**Glacial/interglacial climate variability in southern Spain during the late Early Pleistocene and climate backdrop for early *Homo* in Europe**

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**Abstract**

The oldest evidence of a human presence in western Europe is currently documented at the late Early Pleistocene sites of Barranco León and Fuente Nueva 3 (Guadix-Baza Basin, SE Spain), dated respectively to 1.4 and 1.2 Ma. Understanding the climatic variability that these hominins encountered and coped with is of outstanding importance for placing their activities in an ecological context and understanding their capacity to adapt to changing conditions. Glacial-interglacial variability during this period was considerably less intense than during later phases of the Pleistocene. To date, however, no quantitative estimates are available for this climate variability in Early Pleistocene hominin sites, and no 'cold' reconstructions directly associated with the early hominin occupations of Europe have been performed either. Here stratigraphically constrained quantitative climatic reconstructions are provided for the sites of Barranco León and Fuente Nueva 3, using an improvement on the Mutual Ecogeographic Range method by projecting the niche envelope of the extant representatives of *Ophisaurus* sp. We ascertain differences in temperature and rainfall between the different layers of the two sites, in line with previous reconstructions that revealed warm, humid periods ('interglacial') as well as more temperate but drier periods ('glacial'), consistent with Early Pleistocene climate cyclicity. Our new estimates suggest that late Early Pleistocene hominins, though conditioned to some degree by climatic factors, were able to deal with changing climatic and environmental conditions ('interglacial' and 'glacial') in the southwestern extremity of the European continent.

**Keywords:** Early Pleistocene; glacial/interglacial variability; Amphibia; Squamata; early hominins

## 1. Introduction

Unravelling the climatic context of the Early Pleistocene (between 2.58 and 0.78 Ma) is crucial to understanding the climatic and environmental changes that affected biodiversity and the dynamics of dispersals and extinctions of European terrestrial mammals, including hominins. During this timeframe and up until the Mid-Pleistocene Transition in Europe, cyclical climate change was driven by astronomical-obliquity-dominated 'glacial'-'interglacial' cycles lasting some 41 ka (Lisiecki and Raymo, 2005). These climatic changes resulted in 42 successive cycles of corresponding vegetation, ranging from open landscapes (during glacial periods) to dense forest landscapes (during interglacials) (Leroy et al., 2011). During the Early Pleistocene, an overall trend toward slightly cooler conditions leading to longer glacial phases (Lisiecki and Raymo, 2005) is reflected in the progressively longer phases with open landscapes typically observed for both 'glacial' periods and glacial-interglacial transition periods (Leroy et al., 2011).

Even after decades of research, the migrations of early hominins and their dispersals across the Eurasian continent remain a central topic of discussion. Together with seasonal fluctuations, climate has long been identified as one of the main factors affecting hominin evolution and dispersals, whereas other factors, such as technological innovation, are generally considered background influences (Agustí et al., 2009, 2018; Blain et al., 2021). Leroy et al. (2011) proposed that migrations of early hominins into Europe would only have been possible during the 'glacial' to 'interglacial' transition periods, since full 'glacial' phases would have been too cold, and 'interglacial' to 'glacial' phases too forested. This implies that there would have been 42 narrow windows of opportunity for hominins to disperse into and across Europe during the Early Pleistocene. Other authors (Agustí and Lordkipanidze, 2005, 2011, 2019a) have also pointed out that the expansion of forest cover in Europe around 1.8 Ma

could have allowed early hominins to cross from Africa into the Levantine corridor. Such a pathway would have been hard to traverse during periods of dryness when desert landscapes would have dominated the area (Agustí and Lordkipanidze, 2011, 2019a).

More recently, the range of climatic and environmental values for the occurrence of early hominins in western Eurasia has been estimated by Blain et al. (2021), who propose an ecological model based on a database developed for 23 Early and Middle Pleistocene sites in Spain, called the 'Iberian' ecological model. These authors suggest that rainfall and environmental humidity (expressed as forest cover) may have had a greater impact on the occupation of the territory during the Early and Middle Pleistocene than other factors, such as temperature. Analysis of major Spanish paleoanthropological sites shows them to have *i*) a mean annual temperature (MAT) no colder than 8.4 ºC, *ii*) a mean temperature of the warmest month (MTW) between 16.4 and 27.5 ºC, *iii*) mean annual precipitation (MAP) higher than 732 mm, and *iv*) forest cover between 26 and 41.5% of the total landscape.

In this context, the Guadix-Baza Basin (Granada, Spain) is a key region for research on these issues, given its well-preserved faunal and hominin assemblages that correspond to this chronological framework. The sites of Barranco León (BL) and Fuente Nueva 3 (FN3) are among the oldest and most significant Oldowan occurrences so far discovered outside Africa (Martínez-Navarro et al., 1997; Oms et al., 2000a). Moreover, a deciduous molar attributed to *Homo* sp. from Barranco León is one of the oldest hominin remains found so far in western Europe (Toro-Moyano et al., 2013). These two sites have yielded very rich and well-documented stone tool assemblages (Barsky et al., 2013, 2015a, b, 2018; Titton et al., 2018, 2020, 2021; Toro-Moyano et al., 2010, 2011; Supplementary Note 1). In addition, the fauna from both sites shows clear signs of anthropogenic manipulation, evidenced by the presence of cut and percussion marks on the cortical surface of the bones (Espigares et al., 2019; Yravedra et al., 2021, 2022).

Paleoclimatic and paleoenvironmental reconstructions of BL and FN3 have been undertaken using a variety of proxies and techniques: ecometric and mesowear analyses based on the large-mammal assemblages (Saarinen et al., 2021a); analysis of herpetofaunal assemblages (Blain, 2005, 2009; Bailon, 2010; Blain and Bailon, 2010; Blain et al., 2011, 2016a; Sánchez-Bandera et al., 2020); analysis of small-mammal assemblages (Agustí et al., 2010a, b, 2015a, 2019b); malacofaunal analysis (applied at BL, Albesa and Robles, 2020); isotopic analysis of ostracod shells (Anadón and Gabàs, 2009), of biogenic lacustrine carbonates (Anadón et al., 2015) and of the tooth enamel of large herbivores (Bocherens et al., 2020); pollen analysis (Jiménez Moreno, 2003; Ochando et al., 2022); and taphonomic studies (Yravedra et al., 2021, 2022). Nevertheless, with the exception of the microvertebrate analyses (Agustí et al., 2015a, 2019b; Sánchez-Bandera et al., 2020) and the isotopic analyses of ostracod shells (Anadón and Gabàs, 2009) and biogenic lacustrine carbonates (Anadón et al., 2015), these proxies have been applied to the sites at a broad level, i.e. without taking into account the different levels of their depositional sequences. Overall, these studies indicate that both sites were, in terms of temperature, similar to or warmer than at present and had higher precipitation. Some differences have been detected between BL and FN3, suggesting a particularly wet and warm climate for BL and a more open and drier habitat at least for some layers of FN3

The aim of the present work is to provide a more precise paleoclimatic characterization of the Early Pleistocene of the Guadix-Baza Basin and its hominin-bearing levels, proposing new stratigraphically constrained reconstructions for the different archaeo-stratigraphical levels at BL (levels D1, D2 and E) and FN3 (level 5) on the basis of the amphibian and squamate reptile fossil assemblages.

## 2. Stratigraphic setting and chronology

The Guadix-Baza Basin, located within the Betic Range in the southeastern sector of the Iberian Peninsula (Fig. 1A), yields a continuous record of paleoenvironmental, paleobiological and geological evolution, dating from around 8 Ma to 280 ka (Agustí et al., 2015a). The basin was isolated from the Mediterranean Sea, and the subsequent accumulation of continental sediment of fluviatile and lacustrine origin (clay, silt, sand, and evaporitic calcareous incrustations) filled the Baza Formation (Vera et al., 1985; Soria et al., 1987) and led to the establishment of a large inland lake that occupied this part of the depression from around 5.5 Ma to 0.3 Ma, with marginal areas varying with the fluctuating water level (Vera, 1970; Hüsing et al., 2010). The basin became a catchment area for the present-day Guadalquivir river before 205 ka (Díaz-Hernández and Julià, 2006). It was subsequently infilled by the alluvial Guadix Formation, composed of conglomerates (Viseras, 1991), and by the lacustrine and palustrine Baza Formation, covering the central area (Vera et al., 1985; Anadón et al., 1987).

The sites analyzed in the present work are located in the Baza Formation (Fig. 1B). The chronostratigraphy of the Baza Formation ranges from the Early Pliocene (Agustí, 1986; Garcés et al., 1996; Piñero and Agustí, 2020) to Middle Pleistocene (Agustí et al., 1987; Agustí et al., 2015b). It is composed of three lithostratigraphic members (Vera et al., 1985; Oms et al., 1998, 2000b): the Lower Member (calcareous surface deposits of a lacustrine and palustrine origin); the Intermediate Member (fluvial mudstones and sandstones); and the Upper Member (lacustrine and palustrine deposits resulting from an accumulation of silty calcareous deposits as well as coarser fractions).

The Oldowan archaeo-paleontological sites of BL and FN3 are included in the Upper Member of the Baza Formation, at an altitude of approximately 950 meters above sea level, and separated between them by a distance of 4.1 km. In general (see Fig. 1C), the

succession containing the FN3 site is dominantly palustrine, whereas that containing BL is more lacustrine (Oms et al., 2011). In both cases (see Fig. 1C), the paleo-hydrological conditions (in terms of water salinity and depth) were unstable throughout the accumulation of the sections. A general overview of the sedimentary conditions is summarized here in order better to control for any bias in the paleoecological data.

*2.1 Barranco León*

This site is located around 3 km from the town of Orce. The stratigraphy of the site is divided into the following nine levels, from oldest to youngest (Anadón et al., 2003; Anadón and Gabàs, 2009; Oms et al., 2011; Fig. 1C): level A, beige calcisiltites to calcarenites; level B, black and dark green feldspar quartz muddy sands; level C, beige calcisiltites to calcarenites; level D1, grayish gravels with a sandy matrix; level D2, grayish quartz-bioclastic sands, ending in whitish limestones; level E, fine-to-medium-grained quartz and feldspar sands, with reddish, brown and greenish colorations; level F1, black sandy mudstones; level F2, bioclastic sands of grayish quartz with small chalk nodules in the upper part; and level G, beige-colored sands.

The main environmental features observed in levels D1, D2 and E indicate a marginal freshwater area on the shores of the main saline lake. The freshwater was derived from the adjacent highlands and mixed with surface and hydrothermal waters (Anadón et al., 2015). As shown by micromorphological data (Rodriguez-Rivas, 2009), the presence of freshwater probably attracted humans during the regressive phases of the lake. The faunal content of level D1 has an obvious component of reworking (a parautochthonous component), whereas level D2 is more autochthonous, and level E fully autochthonous.

In terms of archaeo-paleontological content, the most significant levels are D1 and D2. Level D1 (with an average thickness of around 65 cm) is composed of gravels, pebbles, and cobbles, varying from small quartz clasts to palustrine limestone boulders (Anadón and Julià, 2010). The formation of level D1 is associated with a high-energy flash flood depositional event, which brought faunal remains (some anthropogenically modified) and detrital lithic materials (including knapped Oldowan lithics) from an area adjacent to the present-day site (Oms et al., 2011; Titton et al., 2021; Yravedra et al., 2022). Contrastingly, some of the archaeo-paleontological materials present a good state of preservation with little taphonomic alteration (Titton et al., 2021; Yravedra et al., 2022). Along with the refitted and conjoined lithic sets that have been documented (Gibert et al., 1998; Toro-Moyano et al., 2013; Titton et al., 2021), this attests to *in situ* hominin activity taking place in level D1. By contrast, level D2 (around 20 cm thick) records background sedimentation. Both the sands and the microfaunal remains in D2 are similar to those found in level D1.

The stratigraphic sequence of BL has been dated by a variety of methods, including analysis of the large- and small-mammal assemblages, paleomagnetic studies, and electron spin resonance (ESR). ESR dating was applied to optically bleached quartz grains, yielding an age of between 1.02 ± 0.09 Ma in the upper part, and 1.73 ± 0.17 Ma at the base. Levels D1 and D2 were dated to 1.43 ± 0.38 Ma (Toro-Moyano et al., 2013). In general, the evaluations of the ESR range are consistent with the stratigraphy, showing an overall increase in age with depth and ascribing the deposits an Early Pleistocene age. The paleomagnetic studies show the presence of exclusively reverse magnetization throughout the stratigraphic section, indicating a pre-Jaramillo age for all levels of BL (Oms et al., 2000b, 2003, 2011).

The numerical dates are supported by the biochronological data of both micro- and macro-mammal assemblages (Oms et al., 2000a; Agustí et al., 2010a, b; Toro-Moyano et al., 2013). The large-vertebrate association (see Supplementary Notes 2) is typical of the Late

Villafranchian period (Rook and Martínez-Navarro, 2010) and is similar to that of the nearby paleontological site of Venta Micena, dated to ca. 1.6-1.4 Ma (Agustí et al., 2007, 2010b; Duval et al., 2011), despite the presence of *Equus sussenbornensis* and the absence of *Soergelia minor*, which suggest a more recent age for BL. The list of small mammals (see Supplementary Notes 2) is mainly composed of *Mimomys savini* (80% of the rodents). Notable is the presence of *Manchenomys orcensis* (Agustí et al., 2022) and *Allophaiomys* aff. *lavocati*. This assemblage places BL in the regional *Allophaiomys* aff. *lavocati* biozone (Agustí et al., 2010a, b, 2015b), which is where level TE9c of the Sima del Elefante site (Atapuerca) is also situated, biochronologically dated to between 1.5 and 1 Ma (Cuenca-Bescós et al., 2010, 2013). The evolutionary differences between the *M. savini* populations from BL and FN3 suggest that BL is older than FN3 (Lozano-Fernández et al., 2015).

*2.2 Fuente Nueva 3*

FN3 is located east of the town of Orce, on a slope north of the Cañada de Vélez river valley (Fig. 1B), in the village of Fuente Nueva. The general section displays up to 12 levels (Oms et al., 2011; Anadón et al., 2013; see Supplementary Note 3), of which levels 2 and 5 are particularly noteworthy, presenting abundant remains of lithic industries. Furthermore, there is a specimen of *Mammuthus meridionalis* in anatomical connection in level 5, which is associated with hyena coprolites (*Pachycrocuta brevirostris*) and lithic industry (Martínez-Navarro et al., 1997; Toro-Moyano et al., 2010; Espigares et al., 2013). Research by Yravedra et al. (2021) identified traces of human activity on small-, medium-, and very-large-sized animals at the site, highlighting the presence of cut marks on equid, cervid and hippopotamus bones.

The stratigraphic succession at FN3 has been dated by the large- and small-mammal assemblages, paleomagnetic studies, and ESR. ESR data give and age of 1.19 ± 0.21 Ma (Duval, 2008; Duval et al., 2012). The paleomagnetic studies reveal reverse polarity (Oms et al., 2000b), which, in conjunction with the ESR data, suggests an age prior to the Jaramillo subchron (1.07-0.99 Ma; Oms et al., 2003, 2011; Álvarez et al., 2015). Its large-vertebrate assemblage, with a striking abundance of *M. meridionalis* remains (Supplementary Notes 2), is also characteristic of the Late Villafranchian period (Rook and Martínez-Navarro, 2010) and is similar to that of the nearby site of Venta Micena. This is in spite of the presence of *Ammotragus europaeus* and the absence of *Soergelia minor*, which suggest a more recent age for the site of FN3. The taxonomic list of small mammals, which includes *Allophaiomys* aff. *lavocati*, *Mimomys savini* and *Manchenomys orcensis* (Agustí et al., 2010a, b, 2015b, 2022; Supplementary Notes 2), fits within the same biozone as that proposed for BL: the *Allophaiomys* aff. *lavocati* biozone (Agustí et al., 2010a, b, 2015b). As noted above, however, the evolutionary stages of *M. savini* suggest that FN3 is more recent than BL (Lozano-Fernández et al., 2015).

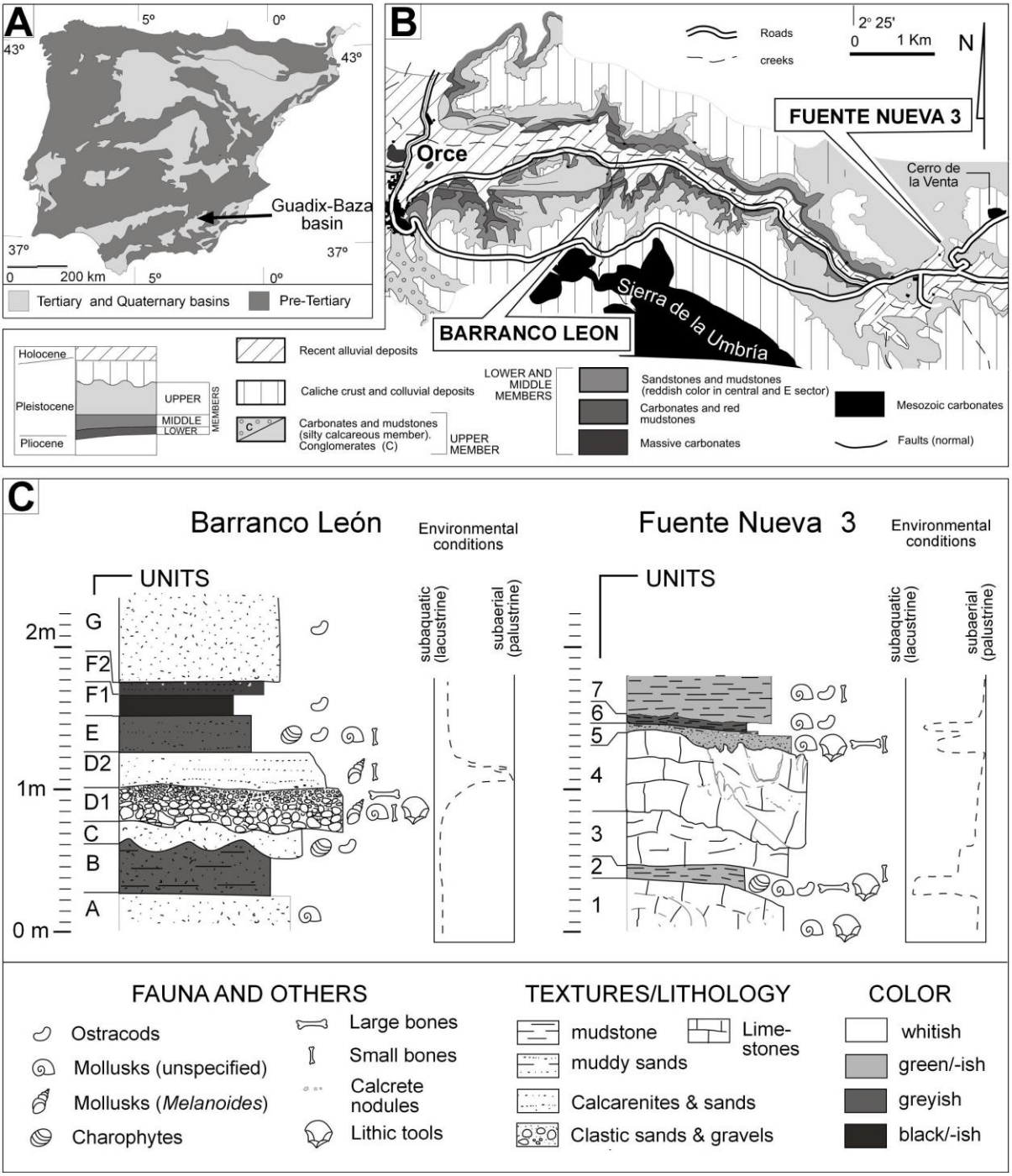


**Figure 1. A**: Location of the Guadix-Baza Basin in the context of the Cenozoic basins of the Iberian Peninsula. **B**: Geological units around Orce and location of the sites of BL and FN3. **C**: BL and FN3 sections with indications of the levels and environmental conditions of deposition documented by sedimentology and invertebrate organisms (from Sánchez-Bandera et al., 2020). Abbreviations: km = kilometers, m = meters.

## 3. Material and methods

### *3.1 Amphibian and reptile assemblages*

The amphibian and squamate reptile fossil remains presented in this study are from levels D1, D2 and E of BL and level 5 of FN3. They have already been interpreted from a paleoenvironmental perspective by means of the habitat weighting method (Sánchez-Bandera et al., 2020). The taxonomic list recorded at BL is composed overall of 13 species: six anurans (*Discoglossus* sp., *Pelobates cultripes*, *Epidalea calamita*, *Bufotes viridis* s.l., *Hyla* sp. and *Pelophylax* cf. *perezi*), two lizards (an indeterminate large-sized lizard and *Ophisaurus* sp.) and five snakes (*Malpolon monspessulanus*, *Natrix maura*, *Natrix natrix* s.l., cf. *Coronella* sp. and *Zamenis scalaris*). The faunal list of FN3-5 is composed of seven species: three anurans (*Discoglossus* sp., *Pelobates cultripes* and *Pelophylax* cf. *perezi*), one lizard (an indeterminate large-sized lizard) and three snakes (*Malpolon monspessulanus*, *Natrix maura* and cf. *Coronella* sp.) (Sánchez-Bandera et al., 2020; Supplementary Table S1). The species diversity and richness of these samples have been analyzed and compared, revealing significant differences between the BL and FN3-5 assemblages, the latter being less rich in terms of biodiversity (Martínez-Monzón et al., 2022).

The herpetofauna show affinities for Mediterranean environments, and most of the species still have present-day representatives in the Orce region (Blain et al., 2016a). The only taxa currently absent in the Iberian Peninsula are the toads of the group *Bufotes viridis* s.l. (documented in level D1 of BL) and the anguid *Ophisaurus* sp. (documented in levels D1, D2 and E of BL) (Sánchez-Bandera et al., 2020). *Bufotes viridis* s.l. is not taken into account in this study since its affinities with Early Pleistocene remains from Spain are still unclear (Blain et al., 2010).

The genus *Ophisaurus* (*sensu* Klembara et al., 2014) includes what were formerly considered separate genera: *Ophisaurus* s.s. from North America, *Dopasia* from southeast Asia, and *Hyalosaurus* from northern Africa. In accordance with the dental characters of the fossils recovered in BL (Blain, 2005, 2009; Blain and Bailon, 2010, 2019), North American species (*Ophisaurus attenuatus*, *O. ceroni*, *O. compressus*, *O. incomptus*, *O. mimicus*, and *O. ventralis*) can be ruled out. Consequently, the extant *Ophisaurus* spp. taxa used in this study to infer the most probable climate envelope for our fossil taxa are those from southeast Asia (*O. buettikoferi*, *O. ludovici*, *O. hainanensis*, *O. sokolovi*, *O. harti* and *O. wegneri*) and North Africa (*Hyalosaurus koellikeri*). *H. koellikeri* is found in central-western Morocco (Escoriza and Comas, 2015; Martínez de Mármol et al., 2019). The southeast Asian species of *Ophisaurus* are distributed (according to the International Union for Conservation of Nature; IUCN, 2021) in Vietnam (*O. ludovici* and *O. harti* in the Hanoi region, and *O. sokolovi* in Gia Lai Province), in Hainan Province in China (*O. hainanensis*), in Borneo (*O. buettikoferi*) and in West Sumatra (*O. wegneri*).

### *3.2 Paleoclimatic reconstructions*

In order to obtain paleoclimatic estimates for levels D1, D2 and E of BL and level 5 of FN3, a series of different procedures were applied to the fossil assemblages, depending on whether or not they include the "exotic" taxon *Ophisaurus* sp.

#### *3.2.1 Mutual Ecogeographic Range*

The Mutual Ecogeographic Range (MER) method (Blain et al., 2009, 2016a) was used to identify the current geographical range common to the extant herpetofaunal species present in each level. The MER method is based on presence/absence (and not abundance) and so is not particularly affected by taphonomic biases and/or over-representation of some species in the sites (Blain et al., 2016a). This method assumes that the species' ecological niche is preserved over time, so fossil species had the same climatic tolerances and preferences as their living counterparts (Jackson and Overpeck, 2000; Jackson and Williams, 2004). Since most of the taxa have modern distributions restricted to the Iberian Peninsula, their current spatial distributions were obtained from Loureiro et al. (2008) for Portugal, and SIARE (AHE, 2020) for Spain. Both are represented in a geographic information system (WGS 84 datum) with a 10 × 10 km square grid. In cases where species-level identification was not achieved (i.e., *Discoglossus* sp., *Hyla* sp. and cf. *Coronella* sp.), all the extant species belonging to the genus were taken into consideration.

Given that the MER method is based on the current geographical range common to the extant species present in each level, it does not allow to include in the analysis taxa that are currently absent from the geographical extension under analysis. In order to obtain a more precise paleoclimatic estimates taking into account the "exotic" taxon *Ophisaurus* sp., we propose a variation on the MER method. This new procedure consists in the modeling and projection over the distribution areas obtained by MER of the niche envelope of the extant representatives of *Ophisaurus* sp.

### *3.2.2 Modeling the* Ophisaurus *sp. ecological niche*

The climatic range of the "exotic" taxon *Ophisaurus* sp. was projected over the MER overlaps of the Iberian Peninsula in order to eliminate the MER areas where this taxon would not have been able to survive. To include the climatic range of *Ophisaurus* sp. (i.e. including *Hyalosaurus koellikeri* and the SE Asian *Ophisaurus* spp.) in the overlapping process, we applied the Uncertain Distribution Area-Occupied Distribution Area (UDA-ODA) discrimination technique (Fagoaga et al., 2019) to its distribution areas. This procedure is a refinement of the MER method using geographic information systems (GIS) (Fagoaga et al., 2019). It provides more precise information on a specific species' distribution, making it possible to build more accurate scenarios (ODAs) that can be used in the overlapping process (superior to the coarse-grained distributions proposed by many atlases).

The initial distribution areas of *H. koellikeri* considered in this study are in line with Escoriza and Comas (2015). Starting from the distribution areas provided by Bons and Geniez (1996), these authors eliminated those areas where the occurrence of *H. koellikeri* may be altered by anthropic landscape modifications. Additionally, we removed the area of the Debdou Valley (Morocco), where the specimens consist of isolated populations, and old and/or unconfirmed records of *H. koellikeri (*Bons and Geniez, 1996; de Pous et al., 2011).

In the absence of more detailed studies, the initial distribution areas of the SE Asian *Ophisaurus* spp. under consideration are those provided by the International Union for Conservation of Nature (IUCN, 2021). To obtain the ODA of the extant *Ophisaurus* spp. we removed those areas above their upper elevation limits (Fig. 2A, 2B). The upper elevation limit for *H. koellikeri* is 2,000 m (Bons and Geniez, 1996; Supplementary Table S2), as it is for the SE Asian *Ophisaurus* spp. taking all the taxa in the group into account. This upper limit pertains to *O. harti* (Lin et al., 2003; Supplementary Table S2).

To model the *Ophisaurus* sp. niche, the vegetation cover requirements of *H. koellikeri* provided by Escoriza and Comas (2015) were analyzed from the resulting

distribution areas (ODA). These authors argue that the proportion of tree crown cover is the variable that best explains the occurrence of *H. koellikeri*, and to a lesser extent other abiotic factors such as substrate, topography, and climatic conditions (de Pous et al., 2011; Escoriza and Comas, 2015). *H. koellikeri* inhabits forests and/or woodlands (68% average tree crown cover) mainly composed of evergreen oaks (*Quercus ilex* and *Q. suber*, 68.43%, Escoriza and Comas, 2015). From the values obtained for this ecological variable, the niche was modeled taking into account the mean +/- SD range in order to remove outliers.

The Occupied Distribution Area (ODA) of *H. koellikeri*, obtained by removing those areas above its upper elevation limit (2,000 m; Fig. 2A), enabled us to extract the areas with evergreen broadleaf tree cover (Tuanmu and Jetz, 2019; Fig. 2C) and obtain the vegetation cover requirements of *H. koellikeri*. The evergreen broadleaf tree cover values (Fig. 2C) range (mean +/- SD) from 13.1 to 28.3% (percentage cover per $km^2$). This range includes 95% of the extant distribution of *H. koellikeri*. From this range, the lowest value (mean – SD, 13.1%), taken to be the minimal optimum vegetation cover requirement of *H. koellikeri*, was selected as the ecological niche for this species.

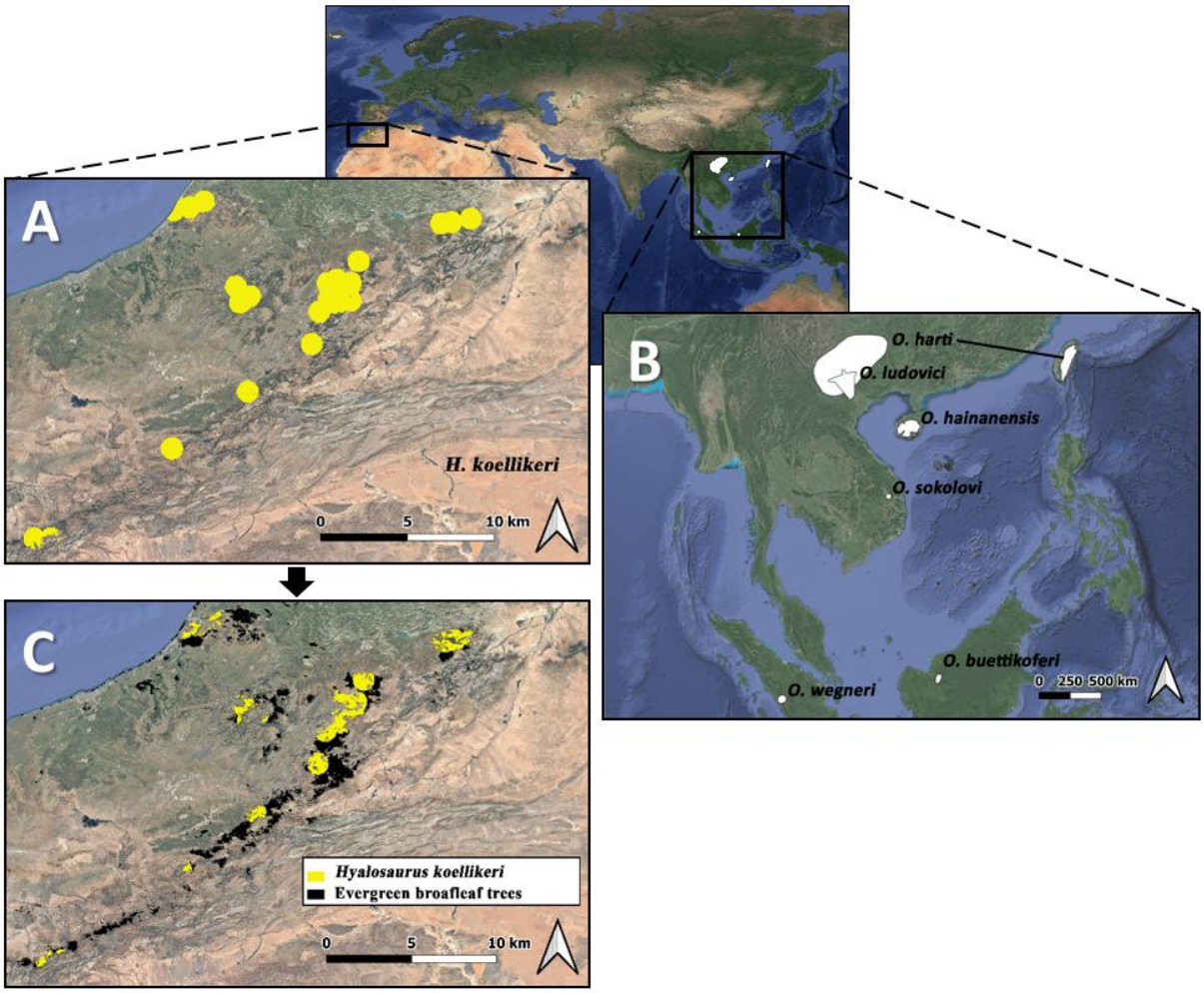


**Figure 2**. Distribution areas of the extant *Ophisaurus* spp. taxa (i.e. including SE Asian *Ophisaurus* spp. and *Hyalosaurus koellikeri*). **A**: Distribution area of *H. koellikeri* after removing the Debdou Valley area and those areas above its upper elevation limit (2,000 m; modified from the distribution area provided by Escoriza and Comas, 2015). **B**: Distribution areas of *Ophisaurus* spp. in Asia (*O. buettikoferi*, *O. hainanensis*, *O. ludovici*, *O. sokolovi*, *O. harti* and *O. wegneri*) after removing the areas above their upper elevation limit (2,000 m; modified from the distribution areas provided by the International Union for Conservation of Nature, IUCN, 2021). **C**: Distribution area of *H. koellikeri* obtained by selecting the areas with evergreen broadleaf tree cover (yellow areas), and the evergreen broadleaf tree cover distribution in central-western Morocco (black areas; class 2 of the global 1-km consensus land cover, Tuanmu and Jetz, 2019). Abbreviations: km = kilometers.

*3.2.3 Climatic parameters*

Annual (MAT, mean annual temperature; MAP, mean annual precipitation) and monthly climatic parameters (mean monthly temperature; mean monthly precipitation) were extracted from the final overlapping areas of climate layers from WorldClim 2.1, with a 30 arcsecond resolution grid (Fick and Hijmans, 2017). The same climatic parameters were calculated for the Orce municipality nowadays (1970-2000, with a 325 $km^2$ area). Datasets were processed using the ArcGIS 10.3 application (ESRI, 2014). The mean and standard deviation were calculated using the statistical program IBM SPSS Statistics 22 (IBM Corp. Released, 2013).

To measure aridity, we used the Gaussen, Lautensach-Meyer, Dantin-Revenga and De Martonne indexes (see for example Muñoz-Delgado, 2003). The Gaussen index ($P < 2 \times T$) regards a dry month as occurring when its pluviometric level (P), measured in mm, is less than twice the value of the average temperature in ºC for that month (T). The Lautensach-Meyer index considers a dry month if its pluviometric level (P), measured in mm, is less than 30 mm. The Dantin-Revenga index is calculated as 100 x MAT/MAP, and the De Martonne aridity index as MAP/(MAT + 10). Climatograms were produced in order to achieve a better visualization of the monthly evolution of temperature and precipitation, applying the scale $P = 2 \times T$ to evaluate directly the Gaussen index.

A point of reference is provided by the present-day values obtained for the Orce region, which indicate a continental Mediterranean climate with cold winters due to altitude (1,000 m above sea level), including sporadic snowfalls and minimum temperatures often below freezing. Summer tends to be hot with temperatures that consistently exceed 30 ºC in July and August and occasionally reach above 40 ºC. Though concentrated in the autumn and

spring, precipitation can occur throughout the year. The MAT is 13 ºC, and the MAP is 437 mm (Table 1; Fick and Hijmans, 2017). The average difference between the warmest and coldest month is 20.3 ºC. The arid period in summer (from June to September) lasts four months.

### *3.3 Statistical analyses*

Independent-sample Student's *t*-tests were performed to test for statistical differences in the climatic parameters (MAT and MAP) between BL (levels D1, D2 and E) and FN3 (level 5). All statistical analyses were run using the statistical program IBM SPSS Statistics 28 (IBM Corp. Released, 2021), and differences were considered significant at $p < 0.05$.

## 4. Results

### *4.1 Paleoclimate inferred for Barranco León and Fuente Nueva 3*

Past climatic data derived by applying the MER method (FN3-5) and the MER method with the projected *Ophisaurus* sp. niche envelope (BL levels) are illustrated in Figures 4 and 5, and a climatic interpretation is synthesized in Supplementary Table S3.

For BL, the size of the area derived from the projection of the *Ophisaurus* sp. niche envelope over the resulting MER is 31 $km^2$ (for BL-D1), 30.8 $km^2$ (for BL-D2), and 126.5 $km^2$ (for BL-E). These areas are located today on the Atlantic seashore of northern Portugal and Galicia and at the southernmost point of the Iberian Peninsula (Fig. 3). The MAT and MAP for BL-D1 are 16.8 ºC and 767 mm, respectively, and for BL-D2 16.6 ºC and 793

mm. Level E yielded MAT and MAP values of 16.4 ºC and 835 mm (Table 1). The climate inferred for these three levels is warm, with a low atmospheric temperature range, warm summers, and mild winters. Rainfall was abundant with an irregular distribution, occurring mainly during winter and spring. The aridity indexes suggest a semi-arid (or humid according to the De Martonne index), continental Mediterranean climate with four dry months in summer (Fig. 4, Table 2).

In the case of FN3-5, the overlap gives a total area of 63,877 $km^2$, with a more generalist distribution mainly concentrated on the west and southwest of the Iberian Peninsula (Fig. 3). The MAT is 14.7 ºC, and the MAP is 618 mm (Table 1). The climate during the accumulation of this level can be described as warm with a high atmospheric temperature range, warm summers, and temperate winters. Rainfall was sparse with an irregular distribution, occurring primarily during winter and spring. The aridity indexes suggest a semi-arid (or semi-humid according to the De Martonne index), continental Mediterranean climate with four dry months in summer (Fig. 4, Table 2).

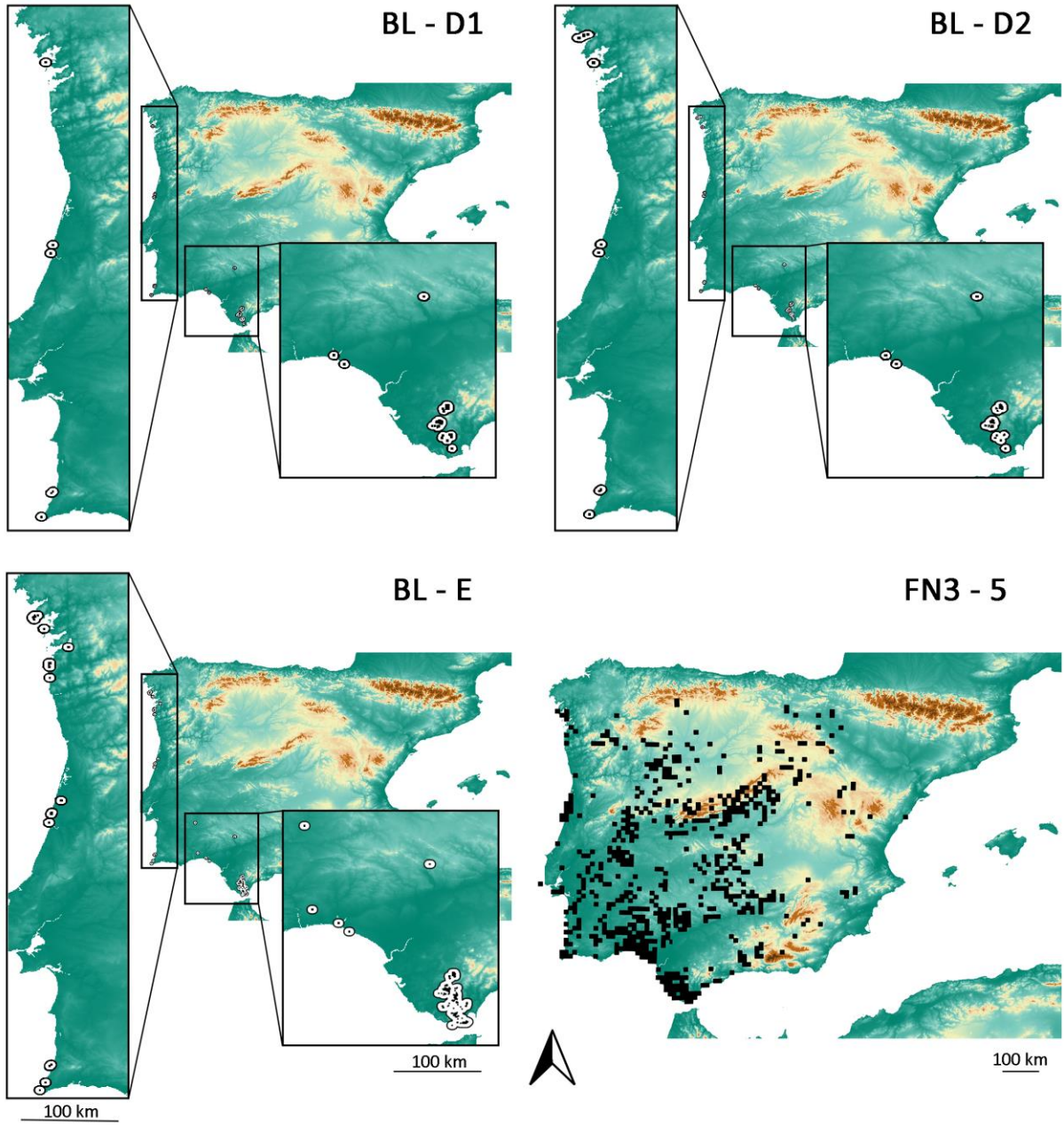


**Figure 3.** Final overlapping areas of the current distribution of the amphibians and squamate reptiles for BL levels D1, D2 and E, and FN3 level 5 (black areas). White areas correspond to the 5 km buffer applied to the overlapping areas of the BL levels to visualize them better. Abbreviations: km = kilometers.

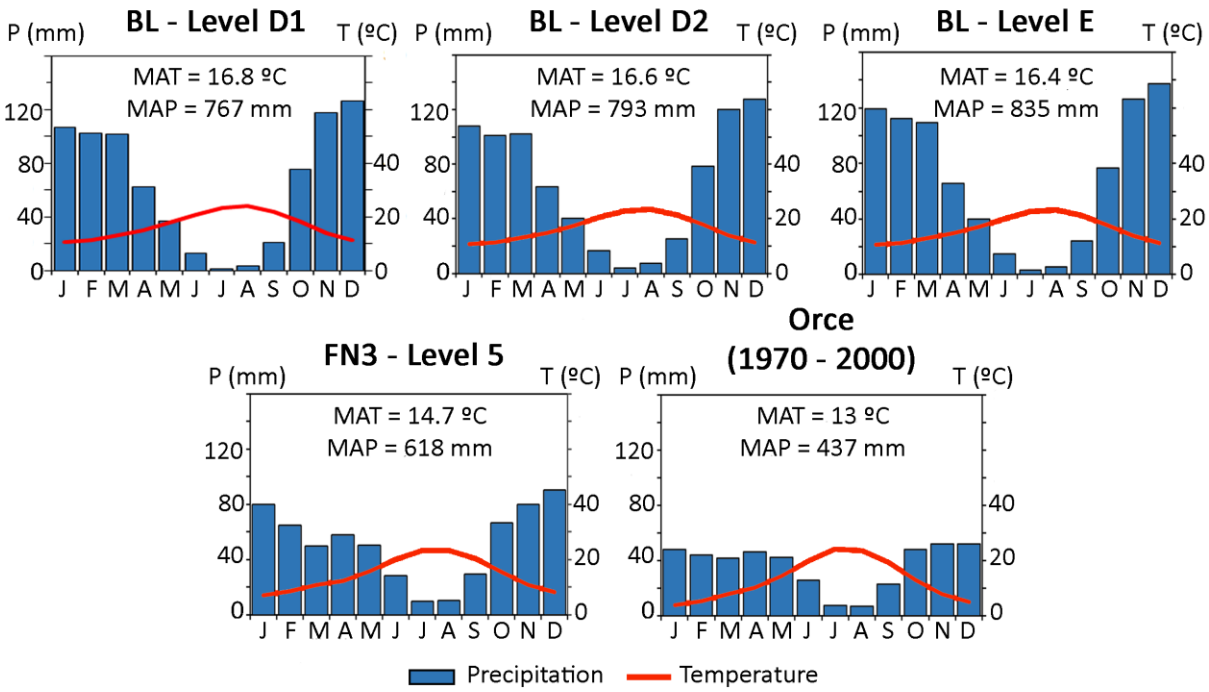


**Figure 4**. Climatograms showing the quantitative climate reconstructions of levels D1, D2 and E of BL, and level 5 of FN3, applying the scale P = 2 x T. Abbreviations: P = precipitation, T = temperature, MAT = mean annual temperature, and MAP = mean annual precipitation.

**Table 1**. Climate values for the present-day Orce region (1970-2000; data from WorldClim 2.1, Fick and Hijmans, 2017) and climate values (in ºC for temperature and mm for precipitation) calculated by the Mutual Ecogeographic Range method with the UDA-ODA discrimination methodology. Abbreviations: MAT = mean annual temperature, MAP = mean annual precipitation, SD = standard deviation, MIN = minimum, MAX = maximum.

| | **Temperature (ºC)** | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | MAT | J | F | M | A | M | J | J | A | S | O | N | D |
| Orce (1970-2000) | 12.9 | 3.8 | 5.4 | 8 | 10.3 | 14.5 | 19.8 | 24.1 | 23.7 | 19.2 | 13.1 | 8 | 4.9 |
| BL - D1 | | | | | | | | | | | | | |
| MEAN | 16.8 | 10.7 | 11.4 | 13.3 | 15 | 17.7 | 20.8 | 23.4 | 23.9 | 21.8 | 18.1 | 14 | 11.3 |
| SD | 0.53 | 0.8 | 0.7 | 0.6 | 0.5 | 0.7 | 0.8 | 1.1 | 1.1 | 0.7 | 0.5 | 0.6 | 0.7 |

| | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| MIN | 14.7 | 7.9 | 9.5 | 12 | 13.8 | 15.3 | 17.9 | 19 | 19.4 | 18.6 | 16.4 | 12.1 | 8.6 |
| MAX | 17.8 | 11.6 | 12.3 | 14.1 | 16.2 | 20.3 | 22.8 | 26.4 | 26.3 | 22.9 | 19.2 | 14.9 | 12.1 |
| BL - D2 | | | | | | | | | | | | | |
| MEAN | 16.6 | 10.6 | 11.3 | 13.1 | 14.9 | 17.4 | 20.5 | 23 | 23.5 | 21.5 | 17.9 | 13.8 | 11.2 |
| SD | 0.8 | 0.7 | 0.7 | 0.6 | 0.7 | 1.1 | 1.2 | 1.7 | 1.7 | 1.3 | 0.8 | 0.6 | 0.7 |
| MIN | 14.1 | 7.9 | 9.5 | 11.6 | 12.8 | 14.5 | 17 | 18.7 | 19.3 | 17.9 | 15.5 | 12.1 | 8.6 |
| MAX | 17.8 | 11.6 | 12.3 | 14.1 | 16.2 | 20.3 | 22.8 | 26.4 | 26.3 | 22.9 | 19.2 | 14.9 | 12.1 |
| BL – E | | | | | | | | | | | | | |
| MEAN | 16.4 | 10.7 | 11.2 | 13 | 14.8 | 17.1 | 20.2 | 22.7 | 23.2 | 21.2 | 17.8 | 13.9 | 11.4 |
| SD | 0.8 | 0.7 | 0.7 | 0.7 | 0.7 | 0.9 | 1 | 1.3 | 1.4 | 1.1 | 0.8 | 0.7 | 0.8 |
| MIN | 13.3 | 7.9 | 8.8 | 14.2 | 12 | 13.9 | 16.9 | 18.5 | 18.6 | 17.4 | 14.5 | 10.8 | 8.6 |
| MAX | 17.8 | 12.2 | 12.7 | 10.6 | 16.2 | 20.3 | 22.8 | 26.4 | 26.3 | 22.9 | 19.2 | 15.2 | 12.8 |
| FN3 – 5 | | | | | | | | | | | | | |
| MEAN | 14.7 | 7.2 | 8.5 | 10.7 | 12.3 | 15.7 | 20 | 23.4 | 23.2 | 20.3 | 15.4 | 10.9 | 8.2 |
| SD | 2.3 | 2.8 | 2.6 | 2.5 | 2.4 | 2.2 | 2 | 2.2 | 2.1 | 2.2 | 2.6 | 2.8 | 2.8 |
| MIN | 7.8 | 0.3 | 1.1 | 3.2 | 4.7 | 8.4 | 13.4 | 17.1 | 17.3 | 13.8 | 8.1 | 3.8 | 1.4 |
| MAX | 18.4 | 12.7 | 13.2 | 14.6 | 16.2 | 19.6 | 23.8 | 27.5 | 27.1 | 24.1 | 19.5 | 15.9 | 13.8 |

| | **Precipitation (mm)** | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | MAP | J | F | M | A | M | J | J | A | S | O | N | D |
| Orce (1970-2000) | 437 | 48 | 44 | 41 | 46 | 42 | 26 | 7 | 7 | 23 | 48 | 52 | 52 |
| BL - D1 | | | | | | | | | | | | | |
| MEAN | 767 | 107 | 102 | 102 | 62 | 36 | 13 | 1 | 3 | 21 | 75 | 118 | 126 |
| SD | 72 | 13 | 13 | 12 | 6 | 7 | 0 | 1 | 2 | 5 | 6 | 11 | 14 |
| MIN | 467 | 60 | 51 | 58 | 37 | 27 | 9 | 1 | 1 | 19 | 59 | 74 | 69 |
| MAX | 974 | 139 | 129 | 125 | 86 | 72 | 39 | 10 | 13 | 46 | 102 | 135 | 145 |
| BL - D2 | | | | | | | | | | | | | |
| MEAN | 793 | 108 | 101 | 102 | 63 | 40 | 16 | 4 | 7 | 25 | 78 | 120 | 127 |
| SD | 113 | 14 | 13 | 12 | 7 | 14 | 11 | 8 | 11 | 15 | 10 | 14 | 15 |
| MIN | 467 | 60 | 51 | 58 | 37 | 27 | 9 | 1 | 1 | 19 | 59 | 74 | 69 |
| MAX | 1113 | 139 | 129 | 125 | 86 | 79 | 47 | 28 | 42 | 71 | 108 | 154 | 158 |

| | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| BL – E | | | | | | | | | | | | | |
| MEAN | 835 | 120 | 112 | 109 | 66 | 40 | 15 | 3 | 6 | 24 | 77 | 126 | 137 |
| SD | 151 | 19 | 17 | 14 | 12 | 16 | 11 | 7 | 8 | 14 | 17 | 16 | 20 |
| MIN | 467 | 60 | 51 | 50 | 37 | 27 | 8 | 0 | 1 | 17 | 59 | 73 | 69 |
| MAX | 1593 | 193 | 191 | 143 | 135 | 103 | 63 | 33 | 39 | 79 | 162 | 190 | 265 |
| FN3 – 5 | | | | | | | | | | | | | |
| MEAN | 618 | 80 | 65 | 50 | 58 | 51 | 28 | 10 | 10 | 30 | 67 | 80 | 90 |
| SD | 234 | 38 | 33 | 25 | 17 | 18 | 13 | 8 | 8 | 14 | 24 | 31 | 37 |
| MIN | 328 | 21 | 17 | 21 | 33 | 23 | 10 | 0 | 2 | 14 | 35 | 24 | 25 |
| MAX | 1818 | 257 | 221 | 158 | 145 | 143 | 71 | 46 | 42 | 108 | 189 | 226 | 273 |

**Table 2.** Climatic interpretation of the climatograms obtained for BL (levels D1, D2 and E), FN3 (level 5), and the present-day Orce region (1970-2000). Abbreviations: MAT = mean annual temperature, temp. = temperate, t. = temperature, m. = months, MTC = mean temperature of coldest month, MAP = mean annual precipitation, Dist. = distribution, p. = precipitation, I. = index, Medit. = Mediterranean, semi-a. = semi-arid, and semi-h. = semi-humid.

| | Barranco León - Level D1 | | Barranco León - Level D2 | | Barranco León - Level E | | Fuente Nueva 3 - Level 5 | | Orce (1970-2000) | |
|---|---|---|---|---|---|---|---|---|---|---|
| MAT | 16.8°C | warm | 16.6°C | warm | 16.4°C | warm | 14.7°C | temp. | 12.9°C | temp. |
| Atmospheric t. range | 13.19°C | medium | 12.85°C | low | 12.56°C | low | 16.2°C | high | 20.3°C | very high |
| Summer t. | 2 m.>22°C | warm | 2 m.>22°C | warm | 2 m.>22°C | warm | 2 m.>22°C | warm | 2 n.>22°C | warm |
| Winter t. | MTC=10.7°C | mild | MTC=10.6°C | mild | TC=10.7 | mild | MTC=7.2°C | temp. | ATC=3.8°C | cold |
| MAP | 767 mm | low | 793 mm | low | 835 mm | abundant | 618 mm | low | 437 mm | low |
| Dist. of rainfall | irregular | winter | irregular | winter | irregular | winter | irregular | winter | irregular | winter |
| Type of p. | rain | | rain | | rain | | rain | | rain | |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Gaussen I. | 4 | Medit. | 4 | Medit. | 4 | Medit. | 4 | Medit. | 4 | Medit. |
| Lautensach-Mey | 4 | semi-a | 4 | semi-a. | 4 | semi-a. | 4 | semi-a. | 4 | semi-a. |
| Dantin-Revenga I. | 2.2 | semi-a. | 2.1 | semi-a. | 2 | semi-a. | 2.4 | semi-a. | 3 | semi-a. |
| De Martonne I. | 28.7 | semi-h. | 29.9 | semi-h. | 31.6 | humid | 25.1 | semi-h. | 19.1 | semi-a. |

Comparison with the current climatic data for the Orce region (Fig. 5B) shows the estimated MAT for BL (levels D1, D2 and E) to be higher than at present (ΔMAT = +3.9 ºC, + 3.6 ºC and +3.5 ºC respectively), with an increase in temperature in winter (ΔMTC = +8.4 ºC, + 8.5 ºC and +8.4 ºC respectively) and a decrease in summer (ΔMTW = -4.8 ºC, -5.3 ºC and -5.6 ºC respectively). The MAP is higher, as suggested by the values of the De Martonne aridity index, which for the BL levels are around 30 (humid/semi-humid climate), whereas currently in Orce the value is slightly below 20 (semi-arid climate). In the case of FN3-5, the estimated MAT is warmer (ΔMAT = +1.8 ºC). The temperature is warmer in winter (ΔMTC = +4.4 ºC) and colder in summer (ΔMTW = -2.7 ºC). The total rainfall is higher (ΔMAP = +180.4 mm) than at present, as suggested by the De Martonne aridity index, whose value exceeds 20 (semi-humid climate) at FN3-5. There are also differences in the distribution of precipitation over the year. The precipitation was more abundant during the early autumn and winter (October to February), whereas in spring and summer it was similar to present values, suggesting greater rainfall seasonality.

*4.2 Statistical analyses*

Despite the similarities in the climatic interpretation of the BL levels and FN3-5, independent-sample Student's *t*-tests show significant differences in terms of temperature

and precipitation between the respective means registered at the two sites (*t*-test, $p < 0.05$) (Table 3).

**Table 3**. Statistical comparisons between the means for the climatic parameters at BL (D1, D2 and E) and FN3 (level 5). *P*-value = probability of rejecting the null hypothesis ($p > 0.05$). Abbreviations: MAT = mean annual temperature, MAP = mean annual precipitation, and ns = not significant.

| **MAT** | | | |
|---|---|---|---|
| (*p*-values) | BL-D2 | BL-E | FN3-5 |
| BL-D1 | ns | <0.02 | < 0.02 |
| BL-D2 | | ns | <0.02 |
| BL-E | | | <0.05 |
| **MAP** | | | |
| (*p*-values) | BL-D2 | BL-E | FN3-5 |
| BL-D1 | ns | <0.01 | < 0.0001 |
| BL-D2 | | ns | <0.00001 |
| BL-E | | | <0.00001 |

## 5. Discussion

In light of the temperature and precipitation estimates obtained from levels BL-D1, D2, E and FN3-5 (Table 1), the following points are discussed below: *1*) the contribution of the results to what is known of the Early Pleistocene terrestrial climate; *2*) a comparison of our results with previous paleoclimatic and paleoenvironmental reconstructions of BL and FN3 based on other proxies; and *3*) the integration of our results into the recently proposed

ecological niche for the early hominins in western Europe, with a view to shedding light on their ecological tolerance.

*5.1 Early Pleistocene climate variability*

The climatic conditions in the southeastern Iberian Peninsula during the Early Pleistocene were under the influence of cyclical changes, fluctuating from long warm-humid phases ('interglacial') to short cold-dry phases ('glacial'), as attested by the pollen assemblages of the Palominas core (around 40 km from BL and FN3) (Altolaguirre et al., 2019, 2020). These studies show that the 'interglacial' periods were warmer than today, whereas the 'glacial' periods were characterized by temperatures close to those currently recorded. Results from pollen data also indicate that the oscillations in precipitation recorded between each phase were not extreme, which could have led to the development of mosaic environments during the 'glacial' phases. These observations are in agreement with our estimated climatic values. The higher temperature and precipitation values estimated for BL (levels D1, D2 and E) correspond to an 'interglacial' phase, whereas the lower temperature and precipitation values obtained for FN3 (level 5) correspond to a 'glacial' phase. This attribution is also inferred from the paleoenvironmental reconstructions based on the same paleoherpetofaunal assemblages carried out by Sánchez-Bandera et al. (2020), which show a predominance of woodlands at BL, with more humid, water-edge environments, compared with more open, drier, and rocky environments at FN3-5.

BL and FN3 span a time interval between ca. 1.4 and ca. 1.2 Ma, which, together with their paleoclimatic and paleoenvironmental characterization, allows us to link the analyzed levels with a globally warmer and wetter Early Pleistocene period attributable to phase 3 of Agustí et al. (2009). Accordingly, the warm and wet conditions of BL-D1, D2 and

E could correspond with an ‘interglacial’ stage, whereas the cold and dry conditions estimated at FN3-5 correspond with a ‘glacial’ stage within a globally warmer-wetter period on a larger time scale.

To situate the levels under analysis within an idealized model of Mediterranean glacial-interglacial vegetation cycles, we carefully adapted a Late Pleistocene environmental succession (following the glacial-interglacial model developed by Tzedakis, 2007), as no similar vegetation phase models were available for the Early Pleistocene. These latter interglacial-glacial cycle models for southern European sites (Tzedakis, 2007) show a pre-temperate phase of open woodland (a cool and dry phase), followed by a temperate phase, characterized by an early expansion of deciduous *Quercus*, Mediterranean sclerophylls, followed by *Carpinus*, *Ostrya*, *Abies*, *Fagus* and in some cases *Picea*, and a post-temperate phase (a cool and drier phase) of open woodland that occurred before the installation of a glacial steppe (a cold and dry phase).

The vegetation phases and their succession within a glacial-interglacial cycle, as proposed by Tzedakis (2007) for the Late Pleistocene, have been said to be similar to those recorded in the Early Pleistocene (e.g. Leroy et al., 2011), although the duration of these phases differed. Climatic oscillations during the Early Pleistocene prior to the Mid-Pleistocene Transition were less severe compared with those of the Middle and Late Pleistocene (Ehlers and Gibbard, 2008). True eccentricity-driven glacial phases like those of the Late Pleistocene did not take place during the Early Pleistocene, when cold and dry periods were weaker and shorter (Ehlers and Gibbard, 2008; Leroy et al., 2011; Altolaguirre et al., 2019). These periods would have been milder and more similar to modern ones, with shorter or even non-existent extreme glacial phases, characterized by widespread open landscapes and open forests, rather than steppe-like landscapes (Leroy et al., 2011; Altolaguirre et al., 2019).

When these paleoclimatic data are combined with data from Sánchez-Bandera et al. (2020) within this adapted glacial-interglacial model, we can tentatively correlate the analyzed succession of BL with the temperate phase. BL-D1 and D2 are associated with a relatively forested, warm, and humid phase (Fig. 5A), since the climate inferred in both levels is warm with a low atmospheric temperature range, and the resulting landscape consists of humid, Mediterranean-type woodland (23.3-28.3% open-humid; 25.6-28.3% woodland). Level E is correlated with a cool and humid phase with a more open and less forested landscape (Fig. 5A), as this level shows data corresponding to somewhat cooler conditions than BL-D1 and D2 and indicates an open landscape (46% open-dry) with humid and wooded areas (18% open-humid; 13% woodland). FN3-5 can be associated with an advanced cool and dry phase, with an open landscape and sparse woodland elements (Fig. 5A). The climate estimates suggesting a semi-arid continental Mediterranean climate are more in accordance with a cool and dry phase than with a cold and dry phase (a glacial maximum). The FN3-5 accumulation reveals the existence of an open and rather dry landscape (65% open-dry; 17.5% open-humid), as reconstructed by Sánchez-Bandera et al. (2020).

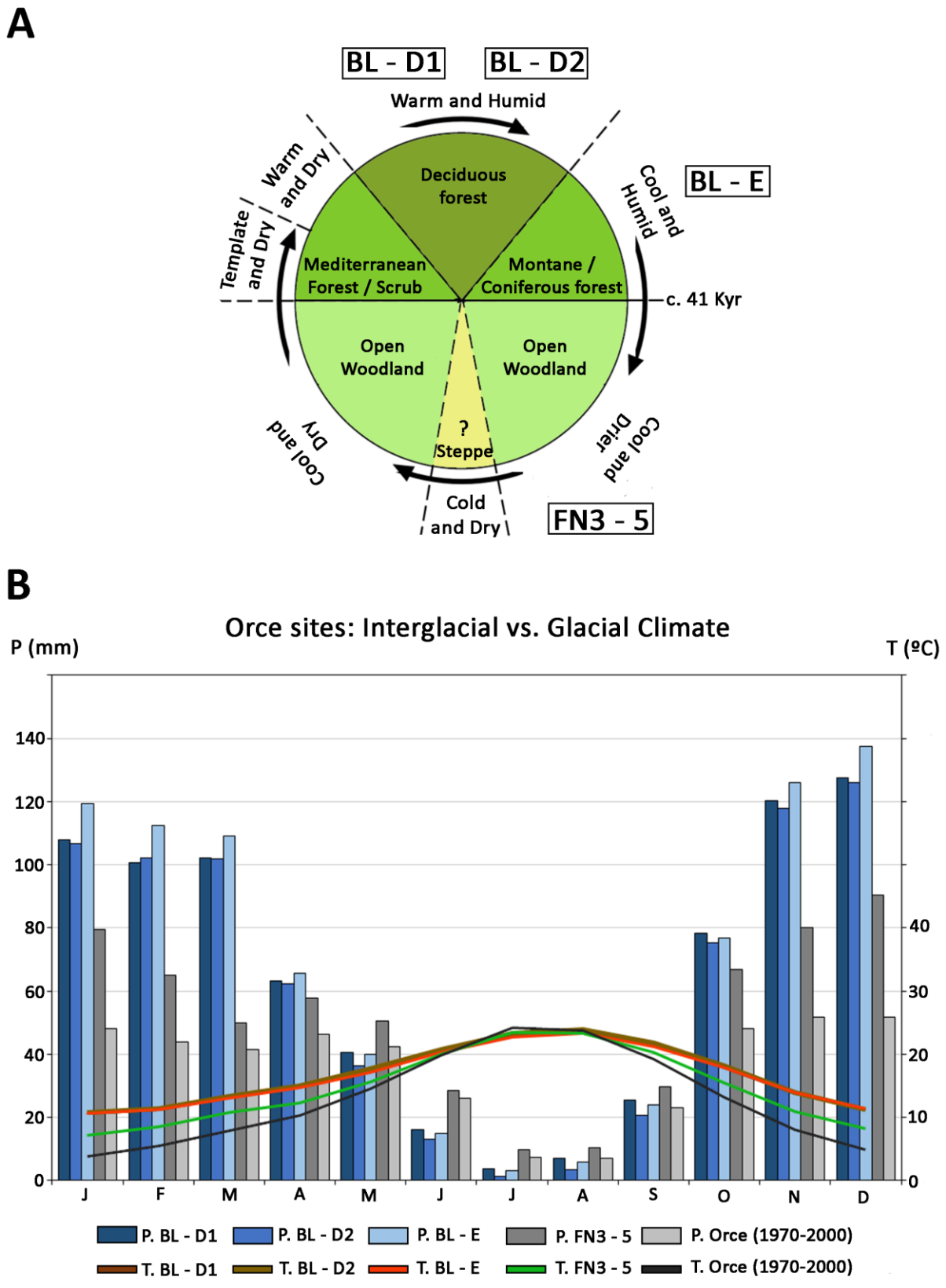


**Figure 5. A**: Correlation of levels D1, D2 and E of BL, and level 5 of FN3 with an idealized glacial-interglacial vegetation cycle based on a southern European model (modified from

Tzedakis, 2007). **B**: Comparative climatogram showing the quantitative climate reconstructions of levels D1, D2 and E of BL, and level 5 of FN3, plus the modern climate values for the Orce region (1970-2020; calculated from WorldClim 2.1 data, Fick and Hijmans, 2017), applying the scale P = 2 x T. Abbreviations: P = precipitation, T = temperature, MAT = mean annual temperature, and MAP = mean annual precipitation.

*5.2 Comparison with previous reconstructions for BL and FN3*

Our paleoclimatic results are in agreement with the other proxies from BL and FN3 and previous paleoclimatic studies. To date, only the microvertebrates and pollen have been studied paleoenvironmentally for each level.

As regards the microvertebrates, paleoclimatic and paleoenvironmental analysis have been performed. Our reconstructions are a step forward from previous paleoclimatic reconstructions based on the herpetofaunal assemblages carried out by Blain et al. (2011, 2016a), at a time when microvertebrates were not recovered in a well-constrained stratigraphical context. The calculated MAT for BL is 16.8 ºC and MAP 700 mm (16.9 ºC and 741 in Blain et al., 2011), and for FN3 MAT 16.4 ºC and MAP 738 mm (16 ºC and 753 mm in Blain et al., 2011) (Table 4). These authors suggest a very similar climatic context for both sites, characterized by warm and humid Mediterranean climate, in agreement with our results. Our stratigraphically constrained reconstructions allowed us to individually analyse the archaeological level 5 of FN3, which shows colder temperatures and drier conditions than previously reported considering all the levels together.

A paleoenvironmental characterization of levels D1 and D2 of BL was performed on the basis of a reduced number of amphibians, reptiles, and micromammals by means of the habitat weighting method (Agustí et al., 2015a). The results demonstrate the

presence of significant bodies of water when both levels were formed and show that an open landscape was always present in the area surrounding the lake. The results from level D1 reveal a predominance of woodland elements (35%), followed by open humid (27.1%), rocky (20%), and open dry elements (17.9%), whereas the results for level D2 show open humid elements (41.2%) to be predominant, followed by woodland elements (30%) and open dry elements (27.1%), with a few small mammals characteristic of rocky habitats (3.8%). These results suggest a possible tendency toward more humid conditions, with a greater prevalence of woodland elements moving upward from the base of the stratigraphic sequence. More recent results for these same levels (Sánchez-Bandera et al., 2020), also including data for level E, show a slight increase in woodland elements (25.7% in level D1 as opposed to 28.3% in D2), together with an increase in arid conditions in level D2 (28.3%) compared with D1 (25.6%). Nevertheless, taken in conjunction with the results from level E, which indicate 46% open-dry elements and 13% woodland elements, the stratigraphic sequence of BL shows a tendency toward more arid conditions with a lower woodland density (Sánchez-Bandera et al., 2020). Regarding FN3, there are two taxa that are ubiquitous at the site: *M. savini* and *M. orcensis*, the latter being a new species that has also been identified at the Early Pleistocene site of Quibas (Murcia, Spain) (Agustí et al., 2022). *M. savini* is the direct ancestor of *Arvicola*, the water vole, and as such it can be presumed to have had aquatic habits, implying the presence of water. By contrast, *M. orcensis* is a hypsodont species without tooth roots that is practically absent from BL, yet it is the only arvicolid present at Quibas where there is scarcely a trace of water (Piñero et al., 2016). Accordingly, we assume that *M. orcensis* was an ubiquitous form or a species adapted to open environments. Given the further presence of *Allophaiomys* aff. *lavocati*, we suggest that FN3 was a more open and less aquatic habitat than BL.

Pollen studies have been performed for BL (levels A5, D1, D2 and E2) and for FN3 (levels 1 to 7) (Ochando et al., 2022). The pollen spectra of BL suggest open

Mediterranean formations with a particular abundance of junipers and a significant presence of oaks, pines, and olives. The presence of *Pistacea* in levels A5, D1 and E2 indicates that the climate was not excessively severe (Altolaguirre et al., 2019). For FN3, the pollen signal seems to reflect a mosaic landscape inherent to high geodiversity or to riverine valleys, depressions, and lacustrine valleys. Amaranthaceae is abundant in FN3 and probably reflects saline soils in the catchment area, which would have extended during dry phases such as those represented by levels 4 and 5, where an opening of the local landscape may have occurred. The authors note that comparing the BL and FN3 pollen records is challenging due to variations in sampling resolution, but the general situation in both sites suggests the coexistence of a mosaic of vegetation including mixed oak-pine forests, juniper-dominated formations, a prevalence of Mediterranean summer-drought conditioned vegetation, and a relatively high diversity of trees indicative of a glacial refuge. Both xerophytic scrub and riparian forests developed in the vicinity of the sites. This characterization of the vegetation fits with the paleoenvironmental reconstructions based on microvertebrates and with the paleoclimatic reconstructions presented here, supporting the presence of a more open and drier habitat in FN3 than in BL, and milder climatic conditions in BL, especially in level D1.

The reconstructions of the vegetation type and climate in BL and FN3 based on large-mammal ecometrics are in broad agreement with the more detailed paleoenvironmental and vegetation reconstructions based on microvertebrates and pollen, although the large-mammal communities lack the resolution necessary to distinguish paleoenvironmental differences between the layers in BL and FN3. Similarly, the estimates obtained from microvertebrates and large-mammal ecometrics indicate environments that were – in terms of temperature – similar to or warmer than at present. Whereas the estimated precipitation values indicate a semi-arid (or semi-humid) climate, all the models indicate higher precipitation for both BL and FN3 than in the area today (Saarinen et al., 2021a). The large-mammal-based

estimates suggest that BL and FN3 are similar, but the presence of *Ammotragus europaeus* with its plain selenodont dental pattern suggests FN3 slightly more arid than BL, consistent with the climatic estimates based on small vertebrates. The broad vegetation type inferred from the large-mammal ecometrics for both BL and FN3 is Mediterranean woodland with productivity slightly higher than at present, which probably reflects the presence of permanent groundwater sources sustaining wetlands and riparian wooded vegetation. Grazing ungulates are rare in BL and FN3, with only *E. altidens* showing a grass-dominated mixed-feeding dietary signal (which is more mixed than that of most other populations of this typically grazing equid; Saarinen et al., 2021a, b). The quantitative climate estimates provided in Saarinen et al. (2021a) for both sites (MAT = 20.7 º C and MAP = 602 mm; Table 4), differ from our results. This is due to *i*) the differences in the resolution degree between herpetofauna and large-mammals species as paleoecological proxies, and *ii*) in Saarinen et al. (2021a) the sites are analysed broadly, without taking into account the different levels. This is because again stratigraphical context is not always available for old excavation campaigns, from where part of the studied material comes. Nevertheless, our more constrained reconstructions fit within the paleoclimatic characterization suggested in Saarinen et al. (2021a) for both BL and FN3, indicating a Mediterranean climate with similar to or warmer temperatures and higher precipitations than at present.

Additionally, isotopic analyses were performed on tooth enamel powders collected from herbivorous mammal specimens (including cervids, bovids, equids, rhinoceros, hippopotamus, and mammoths) from the Venta Micena, BL and FN3 sites (Bocherens et al., 2020). Carbon isotope results from the three sites show that the plants foraged by herbivores were essentially C3 species (trees, shrubs, and C3-grass adapted to a mild growth season), which is consistent with tooth wear results indicating browsing or mixed feeding, with a preference for browsing in most cases. The consumption of C4 plants by some herbivores has

been detected only in BL, which is in agreement with ecometric and herpetofaunal results indicating a particularly wet and warm climate for this site compared to both others. In addition, in the context of a Mediterranean climate with four-month aridity in summer, isotopic variations within teeth suggest significant changes in foraging over the course of a year. This could be related to local seasonal changes or mobility across areas with different vegetation types. This broad climate characterization of BL and FN3 may be related with the globally warm and humid phase 3 described by Agustí et al. (2009) for between 1.4 and 1.1 Ma. Our new stratigraphically constrained paleoclimatic reconstructions reveal some glacial-interglacial variability within this wider Early Pleistocene warm and humid period.

**Table 4.** Comparison between the results of the present study and the previous paleoclimatic estimates obtained for BL and FN3. Estimates by Blain et al. (2011, 2016a) are based on paleoherpetofauna and estimates by Saarinen et al. (2021a) are based on the ecometric of ungulates. Mean +/- SD range values in parenthesis. *Confidence intervals for working with the model fit are effectively zero (perfectly confident in terms of sampling). There are, of course, uncertainties in the data, but they are not due to a small sample (Oksanen et al., 2019). Abbreviations: MAT = mean annual temperature (in °C), and MAP = mean annual precipitation (in mm).

| **MAT (in °C)** | | | | |
|---|---|---|---|---|
| **Site** | **BL** | | | **FN3** |
| Blain et al. (2011) | D<br>16.9<br>(14.0-18.5) | | - | 16.0<br>(9.0-18.5) |
| Blain et al. (2016a) | D<br>16.8<br>(15.0-18.5) | | - | 16.4<br>(12.0-18.5) |
| Saarinen et al. (2021a) | 20.7* | | | 20.7* |
| **This study** | D1 | D2 | E | 5 |

| | | | | |
|---|---|---|---|---|
| | **16.8** (14.7-17.8) | **16.6** (14.1-17.8) | **16.4** (13.3-17.8) | **14.7** (7.8-18.4) |

| **MAP (in mm)** | | | | |
|---|---|---|---|---|
| **Site** | **BL** | | | **FN3** |
| Blain et al. (2011) | D | | - | 753 (400-1500) |
| | 741 (400-1000) | | | |
| Blain et al. (2016a) | D | | - | 738 (500-1200) |
| | 700 (500-1100) | | | |
| Saarinen et al. (2021a) | 602* | | | 602* |
| **This study** | D1 | D2 | E | 5 |
| | **767** (467-974) | **793** (467-1113) | **835** (467-1593) | **618** (328-1818) |

*5.3 New insights into the early hominin ecological niche*

The new climatic estimates presented in this work update the association of BL and FN3 with the 'Iberian' ecological model. Blain et al. (2021) suggest that BL and FN3 can be considered exceptions due to their low precipitation and high temperatures (following the data provided by Blain et al., 2016a) and their percentage of forest cover of around 25%, which is more indicative of a relatively open landscape than a dense forest. All these factors run counter to the 'Iberian' ecological model. Our results for BL (levels D1, D2 and E) show similar temperatures to those proposed by Blain et al. (2021) and somewhat higher precipitation (+67, +93 and +135 mm, respectively), which would be closer to the climate space of the 'Iberian' ecological model but still rather low. In the case of FN3-5, the new estimates show colder temperatures (-1.8 ºC) and drier conditions (-120 mm) than previously estimated, still slightly drier than the reconstructed hominin climate space. This new, drier characterization of FN3-5 emphasizes the difference between this specific level and the 'Iberian' ecological model. Nevertheless, the permanence of the lake system and fresh water sources documented (El Hamouti and Gibert, 2012; Anadón et al., 2015; Granados et al.,

2021), together with its associated marshland vegetation, could have compensated the scarcity of rainfall during most of the year, providing early hominins with a stable source of plant food (Altolaguirre et al., 2021). On the other hand, the area generated for the potential distribution of early hominins by Blain et al. (2021) suggests that the Iberian Peninsula, though presenting inhospitable continental areas, also had large favorable areas covering the Atlantic seashore of northern Portugal and Galicia, the Cantabrian Range, the area around the Pyrenees, and the southernmost area of the Peninsula near the Strait of Gibraltar. The areas obtained by MER overlaps are in agreement with these potential distribution inferences. The overlaps obtained from BL-D1, D2 and E are predominantly located on the Atlantic seashore of northern Portugal and Galicia and at the southernmost point of the Peninsula (Fig. 3), whereas the overlaps from FN3-5, though showing a more generalist distribution, are mainly concentrated in the west and southwest of the Iberian Peninsula (Fig. 3), near these inferred potentially favorable areas.

Another issue to be discussed is the delay observed in the first hominin settlement in western Europe. Prior to this globally warm and humid period (phase 3, according to Agustí et al., 2009), an Early Pleistocene cold and dry period is well documented in sites such as Bagur 2 (Girona, Spain) and the Pirro Nord karstic complex (ca. 1.5 Ma, southern Italy). This globally colder period, coeval with the Iberian locality of Venta Micena (ca. 1.6 Ma) (Guadix-Baza Basin), which also lacks a hominin record, corresponds to phase 2 of Agustí et al. (2009). This cold, dry period has been argued to be the putative factor that delayed the first occupation of Europe, after the warm but dry climate conditions registered at sites like Dmanisi (Georgia) (Blain et al., 2014, 2022) or the coeval Barranco de los Conejos (Guadix-Baza Basin) (Agustí et al., 2009, 2010b, 2013). To date, quantitative estimates of temperature and precipitation for the globally cold, dry Early Pleistocene period with which we compare our data are only available for the Pirro Nord sites (except PN13, which is not yet fully studied, Blain et al., 2019c). FN3-5, despite the cold and dry conditions estimated, shows a warmer

annual temperature (+2 ºC) and lower annual precipitation values (-109 mm) than the mean of the coldest and driest Pirro Nord sites (i.e., PN2, PN5b, PN11 and PN12; Blain et al., 2019a), and also a somewhat warmer annual temperature (+1 ºC) and lower annual precipitation values (-132 mm) than the mean of the warmer and wetter Pirro Nord sites (i.e., PN1, PN5, PN9, PN16 and PN17; Blain et al., 2019a). Accordingly, the data available for the Venta Micena and Pirro Nord sites (which are older localities than BL and FN3) seem to indicate a colder and drier environmental scenario than that proposed for BL and, to a lesser extent, FN3, these latter sites occurring in the context of a globally warmer and more humid (interglacial) phase.

Cold, dry conditions have been documented at the FN3-5, Bagur 2, Pirro Nord and Venta Micena sites, yet a hominin presence has only been evidenced in FN3-5. The hominin presence in the latter site is likely to reflect the fact that hominins were already present in the Guadix-Baza Basin, as is attested in BL (at ca. 1.4 Ma), whereas their absence from other western European sites (at ca. 1.5 Ma) may be associated more with the difficulties of reaching these places due to the globally cold conditions registered during the 1.8–1.4 Ma time interval in Europe (Agustí et al., 2009; Blain et al., 2021). Once hominins were established in the Guadix-Baza Basin, the presence of terrestrial aquatic environments and wetlands with fresh water sources (El Hamouti and Gibert, 2012; Anadón et al., 2015) might well have helped them to persist when the climatic conditions became colder and drier (Altolaguirre et al., 2021).

## 6. Conclusions

Our results shed light on the ecological tolerance of early hominins, improving our understanding of their distribution and the delays observed in their dispersal across western Eurasia. There are no other archaeological sites in the Iberian Peninsula with similar climatic conditions during the Early Pleistocene to those of BL and FN3. These localities, with the

oldest evidence of humans recorded, are thus underlined as key sites. Even so, a larger herpetofaunal sample is needed from other levels of FN3 in order to establish whether the tendency toward aridity inferred paleoenvironmentally in Sánchez-Bandera et al. (2020) was continuous, or whether the FN3 sequence corresponds to a multi-cyclical paleoclimatic model. We suggest that Early Pleistocene hominins, though conditioned to some extent by climatic factors, were able to cope with changing climatic and environmental conditions, both 'interglacial' and 'glacial', within a globally warm and humid period in the southwestern extremity of the European continent. The conclusions are as follows:

1. BL exhibits a warm and humid/semi-humid climate during the accumulation of levels D1 and D2, and a warm (but cooler) and humid climate during level E. These climatic conditions are indicative of a warm ('interglacial') phase within the variability of the Early Pleistocene climate, whereas FN3-5 is reconstructed as cold and semi-humid, correlating with a cold ('glacial') phase.

2. For the first time, quantitative estimates of temperature and precipitation are provided to show the 'glacial'-'interglacial' variability of the late Early Pleistocene climate within a composite archaeopaleontological stratigraphic sequence.

3. The projection of the niche envelope of "exotic" or "extinct" taxa over previously established MER overlaps represents an improvement on previous MER procedures, making it possible to include in the analysis taxa that are currently absent from the geographical extension under analysis.

4. These new paleoclimatic results are consistent with previous reconstructions, which indicate a humid, wooded biotope for BL and a more open, drier biotope for FN3-5. This suggests that late Early Pleistocene hominins, though conditioned to some degree by climatic factors, were able to deal with changing climatic and environmental conditions in the southwest of the European continent.

## Author statement

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