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Abstract

The Viking maritime expansion from Scandinavia (Denmark, Norway, and Sweden) marks one of the swiftest and most far-flung cultural transformations in global history. During this time (c. 750 to 1050 CE), Viking sailors reached Greenland, North America, and large parts of western Eurasia, and left a legacy that persists today. To understand the genetic structure and influence of the Viking expansion, we sequenced the genomes of 442 ancient humans from across Europe and Greenland ranging from the Bronze Age (c. 2400 BCE) to the early Modern period (c. 1600 CE), with particular emphasis on the Viking Age. We find that the period preceding the Viking Age was accompanied by foreign gene flow into Scandinavia from the south and east: spreading from Denmark and eastern Sweden to the rest of Scandinavia. Despite the close linguistic similarities of modern Scandinavian languages, we observe genetic structure within Scandinavia, suggesting that regional population differences were already present 1,000 years ago. We find evidence for a majority of Danish Viking presence in England, Swedish Viking presence in the Baltic, and Norwegian Viking presence in Ireland, Iceland, and Greenland. Additionally, we see substantial foreign European ancestry entering Scandinavia during the Viking Age. We also find that several of the members of the only archaeologically well-attested Viking expedition were close family members. By comparing Viking Scandinavian genomes with present-day Scandinavian genomes, we find that pigmentation-associated loci have undergone strong population differentiation during the last millennia. Finally, we are able to trace the allele frequency dynamics of positively selected loci with unprecedented detail, including the lactase persistence allele and various alleles associated with the immune response. We conclude that the Viking diaspora was characterized by substantial foreign engagement: distinct Viking populations influenced the genomic makeup of different regions of Europe, while Scandinavia also experienced increased contact with the rest of the continent.

Introduction

The three centuries from approximately 750 to 1050 CE mark a pivotal change for the peoples of Scandinavia. The maritime transformation commonly known as the Viking Age (VA) altered the political, cultural and demographic map of Europe in ways that are evident even today. The Vikings established systems of trade and settlement that stretched from the northern fringe of the American continent to the Asian steppe[1]. They also exported new ideas, technologies, language, beliefs, and practices to these lands. In the process, they gradually developed new socio-political structures, assimilated cultural influences, and adopted the Christian faith[2].

Currently, most of our understanding of the VA is based on written sources and archaeological evidence. The VA as a historical period has been framed by the first clearly documented raid on the British monastery of Lindisfarne in 793 CE, and the defeat of a Norwegian army at Stamford Bridge in 1066 CE. More recent perspectives emphasize long-term, multi-causal social processes with after-effects that varied greatly by region[3–5]. Similarly, the notion of a Viking "expansion", implying deliberate drive and purpose, has been supplemented by the more fluid concept of a "diaspora" that developed over time[2]. Under this framework, however, the role of demographic dynamics has remained unclear, as has the question of whether VA Scandinavia was genetically structured or represented a largely homogenous population. Similarly, we still do not know to what extent Vikings mixed with the local populations they encountered and how much foreign ancestry was brought back to Scandinavia.

In order to explore the genomic history of the Viking era, we shotgun sequenced 442 ancient human remains dating from the Bronze Age c. 2400 BCE to the early Modern (EM) period c. 1600 CE (Fig. 1). The ancient samples are divided into five broad categories mentioned in Figure 1a. The majority of individuals (n=376) were sequenced to between 0.1 and 11X average depth of coverage. The dataset includes Bronze Age (n=2) and Iron Age (n=10) individuals from Scandinavia; Early VA (n=43) individuals from Estonia (n=34), Denmark (n=6), and Sweden (n=3); ancient individuals associated with Norse culture from Greenland (n=23), VA individuals from Denmark (n=78), Faroe Islands (n=1), Iceland (n=17), Ireland (n=4), Norway (n=29), Poland (n=8), Russia (n=33), Sweden (n=118), Isle of Man (n=1), Scotland (n=8), England (n=32), Wales (n=1), and Ukraine (n=3), as well as individuals from the medieval and early Modern periods from Faroe Islands (n=16), Italy (n=5), Norway (n=7), Poland (n=2), and Ukraine (n=1). The VA individuals were supplemented with additional published genomes from Sigtuna (n=21, samples VK557-VK578), Sweden[6], and Iceland[7] (Supplementary Table 3). The skeletons originate from major archaeological sites of VA Scandinavian settlements and activities from Europe to Greenland (Supplementary Table 1, Extended Data Fig. 1). The data from the ancient individuals were analyzed together with previously published data from a total of 3,855 present-day individuals across two reference panels (Supplementary Note 6), and data from 1,118 ancient individuals (Supplementary Table 3).

Scandinavian genetic ancestry and the beginnings of the Viking era

Although VA Scandinavians shared a common cultural, linguistic, and material background, there was no common word for Scandinavian identity at that time[1]. The word "Viking" is used in contemporary sources to mean approximately a "pirate" or "sea warrior", and has been adopted in modern scholarly usage to denote travelers and diasporas of Scandinavian origins, language, and culture[2]. As such, there is no single "Viking world", but a coalescence of "Viking worlds" marked by rapidly growing maritime exploration, trade, war, and settlement, following the adoption of deep-sea navigation among the coastal populations of Scandinavia and the Baltic Sea area[8,9]. Thus, it is unclear to what extent the Viking-phenomenon refers to people with a recently shared genetic background and how far population changes accompanied the transition from the Scandinavian Iron Age into the Viking era.

To assess the genetic relationship of VA Scandinavians with that of other ancient European individuals, we performed genetic clustering using multi-dimensional scaling (MDS) on a pairwise identity-by-state (IBS) sharing matrix, as well as latent mixed-ancestry models (Admixture)[10]. We additionally used uniform manifold approximation and projection (UMAP)[11] on the MDS dimensions to visualize fine-scale genetic structure. We find that the majority of our samples broadly cluster within the range of other European Bronze Age (BA) and Iron Age (IA) populations, characterized by an ancestry component that is related to pastoralist populations from the Pontic-Caspian steppe (Fig. 2a, Extended Data Fig. 2 and 3) entering Europe around 3000 BCE[12,13]. The UMAP analysis reveals additional structure among the VA individuals, distributed within a broad area anchored by three ancestry clusters: Pre-Neolithic European hunter-gatherers (Fig. 2b, top right); Neolithic farmers from Anatolia and Europe (Fig. 2b, bottom right); and early BA Steppe pastoralists (Fig. 2b, left). We observe notable differences in the distribution of individuals from different geographic regions, indicating complex fine-scale structure among the different groups (Extended Data Fig. 3 and Fig. S8.13). For example, many VA individuals from the island of Gotland cluster with BA individuals from the Baltic region, indicating mobility across the Baltic Sea. We also identify some clear outliers: A late Neolithic / early BA individual from northern Norway who clusters with pre-Neolithic hunter-gatherers from Norway (VK531); an individual with East Asian-related ancestry who groups with ancient Saami individuals from Finland (VK518); and four Medieval individuals from Foggia in southern Italy with affinities to BA Mycenaean individuals from Greece (Fig. 2 and Extended Data Fig. 3).

We further characterized the deep genetic ancestry of the study individuals, by using f_4-statistics and ancestry modelling with distal sources using *qpAdm*. We find that IA individuals from Scandinavia show higher affinity with Steppe Pastoralists (Yamnaya_EBA) than with Anatolian farmers, similar to their late Neolithic and early BA predecessors (Extended Data Fig. 4a). In VA Scandinavians we find marked variation in ancestry among the different regions. Individuals from Norway are distributed similarly to earlier IA individuals, whereas groups from both Sweden and Denmark include many individuals with greater affinity to Anatolian farmers (Extended Data Fig. 4a). Ancestry modelling with *qpAdm* using the three established distal source groups for Europeans individuals was successful ($p>0.05$) for many groups, showing only subtle differences in their composition (Extended Data Fig. 4b). Nevertheless, the three-way model was rejected in a number of cases, for which we added additional distal source populations representing "Ancient North Eurasian" (ANE) ancestry (Botai_EBA), Caucasus hunter-gatherer ancestry (CaucasusHG_M), or East Asian ancestry (XiongNu_IA). We find that a four-way model including a small amount of East Asian ancestry provides a good fit for groups from the Baltic region, Sweden, and Norway (Extended Data Fig. 4c). This signal is consistent with gene flow involving Siberian ancestry as previously documented or with local admixture with populations with East Asian ancestry such as the Saami[14–16].

Finally, we carried out ancestry modelling with proximate sources to investigate continuity between European IA and VA groups. Using *qpAdm*, we find that models with a single IA source group cannot be rejected for most VA groups. Nevertheless, there is variation in which source group can be fit between the different VA groups. They broadly fall into two categories. On the one hand, groups that can mainly be fit using British IA sources include most Danish VA groups, as well as those from the British Isles. Groups from Norway, Sweden, and the Baltic, on the other hand, can mainly be fit using Scandinavian IA groups (Extended Data Fig. 5a). Notable exceptions are the individuals from Kärda in Southern Sweden, for which only the early Medieval Longobard individuals from Hungary can be fit as a single source group ($p > 0.01$; Extended Data Fig. 5a). Groups with poor one-way fits can be successfully modelled by including either additional northeastern ancestry (e.g. Ladoga_VA, fit using Saami_IA or XiongNu_IA sources) or additional southeastern ancestry (e.g. Jutland_VA, fit using Anatolia_BA source) (Extended Data Fig. 5b). Overall, our findings suggest that the genetic makeup of VA Scandinavia largely derives from ancestry of the preceding IA populations, but also reveal subtle differences in their ancestry and ongoing gene flow from both the south and east. These observations are consistent with archaeological claims of wide-ranging demographic turmoil in the aftermath of the Roman Empire with consequences for the Scandinavian populations during the late Iron Age[17,18]. We caution, however, that sampling for the periods preceding the VA is still sparse, and hence our samples may not provide a full picture of the genetic diversity across Scandinavia or in the rest of Europe during that period. Furthermore, methods based on shared genetic drift such as *qpAdm* are expected to have low power to disentangle fine-scale differences among groups with low genetic differentiation such as those observed in ancient Europeans from the BA onwards.

Genetic structure within VA Scandinavia

By the end of the Iron Age in the 8th century CE, Scandinavia formed a patchwork of conflicting and competing kingdoms with a shared cultural background. For centuries, a political economy based on raiding, trading, and gifts had been common[5]. However, the cause for the development of this economic and political system into the more organized maritime society of the Viking era remains debated[5]. It is commonly argued that seafaring[9,19] contributed to the creation of the densely interlinked Scandinavia of the VA[2,20,21].

To disentangle the fine-scale population structure within VA Scandinavia, we performed genotype imputation on a subset of 298 individuals with sufficient (>0.5X) coverage (289 from this study + 9 published[6]) and inferred genomic segments shared via identity-by-descent (IBD) within the context of a reference panel of 1,464 present-day Europeans using IBDseq, which was subsequently used in the UMAP analysis. We find that VA Scandinavians generally cluster into three groups according to their geographic origin and have close affinities with their respective present-day counterparts in Denmark, Sweden, and Norway (Fig. 3a). Closer inspection of the distributions for the different groups reveals additional complexity in their genetic structure (Fig. S10.1). We find that the "Norwegian" cluster includes Norwegian IA individuals, who are distinct from both Swedish and Danish IA individuals. The latter two groups of individuals cluster with the majority of central and eastern Swedish VA individuals. Many individuals from southwestern Sweden (e.g. Skara) cluster with Danish present-day individuals from the eastern islands (Funen, Zealand), skewing towards the "Swedish" cluster with respect to early and more western Danish VA individuals (Jutland). Some individuals have strong affinities with Eastern Europeans, particularly those from the island of Gotland in eastern Sweden. The latter likely reflects individuals with Baltic ancestry, as clustering with Baltic BA individuals is evident in the IBS-UMAP analysis (Fig. 2b) and through f_4-statistics (Fig S9.1).

To further quantify the within-Scandinavia population structure, we used ChromoPainter[22] to identify long, shared haplotypes among sequenced individuals using a reference panel enriched with Scandinavian individuals (n=1,464, see Supplementary Notes 6 and 11). Our approach detects subtle population structure present during the VA in Scandinavia. Supplementary Figures S11.1-10 and Supplementary Note 11 describe the supervised method that we used to obtain power to robustly identify local ancestry variation in the presence of sequencing rate variation. We find at least four major ancestry components in Scandinavia, each with affinities with a present-day population (Fig. S11.11) which we will refer to as "Danish-like", "Swedish-like", "Norwegian-like," and "North Atlantic" (that is "British-like"). We emphasize that the correspondence between these ancestries and present-day inhabitants of the respective countries is not exact or exclusive. The "North Atlantic" component may reflect originally pre-Roman "Celtic" individuals who occupied the British Isles and were brought into Scandinavia. Vikings were famously mobile and the sampling is heavily structured, so these results (Fig. S11.12) contain significant complexity over time and space, which we expand on below. However, average ancestry results can be visualised (Fig. 4) using spatial interpolation[23] to account for sampling locations (Supplementary Note 12). This highlights spatio-temporal patterns for which we report only statistically significant trends (Table S11.2) in a regression analysis (Supplementary Note 11).

During the VA, we mostly find high levels of Norwegian-like and Swedish-like components in Norway and Sweden, respectively, while "Danish-like" and "North Atlantic" components are more widespread within Scandinavia (Fig. 4, S11.12 and Supplementary Table 6). Notably, the "Swedish-like" component is higher in Salme, Estonia, than in Sweden (Fig S11.12), because our sampling scheme included several individuals from the famous Salme ship burial, which archaeological and isotopic data suggest was of Scandinavian origin[24,25]. While in general individuals from most of the Scandinavian VA settlements (Fig. S11.12) show mixed (Danish, Norwegian, and Swedish) genetic ancestries, VA individuals from Jutland (Denmark) do not have significant "Swedish-like" or "Norwegian-like" genetic components. Furthermore, gene flow within Scandinavia appears to be broadly from south to north, dominated by Danish Vikings moving into what are now Norway and Sweden (Table S11.2).

Although the majority of the Viking genomes within Scandinavia and abroad show affinities to Danish, Norwegian, Swedish, or British populations, there are some notable exceptions. We identified two ancient individuals (VK518 and VK519) originating from northern regions of Norway (Nordland), which have affinities to present-day Saami. This signal is weaker for VK519, indicating that he might have also had "Norwegian-like" ancestors. Given the geographic provenance of these samples, it was not unexpected to find individuals with "Saami-like" ancestry among the VA samples. However, as VK519 is an admixed individual with both "Norwegian-like" and "Saami-like" ancestries, it appears that genetic contacts between these groups were already underway in VA Norway.

Importantly, the genetic data is structured by topographic boundaries rather than by present-day country borders. Thus, the south-western part of Sweden in the VA is genetically more similar to Danish VA populations than the eastern regions of mainland Sweden (i.e. the area around the Mälaren Valley), likely due to geographic barriers that prevented gene flow in Sweden.

We quantified genetic diversity in our samples using two measures: conditional nucleotide diversity (Supplementary Note 9) and variation in inferred ancestry based on ChromoPainter results (Supplementary Note 11; Extended Data Fig. 6 and Fig. S11.13). We also visualised it as the spread of individuals on the MDS plot based on a pairwise IBS sharing matrix (Fig. 3b). We find overall high nucleotide diversity among most VA groups, with diversity values exceeding those of earlier Neolithic or BA groups, and only slightly lower than the highly diverse IA individuals from the British Isles (Fig. S9.5). Both measures of diversity vary significantly across locations. Denmark and southern parts of Sweden have the highest genetic diversity in the region (Fig. 3b) and also possess high diversity in inferred ancestries, suggesting that these regions may have been centers of interaction and trade during this time. Interestingly, on Gotland, there are much more "Danish-like", "British-like", and "Finnish-like" genetic components than "Swedish-like" components, supporting the notion that the island may have been marked by extensive maritime contacts during the VA. Our two Gotland sampling sites, Fröjel and Kopparsvik, have long been argued to contain non-local individuals[26], but recent Sr-isotope analyses have suggested otherwise[27,28]. North Norway also has high diversity in inferred ancestry due to its mixture of "North Atlantic" and "Norwegian-like" ancestry.

On Öland and in Skara (both in southern Sweden), we observe high genetic and ancestry diversity (Extended Data Fig. 6). The high Sr and O isotope variation in Öland has previously suggested: (i) a high proportion (68%) of non-locals, (ii) high diversity in geographical origins and (iii) long distance migration in Öland[29]. Thus, the genetic diversity observed for Öland in the VA fits well with all of these results.

In conclusion, the results for Gotland and Öland agree with the archaeological record in suggesting that Öland and Gotland were important maritime communities from the Roman period onwards[30,31]. A similar pattern is observed at a few archaeological sites from the central Danish islands, such as Langeland, although at a lower scale. Interestingly, genetic diversity here increases from the early to the late VA, suggesting increasing interregional interaction.

Our findings provide evidence for population structure within VA Scandinavia[2,9,19–21]. We see evidence of cosmopolitan centers like Skara and trade-oriented islands like Gotland and Öland to the south, where we find higher diversity of ancestries than in the rest of Scandinavia. These patterns are consistent with a restricted number of sea routes between the different Scandinavian areas and beyond.

Viking migrations

Viking society is particularly famous for its ship technology, allowing for fast transport of large numbers of individuals in a single vessel[32]. These vessels enabled the Vikings not only to carry out lucrative raids and extend trade routes across Western Eurasia, but also to reach and settle lands in the North Atlantic[33–36]. Based on historical and archaeological data, Vikings were present in both western and eastern Europe, reaching perhaps as far as the Pontic Steppe and the Middle East[37,38]. It is commonly believed that the westward migrations and raids were mainly carried out by people from what are now Norway and Denmark in the 9th and 10th centuries CE. In contrast to the western movements, the eastward expansions are commonly believed to have been carried out by Swedish Vikings, trading along navigable river systems and overland caravan routes[38]. These people formed a major component in the complex ethnic group known as the Rus, and are also credited for being active in the formation of the first Russian state[39,40].

Overall, our fine-scale ancestry analyses based on genomic data are largely consistent with the Viking expansion patterns inferred from archaeology (Figs. 3, 4 and S11.12). The eastward movements mainly involved individuals with “Swedish-like” ancestry, while Viking individuals with “Norwegian-like” ancestry travelled to Iceland, Greenland, Ireland, and the Isle of Man. It is worth mentioning that the expansion of the Vikings in Iceland and Greenland was also accompanied by individuals with “North Atlantic” ancestry, which is consistent with previous studies [7,41]. A “Danish-like” ancestry component is more pronounced in present-day England, which is also in accordance with historical records[42] and still visible in place-names[40], surnames[43], and modern genetics[44,45]. Importantly, however, it is currently impossible for us to distinguish “Danish-like” ancestry in the British Isles from that of the Angles and Saxons, who migrated in the 5th-to-6th centuries CE from Jutland and Northern Germany.

The ancient individuals from two execution sites in England (Dorset and Oxford) have significant “North Atlantic” ancestry, as well as “Danish-like” and “Norwegian-like” ancestries. If these represent Viking raiding parties that were defeated and captured, as has been suggested[46,47], this implies such forces were composed of individuals from different places of origin. This pattern is also suggested by isotopic data from the warrior cemetery in Trelleborg, Denmark[48]. Similarly, the presence of "Danish-like" ancestry in an ancient sample from Gnezdovo (Eastern Europe) indicates that the eastern migrations were not entirely composed of Vikings from Sweden.

However, in some cases, localities seem to have taken up Viking culture while incorporating little to no Scandinavian ancestry components, suggesting that the "Viking" identity was not always necessarily associated with Scandinavian genetic ancestry. Archaeological evidence indicates that four higher coverage VA individuals from three different archaeological sites in the Orkney Islands have Scandinavian cultural links[49,50]. However, two (VK202 and VK207) of these samples have over 85% "North Atlantic" ancestry and are genetically similar to present-day Irish and Scottish populations (Figs S11.3, S11.12, S11.14, Supplementary Table 6), which is in contrast to the available isotopic evidence[51]. Haplotype-based analyses corroborate that two of these samples possess local genetic ancestries, with little Scandinavian contribution, aligning them with two local Pictish skeletons. The other two individuals - VK204 and VK205 - displayed c. 50% "Norwegian-like" and "Danish-like" ancestries (Supplementary Table 6), respectively, which may indicate admixture between the locals and Scandinavians in Orkney during the VA. These are likely the first Pictish genomes published to date ("Evidence for Pictish Genomes", Supplementary Note 11). Interestingly, a similar (>80% "North Atlantic" ancestry) individual was found in Ireland (VK545) and five in Scandinavia. This implies that Pictish populations may have been integrated into Scandinavian culture by the VA. Lastly, one of the Orkney samples (VK204) appears to have an uncommon karyotype (likely XXY). Given the relatively high present-day rate of occurrence of Klinefelter syndrome (roughly 1 in 576 males)[52], it is not particularly surprising to observe such a case in such large number of ancient samples.

Gene flow into Scandinavia during the Viking era

Archaeological findings and the written sources support the hypothesis that Viking back-migrations and interaction between the newly settled areas and Scandinavia were common[2,53]. Presumably, if these movements took place, native ancestry from these areas must have also been introduced into Scandinavia. We therefore aimed to assess the levels of non-Scandinavian ancestry in Scandinavia during the VA.

Using fineStructure[22], we find that the levels of non-Scandinavian ancestry in Danish, Norwegian, and Swedish Vikings agree with known trading routes (Supplementary Notes 11 and 12). The most obvious genetic signals are from Finnish and Baltic sources into the area of what is now modern Sweden, including Gotland. These ancestries are present at considerably lower levels or are completely absent in most individuals from Denmark and Norway. A substantial interaction across the Baltic Sea is also suggested by objects from Finland found in graves in Middle Sweden, although recent Sr-isotope analyses are inconclusive regarding the origins of the buried individuals[54,55]. In contrast, western regions of Scandinavia have much higher levels of ancestry from the British Isles (Supplementary Notes 11 and 12). We also observe several individuals (Supplementary Table 6) with large amounts of South European ancestry in Denmark (e.g. VK365 and VK286 from Bogøvej) and southern Sweden (e.g. VK442 and VK350 from Öland, and VK265 from Kärda) during the VA (Fig. 4). No such individuals are found among our Scandinavian IA samples, though we stress that our sampling for this period is more limited than for the other two. The discovery of individuals with ancestry from Southern Europe and the British Isles is the first direct evidence for movement into Scandinavia from these regions. The directions of interaction marked by these individuals is consistent with the major directions of gene flows outwards from Scandinavia also seen in the data.

Surprisingly, individuals from the Kärda site show high amounts of Southern European ancestry when chromosome painting is used. They also show genetic similarity to early Medieval groups from southern Europe such as the Longobards from Hungary in the qpAdm analysis (Extended Data Fig. 5a). The site is located far inland, in south-west Sweden, making this similarity quite unexpected, given that the samples are AMS-dated to the middle of the VA. Studies of VA burial customs suggest that the Småland area was characterized by locally confined cultural groups[56]. The genetic data suggest that this pattern of cultural isolation was sustained in marked contrast to contemporary coastal and island communities. Consistent with this hypothesis we find that the individuals from Kärda show a marked reduction in nucleotide diversity compared to other VA groups (Fig. S9.1).

Disappearance of the Greenlandic Norse

From around 980 to 1440 CE southwest Greenland was settled by people of Scandinavian descent. They likely descended from Icelandic Vikings who established a settlement there at the end of the 10th century CE[35,57]. It is believed that the Norse also reached Newfoundland, from Greenland around 1000 CE, although no permanent settlement was established[36]. The fate of the Norse in Greenland remains debated, but probable causes of their disappearance are social or economic processes in Europe (e.g. political relations within Scandinavia and changed trading systems) and natural processes, like climatic change[35,58,59].

We see no evidence of long-term inbreeding in the Greenlandic Norse genomes, though we note that we only have one high-coverage genome from the later period of occupation of Greenland (Supplementary Note 10; Figs. S10.2 and S10.3). This suggests a depopulation scenario over approximately 100 years which would be in line with previous demographic models[60], as well as the archaeology. Indeed, the latter indicates that marginal farms in the Western Settlement and the northern and southern parts of the Eastern Settlement were abandoned from about 1200 CE, with no converse intensification of settlement in the central areas.

We also find no evidence of ancestry from local populations from the Western Atlantic (Paleo Eskimo, Inuit, or Native American) in the Norse genomes (Fig. S9.4), which accords with previous studies of the skeletal remains[60]. This suggests that either sexual interaction did not take place or that, if it did, then it was on a very small scale with the children remaining in the native communities. In terms of genetic ancestry of the Greenlandic Norse, we find evidence of admixture between Scandinavians (mostly from Norway) and individuals from the British Isles, similar to the first settlers of Iceland[7], which supports the archaeological and historical links between the Greenlandic Norse and the Icelandic Vikings.

Genetic composition of the earliest Viking expedition and kinship findings

Maritime raiding has been a constant of seafaring cultures for millennia. However, the VA is unusual in that it is partly defined by such activity[61]. Despite the historical importance of Viking raiding, the exact nature and composition of these war parties is unknown[5]. One raiding or diplomatic expedition has left direct archaeological traces, at Salme in Estonia, where 41 Swedish Vikings who died violently were buried in two boats accompanied by high-status weaponry[24,25]. Importantly, the Salme boat-burial predates the first textually documented raid (in Lindisfarne in 793) by nearly half a century.

Comparing the genomes of 34 individuals from the Salme burial using kinship analysis, we find that these elite warriors included four brothers buried side by side and a 3rd degree relative of one of the four brothers (Supplementary Note 4). In addition, members of the Salme group had very similar ancestry profiles when compared to the profiles of other Viking burials (Supplementary Notes 10 and 11). This suggests that this raid was conducted by relatively genetically homogeneous group of people of high status, including close kin. Isotope analyses indicate that the crew came from the Mälaren area in Eastern Sweden[25] which confirms that Baltic-Mid-Swedish interaction occurred early in the VA.

Intriguingly, we identified several additional pairs of kin among the other Viking genomes. One is a pair of 2nd degree male relatives (i.e. half-brothers, nephew-uncle, or grandson-grandfather) from two locations separated by the North Sea: one of the samples (VK279) was excavated in Denmark (Galgedil site on Funen; this cemetery was also analyzed for strontium with a group of non-locals there) while the other individual (VK144) was found in the UK (the aforementioned Oxford site). Another pair of individuals with 3rd or 4th degree relatedness (e.g. cousins) was discovered in Sweden, namely a male sample excavated on the island of Öland (VK342) and a female individual from Skämsta, Uppsala (VK527), some 300-400 kilometers apart.

Positive selection in Europe in the last 10,000 years

The availability of hundreds of genomes from the IA and VA - in combination with previously published Mesolithic, Neolithic, and BA genomes[12,13,62,63] - permits us to directly investigate the role of positive selection using time series of allele frequencies from the last ten millennia of European history. We looked for SNPs whose allele frequencies changed significantly in the last 10,000 years using a newly developed method called "neoscan". Implemented in the Ohana software package[64,65], neoscan can detect strong allele frequency shifts in time that cannot be explained by temporal changes in genome-wide genetic ancestry alone (Supplementary Note 14).

Figure 5a shows the resulting likelihood ratio scores in favor of selection looking at the entire 10,000-year period (top, "general" scan), the period up to 4,000 BP (middle, "ancient" scan) and the period from 4,000 BP up to the present (bottom, "recent" scan). The strongest candidate for selection - especially in the "recent" scan - is a cluster of SNPs near the LCT gene - a signal that has been extensively characterized in the past[66,67]. The rise in frequency of the lactase persistence allele to its present-day levels in Northern Europe is, however, poorly understood. We know that this rise must have occurred after the BA, a time at which this allele was still segregating at low frequencies[12,62]. Based on the archaeological record, we also know that VA Scandinavians used a variety of dairy products as an essential part of their daily food intake. Our dataset allows us, for the first time, to directly assess the frequency of the lactase persistence allele (at SNP rs4988235, upstream of the LCT gene) in Scandinavia during the IA and VA, and trace its evolution since the BA.

Figure 5b shows that VA groups had very similar allele frequencies at the LCT lactase persistence SNP to those found in present-day northern European populations. In contrast, the persistence allele was at low frequencies in BA Scandinavians, as well as Corded Ware and Bell Beaker cultures from central Europe, even though there is evidence for milk consumption in these regions by that time. The allele frequency in IA samples is at intermediate levels (c. 37.5%), suggesting this rise in frequency must indeed have occurred during the Iron Age (c. 1500-2500 years ago), but was largely complete at the onset of the VA. Interestingly, the allele frequency of the allele is much higher (c. 40%) in the BA population from the neighboring Baltic Sea region than in BA Scandinavia. Given the geographic and cultural proximity of Scandinavia and the Baltic region, this may suggest gene flow between the two regions resulting in increased frequency of lactase persistence in Scandinavia during the Iron Age.

Other candidates for selection include previously identified regions like the TLR1/TLR6/TLR10 region, the HLA region, SLC45A2 and SLC22A4[62]. We also find several new candidate regions for selection in the "ancient" scan, which includes sweeps that must have occurred before the Viking period, and may point to shared phenotypes between ancient Vikings and present-day Scandinavians. Querying the allele frequency of these SNPs also allows us to determine whether some of the initially selected alleles then decreased in frequency during the last few millennia or whether they remained stable at high frequencies from the VA until the present (Supplementary Note 14). These ancient-sweep candidate regions include a region overlapping the DCC gene, which has been implicated in colorectal cancer[68] and another overlapping the AKNA gene, which is involved in the secondary immune response by regulating CD40 and its ligand[69]. This highlights the utility of using ancient DNA to detect signatures of ancient selective events that may be too difficult to detect using present-day data alone.

Pigmentation-associated SNPs

Exploring twenty-two SNPs with large effects associated with eye color and hair pigmentation, we observe that their frequencies are very similar to those of present-day Scandinavians (Supplementary Note 13). This suggests that pigmentation phenotypes in VA Scandinavians may not have differed much from the present-day occupants of the region (although see section on complex traits below for an analysis including alleles of small effect). Nevertheless, it is important to stress that the genotypes of these SNPs are not fixed across the sequenced samples, and that there is therefore not a single "Viking phenotype". For example, two of the ancient samples with the highest coverage have different pigmentation phenotypes: VK42 from Skara, Sweden has alleles associated with brown eyes and dark hair coloration while VK1 from Greenland has alleles associated with blue eyes and lighter hair.

Evolution of complex traits in Scandinavia

To search for signals of recent population differentiation of complex traits, we compared genotypes of VA samples with those of a present-day Scandinavian population for a range of trait-associated SNP markers. We selected 16 traits for which summary statistics from well-powered genome-wide association studies (GWAS) were available through the GWAS ATLAS (https://atlas.ctglab.nl)[70]. For comparison with the VA samples we used a random population subset of the IPSYCH case-cohort study of individuals born in Denmark between 1981-2011[71]. We derived polygenic risk scores (PRS) for the 16 traits, based on independent genome-wide significant allelic effects and tested for a difference in the distribution of polygenic scores between the two groups, correcting for sex and ancestry-sensitive principal components (Supplementary note S15).

We observed a significant difference between the polygenic scores of VA samples and present-day Danish population samples for three traits; black hair color ($P = 0.00089$), standing height ($P = 0.019$) and schizophrenia ($P = 0.0096$) (Extended Data Fig. 5). For all three traits, the polygenic score was higher in the VA group than in the present-day Danish group. However, the observed difference in PRS for height and schizophrenia between the groups did not remain significant after taking into account the number of tests. A binomial test of the number of black hair color risk alleles found in higher frequency in the VA sample and the present-day sample, also returned a significant difference (65/41; $P = 0.025$), which suggests that the signal is not entirely driven by a few large-effect loci.

Thus, we only find evidence for systematic changes in combined frequencies of alleles affecting hair color (and possibly also height and schizophrenia), among the anthropometric traits and complex disorders we tested. Also, we cannot conclude whether the observed difference in allele frequencies are due to selection acting on these alleles between the VA and the present time or to some other factors (such as more ethnic diversity in the VA sample), nor can we conclude whether a similar change has occurred in other Nordic populations than the Danish.

Genetic legacy of the Vikings in present-day populations

To test whether present-day Scandinavians share increased ancestry with their respective ancient Viking counterparts, we first inferred D-statistics of the form D (YRI, ancient; present-day population 1, present-day population 2), which contrast allele sharing of a test ancient individual with a pair of present-day test populations. We find subtle but noticeable shifts of Viking Age individuals from Scandinavia towards their present-day counterparts in the distributions of these statistics (Extended Data Fig. 5c; Figs S9.2 and S9.3).

We further examined variation in present-day populations using fineSTRUCTURE, and then described these present-day groups by their ancestry from ancient populations (Supplementary Note 11, Fig. S11.14). We find that within Scandinavia, present-day populations are still structured according to the ancient Viking population groups. The component that we associated as “Norwegian-like” is present at

45-65% in present-day Norway. Similarly, the ancient "Swedish-like" ancestry is present at 15-30% within Sweden. Of the four Swedish clusters, one is more related to the ancient Finnish than the "Swedish-like" ancestry, and a second is more related to Danes and Norwegians. "Danish-like" ancestry is now high across the whole region.

Outside of Scandinavia, the genetic legacy of the Vikings is consistent, though limited. A small Scandinavian ancestry component is present in Poland (up to 5%). Within the British Isles, it is difficult to assess how much of the "Danish-like" ancestry is due to pre-existing Anglo-Saxon ancestry; but it is likely to be similar to the "Norwegian-like" ancestry at around 4%. The genetic impacts are stronger in the other direction. While some "British-like" individuals in Orkney became "Scandinavian" culturally, others found themselves in Iceland, Norway and beyond leaving a genetic legacy that persists today. Present-day Norwegians vary between 12 and 25% in their "British-like" ancestry, whilst this ancestry is a more uniform 10% in Sweden. Separating the VA signals from more recent population movements is difficult, but these numbers are consistent with our VA estimates.

Discussion

Until now, our main understanding of the VA was largely based on a combination of historical sources and archaeological evidence. These often characterize the VA as a period of high mobility and interaction among populations. Networks of trade were established, connecting distant regions within Scandinavia through established waterways with significant movement between regions. It has also been viewed as a time during which links were created to regions outside Europe, from the Pontic Steppe in the east to parts of the North American Atlantic coast in the west.

Our genomic analyses add complexity to this simple picture. We largely reconstruct the long-argued movements of Vikings outside Scandinavia: Danish Vikings going to Britain, Norwegian Vikings moving to Ireland, Iceland, and Greenland, and Swedish Vikings sailing east towards the Baltic and beyond. However, we also see evidence of individuals with ancient Swedish and Finnish ancestry in the westernmost fringes of Europe, whilst Danish-like ancestry is also found in the east, defying modern historical groupings. It is likely that many such individuals were from communities with mixtures of ancestries, likely thrown together by complex trading, raiding, and settling networks that crossed cultures and the continent.

Our observations also suggest that the different parts of Scandinavia were not evenly connected, as has often been assumed. Despite relatively fast and easy communication between the coastal regions of

Denmark, Norway, and Sweden, we find that clear genetic structure was present in VA Scandinavia. In fact, our data indicate that VA Scandinavia consisted of a limited number of transport zones and maritime enclaves[72] where contact was made with Europe, while the remaining regions had limited external gene flow with the rest of the Scandinavian continent. Some VA Scandinavian locations are relatively homogeneous both in terms of genetic diversity and patterns of ancestry; particularly mid-Norway, Jutland, and the Atlantic settlements, which contain predominantly Norwegian-like and "North Atlantic" (including possibly pre-Anglo Saxon British) ancestry. Indeed, one of the clearest vectors of contrast observed in this study is between the strong genetic variation seen in relatively populous coastal and southern trading communities such as in the islands Gotland and Öland, and the reduced diversity in less populated (mostly inland) areas in Scandinavia[73–75] (Fig. 3, Extended Data Fig. 5; Supplementary Notes 9 and 11). The high genetic heterogeneity in coastal communities may have been due to increased population size, which would extend both spatially and further back in time the urbanization model for the Late VA city of Sigtuna proposed by Krzewińska et al.[6] who suggested that more cosmopolitan trading centers were already present at the end of the VA in Northern Europe.

Interestingly, our findings correspond with palaeodemographic studies based on place-name evidence and archaeological distributions suggesting population density was higher in Denmark than elsewhere in VA Scandinavia[76]. Gene flow from Denmark to the north is also paralleled by the linguistic affinities of the medieval Scandinavian languages: The Icelandic law text Grágás states that the common language of Swedes, Norwegians, Icelanders, and Danes was dǫnsk tunga ("Danish tongue")[77]. It appears that the formation of large-scale trading and cultural networks that spread people, goods, and warfare took time to affect the heartlands of Scandinavia, which received much more restricted gene flow, retaining pre-existing genetic differences between Scandinavian populations. This pattern of behavior seems to prevail from the beginning of the Viking diaspora to its end at the beginning of the medieval period.

Lastly, our findings also show that Vikings are not simply a direct continuation of the Scandinavian Iron Age groups. Rather than simple continuity, we observe foreign gene flow from the south and east into Scandinavia, starting in the IA, and continuing throughout the duration of the Viking period from an increasing number of sources. This contradicts the myth of the Vikings as people of pure local Scandinavian ancestry. In fact, we found many Scandinavian and North Atlantic VA individuals with high levels of non-Scandinavian ancestry, both within and outside Scandinavia, suggesting ongoing gene flow with different people across Europe.

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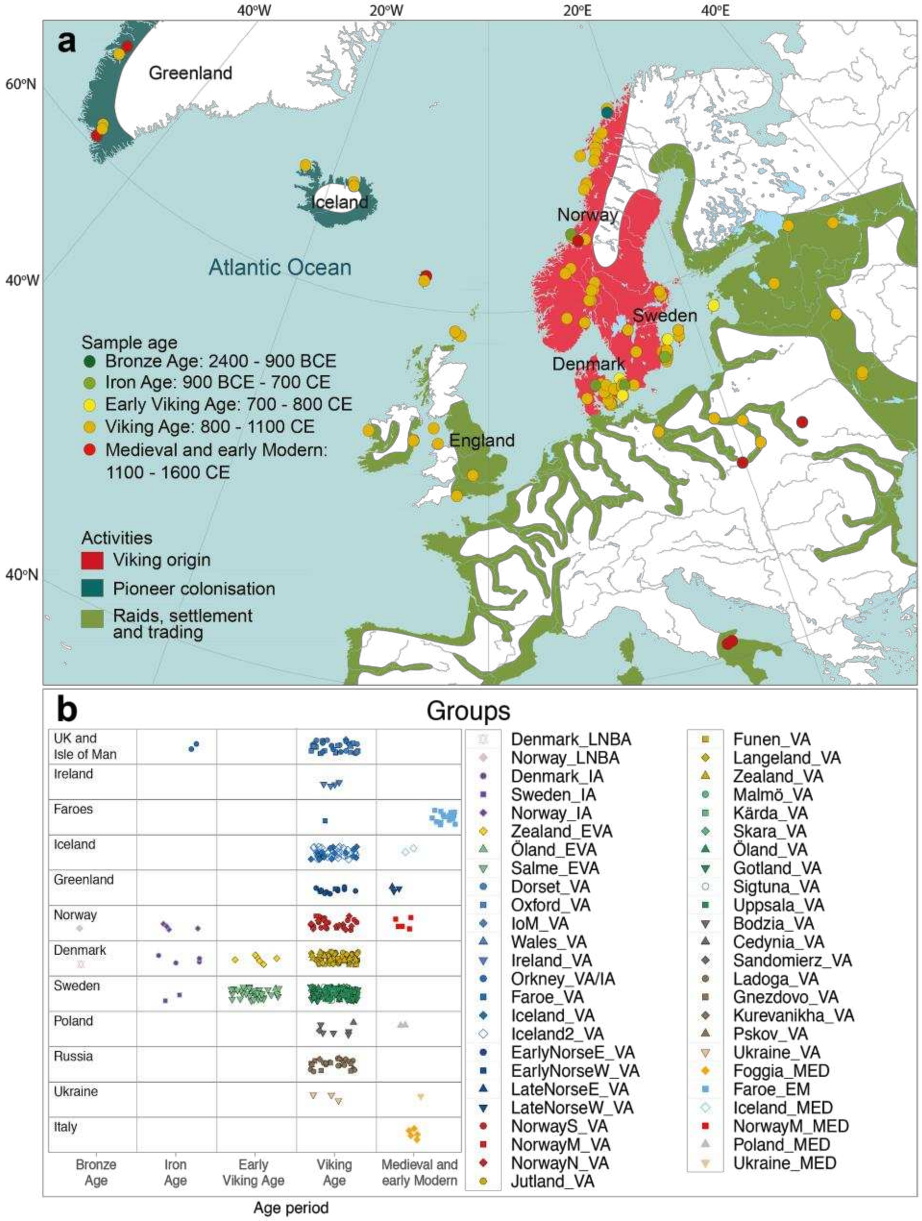


Fig. 1: Viking Age genomic dataset overview. a, Map of the "Viking World" from 8th till 11th centuries, showing geographic location and broad age category (coloured symbols) of sites with new ancient samples reported in this study. **b,** all new ancient individuals from this study (n=442) and published VA samples from Sigtuna[6] and Iceland[7] categorized based on their spatio-temporal origin. The ancient samples are divided into the following five broad categories: Bronze Age (BA), Iron Age (IA), Early Viking Age (EVA), VA and Medieval (MED) / early Modern (EM). Random jitter has been added along the x-axis in each category to aid visualization. LNBA - Late Neolithic/Bronze Age; NorseW - Norse Western settlement; NorseE - Norse Eastern settlement; NorwayS - southern Norway; NorwayN - northern Norway; NorwayM - middle Norway

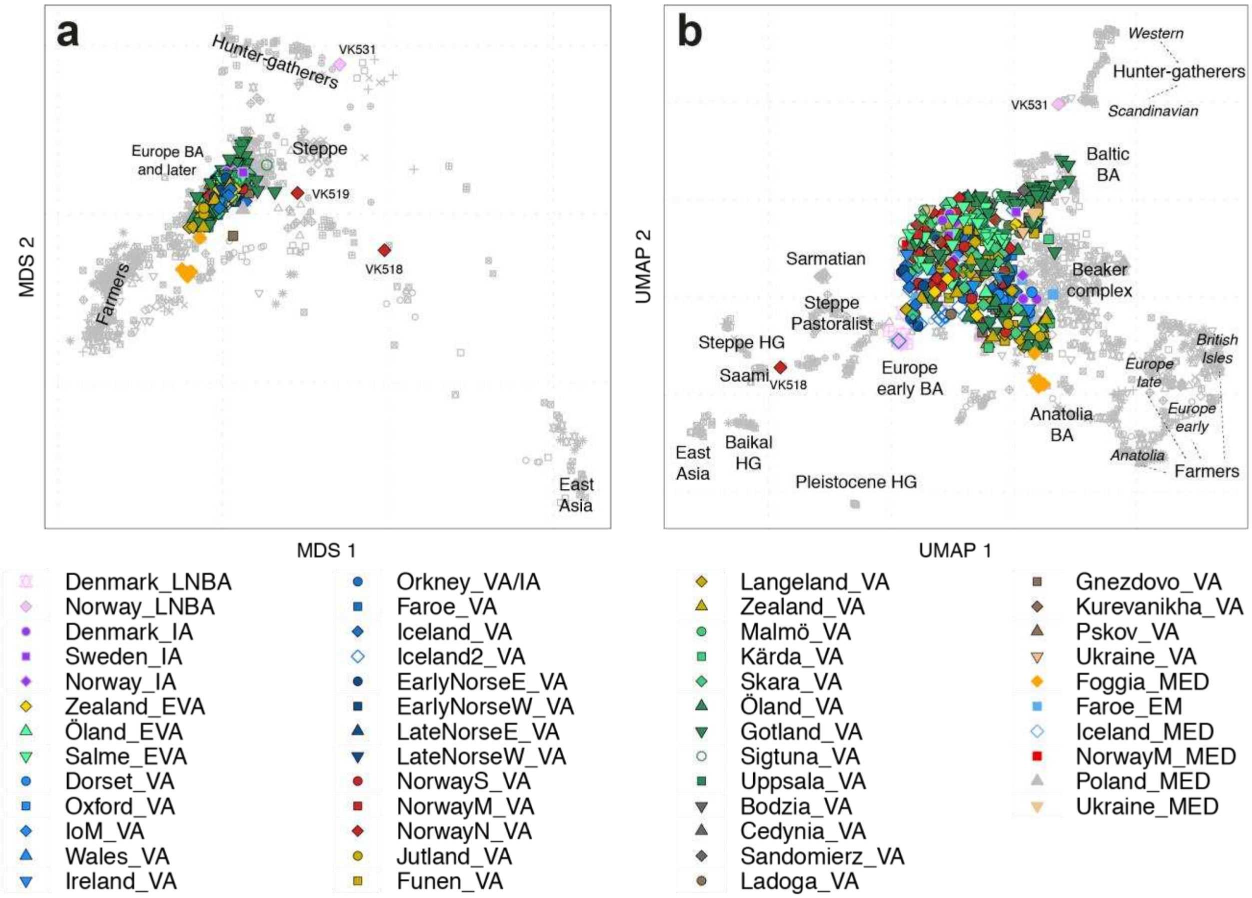


Fig. 2: Genetic structure of VA samples. **a**, Multidimensional scaling (MDS) plot based on a pairwise identity-by-state (IBS) sharing matrix of the VA and other ancient samples (Supplementary Table 3). **b**, Uniform manifold approximation and projection (UMAP) analysis of the same dataset as in plot (**a**).

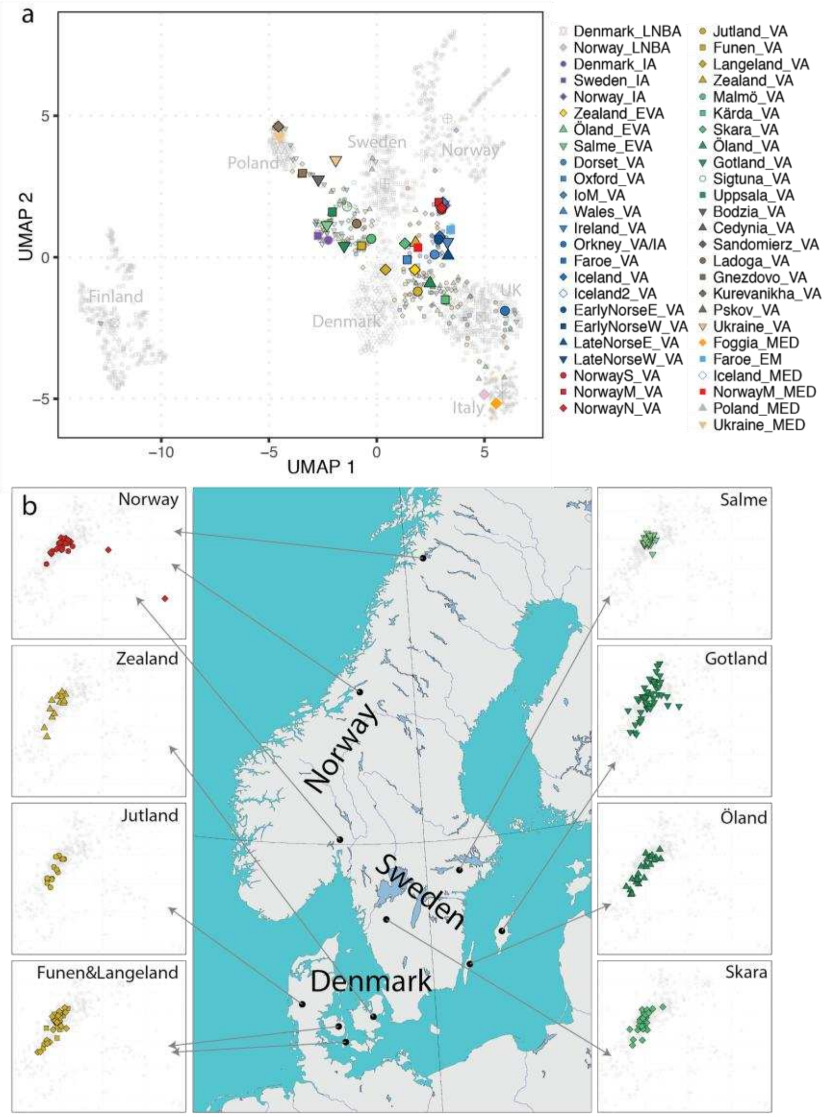


Fig. 3: Genetic structure and diversity of ancient samples. **a**, Uniform manifold approximation and projection (UMAP) analysis of the ancient and modern Scandinavian individuals based on the first 10 dimensions of MDS using identity-by-descent (IBD) segments of imputed individuals. Large symbols indicate median coordinates for each group. **b**, Genetic diversity in major Scandinavian VA populations. Plots next to the map show MDS analysis based on a pairwise IBS sharing matrix. Here "Norway" represents all the sites from Norway. The scale is identical for all the plots.

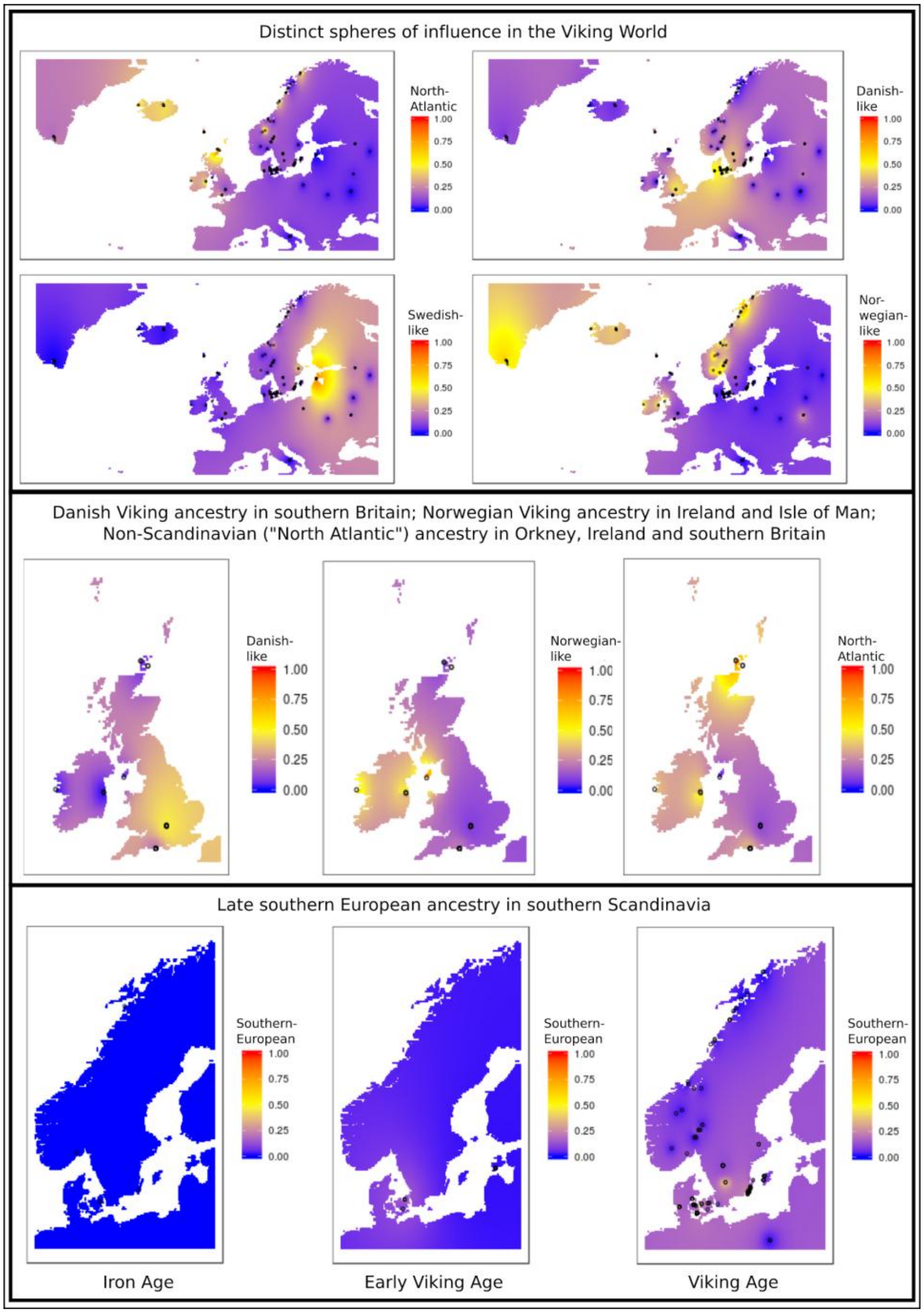


Fig. 4: Spatiotemporal patterns of Viking and non-Viking ancestry in Europe during the IA, EVA and VA. We performed inverse distance weighting interpolation of the ancestry painting proportions of each individual genome on a dense grid of points covering the European continent, to better visualize the distribution of ancestry paintings at different periods (Supplementary Note 12). The "Swedish-like" ancestry is the highest in present-day Estonia due to the ancient samples from the Salme ship burial, which originated from the Mälaren Valley of Sweden, according to archaeological sources.

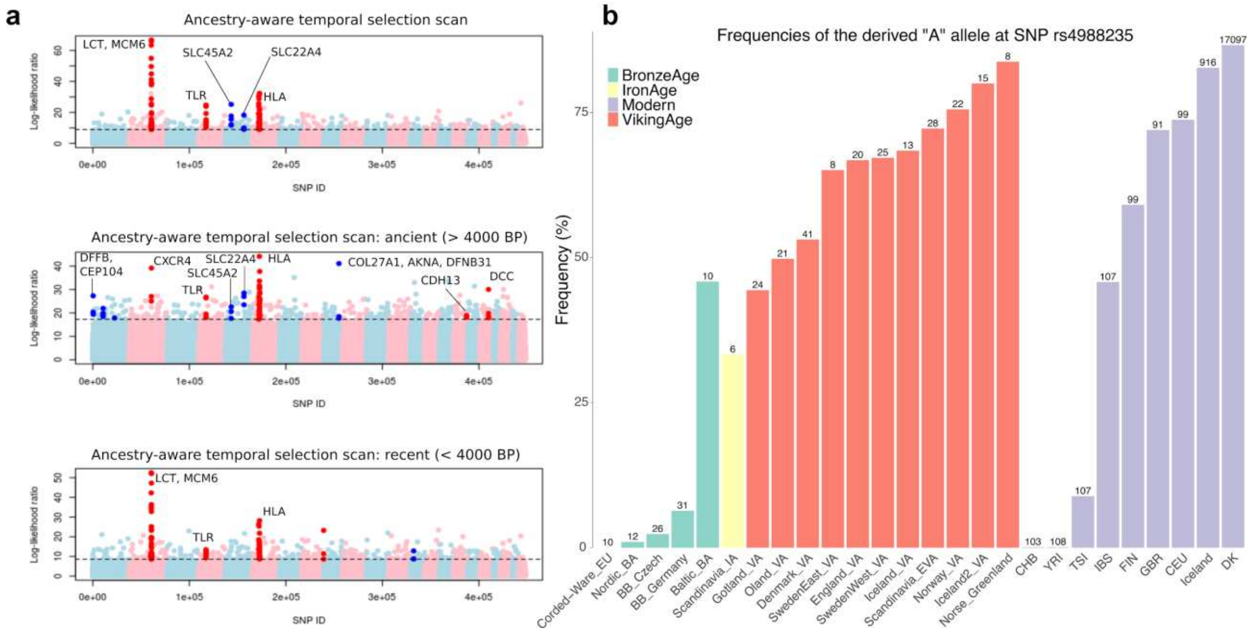
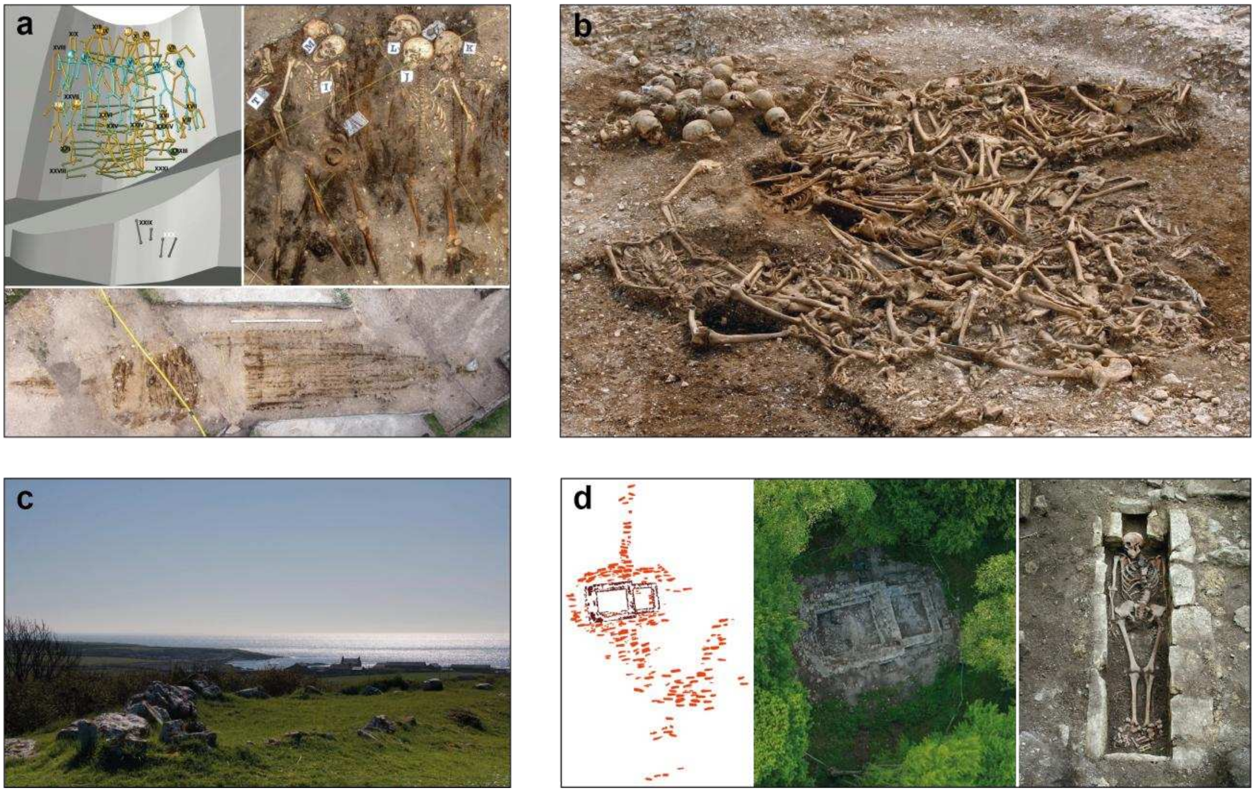


Fig. 5: Positive selection in Europe. a, Manhattan plots of the likelihood ratio scores in favor of selection looking at the entire 10,000-year period (top, "general" scan), the period up to 4,000 BP (middle, "ancient" scan) and the period from 4,000 BP up to the present (bottom, "recent" scan). The highlighted SNPs have a score larger than the 99.9% quantile of the empirical distribution of log-likelihood ratios, and have at least two neighboring SNPs (+/- 500kb) with a score larger than the same quantile. **b**, Frequencies of the derived "A" allele rs4988235 SNP responsible for lactase persistence in humans for different Viking-Age groups, present-day populations from the 1000 Genomes Project as well as relevant Bronze Age population panels. The numbers at the top of the bars denote the sample size on which the allele frequency estimates are based.

Extended Data Figures

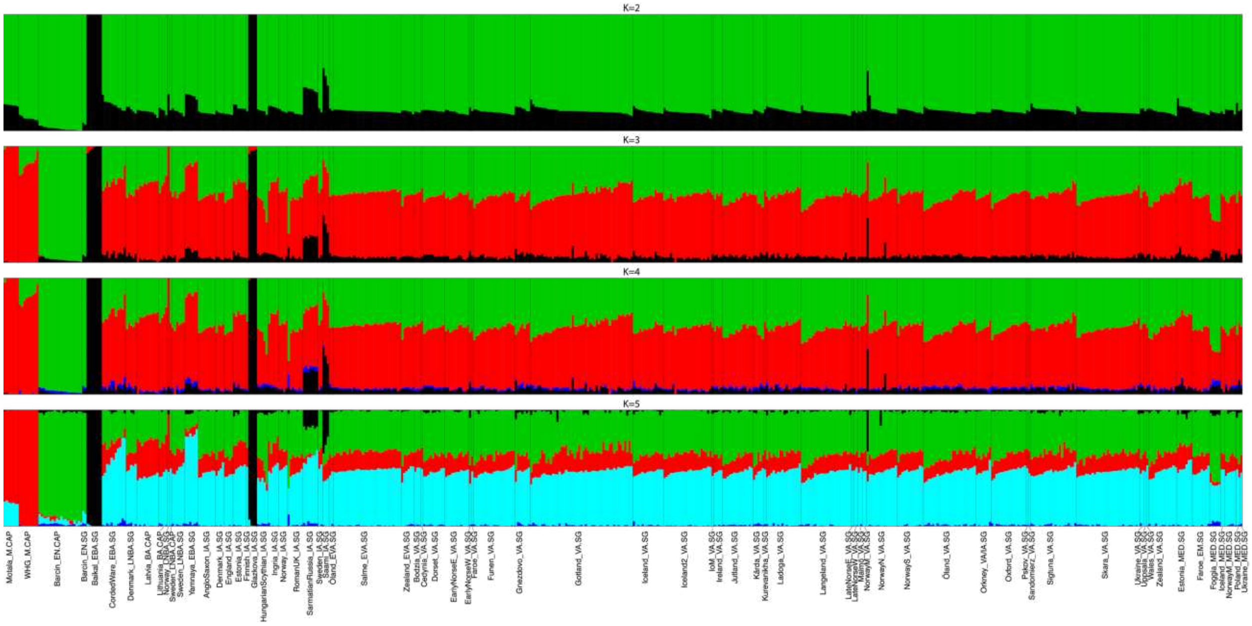
Extended Data Fig. 1: Viking Age archaeological sites.



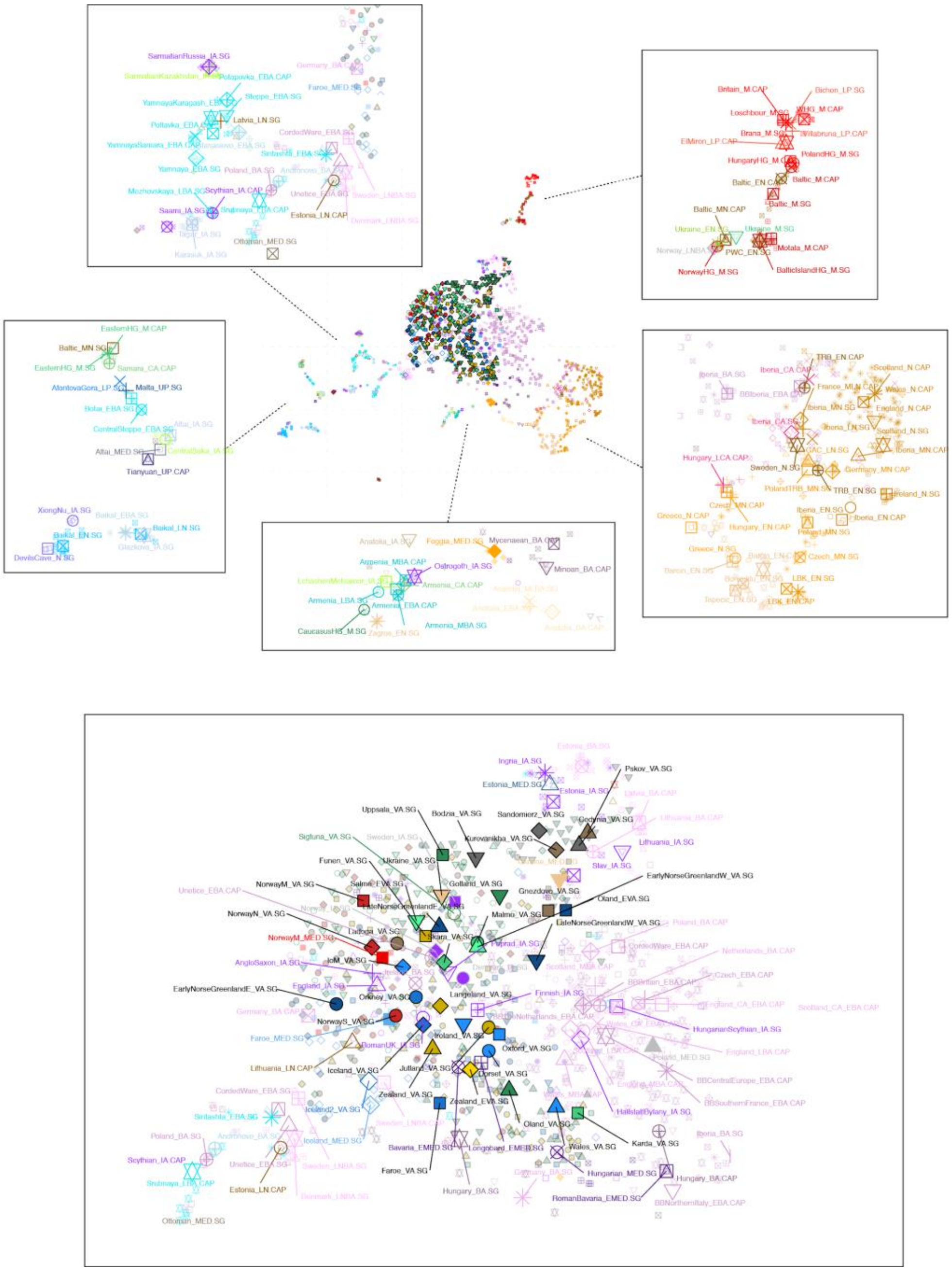
Examples of a few archaeological Viking Age sites and samples used in this study. **a,** Salme II ship burial site of Early Viking Age excavated in present-day Estonia: schematic representation of skeletons (upper left-hand corner image) and aerial images of skeletons (upper right-hand corner and lower images). **b,** Ridgeway Hill mass grave dated to the 10th or 11th century, located on the crest of Ridgeway Hill, near Weymouth, on the South coast of England. Around 50 predominantly young adult male individuals were excavated. **c,** The site of Balladoole: around AD 900, a Viking was buried in an oak ship at Balladoole, Arbory in the south east of the Isle of Man. **d,** Viking Age archaeological site in Varnhem, Sweden: Schematic map of the church foundation (left) and the excavated graves (red markings) at the early Christian cemetery in Varnhem; foundations of the Viking Age stone church in Varnhem (middle) and the remains of a 182 cm long male individual (no. 17) buried in a lime stone coffin close to the church foundations (right).

Extended Data Fig. 2: Model-based clustering analysis

Admixture plot (K=2 to K=5) for 567 ancient individuals spanning 71 different populations. This figure is a subset of most relevant individuals and populations from Figure S7.2, see Supplementary Note 7 for details. This plot consists of 378 ancient samples from this study; VA samples from Sigtuna, Sweden[6] (n=21); Iceland[7] (n=22) and other ancient comparative groups (n=146).

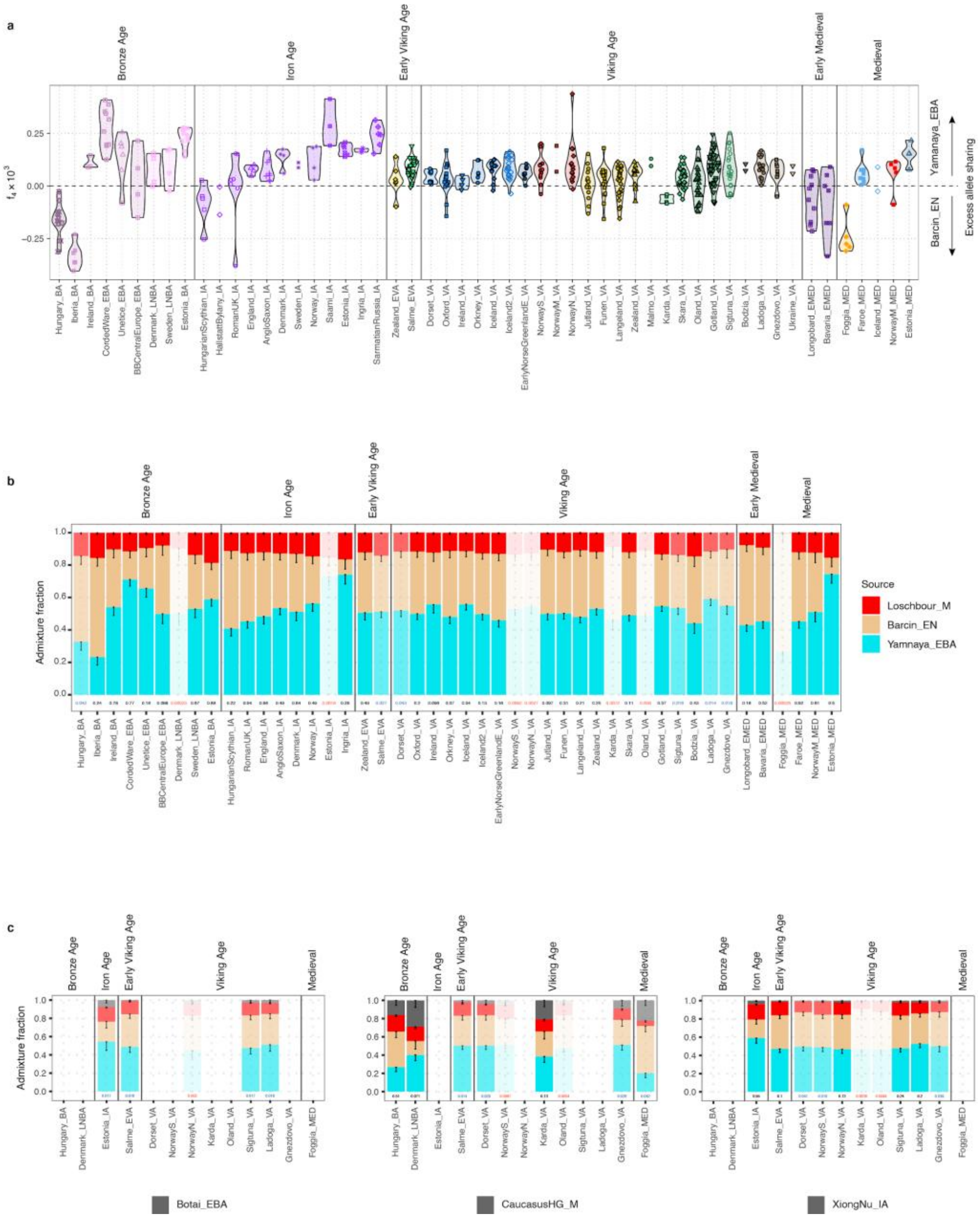


Extended Data Fig. 3: Fine-scale population structure



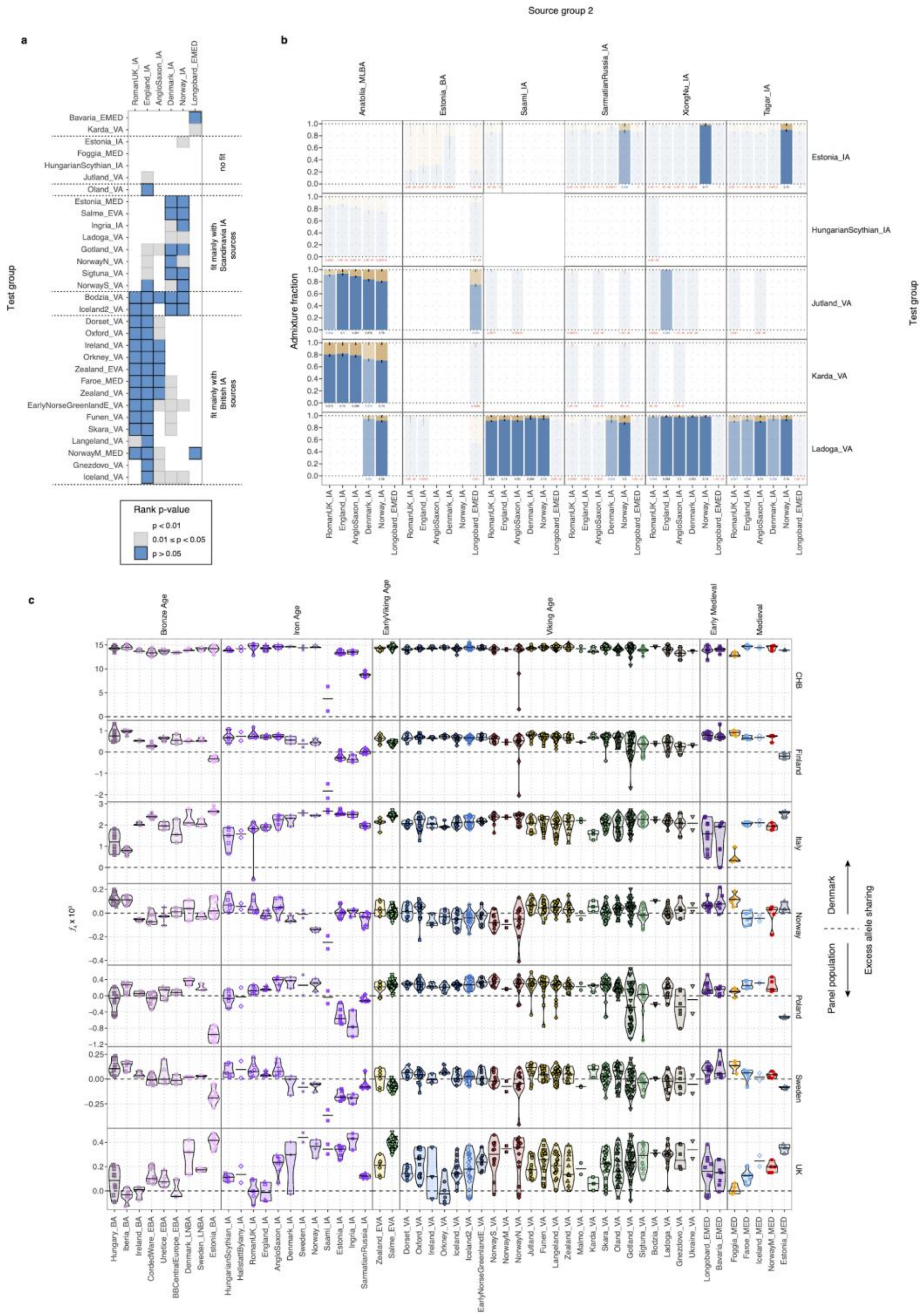
The point cloud at the top center shows an alternative view of the UMAP result from Figure 2b, with all ancient individuals coloured based on analysis group. The framed panels surrounding the point cloud highlight particular ancestry clusters as indicated, with labels and larger symbols corresponding to the median coordinates for the respective group. The larger bottom panel similarly shows median group coordinates for the large central point cloud, which includes the vast majority of European individuals from the Bronze Age onwards.

Extended Data Fig. 4: Ancestry modelling for distal sources



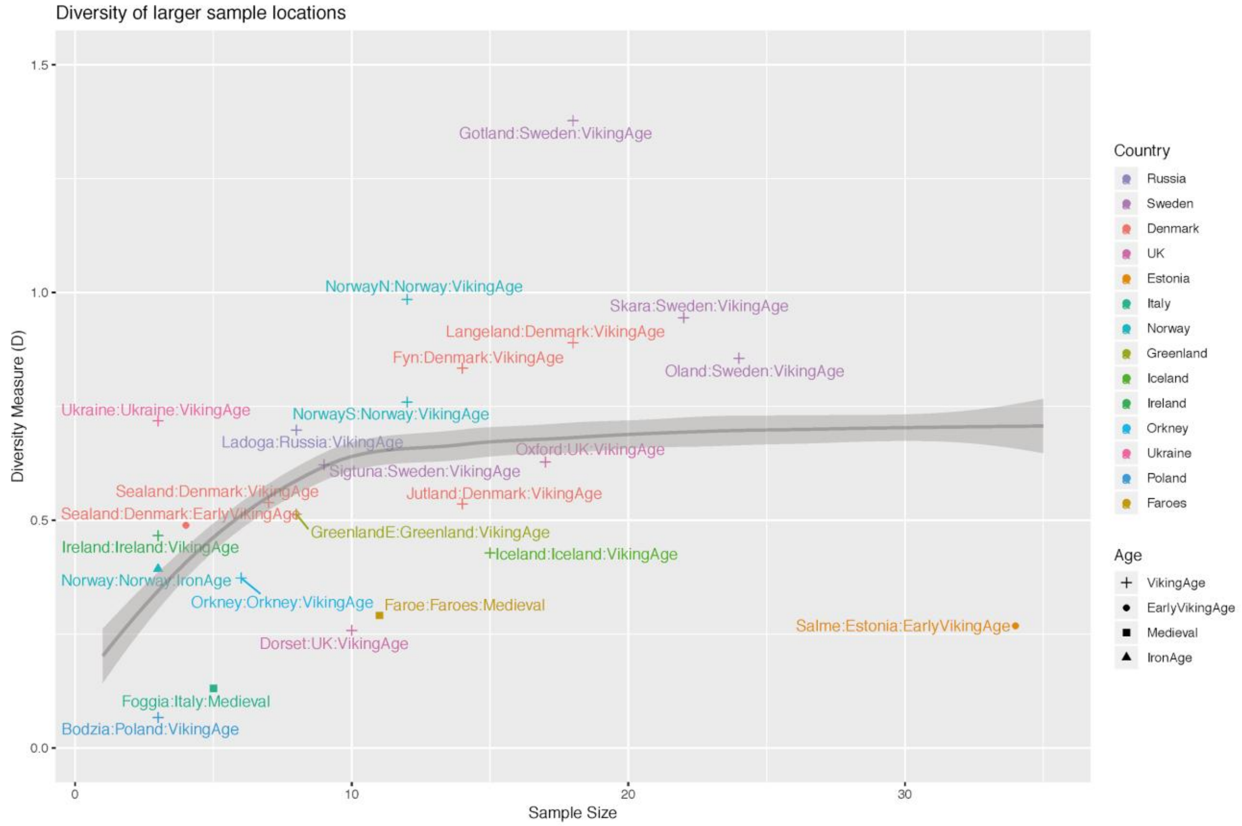
a, Contrasting allele sharing between Anatolian farmers (Barcin_EN) and Steppe pastoralists (Yamnaya_EBA) for European individuals from the Bronze Age and later, using f_4(YRI,test individual;Barcin_EN,Yamnaya_EBA). Only individuals with a minimum of 1,000,000 SNPs with genotypes and groups with at least two such individuals are plotted. **b,** Ancestry proportions of analysis groups from Bronze Age and later inferred using *qpAdm*. Target groups were modelled using three distal sources representing European hunter-gatherer (Loschbour_M), Anatolian farmer (Barcin_EN) and Steppe pastoralist (Yamnaya_EBA) ancestry. **c,** Ancestry proportions of analysis groups for which the three source model was rejected ($p < 0.05$). Target groups were modelled including one additional distal source representing either Steppe hunter-gatherer (Botai_EBA), Caucasus hunter-gatherer (CaucasusHG_M) or East Asian-related (XiongNu_IA) ancestry.

Extended Data Fig. 5: Ancestry modelling for proximate sources



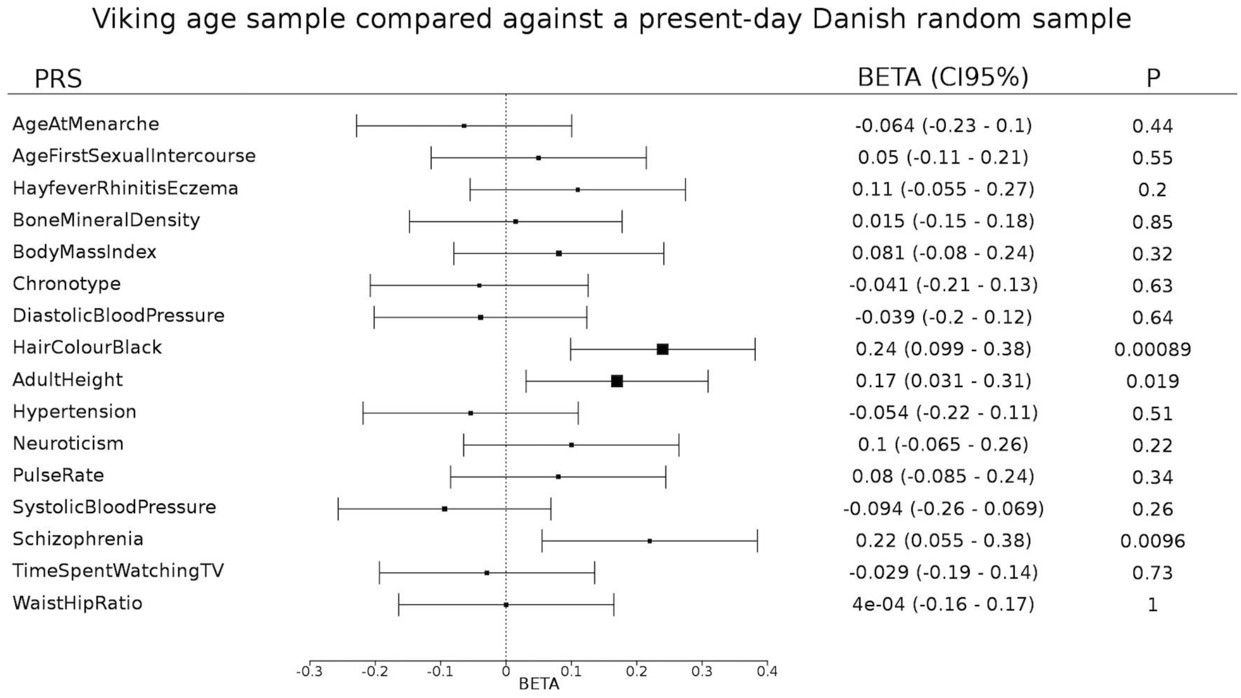
a, Testing for continuity between European Iron Age and later Viking Age and Medieval groups. Couloured squares depict whether a particular target group (row) can be modelled using a single source group (column). P-values for f_4 rank of 0 (corresponding to a single source group) were obtained using *qpAdm* with a set of 15 outgroups which included European Bronze Age groups preceding the source groups. **b,** Two−way admixture ancestry proportions of target groups for which a single source was rejected (p ≤ 0.05). Target groups were modelled using additional proximate Bronze and Iron Age sources. For both **a, b,** only ancient groups containing at least three individuals with a minimum of 1,000,000 SNPs with genotypes are plotted **c,** Contrasting allele sharing between present-day Denmark and other population, using f_4(YRI,test individual;Panel population,Denmark). Only individuals with a minimum of 50,000 SNPs with genotypes and groups with at least two such individuals are plotted. Median values for distributions are indicated with horizontal lines.

Extended Data Fig. 6: Ancestry diversity of different population groups



Diversity of different labels (i.e. sample locations combined with historical age) are shown as a function of their sample size. The Diversity measure is the Kullback-Leibler divergence from the label means, capturing the diversity of a group with respect to the average of that group; see text for details. Larger values are more diverse, though a dependence on sample size is expected. The simulation expectation for the best-fit to the data (0=0.2) is shown.

Extended Data Fig. 7: Polygenic risk scores

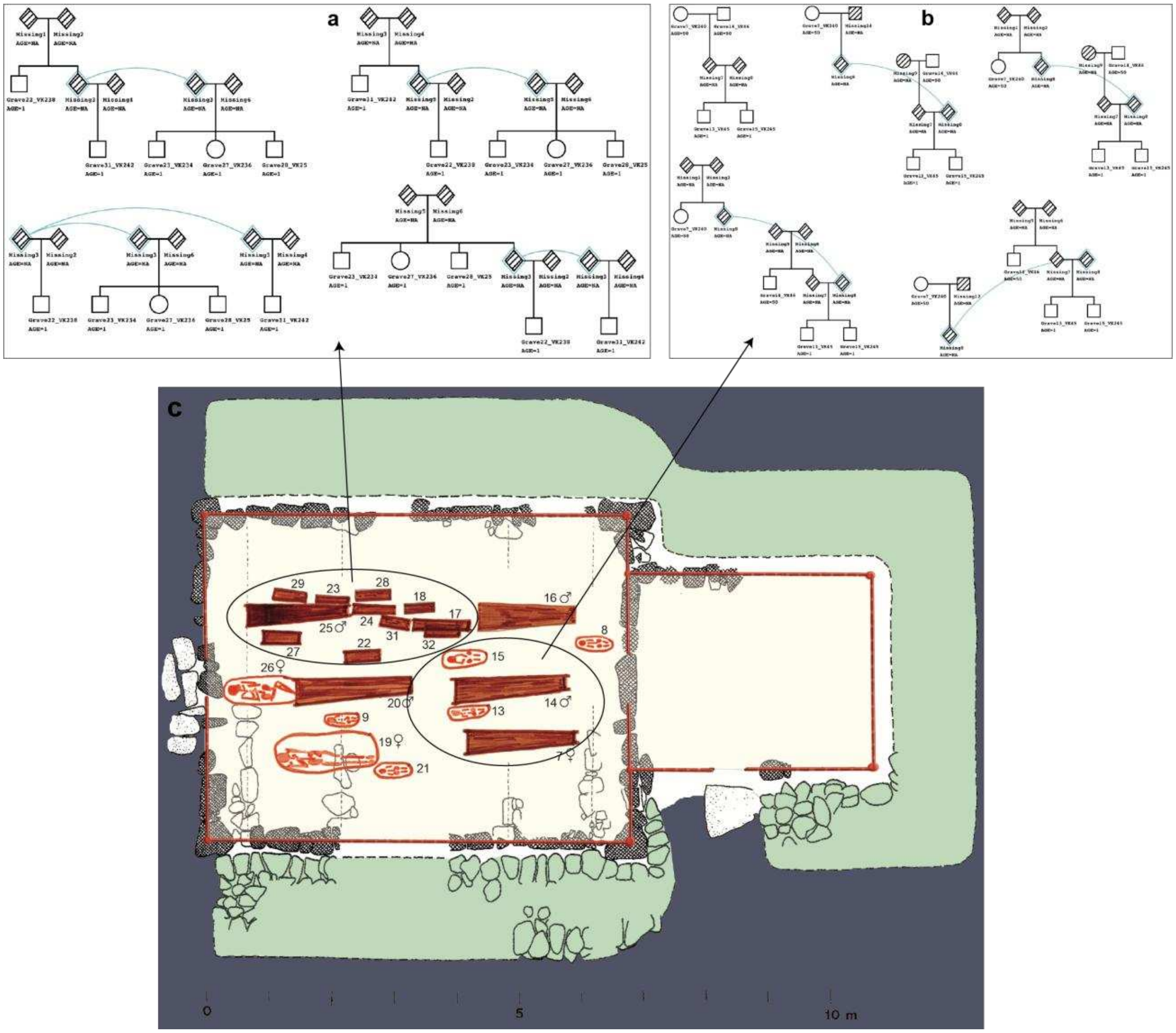


Viking age sample compared against a present-day Danish random sample

PRS	BETA (CI95%)	P
AgeAtMenarche	-0.064 (-0.23 - 0.1)	0.44
AgeFirstSexualIntercourse	0.05 (-0.11 - 0.21)	0.55
HayfeverRhinitisEczema	0.11 (-0.055 - 0.27)	0.2
BoneMineralDensity	0.015 (-0.15 - 0.18)	0.85
BodyMassIndex	0.081 (-0.08 - 0.24)	0.32
Chronotype	-0.041 (-0.21 - 0.13)	0.63
DiastolicBloodPressure	-0.039 (-0.2 - 0.12)	0.64
HairColourBlack	0.24 (0.099 - 0.38)	0.00089
AdultHeight	0.17 (0.031 - 0.31)	0.019
Hypertension	-0.054 (-0.22 - 0.11)	0.51
Neuroticism	0.1 (-0.065 - 0.26)	0.22
PulseRate	0.08 (-0.085 - 0.24)	0.34
SystolicBloodPressure	-0.094 (-0.26 - 0.069)	0.26
Schizophrenia	0.22 (0.055 - 0.38)	0.0096
TimeSpentWatchingTV	-0.029 (-0.19 - 0.14)	0.73
WaistHipRatio	4e-04 (-0.16 - 0.17)	1

Polygenic risk scores (PRS) for 16 complex human traits in Viking Age samples from Denmark, Sweden and Norway compared against a reference sample of >20,000 Danish-ancestry individuals randomly drawn from all individuals born in Denmark in 1981-2011. The PRS is in each case based on allelic effects for >100 independent genome-wide significant SNPs from recent GWAS of the respective traits. Only PRS for black hair colour is significantly different between the groups after taking account of multiple testing, although PRS for height and schizophrenia are considerably elevated as well in the Viking Age samples.

Extended Data Fig. 8: Kinship analysis of ancient samples from Sandoy Church 2 site in Faroe Islands.



a, Reconstruction of four most likely pedigree networks for one (Family-1) of the three families in Sandoy Church 2 site in Faroe Islands. **b,** Five most likely pedigree networks for the Family-2: the most “parsimonious” network (top left) is likely to represent the true family relationship between the individuals (i.e. grandparents and grandsons) based on the burial pattern of the graves as shown at the bottom image (**c**). Ages of the individuals are approximate to help pedigree reconstructions. Blue diamond shapes and lines in each possible pedigree reconstruction represent the same individual.