

# 1 Population genomics of the Viking world

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85

86

87 **Abstract**

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

111

## 112 **Introduction**

113 Three centuries from approximately 750 to 1050 CE mark a pivotal change for the peoples of  
114 Scandinavia. The maritime transformation commonly known as the Viking Age (VA) altered the  
115 political, cultural and demographic map of Europe in ways that are evident even today. The Vikings  
116 established systems of trade and settlement that stretched from the eastern American seaboard to the  
117 Asian steppe<sup>1</sup>. They also exported new ideas, technologies, language, beliefs and practices to these  
118 lands. In the process, they gradually developed new socio-political structures, assimilated cultural  
119 influences, and adopted the Christian faith<sup>2</sup>.

120

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

131 In order to explore the genomic history of the Viking era, we shotgun sequenced 442 ancient human  
132 remains, from the Bronze Age c. 2400 BC to the Medieval Age c. 1600 AD (Fig. 1). The majority of  
133 these individuals (n=376) were sequenced to between 0.1 and 11X average depth of coverage. The  
134 dataset includes Bronze Age (n=2) and Iron Age (n=10) individuals from Scandinavia; Early Viking  
135 Age (n=43) individuals from Estonia (n=34), Denmark (n=6) and Sweden (n=3); ancient individuals  
136 associated with Norse culture from Greenland (n=23), VA individuals from Denmark (n=78), Faroe  
137 Islands (n=1), Iceland (n=17), Ireland (n=4), Norway (n=29), Poland (n=8), Russia (n=33), Sweden  
138 (n=118), UK (n=42), Ukraine (n=3) as well as medieval individuals from Faroe Islands (n=16), Italy  
139 (n=5), Norway (n=7), Poland (n=2) and Ukraine (n=1). The VA individuals were supplemented with  
140 additional published genomes (n=21) from Sigtuna, in Sweden<sup>6</sup>. The skeletons originate from major  
141 archaeological sites of VA Scandinavian settlements and activities from Europe to Greenland  
142 (Supplementary Table 1). The data from the ancient individuals were analyzed together with

143 previously published data from a total of 3,855 present-day individuals across two reference panels,  
144 and data from 922 individuals of ancient origin (Supplementary Note 6).

## 145 146 **Scandinavian genetic ancestry and the beginnings of the Viking era**

147 Although VA Scandinavians shared a common cultural, linguistic and material background, there  
148 was no common word for Scandinavian identity at that time<sup>1</sup>. The word ‘Viking’ is used in  
149 contemporary sources to mean a ‘pirate’ or ‘sea warrior’<sup>2</sup>. As such, there is no single ‘Viking world’,  
150 but a coalescence of ‘Viking worlds’ marked by rapidly growing maritime exploration, trade, war  
151 and colonization, following the adoption of deep-sea navigation among the coastal populations of  
152 Scandinavia and the Baltic Sea area<sup>7,8</sup>. Thus, it is unclear whether the Viking-phenomenon refers to  
153 people with a recently shared genetic background and if foreign influence initiated or accompanied  
154 the transition from the Scandinavian Iron Age into the Viking era.

155 To assess the genetic relationship of the VA Scandinavians with that of earlier European peoples, we  
156 performed genetic clustering using multi-dimensional scaling (MDS) on a pairwise identity-by-state  
157 (IBS) sharing matrix, as well as latent mixed-ancestry models (Admixture)<sup>9</sup>. We find that the majority  
158 of our samples broadly cluster within the range of European Bronze Age (BA) and Iron Age (IA)  
159 populations, characterized by an ancestry component that is related to pastoralist populations from  
160 the Pontic-Caspian steppe (Fig. 2a and Extended Data Fig. 2) entering Europe around 5000 BP<sup>10,11</sup>.  
161 A different dimensionality reduction technique using uniform manifold approximation and projection  
162 (UMAP) revealed additional fine-scale genetic structure. European individuals from the Bronze Age  
163 and onwards are generally distributed within a broad area anchored by four ancestry clusters across  
164 the two UMAP dimensions: Early BA individuals from the Steppe; pre-BA Neolithic Europeans;  
165 Baltic BA individuals; and Scandinavian IA and early VA individuals (Fig. 2b). We observe a wide  
166 range of distributions for VA individuals within this broad area, with notable differences between  
167 geographic regions (Fig. S8.10), indicating complex fine-scale structure among the different groups.  
168 Modelling Scandinavian groups from the BA and onwards as mixtures of three ancestral components  
169 (Mesolithic hunter-gatherers; Anatolian Neolithic; Steppe early BA), again revealed subtle  
170 differences in their composition. We find that the transition from the BA to the IA is accompanied by  
171 a reduction in Neolithic farmer ancestry, with a corresponding increase in both Steppe-like ancestry  
172 and hunter-gatherer ancestry (Extended Data Fig. 6). While most groups show a slight recovery of  
173 farmer ancestry during the VA, there is considerable variation in ancestry across Scandinavia. In  
174 particular, we observe a wide range of ancestry compositions among individuals from Sweden, with

175 some groups in southern Sweden showing some of the highest farmer ancestry proportions (40% or  
176 more in individuals from Malmö, Kärda or Öland). Ancestry proportions in Norway and Denmark on  
177 the other hand appear more uniform (Extended Data Fig. 6). Finally, we detect an influx of low levels  
178 of “eastern” ancestry starting in the early VA, mostly constrained among groups from eastern and  
179 central Sweden as well as some Norwegian groups (Extended Data Fig. 6). Testing of putative source  
180 groups for this “eastern” ancestry revealed differing patterns among the Viking Age target groups,  
181 with contributions of either East Asian- or Caucasus-related ancestry (Supplementary Note 10).  
182 Overall, our findings suggest that the genetic makeup of VA Scandinavia derives from mixtures of  
183 three earlier sources: Mesolithic hunter-gatherers, Neolithic farmers, and Bronze Age pastoralists.  
184 Intriguingly, our results also indicate ongoing gene flow from the south and east into Iron Age  
185 Scandinavia. Thus, these observations are consistent with archaeological claims of wide-ranging  
186 demographic turmoil in the aftermath of the Roman Empire with consequences for the Scandinavian  
187 populations during the late Iron Age<sup>12,13</sup>. We caution, however, that our sampling for the periods  
188 preceding the VA is still sparse, and hence do not provide a full picture of the genetic diversity across  
189 Scandinavia during that period.

190

### 191 **Genetic structure within Viking-Age Scandinavia**

192 By the end of the Iron Age in the 8<sup>th</sup> century CE, Scandinavia formed a patchwork of conflicting and  
193 competing kingdoms with a shared cultural background. For centuries, a political economy based on  
194 raiding, trading and gifts had been common<sup>5</sup>. However, the cause for the development of this  
195 economic and political system into the more organized maritime society of the Viking era remains  
196 debated<sup>5</sup>. It is commonly argued that seafaring<sup>8,14</sup> contributed to create a densely interlinked  
197 Scandinavia during the Viking era<sup>2,15,16</sup>.

198 To disentangle the fine-scale population structure within VA Scandinavia, we performed genotype  
199 imputation on a subset of 300 individuals with sufficient coverage (>0.5X) and inferred genomic  
200 segments shared via identity-by-descent (IBD) within the context of a reference panel of 1,464  
201 present-day Europeans, using IBDseq. We find that VA Scandinavians on average cluster into three  
202 groups according to their geographic origin, shifted towards their respective present-day counterparts  
203 in Denmark, Sweden and Norway (Fig. 3a). Closer inspection of the distributions for the different  
204 groups reveals additional complexity in their genetic structure (Fig. S10.1). We find that the  
205 ‘Norwegian’ cluster includes Norwegian IA individuals, who are distinct from both Swedish and  
206 Danish IA individuals which cluster together with the majority of central and eastern Swedish VA

207 individuals. Many individuals from southwestern Sweden (e.g. Skara) cluster with Danish present-  
208 day individuals from the eastern islands (Funen, Zealand), skewing towards the ‘Swedish’ cluster  
209 with respect to early and more western Danish VA individuals (Jutland). Some individuals have  
210 strong affinity with Eastern Europeans, particularly those from the island of Gotland in eastern  
211 Sweden. The latter likely reflects individuals with Baltic ancestry, as clustering with Baltic BA  
212 individuals is evident in the IBS-UMAP analysis (Fig. 2b) and through  $f_4$ -statistics (Extended Data  
213 Fig. 4).

214 To further quantify the within-Scandinavia population structure, we used ChromoPainter<sup>17</sup> to identify  
215 long, shared haplotypes among sequenced individuals using a reference panel enriched with  
216 Scandinavian populations (n=1,675 individuals, see Supplementary Notes 6 and 11). Our approach  
217 detects subtle population structure present during the VA in Scandinavia. Supplementary Figures  
218 S11.1-10 and Supplementary Note 11 describe the supervised method that we used to obtain power  
219 to robustly identify local ancestry variation in the presence of sequencing rate variation. We find at  
220 least four major ancestry components in Scandinavia, each with affinities with a present-day  
221 population (Fig. S11.11): a Danish-like, a Swedish-like, a Norwegian-like and a British-like  
222 component. Henceforth, we call this latter component ‘North Atlantic’, and we suspect it may reflect  
223 originally Celtic individuals that occupied the British Isles and were brought into Scandinavia. We  
224 refer to the first three ancestries as ‘Danish-like’, ‘Swedish-like’ and ‘Norwegian-like’, though we  
225 emphasize that the correspondence between these ancestries and present-day inhabitants of the  
226 respective Scandinavian countries is by no means exact or exclusive. During the VA, we mostly find  
227 high levels of Norwegian-like and Swedish-like components in Norway and Sweden, respectively,  
228 while Danish-like and ‘North Atlantic’ components are more widespread within Scandinavia (Fig.  
229 S11.12 and Supplementary Table 6). Notably, the ‘Swedish-like’ component is higher in Salme,  
230 Estonia, than in Sweden, because our sampling scheme included several individuals from the famous  
231 Salme Viking ship burial, of which archaeological and isotopic data suggest a Scandinavian  
232 origin<sup>18,19</sup>. While in general individuals from most of the Scandinavian VA settlements show mixed  
233 (Danish, Norwegian and Swedish) genetic ancestries, VA individuals from Jutland (Denmark) do not  
234 have significant Swedish-like or Norwegian-like genetic components. Furthermore, gene flow within  
235 Scandinavia appears to be broadly northwards, dominated by Danish Vikings moving into what are  
236 now Norway and Sweden (Table S11.2; see Supplementary Note 11).

237 Although the majority of the Viking genomes within Scandinavia and abroad show affinities to  
238 Danish, Norwegian, Swedish or British populations, there are some notable exceptions. We identified

239 two ancient individuals (VK518 and VK519) originating from northern regions of Norway  
240 (Nordland), which have affinities to present-day Saami. This signal is weaker for VK519, indicating  
241 that he might have also had Norwegian-like ancestors. Given the geographic provenance of these  
242 samples, it was not unexpected to find individuals with Saami-like ancestry among the VA samples.  
243 However, as VK519 is indeed an admixed individual with both Norwegian-like and Saami-like  
244 ancestries, it appears that genetic contacts between these groups were already underway in VA  
245 Norway.

246 Importantly, present-day country boundaries are not always well reflected in the genetic data. Thus,  
247 the south-western part of Sweden in the VA is genetically more similar to Danish VA populations  
248 than the eastern regions of mainland Sweden (i.e. the area around the Mälaren Valley), likely due to  
249 geographic barriers that prevented gene flow in Sweden.

250 We quantified genetic diversity in our samples using two measures: conditional nucleotide diversity  
251 (Supplementary Note 9) and variation in inferred ancestry (Supplementary Note 11; Extended Data  
252 Fig. 5 and Fig. S11.13). We find overall high nucleotide diversity among most Viking-Age groups,  
253 with diversity values exceeding those of earlier Neolithic or BA groups, and only slightly lower than  
254 the highly diverse IA individuals from the British Isles (Fig. S9.1). Both measures of diversity vary  
255 significantly across locations. Denmark and Gotland in Sweden have the highest genetic diversity in  
256 the region, suggesting that these regions may have been centers of interaction and trade during this  
257 time. They also possess high diversity in inferred ancestries. North Norway also has high diversity in  
258 inferred ancestry due to its mixture of ‘North Atlantic’ and ‘Norwegian-like’ ancestry.

259 Interestingly, on Gotland, there are much more Danish-like, British-like and Finnish-like genetic  
260 components than Swedish-like components, supporting the notion that the island may have been  
261 marked by extensive maritime contacts during the VA. Our two Gotland sampling sites, Fröjel and  
262 Kopparsvik, have traditionally been argued to contain non-local individuals<sup>20</sup>, but recent Sr-isotope  
263 analyses have suggested otherwise<sup>21,22</sup>.

264 On Öland in Sweden, we observe high genetic diversity and the most variable patterns of recent  
265 ancestry (Extended Data Fig. 5) in Scandinavia. Sr and O isotope variation in these samples, and  
266 more contemporary samples from Öland have concluded that there is: (i) a high proportion (68%) of  
267 non-locals, (ii) high diversity in geographical origins and (iii) long distance migration<sup>23</sup>. Thus, the  
268 genetic diversity observed for Öland in the VA fits well with all of these results.

269 In conclusion, the results for Gotland and Öland agree with the archaeological record, suggesting that  
270 Öland and Gotland were important trading posts from the Roman period onwards<sup>24,25</sup>. A similar



271 pattern is observed at a few archaeological sites from the central Danish islands, such as Langeland,  
272 although at a lower scale. Interestingly, genetic diversity here increases from the early to the late VA,  
273 suggesting increasing interregional interaction.

274 Our findings do not agree with the view of an overall highly connected population in Viking  
275 Scandinavia<sup>2,8,14-16</sup>. Rather, we find clear genetic population structure within Scandinavia. We see  
276 evidence of a few cosmopolitan centers to the south, in southern Sweden and Denmark, where we see  
277 higher diversity of ancestries than in the rest of Scandinavia. These patterns are consistent with a  
278 restricted number of sea routes between the different Scandinavian areas and beyond.

279

### 280 **Viking migrations**

281 Viking society is particularly famous for its ship technology, allowing for fast transport of large  
282 numbers of individuals in a single vessel<sup>26</sup>. These vessels enabled the Vikings not only to carry out  
283 lucrative raids and extended trade routes across Western Eurasia, but also to reach and settle lands in  
284 the North Atlantic<sup>27-30</sup>. Based on historical and archaeological data, Viking presence extended into  
285 both western and eastern Europe, reaching perhaps as far as the Pontic Steppe and the Middle  
286 East<sup>31,32</sup>. It is commonly believed that the westward migrations and raids were mainly carried out by  
287 people from what are now Norway and Denmark in the 9<sup>th</sup> and 10<sup>th</sup> centuries CE. In contrast to  
288 western movements, eastward expansions are commonly believed to have been carried out by  
289 Swedish Vikings, trading along navigable river systems and overland caravan routes<sup>32</sup>. Swedish  
290 Vikings (the ‘Rus’) are also credited for being active in the formation of the first Russian state<sup>33,34</sup>.  
291 Overall, our fine-scale ancestry analysis based on genomic data largely support the Viking expansion  
292 patterns inferred from archaeology (Figs. 3, 4 and S11.12). The eastward movements mainly involved  
293 individuals with Swedish-like ancestry, while the Viking individuals with Norwegian-like ancestry  
294 travelled to Iceland, Greenland, Ireland and the Isle of Man. A Danish-like ancestry component is  
295 more pronounced in present-day England, which is also in accordance with historical records<sup>35</sup> and  
296 still visible in place-names<sup>34</sup>, and modern genetics<sup>36,37</sup>. Importantly, however, it is currently  
297 impossible for us to distinguish Danish-like ancestry in the British Isles from that of the Angles and  
298 Saxons, who migrated in the 5<sup>th</sup>-to-6<sup>th</sup> centuries CE from Jutland and Northern Germany.

299 Interestingly, the ancient individuals from two execution sites in England (Dorset and Oxford) have  
300 significant local ‘North Atlantic’ ancestry, as well as Danish-like and Norwegian-like ancestries. If  
301 these represent Viking raiding parties coming to grief, as has been suggested<sup>38,39</sup>, this implies such  
302 forces were composed of individuals from different places of origin. This pattern is also suggested

303 by isotopic data from the warrior cemetery in Trelleborg, Denmark<sup>40</sup>. Similarly, the presence of  
304 Danish-like ancestry in an ancient sample from Gnezdovo (Eastern Europe) indicates that the eastern  
305 migrations were not entirely composed of Vikings from Sweden.  
306 However, in some cases, localities seem to have taken up Viking culture while incorporating little to  
307 no Scandinavian ancestry components, suggesting that the “Viking” identity was not always  
308 necessarily associated with Scandinavian genetic ancestry. Archaeological evidence indicates that the  
309 six higher coverage VA individuals from three different archaeological sites in the Orkney Islands  
310 have Scandinavian cultural links<sup>41,42</sup>. However, four (VK201, VK202, VK203 and VK207) of these  
311 samples have over 85% “UK” ancestry and are genetically similar to present-day Irish and Scottish  
312 populations (Figs 3a and S10.1, Supplementary Table 6), which is in contrast to the isotopic  
313 evidence<sup>43</sup>. Haplotype-based analyses corroborate that four of these samples possessed local genetic  
314 ancestries, with little Scandinavian contribution. Only two individuals - VK204 and VK205  
315 - displayed c. 50% Norwegian and Danish ancestries (Supplementary Table 6), respectively, which  
316 may indicate admixture between the locals and Scandinavians on the Orkney Islands during the VA.  
317 The four ancient genomes of Orkney individuals with little Scandinavian ancestry may be the first  
318 ones of Pictish people published to date (Supplementary Note 12). Yet a similar (>80% “UK”  
319 ancestry) individual was found in Ireland (VK545) and five in Scandinavia, implying that Pictish  
320 populations were integrated into Scandinavian culture by the Viking Age.

321

### 322 **Gene flow into Scandinavia during the Viking era**

323 Archaeological findings and the written sources support the hypothesis that Viking back migrations  
324 and interaction between the newly settled areas and Scandinavia occurred as part of the process<sup>44</sup>.  
325 Presumably, if these migrations took place, native ancestry from these areas must have also been  
326 introduced into Scandinavia. We therefore aimed to assess the levels of non-Scandinavian ancestry  
327 emerging in Scandinavia during the VA.

328 Using fineStructure<sup>17</sup>, we find that the levels of non-Scandinavian ancestry in the Danish, Norwegian  
329 and Swedish Vikings agree with known trading routes (Supplementary Notes 11 and 12). The most  
330 obvious genetic signals are from Finnish and Baltic sources into the area of what is now modern  
331 Sweden, including Gotland. These ancestries are present at considerably lower levels or are  
332 completely absent in most individuals from Denmark and Norway. A substantial interaction across  
333 the Baltic Sea is also suggested by objects from Finland found in graves in Middle Sweden, albeit  
334 recent Sr-isotope analyses are inconclusive regarding the origin of the buried individuals<sup>45,46</sup>. In

335 comparison, western regions of Scandinavia have much higher levels of ancestry from the British  
336 Isles, in comparison with the eastern regions of Sweden (Supplementary Notes 11 and 12). We also  
337 observe several individuals (Supplementary Table 6) with large amounts of South European ancestry  
338 in Denmark and southwest Sweden during the Viking period (Fig. 4). No such individuals are found  
339 among our Scandinavian Iron Age samples, though we stress that our sampling for this period is more  
340 limited than for the other two. The discovery of individuals with ancestry from Southern Europe and  
341 the British Isles is the first direct evidence for movement into Scandinavia from these regions. The  
342 directions of interaction marked by these individuals is consistent with the major directions of gene  
343 flows outwards from Scandinavia also seen in the data.

344 Surprisingly, three individuals from the Kärda site show much higher genetic similarity to Late  
345 Neolithic/Early Bronze Age Danish individuals than to all other VA individuals in the dataset. The  
346 site is located far inland, in south-west Sweden. This similarity is quite unexpected, given that the  
347 samples are AMS-dated to the middle of the VA, and consistent with the presence of Caucasus-related  
348 ancestry inferred in the qpAdm ancestry modelling. Studies of VA burial customs suggest that the  
349 Småland area was characterized by locally confined cultural groups<sup>47</sup>. The genetic data suggest that  
350 this pattern of cultural isolation was sustained in marked contrast to contemporary coastal and island  
351 communities. Consistent with this hypothesis we find that the individuals from Kärda show a marked  
352 reduction in nucleotide diversity compared to other VA groups (Fig. S9.1), although they also have  
353 high amounts of Southern European ancestry.

354

### 355 **Disappearance of the Greenlandic Norse**

356 From around 980 to 1440 CE South-west Greenland was settled by peoples of Scandinavian (Norse)  
357 descent. They likely originated from Icelandic Vikings who established a colony there at the end of  
358 the 9<sup>th</sup> century CE<sup>29,48</sup>. It is believed that the Norse also reached Labrador, North America, from  
359 Greenland around 1000, although no permanent settlement was established<sup>30</sup>. The fate of the Norse  
360 in Greenland remains debated, but probable causes of their disappearance are social or economic  
361 processes in Europe (e.g. political relations within Scandinavia and changed trading systems) and  
362 natural processes, like climatic changes<sup>29,49,50</sup>.

363 We see no evidence of long-term inbreeding in the Greenlandic Norse genomes, though we note that  
364 we only have one high-coverage genome from the later period of occupation of Greenland  
365 (Supplementary Note 10; Figs. S10.2 and S10.3). This suggests a depopulation scenario over  
366 approximately 100 years which would be in line with previous demographic models<sup>51</sup>, as well as the

367 archaeology. Indeed, the latter indicates that marginal farms in the Western Settlement and the  
368 northern and southern parts of the Eastern Settlement were abandoned from about 1200 CE, with no  
369 converse intensification of settlement in the central areas.

370 We also find no evidence of ancestry from local populations from the Western Atlantic (Paleo  
371 Eskimo, Inuit or Native American) in the Norse genomes. This is in accordance with previous  
372 physical anthropological studies of the skeletal remains<sup>51</sup>. This suggests that either sexual interactions  
373 did not take place or that, if they did, then on a very small and incidental scale with the children  
374 remaining in the native communities. In terms of genetic ancestry of the Greenlandic Norse, we find  
375 evidence of admixture between Scandinavians (mostly from Norway) and individuals from the British  
376 Isles, similar to the first settlers of Iceland<sup>52</sup>, which supports the archaeological and historical links  
377 between the Greenlandic Norse and the Icelandic Vikings.

378

### 379 **Genetic composition of the earliest Viking expedition and kinship findings**

380 Maritime raiding has been a constant of seafaring cultures for millennia. However, the VA is unusual  
381 in that it is partly defined by such activity<sup>53</sup>. Despite the historical importance of Viking raiding, the  
382 exact nature and composition of these war parties is unknown<sup>5</sup>. Only one Viking raiding or diplomatic  
383 expedition has left direct archaeological traces, at Salme in Estonia, where 41 Swedish Vikings who  
384 died violently were buried in two boats accompanied by high-status weaponry<sup>18,19</sup>. Importantly, the  
385 Salme boat-burial predates the first textually documented raid (in Lindisfarne in 793) by nearly half  
386 a century.

387 Comparing the genomes of 34 individuals from the Salme burial using kinship analyses, we find that  
388 these elite warriors included four brothers buried side by side and a 3rd degree relative of one of the  
389 four brothers (Supplementary Note 4). In addition, members of the Salme group had very similar  
390 ancestry profiles, in comparison to the profiles of other Viking burials (Supplementary Notes 10 and  
391 11). This suggests that this raid was conducted by genetically homogeneous people of high status,  
392 including close kin. Isotope analyses indicate that the crew descended from the Mälaren area in  
393 Eastern Sweden<sup>19</sup> thus confirming that the Baltic-Mid-Swedish interaction took place early in the  
394 VA.

395 Intriguingly, we identified several additional pairs of kin among the other Viking genomes. One is a  
396 pair of 2<sup>nd</sup> degree male relatives (i.e. half-brothers, nephew-uncle or grandson-grandfather) from two  
397 locations separated by the North Sea: one of the samples (VK279) was excavated in Denmark  
398 (Galgedil site on Funen; this cemetery was also analyzed for strontium with a group of non-locals

399 there) while the other individual (VK144) was found in the UK (Oxford site). Another pair of  
400 individuals with 3<sup>rd</sup> or 4<sup>th</sup> degree relatedness (e.g. cousins) was discovered in Sweden, namely a male  
401 sample excavated on the island of Öland (VK342) and a female individual from Skämsta, Uppsala  
402 (VK527), some 300-400 kilometers apart. Interestingly, the female from Uppsala (VK527) also had  
403 a brother (VK517), and both siblings display a rare genetic disorder of abnormal skeletal  
404 development: spondyloepiphyseal dysplasia. Given the very low frequency of this disorder, the close  
405 family ties between these individuals were expected by the archaeologists<sup>22</sup>. Such long-distance  
406 relationships in our dataset underscore the degree of individual-level mobility during the Viking era.  
407

### 408 **Positive selection in Europe in the last 10,000 years**

409 The availability of hundreds of genomes from the IA and VA - in combination with previously  
410 published Mesolithic, Neolithic and Bronze Age genomes<sup>10,11,54,55</sup> - permit us to directly investigate  
411 the role of positive selection using time series of allele frequencies from the last ten millennia of  
412 European history. We looked for SNPs whose allele frequencies changed significantly in the last  
413 10,000 years, using a newly developed method called “neoscan” that is implemented in the Ohana  
414 software package<sup>56,57</sup>, and that can detect strong allele frequency shifts in time that cannot be  
415 explained by temporal changes in genome-wide genetic ancestry alone (Supplementary Note 14).  
416 Figure 5a shows the resulting likelihood ratio scores in favor of selection looking at the entire 10,000-  
417 year period (top, “general” scan), the period up to 4,000 BP (middle, “ancient” scan) and the period  
418 from 4,000 BP up to the present (bottom, “recent” scan). The strongest candidate for selection -  
419 especially in the “recent” scan - is a cluster of SNPs near the LCT gene - a signal that has been  
420 extensively characterized in the past<sup>58,59</sup>. The rise in frequency of the lactase persistence allele to its  
421 present-day levels in Northern Europe is, however, poorly understood. We know that this rise must  
422 have occurred after the Bronze Age, a time at which this allele was still segregating at low  
423 frequencies<sup>10,54</sup>. Based on the archaeological record, we also know that VA Scandinavians used a  
424 variety of dairy products as an essential part of their daily food intake. Our dataset allows us, for the  
425 first time, to directly assess the frequency of the lactase persistence allele (at SNP rs4988235,  
426 upstream of the LCT gene) in Scandinavia during the Iron Age and VA, and trace its evolution since  
427 the Bronze Age.

428 Figure 5b shows that VA groups had very similar allele frequencies at the LCT lactase persistence  
429 SNP to those found in present-day northern European populations. In contrast, the persistence allele  
430 was at low frequencies in Bronze Age Scandinavians, as well as Corded Ware and Bell Beaker

431 cultures from central Europe, even though there is evidence for milk consumption in these regions by  
432 that time. The allele frequency in Iron Age samples is at intermediate levels (c. 37.5%), suggesting  
433 this rise in frequency must indeed have occurred during the Iron Age (c. 1500-2500 years ago), but  
434 was largely complete at the onset of the VA. Interestingly, the allele frequency of the allele is much  
435 higher (c. 40%) in the Bronze Age population from the neighboring Baltic Sea region than in Bronze  
436 Age Scandinavia. Given the geographic and cultural proximities between Scandinavia and the Baltic  
437 region, this may suggest gene flow between the two regions resulting in increased frequency of lactase  
438 persistence in Scandinavia during the Iron Age.

439 Other candidates for selection include previously identified regions like the TLR1/TLR6/TLR10  
440 region, the HLA region, SLC45A2 and SLC22A4<sup>54</sup>. We also find several new candidate regions for  
441 selection in the “ancient” scan, some of which contain SNPs where the selected allele rose in  
442 frequency early in the Holocene but then decreased later on (Supplementary Note 14). These  
443 candidate regions include a region overlapping the DCC gene, which has been implicated in  
444 colorectal cancer<sup>60</sup> and another overlapping the AKNA gene, which is involved in the secondary  
445 immune response by regulating CD40 and its ligand<sup>61</sup>. This highlights the utility of using ancient  
446 DNA to detect signatures of selection that may have been erased by recent selective dynamics.

447

#### 448 **Pigmentation-associated SNPs**

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

459

#### 460 **Evolution of complex traits in Scandinavia**

461 To search for signals of recent population differentiation of complex traits, we compared genotypes  
462 of Viking age samples with those of a present-day Scandinavian population for a range of trait-

463 associated SNP markers. We selected 16 traits for which summary statistics from well-powered  
464 genome-wide association studies (GWAS) were available through the GWAS ATLAS  
465 (<https://atlas.ctglab.nl>)<sup>62</sup>. For comparison with the Viking age samples we used a random population  
466 subset of the IPSYCH case-cohort study of individuals born in Denmark between 1981-2011<sup>63</sup>. We  
467 derived polygenic risk scores (PRS) for the 16 traits, based on independent genome-wide significant  
468 allelic effects and tested for a difference in the distribution of polygenic scores between the two  
469 groups, correcting for sex and ancestry-sensitive principal components (Supplementary note S15).  
470 We observed a significant difference between the polygenic scores of VA samples and current Danish  
471 population samples for three traits; black hair color ( $P = 0.00089$ ), standing height ( $P = 0.019$ ) and  
472 schizophrenia ( $P = 0.0096$ ) (Extended Data Fig. 5). For all three traits, the polygenic score was higher  
473 in the VA group than in the present-day Danish group. The observed difference in PRS for height and  
474 schizophrenia between the groups did however not remain significant after taking into account the  
475 number of tests. A binomial test of the number of black hair color risk alleles found in higher  
476 frequency in the VA sample and the present-day sample, also returned a significant difference (65/41;  
477  $P = 0.025$ ), which suggests that the signal is not entirely driven by a few large-effect loci.  
478 Thus, we only find evidence for systematic changes in combined frequencies of alleles affecting hair  
479 color (and possibly also height and schizophrenia), among all the anthropometric traits and complex  
480 disorders we tested. Also, we cannot conclude whether the observed difference in allele frequencies  
481 are due to selection acting on these alleles between the Viking Age and the present time or to some  
482 other factors (such as more ethnic diversity in the VA sample), nor can we conclude whether a similar  
483 change has occurred in other Nordic populations than the Danish.

484

### 485 **Genetic legacy of the Vikings in present-day populations**

486 To test whether present-day Scandinavians share increased ancestry with their respective ancient  
487 Viking counterparts, we first inferred D-statistics of the form  $D(\text{YRI, ancient; present-day } X, \text{ present-}$   
488  $\text{day DK})$ , which contrast allele sharing of a test ancient individual with a present-day test population  
489  $X$  and present-day Danes. We find subtle but noticeable shifts of ancient individuals towards their  
490 present-day counterparts in the distributions of these statistics (Extended Data Fig. 3). We further  
491 examined variation in present-day populations using fineSTRUCTURE, and then described these  
492 present-day groups by their ancestry from ancient populations (Fig. S11.14).  
493 We find that within Scandinavia, present-day populations are still structured according to the ancient  
494 Viking population groups. The component that we associated as Norwegian-like is present at 45-65%

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

499 Outside of Scandinavia, the genetic legacy of the Vikings is consistent, though limited. A small  
500 component is present in Poland (up to 5%) and the south of Europe. Within the British Isles, it is  
501 difficult to assess how much of the Danish-like ancestry is due to pre-existing Anglo-Saxon ancestry;  
502 however, the Norwegian-like ancestry is consistently around 4%. The Danish-like contribution is  
503 likely to be similar in magnitude and is certainly not larger than 16% as found in Scotland and Ireland.  
504 The lack of strong variation in ancestry from Scandinavia makes sense if the Vikings did not maintain  
505 a diaspora identity over time but instead integrated into the respective societies in which they settled.  
506 The genetic impacts are stronger in the other direction. The ‘British-like’ populations of Orkney  
507 became ‘Scandinavian’ culturally, whilst other British populations found themselves in Iceland and  
508 Norway, and beyond. Present-day Norwegians vary between 12 and 25% in their ‘British-like’  
509 ancestry, whilst it is still (a more uniform) 10% in Sweden. Separating the VA signals from more  
510 recent population movements is difficult, but these numbers are consistent with our VA estimates.

511

## 512 **Discussion**

513 Until now, our main understanding of the VA was largely based on a combination of historical sources  
514 and archaeological evidence. These often characterize the VA as a period of high mobility and  
515 interaction between peoples. Networks of trade were established, connecting distant regions within  
516 Scandinavia through established waterways with significant movement between regions. It has also  
517 been viewed as a time where links were created to regions outside Europe, from the Pontic Steppe in  
518 the east to North America in the west.

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



527 Our observations also suggest that the different parts of Scandinavia were not as evenly connected,  
528 as has often been assumed. Despite relatively fast and easy communication between the coastal  
529 regions of Denmark, Norway, and Sweden, we find that clear genetic structure was present in Viking-  
530 Age Scandinavia. In fact, our data indicate that Viking Scandinavia consisted of a limited number of  
531 transport zones and maritime enclaves<sup>64</sup> where contact was made with Europe, while the remaining  
532 regions had limited external gene flow with the rest of the Scandinavian continent. Some Viking-Age  
533 Scandinavian locations are relatively homogeneous both in terms of genetic diversity and patterns of  
534 ancestry; particularly mid-Norway, Jutland, and the Atlantic settlements, which contain  
535 predominantly Norwegian-like and ‘North Atlantic’ (including pre-Anglo Saxon British) ancestry.  
536 Indeed, one of the clearest vectors of contrast observed in this study is between the strong genetic  
537 variation seen in relatively populous coastal trading communities such as in the islands Gotland and  
538 Öland, and the reduced diversity in less populated (mostly inland) areas in Scandinavia. Such high  
539 genetic heterogeneity, which was likely due to increased population size, extends the urbanization  
540 model of Late Viking Age city of Sigtuna proposed by Krzewińska et al.<sup>6</sup> both spatially and further  
541 back in time.

542 Interestingly, our findings correspond with paleodemographic studies based on place-name evidence  
543 and archaeological distributions suggesting population density was higher in Denmark than elsewhere  
544 in Viking-Age Scandinavia<sup>65</sup>. Gene flow from Denmark to the north is also paralleled by the linguistic  
545 affinities of the medieval Scandinavian languages: The 12th-century Icelandic law text Grágás states  
546 that the common language of Swedes, Norwegians, Icelanders, and Danes was *dönsk tunga* (‘Danish  
547 tongue’)<sup>66</sup>. It appears that the formation of large-scale trading and cultural networks that spread  
548 people, goods and warfare took time to affect the heartlands of Scandinavia, which received much  
549 more restricted gene flow, retaining pre-existing genetic differences between Scandinavian  
550 populations. This pattern of behavior seems to prevail from the beginning of the Viking diaspora to  
551 its end at the beginning of the medieval period.

552 Our findings also show that Vikings are not simply a direct continuation of the Scandinavian Iron  
553 Age groups. Rather than simple continuity, we observe foreign gene flow from the south and east  
554 into Scandinavia, starting in the Iron Age, and continuing throughout the duration of the Viking  
555 period from an increasing number of sources. Our findings also contradict the myth of the Vikings as  
556 peoples of pure local Scandinavian ancestry. In fact, we found many Viking Age individuals with  
557 high levels of foreign ancestry, both within and outside Scandinavia, suggesting ongoing gene flow  
558 with different peoples across Europe. Indeed, it appears that some foreign peoples contributed more

559 genetic ancestry to Scandinavia during this period than the Vikings contributed to them which could  
560 partially be due to smaller effective population size of the VA Scandinavians as opposed to their  
561 continental and British neighbors.

562

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582

583

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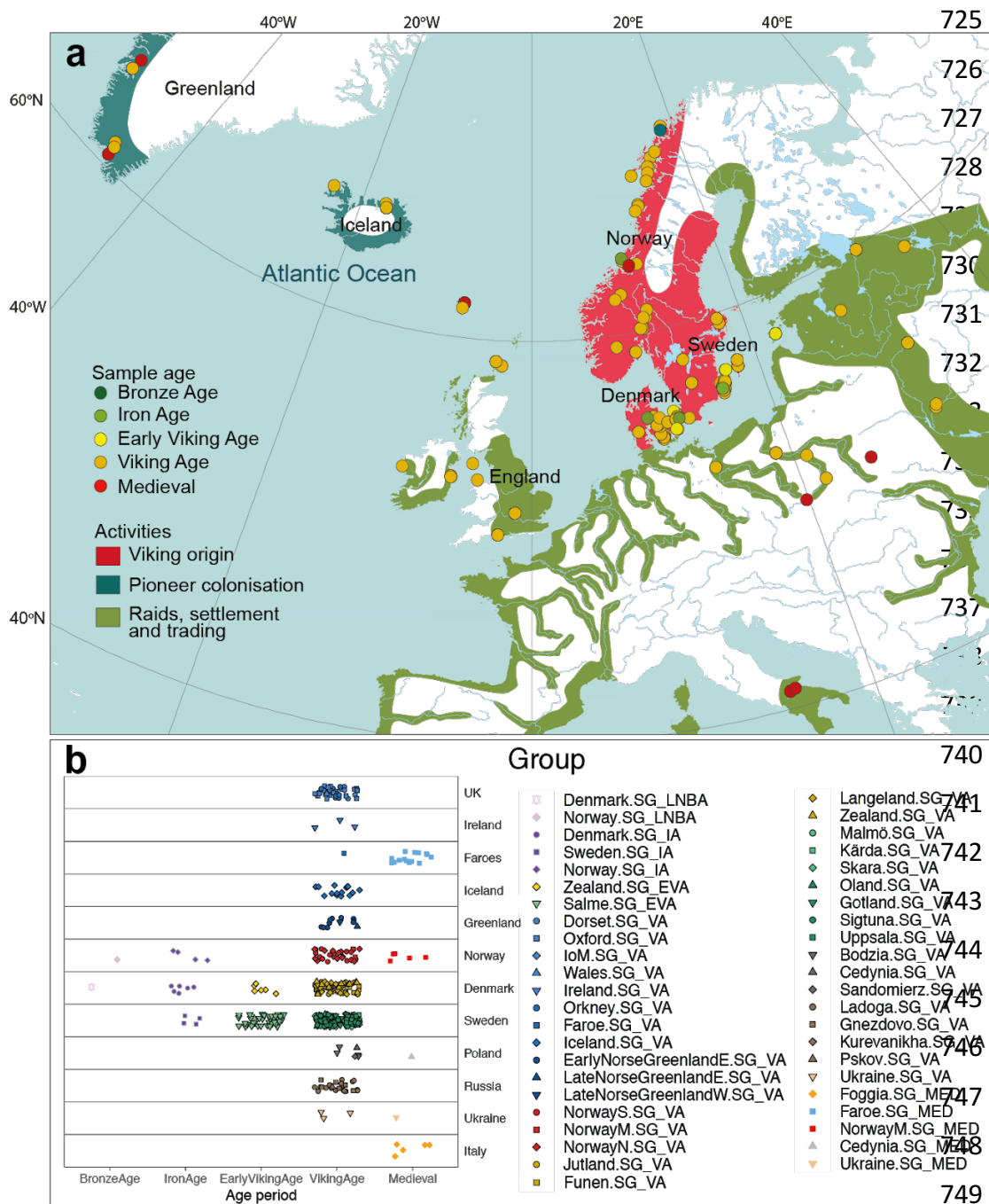
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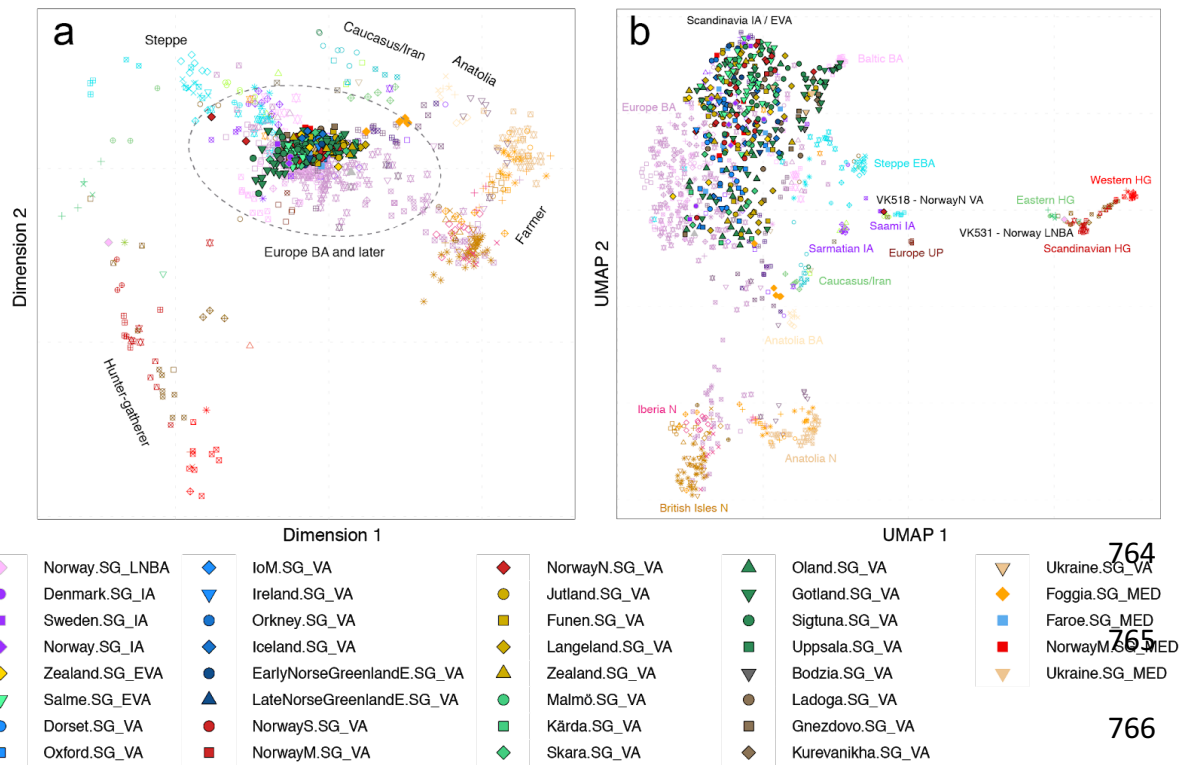


750 **Fig. 1: Map of the “Viking World” from 8<sup>th</sup> till 11<sup>th</sup> centuries.** Different symbols on the map (a)  
 751 correspond to ancient sites of a specific age/culture. The ancient samples are divided into the  
 752 following five broad categories: Bronze Age (BA) - c. 2500 BC - 900 BC; Iron Age (IA) - c. 900 BC  
 753 to 700 CE; Early Viking Age (EVA) - c. 700 to 800 CE; VA - c. 800 to 1100 CE; Medieval - c. 1100  
 754 to 1600 CE. **b**, All ancient individuals from this study (n=442) and published VA samples (n=21)  
 755 from Sigtuna<sup>6</sup> are categorized based on their spatio-temporal origin.

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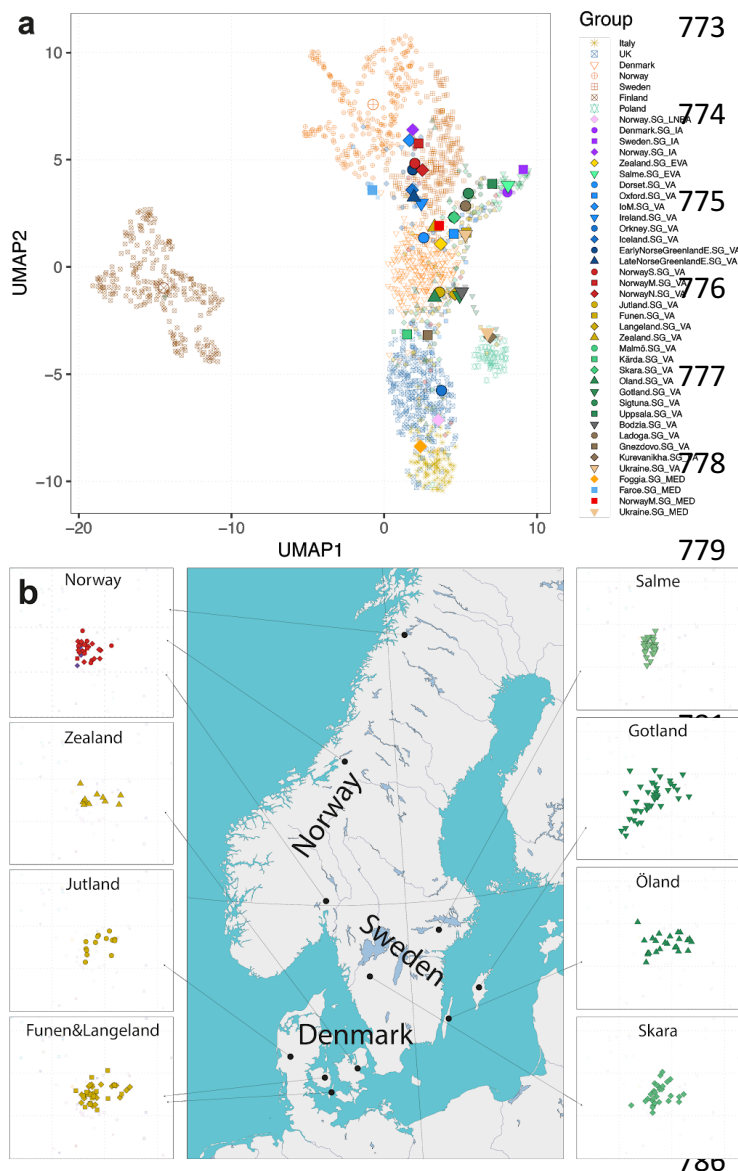
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767 **Fig. 2: Genetic structure of VA samples.** **a**, Multidimensional scaling (MDS) plot based on a  
 768 pairwise identity-by-state (IBS) sharing matrix of the VA and other ancient samples (Supplementary  
 769 Table 3). **b**, Uniform manifold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

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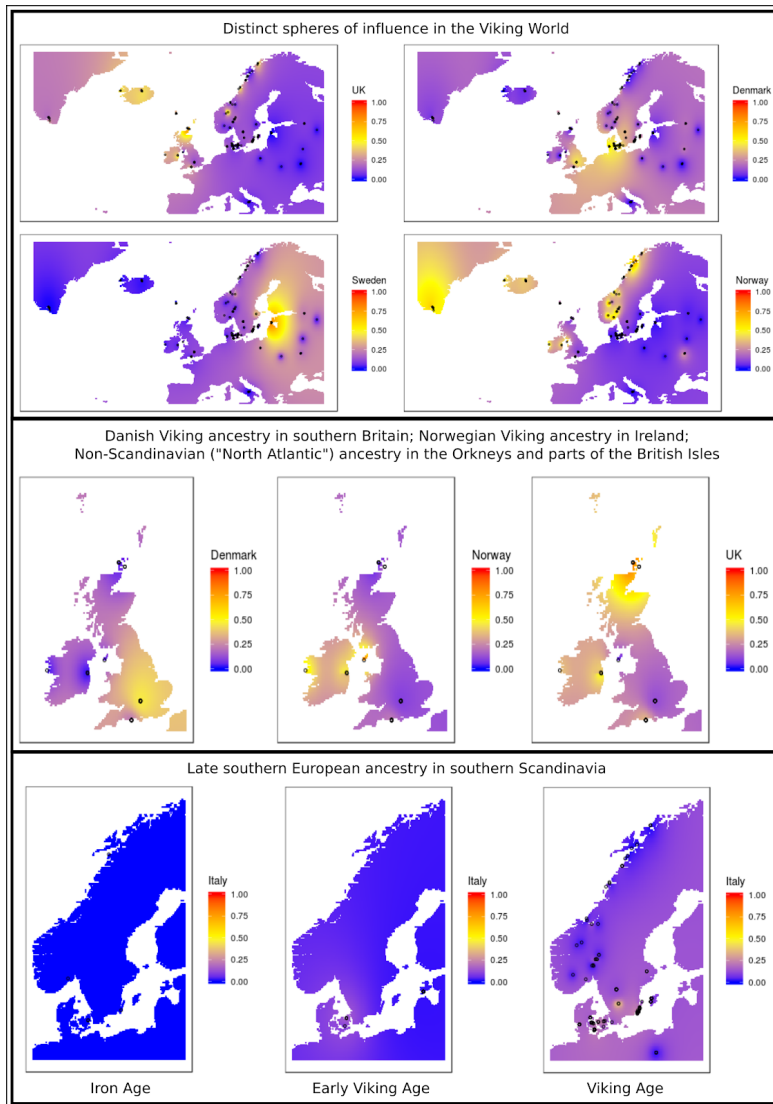
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787 **Fig. 3: Genetic structure and diversity of ancient samples.** **a**, Uniform manifold approximation  
 788 and projection (UMAP) analysis of the ancient and modern Scandinavian individuals based on the  
 789 first 10 dimensions of MDS using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

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816 **Fig. 4: Spatiotemporal patterns of Viking and non-Viking ancestry in Europe during the IA,**  
817 **EVA and VA. UK = ‘British-like’/ ‘North Atlantic’ ancient ancestry component. Sweden =**  
818 **‘Swedish-like’ ancient ancestry component. Denmark = ‘Danish-like’ ancient ancestry component.**  
819 **Norway = ‘Norwegian-like’ ancient ancestry component. Italy = ‘Southern European-like’ ancestry**  
820 **component. See Table S11.2 for statistical tests. The ‘Swedish-like’ ancestry is the highest in present-**  
821 **day Estonia due to the ancient samples from the Salme ship burial, which originated from the Mälaren**  
822 **Valley of Sweden, according to archaeological sources.**

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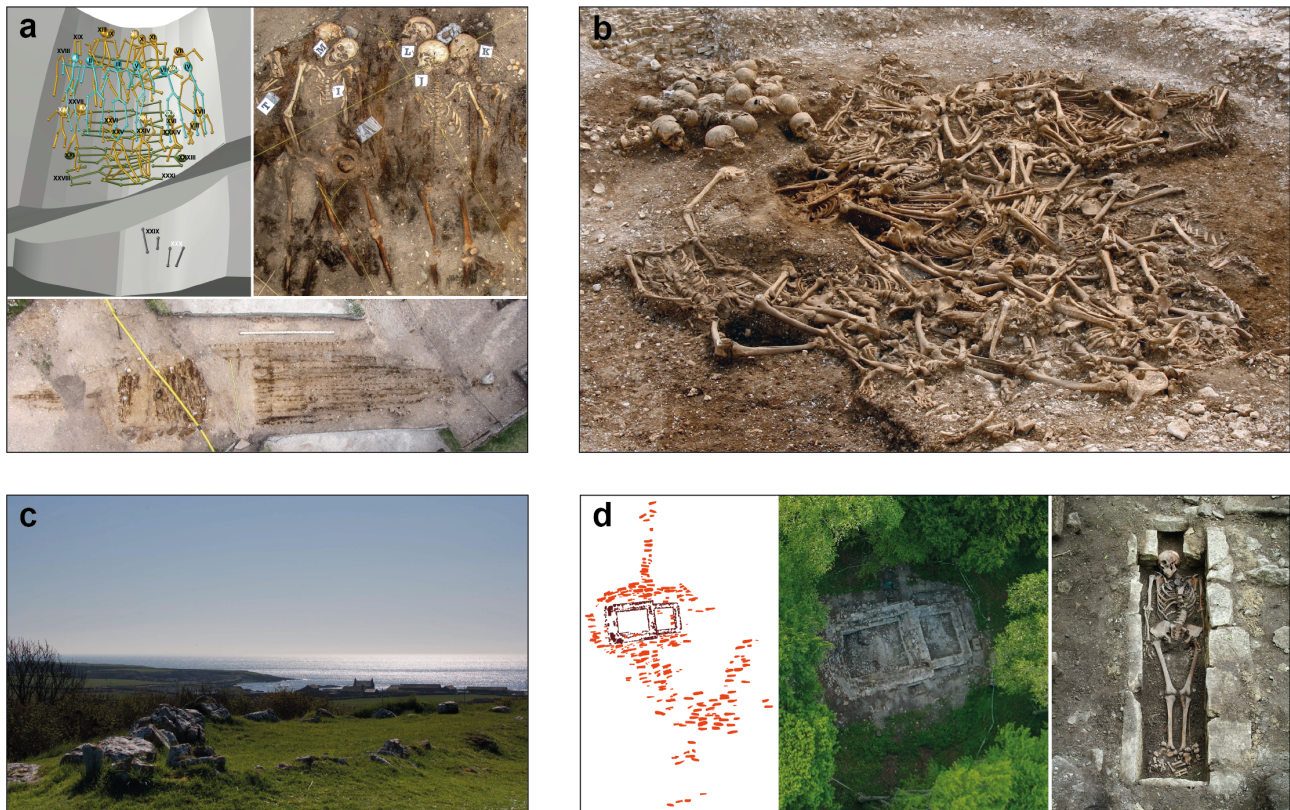


837 **Extended Data Figures**

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839 **Extended Data Fig. 1: Viking Age archaeological sites.**

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

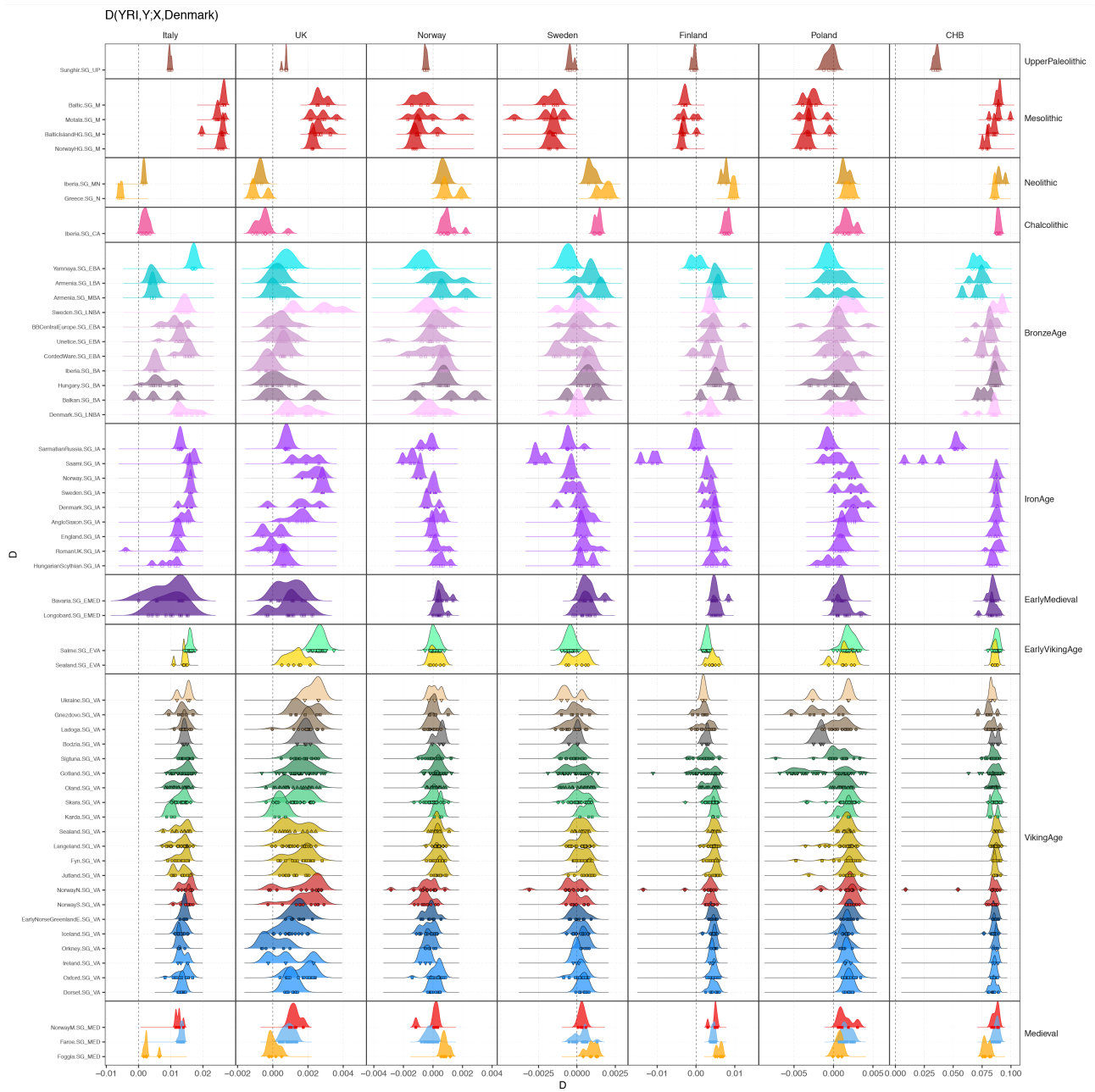
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865 **Extended Data Fig. 3: Symmetry tests of genetic affinity of ancient individuals**  
 866 **with contemporary populations.**

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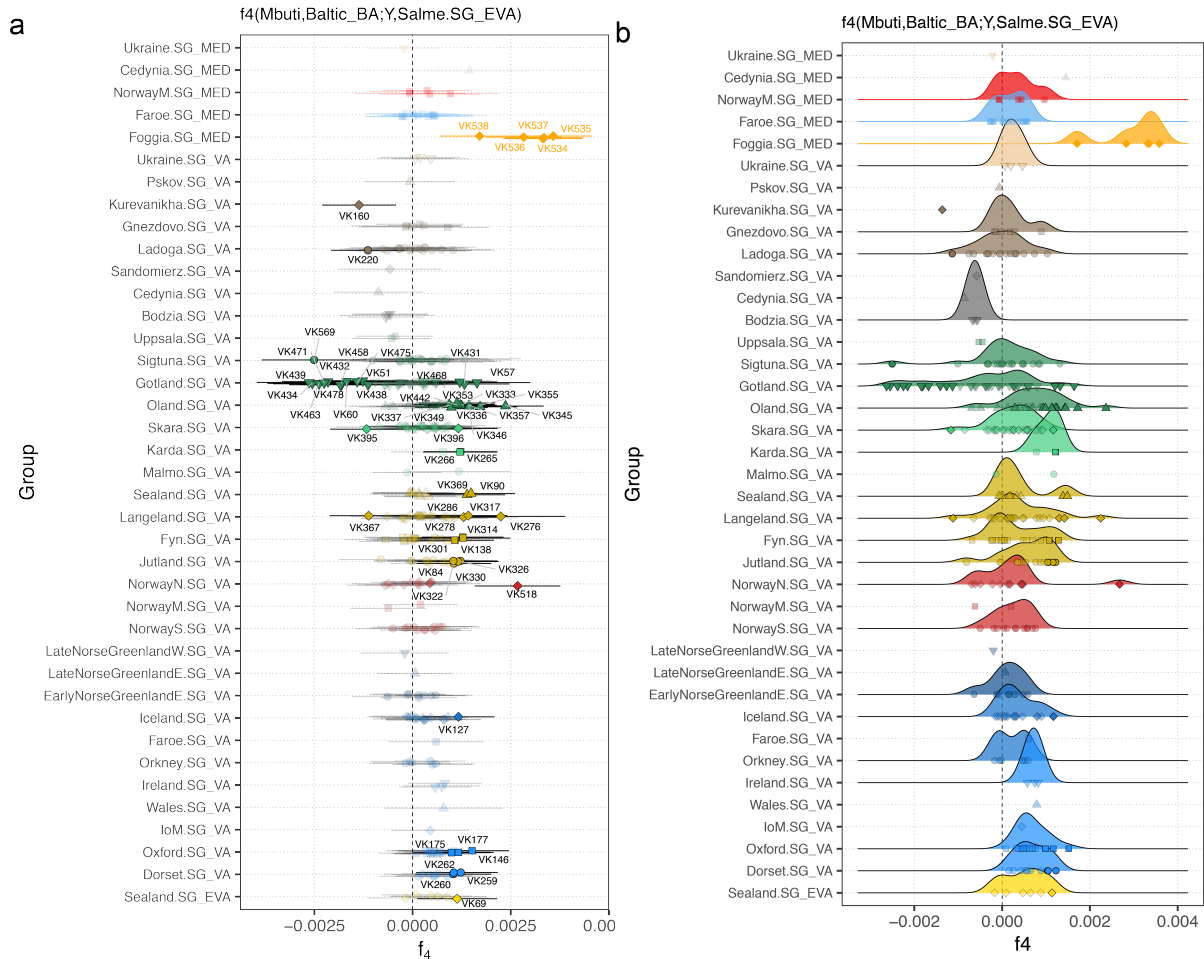
870 Panels show D-statistics of the form  $D(YRI, Y; X, Denmark)$ , which contrast allele sharing of an  
 871 ancient individual Y with either contemporary population X or Denmark. Plot symbols show point  
 872 estimates, and density plots distributions across all individuals per analysis group.

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875 **Extended Data Fig. 4: Symmetry tests for genetic affinity with Baltic Bronze**  
 876 **Age**

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879 Panels show  $f_4$ -statistics of the form  $f_4(\text{Mbuti,Baltic\_BA};Y, \text{Salme.SG\_EVA})$ , which contrast allele  
 880 sharing of Baltic\_BA with either a test individual Y or Salme.SG\_EVA. **a**, point estimates and error  
 881 bars ( $\pm 3$  standard errors) for each target individual, aggregated by analysis group. Individuals with  
 882 significant  $f_4$ -statistics ( $|Z| \geq 3$ ) are indicated without transparency and respective sample IDs. **b**, as  
 883 in **(a)**, with density plot for distributions across all individuals per analysis group.

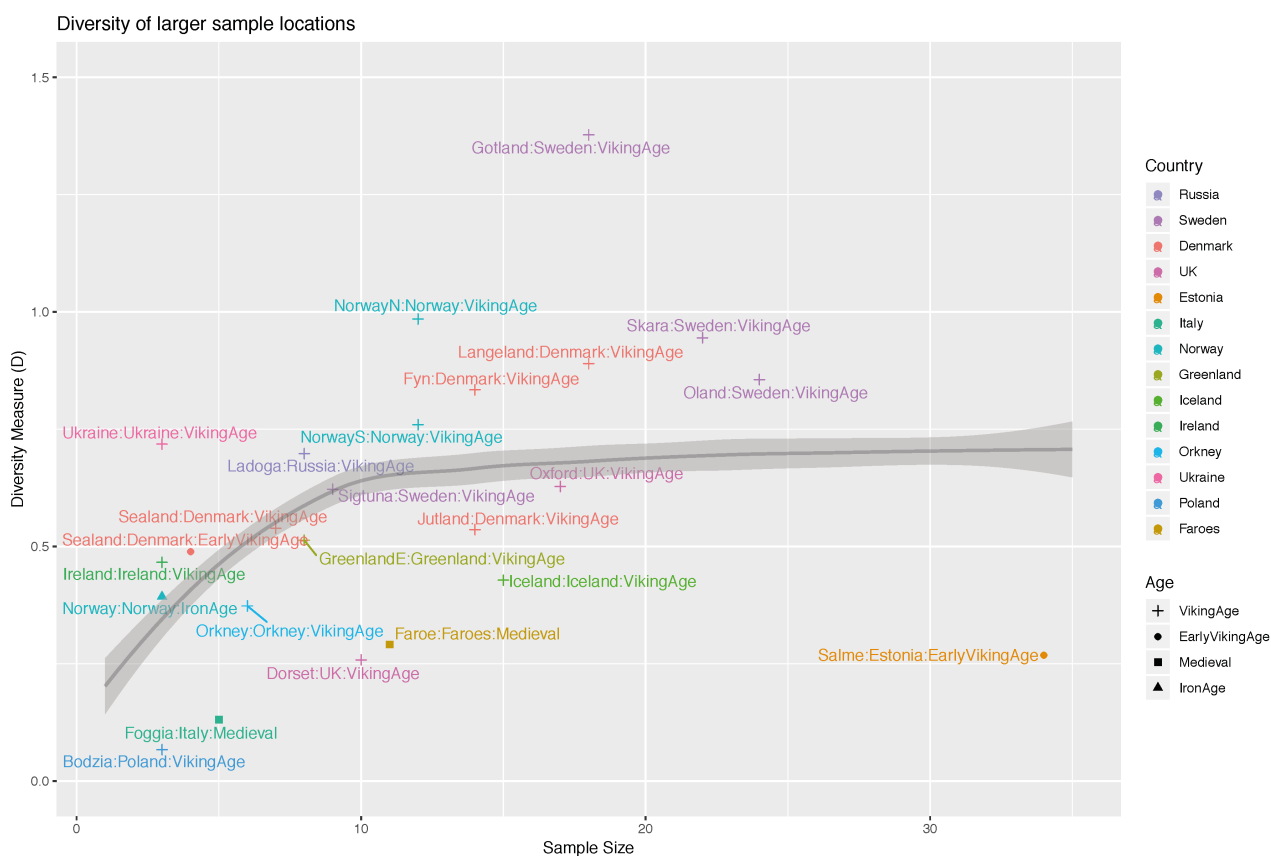
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886 **Extended Data Fig. 5: Ancestry diversity of different population groups**

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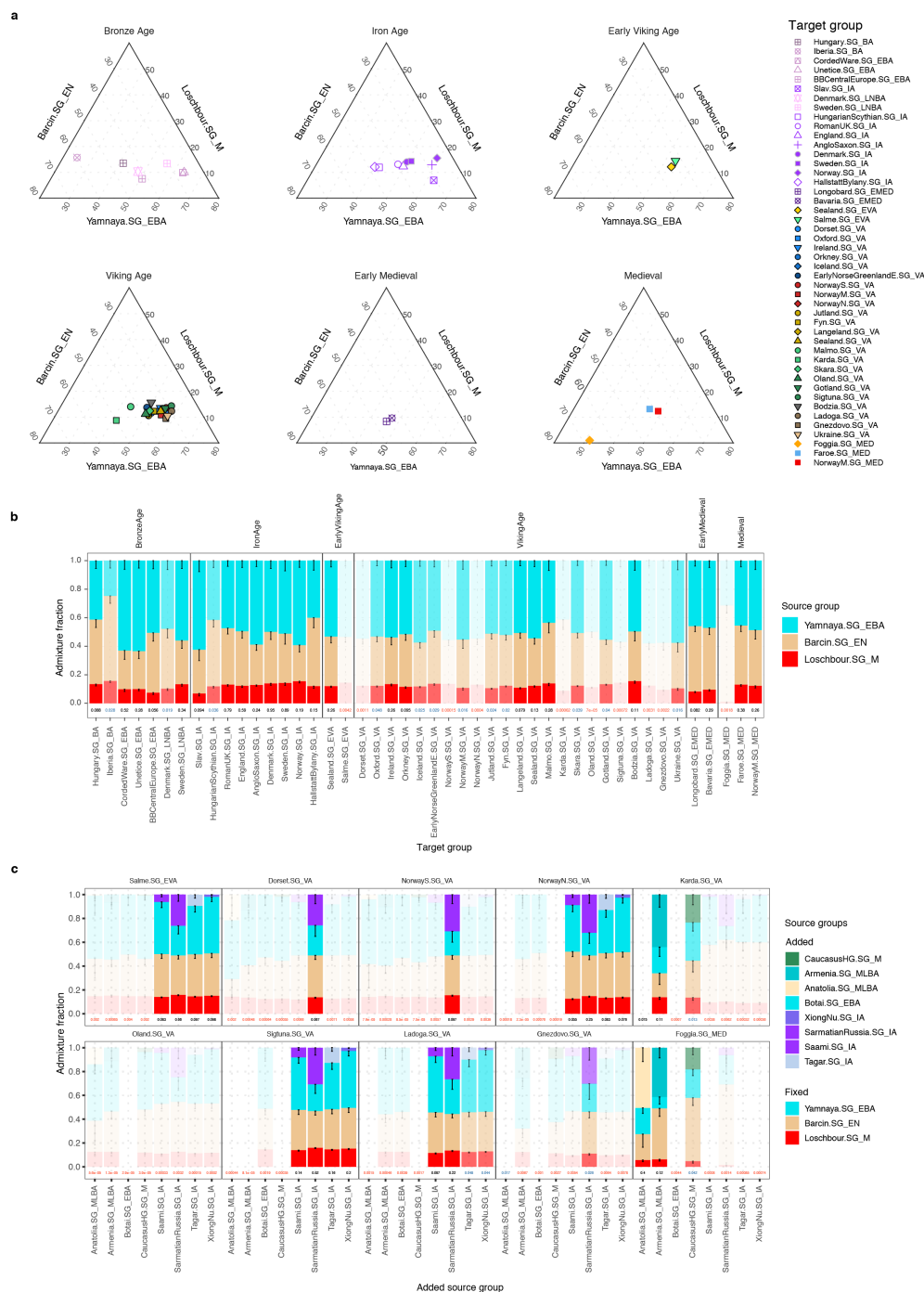
889 Diversity of different labels (i.e. sample locations combined with historical age) are shown as a  
 890 function of their sample size. The Diversity measure is the Kullback-Leibler divergence from the  
 891 label means, capturing the diversity of a group with respect to the average of that group;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

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896 **Extended Data Fig. 6: Ancestry modelling using qpAdm**

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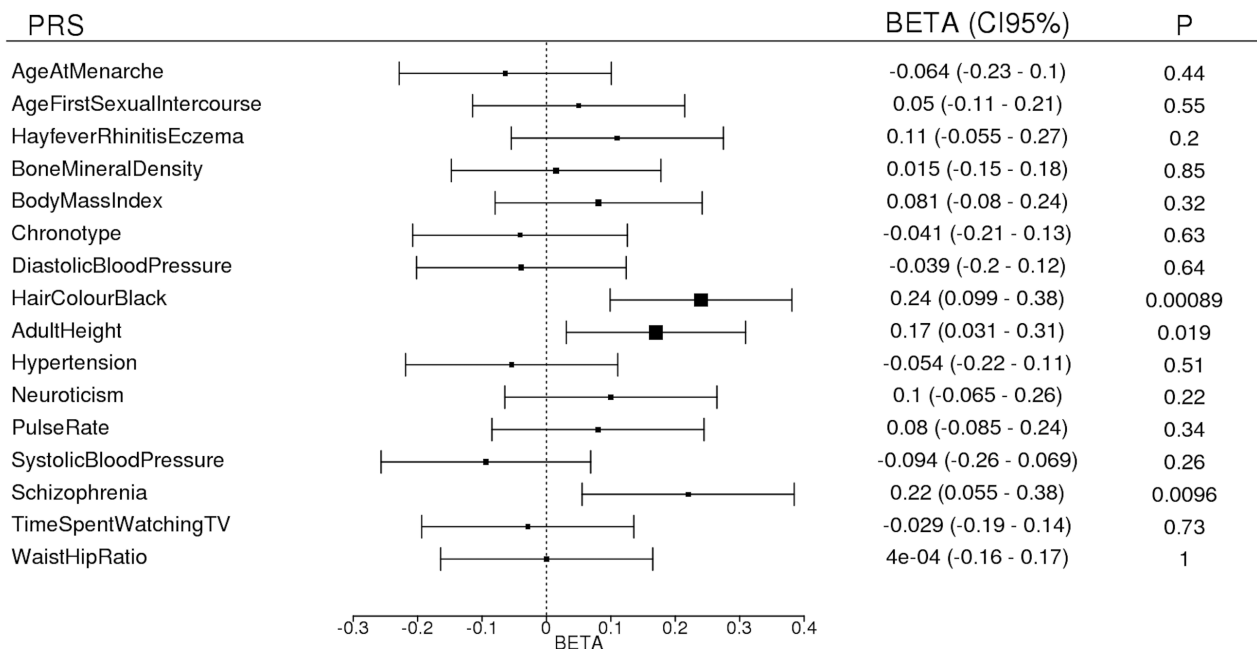
900 **a**, Ternary plots of ancestry proportions for a three-way model of Mesolithic hunter-gatherer  
 901 (Loschbour.SG\_M), Neolithic farmer (Barcin.SG\_EN) and Bronze Age Steppe herders  
 902 (Yamnaya.SG\_EBA). **b**, Bar plots with ancestry proportions as in **(a)**, with error bars indicating  
 903 standard errors and transparency/text colors indicating p-value for model fit (no transparency/black:  
 904  $p \geq 0.05$ ; light transparency/blue:  $0.05 > p \geq 0.01$ ; strong transparency/red:  $p \leq 0.01$ ). **c**, Ancestry  
 905 proportions of four-way models including additional putative source groups for target groups for  
 906 which three-way fit was rejected ( $p \leq 0.01$ ); transparency/text colors as in **(b)**

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908 **Extended Data Fig. 7: Polygenic risk scores**

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Viking age samples compared against contemporary Danish random sample



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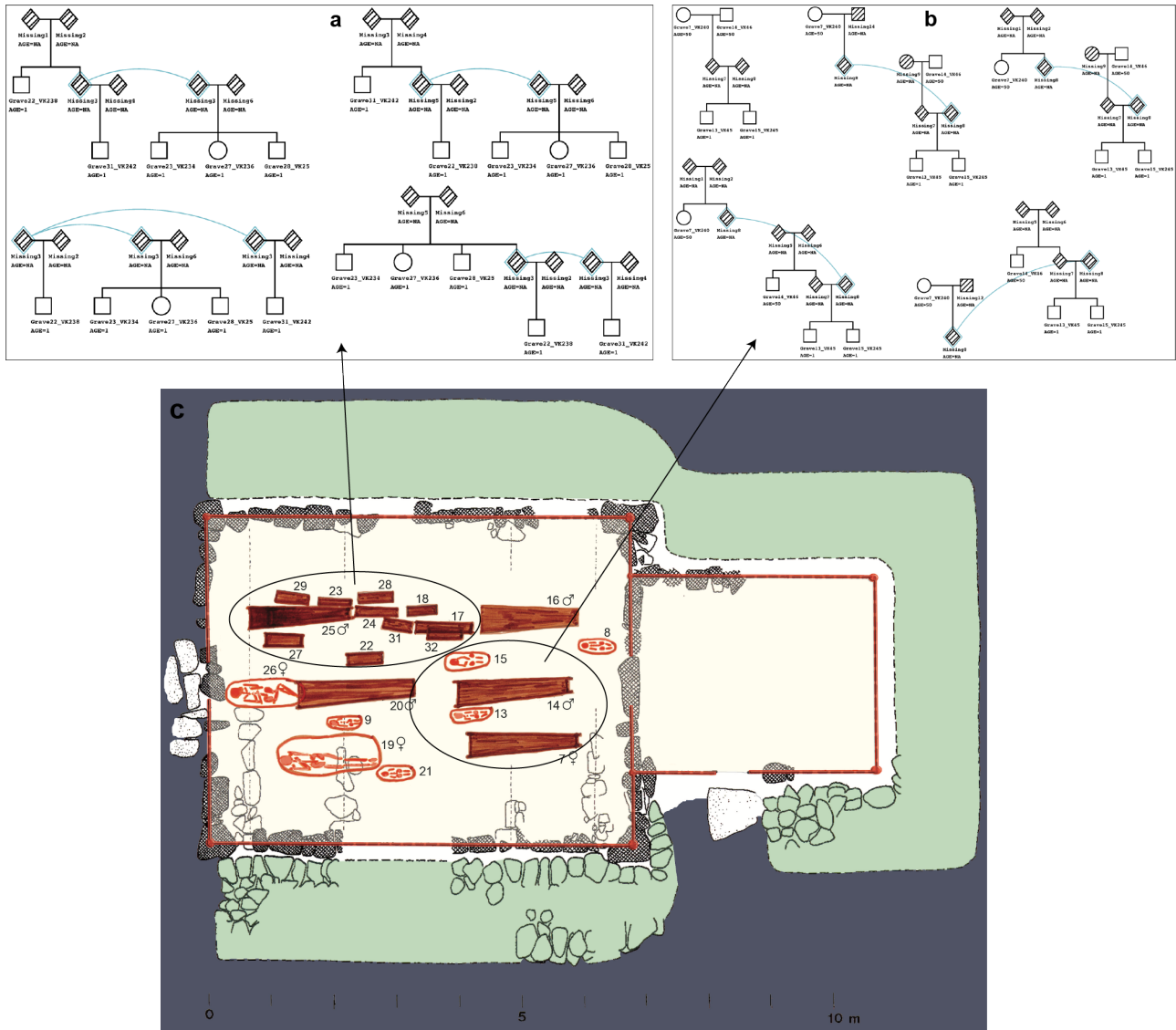
912 Polygenic risk scores (PRS) for 16 complex human traits in Viking Age samples from Denmark, Sweden and  
 913 Norway compared against a reference sample of >20,000 Danish-ancestry individuals randomly drawn from  
 914 all individuals born in Denmark in 1981-2011. The PRS is in each case based on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

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920 **Extended Data Fig. 8: Kinship analysis of ancient samples from Sandoy Church**  
 921 **2 site in Faroe Islands.**

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924

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