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Lynx gene flow in Fennoscandia

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LYNX GENE FLOW IN FENNOSCANDIA

Estimation of gene flow within the Fennoscandian lynx population

Report from SLU Wildlife Damage Center 2024–2

Authors Heather Hemmingmoore[1], Mikael Åkesson[1], Anna Danielsson[1], Göran Spong[2], Oddmund Kleven[3], Alexander Kopatz[3], Katja Holmala[4], Henrik Andrén[1]

Heather Hemmingmoore Orcid ID: 0000-0002-3550-8475
Mikael Åkesson Orcid ID: 0000-0002-4325-8840
Göran Spong Orcid ID: 0000-0002-1246-5046
Oddmund Kleven Orcid ID: 0000-0003-0267-6795
Alexander Kopatz Orcid ID: 0000-0002-9139-1179
Katja Holmala Orcid ID: 0000-0002-1346-4475
Mikael Åkesson Orcid ID: 0000-0002-4325-8840
Henrik Andrén Orcid ID: 0000-0002-5616-2426

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[1] Grimsö Wildlife Research Station, Department of Ecology, Swedish University of Agricultural Sciences, SE-739 93 Riddarhyttan, Sweden
[2] Molecular Ecology Group, Wildlife, Fish, & Environmental Studies, SLU, SE-90183 Umeå, Sweden
[3] Norwegian Institute for Nature Research, Høgskoleringen 9, NO-7034 Trondheim, Norway
[4] Natural Resources Institute Finland (Luke), University of Helsinki, Helsinki, Finland

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Heather Hemmingmoore, Mikael Åkesson, Anna Danielsson, Göran Spong, Oddmund Kleven, Alexander Kopatz, Katja Holmala, Henrik Andrén

Abstract

This study assesses the connectivity and gene flow between Eurasian lynx (*Lynx lynx*) populations in Finland and Scandinavia for the purpose of providing data for the evaluation of favorable conservation status for the European Union Habitats Directive. Using tissue samples from deceased lynx in Fennoscandia, i.e., Sweden, Norway, and Finland, collected between 2019 and 2022, we genotyped these samples using 91 single nucleotide polymorphisms (SNPs). A separate data set was used for validation, consisting of 73 samples from Scandinavia collected between 2010 and 2015 that were RAD sequenced and genotyped using 881 SNPs. We assessed genetic structure within all of Fennoscandia, as well as genetic differentiation and recent gene flow between Scandinavia (Sweden, Norway) and Finland. We also estimated individual relatedness to identify first order relatives, or immediate family members, for the purpose of assessing contemporary connectivity. The results suggest distinct genetic differentiation between the Scandinavian and Finnish lynx populations, with migration rates of approximately eight migrants per generation in either direction, which is comparably low but likely sufficient to prevent complete genetic isolation. These findings have significant implications for lynx conservation strategies under the European Habitats Directive. They underscore the importance of maintaining genetic diversity and facilitating connectivity between transboundary populations, highlighting the need for collaborative management approaches between Sweden, Norway, and Finland.

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Introduction

When populations of wide-ranging, terrestrial species span international borders, different management approaches can have varying impacts on the composition, genetic diversity and structure of these transboundary species (Mason et al. 2020). Thus, it is crucial to understand their population structure and potential barriers in border regions, including whether a single population spans the border, or whether animals on either side belong to distinct populations. If the populations on either side of a boundary exhibit genetic differentiation, it is suggesting population subdivision and therefore it might be important to determine the extent of gene flow between them. Such knowledge provides crucial implications for the genetic health and diversity of each population.

The Eurasian lynx (*Lynx lynx*) is one such transboundary species. It is on Annex IV of the European Habitats Directive, which are defined as "species of Community interest (i.e., endangered, vulnerable, rare or endemic in the European Community) in need of strict protection" (Directive 92/43/EEC). There are eleven distinct populations in Europe (Chapron et al 2014, von Arx et al. 2021), which include the Scandinavian population in Norway and Sweden, and the Karelian population in Finland, which has been previously found to be connected to northwestern Russia (Chapron et al. 2014, von Arx et al. 2021). In this report, we refer to the "Finnish population" rather than the "Karelian population" since our analysis only considers lynx in Finland, which we acknowledge is a subset of the larger Karelian population (Mueller et al. 2022). The lynx population in Scandinavia has recovered to 1200 – 1600 individuals in Sweden and to 350 – 500 individuals in Norway in winter 2022/2023 (Frank & Tovmo 2023) after almost complete extirpation in the early 20th century due to a management policy of paying bounties for pelts (Lönnberg 1930). In Finland, lynx were also nearly extirpated in the mid 20th century (Luikkonen et al. 2009) and have recovered to 2400 – 2600 lynx in the 2022 monitoring season, the majority of which occurred in southern Finland outside the reindeer husbandry area (Valtonen et al. 2023).

Although the Scandinavian and Finnish populations share a similar history of intense persecution in the past, the small populations from which they each recovered in the 20th century were geographically and genetically separated (Hellborg et al. 2002). Scandinavian lynx show lower genetic diversity than their Finnish conspecifics (Spong and Hellborg 2002, Förster et al. 2018, Mueller et al. 2022) and are among the least genetically diverse populations of Eurasian lynx according to analyses of microsatellites and mitochondrial DNA (Schmidt et al. 2011, Ratkiewicz et al. 2012), and recent genome-wide analyses (Lucena-Perez et al. 2020, Mueller et al. 2022), likely due to their geographic isolation from the rest of the continent. Previous analysis with microsatellites and mitochondrial DNA identified structure within the Scandinavian population along a north-south gradient, consistent with the recent bottleneck event and with a pattern of isolation by distance (Hellborg et al. 2002). East-west structure has also been identified within Scandinavia which may not be fully explainable by isolation by distance, and which may predate the population bottleneck (Rueness et al. 2003). A similar pattern of sub structure has not been identified in Finland. Female kin clusters have been identified, with male admixture (Holmala et al. 2018, Herrero et al. 2021). Although Finland and Scandinavia both went through a population bottleneck, the Finnish population has recovered its genetic diversity likely due to its connectivity to Russian Karelia, whereas the Scandinavian population retains relatively higher homozygosity and inbreeding levels, likely due to its geographic isolation from other lynx populations (Mueller et al. 2022). Also, other large carnivore species, such as brown bears (*Ursus arctos*), wolves (*Canis lupus*) and wolverines (*Gulo gulo*), display a similar structural pattern (Åkesson et al. 2021, Kopatz et al. 2021, Lansink et al. 2022).

The objective of this study was to examine the current population structure and gene flow between the Scandinavian and Finnish lynx populations, specifically to provide information for the assessment of favorable conservation status of lynx in Sweden for the European Habitats Directive (reporting 2025 Article 17). Therefore, in this report, we investigate population structure, gene flow, and individual relatedness, for the purpose of assessing the degree of population differentiation and genetic exchange between lynx in Finland and Scandinavia.

Material and Methods

Data collection and genotyping

Fluidigm

This analysis was conducted using a representative number of tissue samples from deceased lynx that were legally shot or killed in traffic in Sweden (n=447), Norway (n = 100), and Finland (n = 102) between 2019 and 2022 (Table 1). Sample collection was not constrained geographically within each country. DNA extractions for all samples took place at Grimsö Wildlife Research Station, Swedish University of Agricultural Sciences (SLU), and the Norwegian samples were also extracted at Norwegian Institute for Nature Research (NINA). All samples were genotyped using 96 single nucleotide polymorphisms (SNPs), 93 of which were autosomal markers and three on the Y chromosome. The Fluidigm SNP array that we used for genotyping was developed for the purpose of sex determination, individual identification and relatedness estimation of lynx within the Scandinavian population. All samples were genotyped at SLU, Grimsö Wildlife Research Station and the Norwegian samples were also genotyped at the NINA genetics lab in Trondheim, Norway. The data was filtered to remove markers on the Y chromosome, markers with more than 20% missing data, and individuals with missing genotypes at more than eight SNPs, resulting in 91 SNPs and 539 individuals being retained (Table 1).

Table 1: Number of tissue samples from lynx (*Lynx lynx*) genotyped by our SNP panel

Country	Final number of samples	Years	DNA Extraction & Genotyping Location	Min/ Max Latitude (WGS84)
Finland	82	2020-2022	Grimsö	60.18/ 67.39
Norway	100	2019-2021	NINA and Grimsö	55.44/ 67.92
Sweden	357	2019-2022	Grimsö	58.41/ 70.39

RAD Sequencing

An independent data set was used to validate our findings from the data set detailed above, consisting of tissue samples from deceased lynx that were legally shot or killed in traffic in Sweden (n=37) and Norway (n=36) between 2010 and 2015. DNA from these samples was extracted at the Swedish University of Agricultural Sciences, Umeå and sequenced by NGI Sweden using Restriction Site-Associated DNA (RAD) Sequencing, a next generation sequencing technique that enables more SNPs to be called than is possible with a Fluidigm panel (Catchen et al. 2013, Rochette and Catchen 2017).

Markers were excluded that contained more than 25% missing data, with a minor allele count lower than three, and that were significantly outside of Hardy-Weinberg equilibrium. After quality control and filtering, this method yielded 881 SNP markers.

Population structure

Discriminant analysis of principal components

We conducted a DAPC analysis, which is a multivariate approach designed to identify groups or clusters of genetically closer or related individuals with priori population definitions to assign membership probabilities for each population to each individual. We ran this analysis with k=2 and k=3 populations, using Scandinavia and Finland as two separate populations, since they are two distinct populations of lynx (Förster et al. 2018, Mueller et al. 2022).

Cluster analysis

Population genetic structure was also assessed using the find.cluster function in the adegenet package in R (Jombart 2010, Jombart and Ahmed 2011). This function utilizes the DAPC method. DAPC does not rely on specific and theoretical assumption for analysis, e.g., that the groups of genotypes should be in Hardy-Weinberg equilibrium. Initially, it performs a principal component analysis (PCA) to transform the original genetic data into uncorrelated variables, capturing the major axes of genetic variation. Then, a K-means clustering algorithm partitions the samples based on these principal components, aiming to minimize the variance within clusters and maximize the variance between them. The Bayesian Information Criterion (BIC) assesses multiple potential values of K (number of clusters) to determine the most suitable number of genetic groups in the dataset.

Structure

We assessed population structure using the Structure software (Pritchard et al. 2000), which uses a Bayesian clustering approach to assign individuals to K populations characterized by a set of allele frequencies at each locus. In this method, allele frequencies are used to probabilistically place individuals into one or more genetic groups, allowing for the detection of mixed ancestry. The approach identifies the number of clusters that best fit the data by maximizing the likelihood of the observed genotypes given the inferred allele frequencies. The number of clusters, k, was set to vary from 1 to 13 in separate runs to determine the most likely number of populations, with ten iterations per k value. The admixture model was selected, allowing for individuals to have ancestry from multiple populations. The burn-in period was set at 100,000 with an additional 500,000 Markov Chain Monte Carlo (MCMC) replications for data collection. The online tools Structure Harvester (Earl and vonHoldt 2012) and Structure Selector (Li and Lui 2018) were used to calculate the mean likelihood values for all values of k across all iterations of the Structure software, for the purpose of identifying the most likely number of genetic clusters (Evanno et al. 2006, Puechmaille et al. 2016).

Population differentiation

F_{ST} captures the amount of genetic difference that can be explained by the difference between populations. We calculated F_{ST} values between Finland and Scandinavia, and also between Sweden, Norway, and Finland, using the *hierfstat* package in R (Goudet and Jombart 2015). Observed heterozygosity was also calculated for each population.

Relatedness

We estimated individual relatedness using the *snpgdsIBDMLE* function from the *SNPRelate* package in R (Zheng et al. 2012). This function calculates the maximum likelihood estimates (MLE) of identity-by-descent (IBD) sharing probabilities based on SNP genotype data. The resultant IBD values were used to assess relatedness coefficients.

Relatedness was assessed for the RADseq data set using the relatedness flag in *vcftools*, which is command line software for working with genomic data in the form of vcf files (Danecek et al. 2011). This method calculates relatedness between pairs of individuals using the Ajk statistic (Yang et al. 2010).

First order relatives

First order relatives, or those with a relatedness value of approximately 0.5, represent a parent/offspring or full sibling relationship. We calculated and mapped the locations of all first order relatives, which we defined as a relatedness value of 0.5 to 0.75 in order to understand where family members were spreading in relation to each other.

Isolation by distance

Geographic distance was calculated between all sample locations using QGIS version 3.22. Mantel tests were used to test for isolation by distance, or the correlation between genetic and geographic distance between individuals using the vegan R package (Oskanen et al. 2022). Isolation by distance was calculated between all samples, and also within the Finnish and Scandinavian populations separately due to the geographic division of the Baltic Sea.

Gene flow

To estimate contemporary gene flow between Finland and Scandinavia, we utilized the *BayesAss3-SNP* software, which estimates migration rates between populations without assuming migration-drift equilibrium (Wilson and Rannala 2003, Mussman et al. 2019). For each population, the analysis was run with 1 million Markov Chain Monte Carlo (MCMC) iterations, a burn-in of 100,000 iterations, and a sampling frequency of 100 iterations. Convergence of the chains was assessed by visual inspection of trace plots (Meirmans 2014). The resultant posterior distributions of migration rates probabilities were used to determine the direction and frequency of recent gene flow between Finland and Scandinavia.

Results

Population structure

All the methods found a clear distinction between the Finnish and Scandinavian lynx populations, which aligns with previous knowledge of lynx population structure across Europe (Förster et a. 2018, Mueller et al. 2022). The Structure analysis, discriminant analysis of principal components, and cluster analysis each identified a single immigrant in Sweden from the Finnish population, sample number V0773/21, an adult female that passed away in Sweden near the Finnish border. The RADseq validation data set was not used to differentiate between Finland and Scandinavia because no Finnish samples were included.

Within Scandinavia, more population structure was identified than within Finland, indicating that the SNPs identified from Scandinavian samples are more variable in Scandinavia compared to Finland. However, the genetic clusters identified are not spatially distinct, suggesting that these are potential lineages and not separate sub-populations. The RADseq validation data set found a single cluster encompassing all of Scandinavia to be the most parsimonious model. Detailed results from each method are as follows:

Discriminant analysis of principal components (DAPC)

The DAPC analysis conducted with k=2 genetic clusters assigned all Finnish individuals to a single genetic cluster with more than a 99.8% probability. It also assigned sample number V0773/21 from Sweden to the Finnish population with a 100% probability. A second individual within Sweden (V0838/19) was given a 10% assignment to the Finnish population, with all other individuals within Scandinavia having less than a 1% probability of Finnish assignment (Figures 1 and 2). When the DAPC analysis was conducted with k=3 genetic clusters, all Finnish individuals were likewise assigned to the same genetic cluster.

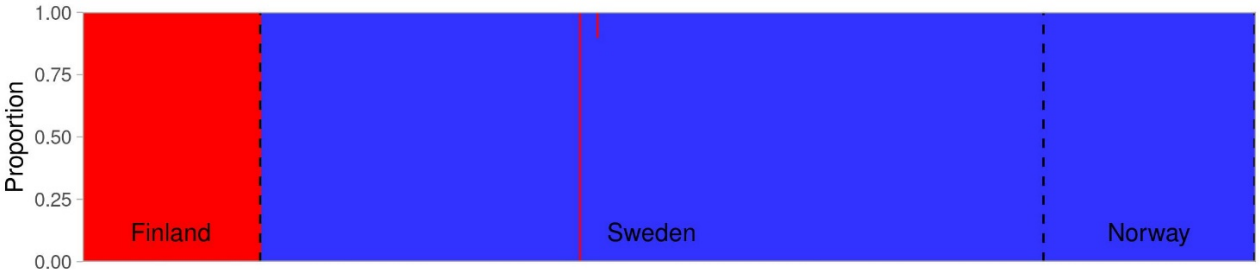

Figure 1: DAPC assignments for all individuals between Finland and Scandinavia, k=2. Each individual is a stacked bar, for which the proportion of their assignment to each cluster is a different color.

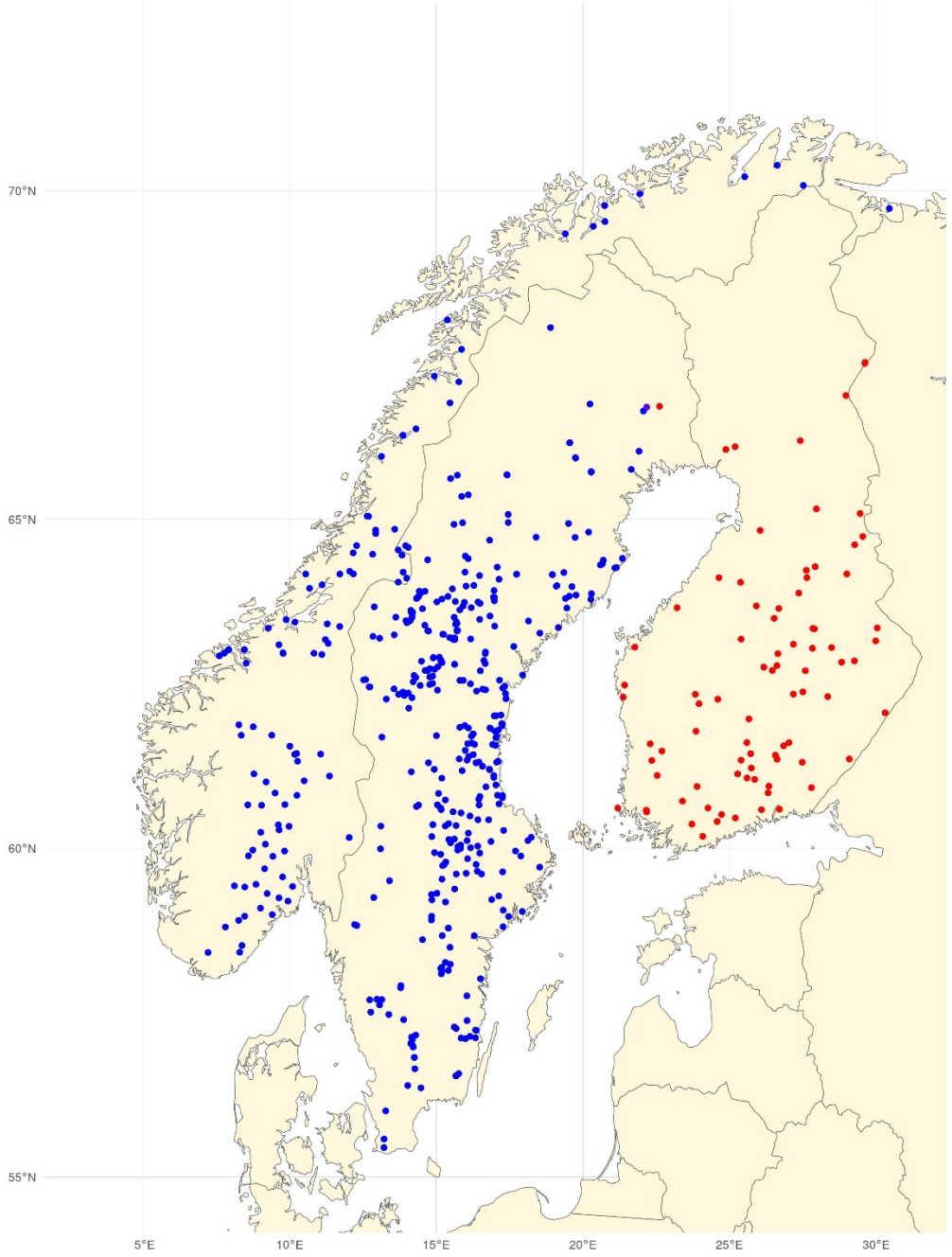

Figure 2: Percentage assignment to the Finnish population cluster according to the DAPC analysis, with red = 100% and blue = 0%, with intermediate shades indicating admixture.

Cluster analysis

The cluster analysis identified eight genetic clusters, seven of which occur in Scandinavia, with Finland as a single cluster (Figure A4). A single sample in Sweden (number V0773/21), an adult female killed in 2021, was assigned to the Finnish cluster, which was the same sample assigned to Finland by Structure and DAPC. The optimal number of clusters (k) was sensitive to the number of principal components (PCs) specified in the analysis, with more granular structure and therefore a greater number of clusters identified as the number of PCs declined. This analysis used 45 PCs, which capture approximately 80% of the variation in the data.

The same analysis for the RADseq validation data set yielded an optimal value of k=1 cluster, suggesting that the Scandinavian lynx is a single, relatively homogenous population. As in the case of the Fluidigm data set, the optimal value of k was sensitive to the number of principal components retained, and we used 45 PCs, which captures approximately 80% of the variation in the data.

Structure analysis

The Structure analysis identified more admixture than did the DAPC and cluster analysis (Figures 3 and 4). Using just the mean likelihood values from the Bayesian clustering approach employed by Structure, k = 12 appears to be the optimal number of clusters (Pritchard et al. 2000) (Figure A1). When K=12, similar clusters are assigned to those assigned using the *find.clusters* function in *adegenet* (Figure A4), with a single cluster in Finland and distinct clusters in southern Norway, northern Norway, and southern Sweden, with overlap in central Sweden and Norway. However, when the method employed by Puechmaille (2016) is used to account for spurious clusters, the optimal value for k drops to three (Figure A2), while the method employed by Evanno et al. (2006) suggests k = 2 clusters (Figure A3). For k=2, the samples separate into Finland and Scandinavia, with the same single sample identified as an immigrant from Finland to Sweden.

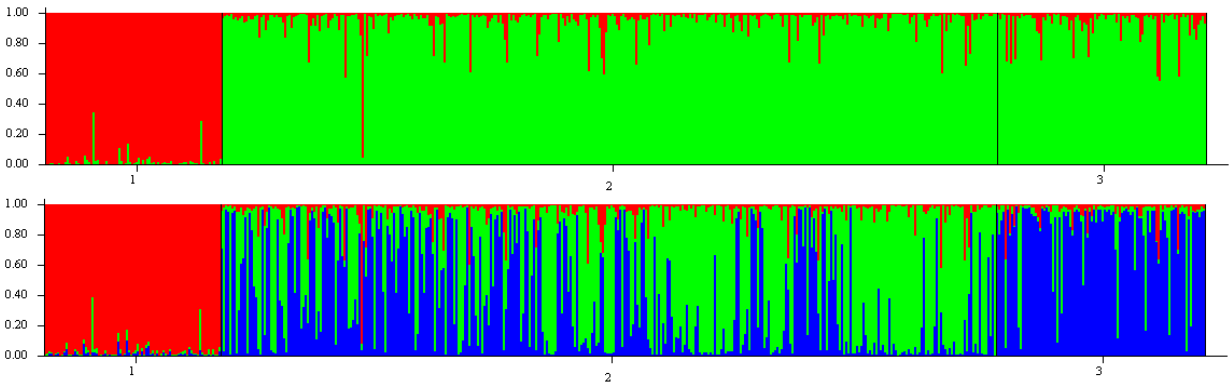

Figure 3: Population cluster assignment based on results from STRUCTURE. Population 1 = Finland, Population 2 = Sweden, Population 3 = Norway. Top, k=2 clusters, bottom, k=3 clusters. Each individual is a stacked bar, for which the proportion of their assignment to each cluster is a different color. The individual in the Swedish cluster (2) with a red bar is V0773/21, the single lynx in Sweden that was assigned to Finland.

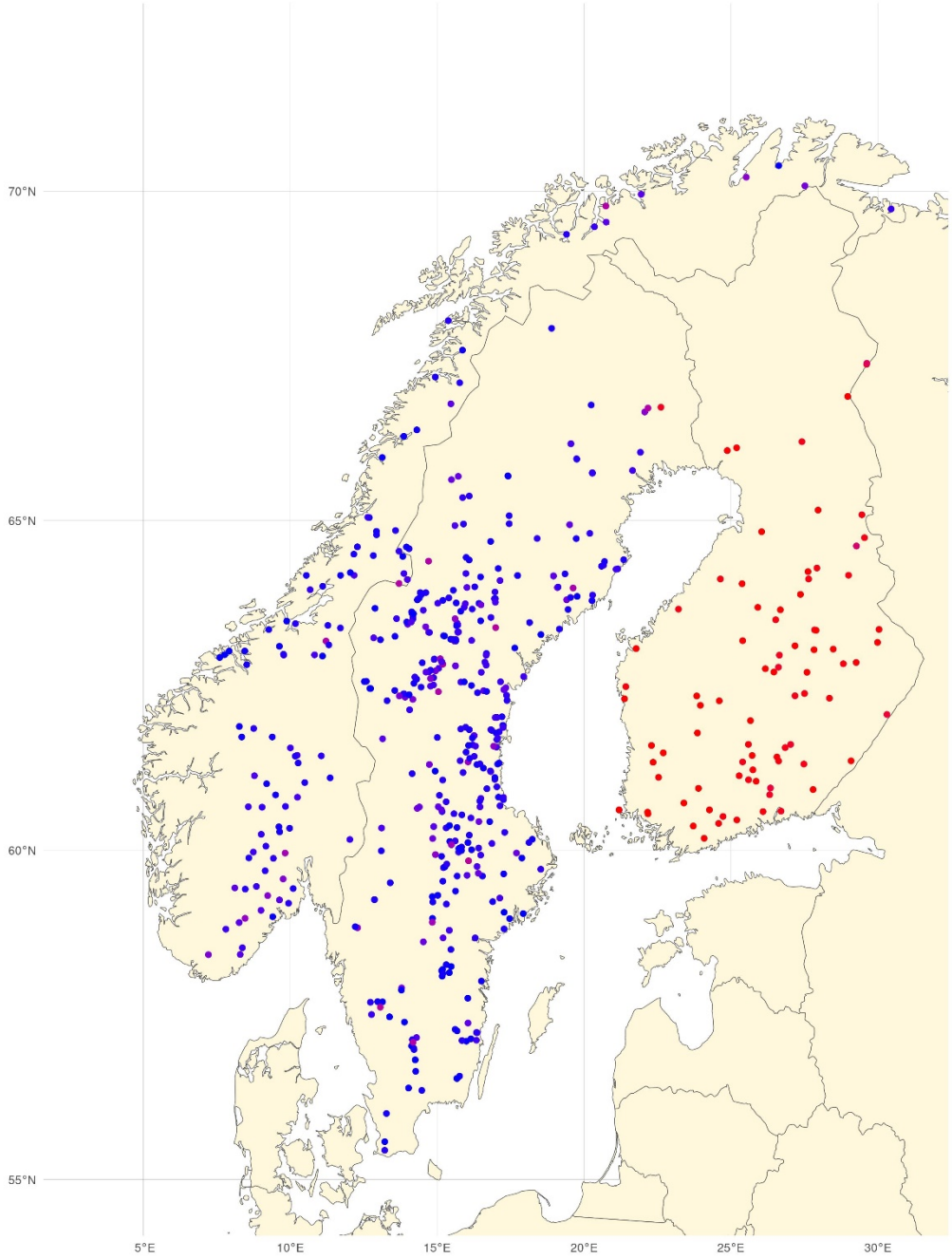

Figure 4: Percentage assignment to the Finnish population cluster according to the STRUCTURE analysis, with red = 100% and blue = 0%, with intermediate shades indicating admixture.

An assignment from Structure (q) indicates the proportion of an individual's genome that originates from each of the inferred clusters or populations. The value of q ranges from 0 to 1 for each cluster, and the sum of each individual's q-values across all clusters (k) should be one.

For k = 2, there is a high level of alignment between cluster assignment and population, with all Finnish samples assigned to the same cluster with a mean q of 0.977 ± 0.051 sd. All Scandinavian samples except one were assigned to a different single cluster 0.947 ± 0.092 sd. As with the DAPC

analysis, a single individual in Sweden (V0773/21) was assigned to the Finnish cluster with an assignment value (q) of 0.954 (95.4%), indicating that she is a migrant from Finland.

When a third cluster was evaluated (k=3), the strong alignment between Finnish samples was retained. All Finnish samples as well as Sample V0773/21 from Sweden were still assigned to a single cluster, while there was more admixture between Norway and Sweden (Table 2).

Admixed individuals are those with ancestry from more than one cluster, with thresholds of 70%, 80% or 90% assignment to a single cluster commonly used to define admixed individuals (e.g., Kopatz et al. 2014, Bhat et al. 2014). Within Finland, only four samples (4.8%) had a q value below 0.9, meaning more than 10% of their ancestry was assigned to the Scandinavian cluster. Of these, only two were below 0.8, and one below 0.7, at 0.71 and 0.63 respectively. This result suggests very little gene flow eastward from Scandinavia into Finland, as we found no migrants, minimal admixture with Structure, and no admixture with the DAPC and cluster analysis. Within Scandinavia, the Structure analysis indicated that 62 lynx may have some Finnish ancestry, although this result should be interpreted with caution, as the potential admixture is minimal

Table 2: Mean cluster assignment for lynx from each country, for k=2 and k=3 clusters

	K=2		**K=3**		
	Cluster 1	Cluster 2	Cluster 1	Cluster 2	Cluster 3
Finland	.975	.024	.962	.022	.017
Norway	.068	.932	.042	.136	.821
Sweden	.049	.951	.048	.552	.400

Population differentiation

F_{ST} values, which capture the proportion of variation that is explainable by population, found a 13.6% difference between Finland and Scandinavia. When populations are compared by country, we found a 13.9% difference between Sweden and Finland, and a 14.0% difference between Norway and Finland, with just a 2% difference between Norway and Sweden. The F_{ST} values between the two Scandinavian countries and Finland are in alignment with the F_{ST} value between Norwegian and Finnish lynx identified previously using RADseq data (Mueller et al. 2022). The 2% difference between Sweden and Norway is not surprising because it is consistent with F_{ST} values between geographically separated clusters within the same population, as Finland and Karelia also have an F_{ST} value of 2% (Mueller et al. 2022).

Relatedness

First order relatives

We found 359 pairs of likely first order relatives within the Fluidigm data set, with no relative pairs between Scandinavia and Finland (Figure 5a). There were no relative pairs in which one member of the dyad was found in Scandinavia and another in Finland. Within the RADseq data set, eleven first order relative pairs were identified within Scandinavia, containing 17 lynx (Figure 5b).

Isolation by distance

Neither data set display an effect of isolation by distance. Mantel tests resulted in a negative correlation between relationship coefficient and geographic distance, with p values approaching one, suggesting the correlation likely occurred entirely by chance (Table 3).

Table 3: Mantel test results for isolation by distance

	Correlation	P value
Fluidigm – Scandinavia	-0.156	1
Fluidigm – Finland	-0.115	0.992
RADseq – Scandinavia	-0.3892	1

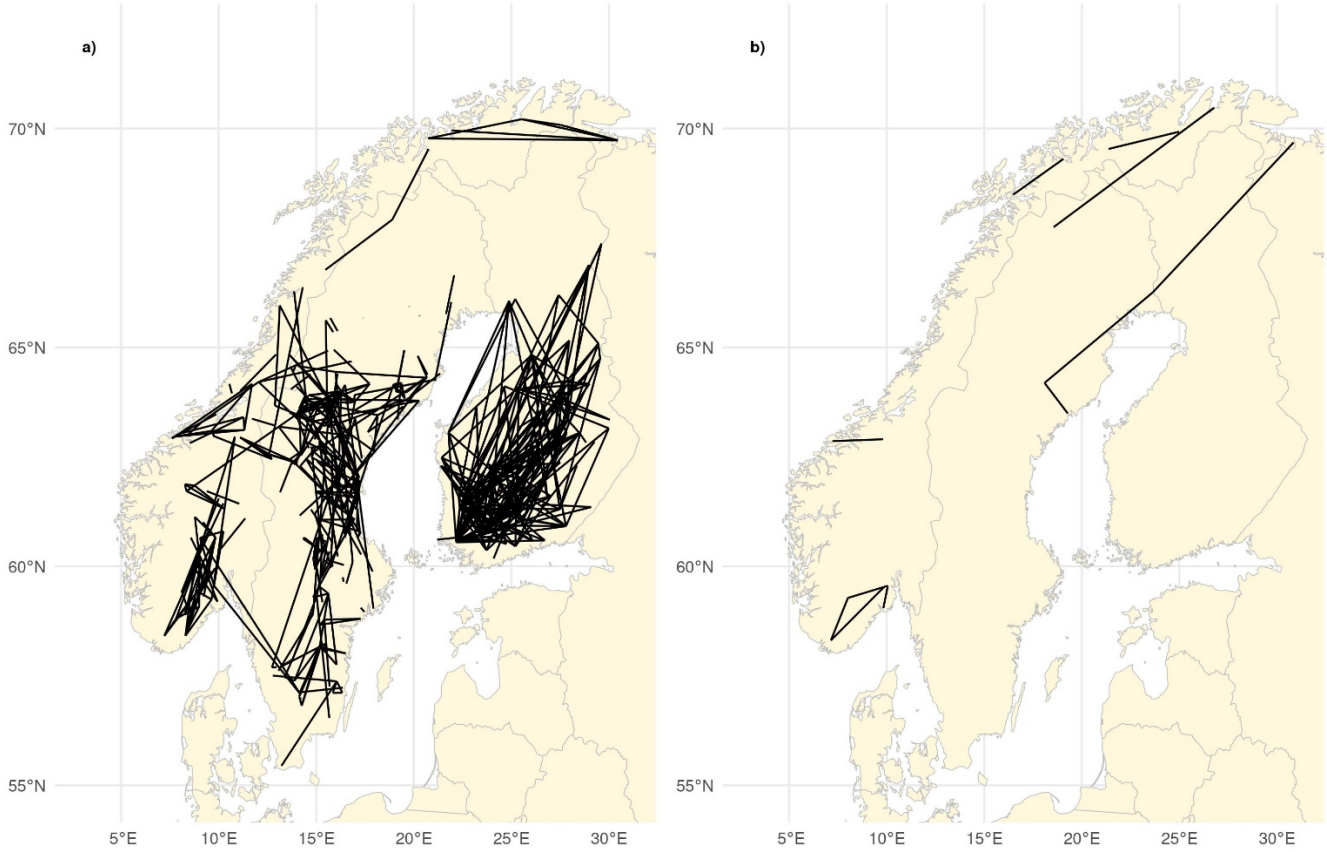

Figure 5: The end of each line is the location of one member of a pair of first order relatives (R=0.5 to 0.75), likely a parent-offspring or full sibling pair. Panel a) shows first order relatives within the Fludigm data set (n=359 pairs containing 409 individuals, or 76% of the data set); Panel b) shows first order relative pairs within the RADseq validation data set (n=11 pairs containing 17 individuals, or 23% of the data set).

Gene flow

Migration rate between the populations was estimated to 0.49% (± 0.48%) migration rate per generation from Finland into Scandinavia, and an estimated 0.35% (± 0.16%) migration rate from Scandinavia into Finland. As recent population size in Scandinavia was estimated to be 1550 – 2100 individuals (Frank & Tovmo 2023), the effective number of migrants per generation from Finland to Scandinavia is estimated to be 8 – 10. As the Finnish population was recently estimated to be 2400 – 2600 lynx, the effective number of migrants per generation from Scandinavia to Finland is estimated to be 8 – 9 (Ministry of Agriculture and Forestry of Finland 2021), or could potentially be higher depending on the size of the greater Karelian population. Although the estimated migration rate is higher than may be expected given the single Finnish migrant detected in Scandinavia, a result that differs substantially from the estimate is not surprising given the wide confidence interval in both the estimated migration rate and population size.

Discussion

Finland and Scandinavia

Our results show that Finland and Scandinavia are home to two distinct Eurasian lynx populations, which is well established from both a demographic and genetic point of view (Hellborg et al 2002, Chapron et al. 2014, Förster et al 2018, Mueller et al. 2022). Although the two populations are distinct, our results show that they are not completely isolated from each other, in that one individual in the data set in Sweden clearly originated from the Finnish population. However, relatively little gene flow occurs between Finland and Scandinavia. While *Structure* identified admixture that *adegenet* did not find, both methods found a single individual lynx in Scandinavia that was identified as a Finnish immigrant. No lynx in were Finland assigned to the Scandinavian population. No close relatives were found between Finland and Scandinavia, and the rate of migration was found to be less than half of one percent per generation in either direction. Although immigration is low, it does likely exceed one migrant per generation, which is the minimum amount of immigration a population needs in order to not experience a loss of genetic variation (Mills & Allendorf 1996). This estimate of an immigration rate of eight to nine individuals per generation is feasible despite our identification of only a single immigrant, as lynx can travel long distances in a single generation as shown by the distances we detected between first order relatives. This capability in combination with the lack of impeding habitat features, suggest that these populations likely have connectivity, even if we have detected only the occasional event.

Despite the long distance dispersal capability of lynx (Samelius et al. 2012, Hemmingmoore et al. manuscript b), transboundary gene flow between Scandinavia and Finland is relatively low, and lower than that of other large carnivores, i.e. brown bears (Kopatz et al. 2019, Kopatz et al. 2021) and wolverines (Kleven et al. 2019, Lansink et al. 2022). The lynx population is sparse on both sides of the border, with only sporadic occurrence in northern Finland and areas of permanent and sporadic occurrence near the Finnish border in Norrbotten County in northern Sweden (Chapron et al. 2014, Frank and Tovmo 2023, Valtonen et al. 2023) (Figures A6 and A7). Management maintains low lynx densities in the reindeer husbandry area in northern Finland, as only 50-75 of the country's approximately 2400-2600 lynx occurred in the reindeer husbandry area (Ministry of Agriculture and Forestry of Finland 2021, Valtonen et al. 2023). Likewise in Sweden, the minimum population

threshold of the northernmost county of Norrbotten is 17 family groups or 11% of the total national minimum threshold, although Norrbotten occupies 22% of Sweden (SEPA 2019). Therefore, management policies in both countries contribute to low numbers of lynx in areas surrounding the national border, which may have contributed to this limited gene flow.

The discrepancy in the number of admixed individuals between the *Structure* results and DAPC results from *adegenet* might arise due to methodological differences in how each tool performs its calculations. Structure's Bayesian clustering approach seeks to capture subtle population structure, while DAPC's linear discriminant analysis of principal components seek to maximize similarity within clusters and differences between them, which might accentuate distinctions between groups. The different results could also be reflective of hierarchical population genetic structure on local, regional and large scales as well as the population history, which will be investigated further in future work.

Within Scandinavia

The population structure within Scandinavia as identified within the Fluidigm data set was unexpected given the presence of some individuals long distances between first order relatives (Figure 5), the lack of population structure recently identified in southern Sweden (Hemmingmoore et al. *manuscript b*), and the comparative homogeneity of the Finnish population. The comparative lack of structure in Finland has been found in previous research (Hellborg et al. 2002), and could potentially be explained by latent effects of the prior bottleneck, exacerbated by potential landscape barriers such as the Scandinavian mountain range (Hellborg et al. 2002, Rueness et al. 2003). As the markers are less variable in Finland, the power to detect structure with that data is also lower.

However, the RADseq validation data set gave a single Scandinavian genetic cluster as the most parsimonious result, and did not reflect the high level of structure found in the Fluidigm data set. The reason for this is likely because the SNP markers used in the primary data set of this study were selected to identify fine scale genetic structure in Scandinavia for the purpose of individual and familial identification, and identification of immigrants. Therefore, markers with high minor allele frequency were selected as the most informative in individual and familial differentiation within the Scandinavian population, which could potentially skew the results toward showing more fine scale structure in Scandinavia than in Finland. This view is supported by the observed heterozygosity (H_O) within each data set; (H_O) for the RADseq data set of 0.267 aligns with previous studies, which have found Scandinavian lynx to be among the populations with the lowest heterozygosity (Ratkiewicz et al. 2012, Förster et al. 2018, Mueller et al. 2022). H_O for the Fluidigm data set is significantly higher at 0.44. This makes sense given that markers with a high level of heterozygosity in Scandinavia are likely to be overrepresented in this situation. H_O for the Finnish population, based on the Fluidigm data set of 0.351, is in alignment with previous studies, suggesting that any effect of ascertainment bias in the Fluidigm data set is toward overrepresentation of heterozygosity in Scandinavia, rather than underrepresentation of heterozygosity in Finland.

This result suggests that Scandinavian lynx are a single population with no meaningful geographic separation despite the identification of genetic clusters. The long geographic distances between first order relatives and lack of isolation by distance identified in both data sets, suggest that geography does not pose a barrier to finding mates, and all of Scandinavia can be considered a continuous population. This result is not surprising given the long distance dispersal capabilities of lynx (Samelius et al. 2012) and the finding that the population in central and southern Sweden is essentially

panmictic, with no genetic structure developing spatially or temporally during the southward recolonization of lynx (Hemmingmoore et al. *manuscript b*).

Conclusion

The rate of migration between these two populations is important from both a biological and management point of view. Biologically, the Scandinavian population retains a relatively high degree of homozygosity and inbreeding due to its historic bottleneck and geographic isolation, while the Finnish population has largely overcome its prior bottleneck likely due to eastward connectivity (Mueller et al. 2022). Therefore, the Scandinavian population would especially benefit from influx of individuals from the Finnish population, and we have found that only limited migration occurs. The boundary between populations almost perfectly aligns with national borders between Finland and northern Sweden and Norway. Although political boundaries are human constructs, they can either create or correspond to barriers that are biologically relevant to animal movement and genetic connectivity, which seems to be the case in this instance. As a transboundary species listed on Annex IV of the EU Habitats Directive (Directive 92/43/EEC) and in Appendix II of the Convention of Migratory Species of Wild Animals (CMS COP 14), the lynx is a politically important species at the European Union level as well as globally. The Therefore, management practices that facilitate cross border gene flow, especially from Finland to Scandinavia, would support the population.

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Appendix

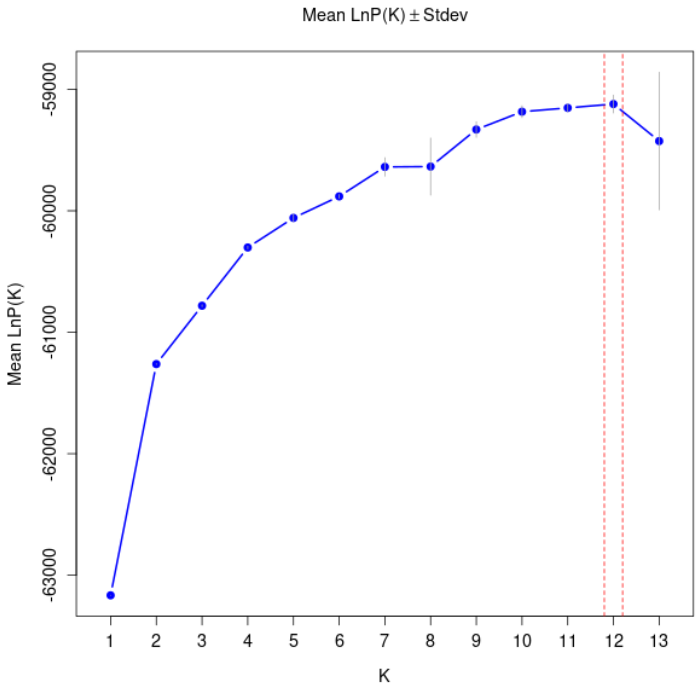

Figure A1: The mean likelihood value for each value of k as calculated by STRUCTURE, identifying k=12 as optimal.

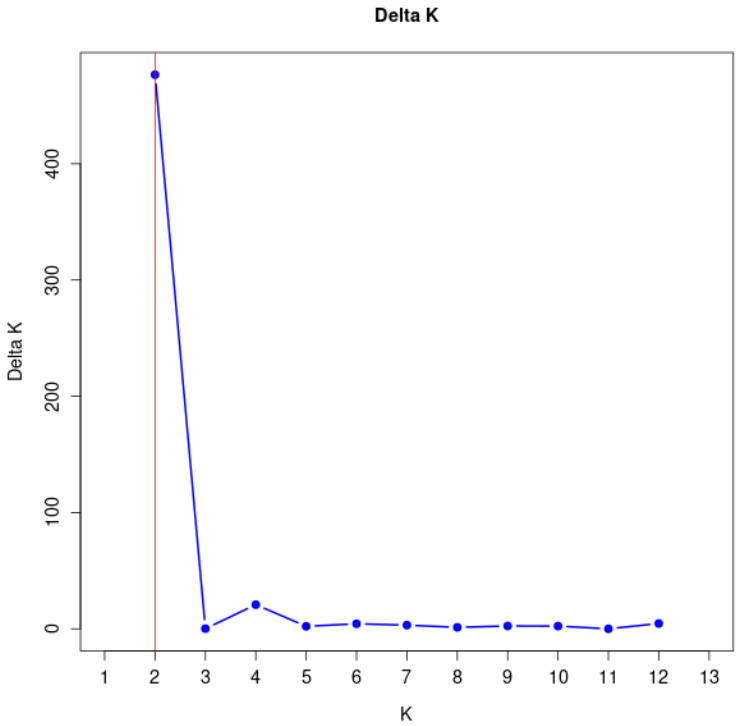

Figure A2: The change in likelihood value for each value of k as calculated by STRUCTURE, identifying k=2 as optimal according to the Evanno method (Evanno et al. 2006).

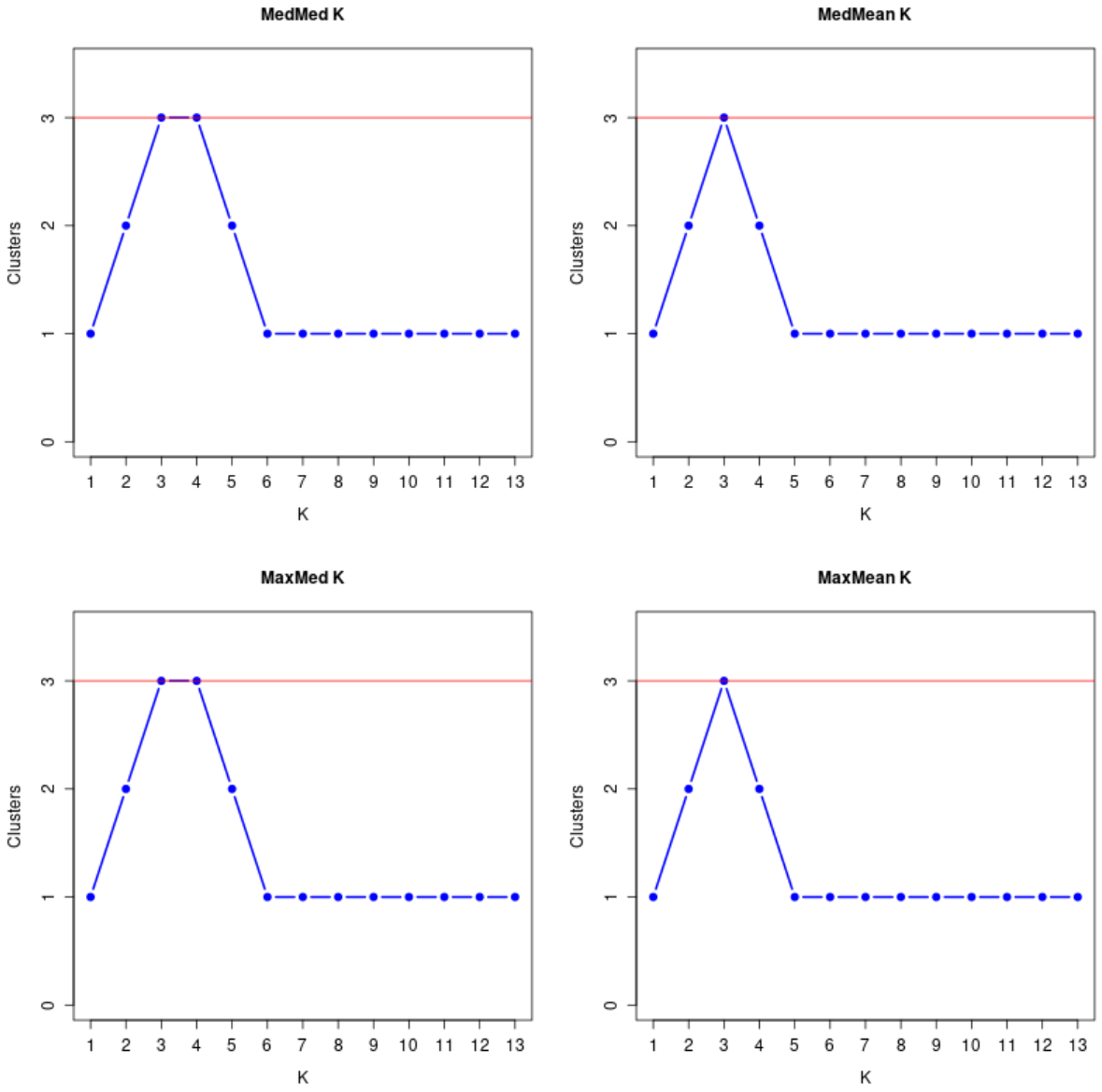

Figure A3: The optimal value of k as calculated by STRUCTURE, after removing spurious clusters (Puechmaille et al. 2016)

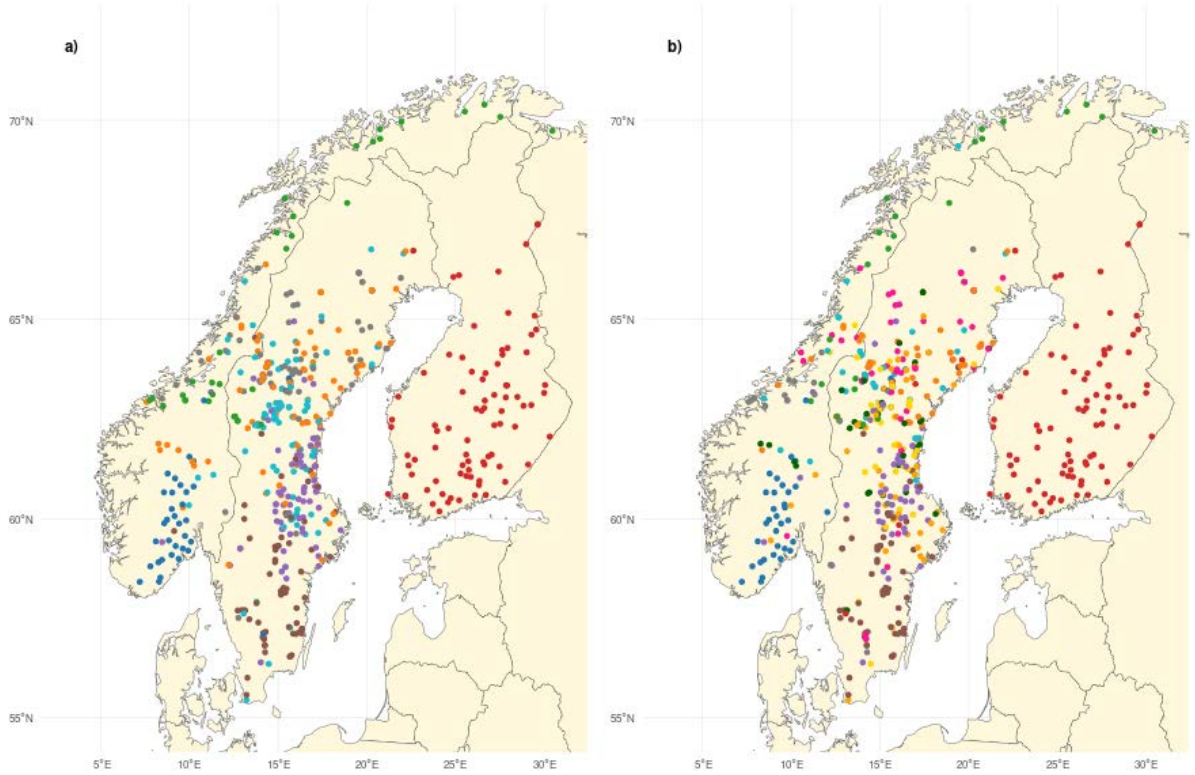

Figure A4: Population cluster assignment. Each dot represents a single sample (deceased lynx) location, colored according to its population cluster assignment. a) shows the eight cluster assignments from adegenet and b) shows the twelve cluster assignments from STRUCTURE.

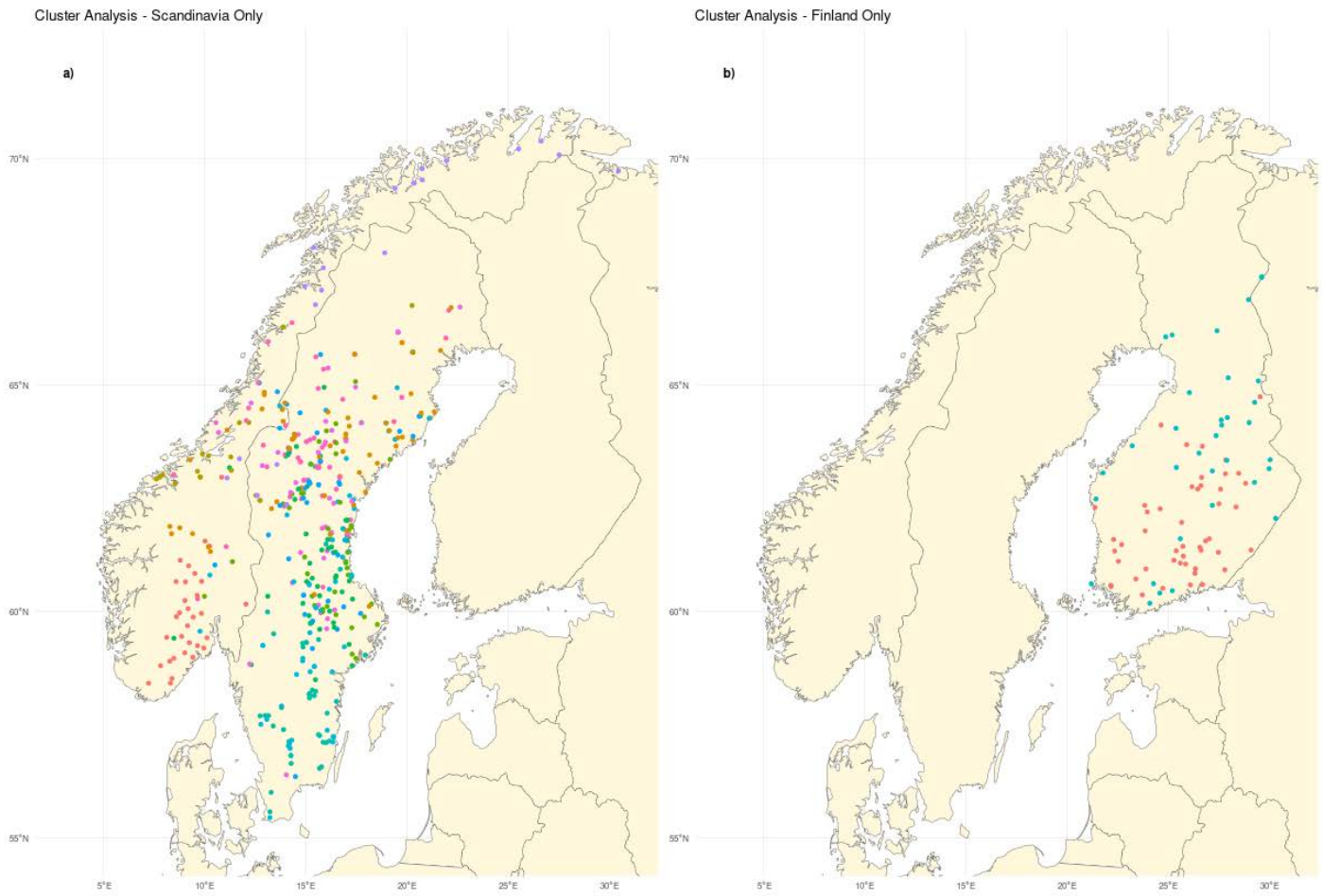

Figure A5: Population cluster assignment for each region assessed individually.

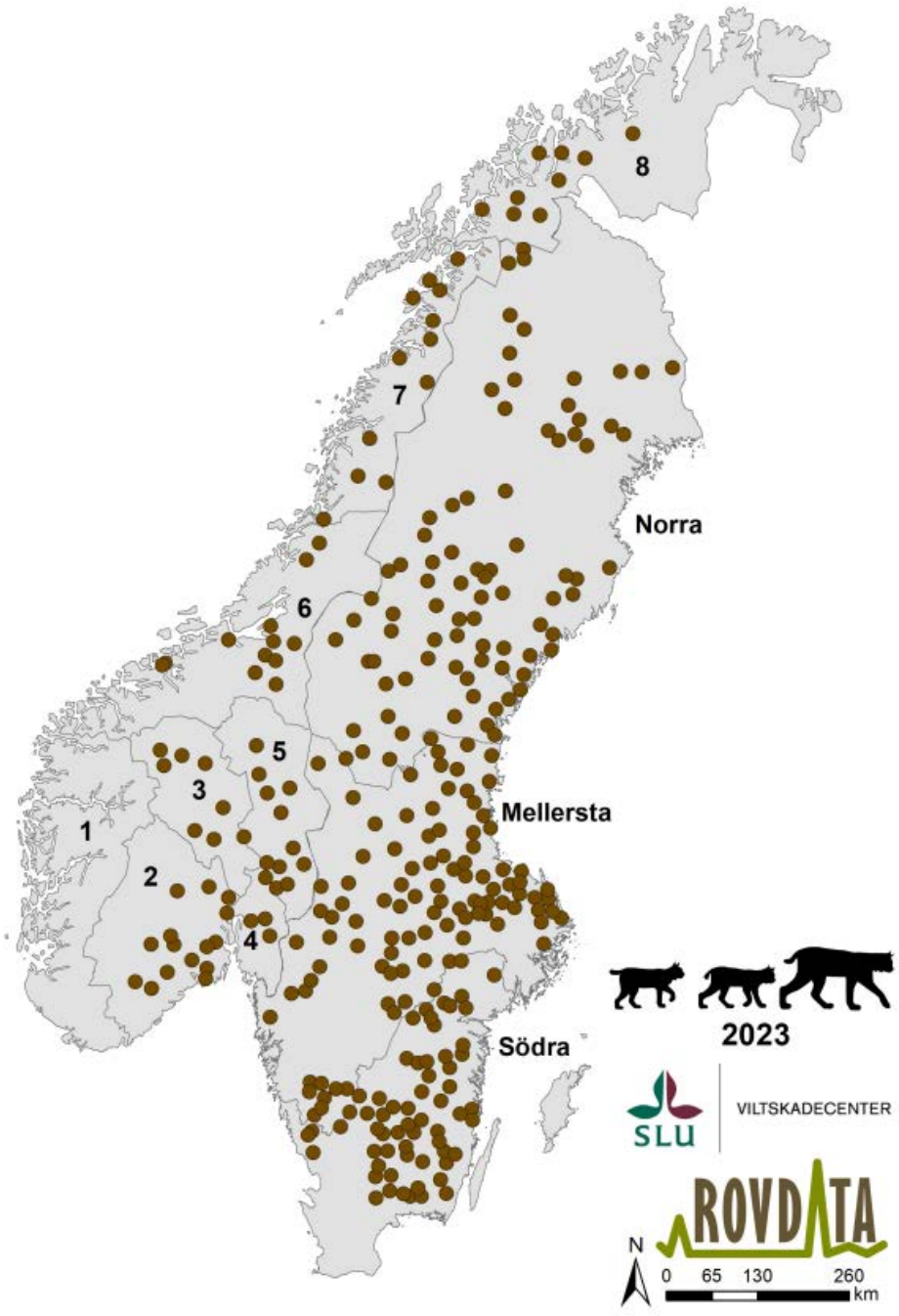

Figure A6: Figure 3 in Frank & Tovmo (2023): Map showing lynx family groups in the Scandinavian region during the season 2022/2023. Based on carnivore regions in Norway and lynx management areas in Sweden. Source: Rovbase

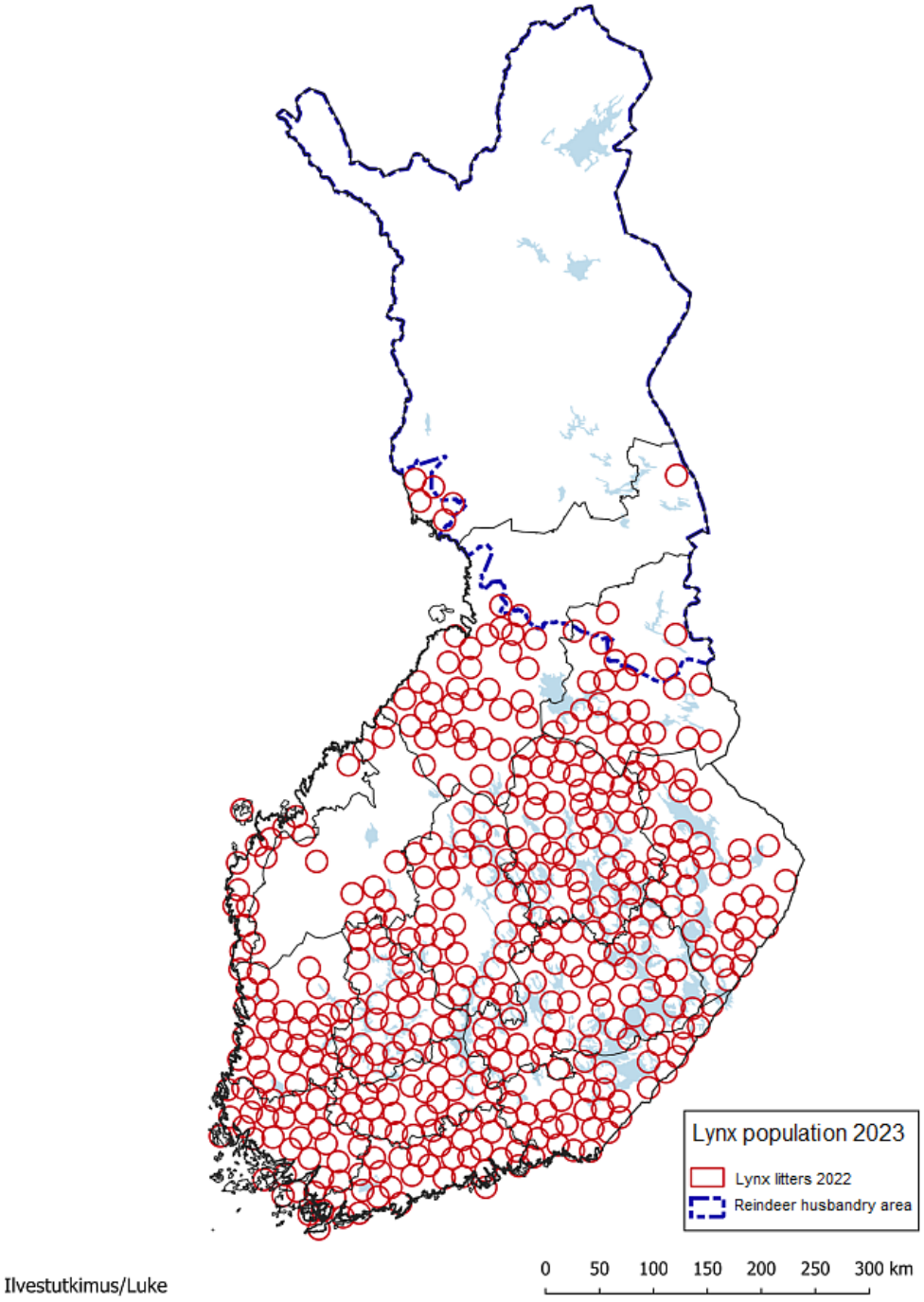

Figure A7: Figure 4 in Valtonen et al. (2023). An estimate of separate lynx litters derived from litter observations in the year 2022. The circle representing a litter is a visual representation of the possible location of the home range, not an estimate of the actual boundary of the home range. Map: Luke."

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