Early Nordic genetics (and some Gaulish too)

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DNA from archaeological remains shows that immigration to Scandinavia was exceptional during the Viking period

Date: January 5, 2023

Source: Stockholm University

Summary: A new study based on 297 ancient Scandinavian genomes analysed together with the genomic data of 16,638 present day Scandinavians resolve the complex relations between geography, ancestry, and gene flow in Scandinavia -- encompassing the Roman Age, the Viking Age and later periods. A surprising increase of variation during the Viking period indicates that gene flow into Scandinavia was especially intense during this period.

FULL STORY

A new study based on 297 ancient Scandinavian genomes analysed together with the genomic data of 16,638 present day Scandinavians resolve the complex relations between geography, ancestry, and gene flow in Scandinavia -- encompassing the Roman Age, the Viking Age and later periods. A surprising increase of variation during the Viking period indicates that gene flow into Scandinavia was especially intense during this period.

An international study coordinated from Stockholm and Reykjavik investigates the development of the Scandinavian gene pool over the latest 2000 years. In this effort the scientists relied on historic and prehistoric genomes, and from material excavated in Scandinavia. These ancient genomes were compared with genomic data from 16,638 contemporary Scandinavians. As the geographical origin and the datings were known for all these individuals, it was possible to resolve the development of the gene pool to a level never realised previously.

Dr Ricardo Rodríguez Varela at the Centre for Palaeogenetics*, who analysed all the data and extracted some of the ancient DNA used in the study, explains: "With this level of resolution we not only confirm the Viking Age migration. We are also able to trace it to the east Baltic region, the British-Irish Isles and southern Europe. But not all parts of Scandinavia received the same amounts of gene flow from these areas. For example, while British-Irish ancestry became widespread in Scandinavia the eastern-Baltic ancestry mainly reached Gotland and central Sweden."

The gene pool bounced back after the Viking period

Another new discovery in this study was what happened to the gene pool after the Viking period. The scientists were surprised to find that it bounced back in the direction of what it looked like before the Viking period migration.

Professor Anders Götherström at the Centre for Palaeogenetics, who is a senior scientist on the study, is intrigued: "Interestingly, the non-local ancestry peaks during the Viking period while being lower before and after. The drop in current levels of external ancestry suggests that the Viking-period migrants got less children, or somehow contributed proportionally less to the gene pool than the people who were already in

Scandinavia."

Yet a new discovery was the history of the northern Scandinavian gene pool. There is a genetic component in northern Scandinavia that is rare in central and western Europe, and the scientists were able to track this component in northern Scandinavia through the latest 1000 years.

Dr Ricardo Rodríguez Varela comments, "We suspected that there was a chronology to the northern Scandinavian gene pool, and it did indeed prove that a more recent influx of Uralic ancestry into Scandinavia define much of the northern gene pool. But if it is recent, it is comparatively so. For example, we know that this Uralic ancestry was present in northern Scandinavia as early as during the late Viking period."

Based on well-known Swedish archaeological sites

The study is based on a number of well-known Swedish archaeological sites. For example, there are genomes from the 17th century warship Kronan, from the Viking and Vendel period boat burials in the lake Mälaren Valley, and from the migration period ring fortress Sandby borg on Öland.

Anders Götherström conclude: "We were working on a number of smaller studies on different archaeological sites. And at some point it just made sense to combine them into a larger study on the development of the Scandinavian gene pool.

The study, published today in *Cell*, is an international effort with several collaborators, but it was led by Dr Ricardo Rodríguez Varela and Professor Anders Götherstörm at Stockholm University, and Professor Agnar Helgason, and Kristján Moore at deCODE in Reykavijk.

*The Centre for Palaeogenetics (CPG) is a joint venture between Stockholm University and the Swedish Museum of Natural History.

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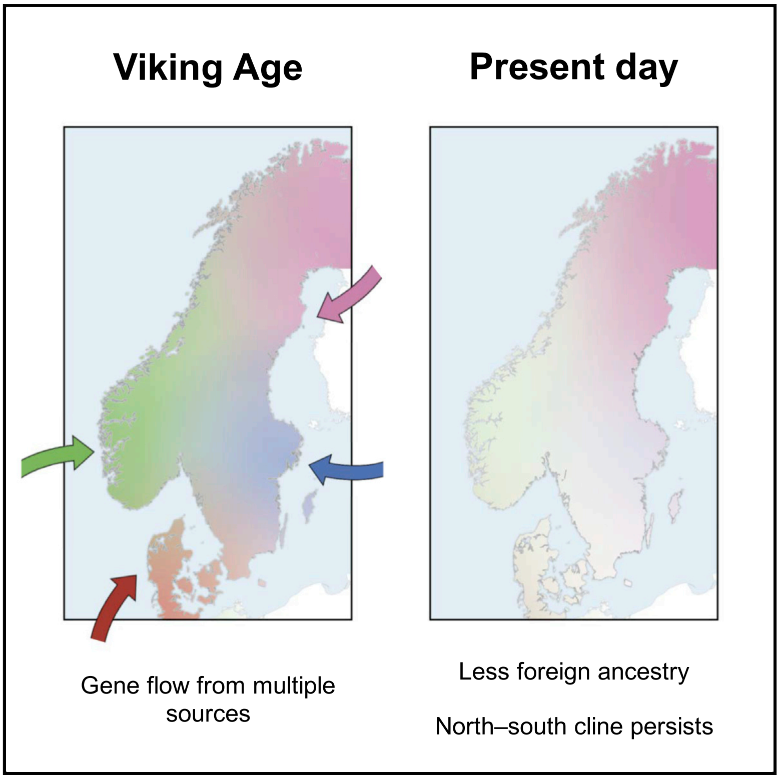
Article

The genetic history of Scandinavia from the Roman Iron Age to the present

Graphical abstract



Highlights

- British-Irish ancestry has an impact on Scandinavia from the Viking period onward
- Eastern Baltic ancestry is more localized to Gotland and central Sweden
- Modern Scandinavians have less non-local ancestry than Viking Age samples
- The north-south genetic cline is mainly due to differential levels of Uralic ancestry

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In brief

The analysis of 297 ancient genomes, spanning the last 2,000 years of Scandinavian history, sampled from historically important archeological sites, resolves the complex relationship between geography, ancestry, and gene flow throughout the study period in Scandinavia, including across the Viking Age.

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Article

The genetic history of Scandinavia from the Roman Iron Age to the present

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SUMMARY

We investigate a 2,000-year genetic transect through Scandinavia spanning the Iron Age to the present, based on 48 new and 249 published ancient genomes and genotypes from 16,638 modern individuals. We find regional variation in the timing and magnitude of gene flow from three sources: the eastern Baltic, the British-Irish Isles, and southern Europe. British-Irish ancestry was widespread in Scandinavia from the Viking period, whereas eastern Baltic ancestry is more localized to Gotland and central Sweden. In some regions, a drop in current levels of external ancestry suggests that ancient immigrants contributed proportionately less to the modern Scandinavian gene pool than indicated by the ancestry of genomes from the Viking and Medieval periods. Finally, we show that a north-south genetic cline that characterizes modern Scandinavians is mainly due to the differential levels of Uralic ancestry and that this cline existed in the Viking Age and possibly earlier.

INTRODUCTION

The ancestry of most modern European populations can primarily be traced, in slightly variable proportions, to the following three ancient genetic sources: European Mesolithic hunter-gatherers, Anatolian Neolithic farmers, and early Bronze Age groups from the Steppe (e.g., Skoglund et al.,[1] Lazaridis et al.,[2] and Haak et al.[3]). The mixing of these sources in Scandinavia is relatively well documented.[1,4–6] However, the extent and impact of migration into Scandinavia after the Bronze Age is less clear.

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Two studies based on ancient DNA (aDNA) indicate gene flow into Scandinavia during the Viking Age (750–1050 CE).[7,8] Other studies of modern Scandinavians have described a marked northward increase in Uralic ancestry,[9–11] which is likely linked to gene flow of Uralic ancestry to the eastern Baltic region toward the end of the Bronze Age.[12]

At the end of the Roman Iron Age (1–400 CE) and the beginning of the migration period (400–550 CE), Scandinavia saw the emergence of new hierarchies, with religious, social, and economic power concentrated among ruling elites, profiting from social networks reaching far into the Roman Empire.[13] Long-distance trading and mercenary activities provided means to acquire and accumulate wealth and status in a hierarchical and unstable political power structure.[13–17] However, the impact of migration during these periods on the Scandinavian gene pool is not well known.

The Viking Age is associated with a marked increase in the flow of goods, customs, technology, and people to and from Scandinavia relative to preceding periods.[18] One indication of migration during this period is the observation of gene flow into Scandinavia from the south, west, and east.[7,8]

Here, we make use of an extensive set of 297 ancient Scandinavian genomes spanning a 2,000-year transect from the beginning of the Roman Iron Age (1st century) to the 19th century, and genotypes from 16,638 modern individuals from Denmark and each county of Norway and Sweden to assess the impact of migration on the Scandinavian gene pool (Figure 1). We combine new whole genome sequence (WGS) data from 48 ancient individuals (Table S1A) with previously published WGS data from 249 ancient individuals[7,8,19,20] (Table S1B), including additional sequence depth for 13 previously published Viking Age individuals from the Swedish town Sigtuna.[7] The new sites include boat burials, chamber burials, and archeological sites like the migration period Sandby borg ringfort and 12 individuals from the Swedish warship Kronan that sank in 1676 CE near the island Öland off the southeast coast of Sweden. The individuals were classified into five periods: Pre-Viking (1–749 CE), Viking (750–949 CE), Late Viking (950–1099 CE), Medieval (1100–1349 CE), and Post-Medieval period (1350–1850 CE) (Figure 1). The former periods are used here as a chronological shorthand label that is not intended to imply that all individuals from the Viking or Late Viking periods were actually "Vikings," just individuals living during these periods. By partitioning the gene pool of Scandinavia geographically and chronologically, it is possible to make inferences about the nature and magnitude of the events that shaped it from the end of the Roman Iron Age to the present. In particular, we have two main aims. First, to document the timing and geographical extent of gene flow into Scandinavia during this period. Second, to investigate when and how the currently observed north-south genetic cline was formed in Norway and Sweden and to what extent shifts in genetic ancestry played a role in this process.

RESULTS

New genomic data from 77 ancient Scandinavians

We generated WGS data from 64 new and 13 previously published individuals.[7] All the individuals exhibit typical features of aDNA,[21] including short-read length and cytosine deamination concentrated at the end of reads (Table S1). DNA contamination was estimated for both X chromosome and mitochondrial DNA (mtDNA), as described in Ebenesersdóttir et al.[22] (Table S1). We considered samples with two X chromosomes to be contaminated if they showed contamination (> 10%) for the mtDNA and samples with one X chromosome to be contaminated if they showed contamination (> 10%) for both X chromosome and mtDNA. From the new generated WGS data, we removed individuals with autosomal coverage < 0.1× (n = 10) (Table S1A) and the individual with lower coverage from each pair of genetically related individuals with a k0 value < 0.8 and pi_HAT > 0.06 (third-degree kinship) (n = 6) (Table S2; STAR Methods). The remaining 48 new individuals had an autosomal coverage ranging from 0.11 to 64.84× (median = 1.33) (Table S1A). In total, 48 new and 249 published ancient genomes were used in subsequent analyses.

The origin and fate of gene flow into Scandinavia

To explore the nature and extent of genetic differences between ancient individuals from the five different periods, we first

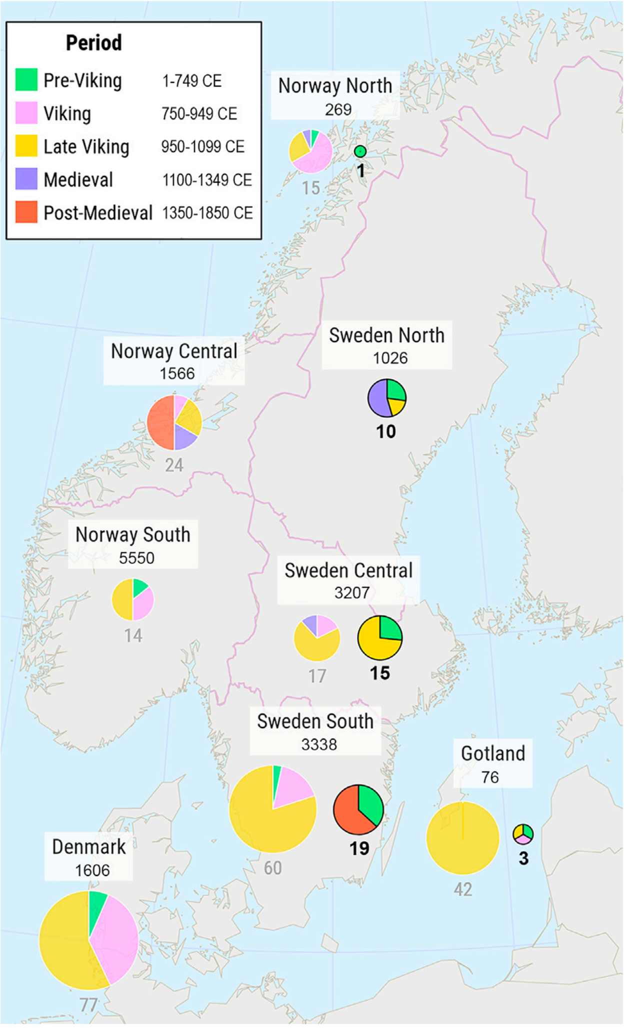


Figure 1. Map summarizing sample locations of ancient Scandinavian genomes analyzed in this study

Faded pie charts represent previously published samples, and pie charts with dark outlines represent newly presented samples. The numbers in brackets represent the number of modern Scandinavians sampled in each region.
See also Table S1.

projected them onto a principal component analysis (PCA) based on microarray genotypes for 168,599 SNPs from 9,052 modern individuals from 67 west Eurasian populations (Figure 2; see Table S3 and STAR Methods). The first principal component (PC1) separates modern individuals according to a north-south geographical axis, whereas the second principal component (PC2) separates them according to an east-west axis. Modern Scandinavians, placed in the top-right of the PCA plot, are well differentiated from most western European and Baltic populations (Wilcoxon test p value < 2.2e−16, see Table S4).

Interestingly, the mean projected PC1 and PC2 coordinates of ancient Scandinavians change over time (Figures 2A and S1A–S1P). First, the Pre-Viking individuals are significantly different from modern Scandinavians for both PC1 and PC2 (Wilcoxon test p values 1.107e−11 and 0.0057, respectively; Figure 2A; Table S4). They are consistently shifted toward the positive values for PC1 in the direction of Neolithic and Mesolithic Scandinavian hunter-gatherers, with some individuals falling outside the range of all modern Europeans (Figure S1Q). The Viking and Late Viking groups are also significantly different from modern Scandinavians on PC1, but in the opposite (negative) direction (Wilcoxon test p values are 0.0199 and 0.0084, respectively). In contrast, the more recent Medieval and Post-Medieval Scandinavians are not significantly differentiated from their modern counterparts on PC1 (Wilcoxon test p values are 0.1299 and 0.2509, respectively). However, for PC2, Post-Medieval Scandinavians are significantly different from their modern counterparts (Wilcoxon test p value 1.142e−6) (Table S4).

Our results indicate a surge of gene flow from the British-Irish Isles into Scandinavia during the Viking period, with additional gene flow from the east in the Late Viking period, consistent with results reported in a previous study.[8] We formally tested for the impact of gene flow into Scandinavia from different sources across time using f_4-statistics of the form f_4(Mbuti, ancient group; Danish, modern population). Here, the Mbuti represents an outgroup, the modern population is a proxy for a potential ancient non-Scandinavian source population and individuals from Denmark represent the southernmost Scandinavian population. To detect gene flow from the west, south, and east of Europe into the different temporal groups of Scandinavia, we selected three modern populations as proxies for different European regions: Irish for west (British-Irish), Sardinian for south (south Europe), and Lithuanian for east (Baltic). To better understand the timing and geographical extent of gene flow from east, west, and south Europe into Scandinavia, we split the ancient individuals from Norway and Sweden by sub-regions: north, central, and south, with the Swedish island of Gotland as a separate region (Figure 1).

We find that affinity to the three non-Scandinavian source populations is low in the Pre-Viking period but higher in nearly all other subsequent periods of ancient Scandinavians, consistent with gene flow from these regions into Scandinavia during the Viking period (Figures 3A–3C).

Figure 3A indicates a marked gene flow of eastern Baltic ancestry into Gotland during the Viking and Late Viking periods, a natural entry point to Sweden from the East, followed by a more gradual increase in central and south Sweden until the Post-Medieval period. Interestingly, present-day individuals from the south and central regions of Sweden are characterized by relatively low levels of eastern Baltic ancestry—similar to those from the Pre-Viking period. Figure 3A shows a lesser degree of eastern Baltic ancestry in northern Sweden and the regional groups of Norway across the different periods, consistent with their greater geographical distance from eastern Baltic source populations.

Figure 3B reveals a slightly different pattern of gene flow of British-Irish ancestry into Scandinavia, with uniformly low levels in Pre-Viking groups but with marked early increases during the Viking period in south Sweden and Denmark. In south Sweden, British-Irish ancestry then decreases to its modern level over time but remained significantly greater than in the Pre-Viking period. In all seven Scandinavian regions with Pre-Viking period individuals, we see a consistently higher level of British-Irish

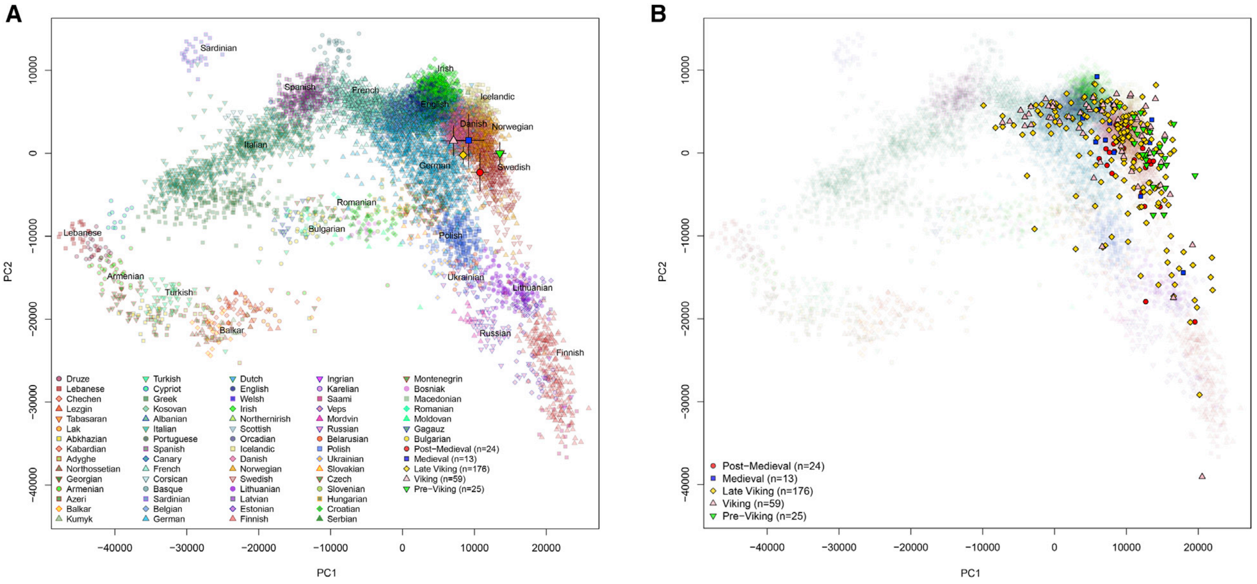


Figure 2. Genotypes from ancient Scandinavians projected onto the first two principal components of modern West Eurasians

(A) The mean and 95% confidence interval for each ancient group for PC1 and PC2.

(B) All ancient individuals from the five different periods.

See also Figure S1 and Table S3.

ancestry in modern populations than in Pre-Vikings. This points to a lasting and widespread gene flow from the British-Irish Isles into Scandinavia, most likely due to migration during the Viking period. Nonetheless, the overall magnitude of British-Irish gene flow into Scandinavia appears to have been small, as witnessed by the relatively clear distinction between modern populations from Scandinavia and the British-Irish Isles.[22]

Overall, the ancient Scandinavian groups have a greater affinity to modern Irish individuals than to modern Sardinians (Figures 3B and 3C). Nonetheless, the patterns of affinity across regions and periods are broadly similar, indicating that these two test populations partly capture the same signal of gene flow. Indeed, when the two f_4 models are calculated per ancient individual, we observe a correlation coefficient of 0.735 ($p < 2.2e{-}16$). However, both the PCA in Figure 2B and a direct comparison of the f_4 results for British-Irish and Sardinian ancestry (Figures S2A and S2B) indicate that these ancestries can be distinguished and that both individuals with British-Irish ancestry and south European ancestry were present in Scandinavia during the Viking period, as previously shown by Margaryan et al.[8] These conclusions are further supported by results based on the qpAdm method (Figures 4 and S3A for extended version).

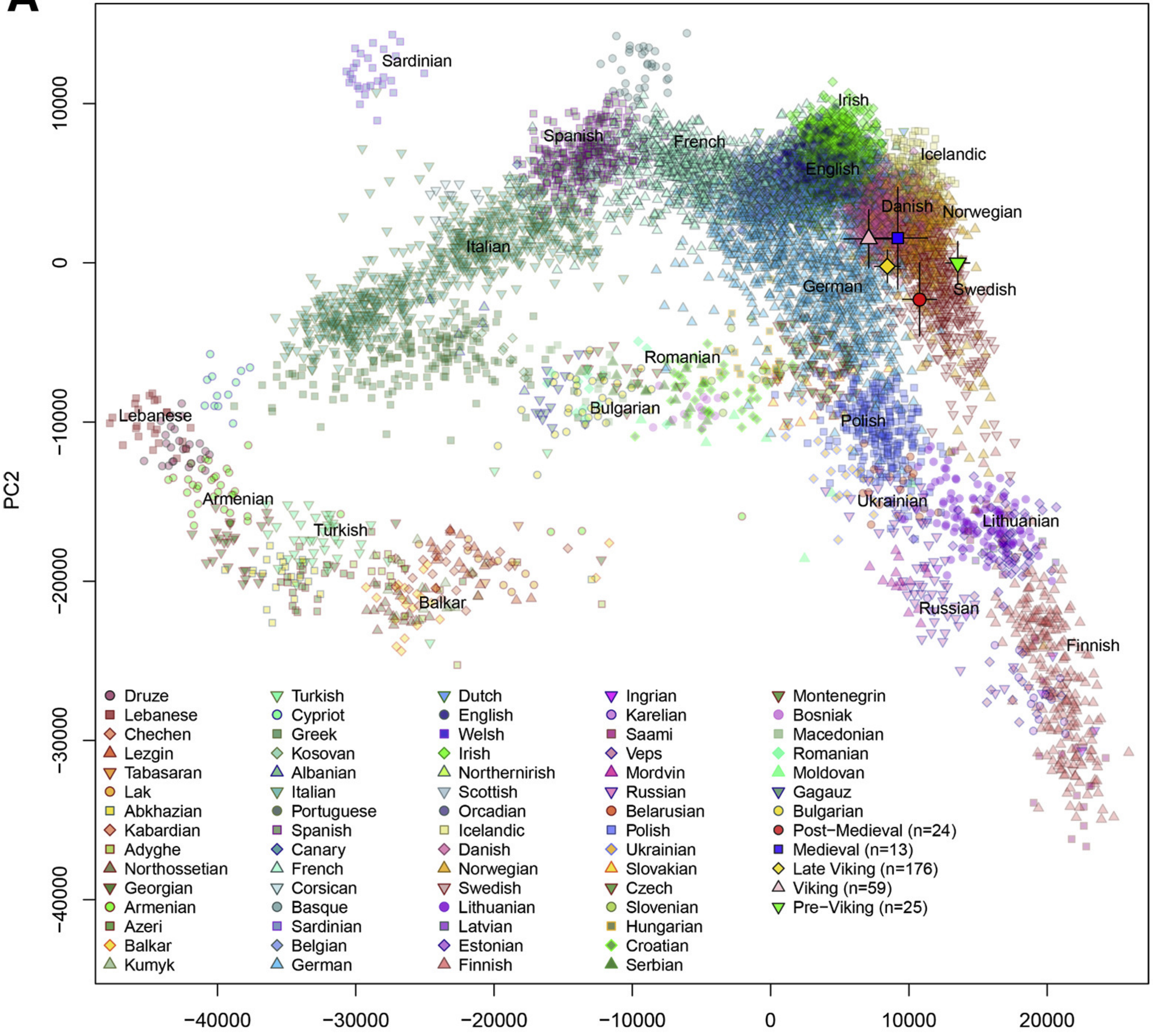
A definitive example of British-Irish gene flow is the Late Viking period female (sal002) found in central Sweden, who appears fully British-Irish in ancestry (Figures S2A and S3B; Tables S5 and S6). Although our results indicate minimal gene flow into Scandinavia from the British-Irish Isles before the Viking period, we find one interesting exception in individual VK213, a young female excavated in Gerdrup, Denmark, and dated to the 5th century (391–527 CE).[8,23] She has the third-highest f_4 value for British-Irish ancestry among the 297 ancient individuals found in Scandinavia, with PCA projections and qpAdm results indicating that this female is likely to have traced most of her ancestry to the British-Irish Isles (Figures S2A and S3B; Tables S5 and S6). This finding raises the possibility that VK213 ended up in Denmark as an indirect consequence of the Anglo-Saxon migration to the British Isles.

To investigate possible sex bias in the gene flow into Scandinavia, we compared previously described f_4-statistic analyses of the form f_4(Mbuti, PopX; Danish, PopC) based on autosomal loci with equivalent analyses based only on X chromosome loci. Although we note that the X chromosomal f_4-statistics have wide standard errors due to the smaller number of loci used, the results shown in Figure 5 provide at least tentative evidence that gene flow into Scandinavia of eastern Baltic ancestry and, to a lesser extent, also British-Irish ancestry was female biased. We also observe direct evidence for gene flow from the British-Irish Isles through males, in the form of two Late Vikings (VK31 and VK405) and one Medieval (wes008) individual carrying the British-Irish-characteristic[24] Y-haplogroup R1b1a1b1a1a2c (Table S1).

The north-south genetic cline in Scandinavia

Previous studies have reported a marked north-south cline of genetic variation in present-day Scandinavia.[9–11] The differentiation of northern Scandinavians has been attributed to a combination of genetic drift due to small population size and gene flow from Uralic-speaking groups.[9] To explore the geographical pattern of Uralic-associated ancestry in modern Scandinavians, we first calculated an f_4-statistic of the form f_4(Mbuti, X; Danish, Finnish) for the complete set of 16,638 modern Scandinavians, where the Danes and Finns represent the southern and northern ends of the cline, respectively, and X represents each of the 19

A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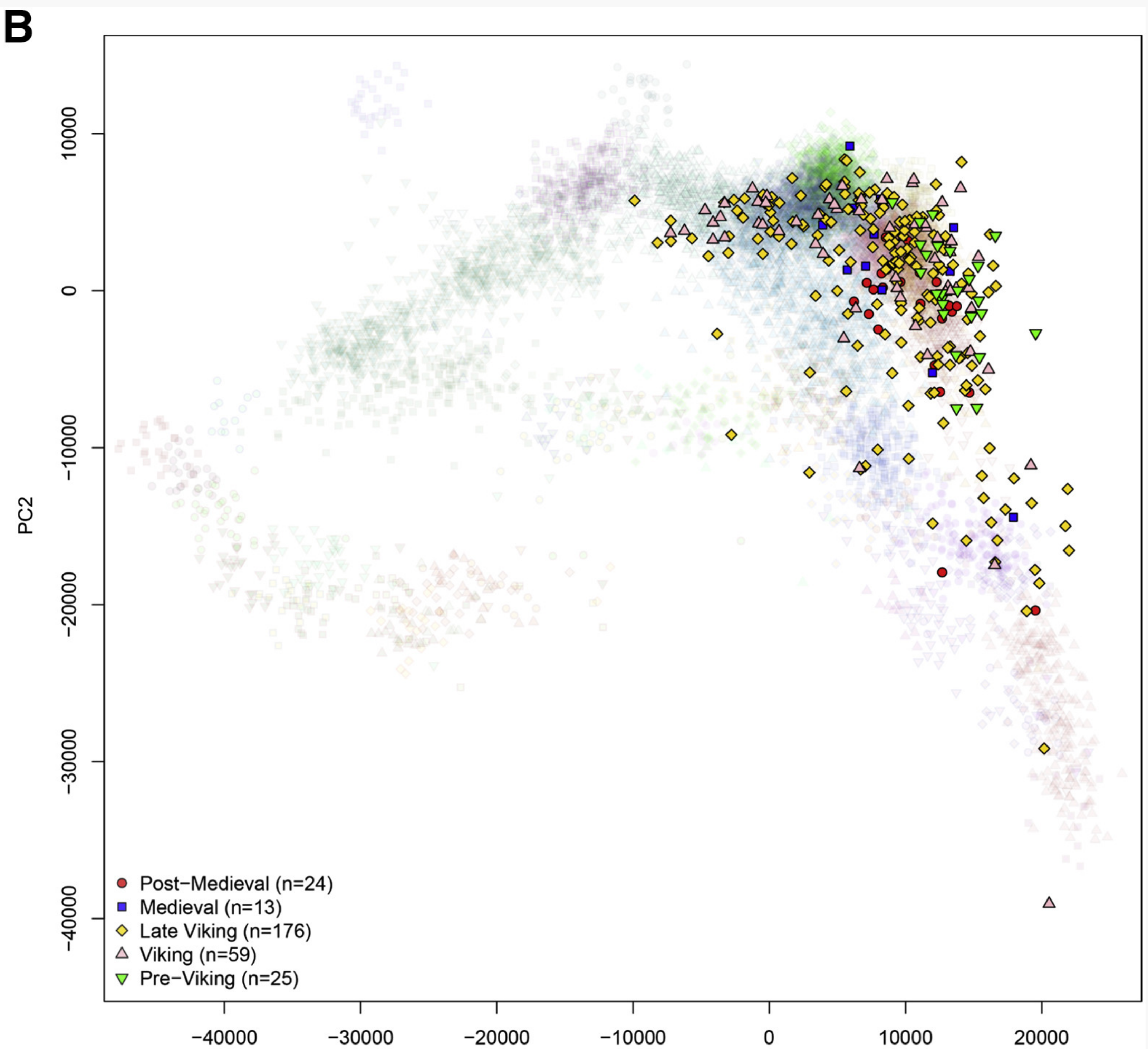
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▲ Viking (n=59)
▼ Pre−Viking (n=25)

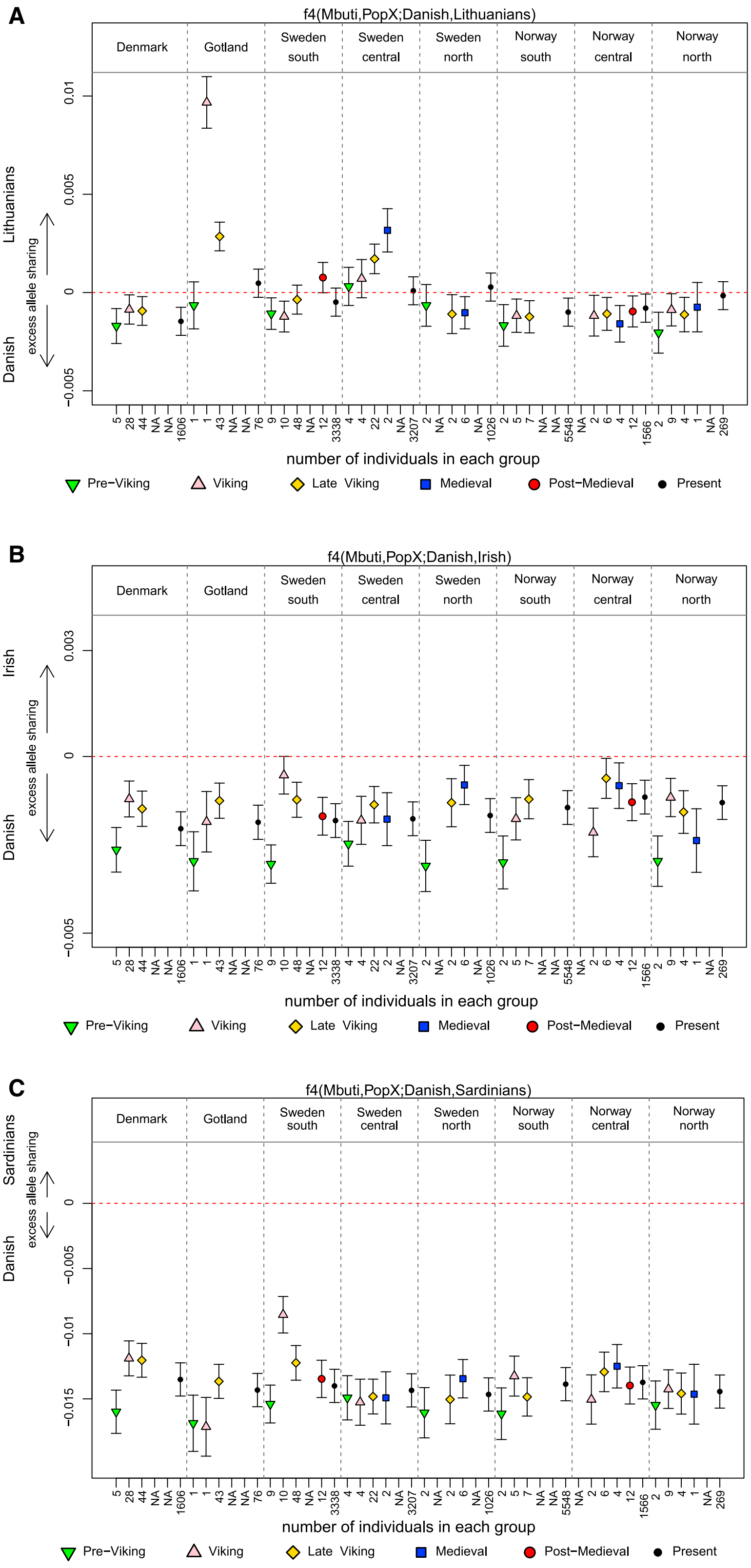


Figure 3. f_4-statistics plots

The f_4-statistics are based on the test f_4(Mbuti, PopX; Danish, modern test population), showing the contrasting allele sharing of the ancient and modern Scandinavian groups divided in period and regions between a modern test population and modern Danish populations. The sample size of each Scandinavian group is represented on the x axis. PopX represents the populations in the legend, and the bars show a 95% confidence interval.

(A) Lithuanians as the test population.

(B) Irish as the test population.

(C) Sardinians as the test population.

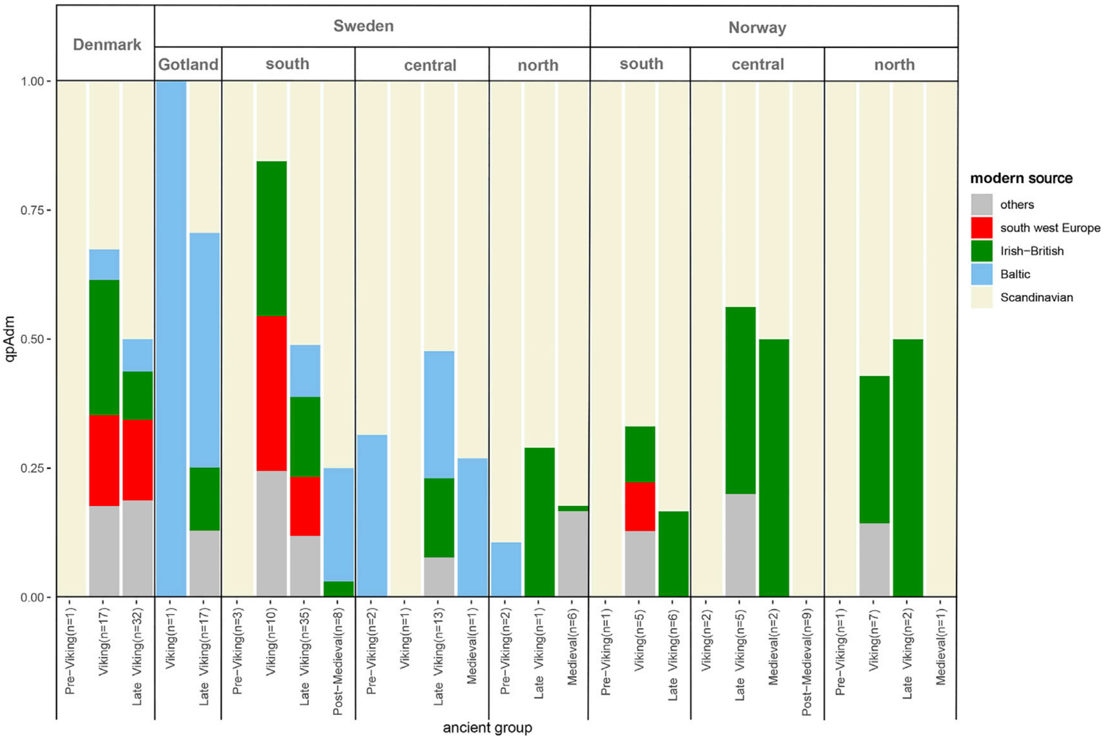
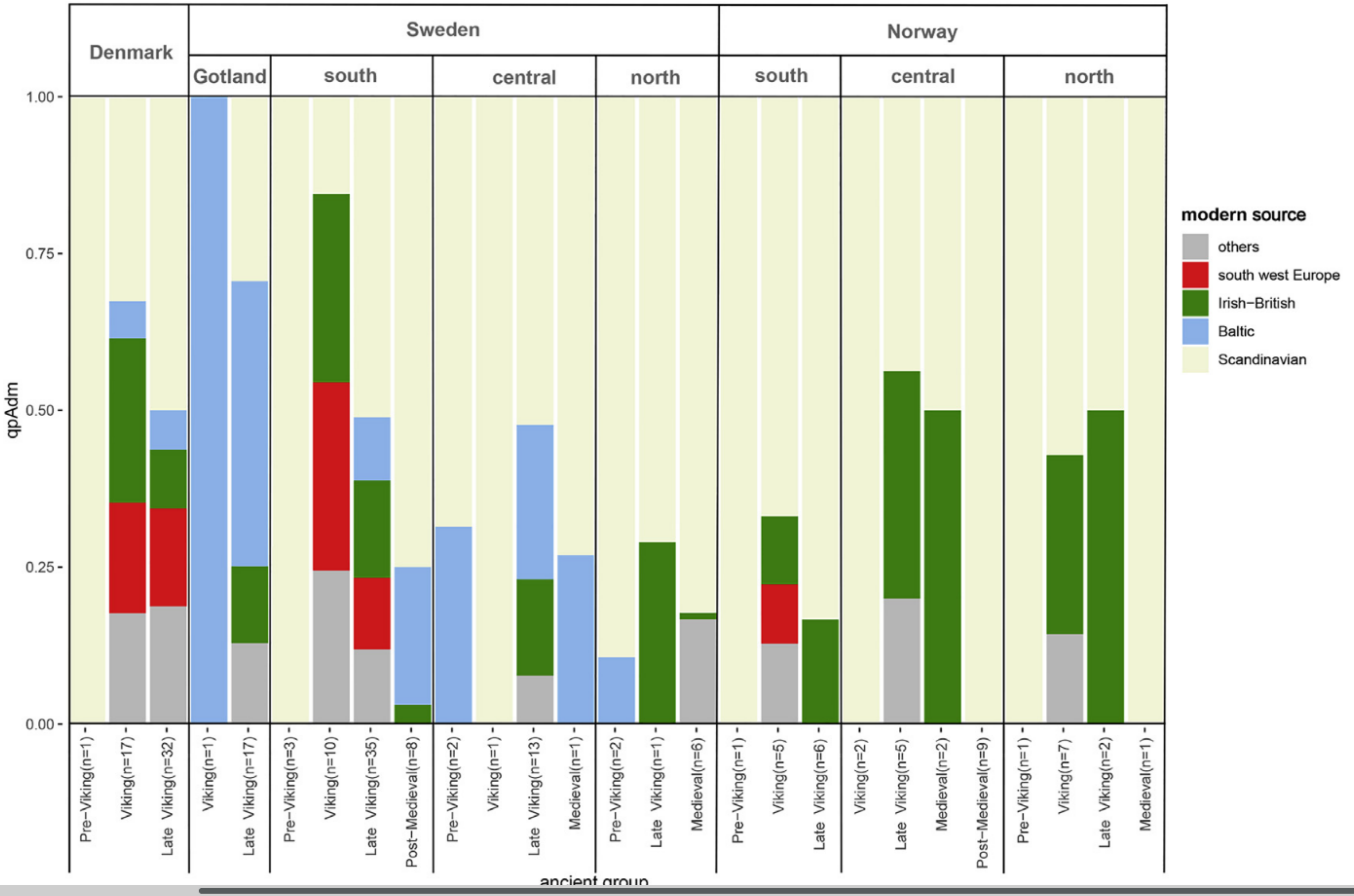


Figure 4. Simplified qpAdm plot using modern populations as sources
Only samples with $p > 0.01$ and coverage >0.5× are shown.
See also Figure S3A and Table S6.

Norwegian or 21 Swedish counties. Finns represent a Uralic source population on the grounds that they are a neighboring population with relatively high levels of Uralic ancestry[25] and speak a language that belongs to the Uralic family. Figure 6A shows a clear clinal pattern of southward declining Uralic ancestry in both countries, which is more marked and linear in Sweden than in Norway. An almost identical pattern is seen for East Asian and Native American ancestry, used here as proxies of Siberian-Uralic ancestry (Figure 6B). These were estimated with a supervised run of ADMIXTURE using five training populations from the 1000 genomes dataset (Utah residents with Northern and Western European ancestry [CEU], Indian Telugu in the UK [ITU], Han Chinese in Beijing, China [CHB], Peruvian in Lima Peru [PEL], and Yoruba in Ibadan, Nigeria [YRI]) (Figure S4). To further explore the north-south differences, we used the first 10 PCs in a PCA based on the 16,638 modern Scandinavians (Figure S3C) to calculate the average Euclidean PC distance between the 1,606 modern Danes and each of the 7,385 modern Norwegian and 7,647 modern Swedish individuals. Summarizing these distances by counties in Norway and Sweden, we yet again observe a clinal pattern, with the greatest PC distances in the north (Figures 6C and 6D). We note that these PC distances do not specifically target Uralic ancestry but rather reflect any differences picked up by the PCs. Thus, the observation that f_4(Mbuti, X; Danish, Finnish), East Asian (CHB) ancestry, and Native American (PEL) ancestry account for 80% of the variation in PC distance to modern Danes in linear regression (Table S7), indicates that the clinal pattern of genetic variation between northern and southern Scandinavia is primarily due to differential levels of Uralic ancestry.

We calculated the same statistics for the 297 ancient individuals from different regions of Scandinavia in an attempt to shed light on when and how the north-south cline appeared. Figure 7 shows one scatterplot for each period, comparing ancient individuals and modern regional groups using two of these statistics: f_4(Mbuti, X; Danish, Finnish) and the PCA distance from Danish. These results show that some version of the north-south cline existed from at least the Viking period onward. In particular, the two Viking Age samples from northern Norway with extreme values for both statistics (VK519 and VK518, the latter carrying the Saami-characteristic mitochondrial haplogroup U5b1b1a[26]) show that individuals with Uralic ancestry had settled in northern Scandinavia at that time and that ADMIXTURE was taking place with groups characterized by south Scandinavian ancestry. However, more data from ancient individuals from the central and northern regions of Scandinavia are required to determine the extent to which the latitudinal shape of the cline developed from the Viking period to the present.

In modern Scandinavians, we also see the cline reflected in the geographical distribution of the Uralic-associated[27] Y-haplogroup N1a1 (Figures S5A and S6A) and its association with the autosomal ancestry cline ($p < 1.6e{-14}$ for logit regression of N1a1 presence on CHB+PEL ancestry, f_4(Mbuti, X; Danish, Finnish) or PC1 coordinate on Figures S3C and S6B). Thus, it may be that N1a1 entered Scandinavian populations via the same Uralic gene flow that generated the north-south


Denmark
Sweden
Norway
Gotland
south
central
north
south
central
north
qpAdm
1.00
0.75
0.50
0.25
0.00
Pre−Viking(n=1)
Viking(n=17)
Late Viking(n=32)
Viking(n=1)
Late Viking(n=17)
Pre−Viking(n=3)
Viking(n=10)
Late Viking(n=35)
Post−Medieval(n=8)
Pre−Viking(n=2)
Viking(n=1)
Late Viking(n=13)
Medieval(n=1)
Pre−Viking(n=2)
Late Viking(n=1)
Medieval(n=6)
Pre−Viking(n=1)
Viking(n=5)
Late Viking(n=6)
Viking(n=2)
Late Viking(n=5)
Medieval(n=2)
Post−Medieval(n=9)
Pre−Viking(n=1)
Viking(n=7)
Late Viking(n=2)
Medieval(n=1)
ancient group
modern source
others
south west Europe
Irish−British
Baltic
Scandinavian

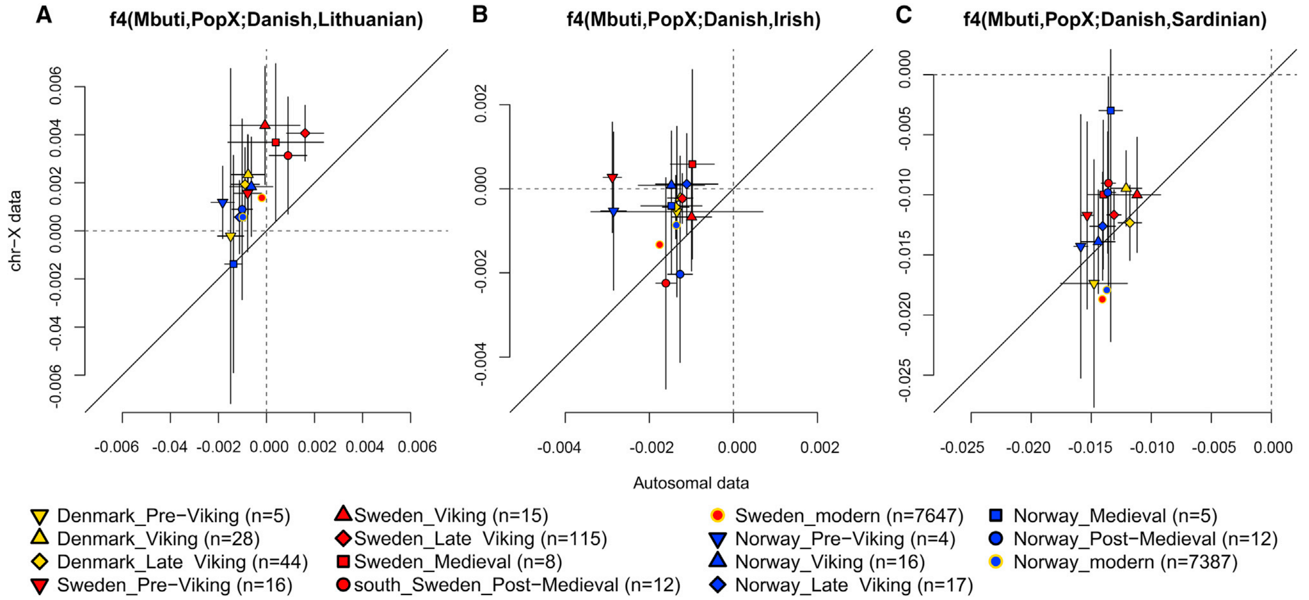


Figure 5. Sex bias f_4-statistic

Scatter plot of the form f_4(Mbuti, PopX; Danish, PopC) where PopX represents the ancient individuals grouped by period and country and the modern populations from Sweden and Denmark whereas PopC represents modern Lithuanians, Irish, and Sardinians. In the x axis are the results using autosomal SNPs, and in the y axis are the results of the X chromosome SNPs. Bars represent 95% confidence intervals.

(A) Lithuanian as PopC.

(B) Irish as PopC.

(C) Sardinians as PopC.

cline. Interestingly, however, the earliest Scandinavian N1a1 carriers we observe that six Pre-Vikings (200–520 CE) from four sites in eastern Sweden show less northern affinity than modern Norwegian and Swedish N1a1 carriers (t tests for CHB+PEL ancestry p = 0.040, f_4[Mbuti, X; Danish, Finnish] p = 0.087, PC1 coordinate on Figure S3C p = 0.0009; Figure S6B). Conversely, the 13 Viking to Post-Medieval N1a1 carriers are not significantly different to modern carriers (CHB+PEL ancestry p = 0.168, f_4(Mbuti, X; Danish, Finnish) p = 0.365, PC1 coordinate on Figure S3C p = 0.629). This may indicate a more ancient initial introduction of N1a1 into Scandinavia before its later dispersal along the modern cline of north-south ancestry.

It is not possible to tell from our results whether the north-south cline existed in some form before the Viking period, as none of the 25 Pre-Viking period individuals have substantial levels of Uralic ancestry. Figure 7A shows a very subtle upward curve of points that can, at best, be interpreted as suggestive evidence of some Uralic ancestry. At the end of this curve is a female (rtp003) from Rombäck in Västernorrland in northern Sweden dating to 450–500 CE, who has both the highest f_4 value among Pre-Viking period individuals and is also assigned a small proportion (1.4%) of Native American (PEL) ancestry, which may be indicative of Uralic ancestry (Table S8). However, additional individuals from the Pre-Viking period are needed to provide more definitive evidence.

From the Post-Medieval period, the only individuals showing notable levels of Uralic ancestry are four crew members of the warship Kronan (kro006, kro009, kro011, and kro014) (Figure 7E), two of whom carry Y-haplogroup N1a1. Of the 24 individuals from this period, 12 are from the Kronan shipwreck and 12 are from central Norway. All the Kronan crew members are assigned to south Sweden in this study because that is where the wreck was found, and their remains were recovered. However, historical records indicate that infantry soldiers were recruited from the northern counties of Sweden like Västerbotten, sailors from the southeast coast of Sweden, and some officers from Finland,[28,29] which fits well with our results (Figures S1R and S2A; Table S5).

DISCUSSION

Our analyses of the impact of gene flow on the different regions of Scandinavia across 2,000 years, from the beginning of the Roman Period to the present, indicate a major increase during the Viking period and a potential bias toward females in the introduction of eastern Baltic and, to a lesser extent, British-Irish ancestries. Gene flow from the British-Irish Isles during this period seems to have had a lasting impact on the gene pool in most parts of Scandinavia. This is perhaps not surprising, given the extent of Norse activities in the British-Irish Isles, starting in the 8th century with recurrent raids and culminating in the 11th century North Sea Empire, the personal union that united the kingdoms of Denmark, Norway, and England.[18] The circumstances and fate of people of British-Irish ancestry who arrived in Scandinavia at this time are likely to have been variable, ranging from the forced migration of slaves to the voluntary immigration of more high-ranking individuals such as Christian missionaries and monks. The female sal002 found in a boat burial in Sala in

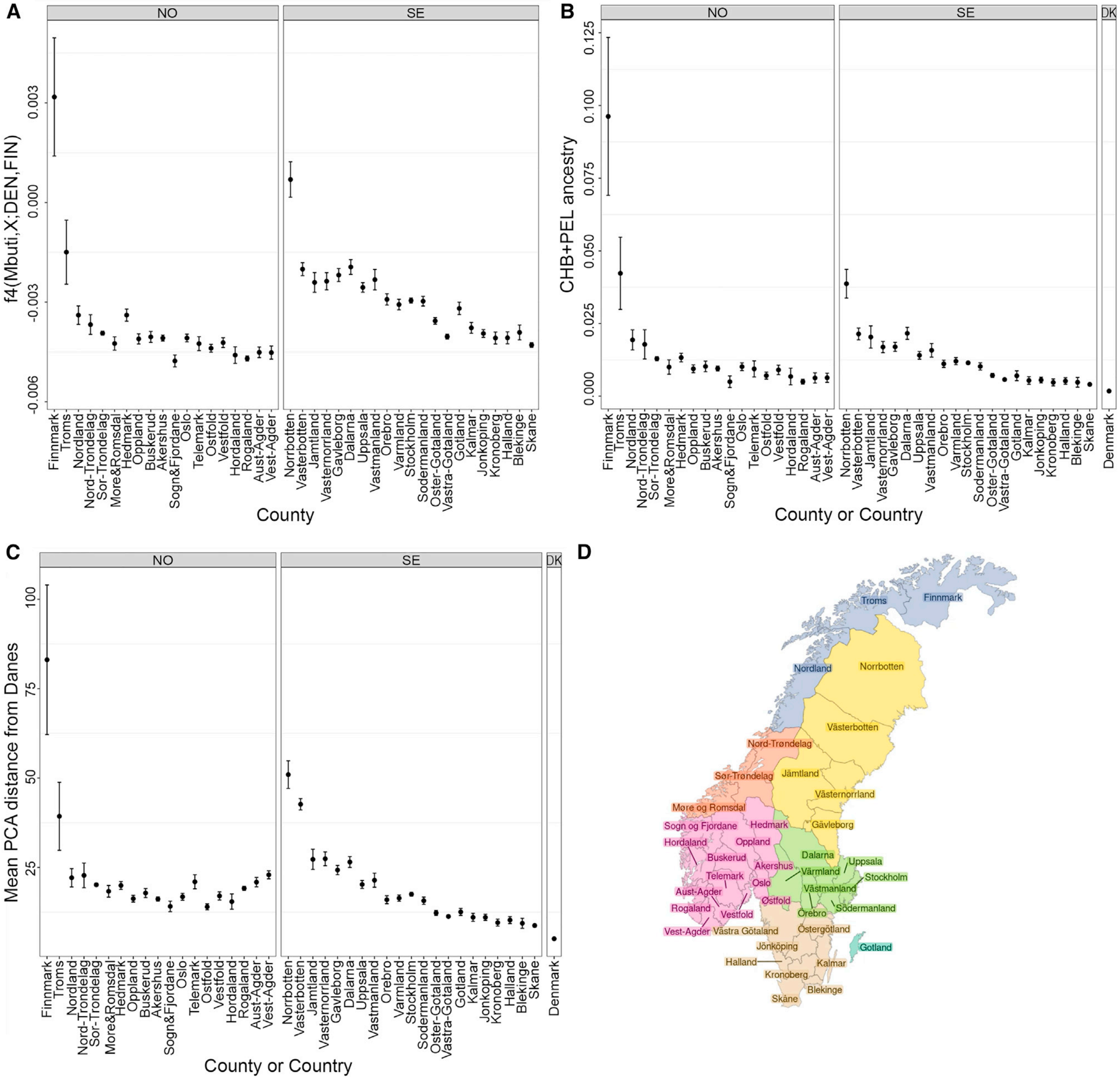


Figure 6. North-south cline of Uralic ancestry across Norwegian and Swedish counties ordered from most northern to southernmost

(A) f_4-statistics based on the test f_4(Mbuti, county; Danish; Finnish) showing the contrasting allele sharing of each modern Swedish and Norwegian county between modern Danes and Finns. Bars represent 95% confidence intervals.

(B) Percentage of CHB and PEL ancestry in the ADMIXTURE analyses (Figure S6). Bars represent 95% confidence intervals.

(C) Average Euclidean PC distance between modern Danes and modern Norwegian and Swedish individuals using the first 10 PCs from a PCA based on the 16,638 modern Scandinavians. Bars represent 95% confidence intervals.

(D) Map of the Norwegian and Swedish counties.

central Sweden from the Late Viking period represents an interesting case.[30] She appears fully British-Irish in ancestry, and the character of her burial indicates that she probably had a high social status in the community that buried her.[31] The situation may have been very different for VK213, a female from Gerdrup, Denmark, dated to the 5th century, who is also British-Irish in ancestry but appears to have been buried without any grave goods.[23] Although this finding indicates that British-Irish gene flow into Scandinavia began at least as early as the 5th century during the Anglo-Saxon migration to the British Isles, our results suggest that most of it likely occurred during the Viking Age. Although its overall impact on the gene pool was small, we

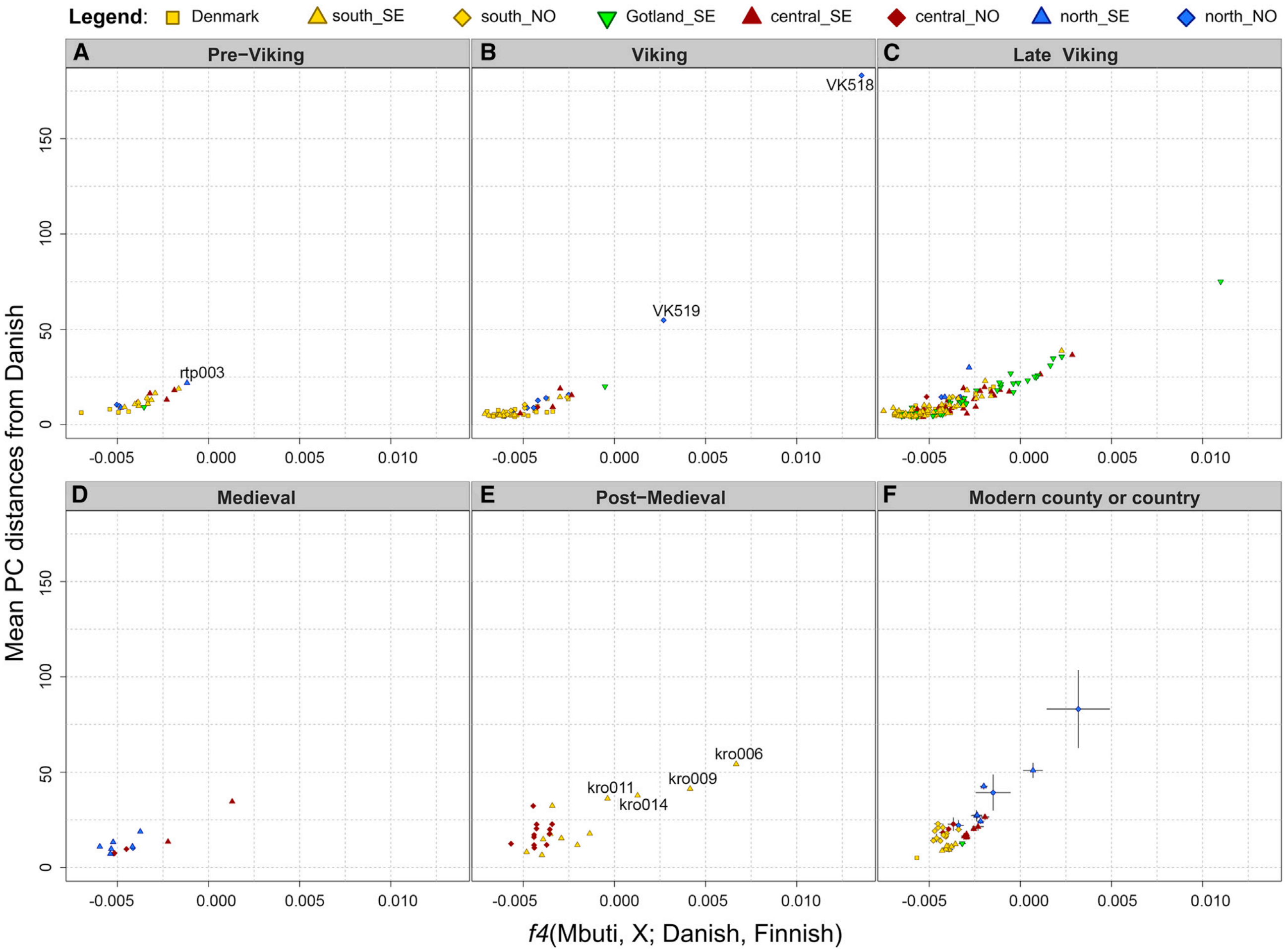


Figure 7. Scatter plots showing Uralic ancestry versus distances to Danish in the ancient individuals and the modern Scandinavian counties/countries

In the x axis, we show the Uralic affinity using f_4-statistics based on the test f_4(Mbuti, X; Danish; Finnish), and in the y axis, the average Euclidean PC distance between each individual/county or country and Danish using the first 10 PCs from a PCA based on the 16,638 modern Scandinavians. (A–E) Display ancient individuals divided into periods, and (F) show populations instead of individuals from Denmark and each county of Sweden and Norway. Bars represent 95% confidence intervals.

See also Table S8.

show that British-Irish gene flow had a lasting impact on all regions of Scandinavia, such that modern Scandinavians have more British-Irish ancestry than Pre-Viking period individuals from the same regions (Figure 3B).

Curiously, we see a tendency for the magnitude of British-Irish ancestry to be greater during the Viking and Late Viking periods than in the present, particularly in south Sweden, where we have relatively large sample sizes for the different periods. This represents a generalization of a trend recently demonstrated on a local scale for Trondheim.[19] A more striking pattern of this kind is seen for eastern Baltic ancestry in Gotland and central Sweden (Figure 3A). The increase of eastern Baltic ancestry in these regions during the Viking Age is consistent with historical sources attesting to contacts such as tributary relations, trade, conflicts, and treaties (e.g., Blomkvist[32,33] and Zachrisson[34]). However, the notable drop in eastern Baltic ancestry in modern individuals from these regions relative to their predecessors requires further attention. There are three conceivable explanations for such a large changeover in a relatively short period of time. First, intervening gene flow from other regions with less such ancestry. Second, past restrictions on reproduction due to a social hierarchy that was stratified in some way by ancestry (similar to that postulated by Ebenesersdóttir et al.[22] in relation to Norse and Gaelic ancestry during the first generations of settlement in Iceland). Third, an overrepresentation in the archeological record of individuals with a particular ancestry relative to those alive at that time and in that place, for example, due to ancestry-related differences in funerary traditions. It is thought that cremation was the dominant funerary tradition in Scandinavia during the Iron Age until the Early Viking Age; hence, any remains from this period that yield DNA are, in an important sense, exceptional. Also, several Viking and Late Viking period samples derive from urban environments with extensive trade networks rather than rural communities.[7,8] Thus, it is possible that the available ancient genomes from the Viking and Late Viking periods are not a random sample from all ancestors of modern Scandinavians that lived during those periods. Based on current evidence, it is hard to determine which of the three explanations listed above might account for the apparent regionally specific decline in eastern Baltic and British-Irish ancestry or whether more than one may have had an impact. Although our study is based on a relatively large number of ancient genomes, even more will be needed to answer such fine-scale questions about the evolution of gene pools in time and space.

We also shed light on the nature and origin of the currently observed north-south clinal pattern of genetic variation in Scandinavia, showing that it is mainly due to northwardly increasing Uralic ancestry that was present during the Viking period and perhaps earlier. The subset of crew members from the Kronan warship who cluster with present-day Finnish (Figures S1R and S2A; Table S5) provides a relatively late example of the kinds of migratory forces that continued the spread of Uralic ancestry within Scandinavia. With more ancient genomes from northern Scandinavia, it may be possible to both determine when groups with Uralic ancestry first entered the region and to more fully document how the distinctive modern cline emerged from subsequent bidirectional gene flow between north and south. Overall, however, our study demonstrates that like in the case of so many other human groups,[22,35–37] the long-term demographic history of Scandinavians has been characterized by gene flow from several different source populations, with an extensive impact in the case of the north-south cline of Uralic ancestry.

Limitations of the study

The lack of samples from the period 500 BCE to 1 CE, partly because cremation was the main funerary tradition during this period, resulted in this study being restricted to the last 2,000 years of Scandinavian genetic history.

STAR★METHODS

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AUTHOR CONTRIBUTIONS

Conceived and designed the study, A.G., A.H., R.R.-V., K.H.S.M., J.S., T.Z., M.K., S.S.E., and G.M.K.; laboratory work, R.R.-V., M.K., N.K., V.K.L., V.S., L.G.-F., and L. Alrawi; bioinformatic analysis, A.H., R.R.-V., K.H.S.M., S.S.E., and G.M.K.; modern and ancient reference datasets preparation, K.H.S.M., S.S.E., M.K., E.G., G.L.C., E.H., I.K., T.O., L. Alfredsson, T.F.H., T.W., C.B., A.R.M., K.S., M.J., P.S., P.P.-R., A.O., E.D., L. Alrawi, M.J., M.T.P.G., and S.G.; archeological support, T.Z., J.S., A.K., L.P.-D., C.A., B.B., B.S., P.P.-R., A.C., G.T.-W., F.G., C.H.-J., K.L., L.E., H.V., A.G., M.K., and R.R.-V.; writing – review & editing, A.H., A.G., R.R.-V., K.H.S.M., and S.S.E. with input from all co-authors; funding acquisition, A.G.; supervision, A.H. and A.G.

DECLARATION OF INTERESTS

A.H., K.H.S.M., K.S., and S.S.E. are employees of deCODE genetics.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Biological samples		
Ancient Human skeletal element	This study	als001, Swedish History Museum, Inventory number SHM 10035, 10289, 20061
Ancient Human skeletal element	This study	als007, Swedish History Museum, Inventory number SHM 10035, 10289, 20061
Ancient Human skeletal element	This study	als010, Swedish History Museum, Inventory number SHM 10035, 10289, 20061
Ancient Human skeletal element	This study	als015, Swedish History Museum, Inventory number SHM 10035, 10289, 20061
Ancient Human skeletal element	This study	bro100, Swedish History Museum, Inventory number SHM33379
Ancient Human skeletal element	This study	enb508, Swedish History Museum, Inventory number SHM15268
Ancient Human skeletal element	This study	frc007, Jamtli
Ancient Human skeletal element	This study	ful001, Swedish History Museum Inventory number 20724
Ancient Human skeletal element	This study	gam872, Swedish History Museum, Inventory number SHM34835
Ancient Human skeletal element	This study	gor164, Swedish History Museum, Inventory number SHM34347
Ancient Human skeletal element	This study	gor358, Swedish History Museum, Inventory number SHM34347
Ancient Human skeletal element	This study	hav001, Swedish History Museum, Inventory number SHM8064
Ancient Human skeletal element	This study	hvr009, The Directorate for Cultural Heritage: Askeladden ID 114142-1.
Ancient Human skeletal element	This study	kro001, Kalmar County Museum, Kronan 38C K16
Ancient Human skeletal element	This study	kro002, Kalmar County Museum, Kronan 25C K14
Ancient Human skeletal element	This study	kro004, Kalmar County Museum, Kronan 5C K2
Ancient Human skeletal element	This study	kro006, Kalmar County Museum, Kronan 26C K18
Ancient Human skeletal element	This study	kro008, Kalmar County Museum, Kronan 6C K9
Ancient Human skeletal element	This study	kro009, Kalmar County Museum, Kronan 31C K1
Ancient Human skeletal element	This study	kro010, Kalmar County Museum, Kronan 42C K17
Ancient Human skeletal element	This study	kro011, Kalmar County Museum, Kronan 50C K13
Ancient Human skeletal element	This study	kro012, Kalmar County Museum, Kronan 8C K8
Ancient Human skeletal element	This study	kro013, Kalmar County Museum, Kronan 3C K11
Ancient Human skeletal element	This study	kro014, Kalmar County Museum, Kronan 27C K6
Ancient Human skeletal element	This study	kro015, Kalmar County Museum, Kronan 43C K4
Ancient Human skeletal element	This study	kvi001, Swedish History Museum, Inventory number SHM19888
Ancient Human skeletal element	This study	lau001, Gotland's museum
Ancient Human skeletal element	This study	lov001, Swedish History Museum, Inventory number SHM29401
Ancient Human skeletal element	This study	rtp001, Swedish History Museum, Inventory number SHM20438
Ancient Human skeletal element	This study	rtp003, Swedish History Museum, Inventory number SHM20438

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REAGENT or RESOURCE	SOURCE	IDENTIFIER
Ancient Human skeletal element	This study	sal002, Swedish History Museum, Inventory number SHM11357
Ancient Human skeletal element	This study	snb010, Kalmar County Museum
Ancient Human skeletal element	This study	snb012, Kalmar County Museum
Ancient Human skeletal element	This study	snb013, Kalmar County Museum
Ancient Human skeletal element	This study	snb014, Kalmar County Museum
Ancient Human skeletal element	This study	snb017, Kalmar County Museum
Ancient Human skeletal element	This study	snb018, Kalmar County Museum
Ancient Human skeletal element	This study	snb019, Kalmar County Museum
Ancient Human skeletal element	This study	stg018, Sigtuna Museum
Ancient Human skeletal element	This study	ven001, Swedish History Museum, Inventory number SHM9785
Ancient Human skeletal element	This study	vls696, Swedish History Museum, Inventory number SHM34069
Ancient Human skeletal element	This study	wes001, Swedish History Museum, Inventory number SHM32079
Ancient Human skeletal element	This study	wes003, Swedish History Museum, Inventory number SHM32079
Ancient Human skeletal element	This study	wes004, Swedish History Museum, Inventory number SHM32079
Ancient Human skeletal element	This study	wes005, Swedish History Museum, Inventory number SHM32079
Ancient Human skeletal element	This study	wes007, Swedish History Museum, Inventory number SHM32079
Ancient Human skeletal element	This study	wes008, Swedish History Museum, Inventory number SHM32079
Ancient Human skeletal element	This study	wes056, Swedish History Museum, Inventory number SHM32079
Chemicals, peptides, and recombinant proteins		
Proteinase K	VWR Sweden	Cat#1.24568.0100
EDTA buffer solution pH 8.0 (0.5 mol/l) for biotechnology, sterile	VWR Sweden	Car#E522-100ML
Sodium acetate	Sigma Aldrich Sweden	Cat#S2889
Guanidine hydrochloride	Sigma Aldrich Sweden	Cat#50933
Isopropanol	Sigma-Aldrich Sweden	Cat#67-63-0
Tween-20	Sigma-Aldrich Sweden	Cat#9005-64-5
Sodium phosphate PH 6.0	VWR Sweden	Cat#101447-426
ATP	Fermentas/Thermo Scientific	Cat#R0441
T4 Polynucleotide Kinase	Thermo Scientific	Cat#EK0032
T4 DNA Polymerase	Fermentas/Thermo Scientific	Cat#EP0062
Bst polymerase (supplied with 10X ThermoPol reaction buffer)	NEB/BioNordika	Cat#M0275S
AmplitTaq Gold	Invitrogen/life technologies	Cat#4311816
ATP	Fermentas/Thermo Scientific	Cat#R0441
10X Tango Buffer	Fermentas/Thermo Scientific	Cat#BY5
High Pure Viral Nucleic Acid Large Volume Kit	Roche	Cat#5114403001
T4 DNA Ligase	Fermentas/Thermo Scientific	Cat#EL0011
Min Elute PCR Purification Kit	QIAGEN	Cat#28006
PEG-4000	Sigma	Cat#1546569
Agencourt AMPure XP beads (60ml)	Beckman Coulter	Cat#A63881

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REAGENT or RESOURCE	SOURCE	IDENTIFIER
Critical commercial assays		
High Sensitivity DNA (chips + reagents) (Bioanalyzer 2100)	Agilent Technologies	Cat#5067-4626
Deposited data		
European Nucleotide Archive	PRJEB57364	(ERS13672864: ERS13672799)
Oligonucleotides		
IS1_adapter.P5:5^0-A*C*A*C*TCTTTCC CTAC ACGACGCTCTTCCG*A*T*C*T-3^0 (* indicates a PTO bond)	Meyer and Kircher[38]	Biomers
IS2_adapter.P7:5^0-G*T*G*A*CTGGAGTT CAG ACGTGTGCTCTTCCG*A*T*C*T-3^0 (* indicates a PTO bond)	Meyer and Kircher[38]	Biomers
IS3_adapter.P5+P7: 50-A*G*A*T*CGGAA*G*A*G*C-30(* indicates a PTO bond)	Meyer and Kircher[38]	Biomers
IS4:(5^0-AATGATACGGCGACCACCGAGATCTA CACTCTTTCCCTACACGACGCTCTT 3^0)	Meyer and Kircher[38]	Biomers
P7 indexing: (5^0-CAAGCAGAAGACGGCATAC GAGATxxxxxxxGTGACTGGAGTT CAGACG TGT 3^0) where x is one of 228 different 7 bp indexes provided in Meyer and Kircher[38]	Meyer and Kircher[38]	Biomers
Software and algorithms		
R	R Core Team[39]	https://www.R-project.org/
AdapterRemoval (v. 2.3.1)	Schubert et al.[40]	https://github.com/MikkelSchubert/adapterremoval
BWA aln/samse (v. 0.7.10)	Li and Durbin[41]	http://bio-bwa.sourceforge.net/
FilterUniqueSAMCons.py	Kircher[42]	https://bioinf.eva.mpg.de/fastqProcessing/
PMDtools (v.v 0.60)	Skoglund et al.[43]	https://github.com/pontussk/PMDtools
samtools (v. 1.9)	Li et al.[44]	https://github.com/samtools/samtools
MapDamage 2.0	Jónsson et al.[45]	https://ginolhac.github.io/mapDamage/
PicardTools v.1.21.3,	N/A	(http://broadinstitute.github.io/picard/)
BEDtools-2.29.2	Quinlan et al.[46]	https://bedtools.readthedocs.io/en/latest/
KING	Manichaikul et al.[47]	https://www.kingrelatedness.com/
ANGSD (v. 0.911)	Korneliussen et al.[48]	http://popgen.dk/angsd/index.php/ANGSD
EIGENSOFT (v. 6.0.1)	Patterson et al.[49]	https://github.com/DReichLab/EIG
AdmixTools (v. 3.0)	Patterson et al.[50]	https://github.com/DReichLab/AdmixTools
ADMIXTURE (v. 1.3.0)	Alexander et al.[51]	https://dalexander.github.io/admixture/download.html
PLINK (v. 1.9)	Chang et al.[52]	(https://www.cog-genomics.org/plink/1.9/)
lcMLkin	Lipatov et al.[53]	https://github.com/COMBINE-lab/maximum-likelihood-relatedness-estimation

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources and reagents should be directed to and will be fulfilled by the lead contact, RRV (ricardo.rodriguez.varela@arklab.su.se).

Materials availability

This study did not generate new unique reagents.

Data and code availability

The new aligned to NCBI build 38 (mapped, filtered and rescaled BAM files) sequence data reported in this paper can be accessed and downloaded from the European Nucleotide Archive (ENA) under the following study accession number: PRJEB57364 (ERS13672864: ERS13672799).

Data are available in the main text or supplementary figures.

Any additional information required to reanalyze the ancient data reported in this study is available from the lead contact upon request.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Description of archaeological sites and archaeological material

*When listing samples at the end of each section below, we use (XY) for individuals that are genetically males and (XX) to refer to individuals that are genetically females. We used bold letters when genetic sex contradicts the archaeological or osteological sex determination.

Alsike

Tuna in Alsike parish, Uppland (Sweden), situated by the water route leading towards Old Uppsala, is known for its burial ground containing inhumation burials in chambers and boats under flat ground. The site was found by a local farmer in 1893. Excavations were made in 1895 and in 1928, and a full report of all fieldwork was published in 1934.[54] The oldest of the graves is a well-furnished early Vendel period burial (c. 550 CE) in a possible chamber and a child burial from the same period. Stray objects from the Migration period (c. 440–560 CE) could belong to older settlement remains at the site, or rather older burials that were ruined when later burials were constructed. Following the early Vendel period burials, there seems to have been a lacuna of c. 200 years in the excavated graves before the site was used for burials again c. 750, continuing throughout the whole Viking Age (750–1050 CE). Ten Viking Age boat burials for both men and women have been found, as well as four Viking Age burials of uncertain type or in chambers.[54,55] The shallow depressions that are still seen on the site likely represent more burials that were not excavated.

Grave XIV found in the eastern part of the burial ground is a weapon burial with one individual (als001), identified as a male based on archaeological analyses. The burial was furnished with a sword among other things. At the man's waist were sword fittings in silver, including a belt buckle with inlays of garnet cloisonné set in gold, a unique piece for the region where the garnets are from India.[54,56] Stones framed the body, which may have been placed in a wooden coffin in a shroud, features that are linked to changes in burial traditions.[57] Some scholars have suggested that the male had spent some time abroad (e.g., Arrhenius[56]). However, strontium isotopic value from molar teeth suggests that the individual was local to the Mälar region.[58] The burial is typologically dated to the transition between the Migration and Vendel periods c. 540/550–610/620 CE.[57]

Sample als010 comes from a tooth taken from a cranium which in the museum archives has been associated with boat burial XI, featuring a boat of unknown type. However, the cranium does not match the post-cranial remains from the burial, so is likely from another individual. While the skeletal material from the cemetery at Tuna in Alsike is generally very well preserved, there is some uncertainty in the first recovery by the local farmer as well as in subsequent antiquarian handling. Thus, the identification of individuals must be done with caution. Nevertheless, the individuals are as a group connected to the site. Grave XII, situated next to grave XI, was a double burial (one of the interred individuals sampled as als007) with weapons but only a single set of objects, indicating the other individual was buried without grave goods. Two horses, two dogs, a capercaillie and a black grouse were among the grave goods. The grave is typologically dated to c. 950–1000 CE.[54]

In the western part of the burial ground was boat grave III, dated to c. 800–900 CE. The grave goods consisted of mostly female dress accessories as well as some weapons, along with two horses and a dog. The human remains were in a heap, which indicated that the grave had been opened before the excavation.[54] Grave VI is a double keelboat burial for a male and a female, dated to c. 900–950 CE, furnished with weapons and jewellery such as oval brooches and beads.[54] Grave IX, possibly a chamber burial, was dated to c. 900–1050 CE. The grave goods included several animals, but few objects compared to other graves excavated at the site.[54] The remains (als002) in Grave IX were archaeologically identified as female.

Samples: als001 (XY) = grave XIV, als002 (**XY**) = grave IX, als007 (XY) = grave XII, ind. 2, als010 (XX), als014 (XX) = grave VI, als015 (XY) = grave III

Curated at: Swedish History Museum, Inventory number SHM 10035, 10289, 20061

Alstahaug

Horvnes in Alstahaug municipality, Nordland County, Norway (66 N, 12 15′E) is situated just south of the Arctic Circle on the coast of the southern part of Nordland. The site is located on the same isthmus in the mouth of a fjord as the farm Sandnes, which is mentioned as a magnate farm in the 9th century in *Egils Saga Skalla-Grímssonar*.[59] Archaeological excavations have revealed a large dwelling site at Sandnes with activities starting around the beginning of the CE.[60] The Horvnes burial is one of few known in Sandnes where people were buried before Christianization in the 11th century.[61] The grave, a stone cist or small chamber, built of eleven big boulders, situated in a low cairn, 7,5 m in diameter, was excavated in 2008 by NTNU, University Museum in Trondheim. At least six individuals were buried in the Horvnes grave during the Iron Age, spanning a period of at least 1000 years. All the deceased individuals were inhumated, which is consistent with the burial practice at this time in Northern Norway. According to radiocarbon dating, the oldest burial took place around 100 BCE and the youngest one around 900 CE. It seems that it was after the last burial that the cist was covered by the cairn. One of the stones in the cairn had a cross, probably a Christian cross, and may have marked the end of the pagan burials in the cist.[61,62]

According to osteological investigations, the individual (hvr009) died around the age of 30.[63,64] This individual (hvr009) is directly radiocarbon dated to the Roman Iron Age, 60–215 CE 95.4% probability (1888±29BP, Ua-75069) calibrated using OxCal v4.4.4[65] and IntCal 13 atmospheric curve.[66]

Samples: hvr009 (XX) = M500AD Horvnes 2008.

Curated at: Norwegian University of Science and Technology, University Museum: Museum number T24129.

The grave cairn: The Directorate for Cultural Heritage: Askeladden ID 114142-1.

Eksta

The remains of a female skeleton were accidentally found in 1931 in a gravel pit in Kvie (kvi001), five kilometres off the coast in Eksta parish in southwestern Gotland (Sweden). The remains were revealed to be part of an inhumation burial, poorly furnished with only two eyed bone pins, and five beads: two of shell, two natural stones and one amber bead, and a piece of iron thread. Four more graves were later excavated and were typologically dated to the Viking Age (RAÄ Eksta 108:1[67]). Although belonging to the Viking Age, kvi001's inhumation does not resemble a traditionally Gotlandic female burial. This may indicate that the individual could have been of low social standing, possibly a thrall. The cranium of the individual had been artificially deformed, unclear though if caused by head flattening or binding. This is most unusual, but is known in three cases in the skeletal material dated to the Viking Age that has been recovered in present Sweden. Osteologically, the skeletal parts were determined as belonging to a female 55–60 years of age.[68]

Samples: kvi001 (XX) = Swedish History Museum Inventory number SHM 19888:1 or grave 3/1931

Curated at: Swedish History Museum, Inventory number SHM19888

Enbacken

The grave field Enbacken (RAÄ 89) is situated on the grounds of the settlement Årsta is one of five grave fields located in Uppsala parish, Uppland (Sweden). The burial ground, which seems to have been used for a relatively short period, consisted of approximately 35 graves, 23 of which were examined by archaeologists in multiple excavations from the end of the 19th century to 2004.[69,70] The majority of the graves were inhumations, but there were also cremation burials. All but one grave, were dated to the late Viking Age. The graves mainly consisted of stone settings in various forms. Most individuals were buried in a southeast-northwest orientation, in a supine position with or without a coffin. Except for nails from the coffins and some knives, only objects that could be related to the deceased's clothes were documented. The grave constructions, lack of clear grave goods and the finds of knives are interpreted as Christian features.[70] In grave A (SHM15268:2A) (enb200), which consisted of a flat mound with an irregular stone setting, the skeleton of an adult man was found who was dated to 893-1044 CE with 93.6% probability (1040±40 BP, Ua-23887).[69] Some of the graves excavated in 1913 cannot be related to the exact grave description and hence lack a grave number today. The skeleton of "SHM15268: box 5086" (enb508) belongs to this group and was, after the osteological analysis, identified as an adult woman.[69]

Samples: enb200 (XY) = SHM15268:2A, enb508 (XX) = SHM15268: box 508

Curated at: Swedish History Museum, Inventory number SHM15268; and Uppsala museum, Inventory number UM29596

Frösön

The church on Frösön (Sweden) is dated to the period late 12th and early 13th century. In the autumn of 2014, the local museum Jamtli conducted archaeological investigations on the church's northern side, next to the wall surrounding the churchyard. In total, 41 burials in different stages of preservation were recovered. No grave goods were found. A few disarticulated crania were recovered that originated from burials that had been disturbed by later burials.[71] The analysed sample comes from one of these disarticulated crania (frc007) that was recovered in association with burial 8. The cranium probably comes from an older burial that had been disturbed by burial 8. The cranium may be roughly dated to the period 950–1150 CE.

Samples: frc007 (XX)

Curated at: Jamtli (the regional open-air museum of Jämtland and Härjedalen)

Fullerö

Fullerö is situated five km north of old Uppsala (Sweden), directly north of the famous Valsgärde boat burial ground. The burial from Fullerö is a richly furnished inhumation male chamber burial radiocarbon dated to the late Roman Iron Age, 242–385 CE 95.4% probability (1732±29BP, Ua-53935). Although the grave had been opened and robbed, it was still remarkably richly furnished and unique.[57,72] The chamber burial was placed in a mound belonging to the first generation of mounds that started to be erected in the early Roman Iron age in the region north of lake Mälaren.[73] The burial chamber is the largest c. 10 m^2 (NNE–SSW) of all known in the lake Mälar region and northern Sweden from CE 200–700.[57] The human skeletal parts that remained were a collar and a rib bone with healed trauma belonging to a middle-aged large, muscular male,[74,75] emphasising the impression that the grave was built for a trained male warrior. The gold finger rings, one of them the largest gold finger ring ever found in Sweden, were probably military honours; the chain mail, belt and the boar-like tusks, and canines from pigs, probably for a horse fitting, may indicate that the man had been in Roman service. In the grave was a worn gold coin used as a pendant, struck for the Roman emperor Maximian Hercules 291CE.[76,77] Bones from a dog and a goshawk were found in the chamber, as well as a phalanx from a bear, suggesting that bear skin was placed with the deceased. The goshawk represents the earliest evidence of hunting with birds of prey in the region, a tradition that otherwise belongs to the 6th century.[78,79] The numerous (more than 20) domestic species in the mound filling are interpreted as animals used for the burial feast.[75,78]

Samples: ful001 (XY) = indiv1 Fullerö

Curated at: Swedish History Museum, Inventory number SHM20724

Gammelbyn

At an archaeological survey in 1975, 15 Viking Age to Early Middle Age inhumation graves were excavated. The graves belonged to the grave field Gammelbyn ID (3:1), Börstil parish, in north-eastern Uppland (Sweden).[80] The grave field (RAÄ 135) is located not far from other contemporary cemeteries, settlements and a trading post in a coastal landscape near the Baltic Sea.[81] The grave field consisted of two parts with different elevations in the terrain. In the upper part of the cemetery, there were stone settings where the graves were oriented in a north-south direction. In most cases, the deceased were placed in hollowed-out logs, but there were also wooden coffins made of planks, and one individual had been placed in a crouched position.[80,81] In the lower part of the grave field, which is believed to be somewhat younger, there were additional stone settings but also graves without a visible superstructure. The majority of the graves in this area had an east-west orientation with no artefacts documented in the graves. The coffins were made of planks and had recessed ends. The osteological analysis showed that both adult men and women and children as young as two to three years old had been buried at the grave field (Kjellström, unpublished). In one of the graves from the upper part, there was a coin found (a German-minted *pfenning*) dated to 1030 CE.[81] Other grave goods, including iron knives and nails, were also found (SHM dnr 602-1008-2007 RAÄ dnr 321-4499-2004). The grave with the most well-preserved osseous material was grave 8, which was one of three double graves at the site, where the skeletons of an adult man (gam872 in A8F25) and a woman (A8F26) were discovered.[82] Apart from possible traces of a coffin belonging to the man, there were no grave goods in the grave.

Samples: gam872 (XY)= burial A8F25

Curated at: Swedish History Museum, Inventory number SHM34835

Gannor

Gannor in Lau parish in south-eastern Gotland (Sweden) is situated in the northern part of ‘‘Lau backar’’, a huge burial ground with many destroyed graves, with c. 500 grave monuments still visible. A chamber burial was accidentally found when a large stone was removed by a local farmer.[83] Based on archaeological and osteological evidence, the remains (lau001) found in the burial cist were identified as a female, buried c. 600 CE. She was found in a crouched position with the remains of an infant placed on her left shoulder, her left hand placed at the infant’s head and her right hand at the infant’s feet. The woman was placed on a bear skin, while the infant was wrapped in a lynx skin. She was furnished with two bronze needles placed by her head, two animal brooches at her shoulders and a unique gilded crab brooch at the neck.[83,84] The well-furnished woman would likely have had a prominent position at the farm. An earlier study has shown that the mitochondrial DNA sequence of the child was incomplete, but shared sufficiently many mutations with the mtDNA of the woman that it is most likely that the two were mother and daughter; nevertheless, they could also represent other types of close maternal relationships (e.g. that of a grandmother and a grandchild[85]).

Close by was a similar grave of another individual, osteologically determined as a probable female and archaeologically gendered as such (lau003). Her burial was not as richly furnished as lau001, and she had only received one animal head brooch and 20 large beads. Like lau001, she was buried in a crouched position c. 600 CE.[83] She was determined to be c. 20 years of age (grave 2[84]).

The richly-furnished woman (lau001) belonged to a mtDNA haplogroup (U5a1b1h) that was different from that of the woman (lau003) in the less well-furnished grave (H2a1). Consequently, they cannot have had the same mother, nor can the older woman be the mother of the younger woman.[85]

Samples: lau001 (XX) = grave A1, lau003 (XX) = grave A2

Curated at: Gotland’s museum

Görla

Görla in Frötuna parish, Uppland (Sweden), is situated in what was once the Viking coastline of eastern Sweden. An excavated late Viking Age burial ground (900–1100 CE) at the site yielded inhumations located in mounds and under flat ground and a single cremation burial in a mound. The burial ground was placed directly on top of a Migration period farm site, and one of the Viking burial mounds had re-used the postholes of the former house for the construction of posts for the ditches that surrounded the mound. Based on osteological analyses, the individuals found in the mounds are males. Interestingly, some mounds were constructed before the burials of the bodies took place, which is uncommon.[86,87] This was probably done to underline property rights.[88] The graves of the individuals that were osteologically determined as females or children were placed under flat ground.[86]

The individual in grave 161, osteologically assessed as a female younger than 45 years, was accompanied by grave goods in the form of a belt buckle of iron, an animal-style ornamented strap divider of bronze and a knife dated to the late Viking Age.[86] The grave was placed in the midship of the former house III.[86] In grave 358 was a well-preserved skeleton, osteologically determined as a female of 30-60 years. While grave 16 contained the skeleton of an adult man.[86]

Samples: gor161 (**XY**) = grave 161, gor164 (XY) = grave 16, gor358 (XX) = grave 358

Curated at: Swedish History Museum, Inventory number SHM34347

Havor

The Iron Age burial ground at Havor in Hablingbo on southern Gotland (Sweden) encompasses c. 400 graves covering the period Pre-Roman Iron Age to Viking Age, where 70 are Viking Age burials.[67] The grave field is known for its high quantity of re-used graves.[67] One of the Viking Age inhumation burials was a stone setting c. 5 metres in diameter (grave 192). On the upper level of the grave, a skeleton was found in disorder, placed there ’much later’ according to the excavator Gabriel Gustafsson. The primary burial (placed S-N) contained an archaeologically gendered female and was furnished with double sets of animal-head brooches, beads, knives, a comb, an armring, pendants, needles, a sewing kit and a spindle whorl.[67] The grave is typologically dated to c. 1000–1100 CE.[89] The cranium of the individual had been artificially deformed, unclear though if it was caused by head flattening or binding. Osteologically the individual is determined as a female 55–60 years of age.[68] The artificially deformed head is a most unusual feature. However, it is known in three cases in the skeletal material dated to the Viking Age that has been recovered in present Sweden.

Samples: hav001 (XX) = Swedish History Museum Inventory number 8064:192

Curated at: Swedish History Museum, Inventory number SHM8064

Kronan

The Royal man-of-war ''Kronan'' was, when built, the biggest, most heavily armed vessel of the Swedish navy and only outsized by two other ships in the world. Well adorned and intended to impress and inspire awe, it was destined to be the Swedish navy's new flagship.[90]

The ship sank in 1676, after only four years of service, off the coast of Öland, near Hulterstad (Sweden), on its way to engage the combined Danish and Dutch navy. Most of the crew drowned, and expensive equipment, such as cannons of varying sizes and weights, and coins, were lost in the shipwreck. The basic crew consisted of 500 seamen and 300 soldiers; on this journey, there were 50 additional infantrymen. According to the historical records, out of a crew of 850 men, only 42 are known to have survived. More than 180 men washed ashore in the days that followed the catastrophe, meaning that approximately 600 men were left in the depth of the sea. The crew of approximately 850 men (sailors and soldiers) was a complete miniature society, almost the size of a medium-sized Swedish town. As a result, the Kronan crew represents a cross-section of the contemporary male population in the country. The age varies from twelve-year-old ship boys to sixty-year-old mates. The social status of the men spanned from the lowest to the highest (i.e. officers often being from the country's nobility).[28,90,91] According to historical record, the soldiers belonged to the infantry regiment of Västerbotten in the north of Sweden, whereas the sailors were recruited from Öland, Åland and Stockholm in eastern Sweden.[28,29] Only 110 casualties are known by name and occupation.[29]

Samples: kro001 (XY) = indiv Kronan 38C K16, kro002 (XY) = indiv Kronan 25C K14, kro004 (XY) = indiv Kronan 5C K2, kro006 (XY) = indiv Kronan 26C K18, kro008 (XY) = indiv Kronan 6C K9, kro009 (XY) = indiv Kronan 31C K1, kro010 (XY) = indiv Kronan 42C K17, kro011 (XY) = indiv Kronan 50C K13, kro012 (XY) = indiv Kronan 8C K8, kro013 (XY) = indiv Kronan 3C K11, kro014 (XY) = indiv Kronan 27C K6, kro015 (XY) = indiv Kronan 43C K4

Curated at: Kalmar county Museum

Rombäck

The burials from Rombäck were located on a sandy ridge a few hundred metres east of Getterån, near the river Ljungan, in Torp parish, Medelpad (Sweden). The inhumation graves were oriented E-W, probably buried under flat ground were accidentally discovered in 1933 by road workers at Knaggsveden, on grounds belonging to the vicarage at Rombäck.[92] Some of the burials had wooden remains after coffins. Two graves were examined by a local person, while the third was examined by a man sent out by the National Board of Antiquities.[93] According to the report, three individuals, or possibly all four of them, were placed face down, i.e. in prone burials, which is unique for the Migration period in Sweden and as far as we know for all of Scandinavia. Both iron and bone material were poorly preserved because of the sandy soils. Furthermore, the bones had been sorted into categories, with long bones, for instance, collected in one parcel. Thus, the individual skeletal remains had been mixed. Grave 3, which was not possible to sex archaeologically, contained an iron ring with remains of bronze and textile, and parts of a wooden object. Graves 2 and 4 were archaeologically determined as male, based on the strike-a-light stones and a weapon. Grave 2 contained a strike-a-light stone and a knife, while grave 4 contained a 50 cm long spearhead that was found by the body, as well as an oval strike-a-light stone, an iron object, and two sets of gilded clasps with remaining textile and fur skin.[94,95]

Samples: rtp001 (XY) = grave 2, rtp003 (XX) = grave 3, rtp004 (XY) = grave 4, rtp005 (XX) = grave 3

Curated at: Swedish History Museum, Inventory number SHM20438

Sala

The Sala boat burial was found by the river Sagån at Sala's old silver ore smelting furnace (Sweden). The burials dated to the Viking Age were originally placed on an island called Brytilsholmen, in the middle of the river.[55,96] The remains of four individuals were accidentally found and partly excavated. Two of them were buried in boats, and two in "chests" or sledges. Two of the individuals were more prominently interred. The archaeologically determined well-furnished female in grave 1 was placed in a logboat with a pair of oval brooches, an equal-armed brooch, four round iron jewellery pendants, a bronze chain, 58 glass beads, a knife, potsherds and a bent iron rod.[96,97] Grave 2 (sal002) also a logboat contained a woman though less well furnished, with two mismatched oval brooches and an equal-armed brooch, and a wooden box. She was buried several generations later, c. 950–1000 CE. Her genetic affinities resemble the modern genetic variation in the British-Irish Isles. The strontium isotope values of her teeth, however, show that she was probably born and raised locally. Her ancestry, together with her isotopic data, allow us to speculate that she could be a second-generation immigrant with parents with a British-Irish Isles genetic origin. The archaeologically determined female in grave 3 (sal003) was furnished with a pair of oval brooches, an equal-armed brooch, two cast pendants of tin and four glass beads. This woman was placed in a wooden chest without a bottom, and its frame was put on top of the head of the woman. Tooth wear indicated that she was middle-aged or older.[96] The brooches are contemporary with those of the woman in the first grave, and thus both were buried c. 800–850 CE.[97] The strontium isotope values of the woman's teeth indicate that she had not grown up in Sala but moved in. Grave 4 was a deviant burial, a male that had been placed prone, with his lower legs lying disorderly in the clay. Possibly the man could have been overturned, together with the stretcher, into the burial pit.[31,75]

Samples: sal002 (XX) = grave 2, sal003 (XX) = grave 3

Curated at: Swedish History Museum, Inventory number SHM11357

Sandby Borg

Sandby borg is a Migration Period (400–550 CE) ringfort on Öland, an island off the southeast coast of Sweden. The archaeological analyses suggest that a large proportion of the site's inhabitants were killed in an organised attack, after which the settlement was immediately and permanently abandoned.[98,99] The killing was dated to the late 5th century according to typological evidence.[100] To date, around ten per cent of the ringfort interior has been excavated, revealing at least thirty distinct individuals. All age groups, from infants to old adults are represented among the human remains. The locations of the bodies and patterns of perimortem trauma are more consistent with a massacre than with a battle.[98,99] The abrupt end of Sandby borg provides a rare opportunity to study human aDNA from the Scandinavian Migration Period, as the bodies were left *in situ* and not subjected to mortuary practices, which in this context typically featured cremation.[101,102]

We sampled a minimum of 15 different individuals from Sandby borg for whole genome sequencing of which nine provided sufficient depth to allow estimates of molecular sex (Table S1). Our results indicate that individual snb018 (a young adult) is so far the only female among the victims of the massacre. For seven of the nine individuals, we recovered genomes with sufficient coverage (1.04–5.42x) to perform population genomic analyses. Of these samples, the morphology shows that snb017 was a child (6–8 years old), snb014 was an elderly male, and the rest were young adults or adolescents.[98] The female individual snb018 was found in the alley next to house 4, individuals snb017, snb019 and snb014 were found together inside house 4,[103] and individuals snb010, snb012 and snb013 were found together inside house 40.[98]

Samples: snb010 (XY) = indiv 7, snb012 (XY) = indiv 6, snb013 (XY) = indiv 2, snb014 (XY) = indiv 15, snb017 (XY) = indiv12, snb018 (XX) = indiv 18, snb019 (XY)= indiv 13.

Curated at: Kalmar County Museum

Såsta, Broby bro

In close proximity to a runestone (U135) and a stone setting in Broby bro, Såsta 3:1, Täby parish, Uppland (Sweden), three previously unknown inhumation burials were found in 1995.[104] The graves were located northeast of a burial ground (RAÄ 36) with mainly cremation graves from the early Iron Age. The runestone, together with two others (U136 and U137), belonged to the Jarlabanke family, and the buried individuals have been interpreted as descendants of the same family.[104] The individuals were buried stretched out on their backs with their arms at their sides, and the graves had an east-west orientation. In grave 1 (bro100) there was a coffin with an elderly man with a piece of textile (most likely silk) that is believed to have belonged to the left sleeve still in place.[105] In grave 3 (bro300), which lacked a visible superstructure, an elderly woman was buried in a coffin made of a hollowed-out log. The woman had been buried together with a knife and a wooden box with a key, containing two silver coins, a silver ring, and three weights of iron or bronze. Based on the *terminus post quem* of the coin, the grave was arranged after 1025 CE.[104] The items in the grave of the woman are believed to reflect her high social status. Later excavations have revealed other graves with a fairly homogeneous character at the site, and all are now considered to belong to the same early Christian grave field (RAÄ 42).[106]

Samples: bro100 (XY) = burial 1, bro300 (XX) = burial 3

Curated at: Swedish History Museum, Inventory number SHM33379

Sigtuna

At the end of the 10th century (c. 970/980 CE), the town Sigtuna was founded on a peninsula in Lake Mälaren (Sweden) connected to the Baltic sea. The town quickly grew to a central hub, a judicial, administrative centre for an increasingly centralised royal power,[107–109] and for the Christian mission from both England and the Hamburg-Bremen archdiocese.[110] This is manifested not least by the fact that Sigtuna's second king, Olof Skötkonung, is depicted on the first coin minted in Sweden. The town was structured so that oblong town yards with several buildings and alleys, were organised at right angles to a wood-paved main street parallel to the shoreline.[111] The rich amount of finds and the non-local character of the artefacts indicate extensive contact with the outside world. These connections reached the whole of Europe but the networks appear to have been especially expansive towards Novgorod and the east (e.g., Krzewińska et al.,[7], Wikström,[111] and Roslund[112,113]). Some researchers have argued that Sigtuna was primarily a gathering place for the households of the local elite in the Mälaren Valley,[114] while others maintain that it was primarily a gathering place for long-distance guests and emphasised its international character, set apart from the rural countryside.[115] Possibly the answer lies in between as results from isotope and genetic analyses from sampled individuals indicate that people from both the immediate area and long distances visitors were buried in the town.[7,116] The town dwellers were, during the first burial phase (c. 970-1100) buried in a variety of contexts: in small burial grounds with superstructures such as small mounds and stone settings, or in graveyards under flat ground, without an associated church, while some at early churchyards by a wooden church; all of these burial contexts were located in a semi-circle around the settlement.[117,118] With time, starting probably as early as in the late 11th century, six Romanesque stone churches, with associated churchyards, were erected.[107,117] One of the churches (known as Biskopskyrkan or Church 1), located in the block Sankt Gertrud, has been excavated on several occasions and 167 skeletons analysed.[119] A recalibration of the individual in grave 18 (stg018) from the excavation in 1983, dated the individual to 892–1031 CE at 95.4% probability (1055 ±40 BP, Ua-22724).[65] The graves in Sigtuna follow in general a Christian expression, with no or few documented objects, and when present most are from to the clothes of the deceased.

Samples: stg018 (XX) = burial 18 (Kv St Gertrud 2980/83)

Curated at: Sigtuna Museum

Ströja

At Ströja, Kvillinge parish, Östergötland (Sweden) recent archaeological investigations revealed the remains of an elite farm with a sacrificial site, established c. 450 CE[120] Hjulström and Lindeberg forthcoming. By c. 650 CE the site grew in importance: the activities at the sacrificial site became more frequent, a marketplace was established, the hall buildings were relocated and the archaeological material became richer. The gold foil figures found at the site indicate that Ströja was linked to other elite residences in Northern Europe. At an outdoor sacrificial site bone fragments of four human skulls had been placed in, or close to, ritual deposit layers with a large amount of fire-cracked stones and animal bones. Three of the skull fragments were directly related to the ritual deposit layers and the fourth was found on top of a nearby hearth. Of the three skull fragments from the ritual deposit layer, one had been placed in a post hole and one had been placed in a red layer (unknown though what caused the colouring). In, or related to the red layer were also bones from horses (one showing signs of severe blows to the extremities), a lower jaw of a wolf and a deposition of amulets of miniature weapons (a sword, a spear, and a shield). One of the four skull fragments were analysed in this study, come from a female individual dated to the late 8th century. This individual was an adult, radiocarbon dated to 715–941 CE with 95.4 % probability (1200±30 BP, Beta-323616) (find 101, str002), and was found in the red layer 3766. The other individual radiocarbon dated to 662–775 CE with 95.4 % probability (1280±30 BP, Beta-384620), was found by a post hole in the northern part of the layer with fire-cracked stones (find 3838, str004, Hjulström and Lindeberg forthcoming).

Samples: str002 (XX) = individual 101 in layer 3766; str004 = individual 3838

Curated at: - not yet in an Inventory

Turinge

The grave field at Åby, Turinge parish, Södermanland (Sweden) was discovered during a rescue excavation in the early 1970s. The burial ground was an early Christian burial ground set in the rural landscape of the farm Åby and had been in use during the late Viking Age, c. 1000–1100 CE. It consisted of 69 graves; 23 cremation burials covered by low stone settings and 46 inhumations. Of the latter, only 12 held preserved human remains due to the acidity of the soils.[121] At the edge of the burial ground under flat ground was a Viking Age boat burial for an archaeologically determined female. It was well furnished with oval brooches; unfortunately, the human bones were too poor to be included in this study. Directly east of the boat burial was grave 8; it was dug into a heap of fire-cracked stones from the Bronze Age (tur001). It was radiocarbon dated at 95.4% probability to the late Viking Age, 1028–1159 CE (938±28 BP, Ua-63132). The grave goods consisted of a knife, iron mounting and a piece of flint which indicated a male burial. At the burial ground were also inhumations under flat ground, among them grave 71 in the eastern part of the cemetery. The grave (tur003) contained no grave goods, but the skeletal remains were dated to the late Viking Age, with a 93.9% probability of dating to 904–1115 CE (1028±28 BP, Ua-63133).

Samples: tur001 (XY) = grave 8, tur003 (XX) = grave 71

Curated at: Swedish History Museum, Inventory number SHM34902

Valsgärde

The cemetery at Valsgärde is situated three km north of Old Uppsala (Sweden), on a hill by the river Fyris in Uppland. It is famous for its richly furnished boat burials, 15 in all, marked by shallow depressions. There are also 15 other types of inhumations, of which several are chamber burials and 62 cremation burials. The burial ground was in use from the Pre-Roman Iron Age, and after a lacuna, the burials continued from the Late Roman Iron Age until the late 11th or early 12th century.[122] Boat burial 6 is one of the most spectacular boat burials, placed near the crest of the hill just below the only mound on the site. The former is typologically dated to c. 650/660–700/710 CE,[122] and contained many grave goods, including a helmet, three shields, two long swords, two weapon knives, a lance, arrows, two belts, kitchen utensils, tools such as axes, thong, hammer and iron bars of different types, animals such as horses, dogs and birds of prey.[123,124] A few bone fragments remained of the deceased, which was an exception as boat burials normally are nearly void of human bones, while animal bones usually are much better preserved (e.g. Ljungkvist[122]). The deceased had been placed under a cover on a feather bedding. The individual had not been dressed, but metal objects like a suit of armour, helmet and weapons wrapped in textiles were found in the grave.[125]

Samples: vlg006 (XY) = boat grave 6

Curated at: Uppsala university Museum Gustavianum, Inventory number UMF 5906

Valsta

Valsta grave field (RAÄ 59) in Norrsunda parish, Uppland, (Sweden) is located between Stockholm and Uppsala, not far from Lake Mälaren, in a region rich in other contemporary sites involving graves and settlement remains. Children and adults of both sexes have been buried at Valsta since the Roman Iron Age; an archaeological survey in 1992-1993 also revealed 63 graves from the Viking Age to Early Middle Ages (750–1150 CE).[126] The grave field was clearly used by several generations of settlers at the site.[127] Among these were both cremation and inhumation graves, of which the latter consisted of burial mounds and stone settings of varied character; some graves were not visible above ground. Artefacts were found in cremations and inhumation graves, but the latter category had fewer objects, primarily related to caskets or the deceased's clothes. However, weapons, coins, urns, scissors, boxes and pear sets were also documented. Based on the radiocarbon dates of the individuals and the style of artefacts it seems that both funeral traditions (i.e. cremation and inhumations) were practised concurrently for a period. In some of the inhumation graves, traces of oak wood caskets were documented. Among the inhumation burials, a supine position of the bodies (with varied orientations) was the most common. However, there are exceptions: the woman in grave 69 (vls696) dated to 996–1192 CE (950±50 BP, Ua-6157) was buried prone, and the man in grave 75 (vls757) dated to 987–1185 CE (965±50 BP, Ua-6160) was found in a crouched position.[126]

Samples: vls696 (XX) = grave A69 F663:20, vls757 (XY) = grave A75 F755:17

Curated at: Swedish History Museum, Inventory number SHM34069

Västerhus

The large magnate's farm Västerhus was located on the island Frösön, Jämtland, in northwest Sweden. The lord and his family at Västerhus are believed to have served as representatives of the king and to have had a fiscal role in the region.[128] In association with the farm was a churchyard, which was completely excavated in 1947–1952. The churchyard has been dated from the 11th to the 14th century.[129] In the churchyard, women were buried to the north of the church and men to the south, and a hierarchical social order of the buried has been assumed to reflect contemporary Norwegian laws.[129,130] Since the publication of the first osteological analysis of the 371 skeletons in 1960, several studies have been performed focusing on the living conditions of the population at the site.[130,131] The majority of the graves had an east-western orientation, and with some exceptions, the dead were in a supine position, some in wooden caskets.[129] Few objects were identified among the buried, but coins, a bronze buckle, iron knives, a lead alloy pilgrim badge (depicting St Martin of Tours), and scallop shells were documented.[130] The scallop shells were discovered in grave 200a (wes007) radiocarbon dated to 1163–1262 (828 ± 29 BP, Ua-62712) and grave 56 (wes056) radiocarbon dated to 1016–1155 cal 95.4% (972 ± 29 BP, Ua-62567). The scallop shells are associated with the shrines at Santiago de Compostela, implying that these two individuals (male and female) may have completed the pilgrimage to Spain.[132] Three of the sampled burials (30, 56, and 67) were recovered North of the church, while the other four were found South of the church (122, 127, 138, 200a).

Samples: wes001 (XX) = grave 30, wes003 (XX) = grave 67, wes004 (XY) = grave 138, wes005 (XY) = grave 122, wes007 (XY) = grave 200a, wes008 (XY) = grave 127, wes056 (XX) = grave 56.

Curated at: Swedish History Museum, Inventory number SHM32079

Vendel

The boat-grave cemetery at Vendel in northern Uppland (Sweden) was discovered by accident in 1881. It was only visible through shallow depressions in the ground next to the church at Vendel, the former settlement site for Tuna in Vendel.[133] The burial site consists of fourteen graves: twelve boat graves and two chamber graves.[134] Most of the graves had been robbed/opened; only two graves had been undisturbed, and grave XIV (ven001), excavated in 1893, was one of them. The individual in grave XIV was archaeologically sexed as male. The deceased had probably been placed in a seated position in the stern of the eight-metre-long boat. Remains of the cheekbone were preserved inside the helmet.[134] The boat grave is dated to 560/570 – 610/620 CE.[57,122,135] It belongs to the first generation of burials at Vendel.[134] The burial is unique among the known boat graves from both Vendel and Valsgärde, as the man seems to have been buried half-seated fully dressed in a tunic - garments of fine linen tabby and woollen twill - with a belt around his waist, wearing a helmet and placed on a feather cushioned bed.[125]

Samples: ven001 (XY) = grave XIV

Curated at: Swedish History Museum, Inventory number SHM9785

Viken, Lovö

The burial site at Vikby (Viken) is situated at a former bay of the island of Lovö, Lovö parish, Uppland (Sweden) exposed towards the Baltic inlet.[136] It is renowned for three chamber burials from the Migration period, although the burial ground consisted of more than 20 graves, both cremations and inhumations from the Migration and Merovingian Periods.[136,137] The most well-furnished was chamber grave 3 (lov002), containing an individual archaeologically and osteologically determined as male, with a sword and sword belt and 50 gaming pieces among other grave goods. The grave is dated to 475–510/520 CE.[57,136,137] Contemporary to grave 3 was an adjacent burial, grave 1, osteologically also determined as male.[136] Based on osteological analysis, both individuals have been identified as older males.[136] The graves were interpreted as having been opened/robbed.[136,137] This interpretation has been questioned for grave 3,[56] as it contained a complete sword, sword belt, lance, arrows, and shield.[135] The genetically determined female XX karyotype of lov001 contradicts the male osteological assignment. A female assignment is consistent with the fact that there were no male-characteristic objects in grave 1. Instead, among the grave goods were a bead, a small gold finger ring, clasps, a spindle whorl and a scraper of elk antler (hide scraper[136]). This would indicate that the grave was erected over a woman.

Samples: lov001 (**XX**) = grave A1, lov002 (XY) = grave A3

Curated at: Swedish History Museum, Inventory number SHM29401

METHOD DETAILS

DNA extraction

The human remains were sampled in the aDNA facilities at the Archaeological Research Laboratory, Stockholm University (Sweden). All samples were decontaminated prior to analysis with a 0.5% sodium hypochlorite solution and UV irradiated (6 J/cm^2 at 254 nm). After removing the surface, bone was drilled to powder and the root tip of the teeth was cut with a multitool drill (Dremel) to get approximately 80 to 150 mg of bone powder/root tip.

The root tip samples were placed in an Eppendorf tube in 1 ml of pre-digestion buffer (0.45 M EDTA pH 8.0) at 37°C in a hybridization oven. After 30 minutes the supernatant was removed to reduce the microbial and exogenous DNA. Following this pre-digestion step, 1 ml extraction buffer (0.45 M EDTA pH 8.0 and 0.25 mg/ml of proteinase K) was added to all the samples and they were incubated at 37°C in the hybridization oven for 1-4 days until all powder/ root tip was dissolved. The extraction was conducted following Dabney et al.,[138] with 1 ml of digested extract being combined with 13 ml of binding buffer containing 5 M guanidine hydrochloride, 40% (vol/vol) isopropanol, 0.05% Tween-20 and 90 mM sodium acetate (pH 5.2). 50 ml silica columns (Roche, High Pure Viral Nucleic Acid Large Volume Kit) were used for purification and the DNA was eluted in 45 μl of EB buffer (Qiagen). The remaining samples were extracted following a slightly different protocol, as described in Krzewinska et al.[7] The extraction buffer contained 1 ml of 0.5 M EDTA (pH 8.0), 1 M urea, and 10 ul of proteinase K (10 mg/ml). After digestion for 48 hours at 37°C in the hybridization oven, the 1 ml of extract was centrifuged at max speed and the supernatant was concentrated to 100 μl using Amicon Ultra centrifugal filters and purified to 110 μl of cleaned product using a MinElute kit (Qiagen).

Library preparation and sequencing

20 μl of extract was used to prepare blunt-end ligation DNA libraries coupled with P5 and P7 adapters and indexes as described in Meyer and Kircher.[38] Blank controls were used during every step of library preparation and amplification. The optimal number of PCR cycles for library amplification was determined with qPCR. The amplification reactions had a total volume of 50 μl, with 5 μl DNA library, and the following in final concentrations: 1 X AmpliTaq Gold Buffer, 2.5 mM $MgCl_2$, 250 μM of each dNTP, 2.5 U AmpliTaq Gold (Thermo Fisher Scientific, Waltham, MA), and 200 nM each of the IS4 primer and index primer.[38] PCR was done with the following conditions: an activation step at 94°C for 10 min followed by 8–20 cycles of 94°C for 30 s, 60°C for 30 s, and 72°C for 45 s, and a final elongation step of 72°C for 10 min. Four amplification reactions with the same indexing primer were made for each library to increase complexity. Finally, the amplified libraries were pooled and purified with AMPure XP beads (Agencourt; Beckman Coulter, Brea, CA), and the fragment size and concentration were checked using BioAnalyzer with the High Sensitivity Kit (Agilent Technologies, Cary, NC).

The samples with the highest proportion of endogenous human content in the conventional blunt-end libraries were also damage-repaired with a USER enzymatic treatment to remove deaminated cytosine sites[139] before further deep-sequencing.

QUANTIFICATION AND STATISTICAL ANALYSIS

Processing and alignment of sequencing reads

Purified libraries were pooled in equimolar concentration and sequenced on an Illumina HiSeq X at the SciLife Sequencing Centre in Stockholm. Sequencing reads were demultiplexed according to the index of each sample sequence. AdapterRemoval v.2.3.1[40] was used to remove adapter sequences, short reads (<25bp), and regions of consecutive low-quality bases and ambiguous bases (N's). Subsequently, reads were aligned to NCBI build 38 of the human reference genome using the Burrows-Wheeler Algorithm, as implemented by BWA v. 0.7.10,[41] with the seed disabled (-1024) to improve accuracy and the minimum base quality set to 15. Base quality scores were rescaled with MapDamage 2.0[45] to exclude likely-damaged bases. Mapped reads were filtered on a library-based level for PCR and optical duplicates using PicardTools v.1.21.3, (http://broadinstitute.github.io/picard/). Only mapped reads with Phred-scaled mapping quality (mapQ) scores $\geq$30 were kept. Read depth and coverage were determined using BEDtools-2.29.2[46] and an in-house python script. Ancient genomes from previously published studies (Table S1B) were processed in the same way after their read data were downloaded. As the sequencing depth for most of the ancient individuals was too low to call diploid genotypes, haploid genotypes were used for all analyses, obtained by randomly selecting a single read for each position of interest from those with base quality $\geq$30.

Data validation

We used several approaches to validate the dataset. Firstly, all libraries yielded short read lengths (Table S1), and patterns of cytosine deamination estimated with MapDamage2.0[45] were consistent with aDNA expectations for samples that were not USER treated (Table S1). Secondly, we estimated contamination affecting mtDNA by estimating the frequency of minor alleles at positions where the major allele was rare following Ebenesersdóttir et al.[22] (Table S1). Thirdly, we used the 'Contamination' program in ANGSD[48] v.0.911 to estimate X-chromosome contamination in males, as described in Rasmussen et al.[140] We only considered bases with quality $\geq$20 and reads with mapping quality $\geq$30. ANGSD applies two different methods to estimate the contamination rate: Method 1 considers all bases, providing greater power while assuming that errors are independent between reads and sites. However, Method 2 does not have this bias, as it randomly samples a single read at each site, but is also less precise than Method 1. Contamination estimates are shown in Table S1. Finally, sex was assigned following the method described in Skoglund et al.[141] (Table S1), with clear assignments obtained for all samples.

Kinship analysis lcMLkin

Kinship relations between the individuals analysed in this study were estimated with the program lcMLkin[53] using bam files mapped to the GRCh37 Genome. We selected a panel of 1,681,497 transversion SNPs from the Estonian Genome Diversity Project (EGDP)[142] in order to avoid post-mortem damage bias in our samples. The genotype likelihoods of the selected SNPs positions were called using 'SNPbam2vcf.py' following a maf=0.15 and using the population allele frequencies from 507 ancient individuals.

Reference population datasets

European reference panel

To help identify the ancestries of our ancient individuals, we compiled an autosomal genomic reference dataset of modern, mostly European individuals comprising 10,083 individuals (9,052 of which shown on PCA figures) containing genotypes for 168,599 variants. The sources used are described in Table S3 and consist of a variety of data sources that are either publicly available, available on request from external groups, or available only to researchers at deCODE genetics.

In order to maximise the final count of intersecting variants and to avoid some sources of batch effects, we selected only data genotyped on a set of Illumina microarrays with high overlapping marker content (600 series, Omni series). For some data sources, this involved restricting to a subset of samples that were chipped on acceptable microarrays, as identified in provided metadata or by analysing per-sample missingness (as for e.g. "urnikyte_lithuania").

All merging was performed while correcting for strand flips and discarding all ambiguous A/T and C/G SNPs. PLINK 1.9 was used at all steps.

QC, ancestry outliers, and inferred geographic/ancestry labels. For the subset of desired populations from each data source, we used PLINK to apply per-variant (–geno) and per-individual (–mind) genotype missingness filters of 3% and exclude non-autosomal variants, and then used KING –unrelated to remove one from each pair of duplicate samples and relatives closer than second degree. After merging, KING –unrelated was again run to identify and remove duplicates and relatives closer than second degree between sources. For ancestry analysis, we removed variants with MAF <1% and variants in long-range high-LD regions.[143]

We then identified and removed genetic ancestry outliers. For some data sources that we expected to have a greater proportion of individuals with recent, very divergent genetic ancestry (i.e. continental-level outliers), we first ran ADMIXTURE on LD-pruned data (plink –indep-pairwise 200 25 0.4) supervised on the 1000G populations CEU, CHB, ITU, PEL, and YRI, and then removed 190 clear outliers by inspection.

We then merged all remaining individuals and performed principal components analysis (PCA) in smartpca with “ldregress: 200” and “ldposlimit: 100000” to identify less divergent (i.e. within-continent) genetic ancestry outliers.

We aimed to use the most granular level of information when assigning population/group labels to samples. Samples have a top-level group label (e.g. “Norwegian”) as well as lower-level regional and ancestry labels (e.g. “Norwegian_Troms_SaamiInferred”). In the figures in this paper that display the European reference PCA, we only show the top-level label.

In a small number of cases, we also assigned labels based on genetic ancestry. Specifically, we noticed two sets of distinctive outliers: one that included individuals labelled “French” and “Spanish” who localised with individuals labelled "Basque Spain" and "Basque France"; and another comprising individuals with labels "Norwegian", "Swedish", and "Finnish", who landed on three sparse clines lying between a shared pole and each of the three main clusters for the respective countries. After inspecting supervised ADMIXTURE assignments, the available information on sub-country region of origin, and analyses that we had performed on some of these individuals in other publications, we concluded that the set of “French” and “Spanish” outliers likely carried Basque ancestry, and the “Norwegian”, “Swedish”, and “Finnish” outliers likely carried Saami ancestry. These ancestries are unusually informative for identifying several kinds of modern and ancient ancestries. Furthermore, Basque were represented at low counts in our geographic/ancestry labels, and Saami not at all. For these reasons, we decided to delineate these two outlier regions using (arbitrarily chosen) PC coordinate criteria and appended "_BasqueInferred" or "_SaamiInferred" to the geographic/ancestry labels of the contained individuals.

We then used an unsupervised method which we refer to as “MVE” (minimum volume ellipsoid, in which we define Mahalanobis distance outliers of a specified quantile, such as 99.9%, from an estimated “true” multivariate distribution found using the R function MASS::cov.mve) to identify per-population outliers in the PC coordinates. We also made sure not to remove individuals as outliers if they carried a lower-level population label which we suspected could be associated with distinctive ancestry but could nonetheless rationally be placed under the top-level label (e.g. "Greek_Turkey", "Croatian_Herzegovina", "Russian_Arkhangelsk"). 433 individuals were removed as outliers at this stage, leaving 10,083 individuals.

We then performed another PCA to confirm that no obvious genetic ancestry outliers remained. However, because they were oversampled and dominated the PC space, we decided to create a subset in which we reduced the number of "Italian" individuals from 1,144 to 700 and "Finnish" from 856 to 300, leaving 9,052 individuals. The PC coordinates generated from this downsampled reference set were used in all the figures in this paper.

Scandinavian reference panel

We also created a reference panel of 16,638 individuals of Scandinavian ancestry (see Table S3). For each dataset, we removed individuals with missingness greater than 3%, the higher-missingness individual from each pair of duplicates or monozygotic twins marked by KING –duplicate, non-autosomal variants, variants with missingness greater than 3%, and variants deviating from Hardy-Weinberg equilibrium by $p < 10^{-20}$. For ancestry analysis, we also removed long-range high-LD regions[143] and variants with MAF less than 1%. Individual ancestry outliers were removed using ADMIXTURE and PCA according to a similar procedure as the one described above, making sure that individuals of putatively Finnish or Saami ancestry were not removed. For the Swedish and Norwegian datasets, we restricted to individuals for which county of residence (Swedish län or Norwegian fylke) was known.

Y-chromosome and mtDNA haplogroups

We used the method of Ebenesersdottir et al.[22] to call consensus mtDNA sequences (Table S1). Y-chromosome haplogroups were assigned to the ancient and modern Scandinavian males using the ISOGG 2019 Y-chromosome tree (Figure S5A; Tables S1).[144] The ISOGG 2019 database is based on 71,405 loci, each of which marks a mutation on the human Y-chromosome tree. For each SNP in the dataset, we determined whether our ancient sample carried the derived or ancestral allele (according to majority alleles with base quality ≥ 30), and assigned each individual to the branch in the tree most consistent with the overall configuration of derived alleles observed.

Principal components analysis

Principal components analysis was performed on modern reference data using the smartpca module in EIGENSOFT (v.6.0.1).[49] No outlier iterations were performed, and the parameters ''ldregress: 200'' and ''ldposlimit: 100000'' were used to perform LD regression. Pseudohaploid ancient data was projected onto principal components using an in-house script that accounts for missingness by multiplying coordinates by a factor relating to the sample's genome-wide missingness.[49,145]

f-statistics

Patterson's *f*-statistics were calculated using in-house scripts based on ADMIXTOOLS package v. 3.0.[50]

ADMIXTURE

ADMIXTURE v.1.3[51] was run on each ancient sample separately supervised on whole-genome sequence data from five populations from the 1000 Genomes project[146] (Utah residents with Northern and Western European ancestry (CEU); Indian Telugu in the U.K. (ITU), Han Chinese in Beijing, China (CHB); Peruvian in Lima, Peru (PEL); and Yoruba in Ibadan, Nigeria (YRI). From the training data, we filtered out variants with more than 3% missingness, non-autosomal variants, variants in long regions of high linkage disequilibrium,[143] and also filtered out individuals in second-degree or closer kinship pairs according to KING, as well as 12 individuals who were possibly ancestry outliers according to PCA and ADMIXTURE analysis. For each run of ADMIXTURE, we restricted the training data to the variants that intersected with the non-missing variants in the test individual and LD-pruned those variants using plink –indep-pairwise 200 25 0.4.

qpAdm

We used the R package admixtools (https://github.com/uqrmaie1/admixtools) to generate allele frequency products for each ancient individual with depth > 0.5x and several modern reference populations from the west Eurasian reference set (Danish, Swedish, Finnish, Lithuanian, Polish, Ukrainian, Hungarian, Romanian, Irish, English_Oxfordshire, Dutch, German, French, Spanish, Sardinian, Italian_Tuscany, Lezgin, Greek, Basque [comprising both Basque_France and Spanish_PaisVasco], Turkish, and Lebanese_Christian), using a block jackknife size of 1 Mb. Modern rather than ancient sources were used in order to avoid biases and artefactual attraction between differently processed aDNA data. We then used these allele frequency products as the input of qpadm_rotate,[147] placing all the modern reference populations in the ''left-right'' position. For convenience, we defined a modified version of the function which did not attempt to run models involving more than three sources. In the output, we filtered for only ''plausible'' models for which all ancestry proportions were in the interval [0,1] and gave p-values greater than 0.01. To create the summarised plots, we selected one model per individual by taking the filtered models with the least number of sources and choosing the one which gave the highest p-value. It is likely that some of the individual runs of qpAdm violate the assumption of no gene flow from references to sources, and ranking by *p*-value is not considered best practice;[147] however, we observed that the models selected by this procedure agreed with results from other analyses. Next, we calculated the mean proportions of each ancestry across the samples in each grouping of geographical region and time period. We then plotted the results using each individual source (Figure S3A) and merging the sources into five different groups; Irish-British (Irish and English_Oxfordshire), South-West Europe (French and Spanish), Scandinavian (Swedish and Danish), Baltic (Lithuanians, Finnish, Ukrainians and Polish), Others (Dutch, Germans, Hungarians and Romanians) (Figure 4).

Supplemental figures

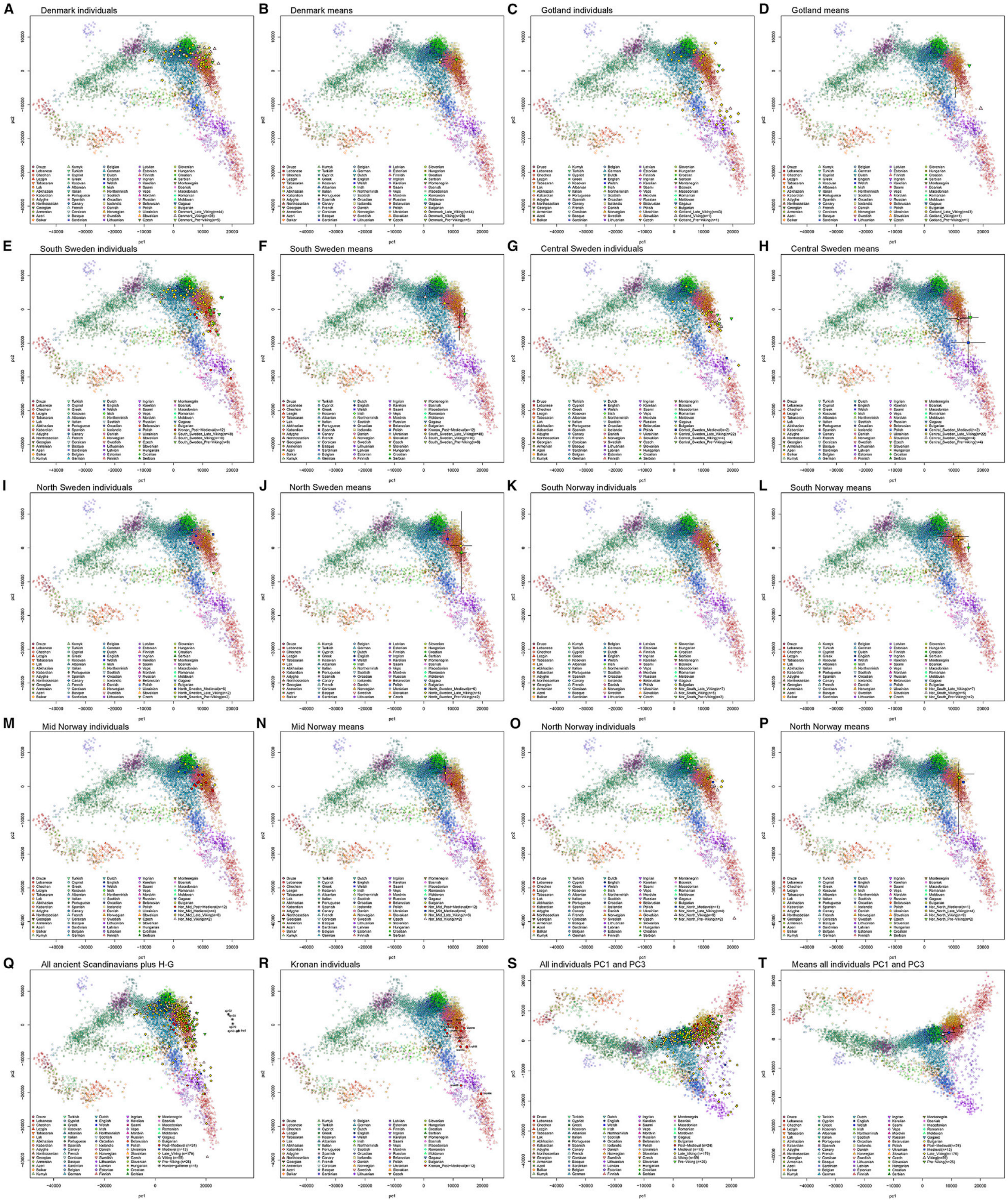

Figure S1. Ancient Scandinavians projected onto the first two or three principal components of modern West Eurasians, related to Figure 2

(A–R) Ancient Scandinavians projected onto the first two principal components.

(S and T) Ancient Scandinavians projected onto the first and the third principal components.

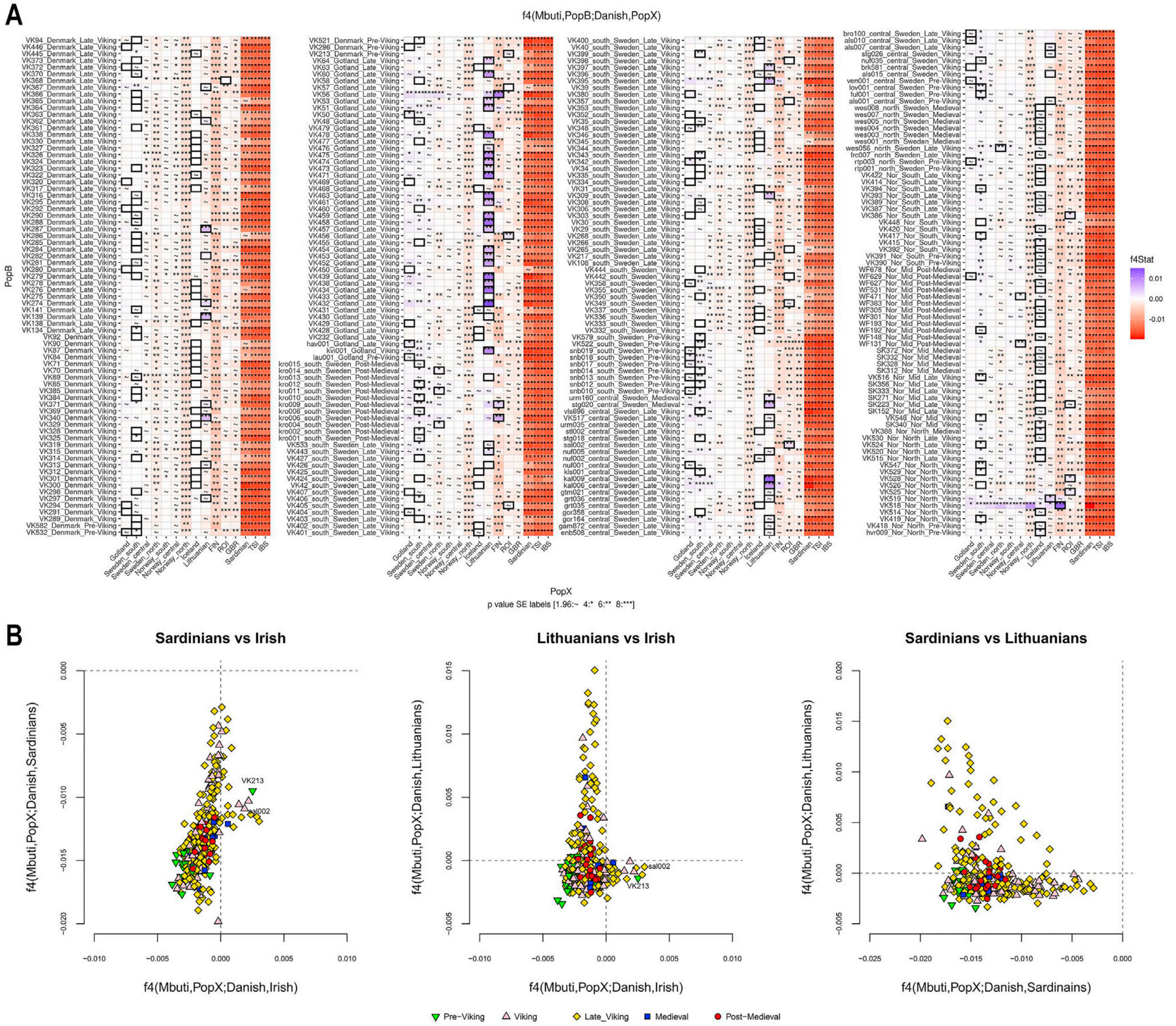

Figure S2. ***f_4*-statistic analyses on ancient individuals, related to Figure 3**

(A) Heatmap. f_4-statistic of the form f_4(Mbuti, Pop B; Danish, PopX). Pop X represent modern populations, and Pop B the ancient individuals. The highlighted squares in each row indicate the highest positive value.

(B) Scatterplots of the f_4-statistic results of the form f_4(Mbuti, ancient individuals; Danish, modern population) versus f_4(Mbuti, ancient individuals; Danish, modern population 2) reflecting the possible correlations of shared genetic drift of each Scandinavian ancient individual with different pairs of modern proxy population.

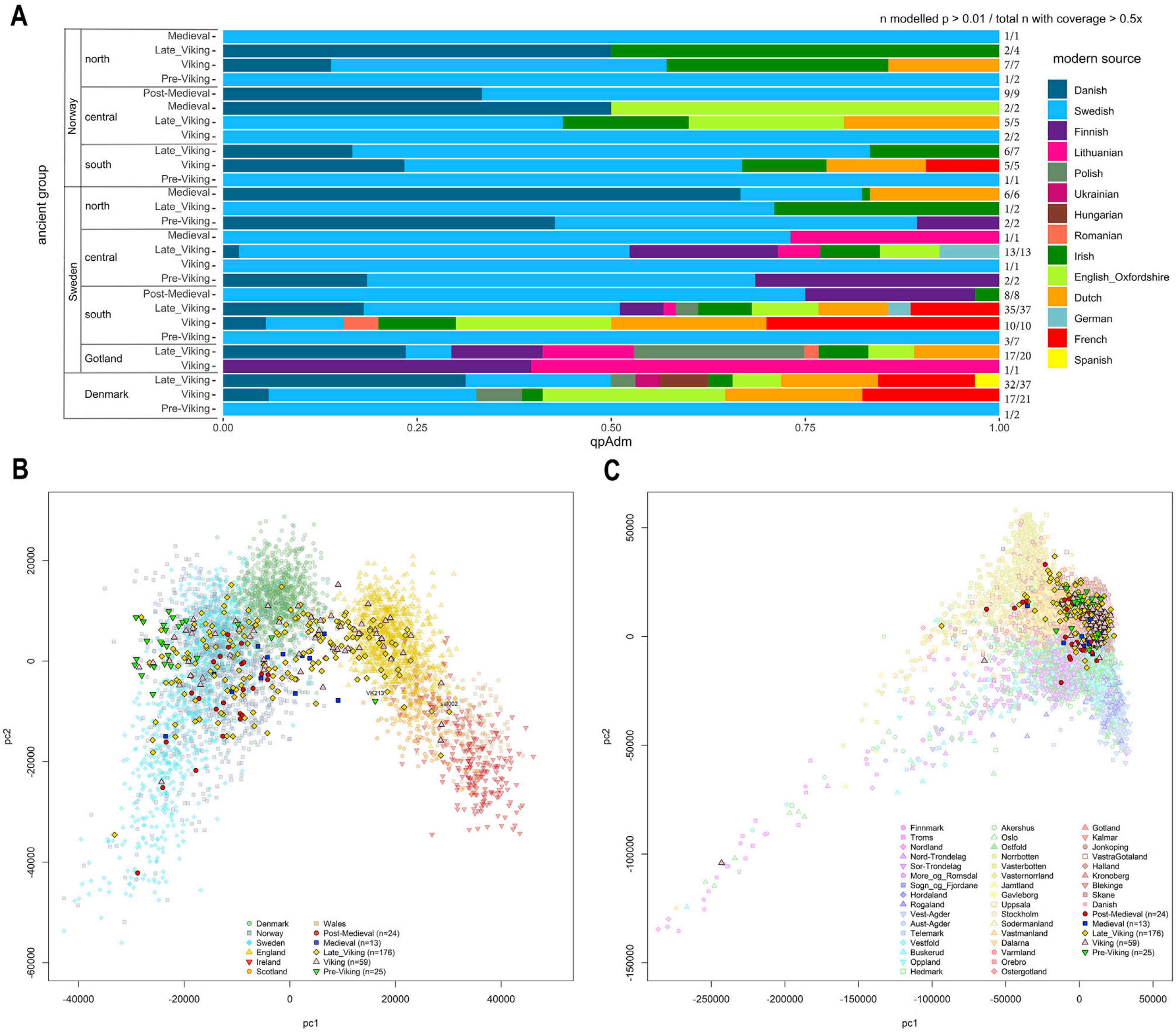

Figure S3. qpAdm and PCA projections of the ancient individuals, related to Figures 2, 4, 6, and 7

(A) qpAdm using 21 modern sources. Only samples with p > 0.01 and coverage >0.5× are plotted. Sardinians, Italian_Tuscany, Greeks, Lezgin, Basque, Turkish, and Lebanese_Christian did not appear in successful models and are not shown in the legend.

(B) Ancient Scandinavians projected onto the first two principal components of modern Scandinavians and the British-Irish Isles.

(C) Ancient Scandinavians projected onto the first two eigenvectors of a PCA from 16,638 modern Scandinavian populations.

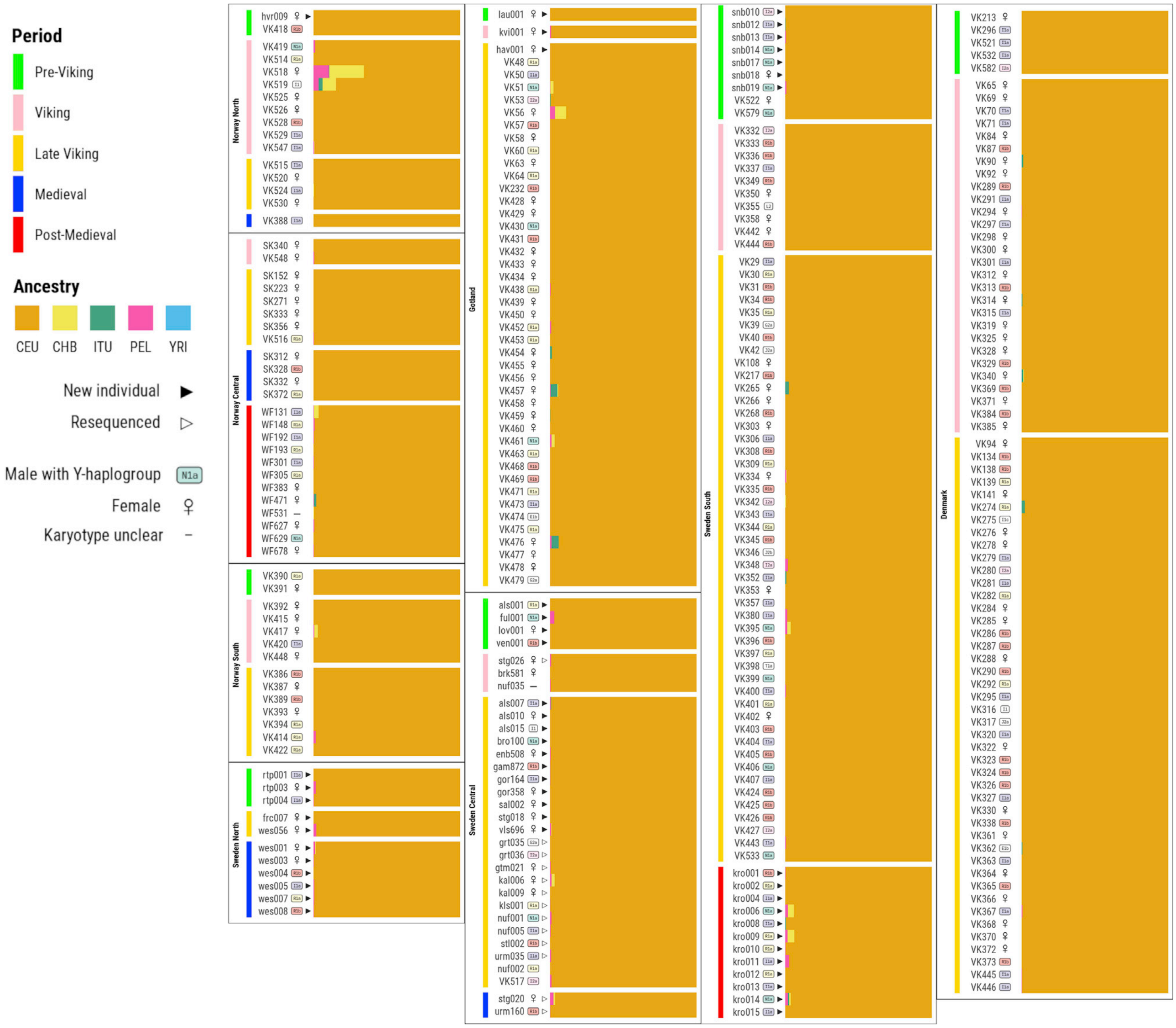

Figure S4. ADMIXTURE, related to Figures 6 and 7

Supervised run of ADMIXTURE using five training populations from the 1000 genomes (Utah residents with Northern and Western European ancestry [CEU], Indian Telugu in the UK [ITU], Han Chinese in Beijing, China [CHB], Peruvian in Lima Peru [PEL], and Yoruba in Ibadan, Nigeria [YRI]).

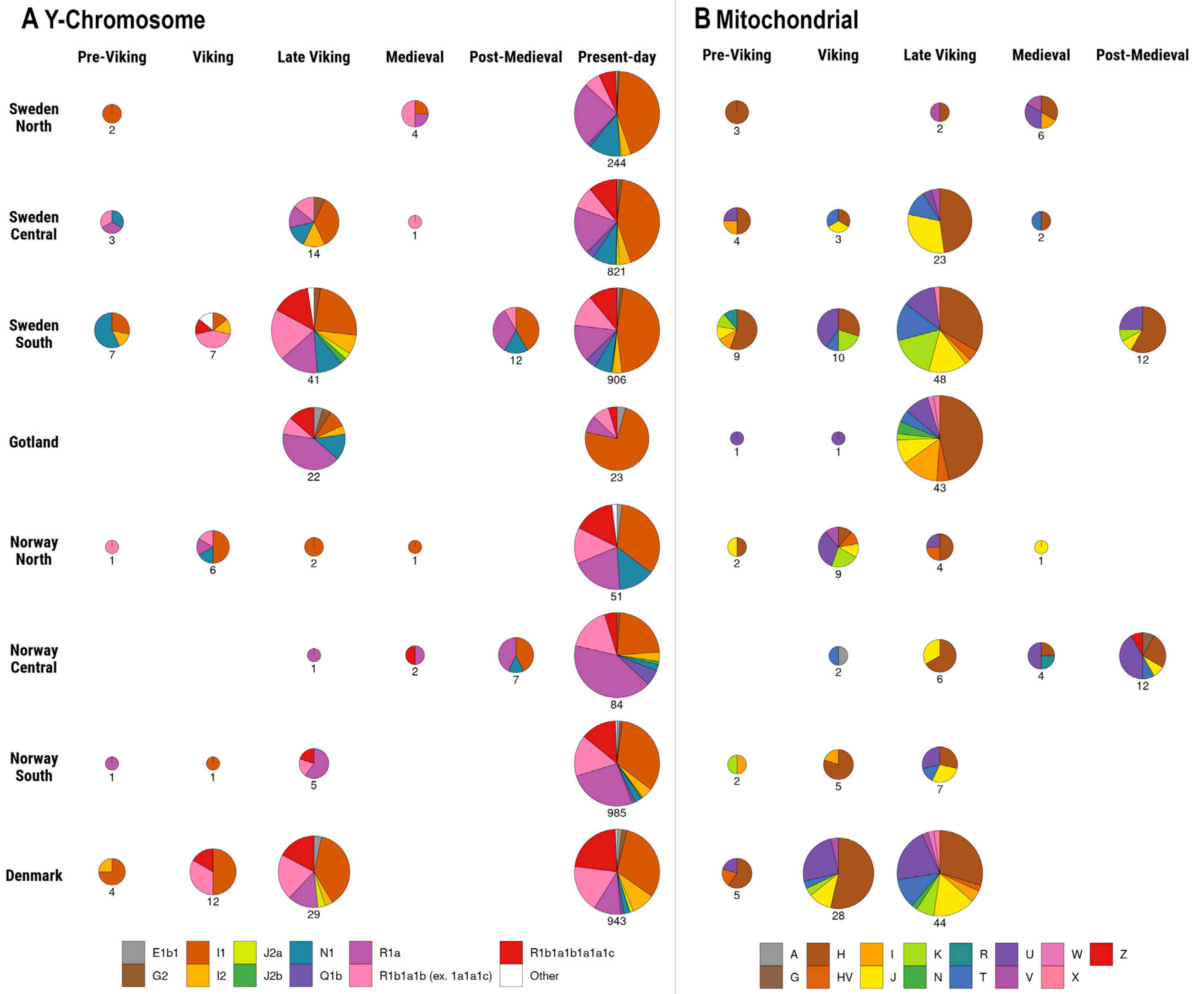

Figure S5. Uniparental haplotype distribution across different periods, countries, or regions, related to STAR Methods

(A) Y chromosome.

(B) Mitochondrial.

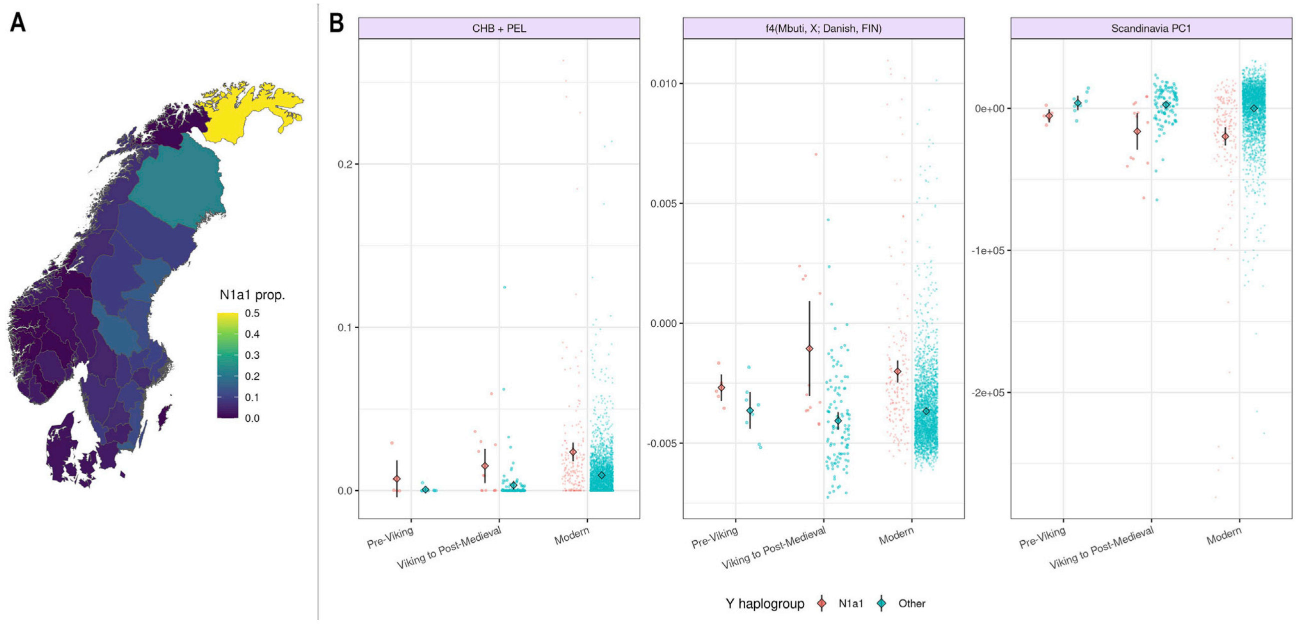

Figure S6. Y chromosome haplotype N1a1 distribution, related to Figures 6 and 7

(A) Modern frequency of the Y chromosome haplotype N1a1 across Scandinavia.

(B) N1a1 status in Norwegians and Swedes by time period and “northern cline” measure (bars are 2 SEs).

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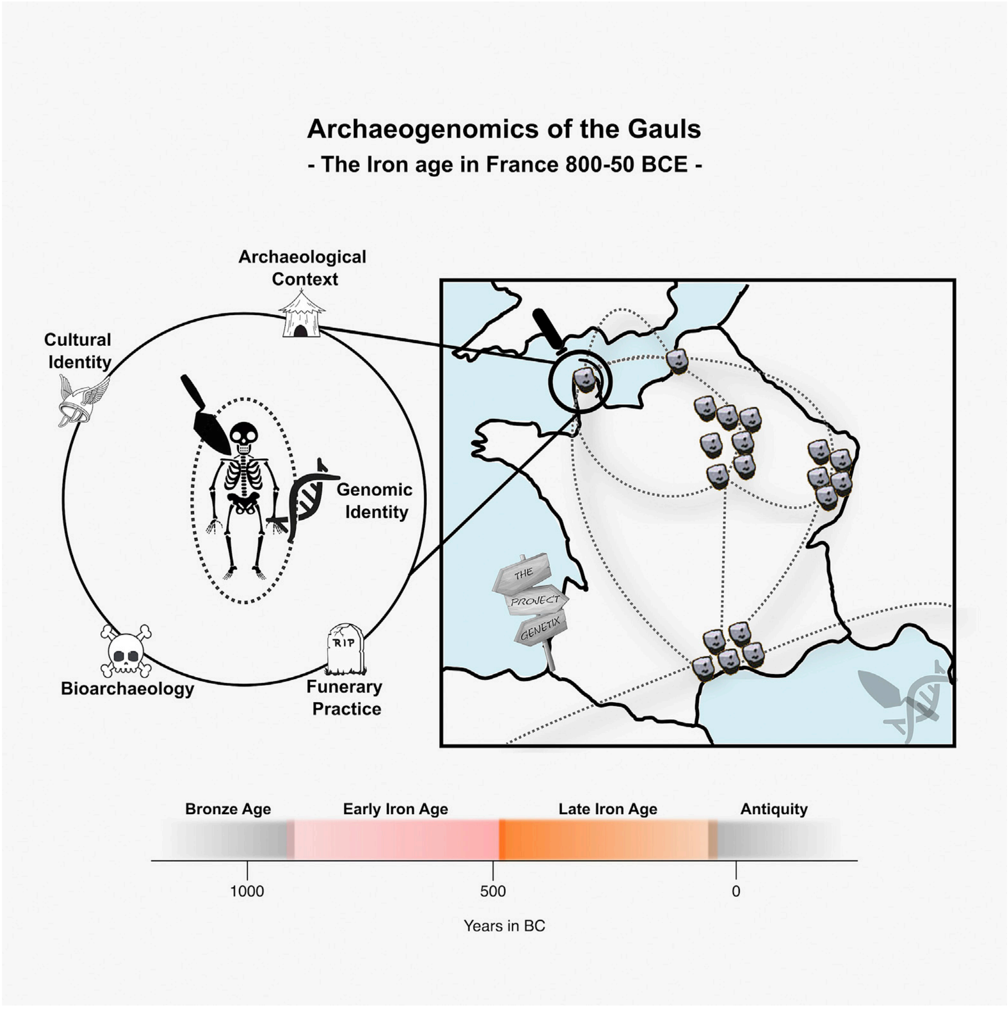
Origin and mobility of Iron Age Gaulish groups in present-day France revealed through archaeogenomics



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Highlights

49 low coverage genomes from 27 sites from France, dated to ≈1200–80 years cal BCE

No major migration or population turnover between Bronze and Iron Age in France

A gradual North/South genetic structuration of IA populations

Evidence of individual mobility between regions and neighboring countries

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Article

Origin and mobility of Iron Age Gaulish groups in present-day France revealed through archaeogenomics

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Continued

SUMMARY

The Iron Age period occupies an important place in French history because the Gauls are regularly presented as the direct ancestors of the extant French population. We documented here the genomic diversity of Iron Age communities originating from six French regions. The 49 acquired genomes permitted us to highlight an absence of discontinuity between Bronze Age and Iron Age groups in France, lending support to a cultural transition linked to progressive local economic changes rather than to a massive influx of allochthone groups. Genomic analyses revealed strong genetic homogeneity among the regional groups associated with distinct archaeological cultures. This genomic homogenization appears to be linked to individuals' mobility between regions and gene flow with neighbouring groups from England and Spain. Thus, the results globally support a common genomic legacy for the Iron Age population of modern-day France that could be linked to recurrent gene flow between culturally differentiated communities.

INTRODUCTION

The French Iron Age holds an important place in French history because Gaulish communities are regularly presented to the general public as the direct ancestors of French populations. This major interest has led to an impressive number of archaeological studies describing Iron Age communities through their material culture and funerary practices and questioning their cultural origins and affinities. Despite this interest, questions concerning the cultural and biological processes underlying the emergence and expansion of Iron Age cultures remain intensely debated. Thus, the transition between the Bronze Age (BA) and the Iron Age (IA) was first linked to the rapid shift from bronze to iron technologies between Hallstatt B3 and Hallstatt C (approximately 800 BC). However, this clear cut-off does not appear to reflect the regional archaeological reality that there was a gradual transition to the use of iron instead of a rapid substitution (Verger, 2015). Moreover, the cultural transformations associated with the transition span over two centuries encompassing the late Bronze Age and the first phase of the Iron Age and appear to have followed different rhythms that varied by region (Verger, 2015). Debates also concern the modes of emergence of the Late Iron Age culture *La Tène*, associated with groups generally referred to as 'Celts' and spread over a large part of Europe, spanning from Bohemia to the Atlantic (Roure, 2020). Thus, some authors propose an advent of this cultural entity in Central Europe and Bohemia before its expansion through the migration of groups bringing cultural developments from the northern Alpine area to the rest of Europe (Kruta, 2000; Brun, 2017). Other authors propose a multiregional origin of the *La Tène* culture through the evolution of a mosaic of cultural complexes ('multipolar genesis in networks'; Milcent, 2006) connected by common markers such as art without implying major migration. According to this view, the 'Celts' would be defined as a multitude of related people with different cultural practices (Lejars and Gruel, 2015).

The great amount of archaeological data available for Iron Age groups from the French territory strikingly contrasts with the near absence of genomic data for the human groups concerned. In the archaeology of death and in the study of ancient human group dynamics, palaeogenetic analyses have led to considerable advances. From the Palaeolithic to the Bronze Age periods, ancient DNA (aDNA) studies have provided arguments complementary to the archaeological evidence to reconstruct the dynamics of the groups at the European macroregional scale (see Liu et al., 2021 for a recent review) and discussions on the social functioning of communities at the local scale (documenting, for example, residence rules or filiation systems; e.g., Mittnik et al., 2019). Despite the considerable increase in palaeogenomic analyses over the last decade, some territories or periods remain poorly documented. In that respect, the French territory remained neglected in palaeogenomic studies in Europe until the very recent publication of three studies targeting this key crossroad region in Western Europe (Brunel et al., 2020; Rivollat et al., 2020; Seguin-Orlando et al., 2021). Nevertheless, genetic and genomic data for IA period from French territory remain scarce, with mitochondrial data for 91 individuals and low-coverage genomes for 19 individuals (Fischer et al., 2018, 2019; Brunel et al., 2020). To date, the underrepresentation of IA populations in palaeogenomic studies, compared with prior periods, can be extended to the European scale, with a total of 44 mitochondrial sequences from Germany, Spain and Italy (Knipper et al., 2014; Núñez et al., 2016; Serventi et al., 2018) and a total of 27 genomic data points from England (Martiniano et al., 2016; Schiffels et al., 2016), Bulgaria (Mathieson et al., 2018), Croatia (Mathieson et al., 2018), Spain (Olalde et al., 2019), Hungary (Gamba et al., 2014), Montenegro (Allentoft et al., 2015), Estonia (Saag et al., 2019) and Germany (Furtwängler et al., 2020).

These observations are particularly frustrating given that only the acquisition of representative palaeogenomic data for French Iron Age groups and their comparison with archaeological data can allow to directly characterize the biological processes potentially involved in the cultural transformations documented between the Bronze Age and Iron Age or between the Early and the Late Iron Age periods. Furthermore, compelling genomic data for these ancient communities provide the only way to test for correlation between the cultural and biological diversities of groups and question modes of exchanges between populations. Finally, genomic data obtained at the local scale can provide major insights into the social organization of communities. For older periods, whether the Neolithic or Bronze Age, palaeogenomic studies have revealed recurrent patrilocal residence rules, patrilineal filiation systems or differences in social level (see, for example, Lacan et al., 2011; Mittnik et al., 2019). For the Iron Age, the indirect testimonies left by Greeks and Romans (such as *DeBello Gallico* from Julius Caesar, even if they must be considered with caution) mentioned a very hierarchical society characterized by a patrilineal system of filiation. Thus, obtaining genomic data for the Iron Age communities represents a unique opportunity to compare biological, archaeological and textual data.

The outstanding questions presented above and the great potential of the combination of archaeological, textual and genomic data in an attempt to resolve them motivated us to better document the genomic diversity of the Gaulish populations. For this purpose, we targeted 145 individuals from 27 sites spread over the extant French territory and distributed throughout the IA period to optimize our chance of documenting the gene pool of a representative set of French Iron Age individuals. The wide chronological distribution of the dataset permitted us to address questions of origin and evolution of the groups, whereas the wide geographical distribution of the samples allowed us to test for interregional gene flow. Notably, some archaeological evidence highlighted particular exchange networks with the groups from the surrounding areas, such as the example of the necropolis of Urville-Nacqueville, sharing clear archaeological features (roundhouses, Durotrigian burials, etc.) with contemporaneous groups from Britain (Lefort et al., 2015). Finally, we also targeted sites associated with different funerary practices to better understand the biological identity and potential selection of the individuals buried.

RESULTS

The Iron Age genomic dataset from France

A total of 145 individuals were targeted for palaeogenomic analyses (Table S1). DNA was extracted, and DNA libraries were built with a partial uracil-DNA glycosylase treatment, allowing for the assessment of postmortem deamination patterns (2%–29%) expected for ancient DNA data. Initial screening via shotgun sequencing of 1 to 2 million reads was used to select libraries with an amount of endogenous DNA above 15%, leading to the exclusion of 92 individuals. For the remaining individuals who passed these quality criteria, we sequenced the libraries to an average depth of 0.178× (Table S2). We found overall negligible level of contamination in our dataset by testing for heterozygosity of polymorphic sites on the X

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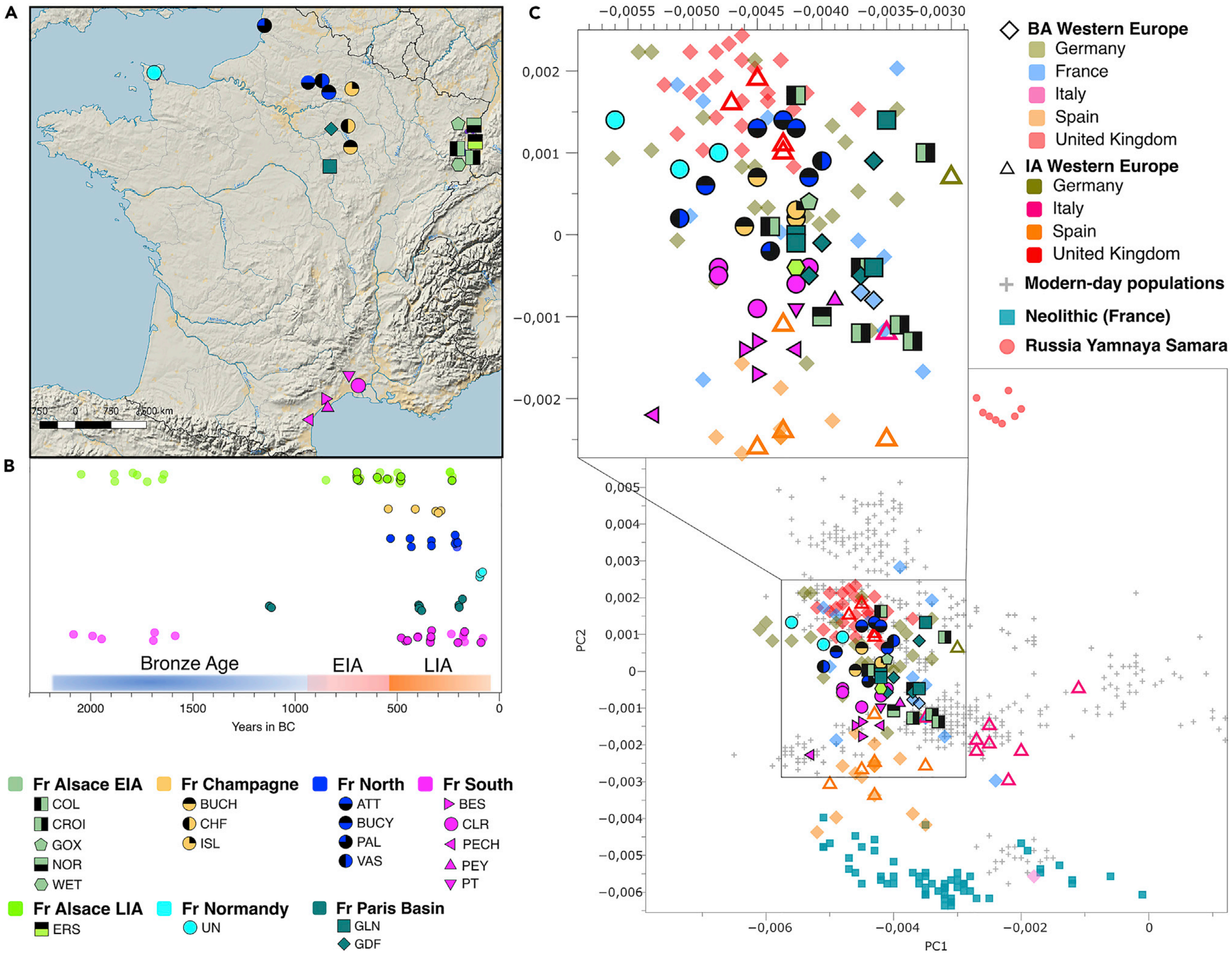

Figure 1. Overview of our dataset

Each colour represents a region, and each symbol represents a site.

(A) Location of samples included in the study.

(B) Timeline of BA and IA individuals with genomic data for the territory corresponding to present-day France. Circles without black outline represent previously published samples.

(C) Principal component analysis of western samples from the Neolithic until the Iron Age projected onto the genomic variability of present-day populations.

chromosome in males (Table S3). The dataset resulting from these successive quality selections encompasses low-coverage genomes for 49 individuals originating from 27 sites, dating from the Bronze Age (*n* = 2) and the Iron Age periods (*n* = 47). We compiled the IA data with 18 low-coverage genomes already published for IA groups from France (Brunel et al., 2020), leading to a total of 65 low-coverage genomes distributed in 6 geographical areas: Alsace (*n* = 20), Champagne (*n* = 5), Normandy (*n* = 3), North (*n* = 10), South (*n* = 18) and Paris Basin (*n* = 9) (see Figure 1A, STAR Methods and Tables S1 and S3). The IA dataset is unbalanced in terms of the chronological distribution of the individuals, with 11 individuals dated to the Early Iron Age and 54 dated to the Late Iron Age period (Figure 1B). This can be partly explained by the funerary treatment and the use of cremation (see, for example, Dedet, 2004 for southern France). The few human remains (from southern or north-western France) available for genomic analyses represent deceased who escaped cremation and benefited from non-ordinary funerary practices. Therefore, the corpus available for genomic analysis may not be representative of the entire population living at the time. For instance, for southern France, genetically analyzed individuals correspond to severed heads (see STAR Methods. site of Le Cailar) or to neonates buried in settlements (see STAR Methods. site Le Plan de la Tour). The dataset is also unbalanced in terms of regional representativeness, with the Normandy region providing the lowest number of genomes due to the low DNA conservation in the coastal Urville-Nacqueville necropolis targeted (Table S1). Finally, among the 65 individuals, if 33 were males and 32 were females, the sex ratio within each region was unbalanced, with notably more females in Alsace and more males in the South (Table S2). With this frame in mind, we analyzed our data with published ancient individuals (n = 5225) genotyped on the 1240k panel (Mathieson et al., 2015) as well with modern (n = 6461) individuals from a panel of modern-day worldwide populations genotyped on the Affymetrix Human Origins (HO) panel. From the present study's dataset, 65 individuals with more than 20,000 SNPs on the 1240k panel were used for the downstream genome-wide analyses (see STAR Methods and Table S2). We found no first-degree relatives among IA individuals from present-day France allowing us to keep the full dataset for downstream analyses (see STAR Methods, Table S3 and Figure S4).

We first explored our data qualitatively using principal component analysis (PCA) by projecting the ancient genomes onto the genetic variation of an HO set of west Eurasians (Figures 1C and S1). French IA individuals fall within the genomic variability of the modern-day French population. IA samples from Spain and Great Britain also fall within modern-day populations from the same region, highlighting a certain degree of continuity from the Iron Age to modern-day populations in Western Europe, confirming previous results based on mitochondrial DNA (Fischer et al., 2018). The PCA also shows a clinal distribution of our IA French samples according to their latitudinal position: the northern samples are closer to the extant Great Britain population, and the southern samples are closer to the Spanish population (Figure S1). These observations are fully consistent with genomic studies conducted on modern Europeans and highlight a geographically and genomic intermediate position of the French groups between north-western and south-western European populations (Novembre et al., 2008).

To test further the genomic variability of the new IA genomes, we grouped the individuals among different chrono-cultural groups, i.e., according to their region of origin and, when possible, to their dating (Early versus Late Iron Age): EIA_Alsace (from 800 BC to 450 BC), LIA_Alsace (from 450 BC to 50 BC), IA_Champagne, IA_Normandy, IA_North, IA_Paris_Basin and IA_South. We then carried out a *qpWave* analysis iterated overall individuals in the pool, testing for significant evidence of heterogeneity relative to the remaining chrono-cultural group (see STAR Methods and Figure 2). Individuals were considered genomic outliers from the chronological-cultural group from which they originate when the *qpWave* p value was <0.05 (Fernandes et al., 2020). This resulted in the identification of six individuals as outliers: BES1248, PECH3 and PEY163 stand as outliers from the IA_South group, CROI11 from the EIA_Alsace group, COL239 from the LIA_Alsace group and GDF1341 from the IA_Paris_Basin group. The analyses at the regional level were consequently conducted separately on these individuals and their chrono-cultural groups. The outlier status of these special individuals will be further discussed.

Genomic continuity from the Bronze Age to the Iron Age

The PCA highlighting Bronze and Iron Age samples from Europe shows relative genomic continuity between groups from the two periods (Figure 1C). To further explore this continuity, we performed a *qpWave* analysis to test whether the regional Bronze and Iron Age groups form a clade. Analyses permitted us to demonstrate an absence of discontinuity (no significant differentiation) between the BA and IA groups in southern France but not in Alsace or in the Paris Basin (Figure 2). The scarcity of data available for the Bronze Age in the Paris Basin (n = 2) might not reflect the diversity of the BA population of this region, which could explain this result. Nevertheless, the absence of continuity between both periods in Alsace is documented by a satisfying number of samples and may be linked to notable gene flow in this crossroads region during both periods. Interestingly, the EIA_Alsace and LIA_Alsace groups form a clade, which is consistent with some genetic continuity between periods yet recognizing important cultural transformations (see STAR Methods). Moreover, when looking at the three main ancestral components that contributed to the genomic composition of western European populations, i.e., pre-Neolithic western Hunter-Gatherers (*WHG* component), Early Neolithic farmers (*Anatolia_N*) and steppe-legacy brought by Bell Beaker groups (*Russia_EMBA_"Yamnaya*; Haak et al., 2015) with *qpAdm* modelling, we observe no significant differences for the last two components between BA and IA populations of southern and northern France (Figures 3A, 3B, and S7) whereas differences exist at the regional level (Figure S8). This indicates the absence of major genetic input from populations with different genetic legacy in the genetic make-up of French IA groups. We then performed *qpAdm* analyses to assess whether the regional Iron Age groups in France could be only explained with the French Bronze Age groups or with supplementary BA groups as sources (see STAR Methods and Table S4). We tested different models and found that all French IA groups could be

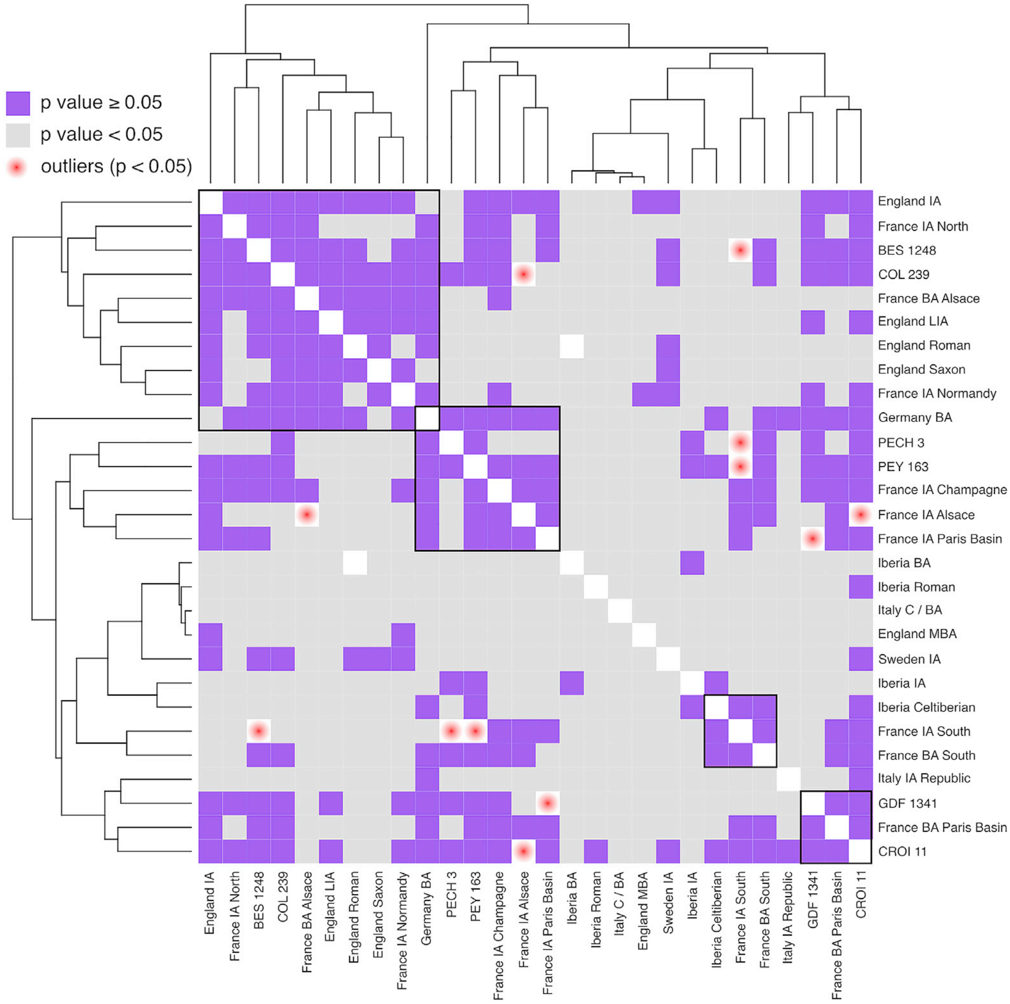

Figure 2. Pairwise *qpWave* testing to detect outliers

Grey-coloured models have a p value of less than 0.05 and were rejected, pink-coloured models have a p value of more than 0.05. Orange circles represent outliers from the chronological-cultural group from which they originate (p value <0.05).

explained by one or two French BA groups as sources. Notably, the fact that the EIA_Alsace and LIA_Alsace group gene pools could be explained by a combination of local BA_Alsace and nonlocal BA_South groups as sources reinforces the status of the region as a gene flow crossroad. Although alternative models involving BA sources from other European regions (Table S5) are also statistically possible, following a principle of parsimony, we preferentially suggest that the French IA groups directly derive from the previous French BA groups.

However, when considering uniparental markers, the genetic continuity between the BA and IA groups from French territory can be only partially identified. A total of 86 mitochondrial and 33 Y chromosome lineages were compiled for the French IA sample (see STAR Methods). Despite a great diversity of mitochondrial lineages among French IA groups, nearly 26% of the individuals could be characterized as belonging to haplogroup H. Even though important regional variability in haplogroup frequencies must be pointed out, haplogroup H represents almost 50% of the lineages in IA_North but less than 30% in IA_South groups (Table S3). Notable increases in haplogroup H and J frequencies between French BA and IA can also be highlighted (Figure S2). Regarding the Y chromosome lineages, we observed an increase in Y chromosome diversity in the Iron Age. We identified four major haplogroups in the French IA dataset: haplogroups I1, I2, and G2, which were dominant during the Neolithic in Western Europe, and the overrepresented R1b1a

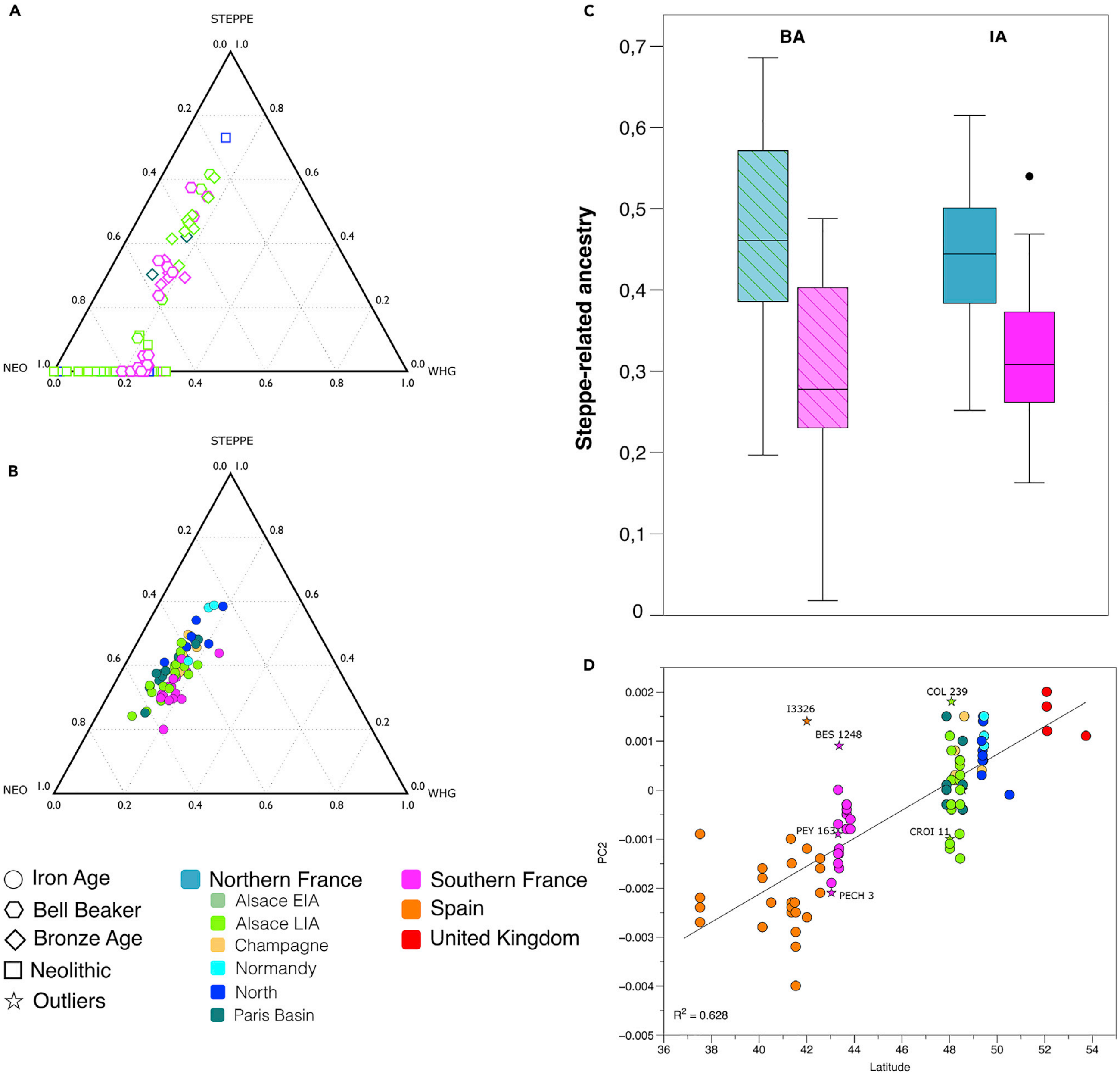

Figure 3. Distribution and average level of ancestral components in IA samples from Western Europe

Each colour corresponds to a region (France) or a country.

(A) Triplot of *qpAdm* values for the Anatolia Neolithic (NEO), steppe and western Hunter-Gatherer components (WHG) for individuals from the Neolithic to the Bronze Age from France (B) Triplot of *qpAdm* values for the Anatolia Neolithic (NEO), steppe and western Hunter-Gatherer components (WHG) for individuals from Iron Age from France.

(C) Evolution of *qpAdm* values for the Steppe related ancestry component in southern and northern French regions, between the Bronze and Iron Age periods.

(D) Relation between the latitudinal position of the archaeological sites where Western Europe IA individuals were found and PC2 values (PCA calculated on the genetic variation of an HO set of west Eurasians).

haplogroup associated with steppe-related migration (69%) (Table S3 and Figure S3) whereas BA males carry only R1b (or R*) haplogroups (Brunel et al., 2020). Nevertheless, it remains to be seen whether the variations observed between BA and IA periods are related to the small amount of data available or to maternal/paternal gene pool shifts linked to specific microevolution processes.

Overall, the compiled results reinforce the archaeological hypothesis that explains the transition from the Bronze Age to the Iron Age by political and economic crisis combined with social changes rather than by major migration or population turnover for the territory of present-day France. These genomic results are in line with more recent archaeological hypotheses that have tended to rule out the involvement of major invasion/migration in the cultural transition (Garcia and Le Bras, 2017). Recent re-evaluations of the archaeological data have indeed indicated progressive cultural evolution during these periods, such as the gradual use of iron (instead of an abrupt substitution from one material to another) or the progressive evolution of pottery (Verger, 2015). Complicating the scenario, recent archaeological studies have even revealed different cultural evolution rhythms depending on the regions or on the type of material studied (Milcent, 2009; Verger, 2015). Finally, the genomic data gathered for the Early and Late Iron Age in the Alsace region is consistent with genetic continuity throughout the Iron Age period. Even if the data in hand are restricted to the Alsace region, they support the view that the emergence of the La Tène culture was not necessarily linked to a major influx of populations/genes.

Genomic and cultural diversity among the Gauls

As previously mentioned, the PCA performed on the French IA dataset highlighted a clear latitudinal distribution of individuals (Figure 1C). The genetic differentiation projected on the PC2 axis is positively correlated with the latitudinal position of the sites where were found the samples in France ($r^2 = 0.59$, Pearson). This correlation even increases when adding IA individuals from Iberian Peninsula and England (Figure 3C, $r^2 = 0.628$). However, the f3 statistic applied in the form *f3* (*Mbuti*, *Ind1*, *Ind2*) showed no clear grouping of individuals in relation to their region of origin (Figure S5). To better characterize the genomic variability perceived between French IA individuals, we ran an f3 statistic in the form *f3* (*Mbuti*, *X*, *Ind*), where X represents an ancestral component (*WHG*, *Anatolia_N* and *Russia_EMBA_Yamnaya*). The results clearly pointed out differences between regions of France with a greater affinity between IA_South and the *Anatolia_N* component, whereas IA groups from northern French (notably Normandy) regions present more affinity with the *Steppe-legacy* component (Figure S6 and Table S6). To more precisely quantify these gradual affinities, we performed a *qpAdm* analysis modeling the IA French groups with these three components as source populations (Table S7). The modeling results clearly confirm that a decreasing north to south gradient in the steppe-related component among IA French groups is inversely correlated with an increase in the early farmer component (Figures 3A and S8). The scarcity of data from Bronze Age periods did not allow us to compare these differential affinities at a fine regional scale for this period, but it is worth noting that the distribution of available data into two separated groups, North versus South, permitted us to observe the same tendency (Figures 3B and S7). This steppe-related ancestry gradient is well established for modern-day European populations (Haak et al., 2015) and appears to be well established in French territory, at least since the BA period.

To test for specific genomic affinities between IA French regional groups or individuals, we performed f3-outgroup statistics in the form *f3* (*Mbuti*, *Region*, *Region*), where Region represents the individuals grouped by geographical affinities (without the previously defined outliers), and in the form *f3* (*Mbuti*, *X*, *X*), where *X* represents individuals from the study (Figure S5). Neithertype of test permitted the detection of any specific affinity between regional groups or individuals. Finally, we also computed f3 statistics in the form *f3* (*Mbuti*, *Site*, *Site*), where *Site* represents all the individuals discovered within the same archaeological site, and, once again, we did not detect any affinity between funerary groups. We then performed an MDS based on the genetic distance (1-*f3 (Mbuti, Site, Site)*) and did not detect any correlation between genetic and geographical distances between sites. A Mantel test comparing a matrix of genetic distances (1-f3) and a matrix of geographical distances between the sites, with the assumption (H_0) being ''there is no correlation between the two matrices'', permitted us to confirm the absence of statistical correlation between both types of distances (p value = 0.3931607).

All the statistical tests performed on IA French groups consequently highlighted an extremely gradual genetic structuration of populations distributed across the present-day French territory, complicating the demonstration of statistically significantly differentiated groups. This major observation supports the hypotheses of a common genomic legacy of the populations dispersed throughout this vast area (Collis, 2003; Roure, 2020). This very weak large-scale genomic pattern contrasts with the cultural variability documented among the regions concerned, which remained important enough during the whole Iron Age period for archaeologists to propose to differentiate the Mediterranean, Atlantic, Hallstattian and Latenian Celts (Bouffier and Garcia, 2012; Garcia, 2006). A recent archaeological scenario implies a multipolar cultural evolution of regional groups sharing some common cultural traits, such as language, religion, and social relations and ornaments and metal furniture (Milcent, 2006, 2009). Combined with the lack of genetic discontinuity pointed out between BA and IA French groups and the global low genetic structuration of groups throughout the IA period, data clearly reinforce a scenario in which regional groups linked through a rich network of cultural and biological exchanges evolve.

Interestingly, biological exchanges between regional French IA groups could be reinforced by the recurrent characterization of genetic outliers, grouping both men and women (see Table S2), which could demonstrate individual interregional mobility. We performed an f3 statistic analysis in the form *f3* (*Mbuti*, *Individual*, *Region*) to assess a possible region of origin for each outlier, and we plot the results in Figure 4. The results indeed highlighted genomic affinities between these outliers and French IA groups from other regions representing possible regions of origin of the individuals or possible origins of their direct ancestors. These affinities are also visible through the *qpWave* analysis (Figure 2). Interestingly, from an archaeological point of view, nothing distinguishes the genetically defined outlier individuals from the others discovered at the same site. This would indicate the full cultural integration of individuals originating from distinct regions. Nevertheless, two exceptions can be pointed out for outlier BES1248 and PECH3. The individual BES1248, from the Bessan site, was found in a single burial, whereas cremation was the predominant funerary practice in southern France during this period (Dedet, 2004). However, the other only adult buried in Bessan (BES1249) does not appear as a genetic outlier and, therefore, impedes drawing any conclusion about the link between outlier status and special funerary features in this case. PECH3 was found in the filling of a ditch associated with the remains of equids contemporary with the ritual phase following the destruction of the Pech Maho site (see STAR Methods for site description). The possibility of an exogenous origin for this individual is particularly interesting as it could reinforce the historical hypothesis of the destruction of the site in relation to the Second Punic War between Rome and Carthage. Interestingly, Olalde et al. (2019) also found a genetic outlier (individual I3326; Figure 3C) in the Ullastret site on the Iberian Peninsula, where many Latenian swords, locally produced, were discovered. This evidence reinforces the idea of important exchanges of goods, people and skills among IA communities. On the other hand, at the Cailar site, where archaeologists have highlighted the practice of severed heads (Ciesielski et al., 2014; STAR Methods; Ghezal et al., 2019), as at Ullastret and Pech Maho, all the individuals analyzed form a genetically homogeneous group and fall within the genetic diversity observed for southern France. Therefore, no genetic element supports the hypothesis of a distant origin for these individuals, whose heads were probably used as trophies. All these specific cases highlight the impressive variability and complexity of interrelation between IA individuals' genetic and archaeological identities.

Interactions between western European contemporaneous groups

Given the gene flow characterized between French IA groups, we tested for equivalent biological interactions with groups from other western European areas. We have seen that PCA and *qpAdm* analyses highlighted special affinities between IA groups from southern France and Spain and from north-western France and England (Figures 1C and S8). We, therefore, explored these specific affinities through an f3 statistic in the form *f3* (*Mbuti*, *IA France*, *IA other*), where *IA other* represents IA groups from regions other than French territory and considering either individuals, sites or regions (see STAR Methods). Unfortunately, palaeogeneomic data are still poor or missing for several bordering regions, such as Germany, which limits this part of our study. The performed test did not permit us to significantly differentiate any specific genetic affinities with IA from the European regions documented, surely linked to the very low genomic differentiation of all the groups concerned. *qpWave* analyses performed between regional groups and other European contemporaneous groups highlight clustering of northern France and north Europe (England and Sweden) IA groups whereas the Gauls of southern France stand out from this cluster but appear closer to the Celtiberians from Iberian Peninsula (Figure 2). Finally, no genetic affinity was found between Greece or Italy and the populations of the IA of the current French territory. Genomic affinities perceived between IA groups from south-western France and northern Spain are expected because they belong to the same cultural entity called ibero-languedocian (Gailledrat, 1997; Py, 1993). Similar types of ceramics and weapons, are indeed found on both sides of the Pyrenees during the IA. Moreover, the settlements and fortifications found in respective regions are quite similar, and some scholars have even proposed the shared use of the Iberian language by the concerned groups (Mullen, 2013). Similarly, the genomic affinity detected between the IA groups from north-western France and England is not surprising. Indeed, the north-western French groups are represented by individuals originating from the Urville-Nacqueville necropolis (Normandy), where specific archaeological features, such as roundhouses, are clearly related to the English IA cultural

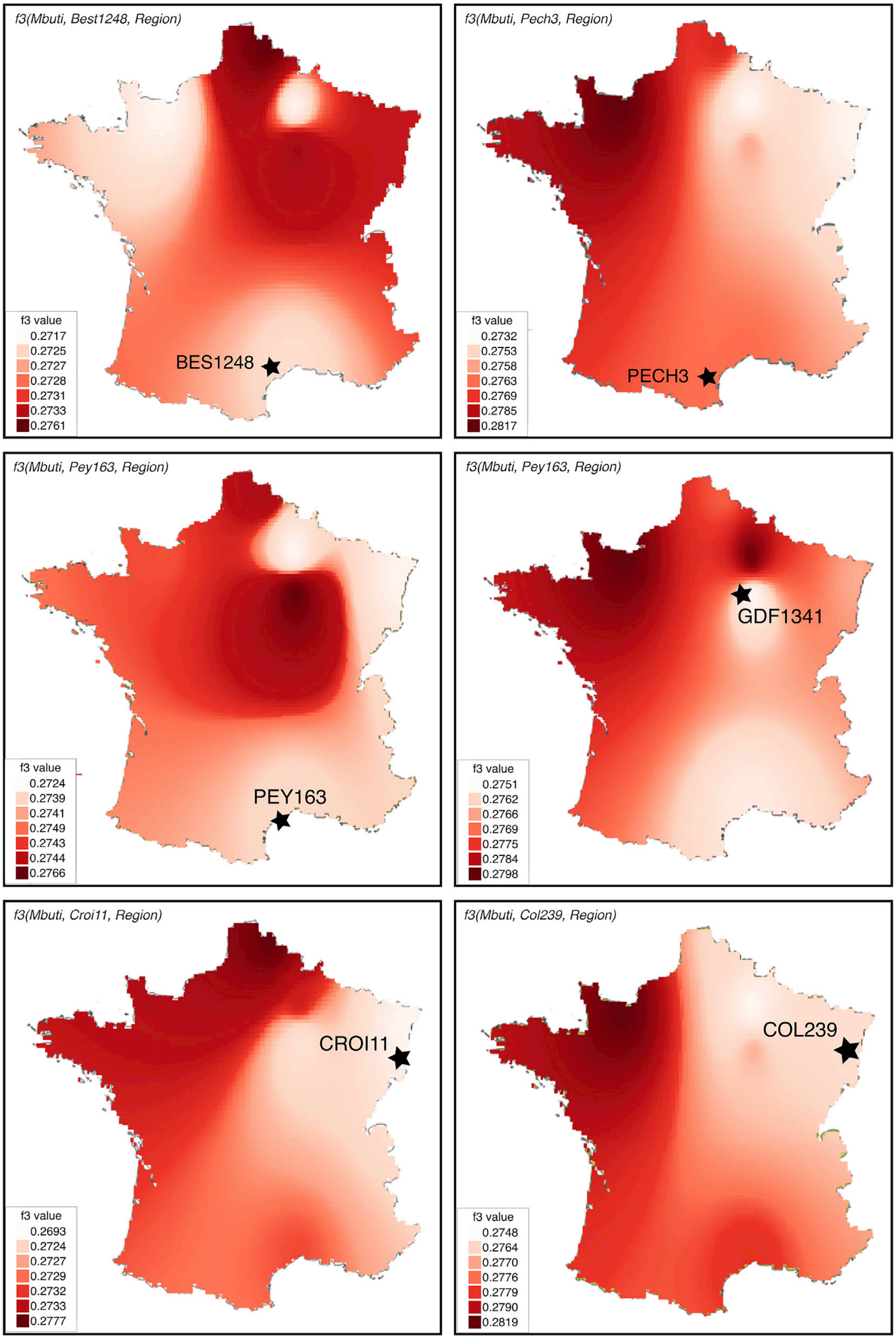

Figure 4. Plot results of the f3-outgroup statistic in the form f3 (Mbuti, Outlier, Region), where "Region" corresponds to Iron Age individuals grouped according to their region of origin

sphere (Lefort et al., 2015). Moreover, Normandy and South England are part of a well-documented network of exchanges during the Bronze Age (Atlantic BA and Manche-Mer du Nord Complex; Marcigny et al., 2017) and the Iron Age periods (part of the medio-Atlantic Iron Age; Milcent, 2006). It is finally worth adding that the three individuals from Urville-Nacqueville that provided genomic data are three males, all buried in the so-called ''Durotrigian'' position, which is well known in Dorset (Fitzpatrick, 2011; Lefort et al., 2015). Consequently, we cannot exclude that these individuals might originate from southern England and may not be representative of the whole population buried at Urville-Nacqueville (Fischer et al., 2018, 2019). Regardless of the case, the correlation between exogenous material, cultural variations, and gene flow with groups from other regions found in these specific contexts cannot be extended to the full IA archaeological landscape. This is notably the case for the necropolis of Peyrou (southern France, 6th–4th centuries BC), where the funerary treatment of the deceased and the material deposited in the tombs provided clear evidence of the establishment of Greek settlers in the region after an intermittent phase of contacts. However, none of the individuals analyzed (*n*= 3, male or female) from the necropolis show peculiar genetic affinity with Greece or the Mediterranean Basin. Interestingly, the individual who stands as an outlier (PEY163) seems to have more affinities with the Paris Basin and did not point out to the Mediterranean area (Figures 2 and 4). As our study is not exhaustive for this site, it is quite possible that the analysis of a larger number of individuals would allow one to highlight the presence of Greek settlers in this necropolis. Indeed, Greek colonies are a very particular environment, where the surrounding native population can live among the Greek settlers (Dedet, 2015). However, this example once again demonstrates that funerary practices and/or exogenous material do not constitute reliable evidence of allochthonous individuals, as already described for other periods/regions (O'Sullivan et al., 2018).

An important result is also the greater dispersion of IA_Alsace individuals in the PCA, overlapping groups from IA_South, IA_North, IA_Paris_Basin or IA_Champagne. This dispersion points to higher genetic diversity within this regional group, which could be evidence of higher gene flow (Figure 1C). The Alsace region is regularly characterized as a ''crossroads'', an axis of transit and exchange, because of the presence of the Rhine River, which has constituted a major communication link between western and central Europe through history. Nevertheless, the genetic exchanges characterized for the IA period do not appear to find a special echo in the material culture. During the Early Iron Age, archaeological records suggest material exchanges between southern Alsace and southwestern Germany (Bavaria, Baden-Württemberg), whereas northern Alsace shared contacts with the Lower Rhine Valley. If the arrival during the Hallstatt period of material described as exogenous (amber from the Baltic region, coral from the Mediterranean, Etruscan imports, etc.) could testify to a notable increase in north-south trade, this kind of material remains very occasional. Therefore, even if cultural exchanges with neighbouring regions are verified, contributions from further distances remain apparently limited.

Functioning of communities

To start documenting the local functioning of French IA groups, we performed an analysis to detect long runs of homozygosity (ROH, Ringbauer et al., 2021). We observed that the number of ROHs of 4–8 cM tended to decrease during the Iron Age following the general tendency observed since the Mesolithic, a result explained by a progressive increase in the mating populations and/or an increase in long-distance gene flow (Figure S10). Few archaeological studies have focused on the IA population demography; nonetheless, a study conducted on funerary data by Isoardi (2008) found an increase in population size at the end of the Early Iron Age in the Southern Alps, Provence and probably in the Rhone and Saone valleys, followed by a slight decrease around the mid-4th century BC. They also noted that population size tended to increase during the second half of the 3rd century BC. Various studies have also demonstrated the importance of exchange networks at varying distances during the Iron Age, as evidenced, for example, by the Greek bronze crater in the tomb of Vix (Early Iron Age, Joffroy, 1954) or the Roman amphorae discovered at Urville-Nacqueville (Late Iron Age, Lefort et al., 2015), but we found no evidence of such long-distance exchanges in our data. Such events might have been restricted to a few individuals playing an important role in Iron Age society but having a limited impact on the genetic pool.

Finally, we detected multiple long ROH on different chromosomes in one individual, COL 336 (Alsace), who can be interpreted as the offspring of a first-degree incestuous union (parent-offspring or full siblings) (Figure S11). Intriguingly, the Colmar site includes several burials in pits without any grave goods or weapons accompanying the deceased, whereas the main funerary practice for this period and this region is the inhumation in small funerary complexes of tumuli. Therefore, even if the observed funerary treatment of COL

336 does not differ from that of any other individuals from the site, it could be considered as a relegation-type burial. This could be linked to a rejection by the IA society of this incestuous practice. This is in opposition to what has been described at the site of Newgrange for Neolithic period (Cassidy et al., 2020), where the presence of consanguineous individual on one of the most spectacular Megalithic mount of Europe was interpreted as the evidence of a high hierarchical society with complex chiefdoms. To explore more in details the social organization of IA groups and compare it with historical sources, a more exhaustive genomic dataset would be necessary.

DISCUSSION

In this study, we recovered 49 genomes from BA and IA individuals widely distributed within present-day France. With this valuable dataset in hand, we were unable to detect a genetic discontinuity between the Bronze and Iron Age communities of France, as already mentioned by Brunel et al. (2020). Our dataset also highlighted a north to south gradient for steppe-related ancestry inversely correlated with the Early Neolithic Farmer one. Moreover, the distribution and proportion of these legacy components remain stable between Bronze and Iron Age periods. This is perfectly in line with recent archaeological evidence considering that the transition from the Bronze to the Iron Age was a consequence of social and political changes from the 8th century BC onwards. If no evidence of migration event could be highlighted since the BA, although events of this type involving populations with the same genetic characteristics are hard to perceive, we were able to detect mobility at the individual scale between regions and gene flow with neighbouring groups from England and Spain. Of great interest, these genetic outliers were not always distinguishable from an archaeological perspective, which could mean that they were fully integrated within the community. Although analyses allow us to propose a possible region of origin for these outliers, Sr isotope analyses would be of great interest to complete the individual mobility scenario. Interestingly, these networks are visible not only in the French territory but also on the western European scale. Indeed, we were able to detect specific affinities between northern/north-western France and England IA communities and between southern France and Spain communities. This result is consistent with archaeological evidence, such as the presence of roundhouses and so-called ‘Durotrigian’ buried in Urville (Normandy) and the definition of the ‘Ibero-languedocian’ complex in the South. Globally, the results proposed reinforce the idea that ‘Celts’ derived from local BA populations that evolved progressively between regional groups sharing some common cultural traits and linked through a network of cultural and biological exchanges.

Limitations of study

Due to the extensive use of cremation in the period considered, the highly variable DNA preservation among sites and the unequal distribution of archaeological discoveries among regions, the genomic dataset obtained remains differentially distributed among regions and periods.

STAR★METHODS

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SUPPLEMENTAL INFORMATION

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Conceptualisation: CEF, MFD, MP. Data curation: CEF, MHP, ID, MFD, MP. Resources: HBE, AB, EC, BD, SD, FC, EG, SG, AG, AB, GK, FL, AL, AM, FM, SO, CP, EP, SP, IR, MRZ, RR, CT, YT and SR. Formal analysis: CEF, MFD, MP. Funding acquisition: SR, MFD, MP. Writing – original draft: CEF, MFD, MP. Writing – review & editing: all.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Biological samples		
osteological remain	this study	Att27
osteological remain	this study	Att3
osteological remain	this study	Att52-2
osteological remain	this study	BES1096B
osteological remain	this study	BES1154
osteological remain	this study	BES1249
osteological remain	this study	BFT228
osteological remain	this study	BLH447
osteological remain	this study	BPV1445
osteological remain	this study	BPV1455
osteological remain	this study	BUCH48-1
osteological remain	this study	BUCH48-2
osteological remain	this study	BUCH82
osteological remain	this study	CHF106
osteological remain	this study	CLR23
osteological remain	this study	CLR24
osteological remain	this study	CLR31
osteological remain	this study	CLR35
osteological remain	this study	CLR44
osteological remain	this study	Col239
osteological remain	this study	Col330
osteological remain	this study	CROI1-4
osteological remain	this study	CROI11
osteological remain	this study	CROI12-2
osteological remain	this study	ERS83-2
osteological remain	this study	GDF1231
osteological remain	this study	GDF1264
osteological remain	this study	GDF1341
osteological remain	this study	GDF1348
osteological remain	this study	GDF1349B
osteological remain	this study	GLN126A
osteological remain	this study	GLN126B
osteological remain	this study	GLN141
osteological remain	this study	GLN29-A
osteological remain	this study	GLN32
osteological remain	this study	Gox287
osteological remain	this study	ISL6950
osteological remain	this study	PAL170
osteological remain	this study	Pech3
osteological remain	this study	Pech9
osteological remain	this study	PEY73

(*Continued on next page*)

Continued

REAGENT or RESOURCE	SOURCE	IDENTIFIER
osteological remain	this study	PT7
osteological remain	this study	SCPG2
osteological remain	this study	UN129
osteological remain	this study	UN19
osteological remain	this study	UN85
osteological remain	this study	VAS75
osteological remain	this study	VAS79-2
osteological remain	this study	WET429
Chemicals, peptides, and recombinant proteins		
Proteinase K 100MG	Sigma Aldrich	Cat# 3115879001
Buffer QG	Qiagen	Cat#19063
OneTaq® 2X Master Mix with Standard Buffer	New England Biolabs	Cat# M0482L
Phusion® High-Fidelity DNA Polymerase	New England Biolabs	Cat# M0530L
NEBNext End Repair Module	New England Biolabs	Cat# E6050L
NEBNext Quick Ligation Module	New England Biolabs	Cat# E6056L
USER Enzyme	New England Biolabs	Cat# M5505L
Critical commercial assays		
MinElute PCR Purification kit	QIAGEN	Cat# 28006
Qubit dsDNA HS Assay Kit	Thermo Fisher Scientific	Cat# Q32854
NextSeq 500/550 High Output Kit v2.5 (150 Cycles)	Illumina	Cat# 20024907
Agilent High Sensitivity DNA Kit	Agilent	Cat# 5067-4627
Deposited data		
Raw and analyzed data	This study	ENA Project: PRJEB50940
Software and algorithms		
READ	Monroy Kuhn et al., 2018	https://bitbucket.org/tguenther/read/src/master/
Admixtools	Patterson et al., 2012	https://github.com/DReichLab/AdmixTools
Yleaf	Ralf et al., 2018	https://github.com/genid/Yleaf
Haplogrep	Dür et al., 2021	https://github.com/seppinho/haplogrep-cmd
ANGSD	Korneliussen et al., 2014	https://github.com/ANGSD/angsd
smartPCA		https://github.com/DReichLab/EIGtree/master/POPGEN
bamUtil		bamUtil 71 https://github.com/statgen/bamUtil
EAGER	Peltzer et al., 2016	https://github.com/apeltzer/eager-gui
AdmixR	Petr et al., 2019	https://github.com/bodkan/admixr

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources and reagents should be directed to and will be fulfilled by the lead contact, Melanie Pruvost (melanie.pruvost@u-bordeaux.fr).

Materials availability

Raw sequence data and alignments are available at the European Nucleotide Archive (ENA) under accession number ENA PRJEB50940.

Data and code availability

- Genomic data have been deposited at the European Nucleotide Archive (ENA) and are publicly available as of the date of publication. Accession numbers are listed in the key resources table. All other previously published genomic data used in this study is available at the sources referenced in the quantification and statistical analysis section.
- This paper does not report original code.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Archaeological and anthropological information

Nordhouse, lieu-dit "Buerckelmatt" (Bas-Rhin)

Person in charge: S. Plouin, F. Lambach

The necropolis of Nordhouse, formed by six tumuli, is located approximately 20 km south of Strasbourg within the alluvial plain of Ill river. These tumuli are mostly dated from the Late Bronze Age IIIb, with cremation materials deposited in the center of a ditched circular enclosure. Accompanied by rich ceramic items, cremated human remains were placed within a wooden architecture. Characteristic potteries from the same phase were found in the eastern sector of each ditch.

The necropolis of Nordhouse was then occupied between the 7th and 4th centuries BCE (between Hallstatt C2 and La Tène B1). During the first and early Iron Ages, numerous weed burials were deposited in the tumulus, and each monument hosted between 14 and 27 graves. A total of 101 burials were found. An exceptional female tomb stands out for the abundance and richness of its grave goods, including glass, amber, coral, a large shell from the Red Sea and many gold ornaments.

In the present paper we used the genomic results previously published for four individuals (Brunel et al., 2020), originating from 3 different monuments. Human remains NOR3-15 (an adult female buried with various ornaments) and NOR3-6 (an adult, possible female, buried with an infant and various ornaments) were discovered in tumulus 3, whereas NOR2B6 (an adult male buried with an infant) and NOR4-4 (a young female buried with various ornaments, potentially corresponding to an aristocratic individual) were found in tumulus 2 and 4, respectively.

Author of entry: S. Plouin and F. Lambach

References: in prep

Sainte Croix en plaine (Haut-Rhin)

Person in charge: F. Chenal, Y. Thomas, S. Plouin

On the territory of the commune of Sainte-Croix-en-Plaine, located 11 km south of Colmar (in Alsace, Haut-Rhin), one of the largest funeral complexes discovered in the department extends over more than one hectare. It has been the subject of several preventive excavation campaigns, in 1979–1981, 1997, 1999 and 2005. More than a hundred funerary structures have been unearthed there, mainly within mounds of which only the circular ditches that surrounded them remain today.

The results of these excavations have provided invaluable information on the knowledge of regional funeral practices between the end of the 2nd and the middle of the 1st millennium BC. The alternation of burial and cremation practices and the occasional presence of wooden containers adapted to the morphology of the deceased could be notably pointed out.

The funerary structures included a rich material consisting mainly of ceramics and female bronze ornaments dated between the 7th and early 4th centuries BC. Most of them were produced from bivalve stone moulds, in which the metal was cast. The objects were then embellished with a chiselled or engraved decoration that may have completely covered them. The most remarkable bracelets are local products and represent major testimonies of Celtic craftsmanship.

In the present study, we propose genomic results from four individuals from this site. Three of them were discovered in the 'Oberes Holzackerfel' location: Croi1-4 (an adult buried with an exceptional iron razor, S1-4), Croi11 (an adult buried in one of the richest burials on the site, deposited with several grave goods such as an amber bead, S11-2) and Croi12-2 (an adult buried with a lignite bracelet, S12-2). Individual SCPG2 was excavated in the 'Oberholtzackerfeld/Echangeur Gendarmerie' location.

These individuals were combined to the Jeb8, originating from the same site and previously published in Brunel et al., 2020.

Author of entry: F. Chenal

References: in prep

Colmar "Jardin des Aubépines" (Haut-Rhin)

Person in charge: M. Roth-Zehner, A. Mauduit.

The settlement of "Jardin des Aubépines" is located in the southwest of the commune of Colmar on a loess layer very favorable for the establishment of pre- and protohistoric deposits. Excavation of the site has established the presence of an imposing ensilage site that begins at Hallstatt B1 and ends at La Tène B1.

Nine individuals (2 women, 2 men, 2 immature and 3 undetermined adults; anthropological study: A. Mauduit) were deposited in silos. Some subjects (ST.336, ST.363) were deposited at the bottom of the structures. In all other cases, the burials were deposited when the silo was already beginning to fill in. Some of them were adorned with bronze or iron fibulae attributable to La Tène B1, bracelets and anklet rings. The silo fillings also delivered ceramics from the same period (Landolt et al., 2010, 2012).

The selection of the individuals deposited in these special structures does not appear to be governed by biological criteria such as age or gender. When compared to funerary groups recovered in cemeteries, no special features could be observed, whether at the level of health status (they have no more pathologies or stress markers), of the goods accompanying the deceased, or of the positions and orientations of the individuals.

At the proximity of the two silos grouping the human deposits, a silo containing the deposit of approximately ten animals (st. 235), whose skeletons are complete, is noteworthy. The localization of this animal deposit raises the question of its association with the human burials discovered nearby. Among the animals, archaeologists could identify a horse (a small Gallic horse) from which the skull was removed, several dogs, one of which was found in a suit (a large dog), at least one piglet and several lambs. The animals discovered in this structure 235 were deposited with great care and therefore cannot be considered as usual rejects from habitat context.

In the present study, we present genomic data for three individuals: Col239 corresponding to an adult (30–60 years old) male buried with some grave goods, Col330 corresponding to an adult (30–39 years old) male and Col336 corresponding to a young (15–25 years old) female buried with a copper bracelet and presenting a spinal injury that might have been infectious. These individuals were combined to two other individuals, Col153A and Col153i, originating from the same site and previously reported by Brunel et al., 2020.

Author of entry: M. Roth-Zehner

Wettolsheim "Ricoh" (Haut-Rhin)

Person in charge: C. Jeunesse, M. Roth-Zehner

The Hallstattian Necropolis "Ricoh" (1987–1990) is located on loessic land to the east of the Wettolsheim municipality. It covers an area of approximately 1.2 ha and consists of ten burial circles grouping a total of 38 burials and 19 cremations. Half of the tombs are located outside the burial enclosure. The occupation of the necropolis begins at Hallstatt B2/B3-Hallstatt C and ends at Hallstatt D1. The cremations belong to the initial phase, while the burials mainly date from Hallstatt C2 and D1. The deceased were found placed in wooden containers into large tombs, with a series of vases regularly placed near their feet. Some individuals were adorned with bronze bracelets presenting geometric decorations typical of the Upper Rhine plain, as well as bracelets of lignite, bronze belts, amber and glass beads (Jeunesse, 1988).

In the present paper, we present the results for individual Wet429, a young male.

Author of entry: M. Roth-Zehner

Goxwiller (ZAC PAEI, Bas-Rhin)

Person in charge: S. Goepfert

Goxwiller is located approximately 25 km southwest of Strasbourg and 5 km east of the Vosges foothills, on a terrace made up of loessic wind deposits. The excavation, carried out in 2011, covers a total area of 3.8 ha.

The first indications of occupation date back to the early Bronze Age and correspond to a well and a pit. After a hiatus of several centuries, a final Bronze Age IIIa complex, consisting of seven widely dispersed structures, was established on the right-of-way. These structures belong to a domestic ensemble whose exact nature cannot be established.

The Early Iron Age is the period best represented on the site with 96 structures that can be attributed to the Hallstatt period. Apart from a few miscellaneous excavations (polylobed pits, oblong pits, simple pits), the majority of the structures identified correspond to silos that hosted at least 45 individuals. Three of the silos had a particular filling, indicating that they had been reintervened or excavated in their center. One of them, St.287, yielded the skeleton of a child aged between 7 and 11 years old. The skeleton, which was deposited in the original structure, was only superficially affected by the reintervention, which seems to have been quickly filled in. One of the skeletal bones was radiocarbon dated indicating a range covering the entire Hallstattian period (excluding Ha D3): 791-519 BC to 2 σ (Poz-47205, 2510 ± 35 BP).

Here, we present data for Gox287, a young individual (7–11 years old).

Author of entry: S. Goepfert

Erstein (Untergasse, Bas-Rhin)

Person in charge: F. Abert

In 2016, a survey archaeological excavation at the Erstein "Untergasse" uncovered an important diachronic site with more than 1,300 archaeological structures.

A first occupation of the Second Iron Age was identified in the western part of the site, encompassing approximately ten burials with exceptional artefacts dated from La Tène B. The burial installation in a rough circle in a restricted space indicates that they were probably originally surmounted by a burial mound. A few nonfuneral structures are also attributable to La Tène, including a silo that provided numerous fragments of ceramics typical of this period and a ditch that crosses the right-of-way from east to west.

The Gallo-Roman period is also represented on the site, particularly in the eastern half of the right-of-way. The structures could only be poorly documented, as most of them have not been excavated. Nevertheless, they have been the subject of a removal of surface material after they had been stripped.

The main occupation of the site dates back to the early Middle Ages. It covers the entire stripped surface and is exceptional in terms of size, density and organisation. It also has the particularity of combining settlement structures with funerary areas. Numerous archaeological structures intersect here, bearing witness to a dense and long-lasting human activity. The settlement contains numerous hut bottoms, storage structures (silos and cellars), wells, post hole drawing plans of buildings and numerous pits. Most of these remains are organised around two or three parallel axes, corresponding to communication routes oriented along a north-south axis.

The funerary structures can be divided into two distinct types. In the western part of the site, isolated burials or graves in groups of two to three graves are present among the habitat remains. To the east, along the northern boundary of the excavation, a small cemetery contains numerous burials, the density of which and some overlaps indicate that they were isolated from the habitat in a reserved space which suggests the existence of a religious building nearby.

Here we present genomic results for Ers83-2, a young individual (approximately 10 years old). This individual was combined to three other samples (Ers1164, Ers86 and Ers88) previously published in Brunel et al., 2020.

Author of entry: F. Abert

Buchères « PLA - secteur 1A » (Aube)

Person in charge: V. Desmarchelier

In 2014, an excavation was carried out in the Aube Logistics Park, in the commune of Buchères, in the south of the Troyes conurbation. This operation was part of the PLA development project, which began with archaeological diagnostics in September 2004. The two stripping operations of 2014 - D41 and D42 - were located to the southeast of this project, in the area known as the ''Vignes Neuves'' and about 700 m from the Fontaines deSavoie stream, which crosses the Logistics Park from north to south. They are about 100 meters apart and are located on a plateau which also concentrates excavation operations D01 (2005), D37 (2011) and D43 (2015). Overall, over the whole of the PLA, the various operations have revealed occupations of domestic or funerary nature, from the early LBK to the modern period. The 2014 excavation has uncovered structures covering approximately 1 ha, indicating discontinuous occupation from the ancient Mesolithic to the modern period.

The Second Iron Age is the period best represented. Nearly 20 silos - two with burials and two with dog deposits - associated with pits, post holes, a polylobed pit and a hole containing human skeletons are evidence of domestic occupation in this sector (Desmarchelier, 2020).

Almost all of the silos delivered ceramic that permitted anchoring their use as a dump at the end of La Tène A2 and during La Tène B1. Interestingly, this period is poorly represented at the local scale despite the start of a peak in the intensity of this type of storage during this period in northern France. There is no dating evidence to establish a proven succession of structures over time, all falling within a broad framework of approximately one hundred years at the beginning of the Second Iron Age. However, as no overlap between structures has been observed, a contemporary or chronologically very close use of the structures can be assumed. Mostly consisting of small domestic waste, the assemblages from the silos do not evoke any particular activity other than conversion into domestic dumps or - in the case of dog dumps or burials - for ritual or funerary purposes.

The hole, located to the east of the pickling, was in itself an enigma because of the human skeletons discovered at a considerable depth in its filling. In addition to these deceased, deposited respectively at 3.90 and 5 m deep, this structure also revealed numerous remains of fauna at 7 m deep. Certain clues related to decomposition indicated the presence of localised empty spaces inducing a cover of the structure above the human remains. These men did not appear to have suffered from any pathology, traumatic or infection, apart from a sprained right ankle observed for one individual. There is no evidence to indicate the context of their deposition, whether it was an accidental and fatal fall or a burial with a cover.

Since the first archaeological interventions in the Logistic Park in 2005, 23 individuals have therefore been discovered in 14 silos and one pit, most of which were deposited on the dome of the first fill or closer to the bottom of the structure, between Hallstatt C and Tène C. Likewise, like the deceased from the PLA as a whole, the individuals discovered in the silos and the hole are on the whole lacking in stress indicators and pathologies, with signs of senescence being rare and not very intense.

In the absence of more eloquent evidence, the location of the habitat on which these structures depended remains hypothetical. In fact, even if it can be assumed that it was located close to those that delivered most of the furniture, no characteristic structure was found there. It should be pointed out that, with regard to this chronological phase, small, lightly built dwellings have little chance of being preserved, as the batteries of silos, due to their depth, are more easily resistant to erosion.

Here we present the genomic results for two individuals: Buch48-1 and Buch48-2 who are two adult males deposited in wells, which is quite rare for the period and the region.

Author of entry: I. Richard

Buchères, Moussey, Saint-Léger-près-Troyes « PLA – D37 et D38 » (Aube)

Person in charge: C. Paresys

In 2011, Inrap carried out an archaeological excavation in the commune of Buchères, in the ''Parc Logistique de l'Aube'' (Aube, Champagne Ardenne). This excavation, with a total area of 12,395 m^2, divided into two separate windows, uncovered several sets of structures covering a vast chronological field from the Neolithic to the contemporary period and different functions (land use, funerary, agricultural; Paresys, 2014).

The main occupation of the site is materialised through eleven funerary enclosures of various shapes, nine circular, one quadrangular and one elliptical. Some ceramic fragments were found in their filling, divided into two main periods, the end of the Neolithic and the end of the first Iron Age. Radiocarbon analyses are consistent with these two periods, and three of the oldest enclosures could be chronologically located between the Neolithic and the end of the Bronze Age. In fact, an enclosure dating from the Early Bronze Age was discovered nearby at the time of the diagnosis in 2005.

Burials dated between Hallstatt C and Tène A were found in three of these enclosures, two in the area bounded by the ditch, the last of which intersected the ditch of enclosure D37F0062.

The storage of grain is illustrated by five silos distributed over the two picklings. Four of them then housed six deceased, two of them with metal furniture. Of the deceased deposited in the same structure, two were simultaneous and two others deferred in time. These deceased are more recent than those buried in the enclosures between Tène B and Tène C.

In the present study, we present genomic results for individual BUCH82, an adult discovered in a silo.

Author of entry: I. Richard

Champfleury « RN 51 » (Marne)

Person in charge: S. Culot

The Champfleury ''RN 51'' (Marne) site is located south of the city of Reims (less than 6.5 km from its ancient center). It is located on the eastern slopes of the Rouillat valley, which slopes slightly from east to west, at altitudes of 107 and 100 m respectively. It is also bordered to the east by one of the many dry valleys encountered in the chalk plain. One of the nearest prominences is less than 1 km to the west, rising to 121 m. Further south, the Montagne deReims, the flagship of this sector, overlooks the plain from a height of 283 m.

The excavation operation uncovered seven sepulchral pits grouping ten individuals, distributed over three distinct groups (Culot, 2012). These burials probably belong to an even larger necropolis, continuing southwards (Champfleury, ''A Mi Champs'',Bonnabel, 2011). The illustrated funerary practice is characteristic of the early Second Iron Age and classic of the Aisne-Marne archaeological culture as defined by J.-P. Demoule (1999). The material associated with the deceased permitted to specify the chronology, ranging from La Tène A (475–400 BC) to La Tène B1 (400–325 BC).

Here we present the genomic results for individual CHF106, an adult male buried with several grave goods.

Author of entry: I. Richard

Isles-sur-Suippe « Les Sohettes » (Marne)

Person in charge: A.-C. Baudry

The Isles-sur-Suippe site is located in the Marne Department, 16 km northeast of Reims. Excavated in 2014 by Inrap (Baudry, 2021), this 4.8 hectare site consists of four sectors covering the chronological periods of the end of the Second Iron Age, Antiquity and the First World War.

The protohistoric occupation consists of an enclosed habitat from the transition between the final La Tène and the beginning of Antiquity. The chronological question is crucial in the case of Isles-sur-Suippe. In fact, approximately fifty architectural units (buildings on posts, palisades) associated with holes, are organised within an enclosure of more than 1.8 ha in surface area. The first elements of dating obtained from the ceramic study and radiocarbon analysis show a relatively short period of occupation of about 150 years, without any apparent chronological hiatus.

One of the pits, pit 6950, was discovered on the edge of the settlement, about 50 m east of the enclosure ditch. It is circular and narrow in cross-section, dug into a compact chalk substrate at least 6 m deep. In its central part, at a depth of 2.5 m, a deposition zone was discovered, containing animal carcasses and the skeleton of a young man. No perennial furniture was found next to this individual except a large ceramic shard. A second deposit was found at the bottom of the shaft, this time consisting of an isolated millstone. The deposit of the animals and the deceased in the pit, because they were very close in time, strongly link the treatment of cattle and humans. It is hypothesised that these deposits were the result of the same operating chain, the purpose of which remains to be elucidated. These practices, which stand outside of usual funerary practices between the 2nd and 1st centuries BC, raise questions about the purpose of this deposit and the practices that may lead to the association of humans and cattle.

Here we present the genomic results for individual ISL6950, the young male recovered in this special structure.

Author of entry: I. Richard

Urville-Nacqueville (Manche)

Person in charge: S. Rottier, A. Lefort

The site of Urville-Nacqueville, Normandy, is an Iron Age coastal settlement and funerary site excavated between 2011–14 and again in 2017. This port, located along the Channel, is characterised by the presence of an artisanal sector and a vast cemetery.

The Iron Age activity focuses on the period 120–80 BC and displays significant links with southern Britain, both in terms of the settlement evidence (e.g. the presence of roundhouses, Kimmeridge shale etc) and burial rites (with some adults individuals buried in a position similar to that seen in the Durotigian region of southwest England; Lefort et al., 2015).

The excavations of the Urville-Nacqueville necropolis revealed 112 graves (78 burials and 34 cremations) containing the remains of at least 127 individuals (of which 41 were cremated). The inhumations are dominated by subadults, and the cremations concern principally adults. The funerary space is organised through the presence of an enclosure in the northeast. Some unusual funerary practices are observed at Urville-Nacqueville, such as deliberate removal of skulls and extra skulls in some burials. This site is also outstanding for the period and the area for its size. Indeed, for the Second Iron Age in Normandy were mainly found small cemeteries of less than 30 individuals, usually cremated and lacking evidence for subadults (Chanson et al., 2011).

Here, we present genomic results for three adult male individuals buried in the so-called 'Durotrigian' position: UN 129, UN 19 and UN 85.

Author of entry: C-E Fischer

Attichy-Bitry

The La Tène necropolis of Attichy-Bitry ''Le Buissonet'' is located in the Oise between the towns of Compiègne and Soissons, on the right bank of the Aisne. Partly destroyed by an antiquarian settlement, 11 burials are spread over about 1300 m^2, grouping 12 individuals, 6 adults, 5 children and 1 individual of undetermined age. The usual funerary practices discovered in the region consist in individual cremated burials. The deceased wore a panoply of ornaments and clothing accessories made of bronze, iron or lignite, with the men also wearing equipment consisting of weapons. In addition to this, there are also toiletries or tools, chariot parts, deposits of meat and ceramic containers for the presentation and consumption of food or liquids. The highest hierarchical rank of this community is expressed in two chariot tombs and a tomb with a circular enclosure where a young child was buried. The funerary occupation of Attichy seems to have extended throughout part of the 3rd century, a period characterised by the abandonment of burial in favor of cremation. The Attichy necropolis can probably be linked to the Aisne-Marne cultural group with a later adoption of cremation for all individuals at the end of the Middle La Tène.

Here we present genomic data for three individuals: Att3, Att27 and Att52-2, that were combined to the individual Att26, previously published in Brunel et al. (2020).

Author of entry: S. Desenne

Bucy le Long

The necropolis of Bucy-le-Long ''la Héronnière - la Fosse Tounise'' is located on the right bank of the Aisne, 3 km upstream from Soissons in the Aisne. It is located on a sandy prominence of the alluvial terrace, overhanging the river. It was occupied between the 5th and 4th centuries BC. The necropolis covers an area of 2.5 hectares and originally contained around 350 graves, of which 235 have been excavated. Burial is the main mode of deposit and only two cremation graves have been found in the complex. All age groups of adults are present (from 18 to over 80 years old) but the proportion of young adults is important here and the elderly individuals are few. Furthermore, despite the high theoretical infant mortality within this type of population, the bulk of the children are missing. The study of pathologies has not revealed any significant deficiencies or war trauma. The state of health is satisfactory, and the perceived traces of arthrosis and rheumatic pathologies are related to the age of the deceased and the repetition of physical tasks. The funeral practices adopted by this population is dressed burial. The women are distinguished by their finery and the men by their weaponry. The rest of the material consists of toiletries, rare tools, ceramic dishes, and foodstuffs, of which only the bones of the meat remain. The elite individuals are distinguished by a monumental tomb known as a ''chariot tomb''.They are buried on a horse-drawn vehicle, a symbol of power.

The necropolis of Bucy-le-Long ''Le Fond du Petit Marais'', located on the right bank of the Aisne, 5 km west of Soissons, covers 3,200 m2. It comprises 66 burials and 15 monuments organised in a linear fashion along a north/south axis, in two distinct groups separated by at least 30m. Its occupation began at La Tène C1, with the burial ritual, and continued at La Tène C2 and then D1 with the cremation ritual. The deceased are mostly equipped with clothing accessories and food offerings. The most richly endowed tombs are provided with bronze vessels (basins, buckets) and one of them has yielded elements of a chariot.

Here, we present genomic data for two individuals: BFT228, from 'La Fosse Tounise' and BLH447, from 'La Heronniere'. They were added to the individual from 'Le Fond du Petit Marais', BFM265, previously published in Brunel et al., 2020.

Author of entry: S. Desenne

La Piece a Liards

Person in charge: S. Oudry

The Etaples necropolis is located along the Channel coast, near the Canche estuary. It is dated to the Middle/Final Hallstatt (Ha D1-D2) and more specifically to the 6th century BC. One of the main features of this necropolis is a specific funerary ritual corresponding to burial in a lateral bent position. Furthermore, it is the only site in the region dating from this period (Henton et al., n.d.). The pits, which are large and structured, are dug out of chalk. Part of them are arranged inside a quadrangular ditch. Comparisons are to be searched about 200 km further south, in Calvados at Basly and Ifs. The convergence of several funerary features concerning the body suggests strong affinities with the funerary systems in use in the communities settled along the Channel coast at the end of the First Iron Age.

Here we present genomic data for Pal170, an adult buried with a bronze ring.

Author of entry: S. Oudry

Vasseny

The necropolis of Vasseny ''au Dessus du Marais'', ''Dessus des Groins'' is located between the towns of Soissons and Reims, in a meander of the Vesle, a few kilometers from its confluence with the Aisne, on the middle alluvial terrace of the left bank of the river.

The necropolis contains 40 tombs spread over a short period of a century, from the second half of the 5th century to the middle of the 4th century BC. The spatial distribution of the burials shows an irregular grid of four concentrations spread over almost one hectare. The ritual of burial is predominant, although at the turn of the 4th and 3rd centuries BC, cremation seems to develop. Only one case of cremation is recognised at Vasseny among 39 burials. The latter correspond, for the most part, to the graves of adults. The deceased present a panoply specific to their sex and rank. The women wear finery (torque, bracelet, pendants, fibula, earrings, etc.) whereas the men are equipped with weapons (dagger, sword, shield, spears and javelins). To these elements are sometimes added toiletries, tools and more frequently food offerings in the form of pieces of meat and ceramic containers intended for the presentation and consumption of food or liquids.

The highest hierarchical rank of this community is expressed in three graves of individuals, two men and one woman, buried on a chariot.

The Vasseny necropolis is part of the Aisne-Marne cultural group as a whole and shows a high degree of homogeneity in the funerary practices of this period. This medium-sized site is part of a geographical network organised on three levels of social integration perceptible within the Aisne-Marne cemeteries.

Here we present genomic data for two individuals: Vas75 and Vas79-2.

Author of entry: S. Desenne

Barbuise 'Les Grèves deFrécul' and 'La Saulsotte' (Aube)

Person in charge: S. Rottier

The site of Barbuise, located in the department of Aube, on the right side of the Seine, is composed of a group of localities discovered as early as the XIX^{e} century. In 1832, an inventory of the megaliths was carried out by the Société Académique de l'Aube and several menhirs and dolmens at Courtavant and La Saulsotte were surveyed. However, it was not until 1937 that the Latenian cemetery known as ''Les Grèves deFrécul'' was discovered and partially excavated by Henri Lamarre.

The site ''Les Grèves deFrécul'' was occupied during the Iron Age, between the 5th and the 3rd centuries BC.

Several excavations were carried out from 1937 to 1975 and revealed 150 burials in five enclosures. The site was then part of rescue excavations during the 1990s and was reexcavated in 2000. During the last excavation, more than 100 burials were counted and almost all of them were associated with a funerary enclosure. However, it is important to note that among all these graves, only 15 are considered to be intact, i.e. not excavated by H. Lamarre in the 1930 and 1940s (Rottier and Piette, 2001).

Here we present genomic results for five individuals from the Iron Age as well as two samples from the Bronze Age. From the Iron Age period, GDF1231 (enclosure E17), GDF1264 (enclosure E8) and GDF1341 (enclosure E19) are females whose the age at death could not be estimated. Two other individuals originating from enclosure E19 were analysed and correspond to an immature individual (GDF1348), and an adult female (GDF1349-A). From the Bronze Age period, genomic data were obtained for individuals BPV1445 and BPV1455.

Author of entry: C-E Fischer

Gurgy 'Les Noisats' (Yonne)

Person in charge: S. Rottier

Gurgy's site 'Les Noisats', occupied between 3rd and 1st centuries BC, is located in the department of Yonne (89), on the right side of the river Yonne. This relatively short period of occupation represents about 7 generations (one generation corresponding to 28 years; Moorjani et al., 2016).

This deposit was first investigated in 1997 by S. Collet and F. Müller. The authors mentionned a few poorly dated structures of minimal interest, but pointed to the presence of an important funerary site from Early and the Late Iron Age associating a circular enclosure and a quadrangular enclosure, comparable to those discovered at the Gurgy 'La Picardie' site, located a few hundred meters away. The funerary complex was excavated by S. Rottier in 2004. It consists in a mound of around 700 m^2 which yielded 40 individuals spread among 35 graves. It should be noted that the mound has been levelled and that only the deepest and latest graves remain (Mordant and Rottier, 2004), so the number of individuals does not represent the group as a whole.

Here we present genomic data for four individuals originating from this mound. Sample GLN29-A corresponds to a male between 7 and 13 years old, GLN32 corresponds to an adult male with a missing skull, whereas GLN126 and GLN141 correspond to two adult females buried in the northern part of the tumulus.

Author of entry: C-E Fischer

Oppidum du Plan de la Tour (Gailhan, Gard)

Person in charge: B. Dedet

The settlement of Plan de la Tour (Gailhan, Gard) is located in eastern Languedoc, in the foothills of the Cevennes. It was occupied between the 5th and 4th centuries BC. The excavation delivered the burials of more than twenty subadults. These deceased were not incinerated, while cremation is the rule in this region for adults admitted to the village cemetery. They were buried in a small pit of the size of the body inside the houses. The bodies are not swaddled, as shown by the observation of the position of the limbs.

Here, we present genomic results for one perinatal individual PT7 (sepulture B2, inhumation W18-23-2). This individual was combined to individual PT2, previously published in Brunel et al., 2020.

Oppidum dePech Maho (Sigean, Aude)

Person in charge: E Gailledrat

Pech Maho (Sigean, Aude) is a small fortified trading post founded at the middle of the 6th century BC and abandoned at the end of the 3rd century BC.

The settlement acted as a place of exchange and meeting between native populations and Mediterranean merchants (Greek, Etruscans, Iberians). Domestic levels yielded some graves of very young children.

Here we present genomic results for two individuals: sample PECH3 that was found in a deposit (Sep. 71289, obj-71289-1) and corresponds to an adult male, and sample PECH9 that corresponds to a perinatal found on dumping ground.

They were combined to two other individuals, previously published in Brunel et al. (2020): sample PECH5 originating from an isolated grave (Sep. 46101, obj-46101-2) and corresponding to a young male (15–18 years old) and sample PECH8 also originating from an isolated grave (Sep. 47003, obj-47003-1) and corresponding to an adult male.

La nécropole du Peyrou 2 (Agde, Hérault)

Person in charge: B. Dedet

The Peyrou site at Agde (Hérault), groups an incineration necropolis functioning during the second half of the 7th century BC (Peyrou 1) and a necropolis hosting 35 burials revealing very different funerary practices (Peyrou 2) and used from the end of the 5th century to the middle of the 2nd century BC. Among the sub-adults, 8 perinatals or infants were found buried in a vase. Adults were buried only with objects relating to the mortuary toilet (perfume vases) or a symbolic tribute with no difference according to the sex of the deceased. These practices are identical to the Greeks' rituals, very different from those of the surrounding region during the Iron Age. Ancient texts attest to the existence of a trade settlement created by the Greek colonists of Marseilles in this place at this time.

Here we report genomic data for individual PEY73, an adult female buried with a pouring vase. These results were combined to those previously published in Brunel et al. (2020) for two other samples: PEY53, an adult female buried with some grave goods, and PEY163, an adult male buried without any grave goods.

La Monédière (Bessan, Hérault)

Person in charge: A Beylier

La Monédière (Bessan, Hérault) site yielded a small collection of burials dated from the 2nd century BC.

The site of La Monédière is the place of a Gallic fortified settlement occupied between the early 6th century and the end of the 5h century BC. Covering an area of nearly 4 ha, this settlement occupies a slight relief on the right bank of the Hérault river. Its foundation appears closely linked to very early contacts made in this part of the Gulf of Lyon with the Mediterranean societies and the establishment, at the mouth of the Herault, of the Agde littoral counter which is roughly 6 km away. The trading activities, indicated by the abundance of products imported from the Greek or Etruscan world, are generally at a level higher than that observed in neighboring establishments. The quantity of amphora reveals the involvement of this site in trade networks uniting the coast and the interior, as well as its role in the redistribution of the products transported from the Mediterranean within the framework of Mediterranean trade, by land or waterways. Benefiting from a favorable geographical position, La Monédière stands as an essential marketplace and a privileged meeting place between natives and Greeks, to such an extent that the question of the *in situ* installation of a Hellenic community was raised. Its occupation was interrupted towards the end of the 5th century BC at the time of the foundation of the colony of Agde/Agathè by Marseilles. In the course of the 2nd century BC, the site was revisited. At this time, a funeral complex was established, yielding a small collection of burials associated with a very poorly known settlement, which could be an integral part of the chôra of the Agathe colony.

Here we present the genomic results for two immatures and one adult. Samples BES1096B and BES1154 are dated to the 5th century BC and correspond to two immatures buried in the settlement, a funerary practice common for the area and the period. The last sample, BES1249 corresponds to an adult found in the cemetery dated to the 2nd century BC, whose burial is not representative of the funerary gestures for the area and period, where adults are mostly cremated. These individuals were combined to BES1248, another adult previously published in Brunel et al., 2020.

Le Cailar (Cailar, Gard)

Person in charge: R. Roure

The site of Le Cailar, south of Nîmes, is an important laguna harbour of the Iron Age. It has been studied since the 2000s and archaeological excavations have shown that the settlement has been occupied since the 6th century BC and was involved in the exchanges with Greek Marseille and all of the Mediterranean. The protohistoric and ancient occupation of Le Cailar lies at the confluence of Vistre and Rhôny. During the whole 3rd century BC, many severed head and metal weapons were displayed on a large public place near the fortification. About 2700 fragments of human bones were recorded during ten excavation campaigns, almost all belonging to the skull. Chemical analyses proved that those heads were embalmed (Ghezal et al., 2019).

Here we present genomic results for five individuals represented by skull deposits: CLR23, CLR24, CLR31, CLR35 and CLR44. All samples were males and were recovered from the public place, within the walls.

METHOD DETAILS

DNA extraction and sequencing

All experiments were performed in the ancient DNA facilities at the PACEA laboratory (CNRS, University of Bordeaux, France). aDNA was preferentially extracted from petrous bones but for some individuals, teeth or even intact long bones were selected (see key resources table). Bone surface was decontaminated before extraction, *ie*.scraped, cleaned with diluted bleach and exposed to ultraviolet (UV) light for each side for 20 min. After soft surface abrasion with a drill, sampling was performed using a clean drill into the denser regions around the cochlea of the petrous bone or into the cortical part of the long bones. Teeth were completely ground to fine powder.

Between 100-250 mg of bone/tooth powder was used for each extraction. aDNA was extracted using a two-steps procedure adapted from Damgaard et al.(2015), and purified by a silica based method on a MinElute column (QIAGEN) (see Brunel et al., 2020).

For all DNA extract, double-stranded libraries were built from 10 to 25μL of DNA template, following a protocol proposed by Meyer and Kircher (2010) and using unique index pairs (Kircher et al., 2012). A partial uracil-DNA-glycosylase (UDG half) treatment was applied to remove deaminated cytosines except for the final nucleotides at the 5′and-3′ reads ends to preserve part of the damage pattern characteristic for ancient DNA (Rohland et al., 2015).

We first screened all indexed libraries via shotgun sequencing targeting around 1 million reads. Libraries were pooled and sequenced on an Illumina NextSeq 500 (2x75bp reads) at Institut deRecherches Biomédicales des Armées (Paris, France). Reads were analysed with EAGER (Peltzer et al., 2016) to process the raw data and to select satisfying libraries for deeper sequencing. Selection criteria included sufficient endogenous DNA proportion (>15%), complexity of the library and presence of damage patterns characteristic for aDNA (see Table S1 for shotgun screening results). Selected librairies were then more deeply sequenced on the same platform in order to obtain low-coverage genomes of at least 0.1× (Table S2).

Read processing, alignment and post-mortem damage

Raw sequence data were processed using EAGER (Peltzer et al., 2016) with the following steps. Reads were trimmed for adaptor sequences and collapsed into single reads using ClipandMerge software. Reads were mapped against the Human Reference Genome hs37d5 with BWA (Burrows-Wheeler Aligner) v0.7.12 (Li and Durbin, 2010), and duplicate reads with the same orientation and start and end positions were removed using DeDup v0.12.1. Reads with a mapping quality phred score <30 were excluded. MapDamage v.2.0.6 was used to observe characteristic aDNA damage patterns, before trimming two bases at the ends of each read to remove residual deaminations with BamUtil (https://genome.sph.umich.edu/wiki/BamUtil:_trimBam). A summary of quality statistics is given in Table S3

QUANTIFICATION AND STATISTICAL ANALYSIS

Sex determination

Genetic sex was calculated using the methods described in Skoglund et al. (2013) estimating the fraction of reads mapping to Y chromosome out of all reads mapping to either X or Y chromosome (see Table S2).

Contamination estimates

We used the ANGSD (Analysis of Next Generation Sequencing Data) package to test for heterozygosity of polymorphic sites on the X chromosome in male individuals, applying a contamination threshold of 5% (Table S2). Contamination estimates were extremely low and permitted us to keep all samples for further analyses.

Uniparental markers

To process mitochondrial DNA data, reads were mapped to the revised Cambridge Reference Sequence (rCRS- GenBank Accession NumberNC_120920.1). VCF files were built using bcftools mpileup and then submitted to HaploGrep 2 (Weissensteiner et al., 2016) in order to determine mitochondrial haplotypes (Table S2). Reliable characterization of maternal lineage could be conducted for 43 individuals. The combination of our mitochondrial dataset with the maternal genomes published by Brunel et al. (2020) permits to confirm the prominence of haplogroups H (25,58%), J (20,93%), K and U (both at 15,12%) among French

IA groups. Large chronological groups, from the Palaeolithic to the Bronze Age period, were constituted to figure out the diachronic evolution of maternal lineages frequencies on the French territory by combining our dataset with previous published data (Brunel et al., 2020; Fischer et al., 2018, 2019; Fu et al., 2016; Olalde et al., 2018; Rivollat et al., 2020, Figure S2).

Y chromosome haplotypes were called using Yleaf statistical package for each male individual (Ralf et al., 2018).All the 29 male individuals identified in our dataset had sufficient coverage for Y haplotype assessment (see Table S2). Most individuals were found to carry haplogroup R1b1a (69%), other males belonging to haplogroups G2a2 (17,24%), I1 and I2 (both at 6,9%). We compiled our dataset with previous published data (Brunel et al., 2020; Fu et al., 2016; Olalde et al., 2018; Rivollat et al., 2020) to study the evolution of the frequencies of Y chromosome haplogroups from the Palaeolithic to the Iron Age (Figure S3).

Kinship analyses

We estimated the degree of genetic relatedness between our individuals by applying Relationship Estimation from Ancient DNA (READ; Monroy Kuhn et al., 2018). Of the 61 French Iron Age individuals for which low coverage genomes are available (Figure S4), we identified only three individuals presenting a 2nd degree of relatedness at Attichy-Bitry (North): individual ATT27, individual ATT3 and individual ATT52-2. The other individual from Attichy (ATT26) shares no biological link up to the 3rd degree with the others.

Inbreeding and diversity estimates

To detect potential inbreeding among the French IA groups and individuals, we calculated length of runs of homozygosity (ROH; Ringbauer et al., 2021) using the software HapROH on individuals carrying more than 300,000 SNPs. We performed hapROH to the pseudo haploid data of 1240k SNPs to detect runs of homozygosity longer than 4 centimorgan for all IA individuals.

Of the individuals providing suitable coverage for this analysis, only individual COL336 from the Iron Age site of Colmar ''Jardin des Aubépines'' (Haut-Rhin) showed evidence for long ROH greater than 50 cM. The sum and length distribution of ROH measured for COL336 suggest their parents were first-degree relatives (Figure S11), i.e., parent-offspring or full siblings (whose offspring will have a quarter of their genome in ROH). This individual was found deposited in a silo without any particular care. The overall absence of long ROH for other French IA individuals or groups indicate that the groups considered were sufficiently large or with controlled union rules to avoid inbreeding (Figure S10).

Principal component analysis

PCA analysis was run with the Human Origins reference panel for 592,998 autosomal genotypes in 796 west Eurasian modern individuals using smartpca v10210 (EIGENSOFT) with the options lsqproject:YES and shrinkmode: YES, using 51 modern populations to calculate eigenvectors on which aDNA samples were projected. Genotypes were downloaded from David Reich's website (dataset v44.3.1240K_HumanOrigins, available at https://reich.hms.harvard.edu/allen-ancient-dna-resource-aadr-downloadable-genotypes-present-day-and-ancient-dna-data) and merged with our dataset. Projections on the first two PCs are provided in Figures 1C and S1.

Genetic clustering and outlier detection

To prepare our dataset for analyses, we divided individuals in six regions and, when possible, in chronological sub-groups: EIA_Alsace (from 800 BC to 450 BC), LIA_Alsace (from 450 BC to 50 BC), IA_Champagne, IA_Normandy, IA_North, IA_Paris_Basin and IA_South (see Table S2).

We carried a *qpWave* from the ADMIXTOOLS package (https://github.com/DReichLab) iterated overall individuals in the pool, testing for significant evidence of heterogeneity relative to a sub-pool of all individuals in the main cluster (except the test individual when it was part of the main cluster). The right set panel A was composed of: Mbuti.DG, Ethiopia_4500BP_published.SG, CHG, Russia_EHG, Russia_Ust_Ishim_HG_published.DG, Czech_Vestonice16, Russia_MA1_HG.SG, Israel_Natufian, Jordan_PPNB_published, Iberia_ElMiron, Anatolia_N_published, Morocco_LN.SG, WHG, Iran_GanjDareh_N, and Russia_EBA_Yamnaya_Samara. We identified outliers from the main cluster individuals when the *qpWave* p-value was $p < 0.05$ (Fernandes et al., 2020).

We found six individuals spending as outliers from the chronological and regional group to which they belong:

- •Bes1248 stands as an outlier from the South_IA group
- •Croi11 stands as an outlier from the Alsace_IA_1 group
- •Col239 stands as an outlier from the Alsace_IA_2 group
- •GDF1341 stands as an outlier from the Paris_Basin_IA group
- •Pech3 stands as an outlier from the South_IA group
- •Pey163 stands as an outlier from the South_IA group

Therefore, these individuals were not included in the analyses at the regional level.

We run *qpWave* analyses with the same reference panel comparing BA and IA groups from the French territory and Europe to test for statistically significant differentiation. We created a similarity matrix, which was then used to generate the heatmap using the heatmap.2 function of the R-package gplots (Warnes et al., 2019) (Figure 2).

f3-outgroup and f4-statistics

Outgroup *f3*-statistics were calculated using qp3Pop and *f4*-statistics using *qpDstat* with the *f4* mode from ADMIXTOOLS (https://github.com/DReichLab). We used the 1240K panel to optimize the number of SNPs covered by the ancient individuals and get more resolution in the statistic tests. Standard errors were calculated with the default block jacknife.

To test for specific genomic affinities between IA individuals, we performed a f3-outgroup statistics in the form *f3* (*Mbuti*, *Ind*, *Ind*). The results were plotted in a heatmap (Figure S5) using the heatmap.2 function of the R-package gplots (Warnes et al., 2019). The heatmap shows no specific affinities between individuals from the same site or region (ATT27 and ATT52-2 were removed from this analysis as they present 2nd-degree genetic relatedness between them and with ATT 3).

To determine if a specific ancestral legacy could explain the outlier status of the individuals, we performed f3-outgroup statisticin the form *f3* (*Mbuti*, *X*, *Outliers/Region*) with X being either one of the three major genetic components of the European population: *WHG*, *Anatolia Neolithic* and *Russia_Samara_EBA_Yamnaya*. The results show that some individuals (Bes1248, Col239) seem to have excess in the Yamnaya component compared to their group of origin (Figure S6). We also performed a *f3* (*Mbuti*, *Outlier*, *Region*) for each outlier and each region. The results were plotted on maps using QGis v.3.10 (https://www.qgis.org/en/site/, Figure 4).

To test if the Yamnaya component distribution permitted any significant differentiation between IA groups from UK, French regions (North, Alsace, the Paris Basin, Champagne, the South) and the Iberian Peninsula, we also performed a f4 statistical analysis, in the form *f4* (*Mbuti*, *Russia_Samara_EBA_Yamnaya*; *PopA*, *PopB*), where PopA and PopB represented Iron Age groups. The only IA groups found to be genetically differentiated from other groups according to the steppe component are the groups from United Kingdom and Normandy (for which this component is the most important) versusall other IA groups. Interestingly, the f4 test *f4* (*Mbuti*, *Russia_Samara_EBA_Yamnaya*; *IA Normandy*, *IA UK*) is not significant, showing similar proportions for this component between the UK and Normandy groups (Table S6).

Population modeling

We used *qpAdm* from the ADMIXTOOLS package (https://github.com/DReichLab) to estimate admixture proportions for all French IA individuals. To assess the percentage of the three major components *WHG*, *Anatolia Neolithic* and *Russia_Samara_EBA_Yamnaya* into each individual, we performed a *qpAdm* analysis with the reference panel B composed of: Mbuti.DG, Ethiopia_4500BP_published.SG, CHG, Russia_EHG, Russia_Ust_Ishim_HG_published.DG, Czech_Vestonice16, Russia_MA1_HG.SG, Israel_Natufian, Jordan_PPNB_published, Iberia_ElMiron). Results are presented in the Figure 3A and detailed in Figure S9 and in Table S7. In a second model, we performed *qpAdm* analyses to assess if the various

Iron Age groups in France could be modelled with ancestry represented by Bronze Age groups using different combinations of BA groups from different regions of France, England, Germany, Italy and Spain with the reference panel A (Tables S4 and S5).

Data and software availability

Raw sequence data and alignments are available at the European Nucleotide Archive (ENA) under accession number ENA: PRJEB50940.

ADDITIONAL RESOURCES

Our study has not generated or contributed to a new website/forum and it is not part of a clinical trial.

Current Biology

Report

The genetic history of Greenlandic-European contact

Highlights

- The present-day Greenlandic population has substantial amounts of European ancestry
- Denmark is the main source of this European ancestry
- There is little evidence of European ancestry from pre-colonial European contact
- The timing of much of the European admixture is very recent

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In brief

The Greenlandic Inuit have had extensive historical contact with Europeans, and the present-day Greenlandic population has substantial amounts of European ancestry. Waples et al. use genetic data to investigate the origin of this ancestry. They show that much of it is Danish and find little evidence of it being from pre-colonial European contact.

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Current Biology

Report

The genetic history of Greenlandic-European contact

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SUMMARY

The Inuit ancestors of the Greenlandic people arrived in Greenland close to 1,000 years ago.[1] Since then, Europeans from many different countries have been present in Greenland. Consequently, the present-day Greenlandic population has ~25% of its genetic ancestry from Europe.[2] In this study, we investigated to what extent different European countries have contributed to this genetic ancestry. We combined dense SNP chip data from 3,972 Greenlanders and 8,275 Europeans from 14 countries and inferred the ancestry contribution from each of these 14 countries using haplotype-based methods. Due to the rapid increase in population size in Greenland over the past ~100 years, we hypothesized that earlier European interactions, such as pre-colonial Dutch whalers and early German and Danish-Norwegian missionaries, as well as the later Danish colonists and post-colonial immigrants, all contributed European genetic ancestry. However, we found that the European ancestry is almost entirely Danish and that a substantial fraction is from admixture that took place within the last few generations.

RESULTS

Background

The Greenlanders are mainly descendants of the Inuit of the Thule culture[3] that entered Northern Greenland from Canada around the 12th century.[1,4] At that time, the Norse had lived in the southern part of the island since 985 CE; they stayed in Greenland until approximately 1450 CE. Previous genetic research has not provided support for gene flow between the Norse and Inuit.[2] However, since the 16th century, thousands of Europeans from various countries either visited or moved to Greenland, and there has been substantial gene flow from Europe into the Greenlandic population.[2,5–7] This European contact with Greenland can be divided into three time periods: pre-colonial; colonial; and post-colonial (Figure 1). Pre-colonial contact was initially limited to exploration and trade, such as when a search for the Northwest Passage led English explorers to Greenland in the 1500s.[8] From the early 18th century, European whaling efforts off the west coast of Greenland brought whalers into contact with the Greenlandic Inuit. Initially, it was the Dutch who dominated European whaling, but in the latter half of the century, the whalers were also German, primarily Frisian, British, and Danish-Norwegian.[8,9] In 1721, the arrival of the Danish-Norwegian missionary priest Hans Egede marked the beginning of the colonial period, leading to a new and more permanent type of contact between Greenlandic Inuit and Europeans, although whaling was still a primary draw, with, e.g., 107 Dutch ships that year. In addition to Danish-Norwegian missionaries, the German Moravian Brethren established religious missions in the period 1733–1900, located in Nuuk and several other locations.[8] In 1751, Denmark-Norway expanded colonial activities and claimed a monopoly on trade,[8] and since then, the primary contact between Greenlanders and Europeans has been with the Kingdom of Denmark. Denmark-Norway remained a conglomerate state until 1814,[10] after which Greenland became an exclusively Danish colony, and in 1953, it became an equal part of the Kingdom of Denmark. The post-colonial period has seen a significant influx of mainly Danish workers but also seasonal fishers, primarily from Portugal and the Faroe Islands.[8,11]

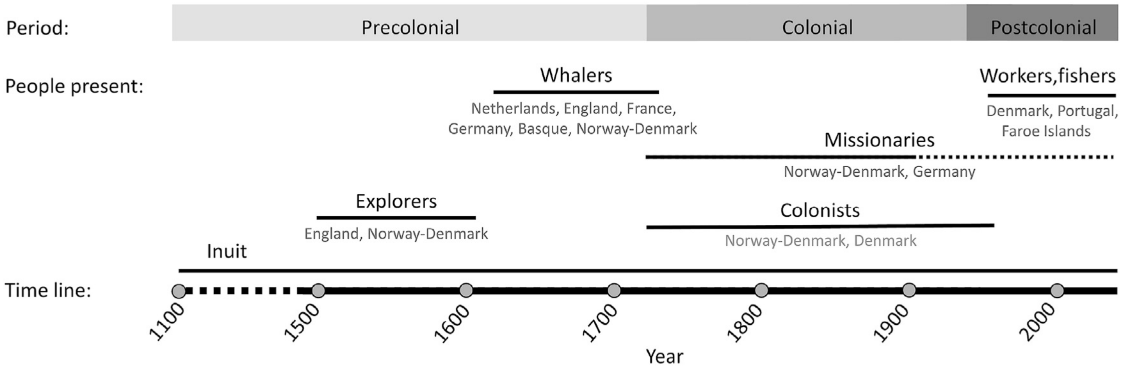

Figure 1. Timeline of significant Greenlandic-European contact

The timeline covers the time since the arrival of the Inuit in Greenland. The presence of different groups of people are shown by horizontal bars. Times are approximate. The most relevant European countries are listed under each group.

Although there was a systematic documentation of marriages between Inuit and Scandinavians from the 1740s,[8,10,12] the degree of admixture prior to the colonial period is largely unknown. However, the extensive whaling and trading activities of the Dutch have led to a common belief in Greenland that admixture with Dutch whalers was relatively common.[13] And notably, any European contribution to the Greenlandic gene pool prior to the 20th century could have an outsized impact compared to more recent admixture, because the population of Greenland has recently greatly expanded, from less than 6,000 in 1789 to more than 55,000 today.[14] Thus, prior to performing this study, we hypothesized that especially Denmark but also the Netherlands, Germany, and Norway all made non-negligible ancestry contributions. Here, we investigated this hypothesis by analyzing dense SNP array data from 3,972 Greenlanders from 15 different locations (Figure S1).

Inference of European admixture sources

Using the genetic data from the Greenlanders, we inferred admixture proportions (Figure S2; see also Data S1) and identified related individuals. Based on the results, we obtained a set of unrelated admixed Greenlanders with both Inuit and European ancestry (n = 1,582) and a set of 181 unrelated, unadmixed Greenlanders with only Inuit ancestry. Genetic data from these individuals were then combined with SNP array data from 8,275 individuals from 14 different European countries, including Denmark, Norway, Sweden, Germany, the UK, and the Netherlands (Figure S1). After quality control and merging, we were left with a combined dataset with 135,702 SNPs, 1,582 admixed Greenlanders, and 8,456 reference individuals. Next, we applied the program ChromoPainter[15] to this dataset to reconstruct ("paint") the genomes of the admixed Greenlandic individuals as mixtures of the haplotypes in the reference individuals (Table S1). The main outcome of this analysis was an estimate for each admixed Greenlander (and each reference individual) of over how much of their genome they are most closely related ancestrally to each of the reference individuals. These estimates were summarized in a so-called coancestry matrix (Figure S3).

We then estimated the genetic contribution from the unadmixed Greenlandic Inuit and each of the 14 different European countries to the ancestry of the admixed individuals in Greenland by applying the program SOURCEFIND[16] to a summary of the

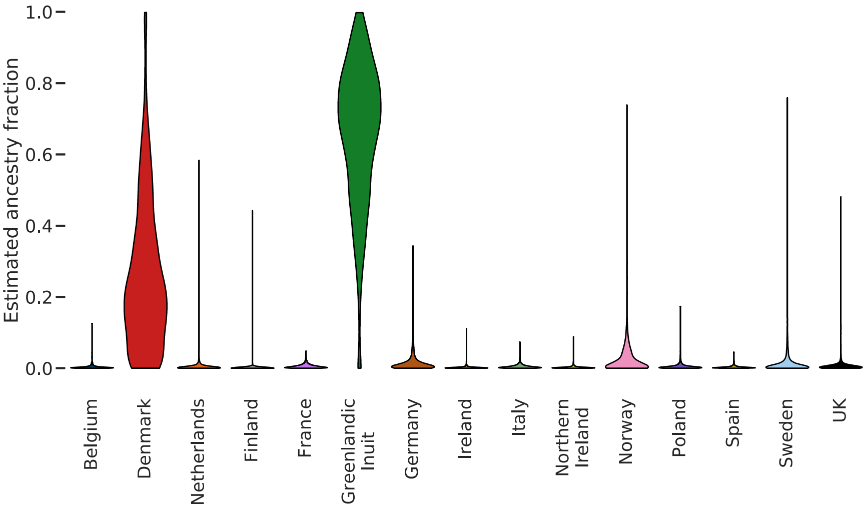

Figure 2. Violin plot of per-country ancestry estimates

Results shown are produced by SOURCEFIND from the analysis where inference was performed on each admixed individual separately. Each source country has a violin showing the distribution of the estimated mean ancestry fraction from that country, across all admixed individuals. Each admixed individual appears in the distribution for each country. Violins are scaled to all have the same max width.

Table 1. Inferred ancestry across 1,582 admixed Greenlandic individuals

	No. of reference individuals	Individual-based			Group-based
		≥1%	≥5%	≥20%	
Belgium	537	0.0% (0)	0.0% (0)	0.0% (0)	0.1%
Denmark	327	76.4% (1,208)	69.5% (1,100)	35.8% (567)	31.6%
Finland	580	0.6% (9)	0.3% (5)	0.1% (1)	0.0%
France	478	0.0% (0)	0.0% (0)	0.0% (0)	0.2%
Greenlandic Inuit	181	98.3% (1,555)	98.3% (1,555)	97.4% (1,541)	65.6%
Germany	1,000	0.1% (1)	0.1% (1)	0.0% (0)	0.3%
Ireland	344	0.2% (3)	0.2% (3)	0.0% (0)	0.1%
Italy	745	0.0% (0)	0.0% (0)	0.0% (0)	0.2%
The Netherlands	1,000	0.1% (1)	0.1% (1)	0.1% (1)	0.1%
Northern Ireland	61	0.0% (0)	0.0% (0)	0.0% (0)	0.1%
Norway	942	17.8% (281)	6.2% (98)	1.1% (18)	0.7%
Poland	57	0.1% (2)	0.1% (1)	0.0% (0)	0.2%
Spain	204	0.0% (0)	0.0% (0)	0.0% (0)	0.2%
Sweden	1,000	3.5% (56)	1.3% (20)	0.1% (1)	0.3%
UK	1,000	0.3% (5)	0.2% (3)	0.1% (1)	0.2%

Results from both individual-based and group-based analyses are shown. The first column gives the number of reference individuals from each source. For individual-based, the values shown are the assignment to country at 1%, 5%, and 20% ancestry thresholds. The percentage values are the percentages of admixed Greenlandic individuals inferred to have at least 1%, 5%, or 20% ancestry from each source country. The numbers in parentheses are the number of individuals in each category. To be counted here, an individual must have had at least 1%, 5%, or 20% ancestry with a posterior probability above 99%. For group-based, the values shown are the percentage of the ancestry of the group of 1,582 admixed Greenlanders inferred to come from each country. All the results were inferred using SOURCEFIND. See also Table S2.

output from ChromoPainter. SOURCEFIND is a Markov chain Monte Carlo (MCMC) method that produces statistical samples from a posterior distribution of the ancestry contributions for a group of target individuals. In this case, the target individuals were the admixed Greenlanders and the possible ancestry sources were the reference countries. These statistical samples can then be summarized in different ways that are informative about the ancestral contribution of each of the reference countries. We applied this method to each admixed Greenlander separately to obtain individual-level resolution but also tried to analyze all the admixed Greenlanders jointly in one group in an attempt to reduce noise in our ancestry estimates.

When performing inference on each admixed individual separately, we first summarized the SOURCEFIND results using the posterior mean of the ancestry proportion from each country per individual to get a simple overview (Figure 2). Based on this, we estimated the 1,582 admixed Greenlanders to have an average of 65.6% Greenlandic Inuit ancestry and 34.4% European ancestry, with the far majority of the latter being Danish. To obtain a more detailed picture of the SOURCEFIND results, we also counted the number of individuals that were assigned at least 5% ancestry from any country with high probability (posterior probability > 0.99). When doing so, we found 1,100 of the 1,582 admixed Greenlandic individuals (69.5%) were assigned at least 5% Danish ancestry, the most of any European country (Table 1). The only other European countries found to contribute more than 5% ancestry to five or more individuals are all Nordic countries: Norway with 98 (6.2%); Sweden with 20 (1.3%); and Finland with 5 (0.3%). A few other countries were inferred to contribute more than 5% ancestry for 1–5 individuals: UK (0.2%); Ireland (0.2%); Poland (0.1%); Germany (0.1%); and the Netherlands (0.1%). The same overall pattern is observed with a lower 1% ancestry threshold (Table 1), with different posterior probability thresholds or a different prior (Table S2). Only four individuals with more than 20% European ancestry were inferred to have ancestry from countries other than Denmark or Norway (Table 1).

We obtained similar results in the group-based analysis, with an estimated Inuit ancestry fraction of 65.6% and European fraction of 34.4% (95% credible interval = 33.5%–36.0%) (Table 1). Please note these results pertain to the admixed Greenlandic individuals and do not reflect the Greenlandic population as a whole, which is estimated to have approximately 25% European ancestry.[2] The Danish ancestry fraction among admixed Greenlanders was 31%, with no other European country contributing more than 1%. This translates to Denmark making up 91% of the total estimated European ancestry, with the only other country contributing more than 1% of the European ancestry being Norway at 2.1% (Table 1). Notably, we performed a range of additional analyses to ensure the validity of these results (Data S2).

Investigating European admixture in the last few generations

To further characterize the history of European admixture in Greenland, we performed an analysis to investigate the timing of admixture in Greenland. Specifically, we inferred local ancestry, Inuit or European, along the genome of each admixed Greenlander to estimate the proportions of the genome where each admixed individual has (1) inherited both alleles from Inuit ancestors, (2) inherited both alleles from European ancestors, or (3) inherited one allele from an Inuit ancestor and one allele from a European ancestor. These fractions are informative about the time of admixture because individuals with different admixture histories have different expected ternary fractions (see Figure 3A for some examples). We chose to estimate "ternary ancestry fractions" instead of using standard methods for timing of admixture based on admixture tract lengths (e.g., Pool and Nielsen[17] and Gravel[18]), because the number of phasing switch

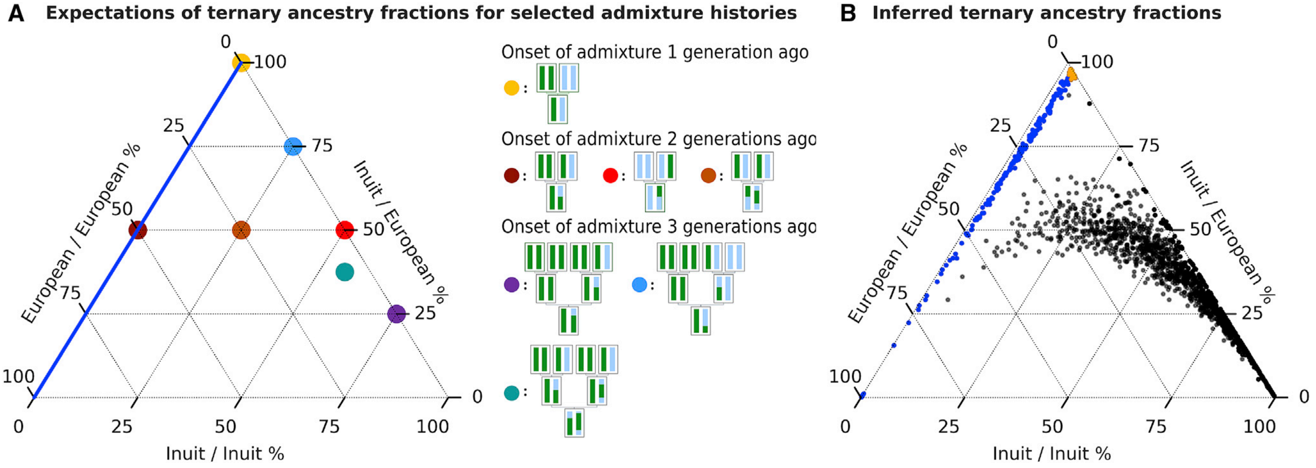

Figure 3. Ternary ancestry fractions, i.e., the fraction of the genome where (1) both alleles have Inuit ancestry, (2) both alleles have European ancestry, or (3) one allele has Inuit ancestry and one has European ancestry

The three corners of the plots represent genomes with all loci having two European alleles (bottom left), two Inuit alleles (bottom right), or one Inuit and one European alleles (top).

(A) Expected ternary ancestry fractions. Colored dots show the expected ternary fractions for individuals with 7 selected admixture histories illustrated in the legend by pedigrees, where green indicates Inuit ancestry and light blue indicates European ancestry. The admixture histories include Greenlanders with admixture from one European parent (yellow); one European grandparent (dark brown); two European grandparents, one on each parental side (red); three European grandparents (light brown); one European great-grandparent (blue), two European great-grandparents, one on each parental side (blue-green); and, finally, three European great-grandparents, all on the same parental side (purple). The left axis in blue indicates fractions that are expected for individuals with at least one European parent because it has no sites with two Inuit alleles.

(B) Inferred ternary ancestry fractions. Colored dots show the inferred ternary ancestry fractions for each of the 1,582 admixed Greenlanders. The colors convey the way we have categorized the individuals: individuals inferred to have one Greenlandic parent and one European parent are yellow; the remaining individuals inferred to have a European parent shown in blue; and other individuals are shown in black.

See also Table S3.

errors was large relative to the recombination rate since admixture, which we feared would markedly affect the timing estimates. In contrast, the ternary ancestry fractions are robust to phasing switch errors.

Among the 1,582 admixed Greenlanders, 250 have ternary fractions that are consistent with having at least one fully European ancestry parent (Figure 3B, blue and yellow dots). Of these, 27 have two European alleles at nearly every genomic position (yellow dots on Figure 3B), suggesting they have two European parents. Together, these 277 (223 + 2 × 27) European ancestry parents account for >8% of the ancestors of the admixed individuals (277/[2 × 1,582]) and for almost 25% of the total European ancestry in Greenland. The ternary ancestry fractions of the remaining individuals are largely consistent with second and third generation admixture with Europeans, as shown in Figure 3A (dots near the right axis). However, it is important to emphasize that, due to variance in recombination and nonrandom mating, these fractions could also be the result of older admixture.

Among the group of admixed Greenlanders with at least one European-ancestry parent, Denmark was by far the largest European ancestry source, making up 98.4% of the European ancestry, with no other country contributing more than 1% (Table S3). In contrast, the group of Greenlanders without a European parent, i.e., a group for which the admixture must have taken place less recently than for the group with at least one European parent, was inferred to have contributions from Norway (3.8%), Germany (2.1%), and Sweden (1.6%), with Denmark constituting 85.7%.

DISCUSSION

Before discussing the results in a historical perspective, we should consider how the study design imposes limitations in the conclusions that can be drawn from the analysis. Briefly, we do not believe that the current study imposes major limitations that pertain to the conclusions presented here; for further details and discussion on this topic, please see Data S2.

The genetic analyses suggest that the European ancestry of the present-day Greenlanders is predominantly Danish and the result of very recent gene flow. This indicates that European activities prior to colonization did not have a significant impact on the current genetic composition of the population in Greenland, in contrast both to common beliefs in Greenland[13] and our own initial hypothesis.

The lack of genetic ancestry originating from the early exploration activities by the British is perhaps the least surprising, because these activities only involved a few ships. Similarly, the relatively small amount of ancestry originating from German Moravian missionaries, who stayed in Greenland for about 170 years until 1900, may be explained by the restrictions that the Moravian Brethren put on intermarriage with the Greenlandic population.[19]

However, the lack of ancestry from whaling countries, especially the Netherlands, is surprising given the common beliefs in Greenland as well as the historical records suggesting a high number of Dutch ships around Greenland's coasts for a substantial period of time.[8,9] This result may be explained by a number of factors. First, early European whalers often did not spend the winter in

Greenland.[13] Second, Dutch, English, and other European whaling activities were reduced by the economic monopoly imposed in 1751 by Denmark-Norway. Finally, it has been postulated that first contact with Europeans was followed by severe epidemics and that the interaction with the Dutch around Disko Island led to some of the first incidents of epidemics in the region.[13] A well-documented example was a severe smallpox epidemic in Nuuk in the 1730s following the arrival of European ships.[13] It is possible that these epidemics could have impacted early patterns of European ancestry and reduced the impact of early admixture.

Our results suggest that most of the European ancestry is from after colonization was initiated. This result is consistent with the fact that most of the Greenlandic individuals without any European ancestry live in the very north as well as the east coast of Greenland,[2] because colonial activities were initiated later in the north (1909) and east (1894) than in the southwest (1721). Also, we found a higher fraction of Norwegian, Swedish, and German ancestry among the Greenlanders without at least one European-ancestry parent, which aligns well with the family registries from the colonial period. The large amount of inferred Danish ancestry, especially within the last generation, is consistent with historical records showing that the influx of Danes to Greenland in the post-colonial period since the 1950s marked a substantial increase in the European immigration rate.

Hence, taken together, although at first perhaps surprising, the results of this study seem consistent with recent demographic trends in Greenland and with historical records of European contact.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

Supplemental Information can be found online at https://doi.org/10.1016/j.cub.2021.02.041.

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AUTHOR CONTRIBUTIONS

A.A. and I.M. conceived and supervised the study. R.K.W., A.L.H., A.A., and I.M. finalized the specific research questions. R.K.W., A.A., and I.M. designed the statistical analyses with input from G.H. and E.J. R.K.W., E.J., A.A., and I.M. created and quality controlled the genetic datasets. R.K.W. performed the statistical analyses with input from I.M., A.A., and G.H. A.L.H. and I.S. provided the historical and contemporary context for the study. M.E.J., C.V.L.L., and P.B. collected and provided context for the Greenlandic samples. T.H., N.G., M.K.A., A.A., and I.M. designed the overall genetic study of the Greenlanders. R.K.W., A.L.H., I.S., A.A., and I.M. wrote the majority of the manuscript with input from all other co-authors.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Biological samples		
European genotype data	[20,21]	EGAD00000000120, EGAD00010000124, EGAD00010000288, EGAS00001002641
Greenlandic genotype data (Metabochip)	[22]	EGAD00010001427, EGAD00010001428
1000 Genomes data	[23]	CHB, YRI, CEU
Deposited data		
Greenlandic genotype data (MEGA)	this paper, available at https://www.ebi.ac.uk/ega/studies/EGAS00001004933	EGAS00001004933
Software and algorithms		
CHROMOPAINTER (v2)	[15]	https://people.maths.bris.ac.uk/∼madjl/finestructure-old/chromopainter_info.html
GLOBETROTTER (v Dec.30.2016)	[24]	https://people.maths.bris.ac.uk/∼madjl/finestructure/globetrotter.html
fineSTRUCTURE (v2, v4)	[15]	https://people.maths.bris.ac.uk/∼madjl/finestructure/finestructure.html
SOURCEFIND (v2)	[16]	Contact Garrett Hellenthal at ghellenthal@gmail.com
ADMIXTURE (v1.3.0)	[25]	http://dalexander.github.io/admixture/
PLINK (v1.9)	[26]	https://www.cog-genomics.org/plink2
RFMix (v2)	[27]	https://github.com/slowkoni/rfmix
relateAdmix	[28]	https://github.com/aalbrechtsen/relateAdmix
PCAngsd	[29]	https://github.com/Rosemeis/pcangsd

RESOURCE AVAILABILITY

Lead contact

Further information and requests should be directed to and will be fulfilled by the Lead Contact, Ida Moltke (ida@binf.ku.dk).

Materials availability

This study did not generate new unique reagents.

Data and code availability

The accession number for the Greenlandic genotype data from the Multi-ethnic genotyping array (MEGA) reported in this paper is EGA: EGAS00001004933. The Greenlandic genotype data onthe Metabochip are available from the European Genome-phenome Archive (https://ega-archive.org) under the accession EGA: EGAS00001002641. The European reference datasets are also available at the European Genome-phenome Archive with accessions EGAD00000000120, EGAD00010000124, EGAD00010000288, and EGAD00010000632. The 1000 Genomes data are publicly available from the 1000 Genomes Project (https://www.internationalgenome.org/data).

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Study participants were Greenlandic individuals from two population surveys: the Inuit Health in Transition (IHIT, n = 3115) and a survey consisting of Greenlanders living in Greenland (B99, n = 1401), and Greenlanders living in Denmark (BBH, n = 547).[30,31] The cohorts have participants from 15 different locations in Greenland from Qaanaaq in the northwest to Tasiilaq in the southeast, (Figure S1) as well as Greenlanders living in Denmark.

The participants gave oral and written consent to participate in the health surveys and subsequently they were mailed information about the population genetics analyses with an option to opt out at any time. The approval for population genetics analyses was given by the Commission for Scientific Research in Greenland (project 2014-08, 2014-098017).

To represent potential European source countries, we selected individuals from 14 different European countries (n = 14,385): The UK, Sweden, Germany, Norway, Italy, Finland, Belgium, the Netherlands (Dutch), France, Ireland, Denmark, Spain, Northern Ireland, and Poland.

METHOD DETAILS

Greenlandic genotype data

All Greenlandic participants were genotyped on two SNP arrays: the CardioMetaboChip (196,224 SNPs)[2,22,32] and the Multi-Ethnic Global Array (∼1.5M SNPs).[33] Data from these two SNP arrays were merged on the plus strand and 3972 individuals with genotypes from both SNP arrays and a missing rate below 0.02 were retained. From these we removed singletons, sites not on an autosome, as well as sites with a significant ($p < 1e\text{-}10$) deviation from Hardy-Weinberg equilibrium in a test that accounts for admixture.[29]

European genotype data

The European SNP array data are from the Wellcome Trust Case Control Consortium (EGAD00000000120, EGAD00010000124, EGAD00010000288, EGAD00010000632),[20,21] and were selected to represent a broad spectrum of potential European admixture sources in Greenland (Figure S1). The European datasets were lifted to hg19 and put on the plus strand, and sites with rates of missing data > 0.05 were removed prior to merging. We also excluded sites within the MHC region and within the HsInv0501 inversion on chromosome 8, as well as sites with more than two alleles. Finally, we limited the number of individuals from each European country to at most 1000 and confirmed that there were no related individuals within each European country.

1000 Genomes Data

For the ADMIXTURE analyses and local ancestry analyses with RFmix (see below) we selected the Han Chinese in Beijing (CHB), Yoruba in Ibadan (YRI), and Utah residents with Northern and Western European Ancestry (CEU) population samples from the Thousand Genomes Project (1000G),[23] for a total of 310 individuals. We used the phased genotypes from phase 3 aligned to GRCh37.

Merged Greenlandic and European reference data

For the haplotype-based analyses we worked on a dataset where the Greenlandic data and the European reference samples were merged. We kept all sites present in both datasets and excluded 52 sites with more than 2% missing data. The resulting merged dataset had 135,702 loci and 12,247 individuals with a total genotyping rate of 0.9995 and all loci with a minor allele count of at least 5.

The merged Greenlandic-European dataset was split by chromosome and phased without a reference panel using SHAPEIT[34] (v2.r904) with default settings, using the HapMap phase II recombination map for hg19.

After merging and phasing, we removed close relatives among all Greenlandic individuals by retaining at most one individual from each pair of individuals with a coefficient of relatedness > 0.2. Then we split the remaining Greenlanders into two sets based the results of a K = 2 ADMIXTURE: 1) the un-admixed Greenlanders with >99% inferred Inuit ancestry, and 2) the admixed Greenlanders with > % inferred European ancestry, for additional details see Data S1. From the second set, we removed seventeen Greenlandic individuals estimated to have >5% African or >7% Asian ancestry in a K = 4 ADMIXTURE analyses including 1000 genomes samples from China (CHB), Nigeria (YRI), the US (CEU). These thresholds were selected to exclude individuals that differed markedly from the majority of other Greenlandic individuals (data not shown) and to be able to avoid having to include any Asian and African reference samples in our fine-scale analyses. We also excluded admixed Greenlandic individuals living in Denmark as these individuals may be more likely to have Danish ancestry than other European ancestries. This left us with a dataset consisting of 1582 not closely related Greenlanders with European admixture (admixed samples), 181 not closely related unadmixed Greenlanders (Inuit reference samples), and 8303 European reference samples.

Based on the results of a pilot ChromoPainter analysis, we subsequently excluded 28 of the European reference samples because they were significant outliers (z-score > 5), based on comparing their total chunk counts to the rest of the individuals from their country (not shown). An atypically high number of chunks can be indicative of low data quality. This resulted in a final set of 8275 European reference samples (Figure S1) and thus 8275+181 = 8456 reference samples in total and 1582 not closely related Greenlanders with European admixture. These data were used to infer ancestry contributions, for details of this analysis see the Quantification and statistical analysis section and Data S2.

Merged Greenlandic and 1000G data

To construct a dataset for the ADMIXTURE and local ancestry analyses, we merged the Greenlandic genotype data with data from 310 individuals from three 1000G populations: Han Chinese in Beijing (CHB), Yoruba in Ibadan (YRI), and Utah residents with Northern and Western European Ancestry (CEU). We subsequently removed 46 sites with a greater than 0.25 frequency difference in the CEU individuals compared to the European admixture component in the K = 2 analysis (see below), retaining 521,622 overlapping sites.

QUANTIFICATION AND STATISTICAL ANALYSIS

ADMIXTURE analyses

We performed two different ADMIXTURE[25] analyses to facilitate the generation of input data for our main analyses: 1) an unsupervised K = 2 ADMIXTURE analysis of all 3972 Greenlandic individuals assuming an Inuit and a European ancestry component, following a previous study[2] and 2) a supervised K = 4 ADMIXTURE analysis of the Greenlandic individuals combined with individuals of European, Asian and African descent to investigate if there are any ancestry from Asian and African populations. We used the K = 2 analysis (Figure S2) to create two sets of Greenlandic individuals: "unadmixed" and "admixed" with > 99% or < 99% Inuit ancestry respectively. These unadmixed individuals were used as a reference for the Greenlandic Inuit ancestry component, while the admixed individuals were the subject of the main analyses; for a more detailed discussion, see Data S1.

Before the unsupervised K = 2 analysis, we applied a minor allele frequency (MAF) filter of 0.05 to the Greenlandic dataset described above (n = 3972), resulting in a dataset with 538,514 sites. For the supervised K = 4 admixture analysis, we selected the Han Chinese in Beijing (CHB), Yoruba in Ibadan (YRI), and Utah residents with Northern and Western European Ancestry (CEU) populations as proxies for Asian, African, and European ancestry, respectively.

For each analysis, we ran each ADMIXTURE (v1.3.0) ten times and selected the run with the maximum likelihood, checking convergence by ensuring multiple other runs within two log-likelihood units.

Relatedness estimation

To estimate relatedness coefficients for the Greenlandic individuals we used relateAdmix.[28] This method accounts for admixture by estimating individual allele frequencies when estimating pairwise identity by descent (IBD) coefficients (k_1, k_2) based on genome-wide ancestry proportions for each individual. We used the K = 2 genotype data and ADMIXTURE estimates of these genome-wide ancestry proportions. To estimate relatedness for the Europeans we applied the IBD inference function (–genome) in PLINK2[26,35] to the genotype data from all the Europeans.

Chromosome painting

We characterized the coancestry between Greenlanders and Europeans with the haplotype-based method ChromoPainter.[15] This method is based on a Hidden Markov model (HMM) that statistically reconstructs ("paints") a target haplotype as a mixture of a set of reference haplotypes while exploiting linkage disequilibrium among nearby SNPs. We combined the reference individuals from Greenland (n = 181) and Europe (n = 8275), with the unrelated admixed Greenlanders (n = 1582) to construct the dataset for this analysis (n = 10038). First, we painted each reference individual using all other reference individuals, then, we painted each admixed Greenlander using all reference individuals. We specified constant mismatch ($\mu = 2.04 \times 10e\text{-}5$) and switch rate ($N_e = 103.35$) parameters across all analyses, which we estimated as the weighted mean values using data from chromosomes 1, 4, 15, and 22 in a subset of 168 individuals chosen to represent all reference populations, using 10 iterations of the expectation-maximization (EM) algorithm implemented in ChromoPainter. For all these analyses, we used the same recombination map as during haplotype phasing.

ChromoPainter quantifies coancestry using two different measures, one based on the length of the genome copied from each donor in centiMorgans (cM), deemed "chunk lengths" by the program, and the second based on simple counting of the number of distinct ancestry chunks copied from each donor, deemed "chunk counts." Unless otherwise noted, we used the chunk lengths measure in downstream analyses. For summaries of the ChromoPainter analysis, see Table S1 and Figure S3.

Ancestry contributions from the European reference countries

We estimated the ancestry contributions from each European reference country and Greenland with SOURCEFIND (v2),[16] based on summaries of the coancestry matrix estimated by ChromoPainter. We summarized the ChromoPainter output into a vector of length 15 for each admixed Greenlander and reference individual, with this vector containing the proportion of DNA by which that person is painted by individuals from each of the 15 reference populations. For each reference population, we averaged these vectors across individuals. We then applied SOURCEFIND to form the vector of each admixed Greenlander as a mixture of those from the reference populations. This is a Markov Chain Monte Carlo (MCMC) approach which puts a prior on the expected number of contributing reference populations and provides an estimate of the genetic contribution of the unadmixed Greenlandic Inuit and each of the 14 different European countries to the ancestry of the admixed individuals in Greenland, while accounting for sample size differences among reference populations. We conducted this analysis in two ways: 1) to each admixed Greenlander individually 2) to the entire set of admixed Greenlanders as a group. The individual-based analysis allowed us to investigate the range of individual-level patterns of European ancestry, while the group analysis considers a large number of individuals at once and estimates the ancestry sources of the mathematically-average admixed Greenlander. The later was done to reduce the noise from averaging the estimates of the individual-based analysis. For additional analyses related to validating the ancestry inference, please see Data S2.

To ensure convergence was reached in the SOURCEFIND analyses, we ran 5 MCMC chains for each analysis and compared variance within and between separate chains with the Rhat diagnostic.[36] Each chain was run with 1M iterations, a 100K burn-in and a thinning factor of 1000. We tested that we discarded enough to burn-in by computing Rhat while discarding the first 500K iterations and compared these values to the shorter burn-in (data not shown). For each ancestry source in each individual the Rhat diagnostic was consistent with MCMC convergence; mean Rhat across all chains was 1.0001, and the max value was 1.0044. For most of our SOURCEFIND analyses we used default priors with eight eligible sources and a mean of four sources expected to contribute.

However, we tested if the results were robust to choice of prior by also running additional analyses with a more sparse prior with eight eligible sources and two sources expected to contribute.

Investigating European admixture in the last few generations

To investigate the timing of European admixture, we assigned local ancestry, either Inuit or European, in each admixed Greenlandic individual using RFMix (v2).[27] In this analysis, we used the same Inuit reference individuals as in the ChromoPainter analysis, along with CEU individuals from 1000G to represent the European ancestry, this allowed us to utilize the larger number of overlapping loci with the 1000G dataset. RFMix was run with default parameters, except we specified two different admixture dates, either 3 or 8 generations ago, to ensure that our results were robust to this choice. We used genotype data from the merged Greenlandic and 1000 Genomes datasets with 521,622 sites, split by chromosome and phased without a reference panel. After phasing, the reference Inuit and CEU individuals were used as the ancestry references for local ancestry inference in the admixed Greenlanders.

We summarized the results for each individual by calculating the fraction of the genome, in cM, that has either two Inuit alleles, two European alleles, or one Inuit and one European allele. We found a few chromosomal regions, such as near the edge of chromosomes, with local ancestry fractions that were outliers relative to the rest of the genome, suggesting potential problems with the inference of local ancestry in these regions, or local genomic factors affecting ancestry. To address this, we removed 88 out of 26008 (0.3%) genomic windows of local ancestry calls with less than 62.5% Inuit ancestry or with more than 72.5% Inuit ancestry, for a total exclusion of 3.76 cm.

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Supplemental Information

The genetic history

of Greenlandic-European contact

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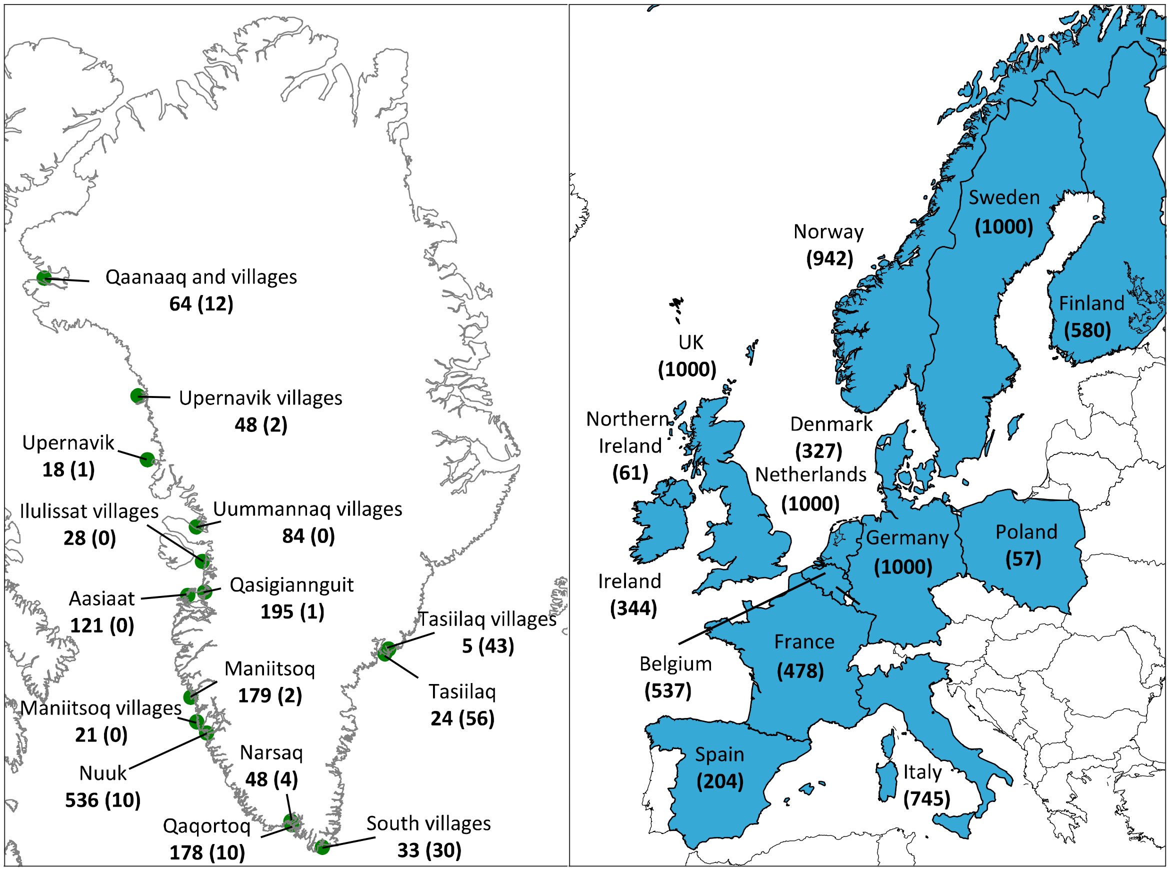

Figure S1. Geographic locations of Greenlandic and European individuals included in the study, related to STAR Methods. Numbers outside parentheses give the number of admixed Greenlandic individuals included from each location in Greenland. Numbers in parentheses give the number of individuals included in the reference panel from each location. There is a total of 1582 unrelated admixed Greenlanders and 8456 reference individuals.

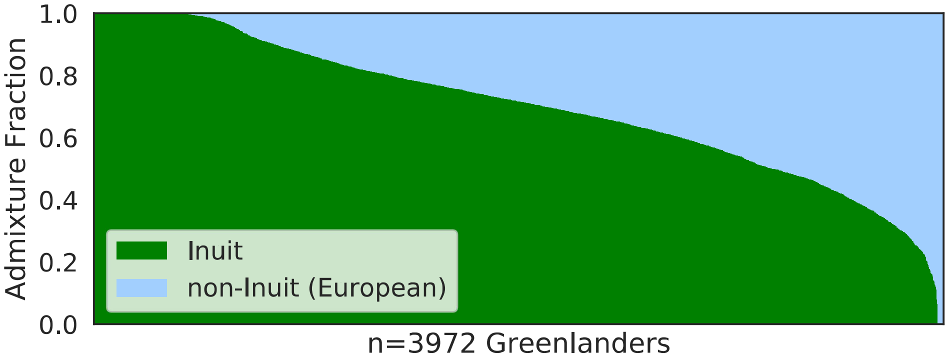

Figure S2. ADMIXTURE analysis (K=2), related to STAR Methods. Stacked bar plot of admixture proportions estimated for 3972 Greenlanders using an unsupervised ADMIXTURE analysis assuming two admixing populations (K=2), Inuit and European. Each individual is depicted as a thin vertical line with the Greenlandic Inuit ancestry proportion shaded green and the European ancestry proportion shaded light blue. This analysis was used to identify admixed and non-admixed Greenlanders for subsequent analyses.

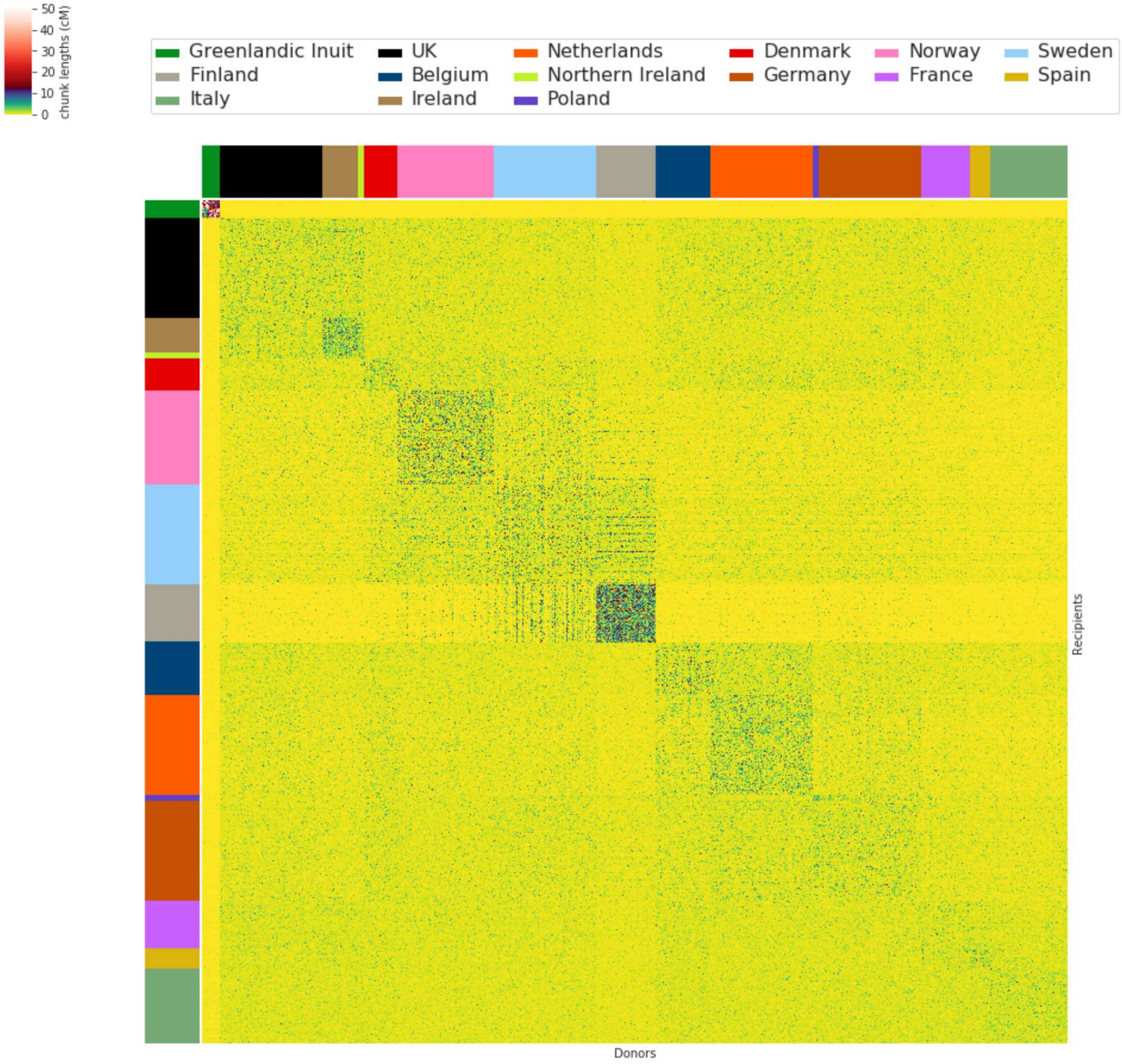

Figure S3. Heatmap of the coancestry matrix estimated by ChromoPainter, related to STAR Methods. The coancestry matrix was estimated between the 8456 reference individuals using ChromoPainter based on chunk lengths (the length of the genome copied from each donor in centiMorgans). Colors along the axes show the country of origin for each individual.

Chr	cM	# of SNPs	Mean # of chunks	Mean # of SNPs per chunk
1	292.1	10398	524.4	19.8
2	274.3	11109	502.4	22.1
3	227.1	9419	428.0	22.0
4	219.4	8233	402.4	20.5
5	208.6	7976	386.8	20.6
6	197.8	9336	367.4	25.4
7	189.5	7774	354.2	21.9
8	177.4	7189	312.7	23.0
9	179.4	6599	311.4	21.2
10	182.2	7070	331.7	21.3
11	161.5	6685	306.1	21.8
12	173.9	6697	320.3	20.9
13	128.3	4915	241.9	20.3
14	115.5	4430	224.2	19.8
15	150.8	4346	233.8	18.6
16	130.7	4496	246.4	18.2
17	127.9	4039	243.5	16.6
18	119.7	3907	224.5	17.4
19	106.6	2914	201.7	14.4
20	109.8	3698	207.8	17.8
21	63.5	2251	120.8	18.6
22	72.4	2221	133.7	16.6

Table S1. Chromosome-level summary of ChromoPainter analyses, related to STAR Methods. Summary of ChromoPainter results from each chromosome showing the number of SNPs and the number of distinct ancestry chunks on each chromosome. Chunk values are averages across all analyzed individuals, including both reference and admixed individuals.

	>=1%			>=5%			>=20%		
With original prior	95.0%	99.0%	99.9%	95.0%	99.0%	99.9%	95.0%	99.0%	99.9%
Belgium	0.1%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%
Denmark	81.4%	76.4%	70.1%	75.2%	69.5%	63.3%	40.4%	35.8%	30.5%
Netherlands	0.2%	0.1%	0.1%	0.1%	0.1%	0.1%	0.1%	0.1%	0.1%
Finland	0.7%	0.6%	0.4%	0.3%	0.3%	0.3%	0.1%	0.1%	0.1%
France	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%
Greenlandic Inuit	98.3%	98.3%	98.3%	98.3%	98.3%	98.3%	97.5%	97.4%	97.3%
Germany	0.6%	0.1%	0.0%	0.3%	0.1%	0.0%	0.0%	0.0%	0.0%
Ireland	0.4%	0.2%	0.2%	0.3%	0.2%	0.0%	0.0%	0.0%	0.0%
Italy	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%
Northern Ireland	0.1%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%
Norway	23.0%	17.8%	13.3%	8.4%	6.2%	4.7%	1.3%	1.1%	1.1%
Poland	0.5%	0.1%	0.0%	0.2%	0.1%	0.0%	0.0%	0.0%	0.0%
Spain	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%
Sweden	5.7%	3.5%	2.1%	2.0%	1.3%	0.8%	0.2%	0.1%	0.1%
UK	0.5%	0.3%	0.2%	0.3%	0.2%	0.2%	0.1%	0.1%	0.1%
With sparse prior									
Belgium	0.1%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%
Denmark	81.7%	77.0%	70.9%	76.1%	70.9%	64.7%	42.0%	36.9%	31.0%
Netherlands	0.2%	0.1%	0.1%	0.1%	0.1%	0.1%	0.1%	0.1%	0.1%
Finland	0.7%	0.6%	0.4%	0.3%	0.3%	0.3%	0.1%	0.1%	0.1%
France	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%
Greenlandic Inuit	98.3%	98.3%	98.3%	98.3%	98.3%	98.3%	97.5%	97.4%	97.3%
Germany	1.2%	0.1%	0.1%	0.6%	0.1%	0.0%	0.1%	0.0%	0.0%
Ireland	0.4%	0.2%	0.2%	0.3%	0.2%	0.0%	0.0%	0.0%	0.0%
Italy	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%
Northern Ireland	0.1%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%
Norway	22.6%	17.5%	13.0%	8.3%	6.1%	4.9%	1.3%	1.1%	1.1%
Poland	0.4%	0.1%	0.1%	0.2%	0.1%	0.0%	0.0%	0.0%	0.0%
Spain	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%
Sweden	5.9%	3.7%	2.3%	2.4%	1.3%	0.8%	0.2%	0.1%	0.1%
UK	0.5%	0.3%	0.2%	0.4%	0.3%	0.2%	0.1%	0.1%	0.1%

Table S2. Assignment to country at 1%, 5% and 20% ancestry thresholds across 1582 admixed Greenlanders, related to Table 1. The percentage values shown are the percentage of individuals inferred to have at least 1%, 5% or 20% ancestry from each source country, as in Table 1 in the main text. Sub-columns give percentages at different posterior probability thresholds: 95.0%, 99.0% and 99.9% (99.0% was used in Table 1). Top sub-table shows results with the original prior used to obtain Table 1, bottom sub-table shows results with a more sparse prior. The assignment analysis was conducted with SOURCEFIND using an individual-based approach.

	Recent admixture	Older admixture
Greenlandic Inuit	33.7%	71.6%
European (combined)	66.3%	28.4%
Denmark	98.4%	85.7%
Norway	0.5%	3.8%
UK	0.1%	0.9%
Sweden	0.1%	1.6%
Germany	0.1%	2.1%
France	0.1%	1.3%
Northern Ireland	0.1%	0.5%
Belgium	0.1%	0.6%
Netherlands	0.1%	0.3%
Spain	0.1%	0.8%
Ireland	0.1%	0.4%
Italy	0.1%	1.1%
Poland	0.1%	0.9%
Finland	0.0%	0.1%

Table S3. Ancestry estimates for groups of two groups of admixed Greenlanders, related to Figure 3. Ancestry estimates for groups of admixed Greenlanders with (n=250) and without (n=1332) a European-ancestry parent, here denoted "recent admixture" and "older admixture", respectively. The Greenlandic Inuit and combined European values are raw means, whereas the values for specific countries are the percentages of the European ancestry they constitute (they are divided by the value of "European (combined)". The European countries are listed in order of their mean value in the recent admixture column.

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Is Iceland’s language a Norse code – or legacy of Celtic settlers?

Gaelic origins of Icelandic words and landmarks challenge orthodox view of Viking heritage, says author

A book says Iceland’s language, landscape and early literature were strongly influenced by Celtic settlers. Photograph: Birdigol/Getty Images

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According to folklore, a Gaelic-speaking warrior queen called Aud was among Iceland’s earliest settlers. Her story is central to an emerging theory that Scottish and Irish Celts played a far bigger role in Iceland’s history than realised.

A book by Thorvaldur Fridriksson, an Icelandic archaeologist and journalist, argues that Gaelic-speaking Celtic settlers from Ireland and western Scotland had a profound impact on the Icelandic language, landscape and early literature.

Aud had been queen of Viking Dublin in the ninth century before taking her family, and Scottish and Irish crewmen, on the voyage to Iceland. Fridriksson believes that through settlers such as Aud, Gaelic language and culture were integral to Iceland's early history.

He has compiled a list of common Icelandic words and, with other academics, identified Icelandic landmarks that he believes have Gaelic roots. Iceland's *skaldic* poetry, *edda* poetic traditions and the sagas upon which Iceland's history is based were heavily influenced by Gaelic culture and immigrants, he argues.

"Every Icelander who has been living for a long time in another Scandinavian country – who has learned to speak Norwegian, Danish or Swedish very well – comes home back to Iceland, hears words in Icelandic never spoken in these languages," Fridriksson said.

"And I started to look at these words and I found them in Gaelic dictionaries, so I began to look at placenames, and a very great deal of Icelandic placenames, mountains, spaces – very important placenames – are very hard to explain in a Scandinavian way."

The theory, which is controversial, challenges the orthodox view that Iceland is a wholly Viking place, founded 1,100 years ago as part of Viking conquests and expansion along the Atlantic's north-eastern seaboard.

The Bárðarbunga volcano in Iceland is said to come from the Gaelic word for guardian (bàrd). Photograph: Arctic-Images/Corbis

It has growing support among academics after groundbreaking DNA research over the past 20 years by the deCODE genetics company in Reykjavik and the University of Oxford found that 63% of

Iceland’s earliest female settlers were of Irish and Scottish origin, as were 20% of early male settlers.

Many are assumed to have been women enslaved by Vikings during their conquest of the Gaelic-speaking Hebrides and eastern Ireland around Dublin, founded by the Vikings in the ninth century. Before the Vikings arrived in Iceland, early Christian Irish hermits, known as *papar*, founded small settlements there.

The DNA evidence upended a long-held belief that Icelanders were almost entirely of Norwegian heritage, a stance central to Iceland’s quest for independence from Denmark in 1918. Icelandic nationalists greatly downplayed evidence that enslaved Celts had helped populate the island.

In a recent paper on Iceland’s Irish links, called Gaelic Whispers, Prof Gísli Sigurðsson of the Árni Magnússon Institute in Reykjavik showed that many of Fridriksson’s arguments are gaining currency. But Sigurðsson said that not all of his claims were substantiated. More work by linguists, particularly specialists in early Gaelic, was needed, he added.

“It is now well established that the first population in Iceland was much more mixed than previously accepted and therefore, the question of linguistic influence from the Gaelic needs to be addressed more seriously than scholars have been willing to do hitherto,” Sigurðsson said.

Fridriksson believes differences in social status meant that in some cases, the Gaelic influence was subtle or lost; in other cases, it was clear.

Aud’s story shows that high-status Gaelic-speaking women, who voluntarily married Viking men, were among the settlers. In the early medieval period, Shetland, Orkney and the Outer Hebrides were Viking kingdoms. Aud, known as Auður djúpúðga in Iceland, is said to have freed the enslaved Celts who sailed under her command from Scotland, settling in western Iceland.

He said the names of many of Iceland’s largest volcanoes have clear Gaelic roots, such as Bárðarbunga (from the Gaelic for guardian, “bàrd”) and Hekla (from the Gaelic for terrifying, “eagal”). That meant they were named by high-status people, as were other landmarks.

Fridriksson hopes his book, Keltar, which has yet to be translated into English, will prompt debate and academic investigation. “The Gaelic influences in our culture are much deeper and greater than people believed up to now,” he said.

That intermingling with Viking cultures enriched Iceland, he added, as did the heavy exposure to Celtic Christianity among Viking converts from the monastic settlement on the Hebridean island of Iona, which played a pivotal role in the spread of early Christianity across northern Britain.

“The best of the so-called Viking culture is from the Gaelic areas; it’s the poetry, the music,” Fridriksson said.

Icelandic words believed to be derived from early Irish and Scots Gaelic

Lyf – Icelandic for medicine, from the Gaelic “luibh”, for herbs

Glíma – Icelandic wrestling, from the early Gaelic “gliad”, meaning battle

Ljómi – Icelandic for glow, from the Gaelic “laom”, meaning fire

Hrútur – Icelandic for ram, from the Gaelic “reithe”

Strákur – Icelandic for boy, derived from the Gaelic “strácair”

Source: Keltar by Thorvaldur Fridriksson