

Ancient genomes indicate population replacement in Early Neolithic Britain

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The roles of migration, admixture and acculturation in the European transition to farming have been debated for over 100 years. Genome-wide ancient DNA studies indicate predominantly Aegean ancestry for continental Neolithic farmers, but also variable admixture with local Mesolithic hunter-gatherers. Neolithic cultures first appear in Britain circa 4000 bc, a millennium after they appeared in adjacent areas of continental Europe. The pattern and process of this delayed British Neolithic transition remain unclear. We assembled genome-wide data from 6 Mesolithic and 67 Neolithic individuals found in Britain, dating 8500–2500 bc. Our analyses reveal persistent genetic affinities between Mesolithic British and Western European hunter-gatherers. We find overwhelming support for agriculture being introduced to Britain by incoming continental farmers, with small, geographically structured levels of hunter-gatherer ancestry. Unlike other European Neolithic populations, we detect no resurgence of hunter-gatherer ancestry at any time during the Neolithic in Britain. Genetic affinities with Iberian Neolithic individuals indicate that British Neolithic people were mostly descended from Aegean farmers who followed the Mediterranean route of dispersal. We also infer considerable variation in pigmentation levels in Europe by circa 6000 bc.

The transition to farming marks one of the most important ecological shifts in human evolution. The processes by which this transition occurred have been a matter of intense debate for over a century^{1–3}, although across continental Europe ancient DNA studies indicate a predominant role for expanding Neolithic farmer populations of mostly Aegean ancestry (Aegean Neolithic Farmers (ANF))^{4–15}. ANF-derived populations dispersed throughout Europe via two major routes: one along the Mediterranean and the other through Central and into Northern Europe^{7,11}. Both dispersing populations introgressed repeatedly with local Mesolithic foragers, which gradually increased their proportion of European Mesolithic ancestry^{7,13–15}.

The nature of the Neolithic transition in Britain remains unclear because of the millennium-long delay in its appearance after the establishment of farming in adjacent regions of continental Europe^{1–3}, and the lack of genome-wide data from British Mesolithic hunter-gatherers. Although there is universal agreement among archaeologists that there was a dramatic change in material culture in Britain around 4000 bc, there are divergent views regarding the extent to which this change was influenced by cultural or demographic processes^{1–3}. The British Isles lie furthest from the Aegean origin^{4–15} of the migrating farmers that influenced the

development of the Neolithic across Europe, are geographically isolated from continental Europe by large bodies of water and had maritime climates which differ from the majority of mainland Europe—all factors that may have altered the nature of the adoption of farming. The relationship between British and continental European Mesolithic populations is also of interest, as Britain geographically abuts two genetically distinct but contemporaneous populations, Western European and Scandinavian Mesolithic hunter-gatherers (WHGs and SHGs, respectively), and could have potentially harboured ancestry from earlier (~19000–15000 bc) Magdalenian Palaeolithic hunter-gatherer populations^{16–18}.

Results

Here, we report whole-genome data from 6 Mesolithic (including ‘Cheddar Man’ from Gough’s Cave, Somerset, England) and 16 Neolithic British individuals, and combine these with data from 51 previously published Neolithic British individuals¹² to characterize the Mesolithic to Neolithic transition in Britain (Fig. 1 and Supplementary Fig. 16). Our Mesolithic samples date from 8750–8459 calibrated (cal.) bc (Early Mesolithic Aveline’s Hole, Somerset, England) to 4256–3803 cal. bc (Late Mesolithic Cnoc Coig, Oronsay, western Scotland). Our Neolithic samples date

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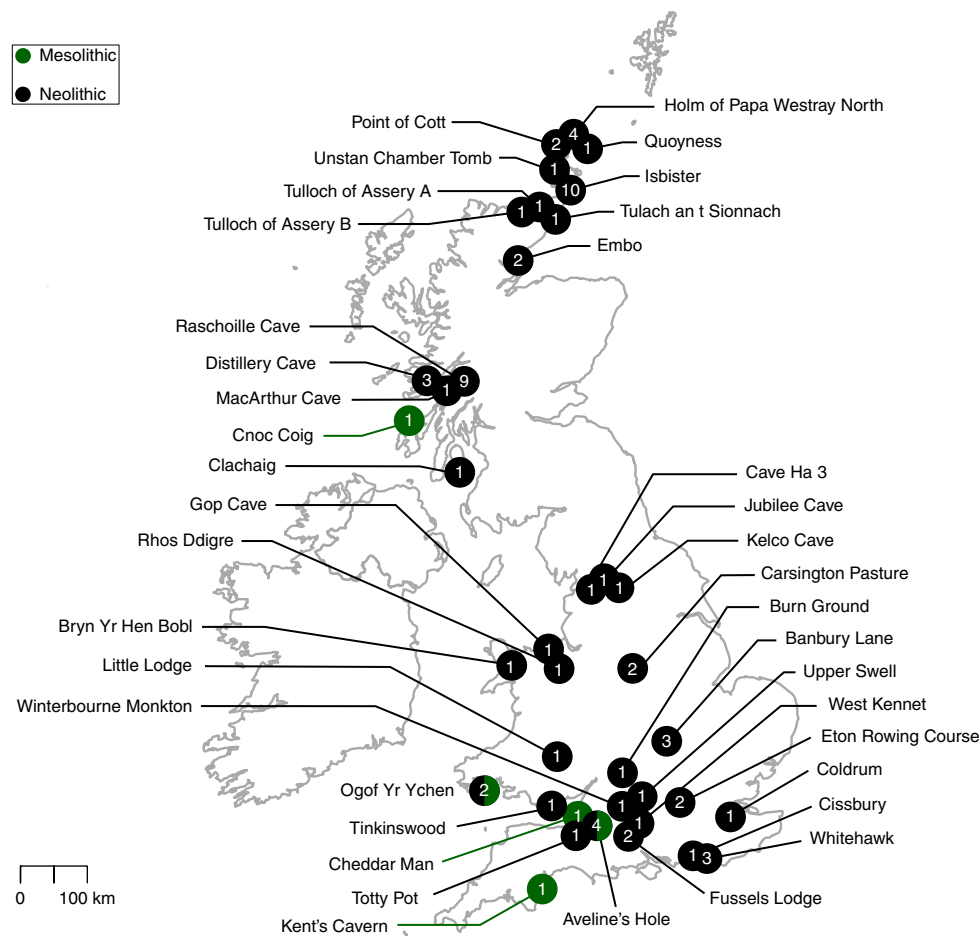


Fig. 1 | Map of sample locations. Geographical locations of British samples analysed here. Numbers indicate total samples obtained from a given location.

from 3951–3780 cal. bc (Early Neolithic McArthur Cave, western Scotland) to 2570–2347 cal. bc (Late Neolithic Isbister, Orkney, Scotland). We combined data generated in two different ways. For 35 individuals, we generated new whole-genome shotgun sequencing data, including full genomes from British Mesolithic (at $\times 2.3$) and Neolithic (at $\times 10.7$) individuals. For all samples we enriched next-generation sequencing libraries for approximately 1.24 million single nucleotide polymorphisms (SNPs) (median coverage $\times 0.88$). When available, we merged data obtained from both methods and identified the most likely allele at each locus (see Methods). These were combined with ancient genomic data from 67 previously reported individuals^{4–7,9–12,14,16–22} (see Supplementary Table 1) and modern genomic data from diverse global populations²³.

All British Mesolithic individuals cluster with Western and Scandinavian hunter-gatherers in a principal components analysis (Fig. 2). By contrast, all directly dated individuals who post-date 4000 bc and undated individuals associated with Neolithic monuments cluster tightly near Iberian and Central European Middle Neolithic individuals. By examining the degree of allele sharing of British Mesolithic individuals with various European hunter-gatherer individuals/groups (SHG, Eastern Hunter Gatherers (EHG) and El Mirón, see Supplementary Figs. 1–4), we were able to attribute these confidently to the WHG group. Comparison of British Mesolithic individuals to different Mesolithic WHGs (Berry au Bac, France; Ranchot88, France; Loschbour, Luxembourg; La Braña, Spain; KO1, Hungary; Supplementary Figs. 5, 6 and 11–14) indicates that all most closely resemble Loschbour. When we compared the remaining British Mesolithic genomes to Loschbour and Cheddar Man

(our highest-coverage British Mesolithic sample, approximately $\times 2.3$), we found no major excess of shared drift for either individual, indicating that Loschbour, Ranchot88 and the British Mesolithic samples do not form separate clusters (Supplementary Fig. 7).

To investigate the proportions of Aegean farmer-related ancestry in the British samples, we modelled these as mixtures of ANFs and European WHGs using the qpAdm method, which studies ensembles of f_4 statistics (Fig. 3 and Supplementary Fig. 8)²⁴. The genomes of all British Mesolithic individuals can be explained almost entirely by WHG ancestry, the remainder ($< 7.3\%$) probably stemming from poorly matching portions of the genome. Most of the ancestry in all British Neolithic individuals could be attributed to ANFs ($> 56\%$, $\sim 74\%$ on average), indicating a substantial shift in ancestry with the transition to farming. To investigate the proximate source of ANF ancestry in British Neolithic individuals, we examined affinities with Early Neolithic individuals from Iberia and Central Europe. We compare Early to Middle Neolithic individuals as the latter are contemporary with the British Early Neolithic, making these an unlikely direct source. For all British Neolithic individuals considered we inferred more shared drift with Early Neolithic Iberians (Fig. 4a and Supplementary Fig. 9). However, these f_4 statistic-based inferences may be sensitive to levels of WHG admixture, such that the similarity in WHG admixture proportions in Early Neolithic Iberian and British samples, but lower estimates in Central European Early Neolithic individuals, is driving the inference of an Iberian rather than Central European source for Early British farmers. To examine this possibility in more detail, we performed a more powerful haplotype-based analysis.

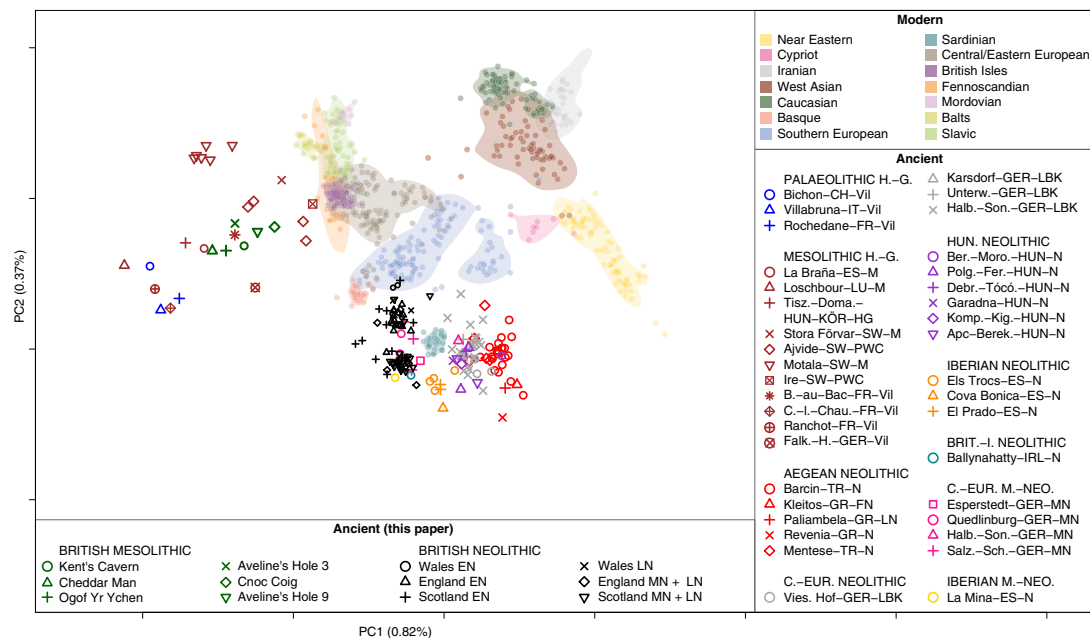


Fig. 2 | Principal component analysis of modern and ancient West Eurasians. British and additional ancient samples are projected onto the reference space computed on present-day West Eurasian populations. See Methods for computational details and Supplementary Table 1 for information on the samples. PC, principal component. Site Abbreviations: Tisz. Doma., Tiszasszölös-Domaháza; B.-au-Bac, Berry-au-Bac; C.-l.-Chau., Cuiy-les-Chaudardes; Falk., Falkensteiner Höhle; Vies. Hof, Viesenhäuser Hof; Unterw., Unterwechel; Halb.-Son., Halberstadt-Sonntagsfeld; Ber.-Moro., Berettyóújfalu-Morotva-liget; Polg.-Fer., Polgár-Ferenci-hát; Debr.-Tócó., Debrecen Tócsapart Erdoalja; Komp.-Kig., Kompolt-Kigyóser; Apc-Berek., Apc-Berekalja I.; Salz.-Sch., Salzmuende-Schiebzig. Region: Brit-I, British Isles; C.-Eur., Central European; CH, Switzerland; ES, Spain; FR, France; GER, Germany; GR, Greece; HUN, Hungary; IRL, Ireland; IT, Italy; LU, Luxembourg; SW, Sweden; TR, Turkey. Plei., Pleistocene; H.-G., hunter-gatherer; Vil., Villabruna Cluster. Cultural Horizon: KÖR, Körös; EN, MN and LN, Early, Middle and Late Neolithic, respectively; M, Mesolithic; N, Neolithic; PWC, Pitted Ware Culture; LBK, Linearbandkeramik.

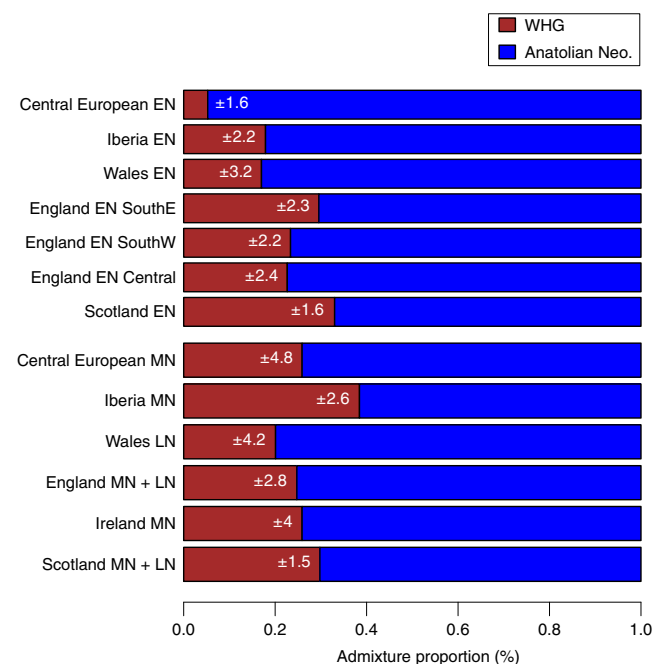


Fig. 3 | WHG and ANF ancestry components of British and Central European Neolithic populations. Relative WHG and ANF ancestry in Early and Middle Neolithic British and continental European populations quantified by qpAdm. Percentages indicate error estimates computed by block jack-knifing with a block size of 5 centimorgans (cM) (ref. ²⁴). See Methods for computational details and Supplementary Table 1 for lists of samples grouped into WHG and the different Neolithic populations. Neo., Neolithic; SouthE, South-East; SouthW, South-West.

Using a chromosome-painting approach²⁵, we obtained patterns of haplotype matching between our high-coverage British Neolithic sample and a global modern reference panel (Supplementary Data 7). We found similar patterns of donor haplotype matching in the British Neolithic genome to those inferred for other high-coverage Neolithic genomes from Ireland and Iberia. These were more similar than the same profiles obtained for high-coverage Neolithic genomes from Central Europe (Fig. 5a). Inferred ancestry coefficients (see Methods) further support this connection between the British, Irish and Iberian Neolithic⁶ and are consistent with the same ancestral populations bringing the Neolithic to Britain and Ireland (Fig. 5b,c and Supplementary Table 8). Additional modelling using global modern populations²⁶ as ancestry surrogates suggests that this population is best represented today by components found in French and Spanish peoples (Fig. 5c and Supplementary Table 9).

To test for a potential second ANF ancestry stream from Central Europe, we explicitly modelled WHG and Early Neolithic populations in qpGraph (see Supplementary Fig. 23 and Supplementary Table 10). The results suggest that the limited Central European Neolithic admixture we find in British Neolithic populations is regionally structured, with populations from England showing the highest levels of admixture followed by those from Scotland. We infer no Central European admixture in Neolithic farmers from Wales. However, we caution that the model fits are poor and so these inferences should be considered preliminary.

We inferred some notable geographic structure in WHG admixture proportions among the British Early Neolithic individuals (see Supplementary Table 4 for statistical comparison of inferred WHG admixture proportions); those from Wales retain the lowest levels of WHG admixture, followed by those from South-West and Central England. Neolithic individuals from

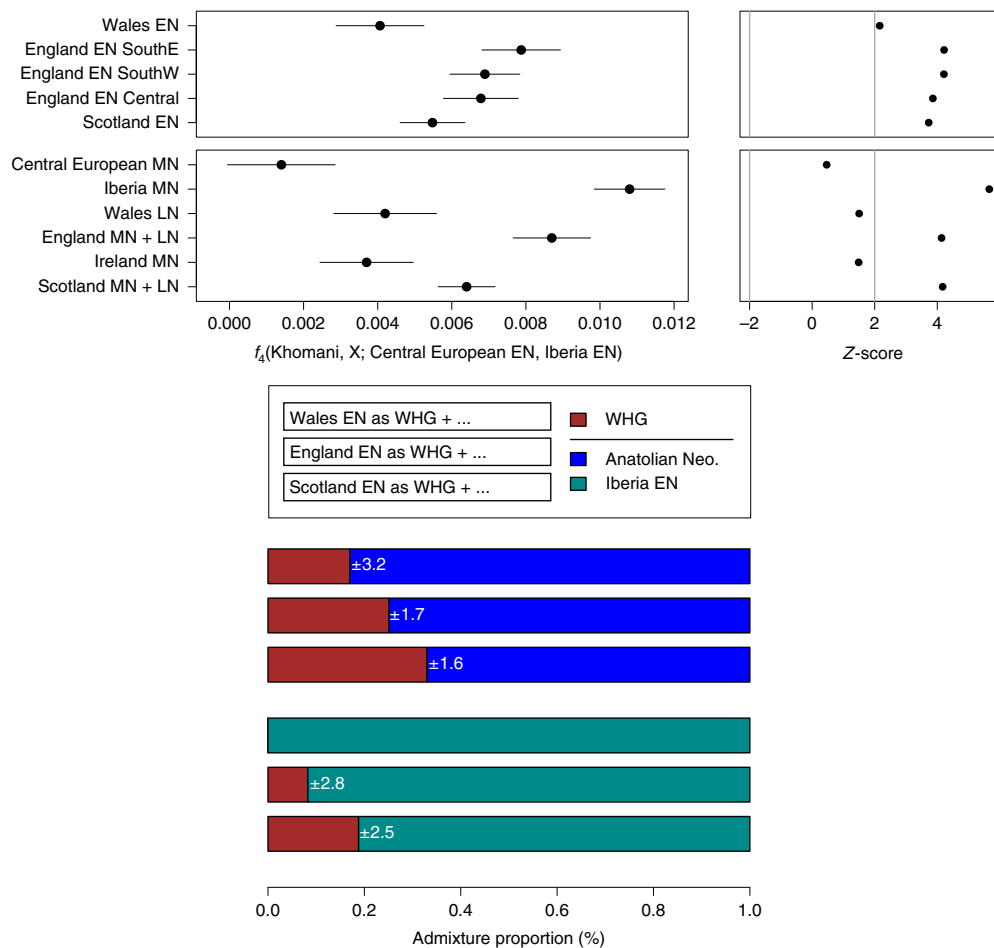


Fig. 4 | Affinities of British and continental Neolithic populations. Top, We computed f_4 statistics of the form f_4 (Khomani, test; Central European EN, Iberia EN) for different British EN, MN and LN and continental MN populations to compare shared drift to Central European EN and Iberian EN populations. A positive Z-score > 2 corresponds to a significant affinity to the Iberian EN over Central European EN population. Bottom, Quantification of excess WHG ancestry in British EN compared to the Iberian EN population. We computed qpAdm estimates of WHG and Anatolian and Iberian ANF populations in EN samples from Wales, England and Scotland. See Supplementary Table 1 for lists of samples grouped into WHG and the different Neolithic populations. The three white bars and the coloured boxes indicate how the bars below them are derived. Percentages and bars indicate error estimates computed by block jack-knifing with a block size of 5 cM (ref. ²⁴).

South-East England and Scotland show considerably higher WHG admixture proportions. These proportions remain stable from the Early into the Middle/Late Neolithic. To infer levels of WHG introgression occurring between Iberian Early Neolithic populations and early British farmers, we estimated admixture proportions using qpAdm²⁴. We detected little excess (~10%) WHG ancestry beyond that already present in Iberian Early Neolithic individuals, supporting little or no additional admixture with British hunter-gatherers, particularly in Wales and South-West and Central England (Figs. 3, 4b and Supplementary Table 4). This result appears to be slightly at odds with the f_4 results presented in Supplementary Fig. 7, which indicate that some British Neolithic samples share genetic affinities with Cheddar Man over Loschbour, although it is difficult to say in these cases whether this is due to genuine substantial admixture with British WHGs or with other WHGs in northern Europe. We regressed individual WHG ancestry proportions in British Neolithic farmers (shown in Supplementary Fig. 8) against latitude and longitude and found a notably positive south-west to north-east cline (Supplementary Fig. 15).

To further explore WHG introgression in Britain we applied ALDER²⁷ to pairs of Early Neolithic regional samples to estimate the timing of WHG/ANF admixture events (Supplementary Table 3).

Only Early Neolithic farmers from western Scotland show evidence of WHG introgression within ten generations. Two individuals from Raschoille Cave had estimated introgression events occurring 4.0 ± 3.4 generations before they lived, which is sufficiently recent in their past that it probably occurred in Britain. The elevated levels of WHG ancestry we see in Neolithic samples from South-East England are older, and therefore probably a result of farmer–forager interactions in mainland Europe. Chronological modelling (using OxCal 4.3 (ref. ²⁸)) of available direct Early Neolithic radiocarbon data from individuals showing ANF ancestry suggests that continental farmers arrived in Britain by 3975–3722 cal. BC (95% confidence interval), 481 years after to 27 years before (95% confidence interval) the death of our latest Mesolithic individual showing no ANF ancestry (Supplementary Data 6). Our model suggests that continental farmers arrived marginally earlier in the west (although see the discussion in Supplementary Data), and rapidly dispersed to other regions of Britain (including the Orkney Islands). The latest regional appearance of ANF ancestry is in Central England and occurs 59 to 386 years (95% confidence interval) after it first appears in Britain.

To explore variation in pigmentation of European populations, we predicted pigmentation in higher-coverage Mesolithic and Neolithic Europeans using HIrisplex-S²⁹. We infer that Cheddar Man mostly probably had blue/green eyes, dark brown (possibly

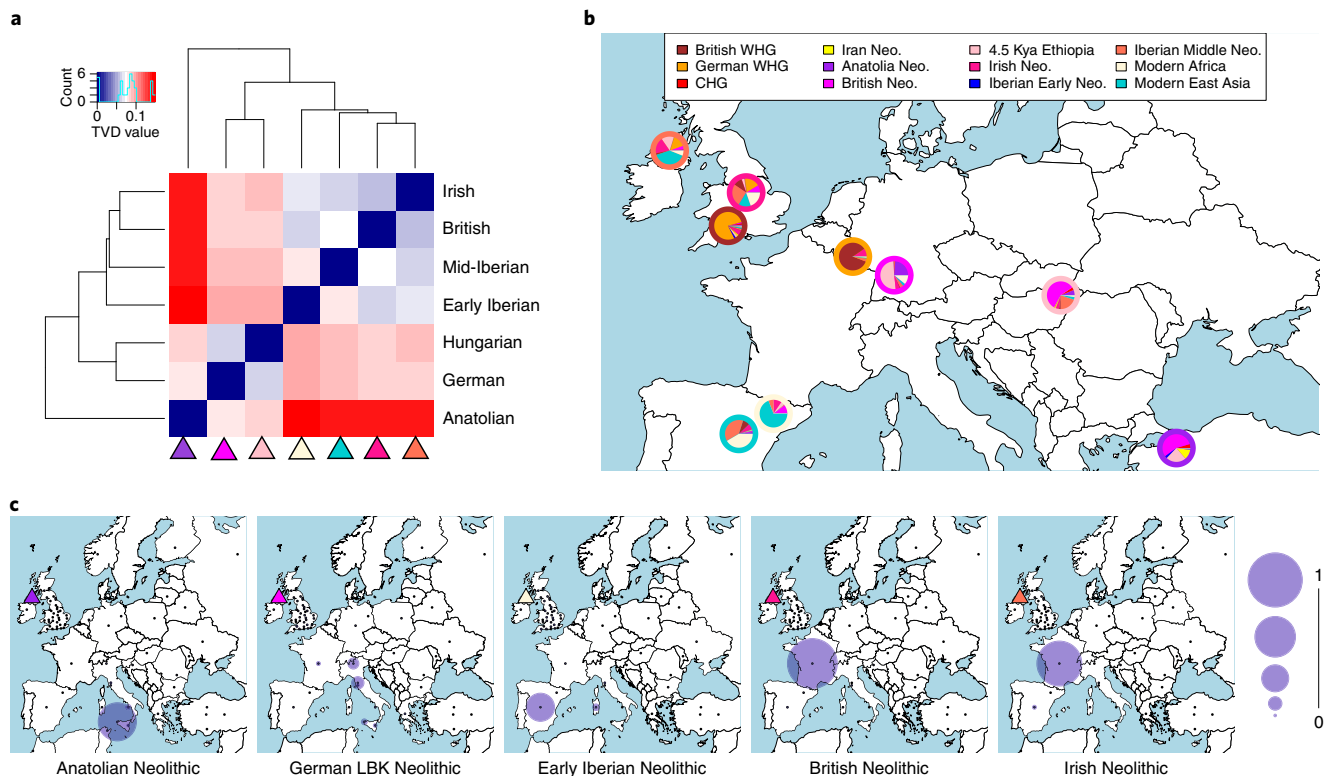


Fig. 5 | Patterns of haplotype sharing across high-coverage aDNA samples. a, Hierarchical clustering of total variation distance (TVD) between CHROMOPAINTER inferred haplotype-sharing profiles of seven high-coverage Neolithic individuals when compared to a global modern reference panel. **b**, Inferred ancestry proportions (SOURCEFIND inferred mixing coefficients) of high-coverage ancient genomes, coloured as per the legend and outer pie ring colour, relative to a panel of ancient genomes, plus modern Yoruba and Han (as given in the legend at the top). Raw proportions and standard errors are provided in Supplementary Table 8. CHG, Caucasus hunter-gatherer. **c**, Inferred ancestry proportions of five high-coverage Neolithic individuals (triangles coloured as in **b**) relative to a global modern reference panel. The size of the blue circle provides the majority of inferred contributions, as given by the scale at bottom right, with all possible modern contributors denoted by a black dot. Raw proportions and standard errors are provided in Supplementary Table 9.

black) hair and dark or dark to black skin, whereas our highest-coverage Early Neolithic individual had brown eyes, black (possibly dark brown) hair and dark to intermediate skin (see Supplementary Data 3). Together with the pigmentation prediction outcomes we obtained for Loschbour and La Braña, these results imply that different pigmentation levels co-existed in Europe by around 6000 BC.

Discussion

The six British Mesolithic genomes examined here are typical of WHGs, indicating that this population spread to the furthest north-western point of Early Holocene Europe after moving from south-eastern Europe, or further east, from approximately 12000 BC¹⁷. This genetic similarity among British and European Mesolithic individuals spans a period in Britain (circa 8500–4000 BC) that includes the cultural transition to the Late Mesolithic and the separation of Britain from continental Europe. Our analyses indicate that the appearance of Neolithic practices and domesticates in Britain circa 4000 BC was mediated overwhelmingly by immigration of farmers from continental Europe^{1,2}, and strongly reject the hypothesized adoption of farming by indigenous hunter-gatherers as the main process³. British farmers were substantially descended from Iberian Neolithic-related populations whose ancestors had expanded along a Mediterranean route^{6,11}, although with a minority portion of their ancestry from populations who took the Danubian route¹². The affinities we find between Neolithic individuals from the British Isles and modern individuals from France are consistent with populations sharing ancestry with Neolithic groups in Iberia moving into

northern France via the Atlantic seaboard and/or southern France, mixing to a limited degree with Neolithic populations from Central Europe before travelling across the English Channel^{1,2,30}.

One explanation for the British Neolithic cline in WHG ancestry is that a single population moved across Britain from a western entry point and progressively admixed with local hunter-gatherers. This scenario is consistent with the western distribution of megalithic cultures along the Atlantic seaboard³¹, and is supported by radiocarbon evidence suggesting a marginally earlier date for the arrival of ANF ancestry in the west of Britain¹. However, the lack of evidence for substantive WHG introgression into British Neolithic populations—outside of western Scotland—favours this cline, reflecting multiple source populations with variable proportions of WHG admixture having entered different parts of Britain. This interpretation is consistent with archaeological evidence for regional British Neolithic cultures showing links to varied parts of mainland Europe² and our qpGraph analysis indicating geographically structured Neolithic Central European admixture. Overall, the regional variation in ancestry of British Neolithic populations probably reflects both differing degrees of admixture between farmers and local foragers (for example, western Scotland) and multiple continental source populations carrying variable WHG and Neolithic Central European ancestry.

Evidence for only low levels of WHG introgression among British Early Neolithic people is striking given the extensive and complex admixture processes inferred for continental Neolithic populations^{7,13–15,32,33}. Low levels of admixture between these

two groups on the wave front of farming advance in continental Europe have been attributed to the maintenance of cultural and reproductive boundaries for up to two millennia after initial contact, before more extensively mixing³². Similarly, isotopic and genetic data from the west coast of Scotland suggest the potential co-existence of genetically distinct hunter-fisher-gatherers and farmers, albeit for a maximum of a few centuries³⁴. However, there is no evidence for a resurgence of WHG ancestry in the British Neolithic, consistent with limited evidence for Mesolithic cultural artefacts in Britain beyond 4000 BC^{1,2}, and with a major dietary shift from marine to terrestrial resources at this time (see Supplementary Data 5)³⁵.

Conclusion

In contrast to other European regions, the transition to farming in Britain occurred with little introgression from resident foragers—either during initial colonization or throughout the Neolithic. This may reflect low Late Mesolithic population density in Britain and/or an introduction of farming by populations who had mastered the technologies needed to thrive in northern and western continental Europe during the previous two millennia^{1,2}.

Methods

Ancient DNA extraction and sequencing. The DNA extractions and library preparations for all samples with newly reported data were conducted in a dedicated ancient DNA laboratory (NHM, London). We used approximately 25 mg of finely drilled bone powder and followed the DNA extraction protocol described in ref. ³⁶, but replaced the Zymo-Spin V column binding apparatus with a high pure extender assembly from the High Pure Viral Nucleic Acid Large Volume Kit (Roche). Library preparations followed the partial uracil–DNA–glycosylase treatment described in ref. ³⁷ and a modified version of the protocol described in ref. ³⁸. Library modifications: the initial DNA fragmentation step was not required, and all clean-up steps used MinElute PCR purification kits (Qiagen). The index PCR step included double indexing³⁹, the polymerase AmpliTaq Gold and the addition of 0.4 mg ml⁻¹ bovine serum albumin. The index PCR was set for 20 cycles with three PCR reactions conducted per library. Libraries were screened for DNA preservation on an Illumina NextSeq platform, with paired-ends reads. Promising libraries were further enriched at the NHM using in-solution hybridization capture enrichment kits (Mybait-3) from MYcroarray. The baits were designed to cover around 20,000 SNPs (5,139 functional and 15,002 neutral SNPs) at $\times 4$ tiling. The capture protocol followed the manufacturer's instructions in Mybait manual v.3. Captured libraries were sequenced on an Illumina NextSeq platform (NHM) using paired-ends reads. Newly reported data from 36 of these libraries were also obtained at the dedicated ancient DNA laboratory in Harvard Medical School by enrichment in solution for approximately 1.24 million targeted SNPs. We sequenced these libraries on an Illumina NextSeq500 instrument, iteratively sequencing more until we estimated that the additional number of targeted SNPs hit per newly generated sequence was fewer than one per 100.

Bioinformatics. All sequence reads underwent adapter and low-quality base trimming, and overlapping reads pairs were collapsed with AdapterRemoval⁴⁰. Non-collapsed reads and those of length less than 30 base pairs were discarded, and the remaining aligned against the hs37d5 human reference genome with the Burrows–Wheeler Aligner⁴¹. Mapped reads with a mapping quality of at least 30 were merged per individual and realigned around InDels with GATK⁴². Resulting BAM files were split by flowcell and lane, and empirical ATLAS⁴³ post-mortem damage patterns estimated per individual per lane for lanes with at least 5.5 million reads, otherwise per individual per flowcell. ATLAS BQSR (base quality score recalibration) tables were generated per lane for lanes with at least 5.5 million reads, otherwise per flowcell. We generated recalibrated BAM files per individual with ATLAS recalBAM, and used these to estimate mitochondrial contamination and determine mitochondrial and Y-chromosome haplogroups with ContamMix⁴⁴, Yleaf⁴⁵ and Phy-Mer⁴⁶. We considered mitochondrial contamination to be tolerable if 0.98 was included in the confidence intervals. Haploid genotypes were called with ATLAS 'allelePresence' with theta fixed at 0.001, determining the most likely base at a given position. Heterozygosity estimates, shown in Supplementary Fig. 10, were computed with ATLAS 'estimate Theta' and a default window size of 1 megabase pair, excluding windows that overlap with telo- or centromeres.

Principal component analysis. Principal component analysis was performed with LASER⁴⁷ following the approach described previously⁷. After generating a reference space of modern West Eurasian individuals¹⁰, we projected the BAM files of ancient reference individuals (see Supplementary Table 1 for references) and the British individuals presented here into the reference space via Procrustes analysis implemented in LASER.

f-statistics. The *f*-statistics presented here, that is outgroups f_3, f_4 , qpAdm and qpGraph, were computed with qpPop and qpDstat in f_4 mode, and qpAdm and qpGraph from the ADMIXTOOLS⁴⁴ package with default parameters on the positions defined by the *HOIII* set of SNPs⁷. Ancient individuals analysed here are listed in Supplementary Table 1, including the explanation of all population labels used (WHG, SHG and so on). Modern reference individuals were first published in ref. ²³. All qpAdm runs used the set of outgroups Han, Karitiana, Mbuti, Onge, Papuan, Mota, Ust'-Ishim, MA1, El Mirón, GoyetQ116-1.

ALDER. We used ALDER²⁷ to estimate the dates of admixture between WHG and ANF. All combinations we tested are listed in Supplementary Table 3, which consisted of the pairs or groups of individuals specified in the first column and WHG and ANF (individuals constituting WHG and ANF are given in Supplementary Table 1).

Chronological modelling. We used OxCal 4.3 (ref. ²⁸) to produce chronological models of the arrival and spread of ANF ancestry into Britain (Supplementary Data 6). We used Early Neolithic (4000–3500 BC) radiocarbon dates only from those obtained from material or individuals where there were palaeogenetic data indicating ANF ancestry. We divided these samples into five regional populations: Western Britain, Central England, Eastern England, Western Scotland and the Orkney Isles. Dates associated with each region were grouped as Phases (Supplementary Fig. 19). We used the Boundary function to produce probability distributions for the arrival of ANF ancestry in Britain as a whole, and for each region. We used the Difference function to produce probability distributions for the time between the death of the latest individual with wholly WHG ancestry and the arrival of populations with ANF ancestry, as well as between the arrival of ANF ancestry in Britain as a whole and the different regions of Britain.

Haplotype-based analyses. We used CHROMOPAINTER²⁵ to summarize DNA patterns in our ancient individuals, including other high-coverage, publicly available ancient genomes from relevant cultures and time periods, to infer the proportion of DNA for which ancient individuals most closely matched to those from a global panel of modern donor groups^{48–50}. This panel included many population samples from across West Eurasia, as well as 35 labelled groups from within the British Isles. We generated matching profiles when considering SNPs independently (allele sharing) and also when considering the correlations between neighbouring SNPs (haplotype sharing). To do so we first merged high-quality diploid calls for our selected high-coverage ancient genomes and jointly phased the resultant dataset of 159,287 SNPs using SHAPEIT v.2 (ref. ⁵¹). We performed additional mixture modelling on our generated allele- and haplotype-sharing profiles implemented in SOURCEFIND²⁶ to form target groups as mixtures of the DNA-sharing profiles of other included groups. We performed two sets of analyses: (1) using all modern groups (or a subset of) to model the ancestry of ancient individuals and (2) using different sets of ancient individuals, plus the modern Yoruba and Han, to model the ancestry of modern worldwide groups. Further details are provided in Supplementary Data 7.

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

BAM files (one file per library, before realigning around InDels; see Supplementary Table 1) have been deposited at the European Nucleotide Archive under study accession PRJEB31249.

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Author contributions

I.B. and M.G.T. conceived the project. Y.D., S.B., Z.F., O.C. and T.B. contributed to the project design. S.B., Y.D., T.B., L.v.D., N.R., S.M., I.O., M.F., M.M., J.O., N.B., K.S., R.M., S.C. and S.W. generated and analysed data. I.B., M.G.T., Y.D., S.B., T.B., M.K., S.W., G.H., I.A., R.S., O.C., A.S., M.P.P., C.S. and D.R. contributed to the sampling strategy and the interpretation of results. I.B., M.G.T., Y.D., S.B. and T.B. wrote the paper, with contributions from all other authors.

Competing interests

The authors declare no competing interests.

Additional information

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