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Alexander Kopatz, Oddmund Kleven, Jonas Kindberg, Ilpo Kojola, Jouni Aspi, Göran Spong, Niclas Gyllenstrand, Love Dalén, Ida Fløystad, Snorre B. Hagen, Øystein Flagstad

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Male brown bear photographed in Finland © Alexander Kopatz

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NØKKELORD
Europeisk brunbjørn, Fennoskandia, Finland, genflyt, konnektivitet, migrasjon, populasjons genetisk struktur, Skandinavia, *Ursus arctos*

Abstract

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Background
The populations of brown bear (*Ursus arctos*) in northern Europe have been recovering or are in the process of recovery from a severe demographic bottleneck. Especially in the main populations of Scandinavia and Finland, the number of individuals has been increasing substantially, compared to the population sizes estimated 20 years ago. Also, the populations have spatially expanded, putatively restoring connectivity and gene flow between these two, formerly separated populations. The Swedish Environmental Protection Agency (Naturvårdsverket) assigned a project to assess the connectivity and gene flow between the eastern and western parts of Fennoscandia, Finland and Scandinavia.

Objective
Our objective was to detect possible immigration of brown bears from eastern Fennoscandia, specifically Finland, into Scandinavia.

Material and Methods
For the first time with continuous sampling of brown bears, we assessed the population genetic structure and gene flow between the brown bear populations of Scandinavia and Finland. We based our analyses on the dispersing sex, male brown bears, as females tend to be philopatric. Our target area was the county of Norrbotten in northern Sweden, at the border to Finland and Norway, representing the most likely area for potential eastern immigrants into Sweden. Previous research did not reveal any influx from Finland into Sweden. However, brown bear samples from Norrbotten have to a very limited degree been included in earlier studies on genetic connectivity in the area. In addition to a large number of samples from Norrbotten and northern Finland, we included genotypes sampled in regions surrounding the target area: Västerbotten in Sweden, Troms and Finnmark in Norway and southern Finland. We utilized all samples and genotypes from male bears available, and, also, genotyped recently collected samples of male brown bears from the study area. Analyses on population genetic structure and gene flow among regions were based on 924 individual male brown bear STR-genotypes (12 short tandem repeats or microsatellite markers). In order to reveal patterns of male dispersal and the distribution of male linages we used brown bear samples genotyped with nine Y-chromosomal STRs from 826 males.

Results
Four different genetic clusters were identified. Assignment values for the different genotypes showed evidence of immigration of brown bears from Finland into Sweden for the first time. However, more individuals from Sweden dispersed into northern Finland than in the opposite direction. Reflective of the genetic structure, estimations resulted in asymmetrical rates of gene flow between Finland and Sweden; 1% immigration rate was detected from the east, northern Finland and Finnmark, into Norrbotten, while there was a rate of about 8% immigration from Norrbotten into northern Finland. Given the current population size, we estimated that 4.6 to 5.5 bears from the eastern populations immigrate into Norrbotten effectively per generation. Indirect methods, reflecting historical gene flow, estimated an effective number of migrants between 1.27 to 2.53 brown bears per generation between Norrbotten and Finland. The level of gene flow appears to surpass the suggested one-migrant-per-generation rule, an established standard or rule of thumb to minimize loss of genetic variation and thus counter genetic isolation. The assessment of male lineages using Y-chromosomal markers showed a similar picture with comparably more brown bears carrying haplotypes from Scandinavia in Finland, suggesting higher influx of individuals in west-east direction than the opposite way. Furthermore, STR- as well as Y-

STR-analyses suggest the northernmost Norwegian county of Finnmark as another transition area or connectivity-corridor between the eastern and western brown bear populations in northern Europe.

Conclusion
Although levels of gene flow from Finland and Finnmark to Scandinavia appear to be relatively low, the results of this study showed immigration of brown bears from the east into Sweden for the first time. This influx might be indicative of further expansion of eastern populations and representative of an expansion front coming from the recovering Finnish brown bear population. However, it might also be that the now detected gene flow may be due to the continuous sampling applied for the first time in this study, which has not been the case in earlier studies assessing the connectivity between brown bear populations from the eastern and western parts of northern Europe.

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Sammendrag

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Bakgrunn og målsetning
Etter en alvorlig demografisk flaskehals på 18- og 1900-tallet, har brunbjørnen (*Ursus arctos*) de siste tiårene tatt seg betydelig opp både i antall og utbredelse i Nord-Europa. Det er spesielt i Skandinavia og Finland at antall individer har økt kraftig, sammenlignet med bestandsstørrelsen bare 20 år tilbake. Økningen i antall har vært ledsaget av en betydelig ekspansjon av utbredelsen, som potensielt er i ferd med å gjenopprette konnektvitet og genflyt mellom disse to, tidligere isolerte bestandene. Her rapporterer vi fra et prosjekt, iverksatt av Naturvårdsverket og støttet av Miljødirektoratet, der målsetningen var å undersøke konnektivitet og genflyt mellom våre østlige nabobestander og vestlige deler av Fennoskandia, dvs. identifisere eventuelle immigranter fra Finland i Skandinavia og undersøke i hvilken grad de bidrar i reproduksjon.

Metoder
Med kontinuerlig representasjon av prøver, som for første gang dekket store deler av Fennoskandia, undersøkte vi den populasjonsgenetiske strukturen og genflyt mellom brunbjørnbestandene i Sverige og Finland. Vi baserte våre analyser på hanner, siden hunnbjørner er såkalt filopatriske, dvs at de etablerer seg i eller i direkte tilknytning til morens hjemmeområde. Vårt fokusområde var Norrbotten, som grenser mot både Norge og Finland og representerer det mest sannsynlige området for potensielle immigranter fra øst. I tidligere studier har man ikke funnet immigranter fra Finland i Sverige. Prøver fra Norrbotten har imidlertid i svært liten grad inngått i disse studiene. I tillegg til et stort antall prøver fra Norrbotten, inkluderte vi genetiske data fra omkringliggende områder som Västerbotten, Troms, Finnmark og Finland. Vi brukte alle genetiske data som var tilgjengelig fra tidligere bjørneanalyser i området og genotypet i tillegg nyere innsamlet materiale fra det samme området. Totalt inkluderte vi genetiske data på 12 autosomale STR-markører (mikrosatelitter) for 924 hanner. For ytterligere analyse av hannenes migrasjonmønster, inkluderte vi data fra ni Y-kromosom-markører fra 826 hanner, som spesifikt representerer hannenes slektslinjer.

Resultater
Fire genetiske grupper ble identifisert i Fennoskandia. Fra parametre for genetisk opphav dokumenterte vi for første gang immigranter fra Finland i Sverige. Dog var det betydelig flere bjørner med svensk opphav i Finland enn vice versa. I tråd med dette bekreftet våre analyser såkalt asymmetrisk genflyt, med 1 % immigrasjonsrate fra øst (Finland/Finnmark) til Norrbotten mot 8 % immigrasjon fra Norrbotten til nord-Finland. Gitt dagens bestandsstørrelse av brunbjørn i Fennoskandia, anslår vi en effektiv immigrasjon på mellom 4,6 og 5,5 reproduserende bjørner med østlig opphav til Norrbotten pr generasjon. Indirekte metoder, som i større grad reflekterer historisk genflyt, anslår et effektivt antall innvandrere mellom 1,27 til 2,53 bjørner. De anslåtte nivåene av immigrasjon synes å være tilstrekkelig i forhold til den anbefalte «en-migrant-per-generasjon»-regelen, en etablert standard for å unngå tap av genetisk variasjon og motvirke genetisk isolasjon. Y-kromosom dataene, som altså spesifikt representerer hannenes slektslinjer, viste et tilsvarende bilde med høyere immigrasjon til Finland fra Sverige enn vice versa. Et relativt stort antall bjørner i Finnmark hadde en østlig genetisk signatur, som viser at dette fylket har et stort potensiale som konnektivitetskorridor mellom våre østlige nabobestander og resten av Skandinavia.

Konklusjon
Selv om immigrasjon og genflyt fra Finland og Finnmark til resten av Skandinavia fortsatt framstår relativt begrenset, dokumenterer dataene i denne studien for første gang immigrasjon av bjørner med østlig opphav til Sverige. Dette kan tyde på at ekspansjonsfronten i en stadig

økende finsk bjørnebestand har beveget seg vestover de siste årene. Tidsperspektivet her er dog noe usikkert, siden vi ikke kan utelukke at pågående genflyt nå endelig blir dokumentert som et resultat av en representativ prøveinnsamling, der vi for første gang hadde en kontinuerlig prøveinnsamling fra store deler av Fennoskandia.

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Contents

Foreword

This report presents results from analyses of genetic structure and connectivity with two different marker types (STRs/microsatellites and male inherited Y-STRs) for more than 900 individual males from the Fennoscandian brown bear population. A large number of new samples were genotyped and analysed to achieve the goal of this study. This genotyping was performed at the genetic laboratories of the Norwegian Institute for Nature Research (NINA) in Trondheim and at the Center for Genetic Identification (CGI) at the Swedish Museum of Natural History in Stockholm. The main goal of the project was to examine gene flow and immigration from Finland into Sweden. The project was commissioned by the Swedish Environmental Protection Agency (Naturvårdsverket) and the Norwegian Environment Agency (Miljødirektoratet).

An earlier version of the report has been peer-reviewed independently by three international experts in the field. The review process has been led and coordinated by Per Sjögren-Gulve from the Swedish Environmental Protection Agency (Naturvårdsverket).

We would like to thank everyone who has contributed to the collection of samples, the lab-work and compiling genotype data. We would also like to thank Per Sjögren-Gulve, who has been our contact person at the Swedish Environmental Protection Agency.

Trondheim, March 2019

Alexander Kopatz, Oddmund Kleven and Øystein Flagstad

1 Introduction

Once almost extirpated throughout the continent, the brown bear (*Ursus arctos*) has made a successful return across northern Europe. Populations have been recovering and individuals have been and still are expanding into areas from which they were wiped out (Chapron et al. 2014). Brown bear populations in Scandinavia and Finland have recovered, especially during the 1990s (Swenson et al. 1995 and 1998; Kojola and Laitala 2000). Despite these documented increases in population sizes in Fennoscandia, previous studies on the genetic connectivity among brown bears of neighbouring Scandinavia and Finland (incl. Russian Karelia) reported considerable genetic differentiation between eastern and western parts in northern Europe. Largest differentiation was found between the brown bears from Scandinavia versus individuals from Finland and northwestern Russia (Schregel et al. 2012; Kopatz et al. 2014; Schregel et al. 2015; Schregel et al. 2018), with further, local or fine-scale structure of the respective bear populations (Manel et al. 2004; Tammeleht et al 2010; Norman et al. 2013; Kopatz et al. 2014; Schregel et al. 2017).

Over the last two decades, numerous studies have assessed the genetic structure of the Scandinavian brown bear population and reported the same subdivision into a southern, central and northern genetic cluster (see e.g. Waits et al. 2000; Manel et al. 2004; Xenikoudakis et al. 2015; Schregel et al. 2017). Studies on the genetic structure of the Finnish brown bear population showed that it is subdivided into a northern and southern genetic group (Kopatz et al. 2014), but differentiation between these two units has been diminishing (Hagen et al. 2015; Kopatz et al. 2017). Although varying in densities, nowadays brown bears are distributed nearly continuously in the northern parts of Fennoscandia. The earlier studies to assess gene flow between east and west combining samples from Scandinavia and Finland did not have complete coverage and continuous sampling across the specific transborder-area between northern Sweden and northern Finland. Those studies were lacking brown bear samples and thus genotypes from Norrbotten (Schregel et al. 2012; Kopatz et al. 2014) and northern Finland (Schregel et al. 2012), areas crucial to assess connectivity levels between the populations of Sweden and Finland. Merely one study analysing Y-chromosomal data and Y-haplotype diversity and distribution among male brown bears in northern Europe included the stated regions, suggesting a substantial division between the populations from Scandinavia and Finland (Schregel et al. 2015).

The objective of this study was to investigate and identify possible immigration from the Finnish bear population into Sweden, but also to quantify the number of bears migrating from Sweden into Finland. Based on previous research on the dispersal of brown bears, we focused on male brown bears only, since males are the dispersing sex and therefore assumed to be the driver behind dispersal and gene flow (Støen et al. 2006; Zedrosser et al. 2007). We reassessed the levels of genetic connectivity and gene flow between the brown bear populations in Scandinavia and Finland by focusing on the area where these populations meet: Norrbotten, from which samples were lacking in previous studies, and northern Finland. In addition, we included genotypes sampled in the neighbouring areas: Västerbotten in Sweden, Troms and Finnmark in Norway and southern Finland to gain a more comprehensive picture on the overall connectivity among brown bears in northern Europe.

2 Material and Methods

2.1 Data collection and molecular analyses

We compiled published individual brown bear autosomal STR genotypes (short-tandem repeats or microsatellites) from Norrbotten and Västerbotten (Sweden), Troms and Finnmark (Norway) and the whole of Finland (Kopatz et al. 2012, 2014 and 2017; Schregel et al. 2012 and 2017). A STR-genotype profile consisted of eight markers which have been used for individual identification during the non-invasive genetic monitoring over more than a decade in northern Europe (Andreassen et al. 2012). The same eight to 12 autosomal STR-markers have been used also in previous genetic research studies in the area (MU05, MU09, MU10, MU23, MU50, MU51, MU59, G10L and MU15, G1A, G1D and G10B; Kopatz et al. 2012 and 2014; Schregel et al. 2012, 2015 and 2017). These markers have been selected on their informativeness and success in genotyping of difficult template DNA, such as in feces or hairs (Kopatz et al. 2012; Andreassen et al. 2012). Also, earlier studies have shown that these STRs display no linkage across markers and populations in Fennoscandia and western Russia (Kopatz et al. 2012 and 2014; Schregel et al. 2012). When possible, we updated the existing data from eight to twelve STR-markers and added DNA-profiles (12 STRs) from recently collected male brown bear samples. This resulted in 892 full genotypes with 12 markers. For 32 genotypes, consisting of eight STR-markers, it was not possible to increase the profile to twelve markers due to lack of sample material. Yet, they were included in the study, giving a total data set of 924 brown bear autosomal STR-genotypes (**Table 1**, **Figure 1**).

***Table 1**: Autosomal- and Y-STR-genotype collection of male brown bears across northern Fennoscandia.*

Number of samples …	Sweden		Finland		Norway		Sum
	Västerbotten	Norrbotten	Northern Finland	Southern Finland	Troms	Finnmark	
… genotyped with STRs	63	399	78	240	24	120	**924**
… genotyped with Y-STRs	41	363	87	227	19	89	**826**
Time period	2015-2017	2005-2017*	2005-2017#	2010-2018	2006-2016	2005-2017	

** data also included one sample from 1996 and one sample from 1997.*

 # data also included one sample from 1997, 1998, 2002 and 2003.

To assess the geographical distribution of male lineages and male dispersal patterns across the study area we also used Y-chromosomal genetic markers. A limited set of individuals has previously been genotyped with nine Y-STR-markers with fragment lengths from 126 to 412 bp (UarY318.1, UarY318.2, UarY318.4, Uar318.6, Uar318.9, UarY369.1, Uar369.4, UarY15020.1, Uar69217.1; Bidon et al. 2014; Schregel. et al. 2015). We added to these data by genotyping the same samples as described above for autosomal STR-genotyping. Of the 924 genotyped male brown bear samples, 98 showed missing data on at least one marker and could not be assigned to a specific Y-haplotype, resulting in a total of 826 complete Y-STR-profiles (**Table 1**).

The laboratory procedures followed the strict guidelines for forensic examination of animal DNA material (Linacre et al. 2011). Specificity, sensitivity and forensic evaluation of the STR-markers are reported in Andreassen et al. (2012). For non-invasive genetic samples, such as feces and hair, STR-markers showing heterozygous results (two different alleles) were run twice and homozygous results (two similar alleles) were replicated three times to assure feasibility of the results. All runs across all markers were required to be consistent to assign individual identity. Single negative results were accepted if the other results were consistent for the rest of the profile (Kopatz et al. 2012). In order to be able to compare the genotypes, the new runs and matching were calibrated. Bin-sets and allele scoring was calibrated among the two different laboratories performing the new genotyping; the Norwegian Institute for Nature Research (NINA) and the Center of Genetic Identification (CGI) at the Swedish Museum of Natural History. The same has been done to the archived genotype data of the genetic monitoring in Norway and Sweden by exchanging, running and scoring reference samples of northern European brown bears.

We focused on male brown bears which were mainly sampled during the last 12 years (2005-2017) representing about one generation in this species (Tallmon et al. 2004; Waples et al. 2014). However, due to limited number of samples from certain areas, specifically northern Finland, we included an additional six genotypes (northern Finland: 4 and Norrbotten: 2) from previously sampled individuals (1996 to 2003) to achieve as representative sample coverage as possible. After sample and genotype collection the data was quality checked and we verified uniqueness of each genotype using GIMLET version 1.3.3 (Valiere 2002) to detect possible recaptures of the same individual. Exact geographic sampling location (longitude and latitude) was available from all but 13 individuals.

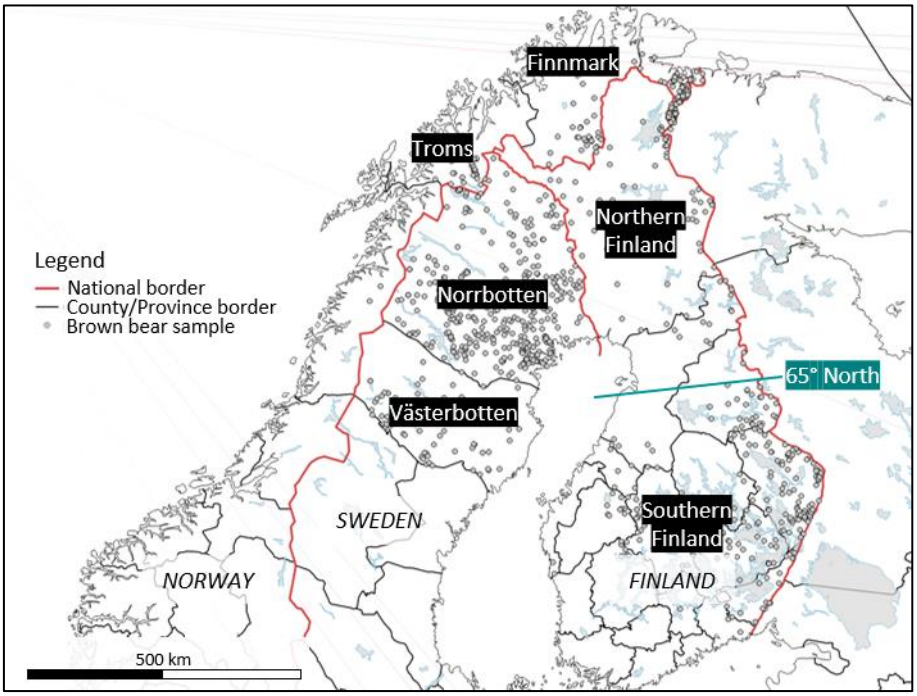

***Figure 1**: Study area and all 924 locations of brown bear samples used in this study. The map contains also borders among countries, counties and provinces as well as a line denoting 65° latitude north, which was used as a border line to distinguish between brown bear samples collected in northern and southern Finland.*

In consideration on previous studies on genetic population structure in the area and due to varying management schemes, samples and genotypes of brown bears from Sweden and Norway were grouped based in which country and county they were sampled. In Finland, we grouped the samples based on latitude into northern and southern Finland with the 65° latitude as separator line. In that way, the northern part connotes approximately with the area of the reindeer husbandry area in Finland. The 318 genotypes from Finland could therefore be grouped to 78 genotypes sampled in northern Finland and 240 genotypes from southern Finland (**Figure 1**, **Table 1**).

2.2 Genetic population structure

We used two different analyses to assess at the population genetic structure of male brown bears in the study area. First, we applied the Bayesian algorithm in STRUCTURE (Pritchard et al. 2000) to identify the population genetic structure within the STR-genotyped data. We tested for the number of subpopulations (K=2 to K=10), using a burnin of 100,000 and 1,000,000 iterations with a repetition of 10 runs. We used admixture model, as we assumed that each individual contained at least parts of their genome from one or more of the K populations. The sampling locations were not used to infer the genetic structure and thus LOCPRIOR function was not applied. Over such a large scale, hierarchical population substructure might be present (Pritchard et al. 2000; Frantz et al. 2009; Anderson et al. 2010; Janes et al. 2017). Thus, the results were post-processed using the algorithms of Evanno et al. (2005) and Puechmaille (2016) to suggest the most likely number of genetic clusters. Eventually, we used CLUMPAK to identify the run most representative of the population structure suggested (Kopelman et al. 2015). In order to reveal the level of differentiation, we estimated pairwise F_{ST} (Weir and Cockerham 1984) among the identified genetic clusters with the program ARLEQUIN version 3.5.2.2 (Excoffier and Lischer 2010).

We further used a discriminant analyses of principal components method (DAPC) (Jombart et al. 2010) in the package ADEGENET (Jombart 2008) in R 3.5.2 (R Core Team 2019). DAPC is not assuming any population genetic model or subdivision but applies multivariate clustering in which individual genotypes are grouped by genetic similarity to visualize genetic hierarchical structure not assuming any specific population genetic model (Jombart et al. 2010). DAPC-analysis has been performed in accordance to the recommendations by Jombart and Collins (2015).

2.3 Gene flow and migration

We assessed possible gene flow among the geographic regions by estimating self-recruitment and directional gene flow using the STR-data with the program BAYESASS Version 3 (Wilson and Rannala 2003). The algorithm applies a Bayesian, non-equilibrium population assignment method to reveal recent or current unidirectional gene flow among populations during the latest, one to three generations. BAYESASS estimates the posterior probability of each genotype's migration-history based on few assumptions compared to e.g. STRUCTURE. For example, the latter incorporates expectations to Hardy-Weinberg-equilibrium, often violated in fragmented, natural populations. Migration rates and individual migrant ancestries were estimated in ten independent runs using a burnin of 10^6 iterations and $21x10^6$ iterations to counter potential convergence issues (Faubet et al. 2007). The analyses were adjusted for allele frequency (0.07), inbreeding coefficient (0.05) and migration (0.15) as suggested for more accurate estimations (Faubet et al. 2007) and applied in earlier studies on gene flow among brown bears in the area (Schregel et al. 2012 and 2017). Also, a random seed for each run was used to allow tests of convergence among the results of each run. We also enabled the trace option to monitor convergence. After completion we tested for consistency and convergence of the estimated migration rates (Meirmans 2014). The effective number of immigrants per generation were estimated

for Norrbotten and Finland by multiplying the migration rate with the estimated population sizes in the two recipient populations (Kobayashi et al. 2018).

To reflect historical levels of gene flow, we applied two indirect methods to assess the level of gene flow. First, we used the private allele method (Slatkin 1985) included in the program GENEPOP (Rousset 2008), which also corrects for sample size, to estimate the effective number of migrants among the regions per generation, and specifically between Norrbotten and Finland. In addition, we estimated the number of migrants between the identified genetic clusters in Norrbotten and Finland by applying Wright's statistics (Wright 1951) and utilizing the acquired pairwise F_{ST}-values (see 2.2).

2.4 Distribution of male lineages

An earlier study using Y-chromosomal markers on brown bears across northern Europe and northwestern Russia identified 36 different haplotypes (Schregel et al. 2015). We used the previously published Y-haplotypes also in this study and utilized the previously identified haplotypes to score the haplotypes found in the newly genotyped individuals. This allowed us to assess the distribution of male lineages across the study area. In that way, also new, unidentified haplotypes could be identified.

3 Results and discussion

3.1 Recaptures

This is the first time such a comprehensive genotype data set of brown bears from Sweden, Finland and Norway has been compiled, merged and analysed. The genotype data originated from different monitoring schemes on non-invasive genetic sampling and tissue samples from legally harvested individuals. Thus, roaming and migrating brown bear individuals may have been sampled more than once in different regions across the study area. Therefore, we tested the data for possible recaptures of individual brown bears. Indeed, during quality assurance of the genetic data (STRs and Y-STRs), we detected a total of 17 recaptures of individual brown bears (**Table A1**). Two individuals formerly detected non-invasively in northern Finland, Lapland, were also shot in the same area. Two individuals sampled non-invasively earlier in eastern Finnmark were identified among shot bears in Finland. Six brown bears sampled non-invasively in Troms were shot in Norrbotten, and, six individuals sampled in Norrbotten were among harvested bears in the same region later. Just one brown bear, which has been identified during non-invasive genetic monitoring near Anarjohka in Finnmark was shot later in Norrbotten. Among these data, the latter is the only individual recorded to have moved from east to west. Most of the recaptures suggested that male brown bears seem much less likely to disperse from east to west; from Finland to Scandinavia, than vice versa. However, this result should be treated with caution as its main purpose was to ensure that only unique genotypes were used to assess genetic connectivity and to remove identical genotypes originating from two samples. These recaptures may also be reflective of the sampling effort and thus might not be representative for the brown bears in parts of the study area. The observed difference of dispersal-events may be an indication of directional gene flow and thus might be investigated further in the future, e.g. by more systematically and increased sampling effort.

3.2 Genetic population structure

The plot of the mean likelihood values resulting from the Bayesian clustering approach with STRUCTURE did not reach a clear plateau to be suggestive on the likely number of genetic clusters in the sample (**Appendix Figure A1**). For such reasons the results by STRUCTURE can be post-processed to reveal the most likely number of genetic clusters present in the data. The approach by Evanno et al. (2006) suggested K=2 genetic clusters (**Figure A2**). The approach described by Puechmaille (2016) suggested K=4 as the most likely number of genetic clusters (**Figure A3**). The bar plots illustrating the assignment of each brown bear genotype for the clusters K=2-5 are shown in **Figure A4**. Based on previous studies assessing the genetic population structure of brown bears in the region, K=2 as well as K=4 as the number of genetic clusters suggested, are feasible and representative of the hierarchical genetic substructure present (Janes et al. 2017). First, K=2 clusters highlights the east-west division, Scandinavia vs. Finland and Finnmark, among brown bears, as it has been shown previously (Schregel et al. 2012; Kopatz et al. 2014). The substructure with K=4 genetic clusters is representative of further subdivision into more local or fine-scale population structure (**Figure 2**), which also has been identified earlier in Sweden (Manel et al. 2004; Norman et al. 2013; Schregel et al. 2017), Finland (Tammeleht et al. 2010; Kopatz et al. 2014) and eastern Finnmark (Schregel et al. 2017).

Among the four identified genetic clusters (**Figure 2**), one cluster consisted of genotypes mainly sampled in Västerbotten, Norrbotten and Troms. As this cluster appears to be reflective of genotypes from Västerbotten we called this cluster accordingly (cluster “Västerbotten”). A second cluster grouped brown bears mainly sampled in Norrbotten and Troms (cluster “Norrbotten/Troms”), but some genotypes were also collected in northern Finland and Finnmark. Genotypes sampled mainly in northern Finland and Finnmark were assigned to a third cluster (cluster: “Northern Finland/Finnmark”). The fourth genetic cluster consisted of genotypes from individuals mainly sampled in southern Finland (cluster: “Southern Finland”), but genotypes assigned to this

cluster were also sampled in northern Finland and Norrbotten (**Figure 2** and **Figure 3**). While most genotypes from the different genetic clusters showed a large degree of geographical grouping (Finland and Finnmark), distribution of genotypes also displayed clear geographical overlap (northern Finland and Norrbotten, northern and southern Finland). Brown bear genotypes sampled in Västerbotten, Troms, Finnmark and southern Finland were mainly assigned to one genetic cluster.

Overall, the differentiation among the genetic clusters showed moderate and significant pairwise F_{ST}-values (**Table 2**), and, slightly lower compared to the numbers reported in earlier studies (Schregel et al. 2012). The clusters of Norrbotten/Troms vs. northern Finland/Finnmark had an F_{ST}-value of 0.09, while Schregel et al. (2012) calculated an F_{ST} of 0.11 between Kainuu in eastern Finland and Russian Karelia vs. Västerbotten. One reason for the difference could be that Schregel et al. (2012) had no continuous sampling and brown bears from Norrbotten and northern Finland were not included in their analyses. Also, F_{ST} is reflective of large, historical time spans (Whitlock and McCauley 1999), and thus most likely representative of the severe demographic bottleneck and separation both large brown bear populations in the east and west of Fennoscandia experienced in the past.

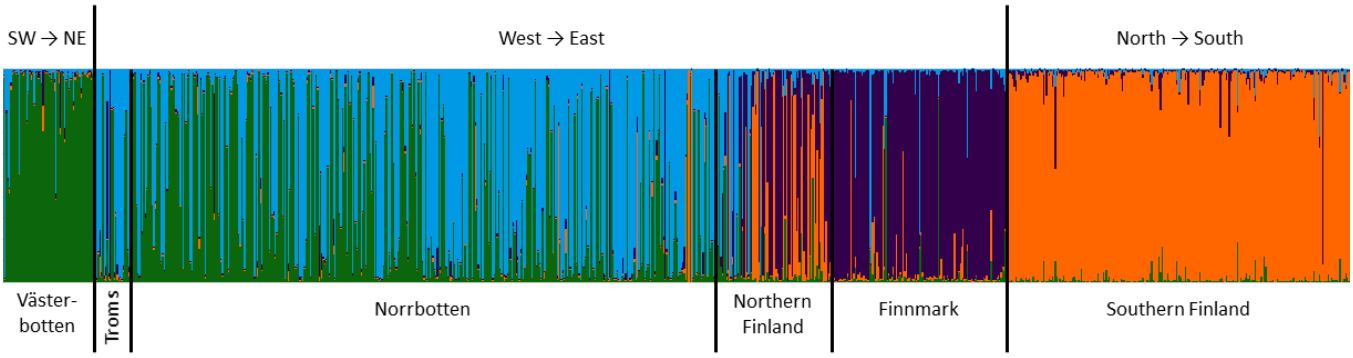

***Figure 2**: Bayesian clustering results of 924 male northern European brown bear STR-genotypes with the program STRUCTURE (Pritchard et al. 2000). The bar plot shows the assignment probabilities for each brown bear genotype for K=4 genetic clusters. The higher the bar of a certain cluster (colour) the more likely the genotype originates from the respective genetic cluster. Genotypes are in specific geographic order, as indicated on the top and the region the samples were collected, as indicated at the bottom.*

STRUCTURE reports individual assignment values (q) for each genotype to each identified genetic cluster. In previous studies a threshold of q=0.7 (70%) has been applied to distinguish between unambiguously assigned genotypes and unassigned or admixed genotypes (Tammeleht et al. 2010; Pelletier et al. 2012; Kopatz et al. 2014). An individual genotype with an assignment value of q≥0.7 for a different cluster and area than it was sampled in may suggest that this individual is most likely a migrant from the assigned genetic group. The presence of such genotypes in an area, especially in Norrbotten and northern Finland, may suggest a transition zone between or among the identified genetic clusters. Genotypes from sampled brown bears in Norrbotten and northern Finland also showed genotypes with low assignment values of q<0.7 caused by mixed ancestry of the individuals as those individuals received genes from more than one genetic cluster (**Figure 2** and **Figure 3**). Admixed genotypes are characterized by ambiguous cluster assignment due to low assignment values for each cluster which is caused by mixed ancestry of the individuals. Most admixed genotypes were found in Norrbotten illustrating admixture among brown bears from Västerbotten and Norrbotten, two clusters shaped by

isolation-by-distance (Schregel et al. 2018).The genotypes sampled in northern Finland displayed a mix of individuals assigned to the gene pools found in northern Finland, Finnmark, Norrbotten and southern Finland suggesting that this seems to be an area where brown bears from the surrounding areas meet and reproduce. Overall, we found 72 (7.79%) genotypes with mixed ancestry and thus ambiguous cluster assignment across the study area, which is illustrative of the distinctiveness of the genetic groups in the area, especially between Sweden and Finland.

In Norrbotten we identified two genotypes assigned to the cluster of northern Finland and Finnmark and four individuals assigned to southern Finland. One similar genotype was sampled in Troms. One individual with admixed ancestry but highest assignment value (q) for the northern Finnish/Finnmark cluster was also found in Norrbotten. Two similar individuals were sampled in Troms. Two admixed genotypes with highest assignment for the southern Finnish cluster were also identified in Norrbotten (**Figure 3**). Previous studies have not identified such influx. This may reflect increased immigration since the last assessment (Kopatz et al. 2014) from the expanding Finnish brown bear population, specifically from the southern genetic cluster in Finland (Hagen et al. 2015; Kopatz et al. 2017). Or, alternatively, is due to the comprehensive sampling effort, which led to the detection of these individuals.

We found 13 genotypes in northern Finland, and three in eastern Finnmark, which originated from the genetic cluster of Norrbotten/Troms. Further, we found two genotypes in eastern Finnmark and one in northern Finland originating from the cluster of Västerbotten (**Figure 3**). Influx of eight brown bears from Norrbotten into northern Finland has been reported earlier (Kopatz et al. 2014). However, the genotype data from Sweden in that study was only based on brown bear samples collected in Västerbotten. Further, the occurrence of admixed genotypes among clusters in the area, and especially between Norrbotten and northern Finland, suggests reproductions among individuals from different genetic groups and regions.

***Table 2**: Pairwise F_{ST}-values for male brown bears in northern Europe among the four identified genetic clusters of Västerbotten (VB), Norrbotten and Troms (NB/TR), northern Finland and Finnmark (NF/FM) and southern Finland (SF). All estimates were significant (P<0.01).*

	VB	NB/TR	NF/FM	SF
VB	-			
NB/TR	0.04	-		
NF/FM	0.09	0.09	-	
SF	0.12	0.13	0.06	-

The DAPC-analysis showed a very similar picture of the genetic grouping among brown bears across the study area. Genotypes from individuals in Västerbotten, Norrbotten and Troms grouped closely together in one distinctive group (**Figure 4**), whereas individuals sampled in southern and northern Finland as well as Finnmark formed three other groups, but with considerable overlap. Also, the groups of bears from northern Finland and Troms and Norrbotten showed substantial overlap, suggesting a certain degree of connectivity among neighbouring populations of brown bears in the study area (**Figure 4**).

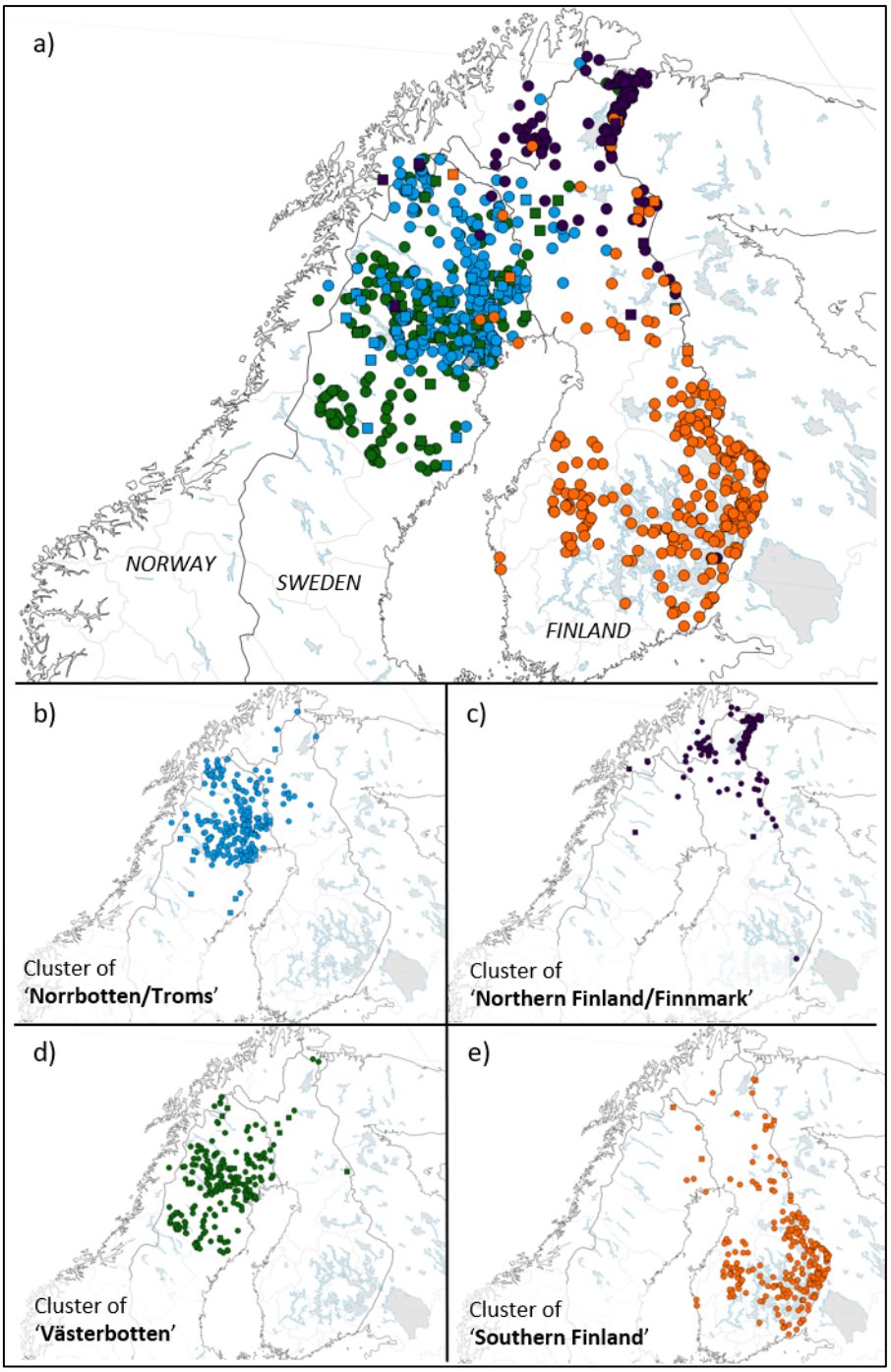

***Figure 3**: Sample locations and distribution of 924 male STR-genotypes in accordance to their assignment to a genetic cluster with the program STRUCTURE (Pritchard et al. 2000). Colours correspond to the bar plot for K=4 cluster of the STRUCTURE-results as shown in **Figure 1**. Genotypes with unambiguous assignment values (q≥0.7) are shown in circles, admixed genotypes (q<0.7) as squares and coloured based on the highest assignment value and the colour of the respective cluster. Map a) shows all genotypes and locations while the distributions of each genetic cluster are shown separately in b) to e).*

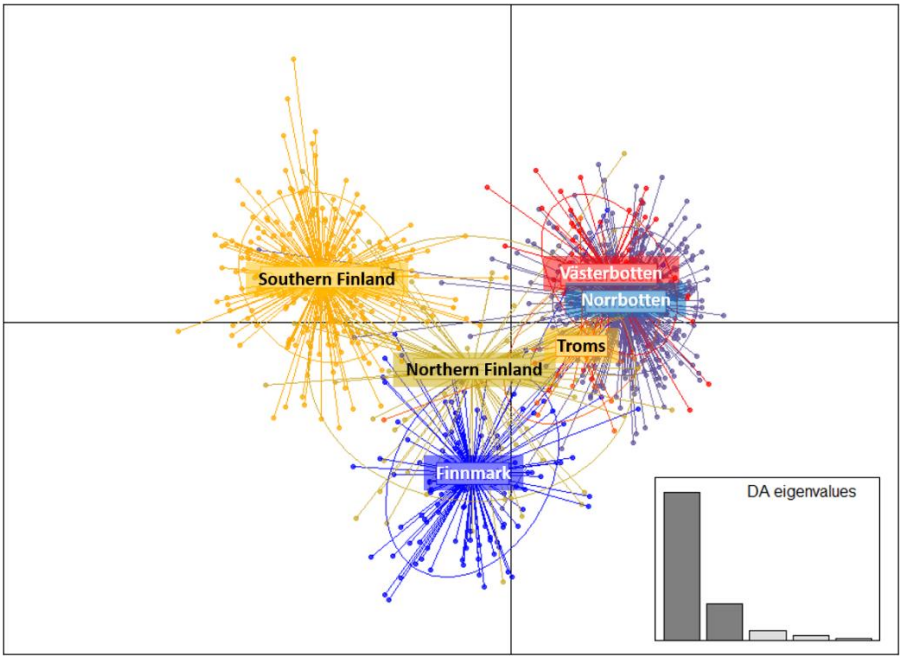

***Figure 4**: Discriminant analysis of principal components (DAPC) scatterplot (Jombart et al. 2010) showing the first two principal components for 924 male brown bears sampled in the different regions and genotyped with 12 STR-markers. Discriminant analysis (DA) eigenvalues are shown in the inset.*

3.3 Gene flow and migration

Migration rates estimated with BAYESASS reflect contemporary or recent migration and gene flow per generation. All ten runs among the regions were consistent and convergent (**Figure A5**). Although very similar across runs, we here present the estimates of the run with the lowest deviance (**Table 3**, **Figure A6**) as suggested by Meirmans (2014). Self-recruitment was lowest in northern Finland with 68%, Troms with 82% and Norrbotten with 89%. High self-recruitment was found with about 91% in Västerbotten, 93% in Finnmark and 98% in southern Finland. The directional migration rates estimated are suggestive of asymmetrical gene flow between northern Finland and Norrbotten: while about 8% influx per generation from Norrbotten into northern Finland has been estimated, the influx from northern Finland into Norrbotten was 0.1%. Further, the results show that Norrbotten receives about 0.3% of genes from Finnmark and 0.6% from southern Finland, which sums up to about 1% of influx of eastern genotypes into Norrbotten per generation. Relatively high rates of immigration were estimated for Troms with about 9% from Norrbotten, 4% from Finnmark and 1% from northern Finland per generation. Northern Finland also seem to receive high rates of gene flow with estimated rates of 12% from Finnmark and 9% from southern Finland, per generation.

BAYESASS also reports the assignment of each genotype being a F0- (first generation migrant) or F1-migrant (second generation migrant) as well as likely being a non-migrant. In our data, these results identified four F0-migrants and four F1-migrants from Finland in Norrbotten (**Table 4**). 15 F0-migrants and nine F1-migrants from Sweden and Troms (one individual) were identified in Finland (**Table 4**). Migrants were also detected among Norrbotten, Troms and Finnmark. These results correspond with the results of the STRUCTURE analysis, with F0-migrants being mainly assigned to a genetic cluster and F1-migrants showing often admixed ancestry, as to be expected (see 3.2, **Figure 2** and **Table 4**).

***Table 3**: Percentage of self-recruitment, directional migration and gene flow of male brown bears in northern Europe among regions, estimated with the program BAYESASS (Wilson and Rannala 2003). Self-recruitment is presented in the diagonal, shaded cells. Directional gene flow and migration is given above and below the diagonal. Standard deviations (SD) calculated by the software are also presented behind the estimations. The regions have the following abbreviations: Västerbotten (VB), Troms (TR), Norrbotten (NB), northern Finland (NF), Finnmark (FM) and southern Finland (SF). Estimations of self-recruitment in, and migration rates into Norrbotten are highlighted in green and into northern Finland (NF) from Norrbotten (NB) are highlighted in blue.*

	From VB	SD	From TR	SD	From NB	SD	From NF	SD	From FM	SD	From SF	SD
to VB	**0.906**	0.024	0.006	0.006	0.073	0.024	0.005	0.005	0.005	0.005	0.005	0.005
to TR	0.018	0.016	**0.823**	0.038	0.093	0.037	0.012	0.011	0.043	0.021	0.011	0.011
to NB	0.082	0.013	0.018	0.005	**0.891**	0.014	0.001	0.001	0.003	0.002	0.006	0.002
to NF	0.010	0.008	0.011	0.007	0.083	0.017	**0.680**	0.011	0.125	0.022	0.091	0.019
to FM	0.004	0.003	0.013	0.006	0.019	0.008	0.031	0.013	**0.931**	0.015	0.004	0.004
to SF	0.002	0.002	0.002	0.002	0.002	0.002	0.008	0.006	0.002	0.002	**0.983**	0.007

We utilized the estimates on gene flow (**Table 3**) to calculate the effective number of migrants per generation by multiplying the estimated rate with the estimated number of brown bears in the region (Kobayashi et al. 2018). Latest assessments estimated 463 to 549 brown bears in Norrbotten (Kindberg and Swenson 2017) and 326 to 415 bears in the northern Finland (reindeer-husbandry area) and 1965 to 2279 bears in the other, southern parts of Finland (Heikkinen and Kojola 2018). Based on these numbers and our estimates on gene flow among the regions, 0.46 to 0.55 bears immigrate effectively from northern Finland, 1.39 to 1.65 bears from Finnmark, and, 2.78 to 3.29 bears from southern Finland into Norrbotten per generation. In the opposite direction, from Norrbotten, 27.1 to 34.5 bears immigrate into northern Finland and 3.9 to 4.6 bears into southern Finland per generation. Given the current estimates of population sizes, the total sum of brown bears immigrating from the neighbouring populations in the east to Norrbotten thus adds up to 4.6 to 5.5 individuals effectively per generation.

In order to assess the level of gene flow between the whole of Finland and Norrbotten, we repeated the BAYESASS-analysis by using only genotypes from Norrbotten and genotypes from northern and southern Finland. This analysis was repeated three times and results were consistent and showed a rate of 0.0083 (~0.8%) from Finland into Norrbotten, while a gene flow rate of 0.0463 (~0.4%) was estimated from Norrbotten into Finland (**Table 5**). Again, the results are suggestive of asymmetrical gene flow between Finland and Sweden. In combination with the actual estimated census sizes of brown bears these suggested 3.9 to 4.6 brown bears per generation immigrating effectively from Finland into Norrbotten and 106 to 125 brown bears immigrate to Finland from Norrbotten per generation.

***Table 4**: Detected migrants in the data sorted by the region the sample was collected in and if the genotype was identified as F0 or F1 migrant. Each row represents one individual genotype with its ID, age, assignment by the program STRUCTURE and BAYESASS (see also **Table A2**) as well as the Y-haplotype (Y-HT). The regions have the following abbreviations: Västerbotten (VB), Troms (TR), Norrbotten (NB), northern Finland (NF), Finnmark (FM) and southern Finland (SF). "Admixed" genotypes under STRUCTURE indicate individuals with mixed ancestry and therefore could not be assigned unambiguously to one of the identified four genetic clusters (see 3.2.).*

	Assignment	ID	Age	STRUCTURE	BAYESASS	Y-HT
To Norrbotten	F0 from SF	NB2010_M003551	4	SF	F0 from SF	3.09
	F0 from SF	NB2013_M406262	7	SF	F0 from SF	FIN.HET.X.04
	F0 from NF/FM	NB2013_M406573	3	NF/FM	F0 from FM	3.04
	F0 from FM	NB2015_M407762	3	NF/FM	F0 from FM	2.07
	F1 from SF	NB2012_M004696	1	Admixed	F1 from SF	3.09
	F1 from SF	NB2008_M004741	3	Admixed	F1 from SF	1.01
	F1 from SF	NB2012_M405845	4	SF	F1 from SF	3.09
	F1 from SF	NB2013_M406480	2	Admixed	F1 from SF	3.09
To Troms	F0 from FM	TR2014_TR50	-	NF/FM	F0 from FM	1.01
	F1 from FM	TR2008_TR25	-	Admixed	F1 from FM	2.02
	F1 from FM	TR2016_TR57	-	Admixed	F1 from FM	-
To northern Finland	F0 from NB	FI1997_27_97	-	NB/TR	F0 from NB	2.05
	F0 from NB	FI2002_2730	3	Admixed	F0 from NB	2.05
	F0 from NB	FI2007_6429	2	NB/TR	F0 from NB	3.09
	F0 from NB	FI2009_7457	1	VB	F0 from NB	2.08
	F0 from NB	FI2009_7510	4	NB/TR	F0 from NB	2.05
	F0 from NB	FI2009_7511	5	NB/TR	F0 from NB	2.05
	F0 from NB	FI2011_9041	2	NB/TR	F0 from NB	2.05
	F0 from NB	FI2011_9465	2	NB/TR	F0 from NB	FIN.HET.X.04
	F0 from NB	FI2012_9843_FI112	6	NB/TR	F0 from NB	2.05
	F0 from NB	FI2012_9957	3	NB/TR	F0 from NB	2.08
	F0 from NB	FI2013_10977	2	NB/TR	F0 from NB	2.05
	F0 from NB	FI2014_12035	3	NB/TR	F0 from NB	2.05
	F0 from NB	FI2015_12103	2	NB/TR	F0 from NB	2.05
	F0 from NB	FI2017_13330	1	NB/TR	F0 from NB	3.09
	F0 from TR	FI2013_10978	8	Admixed	F0 from TR	2.02
	F1 from NB	FI1998_209	2	NB/TR	F1 from NB	3.2
	F1 from NB	FI2003_3186	2	Admixed	F1 from NB	2.08
	F1 from NB	FI2013_10595	15	Admixed	F1 from NB	2.05
	F1 from NB	FI2015_12067	1	Admixed	F1 from NB	2.02
	F1 from NB	FI2016_12990	3	SF	F1 from NB	3.15
	F1 from NB	FI2017_13329	6	NF/FM	F1 from NB	2.05
	F1 from NB	FI2017_13389	3	Admixed	F1 from NB	2.32
	F1 from NB/VB	FI2007_LL026	-	VB	F1 from NB	2.05
	F1 from VB	FI2010_8332	4	Admixed	F1 from VB	2.05
To Finnmark	F0 from NB	FM2011_FI124+	2	NB/TR	F0 from NB	2.05
	F0 from NB	FM2016_FI212+	2	NB/TR	F0 from NB	3.21
	F0 from TR	FM2008_FI079	-	NB/TR	F0 from TR	2.05
	F0 from TR	FM2015_FI178	-	VB	F0 from TR	2.05
	F1 from NB	FM2007_FI062	-	VB	F1 from NB	2.05
	F1 from NB	FM2010_FI099	-	Admixed	F1 from NB	1.01
	F1 from NB	FM2011_FI123_LL43	-	Admixed	F1 from NB	1.01
	F1 from NB	FM2011_FI130_LL32	-	Admixed	F1 from NB	3.21
	F1 from TR	FM2015_FI179	-	Admixed	F1 from TR	2.05

***Table 5**: Percentage of self-recruitment and directional migration and gene flow of male brown bears between the county of Norrbotten in Sweden and Finland, estimated with the program BAYESASS (Wilson and Rannala 2003). Self-recruitment is presented in the diagonal, shaded cells. Directional gene flow and migration is given above and below the diagonal. Standard deviations (SD) calculated by the software are also presented behind the estimations. The regions have the following abbreviations: Norrbotten (NB) and Finland (F).*

	From NB	SD	From F	SD
to NB	**0.992**	0.003	0.008	0.003
to F	0.046	0.007	**0.954**	0.007

The private allele method estimated *Nm*=1.70 as the effective number of migrants between Norrbotten and northern Finland (**Table 6**). Further, the number of effective migrants between southern Finland and Norrbotten was *Nm*=0.57 and between Finnmark and Norrbotten *Nm*=1.05 brown bears. When comparing only Norrbotten and the whole of Finland, *Nm*=1.27 was the estimated effective number of migrants. We used pairwise F_{ST}-values (**Table 2**) to estimate the effective number of migrants between the genetic cluster of Norrbotten/Troms versus northern Finland/Finnmark *Nm*=2.53 and between Norrbotten/Troms and southern Finland *Nm*=1.67. These estimates are lower than the estimates based on the current gene flow. Indeed, lower numbers for *Nm* using this method are to be expected as they are also affected by long-term processes (Slatkin 1987) and most likely influenced by the period characterized by the lack of connectivity between the Scandinavian and Finnish brown bear population.

***Table 6**: Number of effective migrants (Nm) per generation estimated using the private allele method (Slatkin 1985) among brown bears from regions in northern Europe. The regions have the following abbreviations: Västerbotten (VB), Troms (TR), Norrbotten (NB), northern Finland (NF), Finnmark (FM) and southern Finland (SF).*

	VB	TR	NB	NF	FM	SF
VB	-					
TR	1.04	-				
NB	4.38	0.94	-			
NF	1.28	1.55	1.70	-		
FM	0.51	0.96	1.05	3.91	-	
SF	0.27	0.31	0.57	2.81	0.63	-

Overall, the level of gene flow from the east into Norrbotten surpasses the suggested one-migrant-per-generation rule, an established standard or rule of thumb to minimize loss of genetic variation and thus counter genetic isolation (Mills and Allendorf 1996; Wang 2004). For deeper assessment on dispersing individuals, female brown bears should be included in future analyses, as the detected gene flow should lead to juvenile females with mixed ancestry. Also, reconstruction of pedigrees and family groups is necessary. However, such analyses require higher resolution than the twelve applied STR markers provide, for example a SNP-chip with a larger number of SNPs (Norman et al. 2013).

3.4 Distribution of male lineages

The Y-haplotype distribution is reflective of male gene flow as the Y-chromosome is inherited from male to male-offspring and thus can be used to assess genetic structure and gene flow among male individuals. Among the 826 Y-STR-genotypes we found a total of 33 different haplotypes, of which seven had not been detected in these populations before. For a better overview on the distinctive haplotype diversity and distribution between Sweden and Finland, we present haplotypes in accordance to their abundance in the west (Scandinavia) and east (Finland and Finnmark). The distribution in Finland and eastern Finnmark showed a high diversity of Y-haplotypes with a total of 31 different haplotypes identified (**Figures 5-8**). In Scandinavia, we found a total of only six haplotypes of which four also were present in the east.

A previous assessment, which data for the study area has been included here, detected four Y-haplotypes in Scandinavia, of which two (2.05 and 2.08) were distinctive for brown bears in the west and the two others (2.02 and 3.09) were found across Fennoscandia (Schregel et al. 2015). In this study, we found 20 individuals carrying haplotype 2.05 in Finland and 10 in eastern Finnmark. Also, we detected four individuals with haplotype 2.08 in northern Finland, suggesting gene flow from Scandinavia to the east (**Figure 6**). One haplotype previously detected only in the far east, in the Russian Republic of Komi (haplotype 2.28; Schregel et al. 2015), was now also detected in a brown bear sampled in Troms (**Figure 5**). Furthermore, four individuals carrying haplotype 2.07 and two individuals with haplotype 1.01 were sampled in Norrbotten and Troms, also suggesting the occurrence of gene flow in the east-west direction; from Finland to Scandinavia (**Figure 5**). Nonetheless, the variation in the occurrence and diversity of the various haplotypes across the area is highly suggestive of different population histories and recovery processes. While only six haplotypes were recorded in Scandinavia, eastern brown bears in Finland and Finnmark carried 31 different Y-haplotypes.

Five of the seven new Y-haplotypes, previously not detected, were found in Finland and Finnmark, whereas two were found in brown bears sampled in Norrbotten (**Figure 7**). To what extent these two latter haplotypes are distinctive for Scandinavia cannot be said with certainty as they were found in single individuals only. These two haplotypes are not the haplotypes reported as extinct in Scandinavia (Schregel et al. 2015) but could be representative for immigration and reflective of the high diversity of haplotypes to the east.

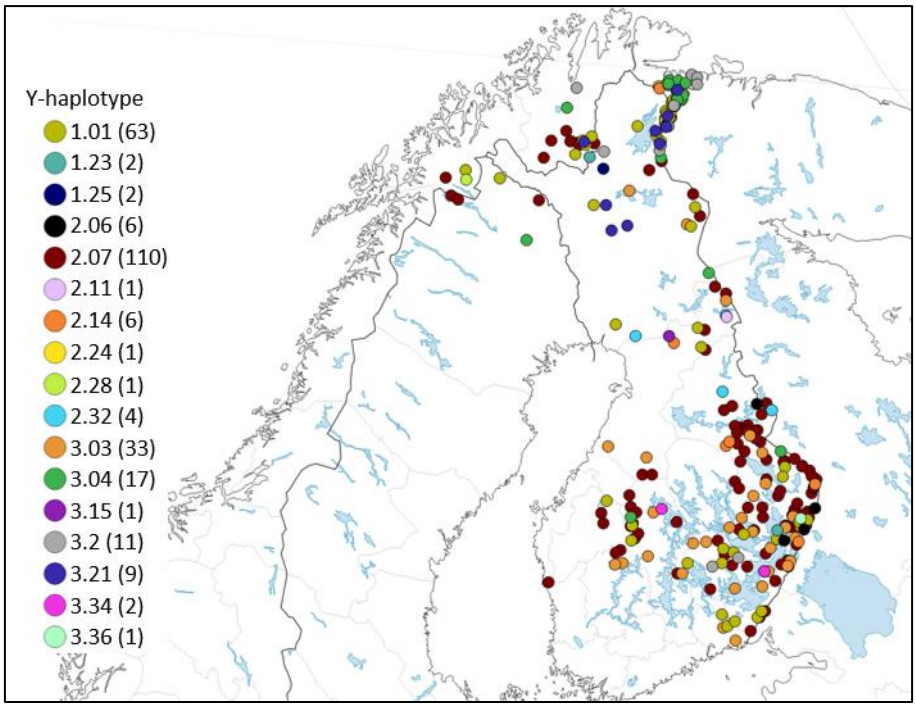

***Figure 5**: Sampling location and geographical distribution of 17 Y-chromosome haplotypes previously identified (and number of individuals in brackets) and characteristic in north-eastern Europe (Finland, north-eastern Norway) among brown bears in the study area.*

Unexpectedly, one Y-STR-marker showed so called pseudoheterozygosity, i.e. two different alleles at one Y-chromosomal marker. In haploid markers, as for Y-chromosomal-specific markers, such pseudoheterozygosity may be caused by gene conversions during meiosis (Sachidanandam et al. 2001; Hallast et al. 2013). Pseudoheterozygosity at this Y-STR-marker (UarY15020.1) was described for brown bears from central and central-eastern Europe only (Bidon et al. 2014) and has not been reported in northern Europe (Schregel et al. 2015). Usually, such a marker is removed from further, especially statistical analysis (Kutschera et al. 2014). However, here, we only report its first-time detection and occurrence in northern Europe and present the geographical distribution (**Figure 8**). If these alleles of pseudoheterozygosity are treated as distinctive alleles, this resulted in five distinctive Y-haplotypes. The geographical location of the brown bears carrying this variant showed geographical grouping indicating most likely distinctive male lineages and family groups. These brown bears were mainly detected in Finland; however, one individual was sampled in Norrbotten, yet another indication of immigration from the east (**Figure 8**).

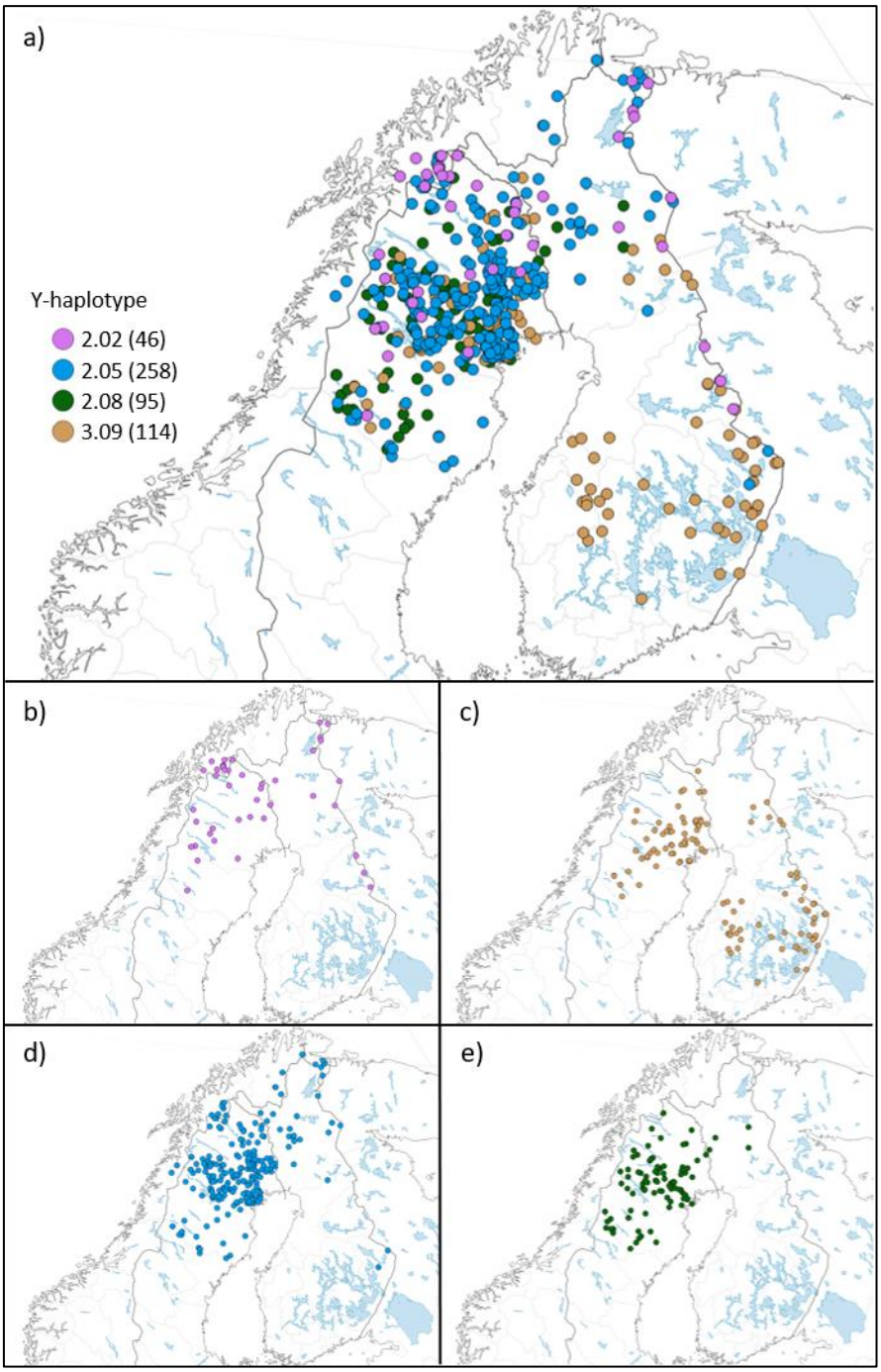

***Figure 6**: Sampling location and geographical distribution of the four, previously detected Y-chromosome haplotypes (and number of individuals in brackets) among brown bears specifically found only in Sweden but also Norway and Finland. a) shows these four Y-haplotypes together while b) to e) present their distribution separately.*

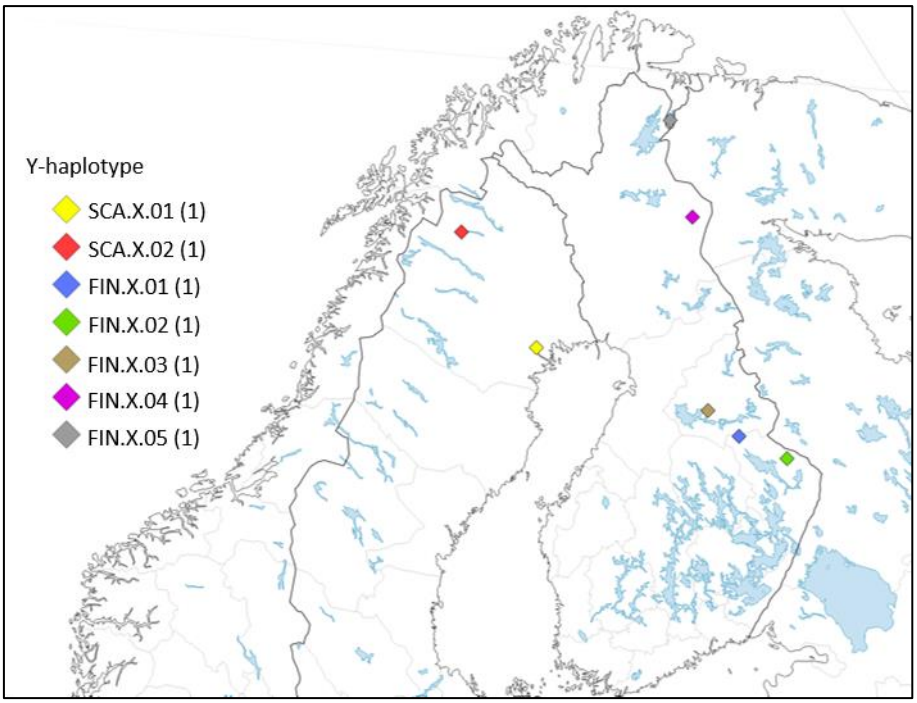

***Figure 7**: Sampling location and geographical distribution of the seven, newly detected Y-chromosome haplotypes among brown bears in Sweden, Norway and Finland.*

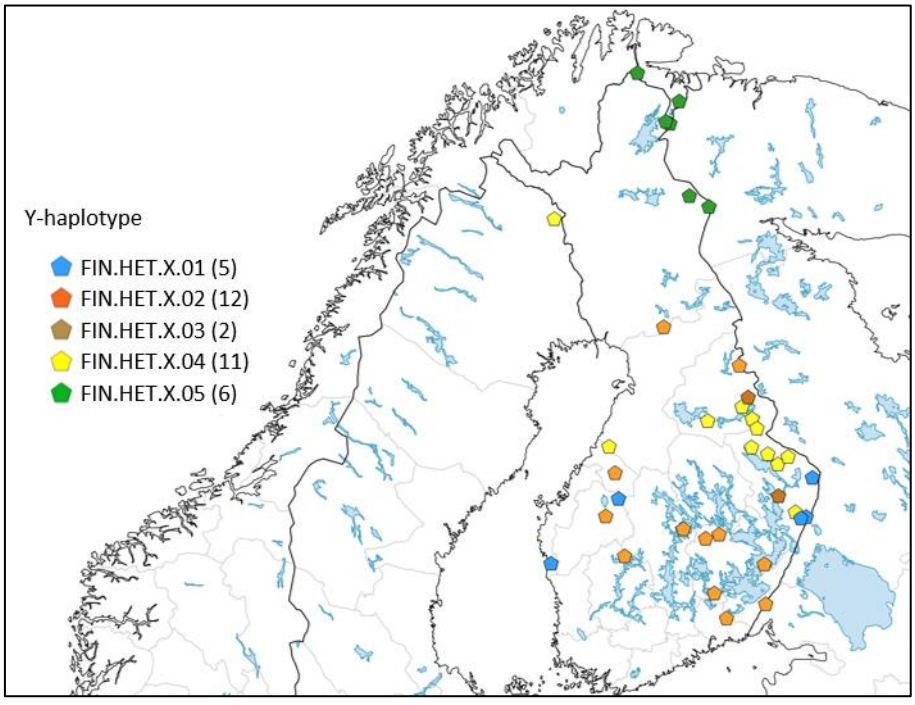

***Figure 8**: Sampling location and geographical distribution of brown bear haplotypes carrying the "pseudoheterozygous" variant of Y-STR-marker UarY15020.1 in northern Europe.*

4 Conclusion

This project represents the first investigation to include a continuous distribution of samples across the study area to assess the genetic connectivity between the Scandinavian and the Finnish brown bear population. Our results show that the brown bear populations of Sweden and Finland, as well as northern Norway, are not genetically isolated from each other. Specifically, brown bear genotypes assigned to the genetic cluster of Norrbotten in Sweden were also found in northern Finland and Finnmark. Genotypes belonging to the Finnish cluster were found in Norrbotten, but in much lower numbers. Estimations resulted in asymmetrical rates of current gene flow between east and west: 1% immigration was detected from eastern Fennoscandia into Norrbotten, while there was about 8% immigration from Norrbotten into Finland. Given the current population size, we estimated that 4.6 to 5.5 bears from the eastern populations immigrate into Norrbotten effectively per generation. Indirect measures of gene flow estimated 1.27 to 2.53 number of migrants between the genetic groups of Norrbotten and Finland. Overall, the level of gene flow surpasses the suggested one-migrant-per-generation rule.

Analysis of the population genetic structure showed distinctive subdivision among brown bears from Sweden and Finland, while the genetic clusters identified within the countries displayed considerable geographical overlap. Nonetheless, we found 8 individuals with genetic origin from the eastern populations in Norrbotten, which has not been reported before, showing immigration from the east into Sweden. Substantially more, 24 individual brown bears with Scandinavian origin were sampled in Finland. The reasons for this asymmetry are unknown but could be related to differences in brown bear densities in Norrbotten and northern Finland. Also, this pattern may be reflective of the earlier initiated expansion of the Swedish brown bear population, and therefore also earlier immigration into Finland. The Finnish brown bear population has also been expanding but, based on our results, with the expansion front now arriving in northern Sweden, represented by a few individuals of eastern origin detected herein. Individual brown bears assigned to the genetic cluster of northern Finland and Finnmark were also found in Troms, suggesting gene flow from east to west through Finnmark. Also, in Finnmark genotypes from the cluster in Norrbotten were sampled.

The distribution of Y-chromosome lineages displayed a similar picture as the results based on STRs. We detected more individuals carrying distinctive haplotypes of Swedish origin in Finland than the other way around. While for example numerous individuals with haplotype 2.05 (a typical Scandinavian haplotype) were sampled in Finland, only a few individuals carrying some of the numerous haplotypes identified in Finland and eastern Finnmark were found in northern Sweden. Still, these results also suggest sufficient, although asymmetric, gene flow between the brown bear populations in Finland and Sweden. The results further suggest that one should aim at transborder management of brown bears in the area.

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7 Appendices

***Table A1**: Previously identified brown bear individuals, sampled non-invasively in Norway, Sweden and Finland and which were identified (recaptured) later during legally harvest.*

Brown bear genotype 1	Country 1	Brown bear genotype 2	Country 2	Notes
LL23	Finland	**12092**	Finland	LL23 was sampled noninvasively 2007 in Finnish Lapland and shot 2015 in Finland (12092).
LL42	Finland	**8884**	Finland	LL42 was sampled noninvasively 2011 in Finnish Lapland (no coordinates) and was shot later, also in 2011, in Finland (8884).
FI112	Norway	**9843**	Finland	FI112 was sampled noninvasively 2010 in Finnmark and shot 2012 in Finland (9843).
FI118	Norway	**12036**	Finland	FI118 was sampled noninvasively 2011,2012,2013, 2014 in Finnmark, shot 2014 in Finland (12036).
FI168	Norway	**M407762**	Sweden	FI168 was sampled noninvasively 2013,2014,2015 in Finnmark (near Anarjohka) and shot 2015 in Norrbotten (M407762).
TR12 BD14-030	Norway	**M001165**	Sweden	TR12 was sampled noninvasively 2008 in Troms and shot 2008 in Norrbotten (M001165).
TR18 BD1370	Norway	**M004683**	Sweden	TR18 was sampled noninvasively 2008, 2009, 2010, 2011 in Troms, sampled noninvasively 2010 in Norrbotten and shot 2012 in Norrbotten (M004683).
TR3 BD14-273	Norway	**M003284**	Sweden	TR3 was sampled noninvasively 2006, 2007, 2008, 2009 in Troms and shot 2010 in Norrbotten (M003284).
TR33 BD14-108	Norway	**M003819**	Sweden	TR33 was sampled noninvasively 2009 in Troms and shot 2011 in Norrbotten (M003819).
TR36	Norway	**M405868**	Sweden	TR36 was sampled noninvasively 2010, 2011, 2012 in Troms and shot 2012 in Norrbotten (M405868).
TR44	Norway	**M407920**	Sweden	TR44 was sampled noninvasively 2013, 2014 in Troms and shot 2015 in Norrbotten (M407920).

Brown bear genotype 1	Country 1	Brown bear genotype 2	Country 2	Notes
BD1035 BD273	Sweden	**M407277**	Sweden	BD273 was sampled noninvasively 2010 in Norrbotten, GPS-collared in 2012 in Norrbotten and shot in 2014 in Norrbotten (M407277).
BD1095 BD268	Sweden	**M405825**	Sweden	BD268 was sampled noninvasively 2010 in Norrbotten, GPS-collared in 2012 and shot 2012 in Norrbotten (M405825).
BD1195 BD265	Sweden	**M406584**	Sweden	BD265 was sampled noninvasively in 2010 in Norrbotten, GPS-collared 2012 and shot 2013 in Norrbotten (M406584).
BD252 NO22	Sweden	**M407016**	Sweden	BD252 NO22 was sampled from marking in Norrbotten in 2011, noninvasively in Nordland, Norway in 2013 and shot in Norrbotten in 2014 (M407016).
BD267	Sweden	**M405846**	Sweden	BD267 has been sampled from marking earlier the same year in Norrbotten and shot 2012 in Norrbotten (M405846).
BD279 BD1186	Sweden	**M406536**	Sweden	BD279 was sampled noninvasively 2010 in Norrbotten, marked in 2013 and shot 2013 in Norrbotten (M406536).

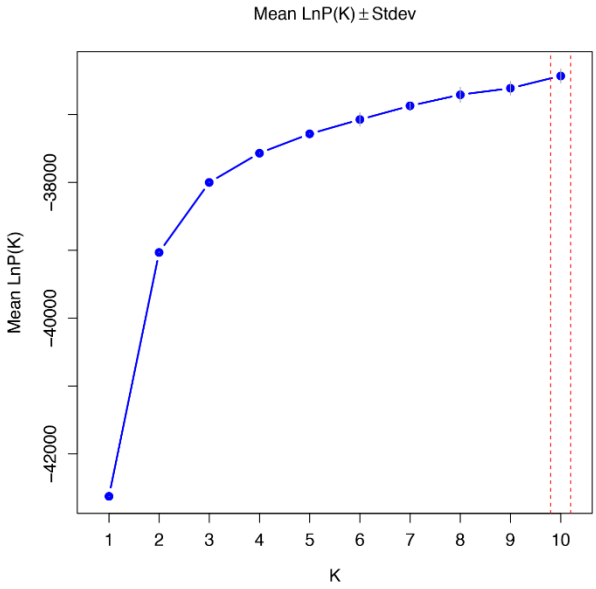

***Figure A1**: Results of the mean likelihood of Bayesian clustering for K=1 to 10 clusters over 10 independent runs of 924 male, northern European brown bears with the program STRUCTURE enabling admixture model and disabled LOCPRIOR option (Pritchard et al. 2000).*

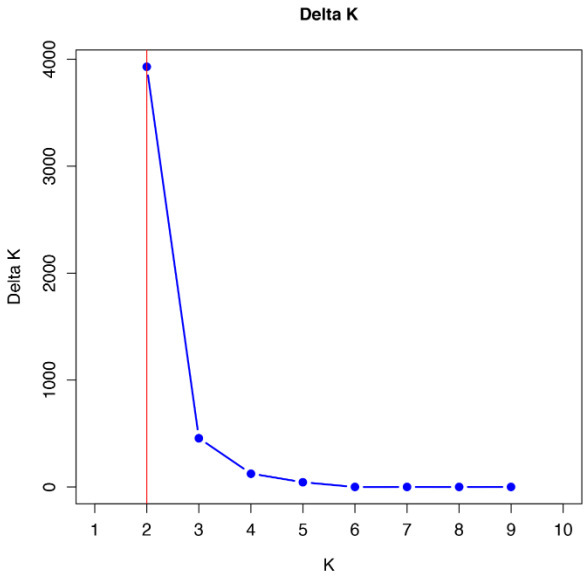

***Figure A2**: Estimate of the most likely number of genetic clusters (ΔK) using the approach described by Evanno et al. (2006).*

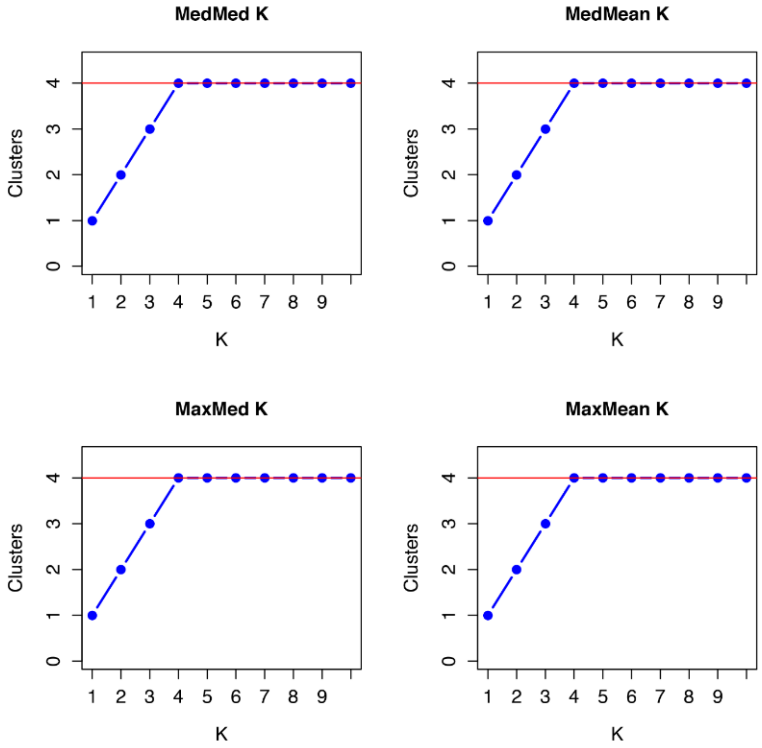

***Figure A3**: Estimate of the most likely number of genetic clusters (K) using the approach described by Puechmaille (2016).*

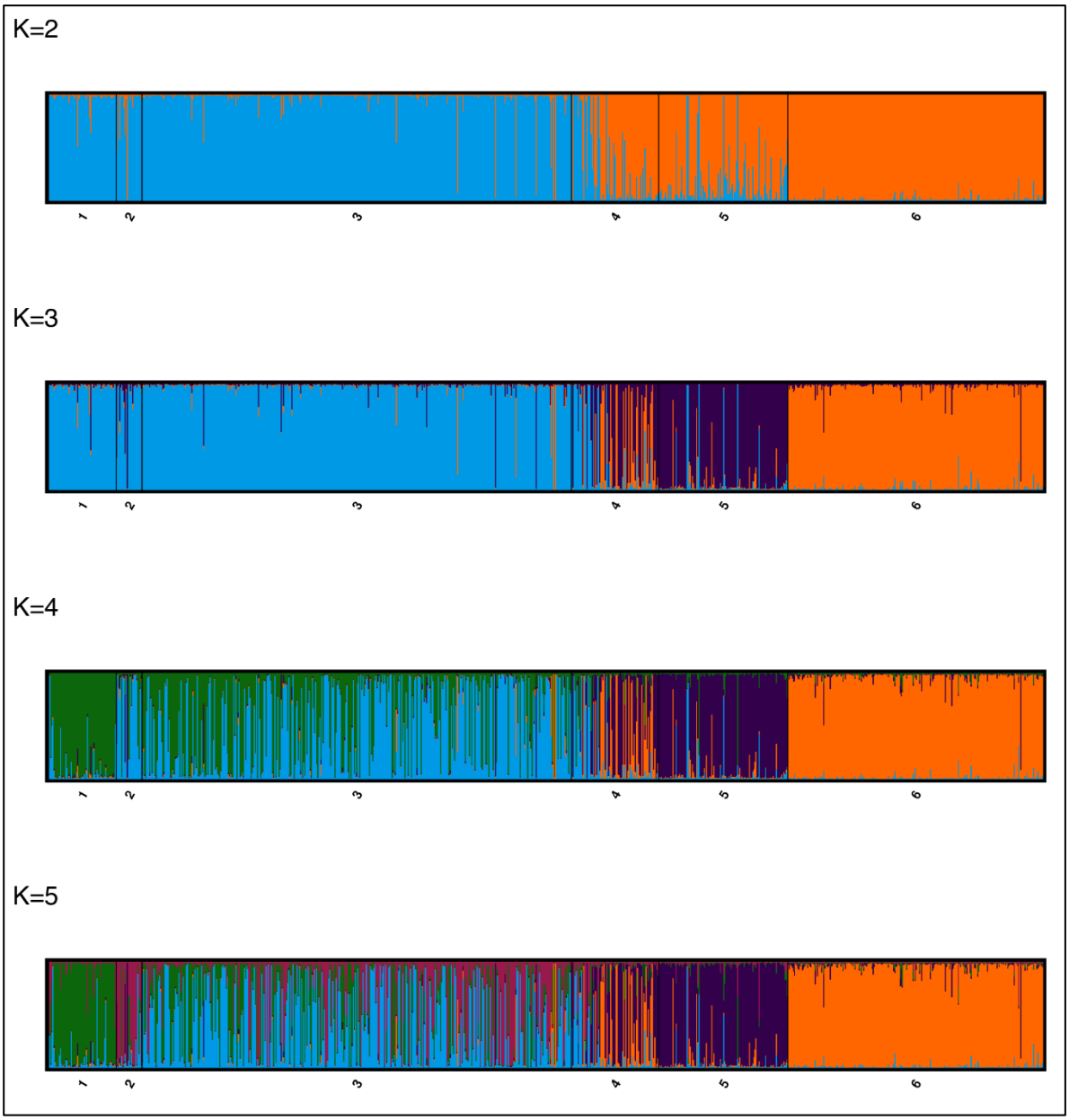

***Figure A4**: Bar plots for K=2-5 of the Bayesian clustering of 924 male, northern European brown bears with the program STRUCTURE and CLUMPAK-averaged outputs for 10 independent runs of the program CLUMPAK (Kopelman et al. 2015). The genotypes are sorted geographically, as described in **Figure 1** and numbers correspond to the sampling areas Västerbotten (1), Troms (2), Norrbotten (3), northern Finland (4), Finnmark (5) and southern Finland (6).*

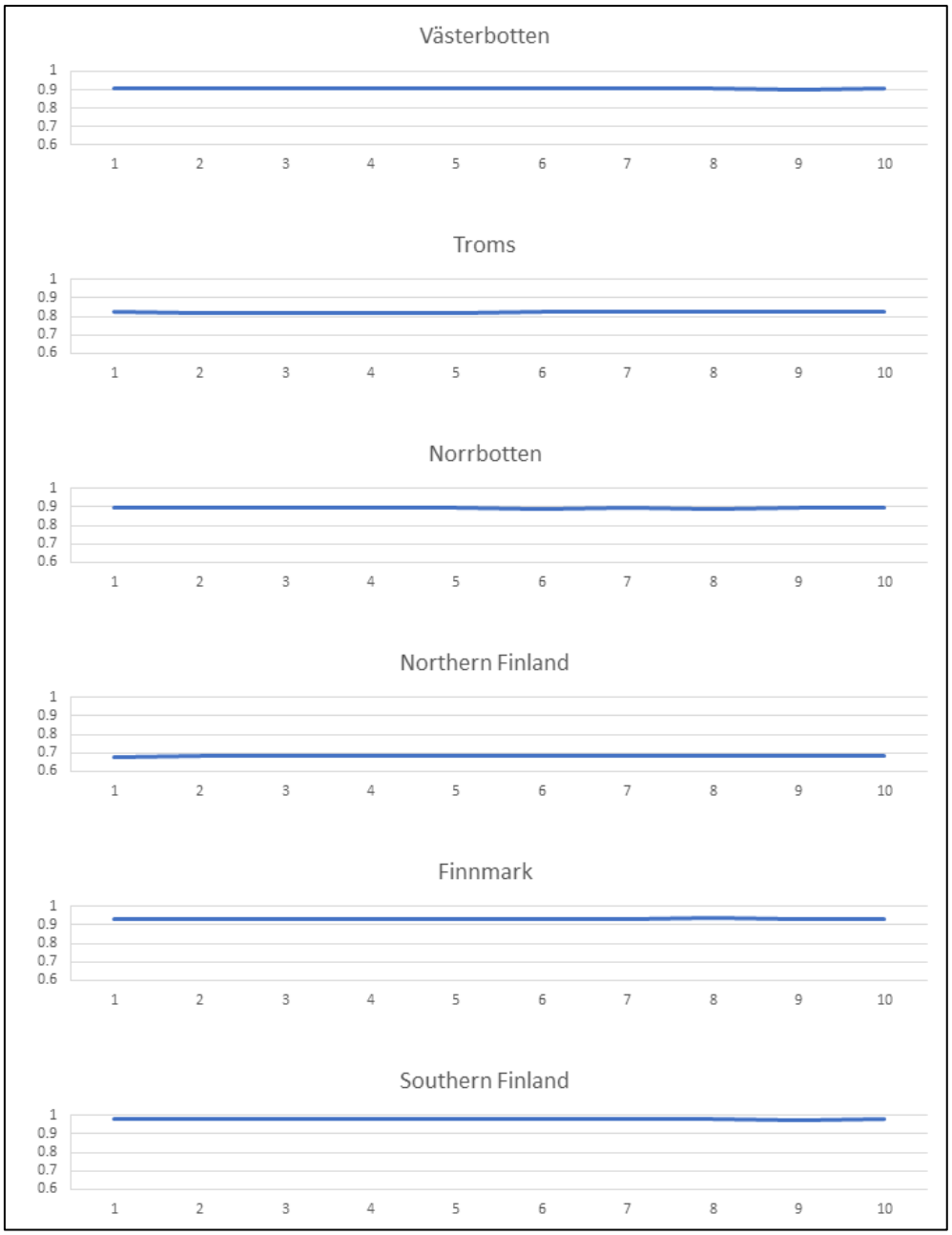

***Figure A5**: Consistency in the estimates of the non-migrant proportion in ten independent runs of BAYESASS (Wilson and Rannala 2003) for male brown bears from six different regions in northern Europe.*

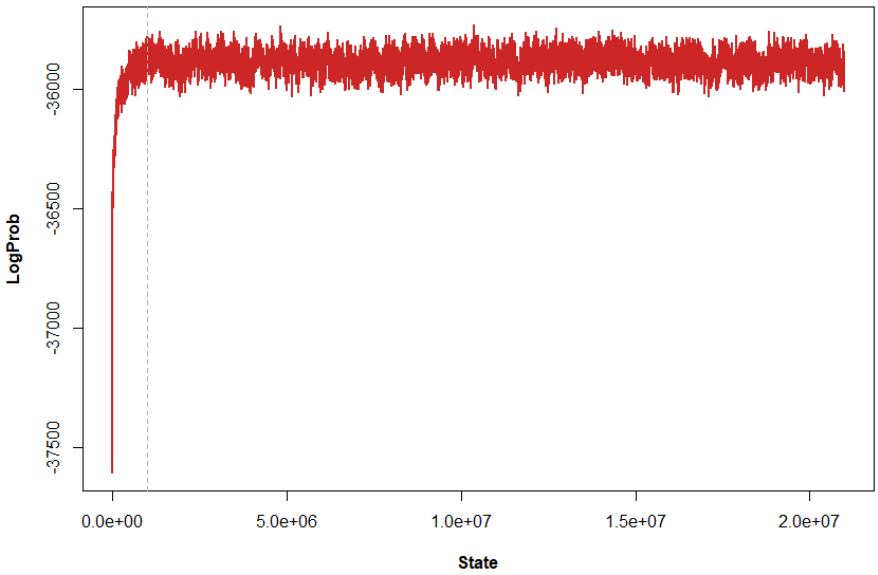

***Figure A6**: Probability for the run used in the results presented for the estimation of self-recruitment and migration among the different regions in northern Europe, estimated using BAYESASS (Wilson and Rannala 2003). Burnin phase indicated by the dotted line (script published by Meirmans 2014).*

***Table A2**: Detected migrants sorted by the region the sample was collected in. Each row represents one individual genotype with its ID and assignment value for the identified genetic clusters by the programs STRUCTURE and BAYESASS. The regions and genetic clusters have the following abbreviations: Västerbotten (VB), Troms (TR), Norrbotten (NB), northern Finland (NF), Finnmark (FM) and southern Finland (SF); the subsequent numbers in the BAYESASS assignment represents non-migrant (0), F0-migrant (1) and F1-migrant (2); see also **Table 3**. Last row shows on how many autosomal STRs have been used in the analyses.*

		STRUCTURE assignment				BAYESASS assignment																	
	ID	VB	NB/TR	NF/FM	SF	VB0	VB1	VB2	TR0	TR1	TR2	NB0	NB1	NB2	NF0	NF1	NF2	FM0	FM1	FM02	SF0	SF1	SF2	STRs
To Norrbotten	NB2010_M003551	0.003	0.004	0.004	0.989	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	12
	NB2013_M406262	0.003	0.002	0.004	0.991	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	12
	NB2013_M406573	0.005	0.008	0.97	0.017	0	0	0	0	0	0	0	0	0	0	0.181	0.054	0	0.727	0.038	0	0	0	12
	NB2015_M407762	0.011	0.008	0.977	0.005	0	0	0	0	0	0	0	0	0	0.001	0	0	0.999	0	0	0	0	0	12
	NB2012_M004696*	0.022	0.222	0.077	0.68	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.001	0.999	12
	NB2008_M004741	0.333	0.253	0.012	0.403	0	0	0.007	0	0.001	0.004	0.001	0	0	0	0	0.001	0	0	0	0	0	0.986	12
	NB2012_M405845	0.017	0.252	0.014	0.716	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.034	0.966	12
	NB2013_M406480	0.012	0.403	0.011	0.574	0	0	0	0	0	0.003	0	0	0	0	0	0.004	0	0	0.022	0	0	0.971	12
To Troms	TR2014_TR50	0.007	0.004	0.978	0.011	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	12
	TR2008_TR25	0.063	0.318	0.607	0.011	0	0	0	0.013	0	0	0	0	0.112	0	0	0.004	0	0.001	0.863	0	0	0.007	12
	TR2016_TR57	0.199	0.154	0.641	0.006	0	0	0.004	0.003	0	0	0	0	0.006	0	0.001	0.05	0	0.032	0.904	0	0	0	8
To northern Finland	FI1997_27_97	0.071	0.881	0.043	0.004	0	0	0.001	0	0	0	0	0.96	0.039	0	0	0	0	0	0	0	0	0	12
	FI2002_2730	0.525	0.461	0.005	0.01	0	0.006	0	0	0	0	0	0.991	0.003	0	0	0	0	0	0	0	0	0	12
	FI2007_6429	0.009	0.96	0.013	0.018	0	0	0	0	0	0	0	0.947	0.053	0	0	0	0	0	0	0	0	0	12
	FI2009_7457	0.876	0.117	0.003	0.004	0	0.002	0	0	0	0	0	0.995	0.003	0	0	0	0	0	0	0	0	0	12
	FI2009_7510	0.013	0.975	0.007	0.005	0	0	0	0	0	0	0	0.955	0.044	0	0	0	0	0	0.001	0	0	0	12
	FI2009_7511	0.309	0.677	0.009	0.005	0	0	0	0	0	0	0	0.996	0.004	0	0	0	0	0	0	0	0	0	12
	FI2011_9041	0.016	0.971	0.005	0.009	0	0	0	0	0	0	0	0.956	0.044	0	0	0	0	0	0	0	0	0	12
	FI2011_9465	0.03	0.959	0.008	0.004	0	0	0	0	0	0	0	0.992	0.008	0	0	0	0	0	0	0	0	0	12
	FI2012_9843_FI112	0.02	0.972	0.005	0.003	0	0.001	0	0	0.311	0	0	0.684	0.004	0	0	0	0	0	0	0	0	0	12
	FI2012_9957	0.025	0.968	0.004	0.003	0	0	0	0	0	0	0	0.998	0.002	0	0	0	0	0	0	0	0	0	12
	FI2013_10977	0.238	0.704	0.033	0.025	0	0	0	0	0	0	0	0.988	0.012	0	0	0	0	0	0	0	0	0	12
	FI2014_12035	0.016	0.961	0.015	0.008	0	0	0.002	0	0	0	0	0.76	0.237	0	0	0	0	0	0.001	0	0	0	12
	FI2015_12103	0.014	0.973	0.008	0.005	0	0	0	0	0	0	0	0.995	0.005	0	0	0	0	0	0	0	0	0	12
	FI2017_13330	0.165	0.827	0.004	0.004	0	0	0	0	0	0	0	0.999	0.001	0	0	0	0	0	0	0	0	0	12
	FI2013_10978	0.031	0.583	0.373	0.013	0	0	0	0	0.946	0.054	0	0	0	0	0	0	0	0	0	0	0	0	12

		STRUCTURE assignment				BAYESASS assignment																
	ID	VB	NB/TR	NF/FM	SF	VB0	VB1	VB2	TR0	TR1	TR2	NB0	NB1	NB2	NF0	NF1	NF2	FM0	FM1	FM02	SF0	SF1	SF2	STRs
	FI1998_209	0.086	0.667	0.214	0.033	0	0	0.064	0	0.022	0.03	0	0.226	0.626	0	0	0	0	0.02	0.012	0	0	0	12
	FI2003_3186	0.546	0.204	0.201	0.049	0	0.002	0.061	0	0	0.007	0	0.067	0.782	0.001	0	0	0	0.004	0.076	0	0	0	12
	FI2013_10595	0.046	0.047	0.485	0.422	0	0	0.004	0	0	0.002	0	0	0.387	0.152	0	0	0	0.028	0.189	0	0.01	0.228	12
	FI2015_12067	0.186	0.253	0.171	0.39	0	0	0.01	0	0	0	0	0.003	0.662	0.019	0	0	0	0.008	0.117	0	0.074	0.107	12
	FI2016_12990	0.02	0.166	0.048	0.767	0	0	0.003	0	0	0.057	0	0	0.438	0.109	0	0	0	0	0.014	0	0.017	0.362	12
	FI2017_13329	0.011	0.125	0.848	0.016	0	0	0.001	0	0	0.016	0	0	0.702	0.003	0	0	0	0.079	0.198	0	0	0.001	12
	FI2017_13389	0.491	0.075	0.141	0.293	0	0	0.048	0	0	0.016	0	0.013	0.437	0.03	0	0	0	0	0.013	0	0.109	0.334	12
	FI2007_LL026	0.686	0.282	0.022	0.01	0	0	0.005	0	0	0.005	0	0.221	0.762	0	0	0	0	0	0.007	0	0	0	12
	FI2010_8332	0.229	0.134	0.231	0.405	0	0	0.664	0	0	0.15	0	0	0.124	0.007	0	0	0	0	0.017	0	0	0.038	12
To Finnmark	FM2011_FI124+	0.149	0.838	0.006	0.006	0	0	0	0	0.001	0	0	0.997	0.002	0	0	0	0	0	0	0	0	0	12
	FM2016_FI212+	0.158	0.774	0.057	0.011	0	0.001	0.001	0	0	0	0	0.759	0.097	0	0.065	0.073	0.004	0	0	0	0	0	12
	FM2008_FI079	0.076	0.909	0.011	0.004	0	0	0	0	0.985	0.011	0	0.001	0.003	0	0	0	0	0	0	0	0	0	8
	FM2015_FI178	0.861	0.132	0.004	0.003	0	0.001	0	0	0.979	0	0	0.02	0	0	0	0	0	0	0	0	0	0	12
	FM2007_FI062	0.772	0.219	0.004	0.005	0	0.006	0	0	0	0	0	0.993	0.001	0	0	0	0	0	0	0	0	0	12
	FM2010_FI099	0.097	0.095	0.567	0.242	0	0	0.019	0	0	0.008	0	0	0.655	0	0.002	0.082	0.223	0	0	0	0.001	0.01	12
	FM2011_FI123_LL43	0.06	0.376	0.551	0.013	0	0	0.002	0	0	0.003	0	0.004	0.775	0	0	0.013	0.203	0	0	0	0	0	12
	FM2011_FI130_LL32	0.068	0.508	0.371	0.053	0	0	0.001	0	0	0.01	0	0	0.978	0	0	0.005	0.006	0	0	0	0	0	12
	FM2015_FI179	0.144	0.419	0.406	0.031	0	0	0.003	0	0.008	0.919	0	0	0.069	0	0	0	0.001	0	0	0	0	0	12

** Individual has been sampled non-invasively in FM and harvested legally in NB.*

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NINA Report

The Norwegian Institute for Nature Research, NINA, is as an independent foundation focusing on environmental research, emphasizing the interaction between human society, natural resources and biodiversity.

NINA was established in 1988. The headquarters are located in Trondheim, with branches in Tromsø, Lillehammer, Bergen and Oslo. In addition, NINA owns and runs the aquatic research station for wild fish at Ims in Rogaland and the arctic fox breeding center at Oppdal.

NINA's activities include research, environmental impact assessments, environmental monitoring, counselling and evaluation. NINA's scientists come from a wide range of disciplinary backgrounds that include biologists, geographers, geneticists, social scientists, sociologists and more. We have a broad-based expertise on the genetic, population, species, ecosystem and landscape level, in terrestrial, freshwater and coastal marine ecosystems.

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