



# Historical and social-cultural processes as drivers for genetic structure in Nordic domestic reindeer

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## Abstract

We have analyzed DNA microsatellites and the mitochondrial control region in reindeer from 31 different husbandry areas in Norway, Sweden, and Finland in order to better understand the processes that underlie the genetic variability of the Nordic domestic herds. The distinct differentiation found in the nuclear markers but less so in the mitochondrial marker gives evidence of an origin from a common ancestral population which later evolved into the two main gene pools characterizing the nuclear genomes of domestic reindeer in Finland and most of Sweden and Norway. Analyses of temporal trends in effective population size give evidence of a rapid increase in number of reindeer before the population growth associated with the pastoral transition. This implies that the ancestry of contemporary domestic reindeer lay among a rapidly growing wild population possibly located in the boreal areas of eastern Fennoscandia or European Russia. The evolution of reindeer husbandry in Finland, perhaps with input from European Russia, which later spread to northern Norway could explain the shared genomic pattern observed in these areas today. The structured selection of productive female-centered herds may explain the genetic structure in other parts of Norway and in Sweden. The further substructuring of the Swedish/ Norwegian gene pool appears to follow the traditional language borders with the South Sámi language dominating the southern and the Central Sámi language in the more northern genetic subclusters. This suggests that traditional knowledge, cultural identities, and herd migrations have contributed to shape the genetic structure seen today. Ecological gradients are more pronounced within as compared to between the genetic clusters, giving further evidence that historical and social-cultural processes are important drivers for the genetic differentiations found in domestic reindeer across the Nordic countries.

## KEYWORDS

domestication, microsatellites, mitochondrial DNA, reindeer pastoralism, Sámi

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## 1 | INTRODUCTION

Domestication of reindeer, *Rangifer tarandus*, and the emergence of large-scaled reindeer herding laid the foundation for one of the most fundamental social transformations that has occurred in Circumpolar North (Hansen & Olsen, 2014; Krupnik, 1993). Today, the reindeer husbandry as a livelihood is increasingly threatened due to climate change (Pape & Löffler, 2012; Vors & Boyce, 2009) and land use changes (Horstkotte, 2013; Sandström, 2015; Skarin & Åhman, 2014). Future adaptation, selection, and improvement of reindeer husbandry are dependent on the genetic variability that exists in the animal resources (FAO, 2007, 2015; Groeneveld et al., 2010). Hence, more knowledge on the processes involved in driving and maintaining genetic variation and structure is currently needed in order to ensure the viability of the already vulnerable reindeer herding industry.

Reindeer husbandry is mainly confined to Eurasia. Among the world's total stock of nearly 2,000,000 domestic reindeer, ~2/3 are found in Russia and 1/3 in the Nordic countries (i.e., Norway, Sweden, and Finland). Today, the number of domestic reindeer is approximately 200,000 in each of the Nordic countries and the husbandry area covers approximately 30%–50% of the area in each. Today's reindeer husbandry is characterized by keeping herds of reindeer on natural pastures in a herding regime with relatively distant human contact. The herds are usually gathered few times per year when calves are marked and where animals are separated into slaughter and breeding animals (Figure 1). Choice of breeding animals is usually based on individual assessment of phenotypes directed toward calf growth and survival (Danell, 1999; Muuttoranta, 2014).

Modern Nordic reindeer husbandry is tightly linked to maintaining higher herd sizes with the contemporary pastoral economics associated with sale of meat from slaughtered calves (Næss, 2010). In contrast, the herders in the deep past used their animals mostly for transportation (Bjørklund, 2013; Ingold, 1986) and/or as decoy animals to attract wild reindeer (Tornæus & Wiklund, 1900). Today's reindeer husbandry has developed through a gradual transition from a hunting economy to reindeer pastoralism driven by diverse economic, social, and ecological forces, including the pressures of



FIGURE 1 Nordic domestic reindeer on winter pastures

colonialism, the market economy, and the collapse in the numbers of wild reindeer (Ingold, 1986; Vorren, 1973). During the 16th–17th centuries, there was a change toward increasing small-scale intensive herding, usually following a nomadic lifestyle, based on provision of transport and food products including milking. (Manker, 1953; Nieminen, 1992). During the 18th and 19th centuries, there was a further development characterized by increasingly large-scale, extensive reindeer pastoralism where the herders subsisted primarily on domestic reindeer (Bjørklund, 2013; Ingold, 1986).

During the early phase of the pastoral transition in Fennoscandia, there were no national borders restricting the seasonal migrations of the herders between their summer grazing at the coastal areas and winter grazing in the forested or mountainous inland. At the beginning of the 19th century, the yearly movements of reindeer were extensive with tens of thousands of crossings of what is now today the international borders between the countries. It was not until major geo-political conflicts during the 19th century, including the loss of Finland from Sweden to Russia in 1809, that the borders between the different nation states dissected the formerly seasonal migration pattern (Aarseth, 1989). The closure of the borders between Russia-Finland and both Norway in 1852 and Sweden in 1889 caused a loss of winter grazing areas in what is now Russian Karelia and Kola peninsula. During the last century, the reindeer migrations have been further reduced by reindeer grazing conventions between the national states and by the increased regulation within countries of the husbandry areas into more local administrative units with own pasture areas and migration routes.

The Nordic reindeer husbandry is a highly diverse social-ecological system, which in the case of Sámis evolved as an adaptation to natural conditions, history, competing land use, and legal rights (Holand et al., 2021; Käyhkö & Hortskotter, 2017; Manker, 1953). Their traditional nomadic herding systems range from alpine tundra forms characterized by long seasonal migrations frequently found in northern Norway and Sweden, to coastal forms, with local seasonal migrations found particularly in mid-part of Norway, and taiga forms typically seen in Sweden and Finland with year-around grazing in the forest zone confined to relatively small areas (Manker, 1953, 1968; Riseth et al., 2018). In contrast to Norway and Sweden, where Sámi almost exclusively practice reindeer husbandry, all local citizens are entitled to own reindeer in Finland. The Finnish Sámi husbandry is mainly confined to the most northerly areas. In the mountainous areas of south-central Norway, which is outside the Sámi herding areas, there are local farmers practicing reindeer husbandry. Besides the national and ethnic diversity, there are social-cultural gradients within the Sámi society represented by the various Sámi language dialects (Sammalahti, 1998). These linguistic and cultural boundaries do not correspond to the national borders and most of the dialects are spoken in multiple countries. The dialects can be grouped into the main languages of Eastern Sámi spoken mainly on the Kola Peninsula in northwestern Russia, Central Sámi in northern Finland, Sweden, and Norway and Southern Sámi spoken in southern parts of Norway and Sweden (Hermanstrand et al., 2019).

Molecular markers are widely used to characterize genetic structure and to reveal and dissect evolutionary and cultural processes that could explain the genetic variation. In reindeer, mitochondrial DNA (mtDNA) and DNA microsatellites are suitable and often used markers that may complement each other as they exhibit different properties and modes of inheritance. MtDNA is particularly suitable in analyzing demographic and evolutionary history due to its maternal and nonrecombining mode of inheritance, while microsatellites on the other hand have shown to be a highly appropriate marker to uncover ongoing demographic processes and genetic structure as they are highly variable and biparentally inherited (Klüttsch et al., 2016; Kvie et al., 2019; McDevitt et al., 2009; Polfus et al., 2017; Røed et al., 2008; Weckworth et al., 2012; Yannic, Pellissier, Le Corre, et al., 2014; Yannic, Pellissier, Ortego, et al., 2014). These markers revealed a genetic similarity between the domestic reindeer of Norway and Finland, while the domestic reindeer of Kola Peninsula Russia reindeer (Røed et al., 2008). This implies at least two independent origins of reindeer husbandry in the Nordic countries and in Russia. However, the samples taken from domestic reindeer herds included in Røed et al. (2008) were few and spatially dispersed, making it difficult to argue for a uniform genetic structure of the domestic reindeer resources across the Nordic countries.

In the present study, we have expanded our dataset considerably by analyzing reindeer from 31 different reindeer husbandry areas in Norway, Sweden, and Finland. To obtain a better understanding of ancient and more recent processes that affects the genetic structure and variation in domestic reindeer, we used both nuclear microsatellites and the mtDNA control region. More specifically, we used these markers to examine the existence of a genetic structure for the Nordic domestic reindeer herds owing to possibly both demographic processes during the history of domestication, and ecological and social-cultural gradients for the different herding systems. We approached the latter by testing for possible relationships between genetic structure and the different vegetation regions, national states, ethnicity, and languages that characterize the different herding areas.

## 2 | MATERIAL AND METHODS

### 2.1 | Sample collection

Reindeer husbandry within the Nordic countries is organized in separate administrative units termed “districts” in Norway, “Sami vilages” in Sweden, and “co-operatives in Finland.” The 904 reindeer samples analyzed in this study were from 31 administrative units in Norway (area 1–14), Sweden (area 15–22), and Finland (area 23–31; Table 1, Figure 2). The samples were blood or tissue samples obtained at the slaughterhouses during 2015–2018.

Our sampling was designed to cover, besides the wide geographical range of the husbandry areas, possible social-cultural and ecological gradients. Nationality, ethnicity, and Sámi languages traditionally

spoken within the respective reindeer husbandry areas were used as proxies for the social-cultural gradients. Sámi versus non-Sámi was used as proxy for ethnicity. The relevant Sámi languages were defined as Central Sámi including the languages of Northern Sámi, Lule Sámi and Pite Sámi, and South Sámi, the latter also including the Ume Sámi language. The Central versus South Sámi reindeer herding districts on both side of the national borders of Norway and Sweden were assigned according to Hermanstrand et al. (2019). The area defined by husbandry area 14 in northeastern Norway belonged traditionally to the Eastern Sámi spoken area but is here classified as Central Sámi area. In 1826, when the border was drawn between Norway and Russian, this area became part of Norway with subsequent strong influence of both Norwegian, Finnish, and North Sámi cultures (Andresen, 1989; Niemi, 1994). The vegetation characterizing the different herding areas was used as proxy for the ecological variable. We used the classification of a Boreal versus Alpine and Sub-Alpine regions as given in Abrahamsen et al. (1984). Herds with seasonal migration using the Alpine region most of the year but straying partly within the Boreal region during winter (area 18 and 20) were classified to the Alpine region.

### 2.2 | Laboratory methods

DNA was extracted from blood and tissue samples using DNeasy Blood and Tissue Kits (Qiagen) following the manufacture's protocol. All samples were analyzed for 18 microsatellite loci amplified by PCR and scored as product sizes as given in Mysterud et al. (2019). The mtDNA sequences comprised of 487 samples distributed between areas (Table 1). A 503 bp long fragment of mitochondrial control region (CR) was amplified and sequenced with primer sequences, PCR amplification, and sequence protocol as given in Kvie et al. (2016). The amplified sequences were trimmed down to a final 432 bp fragment.

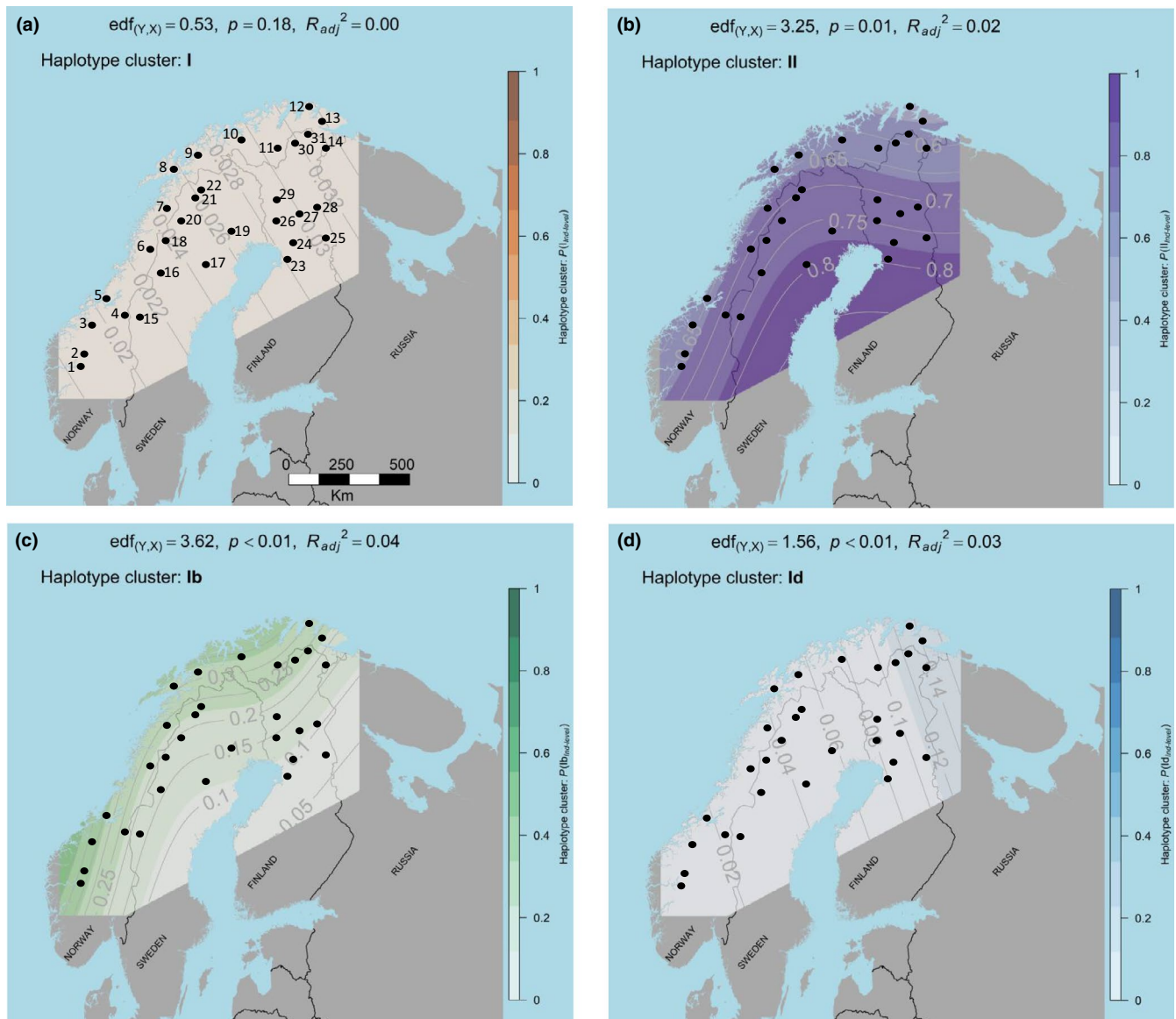
### 2.3 | MtDNA data analyses

DnaSP (Librado and Rozas (2009) was used to calculate mtDNA diversity in terms of number of different haplotypes ( $N_h$ ), haplotype diversity ( $H_d$ ), and nucleotide diversity ( $\pi$ ). ARLEQUIN v3.5 (Excoffier & Lischer, 2010) was used to obtain site pairwise  $F_{ST}$  estimates based on haplotype frequencies, as well as to perform a Mantel test to examine if there was an association between genetic distances and geographical distances. Statistical significance was evaluated after 1,000 permutations. BEAST v1.8.0 (Drummond et al., 2012) was used to construct a Bayesian phylogeny of the identified mtDNA haplotypes. The analyses were run with an HKY G + I substitution model with strict molecular clock for  $10^8$  generations with tree sampled every  $10^4$  iterations. TreeAnnotater v1.7.5 (Drummond et al., 2012) was subsequently used to create a maximum clade credibility tree that represents the posterior distribution. Sequences from previously described CR haplotype clusters were included in a

TABLE 1 Microsatellite and the mtDNA CR variation in reindeer from husbandry areas herded in different vegetation zones and by different ethnic groups in the Nordic countries

Area code	Sample area	Country	Population size (N)	Vegetation region	Ethnicity	Language group	Microsatellites			MtDNA CR region			
							n	Na	uHe	n	Nh	$\pi$	Hd
1	Filefjell	Norway	3,000	Alpine	Norwegian	Norwegian	48	7.22	0.69	16	5	0.015	0.717
2	Lom	Norway	2,400	Alpine	Norwegian	Norwegian	33	6.39	0.70	16	3	0.014	0.608
3	Trollheimen	Norway	1,600	Alpine	Sámi	South Sámi	33	6.11	0.68	19	3	0.015	0.503
4	Riast/Hylling	Norway	4,500	Alpine	Sámi	South Sámi	24	5.94	0.67	14	7	0.016	0.758
5	Fosen	Norway	2,100	Boreal	Sámi	South Sámi	37	5.89	0.66	16	4	0.008	0.442
6	Børgefjell	Norway	900	Alpine	Sámi	South Sámi	34	6.17	0.68	16	3	0.015	0.492
7	Saltfjellet	Norway	3,500	Alpine	Sámi	Central Sámi	33	6.83	0.71	16	3	0.013	0.667
8	Kanstadford	Norway	600	Sub-Alpine	Sámi	Central Sámi	33	5.67	0.65	14	4	0.020	0.692
9	Hjertinden	Norway	800	Sub-Alpine	Sámi	Central Sámi	34	6.61	0.67	17	7	0.015	0.662
10	Beahcegealli	Norway	2,700	Sub-Alpine	Sámi	Central Sámi	24	6.39	0.69	17	6	0.016	0.778
11	Karasjok-vest	Norway	22,000	Sub-Alpine	Sámi	Central Sámi	34	6.94	0.69	15	7	0.021	0.867
12	Nordkinhalvøya	Norway	5,800	Sub-Alpine	Sámi	Central Sámi	24	6.44	0.72	19	8	0.020	0.813
13	Varanger	Norway	11,000	Sub-Alpine	Sámi	Central Sámi	25	6.94	0.71	13	5	0.015	0.628
14	Pasvik	Norway	2,500	Sub-Alpine	Sámi	Central Sámi	34	8.22	0.72	15	4	0.015	0.705
15	Handölsdalen	Sweden	6,000	Alpine	Sámi	South Sámi	30	6.22	0.68	16	2	0.017	0.533
16	Vilhelmina södra	Sweden	9,000	Alpine	Sámi	South Sámi	41	6.56	0.68	15	5	0.008	0.476
17	Malå	Sweden	6,200	Boreal	Sámi	South Sámi	29	6.67	0.71	14	4	0.012	0.582
18	Gran	Sweden	5,000	Alpine	Sámi	South Sámi	31	6.28	0.68	16	5	0.018	0.725
19	Udtdja	Sweden	2,800	Boreal	Sámi	Central Sámi	17	6.33	0.70	16	5	0.016	0.650
20	Luokta-Mávas	Sweden	10,000	Alpine	Sámi	Central Sámi	24	6.44	0.70	16	5	0.013	0.600
21	Sirges	Sweden	15,500	Alpine	Sámi	Central Sámi	24	6.06	0.67	19	3	0.009	0.292
22	Unna Tjerusj	Sweden	8,000	Alpine	Sámi	Central Sámi	28	6.06	0.67	16	4	0.005	0.442
23	Kiiminiki	Finland	900	Boreal	Finnish	Finnish	26	6.06	0.67	14	6	0.018	0.791
24	Kuukas	Finland	1,500	Boreal	Finnish	Finnish	25	6.78	0.72	15	5	0.013	0.629
25	Oivanki	Finland	2,300	Boreal	Finnish	Finnish	26	6.89	0.74	13	3	0.013	0.500
26	Poikajärvi	Finland	4,300	Boreal	Finnish	Finnish	22	6.67	0.72	16	3	0.010	0.508
27	Hirvasniemi	Finland	2,200	Boreal	Finnish	Finnish	26	6.78	0.73	17	7	0.015	0.721
28	Pohjois-Salla	Finland	4,700	Boreal	Finnish	Finnish	28	6.79	0.73	14	6	0.013	0.736
29	Alakylä	Finland	5,000	Boreal	Finnish	Finnish	27	7.22	0.71	18	5	0.013	0.693
30	Paistunturi	Finland	7,200	Sub-Alpine	Sámi	Central Sami	26	6.67	0.68	12	4	0.012	0.455
31	Kaldoaivi	Finland	5,400	Sub-Alpine	Sámi	Central Sami	24	7.28	0.71	17	6	0.016	0.801

Note: N represents the approximate number of reindeer kept within each area, whereas n represents the number of reindeer analyzed. Genetic variation is given as mean number of different alleles (Na) and unbiased expected heterozygosity (uHe) for the microsatellites. MtDNA CR variation is given as number of haplotypes (Nh), nucleotide diversity ( $\pi$ ), and haplotype diversity (Hd).



**FIGURE 2** Predicted probabilities of distribution of individual mtDNA CR cluster in Nordic domestic reindeer related to geographic coordinates from a logistic regression model using a generalized additive model. Locations of sampled husbandry areas given as black dots with area codes numbered in a mainly south-north direction within each country

separate Bayesian analysis to designate sequences from the current study to previously described haplotype clusters (Kvie et al., 2016). Convergence for the phylogeny was assessed in TRACER (Rambaut et al., 2014) giving the effective sample size for all parameters above the general recommendation ( $ESS > 200$ ). Genealogical relationships among haplotypes were examined by constructing a network using Network v4.6 (ref.fluxus-engineering.com).

We applied generalized additive models (GAMs: Wood, 2006), using the mgcv-library in R (R Core Team 2020), to analyze the probability that the individuals belonged to the identified haplotype clusters. Separate analyses were done for each cluster with individual haplotypes treated as a binary response using a logit-link function and assuming a binomial distribution (Zuur et al., 2010). The probability for a given cluster assignment was modeled as a function of the geographical coordinates ( $X$ =East-West positions;  $Y$ =South-North

positions) for the sampled populations as follows: “gam(response~s( $X,Y$ ,bs='ts', $k=5$ ,family=binomial(link='logit'))”. The predictions from the GAMs, back-transformed from logit to probability scale, were then plotted on maps.

Signs of sudden demographic expansion were tested by using the mismatch distribution of haplotypes within haplotype clusters as implemented in ARLEQUIN v3.5 and with 10,000 bootstrap replicates. The sum of squared deviations (SSD) was used to test the fit of the observed data to the model of sudden demographic expansion. If the validity of the model is confirmed, the time since the putative expansion event can be estimated from  $\tau (=2\mu t)$  where  $\tau$  represents the expected number of differences,  $\mu$  the mutation rate and  $t$  the time since divergence. We also performed two neutrality tests, Fu's  $F_s$  and Fu and Li's  $D$  (Fu, 1997; Fu & Li, 1993), implemented in DnaSP, to detect departure from mutation-drift

**TABLE 2** Demographic expansion statistics for mtDNA CR haplogroups of domestic reindeer in Nordic countries

Haplotype cluster	Nh	SSD	Fu's Fs	Fu and Li's D	Nucleotide difference		Expansion time	
					$\tau$	CI (95%)	Years ago	CI (95%)
II	18	0.17***	-25.90***	-2.50*	2.16	1.00–3.24	6,100	2,800–9,100
Ib	10	0.30**	-11.21***	-2.22*	1.80	0.29–4.04	5,000	800–11,300

Note: Number of haplotypes (Nh), sum of square deviation (SSD), Fu's Fs and Fu and Li's D with corresponding *p* values (\*0.01 < *p* < .5, \*\*0.001 < *p* < .01, \*\*\**p* < .001), and estimate of nucleotide differences ( $\tau$ ) with 95% confidence interval (CI) are given.

equilibrium. The temporal trends in effective population size were reconstructed with Bayesian Skyline Plot implemented in BEAST using uncorrelated clock rate and with MCMC simulations and tree sampling as described before. Model of constant versus skyline coalescent was tested by comparing AICM (Baele et al., 2012) as implemented in TRACER.

## 2.4 | Microsatellite data analyses

GenALEX v.6.5 (Peakall & Smouse, 2012) was used to calculate microsatellite genetic diversity and to test for deviations from expectations under Hardy–Weinberg equilibrium (HWE). ARLEQUIN v3.5 was used to estimate pairwise genetic differentiation using the  $F_{ST}$  values (Weir & Cockerham, 1984) and to perform a Mantel as described above for the mtDNA data,

Genetic structuring of microsatellite variation at an individual level was analyzed in the software STRUCTURE (Pritchard et al., 2000) based on the admixture model, correlated allele frequencies, no a priori group membership, 30,000 burn-in cycles, and 300,000 MCMC iterations. We tested for up to 10 populations ( $K = 1-10$ ), each with five repetitions. Mean posterior probability and Evanno's Delta *K* method (Evanno et al., 2005) were obtained in Structure Harvester (Earl & von Holdt, 2012). We used CLUMMP version 1.1.2 (Jakobsson & Rosenberg, 2007) with the FullSearch algorithm and 1,000 repeats, to find the optimal alignment of clusters across all five runs for the selected number of *K*'s. For the graphical display of genetic structure, we used the program Distruct (Rosenberg, 2004). Interference of ancestry distribution (i.e., Q-matrix in STRUCTURE) was displayed on a geographic map using POPSutilities (<http://membres-timc.imag.fr/Olivier.Francois/POPSutilities.R>).

The association between the individual ancestry coefficients, provided as probabilities defined as [0–1], to the clusters in STRUCTURE, and socio-ecological variables was modeled using beta regression (Cribari-Neto & Zeileis, 2010) and the betareg package (Zeileis et al., 2020) in R. Selecting one model for inference based on a predefined set of candidate models was performed using the second-order Akaike's information criterion (AICc: e.g., Burnham & Anderson, 2002) and the R-package AICcmovavg (Mazerolle 2019). We defined four candidate models, each of which only contained one predictor at a time: (a) Country; (b) Ethnicity; (c) Language group; and (d) Vegetation region. Additionally, we used standard modeling diagnostics plots in order

to assess if the selected models fulfilled the underlying assumptions for these models (Zuur et al., 2010).

## 3 | RESULTS

### 3.1 | Genetic variation and demographic history

Levels of genetic variation for the microsatellite loci were high for all sampled areas (Table 1) with mean number of alleles ( $N_a$ ) across all units of 6.588 (SE 0.082) and unbiased expected heterozygosity ( $uHe$ ) of 0.687 (SE 0.006). Test of deviation from HWE in each locus-area combination revealed the majority (98.4%) of these tests to be nonsignificant after performing the Bonferroni correction. The nine significant deviations were all among different loci spread among eight different sample areas. We have used all 18 loci in further analyses as no locus or herd were over-represented among the significant deviations. Standard estimates of mtDNA polymorphism of the 432 bp CR fragment among the 487 reindeer analyzed gave 38 different haplotypes, haplotype diversity ( $H_d$ ), and nucleotide diversity ( $\pi$ ) equal to 0.657 ( $\pm 0.021$ ) and 0.015 ( $\pm 0.006$ ). In contrast to the general trend of relatively high levels of microsatellite variation, CR diversity varied substantially among the populations under study (Table 1).

The Bayesian phylogenetic tree reconstruction of the 38 mtDNA haplotypes showed all haplotypes to belong to a few well-supported clusters/subclusters recognized and labeled II, Ib, and Id together with cluster I haplotypes that did not assign to any subclusters (Figure S1a). The minimum spanning tree (Figure S1b) illustrates that cluster II and subcluster Ib consisted of one haplotype at high frequency, with all other haplotypes radiating from these by one to two mutations.

The mismatch distribution analyses supported a sudden demographic expansion model for both cluster II and Ib haplotypes in using both SSD, Fu's Fs and Fu and Li's *D* statistics (Table 2). The time since expansion using a mutation rate of  $\mu = 0.826 \times 10^{-6}$  (Røed et al., 2014) was estimated to 6,100 (95% CI: 2,800–9,100) and 5,100 (95% CI: 800–11,200) Years Before Present (YBP) for the two respective clusters.

Comparisons of demographic history models indicated that the skyline population size model was a better fit to the data than the constant size model (AICM 1928.40  $\pm$  0.04 vs. 1958.85  $\pm$  0.06). The Bayesian skyline plot indicated a relative stable female effective population size until around 2,500 YBP after which the population

rapidly increased (Figure S2). The estimated substitution rate was  $1.00 \times 10^{-6}$  substitutions per site per year (coefficient of variance  $0.124 \times 10^{-6}$ ).

### 3.2 | Genetic differentiation and spatial structure

The Mantel test indicated a significant correlation between pairwise geographical distance and genetic distance for the microsatellites ( $p < .001$ ,  $R^2 = 0.26$ ), but not for the mtDNA ( $p > .2$ ,  $R^2 = 0.002$ ). The Mantel tests for the microsatellites within each country were all significant ( $p < .001$ ). Based on the microsatellite data, pairwise genetic differences among areas showed a high degree of divergence, with a trend of less differentiation between neighboring areas and among areas within countries, as compared to between countries (Table S1). Particularly, the areas in Finland were significantly different when compared with most areas in Norway and Sweden, except from the most northern area in Finland (area 31) which was similar to area 13 in northern Norway. Also, absence of genetic differentiation between several areas in Sweden and Norway was evident. The mtDNA data showed much less genetic differentiation except from area 11 and 14, which were significantly different from most other areas (Table S1). These two areas stand out as they show a dominance of haplotypes belonging to haplotype subcluster Ib (area 11) and Id (area 14), while most other areas show predominance of cluster II haplotypes (Figure S3).

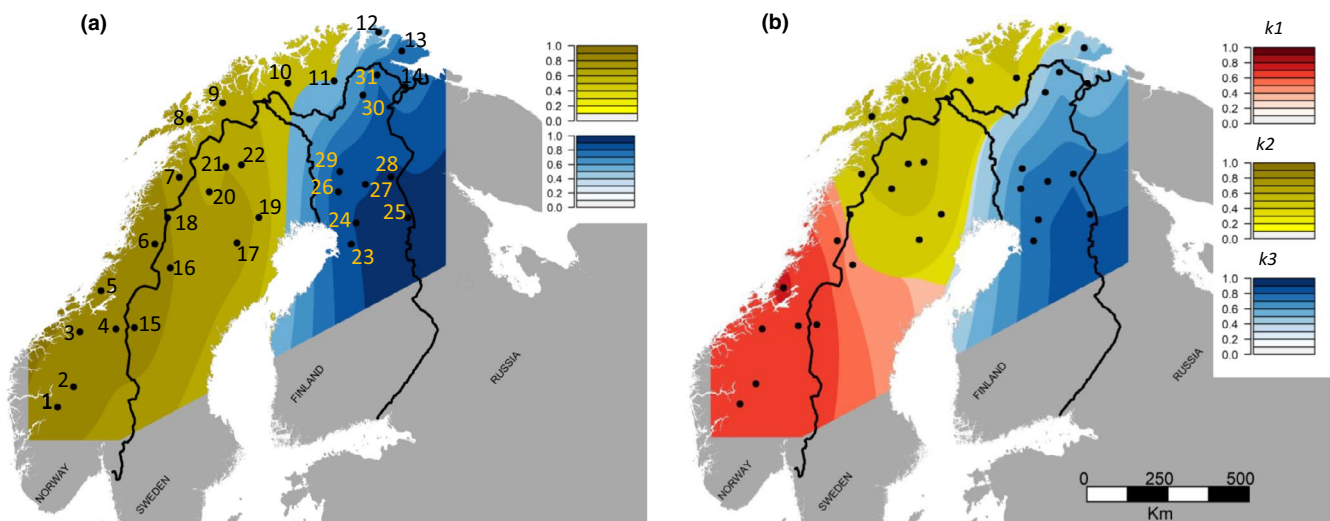
In the spatial analyses of haplotype cluster assignment using a logistic GAM, we revealed a significant spatial effect of haplotype cluster II, Ib, and Id, but not for I (Figure 2). The estimated probability to observe haplotype cluster II was generally high (0.60–0.85) with a trend of increasing frequencies from west to east, and a southward increase for the more eastern areas, giving the highest frequencies in eastern Sweden and southern Finland (Figure 2b). The probability to observe cluster Ib was more variable (0.05–0.50) with a trend of

increasing frequencies from east to west with highest frequencies in Norway (Figure 2c). There was relatively low estimated probability to observe both haplotype cluster I (0.02–0.03) and Id (0.02–0.14). The spatial trend for cluster Id was a north-eastward increase with highest frequencies in northeastern Norway and northern Finland (Figure 2d). The alternative analysis, using a single multinomial GAM instead of running four different logistic models, did to a large degree result in the same conclusions as the logistic model above (Figure S4).

Analyzing microsatellite genetic structure, based on individual assignment analysis, revealed significant increase in mean likelihood up to three populations (Figure S5a) with Delta K values suggesting a main structure of two gene pools (Figure S5b). The main structure showed Finnish reindeer to dominate one cluster while both Swedish and Norwegian reindeer dominate the other, with the exception of a few herds in the most northern parts of Norway, which share its gene pool with Finnish reindeer (Figure 3a; Figure S5c). Further increase in mean likelihood up to three populations indicates a substructure where the Swedish-Norwegian gene pool appears to be separated into a southern cluster ( $k1$ ) and a northern cluster ( $k2$ ), again with the exception of a small area in northern Norway showing similarity to the cluster ( $k3$ ) dominating Finnish reindeer (Figure 3b; Figure S5c). The geographic separation between the clusters  $k1$  and  $k2$  was more pronounced in Norway as compared to Sweden, where several of the geographically intermediate areas appeared to have a mixed ancestry of both the southern and northern subcluster (Figure S5c).

### 3.3 | Relationship between genetic structure and social-ecological variables

In the individual ancestry coefficients at  $K = 3$  in STRUCTURE, Language group had the by far best support in our data as the difference in AICc values for the second-ranked model was 364.111,



**FIGURE 3** Spatial interference of the microsatellite ancestry distribution (i.e., Q-matrix in STRUCTURE) of domestic reindeer in Nordic countries for (a) the main structure ( $K = 2$ ) and (b) the three-parted structure ( $K = 3$ ). Locations of sampled husbandry areas given as black dots with area codes numbered in a mainly south-north direction within each country

**TABLE 3** The relative support for each social–ecological candidate model (*i*) in the assessment of individual ancestry coefficients (i.e., the Q-matrix in STRUCTURE at *K* = 3) based on differences in AICc values ( $\Delta_i$ ) and Akaike's weights ( $w_i$ )

<i>i</i>	Predictors	<i>N</i>	Prob ( <i>k</i> 1)		Prob ( <i>k</i> 2)		Prob ( <i>k</i> 3)	
			$\Delta_i$	$w_i$	$\Delta_i$	$w_i$	$\Delta_i$	$w_i$
1	Country	3	401.240	<0.001	76.752	<0.001	3.834	0.128
2	Ethnicity	2	586.525	<0.001	82.420	<0.001	506.205	<0.001
3	Language group	4	<b>0</b>	<b>1.000</b>	<b>0</b>	<b>1.000</b>	<b>0</b>	<b>0.872</b>
4	Vegetation region	3	364.111	<0.001	134.901	<0.001	455.880	<0.001

Note: *N* represents number of parameters in the model. The clusters represent those dominating reindeer in, respectively, southern Norway and Sweden (*k*1), northern Norway and Sweden (*k*2) and Finland (*k*3). The models in bold was selected and used for inference as their  $\Delta_i$  was zero.

76.752, and 3.834 in the analyses of the clusters dominating in respectively southern Norway and Sweden (*k*1), northern Norway and Sweden (*k*2) and Finland (*k*3) (Table 3). This is even clearer when as judged by the Akaike's weights for the first-ranked model (Table 3). In the analysis of *k*3, Country was the second-ranked model and the analysis where the difference between the first- and second-ranked model was the least. Nonetheless, even for this set of candidate models, the Akaike's weights clearly favored the selected model over any other models (Table 3). In all analyses, Language group explained a considerable amount of variance as the coefficient of determination ( $R^2$ ) was 0.54 for *k*1, 0.58 for *k*2, and 0.30 for *k*3 (Table S2).

## 4 | DISCUSSION

### 4.1 | Genetic variation and demographic history

Our results from analyzing domestic reindeer in the Nordic countries revealed genetic variation both within and between reindeer husbandry areas. The general pattern of relatively high amount of microsatellite variation within all husbandry areas indicates large effective population sizes with limited effects of inbreeding and genetic drift. Most of the herds sampled for this study have relatively large population sizes within their administrative units. Besides, several neighboring herds showed little genetic differentiation indicating gene flow between areas. Large population sizes make genetic drift less prominent and, hence, contribute to maintaining a high level of variation (Frankham, 1996). However, some level of genetic drift due to low population size and isolation is indicated by the reduced amount of microsatellite variation observed in husbandry area 8 in Norway. This area has a herding regime that involves isolation on an island all year around, and it represents the area with smallest population size. Further genetic drift due to isolation by distance (Slatkin, 1993) may have contributed to the relatively large fraction (~26%) of the genetic differentiation in the microsatellite data that is explained by geographic distance. However, the generally high levels of variation and distinct spatial structure for the microsatellites indicate that other processes associated with geographic coordinates are more

likely the main reason for the relatively high association between the genetic and geographic distance.

In contrast to the microsatellites, levels of mtDNA diversity varied considerably among the husbandry areas. Furthermore, several herds showed reduced levels of mtDNA variation, which may indicate previous bottlenecks and small effective population sizes related to the female segment. The discrepancy between microsatellite and mtDNA variation can probably be explained by mtDNA being more prone to genetic drift, faster fixation, and subsequent lower levels of variation, as its effective population size is only one-fourth of microsatellites (Moore, 1995). Alternatively, it can reflect more male than female reindeer mobility and introgression within the Nordic reindeer husbandry system.

Domestication of animals is commonly considered as a rare event that has occurred in a limited number of regions (Clutton-Brock, 1999; Diamond, 2002). During the early stages of the domestication process, domesticates often experience a reduction in effective population sizes due to inbreeding and genetic drift, which typically results in mtDNA haplotypes clustering into a few lineages (Larson & Burger, 2013). As given from the current study, this appears also to characterize the Nordic domestic reindeer. Comparison of ancient and modern DNA in reindeer from both northern Norway and Finland have revealed a significant genetic change in the mitochondrial since medieval times characterized by loss of native haplotypes together with introduction of new ones (Bjørnstad et al., 2012; Heino et al., 2021; Røed et al., 2018). Most of these introduced haplotypes belonged to haplotype cluster II and Ib, which, as seen in this study, became the dominant haplotypes in most Nordic domestic herds. The growth of the Nordic domestic reindeer population from a limited number of maternal lineages is similar to the pattern recently reported for the large Nenets domestic reindeer population in Northwestern Siberia, (Røed et al., 2020). However, the Nenets domestic reindeer was characterized by dominance of CR cluster Ie haplotypes which seems to be absent among Nordic domestic reindeer. Our data therefore give additional support to two independent origins of reindeer husbandry in the Nordic countries and in Northwestern Siberia (Røed et al., 2008). Further, our data suggest that the emergence of both Sámi and Nenets pastoralism involved actual translocation of a special type of animal. This shows that the domestication of reindeer probably has followed the same



pattern as has been documented for several other animals (Clutton-Brock, 1999; Larson & Burger, 2013).

The domestic reindeer in Russia and the Nordic countries have shown to have independent origins; however, some degree of gene flow between the two regions is evident. The distribution of CR cluster I among the Nordic reindeer was mainly limited to the most northeastern areas with highest frequency in herding district 14 in Norway located along the Russian border. This CR cluster appears also to be present in domestic reindeer from Kola Peninsula and Yamal District in European Russia (Kvie et al., 2016; Røed et al., 2008). The introduction of domestic reindeer from the East to the northern Nordic areas may have taken place already in prehistoric times through the eastern exchange and trade that developed during the last two millennia BC (Hansen & Olsen, 2014), or through long-distance migrations such as the migration of Komi and Nenets reindeer herders from the eastern part of the White Sea to Kola Peninsula in the late 19th century.

The dominance of haplotype CR cluster II within the Nordic domestic reindeer may indicate a common domestic ancestry in association with the distribution and history of this lineage. Cluster II is suggested to have evolved during the last glaciation period in refugia isolated from the large Beringia refugium and then colonized new pastures toward the North as the ice retreated (Flagstad & Røed, 2003). The present estimate of roughly 5–6000 YBP since sudden population expansion of both this and the Ib lineage, may indicate events possibly associated with colder climate following the Holocene warm period (9000–5000 YBP, Kaufman et al., 2004). However, these time estimates for sudden expansion may be somewhat upward biased as the domestic herds have increased significantly over the last few centuries with the probability that some haplotypes represent mutations over this time span. This is indicated by the Bayesian skyline plot identifying the rapid population increase around 2,500 YBP which could be due to the cold period following the late Bronze Age (4500–2500 YBP, Solantie, 2005). Both events may have caused isolation followed by a sudden expansion of the population due to colder and more favorable climate. Nevertheless, this is well before the emergence of large-scale reindeer husbandry (Ingold, 1986; Vorren, 1973) and points toward an ancestry of present domestic reindeer among one or a few rapidly growing wild populations.

Probable refuge areas for an ancestral wild population characterized by the CR cluster II haplotypes would be along the colonization route for reindeer toward the north, possibly in present taiga areas in Sweden and Finland or in European Russia. The high frequency of cluster II lineage among extant domestic herds in the taiga regions in Sweden and Finland may give support to this scenario. Today, this is the habitat for the wild Finnish forest reindeer (*R.t. fennicus*) native to Finland and European Russia (Banfield, 1961). An origin of the Scandinavian domestic reindeer from this population was early suggested by Lönneberg (1909) based on morphological data and later supported by several others (Banfield, 1961; Ekman, 1948; Siivonen, 1975). Historically, the Finnish forest reindeer had a much wider distribution area that

probably included most of northern Finland and Sweden, as well as large parts of European Russia. The population became extinct, first in Sweden, and later, in the early 20th century, also in Finland, but then recovered as some herds migrated from Russia to Kainuu district in Finland during the 1950s (Nieminen, 2013). Previous microsatellite analyses of Eurasian wild and domestic reindeer have revealed that while Russian wild and domestic reindeer cluster together, the Nordic domestic reindeer cluster together with Finnish wild reindeer (Røed et al., 2008). The most typical domestic CR cluster II haplotype has been reported to be present in this population, although in low frequency (Røed et al., 2008). A more common distribution of this haplotype that has changed due to effects of bottlenecks and genetic drift might be the case. Also, an early influx of CR cluster II haplotypes from further east is possible. Heino et al. (2019) reported on genetic continuity between 4000-year-old reindeer remains from Volga-Kama region in eastern parts of European Russia and present-day wild reindeer from the taiga zone further northwest in Russia. Their mitogenomic study revealed four out of six studied individuals to have haplotypes belonging to mtDNA CR cluster II.

In Finland, the early nomadic reindeer husbandry is suggested to have spread from the mountain areas of northern Sweden and Norway to Käsivarsi area in northwestern Finland at the beginning of the 17th century, from where the large-scale reindeer herding gradually spread to other areas (Kortesalmi, 2008; Nieminen, 2006). During the 17<sup>th</sup>–18th centuries, there was also frequent trade and transport of animals between the Finnish herders and the indigenous reindeer herding people further east (Kuusela et al., 2016; Nieminen, 2006; Ylimaunu et al., 2014). At that time, the taiga type of reindeer husbandry was common in the coniferous forests on both sides of the present border between Finland and Russia (Koz'min, 2003). This implies a possible transfer of both knowledge and animals from these areas into the more northern reindeer herding cultures. While milking culture appears to have been an important feature of the early reindeer husbandry in western Fennoscandia (Aronsson, 1991; Nieminen, 1992), the early taiga reindeer husbandry is characterized by keeping small herds mostly for transport (Koz'min, 2003). Small-scale transport-based herds are known to often favor a larger distribution of male reindeer. The distinct differentiation observed in biparental markers but less so in maternal markers between extant reindeer in Finland and combined Sweden and Norway could reflect historic different breeding priorities related to sex. Import from Finland mostly to northern Norway of particularly strong male reindeer for transport purposes, and with an eastern ancestry, could explain the present shared genomic pattern between these areas. A more persistent holding of productive female-based herds, primarily used for subsistence (including milking), may have been decisive for the gene pools in other parts of Norway and in Sweden. Further, the opposite east-west gradient for mtDNA CR cluster II and Ib could possibly reflect the use of breeding females with different ancestries during the early emergence of reindeer pastoralism in, respectively, Finland and combined Sweden and Norway.

## 4.2 | Genetic structure and relationships to social-ecological variables

Also, more recent social-ecological processes, including the complex demarcation history among the involved national states, have most likely influenced the genetic structure of the Nordic reindeer herds. Particularly, the border closures between Russia-Finland and both Norway and Sweden during the 19th century restricted the Nordic reindeer herders' pastoral livelihood (Käyhkö & Hortskotte, 2017; Riseth et al., 2016) and may have further differentiated the reindeer genetic resources in respectively Finland and combined Sweden and Norway. Before the border closing between Russia-Finland and Norway in 1852 as many as 50,000 reindeer from the Norwegian side had winter pastures in Finland, and 15,000 reindeer from the Finnish side had summer pastures in Norway (Pedersen, 2001). Migration between Norway and Finland via Sweden was still an option for some herders, but a second border closure between Russia-Finland and Sweden in 1889 caused the loss of winter grazing areas in Russia-Finland also to Swedish herders. The restriction of traditional cross-border migration routes of the reindeer led to a buildup of animals in northernmost Sweden resulting in shortage of grazing resources with subsequent relocation of reindeer and herders to southern parts (Riseth et al., 2016).

The genetic relationship of the two most northeastern husbandry districts in Norway (area 13 and 14) mainly to the genetic cluster dominating in Finland may reflect both the period before the border was drawn between Norway and Russia in 1826, and later when there was a strong influence of Finnish culture and reindeer herding to northeastern Norway. The Finnish influence had a peak during 1920–1944 when the Petsamo area on the Russian side of the present border between Norway and Russia was part of Finland (Niemi, 1994). During these periods, the Skolt Sami, which belongs to the Eastern-Sami language group, practiced reindeer husbandry on both sides of the border.

On the other hand, the border closure between Norway and Sweden appears not to have created similar genetic diversification. This, despite the significant loss of access of particularly Swedish herders to important trading routes, as well as grazing grounds along the Norwegian coast by the Reindeer Grazing Convention of 1919 between Sweden and Norway after the dissolution of the Swedish-Norwegian Union in 1905 (Riseth et al., 2016). Rather than differentiation following the national borders, we found a separation of the reindeer genetic resources within Norway and Sweden that comprise a southern and a northern cluster, and which probably reflects social-ecological processes across these countries. The social-ecological processes tested for in this study are not all definite variables due to both frequent movement and mixing of people belonging to different language groups, and migrations of reindeer herds across several vegetation regions. Despite the ambiguous classifications, the proxies used for all social-ecological processes were significantly associated with the three-parted genetic structure with the language traditionally spoken within the respective reindeer husbandry areas best explaining the genetic structure. Particularly in Norway

did the distribution of the genetic clusters follow the traditional language borders with South Sámi dominating the southern and Central Sámi in the more northern subcluster. Reindeer in the two husbandry areas outside the Sámi herding areas in Norway (area 1 and 2) have an ancestry from animals bought from South Sámi people (Kolden, 1996; Opdal, 1956), and they both assigned to the most southern subcluster. In Sweden, significant genetic introgression of the northern subcluster among the traditionally South Sámi areas is evident. However, this is not surprising considering the large-scaled relocations of Central Sámi herders with their reindeer to southern areas, both after the closure of the borders toward Russia-Finland in 1889 (Riseth et al., 2016) and during more recent time (Åhren, 1979).

The significant explanations of the genetic three-parted substructure by all social-ecological proxies reflect in addition to genetic effects of divergence, high correlation between the proxies, as boreal herding is mainly practiced by local farmers in Finland. There were no obvious differences in herding forms between as compared to within the two genetic subclusters in Sweden and Norway. The reindeer sampled along the gradient from the coastal climate in northern Norway, across the alpine area in inland Sweden to more coastal and forested areas in northeastern Sweden assigned to the same genetic cluster. This implies that the ecological gradients for the husbandries probably reflect adaptive plasticity rather than genetic adaptations. High levels of adaptive plasticity in domestic reindeer are given by the many successful translocations of domestic animals to establish wild populations in new habitats. Among others, small groups of domestic reindeer from Norway were used to establish wild populations on both Iceland in late 18th (Thórisson, 1980) and on the sub-Antarctic island of South Georgia in early 20th century (Leader-Williams & Payne 1980), both of which grew to several thousand animals during the subsequent century.

The present results of social-cultural gradients to best explain the genetic structure of the Nordic domestic herds do not imply that there are no ecological-driven adaptive processes associated with diverging selection. Close monitoring of a domestic herd in Finland over nearly 50 years has documented continued directional selection in fitness traits with climate change as a probable driving force for the adaptive landscape to have changed (Holand et al., 2020). Still, the climatic gradients are more pronounced within as compared to between the detected genetic clusters suggesting these to reflect primarily the different history and spread of the pastoralist culture and secondary to different social-cultural gradients within the Nordic reindeer husbandry system.

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## CONFLICT OF INTEREST

We declare no conflicts of interest.

## AUTHOR CONTRIBUTION

**Knut Håkon Røed:** Conceptualization (lead); Data curation (lead); Formal analysis (lead); Funding acquisition (equal); Investigation (lead); Methodology (lead); Project administration (equal); Resources (lead); Software (lead); Supervision (supporting); Validation (lead); Visualization (equal); Writing-original draft (lead). **Kjersti Kvie:** Data curation (supporting); Formal analysis (supporting); Methodology (supporting); Software (supporting); Writing-original draft (supporting). **Bård-Jørgen Bårdsen:** Data curation (supporting); Formal analysis (supporting); Methodology (supporting); Software (equal); Visualization (equal); Writing-original draft (supporting). **Sauli Laaksonen:** Conceptualization (supporting); Funding acquisition (supporting); Investigation (supporting); Resources (supporting); Writing-original draft (supporting). **Hannes Lohi:** Formal analysis (supporting); Funding acquisition (supporting); Investigation (supporting); Resources (supporting); Writing-original draft (supporting). **Jouko Kumpula:** Conceptualization (supporting); Resources (supporting); Writing-original draft (supporting). **Kjell-Åke Aronsson:** Investigation (supporting); Resources (supporting); Writing-original draft (supporting). **Birgitta Åhman:** Data curation (supporting); Investigation (supporting); Resources (supporting); Writing-original draft (supporting). **Jørn Våge:** Funding acquisition (supporting); Resources (supporting); Writing-original draft (supporting). **Øystein Holand:** Conceptualization (supporting); Funding acquisition (equal); Writing-original draft (supporting).

## DATA AVAILABILITY STATEMENT

DNA sequence data for this study are available in the Sequence Database at the National Centre for Biotechnical Information (NCBI) (GenBank ID: MW936658–MW937144). DNA microsatellite data are available in Dryad (<https://doi.org/10.5061/dryad.j9kd51ccg>).

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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