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Oddmund Kleven, Robert Ekblom, Göran Spong, Gerhardus M. J. Lansink, Jouni Aspi, Scott Creel, Ilpo Kojola, Alexander Kopatz, Anni Koskela, Laura Kvist, Navinder Singh, Jonas Kindberg, Hans Ellegren, Øystein Flagstad

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Wolverine photographed in eastern Finland © Matti Pihlatie

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Abstract

Kleven, O., Ekblom, R., Spong, G., Lansink, G. M. J., Aspi, J., Creel, S., Kojola, I., Kopatz, A., Koskela, A., Kvist, L., Singh, N., Kindberg, J., Ellegren H. & Flagstad, Ø. 2019. Estimation of gene flow into the Scandinavian wolverine population. NINA Report 1617. Norwegian Institute for Nature Research.

Commissioned by the Swedish Environmental Protection Agency (SEPA), a project was conducted to provide data for the current evaluation of favourable conservation status of the wolverine in Sweden. In this report we present the results from this project, in which the main aim was to estimate gene flow into the Scandinavian, and in particular the Swedish wolverine population. Applying different genetic markers, a comprehensive sampling and various statistical approaches, we examined the population genetic structure and connectivity of wolverines in Fennoscandia. We found that wolverines in central Scandinavia were genetically different from those in northern Fennoscandia (i.e., the counties Troms and Finnmark in northern Norway, the northernmost part of Norrbotten in Sweden, and most of Lappland in northern Finland), and wolverines in southern Finland formed a separate genetic cluster. Although there was evidence of genetic substructuring, the change was gradual and showed a pattern of isolation-by-distance. Dispersal events were common but not symmetrical between the identified genetic clusters. Migration rates between central Scandinavia and northern Fennoscandia, as well as from northern Fennoscandia to southern Finland, was moderate, while it was low from southern Finland to the other two sub-populations. Based on the current population size, we estimated that 15-22 wolverines from northern Fennoscandia, and 0.04-0.46 wolverines from southern Finland have migrated into the central Scandinavian sub-population, which included a large part of the Swedish wolverine population, per generation. Despite limited influx of eastern wolverines, our findings indicate the potential for gene flow into the Swedish population, and most likely so through the corridor in northern Fennoscandia.

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Sammendrag

Kleven, O., Ekblom, R., Spong, G., Lansink, G. M. J., Aspi, J., Creel, S., Kojola, I., Kopatz, A., Koskela, A., Kvist, L., Singh, N., Kindberg, J., Ellegren H. & Flagstad, Ø. 2019. Estimering av genflyt til den Skandinaviske jerv populasjonen. NINA Rapport 1617. Norsk institutt for naturforskning.

På oppdrag fra Naturvårdsverket ble et prosjekt gjennomført for å fremskaffe data til en forestående vurdering av bevaringsstatus for jerv i Sverige. I denne rapporten presenterer vi resultatene fra dette prosjektet, hvor hovedformålet var å estimere genflyt til den skandinaviske, og spesielt til den svenske jerv-bestanden. Ved å benytte ulike genetiske markører, et betydelig antall prøver og ulike statistiske analyser, undersøkte vi populasjonsgenetisk struktur og konnektivitet blant jerv i Fennoskandia. Vi fant at jerv i den sentrale delen av Skandinavia var genetisk forskjellig fra jerv i det nordlige området av Fennoskandia (det vil si fylkene Troms og Finnmark, den nordligste delen av Norrbotten i Sverige og det meste av Lappland i Nord-Finland), og at jervene i det sørlige Finland utgjorde en egen genetisk gruppe. Selv om det var evidens for genetisk strukturering, var endringene gradvise og viste et mønster som samsvarte med isolasjon basert på geografisk avstand. Vandringer var vanlige, men de forekom ikke i like stor grad mellom de ulike genetiske gruppene. Migrasjonsratene mellom midt-Skandinavia og nordlige Fennoskandia, samt fra nordlige Fennoskandia til sørlige Finland, var moderat, mens det var lavt fra sørlige Finland til de andre to delpopulasjonene. Basert på den nåværende bestandsstørrelsen, estimerte vi at 15-22 jerver fra nordlige Fennoskandia, og 0,04-0,46 jerver fra sørlige Finland har migrert til den midt-skandinaviske delpopulasjonen, som inneholder er stor andel av den svenske jerv-bestanden, per generasjon. På tross av begrenset immigrasjon av jerv fra østlige områder, så indikerer våre resultater at det er potensiale for genflyt inn til den svenske populasjonen av jerv, og da spesielt via korridoren i det nordlige Fennoskandia.

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Contents

Foreword

This report present results from analyses of genetic structure and connectivity based on different marker types (microsatellites and single-nucleotide polymorphisms, SNPs) and performed for a large number of individuals from the northern Fennoscandian wolverine population. The microsatellite part was led by Uppsala University while the SNP part was led by NINA. The aim of the project was to examine gene flow from Finland into Sweden/Norway. The project was commissioned by the Swedish Environmental Protection Agency (SEPA), in order to provide data for the current evaluation of favourable conservation status of the wolverine in Sweden.

We would like to thank all who has contributed to the collection of samples and to the lab-work. The report was subject to peer-review and we thank reviewers for constructive comments.

We would also like to thank Per Sjögren-Gulve who has been our contact person, and coordinator of the peer-review process, at the Swedish Environmental Protection Agency. The Swedish Environmental Protection Agency has financed this study.

Trondheim and Uppsala, March 2019

Oddmund Kleven and Robert Ekblom

1 Introduction

Historically, the wolverine *Gulo gulo* was found in large parts of Finland, Norway and Sweden, but persecution during the 19th and 20th century led to a dramatic population decline (Chapron et al. 2014). Since the protective legislation in the late 1960s and early 1970s the species has gradually recovered (Chapron et al. 2014), and the population size is recently estimated to be approximately 890 individuals in Norway and Sweden (Tovmo et al. 2018) and 270-300 individuals in Finland (https://www.luke.fi/uutiset/ahmakanta-kasvussa-lahes-koko-maassa/). The wolverine is currently listed as endangered on the national red list for species in Finland (Liukko et al. 2015) and Norway (Henriksen & Hilmo 2015), while it is listed as vulnerable in Sweden (Anonymous 2015).

Limited genetic connectivity with neighbouring populations and low levels of genetic variation may negatively impact the evolutionary potential of populations or species (Frankham et al. 2010). Despite considerable recent population expansion, the levels of gene flow into the Scandinavian wolverine population seem to be restricted. Previous studies of population genetic structure (Flagstad et al. 2012, Walker et al. 2001) have identified three genetic clusters in Scandinavia and northern Finland: 1) wolverines in southwestern Norway, 2) wolverines in south-eastern and central Norway, as well as most of Sweden, 3) wolverines in the northernmost part (north of Torneträsk) of Sweden, northern Norway (Troms and Finnmark counties) and northern Finland. Previous studies revealed very low genetic variability for both microsatellite markers (Walker et al. 2001), mitochondrial DNA (Ekblom et al. 2014) and genome wide single-nucleotide polymorphisms (SNPs) (Ekblom et al. 2018) indicating low rates of immigration into the Scandinavian wolverine population. Limited knowledge is, however, available concerning the wolverines in southern Finland, but some evidence suggests high genetic differentiation from the three other populations (Flagstad et al. 2012, Koskela 2013).

The main aim of this study was to assess contemporary gene flow into the Scandinavian wolverine population to provide data for the current evaluation of favourable conservation status of the species in Sweden. A combination of different genetic marker systems, comprehensive and continuous sampling of wolverines from Finland and northern Scandinavia, as well as various statistical approaches was applied to analyse population genetic structure and genetic connectivity.

2 Material and methods

2.1 Material

As the main aim of the project was to estimate gene flow from Finland into Sweden, we focused our sampling on Finland and northern Sweden, but also included samples from other areas to obtain a good geographic representation of wolverines throughout its distribution in central and northern Fennoscandia. For samples from Norway, Sweden and northern Finland, we selected among individuals that had already been microsatellite genotyped as part of the national monitoring programmes in Norway and Sweden (Flagstad et al. 2018). Some of the samples from northern Finland and all from southern Finland were obtained from an ongoing research project. All these latter samples had already also been genotyped with microsatellite markers. The samples represented various source material for DNA, i.e., tissue from shot individuals, as well as hair, scats and urine from non-invasive tracking. The majority (95%) of the included samples were collected during the years 2009 to 2018 (the last two wolverine generations), while the remaining samples had been collected from 1983 to 2008. A total of 1278 individuals were included for the microsatellite analyses and 1717 individuals for the SNP analyses.

2.2 Methods

2.2.1 Microsatellites

For population genetic analyses we utilised microsatellite data from 18 loci (**Supplementary table 1**) genotyped according to previously published methodology (Brøseth et al. 2010, Flagstad et al. 2004). Briefly, for non-invasive samples a consensus genotype was created based on at least three independent PCR replicates. To calibrate microsatellite genotypes across labs, a few samples from Finland, Norway and Sweden were analysed in one lab. Descriptive population genetic statistics were estimated using GenePop 4.2 (Raymond & Rousset 1995), Arlequin 3.5 (Excoffier & Lischer 2010) and adegenet 2.1.1 (Jombart 2008). Population clustering were inferred using the software Structure 2.3.4 (Pritchard et al. 2000), applying the admixture model with a burn-in phase of 50,000 iterations followed by a run-phase of 200,000 iterations (or Markov Chain Monte Carlo chains) and posterior probability values for K (number of clusters) varying between 1 and 6. Population admixture analysis based on pre-defined populations (including identification of potential migrants as well as individuals with mixed ancestry) was performed using BAPS 6.0 (Corander et al. 2003). Migration rates were estimated using BayesAss (Wilson & Rannala 2003) applying default settings. Additional data handling and plotting were done using R 3.3.1 (R Core Team, 2016).

2.2.2 SNPs

All samples (i.e., available DNA-extracts) were genotyped using 96 SNPs, recently identified by sequencing wolverines from Finland, Norway and Sweden (Spong et al. unpublished data). This panel of 96 SNPs included one polymorphic mitochondrial marker, three monomorphic Y-chromosome markers used for sexing and 92 autosomal markers. The SNPs were genotyped on a 96.96 Dynamic Array using the Fluidigm EP1 instrument according to the manufacturer's protocol and scored using the Fluidigm SNP genotyping analysis software (https://www.fluidigm.com/software). Most of the Swedish samples were SNP genotyped at SLU in Umeå, while all samples from Norway and Finland, as well as some of the samples from Sweden were SNP genotyped at NINA's DNA-lab in Trondheim. A total of 1717 individuals were successfully genotyped at a minimum of 87 autosomal SNPs and included in the downstream SNP-analyses. To calibrate SNP genotypes across labs, a few samples from Finland, Norway and Sweden were analysed in one lab.

Population clustering using the software Structure and estimation of migration rates using BayesAss were also analysed with the SNP data set. However, as the results were qualitatively similar to the microsatellite results, they were not included in this report.

Population structure using the non-model-based method spatial principal component analysis (sPCA) was analysed in the R package “adegenet” 2.1.1 (Jombart 2008) in R 3.3.2 (R Core Team, 2016). Contemporary gene flow was analysed with ML-relate (Kalinowski et al. 2006) and SNPRelate (Zheng et al. 2012).

3 Results

3.1 Microsatellites

3.1.1 Population structure and clustering of individuals

We identified microsatellite population genetic sub-structure in the sampled Fennoscandian population with a best fit of data for four genetic clusters (**figure 1**), using the algorithm of Evanno et al. (2005).

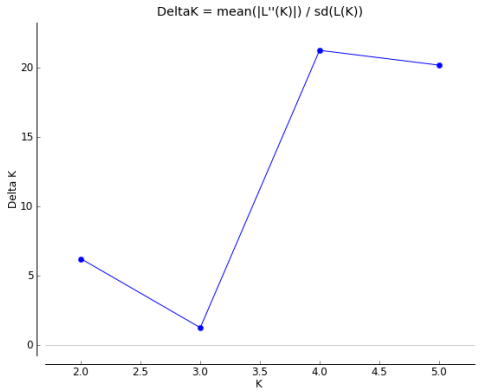

Figure 1. *Results from Structure analysis showing K=4 as the best fit of the data. Evaluation of the optimal level of clustering was according to the delta K method (Evanno et al. 2005)*.

However as seen in the structure bar-plot (**figure 2**), there is a large mixture of individuals from different genetic clusters in each of the geographic locations, except in southern Finland. Furthermore, there seems to be an isolation-by-distance pattern of genetic variation where individuals sampled close to the border of the adjacent population has a higher degree of mixed genetic clustering.

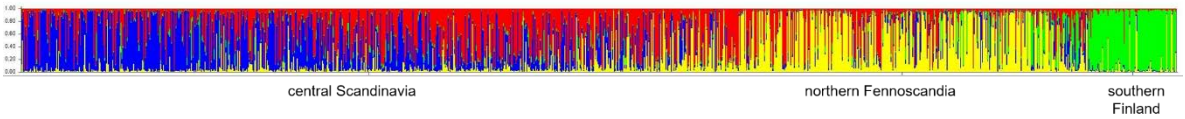

Figure 2. *Bar plot from Structure analysis (K=4) where the colour of each vertical line represents the population assignment for one individual. Individuals are ordered from south to north (central Scandinavia), west to east (northern Fennoscandia) and north to south (southern Finland)*.

We used a principal component analysis (PCA) approach to reduce the number of dimensions in the genotype space. The first PCA dimension identified north-south structure in the central Scandinavian population while the third dimension separated the genotypes from southern Finland (**figure 3**). Individual clustering in BAPS yielded similar results (**figure 4**).

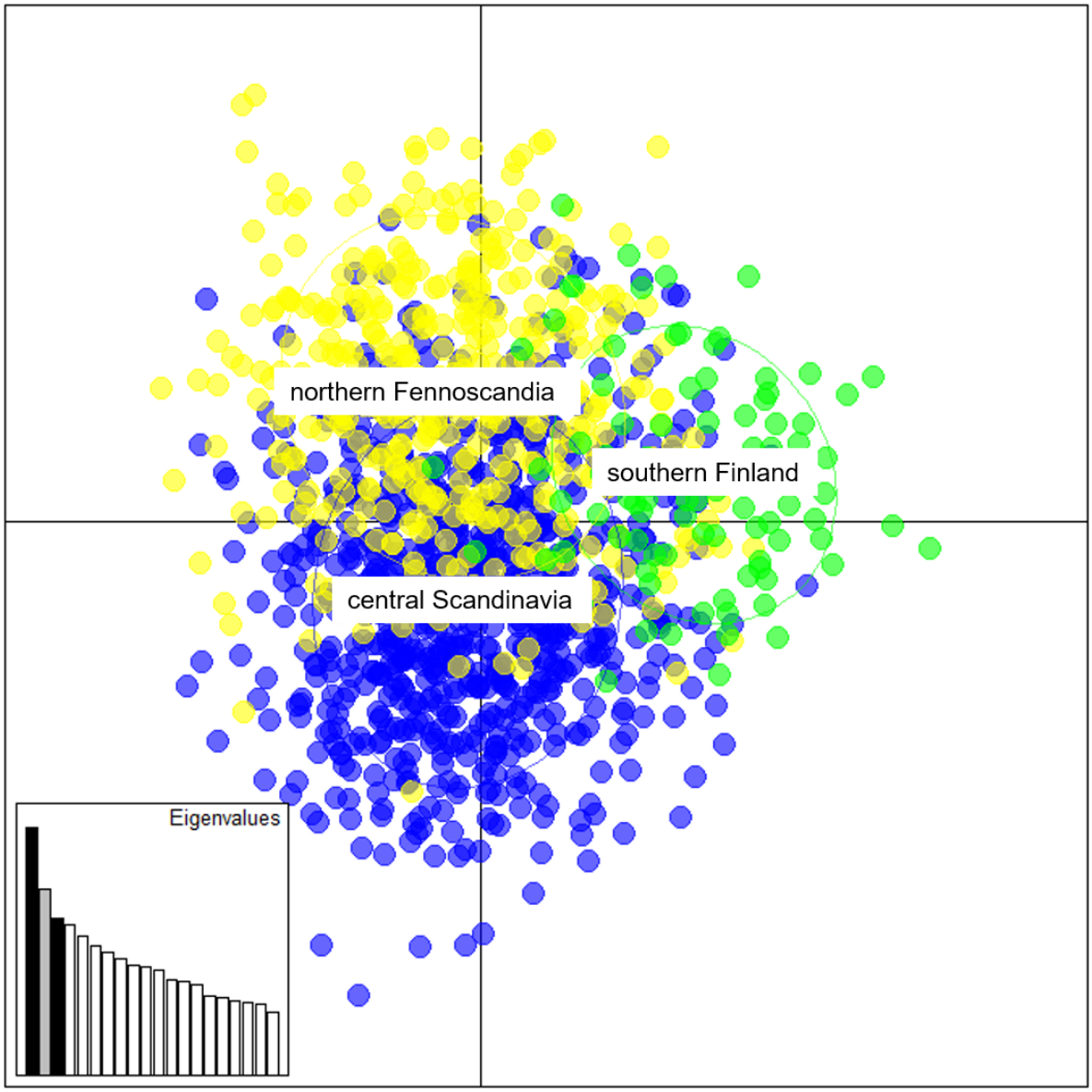

Figure 3. *Scatter plot of PCA dimension 1 (Y-axis) and 3 (X-axis), samples are colour coded according to geographic origin (blue = central Scandinavia, yellow = northern Fennoscandia, green = southern Finland).*

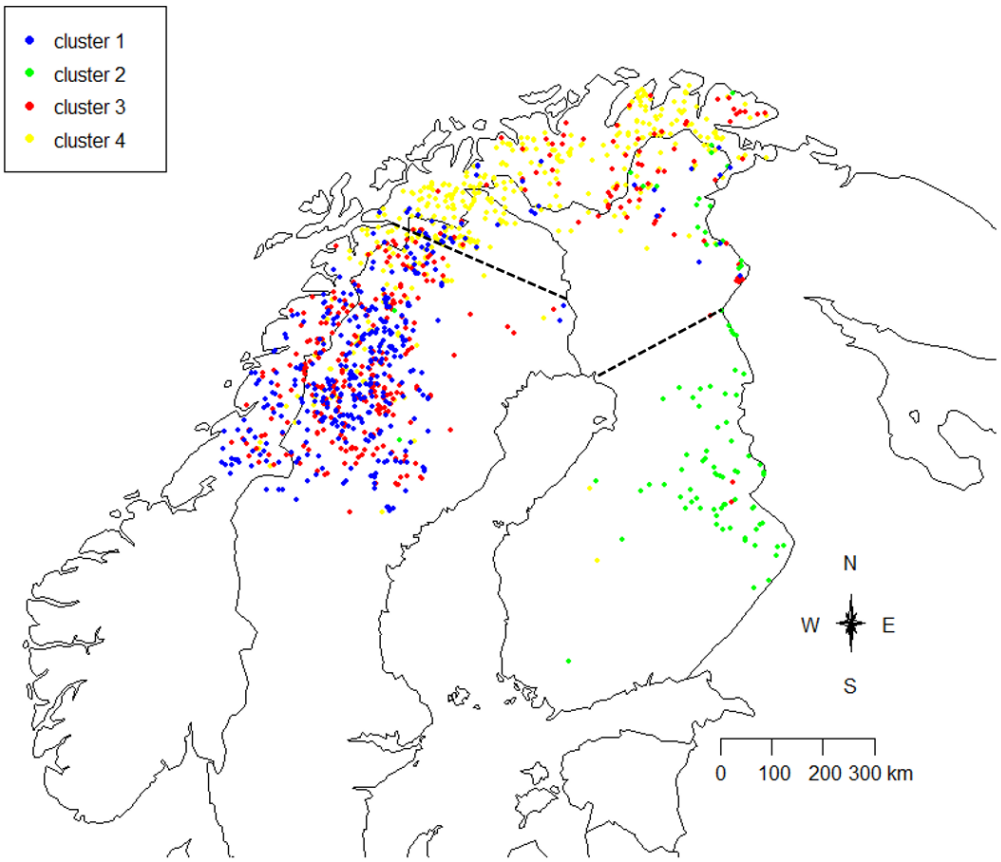

Figure 4. *Map showing the geographic localities for all samples included in the microsatellite analyses. Colours according to the genetic clustering produced using BAPS (K=4). Dashed lines indicate borders between the three inferred subpopulations (central Scandinavia, northern Fennoscandia and southern Finland).*

3.1.2 Analysis of migration rates

In order to investigate migration rates and admixture events, we divided the samples into three subpopulations: central Scandinavia, northern Fennoscandia and southern Finland. The borders between these were based on population genetic structure inferences using both microsatellite markers, SNP-markers and mtDNA haplotypes, as well as knowledge from previous population genetic studies (Ekblom et al. 2018, Walker et al. 2001), but the exact position of the boundaries were still somewhat arbitrarily chosen as the population subdivision in northern Fennoscandia is not entirely clear. There was low but significant ($p < 0.00001$, for all pairwise comparisons) population structure among these sub-populations, with F_{ST} values ranging between 0.040 and 0.114 (**table 1**).

Table 1. *Pairwise levels of genetic differentiation (F_{ST} above diagonal and Rho_{ST} below diagonal) between the three genetically inferred sub-populations of wolverine in Fennoscandia, as determined using Arlequin.*

Rho_{ST}\F_{ST}	Central Scandinavia	Northern Fennoscandia	Southern Finland
C-Scandinavia	-	0.033	0.119
N-Fennoscandia	0.037	-	0.111
Southern Finland	0.095	0.085	-

Using the private alleles method implemented in GenePop, we estimated the number of migrants per generation (Nm) to 0.24 (that this represents migration events across all sub-populations and in both directions). However, the mean frequency of private alleles was low (p(1) = 0.040), resulting in relatively limited power in this analysis. In addition, this approach is prone to historical isolation, potentially leading to an underestimation of current levels of gene flow (Epps & Keyghobadi 2015).

Attempts to estimate contemporary migration rates with BayesAss, which uses assignment methods in a Bayesian framework, revealed overall moderate migration rates between central Scandinavia and northern Fennoscandia, as well as from northern Fennoscandia to southern Finland, while it was low from southern Finland to the other two sub-populations. (**table 2**). The fraction of individuals in central Scandinavia with southern Finnish origin was estimated to only 0.06 %, and the corresponding fraction in northern Fennoscandia was 0.95 %. Migration rates in the opposite direction (into southern Finland) were higher (**table 2**).

Table 2. *Migration rates (m = the fraction of individuals in population X that were migrants derived from population Y, per generation), as determined using BayesAss. Standard deviations (SD) are given in parentheses.*

Population X	Migration rate (m) from population Y*		
	Central Scandinavia	Northern Fennoscandia	Southern Finland
C-Scandinavia	-	0.0445 (±0.0082)	0.0006 (±0.0005)
N-Fennoscandia	0.0810 (±0.0178)	-	0.0095 (±0.0035)
Southern Finland	0.0080 (±0.0067)	0.0613 (±0.0168)	-

**When multiplied with population size (of the recipient population) this will give the number of migrants per generation.*

To calculate the number of migrants per generation we multiplied the estimated migration rates (95% confidence limits) with the estimated mean population size of wolverines. As the main focus was on migration into the Swedish population and the fact that we lacked proper population size estimates from the Finnish population, we calculated only the number of migrants into central Scandinavia, which contained a large part of the Swedish wolverine population. The population size of wolverines for central Scandinavia was estimated to 416 adult (one-year and older) individuals based on the method described by Landa et al. (1998) using the average number of dens from the years 2016-2018 (Tovmo et al. 2018, Tovmo & Mattisson 2018). Based on these numbers, 15-22 wolverines from northern Fennoscandia and 0.04-0.46 wolverines from southern Finland were estimated to have migrated into the central Scandinavian sub-population per generation.

3.1.3 Admixture analysis

Admixture analysis in BAPS revealed 33 individuals in central Scandinavia with a mismatch between the geographic sampling location and the genetic population assignment, and 26 individuals with a possibly mixed ancestry (Supplementary Table 2). However, many of these were

sampled very close to the borders between the different subpopulations (**figure 5** and **figure 6**). Six individuals with a possible mixed southern Finland-Fennoscandian ancestry were identified in the central Scandinavian population. All of these had between 15% and 50% genetic content assigning to the population in southern Finland (thus possibly constituting first or second-generation offspring of migrant individuals).

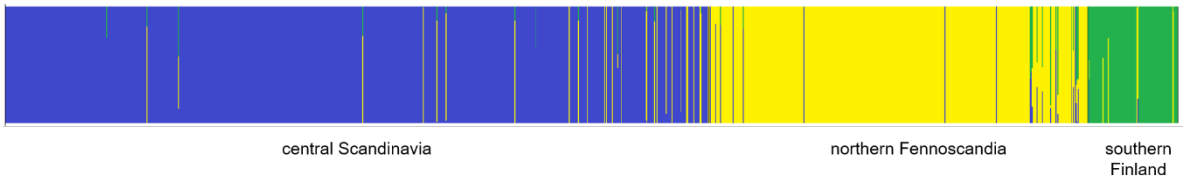

Figure 5. *Results from the admixture analysis performed in BAPS. Blue vertical lines represent individuals genetically assigned to the central Scandinavian population, yellow lines represent individuals assigned to the northern Fennoscandian population and green lines represent individuals assigned to the southern Finnish population. Lines with more than one colour represent individuals assigned to mixed ancestry (possible first or second-generation migrants)*.

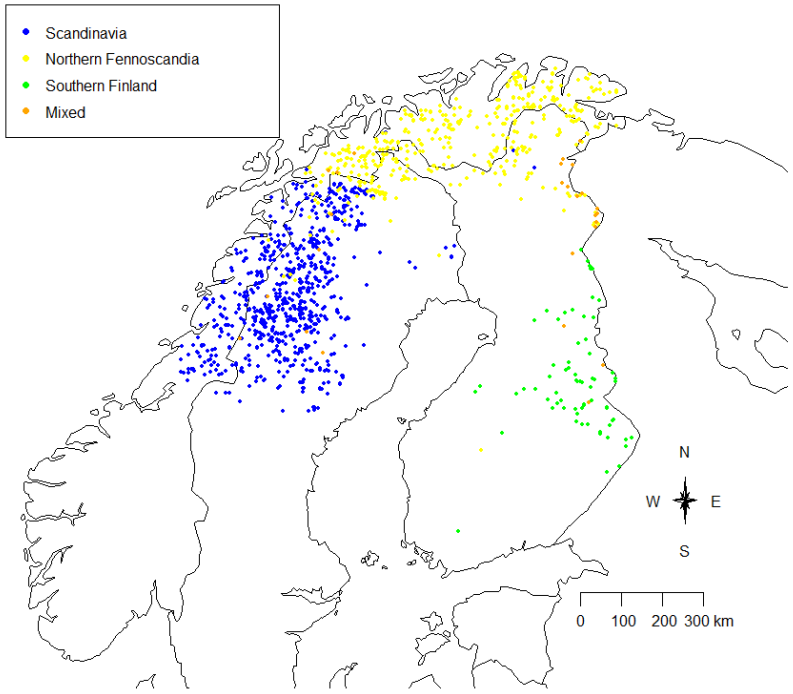

Figure 6. *Map showing the sampling location of each individual colour-coded by genetically assigned ancestry from the admixture analysis performed in BAPS, colours as in figure 5 but with mixed ancestry in orange.*

3.2 SNPs

3.2.1 Mitochondrial haplotypes

The single mitochondrial SNP marker amplified two different alleles/haplotypes (C or T) (**figure 7**). Only one of the haplotypes (C) was detected in Scandinavia, except for a few individuals in the north-eastern part of Norway close to the Russian border that represented the other haplotype, T. In Finland both haplotypes appeared, with haplotype T found in the majority of individuals in the south while only appearing along the Russian border in Finnish Lappland (**figure 7**).

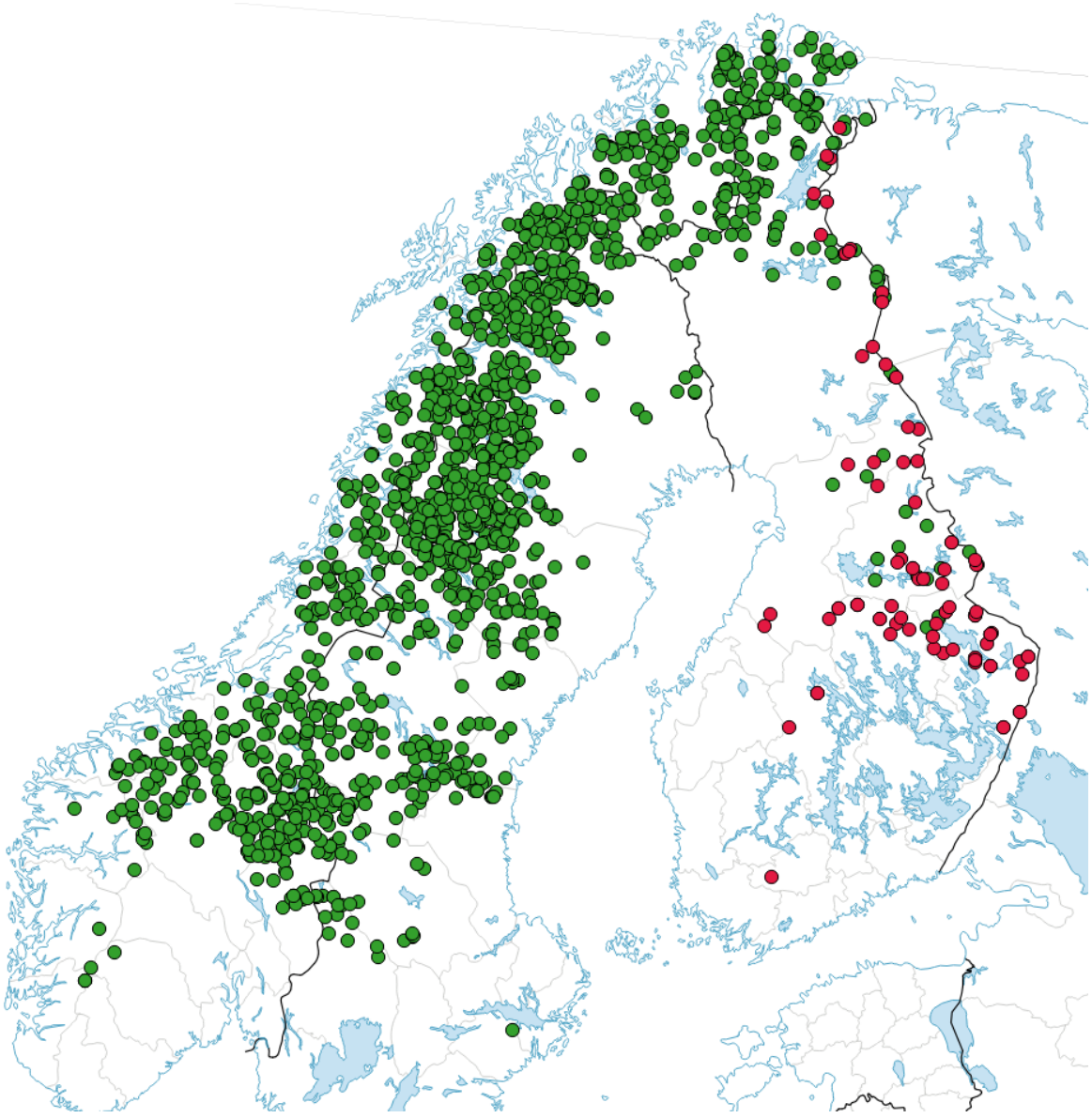

Figure 7. *Map showing the geographical distribution of two different haplotypes (C = green and T = red) detected at a single mitochondrial SNP marker*.

3.2.2 Spatial principle component analysis and contemporary gene flow

The spatial PCA identified spatial structuring in Fennoscandia (**figure 8**), most likely caused by isolation by distance (**Supplementary figure 1**). The change was gradual and continuous and did not show strong subpopulation divisions. Indeed, more detailed analyses of kinship patterns (**figure 9**) confirmed that dispersal events between the clusters identified in the previous analyses were common. Note also that dispersal events followed the shape of the distribution. No links across open water were detected, strongly suggesting that spurious kinship assignments were absent or very rare.

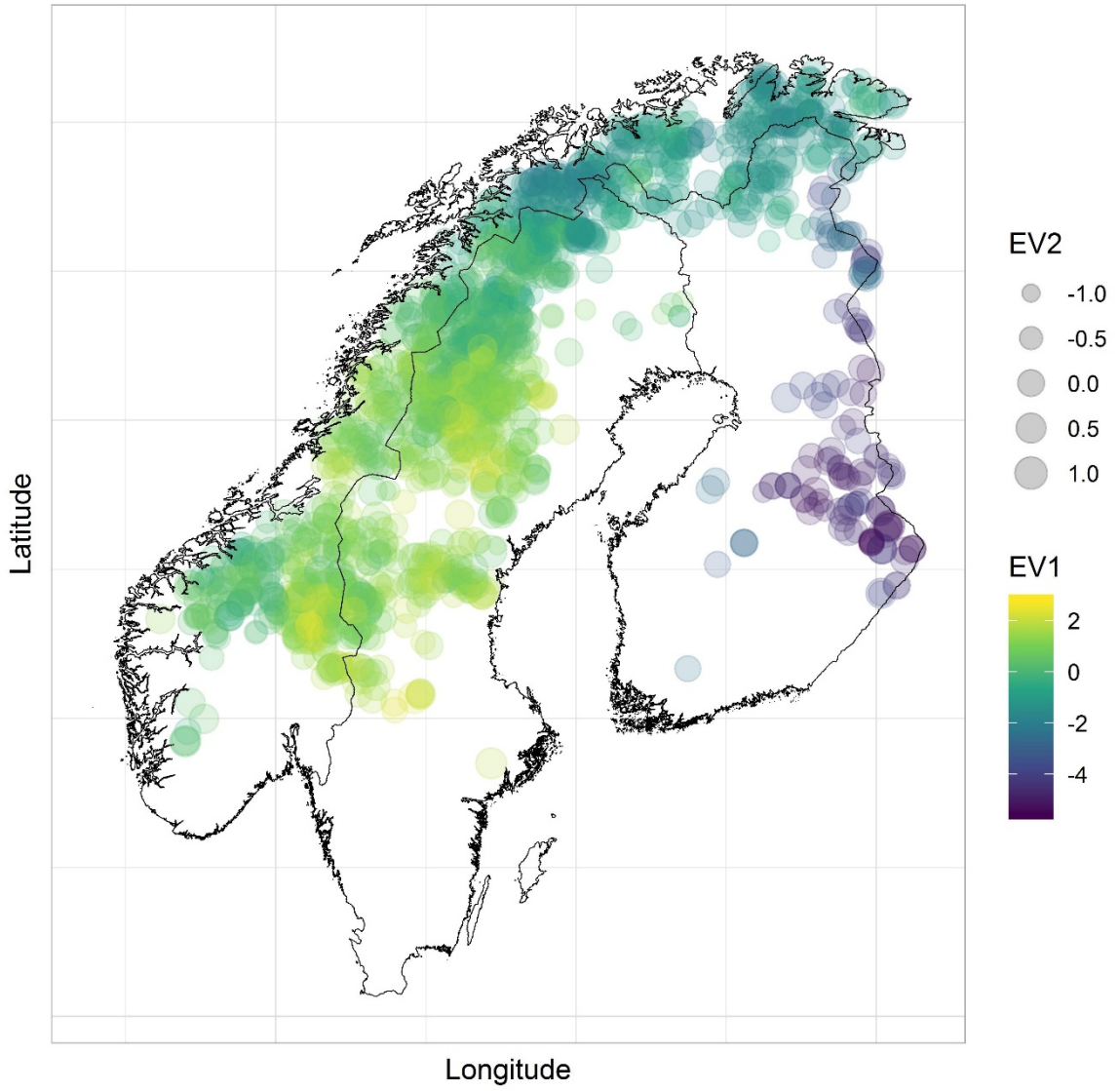

Figure 8. *Results from a spatial PCA plotted onto a map (run in the R package 'adegenet'). EV stands for eigenvector, where positive values indicate global structure and negative values local structure. Global structures exhibit positive spatial autocorrelation while local structures display negative spatial autocorrelation. This approach (in contrast to the algorithms used by the software Structure) does not use assumptions of Hardy-Weinberg equilibrium to delineate clusters. As can be seen in the figure, both EV1 and EV2 show a weak global structure overall, with the exception of the southern Finnish population.*

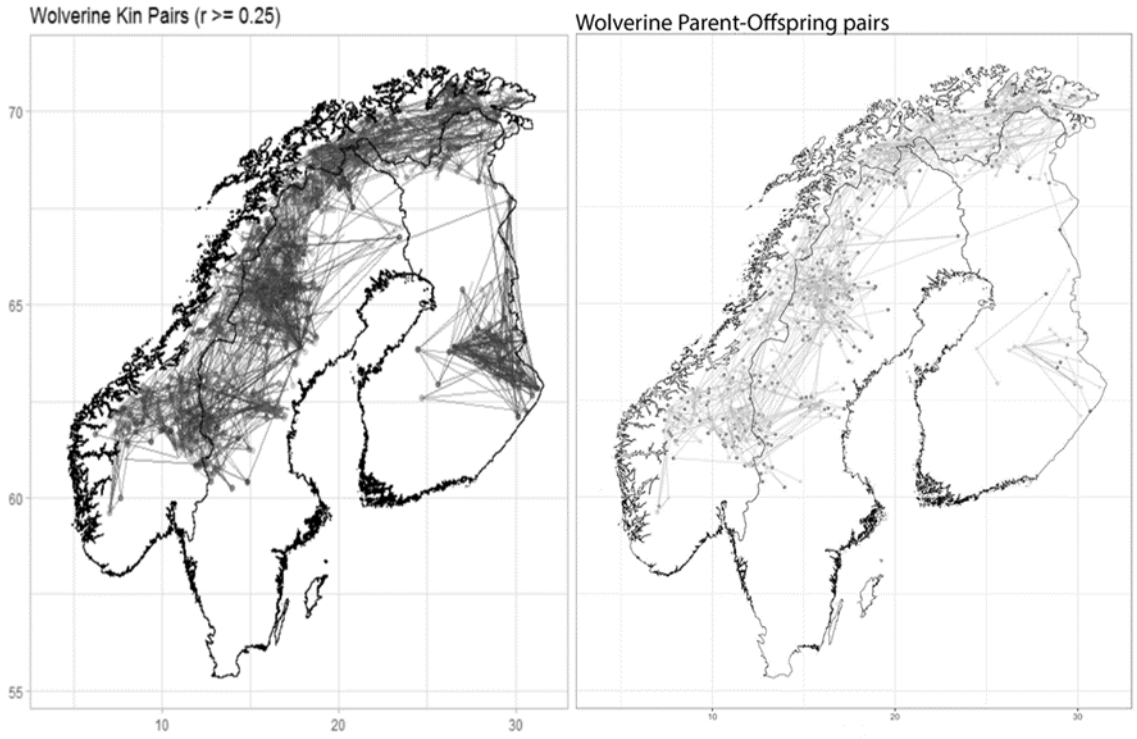

Figure 9. *Analyses of contemporary gene flow (within the last two generations). Analyses for left panel run in SNPRelate and for the right panel in the software ML-relate, both plotted in R using 'ggplot'. For both panels, individuals in pairs are linked by solid lines. The left panel shows kinship pairs including and above second order kin (i.e. r>0.25, or two generations). The right panel shows only parent-offspring pairs (i.e. r=0.5)*.

4 Discussion

All analyses presented herein showed low but significant levels of genetic differentiation in the Fennoscandian wolverine population, especially across Norway, Sweden, and northern Finland. Despite some genetic structuring, levels of gene flow appeared to be quite high across this entire area. However, genetic differentiation between southern Finland and the rest of Fennoscandia was stronger, suggesting limited gene flow. Nevertheless, we found several individuals in northern Fennoscandia that seemed to represent a southern Finnish or eastern genetic signature, showing the potential for immigration also to Scandinavia.

The apparent genetic structure across Norway, Sweden and northern Finland was more likely a result of isolation-by-distance, rather than true population differentiation with limited dispersal among subpopulations. Indeed, it has been shown that software such as Structure and BAPS will force continuous variation into discrete patterns of population differentiation and thus overestimate the extent of genetic clustering (Frantz et al. 2009). Low levels of differentiation and good connectivity across Scandinavia and northern Finland was supported by the sPCA, showing a global genetic signature throughout this area, and corroborated by a gene flow estimate of 4.5% between northern Fennoscandia and central Scandinavia. Furthermore, the kinship analyses revealed that dispersal between the genetic clusters were common.

The wolverines from southern Finland showed a different genetic signature, with several private alleles and one common mtDNA haplotype that was only found in a few individuals outside southern Finland; all of them in the eastern part of northern Fennoscandia. Accordingly, southern Finland formed a separate cluster in the spatial structure modelling with a low estimated migration rate to Fennoscandia, leading to a highly localized genetic signature, as demonstrated from the sPCA and further supported by the kinship analyses. All these figures pointed to limited connectivity between southern Finland and Scandinavia. Importantly though, the “southern Finland” mtDNA haplotype was found in northern Finland and the very eastern part of Scandinavia and some additional individuals with a complete or partial “southern Finnish” genetic signature were present in the same area. Indeed, as wolverines are continuously distributed throughout Scandinavia and northern Finland with good connectivity between different parts of the population, there is a strong potential for immigration and gene flow, which may eventually lead to the influx of “eastern” alleles into Scandinavia. Although wolverines on average do not disperse far (Vangen et al. 2001), they do have large dispersal capacities (Packila et al. 2017).

Implications for conservation

While our analyses demonstrated relatively high levels of gene flow across most of Fennoscandia, wolverines from southern Finland showed a different genetic signature, indicating lower connectivity to this part of Fennoscandia. Our attempt to quantify gene flow suggests that the current effective number of migrants from southern Finland to the remaining Fennoscandia was probably less than one individual per generation, whereas migration in the opposite direction was potentially larger. The estimates on migration rate from northern to southern Finland may however have been overestimated due to human-assisted translocation of 16 wolverines from northern to southern Finland during the years 1979-1998 (Pohja-Mykrä & Kurki 2008).

Long-term maintenance of genetic diversity in any population requires one migrant per generation (Mills & Allendorf 1996). This emphasizes the need for higher influx of eastern wolverines to Scandinavia in the years to come. That said, we found several individuals in the north-eastern part of Fennoscandia representing a southern Finnish or eastern genetic signature. Also, in our sample of 1278 individuals, six wolverines sampled further to the southwest in Scandinavia showed a mixed southern Finland/Scandinavian ancestry. These figures indicate the potential for immigration and gene flow into the Scandinavian wolverine population.

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6 Appendices

Supplementary Table 1 Allele frequencies for each of the 18 genotyped microsatellite loci.

Locus	Allele	Scandinavia	N Fennoscandia	S Finland	All
Gg7					
	168	0.495	0.337	0.349	0.432
	170	0.505	0.662	0.552	0.56
	166	0	0.001	0.099	0.008
	Sample size	1530	826	192	2548
Gg14					
	189	0.441	0.478	0.392	0.449
	199	0.461	0.459	0.5	0.464
	197	0.093	0.06	0.011	0.076
	201	0.005	0.002	0.097	0.011
	Sample size	1530	812	186	2528
Gg42					
	205	0.095	0.14	0.129	0.112
	203	0.157	0.077	0.14	0.13
	201	0.749	0.783	0.731	0.758
	Sample size	1532	820	186	2538
Mvis72					
	262	0.416	0.584	0.443	0.473
	264	0.431	0.351	0.427	0.405
	266	0.153	0.065	0.13	0.123
	Sample size	1516	818	192	2526
Mvis75					
	135	0.184	0.328	0.245	0.235
	139	0.246	0.109	0.005	0.183
	137	0.437	0.473	0.214	0.432
	133	0.133	0.09	0.531	0.149
	131	0	0	0.005	0
	Sample size	1534	826	196	2556
Gg216					
	174	0.337	0.342	0.2	0.336
	172	0.321	0.093	0.2	0.242
	180	0.31	0.524	0.36	0.383
	176	0.032	0.041	0.24	0.039
	Sample size	1534	804	50	2388
Gg234					
	91	0.602	0.717	0.474	0.629
	97	0.334	0.167	0.099	0.262
	101	0.01	0.076	0.005	0.031
	95	0.054	0.039	0.417	0.076
	93	0	0	0.005	0
	Sample size	1534	824	192	2550

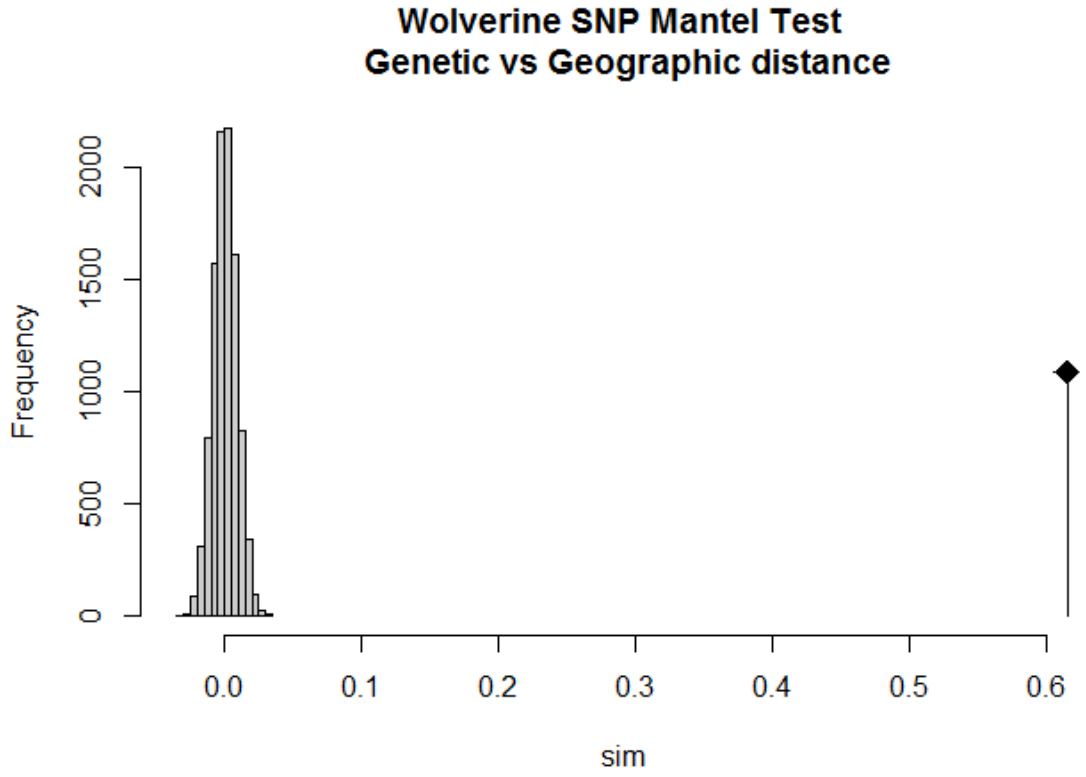
Gg443					
	95	0.694	0.797	0.633	0.723
	99	0.303	0.199	0.02	0.248
	97	0.002	0.004	0.041	0.005
	91	0.001	0	0.306	0.024
	Sample size	1530	824	196	2550
Gg452					
	115	0.644	0.412	0.189	0.534
	113	0.175	0.134	0.199	0.164
	111	0.148	0.352	0.5	0.24
	119	0.034	0.099	0.077	0.058
	117	0	0.004	0.036	0.004
	Sample size	1532	822	196	2550
Gg454					
	133	0.43	0.622	0.228	0.476
	139	0.143	0.029	0.006	0.097
	131	0.174	0.198	0.144	0.179
	137	0.209	0.124	0.372	0.194
	135	0.043	0.027	0.25	0.053
	Sample size	1528	788	180	2496
Gg465					
	173	0.269	0.438	0.151	0.315
	183	0.573	0.453	0.677	0.542
	181	0.158	0.09	0.005	0.124
	177	0	0.019	0.161	0.018
	171	0	0	0.005	0
	Sample size	1532	826	192	2550
Gg470					
	113	0.169	0.254	0.428	0.215
	115	0.831	0.746	0.572	0.785
	Sample size	1518	764	194	2476
Gg101					
	145	0.168	0.066	0.065	0.131
	151	0.692	0.751	0.783	0.714
	143	0.128	0.169	0.087	0.141
	147	0.001	0.003	0.065	0.003
	153	0.01	0.011	0	0.01
	149	0.001	0	0	0.001
	Sample size	1502	792	46	2340
Gg25					
	158	0.129	0.228	0.04	0.16
	166	0.376	0.57	0.32	0.44
	164	0.495	0.202	0.46	0.396
	160	0	0	0.18	0.004
	Sample size	1524	802	50	2376

Gg471					
	115	0.658	0.628	0.744	0.654
	117	0.342	0.372	0.256	0.346
	Sample size	1512	792	168	2472
Lut604					
	115	0.66	0.542	0.6	0.619
	121	0.34	0.458	0.4	0.381
	Sample size	1522	802	50	2374
Mvis57					
	119	0.519	0.343	0.266	0.443
	115	0.255	0.183	0.031	0.215
	111	0.209	0.318	0.469	0.264
	121	0.001	0.011	-	0.004
	113	0.016	0.145	0.146	0.067
	117	0	0	0.078	0.006
	109	0	0	0.01	0.001
	Sample size	1526	808	192	2526
Tt4					
	180	0.891	0.918	0.435	0.866
	182	0.101	0.081	0.559	0.128
	184	0.009	0.001	0.005	0.006
	Sample size	1520	804	186	2510

Supplementary Table 2 List of individuals with mismatch between geographic origin and genetic assignment and with mixed ancestry. Results from admixture analysis in BAPS.

Individual	Geographic origin	Proportion of genome represented by population cluster		
		Scandinavia	N Fennoscandia	S Finland
Ind2997	Scandinavia	0	0.75	0.25
Ind2472	Scandinavia	0	1	0
Ind2483	Scandinavia	0	1	0
Ind1942	Scandinavia	0	0.83	0.17
Ind1247	Scandinavia	0.12	0.45	0.43
Ind1398	Scandinavia	0	0.99	0.01
Ind1423	Scandinavia	0.01	0.87	0.12
Ind1443	Scandinavia	0.02	0.92	0.06
Ind5268	Scandinavia	0	0.88	0.12
Ind5762	Scandinavia	0	1	0
Ind1448	Scandinavia	0	0.88	0.12
Ind5154	Scandinavia	0	1	0
Ind1449	Scandinavia	0	1	0
Ind1342	Scandinavia	0	1	0
Ind5234	Scandinavia	0	1	0
Ind6112	Scandinavia	0.02	0.94	0.04
Ind5146	Scandinavia	0	1	0

Ind6151	Scandinavia	0	0.87	0.13
Ind1455	Scandinavia	0	1	0
Ind5021	Scandinavia	0.08	0.92	0
Ind6172	Scandinavia	0	1	0
Ind1403	Scandinavia	0.09	0.88	0.03
Ind5032	Scandinavia	0	1	0
Ind1244	Scandinavia	0	1	0
Ind5219	Scandinavia	0	1	0
Ind6052	Scandinavia	0	0.94	0.06
Ind6053	Scandinavia	0	1	0
Ind1341	Scandinavia	0.47	0.12	0.41
Ind1394	Scandinavia	0.64	0	0.36
Ind1431	Scandinavia	0.73	0	0.27
GgF0006	N Fennoscandia	0.17	0.16	0.67
Ind6096	N Fennoscandia	1	0	0
Ind1288	N Fennoscandia	0.84	0	0.16
Ind5209	N Fennoscandia	1	0	0
Ind5757	N Fennoscandia	0.81	0	0.19
Ind2036	N Fennoscandia	0.99	0	0.01
Ind6083	N Fennoscandia	1	0	0
Ind3039	N Fennoscandia	1	0	0
Ind3014	N Fennoscandia	0.38	0	0.62
Ind2977	N Fennoscandia	0.44	0	0.56
Ind3020	N Fennoscandia	0.13	0.02	0.85
Ind2978	N Fennoscandia	0.63	0	0.37
Ind3025	N Fennoscandia	0.37	0	0.63
Ind3036	N Fennoscandia	1	0	0
Ind3030	N Fennoscandia	0.29	0.09	0.62
Ind2987	N Fennoscandia	0.85	0.15	0
Ind3023	N Fennoscandia	0.14	0.33	0.53
Ind3059	N Fennoscandia	0.08	0.16	0.76
Ind3086	N Fennoscandia	0.31	0.31	0.38
Ind3017	N Fennoscandia	0.01	0.36	0.63
Ind3046	N Fennoscandia	0.27	0.21	0.52
Ind3015	N Fennoscandia	0.31	0.21	0.48
GgF0081	S Finland	0.37	0.17	0.46
Ind3069	S Finland	0	0.56	0.44
GgF0090	S Finland	0	0.73	0.27
GgF0011	S Finland	0	0.99	0.01
GgF0012	S Finland	0.21	0.79	0
GgF0013	S Finland	0	1	0
GgF0037	S Finland	0	0.96	0.04



Supplementary Figure 1 *Randomization test (Mantel) showing a highly significant isolation by distance pattern when plotting pairwise relatedness values against geographic distances. The histogram in the left part of the graph shows the randomized distribution of correlations and the single line to the right the actual correlation in the data.*

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