

1 Pliocene to Middle Pleistocene climate history in the Guadix-Baza Basin, and the
2 environmental conditions of early *Homo* dispersal in Europe

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39

40 **Abstract**

41 The Guadix-Baza Basin (GBB) in Andalucía, Spain, comprises palaeontological and archaeological
42 sites dating from the Early Pliocene to the Middle Pleistocene, including some of the earliest sites
43 with evidence for the presence of early humans (*Homo* sp.) in Europe. Thus, the history of climate
44 and environments in this basin contributes significantly to our understanding of the conditions
45 under which early humans spread into Europe during the Early Pleistocene. Here we present
46 estimates of precipitation and primary productivity in the GBB from the Pliocene to the Middle
47 Pleistocene based on dental ecometrics in fossil communities of large herbivorous mammals, and
48 perform an ecometrics-based distribution modelling to analyse the environmental conditions of
49 Early and Middle Pleistocene human sites in Europe. Our results show that Early Pleistocene
50 humans generally occupied on average relatively diverse habitats with ecotones, such as woodlands
51 and savannas, but avoided very open and harsh (cool or dry) environments. During the Middle
52 Pleistocene in Europe, humans occupied a comparatively much broader range of environments than
53 during the Early Pleistocene, but were on average more concentrated in environments where the
54 dental ecometric of mammals indicate wooded palaeoenvironments. In the earliest human
55 occupation sites of the GBB, Barranco León and Fuente Nueva 3, the mean annual precipitation and
56 net primary production estimates indicate climatic conditions close to modern Mediterranean
57 sclerophyllous woodland environments, but with slightly higher primary productivity, indicating
58 some similarity with East African woodlands. On the other hand, the environments did not resemble
59 African grassland savannas. The browse-dominated diets of ungulates from Barranco León and
60 Fuente Nueva 3 further suggest palaeoenvironments where grasses were a minor component of the
61 vegetation. In the slightly older site of Venta Micena that has no evidence for the presence of
62 hominins, dental ecometric estimates indicate climate and environments similar to Mediterranean
63 “forest steppe” environments existing in the surroundings of Baza today. Grasses were prevalent in
64 the diet of some taxa, especially equids, in Venta Micena, but most of the species show browse-
65 dominated diets even there.

66 **1. Introduction**

67 Understanding the environmental conditions under which early humans dispersed into Iberia during
68 the Early and Middle Pleistocene is a key issue for understanding what enabled them to expand and
69 how they interacted within different environments. Dental ecometrics and body size of large
70 herbivorous mammals have been associated with various aspects of vegetation and climate
71 (Fortelius et al., 2002; Liu et al., 2012; Saarinen, 2014; Saarinen et al., 2016; Zliobaitė et al., 2016;
72 Fortelius et al., 2016; Zliobaitė et al., 2018; Oksanen et al., 2019). Here we use dental ecometric
73 variables and mean body size in fossil ungulate communities to predict presence of humans (species
74 distribution of humans) during the Early and Middle Pleistocene in Europe. The model is calibrated
75 on fossil and archaeological evidence from Pleistocene localities of Europe.

76 Much of the debate about the environmental conditions during these episodes of earliest human
77 dispersions has centered around the question of whether they occurred in the context of grasslands
78 or wooded grasslands, similar to African grassland savannas (the “savannahstan”-hypothesis;

79 Dennel and Roebrooks, 2005), or rather in woodlands or even closed forests (Belmaker, 2010;
80 Dennel, 2010; Levin, 2015; Patterson et al., 2017a, b; Belmaker and O'Brien, 2018). Also, the
81 importance of water-edge habitats for early humans has been discussed (Cohen et al., 2012). Early
82 human evolution in the Early Pleistocene of East Africa took place in the broad context of opening
83 landscapes and the spread of C4 grasses, but in fact the environments where early humans occurred
84 were diverse, with fine-scale spatial and temporal variation in woody cover (Carrión et al., 2011,
85 2019; Levin, 2015; Patterson et al. 2017a, b). It has been suggested that the earliest human
86 expansion out of Africa into Southern and Eastern Asia occurred in grassland, wooded grassland
87 and woodland habitats similar to modern African savannas (Dennel and Roebrooks, 2005; Dennel,
88 2010). However, this “savannahstan-hypothesis” *sensu stricto* is not consistently supported by
89 multi-proxy analyses of environmental conditions in the Early Pleistocene human occupation sites
90 in Eurasia. Based on indicator species and ecological diversity analysis, it has been suggested that
91 the earliest human occurrence sites in Eurasia, such as Dmanisi (Georgia), and ‘Ubeidiya (Israel),
92 had palaeoenvironments similar to African savannas (Dolukhanov, 2000; Palmquist, 2002;
93 Martinez-Navarro et al., 2004). However, taxonomic diversity measurements using correspondence
94 analyses indicate that their palaeoenvironments differed from African savannas, comprising instead
95 a mixture of temperate forest and Mediterranean woodland elements (Belmaker, 2006, 2010a, b).
96 Other palaeoenvironmental proxies from Dmanisi (such as pollen, phytoliths and carpological
97 remains) indicate landscapes that could be interpreted to be savanna-like in a physiognomic or
98 structural sense, but not taxonomic sense, being instead dominated by temperate oak forest elements
99 with grassy vegetation (Messenger et al., 2010). Mesowear analysis of the ungulate fauna in
100 ‘Ubeidiya further supports a wooded palaeoenvironment, being dominated by ungulates with
101 browsing diets (Belmaker and O'Brien, 2018). Moreover, the earliest human occupation sites in
102 Eastern Asia do not appear to have been consistently savanna-like. For example, the
103 palaeoenvironments in the Nihewan basin (ca. 1.7 – 1 Ma) included elements of temperate
104 woodlands and grasslands (Peterson et al., 2003; Teague and Potts, 2007), while the
105 palaeoenvironment of Gonwangling (ca. 1.2 Ma) has been interpreted as subtropical montane forest
106 (Teague and Potts, 2007).

107

108 *1.1. Research history of climate and palaeoenvironments in the Guadix-Baza Basin during the* 109 *Pleistocene*

110 The Guadix-Baza Basin (GBB) (Andalucía, Spain) is a sedimentary basin, with an extensive record
111 of palaeontological and archaeological sites ranging from the Pliocene to the Middle Pleistocene
112 (ca. 4.5 – 0.4 Ma), including Barranco León and Fuente Nueva 3 (ca. 1.4 – 1.2 Ma), which are
113 among the earliest sites with solid evidence of the presence of humans (*Homo* sp.) in Europe (Toro-
114 Moyano et al., 2013). Somewhat contradictory palaeoenvironmental information from the
115 Pleistocene sites in the GBB has been published based on different methods. For example,
116 Palmqvist et al. (2003) interpreted the palaeoenvironment of Venta Micena to have been similar to
117 East African savannas on the basis of faunal analysis, whereas a Mediterranean woodland
118 environment was suggested by Belmaker (2006). Most analyses indicate a predominance of
119 Mediterranean woodland and open environments in the basin during much of the Early Pleistocene
120 (e.g., Alberdi et al., 2001; Belmaker, 2006, 2010a; Agustí et al., 2010; Blain et al., 2011; Sánchez-
121 Bandera et al., 2020; Altolaguirre et al., 2020, 2021). The presence of the Baza palaeolake, and
122 changes in its water-level, have been key elements affecting the palaeoecology of the basin, by
123 providing a constant supply of water and palustrine environments around the lake (Oms et al.,

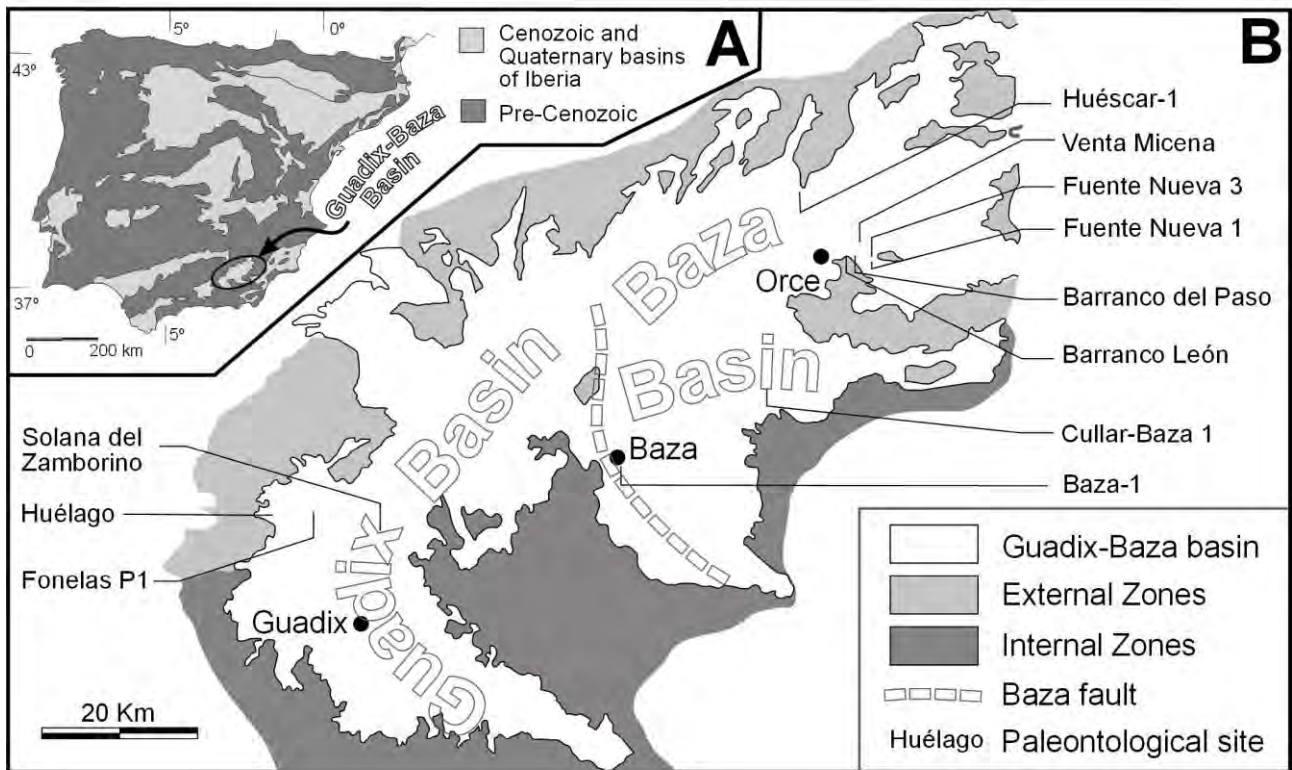
124 2011). Furthermore, the “Galerian turnover pulse” in mammal faunas (ca. 1.0 – 0.9 Ma) has been
125 associated with the arrival of early humans in Europe (Azanza et al., 2000), although many of the
126 earliest European sites, including Barranco León and Fuente Nueva 3, now seem to predate this
127 event. Nonetheless, the arrival of some new species, such as the very large cervid *Praemegaceros*
128 *verticornis* (that was proposed as the marker of the Galerian Mammal Age; Gliozzi et al. 1997) and
129 the large equid *Equus suessenbornensis*, may be associated with the arrival of early humans,
130 suggesting perhaps either a common dispersal event or a change of environmental conditions that
131 favored the dispersal of these taxa in Europe.

132 In the northern margin of the GBB, on the Baza palaeo-lakeshore, swampy conditions are
133 reconstructed at the earliest Pleistocene site of Huélago (ca. 2.6 Ma) as indicated by the depositional
134 environment, taphonomy and the abundance of browsing large herbivores in the mammal fauna. All
135 this evidence suggests abundant wooded or bushy environments in the surroundings (Alberdi et al.,
136 2001). Similarly, both the late Early Pleistocene site of Huéscar 1 (ca. 1.1 Ma according to Alberdi
137 et al., 2001; 900-800 ka according to Ros-Montoya et al., 2019, and 574 – 410 ka according to
138 Demuro et al., 2015) and the early Middle Pleistocene site of Cúllar-Baza 1 (0.7 Ma) have
139 palustrine depositional environments and diverse faunas of browsing ungulates. This indicates a
140 swampy lake- shore environment, surrounded by woodlands or shrublands in Huéscar 1, but the
141 lack of closed-forest mammal taxa indicates open, sparsely forested environments with dry periods
142 (Alberdi et al., 2001).

143 Near the village of Orce, the sites of Venta Micena, Barranco León and Fuente Nueva 3 provide
144 essential data for contributing to discussions about the early human occupation of Europe. Despite
145 intensive excavations, the oldest of these sites, Venta Micena, dated to ca. 1.6 – 1.4 Ma (Duval et al.
146 2010), has not yielded any conclusive evidence for the presence of early humans. In contrast,
147 abundant Oldowan stone tools and bones with anthropogenic modifications have been discovered in
148 Barranco León (1.81 – 1.05 [1.43 ± 0.38], Barsky et al., 2010; Toro-Moyano et al., 2013; Blain et
149 al., 2016; Espigares et al., 2019; Tilton et al., 2019; 2020) and Fuente Nueva 3 (1.4 – 0.98 [1.19 ±
150 0.21], Barsky et al., 2010; Duval, 2008; Duval et al., 2012; Espigares et al., 2019). In addition,
151 Barranco León yielded a fossil human tooth (Toro-Moyano et al., 2013). Palustrine depositional
152 environments near the Baza lakeshore have been evidenced for all these sites (Oms et al., 2011).
153 The palaeoenvironment in Venta Micena was interpreted as similar to African savannas by
154 Palmqvist et al. (2003), based on analyses of feeding ecology and locomotion types of large
155 mammals. However, taxonomic correspondence analysis of large mammals (Belmaker, 2006,
156 2010a) indicates that the palaeoenvironment comprised elements of Mediterranean woodlands and
157 temperate forests and was thus quite different from African savannas. Rodent faunas indicate that
158 the precipitation and temperature in Venta Micena were roughly similar to present (Agustí et al.,
159 2010). The reconstructions of palaeoclimate and palaeoenvironments for Barranco León and Fuente
160 Nueva 3 indicate temperature conditions similar to present, but higher precipitation, with
161 Mediterranean woodland/shrubland -type vegetation (Agustí et al., 2009, 2010; Blain et al., 2011,
162 2016; Sánchez-Bandera et al., 2020). The vegetation type in level D1 at Barranco León, containing
163 most of the faunal remains and evidence of human presence in BL, is described as a wooded
164 environment. In contrast, the environmental conditions at Fuente Nueva 3 are now reconstructed as
165 more open and dryer than at Barranco León, based on the amphibian and reptile fauna (Sánchez-
166 Bandera et al., 2020).

167 In this study we provide further information about the palaeoenvironmental conditions in the GBB
168 from the Early Pliocene (ca. 4.5 Ma) to the Middle Pleistocene (ca. 0.4 Ma), based on dental

169 ecometrics, average body size and diet of large herbivorous mammals. We further discuss the
 170 palaeoenvironments of the earliest human occupation sites, Barranco León and Fuente Nueva 3, in
 171 the wider context of early human palaeoenvironments in Europe, based on distribution modelling of
 172 preferred environments during the Early and Middle Pleistocene of Europe.



173
 174 **Figure 1.** Map of the Guadix-Baza Basin with the localities.

175
 176 **2. Materials and methods**

177 *2.1. Materials*

178 The mammal fossils from Venta Micena, Barranco León and Fuente Nueva 3 used in this study are
 179 housed in the Archaeological Museum of Granada, Andalucía, Spain. Large mammal faunal lists of
 180 European Early and Middle Pleistocene fossil mammal localities and archaeological sites were
 181 collected from literature (references in Supplementary Table S1). Stratigraphic and
 182 sedimentological data for the GBB were also collected. In total, dental ecometric values and mean
 183 body size indices from 12 localities from the GBB and altogether 92 Early and Middle Pleistocene
 184 European localities were used in this study (Supplementary Tables S1 and S2). The localities were
 185 chosen based on the following criteria: 1) the fauna include at least 5 species of large herbivorous
 186 mammals, 2) the mammalian fauna and the possible evidence of human occupation can be shown to
 187 be associated, as far as can be told from the stratigraphy, 3) the fossil assemblage does not show
 188 obvious irregularities due to sorting by human or carnivore activities, or due to other taphonomic
 189 processes.

190 *2.2. Dental ecometric trait data*

191 We use dental ecometric traits within large mammal communities to model mean annual
192 temperature (MAT), minimum annual temperature (MINT), mean annual precipitation (MAP) and
193 net primary production (NPP) of GBB localities and other Early and Middle Pleistocene European
194 localities. Such an approach is taxon-free (Damuth et al., 1992) in the sense that the inference of
195 past conditions is based on generalized dental ecometric traits rather than individual adaptations of
196 taxa, even if the traits are coded at species-level and are in this sense based on species lists per
197 localities. It has been demonstrated that dental ecometric traits are not significantly influenced by
198 non-ecological processes such as phylogenetic conservatism or spatial autocorrelation, and are
199 instead primarily driven by climatic variables (Lawing et al., 2017). Dental ecometric traits for the
200 large herbivorous mammal species present in the GBB and other locations in Early and Middle
201 Pleistocene Europe were determined following the coding of Liu et al. (2012) and Zliobaite et al.
202 (2018). The dental ecometric traits were observed from second upper molar in ungulates, or from
203 the third upper molar in pigs and proboscideans. The traits were scored at the species level.
204 They include:

- 205 - Hypsodonty, HYP (tooth crown height): 1 (brachydont), 2 (mesodont) or 3 (hypsodont).
206 Hypsodonty is an adaptation for increasing functional durability of dentition. Mean ordinated
207 hypsodonty in large mammal communities is correlated with precipitation through the link of high
208 abrasion on teeth in dry climatic conditions, possibly because of multiple factors, including aeolian
209 dust accumulation and prevalence of grasses with phytoliths in dry environments (e.g., Fortelius et
210 al., 2002; Liu et al., 2012).
- 211 - Longitudinal loph count, LOP: the number of elongated cutting edge structures that are oriented in
212 the direction of the tooth row (for example rhinoceroses have one (the ectoloph), ruminants and
213 horses have two (the buccal and lingual "lophids" formed by the flattened cusps), and
214 proboscideans have none (because all the lophs are transverse)). LOP is correlated with temperature
215 (high LOP value indicating cool climate), because longitudinal lophs are most abundant in
216 ungulates feeding seasonally on bark and branches of deciduous trees that drop their leaves during
217 cold months (e.g., Liu et al., 2012).
- 218 - Horizodonty (HOD): the amount of transverse cusp pairs or lophs; the categories are: 1
219 (brachyhorizodont: two cusp pairs or lophs, this includes most herbivorous mammals), 2
220 (mesohorizodont: three cusp pairs or lophs, this happens e.g. in some pigs with enlarged last
221 molars), 3 (hypsohorizodont: more than three cusp pairs or lophs, this includes mostly mammutids,
222 gomphotheres and elephants, and some derived pigs such as warthog). Horizodonty is associated
223 with increase in tooth volume by increasing lophs or cusp pairs, and is associated with functional
224 durability of dentition (Zliobaite et al., 2016).
- 225 - Presence of acute lophs (AL): 1 (present), 0 (absent); these are sharp, cutting lophs that maintain
226 sharp facets when worn, such as the ectoloph of most rhinos, the chisel-like lophs of tapirs, and the
227 sharp buccal lophs of most cervids, but e.g. horses and almost all (hypsodont) bovids lack these.
228 Acute lophs are typical for browsers in forested environments (Zliobaite et al., 2016, 2018) If in
229 doubt, AL for selenodonts is assigned if mesowear is sharp. The proportion of acute lophs in a
230 community is correlated with temperature today, as it is highest in deciduous forest communities
231 where most ungulate species cut branches when leaves are dropped during cold season (see also
232 Oksanen et al., 2019).

- 233 - Presence of obtuse lophs (OL): 1 (present), 0 (absent); these are "blunt" lophs that become basin-
 234 like without maintaining sharp facets when worn (e.g., the transverse lophs in rhinos, hippos,
 235 gomphotheres and elephants, and most of the "lophs" in bovids and equine horses).
- 236 - Structural fortification of cusps (SF): 1 (present), 0 (absent); these are any morphological features
 237 of the cusps that make the cusp stand out from the occlusal surface (by resisting wear) in worn
 238 teeth. The most typical examples of such structures are: buccal cusps with bulbous, thickened
 239 lingual enamel loops in some ruminants (e.g. reduncine antelopes and bovines), cusps with
 240 heavily folded enamel (e.g. in many pigs such as *Sus scrofa*), and molars with raised central ridges
 241 formed by conules or thickened enamel edges (e.g. in *Hippopotamus*). Structural fortification
 242 occurs in modern herbivorous mammal communities in fresh-grass grazers and mixed-feeders in
 243 wooded habitats, primarily in forests and wetlands, and are thus indicators of such habitats
 244 (Zliobaite et al., 2018).
- 245 - Occlusal topography (OT): 1 (flat), 0 (non-flat); this refers to the overall shape of the worn
 246 occlusal surface of the teeth in bucco-lingual direction. Flat occlusal topography is typical for
 247 grazing ungulates such as horses.
- 248 -Plain selenodonty (PS): 1 (present), 0 (absent): this is a combination of traits where longitudinal
 249 loph count is 2, only obtuse lophs are present, there is no structural fortification, no coronal cement
 250 and the occlusal topography is non-flat. This dental morphology type is particularly abundant in
 251 ruminants and camels inhabiting relatively harsh environments, such as deserts and montane
 252 environments.
- 253 -Bunodonty (BUN): 1 (present), 0 (absent); bunodonty refers to dental morphology with separate
 254 cusps that are not fused into elongated, loph-like structures. This dental morphology type is typical
 255 for omnivores and frugivores such as most suids and primates. High proportion of bunodont taxa
 256 indicates relatively warm and humid forest environments.

257 We used mesowear analysis (Fortelius and Solounias, 2000) for reconstructing the dietary
 258 composition of herbivorous mammals in an attrition-abrasion (browse vs. grass) continuum for the
 259 three localities from the vicinity of the village of Orce, Venta Micena, Barranco León and Fuente
 260 Nueva 3. Average mesowear signal in the ungulate communities from the Orce sites provides
 261 further information about the vegetation type at the Orce sites. The mesowear method is based on
 262 scoring the relief and shape of worn ungulate molar teeth, which reflects the degree of abrasion
 263 caused by grass on the molar surface, and allows comparing the dietary composition in the fossil
 264 ungulate populations with known diets of extant ungulates by hierarchical clustering (Fortelius and
 265 Solounias, 2000). Mesowear was scored at the specimen-level. The hierarchical clustering was
 266 performed using Ward's method with Euclidean distances. The clustering was performed in two-
 267 dimensional space, based on the shape and relief scores of the traditional mesowear scoring system
 268 of Fortelius and Solounias (2000).

269 2.3. *Locality mean body size indices*

270 In addition to the dental ecometric traits (crown types and mesowear), body mass estimates were
 271 calculated for a large set of large herbivorous mammals from the 92 Early and Middle Pleistocene
 272 European localities. Relative body size indices were calculated for each locality by calculating the
 273 mean body mass of ungulate species within each locality and dividing these locality means with the
 274 highest mean body mass in the total set of localities. For the body mass estimates, we used
 275 primarily postcranial bone measurements utilising the regression equations of Scott (1990) for bone

276 measurements and body mass in modern ungulates. These were complemented by body mass
277 estimates based on second upper and lower molar lengths for taxa for which postcranials were not
278 available, using the equations of Janis (1990).

279 Relative body size indices were calculated for each of the 92 Early and Middle Pleistocene
280 localities. This was done using the following method: 1) Measurements of postcranial bones or
281 molar teeth were obtained from the literature (or measuring in museums by JS) and used for
282 calculating body mass estimates (preferably for populations of the species within localities, but if
283 measurement data of a species was lacking for a locality, total mean body mass estimate for the
284 species was used instead). 2) Mean body mass was calculated for each locality as the mean value of
285 the body mass estimates of each ungulate species in the locality (palaeopopulations). 3) Relative
286 body mass indices (BM_{loc}) were calculated for each locality by dividing their mean body mass
287 value with the largest mean body mass value in the total set of 92 localities. Thus, the locality with
288 the largest BM_{loc} has the value 1, and all the other localities have values between 0 and 1. The
289 mean body mass indices of the localities were then used in the human distribution modelling
290 analysis as an additional ecometric trait, as average body size of ungulates correlates with habitat
291 openness on one hand, and resource quality and availability on the other hand (see Saarinen, 2014,
292 Saarinen et al., 2016). Proboscidea was omitted from the body size categories because of lack of
293 resolution in the body mass estimate data. The normalised body mass indices for the localities are
294 composite values that take into account the relative size of the species (whether on average small-
295 or large- sized species are dominant in the localities) and for abundantly sampled species, body
296 mass variation within species.

297 *2.4. Mean annual precipitation, mean annual temperature and net primary production estimates for* 298 *the Pliocene – Pleistocene of Guadix-Baza Basin*

299 Mean annual precipitation and net primary productivity in the GBB localities ranging from the
300 Pliocene (ca. 4.5 Ma) to the Middle Pleistocene (ca. 400 ka) were estimated based on hypsodonty,
301 longitudinal loph count and presence of acute lophs, averaged in the large herbivorous mammal
302 assemblages, using the equations by Oksanen et al. (2019). Based on these estimates, the climate
303 history in the GBB from the Early Pliocene to the Middle Pleistocene is discussed. The equations
304 for the estimation are:

305 Mean annual temperature (MAT) = $27 - 28.5 \times AL$

306 Mean temperature of coldest month (MINT) = $18 - 42.9 \times AL$

307 Mean annual precipitation (MAP) = $2.491 - 289 \times HYP - 841 \times LOP$

308 Net primary production (NPP) = $2601 - 144 \times HYP - 935 \times LOP$

309 The climatic variables (MAT, MINT and MAP) for the modern surroundings of Baza were obtained
310 from long-term weather observation data (<https://en.climate-data.org/europe/spain/andalusia-252/>).
311 NPP for the modern Baza area was estimated from dental ecometrics of a combined species
312 assemblage of wild ungulates and domestic ungulates that are herded in that region today. This
313 approach is justified based on the observation that adding feral domestic ungulates in dental
314 ecometrics -based estimates of climate and vegetation type compensate for the bias in the ecometric
315 signal caused by the loss of ungulate species by human interference, for example as has been
316 observed in the Sahel today (Zliobaite et al., 2018).

317 The MAP, MINT and NPP estimates of the GBB localities based on dental ecometrics were
318 compared with both estimated and measured values for modern biomes and ecosystems using
319 hierarchical clustering. For the comparisons, dental ecometric estimates of MAP, MINT and NPP
320 were calculated for selected modern IUCN sites from Eurasia, North America and East Africa, and
321 several Early and Middle Pleistocene early human sites from Africa, in order to evaluate the
322 similarity of the GBB sites with modern environments and African early human sites
323 (supplementary Table S3). In addition, measured MAP, MINT and NPP values for the modern
324 biomes were calculated from the values reported by Olson et al. (2013) and compared with the
325 dental ecometric estimates of MAP, MINT and NPP of the GBB sites (supplementary Table S4).
326 The hierarchical clustering was performed using Ward's method, with the Euclidean distances. The
327 MAP, MINT and NPP values were normalised for the hierarchical clustering analyses.

328 The IUCN sites for the comparison of ecometric estimates from the Pliocene and Pleistocene GBB
329 localities were chosen to represent a wide range of modern environments that are relatively
330 undisturbed by human activities and contain diverse large herbivorous mammal faunas, including
331 boreal forests (Nahanni NP and British Columbia), boreal forest-grassland mosaic (Yellowstone),
332 European temperate forest (Bialowieza NP), Mediterranean high-altitude forest (Sierra Nevada NP),
333 Mediterranean low-altitude woodland/shrubland (near Baza), and a series of tropical African
334 environments from rainforest (Nouabale-Ndoki NP) to grassland savanna (Serengeti) and dry
335 shrubland/woodland (near Nairobi). In addition, dental ecometric estimates from a wide range of
336 African early human sites were chosen for comparison, including Lake Turkana region, Kenya,
337 Olduvai, Tanzania and Swartkrans, South Africa (supplementary Table S3).

338 To complement the hierarchical clustering analysis of the GBB sites, we use MAP ranges of
339 modern Mediterranean biomes (Quézel and Médail, 2003; Suc and Popescu, 2005) as a further
340 reference point for discussing the palaeoenvironments of the GBB sites.

341 *2.5. Modelling of the environmental conditions under which early humans occurred in the Early –* 342 *Middle Pleistocene in Europe*

343 For the modelling of early human habitats in Early and Middle Pleistocene in Europe, we used a
344 tailored species distribution modelling approach. The modelling task was to predict the probability
345 of presence or absence of humans based on ecometric contexts of large mammal communities on
346 sites. The model itself was a logistic regression fit via generalised linear modelling. The
347 presence/absence of humans was coded for 92 Early and Middle Pleistocene palaeontological and
348 archaeological localities from Europe, and dental ecometric traits of large herbivorous mammals
349 were used as the predictive variables for the probability of human presence. We experimented on
350 the analysis using different combinations of traits in the analysis (but with a maximum of 5 traits at
351 time to avoid overfitting) and ended up with a model using hypsodonty (HYP), acute lophs (AL),
352 structural fortification (SF) for Early Pleistocene and Middle Pleistocene localities, and HYP, AL,
353 SF and locality mean body size indices (BM) for the complete set of localities. We evaluated how
354 well the model predicts presence of humans by applying a leave-one out approach to compute the
355 average Area Under the Roc Curve (Fielding and Bell, 1997). In addition, we used mean absolute
356 errors and confidence statistics over the wrights og input variables in the models to compare the
357 performance of the models.

358 We performed principal component analyses (PCA) to further explore the effect of ecometric traits
359 on the presence/absence of humans in Early Pleistocene and Middle Pleistocene localities
360 separately, and the presence of Early Pleistocene, early Middle Pleistocene and late Middle

361 Pleistocene human sites in the complete set of localities. This was done in order to compare the
362 relative and common associations of the ecometric traits with human presence. Partial per cent
363 contribution of the ecometric traits on the principal components were used for evaluating the
364 significance of associations of the constituent ecometric traits on human presence, and generalised
365 conclusions about the environmental conditions of most Pleistocene European human presence sites
366 are discussed based on this analysis.

367

368 **3. Results**

369 *3.1. Pliocene to Middle Pleistocene history of climate and net primary production in the Guadix-* 370 *Baza Basin*

371 Mean annual precipitation (MAP) and net primary production (NPP) estimates based on dental
372 ecometrics in large herbivorous mammal communities indicate a drastic decline from ca. 870 to ca.
373 450 mm/a in MAP and from ca. 1130 to ca. 700 g(C)/m²/a in NPP from the Early Pliocene of Baza
374 1 (ca. 4.6 Ma) to the Plio-Pleistocene boundary of Huélago (ca. 2.6 Ma) in the GBB (Table 1,
375 Figure 1). After this, Fuente Nueva 1 (ca. 2.2 Ma) and Fonelas P-1 (ca. 2 Ma) as well as Venta
376 Micena (ca. 1.6 Ma) have the lowest estimated MAP and NPP, while Barranco del Paso (ca. 1.8
377 Ma) with intermediate age has relatively high MAP and NPP estimates. After the drop at ca. 1.6 Ma
378 in Venta Micena, the MAP and NPP estimates become more homogenous and equable, ranging
379 from ca. 600 to 700 mm MAP and 900 – 1050 g(C)/m²/year NPP. The MAP in the GBB today is
380 around 450 mm (ca. 470 mm in Guadix, ca. 430 mm in Baza, [https://en.climate-](https://en.climate-data.org/europe/spain/andalusia)
381 [data.org/europe/spain/andalusia](https://en.climate-data.org/europe/spain/andalusia)), which is similar to the estimated value for Fuente Nueva 1 and
382 Venta Micena, while the rest of the Pleistocene localities in the GBB are estimated to have higher
383 mean annual precipitation values. Also the NPP value of modern surroundings of Baza, including
384 semi-feral domestic ungulates, is similar to the estimated values for Fuente Nueva 1 and Venta
385 Micena (Table 1).

386 In the hierarchical clustering of dental ecometric- based MAP, MINT and NPP estimates, Venta
387 Micena and Fuente Nueva 1 consistently cluster together with modern surroundings of Baza (Fig. 3
388 a and b), and with modern Mediterranean oak and pine woodland biomes (Fig 3 b). Huélago and
389 Fonelas P-1, together with Dmanisi, consistently form a cluster of their own next to the cluster
390 containing modern Baza and Mediterranean forests in Fig. 3 a and b. Baza 1, Solana del Zamborino
391 and Barranco del Paso cluster together with Bialowieza forest and Sierra Nevada National Park,
392 indicating temperate forest-dominated palaeoenvironments. The rest of the GBB sites, including BL
393 5 and FN 3, form a cluster of their own together with modern African woodland/shrubland and
394 some Pleistocene African sites, and this cluster is separate from modern African grassland savanna
395 (Serengeti plains) and most of the Pleistocene East African hominin sites (Fig. 3 a). Also ‘Ubeidiya,
396 Israel, clusters together with these sites.

397 A further comparison of the MAP values of the GBB sites with MAP ranges of modern
398 Mediterranean biomes (Quézel and Médail, 2003; Suc and Popescu, 2005) indicates that Huélago,
399 Fuente Nueva 1, Fonelas P-1, Mencal 9 and Venta Micena, together with modern environment of
400 Baza, fall within the range of modern “forest steppe” with *Artemisia*, *Pinus halepensis* and scarce
401 evergreen *Quercus* (Table 1). In contrast, Barranco del Paso, Fuente Nueva 3, Barranco León,
402 Huéscar 1 and Cúllar Baza 1 are within the range of evergreen forests dominated by sclerophyllous
403 *Quercus* and *Pinus*, and Baza 1 and Solana del Zamborino have higher MAP values indicating

404 affinity with mixed forest of deciduous *Quercus*, *Fagus* and conifers (Table 1). We consider these
 405 vegetational interpretations as further reference to the vegetation at the GBB sites, but note that
 406 these are likely to be oversimplified as they do not take into account temperature and NPP (see
 407 Discussion).

408

409 **Table 1.** Mean annual precipitation (MAP), minimum annual temperature (MINT) and net primary
 410 production estimates for the GBB sites, based on mammalian dental ecometrics (Oksanen et al.
 411 2019). Modern MAP and MINT values for the vicinity of Baza are from climate observation data
 412 (<https://en.climate-data.org/europe/spain/andalusia>) and the modern NPP value is estimated from
 413 dental ecometrics of large wild and domestic ungulates occurring in the area today. The
 414 Mediterranean vegetation zones (Quézel and Médail, 2003) indicated in the last column are: 1)
 415 Forest-steppe with *Artemisia*, *Pinus halepensis*, *Juniperus* and scarce evergreen *Quercus* (250 <
 416 MAP < 600 mm), 2) Evergreen forest with sclerophyllous oaks, *Pinus pinaster* and *P. pinea* (600 <
 417 MAP < 800 mm) and 3) Mixed forest with deciduous oaks, *Fagus* and conifers (MAP > 800 mm).

Age (Ma)	Locality	presence of humans	MAP (mm)	MINT (°C)	NPP (g(C)/m ² /a)	vegetation type estimated from MAP range of modern Mediterranean vegetation zones (Quézel and Médail 2003)
4.6	Baza 1	absent	873	[0]	1131	3
2.6	Huélogo	absent	447	0.5	691	1
2.2	Fuente Nueva 1	absent	384	10	713	1
2	Fonelas P-1	absent	543	1.5	797	1
1.8	Barranco del Paso	absent	678	1	975	2
1.7	Mencal 9	absent	538	13	882	1
1.6	Venta Micena	absent	449	11	767	1
1.4	Barranco León	present	602	8.5	914	2
1.2	Fuente Nueva 3	present	602	8.5	914	2
0.9	Huéscar 1	present?	708	12	1049	2
0.7	Cúllar Baza 1	present	602	8.5	914	2
0.4	Solana del Zamborino	present	945	2	1221	3
0	Modern (around Baza)	present	433	7	683	1

418

419

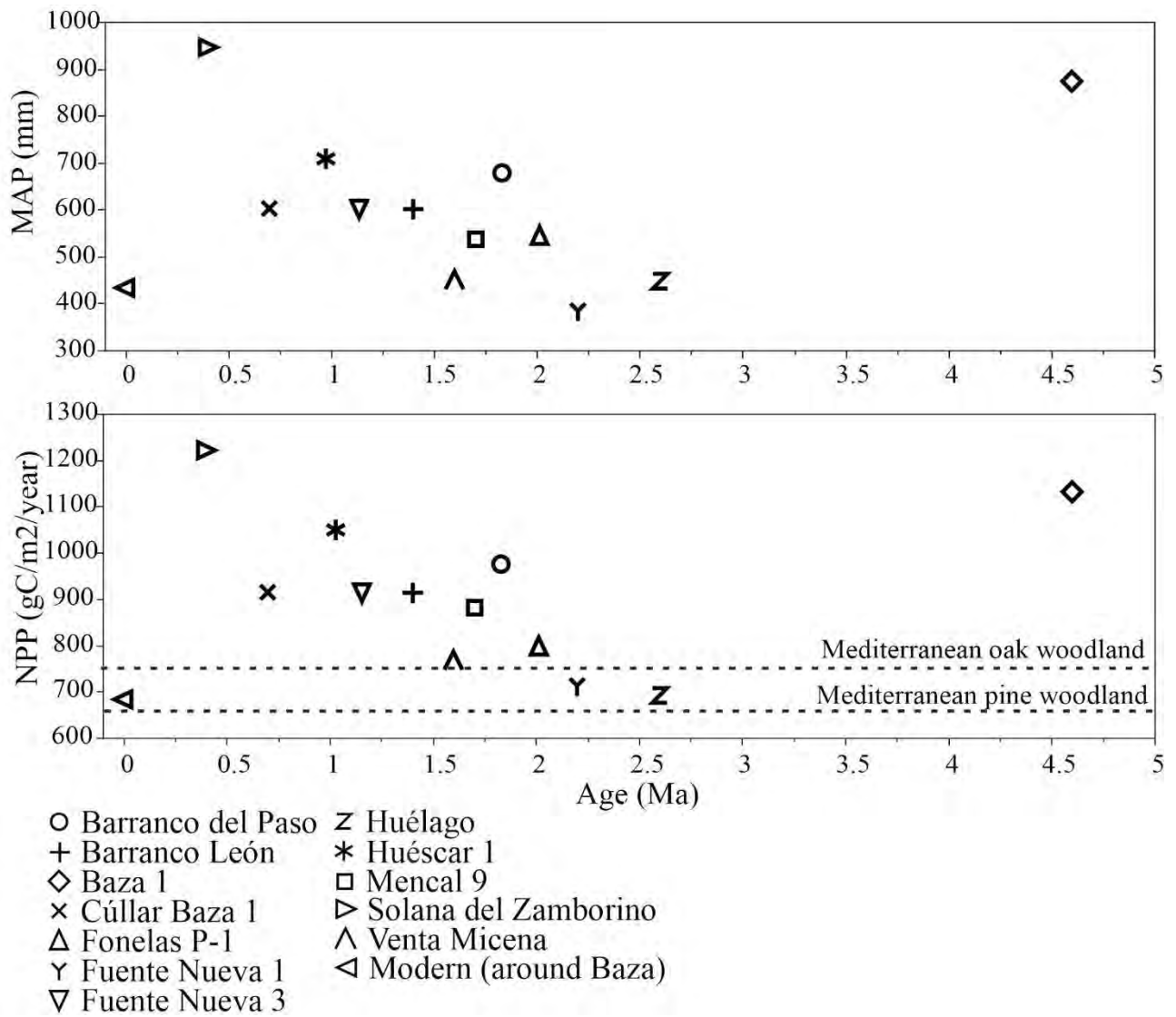
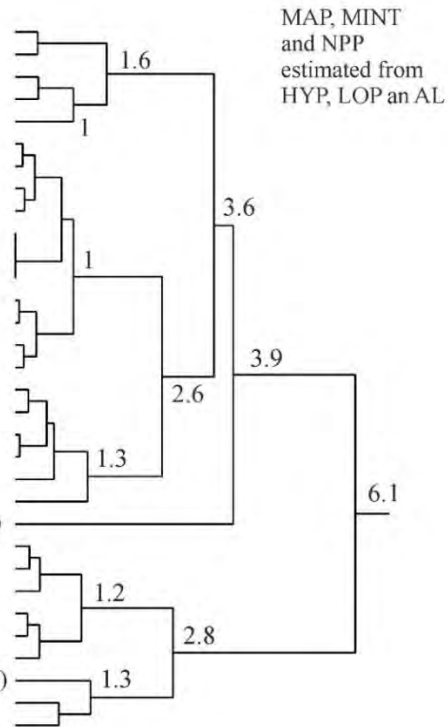


Figure 2. Mean annual precipitation and net primary production in the Guadix-Baza Basin from the Early Pliocene to the Middle Pleistocene as estimated from dental ecometrics of large herbivorous mammals using the equations published by Oksanen et al. (2019).

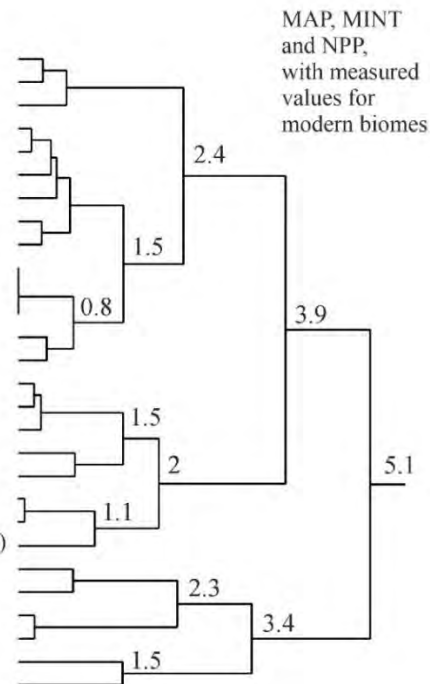
a

Baza 1
 Solana del Zamborino
 Barranco del Paso
 Sierra Nevada NP (IUCN site 143210)
 Bialowieza forest (IUCN site 13410)
 Mencil 9
 Nattoo FM
 woodland/shrubland near Nairobi (IUCN site 99719)
 Swartkrans Cave
 Fuente Nueva 3
 Barranco León 5
 Cúllar-Baza 1
 Huéscar 1
 Olduvai Bed IV
 Koobi Fora 10-KBS
 Serengeti (INCN site 98913)
 'Ubeidiya
 Koobi Fora 105-Upper Burgi
 Nariokotome FM
 Olduvai Bed II
 Kanjera 1
 Koobi Fora 1-Okote
 Tropical rainforest, Nouabale-Ndoki NP (IUCN site 200515)
 Fuente Nueva 1
 Venta Micena
 Baza, modern (including domestic)
 Huélago
 Dmanisi
 Fonelas P-1
 Boreal Montane Fores, British Columbia (IUCN site 126218)
 Nahanni National Park (IUCN site 114943)
 Yellowstone (IUCN site 132729)



b

Baza 1
 Solana del Zamborino
 Barranco del Paso
 Fuente Nueva 1
 Venta Micena
 Mediterranean pine forest
 Mencil 9
 Modern (around Baza)
 Mediterranean oak forest
 Fuente Nueva 3
 Barranco León 5
 Cúllar-Baza 1
 Huéscar 1
 'Ubeidiya
 Huélago
 Dmanisi
 Fonelas P-1
 Temperate forest
 Temperate C4 grassland
 Boreal forest
 Cold/temperate C3 grassland
 Temperate arid shrubland (Argentina)
 Deciduous tropical forest
 Humid savanna (Ivory Coast)
 C4 grassland (Nairobi NP, Kenya)
 Tropical C4 grassland
 Evergreen tropical forest
 Subtropical forest (NE India)



424

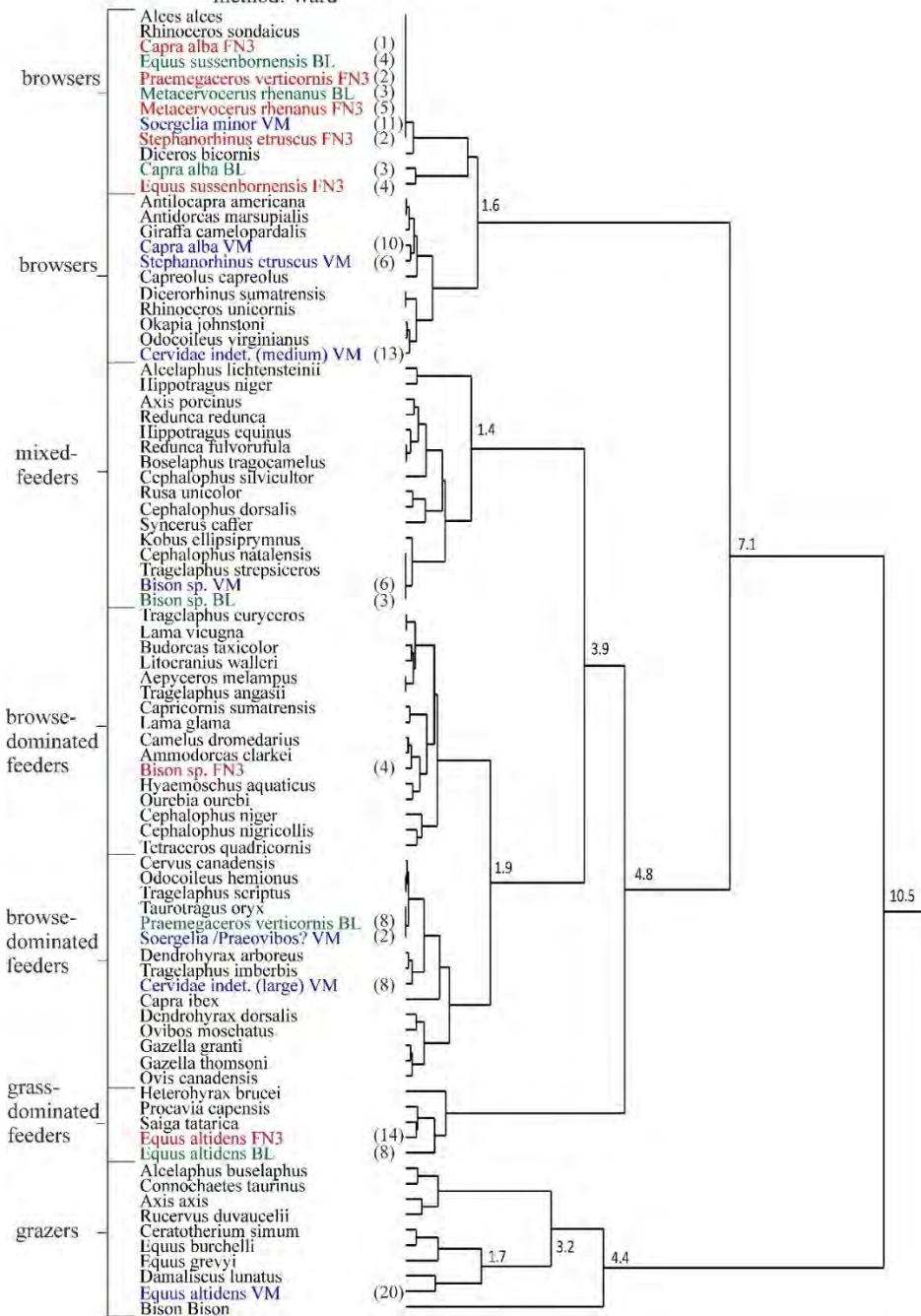
425 **Figure 3.** Hierarchical clustering of the Pleistocene Guadix-Baza sites based on MAP, MINT and
 426 NPP estimated from dental ecometrics with a) dental estimates of MAP, MINT and NPP for
 427 modern IUCN sites and Pleistocene African hominine sites, and b) reported MAP, MINT and NPP
 428 for modern biomes (Chirici et al., 2007; Olson et al., 2013). The Euclidean distance values marking
 429 branch lengths are indicated for 11 first branches. The GBB localities in separate clusters are
 430 marked with different colours. Dmanisi and 'Ubeidiya are included as examples of earliest Eurasian
 431 human sites outside the GBB.

432

433 3.2. Mesowear analysis of the large herbivorous mammals from the Orce sites

434 The results show that most of the Orce ungulate species from all the three localities (Venta Micena,
435 Fuente Nueva 3 and Barranco León) are clustered with extant ungulates that have predominantly
436 browsing and browse-dominated diets (Figure 4). Only *Equus altidens* shows mesowear signals that
437 in Venta Micena indicate purely grazing diet similar to extant zebras and white rhinoceros, and in
438 Barranco León and Fuente Nueva 3 grass-dominated but mixed diet similar to extant saiga antelope
439 and rock hyrax. Abundance of sharp cusps but low relief in *E. altidens* molars from BL and FN3
440 indicates a significant dietary element of some sort of tough vegetation that was not very abrasive.
441 Somewhat surprisingly, the larger species of horse, *Equus cf. suessenbornensis*, from Barranco
442 León and Fuente Nueva 3 have mesowear signals similar to extant browsers such as moose and
443 Javan rhinoceros, although they are represented by relatively small sample sizes. There is a slight
444 but interesting difference between Venta Micena and the rest of the Orce sites, especially in the
445 estimated diet of the horses: the browsing large species of horse (*E. cf. suessenbornensis*) is absent
446 from Venta Micena and the diet of the smaller species, *E. altidens*, is more grass-dominated in VM
447 than in the other sites.

Hierarchical clustering
 -variables: % high cusps, % sharp cusps, % blunt cusps
 -method: Ward



448

449 **Figure 4.** Hierarchical clustering of mesowear of the Orce ungulates with extant ungulate species,
 450 based on percentage of high relief, percentage of sharp cusps and percentage of blunt cusps
 451 (following the methodology of Fortelius and Solounias, 2000). Dietary interpretations are based on
 452 known diets of the modern ungulate species in the clusters (see Fortelius and Solounias, 2000). The
 453 ungulate taxa from Barranco León (BL) are marked in green colour, the ones from Fuente Nueva 3
 454 (FN3) in red, and the ones from Venta Micena (VM) in blue. The numbers in brackets indicate
 455 number of dental specimens used for each ungulate palaeopopulation from the Orce sites. Half
 456 square Euclidean distances are indicated for the first 10 clusters.

457

458 3.3. Early human (*Homo sp.*) habitat modelling based on dental ecometrics and body size of large
459 herbivorous mammals

460 We selected the following model for predicting human occurrence for the complete set of Early and
461 Middle Pleistocene localities, based on estimated coefficients of dental traits, their p-values,
462 accuracy as area under ROC and the mean absolute error:

463 $P(\text{occurrence}) = 1 / (1 + e^{-Z})$, where $Z = -15.852 + 3.542 \cdot \text{HYP} + 10.662 \cdot \text{SF} + 9.526 \cdot \text{AL} +$
464 $5.327 \cdot \text{BMloc}$.

465 In the model for all Early and Middle Pleistocene localities, the strongest significant positive effect
466 for the probability of human presence is given by percentage of the presence of acute lophs (AL),
467 followed by percentage of structural fortification (SF) in the large mammal communities (Table 2).
468 When the model is divided into Early Pleistocene and Middle Pleistocene separately, hypsodonty
469 (HYP), structural fortification (SF) and acute lophs (AL) remain the most significant constituents of
470 the model, but the model is different for Early Pleistocene and Middle Pleistocene. In the Early
471 Pleistocene, the most significant positive correlation for the probability of human presence is
472 provided by structural fortification, whereas in the Middle Pleistocene the most significant
473 correlation is with acute lophs (Table 2.)

474 Component 1 in the principal component analysis of human presence based on the traits
475 corresponds to 46.5 % of variation in human presence and it is contributed by the opposite effects of
476 SF+AL+BMloc and PS+HYP (Figure 4). Component 2 corresponds to 38.6 % of the variation in
477 human presence and is mainly driven by the opposite effects of PS and SF+BMloc.

478 In general, human occurrence is concentrated in localities with high values of acute lophs (AL),
479 structural fortification (SF), high mean body mass index of ungulates in localities (BM_loc), mean
480 bunodonty (BUN) and mean horisodonty (HOD), moderate values of hypsodonty (HYP) and low
481 values of plain selenodont ecomorphs (PS) (Appendix, Fig A.1). The positive correlation with the
482 presence of Early Pleistocene *Homo sp.* is dominated by the effects of high percentage of structural
483 fortification and high locality mean body size index, while the correlation with the Middle
484 Pleistocene humans varies more is more strongly driven by high percentage of acute lophs (Figure
485 4). Furthermore, within the Middle Pleistocene, the Early Middle Pleistocene human sites are more
486 associated with high percentage of acute lophs (AL) than the Late Middle Pleistocene localities
487 (Appendix, Fig A.1).

488 Human habitat suitability scores were calculated based on the total dental ecometric model
489 prediction for all the 92 Early and Middle Pleistocene European localities included in this study and
490 compared with the presence or absence of humans in the localities. The human habitat suitability
491 scores for the localities, ranked from highest to lowest, are presented in supplementary Table S5.
492 Since the model was fit on observed presence-absence data, the sites where the evidence for human
493 presence is lacking generally have the lowest habitat suitability scores and sites where humans are
494 present have the highest scores, but there are some notable exceptions to this pattern. Most notably,
495 several localities with evidence for human presence have lower-than-average estimated habitat
496 suitability scores (Atapuerca TE9c, Bisnik Cave, Visogliano, Orgnac 3, Caune de l' Arago,
497 Pakefield, Swanscombe, Pirro Nord, Hoxne, Vallparadis, Dmanisi and Cúllar-Baza 1). Of these,
498 Orgnac 3, cool stage levels of Caune de l' Arago and Bisnik Cave are characterised by the presence
499 of cold-climate taxa such as *Coelodonta* and *Rangifer tarandus*, indicating harsh climatic conditions
500 in this respect. In contrast, some sites with no evidence for human presence have higher-than-

501 average habitat suitability scores, suggesting that conditions there could have been suitable for
 502 humans, or more specifically, that condition there were quite similar to those where humans have
 503 found. Such sites without evidence for human presence but with high suitability estimates are the
 504 Early Pleistocene sites Colle Curti, Cesi, Castagnone and Monte Riccio in Italy and the early
 505 Middle Pleistocene sites of Mosbach and Prezletice in Central Europe. According to the model
 506 prediction, the Orce human sites Barranco León and Fuente Nueva 3 have a higher habitat
 507 suitability score for early humans than Venta Micena where evidence of human presence is lacking.

508 The colour-interpolated maps of human habitat suitability scores in Europe through time indicate
 509 geographical patterns of habitat suitability that reflects the history of early human dispersals in
 510 Europe (Figure 5). Some of the earliest indication of increase in habitat suitability for humans (as
 511 predicted by the model) occur in the first phase of Early Pleistocene (2.6 – 1.8 Ma) in Central Italy.
 512 During the second phase of Early Pleistocene (1.8 – 0.7 Ma) the areas of highest estimated human
 513 habitat suitability scores are centred in Southern Spain, Central Italy and in the Black Sea coast.
 514 During the early Middle Pleistocene, Central Europe and Southern England show a notable increase
 515 in the estimated human habitat suitability scores. In the late Middle Pleistocene, most of the
 516 European site have relatively high habitat suitability scores, except for a few sites indicating cold
 517 climatic conditions, such as Orgnac 3.

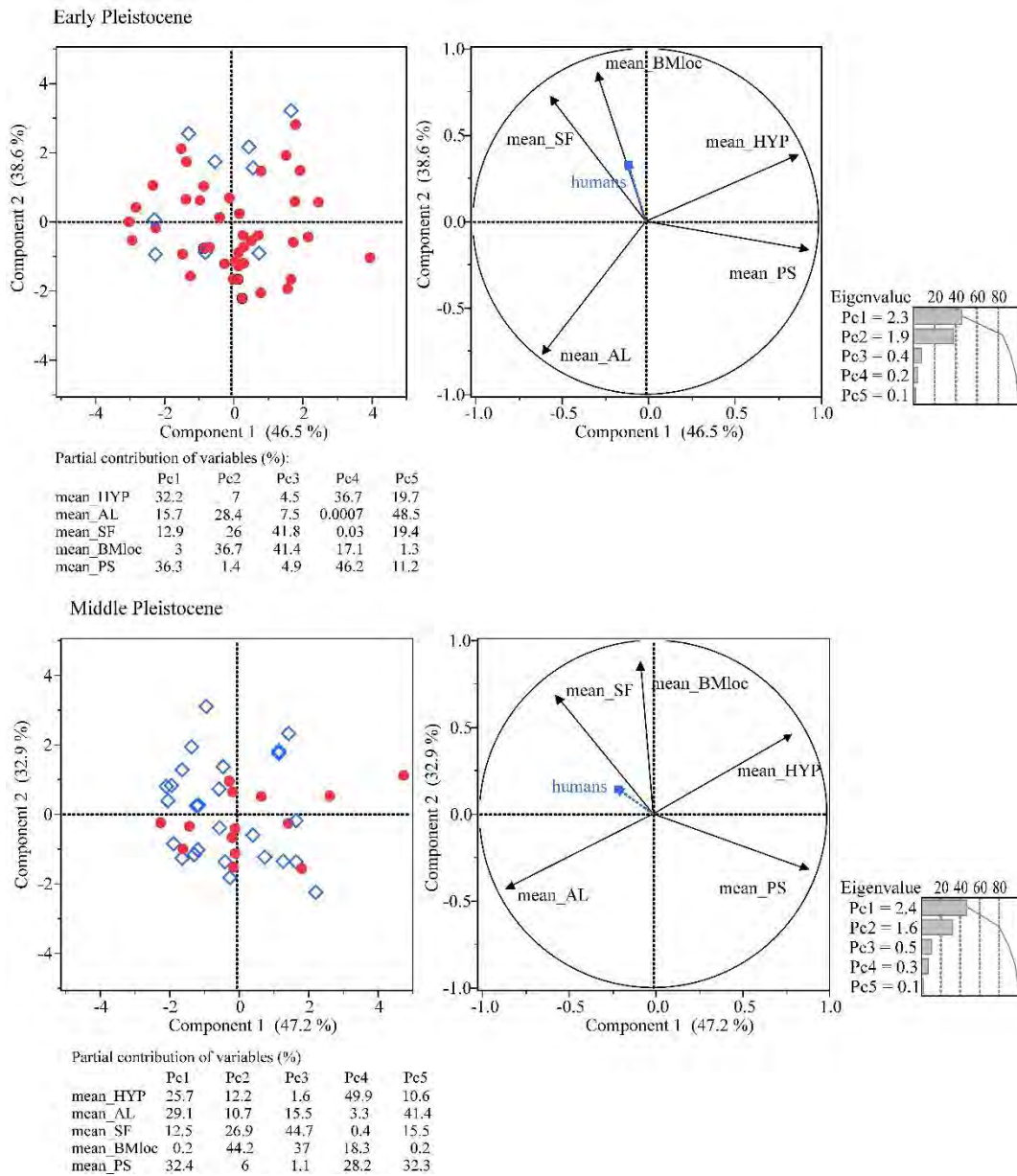
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519 **Table 2.** Coefficients for the dental ecometric traits from the generalised linear model prediction for
 520 the probability of human occurrence in Early and Middle Pleistocene Western Eurasian sites.
 521 Positive coefficients indicate positive correlation with the probability of human occurrence.
 522 Hypsodonty, acute lophs, structural fortification and locality mean body mass index have positive
 523 effects for the probability of human occurrence.

Sample	variables	coefficient	standard error	z value	Pr(> z)	Mean absolute error	Accuracy as area under ROC
Early Pleistocene	intercept	-12.812	8.934	-1.434	0.15		
	HYP	3.834	3.016	1.252	0.21		
	SF	11.035	4.997	2.209	0.03		
	AL	3.705	6.69	0.554	0.56	0.20	0.76
Middle Pleistocene	intercept	-7.502	6.108	-1.228	0.219		
	HYP	2.112	2.100	1.006	0.315		
	SF	5.792	4.612	1.256	0.209		
	AL	7.095	5.157	1.376	0.169	0.34	0.63
Total	intercept	-15.852	5.04	-3.145	0.002		
	HYP	3.542	1.603	2.21	0.03		
	SF	10.662	2.926	3.644	0.0003		
	AL	9.526	3.631	2.624	0.009		
Total	BMloc	5.327	3.965	1.347	0.18	0.29	0.76

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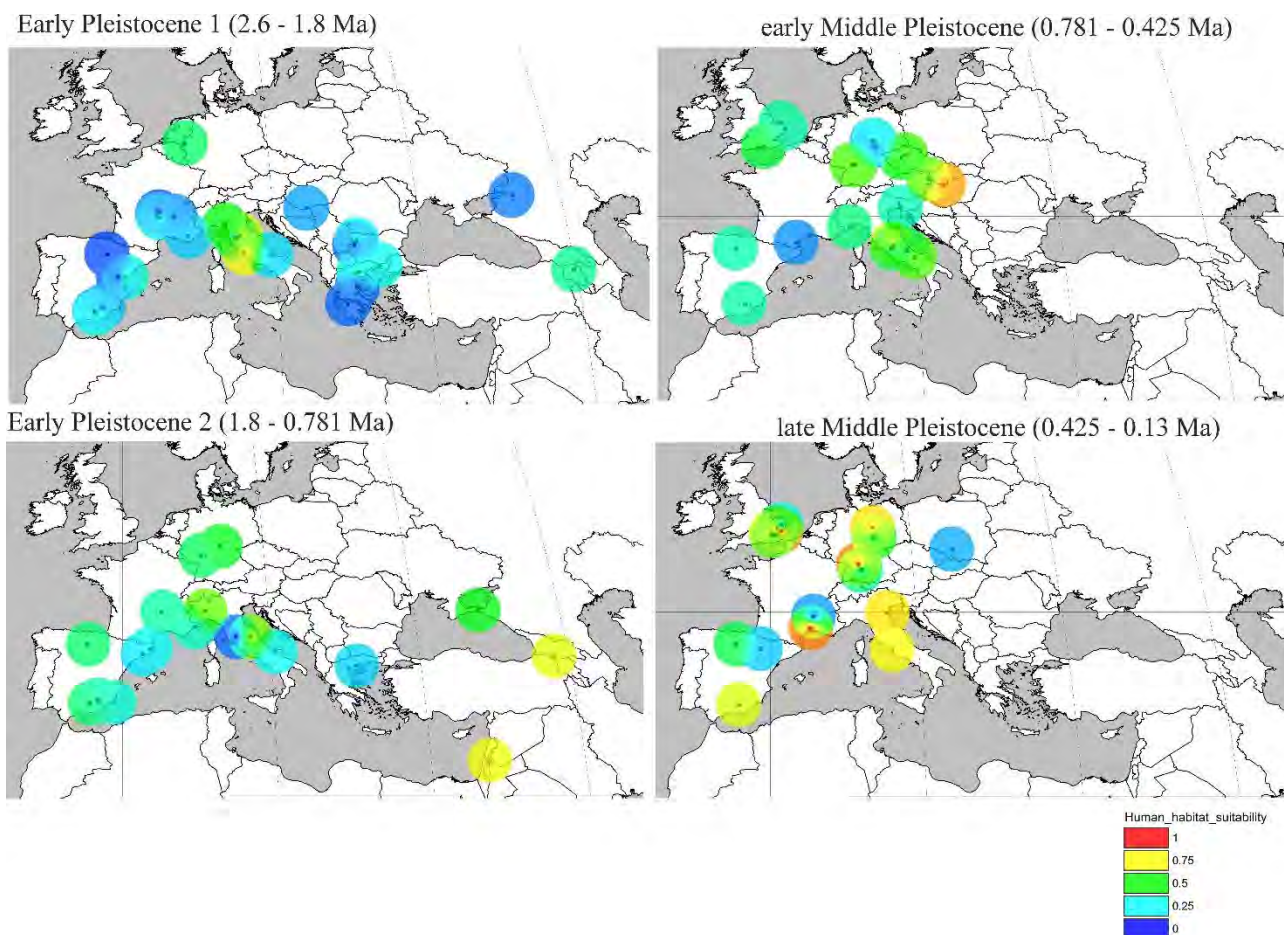
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526

527 **Figure 5.** Principal component analysis of human and non-human sites in Western Eurasia during
 528 the Early and Middle Pleistocene. The red dots mark localities where evidence of the presence of
 529 humans is lacking, and the open blue diamond symbols mark localities where humans were present.
 530 During the Early Pleistocene, most of the human occurrence sites are characterised by relatively
 531 high values of structural fortification and mean body mass, while sites with high hypsodonty and PS
 532 values suggesting “harsh” environments show an almost complete absence of human occurrence. In
 533 the Middle Pleistocene, the human sites are more evenly distributed over the ecometric space but
 534 are more concentrated towards sites with relatively high values of acute lophs, structural
 535 fortification and mean body mass, suggesting on average relatively wooded palaeoenvironments.

536



537

538 **Figure 6.** Colour-interpolated maps of probability of human presence (human habitat suitability
 539 estimated from dental ecometric variables and locality body mass indices) for Early and Middle
 540 Pleistocene Western Eurasian sites. Blue indicates poor suitability for humans and red indicates the
 541 highest suitability, with the spectrum from light blue to green and yellow indicating increasing
 542 habitat suitability. In the earliest phase of Early Pleistocene, the earliest human site in Eurasia
 543 (Dmanisi, Georgia), Tegelen (Netherlands) and especially Central Italian sites have the highest
 544 suitability scores. In the later phase of Early Pleistocene, areas of highest suitability are centered
 545 around the Black Sea coast, Andalusia and Central Italy. In the early Middle Pleistocene, there is
 546 high variation in the habitat suitability, with many Central European and Italian sites getting high
 547 suitability scores. In the late Middle Pleistocene, habitat suitability is mostly high, being highest in
 548 the Mediterranean coast, Central Europe and Southern England, but poor in a few localities that
 549 indicate cold climate.

550

551 4. Discussion

552 The Guadix-Baza Basin in Andalucía, Spain, has particular relevance for the question of early
 553 human habitats and dispersals, as the archaeological and palaeontological sites of Barranco León
 554 and Fuente Nueva 3 (both ca. 1.4 Ma in age) have provided some of the earliest evidence for the
 555 presence of early humans (*Homo* sp.) in Europe (Toro-Moyano et al., 2013). Understanding the
 556 history of climatic and environmental conditions in the GBB and elsewhere in the Early Pleistocene
 557 of Europe is highly important for understanding the underlying environmental conditions under

558 which early human dispersal to Europe happened, and ecometric and palaeoecological analyses
559 from fossil mammals provide new, previously understudied insights into these.

560 Fossil molar teeth of large herbivorous mammals are abundantly available for the Pliocene to
561 Middle Pleistocene fossil localities in the GBB, and thus the dental ecometrics of large herbivorous
562 mammals provide, to our knowledge, thus far the most comprehensive record of climate and
563 environmental history in the archaeological and palaeontological sites in GBB and elsewhere in
564 Europe during the Early and Middle Pleistocene.

565

566 *4.1. Pliocene to Pleistocene climate and palaeoenvironments in the GBB – high-productivity* 567 *woodland ecosystems in the Mediterranean climatic realm*

568 MAP, MINT and NPP estimated from dental ecometric traits in large herbivorous mammal
569 communities indicate a prevalence of palaeoenvironments that are most closely clustered with
570 modern Mediterranean forests than other extant biomes for the GBB sites. The high MAP and NPP
571 estimates for the Pliocene site of Baza 1 (ca. 4.5 Ma; Piñero et al., 2017; Ros-Montoya et al., 2017),
572 the Early Pleistocene Barranco del Paso (ca. 1.8 Ma; Gibert et al., 1992) and the Middle Pleistocene
573 Solana del Zamborino (ca. 0.4 Ma; Jiménez-Arenas et al., 2011; Álvarez-Posada et al., 2017;
574 although see Scott and Gibert, 2009) indicate a much more humid climate and more high-
575 productivity palaeoenvironments than in the GBB today. Hierarchical clustering of these sites with
576 modern IUCN sites indicates a close similarity to the temperate mixed forests of Bialowieza and
577 Sierra Nevada National Parks. This interpretation is further supported by comparison of estimated
578 MAP with the MAP range of modern Mediterranean biomes (Quézel and Médail, 2003; Suc and
579 Popescu, 2005), where Baza 1 and Solana del Zamborino fall within the range of mixed forests with
580 deciduous oaks, *Fagus* and conifers. According to Fauquette et al. (1999), the taxonomic
581 composition of the vegetation in the Mediterranean environments was largely similar to present
582 already in the Pliocene, with the exception of additional presence of subtropical elements such as
583 Taxodiaceae, *Sequoia*, *Engelhardia* and *Symplocos*.

584 During the Early Pleistocene, the localities of Fuente Nueva 1 (ca. 2.2 Ma) and Venta Micena (ca.
585 1.6 Ma) show MAP and MINT estimates that are similar to the present MAP and MINT in the
586 GBB, and NPP estimates that are similar to values estimated from dental ecometrics of large
587 mammals around Baza today and measured values for modern Mediterranean woodland or forest
588 steppe environments. Huélago (ca. 2.6 Ma) and Fonelas P-1 (ca. 2 Ma) also consistently cluster next
589 to the cluster containing estimated MAP, MINT and NPP for modern Baza and measured values for
590 modern Mediterranean woodlands, but they differ mainly in having cooler estimated mean
591 temperatures of coldest month (MINT) than at present. Comparison of the MAP estimates of the
592 GBB sites with MAP ranges of modern Mediterranean biomes (Quézel and Médail, 2003; Suc and
593 Popescu, 2005) provides an additional reference for comparing the vegetation types in the GBB
594 localities. According to this classification, MAP range between 250 and 600 mm/a correspond with
595 forest steppe habitats with *Artemisia*, *Pinus halepensis*, *Juniperus* and scarce evergreen *Quercus*.
596 The modern environment around Baza, as well as the fossil sites of Huélago, Fuente Nueva 1,
597 Fonelas P-1 Mencil 9 and Venta Micena fall within this MAP range.

598 The rest of the Early and Middle Pleistocene localities in the GBB, including the earliest human
599 occupation sites of Fuente Nueva 3 and Barranco León, are clustered together with African
600 woodland or shrubland environments, the Early Pleistocene Natoo Formation from West Turkana,

601 Kenya, and the Early Pleistocene site of Swartkrans, South Africa, based on dental ecometric
602 estimates of MAP, MINT and NPP. Furthermore, these sites form a cluster of their own that is more
603 closely clustered with the modern Mediterranean forests than other modern biomes when compared
604 with reported MAP, MINT and NPP for modern biomes (data from Chirichi et al., 2007, Olson et
605 al., 2013). In these environments, the estimated precipitation varies from similar to somewhat
606 higher than today in the GBB and is lower than in temperate forest biomes, but NPP estimates are
607 higher than in modern Mediterranean and temperate forests. On the other hand, the estimated
608 precipitation and NPP are lower than in modern tropical forests and humid savannas, and estimated
609 NPP is significantly higher than in C4 grassland savannas. After the relatively dry conditions at
610 Venta Micena, precipitation and NPP increased around 1.4 Ma at Barranco León and Fuente Nueva
611 3, the oldest human sites in the GBB. The dental ecometrics-based estimates of MAP (602 mm) and
612 NPP (914 g(C)/m²/a) are higher than today in the GBB, while estimated minimum annual
613 temperature is similar to present (8.5°C). Herpetofauna from these sites indicates that temperature
614 and precipitation in BL and FN 3 were higher than at present (Blain et al., 2011, 2016), and the
615 vegetation would have been dominated by relatively open woodland type (Blain et al., 2011;
616 Sánchez-Bandera et al., 2020). MAP range between 600 and 800 mm/a in modern Mediterranean
617 realm indicates the presence of evergreen forests with sclerophyllous oaks (e.g. *Quercus ilex-*
618 *coccifera*) and pines, and the fossil sites of Barranco del Paso, Fuente Nueva 3, Barranco León,
619 Huéscar 1 and Cúllar-Baza 1 fall within this vegetation category by modern analogue. However,
620 note the affinity of these sites with African woodland habitats in the hierarchical clustering which
621 also uses MINT and NPP values in addition to MAP, indicating perhaps a slightly higher-
622 productivity environment than modern Mediterranean sclerophyllous forests. In summary, the
623 climatic and productivity estimates for the earliest human occupation sites in the GBB (FN3 and
624 BL) were climatically within the range of modern Mediterranean evergreen oak and pine forest
625 environments, but had relatively high NPP, indicating similarity to African dry
626 woodlands/shrublands. However, these environments differed from African grass-dominated
627 savannas. In this regard, BL and FN3 were similar to some African early human sites (Swartkrans
628 and Nattoo Formation), as well as ‘Ubeidiya, Israel, but were different from most of them that
629 indicate palaeoenvironments similar to extant grass-dominated savannas of Serengeti, such as
630 Upper Burgi and KBS Members of Koobi Fora Formation in East Turkana, Nariokotome Member
631 in West Turkana, Olduvai Bed IV, and Kanjera.

632 The interpretation of woodland or shrubland environments, without a significant grassy component
633 of undergrowth, at BL and FN3 is further supported by the mesowear analysis of the ungulate
634 communities. In both sites, vast majority of the ungulate species show mesowear values that cluster
635 together with modern browsers such as *Alces alces* and *Rhinoceros sondaicus* (most of the species)
636 or with browse-dominated mixed-feeders such as *Taurotragus oryx* (the large cervid, cf.
637 *Praemegaceros verticornis*, from BL) or *Tragelaphus strepsiceros* (the large bovines from Barranco
638 León and Fuente Nueva 3). Most notably, even the larger species of horse (cf. *Equus*
639 *suessenbornensis*) from both of the sites clusters with the browsers, while the smaller species of
640 horse (*E. altidens*) is the only species from BL and FN3 that clusters with the extant grass-
641 dominated feeders saiga antelope (*Saiga tatarica*) and rock hyrax (*Procavia capensis*). Such a
642 prominence of browsing diets in the ungulate communities indicates a palaeoenvironment that could
643 not have been grass-rich, and provided rather rich foliage of trees, shrubs or dicotyledonous herbs.
644 Also, the ungulate assemblage from Venta Micena, with estimated dryer climatic conditions, shows
645 an abundance of browsing and browse-dominated feeders, but a higher proportion of mixed-feeders
646 and only one species of horses (*Equus altidens*), which has the only truly grazing mesowear signal

647 of all the ungulates in the Orce sites, clustering with modern grazers such as zebras (*Equus*
648 *burchelli* and *E. grevyi*), tsessebe (*Damaliscus lunatus*) and prairie bison (*Bison bison*). The
649 mesowear data thus indicates a more open and grass-rich palaeoenvironment in Venta Micena than
650 in BL and FN3.

651 The climatic range estimated for most of the Pleistocene GBB sites (including the Orce sites) falls
652 within a temperature and precipitation regime under which the biome cannot be estimated directly
653 from the climate, because other factors such as soil fertility, fire and the top-down influence of large
654 mammal herbivory have a profound impact on the vegetation type (Bond, 2005; Kujper et al.,
655 2015). The NPP estimated by large mammal dental ecometrics represents primary productivity
656 edible by the herbivorous mammals, and the high diversity and body size range of the Early
657 Pleistocene large mammal communities is expected to reflect relatively high NPP. In the surviving
658 natural temperate forests today, such as Bialowieza, the large herbivorous mammals such as
659 European bison, moose, red deer and feral horses, do not create significant open environments, but
660 instead affect the species composition of the trees (Kujpers et al., 2015). Unfortunately, we are
661 currently lacking temperate and Mediterranean environments with a diversity of large mammals
662 even nearly as high as during the Early Pleistocene, making it challenging to estimate the effect of
663 large herbivores on vegetation. For example, the effect of elephants on tree cover can be significant
664 in some environments (Guldemond et al., 2008), and this effect could have been prominent in the
665 Pleistocene but is currently lacking in temperate and Mediterranean environments. The difficulty of
666 assessing how drastic the effect of large herbivores on vegetation was in the past, especially as
667 reliable estimates of herbivore population sizes are lacking, was acknowledged by Bradshaw et al.
668 (2003). However, they conclude that the balance of paleoenvironmental evidence indicates mostly a
669 rather local effect of herbivory on otherwise mostly forested landscapes during the Late Pleistocene
670 and especially Holocene in Northern Europe.

671 The similarity of Venta Micena to modern Mediterranean “forest steppe” and the present climatic
672 conditions and productivity around Baza, and the affinity of FN3 and BL with Mediterranean
673 evergreen forests with lack of significant grass undergrowth, probably relate to the difference in
674 seasonality of rainfall patterns in the Mediterranean realm and East Africa. The seasonality of
675 precipitation in East Africa includes two rainy seasons, whereas the Mediterranean climate is
676 characterised by one rainy season in the winter and hot and dry summers. Drought-tolerant trees and
677 shrubs have an advantage during the hot and dry summer in the Mediterranean realm, while grasses
678 that require more evenly distributed annual rain are in disadvantage there especially due to extended
679 autumn drought (Dallman, 1998; Nogueira et al., 2017). On the other hand, grass-dominated
680 savannas in East Africa thrive under conditions with two rain seasons (e.g., Hesla et al., 1985). Such
681 dissimilarity in the rainfall pattern could largely explain the grass-poor environments in the GBB
682 and the on average more grass-dominated environments of the hominin sites of East Africa during
683 the Pleistocene.

684 Whatever the case, it is evident from the scarcity of grazers that the vegetation in the Orce sites was
685 not dominated by grasses and would thus not likely have been particularly similar to modern
686 African grasslands or grass-dominated savannas. Thus, our results do not support the
687 “savannahstan” hypothesis (Dennel and Roebrooks, 2005; Dennel, 2010) for the GBB sites, at least
688 if the “savannahstan” is understood in the strict sense to be similar in environmental condition to
689 African savannas with grassy undergrowth. Although never dominant, Poaceae is relatively
690 frequent in the pollen record from Palominas lake sequence in the GBB (Altolaguirre et al., 2020),
691 but its fluctuations do not parallel those of the xerophytic component. This leaves open the

692 possibility that a portion of the total count is due to local overrepresentation of grass pollen (e.g.
693 marginal and/or basinal vegetation). Furthermore, it cannot be discarded that grasses could have
694 increased regionally during wet interglacials. Today, hard-leaved perennial grasses such as *Lygeum*
695 *spartum* (on marls and gypsum soils) and *Stipa tenacissima* (on limestones) dominate the local
696 vegetation, but this was clearly not the case during the Early and Middle Pleistocene.

697 In summary, the climate and productivity estimates from the dental ecometrics of the large
698 herbivorous mammal community indicate palaeoenvironments similar in vegetation structure to
699 Mediterranean woodlands, with temperature close to present and annual precipitation and NPP
700 slightly higher than at present in Baza. This raises the question of what these environments were
701 like in terms of resources available for the early humans. The predominantly browse-dominated
702 mesowear signals of ungulates suggests a palaeoenvironment where grasses were not a dominant
703 element in the vegetation, but the browse-dominated mesowear does not further separate whether
704 the browse was mainly obtained from trees, shrubs or non-grass herbs. The Palominas pollen core
705 indicates a high variation in the vegetation in the GBB during the Early Pleistocene, ranging from
706 open grass and *Artemisia* -dominated during dry phases to diverse deciduous/evergreen *Quercus*
707 woodland and wetland during the humid phases (Altolaguirre et al., 2019). Pollen record from a
708 sedimentary section in Palominas provides a reference to the vegetation cycles in the GBB during
709 the Early Pleistocene roughly between the MIS 53 and MIS 34, suggesting that the levels indicating
710 warm and humid conditions correspond with the conditions present in BL and FN3 (Altolaguirre et
711 al., 2019). The evidence from mammal ecometrics, herpetofauna and ungulate mesowear all point at
712 relatively somewhat more humid than present conditions and non-grassy environments in Barranco
713 León and Fuente Nueva 3, which would more likely correspond with the woodland-type vegetation
714 in the Palominas core. The inferred vegetation of such phases of the Palominas core is generally
715 forested with some degree of openness and dominated by deciduous and evergreen *Quercus*, with a
716 diversity of mesophytes such as *Carpinus*, *Acer*, *Juglans*, *Corylus*, *Populus*, *Salix*, *Ulmus*,
717 *Castanea*, *Fagus* and *Buxus*, and thermophytes such as *Olea*, *Pistacia*, *Coriaria*, *Tamarix*, *Phlomis*,
718 *Myrica*, in addition to genera today extinct in the western Mediterranean such as *Eucommia*,
719 *Parrotia*, *Cathaya*, *Aralia*, *Zelkova*, *Pterocarya*, *Tsuga* and *Nyssa* (Altolaguirre et al., 2019, 2020).
720 The sediments at BL and FN3 were deposited during a phase when the Baza Lake in the GBB was
721 relatively large due to basin dynamics (Oms et al., 2011). Sedimentological evidence indicates a
722 palustrine depositional environment for both BL and FN3 (Oms et al., 2011 and references therein),
723 and the presence of wetlands is further attested by faunal elements such as the abundance of
724 hippopotamus (*Hippopotamus antiquus*) in these localities.

725 These wooded phases are intersected in the Palominas core by phases during which the vegetation
726 became steppe-like, dominated by pollen of *Artemisia*, *Ephedra*, Chenopodioideae, Asteraceae, and
727 Poaceae. The conditions during those stages were climatically probably similar to present
728 conditions, possibly allowing the early humans to survive in the area through the glacial stages and
729 to thrive during the warm, humid phases such as those at BL and FN3 (Altolaguirre et al., 2019).

730

731 4.2. Early human palaeoenvironments in Europe – savannas, forests or wetlands?

732 In a broader perspective, the dental trait distribution of large herbivorous mammals across Europe
733 during the Early and Middle Pleistocene indicates on average relatively high-productivity and
734 wooded environments, and avoidance of the harshest environmental conditions. This is illustrated
735 by the positive correlation of high values of AL, SF, BMloc and BUN, and negative correlation of

736 high values of PS with human presence throughout the Early and Middle Pleistocene in Europe.
737 Large average body size in ungulate communities, particularly in the temperate zone such as in
738 Europe during the Quaternary, indicates moderately open habitats but also high resource quality and
739 availability (Saarinen, 2014; Saarinen et al., 2016). These environments, where ungulate
740 communities have high proportion of acute lophs, structural fortification and large average body
741 size, would have likely provided diverse resources for the early humans. In many cases there is also
742 evidence of the presence of significant bodies of water and waterside environments, as indicated by
743 the frequent co-occurrence of *Hippopotamus* with early humans in Europe. The importance of
744 bodies of water for ancient human occupation is prominently attested by archaeological data (e.g.
745 Cohen et al., 2012). Furthermore, Devès et al. (2014) found a suggestive association of early *Homo*
746 with marshy/lakeside environments, where they suggest relatively low-risk exploiting large animals
747 such as elephants would have been possible, and the use of rougher terrains was a secondary
748 strategy used in the absence of large, water-dependent herbivores.

749 Despite these interpretations of average environmental conditions in early human occupation sites,
750 open questions remain. One of these is how the top-down effect of humans and carnivores on the
751 herbivore community is reflected in the ecometric signal of the early human environments. The
752 sampling of the Early and Middle Pleistocene sites for the dental ecometric analysis was made with
753 caution in regard to sampling biases, including those introduced by selection of prey animals by
754 carnivores and humans. For this reason, sites with accumulations gathered primarily by human or
755 carnivore activities were avoided, such as carnivore dens and human dwellings. Furthermore, no
756 systematic difference in the species composition between human sites and non-human sites was
757 observed in the herbivorous mammal communities. However, this does not preclude the possibility
758 of human influence in the herbivorous mammal communities. Whether this matters for the
759 ecometric estimates of temperature, precipitation and NPP depends on whether human influence
760 changes the selection of herbivorous mammal species in the localities in a way that obscures the
761 environmental signal. As we selected all sites with more than five large herbivorous mammal
762 species present, and the species within the assemblages typically represent a wide range of
763 ecometric traits, it is unlikely that a systematic bias from human influence would obscure the
764 environmental signal.

765 The principal component analysis where Early Pleistocene sites with human presence (*Homo* sp.),
766 early Middle Pleistocene sites (cf. *Homo heidelbergensis*) and late Middle Pleistocene sites (cf.
767 *Homo neanderthalensis*) are separated, provides additional information that points at interesting
768 differences in the habitat preference of these different “chronospecies” of *Homo*. The particularly
769 high correlation of Early Pleistocene *Homo* and late Middle Pleistocene *Homo neanderthalensis*
770 with sites where the ungulate assemblages show high proportion of structurally fortified cusps in
771 molars and large average body size indicate that they were mostly associated with woodland-type
772 environments. On the other hand, the early Middle Pleistocene *Homo* are particularly associated
773 with sites where the ungulate communities have a high proportion of acute lophs, indicating
774 forested environments and perhaps cooler climatic conditions (Oksanen et al., 2019). This
775 observation is interesting in the light of archaeological discoveries. For example, the earliest
776 evidence of human occurrence in Britain comes from the ca. 900 ka site of Happisburgh 3, where
777 the proxy evidence indicates relatively cool climatic conditions and vegetation dominated by
778 conifers, possibly similar to the southern edge of boreal forest, such as today in Southern Sweden
779 (Parfitt et al., 2010; Farjon et al., 2020).

780 The earliest human occupation in Europe during the Early Pleistocene thus seems to concentrate in
781 relatively equable and wooded but diverse environments, and our analysis also suggests that the
782 dispersal of early *Homo* into Europe roughly followed the distribution of such environments
783 through time, the conditions being best first in the Caucasus region and the Mediterranean (Spain
784 and Northern Italy). This is in accordance with the ecological model proposed by Blain et al.
785 (2021), based on herpetofaunal assemblages, who suggested that rainfall and environmental
786 humidity (expressed as forest cover) may have had an impact on the occupation of the territory
787 during the Early and Middle Pleistocene more than other factors as temperature. Agustí and
788 Lordkipanidze (2019) suggested that early hominines in Eurasia would have favoured wooded
789 environments because of safer scavenging opportunities compared to open savanna environments,
790 and argued that the early dispersal of *Homo* from Africa to the Caucasus region (Dmanisi) would
791 have followed the distribution of such wooded habitats ca. 1.8 Ma. However, the continuous
792 presence of humans in Europe since the Early Pleistocene might indicate that they were able to
793 survive periods of climatic deterioration and the spread of more steppe-like environments, perhaps
794 leaving no traces in the archaeological record because of diminished population sizes. For example,
795 Altolaguirre et al. (2019) suggested that while humans first appeared in the GBB under relatively
796 humid and wooded conditions, they could have survived there during the coming glacial stages
797 when the climate became dryer but not much cooler, approaching modern conditions. This
798 interpretation is supported by Sánchez-Bandera et al. (2020). Overall, the archaeological records
799 indicate that *Homo* sp. was a frequent but not abundant species in European Early Pleistocene
800 localities (Rodríguez et al., 2015).

801 The importance of local conditions, often phytogeographically linked to micro- and mesoclimates
802 and/or strong edaphism (Carrión et al., 2019), should not be underestimated, and while general
803 climates could be cold dry and regional vegetation open woodland and steppe, the highly complex
804 orography of the surrounding mountains may well have favoured the existence of biodiversity
805 strongholds where ecologically disparate species cohered in time and space during hundreds of
806 millennia. The study case of the mid-Pleistocene Neanderthal Cova de Bolomor, northwards in
807 Valencia, is particularly pertinent (Ochando et al., 2019). This scenario could explain why
808 Arctotertiary taxa mix up with xerothermophilous scrub in Palominas (Altolaguirre et al., 2020).
809 Needless to say, these phytodiversity reservoirs would be crucial to recolonization patterns during
810 interglacials (Carrión et al. 2018).

811 *4.3. Early human occupation – boundary conditions vs. attractions?*

812 Some of the Early Pleistocene human occupation sites with relatively low predicted human habitat
813 suitability score have lower mean hypsodonty values, but moderate structural fortification and r
814 acute loph values (e.g. TE9c of Atapuerca, Vallparadís level 12). Pollen and small vertebrate
815 records indicate the presence of abundant wooded vegetation and relatively high precipitation at
816 TE9c (Blain et al., 2010; Huguet et al., 2017) and at Vallparadís (Martínez et al., 2010). Dmanisi,
817 Georgia, which is the earliest of the human occupation sites, has the lowest habitat suitability score
818 of all the Early Pleistocene human occupation sites. This may be understandable because there is a
819 large geographic distance and different fauna in Dmanisi compared with the other European early
820 Pleistocene human sites, which occur on average much further west.

821 Humans are opportunistic in terms of diet and habitat requirements and use tools to overcome
822 limitations set by environmental conditions. It is thus not surprising that the Pleistocene human
823 occupation sites indicate a wide range of environments based on proxy data and dental ecometric

824 modelling. The presence of humans at sites with the lowest human habitat suitability scores based
825 on the dental ecometric model, such as TE9c, Vallparadis and Dmanisi, could reflect other
826 attractions, such as raw material for tool making that spurred the hominins to overcome the
827 challenges presented by the less-than-optimal environmental conditions. In TE9c the raw materials
828 for the stone tools were gathered from the vicinity of the site at a range of less than 2 km (Huguet et
829 al., 2017). At Dmanisi, the range of volcanic and other rock types present in the area would have
830 provided a high diversity of lithic raw materials (Baena et al., 2010). This could also, to some
831 extent, be the case for the earliest human sites in the GBB (Barranco León and Fuente Nueva 3) as
832 while the human habitat suitability score for them is moderately good, the value of the basin for
833 human occupation could have been enhanced by the availability of lithic raw materials, especially
834 flint (Barsky et al., 2010; Titton et al., 2021).

835

836 **5. Conclusions**

837 According to our mammalian dental ecometric estimates, mean annual precipitation and primary
838 productivity decreased in the GBB from the Pliocene to the Pleistocene, but showed intensive
839 fluctuation thereafter reaching a higher level again during the earliest human occupation in the sites
840 of Barranco León and Fuente Nueva 3 (1.4 – 1.2 Ma). Overall, the estimated environmental
841 conditions in the GBB during the Pleistocene ranged from conditions similar to modern
842 Mediterranean woodlands and shrublands to woodland and forest environments with higher primary
843 production. The dietary spectrum of the ungulates from the Orce sites, especially Barranco León
844 and Fuente Nueva 3, is heavily dominated by browsers and browse-dominated feeders, suggesting a
845 palaeoenvironment where grasses were not a significant element of the herbivorous mammals' diet.
846 In Venta Micena (ca. 1.6 – 1.4 Ma) especially the equids show a more grass-dominated dietary
847 signal, although most of the ungulates there were also browse-dominated feeders.

848 Early human distribution modelling in the Early and Middle Pleistocene of Europe based on dental
849 ecometrics of large herbivorous mammals indicates that the environments where humans occurred
850 during the Early Pleistocene were mostly woodland -dominated environments, whereas in the
851 Middle Pleistocene, humans dispersed to a wide range of environments, being somewhat more
852 concentrated in forest environments.

853

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875

876 **Data availability**

877 The data used for the analyses in this study are provided in supplementary tables S1-S4. Further
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880

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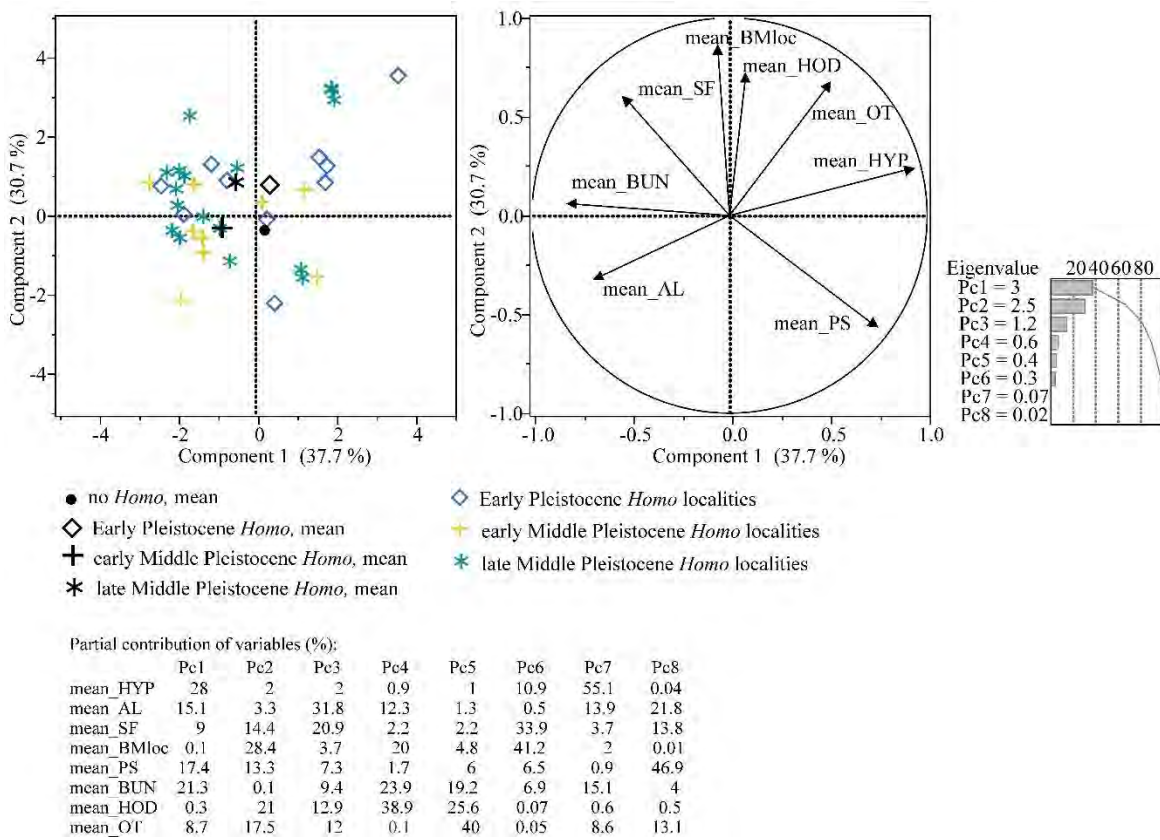
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Appendix



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1148 **Figure A.1.** Principal component analysis of localities with Early Pleistocene *Homo*, early Middle
 1149 Pleistocene *Homo* and late Middle Pleistocene *Homo*, with effect of individual dental traits on the
 1150 principal components. Early and late Middle Pleistocene *Homo* localities are concentrated on
 1151 environments with relatively high SF, HOD and OT values, which early Middle Pleistocene *Homo*
 1152 localities are associated with localities where average AL and BUN values are high. Localities
 1153 without evidence for the presence of *Homo* are associated with high mean PS (only mean is
 1154 indicated).

Author contributions:

- Juha Saarinen: collected most of the mesowear and ecometric data, performed the analyses, made the figures (except Fig 1) and wrote most of the text (main role in planning and preparing the research and the manuscript)
- Otto Oksanen: major role in data collecting, especially species lists of Pleistocene localities; contributed to writing the manuscript
- Indrė Žliobaitė: major role in designing the human habitat distribution modelling and the R-code for that analysis; contributed to writing the manuscript
- Mikael Fortelius: significant role in collecting mesowear data and Guadix-Baza locality data, planning the research and writing the manuscript
- Daniel DeMiguel, Beatriz Azanza, Hervé Bocherens, Carmen Luzón, José Yravedra, Lloyd Courtenay, Hugues-Alexandre Blain, Christian Sánchez-Bandera, Alexia Serrano-Ramos, Juan José Rodríguez-Alba, Suvi Viranta, Deborah Barsky, Jose Solano-García, Miikka Tallavaara, Oriol Oms, Jordi Agustí, Juan Ochando and José S. Carrión: all authors contributed to data collecting and/or discussions concerning data analyses, and writing parts of the manuscript
- Juan Manuel Jiménez-Arenas: contributed to directing data collection and writing the manuscript