POPULATION GENOMICS OF STONE AGE EURASIA

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Summary

Several major migrations and population turnover events during the later Stone Age (after c. 11,000 cal. BP) are believed to have shaped the contemporary population genetic diversity in Eurasia. While the genetic impacts of these migrations have been investigated on regional scales, a detailed understanding of their spatiotemporal dynamics both within and between major geographic regions across Northern Eurasia remains largely elusive. Here, we present the largest shotgun-sequenced genomic dataset from the Stone Age to date, representing 317 primarily Mesolithic and Neolithic individuals from across Eurasia, with associated radiocarbon dates, stable isotope data, and pollen records. Using recent advances, we imputed >1,600 ancient genomes to obtain accurate diploid genotypes, enabling previously unachievable fine-grained population structure inferences. We show that 1) Eurasian Mesolitic hunter-gatherers were more genetically diverse than previously known, and deeply divergent between the west and the east; 2) Hitherto genetically undescribed hunter-gatherers from the Middle Don region contributed significant ancestry to the later Yamnaya steppe pastoralists; 3) The genetic impact of the transition from Mesolithic hunter-gatherers to Neolithic farmers was highly distinct, east and west of a “Great Divide” boundary zone extending from the Black Sea to the Baltic, with large-scale shifts in genetic ancestry to the west. This include an almost complete replacement of hunter-gatherers in Denmark, but no substantial shifts during the same period further to the east; 4) Within-group relatedness changes substantially during the Neolithic transition in the west, where clusters of Neolithic farmer-associated individuals show overall reduced relatedness, while genetic relatedness remains high until ~4,000 BP in the east, consistent with a much longer persistence of smaller localised hunter-gatherer groups; 5) A fast-paced second major genetic transformation beginning around 5,000 BP, with Steppe-related ancestry reaching most parts of Europe within a 1,000 years span. Local Neolithic farmers admixed with incoming pastoralists in most parts of Europe, whereas Scandinavia experienced another near-complete population replacement, with similar dramatic turnover-patterns also evident in western Siberia; 6) Extensive regional differences in the ancestry components related to these early events remain visible to this day, even within countries (research conducted using the UK Biobank resource). Neolithic farmer ancestry is highest in southern and eastern England while Steppe-related ancestry is highest in the Celtic populations of Scotland, Wales, and Cornwall. Overall, our findings show that although the Stone-Age migrations have been important in shaping contemporary genetic diversity in Eurasia, their dynamics and impact were geographically highly heterogeneous.

Keywords:
Population genomics, ancient DNA, Mesolithic, Neolithic, UK Biobank

Introduction

It is argued that genetic diversity in contemporary western Eurasian human populations was largely shaped by three major migrations in the Stone Age: hunter-gatherers occupying the area since c. 45,000 BP; the Neolithic farmers expanding from the Middle and Near East c. 11,000 BP; and Steppe pastoralists coming out of the Pontic steppe c. 5,000 BP, signalling the final stages of the Stone Age and the beginning of the Bronze Age [1–5]. However, due to a paucity of genomic data from skeletons older than 8 ka, knowledge of the population structure in the Mesolithic period and how it was formed is limited, and compromise our ability to understand the subsequent demographic transitions. Also, most ancient DNA (aDNA) studies have thus far been restricted to individuals from Europe, hampering our ability to understand the wider impact of these events. The spatiotemporal mapping of population dynamics east of Europe, including Siberia, Central- and Northern Asia during the same time period is limited. In these regions the local use of the term 'Neolithic' typically refers to new forms of lithic material culture, and/or the presence of ceramics[6]. For instance, the Neolithic cultures of the Central Asian Steppe possessed pottery, but retained a hunter-gatherer economy alongside stone blade technology similar to the preceding Mesolithic cultures[7]. The archaeological record testifies to a boundary, ranging from the eastern Baltic to the Black Sea, east of which hunter-gatherer societies persisted for much longer than in western Europe[8]. However, the possible population genomic implications of this phenomenon is not known. Another enigma in the neolithisation debate is that of Scandinavia [9]. The introduction of farming reached a 1,000-year standstill at the doorstep to Southern Scandinavia before finally progressing into Denmark around 6 ka. It is not known what caused this delay, and whether the transition to farming in Denmark was facilitated by the migration of people (demic diffusion), similar to the rest of Europe[10–13] or mostly involved cultural diffusion[14–16]. Lastly, although analyses of ancient genomes have uncovered large-scale migrations from the Pontic Steppe both into Europe and Asia around 5 ka, the details of this transforming demographic process has remained largely unresolved.

To investigate these formative processes of the early Eurasian gene pools, we conducted the largest aDNA study on human Stone Age skeletal material to date. We sequenced the genomes of 317 radiocarbon-dated (AMS) primarily Mesolithic and Neolithic individuals, covering major parts of Eurasia, and combined them with published shotgun-sequenced data to impute a dataset of >1600 diploid ancient genomes. Genomic data from 100 AMS-dated individuals from Denmark supported detailed analyses of the Stone Age population dynamics in Southern Scandinavia. When combined with genetically-predicted phenotypes, proxies for diet ($\delta^{13}C/\delta^{15}N$), mobility ($^{87}Sr/^{86}Sr$) and vegetation cover (pollen) we could connect this with parallel shifts in phenotype, subsistence and landscape.

Results/Discussion

Samples and data

Our primary data consists of genomes from 317 ancient individuals (Fig 1, Extended data fig. 2, Supplement Table I). A total of 272 were radiocarbon dated within the project, while 39 dates were derived from literature and 15 by archaeological context. Dates were corrected for marine and freshwater reservoir effects (Supplementary Note 7) and ranged from the Upper Palaeolithic (UP) c. 25,700 calibrated years before present (cal. BP) to the mediaeval period (c. 1200 cal. BP). However, 97% of the individuals (N=309) span 11,000 cal. BP to 3,000 cal. BP, with a heavy focus on individuals associated with various Mesolithic and Neolithic cultures.

Geographically, the sampled skeletons cover a vast territory across Eurasia, from Lake Baikal to the Atlantic coast and from Scandinavia to the Middle East, deriving from contexts that include burial mounds, caves, bogs and the seafloor (Supplementary Notes 5-6). Broadly, we can divide our research area into three large regions: 1) central, western and northern Europe, 2) eastern Europe including western Russia and Ukraine, and 3) the Urals and western Siberia. Samples cover many of the key Mesolithic and Neolithic cultures in Western Eurasia, such as the Maglemose and Ertebølle in Scandinavia, the Cardial in the Mediterranean, the Körös and Linear Pottery (LBK) in SE and Central Europe, and many archaeological cultures in Ukraine, western Russia, and the trans-Ural (e.g. Veretye, Lyalovo, Volosovo, Kitoi). Our sampling was particularly dense in Denmark, from where we present a detailed and continuous sequence of 100 genomes spanning the Early Mesolithic to the Bronze Age. Dense sample sequences were also obtained from Ukraine, Western

Russia, and the trans-Ural, spanning from the Early Mesolithic through the Neolithic, up to c. 5,000 BP.

Ancient DNA was extracted from dental cementum or petrous bone and the 317 genomes were shotgun sequenced to a depth of 0.01X to 7.1X (mean = 0.75X, median = 0.26X), with >1X coverage for 81 genomes. We utilised a new method optimised for low-coverage data[17] to impute genotypes using the 1000 Genomes phased data as a reference panel. We also applied this to >1300 previously published shotgun-sequenced genomes (Supplemental Table VII), resulting in a dataset of 8.5 million common SNPs (>1% Minor Allele Frequency (MAF) and imputation info score > 0.5) for 1,664 imputed diploid ancient genomes (see Supplementary Note 2). To validate imputation, 42 high coverage (5X to 39X) genomes were downsampled for testing (see also Mota et al. *submitted*[1]*. While 1X genomes provided remarkably high imputation accuracy (closely matching that obtained for modern samples, Extended Data Fig. 1A-D), African genomes had lower accuracy due to poor representation of this ancestry in the reference panel. Imputation accuracy was influenced by both MAF and coverage (Supplementary Fig. S2.3). We found that coverage as low as 0.1X and 0.4X was sufficient to obtain r^2 imputation accuracy of 0.8 and 0.9 at common variants (MAF≥10%), respectively. We conclude that ancient European genomes can be imputed confidently from coverages above 0.4X and highly valuable data can still be obtained from genome coverage as low as 0.1X when using specific QC on the imputed data (although at very low coverage a bias arises towards the major allele, see Supplementary Note 2). For most downstream analyses, samples with low coverage or sites with low MAF were filtered out (depending on the specific data quality requirements) yielding 1,492 imputed ancient genomes (213 sequenced in this study) after filtering individuals with very low coverages (<0.1X) and/or low imputation quality (average genotype probability < 0.8) and close relatives. Overall, this dataset allows us to characterise the ancient cross-continental gene pools and the demographic transitions with unprecedented resolution.

We conducted a broad-scale characterization of this dataset using principal component analysis (PCA) and model-based clustering (ADMIXTURE), recapitulating and providing increased resolution into previously described ancestry clines in ancient Eurasian populations (Fig. 1; Extended Data Fig. 2; Supplementary Note 3d). Strikingly, inclusion of the imputed ancient genomes in the inference of the principal components reveals much higher variance among the ancient groups than previously anticipated using projection onto a PC-space inferred from modern individuals alone (Extended Data Fig. 2). This is particularly notable in a PCA of West Eurasian individuals, where genetic variation among all present-day populations is confined within a small central area of the PCA (Extended Data Fig. 2C, D). These results are consistent with much higher genetic differentiation between ancient Europeans than present-day populations, reflecting lower effective population sizes and genetic isolation among ancient groups.

To obtain a finer-scale characterization of genetic ancestries across space and time, we assigned imputed ancient genomes to genetic clusters by applying hierarchical community detection on a network of pairwise identity-by-descent (IBD)-sharing similarities[18] (Extended Data Fig. 3; Supplementary Note 3c). The obtained clusters capture fine-scale genetic structure corresponding to shared ancestry within particular spatiotemporal ranges and/or archaeological contexts, and were used as sources and/or targets in supervised ancestry modelling (Extended Data Fig. 4; Supplementary Note 3i). We focus our subsequent analyses on three panels of putative source clusters reflecting different temporal depths: “deep”, using a set of deep ancestry source groups

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reflecting major ancestry poles; “postNeol”, using diverse Neolithic and earlier source groups; and “postBA”, using Late Neolithic and Bronze Age source groups (Extended Data Fig. 4).

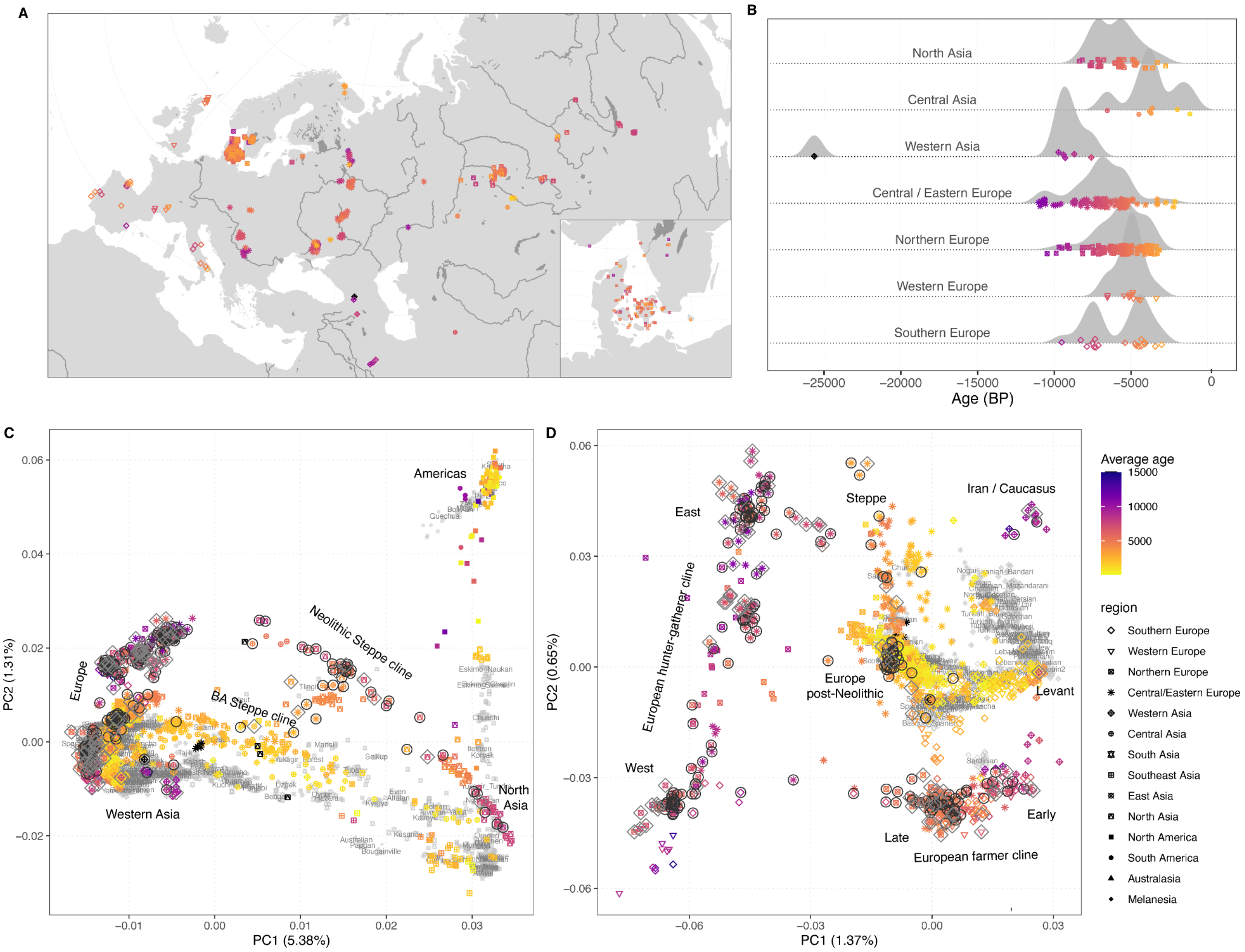

Fig 1. Sample overview and broad scale genetic structure. (A), (B) Geographic and temporal distribution of the 317 ancient genomes reported here. Age and geographic region of ancient individuals are indicated by plot symbol colour and shape, respectively. Random jitter was added to geographic coordinates to avoid overplotting. (C), (D) Principal component analysis of 3,316 modern and ancient individuals from Eurasia, Oceania, and the Americas (C), as well as restricted to 2,126 individuals from western Eurasia (west of Urals) (D). Principal components were defined using both modern and imputed ancient genomes passing all filters, with the remaining low-coverage ancient genomes projected. Ancient genomes sequenced in this study are indicated with black circles (imputed genomes passing all filters, n=213) or grey diamonds (pseudo-haploid projected genomes, n=104). Genomes of modern individuals are shown in grey, with population labels corresponding to their median coordinates.

Deep population structure of western Eurasians

Our study comprises the largest genomic dataset on European hunter-gatherers to date, including 113 imputed hunter-gatherer genomes of which 79 were sequenced in this study. Among them, we report a 0.83X genome of an Upper Palaeolithic (UP) skeleton from Kotias Klde Cave in Georgia, Caucasus (NEO283), directly dated to 26,052 - 25,323 cal BP (95%). In the PCA of all non-African individuals, it occupies a position distinct from other previously sequenced UP individuals, shifted towards west Eurasians along PC1 (Supplementary Note 3d). Using admixture graph modelling, we find that this Caucasus UP lineage derives from a mixture of predominantly West Eurasian UP hunter-gatherer ancestry (76%) with ~24% contribution from a "basal Eurasian" ghost population, first observed in West Asian Neolithic individuals[19] (Extended Data Fig. 5A). Models attempting to reconstruct major post-LGM clusters such as European hunter-gatherers and Anatolian farmers without contributions from this Caucasus UP lineage provided poor admixture graph fits or were rejected in *qpAdm* analyses (Extended Data Fig. 5B,C). These results thus suggest a central role of the descendants related to this Caucasus UP lineage in the formation of later West Eurasian populations, consistent with recent genetic data from the nearby Dzudzuana Cave, also in Georgia[20].

We performed supervised admixture modelling using a set of twelve possible source clusters representing Mesolithic hunter-gatherers from the extremes of the HG cline, as well as temporal or geographical outgroups of deep Eurasian lineages (Fig 2A). We replicate previous results of broad-scale genetic structure correlated to geography in European hunter-gatherers after the LGM[12], while also revealing novel insights into their fine-scale structure. Ancestry related to southern European hunter-gatherers (source: Italy_15000BP_9000 BP) predominates in western Europe. This includes Denmark, where our 28 sequenced and imputed hunter-gatherer genomes derive almost exclusively from this cluster, with remarkable homogeneity across a 5,000 year transect (Fig. 3A). In contrast, hunter-gatherer individuals from the eastern and far northern reaches of Europe show the highest proportions of Russian hunter-gatherer ancestry (source: RussiaNW_11000BP_8000BP; Fig. 2B, D), with genetic continuity until ~5,000 BP in Russia. Ancestry related to Mesolithic hunter-gatherer populations from Ukraine (source: Ukraine_10000BP_4000BP) is carried in highest proportions in hunter-gatherers from a geographic corridor extending from south-eastern Europe towards the Baltic and southern Scandinavia. Swedish Mesolithic individuals derive up to 60% of their ancestry from that source (Fig. 2C). Our results thus indicate northwards migrations of at least three distinct waves of hunter-gatherer ancestry into Scandinavia: a predominantly southern European source into Denmark; a source related to Ukrainian and south-eastern European hunter-gatherers into the Baltic and southern Sweden; and a northwest Russian source into the far north, before venturing south along the Atlantic coast of Norway[21] (Fig. 2). These movements are likely to represent post glacial expansions from refugia areas shared with many plant and animal species[22,23].

Despite the major role of geography in shaping European hunter-gatherer structure, we also document more complex local dynamics. On the Iberian Peninsula, the earliest individuals, including a ~9,200-year-old hunter-gatherer (NEO694) from Santa Maira (eastern Spain), sequenced in this study, show predominantly southern European hunter-gatherer ancestry with a minor contribution from UP hunter-gatherer sources (Fig. 3). In contrast, later individuals from Northern Iberia are more similar to hunter-gatherers from eastern Europe, deriving ~30-40% of their ancestry from a source related to Ukrainian hunter-gatherers[24,25]. The earliest evidence for this gene flow is observed in a Mesolithic individual from El Mazo, Spain (NEO646) that was dated, calibrated and reservoir-corrected to c. 8,200 BP (8365-8182 cal BP, 95%) but context-dated to slightly older (8550-8330 BP, see[26]). The younger date coincides with some of the oldest Mesolithic geometric microliths in northern Iberia, appearing around 8,200 BP at this site[26]. In southern Sweden, we find higher amounts of southern European hunter-gatherer ancestry in late Mesolithic coastal individuals (NEO260 from Evensås; NEO679 from Skateholm) than in the earlier Mesolithic individuals from further inland, suggesting either geographic genetic structure in the Swedish Mesolithic population or a possible eastward expansion of hunter-gatherers from Denmark, where this ancestry prevailed (Fig. 3). An influx of southern European hunter-gatherer-related ancestry in Ukrainian individuals after the Mesolithic (Fig. 3) suggests a similar eastwards expansion in south-eastern Europe[12]. Interestingly, two herein reported ~7,300-year-old imputed genomes from the Middle Don River region in the Pontic-Caspian steppe (Golubaya Krinitsa, NEO113 & NEO212) derive ~20-30% of their ancestry from a source cluster of hunter-gatherers from the Caucasus (Caucasus_13000BP_10000BP) (Fig. 3). Additional lower coverage (non-imputed) genomes from the same site project in the same PCA space (Fig. 1D), shifted away from the European hunter-gatherer cline towards Iran and the Caucasus. Our results thus document genetic contact between populations from the Caucasus and the Steppe region as early as 7,300 years ago, providing documentation of continuous admixture prior to the advent of later nomadic Steppe cultures, in contrast to recent hypotheses, and also further to the west than previously reported[12,27].

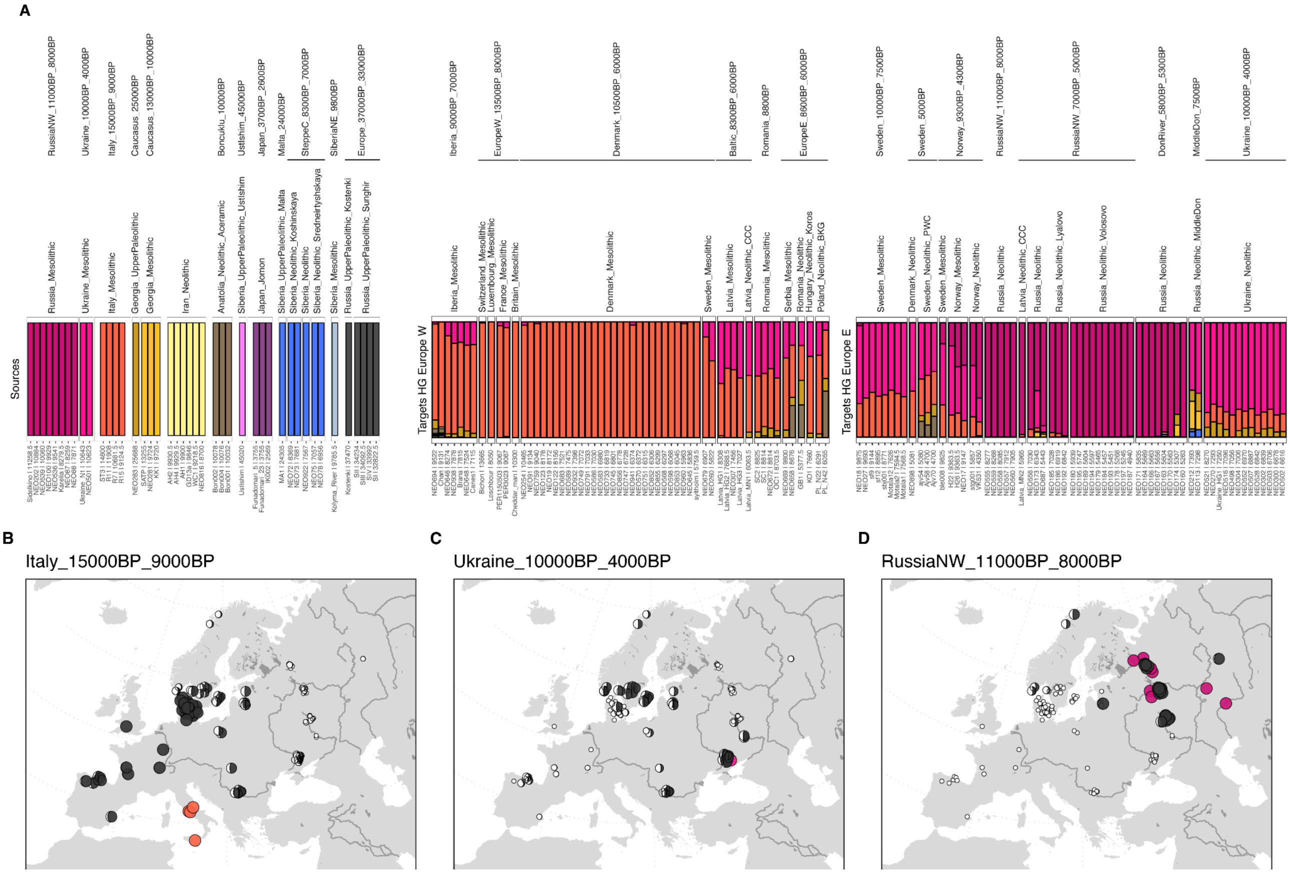

Fig 2. Genetic structure of European hunter-gatherers (A) Ancestry proportions in 113 imputed ancient genomes representing European hunter-gatherer contexts (right) estimated from supervised non-negative least squares analysis using deep Eurasian source groups (left). Individuals from target groups are grouped by genetic clusters. (B)-(D) Moon charts showing spatial distribution of ancestry proportions in European hunter-gatherers deriving from three deep Eurasian source groups; Italy_15000BP_9000BP; Ukraine_10000BP_4000BP; RussiaNW_11000BP_8000BP (source origins shown with coloured symbol). Estimated ancestry proportions are indicated by both size and amount of fill of moon symbols.

Major genetic transitions in Europe

Previous ancient genomics studies have documented multiple episodes of large-scale population turnover in Europe within the last 10,000 years[1,2,4,8,11–13,24,28–31]. The 317 genomes reported here fill important knowledge gaps, particularly in northern and eastern Europe, allowing us to track the dynamics of these events at both continental and regional scales.

Our analyses reveal profound differences in the spatiotemporal neolithisation dynamics across Europe. Supervised admixture modelling (using the “deep” set) and spatiotemporal kriging[32] document a broad east-west distinction along a boundary zone running from the Black Sea to the Baltic. On the western side of this “Great Divide”, the Neolithic transition is accompanied by large-scale shifts in genetic ancestry from local hunter-gatherers to farmers with Anatolian-related ancestry (Boncuklu_10000BP; Fig. 3; Extended Data Fig. 4, 6). The arrival of Anatolian-related ancestry in different regions spans an extensive time period of over 3,000 years, from its earliest evidence in the Balkans (Lepenski Vir) at ~8,700 BP[12] to c. 5,900 BP in Denmark. On the eastern side of this divide, no ancestry shifts can be observed during this period. In the East Baltic region (see also[33]), Ukraine and Western Russia local hunter-gatherer ancestry prevailed until ~5,000 BP without noticeable input of Anatolian-related farmer ancestry (Fig. 3; Extended Data Fig. 4, 6). This Eastern genetic continuity is in remarkable congruence with the archaeological record showing persistence of pottery-using hunter-gatherer-fisher groups in this wide region, and delayed introduction of cultivation and husbandry by several thousand years (Supplementary Note 4).

From approximately 5,000 BP, an ancestry component appears on the eastern European plains in Early Bronze Age Steppe pastoralists associated with the Yamnaya culture and it rapidly spreads across Europe through the expansion of the Corded Ware complex (CWC) and related cultures[1,2]. We demonstrate that this "steppe" ancestry (Steppe_5000BP_4300BP) can be modelled as a mixture of ~65% ancestry related to herein reported hunter-gatherer genomes from the Middle Don River region (MiddleDon_7500BP) and ~35% ancestry related to hunter-gatherers from Caucasus (Caucasus_13000BP_10000BP) (Extended Data Fig. 4). Thus, Middle Don hunter-gatherers, who already carried ancestry related to Caucasus hunter-gatherers (Fig. 2), serve as a hitherto unknown proximal source for the majority ancestry contribution into Yamnaya genomes. The individuals in question derive from the burial ground Golubaya Krinitsa (Supplementary Note 3). Material culture and burial practices at this site are similar to the Mariupol-type graves, which are widely found in neighbouring regions of Ukraine, for instance along the Dnepr River. They belong to the group of complex pottery-using hunter-gatherers mentioned above, but the genetic composition at Golubaya Krinitsa is different from the remaining Ukrainian sites (Fig 2A, Extended Data Fig. 4). We find that the subsequent transition of the Late Neolithic and Early Bronze Age European gene pool happened at a faster pace than during the neolithisation, reaching most parts of Europe within a ~1,000-year time period after first appearing in the eastern Baltic region ~4,800 BP (Fig. 3). In line with previous reports we observe that beginning c. 4,200 BP, steppe-related ancestry was already dominant in individuals from Britain, France and the Iberian peninsula.[13,28,34]. Strikingly, because of the delayed neolithisation in Southern Scandinavia these dynamics resulted in two episodes of large-scale genetic turnover in Denmark and southern Sweden within roughly a 1,000-year period (Fig. 3).

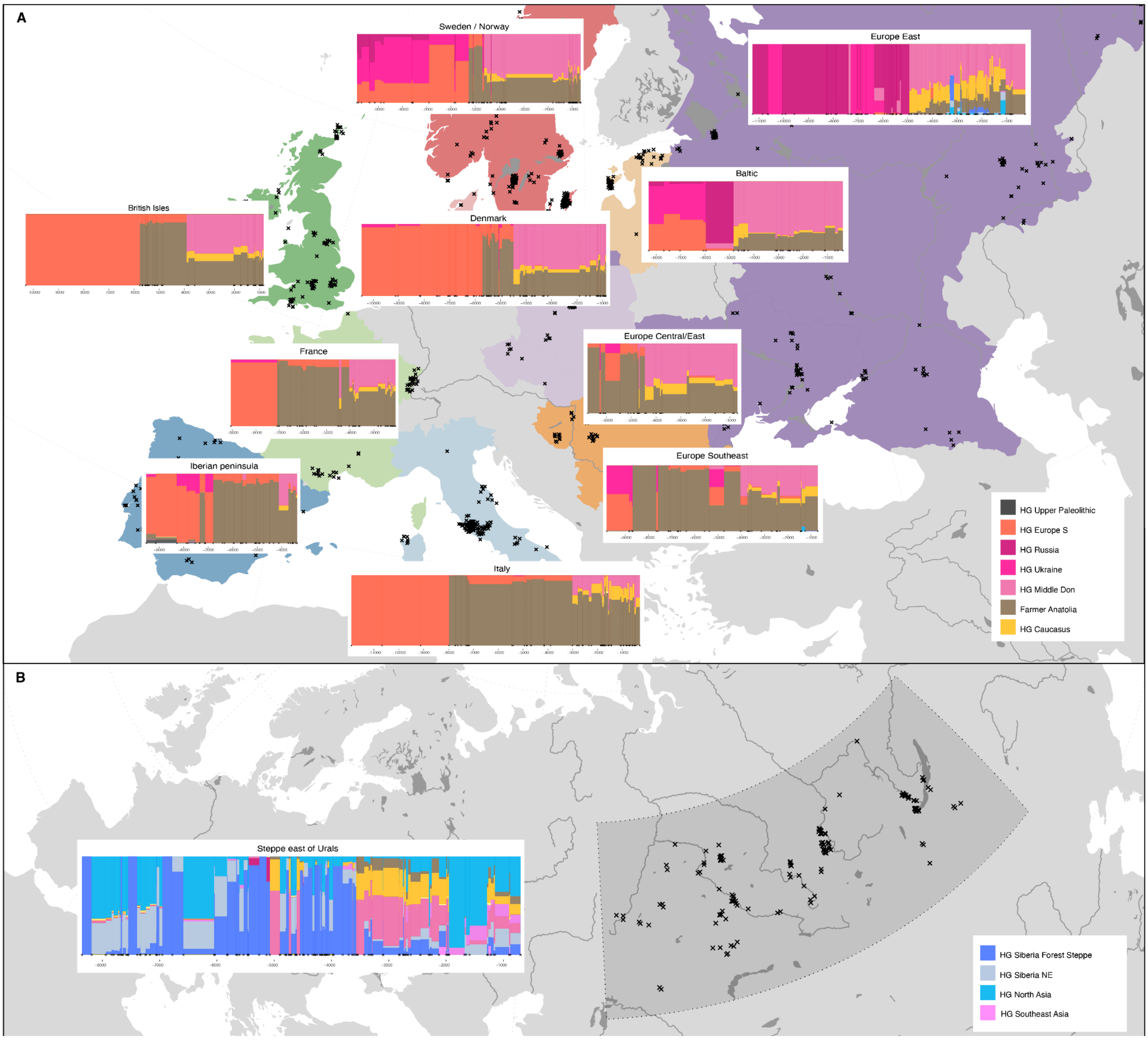

Fig. 3. Genetic transects of Eurasia. Regional timelines of genetic ancestry compositions within the past 15,000 years in western Eurasia (top) and the Eurasian Steppe belt east of the Urals (bottom). Ancestry proportions in 972 imputed ancient genomes from these regions (covering c. 12,000 BP to 500 BP), inferred using supervised admixture modelling with the "deep" hunter-gatherer ancestry source groups. Geographic areas included in timelines are indicated with fill colour (west Eurasia) and grey shading (eastern Steppe region). Excavation locations of the ancient skeletons are indicated with black crosses. Coloured bars within the timelines represent ancestry proportions for temporally consecutive individuals, with the width corresponding to their age difference. Individuals with identical age were offset along the time axis by adding random jitter, ages. We note that the inclusion of only shotgun-sequenced samples may affect the exact timing of events in some regions from where such data are sparse.

We next investigated fine-grained ancestry dynamics underlying these transitions. We replicate previous reports[2,5,11–13,31,35] of widespread, but low-level admixture between immigrant early European farmers and local hunter-gatherers resulting in a resurgence of HG ancestry in many regions of Europe during subsequent centuries (Extended Data Fig. 7). The resulting estimated hunter-gatherer ancestry proportions rarely exceed 10%, with notable exceptions observed in individuals from south-eastern Europe (Iron Gates), Sweden (Pitted Ware Culture) as well as herein reported Early Neolithic genomes from Portugal (western Cardial), estimated to harbour 27% – 43% Iberian hunter-gatherer ancestry (Iberia_9000BP_7000BP). The latter result, suggesting extensive first-contact admixture, is in agreement with archaeological inferences derived from modelling the spread of farming along west Mediterranean Europe[36]. Neolithic individuals from Denmark show some of the highest overall hunter-gatherer ancestry proportions (up to ~25%), mostly derived from Western European-related hunter-gatherers (EuropeW_13500BP_8000BP) supplemented with marginal contribution from local Danish hunter-gatherer groups in some individuals (Extended Data Fig. 7D; Supplementary Note 3f). We estimated the timing of the admixture using the linkage-disequilibrium-based method DATES[37] at ~6,000 BP. Both lines of evidence thus suggest that a significant part of the hunter-gatherer admixture observed in Danish individuals occurred already before the arrival of the incoming farmers in the region (Extended Data Fig. 7), and further point towards Central Europe as a key region in the resurgence of HG ancestry. Interestingly, the genomes of two ~5,000-year-old male individuals (NEO33, NEO898) from Denmark were entirely composed of Swedish hunter-gatherer ancestry, and formed a cluster with Pitted Ware Culture (PWC) individuals from Ajvide on the Baltic island of Gotland (Sweden)[38–40]. Of the two individuals, NEO033 also displays an outlier Sr-signature (Fig. 4), potentially suggesting a non-local origin matching his unusual ancestry. Overall, our results demonstrate direct contact across the Kattegat and Öresund during Neolithic times (Extended Data Fig. 3, 4), in line with archaeological findings from Zealand (east Denmark) showing cultural affinities to PWC on the Swedish west coast[41–44].

Further, we find evidence for regional stratification in early Neolithic farmer ancestries in subsequent Neolithic groups. Specifically, southern European early farmers appear to have provided major genetic ancestry to Neolithic groups of later dates in Western Europe, while central European early farmer ancestry is mainly observed in subsequent Neolithic groups in eastern Europe and Scandinavia (Extended Data Fig. 7D-F). These results are consistent with distinct migratory routes of expanding farmer populations as previously suggested[45]. For example, similarities in material culture and flint mining activities could suggest that the first farmers in South Scandinavia originated from or had close social relations with the central European Michelsberg Culture[46].

The second continental-wide transition from Neolithic farmer ancestry to Steppe-related ancestry differs markedly between geographic regions. The contribution of local farmer ancestry to the incoming groups was high in eastern, western and southern Europe, reaching >50% on the Iberian Peninsula (“postNeol” set; Extended Data Fig. 4, 6B, C)[24]. Scandinavia, however, portrays a dramatically different picture, with a near-complete replacement of the local population inferred across all sampled individuals (Extended Data Fig. 7B, C). Following the second transition, farmer-related ancestry remains in Scandinavia, but the source is now different. It can be modelled as deriving almost exclusively from a genetic cluster associated with the Late Neolithic Globular Amphora Culture (GAC) (Poland_5000BP_4700BP; Extended Data Fig. 4). Strikingly, after the Steppe-related ancestry was first introduced into Europe (Steppe_5000BP_4300BP), it expanded together with GAC-related ancestry across all sampled European regions (Extended Data Fig. 7I). This suggests that the spread of steppe-related ancestry throughout Europe was predominantly mediated through groups that were already admixed with GAC-related farmer groups of the eastern European plains. This finding has major implications for understanding the emergence of the CWC. A stylistic connection from GAC ceramics to CWC ceramics has long been suggested, including the use of amphora-shaped vessels and the development of cord decoration patterns[47]. Moreover, shortly prior to the emergence of the earliest CWC groups, eastern GAC and western Yamnaya groups exchanged cultural elements in the forest-steppe transition zone northwest of the Black Sea, where GAC ceramic amphorae and flint axes were included in Yamnaya burials, and the typical Yamnaya use of ochre was included in GAC burials[48], indicating close interaction between these groups. Previous ancient genomic data from a few individuals suggested that this was limited to cultural influences and not population admixture[49]. However, in the light of our new genetic evidence it appears that this zone, and possibly other similar zones of contact between GAC and

Yamnaya (or other closely-related steppe/forest-steppe groups) were key in the formation of the CWC through which steppe-related ancestry and GAC-related ancestry co-dispersed far towards the west and the north[cf. 50]. This resulted in regionally diverse situations of interaction and admixture[51,52] but a significant part of the CWC dispersal happened through corridors of cultural and demic transmission which had been established by the GAC during the preceding period[53,54].

Fine-scale structure and multiproxy analysis of Danish transect

We present a detailed and continuous sequence of multiproxy data from Denmark, from the Early Mesolithic Maglemose, via the Kongemose and Late Mesolithic Ertebølle epochs, the Early and Middle Neolithic Funnel Beaker Culture and the Single Grave Culture, to Late Neolithic and Bronze Age individuals (Fig. 4). To integrate multiproxy data from as many skeletons as possible we made use of non-imputed data for the admixture analyses (Supplementary Note S3d) which were not restricted to the >0.1X coverage cut-off used elsewhere. This provided genetic profiles from 100 Danish individuals (Fig. 4), spanning c. 7,300 years from the earliest known skeleton in Denmark (the Mesolithic "Koelbjerg Man" (NEO254, 10,648-10,282 cal. BP, 95% probability interval) and formerly known as the "Koelbjerg Woman"[55]), to a Bronze Age skeleton from Hove Å (NEO946) dated to 3322-2967 cal. BP (95%). Two shifts in genomic admixture proportions confirm the major population genetic turnovers (Fig. 4) that was inferred from imputed data (Fig. 3). The multiproxy evidence, however, unveils the dramatic concomitant changes in all investigated phenotypic, environmental and dietary parameters (Fig. 4).

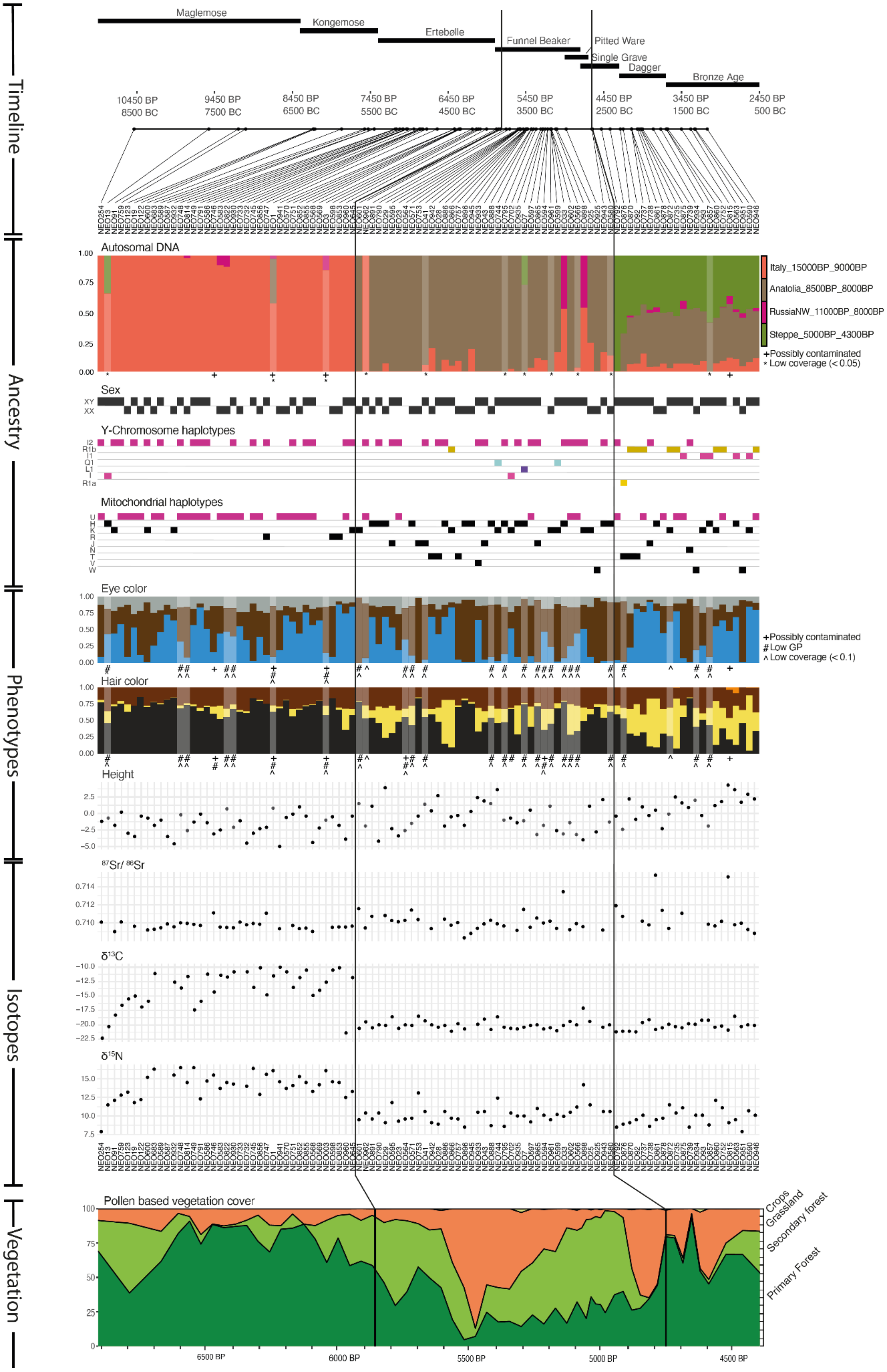
Timeline
Maglemose
Kongemose
Ertebølle
Funnel Beaker
Pitted Ware
Single Grave
Dagger
Bronze Age
10450 BP 8500 BC
9450 BP 7500 BC
8450 BP 6500 BC
7450 BP 5500 BC
6450 BP 4500 BC
5450 BP 3500 BC
4450 BP 2500 BC
3450 BP 1500 BC
2450 BP 500 BC
Ancestry
Autosomal DNA
1.00
0.75
0.50
0.25
0.00
Italy_15000BP_9000BP
Anatolia_8500BP_8000BP
RussiaNW_11000BP_8000BP
Steppe_5000BP_4300BP
+ Possibly contaminated
* Low coverage (< 0.05)
Sex
XY
XX
Y-Chromosome haplotypes
I2
R1b
I1
Q1
L1
I
R1a
Mitochondrial haplotypes
U
H
K
R
J
N
T
V
W
Phenotypes
Eye color
1.00
0.75
0.50
0.25
0.00
+ Possibly contaminated
# Low GP
^ Low coverage (< 0.1)
Hair color
1.00
0.75
0.50
0.25
0.00
Height
2.5
0.0
−2.5
−5.0
Isotopes
⁸⁷Sr/ ⁸⁶Sr
0.714
0.712
0.710
δ¹³C
−10.0
−12.5
−15.0
−17.5
−20.0
−22.5
δ¹⁵N
15.0
12.5
10.0
7.5
Vegetation
Pollen based vegetation cover
100
75
50
25
0
6500 BP
6000 BP
5500 BP
5000 BP
4500 BP
Crops
Grassland
Secondary forest
Primary Forest

Fig 4. Genetic, dietary and environmental shifts in Denmark through time. Two dramatic population turnovers are evident from chronologically-sorted multiproxy data representing 100 Danish Stone Age and early Bronze Age skeletons sequenced in this study. The figure shows concomitant changes in several investigated parameters including (from the top) admixture proportions from non-imputed autosomal genome-wide data, Y-chromosomal and mitochondrial haplogroups, genetic phenotype predictions (based on imputed data) as well as $^{87}Sr/^{86}Sr$ and $\delta^{13}C$ and $\delta^{15}N$ isotope data as possible proxies for mobility and diet, respectively. Predicted height values represent differences (in cm) from the average height of the present-day Danish population, based on genotypes at 310 height-associated loci; probabilities for the indicated natural eye and hair colours are based on genotypes at 18 pigmentation-associated loci with grey denoting probability of intermediate eye colour (including grey, green and hazel) (Supplementary Note 3i). Lower panel shows changes in vegetation, based on pollen analyses at Lake Højby in Zealand (Supplementary Note 11). Note that this vegetation panel covers a shorter time interval than the other panels. Black vertical lines mark the first presence of Anatolian Neolithic farmer ancestry and Steppe-related ancestry, respectively.

During the Danish Mesolithic, individuals from the Maglemose, Kongemose and Ertebølle cultures displayed a remarkable genetic homogeneity across a 5,000 year transect deriving their ancestry almost exclusively from a southern European source (source: Italy_15000BP_9000BP) that later predominates in western Europe (Fig. 2). These cultural transitions occurred in genetic continuity, apparent in both autosomal and uniparental markers, which rules out demic diffusion and supports the long-held assumption of a continuum of culture and population[56–58]. Genetic predictions (see Supplementary Note 3i) indicate blue eye pigmentation with high probability in several individuals throughout the duration of the Mesolithic, consistent with previous findings [1,13,35]. In contrast, none of the analysed Mesolithic individuals display high probability of light hair pigmentation. Height predictions for Mesolithic individuals generally suggest slightly lower and/or less variable stature than in the succeeding Neolithic period. However, we caution that the relatively large genetic distance to modern individuals included in the GWAS panel produces scores that are poorly applicable to Mesolithic individuals and are dependent on the choice of GWAS filters used (see Irving-Pease et al. *submitted*[2*]). Unfortunately, only a fraction of the 100 Danish skeletons included were suitable for stature estimation by actual measurement, why these values are not reported.

Stable isotope $\delta^{13}C$ values in collagen inform on the proportion of marine versus terrestrial protein, while $\delta^{15}N$ values reflect the trophic level of protein sources[59,60]. Both the Koelbjerg Man and the second earliest human known from Denmark, (Tømmerupgårds Mose – not part of the present study; see[61]) showed more depleted dietary isotopic values, representing a lifestyle of inland hunter-fisher-gatherers of the Early Mesolithic forest. A second group consisted of coastal fisher-hunter-gatherers dating to the late half of the Maglemose epoch onwards (Supplementary Figs. S9.1 and S9.2). During this period global sea-level rise gradually changed the landscape of present-day Denmark from an interior part of the European continent to an archipelago, where all human groups had ample access to coastal resources within their annual territories. Increased $\delta^{13}C$ and $\delta^{15}N$ values imply that from the late Maglemose marine foods gradually increased in importance, to form the major supply of proteins in the Ertebølle period[61,cf. 62]. Interestingly, broadly consistent $^{87}Sr/^{86}Sr$ isotope ratios throughout the Mesolithic indicate limited longer-range mobility, in agreement with the evidence for genetic continuity reported here and modelled in previous work[63,64 Fig. 3], and/or dietary sources from homogeneous environments.

The arrival of Anatolian farmer-related ancestry at c. 5,900 BP in Denmark resulted in a population replacement with very limited genetic contribution from the local hunter-gatherers. The shift was

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[2*] E.K.I-P, A.R-M, A.I., A.P., A.F., W.B., K.G.S, .A.S.H., R.Macleod, F.D., R.A.H, T.V., H.M., A.V., L.V., A.J. Stern, G.S., A. Ramsøe, A.J. Schork, A. Rosengren, K.K., P.H.S., D.J.L., R.D., T.S.K., T.W., M.E.A., M.S., R.N., F.R., E.W., *The Selection Landscape and Genetic Legacy of Ancient Eurasians. (Submitted)*

abrupt and brought changes in all the measured parameters. It is a clear case of demic diffusion, which settles a long-standing debate concerning the neolithisation process in Denmark[9,46,65,66], at least at a broader population level. The continuing use of coastal kitchen middens well into the Neolithic[67,68] remains, however, an enigma. It is unknown if these sites represent local remnants of Mesolithic groups that survived in partly acculturated form, or middens taken over by the newcomers. Concomitant shifts in both autosomal and uniparental genetic markers show that the migration by incoming farmers was not clearly sex-biased but more likely involved family units. Diet shifted abruptly to a dominance of terrestrial sources evidenced by $\delta^{13}C$ values around -20 ‰ and $\delta^{15}N$ values around 10 ‰ in line with archaeological evidence that domesticated crops and animals were now providing the main supply of proteins (Supplementary Note 9). Isotope values remained stable at these levels throughout the following periods, although with somewhat greater variation after c. 4,500 BP. However, five Neolithic and Early Bronze Age individuals have $\delta^{13}C$ and $\delta^{15}N$ values indicating intake of high trophic marine food. This is most pronouncedly seen for NEO898 (Svinninge Vejle) who was one of the two aforementioned Danish Neolithic individuals displaying typical Swedish hunter-gatherer ancestry. A higher variability in $^{87}Sr/^{86}Sr$ values can be seen with the start of the Neolithic and this continues in the later periods, which suggests that the Neolithic farmers in Denmark consumed food from more diverse landscapes and/or they were more mobile than the preceding hunter-gatherers (Supplementary Note 10). The Neolithic transition also marks a considerable rise in frequency of major effect alleles associated with light hair pigmentation[69], whereas polygenic score predictions for height are generally low throughout the first millennium of the Neolithic (Funnel Beaker epoch), echoing previous findings based on a smaller set of individuals[35,70].

We do not know how the Mesolithic Ertebølle population disappeared. Some may have been isolated in small geographical pockets of brief existence and/or adapted to a Neolithic lifestyle but without contributing much genetic ancestry to subsequent generations. The most recent individual in our Danish dataset with Mesolithic WHG ancestry is “Dragsholm Man” (NEO962), dated to 5,947-5,664 cal. BP (95%) and archaeologically assigned to the Neolithic Funnel Beaker farming culture based on his grave goods[71,72]. Our data confirms a typical Neolithic diet matching the cultural affinity but contrasting his WHG ancestry. Thus, Dragsholm Man represents a local person of Mesolithic ancestry who lived in the short Mesolithic-Neolithic transition period and adopted a Neolithic culture and diet. A similar case of very late Mesolithic WHG ancestry in Denmark was observed when analysing human DNA obtained from a piece of chewed birch pitch dated to 5,858–5,661 cal. BP (95%)[73].

The earliest example of Anatolian Neolithic ancestry in our Danish dataset is observed in a bog skeleton of a female from Viksø Mose (NEO601) dated to 5,896-5,718 cal. BP (95%) (and hence potentially contemporaneous with Dragsholm Man) whereas the most recent Danish individual showing Anatolian ancestry without any Steppe-related ancestry is NEO943 from Stenderup Hage, dated to 4,818-4,415 cal. BP (95%). Using Bayesian modelling we estimate the duration between the first appearance of farmer ancestry to the first appearance of Steppe-related ancestry in Denmark to be between 876 and 1100 years (95% probability interval, Supplementary Note 8) indicating that the typical Neolithic ancestry was dominant for less than 50 generations. The arrival of steppe-related ancestry signals the rise of the Corded Ware derived cultures in Denmark (i.e. Single Grave Culture), followed by the Dagger epoch and the Bronze Age cultures. While this introduced a major new component in the Danish gene pool, it was not accompanied by apparent shifts in diet. Our complex trait predictions indicate an increase in “genetic height”, which is consistent with Steppe individuals (e.g., Yamnaya) being genetically taller on average[35]; [c.f. 70,74].

These major population turnovers were accompanied by significant environmental changes, as apparent from the high-resolution pollen diagram from Lake Højby in Northwest Zealand reconstructed using the Landscape Reconstruction Algorithm (LRA[75], Supplementary Note 11). While the LRA has previously been applied at low temporal resolution regional scale [e.g. 76,77], and at local scale to Iron Age and later pollen diagrams [e.g. 78,79], this is the first time this quantitative method is applied at local scale to a pollen record spanning the Mesolithic and Neolithic periods in Denmark. Comparison with existing pollen records show that the land cover changes demonstrated here reflect the general vegetation development in eastern Denmark, while the vegetation on the sandier soils of western Jutland stayed more open throughout the sequence (Supplementary Note 11). We find that during the Mesolithic (i.e. before c. 6,000 BP) the vegetation was dominated by primary forest trees (*Tilia, Ulmus, Quercus, Fraxinus, Alnus* etc.). The forest composition changed towards more secondary, early successional trees (*Betula* and then *Corylus*) in the earliest Neolithic, but only a minor change in the relationship between forest and open land is recorded. From c. 5,650 BP deforestation intensified, resulting in a very open grassland-dominated landscape. This open phase was short-lived, and secondary forest expanded from 5,500 to 5,000 BP, until another episode of forest clearance gave rise to an open landscape during the last part of the Funnel Beaker epoch. We thus conclude that the agricultural practice was characterised by repeated clearing of the forest with fire, followed by regrowth. This strategy changed with the onset of the Single Grave Culture, when the forest increased again, but this time dominated by primary forest trees, especially *Tilia* and *Ulmus*. This reflects the development of a more permanent division of the landscape into open grazing areas and forests. In contrast, in western Jutland this phase was characterised by large-scale opening of the landscape, presumably as a result of human impact aimed at creating pastureland[80].

Finally, we investigated the fine-scale genetic structure in southern Scandinavia after the introduction of Steppe-related ancestry using a temporal transect of 38 Late Neolithic and Early Bronze Age Danish and southern Swedish individuals. Although the overall population genomic signatures suggest genetic stability, patterns of pairwise IBD-sharing and Y-chromosome haplogroup distributions indicate at least three distinct ancestry phases during a ~1,000-year time span: i) An early stage between ~4,600 BP and 4,300 BP, where Scandinavians cluster with early CWC individuals from Eastern Europe, rich in Steppe-related ancestry and males with an R1a Y-chromosomal haplotype (Extended Data Fig. 8A, B); ii) an intermediate stage where they cluster with central and western Europeans dominated by males with distinct sub-lineages of R1b-L51 (Extended Data Fig. 8C, D; Supplementary Note 3b) and includes Danish individuals from Borreby (NEO735, 737) and Madesø (NEO752) with distinct cranial features (Supplementary Note 5); and iii) a final stage from c. 4,000 BP onwards, where a distinct cluster of Scandinavian individuals dominated by males with I1 Y-haplogroups appears (Extended Data Fig. 8E). Using individuals associated with this cluster (Scandinavia_4000BP_3000BP) as sources in supervised ancestry modelling (see "postBA", Extended Data Fig. 4), we find that it forms the predominant source for later Iron and Viking Age Scandinavians, as well as ancient European groups outside Scandinavia who have a documented Scandinavian or Germanic association (e.g., Anglo-Saxons, Goths; Extended Data Fig. 4). Y-chromosome haplogroup I1 is one of the dominant haplogroups in present-day Scandinavians, and we document its earliest occurrence in a ~4,000-year-old individual from Falköping in southern Sweden (NEO220). The rapid expansion of this haplogroup and associated genome-wide ancestry in the early Nordic Bronze Age indicates a considerable reproductive advantage of individuals associated with this cluster over the preceding groups across large parts of Scandinavia.

Hunter-gatherer resilience east of the Urals

In contrast to the significant number of ancient hunter-gatherer genomes from western Eurasia studied to date, genomic data from hunter-gatherers east of the Urals remain sparse. These regions are characterised by an early introduction of pottery from areas further east and were inhabited by complex hunter-gatherer-fisher societies with permanent and sometimes fortified settlements[81] (Supplementary Note 4).

Here, we substantially expand the knowledge on ancient Stone Age populations of this region by reporting new genomic data from 38 individuals, 28 of which date to pottery-associated hunter-gatherer contexts [e.g. 82] between 8,300-5,000 BP (Supplementary Table II).The majority of these genomes form a previously only sparsely sampled[37,83] "Neolithic Steppe" cline spanning the Siberian Forest Steppe zones of the Irtysh, Ishim, Ob, and Yenisei River basins to the Lake Baikal region (Fig. 1C; Extended Data Fig. 2A, 3E). Supervised admixture modelling (using the "deep" set of ancestry sources) revealed contributions from three major sources in these hunter gatherers from east of Urals: early West Siberian hunter-gatherer ancestry (SteppeC_8300BP_7000BP) dominated in the western Forest Steppe; Northeast Asian hunter-gatherer ancestry (Amur_7500BP) was highest at Lake Baikal; and Paleosiberian ancestry (SiberiaNE_9800BP) was observed in a cline of decreasing proportions from northern Lake Baikal westwards across the Forest Steppe[83] (Extended Data Figs. 4, 9).

We used these Neolithic hunter-gatherer clusters ("postNeol" ancestry source set, Extended Data Fig. 4) as putative source groups in more proximal admixture modelling to investigate the spatiotemporal dynamics of ancestry compositions across the Steppe and Lake Baikal after the Neolithic period. We replicate previously reported evidence for a genetic shift towards higher Forest Steppe hunter-gatherer ancestry (SteppeCE_7000BP_3600BP) in Late Neolithic and Early Bronze Age individuals (LNBA) at Lake Baikal[83,84]. However, ancestry related to this cluster is already observed at ~7,000 BP in herein-reported Neolithic hunter-gatherer individuals both at Lake Baikal (NEO199, NEO200), and along the Angara river to the north (NEO843). Both male individuals at Lake Baikal belonged to Y-chromosome haplogroup Q1, characteristic of the later LNBA groups in the same region. (Extended Data Fig. 3, 6A). Together with an estimated date of admixture of ~6,000 BP for the LNBA groups, these results suggest gene flow between hunter-gatherers of Lake Baikal and the south Siberian forest steppe regions already during the Early Neolithic. This is consistent with archaeological interpretations of contact. In this region, bifacially flaked tools first appeared near Baikal[85] from where the technique spread far to the west. We find its reminiscences in Late Neolithic archaeological complexes (Shiderty 3, Borly, Sharbakty 1, Ust-Narym, etc.) in Northern and Eastern Kazakhstan, around 6,500-6,000 BP[86,87]. Our herein-reported genomes also shed light on the genetic origins of the Early Bronze Age Okunevo culture in the Minusinsk Basin in Southern Siberia. In contrast to previous results, we find no evidence for Lake Baikal hunter-gatherer ancestry in the Okunevo[83,84], suggesting that they instead originate from a three-way mixture of two different genetic clusters of Siberian forest steppe hunter-gatherers and Steppe-related ancestry (Extended Data Fig. 4D). We date the admixture with Steppe-related ancestry to ~4,600 BP, consistent with gene flow from peoples of the Afanasievo culture that existed near Altai and Minusinsk Basin during the early eastwards' expansion of Yamnaya-related groups[1,84].

From around 3,700 BP, individuals across the Steppe and Lake Baikal regions display markedly different ancestry profiles (Fig. 3; Extended Data Fig. 4D, 9). We document a sharp increase in non-local ancestries, with only limited ancestry contributions from local hunter-gatherers. The early stages of this transition are characterised by influx of Yamnaya-related ancestry, which decays over time from its peak of ~70% in the earliest individuals. Similar to the dynamics in western Eurasia, Yamnaya-related ancestry is here correlated with GAC-related farmer ancestry (Poland_5000BP_4700BP; Extended Data Fig. 9G), recapitulating the previously documented eastward expansion of admixed Western Steppe pastoralists from the Sintashta and Andronovo complexes during the Bronze Age[1,37,88]. However, GAC-related ancestry is notably absent in individuals of the Okunevo culture, providing further support for two distinct eastward migrations of Western Steppe pastoralists during the early (Yamnaya) and later (Sintashta, Andronovo) Bronze Age. The later stages of the transition are characterised by increasing Central Asian (Turkmenistan_7000 BP_5000BP) and Northeast Asian-related (Amur_7500BP) ancestry components (Extended Data Fig. 9G). Together, these results show that deeply structured hunter-gatherer ancestry dominated the eastern Eurasian Steppe substantially longer than in western Eurasia, before successive waves of population expansions swept across the Steppe within the last 4,000 years, including a large-scale introduction of domesticated horse lineages concomitant with new equestrian equipment and spoke-wheeled chariotry[1,37,88,89].

Genetic legacy of Stone Age Europeans

We inferred distributions of Stone Age and Early Bronze Age ancestry components across modern populations by performing chromosome 'painting'[90] on UK Biobank individuals, using a pipeline adapted from GLOBETROTTER[91](Supplementary Note 3h), and admixture proportions estimated by Non-Negative Least Squares. We selected a total of 24,511 individuals of typical ancestral backgrounds from 126 countries from the UK Biobank using a custom pipeline (Supplementary Note 3g).

The various hunter-gatherer ancestries are not homogeneously distributed amongst modern populations (Fig. 5). WHG-related ancestry is highest in present-day individuals from the Baltic States, Belarus, Poland, and Russia; EHG-related ancestry is highest in Mongolia, Finland, Estonia and Central Asia; and CHG-related ancestry is maximised in countries east of the Caucasus, in Pakistan, India, Afghanistan and Iran, in accordance with previous results[92]. The CHG-related ancestry likely reflects both Caucasus hunter-gatherer and Iranian Neolithic signals, explaining the relatively high levels in south Asia[93]. Consistent with expectations[94,95], Neolithic Anatolian-related farmer ancestry is concentrated around the Mediterranean basin, with high levels in southern Europe, the Near East, and North Africa, including the Horn of Africa, but is less frequent in Northern Europe. This is in direct contrast to the Steppe-related ancestry, which is found in high levels in northern Europe, peaking in Ireland, Iceland, Norway, and Sweden, but decreases further south. There is also evidence for its spread into southern Asia. Overall, these results refine global patterns of spatial distributions of ancient ancestries amongst modern populations.

The availability of a large number of modern genomes (n=408,884) from self-identified “white” British individuals who share similar PCA backgrounds[96] allowed us to further examine the distribution of ancient ancestries at high resolution in Britain (Supplementary Note 3h). Although regional ancestry distributions differ by only a few percent, we find clear evidence of geographical heterogeneity across the United Kingdom as visualised by assigning individuals to their birth county and averaging ancestry proportions per county (Fig. 5, inset boxes). The proportion of Neolithic farmer ancestry is highest in southern and eastern England today and lower in Scotland, Wales, and Cornwall. Steppe-related ancestry is inversely distributed, peaking in the Outer Hebrides and Ireland, a pattern only previously described for Scotland[97]. This regional pattern was already evident in the Pre-Roman Iron Age and persists to the present day even though immigrating

Anglo-Saxons had relatively less Neolithic farmer ancestry than the Iron-Age population of southwest Briton (Extended Data Fig. 4). Although this Neolithic farmer/steppe-related dichotomy mirrors the modern 'Anglo-Saxon'/'Celtic' ethnic divide, its origins are older, resulting from continuous migration from a continental population relatively enhanced in Neolithic farmer ancestry, starting as early as the Late Bronze Age[98]. By measuring haplotypes from these ancestries in modern individuals, we are able to show that these patterns differentiate Wales and Cornwall as well as Scotland from England. We also found higher levels of WHG-related ancestry in central and Northern England. These results demonstrate clear ancestry differences within an 'ethnic group' (white British) traditionally considered relatively homogenous, which highlights the need to account for subtle population structure when using resources such as the UK Biobank genomes.

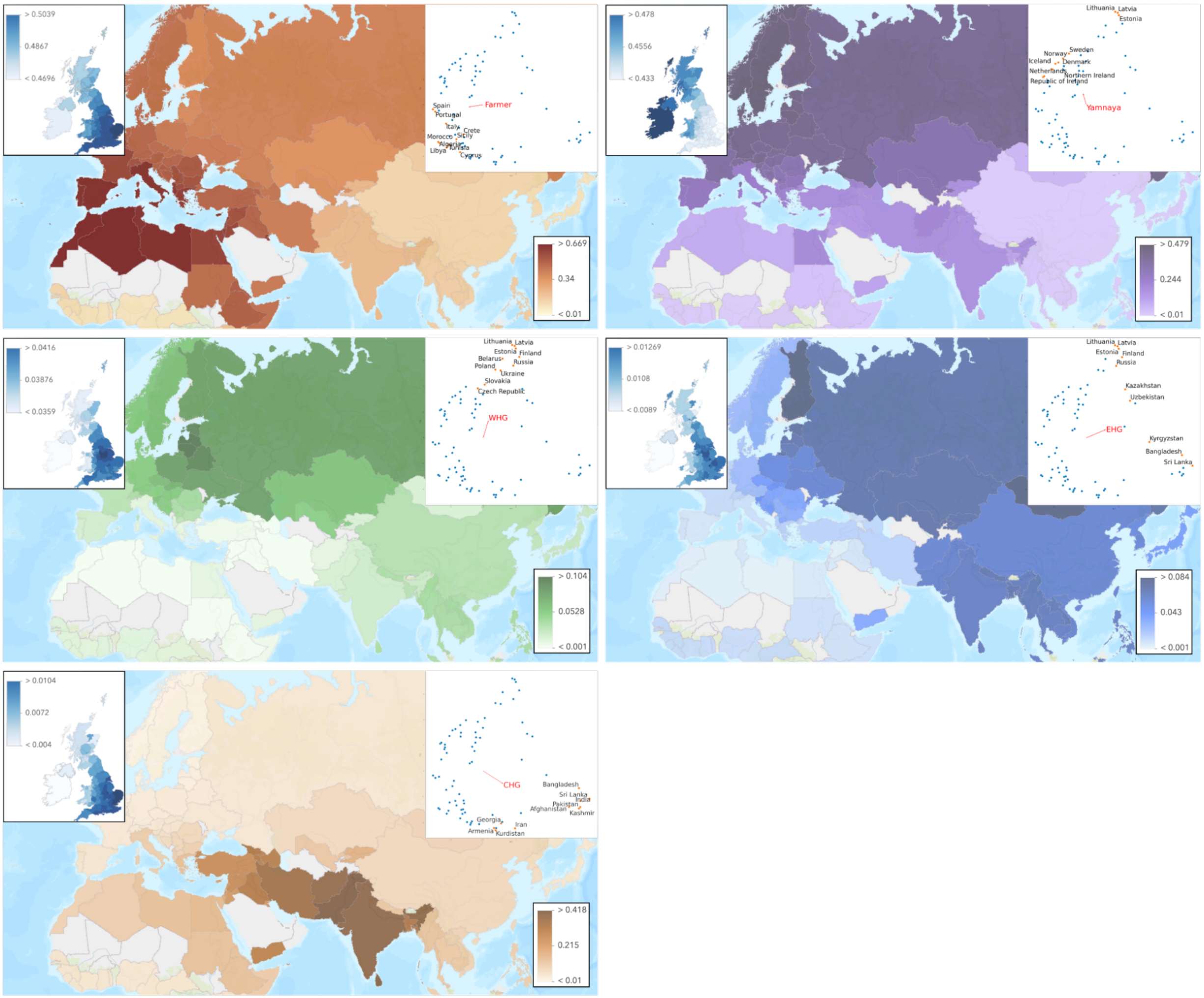


Fig 5. The genetic legacy of Stone Age ancestry in modern populations.
From top left clockwise: Neolithic Farmer, Yamnaya, Caucasus hunter-gatherer, Eastern hunter-gatherer, Western hunter-gatherer. Panels show average admixture proportion in modern individuals per country estimated using NNLS (large maps), average per county within the UK (top left insert), and PCA (PC2 vs PC1) of admixture proportions, with the top 10 highest countries by admixture fraction labelled and PCA loadings for that ancestry.

Sociocultural insights

We used patterns of pairwise IBD sharing between individuals and runs of homozygosity (ROH) within individuals (measured as the fraction of the genome within a run of homozygosity f(ROH)) to examine our data for temporal shifts in relatedness within genetic clusters. Both measures show clear trends of a reduction of within-cluster relatedness over time, in both western and eastern Eurasia (Fig. 6). This pattern is consistent with a scenario of increasing effective population sizes during this period[99]. Nevertheless, we observe notable differences in temporal relatedness patterns between western and eastern Eurasia, mirroring the wider difference in population dynamics discussed above. In the west, within-group relatedness changes substantially during the Neolithic transition (~9,000 to ~6,000 BP), where clusters of Anatolian farmer-associated individuals show overall reduced IBD sharing and f(ROH) compared to clusters of HG-associated individuals (Fig. 6A,C). In the east, genetic relatedness remains high until ~4,000 BP, consistent with a much longer persistence of smaller localised hunter-gatherer groups (Fig. 6B,D).

Next, we examined the data for evidence of recent parental relatedness, by identifying individuals harbouring > 50cM of their genomes in long (>20cM) ROH segments[100]. We only detect 39 such individuals out of a total sample of 1,540 imputed ancient genomes (Fig. 6E), in line with recent results indicating that close kin mating was not common in human prehistory[31,92,100,101]. With the exception of eight ancient American individuals from the San Nicolas Islands in California[102], no obviously discernible spatiotemporal or cultural clustering was observed among the individuals with recent parental relatedness. Interestingly, an ~1,700-year-old Sarmatian individual from Temyaysovo (tem003)[103] was found homozygous for almost the entirety of chromosome 2, but without evidence of ROHs elsewhere in the genome, suggesting an ancient case of uniparental disomy. Among several noteworthy familial relationships (see Supplementary Fig. S3c.2), we report a Mesolithic father/son burial at Ertebølle (NEO568/NEO569), as well as a Mesolithic mother/daughter burial at Dragsholm (NEO732/NEO733).

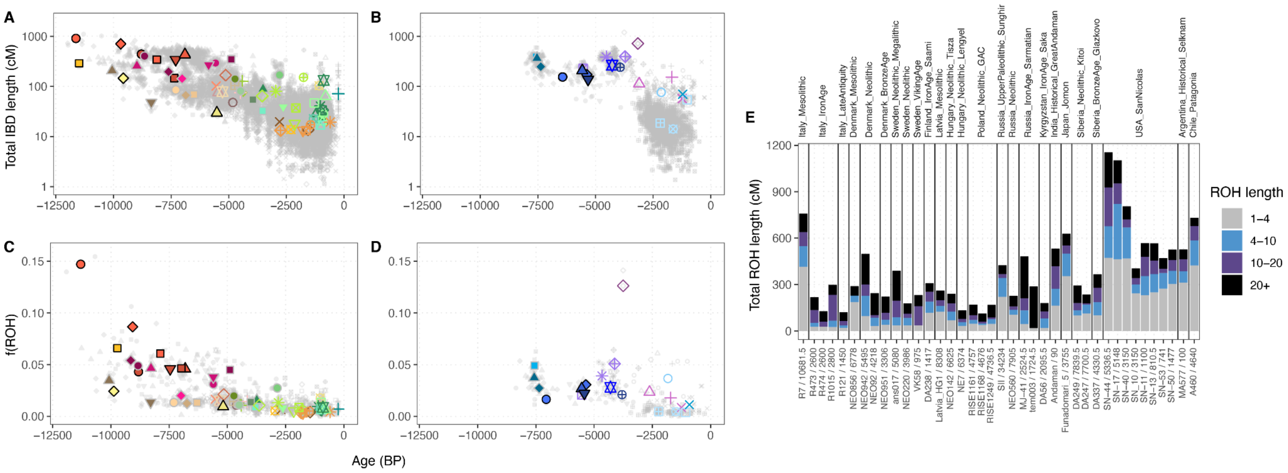


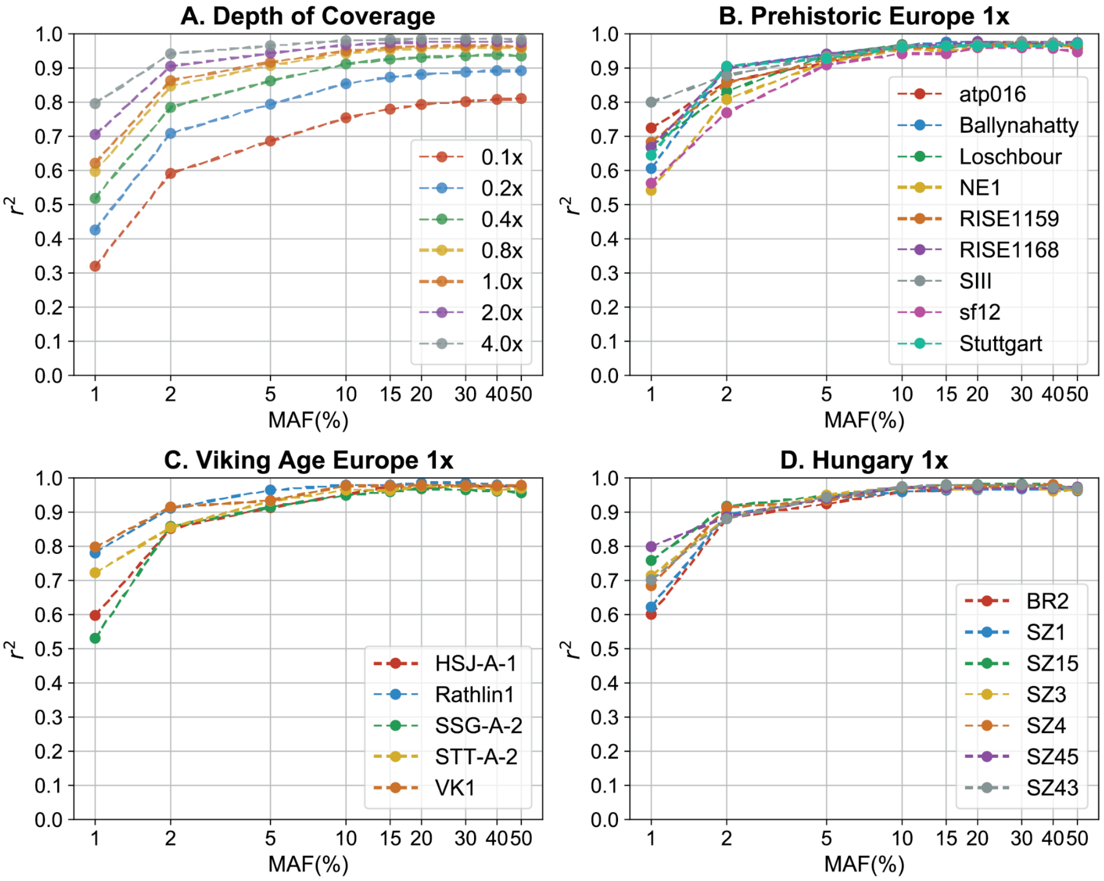
Fig 6. Patterns of co-ancestry. (A)-(D) Panels show within-cluster genetic relatedness over time, measured either as the total length of genomic segments shared IBD between individuals (A, B) or the proportion of individual genomes found in a run of homozygosity f(ROH) (C,D). Results for both measures are shown separately for individuals from western (A, C) or eastern Eurasia (B, D). Small grey dots indicate estimates for individual pairs (A, B) or individuals (C, D), with larger coloured symbols indicating median values within genetic clusters. (E) Distribution of ROH lengths for 39 individuals with evidence for recent parental relatedness (>50 cM total in ROHs > 20 cM).

Conclusion

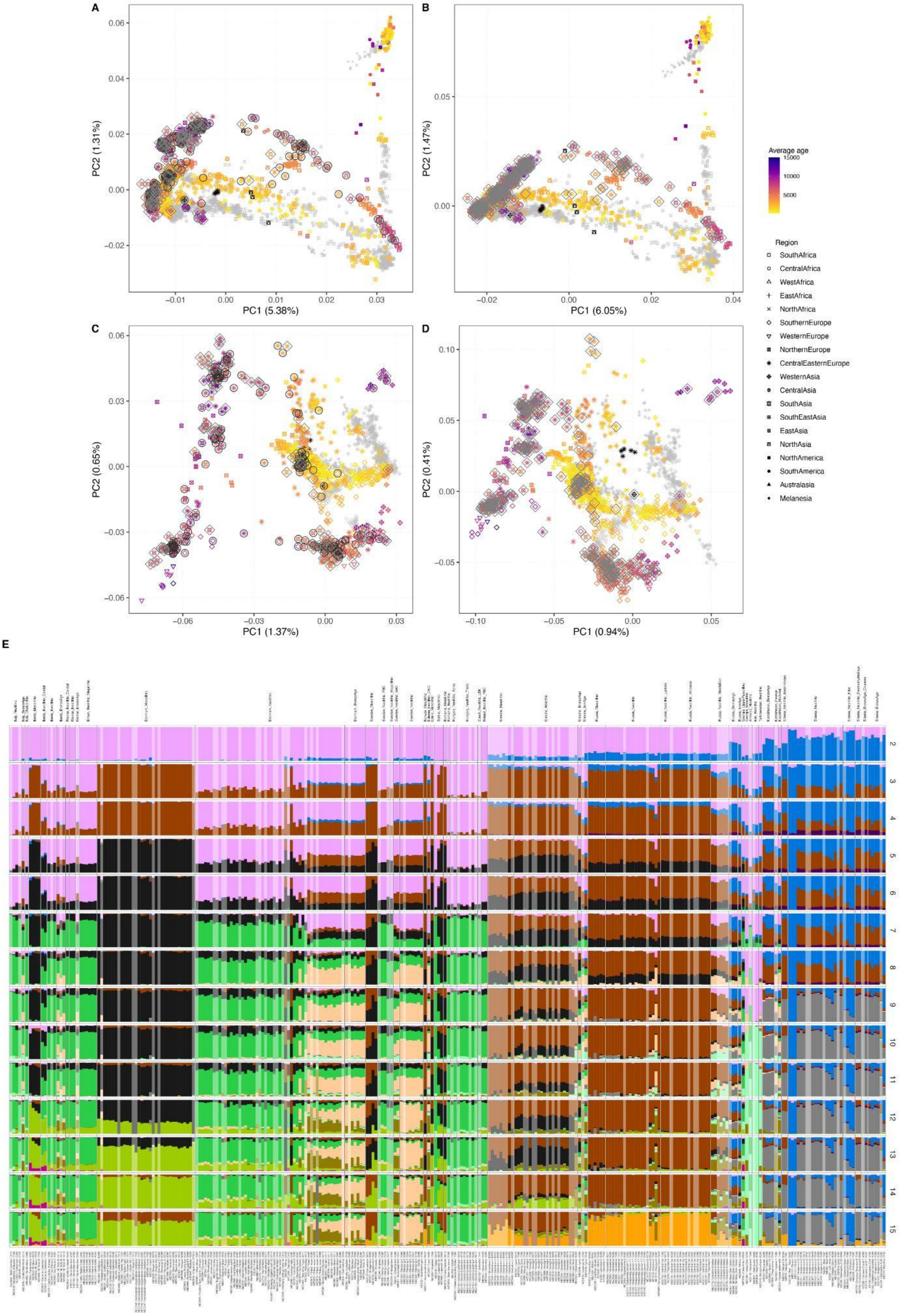
The large-scale nature of our genomic study allows for fundamental insights into the population dynamics of Stone Age Eurasia in unprecedented detail. We demonstrate the existence of a clear east-west genetic division extending from the Black Sea to the Baltic, mirroring observations from

Stone Age material culture, and persisting over several millennia. By imputing >1600 ancient genomes we recover the full scale of ancient genetic diversity in prehistoric Eurasia and show that previous estimates have been severely underestimated. We show that the genetic impact of the Neolithic transition was highly distinct east and west of this boundary. We identify a hitherto unknown source of ancestry in hunter-gatherers from the Middle Don region contributing ancestry to the Yamnaya pastoralists, and we document how the later spread of steppe-related ancestry into Europe was very rapid and mediated through people showing admixture related to the Anatolian farmer-associated Globular Amphora Culture. Finally, we report two near-complete population replacements in Denmark within just 1,000 years, concomitantly with major changes in material culture, ruling out cultural diffusion as a main driver and settling generation-long archaeological debates. Our study reveals that the devil lies in the detail: although the migrations during the Stone Age were crucial in shaping contemporary Eurasian genetic diversity as argued in recent years [104–106], their mode and impact varied extensively across time and space.

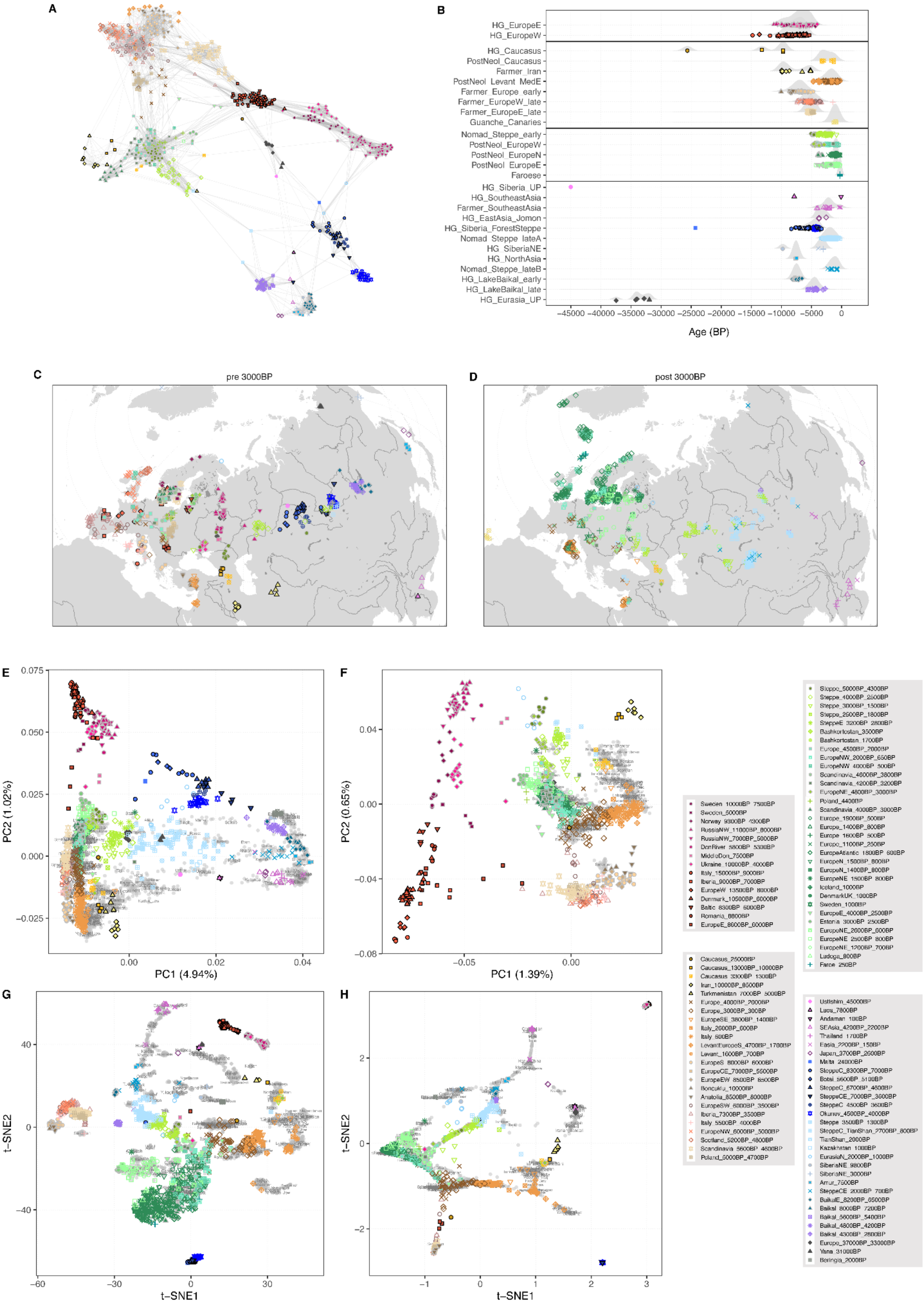
Extended Data Figures



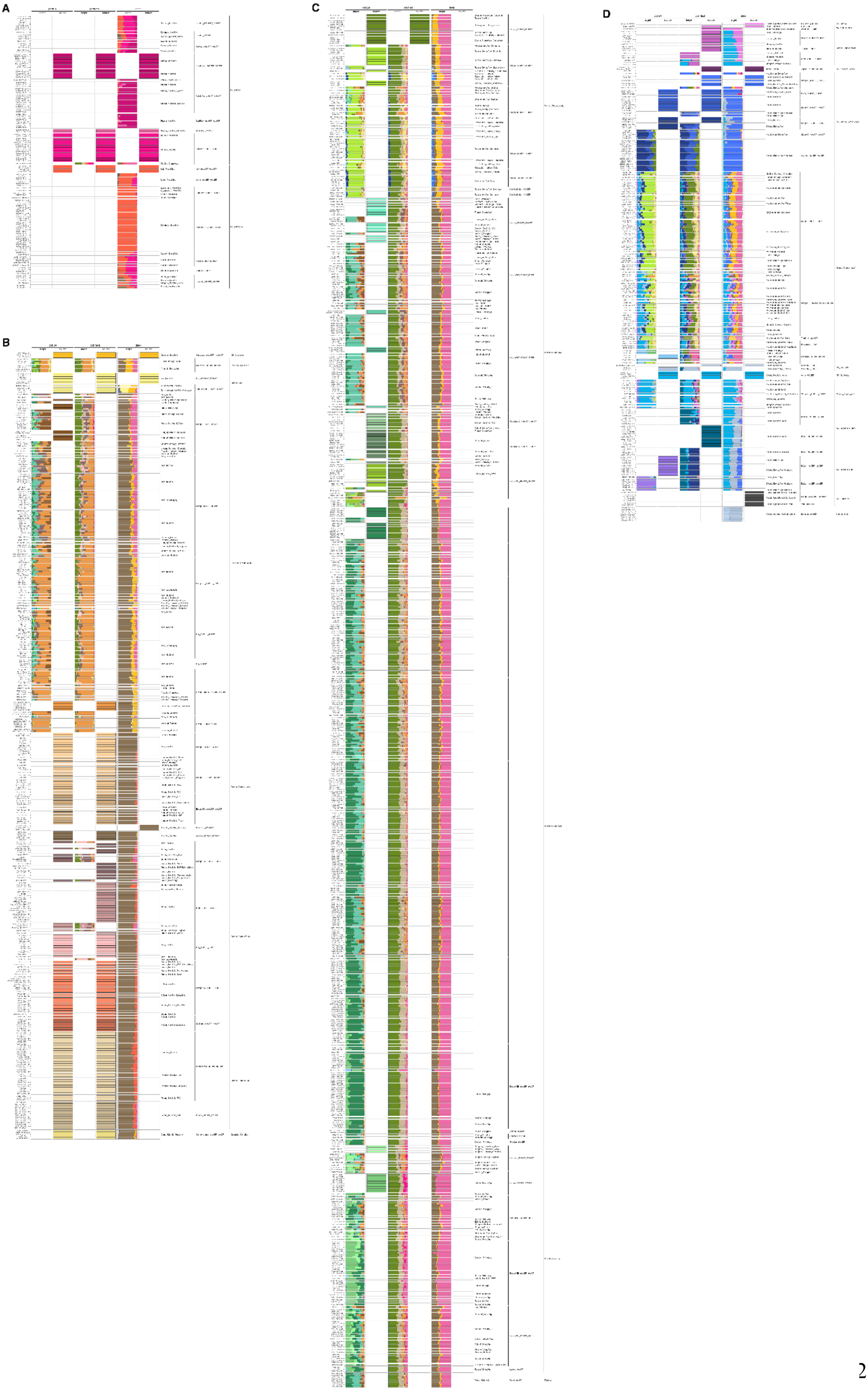
Extended Data Fig.1. Imputation accuracy of aDNA. Panel A shows imputation accuracy across the 42 high-coverage ancient genomes when downsampled to lower depth of coverage values. Panels B-D show imputation accuracy for 1X depth of coverage across 21 high-coverage ancient European genomes. In panels A-D, imputation accuracy is shown as the squared Pearson correlation between imputed and true genotype dosages as a function of minor allele frequency of the target variant sites.


A
PC1 (5.38%)
PC2 (1.31%)
B
PC1 (6.05%)
PC2 (1.47%)
C
PC1 (1.37%)
PC2 (0.65%)
D
PC1 (0.94%)
PC2 (0.41%)
Average age
15000
10000
5000
Region
SouthAfrica
CentralAfrica
WestAfrica
EastAfrica
NorthAfrica
SouthernEurope
WesternEurope
NorthernEurope
CentralEasternEurope
WesternAsia
CentralAsia
SouthAsia
SouthEastAsia
EastAsia
NorthAsia
NorthAmerica
SouthAmerica
Australasia
Melanesia
E
2
3
4
5
6
7
8
9
10
11
12
13
14
15

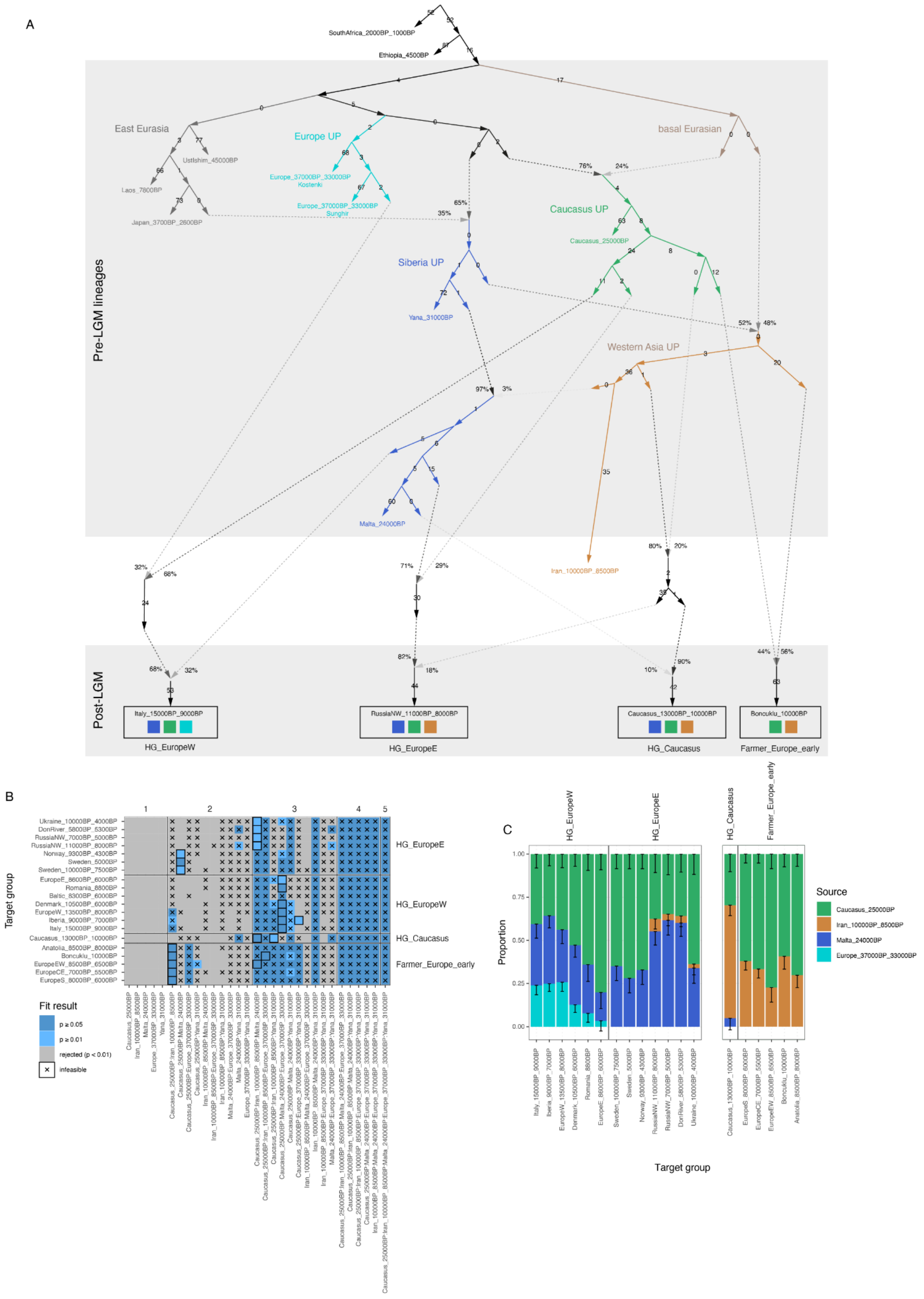
Extended Data Fig. 2. Genetic structure of the 317 herein-reported ancient genomes. (A)-(D) Principal component analysis of 3,316 modern and ancient individuals from Eurasia, Oceania and the Americas (A, B), as well as restricted to 2,126 individuals from western Eurasia (west of Urals) (C, D). Shown are analyses with principal components inferred either using both modern and imputed ancient genomes passing all filters, and projecting low coverage ancient genomes (A, C); or only modern genomes and projecting all ancient genomes (B, D). Ancient genomes sequenced in this study are indicated either with black circles (imputed genomes) or grey diamonds (projected genomes). (E) Model-based clustering results using ADMIXTURE for 284 newly reported genomes (excluding close relatives and individuals flagged for possible contamination). Results shown are based on ADMIXTURE runs from K=2 to K=15 on 1,584 ancient individuals. Low-coverage individuals represented by pseudo-haploid genotypes are indicated with alpha transparency.


A
B
HG_EuropeE
HG_EuropeW
HG_Caucasus
PostNeol_Caucasus
Farmer_Iran
PostNeol_Levant_MedE
Farmer_Europe_early
Farmer_EuropeW_late
Farmer_EuropeE_late
Guanche_Canaries
Nomad_Steppe_early
PostNeol_EuropeW
PostNeol_EuropeN
PostNeol_EuropeE
Faroese
HG_Siberia_UP
HG_SoutheastAsia
Farmer_SoutheastAsia
HG_EastAsia_Jomon
HG_Siberia_ForestSteppe
Nomad_Steppe_lateA
HG_SiberiaNE
HG_NorthAsia
Nomad_Steppe_lateB
HG_LakeBaikal_early
HG_LakeBaikal_late
HG_Eurasia_UP
−45000 −40000 −35000 −30000 −25000 −20000 −15000 −10000 −5000 0
Age (BP)
C
pre 3000BP
D
post 3000BP
E
0.075
0.050
0.025
0.000
−0.025
PC2 (1.02%)
0.00 0.02 0.04
PC1 (4.94%)
F
0.04
0.00
−0.04
−0.08
PC2 (0.65%)
−0.05 0.00
PC1 (1.39%)
G
40
0
−40
t−SNE2
−60 −30 0 30
t−SNE1
H
2
0
−2
t−SNE2
−1 0 1 2 3
t−SNE1
Sweden_10000BP_7500BP
Sweden_5000BP
Norway_9300BP_4300BP
RussiaNW_11000BP_8000BP
RussiaNW_7000BP_5000BP
DonRiver_5800BP_5300BP
MiddleDon_7500BP
Ukraine_10000BP_4000BP
Italy_15000BP_9000BP
Iberia_9000BP_7000BP
EuropeW_13500BP_8000BP
Denmark_10500BP_6000BP
Baltic_8300BP_6000BP
Romania_8800BP
EuropeE_8600BP_6000BP
Caucasus_25000BP
Caucasus_13000BP_10000BP
Caucasus_3300BP_1300BP
Iran_10000BP_8500BP
Turkmenistan_7000BP_5000BP
Europe_4000BP_2000BP
Europe_3000BP_300BP
EuropeSE_3800BP_1400BP
Italy_2600BP_600BP
Italy_600BP
LevantEuropeS_4700BP_1700BP
Levant_1600BP_700BP
EuropeS_8000BP_6000BP
EuropeCE_7000BP_5500BP
EuropeEW_8500BP_6500BP
Boncuklu_10000BP
Anatolia_8500BP_8000BP
EuropeSW_6000BP_3500BP
Iberia_7300BP_3500BP
Italy_5500BP_4000BP
EuropeNW_6000BP_5000BP
Scotland_5200BP_4800BP
Scandinavia_5600BP_4600BP
Poland_5000BP_4700BP
Steppe_5000BP_4300BP
Steppe_4000BP_2500BP
Steppe_3000BP_1500BP
Steppe_2500BP_1800BP
SteppeE_3200BP_2800BP
Bashkortostan_3500BP
Bashkortostan_1700BP
Europe_4500BP_2000BP
EuropeNW_2000BP_650BP
EuropeNW_4000BP_500BP
Scandinavia_4600BP_3800BP
Scandinavia_4200BP_3200BP
EuropeNE_4800BP_3000BP
Poland_4400BP
Scandinavia_4000BP_3000BP
Europe_1900BP_500BP
Europe_1400BP_800BP
Europe_1600BP_500BP
Europe_1100BP_250BP
EuropeAtlantic_1800BP_600BP
EuropeN_1500BP_800BP
EuropeN_1400BP_800BP
EuropeNE_1500BP_800BP
Iceland_1000BP
DenmarkUK_1000BP
Sweden_1000BP
EuropeE_4000BP_2500BP
Estonia_3000BP_2500BP
EuropeNE_2600BP_600BP
EuropeNE_2500BP_800BP
EuropeNE_1200BP_700BP
Ladoga_800BP
Faroe_250BP
UstIshim_45000BP
Laos_7800BP
Andaman_100BP
SEAsia_4200BP_2200BP
Thailand_1700BP
Easia_2200BP_150BP
Japan_3700BP_2600BP
Malta_24000BP
SteppeC_8300BP_7000BP
Botai_5600BP_5100BP
SteppeC_6700BP_4600BP
SteppeCE_7000BP_3600BP
SteppeC_4500BP_3600BP
Okunev_4500BP_4000BP
Steppe_3500BP_1300BP
SteppeC_TianShan_2700BP_800BP
TianShan_2000BP
Kazakhstan_1000BP
EurasiaN_2000BP_1000BP
SiberiaNE_9800BP
SiberiaNE_3000BP
Amur_7500BP
SteppeCE_2000BP_700BP
BaikalE_8200BP_6500BP
Baikal_8000BP_7200BP
Baikal_5600BP_5400BP
Baikal_4800BP_4200BP
Baikal_4300BP_2800BP
Europe_37000BP_33000BP
Yana_31000BP
Beringia_2000BP

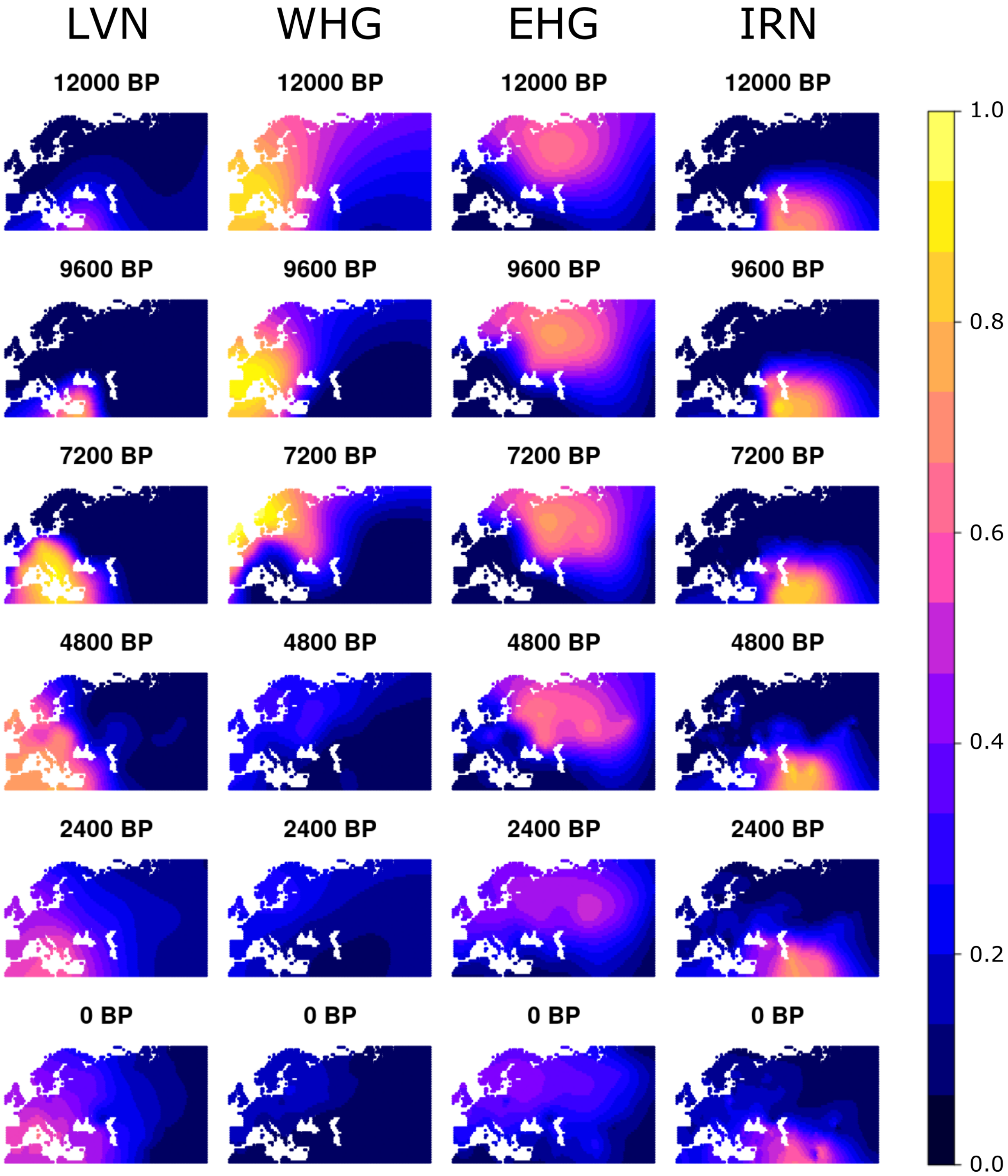
Extended Data Fig. 3. Genetic clustering of ancient individuals. Genetic clusters inferred from pairwise identity-by-descent (IBD) sharing of 1,401 ancient Eurasian individuals, indicated using colored symbols throughout (A) Network graph of pairwise IBD sharing between 596 ancient Eurasians predating 3,000 BP, highlighting within- and between-cluster relationships. Each node represents an individual, and the width of edges connecting nodes indicates the fraction of the genome shared IBD between the respective pair of individuals. Network edges were restricted to the 10 highest sharing connections for each individual, and the layout was computed using the force-directed Fruchterman-Reingold algorithm. (B) Temporal distribution of clustered individuals, grouped by broad ancestry cluster. (C), (D) Geographical distribution of clustered individuals, shown for individuals predating 3,000 BP (C) and after 3,000 BP (D). (E)-(H) Fine-scale population structure among genetic clusters. Modern individuals are shown in grey, with population labels corresponding to their median coordinates. (E), (F) PCA of 3,119 Eurasian (E) or 2,126 west Eurasian (F) individuals. (G), (H) t-distributed stochastic neighbour embedding (t-SNE) using the first 12 principal components of the all Eurasian panel (E). Shown are embeddings with two different exaggeration factors ρ, emphasising local (G, ρ=1) or global (H, ρ=30) structure.


A
B
C
D

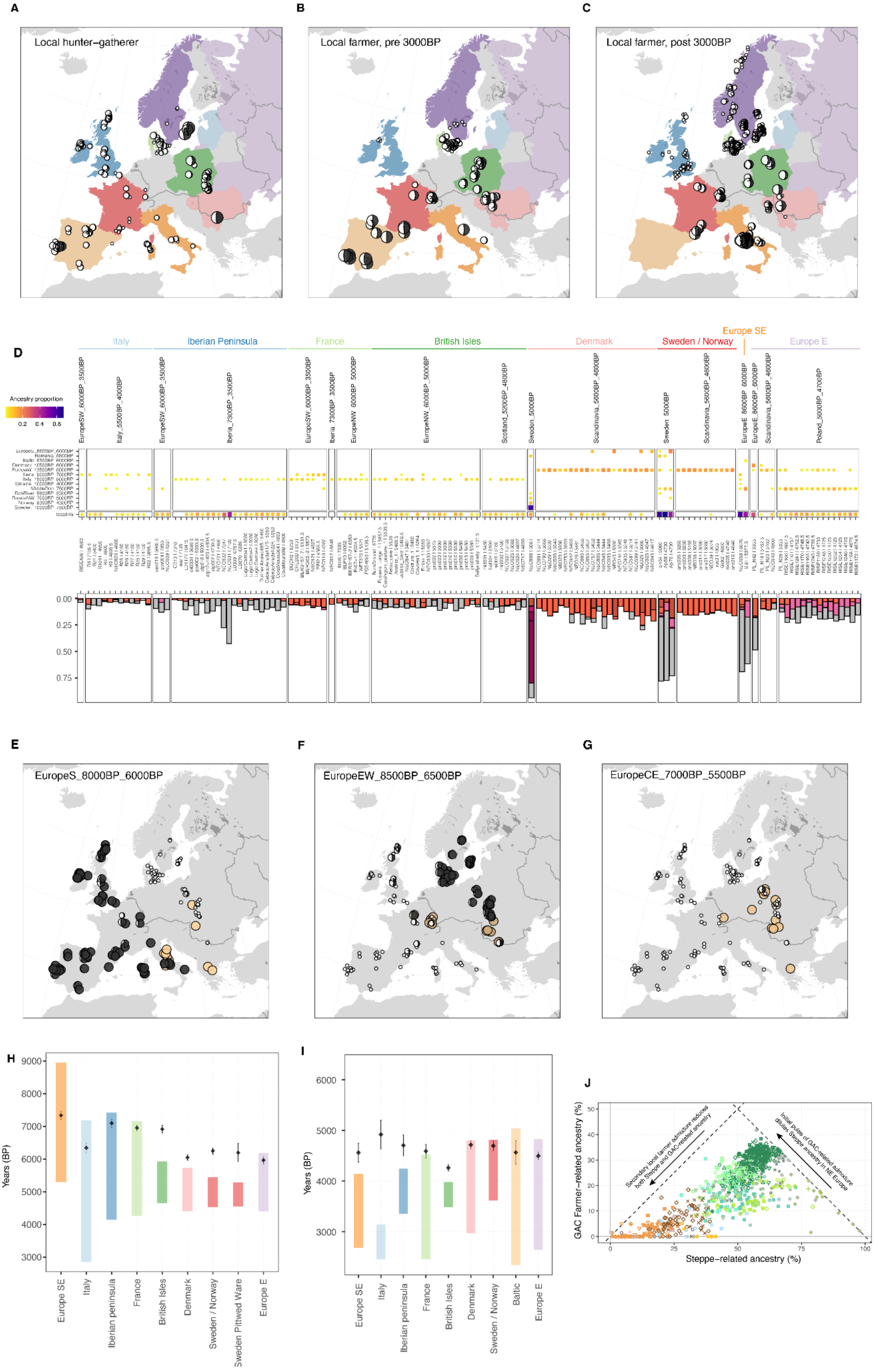
Extended Data Fig. 4. Admixture modelling. Supervised admixture modelling using non-negative least squares on IBD sharing profiles. Panels (A)-(D) show estimated ancestry proportions of four global Eurasian clusters, corresponding to (A) European hunter-gatherers before 4,000 BP; (B) Individuals from Europe and Western Asia from around 10,000 BP until historical times, including Anatolian-associated (Neolithic) farmers, Caucasus hunter-gatherers and recent individuals with genetic affinity to the Levant; (C) European individuals after 5,000 BP, as well as pastoralist groups from the Eurasian Steppe; (D) Central, East and North Asian individuals with east Eurasian genetic affinities. Column pairs show results of modelling target individuals (left columns) using three panels of increasingly distal source groups (right columns): "postBA": Bronze Age and Neolithic source groups; "postNeol", Bronze Age and later targets using Late Neolithic/early Bronze Age and earlier source groups; "deep", Mesolithic and later targets using deep ancestry source groups. Note that some clusters of individuals can be either sources or targets across distinct panels.



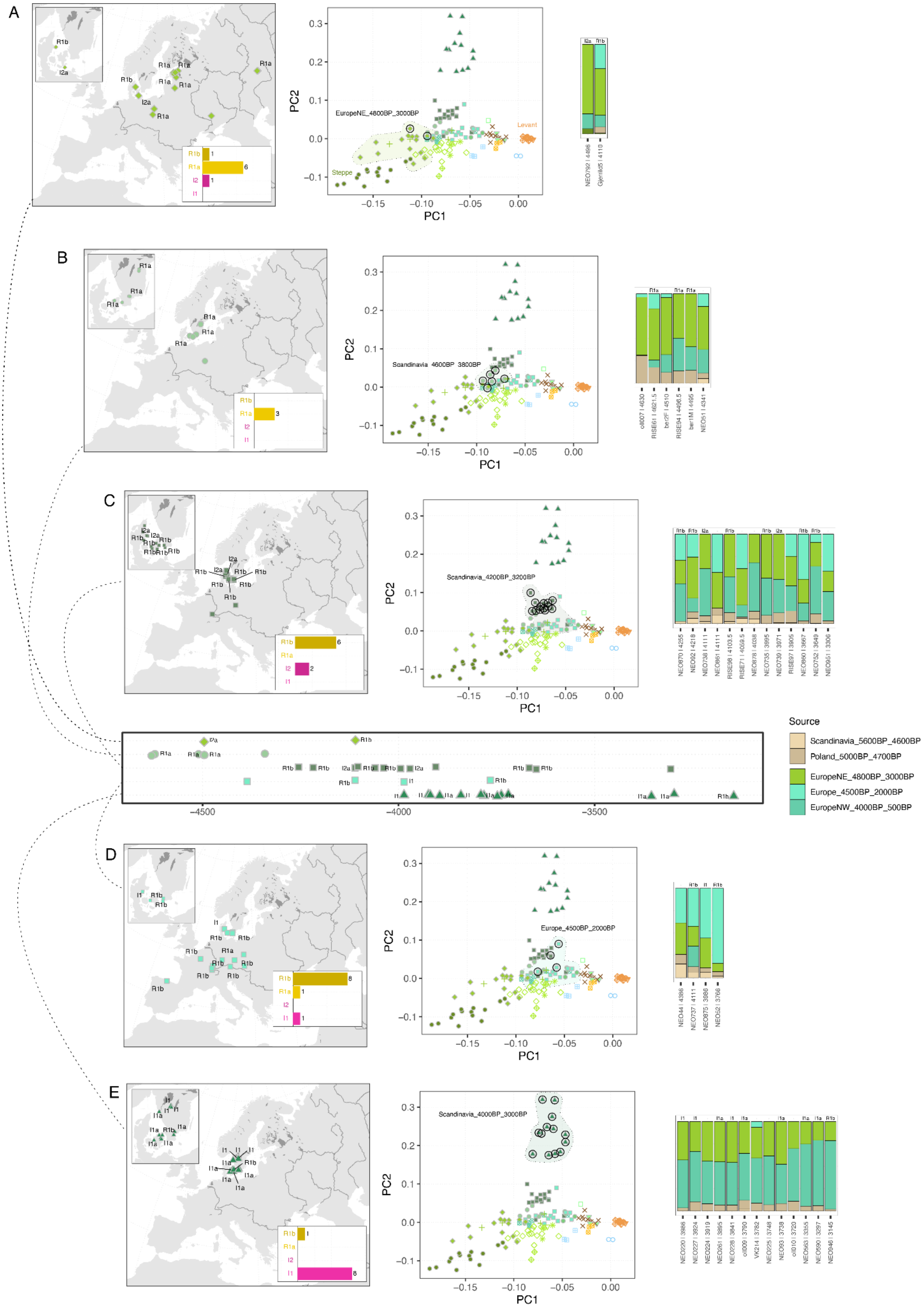
Extended Data Fig. 5. Deep Eurasian population structure. (A) Admixture graph fit relating deep Eurasian lineages predating the Last Glacial Maximum (LGM) to later West Eurasian ancestry clusters (worst |Z| = 3.65). (B) Rotating outgroup *qpAdm* analysis showing fit results for modelling post-LGM target groups as mixtures of all possible combinations involving one to five source groups. Colours of the individual matrix cells indicate the fit for a particular model, either rejected at p<0.01 (grey), 0.01≤ p<0.05 (light blue) or p ≥ 0.05 (dark blue). Cells with crosses indicate infeasible models involving negative admixture proportions. (C) Estimated ancestry proportions from *qpAdm* for post-LGM target groups inferred from the model fitting with least number of source groups.



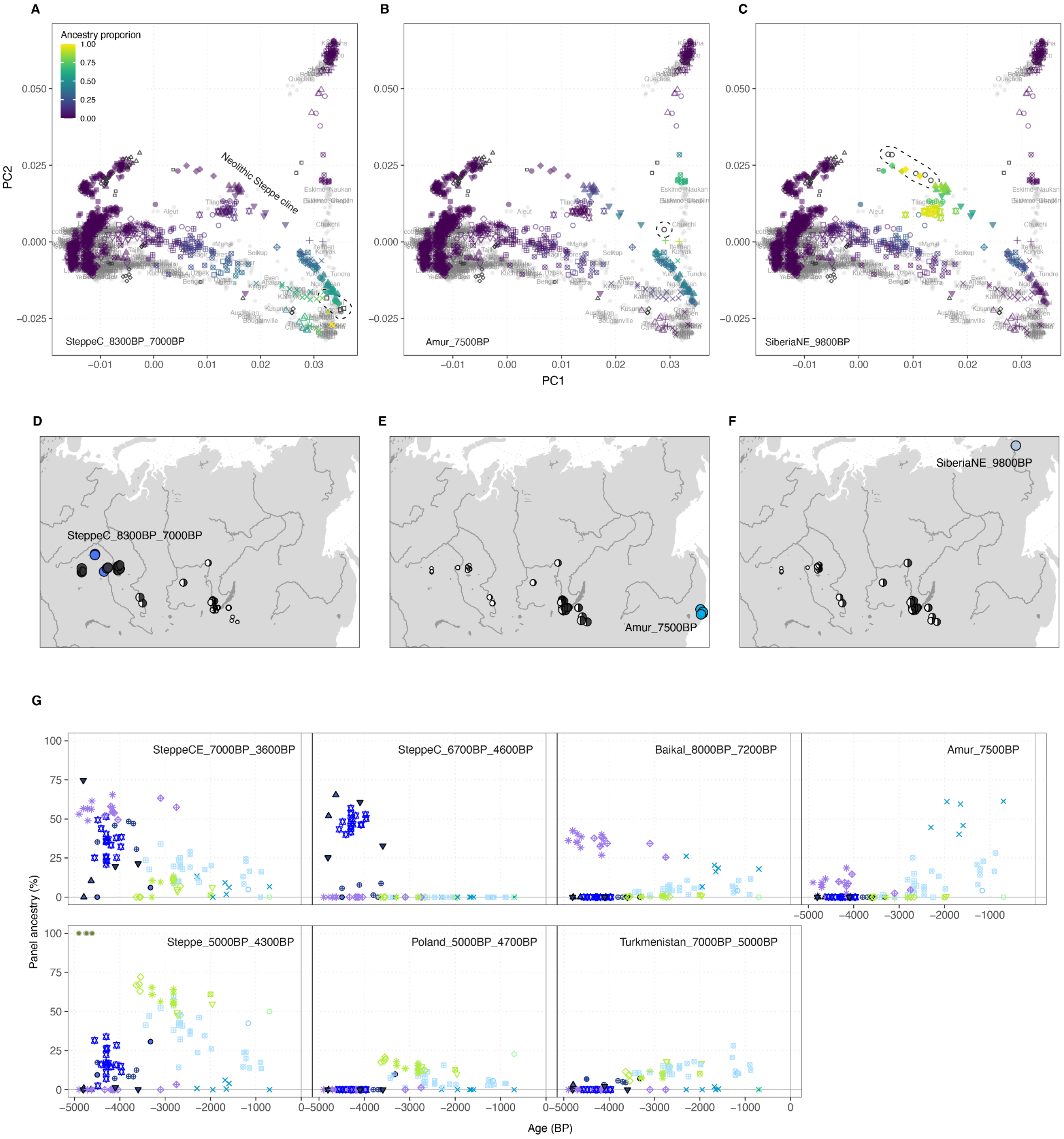
Extended Data Fig 6. Spatiotemporal kriging of four major ancestry clusters over the last 12,000 years of human history. LVN = ancestry maximised in Anatolian farmer populations. WHG = ancestry maximised in western European hunter-gatherers. EHG = ancestry maximised in eastern European hunter-gatherers. IRN = ancestry maximised in Iranian Neolithic individuals and Caucasus hunter-gatherers.


A
Local hunter−gatherer
B
Local farmer, pre 3000BP
C
Local farmer, post 3000BP
D
Italy
Iberian Peninsula
France
British Isles
Denmark
Sweden / Norway
Europe SE
Europe E
Ancestry proportion
0.2
0.4
0.6
EuropeSW_6000BP_3500BP
Italy_5500BP_4000BP
EuropeSW_6000BP_3500BP
Iberia_7300BP_3500BP
EuropeSW_6000BP_3500BP
Iberia_7300BP_3500BP
EuropeNW_6000BP_5000BP
EuropeNW_6000BP_5000BP
Scotland_5200BP_4800BP
Sweden_5000BP
Scandinavia_5600BP_4600BP
Sweden_5000BP
Scandinavia_5600BP_4600BP
EuropeE_8600BP_6000BP
EuropeE_8600BP_6000BP
Scandinavia_5600BP_4600BP
Poland_5000BP_4700BP
EuropeE_8600BP_6000BP
Romania_8800BP
Baltic_8300BP_6000BP
Denmark_10500BP_6000BP
EuropeW_13500BP_8000BP
Iberia_9000BP_7000BP
Italy_15000BP_9000BP
Ukraine_10000BP_4000BP
MiddleDon_7500BP
DonRiver_5800BP_5300BP
RussiaNW_7000BP_5000BP
Norway_8300BP_4300BP
Sweden_10000BP_7500BP
localHG
0.00
0.25
0.50
0.75
E
EuropeS_8000BP_6000BP
F
EuropeEW_8500BP_6500BP
G
EuropeCE_7000BP_5500BP
H
Years (BP)
9000
8000
7000
6000
5000
4000
3000
Europe SE
Italy
Iberian peninsula
France
British Isles
Denmark
Sweden / Norway
Sweden Pittwed Ware
Europe E
I
Years (BP)
6000
5000
4000
3000
Europe SE
Italy
Iberian peninsula
France
British Isles
Denmark
Sweden / Norway
Baltic
Europe E
J
GAC Farmer−related ancestry (%)
50
40
30
20
10
0
Steppe−related ancestry (%)
0
25
50
75
100
Secondary local farmer admixture reduces both Steppe and GAC-related ancestry
Initial pulse of GAC-related admixture dilutes Steppe ancestry in NE Europe

Extended Data Fig. 7. Genetic transitions in Europe. (A)-(C) Ancestry proportions contributed from preceding local groups to later individuals during the two major western Eurasian genetic transitions. (A) contribution to individuals with Anatolian-derived farmer ancestry from preceding local hunter-gatherer groups; (B,C) contribution to individuals with Steppe-related ancestry from preceding local Anatolian farmer-derived groups. Coloured areas in all maps indicate the geographic extent of individuals included in respective regions. (D) Composition of hunter-gatherer ancestry proportions from different source groups in individuals with farmer ancestry, shown as heatmap (top) and barplots (bottom). Grey bars represent contributions from local hunter-gatherers (E)-(G) Moon charts showing spatial distribution of estimated ancestry proportions for European farmer individuals derived from three clusters of early Neolithic European farmers (locations indicated with coloured symbols). Estimated ancestry proportions are indicated by size and amount of fill of moon symbols. (H, I) Estimated time of admixture between (H) local hunter-gatherer groups and farmers and (I) eastern European farmers with GAC-related ancestry and Steppe pastoralist groups. Black diamonds and error bars represent point estimate and standard errors of admixture time, coloured bars show temporal range of included target individuals. The time to admixture was adjusted backwards by the average age of individuals for each region. (J) Correlation between estimated proportions of Steppe-related and GAC farmer-related ancestries, across west Eurasian target individuals. Symbol shape and colour indicate the genetic cluster of respective individuals.


A
R1b
I2a
R1a
R1b
I2a
R1b 1
R1a 6
I2 1
I1
PC2
PC1
0.3
0.2
0.1
0.0
−0.1
−0.15
−0.10
−0.05
0.00
EuropeNE_4800BP_3000BP
Steppe
Levant
I2a
R1b
NEO792 | 4486
Gjerrild5 | 4110
B
R1a
R1b
R1a 3
I2
I1
Scandinavia_4600BP_3800BP
oll007 | 4630
RISE61 | 4621.5
ber2F | 4510
RISE94 | 4496.5
ber1M | 4495
NEO51 | 4341
C
R1b
I2a
R1b 6
R1a
I2 2
I1
Scandinavia_4200BP_3200BP
NEO870 | 4255
NEO92 | 4218
NEO738 | 4111
NEO861 | 4111
RISE98 | 4103.5
RISE71 | 4059.5
NEO878 | 4038
NEO735 | 3995
NEO739 | 3971
RISE97 | 3905
NEO860 | 3667
NEO752 | 3649
NEO951 | 3306
−4500
−4000
−3500
Source
Scandinavia_5600BP_4600BP
Poland_5000BP_4700BP
EuropeNE_4800BP_3000BP
Europe_4500BP_2000BP
EuropeNW_4000BP_500BP
D
I1
R1b
R1a
R1b 8
R1a 1
I2
I1 1
Europe_4500BP_2000BP
NEO44 | 4386
NEO737 | 4111
NEO875 | 3986
NEO52 | 3766
E
I1
I1a
R1b
R1b 1
R1a
I2
I1 8
Scandinavia_4000BP_3000BP
NEO220 | 3986
NEO227 | 3824
NEO224 | 3919
NEO261 | 3895
NEO228 | 3841
oll009 | 3790
VK214 | 3782
NEO225 | 3748
NEO93 | 3738
oll010 | 3720
NEO563 | 3355
NEO590 | 3297
NEO946 | 3145

Extended Data Fig. 8. Fine-scale structure in Late Neolithic Scandinavians. (A)-(E) Geographic locations and PCA based on pairwise IBD sharing (middle) of 148 European individuals predating 3,000 BP. Geographic locations are shown for 65 individuals belonging to the five genetic clusters observed in 38 ancient Scandinavians (temporal sequence shown in timeline in centre of plot). Individual assignments and frequency distribution of major Y chromosome haplogroups are indicated in maps and timeline. Plot symbols with black circles indicate the 38 Scandinavian individuals in the PCA panels. Ancestry proportions for the 38 Scandinavian individuals estimated using proximal source groups from outside Scandinavia ("postNeolScand" source set) are shown on the right of the respective cluster results.



Extended Data Fig. 9. Genetic transformations across the Eurasian Steppe. (A)-(C) Principal component analysis of modern and ancient individuals from Eurasia, Oceania and the Americas, highlighting estimated ancestry proportions from “deep” Siberian ancestry sources (individuals highlighted with dashed line). Present-day individuals are shown in grey, with population labels corresponding to their median coordinates. (D)-(E) Moon charts showing spatial distribution of estimated ancestry proportions of Siberian hunter-gatherers before 5,000 BP from “deep” Siberian ancestry sources (names and locations indicated with coloured symbols). Estimated ancestry proportions are indicated by size and amount of fill of moon symbols. (G) Timelines of ancestry proportions from “postNeol” sources in Central and North Asian ancient individuals after 5,000 BP. Symbol shape and colour indicate the genetic cluster of each individual.

Data availability

All collapsed and paired-end sequence data for novel samples sequenced in this study will be made publicly available on the European Nucleotide Archive, together with trimmed sequence alignment map files, aligned using human build GRCh37. Previously published ancient genomic data used in this study is detailed in Supplementary Table VII, and are all already publicly available. Bioarchaeological data (including Accelerator Mass Spectrometry results) are included in the online supplementary materials of this submission.

Code availability

All analyses relied upon available software which has been fully referenced in the manuscript and detailed in the relevant supplementary notes.

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Ethics declarations

Competing interests

The authors declare no competing interests.