



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

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ABSTRACT

The Guadix-Baza Basin (GBB) in Andalucía, Spain, comprises palaeontological and archaeological sites dating from the Early Pliocene to the Middle Pleistocene, including some of the earliest sites with evidence for the presence of early humans (*Homo* sp.) in Europe. Thus, the history of climate and environments in this basin contributes significantly to our understanding of the conditions under which early humans spread into Europe during the Early Pleistocene. Here we present estimates of precipitation and primary productivity in the GBB from the Pliocene to the Middle Pleistocene based on dental ecometrics in fossil communities of large herbivorous mammals, and perform an ecometrics-based distribution modelling to analyse the environmental conditions of Early and Middle Pleistocene human sites in Europe. Our results show that Early Pleistocene humans generally occupied on average relatively diverse habitats with ecotones, such as woodlands and savannas, but avoided very open and harsh (cool or dry) environments. During the Middle Pleistocene in Europe, humans occupied a comparatively much broader range of environments than during the Early Pleistocene, but were on average more concentrated in environments where the dental ecometric of mammals indicate wooded palaeoenvironments. In the earliest human occupation sites of the GBB, Barranco León and Fuente Nueva 3, the mean annual precipitation and net primary production estimates indicate climatic conditions close to modern Mediterranean sclerophyllous woodland environments, but with slightly higher primary productivity,

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indicating some similarity with East African woodlands. On the other hand, the environments did not resemble African grassland savannas. The browse-dominated diets of ungulates from Barranco León and Fuente Nueva 3 further suggest palaeoenvironments where grasses were a minor component of the vegetation. In the slightly older site of Venta Micena that has no evidence for the presence of hominins, dental ecometric estimates indicate climate and environments similar to Mediterranean “forest steppe” environments existing in the surroundings of Baza today. Grasses were prevalent in the diet of some taxa, especially equids, in Venta Micena, but most of the species show browse-dominated diets even there.

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1. Introduction

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

Much of the debate about the environmental conditions during these episodes of earliest human dispersions has centered around the question of whether they occurred in the context of grasslands or wooded grasslands, similar to African grassland savannas (the “savannahstan”-hypothesis; Dennell and Roebroeks, 2005), or rather in woodlands or even closed forests (Belmaker, 2010a,b; Dennell, 2010; Levin, 2015; Patterson et al., 2017a,b; Belmaker and O'Brien, 2018). Also, the importance of water-edge habitats for early humans has been discussed (Cohen et al., 2012). Early human evolution in the Early Pleistocene of East Africa took place in the broad context of opening landscapes and the spread of C4 grasses, but in fact the environments where early humans occurred were diverse, with fine-scale spatial and temporal variation in woody cover (Carrión et al., 2011, 2019; Levin, 2015; Patterson et al., 2017a,b). It has been suggested that the earliest human expansion out of Africa into Southern and Eastern Asia occurred in grassland, wooded grassland and woodland habitats similar to modern African savannas (Dennell and Roebroeks, 2005; Dennell, 2010). However, this “savannahstan-hypothesis” *sensu stricto* is not consistently supported by multi-proxy analyses of environmental conditions in the Early Pleistocene human occupation sites in Eurasia. Based on indicator species and ecological diversity analysis, it has been suggested that the earliest human occurrence sites in Eurasia, such as Dmanisi (Georgia), and ‘Ubeidiya (Israel), had palaeoenvironments similar to African savannas (Dolukhanov, 2000; Palmqvist, 2002; Martínez-Navarro, 2004). However, taxonomic diversity measurements using correspondence analyses indicate that their palaeoenvironments differed from African savannas, comprising instead a mixture of temperate forest and Mediterranean woodland elements (Belmaker, 2006, 2010a, b). Other palaeoenvironmental proxies from Dmanisi (such as pollen, phytoliths and carpological remains) indicate landscapes that could be interpreted to be savanna-like in a physiognomic or structural sense, but not taxonomic sense, being instead dominated by temperate oak forest elements with grassy vegetation (Messenger et al., 2010). Mesowear analysis of the ungulate fauna in ‘Ubeidiya further supports a wooded palaeoenvironment, being dominated by ungulates with browsing diets (Belmaker and O'Brien, 2018).

Moreover, the earliest human occupation sites in Eastern Asia do not appear to have been consistently savanna-like. For example, the palaeoenvironments in the Nihewan basin (ca. 1.7–1 Ma) included elements of temperate woodlands and grasslands (Peterson et al., 2003; Teague and Potts, 2007), while the palaeoenvironment of Gonwangling (ca. 1.2 Ma) has been interpreted as subtropical montane forest (Teague and Potts, 2007).

1.1. Research history of climate and palaeoenvironments in the Guadix-Baza Basin during the pleistocene

The Guadix-Baza Basin (GBB) (Andalucía, Spain) is a sedimentary basin, with an extensive record of palaeontological and archaeological sites ranging from the Pliocene to the Middle Pleistocene (ca. 4.5–0.4 Ma), including Barranco León and Fuente Nueva 3 (ca. 1.4–1.2 Ma), which are among the earliest sites with solid evidence of the presence of humans (*Homo* sp.) in Europe (Toro-Moyano et al., 2013). Somewhat contradictory palaeoenvironmental information from the Pleistocene sites in the GBB has been published based on different methods. For example, Palmqvist et al. (2003) interpreted the palaeoenvironment of Venta Micena to have been similar to East African savannas on the basis of faunal analysis, whereas a Mediterranean woodland environment was suggested by Belmaker (2006). Most analyses indicate a predominance of Mediterranean woodland and open environments in the basin during much of the Early Pleistocene (e.g., Alberdi et al., 2001; Belmaker, 2006, 2010a; Agustí et al., 2010; Blain et al., 2011; Sánchez-Bandera et al., 2020; Altolaguirre et al., 2020, 2021). The presence of the Baza palaeolake, and changes in its water-level, have been key elements affecting the palaeoecology of the basin, by providing a constant supply of water and palustrine environments around the lake (Oms et al., 2011). Furthermore, the “Galerian turnover pulse” in mammal faunas (ca. 1.0–0.9 Ma) has been associated with the arrival of early humans in Europe (Azanza et al., 2000), although many of the earliest European sites, including Barranco León and Fuente Nueva 3, now seem to predate this event. Nonetheless, the arrival of some new species, such as the very large cervid *Praemegaceros verticornis* (that was proposed as the marker of the Galerian Mammal Age; Gliozzi et al., 1997) and the large equid *Equus suessenbornensis*, may be associated with the arrival of early humans, suggesting perhaps either a common dispersal event or a change of environmental conditions that favoured the dispersal of these taxa in Europe.

In the northern margin of the GBB, on the Baza palaeolakeshore, swampy conditions are reconstructed at the earliest Pleistocene site of Huélago (ca. 2.6 Ma) as indicated by the depositional environment, taphonomy and the abundance of browsing large herbivores in the mammal fauna. All this evidence suggests abundant wooded or bushy environments in the surroundings (Alberdi et al., 2001). Similarly, both the late Early Pleistocene site of Huéscar 1 (ca. 1.1 Ma according to Alberdi et al., 2001; 900–800 ka according to Rodríguez et al., 2015, and 574–410 ka according to Demuro et al., 2015) and the early Middle Pleistocene site of

Cúllar-Baza 1 (0.7 Ma) have palustrine depositional environments and diverse faunas of browsing ungulates. This indicates a swampy lake-shore environment, surrounded by woodlands or shrublands in Huéscar 1, but the lack of closed-forest mammal taxa indicates open, sparsely forested environments with dry periods (Alberdi et al., 2001).

Near the village of Orce, the sites of Venta Micena (VM), Barranco León (BL) and Fuente Nueva 3 (FN3) provide essential data for contributing to discussions about the early human occupation of Europe. Despite intensive excavations, the oldest of these sites, VM, dated to ca. 1.6–1.4 Ma (Duval et al., 2010), has not yielded any conclusive evidence for the presence of early humans. In contrast, abundant Oldowan stone tools and bones with anthropogenic modifications have been discovered in BL (1.81–1.05 [1.43 ± 0.38], Barsky et al., 2010; Toro-Moyano et al., 2013; Blain et al., 2016; Espigares, 2019; Tilton et al., 2020; Tilton et al., 2021) and FN3 (1.4–0.98 [1.19 ± 0.21], Barsky et al., 2010; Duval, 2008; Duval et al., 2012; Espigares, 2019). In addition, BL yielded a fossil human tooth (Toro-Moyano et al., 2013). Palustrine depositional environments near the Baza lakeshore have been evidenced for all these sites (Oms et al., 2011). The palaeoenvironment in VM was interpreted as similar to African savannas by Palmqvist et al. (2003), based on analyses of feeding ecology and locomotion types of large mammals. However, taxonomic correspondence analysis of large mammals (Belmaker, 2006, 2010a) indicates that the palaeoenvironment comprised elements of Mediterranean woodlands and temperate forests and was thus quite different from African savannas. Rodent faunas indicate that the precipitation and temperature in VM were roughly similar to present (Agustí et al., 2010). The reconstructions of palaeoclimate and palaeoenvironments for BL and FN3 indicate temperature conditions similar to present, but higher precipitation, with Mediterranean woodland/shrubland-type vegetation (Agustí et al., 2009, 2010; Blain et al., 2011, 2016; Sánchez-Bandera et al., 2020). The vegetation type in level D1 at Barranco León, containing most of the faunal remains and evidence of human presence in BL, is described as a wooded environment. In contrast, the environmental conditions at FN3 are now reconstructed as more open and dryer than at BL, based on the amphibian and reptile fauna (Sánchez-Bandera et al., 2020).

In this study we provide further information about the palaeoenvironmental conditions in the GBB from the Early Pliocene (ca. 4.5 Ma) to the Middle Pleistocene (ca. 0.4 Ma), based on dental ecometrics, average body size and diet of large herbivorous mammals. We further discuss the palaeoenvironments of the earliest human occupation sites, BL and FN3, in the wider context of early human palaeoenvironments in Europe, based on distribution modelling of preferred environments during the Early and Middle Pleistocene of Europe.

2. Materials and methods

2.1. Materials

The mammal fossils from Venta Micena, Barranco León and Fuente Nueva 3 used in this study are housed in the Archaeological Museum of Granada, Andalucía, Spain. Large mammal faunal lists of European Early and Middle Pleistocene fossil mammal localities and archaeological sites were collected from literature (references in Supplementary Table S1). Stratigraphic and sedimentological data for the GBB were also collected. In total, dental ecometric values and mean body size indices from 12 localities from the GBB and altogether 92 Early and Middle Pleistocene European localities were used in this study (Supplementary Tables S1 and S2). The localities were chosen based on the following criteria: 1) the fauna include at least 5 species of large herbivorous mammals, 2) the

mammalian fauna and the possible evidence of human occupation can be shown to be associated, as far as can be told from the stratigraphy, 3) the fossil assemblage does not show obvious irregularities due to sorting by human or carnivore activities, or due to other taphonomic processes.

2.2. Dental ecometric trait data

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

- Hypsodonty, HYP (tooth crown height): 1 (brachydont), 2 (mesodont) or 3 (hypodont). Hypsodonty is an adaptation for increasing functional durability of dentition. Mean ordinated hypsodonty in large mammal communities is correlated with precipitation through the link of high abrasion on teeth in dry climatic conditions, possibly because of multiple factors, including aeolian dust accumulation and prevalence of grasses with phytoliths in dry environments (e.g., Fortelius et al., 2002; Liu et al., 2012).

- Longitudinal loph count, LOP: the number of elongated cutting edge structures that are oriented in the direction of the tooth row (for example rhinoceroses have one (the ectoloph), ruminants and horses have two (the buccal and lingual “lophids” formed by the flattened cusps), and proboscideans have none (because all the lophids are transverse)). LOP is correlated with temperature (high LOP value indicating cool climate), because longitudinal lophids are most abundant in ungulates feeding seasonally on bark and branches of deciduous trees that drop their leaves during cold months (e.g., Liu et al., 2012).

- Horizodonty (HOD): the amount of transverse cusp pairs or lophids; the categories are: 1 (brachyhorizodont: two cusp pairs or lophids, this includes most herbivorous mammals), 2 (mesohorizodont: three cusp pairs or lophids, this happens e.g. in some pigs with enlarged last molars), 3 (hypsohorizodont: more than three cusp pairs or lophids, this includes mostly mammutids, gomphotheres and elephants, and some derived pigs such as warthog). Horizodonty is associated with increase in tooth volume by increasing lophids or cusp pairs, and is associated with functional durability of dentition (Žliobaite et al., 2016).

- Presence of acute lophids (AL): 1 (present), 0 (absent); these are sharp, cutting lophids that maintain sharp facets when worn, such as the ectoloph of most rhinos, the chisel-like lophids of tapirs, and the sharp buccal lophids of most cervids, but e.g. horses and almost all (hypodont) bovids lack these. Acute lophids are typical for browsers in forested environments (Žliobaite et al., 2016; 2018) If in doubt, AL for selenodonts is assigned if mesowear is sharp. The proportion of acute lophids in a community is correlated with temperature today, as it is highest in deciduous forest communities where most

ungulate species cut branches when leaves are dropped during cold season (see also Oksanen et al., 2019).

- Presence of obtuse lophs (OL): 1 (present), 0 (absent); these are “blunt” lophs that become basin-like without maintaining sharp facets when worn (e.g., the transverse lophs in rhinos, hippos, gomphotheres and elephants, and most of the “lophs” in bovids and equine horses).

- Structural fortification of cusps (SF): 1 (present), 0 (absent); these are any morphological features of the cusps that make the cusp stand out from the occlusal surface (by resisting wear) in worn teeth. The most typical examples of such structures are: buccal cusps with bulbous, thickened lingual enamel loops in some ruminants (e.g. reduncine antelopes and bovines), cusps with heavily folded enamel (e.g. in many pigs such as *Sus scrofa*), and molars with raised central ridges formed by conules or thickened enamel edges (e.g. in *Hippopotamus*). Structural fortification occurs in modern herbivorous mammal communities in fresh-grass grazers and mixed-feeders in wooded habitats, primarily in forests and wetlands, and are thus indicators of such habitats (Zliobaite et al., 2018).

- Occlusal topography (OT): 1 (flat), 0 (non-flat); this refers to the overall shape of the worn occlusal surface of the teeth in buccolingual direction. Flat occlusal topography is typical for grazing ungulates such as horses.

- Plain selenodonta (PS): 1 (present), 0 (absent): this is a combination of traits where longitudinal loph count is 2, only obtuse lophs are present, there is no structural fortification, no coronal cement and the occlusal topography is non-flat. This dental morphology type is particularly abundant in ruminants and camels inhabiting relatively harsh environments, such as deserts and montane environments.

- Bunodonty (BUN): 1 (present), 0 (absent); bunodonty refers to dental morphology with separate cusps that are not fused into elongated, loph-like structures. This dental morphology type is typical for omnivores and frugivores such as most suids and primates. High proportion of bunodont taxa indicates relatively warm and humid forest environments.

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

2.3. Locality mean body size indices

In addition to the dental ecometric traits (crown types and mesowear), body mass estimates were calculated for a large set of large herbivorous mammals from the 92 Early and Middle Pleistocene European localities. Relative body size indices were calculated for each locality by calculating the mean body mass of ungulate species within each locality and dividing these locality means with the highest mean body mass in the total set of

localities. For the body mass estimates, we used primarily postcranial bone measurements utilising the regression equations of Scott (1990) for bone measurements and body mass in modern ungulates, and Christiansen (2004) for proboscideans. These were complemented by body mass estimates based on second upper and lower molar lengths for taxa for which postcranials were not available, using the equations of Janis (1990).

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

2.4. Mean annual precipitation, mean annual temperature and net primary production estimates for the pliocene – pleistocene of Guadix-Baza Basin

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

$$\text{Mean annual temperature (MAT)} = 27 - .28.5 \times AL$$

$$\text{Mean temperature of coldest month (MINT)} = 18 - .42.9 \times AL$$

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

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

The climatic variables (MAT, MINT and MAP) for the modern surroundings of Baza were obtained from long-term weather observation data (<https://en.climate-data.org/europe/spain/andalusia-252/>). NPP for the modern Baza area was estimated from dental ecometrics of a combined species assemblage of wild ungulates and domestic ungulates that are herded in that region today. This approach is justified based on the observation that adding feral domestic ungulates in dental ecometrics -based

estimates of climate and vegetation type compensate for the bias in the ecometric signal caused by the loss of ungulate species by human interference, for example as has been observed in the Sahel today (Zliobaite et al., 2018).

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

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

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

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

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

We performed principal component analyses (PCA) to further explore the effect of ecometric traits on the presence/absence of humans in Early Pleistocene and Middle Pleistocene localities separately, and the presence of Early Pleistocene, early Middle Pleistocene and late Middle Pleistocene human sites in the complete set of localities. This was done in order to compare the relative and common associations of the ecometric traits with human presence. Partial per cent contribution of the ecometric traits on the principal components were used for evaluating the significance of associations of the constituent ecometric traits on human presence, and generalised conclusions about the environmental conditions of most Pleistocene European human presence sites are discussed based on this analysis.

3. Results

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

Mean annual precipitation (MAP) and net primary production (NPP) estimates based on dental ecometrics in large herbivorous mammal communities indicate a drastic decline from ca. 870 to ca. 450 mm/a in MAP and from ca. 1130 to ca. 700 g(C)/m²/a in NPP from the Early Pliocene of Baza 1 (ca. 4.6 Ma) to the Plio-Pleistocene boundary of Huélago (ca. 2.6 Ma) in the GBB (Table 1, Fig. 2). After this, Fuente Nueva 1 (ca. 2.2 Ma) and Fonelas P-1 (ca. 2 Ma) as well as Venta Micena (ca. 1.6 Ma) have the lowest estimated MAP and NPP, while Barranco del Paso (ca. 1.8 Ma) with intermediate age has relatively high MAP and NPP estimates. After the drop at ca. 1.6 Ma in Venta Micena, the MAP and NPP estimates become more homogeneous and equable, ranging from ca. 600–700 mm MAP and 900–1050 g(C)/m²/year NPP. The MAP in the GBB today is around 450 mm (ca. 470 mm in Guadix (<https://en.climate-data.org/europe/spain/andalusia/guadix-57014/>), ca. 430 mm in Baza (<https://en.climate-data.org/europe/spain/andalusia/baza-56902/>)), which is similar to the estimated value for Fuente Nueva 1 and Venta Micena, while the rest of the Pleistocene localities in the GBB are estimated to have higher mean annual precipitation values. Also the NPP value of modern surroundings of Baza, including semi-feral domestic ungulates, is similar to the estimated values for Fuente Nueva 1 and Venta Micena (Table 1).

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

A further comparison of the MAP values of the GBB sites with MAP ranges of modern Mediterranean biomes (Quézel and Médail, 2003; Suc and Popescu, 2005) indicates that Huélago, Fuente Nueva 1, Fonelas P-1, Mencil 9 and Venta Micena, together with modern environment of Baza, fall within the range of modern "forest steppe" with *Artemisia*, *Pinus halepensis* and scarce evergreen *Quercus* (Table 1). In contrast, Barranco del Paso, Fuente Nueva 3, Barranco León, Huéscar 1 and Cúllar-Baza 1 are within the range of

Table 1

Mean annual precipitation (MAP), minimum annual temperature (MINT) and net primary production estimates for the GBB sites, based on mammalian dental ecometrics (Oksanen et al., 2019). Modern MAP and MINT values for the vicinity of Baza are from climate observation data (<https://en.climate-data.org/europe/spain/andalusia/baza-56902/>) and the modern NPP value is estimated from dental ecometrics of large wild and domestic ungulates occurring in the area today. The Mediterranean vegetation zones (Quézel and Médail, 2003) indicated in the last column are: 1) Forest-steppe with *Artemisia*, *Pinus halepensis*, *Juniperus* and scarce evergreen *Quercus* (250 < MAP < 600 mm), 2) Evergreen forest with sclerophyllous oaks, *Pinus pinaster* and *P. pinea* (600 < 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	Huélago	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

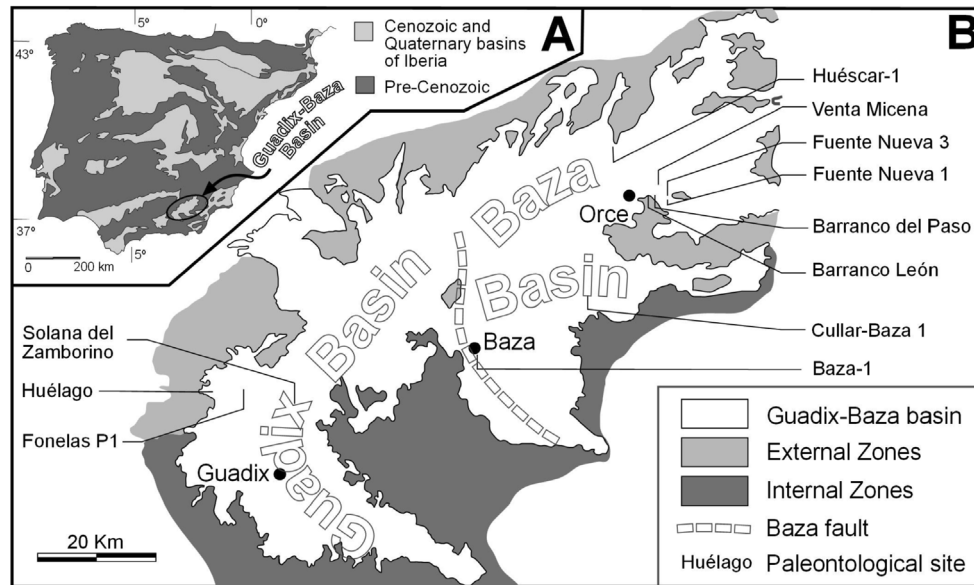


Fig. 1. Map of the Guadix-Baza Basin with the localities.

evergreen forests dominated by sclerophyllous *Quercus* and *Pinus*, and Baza 1 and Solana del Zamborino have higher MAP values indicating affinity with mixed forest of deciduous *Quercus*, *Fagus* and conifers (Table 1). We consider these vegetational interpretations as further reference to the vegetation at the GBB sites, but note that these are likely to be oversimplified as they do not take into account temperature and NPP (see Discussion).

3.2. Mesowear analysis of the large herbivorous mammals from the orce sites

The results show that most of the Orce ungulate species from all the three localities (Venta Micena, Fuente Nueva 3 and Barranco León) are clustered with extant ungulates that have predominantly browsing and browse-dominated diets (Fig. 4, see Supplementary Table S5 for a summary of mesowear results of the Orce ungulates). Only *Equus altidens* shows mesowear signals that in VM

indicate purely grazing diet similar to extant zebras and white rhinoceros, and in BL and FN3 grass-dominated but mixed diet similar to extant saiga antelope and rock hyrax. Abundance of sharp cusps but low relief in *E. altidens* molars from BL and FN3 indicates a significant dietary element of some sort of tough vegetation that was not very abrasive. Somewhat surprisingly, the larger species of horse, *Equus suessenbornensis*, from BL and FN3 have mesowear signals similar to extant browsers such as moose and Javan rhinoceros, although they are represented by relatively small sample sizes. There is a slight but interesting difference between Venta Micena and the rest of the Orce sites, especially in the estimated diet of the horses: the browsing large species of horse (*E. suessenbornensis*) is absent from Venta Micena and the diet of the smaller species, *E. altidens*, is more grass-dominated in VM than in the other sites.

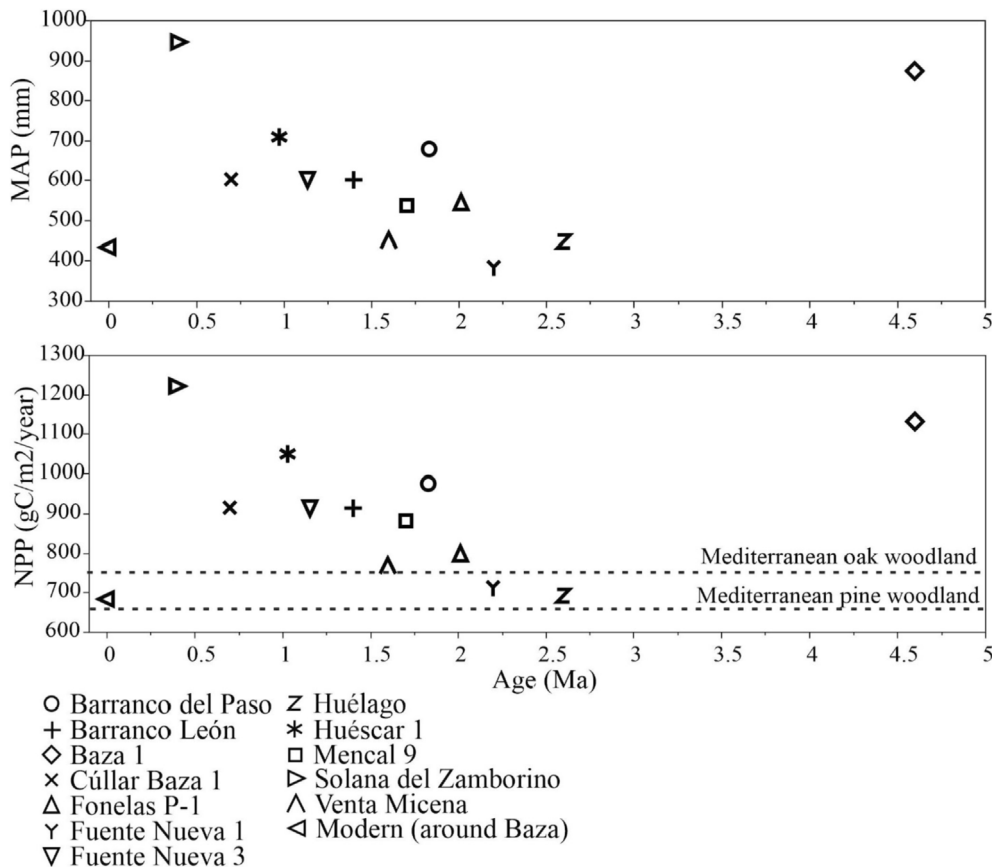


Fig. 2. Mean annual precipitation and net primary production in the Guadix-Baza Basin from the Early Pliocene to the Middle Pleistocene as estimated from dental ecometrics of large herbivorous mammals using the equations published by Oksanen et al. (2019).

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

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

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

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

Component 1 in the principal component analysis of human presence based on the traits corresponds to 46.5% of variation in human presence and it is contributed by the opposite effects of SF + AL + BMloc and PS + HYP (Fig. 5). Component 2 corresponds to 38.6% of the variation in human presence and is mainly driven by the opposite effects of PS and SF + BMloc.

In general, human occurrence is concentrated in localities with

high values of acute lophs (AL), structural fortification (SF), high mean body mass index of ungulates in localities (BM_loc), mean bunodonty (BUN) and mean horisodonty (HOD), moderate values of hypsodonty (HYP) and low values of plain selenodont ecomorphs (PS) (Appendix, Fig. A.1). The positive correlation with the presence of Early Pleistocene *Homo sp.* is dominated by the effects of high percentage of structural fortification and high locality mean body size index, while the correlation with the Middle Pleistocene humans varies more is more strongly driven by high percentage of acute lophs (Fig. 5). Furthermore, within the Middle Pleistocene, the Early Middle Pleistocene human sites are more associated with high percentage of acute lophs (AL) than the Late Middle Pleistocene localities (Appendix, Fig. A.1).

Human habitat suitability scores were calculated based on the total dental ecometric model prediction for all the 92 Early and Middle Pleistocene European localities included in this study and compared with the presence or absence of humans in the localities. The human habitat suitability scores for the localities, ranked from highest to lowest, are presented in Supplementary Table S6. Since the model was fit on observed presence-absence data, the sites where the evidence for human presence is lacking generally have the lowest habitat suitability scores and sites where humans are present have the highest scores, but there are some notable exceptions to this pattern. Most notably, several localities with evidence for human presence have lower-than-average estimated habitat suitability scores (Atapuerca TE9c, Bisnik Cave, Visogliano, Orgnac 3, Caune de l'Arago, Pakefield, Swanscombe, Pirro Nord, Hoxne, Vallparadis, Dmanisi and Cúllar-Baza 1). Of these, Orgnac 3, cool stage levels of Caune de l'Arago and Bisnik Cave are

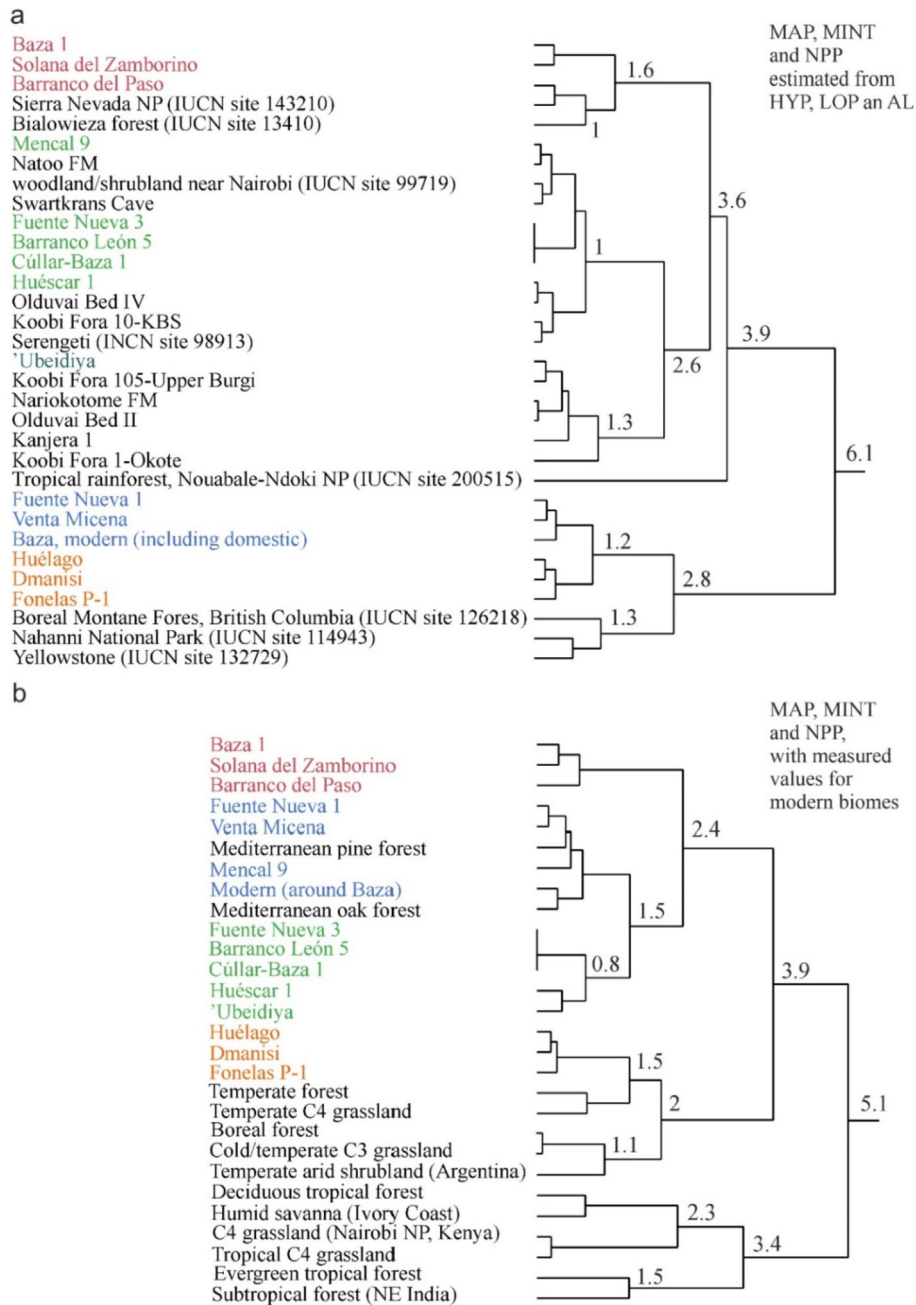


Fig. 3. Hierarchical clustering of the Pleistocene Guadix-Baza sites based on MAP, MINT and NPP estimated from dental ecometrics with a) dental estimates of MAP, MINT and NPP for modern IUCN sites and Pleistocene African hominine sites, and b) reported MAP, MINT and NPP for modern biomes (Chirici et al., 2007; Olson et al., 2013). The Euclidean distance values marking branch lengths are indicated for 11 first branches. The GBB localities in separate clusters are marked with different colours. Dmanisi and 'Ubeidiya are included as examples of earliest Eurasian human sites outside the GBB. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

characterised by the presence of cold-climate taxa such as *Coelodonta* and *Rangifer tarandus*, indicating harsh climatic conditions in this respect. In contrast, some sites with no evidence for human presence have higher-than-average habitat suitability scores, suggesting that conditions there could have been suitable for humans, or more specifically, that condition there were quite similar to those where humans have found. Such sites without evidence for human presence but with high suitability estimates are the Early Pleistocene sites Colle Curti, Cesi, Castagnone and Monte Riccio in Italy and the early Middle Pleistocene sites of Mosbach and Prezletice in Central Europe. According to the model prediction, the Orce human

sites Barranco León and Fuente Nueva 3 have a higher habitat suitability score for early humans than Venta Micena where evidence of human presence is lacking.

The colour-interpolated maps of human habitat suitability scores in Europe through time indicate geographical patterns of habitat suitability that reflects the history of early human dispersals in Europe (Fig. 6). Some of the earliest indication of increase in habitat suitability for humans (as predicted by the model) occur in the first phase of Early Pleistocene (2.6–1.8 Ma) in Central Italy and Dmanisi, Georgia. During the second phase of Early Pleistocene (1.8–0.7 Ma) the areas of elevated human habitat suitability scores

Table 2

Coefficients for the dental ecometric traits from the generalised linear model prediction for the probability of human occurrence in Early and Middle Pleistocene Western Eurasian sites. Positive coefficients indicate positive correlation with the probability of human occurrence. Hypsodonty, acute lophes, structural fortification and locality mean body mass index have positive 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	0.20	0.76
	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		
Middle Pleistocene	intercept	-7.502	6.108	-1.228	0.219	0.34	0.63
	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		
Total	intercept	-15.852	5.04	-3.145	0.002	0.29	0.76
	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		
	BMloc	5.327	3.965	1.347	0.18		

the Early Pleistocene of Europe is highly important for understanding the underlying environmental conditions under which early human dispersal to Europe happened, and ecometric and palaeoecological analyses from fossil mammals provide new, previously understudied insights into these.

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

4.1. Pliocene to pleistocene climate and palaeoenvironments in the GBB – high-productivity woodland ecosystems in the mediterranean climatic realm

MAP, MINT and NPP estimated from dental ecometric traits in large herbivorous mammal communities indicate a prevalence of palaeoenvironments that are most closely clustered with modern Mediterranean forests than other extant biomes for the GBB sites. The high MAP and NPP estimates for the Pliocene site of Baza 1 (ca. 4.5 Ma (Piñero et al., 2017; Rodríguez et al., 2015), the Early Pleistocene Barranco del Paso (ca. 1.8 Ma; Gibert et al., 1992) and the Middle Pleistocene Solana del Zamborino (ca. 0.4 Ma; Janis, 1990; Álvarez-Posada et al., 2017); although see (Scott and Gibert, 2009)) indicate a much more humid climate and more high-productivity palaeoenvironments than in the GBB today. Hierarchical clustering of these sites with modern IUCN sites indicates a close similarity to the temperate mixed forests of Bialowieza and Sierra Nevada National Parks. This interpretation is further supported by comparison of estimated MAP with the MAP range of modern Mediterranean biomes (Quézel and Médail, 2003; Suc and Popescu, 2005), where Baza 1 and Solana del Zamborino fall within the range of mixed forests with deciduous oaks, *Fagus* and conifers. According to Fauquette et al. (1999), the taxonomic composition of the vegetation in the Mediterranean environments was largely similar to present already in the Pliocene, with the exception of additional presence of subtropical elements such as Taxodiaceae, *Sequoia*, *Engelhardia* and *Symplocos*.

During the Early Pleistocene, the localities of Fuente Nueva 1 (ca. 2.2 Ma) and Venta Micena (ca. 1.6 Ma) show MAP and MINT estimates that are similar to the present MAP and MINT in the GBB, and NPP estimates that are similar to values estimated from dental ecometrics of large mammals around Baza today and measured values for modern Mediterranean woodland or forest steppe environments. Huélago (ca. 2.6 Ma) and Fonelas P-1 (ca. 2 Ma) also

consistently cluster next to the cluster containing estimated MAP, MINT and NPP for modern Baza and measured values for modern Mediterranean woodlands, but they differ mainly in having cooler estimated mean temperatures of coldest month (MINT) than at present. Comparison of the MAP estimates of the GBB sites with MAP ranges of modern Mediterranean biomes (Quézel and Médail, 2003; Suc and Popescu, 2005) provides an additional reference for comparing the vegetation types in the GBB localities. According to this classification, MAP range between 250 and 600 mm/a correspond with forest steppe habitats with *Artemisia*, *Pinus halepensis*, *Juniperus* and scarce evergreen *Quercus*. The modern environment around Baza, as well as the fossil sites of Huélago, Fuente Nueva 1, Fonelas P-1 Mencal 9 and Venta Micena fall within this MAP range.

The rest of the Early and Middle Pleistocene localities in the GBB, including the earliest human occupation sites of Fuente Nueva 3 (FN3) and Barranco León (BL), are clustered together with African woodland or shrubland environments, the Early Pleistocene Nattoo Formation from West Turkana, Kenya, and the Early Pleistocene site of Swartkrans, South Africa, based on dental ecometric estimates of MAP, MINT and NPP. Furthermore, these sites form a cluster of their own that is more closely clustered with the modern Mediterranean forests than other modern biomes when compared with reported MAP, MINT and NPP for modern biomes (data from Chirici et al., 2007; Olson et al., 2013). In these environments, the estimated precipitation varies from similar to somewhat higher than today in the GBB and is lower than in temperate forest biomes, but NPP estimates are higher than in modern Mediterranean and temperate forests. On the other hand, the estimated precipitation and NPP are lower than in modern tropical forests and humid savannas, and estimated NPP is significantly higher than in C4 grassland savannas. After the relatively dry conditions at Venta Micena, precipitation and NPP increased around 1.4 Ma at BL and FN3, the oldest human sites in the GBB. The dental ecometrics-based estimates of MAP (602 mm) and NPP (914 g(C)/m²/a) are higher than today in the GBB, while estimated minimum annual temperature is similar to present (8.5 °C). Herpetofauna from these sites indicates that temperature and precipitation in BL and FN 3 were higher than at present (Blain et al., 2011, 2016), and the vegetation would have been dominated by relatively open woodland type (Blain et al., 2011; Sánchez-Bandera et al., 2020). MAP range between 600 and 800 mm/a in modern Mediterranean realm indicates the presence of evergreen forests with sclerophyllous oaks (e.g. *Quercus ilex-coccifera*) and pines, and the fossil sites of Barranco del Paso, FN3, BL, Huéscar 1 and Cúllar-Baza 1 fall within this vegetation category by modern analogue. However, note the affinity of these sites with African woodland habitats in the hierarchical clustering which also uses MINT and NPP values in addition to MAP, indicating perhaps a

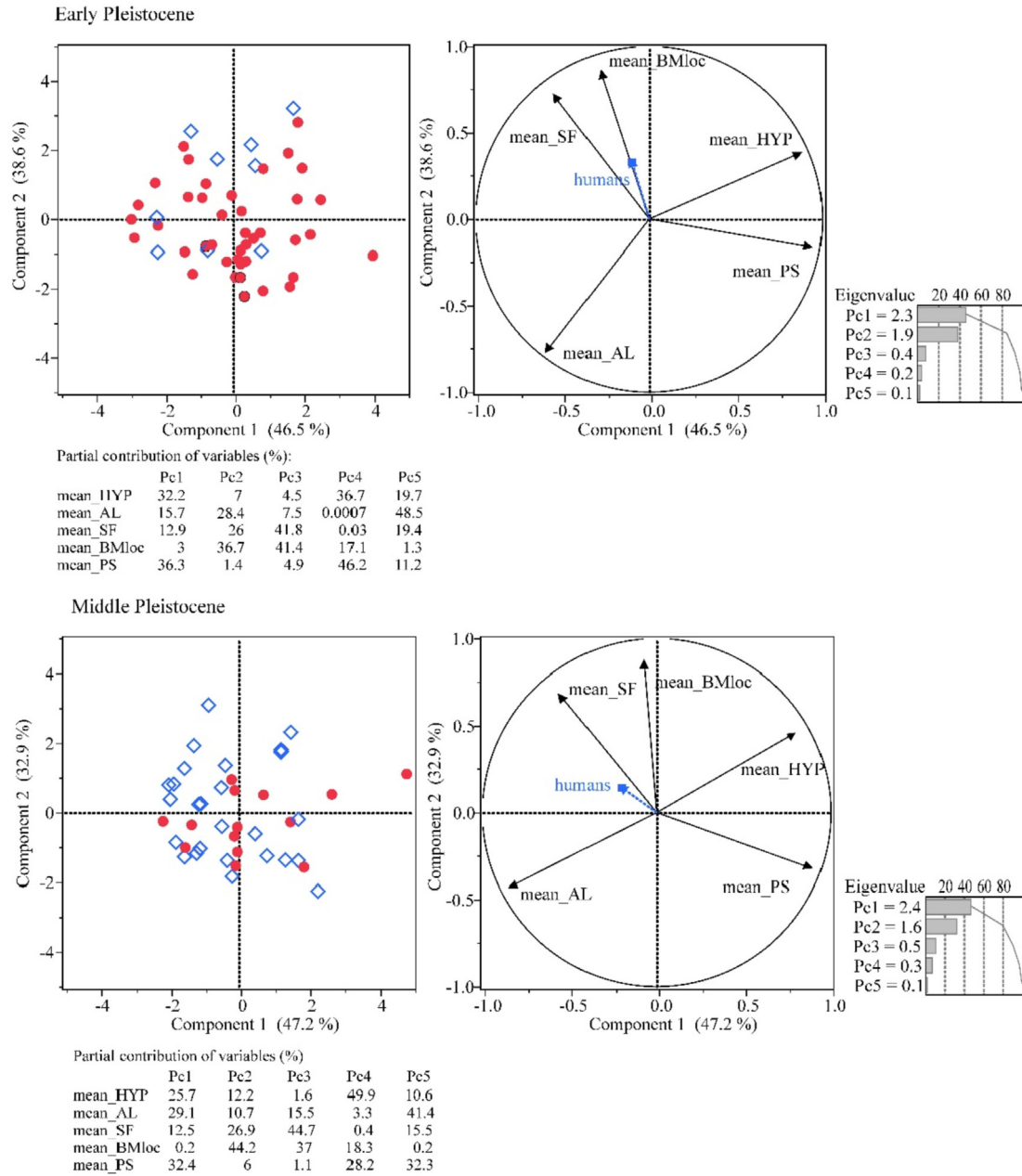


Fig. 5. Principal component analysis of human and non-human sites in Western Eurasia during the Early and Middle Pleistocene. The red dots mark localities where evidence of the presence of humans is lacking, and the open blue diamond symbols mark localities where humans were present. During the Early Pleistocene, most of the human occurrence sites are characterised by relatively high values of structural fortification and mean body mass, while sites with high hypsodonty and PS values suggesting “harsh” environments show an almost complete absence of human occurrence. In the Middle Pleistocene, the human sites are more evenly distributed over the ecometric space but are more concentrated towards sites with relatively high values of acute lophs, structural fortification and mean body mass, suggesting on average relatively wooded palaeoenvironments. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

slightly higher-productivity environment than modern Mediterranean sclerophyllous forests. In summary, the climatic and productivity estimates for the earliest human occupation sites in the GBB (FN3 and BL) were climatically within the range of modern Mediterranean evergreen oak and pine forest environments, but had relatively high NPP, indicating similarity to African dry woodlands/shrublands. However, these environments differed from African grass-dominated savannas. In this regard, BL and FN3 were similar to some African early human sites (Swartkrans and Ntoto Formation), as well as ‘Ubeidiya, Israel, but were different from most of them that indicate palaeoenvironments similar to extant grass-dominated savannas of Serengeti, such as Upper Burgi and KBS

Members of Koobi Fora Formation in East Turkana, Nariokotome Member in West Turkana, Olduvai Bed IV, and Kanjera.

The interpretation of woodland or shrubland environments, without a significant grassy component of undergrowth, at BL and FN3 is further supported by the mesowear analysis of the ungulate communities. In both sites, vast majority of the ungulate species show mesowear values that cluster together with modern browsers such as *Alces* and *Rhinoceros sondaicus* (most of the species) or with browse-dominated mixed-feeders such as *Taurotragus oryx* (the large cervid, cf. *Praemegaceros verticornis*, from BL) or *Tragelaphus strepsiceros* (the large bovines from BL and FN3). Most notably, even the larger species of horse (cf. *Equus suessenbornensis*) from both of

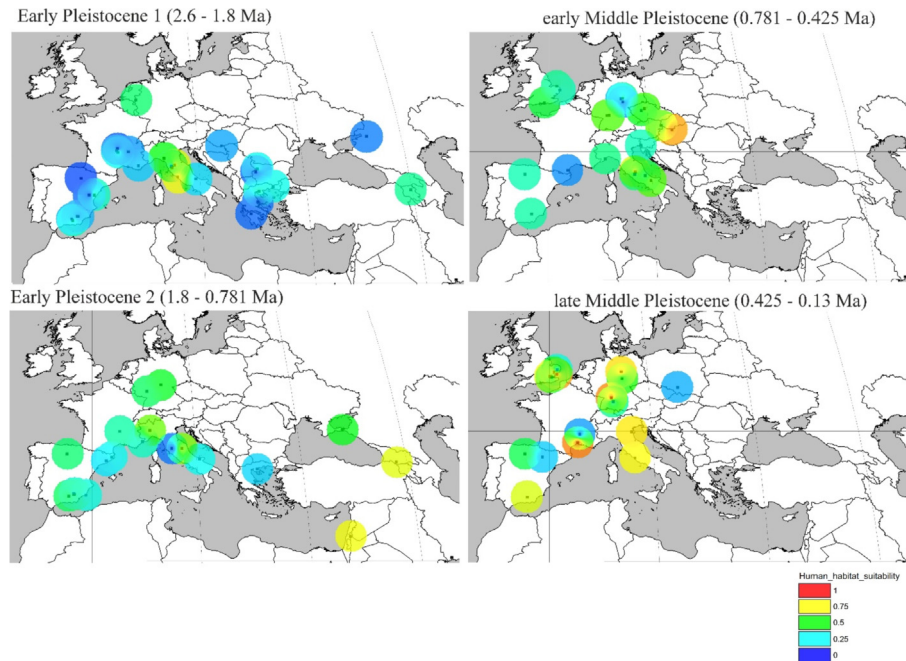


Fig. 6. Colour-interpolated maps of probability of human presence (human habitat suitability estimated from dental ecometric variables and locality body mass indices) for Early and Middle Pleistocene Western Eurasian sites. Blue indicates poor suitability for humans and red indicates the highest suitability, with the spectrum from light blue to green and yellow indicating increasing habitat suitability. In the earliest phase of Early Pleistocene, the earliest human site in Eurasia (Dmanisi, Georgia), Tegelen (Netherlands) and especially Central Italian sites have the highest suitability scores. In the later phase of Early Pleistocene, areas of highest suitability are centered around the Black Sea coast, Andalusia and Central Italy. In the early Middle Pleistocene, there is high variation in the habitat suitability, with many Central European and Italian sites getting high suitability scores. In the late Middle Pleistocene, habitat suitability is mostly high, being highest in the Mediterranean coast, Central Europe and Southern England, but poor in a few localities that indicate cold climate. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

the sites clusters with the browsers, while the smaller species of horse (*E. altidens*) is the only species from BL and FN3 that clusters with the extant grass-dominated feeders saiga antelope (*Saiga tatarica*) and rock hyrax (*Procapra capensis*). Such a prominence of browsing diets in the ungulate communities indicates a palaeoenvironment that could not have been grass-rich, and provided rather rich foliage of trees, shrubs or dicotyledonous herbs. Also, the ungulate assemblage from Venta Micena, with estimated dryer climatic conditions, shows an abundance of browsing and browse-dominated feeders, but a higher proportion of mixed-feeders and only one species of horses (*Equus altidens*), which has the only truly grazing mesowear signal of all the ungulates in the Orce sites, clustering with modern grazers such as zebras (*Equus burchelli* and *E. grevyi*), tsessebe (*Damaliscus lunatus*) and prairie bison (*Bison*). The mesowear data thus indicates a more open and grass-rich palaeoenvironment in Venta Micena than in BL and FN3.

The climatic range estimated for most of the Pleistocene GBB sites (including the Orce sites) falls within a temperature and precipitation regime under which the biome cannot be estimated directly from the climate, because other factors such as soil fertility, fire and the top-down influence of large mammal herbivory have a profound impact on the vegetation type (Bond, 2005; Kujper et al., 2015). The NPP estimated by large mammal dental ecometrics represents primary productivity edible by the herbivorous mammals, and the high diversity and body size range of the Early Pleistocene large mammal communities is expected to reflect

relatively high NPP. In the surviving natural temperate forests today, such as Białowieża, the large herbivorous mammals such as European bison, moose, red deer and feral horses, do not create significant open environments, but instead affect the species composition of the trees (Kujper et al., 2015). Unfortunately, we are currently lacking temperate and Mediterranean environments with a diversity of large mammals even nearly as high as during the Early Pleistocene, making it challenging to estimate the effect of large herbivores on vegetation. For example, the effect of elephants on tree cover can be significant in some environments (Guldemond et al., 2017), and this effect could have been prominent in the Pleistocene but is currently lacking in temperate and Mediterranean environments. The difficulty of assessing how drastic the effect of large herbivores on vegetation was in the past, especially as reliable estimates of herbivore population sizes are lacking, was acknowledged by Bradshaw et al. (2003). However, they conclude that the balance of paleoenvironmental evidence indicates mostly a rather local effect of herbivory on otherwise mostly forested landscapes during the Late Pleistocene and especially Holocene in Northern Europe.

The similarity of Venta Micena to modern Mediterranean “forest steppe” and the present climatic conditions and productivity around Baza, and the affinity of FN3 and BL with Mediterranean evergreen forests with lack of significant grass undergrowth, probably relate to the difference in seasonality of rainfall patterns in the Mediterranean realm and East Africa. The seasonality of

precipitation in East Africa includes two rainy seasons, whereas the Mediterranean climate is characterised by one rainy season in the winter and hot and dry summers. Drought-tolerant trees and shrubs have an advantage during the hot and dry summer in the Mediterranean realm, while grasses that require more evenly distributed annual rain are in disadvantage there especially due to extended autumn drought (Dallman, 1998; Nogueira et al., 2017). On the other hand, grass-dominated savannas in East Africa thrive under conditions with two rain seasons (e.g., Hesla et al., 1985). Such dissimilarity in the rainfall pattern could largely explain the grass-poor environments in the GBB and the on average more grass-dominated environments of the hominin sites of East Africa during the Pleistocene.

Whatever the case, it is evident from the scarcity of grazers that the vegetation in the Orce sites was not dominated by grasses and would thus not likely have been particularly similar to modern African grasslands or grass-dominated savannas. Thus, our results do not support the “savannahstan” hypothesis (Dennell and Roebroeks, 2005; Dennell, 2010) for the GBB sites, at least if the “savannahstan” is understood in the strict sense to be similar in environmental condition to African savannas with grassy undergrowth. Although never dominant, Poaceae is relatively frequent in the pollen record from Palominas lake sequence in the GBB (Altolaguirre et al., 2020), but its fluctuations do not parallel those of the xerophytic component. This leaves open the possibility that a portion of the total count is due to local overrepresentation of grass pollen (e.g. marginal and/or basinal vegetation). Furthermore, it cannot be discarded that grasses could have increased regionally during wet interglacials. Today, hard-leaved perennial grasses such as *Lygeum spartum* (on marls and gypsum soils) and *Stipa tenacissima* (on limestones) dominate the local vegetation, but this was clearly not the case during the Early and Middle Pleistocene.

In summary, the climate and productivity estimates from the dental ecometrics of the large herbivorous mammal community, and the comparison of those with modern biomes, indicate palaeoenvironments similar in vegetation structure to Mediterranean woodlands for the earliest human occupation sited in the GBB (BL and FN3), with temperature close to present and annual precipitation and NPP slightly higher than at present in Baza. This raises the question of what these environments were like in terms of resources available for the early humans. The predominantly browse-dominated mesowear signals of ungulates suggests a palaeoenvironment where grasses were not a dominant element in the vegetation, but the browse-dominated mesowear does not further separate whether the browse was mainly obtained from trees, shrubs or non-grass herbs. The Palominas pollen core indicates a high variation in the vegetation in the GBB during the Early Pleistocene, ranging from open grass and *Artemisia* -dominated during dry phases to diverse deciduous/evergreen *Quercus* woodland and wetland during the humid phases (Altolaguirre et al., 2019). Pollen record from a sedimentary section in Palominas provides a reference to the vegetation cycles in the GBB during the Early Pleistocene roughly between the MIS 53 and MIS 34, suggesting that the levels indicating warm and humid conditions correspond with the conditions present in BL and FN3 (Altolaguirre et al., 2019). The evidence from mammal ecometrics, herpetofauna and ungulate mesowear all point at relatively somewhat more humid than present conditions and non-grassy

environments in BL and FN3, which would more likely correspond with the woodland-type vegetation in the Palominas core. The inferred vegetation of such phases of the Palominas core is generally forested with some degree of openness and dominated by deciduous and evergreen *Quercus*, with a diversity of mesophytes such as *Carpinus*, *Acer*, *Juglans*, *Corylus*, *Populus*, *Salix*, *Ulmus*, *Castanea*, *Fagus* and *Buxus*, and thermophytes such as *Olea*, *Pistacia*, *Coriaria*, *Tamarix*, *Phlomis*, *Myrica*, in addition to genera today extinct in the western Mediterranean such as *Eucommia*, *Parrotia*, *Cathaya*, *Aralia*, *Zelkova*, *Pterocarya*, *Tsuga* and *Nyssa* (Altolaguirre et al., 2019, 2020). The sediments at BL and FN3 were deposited during a phase when the Baza Lake in the GBB was relatively large due to basin dynamics (Oms et al., 2011). Sedimentological evidence indicates a palustrine depositional environment for both BL and FN3 (Oms et al., 2011 and references therein), and the presence of wetlands is further attested by faunal elements such as the abundance of hippopotamus (*Hippopotamus antiquus*) in these localities. Freshwater sources at the periphery of the main Baza saline palaeolake would have provided a constant supply of groundwater (Anadón et al., 2015) that may have overcome the limits imposed by rainfall on the vegetation, and supported high-productivity palustrine environments (Oms et al., 2011).

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

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

In a broader perspective, the dental trait distribution of large herbivorous mammals across Europe during the Early and Middle Pleistocene indicates on average relatively high-productivity and wooded environments, and avoidance of the harshest environmental conditions. This is illustrated by the positive correlation of high values of AL, SF, BMloc and BUN, and negative correlation of high values of PS with human presence throughout the Early and Middle Pleistocene in Europe. Large average body size in ungulate communities, particularly in the temperate zone such as in Europe during the Quaternary, indicates moderately open habitats but also high resource quality and availability (Saarinen, 2014; Saarinen et al., 2016). These environments, where ungulate communities have high proportion of acute lophs, structural fortification and large average body size, would have likely provided diverse resources for the early humans. In many cases there is also evidence of the presence of significant bodies of water and waterside environments, as indicated by the frequent co-occurrence of *Hippopotamus* with early humans in Europe. The importance of bodies of water for ancient human occupation is prominently attested by archaeological data (e.g. Cohen et al., 2012). Furthermore, Devès et al. (2014) found a suggestive association of early *Homo* with marshy/lakeside environments, where they suggest relatively low-risk exploiting large animals such as elephants would have been possible, and the use of rougher terrains was a secondary strategy

used in the absence of large, water-dependent herbivores.

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

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

The earliest human occupation in Europe during the Early Pleistocene thus seems to concentrate in relatively equable and wooded but diverse environments, and our analysis also suggests that the dispersal of early *Homo* into Europe roughly followed the distribution of such environments through time, the conditions being best first in the Caucasus region and the Mediterranean (Spain and Northern Italy). This is in accordance with the ecological model proposed by Blain et al. (2021), based on herpetofaunal assemblages, who suggested that rainfall and environmental humidity (expressed as forest cover) may have had an impact on the occupation of the territory during the Early and Middle Pleistocene more than other factors as temperature. Agustí and Lordkipanidze

(2019) suggested that early hominines in Eurasia would have favoured wooded environments because of safer scavenging opportunities compared to open savanna environments, and argued that the early dispersal of *Homo* from Africa to the Caucasus region (Dmanisi) would have followed the distribution of such wooded habitats ca. 1.8 Ma. However, the continuous presence of humans in Europe since the Early Pleistocene might indicate that they were able to survive periods of climatic deterioration and the spread of more steppe-like environments, perhaps leaving no traces in the archaeological record because of diminished population sizes. For example, Altolaguirre et al. (2019) suggested that while humans first appeared in the GBB under relatively humid and wooded conditions, they could have survived there during the coming glacial stages when the climate became dryer but not much cooler, approaching modern conditions. This interpretation is supported by Sánchez-Bandera et al. (2020). Overall, the archaeological records indicate that *Homo* sp. Was a frequent but not abundant species in European Early Pleistocene localities (Rodríguez et al., 2015).

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

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

Some of the Early Pleistocene human occupation sites with relatively low predicted human habitat suitability score have lower mean hypsodonty values, but moderate structural fortification and acute loph values (e.g. TE9c of Atapuerca, Vallparadís level 12). Pollen and small vertebrate records indicate the presence of abundant wooded vegetation and relatively high precipitation at TE9c (Blain et al., 2010; Hugué et al., 2017) and at Vallparadís (Martínez et al., 2010). Dmanisi, Georgia, which is the earliest of the human occupation sites (García et al., 2010), has a comparatively low human habitat suitability score, which is, however, notably elevated in comparison to most Early Pleistocene sites of comparable age.

Humans are opportunistic in terms of diet and habitat requirements and use tools to overcome limitations set by environmental conditions. It is thus not surprising that the Pleistocene human occupation sites indicate a wide range of environments based on proxy data and dental ecometric modelling. The presence of humans at sites with the lowest human habitat suitability scores based on the dental ecometric model, such as TE9c, Vallparadís and Dmanisi, could reflect other attractions, such as raw material for

tool making that spurred the hominins to overcome the challenges presented by the less-than-optimal environmental conditions. In TE9c the raw materials for the stone tools were gathered from the vicinity of the site at a range of less than 2 km (Huguet et al., 2017). At Dmanisi, the range of volcanic and other rock types present in the area would have provided a high diversity of lithic raw materials (Baena et al., 2010). This could also, to some extent, be the case for the earliest human sites in the GBB (Barranco León and Fuente Nueva 3) as while the human habitat suitability score for them is moderately good, the value of the basin for human occupation could have been enhanced by the availability of lithic raw materials, especially flint (Barsky et al., 2010; Tittton et al., 2021).

5. Conclusions

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

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

Data availability

The data used for the analyses in this study are provided in [Supplementary Tables S1-S5](#). Further details on raw-data collection and sources can be inquired from the corresponding author: juha.saarinen@helsinki.fi.

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.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix

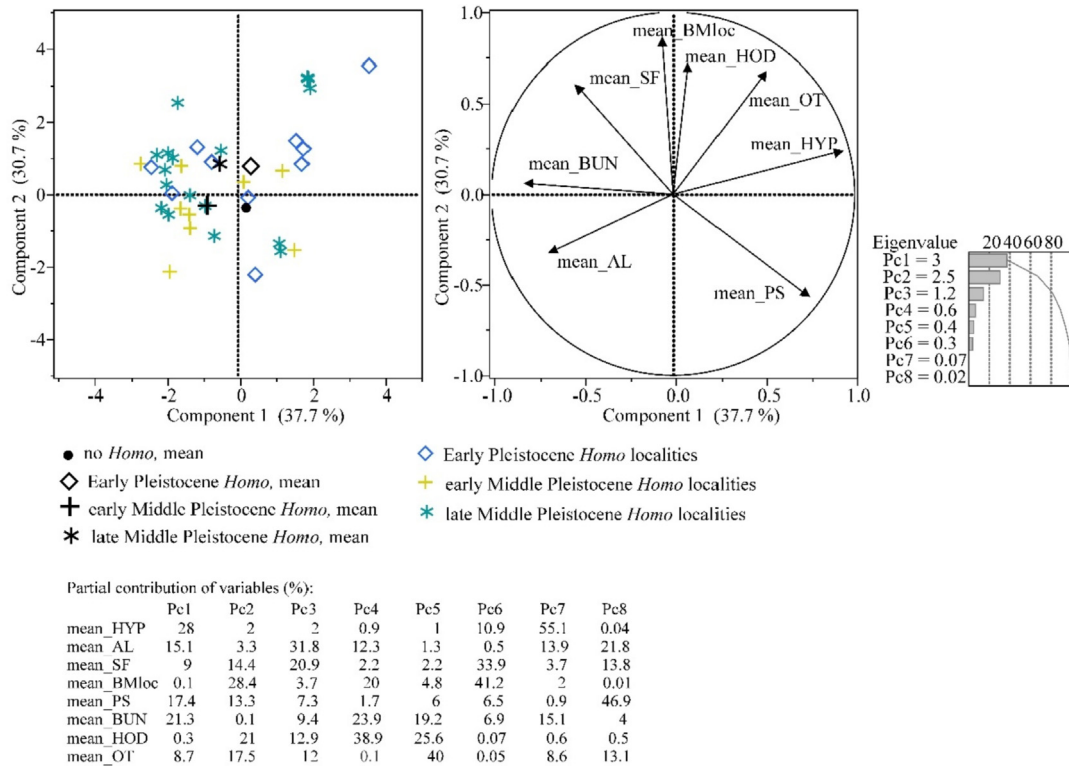


Figure A.1. Principal component analysis of localities with Early Pleistocene *Homo*, early Middle Pleistocene *Homo* and late Middle Pleistocene *Homo*, with effect of individual dental traits on the principal components. Early and late Middle Pleistocene *Homo* localities are concentrated on environments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

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.quascirev.2021.107132>.

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