Tracing the Spread of Celtic Languages using Ancient Genomics

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Summary

Celtic languages, including Irish, Scottish Gaelic, Welsh and Breton, are today restricted to the Northern European Atlantic seaboard. However, between 3 and 2 thousand years before present (BP) Celtic was widely spoken across most of Europe. While often associated with Bell Beaker-related populations, the spread of this prominent Indo-European linguistic cluster remains debated[1–7]. Previous genomic investigations have focused on its arrival to specific regions: Britain[8], Iberia[9] and Southwestern Germany[10]. Here, we utilize new genomic data from Bronze and Iron Age Europe to investigate the population history of historically Celtic-speaking regions, and test different linguistic theories on the origins and early spread of the Celtic languages. We identify a widespread demographic impact of the Central European Urnfield Culture. We find ancestry associated with its Knovíz subgroup in the Carpathian Basin to have formed between 4 – 3.2 kyr BP, and subsequently expanded across much of Western Europe between 3.2 and 2.8 kyr BP. This ancestry further persisted into the Hallstatt Culture of France, Germany and Austria, impacting Britain by 2.8 kyr BP and Iberia by 2.5 kyr BP. These findings support models of an Eastern Central rather than a Western European center of spread for a major component of all the attested Celtic languages. Our study demonstrates, yet again, the power of ancient population genomics in addressing long-standing debates in historical linguistics.

Main

Ancient DNA studies have transformed our ability to track human migrations and interactions, radically improving our understanding of the archaeological record and the formation of linguistic landscapes. Despite these advances, significant challenges remain,

46 particularly in more recent prehistory and at which time various regions were affected by
47 consecutive and increasingly subtle genetic shifts. One key question concerning the cultural
48 formation of Bronze and Iron Age Europe involves the origins and dispersal of the Celtic
49 languages.
50
51 Europe's present-day linguistic landscape is dominated mainly by Romance, Germanic and
52 Slavic languages, which expanded relatively recently during the Iron Age, mainly following
53 the rise of the Roman Empire and the so-called Barbarian Invasions[11–14]. Prior to these
54 events, however, Celtic languages featured prominently among the continent's linguistic
55 identities. These included Lepontic in the Alpine region, Celtiberian in Iberia, and a diverse
56 range of Gaulish or closely related dialects extending across present-day France, Central
57 Europe, Northern Italy, the Balkans, and even parts of Anatolia[15,16]. In the modern era, Celtic
58 languages have retreated to the Northwestern Atlantic fringe, where they persist as the
59 Goidelic varieties Irish and Scottish Gaelic, and the Brittonic varieties Welsh and Breton, the
60 latter having back-migrated to the continent possibly reflecting pressure from the Anglo-
61 Saxon settlements[16–20].
62
63 Although alternative interpretations exist[21–23], several recent genomic studies have linked the
64 broader spread of the Indo-European language family to migrations of Steppe-derived
65 populations of the Yamnaya Culture during the 5th millennium BP (calibrated years before
66 present/1950 CE)[24–29]. These migrations introduced Steppe-related ancestry into Europe and
67 through admixture with populations of Neolithic farmer-related ancestry (including the
68 Globular Amphora Culture with Northeast European Hunter-Gatherer ancestry, European
69 Farmers with Western Hunter-Gatherer ancestry, and Bronze Age Anatolians with Caucasus
70 Hunter-Gatherer ancestry[30]), gave rise to key groups relevant to Bronze and Iron Age Europe.

Genetic analyses reveal admixture between Corded Ware and Globular Amphora-related groups during the Bronze Age, with widespread dissemination of this ancestry across Europe by 4,800 BP[30]. In Western Europe, Bell Beaker populations incorporated additional European Farmer-related ancestry, which remained absent in northern Europe until the Migration Period[31].

Steppe-impacted populations of the archeological Bell Beaker phenomenon have been proposed as carriers of several Indo-European dialects, potentially also including the linguistic ancestor of Celtic[1,3,7,32–34]. Recent studies on Britain have identified genetic transitions around 4500 BP and again between 3200–2800 BP, marking potential entry points for Celtic languages in this part of Europe[8,35,36]. While there have been suggestions of links between the later of these migrations to the British Isles and the Urnfield-associated Knovíz Culture of the Czech Republic[8] , studies of Iron Age genomes from the intermediate regions, France[37] and Southwest Germany[10], have found no general evidence of discontinuity from the Bronze Age to the Iron Age. As a result, the exact area in which Celtic formed and the timeframe of its wider European expansion remain contentious[38]. The debate is currently focused around three main models: (1) a Late Neolithic/Early Bronze Age spread along the Atlantic seaboard linked to the Bell Beaker Culture[5,6,39,40]; (2) a Bronze Age spread from France, Iberia or Northern Italy[1,4,41]; and (3) a Late Bronze Age/Early Iron Age spread from Central Europe associated with the Hallstatt and La Tène Cultures[42–45]. Thus, the appearance and dispersal of the Celtic language constitutes a key question concerning the cultural formation of Bronze and Iron Age Europe.

In an accompanying paper, we report the generation of 752 new genomes, including 126 originating from France, Germany, Austria, and the British Isles, which are of immediate

relevance to these questions (Fig. 1). The final filtered dataset included imputed genomes from 4587 individuals (Supplementary Table S1.1), which were clustered using a hierarchical clustering method leveraging the total length of shared identity-by-descent (IBD) fragments between all individuals. We expand upon the results of[31] by focussing on the broad region spanning Western, Southern and Central Eastern Europe.

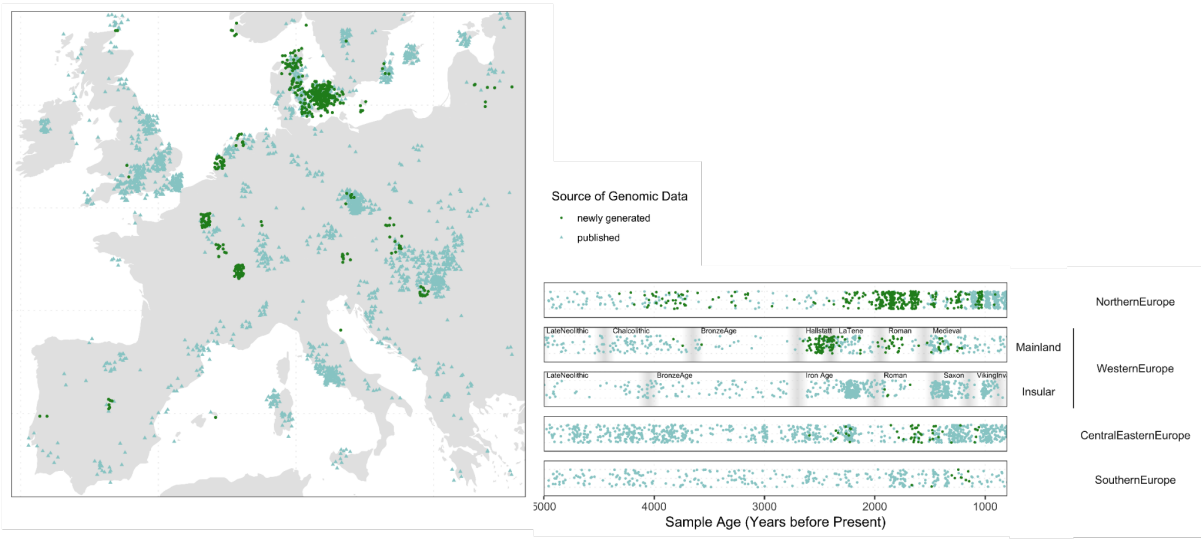

Fig. 1. Geographic and temporal sampling of the subset of ancient individuals included in the final dataset. Newly generated (green) and published (light blue) ancient individuals from the Late Neolithic / Early Bronze Age to the Viking Age. Grey bars on the timeline represent the boundary between historical periods for Western Europe.

The spatio-temporal distributions of the Bell Beaker-related populations

Our understanding of the early spatio-temporal distribution of the Bronze Age antecedents of the attested Celtic languages is limited by the absence of a written record. As recent studies on western Europe have shown a link between Celtic and Bell Beaker ancestry[31,46], insight into the formation of this ancestry profile and its geographical distribution through time may further our understanding of Celtic linguistic prehistory. We first repeated the IBD Mixture

Modelling analyses and ordinary global spatio-temporal kriging from[31] that revealed population structure that distinguishes northeastern from southwestern Europe from the Bronze Age onwards and found a strongly significant association linking individuals from Corded Ware archaeological contexts and later Germanic-speaking regions, and Bell Beaker archaeological contexts and later Celtic-speaking regions.

In brief, through IBD Mixture Modelling a palette is created for every ancient individual in the dataset, representing the proportion of IBDshared with all clusters in the dataset. Individuals from clusters are then chosen as 'sources' and others as 'targets', who are modelled using non-negative least squares. The use of non-negative least square modelling has been routinely applied using chromopainter chunks shared between ancient source and target sets[47], however recent studies have shown that using shared IBD segments between ancient individuals is effective at recovering finescale detail[30]. A strength of this method is that target palettes are modelled as combinations of potential sources palettes, meaning information from all other individuals in the dataset is incorporated into the modelling, rather than relying solely on the sharing of segments between the source and target individuals. When applied to densely sampled regions like Holocene Western Eurasia, sources and targets separated by 10,000 years continue to be modelled reliably[31] . By then performing spatio-temporal kriging[48] using the results from the IBD Mixture Modelling, we interpolate ancestry proportions for points in time and space where genetic data is not available.

We first compared the spatio-temporal kriging results at around ~4300 BP, when ancestry associated with Bell Beaker population first peaks, to ~2500 BP, where the written record documents the geographical distribution of Celtic across Europe. During this period, the range of Corded Ware-related ancestry remains stable (Fig. 2A, D), but Bell Beaker-related

138 ancestry expands (Fig. 2B, E) and European Farmer-related ancestry contracts,

139 correspondingly (Fig. 2C, F).

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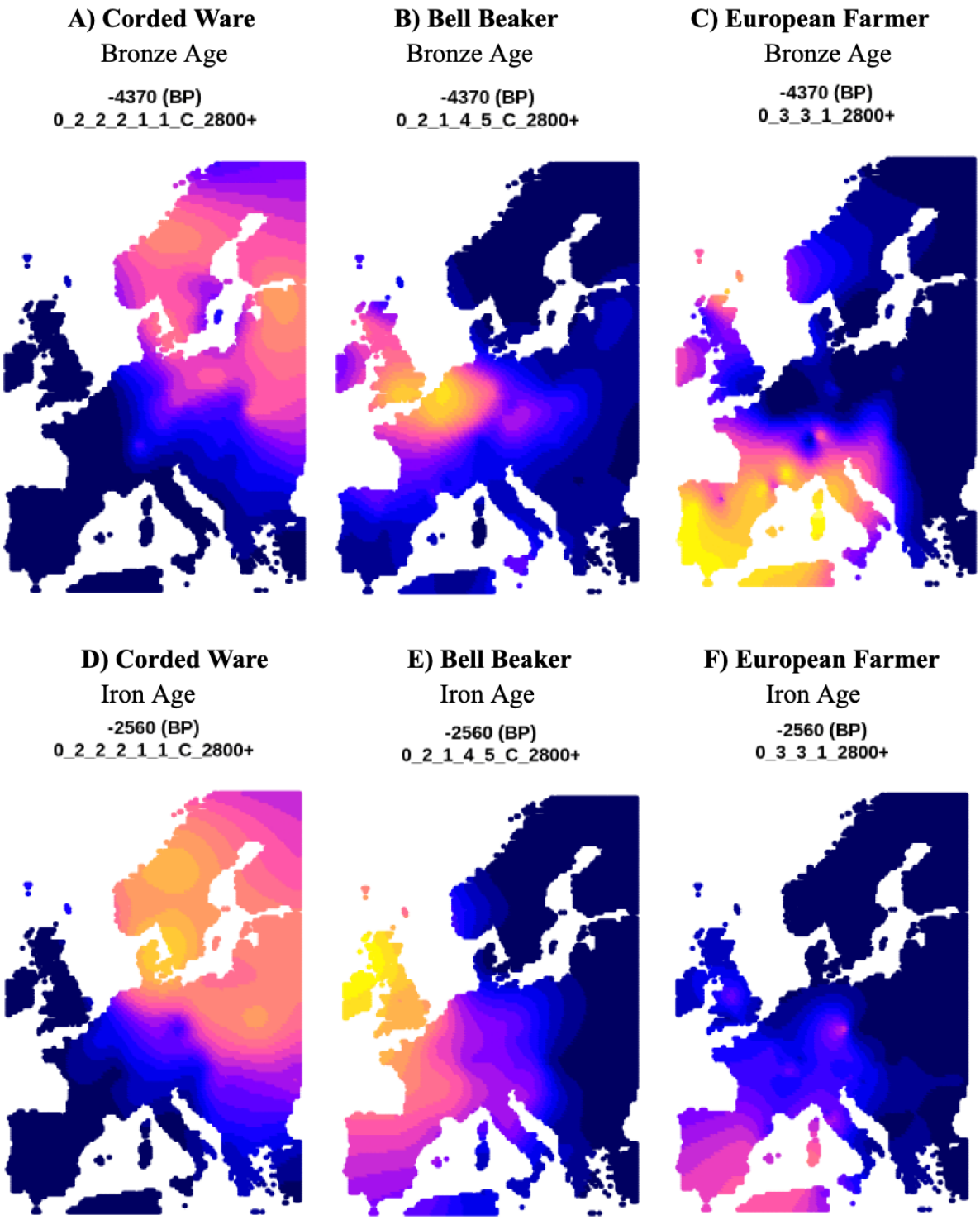

Fig. 2. Spatio-temporal kriging results showing the distribution of Corded Ware- (A,D) , Bell Beaker- (B, E) and European Farmer-related (C,F) ancestry at 4300 BP (upper

panel) and 2500 BP (lower panel). Brighter colours indicate a higher proportion of ancestry modelled. Kriging was performed on the IBD Mixture Modelling set C2 results.

Based on direct sampling, we find early evidence of Bell Beaker-related ancestry being present in France by 4463 BP, the Netherlands by 4384 BP, on the British-Irish Isles by ~4300 BP (England: 4333 BP, Scotland: 4312 BP, Ireland: 3906), and reaching southern Europe by ~4300 BP (Spain 4367 BP, Portugal 4158 BP, Italy 4212 BP). Despite occurring at a similar time, the proportion of Bell Beaker-related ancestry in France, Spain and Italy is less than that of Britain and the Netherlands (Supplementary Fig. S1.5). Further east, the Bell Beaker period was preceded by the Corded Ware Culture. This transition is mirrored genetically in which the Bell Beaker-related individuals follow, or overlap with the end of, the temporal distribution of Corded Ware-related individuals. This is seen in Germany (CWC-related 4703–4358 BP, BB-related by 4439), Hungary (BB-related by 4299 BP, other CWC-related from the same time), Czech Republic (CWC-related 4739–4477 BP, BB-related by 4333), and Poland (CWC-related 4705–4239 BP, BB-related by 4250 BP). Additionally, in all regions, we found a strong temporal correlation between the arrival of Beaker-related ancestry and Y-chromosome haplogroup R-P312, confirming their association (Supplementary Note S3).

Throughout the Bronze and Iron Age, multiple eastward and westward migrations are evident at the peripheries of the region of Bell Beaker-related ancestry. This can be seen, for example, in the Czech Republic, with the expansion of Bell Beaker-related ancestry evident during the Bell Beaker period in place of Corded Ware-related ancestry, and the subsequent reduction during the Únětice period with the reappearance of Corded Ware-related ancestry from the east (Extended Data Fig. 1). However at present, our understanding of migrations

occurring within the Bell Beaker-related region remains restricted to specific areas[8–10], rather than the region as a whole.

Population dynamics during the Bronze and Iron Age

While the genetic borders of Bell Beaker-related ancestry place a likely temporal and geographical boundary within which Celtic formed, understanding the population dynamics within this region may provide insight into whether this Iron Age linguistic landscape developed during a period of genetic continuity or disruption. We hence first attempted to identify the early genetic structure of the region. The occurrence of admixture between Steppe-related and European Farmer-related ancestry in Southern Europe has been well documented in ancient DNA studies[24,25,35,49]; therefore, we set out to assess whether this potentially distinct Farmer ancestry from across Western and Southern Europe could be used as a later proxy for migrations in the region.

Across Europe, we found a series of IBD clusters containing individuals of primarily European Farmer ancestry restricted to specific regions of Europe. To assess how these groups contributed to Bronze and Iron Age Bell Beaker-related populations, we performed IBD Mixture Modelling (Supplementary Note S1). We included source individuals from clusters associated with Neolithic British-Irish Isles (0_3_1_2800+), France and Iberia (0_3_2_4_4_1_2800+), Italy (0_3_2_5_2_2_2_2800+) and the Czech Republic (0_3_3_1_2800+), encompassing proposed homelands for Celtic. In addition, we included a series of Neolithic-related outgroups, Bronze Age Anatolia (0_3_4_1_1_2800+), Polish Globular Amphora Culture (0_3_3_3_C_2800+) and early Anatolian Farmers (Early Anatolian 0_3_4_3_3_2_2_2800+).

Despite relatively dense sampling now existing across the region of interest during the Bronze and Iron Age, very few genomes exist from the Late Bronze Age as a result of the widespread practice of cremation associated with the Urnfield Culture. We therefore first focus on the peripheries of the region of Bell Beaker-related ancestry, England and the Czech Republic, where dense sampling exists throughout the entire period, and France, where the previously sparse sampling has been greatly improved.

To visualise these changes through time, we first binned samples into the Early Bronze Age (4800–4000 BP), Middle Bronze Age (4000–3200 BP), Late Bronze Age (3200–2800 BP) and two Iron Age bins (2800–2470 BP and 2470–2000 BP), and plotted the proportion of ancestry modelled for each individual in (Fig. 3.).

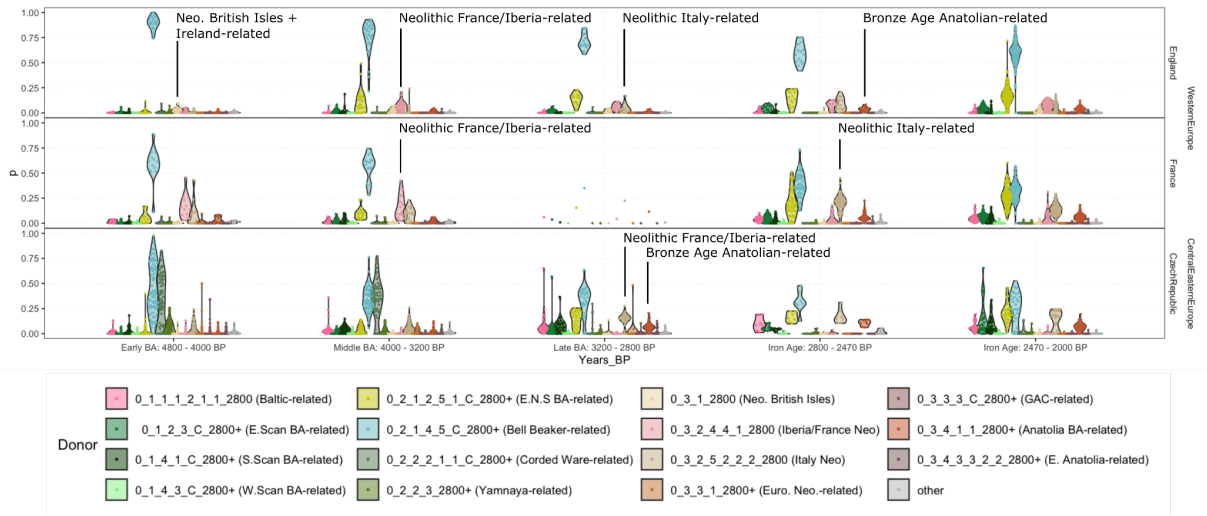

Fig. 3. IBD Mixture Modelling results (Set C3) for Bronze and Iron Age England, France and the Czech Republic. The shifts in relevant Neolithic Farming-related ancestries have been annotated. The full set of IBD Mixture Modelling results can be found in Supplementary Fig. S1.1.

For England, we find a series of transitions in the prominent farming ancestries present for each time slice (Fig. 3). Initially, between 4800–4000 BP, we find a individuals are modelled with a high proportion of Bell Beaker related ancestry, and the tendency to have a slightly higher proportion of local British-Irish Isles Neolithic ancestry, relative to the other Neolithic-related ancestries. By the Middle Bronze Age (4000–3200 BP), the highest Farmer-related ancestry is French/Iberian Neolithic-related rather than the local Neolithic ancestry, consistent with recent studies suggesting migrations from the mainland[8,36]. This migration, specifically the Iberian connection, is further supported by evidence that the UK received copper from Iberia during this phase (3350/3250–750 BP)[41]. However, in the Late Bronze Age, we see a shift, in which the proportion of Italian Neolithic ancestry has increased to similar proportions to that of French/Iberian Neolithic. In the Iron Age, similar patterns are seen, with the additional appearance of Bronze Age Anatolian-related ancestry. The changes in Farming ancestry present are suggestive of migrations from distinct regions of Europe in which local farming ancestry was incorporated.

In France, we see a similar transition (Fig. 3). During the Early and Middle Bronze Age, more local French/Iberian- than Italian Neolithic-related ancestry tends to be present. By the Iron Age, the relative proportions have swapped, so Italian Neolithic-related ancestry is the highest, accompanied by Bronze Age Anatolian ancestry. Due to the lack of samples from the Late Bronze Age, the time of this transition cannot be directly measured. However, the increased proportion of Italian Neolithic-related ancestry during the Late Bronze Age on the British Isles suggests it was present in France by this time.

Further east, in the Czech Republic, we see the increase of Italian Neolithic-related and Bronze Age Anatolian-related ancestry between 3200–2800 BP (Fig. 3). We also note that we

detect no evidence of French/Iberian Neolithic ancestry. By splitting further into the cultural phases for the region, we find that this ancestry profile in the Czech Republic occurred by 3300 BP, in individuals associated with the Tumulus Culture and continuing into the Knovíz and Hallstatt Periods (Extended Data Fig. 1).

To understand how these Neolithic Farmer-related ancestries spread during the Bronze and Iron Age more broadly, we performed spatio-temporal kriging on the IBD Mixture Modelling results for these ancestries (Extended Data Fig. 2). For the three European Farmer related ancestries, we see the proportion of ancestry modelled decreasing through time. However, while we see a general range reduction of the British and French/Iberian Neolithic-related ancestries, we find an increase in the geographical range of the Italian Neolithic-related and Bronze Age Anatolian-related ancestries throughout these periods.

To model more directly, we included Bronze Age sources from the regions in which the distinct farming ancestries associated with the migrations were found. Relevant to the Middle Bronze Age migrations to the British-Irish Isles, we included individuals from France and Iberia, who are modelled primarily as Bell Beaker- and the local French/Iberian Bronze Age-related ancestry (0_3_2_2_2800+). Relevant to the appearance of Italian Neolithic and Bronze Age Anatolian-related ancestry in Western Europe by the Iron Age, we included individuals from Hungary/Serbia (0_3_4_2_2_C_2800+). Consistent with the results found from using the Farmer-related ancestries as a proxy, we find the appearance of Bronze Age French/Iberian ancestry appearing in England during the Middle Bronze Age, and the Hungarian/Serbian Bronze Age reaching widespread distributions during the Iron Age (Fig. 4). In the Czech Republic, we find almost all individuals being modelled with a large proportion of Hungarian/Serbian ancestry during the Late Bronze Age.

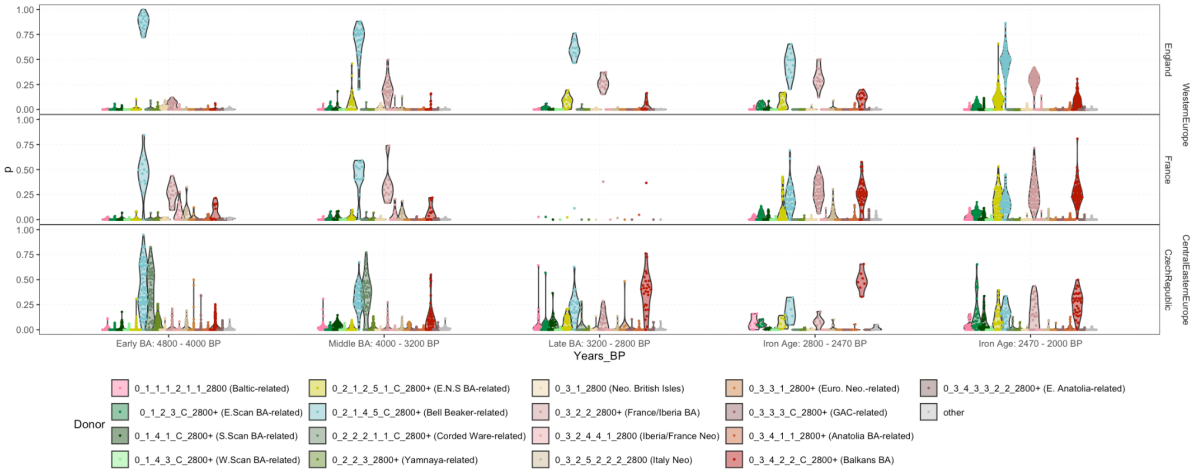

Fig. 4. IBD Mixture Modelling results for England, France and the Czech Republic during the Bronze and Iron Age, highlighting the Southeast (Hungarian/Serbian) and Southwest (France Iberian) European Bronze Age ancestries.

To understand how these Bronze Age-related ancestries spread during the Bronze and Iron Age more broadly, we performed spatio-temporal kriging on the IBD Mixture Modelling results for these ancestries (Fig. 5). The full set of IBD Mixture Modelling results can be found in Supplementary Fig. S1.1.

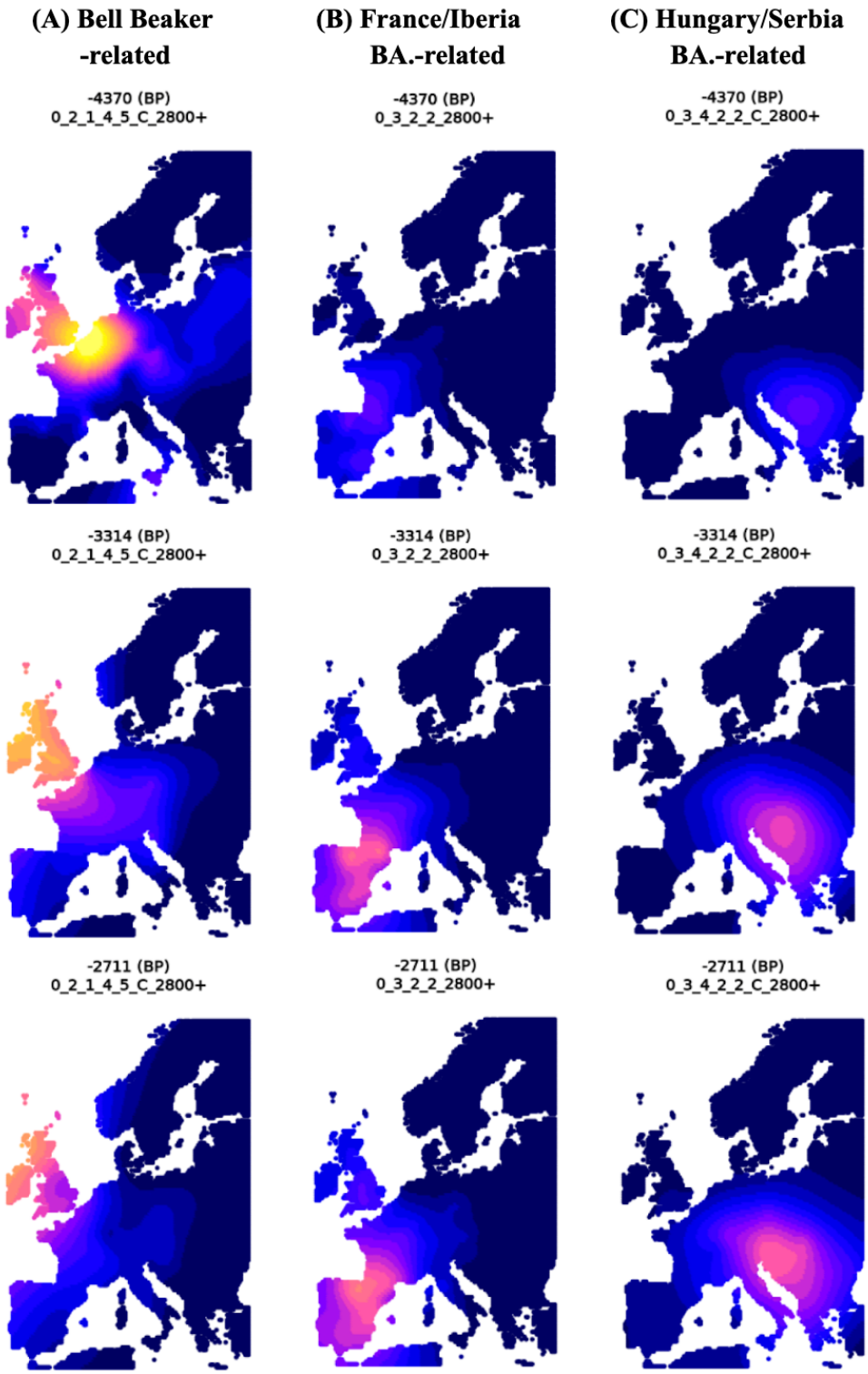

Fig. 5. Spatio-temporal kriging results for (A) Bell Beaker-related, (B) Bronze Age France/Iberia related, and (C) Hungary/Serbia-related sources from IBD Mixture Modelling set C4.

Next, we included individuals from the Late Bronze Age from the Czech Republic, associated with the Urnfield subgroup of the Knovíz Culture, as a source, who were modelled above with high proportions of Hungarian/Serbian ancestry (Extended Data Fig. 1). In the early Iron Age (2800–2470 BP), we find this ancestry modelled across Western Southern and Eastern Central Europe in varying proportions, complemented by more local sources (Extended Data Fig. 3.). In England, the highest proportion tends to be modelled as Bell Beaker-related, followed by Knovíz-related and French/Iberian Bronze Age-related. In contrast, on the mainland, the proportion of ancestry modelled as Bell Beaker-related tends to be low or absent, with the Steppe ancestry in these individuals better modelled by the other Bronze Age sources, i.e. Bronze Age Knovíz-related, French/Iberia and Hungary/Serbia. Compared to England, the impact of Knovíz-related ancestry is particularly high in France, Germany and the Czech Republic. In Austria, we note considerable diversity at the eponymous Hallstatt site, with individuals modelled with particularly high proportions of either Knovíz or Hungarian/Serbia Bronze Age-related ancestry, more similar to Hungary, Slovenia and Slovakia, where the Hungarian/Serbian Bronze Age-related ancestry is modelled in high proportions.

Finally, we included a Bronze Age source from Britain and Ireland (Set C6), corresponding to the fixed ‘left’ population described in the qpAdm analyses below. In England from the Late Bronze Age until the Migration Period, individuals tend to be modelled primarily by the British-Irish Bronze Age ancestry, with some Knovíz or French/Iberian Bronze Age-related ancestry (Supplementary Fig. S1.9). Notably, the East Yorkshire individuals are modelled with very high proportions of the local British-Irish Ancestry (Supplementary Fig. S1.1). In France, Iron Age individuals tend to be modelled primarily by the Knovíz and French/Iberian Bronze Age-related ancestries, but with little to no British-Irish Bronze Age-related ancestry.

307 Notable outliers with high British-Irish Bronze Age ancestry in France include two
308 individuals from the Urville-Nacqueville necropolis in Normandy, a site archaeologically
309 linked with Southern England[37], one of whom carries a typical British-Irish Beaker paternal
310 lineage (R1b-L21).
311
312 The resolution to distinguish between these regions is also informative in relation to
313 Migration Period movements. Some of the Migration Period individuals from Britain carry
314 high proportions of Knovíz-related ancestry and little to no British-Irish Bronze Age-related,
315 suggestive of migrations from or admixture on the continent (Supplementary Figure S1.1).
316 Migration Period migrations into Denmark and Sweden detected elsewhere revealed that
317 people carrying some continental ancestry[12,50], but primarily of Scandinavian ancestry[31],
318 arrived in Denmark and Southern Sweden by the Viking Period; here we provide further
319 insight into the source of the continental ancestry: the influx of small proportions of
320 continental ancestry is modelled as Knovíz and Hungary/Serbia Bronze Age-related ancestry,
321 generally lacking British-Irish Bronze Age and French/Iberian Bronze Age. As such, we can
322 exclude the Netherlands, France, Britain and Ireland as a source of this continental ancestry,
323 and infer a source region further east. This stands in direct contrast to Norway, where high
324 proportions of the British-Irish Bronze Age-related ancestry are detected in most individuals
325 with non-local ancestry, consistent with previous studies[50].
326
327 To confirm the occurrence of these migrations using a more conventional method, we ran a
328 series of qpAdm analyses (Supplementary Note S2). In all models, we fixed a British-Irish
329 Isles Bronze Age group as a 'left' source population (included in set C6 of the IBD Mixture
330 Modelling). We performed a series of 1, 2 and 3 source population models. For the 2 and 3
331 source population models we used a rotational approach, in which all possible combinations

of a series of Neolithic Farming-related (British-Irish Isles: 0_3_1_2800+, France/Iberia: 0_3_2_4_4_1_2800+, Denmark: 0_3_3_2_2_2_C_2800+, Italy (early): 0_3_4_3_5_4_C_2800+, Italy (late): 0_3_2_5_2_2_2_2800+, Czech Republic: 0_3_3_1_2800+, Poland (Globular Amphora Culture): 0_3_3_3_C_2800+, Bronze Age Anatolia: 0_3_4_1_1_2800+) and Bronze Age European (Bronze Age France/Iberia: 0_3_2_2_2800+, Hungary/Serbia: 0_3_4_2_2_C_2800+) populations were placed either as the 'left' or 'right' groups. As outgroups, we included populations from across Eurasia and Africa. The full list of individuals can be found in Supplementary Table S2.4.

From the IBD Mixture Modelling results, the occurrence of three distinct migrations is apparent on the British-Irish Isles. When using qpAdm, only in the earliest period (4800–4000 BP) do we see individuals being consistent under the 1 pop model, with the local Bell Beaker source (Fig. 6). In contrast, in the Middle Bronze and Late Bronze Age, only 2 population models are not rejected, with multiple possible Neolithic sources, or Bronze Age France/Iberia, but not Bronze Age Serbia/Hungary. In the Iron Age transects, no 1 or 2 population models are consistent with the data. In the first (2800–2470 BP), the only models not rejected include Bronze Age Serbia/Hungary. In the second (2470–2200 BP), the only non-rejected model (with marginal significance) includes Bronze Age Serbia/Hungary.

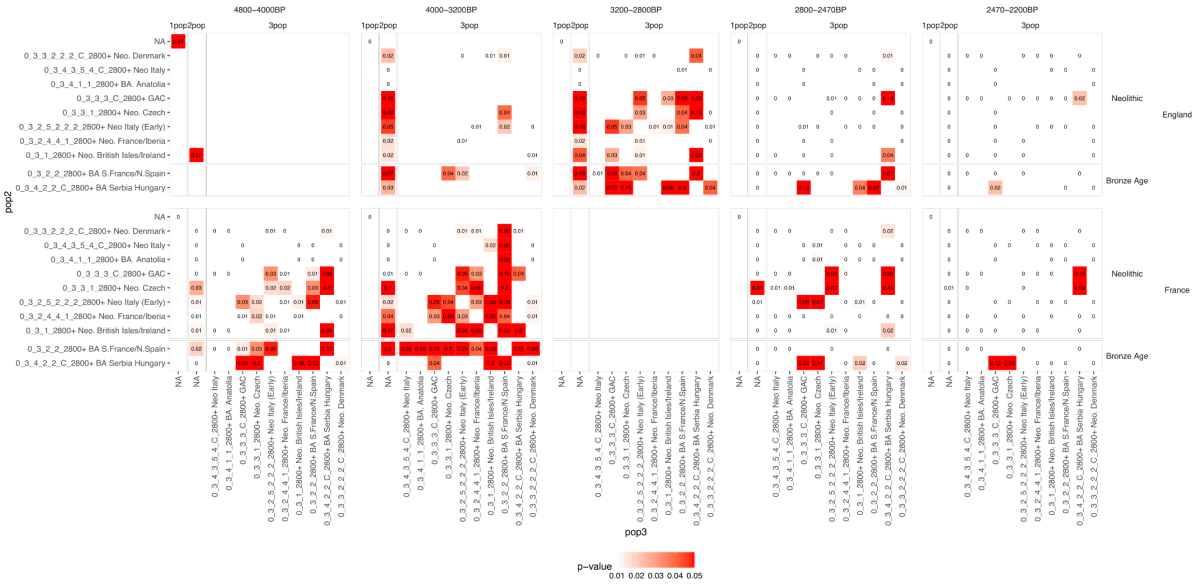

Fig. 6. P-values for rotating qpAdm models for the five time transects from England and France. For all models, Pop1 is fixed as the English Bell Beaker-related cluster. For the 2 population model, the second pop is listed on the Y axis. For the three population mode, the third population is listed on the X axis. P-values for feasible models are shown for each model.

In France, no 1 population model is consistent with the data (Fig. 6.). For the 4800–4000 BP bin, a Neolithic farming group or the local Bronze Age source are weakly significant. For the 4000–3200 BP bin, multiple Neolithic farming groups or the local Bronze Age group are not rejected, but not the Bronze Age Hungary/Serbia group. During the Iron Age a single Neolithic Farmer is feasible in a 2 population model for the earlier bin, but not the later. In both, multiple 3 population models including Bronze Age Hungary/Serbia but not France/Spain fail to be rejected.

We find these results do not contradict, and are broadly consistent with the IBD Mixture Modelling results. We therefore conclude that in England, migrations from at least three distinct populations occurred. Following the first arrival of Steppe ancestry, we find Middle

and Late Bronze Age groups can be modelled only with additional ancestry from Mainland Southern and Western Europe. In contrast the Iron Age population requires ancestry from more Eastern Central Europe to be well modelled, likely occurring at the end of the Bronze Age. In France a similar result is found; in the Iron Age, populations can only be modelled when including a Bronze Age source from Eastern Central Europe, indicating here too, migrations occurred from the east.

Additionally, we find some level of support to these migrations from Y-chromosome haplogroups. While R-P312 is closely linked spatiotemporally with Bell Beaker ancestry, its subhaplogroups exhibit great geographical structure, particularly in the Bronze Age, with R-L21 dominant in Britain and Ireland[3,8], R-DF27 in Iberia and France[9,51,52], and R-U152 in Central Europe and Northern Italy[24,35,53,54] (Supplementary Note S3). This distribution provides a framework for understanding later population movements. Consistent with IBD Mixture Modelling results, we see R-DF27 appearing in England during the Middle Bronze Age[8,37], likely from Iberia/France, and R-U152 reaching both England and France at the end of the Bronze Age[8,37,55]. In France, most occurrences are associated with Hallstatt and Gaulish contexts, further reinforcing this connection.

Discussion

The Late Bronze Age was a period of cultural transitions that were formative to the successive Iron Age, including the rise of intensified agriculture, metal craftsmanship and new forms of warfare. Archaeologically, this era saw the emergence and expansion of the Urnfield Culture (3300–2750 BP) across much of Europe[56,57]. Several factors contributed to its expansion, including the aforementioned advancements in metalworking and agricultural techniques, which provided economic stability and surplus[58]. The introduction of new crops,

393 such as millet, may have further aided population growth[59,60]. This fostered expansion and
394 facilitated the long-distance exchange of important commodities, including bronze, salt, and
395 other raw materials[61]. In contrast, the northward expansion from Central Europe into northern
396 Germany and southern Scandinavia appears to have culminated in a significant defeat, as
397 suggested by the Tollense battle around 3200 BP[62] and evident also from the lack of Knovíz-
398 related ancestry in Scandinavia prior to the Migration Period.
399
400 Notably, the Urnfield Period saw the introduction of a new collective burial rite based on
401 cremation to different regions of Europe[63]. We therefore lack direct genomic evidence for this
402 culture, with the exception of the Urnfield subgroup of the Knovíz Culture, known for its
403 settlement expansion and metallurgical advancements[58]. We nevertheless find that the
404 sporadic appearance of this ancestry in England during the Urnfield Period, followed by its
405 widespread presence by the Hallstatt Period, suggests that populations associated with the
406 wider Urnfield Culture were genetically similar to those of the Knovíz Culture. Our results
407 are therefore in accordance with evidence of the westward expansion of the Urnfield Culture
408 into France[58] and Northeast Iberia[64], suggested previously only by limited ancient DNA
409 data[9,65].
410
411 Our results stand in contrast to recent studies on Iron Age France[37] and Southwest
412 Germany[10], where qpAdm analyses do not reject models in which early Iron Age populations
413 are modelled by local Bronze Age populations. This different outcome likely results from the
414 application of less fine-scale methods and inclusion of fewer ancient samples. The benefit of
415 IBD Mixture Modelling in providing resolution at the individual level is also apparent from
416 the ability to detect diversity within a population, when compared to qpAdm analyses which
417 are typically run at a population level to achieve statistical significance. Notably, the

418 identification of the outlier individuals from Iron Age Normandy, France with elevated
419 British-Irish Bronze Age ancestry, is consistent with archaeological evidence for this site
420 suggesting origins in Southern England[37].
421
422 Consistent with previous studies on the British-Irish Isles[10], we observe the appearance of
423 Neolithic-related ancestry during the Middle to Late Bronze Age. Here, however, we are able
424 to distinguish between multiple migration waves: the initial Bell Beaker migrations, a second
425 French/Iberian Bronze Age migration, and a final Knovíz-related migration from Eastern
426 Central Europe. We further confirm links between a Middle Bronze Age outlier from
427 Margetts Pit with high Early European Farming ancestry and the Knovíz individuals of
428 Central Europe; we find this individual modelled with a high proportion of Knovíz-related
429 ancestry (Supplementary Figure S1.1, Set C5). However, we note that this individual is also
430 modelled with additional Italian- and France/Iberia Neolithic-related ancestry, likely
431 representing admixture from mainland Western Europe. When using the C5 source set, later
432 individuals from Iron Age Britain generally lack Italian Neolithic-related ancestry, indicating
433 that this individual was not representative of the migration into the British-Irish Isles by the
434 Iron Age.
435
436 Unlike the Steppe migrations across Neolithic Europe, now widely associated with the onset
437 of the Indo-European language dispersal[24,25], the Bronze Age migrations discussed here likely
438 involved groups already speaking diverged Indo-European dialects. While historically
439 Germanic-speaking groups primarily carried Corded Ware-associated ancestry and expanded
440 from Northern Europe during the Iron Age[13,31,66], Bell Beaker-associated groups, although
441 culturally and linguistically diverse[38], more likely mediated Indo-European dialects ancestral
442 to Italic and Celtic ("Italo-Celtic", Supplementary Note S4)[46]. A potential remnant of these

443 dialects is Lusitanian in Iberia. Under a model of multiple Bell-Beaker related migrations into
444 Ibera, the presence of this Italo-Celtic language, whose specific relation to Celtic remains
445 ambiguous (Supplementary Note S4), may be the result of the initial intrusion into Iberia.
446
447 In the British-Irish Isles, as well as in Iberia and France, a large proportion of the local
448 Bronze Age ancestries persists throughout the Iron Age, strengthening models in which the
449 historically known varieties of Italo-Celtic evolved locally during these eras. Previous studies
450 have indeed highlighted the possibility that Celtic languages, specifically the linguistic
451 predecessors of Goidelic and Brittonic, were introduced to Britain from France during the
452 Middle to Late Bronze Age[7]. This is supported by our own detection of France/Iberia Bronze
453 Age-related ancestry and consistent with Atlantic models suggesting that Celtic emerged in
454 Central-West Europe[1,41]. However, we find no evidence of this ancestry reaching Eastern
455 Central Europe, where Celtic was spoken during the Iron Age, indicating that this migration
456 does not account for the spread of Celtic as a whole.
457
458 Furthermore, the expansion of Knovíz-related ancestry from Eastern Central Europe detected
459 here, continuing into Hallstatt and La Tène populations, provides new evidence supporting
460 the linguistic model in which Celtic languages were mediated to France, Britain, Iberia and
461 Italy during the Late Bronze Age by populations associated with the Urnfield Culture[67,68].
462 This aligns with the association of the Lepontic language with the Urnfield-derived
463 Golasecca Culture of Northern Italy[69], as well as the Urnfield-type weaponry of ~3200–3000
464 BP depicted on Late Bronze Age warrior stelae of the Southwestern Iberian Peninsula[70–72].
465 Late Bronze Age Urnfield influences were notably highlighted in the discussion on the arrival
466 of the Celtic languages in Britain by archaeologist and linguist V. G. Childe[68]. However,
467 further intrusions to Ireland, suggested to have occurred either in the Late Bronze Age or Late

Iron Age[7], cannot be evaluated here due to the absence of genomes from Ireland for the period between 3500 and 1200 BP.

Conclusion

Here, we demonstrate that it is feasible to resolve various Bell Beaker-associated migrations. By exploring the hitherto elusive genomic impact of the Urnfield Culture, we highlight the potential for further understanding the formation of the distinct linguistic landscapes under scrutiny, once a sufficient number of ancient genomes from these regions is available.

Concretely, our findings support a major component of the Celtic languages forming in, and spreading from, Bronze Age Eastern Central Europe in association with the archaeological Urnfield, Hallstatt and La Tène Cultures[42,68,73]. They do not, in contrast, support a dispersal from Southern France or Iberia linked with Bronze Age migrations to the British Isles[1,2,41] or along the Atlantic seaboard having arrived there with the Late Neolithic Bell Beaker Culture[5,6,39]. Such scenarios require a spread of Celtic contrary to the identified demographic movements. Thus, the evaluation of contrastive hypotheses concerning the emergence and early spread of the Celtic languages yet again demonstrates the power of past population genomics in addressing long-standing debates in historical linguistics.

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682

683 # Methods

684 **Dataset preparation**

685 The 578 new ancient individuals included in the analyses here are part of a larger dataset of
686 712 ancient shotgun sequenced genomes from [31]. Details on the sampling, data generation,
687 quality checks, site description and detailed metadata can be found in [31]. In brief, ancient
688 samples were visually identified as suitable for processing. Samples were drilled, pre-
689 digested [74] , extracted [24], built into libraries [75,76], and sequenced on Illumina Hiseq 4000 and
690 Novaseq 6000 platforms. Sequenced reads were mapped against the human reference genome
691 (hg19), and authenticated based on the length of reads, damage patterns, endogenous rates
692 and presence of contamination. All samples with a genomic coverage greater than 0.1X were
693 imputed, and close relatives identified using ngsRelate (v2) [77] were excluded for IBD based
694 analyses.
695 Genomes were imputed using Glimpse[78] against the 1000 Genomes (1000G) v5 phase 3
696 dataset[79]. Shared IBD segments were called using IBDseq [80] using default parameters.
697 Segments with a LOD score <3 and hotspot regions [30] with excess sharing were excluded. A
698 detailed description can be found in [31].
699

700 **IBD Mixture Modelling**

701 To identify fine-scale structure, we applied IBD Mixture Modelling[30]. We relied on the
702 dataset and IBD Clustering from [31]. The cluster IDs for all individuals included in the dataset
703 can be found in Supplementary Table S1.1. The 4587 ancient individuals in the dataset were
704 determined to be suitable for IBD Mixture Modelling based on a series of filtering steps for
705 genomic coverage (0.1X for shotgun sequenced data, 1X for 1240K capture data), average
706 genotype probability for the 1240K captures sites (0.9) and the removal of close relatives.
707 The final dataset included 690,211sites, being those that intersected with the sites 1000

708 Genomes panel and the 1240K sites, that pass the 1000 Genomes mappability mask, and an
709 imputation INFO score of 0.5.
710
711 For each of the 4587 ancient individuals in the dataset, a palette was created, representing the
712 proportion of sharing with all other clusters, and with the other individuals in their own
713 cluster. The proportions were normalised by the number of individuals in each cluster. To
714 account for the fact that the sharing within the individuals own cluster has n-1 individuals,
715 sharing with all other clusters excludes one individual at random. As a result, clusters with a
716 single individual do not contribute to other individuals' palettes. All segments greater than
717 1cM, with a lod score greater than 3 that did not originate from a hotspot of IBD sharing [30]
718 were included in the palettes. IBD Mixture Modelling was then undertaken using these
719 palettes, by modelling the target individual using non-negative least squares[81], as described in
720 [30]. Standard errors of the ancestry proportions were calculated using a weighted block
721 jackknife, leaving out each chromosome.
722
723 **Spatio-temporal kriging**
724 To understand the trends in ancestry through time, we performed spatiotemporal kriging [48] to
725 interpolate IBD Mixture Modelling results for points in time and space where genetic data is
726 not available. For the ancestry of particular relevance for Set 2 (Corded Ware-, Bell Beaker-
727 and European Farmer-related) and Set C3 (Neolithic British Isles/Ireland-, Neolithic
728 France/Iberia-, Neolithic Italy- and Bronze Age Anatolia-related), we fit spatiotemporal
729 variograms via a metric covariance model [82].
730
731 **qpAdm analyses**

qpAdm analyses were undertaken on the 690,211 sites of the dataset described above, using admixtools2[83]. Populations were placed into three sets: left_fixed, right_fixed or rotational (Supplementary Table S2.4). The 'left_fixed' population was included as a potential source in all qpAdm analyses. The 'right_fixed' population was included as outgroups in all analyses. In 1 population models, all 'rotational' populations were included as outgroups. For 2 population models, one 'rotational' population was placed together with the 'left_fixed' population as potential sources, and all others as outgroups, in all possible combinations. For 3 population models, two 'rotational' populations were placed together with the 'left_fixed' population as potential sources, and all others as outgroups, in all possible combinations.

Data availability

Sequence data for the new 578 ancient genomes can be found in the ENA under accession: xxxxxxxx. The public 4009 ancient genomes included in the dataset are listed in Supplementary Table S1.1, with additional details provided in Supplementary Note S4 of the accompanying paper [31].

Methods References

References 74 - 82.

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Author contributions

EW initiated the study. HMC, GK, EW led the study. HMC, GK, MS, EW conceptualised the study. KK, MS, EW supervised the research. GK, JK, JL, KK, MS, EW acquired funding for research. HMC, TP, MS were involved in data analysis. HMC, GK, JK, JL, KK, EW drafted the main text. HMC, GK, TP, JK, JL, KK, MS drafted supplementary notes and materials. HMC, GK, TP, JK, JL, JPD, KK, MS, EW involved in reviewing and editing drafts.

Ethics declarations

The authors declare no competing interests

Additional Information

Supplementary Information is available for this paper.

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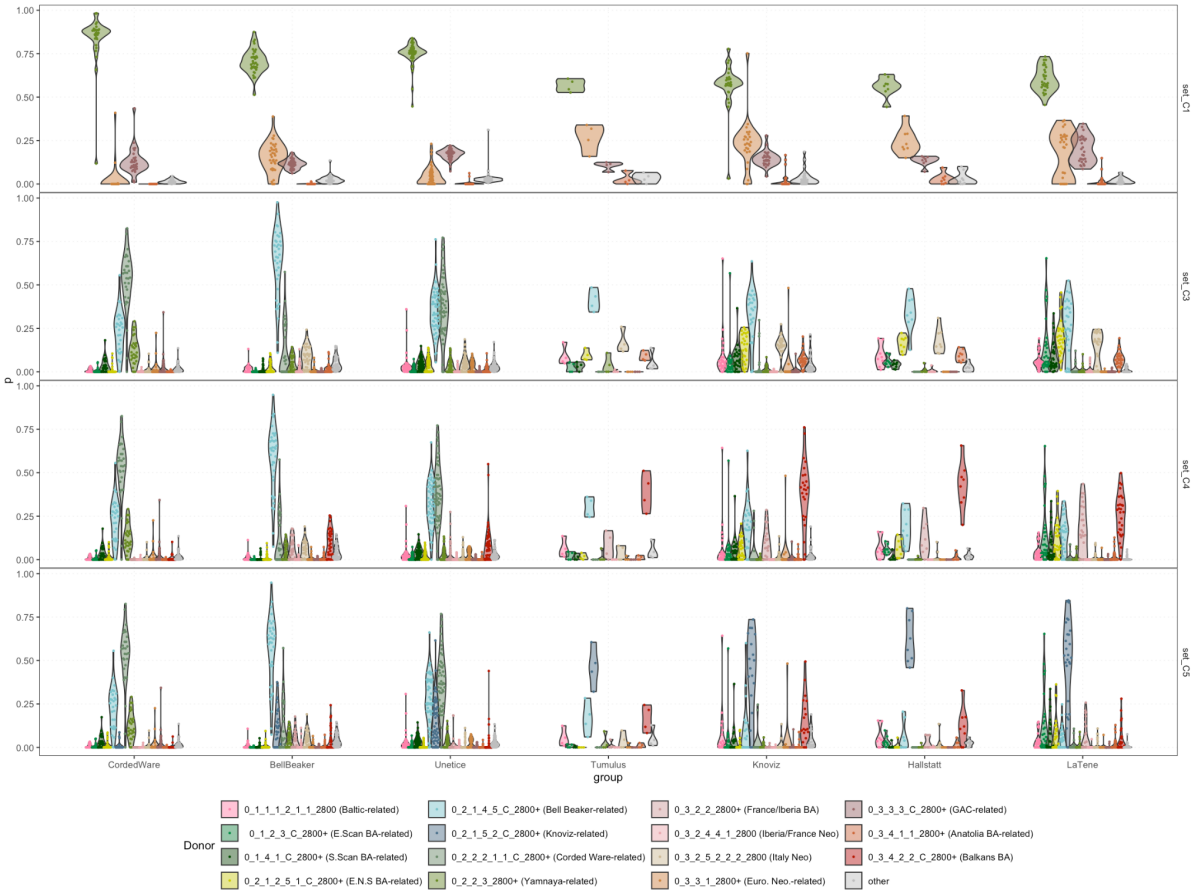
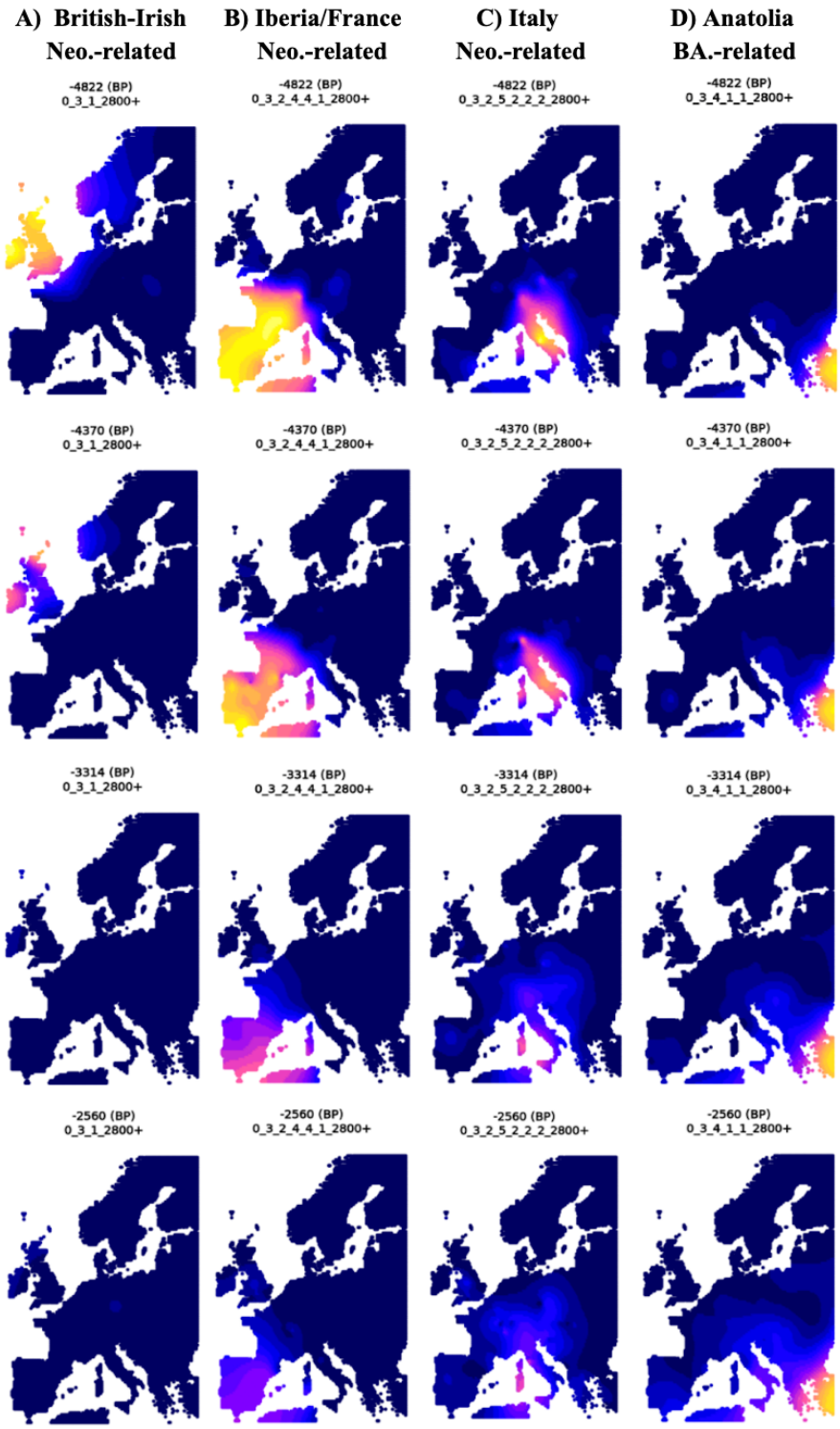
Extended Data Figures

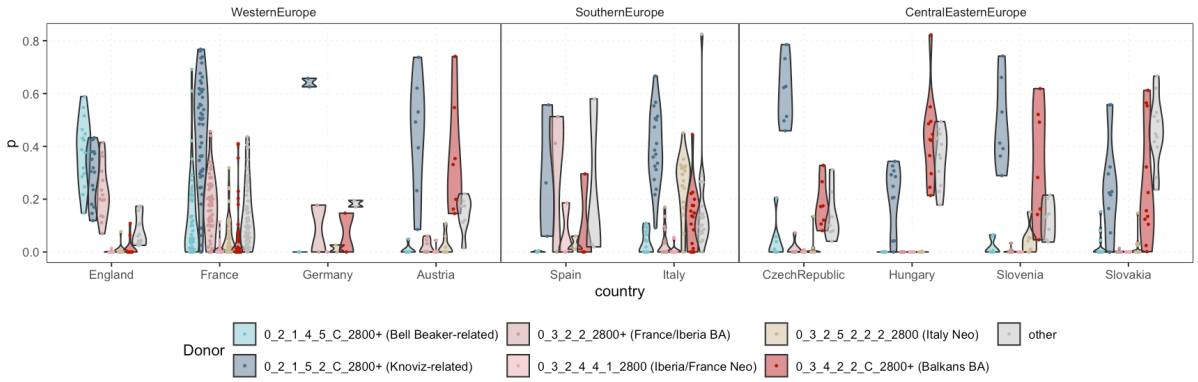


Extended Data Fig. 1. IBD Mixture Modelling Results for samples associated with archaeological cultures/complexes from the Czech Republic for different archeological periods. Cultures are ordered from oldest (left) to youngest (right)**.** The top panel (set C1) highlights decreasing Yamnaya ancestry (olive green) and varying Farming (related ancestry) through time. The second panel (set 3) highlights transitions between Corded Ware (grey-green) and Bell Beaker (light blue) ancestry, and the various farming-related ancestries. The

third panel (set C4) highlights the appearance of the Balkans Bronze Age (red) ancestry from the Tumulus Culture onwards. The lower panel (set C5) models the Knovíz-related ancestry (dark blue) directly.



Extended Data Fig. 2. Spatio-temporal kriging of from IBD Mixture Modelling for European Farmer-related source groups from (A) British Isles, (B) Iberia/France, (C) Italy and (D) Bronze Age Analolia. Kriging results from around the time of arrival of Steppe ancestry (4822 BP), the start of the Bell Beaker migrations (4300 BP), the Middle/Late Bronze Age (3314 BP) and the Iron Age (2560 BP) are shown (top to bottom). Kriging was performed on the IBD Mixture Modelling set C3 results.



Extended Data Fig. 3. Ancestry Proportions from IBD Mixture Modelling set C5 for the early Iron Age (2800 -2470 BP), showing the relevant ancestry sources.