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

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

207

208 “Migration” is a central concept in population genetics as well as in archaeology, but its
209 meaning has evolved in divergent ways in the course of the development of these disciplines,
210 which has sometimes contributed to misunderstandings¹. Population geneticists use “migration”
211 to refer to any movement of genetic material from one geographic region to another, but from
212 an archaeological perspective this definition is too broad, as it means that even low-level
213 symmetrical exchanges of mates between adjacent communities would be considered migration.
214 In archaeology, the concept of migration is also haunted by its politicization in the early
215 twentieth century, when invasion was sometimes argued to be the primary mechanism for the

216 spread and dominance of specific ethnic groups², a theory that was used to justify claims on
217 territory and wars of aggression³. 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 Caesar⁴. 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 study⁹ 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

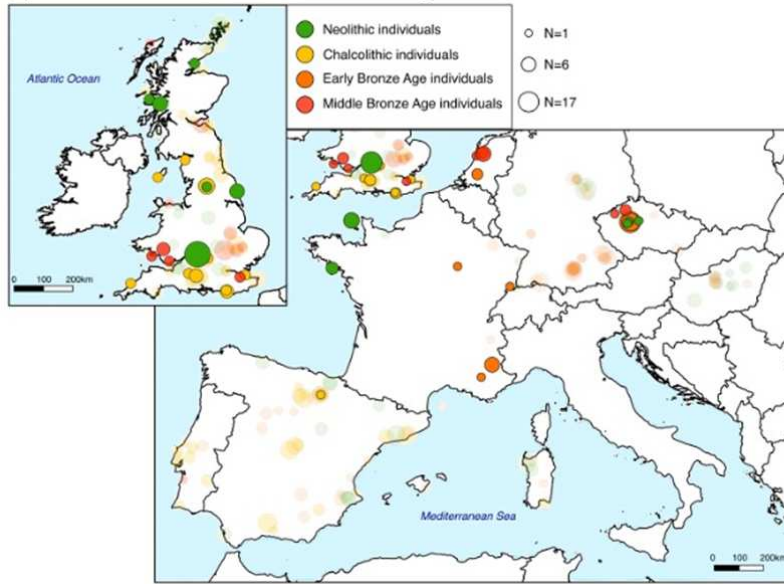
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258 We generated new ancient DNA data beginning in the Neolithic but focusing on the period from
259 the Middle Bronze Age (defined here as beginning around 1550 BCE) through to the end of the
260 pre-Roman Iron Age (defined here as 43 CE) (Supplementary 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 DNA¹⁵⁻¹⁷, 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 DNA¹⁶, or those that were first degree
282 relatives of other higher coverage individuals in the dataset²⁴ (Online Tables 6 and 7), or those
283 that had too low coverage for accurate ancestry inference which we define as <30,000 single

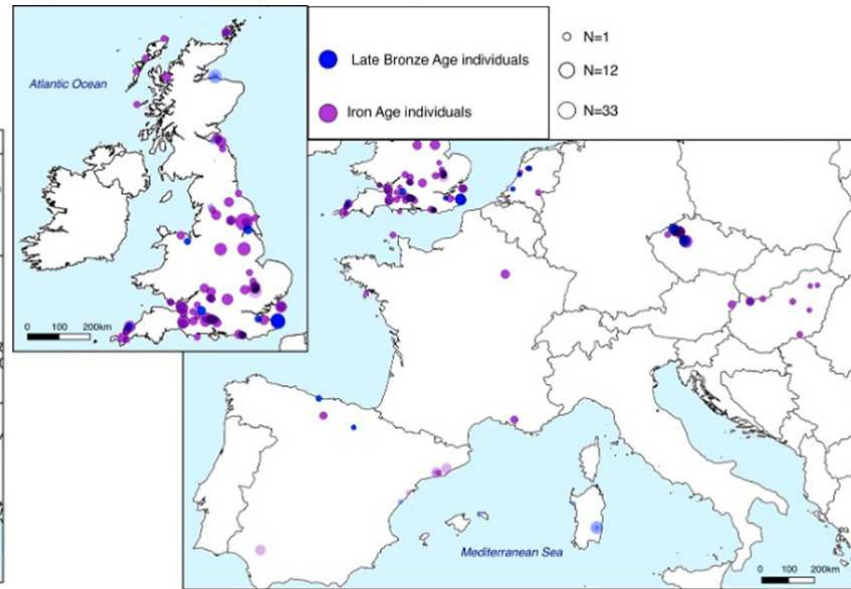
284 nucleotide polymorphisms (SNPs) covered. However, we report data for all individuals. Figure
285 1 shows a map of all the newly reported individuals. We identified 283 individuals from 96
286 families as being genetically related (within the third degree) to at least one other individual in
287 the 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 sites²⁵ (Extended Data Figure 1,
291 Supplementary Information section 3).

292

(a) Neolithic to Middle Bronze Age



(b) Late Bronze Age to Iron Age

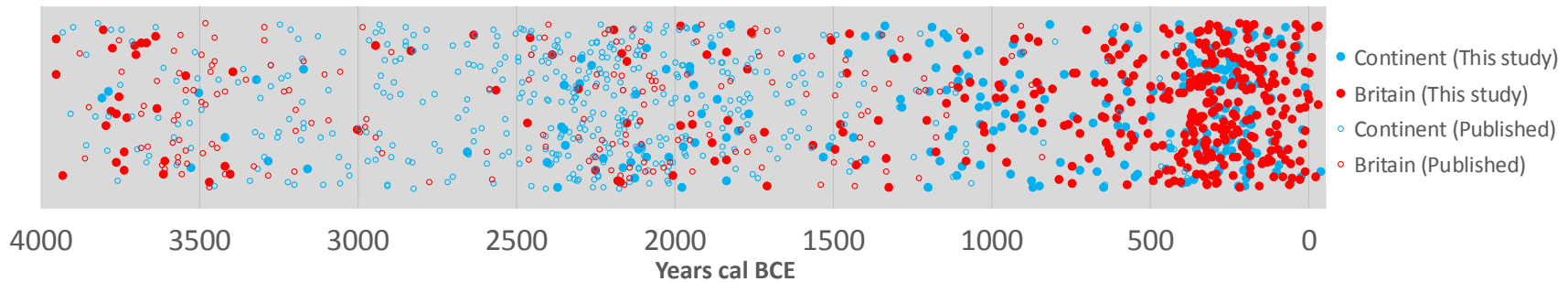


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(c) Time distribution of analysed individuals

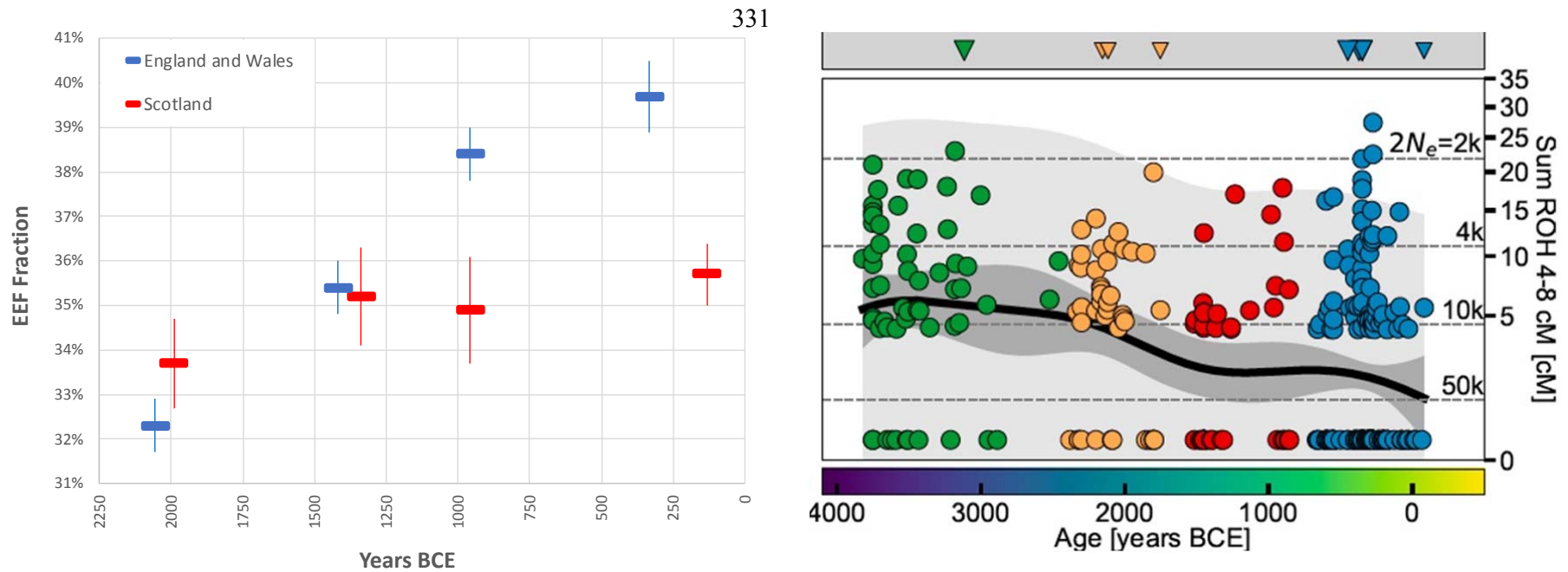


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297

298 **Figure 1: Ancient DNA dataset.** (a) Geographic distribution of the Neolithic to Middle Bronze Age and (b) Late Bronze Age to Iron Age
 299 individuals analysed in this study; we show newly reported data in intense colors and previously published data in pale colors. (c) Temporal
 300 distribution of the newly reported individuals. To reduce overlap of points, we sample the date of each individual from their posterior
 301 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



334 **Figure 2: A high resolution ancient DNA time transect through Britain.** (Left) An increase in EEF ancestry in southern but not northern Britain.
 335 We show $qpAdm$ estimates for all individuals passing basic quality control, divided into four periods (C/EBA, MBA, LBA and IA). X-axis positions
 336 are the average point estimates of dates for individuals in each time frame. Here and elsewhere we show one standard error. (Right) We show
 337 inferred effective population size ($2N_e$) based on short 4-8 centimorgan runs of homozygosity (ROH) using the hapROH software²⁸, with 95%
 338 confidence intervals shown in dark grey (individuals with large proportions of their genome in large runs of homozygosity as expected for unions
 339 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
 340 CE is inferred to have occurred during the EBA-to-MBA transition, coinciding with the beginning of the migration we detect into Britain.

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	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%

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).

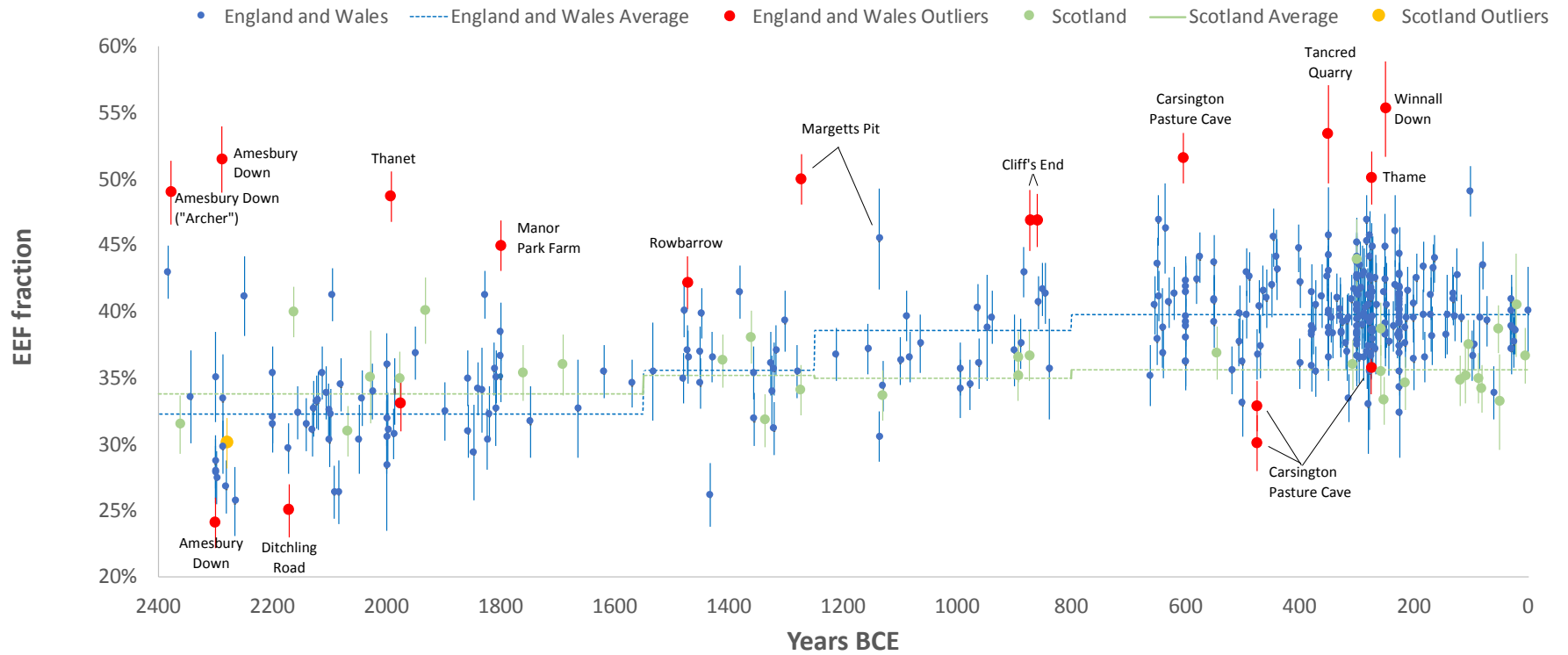
354
 355 Second, we observe high variability in EEF ancestry in the C-EBA, before proportions of EEF
 356 ancestry become relatively homogeneous by ~2100 BCE⁹ (Figure 3). This heterogeneity is
 357 apparent at C-EBA Amesbury Down where EEF ancestry in some burials is significantly below
 358 the period average of 32.3±0.6% (e.g. I2417 at 24.1±1.9% (P=1x10⁻⁸)), whereas in others it is
 359 above the average (e.g. I2416 at 51.5±2.5% (P=3x10⁻⁸) and I14200 at 49.0±2.4% (P=2x10⁻⁷)).

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 Europe²⁹. 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 ancestry²³. 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±3.4% 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±1.9% EEF ancestry (P<10⁻¹² for an excess compared to the MBA average of 35.4±0.6%),
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±3.8%, 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±0.8% by that time. We highlight two individuals at Cliffs End Farm in Kent with
391 significantly elevated EEF ancestry at 46.9±2.3% (I14865 dating to 967-811 calBCE (2735±30
392 BP, GrA-37713), P=1x10⁻⁴ for an excess) and 46.9±2.0% (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 origin³¹, 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

403 **Figure 3: By-individual analysis of the British time transect.** Estimates of EEF ancestry and one standard error for all individuals in the British
404 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
405 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
406 archaeological context date range). The averages for the main clusters in both southern and northern Britain in each period are shown in dashed
407 lines; significant outliers at the ancestry tails are shown in red (for England and Wales) and orange (for Scotland). Outliers like the three Middle
408 and Late Bronze individuals at Margetts Pit and Cliffs End could reflect the source population for the increase in EEF ancestry in the LBA.

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 ($P=8 \times 10^{-8}$ 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 lived²⁸. 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, Iberia³², Hungary, and France³³ (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

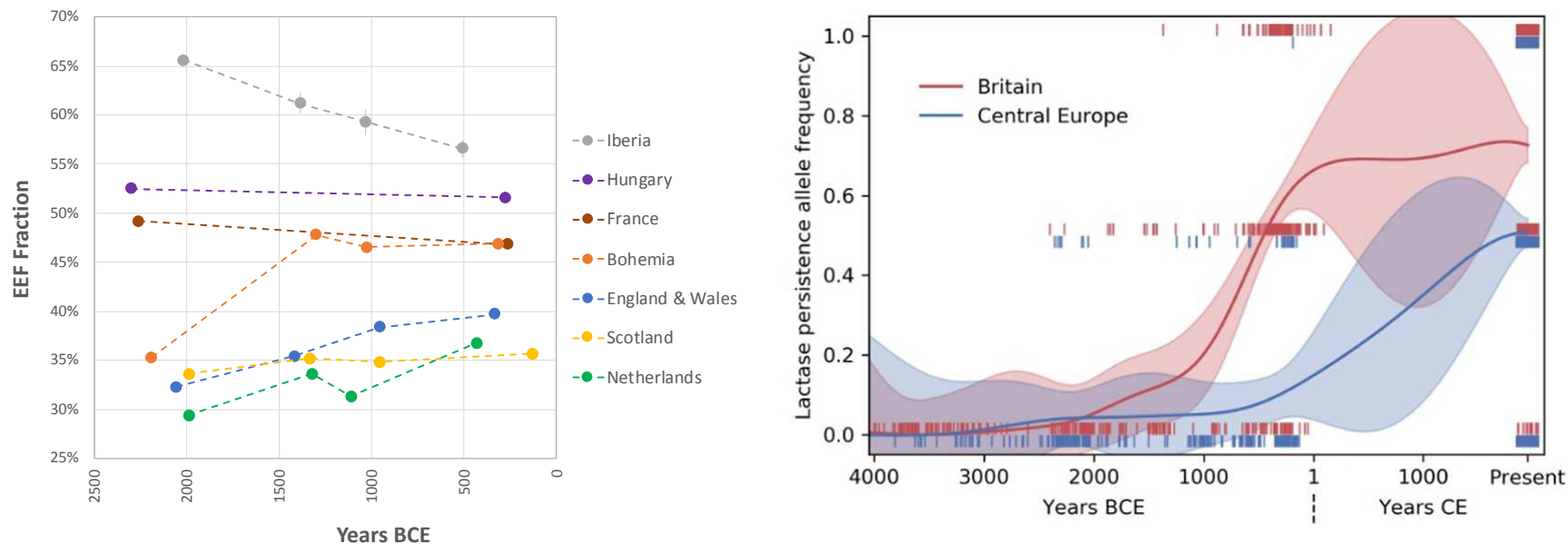
443 1300-800 BCE across much of Central Europe. Later individuals have similar EEF proportions,
444 consistent with continuity through the LBA-IA with earlier Urnfield-associated groups. By
445 contrast, in M-LBA France and Hungary there was little change in average EEF ancestry, and
446 this ancestry 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 Europe²⁰, we
460 obtain an unexpected result for the A allele at the polymorphism *MCM6-LCT* rs4988235
461 correlated with lactase persistence into adulthood²⁰ (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% today³², 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 region³⁶) than it does in mainland Europe. We estimate that this
487 haplogroup was already present at $88 \pm 6\%$ 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 Mesolithic¹¹ and Neolithic^{9,11} people of the islands.



493 **Figure 4: Geographic differences in ancestry component and lactase persistence allele frequency.** (Left) North-South ancestry convergence.
 494 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
 495 dotted lines show which points are regionally grouped and should not be interpreted as implying a smooth change in ancestry over time. (Right)
 496 The allele conferring lactase persistence began rising in frequency earlier in Britain than in Central Europe suggesting different selection
 497 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
 498 persistence allele at SNP rs4988235 by using the GaussianProcessRegressor function from the Scikit-learn library in Python with parameter
 499 $\alpha=0.1$ and $1 \times \text{RationalQuadratic}$ kernel with parameter $\text{length_scale_bounds}=(1, 1000)$. We used the GLIMPSE³⁷ software to impute diploid
 500 genotype posterior probabilities (GP), restricting to samples with $\max(\text{GP}) > 0.9$ for this SNP. The analysis includes 376 ancient individuals from
 501 Britain and 261 from Central Europe (Czech Republic, Slovakia, Croatia, Hungary, Austria, and Slovenia); to represent modern Britain we used
 502 a pool of 190 CEU and GBR individuals from the 1000 Genomes Project³⁸, and to represent modern Central Europe we use 288 from modern
 503 Czechia³⁹. 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
 504 vertical bar, and we show in shading the inferred 95% confidence interval for the allele frequency at each time point output by the Gaussian
 505 process. We confirmed the significantly earlier rise in frequency of the allele in Britain by randomly sampling a single sequence at each
 506 position; Extended Data Figure 5 shows that in the IA the derived allele frequency was 51% in Britain (46-56% 95% confidence interval)
 507 compared to 11% (4-19%) for Bohemia.

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 ($42.6 \pm 4.4\%$) to E-MBA Occitanie ($44.1 \pm 3.4\%$) to Cliffs End
528 ($50.3 \pm 5.3\%$) to IA Hauts de France ($69.6 \pm 7.8\%$) (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 $\sim 50\%$ genome-wide population turnover by the end of this period is substantially
531 larger than the estimate ($23 \pm 8\%$) derived by estimating the degree of population turnover
532 needed to decrease the proportion of L21/M529 Y chromosome haplogroups from $88 \pm 6\%$ in
533 C/EBA Britain to $66 \pm 5\%$ 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 $\sim 79\%$ 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 data⁴¹ (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	<i>n</i>	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 practice⁴². 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 water⁴³⁻⁴⁵. 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 Europe⁴⁶,
 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 LBA⁵². 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 franca⁵³.
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 Scotland⁵⁴. 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 tradition⁵⁵—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 $51\pm 6\%$ in south-central England to $31\pm 5\%$ and $32\pm 5\%$ in northern England and the Midlands
617 (Table 1). Thus, the Iron Age was a period when material culture was increasingly regional in
618 character⁵⁶; 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 $45\pm 5\%$ ^{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 Europe⁵⁹. 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.

638 **Methods**

639

640 **Ancient DNA laboratory work.** In dedicated clean rooms at Harvard Medical School, the
641 University of Vienna, the Natural History Museum in London, and the University of
642 Huddersfield, as well as during sampling trips, we obtained powder from ancient bones and
643 teeth using a variety of methods including sandblasting, drilling and milling^{60,61}. We
644 extracted DNA using a variety of methods⁶²⁻⁶⁴, and prepared double- or single-stranded
645 libraries almost all of them treated with the enzyme Uracil DNA Glycosylase (UDG) to
646 reduce characteristic errors associated with ancient DNA degradation^{16-18,65}. We enriched
647 these sequences manually or in multiplex using automated liquid handlers for sequences
648 overlapping the mitochondrial genome^{21,66} as well as about 1.24 million single nucleotide
649 polymorphisms (“1240K capture”)¹⁹. We pooled enriched libraries which we had marked
650 with unique 7-base pair internal barcodes and/or 7- to 8-base pair indices and sequenced on
651 Illumina NextSeq500 or HiSeqX10 instruments using paired-end reads of either 76 base pairs
652 or 101 base pairs in length (Online Table 3).

653

654 **Bioinformatic analysis.** After trimming barcodes and adapters⁷, we merged read pairs that
655 had at least 15 base pairs of overlap allowing no more than one mismatch. We aligned
656 merged sequences to the mitochondrial reference genome RSRS⁶⁷ or the human reference
657 genome hg19 using *BWA* version 0.6.1⁶⁸. After identifying PCR duplicates by tagging all
658 aligned sequences with the same start and stop positions and orientation and in some cases in-
659 line barcodes, we selected a single copy of each such sequence that had the highest base
660 quality scores. For subsequent analysis, we trimmed the last 2 bases of each sequence for
661 UDG-treated libraries and the last 5 bases for non-UDG-treated libraries to reduce the effects
662 of characteristic errors associated with ancient DNA degradation. We built mitochondrial
663 consensus sequences, determined mitochondrial haplogroups using *HaploGrep2*⁶⁹, and
664 estimated the match rate to the consensus sequence using *contamMix* v.1.0-12⁷⁰ for
665 mitochondrial genomes with an average coverage of at least 2-fold. To represent the
666 autosomal data, we randomly sampled a single sequence covering each of the 1.24 million
667 SNP targets, and estimated coverage based on these targeted SNPs. We used *ANGSD* to
668 estimate contamination based on polymorphism on the X chromosome in males with at least
669 200 SNPs covered twice (males should be non-polymorphic if their data are
670 uncontaminated)²³. We automatically determined Y chromosome haplogroups using both
671 targeted SNPs and off-target sequences aligning to the Y chromosome based on comparisons

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 libraries¹⁶ and >10% for single-
685 stranded USER-treated libraries and double-stranded non-UDG-treated libraries⁷¹. 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 individuals⁷². 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 individuals⁷³. We computed f_4 -statistics and F_{ST} and carried out
700 *qpWave* and *qpAdm* analyses using ADMIXTOOLS²⁷
701 (<https://github.com/DReichLab/AdmixTools>). We inferred relatives up to the third to fifth
702 degree using a previously described method²⁴.

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 approach²⁰. 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 4.4.2⁷⁴ and IntCal20⁷⁵.

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

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739 **Extended Data Table 1: Ancestry change over time in Britain**

	Sample size	qpAdm results						Tests for difference in ancestry proportions between row and column (below diagonal qpWave, above-diagonal f4-statistic)																			
		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	0.063	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	< 10 ⁻¹²	0.063	< 10 ⁻¹²	< 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	0.16	0.16	1x10 ⁻⁹	1x10 ⁻⁵	0.0016	2x10 ⁻⁵	< 10 ⁻¹²	0.89	2x10 ⁻⁸	< 10 ⁻¹²	< 10 ⁻¹²	< 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	0.083	0.083	0.0090	0.011	0.091	0.016	< 10 ⁻¹²	0.45	3x10 ⁻⁵	< 10 ⁻¹²	< 10 ⁻¹²	< 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	..	< 10 ⁻¹²	< 10 ⁻¹²	0.018	0.018	0.81	0.58	0.80	0.92	< 10 ⁻¹²	0.016	0.0087	< 10 ⁻¹²	< 10 ⁻¹²	< 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	0.0011	5x10 ⁻⁷	0.011	0.0015	9x10 ⁻⁴	< 10 ⁻¹²	4x10 ⁻⁶	0.80	< 10 ⁻¹²	< 10 ⁻¹²	< 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	< 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	< 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	< 10 ⁻¹²	< 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	< 10 ⁻¹²	< 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	< 10 ⁻¹²	< 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	< 10 ⁻¹²	< 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	< 10 ⁻¹²	< 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	< 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	< 10 ⁻¹²	< 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	< 10 ⁻¹²	< 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	< 10 ⁻¹²	..	

740 **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
 741 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 f₄(Row population, Column
 742 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)
 743 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.
 744
 745

746 **Extended Data Table 2: Genetic substructure among regions in Iron Age Britain.** As shown in Online Table 12 and in Table 1, the significant
 747 differences between pairs of populations in England and Wales are in principle consistent with being driven by just a single migration from
 748 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	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	
Scotland	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

762 **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
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.

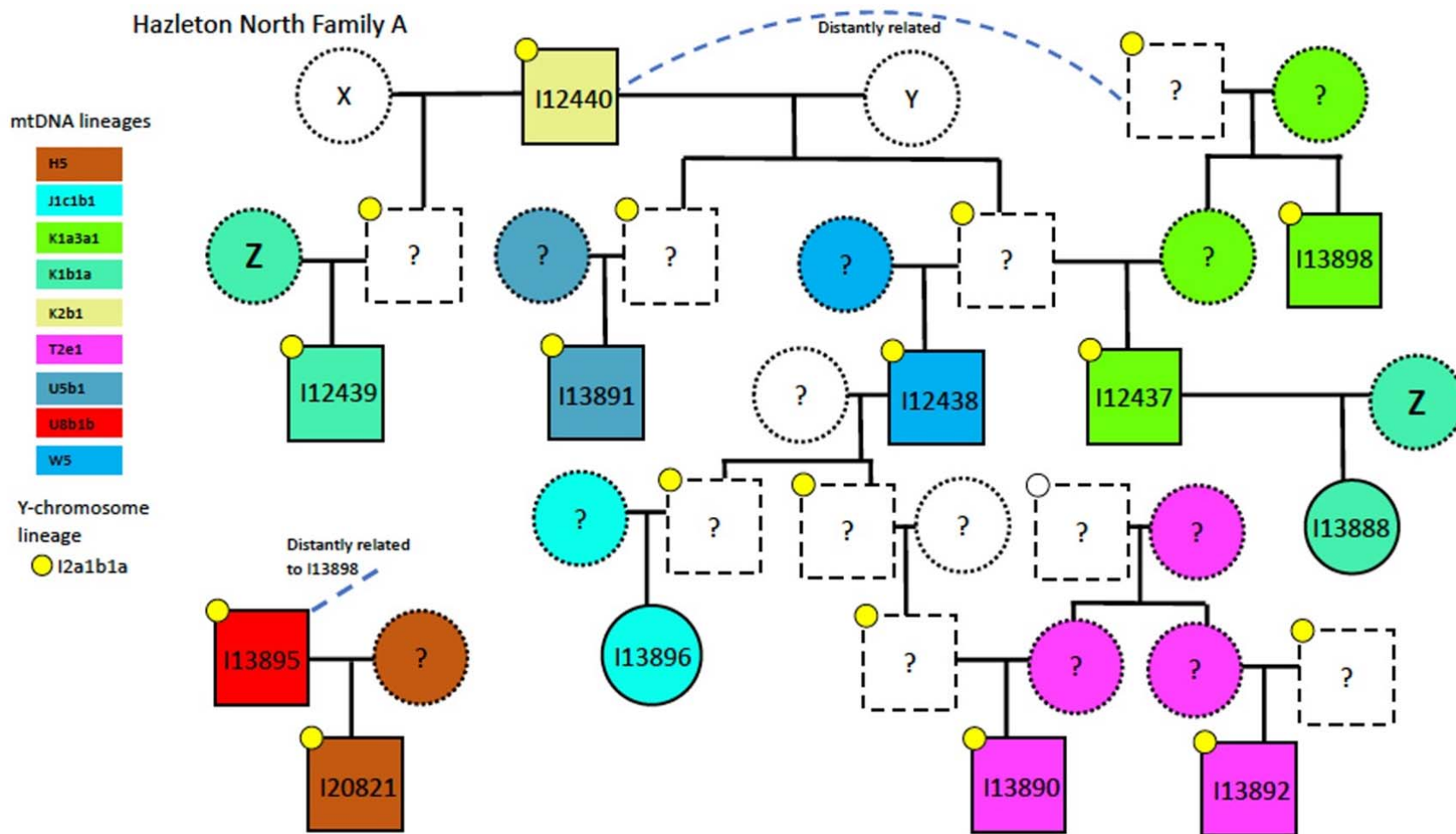
763
764

765 **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

766
767 **Note:** We compute inbreeding-corrected F_{ST} , which samples a single allele from each locus to represent each individual.

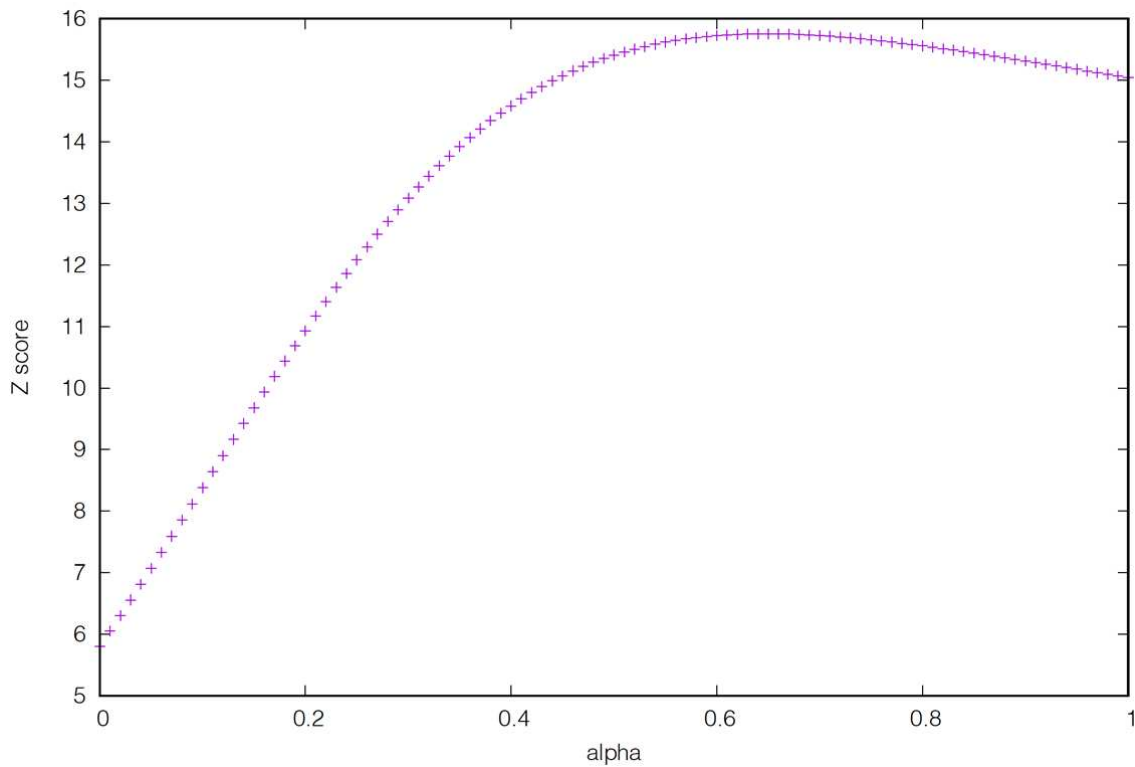
768 **Extended Data Figure 1: Hazleton North Extended Family.** The family structure is a best-guess reconstruction based on detection of pairs of
 769 relatives and patterns of sharing of segments of DNA that are identical by descent from a common ancestor. The evidence of a large pedigree of
 770 relatives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



771

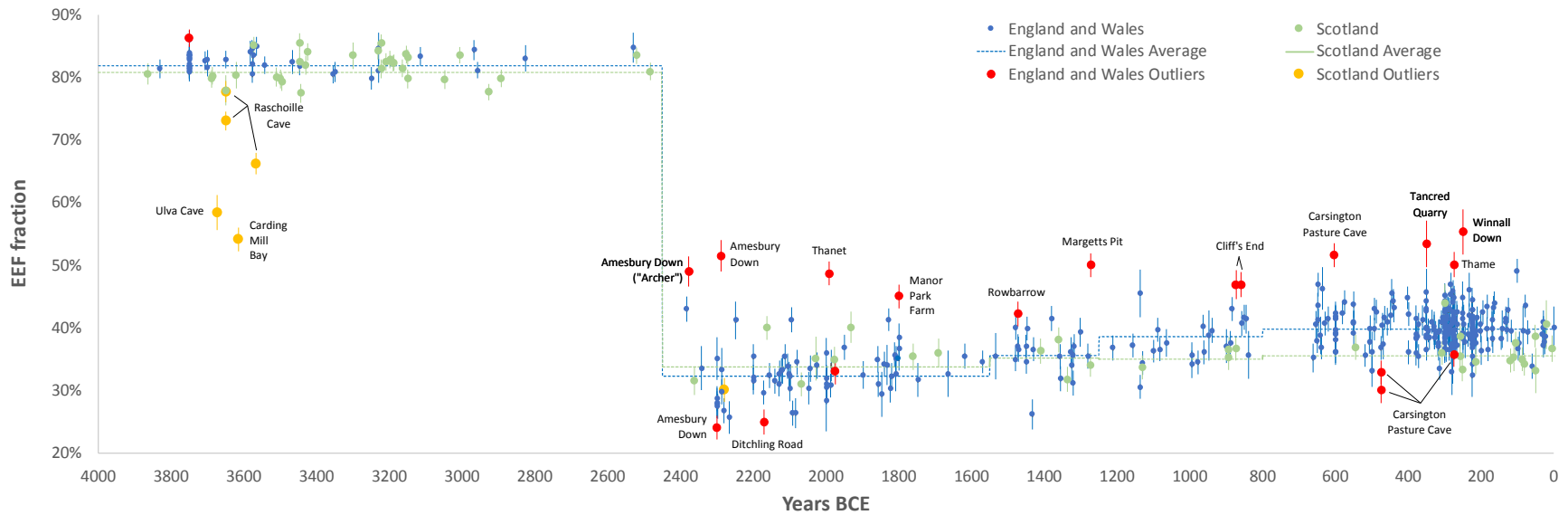
772 **Extended Data Figure 2: Post-MBA Britain was not a mix of earlier British populations.**

773 We computed $f_4(\text{Karitiana}, \text{Netherland_BellBeaker}; \text{England.and.Wales_IA},$
774 $\alpha(\text{England.and.Wales_N}) + (1-\alpha)(\text{England.Wales_C.EBA}))$. 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

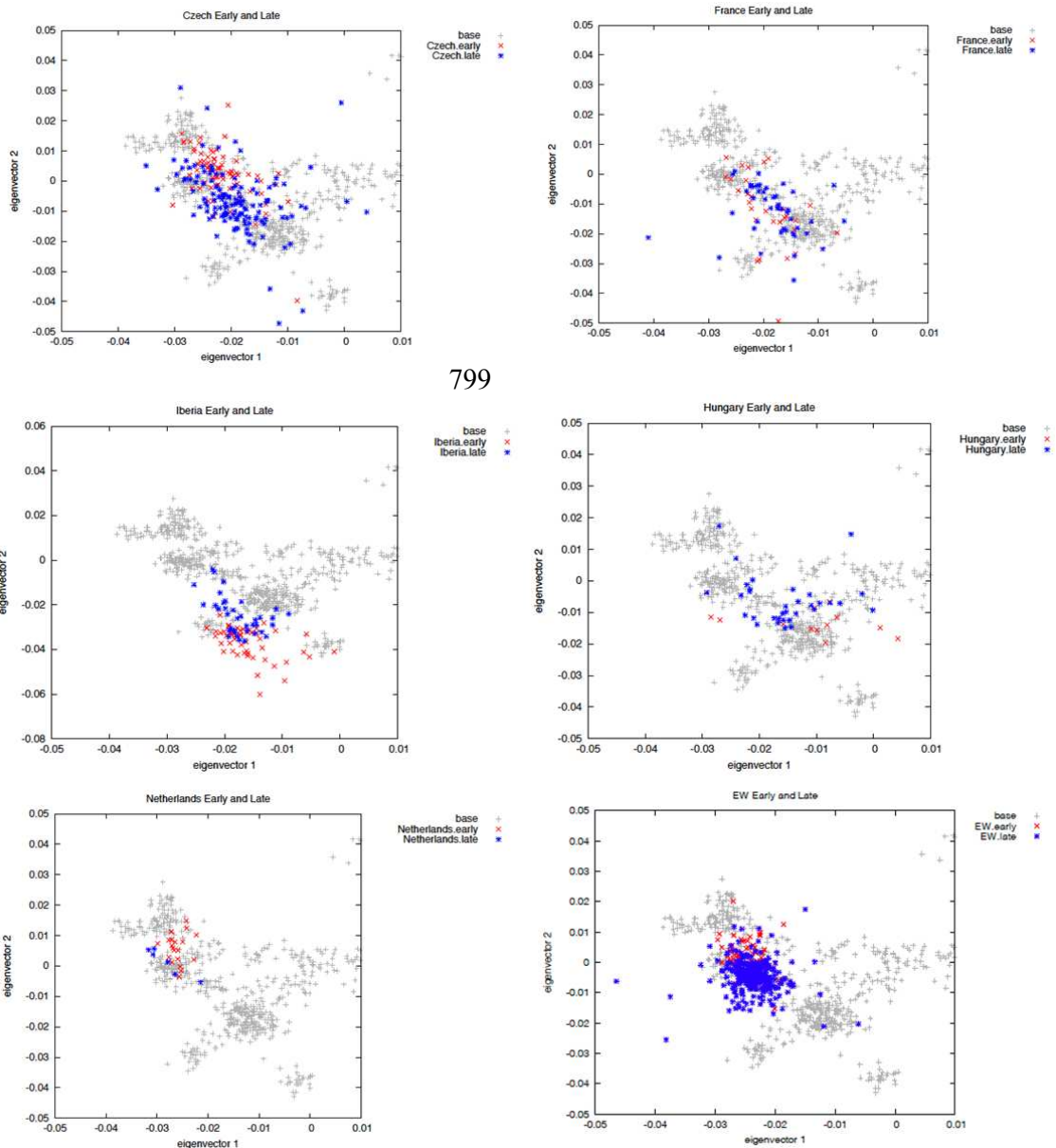
782 **Extended Data Figure 3: By-individual analysis of the British time transect.** This is a version of Figure 3 with the time transect extended into
 783 the Neolithic period. Estimates of EEF ancestry and one standard error are shown for all individuals in the British time transect that pass basic
 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.



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790 **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.

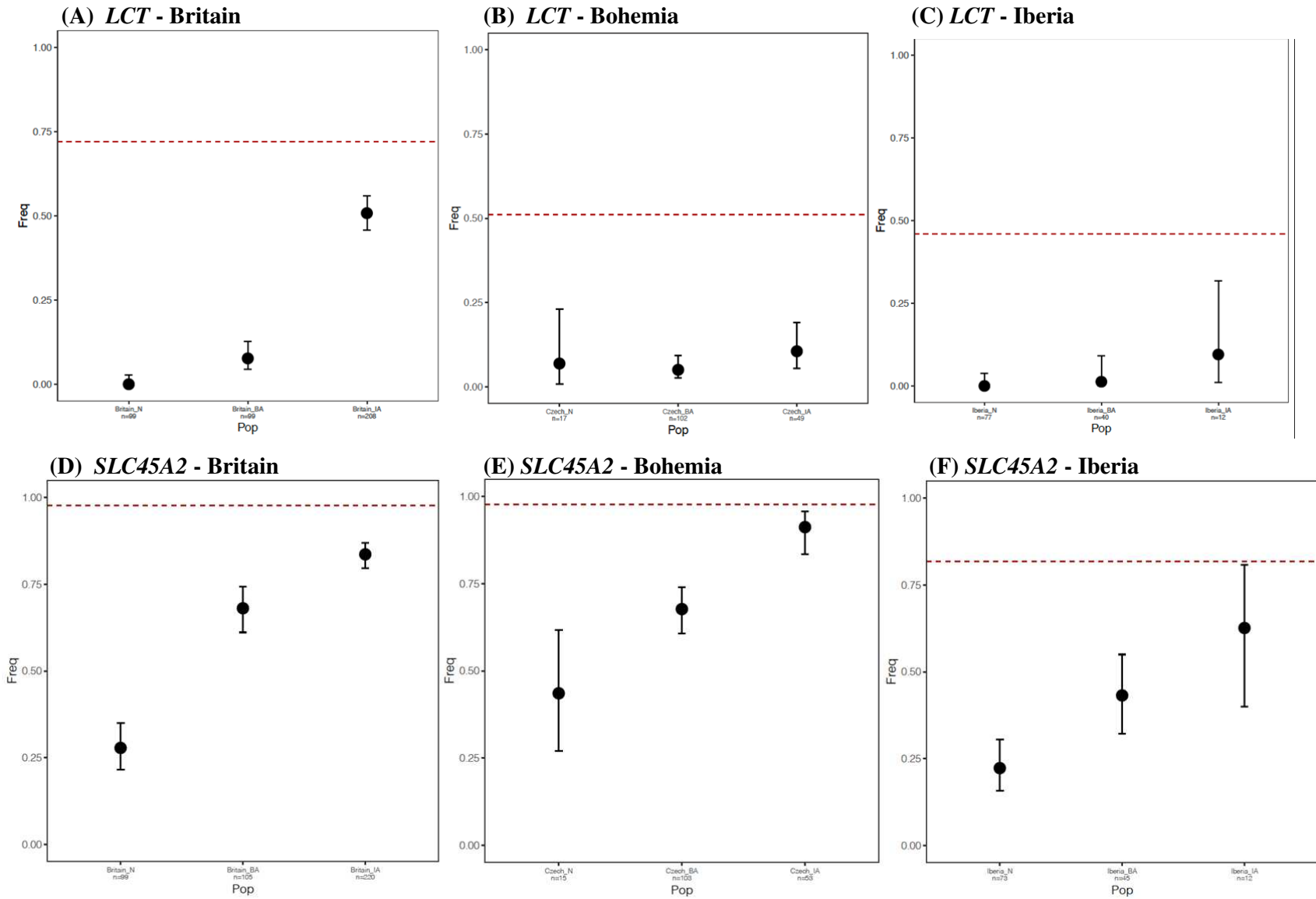


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803 **Extended Data Figure 5: Frequency change over time at two phenotypically important alleles.** (Top) The lactase persistence allele at
 804 rs4988235. (Bottom) The light skin pigmentation allele at rs16891982. In Britain the rise in frequency 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



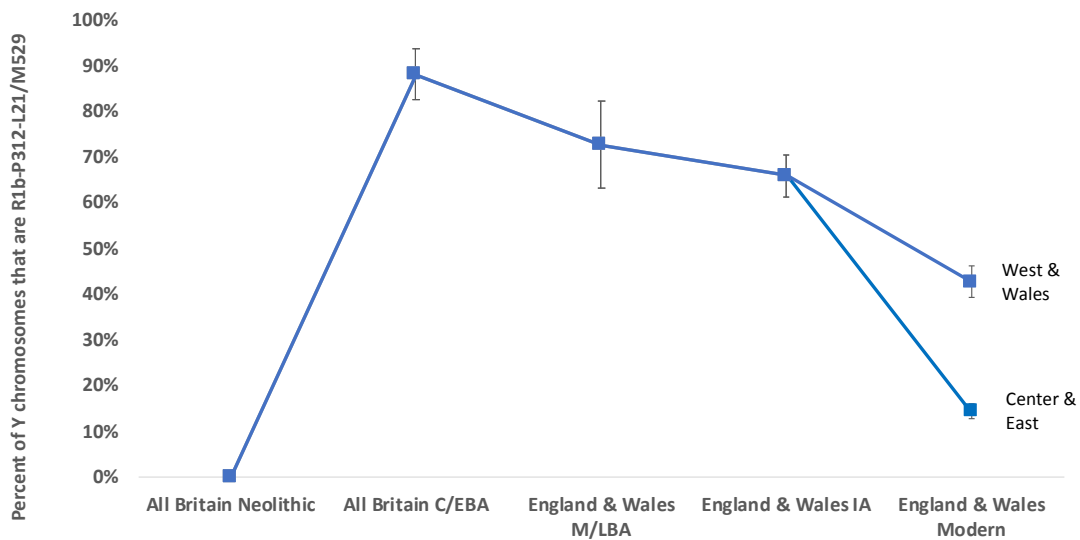
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811 **Extended Data Figure 6: Y chromosome haplogroup frequencies in the British transect.**

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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