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Potential for increased connectivity between differentiated wolverine populations

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ABSTRACT

Information on genetic population structure provides important knowledge for species conservation. Yet, few studies combine extensive genetic data to evaluate the structure and population dynamics of transboundary populations. Here we used single nucleotide polymorphisms (SNPs), microsatellites and mitochondrial haplotypes to analyze the genetic population structure of wolverines (*Gulo gulo*) across Fennoscandia using a long-term monitoring dataset of 1708 individuals. Clear population subdivision was detected between the Scandinavian and the eastern Finnish population with a steep cline in the contact zone. While the Scandinavian population showed isolation by distance, large swaths of this population were characterized by high connectivity. Areas with high resistance to gene flow are likely explained by a combination of factors, such as historical isolation and founder effects. From a conservation perspective, promoting gene flow from the population in eastern Finland to the northwest of Scandinavia could augment the less variable Scandinavian population, and increase the demographic resilience of all subpopulations. Overall, the large areas of low resistance to gene flow suggest that transboundary cooperation with aligned actions of harvest and conflict mitigation could improve genetic connectivity across Finland, Sweden, and Norway.

1. Introduction

Genetic diversity is fundamental for both the short-term and long-term viability, and thus resilience of a population or a species (Frankham, 2005). Genetic diversity is influenced by a multitude of factors, one of which is fragmentation of populations. Fragmentation potentially causes limited connectivity among populations, leading to isolation. Knowledge of the genetic composition and connectivity of a species or population is therefore crucial for its conservation and management (Laikre et al., 2009). One way to study genetic variation is to assess the population structure, and how the degree of structuring is enhanced by limited genetic connectivity and thus low gene flow among regions. Low gene flow can have a direct impact on evolutionary and ecological processes within subpopulations, causing loss of adaptive potential and increase of deleterious effects of inbreeding and drift (Lowe and Allendorf, 2010). Movement of individuals, e.g. due to (natal) dispersal, followed by settlement and reproductions of these dispersers, can lead to exchange of genetic material between different populations. Increasing dispersal then can result in constant exchange of individuals and thus high genetic connectivity safeguarding long-term genetic benefits for

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the populations (Lowe and Allendorf, 2010).

All populations are genetically structured at different spatial scales (Chakraborty, 1993). Thus, one of the key aspects of conservation genetics is to identify the relevant scale of subdivision occurring and where conservation measures can be most effectively applied to preserve genetic variation (Anderson et al., 2010). The relevant spatial scale varies depending on the ecology of the focal species, which will be reflected in the genetic structure. Considering large carnivores, for example, genetic structure needs to be studied on adequate geographic scales to account for potential large home range sizes and long-distance dispersal capacities (Anderson et al., 2010; Cayuela et al., 2018). Such factors can lead to spatial population subdivision reflected by large-scale genetic clusters further shaped by historical events (e.g. post-glacial recolonization: Taberlet et al., 1998; Hewitt, 1999), natural barriers (e.g. large open waters: Hapeman et al., 2011), anthropogenic disturbances (e.g. habitat fragmentation caused by resource extraction: Singh et al., 2017), and ecological heterogeneity (Dures et al., 2020). As an example, the population structure in the continuous range of moose (*Alces alces*) reflects a bidirectional recolonization of Fennoscandia; from the east via Russia and from the southwest via Western Europe (Kangas et al., 2015). On the other hand, genetic structure might also prevail due to anthropogenic effects, such as regional variation in harvest rates. For example, large carnivores are regularly legally harvested in the reindeer husbandry area in northern Finland to mitigate for depredation losses on semi-domesticated reindeer (Kojola et al., 2006; Kopatz et al., 2021), but not in regions outside the reindeer husbandry area.

In addition to such large-scale genetic structures reflecting population subdivision, local processes (e.g. territoriality or family group structures) may impact gene flow resulting in fine-scale genetic clusters (Schregel et al., 2018). Recently developed methodologies can reveal these fine-scale genetic clusters within populations, using, for example, deviations from the isolation by distance (IBD) trend (Keis et al., 2013; Tang et al., 2019), a pattern where genetic differentiation increases with geographic distance (Wright, 1943). IBD residuals can be used to reveal areas with restricted and enhanced gene flow. Such IBD resistance mapping has proven useful to pinpoint the key areas of interest to preserve or stimulate genetic diversity (Schregel et al., 2018).

Assigning genetic population structure based on Bayesian clustering methods might be challenging when sampling is discontinuous (Bradburd et al., 2018), which is a common feature while studying animals in the wild using non-invasive methods. Spurious genetic clusters might be detected, especially when IBD is present (Frantz et al., 2009; Schwartz and McKelvey, 2009). To illustrate, studies on brown bears (*Ursus arctos*) using nuclear DNA revealed genetic clustering within an otherwise continuous Fennoscandian range without obvious geographical barriers (Kopatz et al., 2014; Schregel et al., 2017). However, a more recent study using IBD resistance mapping demonstrated that part of the structure was an artefact of IBD (Schregel et al., 2018).

As a typical representative species of the northern taiga and tundra, the wolverine (*Gulo gulo*) is relatively widespread throughout the northern parts of Fennoscandia (Fig. 1), although at low densities (Chapron et al., 2014). Like all large carnivores in northern Europe, wolverines declined dramatically during the 20th century but have gradually recovered, likely due to complete national protection in 1968 in Sweden, and in 1982 in Norway and Finland (Chapron et al., 2014; Persson et al., 2015). The current distribution is geographically continuous within Fennoscandia and eastwards. Estimates of present numbers (in 2021) are 390–400 individuals in Finland (mainly based on winter wildlife triangle counts; Kojola et al., 2021), 639–724 individuals in Sweden and 358–418 in Norway (obtained using genotype-based capture-recapture modelling; Kleven et al., 2022). Population numbers east of Fennoscandia are much more uncertain, but are estimated to 450–610 individuals in north-western Russia (combining estimates of two regions from Danilov et al., 2018). Two populations are defined in EU policy (Boitani et al., 2015), the Karelian and the Scandinavian population (Fig. 1b). Population genetic studies on Fennoscandian wolverines have revealed that genetic variation and effective population sizes are low (Walker et al., 2001; Ekblom et al., 2018; Lansink et al., 2020; Sugiyama et al., 2022). In Fennoscandia, wolverines have low mitochondrial diversity with a single haplotype found throughout Scandinavia (Walker et al., 2001; Ekblom et al., 2014) and one additional in Finland (Lansink et al., 2020). Two genetic clusters have been detected within Finland based on microsatellites, separating northern and eastern Finland (Lansink et al., 2020). In addition, a small population in south-western Finland was found to carry the genetic signature of northern Finland due to translocations that were conducted between

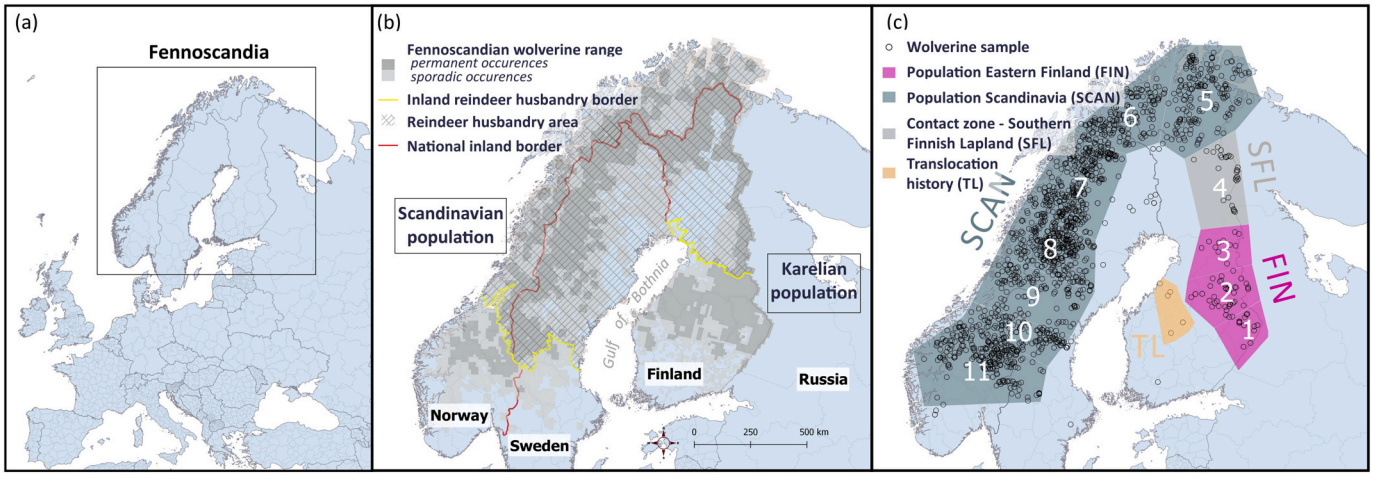

Fig. 1. Location of the study area, Fennoscandian wolverine range and multi-year DNA-based sampling scheme. a) Map of Europe indicating Fennoscandia. b) The wolverine range in Fennoscandia with two populations as defined in EU policies (Boitani et al., 2015). The wolverine range for 2012–2016 is depicted at a 10 × 10 km grid scale with permanent occurrences (i.e. reproducing individuals documented) in dark grey and sporadic occurrences (i.e. wolverine presence without documented reproductive events) in beige following Kaczensky et al. (2021). The southern borders of the reindeer husbandry area (crossed pattern) are marked in yellow. National inland borders for Finland, Norway and Sweden are marked in red. c) Map of study area including all wolverine sample locations ($N = 1708$) and the pre-defined sampling regions. The 11 sampling regions follow the continuity of the population throughout Fennoscandia. A separate region "TL" (yellow) represents a region with translocation history in western Finland. The geographically continuous sampling regions are coloured by populations Scandinavia (dark grey) and eastern Finland (pink), aside from the contact zone in southern Finnish Lapland (light grey). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

1979 and 1998 (Lansink et al., 2020).

The previous studies on genetic population structure of wolverines in Fennoscandia were conducted either on a national scale (Lansink et al., 2020) or within one population (Walker et al., 2001; Flagstad et al., 2004; Ekblom et al., 2018). To examine the genetic population structure of wolverines across Fennoscandia, we took advantage of an extensive dataset including 1708 individuals, predominantly non-invasively sampled throughout Finland, Norway and Sweden during the last two decades. This data set was available from present, transboundary collaborative DNA-based monitoring and data sharing among these countries (e.g. Gervasi et al., 2016; Bischof et al., 2020). We specifically investigated if the patterns of population structure could have emerged purely via the effect of geographic distance on genetic variation (i.e. IBD) or if they reflect population subdivision on one or multiple scales, or are a combination of both. Our study illustrates the importance of transboundary collaboration to conserve the wolverine, which is listed as *Endangered* in Norway (Henriksen and Hilmo, 2015) and Finland (Hyvärinen et al., 2019), and *Vulnerable* in Sweden (Swedish Species Information Centre, 2020).

2. Material and methods

2.1. Sampling

Wolverine samples in Finland, Norway and Sweden were collected through non-invasive, nationwide monitoring programs focusing on scat, hair, and urine collection (Fig. 1c) (Bischof et al., 2020; Lansink et al., 2020). Tissue samples from dead individuals were also included. The majority (96%) of the samples were collected between 2009 and 2019, while the remaining samples were from 1999 to 2008. Wolverine generation time is approximately six years (Rauset et al., 2015), thus, samples were mainly from the two most recent wolverine generations. The older samples were both from Sweden and Finland (Table S1). DNA from the samples was extracted with various established protocols using commercial kits (Appendix A Supplementary data, Sampling).

2.2. Molecular analyses

A total of 1708 individuals (Sweden ($N = 815$); Norway ($N = 705$); Finland ($N = 188$)) were genotyped with a recently developed Fluidigm SNP array (G. Spong, O. Kleven, Ø. Flagstad, A. Norman, B. Schiffthaler, I. Kojola, S. Kokko, J. Kindberg, unpublished data). Briefly, the SNP array consisted of 96 single nucleotide polymorphisms (SNPs), including one polymorphic mitochondrial marker (16S rRNA), three monomorphic Y-chromosome markers used for sexing and 92 autosomal markers. The autosomal SNPs had been identified by Restriction site Associated DNA (RAD) sequencing 96 wolverines from across Fennoscandia and selected primarily based on high minor allele frequency (>0.2) to facilitate individual identification and relatedness estimation. The samples were genotyped on a 96.96 Dynamic Array using the Fluidigm Biomark or EP1 instrument according to the manufacturer's protocol and scored using the Fluidigm SNP genotyping analysis software.

All individuals included were previously genotyped with at least 14 wolverine- or mustelid-specific microsatellite loci (for details see Lansink et al., 2020). For non-invasive samples, a consensus genotype was created based on at least three independent PCR replicates. To calibrate microsatellite genotypes across laboratories, 16 Finnish individuals were genotyped in both Norway and Finland, and 10 Finnish individuals in both Sweden and Finland. For calibration between the laboratories in Norway and Sweden, 20 Norwegian wolverines were genotyped in both laboratories. After quality control (Appendix A Supplementary data, Molecular analyses), the final dataset consisted of 88 autosomal SNPs, 1 mitochondrial SNP and 11 microsatellites (Table S2).

Individuals were grouped into 11 sampling regions following the continuity of the wolverine range throughout Fennoscandia (Fig. 1c; Fig. S1). The sampling regions were designed to compare the population structure analyses with the IBD analysis, while incorporating prior knowledge on population subdivision and translocation history (Lansink et al., 2020). Sampling region 4 represents southern Finnish Lapland, which was previously identified as a contact zone between two genetic clusters (Lansink et al., 2020). A separated sampling region TL represents a western Finnish region with translocation history (Lansink et al., 2020). The sampling regions were further pooled into populations in eastern Finland (1–3) and Scandinavia (5–11), supported by the results of the population structure analyses in this study and, thus, for consistency between analyses in this study, we did not modify the prior groupings (Fig. 1c).

2.3. Population structure

The geographic distribution of mitochondrial haplotypes based on one 16S SNP locus was visualized using software QGIS (QGIS Development Team, 2018). Further genetic population structure was determined by applying model-free clustering methods for both autosomal SNPs and microsatellites, as non-Bayesian methods fit well to geographically continuously distributed populations (Manel et al., 2005) and do not follow any particular genetic model (Jombart et al., 2008; Jombart et al., 2010). We used two multivariate methods, the discriminant analysis of principal components (DAPC) (Jombart et al., 2010) and spatial principal component analysis (sPCA) (Jombart et al., 2008) both implemented in the package adegenet v 2.1.2 (Jombart, 2008) in software R (R Core Team, 2020). Additionally, population differentiation was estimated with G_{ST} (Nei, 1973; Nei, 1978) and Jost's D_{est} (Jost, 2008) using the R package MMOD (Winter, 2012). Based on microsatellites, genetic diversity was estimated for each population by the observed (H_O) and expected heterozygosities (H_E), allelic richness (A_R) and private allelic richness (A_P) using Genalex v. 6.5 (Peakall and Smouse, 2012) and HP-rare v.6–2006 (Kalinowski, 2005) (Appendix A Supplementary data, Population structure).

2.4. IBD

The relationship between geographic and genetic distance was assessed for SNPs and microsatellites using pairwise $F_{ST}/(1\text{-}F_{ST})$ (Rousset, 1997) and the logarithm of genetic distance (Slatkin, 1993) in Spagedi v. 1.5 (Hardy and Vekemans, 2002). Pairwise $F_{ST}/(1\text{-}F_{ST})$ estimates were calculated for the geographically continuous 11 sampling regions and geographic distances were calculated around the Gulf of Bothnia (Appendix A Supplementary data, IBD - Fig. S1).

2.5. IBD resistance mapping

A test for spatial autocorrelation in our dataset was performed to approximate the scale of spatial genetic structure (Anderson et al., 2010) within Fennoscandia. Global multilocus kinship correlograms using Nason's F_{ij} (Loiselle et al., 1995; Kalisz et al., 2001) were constructed for both populations (eastern Finland and Scandinavia) for SNPs and microsatellites with the R package EcoGenetics v. 1.2.1–5 (Roser et al., 2017).

The R package ResDisMapper (Tang et al., 2019) was used to assess regions of potential high and low IBD residuals throughout the Fennoscandian wolverine range. To incorporate the population structure within Fennoscandia, IBD resistance mapping was applied also separately for the two populations; Scandinavia and eastern Finland. In IBD resistance mapping, areas where significantly positive IBD residuals coalesce represent regions where gene flow is hindered (Tang et al., 2019). On the other hand, areas with significant negative IBD residuals facilitate gene flow. For both microsatellites and SNPs, each population was tested with the recommended six genetic distance methods and linear vs. non-linear IBD trend lines (Appendix A Supplementary data, IBD Resistance mapping).

2.6. Assignment accuracy

The assignment accuracy of the populations was tested for both types of markers using principal component analyses and Monte-Carlo cross-validation, as implemented in the R package assignPOP (Chen et al., 2018). Further, we examined how individuals were assigned in the contact zone of southern Finnish Lapland (4) and in western Finland (TL [translocation history]), and we tested the ability of the assignment to detect substructure within Scandinavia (Appendix A Supplementary data, Assignment accuracy).

3. Results

3.1. Population structure

The single mitochondrial 16S SNP marker separated Scandinavia from eastern Finland (Fig. 2). Two geographically clustered mitochondrial SNP haplotypes were detected with a contact zone in Finland.

Discriminant analysis of principal components (DAPC) suggested large-scale clustering in Scandinavia following a geographic cline while clearly separating southeastern Finland from other parts of the range using the autosomal SNPs and microsatellites (Fig. 3; Fig. S2). The first discriminant function (50.6% of total variance for SNPs - 40.5% for microsatellites) divided southeastern Finland from Scandinavia. The contact zone of the two populations is located approximately in southern Finnish Lapland (i.e. sampling region 4; Fig. 1c). Using SNP data, individuals ($N = 8$) from western Finland (TL) either grouped with one of the populations or occurred in between them (Fig. 3), but when using microsatellites, they grouped mostly with the Scandinavian population (Fig. S2). The second discriminant function grouped south-western Scandinavia nearby southeastern Finland for both SNPs and microsatellites. DAPC without prior groupings supported the main results by forming a separated genetic cluster of wolverines from southeastern Finland for both marker sets (Fig. S3). Spatial principal component analysis (sPCA) revealed the same pattern as DAPC and separated southeastern Finnish individuals from Scandinavian individuals (Appendix A Supplementary data, sPCA - Fig. S4–S7).

Pairwise comparison between eastern Finland and Scandinavia resulted in an estimate of population differentiation for SNPs of $G_{ST} = 0.092$ (95% CI = 0.088–0.096) and Jost's $D_{est} = 0.151$ (95% CI = 0.145–0.156), while for microsatellites of $G_{ST} = 0.067$ (95% CI = 0.057–0.076) and Jost's $D_{est} = 0.164$ (95% CI = 0.141–0.187). Genetic

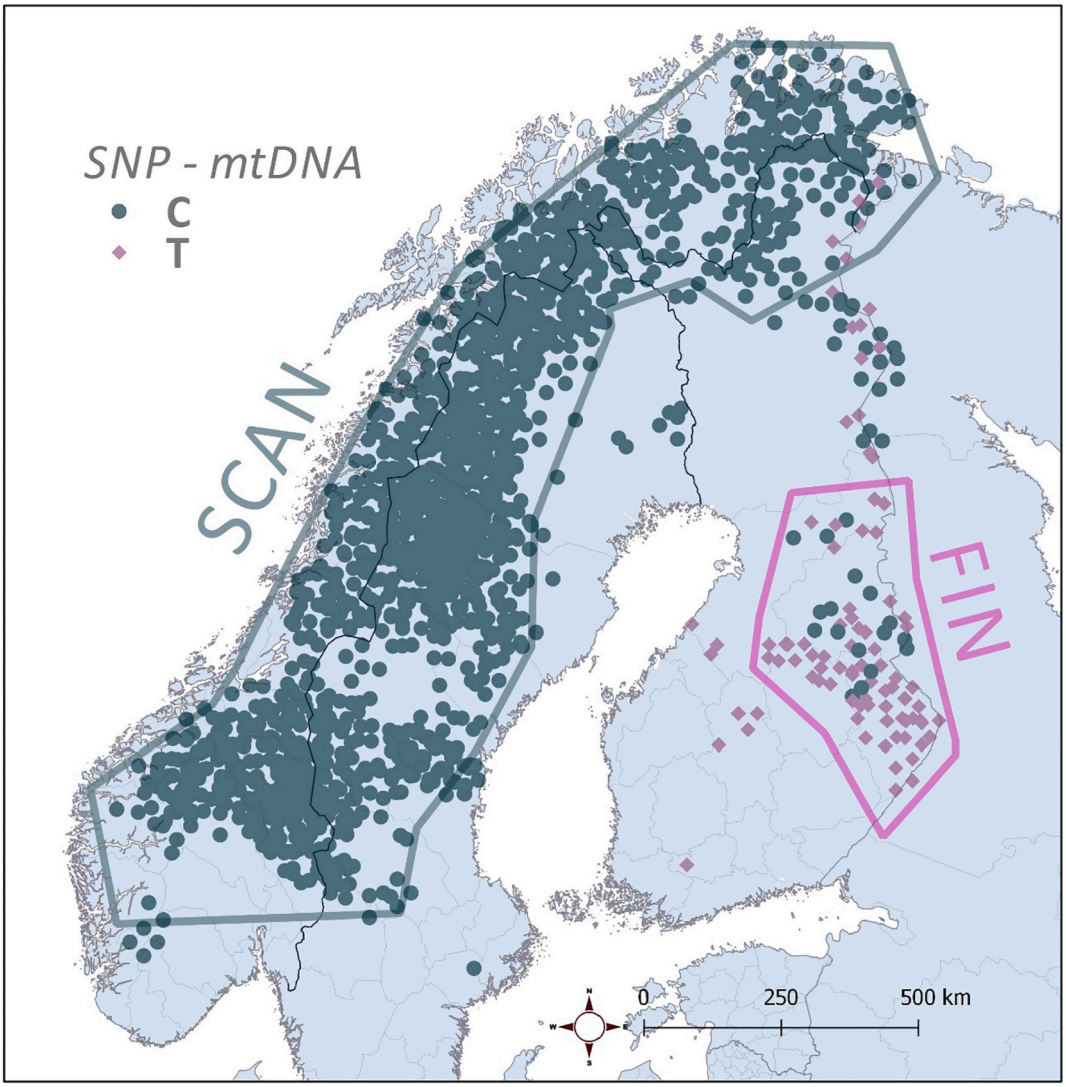

Fig. 2. Geographical distribution of two different haplotypes (C = dark grey dots and T = pink squares) detected by a single mitochondrial 16S SNP marker for 1708 wolverine individuals in Fennoscandia. The Scandinavian (SCAN) and the eastern Finland (FIN) populations are depicted by coloured outlines following the predefined sampling regions. Nearby samples were visualized using point displacement. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

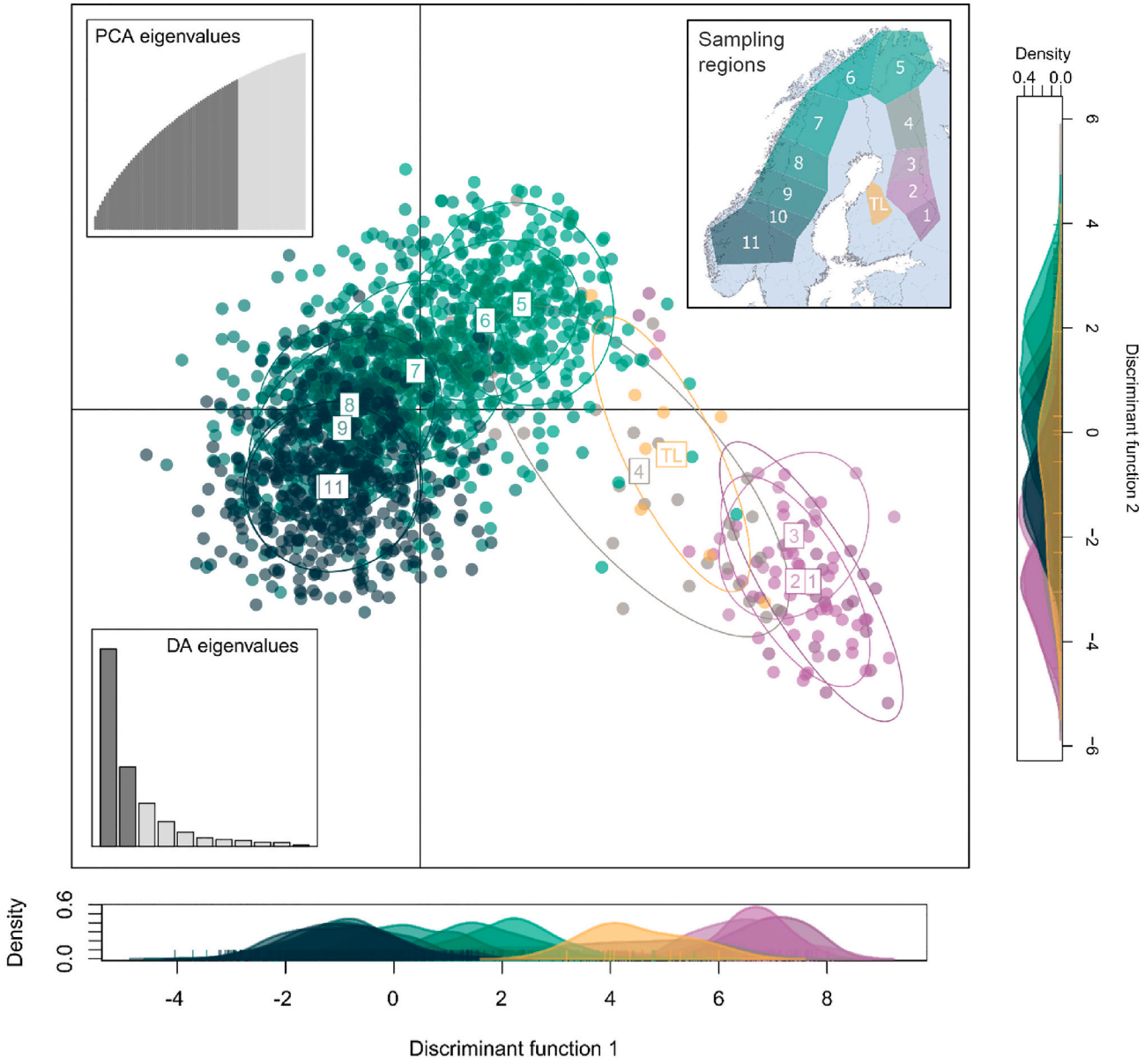

Fig. 3. Results of discriminant analysis of principal components (DAPC) for wolverines ($N = 1701$) in Fennoscandia using 88 SNPs with, as prior groupings, the pre-defined sampling regions. Scatter plot shows the first two discriminant functions explaining 50.6% (function 1) and 20.4% (function 2) of the total variance. Each dot represents an individual, which is coloured by sampling region. Arbitrarily chosen sampling regions follow the Fennoscandian wolverine range geographically (insert top right). Sampling regions in the scatter plot are emphasized by ellipses with the same colours. Sampling region "TL" represents the western Finnish region with translocation history. The ellipse and label of sampling region "11" cover to a large extent sampling region "10" due to high similarity. The top left and bottom left inserts show the PCA eigenvalues and DA eigenvalues, where the retained eigenvalues are in dark grey. Both discriminant functions are depicted separately besides the corresponding axes of the main plot. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

diversity based on microsatellites was higher in eastern Finland ($H_O = 0.554$, $H_E = 0.558$, $A_R = 3.45$, $A_P = 0.57$) than in Scandinavia ($H_O = 0.490$, $H_E = 0.509$, $A_R = 3.25$, $A_P = 0.36$).

3.2. Isolation by distance

We found a significant pattern of IBD among the geographically continuous sampling regions with both SNPs ($R^2 = 0.453$; $b = 0.097$; $P < 0.001$) and microsatellites ($R^2 = 0.392$; $b = 0.073$; $P < 0.001$) (Fig. 4). When grouping the sampling regions according to pre-defined populations (i.e. eastern Finland and Scandinavia), while excluding the intermediate sampling region in southern Finnish Lapland, the IBD model fitted better, though with a gentler IBD regression slope. The IBD regression slope was with SNPs ($R^2_{FIN} = 0.830$; $b_{FIN} = 0.033$; $P_{FIN} = 0.336$ vs. $R^2_{SCAN} = 0.786$; $b_{SCAN} = 0.032$; $P_{SCAN} < 0.001$) and with microsatellites ($R^2_{FIN} = 0.375$; $b_{FIN} = 0.031$; $P_{FIN} = 0.335$ vs. $R^2_{SCAN} = 0.702$; $b_{SCAN} = 0.040$; $P_{SCAN} = 0.001$). Within the Scandinavian population, the northern sampling regions were most differentiated from the central and southern ones with SNPs (Fig. 4). The sampling region of southern Finnish Lapland was genetically more similar to eastern Finland in SNP data, while it was more similar to the Scandinavian population in microsatellite data (Fig. 4).

3.3. IBD resistance mapping

The spatial autocorrelation tests revealed that pairwise distances within 350 km were the most relevant to explain spatial structure for wolverines in Scandinavia, whereas clustering took place on a smaller

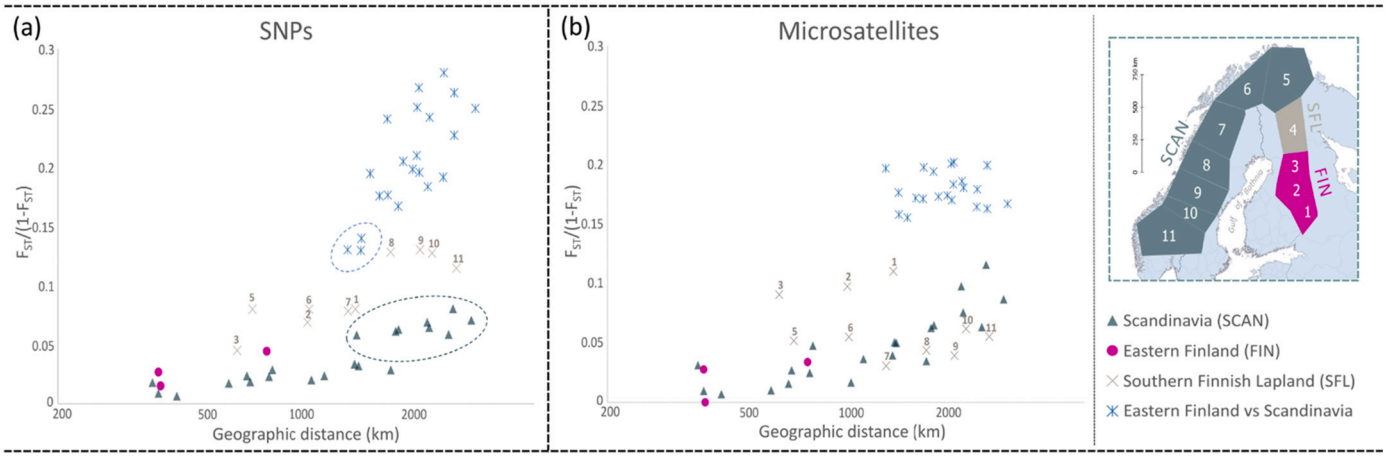

Fig. 4. Geographic distance in relation to genetic distance on a logarithmic scale between 11 arbitrarily defined sampling regions (see map insert) for Fennoscandian wolverines using a) 88 SNPs (N = 1693) and b) 11 microsatellites (N = 1612). Pairs of sampling regions are depicted by comparisons within populations (i.e. Scandinavia [SCAN] and eastern Finland [FIN]) and between populations, except for Southern Finnish Lapland (SFL). For SFL, each pair is numbered according to the paired region to illustrate the difference between SNPs and microsatellites. In a) the sample pairs within the dark-striped oval consist of the most northern Scandinavian sampling regions (5 and 6) vs. central and southern Scandinavian sampling regions (8, 9, 10, 11). The sample pairs within the blue-striped oval consist of between-populations comparisons of the most northern eastern Finland sampling region (3) vs most northern Scandinavian sampling region (5, 6, 7). In b), one pairwise estimate was negative but marked as zero. The Gulf of Bothnia was defined as non-traversable when calculating the geographic distances. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

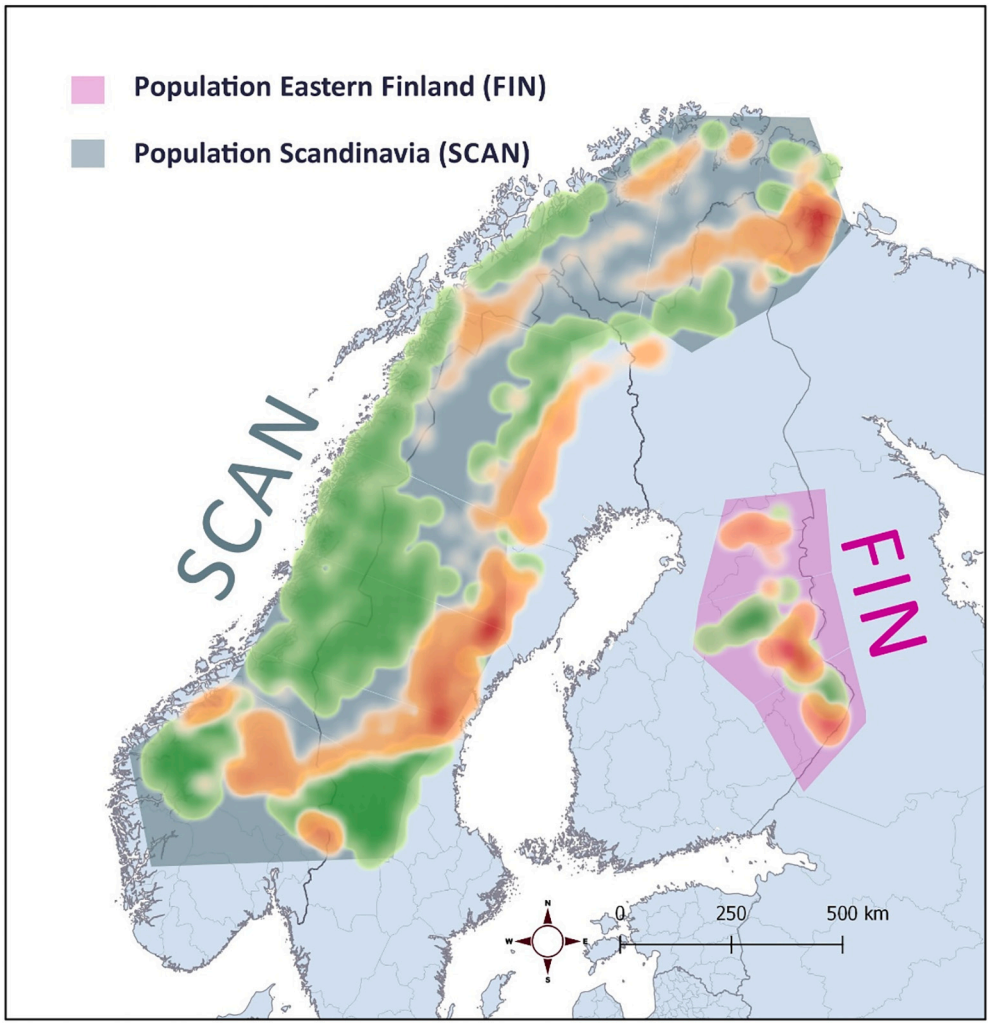

Fig. 5. Combined results of IBD resistance mapping for two Fennoscandian wolverine populations following the ResDisMapper method using 88 SNPs. IBD residual-based resistances were calculated using pairs of individuals sampled within 350 km for Scandinavia (N = 1580) and 100 km for eastern Finland (N = 83). The IBD residuals were taken from an IBD plot using Reynolds' distance and a non-linear trend line for Scandinavia, while Prevostís distance and a linear trend line were used for eastern Finland. The Scandinavian (dark grey) and the eastern Finland (pink) populations are depicted by polygons following the predefined sampling regions. The map consists of areas of statistically high (orange, red) and low (green) resistance to gene flow areas. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

scale within eastern Finland (<100 km) (Fig. S9 and S10). The IBD resistance mapping on both complete data sets, with various genetic distance methods and sample pair distances, supported the population structure results in Section 3.1 (Fig. S11-S16). A high resistance area (i.e. significant positive IBD residuals) was detected between eastern Finland and northern Fennoscandia, and an additional resistance area was detected in western Finland (Fig. S13–S16).

Analyzing the two populations separately, the IBD resistance mapping revealed several regions of high and low resistance departing from the general IBD trend within both populations (Fig. 5; Fig. S17–S24). In the Scandinavian population, a significantly high resistance area was detected with SNPs separating southwestern Norway as well as southern Scandinavia from the rest of Scandinavia, which was otherwise predominantly characterized by low resistance (i.e. significantly negative IBD residuals) (Fig. 5; Fig. S18). The eastern lowland edge of Scandinavia was mostly an area of high resistance. In northern Scandinavia, areas of high resistance were found in the northern border area of Sweden and Norway, and Norway and Finland. With microsatellites, the IBD resistance mapping revealed few similarities with SNPs, instead resistance mapping seemed to be interrupted by a strong north-south trend and only few regions were statistically significant (Fig. S20). In eastern Finland, two regions of low resistance alternated with areas of high resistance irrespective of the marker set used (Fig. 5; Fig. S22–S24).

3.4. Assignment accuracy

Individuals from populations in eastern Finland and Scandinavia were accurately assigned to their population of origin using the 88 SNPs ($mean_{FIN}$ = 97%, SD_{FIN} = 4%; $mean_{SCAN}$ = 99%, SD_{SCAN} = 0%) (Fig. S25), while cross-assignment was very low ($mean_{FIN->SCAN}$ = 3%, $SD_{FIN>SCAN}$ = 4%; $mean_{SCAN->FIN}$ = 1%, $SD_{SCAN->FIN}$ = 0%). For the 11 microsatellites, self-assignment to populations was less accurate ($mean_{FIN}$ = 70%, SD_{FIN} = 16%; $mean_{SCAN}$ = 61%, SD_{SCAN} = 10%) and cross-assignment more likely ($mean_{FIN->SCAN}$ = 30%, $SD_{FIN>SCAN}$ = 16%; $mean_{SCAN->FIN}$ = 39%, $SD_{SCAN->FIN}$ = 10%) (Fig. S26).

Individuals from southern Finnish Lapland were assigned with the SNPs to population eastern Finland (mean = 37%) or to Scandinavia (mean = 63%), though without detecting a geographic cline (Fig. S27). Wolverines (N = 8) from western Finland were strongly assigned to Scandinavia using the SNPs (mean = 87%) (Fig. S28). Dividing the dataset into five subpopulations, the highest assignment accuracy was for eastern Finland (mean = 93%, SD = 2%), followed by northern Scandinavia (mean = 79%, SD = 5%) and southern Scandinavia (mean = 67%, SD = 14%), whereas lower assignment accuracies were detected in southwestern Norway (mean = 58%, SD = 15%) and central Scandinavia (mean = 52%, SD = 10%) using the SNPs (Fig. S29).

4. Discussion

4.1. Population structure

Our study shows that species occurring at low densities, due to large home ranges and territorial behavior, can exhibit cryptic population structures across an apparently continuous distribution range, which needs to be taken into account when planning conservation actions. We found that the genetic structure of Fennoscandian wolverines is characterized by a strong subdivision between Scandinavia and southeastern Finland (i.e. part of the Karelian population), even though these populations have recovered both numerically and spatially in the last decades (Chapron et al., 2014). Our result aligns with the previously detected population structure within Finland (Lansink et al., 2020) and further demonstrates that wolverines of northern Finland belong genetically to the Scandinavian population. Similar population history and subdivision have also been identified in other large carnivores in Fennoscandia. Both Eurasian lynx (*Lynx lynx*) and brown bear went through a severe population bottleneck before the recovery during the last decades (Chapron et al., 2014). Both species show genetic structuring in Fennoscandia, especially in divergence between Finland and Scandinavia (Hellborg et al., 2002; Kopatz et al., 2021). Notably, the zone where brown bear populations of Karelia and Scandinavia meet (Kopatz et al., 2021), coincides with the contact zone of the two wolverine populations identified in this study. Similarly, the population subdivision of Fennoscandian wolverines is likely a reflection of the severe 20th century demographic bottleneck caused by human persecution. Though previously continuously distributed throughout Fennoscandia, during the bottleneck, the population was separated into refuges in the northern parts of the Scandinavian Mountains and in Russian Karelia (Fig. 1b) (Landa et al., 2000). A combination of extremely low numbers, followed by genetic drift, likely caused these refuges to develop their own genetic signatures through loss of some alleles and increase in others (Nei et al., 1975). After the implementation of protective legislation, both remnants recovered gradually and merged, but the genetic signature of the past remained. This delay could be ascribed to the low reproductive output of wolverines (Persson et al., 2006) and human-caused mortality (i.e. harvest, poaching) (Persson et al., 2009; Gervasi et al., 2015), which contribute to slow population recovery. Past genetic signatures detectable for several decades within wolverine populations have previously been shown in south-western Norway (Flagstad et al., 2004) and western Finland (Lansink et al., 2020). Our findings also confirm the previous results showing that the translocations three decades ago are still detectable in western Finland with genetic assignment tests (Lansink et al., 2020).

We found that wolverines have two mitochondrial 16S SNP haplotypes with the same clear-cut population differentiation between Scandinavian and eastern Finnish populations as with nuclear markers. Previously, using a fragment of mtDNA control region sequences, two haplotypes were detected within Finland without a clear contact zone. One of these is the sole haplotype in Scandinavia and the other is scarcely distributed in eastern Finland (Walker et al., 2001; Lansink et al., 2020). A comparison of individuals analysed for both, the mitochondrial 16S SNP and control region haplotypes, revealed that the more common of the control region haplotypes co-occur with both 16S SNPs, whereas the rarer haplotype co-occurs only with the eastern Finnish 16S SNP. Thus, by combining these results, we concluded that Fennoscandian wolverines have at least three mitochondrial haplotypes, all present in Finland but only one in Scandinavia. Interestingly, Scandinavian lynx have also been reported to have a single mitochondrial haplotype, whereas Finnish lynx has additional three haplotypes (Hellborg et al., 2002). The low mitochondrial haplotype diversity in Scandinavia could be due to the location of the population on the far western periphery of the Eurasian range. Similarly, only a few haplotypes were found in the peripheral southernmost populations in North America (Zigouris et al., 2013). Finally, while several wolverine studies comparing mitochondrial and nuclear markers have found incongruent results for population genetic structure (Chappell et al., 2004; Tomasik and Cook, 2005; Cegelski et al., 2006), we found an overall agreement between the two marker systems.

4.2. Resistance to gene flow and isolation by distance

Populations with low genetic variation benefit from gene flow from genetically more diverse populations. In particular, knowledge on areas where gene flow is hampered aids to pinpoint regions, where targeted management actions would be most effective to improve genetic connectivity. Our data pointed out several areas where wolverine gene flow is either facilitated or impeded. We also detected that the relevant geographic scale might be population-specific. Indeed, gene flow within the eastern Finland population occurred on a smaller scale (<100 km) than within the Scandinavian population (<350 km). Positive spatial autocorrelation up to 350 km in the Scandinavian population reflects the high dispersal capacity of wolverines (Vangen et al., 2001; Flagstad et al., 2004). Although the exact distances cannot be compared

(Vekemans and Hardy, 2004), positive autocorrelation on such a large scale has not previously been recorded for wolverines (Schwartz et al., 2009; Balkenhol et al., 2020). The difference between the Fennoscandian populations suggests that gene flow is more limited in eastern Finland compared to Scandinavia. This may simply be an effect of lower density of wolverines in the more recently established population in southeastern Finland, restricting the need for long-distance dispersal to find unoccupied space to establish a territory (Aronsson, 2017). The patchy results of the IBD resistance mapping in eastern Finland confirms that gene flow is facilitated only in two small areas. However, lower and biased sampling effort (e.g. by using mainly hair snag stations) and the lower sample size may have affected the results in eastern Finland. To obtain a more complete picture of gene flow in the entire Karelian population, a denser sampling scheme that would extend into Russia would be required.

IBD resistance mapping can be used to detect areas where dispersal is limited or facilitated under the assumption that the genetic differentiation is not caused by any other factors, such as mutations, historical events, or source-sink dynamics (Tang et al., 2019). We found a clear pattern of IBD within the two Fennoscandian wolverine populations. However, due to the large scale of this study and the recent demographic changes within the populations, we were unable to differentiate between true resistance to dispersal areas, and areas that are genetically differentiated due to other factors. For example, resistance to gene flow was found towards south-western Norway, separating a small subpopulation from the rest of Scandinavia. A few wolverines might have survived in this area during the bottleneck (Flagstad et al., 2004) and the area still seems to have a distinct genetic signature (Ekblom et al., 2018). That said, there are clear indications that ongoing gene flow counteracts the remaining genetic differentiation, as indicated by one of the lowest self-assignment rates among Scandinavian subpopulations. Our results are in concordance with the previous findings that genetic differentiation of this subpopulation is gradually diminishing (Flagstad et al., 2004), although the gene flow is affected by policy decisions and active management, i.e. extensive harvest to reduce depredation on free ranging livestock (Gervasi et al., 2019). On the other hand, areas of reduced gene flow continue from southern Norway into Sweden (Fig. 5) to regions only recently recolonized by wolverines (Aronsson and Persson, 2017; Mattisson et al., 2020). We suggest that the resistance in these areas might be more pronounced due to founder effects (Eckert et al., 2008), or partly due to incomplete sampling.

Overall, the Scandinavian wolverine population was characterized by large areas of high connectivity shaped by isolation by distance, which has been indicated also by previous studies (Walker et al., 2001; Ekblom et al., 2018). Although the high connectivity continued into northern Finland, a few areas in northern Fennoscandia restricted gene flow from central Scandinavia to northern Scandinavia. This genetic discontinuity was also supported by relatively high back-assignment rates of northern individuals to the northern Scandinavian part of the population. Importantly, the Scandinavian population is exposed to different management regimes in Sweden and Norway, respectively (see below), leading to variation in local densities. This may result in a steeper IBD slope in areas with higher wolverine densities. Although we did not detect within-population variation from our autocorrelograms, it possibly affects the IBD resistance mapping at local scales.

4.3. Comparison of SNPs and microsatellites

We used both SNPs and microsatellites, because these markers have different beneficial properties for inference of population structure (Haasl and Payseur, 2011). SNPs are cost-efficient (von Thaden et al., 2017) and well-suited for low quantity and quality DNA samples (Ekblom et al., 2021), although microsatellites also have proven to be useful for many different monitoring and research purposes such as population size estimations, quantifying territory size or paternity testing (Hedmark et al., 2007; Brøseth et al., 2010; Bischof et al., 2016). Here, we showed that microsatellites worked well to detect the major genetic population structures but appeared to be inadequate for more detailed analysis, such as IBD resistance mapping. For example, based on the SNP analyses, the Scandinavian population showed areas of restricted gene flow, whereas these areas could not be identified from microsatellites. As microsatellites have higher mutation rates than SNPs (Bhargava and Fuentes, 2010), genetic boundaries detected with microsatellites can be more diffuse with ongoing gene flow.

4.4. Implications for management

Transboundary cooperation and joint protective legislation are key components in successful large carnivore conservation (Trouwborst, 2015). Nevertheless, challenges may arise in harmonizing transboundary management when there is national or regional variation in human-carnivore conflicts, cultural values, and political interests. Wolverines in Fennoscandia are managed to sustain viable populations while minimizing damage to free-ranging livestock by applying legal harvest (Swenson and Andrén, 2005). Wolverines are fully protected under the Bern Convention (Council of Europe (a), 2022) throughout Fennoscandia, while in Finland and Sweden additional protection is provided by the European Union's Habitats Directive (Council of Europe (b), 2022). Management regimes differ between Finland, Norway and Sweden (e.g. Swenson and Andrén, 2005), but cooperation to improve transboundary management of wolverines has started (e.g. Hansson-Forman et al., 2018), and in this perspective, our result of the Scandinavian population functioning as one transboundary population, supports the continuation of close collaboration between Norway, Sweden and Finland.

In Sweden, the minimum population size is set to 600 individual wolverines to sustain a favourable conservation status (SEPA, 2014). Norway has a national management goal of 39 annual reproductions (Norwegian Ministry of Climate and Environment, 2005). However, the Norwegian population has been above the goal since early 2000s, and thus, the harvest rate has been substantially higher in Norway than in Sweden during the last decade (Bischof et al., 2020) leading to source-sink dynamics from Sweden to Norway (Gervasi et al., 2019). In northern Finland, the management goal is an evenly distributed wolverine population across the reindeer husbandry area (Fig. 1b) to maintain a connection from Russia to Scandinavia, while also allowing selective removal of individuals causing severe damage (Ministry of Agriculture and Forestry of Finland, 2014). On the other hand, hunting is completely prohibited in the wolverine range south of the reindeer husbandry area. This may explain why wolverine density is low in the contact zone of the two populations despite favourable wolverine habitat and denning conditions. However, the Finnish reindeer husbandry area is critical for the exchange of genetic material between Scandinavia and eastern Finland. Low rates of genetic exchange between the two populations are of concern for the long-term viability, especially for the Scandinavian population, which has low genetic diversity and is only connected to the large Eurasian continental population via the population in eastern Finland.

For the genetically impoverished Scandinavian population, increased connectivity with eastern Finland is needed to facilitate gene flow between the two populations. In a species such as the wolverine, with low reproductive capacity (Persson et al., 2006) and high human-caused mortality (Persson et al., 2009; Gervasi et al., 2015), immigration can have a large impact on the genetic viability. Managers should consider spatial planning of harvest to retain the potential for gene flow between the populations. Specifically, harvest should be avoided or kept at a low level within and nearby areas of high gene flow resistance or areas that connect genetically differentiated (sub)populations, to promote dispersal of wolverine individuals. This is important for resistance areas towards southwestern Norway and in northern Scandinavia, and particularly important for areas in and near southern Finnish Lapland that link the Scandinavian and the eastern Finnish populations. Conflict

mitigation can help to widen the contact zone by promoting dispersal into areas with currently no occurrence, or low density, of the wolverine (e.g. southwestern Finnish Lapland and Swedish eastern Norrbotten). Improved transfer of knowledge to local people on the importance of population connectivity for the overall health of populations might increase tolerance for all four Fennoscandian large carnivore species (wolf *Canis lupus*, bear, lynx and wolverine). Appropriate management actions could contribute to increased connectivity, as suggested by the large areas of low resistance to gene flow in the Scandinavian wolverine population, and thus improve the long-term viability of wolverines in northern Europe.

Data statement

Since the wolverine is an endangered species in the study area, sensitive data (i.e. den locations) will not be released. The genotype data will be available in Mendeley Data at https://doi:10.17632/ffmw658bg2.1 following a two-year embargo from the date of publication.

CRediT authorship contribution statement

Gerhardus M. J. Lansink: Conceptualization, Methodology, Formal analysis, Investigation, Resources, Funding acquisition, Writing - Original Draft, Writing - Review & Editing.

Oddmund Kleven: Conceptualization, Methodology, Project administration, Supervision, Writing - Review & Editing.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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References

Anderson, C.D., Epperson, B.K., Fortin, M., Holderegger, R., James, P.M.A., et al., 2010. Considering spatial and temporal scale in landscape-genetic studies of gene flow. Mol. Ecol. 19, 3565–3575. https://doi.org/10.1111/j.1365-294X.2010.04757.x.

Aronsson, M., Persson, J., 2017. Mismatch between goals and the scale of actions constrains adaptive carnivore management: the case of the wolverine in Sweden. Anim. Conserv. 20, 261–269. https://doi.org/10.1111/acv.12310.

Aronsson, M., 2017. In: 'O Neighbour, Where Art Thou?' Spatial and Social Dynamics in Wolverine and Lynx, From Individual Space Use to Population Distribution, 24. Acta Uni. Agric. Suec, pp. 1652–6880. PhD dissertation.

Balkenhol, N., Schwartz, M.K., Inman, R.M., Copeland, J.P., Squires, J.S., et al., 2020. Landscape genetics of wolverines (*Gulo gulo*): scale-dependent effects of bioclimatic, topographic, and anthropogenic variables. J. Mammal. 101, 790–803. https://doi.org/10.1093/jmammal/gyaa037.

Bhargava, A., Fuentes, F.F., 2010. Mutational dynamics of microsatellites. Mol. Biotechnol. 44, 250–266. https://doi.org/10.1007/s12033-009-9230-4.

Bischof, R., Gregersen, E.R., Brøseth, H., Ellegren, H., Flagstad, Ø., 2016. Noninvasive genetic sampling reveals intrasex territoriality in wolverines. Ecol. Evol. 6, 1527–1536. https://doi.org/10.1002/ece3.1983.

Bischof, R., Milleret, C., Dupont, P., Chipperfield, J., Tourani, M., et al., 2020. Estimating and forecasting spatial population dynamics of apex predators using transnational genetic monitoring. PNAS 117, 30531–30538. https://doi.org/10.1073/pnas.2011383117.

Boitani, L., Alvarez, F., Anders, O., Andren, H., Avanzinelli, E., 2015. In: Key Actions for Large Carnivore Populations in Europe. Institute of Applied Ecology, Rome, Italy, pp. 1–120.

Bradburd, G.S., Coop, G.M., Ralph, P.L., 2018. Inferring continuous and discrete population genetic structure across space. Genetics 210, 33–52. https://doi.org/10.1534/genetics.118.301333.

Brøseth, H., Flagstad, Ø., Wärdig, C., Johansson, M., Ellegren, H., 2010. Large-scale noninvasive genetic monitoring of wolverines using scats reveals density dependent adult survival. Biol. Conserv. 143, 113–120. https://doi.org/10.1016/j.biocon.2009.09.012.

Cayuela, H., Rougemont, Q., Prunier, J.G., Moore, J.-S., Clobert, J., et al., 2018. Demographic and genetic approaches to study dispersal in wild animal populations: a methodological review. Mol. Ecol. 27, 3976–4010. https://doi.org/10.1111/mec.14848.

Cegelski, C.C., Waits, L.P., Anderson, N.J., Flagstad, Ø., Strobeck, C., et al., 2006. Genetic diversity and population structure of wolverine (*Gulo gulo*) populations at the southern edge of their current distribution in North America with implications for genetic viability. Conserv. Genet. 7, 197–211. https://doi.org/10.1007/s10592-006-9126-9.

Chakraborty, R., 1993. Analysis of genetic structure of populations: meaning, methods, and implications. In: Majumder, P.P. (Ed.), Human Population Genetics: A Centennial Tribute to J. B. S. Haldane. Springer US, Boston, MA, pp. 189–206.

Chappell, D.E., Den Bussche, Van, Ronald, A., Krizan, J., Patterson, B., 2004. Contrasting levels of genetic differentiation among populations of wolverines (*Gulo gulo*) from northern Canada revealed by nuclear and mitochondrial loci. Conserv. Genet. 5, 759–767. https://doi.org/10.1007/s10592-004-1976-4.

Chapron, G., Kaczensky, P., Linnell, J.D.C., von Arx, M., Huber, D., et al., 2014. Recovery of large carnivores in Europe's modern human-dominated landscapes. Science 346, 1517–1519. https://doi.org/10.1126/science.1257553.

Chen, K., Marschall, E.A., Sovic, M.G., Fries, A.C., Gibbs, H.L., et al., 2018. assignPOP: an r package for population assignment using genetic, non-genetic, or integrated data in a machine-learning framework. Methods Ecol. Evol. 9, 439–446. https://doi.org/10.1111/2041-210X.12897.

Council of Europe (a), 2022. Convention on the conservation of European wildlife and natural heritage. https://www.coe.int/en/web/conventions/full-list/-/conventions/treaty/104. Accessed 6 May.

Council of Europe (b), 2022. Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora. http://eur-lex.europa.eu/legal-content/EN/TXT/?uri=CELEX:31992L0043. Accessed 6 May.

Danilov, P.I., Panchenko, D.V., Tirronen, K.F., Fyodorov, F.V., Belkin, V.V., 2018. Changes in mammal fauna of the northern palearctic and living range dynamics of the component species. Biol. Bull. 45, 265–277. https://doi.org/10.1134/S1062359018030032.

Dures, S.G., Carbone, C., Savolainen, V., Maude, G., Gottelli, D., 2020. Ecology rather than people restrict gene flow in Okavango-kalahari lions. Anim. Conserv. 23, 502–515. https://doi.org/10.1111/acv.12562.

Eckert, C.G., Samis, K.E., Lougheed, S.C., 2008. Genetic variation across species' geographical ranges: the central–marginal hypothesis and beyond. Mol. Ecol. 17, 1170–1188. https://doi.org/10.1111/j.1365-294X.2007.03659.x.

Ekblom, R., Smeds, L., Ellegren, H., 2014. Patterns of sequencing coverage bias revealed by ultra-deep sequencing of vertebrate mitochondria. BMC Genom. 15, 467. https://doi.org/10.1186/1471-2164-15-467.

Ekblom, R., Aronsson, M., Elsner-Gearing, F., Johansson, M., Fountain, T., 2021. Sample identification and pedigree reconstruction in wolverine (*Gulo gulo*) using SNP

genotyping of non-invasive samples. Conserv. Genet. Resour. https://doi.org/10.1007/s12686-021-01208-5.
Ekblom, R., Brechlin, B., Persson, J., Smeds, L., Johansson, M., et al., 2018. Genome sequencing and conservation genomics in the scandinavian wolverine population. Conserv. Biol. 32, 1–29. https://doi.org/10.1111/cobi.13157.
Flagstad, Ø., Hedmark, E., Landa, A., Brøseth, H., Persson, J., et al., 2004. Colonization history and noninvasive monitoring of a reestablished wolverine population. Conserv. Biol. 18, 676–688. https://doi.org/10.1111/j.1523-1739.2004.00328.x-i1.
Frankham, R., 2005. Genetics and extinction. Biol. Conserv. 126, 131–140. https://doi.org/10.1016/j.biocon.2005.05.002.
Frantz, A.C., Cellina, S., Krier, A., Schley, L., Burke, T., 2009. Using spatial bayesian methods to determine the genetic structure of a continuously distributed population: clusters or isolation by distance? J. Appl. Ecol. 46, 493–505. https://doi.org/10.1111/j.1365-2664.2008.01606.x.
Gervasi, V., Linnell, J.D.C., Brøseth, H., Gimenez, O., 2019. Failure to coordinate management in transboundary populations hinders the achievement of national management goals: the case of wolverines in Scandinavia. J. Appl. Ecol. 56, 1905–1915. https://doi.org/10.1111/1365-2664.13379.
Gervasi, V., Brøseth, H., Nilsen, E.B., Ellegren, H., Flagstad, Ø., et al., 2015. Compensatory immigration counteracts contrasting conservation strategies of wolverines (*Gulo gulo*) within Scandinavia. Biol. Conserv. 191, 632–639. https://doi.org/10.1016/j.biocon.2015.07.024.
Gervasi, V., Brøseth, H., Gimenez, O., Nilsen, E.B., Odden, J., et al., 2016. Sharing data improves monitoring of trans-boundary populations: the case of wolverines in Central Scandinavia. Wildlife Biol. 22, 95–106. https://doi.org/10.2981/wlb.00142.
Haasl, R.J., Payseur, B.A., 2011. Multi-locus inference of population structure: a comparison between single nucleotide polymorphisms and microsatellites. Heredity 106, 158–171. https://doi.org/10.1038/hdy.2010.21.
Hansson-Forman, K., Reimerson, E., Sjölander-Lindqvist, A., Sandström, C., 2018. Governing large carnivores—comparative insights from three different countries. Soc. Nat. Resourc. 31, 837–852. https://doi.org/10.1080/08941920.2018.1447179.
Hapeman, P., Latch, E.K., Fike, J.A., Rhodes, O.E., Kilpatrick, C.W., 2011. Landscape genetics of fishers (Martes pennanti) in the northeast: dispersal barriers and historical influences. J. Hered. 102, 251–259. https://doi.org/10.1093/jhered/esr001.
Hardy, O.J., Vekemans, X., 2002. Spagedi: a versatile computer program to analyse spatial genetic structure at the individual or population levels. Mol. Ecol. Notes 2, 618–620. https://doi.org/10.1046/j.1471-8286.2002.00305.x.
Hedmark, E., Persson, J., Segerström, P., Landa, A., Ellegren, H., 2007. Paternity and mating system in wolverines *Gulo gulo*. Wildlife Biol. 13, 13–30. https://doi.org/10.2981/0909-6396(2007)13[13:PAMSIW]2.0.CO;2.
Hellborg, L., Walker, C.W., Rueness, E.K., Stacy, J.E., Kojola, I., et al., 2002. Differentiation and levels of genetic variation in northern european lynx (*Lynx lynx*) populations revealed by microsatellites and mitochondrial DNA analysis. Conserv. Genet. 3, 97–111. https://doi.org/10.1023/A:1015217723287.
Henriksen, S., Hilmo, O., 2015. The 2015 Norwegian Red List for Species [Norsk rødliste for arter 2015]. Norwegian Biodiversity Information Centre, Trondheim, Norway. ISBN: 978-82-92838-41-9.
Hewitt, G.M., 1999. Post-glacial re-colonization of european biota. Biol. J. Linn. Soc. 68, 87–112. https://doi.org/10.1006/bijl.1999.0332.
Hyvärinen, E., Juslén, A., Kemppainen, E., Uddström, A., Liukko, U.-M., 2019. The 2019 Red List of Finnish Species [Suomen lajien uhanalaisuus – Punainen kirja 2019]. Ministry of Environment and Finnish Environment Institute, Helsinki, Finland. ISBN: 978-952-11-4974-0.
Jombart, T., 2008. Adegenet: a R package for the multivariate analysis of genetic markers. Bioinformatics 24, 1403–1405. https://doi.org/10.1093/bioinformatics/btn129.
Jombart, T., Devillard, S., Dufour, A.B., Pontier, D., 2008. Revealing cryptic spatial patterns in genetic variability by a new multivariate method. Heredity 101, 92–103. https://doi.org/10.1038/hdy.2008.34.
Jombart, T., Devillard, S., Balloux, F., 2010. Discriminant analysis of principal components: a new method for the analysis of genetically structured populations. BMC Genet. 11, 94. https://doi.org/10.1186/1471-2156-11-94.
Jost, L., 2008. GST and its relatives do not measure differentiation. Mol. Ecol. 17, 4015–4026. https://doi.org/10.1111/j.1365-294X.2008.03887.x.
Kaczensky, P., Linnell, J.D.C., Huber, D., Von Arx, M., Andren, H., et al., 2021. Distribution of large carnivores in Europe 2012–2016: distribution maps for brown bear, eurasian lynx, grey wolf, and wolverine. Dryad. https://doi.org/10.5061/dryad.pc866t1p3. Dataset.
Kalinowski, S.T., 2005. Hp-rare 1.0: a computer program for performing rarefaction on measures of allelic richness. Mol. Ecol. Notes 5, 187–189. https://doi.org/10.1111/j.1471-8286.2004.00845.x.
Kalisz, S., Nason, J.D., Hanzawa, F.M., Tonsor, S.J., 2001. Spatial population genetic structure in *trillium grandiflorum*: the roles of dispersal, mating, history, and selection. Evolution 55, 1560–1568. https://doi.org/10.1111/j.0014-3820.2001.tb00675.x.
Kangas, V., Kvist, L., Kholodova, M., Nygrén, T., Danilov, P., et al., 2015. Evidence of post-glacial secondary contact and subsequent anthropogenic influence on the genetic composition of fennoscandian moose (Alces alces). J. Biogeogr. 42, 2197–2208. https://doi.org/10.1111/jbi.12582.
Keis, M., Remm, J., Ho, S.Y.W., Davison, J., Tammeleht, E., et al., 2013. Complete mitochondrial genomes and a novel spatial genetic method reveal cryptic phylogeographical structure and migration patterns among brown bears in North-Western Eurasia. J. Biogeogr. 40, 915–927. https://doi.org/10.1111/jbi.12043.
Kleven, O., Andersskog, I.P.Ø., Brandsegg, H., Eriksen, L.B., Spets, M.H., 2022. DNA-based monitoring of the Scandinavian wolverine population 2021. In: NINA Report 2111. Norwegian Institute for Nature Research. Accessed 6 May.
Kojola, I., Heikkinen, S., Mäntyniemi, S., Ollila, T., 2021. In: Ahmakanta Suomessa 2021. Luonnonvara- ja biotalouden tutkimus 88/2021. Natural Resources Institute Finland, Helsinki, p. 11.
Kojola, I., Aspi, J., Hakala, A., Heikkinen, S., Ilmoni, C., et al., 2006. Dispersal in an expanding wolf population in Finland. J. Mammal. 87, 281–286. https://doi.org/10.1644/05-MAMM-A-061R2.1.
Kopatz, A., Eiken, H.G., Aspi, J., Kojola, I., Tobiassen, C., et al., 2014. Admixture and gene flow from Russia in the recovering northern european brown bear (*Ursus arctos*). Plos One 9, e97558. https://doi.org/10.1371/journal.pone.0097558.
Kopatz, A., Kleven, O., Kojola, I., Aspi, J., Norman, A.J., et al., 2021. Restoration of transborder connectivity for fennoscandian brown bears (*Ursus arctos*). Biol. Conserv. 253, 108936 https://doi.org/10.1016/j.biocon.2020.108936.
Laikre, L., Nilsson, T., Primmer, C.R., Ryman, N., Allendorf, F.W., 2009. Importance of genetics in the interpretation of favourable conservation status. Conserv. Biol. 23, 1378–1381.
Landa, A., Lindén, M., Kojola, I., 2000. Action plan for the conservation of wolverines (*Gulo gulo*) in Europe. In: Council of Europe, pp. 1–45.
Lansink, G.M.J., Esparza-Salas, R., Joensuu, M., Koskela, A., Bujnáková, D., et al., 2020. Population genetics of the wolverine in Finland: the road to recovery? Conserv. Genet. 21, 481–499. https://doi.org/10.1007/s10592-020-01264-8.
Loiselle, B.A., Sork, V.L., Nason, J., Graham, C., 1995. Spatial genetic structure of a tropical understory shrub, *Psychotria officinalis* (Rubiaceae). Am. J. Bot. 82, 1420–1425. https://www.jstor.org/stable/2445869.
Lowe, W.H., Allendorf, F.W., 2010. What can genetics tell us about population connectivity? Mol. Ecol. 19, 3038–3051. https://doi.org/10.1111/j.1365-294X.2010.04688.x.
Manel, S., Gaggiotti, O.E., Waples, R.S., 2005. Assignment methods: matching biological questions with appropriate techniques. Trends Ecol. Evol. 20, 136–142. https://doi.org/10.1016/j.tree.2004.12.004.
Mattisson, J., Höglund, L., Brøseth, H., 2020. Bestandsovervåking av jerv i 2020. Inventering av järv 2020. Bestandsstatus for store rovdyr i skandinavia. Beståndsstatus för stora rovdjur i skandinavien. Miljødirektoratet and Naturvårdsverket 30. https://hdl.handle.net/11250/2684114.
Ministry of Agriculture and Forestry of Finland, 2014. Suomen ahmakannan hoitosuunnitelma (Management plan of Finnish wolverines). Maa- ja metsätalousministeriön julkaisuja 9/2014. Ministry of Agriculture and Forestry of Finland. http://urn.fi/URN:ISBN:978-952-453-872-5.
Nei, M., 1973. Analysis of gene diversity in subdivided populations. PNAS 70, 3321–3323. https://doi.org/10.1073/pnas.70.12.3321.
Nei, M., 1978. Estimation of average heterozygosity and genetic distance from a small number of individuals. Genetics 89, 583. https://doi.org/10.1093/genetics/89.3.583.
Nei, M., Maruyama, T., Chakraborty, R., 1975. The bottleneck effect and genetic variability in populations. Evolution 29, 1–10. https://doi.org/10.2307/2407137.
Norwegian Ministry of Climate and Environment, 2005. Forskrift om forvaltning av rovvilt [Regulation about predator management]. Retrieved from. https://lovdata.no/dokument/LTI/forskrift/2005-03-18-242.
Peakall, R., Smouse, P.E., 2012. GenAlEx 6.5: genetic analysis in excel. Population genetic software for teaching and research–an update. Bioinformatics 28, 2537–2539. https://doi.org/10.1093/bioinformatics/bts460.
Persson, J., Rauset, G.R., Chapron, G., 2015. Paying for an endangered predator leads to population recovery. Conserv. Lett. 8, 345–350. https://doi.org/10.1111/conl.12171.
Persson, J., Ericsson, G., Segerström, P., 2009. Human caused mortality in the endangered scandinavian wolverine population. Biol. Conserv. 142, 325–331. https://doi.org/10.1016/j.biocon.2008.10.028.
Persson, J., Landa, A., Andersen, R., Segerström, P., 2006. Reproductive characteristics of female wolverines (*Gulo gulo*) in Scandinavia. J. Mammal. 87, 75–79. https://doi.org/10.1644/04-.1.
QGIS Development Team, 2018. QGIS geographic information system. Open source geospatial foundation project. https://qgis.osgeo.org.
R Core Team, 2020. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.
Rauset, G.R., Low, M., Persson, J., 2015. Reproductive patterns result from age-related sensitivity to resources and reproductive costs in a mammalian carnivore. Ecology 96, 3153–3164. https://doi.org/10.1890/15-0262.1.
Roser, L.G., Ferreyra, L.I., Saidman, B.O., Vilardi, J.C., 2017. EcoGenetics: an R package for the management and exploratory analysis of spatial data in landscape genetics. Mol. Ecol. Resour. 17, e241–e250. https://doi.org/10.1111/1755-0998.12697.
Rousset, F., 1997. Genetic differentiation and estimation of gene flow from F-statistics under isolation by distance. Genetics 145, 1219–1228.
Schregel, J., Kopatz, A., Eiken, H.G., Swenson, J.E., Hagen, S.B., 2017. Sex-specific genetic analysis indicates low correlation between demographic and genetic connectivity in the scandinavian brown bear (*Ursus arctos*). Plos One 12, e0180701. https://doi.org/10.1371/journal.pone.0180701.
Schregel, J., Remm, J., Eiken, H.G., Swenson, J.E., Saarma, U., et al., 2018. Multi-level patterns in population genetics: variogram series detects a hidden isolation-by-distance-dominated structure of scandinavian brown bears *Ursus arctos*. Methods Ecol. Evol. 9, 1324–1334. https://doi.org/10.1111/2041-210X.12980.
Schwartz, M.K., McKelvey, K.S., 2009. Why sampling scheme matters: the effect of sampling scheme on landscape genetic results. Conserv. Genet. 10, 441–452. https://doi.org/10.1007/s10592-008-9622-1.

Schwartz, M.K., Copeland, J.P., Anderson, N.J., Squires, J.R., Inman, R.M., et al., 2009. Wolverine gene flow across a narrow climatic niche. Ecology 90, 3222–3232. https://doi.org/10.1890/08-1287.1.

SEPA, 2014. National Management Plan for Wolverines – Management Period 2014-2019. Swedish Environmental Protection Agency.

Singh, S.K., Aspi, J., Kvist, L., Sharma, R., Pandey, P., et al., 2017. Fine-scale population genetic structure of the Bengal tiger (*Panthera tigris tigris*) in a human-dominated western Terai Arc Landscape, India. PLOS One 12, e0174371. https://doi.org/10.1371/journal.pone.0174371.

Slatkin, M., 1993. Isolation by distance in equilibrium and non-equilibrium populations. Evolution 47, 264–279. https://doi.org/10.1111/j.1558-5646.1993.tb01215.x.

Sugiyama, Y., Nishita, Y., Lansink, G.M.J., Holmala, K., Aspi, J., et al., 2022. Diversity of the MHC class II DRB gene in the wolverine (Carnivora: mustelidae: *Gulo gulo*) in Finland. PLOS one 17, e0267609. https://doi.org/10.1371/journal.pone.0267609.

Swedish Species Information Centre, 2020. The Swedish Red List 2020. Swedish Agricultural University, Uppsala, Sweden.

Swenson, J.E., Andrén, H., 2005. A tale of two countries: large carnivore depredation and compensation schemes in Sweden and Norway. In: Woodroffe, R., Thirgood, S., Rabinowitz, A. (Eds.), People and Wildlife Conflict or Coexistence? Cambridge University Press, London, pp. 323–339. S.

Taberlet, P., Fumagalli, L., Wust-Saucy, A.G., Cosson, J.F., 1998. Comparative phylogeography and postglacial colonization routes in Europe. Mol. Ecol. 7, 453–464. https://doi.org/10.1046/j.1365-294x.1998.00289.x.

Tang, Q., Fung, T., Rheindt, F.E., 2019. ResDisMapper: an r package for fine-scale mapping of resistance to dispersal. Mol. Ecol. Resour. 20, 819–831. https://doi.org/10.1111/1755-0998.13127.

von Thaden, A., Cocchiararo, B., Jarausch, A., Jüngling, H., Karamanlidis, A.A., et al., 2017. Assessing SNP genotyping of noninvasively collected wildlife samples using microfluidic arrays. Sci. Rep. 7, 10768. https://doi.org/10.1038/s41598-017-10647-w.

Tomasik, E., Cook, J.A., 2005. Mitochondrial phylogeography and conservation genetics of wolverine (*Gulo gulo*) of northwestern North America. J. Mammal. 86, 386–396. https://doi.org/10.1644/BER-121.1.

Trouwborst, A., 2015. Global large carnivore conservation and international law. Biodivers. Conserv. 24, 1567–1588. https://doi.org/10.1007/s10531-015-0894-8.

Vangen, K.M., Persson, J., Landa, A., Andersen, R., Segerström, P., 2001. Characteristics of dispersal in wolverines. Can. J. Zool. 79, 1641–1649. https://doi.org/10.1139/z01-124.

Vekemans, X., Hardy, O.J., 2004. New insights from fine-scale spatial genetic structure analyses in plant populations. Mol. Ecol. 13, 921–935. https://doi.org/10.1046/j.1365-294X.2004.02076.x.

Walker, C.W., Vilà, C., Landa, A., Lindén, M., Ellegren, H., 2001. Genetic variation and population structure in scandinavian wolverine (*Gulo gulo*) populations. Mol. Ecol. 10, 53–63. https://doi.org/10.1046/j.1365-294X.2001.01184.x.

Winter, D.J., 2012. Mmod: an R library for the calculation of population differentiation statistics. Mol. Ecol. Resour. 12, 1158–1160. https://doi.org/10.1111/j.1755-0998.2012.03174.x.

Wright, S., 1943. Isolation by distance. Genetics 28, 114–138.

Zigouris, J., Schaefer, J.A., Fortin, C., Kyle, C.J., 2013. Phylogeography and post-glacial recolonization in wolverines (*Gulo gulo*) from across their circumpolar distribution. PLOS One 8, e83837. https://doi.org/10.1371/journal.pone.0083837.