# Hominins likely occupied northern Europe before one million years ago

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## Abstract

Archaeological evidence suggests hominins first reached northern Europe during marine isotope stage (MIS) 21 or 25 (c. 840 or 950 thousand years ago [Ka]). This contrasts with southern Europe, where hominin occupation is evidenced from MIS 37 to 45 (c. 1.22 or 1.39 million years ago [Ma]). Northern Europe, however, exhibits climatic, geological, demographic, and historical disadvantages when it comes to preserving fossil and archaeological evidence of early hominin habitation. It is argued here that perceived differences in first occupation timings between the two European regions needs to be revised in light of these factors. To enhance this understanding, optimal linear estimation models are run using data from the current fossil and artefact record. Results suggest northern Europe to have first been occupied as early as 1.16 Ma, or as late as 913 Ka. These timings could represent minimum date expectations and be extended through future archaeological and fossil discoveries.

## Keywords

Lower Palaeolithic; Early Pleistocene; Optimal Linear Estimation; Modelling; Hominin Demography; Early Human Dispersal; Temporal Range Estimation

## 1. Introduction

Northern Europe provides the highest latitudinal evidence for Early and Middle Pleistocene hominin populations in the world (Parfitt et al., 2010; Ashton et al., 2014). This high latitude has created a unique climatic, geological, and demographic context for reconstructing when members of the genus *Homo* first came to occupy the region. A context principally characterised by repeated glacial cycles, where severe cold stages are thought to have prevented colonisation events and, once populations did arrive, created significant demographic dips and regional extinctions (Dennell et al., 2011; MacDonald et al., 2012; Moncel et al., 2018; Ashton and Davis, 2021). Conversely, interglacial warm stages provided suitable climatic and ecological conditions for hominins, with fossil and archaeological evidence attesting to the occupation of Europe as far as 53° North during these periods (Parfitt et al., 2010; Ashton and Lewis, 2012; Moncel et al., 2018; Ashton and Davis, 2021; Rodríguez et al., 2021).

Together, this has resulted in a fragmented and sparse evidentiary framework for understanding hominin occupation in northern Europe prior to marine isotope stage (MIS) 13 (circa. 500 thousand years ago [ka]). Indeed, only one fossil and ten archaeological sites have been securely demonstrated to predate this MIS stage (Figures 1 and 2; Table 1), and the limitations this places on our understanding of when hominins were present in northern Europe is well known (e.g., Dennell et al., 2011; MacDonald et al., 2012; Hosfield and Cole, 2018; Roebroeks et al., 2018; Davis et al., 2021). From the evidence that is available, we know that hominins were present at Happisburgh (UK) from at least ~ 800 ka (MIS 21), and potentially as early as 936 – 959 ka (MIS 25), due to the presence of footprints and a small flake and core assemblage (Parfitt et al., 2010; Ashton et al., 2014). Subsequently, either one or two archaeological sites are known from MIS 19, while either two or three sites are known from MIS 17 (Pakefield [UK] is either from MIS 17 or 19; see Table 1). MIS 16 has the only suggested glacial habitation site, with lithics dated to 660 ka having been discovered at Moulin Quignon, France (Antoine et al., 2019). Additional fossil and archaeological sites are known from MIS 15, 560 – 620 ka (Figure 1; Table 1).

In comparison, more southernly regions of Europe – notably the Iberian and Italian peninsulas – display earlier evidence of hominin presence. Indeed, long-lived consensus through the short and long chronology hypotheses suggest hominins to have reached these regions in advance of more northern ones (Roebroeks and van Kolfschoten, 1994; Dennell and Roebroeks, 1996; Roebroeks, 2001; McNabb, 2005; Dennell et al., 2011; MacDonald et al., 2012; Moncel et al., 2018); likely as early as 1.2 - 1.4 million years ago (Ma) in Spain (Carbonell et al., 2008; Toro-Moyano et al., 2011; Toro-Moyano et al., 2013; Lorenzo et al., 2015) and 1.0 - 1.5 Ma in Italy (Arzarello and Peretto, 2010; López-García et al., 2015). Reconciling an early appearance of hominins in southern Europe with a later appearance in northern Europe is not easy, particularly given their close geographic proximity. It is important to note, therefore, that the reliability of some early European lithic sites is questioned in the 'short chronology' and 'Galerian migration' hypotheses (Muttoni et al., 2018; Roebroeks et al., 2018). Notably, the 1.2 – 1.3 Ma hominin fossils from Sima del Elefante (Atapuerca, Spain) are widely accepted (Carbonell et al., 2008; Lorenzo et al., 2015 [although see: Muttoni et al., 2010]).

## 2. Explaining the Early Southern and Late Northern Colonisation Model

Once hominins arrived in northern Europe, glacial periods resulted in an absence, or at least, highly diminished number (Antoine et al., 2019; Moncel et al., 2021), of hominins, while more southernly and south-easterly regions could have acted as refugia for 'source' core populations (Dennell et al., 2011; Ashton and Lewis, 2012; MacDonald et al., 2012; Hosfield and Cole, 2018; Moncel et al., 2018; Ashton and Davis, 2021). This does not, however, explain why hominins did not move into northern Europe during warm interglacials prior to MIS 21 or 25. If hominins were able to occupy northern Europe during an interglacial c. 800 to 900 ka, then why not earlier? Answering this question is important, as the present model has significant implications for our understanding of hominin behaviour; it implies an inability, potentially by *Homo antecessor*, to occupy northern European environments despite warmer interglacial environments being suitable.

Arguments can be constructed for Early Pleistocene interglacial winters being too harsh for hominins without fire or clothing (Gowlett, 2016; Hosfield, 2016; Gilligan, 2017; Scott and Hosfield, 2021). Undoubtedly, this is a meaningful environmental difference between the two European regions, but one that still leaves eight months of the year available for annual migrations or shorter lived, but ultimately unsuccessful, colonisation events (Moncel et al., 2018). Moreover, we do not know the precise tolerance of these hominins for cold environments, whose anatomy was potentially better suited to colder conditions than our own (e.g., Dibble et al., 2017; Wore et al., 2018; Rodríguez et al., 2021). Definitions of 'northern Europe' vary, but assuming this means north of the Alps (approx. 46° North) then these dispersals need not imply movement to Happisburgh in the UK but could include more limited journeys to central or northern France, Belgium, Germany, Austria, or the Czech Republic. Thus, the likelihood that individuals and small groups did not, at least sporadically, venture into northern Europe prior to the earliest physical evidence at Happisburgh may be low.

A potentially more plausible explanation for the perceived 400,000-year gap (0.8 - 0.9 Ma [Happisburg] to 1.2 – 1.3 Ma [level TE9, Sima del Elefante]) between the occupation of southern and northern Europe is that our understanding is inaccurate due to a disparity in the likelihood of finding hominin fossils and lithic artefacts in these regions. Simply, the chances of finding evidence of early hominin occupation is greater in more southern European regions. There are four key reasons for this:

- Due to the above-described absence (or near-absence [Antoine et al., 2019; Moncel et al., 2021]) of hominins during glacial periods and potentially during interglacial winters (Hosfield, 2016; Rodríguez et al., 2021), northern Europe is automatically faced with a diminished fossil and archaeological record relative to more temperate regions. The impact of glacial cycles on hominin populations, and therefore fossil and artefact creation, would have been more muted in the south (Dennell et al., 2011; Hosfield, 2016), ultimately providing a more plentiful archaeological and palaeoanthropological record for us to discover today. This difference is further exaggerated by the reduced ability of higher latitudes to support high density hominin populations (Ashton and Davis, 2021). Simply, southern Europe would have sustained larger numbers of hominins across interglacial, transitional, and glacial periods, resulting in a greater volume of evidence being produced, and in turn, a greater number of fossils and artefacts being preserved for us to discover today.
- Glacial periods are associated with the formation of glaciers in northern European regions. The southern limits of glaciers varied dependent on the marine isotope stage (Böse et al., 2012), but their formation would have destroyed many archaeological and fossil sites formed prior to MIS 6, 10, 12 and 16, and potentially before Happisburgh. The impact of glaciers on site preservation is well known to Lower Palaeolithic archaeologists working in these regions (Gowlett, 2006; Preece and Parfitt, 2012; Moncel et al., 2018; Lewis et al., 2021), and the true scale of damage inflicted on our understanding of hominin occupation is hard to ascertain.
- Northern Europe is also geologically impoverished relative to southern Europe when it comes to the presence of caves and karstic system features suitable for hominin habitation and the preservation of fossils, tools, and other evidence of occupation. It is important to stress that it is not void of such features, but on a relative basis there are fewer. Indeed, Spain and Italy collectively have more carbonate rock than the UK, Germany, Belgium, the Netherlands, Denmark, Poland, Slovakia, and Czech Republic combined (Chen et al., 2017). Further, the few caves that do contain Middle Pleistocene sediments, such as Kent's Cavern and Brixham Cave, were investigated at the inception of the subject, resulting in poorly contextualised artefacts and issues of dating (Cook and Jacobi, 1999). Relative to southern European areas, northern Europe therefore has a poor record of relevant cave or rock shelter deposits and is at a disadvantage when it comes to preserving fossil and archaeological evidence of early hominin habitation (although note that southern pre-Happisburgh sites are also found in open-air locations).
- Finally, south-eastern Britain and northern France have a long history of artefacts being recovered from river terrace gravels with abundant lithic collections archived from Middle Pleistocene sites (Roe, 1968; Wymer, 1999; Harris et al., 2019). This might be thought to redress the north-south imbalance, but the vast majority of quarries are now inaccessible for detailed investigation or dating and most were situated on post-MIS 13 terraces. There are exceptions where higher terraces have been reinvestigated, such as on the Solent (McNabb et al., 2012), the Bytham (Davis et al., 2021; Lewis et al., 2021), the Stour (Key et al., 2022) and the Somme (Antoine et al., 2019). However, all try to contextualise older collections, with small-scale fieldwork programmes compared to the often much larger excavations in southern Europe (e.g. Peretto, 2006; Toro-Moyano et al., 2011; Ollé et al., 2013; Vallverdú et al., 2014; Arzarello et al. 2015). So, despite the long history of research in northern Europe, over the last 50 years there has been a much greater focus on early sites in southern Europe, exacerbating the low chances of discovering

early sites in the north (Roebroeks, 2006). Disentangling the impact of historical happenstance on our present understanding is difficult, but overall it appears to have benefited discoveries in more southern regions.

Together, these demographic, geological, climatic and historical factors have potential to help explain the temporal gap between the earliest evidence of hominins in southern and northern Europe. When balanced against there being relatively few discrete and reliable sites in southern Europe predating Happisburgh (UK) (MacDonald et al., 2012; Moncel et al., 2018; Roebroeks et al., 2018), it can be argued that those we do know of, such as Ataperuca (Bermúdez de Castro et al., 2004; de Lombera-Hermida et al., 2015) and Barranc de la Boella (Vallverdu et al., 2014), do not necessarily portray a true difference in first occupation timing between northern and southern Europe. Instead, their presence (and discovery) results from regional differences in the amount of evidence produced, and the subsequent preservation of that evidence. That is, there is more evidence to find in southern regions, so the few > 1 Ma sites that have been found may be the result of the above noted differences (relative to northern Europe) and not an accurate reflection of hominin occupation. Note that this argument concerns only first arrival dates and is distinct to discussions on length of habitation once populations arrive, frequency of re-colonisation after absence, and comparative population sizes.

These considerations are confounded by the fact that finding evidence of the first hunter gatherer populations in any region is extremely difficult. Low population numbers and poor preservation of evidence – potentially combined with seasonal, migratory occupation patterns in ill-defined geographic regions – all limit the chances of artefact and fossil evidence being found (Surovell and Brantingham, 2007; Meltzer, 2009; Surovell et al., 2009; Prasciunas and Surovell, 2015; Du et al., 2020; Bobe and Wood, 2021; Key et al., 2021a, 2021b). In other words, the chances of finding physical evidence of the *earliest* hominin occupation in any region, let alone Pleistocene northern Europe, is close to zero. Happisburgh is not, therefore, likely to provide a reliable account of when hominins first reached northern Europe.

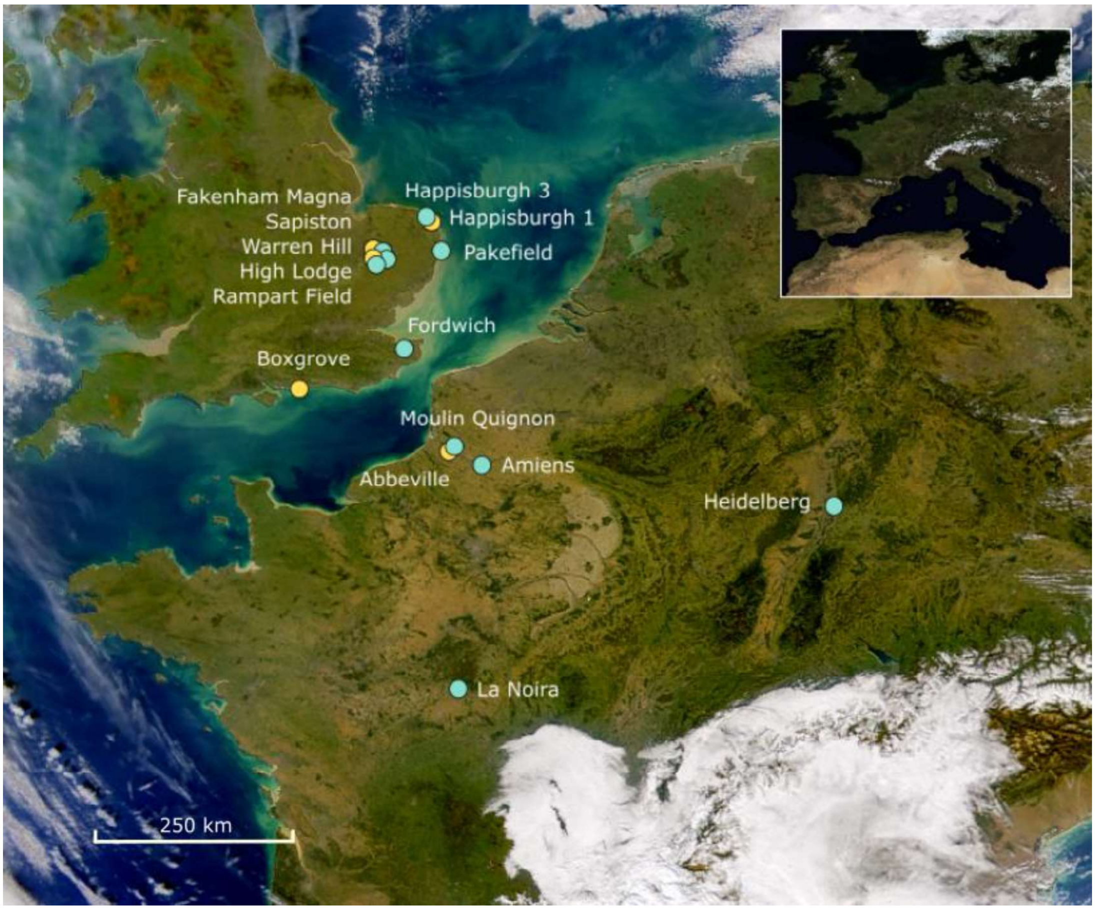

**Figure 1**: The ten oldest sites with evidence of hominin occupation in northern Europe (teal). Five other early sites not included in the main OLE models are included for context (yellow). Note that some of the yellow sites are included in the alternative model scenarios. Original satellite image: NASA Visible Earth Project.

## 3. Building a More Accurate Model for the Earliest Arrival of Hominins in Northern Europe

In the absence of exceptional discoveries and a more comprehensive fossil and archaeological record, how is it possible to identify when hominins first reached northern Europe? A solution to this dilemma was recently introduced to human evolutionary literature in the form of optimal linear estimation (OLE) modelling, a technique able to estimate the earliest or most recent portions of an archaeological and palaeontological phenomena based on existing sparse and fragmentary records (Solow, 2005; Rivadeneira et al., 2009; Key et al., 2021a). That is, OLE can estimate the full temporal range of an artefact or hominin species' presence based on the discoveries made to date. Here, OLE modelling is applied to the combined fossil and archaeological record of northern Europe to provide more accurate estimates for when hominins first came to occupy this region.

Early and Middle Pleistocene demographic patterning in northern Europe has recently been described by Hosfield and Cole (2018) to represent a 'punctuated long chronology' (PLC), whereby cycles of population crashes and increases align with MIS stages. Notably, it is not until after the Anglian glaciation (MIS 12) that they argue for substantive demographic growth and population maintenance in northern Europe. With earlier sites interpreted as evidence of "small scale, fragmented dispersals of hominins" (sites older than c. 700 ka in Table 1) and then "small-scale, biface-making populations" but "within a broad geographic range" (sites aged 500 to 700 ka in Table 1) (Hosfield and Cole, 2018: 157). Others have made similar demographic interpretations for the region, albeit at times with different chronologies (Dennell et al., 2011; Ashton and Lewis, 2012; Roebroeks et al., 2018; Davis et al., 2021). Put plainly, demographic change in northern Europe is hypothesised to be a process of gradual but small population increases as cultural and anatomical mitigations for cold weather increase, interspersed by marked declines during glacial periods. In this scenario, population growth between MIS 21 or 25 and MIS 11 can be viewed as a punctuated distribution (growth) curve broadly aligning with a Weibull distribution (Figure 2B). More substantive populations than those suggested by Hosfield and Cole (2018) in MIS 17 to 13, or lower populations than those illustrated in Figure 2B, still accord well with a Weibull distribution. Other demographic scenarios for northern Europe exist (Figures 2C and 2D), but it is the above-described PLC model that best fits current fossil and archaeological evidence (Hosfield and Cole, 2018; Ashton and Davis, 2021).

Larger populations leave more evidence of their presence in the archaeological and fossil record, meaning those populations are more frequently going to be found by archaeologists and palaeoanthropologists. This helps to explain the gradual increase in site numbers through time seen in Figure 2 (i.e., site identification probability changes monotonically from the point of first colonisation through to population carrying capacity being reached). This relationship underpins why it is so difficult to identify reliably the earliest populations inhabiting a region, and why temporal modelling techniques are needed to gain a more accurate understanding of when these events happened (Surovell and Brantingham, 2007; Meltzer, 2009; Surovell et al., 2009; Prasciunas and Surovell, 2015; Bebber and Key, 2022). The same problem has recently been highlighted for hominin fossil evidence and our subsequent understanding of different species' temporal presence (Du et al., 2020; Bobe and Wood, 2021). Optimal linear estimation modelling (OLE) has been specifically designed to account for low population numbers. Originally used to model the true extinction dates of species after their last sighting by humans (Roberts and Solow, 2003; Solow, 2005), the technique has since been widely applied and recommended within palaeontological extinction scenarios (e.g., Bradshaw et al., 2012; Crees and Turvey, 2014; Pimiento and Clements, 2014; Wang and Marshall, 2016). It is only recently that OLE modelling has been applied in the reverse temporal direction, having been employed to estimate origination ages for Oldowan, Acheulean and Protoaurignacian technologies (Key et al., 2021b; Djakovic et al., 2022). Indeed, it is well known that archaeologists rarely (if ever) discover the first or last occurrences of past cultural phenomena.

## 4. Optimal Linear Estimation

### 4.1 Model Assumptions

OLE has few assumptions relative to alternative temporal modelling techniques (Solow, 2005; Clements et al., 2013; Key et al., 2021a), but for meaningful results to be returned it is important for these assumptions to be met. In the present context this includes the assumption that hominins were present in northern Europe prior to the current oldest physical evidence (in this case Happisburgh [Parfitt et al., 2010]), all fossil and archaeological sites used in the model are independent, search effort does not equate to zero in any given temporal context (that is, archaeologists and palaeoanthropologists are not actively excluding sediments older than Happisburgh in their search efforts), the earliest hominins in northern Europe left traces of their presence through lithic artefacts or bones (and ultimately fossils), and we have no *a priori* reason to think that population pressures were significantly different in one interglacial over another. Search effort could be considered unbalanced between Acheulean and earlier flake-and-core-only assemblages as handaxes are more easily recognised (and thus discovered). This is unavoidable, but search effort for expedient technologies has also been considerable in both northern and southern Europe (e.g., see discussions on the Clactonian and eoliths [Ashton et al., 1992; Ellen, 2013; McNabb, 2020]).

Finally, in the present context, there is the assumption that taphonomic processes are broadly equal or monotonic across the temporal range entered into the model. In other words, if an archaeological site was made in the same location in MIS 15 and MIS 21, then there is the assumption that both would have equal chance of being preserved to the present, or, the period between MIS 21 to MIS 15 would display monotonically increasing preservation probability. As Surovell and colleagues demonstrate (Surovell and Brantingham, 2007; Surovell et al., 2009), this is not a straightforward assumption in all archaeological contexts. Here, however, this is arguably the case for northern Europe between 800 and 600 ka. Northern European stone artefact sites are principally destroyed through glacier formation and fluvial activities, and two of the three most extreme Pleistocene glaciation events happened post-MIS 15. So, irrespective of whether a site was formed in MIS 15 or 21, if a glacier had potential to destroy it (Gowlett, 2006), then it would likely have occurred during MIS 10 or 12 (Preece and Parfitt, 2012). Similarly, Quaternary fluvial terraces (where most pre-MIS 15 lithic artefacts are recovered) form in predictable stages (Bridgland and Westaway, 2014). Once a terrace is formed the river erodes beneath this point, meaning artefacts are saved from further fluvial damage. Incision and erosion can deteriorate Quaternary terraces through time (Bridgland and Westaway, 2014), with this cumulative process potentially impeding the preservation of older sites. It is, however, on a relative scale; all MIS 14 or older sites have been exposed to this process for at least 550,000 years. Moreover, several of the most important (i.e., oldest) sites for the OLE models are not found in such deposits. So, at a very broad level, fluvial disturbance affects artefacts and fossils for broadly equal periods. Fossils may also be destroyed by leaching and other chemical processes, but it is arguably the case that if this is going to influence their preservation it will occur within the space of 600 ka (i.e., an additional 200 to 300 ka would not make a substantive difference). While these broad arguments appear reasonable and the use of the OLE methods appear valid, it is possible that in specific, site-dependent circumstances other taphonomic processes may influence the preservation of early hominin sites.

### 4.2 Archaeological and Fossil Sites

OLE models run to estimate origination timings (i.e., in the reverse temporal direction) require temporal data from the oldest dated occurrences of the investigated phenomenon. Ten occurrences are typically recommended as optimal for OLE (Roberts and Solow, 2003; Solow, 2005; Rivadeneira et al., 2009), making the technique particularly amendable to the fragmented fossil and archaeological record of Pleistocene northern Europe. Northern Europe is defined here as the Alps (approx. 46° North) or more northern latitudes, meaning that pre-Anglian sites in Iberia, Southern France, and Italy are not included in the models.

A thorough review of Palaeolithic and paleoanthropological literature was conducted to identify the oldest fossil and artefactual evidence of hominins in northern Europe (last search effort December 2021). The ten oldest sites identified through this review are presented in Table 1 and Figure 1. These sites represent a 'best-fit' scenario with all being widely accepted in the literature. Several occurrences have been excluded due to their indirect dating methods (e.g., poorly dated terrace sequences), contested 'artefacts', or lack of provenance (see Supplementary Information 1). All excluded occurrences, apart from Untermassfeld in Germany (see: Roebroeks et al., 2018), would be among the youngest dates used in the models, meaning that had they been included, there would only be a minor impact on the estimates produced. The sites of Fakenham Magna (UK) and Sapiston (UK) only display a few artefacts, and although these were identified by strict criteria and a panel of Palaeolithic specialists (Davis et al., 2021, SI), some may still oppose their inclusion on the basis of the small assemblages, but they are included for two reasons. First, irrespective of an assemblage's size, the presence of lithic artefacts at a defined point in time demonstrates the presence of hominins (Davis et al., 2021; Lewis et al., 2021). Second, their inclusion in the models will produce a more conservative estimate relative to their exclusion (i.e., estimates will be more limited and closer to the date of the oldest known artefacts).

The sites of Happisburgh and Pakefield are among the most important considered here as they provide some of the oldest evidence of hominins occupying northern Europe. Thus, they have a relatively great impact on the model's estimates (Key et al., 2021a). Both, however, are associated with two MIS stages. Happisburgh Site 3 is constrained to MIS 21 or MIS 25 (Parfitt et al., 2010), while Pakefield is constrained to MIS 17 or 19 (Parfitt et al., 2005). MIS 17 is the "very youngest" attribution for Pakefield, with an age of MIS 19 being more commonly referenced (Parfitt et al., 2005: 1011; Lewis et al., 2021). Due to these uncertainties, four combinations of data were entered into the OLE models so that versions with all possible Happisburgh and Pakefield MIS associations could be investigated.

In addition to the main 'best-fit' site scenario, two further versions were investigated to illustrate hominin dispersal estimations under alternative site-discovery perspectives, each using the four Happisburgh and Pakefield combinations. The first included the sites of Lunery-Rosières and Pont-de-Lavaud, dated to 1.166 and 1.054 ma, respectively (Despriée et al., 2017, 2018). Both are from central France, slightly south of la Noira, and without independent dating evidence of the ESR age estimates. Rampart Field and Amiens were removed in this scenario. The second version excluded Fakenham Magna and Sapiston (both UK), as in this case the authors preferred geological age is younger than the ESR dates. Abbeville (France) and Happisburgh Site 1 (UK) replaced them in the models.

Each fossil or artefact occurrence had its associated date range identified. These data were drawn directly from published results of radiometric dating methods, or from known marine isotope stage ranges when authors provide only MIS-level chronological associations, following Lisiecki and Raymo (2005) and Railsback et al. (2015). In addition, the author's preferred age for the site or the mean of the date range was also identified. Preferred dates were typically only provided by authors when stratigraphic interpretations allowed more precise dating approximations relative to the use of central tendency values. The use of MIS stages to create input data means results are best interpreted at the MIS level.

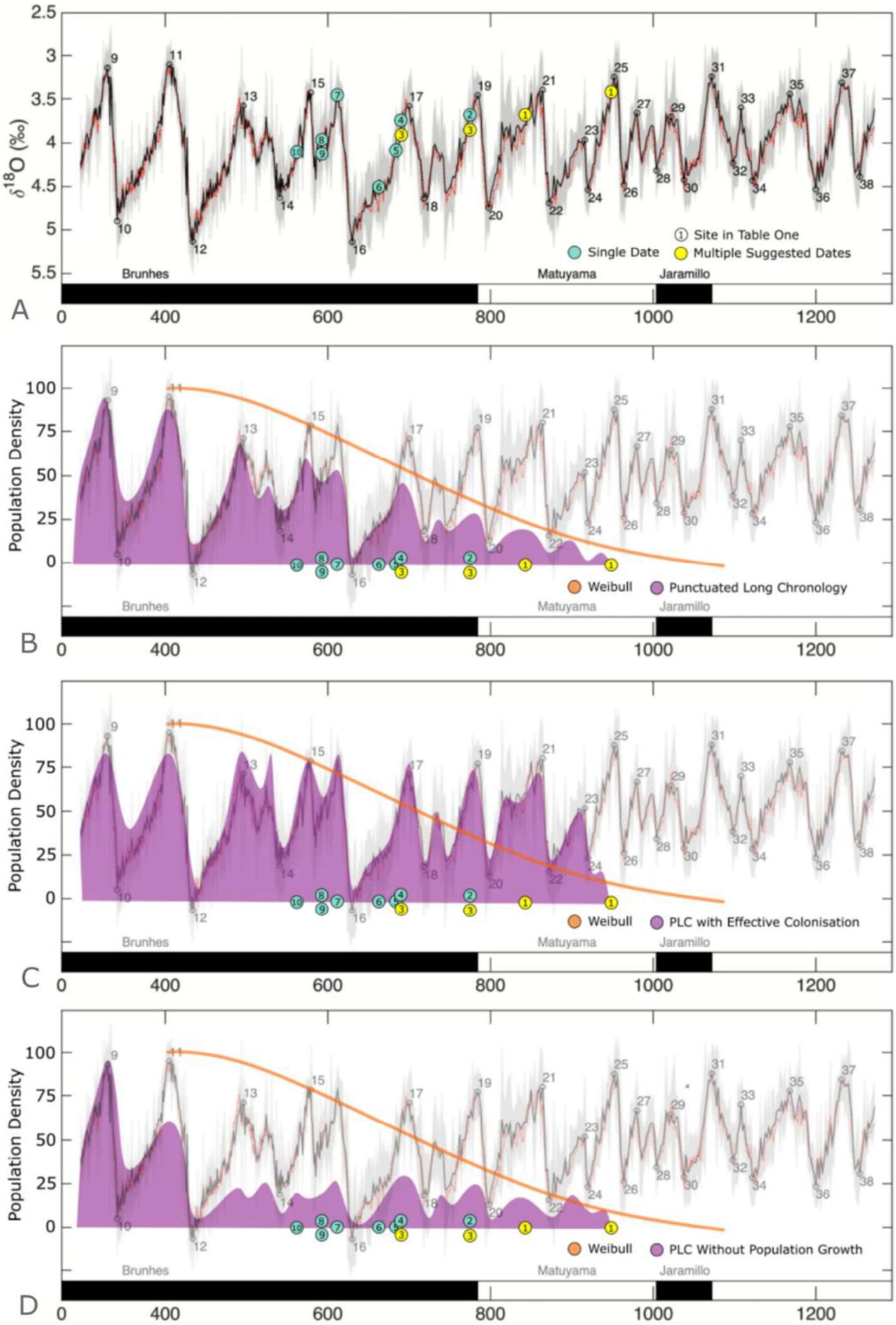


**Figure 2:** The ten archaeological and fossil sites included in the 'best-fit' OLE models presented in the context of Early and Middle Pleistocene marine isotope stages (Figure 2A). Figures 2B, 2C and 2D present hypothetical demographic scenarios for northern Europe following an initial occupation event in MIS 25. Figure 2B represents the punctuated long chronology (PLC) model as proposed by Hosfield and Cole (2018), where populations are slow to increase during initial interglacial periods but following technological and anatomical changes there are increased populations in MIS 15 and 13, before a marked increase in MIS 11. Figure 2C represents a scenario where populations in northern Europe are tightly linked to mean annual temperatures, with winter temperatures, annual resource fluctuations, predation, and disease (for example), not limiting population numbers in one period more than another. Figure 2D represents the standard PLC model (Hosfield and Cole, 2018) without any meaningful population growth until MIS 11. In each, a Weibull distribution curve is presented to demonstrate that the standard punctuated long chronology model (Figure 2B) best fits the assumptions of optimal linear estimation modelling. Note that Happisburgh and Pakefield have both of their proposed ages illustrated (yellow). Versions of these scenarios with complete regional extinction during glacial periods, and interglacial periods without recolonisation, could also be included but are not presented here. The numbers at each peak refer to MIS stages. The original MIS figure is modified from Ahn et al. (2017) under the terms of an CC-BY-NC License.

### 4.3 The OLE Method

OLE uses the timing and chronological spacing of a phenomenon's known occurrences to statistically estimate its full temporal presence. The technique relies on the dates (and their spacing) entered into the model displaying a joint distribution with approximately a 'Weibull form'; an assumption which has already been noted as valid for the present scenario. It then uses the temporal spacing of these dates to determine the shape parameters of the Weibull distribution, which is in turn used to estimate the origination date of the phenomenon in question. Based on the Weibull distribution created, a start point is identified by the model as the date by which another earlier occurrence of the phenomenon should have been found had the phenomenon continued beyond this point (given previous search effort). In the present context, this means the OLE model determines an 'origination point' for hominins entering northern Europe, and if the true earliest date was before this then by now we should have found an artefact or fossil occurrence earlier than Happisburgh. There are no parameters of the model specific to biological or cultural phenomena, and it can be used to investigate temporal presence through a combination of both types of evidence if necessary, so long as all model assumptions are still met (i.e., while fossils do display lower preservation rates relative to stone tools, in the present scenario they equally meet the assumptions outlined in Section 4.1, including site identification probability changing monotonically, and there is no reason to believe their combined probability distribution curve will not meet the model's assumptions).

The formulaic expression of the OLE method is available through diverse sources (e.g., Solow, 2005; Rivadeneira et al., 2009; Key et al. 2021b). This includes Clements et al.'s (2013: 345) experimental testing of the technique, where it is demonstrated to provide "generally accurate and precise estimates" in a range of scenarios. Despite this, the estimates produced in the present study should only be viewed with the same accuracy as the data entered into the models. In this case, model accuracy is limited to individual MIS stages as determined by sites such as Sapiston, Fordwich, Warren Hill and Pakefield (Table 1). Clements (2013) provides an accessible means through which to run OLE models through the R sExtinct package (available via: https://github.com/cran/sExtinct/blob/master/R/OLE.fun.R or the sExtinct package in the CRAN archive). Additionally, the R code used here is available in the Supplementary Information. The OLE method is applied here in reverse such that occurrence age increases towards the past, where $T_1>T_2>...>T_k$ are the *k* earliest occurrences, ordered from the earliest ($T_k$ being the most recent). As there is no specific start date for the time series, the 10th youngest site date was used as the beginning of the period. All calculations were undertaken in R v. 4.0.3 (R Core Team, 2019). All required data is present in Table 1.

Four combinations of site occurrence data were entered into the OLE model, depending on which of the two MIS associations are used for Happisburgh (MIS 21 or 25) and Pakefield (MIS 17 or 19) (Table 1). Three origination estimations were created for each data combination. The first used the original author's preferred age for each site or the mean of the published date range, with the OLE model being run once. Given that many of the sites could only be assigned to individual MIS, the uncertainty of these assignments was addressed using two resampling approaches. Dates were randomly drawn from within each site's date range using either a normal or uniform distribution, and these data were then assessed independently for each distribution type with the OLE method. Normal distributions were defined by standard deviations equal to the half of the difference between the mean value and range bounds. This process was repeated 10,000 times and results were expressed as a mean from all iterations. This was repeated independently for the three site scenarios. All modelled scenarios are detailed in Table 2.

Two types of data relevant to understanding when hominins first entered Europe are produced through the OLE method. The first is $T_O$, which represents the estimated origination date for when hominins first entered northern Europe. In addition, each model also produced a $T_{CI}$ value, which represents the upper bound of each model's confidence interval ($\alpha = 0.05$). This is effectively the date beyond which there is a 5% or less likelihood (as determined by CIs) that hominins were present in northern Europe.

**Table 1**: The ten oldest widely accepted archaeological or hominin fossil occurrences in northern Europe. Four OLE models are run as the oldest archaeological occurrence, Happisburgh (UK), is constrained to *either* MIS 21 or MIS 25, and the second or third oldest, Pakefield (UK), is constrained to *either* MIS 17 or MIS 19 (Table 2). Yet, as some of the oldest dates used, they have a relatively great impact on the model's estimated date and in turn would have substantial implications for the model's predictions. The Mauer mandible is the only hominin fossil old enough to warrant inclusion in the models.

| Ranked Age | Site [1, 12, 13] | | Happisburgh 1 | Happisburgh 2 | MIS Stage | Evidence of Occupation | Reference |
|---|---|---|---|---|---|---|---|
| 1 | Happisburgh Site 3, UK | Mean Date | 947,500 [2] | 840,000 [2] | 25 or 21 | 78 flake and core artefacts | Parfitt et al., 2010 |
| | | Date Range | 936,000 – 959,000 | 814,000 – 866,000 | | | |
| 2 | Fakenham Magna, UK | Mean Date | 775,501 [3] | | 19 | 2 flakes + 1 scraper | Davis et al., 2021; Lewis et al., 2021 |
| | | Date Range | 761,000 – 790,000 | | | | |
| | | | Pakefield 1 | Pakefield 2 | | | |
| 3 [*] | Pakefield, UK | Mean Date | 775,500 [4] | 694,000 [4] | 19 or 17 | 30 flakes, 1 core, 1 retouched flake | Parfitt et al., 2005 |
| | | Date Range | 761,000 – 790,000 | 676,000 – 712,000 | | | |
| 4 [*] | Sapiston, UK | Mean Date | 694,001 [3] | | 17 | 3 flakes | Lewis et al. 2021; Davis et al., 2021 |
| | | Date Range | 676,000 – 712,000 | | | | |
| 5 | la Noira, France | Mean Date | 690, 000 [5] | | 17 | 199 flakes, 57 cores, 58 LCTs | Moncel et al., 2013 |
| | | Date Range | 660,000 – 720,000 | | | | |
| 6 | Moulin Quignon, France | Mean Date | 660,000 | | 16 | 244 flakes, 13 cores, 5 bifaces + historical | Antoine et al., 2019 |
| | | Date Range | 650,000 – 670,000 | | | | |
| 7 | Heidelberg, Germany | Mean Date | 609,000 | | 15 | *Homo heidelbergensis* mandible | Wagner et al., 2010; 2011 |
| | | Date Range | 569,000 – 649,000 | | | | |
| 8 | Fordwich, UK | Mean Date | 592,001 [6] | | 15 | 238 flakes, 4 cores, 4 retouched + > 330 historical handaxes | Key et al., 2022 |
| | | Date Range | 563,000 – 621,000 | | | | |
| 9 | Rampart Field, UK | Mean Date | 592,000 | | 15 | 4 flakes, 1 core, 1 handaxe + historical | Lewis et al. 2021; Davis et al., 2021 |
| | | Date Range | 563,000 – 621,000 | | | | |
| 10 | Amiens, France | Mean Date | 554,000 [8] | | 13 to 15 | 22 flakes, 1 core + historical | Antoine et al., 2015 |
| | | Date Range | 456,000 – 652,000 | | | | |
| n/a [+] | Abbeville, France | Mean Date | 525,000 [9] | | 14 to 15 | 5 flint flakes, 5 bifaces, + historical | Antoine et al., 2016 |
| | | Date Range | 500,000 – 550,000 | | | | |
| n/a [+] | Happisburgh Site 1, UK | Mean Date | 501,000 [10] | | 13 | 478 flakes, 1 handaxe | Lewis et al., 2019 |
| | | Date Range | 478,000 – 524,000 | | | | |
| n/a [+] | Boxgrove, UK | Mean Date | 501,000 | | 13 | Hundreds of bifaces and flakes, *Homo heidelbergensis* fossils | Roberts and Parfitt, 1999 |
| | | Date Range | 478,000 – 524,000 | | | | |
| n/a [+] | Warren Hill, UK | Mean Date | 501,000 [7] | | 13 | 3 flakes + 100's of historical handaxes, flakes, cores | Voinchet et al., 2015; Lewis et al., 2021 |
| | | Date Range | 478,000 – 524,000 | | | | |
| n/a [+] | High Lodge, UK | Mean Date | 492,000 [11] | | 13 | 82 handaxes, 240 retouched flakes, + other and historical | Davis et al., 2021; Ashton et al., 1992 |
| | | Date Range | 478,000 – 506,000 | | | | |

[+] Not included in the OLE models but presented here as well-known sites to provide additional context.
[*] Note that Sapiston and Pakefield change their placing within the OLE model depending on which date is used for the latter.
[1-13] See: Supplementary Information 1

**Table 2**: The different iterations of the OLE models run during the present analyses.

| 'Best Fit' Site Scenarios (Table 1 Sites Ranked 1 – 10) | | | |
|---|---|---|---|
| | **Author preferred or mean published dates** | **Uniform distribution resampling using published date ranges** | **Normal distribution resampling using published date ranges** |
| **Happisburgh MIS 25 and Pakefield MIS 19** | Model 1 | Model 5 | Model 9 |
| **Happisburgh MIS 25 and Pakefield MIS 17** | Model 2 | Model 6 | Model 10 |
| **Happisburgh MIS 21 and Pakefield MIS 19** | Model 3 | Model 7 | Model 11 |
| **Happisburgh MIS 21 and Pakefield MIS 17** | Model 4 | Model 8 | Model 12 |
| **Alternative Site Discovery Scenarios** | | | |
| Model versions 1 to 12, but the sites of Rampart Field and Amiens are excluded and replaced by Lunery-Rosières and Pont-de-Lavaud. (Models 13 to 24) | | | |
| Model versions 1 to 12, but the sites of Fakenham Magna and Sapiston are excluded and replaced by Abbeville and Happisburgh Site 1. (Models 25 to 36) | | | |

## 5. When Did Hominins First Occupy Northern Europe?

OLE models use individual years as units of time, meaning that the origination estimations appear precise relative to the fossil and artefact record from which they are derived. The present results are, however, most reliable when interpreted at the individual MIS level (see above). Four combinations of temporal data were used in the OLE models given current uncertainty regarding the MIS associations of artefacts from Happisburgh and Pakefield. Across all data combinations and model versions for the 'best-fit' scenario (Table 2), the estimated earliest occupation dates for northern Europe ranged between 913,303 (MIS 23) and 1,159,968 (MIS 35) years before present (Table 3). The resampling results align closely with those created using the mean or author preferred data. In all instances the normal and uniform resampling estimates were younger than the mean estimates, but this was only by a maximum of ~ 8,000 years.

Applying an MIS 25 age to Happisburgh resulted in an estimated first arrival for hominins in northern Europe from approximately 1.129 to 1.159 Ma, which accords with either MIS 34 or 35 (Table 3). The upper bound of the different model's confidence interval ($T_{CI}$) is approximately 1.661 to 1.812 Ma. If an MIS 19 association is used for Pakefield then the estimates are more recent, dating to 1.129, 1.132 and 1.136 Ma (across the three versions of the OLE method used here). An MIS 17 association for Pakefield suggests an older first arrival, at 1.152, 1.155, or 1.159 Ma. Notably, these latter results are within the warm MIS 35 interglacial, while those that associated Pakefield with MIS 19 are at the threshold of MIS 33 and 34 (Table 3).

An MIS 21 age for Happisburgh returned estimated first arrival dates of approximately 913 to 935 Ka, which would indicate an MIS 23 or 24 occupation for hominins (Table 3). The upper bound of the different model's confidence interval ($T_{CI}$) is approximately 1.110 to 1.191 Ma. Again, estimates applying an MIS 19 age for Pakefield were ~ 20 Ka, dating to 913, 914 and 917 Ka. If Pakefield dates to MIS 17, then the estimates suggest a 931, 932 or 935 ka arrival for hominins in northern Europe. Notably, all estimates align along glacial and interglacial boundaries (Table 3).

When Sapiston and Fakenham Magna were removed from the site occurrence data, an MIS 25 age for Happisburgh resulted in estimates from approximately 1.178 to 1.215 Ma (Supplementary Information 1). An MIS 21 age for Happisburgh resulted in first occupation timings between 953 to 986 ka. When Lunery-Rosières and Pont de Lavaud were included in the site occurrence data, estimated first occupation dates for northern Europe increase to approximately 1.388 to 1.425 Ma (Supplementary Information 1). There was a limited impact caused by the different age assignments for Happisburgh and Pakefield.

**Table 3:** Estimated origination dates and MIS associations for the first arrival of hominins in northern Europe based on OLE and the region's 'best-fit' known archaeological and palaeoanthropological record. Four data combinations are presented

dependent on the MIS associations used for the sites of Happisburgh (21 or 25) and Pakefield (17 or 19). Presented alongside the origination estimates ($T_O$) are each models' confidence interval ($T_{CI}$).

| | | $T_O$ | | | $T_{CI}$ | | |
|---|---|---|---|---|---|---|---|
| | | Mean estimates | Resampling (normal) | Resampling (uniform) | Mean estimates | Resampling (normal) | Resampling (uniform) |
| Happisburgh 25 & Pakefield 19 | Origination (years BP) | 1,136,609 | 1,132,162 | 1,129,449 | 1,686,733 | 1,673,997 | 1,661,242 |
| | Associated MIS | 34 (1,114 – 1,141 ka) | 34 (1,114 – 1,141 ka) | 34 (1,114 – 1,141 ka) | 59 (1,670 – 1,697.5 ka) | 59 (1,670 – 1,697.5 ka) | 58 (1,642.5 – 1,670 ka) |
| Happisburgh 25 & Pakefield 17 | Origination (years BP) | 1,159,968 | 1,155,696 | 1,152,109 | 1,812,829 | 1,801,410 | 1,783,605 |
| | Associated MIS | 35 (1,141 – 1,190 ka) | 35 (1,141 – 1,190 ka) | 35 (1,141 – 1,190 ka) | 65 (1,802.5 – 1,816 ka) | 64 (1,782 – 1,802.5 ka) | 64 (1,782 – 1,802.5 ka) |
| Happisburgh 21 & Pakefield 19 | Origination (years BP) | 917,214 | 914,498 | 913,303 | 1,119,760 | 1,114,554 | 1,110,611 |
| | Associated MIS | 24 (917 – 936 ka) | 23 (900 – 917 ka) | 23 (900 – 917 ka) | 34 (1,114 – 1,141 ka) | 34 (1,114 – 1,141 ka) | 33 (1,104 – 1,114 ka) |
| Happisburgh 21 & Pakefield 17 | Origination (years BP) | 935,922 | 932,616 | 931,228 | 1,191,908 | 1,185,264 | 1,180,577 |
| | Associated MIS | 24 (917 – 936 ka) | 24 (917 – 936 ka) | 24 (917 – 936 ka) | 36 (1,190 – 1,215 ka) | 35 (1,141 – 1,190 ka) | 35 (1,141 – 1,190 ka) |

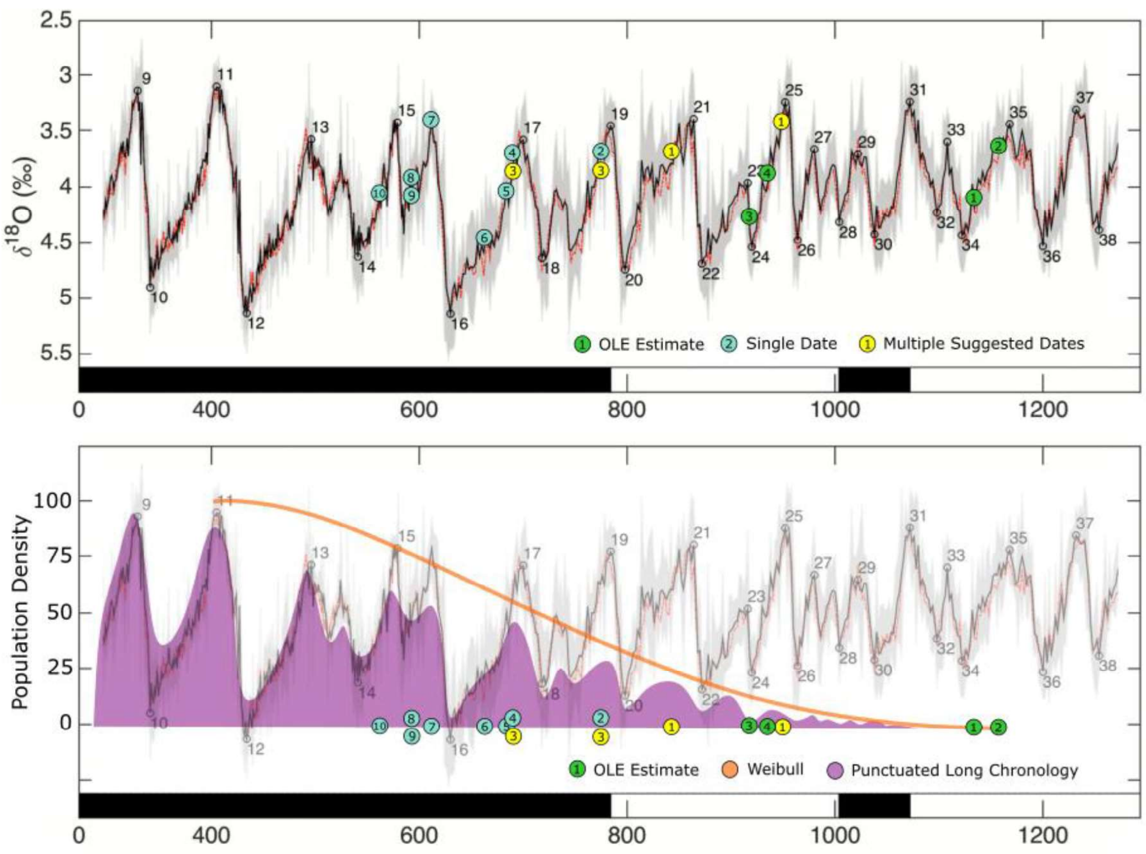


**Figure 3:** Estimated first occupation ages for hominins in northern Europe (blue) alongside the ten earliest known artefact and hominin fossil sites currently known in the region (Table 1; teal and yellow; 'best-fit' site scenario). OLE estimates produced using each site's mean (or the author's preferred) age are depicted. Confidence intervals can be found in Table 3.

## 6. The early occupation of northern Europe

As exceptional as the lithic artefacts and hominin footprints identified at Happisburgh are (Parfitt et al., 2010; Ashton et al., 2014), they are not evidence of the very earliest hominins to have entered northern Europe. Instead, they reflect the current earliest known physical evidence of hominins in the region, as determined by past search efforts. To gain a more accurate understanding of when hominins first reached northern Europe, OLE models have been used to reconstruct the missing portion of the artefact and fossil record and provide the often invisible 'long-tail' to our understanding of hominin demography. As determined by the models, hominins are likely to have first entered northern Europe during MIS 34-35 or MIS 23-25, depending on whether Happisburgh provides evidence of hominins during MIS 25 or 21 (respectively). At a minimum, this is approximately 73,000 to 182,000 years earlier than current evidence suggests, and in several modelled scenarios demonstrates their presence prior to one million years ago.

This reduces discontinuity between the earliest hominin occupation of southern and northern Europe. Importantly, however, based on these models alone, a difference of 100 or 300 ka still exists between the regions and current understanding on why southern Europe was occupied prior to northern Europe need not be overhauled (although see discussion below). Indeed, differences between these regions are still evidenced, along with the associated behavioural implications for hominins (McNabb, 2005; Roebroeks, 2006: Dennell et al., 2011; MacDonald et al., 2012; Hosfield and Cole, 2018). What is presented here, however, is a potentially more realistic scenario where instead of 12 or more marine isotope stages going by before hominins ventured into northern Europe, it *may* be as low as two to four (although see later our discussion concerning southern Europe). As identified in the introduction, these dispersal events need not be successful or prolonged events (Ashton and Davis, 2021); discussion here refers to the first arrival of hominins in these two regions and not the onset of continual occupation.

Of the four date combinations used in the models, the only estimates securely and consistently attributed to a warm interglacial (in this case MIS 35) use an MIS 25 and 17 association for Happisburgh and Pakefield respectively (Table 3). Assuming hominins first entered northern Europe during a warm interglacial (Dennell et al., 2011; Ashton and Davis, 2021), an MIS 25 and 17 association for Happisburgh and Pakefield may be more likely relative to the alternatives of MIS 21 or 19. The strength of this assertion, however, is weakened by the site of Moulin Quignon (France) which dates to 670 – 650 ka (MIS 17a – MIS 16b) and suggests that Middle Pleistocene hominins could survive for at least short periods in reasonably cold climatic conditions (Moncel et al., 2021; Rodríguez et al., 2021). In this scenario, the OLE estimates suggest all date combinations to be feasible (Table 3). Thus, while the OLE models do not provide a great deal of resolution on the dating of Happisburgh and Pakefield, they do provide a small contribution to a now long-lived question. Notably, evidence now suggests that even if Happisburgh Site 3 dates to its lower MIS 21 estimate, it can be stated that hominins were likely present in northern Europe by MIS 23 - 24.

The OLE estimates match Hosfield and Cole's (2018) punctuated long chronology (PLC) hypothesis well; albeit with a longer pre-Anglian tail than the original authors may have predicted. Thus, while the PLC should no longer necessarily reflect an absence of hominins prior to one million years ago, these early populations were still likely characterised by "small scale, fragmented dispersals of hominins… equipped with a flake and core lithic tool kit" (Hosfield and Cole, 2018: 157). The absence and presence of handaxes in northern Europe pre- and post-MIS 16 (respectively), as is currently evidenced in the archaeological record, could have contributed to demographic patterns observed in the PLC model (Hosfield and Cole, 2018; Ashton and Davis, 2021). There is a degree of ambiguity regarding whether a PLC without population growth in subsequent interglacial periods was a possibility (Figure 2D), but it seems unlikely that – even if only minor changes occurred – hominins were not able to cope better with winter or glacial climates through time by means of cultural and anatomical adaptations (see discussion below; Rodríguez et al., 2021). This interpretation is supported through the increasing number of archaeological sites evidenced from MIS 21 through to 15, which could indicate larger populations (see earlier discussion concerning Surovell and Brantingham [2007] and Surovell et al. [2009]).

The removal of Sapiston and Fakenham Magna from the site occurrence data did not substantially alter the model's results relative to the 'best-fit' scenario (estimates were 40 – 50 ka older with their removal). Thus, irrespective of one's views on these sites, hominins are estimated to first reach northern Europe during approximately MIS 35 or MIS 25 (depending on Happisburgh's age). The inclusion of Lunery-Rosières and Pont-de-Lavaud significantly altered the OLE estimates. This is not unexpected as they represented the two oldest occurrences in this alternative model (Key et al., 2021a). In this scenario, hominins are inferred to have first occupied northern Europe during MIS 45 or 47, a date that aligns closely with the earliest known hominin fossils and artefacts in southern Europe (Carbonell et al., 2008; Arzarello and Peretto, 2010; Toro-Moyano et al., 2011; Toro-Moyano et al., 2013; López-García et al. 2015). Depending on one's view of the Lunery-Rosières and Pont-de-Lavaud artefacts and dates, and whether they represent northern European sites, then, the OLE models could provide evidence of hominins first arriving in northern and southern Europe at the same time. As clearly stated by Roebroeks et al. (2018), robust criteria are required for widespread acceptance of sites and OLE estimates are only as strong as the site data used.

This is not the first time that an arrival date in advance of one million years has been suggested for hominins in northern Europe (Garcia Garriga et al., 2013; Landeck and Garcia Garriga, 2016). Importantly, however, the current argument and OLE data have been constructed without the use of contested archaeological sites (bar the Lunery-Rosières and Pont-de-Lavaud scenario) (see: Roebroeks et al., 2018). Moreover, it is important to note that the modelled dates do not confirm the controversial ca. 1.07 Ma occurrence of Untermassfeld (Germany) to be a hominin site, even if its age is within the newly revised temporal framework (Landeck and Garcia Garriga, 2016; Roebroeks et al., 2018). As OLE estimates are derived directly from archaeological and fossil data, their use to validate this record is not appropriate and sites that could potentially contribute to future modelling efforts must be verified by evidence external to the OLE method (i.e., conclusive proof that human-made artefacts or fossils are present).

## 7. Southern and northern Europe: implications of a shorter time-gap for their earliest occupation

Had the OLE method been applied to the current fossil and artefact data-record of southern Europe it is likely that the estimated first arrival of hominins would have been pushed beyond the current 1.2 – 1.4 Ma (Carbonell et al., 2008; Arzarello and Peretto, 2010; MacDonald et al., 2012; Toro-Moyano et al., 2013; Lorenzo et al., 2015). It is unlikely to be above 1.5 to 1.6 Ma due to several of the oldest sites being closely linked in age (see the 'Oldowan' scenario in Key et al. [2021b]), but it could *potentially* increase the chronological gap between northern and southern regions by as much as the current Table 3 models reduce it.

The present northern European models *could*, however, represent a minimum expectation, with estimates potentially increasing should any sites older than Happisburgh be found in northern Europe (see the Lunery-Rosières and Pont-de-Lavaud models already discussed). Indeed, as outlined already, the fossil and archaeological record of northern Europe is hampered in its ability to display evidence of Early and Middle Pleistocene hominins, meaning that direct comparisons of northern and southern European first arrival dates are not appropriate without considering these factors. This includes comparisons derived from OLE models. The arguments for these demographic, geological, climatic and historical limitations are as outlined in Section 2. These factors help explain why multiple fossil and artefact sites equal to or older than Happisburgh exist in southern Europe, without this necessarily being due to an absence of hominins in northern Europe. Moreover, they suggest that northern Europe's 'missing tail' is likely proportionately greater than southern Europe's.

We are *not* claiming that hominins did not reach southern Europe first, but instead that our ability to fairly compare the two regions is impeded and northern Europe is missing a greater proportion of its fossil and archaeological record. Indeed, the current suggested disparity in terms of first hominin presence seems unlikely, and there is good reason to think hominins were present in northern Europe prior to one million years ago. Thus, sites older than Happisburgh likely exist in northern Europe and could be found in the future. In such an event, and given the greater sparsity of the northern European record (and therefore the proportionately greater impact of new discoveries on temporal models), OLE 'origination point' estimates could be pushed back further, and this scenario would imply a shortened time period between the earliest occupation of southern and northern Europe irrespective of whether both regions use OLE (although revised northern European OLE estimates should still be within the present model's confidence intervals). Southern Europe could also identify new, older hominin evidence, but given its current increased preservation and discovery rates (Section 2), the impact of new discoveries will potentially be more muted.

Some ecological models and hypotheses support a shorter first occupation-gap between north and south. At first this would appear to include the Galerian migration hypothesis (Muttoni et al., 2018), which is based on a known faunal turnover in Europe during the late Early Pleistocene Transition (EPT; c. MIS 22). The authors argue that dry, steppic conditions with lower sea-levels provided ecological corridors into Europe for hominins and other species including *Elephas antiquus* and *Mammuthus trogontherii*. Although the hypothesis has an elegance, it does not fit the published age of several southern sites (e.g. Pirro Nord, Atapuerca TE9) and is dependent on revision of their dates (Muttoni et al., 2018). If these multiple southern sites were revised to c. MIS 22, then it is likely that OLE estimates for southern Europe would be lower than those for northern Europe, which would not align with recognised dispersal routes. Thus, a strict interpretation of the Galerian migration hypothesis does not appear consistent with there being a 'long tail' to the known archaeological record of northern Europe. Ecological modelling by Blain et al. (2021), however, provides a different perspective. Based on herpetofaunas from palaeontological sites in Iberia, they identify the floral and faunal environment of European hominins during the Early and early Middle Pleistocene, and demonstrate that these humid woodlands would likely have been found in northern France, south-west England, Belgium and Germany. This suggests there were few archaeologically-detectable ecological reasons preventing a rapid and early occupation of northern Europe, as suggested by the OLE models.

An earlier, pre-MIS 21 or 25, emergence of hominins into northern Europe has implications for several widely discussed behavioural attributes. This includes the capability of hominins to survive northern Europe winters, which has recently been investigated in several detailed studies (Hosfield, 2016, 2020, 2021; Hosfield and Cole, 2018; Rodriguez et al. 2021). Three main cold-weather coping mechanisms have been considered, the first being seasonal migration; although many authors have highlighted the difficulties of long migrations (Hosfield, 2020) and the presence of young children at Happisburgh suggest at least some early groups were not seasonal, adult hunting parties (Ashton et al., 2014). A second coping mechanism could have been physical adaptation through more functional body hair, increased sub-cutaneous fat and a higher basal metabolic rate (Hosfield 2020; Rodriguez et al., 2021). This may be part of the answer, but studies are clear that the third coping mechanism – technological thermal-buffering (i.e., clothing) – would also have been required (Rodriguez et al., 2021). A behaviour which further implies prime access to animal hides through hunting or as top scavengers. Hominin presence in high latitudes may also imply effective food acquisition in regions with relatively dispersed, seasonal resources, which may in turn suggest dependence on near-coastal locations (Parfitt et al., 2010; Cohen et al., 2012; Hosfield, 2020). The present OLE models suggest that all of these behaviours may extend back over a million years.

Finally, several authors have argued that the shorter ~41 ka cycles and unstable climatic conditions towards the onset of the EPT (1.2 - 0.9 ma) may have delayed hominin dispersal into northern Europe, whereas more stable climate with lower seasonality and higher ecological diversity after 0.9 Ma enabled hominin expansion (Kahlke et al., 2011; Hosfield and Cole, 2018). An earlier dispersal, as suggested by the OLE models, implies that human population size and rate of growth was sufficient to allow extension of their geographic range into northern Europe over shorter time-frames with the versatility to deal with unstable environments.

Providing model-based estimates for the first occupation of northern Europe is important for understanding the timing of hominin adaptations to high latitudes. These include biological responses and physical capabilities, technological and behavioural developments, and demographic processes through expansion and contraction. The challenge is to find corroborating evidence for these earlier population incursions given the markedly lower chances of discovery in northern Europe. Notably, major river systems of northern Europe still provide a largely untapped source in the higher terraces for potential evidence of earlier human occupation.

## 8. Conclusion

It is only through continued search efforts that additional physical evidence of Early and Middle Pleistocene hominins will be discovered in northern Europe. What is made clear by the present study is that we can reasonably expect this evidence to stretch as far back as 913 ka to 1.159 ma, but this could represent a minimum expectation that may be pushed back further in the future. Thus, future discoveries may provide physical evidence of hominins in northern Europe before one million years ago. Whether we do find evidence of these early and potentially limited incursions is another question, but as recent discoveries in the Bytham, Somme and Stour Valleys attest, the early Lower Palaeolithic record of northern Europe is not yet exhausted (Antoine et al., 2019; Davis et al., 2021; Lewis et al., 2021; Moncel et al., 2021; Key et al., 2022). In this way, the OLE models act as a temporal guide for future fieldwork investigations while simultaneously providing new data to supplement discussions based on known archaeological, fossil, climatic and palaeoenvironmental evidence (e.g., Dennell et al., 2011; Roebroeks et al., 2018; Moncel et al., 2018; Muttoni et al., 2018; Ashton and Davis, 2021). These models are not the well-dated sites with unambiguous traces of hominin presence requested by Roebroeks et al. (2018); that is, they do not provide conclusive evidence of hominins in northern Europe prior to Happisburgh. Instead, they provide an empirically grounded and theoretically robust scenario based on the current archaeological and fossil record, which is a direct result of past and present search efforts. As future discoveries are made, the OLE estimates can be revised in line with these new data and our understanding on the origination timing of hominins in northern Europe can be refined further. Irrespective of how new discoveries impact future modelling, it is clear that the earliest hominin occupation timings of southern and northern Europe cannot be compared without climatic, geological, demographic and historical differences between these two regions being considered.

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