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

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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

216   spread and dominance of specific ethnic groups[2], a theory that was used to justify claims on

217   territory and wars of aggression[3]. Because of this history, some archaeologists tend to view

218   "migration" as synonymous with *migratory movements* whereby a community consciously

219   plans and executes a long-distance (and permanent) translocation of large numbers of people

220   over a short period (at most a few years), along the lines of the migration of hundreds of

221   thousands of members of the Helvetii described by Julius Caesar[4]. Other archaeologists favour a

222   broader definition that is more compatible with the understanding in population genetics, using

223   "migration" to refer to any process that through a combination of push and pull factors (often

224   related to economic and social forces), results in movement of people from one geographic

225   region to another and significant demographic change over a period that can be as long as

226   centuries[5,6]. An example of a process that would qualify as a migration in this sense would be

227   the eastward movement of people from the Steppe beginning in the third millennium BCE that

228   contributed much of the ancestry of later Europeans[7,8,9,10]. Because we use this broader

229   definition of "migration" here, our key finding of at least three major migrations into Britain in

230   the prehistoric period should not be interpreted as a claim that any of these events were violent

231   "invasions." While social inequality could have been associated with some of these events, the

232   human reality that characterized each of these migrations remains poorly understood and is best

233   addressed through future work integrating archaeology and ancient DNA.

234

235   Whole genome ancient DNA studies have shown that the first Neolithic farmers of Britain

236   ~4000 BCE derived roughly 80% of their ancestry from Early European Farmers (EEF) who

237   originated in Anatolia more than two millennia earlier, and 20% from descendants of Mesolithic

238   hunter-gatherers (Western European Hunter-Gatherers: WHG). The WHG ancestry was almost

239   entirely due to admixture in mainland Europe, indicating that the migrants to Britain in the

240   Neolithic nearly completely absorbed local populations.[9-11] The Neolithic population of Britain

241   was genetically similar to, and almost certainly derived from, contemporaneous populations on

242   the European mainland especially from Iberia and France. This ancestry profile remained stable

243   for about a millennium and a half. However, around 2450 BCE, there was another substantial

244   movement of people into Britain coinciding with the spread of Bell Beaker traditions from

245   mainland Europe,[9] which brought a third major component of 'Steppe ancestry' derived

246   ultimately from people living on the Pontic-Caspian Steppe ~3000 BCE (minimum 90% of

247   ancestry from the new migrants). In the original study[9] reporting this ancestry shift in Britain

248   after ~2450 BCE, no further change in the proportion of EEF ancestry was inferred in the

249   Bronze Age, but that study contained almost no data after 1300 BCE (Figure 1). Today,

250   however, EEF ancestry is significantly higher on average in southern Britain (defined here as

251   England and Wales although we recognize modern boundaries are arbitrary) than in northern

252   Britain (Scotland), raising the question of when this increase in EEF ancestry occurred.[9,12] The

253   rise in EEF ancestry in England and Wales cannot be explained by migrations from northern

254   mainland Europe in the early medieval period (e.g. 'Saxon' or 'Viking' migrations[13,14]), as these

255   populations harbored less EEF ancestry than was present in Bronze Age Britain and hence

256   would have decreased EEF ancestry instead of increasing it as we observe.[9]

257

258   We generated new ancient DNA data beginning in the Neolithic but focusing on the period from

259   the Middle Bronze Age (defined here as beginning around 1550 BCE) through to the end of the

260   pre-Roman Iron Age (defined here as 43 CE) (Supplementary Information Section 1, Online

261   Table 1). We report new data from 409 individuals from the main island of Britain and its small

262   surrounding islands, increasing the number of pre-Roman ancient individuals from Britain to

263   648 and multiplying by 34-fold the number from the combined Late Bronze Age and Iron Age

264   periods (from 10 to 343). We also report new data from 179 individuals from Bohemia (present-

265   day Czech Republic), and additional individuals from France (n=46), Slovakia (n=30), Hungary

266   (n=30), the Netherlands (n=21), Slovenia (n=14), Spain (n=9), and Austria (n=3), mostly dating

267   to the Late Bronze Age (LBA) and Iron Age (IA). We also increased data quality on 28

268   previously published individuals (Online Table 2). To generate these data, we prepared powder,

269   extracted DNA[15-17], and generated sequencing libraries which we almost always pretreated with

270   the enzyme uracil-DNA glycosylase (UDG) to reduce the characteristic cytosine-to-thymine

271   errors of ancient DNA (Online Table 3).[15,16,18] We enriched the libraries in solution and then

272   sequenced them on Illumina instruments (Methods).[19-21] We co-analyzed the data with

273   previously reported data for a total of 5837 ancient and present-day individuals (Online Table

274   4). We clustered individuals by time period and geography aided by 62 radiocarbon dates from

275   bone or teeth that are newly reported in this study (Online Table 5). We also separately labelled

276   individuals that were significantly different in ancestry from the clear majority cluster from

277   each time and region (Supplementary Information Section 2, Online Tables 6 and 7). Although

278   we report data from all individuals, we removed a subset of individuals from the main analysis:

279   those with evidence of contamination based on variation in their mitochondrial sequence or on

280   the X chromosome (the latter only possible in males)[22,23], those with a rate of damage in the

281   final nucleotide lower than is typical for authentic ancient DNA[16], or those that were first degree

282   relatives of other higher coverage individuals in the dataset[24] (Online Tables 6 and 7), or those

283   that had too low coverage for accurate ancestry inference which we define as <30,000 single

284 nucleotide polymorphisms (SNPs) covered. However, we report data for all individuals. Figure

285 1 shows a map of all the newly reported individuals. We identified 283 individuals from 96

286 families as being genetically related (within the third degree) to at least one other individual in

287 the dataset (Online Table 8). The largest family we detect from Britain is a newly-reported set

288 of 11 individuals from the Hazleton North megalithic chambered tomb in Gloucestershire. All

289 11 individuals are connected along the male line consistent with a patrilocal society, as

290 suggested by previous archaeogenetic work on megalithic sites[25] (Extended Data Figure 1,

291 Supplementary Information section 3).

(a) Neolithic to Middle Bronze Age
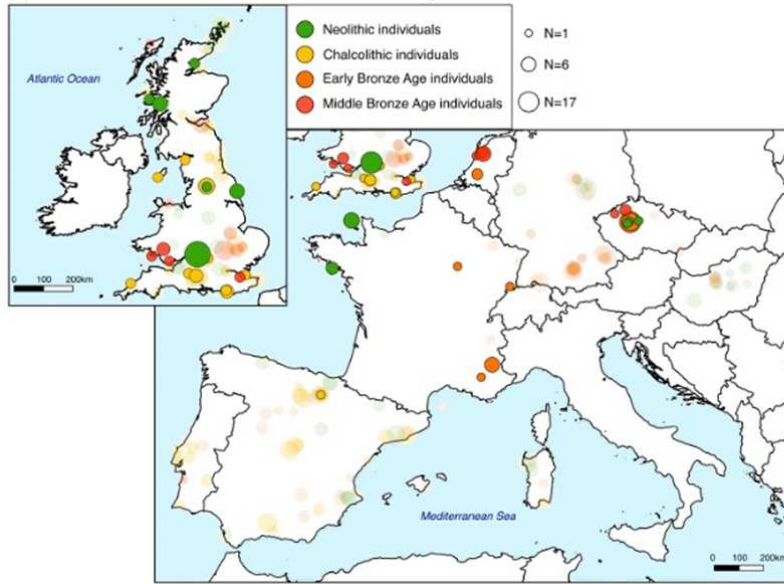
(b) Late Bronze Age to Iron Age
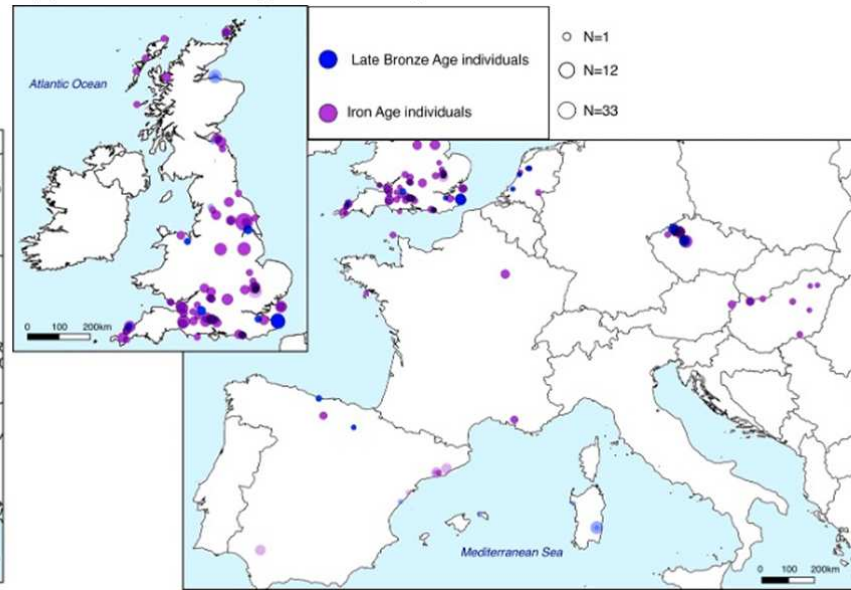
(c) Time distribution of analysed individuals
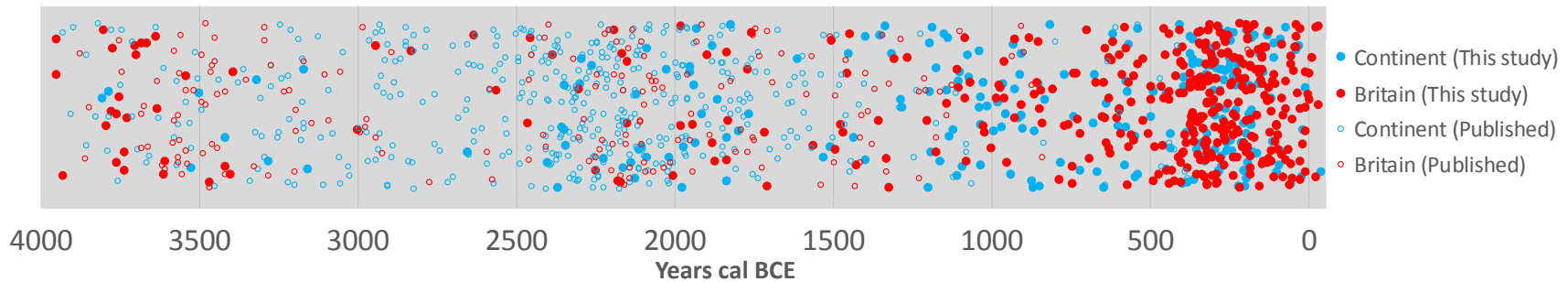
Figure 1: Ancient DNA dataset. (a) Geographic distribution of the Neolithic to Middle Bronze Age and (b) Late Bronze Age to Iron Age individuals analysed in this study; we show newly reported data in intense colors and previously published data in pale colors. (c) Temporal distribution of the newly reported 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.

302   We computed symmetry-f_4 statistics[26,27] between all pairs of analysis clusters from Britain,

303   testing for differences in the rate of allele sharing (shared genetic drift) with two major source

304   populations: Yamnaya pastoralists from the Pontic Caspian Steppe (as a surrogate for Steppe

305   ancestry) and Anatolian farmers (as a surrogate for EEF). We document a significant increase in

306   the degree of allele sharing with EEF populations in England and Wales over time (Extended

307   Data Table 1). To quantify this change, we estimated proportions of the three major ancestry

308   components (EEF, Steppe, and WHG) using *qpAdm*[7], choosing reference and source

309   populations to drive down standard errors. Figure 2 and Extended Data Table 1 document a

310   significant increase in EEF-related ancestry in England and Wales, with the proportion rising

311   from an average of 32.3±0.6% in the Chalcolithic/Early Bronze Age (C/EBA: defined here as

312   2450-1550 BCE, n=64), to 35.4±0.6% in the Middle Bronze Age (MBA: 1550-1250 BCE,

313   n=32), to 38.4±0.8% in the Late Bronze Age (LBA: 1250-800 BCE, n=20), and stabilizing in

314   the Iron Age, when it was 39.7±0.5% (IA: 800 BCE-43 CE, n=249) (here and in what follows,

315   we always quote one standard error). In contrast, there is a barely perceptible change in EEF

316   ancestry in Scotland, with the proportion starting at 33.7±1.0 % in the C-EBA (n=9), then

317   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

318   the IA (n=23). Our dense geographic coverage and large sample size makes it clear that elevated

319   EEF ancestry was widespread in England and Wales by the IA, with average EEF ranging from

320   37.5-40.6% in eight regions of England and Wales, and consistently lower at 35.4-36.0% in

321   three regions of Scotland (Table 1, Extended Data Table 2). We considered the possibility that

322   the rise in EEF ancestry in England and Wales was due to a resurgence of archaeologically less

323   visible populations with more ancestry derived from people living in Britain during the

324   Neolithic. However, our attempts to model IA populations of England and Wales as a mixture

325   of groups who lived in Neolithic and C-EBA Britain failed (always P<10^{-9}, Extended Data

326   Figure 2). We are able to show that this model failure is due to M-LBA populations from

327   Britain harboring significant excess allele sharing with Neolithic populations from mainland

328   Europe that is not observed in earlier groups from Britain (Supplementary Information section

329   4, Extended Data Table 3). The only plausible explanation for these changes in EEF ancestry is

330   new migrations from mainland Europe into southern Britain
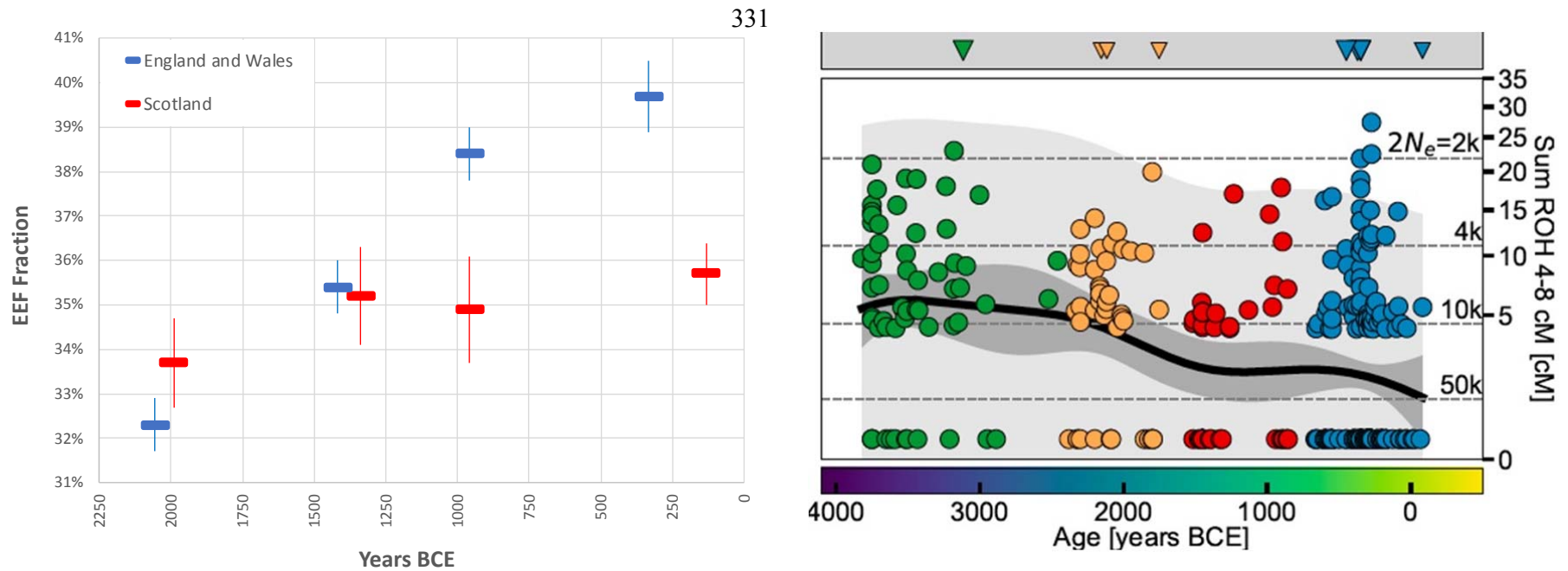
Figure 2: A high resolution ancient DNA time transect through Britain. (Left) An increase in EEF ancestry in southern but not northern Britain. We show qpAdm estimates for all individuals passing basic quality control, divided into four periods (C/EBA, MBA, LBA and IA). X-axis positions are the average 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.

1

341 *Table 1: Variation in ancestry proportions within Iron Age Britain*

Region	*n*	Distal Model				Proximal Model	
		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	7×10^{-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	3×10^{-5}	11.6 ± 1.1%	36.0 ± 1.3%	52.4 ± 1.5%	0.010	20 ± 8%

342 *Notes: Estimates are from qpAdm. For the distal model the right set is (Mbuti, WHGA, Russia Samara EBA Yamnaya, Turkey*
343 *N), and for the proximal model it is these plus (Netherlands Bell Beaker, Poland Globular Amphora). We separate "England*
344 *East Yorkshire" from "England North" because of the large number of samples from East Yorkshire and the distinctive cultural*
345 *context (Arras culture). P-values <0.01 indicate cases where the tested model fit the data poorly so estimates are less reliable.*
346

347 We modelled each individual from Britain using *qpAdm*, labelling significant ancestry outliers

348 (at the p<0.005 level) relative to the main cluster for their time period (Figure 3 and Extended

349 Data Figure 3). We discuss each group of outliers in turn from earliest to latest.

350

351 First and replicating previous results[9,11], we observe a cluster of Neolithic individuals from

352 western Scotland showing high WHG admixture, likely reflecting unions between recent

353 migrants from Europe and indigenous people from Britain (Extended Data Figure 3).

354

355 Second, we observe high variability in EEF ancestry in the C-EBA, before proportions of EEF

356 ancestry become relatively homogeneous by ~2100 BCE[9] (Figure 3). This heterogeneity is

357 apparent at C-EBA Amesbury Down where EEF ancestry in some burials is significantly below

358 the period average of 32.3±0.6% (e.g. I2417 at 24.1±1.9% (P=1×10^{-8})), whereas in others it is

359 above the average (e.g. I2416 at 51.5±2.5% (P=3×10^{-8}) and I14200 at 49.0±2.4% (P=2×10^{-7})).

360 The burials in the low EEF group are plausibly Beaker-period migrants who later mixed with

361 local Neolithic farmers to produce the intermediate proportion of EEF ancestry that prevailed by

362 the end of the EBA. The individual labeled I14200, with significantly elevated EEF ancestry

363 compared to the period average, is the "Amesbury Archer". This individual was located in the

364 most well-furnished burial recovered from the Stonehenge mortuary landscape, and his isotopic

365 profile indicates he spent parts of his childhood outside Britain, possibly the region of the Alps

366 in Central Europe[29]. The Archer's paternal-line ancestry is ultimately derived from Steppe

367 pastoralists as indicated by his Y chromosome haplogroup R1b1a1b1a1a. The simplest

368   explanation is that the Archer migrated to Britain from the Alpine region of mainland Europe

369   and was from a family associated with the Bell Beaker tradition with low Steppe (high EEF)

370   ancestry[23]. However, we cannot rule out more complex scenarios involving recent ancestral

371   admixture in Britain (e.g. his mother not having Steppe ancestry), combined with back-and-

372   forth childhood movements between Britain and Alpine Central Europe. In either case, the

373   Archer's anomalously low Steppe ancestry is important in revealing that Beaker-using people

374   who came to Britain were not socially stratified in such a way that Steppe lineage from eastern

375   Europe necessarily conferred the highest social status. The Archer's 'Companion' (I2565), a

376   burial found next to the Amesbury Archer, had a more typical ancestry proportion for C-EBA

377   Britain ($33.4\pm3.4\%$ EEF; P=0.49 for consistency with the period average). The Archer and the

378   Companion were not closely related genetically (we can rule out first or second degree

379   relationships) despite sharing a rare tarsal malformation and similar grave good assemblages,

380   which has been interpreted as likely to reflect kinship (Supplementary Information section 3).[30]

381

382   Third, we observe outliers with high EEF ancestry in the Late Bronze Age. Individual I13716

383   from Margetts Pit in Kent, dated to 1391-1129 calBCE (3019 ± 31 BP, SUERC-49774), has

384    $50.0\pm1.9\%$ EEF ancestry ($P<10^{-12}$ for an excess compared to the MBA average of $35.4\pm0.6\%$),

385   and she may be derived from one of the sources of migration in mainland Europe. Another

386   individual from the same cemetery (I13617), dated to 1256-1051 calBCE (2946 ± 27 BP,

387   SUERC-49770), also has elevated EEF ancestry of $45.5\pm3.8\%$, although the excess is not

388   significant (P=0.26) due to the larger uncertainty in ancestry estimates reflecting her lower

389   coverage data and due to the fact that the EEF average in England and Wales had increased to

390    $38.6\pm0.8\%$ by that time. We highlight two individuals at Cliffs End Farm in Kent with

391   significantly elevated EEF ancestry at $46.9\pm2.3\%$ (I14865 dating to 967-811 calBCE (2735 ± 30

392   BP, GrA-37713), $P=1x10^{-4}$ for an excess) and $46.9\pm2.0\%$ (I14861 dating to 912-808 calBCE

393   (2713 ± 29 BP, OxA-17804), $P=8x10^{-5}$ for an excess), suggesting continued migration through

394   the LBA. While it is possible in theory that we are observing the effect of a short burst of

395   migration in the late MBA and early LBA followed by co-existence of separate communities

396   with different proportions of EEF ancestry, strontium and oxygen isotope analyses confirms

397   long-distance mobility at Cliffs End Farm by identifying multiple individuals of a non-local

398   origin[31], a finding that is more consistent with continuing migration. Strontium isotope ratios for

399   individual I14861 suggest an origin in Scandinavia or the Alps; the latter would be consistent

400   with their high EEF ancestry.

401

402
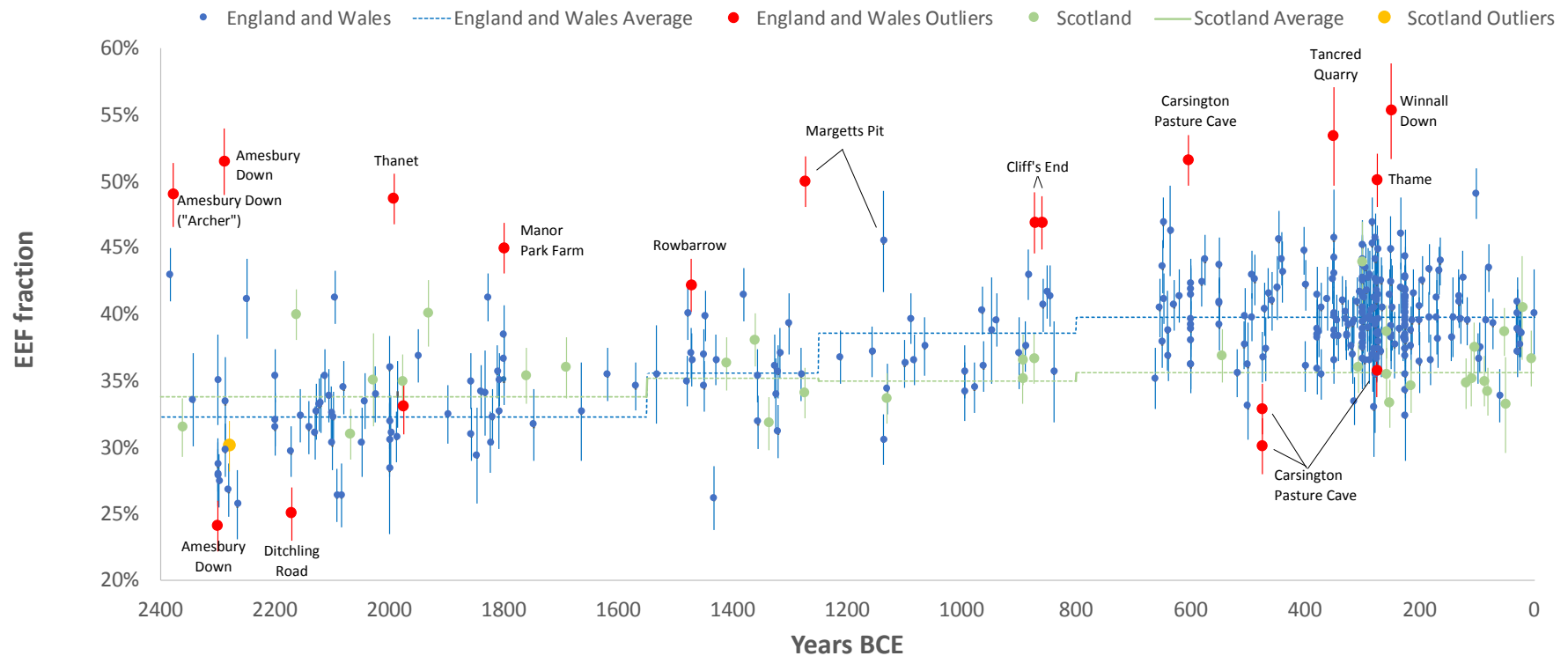
Figure 3: By-individual analysis of the British time transect. *Estimates of EEF ancestry and one standard error for all individuals in the British time transect that pass basic quality control, that fit to a three-way admixture model (EEF + WHG + Yamnaya) at p>0.01 using qpAdm, and that date to 2450-1 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.*

3

409   Fourth, we observe isolated cases of ancestry outliers through the IA. EEF ancestry in I14803

410   from Thame, Oxfordshire (dated to 370-175 calBCE (2204±30 BP, SUERC-95011) is

411   50.1±0.2% which is significantly above the England and Wales IA average of 39.7±0.5%

412   ($P=8\times10^{-8}$ for an excess), and there is extreme diversity of ancestry within burials from

413   Carsington Pasture Cave in Derbyshire (800-150 BCE) with one individual showing

414   significantly elevated EEF ancestry and four others showing reduced EEF ancestry. EEF

415   ancestry proportions in Britain at this time (39.7±0.5%) were lower than in much of Europe, as

416   reflected in the average we observe in contemporary IA individuals from France (46.8±0.8%),

417   Hungary (51.6±0.7%), and Bohemia (46.9±0.6%), and so we would expect to be able to detect

418   any substantial IA migrations from mainland Europe (Figure 4). Thus, while Figure 3 does

419   show isolated individuals from IA Britain with elevated EEF ancestry, the broader lack of a

420   change in EEF ancestry proportion is consistent with a minimal demographic impact of new

421   immigration from mainland Europe and relatively closed and self-sustaining social communities

422   in Britain during the Iron Age.

423

424   We also leverage our large sample-size to infer population size change over four millennia in

425   Britain. For this analysis, we take advantage of the fact that when an individual inherits an

426   identical long stretch of DNA on both their mother's and father's side they must share a recent

427   ancestor; the rate of observation of 4-8 centimorgan segments of genetic homogeneity in a

428   person's genome thus provides information about the number of reproducing individuals living

429   in a population in the last few dozen generations prior to the time individuals lived[28]. We infer

430   an approximately constant population size from the beginning of the Neolithic to the end of the

431   EBA, followed by a roughly five-fold expansion in the EBA-to-MBA transition with no

432   significant evidence of further expansion until the end of the IA (Figure 2B). This suggests that

433   the largest population size change in Britain for the four millennia from ~4000-1 BCE occurred

434   shortly before or concurrent with M-LBA migration from the continent, further highlighting the

435   MBA as a critical period of demographic transition in Britain.

436

437   We co-analyzed our ancient DNA transects through time in Britain with time transects in

438   Bohemia, The Netherlands, Iberia[32], Hungary, and France[33] (Online Table 7, Extended Data

439   Figure 4, Figure 4, and Online Table 9). Average EEF ancestry increased in this period in

440   Bohemia and the Netherlands, just as it did in Britain. The earliest individuals from Bohemia

441   with increased EEF ancestry are associated with artefacts traditionally classified as part of the

442   LBA Knoviz culture, a component of the broader Urnfield cultural complex which spread from

443   1300-800 BCE across much of Central Europe. Later individuals have similar EEF proportions,

444   consistent with continuity through the LBA-IA with earlier Urnfield-associated groups. By

445   contrast, in M-LBA France and Hungary there was little change in average EEF ancestry, and

446   this ancestry decreased in M-LBA Iberia (Extended Data Figure 4, Figure 4, Online Table 9).

447   The general increase in EEF ancestry in northern Europe, and its decrease in southern Europe,

448   reflects a broad process of north-south genetic interchange that affected many regions. There are

449   nonetheless some exceptions from more isolated regions, such as Scotland in the far north

450   (Figure 2), and Sardinia in the far south[34,35] (Online Table 9). We considered the possibility of a

451   single unsampled group admixing from one region into all the others, but such a scenario does

452   not fit the data. For example, people of the LBA Urnfield complex of Central Europe do not fit

453   as a simple source for the new ancestry in Britain (Supplementary Information section 5).

454

455   This study multiplies by almost ten-fold the number of IA individuals with genome-wide data

456   from Central and Western Europe (from 61 to 572), and as a result makes it possible for the first

457   time to track the frequency change of genetic variants with known biological function into the

458   IA (Online Table 10). In addition to showing how variants associated with light skin

459   pigmentation, such as *SLC45A2,* became more common in the IA throughout Europe[20], we

460   obtain an unexpected result for the A allele at the polymorphism *MCM6-LCT* rs4988235

461   correlated with lactase persistence into adulthood[20] (Extended Data Figure 5). Previous work

462   showed that the frequency of this allele in IA Iberia was only a small fraction of its present-day

463   incidence, which we confirm by showing that its frequency was ~10% in the IA compared to

464   ~40% today[32], and in Bohemia where its frequency was ~11% in the IA compared to ~51%

465   today. However, in Britain most of the rise in the frequency of this allele had already occurred

466   by the IA (51% compared to the current 73%), suggesting that selection pressures acted earlier

467   in this region (Figure 4, Extended Data Figure 5). There is no evidence that the main rise in

468   frequency of the lactase persistence allele occurred on the European mainland and came into

469   Britain during the M-LBA migrations, since the Margetts Pit and Cliffs End outliers who are

470   plausible members of the migrating population did not carry the allele, and because we observe

471   that most of the rise in frequency of the lactase allele in Britain occurred in the Middle to Late

472   IA. Specifically, we observe the lactase persistence allele frequency rise from ~14% in the LBA

473   to ~26% in IA samples that we can definitively date to before ~400 BCE, to >50% in the pool

474   of later IA samples. This raises the question of whether milk consumption had an economically

475   or culturally more important role in LBA-IA Britain than it did in Central Europe in this period.

476

477 In contrast to Neolithic and Beaker-associated ancestry transformations in Britain, both of

478 which involved migration from a highly differentiated source, ancestry transformation in the M-

479 LBA was more subtle. Thus, F_{ST} measuring allele frequency differences between a pool of

480 individuals before and after the M-LBA genetic shift in England and Wales was ~0.002 between

481 the C-EBA and LBA-IA, and ~0.001 between the MBA and LBA-IA (Extended Data Table 4).

482 It is important to recognize that the local pre-LBA population in Britain made a substantial

483 genetic contribution to the post-LBA population; it was far from completely replaced. Direct

484 evidence for this comes from Y chromosome haplogroup R1b-P312 L21/M529

485 (R1b1a1a2a1a2c1), which today occurs much more frequently in Britain and Ireland (frequency

486 of 14-71% depending on the region[36]) than it does in mainland Europe. We estimate that this

487 haplogroup was already present at 88±6% in sampled individuals from C-EBA Britain

488 (Extended Data Figure 6, Online Table 11), showing that the population established in Britain

489 by the C-EBA contributed substantially to the ancestry of modern Britain (at least on the male

490 line), in contrast to the genetic legacy of the Mesolithic[11] and Neolithic[9,11] people of the islands.
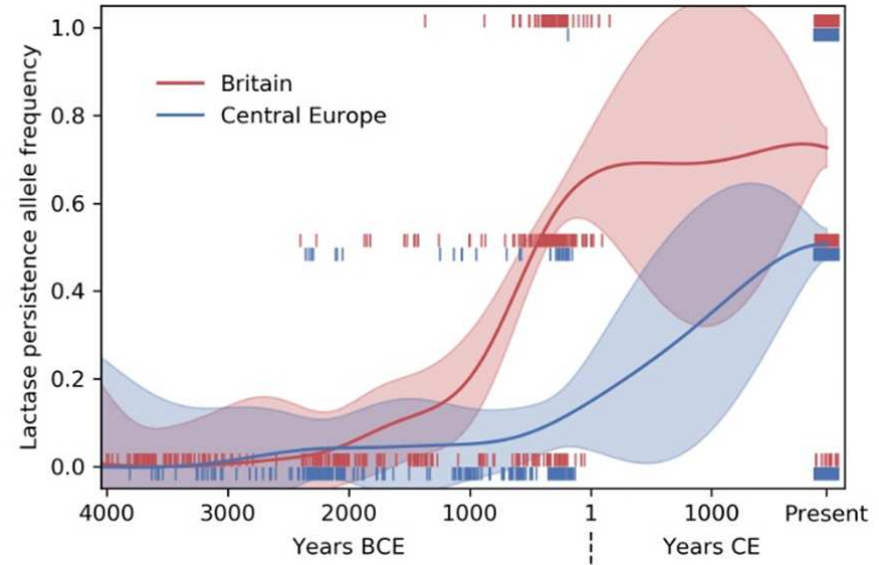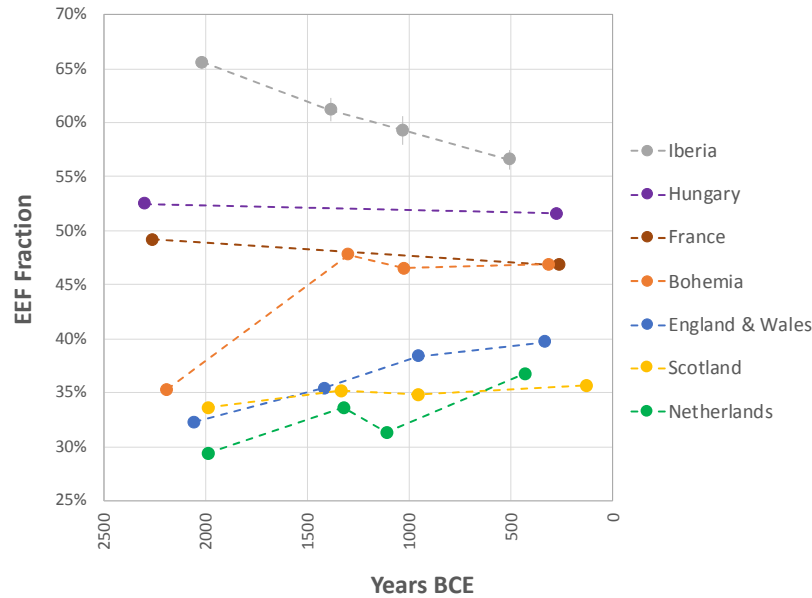
Figure 4: Geographic differences in ancestry component and lactase persistence allele frequency. (Left) North-South ancestry convergence. We show seven ancient DNA time transects for up to four periods (2450-1550 BCE, 1550-1250 BCE, 1250-800 BCE, and 800-50 BCE). The dotted lines show which points are 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.

7

508   To gain insight into the possible sources of the ancestry that spread across England and Wales

509   during the LBA, and to quantify the magnitude of gene flow, we fit the pooled IA individuals

510   from England and Wales as a mixture of a group related to the main C-EBA cluster from

511   England and Wales, and a second source. We examined 71 potential second sources: 69 from

512   mainland Europe, the Margetts Pit outlier, and the pool of two Cliffs End outliers. We then

513   carried out model testing using reference populations in *qpAdm* that had power to distinguish

514   ancestry from C-EBA and IA England and Wales (Supplementary Information Section 6). We

515   identified 17 putative sources that could fit at p>0.05. After probing each with 38 more stringent

516   *qpAdm* testing, we reduced this to six plausible models (Table 2). The Margetts Pit and Cliffs

517   End outliers both fit, consistent with their being immigrants or early generation descendants of

518   immigrants. Our analysis also produces insight into the likely source of migration. Of the other

519   four working surrogates for the source population, three out of four are from France (the one

520   exception is an IA group from Hungary, whose limited data may be the reason for the fit). One

521   fitting source from France is E-MBA Occitanie in the southwest (2100-1200 BCE), a second is

522   IA Occitanie (600-200 BCE) and a third is IA Hauts-de-France (400-100 BCE). The IA groups

523   post-date the LBA ancestry change in Britain by several centuries and so cannot be direct

524   sources; however, they are plausibly descended from earlier populations in their regions or

525   geographic vicinity that could be the true sources. The six fitting models also provide a

526   quantitative estimate of the proportion of novel ancestry arriving into M-LBA England and

527   Wales, ranging from Margetts Pit (42.6±4.4%) to E-MBA Occitanie (44.1±3.4%) to Cliffs End

528   (50.3±5.3%) to IA Hauts de France (69.6±7.8%) (Table 2). Thus, a minimum of around half the

529   ancestry of England and Wales owes its origin to the M-LBA population movements. The

530   estimate of ~50% genome-wide population turnover by the end of this period is substantially

531   larger than the estimate (23±8%) derived by estimating the degree of population turnover

532   needed to decrease the proportion of L21/M529 Y chromosome haplogroups from 88±6% in

533   C/EBA Britain to 66±5% by the IA (Extended Data Figure 6). While these results taken at face

534   value suggest a female-biased spread of mainland European ancestry into Britain in the LBA,

535   this inference is tentative as it assumes that L21/M529 haplogroups were not present among the

536   migrants and that there was no social selection within Britain for L21/M529 male-line lineages;

537   if either assumption was incorrect, we would be underestimating the male contribution. The

538   possibility of female sex bias associated with the ancestry transition in the LBA is striking in

539   light of evidence of Saxon migrations being sex-biased in the reverse direction[40,41]. For

540   example, in present-day Central and Eastern Britain the M529 haplogroup frequency is 14%

541   (Extended Data Figure 6) implying a minimum ~79% male-lineage replacement since IA times,

542   greater than the ~30-40% ancestry contribution from Saxon migrations implied by previous

543   work[13,14] but consistent with estimates based on contemporary Y chromosome data[41] (this

544   computation does not consider the possible contribution of non-Saxon post-IA migrations).

545

546   **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

547
548   *Note: Right populations for the basic ancestry estimate from qpAdm are (Mbuti.SDG, Netherlands_BellBeaker,*
549   *Poland_Globular_Amphora, WHGA, Russia_Samara_EBA_Yamnaya, and Turkey_N). The first source is always*
550   *England C/EBA. This analysis identifies 17 fitting populations at P>0.05 (Supplementary Information section 6*
551   *gives the full list), and here we only show the subset that continues to fit after adding 38 pre-1000BP European*
552   *populations to the reference set, then Bonferroni correcting the lowest p-value for the 38 hypotheses tested.*

553

554   The genetic links we report between England and Wales and parts of mainland Europe are

555   striking in light of the archaeological record. The M-LBA has long been recognized as a time

556   when cultural connections between Britain and regions of mainland Europe intensified. In this

557   period, Britain and Ireland formed part of the 'Atlantic Bronze Age', a network of societies

558   located along the Atlantic façade of Europe (including western Iberia and present-day northern

559   and western France) that shared aspects of material culture and ritual practice[42]. Societies on

560   both sides of the Channel, while far from culturally homogeneous, shared features including

561   elevated enclosures (hillforts), diverse bronze swords and axes, bronze feasting equipment,

562   sources of metals, and ritual deposition of metalwork hoards often around water[43-45]. The

563   similarity in the rites of metalwork deposition suggest that these commonalities did not just

564   reflect exchange of objects and methods of production, but also shared systems of belief. Early

565   models of cultural change in LBA Britain often invoked 'invasion' from Central Europe[46],

566   while more recent discussions have emphasized trade, exchange, economy and the sharing of

567   ideas[42,47]. Our genetic analyses provide overwhelming evidence that major movements of

568   people into Britain occurred during the M-LBA, particularly during a period of intensification

569   of exchange that led to the formation of the 'Manche-Mer du Nord (MMN) complex' among

570   other cultural phenomena[48,49]. Our findings do not establish whether the population movements

571   we detect were a cause or consequence of networks established as part of the Atlantic Bronze

572   Age, but do suggest that interactions between local populations of Britain and new migrants

573   bringing ideas from mainland Europe may be responsible for some of the cultural change we

574   see in M-LBA England and Wales. We do not have sample sizes from the Atlantic façade of

575   mainland Europe that are comparable to what we report from Britain, and thus cannot test if the

576   gene flow between the two regions in the M-LBA was largely unidirectional; ancient DNA

577   sampling from northern France would make it possible to quantify the amount of gene flow in

578   the reverse direction.

579

580   Population movements are often a significant factor in cultural change, including in

581   languages[50,51]. In the context of our results, it is therefore striking that a recent study has

582   proposed that Celtic languages spread into Britain from France likely in the early IA or possibly

583   the LBA[52]. Our identification of substantial M-LBA population movements into Britain from

584   sources that fit populations in France notably better than in Iberia, the Netherlands, and

585   Bohemia adds an independent line of evidence for this scenario. Moreover, our finding of a

586   decrease of EEF ancestry in Iberia, where the proportion was high in the EBA, and the roughly

587   simultaneous increase in Britain where the proportion was low, could, in theory, reflect a Celtic-

588   speaking group of people with intermediate EEF ancestry spreading into both regions, and could

589   help to explain the occurrence of Celtic languages in both regions. Alternatively, this

590   homogenization of EEF ancestry could reflect a generalized increase in mobility over the region

591   and period of the Atlantic Bronze Age, facilitated by the emergence of a Celtic lingua franca[53].

592   While the fact that we do not detect an ancestry change in Scotland might seem like a problem

593   for either of these related proposals, the lack of major ancestry change in Scotland might

594   coincide with the evidence that a non-Celtic language remained in use into the first millennium

595   CE in Scotland[54]. Our finding that there were no major migrations into Britain from the

596   European mainland in the IA suggests that, if Celtic language spread was driven by the

597   movement of people, it is unlikely to have happened in the IA. The adoption in IA Britain of

598   cultural practices that originated in mainland Europe—particularly those linked to the La Tène

599   tradition[55]—were also evidently independent of large-scale population movements, although

600   there certainly were smaller movements of people, as attested by individual IA outliers with

601   high EEF ancestry such as those at Thame or Winnall Down, and individuals with low EEF

602   ancestry such as several at Carsington Pasture Cave (Figure 3).

603

604   In the IA, EEF ancestry was highest in present-day southern England; lower in Wales, the

605   Midlands, and the north of England (2.0-2.3% lower); and lowest in all regions of Scotland

606   (Table 1); suggesting a broad south-north cline of decreasing EEF ancestry. Within the south of

607   Britain we detect six regional groupings with significantly different patterns of allele sharing

608   with mainland groups: Wales, the combined region of northern England and the Midlands, the

609   combined region of southeast and south-central Britain, Cornwall, East Anglia, and East

610   Yorkshire (Extended Data Table 2). To understand this process in more detail, we carried out a

611   *qpAdm* analysis fitting all the British IA groups as mixtures of the England C/EBA population

612   and the six populations in Table 2 that fit as sources for the later migration (Online Table 12).

613   We can fully explain the regional variation in ancestry in the IA in England and Wales as being

614   driven by different proportions of ancestry from the population that spread through the region in

615   the LBA; using Margetts Pit as the source of migration, we obtain estimates ranging from

616   51±6% in south-central England to 31±5% and 32±5% in northern England and the Midlands

617   (Table 1). Thus, the Iron Age was a period when material culture was increasingly regional in

618   character[56]; as we show here, this was accompanied by subtle biological structure. A striking

619   example is in East Yorkshire, where most of our analyzed individuals are associated with Arras

620   Culture burial contexts, comprising square-ditched barrows and occasional chariot burials, and

621   where our estimate of the new ancestry source is 45±5%[57,58]. Similarities between Arras

622   funerary traditions in East Yorkshire and those recorded for IA societies in mainland Europe,

623   particularly the Paris Basin and the Ardennes / Champagne Regions of France and Belgium,

624   have led to suggestions that IA societies in East Yorkshire had been influenced by migrations

625   from mainland Europe[59]. In this context, it is notable that differentiation between IA

626   populations in Britain, as measured by F_{ST}, is highest between East Yorkshire and all other IA

627   populations in England and Wales (Extended Data Table 5). Our analysis suggests that people

628   buried in the style of the Arras Culture did indeed harbor a large proportion of ancestry most

629   likely from France. However, without ancient DNA from the IA from the putative sources in

630   mainland Europe we cannot determine whether this reflects the same M-LBA source that

631   contributed to other southern British populations (followed by isolation within the island of

632   Britain leading to high population-specific genetic drift), or alternatively distinctive migrations

633   from mainland Europe in the IA specifically affecting this region.

634

635   An important direction for future work will be to generate new ancient DNA data from

636   mainland contexts and Ireland to test the alternative scenarios of population history raised here,

637   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

12

672   to the Y chromosome phylogenetic tree from Yfull version 8.09 (https://www.yfull.com/),

673   providing two alternative notations for Y chromosome haplogroups: the first using a label

674   based on the terminal mutation, and the second describing all the associated branches of the

675   Y chromosome tree based on the notation of the International Society of Genetic Genealogy

676   (ISOGG) database version 15.73. (http://www.isogg.org).

677

678   **Determination of ancient DNA authenticity.** We determined ancient DNA authenticity

679   based on five criteria. First, we required that the lower bound of the 95% confidence interval

680   for contamination from *ANGSD* (if we were able to compute it) was <1%. Second, we

681   required that the upper bound of the 95% confidence interval for match rate to mitochondrial

682   consensus sequence (if we were able to compute it) was >95%. Third, we required that the

683   average rate of cytosine-to-thymine errors at the terminal nucleotide for all sequences passing

684   filters was >3% for double-stranded partially UDG-treated libraries[16] and >10% for single-

685   stranded USER-treated libraries and double-stranded non-UDG-treated libraries[71]. Fourth, we

686   required the ratio of sequences mapping to the Y chromosome to the sum of sequences

687   mapping to the X and Y chromosome for the 1240K data to be less than 3% (consistent with

688   a female) or >35% (consistent with a male). Fifth, we required the number of SNPs covered

689   at least once to be at least 5,000 (for most actual population genetic analyses, we required at

690   least 30,000). For some individuals with evidence of contamination, we analyzed only

691   sequences with terminal damage to enrich for genuine ancient DNA by using *pmdtools*,

692   allowing us to rescue data for some individuals[72]. We do not include in our main analyses

693   data from 71 individuals that failed our authenticity criteria (marked as "QUESTIONABLE"

694   in Online Table 1); however, we publish the data as part of this study as a resource.

695

696   **Population genetic analyses.** We used ADMIXTURE to cluster individuals and used Principal

697   Component Analysis as implemented in *smartpca* to visualize gradients of ancestry and genetic

698   drift, using the option *lsqproject* to project ancient individuals onto the patterns of genetic

699   variation learned from modern individuals[73]. We computed f_4-statistics and F_{ST} and carried out

700   *qpWave* and *qpAdm* analyses using ADMIXTOOLS[27]

701   (https://github.com/DReichLab/AdmixTools). We inferred relatives up to the third to fifth

702   degree using a previously described method[24].

703

704   **Allele frequency estimates of variants with functional importance.** We clustered

705   individuals from Britain, Iberia and Czech Republic into 5 temporal groups-3950-2450 BCE,

706   2450-1550 BCE, 1550-1250 BCE, 1250-800 BCE, and 800-50 BCE-matching our

707   periodization into Neolithic, C-EBA, MBA, LBA, and IA in Britain. To estimate the allele

708   frequency of a given SNP in a particular group, we used sequence counts at each SNP

709   position in each individual and used a maximum likelihood approach[20]. We obtained

710   confidence intervals using the Agresti-Coull method implemented in the *binom.confint*

711   function of the R-package *binom.*

712

713   **Accelerator Mass Spectrometry (AMS) radiocarbon dating.** We carried out AMS dating

714   at a variety of laboratories; we refer readers to the individual laboratories for the experimental

715   procedures. We calibrated all dates using OxCal 4.4.2[74] and IntCal20[75].

716

717   **Data availability.** The aligned sequences are available through the European Nucleotide

718   Archive under accession number [to be made available on publication]. Genotype data used in

719   analysis are available at https://reich.hms.harvard.edu/datasets. Any other relevant data are

720   available from the corresponding authors upon reasonable request.

721

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%	..	$< 10^{-12}$	3×10^{-5}	3×10^{-6}	4×10^{-10}	$< 10^{-12}$	$< 10^{-12}$	$< 10^{-12}$	0.68	2×10^{-9}	2×10^{-5}	1×10^{-7}	6×10^{-9}	$< 10^{-12}$	9×10^{-4}	6×10^{-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%	5×10^{-4}	$< 10^{-12}$	..	0.040	$< 10^{-12}$	$< 10^{-12}$	$< 10^{-12}$	$< 10^{-12}$	0.16	1×10^{-9}	1×10^{-5}	0.0016	2×10^{-5}	$< 10^{-12}$	0.89	2×10^{-8}	$< 10^{-12}$
England LBA	17	0.079	11.7%	38.6%	49.7%	0.6%	0.8%	0.9%	5×10^{-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	3×10^{-5}	$< 10^{-12}$
England MBA	25	0.16	11.7%	35.6%	52.7%	0.5%	0.7%	0.8%	1×10^{-8}	$< 10^{-12}$	$< 10^{-12}$	0.0014	..	4×10^{-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%	$< 10^{-12}$	$< 10^{-12}$	$< 10^{-12}$	$< 10^{-12}$	1×10^{-7}	..	$< 10^{-12}$	$< 10^{-12}$	0.0011	5×10^{-7}	0.011	0.0015	9×10^{-4}	$< 10^{-12}$	4×10^{-6}	0.80	$< 10^{-12}$
England Neolithic	35	0.012	17.0%	81.8%	1.2%	0.5%	0.6%	0.6%	$< 10^{-12}$	5×10^{-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%	$< 10^{-12}$	2×10^{-7}	$< 10^{-12}$	$< 10^{-12}$	$< 10^{-12}$	$< 10^{-12}$	1×10^{-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%	3×10^{-8}	$< 10^{-12}$	7×10^{-10}	0.044	7×10^{-4}	1×10^{-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%	1×10^{-7}	$< 10^{-12}$	4×10^{-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%	4×10^{-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%	1×10^{-7}	$< 10^{-12}$	3×10^{-7}	6×10^{-4}	0.093	3×10^{-5}	$< 10^{-12}$	$< 10^{-12}$	0.023	1×10^{-4}	0.0061	0.32	..	$< 10^{-12}$	0.025	0.024	$< 10^{-12}$
Scotland Neolithic	32	2×10^{-5}	17.4%	80.8%	1.8%	0.5%	0.6%	0.6%	$< 10^{-12}$	3×10^{-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	8×10^{-5}	$< 10^{-12}$	$< 10^{-12}$	0.23	0.12	0.073	0.26	0.022	$< 10^{-12}$	..	2×10^{-4}	$< 10^{-12}$
Wales MBA	5	0.59	12.9%	34.3%	52.8%	1.0%	1.3%	1.5%	2×10^{-9}	$< 10^{-12}$	4×10^{-7}	4×10^{-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	$< 10^{-12}$	$< 10^{-12}$	..

740
741
742 **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
743 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*
744 *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)
745 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.

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

749
750

751 **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

752
753 **Note:** We model each group in *qpAdm* as a mixture of a Neolithic and a Chalcolithic/EBA population (first
754 column from England and Wales, second column from Scotland). In each case the reference populations are
755 (*Mbuti.SDG, Netherlands_BellBeaker, Poland_Globular_Amphora, WHGA, Iberia_C, Czech_EBA,*
756 *Italy_Sardinia_EBA, Russia_Samara_EBA_Yamnaya, Turkey_N)*. P-values from *qpAdm* are highlighted if
757 <0.001. We definitively reject the model that people of LBA and IA England and Wales are directly
758 descended from a mixture of Neolithic and C/EBA people from England and Wales (the failure of the models
759 involving Irish populations may not reflect real modeling failure but instead could reflect systematic
760 differences in data properties between shotgun sequencing data and in-solution enrichment data).
761

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		
		N	East Yorkshire	Midlands	Cornwall	Wales	Southcentral	Southeast	East Anglia	North	Scotland Southeast	Scotland West	Scotland Orkney
			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.


771
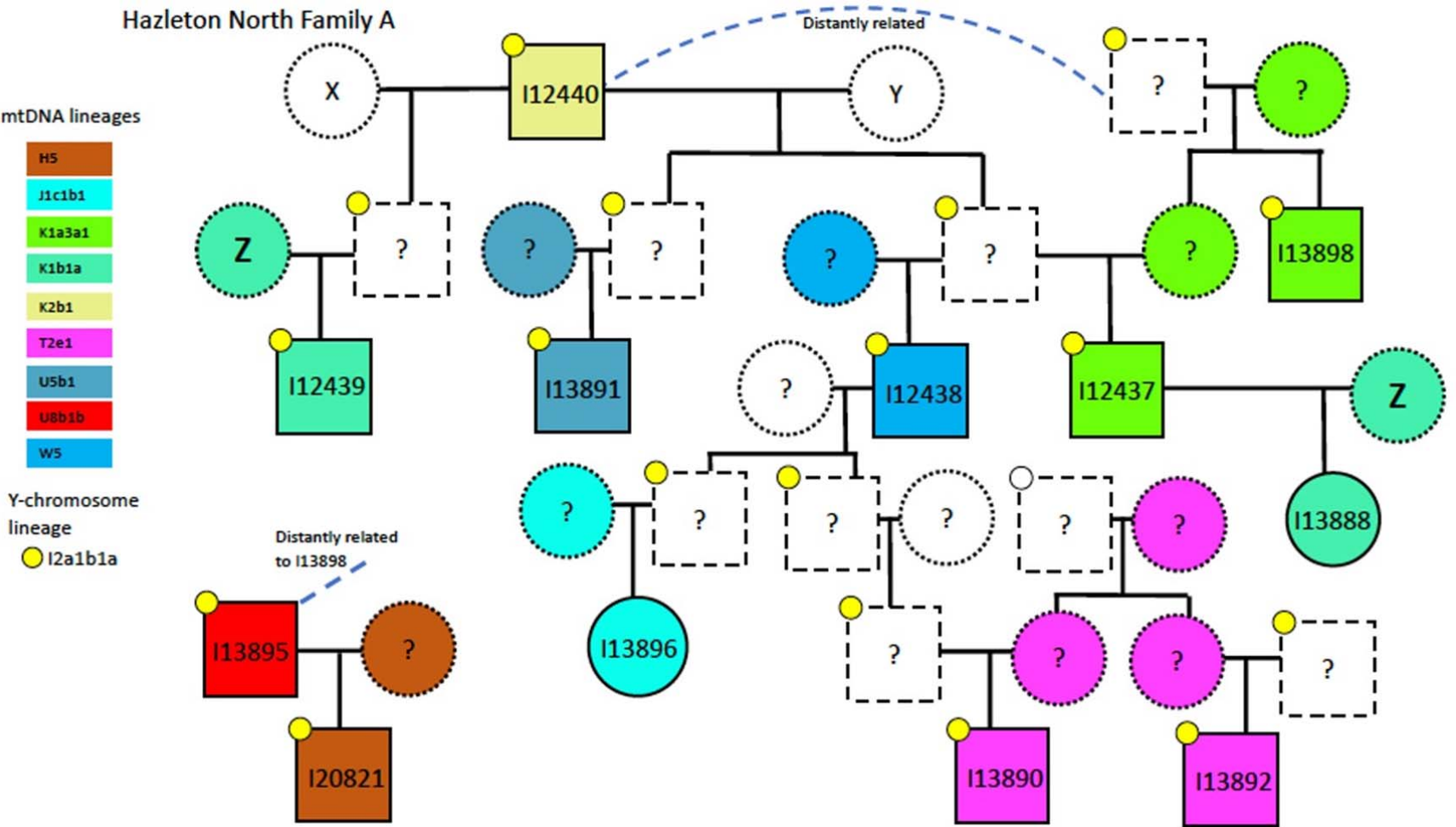
772 **Extended Data Figure 2: Post-MBA Britain was not a mix of earlier British populations.**

773 We computed f_4(*Karitiana, Netherland_BellBeaker; England.and.Wales_IA,*

774 α(*England.and.Wales_N*) + (1-α)(*England.Wales_C.EBA*)). If *England.and.Wales_IA* is a

775 simple mix of *England.and.Wales_N* and *England.Wales_C.EBA* without any additional

776 contribution of ancestry, then for some mixture proportion the statistic will be consistent with

777 zero (Supplementary Information section 4). However, we observe that it is positive for all

778 values of α, showing that Karitiana share more alleles with IA people from England and Wales

779 than do both Neolithic and C/EBA people; thus, they must have ancestry from an additional

780 population deeply related to Karitiana that did not contribute to the earlier groups.

781
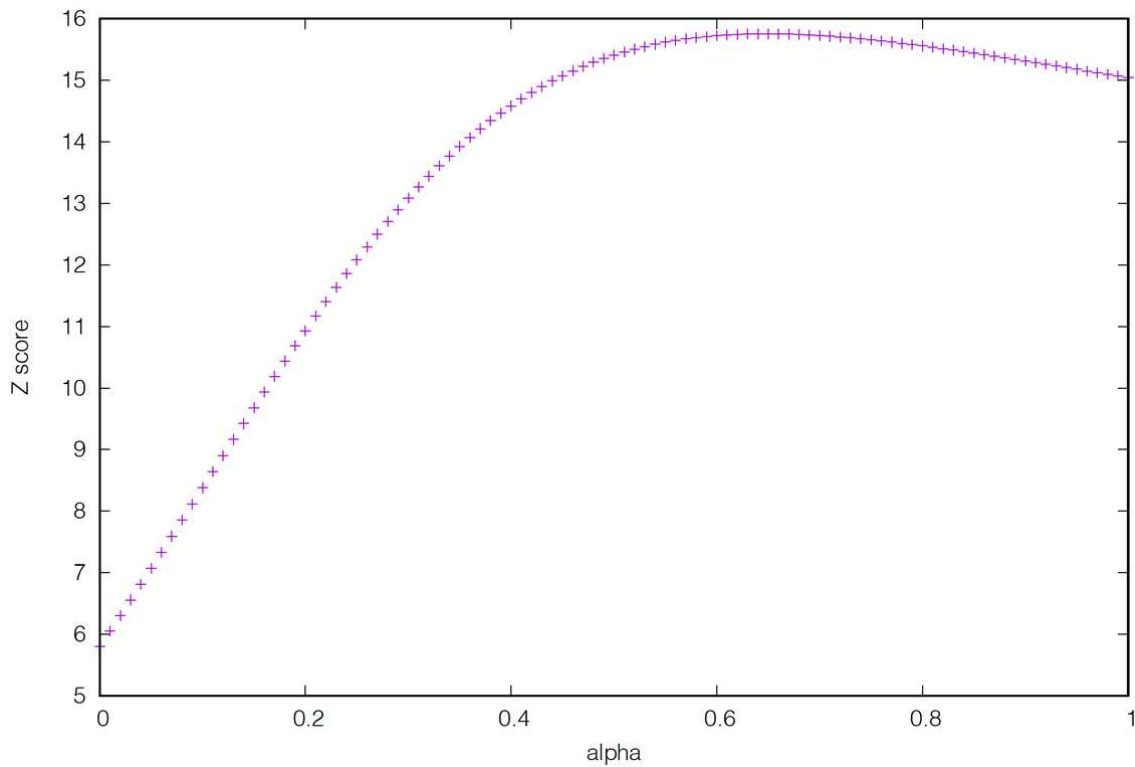
782 **Extended Data Figure 3: By-individual analysis of the British time transect.** This is a version of Figure 3 with the time transect extended into

783 the Neolithic period. Estimates of EEF ancestry and one standard error are shown for all individuals in the British time transect that pass basic

784 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

785 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

786 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

787 southern and northern Britain in each period are shown in dashed lines.
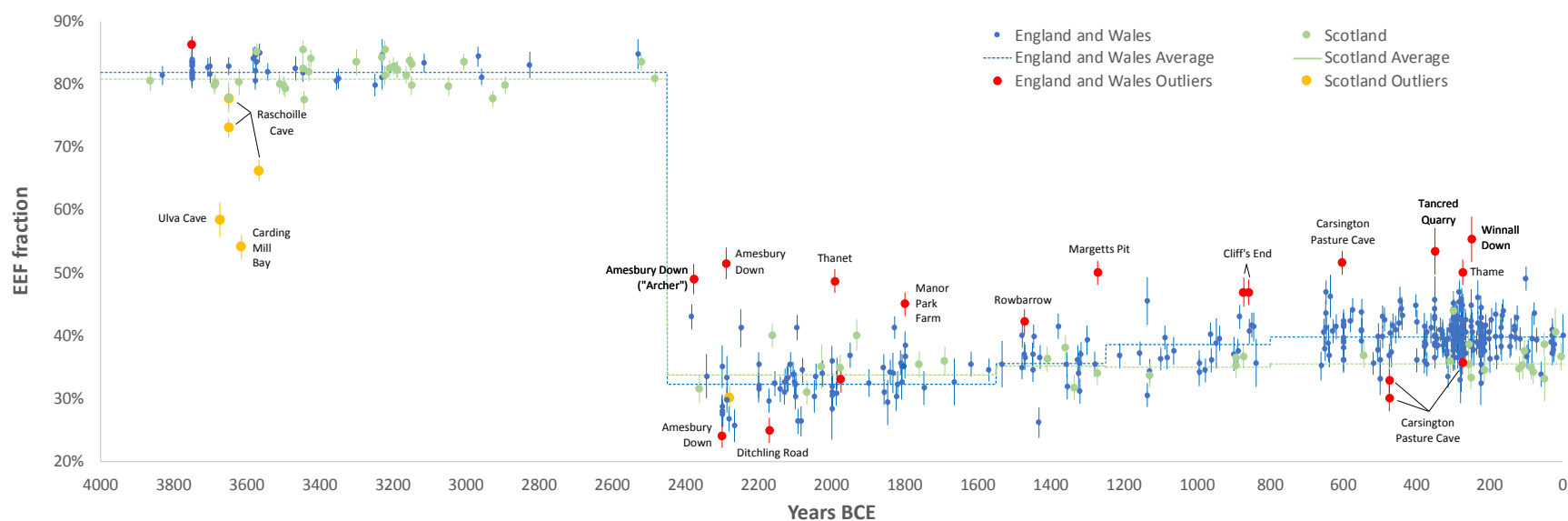
788

789

Extended Data Figure 4: Ancestry change over time in multiple European time transects.

791 Because of the genetic shift we observe in Britain, for each time transect we separated our

792 samples into 'Early' (2250-1350 BCE) and 'Late' (1050-50 BCE). We show PCA plots where

793 the 'base individuals' (light grey) are present populations used to calculate the PCA axes.

794 Populations with high Steppe ancestry are shifted to the top left, and with high EEF and WHG

795 ancestry to the bottom. We see increases in EEF ancestry in more northern regions (England

796 and Wales (EW), Bohemia (Czech), and the Netherlands), decreases in more southern regions

797 (Hungary and Iberia), and no clear average change in France.

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800

802
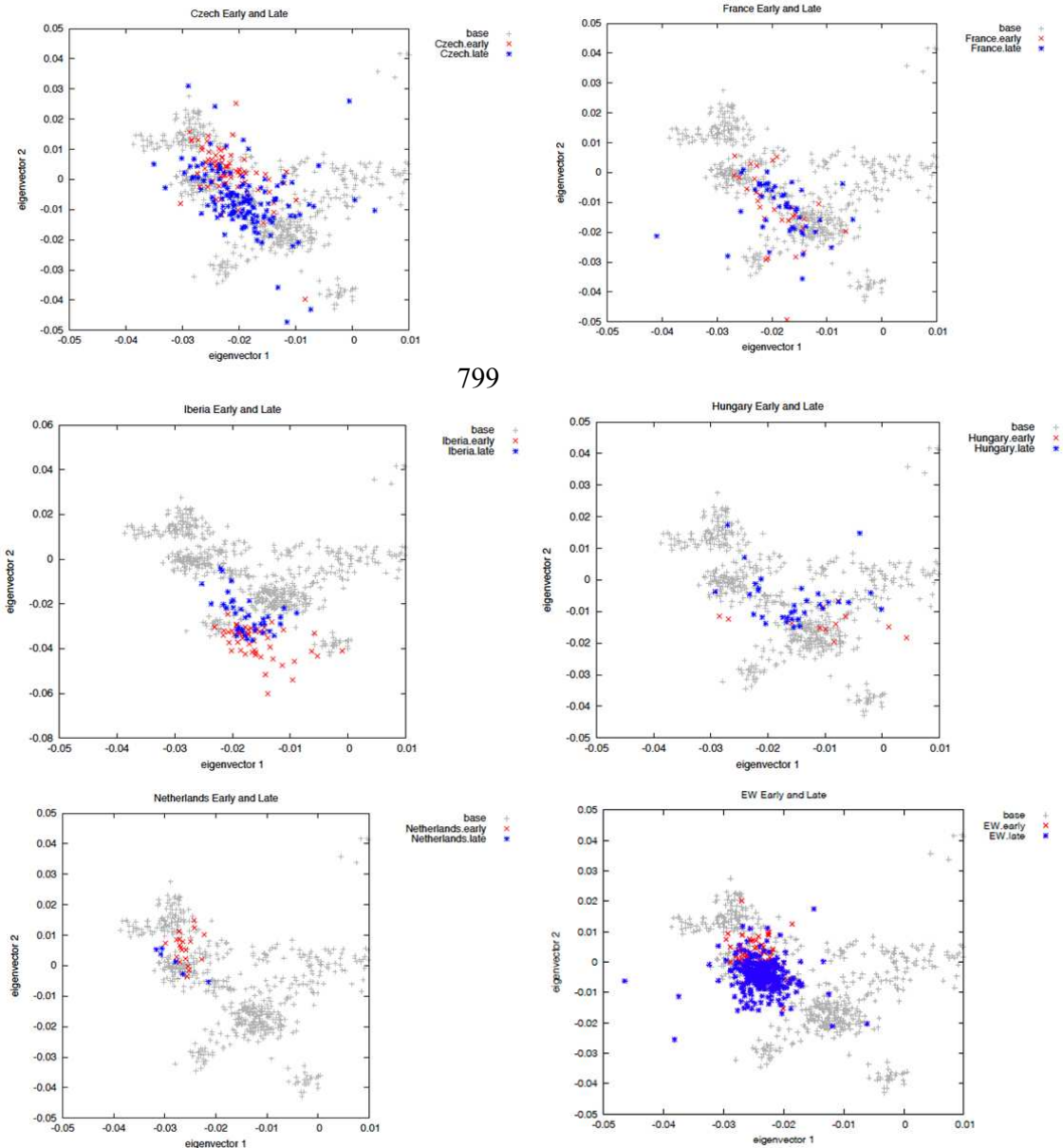
803 **Extended Data Figure 5: Frequency change over time at two phenotypically important alleles.** (Top) The lactase persistence allele at
804 rs4988235. (Bottom) The light skin pigmentation allele at rs16891982. In Britain the rise in frequency of the lactase persistence is significantly
805 earlier than in Bohemia. This analysis is based on direct observation of alleles; imputation results are qualitatively consistent (Figure 4B).
806
807

810
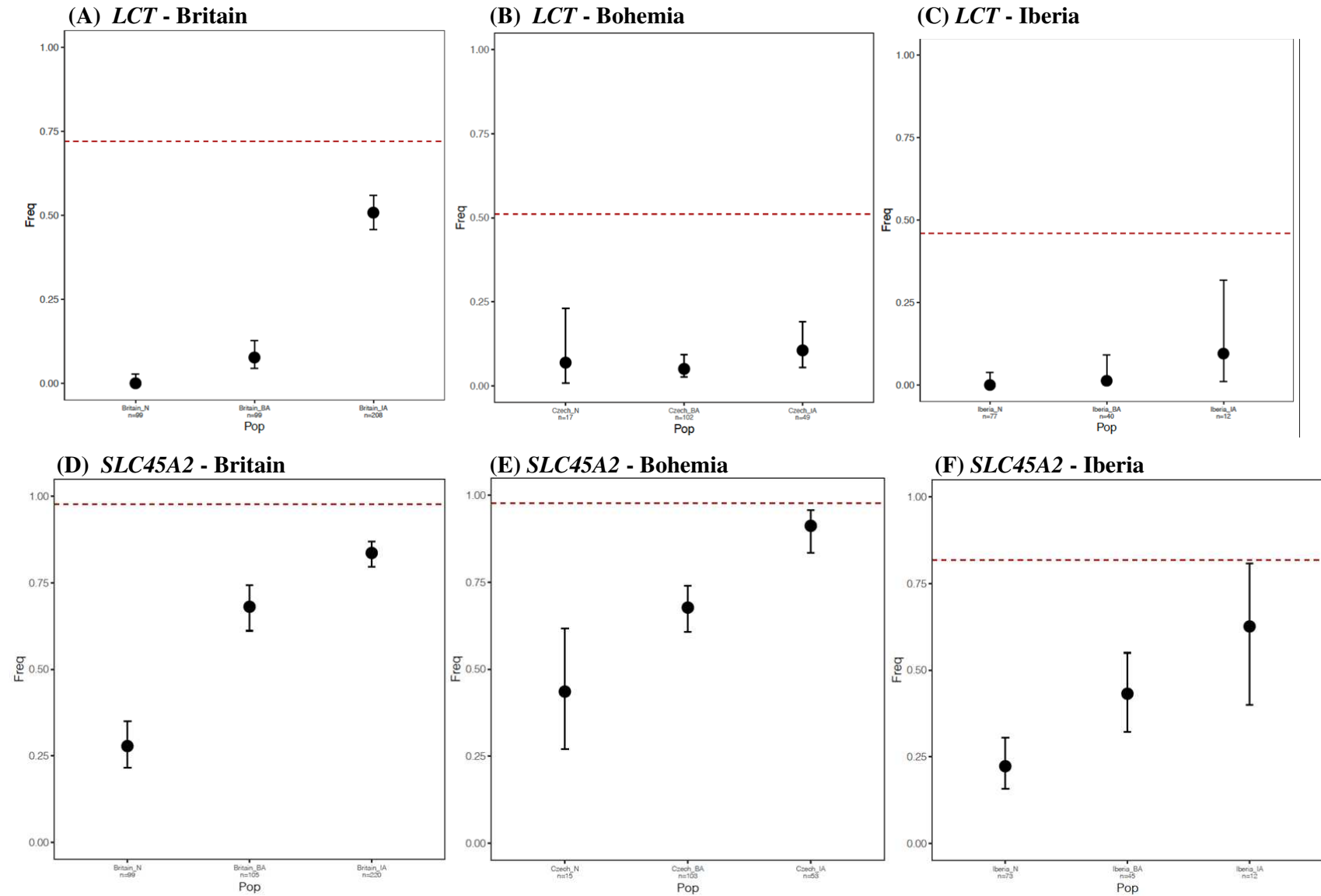
811   **Extended Data Figure 6: Y chromosome haplogroup frequencies in the British transect.**

812   We show the estimated frequency of the characteristically British Y chromosome haplogroup

813   R1b-P312 L21/M529 in all individuals for which we are able to make a determination and

814   which are not first-degree relatives of a higher coverage individual in the dataset. The frequency

815   increases significantly from ~0% in the whole island Neolithic, to 88±6% in the whole island

816   Chalcolithic/EBA. It declines to 73±10% in the MBA and LBA (from this time on restricting to

817   England and Wales because of the autosomal evidence of a change in ancestry in the south but

818   not the north), and to 66±5% in the IA, a significant reduction relative to the Chalcolithic/EBA.

819   There is a further reduction from this time to the present, where the proportion is 43±3% in

820   Wales and the west of England, and 14±2% in the center and east of England potentially due to

821   later immigrants bearing a different distribution of Y chromosome haplogroup frequencies.

822
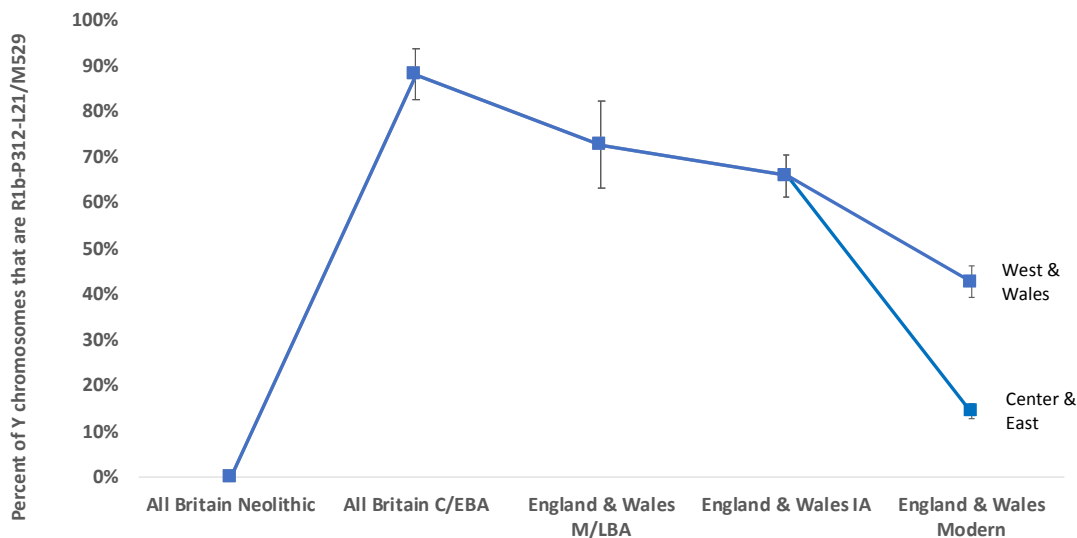
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