Detecting population structure within the Scandinavian lynx *(Lynx lynx)* population

Genetisk struktur hos Skandinaviska lodjur

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Abstract

The Eurasian lynx (*Lynx lynx*), a feline spread all over Eurasia has, as many other carnivores, been severely hunted, and due to this many populations of lynx have suffered from bottlenecks and fragmentation. As bottlenecks and fragmentation may have detrimental effects on the genetic status of a population, researchers have been keen to look closer into the genetic status of the lynx. With the development of next generation sequencing and improved analyses of genetics this research into lynx genetics has been enabled. Research has shown that there indeed are signs of genetic structuring between lynx populations, at least on a larger scale. In this report the genetic structure within the Scandinavian lynx population was examined by analyzing DNA from Swedish and Norwegian. 6 possible clusters were suggested within the population, and all but 4 individuals were successfully assigned into one of these 6 clusters. Further analyses of the fixation between suggested clusters revealed that fixation was very low, implying that the population structure within the Scandinavian lynx population is weak. This is probable as the population suffered briefly from a bottleneck and has later expanded rapidly throughout the two countries, which could be a causation of the weak genetic differentiation within the population.

Introduction

The Eurasian lynx (*Lynx lynx*) is by far the largest and perhaps the most charismatic of the felines on the European continent, and it is the largest of the four extant species within the Lynx genus (von Arx et al. 2005). It is also one of the most widespread species, with a distribution ranging from western Norway into the Siberian north and the Far East of China (Ratkiewicz et al 2014, Rueness et al 2014, Schmidt et al 2011). Its preferred habitat is forested areas, where it may ambush prey such as medium sized ungulates, rodents and grouse (Elmhagen et al. 2007, Pasanen Mortensen et al. 2013, Breitenmoser et al. 2015). If the availability of prey is limited, livestock such as semi-domestic reindeer (*Rangifer tarandus*) or free ranging sheep (*Oves aries*) may become alternative prey, which has led to complex conflicts between owners of livestock and conservation biologists (von Arx et al. 2005, Andrén et al. 2006, Chapron et al. 2014).

Previous studies of the Eurasian lynx in Europe and Scandinavia have suggested that the genetic variability is low to moderate, based on mtDNA and microsatellites (Hellborg et al. 2002, Schmidt et al. 2011, Ratkiewicz et al. 2014, Rueness et al. 2014). As many other carnivores, they were extensively persecuted well into the 20th century, until national laws, directives such as the European Union's Habitat Directive and similar acts protected carnivores, including lynx (Schmidt et al. 2011, Chapron et al. 2014). Since then carnivores all over Europe have increased, at least locally (Schmidt et al. 2011, Chapron et al. 2014). As a consequence of persecution, bottleneck effects have taken place and many lynx populations have become fragmented due to an increasingly fragmented landscape (Schmidt et al. 2011, Chapron et al. 2014, Ratkiewicz et al. 2014, Rueness et al. 2014, Bull et al. 2016). Their remarkable ability to disperse has probably been a valuable aid in the populations' recovery, as dispersal distances have been recorded at up to 450 km and this may stabilize the consequences of fragmentation (Schmidt et al. 2011, Chapron et al. 2014, Aronsson et al. 2016). When so heavily affected by humans, this calls for extensive knowledge regarding the genetic and ecological status of the populations, decreasing the risk of human-induced detrimental consequences.

With the appearance of next generation sequencing in ecological research, the use of the genetic markers Single Nucleotide Polymorphisms (SNP) has shown to be successful regarding identification of individuals, degree of relatedness, mating patterns and home ranges in other large carnivores such as the brown bear (*Ursus arctos*) and the puma (*Puma concolor*) (Hostetler et al. 2013, Norman et al. 2013, Norman & Spong 2015, Fitak et al. 2016, Spitzer et al. 2016). All of these areas are of interest in research of the Eurasian lynx, as they are all relevant regarding monitoring and conservation issues. By identifying individuals successfully the monitoring of the populations expansion and growth might grant further insights into population dynamics, both genetic and social. A better understanding of dispersal patterns might improve managers and researchers possibility to predict the population growth within an area by including any loss or addition of lynxes by migration from or to a neighboring area. Additionally, SNP analyses can be applied to DNA of lesser quality, like DNA collected from fecal matter and hair (Norman & Spong 2015). Non-

invasive methods are arguably beneficial both from an economic and animal welfare perspective, so SNPs might be a valuable tool for genetic monitoring within research and management (Norman et al 2013, Norman & Spong 2015).

The aim of this study is to use SNP as a genetic marker and applying it to research regarding the Scandinavian lynx population; by sequencing and analyzing DNA samples from Swedish and Norwegian lynx to investigate the population genetics and dynamics.

Methods
Sample collection and sequencing
The DNA that was used in this study was collected from dead lynx from both Sweden and Norway, from the northernmost into the south (figure 3), which have been sent to the SVA where they on routine collect DNA from lynx (SVA). DNA from 72 individuals was used for the analyses in this report. These specific lynx were collected between 2010 and 2015. The DNA was extracted with the QIAsymphony DNA kit (Qiagen, Hilden, Germany) following manufacturer's instructions. With gel electrophoresis the DNA quality was visually assessed, using the Kodak Electrophoresis Documentation and Analysis System 120 (Eastman Kodak Company, Rochester, USA). About 1-5 μg of tissue was digested of each DNA sample, individually for 16 hours with EcoR1 (Thermo Fisher Scientific, Massachusetts, USA), following the manufacturer's instructions. By using the Mini Elute Reaction Cleanup kit (Qiagen, Hilden, Germany) the samples were purified and the active enzyme was removed. A second elution was visualized with gel electrophoresis to assess digestions quality. DNA samples which had been digested were sent to the Science for Life Laboratories (SciLifeLab, Stockholm, Sweden) for library construction and preparation. Fragments between 420-720 bp (including adaptors) were excised and blunt end repaired. The fragments were then paired-end sequenced on the platform Illumina HiSeq 2500.

Bioinformatics
Bioinformatic analyses weres performed in Stacks 1.42. SNPs were chosen based on; Minor Allele Frequencies (MAF) > 0.05, sampled in more than 90% of individuals (67 or more), no less than 10bp from the start of the locus and no less than 5bp from the end of the locus. Stacks settings were; m=7, M=1, n=1 where m is minimum depth of coverage required for a stack, M is maximum nucleotide distance between stacks required for a tag and n is the distance allowed between sample tags when generating the catalogue. The SNPs were also filtered based on if they significantly deviated from HW equilibrium. This was tested in Genepop 4.2 on the web - Hardy Weinberg Exact Tests within the population probability test performed for each locus in the population. Markov chain parameters were set to the default setting.

Genetic structure
The software Structure (Pritchard et al 2000) was used for analyzing the population dynamics, seeing how many potential clusters within the population that may be suggested from the genetic data, where K is the number of clusters. The length of Burnin period, the

length of the simulation run, was set to 10 000 and the number of MCMC Reps after Burnin, the length of the simulation after burnin for accurate parameter estimates, was set to 100 000. For each suggested K value there was 15 iterations, and the range of suggested K values were set from 1 - 10. This generated 15 log likelihoods for each K, ln P(D). By calculating the second order rate of change of the likelihood (ΔK), the true value of K should be revealed by a peak in the ΔK value.

L(K) = an average of 15 values of Ln P(D)
L'(K) = L(K)n – L(K)n-1
L''(K) = L'(K)n – L'(K)n-1
Delta K = [L''(K)]/Stdev

When the true K has been calculated, individuals were assigned to different clusters. This was done by comparing the 15 iterations for the calculated true value of K. In each iteration for a suggested K, the individuals in the analysis would be grouped depending on the suggested K. So if for an example, in an iteration for K=4 one would see that perhaps individual 1, 2 and 5 ended up in cluster 3. The cluster number in itself is arbitrary, as in another iteration for K=4 individuals 1,2 and 5 might have ended up in cluster 2, but by looking at which individuals were grouped together repeatedly one can assign these individuals to a cluster. If a number of individuals had been grouped together for more than 45% of the iterations, they were assigned to a cluster.

Fixation indices
When the individuals had been assigned to clusters based on the results in Structure, the fixation between these clusters was tested in Genepop 4.2 on the web, in option 6 - Fst & Other Correlations. An analysis of isolation by distance between groups was performed (suboption 6), were coordinates for each individual were included in the input file. This generated a semi matrix for genetic estimates (F/1-F) and ln (distances) between the clusters. A fitting to a + b ln(distance), values for a and b, ABC bootstrap for slope, point estimates and confidence interval, and a correlation on the isolation by distances is also generated by this analysis.

Results
The filtering of SNPs with low quality in Stacks 1.42 generated 532 markers with SNPs that followed the set conditions mentioned in the method. After additionally filtering of the markers that deviated significantly from HW-equilibrium, there were 522 markers left. The average heterozygosity of these markers was 0.274, the lowest 0.014 and highest 0.603

Population structure
After calculating ΔK, it was revealed as 6, suggesting that there are 6 clusters within the Swedish-Norwegian population. Because of this, the 15 iterations for K=6 were compared to see what individuals that were repeatedly clustered together. 4 individuals could not be assigned into only one cluster, as they had been assigned equally many times into two

different clusters. The remaining 68 individuals were assigned with varying percentages to only one cluster (table 1). 8 individuals were assigned into cluster 1, 14 individuals assigned into cluster 2, 23 individuals were assigned into cluster 3, 14 into cluster 4, 9 into cluster 5 (figure 1 and 2). Of the 4 individuals who could not be assigned into only one cluster, 3 were assigned into cluster 3 and 4, and one individual was assigned into cluster 3 and 5 (Appendix). All but two clusters had both females and males, and had also lynx from both Sweden and Norway (figure 1 and 2). These assignments were then visualized in a map (figure 3).
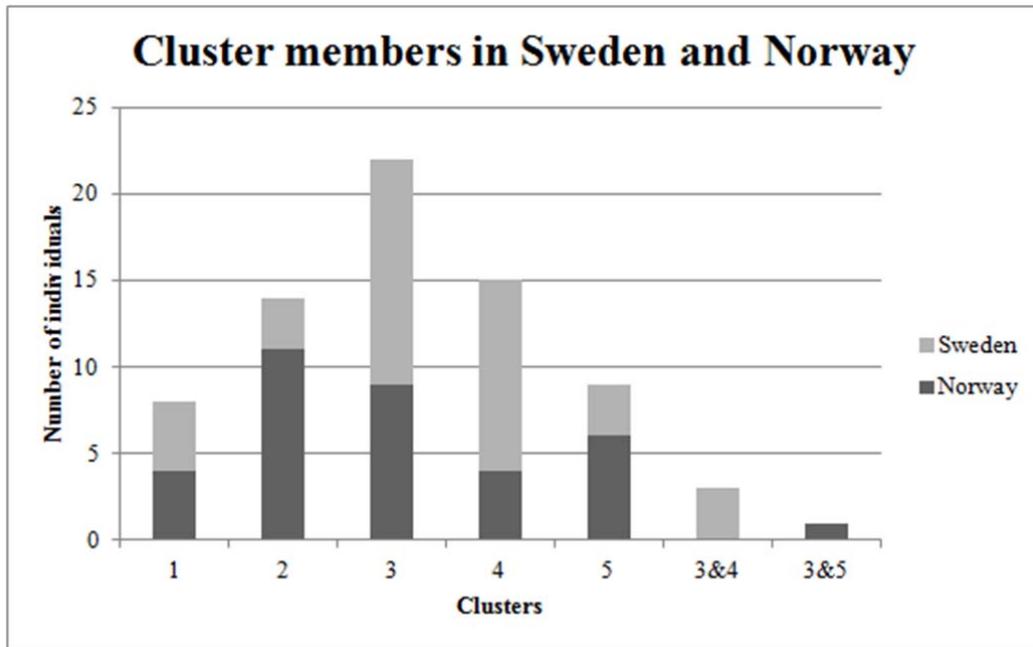

Figure 1. Diagram showing the representation of Sweden and Norway in the different clusters.
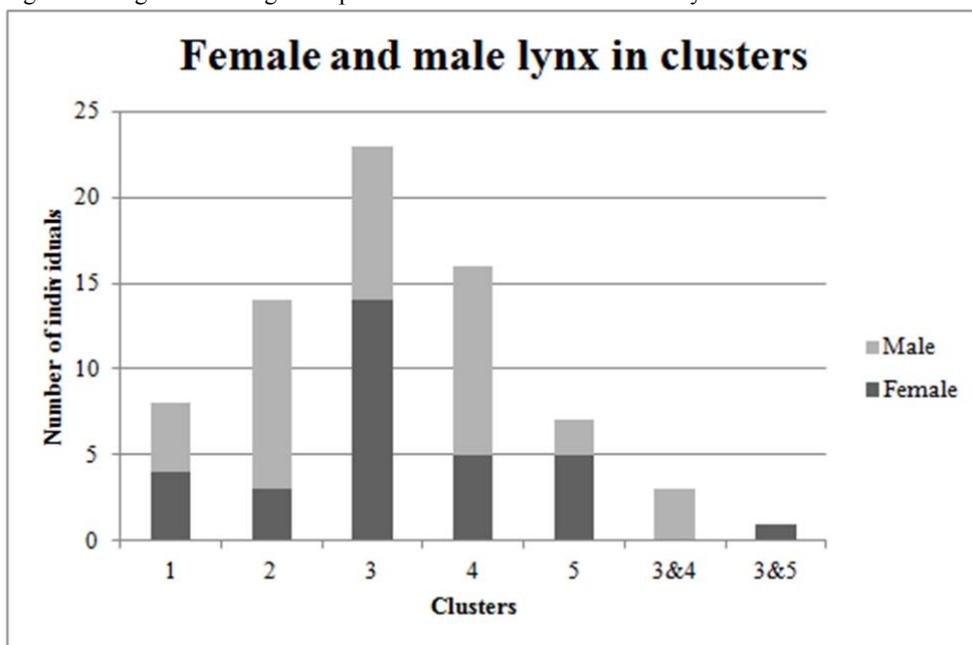

Figure 2. Diagram showing the representation of males and females in the different clusters.
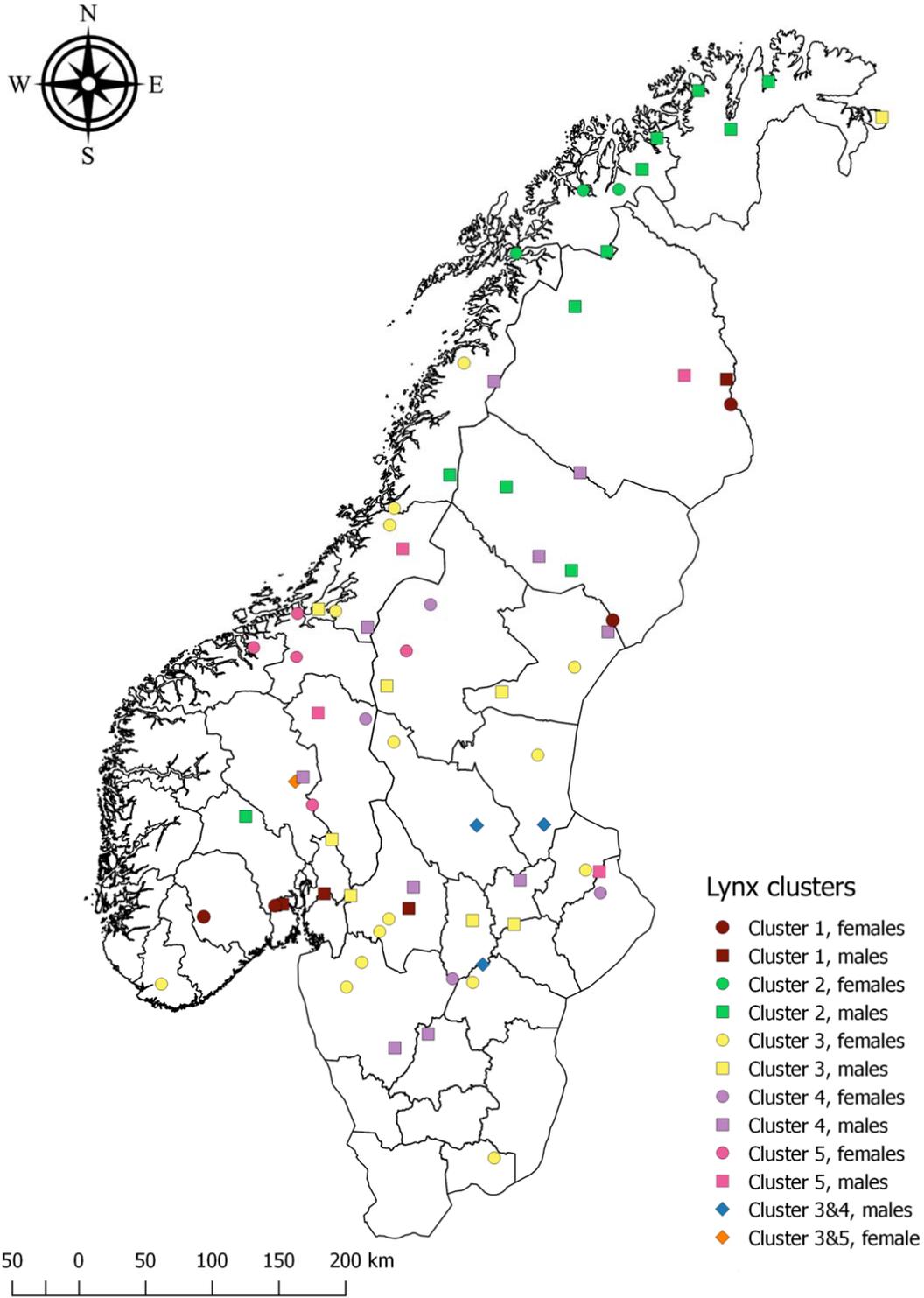
Figure 3. Map illustrating the individuals in their assigned clusters. See legend for details regarding cluster and sex of the lynx.

Fixation indices

The testing of fixation indices between clusters revealed that the level of fixation was very low (tables 1, 2 and 3), and there was no significant correlation between genetic estimates and distance (table 3 and figure 4).

Table 1. Results of the fixation indices between the suggested clusters, were both male and female lynx are included.

	Cluster 1	Cluster 2	Cluster 3	Cluster 4
Cluster 2	0.101635	-	-	-
Cluster 3	0.05272	0.054724	-	-
Cluster 4	0.084037	0.083915	0.011731	-
Cluster 5	0.081756	0.076154	0.023872	0.043026

Table 2. Results of the fixation indices between the suggested clusters, but only female lynx are included.

	Cluster 1	Cluster 2	Cluster 3	Cluster 4
Cluster 2	0,116239	-	-	-
Cluster 3	0,091517	0,05755	-	-
Cluster 4	0,124751	0,108963	0,014194	-
Cluster 5	0,141698	0,089922	0,04762	0,05959

Table 3. The Statistical details for the two analyses

|	Female and Male	Only Female
Fitting F/(1-F) to a + b ln(distance)	a = 0.0533641, b = 0.00432465	a = 0.0763632, b = 0.00578151
Point estimate and 95% confidence interval	0.00432465 [-0.00642333 , 0.014677]	0.00578151 [-0.0208306 , 0.0330465]
Test of isolation by distance (One tailed Pvalue):	Pr(correlation > observed correlation) =0.222 under null hypothesis	Pr(correlation > observed correlation) =0.21 under null hypothesis
Other one tailed Pvalue:	Pr(correlation < observed correlation) =0.816 under null hypothesis	Pr(correlation < observed correlation) =0.802 under null hypothesis
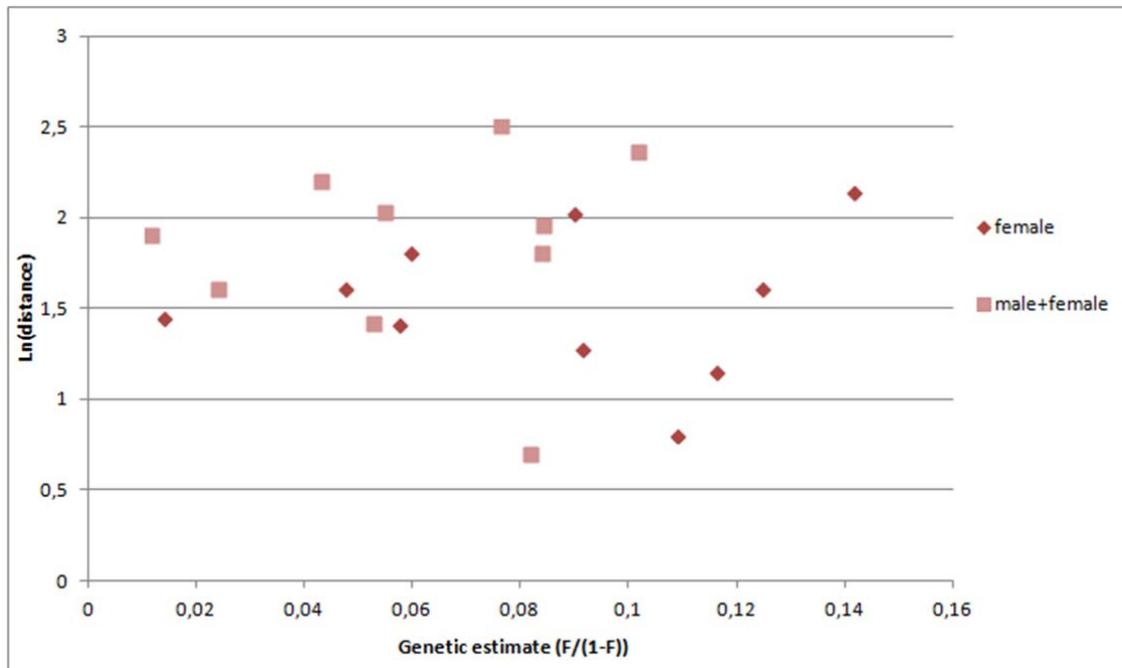
Figure 4. The genetic estimate plotted against the ln(distance). Squares are males and females, diamonds only females included.

Discussion

The analyses of the sampled lynx DNA revealed that there are possibly six clusters, and the coordinates for each individual show that most of these clusters are well spread throughout Sweden and Norway (figure 3). But even though 6 clusters were suggested, the following analysis of genetic estimates showed that the fixation between said clusters was low, suggesting a weak population structure.

The fixation indices reveal that there is no significant differentiation between the suggested clusters, and this could be caused by a number of things. One is that lynx have, according to inventories, expanded both in numbers and distribution the last couple of years, especially in the mid- and southern Sweden (Samelius et al. 2011, Naturvårdsverket). One way of looking closer into this would be to additionally compare the ages of the found lynx and also look into relatedness between individuals, to get a better picture of how dispersal patterns look and how they may affect population structure. This has for example been done for bears in Sweden, where the use of SNP markers successfully revealed dispersal patterns and relatedness between individuals (Norman et al. 2013, Norman & Spong 2015, Spitzer et al. 2016). It is known that lynx may disperse for long distances, and this may also be one of the causes for the structuring in the population (Schmidt et al 2011, Samelius et al 2012, Aronsson et al 2016). Looking at the visualization of the different clusters (figure 3), the suggested cluster are very spread all over the two countries, with some exceptions like cluster 2 and cluster 5, which seem to have a more concentrated distribution, with 2-3 individuals much farther away. These individuals are most often males, which could also support that the weak structure might be caused by dispersal, as males, at least in small spatial scales,

10

generally disperse much farther than females (Samelius et al. 2012, Ratkiewicz et al. 2014, Rueness et al. 2014).

Comparing the fixation indices between the Swedish-Norwegian population and the more continental one could add valuable insights to the bottleneck structure, caused by the Swedish-Norwegian population being relatively isolated from the continental population. With a lower sample number (n=30), the Norwegian population has been compared to lynx from all over Eurasia, and a bottle neck was suggested as the individuals from Norway were significantly differentiated from the rest of the Eurasian lynx (Ratkiewicz et al. 2014). Those 30 individuals were also exclusively Norwegian, with no samples from Sweden. Comparing a larger sample size with the Eurasian population might offer more clarity in just how much of a bottleneck effect that is acting on the Swedish-Norwegian population, which additionally might reveal more details on the nature behind the causation of the weak population structure within the Swedish-Norwegian population.

The number of clusters suggested by Structure was 6, but the sharp eyed will notice that there is not a sixth cluster among the assigned individuals. During the sorting of individuals into different clusters, none of the individuals ended up in a sixth cluster enough times for them to be ultimately assigned to it. About 25 individuals were assigned at least once into that cluster, but never more than for 4 iterations. One reason to why they weren't assigned more into the sixth cluster could perhaps be that they could be some "hybrids" between clusters, and perhaps that the sixth cluster isn't represented enough in the samples for this report.

As males generally disperse farther distances, this may explain the low fixation between clusters (Ratkiewicz et al. 2014, Rueness et al. 2014, table 3,4,5). When males are excluded from the analysis, the fixation is increased, but only slightly (table 3,4,5). The correlation between fixation and distance is not significant in either of the analyses, which points to a weak population structure (table 5). As lynx are highly mobile animals that may disperse for long distances this is not an implausible result (Schmidt et al. 2011, Samelius et al. 2012, Aronsson et al. 2016). One may speculate that lynx struggle to disperse through the reindeer herding area, as their adult mortality is higher within these areas, and the reindeer herding area is quite a substantial portion of the Swedish land area (Andrén et al. 2006). As no significant structure could be found between lynx within and lynx outside the reindeer herding area, it might be easier for lynx to disperse through this area than previously speculated.

One could argue that the time frame 2010-2015 of the sampled individuals is too narrow. Lynx are relatively long lived and the natural adult mortality is low. Additionally, it takes about two years for them to sexually mature, so it might well take some years before any genetic imprints can be seen (Nilsen et al. 2012). A longer time frame might very well grant a better picture of the dispersal dynamics and also adding age as a factor could perhaps reveal more about dispersal patterns. Additionally, making sure that the ages of the sampled individuals is representative of the age distribution of the population could also be valuable. Also, by looking at mtDNA, and relatedness between females, one could further investigate if

females tolerate their daughters' territories overlapping with their own (Ratkiewicz et al 2014, Aronsson, lecture 2016-09-12).

A number of studies have found a pattern between climate and genetic differentiation, which is something future research and monitoring will be able to analyze further (Nilsen et al. 2009, Schmidt et al 2011, Rueness et al. 2014). The specific climate of an area acts as a selective force, affecting the genetic variation within the local population (Nilsen et al. 2009, Schmidt et al 2011, Rueness et al. 2014). It is probable that there would be a gradient of genetic variability following the different climate zones, as there is some differentiation in climate throughout Sweden and Norway.

Further use of SNP rather than molecular markers would most probably be beneficial for research and monitoring, as not only can it be used on DNA of lesser quality, it is by far safer and less invasive than capturing and sedating individuals (Norman & Spong 2015). The possibility to identify individuals without collaring is truly valuable, not only for research but also for the animals' welfare. By identifying individuals successfully with SNP the monitoring of the population would become less invasive and costly. SNPs have been successful for studying dispersal patterns and a better understanding of dispersal patterns might improve managers and researchers possibility to predict the population growth within an area by including any loss or addition of lynxes by migration from or to a neighboring area.

Technical issues
Due to computing errors only 15 iterations for each K was run, as some literature suggests running more iterations so there could be a flaw in this, that more iterations would be needed for an even more precise value. The assignment in itself of the individuals was delicate and there is room for errors within the method. Many individuals were assigned to a number of different clusters; more iterations might reveal a better resolution. However, the fact that many individuals were assigned to several different clusters might simply be caused by a very weak structuring within the Swedish-Norwegian population.

Conclusion
The analyses have shown that there are a number of clusters within the Scandinavian population, many of them transnational and genetic estimates have revealed a weak population structure, which is supported by the species social dynamics, bottleneck effects and the swift expansion of the population into the southern parts of Sweden and Norway. More research into dispersal patterns and the addition of longer time frames to similar analyses would most probably be beneficial for management and monitoring, as this might add more valuable insights into the population growth, structure and social dynamics of the Scandinavian lynx population.

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Appendix

Table 1. Individuals of lynx, what cluster they ultimately were assigned to and how many % of the 15 iterations in Structure they had been put in that cluster.

Individual	Cluster	%	Individual	Cluster	%	Individual	Cluster	%
1	Cluster 3	100	25	Cluster 5	67	49	Cluster 1	67
2	Cluster 3	80	26	Cluster 3	47	50	Cluster 3	80
3	Cluster 1	73	27	Cluster 3	60	51	Cluster 2	100
4	Cluster 4	53	28	Cluster 3 /Cluster 4	40/40	52	Cluster 3	53
5	Cluster 3	80	29	Cluster 4	53	53	Cluster 2	100
6	Cluster 3	93	30	Cluster 3 /Cluster 4	40/40	54	Cluster 2	100
7	Cluster 3	60	31	Cluster 3	60	55	Cluster 5	67
8	Cluster 3	93	32	Cluster 4	60	56	Cluster 4	67
9	Cluster 1	47	33	Cluster 4	47	57	Cluster 2	100
10	Cluster 2	100	34	Cluster 4	60	58	Cluster 2	93
11	Cluster 2	73	35	Cluster 1	67	59	Cluster 5	73
12	Cluster 1	73	36	Cluster 4	53	60	Cluster 2	67
13	Cluster 3	47	37	Cluster 3	87	61	Cluster 2	100
14	Cluster 4	53	38(N)	Cluster 4	53	62	Cluster 2	100
15	Cluster 5	47	39	Cluster 1	73	63	Cluster 5	53
16	Cluster 3	93	40	Cluster 3	73	64	Cluster 1	67

17	Cluster 3	73	41	Cluster 3	80	65	Cluster 5	67
18	Cluster 2	100	42	Cluster 3 /Cluster 5	40/40	66	Cluster 4	60
19	Cluster 4	67	43	Cluster 3	80	67	Cluster 3	80
20	Cluster 5	67	44	Cluster 1	67	68	Cluster 4	60
21	Cluster 3 /Cluster 4	40/40	45	Cluster 2	100	69	Cluster 5	67
22	Cluster 4	53	46	Cluster 2	100	71	Cluster 3	87
23	Cluster 3	87	47	Cluster 3	80	72	Cluster 5	67
24	Cluster 4	53	48	Cluster 2	100	73	Cluster 3	93

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