

1 Towards a Middle Pleistocene terrestrial climate reconstruction based on herpetofaunal
2 assemblages from the Iberian Peninsula: state of the art and perspectives
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29

30 **Abstract**

31

32 The pattern of the varying climatic conditions in southern Europe over the last million
33 years is well known from isotope studies on deep-ocean sediment cores and the long
34 pollen records that have been produced for lacustrine and marine sedimentary sequences
35 from Greece, Italy and the Iberian margin. However, although relative glacial and
36 interglacial intensities are well studied, there are still few proxies that permit
37 quantitative terrestrial temperature and precipitation reconstruction. In this context,
38 fauna-based climate reconstructions based on evidence preserved in archaeological or
39 palaeontological sites are of great interest, even if they only document short windows of
40 that climate variability, because (a) they provide a range of temperature and
41 precipitation estimates that are understandable in comparison with present climate; (b)
42 they may allow the testing of predicted temperature changes under scenarios of future
43 climate change; and (c) quantitative temperature and precipitation estimates for past
44 glacials and interglacials for specific regions/latitudes can help to understand their
45 effects on flora, fauna and hominids, as they are directly associated with those cultural
46 and/or biological events. Moreover such reconstructions can bring further arguments to
47 the discussion about important climatic events like the Mid-Bruhnes Event, a climatic
48 transition between moderate warmths and greater warmths during interglacials. In this
49 paper we review a decade of amphibian- and reptile-based climate reconstructions
50 carried out for the Iberian Peninsula using the Mutual Ecogeographic Range method in

51 order to present a regional synthesis from MIS 22 to MIS 6, discuss the climate pattern
52 in relation to the Mid-Bruhnes Event and the thermal amplitude suggested by these
53 estimates and finally to identify the chronological gaps that have still to be investigated.

54

55 **Keywords:** Vertebrates as climate proxy; Amphibian; Reptile; Mutual Ecogeographic
56 Range; Middle Pleistocene; South-Western Mediterranean.

57

58 **1. Introduction**

59

60 Since Buffon, in his *Époques de la Nature* (1778), suggested that the climate of western
61 Europe must have been much warmer in the past to support the elephants, hippos, big
62 cats and rhinos that were found as fossils, the vertebrate record has been understood to
63 provide information on past climatic conditions, via the use of analogy with modern
64 representatives. At first, studies of fossil vertebrates involved only counting the number
65 of taxa and organisms present in an archaeological or palaeontological excavation and
66 interpretation of these data was done in a qualitative and descriptive way only. Since
67 then there have been many advances in both the methods used for analysis of fossil
68 vertebrate remains and a great increase in scope of the questions. They have been used
69 to address quantitative palaeoenvironmental reconstructions (e.g. Chaline et al., 1995;
70 Lyman and O'Brien, 2005; Villa et al. 2010; Lopes et al. 2013), effect of climatic
71 variability on vertebrates (e.g. Blois and Hadly, 2009; Blois et al., 2010, 2013; Bryson
72 et al. 2010; McDonald and Bryson, 2010), changes in the vertebrate communities over
73 time (e.g. Stewart 2008, 2009; Hofreiter and Stewart, 2009), determination of refuge
74 area (e.g. Stewart and Lister, 2001; Stewart and Cooper, 2008; López-García et al.,
75 2010a), extinction and speciation processes (e.g. Lister, 2004; Nogués-Bravo et al.,

76 2008; Gillespie et al. 2012), impact of vertebrates on flora (e.g. Johnson, 2009a, b; Gill
77 et al., 2009, 2012; Faith, 2011; Brault et al., 2013), evolution of the ecological niches
78 over time (e.g. Martínez-Meyer et al., 2004; Rödder et al., 2013) and finally the most
79 advanced of these approaches involves quantitative reconstruction of palaeoclimatic
80 conditions.

81

82 Methods for the quantitative inference of palaeoclimate using vertebrates dates back to
83 the pioneering work of Brattstrom (1953, 1956), followed in the 1990's by an abundant
84 literature (e.g. Markwick, 1994, 1998; Kay and Maden, 1996; Motuzco and Ivanov,
85 1996; Montuire et al., 1997; Aguilar et al., 1999; Montuire, 1999). The most commonly
86 used vertebrates for palaeoclimatic reconstructions are mammals (of which small
87 mammals dominate over herbivorous megafauna), followed by reptiles and amphibians.
88 The parameters which can be reconstructed using vertebrate remains are principally
89 temperature and precipitation (Table 1).

90

91 Methods for palaeoclimatic reconstructions based on vertebrates have increased both in
92 number and accuracy in recent decades. However the application of most of these
93 methods is restricted to a period or a biome/geographical location, is limited by the
94 availability of a particular proxy or ecometric and in most cases does not permit a
95 reconstruction of both temperature and rainfall. For example, in the case of
96 palaeoclimatic reconstructions with thermal ecology (Brattstrom, 1956; Markwick,
97 1994, 1998; Böhme, 2006, 2008) and the relation size-temperature-metabolic rate
98 (Denny et al., 2009; Makarieva et al., 2005; Sniderman, 2009; Head et al., 2009a, b,
99 2013), only temperature parameters can be inferred. In the case of reconstructions based
100 on hypsodonty (Fortelius et al., 2002, 2006; Damuth et al., 2002; Eronen and Rook,

101 2004; Eronen et al., 2010b, 2011) it is only possible to infer precipitation, a factor that is
102 always subject to large uncertainties for the past (Porch, 2010). Another limitation of
103 some of these methods is that they can only be applied to a species that presents the
104 necessary ecometric, such as the large size of *Titanoboa* (Head et al., 2009a),
105 *Beelzebufo* (Makarieva et al., 2009) and *Barbatorex* (Head et al., 2013) or to a taxon
106 that is restricted today to tropical environments such as Crocodylia (Markwick, 1994,
107 1998).

108

109 Finally, there are other methods that can only be used for more recent periods, such as
110 the Mutual Ecogeographic Range (Martínez-Solano and Sanchiz, 2005; Blain et al.,
111 2009, 2016a), a variant of the numerous methodologies for climate reconstruction which
112 use the modern distribution of species such as the Mutual Climatic Range and the
113 Modern Analogue Technique (see Birks et al., 2010 for a synthesis and comparison),
114 due to the fact that it is necessary to have extant representatives for the species
115 recovered from archaeological sites. This method has been applied mainly to the late
116 Middle and Late Pleistocene-Holocene for small-mammals (e.g. López-García et al.,
117 2008, 2010b, 2011a, b, c, d, 2013a, b; Bañuls et al., 2012, 2013, 2014; Fernández-
118 García and López-García, 2013; Fernández-García, 2014; Rey-Rodríguez et al., 2016;
119 Fagoaga et al., 2017, in press) and back to the earliest Pleistocene for herpetofauna (e.g.
120 Martínez-Solano and Sanchiz, 2005; Blain, 2005, 2009, 2012-14; Blain et al., 2007,
121 2008a, 2009, 2010, 2011a, b, 2012a, b, 2013a, b, c, 2014a, b, c, 2015, 2016a, 2017a, b;
122 Blain and Corchón Rodríguez, 2017; Agustí et al., 2009; Marquina et al., 2017; Villa et
123 al., 2018a, b). Using this method in older periods with extinct taxa (especially
124 mammals) and relating them to their closest current representatives could increase the
125 error in palaeoclimatic reconstruction since the extinct taxon may not necessarily have

126 had the same niche as its current representatives (Rödder et al., 2013), and during the
127 past the biological communities were not necessarily analogous with present ones
128 (Williams and Jackson, 2007; Semken et al., 2010; Urban et al., 2012; Correa-Metrio et
129 al., 2012) and this disparity increases further back in time (Stewart, 2008). The presence
130 of non-analogous or disparate communities is also a problem when reconstructions are
131 based on current biomes or ecoregions, as in the case of the transfer function method
132 (Hernández-Fernández, 2001; Hernández-Fernández and Peláez-Campomanes, 2003,
133 2005; Hernández-Fernández, 2006; Hernández-Fernández and Vrba, 2006; Hernández-
134 Fernández et al., 2007) and the variant of the mutual climate range method of Polly and
135 Eronen (2011), as in the past these biomes or ecoregions did not necessarily exist as
136 today.

137

138 The Mutual Ecogeographic Range (MER) has been applied, under different names (see
139 Lyman, 2016), to fossil amphibians and reptiles at a regional level (Catalonia) or for
140 some Spanish provinces (Granada, Murcia, Burgos, Castellón and Valencia) by Blain
141 (2005, 2009) and at a peninsular scale first by Martínez-Solano and Sanchiz (2005) and
142 since then by Blain et al. (2009) and subsequent publications. According to Birks et al.
143 (2010), the Mutual Climatic Range is part of indicator-species approaches (based on the
144 “presence/absence of one or few taxa”) whereas Modern Analogue Technique is part of
145 assemblage approaches (based on the “presence/absence of many taxa”). As a
146 bioclimate envelope approach is not generated for each taxon, MER seems to be closest
147 to a Modern Analogue Technique. Moreover in contrast to the indicator species
148 approaches, the assemblage approach considers the fossil assemblage as a whole (as we
149 do, even if we are aware that generally a very few ecologically strong indicator species
150 have more weight in such reconstruction than other more ubiquitous ones) and the

151 relative abundances of all the different fossil taxa. In contrast to Modern Analogue
152 Technique it is assumed (as in Mutual Climatic Range approaches) that a taxon has an
153 equal probability of occurrence anywhere within its climate range (Hupper and Solow,
154 2004; Horne and Mezquita, 2008) even if this has been shown not to be true in many
155 empirical studies.

156

157 Assuming niche conservatism, MER involves finding the modern sample(s) that is (are)
158 most similar to the fossil assemblage. Then the past climatic conditions are inferred
159 from the climate variable(s) for the analogous modern sample(s). Application of MER
160 to the Spanish fossil record is possible because most of the fossil Pleistocene
161 amphibians and reptiles belong to extant species, with only a few exceptions (see Blain
162 et al., 2016b for a recent review). The climate reconstruction is then based on the mean
163 of the whole analogous modern samples (expressed here as 10 x 10 km UTM squares)
164 without any weighting as usually the distribution of the obtained values is normal (see
165 for example Martínez-Solano and Sanchiz, 2005). Such a method, based only on
166 absence/presence (and not abundance), is consequently free from taphonomical bias and
167 over-representation of some species in the fossil assemblages that may be more linked
168 with the diet preference of the agent of accumulation or to the close proximity of a
169 particular environment (rocky areas for karst sites or water biotopes for lake sites) than
170 with climate.

171

172 Lobo et al. (2016) verified the assumption that current ecological niches for amphibians
173 represent a reliable inference tool for past environmental conditions. This assumption
174 can also certainly be extended to reptiles. Lobo et al. (2016) also demonstrate that for
175 direct raw inferences, the combined taxa sets do not improve in accuracy with the

176 number of species included (above a certain sample size threshold), but that the
177 precision, however, is quite variable among taxa, reflecting sometimes the effect of non-
178 climatic distributional constraints.

179

180 In the last decade, a number of publications dealt with climate reconstruction from
181 various Pleistocene localities within the Iberian Peninsula based on their preserved
182 fossil amphibians and reptiles (Fig. 1, Table 2). This work enables a regional synthesis
183 of the palaeoclimatic data obtained to date from the herpetofaunal assemblages of the
184 Iberian Peninsula from MIS 22 to MIS 6, i.e. since the first supposed cold glacial to the
185 penultimate glacial. This time period is an interesting interval because it encompasses
186 the last part of the Early-Middle Pleistocene transition (a major transition in climate
187 cyclicity), and shows stronger climatic fluctuations (higher intensity of cold and warm
188 periods) and also intriguing climatic phenomena: the Early-Brunhes and the Mid-
189 Brunhes Events. So, even if microvertebrate based climatic reconstruction is still
190 fragmentary, they remain important and interesting because (a) they provide a range of
191 temperature and precipitation estimates that are understandable in comparison with
192 present climate; (b) they allow the testing of predicted temperature changes under
193 scenarios of future climate change; and (c) quantitative temperature and precipitation
194 estimates for past glacials and interglacials for specific regions/latitudes can help to
195 understand their effects on flora, fauna and hominids, as they are directly associated
196 with those cultural and/or biological events. All these issues will be discussed here in
197 the light of herpetofauna-based temperature estimates and their suggested thermal
198 amplitude and concluding by identifying the chronological gaps that have still to be
199 investigated.

200

201 **2. Material and methods**

202

203 Most of the climatic estimates used in this synthesis were obtained using the same
204 standardized nomenclature and methods, hence we did not encounter any of the
205 problems of differing taxonomy or methods which can often affect synthetic work.

206

207 *2.1. Small vertebrate sampling and taxonomical identification*

208

209 Standardized techniques for the recovery of small vertebrates in Pleistocene
210 archaeological sites are now applied by vertebrate palaeontologists over the whole
211 Iberian Peninsula, independently of archaeological research teams. The small vertebrate
212 fossil remains recovered from studied sites mainly consist of disarticulated bone
213 fragments collected by wet-sieving during field work campaigns. Depending on the
214 excavated surface or sampling strategies, the sediment was water-screened using
215 superimposed 10, 5 and 0.5 mm (or 0.7 mm in some cases) mesh screens and bagged by
216 square, layer and excavation levels. The microfossils were processed, sorted and
217 taxonomically classified with the naked-eye in the larger size fractions and with the help
218 of a binocular microscope under 10x magnification for the smaller size fractions. The
219 resulting cranial and post-cranial elements have been checked by a palaeoherpetologist
220 who separated amphibian and reptile remains from the bones of other small vertebrates.

221

222 The fragments were identified mainly following the general criteria given by Böhme
223 (1977), Bailon (1991, 1999), Sanchiz (1984), Esteban and Sanchiz (1985, 1990),
224 Sanchiz et al. (1993, 2002), Holman (1998) and Gleed-Owen (1998 and 2000) for frogs
225 and toads, Barahona Quintana (1996), Barahona and Barbadillo (1997) for lizards, and

226 Bailon (1991), Szyndlar (1984) and Blain (2005) for snakes. Comparisons were made
227 using the dry skeleton collections mainly of the Museo Nacional de Ciencias Naturales
228 (MNCN, Madrid, Spain), the Muséum national d'Histoire naturelle (MNHN, Anatomie
229 Comparée, Paris, France), and reference collections held at IPHES (Tarragona, Spain).
230 Specific attribution of this material rests principally on the best diagnostic elements.
231 Descriptions and illustrations of the fossil elements for each of the represented species
232 are presented in the source publications (Table 2).

233

234 2.2. *Mutual Ecogeographic Range*

235

236 As described in the source papers (see Table 2), the MER analysis for each site is based
237 on the distribution atlases of the Iberian herpetofauna (Pleguezuelos et al., 2004;
238 Godinho et al., 1999), divided into 10 x 10 km UTM squares. Climatic parameters have
239 been estimated for each UTM square using climatic maps of the Iberian Peninsula (Font
240 Tullot, 2000, based on 1961-1990 values; Ninyerola et al., 2005, based on 1951-1999
241 values). The use of a modern distributional dataset “restricted” to the Iberian Peninsula
242 is supported by the fact that most of the species represented today in the Iberian
243 Peninsula correspond to Iberian endemic species (for example *Discoglossus jeanneae*,
244 *Pelophylax perezi*, *Chalcides bedriagai*), French-Iberian species (*Pelobates cultripes*,
245 *Bufo* gr. *bufo-spinosus*, *Timon lepidus* or *Rhinechis scalaris*) or Ibero-Maghrebian
246 species (*Mauremys leprosa*).

247

248 When searching for analogous assemblages, careful attention has been paid to ensure
249 that the actual current distribution corresponds to the potential ecological/climatic
250 distribution and has not been strongly affected by other limiting or perturbing

251 parameters, such as urbanism, landscape anthropogenic impacts, predation, or
252 competition with another species. For example tortoises (*Testudo* sp.) are usually
253 excluded from the analyses because their actual distribution is too different from their
254 potential distribution. In addition, for Cueva Victoria (Murcia), *Bufo* sp. (*viridis*
255 group) has been excluded from the analysis not only because it is currently absent from
256 the Iberian Peninsula but also because it may represent an extinct taxon and the
257 imprecision of its systematic attribution hampered comparison with extant taxa (Blain et
258 al., 2010a, 2016b).

259

260 For the present synthesis we only used four climatic parameters: mean annual
261 temperature (MAT), mean temperature of the coldest month (MTC), mean temperature
262 of the warmest month (MTW), and mean annual precipitation (MAP). For an accurate
263 comparison between the different sites, sometimes located in different climatic areas
264 within the Iberian Peninsula, the difference from current values (Δ) was calculated, thus
265 allowing us to correct disparities in the estimated climate values between
266 northern/southern and/or inland/littoral sites.

267

268 2.3. *Habitat Weighting*

269

270 In addition to the climatic parameters, the representation of forested habitats (% wood;
271 Table 2) estimated from the composition of the amphibian and reptile assemblage using
272 the Habitat Weighting method (see Blain et al., 2008b for its application to
273 herpetofauna) has been compiled for each site. Even if not representing true
274 environmental successions (because of the geographical and topographical disparities
275 between sites), % wood will be interpreted here in comparison with the different climatic

276 parameters to explore potential correlations with temperature and precipitation, in order
277 to discuss and compare with the palynological reconstructions for southern Europe.

278

279 *2.4. Chronological uncertainty*

280

281 One of the main challenges of such a synthesis is to place the results into a wider,
282 ideally global, stratigraphic context such as that provided by the marine isotope
283 stratigraphy (e.g. Lisiecki and Raymo 2005). In the source papers, the correlation
284 between a particular archaeological context and the marine isotope stratigraphy has
285 usually been done using the range given by absolute (e.g. radiometric) dating at the site
286 informed by the local palaeoclimatic reconstruction. For sites where the source papers
287 provide a detailed discussion of geo- and biochronology, palaeomagnetic data and
288 numeric dates, the age uncertainties have been reported as ellipses in Figure 2.
289 Otherwise, no uncertainty is shown in the figure.

290

291 *2.5. Statistics*

292

293 For the statistical analyses, any repeated result has been deleted from the same
294 stratigraphic level in order to avoid redundancy. Linear regressions have been used with
295 the main goals of (1) evaluating patterns, if they exist, between pairs of climatic and
296 ecological variables and (2) establishing the nature and strength of their relationships
297 from the samples used in our analyses . Linear regression is an approach that permits
298 modeling of the relationship between a dependent variable (y) and, in the case of simple
299 linear regression, an independent or explanatory variable (x). In order to model such
300 relationships we use linear predictor functions (linear models):

301

$$y = a x^b$$

302 where a represents the Y-intercept and b the slope value calculated from two given sets
303 of data.

304

305 Although linear regression has been widely used for prediction, in this paper we mainly
306 use it for evaluating the null hypothesis [$H_0 (b = 0)$] that is, if the slope obtained for
307 each linear regression is equal to 0. If the p -value is <0.05 we can reject the H_0 . In
308 addition, we evaluate the strength of the relationships, denoted by the coefficient of
309 determination (R^2).

310

311 The adjustment technique used in this study is Ordinary Least Squares (OLS) which
312 aims to minimize the sum of the squares of the difference between the observed values
313 of a given dataset and the predicted ones by the linear function (that is, the sum of the
314 squares of the residuals). Regression functions were estimated using the statistical
315 package JMP 13.

316

317 **3. Results**

318

319 *3.1. Climatic and environmental synthesis*

320

321 Table 2 presents the climatic and environmental parameters compiled for this synthesis.
322 The number of observations is 52 corresponding to 10 archaeo-palaeontological sites,
323 some of them represented by different stratigraphic levels and/or different samples.
324 Despite the number of sites/levels represented in this synthesis, it is obvious from Fig. 2
325 that the records do not span the entire interval. It is the case particularly for the period

326 between MIS 16 and MIS 12 (i.e. from 650 ka to 450 ka). Correlation with the MIS
327 stages for the latest Early Pleistocene and early Middle Pleistocene (MIS 22 to MIS 17)
328 are hampered by quite large chronological uncertainties. And finally even for the period
329 between MIS 11 and MIS 6 (i.e. between 400 ka and 140 ka) where there are a larger
330 number of studied localities, many stages and substages are still entirely undocumented,
331 for example MIS 11e, 11d, the whole of MIS 10, and probably also MIS 7d to MIS 6b.

332

333 Despite the incomplete record, this synthesis allows comparison between sites and
334 between periods. Δ MAT estimates range between -3.9°C and $+4.0^{\circ}\text{C}$ relative to current
335 local temperature. Δ MTC ranges between -4.5°C and $+3.1^{\circ}\text{C}$; Δ MTW between -4.1°C
336 and $+2.6^{\circ}\text{C}$; and Δ MAP values are always positive (i.e. higher than current values)
337 reaching up to $+518$ mm in Cal Guardiola during MIS 22.

338

339 When comparing our results with the lettered marine isotope record (Railsback et al.
340 2015) (Fig. 2), it seems that negative peaks in the climate reconstructions, indicating
341 cold conditions, fit well with the isotopic changes taking place in MIS 22 (at Cal
342 Guardiola) and MIS 6 (at Estanque de Tormentas de Butarque H-02) while positive
343 peaks in our climatic reconstructions, indicating warmer conditions, fit well with the
344 isotopic patterns of MIS 11c (Gran Dolina T17) and MIS 9e (Gran Dolina T9). Also, the
345 apparently long-lasting “warmer than present” climatic conditions registered in level
346 TD6 from the Gran Dolina (T55 to T32) seems to fit with the isotopic pattern of MIS
347 21.

348

349 The environmental parameter for forest and shrub land cover (%wood) ranges between
350 a maximum value of 41.5% in Gran Dolina TD6 (T47 = MIS 21) and a minimum value

351 of 11.2% for Cueva Victoria (MIS 22) (Table 2, Fig. 2). In this context, %wood does
352 not represent any palaeoenvironmental temporal evolution as the representation of
353 woodlands also depends on the topography and soils around the different archaeological
354 sites that are not taken into account in this study. For an effective palaeoenvironmental
355 reconstruction, a sort of “ $\Delta\%$ wood” must be evaluated in order to be able to compare
356 how different from the present the woodland cover was for each of the sites.
357 Nevertheless due to the modern human impact on the Iberian landscape such
358 approximations would have been problematic and highly controversial.

359

360 *3.2. Comparison between parameters*

361

362 Table 3 summarizes the results obtained in the regression analyses. When the
363 dependent/independent variable pairs are mean annual temperature (MAT)/mean
364 temperature of the coldest month (MTC) and MAT/mean temperature of the warmest
365 month (MTW) both regressions give slopes that are significantly different from zero. In
366 addition, the coefficients of determination are high, especially that of MTC on MAT.
367 These results are expected because MAT depends on both MTC and MTW. The
368 distribution of the data in the parameter space defined by MTC on MAT (Fig. 3A) is
369 very homogeneous. Nevertheless, the Gran Dolina TD6 sample T47 falls under the
370 lower limit of the confidence interval indicating the lowest MTC value as a function of
371 the MAT value. On the other hand, ETB (H-02) exhibits a high MTW value in relation
372 to MAT (Fig. 3B).

373

374 When the independent variables are those related to temperature and the dependent is
375 the MAP, all regressions provide slopes significantly different from 0 (Fig. 4).

376 Nevertheless, it is noteworthy that MAP on MTW supplies the highest coefficient of
377 determination and the lowest p -value indicating that the MAP is better predicted by the
378 MTW (Fig. 4C). Interestingly, all the slopes present negative values indicating that
379 higher annual precipitations are associated with lower annual and seasonal
380 temperatures. The bivariate plot shows that Cal Guardiola presents a very high rain
381 regime in relation to temperature variables (Fig. 4A, B, C). On the other hand, Ambrona
382 and ETB (H-02) present a low MAP value when plotted against MAT and MTC (Fig.
383 4A, B). In addition, Ambrona and TE-URU display the lowest values when MTW is the
384 independent variable (Fig. 3C).

385

386 Consistent with expectation, Δ MTC and Δ MTW are strongly correlated with Δ MAT
387 (Fig. 5). In the first case, Cal Guardiola falls on the lower limit of the confidence
388 interval and Áridos-1 well beyond the upper one (Fig. 5A). In the second case, Cal
389 Guardiola and Valdocarros II (level 4) are located under the lower limit of the
390 confidence interval while Ambrona is above the upper limit (Fig. 5B). No Δ MT variable
391 (i.e. MAT, MTC and MTW) is significantly correlated with Δ MAP. This last fact is
392 quite surprising however most glacial modeling shows that increase in ice cover is linked
393 with an increase in winter rainfall (e.g. Vigne and Bailon, 2000; Nesje et al., 2008;
394 Hodell et al., 2008), demonstrating that temperature is not necessarily directly correlated
395 with precipitation. This lack of correlation between Δ MAP and Δ MT raises issues for
396 palaeoprecipitation reconstructions based on vertebrate proxy, especially on amphibians
397 that are strongly related with such parameters (Blain et al., 2008b, 2009).

398

399 Considering %wood as the independent variable, the only two regressions that provide
400 slopes significantly different from zero are MTW and MAP (Fig. 6A, B), the second

401 one supplying a higher coefficient of correlation and a lower p -value. Interestingly, the
402 MTW gives a negative slope (Fig. 6A) while the MAP provides a positive one (Fig. 6B)
403 indicating that as a general rule the forest cover (% wood) is higher when summers are
404 colder and the amount of rainfall is larger. In both cases, the variance in the data is high.
405 A particular note is the low value of the tree cover estimated for Ambrona and CDLB
406 (CB3) with respect to the MTW (Fig. 6A).

407

408 Lastly, when the differences between Early-Middle Pleistocene estimates and modern
409 climatic values (Δ) are used as independent variables and the % wood as the dependent
410 one, the low value of the coefficients of determination indicates a weak relationship
411 among these pairs of variables (Fig. 7). The only two regressions that provide slopes
412 statistically different from zero are Δ MAP and Δ MAP. When the independent variable
413 is Δ MAP, Cal Guardiola displays the highest % wood value and Ambrona the lowest
414 one (Fig. 7A). When the independent variable is Δ MAP, Cueva Victoria 2 shows the
415 lowest % wood and Gran Dolina-TD10 (T16) the highest one, although not exceeding
416 the upper limit of the interval of confidence (Fig. 7B).

417

418 **4. Discussion**

419

420 Interglacials (and glacials) are phenomena that can be considered widespread (probably
421 of global extent), even if their regional expression is neither globally uniform or
422 synchronous (PAGES, 2016). Numerous records are used as temperature proxies (like
423 % arboreal pollen or alkenone-based sea surface temperature estimates in marine
424 records) but most of them do not propose temperature estimates comparable with
425 modern climate values. Even after a decade of herpetofauna-based palaeoclimatic

426 quantitative estimates on the Iberian Peninsula, the reconstructed record is still highly
427 fragmentary compared with that resulting from lake and marine pollen or isotopic
428 sequences (see Fig. 2). However, they remain important and interesting because (a) they
429 provide a range of temperature and precipitation estimates that are understandable in
430 comparison with present climate; (b) they allow the testing of predicted temperature
431 changes under scenarios of future climate change (between 1 and 3°C worldwide for
432 next 100 years but up to 6°C for other scenari; e.g. Proistosescu and Huybers, 2017);
433 and (c) quantitative temperature and precipitation estimates for past glacials and
434 interglacials for specific regions/latitudes can help to understand their effects on flora,
435 fauna and hominids.

436

437 *4.1. How cold were the glacial complexes?*

438

439 The uplands of the Mediterranean are thought to have been particularly important
440 centers of biotic refuge. The mountainous peninsulas of southern Europe provided
441 refuge for temperate biota during Quaternary cold stages when northern Europe and the
442 Alps were covered by ice sheets and permafrost, and the lowland areas of the
443 Mediterranean were characterized by cold and dry steppe (Hewitt, 1999). This is
444 thought to be responsible for genetic diversity with a richness of endemic species
445 (Blondel and Aronson, 1999). Pollen records from long lacustrine sequences confirm
446 that the mid-altitudes of this region were a refugial area (wet enough but not too cold)
447 for temperate tree taxa through multiple glacial cycles (Bennett et al., 1991; Tzedakis,
448 1993).

449

450 Among the climatic reconstructions, two localities are particularly interesting for
451 documenting cold periods: Cal Guardiola (tentatively correlated with MIS 22; Agustí et
452 al., 2009) and Estanque de Tormentas de Butarque H-02 (tentatively correlated with
453 MIS6a by Blain et al., 2017b).

454

455 *4.1.1 Marine Isotope Stage 22*

456

457 The palaeontological locality from the latest Early Pleistocene of Cal Guardiola
458 (Barcelona, NE Spain) has yielded fossil remains of the following amphibians and
459 reptiles: *Bufo* gr. *bufo-spinosus* and *Epidalea calamita*, *Rana* cf. *temporaria*, cf. *Testudo*
460 s.l., cf. *Lacerta* s.l. and small sized lacertids and *Natrix* cf. gr. *natrix-astreptophora*
461 (Blain, 2005, 2009). This herpetofauna, as a whole, could be indicative of colder and
462 especially more humid climatic Mediterranean conditions than those which currently
463 occur in this area. Today in the Iberian Peninsula, *B. spinosus*, *E. calamita*, *R.*
464 *temporaria* and *N.* gr. *natrix-astreptophora* are found together in an area included
465 within the Eurosiberian bioclimatic domain. The resulting overlap of their current
466 distribution suggests a MAT = $11.6 \pm 1.9^\circ\text{C}$ and a MAP = 1168 ± 430 mm: i.e. much
467 colder (-3.9°C) and wetter (+ 518 mm) by comparison with modern values for the area.
468 MTC was estimated as $4.5 \pm 2.2^\circ\text{C}$ and MTW $18.9 \pm 1.7^\circ\text{C}$ (Agustí et al., 2009).
469 Summers were then much colder than today (-6.7°C relative to present values) and
470 winter slightly colder (-2.7°C). However this reconstruction must be nuanced by the
471 occurrence of tortoises (cf. *Testudo* s.l.), that would suggest warmer and dryer
472 conditions, even if as said before modern potential distribution for tortoises in the
473 Iberian Peninsula is largely unknown. Landscape reconstruction based on herpetofauna

474 shows the prevalence of a humid environment comprising both open herbaceous areas
475 and wooded areas (37.0 %).

476 By comparison, large mammals from Cal Guardiola have suggested temperate climatic
477 conditions with the occurrence of primates (*Macaca sylvanus* cf. *florentina*; Alba et al.,
478 2008) and hyenas (*Pachycrocuta brevirostris*; Madurell-Malapeira et al., 2009), large
479 expanses of water (indicated by the abundance of hippos) and woodlands (indicated by
480 the large representation of cervids and fallow-deer).

481 In the same way, palaeobotanical analyses (pollen and macroremains) suggested warm-
482 temperate and humid conditions and a vegetal cover composed of a mixed deciduous
483 forest with significant numbers of oaks (*Quercetum mixtum* formations).
484 Thermophilous, mesohygrothermophilous and river forest species are also present,
485 including some taxa rarely recorded for the Pleistocene, e.g., the mesocratic group of
486 species represented by *Juglans*, *Carya* and *Platanus* (Postigo Mijarra et al., 2007). In
487 addition, statistical analysis of herpetofaunal estimates shows that Cal Guardiola
488 displays high rainfall regime and tree coverage in relation to temperature (Fig. 4A, B, C;
489 Fig. 7A).

490 As a result, MER estimates for Cal Guardiola are clearly colder, whereas other proxies
491 suggest warm and humid conditions. However, close comparison between proxies is
492 hampered by the fact that the context of the herpetofaunal remains within the Cal
493 Guardiola stratigraphical sequence is not yet well understood and consequently we have
494 no way to determine whether the studied amphibian and reptile remains are exactly
495 contemporaneous with the recovered large mammals and palaeobotanical remains. In
496 addition, taphonomic studies (Madurell-Malapeira et al., 2012) suggested that the whole
497 assemblage may have been dragged down by a flood event in a mountain spring. Such a
498 flood could have transported cold-tolerant species (like *Rana temporaria*) downstream

499 from higher altitudes, thus lowering temperature estimates for Cal Guardiola.
500 Nonetheless, attribution of the cold period represented by the herpetofaunal assemblage
501 to MIS 22 agrees with the chronological range given by palaeomagnetism,
502 biochronology and absolute dating (ESR-US) for the sequence of the nearby,
503 stratigraphically correlated with Cal Guardiola, site of Vallparadis which is dated
504 between 1.0 and 0.83 Ma (Madurell-Malapeira et al., 2010; Martinez et al., 2010;
505 Lozano-Fernández et al., 2015).

506

507 Consequently, if the Cal Guardiola cold herpetofaunal assemblage corresponds to MIS
508 22 and is not affected by transport, it represents an interesting data point as it documents
509 how cold was the climate during this MIS (centred on 0.87 Ma) representing the first
510 Quaternary ice sheet expansion associated with a sea-level drop of over 100 m (Maslin
511 and Ridgwell, 2005; Muttoni et al., 2007).

512

513 Cueva Victoria is another Iberian palaeontological site recently attributed to MIS 22
514 (Gibert et al., 2016). It is a karstic cavity located near the city of Cartagena (Murcia, SE
515 Spain), first excavated in 1976. Its abundant and well preserved large mammal fauna
516 date from the late Early Pleistocene (1.6 to 0.8 Ma). It is worth mentioning that this site
517 has provided the only specimens of the African cercopithecoid *Theropithecus oswaldi*
518 recovered from Europe. It has also yielded five teeth (Gibert et al., 1995; Ferràndez-
519 Cañadell et al., 2014) and a phalanx (Martínez-Navarro et al., 2005) whose attribution
520 to the genus *Homo* (Gibert and Pons-Moyá, 1984; Ribot Trafi et al., 2012-14) greatly
521 contributed to the media coverage of the site. Earlier analysis of the fauna, based on the
522 stage of evolutionary development of *Stephanorhinus etruscus*, placed the site at 1.6 Ma
523 (Agustí et al., 1987), and Blain et al. (2008a) proposed that the normal chron at the top

524 of Cueva Victoria can best be assigned to the base of the Jaramillo event, with an
525 estimated age of 1.072 ± 0.2 Ma (MIS 31). Gibert et al. (2016) constrain the age of the
526 vertebrate remains from Cueva Victoria by palaeomagnetism, vertebrate biostratigraphy
527 and $^{230}\text{Th}/\text{U}$ dating and interpret the lower reversal (N-R) to be the end of the Jaramillo
528 magnetochron (0.99 Ma). These ages bracket the chronology of the fossiliferous breccia
529 between 0.99 and 0.78 Ma, suggesting that the capping flowstone was formed during
530 the wet MIS 19. Consequently, according to these authors, the age of the breccia in the
531 upper part of Cueva Victoria is $\sim 0.9\text{-}0.85$ Ma (i.e. MIS 22).

532

533 Two palaeoclimatic reconstructions based on herpetofaunal remains have been carried
534 out for Cueva Victoria: the first one using the collections from the first field campaigns
535 of the Museu de Geologia de Barcelona (Blain, 2005, 2009; Blain et al., 2008a; Agustí
536 et al., 2009) and then the collections from the 1984-2009 field campaigns of the Museo
537 Arqueológico Municipal de Cartagena, Murcia (Blain, 2012-2014). No information
538 associated with the material from these two collections permits a more precise
539 stratigraphical localization within the fossiliferous breccia (only the name of the
540 chambers was given on the original labels).

541

542 The first reconstruction (Blain et al., 2008a) is based on the following recovered fauna
543 of anurans and squamate reptiles: cf. *Pelodytes* sp., *Bufo* gr. *bufo-spinosus*, *Blanus*
544 *cinereus*, *Tarentola* sp., *Chalcides* cf. *bedriagai*, *Timon* cf. *lepidus* and indeterminate
545 small lacertids, *Natrix maura*, *Coronella girondica*, *Rhinechis scalaris* and *Malpolon* cf.
546 *monspessulanus* (Blain, 2005, 2009; Blain et al., 2008a). In Cueva Victoria, the overlap
547 resulting from such an assemblage suggested a MAT slightly cooler than present (-
548 1.0°C lower than at present in the area), with cooler winters but warmer summers and

549 above all higher MAP (+ 387 mm). The reconstructed landscape may correspond to an
550 open woodland environment (21.0%). These results match well with the presence in
551 Cueva Victoria of the Hermann's tortoise (*Testudo hermanni*; García-Porta, 2001),
552 whose current distribution in the Iberian Peninsula (restricted to Catalonia) is
553 characterized by MAT above 14°C and MAP below 700 mm (Cheylan, 1981; Llorente
554 et al., 2004).

555

556 The second reconstruction (Blain, 2012-2014) gives more temperate results. It is worth
557 noting that from a statistical point to view, it deviates more strongly from the general
558 trends. The faunal list of the material hosted in the Museo Arqueológico Municipal de
559 Cartagena is composed of 6 anurans (*Pelobates cultripes*, *Pelodytes* sp., *Bufo* gr. *bufo-*
560 *spinosus*, *Epidalea* cf. *calamita*, *Bufo* *viridis* s.l. and *Pelophylax perezii*), 5 lizards
561 (*Tarentola mauritanica*, *Chalcides bedriagai*, *Acanthodactylus erythrurus*, *Timon*
562 *lepidus* and a small indeterminate lacertid) and 3 snakes (*Malpolon monspessulanus*,
563 *Rhinechis scalaris* and *Vipera latastei*). This study completed previous faunal lists of
564 Blain et al. (2008a), adding *P. cultripes*, *B. calamita*, *B. viridis* s.l., *P. perezii*, *A.*
565 *erythrurus* and *V. latastei*. The large abundance of green toads (*B. viridis* s.l.),
566 Montpellier snakes (*M. monspessulanus*) and ladder snakes (*Rh. scalaris*) is indicative
567 of dry conditions, with well developed steppe and rocky environments. Evidence for
568 woody areas is rather scarce (11.2%). This reconstruction is consistent with the presence
569 of *Theropithecus*, a taxon that displayed a diet more based on C₄ plants than *Homo* in
570 Africa (Cerling et al., 2013). Reconstructed climatic parameters suggested a MAT =
571 $17.2 \pm 1.6^\circ\text{C}$, slightly lower (-0.5°C) than modern values, and MAP = 611 ± 160 mm,
572 thus higher (+282 mm) than current values.

573

574 These results seem to indicate that Cueva Victoria was formed during a cold-temperate
575 and wetter period than today but temperature estimates are far warmer than those
576 obtained for the northern Iberian site of Cal Guardiola. Consequently two hypotheses
577 can be made: 1) there was a stronger latitudinal temperature gradient than today, or 2)
578 the chronology of the Cueva Victoria upper breccia should be correlated with early MIS
579 21 and thus, as said by Gibert et al. (2016), would correspond to the first entrance of
580 *Theropithecus* into Europe during or just after MIS 22 (when climate improved but sea-
581 level was not yet high). In this second hypothesis, the second more temperate climate
582 reconstruction based on the herpetofaunal assemblage comprising green toads (*Bufo*
583 *viridis* s.l.), and representing the last appearance of this anuran group in the Iberian
584 Peninsula (Blain et al., 2010a, 2016b), would be correlated with MIS 23. This could
585 also suggest that the disappearance of *Bufo viridis* s.l. from the Iberian Peninsula at
586 that time would have been linked with the harsher conditions of MIS 22.

587

588 4.1.2 Marine Isotope Stage 8

589

590 According to the deep sea oxygen isotope records, MIS 8 does not seem to have been a
591 particularly cold glacial, at least in its early part. This means that it can be difficult to
592 securely correlate sites clearly with either MIS 8 or the end of MIS 9. The Cuesta de la
593 Bajada (Teruel, eastern Spain) herpetofaunal assemblage has recently been suggested as
594 representing cold climatic conditions during part of MIS 8 (Blain et al., 2017a). Cuesta
595 de la Bajada is a Middle Pleistocene site at which some of the earliest evidence of
596 Middle Palaeolithic stone tool traditions and primary access to fleshed cervid and equid
597 carcasses by hominins have been documented (Santonja et al., 2014, 2016),
598 (Domínguez-Rodrigo et al., 2015). The numerical ages derived from the combination of

599 ESR and OSL dating methods indicate that the lowermost level CB3 is between 317 and
600 240 ka, which encompasses MIS 8 and most of MIS 9 (Santonja et al., 2014; Arnold et
601 al., 2016; Duval et al., 2017). These dates are corroborated by the small-mammal study,
602 in particular the morphological state of *Cricetulus (A.) bursae*, *Arvicola* aff. *sapidus* and
603 *Microtus (I.) brecciensis*. This makes it possible to place the site of Cuesta de la Bajada
604 (levels CB3 and CB2) in the advanced, but not final, Middle Pleistocene (Sesé et al.,
605 2016). The large mammal assemblage composed of *Canis lupus*, *Elephas*
606 (*Palaeoloxodon*) *antiquus*, *Stephanorhinus* cf. *hoemitoechus*, *Equus chosaricus*, *Cervus*
607 *elaphus*, *Bos primigenius*, *Rupicapra rupicapra* and *Capra* sp., is also characteristic of
608 the Middle Pleistocene (Santonja et al., 2014).

609

610 The herpetofaunal assemblage from Cuesta de la Bajada is composed of at least 9 taxa,
611 including 6 anurans (*Alytes obstetricans*, *Pelodytes punctatus*, *Bufo* gr. *bufo-spinosus*,
612 *Epidalea calamita*, *Hyla* gr. *arborea-molleri*, and *Pelophylax perezii*), a small-sized
613 lacertid lizard (Lacertidae indet.), and 2 snakes (*Coronella* cf. *girondica* and *Vipera*
614 sp.). *Hyla* gr. *arborea-molleri* is the only species represented in Cuesta de la Bajada that
615 is currently absent in the area (the species is present today in the northwestern Iberian
616 Peninsula) and whose presence would suggest cool and moist climatic conditions. The
617 palaeoclimatic parameters suggest for CB2 and CB3 that MAT was much colder (-2.2°C
618 and -2.5°C, respectively) and MAP much higher (+ 291.9 and +282.3 mm) than today
619 in the Teruel area. The summer was temperate and the winter was cold, with three
620 months of mean temperatures below 6°C. Rainfall was low but its distribution was
621 regular, occurring throughout the year but with the highest levels during winter and
622 spring and lowest levels occurring in the summer (July and August) (Blain et al.,
623 2017a). Summer and winter temperatures are similarly depressed (January and July

624 1.2°C lower than today). The palaeoenvironmental reconstruction based on the
625 herpetofaunal assemblage suggests a sparsely wooded (15-20%) patchy landscape with
626 a large representation of dry herbaceous areas, and scrubland habitats together with
627 aquatic habitats. These reconstructions are consistent with other proxies recovered from
628 Cuesta de la Bajada (pollen, small and large mammals) and other European MIS 8-9
629 palaeoclimatic records (see Blain et al., 2017a), enabling correlation of levels CB2 and
630 CB3 (which are also constrained by the OSL and ESR dates), with the later part of MIS
631 8 (265-257 ka) or MIS 9b (303-290 ka).

632
633 Such a cold climate and minor woodland cover (15 to 20% of the total landscape)
634 described above are similar to that observed in level 2 of the Valdocarros II
635 archaeological site (Madrid, Spain), which is correlated to the latest part of MIS 8 just
636 before Termination III (Blain et al., 2012b). This would suggest that rather similar
637 climatic and environmental conditions were in place during these cold periods over
638 large areas of the inner Iberian Peninsula.

639
640 The archaeological site of Valdocarros II is located in an abandoned meander of the
641 Valdocarros unit. Amino-Acid Racemization provided ages of 254 ± 47 ka BP (made on
642 ostracods *Herpetocypris reptans*) and 262 ± 0.7 ka BP (made on herbivore teeth)
643 corresponding to the end of MIS 8 and the beginning of MIS 7 (Panera et al., 2011).
644 The site consists of four layers (1, 2, 3 and 4), fining upwards from silt to silty-clay,
645 each one 30-50 cm thick and several tens of meters wide. For level 2, the occurrence of
646 *Hyla gr. arborea-molleri* again, which is currently absent from large areas in the south
647 of the Iberian Peninsula, suggest cool and moist climatic conditions, whereas levels 3
648 and 4 show warmer conditions. The reconstructed climate for level 2 is relatively cold

649 with MAT 1.8°C lower than today. These cooler climatic conditions are mainly linked
650 to a greater decrease in the summer (-2.9°C) (Fig. 5B) than in the winter (-1.0°C)
651 temperatures. Even if rather low, the total amount of rainfall is higher than the current
652 level in Madrid. Environmental reconstructions based on the herpetofaunal assemblages
653 suggest that riverine woodlands are somewhat poorly represented in level 2 (less than
654 15% of the total) unlike in more temperate-warm levels 4 and 3 (with woodlands
655 reaching 34%), where the presence of *Bufo* gr. *bufo-spinosus* may indicate more stable
656 climatic conditions than in level 2.

657

658 Finally, among the Pleistocene localities of the Sierra de Atapuerca, the site called Sima
659 del Elefante in its upper part (TE-URU) has fossiliferous levels pertaining to the late
660 Middle Pleistocene (350-250 ka). Two travertine samples from the upper part of TE18
661 Unit were dated using U/Th series, giving 254.727 +13.121/-11.773 ka BP, and 307.175
662 +22.579/-18.868 ka BP (Lombera-Hermida et al., 2015). Such ages were already
663 suggested by the small-mammal biochronological studies that provided an age between
664 ca. 250-350 ka for levels TE18 and TE19, i.e. slightly younger than Atapuerca-TD10
665 and quite similar to Atapuerca-Galería (López-García et al., 2011d). At that time the
666 amphibians and reptiles from the two upper levels TE18 and TE19 were analyzed and
667 have proved to be one of the richest assemblages of all the localities of the Sierra de
668 Atapuerca (Blain et al., 2011b). The faunal list is composed of 18 taxa made up of
669 urodeles (*Salamandra salamandra* and *Lissotriton helveticus*), anurans (*Discoglossus*
670 sp., *Alytes* sp. *Pelobates cultripipes*, *Pelodytes punctatus*, *Bufo* gr. *bufo-spinosus*,
671 *Epidalea calamita*, *Hyla* gr. *arborea-molleri* and cf. *Rana* sp.), a terrestrial tortoise
672 (*Testudo* s.l.), lizards (*Lacerta* s.l., *Podarcis* sp. and *Anguis fragilis*) and snakes (*Natrix*
673 gr. *natrix-astreptophora*, *N. maura*, *Coronella* cf. *giron dica* and *Vipera latastei*). The

674 TE19 assemblage suggested a slightly warmer (+0.4°C) and moister (+95 mm) climate
675 than the current one (Blain et al., 2011b). However, the MAP was low given the
676 estimated temperatures, specifically those for the MTW (Fig. 4C). The landscape was
677 probably composed of a gallery forest (20.0%) along a quiet water river within a
678 Mediterranean environment alternating laterally between dry meadows, rocky or stony
679 areas and open scrubland.

680

681 The presence of charcoal pieces of *Pinus silvestris/nigra* in TE19 together with the
682 abundance of horses has been interpreted as an indicator of cold, dry climatic
683 conditions, with the development of open landscapes (Rosas et al., 2006). However,
684 López-García et al. (2011d) suggested that the presence of horses together with other
685 herbivores such as *Stephanorhinus hemithoecus*, *Cervus elaphus*, *Dama dama* and *Bos*
686 sp. is indicative of open forests, and the occurrence of taxa representative of temperate
687 Europe, such as *C. elaphus* and *D. dama*, could be associated with mild climatic
688 conditions. Moreover, the small mammal assemblage is dominated by temperate-
689 Mediterranean taxa such as *Iberomys brecciensis*, *Terricola atapuerquensis*,
690 *Oryctolagus* sp., *Crocidura* sp., *Miniopterus schreibersii* and *Rhinolophus euryale-*
691 *mehelyi* (López-García et al., 2011d). Ongoing studies of the sublevels within TE19
692 suggest some disparities between them and TE19f may have been much colder than
693 TE19c (Blain, unpublished data). Waiting for a new contextualization of these remains
694 and MER estimates, TE19 may correspond, taking into account dating of the underlying
695 level TE18, to the MIS 10a/9e, the MIS 9b/9a or the MIS 8a/7e transitions.

696

697 *4.1.3 Marine Isotope Stage 6*

698

699 In southwestern Mediterranean Europe, only a very few archaeo-palaeontological sites
700 document the terrestrial faunas of the penultimate glacial. Recently the minimum age of
701 the archaeological site of Estanque de Tormentas de Butarque H-02 (Madrid, Central
702 Spain) has been estimated as MIS 6, based on the occurrence of the proboscidean
703 *Palaeoloxodon antiquus* together with the rodents *Microtus brecciensis* and *M. arvalis*
704 (Laplana et al., 2015; Blain et al., 2017b). TL samples taken from the overlying level
705 yield ages of 84.6 (+12.6/-11.2), 74.9 (+10.2/-9.2) and 56.8 ± 4 ka, respectively
706 (Domínguez Alonso et al., 2009). Although this site is not directly dated, i.e. in the
707 same layer as the fossil assemblage, the ages of the overlying level provides a minimum
708 age of MIS 5 and rodent biochronology suggests a late Middle Pleistocene age between
709 MIS 8 and MIS 6 (Laplana et al., 2015).

710

711 The herpetofaunal assemblage from H-02 (ETB) is composed of at least 10 amphibians
712 and reptiles (Blain et al., 2017b): six anurans (*Discoglossus* sp., *Pelobates cultripes*, cf.
713 *Pelodytes* sp., *Bufo* gr. *bufo-spinosus*, *Epidalea calamita* and *Pelophylax perezii*), one
714 turtle (*Emys* or *Mauremys*), one or two indeterminate lizards (Lacertidae indet.) and two
715 snakes (*Natrix* gr. *natrix-astreptophora* and *Coronella girondica*). Quantitative climate
716 reconstruction applied to the herpetofaunal assemblage suggested a colder (-3.0°C) and
717 slightly wetter (+122.8 mm) climate than present. The temperature difference is greater
718 for winter ($\Delta\text{MTC} = -3.1^\circ\text{C}$) than for summer ($\Delta\text{MTW} = -1.6^\circ\text{C}$), which remains
719 reasonably temperate. A relevant aspect is the low relative amount of rain in relation to
720 annual and winter temperatures (Fig. 4A, B). Palaeoenvironmental reconstruction
721 suggests a large representation of dry environments on the overlying plateau, together
722 with a probable corridor of humid meadows and woodlands (16.9%) along the river
723 where the site is located (Blain et al., 2017b).

724

725 Even if the chronology of the site has still to be constrained, it can be correlated with
726 part of the penultimate glacial (~ 185–135 ka) corresponding to the late Saalian
727 glaciation in Europe. Global sea-level reconstructions (Thompson and Goldstein, 2006;
728 Elderfield et al., 2012; Bintanja et al., 2005) indicate a sea-level drop of more than 100
729 m towards the end of MIS 6 (after 150 ka). Sea surface temperatures were 5°C lower
730 than present as the climate approached a stable maximum glacial state, culminating in
731 one of the largest Quaternary glaciations (Margari et al., 2014). With regard to
732 temperature and precipitation quantification, several different reconstructions have
733 concluded that the climate of at least some intervals in early MIS 6 must have been
734 characterized by temperature depressions (summer and annual) of 8–9°C below modern
735 values and annual precipitation of >2000 mm (and possibly >3000 mm) in the highest
736 mountains in order to form glaciers (Hughes et al., 2007; Hughes and Braithwaite,
737 2008). Modeled atmospheric temperatures for the Northern Hemisphere suggest that
738 extremes were $17 \pm 2.7^\circ\text{C}$ below present (Bintanja et al., 2005). Long pollen sequences
739 from France have also yielded estimates for MAT and MAP (Guiot et al., 1989, 1993).
740 At La Grande Pile (Vosges), the annual temperature was 4 to 8°C lower and
741 precipitation 200 to 800 mm lower than at present in the area. In south-central France,
742 reconstructions for the Les Echets area suggest an MAT 8 to 12°C lower and
743 precipitation 400 to 600 mm less than today. Such results have also been corroborated
744 by the coleopteran assemblage studies in La Grande Pile, with a cold and continental
745 climate reconstructed for the later part of MIS 6 (Ponel, 1995). At a more global scale,
746 modeled temperature reconstructions for the EPICA Dome C record (Masson-Delmotte
747 et al., 2010), for equatorial Pacific Sea Surface Temperature (Medina-Elizalde and Lea,
748 2005) and deep ocean temperature (Zachos et al., 2001; Bintanja et al., 2005) suggest a

749 maximum difference during glacial and interglacial periods for the last 800 ka around -
750 4.0°C or -5.0°C (see Masson-Delmotte et al., 2010 fig. 7).

751

752 Consequently, the ETB (H-02) climate reconstruction may suggest that 1) temperature
753 variations were not extreme and precipitation was sufficient in southern Mediterranean
754 Europe during MIS 6 for the persistence of temperate trees (Blain et al., 2017b) or 2)
755 that the site better matches a cold period of MIS 7 (i.e. MIS 7d) or early MIS 6 and does
756 not correspond with the lowest temperatures.

757

758 *4.2. How warm were the interglacial complexes?*

759

760 Interglacials refer to warm periods, with low ice extent (high sea level); end-members of
761 the glacial cycles (PAGES, 2016). They are often defined as the most prominent peak(s)
762 within each odd-numbered marine isotopic complex and “as warm or warmer than the
763 Holocene”. In this synthesis numerous climate reconstructions show temperatures
764 warmer than present. However, because of dating uncertainties, it is often difficult to
765 correlate archaeological sites to the marine isotope stratigraphy. The highest
766 temperature within the same locality has been thus referred to be the best approximation
767 to the interglacial maximum within general positive temperatures that belong to the
768 interglacial complex as a whole. According to this synthesis, temperature
769 reconstructions higher than present levels seem to be better represented in the Middle
770 Pleistocene Spanish record than colder ones. This could be explained by the fact that
771 interglacial assemblages usually show a higher faunal diversity and are usually
772 associated with a higher intensity or duration of archaeological occupations more
773 susceptible to interest the archaeologists or to be detected.

774

775 *4.2.1 Marine Isotope Stage 21*

776

777 Among the very latest Early Pleistocene sites, the Gran Dolina (or Trinchera Dolina,
778 abbreviated as TD) TD6 level (Burgos, northern Spain) is certainly the best studied
779 archaeological site in Spain that documents a warm-temperate interglacial complex
780 before the Mid-Brunhes Event (Blain et al., 2013a). Here the compiled data are based
781 on the material from partial excavations of the TD sequence during a preliminary
782 evaluation of its archaeological and palaeontological significance known as 'Trinchera
783 Dolina Sondeo Sur' which lasted from 1993 to 1999. Hominin remains were first
784 unearthed in 1994 and 1995 from level TD6. They were dated to slightly more than 780
785 ka on the basis of palaeomagnetic and microfaunal evidence making these, at the time,
786 the oldest known hominins in Europe, and they were described as a new species, *Homo*
787 *antecessor* (Carbonell et al., 1995; Bermúdez de Castro et al., 1997). TD6 has a pre-
788 Matuyama negative polarity (>0.78 Ma) (Parés and Pérez-González, 1995, 1999).
789 Biostratigraphy confirms an Early Pleistocene age (Cuenca-Bescós et al., 1999, 2010,
790 2015, 2016; Cuenca-Bescós and García, 2007). Radiometric dating by ESR dating of
791 optically bleached quartz and U-series methods has provided an age for TD6 of between
792 800 and 880 ka (Falguères et al., 1999; Moreno García, 2011) and consequently TD6
793 has been associated with MIS 21 (Cuenca-Bescós and García, 2007; Cuenca-Bescós et
794 al., 2011; Blain et al., 2012a, 2013a).

795

796 MER estimates gave positive temperatures (between +0.8 and +2.7°C) and higher
797 rainfall (between +308 and +477 mm) for the whole TD6 sequence (Table 2). One of
798 the characteristics of such detailed climate reconstructions is that the highest value is

799 obtained for numerous spits (T50, T48, T45, T44, T43, T41, T40, T37, T36, T35, and
800 T33), and gives the impression of a long-lasting interglacial, something that is also
801 observed in marine isotope records (see Fig. 2). The reconstructed climate is temperate,
802 with a temperate summer and a cold winter (Fig. 3A, B). Rainfall is abundant and its
803 distribution is regular, occurring throughout the year, with the highest levels during
804 spring (Blain et al., 2013a). In comparison with current climatic data, the “interglacial
805 optimum values” can be estimated to be 2.7°C higher, well out of the range of the
806 standard deviation, with a quite similar increase in temperature during summer (+1.9°C)
807 and winter (+1.2°C). MAP is higher (+409 mm) than the current level and occurred
808 principally, as today, during the spring. The duration of the dry period during summer
809 (estimated for level TD6-2, i.e. T38-41; Blain et al., 2013a) is reduced with no dry
810 months, whereas today there are two dry months (July and August). This was also
811 clearly suggested by the values of the De Martonne aridity index, which is higher than
812 30 (humid climate) in TD6-2, whereas for the Burgos weather station the value is lower
813 than 30 (semi-humid climate), suggesting that today conditions are more arid than those
814 occurring during the formation of TD6-2 (Blain et al., 2013a). In conclusion, the overall
815 climate pattern in TD6 is concordant with a Mediterranean climate, with temperate
816 summers and cold winters and rainfall maximums corresponding to spring and autumn.

817

818 Reconstruction from the amphibian and reptile assemblages suggests that during the
819 formation of TD6 level there was a patchy landscape with humid meadows and woody
820 habitats. Some taxa, such as *Alytes obstetricans*, *Bufo* gr. *bufo-spinosus*, *Rana* sp.,
821 *Coronella austriaca* and *Vipera aspis*, preferentially live in open woodlands and/or
822 humid meadows. *Pelobates cultripes* and to a lesser extent *Epidalea calamita* and
823 *Pelodytes punctatus* are inhabitants of drier, open environments with poor and short

824 plant cover and with loose or stony soils, which must have been well represented in the
825 Sierra de Atapuerca calcareous substrate in the vicinity of the cave. Woodlands are
826 reasonably well represented, totalling between 26.2 and 41.5% of the landscape (Table
827 2).

828

829 Such warm and humid conditions are well supported by other proxies, such as
830 palynological studies at Gran Dolina that have documented little pollen preserved for
831 TD6 but documenting more or less open forest cover (around 45–60% arboreal pollen),
832 in which Mediterranean taxa such as *Quercus* type *ilex-coccifera*, *Olea*, *Celtis*, *Pistacia*
833 and *Coriaria* are dominant. Mesophilous taxa such as deciduous *Quercus*, *Acer*, *Tilia*,
834 *Prunus*, *Carpinus* and *Corylus* are also well represented, suggesting a temperate
835 climate, with no intensely cold conditions and rainfall sufficient to maintain deciduous
836 trees (Burjachs, 2001). The high abundance of *Celtis* seeds at TD6 is also a notable
837 proof of Mediterranean conditions (Rodríguez et al., 2011). Large mammals,
838 represented in TD6 by *Canis mosbachensis*, *Mustela palerminea* and *Lynx* sp., also
839 suggest a warm and relatively wooded landscape (Cuenca-Bescós and García, 2007).
840 Nevertheless, the presence of *Mammuthus* sp. shows that open country was also
841 significant at this time. The presence of Mediterranean taxa towards the top of TD6
842 suggests a temperate climate, coinciding with the Mediterranean character of the large
843 porcupine *Hystrix refossa* (Laplana and Cuenca-Bescós, 1996; Cuenca-Bescós et al.,
844 2005). In addition, the presence of *Castor fiber*, the giant shrew *Dolinasorex glyphodon*
845 and *Miomys savini* is notable (Cuenca-Bescós et al., 2005, 2017; Rofes and Cuenca-
846 Bescós, 2009; Lozano-Fernández et al., 2013), indicating the existence of a permanent
847 water stream in the vicinity of the site. Similarly, the birds are predominantly species of
848 open-country and bushland habitats, while the presence of waterfowl (*Anas* sp.) and

849 waders (*Limosa limosa*, *Scolopax rusticola*) constitutes additional evidence supporting
850 the existence of a large body of water (Sánchez-Marco, 1999).

851

852 4.2.2 Marine Isotope Stage 19

853

854 Again in the Sierra de Atapuerca, level TD8 of the Gran Dolina is considered the first
855 Middle Pleistocene fossiliferous level of this sequence. The TD8 level is formed by a
856 succession of brecciated flows of red lutites with gravels and boulders (Parés and Pérez-
857 González, 1999). The Matuyama-Brunhes Boundary has been identified between the
858 TD7 and TD8 levels (Parés and Pérez-González, 1999). In order to date this deposit,
859 several samples were analyzed with different methods. An average age of 600 ka was
860 obtained by ESR and U-series from samples collected from the middle part of the
861 sedimentary deposit (602 ± 52 kyr) (Falguères et al., 1999), thus, it correlates with MIS
862 15. On the other hand, the range of error of one TL date from the base of TD8
863 overlapped the Matuyama-Brunhes Boundary (820 ± 140 kyr) (Berger et al., 2008).
864 Faunal remains were recovered from the middle to lower part of TD8 (the upper part is
865 sterile). The small-mammal assemblage from TD8 corresponds to an older assemblage
866 called TD8a by Cuenca-Bescós et al. (1999) and is characteristic of Atapuerca Faunal
867 Unit 5 (local faunal zones), which corresponds to changes between the Early and
868 Middle Pleistocene (Cuenca-Bescós et al., 2010, 2011, 2016). Sublevel TD8b is
869 characterized by the disappearance of *Mimomys savini* and is now considered to be a
870 different stratigraphic unit called TD8/9. In addition TD8 is peculiar in retaining a
871 species of the giant deer genus *Eucladoceros* and a small rhinoceros. Such a small
872 rhinoceros is common in the late Early Pleistocene. The persistence of these forms

873 suggests that TD8 belongs to the oldest Middle Pleistocene (Blasco et al., 2011)
874 consistent with an attribution to MIS 19.

875

876 The studied amphibians and reptiles derive from the same test pit of ‘Dolina Sondeo
877 Sur’ dug in TD8 during the 1994 field season. The herpetofaunal assemblage is
878 composed of 8 anurans (*Alytes obstetricans*, *Pelobates cultripes*, *Pelodytes punctatus*,
879 *Bufo* gr. *bufo-spinosus*, *Epidalea calamita*, *Hyla* gr. *arborea-molleri*, *Rana* sp., and
880 *Pelophylax* sp., 2 lizards (*Blanus cinereus* and Lacertidae indet.), and 5 snakes (*Natrix*
881 cf. gr. *natrix-astreptophora*, *Natrix* cf. *maura*, *Coronella austriaca*, *Rhinechis scalaris*,
882 and *Vipera* cf. *aspis*). Reconstructed climate is warmer (+1.7°C) and wetter (+409 mm)
883 (Blain et al., 2009) in a similar way to that previously described for MIS 21. A warm
884 climate is coherent with the presence of tortoise (*Testudo* sp.). Pollen studies show an
885 association of temperate Mediterranean woodlands with several Atlantic taxa based on
886 the presence of *Castanea* and *Quercus*, *Betula*, *Acer*, *Alnus*, *Hedera*, *Fagus* and *Salix*
887 (García-Antón, 1989), also suggesting a temperate and humid climate during the
888 formation of TD8.

889

890 4.2.3 Marine Isotope Stage 17

891

892 In the Iberian Peninsula, the site of Cúllar Baza 1 (Granada, southeastern Spain) has
893 been correlated with MIS 17 with an age of 700-600 ka based on the recovered lithic
894 industries (Vega Toscano, 1989), the evolutionary stage of arvicolines (Ruiz-Bustos and
895 Michaux, 1976; Sesé, 1989; Sesé et al., 2016; Agustí et al., 2009, 2010) and the large
896 mammal association that has been correlated with Ponte Galeria Faunal Unit (i.e. MIS
897 18-17; Florindo et al., 2007). It should be noted that some AAR datings yielded an age

898 of 476 ± 24 ka (Ortiz et al., 2000) and 441 ± 27 ka (Torres et al., 1997) for the site,
899 suggesting that it has to be correlated with MIS 11. However such estimates are not
900 coherent with previous studies.

901

902 MER estimates for Cúllar Baza 1 rely on the squamate fauna studied by Barbadillo
903 (1989): *Blanus cinereus*, *Chalcides* cf. *bedriagai*, *Acanthodactylus* cf. *erythrurus*,
904 *Timon* cf. *lepidus*, *Podarcis* sp., cf. *Natrix* sp. and *Rhinechis scalaris*. No amphibians
905 have ever been described from this site, perhaps because of the small size of the sample
906 or taphonomic bias. The squamate assemblage suggests a warm and dry climate (drier
907 than previous Early Pleistocene periods), with the development of dry meadows, rocky
908 areas and Mediterranean open forest areas. The MER method estimates MAT to be 16.5
909 ± 2.2 °C (i.e. $+4.0$ °C in relation with present) and MAP to be 568 ± 204 mm (i.e. $+268$
910 mm in relation with present) (Agustí et al., 2009, 2010).

911

912 According to marine isotope records, MIS 17 does not seem to have been particularly
913 warmer than other interglacials in the marine oxygen isotope record (see for example
914 Fig. 2). The fact that reconstructed temperatures for Cúllar Baza 1 are the highest of all
915 the herpetofauna-based reconstructions may signify that 1) the site is coeval with a
916 particular warm maximum of MIS 17 (i.e. MIS 17c; Fig. 2) or 2) that interglacial
917 warmth was more pronounced in southern Spain or in the continental Guadix-Baza
918 basin than the global record.

919

920 *4.2.4 Marine Isotope Stage 11*

921

922 Three herpetofaunal assemblages in the Iberian Peninsula have been referred to MIS 11
923 (Blain et al., 2015): the base of level TD10 of Gran Dolina (TD10.3) correlated with
924 MIS 11c, Áridos-1 correlated with MIS 11b and Ambrona (AS4 and AS3) correlated
925 with MIS 11a. Compared with today, reconstructed mean annual temperature varies
926 from +2.7 to +0.3°C and mean annual precipitation varies from +311.7 to +74.4 mm,
927 suggesting a progressive decrease in temperature and rainfall from the fully interglacial
928 conditions of MIS 11c to the end of MIS 11. The presence of woodland areas is also
929 well substantiated throughout the duration of MIS 11, at least during the interglacial and
930 interstadial periods (Blain et al., 2015).

931

932 T17 ('Talla 17', an artificial excavation layer within TD10.3) has been correlated with
933 the MIS 11c interglacial on the basis of reconstructed mean annual temperatures which
934 point to a much higher temperature for that archaeological sample than for the other
935 samples from TD10.3 (Blain et al., 2012a). Attribution to MIS 11 relies on
936 biochronological data (middle part of the Middle Pleistocene) and is corroborated by
937 numeric datings, with a combined ESR/U-series age of around 430 ka for the base of
938 level TD10.3 (Berger et al., 2008; Falguères et al., 2013). Higher temperatures obtained
939 for this level are due to the presence of a typical Mediterranean species (*Pelobates*
940 *cultripes*), but the assemblage also included some Eurosiberian taxa (*Rana* sp. and
941 *Vipera aspis*) and the presence of *Hyla* gr. *arborea-molleri*, which is currently absent
942 from large areas in the south of the Iberian Peninsula. The MAT was 12.9°C and the
943 MAP was 867 mm. The reconstructed climate was found to be temperate with warm
944 summers and cold winters, with the mean temperature of the coldest month equal to
945 5.2°C. The total amount of rainfall is higher (Δ MAP= +311.7 mm) than the current
946 level in Burgos.

947

948 While there are numerous palaeoclimatic records of MIS 11 in northern and central
949 Europe (UK, Germany, Czech Republic, France and Poland), such records are relatively
950 scarce in southern Europe (Candy et al., 2014), with just a few marine cores from the
951 western margin of the Iberian Peninsula (de Abreu et al., 2005; Desprat et al., 2005;
952 Martrat et al., 2007; Voelker et al., 2010) and the classic lacustrine pollen records from
953 Ioannina and Tenaghi Philippon in Greece (Tzedakis et al., 2001, 2006; Tzedakis,
954 2005). Moreover, most of these Iberian offshore records only document SSTs, while a
955 single pollen-based analysis by Desprat et al. (2005) described the potential MIS 11
956 climate and environmental succession on the Iberian land mass (deep-sea core MD01-
957 2447). In this analysis the warmest peak of MIS 11c is characterized by MTC and
958 MTW similar to current values and lower MAP (-100 mm). However in many records,
959 MIS 11c is characterized as one of the warmest interglacials of the last 800 ka (PAGES,
960 2016), even warmer than the Holocene. Temperature estimates vary from place to place,
961 but range from similar to the present to warmer (1 or 2 °C above modern levels; Kukla,
962 2003; Rousseau, 2003), in accordance with the herpetofauna-based reconstructed
963 temperatures presented here for the whole interglacial complex.

964

965 *4.2.5 Marine Isotope Stage 9*

966

967 Progressing up through the Gran Dolina TD10 sequence, the next temperature
968 maximum has been found for spit T9 (Fig. 2). In accordance with the numeric datings
969 (around 300 ka) this spit has been correlated with MIS 9 (Blain et al., 2012a).
970 Reconstructed temperature is lower than for spit T17 (MIS 11c), yet a warmer (ΔMAT
971 = +2.8°C) and wetter ($\Delta\text{MAP} = 292 \text{ mm}$) climate than at present in the Burgos area is

972 indicated. Such results are based on samples from the 1993 partial excavations of the
973 TD sequence. Further contextualization of these temperature and precipitation estimates
974 and correlation with the new stratigraphical separations of TD10 by sublevels will be
975 complemented in the future by the ongoing studies on the mammal and herpetofaunal
976 material recovered during the excavation campaigns since 2010 on the whole surface of
977 the level TD10.

978

979 *4.2.6 Marine Isotope Stage 7*

980

981 MIS 7 is rather poorly known in the Iberian Peninsula. Besides the spit T1 (TD10) in
982 the Gran Dolina stratigraphical sequence carefully correlated with MIS 7 by Blain et al.
983 (2012a) (Figure 2), few sites have been attributed to MIS 7.

984

985 New excavations conducted between 2001 and 2005 at Mollet Cave (Serinyà, north-east
986 Spain), led to a more precise characterization of the archaeological and palaeontological
987 contents of level 5, recovery of small vertebrates, and collection of samples for
988 radiometric dating (Maroto et al., 2012; López-García et al., 2014). The results obtained
989 using U-series disequilibrium dating ascribed an age of ca. 215 ka to Level 5, which
990 would correspond to MIS 7c. The faunal association suggests a landscape formed by an
991 open and humid woodland characteristic of an interstadial phase. The herpetofaunal
992 assemblage is represented by a few ubiquitous species as *Pelodytes punctatus*, *Bufo* gr.
993 *bufo-spinosus* and *Vipera* sp. that unfortunately did not permit the application of the
994 MER method.

995

996 Close to the Mediterranean coast another cave, the Cova del Rinoceront (Barcelona,
997 northeastern Spain), has delivered a small vertebrate assemblage, in levels VII and VIII,
998 that has been correlated with MIS 7/6. The exposed stratigraphy has a thickness of 11 m
999 and a width of between 1.5 and 3 m. The sequence can be divided into three main units
1000 (Units 1, 2 and 3), comprising eight layers designated I to VIII (from top to bottom).
1001 The publication by Daura et al. (2015) and López-García et al. (2016) showed that the
1002 chronological range of the upper part of sequence (layers I to III), as determined by U-
1003 Th dating and microfaunal evidence, relates to MIS 5, in agreement with its faunal
1004 composition that indicates widespread temperate conditions (probably equivalent to
1005 MIS 5e), mainly illustrated by the presence of the Mediterranean tortoise.
1006 Even if the maximum age indicated for layer VII by U-Th (~175 ka) implies that layer
1007 VII post-dates MIS 7, the lower part of the sequence's mammal assemblage suggests
1008 warm climatic conditions that do not fit well with an attribution to MIS 6 but better with
1009 an attribution to MIS 7 as the layer VII assemblage is very similar to other small
1010 vertebrate associations from the Mediterranean zone, such as Bolomor level 5 (dated to
1011 ca. 228 ka; Guillem-Calatayud, 2000), Mollet cave (dated to ca. 215 ka; Maroto et al.,
1012 2012; López-García et al., 2014), Valdocarros II (MIS 8 to MIS 7; Sesé et al., 2011a;
1013 Blain et al., 2012b), la Baume Bonne (MIS 8/7; Hanquet, 2011) and Cèdres (MIS 7;
1014 Hanquet, 2011). Consequently further dating would be of interest for better constraining
1015 the age of the lower part of Cova Rinoceront (levels VII and VIII) as well as a detailed
1016 study of the herpetofaunal assemblage that already furnished a nice amphibian and
1017 reptile association with 3 anurans (*Pelobates cultripes*, *Bufo* gr. *bufo-spinosus*,
1018 *Pelophylax* sp.), one lizard (*Anguis fragilis*), and 3 snakes (*Natrix* gr. *natrix-*
1019 *astreptophora*, *Malpolon monspessulanus*, *Vipera* sp.) (Daura et al., 2015; López-
1020 García et al., 2016).

1021

1022 Recently new datings around 200 and 235 ka have been obtained for the site of Preresá
1023 (Manzanares valley, SE Madrid), formerly attributed to MIS 5a (Rubio-Jara, 2011; Sesé
1024 et al., 2011b; Blain et al., 2013c; Panera et al., 2014), and thus suggesting an age
1025 comprised between MIS 7 and early MIS 6 (Moreno et al., in press). MAT 0.3°C higher
1026 than current values obtained for the Preresá herpetofaunal assemblage (Blain et al.,
1027 2013c, in press) may suggest that this site would better be placed, if referring to the new
1028 dating, within MIS 7 than MIS 6. Anyway new analyses must be done to confirm the
1029 MIS attribution of this site.

1030

1031 Finally, as already stated above, the herpetofaunal assemblage from Estanque de
1032 Tormentas de Butarque (H-02) correlated with MIS 6a could also potentially be
1033 correlated with MIS 7d (Blain et al., 2017b, in press). Similarly to MIS8/9, the
1034 differentiation between cold stages of MIS 7 and MIS 6 is far from easy due to the large
1035 chronological uncertainty of the sites under study.

1036

1037 *4.3. Climate pattern, thermal amplitude and coherence of MER estimates*

1038

1039 *4.3.1 Climate pattern and vegetal cover*

1040

1041 Independently of the values of MER estimates, the regression analyses (OLS: Ordinary
1042 Least Squares) raised on one hand that although MTW is strongly correlated with MAT,
1043 the parameter that best drives MAT is MTC. On the other hand, MAP is more correlated
1044 with MTW than with MAT or MTC. In addition, %wood is negatively correlated with
1045 MTW and positively with MAP. MTW and MAP thus seem to be the decisive climatic

1046 parameters for % wood in Mediterranean environments. It is not surprising as today one
1047 of the most limiting factors for fauna and flora in the Mediterranean climate area is the
1048 period of aridity (intensity and length) during summer months (e.g. Blondel and
1049 Aronson, 1999). However MTC has also been said to be, together with MAP, an
1050 important factor having a strong influence on the vegetation and on the formation of
1051 steppe landscape in the Iberian Peninsula (e.g. Suarez Cardona et al., 1992). In our case,
1052 it is probable that even if it fluctuates, MTC does not reach temperatures cold enough to
1053 have had a real impact on % wood. MAP in the MER reconstructions is always higher
1054 than present levels in the Iberian Peninsula. A weak correlation between MAP and
1055 temperature parameters has been found. This suggests that the relation between
1056 temperature and precipitation must have been more complex, and that further
1057 investigations must be done on the distribution of rainfall during the year (winter vs.
1058 summer precipitation) in relation to temperature related to increasing anticyclonic
1059 circulation over the region, causing a northward or southward shift of the mid-latitude
1060 storm track (i.e. Giorgi and Lionello, 2008).

1061

1062 As far as Habitat Weighting estimated local extensions of forest area (% wood) is
1063 concerned, based on the proportion of the amphibian and reptile assemblage with
1064 affinities for open woodland areas in a particular archaeological site, we show here that
1065 the forest cover seems to be higher when summers are colder and the amount of rainfall
1066 is larger. Even if such an assumption is biologically or ecologically coherent, woodland
1067 cover seems to be equally represented between glacial and interglacial intervals, with
1068 the exception of some particular low percentages during MIS 22 (Cueva Victoria) and
1069 MIS 6 (ETB-H02). During interglacial periods % wood reaches only 30-40%. This fact
1070 seems to be in disagreement with pollen studies that usually associate higher Arboreal

1071 Pollen levels with interglacial periods, so higher MAT (and higher MAP, at least during
1072 certain portions of the interglacials). Consequently, amphibians and reptiles do not seem
1073 to register any strong differences in forest cover between glacial and interglacials. Two
1074 possible reasons for this: (a) there were no major changes in forest cover at the site
1075 scale; (b) there were changes in forest cover but the herpetofauna does not register
1076 them. In support of (a), perhaps the sites were situated within refugial areas for
1077 temperate trees. Unfortunately pollen reconstructions at these sites are not rich enough
1078 (particularly in Atapuerca) for documenting the real extent of the vegetal cover. In
1079 support of (b), amphibian and reptile assemblages represent time periods long-enough
1080 to encompass both warm and cold intervals. This last hypothesis regarding the
1081 refugia/stable environment argument might be related to the sedimentation in the cave
1082 or also, as argued for a site like Sima del Elefante TE-URU, to the stratigraphical
1083 precision used for the microvertebrate analysis.

1084

1085 *4.3.2 Thermal amplitude*

1086

1087 What about the thermal amplitude or intensity proposed by MER reconstructions? As
1088 we saw MER climate estimates oscillate roughly between +4°C and -4°C for the
1089 Mediterranean environments. Such intensities are coherent with global records like
1090 Epica Dome C (Masson-Delmotte et al., 2010) but far away from other continental
1091 climate reconstructions such as in central France or northern Germany pollen estimates
1092 (see for example the discussion about MIS 6, with Δ MAT up to -8°C in comparison
1093 with current temperature in mountain areas of the Balkan Peninsula; Hughes et al.,
1094 2007), the reconstructed surface air temperature by Bintanja et al. (2005) suggesting an
1095 extreme of 17°C below present for glacial periods during the last 800 ka or the land-

1096 based proxy surface air temperature anomalies in Eurasia for the Last Glacial Maximum
1097 of -12 to -20°C (Guiot et al., 1993, 1999, 2000; Kageyama et al., 2001, 2006; Allen et
1098 al., 1999). Because of the lack of comparative terrestrial temperature estimates in the
1099 western Mediterranean, it is difficult to know whether our estimate is too warm or the
1100 climate in the Mediterranean area was different (milder or much warmer) in comparison
1101 with other places, altitudes or latitudes. In this context, in our opinion, one of the main
1102 questions is where to place the “0” when comparing with present day climate. Most
1103 climate records do not help in answering such a question as it is often difficult to know
1104 exactly if the reference period is taken for present or for the Holocene maximum; and
1105 how good are reconstructions for the Holocene maximum? Such a calibration of the
1106 palaeoclimate records would help in answering which periods were colder than present
1107 measurements (i.e. 1951-1999) and also to appreciate if interglacials were warmer (and
1108 how much) than today rather than the Holocene maximum. Such data thus would permit
1109 to compare directly vegetation belt distribution in the past or to understand the
1110 palaeobiogeography of some extant species at a precise moment of the Pleistocene.

1111

1112 For discussing such an issue, the comparison with the composite western Iberian
1113 Margin alkenone-based SST record published by Rodrigues et al. (2011) is very
1114 interesting (Fig. 8). This composite record covers the last 600 ka and comes from cores
1115 MD03-2699 (MIS 1-2 and MIS 9 to MIS15; Rodrigues et al., 2011) and MD01-2443
1116 and MD01-2444 (from MIS 1 to MIS 11; Martrat et al., 2007). This is one of the few
1117 records where the comparison with modern temperature is explicitly done (grey areas
1118 on Fig. 8). When compared with the MER estimates it seems, even if such direct
1119 comparison is again hampered by the chronological uncertainties, that MER estimates

1120 are coherent with SST values of the western Iberian Margin. Such a pattern may be
1121 completed in the future by the inclusion of the Late Pleistocene in the comparison.

1122

1123 *4.3.3 Early and Mid-Brunhes Events*

1124

1125 The Mid-Brunhes Event (MBE) corresponds to a climatic transition between MIS 13
1126 and 11 that separates two climatic modes (Fig. 2): (1) Early-Middle Pleistocene
1127 interglacials (780–450 ka), which are characterized by only moderate warmth, and (2)
1128 Middle and Late Pleistocene interglacials (occurring after 450 ka), which are
1129 characterized by greater warmth consistent with, or warmer than, the Holocene. This
1130 event has been observed in a variety of long-term climate records such as the Mapping
1131 Spectral Variability in Global Climate Project (SPECMAP) and the European Project
1132 for Ice Coring in Antarctica (EPICA), many records of sea-surface temperature, and
1133 some long-term speleothem records, but its effect on terrestrial systems is still poorly
1134 understood due to the absence of detailed long-term records of environmental change
1135 (Tzedakis et al., 2006, 2009; Candy et al., 2010). Through their examination of the
1136 British terrestrial sequence, Candy et al. (2010) showed that interglacial climates during
1137 the early Middle Pleistocene were as warm as those that occurred during the late Middle
1138 and Late Pleistocene, suggesting that the MBE was not a global climatic transition, but
1139 was restricted to specific regions, in particular to higher latitudes of the Southern
1140 Hemisphere.

1141

1142 The longest small-vertebrate bearing section in the Iberian Peninsula is represented by
1143 the site of Gran Dolina (Atapuerca), with sediments that document from 1 Ma to
1144 approximately 200 ka years ago (with an important hiatus at the beginning of the

1145 Middle Pleistocene). To date ~40,000 amphibian and squamate bone fragments have
1146 been studied, representing at least 20 taxa, including newts, toads and frogs,
1147 amphisbaenians, lacertids, anguids, and snakes. Such an assemblage permitted the
1148 application of climatic and environmental reconstruction methods to the whole
1149 sequence. The analysis of the differences between the successive interglacial peaks
1150 revealed that (Blain et al., 2012a): 1. Post-MBE interglacials were warmer than pre-
1151 MBE interglacials in accordance with the MBE climate transition as documented by ice
1152 (EPICA and SPECMAP) and sea-surface temperature records; 2. Pre-MBE interglacials
1153 were warmer than present day; 3. The reconstructed MIS 11 mean annual temperature is
1154 slightly warmer than MIS 9, and much warmer than MIS 7 in northern Spain (MIS 5
1155 being absent from the Gran Dolina record); and 4. Post-MBE interglacials had lower
1156 rainfalls than pre-MBE interglacials, resulting in the increasing development of open
1157 dry environments on the Iberian Peninsula. However reappraisal of the conclusion by
1158 Blain et al. (2012a) through the present compilation of data shows that MIS 17 seems to
1159 have been much warmer than any post-MBE interglacials. Such a high temperature
1160 level reconstructed for Cúllar-Baza 1 would be consistent with the observation of Candy
1161 et al. (2010) for the British terrestrial sequence that MBE is not observable in Western
1162 Europe. However conclusions are hampered by the fact that we still lack data for most
1163 of the pre-MBE interglacials like for MISs 13a and 15a and 15e.

1164

1165 Another climate event, the Early Brunhes Event (EBE) suggests a shift to more extreme
1166 glacials between MIS 18 and 16 that separates two climatic modes (Fig. 2): (1) Early-
1167 Middle Pleistocene glacials (780–660 ka), which are characterized by only moderate
1168 cold, and (2) Middle and Late Pleistocene glacials (occurring after 660 ka), which are
1169 characterized by harsher cold maxima consistent with, or colder than, the Last Glacial

1170 Maximum (MIS 2). According to the estimates presented here, MIS 22 seems to have
1171 been as cold as MIS 6 and MIS 8 estimates. In a same way as for MBE, the EBE is
1172 difficult to be appreciated in our reconstructions because of the lack of data for many
1173 glacial periods (i.e. MIS 10a, 12a, 14a, 14c, 16a, 18a, 18e, 20a and 20c) and also mainly
1174 because of the large chronological uncertainty for sites that document cold climate
1175 making difficult to know if they correspond to the glacial maximum or to a less cold
1176 stadial period.

1177

1178 **5. Conclusions**

1179

1180 A decade of amphibian- and reptile-based climate reconstructions carried out for the
1181 Iberian Peninsula using the Mutual Ecogeographic Range method is reviewed in order
1182 to present a regional synthesis from MIS 22 to MIS 6. Conclusions are as follows:

1183

1184 1. Despite the number of sites/levels represented in this synthesis, the records do not
1185 cover the entire interval. It is the case particularly for the period between MIS 16 and
1186 MIS 12 (i.e. from 650 ka to 450 ka). Correlation with the MIS stages for the latest Early
1187 Pleistocene and early Middle Pleistocene (MIS 22 to MIS 17) are hampered by quite
1188 large chronological uncertainties. And finally even for the period between MIS 11 and
1189 MIS 6 (i.e. between 400 ka and 140 ka) where there are a larger number of studied
1190 localities, many stages and substages are still entirely undocumented, for example MIS
1191 11e, 11d, the whole of MIS 10, and MIS 7d to MIS 6b.

1192

1193 2. This synthesis allows comparison between sites and between periods. Δ MAT
1194 estimates range between -3.9°C and $+4.0^{\circ}\text{C}$ relative to current local temperature.

1195

1196 3. Independently of the amplitude and intensity of MER estimates, the statistical
1197 analyses highlighted that although MTW is correlated with MAT, the parameter that
1198 best drives MAT is MTC. MAP is more correlated with MTW than with MAT and
1199 MTC. %wood is negatively correlated with MTW and positively with MAP. MTW and
1200 MAP (i.e. summer aridity) thus seem to be the most important climatic parameters for
1201 %wood in Mediterranean environments.

1202

1203 4. As far as Habitat Weighting estimated local extensions of forest area (%wood) is
1204 concerned, amphibians and reptiles do not seem to register any strong differences in
1205 forest cover, such as those documented by pollen records, between glacial and
1206 interglacials. Either there were no major changes in forest cover at the site scale, or
1207 changes in forest cover were not recorded by the herpetofauna. Further studies are
1208 needed to document if, perhaps the sites were situated within refugial areas for
1209 temperate trees or if amphibian and reptile assemblages represent time periods long-
1210 enough to encompass both warm and cold intervals.

1211

1212 5. The Mid-Brunhes Event (MBE) previously documented in the sequence of Gran
1213 Dolina (Atapuerca; Blain et al., 2012a), is challenged by the climate reconstructions of
1214 the site of Cúllar-Baza 1 (Granada, SE Spain). MIS 17 seems to have been much
1215 warmer than any post-MBE interglacials and thus would suggest in accordance with
1216 observations by Candy et al. (2010) for the British terrestrial sequence that MBE is not
1217 observable in Western Europe. However conclusions are hampered by the fact that we
1218 still lack data for most of the pre-MBE interglacials like for MISs 13a and 15a and 15e.

1219

1220 6. In a same way as for MBE, the Early Brunhes Event (EBE) is difficult to be
1221 appreciated in our reconstructions because of the lack of data for many glacial periods
1222 and also mainly because of the large chronological uncertainty for sites that document
1223 cold climate in terms of knowing if they correspond to the glacial maximum or to a less
1224 cold stadial period. However MIS 22 (Cal Guardiola) seems to have been as cold as
1225 MIS 6 (ETB-H-02).

1226

1227 **Acknowledgements**

1228

1229 This paper is fruit of the workshop “Coping with Climate: The Legacy of *Homo*
1230 *heidelbergensis*” held at the University of Brighton from 2nd to 4th February 2017. We
1231 thank the organizers Dr. Rob Hosfield (University of Reading) and Dr. James Cole
1232 (University of Brighton) for their kind invitation, helpful discussions and encouragement
1233 during the meeting. We strongly acknowledge the numerous and discerning comments
1234 of the two reviewers Salvador Bailon (Paris) and Krister Smith (Frankfurt). This paper
1235 has been mainly funded by the University of Reading and also by projects CGL2016-
1236 80000-P (Spanish Ministry of Economy and Competitiveness) and 2017SGR-859
1237 (Generalitat de Catalunya).

1238

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2401 Captions

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2403 Figure 1. Geographical location within the Iberian Peninsula of the Early-Middle
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2422

2423 Figure 3. Biivariate plot using as independent variable MAT. A: MTC on MAT; B:
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2425

2426 Figure 4. Bivariate plot using as dependent variable MAP. A: MAP on MAT; B: MAP
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2429 Figure 5. Bivariate plot using as dependent variable Δ MAT. A: Δ MAT on Δ MTC; B:
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2455 vegetative activity period (VAP) and drought length (D). References: ¹Brattstrom
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2468 Jeannet (2009, 2010), ³⁵Manzano (2015), ³⁶Vieites et al (2009), ³⁷Holden et al. (2013).

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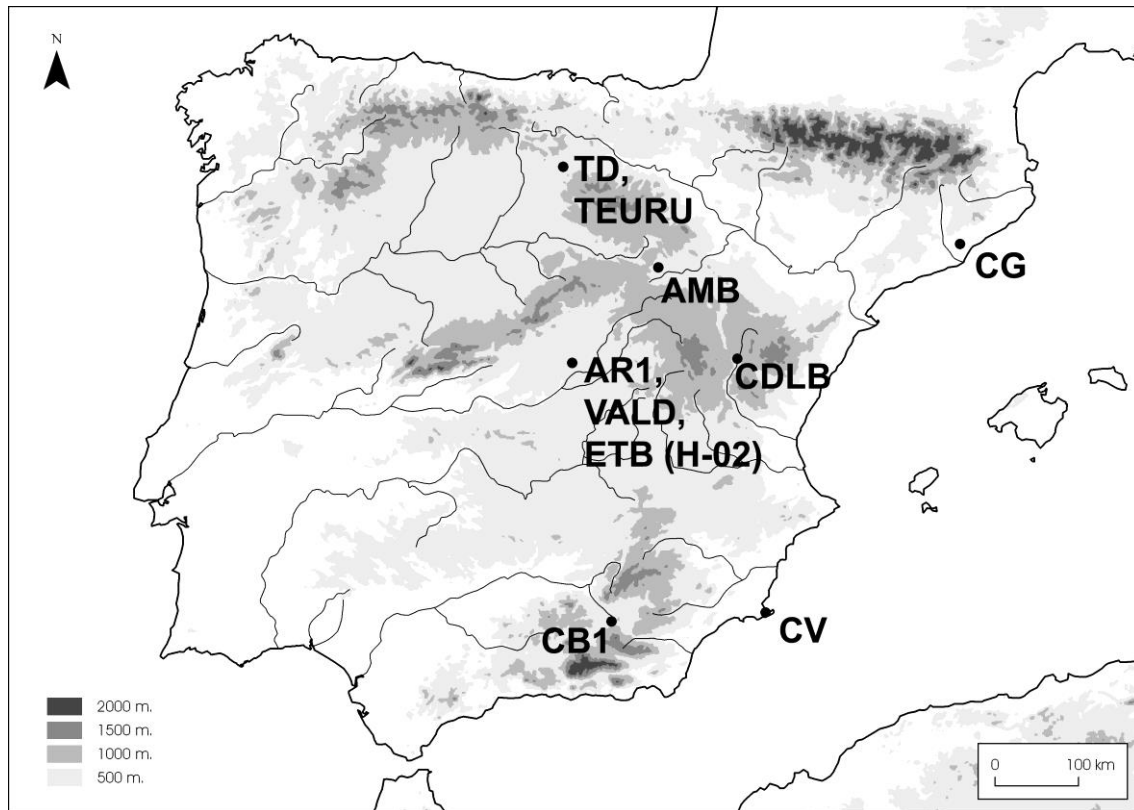
2470 Table 2. Herpetofauna-based Early-Middle Pleistocene Iberian climate and
2471 environmental reconstructions. Abbreviations: Marine Isotope Stage (MIS), mean
2472 annual temperature (MAT), mean temperature of the coldest month (MTC), mean
2473 temperature of the warmest month (MTW), mean annual precipitation (MAP),
2474 representation of woodland and woodland margins in the reconstructed environment
2475 (%wood), standart deviation (SD), difference with current value (Δ). References:
2476 ¹Agustí et al. (2009), ²Blain et al. (2008a), ³Blain (2012-2014), ⁴Blain et al. (2008b),
2477 ⁵Blain et al. (2009), ⁶Blain et al. (2012a), ⁷Blain et al. (2013a), ⁸Blain et al. (2015),
2478 ⁹Blain et al. (2014b), ¹⁰Blain et al. (2017a), ¹¹Blain et al. (2011b), ¹²Blain et al. (2012b),
2479 ¹³Blain et al. (2017b). Grey bands represent the sample that corresponds to the warmest
2480 temperature and consequently have been correlated with the interglacial peak (Blain et
2481 al., 2012a).

2482

2483 Table 3. Descriptive statistics of regression analyses (OLS: Ordinary Least Squares); N:
2484 sample size; R²: coefficient of correlation; *a*: Y–intercept; *b*: slope; H₀ (*b*=0): null
2485 hypothesis for slope zero.

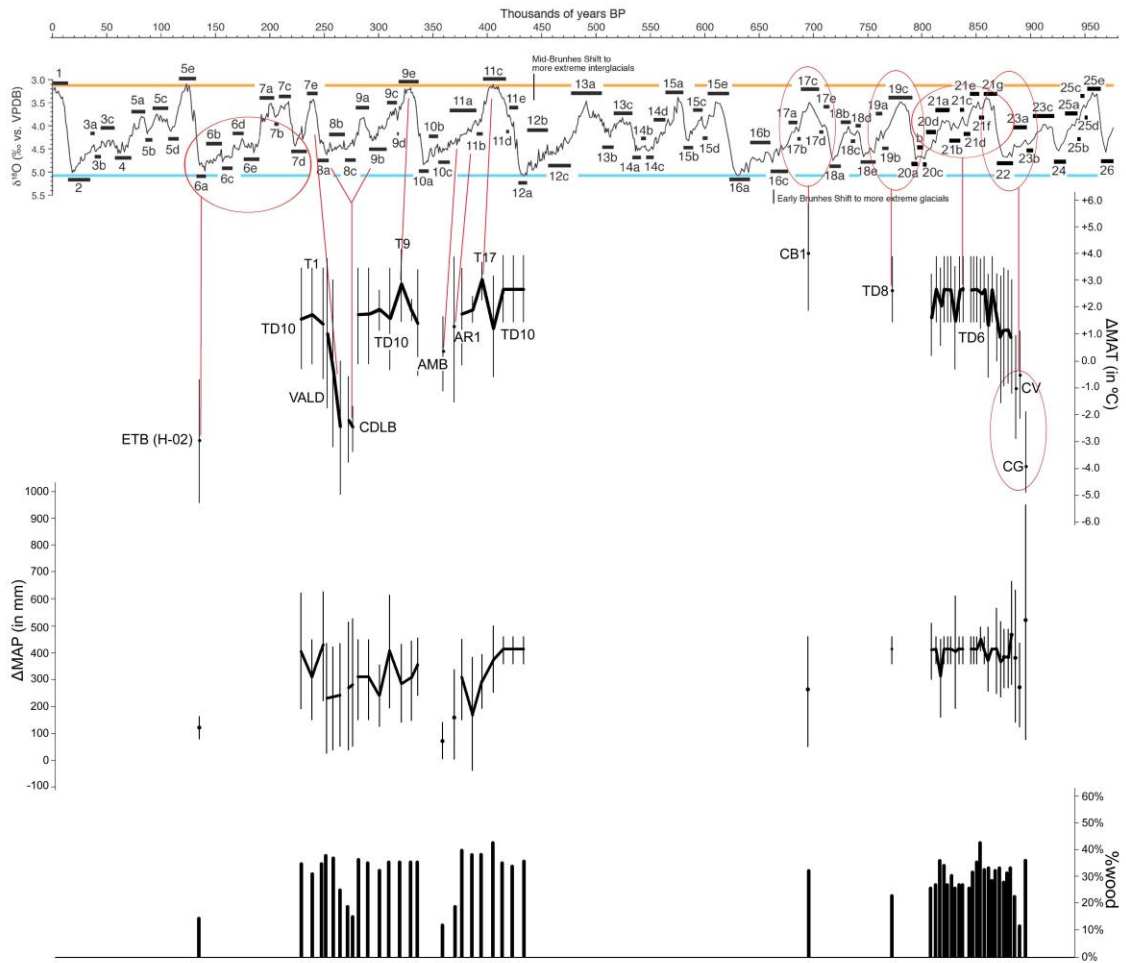
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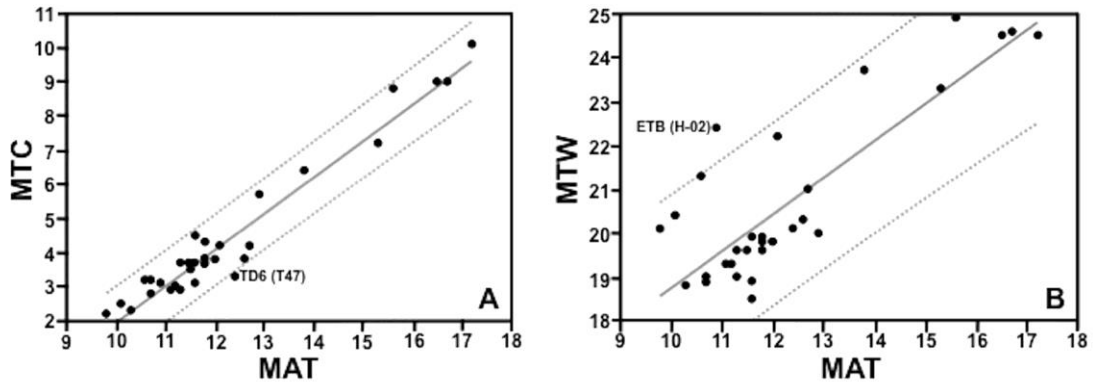
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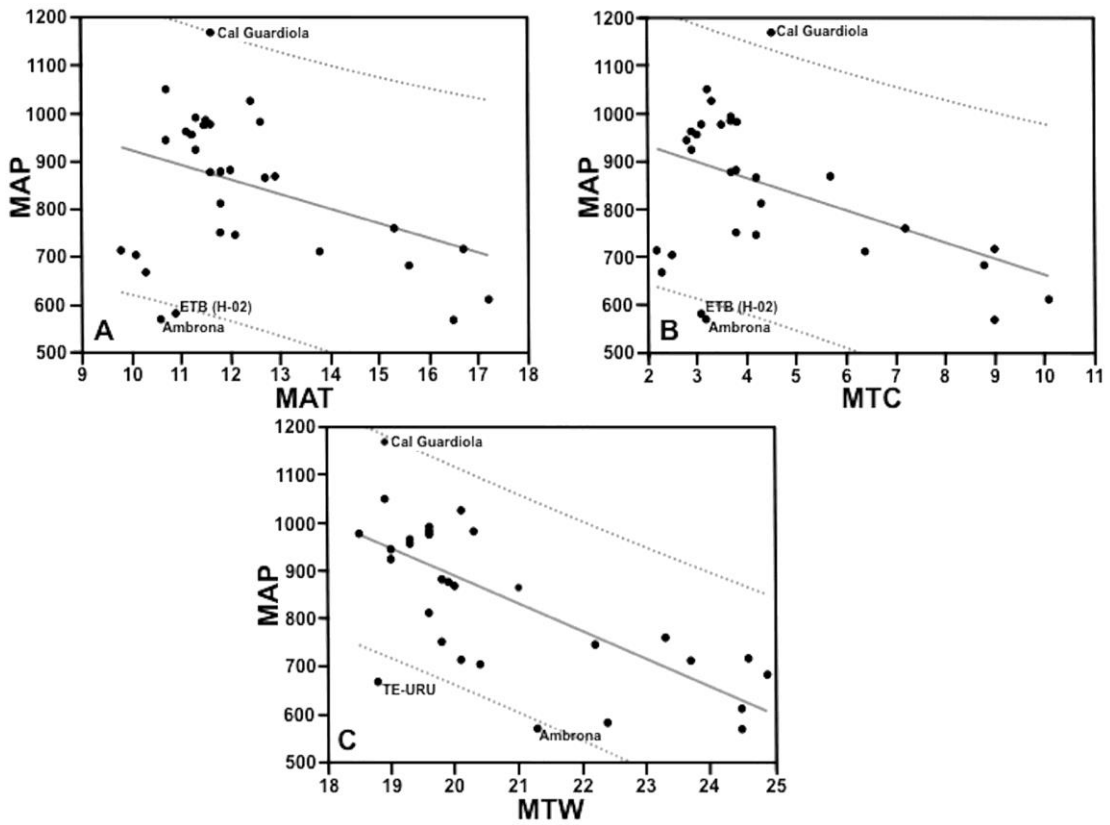
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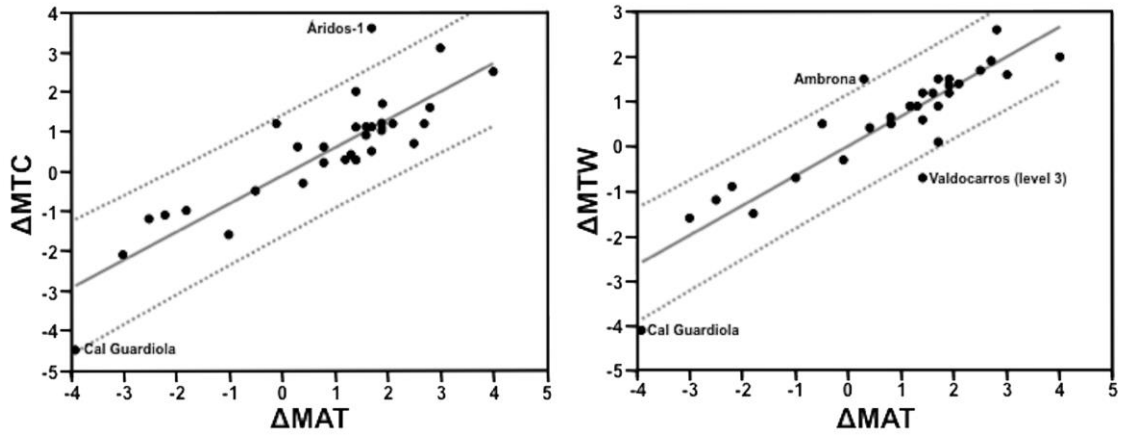
2510 MTW on MAT.



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2512 Figure 4. Bivariate plot using as dependent variable MAP. A: MAP on MAT; B: MAP

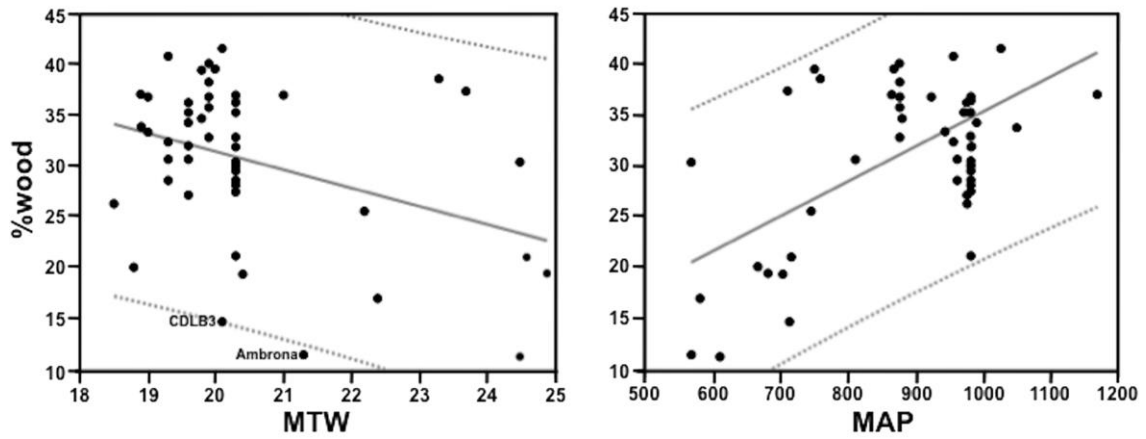
2513 on MTC; C: MAP on MTW.



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2515 Figure 5. Bivariate plot using as dependent variable ΔMAT . A: ΔMAT on ΔMTC ; B:

2516 ΔMAT on ΔMTW .



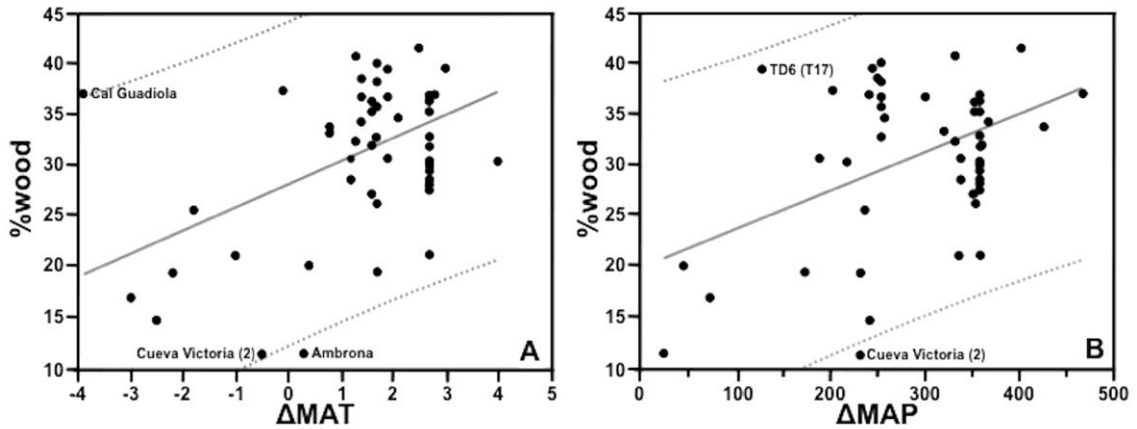
2517

2518 Figure 6. Bivariate plots using as dependent variable % wood. A: % wood on MTW; B:

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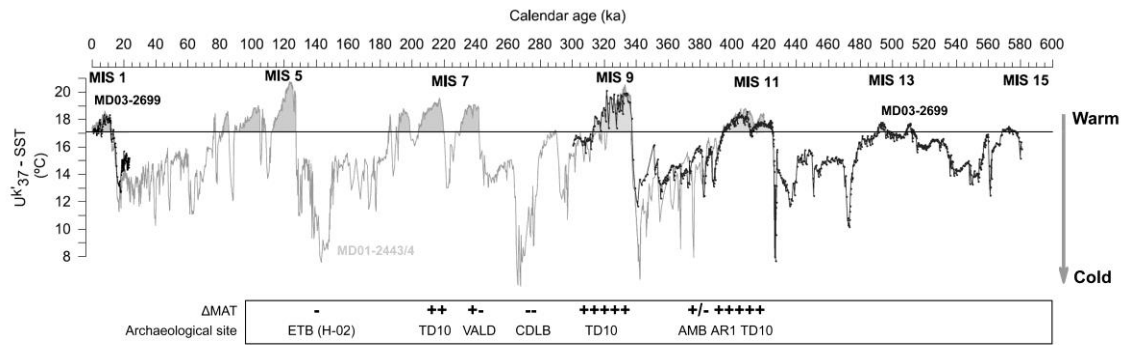
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2555 (2012), ³¹Smith and Polly (2013), ³²Motuzco and Ivanov (1996), ³³Avery (1999), ³⁴
2556 Jeannet (2009, 2010), ³⁵Manzano (2015), ³⁶Vieites et al (2009), ³⁷Holden et al. (2013).

Method	Proxy	Epoch	Region	Temperature	Precipitation	Others	Comparison with other proxies	Refs.
Thermal ecology	Anurans, Squamates, Crocodiles	Cretaceous to Holocene	North-America, Global	MAT, MTC	-	-	Pollen and paleoflora	1, 2, 3
Size-temperature-metabolic rate	Anurans, Squamates	Cretaceous, Paleocene, Eocene, Pleistocene	Africa, Asia, South-America, Australia	MAT	-	-	Sea surface temperature, oxygen isotopes, paleoflora	4, 5, 6, 7
Ecophysiological groups	Fishes, Anurans, Caudates, Allocaudates, Testudines, Squamates	Paleocene to Pleistocene	Europe, Asia, Africa	MAT, MTC, MTW	MAP, Pwm	-	Small-mammals, paleoflora, pollen, oxygen isotopes	8, 9, 10
Transfer functions	Large and small mammals	Pliocene to Holocene	Europe, Asia, Africa	MAT, MTW, MTC, Tp	MAP	MATA, IT, ITC, VAP, D	Paleosoils, pollen, paleoflora, oxygen isotopes	11, 12, 13, 14
Diversity and abundance	Large and small mammals	Miocene to Holocene	Europe, South-America	MAT, MTC, MTW	MAP, MINP	Rainfall seasonality	Paleoflora, hypsodonty, oxygen isotopes	15, 16, 17, 18, 19, 20, 21, 22
Hypsodonty	Large mammals	Miocene, Pliocene	Europe, Asia	-	MAP	-	Paleoflora	19, 23, 25, 26
Mutual Climatic Range and Mutual Ecogeographic Range	Anurans, Caudates, Squamates, Testudines, Large and small mammals	Pleistocene, Holocene	Europe	MAT, MTC, MTW	MAP, MWP, MSP, MSpP, MAuP	Aridity indexes	Pollen, charcoal, mammals, oxygen isotopes	24, 26, 27, 28, 29, 30, 31
Arealogical method of climatograms	Small mammals	Holocene	Europe, Asia	MTC, MTW	MAP	-	-	32
Modern analogues	Small mammals	Pliocene, Pleistocene	Africa	MTW, MTC, maximum interval of monthly temperature	MAP, % of winter rainfall	Aridity index in summer	-	33
Climato-ecological Aptitudes	Small mammals, Amphibians, Reptiles	Pleistocene, Holocene	Europe	MAT, MTC, MTW	MAP	-	-	34, 35
Phylogeny and ENM	Caudates	Cretaceous to Present	Global	MAT	MAP	-	-	36
Insect-damage on vertebrate remains	Large mammals, birds	Pleistocene	North-America	MAT	-	Humidity	Oxygen isotopes	37

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2561 Table 2. Herpetofauna-based Early-Middle Pleistocene Iberian climate and
 2562 environmental reconstructions. Abbreviations: Marine Isotope Stage (MIS), mean
 2563 annual temperature (MAT), mean temperature of the coldest month (MTC), mean
 2564 temperature of the warmest month (MTW), mean annual precipitation (MAP),
 2565 representation of woodland and woodland margins in the reconstructed environment
 2566 (%wood), standart deviation (SD), difference with current value (Δ). References:
 2567 ¹Agustí et al. (2009), ²Blain et al. (2008a), ³Blain (2012-2014), ⁴Blain et al. (2008b),
 2568 ⁵Blain et al. (2009), ⁶Blain et al. (2012a), ⁷Blain et al. (2013a), ⁸Blain et al. (2015),
 2569 ⁹Blain et al. (2014b), ¹⁰Blain et al. (2017a), ¹¹Blain et al. (2011b), ¹²Blain et al. (2012b),
 2570 ¹³Blain et al. (2017b). Grey bands represent the sample that corresponds to the warmest
 2571 temperature and consequently have been correlated with the interglacial peak (Blain et
 2572 al., 2012a).

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Site	sample	MIS	MAT		MTC		MTW		MAP		%wo od	Refs.
			mean \pm SD	Δ	mean \pm SD	Δ	mean \pm SD	Δ	mean \pm SD	Δ		
Cal Guardiola		MIS	11.6 \pm	-			18.9 \pm	-	1168 \pm	+51		1
	22		1.9	3.9	4.5 \pm 2.2	4,5	1.7	4,1	430	8	37.0	
Cueva Victoria		MIS	16.7 \pm	-			24.6 \pm	-	716 \pm	+38		2
	22		1.9	1.0	9.0 \pm 2.3	1,6	1.4	0,7	241	7	21.0	
		MIS	17.2 \pm	-	10.1 \pm	-	24.5 \pm	+0.	611 \pm	+28		3
	22		1.6	0.5	1.7	0,5	0.8	5	160	2	11.2	
Gran Dolina, TD6		MIS	10.7 \pm	+0.		+0.	18.9 \pm	+0.	1049 \pm	+47		4, 5, 6, 7
	T55	21	2.1	8	3.2 \pm 2.0	6	1.6	5	193	7	33.7	
			11.1 \pm	+1.		+0.	19.3 \pm	+0.	961 \pm	+38		
	T54		2.1	2	2.9 \pm 2.2	3	1.7	9	102	9	30.6	
			11.1 \pm	+1.		+0.	19.3 \pm	+0.	961 \pm	+38		
	T53		2.2	2	2.9 \pm 2.3	3	1.7	9	102	9	28.5	
			10.7 \pm	+0.		+0.	19.0 \pm	+0.	943 \pm	+37		
	T52		2.3	8	2.8 \pm 2.3	2	1.8	6	137	1	33.3	
			11.5 \pm	+1.		+1.	19.6 \pm	+1.	983 \pm	+41		
	T51		1.6	6	3.7 \pm 1.7	1	1.3	2	162	1	31.9	
			12.6 \pm	+2.		+1.	20.3 \pm	+1.		+40		
	T50		1.2	7	3.8 \pm 1.9	2	1.2	9	981 \pm 46	9	29.4	
			11.2 \pm	+1.		+0.	19.3 \pm	+0.	955 \pm	+38		
	T49		1.9	3	3.0 \pm 1.9	4	1.5	9	116	3	32.3	
			12.6 \pm	+2.		+1.	20.3 \pm	+1.		+40		
	T48		1.2	7	3.8 \pm 1.9	2	1.2	9	981 \pm 46	9	31.8	
			12.4 \pm	+2.		+0.	20.1 \pm	+1.	1025 \pm	+45		
	T47		1.3	5	3.3 \pm 2.2	7	1.2	7	46	3	41.5	
			12.6 \pm	+2.		+1.	20.3 \pm	+1.		+40		
	T45		1.2	7	3.8 \pm 1.9	2	1.2	9	981 \pm 46	9	36.3	
			12.6 \pm	+2.		+1.	20.3 \pm	+1.		+40		
	T44		1.2	7	3.8 \pm 1.9	2	1.2	9	981 \pm 46	9	30.3	
			12.6 \pm	+2.		+1.	20.3 \pm	+1.		+40		
	T43		1.2	7	3.8 \pm 1.9	2	1.2	9	981 \pm 46	9	27.5	
			12.6 \pm	+2.		+1.	20.3 \pm	+1.		+40		
	T41		1.2	7	3.8 \pm 1.9	2	1.2	9	981 \pm 46	9	28.6	
			12.6 \pm	+2.		+1.	20.3 \pm	+1.		+40		
	T40		1.2	7	3.8 \pm 1.9	2	1.2	9	981 \pm 46	9	28.6	

			11.5 ±	+1.		+0.	19.6 ±	+1.	975 ±	+40	
	T38		1.9	6	3.5 ± 2.0	9	1.7	2	206	3	27.1
			12.6 ±	+2.		+1.	20.3 ±	+1.		+40	
	T37		1.2	7	3.8 ± 1.9	2	1.2	9	981 ± 46	9	29.9
			12.6 ±	+2.		+1.	20.3 ±	+1.		+40	
	T36		1.2	7	3.8 ± 1.9	2	1.2	9	981 ± 46	9	28.1
			12.6 ±	+2.		+1.	20.3 ±	+1.		+40	
	T35		1.2	7	3.8 ± 1.9	2	1.2	9	981 ± 46	9	32.8
			12.0 ±	+2.		+1.	19.8 ±	+1.	880 ±	+30	
	T34		1.4	1	3.8 ± 2.2	2	1.5	4	148	8	34.6
			12.6 ±	+2.		+1.	20.3 ±	+1.		+40	
	T33		1.2	7	3.8 ± 1.9	2	1.2	9	981 ± 46	9	28.1
			11.6 ±	+1.		+0.	18.5 ±	+0.	976 ±	+40	
	T32		1.5	7	3.1 ± 2.1	5	2.1	1	103	4	26.2
Gran Dolina,		MIS	12.6 ±	+2.		+1.	20.3 ±	+1.		+40	
TD8	T28	19	1.2	7	3.8 ± 1.9	2	0.8	9	981 ± 46	9	21.1
Cúllar Baza 1		MIS	16.5 ±	+4.		+2.	24.5 ±	+2.	568 ±	+26	1
		17	2.2	0	9.0 ± 2.8	5	1.3	0	204	8	30.3
Gran Dolina,		MIS	12.6 ±	+2.		+1.	20.3 ±	+1.		+40	
TD10	T21	13	1.2	7	3.8 ± 1.9	2	1.2	9	981 ± 46	9	36.8
			12.6 ±	+2.		+1.	20.3 ±	+1.		+40	
	T20		1.2	7	3.8 ± 1.9	2	1.2	9	981 ± 46	9	35.2
			12.6 ±	+2.		+1.	20.3 ±	+1.		+40	
	T19		1.2	7	3.8 ± 1.9	2	1.2	9	981 ± 46	9	36.3
			11.2 ±	+1.		+0.	19.3 ±	+0.	955 ±	+38	
	T18		1.9	3	3.0 ± 1.9	4	1.5	9	116	3	40.7
		MIS	12.9 ±	+3.		+3.	20.0 ±	+1.	867 ±	+29	
	T17	11c	0.7	0	5.7 ± 1.4	1	1.4	6	101	5	39.5
			11.8 ±	+1.		+1.	19.8 ±	+1.	750 ±	+17	
	T16		0.4	9	3.8 ± 1.9	2	0.4	4	212	8	39.4
			11.6 ±	+1.		+1.	19.9 ±	+1.	876 ±	+30	
	T15		1.8	7	3.7 ± 2.0	1	1.4	5	153	4	40.0
			11.3 ±	+1.		+0.	19.0 ±	+0.	923 ±	+35	
	T12		1.9	4	2.9 ± 1.9	3	1.6	6	122	1	36.7
			11.8 ±	+1.		+1.	19.9 ±	+1.	876 ±	+30	
	T10		0.4	9	3.7 ± 2.0	1	1.4	5	153	4	36.7
			12.7 ±	+2.		+1.	21.0 ±	+2.	864 ±	+29	
	T9	MIS 9	1.3	8	4.2 ± 2.0	6	1.2	6	126	2	36.9
			11.5 ±	+1.		+0.	19.6 ±	+1.	975 ±	+40	
	T8		1.9	6	3.5 ± 2.0	9	1.7	2	206	3	36.2
			11.8 ±	+1.		+1.	19.6 ±	+1.	811 ±	+23	
	T6		0.8	9	4.3 ± 0.7	7	1.2	2	121	9	30.6
			11.6 ±	+1.		+1.	19.9 ±	+1.	876 ±	+30	
	T5		1.8	7	3.7 ± 2.0	1	1.4	5	153	4	35.7
			11.6 ±	+1.		+1.	19.9 ±	+1.	876 ±	+30	
	T4		1.8	7	3.7 ± 2.0	1	1.4	5	153	4	38.2
			11.3 ±	+1.		+1.	19.6 ±	+1.	990 ±	+41	
	T2		2.1	4	3.7 ± 2.1	1	1.5	2	202	8	34.2
			11.6 ±	+1.		+1.	19.9 ±	+1.	876 ±	+30	
	T1		1.8	7	3.7 ± 2.0	1	1.4	5	153	4	32.7
			11.5 ±	+1.		+0.	19.6 ±	+1.	975 ±	+40	
Áridos-1	T0		1.9	6	3.5 ± 2.0	9	1.7	2	206	3	35.2
		MIS	15.1 ±	+1.		+1.	24.1 ±	+0.	624 ±	+16	8, 9
		11b	2.7	2	3.2 ± 2.2	6	2.1	1	164	6	19.4
Ambrona	AS4 &	MIS	10.6 ±	+0.		+0.	21.3 ±	+1.			8
	AS3	11a	1.4	3	3.2 ± 1.3	6	1.2	5	569 ± 70	+74	11.4
CDLB		MIS	-	-	-	-	20.1 ±	-	713 ±	+29	10
	CB3	9/8	9.8 ± 0.8	2.5	2.2 ± 1.2	1.2	1.0	1.2	227	2	14.6
		MIS	10.1 ±	-	-	-	20.4 ±	-	703 ±	+28	
	CB2	9/8	1.6	2.2	2.5 ± 1.5	1.1	1.6	0.9	225	2	19.3
TEURU		MIS	10.3 ±	+0.		-	18.8 ±	+0.	667 ±		11
	TE19	9/8	0.8	4	2.3 ± 0.6	0.3	1.0	4	153	+95	20.0
Valdocarros II			11.4 ±	-	-	-	21.6 ±	-	699 ±	+24	12
	level 2	MIS8a	2.5	2.5	3.1 ± 2.2	2.1	2.2	2.4	185	1	25.5
		MIS	13.8 ±	-		+0.	22.5 ±	-	692 ±	+23	
	level 3	8/7	3.1	0.1	5.7 ± 3.4	5	2.3	1.5	187	4	37.3
		MIS	14.9 ±	+1.		+1.	23.5 ±	-	689 ±	+23	
	level 4	8/7	2.8	0	6.9 ± 3.4	7	2.0	0.5	197	1	38.5
ETB (H-02)			10.9 ±	-	-	-	22.4 ±	-		+12	13
		MIS 6	2.3	3.0	3.1 ± 2.7	2.1	2.1	1.6	581 ± 40	3	16.9

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2576 Table 3. Descriptive statistics of regression analyses (OLS: Ordinary Least Squares); N:
 2577 sample size; R²: coefficient of correlation; *a*: Y-intercept; *b*: slope; H₀ (*b*=0): null
 2578 hypothesis for slope zero.
 2579

	N	R²	a	b	H₀ (<i>b</i>=0)
MTC on MAT	37	0.937	-8.724	1.066	<0.0001
MTW on MAT	37	0.703	10.271	0.845	<0.0001
	N	R²	a	b	H₀ (<i>b</i>=0)
MAP on MAT	37	0.134	1227.059	-30.487	<0.05
MAP on MTC	37	0.198	999.161	-33.656	<0.01
MAP on MTW	37	0.488	2043.132	-57.725	<0.0001
	N	R²	a	b	H₀ (<i>b</i>=0)
ΔMTC on ΔMAT	37	0.746	-0.118	0.708	<0.0001
ΔMTW on ΔMAT	37	0.820	0.013	0.666	<0.0001
	N	R²	a	b	H₀ (<i>b</i>=0)
ΔMAP on ΔMAT	37	0.016	319.389	7.319	0.450
ΔMAP on ΔMTC	37	0.017	332.027	9.213	0.436
ΔMAP on ΔMTW	37	0.001	328.333	2.504	0.850
	N	R²	a	b	H₀ (<i>b</i>=0)
%wood on MAT	37	0.009	35.904	-0.455	0.571
%wood on MTC	37	0.029	33.533	-0.743	0.307
%wood on MTW	37	0.145	67.166	-1.788	<0.05
%wood on MAP	37	0.365	0.994	0.034	<0.0001
	N	R²	a	b	H₀ (<i>b</i>=0)
%wood on ΔMAT	37	0.219	28.085	2.277	<0.005
%wood on ΔMTC	37	0.067	29.284	1.814	0.665
%wood on ΔMTW	37	0.067	29.190	1.713	0.122
%wood on ΔMAP	37	0.197	17.996	0.038	<0.01

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