

1 **Hominins likely occupied northern Europe before one million years ago**

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11 **Abstract**

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

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22 **Keywords**

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

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37 1. Introduction

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

47 Together, this has resulted in a fragmented and sparse evidentiary framework for understanding hominin
48 occupation in northern Europe prior to marine isotope stage (MIS) 13 (circa. 500 thousand years ago [ka]). Indeed,
49 only one fossil and ten archaeological sites have been securely demonstrated to predate this MIS stage (Figures
50 1 and 2; Table 1), and the limitations this places on our understanding of when hominins were present in northern
51 Europe is well known (e.g., Dennell et al., 2011; MacDonald et al., 2012; Hosfield and Cole, 2018; Roebroeks et
52 al., 2018; Davis et al., 2021). From the evidence that is available, we know that hominins were present at
53 Happisburgh (UK) from at least ~ 800 ka (MIS 21), and potentially as early as 936 – 959 ka (MIS 25), due to the
54 presence of footprints and a small flake and core assemblage (Parfitt et al., 2010; Ashton et al., 2014).
55 Subsequently, either one or two archaeological sites are known from MIS 19, while either two or three sites are
56 known from MIS 17 (Pakefield [UK] is either from MIS 17 or 19; see Table 1). MIS 16 has the only suggested glacial
57 habitation site, with lithics dated to 660 ka having been discovered at Moulin Quignon, France (Antoine et al.,
58 2019). Additional fossil and archaeological sites are known from MIS 15, 560 – 620 ka (Figure 1; Table 1).

59 In comparison, more southerly regions of Europe – notably the Iberian and Italian peninsulas – display earlier
60 evidence of hominin presence. Indeed, long-lived consensus through the short and long chronology hypotheses
61 suggest hominins to have reached these regions in advance of more northern ones (Roebroeks and van
62 Kolfschoten, 1994; Dennell and Roebroeks, 1996; Roebroeks, 2001; McNabb, 2005; Dennell et al., 2011;
63 MacDonald et al., 2012; Moncel et al., 2018); likely as early as 1.2 - 1.4 million years ago (Ma) in Spain (Carbonell
64 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
65 (Arzarello and Peretto, 2010; López-García et al., 2015). Reconciling an early appearance of hominins in southern
66 Europe with a later appearance in northern Europe is not easy, particularly given their close geographic proximity.
67 It is important to note, therefore, that the reliability of some early European lithic sites is questioned in the ‘short
68 chronology’ and ‘Galerian migration’ hypotheses (Muttoni et al., 2018; Roebroeks et al., 2018). Notably, the 1.2
69 – 1.3 Ma hominin fossils from Sima del Elefante (Atapuerca, Spain) are widely accepted (Carbonell et al., 2008;
70 Lorenzo et al., 2015 [although see: Muttoni et al., 2010]).

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

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

81 Arguments can be constructed for Early Pleistocene interglacial winters being too harsh for hominins without fire
82 or clothing (Gowlett, 2016; Hosfield, 2016; Gilligan, 2017; Scott and Hosfield, 2021). Undoubtedly, this is a
83 meaningful environmental difference between the two European regions, but one that still leaves eight months
84 of the year available for annual migrations or shorter lived, but ultimately unsuccessful, colonisation events
85 (Moncel et al., 2018). Moreover, we do not know the precise tolerance of these hominins for cold environments,

86 whose anatomy was potentially better suited to colder conditions than our own (e.g., Dibble et al., 2017; Wore
87 et al., 2018; Rodríguez et al., 2021). Definitions of ‘northern Europe’ vary, but assuming this means north of the
88 Alps (approx. 46° North) then these dispersals need not imply movement to Happisburgh in the UK but could
89 include more limited journeys to central or northern France, Belgium, Germany, Austria, or the Czech Republic.
90 Thus, the likelihood that individuals and small groups did not, at least sporadically, venture into northern Europe
91 prior to the earliest physical evidence at Happisburgh may be low.

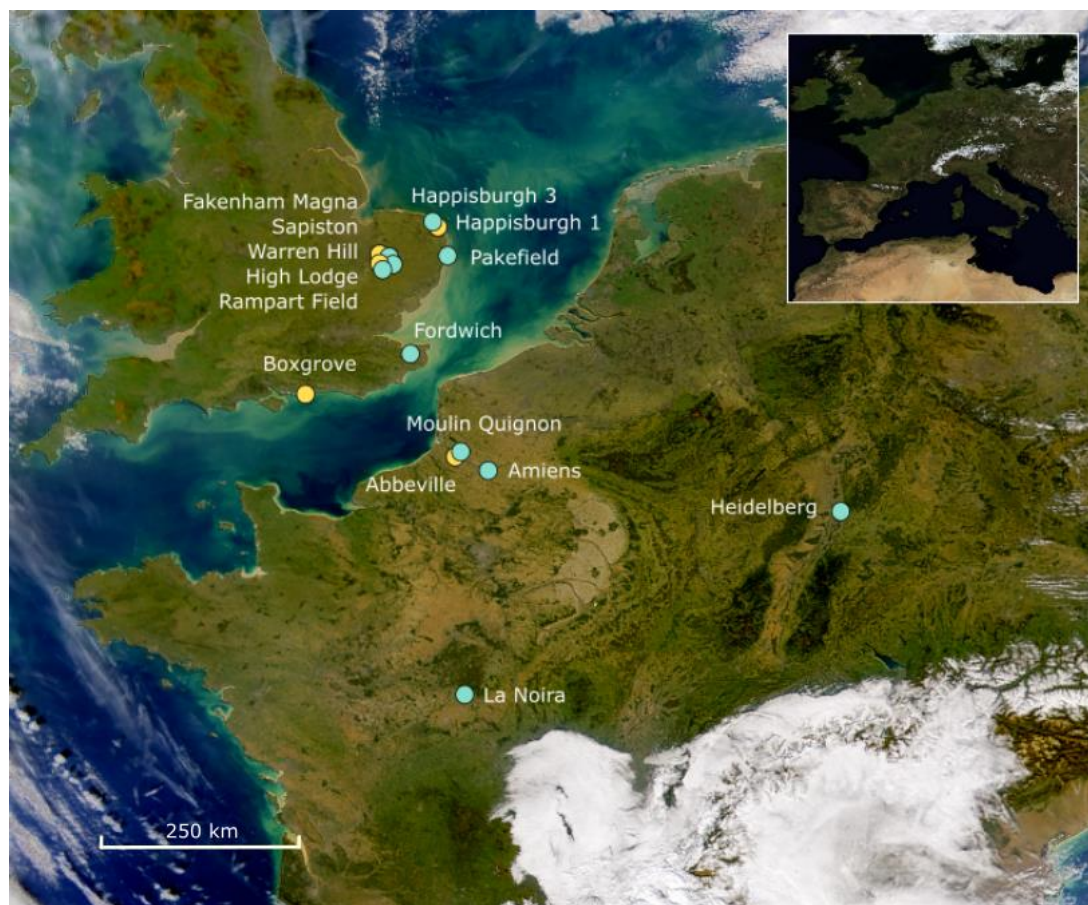
92 A potentially more plausible explanation for the perceived 400,000-year gap (0.8 - 0.9 Ma [Happisburgh] to 1.2 –
93 1.3 Ma [level TE9, Sima del Elefante]) between the occupation of southern and northern Europe is that our
94 understanding is inaccurate due to a disparity in the likelihood of finding hominin fossils and lithic artefacts in
95 these regions. Simply, the chances of finding evidence of early hominin occupation is greater in more southern
96 European regions. There are four key reasons for this:

- 97 • Due to the above-described absence (or near-absence [Antoine et al., 2019; Moncel et al., 2021]) of
98 hominins during glacial periods and potentially during interglacial winters (Hosfield, 2016; Rodríguez et
99 al., 2021), northern Europe is automatically faced with a diminished fossil and archaeological record
100 relative to more temperate regions. The impact of glacial cycles on hominin populations, and therefore
101 fossil and artefact creation, would have been more muted in the south (Dennell et al., 2011; Hosfield,
102 2016), ultimately providing a more plentiful archaeological and palaeoanthropological record for us to
103 discover today. This difference is further exaggerated by the reduced ability of higher latitudes to support
104 high density hominin populations (Ashton and Davis, 2021). Simply, southern Europe would have
105 sustained larger numbers of hominins across interglacial, transitional, and glacial periods, resulting in a
106 greater volume of evidence being produced, and in turn, a greater number of fossils and artefacts being
107 preserved for us to discover today.
- 108 • Glacial periods are associated with the formation of glaciers in northern European regions. The southern
109 limits of glaciers varied dependent on the marine isotope stage (Böse et al., 2012), but their formation
110 would have destroyed many archaeological and fossil sites formed prior to MIS 6, 10, 12 and 16, and
111 potentially before Happisburgh. The impact of glaciers on site preservation is well known to Lower
112 Palaeolithic archaeologists working in these regions (Gowlett, 2006; Preece and Parfitt, 2012; Moncel et
113 al., 2018; Lewis et al., 2021), and the true scale of damage inflicted on our understanding of hominin
114 occupation is hard to ascertain.
- 115 • Northern Europe is also geologically impoverished relative to southern Europe when it comes to the
116 presence of caves and karstic system features suitable for hominin habitation and the preservation of
117 fossils, tools, and other evidence of occupation. It is important to stress that it is not void of such features,
118 but on a relative basis there are fewer. Indeed, Spain and Italy collectively have more carbonate rock
119 than the UK, Germany, Belgium, the Netherlands, Denmark, Poland, Slovakia, and Czech Republic
120 combined (Chen et al., 2017). Further, the few caves that do contain Middle Pleistocene sediments, such
121 as Kent’s Cavern and Brixham Cave, were investigated at the inception of the subject, resulting in poorly
122 contextualised artefacts and issues of dating (Cook and Jacobi, 1999). Relative to southern European
123 areas, northern Europe therefore has a poor record of relevant cave or rock shelter deposits and is at a
124 disadvantage when it comes to preserving fossil and archaeological evidence of early hominin habitation
125 (although note that southern pre-Happisburgh sites are also found in open-air locations).
- 126 • Finally, south-eastern Britain and northern France have a long history of artefacts being recovered from
127 river terrace gravels with abundant lithic collections archived from Middle Pleistocene sites (Roe, 1968;
128 Wymer, 1999; Harris et al., 2019). This might be thought to redress the north-south imbalance, but the
129 vast majority of quarries are now inaccessible for detailed investigation or dating and most were situated
130 on post-MIS 13 terraces. There are exceptions where higher terraces have been reinvestigated, such as
131 on the Solent (McNabb et al., 2012), the Bytham (Davis et al., 2021; Lewis et al., 2021), the Stour (Key et
132 al., 2022) and the Somme (Antoine et al., 2019). However, all try to contextualise older collections, with
133 small-scale fieldwork programmes compared to the often much larger excavations in southern Europe
134 (e.g. Peretto, 2006; Toro-Moyano et al., 2011; Ollé et al., 2013; Vallverdú et al., 2014; Arzarello et al.
135 2015). So, despite the long history of research in northern Europe, over the last 50 years there has been
136 a much greater focus on early sites in southern Europe, exacerbating the low chances of discovering

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

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

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



160

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

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

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

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

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

206 4. Optimal Linear Estimation

207

208 4.1 Model Assumptions

209 OLE has few assumptions relative to alternative temporal modelling techniques (Solow, 2005; Clements et al.,
210 2013; Key et al., 2021a), but for meaningful results to be returned it is important for these assumptions to be met.
211 In the present context this includes the assumption that hominins were present in northern Europe prior to the
212 current oldest physical evidence (in this case Happisburgh [Parfitt et al., 2010]), all fossil and archaeological sites
213 used in the model are independent, search effort does not equate to zero in any given temporal context (that is,
214 archaeologists and palaeoanthropologists are not actively excluding sediments older than Happisburgh in their
215 search efforts), the earliest hominins in northern Europe left traces of their presence through lithic artefacts or
216 bones (and ultimately fossils), and we have no *a priori* reason to think that population pressures were significantly
217 different in one interglacial over another. Search effort could be considered unbalanced between Acheulean and
218 earlier flake-and-core-only assemblages as handaxes are more easily recognised (and thus discovered). This is
219 unavoidable, but search effort for expedient technologies has also been considerable in both northern and
220 southern Europe (e.g., see discussions on the Clactonian and eoliths [Ashton et al., 1992; Ellen, 2013; McNabb,
221 2020]).

222 Finally, in the present context, there is the assumption that taphonomic processes are broadly equal or monotonic
223 across the temporal range entered into the model. In other words, if an archaeological site was made in the same
224 location in MIS 15 and MIS 21, then there is the assumption that both would have equal chance of being preserved
225 to the present, or, the period between MIS 21 to MIS 15 would display monotonically increasing preservation
226 probability. As Surovell and colleagues demonstrate (Surovell and Brantingham, 2007; Surovell et al., 2009), this
227 is not a straightforward assumption in all archaeological contexts. Here, however, this is arguably the case for
228 northern Europe between 800 and 600 ka. Northern European stone artefact sites are principally destroyed
229 through glacier formation and fluvial activities, and two of the three most extreme Pleistocene glaciation events
230 happened post-MIS 15. So, irrespective of whether a site was formed in MIS 15 or 21, if a glacier had potential to
231 destroy it (Gowlett, 2006), then it would likely have occurred during MIS 10 or 12 (Preece and Parfitt, 2012).
232 Similarly, Quaternary fluvial terraces (where most pre-MIS 15 lithic artefacts are recovered) form in predictable
233 stages (Bridgland and Westaway, 2014). Once a terrace is formed the river erodes beneath this point, meaning
234 artefacts are saved from further fluvial damage. Incision and erosion can deteriorate Quaternary terraces through
235 time (Bridgland and Westaway, 2014), with this cumulative process potentially impeding the preservation of older
236 sites. It is, however, on a relative scale; all MIS 14 or older sites have been exposed to this process for at least
237 550,000 years. Moreover, several of the most important (i.e., oldest) sites for the OLE models are not found in
238 such deposits. So, at a very broad level, fluvial disturbance affects artefacts and fossils for broadly equal periods.
239 Fossils may also be destroyed by leaching and other chemical processes, but it is arguably the case that if this is
240 going to influence their preservation it will occur within the space of 600 ka (i.e., an additional 200 to 300 ka
241 would not make a substantive difference). While these broad arguments appear reasonable and the use of the
242 OLE methods appear valid, it is possible that in specific, site-dependent circumstances other taphonomic
243 processes may influence the preservation of early hominin sites.

244 4.2 Archaeological and Fossil Sites

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

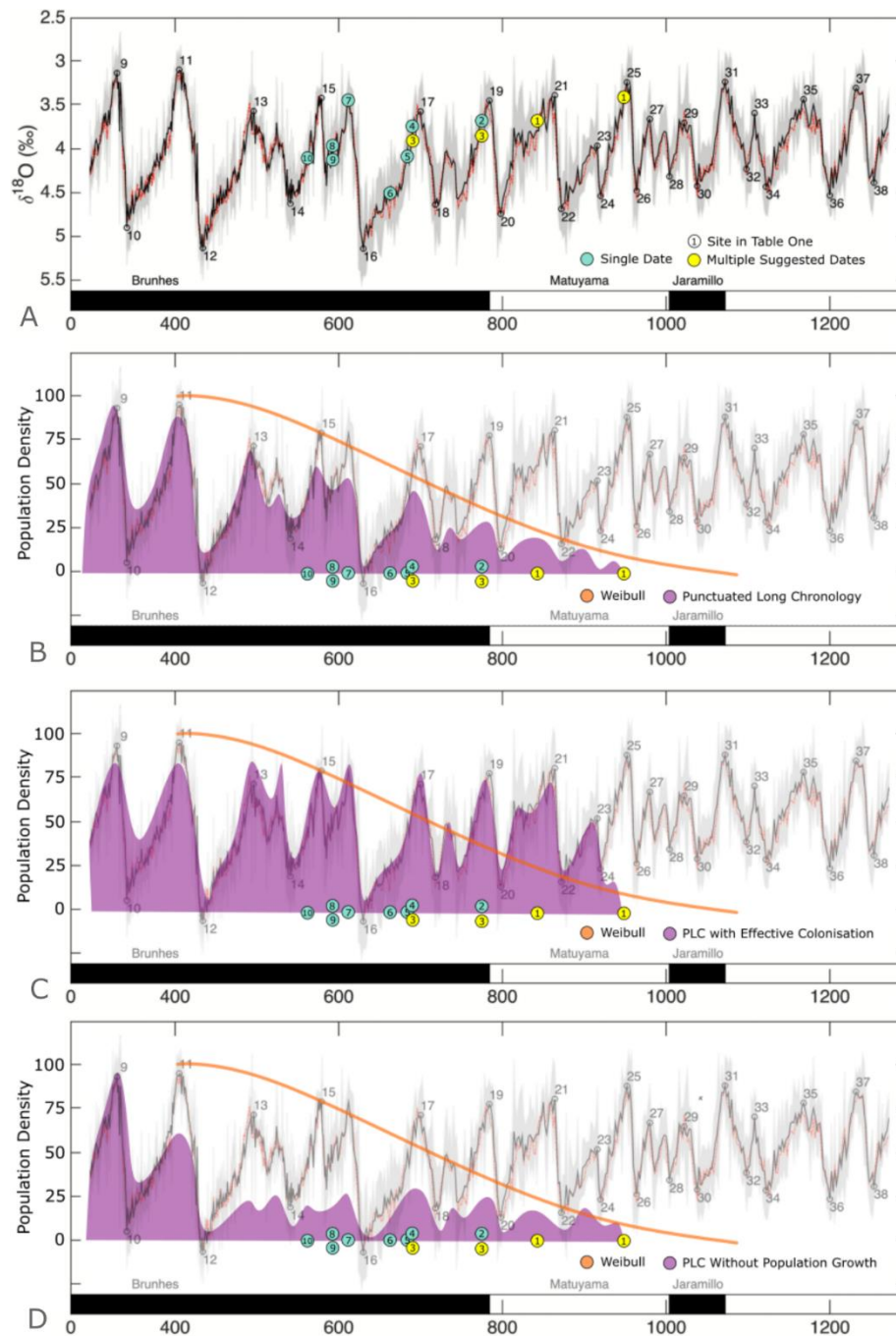
251 A thorough review of Palaeolithic and paleoanthropological literature was conducted to identify the oldest fossil
252 and artefactual evidence of hominins in northern Europe (last search effort December 2021). The ten oldest sites
253 identified through this review are presented in Table 1 and Figure 1. These sites represent a 'best-fit' scenario
254 with all being widely accepted in the literature. Several occurrences have been excluded due to their indirect
255 dating methods (e.g., poorly dated terrace sequences), contested 'artefacts', or lack of provenance (see
256 Supplementary Information 1). All excluded occurrences, apart from Untermassfeld in Germany (see: Roebroeks
257 et al., 2018), would be among the youngest dates used in the models, meaning that had they been included, there
258 would only be a minor impact on the estimates produced. The sites of Fakenham Magna (UK) and Sapiston (UK)

259 only display a few artefacts, and although these were identified by strict criteria and a panel of Palaeolithic
260 specialists (Davis et al., 2021, SI), some may still oppose their inclusion on the basis of the small assemblages, but
261 they are included for two reasons. First, irrespective of an assemblage's size, the presence of lithic artefacts at a
262 defined point in time demonstrates the presence of hominins (Davis et al., 2021; Lewis et al., 2021). Second, their
263 inclusion in the models will produce a more conservative estimate relative to their exclusion (i.e., estimates will
264 be more limited and closer to the date of the oldest known artefacts).

265 The sites of Happisburgh and Pakefield are among the most important considered here as they provide some of
266 the oldest evidence of hominins occupying northern Europe. Thus, they have a relatively great impact on the
267 model's estimates (Key et al., 2021a). Both, however, are associated with two MIS stages. Happisburgh Site 3 is
268 constrained to MIS 21 or MIS 25 (Parfitt et al., 2010), while Pakefield is constrained to MIS 17 or 19 (Parfitt et al.,
269 2005). MIS 17 is the "very youngest" attribution for Pakefield, with an age of MIS 19 being more commonly
270 referenced (Parfitt et al., 2005: 1011; Lewis et al., 2021). Due to these uncertainties, four combinations of data
271 were entered into the OLE models so that versions with all possible Happisburgh and Pakefield MIS associations
272 could be investigated.

273 In addition to the main 'best-fit' site scenario, two further versions were investigated to illustrate hominin
274 dispersal estimations under alternative site-discovery perspectives, each using the four Happisburgh and
275 Pakefield combinations. The first included the sites of Lunery-Rosières and Pont-de-Lavaud, dated to 1.166 and
276 1.054 ma, respectively (Despriée et al., 2017, 2018). Both are from central France, slightly south of la Noira, and
277 without independent dating evidence of the ESR age estimates. Rampart Field and Amiens were removed in this
278 scenario. The second version excluded Fakenham Magna and Sapiston (both UK), as in this case the authors
279 preferred geological age is younger than the ESR dates. Abbeville (France) and Happisburgh Site 1 (UK) replaced
280 them in the models.

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



288

289 **Figure 2:** The ten archaeological and fossil sites included in the ‘best-fit’ OLE models presented in the context of Early and
 290 Middle Pleistocene marine isotope stages (Figure 2A). Figures 2B, 2C and 2D present hypothetical demographic scenarios for
 291 northern Europe following an initial occupation event in MIS 25. Figure 2B represents the punctuated long chronology (PLC)
 292 model as proposed by Hosfield and Cole (2018), where populations are slow to increase during initial interglacial periods but
 293 following technological and anatomical changes there are increased populations in MIS 15 and 13, before a marked increase
 294 in MIS 11. Figure 2C represents a scenario where populations in northern Europe are tightly linked to mean annual
 295 temperatures, with winter temperatures, annual resource fluctuations, predation, and disease (for example), not limiting
 296 population numbers in one period more than another. Figure 2D represents the standard PLC model (Hosfield and Cole, 2018)
 297 without any meaningful population growth until MIS 11. In each, a Weibull distribution curve is presented to demonstrate that
 298 the standard punctuated long chronology model (Figure 2B) best fits the assumptions of optimal linear estimation modelling.
 299 Note that Happpisburgh and Pakefield have both of their proposed ages illustrated (yellow). Versions of these scenarios with
 300 complete regional extinction during glacial periods, and interglacial periods without recolonisation, could also be included but
 301 are not presented here. The numbers at each peak refer to MIS stages. The original MIS figure is modified from Ahn et al.
 302 (2017) under the terms of an CC-BY-NC License.

303 4.3 The OLE Method

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

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

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

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

348 **Table 1:** The ten oldest widely accepted archaeological or hominin fossil occurrences in northern Europe. Four OLE models are
349 run as the oldest archaeological occurrence, Happisburgh (UK), is constrained to *either* MIS 21 or MIS 25, and the second or
350 third oldest, Pakefield (UK), is constrained to *either* MIS 17 or MIS 19 (Table 2). Yet, as some of the oldest dates used, they
351 have a relatively great impact on the model's estimated date and in turn would have substantial implications for the model's
352 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	<i>Homo heidelbergensis</i> 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, <i>Homo heidelbergensis</i> 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				

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⁺ 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

357

358 **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)			

359

360 5. When Did Hominins First Occupy Northern Europe?

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

370 Applying an MIS 25 age to Happisburgh resulted in an estimated first arrival for hominins in northern Europe from
 371 approximately 1.129 to 1.159 Ma, which accords with either MIS 34 or 35 (Table 3). The upper bound of the
 372 different model’s confidence interval (T_{CI}) is approximately 1.661 to 1.812 Ma. If an MIS 19 association is used for
 373 Pakefield then the estimates are more recent, dating to 1.129, 1.132 and 1.136 Ma (across the three versions of
 374 the OLE method used here). An MIS 17 association for Pakefield suggests an older first arrival, at 1.152, 1.155, or
 375 1.159 Ma. Notably, these latter results are within the warm MIS 35 interglacial, while those that associated
 376 Pakefield with MIS 19 are at the threshold of MIS 33 and 34 (Table 3).

377 An MIS 21 age for Happisburgh returned estimated first arrival dates of approximately 913 to 935 Ka, which would
 378 indicate an MIS 23 or 24 occupation for hominins (Table 3). The upper bound of the different model’s confidence
 379 interval (T_{CI}) is approximately 1.110 to 1.191 Ma. Again, estimates applying an MIS 19 age for Pakefield were ~ 20
 380 Ka, dating to 913, 914 and 917 Ka. If Pakefield dates to MIS 17, then the estimates suggest a 931, 932 or 935 ka
 381 arrival for hominins in northern Europe. Notably, all estimates align along glacial and interglacial boundaries (Table
 382 3).

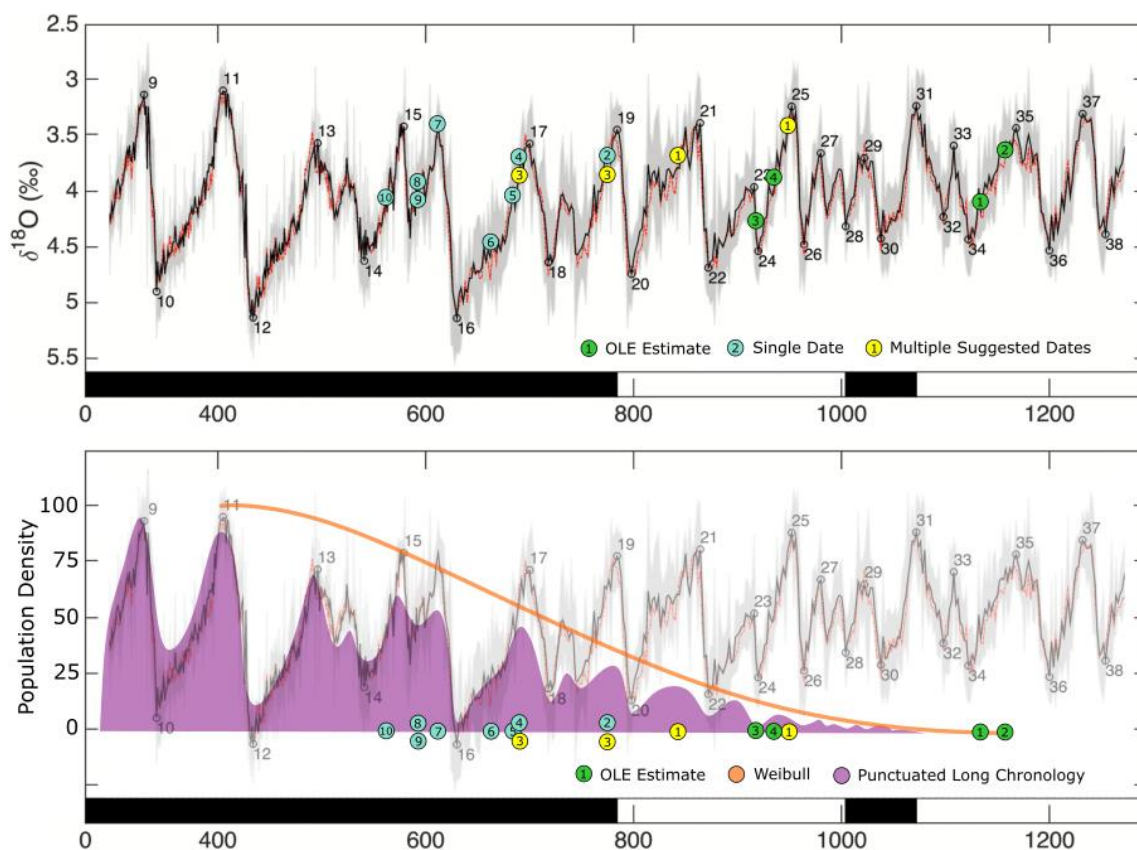
383 When Sapiston and Fakenham Magna were removed from the site occurrence data, an MIS 25 age for
 384 Happisburgh resulted in estimates from approximately 1.178 to 1.215 Ma (Supplementary Information 1). An MIS
 385 21 age for Happisburgh resulted in first occupation timings between 953 to 986 ka. When Lunery-Rosières and
 386 Pont de Lavaud were included in the site occurrence data, estimated first occupation dates for northern Europe
 387 increase to approximately 1.388 to 1.425 Ma (Supplementary Information 1). There was a limited impact caused
 388 by the different age assignments for Happisburgh and Pakefield.

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

391 dependent on the MIS associations used for the sites of Happisburgh (21 or 25) and Pakefield (17 or 19). Presented
 392 alongside the origination estimates (T_0) are each models' confidence interval (T_{CI}).

		T_0			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)

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394

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

398 6. The early occupation of northern Europe

399 As exceptional as the lithic artefacts and hominin footprints identified at Happisburgh are (Parfitt et al., 2010;
 400 Ashton et al., 2014), they are not evidence of the very earliest hominins to have entered northern Europe. Instead,
 401 they reflect the current earliest known physical evidence of hominins in the region, as determined by past search
 402 efforts. To gain a more accurate understanding of when hominins first reached northern Europe, OLE models
 403 have been used to reconstruct the missing portion of the artefact and fossil record and provide the often invisible

404 'long-tail' to our understanding of hominin demography. As determined by the models, hominins are likely to
405 have first entered northern Europe during MIS 34-35 or MIS 23-25, depending on whether Happisburgh provides
406 evidence of hominins during MIS 25 or 21 (respectively). At a minimum, this is approximately 73,000 to 182,000
407 years earlier than current evidence suggests, and in several modelled scenarios demonstrates their presence prior
408 to one million years ago.

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

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

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

445 The removal of Sapiston and Fakenham Magna from the site occurrence data did not substantially alter the
446 model's results relative to the 'best-fit' scenario (estimates were 40 – 50 ka older with their removal). Thus,
447 irrespective of one's views on these sites, hominins are estimated to first reach northern Europe during
448 approximately MIS 35 or MIS 25 (depending on Happisburgh's age). The inclusion of Lunery-Rosières and Pont-
449 de-Lavaud significantly altered the OLE estimates. This is not unexpected as they represented the two oldest
450 occurrences in this alternative model (Key et al., 2021a). In this scenario, hominins are inferred to have first
451 occupied northern Europe during MIS 45 or 47, a date that aligns closely with the earliest known hominin fossils
452 and artefacts in southern Europe (Carbonell et al., 2008; Arzarello and Peretto, 2010; Toro-Moyano et al., 2011;
453 Toro-Moyano et al., 2013; López-García et al. 2015). Depending on one's view of the Lunery-Rosières and Pont-

454 de-Lavaud artefacts and dates, and whether they represent northern European sites, then, the OLE models could
455 provide evidence of hominins first arriving in northern and southern Europe at the same time. As clearly stated
456 by Roebroeks et al. (2018), robust criteria are required for widespread acceptance of sites and OLE estimates are
457 only as strong as the site data used.

458 This is not the first time that an arrival date in advance of one million years has been suggested for hominins in
459 northern Europe (Garcia Garriga et al., 2013; Landeck and Garcia Garriga, 2016). Importantly, however, the
460 current argument and OLE data have been constructed without the use of contested archaeological sites (bar the
461 Lunery-Rosières and Pont-de-Lavaud scenario) (see: Roebroeks et al., 2018). Moreover, it is important to note
462 that the modelled dates do not confirm the controversial ca. 1.07 Ma occurrence of Untermassfeld (Germany) to
463 be a hominin site, even if its age is within the newly revised temporal framework (Landeck and Garcia Garriga,
464 2016; Roebroeks et al., 2018). As OLE estimates are derived directly from archaeological and fossil data, their use
465 to validate this record is not appropriate and sites that could potentially contribute to future modelling efforts
466 must be verified by evidence external to the OLE method (i.e., conclusive proof that human-made artefacts or
467 fossils are present).

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

469 Had the OLE method been applied to the current fossil and artefact data-record of southern Europe it is likely
470 that the estimated first arrival of hominins would have been pushed beyond the current 1.2 – 1.4 Ma (Carbonell
471 et al., 2008; Arzarello and Peretto, 2010; MacDonald et al., 2012; Toro-Moyano et al., 2013; Lorenzo et al., 2015).
472 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
473 ‘Oldowan’ scenario in Key et al. [2021b]), but it could *potentially* increase the chronological gap between northern
474 and southern regions by as much as the current Table 3 models reduce it.

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

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

497 Some ecological models and hypotheses support a shorter first occupation-gap between north and south. At first
498 this would appear to include the Galerian migration hypothesis (Muttoni et al., 2018), which is based on a known
499 faunal turnover in Europe during the late Early Pleistocene Transition (EPT; c. MIS 22). The authors argue that dry,
500 steppic conditions with lower sea-levels provided ecological corridors into Europe for hominins and other species
501 including *Elephas antiquus* and *Mammuthus trogontherii*. Although the hypothesis has an elegance, it does not fit
502 the published age of several southern sites (e.g. Pirro Nord, Atapuerca TE9) and is dependent on revision of their

503 dates (Muttoni et al., 2018). If these multiple southern sites were revised to c. MIS 22, then it is likely that OLE
504 estimates for southern Europe would be lower than those for northern Europe, which would not align with
505 recognised dispersal routes. Thus, a strict interpretation of the Galerian migration hypothesis does not appear
506 consistent with there being a 'long tail' to the known archaeological record of northern Europe. Ecological
507 modelling by Blain et al. (2021), however, provides a different perspective. Based on herpetofaunas from
508 palaeontological sites in Iberia, they identify the floral and faunal environment of European hominins during the
509 Early and early Middle Pleistocene, and demonstrate that these humid woodlands would likely have been found
510 in northern France, south-west England, Belgium and Germany. This suggests there were few archaeologically-
511 detectable ecological reasons preventing a rapid and early occupation of northern Europe, as suggested by the
512 OLE models.

513 An earlier, pre-MIS 21 or 25, emergence of hominins into northern Europe has implications for several widely
514 discussed behavioural attributes. This includes the capability of hominins to survive northern Europe winters,
515 which has recently been investigated in several detailed studies (Hosfield, 2016, 2020, 2021; Hosfield and Cole,
516 2018; Rodriguez et al. 2021). Three main cold-weather coping mechanisms have been considered, the first being
517 seasonal migration; although many authors have highlighted the difficulties of long migrations (Hosfield, 2020)
518 and the presence of young children at Happisburgh suggest at least some early groups were not seasonal, adult
519 hunting parties (Ashton et al., 2014). A second coping mechanism could have been physical adaptation through
520 more functional body hair, increased sub-cutaneous fat and a higher basal metabolic rate (Hosfield 2020;
521 Rodriguez et al., 2021). This may be part of the answer, but studies are clear that the third coping mechanism –
522 technological thermal-buffering (i.e., clothing) – would also have been required (Rodriguez et al., 2021). A
523 behaviour which further implies prime access to animal hides through hunting or as top scavengers. Hominin
524 presence in high latitudes may also imply effective food acquisition in regions with relatively dispersed, seasonal
525 resources, which may in turn suggest dependence on near-coastal locations (Parfitt et al., 2010; Cohen et al.,
526 2012; Hosfield, 2020). The present OLE models suggest that all of these behaviours may extend back over a million
527 years.

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

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

540 **8. Conclusion**

541 It is only through continued search efforts that additional physical evidence of Early and Middle Pleistocene
542 hominins will be discovered in northern Europe. What is made clear by the present study is that we can reasonably
543 expect this evidence to stretch as far back as 913 ka to 1.159 ma, but this could represent a minimum expectation
544 that may be pushed back further in the future. Thus, future discoveries may provide physical evidence of hominins
545 in northern Europe before one million years ago. Whether we do find evidence of these early and potentially
546 limited incursions is another question, but as recent discoveries in the Bytham, Somme and Stour Valleys attest,
547 the early Lower Palaeolithic record of northern Europe is not yet exhausted (Antoine et al., 2019; Davis et al.,
548 2021; Lewis et al., 2021; Moncel et al., 2021; Key et al., 2022). In this way, the OLE models act as a temporal guide
549 for future fieldwork investigations while simultaneously providing new data to supplement discussions based on
550 known archaeological, fossil, climatic and palaeoenvironmental evidence (e.g., Dennell et al., 2011; Roebroeks et
551 al., 2018; Moncel et al., 2018; Muttoni et al., 2018; Ashton and Davis, 2021). These models are not the well-dated
552 sites with unambiguous traces of hominin presence requested by Roebroeks et al. (2018); that is, they do not

553 provide conclusive evidence of hominins in northern Europe prior to Happisburgh. Instead, they provide an
554 empirically grounded and theoretically robust scenario based on the current archaeological and fossil record,
555 which is a direct result of past and present search efforts. As future discoveries are made, the OLE estimates can
556 be revised in line with these new data and our understanding on the origination timing of hominins in northern
557 Europe can be refined further. Irrespective of how new discoveries impact future modelling, it is clear that the
558 earliest hominin occupation timings of southern and northern Europe cannot be compared without climatic,
559 geological, demographic and historical differences between these two regions being considered.

560

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