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Matrilineal diversity and population history of Norwegians

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Abstract

Background: While well known for its Viking past, Norway's population history and the influences that have shaped its genetic diversity are less well understood. This is particularly true with respect to its demography, migration patterns, and dialectal regions, despite there being curated historical records for the past several centuries. In this study, we undertook an analysis of mitochondrial DNA (mtDNA) diversity within the country to elaborate this history from a matrilineal genetic perspective.

Methods: We aggregated 1174 partial modern Norwegian mtDNA sequences from the published literature and subjected them to detailed statistical and phylogenetic analysis by dialectal regions and localities. We further contextualized the matrilineal ancestry of modern Norwegians with data from Mesolithic, Iron Age, and historic period populations.

Results: Modern Norwegian mtDNAs fell into eight West Eurasian (N, HV, JT, I, U, K, X, W), five East Eurasian (A, F, G, N11, Z), and one African (L2) haplogroups. Pairwise analysis of molecular variance (AMOVA) estimates for all Norwegians indicated they were differentiated from each other at 1.68% ($p < 0.001$). Norwegians within the same dialectal region also showed genetic similarities to each other, although differences between subpopulations within dialectal regions were also observed. In addition, certain mtDNA lineages in modern Norwegians were also found among prehistoric and historic period populations, suggesting some level of genetic continuity over hundreds to many thousands of years.

Conclusions: This analysis of mtDNA diversity provides a detailed picture of the genetic variation within Norway in light of its topography, settlement history, and historical migrations over the past several centuries.

KEYWORDS
haplogroup, haplotype, language, mtDNA, Norway

1 | INTRODUCTION

Norway lies on the western edge of the Scandinavian Peninsula, with the majority of the country surrounded by water. Norway is also the longest country in Scandinavia, stretching 1752 km in length, a distance equivalent to the length of the Netherlands to the center of Italy (Hervik et al., 1993). Taking into consideration fjords and islands, the coastline is ~83,000 km in total length (Grabbe et al., 2009).

Topographically, Norway consists of largely mountainous terrain in the innermost parts of most of the country that is broken up into valleys and fjords running through the coastal areas. The highest mountain ranges begin at the horizontal level of Stavanger in the southwest and extend up to Trondheim in central Norway. This stretch includes the Jotunheimen mountain range, home to Norway's highest mountain called Galdhøpiggen at 2469 m (Vistad et al., 2016), which divides the southern and most populated portion of the country into eastern and western halves.

After the Fennoscandian ice sheet covering Norway began to melt during the Last Glacial Maximum ~23,000 years ago, Norway's coastline slowly became inhabited by rich forests and wildlife (Glørstad et al., 2020; Stroeven et al., 2016). Much of the earliest evidence of human settlement, which dates to 10,000 years ago, comes from hunting tools and burial sites found from the southeastern Oslo Fjord all of the way up to Finnmark in the far north (Bang-Andersen, 2003; Günther et al., 2018). These findings suggest that the entire coastline was quickly settled by pioneering groups (Bang-Andersen, 2012), who employed watercraft to move along the long coastline for hunting and fishing (Helskog, 1985).

Based on recent ancient DNA work, Norway was initially settled by hunter-gatherers groups migrating into the country from the both southwest and northeast (Günther et al., 2018). These groups were later partially incorporated into expanding farming cultures (Malmström et al., 2015; Skoglund et al., 2012). A major genetic shift in Norway's population structure occurred after the Viking Age (750–1050 ACE), and has been described in terms of both genomic admixture (Margaryan et al., 2020) and changes in mtDNA haplogroup frequencies (Krzewińska et al., 2015). This shift likely resulted from greater gene flow from the British Isles into modern-day Norway compared with Denmark and Sweden, which, in turn, was due to more frequent maritime routes of the western-dwelling Norse to the British Isles (Margaryan et al., 2020).

These maritime routes continued to shape and influence Norwegian society and culture long after the Viking expansions. Due to its climate, the economic dependence on natural goods varies by region in Norway and requires timely ship-based mechanisms to distribute fresh cargo throughout the rest of the country. The processing and packaging of fish for export also took place either in or near coastal towns along routes of great distance. Extending the length of the western coastline, the Norwegian fisheries industry was dispersed in scattered longitudinal rural settlements rather than more nucleated fishing communities as seen in European countries such as Great Britain, Germany, France, and Denmark (Haaland & Svihus, 2011; Kleppe, 2014; Wickler & Narmo, 2014). By 1850, nearly all Norwegian towns west of Lindesnes in Adger County, Norway's southernmost point, were engaged in the processing and exportation of fish and/or shipping and shipbuilding (Haaland & Svihus, 2011). The majority of the country's 3% arable land in Hedmark and Østfold Counties in the southeast region of Norway was dedicated to growing crops on large farms (Knutsen, 2019). With sparser forests, the central and northern parts of Norway have traditionally relied more on fishing (Knutsen, 2019).

Mass migrations started within Norway around the 1750–1780s (Svalestuen, 1978; Thorvaldsen, 2019) and boomed in the mid-1800s when Norwegians no longer needed official permissions to relocate (Pryser, 1981; Svalestuen, 1978). A large proportion of migrants were young couples looking for better economic opportunities and to expand their families. The most comprehensive and most widely mentioned wave of internal migrants was that from southeastern Norway and southern Trøndelag to the Målselv and Bardu valleys southeast of Tromsø (Thorvaldsen, 2019). Later, between 1750 and 1801, as rural inland farming populations in the southeast became more overpopulated, people moved from the inland districts to the Oslo Fjord for better opportunities in agriculture and timber trade (Dyrvik, 1972; Sølvi, 1979). Similarly, people moved from the inland southeast, west, and central Norway to the northernmost coastlines for cod and herring fishing opportunities (Niemi et al., 2003). Some Norwegians also emigrated after famine and poverty spread in the 19th century. However, the majority could not afford the ship fare and did not want to enter into indentured servitude relocated within the country itself (Sølvi, 1979).

The regional distribution of Norwegians is further reflected in the distinct spoken dialects in those locations, which may have been influenced by maritime routes and internal migration patterns. These dialects vary substantially from each other in terms of grammar, syntax, tone, and pronunciation (Skjekkeland, 2005). The major dialects include Eastern Norwegian (*østnorsk*), Western Norwegain (*vestnorsk*) and Trøndelag in central Norway (*trøndersk*), and Northern Norwegian (*nordnorsk*) (Skjekkeland, 2005; Venås & Skjekkeland, 2020). During Danish rule (1357–1814), a colloquial Norwegian-like Danish was spoken widely by Norwegians who lived in cities and towns. By the first half of the16th century, the Old Norwegian written language had fallen out of favor and, by the 18th century, Danish grammar, pronunciation, and vocabulary were preferred or insisted upon over Norwegian in education and theater (Haugen, 1959). During the less restrictive union between Sweden and Norway (1814–1905), the rise of a unique Norwegian identity led to the return of Norwegian dialects and lexicon back into acceptance (Derry, 2012; Haugen, 1959). As a result of this language history, several elements of the four regional Norwegian dialects have persisted, with several of their distinctive features being preserved (Skjekkeland, 2005).

Mitochondrial DNA (mtDNA) has been a frequently studied source of genetic information for understanding long-term population shifts, diversity, and demographic structure. It is a maternally inherited, nonrecombining DNA molecule at the HVS I region that evolves at a clock-like rate (Soares et al., 2009), making its invaluable for reconstructing populations dynamics based on matrilineal genetic diversity in human populations. Thus, we investigated matrilineal variation in Norway by dialect regions, we attempted to characterize regional mitochondrial DNA (mtDNA) diversity in Norway to determine the influence of dialectal region, subpopulation, and topography on its distribution in the country. We further explored the impact of internal historical migrations on the present-day gene pool.

2 | MATERIALS AND METHODS

2.1 | Mitochondrial DNA data

Data for a total of 1174 partial mtDNA sequences from modern Norwegians were gathered from various published sources, including Krzewińska, 2014; Opdal et al., 1998; Passarino et al., 2002; Helgason et al., 2001. This study also included mtDNA sequences from the GenBank database as of June 1, 2020, that belonged to persons of Norwegian ethnicity and origin. Specific information about the collection location or residence within Norway was available for 64% of the total data set ($n = 755$). Information about these samples, including their GenBank accession numbers and the specific tables within the published sources from which the sequences were obtained, are provided in Table S1.

In addition, partial mtDNA sequences from 1597 non-related individuals with matrilineal Norwegian ancestors were incorporated into this analysis to contextualize the human migration changes within Norway since the early modern ancestors of the 17th to 20th centuries. The mtDNA sequences were obtained on June 1, 2020, from The Norway DNA Project (http://www.norwaydna.no), which is a subproject of the Family Tree DNA database (http://www.familytreedna.com) containing mtDNA sequences submitted by consenting members (The Norway DNA Project Group, 2014). Membership is open to individuals who have a Norwegian background, Norwegian ancestry, or who live in Norway. Location information was derived from individuals submitting their mtDNA data who had also indicated the local region of their earliest known matrilineal ancestor (87%; $n = 1396$), using The Norwegian National Archives (https://www.arkivverket.no/). These archives contain annotated information on Norwegians living from the 17th to the early 20th century that derives from parish records, census records, and village books. For these reasons, this Family Tree DNA data set was used as a proxy for ancestral Norwegian populations, and for this reason its constituent members will be called the "Ancestors."

2.2 | Geographic and dialectic regions of Norway

MtDNA sequences among Modern Norwegians were localized largely to cities, which reflects the current locations of most Norwegians, while mtDNA sequence data among Ancestors were spread throughout towns, villages, and cities within different counties. For comparative purposes, the specific locations were separated into the following geographical regions based on the major dialects of Norway: (1) The *Southeast (Eastern Norwegian dialect) region included Ancestors born or from the settlements of* Hedmark, Oppland, Buskerud, Akershus and Oslo, Telemark, Vestfold, and Østfold Counties. For Modern Norwegians, it compassed the Southeast area of Norway, which largely compasses the capital of Oslo, as well as the above-mentioned neighboring southeastern counties. (2) The *West (Western Norwegian dialect) region included Ancestors born in or from the settlements of* Agder, Rogaland, Hordaland, Sogn and Fjordane (including Førde), and Møre and Romsdal Counties. For Modern Norwegians, it compassed Haugesund (within Rogaland county), Bergen (within Hordaland county), and Førde (within Sogn and Fjordane county). (3) The *Central (Trøndelag Norwegian dialect) region included Ancestors born in or from the settlements of* South-Trøndelag and North-Trøndelag Counties. For Modern Norwegians, this region compassed Trondheim, where samples were taken at St. Olav's Hospital and the population consists of individuals residing in North-Trøndelag County. (4) *The North (Northern Norwegian dialect) region included Ancestors born in or from the settlements of* Nordland, Troms, and Finnmark Counties. For Modern Norwegians, it compassed the same counties.

2.3 | Ethics statement

This study is based on open-access and publicly available data sets. The respective studies from which these data derive have gone through standard protocols to obtain informed consent from participants, clearance, and approval from the respective ethics committees for sample collection and analysis, as outlined in the associated publications.

2.4 | Phylogenetic and statistical analysis

All mtDNA sequences were delimited to reads between nucleotide positions (np) 16,024 to 16,383, that is, the first hypervariable region segment (HVS1) of the mtDNA control region (CR). The HVSI mtDNA sequences were then aligned against the Reconstructed Sapiens Reference Sequence (RSRS), which allows for naming and mapping of the mtDNA haplogroups from an ancestral base (Behar et al., 2012) using MAFFT version 7 (Katoh & Standley, 2013).

Haplogroup classifications of the HSVI sequences were made with HaploGrep2 (Weissensteiner et al., 2016), which uses PhyloTree Build 17 as its reference (van Oven & Kayser, 2009). Haplogrep2 computes the haplogroup classifications on pre-calculated phylogenetic weights that correspond to the occurrence per position in Phylotree Build 17 (http://www.phylotree.org), which, in turn, reflects the mutational stability of a variant.

Haplogrep2 classifications were verified using a maximum likelihood (ML) phylogeny for the unique haplogroups using IQ-TREE 1.6.12 software (http://www.iqtree.org) (Nguyen et al., 2015). The phylogeny was constructed under the general time-reversible nucleotide substitution model with a proportion of invariant sites (TPM3u + F + I + G4) which was inferred in jModelTest (https://github.com/ddarriba/jmodeltest2) as the best fitting model. This tree was then updated to take into account back mutations, (point mutations that revert to the ancestral state) and noncontinuous mutations in accordance with PhyloTree, Build 17 (van Oven & Kayser, 2009). Accordingly, we ignored hot-spot mutations such as cytosine (C) insertions/deletions at position 16,193, and expansions of cytosomes that affect the number of adenosines at positions 16,182 and 16,183, because these common polymorphisms are also excluded from Phylotree, are not diagnostic for a particular haplogroup assignment, and may lead to inaccuracies in algorithmic predictions of phylogenetic organization.

DnaSP 5.10.01 (Librado & Rozas, 2009) was used to calculate the basic parameters of genetic diversity. The analysis of molecular variance (AMOVA) was carried out using Arlequin 3.5.2.2 (Excoffier & Lischer, 2010) and R (R Core Team, 2018). The statistical significance of fixation indices (F*st*) and their respective p-values was estimated by permutation analysis (10,000 permutations) assuming a Tamura-Nei (1993) model with a gamma distribution of 0.26. Comparisons of haplogroup frequencies between geographic or dialectic regions were conducted using a Chi-square or Fisher's exact test, where appropriate.

The structuring of mtDNA sequence diversity by geography was assessed through the analysis of F*st* values with multidimensional scaling (MDS), using the PAST v.2.17b software (Hammer et al., 2001). All analyses were conducted by location listed in the public data sets. Locations were combined into the four main dialect regions of Norway—North, Central, West, and Southeast (Venås & Skjekkeland, 2020)—for both the Ancestor and Modern Norwegian data sets, as outlined above.

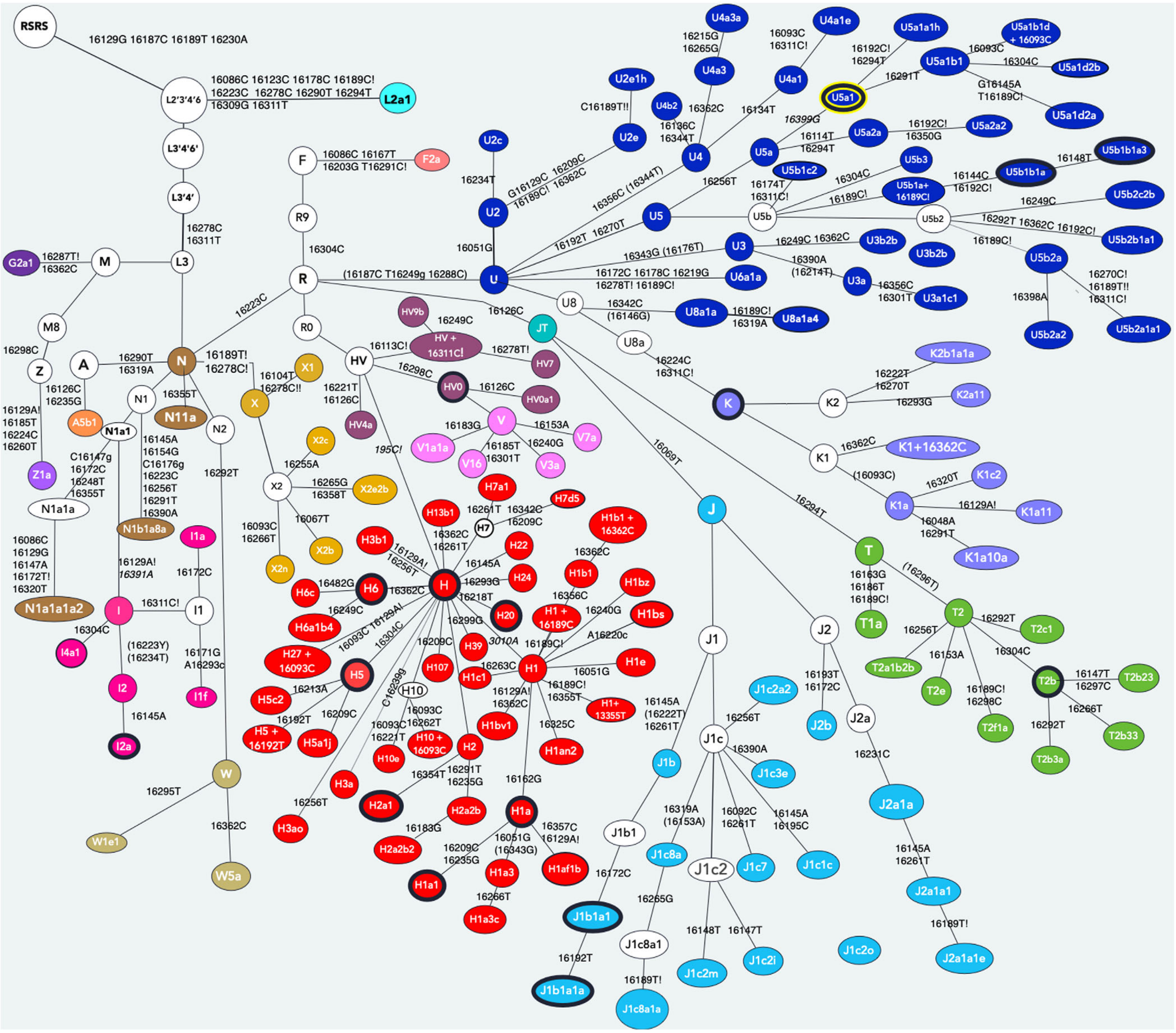

FIGURE 1 Phylogenetic network of maternal lineages represented by mitochondrial DNA. (mtDNA) haplogroups among present-day Norwegians. The white circles indicate haplogroups not found among the Norwegian data. The thick black borders around haplogroups indicate the representation among late Iron Age inhabitants of Norway (Krzewińska et al., 2015). The yellow circle indicates haplogroup representation from Mesolithic inhabitants of Norway, as sequenced by (Günther et al., 2018). Back mutations are indicated with an exclamation mark (!) and two exclamation marks (!!) indicate a double back mutation. Noncontinuous mutations that do not follow through all subsequent haplogroups are indicated in parentheses. Mutations outside of the np16,024–16,383 region that support some regions of the tree are indicated in italics

To estimate population growth over time, we generated a Bayesian skyline plot (BSP) using BEAST 1.10.4, cross-platform program for Bayesian analysis of molecular sequences, (Suchard et al., 2018) with gamma distributed rates (Drummond et al., 2005; Soares et al., 2012; Suchard et al., 2018). Briefly, each Markov chain Monte Carlo (MCMC) sample was based on a run of 10 million generations sampled every 1000 steps, of which the first 1% was discarded to allow for burn-in. The mutation rate of 1.64×10^{-7} (Soares et al., 2009) was used to convert substitution rates into years (x-axis) and coalescent intensities into effective population sizes (y-axis) (Drummond et al., 2005). BEAST outputs were visualized with the Tracer v.1.7.1 program (Rambaut et al., 2018). The BSP analysis was restricted to the database for contemporary Norwegians because the information for the Ancestors' sequences from Family Tree DNA did not specify the individuals' modern familial residence (whether inside or outside Norway).

3 | RESULTS

3.1 | Distribution of Norwegian maternal lineages.

In this study, a total of 1174 Modern Norwegian HVS1 sequences were analyzed. Among them, 151 unique haplogroups were identified based on the Phylotree Build 17 nomenclature (Figure 1). These haplogroups fell into eight West Eurasian (N, HV, JT, I, U, K, X, W), five East Eurasian (A, F, G, N11, Z), and one African (L2) major haplogroups. Overall, 98.4% ($n = 1155$) of Norwegians had a mtDNA that belonged to a West Eurasian maternal lineage.

As can be seen in the haplogroup network displayed in Figure 1, a large number of Modern Norwegian mtDNAs belonged to haplogroups H, J, and U, similar to what has been seen for other northern and western European populations, including the studies on Norwegian mtDNA diversity used in this paper (Helgason et al., 2001; Krzewińska, 2014; Lembring et al., 2013; Li et al., 2014; Passarino et al., 2002). We also noted that the mutational signature of the U5a1 haplotype (16129G, 16187C, 16189T, 16192T, 16223C, 16230A, 16256T, 16270T, 16278C, and 16311T) appearing in this network was also found in the mtDNA of a Mesolithic individual analyzed by (Günther et al., 2018), while sequence motifs for haplogroups HV0, H5, H6, H20, H, H1a, H1a1, H2a1, I2a, J, J1b1a1, J1b1a1a, T2b, U5b1b1a3, and U5b1b1a in contemporary Norwegians were also detected in Iron Age individuals analyzed by Krzewinska and coworkers (Krzewińska et al., 2015).

These results were not unexpected. Recent analysis of the genomic makeup of Viking Age Scandinavians (793–1066 CE) reflected gene flow from other European populations, as well as primarily genetic ancestry from populations preceding the Iron Age (500 BCE–800 CE) (Margaryan et al., 2020). While further analysis is needed to determine whether the observed similarity of the polymorphisms extends further to include whole mitogenomes, these findings suggested that certain haplogroups have been present in the region for many thousands of years.

Of the Modern Norwegian samples, 64% were localized to specific dialectal regions of Norway, whereas 36% could not be localized to any specific region. Nevertheless, the proportion of major haplogroups among those with no locations was similar to the

TABLE 1 Distribution of major mtDNA haplogroups by major dialectal region in Norway among Norwegians

	Southeast $n = 225$		West $n = 257$		Central $n = 268$		North $n = 5$		No location[a] $n = 419$		Total $n = 1174$	
Hg	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%
A	1	0.44	0	0	0	0	0	0	0	0	1	0.09
F	0	0	0	0	1	0.37	0	0	0	0	1	0.09
G	1	0.44	0	0	0	0	0	0	0	0	1	0.09
H	113	50.22	119	45.92	94	35.07	1	20	185	44.15	512	43.6
HV	7	3.1	5	1.95	14	5.22	1	20	13	3.11	40	3.42
I	7	3.11	5	1.95	2	0.74	1	20	15	3.58	30	2.57
J	17	7.55	28	10.89	54	20.16	0	0	50	11.93	149	12.69
JT	2	0.89	0	0	0	0	0	0	0	0	2	0.17
K	10	4.43	10	3.9	20	7.46	0	0	22	5.25	62	5.3
L	0	0	0	0	0	0	0	0	1	0.24	1	0.09
N	2	0.88	3	1.17	4	1.5	0	0	3	0.72	12	1.03
T	19	8.44	16	6.23	23	8.57	0	0	41	9.78	99	8.43
U	39	17.33	53	20.63	44	16.78	1	20	67	16	204	17.41
V	2	0.88	2	0.78	8	2.99	1	20	11	2.63	24	2.06
W	3	1.33	9	3.5	1	0.37	0	0	6	1.43	19	1.63
X	1	0.44	3	1.17	2	0.74	0	0	3	0.72	9	0.79
Z	1	0.44	4	1.56	1	0.37	0	0	2	0.48	8	0.68

Note: All mtDNA sequences were analyzed between np 16,024 and 16,383.

[a] Individuals for whom a geographic place of origin was not listed.

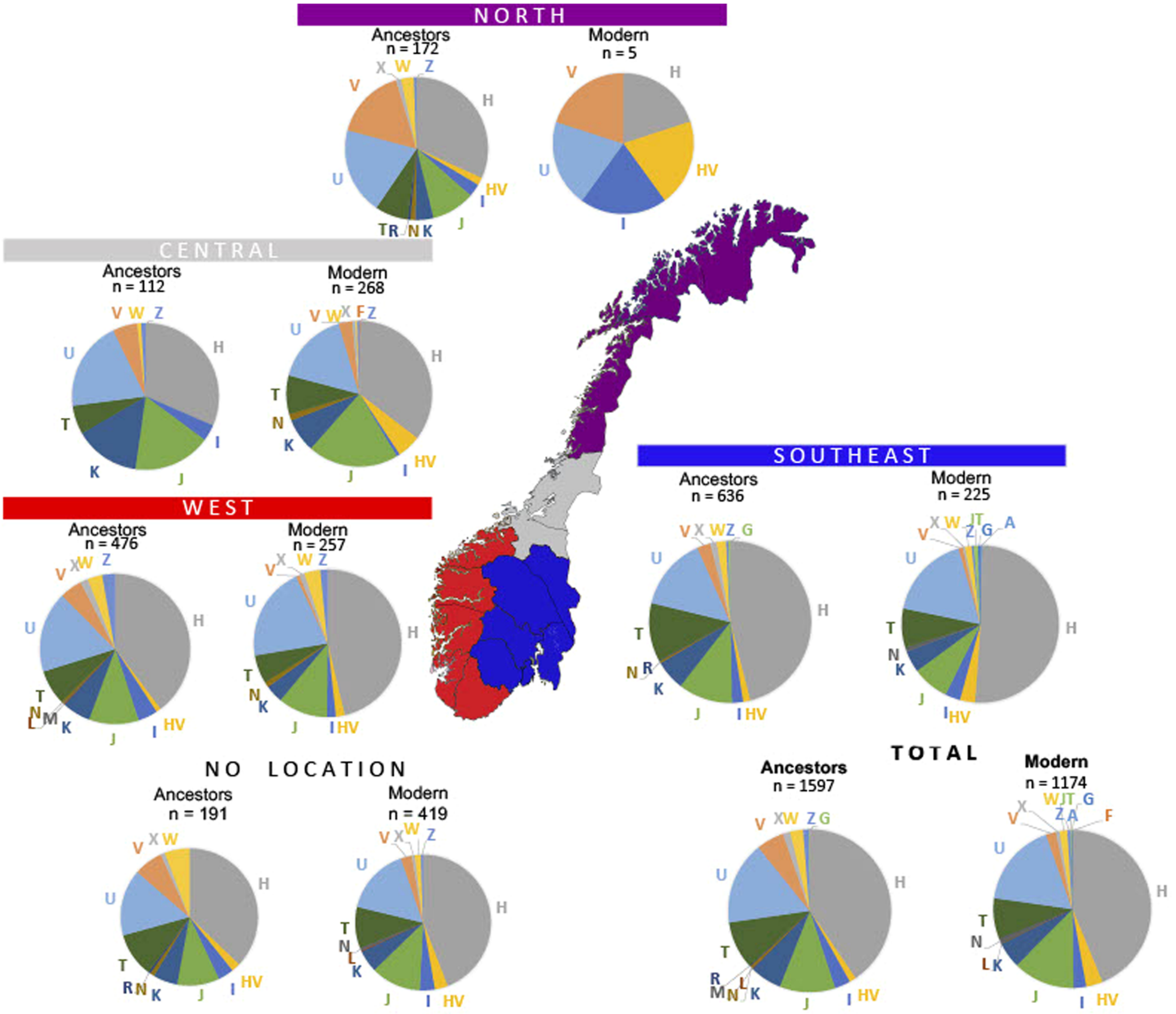

FIGURE 2 Comparison of mtDNA haplogroup distribution among ancestral populations of Norway (17th–20th century) versus the modern population by dialect region. The map of Norway is modified from a public domain map found at: https://en.wikipedia.org/wiki/Counties_of_Norway#/media/File:Nye_fylker_-_regjeringen.no.svg

proportions for Norwegians, overall (Fisher's $p = 0.20$). As a result, the individuals with no location were deemed to be representative of Norway as a whole. Accordingly, the mtDNA gene pool of Norwegians is defined, predominantly, by haplogroups H (44%), U (17%), J (13%), T (8%), K (5%), I (3%), HV (3%), V (2%), and W (2%), while all other haplogroups were present at 1% or less. These frequencies are similar to what was reported in the studies from which these data were obtained (Helgason et al., 2001; Krzewińska, 2014; Passarino et al., 2002).

Haplogroup distribution varied by dialectal region. Haplogroup H was most frequent in the Southeast dialectal region (50%) and least frequent in the Central dialectal region (35%) ($\chi^2 = 14.06$; $p < 0.001$) (Table 1). Haplogroup J appeared at the highest frequency in the Central dialectal region (20%) and the lowest in the Southeast dialectal region (8%) ($\chi^2 = 15.74$; $p < 0.001$). In the Central dialectal region, the haplogroup T occurred at the highest frequency (9%) and the lowest in the West dialectal region (6%), although this difference was not statistically significant ($\chi^2 = 0.33$; $p = 0.56$). Since only five individuals derived from the North dialectal region, the small sample size did not allow for any effective estimate of haplogroup frequencies there. Additional haplogroup detail for these mtDNA sequences are provided in Table S2.

A comparison of the distributional differences among the Modern population compared with the Ancestral population is displayed in Figure 2. Most noticeably, the frequency of haplogroup H in the Ancestral population was higher than in the Southeast dialectal region and lower in the North region ($\chi^2 = 11.31$, $p < 0.001$). Although the difference in the frequency of haplogroup U between the North and

Southeast region was not statistically significant ($\chi^2 = 2.6$, $p = 0.11$), haplogroup U5 appeared at high frequency in the North (for which 92% of the U mtDNAs belong to U5) compared to the Southeast ($\chi^2 = 7.35$, $p = 0.007$) region. The North was distinct from the other regions in the terms of the higher frequency of haplogroup V ($\chi^2 = 11.31$, $p < 0.001$), although haplogroups I and HV occurred at similar frequencies in the Ancestral North compared to the other regions (both $p > 0.05$).

3.2 | Genetic diversity and differentiation.

Overall, the level of genetic variation among Norwegian mtDNA was similar to that seen in other European populations, with about 50% being belonging to haplogroup H and the majority of the rest to other sequences consisting of other West Eurasian lineages described (Côrte-Real et al., 1996; Li et al., 2014; Richard et al., 2007). Summary statistics with the parameters of genetic diversity for Norwegians sorted by dialectal region are shown in Table 2. The HVSI sequences in Norwegians comprised 268 distinct haplotypes defined by 131 variable sites being identified among 1174 individuals. The mean number of nucleotide differences was 3.18, with the Central and West dialectal regions having the highest values (3.52 and 3.16, respectively). Similar values of haplotype and nucleotide diversity among Norwegians were noted in all dialect regions, except the North, for which only five individuals were identified. Each region also had Tajima's D that was consistent with a recent population expansions.

TABLE 2 Diversity indices for Norwegian subpopulations based on mtDNA HVS1 sequences

Population	Samples (*n*)	Haplotypes (h)	Variable sites (s)	Haplotype diversity (hd)	Nucleotide diversity (Pi)	Mean # of nucleotide differences (k)	Tajima D's	*p*-value for Tajima's D
Southeast	225	106	81	0.9271	0.00958	2.971	−2.41	$p < 0.01$
West	257	86	69	0.9192	0.01019	3.159	−2.09	$p < 0.05$
Central	268	81	69	0.9334	0.01134	3.517	−2.05	$p < 0.05$
North	5	4	4	0.9	0.00519	1.6	−1.18	N.S.
No Location	419	142	94	0.9207	0.01004	3.082	−2.27	$p < 0.01$
Total	1174	270	131	0.938	0.01026	3.182	−2.35	$p < 0.001$

Note: "N.S." indicated "not significant."

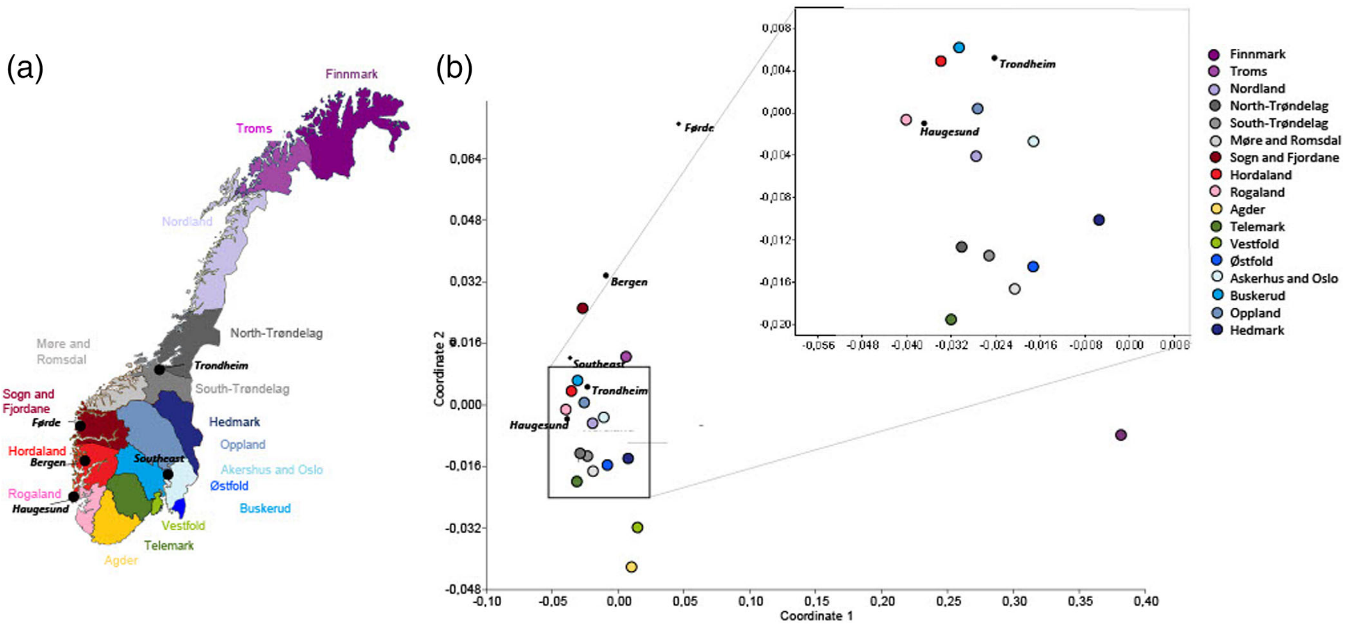

FIGURE 3 Multidimensional scaling plot of mtDNA diversity from specific locations in Norway (a) historical counties of Norway that represent the location of the ancestors' maternal lineages obtained from family tree DNA are in colored dots. Locations in black italics represent areas from which mtDNA data have been obtained among contemporary individuals. (b) A MDS plot of inter-population pairwise *Fst* values calculated from mtDNA HVSI sequences, with a magnified view of the center coordinates. Coordinates 1 and 2 for the modern populations are as follows: Møre and Romsdal (0.55, −0.12), Nordland (−0.13, 0.21), and Finnmark (0.46, 0.55). These points have not been included as the small sample sizes are not representative of mtDNA diversity in these regions and skews the overall plot to present these regions as false outliers

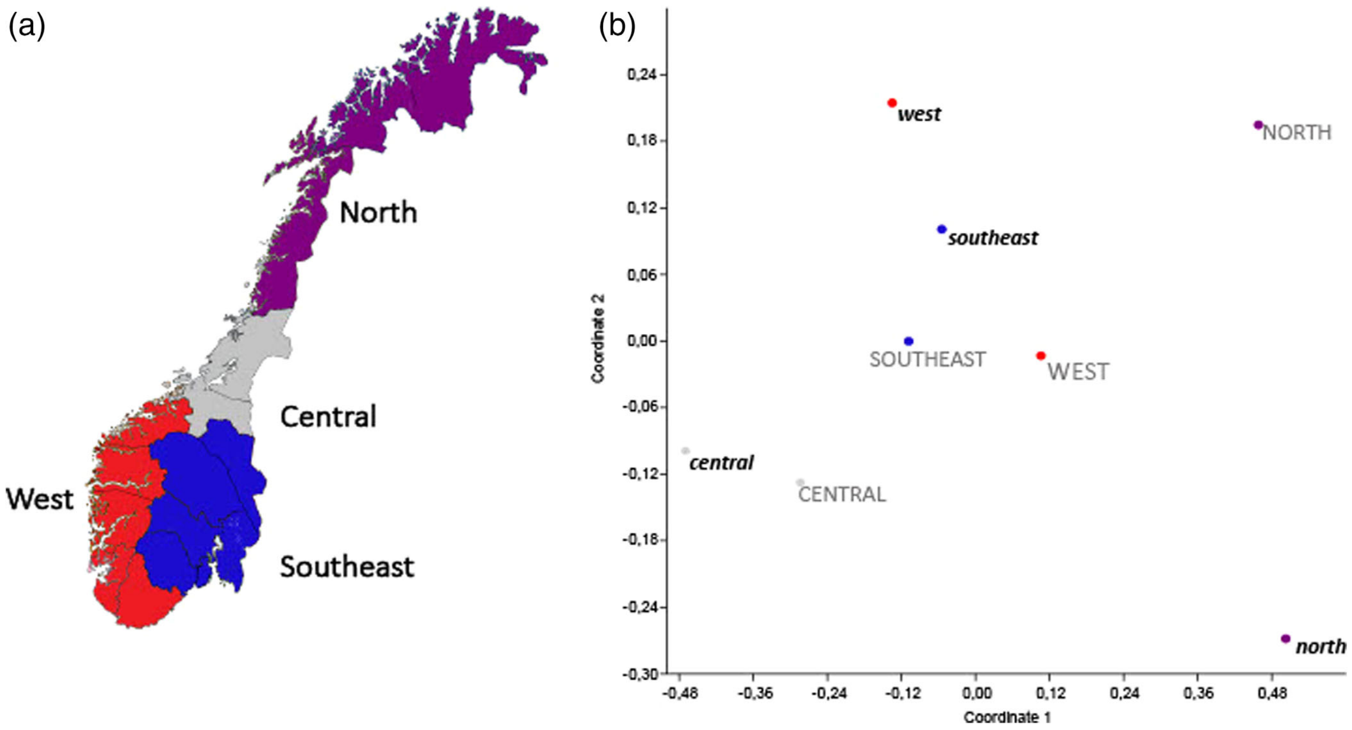

FIGURE 4 Influence of linguistic subdivisions on mtDNA diversity in Norway. (a) Black line divisions indicate the four general dialectal regions of Norway (north, central, southeast, and west). (b) MDS plot of inter-population pairwise *Fst* values calculated from mtDNA HVSI sequence data based on the four dialectal regions of Norway. mtDNA of descendants of historical regions (the ancestors) (capitalized gray font) and modern individuals and their current location in Norway (italicized black font)

3.3 | Inter-population relationships by locality and dialectal region

Using mtDNA data from Norwegians who had submitted information about the geographic location of their earliest matrilineal ancestor from The Norway DNA Project, we plotted these locations and those for modern Norwegians onto the county map of Norway (Figure 3a). Estimation of pairwise *Fst* values from HVSI sequences by specific Norwegian counties showed similarities between the locations for the Ancestral and Modern individuals (Table S3). When comparing the Fst values for Modern cities were compared to those of the Ancestral counties, the extent of differentiation between them was low: Bergen vs. Hordaland ($Fst = 0.0137$; $p = 0.05$); Førde versus Sogn and Fjordane ($Fst = 0.0177$, $p = 0.08$); and Haugesund vs. Rogaland ($Fst = 0.0050$; $p = 0.95$). The exception was Askerhus and Oslo compared with the modern Southeast ($Fst = 0.0092$; $p = 0.03$).

The Ancestral and the Modern Norwegian mtDNA data sets were subjected to AMOVA to determine the influence of geography and language on mtDNA diversity. The results pointed to generally low levels of population differentiation among Norwegians in different subpopulations ($Fst = 1.68\%$, $p < 0.001$) (Table S4). This analysis also showed that there was modest genetic differentiation by large dialectal regions (0.41%, $p < 0.001$) as well as subpopulation (0.81%; $p < 0.001$). Most of the differences came from Ancestral Finnmark, which had moderate genetic differentiation, followed by Ancestral Agder and Modern Førde (Table S3). In fact, the pattern of mtDNA diversity in Ancestral Finnmark differed significantly from that of all other Norwegian counties and Modern cities, with pairwise F*st* values ranging from 0.05 to 0.1 with *p*-values <0.001.

To visualize the genetic relationships between different Norwegian populations, an MDS plot was constructed using the pairwise F*st* values estimated for each of the Norwegian subpopulations (Figure 3b). The results showed that the majority of Norwegian counties were genetically similar, and that Norwegians with ancestry from the counties of the Southeast and Central regions had similar mtDNA backgrounds.

The Ancestral and Modern Norwegian populations were also partly differentiated to some degree based on the four major dialectal regions of the country (Figure 4a,b; Table S5). In general, the Ancestral populations tended to cluster closely toward the center of the plot, while there were greater levels of separation between Modern populations. Notably, the Southeast Modern and Ancestral populations had the lowest pairwise mtDNA distances relative to the other regions of Norway to each other (F*st* all 0.0050–0.0118) (Table S5). The Modern West population was distinct from the Ancestral West ($Fst = 0.0078$; $p < 0.000$). The Modern West population was differentiated from the Ancestral Southeast ($Fst = 0.0119$; $p < 0.001$), but had a lower F*st* value relative to the Modern Southeast ($Fst = 0.0052$; $p = 0.04$). These findings suggest recent changes in the distribution of maternal lineages over the past few centuries that have made the Modern West less dissimilar to the Modern Southeast. By contrast, the Central Modern and Ancestral populations were not significantly different from each other ($Fst = 0.0064$; $p = 0.13$). The North Ancestral population further differed from all other regional

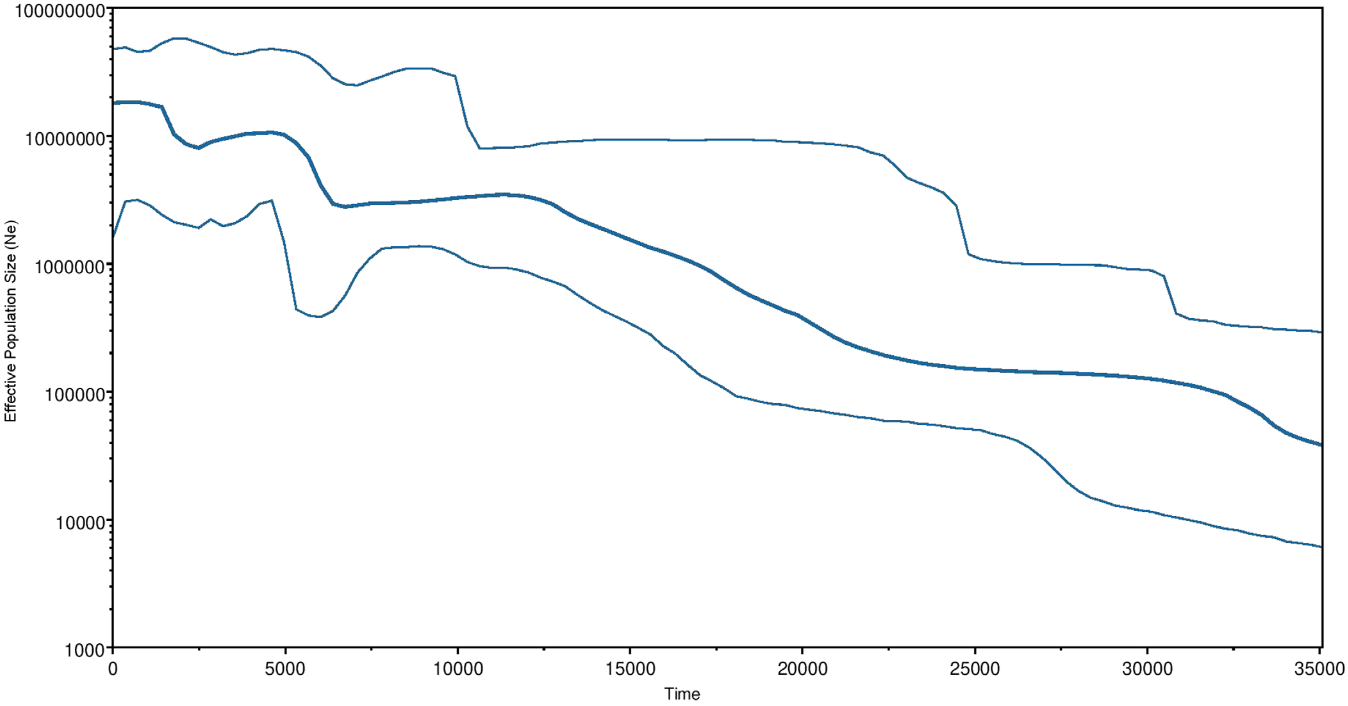

FIGURE 5 A Bayesian skyline plot (BSP) of Norwegian mtDNA sequences. A mutation rate of 1.64×10^{-7} was used to convert substitution rates into years (x-axis) and coalescent intensities into effective population sizes (y-axis)

populations ($p < 0.001$), except for the Modern North, from which it could not be differentiated due to its small sample size.

3.4 | Demography of Norwegian mtDNAs

To better understand the historical demography of the Norwegian population in terms of changes in the effective population size related to coalescent events, a demographic model with Bayesian analysis was conducted using the 1174 Modern samples (Figure 5). The x-axis shows the time from the present in units of thousands of years, and the y-axis is equal to Ne·μ, the product of the effective population size and the HVSI mutation rate calculated by Soares and colleagues (Soares et al., 2009). In this Bayesian skyline plot (BSP), the thick solid line represents the median posterior effective population size through time, while the thin lines show the 95% highest posterior density limits.

As seen in this BSP the effective population size (Ne) slowly grew from about 35 kya and then stabilized around 12 kya as the inland ice sheets began melting at the end of the Late Glacial Maximum (Glørstad et al., 2020). The earlier period of population growth likely corresponds to the initial settlement of the European continent by anatomically modern humans. The population size then increased again around 6 kya, which corresponds to the late Neolithic period when agriculture expanded into Norway (Hjelle et al., 2006). The population further increased from 2.5 to 1.6 to kya (or around 300 to 400 CE) during the Late Bronze Age, when the proto-Norse runic alphabet was established (Imer, 2011).

The BSP appears to slightly overestimate the effective population size based on this data set. However, this result is well within the uncertainty admitted by the 95% hypothetical posterior density limits (and may well be due to the stochastic error associated with this particular simulation). The growth projection was also similar to the BSP estimated from Danish mtDNA sequences using similar methodology (Li et al., 2014).

4 | DISCUSSION

We analyzed mtDNA HVS1 sequences from different Norwegian subpopulations delineated by dialectal region and geography to investigate the source of their matrilineal descent and to identify genetic differences that might be related to population movements. Overall, the Norwegian matrilineal gene pool is represented by a diverse set of mitochondrial lineages that belong primarily to eight West Eurasian haplogroups, which are distributed differently in various regional areas. Our findings indicate that Norwegian mtDNA diversity was modestly influenced by geography, and to lesser extent by language (dialect region).

While Norwegians share many maternal lineages in common, their subpopulations differed slightly from each other in regions linked to known maritime routes around the perimeter of the country rather than latitudinal land-traversing routes. The differences between otherwise closely located regions (e.g., the Ancestral West Norway versus Ancestral Southeast Norway, which were significantly different, $p < 0.001$) were likely shaped by the geographic barrier of tall mountain ranges that prevented frequent close contact between the two regions. As a result, there are genetic similarities between several settlements located along the country's longitudinal coastline that would have been otherwise difficult to reach by land due to the numerous fjords that separate them.

The mountainous regions and fjords that topographically separate regions of Norway have led to maritime travel becoming an essential component of human movements within the country. Maritime activities have molded the development of Norwegian culture and society for many millennia. The importance of marine vessels is reflected in their appearance in early rock art found all over Norway (Ballard et al., 2004; Bjerck, 2012; Ljunge, 2015). While recent archaeological evidence indicates that, by 6180–6680 cal yr BP, people sometimes traveled through the Jotunheimen Mountains that separate the West from the Southeast (Pilø et al., 2020), this travel was likely restricted to the winter months when bogs and streams were frozen over. Ships were also clearly crucial for the Norse expansion during the Viking Age (Østmo, 2003). Moreover, the mid-19th century "golden age" of sailing vessels has been recorded as being a catalyst for major timber and fishing-based economic activities within in Norway that led to eventual economic prosperity (Fischer & Nordvik, 1987; Haaland & Svihus, 2011).

Given its geographical barriers, Norwegians maintained remarkable contact across long distances through maritime travel. The terms "Norway" and "Norwegian" had been in use since at least the 9th century by the Viking Age seafarer Ottar from Hålogaland (in the North), and the petty kingdoms of Norway had been politically unified as a single entity by the 11th century (Bagge, 1995; Larsen, 1950), relatively earlier than other countries of similar size in Europe. Maritime routes remained the primary mode of trade and transportation until the use of motorized vehicles became popular in Norway in the early 20th century (Jentoft & Finstad, 2018) and railway networks expanded, with the Bergen line (*Bergenbanen*) in the West reaching the inland Southeast in 1909 (Haaland & Svihus, 2011). More recent more routes of modern travel may have led to closer genetic similarities between the western city of Bergen and the southeastern city of Oslo in the modern data set.

The detailed locality analyses indicate that Norwegian subpopulations are genetically similar, while Norwegians from Finnmark, and to a lesser extent, Agder and modern Førde, appear to have become moderately differentiated. The observed level of dissimilarity between these regions is similar to what had been reported for Y-chromosome (paternal) lineages in Norwegians (Dupuy et al., 2006). Dupuy et al. (2006) reported regional variation in Y-chromosome variation for Finnmark (north), Sogn and Fjordane (west), and Agder (south), and indicated that these three areas had the highest degree of dissimilarity. While men were more often the migrants who traveled long distances in Norway (Thorvaldsen, 2019), parish registers indicate that many migrations also involved young couples who had given birth to children only after moving to a new locality (Svalestuen, 1978; Thorvaldsen, 2019). By 1920, it was as usual for women as men to be migrants within Norway (Thorvaldsen, 2019).

Some of the observed regional differences may be explained by specific internal migration patterns. First, the difference between Finnmark and other Norwegian regions may be due to its geographical isolation for many centuries. Norwegians have been living in the northernmost parts of the country since at least the 14th century (Opsahl, 2020). However, the population was scattered along coastal areas, and the region was also occupied by the Saami, an indigenous people in Norway that had been seasonally nomadic until the late 19th century (Ahren, 2004). Interestingly, Norwegian Saami populations contain a higher proportion of U5b1b mtDNAs than Norwegians (Dupuy & Olaisen, 1996; Tambets et al., 2004). However, Krzewinska et al. detected this haplogroup in two individuals from the Late Iron Age who had received a Norse burial, suggesting that some Saami individuals may have been assimilated or accepted into Norse society as early as the 10th century CE (Krzewińska et al., 2015).

It is worth noting that the F*st* value of dissimilarity among Norwegians of Ancestral Finnmark are lower than those of Norwegian Saami population. The F*st* values in the order of 0.2 (all $p < 0.05$ for Bergen, Oslo, Førde and Trøndelag) (Saami as reported by Krzewińska, 2014) vs. 0.1 (all $p < 0.001$ for the same regions) (Norwegian Finnmark in this study). No Norwegians in our study nor in the study by Krzewińska, 2014 had F*st* values above 0.2. Thus, while the northern Finnmark subpopulation was somewhat more genetically dissimilar to all other Norwegian subpopulations, the level of genetic dissimilarity is higher among the Norwegian Saami, who also live in the north but who have a distinct history and migration patterns (Tambets et al., 2004).

In the 1780s, a mass movement of settlers from the southern to the more northern regions of Norway was encouraged by the appointed bailiff in order to take advantage of fishing opportunities there (Thorvaldsen, 2019). Involving some 1000 individuals, this northward migration continued until the 1830s, when the introduction of potato farming and smallpox vaccination made southeastern and western Norway more hospitable and prosperous (Gjerde, 1989; Tryland, 2001).

A second and more recent migration is the movement of rural farming populations to city locations in the southeast. Our analysis of modern (primarily urban-located) Norwegians in Oslo and each of the surrounding farming areas, namely, Oppland, Hedmark, and Buskerud, show strong genetic similarities, and suggest that migration from the inland to the coastal southeast during industrialization contributed their genetic make-up. In addition, the economic opportunities within the capital of Oslo have attracted populations from the entire country, which reflected in the diversity of mtDNA haplogroups represented in the area and has continued to the present day. According to the National Statistics Bureau archives, Oslo has had a positive net migration rate (i.e., once Norwegians migrate to Oslo, they tend to settle there permanently), as well as the highest overall migration rate within the country since at least 1966. By contrast, those in northern Norway as well as the rural southeastern areas of Hedmark and Oppland Counties have had negative net migration rates (Longva, 2000). In the south of Norway, Agder County's dependence on shipbuilding and its strategically located southern fishing shores may have kept that part of the country more independent and isolated from the rest of the southeastern regional area (Gjerde, 1989) and more connected with the fishing coasts of the southwest. Much of the Norwegian population today still lives in or near coastal cities, in particular Oslo, Bergen, and Trondheim (Statistics Norway: Statistics Central Bureau, 2020).

A third and different pattern was found for the western part of Norway. While the haplogroup composition of Ancestral populations from Sogn and Fjordane is like other counties of the West, modern Førde has become more heterogeneous over time. According to census records, 17.2 per 1000 individuals from the Sogn municipality emigrated to America yearly from 1856 to 1865, with a total of 6430 emigrants leaving Norway during this period (Gjerde, 1989; Svalestuen, 1978). By 1905, 40% of Sogn and Fjordane inlanders had left for the US, while 20%–30% left in the central parts of Sogn and Fjordane (Gjerde, 1989; Østrem, 2015). As population growth outpaced the available food supply, many Norwegians in the western part of the country were lured by the possibility of owning arable farmland in the northwestern United States that could not be offered in the western Norway (Gjerde, 1989). After Ireland, the second largest number of immigrants to the US and the majority came from Norway, in particular the north-central part of the West (Gjerde, 2007).

We found that the modern Førde population was not significantly different from Ancestral Sogn and Fjordane ($p = 0.08$). Nevertheless, the loss of some maternal lineages may have widened the difference between modern Førde and other Norwegian subpopulations over time. Indeed, the uniqueness of Sogn and Fjordane had been reported based on both Y chromosome variation (Dupuy et al., 2006) and the higher proportion of the Kell (K+) blood group (Kornstad, 1997). In addition, the uniqueness of modern-day Førde may be due to the natural boundaries of the region (Krzewińska, 2014), with the highest peak of Jotunheimen being located at this county's eastern border.

On a larger time scale, our phylogeographic analysis pointed to some founder maternal lineages that are still shared by Norwegians from the earliest inhabitants of the Mesolithic era 9000 BP and Late Iron Age (500 to 1050 CE) (Günther et al., 2018; Krzewińska et al., 2015). The frequency of these haplogroups among the current Norwegian population has changed modestly over time, with slightly higher frequencies of U and K but slightly lower frequencies of H and J (Krzewińska et al., 2015). Furthermore, the early infiltration of Orkney, English, Scottish, Irish, and other Scandinavian lineages through slave trading since the Viking expansion has been reported by Krzewińska et al. (2015), who also showed their continued genetic affinities among the samples from Haugesund, Bergen, Førde, and Trondheim (Krzewińska, 2014).

In more recent times, the diversity of haplogroups among ethnic Norwegians shows a modest expansion. All of the haplogroups present in the Modern Norwegian population were also present among the Ancestor Norwegian population as expected, except for haplogroups N11 and F2a, which are present at low frequency within the Modern population. Because these mtDNAs belong to East Eurasian haplogroups, their presence is likely due to recent immigration of people from regions in which these maternal lineages are more common, that is, South-East Asia. In addition, haplogroup L2, the only maternal lineage of African origin, found both our study and that of Passarino et al., (2002), also appears among one participant in The Norwegian DNA Project (not included in this analysis) and is associated with an individual from the Dominican Republic who arrived in Norway in 1860. A haplogroup L2 mtDNA also appears in the Hordaland Ancestor population in an individual with a Norwegian first name and surname. Thus, L2 mtDNA was introduced into Norway by early immigrants. Conversely, G2a1 and Z1a, which are both haplogroups of East Eurasian origin, have been present among Norwegian Ancestors since at least the 1600s and likely entered the population during recent prehistory. Haplogroup G2a is also present in similarly low frequencies among populations of Central and Eastern Europe, while haplogroup Z is present at about 4% to 7% among Saami populations (Ingman & Gyllensten, 2007; Mielnik-Sikorska et al., 2013; Tambets et al., 2004).

In conclusion, our study provides an extensive survey of mtDNA haplogroup distributions among Norwegians. It reveals the importance of geographic regions as boundaries of gene flow among a people deeply influenced by Norway's topography and maritime travel around the country. The study also serves as a comprehensive framework for understanding how the pattern of genetic variation in the Norwegian population has been shaped by major historical events over several generations. Further studies of Norwegian maternal lineages, specifically those focusing on mitogenome sequence variation, will provide a more comprehensive evolutionary portrait of Norwegian population history, demography, and migration.

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CONFLICT OF INTEREST

All authors report no conflicts of interest.

AUTHOR CONTRIBUTIONS

Dana Kristjansson: Conceptualization; data curation; formal analysis; investigation; methodology; software; validation; visualization; writing-original draft; writing-review & editing. **Jon Bohlin:** Resources; writing-review & editing. **Astanand Jugessur:** Funding acquisition; project administration; writing-review & editing. **Theodore Schurr:** Conceptualization; funding acquisition; investigation; methodology; project administration; resources; supervision; writing-review & editing.

DATA AVAILABILITY STATEMENT

No new data was generated in this study. The data that support the findings of this study are available from public repositories and the published literature. The data obtained from Genbank can be found at https://www.ncbi.nlm.nih.gov/genbank/, reference numbers (AY026032.1-AY025708.1, EU684448.1, EU980593.1, FJ499472.1, FJ652065.1, GU815340.1, HQ153430.1, HQ660704.1, HQ676806.1, HQ698894.1, HQ711364.1, HQ917079.1, JF825889.1, JN603188.1, JQ735910.1, JQ763435.1, JQ898578.1, KC170990.1, KF057946.1, KF817593.1, KJ603459.1, KP136794.1, KP407173.1, KP733897.1, KP969064.1,

KT210950.1, KT886412.1, KU057167.1, KU873089.1. KX129707.1, KX980415.1, KY000078.1, KY115220.1, MF103670.1, MF103671.1, MF116363.1, MF116367.1, MF597726.1, MF693153.1, MG436774.1, MG687433.1, MH142589.1, MH550114.1, MH899455.1, MK434282.1, MK792836.1, MN318468.1, MN599048.1.) Data from the published literature can be found in the following published articles referenced within the bibliography of this article: Opdal SH et al (1998), Table 1, DOI: 10.1080/080352598750031347 and Passarino G et al (2002), Table 3, DOI: 10.1038/sj.ejhg.5200834. Data from Krzewińska, M. (2014). Tables S2-S11 are published in the doctoral thesis Human origins and migrations in Norway inferred from ancient and modern DNA analysis. Theses at University of Oslo are available from the university library upon request (Object ID: 71499613630002201). The FamilyTreeDNA data were derived from the following resource that is openly available: https://www.familytreedna.com/public/Norway?iframe=mtresults.

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REFERENCES

Ahren, M. (2004). Indigenous Peoples' culture, customs, and traditions and customary law - the Saami People's perspective. *Arizona Journal of International and Comparative Law*, *21*, 63. https://heinonline.org/HOL/Page?handle=hein.journals/ajicl21&id=81&div=&collection

Bagge, S. (1995). Nationalism in Norway in the middle ages. *Scandinavian Journal of History*, *20*(1), 1–18. https://doi.org/10.1080/03468759508579290

Ballard, C., Bradley, R., Myhre, L. N., & Wilson, M. (2004). The ship as symbol in the prehistory of Scandinavia and Southeast Asia. *World Archaeology*, *35*(3), 385–403. https://doi.org/10.1080/0043824042000185784

Bang-Andersen, S. (2003). Southwest Norway at the Pleistocene/Holocene transition: Landscape development, colonization, site types, settlement patterns. *Norwegian Archaeological Review*, *36*(1), 5–25. https://doi.org/10.1080/00293650307293

Bang-Andersen, S. (2012). Colonizing contrasting landscapes.: The pioneer coast settlement and inland utilization in southern Norway 10,000-9500 years before present. *Oxford Journal of Archaeology*, *31*(2), 103–120. https://doi.org/10.1111/j.1468-0092.2012.00381.x

Behar, D. M., Van Oven, M., Rosset, S., Metspalu, M., Loogväli, E. L., Silva, N. M., Kivisild, T., Torroni, A., & Villems, R. (2012). A "copernican" reassessment of the human mitochondrial DNA tree from its root. *American Journal of Human Genetics*, *90*(4), 675–684. https://doi.org/10.1016/j.ajhg.2012.03.002

Bjerck, H. (2012). On the outer fringe of the human world: Phenomenological perspectives on anthropomorphic cave paintings in Norway. In K. A. Bergsvik & R. Skeates (Eds.), *Caves in Context: the cultural significance of caves and rockshelters in Europe (pp. 48–64)*. Oxbow Books.

Côrte-Real, H. B. S. M., Macaulay, V. A., Richards, M. B., Hariti, G., Issad, M. S., Cambon-Thomsen, A., Papiha, S., Bertranpetit, J., & Sykes, B. C. (1996). Genetic diversity in the Iberian Peninsula determined from mitochondrial sequence analysis. *Annals of Human Genetics*, *60*(4), 331–350. https://doi.org/10.1111/j.1469-1809.1996.tb01196.x

Derry, T. K. (2012). *A history of Scandinavia: Norway, Sweden, Denmark, Finland and Iceland* (13th ed.). University of Minnesota Press.

Drummond, A. J., Rambaut, A., Shapiro, B., & Pybus, O. G. (2005). Bayesian coalescent inference of past population dynamics from molecular sequences. *Molecular Biology and Evolution*, *22*(5), 1185–1192. https://doi.org/10.1093/molbev/msi103

Dupuy, B. M., & Olaisen, B. (1996). *mtDNA sequences in the Norwegian Saami and main populations* 23–25. Springer, . https://doi.org/10.1007/978-3-642-80029-0_6

Dupuy, B. M., Stenersen, M., Lu, T. T., & Olaisen, B. (2006). Geographical heterogeneity of Y-chromosomal lineages in Norway. *Forensic Science International*, *164*(1), 10–19. https://doi.org/10.1016/j.forsciint.2005.11.009

Dyrvik, S. (1972). Historical demography in Norway 1660-1801: A short survey. *Scandinavian Economic History Review*, *20*(1), 27–44. https://doi.org/10.1080/03585522.1972.10407709

Excoffier, L., & Lischer, H. E. L. (2010). Arlequin suite ver 3.5: A new series of programs to perform population genetics analyses under Linux and windows. *Molecular Ecology Resources*, *10*(3), 564–567. https://doi.org/10.1111/j.1755-0998.2010.02847.x

Fischer, L. R., & Nordvik, H. W. (1987). From Namsos to Halden: Myths and realities in the history of norwegian seamen's wages, 1850-1914. *Scandinavian Economic History Review*, *35*(1), 41–64. https://doi.org/10.1080/03585522.1987.10408081

Gjerde, J. (1989). *From peasants to farmers: The migration from Balestrand, Norway, to the upper middle west*. Cambridge University Press.

Gjerde, J. (2007). Fiksjon, fakta og forskning: seminar om den tidlige utvandringa til Amerika. In O. Østrem (Ed.), *Echoes of freedom: The Norwegian encounter with America*. (48–59). Stavanger, Norway: University of Stavanger.

Glørstad, H., Gundersen, J., Kvalø, F., Nymoen, P., Simpson, D., & Skar, B. (2020). Norway: Submerged stone age from a norwegian perspective. In *Coastal research library* (Vol. 35, pp. 125–140). Springer. https://doi.org/10.1007/978-3-030-37367-2_6

Grabbe, M., Lalander, E., Lundin, S., & Leijon, M. (2009). A review of the tidal current energy resource in Norway. *Renewable and Sustainable Energy Reviews*, *13*, 1898–1909. https://doi.org/10.1016/j.rser.2009.01.026

Günther, T., Malmström, H., Svensson, E. M., Omrak, A., Sánchez-Quinto, F., Kılınç, G. M., Krzewińska, M., Eriksson, G., Fraser, M., Edlund, H., Munters, A. R., Coutinho, A., Simões, L. G., Vicente, M., Sjölander, A., Jansen Sellevold, B., Jørgensen, R., Claes, P., Shriver, M. D., … Jakobsson, M. (2018). Population genomics of Mesolithic Scandinavia: Investigating early postglacial migration routes and high-latitude adaptation. *PLoS Biology*, *16*(1), e2003703. https://doi.org/10.1371/journal.pbio.2003703

Haaland, A., & Svihus, Å. (2011). Coastal and maritime Norway. Art Council Norway, The Norwegian Coastal Administration, The Directorate for Cultural Heritage and Directory of Fisheries. https://ra.brage.unit.no/ra-xmlui/bitstream/handle/11250/176922/Fortellinger_kystNorge_Kyst_og_havlandet_eng.pdf?sequence=1

Hammer, D. A. T., Ryan, P. D., Hammer, Ø., & Harper, D. A. T. (2001). Past: paleontological statistics software package for education and data analysis. *Palaeontologia Electronica*, *4*(1), 1–9. http://palaeo-electronica.orghttp//palaeo-electronica.org/2001_1/past/issue1_01.htm

Haugen, E. (1959). Planning for a standard language in modern Norway. *Anthropological Linguistics*, *1*, 8–21.

Helgason, A., Hickey, E., Goodacre, S., Bosnes, V., Stefánsson, K., Ward, R., & Sykes, B. (2001). mtDNA and the islands of the North Atlantic: Estimating the proportions of Norse and Gaelic ancestry. *American Journal of Human Genetics*, *68*(3), 723–737. https://doi.org/10.1086/318785

Helskog, K. (1985). Boats and meaning: A study of change and continuity in the Alta fjord, arctic Norway, from 4200 to 500 years B.C. *Journal of Anthropological Archaeology*, *4*(3), 177–205. https://doi.org/10.1016/0278-4165(85)90002-9

Hervik, A., Tretvik, T., & Øvstedal, L. (1993). *Norway: Crossing Fjords and Mountains* (pp. 349–365). Springer. https://doi.org/10.1007/978-94-015-8118-9_20

Hjelle, K. L., Hufthammer, A. K., & Bergsvik, K. A. (2006). Hesitant hunters: A review of the introduction of agriculture in western Norway. *Environmental Archaeology*, *11*(2), 147–170. https://doi.org/10.1179/174963106x123188

Imer, L. (2011). The oldest runic monuments in the north. *NOWELE. North-Western European Language EvolutionNOWELE / North-Western European Language EvolutionNOWELE*, *62–63*(63), 169–212. https://doi.org/10.1075/nowele.62-63.04ime

Ingman, M., & Gyllensten, U. (2007). A recent genetic link between Sami and the Volga-Ural region of Russia. *European Journal of Human Genetics*, *15*(1), 115–120. https://doi.org/10.1038/sj.ejhg.5201712

Jentoft, S., & Finstad, B. P. (2018). Building fisheries institutions through collective action in Norway. *Maritime Studies*, *17*(1), 13–25. https://doi.org/10.1007/s40152-018-0088-6

Katoh, K., & Standley, D. M. (2013). MAFFT multiple sequence alignment software version 7: Improvements in performance and usability. *Molecular Biology and Evolution*, *30*(4), 772–780. https://doi.org/10.1093/molbev/mst010

Kleppe, J. I. (2014). Desolate landscapes or shifting landscapes? Late glacial/early post-glacial settlement of northernmost Norway in the light of new data from eastern Finnmark. In F. Riede & M. Tallavaara (Eds.), BAR Intern *Lateglacial and postglacial pioneers in northern Europe*. Archaeopress.

Knutsen, H. (2019). NIBIO POP 6(8)2020.

Kornstad, L. (1997). Frequency of the blood group antigen K and the A1A2BO groups in the Norwegian counties. *Gene Geography: A Computerized Bulletin on Human Gene Frequencies*, *11*(1), 37–46. https://europepmc.org/article/med/9615212

Krzewińska, M. (2014). Human origins and migrations in Norway inferred from ancient and modern DNA analysis. Ph.D., Museum of Cultural Heritage and Department of Biosciences, University of Oslo.

Krzewińska, M., Bjørnstad, G., Skoglund, P., Olason, P. I., Bill, J., Götherström, A., & Hagelberg, E. (2015). Mitochondrial DNA variation in the Viking age population of Norway. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, *370*(1660), 20130384. https://doi.org/10.1098/rstb.2013.0384

Larsen, K. (1950). *A history of Norway* (2nd ed.). Princeton University Press.

Lembring, M., Van Oven, M., Montelius, M., & Allen, M. (2013). Mitochondrial DNA analysis of Swedish population samples. *International Journal of Legal Medicine*, *127*(6), 1097–1099. https://doi.org/10.1007/s00414-013-0908-6

Li, S., Besenbacher, S., Li, Y., Kristiansen, K., Grarup, N., Albrechtsen, A., Sparsø, T., Korneliussen, T., Hansen, T., Wang, J., Nielsen, R., Pedersen, O., Bolund, L., & Schierup, M. H. (2014). Variation and association to diabetes in 2000 full mtDNA sequences mined from an exome study in a Danish population. *European Journal of Human Genetics*, *22*(8), 1040–1045. https://doi.org/10.1038/ejhg.2013.282

Librado, P., & Rozas, J. (2009). DnaSP v5: A software for comprehensive analysis of DNA polymorphism data. *Bioinformatics*, *25*(11), 1451–1452. https://doi.org/10.1093/bioinformatics/btp187

Ljunge, M. (2015). Capturing images: Knowledge, ownership and the materiality of cave art. In A. Klevnäs & C. Hedenstierna-Jonson (Eds.), *Own or be owned: Archaeological approaches to the concept of possession (pp. 131–140)*. Stockholm University.

Longva, S. (2000). Population statistics 1998 with figures as of 1 January 1999.

Malmström, H., Linderholm, A., Skoglund, P., Storå, J., Sjödin, P., Gilbert, M. T. P., Holmlund, G., Willerslev, E., Jakobsson, M., Lidén, K., & Götherström, A. (2015). Ancient mitochondrial DNA from the northern fringe of the Neolithic farming expansion in Europe sheds light on the dispersion process. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, *370*(1660), 20130373. https://doi.org/10.1098/rstb.2013.0373

Margaryan, A., Lawson, D. J., Sikora, M., Racimo, F., Rasmussen, S., Moltke, I., Cassidy, L. M., Jørsboe, E., Ingason, A., Pedersen, M. W., Korneliussen, T., Wilhelmson, H., Buś, M. M., de Barros Damgaard, P., Martiniano, R., Renaud, G., Bhérer, C., Moreno-Mayar, J. V., Fotakis, A. K., … Willerslev, E. (2020). Population genomics of the Viking world. *Nature*, *585*(7825), 390–396. https://doi.org/10.1038/s41586-020-2688-8

Mielnik-Sikorska, M., Daca, P., Malyarchuk, B., Derenko, M., Skonieczna, K., Perkova, M., Dobosz, T., & Grzybowski, T. (2013). The history of Slavs inferred from complete mitochondrial genome sequences. *PLoS One*, *8*(1), e54360. https://doi.org/10.1371/journal.pone.0054360

Nguyen, L.-T., Schmidt, H. A., von Haeseler, A., & Minh, B. Q. (2015). IQ-TREE: A fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Molecular Biology and Evolution*, *32*(1), 268–274. https://doi.org/10.1093/molbev/msu300

Niemi, E., Myhre, J. E., & Kjeldstadli, K. (2003). I nasjonalstatens tid 1814-1940. In K. Kjeldstadli (Ed.), *Norwegian immigration history* (2nd ed.). Oslo, Norway: Pax.

Opdal, S. H., Rognum, T. O., Vege, Å., Stave, A. K., Dupuy, B. M., & Egeland, T. (1998). Increased number of substitutions in the D-loop of mitochondrial DNA in the sudden infant death syndrome. *Acta Paediatrica, International Journal of Paediatrics*, *87*(10), 1039–1044. https://doi.org/10.1080/080352598750031347

Opsahl, E. (2020). Avaldsnes' position in Norway in the 14th century. In D. Skre (Ed.), *Rulership in 1st to 14th century Scandinavia. Royal graves and sites at Avaldsnes and beyond* (pp. 517–529). De Gryuter.

Østmo, E. (2003). When the Norsemen learned to row: A technological innovation for shipping in the early iron age. *Viking: Norwegian Archaeological Yearbook*, *66*, 7–29.

Østrem, N. O. (2015). *Suget frå Amerika - Norgeshistorie*. https://www.norgeshistorie.no/industrialisering-og-demokrati/1546-suget-fra-amerika.html

Passarino, G., Cavalleri, G. L., Lin, A. A., Cavalli-Sforza, L. L., Børresen-Dale, A. L., & Underhill, P. A. (2002). Different genetic components in the Norwegian population revealed by the analysis of mtDNA and Y chromosome polymorphisms. *European Journal of Human Genetics*, *10*(9), 521–529. https://doi.org/10.1038/sj.ejhg.5200834

Pilø, L. H., Barrett, J. H., Eiken, T., Finstad, E., Grønning, S., Post-Melbye, J. R., Nesje, A., Rosvold, J., Solli, B., & Ødegård, R. S. (2020). Interpreting archaeological site-formation processes at a mountain ice patch: A case study from Langfonne, Norway. *The Holocene*, *3*, 469–482. https://doi.org/10.1177/0959683620972775

Pryser, T. (1981). In B. Gjerdåker (Ed.), *På flyttefot: Innanlands vandring på 1800-talet* (pp. 59–69). Det Norske Samlaget.

R Core Team. (2018). R: A language and environment for statistical computing. R Foundation for Statistical Computing.

Rambaut, A., Drummond, A. J., Xie, D., Baele, G., & Suchard, M. A. (2018). Posterior summarization in Bayesian phylogenetics using tracer 1.7. *Systematic Biology*, *67*(5), 901–904. https://doi.org/10.1093/sysbio/syy032

Richard, C., Pennarun, E., Kivisild, T., Tambets, K., Tolk, H. V., Metspalu, E., Reidla, M., Chevalier, S., Giraudet, S., Lauc, L. B., Peričić, M., Rudan, P., Claustres, M., Journel, H., Dorval, I., Müller, C., Villems, R., Chaventré, A., & Moisan, J. P. (2007). An mtDNA perspective of French genetic variation. *Annals of Human Biology*, *34*(1), 68–79. https://doi.org/10.1080/03014460601076098

Skjekkeland, M. (2005). *Dialektar i Noreg–Tradisjon og Fornying*. Høyskoleforlaget. https://scholar.google.com/scholar?hl=no&as_sdt=0%2C5&q=Skjekkeland%2C+M.+%282005%29.+Dialektar+i+Noreg–Tradisjon+og+Fornying.+Kristiansand%3A+Høyskoleforlaget.&btnG

Skoglund, P., Malmström, H., Raghavan, M., Storå, J., Hall, P., Willerslev, E., Gilbert, M. T. P., Götherström, A., & Jakobsson, M. (2012). Origins and genetic legacy of neolithic farmers and hunter-gatherers in Europe. *Science*, *336*(6080), 466–469. https://doi.org/10.1126/science.1216304

Soares, P., Alshamali, F., Pereira, J. B., Fernandes, V., Silva, N. M., Afonso, C., Costa, M. D., Musilová, E., MacAulay, V., Richards, M. B., Černý, V., & Pereira, L. (2012). The expansion of mtDNA haplogroup L3 within and out of Africa. *Molecular Biology and Evolution*, *29*, 915–927. https://doi.org/10.1093/molbev/msr245

Soares, P., Ermini, L., Thomson, N., Mormina, M., Rito, T., Röhl, A., Salas, A., Oppenheimer, S., Macaulay, V., & Richards, M. B. (2009). Correcting for purifying selection: An improved human mitochondrial molecular clock. *American Journal of Human Genetics*, *84*(6), 740–759. https://doi.org/10.1016/j.ajhg.2009.05.001

Sølvi, S. (1979). *Folkevekst og flytting: en historisk-demografisk studie i 1700-årenes Øst-Norge*. Universitetsforlaget. http://urn.nb.no/URN:NBN:no-nb_digibok_2009062901084

Statistics Norway: Statistics Central Bureau. (2020). *Facts about the Population*. https://www.ssb.no/en/befolkning/statistikker/beftett

Stroeven, A. P., Hättestrand, C., Kleman, J., Heyman, J., Fabel, D., Fredin, O., Goodfellow, B. W., Harbor, J. M., Jansen, J. D., Olsen, L., Caffee, M. W., Fink, D., Lundqvist, J., Rosqvist, G. C., Strömberg, B., & Jansson, K. N. (2016). Deglaciation of Fennoscandia. *Quaternary Science Reviews*, *147*, 91–121. https://doi.org/10.1016/j.quascirev.2015.09.016

Suchard, M. A., Lemey, P., Baele, G., Ayres, D. L., Drummond, A. J., & Rambaut, A. (2018). Bayesian phylogenetic and phylodynamic data integration using BEAST 1.10. *Virus Evolution*, *4*(1), 1–5. https://doi.org/10.1093/ve/vey016

Svalestuen, A. A. (1978). Om den Regionale Spreiinga av Norsk Utvandring før 1865. In A. Engen (Ed.), *Utvandringa-Det Store Opbrotet (p. 77)*. Det Norske Samlaget.

Tambets, K., Rootsi, S., Kivisild, T., Help, H., Serk, P., Loogväli, E. L., Tolk, H. V., Reidla, M., Metspalu, E., Pliss, L., Balanovsky, O., Pshenichnov, A., Balanovska, E., Gubina, M., Zhadanov, S., Osipova, L., Damba, L., Voevoda, M., Kutuev, I., … Villems, R. (2004). The Western and eastern roots of the Saami - the story of genetic "outliers" told by mitochondrial DNA and Y chromosomes. *American Journal of Human Genetics*, *74*(4), 661–682. https://doi.org/10.1086/383203

Tamura, K., & Nei, M. (1993). Estimation of the number of nucleotide substitutions in the control region of mitochondrial DNA in humans and chimpanzees. *Molecular Biology and Evolution*, *10*(3), 512–526. https://doi.org/10.1093/oxfordjournals.molbev.a040023

The Norway DNA Project Group. (2014). *FamilyTreeDNA - The Norway DNA - Norge Project*. https://www.familytreedna.com/group-join.aspx?Group=Norway

Thorvaldsen, G. (2019). Internal migration in 19th and 20th century Norway. An overview 1865 to 1960. In *Nominative Data in Demographic Research in the East and the West: Monograph* (pp. 166–184). Publishing house of the Ural University. https://doi.org/10.15826/B978-5-7996-2656-3.10

Tryland, M. (2001). Kopper og koppevirus – 200 år siden første vaksinasjon i Norge. *Tidsskrift for Den Norske Legeforening*. https://tidsskriftet.no/2001/12/medisinsk-historie/kopper-og-koppevirus-200-ar-siden-forste-vaksinasjon-i-norge

van Oven, M., & Kayser, M. (2009). Updated comprehensive phylogenetic tree of global human mitochondrial DNA variation. *Human Mutation*, *30*(2), E386–E394. https://doi.org/10.1002/humu.20921

Venås, K., & Skjekkeland, M. (2020). dialekter i Norge – inndeling – Store norske leksikon. https://snl.no/dialekter_i_Norge_-_inndeling

Vistad, O. I., Wold, L. C., Daugstad, K., & Haukeland, J. V. (2016). Mimisbrunnr climate park – A network for heritage learning, tourism development, and climate consciousness. *Journal of Heritage Tourism*, *11*(1), 43–57. https://doi.org/10.1080/1743873X.2015.1082570

Weissensteiner, H., Pacher, D., Kloss-Brandstätter, A., Forer, L., Specht, G., Bandelt, H. J., Kronenberg, F., Salas, A., & Schönherr, S. (2016). HaploGrep 2: Mitochondrial haplogroup classification in the era of high-throughput sequencing. *Nucleic Acids Research*, *44*(W1), W58–W63. https://doi.org/10.1093/nar/gkw233

Wickler, S., & Narmo, L. E. (2014). Tracing the development of fishing settlement from the iron age to the modern period in northern Norway: A case study from Borgvær in the Lofoten Islands. *Journal of Island and Coastal Archaeology*, *9*(1), 72–87. https://doi.org/10.1080/15564894.2013.810678

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