LETTERS

Early Pleistocene human occupation at the edge of the boreal zone in northwest Europe

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The dispersal of early humans from Africa by 1.75 Myr ago led to a marked expansion of their range, from the island of Flores in the east to the Iberian peninsula in the west[1–5]. This range encompassed tropical forest, savannah and Mediterranean habitats, but has hitherto not been demonstrated beyond 45° N. Until recently, early colonization in Europe was thought to be confined to the area south of the Pyrenees and Alps. However, evidence from Pakefield (Suffolk, UK) at ~0.7 Myr indicated that humans occupied northern European latitudes when a Mediterranean-type climate prevailed[6]. This provided the basis for an 'ebb and flow' model, where human populations were thought to survive in southern refugia during cold stages, only expanding northwards during fully temperate climates[5]. Here we present new evidence from Happisburgh (Norfolk, UK) demonstrating that Early Pleistocene hominins were present in northern Europe >0.78 Myr ago when they were able to survive at the southern edge of the boreal zone. This has significant implications for our understanding of early human behaviour, adaptation and survival, as well as the tempo and mode of colonization after their first dispersal out of Africa.

At Happisburgh Site 3 (Fig. 1) an assemblage of 78 flint artefacts has been excavated from fluvial gravels and laminated estuarine sands and silts that fill a series of stacked, overlapping channels. The assemblage includes cores, flakes and flake tools, with no evidence of hand-axe manufacture (Fig. 2a–h). Many of the artefacts are unabraded, indicating discard at or near the site and minimal fluvial transport. A characteristic of the assemblage is the predominance of large flakes (up to 145 mm) with sharp cutting edges and opposing cortex. The unusual size-range, together with the high proportion of flake tools, indicates that they have been selected and brought into the area for use and that knapping was undertaken elsewhere. The presence of artefacts at several levels in the succession indicates repeated visits to the site.

Happisburgh (52°49′36″ N, 1°31′58″ E) lies on the northeast coast of Norfolk, a rapidly eroding cliffed coastline largely composed of Early and Middle Pleistocene sediments. The locality lies within the Crag Basin that, during periods of high global sea level, was part of a wide embayment at the edge of the North Sea (Fig. 1b). Freshwater, estuarine and inter-tidal sediments of the Cromer Forest-bed Formation (CF-bF) and its shallow marine equivalent, the Wroxham Crag Formation, were deposited in this area during the Early and early Middle Pleistocene[7]. These largely interglacial deposits are famous for their rich flora and fauna[8]. However, despite a long history of investigation, the CF-bF has only recently yielded evidence for human presence[6]. The ancestral River Thames and the now-extinct Bytham River flowed across the region from the west and southwest depositing the Kesgrave and Bytham sands and gravels, respectively[7]. This prolonged phase of fluvial activity ended during the Anglian Stage (marine isotope stage (MIS) 12) with the emplacement of tills and related glacial sediments that comprise the Happisburgh and Lowestoft formations[9].

The artefacts at Happisburgh Site 3 occur within the newly defined Hill House Formation (HHF; Supplementary Information 1), which overlies sands and silts of the Norwich Crag Formation and is succeeded by the Happisburgh and Lowestoft formations. The HHF consists primarily of a series of stacked channels, most filled with lag gravels overlain by laminated sands and silts (Fig. 3). The sedimentology indicates deposition in the lower reaches of a large river,

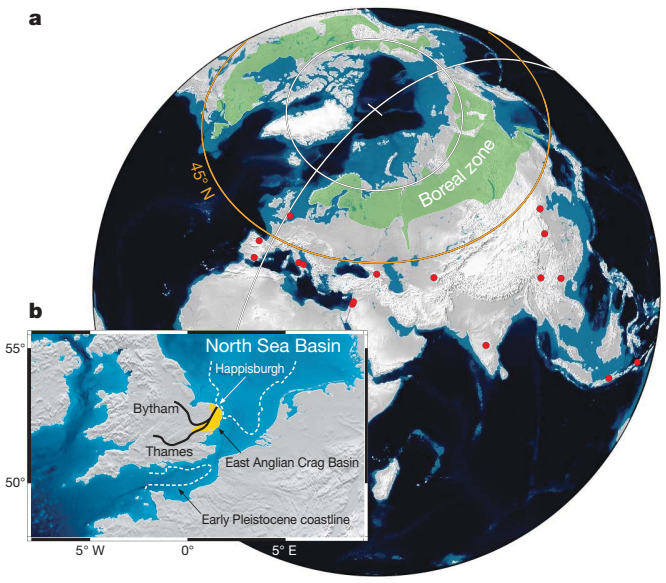

Figure 1 | Location of Happisburgh and other Early Pleistocene archaeological sites in Eurasia. a, Key Early Pleistocene archaeological sites (red dots) in relation to 45° N and the present-day boreal zone. **b**, Reconstruction of the palaeogeography of northwest Europe at the time of the human occupation at Happisburgh, showing the Thames draining into the North Sea ~150 km to the north of its present-day estuary.

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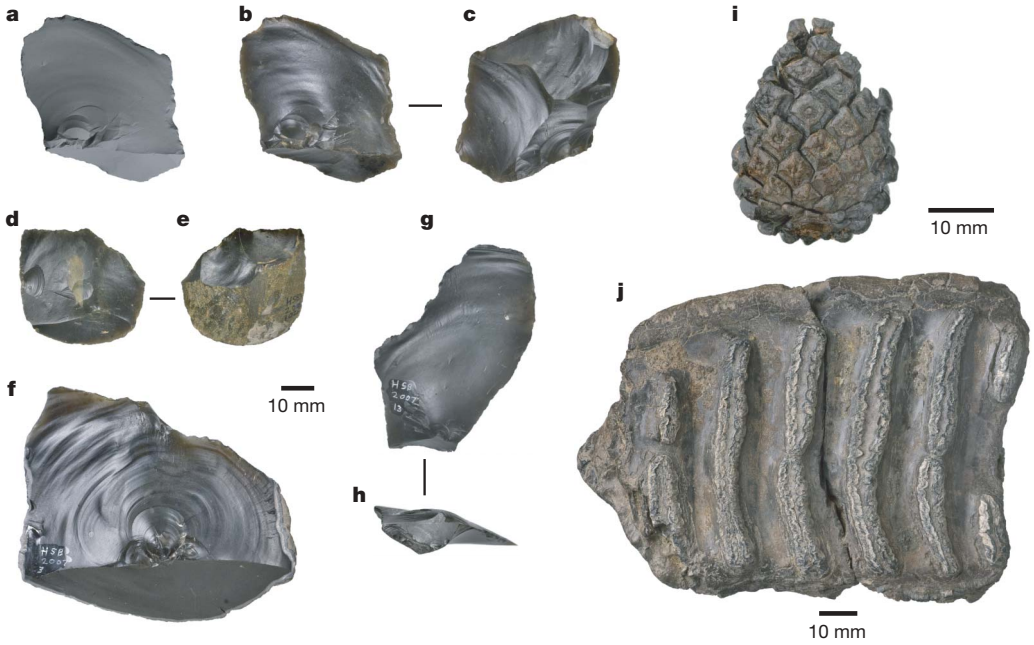

Figure 2 | Early Pleistocene artefacts and biological remains from Happisburgh Site 3. Flint artefacts include hard-hammer flakes, notches, retouched flakes and cores (**a**–**c**, hard-hammer flake; **d**, **e**, multiple notch; **f**, hard-hammer flake; **g**, **h**, hard-hammer flake, showing pronounced point of percussion on plain butt). Supplementary Information includes micro-CT volume rendering of artefacts (still example shown as **a**) with three-dimensional animations (see Supplementary Movies 1–10). **i**, Cone of *Pinus* cf. *sylvestris*. **j**, Upper second molar of *Mammuthus* cf. *meridionalis*.

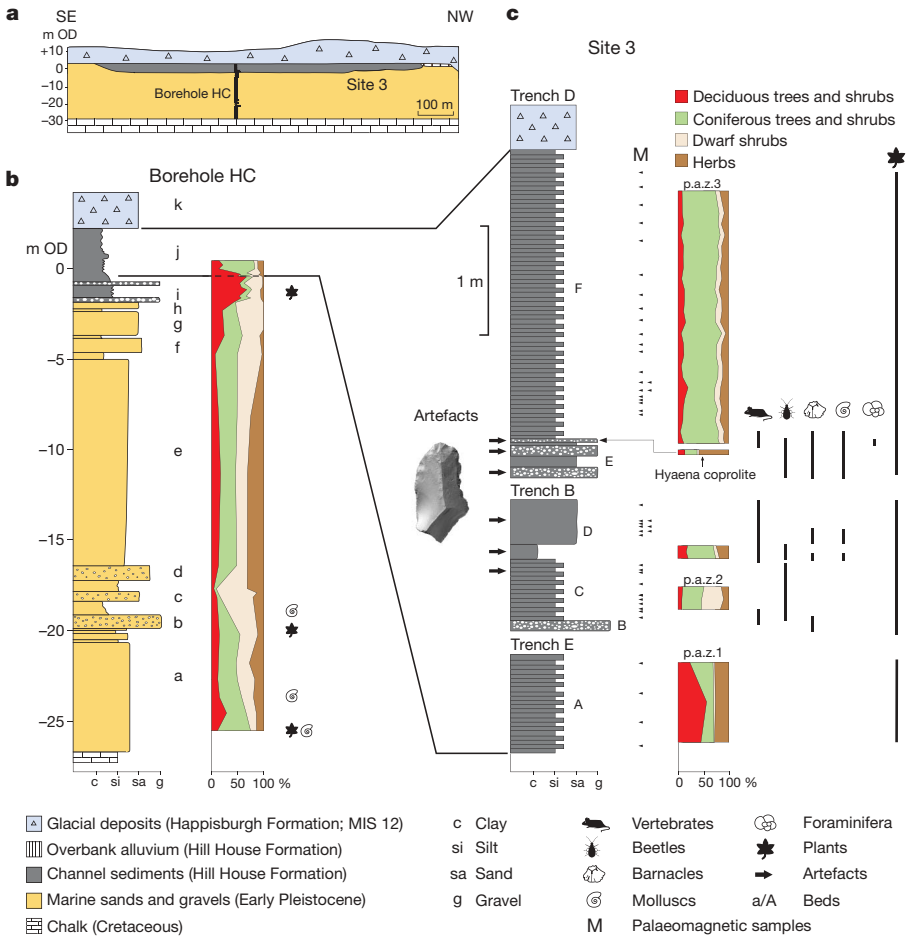

Figure 3 | Stratigraphical context of the Happisburgh Site 3 artefacts and biological remains. **a**, Coastal section, showing the location of Borehole HC and Site 3. OD, Ordnance Datum. **b**, Lithostratigraphy and summary of pollen record for Borehole HC[22]. **c**, Composite lithostratigraphy for Site 3, showing the alternation of coarse-grained channel deposits and estuarine laminated sands and silts. Correlation with borehole HC shows that the artefacts from Site 3 date towards the end of the interglacial; earlier sediments are yet to be investigated for human presence.

probably in the upper part of an estuary. The clast lithology of the gravels can be used to establish the palaeogeographical context of the site. Significantly, the non-local component includes vein quartz and quartzite carried by the river from source areas in the English Midlands. The ratio of vein quartz to quartzite, the predominantly white/colourless appearance of both these lithologies, and the proportion of Carboniferous chert indicate deposition by the ancestral River Thames with some contribution from the Bytham River[7]. In addition, the presence of Lower Greensand chert and Hertfordshire Puddingstone indicates a catchment encompassing southeast England. Among the exotic rocks are acid volcanic clasts probably derived from Ordovician strata in North Wales. This suite is comparable with the volcanic rocks found in the Kesgrave Sands and Gravels[10]. The geological evidence therefore indicates that human occupation occurred in the upper estuarine zone of the River Thames, which flowed into the sea ~150 km north of its present estuary.

The age of the human occupation is constrained by a combination of palaeomagnetism and biostratigraphy. The natural remanent magnetization (NRM) of a sediment can comprise distinct components acquired at different times in the sediment's history. East Anglian Plio-Pleistocene sediments are less than ideal palaeomagnetic recorders; they lack magnetite (except as inclusions within silicate grains or magnetite lamellae in ilmenites), they contain low concentrations of a range of relict magnetic minerals (for example, ferrian ilmenites, ferrimagnetic chromites) and they frequently carry a strong normal polarity overprint from post-depositional formation of the ferrimagnetic iron sulphide mineral, greigite[11,12]. To avoid chemical change during NRM analysis in these organic-rich sediments, thermal demagnetization is precluded. To reduce the possibility of generating spurious, greigite-borne gyroremanences (GRMs) on alternating field demagnetization[13,14], stepwise tumbling alternating field demagnetization is used to remove secondary NRM components and to isolate the characteristic remanent magnetization (ChRM) acquired at or near the time of sediment deposition.

Palaeomagnetic analyses at Happisburgh were undertaken on 45 samples from the laminated silts (beds A, C, D and F) below, within and above the artefact-bearing gravels (Fig. 3). In all but the basal samples, a strong, normal polarity overprint is carried by greigite. Tumbling alternating field demagnetization removes much of this normal overprint and isolates a weak, reversed polarity ChRM (Fig. 4a) or clear great circle trends towards reversed polarity, especially in fields above ~50 milliTesla (mT) (Fig. 4b, Supplementary Information 3 and Supplementary Fig. 1b). The basal samples contain much less greigite, have proportionally less of this normal overprint, and their initial NRMs have negative inclinations (Fig. 4c). Thus, most of the reverse polarity remanence within the Happisburgh sediments is carried not by the (probably) post-depositional greigite[15], but by detrital minerals, with medium to high (>~50 mT) coercivities. The Happisburgh sediments therefore display a reversed polarity, depositional remanence throughout beds A, C, D and F (Supplementary Information 3, Supplementary Fig. 1 and Supplementary Table 1). This indicates deposition during either the Matuyama chron (2.52–0.78 Myr) or during a brief Brunhes chron geomagnetic excursion[16].

The age of the site is further constrained by biostratigraphic evidence. Important plant taxa include *Tsuga* (hemlock) and *Ostrya*-type (hop-hornbeam type), which are unknown in northern Europe after the Early Pleistocene[17]. Key mammalian taxa include *Mammuthus* cf. *meridionalis* (southern mammoth; Fig. 2j), *Equus suessenbornensis* (extinct equid) and at least two species of *Mimomys* (extinct vole), together with *Cervalces latifrons* (extinct elk), *Cervus elaphus* (red deer) and 'advanced' forms of *Microtus* (voles)[18–20]. The overlapping ranges of the plant and mammalian taxa indicate a date towards the end of the Early Pleistocene. This evidence together with the palaeomagnetic data indicates that human occupation occurred towards the end of the Matuyama Chron between 0.99 and 0.78 Myr ago (Fig. 5).

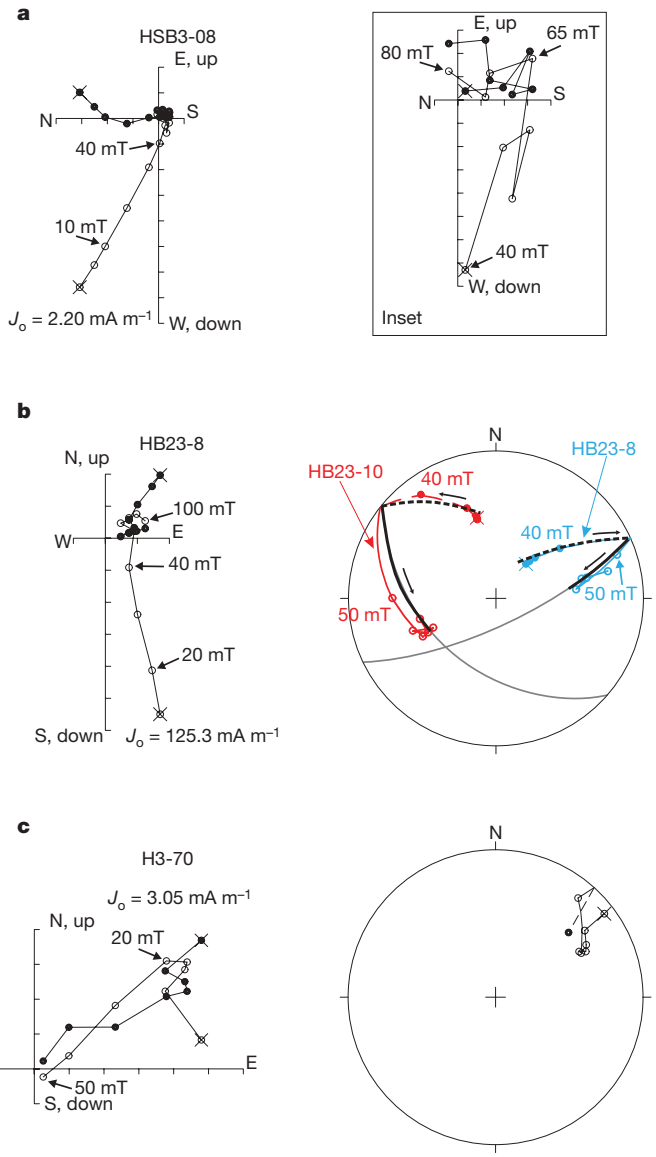

Figure 4 | Representative sample demagnetization data. a, Bed C: HSB3-08, Zijderveld diagram showing reverse polarity component isolated from 65 to 80 mT. **b**, Bed D: HB23-8, Zijderveld diagram and stereo plot of the observed great circle trend from demagnetization data (in blue) from 10 to 100 mT, thick dashed/solid lines indicating lower/upper hemisphere, and their upper hemisphere extension (thin grey line). An intersecting fitted great circle path is also shown on the stereo plot for neighbouring sample HB23-10 (demagnetization data, in red, from 10 to 80 mT). **c**, Bed A: H3-70, Zijderveld diagram and stereo plot showing the removal of a small normal overprint at 10–15 mT, and a reversed NRM component evident up to 50 mT. Filled/open symbols denote projections onto the lower/upper hemisphere. Lower hemisphere projection paths are dashed and upper hemisphere paths are solid. See Supplementary Information 1, Supplementary Fig. 6 for the location of samples.

The environment and climate during the period of human occupation can be reconstructed from a rare combination of terrestrial and marine biota, which include plant remains (for example, pollen, seeds, pine-cones (Fig. 2i) and wood), together with foraminifera, marine molluscs, barnacles, beetles and vertebrates (Supplementary Information 2). Three pollen assemblage zones (p.a.z.) are represented (Fig. 3; Supplementary Information 1 and Supplementary Fig. 8). The first (p.a.z. 1), which pre-dates the artefacts, is indicative of deciduous woodland with *Quercus* (oak), *Ostrya*-type (hop-hornbeam type), *Ulmus* (elm) and *Alnus* (alder). The second (p.a.z. 2) is associated with the earliest artefacts ($n = 2$) and is dominated by heathland taxa (~40% Ericaceae-type), together with *Pinus* (pine) and *Picea* (spruce).

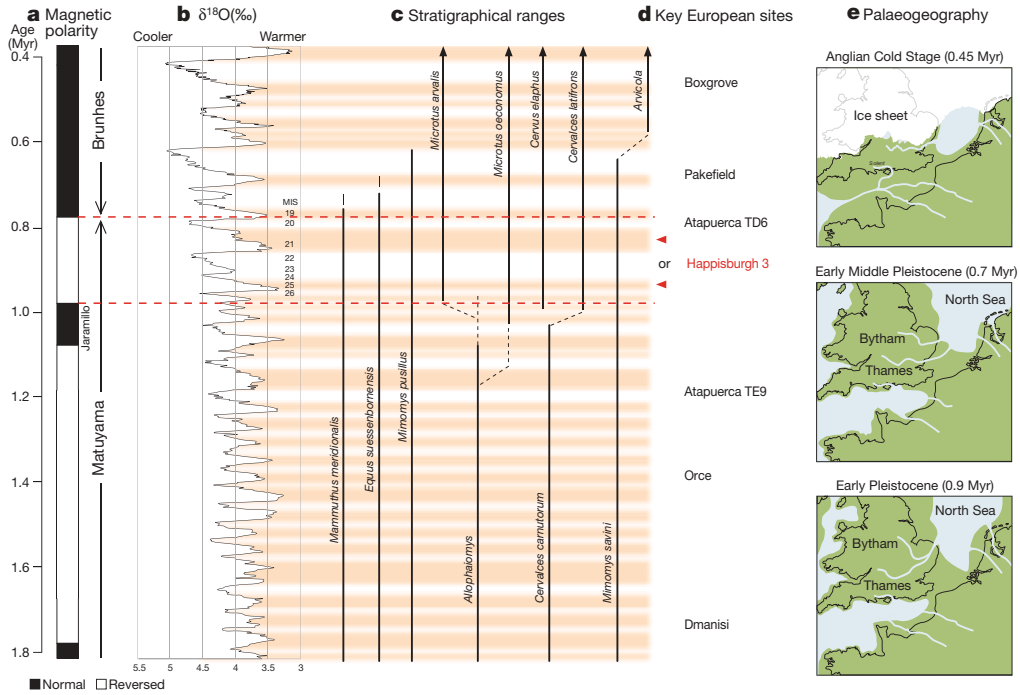

Figure 5 | Dating evidence for Happisburgh 3. **a**–**e**, The age of the artefacts is constrained by the reversed polarity (**a**), the palaeobotany indicating deposition towards the end of an interglacial cycle, that is, cooling limb of odd-numbered isotope stage (**b**), combination of biostratigraphically significant mammals (**c**), and palaeogeographical context when the River Thames entered the North Sea at this site (**e**). This evidence indicates that the artefacts date from either MIS 21 (866–814 kyr) or 25 (970–936 kyr), which are the most prominent warm stages (that is, those most likely to have supported deciduous forest and other thermophilous plants—see Supplementary Information 1) in the period spanning 0.99–0.78 Myr (ref. 29). With the exception of Happisburgh 3, all European Early Pleistocene sites are located south of 45°N (**d**). The oxygen isotope record used to provide the climate record is the LR04 stack[30].

Most of the artefacts ($n = 76$) occur within sands and gravels that are encompassed by p.a.z. 3. This zone is characterized by abundant *Pinus* and *Picea* pollen that, together with conifer wood and pine-cones, indicate regional conifer-dominated forest with deciduous elements forming a minor component. Local grassland is indicated by the range of grazers (*Equus suessenbornensis*, Bovidae and *Microtus* spp.) and by pollen from a hyaena coprolite (Supplementary Information 1). Beetle and plant macrofossil remains indicate a large, slow-flowing river fringed by riparian habitats that included reed-swamp, alder carr, marsh and pools, with forest close by. A large river is also indicated by *Acipenser* cf. *sturio* (sturgeon), and proximity to the estuary and salt marsh is indicated by marine molluscs, barnacles and foraminifera.

Mutual Climatic Range[21] temperature estimates from the beetles (Supplementary Information 1) indicate that mean summer temperatures (between 16 and 18 °C) were similar to or possibly slightly warmer than southern Britain today. The mean winter temperatures (between 0 and –3 °C) were at least 3 °C lower than today, although reconstruction of winter temperatures can be more problematic. These temperature estimates, together with the conifer-dominated woodland, are analogous to the situation that exists in southern Scandinavia today near the transition between the temperate and boreal vegetational zones.

The vegetational succession (p.a.z. 1–3) can be correlated with the upper part of the longer pollen record from borehole HC (ref. 22; Fig. 3a, b). The record at Site 3 is therefore consistent with a position in the second half of an interglacial cycle, with human occupation during the period of cooling climate. The fully temperate conditions indicated by the complete palaeobotanical succession in borehole HC may therefore further constrain human occupation to the end of either MIS 21 (866–814 kyr) or MIS 25 (970–936 kyr) (Fig. 5).

The northern latitude of Happisburgh is in marked contrast to other uncontested Early Pleistocene archaeological sites in Eurasia that all lie south of 45° N (refs 23, 24; Fig. 1). These more southerly sites are associated with a range of habitats from tropical forest in southeast Asia[2], steppe in central Asia[25], to Mediterranean habitats in southern Europe[3]. Happisburgh Site 3 therefore provides the first record of Early Pleistocene occupation of northern forests. Previous models of human expansion and contraction in synchrony with the biota of specific habitats (habitat-tracking), as suggested at Pakefield[6], are not supported by the new evidence, which indicates an ability to survive novel environments as global climate deteriorated towards the end of an interglacial. Investigation of older sediments at Happisburgh will establish at what stage of the interglacial humans first arrived (Fig. 3).

Occupation of northern forests would have presented a range of new challenges to colonising populations from southern Eurasia[26,27]. During interglacials the vegetation of much of northern Europe consisted of dense forest with seasonal plant resource availability. This would have entailed a greater reliance on animal resources during winter months when access to edible plants would have been severely reduced. Northern coniferous forests presented even greater challenges owing to their low usable biomass, being characterized by poor edible plant resources and dispersed herbivore populations. Further difficulties would have included short winter daylight hours for foraging and severe winter cold compared to many parts of southern Europe[28].

The evidence from Happisburgh Site 3 provides a detailed reconstruction of the local landscape and its resources, which can begin to answer some of the questions about human adaptation at this time. The biological data indicate that human occupation was located at an ecotone with access to a variety of resource-rich habitats, including a large tidal river with freshwater pools and marsh on its floodplain, together with salt marsh and coast nearby. The floodplain was dominated by grass, which supported a diverse range of herbivores and

their predators, whereas the surrounding conifer-dominated forest would have sustained a far more restricted range of large mammals. The presence of Early Pleistocene humans in these northern latitudes might therefore be explained by the proximity of this mosaic of habitats. This ecotone provided a much wider range of critically important winter resources such as tubers and rhizomes, shellfish, seaweed and the resident herbivore population than the northern forest alone.

Although the climate at Happisburgh was more continental than that of the present day, winter temperatures would have been ameliorated by an oceanic effect in comparison to the continental landmass at equivalent latitudes. It remains unclear whether expansion into northern latitudes with lower winter temperatures required human physical adaptation, seasonal migration or developments in technology such as hunting, clothing, the use of shelters or control of fire. At present there are no other Early Pleistocene archaeological sites with comparable organic preservation. Therefore the survival of organic materials at Happisburgh and other East Anglian coastal exposures might potentially answer questions about developments in technology.

The artefacts from Happisburgh demonstrate that the East Anglian coast is a key area for understanding the earliest occupation of northern Europe. Accelerated coastal erosion is now exposing new geological sections and an increasing number of Lower Palaeolithic sites, but their locations make them vulnerable to further erosion and sea level rise. The sediments are a largely unexplored archaeological resource, spanning over 80 km of coastline and encompassing a critical period for early human prehistory from ~1.8 to 0.48 Myr. Future investigations in this region will focus on these sediments with the possibility of discovering evidence of even earlier human presence in northern Europe.

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1. Carbonell, E. *et al.* Eurasian gates: the earliest human dispersals. *J. Anthropol. Res.* **64,** 195–228 (2008).
2. Brumm, A. *et al.* Hominins on Flores, Indonesia, by one million years ago. *Nature* **464,** 748–752 (2010).
3. Carbonell, E. *et al.* The first hominin of Europe. *Nature* **452,** 465–469 (2008).
4. Dennell, R. & Roebroeks, W. An Asian perspective on early human dispersal from Africa. *Nature* **438,** 1099–1104 (2005).
5. Roebroeks, W. The human colonisation of Europe: where are we? *J. Quaternary Sci.* **21,** 425–435 (2006).
6. Parfitt, S. A. *et al.* The earliest record of human activity in northern Europe. *Nature* **438,** 1008–1012 (2005).
7. Rose, J., Moorlock, B. S. P. & Hamblin, R. J. O. Pre-Anglian fluvial and coastal deposits in Eastern England: lithostratigraphy and palaeoenvironments. *Quaternary Int.* **79,** 5–22 (2001).
8. Reid, C. *The Geology of the Country around Cromer* (HMSO, London, 1882).
9. Preece, R. C. *et al.* Biostratigraphic and aminostratigraphic constraints on the age of the Middle Pleistocene glacial succession in north Norfolk, UK. *J. Quaternary Sci.* **24,** 557–580 (2009).
10. Hey, R. W. & Brenchley, P. J. Volcanic pebbles from Pleistocene gravels in Norfolk and Essex. *Geol. Mag.* **114,** 219–225 (1977).
11. Maher, B. A. & Hallam, D. F. Magnetic carriers and remanence mechanisms in magnetite-poor sediments of Pleistocene age, southern North Sea margin. *J. Quaternary Sci.* **20,** 79–94 (2005).
12. Maher, B. A. & Hallam, D. F. Palaeomagnetic correlation and dating of Plio/Pleistocene sediments at the southern margins of the North Sea Basin. *J. Quaternary Sci.* **20,** 67–77 (2005).
13. Giddings, J. W., Klootwijk, C., Rees, J. & Groenewoud, A. Automated AF-demagnetization on the 2G-Enterprises through-bore cryogenic magnetometer. *Geol. Mijnb.* **76,** 35–44 (1997).
14. Sagnotti, L. & Winkler, A. Rock magnetism and palaeomagnetism of greigite-bearing mudstones in the Italian peninsula. *Earth Planet. Sci. Lett.* **165,** 67–80 (1999).
15. Roberts, A. P. & Weaver, R. Multiple mechanisms of remagnetization involving sedimentary greigite (Fe_3S_4). *Earth Planet. Sci. Lett.* **231,** 263–277 (2005).
16. Roberts, A. P. Geomagnetic excursions: knowns and unknowns. *Geophys. Res. Lett.* **35,** L17307 (2008).
17. Magri, D., Di Rita, F. & Palombo, M. R. An Early Pleistocene interglacial record from an intermontane basin of central Italy (Scoppito, L'Aquila). *Quaternary Int.*, (2009).
18. Azzaroli, A. in *The early Middle Pleistocene in Europe* (ed. Turner, C.), 45–51 (Taylor & Francis, 1996).
19. Lister, A. M. in *The early Middle Pleistocene in Europe* (ed. Turner, C.), 25–44 (Taylor & Francis, 1996).
20. Maul, L. C. & Markova, A. K. Similarity and regional differences in Quaternary arvicolid evolution in Central and Eastern Europe. *Quaternary Int.* **160,** 81–99 (2007).
21. Atkinson, T. C., Briffa, K. R. & Coope, G. R. Seasonal temperatures in Britain during the past 22,000 years, reconstructed using beetle remains. *Nature* **325,** 587–592 (1987).
22. West, R. G. *The Pre-glacial Pleistocene of the Norfolk and Suffolk Coasts* (Cambridge Univ. Press, 1980).
23. Zhu, R. X. *et al.* New evidence on the earliest human presence at high northern latitudes in northeast Asia. *Nature* **431,** 559–562 (2004).
24. Dennell, R. *The Palaeolithic Settlement of Asia* (Cambridge Univ. Press, 2009).
25. Ranov, V. A., Carbonell, E. & Rodríguez, X. P. Kuldara: earliest human occupation in central Asia in its Afro-Asian context. *Curr. Anthropol.* **36,** 337–346 (1995).
26. Gamble, C. S. *The Palaeolithic Settlement of Europe* (Cambridge Univ. Press, 1986).
27. Roebroeks, W. Hominid behaviour and the earliest occupation of Europe: an exploration. *J. Hum. Evol.* **41,** 437–461 (2001).
28. Dennell, R. Dispersal and colonisation, long and short chronologies: how continuous is the Early Pleistocene record for hominids outside East Africa? *J. Hum. Evol.* **45,** 421–440 (2003).
29. Bintanja, R., van de Waal, R. S. W. & Oerlemans, J. Modelling atmospheric temperatures and global sea levels over the past million years. *Nature* **437,** 125–128 (2005).
30. Lisiecki, L. E. & Raymo, M. E. A. Pliocene–Pleistocene stack of 57 globally distributed benthic $\delta^{18}O$ records. *Paleoceanography* **20,** PA1003 (2005).

Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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Author Contributions S.A.P., N.M.A. and S.G.L. coordinated research on the site, wrote the article and edited the Supplementary Information. Authors contributed in the following areas: archaeology (N.M.A.); CT scans and videos of artefacts (R.L.A.); stratigraphical sequence and palaeogeography (S.G.L. and P.G.H.); palaeomagnetic investigations (B.A.M. and V.K.); mammalian biostratigraphy (S.A.P.); palynology (S.M.P. and M.D.L.); plant macrofossils (M.H.F.); wood (R.G.); foraminifera (J.E.W.); palaeoecology, molluscs and barnacles (R.C.P.); coleoptera (G.R.C.); vertebrates (S.A.P. and N.R.L.). C.B.S. contributed to writing and editing of the paper and is Director of the *Ancient Human Occupation of Britain* Project.

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