Steppe Ancestry in western Eurasia and the spread of the Germanic Languages

Hugh McColl[1], Guus Kroonen[2,3], J. Víctor Moreno-Mayar[1], Frederik Valeur Seersholm[1], Gabriele Scorrano[1], Thomaz Pinotti[1,4], Tharsika Vimala[1], Søren M. Sindbæk[5], Per Ethelberg[6], Ralph Fyfe[7], Marie-José Gaillard[8], Hanne M. Ellegård Larsen[9], Morten Fischer Mortensen[10], Fabrice Demeter[1,11], Marie Louise S. Jørkov[12], Sophie Bergerbrant[13], Peter de Barros Damgaard[1], Morten E. Allentoft[14,1], Lasse Vinner[1], Charleen Gaunitz[1], Abigail Ramsøe[1], Isin Altinkaya[1], Rasmus Amund Henriksen[1], Evan K. Irving-Pease[1,15], Serena Sabatini[16], Anders Fischer[17,16], William Barrie[18], Andrés Ingason[19,1], Anders Rosengren[19,1], Andrew Vaughn[20], Jialu Cao[1], Jacqueline Staring[1], Jesper Stenderup[1], Fulya Eylem Yediay[21,16], Torbjörn Ahlström[22], Sofie Laurine Albris[23], Biyaslan Atabiev[24], Pernille Bangsgaard[1], Maria Giovanna Belcastro[25], Nick Card[26], Philippe Charlier[27,28], Elizaveta Chernykh[29], Torben Trier Christiansen[30], Alfredo Coppa[31], Maura De Coster[32], Sean Dexter Denham[33], Sophie Desenne[34,35], Jane Downes[26], Karin Margarita Frei[9], Olivér Gábor[36], Johan Zakarias Gårdsvoll[23], Zanette Tsigaridas Glørstad[37], Jesper Hansen[38], Stijn Heeren[39], Merete Henriksen[40], Volker Heyd[41], Mette Høj[42], Mads Kähler Holst[43], Rimantas Jankauskas[44], Henrik Janson[45], Mads Dengsø Jessen[23], Jens Winther Johannsen[46], Torkel Johansen[47], Ole Thirup Kastholm[46], Anton Kern†[48], Ruslan Khaskhanov[49], Katrine Kjær[50], Vladimir Kolosov[51], Lisette M. Kootker[32], Anne Christine Larsen[52], Thierry Lejars[53], Mette Løvschal[54,43], Niels Lynnerup[55], Yvonne Magnusson[56], Kristiina Mannermaa[57], Vyacheslav Masyakin[58], Anne Lene Melheim[37], Inga Merkyte[59], Vyacheslav Moiseyev[60], Stig Bergmann Møller[61], Erika Molnár[62], Nadja Mortensen[46], Eileen Murphy[63], Bjarne Henning Nielsen[64], Doris Pany-Kucera[65], Bettina Schulz Paulsson[45], Marcia S Ponce de León[66], Håkon Reiersen[33], Walter Reinhard[67], Antti Sajantila[68,69], Birgitte Skar[70], Vladimir Slavchev[71], Václav Smrčka[72], Lasse Sørensen[73], Georg Tiefengraber[65], Otto Christian Uldum[74], Jorge Vega[75], Daniele Vitali[76], Alexey Voloshinov[77], Sidsel Wåhlin[64,78], Holger Wendling[79,80], Anna Wessman[81], Helene Wilhelmson[82,83], Karin Wiltschke[65], João Zilhao[84], Christoph PE Zollikofer[66], Thorfinn Sand Korneliussen[1], Bruno Chaume[85], Jean-Paul Demoule[86,87], Thomas Werge[19,88], Line Olsen[1], Rasmus Nielsen[89,1], Lotte Hedeager[1], Kristian Kristiansen[1,16], Martin Sikora[1], Eske Willerslev[1,90] *

<u>Affiliations</u>

[1]Lundbeck Foundation GeoGenetics Center, Globe Institute, University of Copenhagen, Copenhagen, Denmark., [2]Leiden University Centre for Linguistics, Leiden University, Leiden, The Netherlands, [3]Department of Nordic Studies and Linguistics, University of Copenhagen, Copenhagen, Denmark, [4]Laboratório de Biodiversidade e Evolução Molecular (LBEM), Universidade Federal de Minas Gerais, Belo Horizonte, Brazil, [5]Centre for Urban Network Evolutions (UrbNet), School of Culture and Society, Aarhus University, Aarhus, Denmark, [6]Museum Sønderjylland, Arkæologi, [7]School of Geography, Earth and

Environmental Sciences, University of Plymouth UK, [8]Department of Biology and Environmental Sciences, Linnaeus University, Kalmar, Sweden, [9]National Museum of Denmark, [10]National Museum of Denmark. Environmental Archaeology and Materials Science, [11]Eco-anthropologie (EA), Dpt ABBA, Muséum national d'Histoire naturelle, CNRS, Université Paris Cité, Musée de l'Homme 17 place du Trocadéro, 75016 Paris, France, [12]Laboratory of Biological Anthropology, Globe Institute, University of Copenhagen, Denmark, [13]Department of Archaeology and Ancient History, Campus Gotland, Uppsala Univeristy, [14]Trace and Environmental DNA (TrEnD) Laboratory, School of Molecular and Life Sciences, Curtin University, Perth, Australia, [15]Section for Molecular Ecology and Evolution, Globe Institute, University of Copenhagen, Copenhagen, Denmark, [16]Department of Historical Studies, University of Gothenburg, Sweden, [17]Sealand Archaeology, Kalundborg, Denmark, [18]Department of Genetics, University of Cambridge, Cambridge, UK, [19]Institute of Biological Psychiatry, Mental Health Services, Copenhagen University Hospital, Roskilde, Denmark., [20]Center for Computational Biology, University of California Berkeley, Berkeley, California, United States of America, [21]Lundbeck Foundation GeoGenetics Center, Globe Institute, University of Copenhagen, Copenhagen, Denmark, [22]Department of Archaeology and Ancient History, Lund University, [23]National Museum of Denmark, Prehistory, Middle Ages and Renaissance, [24]Institute for Caucasus Archaeology, Russia, [25]Department of Biological, Geological and Environmental Sciences - BiGeA, University of Bologna, Via Selmi 3 40126 Bologna, Italy, [26]Archaeology Institute, University of Highlands and Islands, UK, [27]Laboratory Anthropology, Archaeology, Biology (LAAB), UFR of Health Sciences (UVSQ / Paris Saclay University), 2 avenue de la source de la Bièvre, 78180 Montigny-Le-Bretonneux, France, [28]Department of Epidemiology and Public Health, University Hospital Raymond Poincaré (APHP), Garches, France, [29]Udmurt State University, [30]The Historical Museum of Northern Jutland, [31]Department of Environmental Biology, Sapienza University of Rome, [32]Geology & Geochemistry cluster, Department of Earth Sciences, Vrije Universiteit Amsterdam, the Netherlands, [33]Museum of Archaeology, University of Stavanger, [34]Institut national de recherches archéologiques préventives, [35]UMR 8215, CNRS, [36]Janus Pannonius Muzeum,Pécs, Hungary, [37]Museum of Cultural History, University of Oslo, [38]Svendborg Museum, Denmark, [39]Vrije Universiteit Amsterdam, the Netherlands, [40]Institute of archaeology and cultural history, NTNU University museum, [41]Department of Cultures / Archaeology, University of Helsinki, Finland, [42]The Museum Organisation ROMU, Collections, [43]Moesgaard Museum, [44]Vilnius University, Lithuania, [45]Department of Historical Studies, University of Gothenburg, Gothenburg, Sweden, [46]The Museum Organisation ROMU, Archaeology, [47]NTNU University Museum, Department of Archaeology and Cultural History, [48]Natural History Museum, Vienna, [49]Complex Research Institute of the Russian Academy of Sciences, Grozny, Russia, [50]ROMU, [51]The State Hermitage Museum, [52]National Museum of Denmark, Trelleborg, [53]CNRS, Umr 8546, ENS, PSL, Paris, [54]Department of Archaeology and Heritage Studies, Aarhus University, Aarhus, Denmark, [55]Department of Forensic Medicine, University of Copenhagen, Denmark, [56]Malmö museum, 205 80 Malmö, Sweden/Regionmuseet Skåne, Box 134, 291 22 Kristianstad, [57]Department of Cultures, Archaeology, University of Helsinki, Finland, [58]National Academy of Sceinces, Ukraine, [59]Saxo-Instituttet, Copenhagen, [60]Peter the Great Museum of Anthropology and Ethnography (Kunstkamera), Russian Academy of Sciences, Universitetskaya Nab. 3, St. Petersburg, Russia, [61]Nordjyske Museer, Aalborg, Denmark, [62]Department of Biological Anthropology, University of Szeged, Hungary, [63]Archaeology and Palaeoecology, School of Natural and Built Environment, Queen's University Belfast, Northern Ireland, [64]Vesthimmerlands Museum, [65]Natural History Museum Vienna, Austria, [66]Department of Informatics, University of Zurich, [67]Staatliches Konservatoramt, Saarbruecken, Germany, [68]University of Helsinki, [69]Finnish Institute of Health and Welfare, [70]Institute of archaeology and cultural history, NTNU University Museum, Norway., [71]Museum of Archaeology, Varna, Bulgaria, [72]Institute for History of Medicine, First Faculty of Medicine, Charles University, Prague, Czech Republic, [73]The National Museum of Denmark, Prehistory, Middle Ages and Renaissance, [74]The Viking Ship Museum, Roskilde,, [75]Argea Consultores SL, Madrid, Spain, [76]Département de Histoire des Arts et Archéologie, University of Burgundy, France, [77]Institute of Archeology, Moscow, Russia, [78]Vendsyssel Historiske Museum, [79]Salzburg Museum, Austria, [80]Archäologische Staatssammlung, [81]University of Bergen, Department of Cultural History, Norway, [82]Lund University Sweden, [83]Sydsvensk arkeologi, Malmö, Sweden, [84]University of Lisbon - UNIARQ (Centro de Arqueologia da Universidade de Lisboa), Faculdade de Letras, Alameda da Universidade, 1600-214 Lisboa, Portugal, [85]UMR6298, ARTEHIS, CNRS (Centre National de la Recherche Scientifique), Dijon, France, [86]University of Paris I - Panthéon-Sorbonne, [87]UMR 8215 CNRS, [88]Lundbeck Foundation GeoGenetics Center, Globe Institute, Faculty of Health Sciences, University of Copenhagen, Copenhagen, Denmark., [89]Departments of Integrative Biology and Statistics, UC Berkeley, [90]GeoGenetics Group, Department of Zoology, University of Cambridge, Cambridge, UK

* Corresponding author; email: ewillerslev@sund.ku.dk

Summary

Germanic-speaking populations historically form an integral component of the North and Northwest European cultural configuration. According to linguistic consensus, the common ancestor of the Germanic languages, which include German, English, Frisian, Dutch as well as the Nordic languages, was spoken in Northern Europe during the Pre-Roman Iron Age. However, important questions remain concerning the earlier Bronze Age distribution of this Indo-European language branch in Scandinavia as well as the driving factors behind its Late Iron Age diversification and expansion across the European continent. A key difficulty in addressing these questions are the existence of striking differences in the interpretation of the archaeological record, leading to various hypotheses of correlations with linguistic dispersals and changes in material culture. Moreover, these interpretations have been difficult to assess using genomics due to limited ancient genomes and the difficulty in differentiating closely related populations. Here we integrate multidisciplinary evidence from population genomics, historical sources, archaeology and linguistics to offer a fully revised model for the origins and spread of Germanic languages and for the formation of the genomic ancestry of Germanic-speaking northern European populations, while acknowledging that coordinating archaeology, linguistics and genetics is complex and potentially controversial. We sequenced 710 ancient human genomes from western Eurasia and analysed them together with 3,940 published genomes suitable for imputing diploid genotypes. We find evidence of a previously unknown, large-scale Bronze Age migration within Scandinavia, originating in the east and becoming widespread to the west and south, thus providing a new potential driving factor for the expansion of the Germanic speech community. This East Scandinavian genetic cluster is first seen 800 years after the arrival of the Corded Ware Culture, the first Steppe-related population to emerge in Northern Europe, opening a new scenario implying a Late rather than an Middle Neolithic arrival of the Germanic language group in Scandinavia. Moreover, the non-local Hunter-Gatherer ancestry of this East Scandinavian cluster is indicative of a cross-Baltic maritime rather than a southern Scandinavian land-based entry. Later in the Iron Age around 1700 BP, we find a southward push of admixed Eastern and Southern Scandinavians into areas including Germany and the Netherlands, previously associated with Celtic speakers, mixing with local populations from the Eastern North Sea coast. During the Migration Period (1575-1200 BP), we find evidence of this structured, admixed Southern Scandinavian population representing the Western Germanic Anglo-Saxon migrations into Britain and Langobards into southern Europe. During the Migration Period, we detect a previously unknown northward migration back into Southern Scandinavia, partly replacing earlier inhabitants and forming the North Germanic-speaking Viking-Age populations of Denmark and southern Sweden, corresponding with historically attested Danes. However, the origin and character of these major changes in Scandinavia before the Viking Age remain contested. In contrast to these Western and Northern Germanic-speaking populations, we find the Wielbark population from Poland to be primarily of Eastern Scandinavian ancestry, supporting a Swedish origin for East Germanic groups. In contrast, the later cultural descendants, the Ostrogoths and Visigoths are predominantly of Southern European ancestry implying the adoption of Gothic culture. Together, these results highlight the use of archaeology, linguistics and genetics as distinct but complementary lines of evidence.

Introduction

The ~5000 BP spread of Steppe-related ancestry is widely acknowledged as a likely *terminus post quem* for the spread of the Indo-European language family to Europe at large [1,2]. In Northern Europe, the Germanic languages, including German, Dutch, Frisian, English as well as the Nordic languages, constitute one of the dominant components of the historically known linguistic landscape, next to Balto-Slavic and Finno-Saamic. Here, the archaeological Corded Ware culture, including the Battle Axe and Single Grave cultures, as well as the Bell Beaker culture have been proposed as vectors for the introduction of Germanic languages [3–7]. However, a significant time gap of 2~3 millennia exists between these first waves of Steppe-related ancestry (c. 5000 - 4500 BP) and the appearance of the oldest Germanic runic writings in the first centuries CE [8]. Given the current lack of data, it cannot therefore be excluded that undocumented demographic changes during this intervening period shaped Northern Europe's linguistic landscape over the past 4,000 - 4,500 years [9]. During and especially before the Bronze Age, little is known about the distribution of the predecessor of the Germanic languages, at which stage it is referred to as Palaeo-Germanic [10]. Lexical borrowing from Celtic [11] and into Finno-Saamic [12,13] is estimated to have occurred from the Late Bronze Age (3050 - 2500 BP), demonstrating its geographic position relative to these linguistic groups. However, in the absence of other linguistic evidence, the timing of the arrival of Palaeo-Germanic in Scandinavia as well as its trajectory from the Indo-European homeland still remains elusive [14–16].

The northern European Iron Age (~2800 - 1575 BP) and the Migration Period (~1575 - 1200 BP) are characterised by a series of revolutionary transitions: the 'democratisation' of metallurgy through ease of access to iron [17], the rise and fall of the Western Roman Empire [18] and the subsequent 'barbarian' invasions into and within Europe [19–21]. A series of large-scale violent events dominated the political scene and were associated with recruiting warriors from a large and mixed origin [22]. These events coincided with pervasive linguistic shifts, which are still reflected in the present-day European linguistic landscape. Here, for the first time we link these dramatic and contested changes with genetic evidence to determine if they were linked to population movements in northern Europe. Around the middle of the 3rd millennium BP, Palaeo-Germanic saw the effects of a set of defining sound changes, by which it developed into Proto-Germanic, the most recent common ancestor of all Germanic descendant languages [10,23,24]. The Proto-Germanic speech community is assumed to have existed in Southern Scandinavia and Northern Germany throughout the Pre-Roman Iron Age (2500 - 1950 BP) [25,26], with the likely cultural sources being the Nordic Iron Age and the Jastorf culture [16,27]. From the end of the Pre-Roman Iron Age, Proto-Germanic language continuum split into East, North and West Germanic, the latter two likely forming a subclade [28–31]. The process coincided with multiple phases of expansion towards the south related to the fall of the Western Roman Empire, ultimately affecting the major civilizational centres of the Mediterranean in the Migration Period [32].

Of the East Germanic-speaking groups, the Goths were prominent actors in Late Antiquity. They settled in South-East Europe by 1850 BP [33]. Following the Hunnic invasion, some Goths entered the territories of the Roman Empire, contributing to its fall, and established two kingdoms, one in Italy and another in France and Iberia. However, the pre-Migration Period origin of the Goths is contested. Their own oral history records an exodus from Scandinavia across the Baltic Sea [34–37]. Combined with toponymical evidence [38], this resulted in theories of Sweden as the homeland for the Goths [35,36,39]. Modern scholarship, especially from the field of history, have questioned these lines of evidence, and challenged the idea of a Scandinavian origin [40,41]. In addition, archaeologists have questioned traditional interpretations of the East European Wielbark culture as a vector for the Goths [42].

Of the West Germanic-speaking groups several movements subsequent to the East Germanic expansion took place into areas previously inhabited by British Celtic and East Scandinavian populations. One such West Germanic group is the Langobards, who similarly traced their origins back to Southern Denmark or Northern Germany [43,44]. Roman author Tacitus places them around the lower Elbe in the 1st century CE, spread south through Czechia, Hungary, and eventually established a kingdom in Italy from 1350 BP. To the west, in parts of Britain, immigrating West Germanic Anglo-Saxons replaced local Celtic speaking populations. While previous studies have shown that some Goths, Langobards and Anglo-Saxons carried Scandinavian ancestry, confirming the specific origin within Scandinavia has not been possible [45–48]. Whereas the Migration Period was traditionally defined as a period of 'folk migrations' of Germanic and other tribes, recent scholarship is highly divided over the scale of these population movements as well as the authenticity of the origin stories of 'Barbarian' peoples [37,40,49–52]. Thus, the northern European origins, as well as the potential genetic impact of these peoples on their regions of settlement, remain heavily disputed.

In Scandinavia, the populations continued to speak Northwest Germanic dialects well documented in runic inscriptions [53]. During the Migration period (1575 - 1200 BP), radical changes led to the transformation of these dialects into Old Norse, the language spoken by Viking Age Scandinavians from ~1200 until 800 BP [54]. The 350 years after ~1575 BP, which encompassed this period of cultural and linguistic change, was a time of great upheaval in Western and Northern Europe. The period saw volcanic activity resulting in global decreased temperatures [55] and reduced plant growth in Scandinavia, the Justinian plague and population collapse and recovery (Supplementary Note S7.3, S7.4). To what extent the formation of Old Norse may have been linked to these phenomena remains debated.

Hitherto, genetic evidence to collate with the events described above has been lacking. In the wake of two large-scale population replacements across Europe during the Holocene, studies of ancient and modern genomes have suggested a period of relatively stable population structure since the European Bronze Age 5,000 - 3,000 BP, with a gradient of higher ancestry from Neolithic Farmers in southern Europe to higher ancestry from Bronze Age Steppe Pastoralists in Northern Europe [1,2,56]. This genetic continuity contrasts with ideas of the Iron Age and subsequent Migration Period (~2800 - 1200 BP) in Northern Europe as considered by many archaeologists, historians and linguists to be the periods that shaped modern Europe [17,18,37,57]. Migrations within Europe over the last 5,000 years would have represented interactions by much more closely related populations than the arrival of the Neolithic Farmers and Bronze Age Steppe Pastoralists, limiting the possibility of their detection in ancient DNA studies.

Recent studies have shown that with dense ancient DNA sampling, at sufficient sequencing depth for imputation (~0.1X for whole genomes), the detection of fine scale population structure in closely related ancient populations is possible [58–60]. To investigate the spread and diversification of Germanic-speaking populations, we sequenced 710 ancient genomes (Table , Supplementary Note S1A and S1B) from human populations across western Eurasia, with a focus on the northern European Iron Age and the bordering Celtic-speaking region of western Europe (Figure 1). Together with published ancient genomes from around the world, we selected samples with suitable average depth of coverage for imputation based on previous studies [59–61]. After filtering and overlapping with the wealth of publicly available SNP capture data suitable for imputation (~1X on targeted SNPs for 1240k capture), the final dataset contained 578 new and 3,939 published individuals covering 697,179 SNPs (Supplementary Note S5).

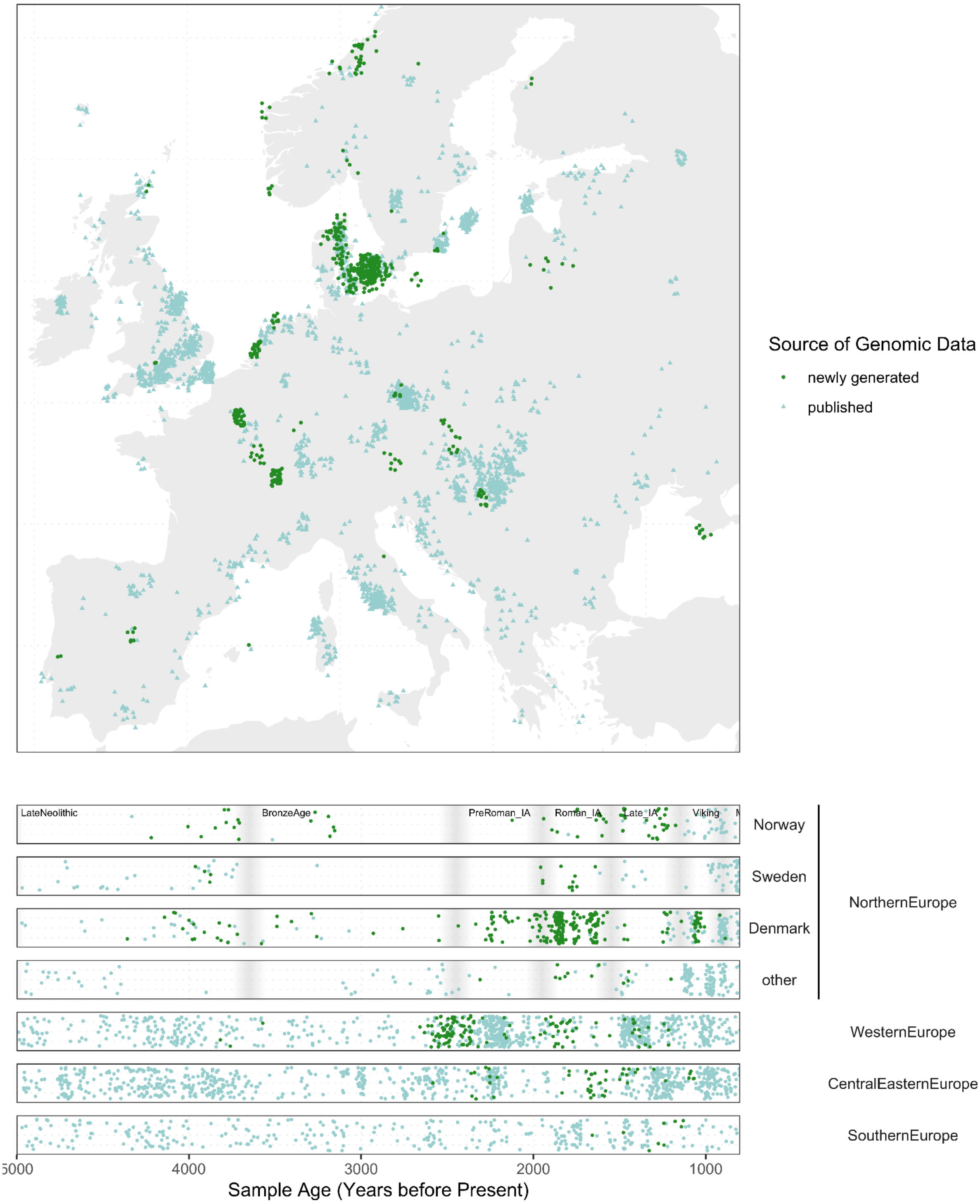


Figure 1. Geographic and temporal sampling of a subset of ancient individuals included in the final dataset, showing all newly generated (green) and published (light blue) ancient individuals from the Late Neolithic / Early Bronze Age throughout the Viking Age. Grey bars represent the boundary between historical periods denoted in the top panel.

Fine-scale resolution of Steppe ancestry in the European BA

For the previously detected major migrations in Europe, the use of f-statistics have been sufficient to confirm demographic transitions between deeply divergent populations. However here, the migrations in question here are between populations that are much more closely related, making these tools unsuitable. As such, we instead explored the genomic affinities between all the individuals in the entire dataset using the identity-by-descent (IBD) hierarchical clustering method and mixture modelling described in [60] which is particularly powerful for discerning closely related genomic ancestries.

Here, clusters are formed on the basis of the long shared genomic segments between all pairs of individuals within the dataset, rather than by proportions of the deeply diverging ancestries that they carry. This hierarchy of the clusters is informative of regional and temporal genetic structure (Figure S6.4.1.1, S6.4.1.2, S6.4.1.3). However, this clustering can be misleading in instance of admixture, exemplified by the Western Scandinavian 0_1_6 cluster. In Western Scandinavia there has been multiple waves of migration from Eastern Scandinavia, which has resulted in the earliest and latest individuals in this cluster share vary little ancestry. However, intermediate samples with varying levels of admixture form a link between the early and late individuals, giving a false impression of continuity.

To overcome this limitation, we relied on the IBD Mixture Modelling (ref) to assess the genetic structure within the clusters (Supplementary Note 6.5). In brief, we create ‘palettes’ for each individual, based on the length of IBD segments shared with all clusters in the dataset. We then define a set of individuals from specific cluster as “sources”, and model the remaining individuals in the dataset (“targets”) as a mixture of all possible source palettes, using a NNLS, similar to chromosome painting [62]. By beginning with the most distal sources relevant to Europe during the Holocene (Western Hunter Gatherers, Eastern Hunter Gatherers, Caucasus Hunter Gatherers, early Anatolian Farmers) and a series of out groups (Supplementary Note x) we find admixture proportions for Bronze Age Europeans consistent with the expectations; for Bronze Age Europe, individuals are modelled in primarily by the source populations for Yamnaya (Caucasus Hunter Gatherer - CHG, and Eastern Hunter Gatherers - EHG) and Anatolian Farmer. By including a more proximal source, Yamnaya, the ancestry previously modelled as CHG and EHG is now modelled by Yamnaya, despite all sources still being present (Figure Supp ADM). We see similar patterns when including proximal admixed European Farmers to a more basal set with the distal Anatolian Farmers and WHG source (Figure Supp ADM2), allowing us to progressively add more source clusters. When two source clusters are used that are too similar, large error bars appear and we reject the model.

From the IBD clustering, we find that the majority of European individuals from 5000 BP fall within four main clusters with a varying geographical distinction for each (Figure 2, Figure S6.4.1.1, Supplementary Note 6.4.1, Table S2). These clusters broadly contain individuals from Yamnaya-, Eastern Corded Ware-, Northern Corded Ware-, and Bell Beaker-related archaeological cultures, respectively. Notably, individuals from each cluster are placed adjacent to each other in a standard western Eurasian PCA (Figure 2, S6.1), and each cluster occupies different positions along the well established cline of Steppe - Farmer ancestry that formed in Europe from the Bronze Age.

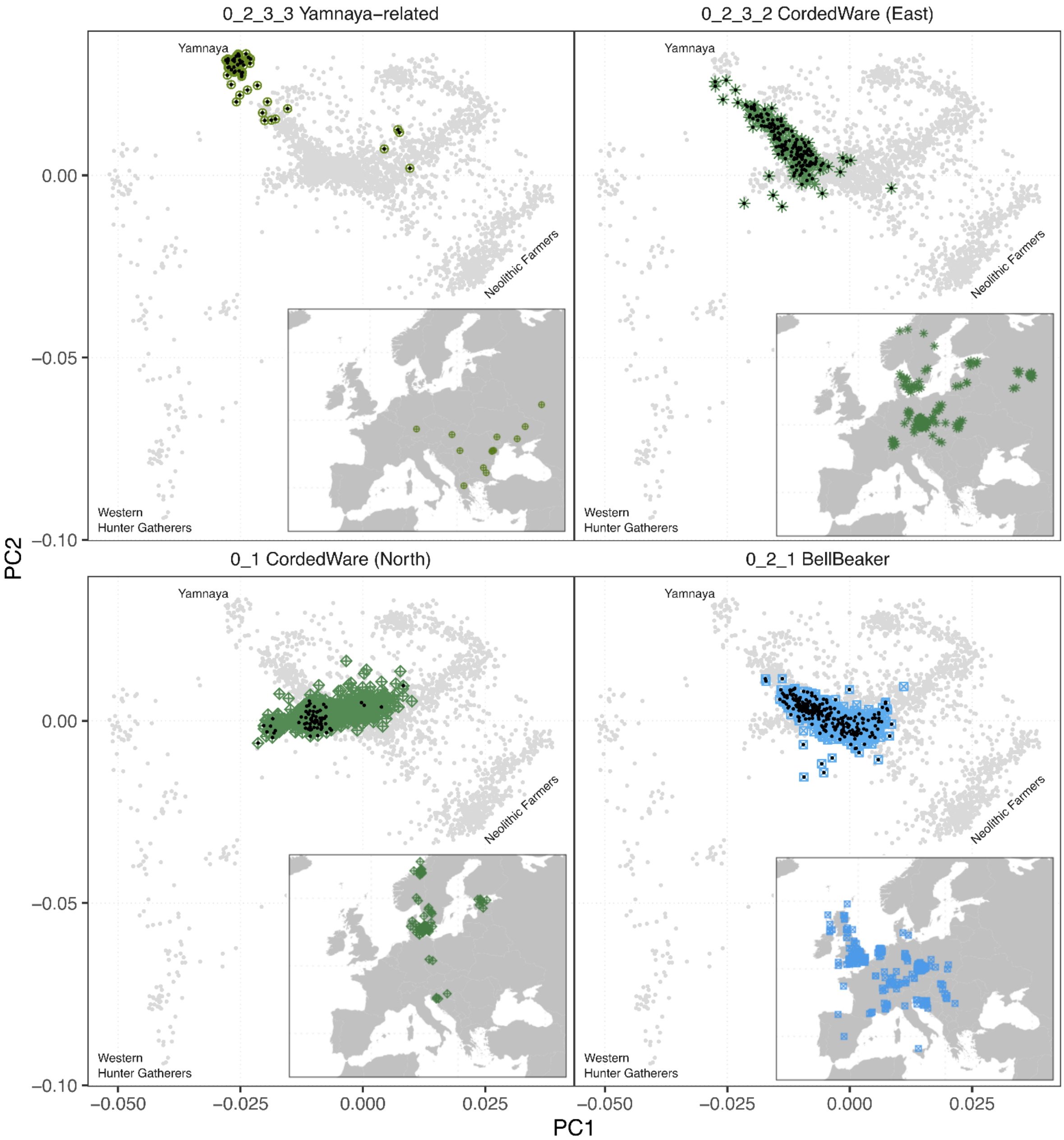
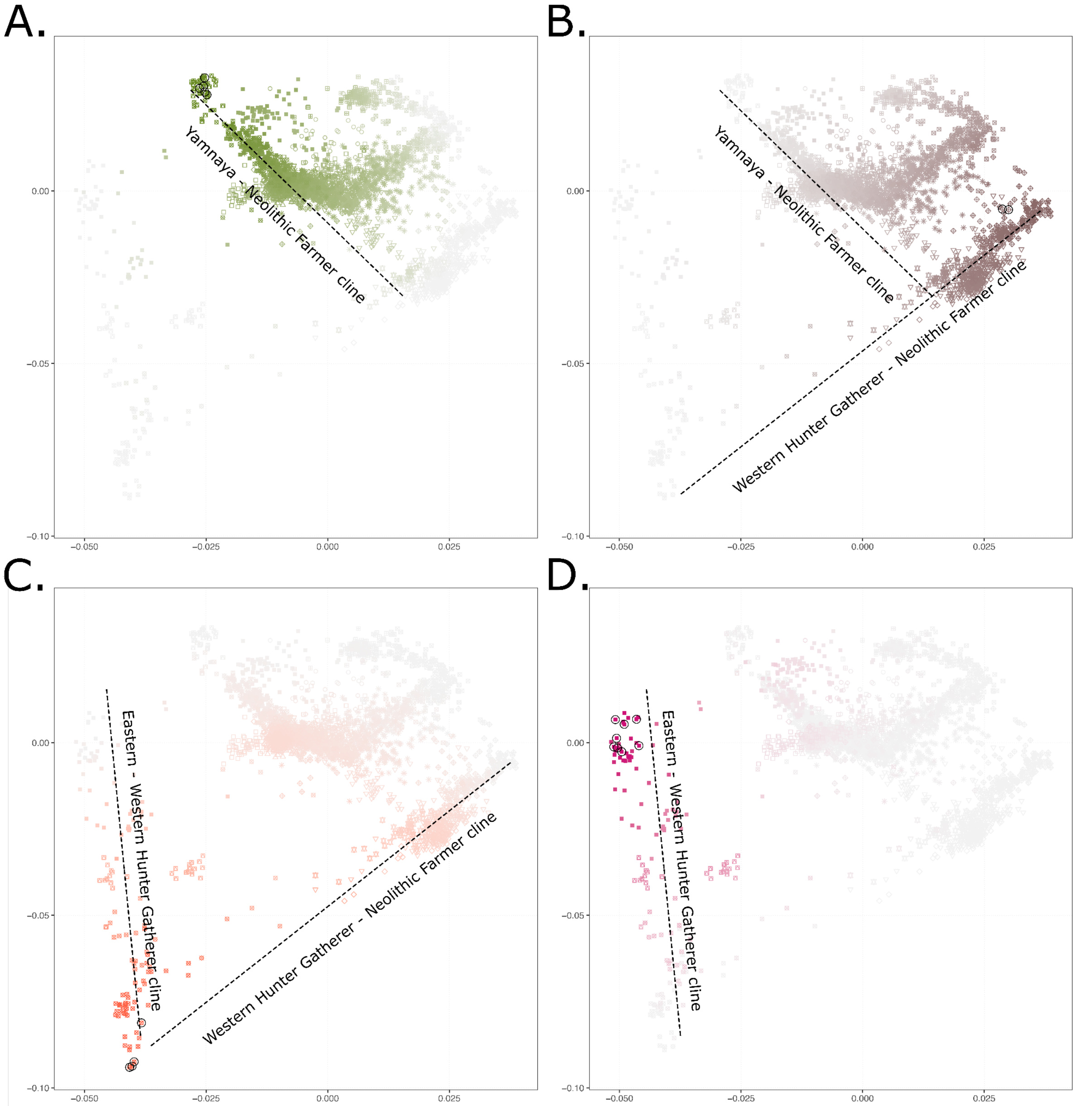


Figure 2. Ancient individuals are highlighted on the western Eurasian PCA and in geographical space for the main four steppe-related clusters. On the PCA, samples older than 2800 BP are indicated with a '.', on the map, only samples older than 2800 BP are shown.

To understand the variation between these clusters in finer detail, we undertook IBD Mixture Modelling (Supplementary Note 6.5). In Extended Data Figure 1 and Figure S6.5.2.1, we plot the admixture proportions inferred by the IBD mixture modelling (Supplementary Note S6.2, Supplementary Fig) on top of the standard western Eurasian PCA to explore the geographic apportionment of each genomic ancestry. We see the relative proportions of Steppe and Farmer-related ancestry along the Yamnaya-Neolithic Farmer cline in Extended Data Figure 1A and B, the relative proportions of Farming- and WHG-related ancestry along respective cline in Extended Data Figure 1B and C, and WHG and EHG along the respective cline in Extended Data Figure 1C and D. Furthermore, this representation of our results revealed a series of novel genetic clines and provide additional resolution to previously found clines within the densely overlapping Bronze Age PCA space.



Extended Data Figure 1. A subset of Mixture modelling results from Auxiliary set 1 displayed on the western Eurasian PCA, (Supplementary Note S6.5.2), showing the clines representing the diversity of western Eurasian Hunter-gatherers, the arrival of Neolithic Farmers in Europe admixing with the local Hunter-gatherers, and the arrival of Yamnaya-related *ancestry admixing with European Farmers. Source individuals are circled, and admixture proportions follow a cline from coloured to grey.*

We first modelled all individuals in the dataset using representatives of the Yamnaya-, Corded Ware (East)- and Bell Beaker-related clusters as sources to explore the relationship between the early individuals from each cluster and later populations in time. To explore interactions with the farming populations present in Europe during this time, we also included representatives of three clusters - the Globular Amphora Culture (GAC) of North East Europe, European Farmers, and Levant / Bronze Age Anatolians. Despite all being modelled primarily with Neolithic Farming ancestry, they are modelled with small proportions of North East European Hunter Gatherer (Latvian/Lithuanian), Western Hunter Gatherer (Italy) and Caucasus Hunter Gatherer ancestry respectively.

We find that the estimated Yamnaya admixture proportions previously shown to decrease along the cline connecting Yamnaya individuals and the dense clustering of BA diversity in Set X (Extended Data Figure 1) to now be modelled by Corded Ware source (Figure 3B). The decrease corresponds with increasing farming-related ancestry, which is here modelled as GAC (Figure 3D, Figure S6.5.1.6.). We interpret this cline to correspond to the admixture with GAC previously documented to occur prior to the arrival of steppe ancestry in Europe [60]. This cline corresponds to one of the four previously mentioned clusters, the 'Corded Ware (East)' cluster (Figure 2).

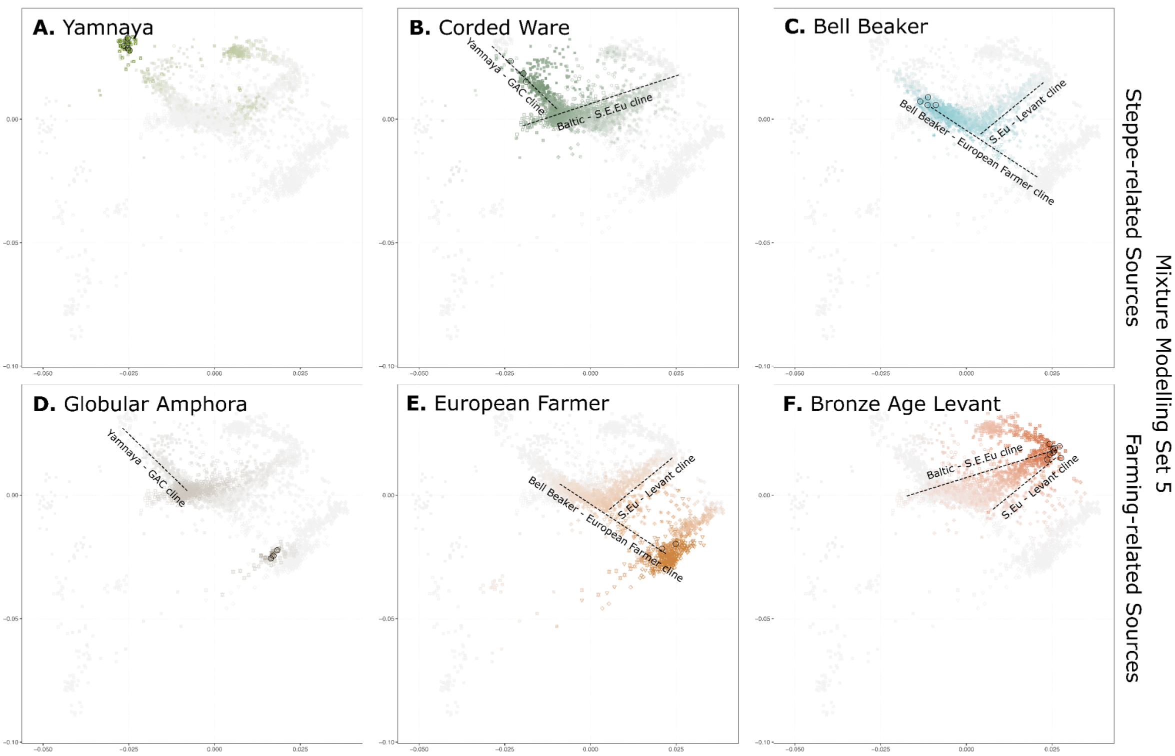


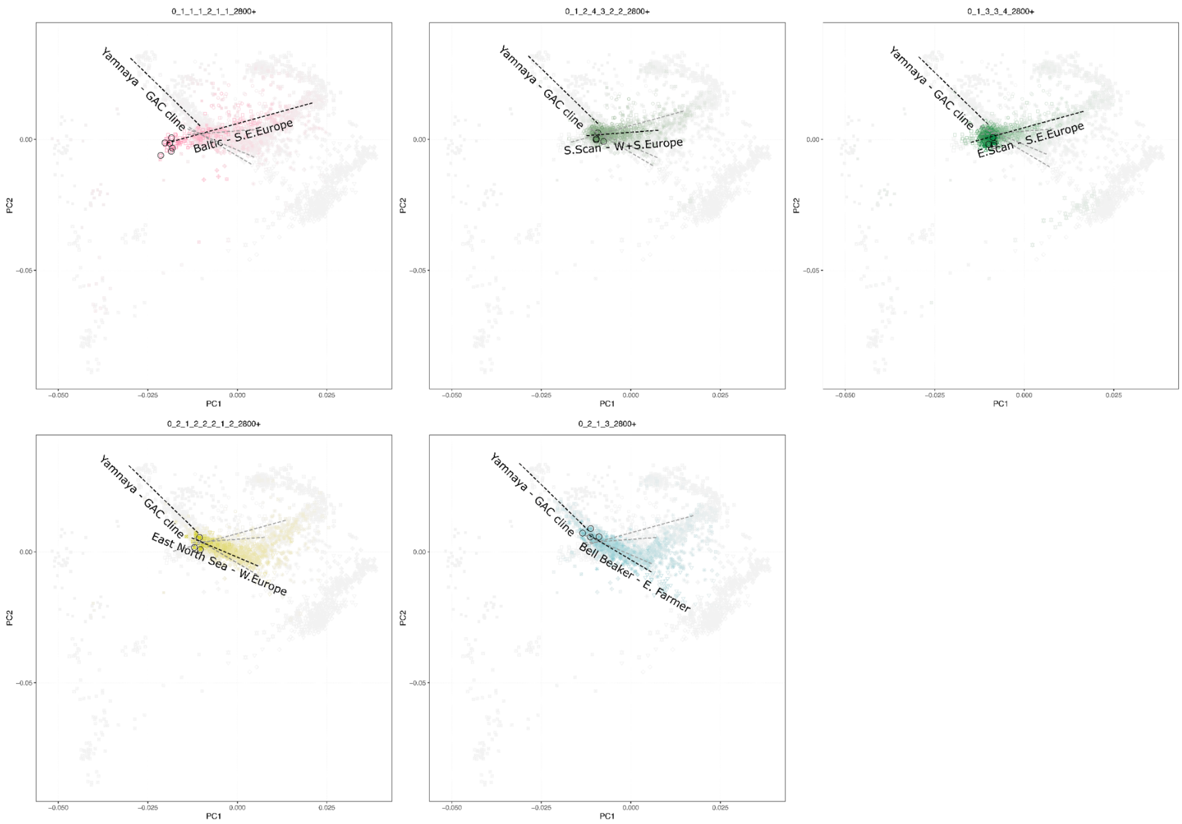
Figure 3. A subset of Mixture modelling results from Set 5 displayed on the western Eurasian PCA, (Supplementary Note S6.5). A subset of IBD Mixture Modelling results from Set 5.

Mixture Modelling Proportions for Steppe Ancestry related clusters A) Yamnaya-reltaed, B) Corded Ware-related and C) Bell Beaker-related, and Farming ancestry related clusters: D) Globular Amphora Culture-related, E) European Farmer-related and F) Levant / Bronze Age Anatolia-related. Source individuals are circled, and admixture proportions follow a cline from coloured to grey. Results shown here are a subset of Figure S6.5.1.3.

Overlapping with the admixed European tip of this Corded Ware (East) cline we find a series of additional clines, representing additional admixture between early European steppe people already carrying GAC ancestry, and additional farming-related groups in Europe. The first cline within this diversity extends from this point to the European Farmer cline. The Steppe ancestry in this cline is modelled by the Bell Beaker-related source (Figure 3C), and the additional Farming ancestry by the European Farmers (Figure 3E). We interpret this cline to represent additional admixture with Farming sources within Europe who themselves carry some Western Hunter Gatherer ancestry. This cline corresponds to another of the four previously mentioned clusters, the ‘Bell Beaker’ cluster (Figure 2). Very few individuals within Europe are modelled as ‘Yamnaya’ when the Corded Ware and Bell Beaker source clusters are included (Figure 3A).

From within the Corded Ware (East) and Bell-Beaker diversity we find an additional two clines extending to the Levant / Bronze Age Anatolians cluster (Figure 3F). The steppe ancestry of first is modelled as Bell Beaker-related, and corresponds to a sub-cluster (Figure S6.1.12) within the main Bell Beaker cluster and contains many Hallstatt and La Tene individuals (Table X), which we interpret as admixture within the range of these cultures, from France to the Black Sea. However, no suitable Bronze Age source cluster could be identified, suggesting a higher degree of continuity and complexity within the Bell Beaker related populations of this region, consistent with previous studies [63]. The steppe ancestry of the second cline is modelled as Corded Ware (East) ancestry (Figure 3B), and corresponds to the Corded Ware (North) cline (Figure 2), which we interpret as admixture between Northeast and Southeast Europe. For both clines, the additional farmer ancestry is modelled as Levant / Bronze Age Anatolian.

The second cline represents admixture with North East Europeans, who form the ‘Corded Ware (North)’ cline (Figure 2) and are modelled as Corded Ware (Figure 3B) and GAC ancestry (Figure 3D). Individuals with varying proportions of Corded Ware, Bell Beaker and Eastern Mediterranean Bronze Age ancestry are present as a cloud between the two clines. Entering this cloud at various angles we find three Corded Ware (North) sub-clusters (Eastern Scandinavian, Southern Scandinavian, Baltic) and one Bell Beaker subcluster (Eastern North Sea), which we interpret as admixture into different regions of Europe with varying proportions of the farming-related sources (Extended Data Figure 2).



Extended Data Figure 2. A subset of Mixture modelling results from Set 5 displayed on the western Eurasian PCA, (Supplementary Note S6.5), showing a admixture proportions for a series of sub-clusters from the Corded Ware and Bell Beaker clusters, revealing clines admixing with groups of varying European Farmer and Bronze Age Western Mediterranean-related ancestry. Source individuals are circled, and admixture proportions follow a cline from coloured to grey.

We find an additional cline at the other end of the Corded Ware (North) cluster, extending towards the Eastern Hunter-gatherers. At the end of this cline, we find Estonian Bronze Age individuals of the 'Baltic' sub-cluster with modelled with additional Eastern Hunter Gatherer ancestry, corresponding to their position in the PCA. Notably, the presence of this ancestry makes the Baltic sub-cluster distinct from the other Corded Ware (North) sub-clusters. Even the Bronze Age individuals with the highest Farmer ancestry from this cluster have higher Eastern Hunter Gatherer ancestry than any Bronze Age individual from the other Corded Ware (Northern) sub-clusters, despite its southern location in Croatia (Figure S6.5.1.4).

Many of the Bronze Age and later Southern European individuals cluster with Neolithic Farmers, as they only carry small amounts of Steppe Ancestry (Supplementary Note S6.4). To identify the source of Steppe Ancestry in these individuals, we applied IBD mixture modelling (Figure M, Suppl section IBD MM) with representatives of the Yamnaya, Corded Ware and Bell Beaker clusters, and find the steppe ancestry of the majority of these more southern individuals to be modelled as Bell Beaker-related ancestry (Figure 4, Source Set 5, Supplementary Note 6.5). By the late Bronze Age onwards, irrespective of clusters, the Steppe ancestry in almost all Europeans can be well modelled by Northern Corded Ware or the Bell Beaker sources (Figure 4). Almost all samples modelled primarily as Corded Ware, Bell Beaker and Yamanaya-related ancestry fall within the regions prescribed to each culture in the archaeological literature (Figure 4).

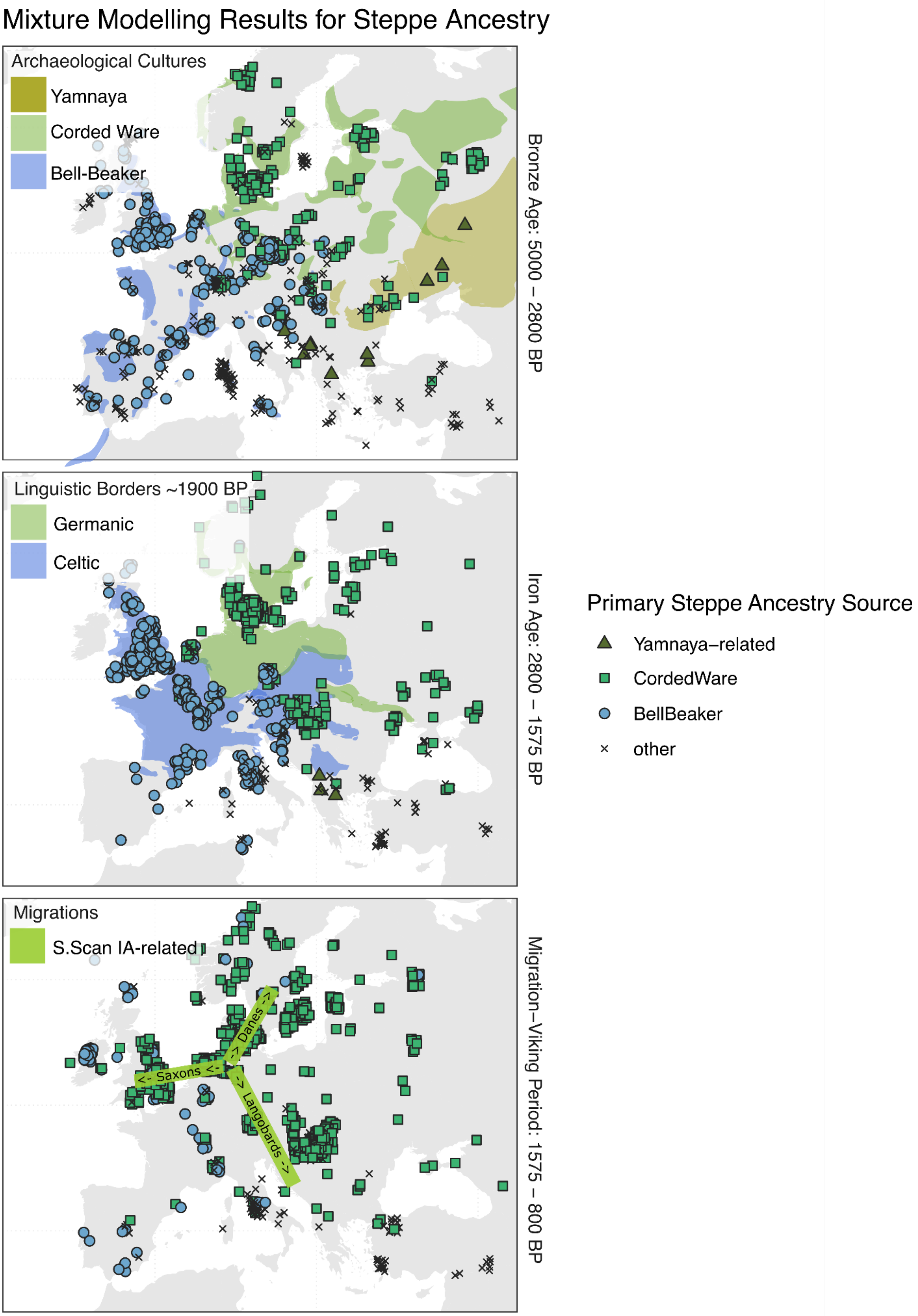


Figure 4. Geographical distributions of major Archaeological Cultures and Language Families and contemporaneous Steppe Ancestry Source. Individuals with less than 10%

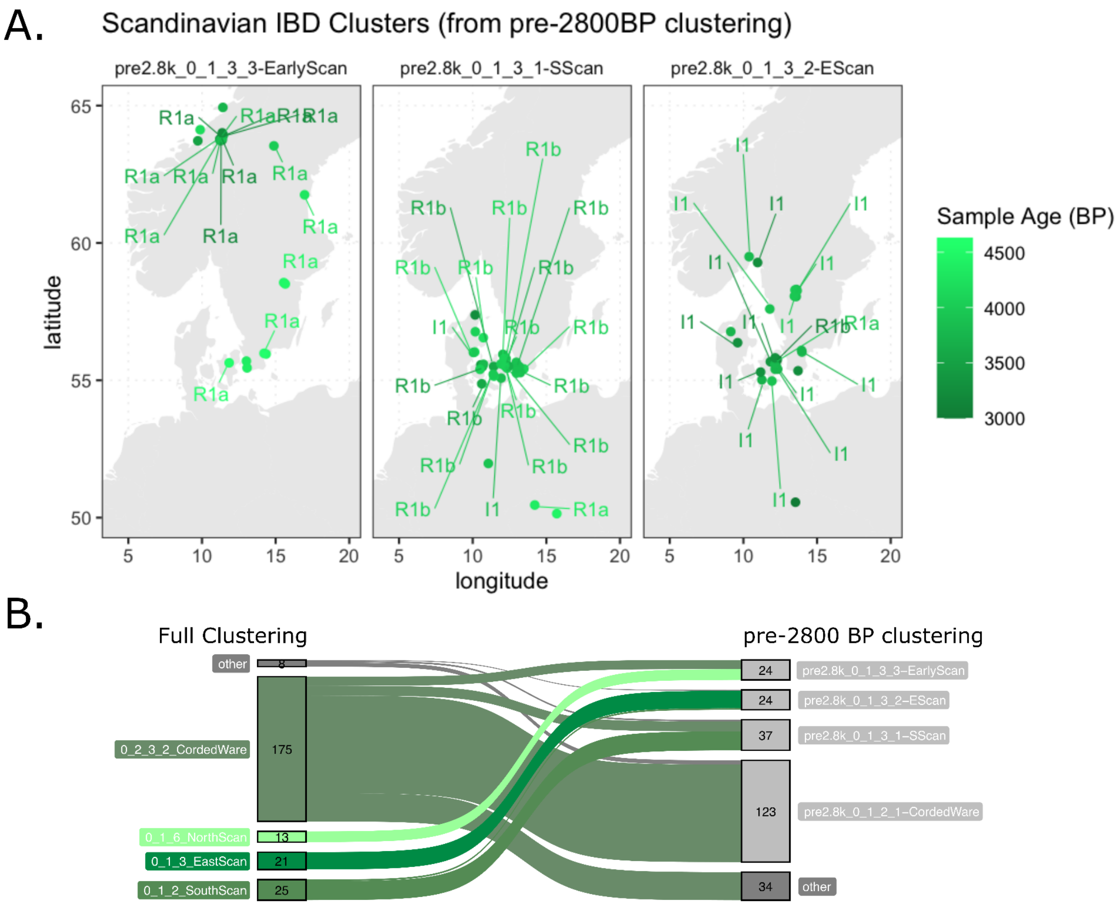
Steppe Ancestry, or less than 66% from one of the source groups are indicated with an 'x'. Archaeological boundaries modified from [64].

The border between these Corded Ware and Bell Beaker Steppe ancestries remains relatively stable throughout the Iron Age, until the fall of the Roman Empire (Figure 4). Beginning in the Migration Period, we see a southward shift of these borders. In Britain, the beginning of the Anglo-Saxon period has previously been linked to a demographic movement from continental Europe [47,65]; this transition is reflected here in the shift among individuals from the Bell Beaker to Corded Ware clusters. In addition, we see a similar but slightly earlier result for the Netherlands and Germany (Figure S6.3.1.1). The presence of Bell Beaker-related ancestry in the Norwegian Viking Period represents previously documented migrations from Celtic regions within Britain and Ireland, however here we detect these migrations as early as the Iron Age (1242 BP, Figure S6.4.2.1).

Population dynamics in Scandinavia from the LNBA to Iron Age

In order to identify whether migrations had occurred within Northern Europe, understanding the substructure within the Bronze Age populations of this region was necessary. We therefore reclustered all ancient samples older than 2800 BP, to remove the impact of later admixture between structured populations present in the Bronze Age (Supplementary Note 6.4.2, Supplementary Table x). Within Scandinavia, three clusters are apparent (Extended Data Figure 4): 1) an early Scandinavian cluster, including the oldest Swedish (Battle Axe Culture) and Danish samples and almost all Norwegians, 2) a later 'Southern Scandinavian' cluster restricted to Denmark and the southern tip of Sweden, and 3) a second later 'Eastern Scandinavian' cluster, spread across Sweden and overlapping with that of the Southern Scandinavia cluster. In all three instances, there is a very close correspondence between Y-haplogroups and the IBD clusters (Extended Data Figure 4A), largely driven by different frequencies of haplogroups I1a-DF29, R1a1a1b1a3a (R1a-Z284) and R1b1a1b1a1a1 (R1b-U106), which are all strongly associated with Scandinavian ancestry (Supplementary Note

6.4.2).



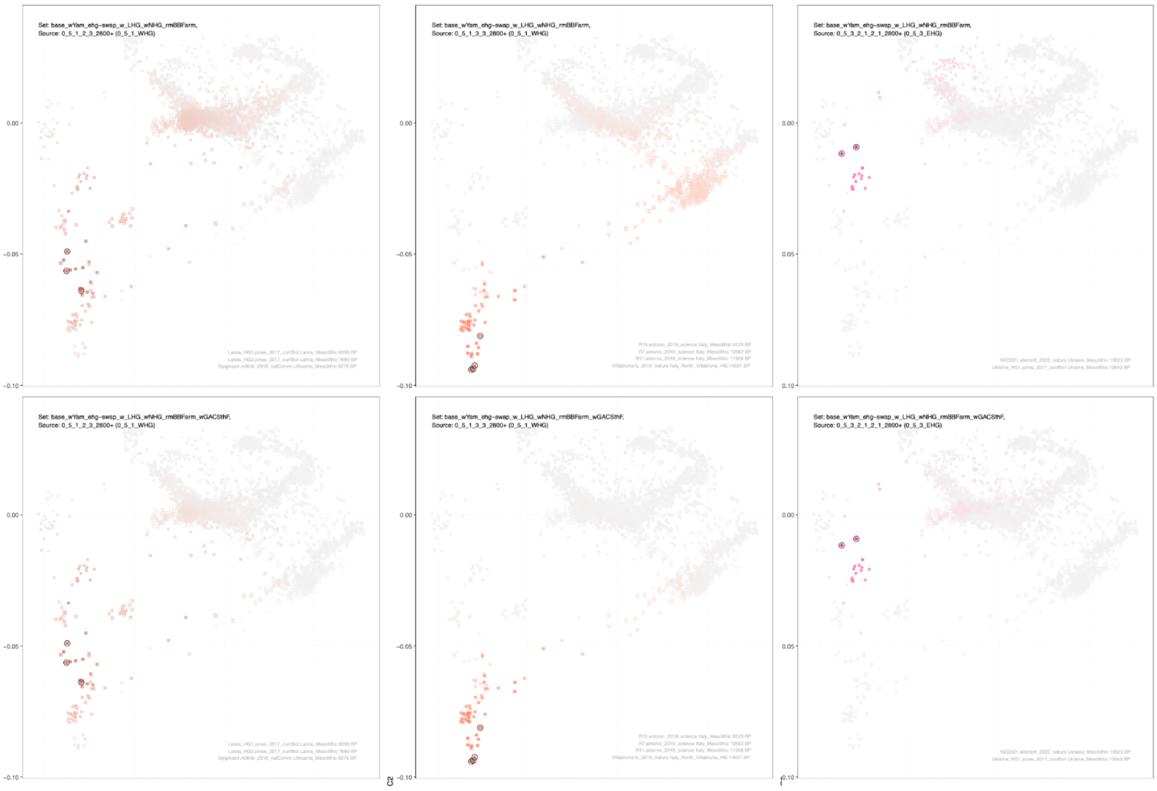
Extended Data Figure 4. (A) Geographical distribution of individuals within the Scandinavian Clusters from the pre-2800 BP re-clustering. For males with sufficient coverage, major Y-haplogroups are noted. (B) Sankey diagram showing the correspondence between the three main Scandinavian clusters and the Eastern Corded Ware clusters in the Full and pre-2800 BP clustering,

We find a large degree of overlap between the Early, Southern and Eastern Scandinavian clusters of the pre-2800 BP individuals and three subclusters detected in the original northern Corded Ware cluster: Western, Southern and Eastern Scandinavian respectively (Supplementary Extended Data Figure 4B, Supplementary Note S6.4.2). A clear difference between the two clustering runs is the reduction from 175 to 123 individuals in the Eastern Corded Ware cluster in the pre-2800 BP clustering. Many of these individuals are instead found in clusters from Northern Europe in the pre-2800 BP clustering. The pre-2800 BP Early Scandinavian cluster contains 24 individuals rather than 13 in the corresponding Western Scandinavian cluster in the full clustering. Similarly, the pre-2800 BP Southern Scandinavian cluster sees 37 individuals rather than 25. From mixture modelling results (Figure S6.4.2.4), we see that the samples that moved from the Eastern Corded Ware cluster in the original modelling are modelled with the smallest amounts of the Eastern, Western and

Southern Scandinavian that is widespread from the late Bronze Age onwards. In contrast, from 4000 BP almost all Scandinavians are well modelled as combinations of Eastern, Western and Southern Bronze Age ancestries. Combined, the results suggest a structured population in Scandinavia present from ~4600 - 4000 BP.

From the more basel set of sources (Set 1) for themixture modelling, we find Yamnaya related ancestry to be modelled as Eastern Hunter-gatherer and Caucasus Hunter-gatherer (Figure S6.5.1.10, S6.5.1.1, S6.5.1.2, S6.5.1.3), as expected [66] . However, the pre-2800 BP Eastern Scandinavians are distinct in the relatively high proportion of Eastern Hunter-gatherer ancestry, compared to Northern and Western Scandinavians (Figure S6.5.1.6, S6.5.1.4*)*. To identify the specific source of this Hunter-gatherer ancestry, we included additional Hunter-gatherer sources from the region (Norway, Sweden, Latvia and Lithuania, Denmark) together with Yamanya and find the Eastern Scandinavians hunter-gatherer ancestry modelled entirely by the Latvian HG source from across the Baltic, rather than the local Scandinavian hunter gatherers (Extended Data Figure 5, Figure S6.5.1.4, Supplementary Note S6.5.1). In contrast, the Southern and Western Scandinavians are modelled with additional Western Hunter-gatherer ancestry (Italian source clusters). These admixture results are consistent with the subtle differences in the distribution of the Scandinavian clusters in the western Eurasian PCA (Supplementary Note 6.1).

The clustering of the Eastern, Northern and Western Scandinavian sub-clusters within the Corded Ware (North Cluster) and the steppe ancestry being modelled as Corded Ware (East) points to a shared history as part of the Corded Ware expansions. However, first detection of Eastern Scandinavians 800 years after the earliest Corded Ware people in Scandinavia, and the presence of a Hunter-gatherer ancestry not local to Scandinavia points to an additional, late arrival into Scandinavia by the ancestors of the Eastern Scandinavians.



Extended Data Figure 5. Mixture Modelling sets showing the Hunter Gatherer admixture in Europe. Row 1 (set X) has no admixed source populations, showing Western Hunter Gatherer ancestry in European Farmers, North Western Hunter Gathers (Latvia, Lituania) admixture in GAC, and Eastern Hunter Gatherer along the 'Baltic' cline. The second row (set Y) includes the admixed Farmer populations, showing the required additional North Western Hunter Gatherer ancestry in Eastern Scandinavians and Eastern Hunter Gatherer ancestry in the Baltic cline.

While the steppe ancestry in the northern European clusters are modelled primarily by the Corded Ware source and the western European clusters by the Bell Beaker source, a Bronze Age Eastern North Sea (ENS) cluster from the coastal region in the overlap between the two cultures is modelled with equal proportions (Figure S6.5.1.7, Suppl Note S6.9.2). This result is also reflected in the position of these Bronze Age samples in the western Eurasian PCA, between the oldest Bell Beaker and Northern Corded Ware samples (Supplementary Note 6.1, Figure S6.1.13). When using an early Bronze Age cluster representing this population, we see genetic continuity between 3700 BP and 1700 BP with little evidence of admixture.

With representatives of each of the additional northern European Bronze Age source clusters, we resolve in more detail the extent of a previously documented expansion of Eastern Scandinavian ancestry [59,60]. By the Iron Age in Scandinavia, almost all individuals are modelled with >50% Eastern Scandinavian ancestry. The impact of this expansion is most apparent on the Danish Islands, followed by Norway (Supplementary Note S6.9.4) and finally the Danish peninsula of Jutland (Figure 5).

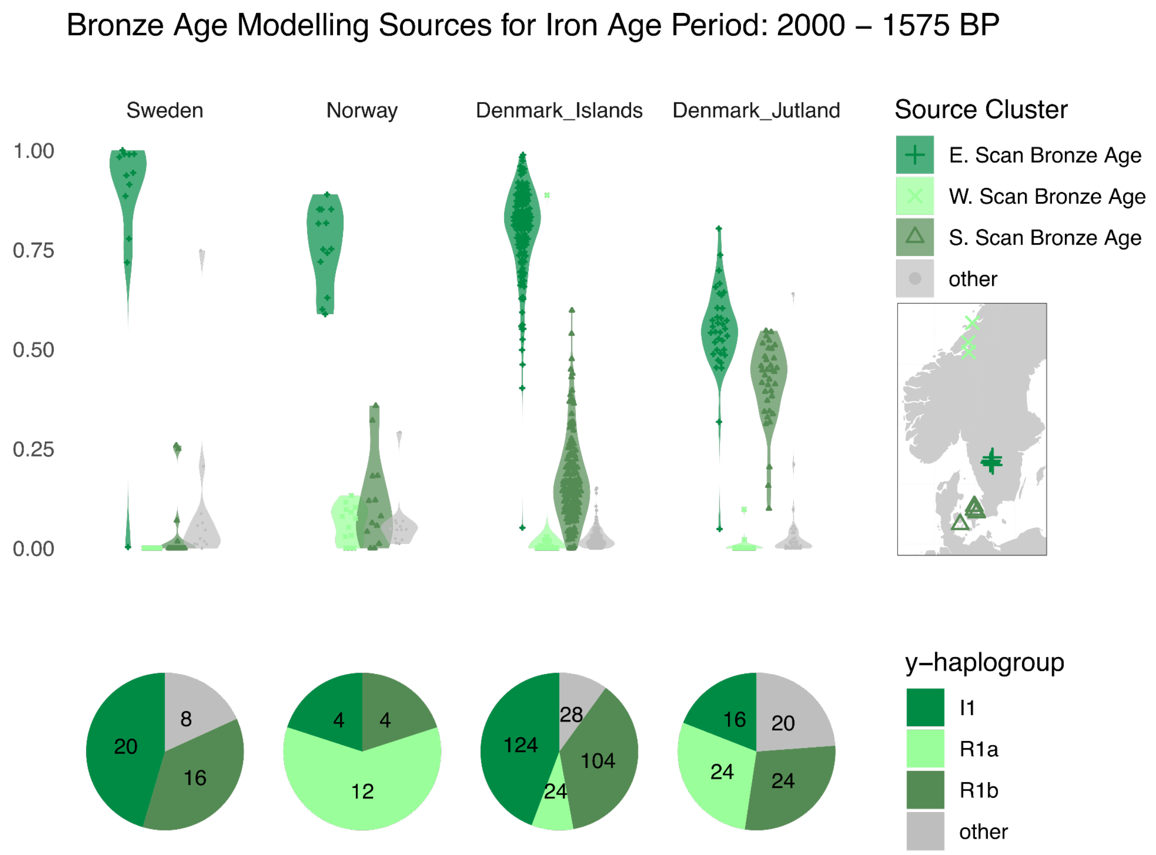


Figure 5. A) Violin Plots showing the proportion of Bronze Age Scandinavian ancestries for each Iron Age individual from Sweden, Norway and Denmark. The highest proportions of E.Scan, W.Scan and S.Scan Bronze Age ancestry are in the local region, despite E.Scan BA being the highest on average in all regions. B) Pie charts showing the proportions of the Y-haplogroups for the Iron Age regions. Despite the low proportion of Western Scandinavaian Bronze Age ancestry in the Norweigians, the proportion of the corresponding R1a haplogroup is high.

During the Bronze Age, there are a number of admixed Norwegian and Danish Bronze Age outliers who carry local and Eastern Scandinavian ancestry. When including these admixed clusters as sources, we find the Scandinavian ancestry of Iron Age Jutlandic individuals modelled entirely as the admixed Danish Bronze Age source. In contrast, the Danish Isles and Norwegian Iron Age populations require additional East Scandinavian ancestry, suggestive of either multiple waves of migration or continuous gene flow (Figure S6.5.2.2). We used DATES [67] to date the admixture time between the Eastern Scandinavians and the Southern Scandinavians, using admixed populations from the Danish Isles Bronze Age, the Danish Isles Iron Age, and the Jutlandic Iron Age (Supplementary Note S6.7, Figure S6.7.1). We observed an overlap between the various target groups during the Bronze Age (~3750 - 3250 BP), shortly after the first detection of Eastern Scandinavian ancestry in Scandinavia. A similar result was seen for the the admixed Western Scandinavian Bronze Age cluster (4200 - 3600 BP).

Expansions of Scandinavian ancestry during the Migration Period

We see these respective proportions of Southern and Eastern Scandinavian Bronze Age ancestry persist throughout the Iron Age (2800 – 1575 BP) in Jutland, the Danish Isles and Southern Sweden. In Jutland during the Iron Age, individuals tend to fall within the Southern Scandinavian cluster (Figure 6), and are modelled with ~55% Southern and ~45% Eastern Scandinavian BA (Figure 5). Further east, individuals fall within the Eastern Scandinavian cluster; on the Danish Isles individuals are modelled as ~20% Southern and ~80% Eastern Scandinavian BA and in Sweden most individuals are modelled as ~100% Eastern Scandinavian BA (Figure 5).

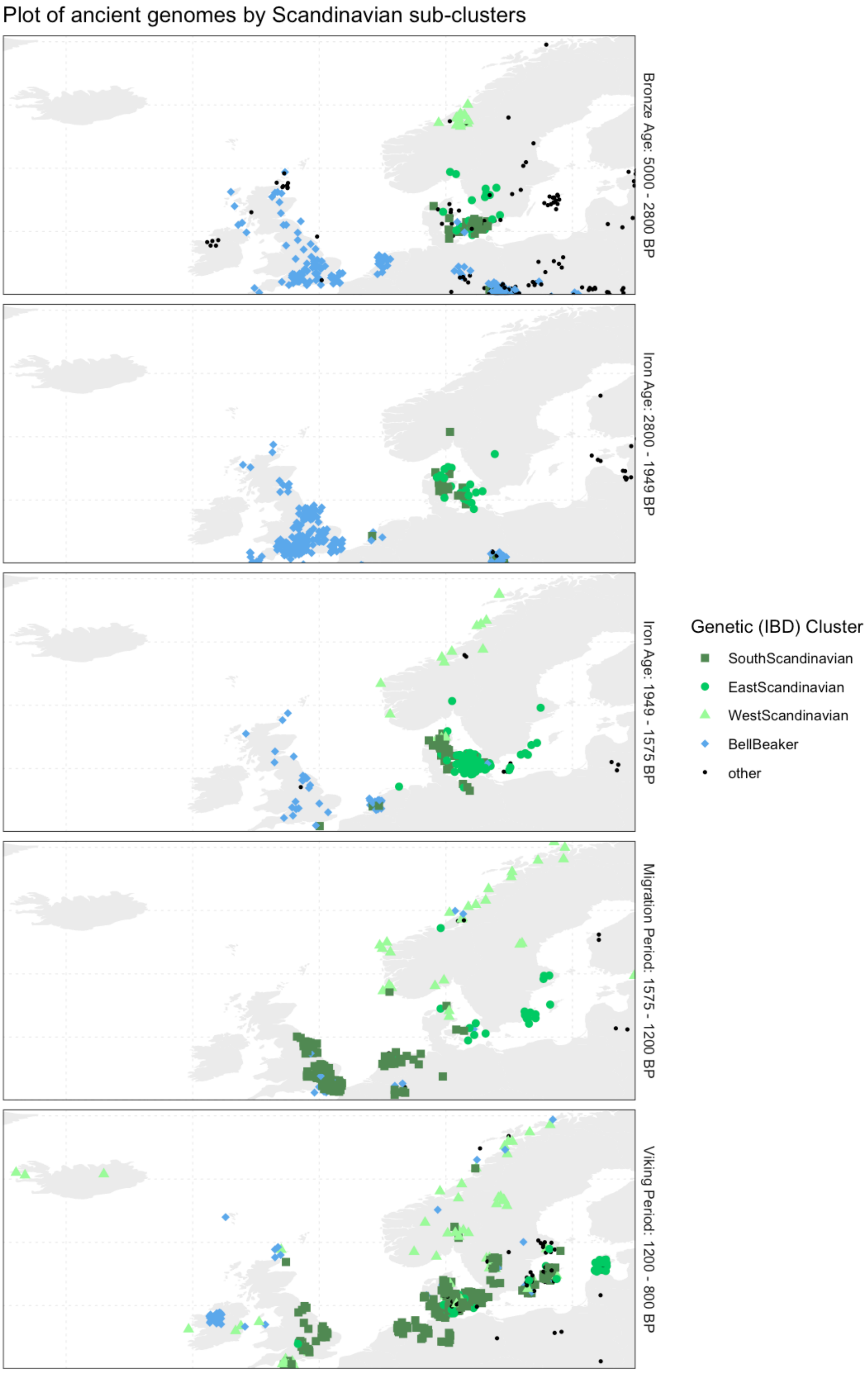
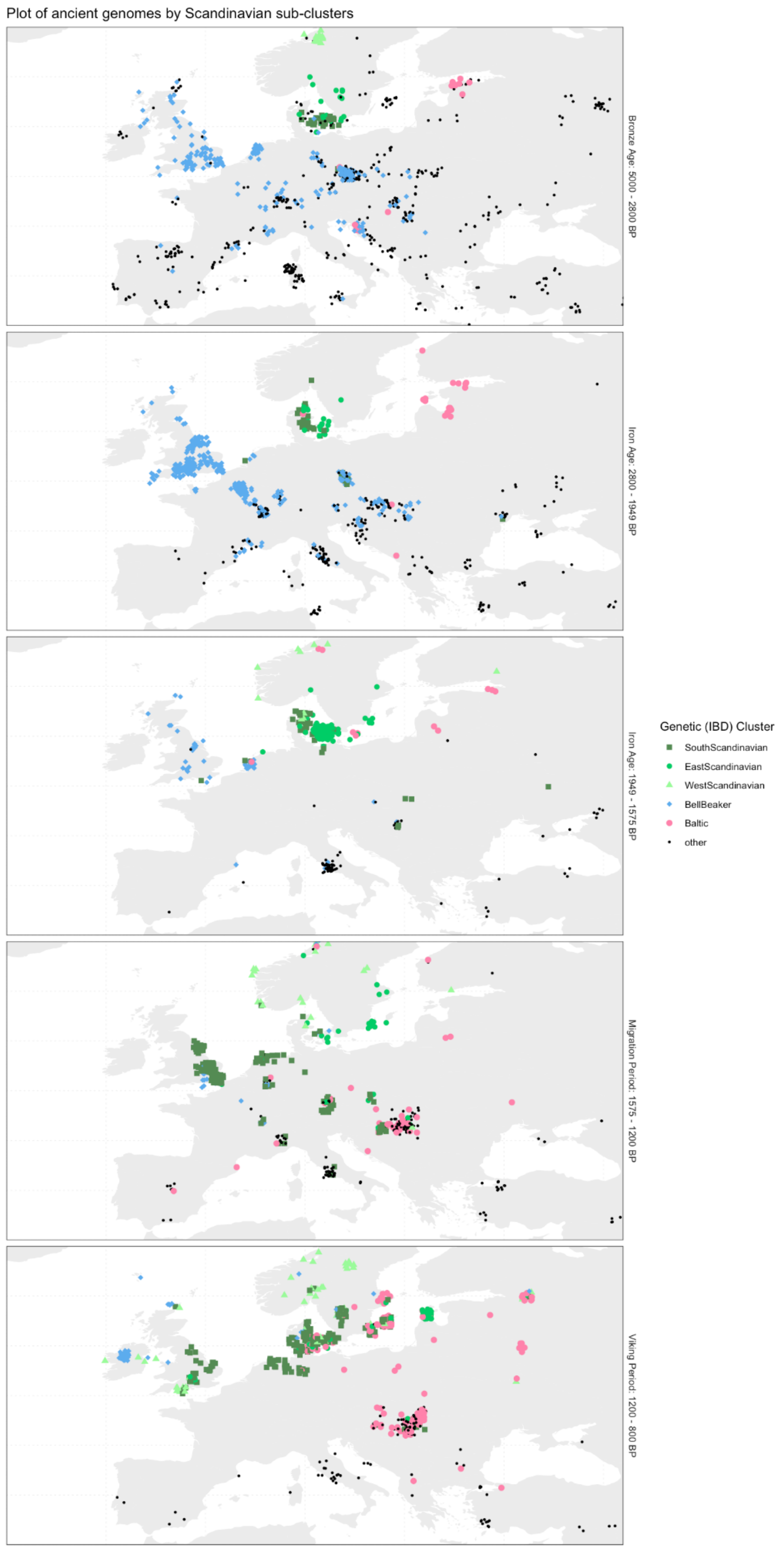


Figure 6. Geographical Distribution of ancient individuals within the Western Scandinavian, Southern Scandinavian, Eastern Scandinavian and Bell Beaker subclusters through time in

Northern Europe. Note: these clusters do not represent the complexities of admixture between clusters (see Supplementary Note S6.4.2.) and should be interpreted together with Mixture Modellings results.

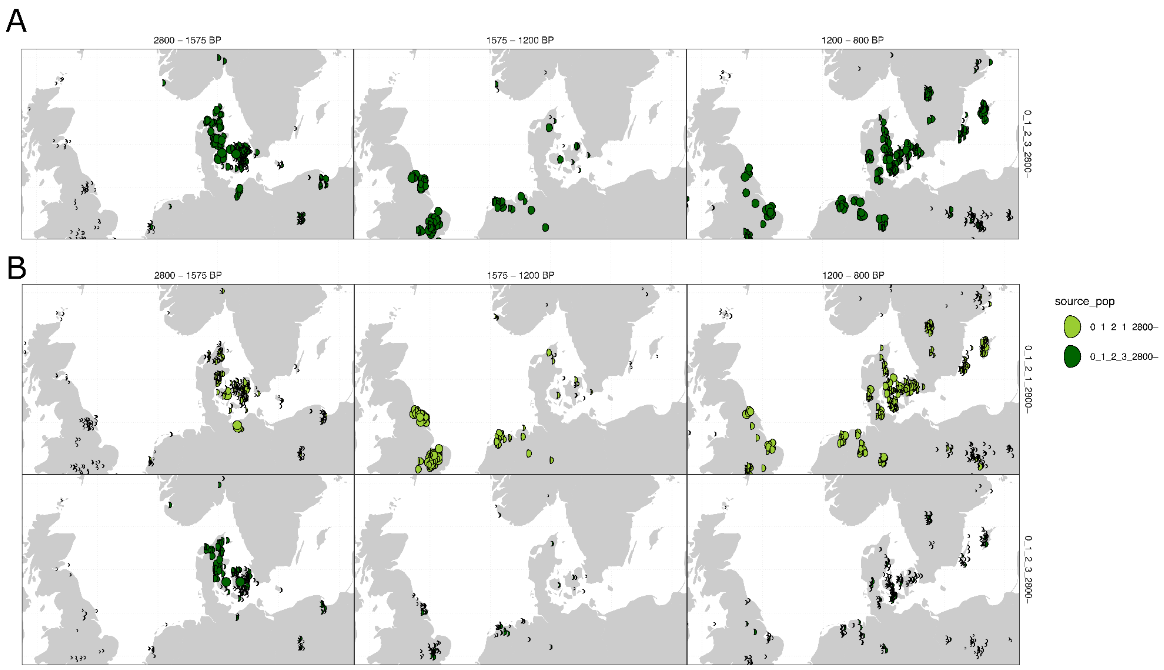
The period between 2800 and 1575 BP is described in the archaeological and historical literature as the time of Germanic migrations moving south into continental Europe (ref). The lack of samples from this period, especially from Germany, limits our ability to determine when these migrations may have occurred. Despite this, we are able to see expansions have occurred at least by the end of the Iron Age and beginning of the Migration Period, when sampling density improves (Extended Data Figure 6).



Extended Data Figure 6. Geographical Distribution of ancient individuals within the Western Scandinavian, Southern Scandinavian, Eastern Scandinavian, Baltic and Bell Beaker subclusters through time in Northern Europe. Note: these clusters do not represent the complexities of admixture between clusters (see Supplementary Note S6.4.2.) and should be interpreted together with Mixture Modellings results.

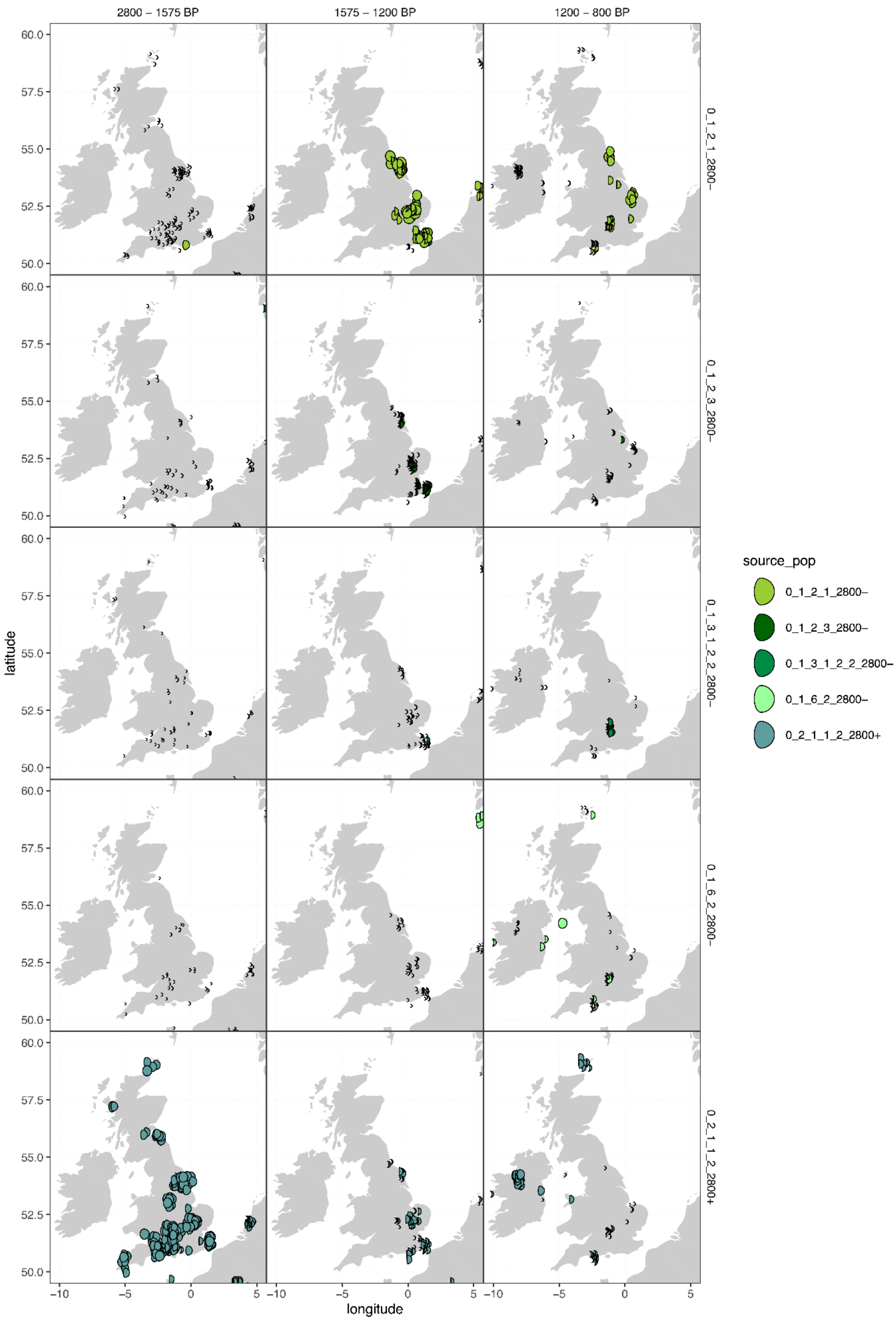
By using Iron Age sources for Western, Southern and Eastern Scandinavians (set 6, Extended Data Figure 6), we are able to ascertain more specific source populations and regions for migrations previously described more broadly to Northern Europe (Gretzinger, Langobards, Stolarek). South of the Nordic region, the Jutlandic Iron Age source to be the primary Scandinavian ancestry to the west (present day Germany, the Netherlands and England). Further east, populations of present-day Poland, Lithuania, Latvia, Estonia, Öland and Finland are primarily mixtures of Eastern Scandinavian and Baltic Bronze Age ancestries.

The arrival of northern continental European ancestry during the Saxon period in England from a broad region ranging from the Netherlands to Southern Sweden has previously been shown [47]. Here we find almost all samples from England fall within the Southern Scandinavian clusters, restricting the range from the Netherlands to Jutland (Extended Data Figure 7). By adding a second Iron Age Southern Scandinavian source from Mecklenburg, Northern Germany, we are able to distinguish between the two Southern Scandinavian IA sources, allowing us to restrict this range further (Extended Data Figure 7). We find Southern Scandinavian ancestry in almost all Saxons from England, Frisians from the Netherlands and Iron Age Germans to be modelled as the Northern German source. Interestingly, the distribution of those two closely related ancestries largely resembles that of the two lineages of the dominant R1b Y-chromosome in the region (Supplemental Section 6.6.4.2). In contrast, individuals from Northern Jutland are modelled primarily as the local Southern Scandinavian IA ancestry.



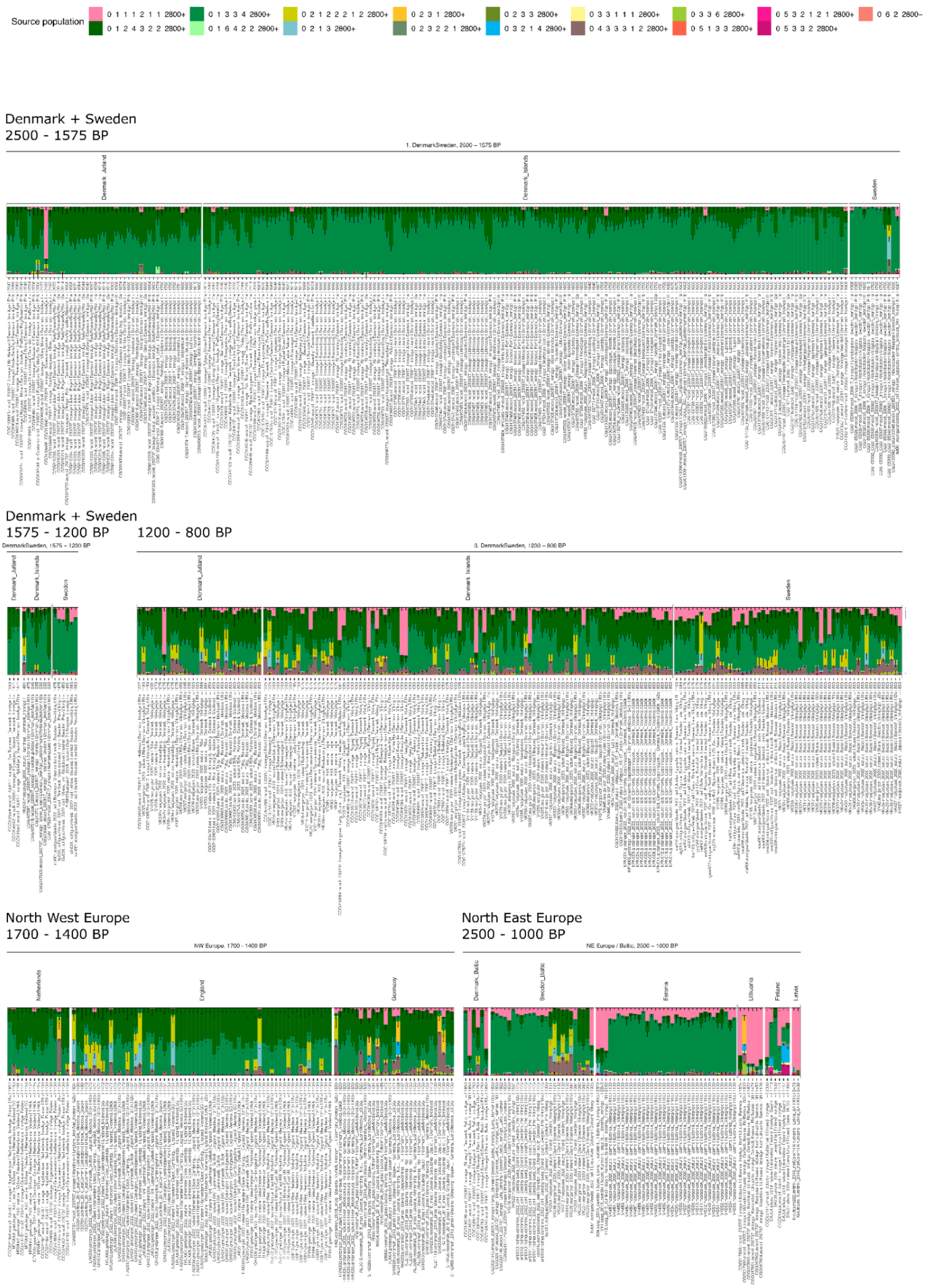
Extended Data Figure 7. A subset of IBD Mixture Modelling results showing the proportion of Southern Scandinavian IA ancestry for Northern Europe for A) Set 7, which contains a single Southern Scandinavian IA source (0_1_2_3, Northern Jutland), in comparison to B) set Y, with two Southern Scandinavian IA sources (0_1_2_3, Northern Jutland and 0_1_2_1 Mecklenburg (Northern Germany). The proportion of ancestry modelled is indicated by the *proportion filled and size of each circle. Full mixture modelling results for Northern Europe are shown in Figure S6.5.1.8 and Figure S6.5.1.8*

In Britain between 1575 and 1200 BP, we find some outliers modelled with North Jutlandic IA rather than North German IA ancestry (Extended Data Figure 8). Although bias in sampling may mean that the specific region and timing of the arrival of individuals with this profile cannot be identified, the heterogeneity present is expected due to the various homelands of the Angles, Saxons and Jutes along the Eastern North Sea coast migrating to Britain during this period. By the Viking Age, we detect Eastern Scandinavian and Western Scandinavian ancestries across Britain and its Islands, representing Viking migrations from Sweden and Norway. Although migration from Denmark is likely during this period, the close relation between the Anglo-Saxons and the Danish Vikings limits our ability to detect this migration.



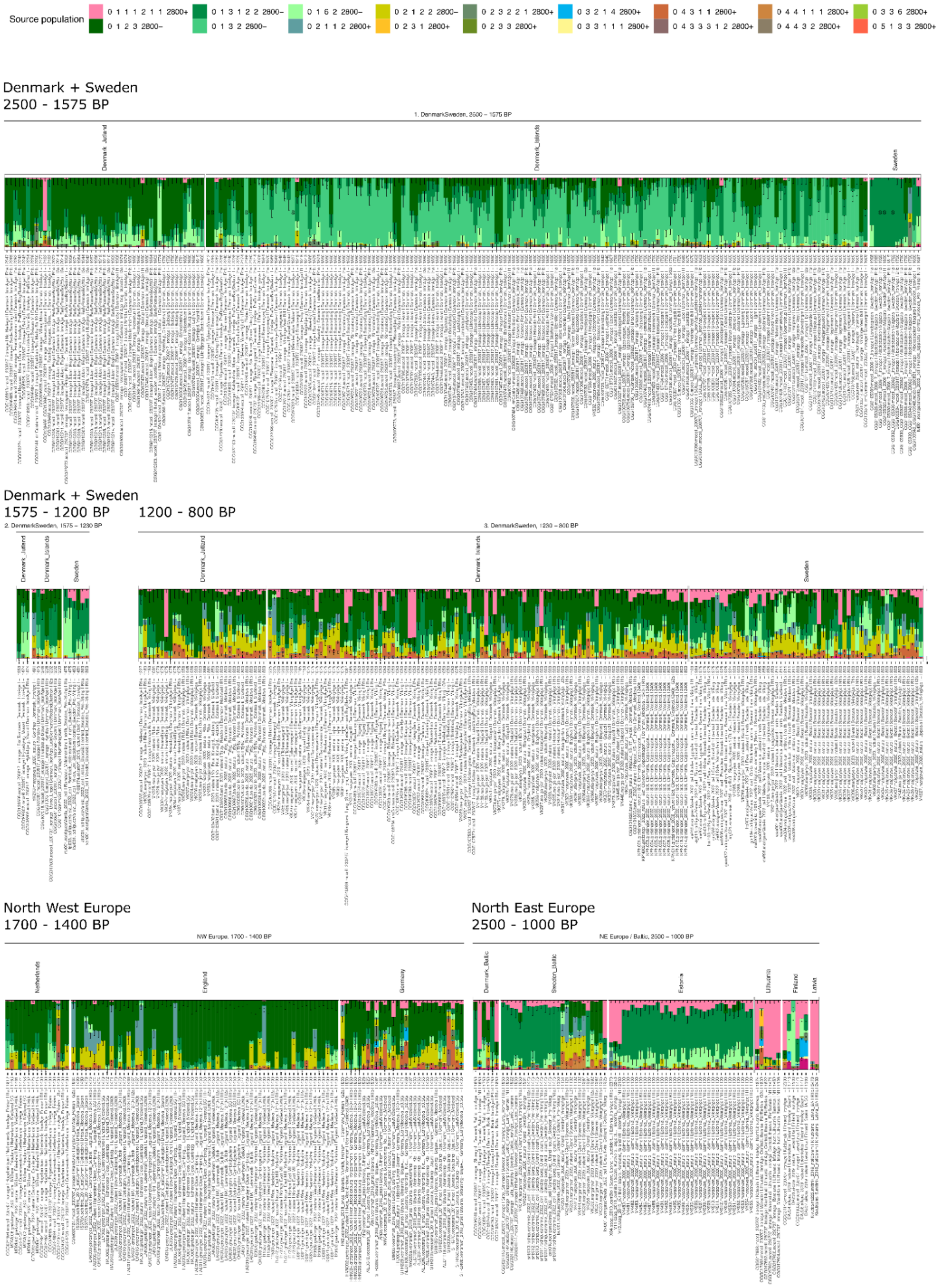
Extended Data Figure 8. A subset of IBD Mixture Modelling results showing the proportion of ancestry for set X. In column 1 (2800 - 1575 BP), the dominant ancestry modelled is 0_2_1_1_2 Celtic Bronze Age. In column 2 (1575 - 1200 BP) during the Anglo Saxon period, a transition causing individuals to be modelled primarily as 0_1_2_1 Southern Scandinavian IA (Mecklenburg, Northern Germany) has occurred, with small proportions of 0_1_2_3 Southern Scandinavian IA (Northern Jutland, Denmark). In column 3 (1200 - 800 BP), the *appearance of other Scandinavian ancstries (cluster 0_1_3_2_2_2 Eastern Scandinavian IA (Sweden) and cluster 0_1_6_2 Western Scandinavian IA (Norway)) is apparent during the Viking Period.*

Similarly, we find another West Germanic speaking population, the Langobards from the Czech Republic, Hungary, and Italy to be modelled as primarily Southern Scandinavian IA (Figure S6.9.6.1), and, accordingly, to carry a few Y haplogroups lineages restricted to Scandinavia. In contrast, we find the (supposed East Germanic-speaking) Polish Wielbark individuals, to be modelled primarily as Eastern Scandinavian. However, most later individuals associated with the originally East Germanic-speaking groups, the Ukrainian Ostrogoths and the Visigoths of Iberia, appear to be locals (Supplementary Note 6.9.6). Two exceptions are from Goths from Iberia, who genetically fall on the Northeast-Southeast Baltic cline (one of which carries a Northern European Y haplogroups), suggesting an origin in North East Europe, but not Eastern Scandinavia specifically. This cline includes populations related to the spread of Slavic populations in Poland, Hungary and the Czech Republic and are to be related to the Baltic Bronze Age ancestry originating in North East Europe (Supplementary Note 6.9.7). With the current sampling, determining a more precise homeland of the Slavic migrations is not yet possible.



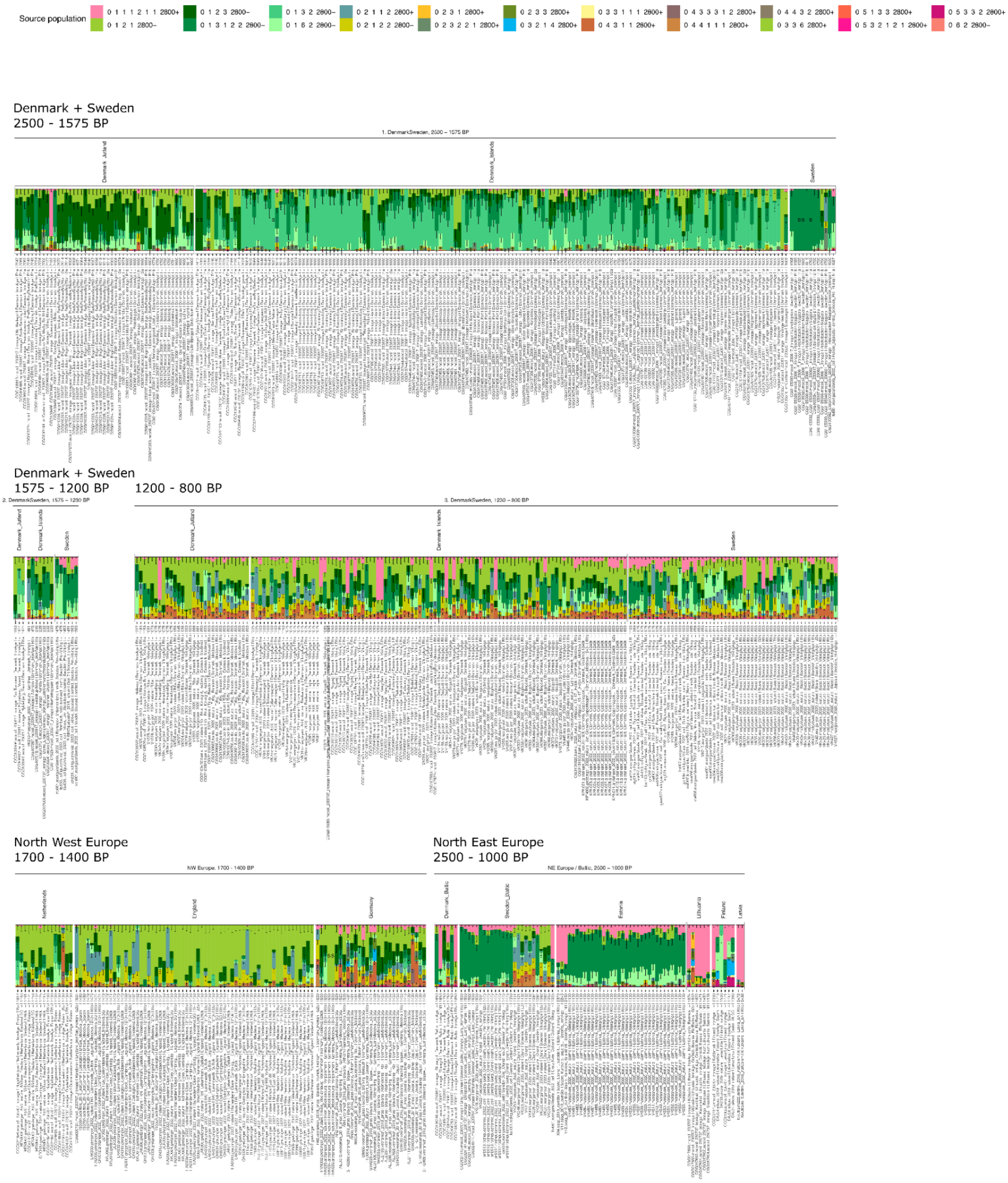
Extended Data Figure 9. A subset of IBD Mixture Modelling results for Bronze Age sources. Row 1 shows the decreasing proportion of Southern Scandinavian ancestry from

Denmark_Jutland to the Islands of Denmark, to Southern Sweden. Row two shows Denmark and Sweden during the Migration Period (1575 - 1200 BP, left) and the Viking Period (1200 - 800 BP, right). Row three shows the surrounding regions to the west (left) and east (right).



Extended Data Figure 10. A subset of IBD Mixture Modelling results for Iron Age sources. Row 1 shows variation from Denmark_Jutland to the Islands of Denmark, to Southern Sweden. Row two shows Denmark and Sweden during the Migration Period (1575 - 1200

BP, left) and the Viking Period (1200 - 800 BP, right). Row three shows the surrounding regions to the west (left) and east (right).



Extended Data Figure 11. A subset of IBD Mixture Modelling results for Iron Age sources, when including two Southern Scandinavian Iron Age sources. Row 1 shows variation from Denmark_Jutland to the Islands of Denmark, to Southern Sweden. Row two shows Denmark and Sweden during the Migration Period (1575 - 1200 BP, left) and the Viking Period (1200 - 800 BP, right). Row three shows the surrounding regions to the west (left) and east (right).

On the Danish Isles we see discontinuity from around 1600 BP (Extended Data Figure 6). Between 1600 BP and 1230 BP the limited number of samples limits our ability to genetically determine the precise timing and nature of this transition. Sampling density improves from 1230 BP, in the 100 years leading up to the Viking Age, by which point we see a distinct transition has occurred. This transition is visible at a variety of resolutions. From the Bronze Age modelling, we see an increase in the proportion of Southern Scandinavian ancestry on Zealand by 1230 BP (Extended Data Figure 9). In the Iron Age (2000 – 1575 BP), the only regions with high proportions of Southern Scandinavian ancestry are Jutland and Germany. In Northern Jutland, the proportion of Southern Scandinavian ancestry remains relatively constant. In both regions, by the Viking Age, many individuals carry a series of ancestries previously only found further south and west – ENS Bronze Age, Bell Beaker/Celtic Bronze Age and European Farmer.

By including the two Iron Age Southern Scandinavian clusters in the sources (Jutland and Mecklenburg) together with two Iron Age Eastern Scandinavian clusters (Danish Isles and Sweden), we are able to further disentangle these migrations (Extended Data Figure 11). The Danish Isles ancestry that was widespread on Zealand from 2200 BP disappears from ~1600 BP. For the few samples between 1600 BP and 1230 BP we find instead a variety of ancestries, Swedish Iron Age, Celtic Iron Age, Norwegian Iron Age, and Jutlandic (check) Iron Age. In Northern Jutland, this additional resolution reveals a transition within the constant proportion Bronze Age Southern Scandinavian ancestry. Prior to 1600 BP it is modelled as North Jutlandic IA ancestry, which gradually shifts to become primarily modelled as North German IA ancestry. Small proportions of Jutlandic IA ancestry are modelled in many later individuals, which is in direct contrast to Zealand, where it appears a population replacement occurred.

From 1230 BP until 800 BP, including the Viking Age, we see most individuals modelled primarily with small proportions of ancestries that prior to 1575 BP were only found south of Scandinavia: ENS ancestry of the East North Sea coast, Northern German ancestry from Mecklenburg and Celtic ancestry of the Britain and Ireland and France, and European Farming ancestry found in western Europe (Extended Data Figures 9 - 11). On Zealand and the Baltic Islands we also detect a number of individuals with Baltic (Estonian Bronze Age) ancestry, similar to populations associated with the Slavic-related populations. In addition to these non-local ancestries, many of these individuals are modelled with small proportions of East, West and South Scandinavian ancestry primarily found within Scandinavia during the Iron Age. Although in Northern Jutland, we have evidence of admixture between the local Iron Age population and the incoming Migration Period population, suggesting that admixture at this time occurred within Scandinavia. However, we cannot exclude the possibility of admixture between the more southern sources and the Scandinavian IA sources occuring in the unsampled regions of Southern Jutland or continental Europe.

The dense sampling and high resolution demographic inference have allowed us to establish a baseline ancestry for various regions, and subsequently identify outliers (Supplementary Note S6.8.1).

Discussion

The Germanic Indo-European language group is frequently assumed to have been introduced by the first major Steppe cultures to arrive in Scandinavia. The Corded Ware culture, appearing around 4800 BP, is generally seen as a likely context [3–6], the local Jutlandic Single Grave culture often taking a central role [16,68,69]. A comparable model sees the appearance of the Bell Beaker culture to Jutland and Norway around 4400 BP as the moment when this language group was introduced [7] . In contrast with these older hypotheses, an East Scandinavian population, which is not detected for another 400-800 years, is revealed here as an alternative vector for the introduction of Germanic, allowing for the proposition of a revised model. Although all Early Bronze Age populations of Scandinavia derive their Steppe ancestry from people of Corded Ware culture, the earliest Scandinavian individuals carry small proportions of local Western Hunter-Gatherer ancestry, whereas the later Eastern Scandinavians are modelled with Lithuanian/Latvian Hunter-Gatherer ancestry (Extended Data Figure 3, Figure S6.5.1.4, Supplementary Note S6.5.1), indicative of a Late Neolithic cross-Baltic migration into Scandinavia. No such migration has to our knowledge been identified in the archaeological record. However, the timing coincides with the introduction of a new, Late Neolithic sheep breed to Scandinavia [70]. It also coincides with the spread of a new burial rite of gallery graves in south Sweden, the Danish islands [71] and Norway [72], a new house type [70,73,74], the first durative bronze networks [75], as well as with the end of an east-west divide in Scandinavia between 4050 and 3650 BP [73].

Archaeologically, the Nordic Bronze Age is a period of strong cultural homogenisation in south Scandinavia, starting around 3500 BP, creating the so-called Nordic Cultural Zone that lasted until 2500 BP. It was accompanied by widespread mobility not least in relation to forging new alliances supporting metal distribution [76]. Although it is possible additional migratory events occurred, our results based on IBD Mixture Modelling (Supplementary Note admixed source) and DATES analyses (Supplementary Note S6.7) suggest that admixture between Bronze Age Southern and Eastern Scandinavians likely occurred in Jutland and the Danish Isles during the Nordic Bronze Age, between 3700 - 3400 BP, and leading to the formation of the Iron Age Southern Scandinavians (Supplementary Note S6.5.1). The formation of the admixed Late Bronze Age Western Scandinavians as Bronze Age Western and Eastern Scandinavian similarly occurred in the overlapping time period of 4200 - 3600 BP (Figure S6.7.1), however by the Iron Age however, Norwegian individuals carry additional East Scandinavian ancestry. Linguistically, the Late Bronze Age is the period during which Palaeo-Germanic donated vocabulary to Finno-Saamic in the east and adopted vocabulary from Celtic in the south, suggesting that it was spoken widely among East Scandinavians distributed between Sweden and Denmark, and possibly also in the Nordic Bronze Age communities in Finland and Estonia [77,78].

The transition from Palaeo- to Proto-Germanic is traditionally characterised by defining phonological changes known as the Germanic sound shifts and took place around the start of the Iron Age (~2600 BP) [8,79]. This defining event has been speculated to result from the assimilation of a different, unknown language [79]. Our results reveal no major admixture events around this period, suggesting that this linguistic phase shift was rather induced by other factors, such as changes in mobility patterns or social hierarchies towards the onset of the Iron Age, or by language-internal developments. At any rate, the persistent genetic border between Southern and Eastern Scandinavians throughout the Iron Age suggested that the Proto-Germanic speech community united these different populations until its dissolution around 2000 BP.

We further find that the IA Southern Scandinavians that arose from admixture between Bronze Age Southern and Eastern Scandinavians are central to understanding the Germanic dispersal. After the Pre-Roman Iron Age, around 2000 BP, Proto-Germanic diverged into North, East and West Germanic. The spread of West Germanic to Germany, the Netherlands and Britain, appears to be closely related to populations migrating from the Jutland Peninsula. In these regions, we see the transition from Bell Beaker-related to the Corded Ware-related Southern Scandinavian ancestry. For Germany and Britain, where Celtic was known to be spoken, this period also saw a linguistic transition to Germanic. In the Netherlands, IA Southern Scandinavians' ancestry became dominant in the place of a distinct Eastern North Sea population. The linguistic affiliation of this population is unknown. According to the linguistic 'Nordwestblock' hypothesis, the Netherlands may have harboured a language distinct from both Celtic and Germanic[80]. Given that ENS is a Bell Beaker subcluster, which is associated with Celtic languages in Britain and France, our results can alternatively be brought in line with theories of Celtic speakers, perhaps including the *Frisii* of the Roman Period, inhabiting the Dutch North Sea coast during the Early Iron Age [81]. Although no unadmixed ENS populations are found during the migration period, the incoming Southern Scandinavians carry small proportions of ENS ancestry, indicating the migrations were not a complete replacement. Dutch coastal areas see a habitation hiatus around 1600 BP and subsequent appearance of a new material culture that is often referred to as Anglo-Saxon in nature [82], mirroring the genetics and timing of the Late Iron Age, linguistically West-Germanic Frisians in this dataset. In addition, we find that the Southern Scandinavian ancestry of these migrating populations is better modelled by individuals near Southern rather than the Northern Jutland, and that the migrating populations often carry varying but minor proportions of ENS ancestry, inherited from the earlier people who previously lived in the region. In contrast to previous studies, which relied on Scandinavian samples postdating the Migration Period [47], we can now reject the Danish Isles and Sweden as a source area for the Anglo-Saxons in Britain, as these were dominated by Eastern Scandinavian ancestry prior to the Viking Age (Figure 6).

While previous studies have identified the presence of some northern European ancestry in Migration Period populations with historically documented ancestral myths about origins in northern Europe [45,48,83], they have not had the resolution to identify a source region with the resolution presented here. Here we show that the Scandinavian ancestry in most of the

Langobards is from Southern Scandinavia, consistent with post-classical origin legends [84]. However, three outlier Langobards from the Czech Republic and Hungary are of Eastern Scandinavian origin. The earliest individuals from Wielbark, Poland (~1900 BP) are primarily of Eastern Scandinavian ancestry, supporting a population migration from a region and population distinct from that of the West and North Germanic populations, a scenario potentially consistent with Gothic oral history. Further south, the later Ostrogoth and Visigoth individuals (1600 - 1100 BP) who were cultural descendents of the earlier Goths, appear similar to local Southern Europeans. The two outliers from Spain have around 50% northern European ancestry, but unlike the earlier Wielbark individuals, they fall along the Northeast-Southeast Baltic cline. The genetic distinction of the Ostrogoth and Visigoth populations from the Eastern Scandinavian Wielbark Goths suggests an adoption of the culture and East Germanic language by the more southern groups.

The subsequent period (1600 - 1200 BP) was one of great turbulence, including the collapse of the Western Roman Empire, the Barbarian migrations, the Justinian plague and the Late Antique Little Ice Age resulting from volcanic eruptions (Figure 7). In the archaeological and historical literature this is considered a period of genetic continuity in Scandinavia despite a reduction in population size (Supplementary Note S7.3, S7.4), however the genetic record now negates this assumption of pervasive genetic continuity from the Iron Age on the Danish Isles, Northern Jutland and Southern Sweden. Due to the scarcity of genomes from this period we rely on other lines of evidence to provide information on the homeland and timing of this migration.

The population in southern Scandinavia after 1200 BP shows hitherto unknown changes compared with the situation in the same areas before 1600 BP. Our results demonstrate the arrival of a strong component of North German IA ancestry, in combination with a series of ancestries previously associated with Celtic-speaking groups and populations carrying European Farmer (in addition to GAC) ancestry from north-western Europe. In the Danish islands, the shift amounts to a virtually complete population replacement. Subsequently these changes are supplemented by a modest arrival of eastern ancestry associated with Slavic populations, who migrated into areas south of the Baltic Sea formerly settled by East Germanic speakers, and noted as a component in Scandinavian samples after 1200 BP.

In the period directly following the volcanic activity (1414 and 1411 BP) and the Justinian Plague (1409 BP), Scandinavia saw a population decline that did not fully recover until around 1300 BP (Supplementary Note S7) [85]. Linguistically, this period is one of central importance to Northern Europe. Runic inscriptions from across Scandinavia testify to a North Germanic language that remained relatively similar to Proto-Germanic during 2000 - 1500 BP. However, during the Migration period (1575 - 1200 BP) the language underwent far-reaching changes resulting in the formation of Old Norse [54]. The glottogenesis of Old Norse thus coincides with a period of social and demographic instability [86]. Following this transition, the originally common Germanic script known as the Elder Futhark was likewise fundamentally remodelled, giving rise to the Younger Futhark that was tailored specifically to Old Norse [87,88], and was taken into use all across Scandinavia.

Old Norse, spoken across a vast area, including Norway, Iceland and Sweden, was by its speakers referred to as *dǫnsk tunga*, i.e. the Danish tongue [89,90]. Across Scandinavia, we see variation in how the populations associated with this language were established. In Denmark and Sweden we show strong genetic evidence suggesting that observed archaeological and linguistic changes are linked to the migration of Iron Age Danes. Based on the genetic heterogeneity of the migrating population and the inability to identify a suitable source population, it appears that between 1500 and 1200 BP was likely the outcome of an amalgamation among several migrating and local groups, comparable to the formation processes among Germanic groups on the continent. In contrast, in Norway, the adoption of Old Norse and similar social changes as seen in South Scandinavia occurred with limited genetic impact from Southern Scandinavian and must have been more cultural in nature. With the exception of a single early Viking sample, the majority of Viking Age Norwegians appear either to carry local ancestry, or to reflect back migrations from Celtic regions of Britain and Ireland. Of note, the border between the East and West Norse languages closely corresponds closely to that of the Southern Scandinavians and Western Scandinavians clusters during the Viking Period (Figure 6).

Combined with linguistic, historical and archaeological evidence, our findings have implications for the prehistory of the Danes. Antique sources mention the Danes living in South Scandinavia by 1450 BP [91,92]. According to oral histories, the South Scandinavian royal lineage of the Danes, as well as those of the Swedes and the Norwegians were initiated between 1550-1500 BP [93] and continued throughout the subsequent periods. The appearance of the Danes appears to coincide with prominent cultural changes. By the late Migration Period (1475 - 1400 BP) a new group of large princely halls was introduced in a number of sites, many of which continued in use until the end of the Viking Age [93–96]. 1550 - 1450 BP saw the development and spread of Germanic animal art, an expression form that was closely tied with religious concepts, and continued to develop until the conversion to Christianity around 1000 BP [37,97,98]. Finally, we see possible evidence of a political shift in the construction of the Dannevirke in Southern Jutland, a south facing moat and rampart earth stretching more than 5 km across the peninsular near Slesvig, whose second phase dates to around 1500 BP [99].

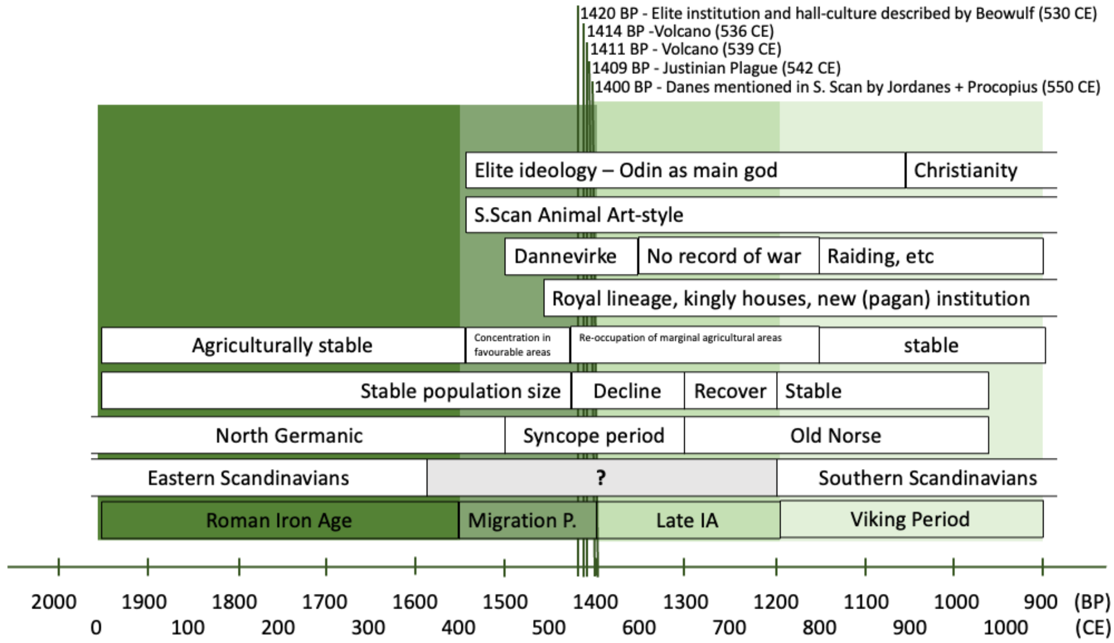


Figure 7. Timeline showing the climatic, cultural, linguistic and genetic shifts in the Danish Isles and Southern Sweden occurring from the Migration Period to the Viking Age.

Thus, the period between 1550 - 1400 BP in Scandinavia covers a number of potentially major population dynamics. The migrations and plague might have caused abandonment of marginal subsistence areas [55]. During the Little Antique Ice Age, although depopulation in marginal areas occurred [100], there was continuity to some degree in more fertile and southern areas [101] also related to intensified food production [102] . This is shown in the pollen data from southernmost Sweden, where woodland regeneration occurs in uplands, with continuity of agricultural production in the most favourable areas (Supplementary Note S7.4). Further north, variation between different climatic zones is noted in southern Norway, with different societal impact from place to place which does not directly correspond with the climatic data [55]. For those who survived, the subsequent improving conditions and relative abundance of resources due to a lower population size would have created the opportunity for rapid expansion, as attested to in historical sources in other areas.

On the present archaeological and historical evidence, we may thus conclude that the major population shift in South Scandinavia between the Roman and the Viking periods was not solely driven by the climate events or plague of 1450 - 1350 BP but instead likely took hold between 1550 and 1450 BP and was associated with the establishment and subsequent expansion of what became the Danes.

The major findings from ancient DNA studies over the last 10 years have primarily concerned large scale transitions of genetically distinct populations detected with a relatively small number of genomes. Here we show how the complexities of demographic events between closely related populations can now be exposed through dense sampling through space and time and the application of improved methodologies. Our findings have important implications for the interpretation of the archaeological record after the Middle Neolithic. They additionally allow us to offer a number of revisions to the formation of West Eurasian ancestry as well as the proposition of a new model for the origin and spread of the Germanic languages. However, the present study also has limitations and raises several new questions.

With the resolution now shown to be possible here, additional sampling from a series of regions will allow a series of questions to be addressed that are currently not possible with the current dataset. Of particular interest is 1) confirming the proposed Bronze Age source of the East Scandinavians along the Baltic coast, 2) identifying the Iron Age border between the East and South Scandinavian IA in continental Europe between Mecklenburg and Gdansk representing the border between East and North West Germanic, 3) determining the more localised regions both along the East North Sea coast and within Britain representing each of the Angles, Saxons and Jutes, and 4) the regions in North East Europe related to source of Baltic and Slavic populations.

Our results additionally call for a reappraisal of the linguistic evidence concerning the hypothetical migration of Germanic from the Baltic into Scandinavia and its trajectory of this linguistic subgroup from the Indo-European steppe. The formation of East Scandinavians out of Baltic populations finds an evident linguistic analogue in the isoglosses shared between the Germanic and Balto-Slavic branches of the Indo-European language family, which point to prehistoric borrowing, a linguistic subclade, or both [103]. On the other hand, the relatively late, Bronze Age arrival of agriculture in the Baltic [104,105] vs the presence in Proto-Germanic of agricultural terms inherited from Indo-European [106] raises a question on the suitability of the archaeological context of this area as a linguistic stepping stone during the Late Neolithic.

Finally, this study highlights fundamental methodological difficulties in establishing correlations – or lack thereof – between genetic, archaeological and linguistic evidence [107,108]. For instance, the immigration of East Scandinavians, central to our new model, has so far not been recognized in the archaeological record. During the Late Iron Age, Northwest Germanic was spoken by both Southern, Eastern and Northern Scandinavians, as demonstrated by runic inscriptions from across Scandinavia, despite persistent genetic boundaries between these populations. Following the Migration Period, southern European individuals exhibit late Germanic burial identities without showing ancestry from Northern Europe. These findings underline the differences in the mechanisms behind the proliferation of genetic, linguistic and cultural features and call for additional interdisciplinary studies on the integration of these diverse lines of evidence on human prehistory.

References

1. Allentoft, M. E. *et al.* Population genomics of Bronze Age Eurasia. *Nature* **522**, 167–172 (2015).
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. Güntert, H. *Der Ursprung der Germanen*. (C. Winter, Heidelberg, 1934).
4. Childe, V. G. *The Aryans: A Study of Indo-European Origins*. (K. Paul, Trench, Trubner & Company, Limited, 1926).
5. Anthony, D. W. Pontic-Caspian Mesolithic and Early Neolithic societies at the time of the Black Sea flood: a small audience and small effects. in *The Black Sea Flood Question: Changes in Coastline, Climate and Human Settlement* (eds. Yanko-Hombach, V., Gilbert, A. S., Panin, N. & Dolukhanov, P. M.) (Springer Science & Business Media, 2006).
6. Kristiansen, K. *et al.* Re-theorising mobility and the formation of culture and language among the Corded Ware Culture in Europe. *Antiquity* **91**, 334–347 (2017).
7. Prescott, C. Dramatic beginnings of Norway's history? Archaeology and Indo-Europeanization. in *Language and Prehistory of the Indo- European Peoples: A Cross-disciplinary Perspective* (ed. Hyllested, A.) (Museum Tusculanum Press, 2017).
8. Kroonen, G., Hedeager, L., Prescott, C. & Kristiansen, K. Questions concerning the Indo-Europeanization of Scandinavia: The Germanic languages. in *Oxford Handbook of Scandinavian Archaeology* (Oxford University Press, Oxford, in press).
9. Sims-Williams, P. An Alternative to 'Celtic from the East' and 'Celtic from the West'. *Camb. Archaeol. J.* **30**, 511–529 (2020).
10. Polomé, E. C. Methodological Aspects of Glotto-and Ethnogenesis of the Germanic Peoples. *Entsteh. Von Sprachen Volkern Giotto- Ethnogenetische Aspekte Eur. Sprachen*

Akten Des **6**, 45–70 (1985).

11. van Sluis, P., Jørgensen, A. R. & Kroonen, G. European Prehistory between Celtic and Germanic: The Celto-Germanic Isoglosses Revisited. in *The Indo-European Puzzle Revisited: Integrating Archaeology, Genetics, and Linguistics* (eds. Willerslev, E., Kroonen, G. & Kristiansen, K.) 193–244 (Cambridge University Press, Cambridge, 2023). doi:10.1017/9781009261753.018.
12. Aikio, A. On Germanic-Saami contacts and Saami prehistory. *Suom.-Ugr. Seuran Aikakauskirja* **2006**, 9–55 (2006).
13. Kallio, P. The Indo-Europeans and the non-Indo- Europeans in prehistoric Northern Europe. in *Language and prehistory of the Indo-European peoples: a cross-disciplinary perspective* (eds. Hyllested, A., Whitehead, B. N., Olander, T. & Olsen, B. A.) (Museum Tusculanum Press, Copenhagen, 2017).
14. Polomé, E. C. Who are the Germanic people? in *Proto-Indo-European: The Archaeology of a Linguistic Problem : Studies in Honor of Marija Gimbutas* (ed. Gimbutas, M.) 216–244 (Institute for the Study of Man, Washington, D.C., 1987).
15. Mallory, J. P. *In Search of the Indo-Europeans: Language, Archaeology and Myth*. (Thames and Hudson, London, 1989).
16. Schmidt, K. H. The Celts and the Ethnogenesis of the Germanic People. *Hist. Sprachforsch. Hist. Linguist.* **104**, 129–152 (1991).
17. Kristiansen, K. *Europe Before History. Cambridge*. (Cambridge University Press, Cambridge, 1998).
18. Heather, P. J. *The Fall of the Roman Empire*. (Pan Books, 2006).
19. Drinkwater, J. F. *The Alamanni and Rome 213-496: (Caracalla to Clovis)*. (OUP Oxford, 2007).
20. Kelly, G. *Ammianus Marcellinus: The Allusive Historian*. (Cambridge University Press,

2008).

21. Wickham, C. *The Inheritance of Rome: A History of Europe from 400 to 1000*. (Penguin UK, 2009).
22. Holst, M. K. *et al.* Direct evidence of a large Northern European Roman period martial event and postbattle corpse manipulation. *Proc. Natl. Acad. Sci.* **115**, 5920–5925 (2018).
23. Fulk, R. D. *A Comparative Grammar of the Early Germanic Languages*. (John Benjamins, 2018). doi:10.1075/sigl.3.
24. Kümmel, M. J. Reconstructing Proto-Germanic. in *Oxford Research Encyclopedia of Linguistics* (2023). doi:10.1093/acrefore/9780199384655.013.931.
25. Nielsen, H. F. *The Germanic Languages: Origins and Early Dialectal Interrelations*. (University of Alabama Press, 1989).
26. Ringe, D. A. *From Proto-Indo-European to Proto-Germanic*. (Oxford University Press, 2017).
27. Schwantes, G. Die Jastorf-Zivilisation. in *Reinecke Festschrift* (eds. Behrens, G. & Werner, J.) (Mainz, 1950).
28. Ringe, D. Proto-Germanic. in *From Proto-Indo-European to Proto-Germanic* (ed. Ringe, D.) 0 (Oxford University Press, 2017). doi:10.1093/oso/9780198792581.003.0004.
29. Salmons, J. 59. The evolution of Germanic. in *Handbook of Comparative and Historical Indo-European Linguistics* vol. 2 1002–1027 (De Gruyter Mouton, 2017).
30. Hansen, B. S. S. & Kroonen, G. J. Germanic. in *The Indo-European Language Family* (ed. Olander, T.) 152–172 (Cambridge University Press, Cambridge, 2022). doi:10.1017/9781108758666.010.
31. Agee, J. R. Using Historical Glottometry to Subgroup the Early Germanic Languages. *J. Ger. Linguist.* **33**, 319–357 (2021).
32. Wolfram, H. *The Roman Empire and Its Germanic Peoples*. (Univ of California Press,

2005).

33. Wolfram, H. *History of the Goths*. (University of California Press, 1990).

34. Jordanes. *The Origin and Deeds of the Goths: In English Version*. (Princeton University Press, 1908).

35. Svennung, J. *Jordanes und Scandia: kritisch-exegetische Studien*. (Almqvist & Wiksell ; O. Harrassowitz, Stockholm, Wiesbaden, 1967).

36. Svennung, J. Jordanes und die gotische Stammsage. in *Studia Gotica. Die eisenzeitlichen Verbindungen zwischen Schweden und Südosteuropa* (ed. Hagberg, U. E.) (Kungl. Vitterhets, Historie och Antikvitets Akademien, Stockholm, 1972).

37. Hedeager, L. *Iron Age Myth and Materiality: An Archaeology of Scandinavia AD 400-1000*. (Routledge, 2011).

38. Andersson, T. Goten: § 1. Namenkundliches. in *Reallexikon der Germanischen Altertumskunde* (eds. Heinrich, B., Steuer, H. & Timpe, D.) vol. 12 402–403 (De Gruyter, 1998).

39. Hachmann, R. Die Goten und Skandinavien. in *Quellen und Forschungen zur Sprach- und Kulturgeschichte der germanischen Völker. N.F.* vol. 34 (De Gruyter, 1970).

40. Goffart, W. Jordanes's 'Getica' and the Disputed Authenticity of Gothic Origins from Scandinavia. *Speculum* **80**, 379–398 (2005).

41. Christensen, A. S. *Cassiodorus, Jordanes and the History of the Goths: Studies in a Migration Myth*. (Museum Tusculanum Press, 2002).

42. Steuer, H. „Germanen" aus Sicht der Archäologie: Neue Thesen zu einem alten Thema. in *„Germanen" aus Sicht der Archäologie* (De Gruyter, 2021). doi:10.1515/9783110702675.

43. Foulke, W. D. Paul the Deacon. History of the Langobards. (1907).

44. Menghin, W. *Die Langobarden. Archäologie und Geschichte*. (Konrad Theiss Verlag,

Stuttgart, 1985).

45. Amorim, C. E. G. *et al.* Understanding 6th-century barbarian social organization and migration through paleogenomics. *Nat. Commun.* **9**, 3547 (2018).

46. Veeramah, K. R. *et al.* Population genomic analysis of elongated skulls reveals extensive female-biased immigration in Early Medieval Bavaria. *Proc. Natl. Acad. Sci.* **115**, 3494–3499 (2018).

47. Gretzinger, J. *et al.* The Anglo-Saxon migration and the formation of the early English gene pool. *Nature* **610**, 112–119 (2022).

48. Stolarek, I. *et al.* Genetic history of East-Central Europe in the first millennium CE. *Genome Biol.* **24**, 173 (2023).

49. Amory, P. *People and Identity in Ostrogothic Italy, 489–554 (Cambridge Studies in Medieval Life and Thought 4th Series 33)*. (Cambridge, 1997).

50. Pohl, W. Memory, Identity and Power in Lombard Italy. in *The Uses of the Past in the Early Middle Ages* (eds. Hen, Y. & Innes, M.) (Cambridge University Press, 2000).

51. Halsall, G. *Barbarian Migrations and the Roman West, 376–568*. (Cambridge University Press, 2007).

52. Heather, P. J. *Empires and Barbarians*. (Macmillan, 2009).

53. Looijenga, T. *Texts and Contexts of the Oldest Runic Inscriptions*. (Brill, Netherlands, 2003).

54. Birkmann, T. 71. A survey of ancient Nordic sources. in *The Nordic languages. An international handbook of the history of the North Germanic languages* 619–625 (De Gruyter Mouton, 2008). doi:10.1515/9783110197051-071.

55. van Dijk, E. *et al.* Climatic and societal impacts in Scandinavia following the 536 and 540 CE volcanic double event. *Clim. Past* **19**, 357–398 (2023).

56. Antonio, M. L. *et al.* Stable population structure in Europe since the Iron Age, despite

high mobility. *eLife* **13**, e79714 (2024).

57. Geary, P. J. *The Myth of Nations: The Medieval Origins of Europe*. (Princeton University Press, 2003).
58. Ringbauer, H. *et al.* ancIBD - Screening for identity by descent segments in human ancient DNA. 2023.03.08.531671 Preprint at https://doi.org/10.1101/2023.03.08.531671 (2023).
59. Allentoft, M. E. *et al.* 100 ancient genomes show repeated population turnovers in Neolithic Denmark. *Nature* **625**, 329–337 (2024).
60. Allentoft, M. E. *et al.* Population genomics of post-glacial western Eurasia. *Nature* **625**, 301–311 (2024).
61. Sousa da Mota, B. *et al.* Imputation of ancient human genomes. *Nat. Commun.* **14**, 3660 (2023).
62. Lawson, D. J., Hellenthal, G., Myers, S. & Falush, D. Inference of Population Structure using Dense Haplotype Data. *PLOS Genet.* **8**, e1002453 (2012).
63. Fischer, C.-E. *et al.* Origin and mobility of Iron Age Gaulish groups in present-day France revealed through archaeogenomics. *iScience* **25**, (2022).
64. Furholt, M. Social Worlds and Communities of Practice: a polythetic culture model for 3rd millennium BC Europe in the light of current migration debates. *Préhistoires Méditerranéennes* (2020) doi:10.4000/pm.2383.
65. Schiffels, S. *et al.* Iron Age and Anglo-Saxon genomes from East England reveal British migration history. *Nat. Commun.* **7**, 10408 (2016).
66. Lazaridis, I. *et al.* The genetic history of the Southern Arc: A bridge between West Asia and Europe. *Science* **377**, eabm4247 (2022).
67. Narasimhan, V. M. *et al.* The formation of human populations in South and Central Asia. *Science* **365**, eaat7487 (2019).

68. Glob, P. V. Studier over den jyske enkeltgravskultur. in *Fortid Og Nutid* 298–302 (Gyldendal, 1945).

69. Iversen, R. & Kroonen, G. Talking Neolithic: Linguistic and Archaeological Perspectives on How Indo-European Was Implemented in Southern Scandinavia. *Am. J. Archaeol.* **121**, 511–525 (2017).

70. Larsson, M. N. *et al.* Ancient Sheep Genomes reveal four Millennia of North European Short-Tailed Sheep in the Baltic Sea region. 2023.06.26.544912 Preprint at https://doi.org/10.1101/2023.06.26.544912 (2023).

71. Müller, J. & Vandkilde, H. The Nordic Bronze Age Rose from Copper Age Diversity: Contrasts in the Cimbrian Peninsula. in *Contrasts of the Nordic Bronze Age* (eds. Austvoll, K. I. et al.) vol. 1 29–48 (Brepols Publishers, Turnhout, 2020).

72. Østmo, E. *Krigergraver: en dokumentarisk studie av senneolittiske hellekister i Norge*. (Kulturhistorisk Museum, Universtitet i Oslo, 2011).

73. Johannsen, J. W. The Late Neolithic Expansion: Ancient and new traditions 2350-1700 BC. *Dan. J. Archaeol.* **12**, 1–22 (2023).

74. Austvoll, K. I. *Seaways to Complexity: A Study of Sociopolitical Organisation Along the Coast of Northwestern Scandinavia in the Late Neolithic and Early Bronze Age*. (Equinox Publishing Limited, 2021).

75. Vandkilde, H. *The Metal Hoard from Pile in Scania, Sweden: Place, Things, Time, Metals, and Worlds around 2000 BCE*. (Aarhus Universitetsforlag, 2017).

76. Kristiansen, K. Contrasting 3rd and 2nd millennium BC mobility in temperate Europe: migration versus trade. in *Moving northward: Professor Volker Heyd's Festschrift as he turns 60* (eds. Lahelma, A. et al.) (The Archaeological Society of Finland, Helsinki, 2023).

77. Aikio, A. An essay on Saami ethnolinguistic prehistory. in *A Linguistic Map of*

Prehistoric Northern Europe (eds. Grünthal, R. & Kallio, P.) vol. 226 63–117 (Société Finno-Ougrienne, Helsinki: Suomalais-Ugrilainen Seura, 2012).

78. Lang, V. Formation of Proto-Finnic – an archaeological scenario from the Bronze Age / Early Iron Age. in *Congressus duodecimus Internationalis Fenno-Ugristarum, Oulu 2015: plenary papers* (eds. Mantila, H., Leinonen, K., Brunni, S., Palviainen, S. & Sivonen, J.) 63–84 (University of Oulu, Oulu, 2015).
79. Hirt, H. Die Urheimat der Germanen: Nachwort. in *Neue Jahrbücher für das klassische Altertum, Geschichte und deutsche Litteratur* vol. 3 570–572 (1899).
80. Hachmann, R., Kossack, G. & Kuhn, H. *Völker zwischen Germanen und Kelten: Schriftquellen, Bodenfunde und Namengut zur Geschichte des nördlichen Westdeutschlands um Christi Geburt*. (Wachholtz, Rhine River Valley, 1962).
81. Schrijver, P. 3. Frisian between the Roman and the Early Medieval Periods: Language contact, Celts and Romans. in *3. Frisian between the Roman and the Early Medieval Periods: Language contact, Celts and Romans* 43–52 (Boydell and Brewer, 2017). doi:10.1515/9781787440630-010.
82. Knol, E. & IJssennagger, N. Palaeogeography and People. in *Frisians and Their North Sea Neighbours: From the Fifth Century to the Viking Age* (eds. Hines, J. & IJssennagger, N.) 5–24 (Boydell & Brewer, 2017).
83. Olalde, I. *et al.* The genomic history of the Iberian Peninsula over the past 8000 years. *Science* **363**, 1230–1234 (2019).
84. Diaconus, P. *History of the Lombards*. (University of Pennsylvania Press, 1974).
85. Arthur, F. *et al.* The impact of volcanism on Scandinavian climate and human societies during the Holocene: Insights into the Fimbulwinter eruptions (536/540 AD). *The Holocene* 09596836231225718 (2024) doi:10.1177/09596836231225718.
86. Knirk, J. E. 73. Runes : Origin, development of the futhark, functions, applications, and

methodological considerations. in *The Nordic Languages: Volume 1* 634–648 (De Gruyter Mouton, 2008). doi:10.1515/9783110197051-073.

87. Barnes, M. P. *Runes: A Handbook*. (Boydell Press, 2012).
88. Schulte, M. Runology and historical sociolinguistics: On runic writing and its social history in the first millennium. *J. Hist. Socioling.* **1**, 87–110 (2015).
89. Ottosson, K. 90. Old Nordic: A definition and delimitation of the period. in *The Nordic languages. An international handbook of the history of the North Germanic languages* vol. 1 787–793 (De Gruyter Mouton, 2002).
90. Riisøy, A. I. Danish Legal Procedure and a Common Scandinavian Law. in *Viking encounters: Proceedings of the Eighteenth Viking Congress* (eds. Pedersen, A. & Sindbæk, S. M.) 220–231 (Aarhus Universitetsforlag, 2020).
91. Jordanes. Chapter 1:23. in *The Gothic History of Jordanes in English Version* (Princeton University Press, 1915).
92. Procopius. *De Bellis [History of the Wars Book I-VIII]*. (Harvard University Press, 1918).
93. Skre, D. 3. Rulership and Ruler's Sites in 1st–10th-century Scandinavia. in *3. Rulership and Ruler's Sites in 1st–10th-century Scandinavia* (ed. Skre, D.) 193–244 (De Gruyter, 2020). doi:10.1515/9783110421101-003.
94. Söderberg, B. Aristokratiskt rum och gränsöverskridande. Järrestad och sydöstra Skåne mellan region och rike 600-1100. *Skrifter. Riksantikvarieämbetet, Arkeologiska undersökningar* vol. 62 (Lund University, 2005).
95. *Viking Dynasties. The Royal Families of Lejre and Uppsala. Between Archaeology and Text*. (Århus University Press, Århus, 2024).
96. Gansum, T. Borre - a royal manor with halls, mounds, harbour and ship graves. in *Viking Age Aristocratic Residences in Northern Europe* (ed. Ravn, M.) (Århus University Press., Århus, in press).

97. Hedeager, L. Poetry and picturing in deep historical time. in *Re-imagining Periphery: Archaeology and Text in Northern Europe from Iron Age to Viking and Early Medieval Periods* (eds. Hillerdal, C. & Ilves, K.) 107–116 (Oxbow Books, 2020).

98. Jørgensen, L. From tribute to the estate system, 3rd-12th century. A proposal for the economic development of the magnates' residences in Scandinavia based on settlement structure from Gudme, Tissø and Lejre. in *Kingdoms and Regionality: Transactions from the 49th Sachsensymposium, 1998 in Uppsala* (ed. Arrhenius, B.) 73–82 (Archaeological Research Laboratory, Stockholm University, Stockholm, 2001).

99. Tummuscheit, A. & Witte, F. The Danevirke: Preliminary Results of New Excavations (2010–2014) at the Defensive System in the German-Danish Borderland. *Offas Dyke J.* **1**, 114–136 (2019).

100. Price, N. Climate change and the Fimbulwinter. in *Oxford Handbook of Scandinavian Archaeology* (Oxford University Press, Oxford, in press).

101. Holst, M. Farmsteads and communities. in *Oxford Handbook of Scandinavian Archaeology* (Oxford University Press, Oxford, in press).

102. McNeill, W. *Plagues and Peoples*. (Knopf Doubleday Publishing Group, 1998).

103. Stang, C. S. *Lexikalische Sonderübereinstimmungen zwischen dem Slavischen, Baltischen und Germanischen*. (Univ.-Forl., 1972).

104. Grikpėdis, M. & Matuzeviciute, G. M. A Review of the Earliest Evidence of Agriculture in Lithuania and the Earliest Direct AMS Date on Cereal. *Eur. J. Archaeol.* **21**, 264–279 (2018).

105. Piličiauskas, G. *et al.* The transition from foraging to farming (7000–500 cal BC) in the SE Baltic: A re-evaluation of chronological and palaeodietary evidence from human remains. *J. Archaeol. Sci. Rep.* **14**, 530–542 (2017).

106. Kroonen, G., Jakob, A., Palmér, A. I., Sluis, P. van & Wigman, A. Indo-European

cereal terminology suggests a Northwest Pontic homeland for the core Indo-European languages. *PLOS ONE* **17**, e0275744 (2022).

107. Greenhill, S. J. Do languages and genes share cultural evolutionary history? *Sci. Adv.* **7**, eabm2472 (2021).

108. Barbieri, C. *et al.* A global analysis of matches and mismatches between human genetic and linguistic histories. *Proc. Natl. Acad. Sci.* **119**, e2122084119 (2022).