K., Amiot, R., Lécuyer, C., Koufos, G. D., Martineau, F., Fourel, F., Kostopoulos D.S.,
1295 Merceron, G., 2013. Late Miocene climatic and environmental variations in northern
1296 Greece inferred from stable isotope compositions ($\delta^{18}\text{O}$, $\delta^{13}\text{C}$) of equid teeth
1297 apatite. *Palaeogeography, Palaeoclimatology, Palaeoecology* 388, 48–57.

1298 Roche, D. M., Dokken, T. M., Goosse, H., Renssen, H., Weber, S. L., 2007. Climate of the
1299 Last Glacial Maximum: sensitivity studies and model-data comparison with the
1300 LOVECLIM coupled model. *Climate of the Past* 3, 205–224.

1301 Rodrigo-Gámiz, M., F. Martínez-Ruiz, S.W. Rampen, S. Schouten, Sinninghe Damsté J. S.,
1302 2014. Sea surface temperature variations in the western Mediterranean Sea over the last 20
1303 kar: A dual-organic proxy (UK'37 and LDI) approach. *Paleoceanography* 29, 87–98.
1304 doi:10.1002/2013PA00246

1305 Rozanski, K., Araguas-Araguas, L., Gonfiantini, R. (1992). Relation between long-term
1306 trends of oxygen-18 isotope composition of precipitation and climate. *Science* 258, 981–
1307 985.

- 1308 Rozanski, K., Sonntag, C., Münnich, K.O., 1982. Factors controlling stable isotope
1309 composition of European precipitation. *Tellus*, 34(2), 142-150. DOI: 10.3402/
1310 tellusa.v34i2.10796.
- 1311 Sanchez Chillón, B., Alberdi, M. T., Leone, G., Bonadonna, F. P., Stenni, B., Longinelli, A.,
1312 1994. Oxygen isotopic composition of fossil equid tooth and bone phosphate: an archive of
1313 difficult interpretation. *Palaeogeography, Palaeoclimatology, Palaeoecology* 107, 317–328.
- 1314 Sánchez-Goñi, M. F., Landais, A., Fletcher, W.J., Naughton, F., Desprat, S., Duprat, J., 2008.
1315 Contrasting impacts of Dansgaard-Oeschger events over a western European latitudinal
1316 transect modulated by orbital parameters. *Quaternary Science Reviews* 27, 1136–1151.
- 1317 Schmidt, S., Andersen, V., Belviso, S., Marty, J. C., 2002. Strong seasonality in particle
1318 dynamics of north-western Mediterranean surface waters as revealed by
1319 $^{234}\text{Th}/^{238}\text{U}$. *Deep Sea Research Part I: Oceanographic Research Papers* 49, 1507–1518.
- 1320 Schmitt, J., Schneider, R., Elsig, J., Leuenberger, D., Lourantou, A., Chappellaz, J., Köhler,
1321 P., Joos, F., Stocker, T.F., Leuenberger, M., Fischer, H., 2012. Carbon isotope constraints
1322 on the deglacial CO_2 rise from ice cores. *Science* 336, 711–714.
- 1323 Schneider von Deimling, T., Ganopolski, A., Held, H., Rahmstorf, S., 2006. How cold was
1324 the last glacial maximum? *Geophysical Research Letters* 33, 14. 10.1029/2006GL026484
- 1325 Schrag, D. P., Adkins, J. F., McIntyre, K., Alexander, J. L., Hodell, D. A., Charles, C. D.,
1326 McManus, J. F., 2002. The oxygen isotopic composition of seawater during the Last
1327 Glacial Maximum. *Quaternary Science Reviews* 21, 331–342.
- 1328 Schubert, B. A., and Jahren, A. H., 2012. The effect of atmospheric CO_2 concentration on
1329 carbon isotope fractionation in C3 land plants. *Geochimica et Cosmochimica Acta* 96, 29–
1330 43.
- 1331 Sima, A., Paul, A., Schulz, M., Oerlemans, J., 2006. Modeling the oxygen-isotopic
1332 composition of the North American Ice Sheet and its effect on the isotopic composition of
1333 the ocean during the last glacial cycle. *Geophysical Research Letters*, 33(15).
1334 doi.org/10.1029/2006GL026923.
- 1335 Skrzypek, G., Wiśniewski, A., Grierson, P. F., 2011. How cold was it for Neanderthals
1336 moving to Central Europe during warm phases of the last glaciation? *Quaternary Science*
1337 *Reviews*, 30, 481–487.
- 1338 Smith, B. N., and Epstein, S., 1971. Two categories of $^{13}\text{C}/^{12}\text{C}$ ratios for higher plants. *Plant*
1339 *Physiology* 47, 380–384.
- 1340 Sommer, R. S., and Nadachowski, A., 2006. Glacial refugia of mammals in Europe: evidence
1341 from fossil records. *Mammal Review* 36, 251–265.
- 1342 Steele, J. H., Thorpe, S. A., Turekian, K. K., 2009. Elements of physical oceanography: a
1343 derivative of the encyclopedia of ocean sciences. Academic Press, 647 pp.
- 1344 Strandberg, G., Brandefelt, J., Kjellström, M. E., Smith, B., 2011. High-resolution regional
1345 simulation of last glacial maximum climate in Europe. *Tellus A: Dynamic Meteorology*
1346 *and Oceanography* 63, 107–125.
- 1347 Straus, L. G., 2018. The Pleistocene–Holocene transition in Cantabrian Spain: current
1348 reflections on culture change. *Journal of Quaternary Science* 33, 346–352.
- 1349 Straus, L. G., 1981. On the habitat and diet of *Cervus elaphus*. *Munibe* 33, 175–182.
- 1350 Straus, L. G., 2000. A quarter-century of research on the Solutrean of Vasco-Cantabria, Iberia
1351 and beyond. *Journal of Anthropological Research* 56, 39–58.
- 1352 Straus, L. G., and Morales, M. R. G., 2012. The Magdalenian settlement of the Cantabrian
1353 region (northern Spain): the view from El Mirón Cave. *Quaternary International* 272, 111–
1354 124.
- 1355 Szostek, K., 2009. Chemical signals and reconstruction of life strategies from ancient human
1356 bones and teeth-problems and perspectives. *Anthropological Review* 72, 3–30.

- 1357 Tarasov, P. E., Volkova, V. S., Webb III, T., Guiot, J., Andreev, A. A., Bezusko, L. G.,
1358 Bezusko, T.V., Bykova, G.V., Dorofeyuk, N.I., Kvavadze, E.V., Osipova, I. M., Panova,
1359 N.K., Sevastyanov, D.V., 2000. Last glacial maximum biomes reconstructed from pollen
1360 and plant macrofossil data from northern Eurasia. *Journal of Biogeography* 27, 609–620.
- 1361 Tazioli, A., Cervi, F., Doveri, M., Mussi, M., Deiana, M., Ronchetti, F., 2019. Estimating the
1362 Isotopic Altitude Gradient for Hydrogeological Studies in Mountainous Areas: Are the
1363 Low-Yield Springs Suitable? Insights from the Northern Apennines of Italy. *Water* 11,
1364 1764. doi.org/10.3390/w11091764
- 1365 Tejada-Lara, J. V., MacFadden, B. J., Bermudez, L., Rojas, G., Salas-Gismondi, R., Flynn, J.
1366 J., 2018. Body mass predicts isotope enrichment in herbivorous mammals. *Proceedings of*
1367 *the Royal Society B: Biological Sciences* 285, 20181020. doi.org/10.1098/rspb.2018.1020
- 1368 Tejero, J.M., Cacho, C., de Quirós, F.B., 2008. Arte mueble en el Auriñaciense cantábrico.
1369 Nuevas aportaciones a la contextualización del frontal grabado de la Cueva de Hornos de
1370 la Peña (San Felices de Buelna, Cantabria). *Trabajos de Prehistoria* 65, 115–123.
- 1371 Texier, J.-P., 2009. Histoire géologique de sites préhistoriques classiques du Périgord : une
1372 vision actualisée : la Micoque, la grotte Vaufréy, le Pech de l'Azé I et II, la Ferrassie, l'abri
1373 Castanet, le Flageolet, Laugerie Haute. *Collection Documents Préhistoriques* 25, Paris,
1374 Comité des travaux historiques et scientifiques.
- 1375 Thompson, I. D., Wiebe, P. A., Mallon, E., Rodgers, A. R., Fryxell, J. M., Baker, J. A., Reid,
1376 D., 2015. Factors influencing the seasonal diet selection by woodland caribou (*Rangifer*
1377 *tarandus tarandus*) in boreal forests in Ontario. *Canadian Journal of Zoology* 93, 87–98.
- 1378 Thunell, R. C., Williams, D. F., 1989. Glacial–Holocene salinity changes in the
1379 Mediterranean Sea: hydrographic and depositional effects. *Nature* 338, 493–496.
- 1380 Trueman, C., Chenery, C., Eberth, D. A., Spiro, B., 2003. Diagenetic effects on the oxygen
1381 isotope composition of bones of dinosaurs and other vertebrates recovered from terrestrial
1382 and marine sediments. *Journal of the Geological Society* 160, 895–901.
- 1383 Tütken, T., Furrer, H., Vennemann, T. W., 2007. Stable isotope compositions of mammoth
1384 teeth from Niederweningen, Switzerland: implications for the Late Pleistocene climate,
1385 environment, and diet. *Quaternary International* 164, 139–150.
- 1386 Tzedakis, P. C., Hughen, K. A., Cacho, I., Harvati, K. (2007). Placing late Neanderthals in a
1387 climatic context. *Nature* 449, 206–208.
- 1388 Vallejo, M. D. S., Cantal, J. A. R., Sánchez, M. C., 2005. La fauna de mamíferos del
1389 Solutrense en la Cueva de Nerja. *Munibe Antropologia-Arkeologia* 57, 255–263.
- 1390 Van Andel, T. H., Davies, W., Weninger, B., 2003. The human presence in Europe during the
1391 last glacial period I: human migrations and the changing climate. In: *Neanderthals and*
1392 *modern humans in the European landscape during the last glaciation*, Editors: T.H. van
1393 Andel; W. Davies, pp. 31-56.
- 1394 Verpoorte, A., Cosgrove, R., Wood, R., Petchey, F., Lenoble, A., Chadelle, J. P., Smith, C.,
1395 Kamermans, H., Roebroeks, W., 2019. Improving the chronological framework for
1396 Laugerie-Haute ouest (dordogne, France). *Journal of Archaeological Science: Reports* 23,
1397 574–582.
- 1398 Vigeant, J., Ribot, I., Hélie, J. F., 2017. Dietary habits in New France during the 17th and
1399 18th centuries: An isotopic perspective. *American Journal of Physical Anthropology* 162,
1400 462–475.
- 1401 Villaret, J. C., Bon, R., Rivet, A., 1997. Sexual segregation of habitat by the alpine ibex in the
1402 French Alps. *Journal of Mammalogy* 78, 1273–1281.
- 1403 Wand, S.J.E., Midgley, G.F., Jones, M.H., Curtis, P.S., 1999. Responses of wild C4 and C3
1404 grass (Poaceae) species to elevated atmospheric CO₂ concentration: a meta-analytic test of
1405 current theories and perceptions. *Global Change Biology* 5, 723-741.

1406 Woillez, M., Kageyama, M., Krinner, G., de Noblet-Ducoudré, N., Viovy, N., Mancip, M.,
1407 2011. Impact of CO₂ and climate on the Last Glacial Maximum vegetation: results from
1408 the ORCHIDEE/IPSL models. *Climate of the Past* 7, 557–577.

1409 Wren, C. D., and Burke, A., 2019. Habitat suitability and the genetic structure of human
1410 populations during the Last Glacial Maximum (LGM) in Western Europe. *PloS one* 14, 6.
1411 doi.org/10.1371/journal.pone.0217996

1412 Yravedra Sainz de los Terreros, J., 2010a. Estrategias de subsistencia en el yacimiento
1413 palaeolítico del Ruso (Igollo de Camargo, Cantabria, España). *Espacio, Tiempo y Forma.*
1414 Serie I, Nueva época. Prehistoria y Arqueología 3, 39–58.

1415 Yravedra Sainz de los Terreros, J., 2010b. Zooarqueología y tafonomía del yacimiento de
1416 Hornos de la Peña (San Felices de Buelna, Cantabria). *Complutum* 2, 69–86.

1417 Yravedra, J., and Brugal, J.-Ph., 2005. Essai sur la biodiversité des associations de grands
1418 mammifères à la fin du Pléistocène dans le Sud-Ouest de l'Europe. In *Homenaje a Jesús*
1419 *Altuna*, 139–162. San Sebastian: MUNIBE (Antropología-Arkeología).

1420 Yravedra, J., Julien, M. A., Alcaraz-Castano, M., Estaca-Gómez, V., Alcolea-González, J., de
1421 Balbín-Behrmann, R., Lécuyer, C., Hillaire-Marcel, C., Burke, A., 2016. Not so deserted...
1422 paleoecology and human subsistence in Central Iberia (Guadalajara, Spain) around the
1423 Last Glacial Maximum. *Quaternary Science Reviews* 140, 21–38.

1424 Yurtsever, Y., 1975. Worldwide survey of stable isotopes in precipitation. Report Isotope
1425 Hydrology Section. Vienna: International Atomic Energy Agency, 40.

1426 Zazzo, A., Lécuyer, C., Mariotti, A., 2004. Experimentally-controlled carbon and oxygen
1427 isotope exchange between bioapatites and water under inorganic and microbially-mediated
1428 conditions. *Geochimica et Cosmochimica Acta* 68, 1–12.

1429
1430

1431
1432
1433
1434
1435
1436
1437
1438
1439
1440
1441
1442
1443
1444
1445
1446
1447
1448

Table captions:

Table 1: Carbon and oxygen isotope compositions of tooth enamel from large herbivorous mammal remains of the LGM recovered from southwest France (Laugerie-Haute), north Spain (El Cierro, El Ruso, El Pendo, Hornos de la Peña), east Spain (Malladetes) and southeast Spain (Nerja). See the Figure 1 for the geographic locations of these archaeological sites. Studied taxa and ^{14}C ages are also provided along with the calculated oxygen isotope compositions of drinking and diet water ($\delta^{18}\text{O}_w$) and the carbon isotope composition of their diet ($\delta^{13}\text{C}_{\text{diet}}$). See the text for more explanations. Calendar ages were determined using the most recent calibration curve data for the Northern Hemisphere, IntCal20 (Reimer et al., 2020). Calibrated date ranges correspond to 92.9% probability (2σ).

Table 2: Synthesis of calculated mean annual air temperatures (MAAT) and mean annual precipitation (MAP) during the LGM, estimated. from the $\delta^{13}\text{C}$ - and $\delta^{18}\text{O}$ -values of tooth enamel carbonate from large herbivorous mammal remains.

1449

1450 **Figure captions:**

1451

1452 Figure 1: Location of the archaeological sites investigated: Laugerie-Haute, in southwestern
1453 France; El Cierro in the Province of Asturias, Hornos de la Peña, El Pendo and El Ruso
1454 in Cantabria, Nerja in the Province of Málaga and Malladetes, in the Province of
1455 Valencia.

1456

1457 Figure 2: Frequency histogram of the calculated $\delta^{13}\text{C}$ -value of mammal diets. Cervidae and
1458 Equidae are represented in blue; Caprinae, in red. The Gaussian curves were obtained
1459 by parametric estimation using PAST4.02 software (Hammer et al., 2001). These curves
1460 may slightly differ from those obtained by least-squares approximations (performed
1461 using 10,000 iterations) according to the general equation of normal distribution as
1462 follows: $y = m1 + m2 * \exp\left(-\frac{(x-m3)^2}{(m4)^2}\right)$. Constant uncertainties are $\pm 1\sigma$. For Cervidae
1463 and Equidae: $m1 = 0.35 \pm 0.37$; $m2 = 7.75 \pm 1.24$; $m3 = -24.02 \pm 0.06$ and $m4 = 0.48 \pm 0.09$
1464 with $R^2 = 0.71$; for Caprinae: $m1 = 0.17 \pm 0.20$; $m2 = 8.33 \pm 0.62$; $m3 = -22.46 \pm 0.03$ and
1465 $m4 = -0.60 \pm 0.05$ with $R^2 = 0.92$.

1466

1467 Figure 3: A) Modern and reconstructed MAP (mm yr^{-1}) for the various French and Spanish
1468 archaeological sites. Modern cities (Cestas-Pierroton for Laugerie-Haute, Santander for
1469 northern Spain, Valencia for Malladates and Almeria for Nerja) in the vicinity of
1470 studied sites were ranked according to increasing MAP that roughly follow a S–N
1471 geographic trend. See Table 2 for the output of calculation. B) estimated MAP taking
1472 into account the lower atmospheric pCO_2 during the LGM relatively to the Holocene
1473 (see section 5.2.1 for a detailed explanation).

1474

1475 Figure 4: Present-day linear relationship between the dew point temperature in °C (T_d) and
1476 the mean weighted $\delta^{18}\text{O}$ -value ($\delta^{18}\text{O}_{\text{mw}}$) of precipitations, extracted from the
1477 IAEA/WMO database. The database was filtered to only include meteorological sites
1478 above $|32^\circ|$ latitude. T_d is the dew point (°C). The equation of the linear regression is T_d
1479 $= 1.30(\pm 0.06)\delta^{18}\text{O}_{\text{mw}} + 15.69(\pm 0.67)$ with $R^2 = 0.83$.

1480

1481 Figure 5: Present-day MAAT– $\delta^{18}\text{O}_{\text{mw}}$ linear relationships extracted from the IAEA/WMO
1482 database. A) Global data above 32°N with 15 outliers removed after linear regression
1483 analysis: $\text{MAAT} = 1.42(\pm 0.04)\delta^{18}\text{O}_{\text{mw}} + 22.02(\pm 0.44)$; B) Global data for sites above
1484 32°N and with a MAAT $> 0^\circ\text{C}$: $\text{MAAT} = 1.40(\pm 0.08)\delta^{18}\text{O}_{\text{mw}} + 21.86(\pm 0.64)$.

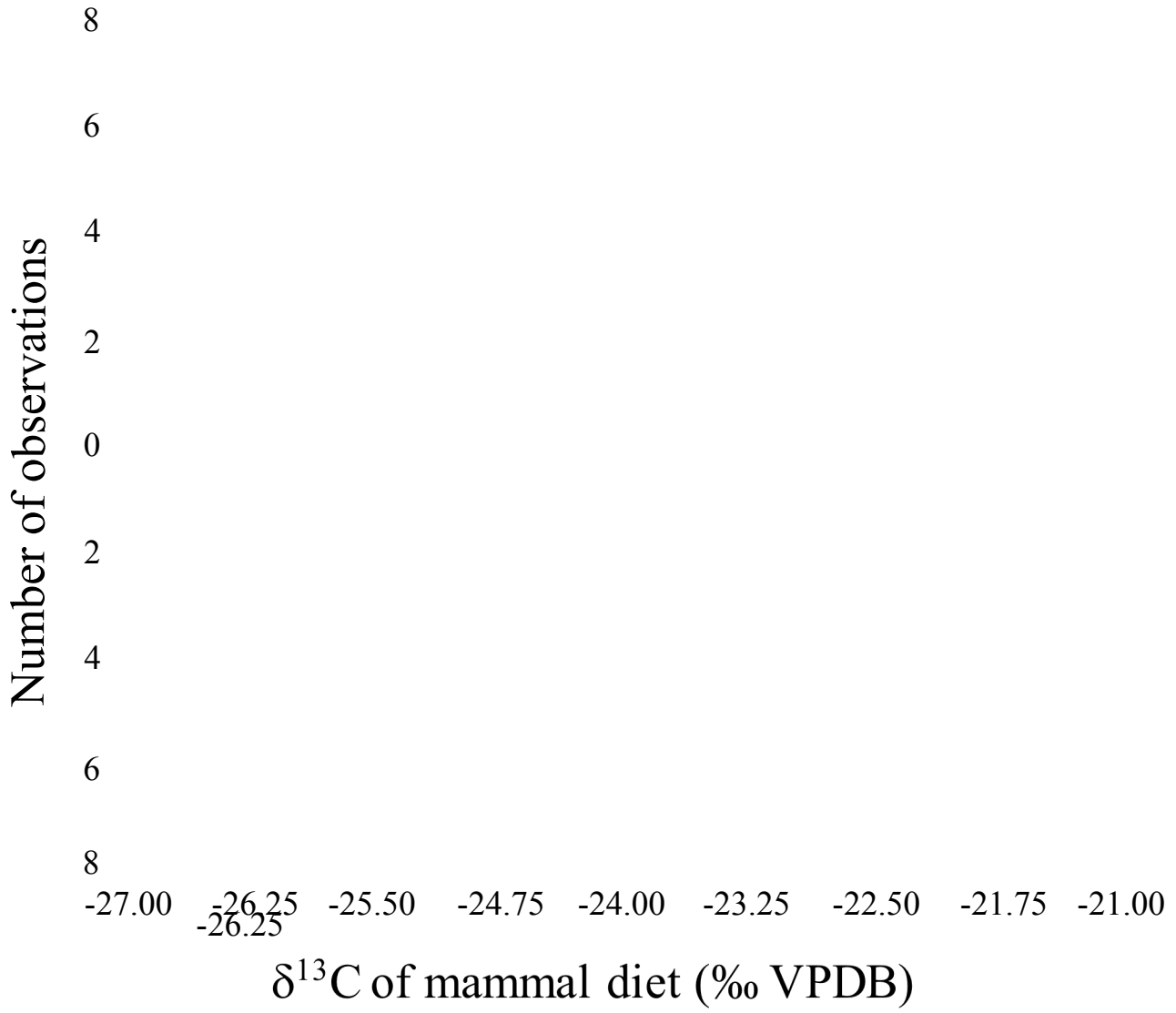
1485

1486 Figure 6: Frequency histogram of $\delta^{18}\text{O}$ of meteoric waters calculated from the $\delta^{18}\text{O}$ of apatite
1487 carbonate from the sampled teeth of Cervidae, Equidae and Caprinae. Archaeological
1488 sites located from northern Spain and SW France, are represented in blue while the
1489 Mediterranean sites of Malladates and Nerja are represented in red. The Gaussian
1490 curves were obtained by parametric estimation using PAST4.02 software (Hammer et
1491 al., 2001). These fitting curves may slightly differ from those obtained by least-squares
1492 approximations (performed by using 10,000 iterations) according to the general
1493 equation of normal distribution as follows: $y = m1 + m2 * \exp\left(-\frac{(x-m3)^2}{m4}\right)$. For Atlantic
1494 sites: $m1 = 1.35\pm 0.79$; $m2 = 13.17\pm 1.57$; $m3 = -9.98\pm 0.09$ and $m4 = 0.97\pm 0.15$ with R^2
1495 $= 0.89$. For Mediterranean sites: $m1 = 0.12\pm 0.84$; $m2 = 3.74\pm 1.09$; $m3 = -5.28\pm 0.19$ and
1496 $m4 = 0.97\pm 0.41$ with $R^2 = 0.70$. The constant uncertainties are $\pm 1\sigma$.

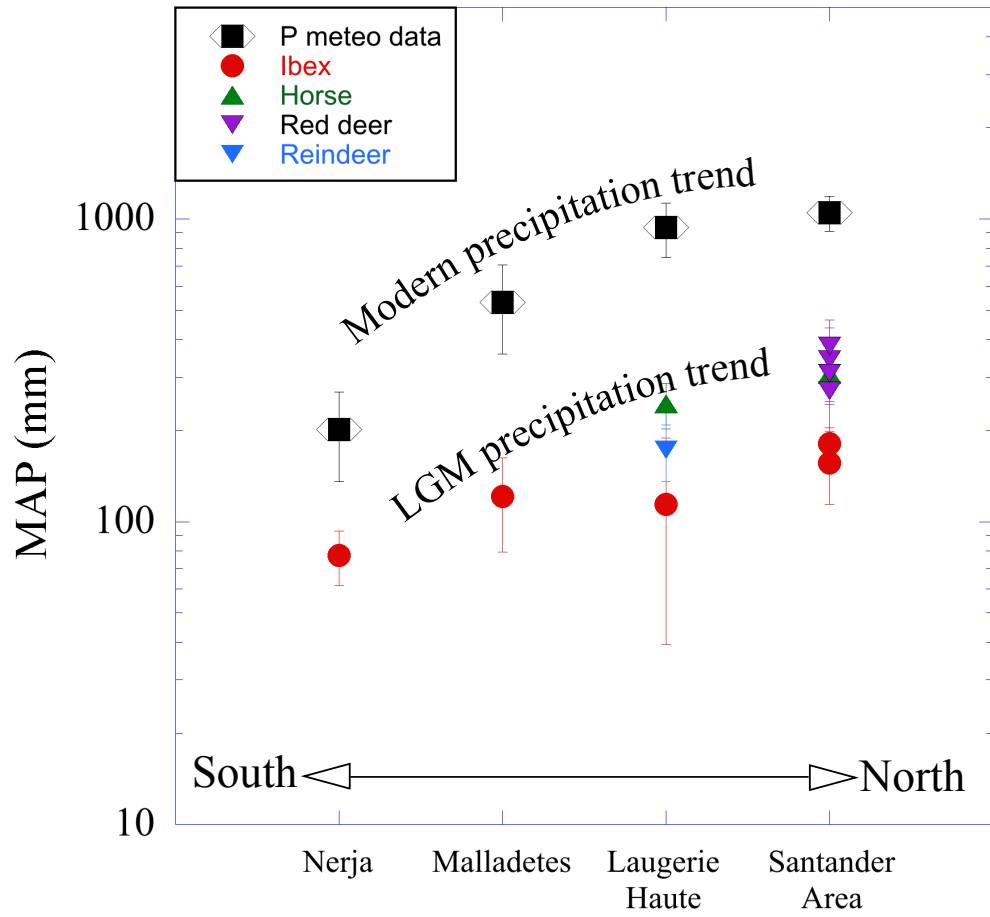
1497

1498 Figure 7: Modern and reconstructed MAAT (°C) of the sampled archaeological sites. Modern
1499 cities (Cestas-Pierroton for Laugerie-Haute, Santander for northern Spain, Valencia for
1500 Malladates and Almeria for Nerja) in the vicinity of studied sites were ranked according
1501 to a decreasing MAAT that roughly follow a S–N trend. See Table 2 for the output of
1502 calculation. Temperatures were calculated assuming an oxygen isotope composition of
1503 oceanic surface waters of +0.8‰ (VSMOW).

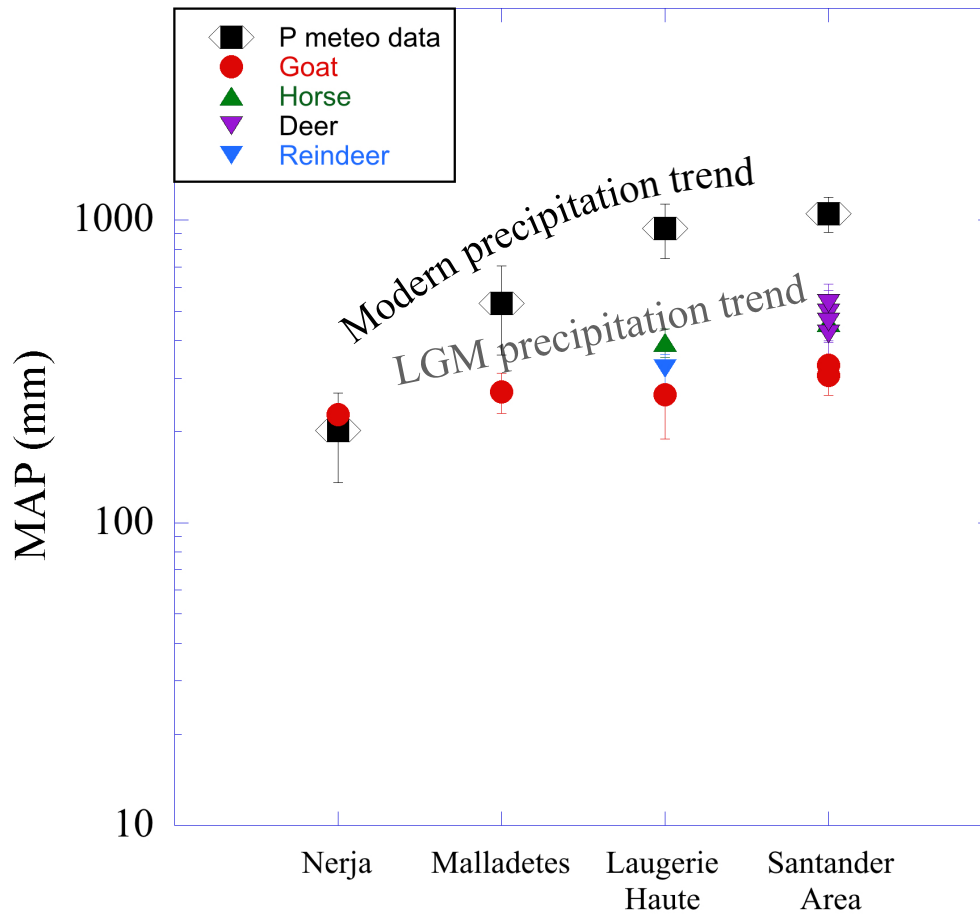




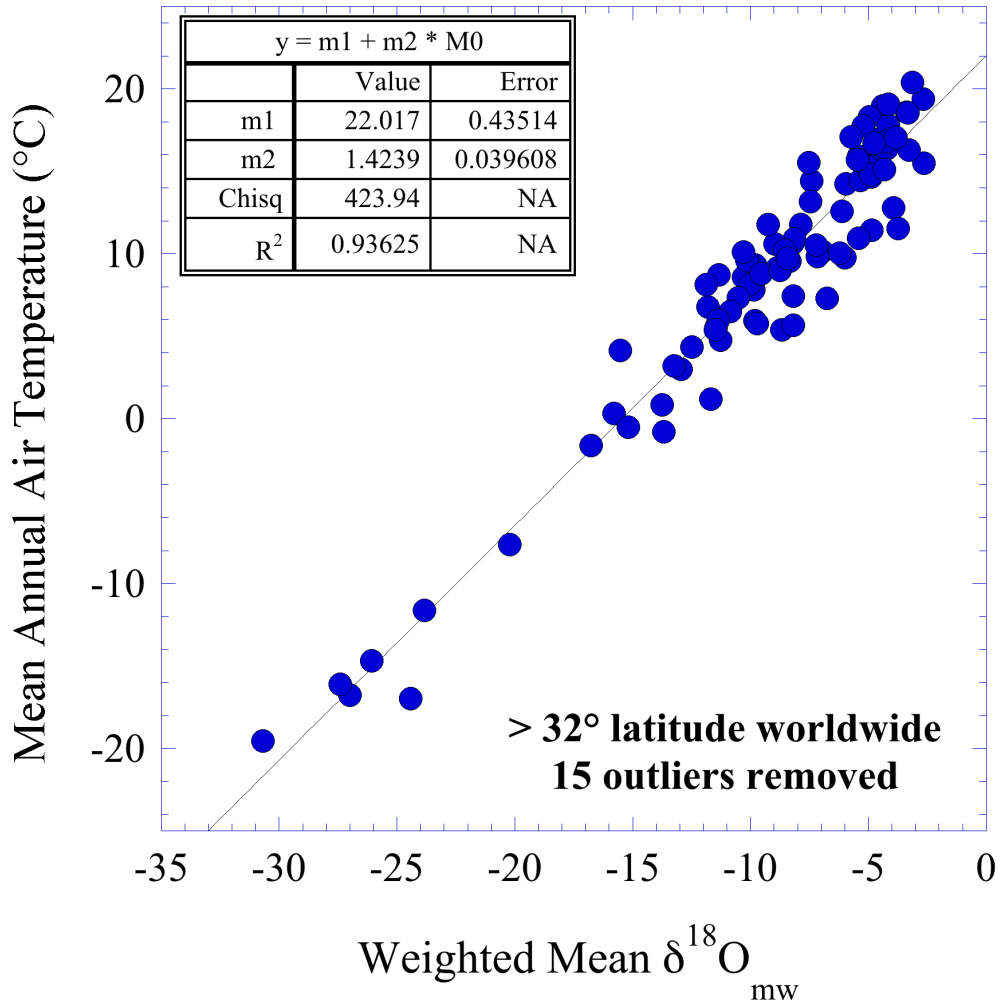
A)



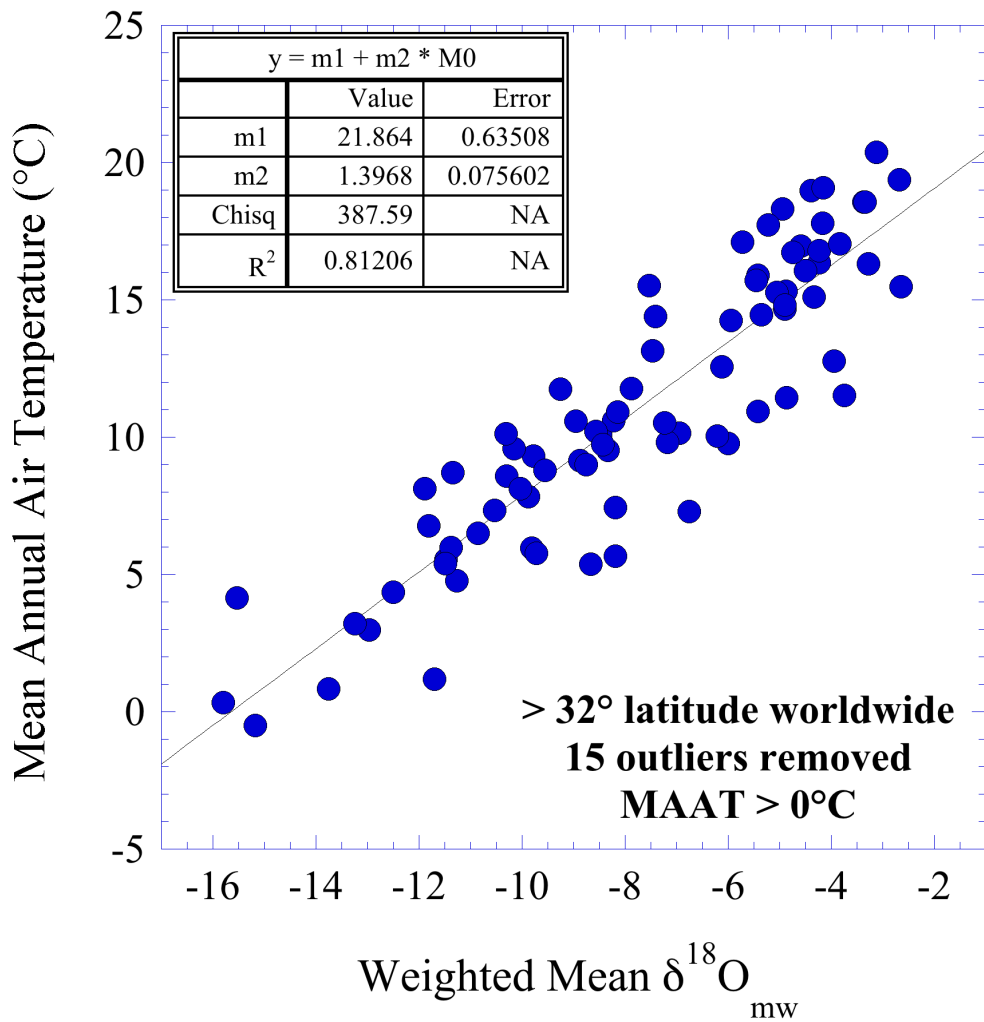
B)

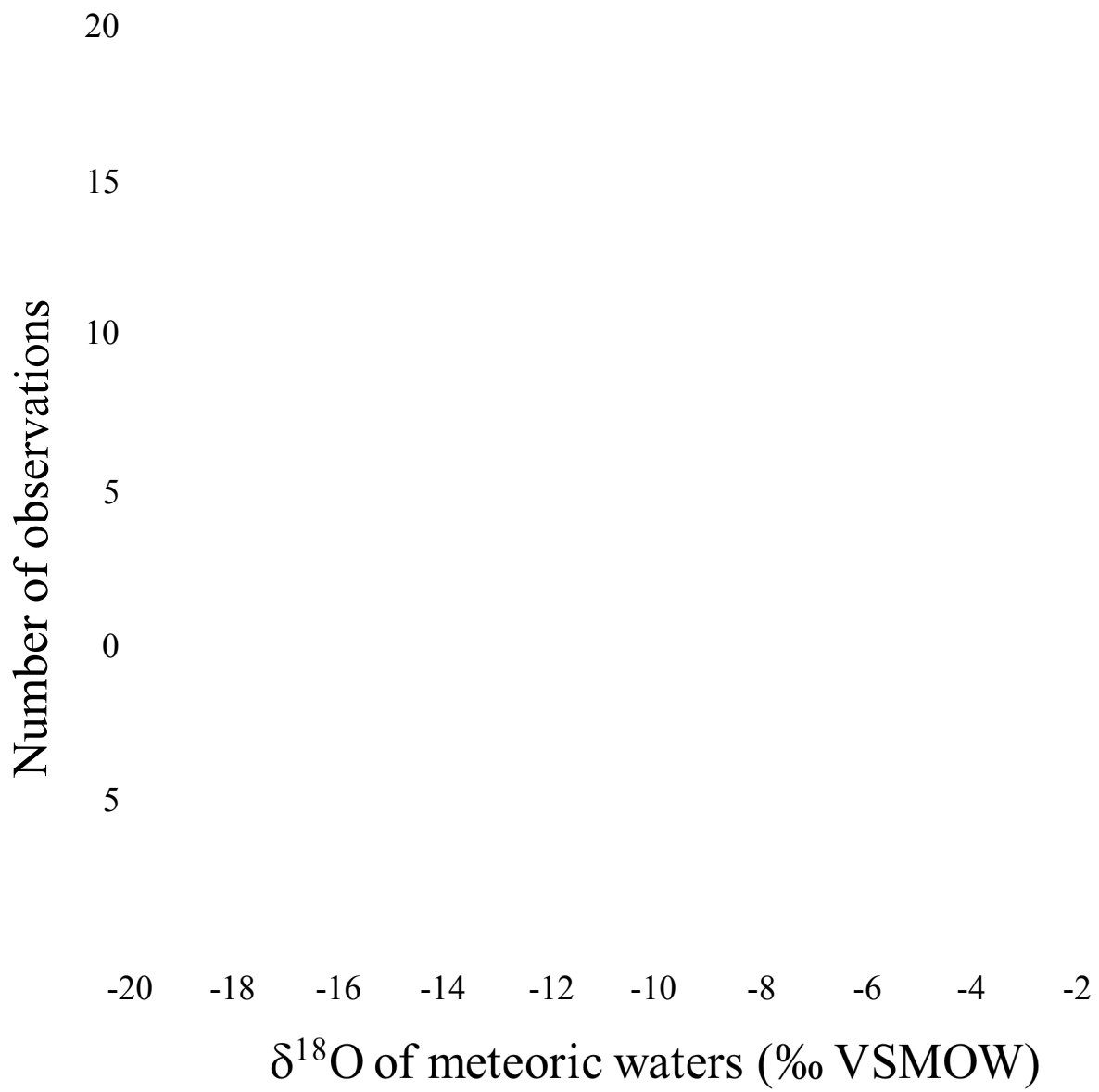


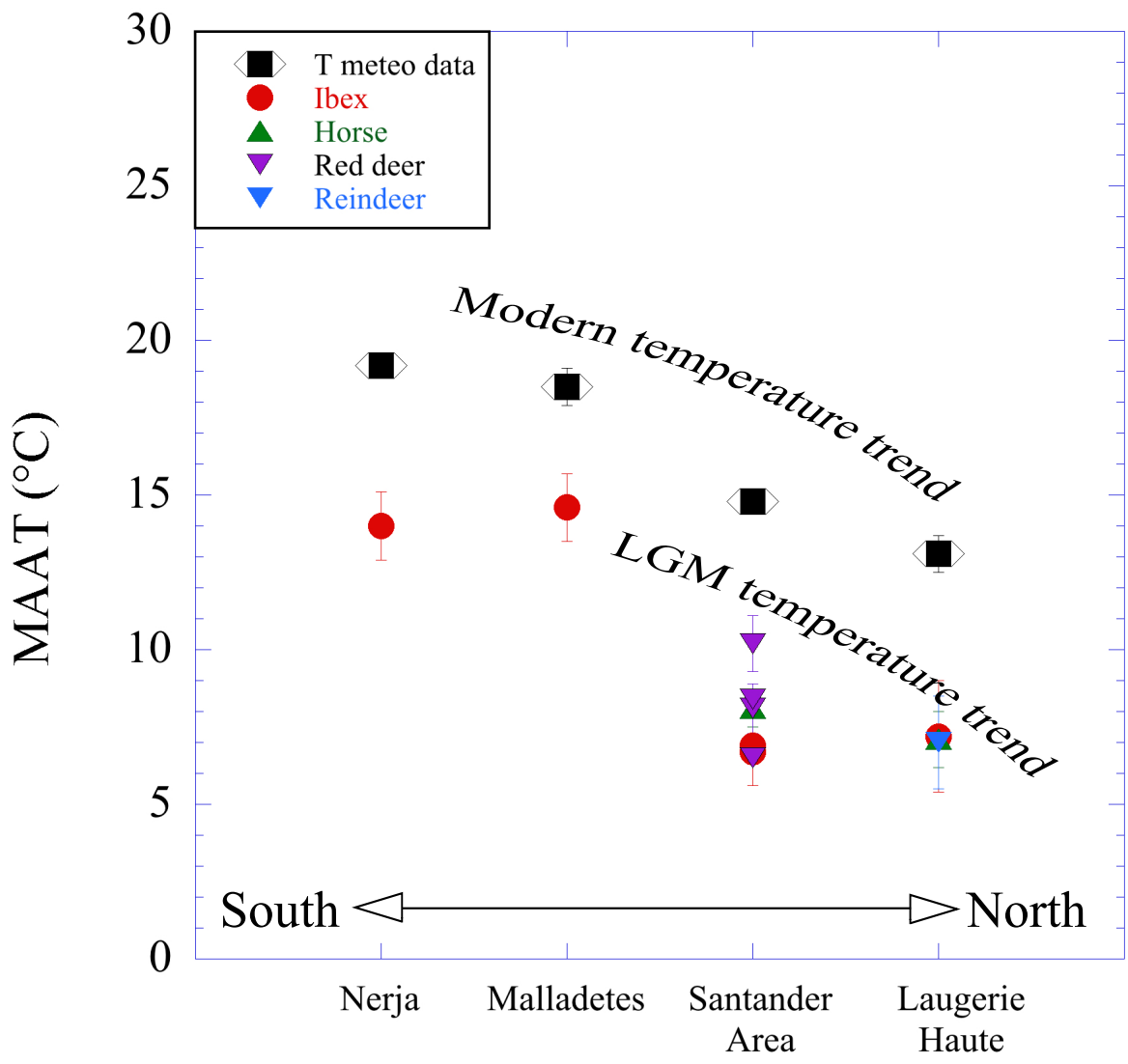
A)



B)







Site	Lab#	Level	¹⁴ C dates BP	+/-	¹⁴ C cal BP	Lithic scale	Taxon	Material	$\delta^{13}C_c$	$\delta^{13}C_{diet}$	$\Delta^{13}C_{leaf}$	P	$\delta^{18}O_c$	$\delta^{18}O_e$	$\delta^{18}O_{p\ calc.}$	$\delta^{18}O_{w\ cor.ice (1.2)}$	$\delta^{18}O_{w\ cor.ice (0.8)}$	T ($\delta^{18}O_{sw} = 1.2$)	T ($\delta^{18}O_{sw} = 0.8$)
					IntCal20 (92.9%)														
									% VPDB	% VPDB	(mm)	% VPDB	% VSMOW	% VSMOW	% VSMOW	% VSMOW	% VSMOW	(°C)	(°C)
El Cierro	EC-1B	G	15580	75	19011-18735	Lower Magdalenian	<i>Cervus elaphus</i>	M3 lower D	-11.21	-24.55	17.99	336	-6.6	24.1	15.1	-10.4	-10.0	6.9	7.5
El Cierro	EC-2B	G	15580	75	19011-18735	Lower Magdalenian	<i>Cervus elaphus</i>	M3 lower D	-11.12	-24.46	17.89	323	-6.1	24.5	15.5	-10.0	-9.6	7.4	8.0
El Cierro	EC-3B	G	15580	75	19011-18735	Lower Magdalenian	<i>Cervus elaphus</i>	M3 lower D	-10.94	-24.28	17.71	298	-6.6	24.0	15.0	-10.5	-10.1	6.8	7.4
El Cierro	EC-4B	G	15580	75	19011-18735	Lower Magdalenian	<i>Cervus elaphus</i>	M3 lower D	-11.42	-24.76	18.22	367	-5.9	24.8	15.8	-9.8	-9.4	7.7	8.3
El Cierro	EC-5B	G	15580	75	19011-18735	Lower Magdalenian	<i>Cervus elaphus</i>	M3 lower D	-10.92	-24.26	17.69	296	-6.7	24.0	15.0	-10.5	-10.1	6.8	7.4
El Cierro	EC-17B	G	15580	75	19011-18735	Lower Magdalenian	<i>Cervus elaphus</i>	M2 lower D	-12.04	-25.38	18.86	463	-6.2	24.5	15.5	-10.1	-9.7	7.4	8.0
El Cierro	EC-19B	G	15580	75	19011-18735	Lower Magdalenian	<i>Cervus elaphus</i>	M2 lower G	-12.28	-25.62	19.11	505	-5.5	25.1	16.1	-9.5	-9.1	8.2	8.8
El Cierro	EC-20B	G	15580	75	19011-18735	Lower Magdalenian	<i>Cervus elaphus</i>	M2 lower G	-11.06	-24.40	17.84	315	-4.8	25.9	16.9	-8.8	-8.4	9.2	9.8
El Cierro	EC-21B	G	15580	75	19011-18735	Lower Magdalenian	<i>Capra pyrenaica</i>	M3 lower G	-10.46	-23.30	16.69	182	-6.3	24.3	15.3	-11.0	-10.6	6.1	6.7
El Cierro	EC-22B	G	15580	75	19011-18735	Lower Magdalenian	<i>Capra pyrenaica</i>	M2 lower G	-10.67	-23.51	16.91	205	-6.0	24.7	15.7	-10.5	-10.1	6.7	7.3
El Cierro	EC-6B	G1	16360	55	19891-19566	Lower Magdalenian	<i>Cervus elaphus</i>	M2 lower G	-11.19	-24.53	17.97	333	-6.2	24.4	15.5	-10.1	-9.7	7.3	7.9
El Cierro	EC-7B	G1	16360	55	19891-19566	Lower Magdalenian	<i>Cervus elaphus</i>	M2 lower D	-11.43	-24.77	18.22	367	-6.3	24.3	15.3	-10.2	-9.8	7.2	7.8
El Cierro	EC-9B	G1	16360	55	19891-19566	Lower Magdalenian	<i>Cervus elaphus</i>	M3 lower D	-10.43	-23.77	17.18	236	-6.0	24.7	15.7	-9.9	-9.5	7.7	8.3
El Cierro	EC-10B	G1	16360	55	19891-19566	Lower Magdalenian	<i>Cervus elaphus</i>	M2 lower G	-11.48	-24.82	18.28	375	-6.6	24.1	15.1	-10.4	-10.0	6.9	7.5
El Cierro	EC-11B	G1	16360	55	19891-19566	Lower Magdalenian	<i>Cervus elaphus</i>	M3 lower G	-11.58	-24.92	18.38	390	-6.4	24.3	15.3	-10.2	-9.8	7.2	7.8
El Cierro	EC-12B	G1	16360	55	19891-19566	Lower Magdalenian	<i>Cervus elaphus</i>	M2 lower G	-10.73	-24.07	17.50	272	-5.8	24.9	15.9	-9.7	-9.3	7.9	8.5
El Cierro	EC-13B	G1	16360	55	19891-19566	Lower Magdalenian	<i>Cervus elaphus</i>	M3 lower G	-11.10	-24.44	17.88	321	-6.0	24.7	15.7	-9.9	-9.5	7.7	8.3
El Cierro	EC-14B	G1	16360	55	19891-19566	Lower Magdalenian	<i>Cervus elaphus</i>	M2 lower G	-10.98	-24.32	17.75	304	-6.2	24.5	15.5	-10.1	-9.7	7.4	8.0
El Cierro	EC-15B	G1	16360	55	19891-19566	Lower Magdalenian	<i>Cervus elaphus</i>	M3 lower G	-10.99	-24.33	17.77	306	-6.5	24.2	15.2	-10.4	-10.0	7.0	7.6
El Cierro	EC-23B	G1	16360	55	19891-19566	Lower Magdalenian	<i>Capra pyrenaica</i>	M2 lower G	-10.33	-23.17	16.56	169	-6.6	24.1	15.1	-11.2	-10.8	5.8	6.4
El Cierro	EC-24E	H	LGM	N/A	N/A	Upper Solutrean	<i>Capra pyrenaica</i>	M2 lower G	-8.93	-21.77	15.09	44	-6.4	24.3	15.3	-11.0	-10.6	6.0	6.6
El Pendo	PE-1B	4	LGM	N/A	N/A	Upper Solutrean	<i>Cervus elaphus</i>	M2/M3? upper G	-10.66	-24.00	17.42	263	-6.1	24.6	15.6	-10.0	-9.6	7.5	8.1
El Pendo	PE-2B	4	LGM	N/A	N/A	Upper Solutrean	<i>Cervus elaphus</i>	M2 upper G	-10.80	-24.14	17.56	280	-5.5	25.2	16.2	-9.4	-9.0	8.3	8.9
El Pendo	PE-3B	4	LGM	N/A	N/A	Upper Solutrean	<i>Cervus elaphus</i>	M3 upper D	-10.52	-23.86	17.27	246	-5.4	25.3	16.3	-9.4	-9.0	8.4	9.0
El Pendo	PE-4B	4	LGM	N/A	N/A	Upper Solutrean	<i>Cervus elaphus</i>	M2 upper G	-10.57	-23.91	17.33	252	-6.2	24.5	15.5	-10.1	-9.7	7.4	8.0
El Pendo	PE-5B	4	LGM	N/A	N/A	Upper Solutrean	<i>Cervus elaphus</i>	M3 upper G	-10.51	-23.85	17.26	244	-5.4	25.3	16.3	-9.3	-8.9	8.4	9.0
El Pendo	PE-6B	4	LGM	N/A	N/A	Upper Solutrean	<i>Cervus elaphus</i>	M3 upper D	-11.04	-24.38	17.81	312	-6.1	24.6	15.6	-10.0	-9.6	7.5	8.1
El Pendo	PE-7B	4	LGM	N/A	N/A	Upper Solutrean	<i>Cervus elaphus</i>	M2 upper D	-10.90	-24.24	17.67	294	-6.1	24.6	15.6	-10.0	-9.6	7.5	8.1
El Ruso	RU-2B	3	16410	210	< 20396 - 19322	Upper Solutrean	<i>Cervus elaphus</i>	M3 upper G	-10.50	-23.84	17.25	243	-3.7	27.1	18.0	-7.9	-7.5	10.5	11.1
El Ruso	RU-3B	3	16410	210	< 20396 - 19322	Upper Solutrean	<i>Cervus elaphus</i>	M2 upper D	-10.59	-23.93	17.35	255	-4.3	26.5	17.4	-8.4	-8.0	9.8	10.4
El Ruso	RU-5B	3	16410	210	< 20396 - 19322	Upper Solutrean	<i>Cervus elaphus</i>	M2 upper G	-12.89	-26.23	19.75	622	-3.7	27.1	18.0	-7.8	-7.4	10.5	11.1
El Ruso	RU-6B	3	16410	210	< 20396 - 19322	Upper Solutrean	<i>Cervus elaphus</i>	M3 upper G	-10.58	-23.92	17.33	253	-4.6	26.1	17.1	-8.7	-8.3	9.4	10.0
El Ruso	RU-7B	3	16410	210	< 20396 - 19322	Upper Solutrean	<i>Cervus elaphus</i>	M2 upper G	-10.84	-24.18	17.60	285	-4.9	25.8	16.8	-8.9	-8.5	9.0	9.6
El Ruso	RU-8B	3	16410	210	< 20396 - 19322	Upper Solutrean	<i>Cervus elaphus</i>	M1 upper G	-10.11	-23.45	16.84	198	-5.6	25.1	16.1	-9.6	-9.2	8.1	8.7
Hornos de la Peña	HP-1e	B	18450	520	23425-21038	Lower Magdalenian	<i>Cervus elaphus</i>	M3 lower G	-11.52	-24.86	18.31	380	-7.4	23.2	14.3	-11.2	-10.8	5.9	6.5
Hornos de la Peña	HP-4B	B	18450	520	23425-21038	Lower Magdalenian	<i>Capra pyrenaica</i>	M2 lower D	-9.64	-22.48	15.84	103	-6.7	23.9	14.9	-11.4	-11.0	5.5	6.1
Hornos de la Peña	HP-5B	B	18450	520	23425-21038	Lower Magdalenian	<i>Capra pyrenaica</i>	M2 lower D	-9.98	-22.82	16.19	134	-6.8	23.9	14.9	-11.4	-11.0	5.5	6.1
Hornos de la Peña	HP-6B	B	18450	520	23425-21038	Lower Magdalenian	<i>Capra pyrenaica</i>	M2 lower D	-10.00	-22.84	16.21	136	-5.3	25.4	16.4	-9.8	-9.4	7.7	8.3
Hornos de la Peña	HP-7e	B	18450	520	23425-21038	Lower Magdalenian	<i>Capra pyrenaica</i>	M3 upper D	-10.71	-23.55	16.95	210	-6.1	24.5	15.6	-10.7	-10.3	6.5	7.1
Hornos de la Peña	HP-7b	B	18450	520	23425-21038	Lower Magdalenian	<i>Capra pyrenaica</i>	M3 upper D	-10.92	-23.76	17.16	233	-6.1	24.6	15.6	-10.7	-10.3	6.5	7.1
Hornos de la Peña	HP-8B	B	18450	520	23425-21038	Lower Magdalenian	<i>Equus caballus</i>	M3 lower D	-10.78	-24.28	17.71	299	-5.9	24.8	15.8	-9.8	-9.4	7.8	8.4
Hornos de la Peña	HP-9B	B	18450	520	23425-21038	Lower Magdalenian	<i>Equus caballus</i>	M3 lower G	-10.90	-24.40	17.84	315	-6.3	24.4	15.4	-10.3	-9.9	7.1	7.7
Hornos de la Peña	HP-11B	B	18450	520	23425-21038	Lower Magdalenian	<i>Rupicapra rupicapra</i>	M3 upper D	-9.90	-22.74	16.11	126	-7.2	23.5	14.5	-11.9	-11.5	4.9	5.5
Hornos de la Peña	HP-12B	B	18450	520	23425-21038	Lower Magdalenian	<i>Rupicapra rupicapra</i>	M3 upper D	-10.40	-23.24	16.63	176	-5.3	25.4	16.4	-9.9	-9.5	7.7	8.3
Hornos de la Peña	HP-13B	B	18450	520	23425-21038	Lower Magdalenian	<i>Rupicapra rupicapra</i>	M3 lower D	-9.97	-22.81	16.17	133	-7.4	23.2	14.3	-12.1	-11.7	4.5	5.1
Hornos de la Peña	HP-14B	B	18450	520	23425-21038	Lower Magdalenian	<i>Rupicapra rupicapra</i>	M2 lower D	-10.22	-23.06	16.44	158	-5.2	25.5	16.5	-9.7	-9.3	7.9	8.5
Laugerie-Haute E.	LH-2B	4 to 8	>17000<19000	N/A	N/A	Magdalenian II	<i>Capra pyrenaica</i>	M2 upper G	-9.24	-22.08	15.42	69	-4.4	26.3	17.3	-8.9	-8.5	9.1	9.7
Laugerie-Haute E.	LH-3B	4 to 8	>17000<19000	N/A	N/A	Magdalenian II	<i>Capra pyrenaica</i>	M2 lower D	-10.82	-23.66	17.06	222	-6.2	24.4	15.4	-10.9	-10.5	6.3	6.9
Laugerie-Haute E.	LH-4B	4 to 8	>17000<19000	N/A	N/A	Magdalenian II	<i>Saiga tatarica</i>	M3 lower G	-10.45	-22.85	16.22	137	-5.5	25.2	16.2	-10.1	-9.7	7.4	8.0
Laugerie-Haute E.	LH-5B	4 to 8	>17000<19000	N/A	N/A	Magdalenian II	<i>Saiga tatarica</i>	M3 lower D	-10.17	-22.57	15.93	111	-4.5	26.2	17.2	-8.9	-8.5	9.0	9.6
Laugerie-Haute E.	LH-6B	4 to 8	>17000<19000	N/A	N/A	Magdalenian II	<i>Saiga tatarica</i>	M2 lower D	-9.87	-22.27	15.62	85	-7.4	23.3	14.3	-12.1	-11.7	4.5	5.1
Laugerie-Haute E.	LH-7B	4 to 8	>17000<19000	N/A	N/A	Magdalenian II	<i>Saiga tatarica</i>	M3 lower G	-9.70	-22.10	15.44	70	-6.2	24.4	15.4	-10.9	-10.5	6.3	6.9
Laugerie-Haute E.	LH-8B	4 to 8	>17000<19000	N/A	N/A	Magdalenian II	<i>Saiga tatarica</i>	M3 lower G	-10.56	-22.96	16.34	148	-5.3	25.4	16.4	-9.8	-9.4	7.7	8.3
Laugerie-Haute E.	LH-14B	4 to 8	>17000<19000	N/A	N/A	Magdalenian II	<i>Saiga tatarica</i>	M3 lower G	-10.19	-22.59	15.95	112	-5.5	25.2	16.2	-10.0	-9.6	7.5	8.1
Laugerie-Haute E.	LH-15B	4 to 8	>17000<19000	N/A	N/A	Magdalenian II	<i>Saiga tatarica</i>	M2 lower G	-10.14	-22.54	15.89	108	-7.4	23.2	14.2	-12.2	-11.8	4.4	5.0
Laugerie-Haute E.	LH-9B	18 to 20	18260	360	22971-21203	Magdalenian 0	<i>Saiga tatarica</i>	M3 upper G	-10.55	-22.95	16.33	147	-5.0	25.7	16.7	-9.5	-9.1	8.3	8.9
Laugerie-Haute E.	LH-13B	18 to 20	18260	360	22971-21203	Magdalenian 0	<i>Rupicapra rupicapra</i>	M3 lower G	-9.52	-22.36	15.71	92	-5.6	25.1	16.1	-10.2	-9.8	7.2	7.8
Laugerie-Haute E.	LH-10B	18 to 20	18260	360	22971-21203	Magdalenian 0	<i>Equus caballus</i>	M3 upper D	-10.59	-24.09	17.51	274	-6.3	24.3	15.3	-10.3	-9.9	7.0	7.6
Laugerie-Haute E.	LH-11B	18 to 20	18260	360	22971-21203	Magdalenian 0	<i>Equus caballus</i>	M3 upper D	-10.10	-23.60	17.00	215	-7.0	23.6	14.7	-11.0	-10.6	6.0	6.6
Laugerie-Haute E.	LH-12B	10 to 16	LGM	N/A	N/A	Magdalenian I	<i>Capra pyrenaica</i>	M3 lower G	-9.66	-22.50	15.86	105	-7.0	23.6	14.7	-11.7	-11.3	5.1	5.7
Laugerie-Haute E.	LH-16B	10 to 16	LGM	N/A	N/A	Magdalenian I	<i>Rangifer tarandus</i>	M3 lower G	-9.92	-23.26	16.64	178	-7.7	22.9	14.0	-10.7	-10.3	6.5	7.1
Laugerie-Haute E.	LH-17B	10 to 16	LGM	N/A	N/A	Magdalenian I	<i>Rangifer tarandus</i>	M3 lower G	-10.18	-23.52	16.92	206	-6.9	23.7	14.7	-9.8	-9.4	7.8	8.4
Laugerie-Haute E.	LH-18B	10 to 16	LGM	N/A	N/A	Magdalenian I	<i>Rangifer tarandus</i>	M3 lower G	-9.47	-22.81	16.18	13							

	MAP (mm)	MAP* (mm)	P (S.D.) (mm)	$\delta^{18}\text{Ow}$ ‰ VSMOW ($\delta^{18}\text{Osw} = +1.2$)	$\delta^{18}\text{Ow}$ ‰ VSMOW ($\delta^{18}\text{Osw} = +0.8$)	$\delta^{18}\text{Ow}$ (S.D.) ‰ VSMOW	MAAT (°C)	MAAT (S.D.) (°C)	T-EUROPE (°C) Skrzypek et al. 2011 ($\delta^{18}\text{Osw} = +1.2$)	T-EUROPE (°C) Skrzypek et al. 2011 ($\delta^{18}\text{Osw} = +0.8$)	S.D.	MAT anomaly (°C) ($\delta^{18}\text{Osw} = +1.2$)	MAT anomaly (°C) ($\delta^{18}\text{Osw} = +0.8$)	MAP anomaly (mm)
Modern meteo data for cities close to the archaeological sites:														
Almeria	202.0	N/A	66.2	-5.8		1.2	19.2	0.4						
Cestas-Pierroton	937.3	N/A	191.5	-5.8		0.7	13.1	0.6						
Santander	1049.9	N/A	140.3	-5.8		0.3	14.8	0.4						
Valencia	531.7	N/A	172.9	-5.2		0.7	18.5	0.6						
MAP, MAT and their anomalies relative to present-days calculated for the studied archaeological sites:														
Nerja (≈Almeria)														
<i>Capra</i>	78	228	16	-5.8	-5.4	0.8	N/A	N/A	13.4	14.0	1.1	-5.8	-5.2	-125
Laugerie-Haute (≈ Cestas)														
Caprinae	118	268	48	-10.4	-10.0	1.2	N/A	N/A	6.9	7.5	1.7	-6.2	-5.6	-819
Caprinae	120	270	39	-9.8	-9.4	0.5	N/A	N/A	7.8	8.4	0.7	-5.3	-4.7	-818
<i>Equus</i>	245	395	42	-11.9	-11.5	0.7	N/A	N/A	6.5	7.1	0.9	-6.6	-6.0	-693
Caprinae	105	255	n.a.	-11.7	-11.3	n.a.	N/A	N/A	5.1	5.7	N/A	-8.0	-7.4	-833
<i>Rangifer tarandus</i>	172	322	37	-10.8	-10.4	1.0	N/A	N/A	6.4	7.0	1.5	-6.7	-6.1	-765
Malladetes (≈Valencia)														
<i>Capra</i>	121	271	42	-5.4	-5.0	0.8	N/A	N/A	14.0	14.6	1.1	-4.5	-3.9	-411
El Cierro (≈ Santander)														
<i>Cervus elaphus</i>	363	513	79	-10.0	-9.6	0.6	N/A	N/A	7.6	8.2	0.8	-7.2	-6.6	-687
<i>Capra</i>	194	344	16	-10.8	-10.4	0.3	N/A	N/A	6.4	7.0	0.4	-8.4	-7.8	-856
<i>Cervus elaphus</i>	323	473	50	-10.1	-9.7	0.2	N/A	N/A	7.4	8.0	0.3	-7.4	-6.8	-727
<i>Capra</i>	169	319	n.a.	-11.2	-10.8	n.a.	N/A	N/A	5.8	6.4	N/A	-9.0	-8.4	-881
El Pendo (≈ Santander)														
<i>Cervus elaphus</i>	270	420	26	-9.8	-9.4	0.3	N/A	N/A	7.8	8.4	0.5	-7.0	-6.4	-780
El Ruso (≈ Santander)														
<i>Cervus elaphus</i>	310	460	156	-8.5	-8.1	0.7	N/A	N/A	9.6	10.2	0.9	-5.2	-4.6	-740
Hornos de la Pena (≈ Santander)														
<i>Cervus elaphus</i>	380	530	n.a.	-11.2	-10.8	n.a.	N/A	N/A	5.9	6.5	N/A	-8.9	-8.3	-670
<i>Capra & Rupicapra</i>	157	307	43	-10.8	-10.4	0.9	N/A	N/A	6.3	6.9	1.3	-8.5	-7.9	-893
<i>Equus</i>	307	457	11	-11.1	-10.7	0.4	N/A	N/A	7.5	8.1	0.6	-7.3	-6.7	-743

MAP = Mean Annual Precipitation in mm

MAP* = Mean Annual Precipitation in mm corrected from the LGM pCO₂ estimate

$\delta^{18}\text{Ow}$ = mean oxygen isotope composition of precipitations

$\delta^{18}\text{Osw}$ = mean oxygen isotope composition of oceanic surface waters

MAAT = Mean Annual Air Temperatures obtained from IAEA/WMO database

MAT = calculated Mean Air Temperatures at archaeological sites

MAT anomaly = anomaly in MAT relative to present-days

MAP anomaly = anomaly in MAP relative to present-days