Article

Large-scale migration into Britain during the Middle to Late Bronze Age

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Present-day people from England and Wales have more ancestry derived from early European farmers (EEF) than did people of the Early Bronze Age[1]. To understand this, here we generated genome-wide data from 793 individuals, increasing data from the Middle to the Late Bronze Age and Iron Age in Britain by 12-fold, and western and central Europe by 3.5-fold. Between 1000 and 875 BC, EEF ancestry increased in southern Britain (England and Wales) but not northern Britain (Scotland) due to incorporation of migrants who arrived at this time and over previous centuries, and who were genetically most similar to ancient individuals from France. These migrants contributed about half the ancestry of people of England and Wales from the Iron Age, thereby creating a plausible vector for the spread of early Celtic languages into Britain. These patterns are part of a broader trend of EEF ancestry becoming more similar across central and western Europe in the Middle to the Late Bronze Age, coincident with archaeological evidence of intensified cultural exchange[2–6]. There was comparatively less gene flow from continental Europe during the Iron Age, and the independent genetic trajectory in Britain is also reflected in the rise of the allele conferring lactase persistence to approximately 50% by this time compared to approximately 7% in central Europe where it rose rapidly in frequency only a millennium later. This suggests that dairy products were used in qualitatively different ways in Britain and in central Europe over this period.

Whole-genome ancient DNA studies have shown that the first Neolithic farmers of the island of Great Britain (hereafter Britain) who lived 3950–2450 BC derived roughly 80% of their ancestry from EEF who originated in Anatolia more than two millennia earlier, and 20% from Mesolithic hunter–gatherers (western European hunter–gatherers (WHGs)) with whom they mixed in continental Europe, indicating that local WHGs in Britain contributed negligibly to later populations[7–9]. This ancestry profile remained stable for about a millennium and a half. From around 2450 BC, there was another substantial migration (Box 1) into Britain (minimum 90% ancestry from the new migrants) coinciding with the spread of Bell Beaker traditions from continental Europe, which brought a third major component: 'Steppe ancestry' derived originally from people living on the Pontic–Caspian Steppe approximately 3000 BC[8]. In the original study[8] reporting this ancestry shift in Britain, no significant average change in the proportion of EEF ancestry was detected from the Chalcolithic/Early Bronze Age (C/EBA) (2450–1550 BC), through the Middle Bronze Age (MBA) (1550–1150 BC) and Late Bronze Age (LBA) (1150–750 BC), to the pre-Roman Iron Age (IA) (750 BC to AD 43). However, that study contained little data after 1300 BC (Fig. 1). Today, however, EEF ancestry is significantly higher on average in southern Britain than in northern Britain, raising the question of when this increase occurred[1,8]. The rise in EEF ancestry cannot be explained by migration from northern continental Europe in the early medieval period, as early medieval migrants had less EEF ancestry than in Bronze Age Britain[10] and hence would have decreased EEF ancestry instead of increased ancestry as we observed[1].

We generated genome-wide ancient DNA data from 403 previously unanalysed individuals from Britain, increasing the number of pre-Roman individuals to 589 and multiplying by 28-fold the number from the combined period of the LBA and IA (from 13 to 359) (Fig. 1, Supplementary Information Section 1, Supplementary Table 1, Methods). We also report data from ancient individuals mostly dating to the LBA and IA from the Czech Republic ($n = 161$), Hungary ($n = 54$), France ($n = 52$), the Netherlands ($n = 28$), Slovakia ($n = 25$), Croatia ($n = 21$), Slovenia ($n = 14$), the Channel Islands ($n = 13$), Spain ($n = 10$), Serbia ($n = 8$), Austria ($n = 3$) and the Isle of Man ($n = 1$). We increased data quality on 33 previously published individuals (Supplementary Table 1). To generate these data (Methods), we prepared powder from bones and teeth, extracted DNA, and generated 1,020 sequencing libraries all pretreated with uracil-DNA glycosylase to reduce characteristic cytosine-to-thymine errors of ancient DNA (Supplementary Table 2). We enriched libraries in solution for a targeted set of more than 1.2 million single-nucleotide polymorphisms, sequenced them, and then co-analysed with previously reported data (Supplementary Table 3). We clustered by time and geography, aided by 123 newly reported radiocarbon dates (Supplementary Table 4). We separately labelled individuals who were significantly different in ancestry from the majority cluster from each time period and region (Supplementary Information Section 2, Supplementary Table 5). Although we report data from all individuals, we removed a subset from the main analysis: those with evidence of contamination, those with a rate of damage in the final nucleotide lower than the typical range for authentic ancient DNA, those who were first-degree relatives of other higher coverage individuals in the dataset, or those with too little data for accurate ancestry inference (less than 30,000 single-nucleotide polymorphisms covered at least once) (Supplementary Table 5, Methods). Figure 1 shows a map of the

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Box 1

Reconciling archaeological and genetic understandings of 'migration'

'Migration' is a central concept in both population genetics and archaeology, but its meaning has evolved in divergent ways in the course of the development of these disciplines[27]. Population geneticists use migration to refer to any movement of genetic material from one region to another, which would see even low-level symmetrical exchanges of mates between adjacent communities as representing migration, whereas archaeologists restrict its use to processes that result in significant demographic change due to permanent translocation of people from one region to another[28]. In European archaeology, discussions of prehistoric migrations have become fraught due to the ways in which theories of migration were exploited politically in the early-to-mid-twentieth century, when movement of large numbers of people over short times was sometimes argued to be a primary mechanism for the spread of ethnic groups, and archaeological reconstructions of such events were used to justify claims on territory[29]. Because of this, some archaeologists prefer to set a high bar for theorizing migration, for example, by restricting its use to cases where there is evidence of organized movements of people over a short time. However, this can make it difficult to recognize the important effects that large-scale movements of people had in prehistory[28], such as the westward movement of people from the Steppe beginning in the third millennium BC that genetic data have shown contributed much of the ancestry of later Europeans[8,30]. We use the term 'migration' here with intention, because the movement of people into Britain that we document was demographically transformative. We emphasize that our findings are not sufficient to prove mass movement over a short time; indeed, our radiocarbon dating and isotopic evidence show that at least some of the migration was drawn out over hundreds of years.

analysed individuals. We identified 123 individuals from 48 families as related (within the third degree) to at least one other newly reported individual in the dataset (Supplementary Table 6).

British ancient DNA time transect

We computed f_4-statistics with Block Jackknife standard errors[11] between all pairs of temporal groupings of individuals in Britain, testing for differences in the rate of allele sharing (genetic drift) with the two major source populations (Steppe and EEF). We document a significant increase in the degree of allele sharing with EEF populations in England and Wales over the Middle to Late Bronze Age (M-LBA) and into the IA (Extended Data Table 1). To estimate the proportions of EEF, Steppe and WHG ancestry, we used qpAdm[12], which takes advantage of the fact that if a 'target' population is a mixture of 'source' populations for which we have close surrogates in our dataset, we can compute all possible f_4-statistics relating the targets and sources to a set of chosen outgroups, and then use qpAdm to find the values of the mixture coefficients α_{EEF}, α_{Steppe}, and α_{Steppe} that fit all the statistics, while also providing a P value for whether the target population can in fact be modelled as a mixture of close relatives of the sources. We carefully chose our set of sources and 'outgroups' to provide much more accurate inferences than previous qpAdm setups due to their large sample sizes and the high degree of leverage that they provide for teasing apart the three major components of European ancestry (Supplementary Information Section 2). Our proxies for the sources are 22 early Balkan Neolithic farmers with minimal hunter–gatherer admixture (EEF), 20 Yamnaya and Poltavka pastoralists (Steppe), and 18 Mesolithic hunter–gatherers from across western Europe (WHG). Our outgroups are close genetic cousins of the three sources—24 Anatolian Neolithic individuals related to EEF, 19 Afanasievo individuals related to Yamnaya Steppe pastoralists, and 41 hunter–gatherers largely from the Danubian Iron Gates related to WHG—and a pool of 9 ancient sub-Saharan African individuals processed using the same in-solution enrichment technology and without evidence of West Eurasian-related admixture.

EEF-related ancestry increased in England and Wales from 31.0 ± 0.5% in the C/EBA (n = 69) to 34.7 ± 0.6% in the MBA (n = 26), to 36.1 ± 0.6% in the LBA (n = 23), and stabilized at 37.9 ± 0.4% in the IA (n = 273) (here and below, we quote one standard error). There was no significant change in Scotland (Fig. 2, Extended Data Table 1). Increased EEF ancestry was widespread in southern Britain by the IA, with point estimates ranging from 36.0% to 38.8% across eight regions of England (Wales sample sizes were too small to provide accurate inference) (Table 1, Extended Data Table 2). We considered the possibility that the rise in EEF ancestry in southern Britain was due to a resurgence of archaeologically less visible populations with more ancestry from people living in Britain in the Neolithic, which we missed due to either geographical biases in sampling or variation across cultural contexts in the way groups treated their dead, for example, through cremation. However, models of people from England and Wales from the IA as a mixture of groups in Neolithic and C/EBA Britain are highly inconsistent with the data at a statistical significance of $P < 10^{-6}$ (Extended Data Fig. 1). This is due to populations from the IA in Britain sharing alleles with some Neolithic populations in continental Europe that were not present in early Neolithic or C/EBA groups in Britain (Supplementary Information Section 3). The most plausible explanation for these patterns is migration of people carrying this distinctive ancestry into southern Britain in the M-LBA.

We modelled ancestry in each individual, labelling significant ancestry outliers relative to most individuals of their period. We highlight key observations (Fig. 3, Extended Data Fig. 2).

First, replicating previous results[8,9], we infer a cluster of Neolithic individuals from western Scotland with high WHG admixture, probably reflecting unions between recent migrants from Europe and descendants of local Mesolithic groups in Britain (Extended Data Fig. 2).

Second, we infer high variability in EEF ancestry in the C/EBA, before EEF ancestry became relatively homogeneous after roughly 2000 BC[8] (Fig. 3). This is apparent at Amesbury Down where EEF ancestry in some burials was significantly below the average of 29.9 ± 0.4% (for example, individual I2417 at 22.2 ± 1.8%), plausibly reflecting migrants during the Beaker period who mixed with local Neolithic farmers to produce the intermediate EEF ancestry that prevailed by the end of the EBA. Others are above the group average including individual I14200 at 45.3 ± 2.2%, known as the 'Amesbury Archer', who was buried in the most well-furnished grave recovered from the Stonehenge mortuary landscape and had an isotopic profile indicating that he spent parts of his childhood outside Britain, possibly in the Alps[13]. The fact that the Archer was a migrant but had too little Steppe ancestry to be from the population that drove Steppe ancestry to the level observed in C/EBA Britain shows that Beaker-associated migrants to Britain were not genetically homogeneous. The 'Companion' (I2565), a burial found next to the Archer whose isotopic profile, like most others at the site, was consistent with a local upbringing, was not an ancestry outlier (32.7 ± 3.0% EEF; Fig. 3). The Archer and the Companion shared a rare tarsal morphology and similar grave goods, which was hypothesized to reflect a close genetic relationship[14] (Supplementary Information Section 4), but our results rule out first-degree or second-degree relatedness.

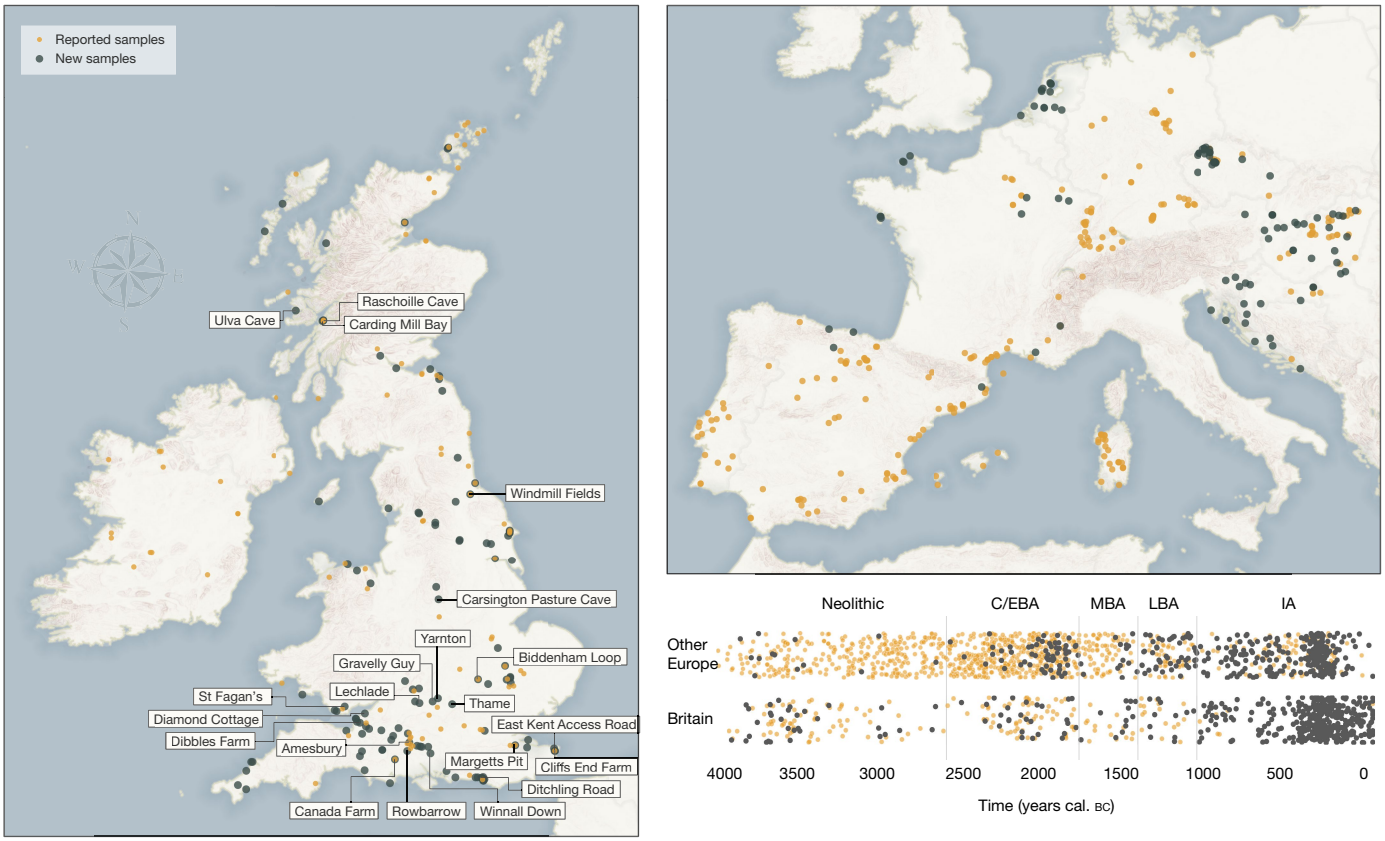

Fig. 1 | Ancient DNA dataset. Geographical distribution of sites and temporal distribution of individuals 4000 BC to AD 43. Newly reported samples are shown in black; published samples are shown in orange. Base maps were made with Natural Earth, and elevation data with Copernicus, European Digital Elevation Model v1.1. The labelled sites on the map of Britain are those with ancestry outliers relative to others of the same period. The timeline shows archaeological periods in the British chronology: Neolithic (3950–2450 BC), C/EBA (2450–1550 BC), MBA (1550–1150 BC), LBA (1150–750 BC) and pre-Roman IA (750 BC to AD 43). To separate points in a way that improves visualization, we added jitter on the *y* axis and we sampled dates based on their probability distributions (using the date means and standard deviations given in Supplementary Table 1).

Third, we observe four outliers with high EEF ancestry in the late MBA and LBA who are candidates for being first-generation migrants or the offspring of recent migrants, all of whom were buried in Kent in the southeasternmost part of Britain. The earlier two are from Margetts Pit: 47.8 ± 1.8% in individual I13716 (1391–1129 cal. BC) and 43.6 ± 1.8% in I13617 (1214–1052 cal. BC). The latter two are from Cliffs End Farm: 43.2 ± 2.0% in individual I14865 (967–811 cal. BC) and 43.4 ± 1.8% in I14861 (912–808 cal. BC). We considered the possibility that we were observing the effect of a short burst of migration in the MBA, which included the Margetts Pit outliers, followed by co-existence of separate communities with different EEF ancestry for at least a couple of hundred years, including the Cliffs End Farm outliers. However, strontium and oxygen isotope analyses have identified multiple individuals of non-local origin at Cliffs End Farm[15], including outlier I14861, suggesting that this was not a single mass migration but instead a stream of migrants over hundreds of years (Supplementary Information Section 5).

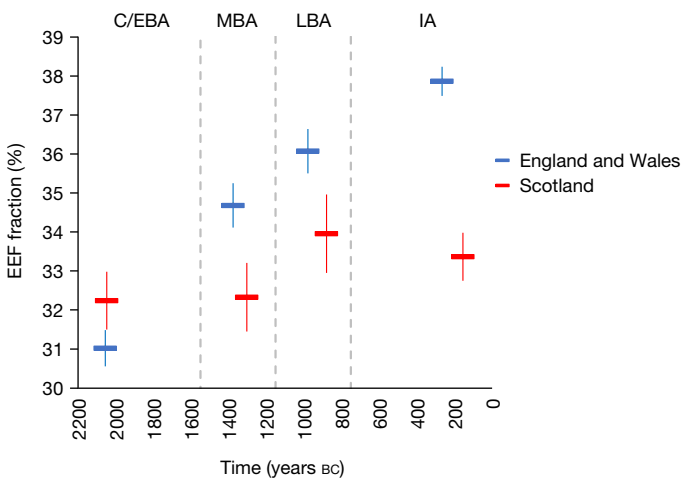

Fig. 2 | Increase in EEF ancestry during the MBA to LBA. EEF ancestry increased in southern Britain beginning with the Margetts Pit MBA outliers but hardly in the north. Estimates from qpAdm are binned into four archaeological periods. Means and one standard error are plotted from a Block Jackknife. Sample sizes in the C/EBA, MBA, LBA and IA are 69, 26, 23 and 273 in England and Wales and 10, 5, 4 and 18 in Scotland, respectively.

Fourth, the fraction of individuals whose ancestry is significantly different from the main group is 17% over the first part of the C/EBA (2450–1800 BC), 4% from the end of the EBA through the beginning of the MBA (1800–1300 BC), 17% from the end of the MBA through the LBA (1300–750 BC), and 3% through the IA (Fig. 3). This is consistent with two periods of relatively high rates of migration into southern Britain in the Chalcolithic and then again in the M-LBA. We considered the possibility that our failure to observe a high rate of outliers in the IA compared with the preceding period was because ancestry had, by this time, homogenized to some extent between Britain and continental regions, which could make outliers more difficult to detect. However, average EEF ancestry in Britain in the IA was 37.9 ± 0.4%, which is substantially different from much of contemporary western and central Europe—52.6 ± 0.6% in Iberia, 49.8 ± 0.4% in Austria, Hungary and Slovenia, 45.4 ± 0.5% in the Czech Republic, Slovakia and Germany, 45.6 ± 0.5% in France and Switzerland, and 34.4 ± 1.2% in the Netherlands (Fig. 4a)—which would have made the

Table 1 | Regional variation in ancestry in IA Britain

		Latitude	Modelling ancestry with pre-Bronze Age sources				Modelling ancestry with Bronze Age sources	
Region	***n***		***P***	**WHG (%)**	**EEF (%)**	**Steppe (%)**	***P***	**Continental (%)**
Scotland								
Orkney	2	59	0.22	14.2±1.1	34.1±1.2	51.6±1.6	0.10	20±9
West	4	58	0.12	13.0±0.8	32.3±1.0	54.7±1.2	0.19	8±7
Southeast	12	56	0.67	12.1±0.6	33.9±0.7	54.0±0.9	0.39	16±5
England								
North	10	54	0.35	13.4±0.6	36.3±0.8	50.3±1.0	0.76	35±5
East Yorkshire	47	54	0.61	13.2±0.4	37.0±0.5	49.8±0.6	0.86	44±4
Midlands	18	53	0.66	12.6±0.5	36.0±0.6	51.4±0.8	0.77	36±4
Southwest	84	53	0.30	13.7±0.4	38.7±0.4	47.6±0.6	0.56	55±5
East Anglia	21	52	0.44	13.5±0.5	37.0±0.5	49.5±0.7	0.52	44±4
Southcentral	38	52	0.32	13.9±0.4	38.8±0.5	47.2±0.6	0.35	56±5
Southeast	3	51	0.13	13.9±0.5	38.3±0.5	47.8±0.6	0.40	52±5
Cornwall	16	50	0.40	13.5±0.5	36.4±0.7	50.1±0.8	0.64	39±5
Wales								
North	1	53	0.20	12.1±1.6	34.7±2.0	53.2±2.5	0.53	22±14
South	2	51	0.66	14.2±1.2	38.6±1.5	47.2±1.8	0.57	53±11

Regions are ordered first by large grouping (Scotland–England–Wales), then latitude. We separate 'England East Yorkshire' from 'England North' because of its distinctive cultural context in the IA (Arras). For the final two columns, we use Britain_C.EBA as the Britain source and the Margetts Pit and Cliffs End Farm pool as the continental source.

majority of migrants from these regions detectable given the less than 2% standard errors in most of our ancestry estimates (Supplementary Table 5). Our sampling from western France and Belgium is poor, and it is possible that EEF ancestry proportions there were similar to Britain, so we cannot rule out migration from this region in the IA. Nevertheless, our results are consistent with reduced migration from continental Europe and suggest a substantial degree of genetic isolation of Britain from much of continental Europe during the IA[16].

Demographic change in Britain is also evident from another aspect of the data: the rate of runs of homozygosity, which can occur when the parents of an individual are closely related. The larger the pool of people from which individuals draw their mates, the less likely it is for parents to be closely related, and thus we can average the number of 4–8 centimorgan (cM) runs of homozygosity segments to estimate the effective size of the pool of people within which people were mating in the approximately 600-year period before the time when the analysed individuals lived[17]. We found that the size of the mating pool increased by roughly fourfold from the Neolithic to the IA (Extended Data Fig. 3), but this should not be interpreted as an estimate of changes in census population size over this period, as mating pool sizes are also affected by changing social customs. First, if the distance over which people ranged to find their mates was higher in some cultural contexts than in others, it would cause mating pool sizes to be different even if there was no difference in population densities; for example, the size of the mating pool may have been less than the island-wide population size if members of communities mixed little with their neighbours[16], or larger if individuals mated not only with people outside their local communities but also outside Britain. Second, we have gaps in sampling, especially at the end of the Neolithic (roughly 3000–2450 BC), which means that demographic processes in such periods may be obscured. Third, owing to the method effectively averaging the size of mating pools over centuries, this analysis may also fail to detect population declines over the space of a few decades.

British change in European context

We co-analysed our ancient DNA time transect in Britain alongside European transects (Fig. 4a, Supplementary Tables 5, 7). The average EEF ancestry increased in north-central Europe (Czech Republic, Slovakia and Germany) just as in Britain, with the first individuals with greatly increased EEF ancestry associated with artefacts that are traditionally classified as part of the Knoviz culture, a component of the broader Urnfield cultural complex (1300–800 BC) that spread across much of central Europe. This is particularly notable as the Knoviz individuals are from a population that is genetically similar to the Margetts Pit and Cliffs End Farm outliers (Supplementary Information Section 6). Later individuals in north-central Europe have similar EEF proportions, consistent with substantial continuity through the LBA to the IA. In France and Switzerland, as well as in south-central Europe (Austria, Hungary and Slovenia), there was little change in average EEF ancestry in the M-LBA, whereas EEF ancestry decreased in Iberia (Spain and Portugal) in the same period. There are two exceptions to this broad pattern of ancestry convergence in Europe—Scotland in the far north, and Sardinia in the far south—both of which have extreme and relatively unchanging proportions of EEF ancestry in this period (Supplementary Table 7).

This study multiplies by almost eightfold the number of IA individuals with genome-wide data from western and central Europe (from 80 to 624; Supplementary Table 5), making it possible to accurately track the frequency change of genetic variants into the IA (Supplementary Table 8). Variants associated with light skin pigmentation at *SLC45A2* became substantially more common throughout Europe in the IA. We obtained an unexpected result for the derived allele at *MCM6-LCT* rs4988235, which is associated with lactase persistence into adulthood (Extended Data Fig. 4). Previous analyses found that its frequency in the IA in sampled parts of continental Europe was a small fraction of its present-day incidence[18]. We document this at high precision in our dataset in Iberia where it was approximately 9% compared with approximately 40% today, and in central Europe (Austria, Hungary, Slovenia, Czech Republic, Slovakia and Germany) where it was approximately 7% compared with approximately 48% today. However, in IA Britain its frequency was 50% compared with the current 73%, showing that intense selection to increase the frequency of this allele acted roughly a millennium earlier in Britain than it did in multiple parts of continental Europe (Fig. 4b, Extended Data Fig. 4). We found no evidence that the frequency rise in Britain was due to M-LBA migration: the Margetts Pit

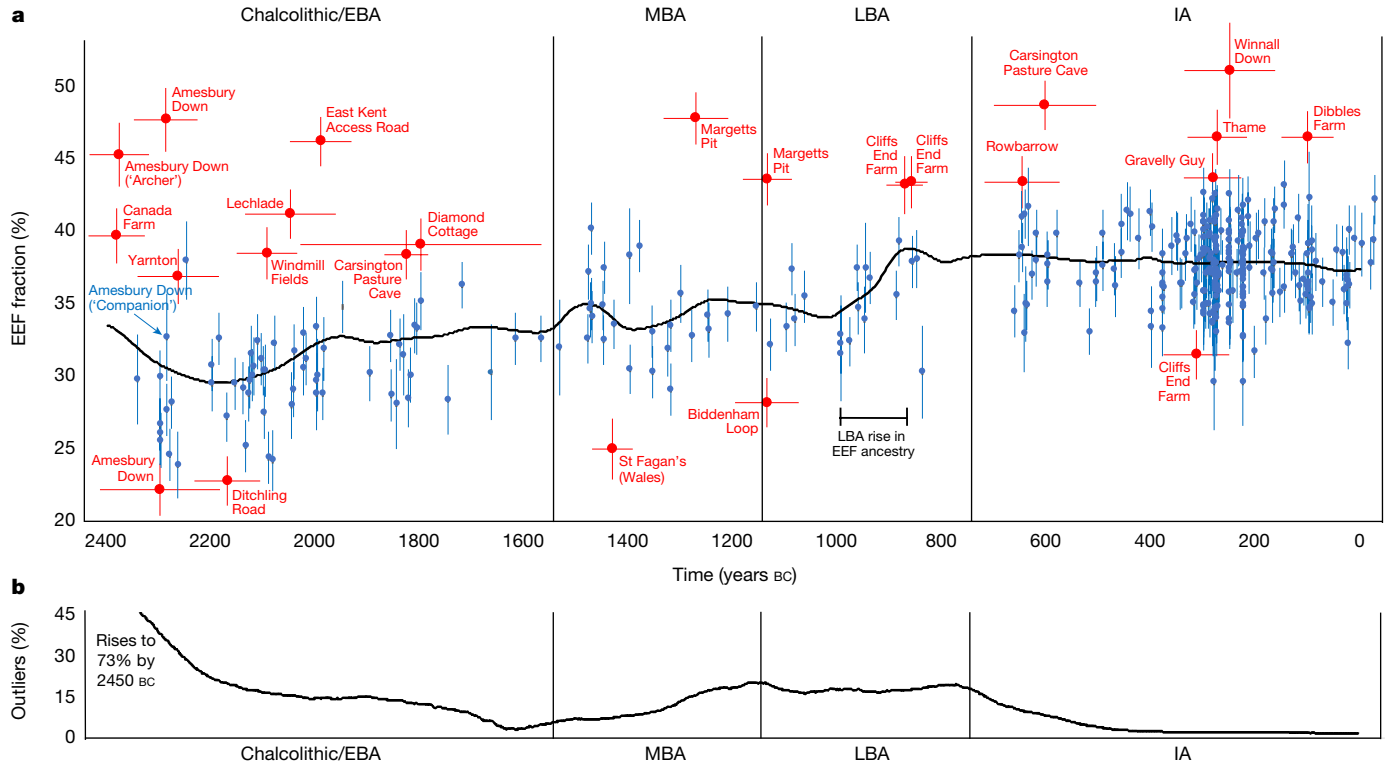

Fig. 3 | By-individual analysis of the southern Britain time transect. **a**, Estimates of EEF ancestry and one standard error for all individuals fitting a three-way admixture model (EEF + WHG + Yamnaya) at $P > 0.01$ using qpAdm; we restricted to 2450 BC to AD 43 using the best date estimate from Supplementary Table 5. Most individuals are in blue, whereas significant outliers at the ancestry tails are in red (outliers are identified as $P < 0.005$ based on a qpWave test from the main cluster from their period and $|Z| > 3$ for a difference in EEF proportion, or $P < 0.1$ and $|Z| > 3.5$). The horizontal bar indicates one standard error for the date (Supplementary Table 5). The black line shows population-wide EEF ancestry at each time obtained by weighting the EEF estimate of each individual by the inverse square of their standard error and the probability that their date falls at that time (based on the mean and standard error in Supplementary Table 5 assuming normality; we filtered out individuals with standard errors of more than 120 years). The incorporation of increased EEF ancestry into the majority of individuals occurred approximately 1000–875 BC. **b**, Proportion of outliers over 300-year sliding windows centred on each point, based on randomly sampling dates of all individuals 100 times assuming normality and their mean and standard deviation in Supplementary Table 5 (removing individuals with EEF errors of more than 0.022 and date errors of more than 120 years). Major periods of migration into Britain are periods with elevated proportions of outliers: between 2450 and 1800 BC (17% outliers) and 1300 and 750 BC (17% outliers again). The fact that there was an elevated rate of outliers before the 1000–875 BC population-wide rise in EEF ancestry may reflect a delay between the time of arrival of migrants and the full incorporation of their genetic ancestry into the population.

and Cliffs End Farm outliers did not carry the allele, and most of the rise in Britain occurred after the M-LBA (Fig. 4b, Supplementary Table 8). This suggests that dairy products were consumed in a qualitatively different way or were economically more important in LBA–IA Britain than in central Europe.

Continental sources of M-LBA migration

The ancestry change in Britain during the M-LBA was more subtle than those associated with the Neolithic and Beaker-period migrations. In England and Wales, allele frequency differentiation between the Neolithic and C/EBA was F_{ST} of approximately 0.02, but between the C/EBA and the IA it was an order of magnitude smaller at F_{ST} of approximately 0.002 (Extended Data Table 1). The pre-LBA population in Britain also made a substantial genetic contribution to the IA population, in contrast to the two earlier major Holocene ancestry shifts[8,9]. Evidence for a substantial contribution from the C/EBA population to later populations also comes from the Y chromosome haplogroup R1b-P312/L21/M529 (R1b1a1a2a1a2c1), which is present at 89 ± 5% in sampled individuals from C/EBA Britain and is nearly absent in available ancient DNA data from C/EBA Europe (Supplementary Table 9). The haplogroup remained more common in Britain than in continental Europe in every later period, and continues to be a distinctive feature of the British Isles as its frequency in Britain and Ireland today (14–71% depending on the region[19]) is far higher than anywhere else in continental Europe (Extended Data Fig. 5).

To gain insight into the possible sources of the M-LBA migrants to southern Britain, the pooled IA individuals from England and Wales were fitted in qpAdm as a mixture of the main C/EBA cluster, and a second source. We tested 65 sources—63 from continental Europe and 2 from Britain (the Margetts Pit and the Cliffs End Farm outlier pools)—and found that 20 fit at $P > 0.05$. We then pooled the genetically similar individuals from Margetts Pit and Cliffs End Farm and performed further testing with more stringent qpAdm setups, leaving eight second sources that consistently fit well with modest standard errors (Table 2, Supplementary Information Section 6). The pool of Margetts Pit and Cliffs End Farm individuals fits as contributing 49.4 ± 3.0% of the ancestry of IA people from southern Britain. Even omitting representatives of the putative source population living in Britain itself, we infer large genetic turnovers, as the seven continental populations that fit as sources are estimated to contribute 24–69% ancestry. Although only one-fifth of the continental candidate populations that we tested are from France, six-sevenths of the fitting populations are from France. Four of these are from Occitanie in southern France (600–200 BC), two from Grand Est in northeastern France (800–200 BC) and one from Spain (a group from approximately 600 BC). These fitting second sources all significantly post-date the ancestry change in Britain and hence cannot be the true sources; however, they are plausibly descended from earlier local populations. An

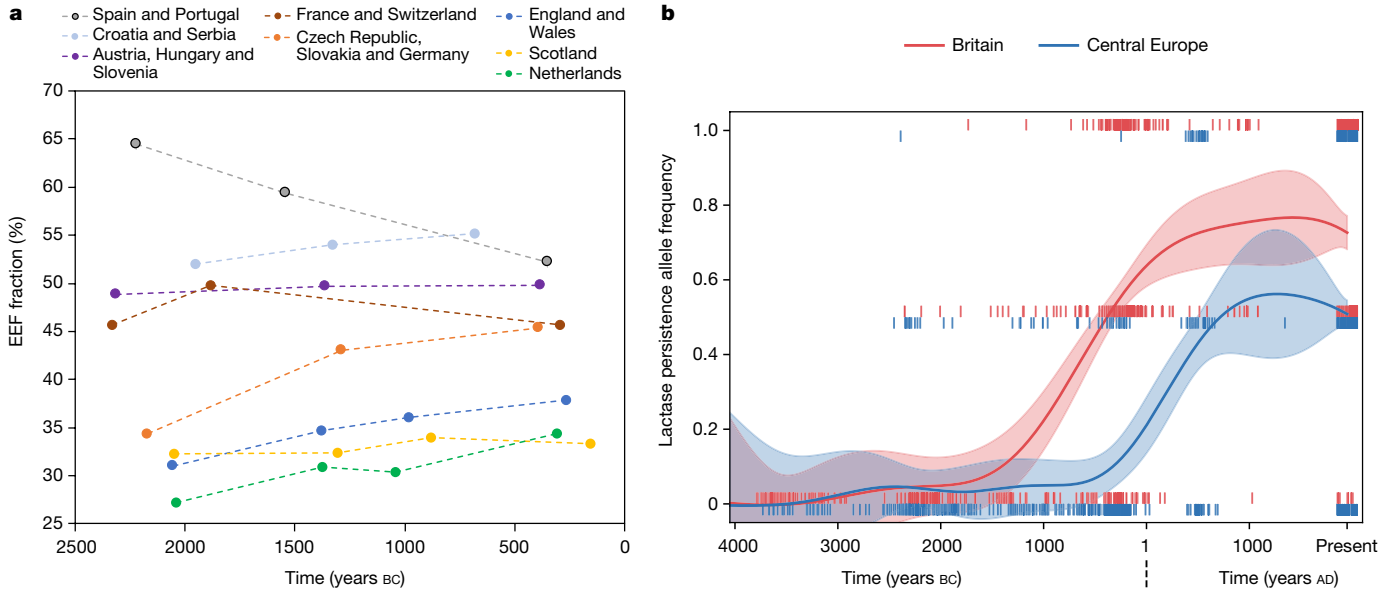

Fig. 4 | Genetic change in Britain in the context of Europe-wide trends. **a**, Eight ancient DNA time transects for up to four periods, plotting the mean of the EEF inference on the *y* axis and using the average of dates of individuals in periods defined for each region as in Supplementary Table 5 on the *x* axis. Sample sizes used to compute each point are given in Supplementary Table 7. The dotted lines connecting points should not be interpreted as implying a smooth change over time and instead are meant to help in visual discernment of which groups of points come from the same time transects. **b**, A major rise in the allele conferring lactase persistence occurred about a millennium earlier in Britain than in central Europe, suggesting different selection regimes and possibly cultural differences in the use of dairy products in the two regions in the IA. This analysis based on imputed data includes 459 ancient individuals from Britain and 468 from central Europe (Czech Republic, Slovakia, Croatia, Hungary, Austria, Germany and Slovenia) (we then co-analysed with present-day individuals; Methods). Each vertical bar represents the derived allele frequency for each individual with values [0, 0.5, 1]; we use jitter on the *x* axis, and the shaded area indicates the inferred 95% confidence interval for the allele frequency at each time point.

origin in France is also suggested by the fact that all of the high EEF outliers in Britain in the M-LBA, as well as all of the individuals from 1000–875 BC who attest to the ramp-up of EEF ancestry to IA levels, are from Kent in far southeastern Britain (Extended Data Fig. 6). The migrant stream began admixing more broadly through southern Britain by the second half of the LBA, as individual I12624 from Blackberry Field, Potterne in Wiltshire, dated to 950–750 BC, had an EEF proportion of 38.1 ± 2.0% consistent with the level that became ubiquitous in southern Britain by the beginning of the IA (Extended Data Fig. 3). As this is the only non-Kent data point from the second half of the LBA, however, more sampling is needed to understand the geographical and temporal course of the spread of this ancestry beyond Kent.

Table 2 | Fitting proxies for the new ancestry source in IA southern Britain

Proxies for source of the new ancestry	*n*	Mean date (BC)	*P* value	Ancestry (%)
Margetts Pit and Cliffs End Farm M-LBA	4	1036	0.07	49.4±3.0
Spain IA Tartessian	2	629	0.16	23.7±1.2
France GrandEst IA1 (shotgun data)	5	620	1.00	48.9±3.7
France Occitanie IA2 (high EEF subgroup, shotgun data)	1	450	0.85	25.8±1.7
France Occitanie IA2 (high WHG subgroup, shotgun data)	1	450	0.39	33.5±4.1
France Occitanie IA2 (shotgun data)	2	400	0.25	53.3±5.4
France Occitanie IA2 (low Steppe subgroup, shotgun data)	2	363	0.33	36.5±2.6
France GrandEst IA2	12	250	0.09	68.5±3.3

We fitted the pooled IA individuals from England and Wales as a mixture of the pooled C/EBA individuals from England and Wales and a proxy for the new ancestry source. The *P* value is from qpAdm's test of fit of each population as a two-way admixture with no correction for multiple hypothesis testing. These results represent eight of the 65 lines in Supplementary Information Section 6, Table S6.1.

Regional variation in IA Britain

Estimates of Margetts Pit and Cliffs End Farm-like ancestry in southern Britain range from 35 ± 5% in northern England to 56 ± 5% in south-central England (Table 1, Extended Data Table 2). The IA was a period when material culture was increasingly regional in character[16], and our results show that this was accompanied by subtle genetic structure, although within southern Britain there is no clear correlation of these admixture proportions to latitude (Table 1). We highlight the case of East Yorkshire, where most individuals are from 'Arras Culture' contexts comprising square-ditched barrows and occasional chariot burials. Similarities to funerary traditions of IA societies in the Paris Basin and Ardennes/Champagne regions have led to suggestions that East Yorkshire was influenced by direct migration from continental Europe in the IA[20]. Our estimate of the Margetts Pit and Cliffs End Farm ancestry source for East Yorkshire burials is 44 ± 4% (Table 1), which is typical for middle latitudes of Britain at this time (East Anglia is similar). However, the East Yorkshire burials are distinctive in another way: regional differentiation in IA Britain, as measured by F_{ST}, is higher between East Yorkshire and other groups than it is between any other pair of IA populations in England and Wales in our dataset (Extended Data Table 2). Comparative data from the continent could make it possible to determine whether this is due to isolation of IA East Yorkshire from the rest of southern Britain, or later streams of migration specifically affecting East Yorkshire.

Archaeological and linguistic context

The period from 1500 to 1150 BC has long been recognized as a time when cultural connections between Britain and regions of continental

Europe intensified, and when societies on both sides of the Channel shared cultural features, including domestic pottery, metalwork and ritual depositional practices[2–6]. From around 750 BC, there is more limited archaeological evidence of contact between Britain and the continent, and our genetic findings concur in showing that, by the beginning of the IA, there is little evidence of demographically significant migration into Britain[2]. Our findings do not establish whether the population movements that we infer were a cause or consequence of M-LBA exchange networks, but they do suggest that interactions between local populations of Britain and new migrants bringing ideas from continental Europe could have been a vector for some of the cultural change that we see in M-LBA England and Wales. Western and central France are much more poorly represented by available genome-wide ancient DNA data than neighbouring regions of Europe, and thus we cannot at present test whether the gene flow between the two regions in this period was largely unidirectional.

Population movements are often an important driver of cultural change, including in the languages people speak. While periods of intense migration, such as the one we infer here, do not always result in language shifts[18], genetic evidence of significant migration is important because it documents demographic processes that are plausible conduits for language spread[21]. Several researchers have interpreted linguistic data as providing evidence for early Celtic languages spreading into Britain from France at the end of the Bronze Age or in the early IA[22,23]. Our identification of substantial migration into Britain from sources that best fit populations in France provides an independent line of evidence in support of this, and points to the M-LBA as a prime candidate for the period of this language spread. While the lack of evidence for M-LBA EEF ancestry change in Scotland could be interpreted as weakening the case that Celtic languages spread into Britain at this time, a later arrival of Celtic languages in Scotland is consistent with evidence that non-Celtic and Celtic languages coexisted there into the first millennium AD[24]. Our finding of a decrease of EEF ancestry in Iberia, where the proportion was relatively high in the EBA, and a roughly simultaneous increase in Britain where the proportion was relatively low in the EBA (Fig. 4a), could, in theory, reflect a Celtic-speaking group of people with intermediate EEF ancestry spreading into both regions, although such a simple model cannot explain all the north–south ancestry convergence in Europe (Supplementary Information Section 7). Nevertheless, the fact that the Margetts Pit and Cliffs End Farm outliers are genetically very similar to the Knoviz culture sample from central Europe (Supplementary Information Section 6) is notable in light of the fact that some scholars have hypothesized that central European Urnfield groups such as Knoviz have links to the spread of Celtic languages[25]. Our failure to find evidence of large-scale migration into Britain from continental Europe in the IA suggests that, if the spread of Celtic languages was driven by large-scale movement of people, it is unlikely to have occurred at this time. The adoption of cultural practices in IA Britain originating in continental Europe—particularly those linked to the La Tène tradition[26]—was also evidently independent of large-scale population movements, although there certainly were smaller movements, attested by individual IA outliers with high EEF ancestry such as those at Thame or Winnall Down (Fig. 3).

An important direction for future work is to generate new ancient DNA data from continental contexts especially in central and western France—and also Ireland—to test the alternative scenarios of population history consistent with the observations in this study, and to develop theories integrating the genetic findings within archaeological frameworks.

Online content

Any methods, additional references, Nature Research reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at https://doi.org/10.1038/s41586-021-04287-4.

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Methods

Ancient DNA laboratory work

All human skeletons analysed in this study were sampled with written permission of the stewards of the skeletons and every individual is represented by at least one co-author. Researchers who wish to obtain further information about specific individuals should write to the corresponding authors and/or the authors who provided the archaeological contextualization for those individuals given in Supplementary Information Section 1. In dedicated clean rooms at Harvard Medical School, the University of Vienna, the Natural History Museum in London, and the University of Huddersfield, as well as during sampling trips, we obtained powder from ancient bones and teeth using methods including sandblasting, drilling and milling[31,32]. We extracted DNA using various methods[33–35], and prepared double-stranded or single-stranded libraries treated with the enzyme uracil DNA glycosylase to reduce characteristic errors associated with ancient DNA degradation[36–39]. We enriched these sequences manually or in multiplex using automated liquid handlers for sequences overlapping the mitochondrial genome[40,41] as well as about 1.24 million single-nucleotide polymorphisms (SNPs)[42]. We pooled enriched libraries, which we had marked with unique 7-bp internal barcodes and/or 7–8-bp indices and sequenced on Illumina NextSeq500 or HiSeqX10 instruments using paired-end reads of either 76 bp or 101 bp in length (Supplementary Table 2).

Bioinformatic analysis

After trimming barcodes and adapters[30], we merged read pairs with at least 15 bp of overlap allowing no more than one mismatch if base quality was at least 20, or up to three mismatches if base qualities were less than 20; we chose the nucleotide of the higher quality in case of a conflict while setting the local base quality to the minimum of the two (for these steps, we used a custom toolkit at https://github.com/DReichLab/ADNA-Tools). We aligned merged sequences to the mitochondrial genome RSRS[43] or the human genome hg19 (GRCh37; https://www.ncbi.nlm.nih.gov/assembly/GCF_000001405.13/) using the samse command[44] of BWA version 0.7.15 with parameters -n 0.01, -o 2, and -l 16500. After identifying PCR duplicates by tagging all aligned sequences with the same start and stop positions and orientation and, in some cases, in-line barcodes using Picard MarkDuplicates (http://broadinstitute.Github.io/picard/), and restricting to sequences that spanned at least 30 bp, we selected a single copy of each such sequence that had the highest base quality score. For subsequent analysis, we trimmed the last two bases of each sequence for UDG-treated libraries and the last five for non-UDG-treated libraries to reduce the effects of characteristic errors associated with ancient DNA degradation. We built mitochondrial consensus sequences, determined haplogroups using HaploGrep2 version 2.1.15 (ref. [45]) and Phylotree version 17, and estimated the match rate to the consensus sequence using contamMix version 1.0-12 (ref. [46]) when coverage was at least twofold. To represent the nuclear data, we randomly sampled a single sequence covering each of the 1.24 million SNP targets, and estimated coverage based on the subset of these targeted SNPs on the autosomes. We used ANGSD version 0.923 to estimate contamination based on polymorphism on the X chromosome in male individuals with at least 200 SNPs covered twice (male individuals should be non-polymorphic if their data are uncontaminated)[47]. We automatically determined Y chromosome haplogroups using both targeted SNPs and off-target sequences aligning to the Y chromosome based on comparisons to the Y chromosome phylogenetic tree from Yfull version 8.09 (https://www.yfull.com/), providing two alternative notations for Y chromosome haplogroups: the first using a label based on the terminal mutation, and the second describing all associated branches of the Y chromosome tree based on the notation of the International Society of Genetic Genealogy (ISOGG) database version 15.73 (http://www.isogg.org). We manually checked the Y chromosome haplogroups for the male individuals in the Britain time transect.

Determination of ancient DNA authenticity

We determined ancient DNA authenticity based on five criteria. First, we required that the lower bound of the 95% confidence interval for contamination from ANGSD (if we were able to compute it) was less than 1%. Second, we required that the upper bound of the 95% confidence interval for match rate to mitochondrial consensus sequence (if we were able to compute it) was more than 95%. Third, we required that the average rate of cytosine-to-thymine errors at the terminal nucleotide for all sequences passing filters was more than 3% for double-stranded partially UDG-treated libraries[39] and more than 10% for single-stranded USER-treated libraries and double-stranded non-UDG-treated libraries (the latter libraries are all from previously published data that we reanalysed here)[48]. Fourth, we required the ratio of sequences mapping to the Y chromosome to the sum of sequences mapping to the X and Y chromosome for the 1240K data to be less than 3% (consistent with a female individual) or more than 35% (consistent with a male individual). Fifth, to report an individual, we required the number of SNPs covered at least once to be at least 5,000 (for most actual population genetic analyses, we required at least 30,000). For some individuals with evidence of contamination, we analysed only sequences with terminal damage to enrich for genuine ancient DNA, allowing us to study more individuals[49]. We do not include data from 71 individuals that failed our authenticity criteria (marked as 'QUESTIONABLE' in Supplementary Table 1) in our main analyses; however, we publish the data as part of this study as a resource.

Approach to chronological uncertainty

We restricted individuals for which we newly report data to those whose date estimate (mean of the posterior distribution from radiocarbon dating, or midpoint of the archaeological context date) is older than AD 43 based on information that we had available as of 1 July 2021. For the great majority of individuals, assignments to chronological periods did not change subsequently. However, there were 23 exceptions, and we study these as part of their original analysis groupings (Supplementary Information Section 8).

Population genetic analyses

We detected runs of homozygosity using hapROH version 0.3 (ref. [17]). We computed f_4-statistics and F_{ST} and carried out qpWave and qpAdm analyses in ADMIXTOOLS version 7.0.2, computing standard errors with a Block Jackknife[50]. For modelling ancestry with pre-Bronze Age sources in qpAdm, we used the outgroup populations (OldAfrica, WHGA, Balkan_N and OldSteppe) using the assignment of individuals to groups as in Supplementary Table 3. For modelling ancestry with M-LBA sources, we used the outgroups (OldAfrica, OldSteppe, Turkey_N, Netherlands_C.EBA, Poland_Globular_Amphora, Spain. Portugal_4425.to.3800BP, CzechRepublic.Slovakia.Germany_3800. to.2700BP, Sardinia_8100.to.4100BP, CzechRepublic.Slovakia.Germany_4465.to.3800.BP, Sardinia_4100.to.2700BP and Spain.Portugal_6500.to.4425BP), using the assignment of individuals to groups specified in either Supplementary Table 3 or Supplementary Table 5.

Relative detection

We inferred relatives up to the third degree as previously described[51].

Allele frequency estimates of variants with functional importance

We clustered individuals into the temporal groupings specified in Supplementary Table 5. To estimate the allele frequency of a given SNP in a particular group for Supplementary Table 8, we used sequence counts at each SNP position in each individual and a maximum likelihood approach[52]. We obtained confidence intervals using the Agresti–Coull method implemented in the binom.confint function of the R package binom. For the imputation-based methodology for studying the trajectory of the lactase persistence allele (Fig. 4b), we used GLIMPSE[37] to impute diploid genotype posterior probabilities (GP)

based on 1000 Genomes Projects haplotypes[38], restricting to samples with max(GP) > 0.9 for this SNP. To represent allele frequencies in modern Britain, we used data from the 1000 Genomes Project, pooling together 190 individuals who were either European American individuals from Utah (CEU) or people of European ancestry from Great Britain (GBR)[38]. To represent modern central Europe, we used 288 individuals from the modern Czech Republic[39]. We visualize the frequency trajectory of the lactase persistence allele at SNP rs4988235 in Fig. 4b using the GaussianProcessRegressor function from the Scikit-learn library in Python with parameter alpha = 0.1 and 1*RationalQuadratic kernel with parameter length_scale_bounds = (1, 1000).

Radiocarbon dating

We carried out accelerator mass spectrometry dating at various laboratories (n = 81 at SUERC, n = 40 at PSUAMS, n = 1 at BRAMS, and n = 1 at Poznan); Supplementary Table 4 specifies the methods that we used and also provides the detailed measurements. We refer readers to the individual laboratories for the experimental protocols. We calibrated all dates using OxCal 4.4.2 (ref. [53]) and IntCal20 (ref. [54]).

Reporting summary

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

Data availability

The raw data are available as aligned sequences (.bam files) through the European Nucleotide Archive under accession number PRJEB47891. The newly generated genotype data are available as a Supplementary Data file. The previously published data co-analysed with our newly reported data can be obtained as described in the original publications, which are all referenced in Supplementary Table 3; a compiled dataset that includes the merged genotypes used in this paper is available as the Allen Ancient DNA Resource at https://reich.hms.harvard.edu/allen-ancient-dna-resourceaadr-downloadable-genotypes-present-day-and-ancient-dna-data. Any other relevant data are available from the corresponding authors on reasonable request.

Code availability

This study uses publicly available software, which we fully reference.

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Competing interests The authors declare no competing interests.

Additional information

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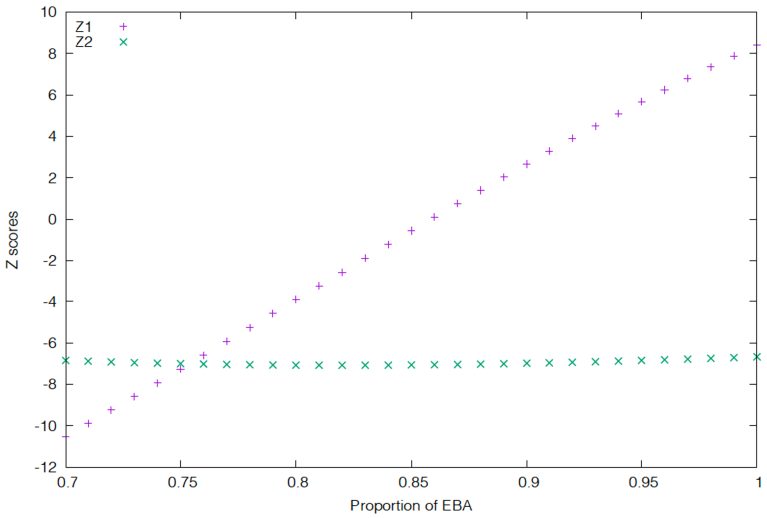
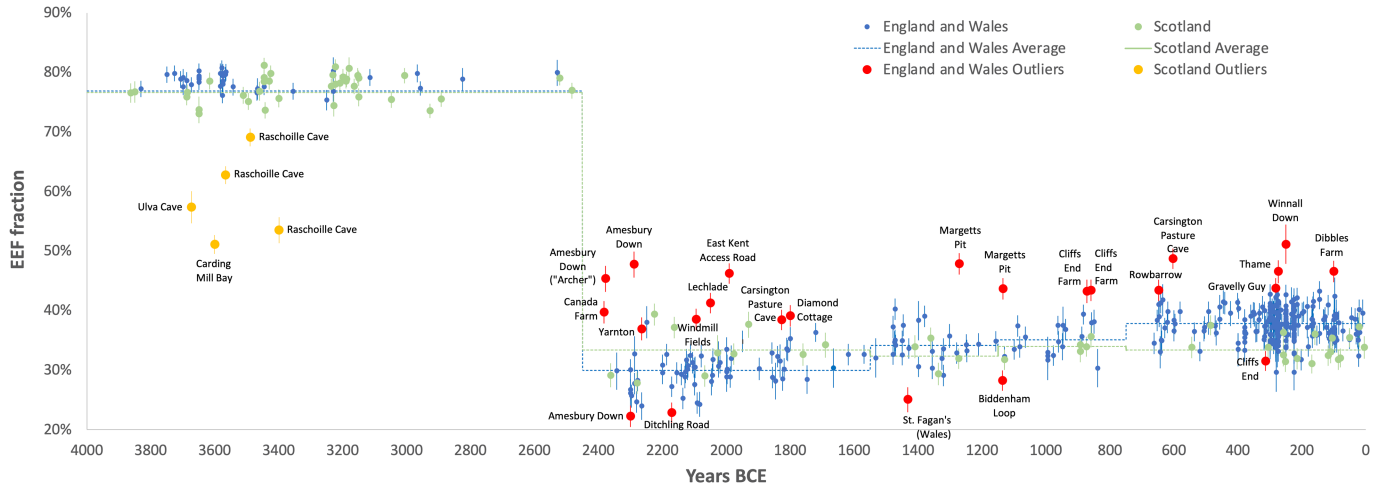
A

Modeled population	N	Neolithic and C/EBA Groups Used in Modeling	
		England/Wales	Scotland
England/Wales MBA	26	0.34	0.046
England/Wales LBA	23	0.023	0.0074
England/Wales IA	273	$<10^{-6}$	$<10^{-6}$
Scotland MBA	5	0.88	0.028
Scotland LBA	4	0.25	0.77
Scotland IA	18	0.0091	0.0028

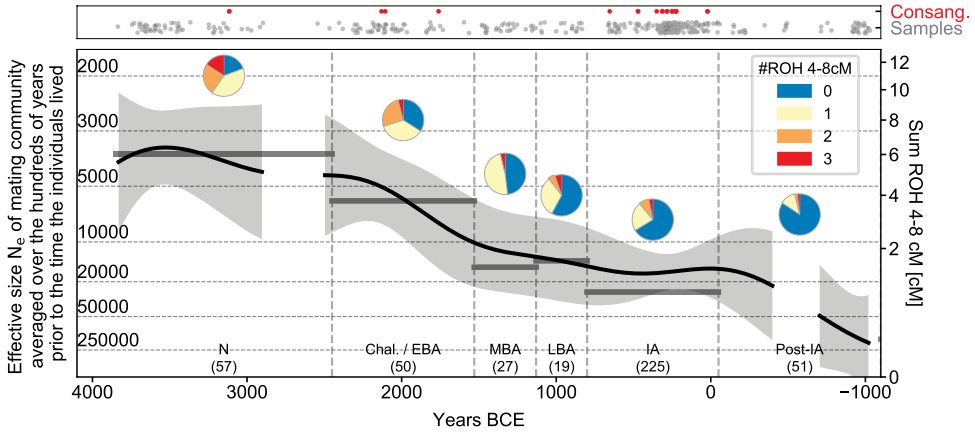
B



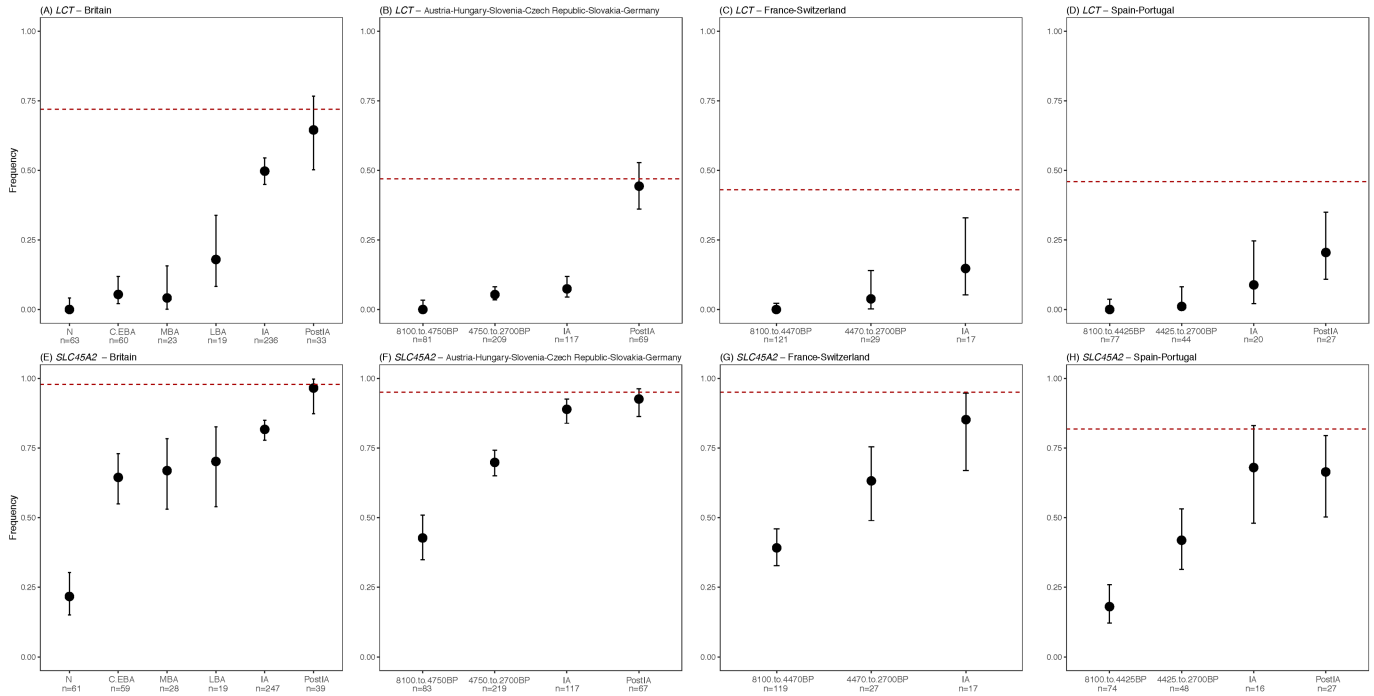
Extended Data Fig. 1 | Post-MBA Britain was not a mix of earlier British populations. a, *qpAdm* p-values for modelling British groups as a mix of Neolithic and Chalcolithic/EBA populations from England and Wales or Scotland (outgroups OldAfrica, OldSteppe, Turkey_N, CzechRepublic.Slovakia.Germany_3800.to.2700BP, Netherlands_C.EBA, Poland_Globular_Amphora, Spain.Portugal_4425.to.3800BP, CzechRepublic.Slovakia.Germany_4465.to.3800.BP, Sardinia_4100.to.2700BP, Sardinia_8100.to.4100BP, Spain.Portugal_6500.to.4425BP). We highlight $p<0.05$ (yellow) or $p<0.005$ (red). Both sources and target populations in this analysis remove outlier individuals ("Filter 2" in Supplementary Table 5); we obtain qualitatively similar results when outlier individuals are not removed (not shown). **b**, To obtain insight into the source of the new ancestry in Britain in the IA, we computed f_4(England.and.Wales_IA, α(England.and.Wales_N) + (1-α)(England.Wales_C.EBA); R1, R2) for different (R1, R2) population pairs. If England.and.Wales_IA is a simple mixture of England.and.Wales_N and England.and.Wales_C.EBA without additional ancestry, then for some mixture proportion the statistic will be consistent with zero for all (R1, R2 pairs). When (R1, R2) = (OldAfrica, OldSteppe) feasible Z-scores (Z1 in the plot) are observed when $\alpha \sim 0.85$, showing that ~85% ancestry from England.and.Wales_C.EBA ancestry is needed to contribute the observed proportion of Steppe ancestry in England.and.Wales_IA. However, when (R1, R2) is (Balkan_N, Sardinian_8100.to.4100BP), we get infeasible Z-scores (Z2) of <-6 across the range where Z1 is remotely feasible. Thus, Iron Age people from England and Wales must have ancestry from an additional population deeply related to Sardinian Early Neolithic groups.



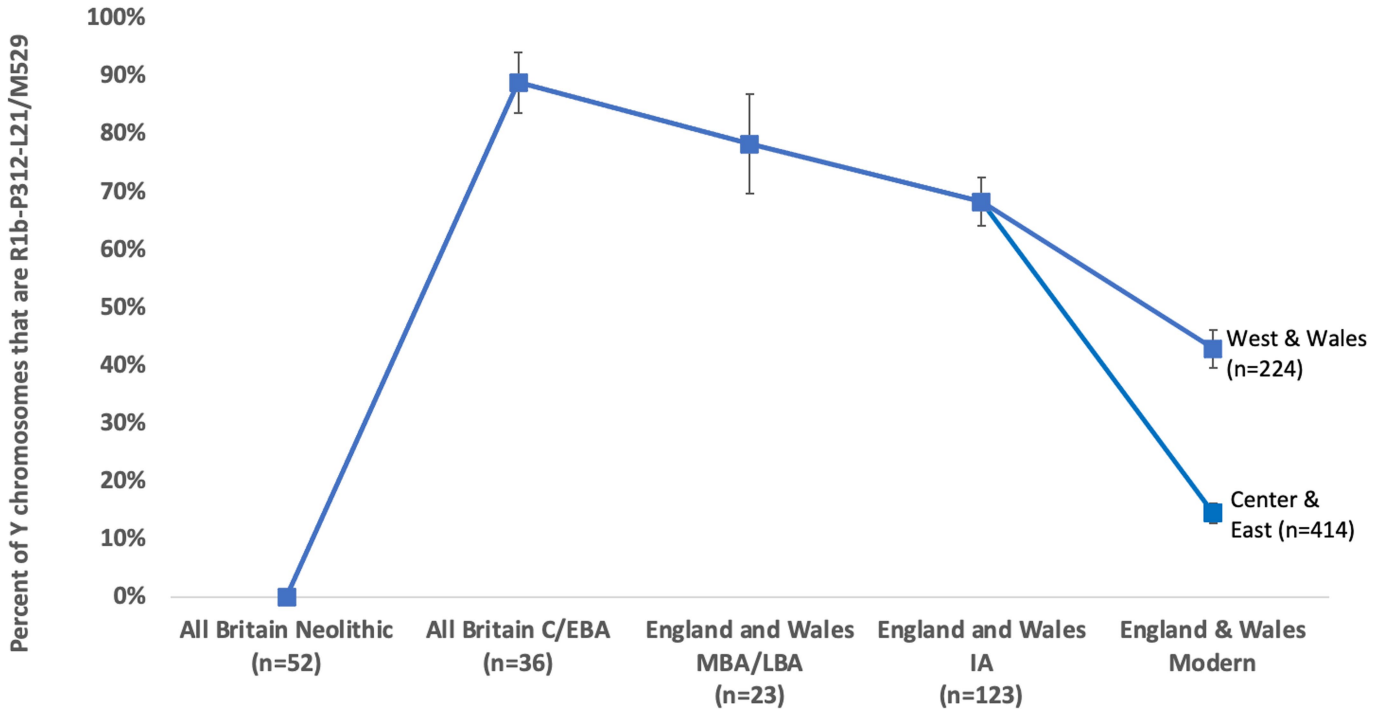
Extended Data Fig. 2 | By-individual analysis of the British time transect. Version of Fig. 3 with the time transect extended into the Neolithic, and adding in individuals from Scotland. We plot mean estimates of EEF ancestry and one standard error bars from a Block Jackknife for all individuals in the time transect that pass basic quality control, that fit to a three-way admixture model (EEF + WHG + Yamnaya) at p>0.01 using *qpAdm*, and for the Neolithic period that fit a two-way admixture model (EEF + WHG) at p>0.01. Individuals that fit the main cluster of their time are shown in blue (southern Britain) and green (Scotland), while red and orange respectively show outliers at the ancestry tails (identified either as p<0.005 based on a *qpWave* test from the main cluster of individuals from their period and |Z|>3 for a difference in their EEF ancestry proportion from the period, or alternatively p<0.1 and |Z|>3.5). The averages for the main clusters in both southern Britain and Scotland in each archaeological period (Neolithic, C/EBA, MBA, LBA and IA) are shown in dashed lines.



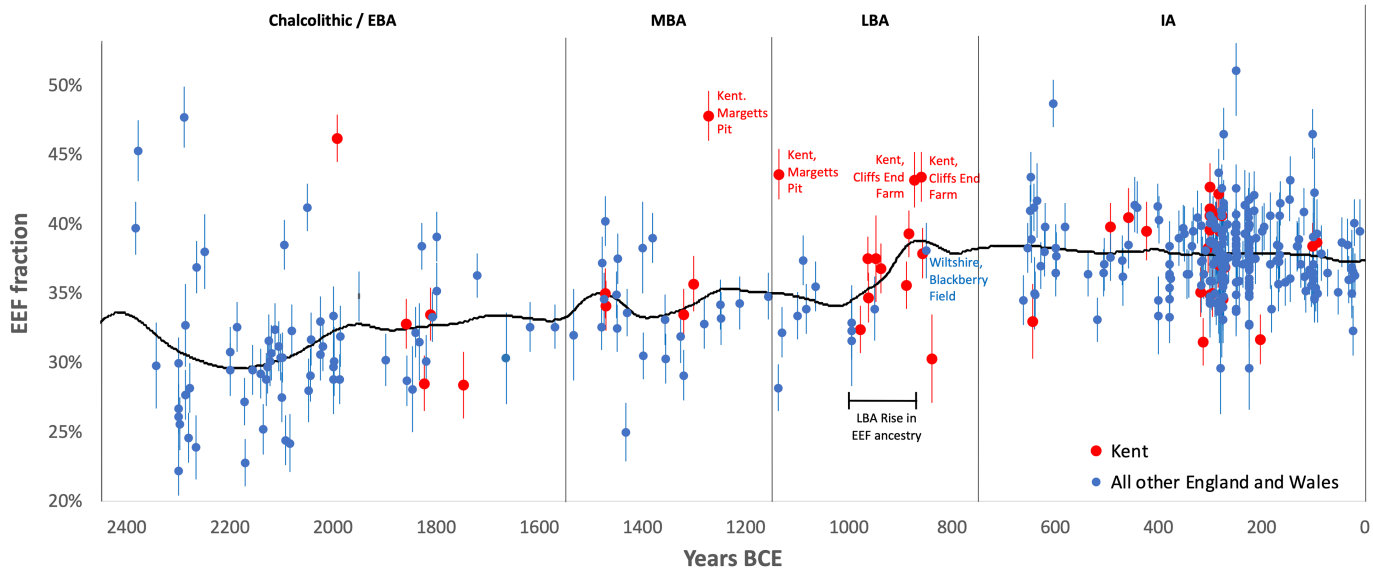
Extended Data Fig. 3 | Changes in the size of the mate pool over time. Close kin unions were rare at all periods as reflected in the paucity of individuals harbouring >50 centimorgans (cM) of their genome in runs of homozygosity (ROH) of >12 cM (red dots in top panel). The number of ROH of size 4–8 cM per individual (bottom panel) reflects the rate at which distant relatives have children, providing information about the sizes of mate pools (Ne) averaged over the hundreds of years prior to when individuals lived; thus, the broad trend of an approximately fourfold drop in Ne from the Neolithic to the IA is robust, but we may miss fluctuations on a time scale of centuries. The thick black lines represent the mean Ne obtained by fitting a mathematical model of a Gaussian process with a 600-year smoothing kernel (gray area 95% confidence interval). The horizontal grey lines show period averages from maximum likelihood which can differ from the mean obtained through the mathematical modelling if the counts do not conform well to a Gaussian process. We interrupt the fitted line for periods with too little data for accurate inference (<10 individuals in a 400-year interval centered on the point).



Extended Data Fig. 4 | Frequency change over time at two phenotypically important alleles. Present-day frequencies are shown by the red dashed lines; sample sizes for each period are labelled at the bottom of each plot; and we show means along with 95% confidence intervals (Supplementary Table 8). (**a**–**d**/Top) Lactase persistence allele at rs4988235. (**e**–**h**/Bottom) Light skin pigmentation allele at rs16891982. In Britain the rise in frequency of the lactase persistence allele occurred earlier than in central Europe. This analysis is based on direct observation of alleles; imputation results are qualitatively consistent (Fig. 4b).



Extended Data Fig. 5 | Y chromosome haplogroup frequency changes over time. Estimated frequency of the characteristically British Y chromosome haplogroup R1b-P312/L21/M529 in all individuals for which we are able to make a determination and which are not first-degree relatives of a higher coverage individual in the dataset. Sample sizes for each period are labelled at the bottom, and we show means and one standard error bars from a binominal distribution. The frequency increases significantly from ~0% in the whole island Neolithic, to 89±4% in the whole island C/EBA. It declines non-significantly to 79±9% in the MBA and LBA (from this time onward restricting to England and Wales because of the autosomal evidence of a change in EEF ancestry in the south but not the north). It further declines to 68±4% in the IA, a significant reduction relative to the C/EBA (P=0.014 by a two-sided chi-square contingency test). There is additional reduction from this time to the present, when the proportion is 43±3% in Wales and the west of England ($P=5x10^{-6}$ for a reduction relative to the IA), and 14±2% in the center and east of England ($P=3x10^{-32}$ for a reduction relative to the IA).



Extended Data Fig. 6 | Version of Fig. 3a contrasting Kent to the rest of southern Britain. We show the period 2450-1 BCE. Each point corresponds to a single individual and we show means and one standard error bars from a Block Jackknife. All the high EEF outliers during the M-LBA are from Kent—the part of the island closest to France—and in addition all the individuals from 1000-875 BCE from the group of samples showing the ramp-up from MBA to IA levels of EEF ancestry are from Kent (5 from Cliffs End Farm and 3 from East Kent Access Road). This suggests the possibility that this small region was the gateway for migration to Britain during the M-LBA. Further sampling from the rest of Britain during the M-LBA is critical in order to understand the dynamics of how this ancestry spread more broadly. However, the fact that the only sample from the second half of the LBA that is not from Kent—I12624 from Blackberry Field in Potterne in Wiltshire at 950-750 BCE—already has a proportion of EEF ancestry typical of the IA in southern Britain—suggests that this ancestry began spreading more broadly by the second half of the LBA.

Extended Data Table 1 | Ancestry change over time in Britain

		qpAdm results *(3-way model)*							*Tests for difference in ancestry between row & column (below diagonal f_4-statistic Z-score, above-diagonal F_{ST})*																							
	Sample size	P-value	WHG	EEF	Steppe	WHG error	EEF error	Steppe	England.and.Wales_N	England.and.Wales_C.EBA	England.and.Wales_MBA	England.and.Wales_LBA	England.and.Wales_IA	England.and.Wales_PostIA	England.and.Wales_Modern	Scotland_N	Scotland_C.EBA	Scotland_MBA	Scotland_LBA	Scotland_IA	Scotland_PostIA	Scotland_Modern	Ireland_N	Ireland_C.EBA	Ireland_PostIA	Ireland_Modern	Channel.Islands_8100.to.5700BP	Channel.Islands_5700.to.4450BP	Channel.Islands_IA
England.and.Wales_N	37	0.7597	20.8%	76.7%	2.6%	0.5%	0.5%	0.6%		0.02	0.0176	0.0171	0.0161	0.0219	0.0226	0.0013	0.0192	0.0188	0.0188	0.0197	0.0206	0.0239	0.0046	0.0275	0.0233	0.0225	0.0177	0.0073	0.0153
England.and.Wales_C.EBA	69	0.3840	12.6%	31.0%	56.4%	0.4%	0.5%	0.6%	-65.7		0.0007	0.0012	0.0017	0.0084	0.0107	0.0204	0.0013	0.0002	0.0013	0.0019	0.006	0.0109	0.0259	0.0112	0.0091	0.0085	0.0357	0.0173	0.0055
England.and.Wales_MBA	26	0.0918	13.5%	34.7%	51.8%	0.5%	0.6%	0.7%	-58.2	-7.3		0.0004	0.0008	0.0066	0.0088	0.0181	0.0011	0.0009	0.0013	0.0016	0.004	0.009	0.0227	0.0099	0.0064	0.0071	0.0333	0.0151	0.0043
England.and.Wales_LBA	23	0.4609	13.6%	36.1%	50.4%	0.5%	0.6%	0.7%	-52.3	-9.9	2.9		0.0006	0.0056	0.007	0.0179	0.0028	0.0012	0.0017	0.0022	0.0037	0.0077	0.0209	0.0089	0.0065	0.0052	0.0319	0.0141	0.0037
England.and.Wales_IA	273	0.3637	13.6%	37.9%	48.5%	0.3%	0.4%	0.5%	-63.9	-19.4	7	2.3		0.0053	0.0073	0.0175	0.0027	0.0011	0.0016	0.0018	0.0035	0.0076	0.0204	0.0099	0.0064	0.0049	0.0306	0.0136	0.0032
England.and.Wales_PostIA	38	0.0002	15.0%	36.6%	48.3%	0.4%	0.5%	0.6%	61	-11	-2.5	1	5.8		0.003	0.0239	0.0085	0.0051	0.0074	0.0076	0.0014	0.0037	0.0188	0.0069	4E-05	0.0024	0.0333	0.017	0.0049
England.and.Wales_Modern	62	0.6315	14.1%	40.0%	45.9%	0.4%	0.4%	0.6%	-61.3	-19.5	-8.8	-4	-3.5	8.5		0.0243	0.0107	0.0071	0.0094	0.0097	0.0034	0.0016	0.0184	0.0083	0.0029	0.0021	0.034	0.0175	0.0072
Scotland_N	44	0.6642	23.1%	74.3%	2.5%	0.4%	0.5%	0.6%	2.7	-65.1	-55.5	-51.3	-64.4	-61.3	-61.6		0.0184	0.0186	0.0182	0.0197	0.0227	0.026	0.0079	0.0296	0.0243	0.0248	0.0196	0.0084	0.0164
Scotland_C.EBA	10	0.1517	13.5%	32.2%	54.3%	0.6%	0.7%	1.0%	52	-3	1.6	4.3	6.4	3.5	7.8	-50.6		0.0011	0.002	0.0022	0.0064	0.0107	0.0243	0.0099	0.0079	0.0098	0.0338	0.0194	0.0067
Scotland_MBA	5	0.5635	14.0%	32.3%	53.7%	0.8%	0.9%	1.1%	45.2	-1.7	2	4.1	6.2	3.9	7.4	-44.8	0.5		0.0009	0.0013	0.0032	0.0074	0.0216	0.0078	0.007	0.0061	0.032	0.0132	0.0036
Scotland_LBA	4	0.8346	12.4%	34.0%	53.7%	0.8%	1.0%	1.2%	39.8	-4	-0.1	1.3	3.2	1	4.2	-40.4	-1.1	1.7		0.0002	0.0047	0.0098	0.0239	0.0101	0.0084	0.0074	0.0357	0.0152	0.007
Scotland_IA	18	0.1850	12.7%	33.4%	54.0%	0.6%	0.6%	0.8%	56.1	-3.8	1.7	4.1	8.4	4.3	10.2	-56	0.2	1.1	-1.4		0.0047	0.0095	0.0251	0.0108	0.0083	0.0069	0.035	0.0178	0.0044
Scotland_PostIA	10	0.4713	12.9%	36.4%	50.7%	0.6%	0.7%	0.9%	50.4	-7.4	-1.5	1.2	3.7	0.3	5.1	48.3	-2.5	-3	-0.6	-2.9		0.0034	0.0189	0.0068	0.0021	0.0015	0.0331	0.0162	0.0037
Scotland_Modern	78	0.7341	14.3%	37.5%	48.2%	0.4%	0.4%	0.6%	62.1	-12.9	-3.5	0.2	5.1	-1.2	7.9	-62.4	-4.2	-4.5	-1.5	-5.5	1		0.0201	0.0089	0.0032	0.001	0.0352	0.0179	0.0078
Ireland_N	51	0.6505	21.6%	77.9%	0.5%	0.4%	0.5%	0.5%	-0.5	-69.3	-59	-54.9	-69.3	-65.8	-65.9	3.3	51.4	45.4	40.9	57.2	52	67.2		0.0238	0.0189	0.019	0.0183	0.0081	0.0158
Ireland_C.EBA	3	0.4166	13.6%	30.5%	55.9%	0.9%	1.2%	1.5%	37.9	1.5	4.7	6.4	8	5.9	9	-38	-3.3	-2.8	-4.3	-3.9	-5.4	-6.6	-38.8		0.0056	0.0068	0.0408	0.0256	0.0094
Ireland_PostIA	3	0.0109	14.0%	34.9%	51.1%	0.9%	1.1%	1.3%	37.6	-3.8	-0.3	1.5	3.1	1.1	4.1	-37.5	1.4	1.8	0	1.3	-0.8	-1.5	38.6	-3.9		0.0027	0.0336	0.0166	0.0049
Ireland_Modern	30	0.6461	12.9%	36.8%	50.3%	0.4%	0.5%	0.7%	57.6	-8.7	0	3.2	7.3	1.3	10.6	-56.8	1.8	1.7	0.5	3.6	-1.2	-3.7	-61.1	-5.5	-0.5		0.0346	0.0161	0.005
Channel.Islands_8100.to.5700BP	3	0.7577	16.1%	82.3%	1.6%	1.3%	1.4%	1.6%	3.5	36.4	33.7	31.8	32.7	33.2	31.8	4.4	33.8	30.8	28.6	33.9	32	33	3.3	29.8	29.3	30.3		0.0126	0.0266
Channel.Islands_5700.to.4450BP	3	0.4611	31.0%	67.1%	1.9%	1.2%	1.3%	1.4%	-7.9	28.1	24.7	23.7	23.8	24.4	22.7	-7	24.1	23.3	20.8	24.9	23.4	24.4	-8.3	23	20.5	21.1	-8.4		0.0099
Channel.Islands_IA	4	0.8603	15.4%	43.9%	40.7%	0.9%	1.2%	1.4%	-28.3	11.3	7.5	6	5.3	6.7	4.2	-27.3	7.3	7.8	6.5	8.5	6.7	6.4	-29.3	9.3	5.9	5.9	22.4	13.8	

We pool all individuals from each period and region removing those failing *qpAdm* modelling at p<0.01 according to Supplementary Table 5. In the left columns are *qpAdm* estimates of ancestry based on pre-Bronze Age source populations for each group. Below diagonal are Z-scores from f_4*(Row population, Column population; Turkey_N, OldSteppe)* (highlighted in red if |Z|>3). Above diagonal are inbreeding-corrected F_{ST} values (highlighted in yellow if F_{ST}>0.005).

Extended Data Table 2 | Fine genetic structure in Iron Age Britain

		qpAdm results *(3-way model)*							*Tests for difference in ancestry between row & column (below diagonal f_4-statistic Z-score, above-diagonal F_{ST})*											
	N	P-value for qpAdm (3-way model)	WHG (3-way model)	EEF (3-way model)	Steppe (3-way model)	WHG err. (3-way model)	EEF err. (3-way model)	Steppe err. (3-way model)	Scotland West	Scotland Southeast	Scotland Orkney	England Midlands	England North	England Cornwall	England East Anglia	England East Yorkshire	England Southeast	England Southwest	England Southcentral	Wales North	Wales South
Scotland West	4	0.12	13.0%	32.3%	54.7%	0.8%	1.0%	1.2%		0.0007	0.0006	0.0032	0.0035	0.0052	0.0035	0.0046	0.0034	0.004	0.0034	n/a	0.0038
Scotland Southeast	12	0.67	12.1%	33.9%	54.0%	0.6%	0.7%	0.9%	0.3		0.001	0.0012	0.0008	0.0028	0.0017	0.003	0.0014	0.0015	0.0019	n/a	0.0018
Scotland Orkney	2	0.22	14.2%	34.1%	51.6%	1.1%	1.2%	1.6%	0.7	1.1		0.0018	0.0013	0.0037	0.0007	0.0029	0.0014	0.0021	0.0021	n/a	0.0074
England Midlands	18	0.66	12.6%	36.0%	51.4%	0.5%	0.6%	0.8%	2.8	3.4	0.9		0.0001	0.0022	0.001	0.0028	0.0008	0.0009	0.0013	n/a	0.0016
England North	10	0.35	13.4%	36.3%	50.3%	0.6%	0.8%	1.0%	2.4	2.6	0.9	0.1		0.0027	0.0005	0.0016	0.0002	0.0007	0.0009	n/a	0.0019
England Cornwall	16	0.40	13.5%	36.4%	50.1%	0.5%	0.7%	0.8%	3.0	3.8	1.1	0.9	0.9		0.0025	0.0041	0.002	0.0021	0.0024	n/a	0.0024
England East Anglia	21	0.44	13.5%	37.0%	49.5%	0.5%	0.5%	0.7%	3.7	4.8	1.7	0.9	1.1	0.1		0.002	0.0007	0.0011	0.0013	n/a	0.0012
England East Yorkshire	47	0.61	13.2%	37.0%	49.8%	0.4%	0.5%	0.6%	4.1	5.4	2.1	1.5	1.7	-0.6	-0.5		0.0022	0.0026	0.0023	n/a	0.0028
England Southeast	36	0.13	13.9%	38.3%	47.8%	0.5%	0.5%	0.6%	5.4	7.2	2.8	-3.8	-3.2	-2.5	-3.4	-3.2		0.0008	0.0005	n/a	0.0008
England Southwest	84	0.30	13.7%	38.7%	47.6%	0.4%	0.4%	0.6%	5.6	8.4	3.3	-4.5	-4.3	-3.3	-3.7	-3.4	0.2		0.0009	n/a	0.0013
England Southcentral	38	0.32	13.9%	38.8%	47.2%	0.4%	0.5%	0.6%	5.6	7.5	3.3	-4.6	-3.6	-2.7	-3.0	-3.3	0.0	-0.2		n/a	0.0013
Wales North	1	0.20	12.1%	34.7%	53.2%	1.6%	2.0%	2.5%	0.8	1.1	2.0	1.9	2.0	2.5	2.9	3.1	3.6	3.6	3.5		n/a
Wales South	2	0.66	14.2%	38.6%	47.2%	1.2%	1.5%	1.8%	-2.7	-3.1	-1.5	-1.6	-1.3	-1.2	-1.0	-0.9	0.0	0.4	0.3	-1.9	

This is an expanded version of Table 1 including not just ancestry estimates for each group but also pairwise population comparisons. We pool all individuals from each period and region removing those failing *qpAdm* modelling at p<0.01 according to Supplementary Table 5. In the left columns are *qpAdm* estimates of ancestry for each group. Below diagonal are Z-scores from f_4*(Row population, Column population; Turkey_N, OldSteppe)* (highlighted in red if |Z|>3). Above diagonal are inbreeding-corrected F_{ST} values (highlighted in yellow if F_{ST}>0.0025).

nature portfolio

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Reporting Summary

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For all statistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.

n/a	Confirmed	
☐	☒	The exact sample size (*n*) for each experimental group/condition, given as a discrete number and unit of measurement
☐	☒	A statement on whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
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☐	☒	A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
☐	☒	For null hypothesis testing, the test statistic (e.g. *F*, *t*, *r*) with confidence intervals, effect sizes, degrees of freedom and *P* value noted *Give P values as exact values whenever suitable.*
☒	☐	For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
☒	☐	For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
☒	☐	Estimates of effect sizes (e.g. Cohen's *d*, Pearson's *r*), indicating how they were calculated

Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	BWA version 0.7.15 and other bioinformatics tools and data workflows (https://github.com/DReichLab/ADNA-Tools and https://github.com/DReichLab/adna-workflow)
Data analysis	hapROH version 0.3, Phylotree version 17, Yfull version 8.09, HaploGrep2 version 2.1.15, contamMix version 1.0-12, ANGSD version 0.923, ADMIXTOOLS version 7.0.2, R-package binom version 1.1-1, OxCal version 4.4.2, IntCal20, ISOGG version 15.73, pmdtools

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Data

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All manuscripts must include a data availability statement. This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A description of any restrictions on data availability
- For clinical datasets or third party data, please ensure that the statement adheres to our policy

The raw data are available as aligned sequences (bam files) through the European Nucleotide Archive under accession number PRJEB47891. The newly generated genotype data are available as a Supplementary data file. The previously published data co-analysed with our newly reported data can be obtained as described in the original publications, which are all referenced in Supplementary Table 3; a compiled dataset that includes the merged genotypes used in this paper is available as the Allen Ancient DNA Resource at https://reich.hms.harvard.edu/allen-ancient-dna-resourceaadr-downloadable-genotypes-present-day-and-ancient-dna-data. Any other relevant data are available from the corresponding authors upon reasonable request.

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Life sciences study design

All studies must disclose on these points even when the disclosure is negative.

Sample size	We report new ancient DNA data from my contexts where ancient DNA has not previously been reported. Although even more powerful inferences could have been made if sample sizes were larger, we make the inferences we can with these samples.
Data exclusions	We excluded ancient samples from this study if they did not fall within its temporal scope based on the information we had available as of July 1 2021 (4000 BCE - 43 CE in Britain, 5500 BCE - 43 CE on the continent). We also excluded samples that did not fall within the geographic scope of the study (Britain and western and Central Europe). After collecting genetic data, we excluded individuals from the analysis dataset as described in the Methods section entitled "Determination of ancient DNA authenticity." Specifically: "We determined ancient DNA authenticity based on five criteria. First, we required that the lower bound of the 95% confidence interval for contamination from ANGSD (if we were able to compute it) was <1%. Second, we required that the upper bound of the 95% confidence interval for match rate to mitochondrial consensus sequence (if we were able to compute it) was >95%. Third, we required that the average rate of cytosine-to-thymine errors at the terminal nucleotide for all sequences passing filters was >3% for double-stranded partially UDG-treated libraries39 and >10% for single-stranded USER-treated libraries and double-stranded non-UDG-treated libraries (the latter libraries are all from previously published data that we reanalysed here)48. Fourth, we required the ratio of sequences mapping to the Y chromosome to the sum of sequences mapping to the X and Y chromosome for the 1240K data to be less than 3% (consistent with a female) or >35% (consistent with a male). Fifth, to report an individual we required the number of SNPs covered at least once to be at least 5,000 (for most actual population genetic analyses, we required at least 30,000). For some individuals with evidence of contamination, we analysed only sequences with terminal damage to enrich for genuine ancient DNA using pmdtools, allowing us to study more individuals49. We do not include in our main analyses data from 71 individuals that failed our authenticity criteria (marked as “QUESTIONABLE” in Supplementary Table 1); however, we publish the data as part of this study as a resource. A total of 97 of the 1020 libraries newly reported for this study are also indicated as “QUESTIONABLE” by these criteria."
Replication	Only a single library can be made from each extract aliquot so no replication from the same extract is possible. However, the data from the 1020 newly reported libraries came from 826 distinct individuals. For the individuals with more than one library, we had internal replication confirming that the libraries were from the same individuals. Another measure of replication also derives from the fact that the ancestry distributions in individuals from the same periods tended to be very similar. As a result of this, key findings in this study are not dependent on single samples. Thus, key findings such as the increase in EEF ancestry in the LBA and IA in Britain, or in the millennium-earlier rise in frequency of the allele conferring lactase persistence in Britain than in Central Europe, are not dependent on single samples.
Randomization	Historical studies are retrospective rather than prospective -- and the actual trajectory of human history has occurred only once -- so randomization of the data into independent processes is not possible. The text contains a caveat about possible biases due to non-random sampling. Specifically, we write: "We considered the possibility that the rise in EEF ancestry in southern Britain was due to a resurgence of archaeologically less visible populations with more ancestry from people living in Britain in the Neolithic, which we could have missed either due to geographic biases in sampling, or variation across cultural contexts in the way groups treated their dead for example through use of cremation. However, models of IA populations of England and Wales as a mixture of groups in Neolithic and C/EBA Britain failed at high significance (Extended Data Fig. 1) due to IA populations sharing more affinity to with some Neolithic populations from continental Europe than they did with Neolithic groups in Britain, implying the arrival of ancestry not present in earlier periods (Supplementary Information section 3). The most plausible explanation is migration into southern Britain in the M-LBA.”
Blinding	Co-analysis of the genetic and archaeological data was central to the study, so we could not be blind to the sample identity.

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study
☒	☐ Antibodies
☒	☐ Eukaryotic cell lines
☐	☒ Palaeontology and archaeology
☒	☐ Animals and other organisms
☒	☐ Human research participants
☒	☐ Clinical data
☒	☐ Dual use research of concern

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging

Palaeontology and Archaeology

Specimen provenance

We describe the provenance of all archaeological specifmens in Supplementary Table 1 and Supplementary Information section 1.

Specimen deposition

The bone and tooth parts that remain after analysis for ancient DNA are under the stewardship of the archaeologists and cultural institutions from which they were sampled. At present, they are either already returned to the sample stewards or they are stored on long-term loan at the ancient DNA laboratories where they were analysed. They can be re-examined upon request to the sample stewards. Researchers who wish to replicate analyses from this study or gather new data on the libraries generated for this study are welcome to make a request for aliquots of those libraries to corresponding author David Reich who will fulfill all reasonable requests.

Dating methods

We carried out Accelerator Mass Spectrometry (AMS) radiocarbon dating at a variety of laboratories (n=81 at SUERC, n=40 at PSUAMS, n=1 at BRAMS, and n=1 at Poz). The details of the experimental process used for dating are presented in Supplementary Table 4 along with quality control measurements and specification of the protocol type used (XAD amino acids or >30kDa gelatin). We refer readers to the individual laboratories for the experimental protocols. We calibrated all dates using OxCal 4.4.2 and IntCal20.

☒ Tick this box to confirm that the raw and calibrated dates are available in the paper or in Supplementary Information.

Ethics oversight

All human skeletons analysed in this study were sampled with written permission of the stewards of the skeletons and every individual is represented by at least one co-author. Researchers who wish to obtain further information about specific individuals should write to the corresponding authors and/or the authors who provided the archaeological contextualisation for those individuals whose names are specified in Supplementary Material section 1.

Note that full information on the approval of the study protocol must also be provided in the manuscript.