

The Beaker phenomenon and the genomic transformation of northwest Europe

A list of authors and their affiliations appears at the end of the paper.

From around 2750 to 2500 BC, Bell Beaker pottery became widespread across western and central Europe, before it disappeared between 2200 and 1800 BC. The forces that propelled its expansion are a matter of long-standing debate, and there is support for both cultural diffusion and migration having a role in this process. Here we present genome-wide data from 400 Neolithic, Copper Age and Bronze Age Europeans, including 226 individuals associated with Beaker-complex artefacts. We detected limited genetic affinity between Beaker-complex-associated individuals from Iberia and central Europe, and thus exclude migration as an important mechanism of spread between these two regions. However, migration had a key role in the further dissemination of the Beaker complex. We document this phenomenon most clearly in Britain, where the spread of the Beaker complex introduced high levels of steppe-related ancestry and was associated with the replacement of approximately 90% of Britain's gene pool within a few hundred years, continuing the east-to-west expansion that had brought steppe-related ancestry into central and northern Europe over the previous centuries.

During the third millennium BC, two new archaeological pottery styles expanded across Europe and replaced many of the more localized styles that had preceded them¹. The expansion of the 'Corded Ware complex' in north-central and northeastern Europe was associated with people who derived most of their ancestry from populations related to Early Bronze Age Yamnaya pastoralists from the Eurasian steppe^{2–4} (henceforth referred to as 'steppe'). In western Europe there was the equally expansive 'Bell Beaker complex', defined by assemblages of grave goods that included stylized bell-shaped pots, copper daggers, arrowheads, stone wristguards and V-perforated buttons⁵ (Extended Data Fig. 1). The oldest radiocarbon dates associated with Beaker pottery are from around 2750 BC in Atlantic Iberia⁶, which has been interpreted as evidence that the Beaker complex originated in this region. However, the geographic origins of this complex are still debated⁷ and other scenarios—including an origin in the Lower Rhine area, or even multiple independent origins—are possible (Supplementary Information section 1). Regardless of geographic origin, by 2500 BC the Beaker complex had spread throughout western Europe and northwest Africa and had reached southern and Atlantic France, Italy and central Europe⁵, where it overlapped geographically with the Corded Ware complex. Within another hundred years, it had expanded to Britain and Ireland⁸. A major debate in archaeology has revolved around the question of whether the spread of the Beaker complex was mediated by the movement of people, culture or a combination of both⁹. Genome-wide data have revealed high proportions of steppe-related ancestry in Beaker-complex-associated individuals from Germany and the Czech Republic^{2–4}, which shows that these individuals derived from mixtures of populations from the steppe and the preceding Neolithic farmers of Europe. However, a deeper understanding of the ancestry of people associated with the Beaker complex requires genomic characterization of individuals across the geographic range and temporal duration of this archaeological phenomenon.

Ancient DNA data

To understand the genetic structure of ancient people associated with the Beaker complex and their relationship to preceding, subsequent and contemporary peoples, we used hybridization DNA capture^{4,10} to enrich

ancient DNA libraries for sequences overlapping 1,233,013 single nucleotide polymorphisms (SNPs), and generated new sequence data from 400 ancient Europeans dated to between approximately 4700 and 800 BC, excavated from 136 different sites (Extended Data Tables 1, 2; Supplementary Table 1; Supplementary Information section 2). This dataset includes 226 Beaker-complex-associated individuals from Iberia ($n = 37$), southern France ($n = 4$), northern Italy ($n = 3$), Sicily ($n = 3$), central Europe ($n = 133$), the Netherlands ($n = 9$) and Britain ($n = 37$), and 174 individuals from other ancient populations, including 118 individuals from Britain who lived both before ($n = 51$) and after ($n = 67$) the arrival of the Beaker complex (Fig. 1a, b). For genome-wide analyses, we filtered out first-degree relatives and individuals with low coverage (fewer than 10,000 SNPs) or evidence of DNA contamination (Methods) and combined our data with previously published ancient DNA data (Extended Data Fig. 2) to form a dataset of 683 ancient samples (Supplementary Table 1). We merged these data with those from 2,572 present-day individuals genotyped on the Affymetrix Human Origins array^{11,12} as well as with 300 high-coverage genomes¹³. To facilitate the interpretation of our genetic results, we also generated 111 direct radiocarbon dates (Extended Data Table 3; Supplementary Information section 3).

Y-chromosome analysis

The Y-chromosome composition of Beaker-complex-associated males was dominated by R1b-M269 (Supplementary Table 4), which is a lineage associated with the arrival of steppe migrants in central Europe after 3000 BC^{2,3}. Outside Iberia, this lineage was present in 84 out of 90 analysed males. For individuals for whom we determined the R1b-M269 subtype ($n = 60$), we found that all but two had the derived allele for the R1b-S116/P312 polymorphism, which defines the dominant subtype in western Europe today¹⁴. By contrast, Beaker-complex-associated individuals from the Iberian Peninsula carried a higher proportion of Y haplogroups known to be common across Europe during the earlier Neolithic period^{2,4,15,16}, such as I ($n = 5$) and G2 ($n = 1$); R1b-M269 was found in four individuals with a genome-wide signal of steppe-related ancestry, and of these, the two with higher coverage could be classified

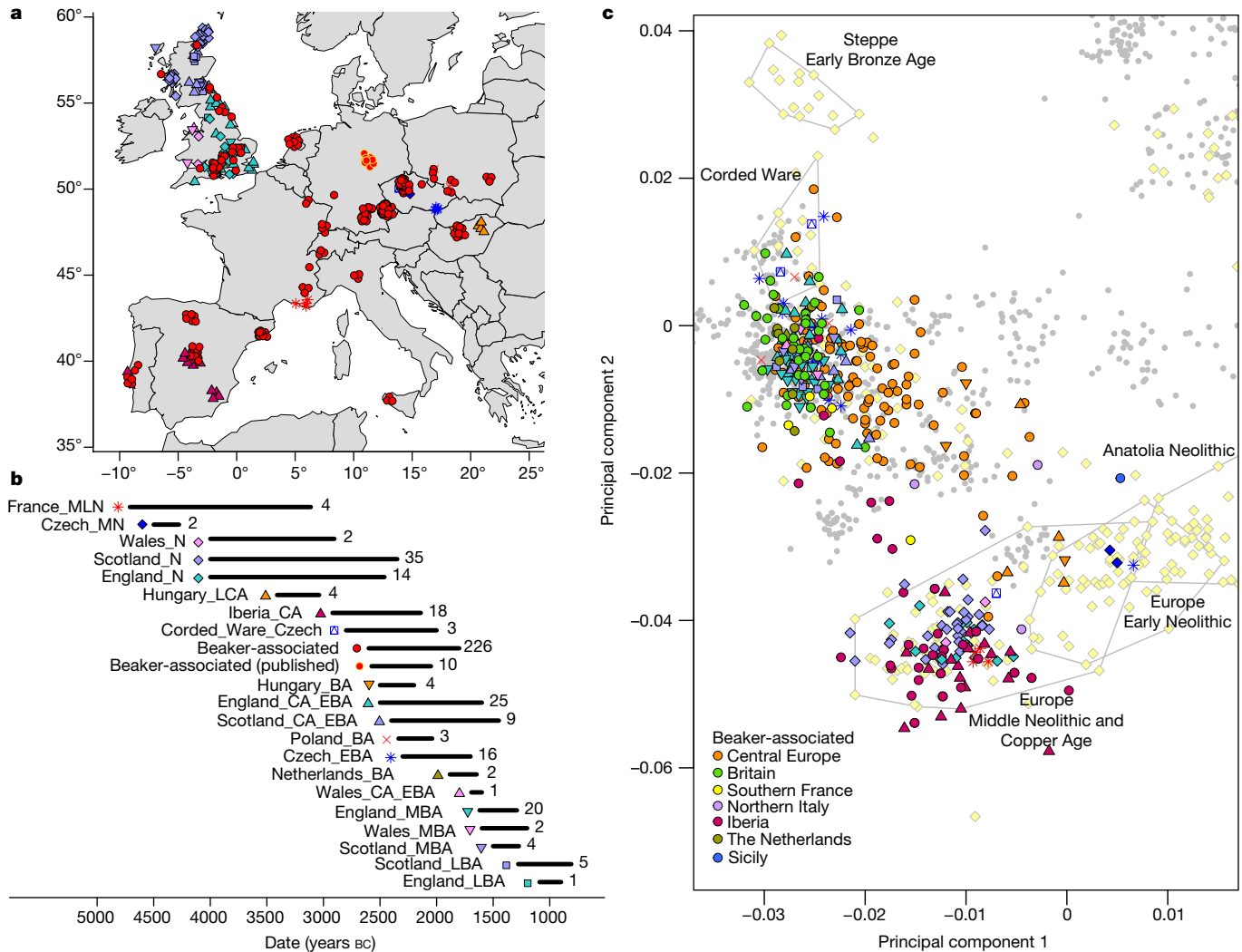


Figure 1 | Spatial, temporal and genetic structure of individuals in this study. **a**, Geographic distribution of samples with new genome-wide data. Random jitter was added for sites with multiple individuals. Map data from the R package ‘maps’. **b**, Approximate time ranges for samples with new genome-wide data. Sample sizes are given next to each bar.

as R1b-S116/P312. The widespread presence of the R1b-S116/P312 polymorphism in ancient individuals from central and western Europe suggests that people associated with the Beaker complex may have had an important role in the dissemination of this lineage throughout most of its present-day distribution.

Spread of people associated with the Beaker complex

We performed principal component analysis by projecting the ancient samples onto the genetic variation in a set of west Eurasian present-day populations. We replicated previous findings¹¹ of two parallel clines, with present-day Europeans on one side and present-day Near Eastern populations on the other (Extended Data Fig. 3a). Individuals associated with the Beaker complex are notably heterogeneous within the European cline along an axis of variation defined by Early Bronze Age Yamnaya individuals from the steppe at one extreme and Middle Neolithic and Copper Age Europeans at the other extreme (Fig. 1c; Extended Data Fig. 3a). This suggests that genetic differentiation among Beaker-complex-associated individuals may be related to variable amounts of steppe-related ancestry. We obtained qualitatively consistent inferences using ADMIXTURE model-based clustering¹⁷. Beaker-complex-associated individuals harboured three main genetic components: one characteristic of European Mesolithic

hunter-gatherers, one maximized in Neolithic individuals from the Levant and Anatolia, and one maximized in Neolithic individuals from Iran and present in admixed form in steppe populations (Extended Data Fig. 3b).

Both principal component analysis and ADMIXTURE are powerful tools for visualizing genetic structure, but they do not provide formal tests of admixture between populations. We grouped Beaker-complex-associated individuals on the basis of geographic proximity and genetic similarity (Supplementary Information section 6), and used qpAdm² to directly test admixture models and estimate mixture proportions. We modelled their ancestry as a mixture of Mesolithic western European hunter-gatherers, northwestern Anatolian Neolithic farmers and Early Bronze Age steppe populations; the first two of these contributed to the ancestry of earlier Neolithic Europeans. We find that in areas outside of Iberia, with the exception of Sicily, a large majority of the Beaker-complex-associated individuals that we sampled derive a considerable portion of their ancestry from steppe populations (Fig. 2a). By contrast, in Iberia such ancestry is present in only 8 of the 32 individuals that we analysed; these individuals represent the earliest detection of steppe-related genomic affinities in this region. We observed differences in ancestry not only at a pan-European scale, but also within regions and even within sites. For instance, at Szigetszentmiklós in Hungary, we

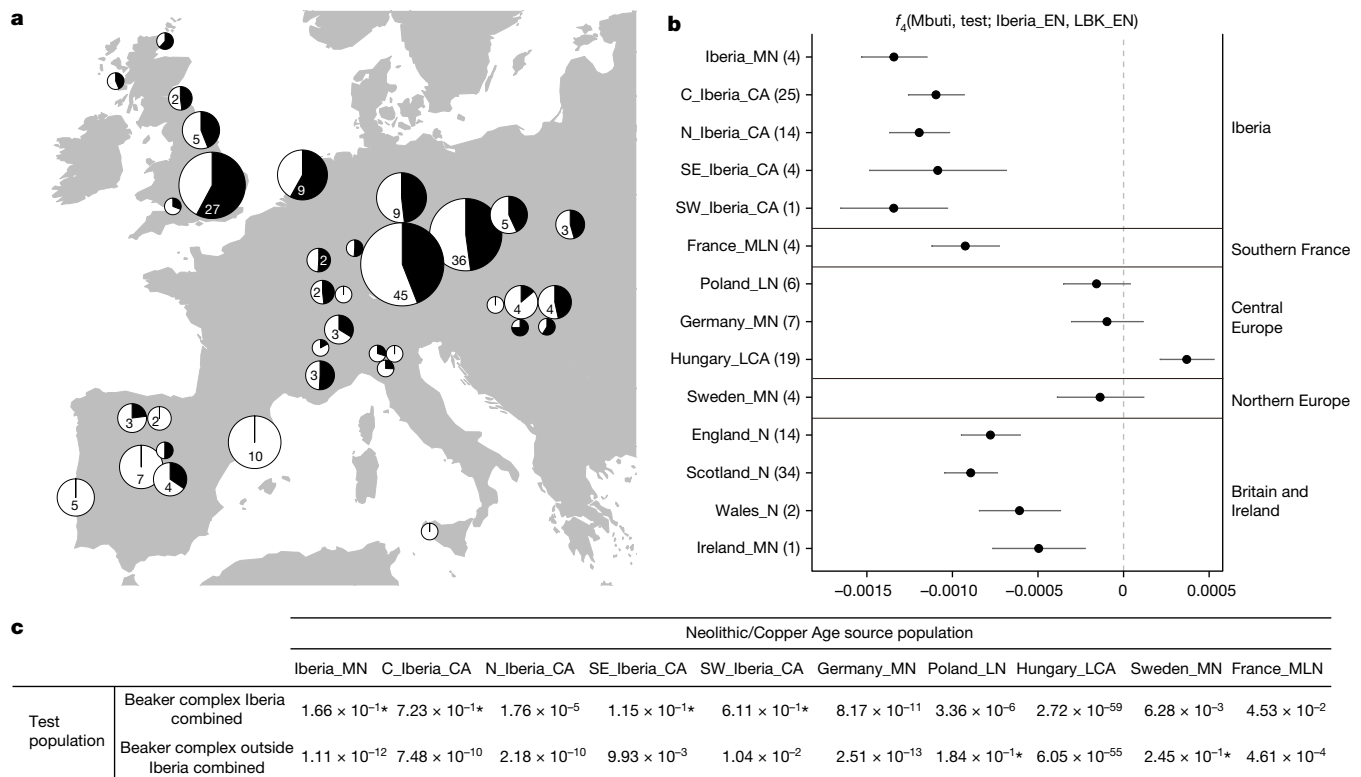


Figure 2 | Investigating the genetic makeup of Beaker-complex-associated individuals. **a**, Proportion of steppe-related ancestry (in black) in Beaker-complex-associated groups computed with qpAdm² under the model ‘Steppe_EBA + Anatolia_N + WHG’ (WHG, Mesolithic western European hunter-gatherers). The area of the pie is proportional to the number of individuals (number shown if more than one). Map data from the R package ‘maps’. **b**, f_4 (Mbuti, test; Iberia_EN, LBK_EN) computed for European populations (number of individuals for each group is given in parentheses) before the emergence of the Beaker complex (Supplementary Information section 7). Error bars represent ± 1 standard errors. **c**, Testing different populations as a source for the Neolithic ancestry component in Beaker-complex-associated individuals. The table shows P values (* indicates values > 0.05) for the fit of the model: ‘Steppe_EBA + Neolithic/Copper Age’ source population.

found roughly contemporary Beaker-complex-associated individuals with very different proportions (from 0% to 75%) of steppe-related ancestry. This genetic heterogeneity is consistent with early stages of mixture between previously established European Neolithic populations and migrants with steppe-related ancestry. One implication of this is that even at local scales, the Beaker complex was associated with people of diverse ancestries.

Although the steppe-related ancestry in Beaker-complex-associated individuals had a recent origin in the east^{2,3}, the other ancestry component—from previously established European populations—could potentially be derived from several parts of Europe, because groups that were genetically closely related were widely distributed during the Neolithic and Copper Ages^{2,4,11,16,18–23}. To obtain insight into the origin of this ancestry component in Beaker-complex-associated individuals, we looked for regional patterns of genetic differentiation within Europe during the Neolithic and Copper Age. We examined whether populations pre-dating the emergence of the Beaker complex shared more alleles with Iberian (Iberia_EN) or central European Linearbandkeramik (LBK_EN) Early Neolithic populations (Fig. 2b). As previously described², Iberian Middle Neolithic and Copper Age populations, but not central and northern European populations, had genetic affinities with Iberian Early Neolithic farmers (Fig. 2b). These regional patterns could partially be explained by differential genetic affinities to pre-Neolithic hunter-gatherer individuals from different regions²² (Extended Data Fig. 4). Neolithic individuals from southern France and Britain are also significantly closer to Iberian Early Neolithic farmers than they are to central European Early Neolithic farmers (Fig. 2b), consistent with a previous analysis of a Neolithic genome from Ireland²³. By modelling Neolithic populations and Mesolithic western European

hunter-gatherers in an admixture graph framework, we replicate these results and show that they are not driven by different proportions of hunter-gatherer admixture (Extended Data Fig. 5; Supplementary Information section 7). Our results suggest that a portion of the ancestry of the Neolithic populations of Britain was derived from migrants who spread along the Atlantic coast. Megalithic tombs document substantial interaction along the Atlantic façade of Europe²⁴, and our results are consistent with such interactions reflecting south-to-north movements of people. More data from southern Britain and Ireland and nearby regions in continental Europe will be needed to fully understand the complex interactions between Britain, Ireland and the continent during the Neolithic²⁴.

The distinctive genetic signatures found in the Iberian populations who preceded the arrival of Beaker complex, when compared to contemporary central European populations, enable us to formally test for the origin of the Neolithic-related ancestry in Beaker-complex-associated individuals. We grouped individuals from Iberia ($n = 32$) and from outside Iberia ($n = 172$) to increase power and evaluated the fit of different Neolithic and Copper Age groups with qpAdm² under the model: ‘Steppe_EBA + Neolithic/Copper Age’. For Beaker-complex-associated individuals from Iberia, the best fit was obtained when Middle Neolithic and Copper Age populations from the same region were used as the source for their Neolithic-related ancestry; we could exclude central and northern European populations as sources of this ancestry ($P < 0.0063$) (Fig. 2c). Conversely, the Neolithic-related ancestry in Beaker-complex-associated individuals outside of Iberia was most closely related to central and northern European Neolithic populations with relatively high hunter-gatherer admixture (for example, Poland_LN, $P = 0.18$ and Sweden_MN, $P = 0.25$), and we could significantly exclude Iberian sources ($P < 0.0104$) (Fig. 2c).

These results support mostly different origins for Beaker-complex-associated individuals, with no discernible Iberia-related ancestry outside of Iberia.

Nearly complete turnover of ancestry in Britain

The genetic profile of British Beaker-complex-associated individuals ($n = 37$) shows strong similarities to that of central European Beaker-complex-associated individuals (Extended Data Fig. 3). This observation is not restricted to British individuals associated with the ‘All-Over-Cord’ Beaker pottery style that is shared between Britain and central Europe: we also find this genetic signal in British individuals associated with Beaker pottery styles derived from the ‘Maritime’ forms, which were predominant earlier in Iberia. The presence of large amounts of steppe-related ancestry in British Beaker-complex-associated individuals (Fig. 2a) contrasts sharply with Neolithic individuals from Britain ($n = 51$), who have no evidence of steppe genetic affinities and cluster instead with Middle Neolithic and Copper Age populations from mainland Europe (Extended Data Fig. 3). A previous study showed that steppe-related ancestry had arrived in Ireland by the Bronze Age²³; here we show that, at least in Britain, it arrived earlier in the Copper Age (which, in Britain, is synonymous with the Beaker period).

Among the continental Beaker-complex groups analysed in our dataset, individuals from Oostwoud, the Netherlands, are the most closely related to the large majority of Beaker-complex-associated individuals from southern Britain ($n = 27$). The two groups had almost identical steppe-related ancestry proportions (Fig. 2a), the highest level of shared genetic drift (Extended Data Fig. 6b) and were symmetrically related to most ancient populations (Extended Data Fig. 6a), which shows that they are likely derived from the same ancestral population with limited mixture into either group. This does not necessarily imply that the Oostwoud individuals are direct ancestors of the British individuals, but it does show that they were closely related genetically to the population—perhaps yet to be sampled—that moved into Britain from continental Europe.

We investigated the magnitude of population replacement in Britain with qpAdm² by modelling the genome-wide ancestry of Neolithic, Copper and Bronze Age individuals, including Beaker-complex-associated individuals, as a mixture of continental Beaker-complex-associated samples (using the Oostwoud individuals as a surrogate) and the British Neolithic population (Supplementary Information section 8). During the first centuries after the initial contact, between approximately 2450 and 2000 BC, ancestry proportions were variable (Fig. 3), which is consistent with migrant communities just beginning to mix with the previously established British Neolithic population. After roughly 2000 BC, individuals were more homogeneous and possessed less variation in ancestry proportions and a modest increase in Neolithic-related ancestry (Fig. 3). This could represent admixture with persisting British populations with high levels of Neolithic-related ancestry or, alternatively, with incoming continental populations with higher proportions of Neolithic-related ancestry. In either case, our results imply a minimum of $90 \pm 2\%$ local population turnover by the Middle Bronze Age (approximately 1500–1000 BC), with no significant decrease observed in 5 samples from the Late Bronze Age. Although the exact turnover rate and its geographic pattern await refinement with more ancient samples, our results imply that for individuals from Britain during and after the Beaker period, a very high fraction of their DNA derives from ancestors who lived in continental Europe before 2450 BC. An independent line of evidence for population turnover comes from uniparental markers. Whereas Y-chromosome haplogroup R1b was completely absent in Neolithic individuals ($n = 33$), it represents more than 90% of the Y chromosomes in individuals from Copper and Bronze Age Britain ($n = 52$) (Fig. 3). The introduction of new mtDNA haplogroups, such as I, R1a and U4, which were present in Beaker-complex-associated populations from continental Europe but not in

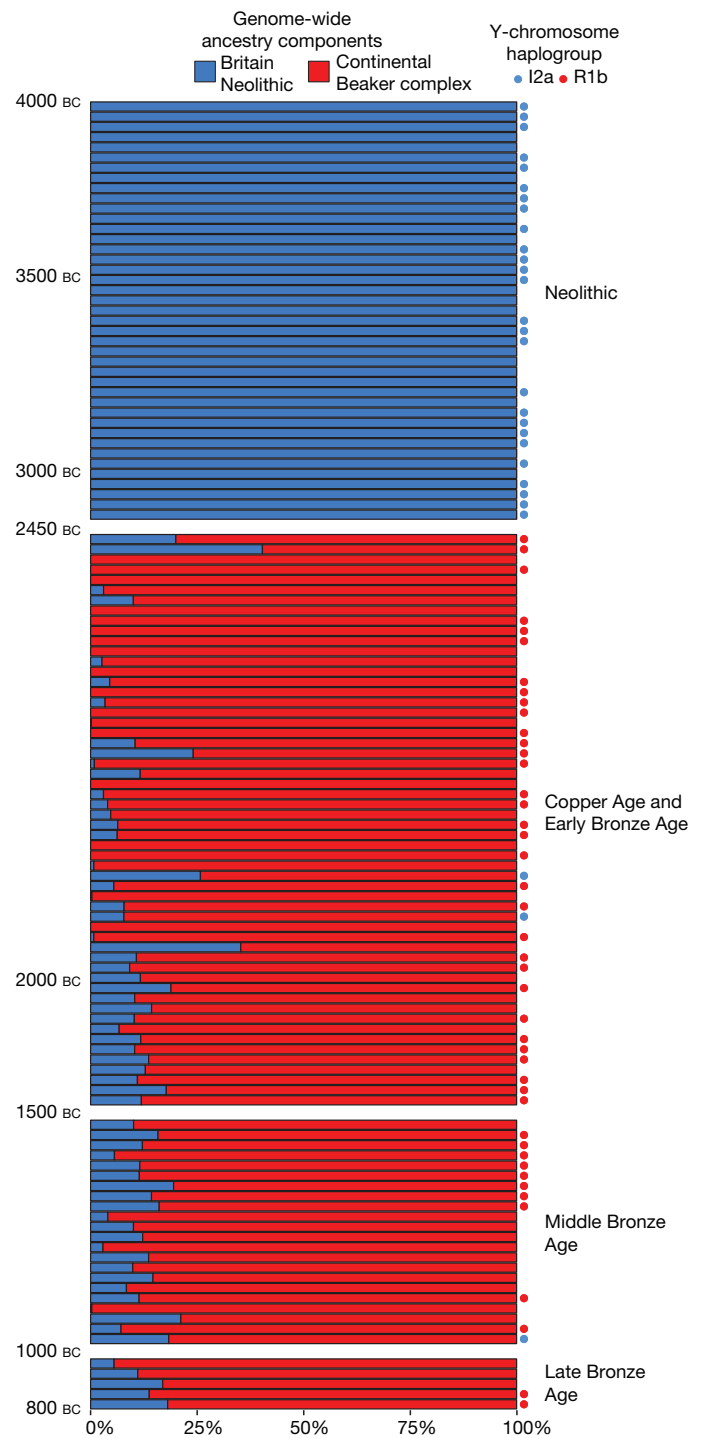


Figure 3 | Population transformation in Britain associated with the arrival of the Beaker complex. Modelling Neolithic, Copper and Bronze Age (including Beaker-complex-associated) individuals from Britain as a mixture of continental Beaker-complex-associated individuals (red) and the Neolithic population from Britain (blue). Each bar represents genome-wide mixture proportions for one individual. Individuals are ordered chronologically and included in the plot if represented by more than 100,000 SNPs. Circles indicate the Y-chromosome haplogroup for male individuals.

Neolithic Britain (Supplementary Table 3), suggests that both men and women were involved in this population turnover.

Our ancient DNA transect-through-time in Britain also enabled us to track the frequencies of alleles with known phenotypic effects. Derived alleles at rs16891982 in *SLC45A2* and rs12913832 in *HERC2/OCA2*,

which contribute to reduced skin and eye pigmentation in Europeans, considerably increased in frequency between the Neolithic period and the Beaker and Bronze Age periods (Extended Data Fig. 7). The arrival of migrants associated with the Beaker complex therefore markedly altered the pigmentation phenotypes of British populations. However, the lactase persistence allele at SNP rs4988235 in *LCT* remained at very low frequencies across this transition, both in Britain and continental Europe, which shows that the major increase in its frequency occurred within the last 3,500 years^{3,4,25}.

Discussion

The term ‘Bell Beaker’ was introduced by late-nineteenth- and early-twentieth-century archaeologists to refer to a distinctive pottery style found across western and central Europe at the end of the Neolithic that was initially hypothesized to have been spread by a genetically homogeneous population. This idea of a ‘Beaker Folk’ became unpopular after the 1960s as scepticism grew about the role of migration in mediating change in archaeological cultures²⁶, although even at the time²⁷ it was speculated that the expansion of the Beaker complex into Britain was an exception—a prediction that has now been borne out by ancient genomic data.

The expansion of the Beaker complex cannot be described by a simple one-to-one mapping of an archaeologically defined material culture to a genetically homogeneous population. This stands in contrast to other archaeological complexes, notably the Linearbandkeramik farmers of central Europe², the Early Bronze Age Yamnaya of the steppe^{2,3} and—to some extent—the Corded Ware complex of central and eastern Europe^{2,3}. Our results support a model in which cultural transmission and human migration both had important roles, with the relative balance of these two processes depending on the region. In Iberia, the majority of Beaker-complex-associated individuals lacked steppe affinities and were genetically most similar to preceding Iberian populations. In central Europe, steppe-related ancestry was widespread and we can exclude a substantial contribution from Iberian Beaker-complex-associated individuals. However, the presence of steppe-related ancestry in some Iberian individuals demonstrates that gene flow into Iberia was not uncommon during this period. These results contradict initial suggestions of gene flow into central Europe based on analysis of mtDNA²⁸ and dental morphology²⁹. In particular, mtDNA haplogroups H1 and H3 were proposed as markers for a Beaker-complex expansion originating in Iberia²⁸, yet H3 is absent among our Iberian Beaker-complex-associated individuals.

In other parts of Europe, the expansion of the Beaker complex was driven to a substantial extent by migration. This genomic transformation is clearest in Britain owing to our densely sampled time transect. The arrival of people associated with the Beaker complex precipitated a demographic transformation in Britain, exemplified by the presence of individuals with large amounts of steppe-related ancestry after 2450 BC. We considered the possibility that an uneven geographic distribution of samples may have caused us to miss a major population that lacked steppe-derived ancestry after 2450 BC. However, our British Beaker and Bronze Age samples are dispersed geographically—extending from the southeastern peninsula of England to the Western Isles of Scotland—and come from a wide variety of funerary contexts (rivers, caves, pits, barrows, cists and flat graves) and diverse funerary traditions (single and multiple burials in variable states of anatomical articulation), which reduces the likelihood that our sampling missed major populations. We also considered the possibility that different burial practices between local and incoming populations (cremation versus inhumation) during the early stages of interaction could result in a sampling bias against local individuals. Although it is possible that such a sampling bias makes the ancestry transition appear more sudden than it in fact was, the long-term demographic effect was clearly substantial, as the pervasive steppe-related ancestry observed during the Beaker period, which was absent in the Neolithic period, persisted during the Bronze Age—and indeed remains predominant in

Britain today². These results are notable in light of strontium and oxygen isotope analyses of British skeletons from the Beaker and Bronze Age periods³⁰, which have provided no evidence for substantial mobility over individuals’ lifetimes from locations with cooler climates or from places with geologies atypical of Britain. However, the isotope data are only sensitive to first-generation migrants and do not rule out movements from regions such as the lower Rhine area or from other geologically similar regions for which DNA sampling is still sparse. Further sampling of regions on the European continent may reveal additional candidate sources.

By analysing DNA data from ancient individuals, we have been able to provide constraints on the interpretations of the processes underlying cultural and social changes in Europe during the third millennium BC. Our results motivate further archaeological research to identify the changes in social organization, technology, subsistence, climate, population sizes³¹ or pathogen exposure^{32,33} that could have precipitated the demographic changes uncovered in this study.

Online Content Methods, along with any additional Extended Data display items and Source Data, are available in the online version of the paper; references unique to these sections appear only in the online paper.

Received 8 May 2017; accepted 4 January 2018.

Published online 21 February 2018.

1. Czebreszuk, J. In *Ancient Europe, 8000 B.C. to A.D. 1000: An Encyclopedia of the Barbarian World* (eds Bogucki, P. I. & Crabtree, P. J.) 476–485 (Charles Scribner’s Sons, 2004).
2. Haak, W. *et al.* Massive migration from the steppe was a source for Indo-European languages in Europe. *Nature* **522**, 207–211 (2015).
3. Allentoft, M. E. *et al.* Population genomics of Bronze Age Eurasia. *Nature* **522**, 167–172 (2015).
4. Mathieson, I. *et al.* Genome-wide patterns of selection in 230 ancient Eurasians. *Nature* **528**, 499–503 (2015).
5. Czebreszuk, J. *Similar But Different. Bell Beakers in Europe* (Adam Mickiewicz Univ., 2004).
6. Cardoso, J. L. Absolute chronology of the Beaker phenomenon north of the Tagus estuary: demographic and social implications. *Trab. Prehist.* **71**, 56–75 (2014).
7. Jeunesse, C. The dogma of the Iberian origin of the Bell Beaker: attempting its deconstruction. *J. Neolit. Archaeol.* **16**, 158–166 (2015).
8. Fokkens, H. & Nicolis, F. *Background to Beakers. Inquiries into Regional Cultural Backgrounds of the Bell Beaker Complex* (Sidestone, 2012).
9. Linden, M. V. What linked the Bell Beakers in third millennium BC Europe? *Antiquity* **81**, 343–352 (2007).
10. Fu, Q. *et al.* An early modern human from Romania with a recent Neanderthal ancestor. *Nature* **524**, 216–219 (2015).
11. Lazaridis, I. *et al.* Ancient human genomes suggest three ancestral populations for present-day Europeans. *Nature* **513**, 409–413 (2014).
12. Lazaridis, I. *et al.* Genomic insights into the origin of farming in the ancient Near East. *Nature* **536**, 419–424 (2016).
13. Mallick, S. *et al.* The Simons Genome Diversity Project: 300 genomes from 142 diverse populations. *Nature* **538**, 201–206 (2016).
14. Valverde, L. *et al.* New clues to the evolutionary history of the main European paternal lineage M269: dissection of the Y-SNP S116 in Atlantic Europe and Iberia. *Eur. J. Hum. Genet.* **24**, 437–441 (2016).
15. Gamba, C. *et al.* Ancient DNA from an Early Neolithic Iberian population supports a pioneer colonization by first farmers. *Mol. Ecol.* **21**, 45–56 (2012).
16. Günther, T. *et al.* Ancient genomes link early farmers from Atapuerca in Spain to modern-day Basques. *Proc. Natl Acad. Sci. USA* **112**, 11917–11922 (2015).
17. Alexander, D. H., Novembre, J. & Lange, K. Fast model-based estimation of ancestry in unrelated individuals. *Genome Res.* **19**, 1655–1664 (2009).
18. Broushaki, F. *et al.* Early Neolithic genomes from the eastern Fertile Crescent. *Science* **353**, 499–503 (2016).
19. Skoglund, P. *et al.* Genomic diversity and admixture differs for Stone-Age Scandinavian foragers and farmers. *Science* **344**, 747–750 (2014).
20. Olalde, I. *et al.* A common genetic origin for early farmers from Mediterranean Cardial and central European LBK cultures. *Mol. Biol. Evol.* **32**, 3132–3142 (2015).
21. Mathieson, I. *et al.* The genomic history of southeastern Europe. *Nature* <https://doi.org/10.1038/nature25778> (2018).
22. Lipson, M. *et al.* Parallel palaeogenomic transects reveal complex genetic history of early European farmers. *Nature* **551**, 368–372 (2017).
23. Cassidy, L. M. *et al.* Neolithic and Bronze Age migration to Ireland and establishment of the insular Atlantic genome. *Proc. Natl Acad. Sci. USA* **113**, 368–373 (2016).
24. Sheridan, J. A. In *Landscapes in Transition* (eds Finlayson, B. & Warren, G.) 89–105 (Oxbow, 2010).

25. Burger, J., Kirchner, M., Bramanti, B., Haak, W. & Thomas, M. G. Absence of the lactase-persistence-associated allele in early Neolithic Europeans. *Proc. Natl Acad. Sci. USA* **104**, 3736–3741 (2007).
26. Clarke, D. L. In *Glockenbecher Symposium, Oberried, 18–23 März 1974* (eds Lanting, J. N. & van Der Waals, J. D.) 460–477 (Bussum, 1976).
27. Clark, G. The invasion hypothesis in British archaeology. *Antiquity* **40**, 172–189 (1966).
28. Brotherton, P. *et al.* Neolithic mitochondrial haplogroup H genomes and the genetic origins of Europeans. *Nat. Commun.* **4**, 1764 (2013).
29. Desideri, J. *When Beakers Met Bell Beakers: an Analysis of Dental Remains (British Archaeological Reports International Series 2292)* (Archaeopress, 2011).
30. Parker Pearson, M. *et al.* Beaker people in Britain: migration, mobility and diet. *Antiquity* **90**, 620–637 (2016).
31. Shennan, S. *et al.* Regional population collapse followed initial agriculture booms in mid-Holocene Europe. *Nat. Commun.* **4**, 2486 (2013).
32. Valtueña, A. A. *et al.* The Stone Age plague and its persistence in Eurasia. *Curr. Biol.* **27**, 3683–3691 (2017).
33. Rasmussen, S. *et al.* Early divergent strains of *Yersinia pestis* in Eurasia 5,000 years ago. *Cell* **163**, 571–582 (2015).

Supplementary Information is available in the online version of the paper.

Acknowledgements We thank D. Anthony, J. Koch, I. Mathieson and C. Renfrew for comments; A. Cooper for support from the Australian Centre for Ancient DNA; the Bristol Radiocarbon Accelerator Mass Spectrometry Facility (BRAMS); A. C. Sousa, A. M. Cóluga, L. Loe, C. Roth, E. Carmona Ballesteros, M. Kunst, S.-A. Coupar, M. Giesen, T. Lord, M. Green, A. Chamberlain and G. Drinkall for assistance with samples; E. Willerslev for supporting several co-authors at the Centre for GeoGenetics; the Museo Arqueológico Regional de la Comunidad de Madrid, the Hunterian Museum, University of Glasgow, the Orkney Museum, the Museu Municipal de Torres Vedras, the Great North Museum: Hancock, the Society of Antiquaries of Newcastle upon Tyne, the Sunderland Museum, the National Museum of Wales, the Duckworth Laboratory, the Wiltshire Museum, the Wells Museum, the Brighton Museum, the Somerset Heritage Museum and the Museum of London for facilitating sample collection. Support for this project was provided by Czech Academy of Sciences grant RVO:67985912; by the Momentum Mobility Research Group of the Hungarian Academy of Sciences; by the Wellcome Trust (100713/Z/12/Z); by Irish Research Council

grant GOIPG/2013/36 to D.F.; by the Heidelberg Academy of Sciences (WIN project 'Times of Upheaval') to P.W.S., J.K. and A.Mi.; by the Swedish Foundation for Humanities and Social Sciences grant M16-0455:1 to K.Kr.; by the National Science Centre, Poland grant DEC-2013/10/E/HS3/00141 to M.Fu.; by a Spanish MINECO grant BFU2015-64699-P to C.L.-F.; by Obra Social La Caixa and a Spanish MINECO grant HAR2016-77600-P to C.L., P.R. and C.Bi.; by the NSF Archaeometry program BCS-1460369 to D.J.K.; by the NFS Archaeology program BCS-1725067 to D.J.K. and T.Ha.; and by an Allen Discovery Center grant from the Paul Allen Foundation, US National Science Foundation HOMOINID grant BCS-1032255, US National Institutes of Health grant GM100233, and the Howard Hughes Medical Institute to D.R.

Author Contributions S.B., M.E.A., N.R., A.S.-N., A.Mi., N.B., M.Fe., E.Har., M.Mi., J.O., K.S., O.C., D.K., F.C., R.Pi., J.K., W.H., I.B. and D.R. performed or supervised laboratory work. G.T.C. and D.J.K. undertook the radiocarbon dating of a large fraction of samples. I.A., K.Kr., A.B., K.W.A., A.A.F., E.B., M.C.-B., D.B., C.Bi., J.V.M., R.M.G., C.Bo., L.Bo., T.A., L.Bü., S.C., L.C.N., O.E.C., G.T.C., B.C., A.D., K.E.D., N.D., M.E., C.E., M.K., J.F.F., H.F., C.F., M.G., R.G.P., M.H.-U., E.Had., G.H., N.J., T.K., K.Ma., S.P., P.L., O.L., A.L., C.H.M., V.G.O., A.B.R., J.L.M., T.M., J.I.M., K.Mc., B.G.M., A.Mo., G.K., V.K., A.C., R.Pa., A.E., K.Kö., T.Ha., T.S., J.Da., Z.B., M.H., P.V., M.D., F.B., R.F.F., A.-M.H.-C., S.T., E.C., L.L., A.V., A.Z., C.W., G.D., E.G.-D., B.N., M.Br., M.Lu., R.M., J.De., M.Be., G.B., M.Fu., A.H., M.Ma., A.R., S.L., I.S., K.T.L., J.L.C., C.L., M.P.P., P.W., T.D.P., P.P., P.-J.R., P.R., R.R., M.A.R.G., A.Sc., J.S., A.M.S., V.S., L.V., J.Z., D.C., T.Hi., V.H., A.Sh., K.-G.S., P.W.S., R.Pi., J.K., W.H., I.B., C.L.-F. and D.R. assembled archaeological material. I.O., S.M., T.B., A.Mi., E.A., M.Li., I.L., N.P., Y.D., Z.F., D.F., D.J.K., P.d.K., T.K.H., M.G.T. and D.R. analysed data. I.O., C.L.-F. and D.R. wrote the manuscript with input from all co-authors.

Author Information Reprints and permissions information is available at www.nature.com/reprints. The authors declare no competing financial interests. Readers are welcome to comment on the online version of the paper. Publisher's note: Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations. Correspondence and requests for materials should be addressed to I.O. (inigo_olalde@hms.harvard.edu) or D.R. (reich@genetics.med.harvard.edu).

Reviewer Information *Nature* thanks C. Renfrew, E. Rhodes, M. Richards and the other anonymous reviewer(s) for their contribution to the peer review of this work.

Iñigo Olalde¹, Selina Brace², Morten E. Allentoft³, Ian Armit⁴§, Kristian Kristiansen⁵§, Thomas Booth², Nadin Rohland¹, Swapan Mallick^{1,6,7}, Anna Szécsényi-Nagy⁸, Alissa Mittnik^{9,10}, Eveline Hahn¹¹, Mark Lipson¹, Iosif Lazaridis^{1,6}, Thomas K. Harper¹², Nick Patterson⁶, Nasreen Broomandkoshbacht^{1,7}, Yoan Diekmann¹³, Zuzana Faltskova¹³, Daniel Fernandes^{14,15,16}, Matthew Ferry^{1,7}, Eadaoin Harney¹, Peter de Knijff¹¹, Megan Michel^{1,7}, Jonas Oppenheimer^{1,7}, Kristin Stewardson^{1,7}, Alistair Barclay¹⁷, Kurt Werner Alt^{18,19,20}, Corina Liesau²¹, Patricia Ríos²¹, Concepción Blasco²¹, Jorge Vega Miguel²², Roberto Menduina García²², Azucena Avilés Fernández²³, Eszter Bánffy^{24,25}, Maria Bernabò-Brea²⁶, David Billoin²⁷, Clive Bonsall²⁸, Laura Bonsall²⁹, Tim Allen³⁰, Lindsey Büster⁴, Sophie Carver³¹, Laura Castells Navarro⁴, Oliver E. Craig³², Gordon T. Cook³³, Barry Cunliffe³⁴, Anthony Denaire³⁵, Kirsten Egging Dinwiddy¹⁷, Natasha Dodwell³⁶, Michal Ernée³⁷, Christopher Evans³⁸, Milan Kuchark³⁹, Joan Francés Farré⁴⁰, Chris Fowler⁴¹, Michiel Hazenbeek⁴², Rafael Garrido Pena²¹, María Haber-Urriarte²³, Elzbieta Haduch⁴³, Gill Hey³⁰, Nick Jowett⁴⁴, Timothy Knowles⁴⁵, Ken Massy⁴⁶, Saskia Pfrengle⁹, Philippe Lefranc⁴⁷, Olivier Lemerrier⁴⁸, Arnaud Lefebvre^{49,50}, César Heras Martínez^{51,52,53}, Virginia Galera Olmo^{52,53}, Ana Bastida Ramírez⁵¹, Joaquín Lomba Maurandi²³, Tona Majó⁵⁴, Jacqueline I. McKinley¹⁷, Kathleen McSweeney²⁸, Balázs Gusztáv Mende⁸, Alessandra Mod⁵⁵, Gabriella Kulcsár²⁴, Viktória Kiss²⁴, András Czene⁵⁶, Róbert Patay⁵⁷, Anna Endrődi⁵⁸, Kitti Köhler²⁴, Tamás Hajdu^{59,60}, Tamás Szeniczey⁵⁹, János Dani⁶¹, Zsolt Bernert⁶⁰, Maya Hoole⁶², Olivia Cheronet^{14,15}, Denise Keating⁶³, Petr Velemínský⁶⁴, Miroslav Dobeš³⁷, Francesca Candilio^{65,66,67}, Fraser Brown³⁰, Raúl Flores Fernández⁶⁸, Ana-Mercedes Herrero-Corral⁶⁹, Sebastiano Tusa⁷⁰, Emiliano Carnieri⁷¹, Luigi Lentini⁷², Antonella Valentini⁷³, Alessandro Zanini⁷⁴, Clive Waddington⁷⁵, Germán Delibes⁷⁶, Elisa Guerra-Doce⁷⁶, Benjamin Neil³⁸, Marcus Brittain³⁸, Mike Luke⁷⁷, Richard Mortimer³⁶, Jocelyne Desideri⁷⁸, Marie Besse⁷⁸, Günter Brücken⁷⁹, Miroslaw Furmanek⁸⁰, Agata Hałuszko⁸⁰, Maksym Mackiewicz⁸⁰, Artur Rapiński⁸¹, Stephany Leach⁸², Ignacio Soriano⁸³, Katina T. Lillios⁸⁴, João Luís Cardoso^{85,86}, Michael Parker Pearson⁸⁷, Piotr Włodarczyk⁸⁸, T. Douglas Price⁸⁹, Pilar Prieto⁹⁰, Pierre-Jérôme Rey⁹¹, Roberto Risch⁸³, Manuel A. Rojo Guerra⁹², Aurore Schmitt⁹³, Joël Serrallongue⁹⁴, Ana Maria Silva⁹⁵, Václav Smrčka⁹⁶, Luc Vergnaud⁹⁷, João Zilhão^{85,98,99}, David Caramelli⁵⁵, Thomas Higham¹⁰⁰, Mark G. Thomas¹³, Douglas J. Kennett¹⁰¹, Harry Fokkens¹⁰², Volker Heyd^{31,103}, Alison Sheridan¹⁰⁴, Karl-Göran Sjögren⁵, Philipp W. Stockhammer^{46,105}, Johannes Krause¹⁰⁵, Ron Pinhasi^{14,15}§, Wolfgang Haak^{105,106}§, Ian Barnes⁵§, Carles Lalueza-Fox¹⁰⁷§ & David Reich^{1,6,7}§

GeoGenetics, Natural History Museum, University of Copenhagen, Copenhagen 1350, Denmark. ⁴School of Archaeological and Forensic Sciences, University of Bradford, Bradford BD7 1DP, UK. ⁵University of Gothenburg, Gothenburg 405 30, Sweden. ⁶Broad Institute of MIT and Harvard, Cambridge, Massachusetts 02142, USA. ⁷Howard Hughes Medical Institute, Harvard Medical School, Boston, Massachusetts 02115, USA. ⁸Laboratory of Archaeogenetics, Institute of Archaeology, Research Centre for the Humanities, Hungarian Academy of Sciences, Budapest 1097, Hungary. ⁹Institute for Archaeological Sciences, Archaeo- and Palaeogenetics, University of Tübingen, Tübingen 72070, Germany. ¹⁰Department of Archaeogenetics, Max Planck Institute for the Science of Human History, Jena 07745, Germany. ¹¹Department of Human Genetics, Leiden University Medical Center, Leiden 2333 ZC, The Netherlands. ¹²Department of Anthropology, The Pennsylvania State University, University Park, Pennsylvania 16802, USA. ¹³Research Department of Genetics, Evolution and Environment, University College London, London WC1E 6BT, UK. ¹⁴Earth Institute and School of Archaeology, University College Dublin, Dublin 4, Ireland. ¹⁵Department of Anthropology, University of Vienna, Vienna 1090, Austria. ¹⁶Research Center for Anthropology and Health, Department of Life Science, University of Coimbra, Coimbra 3000-456, Portugal. ¹⁷Wessex Archaeology, Salisbury SP4 6EB, UK. ¹⁸Center of Natural and Cultural History of Man, Danube Private University, Krems 3500, Austria. ¹⁹Department of Biomedical Engineering, Basel University, Basel 4123, Switzerland. ²⁰Integrative Prehistory and Archaeological Science, Basel University, Basel, Switzerland. ²¹Departamento de Prehistoria y Arqueología, Universidad Autónoma de Madrid, Madrid 28049, Spain. ²²ARGEA S.L., Madrid 28011, Spain. ²³Área de Prehistoria, Universidad de Murcia, Murcia 30001, Spain. ²⁴Institute of Archaeology, Research Centre for the Humanities, Hungarian Academy of Sciences, Budapest 1097, Hungary. ²⁵Romano-Germanic Commission, German Archaeological Institute, Frankfurt am Main 60325, Germany. ²⁶Museo Archeologico Nazionale di Parma, Parma 43100, Italy. ²⁷INRAP, Institut National de Recherches Archéologiques Préventives, Buffard 25440, France. ²⁸School of History, Classics and Archaeology, University of Edinburgh, Edinburgh EH8 9AG, UK. ²⁹10 Merchiston Gardens, Edinburgh EH10 5DD, UK. ³⁰Oxford Archaeology, Oxford OX2 0ES, UK. ³¹Department of Archaeology and Anthropology, University of Bristol, Bristol BS8 1UU, UK. ³²BioArCh, Department of Archaeology, University of York, York YO10 5DD, UK. ³³Scottish Universities Environmental Research Centre, East Kilbride G75 0QF, UK. ³⁴Institute of Archaeology, University of Oxford, Oxford OX1 2PG, UK. ³⁵University of Burgundy, Dijon 21000, France. ³⁶Oxford Archaeology East, Cambridge CB23 8SQ, UK. ³⁷Institute of Archaeology, Czech Academy of Sciences, Prague 118 01, Czech Republic. ³⁸Cambridge Archaeological Unit, Department of Archaeology, University of Cambridge, Cambridge CB3 0DT, UK. ³⁹Labrys o.p.s., Prague 198 00, Czech Republic. ⁴⁰Museu i Poblat Ibèric de Ca n'Oliver, Cerdanyola del Vallès 08290, Spain. ⁴¹School of History, Classics & Archaeology, Newcastle University, Newcastle upon Tyne NE1 7RU, UK. ⁴²INRAP, Institut National de Recherches Archéologiques Préventives, Nice 06300, France. ⁴³Institute of Zoology and Biomedical Research, Jagiellonian University, Kraków 31-007, Poland. ⁴⁴Great Orme Mines, Great Orme, Llandudno LL30 2XG, UK. ⁴⁵Bristol Radiocarbon Accelerator Mass Spectrometry Facility, University of Bristol, Bristol BS8 1UU, UK. ⁴⁶Institut für Vor- und Frühgeschichtliche Archäologie und Provinzialrömische Archäologie,

¹Department of Genetics, Harvard Medical School, Boston, Massachusetts 02115, USA.

²Department of Earth Sciences, Natural History Museum, London SW7 5BD, UK. ³Centre for

Ludwig-Maximilians-Universität München, Munich 80539, Germany.⁴⁷INRAP, Institut National de Recherches Archéologiques Préventives, Strasbourg 67100, France.⁴⁸Université Paul-Valéry - Montpellier 3, UMR 5140 ASM, Montpellier 34199, France.⁴⁹INRAP, Institut National de Recherches Archéologiques Préventives, Metz 57063, France.⁵⁰UMR 5199, Pacea, équipe A3P, Université de Bordeaux, Talence 33400, France.⁵¹TRÉBEDE, Patrimonio y Cultura SL, Torres de la Alameda 28813, Spain.⁵²Departamento de Ciencias de la Vida, Universidad de Alcalá, Alcalá de Henares 28801, Spain.⁵³Instituto Universitario de Investigación en Ciencias Policiales (IUICP), Alcalá de Henares 28801, Spain.⁵⁴Archaeom, Departament de Prehistòria, Universitat Autònoma de Barcelona, Cerdanyola del Vallès 08193, Spain.⁵⁵Department of Biology, University of Florence, Florence 50121, Italy.⁵⁶Salisbury Ltd, Budaörs 2040, Hungary.⁵⁷Ferenczy Museum Center, Szentendre 2100, Hungary.⁵⁸Budapest History Museum, Budapest 1014, Hungary.⁵⁹Department of Biological Anthropology, Eötvös Loránd University, Budapest 1117, Hungary.⁶⁰Hungarian Natural History Museum, Budapest 1083, Hungary.⁶¹Déri Museum, Debrecen 4026, Hungary.⁶²Historic Environment Scotland, Edinburgh EH9 1SH, UK.⁶³Humanities Institute, University College Dublin, Dublin 4, Ireland.⁶⁴Department of Anthropology, National Museum, Prague 115 79, Czech Republic.⁶⁵Soprintendenza Archeologia belle arti e paesaggio per la città metropolitana di Cagliari e per le province di Oristano e Sud Sardegna, Cagliari 9124, Italy.⁶⁶Physical Anthropology Section, University of Philadelphia Museum of Archaeology and Anthropology, Philadelphia, Pennsylvania 19104, USA.⁶⁷Department of Environmental Biology, Sapienza University of Rome, Rome 00185, Italy.⁶⁸46 Cuidad Real Street, Parla 28982, Spain.⁶⁹Departamento de Prehistoria, Universidad Complutense de Madrid, Madrid 28040, Spain.⁷⁰Soprintendenza del Mare, Palermo 90133, Italy.⁷¹Facoltà di Lettere e Filosofia, Università di Palermo, Palermo 90133, Italy.⁷²Soprintendenza per i beni culturali e ambientali di Trapani, Trapani 91100, Italy.⁷³Prima Archeologia del Mediterraneo, Partanna 91028, Italy.⁷⁴Università degli Studi di Palermo, Agrigento 92100, Italy.⁷⁵Archaeological Research Services Ltd, Bakewell DE45 1HB, UK.⁷⁶Departamento de Prehistoria, Facultad de Filosofía y Letras, Universidad de Valladolid, Valladolid 47011, Spain.⁷⁷Albion Archaeology, Bedford MK42 0AS, UK.⁷⁸Laboratory of Prehistoric Archaeology and Anthropology, Department F.-A. Forel for Environmental and Aquatic Sciences, University of Geneva, Geneva 4, Switzerland.⁷⁹General Department of Cultural Heritage Rhineland Palatinate, Department of Archaeology, Mainz 55116, Germany.⁸⁰Institute of Archaeology, University of Wrocław, Wrocław 50-137, Poland.⁸¹Institute of Archaeology, Silesian University in Opava, Opava 746 01, Czech Republic.⁸²Department of Archaeology, University of Exeter, Exeter EX4 4QE, UK.⁸³Departament de Prehistòria, Universitat Autònoma de Barcelona, Cerdanyola del Vallès 08193, Spain.⁸⁴Department of Anthropology, University of Iowa, Iowa City, Iowa 52240, USA.⁸⁵Centro de Arqueologia, Universidade de Lisboa, Lisboa 1600-214, Portugal.⁸⁶Universidade Aberta, Lisboa 1269-001, Portugal.⁸⁷Institute of Archaeology, University College London, London WC1H 0PY, UK.⁸⁸Institute of Archaeology and Ethnology, Polish Academy of Sciences, Kraków 31-016, Poland.⁸⁹Laboratory for Archaeological Chemistry, University of Wisconsin-Madison, Madison, Wisconsin 53706, USA.⁹⁰University of Santiago de Compostela, Santiago de Compostela 15782, Spain.⁹¹UMR 5204 Laboratoire Edytem, Université Savoie Mont Blanc, Chambéry 73376, France.⁹²Department of Prehistory and Archaeology, Faculty of Philosophy and Letters, Valladolid University, Valladolid 47011, Spain.⁹³UMR 7268 ADES, CNRS, Aix-Marseille Univ, EFS, Faculté de médecine Nord, Marseille 13015, France.⁹⁴Service archéologique, Conseil Général de la Haute-Savoie, Annecy 74000, France.⁹⁵Laboratory of Prehistory, Research Center for Anthropology and Health, Department of Life Science, University of Coimbra, Coimbra 3000-456, Portugal.⁹⁶Institute for History of Medicine and Foreign Languages, First Faculty of Medicine, Charles University, Prague 121 08, Czech Republic.⁹⁷ANTEA Bureau d'étude en Archéologie, Habsheim 68440, France.⁹⁸Institució Catalana de Recerca i Estudis Avançats, Barcelona 08010, Spain.⁹⁹Departament d'Història i Arqueologia, Universitat de Barcelona, Barcelona 08001, Spain.¹⁰⁰Oxford Radiocarbon Accelerator Unit, RLAHA, University of Oxford, Oxford OX1 3QY, UK.¹⁰¹Department of Anthropology & Institute for Energy and the Environment, The Pennsylvania State University, University Park, Pennsylvania 16802, USA.¹⁰²Faculty of Archaeology, Leiden University, 2333 CC Leiden, The Netherlands.¹⁰³Department of Philosophy, History, Culture and Art Studies, Section of Archaeology, University of Helsinki, Helsinki 00014, Finland.¹⁰⁴National Museums Scotland, Edinburgh EH1 1JF, UK.¹⁰⁵Max Planck Institute for the Science of Human History, Jena 07745, Germany.¹⁰⁶Australian Centre for Ancient DNA, School of Biological Sciences, University of Adelaide, Adelaide 5005, South Australia, Australia.¹⁰⁷Institute of Evolutionary Biology, CSIC-Universitat Pompeu Fabra, Barcelona 08003, Spain.

§These authors jointly supervised this work.