

Large-Scale Migration into Southern Britain During the Middle to Late Bronze Age

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1 **Present-day populations from England and Wales harbour more ancestry derived from**
2 **Early European Farmers (EEF) than did people of the Early Bronze Age. To study how**
3 **this occurred, we generated genome-wide data from 803 individuals, almost all from the**
4 **Middle to Late Bronze Age and the Iron Age, increasing data in this period from Britain**
5 **by 12-fold, and from Western and Central Europe by more than two-fold. Between 1000-**
6 **875 BCE, EEF ancestry increased in southern Britain (England and Wales) but not in**
7 **northern Britain (Scotland), due to incorporation into the population of a stream of**
8 **migrants who arrived at this time and in previous centuries and who were genetically most**
9 **similar to ancient individuals from France. These migrants cumulatively contributed**
10 **about half the ancestry of Iron Age people of England and Wales, thereby documenting a**
11 **previously unknown demographic process that is a plausible vector for the spread of early**
12 **Celtic languages into Britain. These patterns are part of a broader trend of EEF ancestry**
13 **proportions becoming more similar across Central and Western Europe in the Middle to**
14 **Late Bronze Age, coincident with intensification of cultural exchange and highlighting this**
15 **period as a peak of interaction and mobility. We find no evidence of a comparable rate of**
16 **migration into Britain in the Iron Age. The distinct genetic trajectories of Britain and**
17 **continental Europe in the Iron Age are also exemplified by the fact that the allele**
18 **conferring lactase persistence rose to ~50% frequency in Britain by this time whereas it**
19 **was only ~7% in Central Europe and underwent a comparable rise in frequency only a**
20 **millennium later, a pattern that could only occur if there were qualitative differences in**
21 **how dairy products were used in Britain and in Central Europe.**

22 “Migration” is a central concept in both population genetics and archaeology, but its meaning
23 has evolved in divergent ways in the course of the development of these disciplines¹. Population
24 geneticists use “migration” to refer to any movement of genetic material from one region to
25 another, but from an archaeological perspective this can be too broad, since this definition
26 would see even low-level symmetrical exchanges of mates between adjacent communities as
27 representing migration. Archaeologists generally use “migration” to refer to processes that
28 result in significant demographic change due to directed and permanent translocation of people
29 from one region to another^{2,3}. In European archaeology, discussions of prehistoric migrations
30 have become fraught due to the ways in which theories of migration were exploited for political
31 purposes in the early-mid twentieth century—when movement of large numbers of people over
32 a short period of time was sometimes argued to be a primary mechanism for the spread of ethnic
33 groups⁴ and archaeological reconstructions of such events were used to justify claims on
34 territory⁵. Setting a high bar for theorizing migration, however—for example by only using it

35 when there is clear evidence for organized movements of people over a short period of time—
36 minimizes the important effects that cumulatively large-scale movements are likely to have had
37 in shaping prehistory², such as the westward migration of people from the Steppe beginning in
38 the third millennium BCE that genetic data have unambiguously shown contributed much of the
39 ancestry of later Europeans including eventually people from Britain^{6,7,8,9}. We emphasize that
40 the large-scale Middle to Late Bronze Age migrations we document here unfolded over
41 hundreds of years as attested by our radiocarbon dating data and so cannot all be explained by
42 movement over a short time.

43 Whole genome ancient DNA studies have shown that the first Neolithic farmers of the island of
44 Great Britain (hereafter Britain) who lived 3950-2450 BCE derived roughly 80% of their
45 ancestry from Early European Farmers (EEF) who originated in Anatolia more than two
46 millennia earlier, and 20% from Mesolithic hunter-gatherers (Western European Hunter-
47 Gatherers: WHG)⁸⁻¹⁰. The WHG ancestry in the first British farmers was almost entirely due to
48 admixture in continental Europe, indicating that migrants in the Neolithic brought this WHG
49 ancestry with them and local WHG contributed negligibly to the ancestry of later people in
50 Britain. The Neolithic population of Britain was genetically similar to, and almost certainly
51 derived from, contemporaneous populations from continental Europe, especially Iberia and
52 France. This ancestry profile remained stable for about a millennium and a half. From around
53 2450 BCE, the onset of the Chalcolithic period, there was another substantial movement of
54 people into Britain (minimum 90% of ancestry from the new migrants) coinciding with the
55 spread of Bell Beaker traditions from continental Europe which brought a third major
56 component: ‘Steppe ancestry’ derived originally from people living on the Pontic-Caspian
57 Steppe ~3000 BCE⁸. In the original study⁸ reporting this ancestry shift in Britain, no significant
58 average change in the proportion of EEF ancestry was detected from the Chalcolithic/Early
59 Bronze Age (C/EBA; 2450-1550 BCE), through the Middle Bronze Age (MBA; 1550-1150
60 BCE) and Late Bronze Age (LBA; 1150-750 BCE), to the pre-Roman Iron Age (IA; 750 BCE-
61 43 CE). However, that study contained little data after 1300 BCE (Figure 1). Today, however,
62 EEF ancestry is significantly higher on average in southern Britain (defined here as England and
63 Wales although we recognize modern boundaries are arbitrary) than in northern Britain
64 (Scotland), raising the question of when this increase in EEF ancestry occurred^{8,11}. The rise in
65 EEF ancestry in England and Wales cannot be explained by migration from northern continental
66 Europe in the early medieval period^{12,13}, as early medieval migrant groups harboured less EEF
67 ancestry than was present in Bronze Age Britain and hence would have decreased EEF ancestry
68 instead of increasing it as we observe⁸.

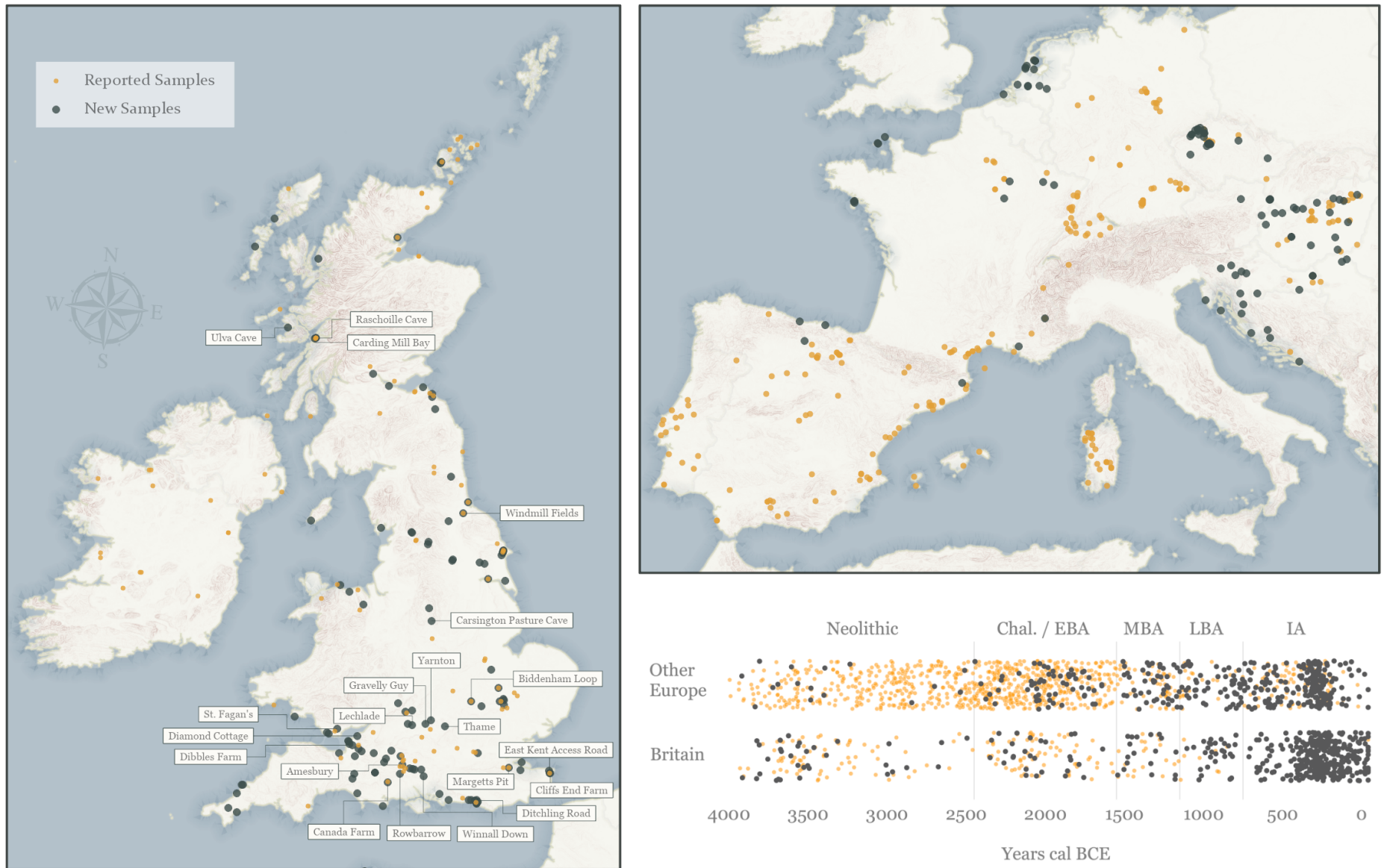
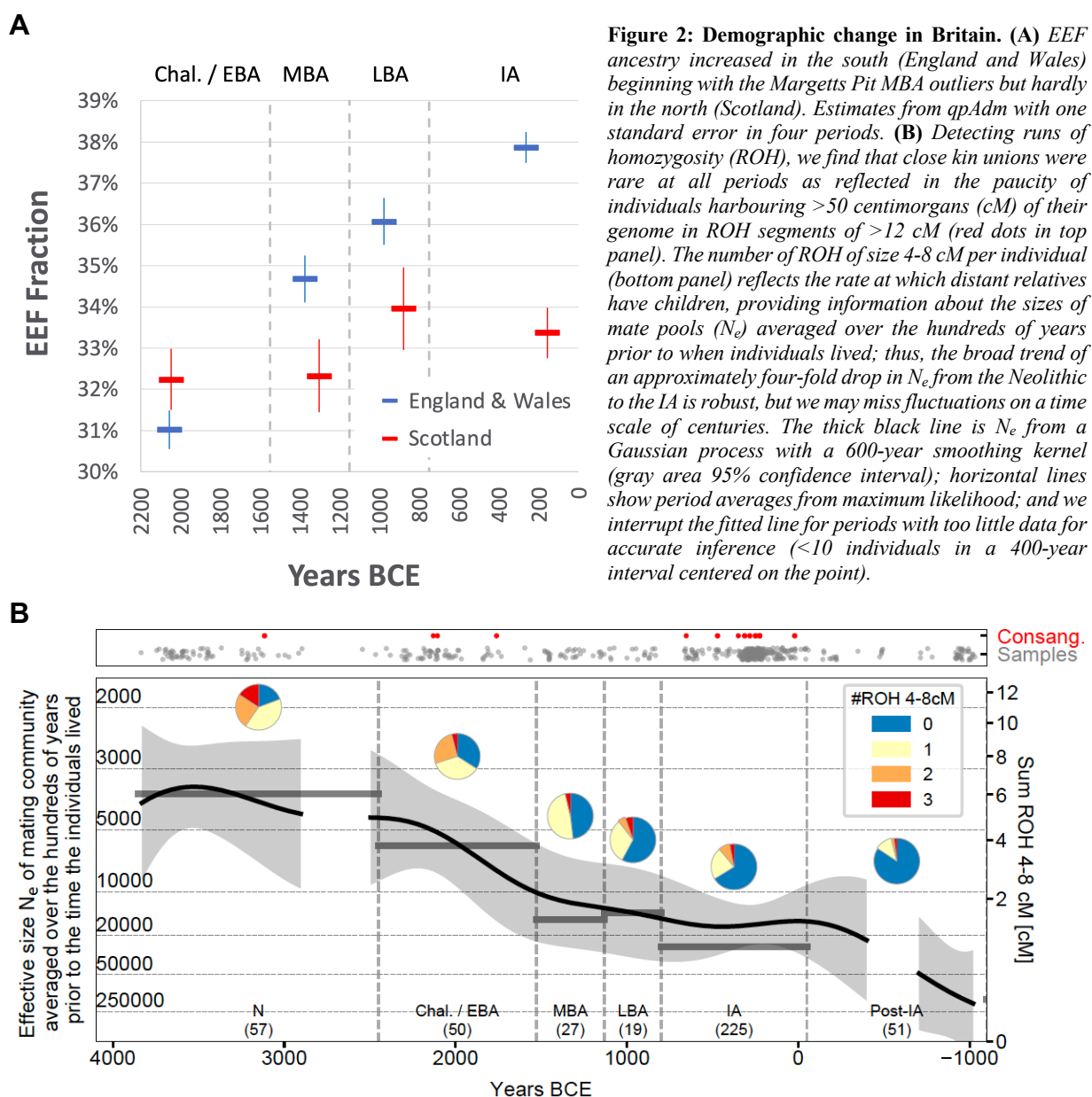


Figure 1: Ancient DNA Dataset. Geographic distribution of sites and temporal distribution of individuals in the period 4000 BCE-43 CE. Newly reported data are in black; published data are in orange. In the map of Britain we label sites that harbour individuals who are ancestry outliers relative to others of the same period. In the timeline we denote the archaeological periods according to the British chronology: Neolithic (3950-2450 BCE), Chalcolithic and Early Bronze Age (C/EBA, 2450-1550 BCE), Middle Bronze Age (MBA, 1550-1150 BCE), Late Bronze Age (LBA, 1150-750 BCE), and pre-Roman Iron Age (IA, 750 BCE-43 CE). To aid visualisation, we add jitter on the Y axis and randomly sample dates from their probability distributions given in Online Table 1.

69 We generated new ancient DNA data from 426 previously unanalysed individuals from Britain,
70 increasing the number of pre-Roman individuals to 608 and multiplying by 28-fold the number
71 from the combined period of the LBA and IA (from 13 to 365) (Fig. 1, Supplementary
72 Information section 1, Online Table 1). We also report data from previously unanalysed ancient
73 individuals mostly dating to the LBA and IA from the Czech Republic ($n=160$), Hungary
74 ($n=54$), France ($n=52$), the Netherlands ($n=28$), Slovakia ($n=25$), Croatia ($n=21$), Slovenia
75 ($n=14$), Spain ($n=10$), Serbia ($n=8$) and Austria ($n=3$). We increased data quality on 33
76 previously published individuals (Online Table 1). To generate these data, we prepared powder
77 from bones and teeth, extracted DNA¹⁴⁻¹⁶, and generated 1033 sequencing libraries all
78 pretreated with the enzyme uracil-DNA glycosylase to reduce characteristic cytosine-to-thymine
79 errors of ancient DNA (Online Table 2)^{14,15,17}. We enriched libraries in solution and sequenced
80 them.¹⁸⁻²⁰ We co-analysed with previously reported data for a total of 5928 ancient and present-
81 day individuals (Online Table 3). We clustered by time and geography aided by 126 newly
82 reported radiocarbon dates (Online Table 4). We separately labelled individuals that were
83 significantly different in ancestry from the majority cluster from each time period and region
84 (Supplementary Information section 2, Online Table 5). Although we report data from all
85 individuals, we removed a subset from the main analysis: those with evidence of contamination
86 based on finding variation in parts of their genome where they are expected to have DNA from
87 only one parent^{21,22}, those with a rate of damage in the final nucleotide lower than is typical for
88 authentic ancient DNA¹⁵, those that were first degree relatives of other higher coverage
89 individuals in the dataset²³, or those that had too little data for accurate ancestry inference
90 (<30,000 single nucleotide polymorphisms (SNPs) covered at least once) (Online Table 5).
91 Figure 1 shows a map of analysed individuals. We identified 127 individuals from 50 families
92 as related (within the third degree) to at least one other newly reported individual in the dataset
93 (Online Table 6).

94 We computed symmetry- f_4 statistics^{24,25} between all pairs of temporal groupings of individuals
95 in Britain, testing for differences in the rate of allele sharing (genetic drift) with the two major
96 source populations (Steppe and EEF); we computed standard errors using a Block Jackknife.
97 We document a significant increase in the degree of allele sharing with EEF populations in
98 England and Wales over the Middle to Late Bronze Age (M-LBA) and into the IA (Extended
99 Data Table 1). To estimate the proportions of EEF, Steppe, and WHG ancestry in any “Target”
100 population²⁶, we leveraged the fact that the magnitudes of f_4 -statistics can be interpreted in
101 terms of mixture fractions. Specifically, $qpAdm$ models the f_4 -statistics in each “Target”

102 population as a linear combination of the f_4 -statistics in populations we use as proxies for the
 103 mixing “Sources.” *qpAdm* computes statistics of the form $f_4(\text{Target}, \text{Source}_i; \text{Outgroup}_j,$
 104 $\text{Outgroup}_k)$ that compare Target and Sources to a set of four “Outgroups” that we optimized to
 105 provide more precise estimates of ancestry proportions than previous *qpAdm* setups
 106 (Supplementary Information section 2). Here, our proxies for the “Sources” are 22 early Balkan
 107 Neolithic farmers with minimal hunter-gatherer admixture (EEF); 20 Yamnaya and Poltavka
 108 pastoralists (Steppe); and 18 Mesolithic hunter-gatherers from across Western Europe (WHG).



109 Applying *qpAdm* to our data, we find that EEF-related ancestry increased in England and Wales
 110 from $31.0 \pm 0.5\%$ in the C/EBA ($n=69$), to $34.7 \pm 0.6\%$ in the MBA ($n=26$), to $36.1 \pm 0.6\%$ in the
 111 LBA ($n=23$), and stabilized in the IA at $37.9 \pm 0.4\%$ ($n=273$) (here and below, we quote one

112 standard error). There is no statistically significant change in Scotland (Figure 2 and Extended
 113 Data Table 1). EEF ancestry was widespread in southern Britain by the IA, averaging 36.0-
 114 38.8% in eight regions of England (Table 1, Extended Data Table 2) (IA Wales sample sizes are
 115 too small to provide accurate inference). Within England, EEF ancestry proportions inferred
 116 over the mostly later IA individuals do not correlate to latitude (Table 1). We considered the
 117 possibility that the rise in EEF ancestry in southern Britain was due to a resurgence of
 118 archaeologically less visible populations with more ancestry from people living in Britain
 119 during the Neolithic. However, our attempts to model IA populations of England and Wales as a
 120 mixture of groups who lived in Neolithic and C/EBA Britain failed at high significance
 121 (Extended Data Figure 1). This is due to LBA and IA populations in Britain sharing excess
 122 alleles with Neolithic populations from continental Europe not seen in earlier groups from
 123 Britain (Supplementary Information section 3). The most plausible explanation is migration
 124 from outside Britain into southern Britain in the M-LBA.

125 We modelled each individual from Britain using *qpAdm*, labelling significant ancestry outliers
 126 relative to most individuals of their period as candidates for migrants or their recent descendants
 127 (Figure 3, Extended Data Figure 2). We discuss each group of outliers from earliest to latest.

Table 1: Regional variation in ancestry in Iron Age Britain

Region	N	Lat- it- ude	Modeling Ancestry With Pre-Bronze Age Sources			Modeling Ancestry with Middle to Late Bronze Age Sources		
			P- value	WHG	EEF	Steppe	P- value	Margetts Pit and Cliffs End Farm-like ancestry
Scotland Orkney	2	59	0.22	14.2 ± 1.1%	34.1 ± 1.2%	51.6 ± 1.6%	0.10	20 ± 9%
Scotland West	4	58	0.12	13.0 ± .8%	32.3 ± 1.0%	54.7 ± 1.2%	0.19	8 ± 7%
Scotland Southeast	12	56	0.67	12.1 ± .6%	33.9 ± .7%	54.0 ± .9%	0.39	16 ± 5%
England North	10	54	0.35	13.4 ± .6%	36.3 ± .8%	50.3 ± 1.0%	0.76	35 ± 5%
England East Yorkshire	47	54	0.61	13.2 ± .4%	37.0 ± .5%	49.8 ± .6%	0.86	44 ± 4%
England Midlands	18	53	0.66	12.6 ± .5%	36.0 ± .6%	51.4 ± .8%	0.77	36 ± 4%
England Southwest	84	53	0.30	13.7 ± .4%	38.7 ± .4%	47.6 ± .6%	0.56	55 ± 5%
England East Anglia	21	52	0.44	13.5 ± .5%	37.0 ± .5%	49.5 ± .7%	0.52	44 ± 4%
England Southcentral	38	52	0.32	13.9 ± .4%	38.8 ± .5%	47.2 ± .6%	0.35	56 ± 5%
England Southeast	3	51	0.13	13.9 ± .5%	38.3 ± .5%	47.8 ± .6%	0.40	52 ± 5%
England Cornwall	16	50	0.40	13.5 ± .5%	36.4 ± .7%	50.1 ± .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%
Wales South	2	51	0.66	14.2 ± 1.2%	38.6 ± 1.5%	47.2 ± 1.8%	0.57	53 ± 11%

Notes: Regions are ordered first by large grouping (Scotland-England-Wales), then reverse order of latitude. For modeling ancestry with pre-Bronze Age sources the right set is (OldAfrica, WHG, Balkan_N, OldSteppe); for modeling of ancestry with M-LBA sources it is 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, Spain.Portugal_6500.to.4425BP. We separate "England East Yorkshire" from "England North" because of East Yorkshire's distinctive cultural context (Arras).

128 First, replicating previous results^{8,10}, we infer a cluster of Neolithic individuals from western
 129 Scotland with high WHG admixture, likely reflecting unions between recent migrants from
 130 Europe and descendants of local Mesolithic groups in Britain (Extended Data Figure 2).

131 Second, we infer high variability in EEF ancestry in the C/EBA, before EEF ancestry became
132 relatively homogeneous after ~2000 BCE⁸ (Figure 3). This is apparent at Amesbury Down
133 where EEF ancestry in some burials is significantly below the average of 29.9±0.4% (e.g. I2417
134 at 22.2±1.8%), and in others above the group average (e.g. I2416 at 47.7±2.2% and I14200 at
135 45.3±2.2%). The low EEF group are plausibly Beaker-period migrants who mixed with local
136 Neolithic farmers to produce the intermediate EEF ancestry that prevailed by the end of the
137 EBA. Within the Beaker-associated burials, individual I14200 with elevated EEF ancestry is
138 known as the “Amesbury Archer”. He was buried in the most well-furnished grave recovered
139 from the Stonehenge mortuary landscape, and his isotopic profile indicates he spent parts of his
140 childhood outside Britain, possibly in the Alps²⁷. The fact that the Archer was a migrant but had
141 too little Steppe ancestry to be from the population that drove Steppe ancestry to the high level
142 observed in C/EBA Britain, shows that Bell Beaker-associated migrants to Britain were not
143 from a homogeneous population. The ‘Companion’ (I2565), a burial found next to the Archer
144 whose isotopic profile like most others at the site is consistent with a local upbringing, was not
145 an ancestry outlier for C/EBA Britain (32.7±3.0% EEF; P=0.47 for consistency with the period
146 average; Figure 3). The Archer and the Companion shared a rare tarsal morphology and similar
147 grave goods that have been hypothesized to reflect a close genetic relationship (Supplementary
148 Information section 4)²⁸, but our results rule out first- or second-degree genetic relatedness.

149 Third, we observe four outliers with high EEF ancestry in the late MBA and LBA who are
150 candidates for being first generation migrants or the offspring of recent migrants from
151 continental Europe, all of whom were buried in Kent in the southeasternmost part of Britain.
152 The earlier two are from the site of Margetts Pit: 47.8±1.8% in individual I13716 (1391-1129
153 calBCE) and 43.6±1.8% ancestry in I13617 (1214-1052 calBCE). The latter two are from Cliffs
154 End Farm: 43.2±2.0% in individual I14865 (967-811 calBCE) and 43.4±1.8% in individual
155 I14861 (912-808 calBCE). We considered the possibility that we are observing the effect of a
156 short burst of migration in the MBA, explaining the Margetts Pit outliers, followed by co-
157 existence of separate communities with different proportions of EEF ancestry for at least a
158 couple of hundred years, thereby explaining the Cliffs End Farm outliers. However, strontium
159 and oxygen isotope analyses identify multiple individuals of non-local origin at Cliffs End
160 Farm²⁹ including the genetic outlier I14861, suggesting that the stream of migrants continued
161 into the second half of the LBA (Supplementary Information section 5).

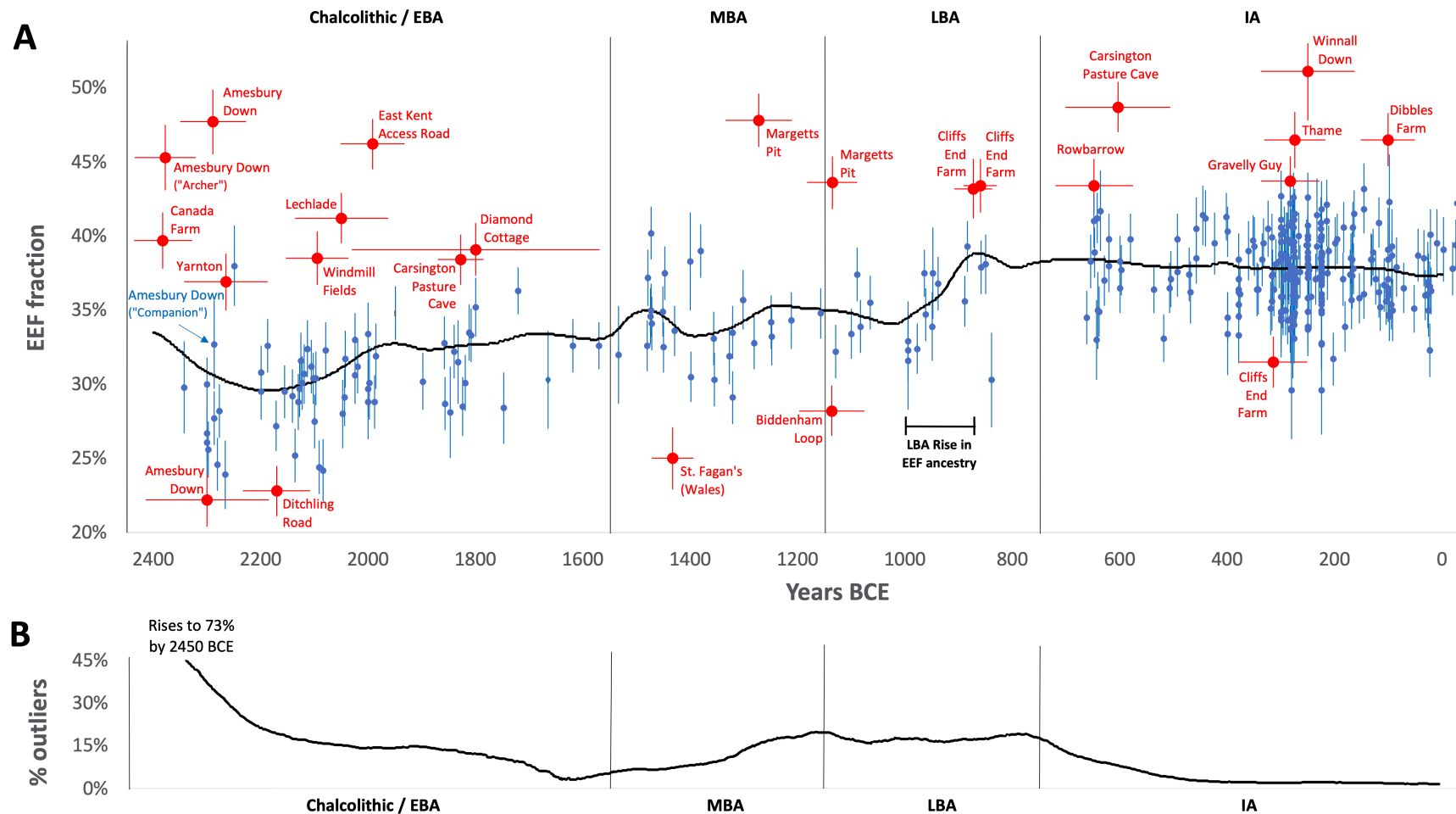


Figure 3: By-individual analysis of the England and Wales time transect. (A) Estimates of EEF ancestry and one standard error for all individuals that fit a three-way admixture model (EEF + WHG + Yamnaya) at $p > 0.01$ using *qpAdm* and date to 2450 BCE–43 CE (we plot the mean of the posterior interval of the ^{14}C date or the mean of the archaeological context range). Most individuals are shown in blue while significant outliers at the ancestry tails are in red with a horizontal error bar to show one standard error for the date (outliers are identified either 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 $|Z| > 3.5$) (Online Table 5). Outliers like the four MBA and LBA individuals at Margetts Pit and Cliffs End Farm fit as the source for the increase in EEF ancestry in the IA. The black line shows an estimate of population-wide EEF ancestry proportion at each time obtained by weighting each individual's EEF estimate by the inverse square of their standard error as well as the probability that their date falls at each point in time (based on the date mean and error given in Online Table 5; we filter out individuals with date errors > 120 years). The incorporation of increased EEF ancestry into the majority of samples occurred ~ 1000 – 875 BCE. **(B)** Proportion of outliers measured over 300-year sliding windows centered on each point; to estimate this we randomly sample dates of all individuals 100 times assuming normality and their mean and standard deviation in Online Table 5 (we remove individuals with EEF errors > 0.022 and date standard errors > 120 years). Major periods of migration into Britain are evident as periods when elevated proportions of individuals are outliers: between 2450–1800 BCE (17% outliers) and 1300–750 BCE (17% outliers again). Our ability to temporally resolve the period of outliers is poorer than our ability to resolve the period of incorporation of increased EEF ancestry into the broader population; thus, for example, the earliest outlier with elevated EEF ancestry in the M-LBA at Margetts Pit 113716 could have died as late as 1129 BCE based on the uncertainty of her ^{14}C date.

162 Fourth, the fraction of individuals whose ancestry is significantly different from the main group
163 is 17% over the first part of the C/EBA (2450-1800 BCE), much lower at 4% from the end of
164 the EBA through the beginning of the MBA (1800-1300 BCE), high again at 17% between the
165 end of the MBA through the LBA (1300-750 BCE), and low again at 3% through the IA (Figure
166 3). This is consistent with two major periods of migration into southern Britain in the
167 Chalcolithic and then again in the M-LBA. We considered the possibility that our failure to
168 observe a high rate of outliers in the IA compared with the immediately preceding period was
169 because ancestry had homogenized to an extent between northern and southern Europe by this
170 time, which could make outliers more difficult to detect. However, the average EEF ancestry in
171 Britain in the IA was $37.9 \pm 0.4\%$, which is substantially different from much of contemporary
172 Western and Central Europe— $52.6 \pm 0.6\%$ in Iberia, $49.8 \pm 0.4\%$ in Austria, Hungary, and
173 Slovenia, $45.4 \pm 0.5\%$ in the Czech Republic, Slovakia and Germany, $45.6 \pm 0.5\%$ in France and
174 Switzerland, and $34.4 \pm 1.2\%$ in the Netherlands (Figure 4A)—which would have made the
175 majority of migrants from these regions detectable given the small standard errors in most
176 individual ancestry estimates of $<2\%$ (Online Table 5). Our sampling from western France and
177 Belgium is poor, and it is possible that EEF ancestry proportions there were similar to Britain,
178 so we cannot rule out migration from this region in the IA. Nevertheless, the lack of a change in
179 EEF ancestry proportion in the IA is consistent with reduced migration from continental Europe
180 and suggests relatively closed and self-sustaining social communities in Britain during the IA³⁰.

181 Demographic change in Britain over our period of study is also evident from another aspect of
182 the data: the rate of observations of runs of homozygosity (ROH), which can occur when a
183 person's parents are relatively closely related. The larger the pool of people from which
184 individuals draw their mates, the less likely it is for parents to be closely related, and thus we
185 can average the number of 4-8 centimorgan (cM) ROH segments to estimate the effective size
186 of the pool of people within which people were mating in the ~600 year period prior to the time
187 when the analysed individuals lived³¹. We find that the size of the mating pool increased by
188 roughly four-fold from the Neolithic to the IA, but we caution that this inference should not be
189 interpreted as an estimate of population size changes over this period as mating pool sizes are
190 also affected by changing social customs. First, if the distance over which people ranged to find
191 their mates was higher in some cultural contexts than in others it would cause the mating pool
192 sizes to be different even if there was no difference in actual population size; for example,
193 mating pool size may be less than the island-wide population size if members of communities
194 mixed little with their neighbours as is plausible in the British IA where there was high regional

195 variation in material culture³⁰, or larger if individuals mated not only with people outside their
196 local communities but also outside Britain. Second, we have a major gap in sampling at the end
197 of the Neolithic (roughly 3000-2450 BCE) and thin sampling at the beginning of the IA, which
198 means that demographic processes in these periods may be missed. Third, due to the method
199 effectively averaging over centuries, this analysis may also fail to detect major population
200 declines over the space of a few decades, if these were followed by rapid population recovery.
201 Future work that complements measurement of changing degree of parental relatedness over
202 time with estimates of changing degree of relatedness of individuals across communities³²
203 should make it possible to examine how much of this signal of increasing size over time was
204 driven by true growth in population size, and how much by increasing rates of gene exchange
205 across geographically dispersed communities.

206 We co-analysed our ancient DNA time transect in Britain alongside European transects (Figure
207 4A, Online Tables 5 and 7). Average EEF ancestry increased in this period in North-Central
208 Europe and the Netherlands, just as in Britain. The first individuals from North-Central Europe
209 (Czech Republic/Slovakia/Germany) with greatly increased EEF ancestry are associated with
210 artefacts traditionally classified as part of the LBA Knoviz culture, a component of the broader
211 Urnfield cultural complex (1300-800 BCE) that spread across much of Central Europe. This is
212 especially striking as the Knoviz individuals are genetically consistent with being from a very
213 similar population as the Margetts Pit and Cliffs End Farm outliers (Supplementary Information
214 section 6). Later individuals in North-Central Europe have similar EEF proportions, consistent
215 with continuity through the LBA-IA with earlier Urnfield-associated groups. By contrast, in
216 MBA and LBA France/Switzerland and South-Central Europe (Austria/Hungary/Slovenia) there
217 was little change in average EEF ancestry, while EEF ancestry decreased in MBA and LBA
218 Iberia (Spain/Portugal). There are also two exceptions to this broad European pattern of
219 ancestry convergence in Europe—Scotland in the far north, and Sardinia in the far south^{33,34}—
220 both of which have extreme proportions of EEF ancestry (Scotland low and Sardinia high)
221 relative to the European average across this period (Online Table 7).

222 Placing Britain within the broader context of Europe is also illuminating with respect to the
223 frequency trajectories of genetic variants of phenotypic importance. This study multiplies by
224 almost eight-fold the number of IA individuals with genome-wide data from Western and
225 Central Europe (from 80 to 624; Online Table 5), making it possible for the first time to
226 accurately track the frequency change of genetic variants into the IA (Online Table 8). In

227 addition to showing how variants associated with light skin pigmentation, such as *SLC45A2*,
228 became more common in the IA throughout Europe¹⁹, we obtain an unexpected result for the
229 derived allele at the polymorphism *MCM6-LCT* rs4988235 correlated with lactase persistence
230 into adulthood¹⁹ (Extended Data Figure 3). Previous work showed that the frequency of this
231 allele in IA Iberia was only a small fraction of its present-day incidence³⁵, which we confirm by
232 showing that its frequency was ~9% in the IA compared to ~40% today. Similarly, in a pool of
233 individuals from Central Europe (Austria, Hungary, Slovenia, Czech Republic, Slovakia and
234 Germany) its frequency was ~7% in the IA compared to ~48% today. However, in Britain, most
235 of the rise in frequency had occurred by the IA (50% compared to the current 73%), suggesting
236 that intense selection acted earlier and the main rise in frequency occurred about a millennium
237 earlier than in Central Europe (Figure 4B, Extended Data Figure 3). We find no evidence that
238 the main rise in frequency of the lactase persistence allele occurred in continental Europe and
239 that its frequency rise in Britain was due to M-LBA migration. Thus, the Margetts Pit and Cliffs
240 End Farm outliers who are plausible members (or recent offspring) of the migrating population
241 did not carry the allele, and most of its frequency rise in Britain occurred after the M-LBA
242 (Figure 4B, Online Table 8). This raises questions about whether dairy products were consumed
243 in a qualitatively different way or were economically more important in LBA-IA Britain than in
244 Central Europe.

245 The ancestry change in Britain we document during the M-LBA was more subtle than the one
246 that occurred during the Neolithic and Beaker-period migrations. In England and Wales, for
247 example, allele frequency differentiation between the Neolithic and C/EBA was $F_{ST} \sim 0.02$, but
248 between the C/EBA and the IA it was an order of magnitude smaller at $F_{ST} \sim 0.002$ (Extended
249 Data Table 1). The pre-LBA population in Britain also made a substantial genetic contribution
250 to the IA population—its genetic signature was not even close to being completely replaced—
251 which contrasts with the two earlier major Holocene ancestry shifts^{8,10}. Direct evidence for a
252 substantial contribution from the earlier population specifically on the male line comes from Y
253 chromosome haplogroup R1b-P312 L21/M529 (R1b1a1a2a1a2c1), which was present at 89±5%
254 in sampled individuals from C/EBA Britain and has always been nearly absent on the continent
255 (Online Table 9), and today occurs much more frequently in Britain and Ireland (frequency of
256 14-71% depending on region³⁶) than in continental Europe (Extended Data Figure 4).

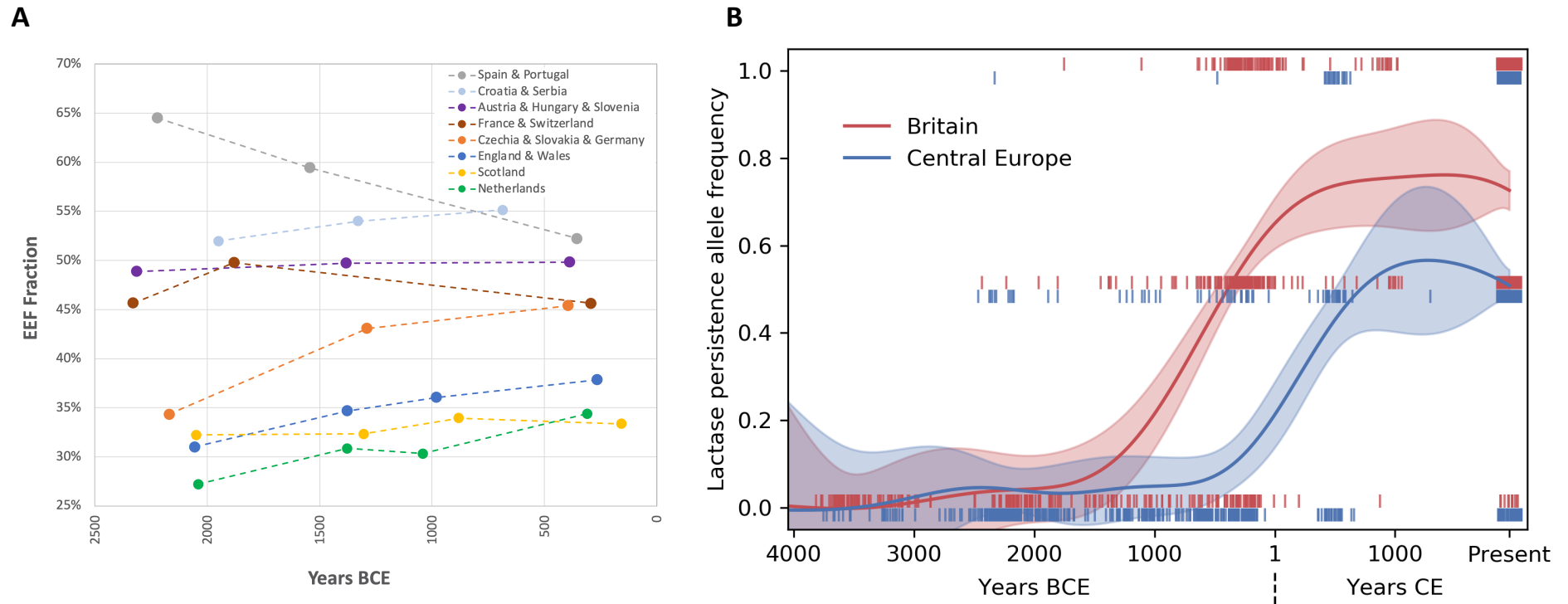


Figure 4: Genetic change in Britain in the context of Europe-wide trends. (A) North-south ancestry convergence. We show eight ancient DNA time transects for up to four periods, using the average of dates of individuals in periods defined for each region as in Online Table 5 (we use the N/C/EBA/MBA/LBA/IA division into archaeological periods for Britain, but avoid using it for most of the rest of Europe because chronological boundaries differ). Dotted lines show which points are regionally grouped and should not be interpreted as implying a smooth change over time. **(B) The allele conferring lactase persistence made its major rise 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.** We visualise the frequency trajectory of the lactase persistence allele at SNP rs4988235 by using the GaussianProcessRegressor function from the Scikit-learn library in Python with parameter $\alpha=0.1$ and $1 \times \text{RationalQuadratic}$ kernel with parameter $\text{length_scale_bounds}=(1, 1000)$. We use the GLIMPSE³⁷ software to impute diploid genotype posterior probabilities (GP), restricting to samples with $\max(\text{GP}) > 0.9$ for this SNP. The analysis includes 459 ancient individuals from Britain and 468 from Central Europe (Czech Republic, Slovakia, Croatia, Hungary, Austria, Germany and Slovenia); to represent modern Britain we use a pool of 190 CEU and GBR individuals from the 1000 Genomes Project³⁸, and to represent modern Central Europe we use 288 individuals from the modern Czech Republic³⁹. Each vertical bar represents the derived allele frequency for each individual with values $[0, 0.5, 1]$; we use jitter on the x-axis for each vertical bar, and we show in shading the inferred 95% confidence interval for the allele frequency at each time point.

257 To gain insight into the possible sources of the ancestry that spread across southern Britain by
258 the end of the LBA, we fit the pooled IA individuals from England and Wales in *qpAdm* as a
259 mixture of a group related to the main C/EBA cluster, and a second source. We tested 65 second
260 sources—63 from continental Europe and 2 from Britain (the Margetts Pit outlier pool, and the
261 Cliffs End Farm outlier pool)—and found that 20 fit at $p > 0.05$; we then pooled the genetically
262 similar Margetts Pit and Cliffs End Farm individuals and performed further *qpAdm* testing with
263 more stringent *qpAdm* setups, leaving eight second sources that consistently fit well with
264 modest standard errors (Table 2, Supplementary Information section 6). The Margetts Pit and
265 Cliffs End Farm pool fit as contributing $49.4 \pm 3.0\%$ of the ancestry of IA southern Britons,
266 providing our best estimate of the degree of genetic turnover. The seven continental populations
267 that fit as sources are estimated to contribute 24-69%; thus, even without results from
268 representatives of the putative source population living in Britain itself, we infer large genetic
269 turnovers. Although only 20% of the continental candidate populations we tested are from
270 France, 86% of the fitting populations are: the fitting populations are four from Occitanie in
271 southern France (600-200 BCE), two from Grand Est in northeastern France (800-200 BCE),
272 and one from Spain (a ~600 BCE group). These fitting second sources all post-date the ancestry
273 change in Britain by hundreds of years and hence they cannot be the true sources; however, they
274 are plausibly descended from earlier local populations. An origin in France is also suggested by
275 the fact that all of the high EEF outliers in Britain in the M-LBA, and all of the 1000-875 BCE
276 individuals that track the ramp-up of EEF ancestry from MBA to IA levels, are from Kent in far
277 southeastern Britain (Extended Data Figure 5). Southwestern individual I12624 from
278 Blackberry Field, Potterne in Wiltshire (950-750 BCE) had a typical EEF proportion for the IA
279 of southern Britain, suggesting the spread of descendants of the migrant stream throughout
280 southern Britain may have already begun by this time, although we caution that this is the only
281 datapoint we have in the second half of the LBA from outside Kent, and so more sampling is
282 needed to understand the geographic and temporal course of the spread of this ancestry. Our
283 data point to the new ancestry being ubiquitous in southern Britain by the beginning of the IA.

Table 2: Populations fitting as proxies for the new ancestry in IA southern Britain

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

284 We can fully explain the significant regional variation in ancestry in IA England and Wales
285 (Table 1 and Extended Data Table 2) as driven by different proportions of ancestry from the
286 population to which the Margetts Pit and Cliffs End Farm individuals belonged, obtaining
287 estimates ranging from 35±5% in northern England to 56±5% in south-central England (Table
288 1). Archaeological data show that the IA was a period when material culture was increasingly
289 regional in character³⁰; as we show here, this was accompanied by subtle genetic structure. We
290 highlight the case of East Yorkshire, where most individuals we analysed are associated with
291 ‘Arras Culture’ contexts comprising square-ditched barrows and occasional chariot burials^{40,41};
292 similarities between Arras funerary traditions and those of IA societies in the Paris Basin and
293 the Ardennes/Champagne regions of France and Belgium have led to suggestions that East
294 Yorkshire was influenced by direct migration from continental Europe in the IA⁴². Our estimate
295 of the Margetts Pit/Cliffs End Farm ancestry source for East Yorkshire burials is 44±4% (Table
296 1) which is typical for middle latitudes of Britain at this time (East Anglia is similar). However,
297 the East Yorkshire burials are distinctive in another way: regional differentiation in IA Britain,
298 as measured by F_{ST} , is higher between East Yorkshire and other groups than between any other
299 pairs of IA populations in England and Wales (Extended Data Table 2). Without ancient DNA
300 from the putative IA sources for the Arras culture in continental Europe, we cannot determine if
301 the genetic differentiation we observe of people in Arras burial contexts is attributable to the
302 subsequent isolation in the IA of the population from the rest of southern Britain, or later
303 streams of migration specifically affecting East Yorkshire that we have limited power to detect.

304 The period from 1500-1150 BCE has long been recognized as a time when cultural connections
305 between Britain and regions of continental Europe intensified, and when societies on both sides
306 of the Channel shared cultural features including domestic pottery, metalwork and ritual
307 depositional practices⁴³⁻⁴⁷. From around 750 BCE there is more limited archaeological evidence
308 of contact between Britain and the continent, with little that would suggest the significant
309 movement of people⁴³. Both the genetic and archaeological data concur in showing that, by the
310 beginning of the IA, there is little evidence of demographically significant migration into
311 Britain. Our findings do not establish whether the population movements we infer were a cause
312 or consequence of M-LBA exchange networks, but they do suggest that interactions between
313 local populations of Britain and new migrants bringing ideas from continental Europe could
314 have been a vector for some of the cultural change we see in M-LBA England and Wales. Much
315 of northern and central France is currently almost entirely unsampled, and thus we cannot at
316 present test if the gene flow between the two regions in this period was largely unidirectional.

317 Population movements are often a significant driver of cultural change, including in the
318 languages people speak. While periods of intense migration such as the one we infer here do not
319 always result in language shifts³⁵, genetic evidence of significant migration is important because
320 it documents demographic processes that are plausible conduits for language spread^{48,49}. Several
321 researchers have interpreted linguistic data as providing evidence for early Celtic languages
322 spreading into Britain from France at the end of the Bronze Age or in the Early Iron Age^{50,51}.
323 Our identification of substantial migration into Britain from sources that best fit populations in
324 France provides an independent line of evidence in support of this, and points to the M-LBA as
325 a prime candidate for the period of this language spread. While the lack of evidence for M-LBA
326 EEF ancestry change in Scotland (Figure 2A) could be interpreted as a concern for the case that
327 Celtic language spread into Britain at this time, in fact a later arrival of Celtic languages in
328 Scotland is entirely consistent with evidence that non-Celtic and Celtic languages coexisted
329 there into the first millennium CE⁵². Our finding of a decrease of EEF ancestry in Iberia, where
330 the proportion was relatively high in the EBA, and a roughly simultaneous increase in Britain
331 where the proportion was relatively low in the EBA (Figure 4a), could, in theory, reflect a
332 Celtic-speaking group of people with intermediate EEF ancestry spreading into both regions,
333 although such a simple model cannot explain all the north-south ancestry convergence in
334 Europe (Supplementary Information section 7); the true gene flows were more complex.
335 Nevertheless, the fact that the Margetts Pit and Cliffs End Farm outliers are genetically very
336 similar to our Knoviz culture sample (Supplementary Information section 6) is striking in light
337 of the fact that some scholars have hypothesized Central European Urnfield groups to have links
338 to Celtic language spread⁵³. In contrast, our failure to find evidence of large-scale migration into
339 Britain from continental Europe in the IA suggests that, if Celtic language spread was driven by
340 large-scale movement of people, it is unlikely to have occurred at this time. The adoption in IA
341 Britain of cultural practices originating in continental Europe—particularly those linked to the
342 La Tène tradition⁵⁴—were also evidently independent of large-scale population movements,
343 although there certainly were smaller movements of people, attested by individual IA outliers
344 with high EEF ancestry such as those at Thame or Winnall Down (Figure 3).

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

349 **Methods**

350

351 **Ancient DNA laboratory work**

352 All ancient human skeletons analysed in this study were sampled with written permission of
353 the stewards of the samples and every sample is represented by at least one co-author.

354 Researchers who wish to obtain further information about specific samples should write to
355 the corresponding authors and/or the authors who provided the archaeological

356 contextualization for those samples in Supplementary Material section 1. In dedicated clean
357 rooms at Harvard Medical School, the University of Vienna, the Natural History Museum in

358 London, and the University of Huddersfield, as well as during sampling trips, we obtained

359 powder from ancient bones and teeth using methods including fine sandblasting, drilling and
360 milling^{55,56}. We extracted DNA using a variety of methods⁵⁷⁻⁵⁹, and prepared double- or

361 single-stranded libraries treated with the enzyme Uracil DNA Glycosylase (UDG) to reduce
362 characteristic errors associated with ancient DNA degradation^{15-17,60}. We enriched these

363 sequences manually or in multiplex using automated liquid handlers for sequences

364 overlapping the mitochondrial genome^{20,61} as well as about 1.24 million single nucleotide

365 polymorphisms (“1240K capture”)¹⁸. We pooled enriched libraries which we had marked

366 with unique 7-base pair internal barcodes and/or 7- to 8-base pair indices and sequenced on

367 Illumina NextSeq500 or HiSeqX10 instruments using paired-end reads of either 76 base pairs

368 or 101 base pairs in length (Online Table 2).

369

370 **Bioinformatic analysis**

371 After trimming barcodes and adapters⁶, we merged read pairs with at least 15 base pairs of

372 overlap allowing no more than one mismatch if base quality was at least 20, or up to three

373 mismatches if base qualities were <20; we chose the nucleotide of the higher quality in case

374 of a conflict while setting the local base quality to the minimum of the two (for these steps we

375 used a custom toolkit at <https://github.com/DReichLab/ADNA-Tools>). We aligned merged

376 sequences to the mitochondrial genome RSRS⁶² or the human genome hg19 (GRCh37,

377 https://www.ncbi.nlm.nih.gov/assembly/GCF_000001405.13/), and aligned these sequences

378 using the *samse* command⁶³ of *BWA* version 0.7.15-r1140 with parameters -n 0.01, -o 2, and -

379 l 16500. After identifying PCR duplicates by tagging all aligned sequences with the same

380 start and stop positions and orientation and in some cases in-line barcodes using Picard

381 MacDuplicates (<http://broadinstitute.github.io/picard/>), and restricting to sequences that

382 spanned at least 30 base pairs, we selected a single copy of each such sequence that had the

383 highest base quality score. For subsequent analysis, we trimmed the last 2 bases of each
384 sequence for UDG-treated libraries and the last 5 for non-UDG-treated libraries to reduce the
385 effects of characteristic errors associated with ancient DNA degradation. We built
386 mitochondrial consensus sequences, determined haplogroups using *HaploGrep*²⁶⁴ and
387 Phylotree version 17, and estimated the match rate to the consensus sequence using
388 contamMix v.1.0-12²¹ when coverage was at least two-fold. To represent the nuclear data, we
389 randomly sampled a single sequence covering each of the 1.24 million SNP targets, and
390 estimated coverage based on the subset of these targeted SNPs on the autosomes. We used
391 *ANGSD* to estimate contamination based on polymorphism on the X chromosome in males
392 with at least 200 SNPs covered twice (males should be non-polymorphic if their data are
393 uncontaminated)²². We automatically determined Y chromosome haplogroups using both
394 targeted SNPs and off-target sequences aligning to the Y chromosome based on comparisons
395 to the Y chromosome phylogenetic tree from Yfull version 8.09 (<https://www.yfull.com/>),
396 providing two alternative notations for Y chromosome haplogroups: the first using a label
397 based on the terminal mutation, and the second describing all the associated branches of the
398 Y chromosome tree based on the notation of the International Society of Genetic Genealogy
399 (ISOGG) database version 15.73. (<http://www.isogg.org>).

400

401 **Determination of ancient DNA authenticity**

402 We determined ancient DNA authenticity based on five criteria. First, we required that the
403 lower bound of the 95% confidence interval for contamination from *ANGSD* (if we were able
404 to compute it) was <1%. Second, we required that the upper bound of the 95% confidence
405 interval for match rate to mitochondrial consensus sequence (if we were able to compute it)
406 was >95%. Third, we required that the average rate of cytosine-to-thymine errors at the
407 terminal nucleotide for all sequences passing filters was >3% for double-stranded partially
408 UDG-treated libraries¹⁵ and >10% for single-stranded USER-treated libraries and double-
409 stranded non-UDG-treated libraries (the latter libraries are all from previously published data
410 that we reanalysed here)⁶⁵. Fourth, we required the ratio of sequences mapping to the Y
411 chromosome to the sum of sequences mapping to the X and Y chromosome for the 1240K
412 data to be less than 3% (consistent with a female) or >35% (consistent with a male). Fifth, to
413 report an individual we required the number of SNPs covered at least once to be at least 5,000
414 (for most actual population genetic analyses, we required at least 30,000). For some
415 individuals with evidence of contamination, we analysed only sequences with terminal
416 damage to enrich for genuine ancient DNA using *pmdtools*, allowing us to study more

417 individuals⁶⁶. We do not include in our main analyses data from 71 individuals that failed our
418 authenticity criteria (marked as “QUESTIONABLE” in Online Table 1); however, we
419 publish the data as part of this study as a resource.

420

421 **Approach to chronological uncertainty**

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

428

429 **Population genetic analyses**

430 We used Principal Component Analysis as implemented in *smartpca* to visualise gradients of
431 ancestry, using the option *lsqproject* to project ancient individuals onto the patterns of genetic
432 variation learned from modern individuals⁶⁷. We computed f_4 -statistics and F_{ST} and carried out
433 *qpWave* and *qpAdm* analyses in ADMIXTOOLS²⁵. We inferred relatives up to the third to fifth
434 degree using a previously described method²³.

435

436 **Allele frequency estimates of variants with functional importance**

437 We clustered individuals into the temporal groups specified in Online Table 5. To estimate
438 the allele frequency of a given SNP in a particular group for Online Table 8, we used
439 sequence counts at each SNP position in each individual and used a maximum likelihood
440 approach¹⁹. We obtained confidence intervals using the Agresti-Coull method implemented
441 in the *binom.confint* function of the R-package *binom*. The imputation-based methodology
442 for studying the trajectory of the lactase persistence allele is described in the Figure 4 legend.

443

444 **Accelerator Mass Spectrometry (AMS) radiocarbon dating**

445 We carried out AMS dating at a variety of laboratories; we refer readers to the individual labs
446 for the experimental procedures. We calibrated all dates using OxCal 4.4.2⁶⁸ and IntCal20⁶⁹.

447

448 **Reporting summary**

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

451 **Data availability**

452 The raw data are available as aligned sequences (bam files) through the European Nucleotide
453 Archive under accession number [to be made available on publication]. Less processed versions
454 of the data (fastq files) are available from the corresponding authors on request, whereas more
455 processed versions of the data (the genotype data obtained by random allele sampling used in
456 analysis) are available at <https://reich.hms.harvard.edu/datasets>. Any other relevant data are
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484 **Author contributions** N.P., I.A. and D.R. conceived the study. N.P., I.O., C.L.-F., P.d.K., I.B.,
485 M.G.T., D.J.K., B.Cun., N.R., R.Pi., I.A., and D.R. supervised the study. T.B., L.Bü., C.-E.F.,
486 O.Ch., S.B., B.A., T.A., K.A., L.A., A.As., C.B.-D., A.Ba., L.Ba., K.B., Z.B., J.Bl., M.Bo.,
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506

507 **Competing interests** The authors declare no competing interests.

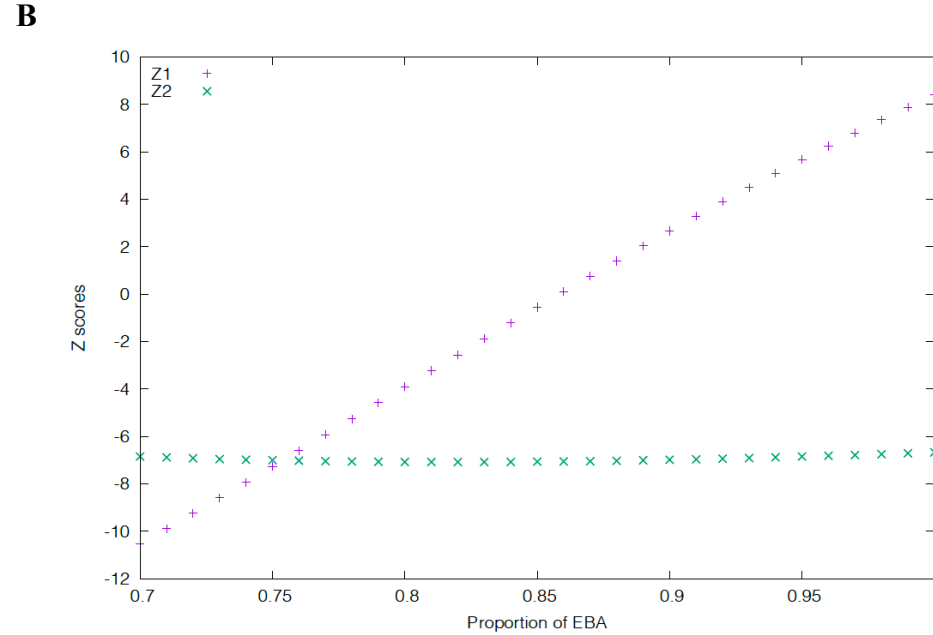
Extended Data Table 2: Fine structure in Iron Age Britain.

	N	<i>qpAdm</i> results (3-way model)						Tests for difference in ancestry between row & column (below diagonal f_4 -statistic Z-score, above-diagonal F_{ST})													
		P-value for <i>qpAdm</i> (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	

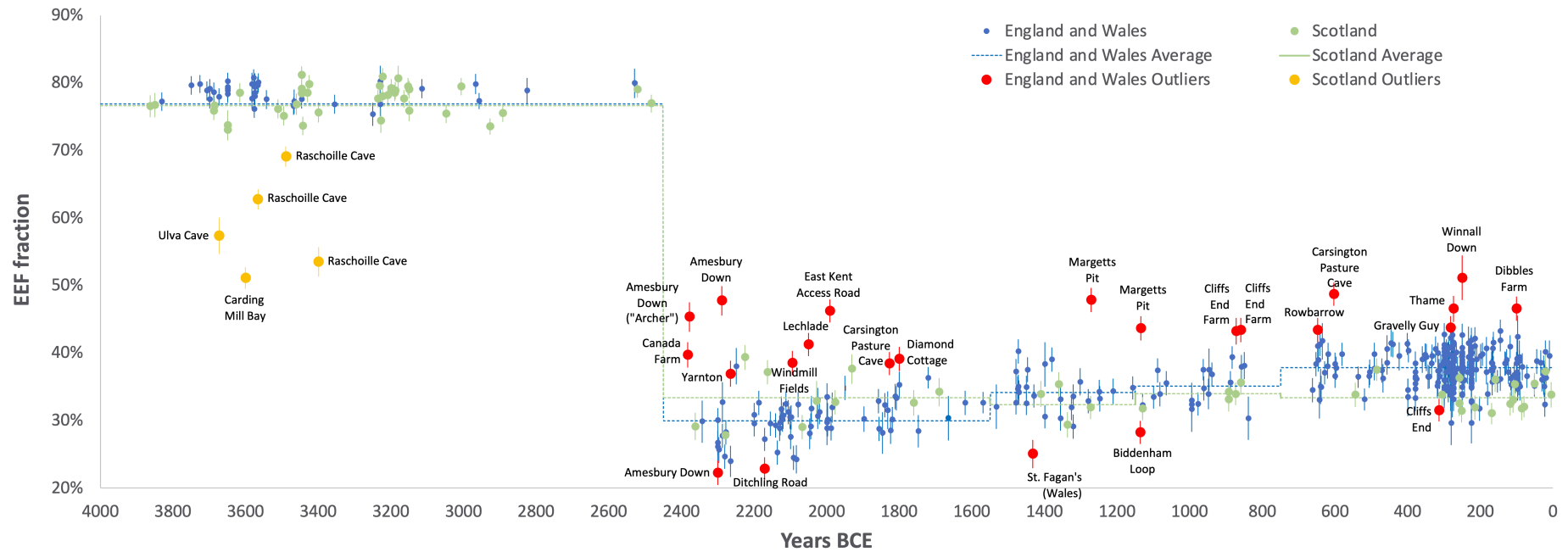
Note: This is an expanded version of Table 1 including not just ancestry estimates for each group but also pairwise population comparisons. We pool all individuals from each period and region removing those failing *qpAdm* modeling at $p < 0.01$ according to Online Table 5). In the left columns are *qpAdm* 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 $F_{ST} > 0.0025$).

A

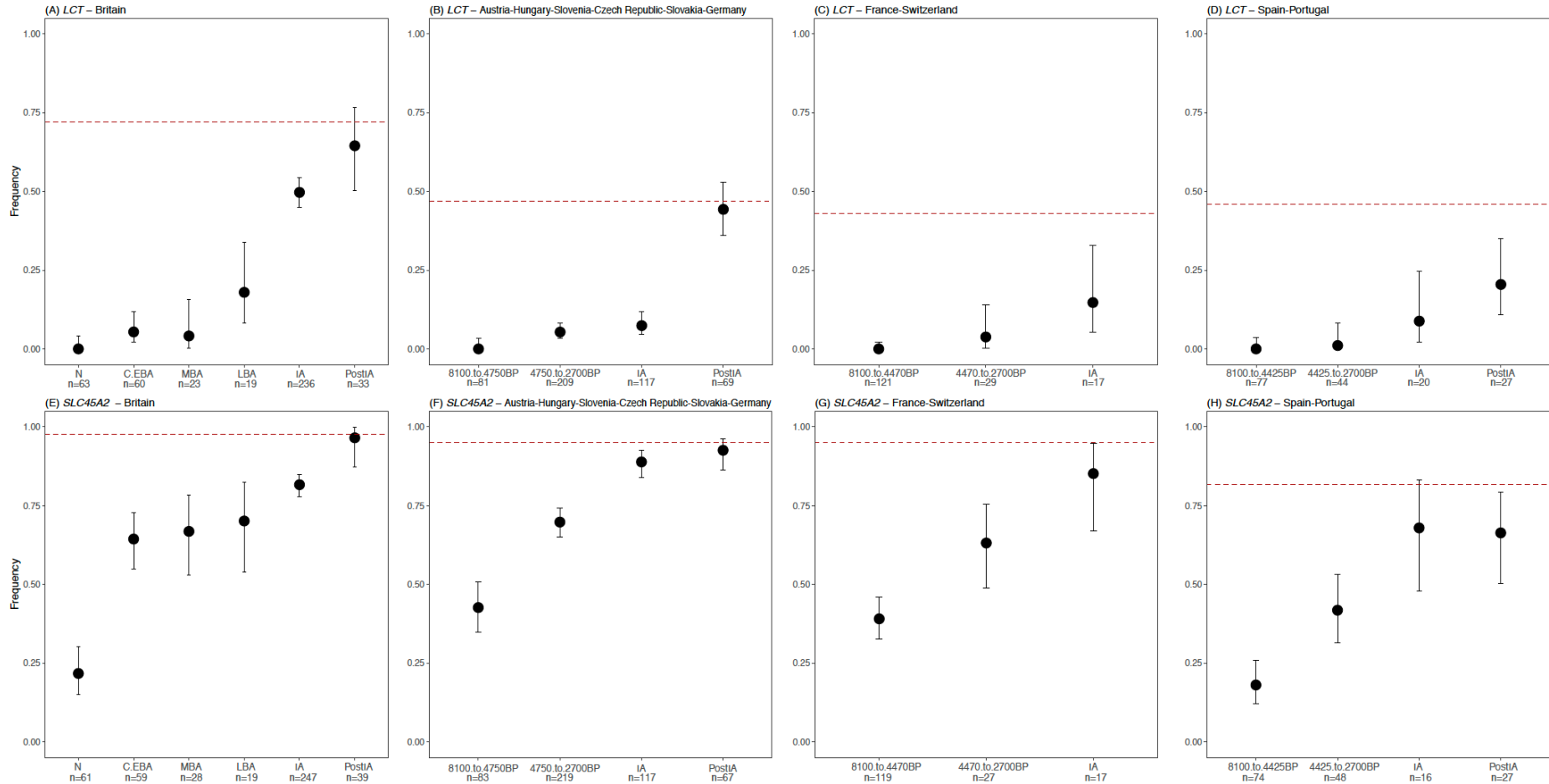
Modeled population	N	Neolithic and C/EBA Groups Used in Modeling	
		England/Wales	Scotland
England/Wales MBA	26	0.34	0.046
England/Wales LBA	23	0.023	0.0074
England/Wales IA	273	<10 ⁻⁶	<10 ⁻⁶
Scotland MBA	5	0.88	0.028
Scotland LBA	4	0.25	0.77
Scotland IA	18	0.0091	0.0028



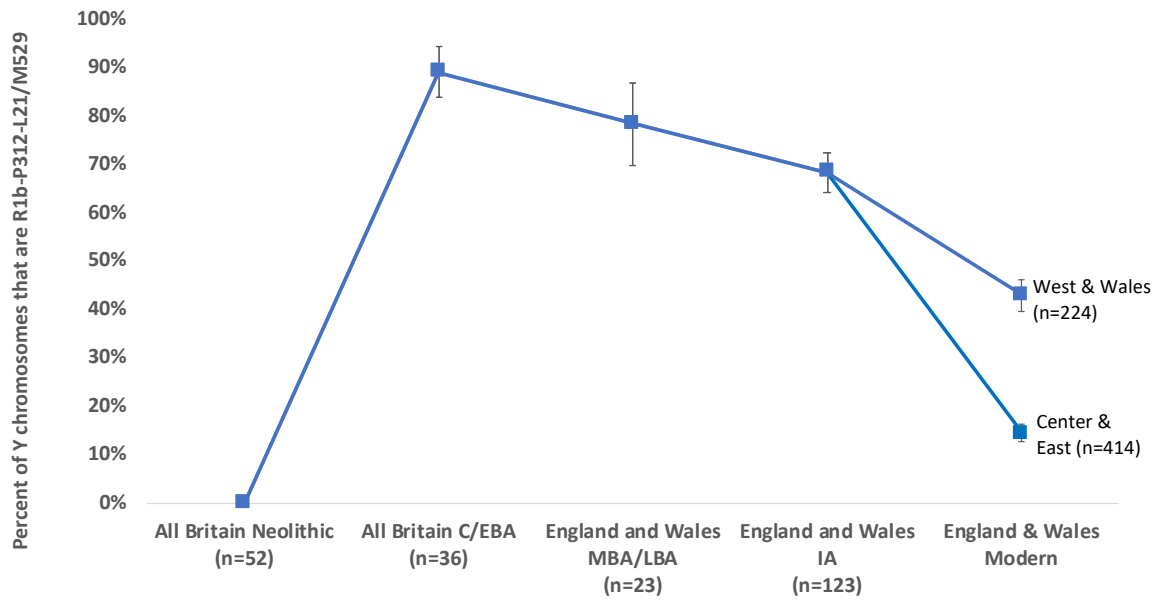
Extended Data Figure 1: Post-MBA Britain was not a mix of earlier British populations. (A) *qpAdm* P-values for modeling British groups as a mix of Neolithic and Chalcolithic/EBA populations from England and Wales, Scotland, or Ireland (outgroups OldAfrica, OldSteppe, Turkey_N, CzechRepublic.Slovakia.Germany_3800.to.2700BP, Netherlands_C.EBA, Poland_Globular_Amphora, Spain.Portugal_4425.to.3800BP, CzechRepublic.Slovakia.Germany_4465.to.3800BP, 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 Online Table 5); we obtain qualitatively similar results when outlier individuals are not removed (not shown). In England and Wales, the main MBA group, and to a marginal extent the main LBA grouping, can be modelled as a mixture of the Neolithic and C/EBA populations; we can reject such a model for the IA (we can more weakly reject this model even for Scotland, whether using England/Wales or Scotland sources, suggesting some of the same stream of migration also affected Scotland albeit probably in a more subtle way). (B) To obtain insight into the source of the new ancestry in Britain in the IA, we computed $f_4(\text{England.and.Wales_IA}, \alpha(\text{England.and.Wales_N}) + (1-\alpha)(\text{England.Wales_C.EBA}); R1, R2)$ for several different (R1, R2) 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 $\sim 85\%$ ancestry from England.and.Wales_C.EBA ancestry is needed to contribute the 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 the other Z-score (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.



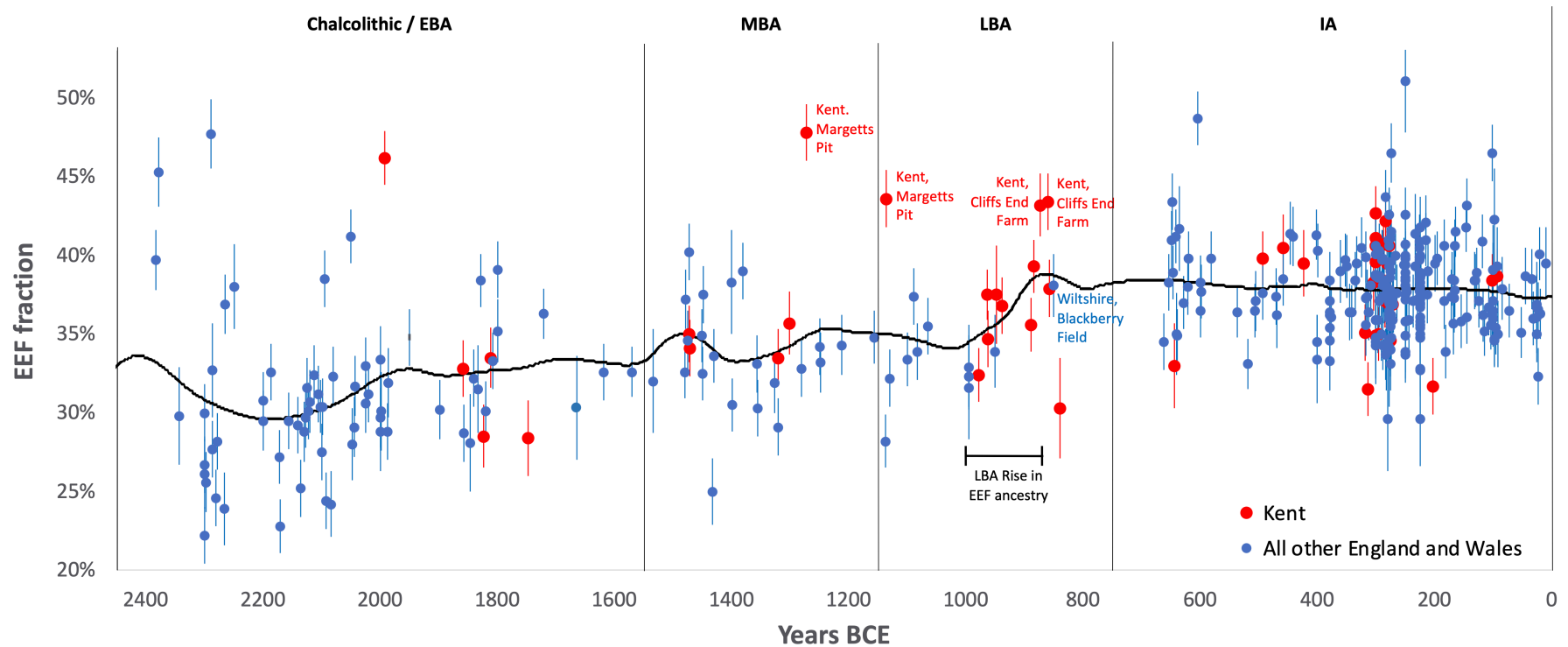
Extended Data Figure 2: By-individual analysis of the British time transect. Version of Figure 3 with the time transect extended into the Neolithic, and showing the individuals from Scotland. Estimates of EEf ancestry and one standard error are shown for all individuals in the British time transect that 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 $p > 0.01$. Blue and green show individuals from southern and northern Britain that fit the average for the main cluster of their time, while red and orange 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 and northern Britain in each archaeological period (Neolithic, C/EBA, MBA, LBA and IA) are shown in dashed lines.



Extended Data Figure 3: Frequency change over time at two phenotypically important alleles. Present-day frequency is shown by the red line. (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 consistent (Figure 4B). Online Table 8 gives full numerical results for 107 phenotypically important alleles.



Extended Data Figure 4: Y chromosome haplogroup frequencies change over time. We show the 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. The frequency increases significantly from ~0% in the whole island Neolithic, to 89±4% in the whole island C/EBA. It declines albeit non-significantly to 79±9% in the MBA and LBA (from this time on restricting to England and Wales because of the autosomal evidence of a change in 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 a further reduction from this time to the present, where the proportion is 43±3% in Wales and the west of England ($P=5 \times 10^{-6}$ for a reduction relative to the IA), and 14±2% in the center and east of England ($P=3 \times 10^{-32}$ for a reduction relative to the IA), potentially due to later migrations bearing a different distribution of Y chromosome haplogroup frequencies.



Extended Data Figure 5: Version of Figure 3A contrasting Kent to the rest of southern Britain. We show the period 2450-1 BCE. All the high EEF outliers at 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 at the M-LBA. Further sampling from the rest of Britain at the M-LBA is critical in order to understand the dynamics of how this ancestry spread more broadly, but the fact that only sample from the LBA that is not from Kent, I12624 from Blackberry Field in Potterne in Wiltshire at 950-750 BCE, already has IA levels of EEF ancestry, suggests that this ancestry began spreading more broadly by the date of this individual.

References

- 508 1 Booth, T. J. A stranger in a strange land: a perspective on archaeological responses
509 to the palaeogenetic revolution from an archaeologist working amongst
510 palaeogeneticists. *World Archaeology* **51**, 586-601,
511 doi:10.1080/00438243.2019.1627240 (2019).
- 512 2 Anthony, D. W. Migration in archeology: The baby and the bathwater. *American*
513 *Anthropologist* **92**, 895-914 (1990).
- 514 3 Altschul, J. H. *et al.* Opinion: To understand how migrations affect human securities,
515 look to the past. *Proc Natl Acad Sci U S A* **117**, 20342-20345,
516 doi:10.1073/pnas.2015146117 (2020).
- 517 4 Kossinna, G. *Die Herkunft der Germanen: Zur Methode der Siedlungsarchäologie.*
518 (Kabitzsch, 1911).
- 519 5 Vander Linden, M. Population history in third-millennium-BC Europe: assessing the
520 contribution of genetics. *World Archaeology*, doi:10.1080/00438243.2016.1209124
521 (2016).
- 522 6 Haak, W. *et al.* Massive migration from the steppe was a source for Indo-European
523 languages in Europe. *Nature* **522**, 207-211, doi:10.1038/nature14317 (2015).
- 524 7 Allentoft, M. E. *et al.* Population genomics of Bronze Age Eurasia. *Nature* **522**, 167-+,
525 doi:10.1038/nature14507 (2015).
- 526 8 Olalde, I. *et al.* The Beaker phenomenon and the genomic transformation of
527 northwest Europe. *Nature* **555**, 190-196, doi:10.1038/nature25738 (2018).
- 528 9 Cassidy, L. M. *et al.* Neolithic and Bronze Age migration to Ireland and establishment
529 of the insular Atlantic genome. *Proc Natl Acad Sci U S A* **113**, 368-373,
530 doi:10.1073/pnas.1518445113 (2016).
- 531 10 Brace, S. *et al.* Ancient genomes indicate population replacement in Early Neolithic
532 Britain. *Nat Ecol Evol* **3**, 765-771, doi:10.1038/s41559-019-0871-9 (2019).
- 533 11 Galinsky, K. J., Loh, P. R., Mallick, S., Patterson, N. J. & Price, A. L. Population
534 structure of UK Biobank and ancient Eurasians reveals adaptation at genes
535 influencing blood pressure. *Am J Hum Genet* **99**, 1130-1139,
536 doi:10.1016/j.ajhg.2016.09.014 (2016).
- 537 12 Leslie, S. *et al.* The fine-scale genetic structure of the British population. *Nature* **519**,
538 309-314, doi:10.1038/nature14230 (2015).
- 539 13 Schiffels, S. *et al.* Iron Age and Anglo-Saxon genomes from East England reveal
540 British migration history. *Nat Commun* **7**, 10408, doi:10.1038/ncomms10408 (2016).
- 541 14 Briggs, A. W. *et al.* Removal of deaminated cytosines and detection of in vivo
542 methylation in ancient DNA. *Nucleic Acids Res* **38**, e87, doi:10.1093/nar/gkp1163
543 (2010).
- 544 15 Rohland, N., Harney, E., Mallick, S., Nordenfelt, S. & Reich, D. Partial uracil-DNA-
545 glycosylase treatment for screening of ancient DNA. *Philosophical transactions of the*
546 *Royal Society of London. Series B, Biological sciences* **370**, 20130624,
547 doi:10.1098/rstb.2013.0624 (2015).
- 548 16 Gansauge, M.-T., Aximu-Petri, A., Nagel, S. & Meyer, M. Manual and automated
549 preparation of single-stranded DNA libraries for the sequencing of DNA from ancient
550 biological remains and other sources of highly degraded DNA. *Nature Protocols* **15**,
551 2279-2300, doi:10.1038/s41596-020-0338-0 (2020).
- 552 17 Gansauge, M. T. *et al.* Single-stranded DNA library preparation from highly degraded
553 DNA using T4 DNA ligase. *Nucleic Acids Res* **45**, e79, doi:10.1093/nar/gkx033
554 (2017).
- 555 18 Fu, Q. *et al.* An early modern human from Romania with a recent Neanderthal
556 ancestor. *Nature* **524**, 216-219, doi:10.1038/nature14558 (2015).
- 557 19 Mathieson, I. *et al.* Genome-wide patterns of selection in 230 ancient Eurasians.
558 *Nature* **528**, 499-503, doi:10.1038/nature16152 (2015).
- 559 20 Fu, Q. *et al.* DNA analysis of an early modern human from Tianyuan Cave, China.
560 *Proc Natl Acad Sci U S A* **110**, 2223-2227, doi:10.1073/pnas.1221359110 (2013).

561 21 Fu, Q. *et al.* A revised timescale for human evolution based on ancient mitochondrial
562 genomes. *Curr Biol* **23**, 553-559, doi:10.1016/j.cub.2013.02.044 (2013).

563 22 Korneliussen, T. S., Albrechtsen, A. & Nielsen, R. ANGSD: Analysis of Next
564 Generation Sequencing Data. *BMC Bioinformatics* **15**, 356, doi:10.1186/s12859-014-
565 0356-4 (2014).

566 23 Kennett, D. J. *et al.* Archaeogenomic evidence reveals prehistoric matrilineal
567 dynasty. *Nat Commun* **8**, 14115, doi:10.1038/ncomms14115 (2017).

568 24 Reich, D., Thangaraj, K., Patterson, N., Price, A. L. & Singh, L. Reconstructing Indian
569 population history. *Nature* **461**, 489-494, doi:10.1038/nature08365 (2009).

570 25 Patterson, N. *et al.* Ancient admixture in human history. *Genetics* **192**, 1065-1093,
571 doi:10.1534/genetics.112.145037 (2012).

572 26 Lazaridis, I. *et al.* Ancient human genomes suggest three ancestral populations for
573 present-day Europeans. *Nature* **513**, 409-413, doi:10.1038/nature13673 (2014).

574 27 Evans, J. A., Chenery, C. A. & Montgomery, J. A summary of strontium and oxygen
575 isotope variation in archaeological human tooth enamel excavated from Britain.
576 *Journal of Analytical Atomic Spectrometry* **27**, 754-764, doi:10.1039/C2JA10362A
577 (2012).

578 28 Fitzpatrick, A. P. *The Amesbury Archer and the Boscombe Bowmen: Early Bell*
579 *Beaker burials at Boscombe Down, Amesbury, Wiltshire, Great Britain: Excavations*
580 *at Boscombe Down*. Vol. 1 (Wessex Archaeology, 2011).

581 29 Millard, A. R. in *Cliffs End Farm, Isle of Thanet, Kent: A Mortuary and Ritual Site of*
582 *the Bronze Age, Iron Age and Anglo-Saxon Period With Evidence for Long-Distance*
583 *Maritime Mobility* (eds J. I. McKinley *et al.*) 135-146 (Wessex Archaeology, 2014).

584 30 Champion, T. C., Haselgrove, C., Armit, I., Creighton, J. & Gwilt, A. *Understanding*
585 *the British Iron Age: An Agenda for Action. A Report for the Iron Age Research*
586 *Seminar and the Council of the Prehistoric Society*. (Trust for Wessex Archaeology,
587 2001).

588 31 Ringbauer, H., Novembre, J. & Steinrücken, M. Human Parental Relatedness
589 through Time - Detecting Runs of Homozygosity in Ancient DNA. *bioRxiv*,
590 2020.2005.2031.126912, doi:10.1101/2020.05.31.126912 (2020).

591 32 Fernandes, D. M. *et al.* A genetic history of the pre-contact Caribbean. *Nature* **590**,
592 103-110, doi:10.1038/s41586-020-03053-2 (2021).

593 33 Fernandes, D. M. *et al.* The spread of steppe and Iranian-related ancestry in the
594 islands of the western Mediterranean. *Nat Ecol Evol* **4**, 334-345, doi:10.1038/s41559-
595 020-1102-0 (2020).

596 34 Marcus, J. H. *et al.* Genetic history from the Middle Neolithic to present on the
597 Mediterranean island of Sardinia. *Nat Commun* **11**, 939, doi:10.1038/s41467-020-
598 14523-6 (2020).

599 35 Olalde, I. *et al.* The genomic history of the Iberian Peninsula over the past 8000
600 years. *Science* **363**, 1230-1234, doi:10.1126/science.aav4040 (2019).

601 36 Busby, G. B. J. *et al.* The peopling of Europe and the cautionary tale of Y
602 chromosome lineage R-M269. *Proceedings of the Royal Society B: Biological*
603 *Sciences* **279**, 884-892, doi:10.1098/rspb.2011.1044 (2012).

604 37 Rubinacci, S., Ribeiro, D. M., Hofmeister, R. & Delaneau, O. Efficient phasing and
605 imputation of low-coverage sequencing data using large reference panels. *bioRxiv*,
606 2020.2004.2014.040329, doi:10.1101/2020.04.14.040329 (2020).

607 38 Auton, A. *et al.* A global reference for human genetic variation. *Nature* **526**, 68-74,
608 doi:10.1038/nature15393 (2015).

609 39 Hubacek, J. A. *et al.* Frequency of adult type-associated lactase persistence LCT-
610 13910C/T genotypes in the Czech/Slav and Czech Roma/Gypsy populations. *Genet*
611 *Mol Biol* **40**, 450-452, doi:10.1590/1678-4685-GMB-2016-0071 (2017).

612 40 Stead, I. M. *The Arras Culture*. (Yorkshire Philosophical Society, 1979).

613 41 Halkon, P. *The Arras Culture of Eastern Yorkshire: Celebrating the Iron Age*.
614 (Oxbow Books, 2020).

- 615 42 Jay, M., Montgomery, J., Nehlich, O., Towers, J. & Evans, J. British Iron Age chariot
616 burials of the Arras culture: a multi-isotope approach to investigating mobility levels
617 and subsistence practices. *World Archaeology* **45**, 473-491,
618 doi:10.1080/00438243.2013.820647 (2013).
- 619 43 Cunliffe, B. *Britain Begins*. (Oxford University Press, 2013).
- 620 44 Koch, J. T., Cunliffe, B.W. *Celtic from the West 2: Rethinking the Bronze Age and the*
621 *Arrival of Indo-European in Atlantic Europe*. (Oxbow Books, 2013).
- 622 45 Needham, S. & Bowman, S. Flesh-hooks, technological complexity and the Atlantic
623 Bronze Age feasting complex. *European Journal of Archaeology* **8**, 93-136,
624 doi:10.1177/1461957105066936 (2005).
- 625 46 Marcigny, C., Bourgeois, J. & Talon, M. in *Rythmes et contours de la géographie*
626 *culturelle sur le littoral de la Manche entre le IIIe et le début du Ier millénaire (chapter*
627 *title: Movement, exchange and identity in Europe in the 2nd and 1st millennia BC:*
628 *beyond frontiers* (eds A. Lehoerff & M. Talon) 63-78 (Oxbow Books, 2017).
- 629 47 Marcigny, C. in *Les Anglais in Normandie (chapter title: Les relations transmanche*
630 *durant l'âge du Bronze entre 2300 et 800 avant notre ère)* 47-54 (2011).
- 631 48 McConvell, P. in *Migration History in World History (chapter title: The archaeo-*
632 *linguistics of migration)* 153-186 (Brill, 2010).
- 633 49 Bellwood, P. S. & Renfrew, C. *Examining the Farming/Language Dispersal*
634 *Hypothesis*. (McDonald Institute for Archaeological Research, 2002).
- 635 50 Sims-Williams, P. An Alternative to 'Celtic from the East' and 'Celtic from the West'.
636 *Cambridge Archaeological Journal* **30**, 511-529, doi:10.1017/S0959774320000098
637 (2020).
- 638 51 Mallory, J. P. *The Origins of the Irish*. (Thames & Hudson Inc., 2013).
- 639 52 Rodway, S. The Ogham inscriptions of Scotland and Brittonic Pictish. *Journal of*
640 *Celtic Linguistics* **21**, 173-234, doi:10.16922/jcl.21.6 (2020).
- 641 53 Herm, G. *The Celts: The people who came out of the darkness*. (Weidenfeld and
642 Nicolson, 1976).
- 643 54 Guggisberg, M. in *Oxford Handbook of the European Iron Age* (ed K. Rebay-
644 Sailsbury C. Haselgrove, P. Wells) (Oxford University Press, 2018).
- 645 55 Pinhasi, R., Fernandes, D. M., Sirak, K. & Cheronet, O. Isolating the human cochlea
646 to generate bone powder for ancient DNA analysis. *Nature Protocols* **14**, 1194-1205,
647 doi:10.1038/s41596-019-0137-7 (2019).
- 648 56 Sirak, K. A. *et al.* A minimally-invasive method for sampling human petrous bones
649 from the cranial base for ancient DNA analysis. *Biotechniques* **62**, 283-289,
650 doi:10.2144/000114558 (2017).
- 651 57 Dabney, J. *et al.* Complete mitochondrial genome sequence of a Middle Pleistocene
652 cave bear reconstructed from ultrashort DNA fragments. *Proc Natl Acad Sci U S A*
653 **110**, 15758-15763, doi:10.1073/pnas.1314445110 (2013).
- 654 58 Korlevic, P. *et al.* Reducing microbial and human contamination in DNA extractions
655 from ancient bones and teeth. *Biotechniques* **59**, 87-93, doi:10.2144/000114320
656 (2015).
- 657 59 Rohland, N., Glocke, I., Aximu-Petri, A. & Meyer, M. Extraction of highly degraded
658 DNA from ancient bones, teeth and sediments for high-throughput sequencing. *Nat*
659 *Protoc* **13**, 2447-2461, doi:10.1038/s41596-018-0050-5 (2018).
- 660 60 Briggs, A. & Heyn, P. in *Methods in Molecular Biology* Vol. 840 143-154 (Springer,
661 2012).
- 662 61 Maricic, T., Whitten, M. & Paabo, S. Multiplexed DNA sequence capture of
663 mitochondrial genomes using PCR products. *PLoS One* **5**, e14004,
664 doi:10.1371/journal.pone.0014004 (2010).
- 665 62 Behar, D. M. *et al.* A "Copernican" reassessment of the human mitochondrial DNA
666 tree from its root. *Am J Hum Genet* **90**, 675-684, doi:10.1016/j.ajhg.2012.03.002
667 (2012).
- 668 63 Li, H. & Durbin, R. Fast and accurate short read alignment with Burrows-Wheeler
669 transform. *Bioinformatics* **25**, 1754-1760, doi:10.1093/bioinformatics/btp324 (2009).

670 64 Weissensteiner, H. *et al.* HaploGrep 2: mitochondrial haplogroup classification in the
671 era of high-throughput sequencing. *Nucleic Acids Res* **44**, W58-63,
672 doi:10.1093/nar/gkw233 (2016).
673 65 Sawyer, S., Krause, J., Guschanski, K., Savolainen, V. & Paabo, S. Temporal
674 patterns of nucleotide misincorporations and DNA fragmentation in ancient DNA.
675 *PLoS One* **7**, e34131, doi:10.1371/journal.pone.0034131 (2012).
676 66 Skoglund, P. *et al.* Separating endogenous ancient DNA from modern day
677 contamination in a Siberian Neandertal. *Proc Natl Acad Sci U S A* **111**, 2229-2234,
678 doi:10.1073/pnas.1318934111 (2014).
679 67 Patterson, N., Price, A. L. & Reich, D. Population structure and eigenanalysis. *PLoS*
680 *genetics* **2**, e190, doi:10.1371/journal.pgen.0020190 (2006).
681 68 Bronk Ramsey, C. Bayesian Analysis of Radiocarbon Dates. *Radiocarbon* **51**, 337-
682 360, doi:10.1017/S0033822200033865 (2009).
683 69 Reimer, P. J. *et al.* The IntCal20 northern hemisphere radiocarbon age calibration
684 curve (0–55 cal kBP). *Radiocarbon* **62**, 725-757, doi:10.1017/RDC.2020.41 (2020).
685