HUMAN EVOLUTION

Ancient genomes from Iceland reveal the making of a human population

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Opportunities to directly study the founding of a human population and its subsequent evolutionary history are rare. Using genome sequence data from 27 ancient Icelanders, we demonstrate that they are a combination of Norse, Gaelic, and admixed individuals. We further show that these ancient Icelanders are markedly more similar to their source populations in Scandinavia and the British-Irish Isles than to contemporary Icelanders, who have been shaped by 1100 years of extensive genetic drift. Finally, we report evidence of unequal contributions from the ancient founders to the contemporary Icelandic gene pool. These results provide detailed insights into the making of a human population that has proven extraordinarily useful for the discovery of genotype-phenotype associations.

Historical sources (*1*) indicate that Iceland was settled by people from Norway and the British-Irish Isles between 870 and 930 CE (*2*, *3*). Throughout the preceding century, the Norse had raided, traded, and settled in the islands and coastal regions of Ireland, Scotland, and northern England (*4*). Settlers in Iceland are thought to number ~8,000 to 16,000 individuals, with the population rarely exceeding 50,000 until 1850 (*3*), after which there was a rapid expansion to its current size of 330,000.

Studies of mitochondrial DNA (mtDNA) and Y-chromosomes from contemporary Icelanders indicate that 62% of their matrilineal ancestry stems from Scotland and Ireland and 75% of their patrilineal ancestry is Scandinavian (*5*–*7*). Moreover, mtDNA control region sequences from 68 Icelandic skeletal remains (~1000 years old) are more similar to contemporary source populations in Scandinavia, Scotland, and Ireland than to contemporary Icelanders (*8*). This was explained by a loss of mtDNA haplotypes from the Icelandic gene pool due to extensive genetic drift (*8*), supported by findings from whole-genome sequencing (WGS), genome-wide association studies (*9*), and population genetics analyses (*10*).

To directly assess the formation and subsequent evolution of a human population, we selected 35 ancient Icelanders for WGS (Fig. 1), most of whom represent the first generations of settlement (*11*) (Table 1 and tables S1 and S2). The 27 individuals passing quality control (*11*) (tables S3 and S4) were sequenced to between 0.18× to 30.7× average read depth (median = 0.71) (Table 1). The data display characteristics of ancient DNA (aDNA), and their authenticity is supported by multiple analyses (*11*) (figs. S1 and S2 and tables S4 to S6).

The sex of 26 of individuals was confidently determined by calculating the proportion of sex chromosome reads that mapped to the Y-chromosome (R_y) (*12*) (fig. S3 and table S7). The result for one individual, YGS-B2, was ambiguous, as R_y = 0.055 exceeded the upper limit for females (0.016) but was below the lower limit for males (0.075). The read depth of sex chromosomes relative to autosomes indicates that YGS-B2, who died before adulthood, carried two X-chromosomes and one Y-chromosome (fig. S4). This is further supported by a clearly assigned Y-chromosome haplogroup and X-chromosome heterozygosity in the range observed for females (table S8). To our knowledge, Klinefelter syndrome has not been reported in aDNA studies to date. Of the 24 individuals from pre-Christian (<1000 CE) burials (Table 1), 19 (79%) were male (X^2 test against expectation of 50%, P = 0.008). As the

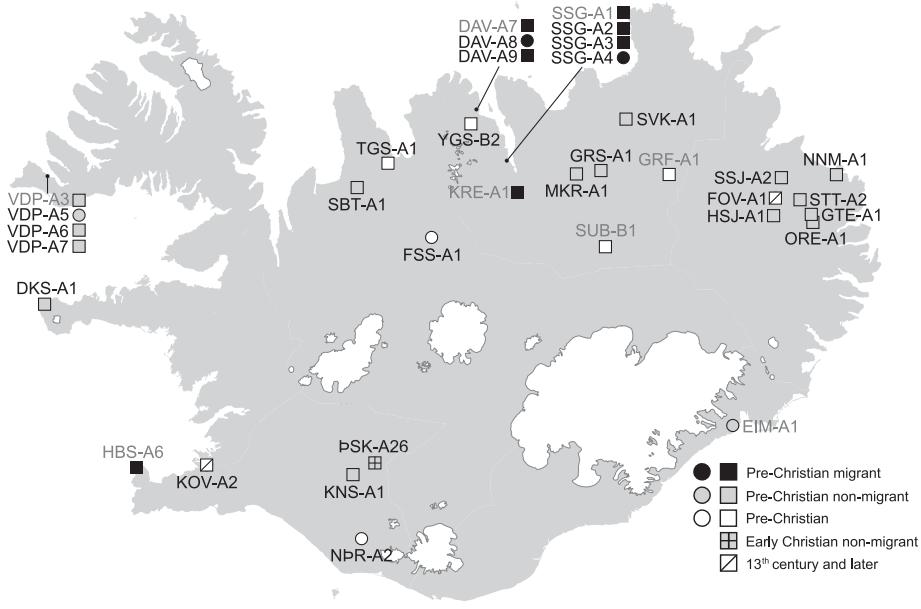

Fig. 1. A map of Iceland showing the locations of skeletal remains sampled for this study. Circles indicate females and squares, males. Eight samples (light gray labels) were ultimately excluded from further analysis.

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individuals were not selected by morphologically predicted sex, this implies sex differences in burial practices during the period (*13*), such that female burials were either rarer or less likely to be discovered in our time.

Little can be inferred about the phenotypes of the ancient Icelanders. However, we report haploid genotypes for a set of rare disease-associated sequence variants discovered in the Icelandic population and variants thought to have been subject to positive selection in Europeans (tables S9 and S10).

We next examined the relationship between the ancient Icelanders and contemporary populations using single-nucleotide polymorphism (SNP) arrays (table S11). As the read depth for most ancient Icelanders was too low to call diploid genotypes, haploid genotypes were used in all analyses (*11*). We performed a principal components analysis (PCA) of 2139 contemporary individuals from 28 European populations. When projected onto the first two principal components (PCs), all ancient Icelanders plot within clusters of contemporary Scandinavians and British-Irish Islanders (fig. S5).

We also performed a PCA restricted to contemporary individuals from Scandinavia (n = 3118), the British-Irish Isles (n = 1436), and Iceland (n = 916) based on 404,066 SNPs. We observed a separation between contemporary Scandinavians and British-Irish Islanders on PC2 (Fig. 2A), reflecting allele frequency differences that have accumulated across several millennia of drift. PC1 reveals an even more marked separation of contemporary Icelanders from their source populations. This divergence is also seen in the distribution of genetic distances (F_{ST}) between Icelanders and their source populations (fig. S6A).

The most likely cause for this divergence of Icelanders is 1100 years of genetic drift resulting from an initial founder event and subsequent small population size (*8*–*10*, *14*). This interpretation is supported by PCA projections of 25 ancient Icelanders (24 pre-Christian and one early-Christian, <1104 CE), all of whom plot within the range of PC1 occupied by contemporary Scandinavians and British-Irish Islanders (Fig. 2A and fig. S7). Accordingly, F_{ST} distances show that allele frequencies in ancient Icelanders are more similar to those of the source populations than to those of contemporary Icelanders (fig. S6B). Furthermore, ancient Icelanders show no evidence of the geographic patterns of genetic variation found in contemporary Icelanders (fig. S8). The implication that source populations experienced much less drift than Icelanders (*8*) is supported by PCA projections of ancient individuals (n = 16) from the British-Irish Isles dating from ~4000 to 1100 calibrated years before the present (*11*) (table S12), who cluster within contemporary British and Irish populations (fig. S9).

Whereas some ancient Icelanders appear to be unadmixed Scandinavian or British-Irish Islanders, others resemble a mixture of these ancestral

Table 1. Summary of genomic sequence data from ancient Icelanders.

Time period	Classification based on $^{87}Sr/^{86}Sr$ values	Sample	Archaeological date	^{14}C dating (cal CE)	Auto. genome depth of coverage (×)	Auto. genome covered (%)	SNP overlap with European ref. (%)†	SNP overlap with North European ref. (%)‡	Sex chr. karyotype	mtDNA haplogroup	chrY haplogroup	$^{87}Sr/^{86}Sr$ ratio
Pre-Christian	**Migrant**	DA-V-A8	<1000	<1050	3.31	89.12	90.14	93.92	XX	H1	–	0.7121
		DAV-A9	<1000	980-1020	0.43	26.66	21.79	22.66	XY	H1	I1	0.7118
		SSG-A2*	<1000	NA§	10.56	94.96	95.58	99.8	XY	J1c3g	R1b1a1a2a1a2c1	0.7095
		SSG-A3*	<1000	NA	0.26	16.37	8.16	8.56	XY	T2b2b	I1	0.7093
		SSG-A4*	<1000	NA	7.26	94.08	94.92	99.08	XX	J1b1a1a	–	0.7117
	Non-migrant	DKS-A1	<1000	NA	0.56	36.43	28.38	29.59	XY	U5a1h	R1a1a1b1a3	0.7088
		GRS-A1	<1000	<1050	0.55	34.77	27.86	29	XY	K1a1b1b	R1a1a1b1a3b	0.7071
		GTE-A1	<1000	NA	0.25	13.54	12.73	13.18	XY	H4a1a4b	R1a1a1b1a3a1	0.7061
		HSJ-A1	<1000	NA	30.74	96.29	95.73	99.99	XY	H3g1	I1a1b3b	0.7074
		KNS-A1	<1000	NA	0.71	43.95	36.2	37.8	XY	H5	R1b1a1a2a1a2c	0.706
		MKR-A1	<1000	<1050	0.18	11.33	11.25	11.68	XY	K1c1b	R1a1a1b	0.7065
		NNM-A1	<1000	NA	0.48	32.83	22.23	23.3	XY	H2a2b5a	R1a1a1b1a3a	0.7062
		ORE-A1	<1000	NA	0.44	26.26	22.88	23.79	XY	K1a3a	R1b1a1a2a1a	0.7087
		SBT-A1	<1000	NA	6.01	93.72	94.36	98.46	XY	H3g1a	I1a2a1a2	0.7084
		SSJ-A2	<1000	NA	0.36	22.41	14.04	14.77	XY	U5a1a1	I1a1b3	0.7077
		STT-A2	<1000	975-1015	12.92	95.62	95.67	99.9	XY	U4b1b1	R1b1a1a2a1a2c1	0.7069
		SVK-A1	<1000	<1050	1.07	67.81	60.95	63.47	XY	I2	I1b	0.7078
		VDP-A5	<1000	NA	1.32	81.88	83.64	87.05	XX	H3	–	0.7085
		VDP-A6	<1000	NA	1.86	85.92	63.06	65.83	XY	H1c3a	R1a1a1b1a3a	0.7089
		VDP-A7	<1000	NA	0.83	70.07	83.15	86.68	XY	H4a1a1	R1b1a1a2a1a1b	0.7085
	Not available	FSS-A1	<1000	NA	0.94	58.92	56.28	58.54	XX	U4a2	–	NA
		NÞR-A2	<1000	NA	0.49	31.88	31.79	32.93	XX	K1a2a	–	NA
		TGS-A1	<1000	943-1024	1.01	59.32	54.86	57.14	XY	T2e1	R1b1a1a2a1a2d	NA
		YGS-B2	<1000	NA	0.27	18.37	14.99	15.67	XXY	J1c1a	R1b1a1a2a1a	NA
Early-Christian	**Non-migrant**	ÞSK-A26	1000–1104	1120	0.77	48.41	44.69	46.45	XY	J1b1a1a	R1a1	0.7061
13th century and later	**Not available**	FOV-A1	>1000	1246-1302	0.68	43.26	37.24	38.91	XY	HV17a	R1b1a1a2a1a2c1a1	NA
		KOV-A2	b. 1678	NA	0.57	36.05	34.03	35.42	XY	H1	R1b1a1a2a1a	NA

*Samples marked with an asterisk symbol (*) were excavated from the same site as samples that have been subjected to radiocarbon dating, yielding the date estimate 980 to 1020 cal CE. †N = 227,056 SNPs. ‡N = 404,066 SNPs. §NA, not available.

groups (*5*–*8*) (Fig. 2A). Contemporary genotyped individuals were grouped into Norse (n = 2138, Norway and Sweden) and Gaelic (n = 459, defined here as Ireland and Scotland, excluding Orkney), and their relationships were tested with *D*-statistics (*15*) in the form *D*(*Yoruba*, *X*; *Norse*, *Gaelic*) (Fig. 2B and table S13).

We ran ADMIXTURE in supervised mode separately for each ancient Icelander with the Norse and Gaelic reference populations, yielding results (Fig. 2C) consistent with both PC2 axis position in Fig. 2A and *D*-statistics (Fig. 2B) (Pearson's $|r| > 0.98$ between all three ancestry assessments). Table 1 shows that Y-chromosomes from the 22 ancient Icelandic males belong to haplogroups common in Norse (I1 and R1a) and in Gaels (R1b1) (*11*) (table S14). An association between I1/R1a status and autosomal Norse ancestry was observed in the 19 pre-Christian males (p = 0.02, one-sided t test, Fig. 2C), consistent with them dating to the first generations of settlement.

We estimated the mean Norse ancestry of the settlement population (24 pre-Christians and one early Christian) as 0.566 [95% confidence interval (CI) 0.431–0.702], with a nonsignificant difference between males (0.579) and females (0.521). Applying the same ADMIXTURE analysis to each of the 916 contemporary Icelanders, we obtained a mean Norse ancestry of 0.704 (95% CI 0.699–0.709). Although not statistically significant (t test p = 0.058), this difference is suggestive. A similar difference of Norse ancestry was observed with a frequency-based weighted least-squares admixture estimator (*16*), 0.625 [Mean squared error (MSE) = 0.083] versus 0.74 (MSE = 0.0037). Finally, the *D*-statistic test *D*(*YRI*, *X*; *Gaelic*, *Norse*) also revealed a greater affinity between Norse and contemporary Icelanders (0.0004, 95% CI 0.00008–0.00072) than between Norse and ancient Icelanders (−0.0002, 95% CI −0.00056–0.00015). This observation raises the possibility that reproductive success among the earliest Icelanders was stratified by ancestry, as genetic drift alone is unlikely to systematically alter ancestry at thousands of independent loci (fig. S10). We note that many settlers of Gaelic ancestry came to Iceland as slaves, whose survival and freedom to reproduce is likely to have been constrained (*17*). Some shift in ancestry must also be due to later immigration from Denmark, which maintained colonial control over Iceland from 1380 to 1944 (for example, in 1930 there were 745 Danes out of a total population of 108,629 in Iceland) (*18*).

For 20 of the 24 pre-Christian Icelanders, strontium isotopes 86 and 87 were measured from dental enamel (*11*), revealing whether they spent their first 6 years in Iceland (nonmigrants) or elsewhere (migrants). Three are deemed migrants on the basis of high $^{87}Sr/^{86}Sr$ ratios (>0.710). These likely first-generation settlers were unmixed; DAV-A8 and DAV-A9 (from the same site) were Norse, and SSG-A4 was Gaelic (Table 1 and Fig. 2C). SSG-A2 and SSG-A3 (from the same site as SSG-A4) have lower $^{87}Sr/^{86}Sr$ ratios, albeit too high for a childhood solely in Iceland. Notably, SSG-A3 is estimated to be an equal mix of Norse and Gaelic, indicating that some admixture occurred before arrival in Iceland, perhaps in Viking settlements in Scotland or Ireland.

One intriguing implication of the extensive drift that has accumulated in the Icelandic gene pool is that DNA samples from earlier generations could be dated through the proportion of drift shared with the contemporary population.

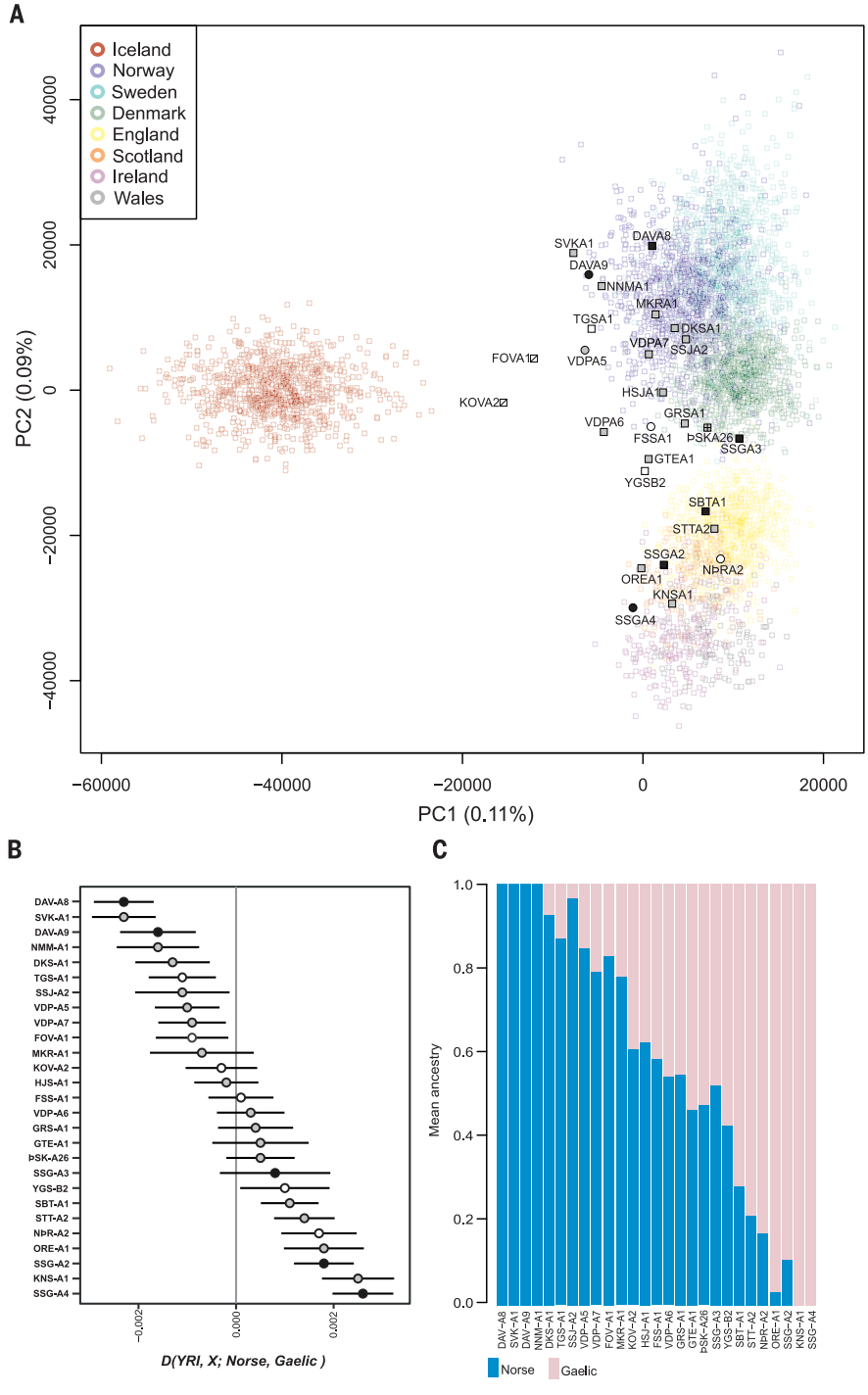

Fig. 2. Ancestry of ancient Icelanders. (**A**) Ancient Icelanders projected onto the first two eigenvectors of a PCA based on contemporary Scandinavians, British-Irish Islanders, and Icelanders. Proportion of variance explained is shown in parentheses. Symbols for ancient individuals are as specified in Fig. 1. (**B**) *D*-statistics reflecting the differential affinity of ancient Icelanders (*X*) to Norse and Gaelic reference populations, with the Yoruba from Nigeria (YRI) as an outgroup (n = 91). Symbols are shaded as in Fig. 1. (**C**) Estimated Norse and Gaelic ancestry proportions for ancient Icelanders using ADMIXTURE in supervised mode.

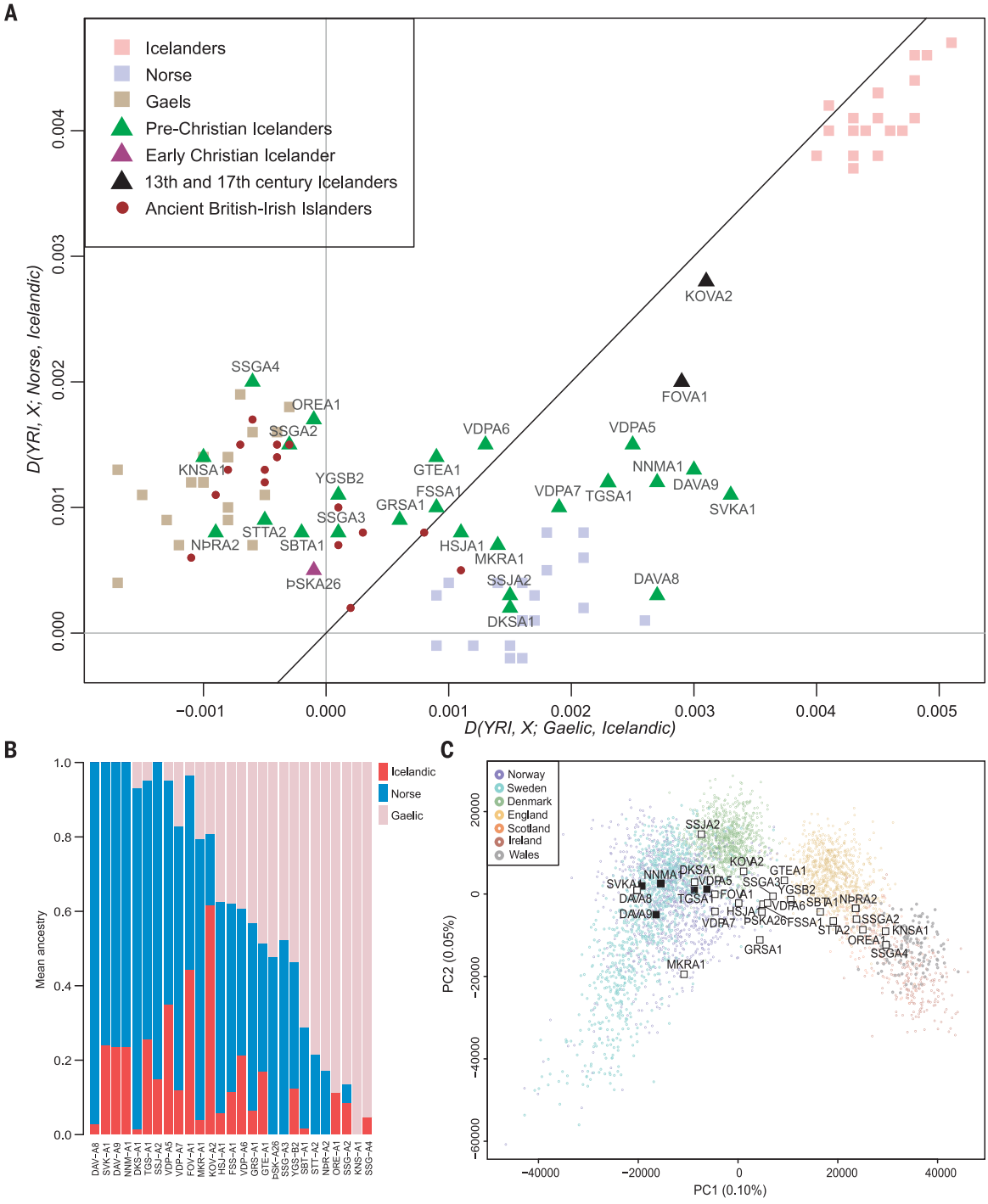

Fig. 3. Shared drift of ancient and contemporary Icelanders. (**A**) Scatterplot of *D*-statistics reflecting Iceland-specific drift. To aid interpretation, we included values for ancient British-Irish Islanders and a subset of contemporary individuals (who were correspondingly removed from the reference populations). (**B**) Estimated Norse, Gaelic, and Icelandic ancestry for ancient Icelanders using ADMIXTURE in supervised mode. (**C**) Ancient Icelanders projected onto a PCA of contemporary Scandinavians and British-Irish Islanders. Black squares denote the five individuals who may have contributed disproportionately to the Icelandic gene pool.

To test this hypothesis, we sequenced two Icelanders from the 13th (FOV-A1) and 17th (KOV-A2) centuries. Projection of their genotypes onto the PCA in Fig. 2A resulted in placement partway between contemporary Icelanders and their source populations, consistent with the genotypes of FOV-A1 and KOV-A2 being shaped by only part of the drift that characterizes modern Icelanders.

A scatterplot of two *D*-statistics, *D*(*YRI*, *X*; *Norse*, *Icelandic*) and *D*(*YRI*, *X*; *Gaelic*, *Icelandic*), for all 27 ancient Icelanders (table S15) effectively distinguishes the signature of Iceland-specific drift (an axis parallel to the diagonal line) from Norse-Gaelic ancestry (perpendicular deviation from that line) (Fig. 3A). Consistent with the PCA in Fig. 2A, pre-Christian Icelanders plot close to contemporary Norse and Gaels. Furthermore,

KOV-A2 is closer to contemporary Icelanders, whereas FOV-A1 plots roughly halfway between them and the contemporary Gaelic and Norse source populations.

Five pre-Christian Icelanders (VDP-A5, DAV-A9, NNM-A1, SVK-A1 and TGS-A1) fall just outside the space occupied by contemporary Norse in Fig. 3A. That these individuals show a stronger signal of drift shared with contemporary Icelanders is also apparent in the results of ADMIXTURE, run in supervised mode with three contemporary reference populations (Norse, Gaelic, and Icelandic) (Fig. 3B). The correlation between the proportion of Icelandic ancestry from this analysis and PC1 in Fig. 2A is $|r| = 0.913$. One possible explanation of this result is misclassification of these individuals as early Icelanders. However, this is doubtful, as they exhibit pre-Christian burial features, early radiocarbon dates (DAV-A9, SVK-A1 and TGS-A1), strontium isotopes inconsistent with being raised in Iceland (DAV-A9) (Table 1), and a high proportion (>87%) of Norse ancestry (DAV-A9, NNM-A1, SVK-A1, and TGS-A1, Fig. 2C).

Contamination from contemporary Icelanders could also affect our results but is negligible in all five individuals (table S4). Three factors could account for the greater shared drift of the five pre-Christian Icelanders with contemporary Icelanders. First, subtle genetic drift in the Norse gene pools might have shifted allele frequencies during the past 1100 years, making contemporary Norse less representative of their ancestors than is the case for Gaels. Second, they might originate from a subpopulation within Scandinavia that is poorly represented by contemporary populations or our reference samples. Third, these five individuals may have contributed disproportionately to the gene pool of contemporary Icelanders.

If genetic drift or population substructure in Scandinavian populations were responsible for their outlying positions (Figs. 2A and 3A), then the five individuals would also be outliers in a PCA generated only using contemporary individuals from Scandinavia and the British-Irish Isles. However, as the five ancient Icelanders fall well within the cluster of contemporary Scandinavians (Fig. 3C), we conclude that they, or close relatives, likely contributed more to the contemporary Icelandic gene pool than the other pre-Christians. We note that this observation is consistent with the inference that settlers of Norse ancestry had greater reproductive success than those of Gaelic ancestry.

Ancient genomes are key to answering questions about the formation and evolution of human populations during recent millennia. The settlement of Iceland occurred around 1100 years ago at the height of the Viking age. Our study reveals a highly admixed Norse and Gaelic gene pool of this founding population that was shaped by substantial genetic drift. The resultant founder events are one reason why the Icelandic population has contributed so much to the discovery of genotype-phenotype associations for rare sequence variants (*9*).

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SUPPLEMENTARY MATERIALS

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Materials and Methods
Supplementary Text
Figs. S1 to S10
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Ancient genomes from Iceland reveal the making of a human population

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Founder effects in modern populations

The genomes of ancient humans can reveal patterns of early human migration (see the Perspective by Achilli *et al.*). Iceland has a genetically distinct population, despite relatively recent settlement (~1100 years ago). Ebenesersdóttir *et al.* examined the genomes of ancient Icelandic people, dating to near the colonization of Iceland, and compared them with modernday Icelandic populations. The ancient DNA revealed that the founders had Gaelic and Norse origins. Genetic drift since the initial settlement has left modern Icelanders with allele frequencies that are distinctive, although still skewed toward those of their Norse founders. Scheib *et al.* sequenced ancient genomes from the Channel Islands of California, USA, and Ontario, Canada. The ancient Ontario population was similar to other ancient North Americans, as well as to modern Algonquian-speaking Native Americans. In contrast, the California individuals were more like groups that now live in Mexico and South America. It appears that a genetic split and population isolation likely occurred during the Ice Age, but the peoples remixed at a later date.

Science, this issue p. 1028, p. 1024; see also p. 964