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Upper Palaeolithic hunter–gatherer societies in the Basque Country (Iberian Peninsula) in the light of palaeoenvironmental dynamics in the last Glacial Period: cultural adaptations and the use of biotic resources

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Abstract

Upper Palaeolithic archaeological sites in the Basque Country have been excavated for over a century. They have yielded a rich palaeoenvironmental record with zoological and botanical remains that have been obtained in stratigraphic series dated precisely by radiocarbon. This information reveals cyclical environmental changes from climates similar to today to drier and extremely cold conditions, when species in current boreal biomes and others now extinct but with similar ecological preferences were present in the region. Moreover, the archaeological sites have provided high-resolution information about the resilience mechanisms of the communities of our own human species. This information allows us to increase the corpus of palaeoclimate data regarding the Marine Isotopic Stage (MIS) 2 and MIS 3 for a critical region within the human population of Eurasia. The aim of this paper is to show how an extraordinary capacity for adaptation to drastic climate changes Upper Palaeolithic hunter–gatherer societies displayed, even though their subsistence depended on biotic resources that alter rapidly.

1. Geographic framework and setting

Cantabrian region, in the northwest of the Iberian Peninsula, forms a cul-de-sac between the Bay of Biscay and the Cantabrian Mountains, with peaks reaching to over 2600 m a.s.l. Geographically, this range represents the prolongation of the Pyrenees, similarly on a general eastwest alignment. However, at the western end of the Pyrenees and the easternmost part of the Cantabrian Mountains, altitudes are lower, with passes at ~600 and 700 m separating the Atlantic part of the Basque Country from the Mediterranean side and the Ebro valley. Different sources of high-quality flint are known on both sides of the watershed (García-Rojas and others, 2020), as well as their distribution in both Atlantic and Mediterranean Palaeolithic deposits. Since the circulation of human groups and animals on both sides of the Pyrenees is also well-known, the Basque Country has gradually lost its character as a corridor with no way out to become a meeting of ways, the so-called Basque Crossroads (Arrizabalaga, 2007; Arrizabalaga and others, 2016). With this name, a broad region on both sides of the Pyrenees leads in different directions (Fig. 1) to a variety of biomes (Cantabrian Spain, northern Iberian plateau, Ebro valley, Pyrenean Piedmont and Aquitaine) where populations and ideas circulated between the Iberian Peninsula and the rest of Europe during the Palaeolithic.

Dated back to ~43 000 cal BP (Higham and others, 2014; Wood and others, 2014), the first technocomplex assigned to the Upper Palaeolithic in this region, the Chatelperronian, has been detected at such sites as Labeko Koba (Arrizabalaga and Altuna, 2000), Ekain (Altuna and Merino, 1984) and Aranbaltza (Rios-Garaizar and others, 2022) (Fig. 1). Four main technocomplexes succeeded it during the Late Marine Isotopic Stage (MIS) 3 and the MIS 2 (Aurignacian, between 41 000 and 32 000 cal BP; Gravettian, between 32 000 and 22 000 cal BP; Solutrean, between 22 000 and 17 500 cal BP and Magdalenian, between 17 500 and 12 000 cal BP: all dates are approximate, based on averages of calibrated radiocarbon sets, such as Marín-Arroyo and others, 2018). These are defined techno-typologically based on the kinds of tools and weapons the human groups made from different types of stone and organic materials like bone, antlers and shells. They also worked with other organic raw materials of both animal origin (hides, tendons, intestines, etc.) and plants (wood, roots, barks, leaves, etc.), but their perishable nature does not allow them to be preserved in our archaeological deposits.

During this long period of time, over 30 000 years, the climate often changed, sometimes to extreme conditions, especially in the coldest phases (Iriarte-Chiapusso and others, 2005, 2016*a*, 2016*b*; Garcia-Ibaibarriaga and others, 2019; Oliva and others, 2019; Bartolomé and others, 2021). This paper will review how multiproxy information, mainly from archaeological sites, is analysed to achieve a detailed palaeoenvironmental reconstruction of the prehistoric

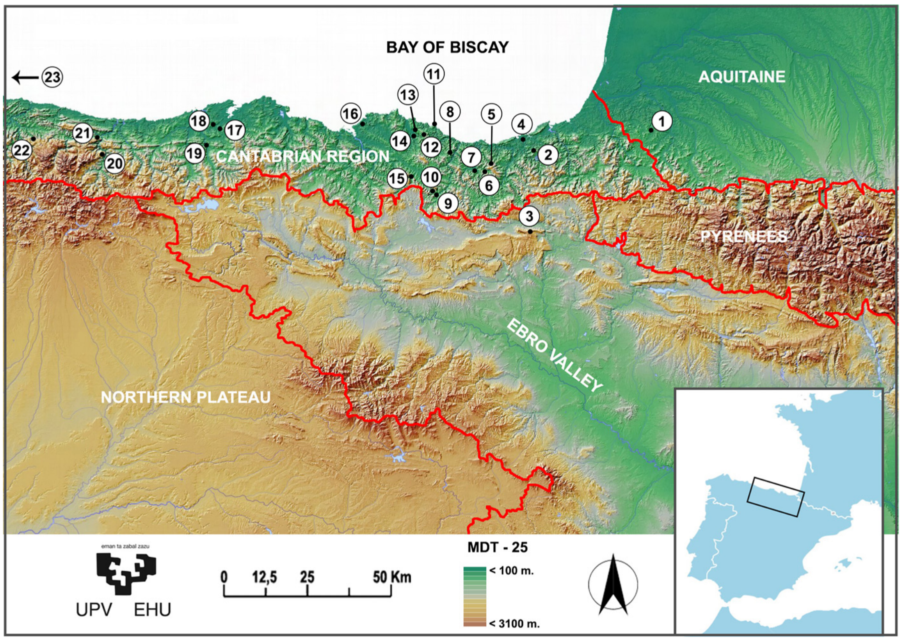

Figure 1. Main sites mentioned along the text: (1) Isturitz cave, (2) Aitzbitarte III cave, (3) Mugarduia Sur Flint workshop site, (4) Ametzagaina camp site, (5) Erralla cave, (6) Amalda cave, (7) Ekain cave, (8) Kiputz palaeontological site, (9) Labeko Koba cave, (10) Lezetxiki cave, (11) Santa Catalina cave, (12) Ondaro cave, (13) Antoliñako Koba cave, (14) Santimamiñe cave, (15) Bolinkoba cave, (16) Aranbaltza camp site, (17) Morín cave, (18) El Pendo cave, (19) El Castillo cave, (20) El Esquilléu cave, (21) Coimbre cave, (22). La Güelga cave, (23) Área Longa limnetic deposit.

past. In a few cases, other types of deposits not formed by humans, such as peat bogs, wetlands and natural traps, are able to add to the volume of data being analysed. In addition, this paper tries to show the resilience that hunter–gatherer societies incorporate into their socio-economic and cultural behaviours to overcome the challenges that arise from a hostile environment.

2. Multiproxy analysis

The palaeoenvironmental analysis is based on the study and interpretation of the sedimentary record through analytical disciplines grouped in different fields, such as geoarchaeology (referring to the sedimentary processes observed), archaeobotany (study of the fossilised remains of plants) and archaeozoology (analysis of evidence of vertebrate and invertebrate animal species). These disciplines obtain results that can be contextualised through their stratigraphic position or by different dating techniques, the main one of which is radiocarbon, applied to their coetaneous context.

This geochronological framing is able to place the information in a sequence and also correlate it with the principal palaeoclimate cores. Since it was developed by Libby (1952), radiocarbon has become the key dating technique for the Upper Palaeolithic in Eurasia. It is a practically universal method (Currie, 2004; Wood, 2015), as modern protocols allow ages of 50 000 BP to be reached, and organic materials like bone and charcoal, which are commonly found at archaeological sites, can be dated. In recent decades, two methodological procedures have improved the precision of the method and enlarged the possibilities of its application. The first was the use of accelerator mass spectrometry, or AMS, which reduced the amount of material that could be dated (Bennett and others, 1977), and the second was the pre-treatment of samples by the ultrafiltration or ABOx techniques, which eliminated contaminating elements that alter the results to a more recent date than the real one (Hedges and others, 1989). With these three consecutive methodological developments, it is now possible to reconstruct the MIS 3 and MIS 2 in southwest Europe with almost calendar-like precision (Reimer and others, 2020). Bayesian modelling has been especially successful in detecting hiatus of data and to fill information in transitional periods.

Geoarchaeology applies the concepts, techniques and knowledge of earth sciences to the study of the processes involved in the creation of the archaeological and/or natural record (Rapp and Hill, 1998). In addition to the macroscopic description of the sedimentary sequence or traditional quantitative sedimentology, micromorphology is another pillar of geoarchaeology. This technique analyses compact sediment samples with microscopic precision to determine the processes and evolution of soils. The samples are extracted from the archaeological section or natural soils without altering them so that thin-sections can be made from them. These are then observed by optical and electronic microscopy to identify the formation of the soil or sediment (Fig. 2). This is linked with its origin as a way to approach the stratigraphic record (Rapp, 1975; Butzer, 1982; Courty and others, 1989; Solé, 1990; Waters, 1992; Rapp and Hill, 1998; Stoops, 2003; Goldberg and Macphail, 2006). Different source areas of the sediments can be identified, as well as important data about the context in which the artefacts, excavated structures and natural deposits are found. This information about the relationship between humans and their environment can define and characterise areas and types of land-use and of raw materials.

Archaeozoology follows slightly different methodological protocols by studying faunal remains. Although remains of molluscs, crustaceans and other invertebrate species may be found, the main attention is focused on vertebrates, differentiated into large and small animals. The study of the remains of large vertebrates consists firstly of taxonomic identification of the remains using reference collections and anatomy atlases (Barone, 1976; Pales and García, 1981). This is followed by biometric analysis (von den Driesch, 1976), in which indeterminable remains are grouped into categories based on their size and weight (Bunn, 1986). In this way, the number of remains, number of specimens, minimum number of individuals and minimum number of elements in the assemblage can be calculated (Grayson, 1984; Klein and Cruz-Uribe, 1984; Lyman, 1994). Finally, macrofauna studies are completed by taphonomic analysis in order to understand the role of humans, carnivores and post-depositional phenomena in the formation of the archaeological deposit (Behrensmeyer, 1978; Villa and Mahieu, 1991; Lyman, 1994; Fernández-Jalvo and Andrews, 2016; Marín-Arroyo and Sanz-Royo, 2022).

For small vertebrates, various methods are used to process the sediment extracted in archaeological and/or palaeontological excavations in order to recover small remains (from classic dry

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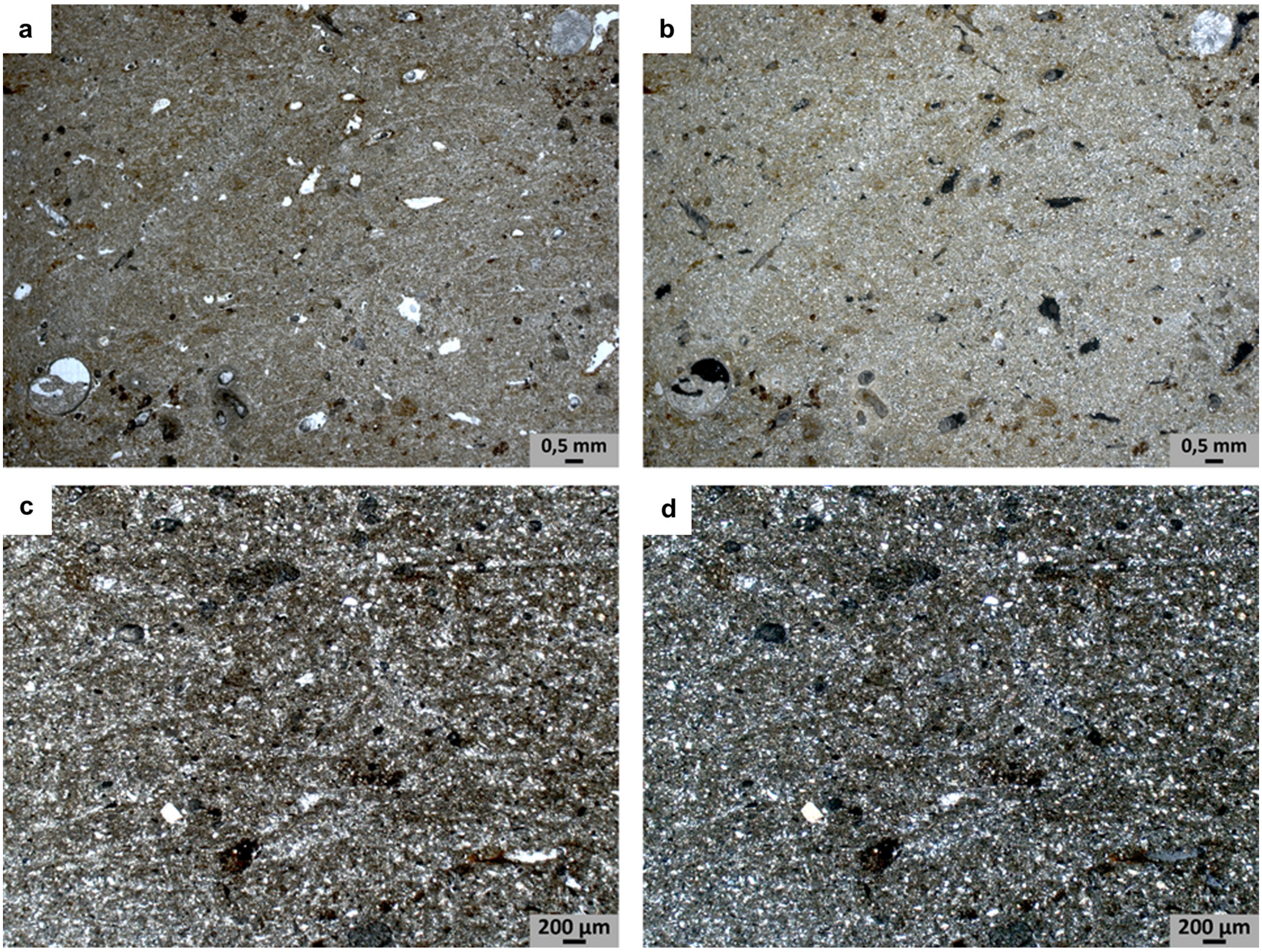

Figure 2. (a–d) Pictures showing micromorphology samples suggesting cold weather conditions in the correlated sediments. The four microphotographs belong to repeated episodes of cryoturbation during sedimentation (Arenaza cave). They are characterised by lenticular and laminated microstructure. The high pressures induced by the crystallisation produced in the ice are crucial for the physical fragmentation of the coarse limestone elements. That is why repeated freezing has favoured the fragmentation of these elements and the fragmentation of fine sediment particles. It has been possible to alter the sediment's size and original colour. In the thawing process, the calcium carbonate precipitated at this time is present in thin micritic coatings and sparitic cavity fillings. In addition, this association with thawing times may be critical to algae growth. That is why some limestone fragments and the basal mass present a lenticular microstructure, where different colours can be seen, indicating that freezing-thawing has occurred at o times (by the authors).

sieving to water screening), since the recovery of the material is the most variable part of the methodology. In order to avoid the loss of the smallest remains of some species, which would distort the palaeoenvironmental information, it is essential that the smallest mesh size should not exceed 0.5 mm. Using a stereomicroscope, the disarticulated bone fragments and isolated teeth are separated from the concentrates, classified, quantified and photographed. Once all the fossil remains have been separated, the next step is to group them according to anatomical criteria and determine their taxonomy (Fig. 3). Along with current material from several reference collections, we can draw on an abundance of specialised bibliographies (such as Bailon, 1991 or Chaline and others, 1974). The taxonomic classification for small mammals is in accordance with Wilson and Reeder (2005), and the systematic nomenclature used for amphibians and reptiles is based on Speybroeck and others (2010). Specific taxonomic attributions are based mainly on the best cranial and/or postcranial diagnostic elements: isolated teeth for the lagomorphs; isolated teeth and mandibles for the rodents (first lower molars for the Arvicolinae); isolated teeth, mandibles and postcranial skeleton for the insectivores; the vertebrae for newts, lacertids and snakes; vertebrae, dental material and osteoderms for *Anguis fragilis*; and the humerus, the ilium and the scapula for the anurans. Palaeoclimate and palaeoenvironmental inferences from microvertebrate fossils are based on knowledge of modern ecological preferences, following the International Union for Conservation of Nature (2022) or Sesé (2016), among others.

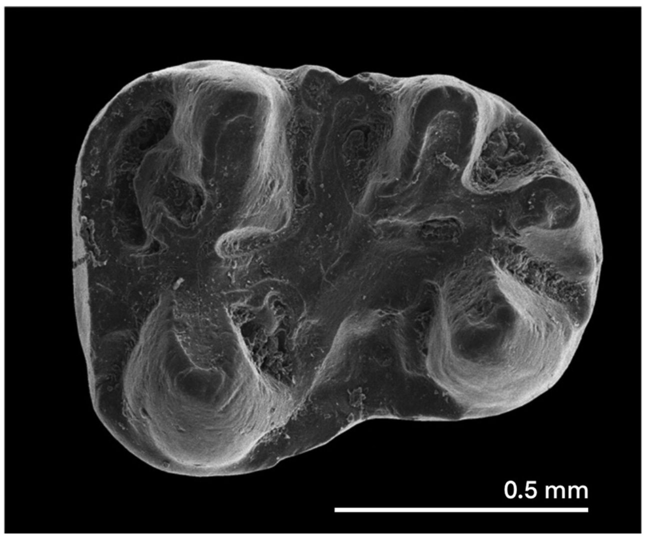

Figure 3. Right first lower molar of *Sicista betulina* from Lezetxiki II (by the authors).

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Palaeobotany is a more inclusive discipline than Archaeobotany, as it includes the study of fossilised botanic remains preserved not only in archaeological sites but in other kinds of deposits (lakes, peat bogs, natural traps, moraines, etc.) to which humans did not contribute directly. Although it includes multiple disciplines related to the identification and interpretation of botanic remains (charcoal, seeds, tubers, diatomic algae, wood, pollen, etc.), in the oldest deposits, it is only usual to find pieces of charcoal and fossilised pollen. In both cases, the analytical protocol comprises sampling, separation of the fossil remains, their identification and graphic representation. The characterisation of the vegetation and its changes during the Upper Pleistocene is accomplished by the study of these remains preserved in the sediment. The information obtained is related directly to the characteristics of each kind of remains (fragments of wood, seeds, fruit, pollen, spores, etc.) and to the sedimentary context in which they were deposited. For this reason, in the geographic area of study, most of our knowledge about changes in the plant communities in the Upper Pleistocene comes from the discipline of palaeo-palynology (the study of fossil pollen and spores) applied to archaeological deposits whose sequences usually cover the longest spans of time (Fig. 4). It was precisely the interest in understanding the kind of environment in which Palaeolithic communities lived that spurred archaeology to apply this discipline to the sites being studied (Leroi-Gourhan, 1959; Boyer-Klein, 1984; Dupré, 1988). Better preservation of the archaeological record in caves and rock shelters means that open-air occupations (affected more by post-depositional processes) are under-represented. Nonetheless, palynological studies of those kinds of sites are achieving highly significant data (Iriarte-Chiapusso and others, 2016*a*, 2016*b*). In the case of non-anthropic deposits, like peat bogs and wetlands, the availability of information decreases significantly because of the lack of long Upper Pleistocene sequences; it was at the end of that period that some peat bogs in the western Pyrenees began to form (Ayerdi, 2022). In contrast, potholes have acted as natural traps for wildlife and have provided interesting information about flora and fauna at different periods in the MIS 5, 4 and 3 (Castaños and others, 2014; Suárez-Bilbao and others, 2016–2017).

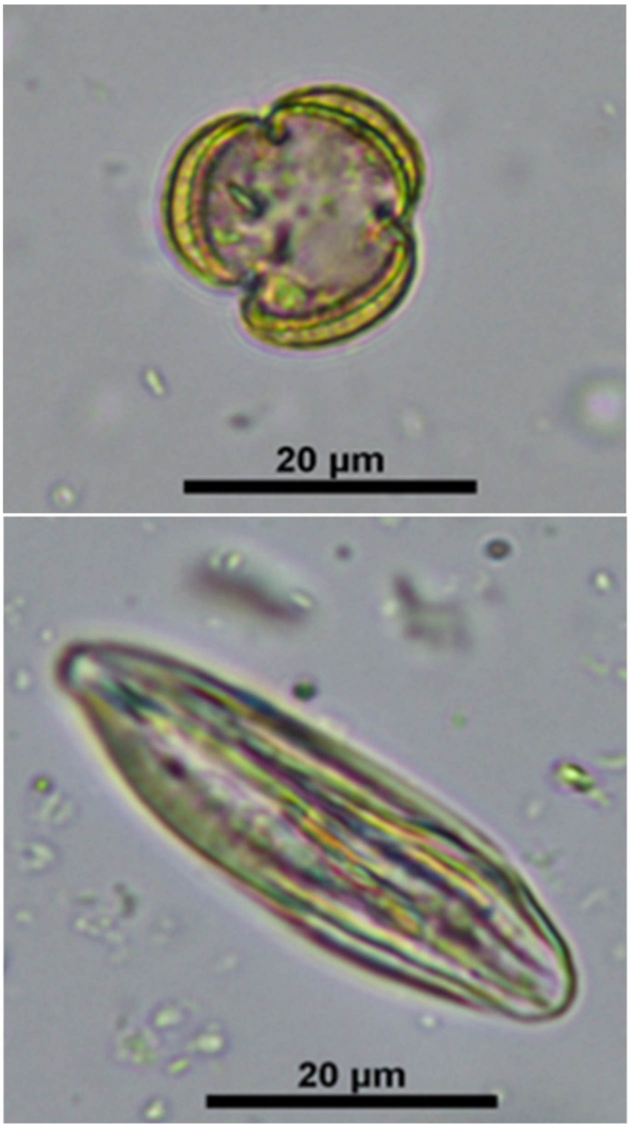

Figure 4. Pollen grains of *Artemisia* (top) and *Ephedra* (bottom) (steppic plants) from the site of Labeko Koba (by the authors).

Large plant remains do not survive so well and therefore are not usually found unless they have been carbonised. Even under that condition, it is difficult to unearth Palaeolithic seeds and/or fruit, apart from the part of the shells that protects the fruit, as in the case of hazelnuts (Arrizabalaga and others, 2003*a*, 2003*b*). Fragments of charred wood come from hearths and provide information about the fuel that human groups selected for their fires. Very rarely, when the site is located in an area of wetlands, wooden tools shaped by humans have been found, although dated in an earlier period than covered by this paper (MIS 5) (Rios-Garaizar and others, 2018).

3. Unravelling the information

One of the most transcendental moments in our history occurred during the chronological framework of the MIS 3 isotope stage: our species (*Homo sapiens*) became the only representative of the *Homo* genus in Europe. The replacement took place in very different biogeographic areas and a very complex climatic period, defined by a relatively rapid succession of climate events, as regionally shown in the archaeological site of Labeko Koba (Arrizabalaga and Altuna, 2000). The alternate stadial and interstadial phases would cause significant variations to the landscape in relatively short periods of time. Several good diachronic series are available in our region, and this paper will add new information to them (Garcia-Ibaibarriaga and others, 2019; Cascalheira and others, 2021; Arrizabalaga and others, 2021).

Although no continuous sequences cover the whole of the MIS 3, some natural deposits, like Area Longa Beach (northwest Iberian Peninsula), record the complexity of the period (Fig. 1). The palynological study determined that three warmer woodland phases alternated with periods of more open vegetation. However, these interstadials were not as warm as interstadials MIS 5b and 5c, and the cold phases were not as cold as MIS 4 and MIS 2 (Gómez-Orellana and others, 2007).

The archaeological site of Labeko Koba (Arrasate, Gipuzkoa) provides another example. Around 42 500 BP, carnivores used the shaft of Labeko Koba as a den, while the occasional human presence (Chatelperronian) may have been motivated by opportunities to scavenge meat, marrow, hide, horn or bone from carcasses left in the cave by the carnivores. While the landscape was characterised by the absence of large forests, the composition of the woodland, which included deciduous species such as hazel, oak and chestnut, indicates that the occupants lived under conditions of climate amelioration (interstadial). However, 1500 years later, the landscape would be dominated by grasses and shrubs, with some cryo-xerophilous taxa (*Artemisa* and *Ephedra*), reflecting a dry and cold climate at that time. In this open landscape lived mammoths, woolly rhinoceros, marmots, arctic foxes, reindeers, etc. (Altuna and Mariezkurrena, 2000; Iriarte-Chiapusso, 2000).

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No micromorphological information is available for that area at that time, but other studies in the Cantabrian region (e.g. the caves of La Güelga, in Cangas de Onís, Asturias; Morín, in Villaescusa, Cantabria; El Pendo, in Camargo, Cantabria and El Castillo, in Puente Viesgo, Cantabria, Fig. 1) have shown that the succession of stadial and interstadial phases during that time was drastic and the main cold phases were not only severe but had geomorphological consequences (Hoyos and Laville, 1982; Maíllo-Fernández and others, 2016; Kehl and others, 2018).

In the Gravettian period, human populations continued to adapt to the environment efficiently enough to be able to occupy mountain areas at over 900 m altitude. In general, open landscapes with few trees (pine and lower frequency of *Juniperus* and/or *Betula*) have generally been identified in the studies performed on cave deposits. Nonetheless, improvements in the climate are occasionally observed, reflected in the dynamics of deciduous trees, heath and grasses (Dupré, 1990).

Animal species associated with a cold climate appear mostly in the first half of the Gravettian, in both archaeological and exclusively palaeontological deposits (Bouchud, 1951; Altuna, 1972; Altuna and Mariezkurrena, 1984; Castaños, 1996): mammoth, woolly rhinoceros (*Coelodonta antiquitatis*) and reindeer (*Rangifer tarandus*). The presence of reindeer in this environment appears to have been scarce, as it has only been identified through isolated remains at Lezetxiki and Aitzbitarte IIII (Altuna and Mariezkurrena, 2011) (Fig. 1), whereas in Isturitz cave, it played a significant role in human subsistence strategies (Passemard, 1944; Bouchud, 1951; Beaufort and Jullien, 1973; Lacarrière, 2008; Normand and others, 2012). Mammoth consumption has also been documented in that cave (Villaluenga and others, 2022).

There are two Gravettian deposits with small vertebrate studies. Cold climatic conditions related to the GS-5.2 event are revealed by the palaeoenvironmental analysis of the small vertebrate assemblages from Ondaro rock-art cave (Nabarniz, Biscay; 240 m a.s.l., Fig. 1; Suárez-Bilbao and others, 2016–2017), as indicated by the relatively high proportion of tundra vole remains (*Microtus oeconomus*) in the stratigraphic sequence (between 9 and 20%). The small vertebrate assemblage provides information for the period between the GS-5.1 and GS-3 at Bolinkoba (Abadiño, Biscay; 388 m a.s.l., Fig. 1), where the total absence of woodland species among the small vertebrates in the Gravettian levels (Garcia-Ibaibarriaga and others, 2015) reveals the predominance of rigorous climatic conditions.

However, this landscape characterisation is totally different from the one obtained by palynological studies carried out at two open-air sites: Ametzagaina (Donostia, Gipuzkoa) and Mugarduia Sur (Urbasa, Navarre) (Fig. 1). The former is near the modern shore of the Bay of Biscay, whereas the latter is in the Sierra de Urbasa at over 900 m a.s.l. on the Mediterranean side of the watershed.

At both of them, interstadial conditions led to broadleaf forests dominating the landscape, although in different ways, as might be expected. At Ametzagaina, alder, birch, hazel and oak were more common than pine and, although the percentages of arboreal pollen are significantly higher than that found in cave sites, the landscape was still quite open, with a predominance of heath and grasses. However, the conditions were not stable, and the high humidity conditions inferred at the base of the sequence (~24 000 BP) gradually reduced (decrease in ferns, heather, alder, hazel and oak) (Tapia and others, 2009).

At Mugarduia South, in contrast, forests dominated the landscape, with higher percentages of birch and hazel than pine, oak, beech and lime at the base of the sequence. Higher up, although the total values of arboreal pollen decrease, the role of hazel, pines, beech and oak stabilised in its composition. Unlike at Ametzagaina, humidity increased over time (Iriarte-Chiapusso, 2013).

One of the most significant palaeoclimate aspects of MIS 2 is the impact of the episode of severe conditions, known as the Last Glacial Maximum (LGM), on the vegetation. Practically half of the modern area of Europe was under the ice, the sea level dropped considerably, and the cold and low environmental humidity determined the vegetation dynamics (Maier and others, 2021). However, palaeoenvironmental studies show that responses to the same climate events are not identical, depending on the biogeographic conditions of each place. This is seen in the deglaciation process in mountain ranges in northern Iberia. Because of the influence of the LGM in Europe, deglaciation would have started after that event. In contrast, several sequences in the Picos de Europa, Basque Mountains and Pyrenees do not coincide with the most extreme climate conditions. Studies suggest that deglaciation had begun earlier, before 35 000 cal BP in the Cantabrian Mountains (Fig. 5) and before 30 000 cal BP in the Pyrenees (Serrano and others, 2013*a*, 2013*b*;

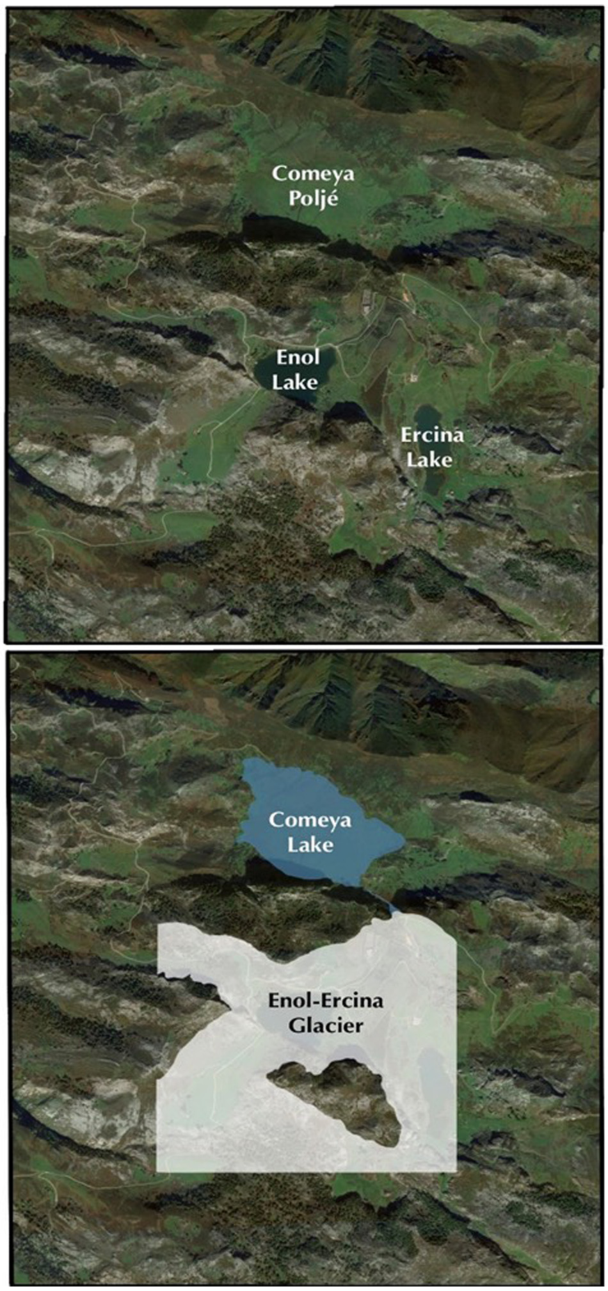

Figure 5. Maximum glacial spread in the current area of Covadonga Lakes (Asturias) ~40 000 cal BP. Based on Moreno and others (2010), over a Google Earth image.

Rodríguez-Rodríguez and others, 2015). After that process had started, the glaciers advanced again in the LGM, but without reaching the maximum extension, they occupied previously (Delmas and others, 2022). In the Basque Mountains, at a lower altitude, the impact of the LGM was almost irrelevant (Rico, 2012). Therefore, Solutrean populations in the Cantabrian region witnessed a smaller extension of the mountain glaciers than in previous societies.

The small vertebrate record also reflects the variability in the climate events that succeeded one another during MIS 2. The palaeontological site of Kiputz IX (Mutriku, Gipuzkoa; 119 m a.s.l.) (Fig. 1) provided a poorly diverse but relatively rich small vertebrate assemblage contemporary with the Solutrean period (Garcia-Ibaibarriaga and others, 2012). This assemblage indicates a predominance of open spaces, although the tree cover increases gradually towards the top of the sequence. The small mammals from the Upper Solutrean at Antoliñako Koba indicate two forest peaks (Rofes and others, 2015), in which the second one was preceded by an increase in rocky habitats (Fig. 1).

In sequences with levels attributed to the Solutrean, the landscape continued to be open (generally with percentages of arboreal pollen below 10%, represented by *Pinus*, accompanied by *Betula* and/or *Juniperus*). The main differences are associated with the degree of humidity rather than with temperature oscillations (Iriarte-Chiapusso, 2011*a*, 2011*b*; García-Ibaibarriaga and others, 2012). However, episodes of climate amelioration have also been detected (Dupré, 1990).

After the LGM, the volume of palaeobotanic information in the north of the Iberian Peninsula increased considerably because of the more significant number of peat and lake sites whose sequences began at that time. The greater density of data shows how local factors such as altitude, latitude, orientation and distance from the sea help to explain the different impacts of global climate change in each biogeographic unit. Consequently, the characteristic composition of synchronic pollen zones may differ depending on their location (Iriarte-Chiapusso and others, 2016*a*, 2016*b*). This, therefore, supports the impression obtained for earlier periods, for which less information is available.

Even in the final stages of the last Glacial Period, the palaeoenvironmental conditions experienced by Magdalenian societies varied considerably as they experienced two episodes of climate deterioration (Oldest and Younger Dryas), separated by the late glacial interstadial (Iriarte-Chiapusso and others, 2016*a*, 2016*b*).

In soil micromorphology studies, the entity of the processes identified hinders their correlation with the rapid climate change in the last Glacial Period (Areso, 1984; Hoyos and Fumanal, 1985; Areso and others, 1990; Pérez-Fernández, 2017, 2021). Cryoturbation processes and the growth of tufaceous structures in many parts of the Cantabrian region confirm the degree of humidity and milder temperatures, especially in the late glacial interstadial (González-Sampériz and others, 2006; González-Amuchástegui and Serrano-Cañadas 2015; Moreno and others, 2010; Aranbarri and others, 2014). The high humidity would explain the accumulation of carbonate by solution and, consequently, the loss of the original organic materials (Pérez-Fernández, 2021).

In general, the climate improvement in the late glacial interstadial anticipated the vegetation changes that occurred in the Holocene. Not only was the tree cover enriched by meso-thermophile taxa in places with most oceanic influence, but also the forests expanded in mountain areas and inland. The increase in the arboreal cover would be the cause of the large percentage of woodland species (40–50%) in small mammal assemblages, as seen in the abundance of *Sorex araneus-coronatus* in Santimamiñe cave (Rofes and others, 2014) (Fig. 1). Despite pollen and/or stratigraphic hiatuses interrupting the sequences, the effects of the climate change that occurred in this interstadial are detected in palynological studies (Iriarte-Chiapusso, 2011*b*).

During the Magdalenian, the only mammal species adapted to a cold climate that tends to appear in faunal records is reindeer, with the shaft of Kiputz IX (Castaños and Castaños, 2018) and the archaeological site of Santa Catalina (Castaños, 2014) as the series containing the largest samples (Fig. 1). The latter site is a good example of how the last cold episodes of MIS 2 were still significant. The site is now on a sea cliff, but in the Upper Magdalenian (Level III) the coastline was 4 km away to the north. Other cold-adapted species like *Phoca* sp., *Alca impennis*, *Fulmarus glacialis* and *Fratercula arctica* also lived in the environment around the cave (Elorza, 2014).

A drop in temperature and episodes of considerable aridity characterise the Younger Dryas (Bartolomé and others, 2015; Bernal-Wormull and others, 2021). Even so, their intensity was less than in the stadials before the last interstadial. Once again, these conditions intensified further from the coast and in the mountains, owing to the impact of the altitudinal gradient. Despite this, while the landscape was more open, there were places where deciduous trees did not disappear and from which the forest would rapidly expand after the start of the Holocene.

4. Human resilience and use of the resources in the environment

From the beginning of the Upper Palaeolithic, the only human species in the southwest of Europe was our own, *H. sapiens*. Therefore, behaviour that is considered uncharacteristic of prehistoric human groups cannot be attributed to biological or anthropological factors. While it is not the subject of the present study, we possess detailed knowledge of the socio-cultural and technological development of the hunter–gatherer bands that originated the regional archaeological record (Fernández-Eraso and Santos, 2007–2008; Arrizabalaga and Iriarte-Chiapusso, 2011*a*). Practically none of the factors involved follows a linear evolution with the possible exception of population size, in which a gradual increase with no setbacks can be appreciated. Hunting strategies, technologies to make weapons and tools in lithic and osseous raw materials, and symbolic behaviour are not without periodical regressions and erratic developments. But the most changeable variable, as explained above, was the environment. Over 30 000 years, environmental changes have been recorded with great frequency and over a wide range, from a climate similar to the present to periods of extreme cold, as shown by vegetation associations of taiga and the presence of boreal animal species like *C. antiquitatis*, *Gulo gulo* and *R. tarandus* (Gómez-Olivencia and others, 2014). Human communities, extremely sensitive to the subsequent changes in biotic resources, always developed mechanisms through material culture and adaptive strategies to adjust to them.

A century after the region's first research on the Upper Palaeolithic, over 300 radiocarbon dates have been obtained, and exhaustive excavations have been carried out at more than 40 archaeological sites. Such a large amount of palaeo-ecological and techno-cultural information cannot be summarised in a brief text. Nonetheless, some of the adaptation mechanisms employed by hunter–gatherer societies in the region, well documented by recent research, will be described below.

The main conceptual change in this topic in recent decades has been an enlargement in the size of the Palaeolithic human world. We were already aware of the Atlantic part of the Basque Crossroads, with its low altitudes and numerous limestone areas with caves that provided refuge, but we have recently discovered that Upper Palaeolithic groups also frequented the Mediterranean side of the watershed, further south but more

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hostile for human occupation in the stadials because of the greater altitude and lower density of caves. Many of the sources of good quality flint are in that area (Tarriño and others, 2015), and therefore the identification of those raw materials at sites on the Atlantic side necessarily attests to habitual visits to those outcrops (Arrizabalaga and others, 2007, 2017). This diversification of biomes also implies the presence of open-air occupations, which were practically unknown before the late 20th century, with different purposes (camps, hunting posts, flint workshops) than those already known (Arrizabalaga and Iriarte-Chiapusso, 2011*b*). Cave sites must be over-represented in a region like the Basque Country, with dense vegetation that hampers the discovery of open-air deposits. Consequently, the environmental signal provided by the cave deposits, which often point to stadial conditions, generated a bias in the palaeoclimate reconstruction of the Upper Palaeolithic (Iriarte-Chiapusso and others, 2016*a*, 2016*b*). As we now know, at least for the Gravettian period, for which the highest density of open-air camps has been documented, caves would have been occupied most during the intense cold conditions of stadials. In other times, when the climatology allowed open-air occupations, there would have been no constraints to the organisation of camps, even at considerable altitude, as in the case of the flint workshop at Mugarduia South (Barandiaran and others, 2013). To complete the palaeoenvironmental reconstruction of those 30 000 years of the Upper Palaeolithic, the contribution of open-air sites is vital to document phases of a more favourable climate and obtain an overall picture with no biases.

From the point of view of adaptive behaviour, the occupation of exterior sites, away from the protection of the caves, is more demanding. It involves better management of fire and weapons and implements for defence, tent-like structures are essential (as well as the logistics for their transport during the periodical movements of the group), and the requirements for clothing and footwear are also stricter to resist the outside temperatures at all times. It has recently been noted, again in the case of the Gravettian (Calvo and others, 2019), that thousands of a very particular lithic implement, the so-called Noailles burin, would have been used to make clothes and other objects from animal skins. Thus, as in many other parts of Europe, the over-representation of caves on the maps of archaeological sites has led to a biased picture that we should start to correct now.

Paradoxically, from this bias that is to be corrected, the picture of the palaeoenvironment that emerges is monotonously cold. Because of this over-representation of cave sequences, studies are more likely to detect colds of varying intensity than climate situations similar to the present or to interstadials. However, an adaptive mechanism to solve the lack of fuel at times of extreme cold has recently been detected. As can be observed in some archaeological levels in Labeko Koba (Iriarte-Chiapusso, 2000) and Aitzbitarte III (Iriarte-Chiapusso, 2011*a*), in some cold pulses, tree cover was reduced to a minimum as it contributed <4% of palynomorphs to pollen samples. It may be supposed that the generation of dead wood to be used as fuel would be so limited and so far spread that alternatives would become essential. At both Mousterian sites (Esquilleu) and Aurignacian (Labeko Koba) and Gravettian locations (Coímbre) (Fig. 1), these alternatives included the use of long bones after the marrow had been removed and they had been broken up. The result, a mass of bone fragments in different stages of carbonisation or calcination, had not been interpreted well, possibly because the practice of collecting all the osseous material recovered during excavation is relatively recent. Thanks to our experimentation, we can affirm that fire with this kind of fuel does not reach very high temperatures (maximum of 250°C) but is very efficient and long-lasting, as it can burn for up to 8 h without needing to add more bones (Yravedra and others, 2005, 2016).

Due to the strategic planning that characterises our species, from the first time modern humans reached the Cantabrian region, changes can be identified in hunting practices (Altuna, 1990). Three decades ago, very few good sequences for the first two-thirds of the Upper Palaeolithic were known in the Basque Country. At that time, the model was rather unbalanced because of the paradigmatic study of Ekain cave (Altuna and Mariezkurrena, 1984), which was a late Magdalenian hunting post specialising in capturing young deer around the time when they gave birth in spring. As well as representing behaviour at the very end of the Palaeolithic, the functional bias of the site did not favour a balanced view of hunting in the whole Upper Palaeolithic. Other deposits that had been excavated shortly before or were being excavated at that time, like Erralla (Altuna and others, 1985) and Amalda (Altuna and others, 1990), provided a contrasting picture that was still not complete for the Early Upper Palaeolithic (Fig. 1). Two studies later corrected that perspective: Labeko Koba and the outer sector at Aitzbitarte III.

The oldest levels are in Labeko Koba (Arrasate), whose deposit starts with Lower Level IX, Chatelperronian, but in a context with only sporadic human presence as it was used by hyenas and other carnivores (Arrizabalaga and others, 2003*a*, 2003*b*; Villaluenga and others, 2012). The first level in which humans were the major contributor to the remains of ungulates is Level VII, Proto-Aurignacian (Arrizabalaga, 2000), and this pattern persisted for about four millennia until the final phase of the old Aurignacian (Level IV). In those four levels, hunting concentrated on large bovids, especially bison, rather than red deer and horses, which are less abundant (Altuna and Mariezkurrena, 2000). Other species are also represented in smaller proportions: chamois, ibex, woolly rhinoceros, mammoth and others even less numerous, clearly brought by humans. This is an important point because a large number of carnivore species, mainly medium-sized ones, are found in the Labeko Koba deposit. Although the sequence is more recent at Aitzbitarte III (outer sector), dated from the late old Aurignacian to the Solutrean, it also attests a gradual specialisation in particular species (Altuna and others, 2011). On most levels, that species is the same as in Labeko Koba: bison (Altuna and Mariezkurrena, 2011).

Unlike the western part of Cantabrian Spain, where the role of horses and bison in the diet continued to be important until the very end of the Upper Palaeolithic, on the Basque Crossroads, those animals would become scarcer among the prey from the Gravettian onwards. This is not because they disappeared from the territory since they continued to be depicted in both parietal and portable art in the Magdalenian. It is paradoxical that in Ekain cave, during the Upper Magdalenian, the most commonly represented animals are horses and bison whereas they hardly appear among the prey at the same site (Altuna and Mariezkurrena, 1984). However, it is likely that they were not as abundant as they had been in the Aurignacian and Gravettian since their decline among the hunted animals is very significant.

The pattern established through sites like Ekain is only valid in those circumstances of the Magdalenian or even the late Magdalenian. In those recent times, a single species makes up over 60% and sometimes even 90% of the identifiable remains. Chamois and ibex are the most common animals at montane sites and in places with crags. In contrast, the preferred prey is red deer at valley sites or reindeer to the north of the Pyrenees. As stated above, thanks to the increasing number of Upper Palaeolithic sequences and radiocarbon dates for their contextualisation, this change in behaviour can be seen to be gradual. Not only do species like bison and horse steadily disappear among the hunted animals, but the degree of specialisation also increases from a majority of a species to an overwhelming dominance in

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later periods. As we have known for some time, in specialised hunting, modern humans were helped by the first dogs; wolves that were accustomed to living with humans until they began to collaborate with them. A recent study has assessed the ascription of a specimen at Erralla to a domestic breed (Hervella and others, 2022). This assistance, together with improvements in the hunters' equipment, increased hunting parties' possibilities of success.

In the last few decades, some biases have been detected in the available information, and it has sometimes been possible to correct them with the use of new surveying and analytical methodologies. The case of open-air occupations, especially in the Gravettian, has been described above. Six camps, hunting posts or flint workshops are now known, which permits a fuller image of the use of the territory (Calvo, 2019; Arrizabalaga and Iriarte-Chiapusso, 2020; Calvo and Arrizabalaga, 2020). Indeed, although it is still difficult to conciliate the archaeological scale expressed in millennia with the historical scale of the groups or individuals who created the record, knowledge gained in the last decade has allowed us to consider the territorialisation of collectives. Upper Palaeolithic hunter–gatherer groups were nomadic in their behaviour and moved across an indeterminate territory in the course of the seasons in order to make use of its resources. To the extent that we are able to define those territories or even establish seasonality patterns in their use, we shall understand much better the motives for that nomadic mobility. Through the distribution of flint artefacts in the region (which is particularly well known for the Gravettian) and examples like that of Ekain, which characterises a cave deposit from the functional and seasonal point of view as a hunting post, we can determine more precisely the parameters that governed the movements of those groups (Fig. 6). Moreover, their mobility seems to have been much more restricted than was thought. For example, on the Basque Crossroads, in practically all the known archaeological levels, more than 95% of the flint came from outcrops in the same area. The occasional exceptions can be classed as flint from an extended region (Cantabria, Asturias, Aquitaine, Dordogne and the Pyrenean Piedmont), apart from some currently unidentified types. Thus, the evidence of the raw materials clearly indicates a closer and more restricted territorial framework than had been imagined previously. This helps to understand the agility with which the human groups responded to drastic environmental changes, apparently without great difficulties: over the long span of time that separates the Chatelperronian from the end of the Palaeolithic, human collectives came to know the territory and its resources perfectly well, and that enabled them to adapt to environmental changes that took place in the time of a few human generations.

5. Final considerations

The perspective on human evolution has changed remarkably. Until 1980, the approach was 'anthropocentric', in which humans were at the centre of the natural world, at the top of the food pyramid. We are now just seen as one more living being on the planet whose history is framed in a global environmental context.

However, contextualising the information obtained, a series of limitations interfere with the definition of the Quaternary palaeoenvironmental dynamics, such as sequence hiatuses or gaps that we do not know well or issues in obtaining reliable dates. Despite these constraints, authentic interdisciplinary studies provide different analytics and allow us to define the complexity of the palaeoclimate and environmental dynamics in this territory

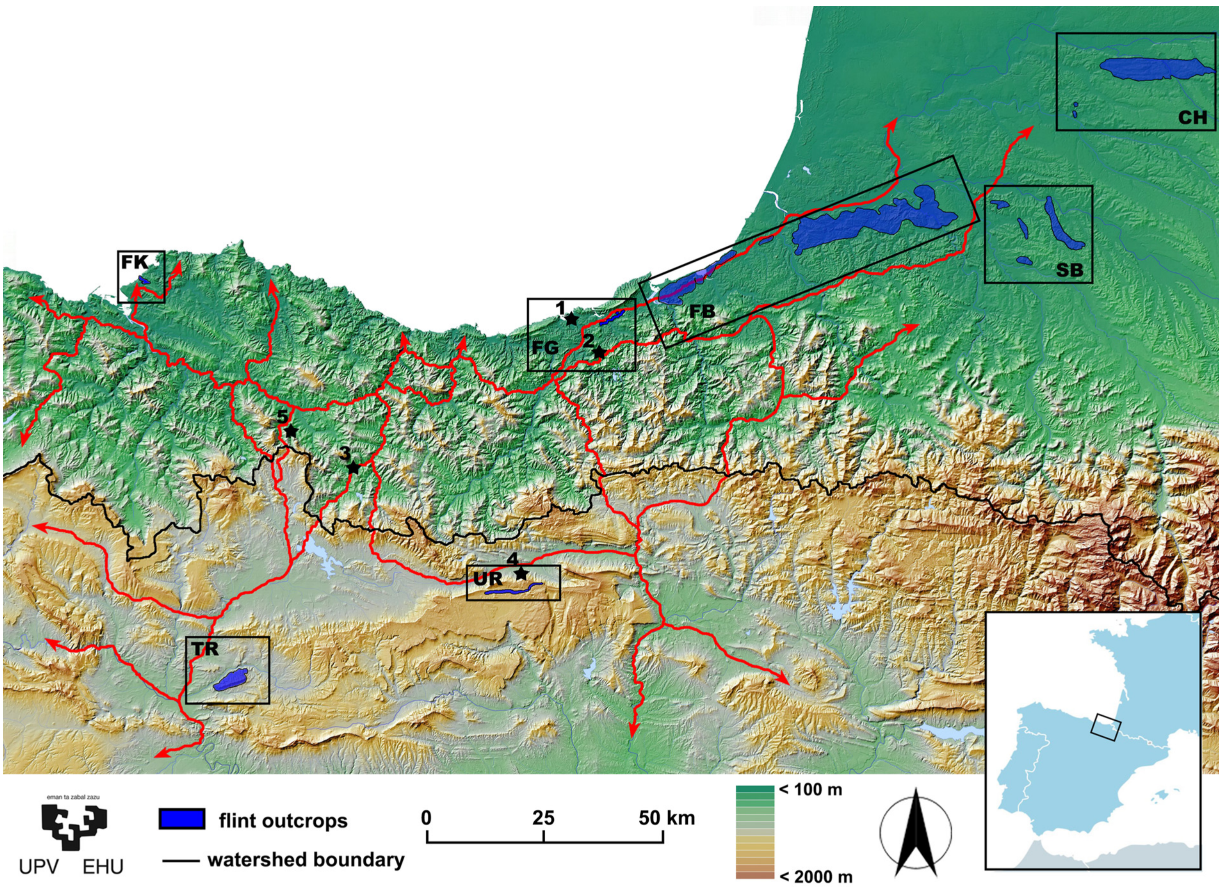

Figure 6. Regional distribution of chert outcrops and presumed routes for the mobility of human groups during the Upper Palaeolithic: (1) Ametzagaina campsite, (2) Aitzbitarte III cave, (3) Labeko Koba cave, (4) Mugarduia Sur Flint workshop site, (5) Bolinkoba cave.

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(with greater availability of data from the LGM onwards). As has been explained, in the same territory, palaeoclimate conditions determine the evolution and adaptation of plant, animal and human communities.

We could continue with more examples of the technological and behavioural changes introduced by the first anatomically modern humans (*H. sapiens*) after they entered the Iberian Peninsula. As the palaeoenvironmental record shows, the ∼30 000 years of the Upper Palaeolithic saw short-cycle environmental changes. Archaeozoological and archaeobotanic data have revealed drastic oscillations between biotic conditions compatible with the present climate on the Basque Crossroads and significantly colder ones, comparable with coastal areas today in the latitude of ∼60–70°N. The demographic curve does not seem to replicate those cycles, as we can observe a slow but sustained growth in the number of known sites and their distribution across the region. Material culture and adaptive mechanisms mediated between the natural environment and human groups: their footwear and clothing let them spread to higher altitudes, hunting weapons and tools enabled them to exploit their surroundings more efficiently and we can imagine that primitive maps allowed them to travel periodically to flint outcrops in short expeditions to acquire new supplies of raw material. All this was made possible by empirical knowledge of the territory, to which they seem to have become linked at an unexpectedly early time, understood on a broad scale and with many reservations. This early territorialisation of the human groups would facilitate resilience and agile adaptation to the sudden climate changes that sometimes took place over just a few centuries.

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