Large Scale Migration into Southern Britain at the End of the Bronze Age

Nick Patterson[1,2,*], Michael Isakov[3,*], Thomas Booth[4,*], Lindsey Büster[5,*], Claire-Elise Fischer[5,*], Inigo Olalde[6,7], Harald Ringbauer[1,2], Ali Akbari[1,6,8], Olivia Cheronet[9,10], Nicole Adamski[6,8], Eveline Altena[11], Rebecca Bernardos[6], Selina Brace[12], Guillermo Bravo[9], Nasreen Broomandkhoshbacht[6,8], Kimberly Callan[6,8], Francesca Candilio[13], Elizabeth Curtis[6,8], Lea Demetz[9], Peter De Knijff[11], Kellie Sara Duffett Carlson[9], Daniel M. Fernandes[9,14], Suzanne Freilich[9], Aisling Kearns[6], Ann Marie Lawson[6,8], Iosif Lazaridis[1,6], Matthew Mah[2,8,6], Swapan Mallick[2,8,6], Kirsten Mandl[9], Adam Micco[2,6], Megan Michel[6,8], Jonas Oppenheimer[6,8], Maria Pala[15], Lijun Qiu[6], Constanze Schattke[9], Kristin Stewardson[6,8], Kadir Toykan-Özdoğan[9], J. Noah Workman[6], Fatma Zalzala[6,8], Zhang Zhao[6], Brendan Culleton[16], Tim Allen[17], Katalin Almássy[18], Christèle Baillif-Ducros[19], Alistair Barclay[20], Ian Barnes[12], László Bartosiewicz[21], Katherine Baxter[22], Madeleine Bleasdale[5], Philippe Boissinot[23], Clive Bonsall[24], Pippa Bradley[25], Marcus Brittain[26], Fraser Brown[17], Lisa Brown[27], Richard Brunning[28], Chelsea Budd[29,30], Sylvain Canet[19], Silvia Carnicero-Cáceres[31], Andrew Chamberlain[32], Sébastien Chauvin[19], Sharon Clough[33], Alfredo Coppa[34], Oliver Craig[5], Matija Črešnar[35,36], Vicki Cummings[37], Robin Daniels[38], Alex Davies[17], Philip De Jersey[39], Jody Deacon[40], Csilla Deminger[41], Peter W. Ditchfield[42], Gail Drinkall[43], Ceiridwen J. Edwards[15], Eszter Istvánovits[44], Christopher Evans[26], Jane Evans[45], Manuel Fernández-Götz[24], Andrew Fitzpatrick[46], Harry Fokkens[47], M. George B. Foody[15], Allison Fox[48], Chris Fowler[49], Michelle Gamble[50], Manuel R. González Morales[51], Borja González-Rabanal[52], Adrian Green[53], Tamás Hajdu[54,55], Derek Hamilton[56], James Harris[57], Chris Hayden[17], Bénédicte Hernu[58], Gill Hey[17], Milan Horňák[59], Andy M. Jones[60], Kevin Kazek[61], Robert A. Kenyon[62], Amal Khreisheh[28], Mark Knight[26], Péter F. Kovács[63], Anita Kozubová[64], Valéria Kulcsár[65], Carles Lalueza-Fox[66], Christophe Le Pennec[67], Michael Legge[68], Matt Leivers[25], Louise Loe[17], Olalla López-Costas[69], Tom Lord[70], James Lyall[71], Philip Mason[72], Andy Maxted[73], Ana B. Marín-Arroyo[74], Lauren McIntyre[17], Jacqueline McKinley[25], Kathleen McSweeney[24], Sophie Meyer[75], Steve Minnitt[76], Joanna Moore[77], Geoff Morley[78], Graham Mullan[79], Margaréta Musilová[80], Benjamin Neil[26], Rebecca Nicholls[81], Cécile Paresys[19], Ricky Patten[26], Krisztina Pesti[82], Coline Pichon[83], Catriona Pickard[24], T. Douglas Price[84], Rebecca Redfern[85], Branislav Resutík[80], Martin B. Richards[15], Alena Šefčáková[86], Alison Sheridan[87], Sabine Skae[88], Mark Stephens[89], Szabolcs Czifra[90], Tamás Szeniczey[54,55], Jonathan Tabor[26], Clenis Tavarez Maria[91], Rachel Terry[92], Mark Thomas[93], Maria Teschler-Nicola[94], Jesús F. Torres-Martínez[95], Julien Trapp[61], Ross Turle[96], Ferenc Ujvári[82], Petr Veleminsky[97], Clive Waddington[98], Paula Ware[89], Paul Wilkinson[99], Linda Wilson[79], Rob Wiseman[26], Eilidh Young[100], Andrej Žitňan[101], Zoltán Pilling[102], Peter Halkon[30], Douglas Kennett[103], Barry Cunliffe[104], Malcolm Lillie[29,30], Nadin Rohland[2,6], Ron Pinhasi[9,10], Ian Armit[5], David Reich[1,2,6,8]

* Co-lead authors:
N. Patterson, M. Isakov, T. Booth, L. Büster, C.-E. Fischer

Correspondence to:
R. Pinhasi (ron.pinhasi@univie.ac.at), I. Armit (ian.armit@york.ac.uk), and D. Reich (reich@genetics.med.harvard.edu)

[1]Department of Human Evolutionary Biology, Harvard University, Cambridge, MA 02138
[2]Broad Institute of MIT and Harvard, Cambridge, MA 02142, USA
[3]Harvard College, Cambridge, MA 02138, USA
[4]The Francis Crick Institute, London, NW1 1AT, UK
[5]Department of Archaeology, University of York, York YO1 7EP, UK
[6]Department of Genetics, Harvard Medical School, Boston, Massachusetts 02115, USA
[7]Institute of Evolutionary Biology, CSIC-Universitat Pompeu Fabra, 08003 Barcelona, Spain
[8]Howard Hughes Medical Institute, Boston, MA 02115, USA
[9]Department of Evolutionary Anthropology, University of Vienna, 1090 Vienna, Austria
[10]Earth Institute and School of Archaeology, University College Dublin, Dublin 4, Republic of Ireland
[11]Department of Human Genetics, Leiden University Medical Center, Leiden 2333 ZC, The Netherlands
[12]Department of Earth Sciences, Natural History Museum, London SW7 5BD, UK
[13]Superintendency of Archaeology, Fine Arts and Landscape for the city of Cagliari and the provinces of Oristano and South Sardinia, 09121 Cagliari, Italy
[14]CIAS, Department of Life Sciences, University of Coimbra, 3000-456 Coimbra, Portugal
[15]Department of Biological and Geographical Sciences, School of Applied Sciences, University of Huddersfield, Queensgate, Huddersfield, HD1 3DH, UK
[16]Institutes of Energy and the Environment, The Pennsylvania State University, University Park, PA 16802, USA
[17]Oxford Archaeology, Oxford, OX2 0ES, UK
[18]Městské Muzeum v Čelákovicích, 250 88 Čelákovice, Czech Republic
[19]Institut National de Recherches Archéologiques Préventives (INRAP), 75685 Paris cedex 14, France
[20]Cotswold Archaeology, Andover, Hampshire, SP10 5LH, UK
[21]Department of Archaeology and Classical Studies, Stockholm University, 106 91 Stockholm, Sweden
[22]Leeds Museums and Galleries, Leeds Discovery Centre, Leeds LS10 1LB, UK
[23]University of Toulouse-Jean Jaurès, 31058 Toulouse, France
[24]School of History, Classics and Archaeology, University of Edinburgh, Edinburgh EH8 9AG, UK
[25]Wessex Archaeology, Salisbury SP4 6EB, UK
[26]Cambridge Archaeological Unit, Department of Archaeology, University of Cambridge, Cambridge CB3 0DT, UK
[27]Wiltshire Museum, Devizes SN10 1NS, UK
[28]South West Heritage Trust, Somerset Heritage Centre, Norton Fitzwarren, Taunton, TA2 6SF, UK
[29]Department of Historical, Philosophical and Religious Studies, Umeå University 901 87, Umeå, Sweden
[30]Department of History, University of Hull, Hull, HU6 7RX, UK
[31]Instituto de Medicina Legal y Ciencias Forenses de Cantabria, Santander, Spain
[32]School of Earth and Environmental Sciences, University of Manchester, Manchester, M13 9PL, UK
[33]Cotswold Archaeology, Cirencester, Gloucestershire, GL7 6BQ, UK
[34]Department of Animal and Human Biology, Section of Anthropology, University of Rome, La Sapienza, 00185 Rome, Italy
[35]University of Ljubljana, Faculty of Arts, Department of Archaeology, Centre for Interdisciplinary Research in Archaeology

[36]Institute for the Protection of Cultural Heritage of Slovenia, Conservation Centre, Centre for Preventive Archaeology, SI-1000 Ljubljana, Slovenia
[37]School of Forensic and Applied Sciences, University of Central Lancashire, Preston, Lancashire PR1 2HE, UK
[38]Tees Archaeology, Hartlepool, TS24 8BT, UK
[39]Guernsey Museums & Galleries, Candie Gardens, St Peter Port, Guernsey, GY1 1UG, UK
[40]National Museum of Wales, Cardiff CF10 3NP
[41]Kuny Domokos Museum, H-2890 Tata, Hungary
[42]Research Laboratory for Archaeology, School of Archaeology, University of Oxford, Oxford OX1 3TG, UK
[43]The Orkney Museum, Kirkwall, Orkney, KW15 1NY, UK
[44]Jósa András Museum, H-4400 Nyíregyháza, Hungary
[45]British Geological Survey, Keyworth Nottingham, Nottinghamshire NG12 5GG, UK
[46]Archaeology and Ancient History, University of Leicester, Leicester, LE1 7RH, UK
[47]Faculty of Archaeology, Leiden University, 2333 CC Leiden, The Netherlands
[48]Manx National Heritage, Eiraght Ashoonagh Vannin, Manx Museum, Douglas IM1 3LY, , Isle of Man
[49]School of History, Classics and Archaeology, Newcastle University, Newcastle upon Tyne NE1 7RU, UK
[50]Heritage and Archaeological Research Practice (HARP), Edinburgh, EH2 3JG.
[51]Instituto Internacional de Investigaciones Prehistóricas de Cantabria (Universidad de
[52]Grupo EvoAdapta, Departamento de Ciencias Históricas, Universidad de Cantabria. Santander, Spain.
[53]The Salisbury Museum, Salisbury SP1 2EN, UK
[54]Department of Biological Anthropology, Eötvös Loránd University, H-1117 Budapest, Hungary
[55]Department of Anthropology, Hungarian Natural History Museum, H-1083 Budapest, Hungary
[56]Scottish Universities Environmental Research Centre (SUERC), East Kilbride, G75 0QF, UK
[57]Corinium Museum, Park Street, Cirencester, GL7 2BX, UK
[58]Musée Saint-Remi, Ville de Reims, CS 80036, 51722 Reims, France
[59]University of Ljubljana, Department of Archaeology, 1000 Ljubljana, Slovenija
[60]Cornwall Archaeology Unit, The, Truro TR1 3AY, UK
[61]Musée de La Cour d'Or, 57000 Metz, France
[62]East Dorset Antiquarian Society (EDAS), Merrow, West Bexington, Dorset, DT2 9DG, UK
[63]Damjanich János Museum, H-5000 Szolnok, Hungary
[64]Archaeological Institute of the Slovak Academy of Sciences, 949 21 Nitra, Slovakia
[65]University of Szeged, Faculty of Arts, Department of Archaeology, H-6722 Szeged, Hungary
[66]Institute of Evolutionary Biology, CSIC-Universitat Pompeu Fabra, Barcelona 08003, Spain
[67]Musee d'Histoire et d'Archeologie, 56000 Vannes, France
[68]School of History, Archaeology and Religion, Cardiff University, Cardiff, CF10 3EU, UK
[69]Facultade de Bioloxía, University of Santiago de Compostela, 15782 Santiago de Compostela, Spain
[70]Lower Winskill Farm, Langcliffe, Settle, BD24 9PZ, UK
[71]Geophiz.biz, West Heslerton, North Yorkshire, YO17 8RQ, UK
[72]Institute for the Protection of Cultural Heritage of Slovenia, Conservation Centre, Centre for Preventive Archaeology, Poljanska 40, SI-1000 Ljubljana, Slovenia
[73]Royal Pavillion and Museums, Brighton BN1 1EE, UK
[74]Grupo EvoAdapta, Departamento de Ciencias Históricas, Universidad de Cantabria, Santander, Spain.

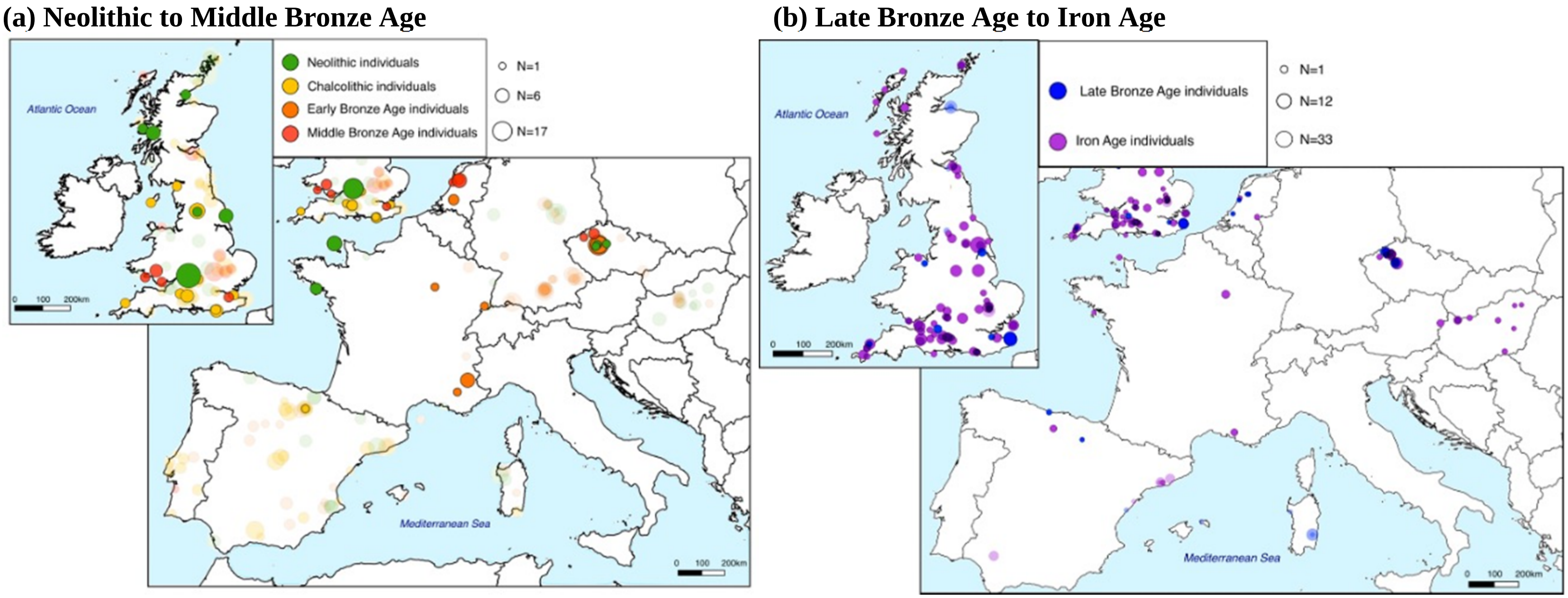
[75]Royal Cornwall Museum, Truro, Cornwall, TR1 2SJ, UK
[76]South West Heritage Trust (retired), Somerset Heritage Centre, Norton Fitzwarren, Taunton, TA2 6SF, UK
[77]Department of Archaeology, Durham University, Durham, DH1 3LE, UK
[78]MOLES Archaeology, Courtwood House, Silver Street Head, Sheffield, S1 2DD, UK
[79]University of Bristol Spelaeological Society, University of Bristol Student Union Building, Queens Road, Bristol, BS8 1LN, UK
[80]Municipal Monument Preservation Institute Bratislava, 811 01, Bratislava, Slovakia
[81]Archaeological and Forensic Sciences, University of Bradford, Bradford, BD7 1DP, UK
[82]Rómer Flóris Museum of Art and History, H-9021 Győr, Hungary
[83]Musée Le Vergeur, 51100 Reims, France
[84]Department of Anthropology, University of Wisconsin-Madison, Madison, Wisconsin 53706, USA
[85]Centre for Human Bioarchaeology, Museum of London, 150 London Wall, London EC2Y 5HN, UK
[86]Slovak National Museum – Natural History Museum, 810 06 Bratislava 16, Slovakia
[87]National Museums Scotland, Edinburgh EH1 1JF, UK
[88]The Dock Museum, Barrow-in-Furness, Cumbria LA14 2PW, UK
[89]MAP Archaeological Practice, Showfield Lane, Malton, North Yorkshire, YO17 6BT, UK
[90]Hungarian National Museum, Archaeological Heritage Protection Directorate, H-1113 Budapest, Hungary
[91]Museo del Hombre Dominicano, Santo Domingo 10204, Dominican Republic
[92]Craven Museum and Gallery, Skipton, BD23 1AH, UK
[93]Research Department of Genetics, Evolution and Environment, University College London, London WC1E 6BT, UK
[94]Natural History Museum Vienna, Department of Anthropology, A-1010 Wien, Austria
[95]Universidad Complutense de Madrid, Facultad de Geografía e Historia, Departamento de Prehistoria, Historia Antigua y Arqueología, Avda. de Séneca, 2
[96]Hampshire Cultural Trust, Winchester, SO23 8RB, UK
[97]Department of Anthropology, National Museum, 115 79, Prague 1, Czech Republic
[98]Archaeological Research Services, Angel House, Portland Square, Bakewell, Derbyshire, DE45 1HB, UK
[99]Swale and Thames Archaeological Survey Company, Faversham, Kent, ME13 8UP, UK
[100]Keswick Museum, Keswick CA12 4NF, UK
[101]AA AVALA s.r.o., 821 04 Bratislava, Slovakia
[102]Independent researcher, H-1097 Budapest, Hungary
[103]Department of Anthropology, University of California, Santa Barbara, CA 93106, USA
[104]Institute of Archaeology, University of Oxford, Oxford OX1 2PG, UK

Present-day populations from England and Wales harbour more ancestry derived from Early European Farmers (EEF) than did people of the Early Bronze Age, suggesting later migrations from mainland Europe. To investigate how this occurred, we report genome-wide data from 740 individuals from Bronze and Iron Age Europe, increasing the number of individuals with such data from Britain by more than 3-fold, and from the Western and Central European Iron Age by about 10-fold. We detect an increase in EEF ancestry in Britain in the Middle to Late Bronze Age around 1300-800 BCE produced by an influx of people most closely matching ancient individuals from France, coincident with or immediately following the most dramatic population growth in Britain in the four millennia prior to the common era: an approximately five-fold increase in population size. These migrations contributed around half of the ancestry of Iron Age people in England and Wales but had little impact in Scotland. We find no evidence of significant movement of people into Britain during the Iron Age after 800 BCE, when patterns of genetic change seem to have been largely independent of those on the mainland. The independent trajectories of genetic variants in Britain in the Iron Age is also reflected in the earlier rise of the lactase persistence allele (~50% by the Iron Age) than in Central Europe (~10%), suggesting a greater reliance on pastoralism in Britain in this period. The evidence for a demographically significant migration into Britain by the end of the Bronze Age but not in the Iron Age raises the possibility that early Celtic languages spread from the vicinity of France into Britain during this time, and decreases the plausibility of later spreads. Europe-wide, EEF ancestry proportions tended to increase in northern Europe and to decrease in the south by the end of the Bronze Age, coincident with an intensification of trade and expanding networks of shared ritual practices and highlighting the end of the Bronze Age as a peak of both cultural interaction and human mobility.

“Migration” is a central concept in population genetics as well as in archaeology, but its meaning has evolved in divergent ways in the course of the development of these disciplines, which has sometimes contributed to misunderstandings[1]. Population geneticists use “migration” to refer to any movement of genetic material from one geographic region to another, but from an archaeological perspective this definition is too broad, as it means that even low-level symmetrical exchanges of mates between adjacent communities would be considered migration. In archaeology, the concept of migration is also haunted by its politicization in the early twentieth century, when invasion was sometimes argued to be the primary mechanism for the spread and dominance of specific ethnic groups[2], a theory that was used to justify claims on territory and wars of aggression[3]. Because of this history, some archaeologists tend to view “migration” as synonymous with *migratory movements* whereby a community consciously plans and executes a long-distance (and permanent) translocation of large numbers of people over a short period (at most a few years), along the lines of the migration of hundreds of thousands of members of the Helvetii described by Julius Caesar[4]. Other archaeologists favour a broader definition that is more compatible with the understanding in population genetics, using “migration” to refer to any process that through a combination of push and pull factors (often related to economic and social forces), results in movement of people from one geographic region to another and significant demographic change over a period that can be as long as centuries[5,6]. An example of a process that would qualify as a migration in this sense would be the eastward movement of people from the Steppe beginning in the third millennium BCE that contributed much of the ancestry of later Europeans[7,8,9,10]. Because we use this broader definition of “migration” here, our key finding of at least three major migrations into Britain in the prehistoric period should not be interpreted as a claim that any of these events were violent “invasions.” While social inequality could have been associated with some of these events, the human reality that characterized each of these migrations remains poorly understood and is best addressed through future work integrating archaeology and ancient DNA.

Whole genome ancient DNA studies have shown that the first Neolithic farmers of Britain ~4000 BCE derived roughly 80% of their ancestry from Early European Farmers (EEF) who originated in Anatolia more than two millennia earlier, and 20% from descendants of Mesolithic hunter-gatherers (Western European Hunter-Gatherers: WHG). The WHG ancestry was almost entirely due to admixture in mainland Europe, indicating that the migrants to Britain in the Neolithic nearly completely absorbed local populations.[9-11] The Neolithic population of Britain was genetically similar to, and almost certainly derived from, contemporaneous populations on the European mainland especially from Iberia and France. This ancestry profile remained stable for about a millennium and a half. However, around 2450 BCE, there was another substantial movement of people into Britain coinciding with the spread of Bell Beaker traditions from mainland Europe,[9] which brought a third major component of ‘Steppe ancestry’ derived ultimately from people living on the Pontic-Caspian Steppe ~3000 BCE (minimum 90% of ancestry from the new migrants). In the original study[9] reporting this ancestry shift in Britain after ~2450 BCE, no further change in the proportion of EEF ancestry was inferred in the Bronze Age, but that study contained almost no data after 1300 BCE (Figure 1). Today, however, EEF ancestry is significantly higher on average in southern Britain (defined here as England and Wales although we recognize modern boundaries are arbitrary) than in northern Britain (Scotland), raising the question of when this increase in EEF ancestry occurred.[9,12] The rise in EEF ancestry in England and Wales cannot be explained by migrations from northern mainland Europe in the early medieval period (e.g. 'Saxon' or 'Viking' migrations[13,14]), as these populations harbored less EEF ancestry than was present in Bronze Age Britain and hence would have decreased EEF ancestry instead of increasing it as we observe.[9]

We generated new ancient DNA data beginning in the Neolithic but focusing on the period from the Middle Bronze Age (defined here as beginning around 1550 BCE) through to the end of the pre-Roman Iron Age (defined here as 43 CE) (Supplementary Information Section 1, Online Table 1). We report new data from 409 individuals from the main island of Britain and its small surrounding islands, increasing the number of pre-Roman ancient individuals from Britain to 648 and multiplying by 34-fold the number from the combined Late Bronze Age and Iron Age periods (from 10 to 343). We also report new data from 179 individuals from Bohemia (present-day Czech Republic), and additional individuals from France (*n*=46), Slovakia (*n*=30), Hungary (*n*=30), the Netherlands (*n*=21), Slovenia (*n*=14), Spain (*n*=9), and Austria (*n*=3), mostly dating to the Late Bronze Age (LBA) and Iron Age (IA). We also increased data quality on 28 previously published individuals (Online Table 2). To generate these data, we prepared powder, extracted DNA[15-17], and generated sequencing libraries which we almost always pretreated with the enzyme uracil-DNA glycosylase (UDG) to reduce the characteristic cytosine-to-thymine errors of ancient DNA (Online Table 3).[15,16,18] We enriched the libraries in solution and then sequenced them on Illumina instruments (Methods).[19-21] We co-analyzed the data with previously reported data for a total of 5837 ancient and present-day individuals (Online Table 4). We clustered individuals by time period and geography aided by 62 radiocarbon dates from bone or teeth that are newly reported in this study (Online Table 5). We also separately labelled individuals that were significantly different in ancestry from the clear majority cluster from each time and region (Supplementary Information Section 2, Online Tables 6 and 7). Although we report data from all individuals, we removed a subset of individuals from the main analysis: those with evidence of contamination based on variation in their mitochondrial sequence or on the X chromosome (the latter only possible in males)[22,23], those with a rate of damage in the final nucleotide lower than is typical for authentic ancient DNA[16], or those that were first degree relatives of other higher coverage individuals in the dataset[24] (Online Tables 6 and 7), or those that had too low coverage for accurate ancestry inference which we define as <30,000 single nucleotide polymorphisms (SNPs) covered. However, we report data for all individuals. Figure 1 shows a map of all the newly reported individuals. We identified 283 individuals from 96 families as being genetically related (within the third degree) to at least one other individual in the dataset (Online Table 8). The largest family we detect from Britain is a newly-reported set of 11 individuals from the Hazleton North megalithic chambered tomb in Gloucestershire. All 11 individuals are connected along the male line consistent with a patrilocal society, as suggested by previous archaeogenetic work on megalithic sites[25] (Extended Data Figure 1, Supplementary Information section 3).



(a) Neolithic to Middle Bronze Age

(b) Late Bronze Age to Iron Age

(c) Time distribution of analysed individuals

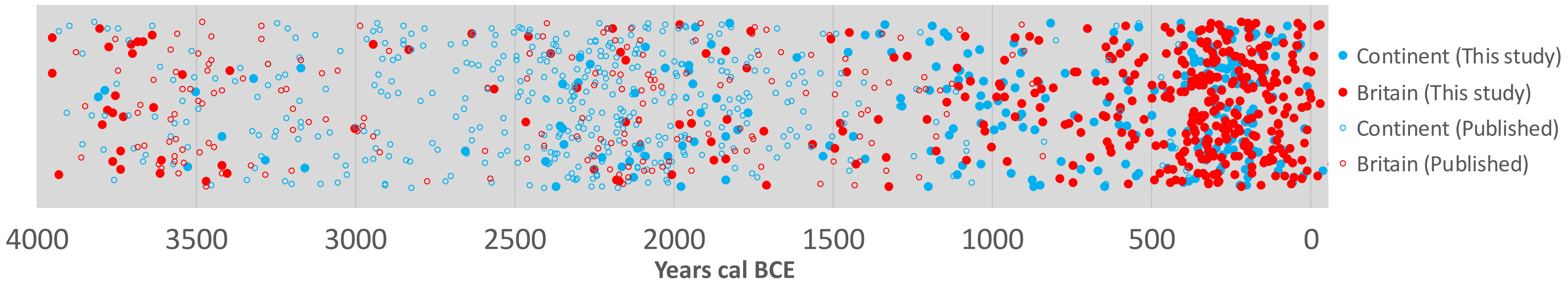


Figure 1: Ancient DNA dataset. *(a) Geographic distribution of the Neolithic to Middle Bronze Age and (b) Late Bronze Age to Iron Age individuals analysed in this study; we show newly reported data in intense colors and previously published data in pale colors. (c) Temporal distribution of the newly reported individuals. To reduce overlap of points, we sample the date of each individual from their posterior distribution (based on their means and standard deviations specified in Online Tables 6 and 7) and add jitter on the Y axis.*

We computed symmetry-f_4 statistics[26,27] between all pairs of analysis clusters from Britain, testing for differences in the rate of allele sharing (shared genetic drift) with two major source populations: Yamnaya pastoralists from the Pontic Caspian Steppe (as a surrogate for Steppe ancestry) and Anatolian farmers (as a surrogate for EEF). We document a significant increase in the degree of allele sharing with EEF populations in England and Wales over time (Extended Data Table 1). To quantify this change, we estimated proportions of the three major ancestry components (EEF, Steppe, and WHG) using *qpAdm*[7], choosing reference and source populations to drive down standard errors. Figure 2 and Extended Data Table 1 document a significant increase in EEF-related ancestry in England and Wales, with the proportion rising from an average of 32.3±0.6% in the Chalcolithic/Early Bronze Age (C/EBA: defined here as 2450-1550 BCE, n=64), to 35.4±0.6% in the Middle Bronze Age (MBA: 1550-1250 BCE, n=32), to 38.4±0.8% in the Late Bronze Age (LBA: 1250-800 BCE, n=20), and stabilizing in the Iron Age, when it was 39.7±0.5% (IA: 800 BCE-43 CE, n=249) (here and in what follows, we always quote one standard error). In contrast, there is a barely perceptible change in EEF ancestry in Scotland, with the proportion starting at 33.7±1.0 % in the C-EBA (n=9), then 35.2±1.1% in the MBA (n=4), reaching 34.9±1.2% in the LBA (n=4), and finally 35.7±0.7% in the IA (n=23). Our dense geographic coverage and large sample size makes it clear that elevated EEF ancestry was widespread in England and Wales by the IA, with average EEF ranging from 37.5-40.6% in eight regions of England and Wales, and consistently lower at 35.4-36.0% in three regions of Scotland (Table 1, Extended Data Table 2). We considered the possibility that the rise in EEF ancestry in England and Wales was due to a resurgence of archaeologically less visible populations with more ancestry derived from people living in Britain during the Neolithic. However, our attempts to model IA populations of England and Wales as a mixture of groups who lived in Neolithic and C-EBA Britain failed (always $P<10^{-9}$, Extended Data Figure 2). We are able to show that this model failure is due to M-LBA populations from Britain harboring significant excess allele sharing with Neolithic populations from mainland Europe that is not observed in earlier groups from Britain (Supplementary Information section 4, Extended Data Table 3). The only plausible explanation for these changes in EEF ancestry is new migrations from mainland Europe into southern Britain

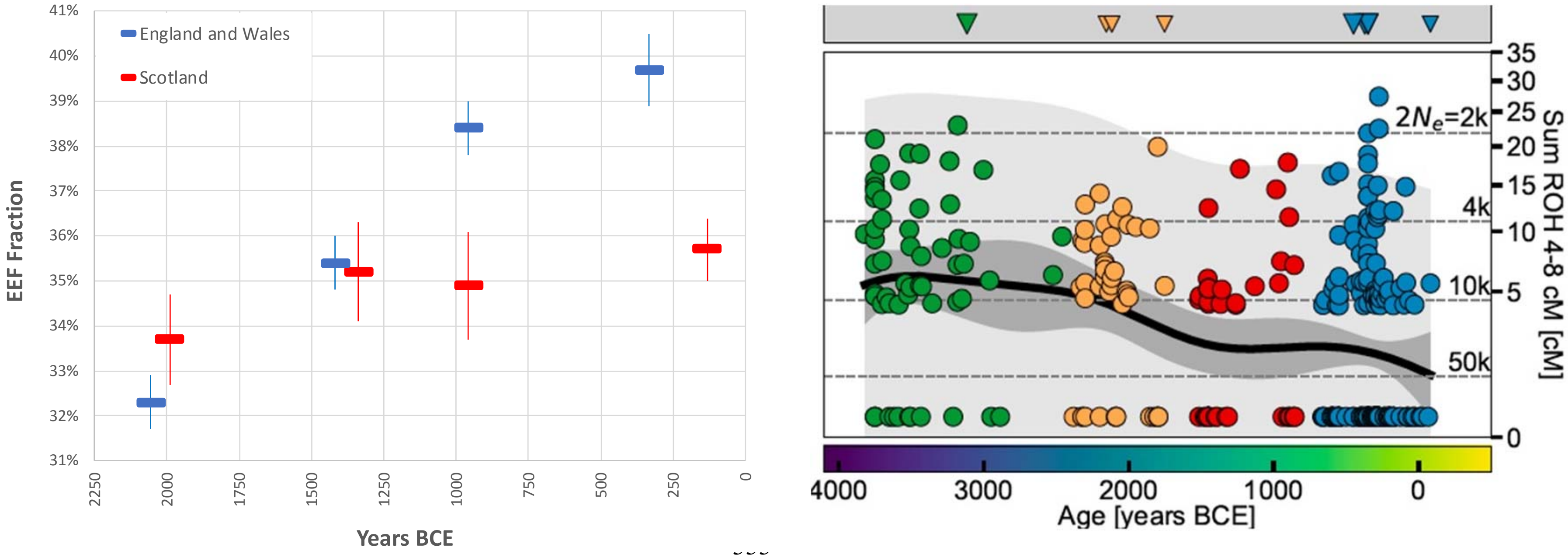


Figure 2: A high resolution ancient DNA time transect through Britain. *(Left) An increase in EEF ancestry in southern but not northern Britain. We show qpAdm estimates for all individuals passing basic quality control, divided into four periods (C/EBA, MBA, LBA and IA). X-axis positions are the average point estimates of dates for individuals in each time frame. Here and elsewhere we show one standard error. (Right) We show inferred effective population size ($2N_e$) based on short 4-8 centimorgan runs of homozygosity (ROH) using the hapROH software*[28]*, with 95% confidence intervals shown in dark grey (individuals with large proportions of their genome in large runs of homozygosity as expected for unions of first or second cousin are shown as inverted triangles). The only significant population size increase in Britain in the four millennia from 4000-1 CE is inferred to have occurred during the EBA-to-MBA transition, coinciding with the beginning of the migration we detect into Britain.*

Table 1: Variation in ancestry proportions within Iron Age Britain

		Distal Model				**Proximal Model**	
Region	***n***	**P-value**	**WHG**	**EEF**	**Steppe**	**P-value**	**Margetts Pit & Cliffs End**
England Southcentral	84	0.164	12.1 ± .5%	40.6 ± .5%	47.4 ± .6%	0.62	50 ± 4%
England Southeast	38	0.719	11.8 ± .5%	40.3 ± .6%	47.9 ± .7%	0.92	47 ± 4%
England East Anglia	20	0.871	12.1 ± .5%	39.2 ± .6%	48.7 ± .8%	0.041	46 ± 5%
England East Yorkshire	35	0.093	11.5 ± .5%	39.5 ± .6%	49.0 ± .7%	0.52	46 ± 5%
England Cornwall	17	0.270	11.5 ± .6%	38.2 ± .7%	50.3 ± .9%	0.17	39 ± 5%
England Midlands	20	0.034	11.7 ± .6%	37.8 ± .7%	50.5 ± .9%	0.33	33 ± 5%
England North	17	0.002	11.2 ± .6%	37.7 ± .8%	51.1 ± .9%	0.50	32 ± 5%
Wales	4	0.115	10.6 ± 1.1%	37.5 ± 1.5%	51.8 ± 1.6%	0.84	44 ± 9%
Scotland West	7	7x10^{-5}	10.5 ± 1.8%	35.4 ± .9%	54.2 ± 1.1%	0.15	25 ± 6%
Scotland Southeast	12	0.032	9.8 ± 1.7%	35.5 ± .9%	54.7 ± 1.0%	0.16	21 ± 5%
Scotland Orkney	4	3x10^{-5}	11.6 ± 1.1%	36.0 ± 1.3%	52.4 ± 1.5%	0.010	20 ± 8%

Notes: Estimates are from qpAdm. For the distal model the right set is (Mbuti, WHGA, Russia Samara EBA Yamnaya, Turkey N), and for the proximal model it is these plus (Netherlands Bell Beaker, Poland Globular Amphora). We separate "England East Yorkshire" from "England North" because of the large number of samples from East Yorkshire and the distinctive cultural context (Arras culture). P-values <0.01 indicate cases where the tested model fit the data poorly so estimates are less reliable.

We modelled each individual from Britain using *qpAdm*, labelling significant ancestry outliers (at the $p<0.005$ level) relative to the main cluster for their time period (Figure 3 and Extended Data Figure 3). We discuss each group of outliers in turn from earliest to latest.

First and replicating previous results[9,11], we observe a cluster of Neolithic individuals from western Scotland showing high WHG admixture, likely reflecting unions between recent migrants from Europe and indigenous people from Britain (Extended Data Figure 3).

Second, we observe high variability in EEF ancestry in the C-EBA, before proportions of EEF ancestry become relatively homogeneous by ~2100 BCE[9] (Figure 3). This heterogeneity is apparent at C-EBA Amesbury Down where EEF ancestry in some burials is significantly below the period average of 32.3±0.6% (e.g. I2417 at 24.1±1.9% (P=1x10^{-8})), whereas in others it is above the average (e.g. I2416 at 51.5±2.5% (P=3x10^{-8}) and I14200 at 49.0±2.4% (P=2x10^{-7})). The burials in the low EEF group are plausibly Beaker-period migrants who later mixed with local Neolithic farmers to produce the intermediate proportion of EEF ancestry that prevailed by the end of the EBA. The individual labeled I14200, with significantly elevated EEF ancestry compared to the period average, is the "Amesbury Archer". This individual was located in the most well-furnished burial recovered from the Stonehenge mortuary landscape, and his isotopic profile indicates he spent parts of his childhood outside Britain, possibly the region of the Alps in Central Europe[29]. The Archer's paternal-line ancestry is ultimately derived from Steppe pastoralists as indicated by his Y chromosome haplogroup R1b1a1b1a1a. The simplest explanation is that the Archer migrated to Britain from the Alpine region of mainland Europe and was from a family associated with the Bell Beaker tradition with low Steppe (high EEF) ancestry[23]. However, we cannot rule out more complex scenarios involving recent ancestral admixture in Britain (e.g. his mother not having Steppe ancestry), combined with back-and-forth childhood movements between Britain and Alpine Central Europe. In either case, the Archer's anomalously low Steppe ancestry is important in revealing that Beaker-using people who came to Britain were not socially stratified in such a way that Steppe lineage from eastern Europe necessarily conferred the highest social status. The Archer's 'Companion' (I2565), a burial found next to the Amesbury Archer, had a more typical ancestry proportion for C-EBA Britain (33.4±3.4% EEF; P=0.49 for consistency with the period average). The Archer and the Companion were not closely related genetically (we can rule out first or second degree relationships) despite sharing a rare tarsal malformation and similar grave good assemblages, which has been interpreted as likely to reflect kinship (Supplementary Information section 3).[30]

Third, we observe outliers with high EEF ancestry in the Late Bronze Age. Individual I13716 from Margetts Pit in Kent, dated to 1391-1129 calBCE (3019±31 BP, SUERC-49774), has 50.0±1.9% EEF ancestry ($P<10^{-12}$ for an excess compared to the MBA average of 35.4±0.6%), and she may be derived from one of the sources of migration in mainland Europe. Another individual from the same cemetery (I13617), dated to 1256-1051 calBCE (2946±27 BP, SUERC-49770), also has elevated EEF ancestry of 45.5±3.8%, although the excess is not significant (P=0.26) due to the larger uncertainty in ancestry estimates reflecting her lower coverage data and due to the fact that the EEF average in England and Wales had increased to 38.6±0.8% by that time. We highlight two individuals at Cliffs End Farm in Kent with significantly elevated EEF ancestry at 46.9±2.3% (I14865 dating to 967-811 calBCE (2735±30 BP, GrA-37713), $P=1\times10^{-4}$ for an excess) and 46.9±2.0% (I14861 dating to 912-808 calBCE (2713±29 BP, OxA-17804), $P=8\times10^{-5}$ for an excess), suggesting continued migration through the LBA. While it is possible in theory that we are observing the effect of a short burst of migration in the late MBA and early LBA followed by co-existence of separate communities with different proportions of EEF ancestry, strontium and oxygen isotope analyses confirms long-distance mobility at Cliffs End Farm by identifying multiple individuals of a non-local origin[31], a finding that is more consistent with continuing migration. Strontium isotope ratios for individual I14861 suggest an origin in Scandinavia or the Alps; the latter would be consistent with their high EEF ancestry.

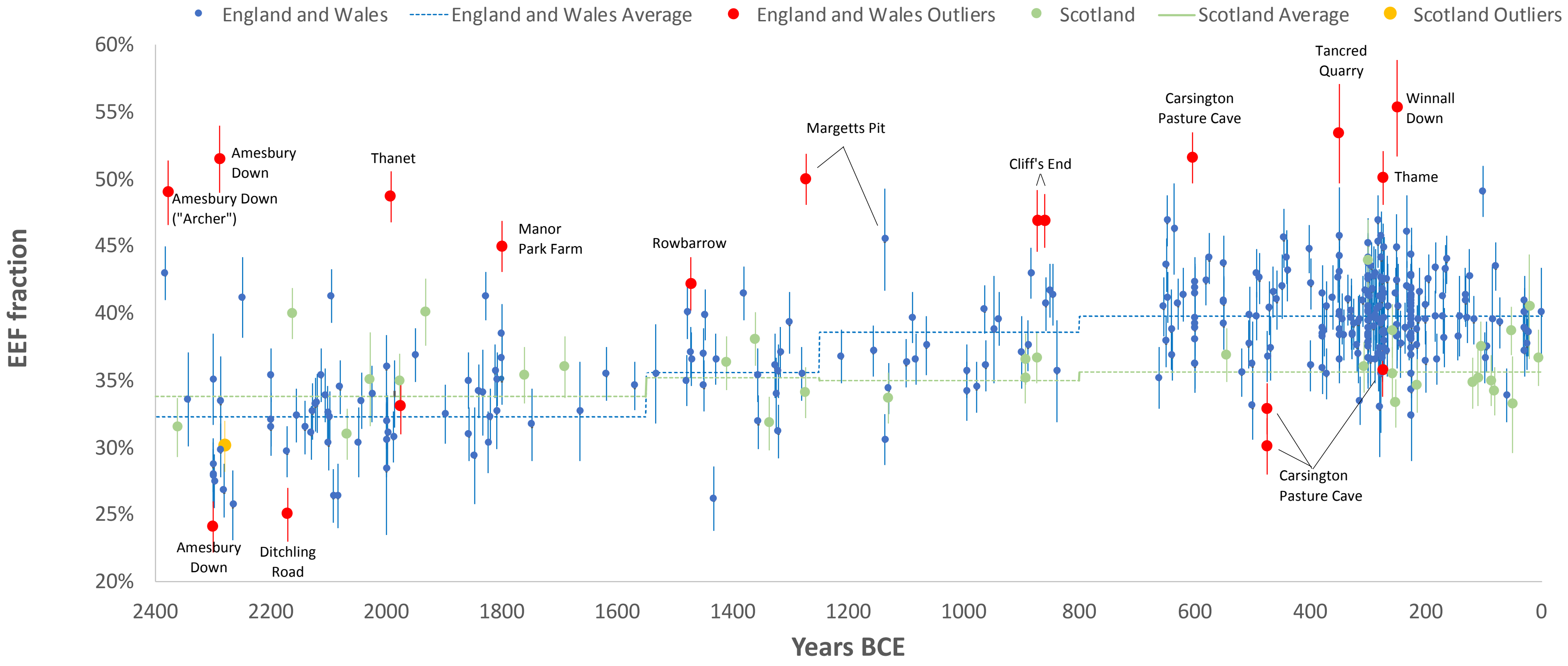


Figure 3: By-individual analysis of the British time transect. *Estimates of EEF ancestry and one standard error for all individuals in the British time transect that pass basic quality control, that fit to a three-way admixture model (EEF + WHG + Yamnaya) at p>0.01 using qpAdm, and that date to 2450-1 BCE (we plot individuals based on the average of the date interval shown in Online Table 6: either a direct radiocarbon date or an archaeological context date range). The averages for the main clusters in both southern and northern Britain in each period are shown in dashed lines; significant outliers at the ancestry tails are shown in red (for England and Wales) and orange (for Scotland). Outliers like the three Middle and Late Bronze individuals at Margetts Pit and Cliffs End could reflect the source population for the increase in EEF ancestry in the LBA.*

Fourth, we observe isolated cases of ancestry outliers through the IA. EEF ancestry in I14803 from Thame, Oxfordshire (dated to 370-175 calBCE (2204±30 BP, SUERC-95011) is 50.1±0.2% which is significantly above the England and Wales IA average of 39.7±0.5% ($P=8x10^{-8}$ for an excess), and there is extreme diversity of ancestry within burials from Carsington Pasture Cave in Derbyshire (800-150 BCE) with one individual showing significantly elevated EEF ancestry and four others showing reduced EEF ancestry. EEF ancestry proportions in Britain at this time (39.7±0.5%) were lower than in much of Europe, as reflected in the average we observe in contemporary IA individuals from France (46.8±0.8%), Hungary (51.6±0.7%), and Bohemia (46.9±0.6%), and so we would expect to be able to detect any substantial IA migrations from mainland Europe (Figure 4). Thus, while Figure 3 does show isolated individuals from IA Britain with elevated EEF ancestry, the broader lack of a change in EEF ancestry proportion is consistent with a minimal demographic impact of new immigration from mainland Europe and relatively closed and self-sustaining social communities in Britain during the Iron Age.

We also leverage our large sample-size to infer population size change over four millennia in Britain. For this analysis, we take advantage of the fact that when an individual inherits an identical long stretch of DNA on both their mother's and father's side they must share a recent ancestor; the rate of observation of 4-8 centimorgan segments of genetic homogeneity in a person's genome thus provides information about the number of reproducing individuals living in a population in the last few dozen generations prior to the time individuals lived[28]. We infer an approximately constant population size from the beginning of the Neolithic to the end of the EBA, followed by a roughly five-fold expansion in the EBA-to-MBA transition with no significant evidence of further expansion until the end of the IA (Figure 2B). This suggests that the largest population size change in Britain for the four millennia from ~4000-1 BCE occurred shortly before or concurrent with M-LBA migration from the continent, further highlighting the MBA as a critical period of demographic transition in Britain.

We co-analyzed our ancient DNA transects through time in Britain with time transects in Bohemia, The Netherlands, Iberia[32], Hungary, and France[33] (Online Table 7, Extended Data Figure 4, Figure 4, and Online Table 9). Average EEF ancestry increased in this period in Bohemia and the Netherlands, just as it did in Britain. The earliest individuals from Bohemia with increased EEF ancestry are associated with artefacts traditionally classified as part of the LBA Knoviz culture, a component of the broader Urnfield cultural complex which spread from

1300-800 BCE across much of Central Europe. Later individuals have similar EEF proportions, consistent with continuity through the LBA-IA with earlier Urnfield-associated groups. By contrast, in M-LBA France and Hungary there was little change in average EEF ancestry, and this ancestry decreased in M-LBA Iberia (Extended Data Figure 4, Figure 4, Online Table 9). The general increase in EEF ancestry in northern Europe, and its decrease in southern Europe, reflects a broad process of north-south genetic interchange that affected many regions. There are nonetheless some exceptions from more isolated regions, such as Scotland in the far north (Figure 2), and Sardinia in the far south[34,35] (Online Table 9). We considered the possibility of a single unsampled group admixing from one region into all the others, but such a scenario does not fit the data. For example, people of the LBA Urnfield complex of Central Europe do not fit as a simple source for the new ancestry in Britain (Supplementary Information section 5).

This study multiplies by almost ten-fold the number of IA individuals with genome-wide data from Central and Western Europe (from 61 to 572), and as a result makes it possible for the first time to track the frequency change of genetic variants with known biological function into the IA (Online Table 10). In addition to showing how variants associated with light skin pigmentation, such as *SLC45A2*, became more common in the IA throughout Europe[20], we obtain an unexpected result for the A allele at the polymorphism *MCM6-LCT* rs4988235 correlated with lactase persistence into adulthood[20] (Extended Data Figure 5). Previous work showed that the frequency of this allele in IA Iberia was only a small fraction of its present-day incidence, which we confirm by showing that its frequency was ~10% in the IA compared to ~40% today[32], and in Bohemia where its frequency was ~11% in the IA compared to ~51% today. However, in Britain most of the rise in the frequency of this allele had already occurred by the IA (51% compared to the current 73%), suggesting that selection pressures acted earlier in this region (Figure 4, Extended Data Figure 5). There is no evidence that the main rise in frequency of the lactase persistence allele occurred on the European mainland and came into Britain during the M-LBA migrations, since the Margetts Pit and Cliffs End outliers who are plausible members of the migrating population did not carry the allele, and because we observe that most of the rise in frequency of the lactase allele in Britain occurred in the Middle to Late IA. Specifically, we observe the lactase persistence allele frequency rise from ~14% in the LBA to ~26% in IA samples that we can definitively date to before ~400 BCE, to >50% in the pool of later IA samples. This raises the question of whether milk consumption had an economically or culturally more important role in LBA-IA Britain than it did in Central Europe in this period.

In contrast to Neolithic and Beaker-associated ancestry transformations in Britain, both of which involved migration from a highly differentiated source, ancestry transformation in the M-LBA was more subtle. Thus, F_{ST} measuring allele frequency differences between a pool of individuals before and after the M-LBA genetic shift in England and Wales was ~0.002 between the C-EBA and LBA-IA, and ~0.001 between the MBA and LBA-IA (Extended Data Table 4). It is important to recognize that the local pre-LBA population in Britain made a substantial genetic contribution to the post-LBA population; it was far from completely replaced. Direct evidence for this comes from Y chromosome haplogroup R1b-P312 L21/M529 (R1b1a1a2a1a2c1), which today occurs much more frequently in Britain and Ireland (frequency of 14-71% depending on the region[36]) than it does in mainland Europe. We estimate that this haplogroup was already present at 88±6% in sampled individuals from C-EBA Britain (Extended Data Figure 6, Online Table 11), showing that the population established in Britain by the C-EBA contributed substantially to the ancestry of modern Britain (at least on the male line), in contrast to the genetic legacy of the Mesolithic[11] and Neolithic[9,11] people of the islands.

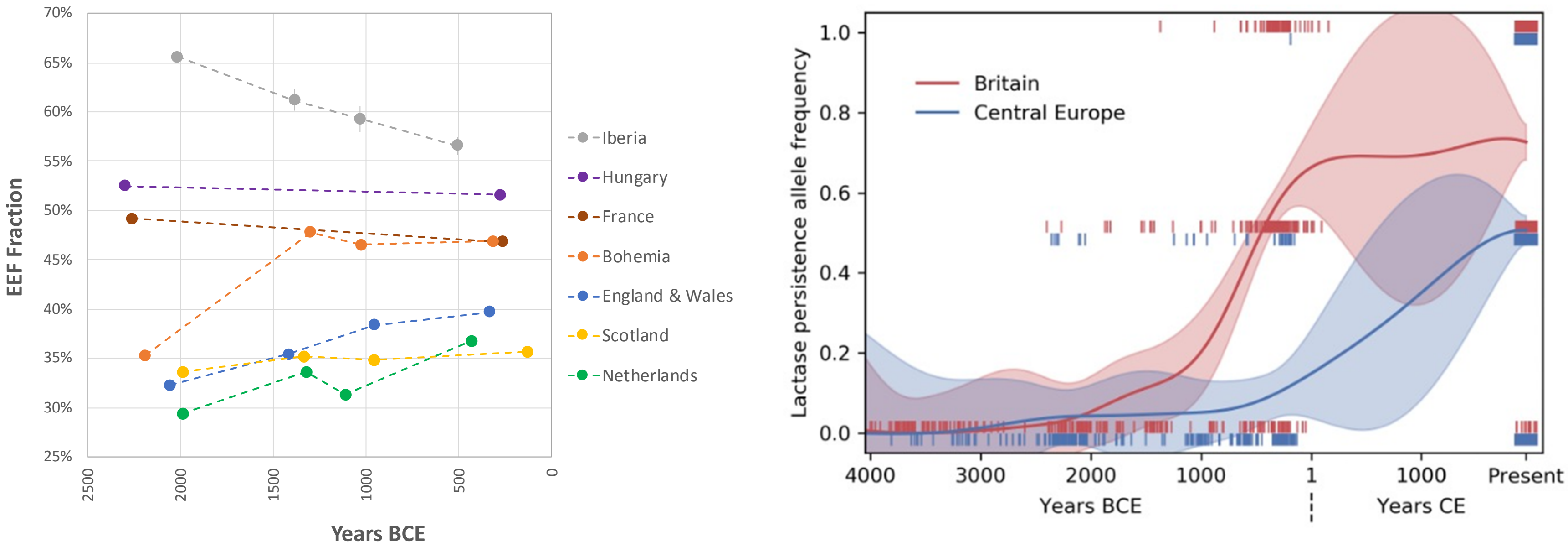


Figure 4: Geographic differences in ancestry component and lactase persistence allele frequency. (Left) *North-South ancestry convergence****.*** *We show seven ancient DNA time transects for up to four periods (2450-1550 BCE, 1550-1250 BCE, 1250-800 BCE, and 800-50 BCE). The dotted lines show which points are regionally grouped and should not be interpreted as implying a smooth change in ancestry over time.* ***(Right)*** *The allele conferring lactase persistence began rising in frequency earlier in Britain than in Central Europe suggesting different selection regimes and possibly cultural differences in the role of dairying in the two regions in the IA. We visualize 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*RationalQuadratic kernel with parameter length_scale_bounds=(1, 1000). We used the GLIMPSE*[37] *software to impute diploid genotype posterior probabilities (GP), restricting to samples with max(GP)>0.9 for this SNP. The analysis includes 376 ancient individuals from Britain and 261 from Central Europe (Czech Republic, Slovakia, Croatia, Hungary, Austria, and Slovenia); to represent modern Britain we used a pool of 190 CEU and GBR individuals from the 1000 Genomes Project*[38]*, and to represent modern Central Europe we use 288 from modern Czechia*[39]*. Each vertical bar represents 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 output by the Gaussian process. We confirmed the significantly earlier rise in frequency of the allele in Britain by randomly sampling a single sequence at each position; Extended Data Figure 5 shows that in the IA the derived allele frequency was 51% in Britain (46-56% 95% confidence interval) compared to 11% (4-19%) for Bohemia.*

To gain insight into the possible sources of the ancestry that spread across England and Wales during the LBA, and to quantify the magnitude of gene flow, we fit the pooled IA individuals from England and Wales as a mixture of a group related to the main C-EBA cluster from England and Wales, and a second source. We examined 71 potential second sources: 69 from mainland Europe, the Margetts Pit outlier, and the pool of two Cliffs End outliers. We then carried out model testing using reference populations in *qpAdm* that had power to distinguish ancestry from C-EBA and IA England and Wales (Supplementary Information Section 6). We identified 17 putative sources that could fit at p>0.05. After probing each with 38 more stringent *qpAdm* testing, we reduced this to six plausible models (Table 2). The Margetts Pit and Cliffs End outliers both fit, consistent with their being immigrants or early generation descendants of immigrants. Our analysis also produces insight into the likely source of migration. Of the other four working surrogates for the source population, three out of four are from France (the one exception is an IA group from Hungary, whose limited data may be the reason for the fit). One fitting source from France is E-MBA Occitanie in the southwest (2100-1200 BCE), a second is IA Occitanie (600-200 BCE) and a third is IA Hauts-de-France (400-100 BCE). The IA groups post-date the LBA ancestry change in Britain by several centuries and so cannot be direct sources; however, they are plausibly descended from earlier populations in their regions or geographic vicinity that could be the true sources. The six fitting models also provide a quantitative estimate of the proportion of novel ancestry arriving into M-LBA England and Wales, ranging from Margetts Pit (42.6±4.4%) to E-MBA Occitanie (44.1±3.4%) to Cliffs End (50.3±5.3%) to IA Hauts de France (69.6±7.8%) (Table 2). Thus, a minimum of around half the ancestry of England and Wales owes its origin to the M-LBA population movements. The estimate of ~50% genome-wide population turnover by the end of this period is substantially larger than the estimate (23±8%) derived by estimating the degree of population turnover needed to decrease the proportion of L21/M529 Y chromosome haplogroups from 88±6% in C/EBA Britain to 66±5% by the IA (Extended Data Figure 6). While these results taken at face value suggest a female-biased spread of mainland European ancestry into Britain in the LBA, this inference is tentative as it assumes that L21/M529 haplogroups were not present among the migrants and that there was no social selection within Britain for L21/M529 male-line lineages; if either assumption was incorrect, we would be underestimating the male contribution. The possibility of female sex bias associated with the ancestry transition in the LBA is striking in light of evidence of Saxon migrations being sex-biased in the reverse direction[40,41]. For example, in present-day Central and Eastern Britain the M529 haplogroup frequency is 14% (Extended Data Figure 6) implying a minimum ~79% male-lineage replacement since IA times, greater than the ~30-40% ancestry contribution from Saxon migrations implied by previous work[13,14] but consistent with estimates based on contemporary Y chromosome data[41] (this computation does not consider the possible contribution of non-Saxon post-IA migrations).

Table 2: Working proxies for the new source of ancestry in Iron Age England

Second Source	*n*	Date range	Basic ancestry estimate	Std. error	P-value basic	P-value model competition
England Margetts Pit outlier	1	1400-1100 BCE	42.6%	4.4%	0.57	0.43
England Cliffs End outliers	2	1000-800 BCE	50.3%	5.3%	0.92	0.77
France Occitanie EMBA	2	2100-1200 CE	44.1%	3.4%	0.17	0.32
France Occitanie IA	6	600-200 BCE	43.5%	3.1%	0.35	0.99
France Hauts De France IA	2	400-100 BCE	69.6%	7.8%	0.42	0.72
Hungary IA Celtic	3	500-1 CE	59.2%	8.6%	0.09	0.43

Note: Right populations for the basic ancestry estimate from qpAdm are (Mbuti.SDG, Netherlands_BellBeaker, Poland_Globular_Amphora, WHGA, Russia_Samara_EBA_Yamnaya, and Turkey_N). The first source is always England C/EBA. This analysis identifies 17 fitting populations at P>0.05 (Supplementary Information section 6 gives the full list), and here we only show the subset that continues to fit after adding 38 pre-1000BP European populations to the reference set, then Bonferroni correcting the lowest p-value for the 38 hypotheses tested.

The genetic links we report between England and Wales and parts of mainland Europe are striking in light of the archaeological record. The M-LBA has long been recognized as a time when cultural connections between Britain and regions of mainland Europe intensified. In this period, Britain and Ireland formed part of the 'Atlantic Bronze Age', a network of societies located along the Atlantic façade of Europe (including western Iberia and present-day northern and western France) that shared aspects of material culture and ritual practice[42]. Societies on both sides of the Channel, while far from culturally homogeneous, shared features including elevated enclosures (hillforts), diverse bronze swords and axes, bronze feasting equipment, sources of metals, and ritual deposition of metalwork hoards often around water[43-45]. The similarity in the rites of metalwork deposition suggest that these commonalities did not just reflect exchange of objects and methods of production, but also shared systems of belief. Early models of cultural change in LBA Britain often invoked 'invasion' from Central Europe[46], while more recent discussions have emphasized trade, exchange, economy and the sharing of ideas[42,47]. Our genetic analyses provide overwhelming evidence that major movements of people into Britain occurred during the M-LBA, particularly during a period of intensification of exchange that led to the formation of the 'Manche-Mer du Nord (MMN) complex' among other cultural phenomena[48,49]. Our findings do not establish whether the population movements we detect were a cause or consequence of networks established as part of the Atlantic Bronze Age, but do suggest that interactions between local populations of Britain and new migrants bringing ideas from mainland Europe may be responsible for some of the cultural change we see in M-LBA England and Wales. We do not have sample sizes from the Atlantic façade of mainland Europe that are comparable to what we report from Britain, and thus cannot test if the gene flow between the two regions in the M-LBA was largely unidirectional; ancient DNA sampling from northern France would make it possible to quantify the amount of gene flow in the reverse direction.

Population movements are often a significant factor in cultural change, including in languages[50,51]. In the context of our results, it is therefore striking that a recent study has proposed that Celtic languages spread into Britain from France likely in the early IA or possibly the LBA[52]. Our identification of substantial M-LBA population movements into Britain from sources that fit populations in France notably better than in Iberia, the Netherlands, and Bohemia adds an independent line of evidence for this scenario. Moreover, our finding of a decrease of EEF ancestry in Iberia, where the proportion was high in the EBA, and the roughly simultaneous increase in Britain where the proportion was low, could, in theory, reflect a Celtic-speaking group of people with intermediate EEF ancestry spreading into both regions, and could help to explain the occurrence of Celtic languages in both regions. Alternatively, this homogenization of EEF ancestry could reflect a generalized increase in mobility over the region and period of the Atlantic Bronze Age, facilitated by the emergence of a Celtic lingua franca[53]. While the fact that we do not detect an ancestry change in Scotland might seem like a problem for either of these related proposals, the lack of major ancestry change in Scotland might coincide with the evidence that a non-Celtic language remained in use into the first millennium CE in Scotland[54]. Our finding that there were no major migrations into Britain from the European mainland in the IA suggests that, if Celtic language spread was driven by the movement of people, it is unlikely to have happened in the IA. The adoption in IA Britain of cultural practices that originated in mainland Europe—particularly those linked to the La Tène tradition[55]—were also evidently independent of large-scale population movements, although there certainly were smaller movements of people, as attested by individual IA outliers with high EEF ancestry such as those at Thame or Winnall Down, and individuals with low EEF ancestry such as several at Carsington Pasture Cave (Figure 3).

In the IA, EEF ancestry was highest in present-day southern England; lower in Wales, the Midlands, and the north of England (2.0-2.3% lower); and lowest in all regions of Scotland (Table 1); suggesting a broad south-north cline of decreasing EEF ancestry. Within the south of

Britain we detect six regional groupings with significantly different patterns of allele sharing with mainland groups: Wales, the combined region of northern England and the Midlands, the combined region of southeast and south-central Britain, Cornwall, East Anglia, and East Yorkshire (Extended Data Table 2). To understand this process in more detail, we carried out a *qpAdm* analysis fitting all the British IA groups as mixtures of the England C/EBA population and the six populations in Table 2 that fit as sources for the later migration (Online Table 12). We can fully explain the regional variation in ancestry in the IA in England and Wales as being driven by different proportions of ancestry from the population that spread through the region in the LBA; using Margetts Pit as the source of migration, we obtain estimates ranging from 51±6% in south-central England to 31±5% and 32±5% in northern England and the Midlands (Table 1). Thus, the Iron Age was a period when material culture was increasingly regional in character[56]; as we show here, this was accompanied by subtle biological structure. A striking example is in East Yorkshire, where most of our analyzed individuals are associated with Arras Culture burial contexts, comprising square-ditched barrows and occasional chariot burials, and where our estimate of the new ancestry source is 45±5%[57,58]. Similarities between Arras funerary traditions in East Yorkshire and those recorded for IA societies in mainland Europe, particularly the Paris Basin and the Ardennes / Champagne Regions of France and Belgium, have led to suggestions that IA societies in East Yorkshire had been influenced by migrations from mainland Europe[59]. In this context, it is notable that differentiation between IA populations in Britain, as measured by F_{ST}, is highest between East Yorkshire and all other IA populations in England and Wales (Extended Data Table 5). Our analysis suggests that people buried in the style of the Arras Culture did indeed harbor a large proportion of ancestry most likely from France. However, without ancient DNA from the IA from the putative sources in mainland Europe we cannot determine whether this reflects the same M-LBA source that contributed to other southern British populations (followed by isolation within the island of Britain leading to high population-specific genetic drift), or alternatively distinctive migrations from mainland Europe in the IA specifically affecting this region.

An important direction for future work will be to generate new ancient DNA data from mainland contexts and Ireland to test the alternative scenarios of population history raised here, and to develop theories integrating the genetic findings within archaeological frameworks.

Methods

Ancient DNA laboratory work. 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 a variety of methods including sandblasting, drilling and milling[60,61]. We extracted DNA using a variety of methods[62-64], and prepared double- or single-stranded libraries almost all of them treated with the enzyme Uracil DNA Glycosylase (UDG) to reduce characteristic errors associated with ancient DNA degradation[16-18,65]. We enriched these sequences manually or in multiplex using automated liquid handlers for sequences overlapping the mitochondrial genome[21,66] as well as about 1.24 million single nucleotide polymorphisms ("1240K capture")[19]. We pooled enriched libraries which we had marked with unique 7-base pair internal barcodes and/or 7- to 8-base pair indices and sequenced on Illumina NextSeq500 or HiSeqX10 instruments using paired-end reads of either 76 base pairs or 101 base pairs in length (Online Table 3).

Bioinformatic analysis. After trimming barcodes and adapters[7], we merged read pairs that had at least 15 base pairs of overlap allowing no more than one mismatch. We aligned merged sequences to the mitochondrial reference genome RSRS[67] or the human reference genome hg19 using *BWA* version 0.6.1[68]. 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, we selected a single copy of each such sequence that had the highest base quality scores. For subsequent analysis, we trimmed the last 2 bases of each sequence for UDG-treated libraries and the last 5 bases for non-UDG-treated libraries to reduce the effects of characteristic errors associated with ancient DNA degradation. We built mitochondrial consensus sequences, determined mitochondrial haplogroups using *HaploGrep2*[69], and estimated the match rate to the consensus sequence using contamMix v.1.0-12[70] for mitochondrial genomes with an average coverage of at least 2-fold. To represent the autosomal data, we randomly sampled a single sequence covering each of the 1.24 million SNP targets, and estimated coverage based on these targeted SNPs. We used *ANGSD* to estimate contamination based on polymorphism on the X chromosome in males with at least 200 SNPs covered twice (males should be non-polymorphic if their data are uncontaminated)[23]. 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 the 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).

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 <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 libraries[16] and >10% for single-stranded USER-treated libraries and double-stranded non-UDG-treated libraries[71]. 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, 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 analyzed only sequences with terminal damage to enrich for genuine ancient DNA by using *pmdtools*, allowing us to rescue data for some individuals[72]. We do not include in our main analyses data from 71 individuals that failed our authenticity criteria (marked as “QUESTIONABLE” in Online Table 1); however, we publish the data as part of this study as a resource.

Population genetic analyses. We used ADMIXTURE to cluster individuals and used Principal Component Analysis as implemented in *smartpca* to visualize gradients of ancestry and genetic drift, using the option *lsqproject* to project ancient individuals onto the patterns of genetic variation learned from modern individuals[73]. We computed f_4-statistics and F_{ST} and carried out *qpWave* and *qpAdm* analyses using ADMIXTOOLS[27] (https://github.com/DReichLab/AdmixTools). We inferred relatives up to the third to fifth degree using a previously described method[24].

Allele frequency estimates of variants with functional importance. We clustered individuals from Britain, Iberia and Czech Republic into 5 temporal groups-3950-2450 BCE, 2450-1550 BCE, 1550-1250 BCE, 1250-800 BCE, and 800-50 BCE-matching our periodization into Neolithic, C-EBA, MBA, LBA, and IA in Britain. To estimate the allele frequency of a given SNP in a particular group, we used sequence counts at each SNP position in each individual and used a maximum likelihood approach[20]. We obtained confidence intervals using the Agresti-Coull method implemented in the *binom.confint* function of the R-package *binom.*

Accelerator Mass Spectrometry (AMS) radiocarbon dating. We carried out AMS dating at a variety of laboratories; we refer readers to the individual laboratories for the experimental procedures. We calibrated all dates using OxCal 4.4.2[74] and IntCal20[75].

Data availability. The aligned sequences are available through the European Nucleotide Archive under accession number [to be made available on publication]. Genotype data used in analysis are available at https://reich.hms.harvard.edu/datasets. Any other relevant data are available from the corresponding authors upon reasonable request.

Acknowledgments

We thank Aurore Schmitt for sharing skeletal material and assisting with archaeological contextualization for six newly reported individuals from the Late Neolithic or Early Bronze Age-associated Villard site. We thank Rachel Crellin for comments on the manuscript. This project received funding from the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation programme (grant agreement No. 834087; the COMMIOS Project to I.A.). M.B.G.F. was funded by The Leverhulme Trust via a Doctoral Scholarship scheme awarded to M.P. and M.B.R. M.L. was supported by the South, West & Wales Doctoral Training Partnership. M.G.'s osteological analyses were funded by Culture Vannin. We acknowledge support for radiocarbon dating and stable isotope analyses as well as access to skeletal material from Manx National Heritage and Alison Fox. For the Blaydon burial, we thank Myra Giesen and Andy Parkin at the Great North Museum for assistance with sample selection. Dating analysis was funded by Leverhulme Trust grant RPG-388. M.G.T. and I.B. were supported by a Wellcome Trust Investigator Award (project 100713/Z/12/Z). The research directed by D.R. was funded by NIH (NIGMS) grant GM100233, the Paul Allen Foundation, the John Templeton Foundation grant 61220, a private donation by Jean-Francois Clin, and the Howard Hughes Medical Institute.

Extended Data Table 1: Ancestry change over time in Britain

		qpAdm results							*Tests for difference in ancestry proportions between row and column (below diagonal qpWave, above-diagonal f4-statistic)*																				
	Sample size	qpAdm P-value	WHG	EEF	Steppe	WHG error	EEF error	Steppe	Channel Islands IA	Channel Islands Neolithic	England IA	England LBA	England MBA	England Chalcolithic/EBA	England Neolithic	Ireland Neolithic	Isle of Man Chalcolithic/EBA	Scotland IA	Scotland LBA	Scotland MBA	Scotland Chalcolithic/EBA	Scotland Neolithic	Wales IA	Wales MBA	Wales Neolithic
Channel Islands IA	2	0.88	13.4%	46.4%	40.2%	1.3%	1.6%	1.9%	..	$< 10^{-12}$	$3x10^{-5}$	$3x10^{-6}$	$4x10^{-10}$	$< 10^{-12}$	$< 10^{-12}$	$< 10^{-12}$	0.68	$2x10^{-9}$	$2x10^{-5}$	$1x10^{-7}$	$6x10^{-9}$	$< 10^{-12}$	$9x10^{-4}$	$6x10^{-11}$	$< 10^{-12}$
Channel Islands Neolithic	3	0.57	11.8%	86.9%	1.3%	1.3%	1.6%	1.6%	$< 10^{-12}$	..	$< 10^{-12}$	$< 10^{-12}$	$< 10^{-12}$	$< 10^{-12}$	0.071	0.074	$< 10^{-12}$	$< 10^{-12}$	$< 10^{-12}$	$< 10^{-12}$	$< 10^{-12}$	0.063	$< 10^{-12}$	$< 10^{-12}$	0.015
England IA	231	0.32	12.0%	39.8%	48.2%	0.4%	0.5%	0.6%	$5x10^{-4}$	$< 10^{-12}$	..	0.040	$< 10^{-12}$	$< 10^{-12}$	$< 10^{-12}$	$< 10^{-12}$	0.16	$1x10^{-9}$	$1x10^{-5}$	0.0016	$2x10^{-5}$	$< 10^{-12}$	0.89	$2x10^{-8}$	$< 10^{-12}$
England LBA	17	0.079	11.7%	38.6%	49.7%	0.6%	0.8%	0.9%	$5x10^{-5}$	$< 10^{-12}$	0.10	..	0.0016	$< 10^{-12}$	$< 10^{-12}$	$< 10^{-12}$	0.083	0.0090	0.011	0.091	0.016	$< 10^{-12}$	0.45	$3x10^{-5}$	$< 10^{-12}$
England MBA	25	0.16	11.7%	35.6%	52.7%	0.5%	0.7%	0.8%	$1x10^{-8}$	$< 10^{-12}$	$< 10^{-12}$	0.0014	..	$4x10^{-8}$	$< 10^{-12}$	$< 10^{-12}$	0.018	0.81	0.58	0.80	0.92	$< 10^{-12}$	0.016	0.0087	$< 10^{-12}$
England Chalcolithic/EBA	54	0.020	11.0%	32.3%	56.7%	0.5%	0.6%	0.7%	$< 10^{-12}$	$< 10^{-12}$	$< 10^{-12}$	$< 10^{-12}$	$1x10^{-7}$		$< 10^{-12}$	$< 10^{-12}$	0.0011	$5x10^{-7}$	0.011	0.0015	$9x10^{-4}$	$< 10^{-12}$	$4x10^{-6}$	0.80	$< 10^{-12}$
England Neolithic	35	0.012	17.0%	81.8%	1.2%	0.5%	0.6%	0.6%	$< 10^{-12}$	$5x10^{-5}$	$< 10^{-12}$	$< 10^{-12}$	$< 10^{-12}$	$< 10^{-12}$	..	0.95	$< 10^{-12}$	$< 10^{-12}$	$< 10^{-12}$	$< 10^{-12}$	$< 10^{-12}$	0.83	$< 10^{-12}$	$< 10^{-12}$	0.18
Ireland Neolithic	28	$< 10^{-12}$	18.0%	83.1%	-1.1%	0.5%	0.6%	0.6%	$< 10^{-12}$	$2x10^{-7}$	$< 10^{-12}$	$< 10^{-12}$	$< 10^{-12}$	$< 10^{-12}$	$1x10^{-11}$	..	$< 10^{-12}$	$< 10^{-12}$	$< 10^{-12}$	$< 10^{-12}$	$< 10^{-12}$	0.77	$< 10^{-12}$	$< 10^{-12}$	0.16
Isle of Man Chalcolithic/EBA	1	0.12	10.4%	46.7%	42.8%	2.3%	3.5%	3.8%	0.49	$< 10^{-12}$	0.17	0.14	0.024	0.0029	$< 10^{-12}$	$< 10^{-12}$	..	0.019	0.013	0.026	0.018	$< 10^{-12}$	0.17	0.0017	$< 10^{-12}$
Scotland IA	23	0.0015	10.4%	35.6%	54.1%	0.6%	0.7%	0.9%	$3x10^{-8}$	$< 10^{-12}$	$7x10^{-10}$	0.044	$7x10^{-4}$	$1x10^{-6}$	$< 10^{-12}$	$< 10^{-12}$	0.052	..	0.49	0.92	0.79	$< 10^{-12}$	0.024	0.008	$< 10^{-12}$
Scotland LBA	4	0.011	10.1%	35.0%	54.8%	0.9%	1.2%	1.3%	$1x10^{-7}$	$< 10^{-12}$	$4x10^{-5}$	0.052	0.047	0.021	$< 10^{-12}$	$< 10^{-12}$	0.047	0.88	..	0.53	0.70	$< 10^{-12}$	0.013	0.063	$< 10^{-12}$
Scotland MBA	4	0.16	12.1%	35.2%	52.6%	0.9%	1.1%	1.3%	$4x10^{-6}$	$< 10^{-12}$	0.011	0.23	0.95	0.015	$< 10^{-12}$	$< 10^{-12}$	0.043	0.31	0.36	..	0.77	$< 10^{-12}$	0.063	0.025	$< 10^{-12}$
Scotland Chalcolithic/EBA	8	0.0060	12.3%	33.8%	53.8%	0.8%	1.0%	1.1%	$1x10^{-7}$	$< 10^{-12}$	$3x10^{-7}$	$6x10^{-4}$	0.093	$3x10^{-5}$	$< 10^{-12}$	$< 10^{-12}$	0.023	$1x10^{-4}$	0.0061	0.32	..	$< 10^{-12}$	0.025	0.024	$< 10^{-12}$
Scotland Neolithic	32	$2x10^{-5}$	17.4%	80.8%	1.8%	0.5%	0.6%	0.6%	$< 10^{-12}$	$3x10^{-6}$	$< 10^{-12}$	$< 10^{-12}$	$< 10^{-12}$	$< 10^{-12}$	0.26	$< 10^{-12}$	$< 10^{-12}$	$< 10^{-12}$	$< 10^{-12}$	$< 10^{-12}$	$< 10^{-12}$	..	$< 10^{-12}$	$< 10^{-12}$	$< 10^{-12}$
Wales IA	4	0.17	10.8%	37.9%	51.3%	1.1%	1.5%	1.6%	0.0092	$< 10^{-12}$	0.97	0.89	0.074	$8x10^{-5}$	$< 10^{-12}$	$< 10^{-12}$	0.23	0.12	0.073	0.26	0.022	$< 10^{-12}$	..	$2x10^{-4}$	$< 10^{-12}$
Wales MBA	5	0.59	12.9%	34.3%	52.8%	1.0%	1.3%	1.5%	$2x10^{-9}$	$< 10^{-12}$	$4x10^{-7}$	$4x10^{-4}$	0.057	0.93	$< 10^{-12}$	$< 10^{-12}$	0.0054	0.027	0.16	0.16	0.042	$< 10^{-12}$	0.0029	..	$< 10^{-12}$
Wales Neolithic	6	0.21	15.9%	80.7%	3.4%	1.0%	1.4%	1.5%	$< 10^{-12}$	0.0016	$< 10^{-12}$	$< 10^{-12}$	$< 10^{-12}$	$< 10^{-12}$	0.44	0.0026	$< 10^{-12}$	$< 10^{-12}$	$< 10^{-12}$	$< 10^{-12}$	$< 10^{-12}$	0.24	$< 10^{-12}$	$< 10^{-12}$	..

Note: We pool all individuals from each period and region while removing from the analysis outlier individuals that fail *qpAdm* modeling at p<0.005 as specified in Online Table 6. In the left columns are *qpAdm* estimates of ancestry for each group for the three-way admixture model. Above the diagonal are 2-sided p-values based on the *Z*-score from f_4*(Row population, Column population; Turkey_Neolithic, Russia_Samara_EBA_Yamnaya)*. Below the diagonal are p-values from Hotelling's T-squared tests from *qpWave* using Left=(Row population, Column population) and Right=(*Mbuti.SDG, Russia_Samara_EBA_Yamnaya, Turkey_N, WHGA*). For the tests of differences in ancestry proportion, P-values are highlighted if <0.001.

Extended Data Table 2: Genetic substructure among regions in Iron Age Britain. As shown in Online Table 12 and in Table 1, the significant differences between pairs of populations in England and Wales are in principle consistent with being driven by just a single migration from mainland Europe affecting different Iron Age groups in different proportions.

			England and Wales								Scotland		
			Southcentral	**Southeast**	**East Yorkshire**	**East Anglia**	**Cornwall**	**Midlands**	**North**	**Wales**	**Orkney**	**Southeast**	**West**
		N	84	38	35	20	17	20	17	4	4	12	7
England & Wales	**Southcentral**	84	■	0.13	$8x10^{-6}$	$2x10^{-4}$	$7x10^{-6}$	$2x10^{-9}$	$8x10^{-9}$	0.23	$<10^{-12}$	$<10^{-12}$	$<10^{-12}$
	Southeast	38	0.38	■	$4x10^{-4}$	0.0056	$6x10^{-4}$	$3x10^{-6}$	$1x10^{-6}$	0.21	$4x10^{-12}$	$<10^{-12}$	$<10^{-12}$
	East Yorkshire	35	0.81	0.81	■	$7x10^{-11}$	0.0012	$7x10^{-4}$	0.0015	0.55	$2x10^{-7}$	$2x10^{-10}$	$2x10^{-10}$
	East Anglia	20	0.0030	0.051	0.11	■	$1x10^{-4}$	$4x10^{-7}$	$7x10^{-9}$	0.04	$<10^{-12}$	$<10^{-12}$	$<10^{-12}$
	Cornwall	17	0.0027	0.014	0.046	0.81	■	0.0016	0.31	0.89	$3x10^{-6}$	$3x10^{-7}$	$2x10^{-10}$
	Midlands	20	$2x10^{-7}$	$9x10^{-6}$	$2x10^{-4}$	0.010	0.074	■	0.059	0.14	$8x10^{-6}$	$2x10^{-4}$	$8x10^{-8}$
	North	17	$5x10^{-5}$	$2x10^{-4}$	0.0024	0.030	0.19	0.66	■	0.76	0.0017	$9x10^{-4}$	$2x10^{-5}$
	Wales	4	0.82	0.83	0.93	0.81	0.78	0.47	0.69	■	0.020	0.0056	0.0051
Scotland	**Orkney**	4	$5x10^{-5}$	$5x10^{-5}$	$3x10^{-4}$	$8x10^{-4}$	0.0085	0.073	0.14	0.091	■	0.023	0.37
	Southeast	12	$4x10^{-11}$	$2x10^{-9}$	$4x10^{-8}$	$4x10^{-6}$	$8x10^{-5}$	0.10	0.0079	0.041	0.012	■	0.14
	West	7	$8x10^{-7}$	$4x10^{-6}$	$3x10^{-5}$	$9x10^{-4}$	0.0091	0.55	0.47	0.22	0.56	0.11	■

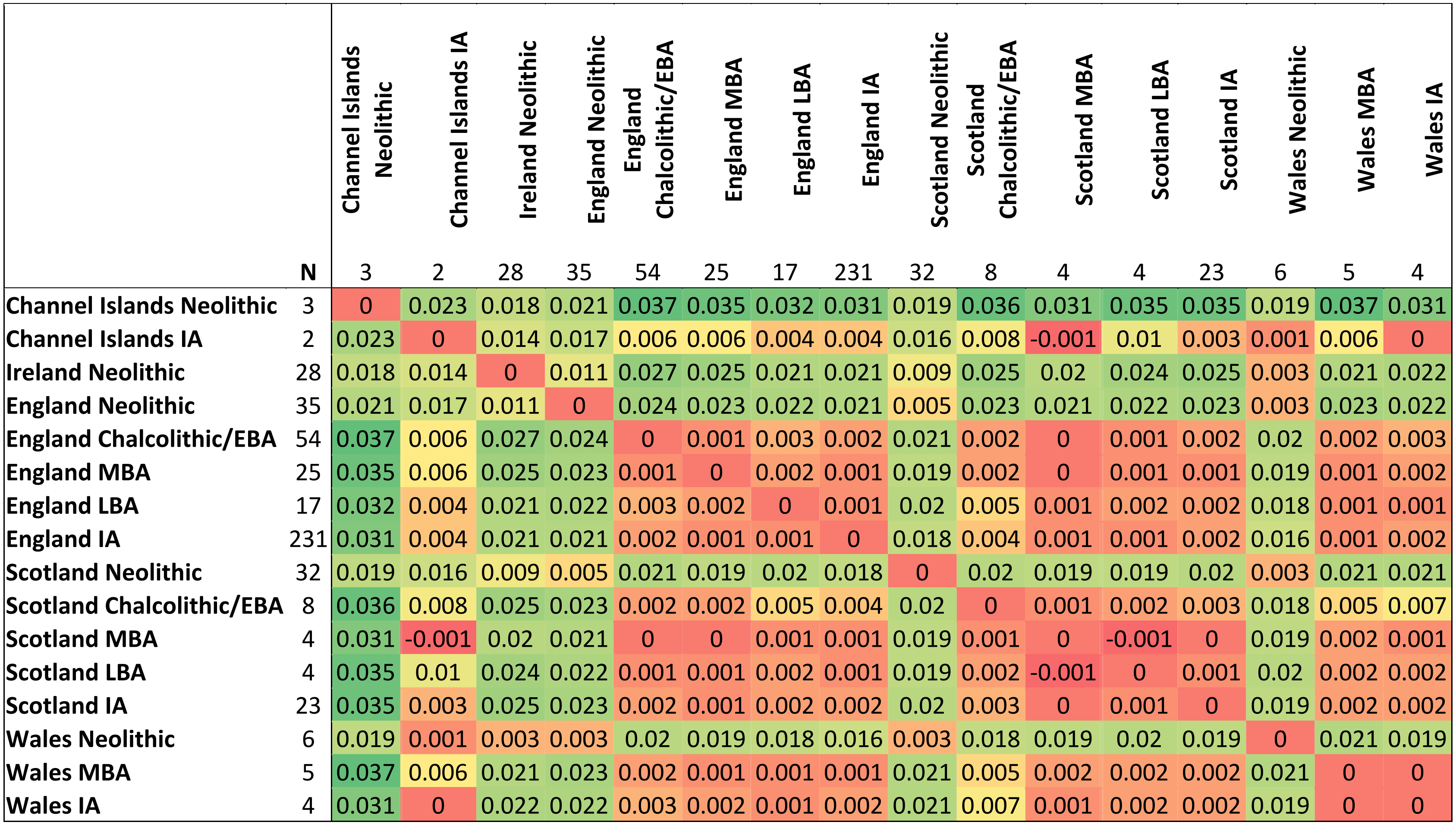
Note: Outgroups for qpWave analyses are: (Below diagonal right set 1) Mbuti.SDG, WHGA, Russia_Samara_EBA_Yamnaya, Turkey_N; (Above diagonal right set 2) Mbuti.SDG, Netherlands_BellBeaker, Poland_Globular_Amphora, Iberia_C, Czech_EBA, Italy_Sardinia_EBA, Russia_Samara_EBA_Yamnaya, Turkey_N

Extended Data Table 3: LBA and Iron Age populations had ancestry absent in earlier people from Britain

Modeled population	P-value for modeling with England/Wales sources	P-value for modeling with Scotland sources
England.and.Wales_N	n/a (defined as a source)	0.033
England.and.Wales_C.EBA	n/a (defined as a source)	0.000078
England.and.Wales_MBA	0.0060	0.00001
England.and.Wales_LBA	$< 10^{-12}$	$< 10^{-12}$
England.and.Wales_IA	$< 10^{-12}$	$< 10^{-12}$
Scotland_N	0.025	n/a (defined as a source)
Scotland_C.EBA	0.000055	n/a (defined as a source)
Scotland_MBA	0.90	0.039
Scotland_LBA	0.0071	0.0066
Scotland_IA	0.012	2×10^{-4}
Isle.of.Man_C.EBA	0.10	0.050
Ireland_N	$< 10^{-12}$	$< 10^{-12}$
Ireland_C.EBA	$< 10^{-12}$	$< 10^{-12}$
Channel.Islands_N	4×10^{-6}	$< 10^{-12}$
Channel.Islands_IA	0.56	0.13

Note: We model each group in *qpAdm* as a mixture of a Neolithic and a Chalcolithic/EBA population (first column from England and Wales, second column from Scotland). In each case the reference populations are (*Mbuti.SDG, Netherlands_BellBeaker, Poland_Globular_Amphora, WHGA, Iberia_C, Czech_EBA, Italy_Sardinia_EBA, Russia_Samara_EBA_Yamnaya, Turkey_N)*. P-values from *qpAdm* are highlighted if <0.001. We definitively reject the model that people of LBA and IA England and Wales are directly descended from a mixture of Neolithic and C/EBA people from England and Wales (the failure of the models involving Irish populations may not reflect real modeling failure but instead could reflect systematic differences in data properties between shotgun sequencing data and in-solution enrichment data).

Extended Data Table 4: Pairwise F_{ST} among coarse population groupings in the British Isles



	N	Channel Islands Neolithic	Channel Islands IA	Ireland Neolithic	England Neolithic	England Chalcolithic/EBA	England MBA	England LBA	England IA	Scotland Neolithic	Scotland Chalcolithic/EBA	Scotland MBA	Scotland LBA	Scotland IA	Wales Neolithic	Wales MBA	Wales IA
N		3	2	28	35	54	25	17	231	32	8	4	4	23	6	5	4
Channel Islands Neolithic	3	0	0.023	0.018	0.021	0.037	0.035	0.032	0.031	0.019	0.036	0.031	0.035	0.035	0.019	0.037	0.031
Channel Islands IA	2	0.023	0	0.014	0.017	0.006	0.006	0.004	0.004	0.016	0.008	-0.001	0.01	0.003	0.001	0.006	0
Ireland Neolithic	28	0.018	0.014	0	0.011	0.027	0.025	0.021	0.021	0.009	0.025	0.02	0.024	0.025	0.003	0.021	0.022
England Neolithic	35	0.021	0.017	0.011	0	0.024	0.023	0.022	0.021	0.005	0.023	0.021	0.022	0.023	0.003	0.023	0.022
England Chalcolithic/EBA	54	0.037	0.006	0.027	0.024	0	0.001	0.003	0.002	0.021	0.002	0	0.001	0.002	0.02	0.002	0.003
England MBA	25	0.035	0.006	0.025	0.023	0.001	0	0.002	0.001	0.019	0.002	0	0.001	0.001	0.019	0.001	0.002
England LBA	17	0.032	0.004	0.021	0.022	0.003	0.002	0	0.001	0.02	0.005	0.001	0.002	0.002	0.018	0.001	0.001
England IA	231	0.031	0.004	0.021	0.021	0.002	0.001	0.001	0	0.018	0.004	0.001	0.001	0.002	0.016	0.001	0.002
Scotland Neolithic	32	0.019	0.016	0.009	0.005	0.021	0.019	0.02	0.018	0	0.02	0.019	0.019	0.02	0.003	0.021	0.021
Scotland Chalcolithic/EBA	8	0.036	0.008	0.025	0.023	0.002	0.002	0.005	0.004	0.02	0	0.001	0.002	0.003	0.018	0.005	0.007
Scotland MBA	4	0.031	-0.001	0.02	0.021	0	0	0.001	0.001	0.019	0.001	0	-0.001	0	0.019	0.002	0.001
Scotland LBA	4	0.035	0.01	0.024	0.022	0.001	0.001	0.002	0.001	0.019	0.002	-0.001	0	0.001	0.02	0.002	0.002
Scotland IA	23	0.035	0.003	0.025	0.023	0.002	0.001	0.002	0.002	0.02	0.003	0	0.001	0	0.019	0.002	0.002
Wales Neolithic	6	0.019	0.001	0.003	0.003	0.02	0.019	0.018	0.016	0.003	0.018	0.019	0.02	0.019	0	0.021	0.019
Wales MBA	5	0.037	0.006	0.021	0.023	0.002	0.001	0.001	0.001	0.021	0.005	0.002	0.002	0.002	0.021	0	0
Wales IA	4	0.031	0	0.022	0.022	0.003	0.002	0.001	0.002	0.021	0.007	0.001	0.002	0.002	0.019	0	0

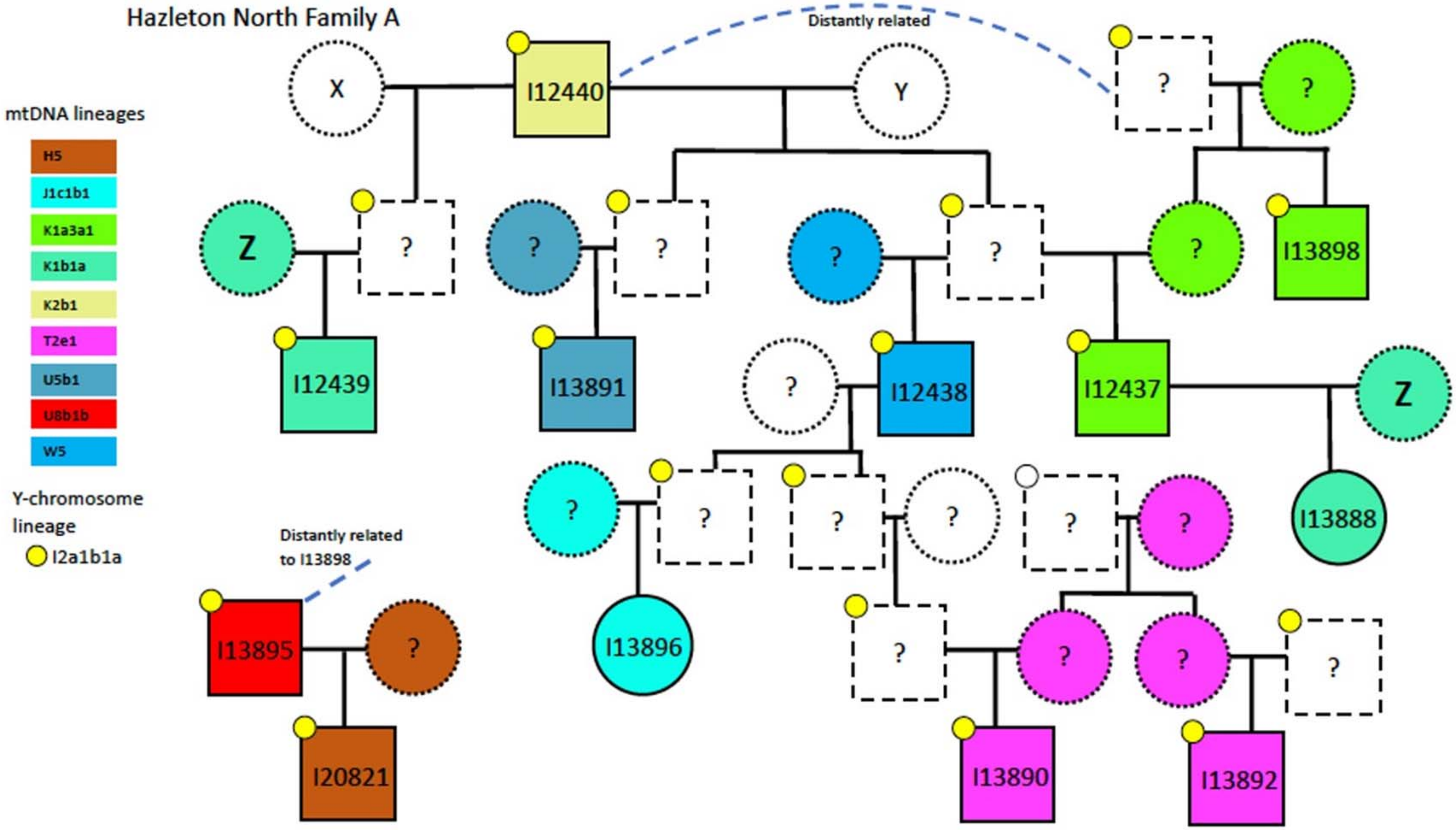
Note: We compute inbreeding-corrected F_{ST}, which samples a single allele from each locus to represent each individual.

Extended Data Table 5: Pairwise F_{ST} among fine-geographic groupings in the British Iron Age

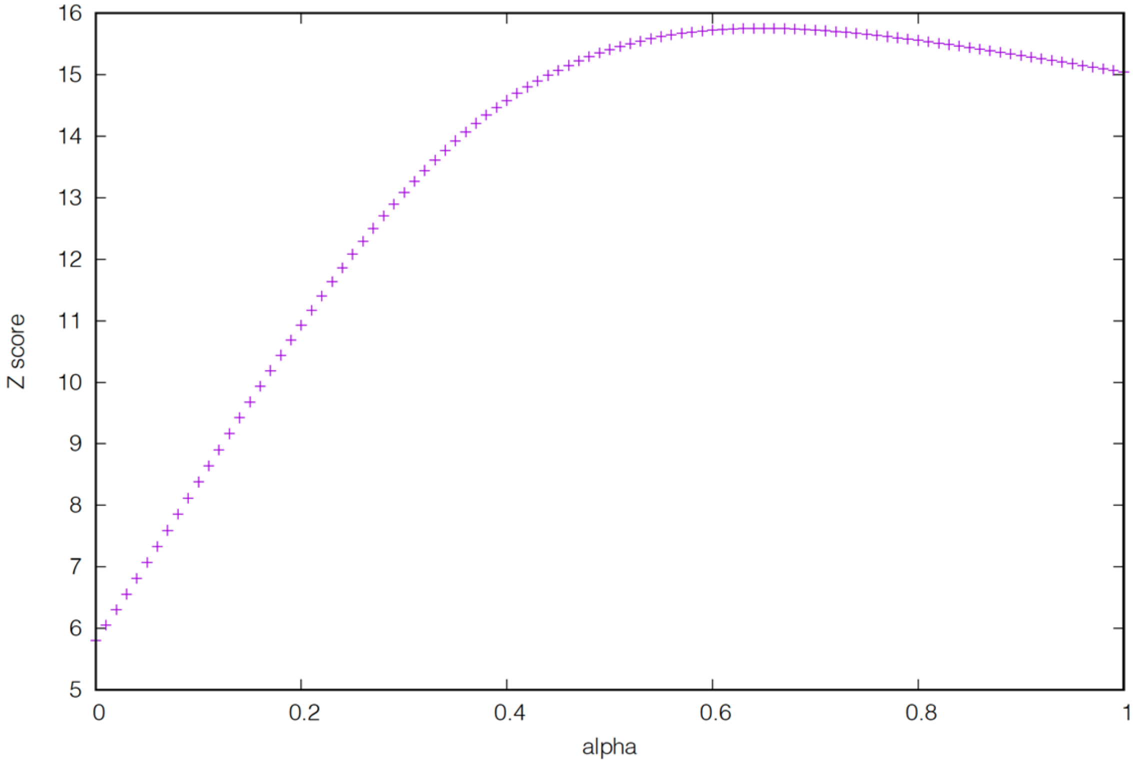
			England and Wales								Scotland		
			East Yorkshire	Midlands	Cornwall	Wales	Southcentral	Southeast	East Anglia	North	Scotland Southeast	Scotland West	Scotland Orkney
		N	35	20	17	4	84	38	20	17	12	7	4
England and Wales	**East Yorkshire**	35	0	0.005	0.005	0.006	0.003	0.003	0.003	0.002	0.004	0.005	0.004
	Midlands	20	0.005	0	0.003	0.004	0.002	0.002	0.002	0.002	0.003	0.004	0.003
	Cornwall	17	0.005	0.003	0	0.003	0.002	0.002	0.002	0.002	0.003	0.004	0.004
	Wales	4	0.006	0.004	0.003	0	0.002	0.002	0.002	0.001	0.002	0.004	0.004
	Southcentral	84	0.003	0.002	0.002	0.002	0	0	0	0	0.002	0.002	0.003
	Southeast	38	0.003	0.002	0.002	0.002	0	0	0	0	0.002	0.002	0.002
	East Anglia	20	0.003	0.002	0.002	0.002	0	0	0	0	0.002	0.003	0.001
	North	17	0.002	0.002	0.002	0.001	0	0	0	0	0.001	0.001	0.001
Scotland	**Scotland Southeast**	12	0.004	0.003	0.003	0.002	0.002	0.002	0.002	0.001	0	0.001	0.002
	Scotland West	7	0.005	0.004	0.004	0.004	0.002	0.002	0.003	0.001	0.001	0	0
	Scotland Orkney	4	0.004	0.003	0.004	0.004	0.003	0.002	0.001	0.001	0.002	0	0

Note: We compute inbreeding-corrected F_{ST}, which samples a single allele from each locus to represent each individual.

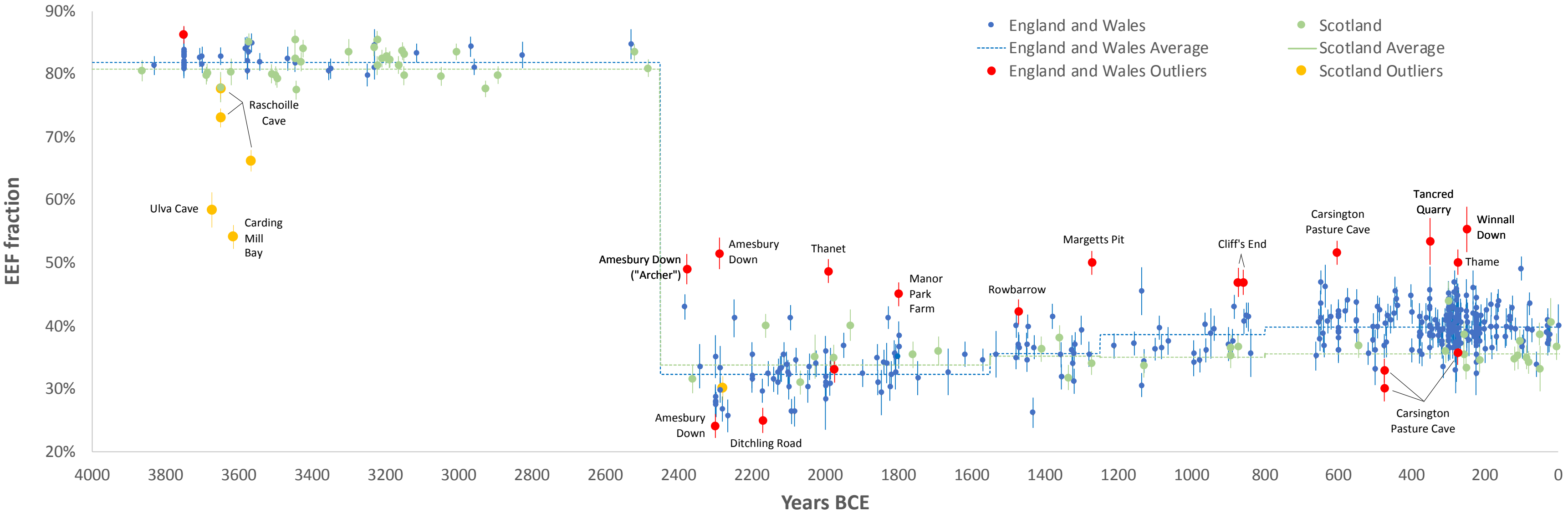
Extended Data Figure 1: Hazleton North Extended Family. The family structure is a best-guess reconstruction based on detection of pairs of relatives and patterns of sharing of segments of DNA that are identical by descent from a common ancestor. The evidence of a large pedigree of relatives connected along the male line is consistent with models of a patrilocal society in the Neolithic period in Britain.



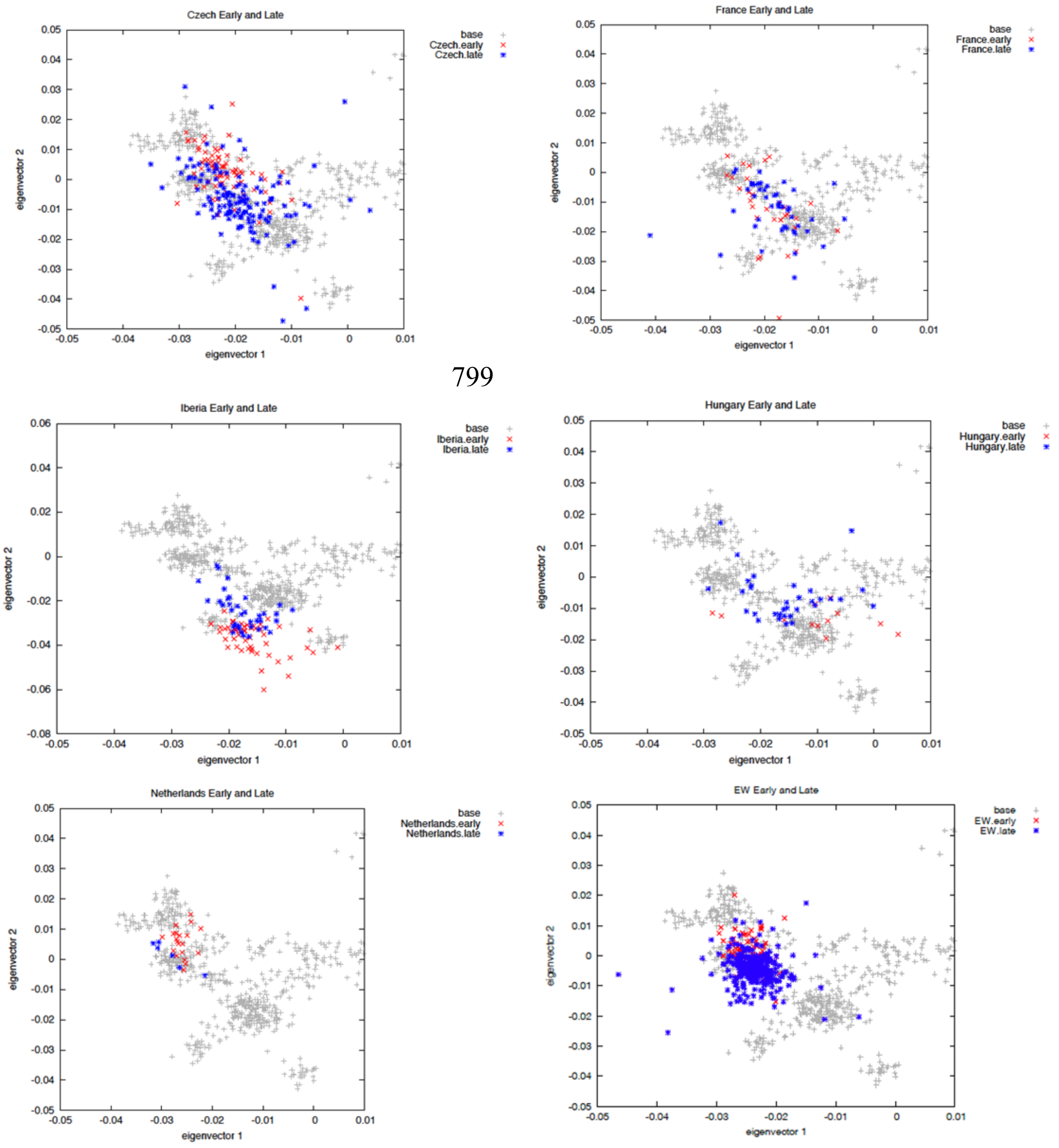
Extended Data Figure 2: Post-MBA Britain was not a mix of earlier British populations. We computed f_4*(Karitiana, Netherland_BellBeaker; England.and.Wales_IA,* α(*England.and.Wales_N*) + (1-α)(*England.Wales_C.EBA)*). If *England.and.Wales_IA* is a simple mix of *England.and.Wales_N* and *England.Wales_C.EBA* without any additional contribution of ancestry, then for some mixture proportion the statistic will be consistent with zero (Supplementary Information section 4). However, we observe that it is positive for all values of α, showing that Karitiana share more alleles with IA people from England and Wales than do both Neolithic and C/EBA people; thus, they must have ancestry from an additional population deeply related to Karitiana that did not contribute to the earlier groups.



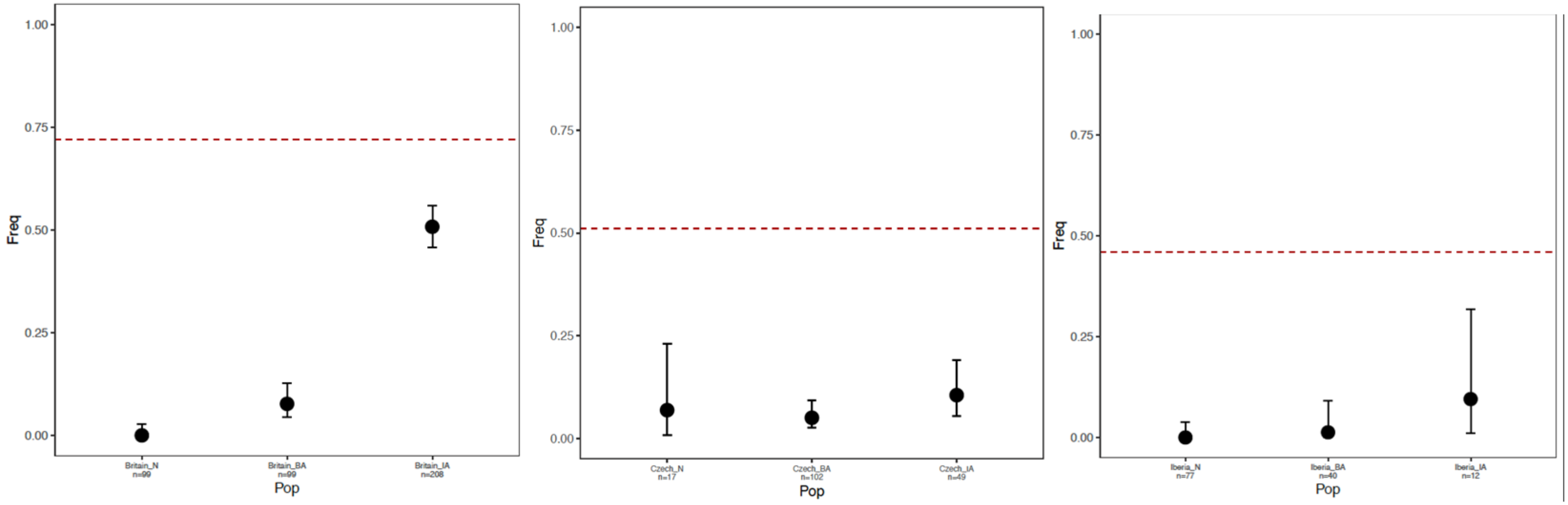
Extended Data Figure 3: By-individual analysis of the British time transect. This is a version of Figure 3 with the time transect extended into the Neolithic period. Estimates of EEF ancestry and one standard error are shown for all individuals in the British time transect that pass basic quality control, 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 significant outliers at the ancestry tails. The averages for the main clusters in both southern and northern Britain in each period are shown in dashed lines.



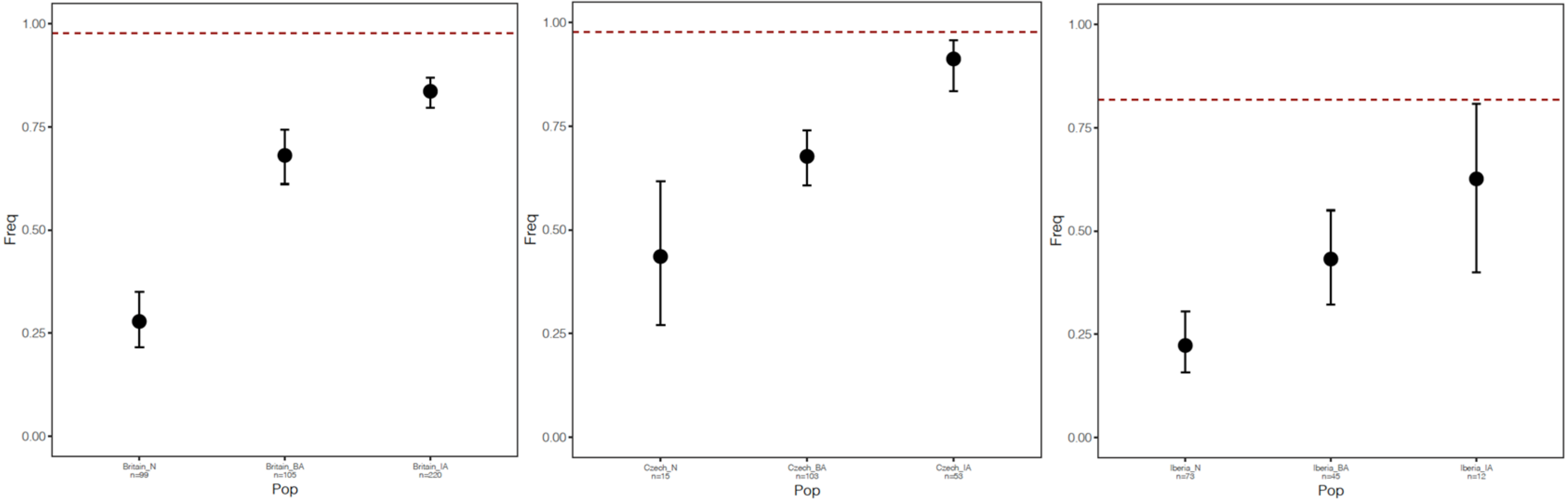
Extended Data Figure 4: Ancestry change over time in multiple European time transects. Because of the genetic shift we observe in Britain, for each time transect we separated our samples into 'Early' (2250-1350 BCE) and 'Late' (1050-50 BCE). We show PCA plots where the 'base individuals' (light grey) are present populations used to calculate the PCA axes. Populations with high Steppe ancestry are shifted to the top left, and with high EEF and WHG ancestry to the bottom. We see increases in EEF ancestry in more northern regions (England and Wales (EW), Bohemia (Czech), and the Netherlands), decreases in more southern regions (Hungary and Iberia), and no clear average change in France.



Extended Data Figure 5: Frequency change over time at two phenotypically important alleles. (Top) The lactase persistence allele at rs4988235. (Bottom) The light skin pigmentation allele at rs16891982. In Britain the rise in frequency of the lactase persistence is significantly earlier than in Bohemia. This analysis is based on direct observation of alleles; imputation results are qualitatively consistent (Figure 4B).

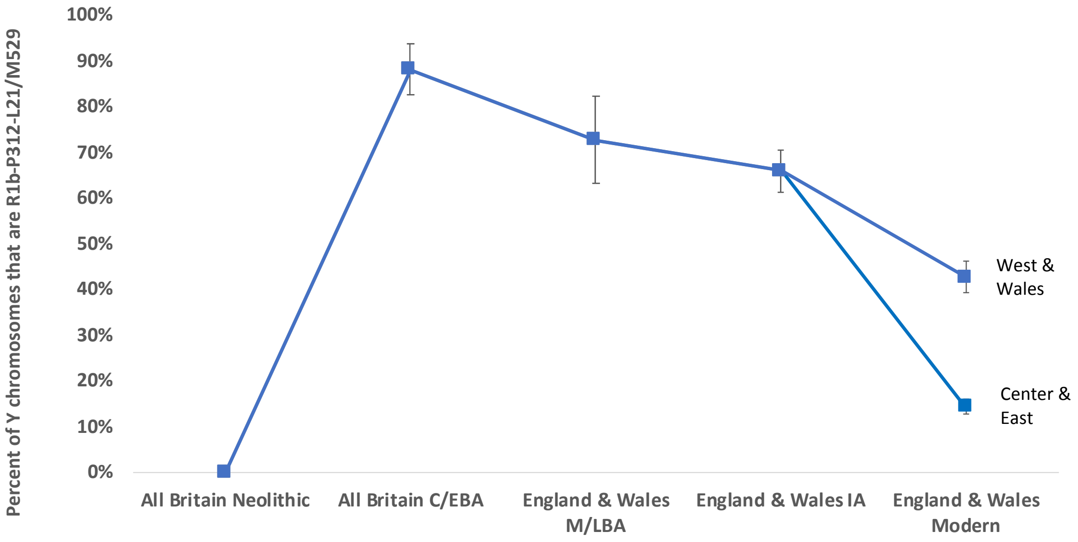


(A) ***LCT*** **- Britain** **(B)** ***LCT*** **- Bohemia** **(C)** ***LCT*** **- Iberia**



(D) ***SLC45A2*** **- Britain** **(E)** ***SLC45A2*** **- Bohemia** **(F)** ***SLC45A2*** **- Iberia**

Extended Data Figure 6: Y chromosome haplogroup frequencies in the British transect. 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 88±6% in the whole island Chalcolithic/EBA. It declines to 73±10% 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), and to 66±5% in the IA, a significant reduction relative to the Chalcolithic/EBA. There is a further reduction from this time to the present, where the proportion is 43±3% in Wales and the west of England, and 14±2% in the center and east of England potentially due to later immigrants bearing a different distribution of Y chromosome haplogroup frequencies.



References

1 Booth, T. J. A stranger in a strange land: a perspective on archaeological responses to the palaeogenetic revolution from an archaeologist working amongst palaeogeneticists. *World Archaeology* **51**, 586-601, doi:10.1080/00438243.2019.1627240 (2019).

2 Kossinna, G. *Die Herkunft der Germanen: Zur Methode der Siedlungsarchäologie*. (Kabitzsch, 1911).

3 Arnold, B. 'Arierdämmerung': Race and Archaeology in Nazi Germany. *World Archaeology* **38**, 8-31 (2006).

4 Caesar, J. *The Gallic wars*. Collector's edn, (Easton Press, 1983).

5 Anthony, D. W. Migration in Archeology: The Baby and the Bathwater. *American Anthropologist* **92**, 895-914 (1990).

6 Altschul, J. H. *et al.* Opinion: To understand how migrations affect human securities, look to the past. *Proc Natl Acad Sci U S A* **117**, 20342-20345, doi:10.1073/pnas.2015146117 (2020).

7 Haak, W. *et al.* Massive migration from the steppe was a source for Indo-European languages in Europe. *Nature* **522**, 207-211, doi:10.1038/nature14317 (2015).

8 Allentoft, M. E. *et al.* Population genomics of Bronze Age Eurasia. *Nature* **522**, 167-+, doi:10.1038/nature14507 (2015).

9 Olalde, I. *et al.* The Beaker phenomenon and the genomic transformation of northwest Europe. *Nature* **555**, 190-196, doi:10.1038/nature25738 (2018).

10 Cassidy, L. M. *et al.* Neolithic and Bronze Age migration to Ireland and establishment of the insular Atlantic genome. *Proc Natl Acad Sci U S A* **113**, 368-373, doi:10.1073/pnas.1518445113 (2016).

11 Brace, S. *et al.* Ancient genomes indicate population replacement in Early Neolithic Britain. *Nat Ecol Evol* **3**, 765-771, doi:10.1038/s41559-019-0871-9 (2019).

12 Galinsky, K. J., Loh, P. R., Mallick, S., Patterson, N. J. & Price, A. L. Population Structure of UK Biobank and Ancient Eurasians Reveals Adaptation at Genes Influencing Blood Pressure. *Am J Hum Genet* **99**, 1130-1139, doi:10.1016/j.ajhg.2016.09.014 (2016).

13 Leslie, S. *et al.* The fine-scale genetic structure of the British population. *Nature* **519**, 309-314, doi:10.1038/nature14230 (2015).

14 Schiffels, S. *et al.* Iron Age and Anglo-Saxon genomes from East England reveal British migration history. *Nat Commun* **7**, 10408, doi:10.1038/ncomms10408 (2016).

15 Briggs, A. W. *et al.* Removal of deaminated cytosines and detection of in vivo methylation in ancient DNA. *Nucleic acids research* **38**, e87, doi:10.1093/nar/gkp1163 (2010).

16 Rohland, N., Harney, E., Mallick, S., Nordenfelt, S. & Reich, D. Partial uracil-DNA-glycosylase treatment for screening of ancient DNA. *Philos Trans R Soc Lond B Biol Sci* **370**, 20130624, doi:10.1098/rstb.2013.0624 (2015).

17 Gansauge, M.-T., Aximu-Petri, A., Nagel, S. & Meyer, M. Manual and automated preparation of single-stranded DNA libraries for the sequencing of DNA from ancient biological remains and other sources of highly degraded DNA. *Nature Protocols* **15**, 2279-2300, doi:10.1038/s41596-020-0338-0 (2020).

18 Gansauge, M. T. *et al.* Single-stranded DNA library preparation from highly degraded DNA using T4 DNA ligase. *Nucleic Acids Res* **45**, e79, doi:10.1093/nar/gkx033 (2017).

19 Fu, Q. *et al.* An early modern human from Romania with a recent Neanderthal ancestor. *Nature* **524**, 216-219, doi:10.1038/nature14558 (2015).

20 Mathieson, I. *et al.* Genome-wide patterns of selection in 230 ancient Eurasians. *Nature* **528**, 499-503, doi:10.1038/nature16152 (2015).

21 Fu, Q. *et al.* DNA analysis of an early modern human from Tianyuan Cave, China. *Proc Natl Acad Sci U S A* **110**, 2223-2227, doi:10.1073/pnas.1221359110 (2013).

22 Fu, Q. *et al.* A revised timescale for human evolution based on ancient mitochondrial genomes. *Current biology : CB* **23**, 553-559, doi:10.1016/j.cub.2013.02.044 (2013).

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

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

25 Sánchez-Quinto, F. *et al.* Megalithic tombs in western and northern Neolithic Europe were linked to a kindred society. *Proceedings of the National Academy of Sciences of the USA* **116**, 9469-9474, doi:10.1073/pnas.1818037116 (2019).

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

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

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

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

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

31 Millard, A. R. in *Cliffs End Farm, Isle of Thanet, Kent: A mortuary and ritual site of the Bronze Age, Iron Age and Anglo-Saxon period with evidence for long-distance maritime mobility* (eds J. I. McKinley *et al.*) 135-146 (Wessex Archaeology, 2014).

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

33 Brunel, S. *et al.* Ancient genomes from present-day France unveil 7,000 years of its demographic history. *Proceedings of the National Academy of Sciences of the United States of America* **117**, 12791-12798, doi:10.1073/pnas.1918034117 (2020).

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

35 Marcus, J. H. *et al.* Genetic history from the Middle Neolithic to present on the Mediterranean island of Sardinia. *Nature communications* **11**, 939, doi:10.1038/s41467-020-14523-6 (2020).

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

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

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

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

40 Thomas, M. G., Stumpf, M. P. H. & Härke, H. Evidence for an apartheid-like social structure in early Anglo-Saxon England. *Proceedings of the Royal Society B: Biological Sciences* **273**, 2651-2657, doi:10.1098/rspb.2006.3627 (2006).

41 Weale, M. E., Weiss, D. A., Jager, R. F., Bradman, N. & Thomas, M. G. Y Chromosome Evidence for Anglo-Saxon Mass Migration. *Molecular Biology and Evolution* **19**, 1008-1021, doi:10.1093/oxfordjournals.molbev.a004160 (2002).

42 Cunliffe, B. *Europe Between the Oceans: 9000 BC-AD 1000*. (Yale University Press, 2008).

43 Cunliffe, B. *Britain Begins*. (Oxford University Press, 2013).

44 Koch, J. T., Cunliffe, B.W. *Celtic from the West 2: Rethinking the Bronze Age and the Arrival of Indo-European in Atlantic Europe*. (Oxbow Books, 2013).

45 Needham, S. & Bowman, S. Flesh-hooks, technological complexity and the Atlantic Bronze Age feasting complex. *European Journal of Archaeology* **8**, 93-136, doi:10.1177/1461957105066936 (2005).

46 Childe, V. G. *The Bronze Age*. 224-225 (Cambridge University Press, 1930).

47 Noort, R. V. d. in *The Oxford Handbook of the European Bronze Age* (ed H. Fokkens; A. Harding) (Oxford University Press, 2013).

48 C. Marcigny, J. B., M. Talon. in *Movement, Exchange and Identify in Europe in the 2nd and 1st Millennia BC: Beyond Frontiers* (ed M. Talon A. Lehoerff) 63-78 (Oxbow Books, 2017).

49 Marcigny, C. in *Les Anglais en Normandie* 47–54 (2011).

50 McConvell, P. in *Migration History in World History* 153-186 (Brill, 2010).

51 P. S. Bellwood, C. R. *Examining the Farming/Language Dispersal Hypothesis*. (McDonald Institute for Archaeological Research, 2002).

52 Sims-Williams, P. An Alternative to ‘Celtic from the East’ and ‘Celtic from the West’. *Cambridge Archaeological Journal* **30**, 511-529, doi:10.1017/S0959774320000098 (2020).

53 Loog, L. *et al.* Estimating mobility using sparse data: Application to human genetic variation. *Proceedings of the National Academy of Sciences* **114**, 12213, doi:10.1073/pnas.1703642114 (2017).

54 Rodway, S. The Ogham Inscriptions of Scotland and Brittonic Pictish. *Journal of Celtic Linguistics* **21**, 173-234, doi:10.16922/jcl.21.6 (2020).

55 Guggisberg, M. in *Oxford Handbook of the European Iron Age* (ed K. Rebay-Sailsbury C. Haselgrove, P. Wells) (Oxford University Press, 2018).

56 Champion, T. C., Haselgrove, C., Armit, I., Creighton, J. & Gwilt, A. *Understanding the British Iron Age: an agenda for action. A Report for the Iron Age Research Seminar and the Council of the Prehistoric Society*. (Trust for Wessex Archaeology, 2001).

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

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

59 Jay, M., Montgomery, J., Nehlich, O., Towers, J. & Evans, J. British Iron Age chariot burials of the Arras culture: a multi-isotope approach to investigating mobility levels and subsistence practices. *World Archaeology* **45**, 473-491, doi:10.1080/00438243.2013.820647 (2013).

60 Pinhasi, R., Fernandes, D. M., Sirak, K. & Cheronet, O. Isolating the human cochlea to generate bone powder for ancient DNA analysis. *Nature Protocols* **14**, 1194-1205, doi:10.1038/s41596-019-0137-7 (2019).

61 Sirak, K. A. *et al.* A minimally-invasive method for sampling human petrous bones from the cranial base for ancient DNA analysis. *Biotechniques* **62**, 283-289, doi:10.2144/000114558 (2017).

62 Dabney, J. *et al.* Complete mitochondrial genome sequence of a Middle Pleistocene cave bear reconstructed from ultrashort DNA fragments. *Proc Natl Acad Sci U S A* **110**, 15758-15763, doi:10.1073/pnas.1314445110 (2013).

63 Korlevic, P. *et al.* Reducing microbial and human contamination in DNA extractions from ancient bones and teeth. *Biotechniques* **59**, 87-93, doi:10.2144/000114320 (2015).

64 Rohland, N., Glocke, I., Aximu-Petri, A. & Meyer, M. Extraction of highly degraded DNA from ancient bones, teeth and sediments for high-throughput sequencing. *Nat Protoc* **13**, 2447-2461, doi:10.1038/s41596-018-0050-5 (2018).

65 Briggs, A. & Heyn, P. in *Methods in Molecular Biology* Vol. 840 143-154 (Springer, 2012).

66 Maricic, T., Whitten, M. & Paabo, S. Multiplexed DNA sequence capture of mitochondrial genomes using PCR products. *PLoS One* **5**, e14004, doi:10.1371/journal.pone.0014004 (2010).

67 Behar, D. M. *et al.* A "Copernican" reassessment of the human mitochondrial DNA tree from its root. *Am J Hum Genet* **90**, 675-684, doi:10.1016/j.ajhg.2012.03.002 (2012).

68 Li, H. & Durbin, R. Fast and accurate short read alignment with Burrows-Wheeler transform. *Bioinformatics* **25**, 1754-1760, doi:10.1093/bioinformatics/btp324 (2009).

69 Weissensteiner, H. *et al.* HaploGrep 2: mitochondrial haplogroup classification in the era of high-throughput sequencing. *Nucleic Acids Res* **44**, W58-63, doi:10.1093/nar/gkw233 (2016).

70 Fu, Q. *et al.* A revised timescale for human evolution based on ancient mitochondrial genomes. *Current biology : CB* **23**, 553-559, doi:10.1016/j.cub.2013.02.044 (2013).

71 Sawyer, S., Krause, J., Guschanski, K., Savolainen, V. & Paabo, S. Temporal patterns of nucleotide misincorporations and DNA fragmentation in ancient DNA. *PLoS One* **7**, e34131, doi:10.1371/journal.pone.0034131 (2012).

72 Skoglund, P. *et al.* Separating endogenous ancient DNA from modern day contamination in a Siberian Neandertal. *Proc Natl Acad Sci U S A* **111**, 2229-2234, doi:10.1073/pnas.1318934111 (2014).

73 Patterson, N., Price, A. L. & Reich, D. Population structure and eigenanalysis. *PLoS genetics* **2**, e190, doi:10.1371/journal.pgen.0020190 (2006).

74 Bronk Ramsey, C. Bayesian Analysis of Radiocarbon Dates. *Radiocarbon* **51**, 337-360, doi:10.1017/S0033822200033865 (2009).

75 Reimer, P. J. *et al.* The IntCal20 Northern Hemisphere Radiocarbon Age Calibration Curve (0–55 cal kBP). *Radiocarbon* **62**, 725-757, doi:10.1017/RDC.2020.41 (2020).