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# The First Occupations of Western Europe: Dispersals and Population Dynamics in the Early to Middle Pleistocene

Carolina Cucart-Mora<sup>1</sup> · Diego Lombao<sup>2,3</sup> · Antonio Pineda<sup>1,4</sup> · Bruno Boemke<sup>5</sup> · Beniamino Mecozzi<sup>6</sup> · Marie-Hélène Moncel<sup>1</sup>

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## Abstract

The occupation of Western Europe is part of a greater process, the first “Out of Africa”. Within this process, a wide chronological gap is documented between the first occupations in Asia and those in Western Europe. The earliest occupations of Western Europe are dated around 1.4–1.2 Ma and located in Southern Europe, in the Iberian Peninsula and Italy. A punctuated advance towards the North is discerned with the first occupations in England being as old as 0.9 Ma. Through a synthesis of up-to-date literature, this paper aims to provide an updated, robust and more integrated understanding of the processes that shaped the earliest human occupations of Western Europe. Throughout our review and analysis, the early occupation of Western Europe is revealed as a complex, multi-phased process marked by episodic population incursions and turnovers. The archaeological record, of which we demonstrate a considerable bias in likelihood of discovery, shows that colonization began around 1.4–1.2 Ma, with successive waves introducing new distinct hominin species, technological repertoires and adaptive strategies. Of these successive waves, at least four are clearly visible in the record, although we acknowledge that with a high probability there were more waves of varying intensities. Integrated technological, faunistic and taphonomic studies will be key going forward. We finally advocate for a multiscale approach based on complex systems theory and an array of computational modelling techniques to gain a more comprehensive and robust knowledge of the process of population of Western Europe.

**Keywords** Early Pleistocene · Early Middle Pleistocene · Western Europe · Hominin dispersals

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Extended author information available on the last page of the article

## Introduction

The occupation of Western Europe is part of a greater process, the first “Out of Africa”. The oldest evidence of human occupation outside Africa is found in Shangchen (China) with an estimated chronology of up to 2.12 Ma (Zhu et al., 2018). These dates are significantly older than those of the Dmanisi site in Georgia (between 1.78 and 1.85 Ma) (Gabunia et al. 1995; de Lumley et al., 2002; Ferring et al., 2011) the gateway to Europe. Other sites with comparable early age have also been identified in China (Ao et al., 2012; Luo et al., 2020; Zhu et al., 2004). At the other end of the Eurasian continent, a greater gap between the earliest human occupations in Africa and Western Europe has been recognized. The earliest documented occupations are dated around 1.4–1.2 Ma and located in Southern Europe. Specifically, the Iberian Peninsula: Orce and Sima del Elefante (Huguet et al., 2016; 2025; Blain et al., 2016; Lozano-Fernández et al., 2015) and from Italian Peninsula site of Pirro Nord (Arzarello et al., 2012; Pavia et al., 2012). This suggests a possible synchrony dispersal around the Mediterranean Europe (Arzarello et al., 2007; López-García et al., 2015). Evidence suggests that southern France was first populated a little later, whereas northern France was first populated around 1.1 Ma maximum (Despriée et al., 2024). In Britain, the human diffusion would take place later, as indicated by the evidence recovered in Happisburgh 3 dated as early as ca. 900 ka (Parfitt et al., 2010).

The relatively late arrival of humans to Western Europe, compared to other parts of Eurasia, remains unclear and could be attributed to a variety of factors, including climatic, ecological and geographical challenges. The questions of when, who and how these early occupations occurred remain subjects of debate. Hominin populations during the Early and early Middle Pleistocene underwent significant climatic, environmental, and cultural changes. This period includes the Early to Middle Pleistocene Transition (EMPT) (ca. 1 Ma to 400 ka), marked by a shift from low-amplitude, high-frequency glacial-interglacial cycles to high-amplitude, low-frequency cycles. Additionally, it encompasses a faunal turnover, characterized by the extinction of the “Villafranchian” fauna and the spread of modern mammalian species.

The aim of this paper is to provide a comprehensive review of the current state of research on the earliest human occupations in Western Europe during the Early Pleistocene and the early Middle Pleistocene. By synthesizing the most recent data and studies, this review seeks to present a detailed overview of the main hypotheses and interpretations regarding key aspects such as paleodemographic trends and dispersal routes and timing. Through this synthesis, the paper aims to provide an updated, robust and more integrated understanding of the processes that shaped the earliest human occupations of Western Europe.

## Climate and Environment

The Early Pleistocene climate was characterised by 41-ka high-frequency glacial-interglacial cycles that were phase-locked to the obliquity-driven isolation cycle. The most significant climatic event within the time frame of this paper is the

emergence of low-frequency, high-amplitude, quasi-periodic 100 ka cycles during the Middle Pleistocene (Clark et al., 2006). The Early-Middle Pleistocene transition (EMPT) (ca. 1 Ma to 400 ka) was characterized by an increase in the severity of glaciations, the decrease of the sea surface temperature, an increase of the ice-volume and a trend towards cooler, more arid climates (Batchelor et al., 2019). The Middle Pleistocene glaciations were severe enough to cause ice sheet development on the continental scale. According to what is observed in the LR04  $\delta^{18}$  stack, the first long glaciation of the Pleistocene occurs at ca. 900 ka (Clark et al., 2006), including Marine Isotope Stage (MIS) 24 and 22 separated by a subtle MIS 23. A substantial increase in global ice volume is evident in deep-sea cores after MIS 22 (Lisiecki & Raymo, 2007). The onset of the more severe climatic conditions from MIS 22 onwards is also visible in a thicker and coarser loess deposit in northern Europe (Dodonov, 2005). In northern Europe, MIS 16, 14 and 12 were particularly severe. In contrast, during MIS 19, 17 and 15, interglacial conditions were similar to present ones (MacDonald et al., 2012; Sassoon et al., 2025).

These climatic changes had a strong influence on plant and animal distribution in mid-latitude Europe. Both fauna and vegetation responded to the climatic cycles. During colder phases, plant and animal populations adapted to temperate conditions retreated to southern refugia (e.g. Iberian Peninsula, Italy and Greece) and when climatic conditions ameliorated, they expanded from there to northern latitudes. The expansion of the ice sheet in the Northern Hemisphere during cold phases shifted vegetation zones southwards, e.g. steppe grassland to woodland and affected faunal populations in a similar fashion, e.g. hippopotamus extended to England in warm phases (Dennell et al., 2011). A climate-coordinated sink-and-source dynamic is observed for fauna and vegetation.

Alongside these dynamics, the paleontological record suffered important transformations at the continental scale. The EMPT records the disappearance of typical Villafranchian large mammals that inhabited the European continent for hundreds of thousands of years and the arrival of newcomers. These new forms were characterised by a high level of adaptability to different climates and environments, allowing them to survive the glacial-interglacial phases of the Middle Pleistocene. Several of these newcomers, or their relative descendants, represent the extant mammal species that still occupy the European continent (Iannucci et al., 2021; van der Made et al., 2017). Other forms, especially due to climatic conditions recognized during the last glacial period, became extinct or survived in other continents (e.g. elephants, hippopotamuses or rhinoceroses).

Research over the last two decades has identified the main faunal reorganisations that reflected the great renewal of terrestrial ecosystems and the mutation of climatic conditions. One of these events occurred during the Epivillafranchian (ca. 1.2—0.8 Ma), when typical Villafranchian taxa started to disappear (Azzaroli et al., 1988; Caloi & Palombo, 1996; Kahlke, 2009; 2006; 2001; Koufos, 2001; Rook & Martínez-Navarro, 2010; Spassov, 2003) and two important elements of the modern European ecosystems diffused from Asia, *Cervus elaphus* and *Sus scrofa* (Bellucci et al., 2015; Iannucci et al., 2021; Kahlke et al., 2011; Markova & Vislobokova, 2016; Martínez-Navarro & Rabinovich, 2011; van der Made et al., 2017). Between the end of the Early Pleistocene and the onset of the Middle Pleistocene, several

characteristic Middle–Late Pleistocene mammals—such as the iconic species *Palaeoloxodon antiquus*, *Crocota crocuta* and *Panthera leo*—appeared and became common components of European faunal assemblages (Mecozzi et al., 2025 and reference therein). The end of the Early Pleistocene also coincides with the extinction of one of the most known carnivorans of Europe, the giant hyaena *Pachycrocota brevirostris* and the almost disappearance of the other carnivoran that dominated that ecological chain at that time, *Homotherium latidens*. These two species, diffused across all continents during the Early Pleistocene, are considered as the most important competitors of the first humans that occupied Europe between 1.5 and 0.8 Ma. The remarkable competition between humans and these two carnivorans will have no equal in the Middle Pleistocene, where paleontological and archaeological evidence indicates less frequent and less pronounced competition compared to earlier periods (Moncel et al., 2023; Rocca et al., 2023a). After the important glacial climatic episode identified as MIS 16, another significant renewal occurred, with the arrival of modern hippopotamuses (*Hippopotamus amphibius*), the more evolved bovids (*Bison priscus* and *Bos primigenius*), the modern horse (*Equus ferus* and *Equus hydruntinus*) and the extinction of their relative ancestors (Boulbes & van Asperen, 2019; Iannucci et al., 2021; Mecozzi et al., 2023, 2024).

At the end of EMPT, European terrestrial ecosystems were quite similar to their modern counterparts, with the exception of the specialised forms both cold (e.g., woolly mammoth and woolly rhinoceros) and warm (e.g., *Palaeoloxodon antiquus* and *Hippopotamus amphibius*) that disappeared from the continent during the Late Pleistocene due to the climatic instability and the pronounced cold climatic conditions recognized during the Last Glacial (MIS 5d-2).

## Western Europe First Occupations

The study of early hominin populations in Western Europe is based on a fragmentary record from relatively few sites (see also supplementary material, table S1). In addition to the paucity of records, the difficulty in obtaining numerical dates, lithic assemblages in secondary positions and doubts surrounding the anthropogenic nature of many of the so-called lithic tools raise more questions than answers for researchers. During the 1980s and 1990s, two hypotheses were put forward: (i) the Young Europe, which claimed that the subcontinent was not occupied until at least 500 ka ago and that *Homo heidelbergensis* was the first hominin to settle, based on Boxgrove's paleoanthropological and cultural evidence (Dennell & Roebroeks, 1996) and (ii) Old Europe, which was based on evidence from sites that at the time were dated to approximately 2 Ma (Bonifay & Vandermeersch, 1991; Gibert & Palmqvist, 1995). Decisive in the debate was the discovery of *Homo antecessor* remains, and mode 1 tools found at Gran Dolina and dated before the Brunhes-Matuyama boundary (Carbonell et al., 1995). Equally relevant is the recent identification of *Homo aff. erectus* in the Sima del Elefante (Huguet et al., 2025). In the meanwhile, several new sites have been discovered, and others have been resurveyed, and their assemblages re-evaluated. In the following section, we review the current state of the chrono-spatial and cultural evidence in relation to the first population.

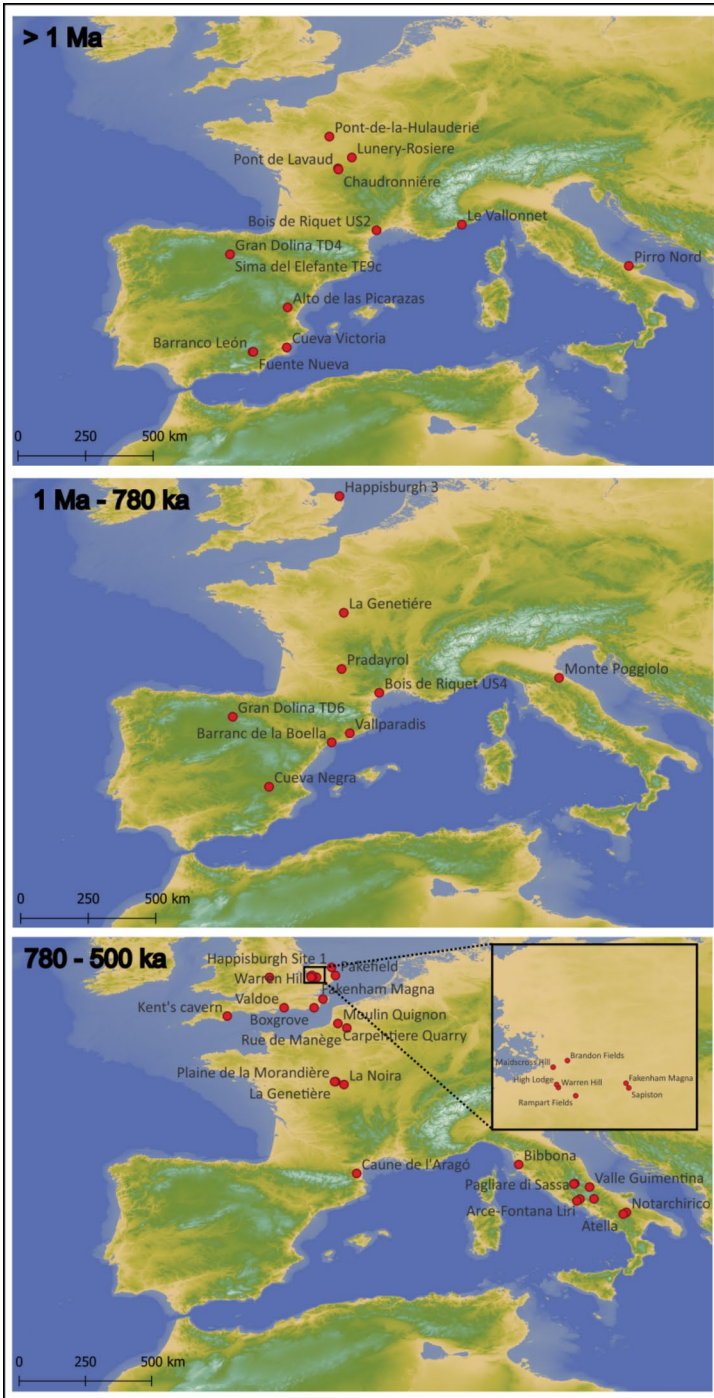
## The Chrono-spatial Record

### –Older than 1 Ma

Two of the oldest hominin sites in Western Europe are Barranco León and Fuente Nueva 3, located on the Iberian Peninsula (Fig. 1). These sites have been dated to approximately 1.4 to 1.2 Ma using a combination of absolute dating, biochronology and palaeoclimatic evidence, correlating the occupations with MIS 49–43 (Blain et al., 2011; Duval et al., 2012; Lozano-Fernández et al., 2015). The significance of the sites lies in their large mode 1 lithic assemblage (Barsky et al., 2016; Tilton et al., 2021) and an infant molar attributed to *Homo* sp. from Barranco León (Toro-Moyano et al., 2013). A potentially older site is Alto de las Picarazas (Spain), which contains a sparse assemblage of mode 1 lithic tools, and bones with evidence of anthropogenic modification. Based on the identified micromammal taxa and their correlations with Venta Micena (Spain), the site has been tentatively dated to between 1.8 and 1.5 Ma (Vicente Gabarda et al., 2016). However, the small lithic assemblage and the reliance on a single absolute date recommends caution. Equally, Cueva Victoria (Spain) was once considered one of the oldest sites, with an estimated age of 1.3–0.9 Ma (Carbonell et al., 1981). However, the lithic assemblage is too limited to be assigned to a specific technocomplex, and it remains unclear whether Early Pleistocene fauna and lithic tools entered the deposit simultaneously. Therefore, there is no evidence supporting the inclusion of the sites among the earliest hominin occupations of the continent.

Pirro Nord (Italy) yielded lithic tools into a fissure filling associated with a rich faunal assemblage bearing evidence of anthropic activity. Initial biochronological analysis dated the infilling to between 1.6 and 1.3 Ma (Arzarello et al., 2012; Pavia et al., 2012). However, recent multi-technique dating of both fossil remains, and host sediment produced dates clustering around 0.8 Ma, consistent with paleomagnetic data correlating the sediment to the Matuyama chron (>0.773 Ma) (Duval et al., 2024). While these numerical dates agree and support the contemporaneity of the sediment, lithic tools and fossils, they are notably younger than the earlier biochronological estimates. This discrepancy raises the possibility that the sediment and fossils may not be coeval, although this is contradicted by taphonomic evidence (Giusti & Arzarello, 2016). The findings suggest a more complex site formation process, leaving the precise age of the archaeological deposit uncertain.

Sima del Elefante, in the Sierra de Atapuerca karstic system (Spain), is one of the most relevant sites on the continent. Three types of remains are found: faunal, lithic and anthropological. TE7 yielded the oldest human remains on the entire continent of Europe: the midface of a hominin ascribed to *Homo* aff. *erectus* (Huguet et al., 2025). TE9c yielded the jaw of an adult hominin (Bermúdez de Castro et al., 2011), and a fifth proximal hand phalanx belonging to an adult individual (Lorenzo et al., 2015) both ascribed to *Homo* sp. Although stratigraphy confirms that TE7 is older than TE9c, the radiometric and biochronological ages of the two contexts are indistinguishable ca. 1.4–1.1 Ma (Huguet et al., 2025). Le Vallonnet (France), where an alternating presence of carnivores and humans is documented, dated at ~1.2 Ma based on U-Pb dating (Michel et al., 2017). The site is associated with a normal polarity (Cobb Mountain interval) corresponding to MIS 36, a cold glacial period



**Fig. 1** Sites distribution in Western Europe at three different time windows. More details about the sites can be found at Table S1

consistent with the faunal assemblage which propose an age of ca. 1 ma for the site (Iannucci et al., 2021). In Italy, the mode 1 artefacts found at Monte Peglia have been dated by biochronology at around 1.07 Ma (MIS 35/33) making them the oldest in the region after Pirro Nord (Ceruleo & Petronio, 2024).

Two sites stand out for documenting the presence of hominins in mid-latitudes before 1 million years ago. The first is Lunery-Rosiere (France). The ESR age of the fluvial deposit matches the Cobb Mountain subchron. This evidence, together with the sedimentary study of the fluvial deposit, led the researchers to conclude that the three occupations took place at the end of a transition between an interglacial and glacial event around 1.1 Ma, and that the site was unoccupied during the glacial maximum (i.e. at the beginning of MIS 36) (Despriée et al., 2024). At Pont-de-Lavaud (France), also in the Loire Basin, about 5000 mode 1 artefacts dated to about 1.1 Ma were recovered (Despriée et al., 2011). Pollen and phytolith analysis revealed the predominance of forest taxa related to a warm and humid climate, i.e. occupation took place during a temperate pulse at the beginning of MIS 31 (Marquer et al., 2011). Two other French sites are attributed to the same period, although their chronology is less certain and their lithic assemblages are very small. These are Pont-de-la-Hulauderie on the Loire River and Chaudronnière on the Creuse River (Despriée et al., 2010, 2011), which were dated by geostatigraphic correlations to around 1 Ma.

–Between 1 Ma and 780 ka

Around the million-year mark are TD3-4 and TD6 from Gran Dolina (Spain). TD3-4, the lowest unit containing anthropic activity evidence, has been dated by biochronology and ESR-OB to approximately 1 Ma (Cuenca-Bescós & García, 2007; Moreno et al., 2015). TD6 has been dated by palaeomagnetism to approximately 936 ka (Parés et al., 2013). However, the TL dates of TD7 (i.e.  $960 \pm 160$  ka), in the overlying level, suggest that the level could be older. The paleoanthropological collection of TD6 consists of 10,880 remains (Mosquera et al., 2018). Among them, human remains from subunit TD6.2 led to the introduction of an additional Pleistocene human species, *Homo antecessor* (Bermúdez de Castro et al., 1997). These remains showed alterations of anthropogenic origin, the earliest case of cultural cannibalism (Carbonell et al., 2010).

In France, Bois de Riquet US2 was originally dated by biochronology to between 1.3 and 1.1 (Bourguignon et al., 2016b), but a range of between 1 and 0.9 Ma was subsequently proposed based on the similarity of the micromammal assemblages to those of the Sima del Elefante (Lozano-Fernández et al., 2019). The presence of hominins at the site is considered limited or sporadic, based on the few anthropogenic modifications documented on bones and some basalt artefacts and manuports (Bourguignon et al., 2016a). A second Middle Pleistocene occupation phase (between 0.68 and 0.78 Ma) has been documented (Bourguignon et al., 2016b). Of similar age is Ca'Belvedere di Monte Poggiolo (Italy), with a fairly large assemblage of lithic remains classified as mode 1 (Peretto et al., 1998). The site was initially dated by magnetostratigraphy and ESR just before or after Jaramillo's normal polarity subchronology, between 1.07 and 0.98 Ma (Falguères, 2003). However, Muttoni et al. (2011) have proposed a different interpretation, attributing the deposit to approximately 859 ka, based on regional scale geo-stratigraphic

investigations. At present, most researchers still opt for the determination between 1 and 0.9 Ma (e.g. Rodríguez and Lozano et al. 2025).

At Vallparadis (Spain), within a rich palaeontological sequence, level 10 yielded mode 1 lithic tools (Martínez et al., 2014). The chronological attribution of the level has been the subject of controversy in recent decades, with initial ESR dating results placing the level between 780 and 960 ka (Duval et al., 2011). Subsequently, biochronological analyses set the age between 980 and 950 ka (Martínez et al., 2014). Later, new ESR dating was carried out and yielded a mean age of  $858 \pm 87$  ka (Duval et al., 2015). Another uncertainty concerns the anthropogenic nature of the lithic artefacts, mostly quartz, as well as the contextual integrity of the assemblage (Madurell-Malapeira et al., 2012). The multiple doubts arising from the cross-evidence recommend a re-evaluation of the context and its materials.

The Happisburgh Site 3 site (UK) provided the oldest surviving evidence of Early Pleistocene hominins in the far southern boreal zone (Parfitt et al., 2010). The age of occupation, established by integrating palaeomagnetism and biochronology, was placed at the end of MIS 21 (814–866 ka) or MIS 25 (936–970 ka) (Parfitt et al., 2010). Human presence has been documented through a small flint lithic tool assemblage ( $n=78$ ). In addition, this site has the oldest human footprints outside Africa, originally attributed to *Homo antecessor* (Ashton et al., 2014), although recent geometric morphometric analysis concluded that the footprints are more similar to *Homo erectus* from Ileret (Kenya) (Wiseman et al. 2020).

The Cueva Negra del Estrecho del Río Quipar and Solana del Zamborino (Spain) were considered once the oldest evidence of mode 2 in Western Europe (Scott & Gibert, 2009; Walker et al., 2013). Cueva Negra sequence has been dated by palaeomagnetism, biostratigraphy of large and small mammals, and a combination of CSUS-ESR and US-ESR between the end of the Jaramillo subchron and the Matuyama-Brunhes boundary (990–772 ka) (Walker et al., 2020). However, the dating of the deposits is not without criticism (see Jiménez-Arenas et al., 2011). A new paleomagnetic study of Solana del Zamborino has established the age of the occupation between 300 and 480 ka in accordance with biochronology (Álvarez-Posada et al., 2017; García-Vadillo et al., 2023). Less controversial is the age from Pradayrol (France) (ca. 900 ka), where a lithic assemblage of fifteen pieces was found and considered by Moncel and Ashton (2018) as possible early attempt at bifacial knapping. Currently, the oldest and most accepted evidence of early Acheulean technology is found at Barranc de la Boella (Spain) (Mosquera et al., 2015, 2016; Ollé et al., 2023; Vallverdú et al., 2014). Palaeomagnetic, cosmogenic and biochronological data place the occupations of the three excavated localities (Pit 1, La Mina and El Forn) at the end of the Early Pleistocene (between 990 and 780 ka) (Vallverdú et al., 2014). One of the localities of the site (Pit 1) corresponds to a kill/butchering site, as illustrated by an association of *Mammuthus meridionalis* and several in situ cores, flakes and large-shaped tools (Fidalgo et al., 2025; Mosquera et al., 2015, 2016; Ollé et al., 2023).

–Between 780 and 500 ka

The second-oldest site in England is Pakefield, which yielded a small Mode 1 lithic assemblage. Three numerical dates, providing minimum ages, are available for the CFbf formation where the artefacts were discovered. These, together

with other studies—including lithostratigraphy, palaeomagnetism, amino acid geochronology and biochronology—indicate an age of approximately 700 ka (Parfitt et al., 2005). This time interval is characterised by a general increase in the number of sites and the emergence of mode 2 lithic assemblages. Two sites represent the earliest mode 2 occupations in England: Fakenham Magna and Sapiston (Davis et al., 2021; Key & Ashton, 2023). The former is attributed to MIS 19 (790–761 ka), while the latter is assigned to MIS 15 (563–621 ka). However, most researchers have excluded these sites from broader analyses, owing to the supposed secondary position of the artefacts at Fakenham and the uncertain chronocultural attribution of the Rampart Fields tools. Rampart Fields itself, attributed to MIS 15 (621–563 ka) through numerical dating and geological correlation, was reported in nineteenth-century quarrying works as a rich source of archaeological artefacts. Unfortunately, the surviving assemblage is currently limited to a few flakes and eight bifaces (Davis et al., 2021).

Likewise, some of the historical handaxes from Maudscross Hill (Davis et al., 2021) and Brandon Fields (Lewis et al., 2021) have been tentatively ascribed to MIS 15. At Maudscross Hill, the deposit has been dated twice (Lewis et al., 2021; Voinchet et al., 2015), yielding four consistent ages that provide a weighted mean of  $542 \pm 34$  ka. These results suggest that the deposit formed prior to MIS 12 (Lewis et al., 2021). Davis et al. (2021) further propose that the handaxes from the gravels of the Timworth Member fall into two groups based on typology and condition: crude and rolled handaxes, which they attribute to reworked MIS 15 palaeosurfaces, and ovate handaxes from Maudscross Hill and Brandon Fields, which are suggested to have derived from the surface of the Timworth Terrace, dated to MIS 11.

In Italy, the site of Notarchirico has yielded the oldest evidence of handaxes in southern Europe (Moncel et al., 2020a, 2020b). The stratigraphic sequence records recurrent occupations during which hominins engaged in butchery activities. However, the interpretation of putative butchery traces in the so-called elephant area has recently been challenged (Pineda et al., 2024). A fragment of a femur attributed to *Homo heidelbergensis* was recovered from the uppermost level of the sequence (level Alfa) (Micarelli et al., 2024). The most recent geochronological investigations, combining  $^{40}\text{Ar}/^{39}\text{Ar}$  and ESR dating, place the entire sequence between approximately 700 and 600 ka. Around the same time that Acheulean assemblages were first documented on the Italian peninsula, several open-air sites with mode 1 lithic industries are also known, including Arce, Fontana Liri, Pagliare di Sassa, Castro di Volsci and Bibbona. Their chronological attribution relies primarily on geological correlations of fluvial terrace systems, suggesting ages as early as MIS 17 (Palombo et al., 2010; Peretto, 2006). Further chronostratigraphic studies are required to refine the chronology of these assemblages. Finally, at Colle Marino, the layer believed to be the origin of the lithic collection has been dated at about 700 ka (Florindo et al., 2021).

In France, lithic assemblages containing Acheulean tools are numerous and provide important insights into the adaptability of hominins to diverse climatic and environmental conditions. The two sites associated with the “La Genetière” formation yielded abundant lithic material, including handaxes, cores and flakes.

ESR dates for La Genetière range between 800 and 470 ka, while those from Plaine de la Morandière fall between 730 and 620 ka (Despriée et al., 2007). However, as the artefacts are in secondary position, these ages should be regarded as minimal chronological boundaries (Despriée et al., 2010). Further north, at Moulin Quignon, a substantial lithic assemblage ( $n=260$ ), including large flakes, cores and five handaxes, was recovered. The Acheulean tools, dated between 670 and 650 ka (Pierre-Antoine et al., 2019), at the onset of MIS 16, suggest that hominins were able to persist under cold climatic conditions, with occupations taking place during a short temperate interval not directly recorded in the sediments. Penecontemporaneous with Notarchirico and Moulin Quignon is the site of La Noira (Hardy et al., 2018), dated between 678 and 638 ka on the basis of numerical dating and palaeomagnetic analyses (Duval et al., 2020). Soleilhac, in the Massif Central, has been numerically dated between 600 and 500 ka, although this chronology remains disputed (Raynal et al., 1995). Moreover, the site has not yielded bifacially worked pieces and has been attributed to mode 1 (Bracco, 1991).

Lastly, Fordwich (UK), formerly a commercial quarry, yielded more than 330 handaxes during extraction activities in the 1920s. The age of this collection has been estimated as MIS 15, based on numerical dating and geological characterisation of nearby sediments (Key et al., 2022). However, these studies were not conducted on the original archaeological context but on two outcrops excavated much later (Bridgland et al. 1998; Key et al., 2022). Establishing a direct correlation between these deposits and the original findspot is problematic, as the quarry has long since closed and little is known about the precise location and stratigraphic characteristics of the artefact-bearing layers, beyond the brief description provided by Smith (1933). The first excavation of the sites led to the attribution of the Fordwich assemblage to MIS 15 (Key et al., 2022). More recently, the excavation and dating of three trenches at Old Park, which contains Fordwich quarry, led Key et al. (2025) to suggest that the terraces of the River Stour were occupied during MIS 17 to MIS 16, possibly during MIS 15. Additionally, they identified two artefact-bearing stratigraphic unit aligned with the cold MIS 13 and MIS 12. Finally, they propose that the historical handaxes are associated with the MIS 17–16 dated gravels.

Isernia La Pineta (Italy) is an extensive open-air site that has yielded abundant lithic and faunal remains. A human deciduous incisor, belonging to a child aged between 5 and 7 years and attributed to *Homo* sp., was also recovered (Lugli et al., 2017; Peretto et al., 2015). The archaeological level has been dated to between 583 and 561 ka (Gallotti & Peretto, 2015; Peretto et al., 2015). Cimitero di Atella (Italy), an open-air site located near Notarchirico, records several episodes of human occupation along the shores of a paleolake. The deposit has been dated to between 580 and 440 ka through a combination of  $^{40}\text{Ar}/^{39}\text{Ar}$ , ESR and correlations with eruptive phases of the Vulture Volcano (Rocca et al., 2023b). Also, close to Notarchirico is the site of Loreto. Level A of the site has yielded a mode 2 lithic assemblage (Carpentieri et al., 2025) dated between MIS 13 and 15 as the last radiometric analyses have not yielded conclusive results (Pereira et al., 2024). At Valle Giumentina (Italy), another lakeshore occupation where both “Clactonian-type” and Acheulean assemblages have been recovered, the sequence has been dated to between MIS 15 and MIS 12 (621–424 ka) (Villa et al., 2016a, 2016b). Finally,

the site of Ficoncella, dated to ca. 500 ka (MIS 15) by tephra layers encapsulating the archaeological horizon, yielded a Middle Pleistocene lithic assemblage lacking handaxes (Aureli et al., 2016).

Caune de l'Arago (France) was once considered one of the oldest examples of mode 2 assemblages in Europe together with Notarchirico. Hominins first present at the site during a cold and dry phase of MIS 14 (560–530 ka) (Falguères et al., 2015). Level P/Q contains finely shaped handaxes and cleavers (Barsky, 2013), together with faunal remains resulting from recurring short-term occupations (Barsky & de Lumley, 2010). Other sites with ages dated to MIS 14 are in France: Rue de Manège is in the Middle Somme Valley, and the technology of the very small lithic assemblage is directed towards the production of flakes (Antoine et al., 2015). Carpentier Quarry is one of classical palaeolithic French sites and was studied on several occasions during the XX and XXI centuries. Although initially allocated to MIS 14 (563–533 ka) Moncel et al., (2021a, 2021b) and Pierre Antoine et al. (2016) have re-evaluated the site and consider that the Acheulean artefacts are to be allocated to MIS 15 and early stages to MIS 14 (550 and 500).

An increase in the number of English sites dated to MIS 13 suggests dispersals of hominins into northern Europe around 500 ka. Happisburgh Site 1 has been attributed to MIS 13 (533–478 ka) or the onset of MIS 12 (478–424 ka) based on lithostratigraphic and biostratigraphic evidence (Lewis et al., 2019). Warren Hill (Davis et al., 2021) and High Lodge (West et al., 2014), located only one kilometre apart on Bytham River terraces, are also dated to MIS 13. Waverley Woods has yielded a small lithic assemblage from a channel deposit likewise attributed to the Bytham River and to MIS 13 (Keen et al., 2006; Shotton et al., 1993). On the West Sussex coastal plain, less than 5 km apart, the sites of Boxgrove and Valdoe share almost identical stratigraphy, and both have been dated to MIS 13 (Preece & Parfitt, 2022). Boxgrove is particularly significant: two incisors attributed to a Middle Pleistocene hominin (Hillson et al., 2010), a tibia (Roberts et al. 1994), an exceptionally large assemblage of handaxes and large mammal remains bearing anthropogenic modifications were all recovered there (Parfitt & Roberts, 1999). Contemporaneous with these sites are handaxes and flakes from Kent's Cavern, found in secondary position but dated to MIS 13 on the basis of associated microfauna (MacDonald et al., 2012). The English record thus indicates sporadic occupations of high latitudes during MIS 25 and MIS 21 (e.g. Happisburgh 3), renewed presence during MIS 15 (e.g. Fordwich, Maidscross Hill and Brandon Fields), but a more stable and recurrent pattern of settlement becoming firmly established from MIS 13 onwards.

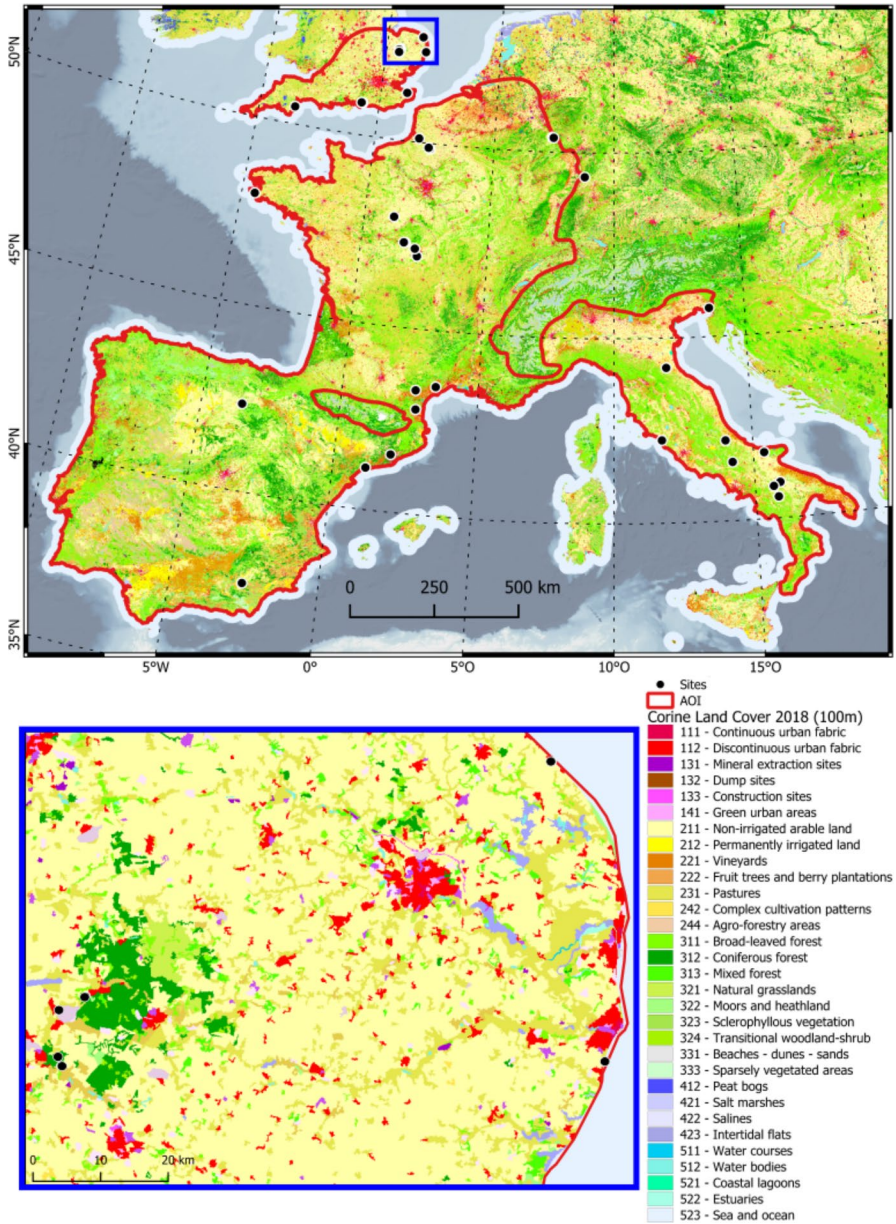
## Representativity of the Archaeological Record

Every archaeological record is subject to time-dependent natural processes, potentially destroying, displacing or obscuring artefacts. These processes include the general taphonomic loss (Coco & Iovita, 2020; Surovell & Brantingham, 2007; Surovell et al., 2009), highly dynamic and destructive erosion event on specific geological systems (Ashton et al., 2011), regional large-scale erosion events (Aurà et al., 2012), and significant sediment build-up, leading to invisibility of sites as, e.g.

in the Carpathian basin (Chu, 2018; Nett et al., 2021). An inventory of archaeological sites such as the one presented above only represents a small subset of all evidence left by our ancestors. The question whether this inventory is representative for the actual distribution of early humans in the paleo-landscape remains hard to answer. Some regional studies have addressed the representativity of the archaeological record, this is the case of Bruxelles and Jerry (2011) for the Garonne Valley Upper Palaeolithic, and the British Early Palaeolithic (Harris et al., 2019). One of the few studies addressing this topic at a supra-regional scale is Boemke et al. (2023), analysing the distribution of 4200 European Upper Palaeolithic occupations. Despite the large sample size, the study showed that the single best predictor of site presence was the contemporary land use, underlining the critical role of external circumstances influencing the probability of discovery. In their study, Boemke et al. (2023) identified three land cover types (i.e. Urban fabric, mineral extraction sites and vineyards) that showed an especially elevated occurrence of sites. Each of these land cover types requires a deep intervention into the sediment which is necessary to detect deeply buried archaeological material Fig. 2. This underlines the big influence of sampling bias on site distribution.

In comparison, archaeological material from the early Middle Pleistocene has been subject to far longer timespans of potential destruction, relocation and/or obscuring sedimentary processes. Therefore, an assessment of the representativity of site distribution is of critical importance to put the results of spatial analyses into perspective. To this goal, we adapted part of the methodology by Boemke et al. (2023) and applied it to our archaeological record on Western European early Middle Pleistocene sites (see Supplementary materials table S3). With the aim of identifying contemporary land use classes that have the biggest impact on the discovery of sites, we conducted spatial intersections between 43 point locations of our archaeological record and both the Corine Land Cover (CLC) dataset with a high thematic resolution but low spatial resolution (44 classes, 100\*100 m spatial resolution, CLMS 2018) (see Fig. 2) as well as the CLC+Backbone dataset with low thematic but high spatial resolution (11 classes, 10\*10 m spatial resolution, CLMS 2018). For the CLC dataset, the years 1990, 2000 and 2018 were used, while CLC+ was only available for the year 2018. In the following paragraphs, only the main results of this analysis are presented. For an overview of all results, see Table S2 in the Supplementary materials.

Despite the large difference in sample size, both the original study and the early Middle Pleistocene site distributions show several similarities when it comes to over- and underrepresentation on certain land cover classes. As such, in our analysis of the CLC dataset, sites were also highly overrepresented on *urban fabric* (up to a factor of 12.4, varying between land cover datasets) as well as *mineral extraction sites* (up to a factor of 81). While these factors of overrepresentation are significantly higher than those found by Boemke et al. (2023), which could be interpreted as a higher predictive strength of the contemporary land use, they need to be considered cautiously as our sample size is significantly smaller. We observed a high over-representation on coastal classes such as *intertidal flats and beaches-dunes-sands*. This can be explained by the depth of sediment-intrusion caused by coastal erosional processes. For the CLC+Backbone dataset, similar trends were observed with the highest over-representation of sites



**Fig. 2** Above, map of Europe showing the study area encircled in red, the archaeological sites over the Corine Land Cover 2018 map. Below, zoom on the map corresponding to eastern England encircled in blue. Details on the analysis can be found in Table S2 and S3

on the classes *sealed* (factor of 4.6) and *non and sparsely vegetated areas* (factor of 6.4). These correspond to the CLC classes urban fabric as well as mineral extraction sites and coastal areas, further underlining the previous results.

Although the results of the geostatistical analysis must be interpreted with caution due to the relatively small sample size of only 43 sites (see Fig. 2), they nonetheless confirm and reinforce existing ideas about the likelihood of discovering early Middle Pleistocene archaeological sites. The pronounced over-representation of sites within certain land-cover types suggests that archaeological deposits are most often encountered in contexts subject to substantial earth disturbance, whether through natural erosion or anthropogenic sediment intrusion. In short, the more disturbed the ground, the higher the probability of site discovery. Conversely, land cover types that primarily affect only the surface level, such as arable land, are under-represented and thus associated with a low probability of discovery. This pattern is consistent with the depth at which most Early and early Middle Pleistocene contexts are located, and with the fact that several have been uncovered during extraction work in commercial quarries, as exemplified by numerous English sites. For the purposes of this study, these results highlight the significant impact that sampling bias is likely to have on the observed distribution of sites. More broadly, they remind us that the spatial patterning of the archaeological record is shaped not only by the environmental preferences of hominin groups, but also by the availability of sedimentary contexts conducive to preservation, as well as by the erosional processes and extractive activities that ultimately expose the remains.

### Paleoanthropological Record

The paleoanthropological record of Western Europe is characterised by the scarcity of hominin remains. Nevertheless, the specimens that have been taxonomically classified provide important insights into the population dynamics of the continent. The earliest hominin fossils in Western Europe are found in the Iberian Peninsula and date to ca. 1.4–1.1 Ma. Among them is a deciduous molar from Barranco León, which could not be assigned to a specific taxon (Toro-Moyano et al., 2013). More significantly, the oldest hominin face in Western Europe was discovered at level TE7 of Sima del Elefante, broadly contemporaneous with the Orce remains. This specimen has been classified as *Homo* aff. *erectus* since researchers argue that although it shows similarities with *Homo erectus*, it also displays notable morphological differences from the fossils usually referred to this taxon (Rosa Huguet et al., 2025). Stratigraphically above, in level TE9c, a phalanx and a mandibular fragment were recovered, although their taxonomic attribution remains inconclusive (Bermúdez de Castro et al., 2011; Carbonell et al., 2008).

Also, within the Sierra de Atapuerca, the unit TD6 of Gran Dolina yielded a partial juvenile face that led researchers to describe a new species, *Homo antecessor* (Bermúdez de Castro et al., 1997). The assemblage, comprising 170 human fossils representing a minimum of eight individuals, has enabled a detailed evaluation of the taxonomic and phylogenetic position of *Homo antecessor* (Bermúdez de Castro et al., 2017). Within the last decade, enamel proteome analysis from a molar fragment has provided molecular evidence suggesting that *Homo antecessor* shared a close evolutionary relationship with the last common ancestor of *Homo sapiens*, *Homo neanderthalensis* and Denisovans (Welker et al., 2016).

Nevertheless, the exact phylogenetic relationships among the Early Pleistocene specimens remain unresolved. Several remains cannot be confidently assigned to any species, and thus, the taxonomic position of *Homo antecessor* continues to be debated, while the classification of *H. aff. erectus* remains provisional. Recent work by Huguet et al. (2025) suggests that a population turnover occurred between the occupations of Sima del Elefante and Gran Dolina. Supporting evidence includes differences in faunal assemblage composition between the two sites (Cuenca-Bescós et al., 2016), hypotheses of a significant decline in habitat suitability during MIS 34 (Margari et al., 2023), and genetic evidence pointing to a severe human bottleneck around 900 ka (Deng et al., 2025; Hu et al., 2023). These findings indicate that Europe was likely inhabited by at least two distinct hominin species during the Early Pleistocene. The mechanisms of this turnover remain uncertain: *Homo antecessor* may have colonised an empty territory following local extinction, or alternatively, it may have briefly overlapped with *Homo aff. erectus* before replacing it.

The period between 900 and 500 ka is marked by the appearance of *Homo heidelbergensis*. The species was first defined from the Mauer mandible (Schoetensack, 1908), and its emergence is generally dated to around 600 ka (Wagner et al., 2011). Between 600 and 500 ka, *Homo heidelbergensis*—whose phylogenetic and taxonomic status remains debated—has been identified at two sites: At Caune de l’Arago, more than 400 remains belonging to at least 30 individuals have been recovered (de Lumley, 2015) and at Notarchirico, where a tibia fragment has been attributed to this taxon (Micarelli et al., 2024). The record is further complemented by a deciduous tooth from Isernia La Pineta, more cautiously assigned to *Homo sp.* (Peretto et al., 2015).

## Technological Behaviour

Between 1.4 and 1.0 Ma, the archaeological record in Western Europe is generally sparse and widely dispersed, making it difficult—or even impossible—to identify consistent, long-term technological and behavioural patterns. Nevertheless, studies of Early Pleistocene lithic assemblages in Western Europe reveal several shared technological features (Carpentieri & Arzarello, 2021; Despriée et al., 2024; Gallotti & Peretto, 2015; Lombao, 2021; Lombao et al., 2023, 2024; Marina Mosquera et al., 2018).

Raw material procurement strategies are characterised by the exploitation of locally accessible (i.e. < 5 km from the site) lithological varieties such as chert, limestone, sandstone, quartz, quartzite and basalt with a wide range of qualities and morphologies. Reduction sequences are mostly short, aimed at obtaining products with a cutting edge (i.e., unretouched flakes and heavy-duty tools). The identification of all the elements of the reduction sequences at Gran Dolina-TD6.2, Monte Poggiolo, Fuente Nueva 3 and Barranco León (Arzarello et al., 2016; Barsky et al., 2022; Carbonell et al., 1999; Moyano et al., 2011; Peretto et al., 1998; Yravedra et al., 2024) suggests systematic in situ knapping of materials. The variability observed in knapping strategies suggests that Early Pleistocene hominins were “situational knappers”, capable of adjusting their *know-how* to the specific characteristics of each

context, depending on the morphology and quality of the available raw materials (Lombao et al., 2023). Direct percussion with a hard hammer is the predominant technique. However, when the blank is small or of low quality, the bipolar-on-anvil technique is preferred over freehand percussion, as observed at sites such as Pont-de-Lavaud, Vallparadís, Fuente Nueva 3, Barranco León, Gran Dolina TD6.2, and Ca' Belvedere di Monte Poggiolo (Arzarello & Peretto, 2010; Barsky et al., 2015; de Lombera-Hermida et al., 2016; García et al., 2013). Most Early Pleistocene mode 1 assemblages in Western Europe contain few, if any, retouched implements. An exception is TD6, where retouched tools are relatively common and appear to be made predominantly on higher-quality raw materials (Mosquera et al., 2018). This has been interpreted either as a more advanced phase in archaic technology (*sensu* Carbonell et al., 2016) or as an outcome of more intense and recurrent site occupation (Lombao, 2021; Lombao et al., 2023).

Around 900 ka, a suite of technological innovations is documented in Western Europe, primarily at Barranc de la Boella (Lombao et al., 2024; Mosquera et al., 2015, 2016; Ollé et al., 2023). The site raises questions on the onset of the early Acheulean technocomplex in Western Europe, characterized by the production of large-shaped tools, particularly picks, which dominate the assemblage at Pit 1 locality. Other large tools, including cleavers, knives, and choppers, are present, though classical handaxes are notably absent (Ollé et al., 2023). This assemblage reflects an expanded technological repertoire, with specialized raw material management. Chert was primarily used to produce flakes and small retouched tools, while schist was employed for large flakes (> 10 cm) and large-shaped tools. Moreover, the spatial and temporal separation of large flake and large tool production suggests a structured organization and a well-planned resource exploitation (Lombao et al., 2024). Core reduction strategies at Barranc de La Boella exhibit a combination of sequential flaking to maximize flake production and opportunistic knapping, similar to mode 1 technological features. Variability in core reduction intensity and volumetric exhaustion further supports the presence of diverse knapping strategies (Lombao et al., 2024).

These technological features indicate the earliest appearance of technological and behavioural changes, described as mode 2 in Western Europe since the late Early Pleistocene (Mosquera et al., 2016; Vallverdú et al., 2014). However, this technocomplex did not replace mode 1. In fact, several sites lacking large cutting tools—such as Gran Dolina TD6, Vallparadís and Happisburgh 3—chronologically overlap with those featuring large cutting tools, including El Barranc de la Boella. Moreover, assemblages without bifaces are also penecontemporaneous with behavioural innovations attributed to mode 2.

The early Middle Pleistocene (780–500 ka) lithic record exhibits substantial variability in the presence, morphology and typology of LCTs, as well as in core knapping strategies (Carpentieri et al., 2023; Moncel et al., 2020a, 2020b, 2022). Initially, researchers distinguished different phases within the Early and Late Acheulean (~ 500 ka) in Europe (Gallotti & Peretto, 2015; Moncel & Schreve, 2016; Mosquera et al., 2013). More recent analyses have identified additional variability within the early Acheulean itself, suggesting different technological phases or population dispersal waves (Lombao et al., 2024; Ollé et al., 2023).

While some early Acheulean behaviours resemble mode 1, such as reliance on locally available raw materials, there is an increasing emphasis on strategic raw material selection in some sites (i.e. Caune de l'Arago). At Bois de Riquet US4, local raw materials appear to have been deliberately chosen for specific tool production, reflecting a minimal degree of planning (Barsky et al., 2015; Bourguignon et al., 2016a). The presence of “giant cores”, partially reduced and likely reserved for later exploitation, further suggests foresight in lithic production. Similarly, at La Noira stratum a, local silicified limestone tablets were selected based on thickness for either flake or handaxe production (García-Medrano et al., 2022; Moncel et al., 2016, 2020a, 2020b, 2021a, 2021b).

The early Acheulean is marked by the production of both large and small flakes, as well as the emergence of LCTs, including cleavers, picks and handaxes. However, considerable typological and technological diversity is observed across different sites. At Barranc de la Boella, picks and cleaver-like tools predominate, whereas later sites, such as la Noira stratum a contains a large quantity of unstandardized heavy-duty tools, with shaping or retouched focused on specific cutting edges (Moncel et al., 2020a).

Handaxes become more frequent in later assemblages, such as La Noira, Notarchirico, and Moulin Quignon, though they remain low in ratio. When present, they often co-occur with partially bifacially worked tools (Antoine et al., 2019; Moncel & Schreve, 2016; Moncel et al., 2019, 2020a, 2020b, 2021a, 2021b). A notable characteristic of early Acheulean sites is the low frequency of large flakes being used for heavy-duty tools or as cores, a pattern that contrasts with later Acheulean assemblages from 500 ka and onwards (Ashton & Davis, 2021; de Lumely, 2015; García-Medrano et al., 2023; Moncel & Ashton, 2018; Moncel et al., 2012; Mosquera et al., 2024; Ollé et al., 2016a, 2016b; Peretto et al., 2016; Rubio-Jara et al., 2016; Santonja & Villa, 2006; Villa et al., 2016a, 2016b). Moreover, regional trends seem to exist with cleavers on flake in the south while lacking in the north-west.

Shaping techniques and handaxe morphologies display significant diversity without a clear trend toward increasing refinement over time during the Early Middle Pleistocene (Moncel & Schreve, 2016). This variability is evident in long sequences such as la Noira and Caune de l'Arago, where archaic crudely made forms persist. At Notarchirico, LCTs appear intermittently across the archaeostratigraphic sequence (Moncel et al., 2019, 2020b).

Despite the technological diversity of early Acheulean assemblages, a broad diachronic pattern can be identified. During the late Early Pleistocene (Barranc de la Boella), picks are present while handaxes are absent, whereas a reversed trend is recognized in the early Middle Pleistocene. These younger assemblages are characterized by a greater emphasis on bifacial tools (i.e. handaxes), while picks and trihedral tools become rare or disappear altogether.

Additionally, core reduction strategies exhibit increasing complexity and volumetric control. While simple unipolar and multipolar knapping strategies characteristic of mode 1 continue to be used, the bifacial centripetal knapping and alternating striking surfaces—become more common with a higher productivity and independence of the raw material constraints. This growing technological

complexity is also seen in the fragmentation of reduction sequences, particularly in the processing of larger blanks and the manufacture of large-shaped tools. As a result, LCTs are often produced in one location, transported to another, and ultimately discarded far from their point of origin.

For instance, La Noira stratum *a* demonstrates a systematic separation of flake and handaxe production, with different reduction strategies for smaller and larger tools. Similarly, the presence of partially reduced “giant cores” at Bois de Riquet US4 suggests that some large blanks were intentionally set aside for later stages of toolmaking. This contrasts with the production of smaller flakes, which typically occurs and is used at the same site (Viallet et al., 2022). The selective transport of LCTs, along with increasingly sophisticated raw material selection, reflects a notable degree of planning and foresight, marking a shift toward more structured technological behaviours in the early Acheulean. In summary, during the first half of the Middle Pleistocene, lithic assemblages reflect a combination of previously recognized mode 1 technological behaviours and emerging new behavioural trends. While locally available raw materials continued to be used within a 5-km radius, raw material selection became increasingly strategic, considering knapping objectives, shape, size and quality. Additionally, more complex knapping techniques, such as bifacial centripetal reduction, became widespread, suggesting a gradual shift toward overcoming raw material constraints (Carpentieri et al., 2023; Lombao et al., 2024; Moncel et al., 2020a, 2020b, 2021a, 2021b). Overall, this technological scenario reflects a period of significant transformation, where the adoption of large-shaped tools varied based on local conditions, including raw material availability, site function and occupation intensity. The potential arrival of new populations with distinct technological behaviours or local evolution over time of isolated or related populations may have further contributed to this variability. Consequently, the early Acheulean in Europe presents a mosaic of technological strategies, where more complex approaches coexisted with opportunistic methods, underscoring the dynamic and evolving nature of this period.

## Subsistence Behaviour

Subsistence inferences regarding the earliest inhabitants of Western Europe are currently very limited, specially for chronologies exceeding one million years, and particularly for sites in North-West Europe. This is due to various factors, including (a) the low number of sites; (b) many assemblages are located on river terraces and thus primarily composed of lithic materials associated with scarce bone remains (e.g., Despriée et al., 2010; García-Garriga, 2014); (c) in assemblages where faunal remains are preserved, evidence of anthropogenic activity is minimal, either as a result of preservation issues affecting bone surfaces and pre-existing modifications (Domínguez-Rodrigo et al., 2007; Pineda & Saladié, 2022) or because these are palimpsests formed in open-air settings during multiple events, where the association between fauna remains and lithic tools is not necessarily proved.

Only two sites in Western Europe allow researchers to make inferences about subsistence behaviour before 1Ma: Sima del Elefante and Fuente Nueva 3. The

main evidence at Fuente Nueva 3 is related to the acquisition and consumption of a partial carcass (primarily cranial and axial skeleton) of a mammoth (*Mammuthus meridionalis*) by hominins. Two interpretations have been proposed. First, Espigares et al. (2013) perceive spatial association between the remains with lithic tools and hyena coprolites. This leads them to suggest a natural death of the mammoth followed by a primary access by hominins, who transported the limb to a different site, followed by hyenas. However, there is no conclusive evidence to confirm whether the death was natural or the result of predation. Second, Yravedra et al. (2024) argue that the coprolites and stone tools are not spatially associated with the mammoth. Nevertheless, they also support the consumption of the carcass by hominins and felids, based on the identification of cut marks and felid tooth marks on the bone surfaces. However, mammoths and other megaherbivores (> 1000 kg) were not the primary prey of Paleolithic human groups, who primarily hunted medium- and large-sized ungulates.

At Sima del Elefante, anthropogenic traces are mainly associated with deer, horse and bovids in the lowest levels of the sequence (> 1.2 Ma) (Huguet et al., 2017, 2025). Although these accumulations were predominantly formed in secondary position due to mudflows (Rosas et al., 2006), the anatomical distribution of cut marks suggests primary access to the carcasses by hominin groups (Huguet et al., 2017), either through hunting or, less likely but not excluded, active scavenging. The consumption of turtles has also been proposed in at least two levels of the site, based on the identification of incisions on the ventral surface of some recovered shell fragments, likely produced during the evisceration of these animals (Blasco et al., 2011). Other assemblages from similar chronologies, such as Barranco Leon, Pirro Nord, Alto de las Picarazas or Bois-de-Riquet, exhibit scarce or no evidence of anthropogenic modification of carcasses, making reliable subsistence inferences limited (Arzarello et al., 2007; Bourguignon et al., 2016a; Giusti & Arzarello, 2016; Moclán et al., 2023; Vicente Gabarda et al., 2016; Yravedra et al., 2022).

From one million years onward, the available evidence and inferences increase. The most paradigmatic case is subunit TD6.2 of Gran Dolina, where an extensive record of faunal and stone tools has been recovered. This level has been interpreted as a residential camp, where hominin groups systematically transported carcasses after hunting (Saladié et al., 2011, 2012). This would reflect a complex development of cooperation among individuals for the acquisition, exploitation and distribution of resources. Furthermore, the absence of carnivore activity has been explained as evidence of the high degree of territorial control exerted by hominin groups (Saladié et al., 2014). Additionally, the *Homo antecessor* remains show cut marks and anthropic breakage, indicating they were treated similarly to other consumed animals. This was interpreted as the earliest evidence of intergroup violence within the genus *Homo*, involving the hunting and subsequent consumption of the most vulnerable individuals from neighbouring groups to decimate their generational continuity and expand territorial dominance (Saladié et al., 2012). Remarkably, evidence of plant and fruit consumption have been found in this same context. Some hackberry (*Celtis* sp.) seeds, which could have provided carbohydrates, fibres and essential micronutrients for a proper metabolic functioning, have been recovered and interpreted as brought into the cave by *Homo antecessor* for consumption (Allué

et al., 2015). In the same assemblage, dental microwear studies of *Homo antecessor* have revealed an abrasive diet rich in hard vegetables, tubers possibly containing sand particles, as well as collagen, connective tissue and raw bone or meat (Pérez-Pérez et al., 2017).

In similar chronologies, Pit 1 of Barranc de la Boella has yielded mammoth remains associated with over four hundred stone tools, cut marks on a rib fragment and indirect evidence from the use-wear analysis of certain flakes, which were likely used for defleshing (Fidalgo et al., 2025; Mosquera et al., 2015; Vallverdú et al., 2014). Exclusive access by hominin groups has been proposed, although the mode of access to the carcass remains unknown. Conversely, the other two assemblages from Barranc de la Boella, La Mina and El Forn, exhibit limited evidence of anthropogenic processing of carcasses (Pineda et al., 2014), and the relationship between fauna and stone tools is not documented. These sites have been interpreted as transit areas, where hominin groups were likely passing through in search of resources, not only meat but also water, plants or raw materials for stone tool production (Pineda et al., 2015, 2017). Once again, other assemblages such as Vallparadís, Monte Poggiolo or Site 3 at Happisburgh do not exhibit clear signs of anthropic activity that would enable reliable subsistence inferences (e.g. (e.g. Arzarello & Peretto, 2010; Martínez et al., 2010; S. A. Parfitt et al., 2010).

A paradigmatic site for the study of hominin carnivorism during the Middle Pleistocene is Notarchirico. At this site, the remains of an adult elephant were found spatially close to lithic tools. The proximity of the artefacts to the faunal remains lead to its interpretation as a butchering site (Cassoli et al., 1993; Piperno & Tagliacozzo, 2001). However, after closer re-examination, this association does not appear to be supported by clear evidence (Pineda et al., 2024), nor has it been conclusively demonstrated at Italian sites such as Cimitero di Atella and Ficoncella (Rocca et al., 2021). In contrast, other sites, including Happisburgh Site 1 (Lewis et al., 2019), Boxgrove (Pope et al., 2021; Smith, 2013), and Caune de l'Aragó (Chen & Moigne, 2018), exhibit clear anthropogenic evidence associated with hunting activities by hominin groups. In Caune de l'Aragó, the active scavenging or opportunistic hunting of various *Stephanorhinus hemitoechus* individuals has been proposed at level F, slightly younger than 500 ka. This would have included acquiring and transporting the carcasses to the cave for intensive processing (Chen and Moigné, 2018). From a similar time frame, at Boxgrove, an almost complete carcass of a large female horse showing clear evidence of processing was recovered in close spatial proximity to bifacial lithic tools and bone tools in the so-called *Horse Butchery Site GTP17*. This assemblage has been interpreted as a butchery site, representing the acquisition and exploitation of the animal's carcass during a single, discrete event (Pope et al., 2021).

In summary, inferences about the subsistence behaviour of Early and early Middle Pleistocene hominins are biased due to the lack of taphonomic studies in many assemblages and the limitations derived from the poor preservation of bone surfaces in most cases (Pineda & Saladié, 2022). Nevertheless, the available data clearly indicate that hominin groups had primary and early access to ungulate carcasses, mostly of medium and large size. There is also evidence for the exploitation of megaherbivores weighing over a tonne, such as mammoths, which may indicate the

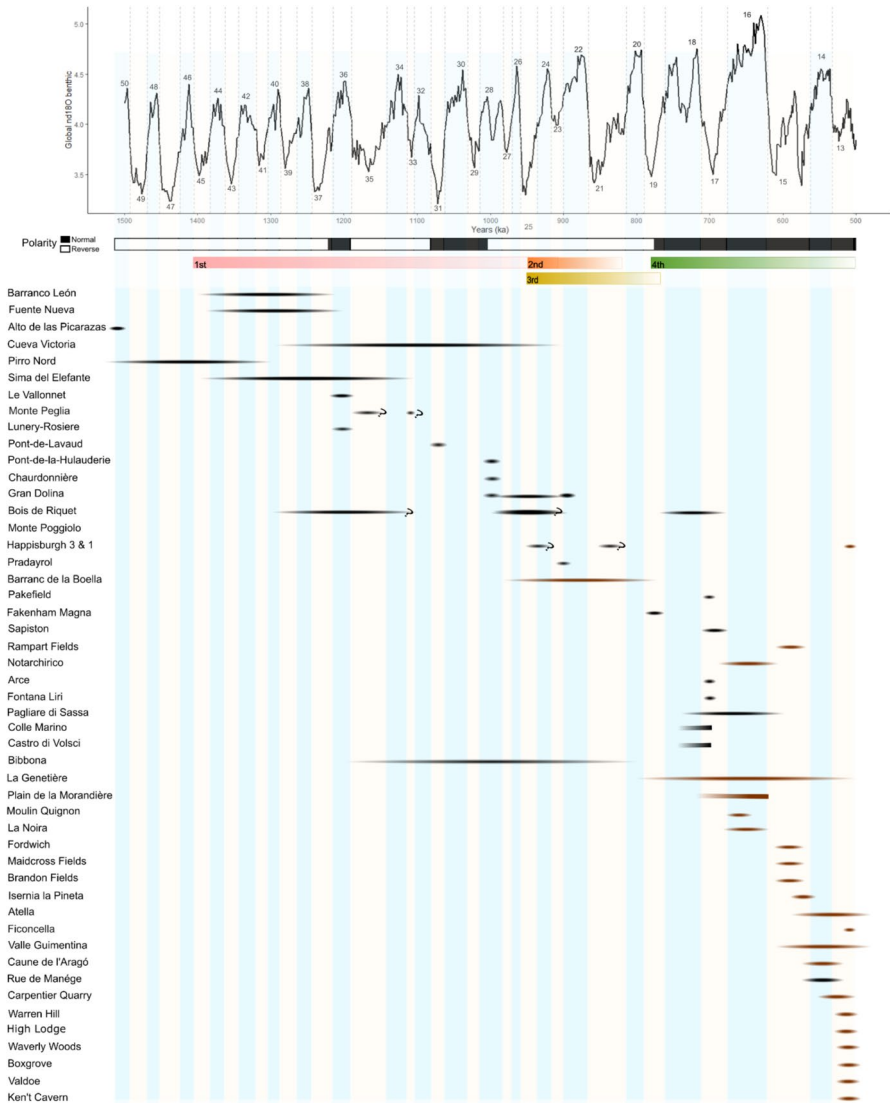
importance of these animals in the acquisition and consumption of meat for these groups.

## Discussion

### What the Record Shows

The study of early Western European populations now seems to have overcome the *old vs young chronology* discussion and established baseline trends. The oldest unequivocal evidence of hominins in Western Europe comes from the Iberian Peninsula and is dated around 1.4–1.2 Ma. As shown in Table S1, the number of sites before 1 Ma is very limited, and the number is even lower when only considering unquestioned dates. The number of sites documented between 1 Ma and 780 ka is not much higher, and it is not until after 500 ka when an increase of population density and distribution is discerned from the archaeological record (French, 2021). Particularly, four dispersal phases of different intensities are visible in the archaeological record (see Fig. 3). The first phase, or the initial arrival, is characterized by the arrival of the first hominins associated with mode 1 (cores-and-flakes technology). Among the most characteristic sites of this phase is Sima del Elefante (TE9 and TE7), which yielded remains ascribed to *Homo* sp. and the partial face of *Homo* aff. *erectus* in association with mode 1 tools (Bermúdez de Castro et al., 2011; Huguet et al., 2025). The evidence of hominin presence is limited to Southern Europe, namely the Iberian Peninsula and Italy. Technology is characterized by simple cores, unretouched and unstandardized flakes, a component of crudely made, heavy-duty tools and the exclusive use of local raw materials. Evidence related to the subsistence during this period remains scarce. Cut marks identified on some bones from Sima del Elefante (Huguet et al., 2025) indicate that human groups had primary access to the carcasses. This pattern is consistent with the results reported by Espigares et al. (2013) and Yravedra et al. (2024) at Fuente Nueva 3. Nevertheless, no reliable inferences can yet be drawn regarding the specific means by which the carcasses were accessed.

The second phase is represented by *Homo antecessor*, found at Gran Dolina TD6 (ca. 900 ka). The interpretation of *Homo antecessor* as a basal taxon in the common lineage of *Homo sapiens*, Neanderthals and Denisovans implies that the dispersal event had an African origin (Welker et al., 2020). When settling this population, they may have encountered an empty territory or a brief overlap in some areas with a very sparse population (Rosa Huguet et al., 2025). This population turnover aligns with a proposed decline in hominin's habitat suitability index around MIS 34 (Margari et al., 2023) and the faunal discontinuity between TD6 and TD9 (Gloria Cuenca-Bescós et al., 2016). Technologically, mode 1 assemblages show greater technical diversity, including a relatively high frequency of retouched tools within the assemblage (Mosquera et al., 2018). At the subsistence strategies level, we find the earliest evidence in Europe of a home base, where *Homo antecessor* would have hunted, transported and extensively processed the carcasses of the obtained preys in a highly competitive context



**Fig. 3** Chronological span of the sites considered in the paper and the four phases of population proposed in the discussion. For more information in the site’s chronology see Table S1

(Saladié et al., 2011, 2014), with clear evidences of cannibalism, being the earliest documented to date (Saladié et al., 2012).

The third phase is marked by the lithic assemblages from Barranc de la Boella, where the oldest LCTs in Europe appear (ca. 990–780 ka). Although the biological agent behind this technology has not yet been identified, the lack of transitional assemblages is interpreted as evidence of mode 2 technologies being an “imported” influence. It has been proposed that it might represent a new population wave into

Europe, possibly related to the populations of ‘Ubeidiya (Israel) dated between 1.4 and 1.2 Ma (Ollé et al., 2023). While the involvement of *Homo antecessor* cannot be ruled out, it is also plausible that another species is responsible. The presence of mode 2 technology at Barranc de la Boella is contemporaneous with mode 1 technology at TD6 (only 500 km apart). The co-occurrence of mode 1 and mode 2 industries, which continues to be documented through the Middle Pleistocene, suggests a complex scenario with potential cultural overlap and the coexistence of distinct technological and regional traditions, rather than a simple linear replacement sequence.

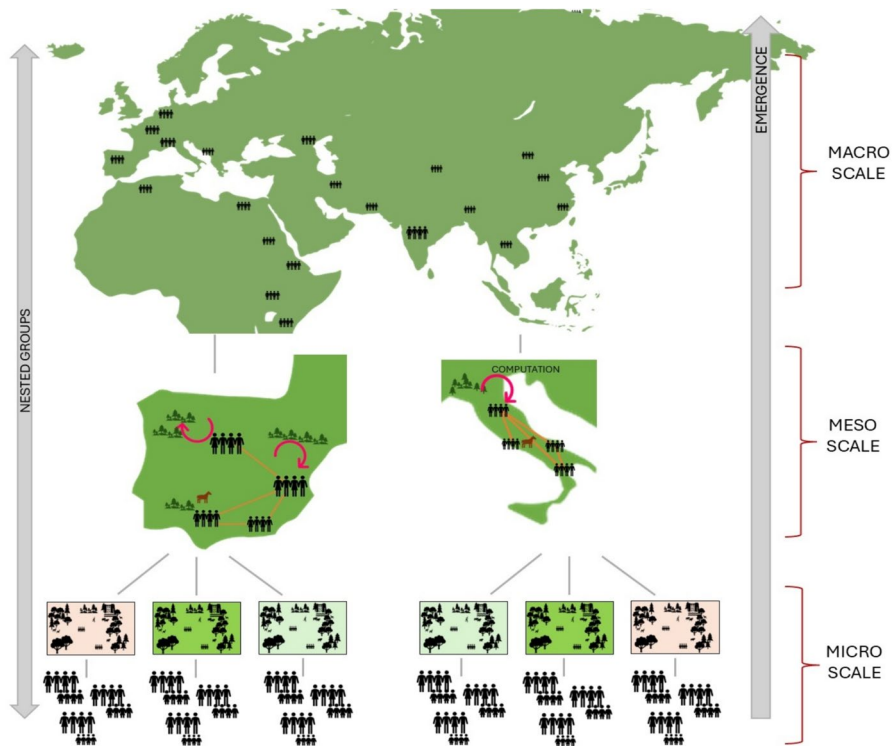
The fourth phase is associated with the appearance in the record of the remains ascribed to *Homo heidelbergensis* (between 780 and 500 ka). Human remains were recovered from Notarchirico, Caune de l’Aragó and Boxgrove. Whether it was a single event or multiple successive entries remains uncertain, although it is proposed that it was a faster and more successful dispersal during a time of ample climatic fluctuations (Moncel et al., 2020a, 2020b). Technologically, this phase shows a growing presence of mode 2 technology, particularly bifacial shaping, although it often coexists with mode 1-type strategies. The adoption of bifacial tools (i.e. handaxes) appears gradual, with significant variability between regions and even within individual sites. It also shows a selective exploitation of raw materials and an increased mobility of tools, especially LCTs. Characteristic of this phase are the assemblages from Notarchirico (Moncel et al., 2020a, 2020b), La Noira stratum a (Moncel et al., 2020a, 2020b) and Moulin Quignon (Pierre Antoine et al., 2019). Importantly, even as these advanced technologies spread, previous mode 1-type technologies continued to exist (see Fig. 3) and are even found intercalated within the same sequence (e.g. Notarchirico—see Moncel et al., 2020a, 2020b) indicating a diverse and non-homogeneous cultural landscape across Europe with persistence of basic, efficient know-how. Overall, the early European Acheulean should not be viewed as a strict rupture with mode 1, but rather as an expansion of the technological repertoire, with overlapping practices and gradual innovation. This perspective is supported by the persistence of mode 1 strategies in several sites, even after the appearance of bifacial tools. It is during this period that we document greater variability in the use of space and in subsistence patterns in Western Europe, including the so-called Horse Butchery Site GTP17 at Boxgrove (Pope et al., 2021) and the evidence of primary access to rhinoceros’ carcasses at Caune de l’Aragó (Chen and Moigné, 2018). Nevertheless, most assemblages still provide only limited possibilities for subsistence inferences.

## Scales and Interplay

The population of Western Europe cannot be conceived as an isolated process that developed in a linear fashion. In fact, it took place within a larger process: the first “Out of Africa”. With a research object of this scale, one of the biggest challenges we face is the manipulation and reconciliation of data and dynamics at different temporal and spatial scales. e.g., How can we scale observations from archaeological sites to understand how populations were affected by climatic oscillations registered in ice and marine cores? Systems theory is a cross-disciplinary framework that allows for the conceptualization and study of hominin populations and their

environment (Burke et al., 2025). This is to say that hominin populations fulfil the features of a Complex Adaptive System (CAS) (Barton 2014; Burke et al., 2025), they are composed of heterogeneous entities; these (whether they are individuals or groups) perceive and react to climate and environment around them and interact with each other with varying frequency and intensity. Equally, from a CAS perspective culture is also a dynamic, complex system that interacts with the Earth and the human system (Burke et al., 2025). The relational and nested structure (Fig. 4) of a complex system, that accounts for emergent phenomena within the system, is a suitable framework to approach the different temporal and spatial scales of our phenomenon of interest and how they are interlinked (Fig. 4). It is the different levels of integration and the nested nature of complex systems that allow us to approach parts of the phenomenon separately but also in its totality. Specifically, we propose the modelling of this process in three different scales: micro, meso and macro as depicted in Fig. 4.

The scale refers to both time and space. The micro scale, or local, would consider individuals as study objects and the time scale spans from one to several years. This scale provides the main source of direct information for understanding the behaviour



**Fig. 4** Characteristics of populations as complex systems with specification of the spatial extent of each of the three scales of study we propose. Adapted from <https://necsi.edu/visualizing-complex-systems-science>

of hominin groups and populations. At this scale, researchers deal with material remains of mostly local activities, and obtain information on the technological behaviour of the group (e.g. Lombao et al., 2024) or their subsistence strategies (e.g. Pineda et al., 2024). Further questions that can be answered at this scale concern the efficiency of hominin groups in exploiting a particular environment (e.g. Reschke et al., 2024), patterns of mobility throughout the year, i.e. how spatial behaviour changes with the seasons, the effects that a particularly brief but marked climatic episode might have on a group, or how the introduction of innovations might affect a group's efficiency in exploiting its environment.

The meso, or regional, scale would focus on various groups and their interaction with each other and with the environment. The regional scale is variable in its specific extent, and the temporal scale is linked to specific climatic events or climatic oscillations. As an example, the work of Hosfield and Cole (2018) investigates the possible drivers of hominin expansion into northern Europe. After examining the records, they conclude that it shows that dispersal was facilitated by the emergence of behavioural plasticity visible through the emergence of mode 2 technology. Another regional study analyses the pollen record and computationally reconstructs changes in habitat suitability indices during the particularly adverse conditions of MIS 34, concluding that these could have caused a population bottleneck (Margari et al., 2023). Studies like this are the basis for answering questions about what happens to human groups occupying the region when substantial environmental changes occur: would the groups disappear or migrate to territories with a more benign environment? How would that affect population distribution and size? The regional scale is also suitable for studying the development of cumulative culture, the loss of cultural capital or the diffusion of innovation and its relationship to population structure and climatic oscillation.

The macro-scale in this case refers to continental or intercontinental processes and focuses on a time interval that can range from a few hundred thousand years to more than a million years. This is the scale we deal with at this paper. We have reviewed the archaeological record that suggests that Western Europe may have been "visited" (*sensu* French, 2021) by multiple waves and therefore experienced several instances of population and depopulation. The "source and sink" model (Dennell et al., 2011) is therefore the explanatory theory that best fits the current archaeological record. It proposes that, during the initial dispersal into western Europe, hominin populations endured glacial periods in southern latitudes, which acted as refuges, and were only able to venture to higher latitudes during the warm phase. The idea that early hominins were sensitive to harsh climates is supported by evidence associating their earliest occupations with mild conditions and predominantly open landscapes (Agustí et al., 2009; Altolaguirre et al., 2019; Blain et al., 2011; Leroy et al., 2011). In recent years, this notion has been challenged to a certain degree by the pioneer population events recorded in France and England. At Lunery-Rosiere, where the occupation took place at the early MIS 36 suggests hominins were capable to adapt to early glacial conditions (Despri   et al., 2024). At Pont du Lavaud (ca. 1.1 Ma), the pollen showed the environment was densely forested (Marquer et al., 2011). At Happisburgh 3, the occupation took place in a northern forest environment with cool continental climate (Parfitt et al., 2010). At

Moulin Quignon, the occupations took place under harsh conditions (Antoine et al., 2015). At present, the degree of tolerance of hominins to harsh/cold environments remains undetermined, although habitat suitability models and other computational approaches seem to be a suitable methodological approach to elucidate this question (e.g. Margarit et al. 2023; Rodríguez et al. 2021).

The question arising from the “sink and source” model concerns the regions from which the source populations would repeatedly disperse in Europe. (Dennell et al., 2011). Within Europe, judging from the current archaeological record, that region could be the Iberian Peninsula. Although previously population continuity had some support (e.g. Bermúdez de Castro et al., 2013; Rosa Huguet et al., 2013), current evidence suggests a population turnover could have taken place during Early Pleistocene (MIS 34) (Margari et al., 2023) correlated with the discontinuity between the occupations of Sima del Elefante and Gran Dolina (Huguet et al., 2025). As for the Middle Pleistocene, Gran Dolina—which records both absences and presences of hominins (Ollé et al., 2016a, 2016b; Mosquera et al., 2013; MacDonald et al., 2012, p. 92.)—mode 1 tools and *Homo antecessor* remains are followed by a hiatus in hominin presence (TD7 and TD8) spanning approximately 900–500 ka (Berger et al., 2008; Moreno et al., 2015; Parés et al., 2013). Subsequently, Acheulean tools appear almost synchronously at the Galería, Gran Dolina TD10 and Sima de los Huesos sites (Ollé et al., 2016a, 2016b). Therefore, based on the longest and most complete record available, the Iberian Peninsula was inhabited for long periods of time, but not continuously. If southern Europe, with mild environmental conditions, was depopulated, it is reasonable to assume that the rest of Europe would also be depopulated too (Dennell et al., 2011). However, as can be seen in Figs. 1 and 3, several European sites are dated within this time interval, which could suggest that the Iberian Peninsula was populated, but the sites were not. On the available evidence, it seems unlikely that the Iberian Peninsula could have acted as a major source of population; some authors consider it more realistic to regard western Europe as a sink for population from Eurasia or even Africa (French, 2021).

The dispersal events visible in the archaeological record appear to originate primarily from Africa (Fig. 4). However, the assumption that Africa was the sole source of population for Eurasia may be an oversimplification amplified by the bias and fragmentation of the archaeological record. Some researchers support the possibility of population exchange between Africa and Eurasia (Dennell, 2008; French, 2021). The routes travelled by hominins during their forays into Europe are equally difficult to elucidate. Dmanisi (South Caucasus, Georgia), at the crossroads between Africa, Asia and Europe, is considered the gateway to Europe. It is suggested that hominins most likely arrived there via the Levantine corridor, the only land corridor between Africa and Europe (Falguères, 2020). The spatial disconnect between Dmanisi and the oldest sites in Western Europe may be bridged by the mode 1 lithic assemblage from Korolevo, dated to approximately 1.42 Ma (Garba et al., 2024). According to the researchers who dated the site, this is the first plausible evidence of a dispersal from the east, from the Levant, through Asia Minor, the Danube corridor and the Pannonian Basin. Hominins could also have crossed via the northern Black Sea. This proposal has been heavily criticized (see Demidenko, 2024) due to the lack of geographic and archaeological evidence connecting the sites and doubts

about the primary position of the dated materials. Two routes involving crossing the sea have been proposed: the crossing from Tunisia to Sicily (Howitt-Marshall & Runnels, 2016) and across the Strait of Gibraltar. It is worth considering that the Sicilian route is archaeologically impossible to trace (Falgueres 2020; Villa, 2001). The passage through the Strait of Gibraltar is supported by a chronostratigraphic model indicating that the Orce sites are the oldest in Europe and that African taxa are present on the Iberian Peninsula (Gibert et al., 2024). Given the difficulty of crossing the strait without rafts even during the Lower Pleistocene (Hölzchen et al., 2016), the feasibility of this crossing has always been in doubt (O'Regan 2008).

As for the waves that introduced LCTs and mode 2 technologies, they are thought to have come from Africa via the Levant. It was suggested that the appearance of LCTs in Barranc de la Boella and Notarchirico was the result of two waves related to Gesher Benot Ya'qov (ca. 900 ka, Israel) (Moncel et al., 2020a, 2020b). The most recent proposal differentiates the origin of the first wave, linking the Barranc de la Boella lithic assemblage to 'Ubeidiya (ca. 1.4 Ma) (Lombao et al., 2024; Ollé et al., 2023). Regardless of the origin, Mode 2 technologies are thought to have dispersed across the northern Mediterranean coastal plains. Regardless of whether these were demic or cultural dispersals, the archaeological record indicates that they occurred, contrary to the view of Mithen and Reed (2001), on multiple occasions. Current research remains open to the possibility that their sources included both Africa and Asia, although most evidence supports an African origin. Unfortunately, given the limitations of the available data, reconstructing the precise routes or corridors of these dispersals remains highly speculative.

One question remains unanswered for researchers regardless of the scale at which we make our observations. The most difficult and most debated question: "why" (Bar-Yosef and Cohen, 2013). Countless explanations, focusing on both intrinsic and extrinsic factors, have been invoked for the possible causes of the spread from Africa to Eurasia: climatic oscillations, population growth, cultural changes, social developments or dietary changes are some of them (Carbonell 2008; Bar-Yosef and Cohen 2013; Carotenuto et al., 2016; Dennell, 2017, van der Made, 2011). In the specific case of Europe, we also ask "why so late?" The chrono-spatial records we review in the "[Western Europe First Occupations](#)" section suggest that the initial dispersal of hominins across Europe was strongly constrained by climate, with the earliest occupations concentrated in climatically favourable southern areas. Occupations northwards before 900–700 ka seem to be limited to favourable pulses or temperate periods. There seems to be some correlation between the generalisation of mode 2 technologies and the emergence of *Homo heidelbergensis*, as well as the stabilisation and increase of western European populations. The factors that drove hominin dispersal across Europe are unclear, and the "push and pull" is not the focus of a discussion more concerned with factors limiting diffusion.

We have defined three manageable and adaptable scales of observation and a suitable theoretical framework to understand how the different levels are embedded within each other. As shown in the section, the study of the archaeological and paleoenvironmental record provides empirical information that allows us to gather data and reconstruct dynamics at these scales. Nevertheless, reconstructing and understanding the first populations of Western Europe is challenged by the fact

that we are reconstructing continental-scale processes from the information found at temporally and spatially isolated spots, i.e. archaeological sites. The empirical record is insufficient to answer overarching questions that entail the interplay of dynamics between scales or causality.

## Conceptual and Methodological Proposal

Understanding the complex interaction between the environment and humans requires a multifaceted approach. First, a comprehensive study of archaeological remains is necessary. Often, the study of sites focuses on a relatively small number and types of evidence. Most of the time, this is due to the scarcity of remains, which only allows for relative dating and an inventory of lithic tools. Palaeontological, taphonomic or palaeoenvironmental studies are scarce. However, paradigmatic sites from this period, such as Gran Dolina, Barranc de la Boella, Notarchirico or Boxgrove, show the potential to open different lines of research. Technological, faunal and taphonomic studies are fundamental, as they deal with the behaviour of archaeological populations. To complement the study of the remains left by hominins, the analysis of mammalian palaeocommunities and other palaeobotanical proxies (e.g. isotopes, macrobotanical remains, pollen and non-pollen palynomorphs) will help us to understand the environment in which they lived and the climate they had to endure. Secondly, an effort needs to be made to assess the quality and representativeness of the record to understand the limits of our interpretations (see Representativity of the Archaeological Record).

Here, we have presented the chronological determinations of Western Europe sites without overlooking the discussion around them (see.). Also, we have carried out our own evaluation of the representativity of the archaeological record (see Representativity of the Archaeological Record). As explained above, the size of the sample recommends caution with the interpretation of the results. Conducting representativeness analyses at the continental scale constitutes a considerable challenge. While regional studies are feasible and yield valuable insights into gaps in the archaeological record, their application has largely been restricted to more recent periods (Boemke et al., 2022; Bruxelles & Jerry, 2011; Harris et al., 2019).

To integrate natural, human and cultural systems, we propose Systems Theory as a conceptual framework, supported by various modelling techniques. A comprehensive blueprint for this approach is presented by Burke et al. (2025), who propose a unified framework that brings together Complex Systems Theory, Evolutionary Theory and Anthropological Theory with the Archaeology of Climate Change to better understand the role of cultural systems within climate models. Building on this foundation, climate change archaeology applies systems theory to model the dynamic interactions between natural and cultural systems, employing Species Distribution Models to reconstruct the spatial extent and variability of habitable landscapes under different climatic regimes. Evolutionary theory further contributes by examining how climate functions as a selective force in both biological and cultural evolution, while Cumulative Cultural models simulate processes of innovation, transmission, and cultural change in relation

to demographic variables such as population size, density and connectivity. Anthropological theory, in turn, emphasizes human agency, historical contingency and cultural diversity, thereby ensuring that the framework remains sensitive to the socio-cultural factors that mediate human responses to environmental change. The overall framework is operationalized through a modelling pipeline that links SDMs (Species Distribution Models) and CCE (Cumulative Culture Evolution) models to generate testable hypotheses about climate-culture interactions (Burke et al., 2025).

In line with the framework proposed by Burke et al. (2025) but adapted to the specific features of the Early and early Middle Pleistocene archaeological record, the methodological approach developed within the LATEurope project (Sommer et al., 2025) places a distinctive emphasis on simulation techniques. Although computational simulations have long been applied to the study of Lower and Middle Pleistocene dispersals—the first simulation of the initial “Out of Africa” expansion, a cellular automaton, dates back more than two decades (Mithen & Reed, 2002)—its use has stagnated in recent years (Hughes et al., 2007; Nikitas & Nikita, 2005; Romanowska et al., 2017). Against this backdrop, the central aim of Lateurope is to investigate why Western Europe was colonized by hominins significantly later than other regions of Eurasia. Within its interdisciplinary framework, the project employs a comprehensive modelling package to reconstruct the spatiotemporal dynamics of hominin occupation in relation to broader environmental and demographic processes across Eurasia and Africa.

Following the general logic of Burke et al. (2025), the LATEurope approach begins with climatic and environmental reconstructions, which are then coupled with hominin presence data to build Species Distribution Models (SDMs), based on presence only algorithms and straightforward assumptions to not overcomplicate the interpretation of results we know will be biased (see Representativity of the Archaeological Record). These SDMs parameterize four simulations—one cellular automaton and three agent-based models—each operating at a different temporal and spatial scale. The first, at the continental scale, explores how shifting environments shaped large-scale dispersal patterns (see Lomborg et al., in press). The second, at the regional scale, investigates how behavioural plasticity emerged in response to climatic variability and influenced hominin survival. The third, at the local scale, evaluates how mobility strategies and subsistence behaviours adapted to immediate conditions and contributed to group survivability (see Reschke et al., in press). These three models will ultimately be integrated into a large-scale agent-based model and validated against the archaeological record. The multi-scale and pluridisciplinary approach of LATEurope shows that it is possible to integrate our three-scale perspective while following the blueprint proposed by Burke et al. (2025).

## Conclusion: Hominin Populations as Part of a Greater System

Despite the limitations of the archaeological and paleoenvironmental record, the study of early hominin presence in Western Europe has moved beyond earlier debates and established several baseline patterns. The earliest evidence of settlement dates between 1.4 and 1.2 Ma with successive waves introducing new distinct hominins species, technological repertoires and adaptive strategies, e.g. mode 1 was gradually displaced by more sophisticated mode 2 technologies. These phases broadly align with climatic oscillations and support a source—sink model of population dynamics, whereby populations expanded northward from southern refugia during interglacial periods and retracted during harsher phases—mirroring patterns observed in other temperate species (Leroy et al., 2011; MacDonald et al., 2012). However, hominins were not merely “dancing to the rhythms of the Pleistocene” (Gamble, 1999, p. 125). Over time, their behaviour evolved in increasingly flexible and innovative ways, as new adaptive strategies in subsistence and technology emerged (Timmermann et al., 2024a, 2024b). Recent evidence from sites such as Melka Kunture (Mussi et al., 2023) further caution against treating early hominin behaviour as uniform or static. Instead highlights the need to view them as cognitively and behaviourally distinct from other members of the faunal guild (Dennell, 2017).

The peopling of Western Europe emerges as a complex, discontinuous and multi-scalar process shaped by ecological constraints, technological innovations, behavioural plasticity and demographic turnover. Rather than reflecting a single wave of colonization, the archaeological record reveals a mosaic of dispersals, population replacements and cultural variability. This study contributes to the field by providing an updated synthesis of the archaeological record that distinguishes at least four major dispersal phases; proposing a multiscale framework—micro, meso and macro—to integrate local site data with broader environmental and demographic dynamics through the lens of complex systems theory. Finally, outline a methodological proposal that combines paleoclimatic reconstructions, Species Distribution Models (SDMs) and a suite of multiscale simulations to examine the interaction between environmental variability and hominin dispersal, adaptation and occupation. Together, these contributions emphasize the value of interdisciplinary and computational approaches for addressing the persistent questions—particularly those related to the drivers of dispersal, the mechanisms of cultural transmission and the behavioural flexibility of early hominin populations. Looking ahead, the integration of archaeological data with computational methods promises to open new avenues of research, enabling us to generate richer insights into the dynamics that shaped the earliest human presence in Western Europe.

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**Data Availability** No datasets were generated or analysed during the current study.

## Declarations

**Competing interests** The authors declare no competing interests.

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## Authors and Affiliations

**Carolina Cucart-Mora**<sup>1</sup>  · **Diego Lombao**<sup>2,3</sup>  · **Antonio Pineda**<sup>1,4</sup>  ·  
**Bruno Boemke**<sup>5</sup>  · **Beniamino Mecozzi**<sup>6</sup>  · **Marie-Hélène Moncel**<sup>1</sup> 

✉ Carolina Cucart-Mora  
carolina.cucartmora@mnhn.fr

- <sup>1</sup> CNRS UMR 7194 HNHP, National Museum of Natural History, Institut de Paleontologie Humaine, Rue René Panhard, Paris 75013, France
- <sup>2</sup> GEPN-AAT, Grupo de Estudos para a Prehistoria do Noroeste Ibérico–Arqueoloxía, Antigüidade E Territorio, Departamento de Historia, Facultade de Xeografía E Historia, Universidade de Santiago de Compostela, Praza da Universidade 1, Santiago de Compostela 15782, Spain
- <sup>3</sup> Centro de Investigación Interuniversitario das Paisaxes Atlánticas Culturais (CISPAC), Edificio Fontán, Cidade da Cultura S/N, Santiago de Compostela 15702, Spain
- <sup>4</sup> Institut Català de Paleoecologia Humana i Evolució Social (IPHES-CERCA), Zona Educacional 4 - Campus Sescelades URV (Edifici W3), Tarragona 43007, Spain
- <sup>5</sup> Department of Geography, Kiel University, Ludwig-Meyn-Straße 8, Kiel 24118, Schleswig-Holstein, Germany
- <sup>6</sup> Department of Environmental Biology, Sapienza University of Rome, P. Le Aldo Moro 5, Rome 00185, Italy