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Genetic consequences of conservation management: the case of the arctic fox (*Vulpes lagopus*) in Scandinavia

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Preface

This thesis is original, unpublished, and written wholly by the author, E. J. K. Hemphill. The project was part of the ECOFUNC project (Understanding ecosystem functionality, expansion, and retreat of species on the Scandinavian mountain tundra under multiple drivers of change), funded by the Norwegian Research Council (grant 244557).

Fieldwork was performed as part of the Norwegian Arctic Fox Monitoring Programme and the Norwegian Arctic Fox Captive Breeding Programme. Both projects are funded by the Norwegain Environment Agency. Molecular analysis was performed at the Norwegian Institute for Nature Research (NINA) in Trondheim.

Cover photo: Morgan Frelsøy, Avisa OPP.

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Elisa J. K. Hemphill,

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Abstract

The Arctic fox (Vulpes lagopus) population in Fennoscandia experienced a drastic demographic and genetic bottleneck in the early 20th century as a result of high hunting pressure. In 2000, despite almost 70 years of protection, the population showed no signs of recovery. The failure to recover was attributed to the combined threats of red fox (Vulpes vulpes) competition, instability in the rodent cycles (the Fennoscandian arctic foxes main food source), and the small and fragmented nature of the population, making it highly susceptible to the risks of inbreeding, genetic drift, and Allee effects.

Beginning in 1998 a number of conservation measures were implemented in order to mitigate the population decline and facilitate re-establishment. These measures included supplementary feeding, red fox culling, and the reintroduction of foxes from a captive breeding program. The positive demographic impact of these strategies has been confirmed, and the population has more than doubled in size during the past decade. This study compares microsatellite data across 8 loci in Scandinavian arctic fox samples collected between 2008 and 2015 in three core populations and five stepping stone areas to investigate whether the recent demographic success of the mid-Scandinavian arctic fox population has been complemented by changes in genetic diversity, genetic differentiation, and connectivity between subpopulations.

The results suggest that genetic diversity at the subpopulation level has increased substantially during the last decade, while genetic differentiation among populations has decreased. Patterns of dispersal complement these findings, highlighting the important role of immigration in ensuring subpopulation and metapopulation persistence. A marked shift in the dynamics of the mid-Scandinavian arctic fox population is evident around 2010/2011, with a substantial increase in dispersal in the system. This shift followed the recolonization of a core habitat region through the release of foxes from the captive breeding program and was synchronized in time with conservation efforts such as supplementary feeding and red fox culling in the stepping stone areas between core populations. Indeed, the evidence of increased genetic diversity and connectivity during the last decade indicate a restoration of metapopulation dynamics in the Scandinavian arctic fox population and an increase in the long-term viability of the species.

Contents

Introduction

During the twentieth century, anthropogenic pressures in the form of habitat destruction, over-exploitation, introduced species, and climate change, have caused severe demographic declines and substantial fragmentation of natural populations (Lande 1998; Wilcove et al. 1998; Laurance et al. 2000; Stuart et al. 2004; Corlett 2007; Brook et al. 2008; Vié et al. 2009; Murphy and Romanuk 2014). Habitat fragmentation is a common threat to biodiversity and has been shown to decrease connectivity (Burel et al. 1998) and reduce genetic diversity in a variety of species (Goossens et al. 2006; Nyström et al. 2006; Bellemain et al. 2007). For species occupying fragmented habitats, empirical studies as well as metapopulation- and population genetic theory emphasize the importance of connectivity for maintaining genetic diversity within populations, and preserving the ability of species to rapidly adapt and persist (Stacey and Taper 1992; Hanski and Gilpin 1997; Hanski 1998; Hanski and Gaggiotti 2004; Barrett and Schluter 2008; Stuart et al. 2014).

Dispersal and genetic drift are considered the most prominent processes influencing connectivity and genetic structure in animal populations (Slatkin 1987; Clobert 2012). Theoretically, species with high intrinsic movement capacity are expected to show high connectivity, increased rates of gene flow, and a lower degree of population structuring (Bohonak 1999; Habel et al. 2015). In practice however, realized patterns of movement and structuring may be influenced by behavioral traits (Surridge et al. 1999; Miller et al. 2010), geographical features such as spatial distance, topographic barriers, and fragmentation (Wright 1943; Slatkin 1987; Diffendorfer et al. 1995; Manel et al. 2003; Hartl and Clark 2007; Manel and Holderegger 2013), or historical factors such as colonization, range expansion, or isolation (Hewitt 1996; Taberlet et al. 1998; Templeton 1998; Hewitt 2000). Additionally, an increasing number of studies have revealed cryptic genetic structures that cannot be explained by either geographical or historical factors, but which instead may be explained by ecological factors such as habitat heterogeneity in resource availability, climate, and inter- or intra-specific competition. Interestingly, many of these studies concern populations of highly mobile carnivoran

mammals (Rueness, Jorde, et al. 2003; Rueness, Stenseth, et al. 2003; Geffen et al. 2004; Sacks et al. 2004; McRae et al. 2005; Pilot et al. 2006; Sacks et al. 2008).

When connectivity within a metapopulation is restricted, reduced gene flow and increased isolation among subpopulations increases subpopulation vulnerability to genetic drift and inbreeding (Jaenike 1973; Frankham et al. 2002). This results in a reduction in genetic variation within populations, and an increase in genetic differentiation among populations (Wright 1931; Jaenike 1973; Nei et al. 1975; Hanski 1998; Hamilton 2011). Loss of genetic variation and inbreeding may, in turn, reduce individual fitness, the ability to resist disease, and evolutionary potential (Lacy 1997; Altizer et al. 2003; England et al. 2003; Fernández et al. 2004; Spielman et al. 2004; Frankham 2005; Willi et al. 2006). In extreme cases, the fitness reduction resulting from genetic drift and inbreeding depression can produce a negative feedback loop or vortex, reducing population size and genetic diversity further (Gilpin and Soulé 1986; Fagan and Holmes 2006). The result is a reduction in long-term population viability, which may ultimately lead to extinction (Gilpin and Soulé 1986; Caughley 1994; Waser and Williams 2001; Keller and Waller 2002; Fagan and Holmes 2006).

Given widespread and continuing habitat fragmentation and population declines (Wilcove et al. 1998; Jenkins 2003; Kinnaird et al. 2003; Vié et al. 2009; Murphy and Romanuk 2014; Ducatez and Shine 2017), preventative and corrective measures may be the only viable solution to avoid extinction of highly endangered species (Che-Castaldo and Neel 2016). The establishment and/or maintenance of habitat corridors and "stepping-stone" habitat patches for endangered species are two such preventative measures that can maintain or restore connectivity (Riordan et al. 2015; Suarez-Rubio et al. 2015). The use of corridors and stepping stones has been shown to increase movement rates of terrestrial mammals (Mech and Hallett 2001) and to increase gene flow, thereby alleviating genetic threats (Aars and Ims 1999; Hale et al. 2001; Carroll et al. 2014). Likewise, reintroduction and translocation of individuals between subpopulations may augment gene flow, thus maintaining genetic variation and mitigating the negative consequences of inbreeding depression (Storfer 1999; IUCN 2012). These strategies have for instance been successfully used to re-establish a viable grey wolf population in Yellowstone national park (Smith et al. 2003;

Vonholdt et al. 2008), and to facilitate genetic rescue of the Florida panther (Johnson et al. 2010). Despite these examples, however, success rates of translocations, re-introductions, and supplementations are highly variable between species, and numerous studies indicate that relocations are not always successful (Fischer and Lindenmayer 2000; Weeks et al. 2011).

The arctic fox (*Vulpes lagopus*) is a medium sized arctic carnivore exhibiting a typical metapopulation structure in the Fennoscandian mountain tundra ecoregion (Herfindal et al. 2010). In Fennoscandia, arctic foxes prey mainly on cyclic rodents, and their population dynamics are tightly linked to the 3- to 5-year rodent cycles (Angerbjörn et al. 1995; Henden et al. 2009). Like many large carnivores in Scandinavia, the arctic fox population experienced a major demographic and genetic bottleneck in the late 19th/early 20th century (Collett 1912; Tannerfeldt and Angerbjörn 1998) as a result of excessive hunting associated with a lucrative fur trade (Lönnberg 1927; Østbye et al. 1978; Linnell et al. 1999; Nyström et al. 2006). After being recognized as endangered in the late 1920's (Lönnberg 1927; Sømme 1932; Høst 1935), the arctic fox was protected by law in Sweden (1928), Norway (1930) and Finland (1938). Despite protected status, however, the population showed little or no indication of population recovery during the following decades (Østbye et al. 1978; Hersteinsson et al. 1989; Angerbjörn et al. 1995; Kaikusalo and Angerbjörn 1995; Tannerfeldt et al. 2002).

While former persecution is accepted as the primary cause of the original population decline (Linnell et al. 2004), a combination of other factors may have influenced the failed recovery of the arctic fox population and may continue to threaten their persistence. Interspecific competition and intraguild predation from red foxes (*Vulpes vulpes*) have been documented to affect the arctic fox negatively (Elmhagen et al. 2002; Tannerfeldt et al. 2002; Pamperin et al. 2006; Selås and Vik 2007; Henden et al. 2010; Rodnikova et al. 2011), as has low food availability caused by fading rodent cycles (Angerbjörn et al. 2001; Ims et al. 2008; Henden et al. 2009; Elmhagen et al. 2011; Cornulier et al. 2013). Furthermore, the small and fragmented nature of the remaining arctic fox subpopulations increase their vulnerability to further population decline as a result of Allee effects (i.e., negative population growth rates at low population size) and inbreeding depression (Loison et al. 2001; Herfindal et al.

2010; Angerbjörn et al. 2013). Climate change may also play a role by reinforcing the aforementioned influences (Fuglei and Ims 2008). In parallel with climate change, the amplitude and regularity of rodent cycles have diminished (Ims et al. 2008; Kausrud et al. 2008; Elmhagen et al. 2011), and increased productivity in alpine regions has facilitated the invasion of red foxes into historically arctic fox dominated habitat (Hersteinsson and Macdonald 1992; Tannerfeldt et al. 2002).

At the end of the 20th century, the entire Fennoscandian arctic fox population was estimated at less than 120 adult individuals (Linnell et al. 1999; Kaikusalo 2000; Elmhagen et al. 2004; Sillero-Zubiri et al. 2004), and possibly as few as 40 -60 individuals (Angerbjörn et al. 2013), divided into three relatively isolated subpopulations (Dalén et al. 2006; Nyström et al. 2006). As the population showed no sign of recovery, it was increasingly evident that some form of active intervention would be necessary to save the arctic fox population from extinction (Linnell et al. 1999; Loison et al. 2001). Beginning in 1998, a number of large-scale conservation actions were implemented in several regions of the Fennoscandian mountain tundra with the goal of mitigating threats associated with increased red fox competition and food resource decline (Direktoratet for Naturforvaltning 2003; Elmhagen 2008). These actions included red fox culling to reduce competition and intraguild interactions, and supplementary feeding to increase arctic fox survival and reproduction (Angerbjörn et al. 2013). Additionally, the Norwegian Arctic Fox Captive Breeding Programme was established with the aim of re-establishing extinct arctic fox populations, strengthening small populations, and facilitating gene flow to reduce the risks of Allee effects and inbreeding depression (Linnell et al. 2004; Landa et al. 2017).

Several studies have confirmed the positive demographic effect of both supplementary feeding and red fox culling, reporting that red fox culling allowed an increase in arctic fox activity (Angerbjörn et al. 2003; Hamel et al. 2013), while supplementary feeding led to an increase in den occupancy, reproduction, litter size and number, and short-term pup survival (Angerbjörn et al. 1991; Tannerfeldt et al. 1994; Angerbjörn et al. 2003; Angerbjörn et al. 2013; Meijer et al. 2013). Additionally, the release of captive-bred individuals through the Norwegian Arctic Fox Captive Breeding Programme was highly successful and resulted in recolonization of three

historically inhabited arctic fox habitats, one of which is currently the largest arctic fox subpopulation in Norway (Ulvund et al. 2016; Landa et al. 2017). In 2015 a minimum of 127 arctic fox litters were born in Sweden and Norway, giving a minimum population size estimate of 254 adult foxes in Scandinavia (Eide et al. 2015). This was more than double, and possible four times greater than the estimated population size in 2000 (Angerbjörn et al. 2013).

While this demographic success provides optimism for the future viability of the arctic fox population, the genetic consequences of the implemented conservation actions have not yet been investigated. Theoretically, increasing connectivity and population size should lead to an increase in genetic diversity and long-term population viability (Ibrahim et al. 1996; Austerlitz et al. 1997; Ramakrishnan et al. 2010). However, despite demographic recovery, populations may still suffer from reduced genetic diversity due to genetic drift that occurs at reduced population size (Groombridge et al. 2000; Larson et al. 2002). Additionally, invasive management strategies such as translocation and reintroduction are associated with a number of risks including "contamination" or genetic swamping of unique remnant subpopulations (Berg 1982; Bertram and Moltu 1986; Sale 1986; Price 1989; Johnson 1990), as well as loss of genetic diversity due to small founder population size (Nei et al. 1975; Berry 1986; Lenney Williams et al. 2002; Maudet et al. 2002). Understanding how conservation actions affect spatial genetic structuring and levels of genetic diversity within fragmented populations is thus essential for understanding the effects of conservation on population viability (Allendorf and Luikart 2009; Hamilton 2011) and evaluating future conservation priorities.

In the present study, I will investigate genetic diversity and genetic structure in the fragmented mid-Scandinavian arctic fox population, with the aim of assessing (i) the extent to which genetic diversity and structure have changed during the past decade (from 2008 to 2015), (ii) how conservation efforts and rodent dynamics have influenced these potential genetic changes, and (iii) how the number and origin of dispersers have varied temporally.

Materials and Methods

Study species, demographic history, and management

The arctic fox (*Vulpes lagopus*) is a medium sized arctic carnivore with a circumpolar distribution in tundra and alpine habitats (Angerbjörn and Tannerfeldt 2014). Arctic foxes are highly adapted to arctic conditions (Fuglei and Ims 2008), and are found in two habitat dependent ecotypes – the "lemming fox" and the "coastal fox" (Braestrup 1941). In Fennoscandia, the arctic fox belongs to the lemming ecotype, feeding primarily on cyclic rodents such as lemmings and voles (Braestrup 1941; Elmhagen et al. 2000). As a result of this specialization, arctic foxes reproduce almost exclusively in the increase and peak phases of the rodent cycle, and population density varies greatly between years (Angerbjörn et al. 1995; Tannerfeldt and Angerbjörn 1998; Strand et al. 1999). Arctic foxes are capable of long-distance movements of more than 1000km (Eberhardt and Hansson 1978; Garrott and Eberhardt 1987; Strand et al. 2000). Such long distance dispersal movements are particularly common in "lemming" foxes (Angerbjörn et al. 2004; Dalén et al. 2005) and occur primarily in years with low lemming density (Braestrup 1941; Wrigley and Hatch 1976).

Following the dramatic population decline in the late 1800s, the once abundant arctic fox population was reduced to only a few hundred individuals distributed across a series of naturally fragmented "habitat islands"(Zetterberg 1945). The low-density populations that remained were more or less isolated, and many disappeared entirely in the post-protection period (Linnell et al. 1999). Between 1988 and 1998, breeding and activity were reported at Hardangervidda, Snøhetta, Børgefjell/Borgafjäll, Kjølifjellet, Blåfjellet/Skjækerfjellet, Hestkjølen, Saltfjellet, Dividalen, Sylane/Helags and Finnmark (Linnell et al. 1999; Direktoratet for Naturforvaltning 2003). However, the population at Børgefjell/Borgafjäll was the only stable population during this period (Linnell et al. 1999), and the population at Snøhetta appeared to have gone extinct in the mid-1990s (Linnell et al. 2004).

Between 1998 and 2008, the EU/LIFE projects SEFALO (1998-2002) and SEFALO+ (2003-2008) implemented supplementary feeding and red fox culling in several

Swedish mountain tundra regions including Helags, Borgafjäll, and Vindelfjällen (Angerbjörn et al. 2013). Between 2010 and 2014 the "Felles Fjellrev" project continued the implementation of red fox culling and supplementary feeding in the aforementioned Swedish regions, additionally implementing the same measures in intermediate "stepping stone" areas between core arctic fox subpopulations in the Norwegian mountain regions Knutshø, Kjølifjellet, Forollhogna, Hestkjølen, and Blåfjellet/Skjækerfjellet (Ericson 2014). The aim of the intervention was to stimulate dispersal between subpopulations and encourage recolonization of previously inhabited arctic fox territories.

The Norwegian Arctic Fox Captive Breeding Programme was established in 2005 (Linnell et al. 1999; Landa et al. 2017). Breeding adults for the program were captured as pups from the seven remaining subpopulations in Fennoscandia (n = 12 original founders) and crossed after careful genetic consideration. The principle focus was to maintain a healthy balance between founder lineages, thereby maintaining genetic diversity from throughout Fennoscandia (Landa et al. 2017). The first release of foxes from the captive breeding program occurred in 2006 at Saltfjellet in northern Norway (n = 2)(Landa et al. 2017). Since then, a total of 301 captive-bred foxes have been released at Saltfjellet (n = 65), Sylane (n = 5), Knutshø (n = 18), Snøhetta (n = 67), Finse (n = 74), and Hardangervidda (n = 72) (Ulvund et al. 2016; Landa et al. 2017). Supplementary feeding was implemented in release regions to encourage demographic growth after release (Angerbjörn et al. 2013). Furthermore, captive-bred foxes were released in January and February, after the harsh fall season when food is scarce and mortality among juveniles and adults is high (Meijer et al. 2008).

Since 1998, the intensity and implementation of red fox culling, supplementary feeding, and captive release have varied both spatially (between subpopulations) and temporally. At Børgefjell/Borgafjäll, both supplementary feeding and red fox culling were implemented, but no captive-bred individuals were released into the population (Angerbjörn et al. 2013; Ulvund et al. 2016). In contrast, released captive-bred individuals, many of whom had a genetic background from Børgefjell/Borgafjäll, were the founders of the re-established Snøhetta population (Landa et al. 2017). Furthermore, supplementary feeding was routinely carried out at Snøhetta following

the first release of captive-bred foxes in 2007, but red fox culling was never implemented (Ulvund et al. 2016). The population at Sylane/Helags experienced relatively strong management efforts throughout the study period, including supplementary feeding, red fox culling, and the release of a small number of captive-bred individuals (n = 5) (Ulvund et al. 2016). Finally, no captive-bred individuals were released in the "stepping stone" subpopulations, with the exception of 18 individuals released at Knutshø in 2008 (n = 4) and 2011 (n = 14) (Ulvund et al. 2016). All other recolonization events between 2008 and 2015 were thus the result of natural dispersal and establishment. For a detailed background of the genetic/geographic background of all captive-bred released foxes, see the Appendix, Table A1. For a full overview of the conservation actions implemented in the study area from 1999 onwards and the annual rodent abundance from 1999 onwards, see the Appendix, Table A2.

Data collection and sampling

The arctic fox samples analyzed in this study originate from eight subpopulations across mid-Scandinavia (Fig. 1) and were obtained during annual surveys of all known active den sites between 2008 and 2015. The sampling sites comprise the majority of suitable arctic fox habitat in mid-Scandinavia, covering an area of 10 300 km^2, and a linear distance North to South of 350 km. The populations at Børgefjell/Borgafjäll, Snøhetta, and Sylane/Helags are referred to as "core" subpopulations as they supported relatively large and stable populations throughout the study period. The remaining populations are referred to as "stepping stone" subpopulations, as they may play a role in facilitating dispersal between core populations. Many of the stepping stone subpopulations were recolonized during the course of the study, and as such, population sizes are low throughout the study.

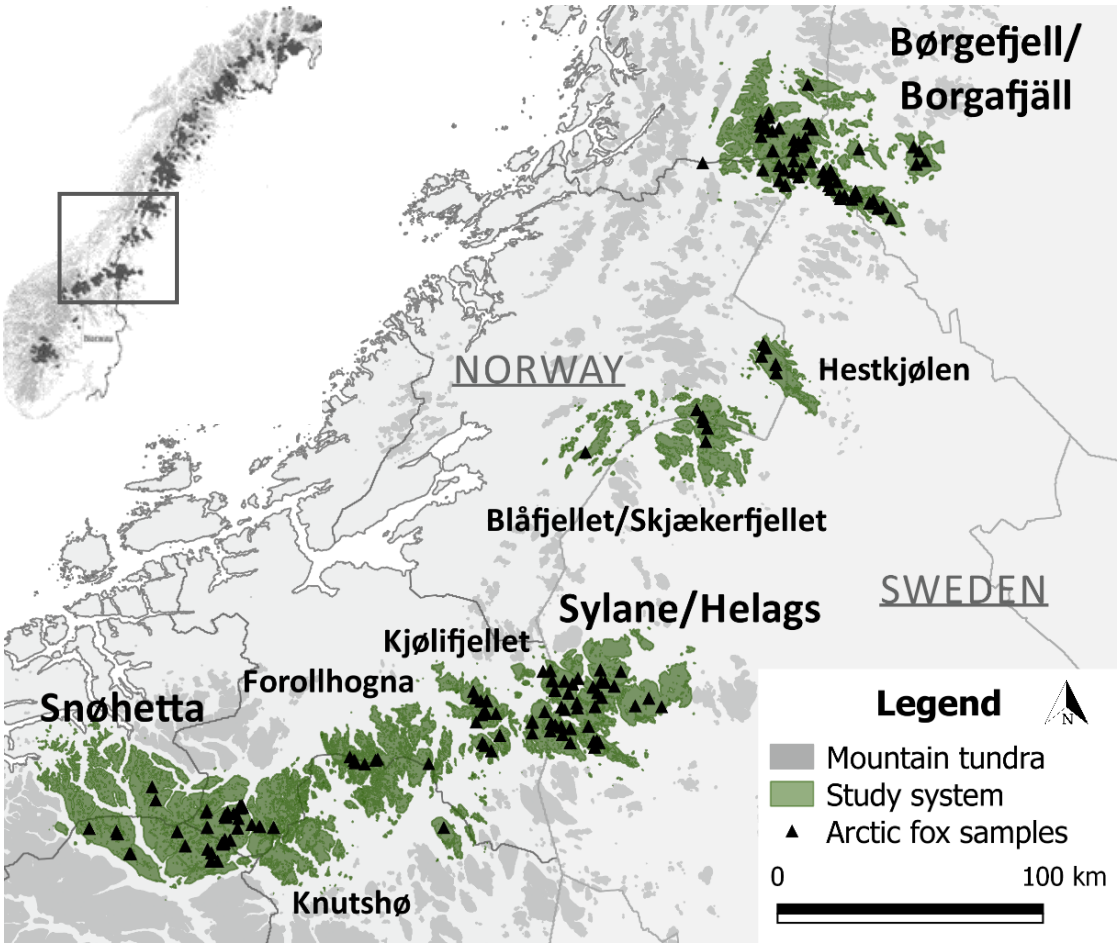

Figure 1. Map of the mountain tundra region in mid-Scandinavia. Dark green areas show the current distribution of the arctic fox, fragmented into eight subpopulations: Snøhetta, Knutshø, Forollhogna, Kjølifjellet, Sylane/Helags, Blåfjellet/Skjækerfjellet, Hestkjølen, and Børgefjell/Borgafjäll. Black triangles indicate geographical sampling locations (den sites) of arctic fox samples collected in mid-Scandinavia between 2008 and 2015. The inset map shows the location of all 645 known den localities in Scandinavia.

In Norway, hair and fecal samples (n = 2620) were collected between 2008 and 2015 from from Snøhetta (n = 840), Knutshø (n = 109), Forollhogna (n = 49), Kjølifjellet (n = 214), Sylane (n = 341), Blåfjellet/Skjækerfjellet (n = 125), Hestkjølen (n = 284), and Børgefjell (n = 658) as part of the national arctic fox monitoring program (Eide et al. 2015). Since mortality rates among young foxes are high during summer and early fall (Garrott and Eberhardt 1982; Tannerfeldt and Angerbjörn 1996; Loison et al. 2001; Meijer et al. 2008), the majority of fecal samples were collected between November 1st and June 1st. This ensured samples collected between November 1st in year *t* and June 1st in year *t + 1* provided a reliable estimate of the genetic composition of the adult (i.e. potentially reproductive) population for year *t + 1*. In Swedish

populations, tissue samples were collected each summer from live-caught pups within the Swedish Arctic Fox Conservation Program during annual ear-marking, and fecal samples were collected in winter during systematic den surveys. Swedish samples were processed at the University of Stockholm, and complete genotypes for n = 290 tissue samples and n = 47 fecal samples were provided to supplement our data for populations occurring along the Norwegian/Swedish border: Blåfjellet/Skjækerfjellet (including Sösjöfjällen on the Swedish side of the border), Sylane/Helags and Børgefjell/Borgafjäll. In order to incorporate the genetic profiles from the tissue samples of Swedish pups into my data set, it was again necessary to account for high pup mortality. To accomplish this, samples from two random pups per litter in year t were selected and used as proxies for the genetic variation represented by their parents in that year. The rest of the samples from each den were excluded from the analyses.

Further supplementation of the dataset was accomplished through review of recapture data from Biomark and Trovan chip readers which record the activity of biochip-marked foxes at the feeding stations (Landa et al. 2017). This allowed confirmation of fox survival and presence for years when physical samples (hair or feces) were lacking. To avoid overestimating population size or survival based on the Biomark and Trovan chip recapture data, only individuals recorded after the 1st of February each year were included in the final dataset. Finally, individual presence was included for intermediate years between recordings, so that for example, if an individual was registered in year t and year *t+3*, their presence was added in years *t+1* and *t+2*. All individuals were only recorded in one subpopulation per year, and intermediate recordings (ex. *t+1* and *t+2*) were assigned to the population in which they had been recorded in previous and subsequent years (ex. *t* and *t+3*).

Molecular analyses

Genomic DNA from n = 2100 Norwegian fecal samples was extracted using FastDNA's SPIN Kit for Soil following the manufacturer's protocol, and from hair samples using the DNeasy Tissue Kit (Qiagen, GmbH, Hilden, Germany) as described by Gagneux et al. (1997). Extracted DNA from all fecal samples was determined for species origin (arctic fox, red fox, or wolverine) following the feces identification method described

by Dalén et al. (2004). Fecal DNA extraction and polymerase chain reaction (PCR) setup were performed in a work area at NINA (Trondheim, Norway) dedicated for low-copy number DNA extractions, in a room separated from the post-PCR laboratory. One negative control well was used in each 96 well PCR plate to monitor for contamination during extraction. Microsatellite variation in DNA from hair and fecal samples was analyzed for 11 polymorphic loci previously developed and shown to be variable for the arctic fox: *CPH3*, *CPH9*, *CPH15* (Fredholm and Winterø 1995), *CXX140*, *CXX173*, *CXX250* (Ostrander et al. 1993), *377*, *606*, *671*, *758* and *771* (Ostrander et al. 1995). Amplification of DNA extracted from feces was carried out in 8.4 µl reactions containing 2.0 µl of DNA extract, 4.0 µl Qiagen multiplex mix, 1.6 µl RNase-free water, and 0.8 µl primer mix. The primer mix contained forward and reverse primers for all 11 microsatellite markers, giving final primer concentrations of 0.06 µM (*CXX140*), 0.08 µM (*CPH9, CXX173, 606*, *671*), 0.15 µM (*CPH3*, *CPH15, CXX250, 377, 771*), and 0.19 µM (*758*). PCR amplifications were performed using a Veriti 96-Well Thermal Cycler (Applied Biosystems). For the fecal samples, the following cycle parameters were used: 95 °C for 15min, followed by 35 cycles of 95 °C for 30 s, 57 °C for 90 s, and 72 °C for 60 s, followed by 60 °C for 30 min. The resulting PCR products were separated electrophoretically on an ABI 3130xl Genetic Analyzer (Applied Biosystems), using GeneScan-500 LIZ DNA Size Standard (Applied Biosystems). PCR set up and amplification for hair samples was carried out following the procedures outlined by Norén et al. (2005, 2016).

The low quality and small number of DNA copies in fecal and hair samples can cause allelic dropout during PCR (Gagneux et al. 1997). To control for this, each amplification was replicated three times. The results from genotyping were scored and interpreted using the software GENEMAPPER 4.0 (Applied Biosystems). Consensus genotypes were then constructed from the replicated PCR runs using the threshold rule that alleles had to appear at least twice to be accepted as heterozygous genotypes, and three times to be accepted as homozygous genotypes.

Quality control and data selection

Of the n = 2100 Norwegian samples analyzed, n = 1543 samples were confirmed to be of arctic fox origin, and n = 945 samples were successfully amplified and

genotyped for at least eight of the eleven loci. Following combination with the supplemental data from Sweden, all sample genotypes were matched using the Excel MS TOOLKIT 3.1 (Park 2001) to detect and exclude all within year repeats. The combined Norwegian/Swedish dataset had large amounts of missing data at locus *CPH15*, *606* and *671* (25%, 22%, and 21% respectively) and these loci were thus excluded from further analyses. After further supplementing the dataset with recapture data and data for intermediate years, the final dataset included n = 868 observations of n = 606 unique individuals from eight subpopulations between 2008 and 2015 (with a maximum of 4 % missing data per locus). Annual minimum population size estimates for all sampled subpopulations are shown in Figure 2, and a summary of this data is available in the Appendix (Table A3).

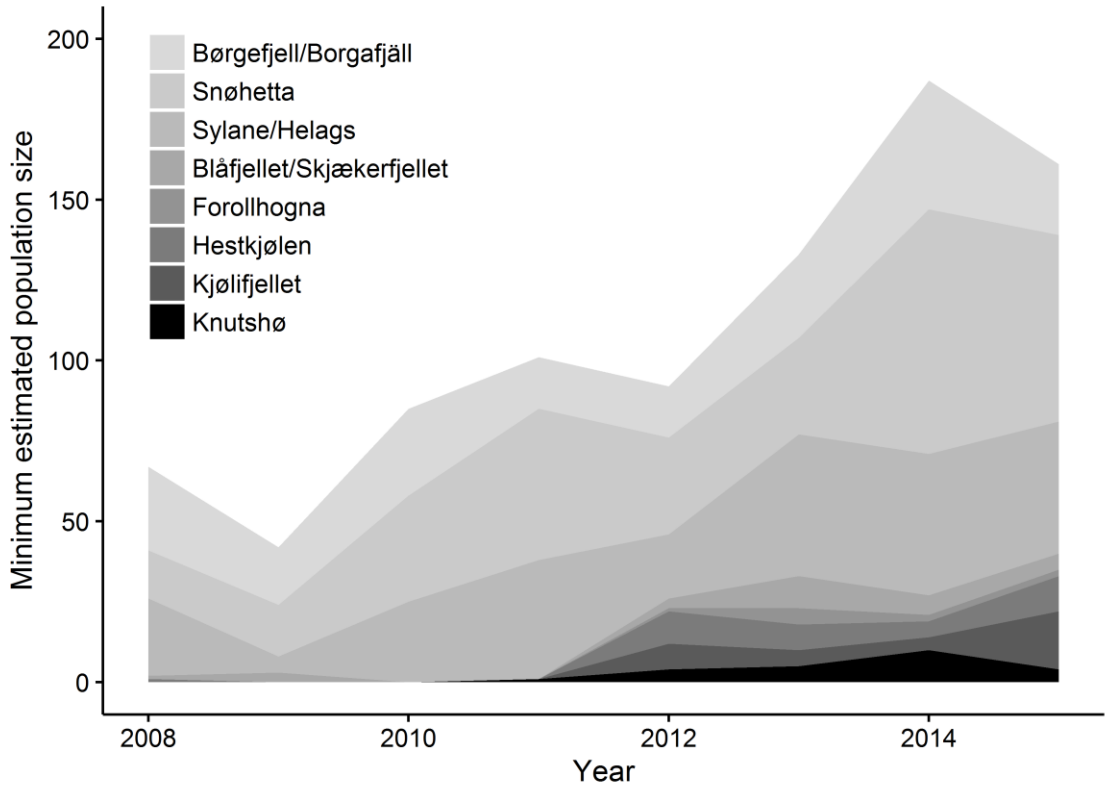

Figure 2. Minimum annual population size estimates for eight mid-Scandinavian arctic fox subpopulations between 2008 and 2015 based on DNA analysis of fecal, hair, and tissue samples, and supplemented with Trovan/Biomark chip recapture data.

To check the quality and reliability of the final microsatellite dataset, tests for null alleles, large allelic dropout, scoring errors due to stutter, deviations from Hardy-Weinberg equilibrium (HWE), and linkage disequilibrium (LD) were performed for

each population across all sampling years, including only unique multilocus genotypes. The probability of two individuals in a population sharing an identical multilocus genotype, or Probability of Identity (PI), was calculated per population per year. The probability of null allele presence, large allelic dropout, or scoring errors due to stutter was tested within a 95% confidence interval using the software MICRO-CHECKER 2.2.3 (Van Oosterhout et al. 2004). Probability of Identity (PI) was calculated using GENALEX 6.5 (Peakall and Smouse 2006, 2012). Potential deviations from Hardy-Weinberg equilibrium (HWE) and linkage disequilibrium (LD) between pairs of loci were tested using Markov chain exact tests (1000 dememorization steps, 5000 batches with 10000 iterations per batch) in GENEPOP 4.2 (Raymond and Rousset 1995; Rousset 2008). To account for the multiple comparisons performed, the Bonferroni correction (Dunn 1961; Rice 1989) was applied to both HWE tests and pairwise LD tests.

Across all years, the probability of two individuals in a population sharing an identical multilocus genotype was $< 3.5 \times 10^{-4}$. Estimates of null allele frequencies suggested possible null alleles in four loci in three populations. However, since null alleles are likely to occur systematically in the same loci across populations and this was not observed, it was considered unlikely that this deviation was due to non-amplified alleles. All loci were therefore retained based on this quality control. After applying the Bonferroni correction (Bonferroni corrected *p*-value = 0.008), three loci in three populations showed significant departures from HWE frequencies (see Appendix, Table A4). As deviation was only detected in 4 out of 64 possible locus-population combinations (8 loci X 8 populations), and no systematic deviation was evident across populations, all loci were retained based on this test. Results of the pairwise LD tests (Bonferroni corrected *p*-value = 0.0002) revealed significant linkage between 17 pairs of loci distributed across four subpopulations (see Appendix, Table A5). More than 50% of the linked locus pairs occurred in the Snøhetta population. However, since none of the loci were consistently linked across subpopulations and deviation was only detected in 31 out of 224 possible locus pair -population combinations (28 locus pairs X 8 populations), all eight loci were kept for subsequent analyses. These initial tests are in accordance with previous genetic studies of the Scandinavian arctic fox which have described variation at these loci and verified their

independence and reliability (Norén et al. 2005; Dalén et al. 2006; Nyström et al. 2006).

Statistical analyses

Using GENALEX 6.5 (Peakall and Smouse 2006, 2012), yearly estimates of genetic diversity for each subpopulation were calculated as the average number of alleles per locus (hereafter referred to as average allelic diversity, n_A), average unbiased expected heterozygosity (hereafter referred to as average expected heterozygosity, H_E), and average observed heterozygosity (H_O). Furthermore, average individual multilocus heterozygosity (I_{MLH}) was calculated in R (R Core Team 2016) as the proportion of heterozygous loci observed, divided by the total number of loci typed for each individual (Hansson et al. 2004), and averaged for each population each year. Genetic differentiation among subpopulations (F_{ST}; Wier and Cockerham 1984) was estimated annually at the metapopulation level, and for subpopulation pairs (pairwise F_{ST}) using GENALEX 6.5 (Peakall and Smouse 2006, 2012). All diversity and differentiation parameters were tested for normality and homogeneity of variance prior to further analyses.

As the arctic fox has a generation length of four years (Linnell et al. 2004), many individuals were represented in multiple sampling years. This created non-independence in diversity and differentiation estimates between years, and as such, parameter estimates and *p*-values from linear regression analyses would have to be interpreted with caution. In order to account for this non-independence, significant temporal variation in diversity and differentiation estimates was assessed by comparing a subset of data including all unique individuals present in 2008/2009 (n = 90) to a subset of data including all unique individuals present in 2014/2015 (n = 288), using a linear mixed model approach in the *lme4* package in R (Bates et al. 2014; R Core Team 2016). Only three individuals were present in both 2008/2009 and 2014/2015, and estimates from these two time periods were therefore assumed to be independent.

For diversity parameters measured at the locus level (n_A, H_E, H_O), differences in average population level diversity between the two sampling periods (2008/2009 vs 2014/2015) were tested including locus as a random factor and population as a fixed

factor. For average I_{MLH}, differences in average population estimates between sampling periods (2008/2009 vs 2014/2015) were tested including population as a fixed factor. Significant interactions between sampling period and population were also tested for all diversity parameters. For the stepping stone populations, insufficient data from 2008/2009 made statistical analysis of temporal change in these subpopulations unreliable. For this reason, temporal differences in genetic diversity between 2008/2009 and 2014/2015 were only tested for the three core populations: Børgefjell/Borgafjäll, Snøhetta, and Sylane/Helags.

To investigate the effects of management efforts (supplemental feeding, red fox culling, and population supplementation/reintroduction) and rodent abundance on inter-annual change in genetic diversity, I composed global models for each diversity parameter (n_A, H_E, H_O, I_{MLH}). In the global models, supplemental feeding, red fox culling and the release of captive-bred individuals were included as continuous covariates, while rodent phase and population were included as fixed factors (Equation 1). Data from all eight subpopulations were included in these analyses.

(1) $\Delta Diversity \sim DensFed_t + RedCulled + ReleasedFoxes_t + RodentPhase_t + Population$

Inter-annual changes in the respective diversity parameters were calculated by subtracting estimates in year *t* from estimates in year *t+1*. Supplementary feeding, red fox culling, and population supplementation/reintroduction were quantified as the number of dens fed (DensFed), the number of red foxes culled (RedCulled), and the number of captive-bred individuals released (ReleasedFoxes) annually in each population, respectively. Rodent abundance (RodentPhase) was classified into four phases: (1) low, (2) increase, (3) peak, and (4) decline, following Angerbjörn et al. (2013). For each diversity parameter, I started by testing the global model that included the main effects of all the factors and covariates. I then proceeded to test all the models nested within the global model using the R package *gmulti* (Calcagno and de Mazancourt 2010; R Core Team 2016). To select the most appropriate model explaining variation in inter-annual change in each of the diversity parameters, I used a modification of Akaike's information criterion (AIC) suitable for small sample sizes (AICc; Burnham and Anderson 2002) and examined r^2 values. The model with the lowest AICc value was assumed to be the most parsimonious model (i.e. the

''best'' model). To further examine the relative likelihood of each model given the data and the set of tested models, I calculated the Akaike weights, w_i, of each model *i*. According to Burnham and Anderson (2002), when models deviated with less than two AICc-units from the best model, and the Akaike weight is small, the most biologically relevant model should be chosen. Based on this knowledge, all models with AICc values within two AICc-units of the best model were retained and considered in my presentation of the results.

To investigate temporal variation in the population structure of the arctic fox in mid-Scandinavia, I tested for differences in estimates of metapopulation level F_{ST} and pairwise F_{ST}, respectively, between the two sampling periods (2008/2009 and 2014/2015). To test differences in metapopulation level F_{ST}, I used a linear mixed model approach in the *lme4* package in R (Bates et al. 2014; R Core Team 2016), including locus as a random factor. Differences in pairwise F_{ST} estimates between the two sampling periods for comparisons between core populations, and core and stepping stone populations were tested using a linear model approach, and pairwise t-tests in R (R Core Team 2016). Temporal variation in pairwise F_{ST} between stepping stone populations was not evaluated due to insufficient data from 2008/2009.

To identify genetic clusters in the metapopulation, a Bayesian Markov Chain Monte Carlo (MCMC) approach was employed using the software STRUCTURE 2.3.4 (Pritchard et al. 2000). The program calculates the log likelihood $\Pr(X|K)$, i.e. the probability of the observed genotypes (X) given a pre-assigned number of genetic clusters (K) in a dataset, and assigns individuals to population clusters accordingly. For each year (2008 to 2015), I independently ran an admixture model with correlated allele frequencies, without using sampling location as a prior. The predetermined number of clusters ranged from one to eight, to include all potential geographical clusters, and ten independent runs were performed for each predefined number of clusters tested. Each run was performed with a burn-in length of 200 000 steps and 500 000 MCMC iterations. To interpret the results from STRUCTURE, I first calculated the probability of each K ($\mathrm{P}(K|X)$) according to the recommendations from Pritchard et al. (2000). Thereafter, I followed the recommendations by Evanno et al. (2005) to determine the most probable number of clusters each year (based on the calculation of the ΔK statistic). Finally, the 10 replicates for each year's STRUCTURE analysis were further

summarized using the software CLUMPP 1.1.2 (Jakobsson and Rosenberg 2007). To further investigate the genetic population structure, a principle component analysis (PCA) was performed separately for each year (2008 to 2015) using the R package *adegenet* (Jombart 2008; Jombart and Ahmed 2011; R Core Team 2016).

To determine the origin (local or immigrant) of arctic fox recruits between 2009 and 2015, I used the maximum likelihood assignment test method implemented in ONCOR (Kalinowski et al. 2007). Based on the results of the aforementioned STRUCTURE analysis, two reference clusters were predefined. In ONCOR, the *Individual Assignment* option was then used to assign each of the new recruits for a particular year (*t*) to the two predefined genetic clusters, based on baseline allele frequencies of these clusters in the previous year (*t-1*). Thus immigrants from 2008 to 2009 were identified by testing assignment of all recruits from the 2008 cohort (i.e. born in 2008 and recorded as present in 2009 and/or later) to each of the two clusters, based on the genetic composition of the adult population in each of the clusters in 2008. For assigning a recruit to a cluster, we used a threshold value (Q) of 0.9. Individuals that assigned ($Q > 0.9$) to a cluster other than that in which they were sampled were considered immigrants.

Results

Temporal changes in genetic diversity within subpopulations

A general increase in average allelic diversity (n_A) was observed across all core populations (Børgefjell/Borgafjäll, Snøhetta, Sylane/Helags) between 2008 and 2015 (Fig. 3a). Average n_A at both Børgefjell/Borgafjäll and Snøhetta increased gradually over time and was significantly higher in 2014/2015 than in 2008/2009 for both populations (Table 1). At Sylane/Helags, average n_A was lower than at either Børgefjell/Borgafjäll and Snøhetta in 2008/2009 (vs. Børgefjell/Borgafjäll: t = -2.594, p < 0.05; vs. Snøhetta: t = -2.075, p = 0.057), although this difference was only significant for the Sylane/Helags – Børgefjell/Borgafjäll comparison. Between 2008/2009 and 2014/2015, average n_A at Sylane/Helags increased by more than 50% (t = 5.351, p < 0.01; Table 1). As a consequence, average n_A at Sylane/Helags was the same as at both Børgefjell/Borgafjäll (t = 0.288, p = 0.778) and Snøhetta (t = 1.000, p = 1.000) by 2014/2015. In the stepping stone populations, average n_A also showed a general pattern of increase over time (Fig. 3b). However, high temporal variation associated with founder effects and small population sizes made interpretation of trends difficult.

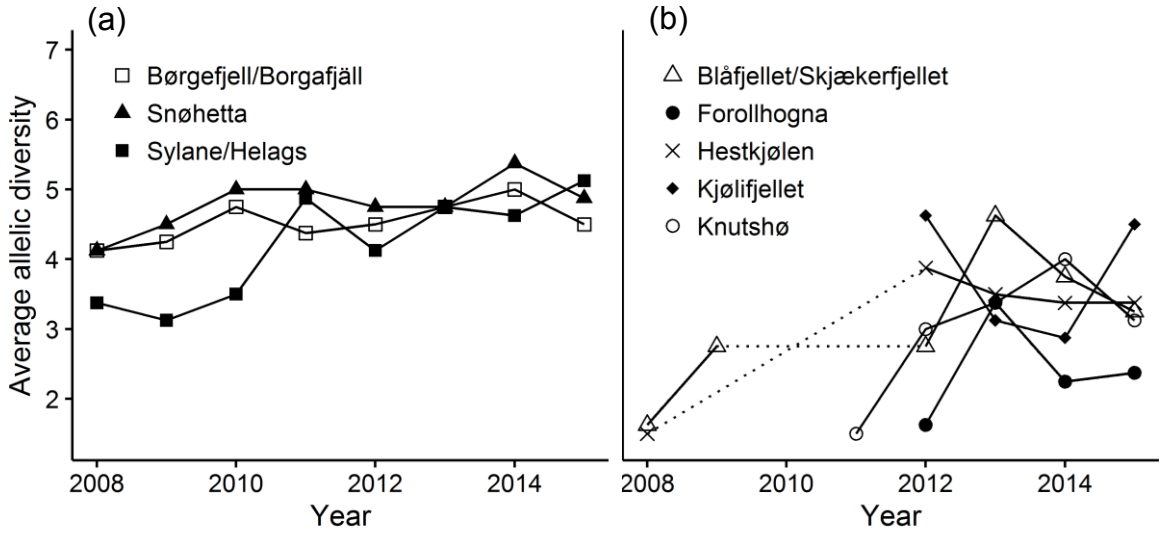

Figure 3. Annual changes in average allelic diversity (n_A) between 2008 and 2015 in (a) core and (b) stepping stone arctic fox subpopulations in mid-Scandinavia. Dotted lines indicate interpolated values for intermediate years with missing data.

Table 1. Mean, and mean difference in four measures of genetic diversity (allelic diversity (n_A), expected heterozygosity (H_E), observed heterozygosity (H_O), and individual multilocus heterozygosity (I_{MLH})) as estimated in three core arctic fox subpopulations in mid-Scandinavia in 2008/2009 and 2014/2015. *p*-values < 0.05 are indicated in bold.

		2008/2009	**2014/2015**	**Difference**			
Parameter	Population	Mean ± SE	Mean ± SE	Mean±SE	df	*t*-value	*p*-value
n_A	Børgefjell/Borgafjäll	4.750 ± 0.412	5.250 ± 0.453	0.500 ± 0.189	7	2.646	**0.033**
	Snøhetta	4.500 ± 0.423	5.375 ± 0.498	0.875 ± 0.227	7	3.862	**0.006**
	Sylane/ Helags	3.500 ± 0.327	5.375 ± 0.324	1.875 ± 0.350	7	5.351	**0.001**
H_E	Børgefjell/Borgafjäll	0.586 ± 0.039	0.613 ± 0.031	0.027 ± 0.032	7	0.844	0.426
	Snøhetta	0.641 ± 0.050	0.676 ± 0.046	0.035 ± 0.032	7	1.099	0.308
	Sylane/ Helags	0.576 ± 0.055	0.609 ± 0.044	0.033 ± 0.029	7	1.131	0.295
H_O	Børgefjell/Borgafjäll	0.589 ± 0.048	0.608 ± 0.043	0.020 ± 0.051	7	0.390	0.708
	Snøhetta	0.699 ± 0.066	0.704 ± 0.053	0.005 ± 0.063	7	0.080	0.939
	Sylane/ Helags	0.601 ± 0.061	0.584 ± 0.047	-0.018 ± 0.038	7	-0.461	0.658
I_{MLH}	Børgefjell/Borgafjäll	0.589 ± 0.034	0.606 ± 0.023	0.017 ± 0.040	90	0.423	0.673
	Snøhetta	0.699 ± 0.035	0.704 ± 0.017	0.005 ± 0.040	111	0.115	0.908
	Sylane/Helags	0.602 ± 0.031	0.583 ± 0.021	-0.018 ± 0.039	110	-0.469	0.640

Neither average expected heterozygosity (H_E) or average observed heterozygosity (H_O) showed any significant difference between 2008/2009 and 2014/2015 in any of the core subpopulations (Fig. 4a, c; Table 1). At Børgefjell/Borgafjäll and Sylane/Helags, average H_O showed high inter-annual variation, while average H_E and H_O at Snøhetta remained relatively high and stable throughout the study period (Fig. 4a, c). Average H_O was significantly higher at Snøhetta than at both Børgefjell/Borgafjäll and Sylane/Helags throughout the study period (vs. Børgefjell/Borgafjäll: $t = 2.101$, $p < 0.05$; vs. Sylane/Helags: $t = 2.213$, $p < 0.05$), while there was no significant difference in average H_E (vs. Børgefjell/Borgafjäll: $t = 1.554$, $p = 0.129$; vs. Sylane/Helags: $t = 1.731$, $p = 0.092$). The stepping stone subpopulations showed a general increase in average H_E over time (Fig. 4b, 4d). However, interpretation of trends in both average H_E and average H_O was difficult due to high temporal variation associated with founder effects and small population size. Average individual heterozygosity (I_{MLH}) showed a temporal trend similar to average H_O in both the core and stepping stone subpopulations but displayed slightly less within year variance (see Table 1).

Influence of conservation efforts on genetic diversity

The analyses revealed that the most parsimonious models explaining variation in all four measures of genetic diversity (H_E, H_O, n_A, I_{MLH}) included only the intercept (Table 2). As one or two models had AICc-values within two AICc-units of the most parsimonious model for each diversity measure, these models were also considered as relevant in explaining the observed variation in genetic diversity (Burnham and Anderson 2002). The number of red foxes shot, the number of captive-bred foxes released, and the rodent phase were included in multiple "top-ranked" models (i.e. $\Delta AICc < 2$) , however none of these parameters explained significant proportions of the observed inter-annual variation in the respective diversity measures (Table 3), and the majority of the models explained less than 2% of the total variance (r^2 values from Table 2). Rodent phase explained between 14 -16 % of the observed inter-annual variation in H_O and I_{MLH} (r^2 of model 2, Table 2c; r^2 of model 2, Table 2d), and was the only variable displaying near-significant parameter effect sizes (Table 3).

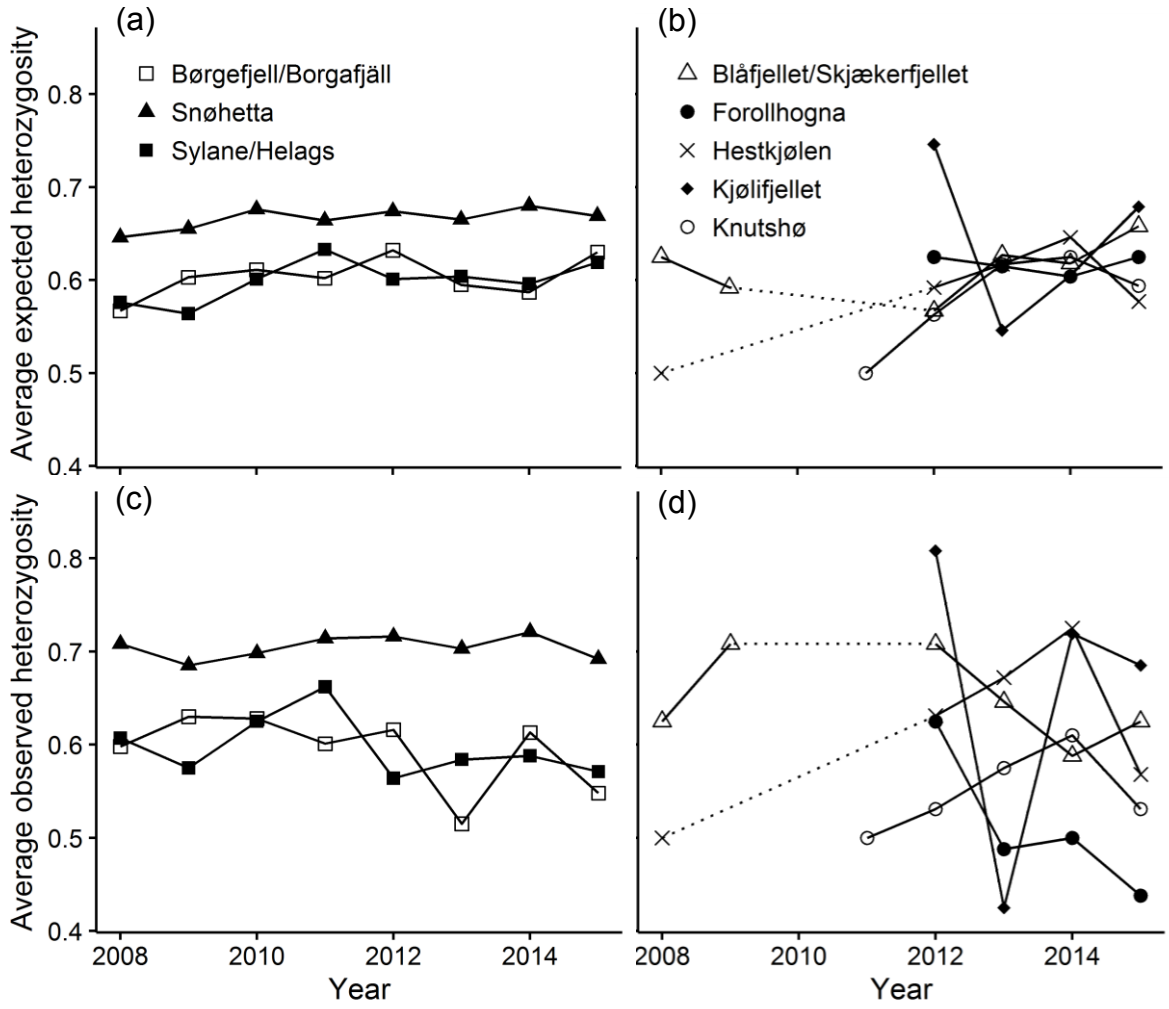

Figure 4. Annual changes in average expected heterozygosity (H_E) in (a) core and (b) stepping stone arctic fox subpopulations, and average observed heterozygosity (H_O) in (c) core and (d) stepping stone arctic fox subpopulations in mid-Scandinavia between 2008 and 2015. Dotted lines indicate interpolated values for intermediate years with missing data.

Table 2. AICc ranking of generalized linear models testing whether conservation efforts (DensFed, RedCulled, ReleasedFoxes) and rodent phase (RodentPhase) explain variation in inter-annual variation in four measures of genetic diversity in mid-Scandinavian arctic fox populations between 2008 and 2015. Only models within 2 AICc-units of the best model for each diversity parameter are shown here. The measures of genetic diversity are (a) average allelic diversity (n_A), (b) average expected heterozygosity (H_E), (c) average observed heterozygosity (H_O), and (d) average individual multilocus heterozygosity (I_{MLH}). AICc for the top-ranked models (Rank 1) were (a) 93.06, (b) - 21.99, (c) -65.90 and (d) -64.83.

	Rank	Models	K	ΔAICc	*w*AICc	r^2
(a) n_A						
	1	Intercept	1	0	0.349	0.0
	2	RedCulled	2	1.636	0.154	0.019
	3	ReleasedFoxes	2	1.705	0.149	0.017
(b) H_E						
	1	Intercept	1	0	0.397	0.0
	2	RedCulled	2	1.8	0.162	0.015
(c) H_O						
	1	Intercept	1	0	0.275	0.0
	2	RodentPhase	4	0.893	0.176	0.160
	3	RedCulled	2	1.956	0.104	0.011
(d) I_{MLH}						
	1	Intercept	1	0	0.301	0.0
	2	RodentPhase	4	1.43	0.148	0.149

Temporal changes in genetic structure

At the metapopulation level, genetic differentiation (F_{ST}) decreased by 49% over the study period, from 0.235 (± 0.036) in 2008/2009 to 0.120 (± 0.012) in 2014/2015 (t = -2.425, p < 0.05; Fig. 5a). Average pairwise F_{ST} between the core populations showed a gradual but non-significant decrease over time from 0.073 (± 0.019) in 2008/2009 to 0.050 (± 0.014) in 2014/2015 (t = -0.959, p = 0.392; Fig. 5b). F_{ST} between Snøhetta and Børgefjell/Borgafjäll remained stable throughout the study period. For pairwise comparisons between the core and stepping stone populations, the reduction in differentiation was much more dramatic, with F_{ST} decreasing by 68% from 0.201 (± 0.046) in 2008/2009 to 0.065 (± 0.008) in 2014/2015 (t = -4.431, p < 0.001; Fig. 5c). For pairwise comparisons between stepping stone populations, a general pattern of decreased differentiation was observed (Fig. 5d). However, interpretation of the trends was difficult due to small population size.

Table 3. Parameter estimates and levels of significance are from univariate generalized linear models testing the effects of conservation efforts (DensFed, RedCulled, ReleasedFoxes), and rodent abundance (RodentPhase) on inter-annual change in four measures of genetic diversity in arctic foxes sampled in eight mid-Scandinavian subpopulations between 2008 and 2015. The measures of genetic diversity are (a) average allelic diversity (n_A), (b) average expected heterozygosity (H_E), (c) average observed heterozygosity (H_O), and (d) average individual multilocus heterozygosity (I_{MLH}).The top-ranked models based on AICc are shown (see Table 2). For the Likelihood Ratio Tests, the chi-square statistic gives the difference in -2 log-likelihoods between the model presented and a reduced model, including only the intercept.

			Parameter estimates				**Likelihood Ratio Tests**		
	Rank	Models	Parameter	*Estimate* ± *SE*	*t*-value	*p*-value	Chi-Square	df	Sig.
(a) n_A	*2*	RedShot	Red Shot	0.003 ± 0.003	0.834	0.410	0.728	1	0.394
	3	ReleasedFoxes	Released Foxes	0.020 ± 0.025	0.794	0.433	0.659	1	0.417
(b) H_E	*2*	RedShot	Red Shot	0.000 ± 0.000	0.733	0.468	0.564	1	0.453
(c) H_O	*2*	RodentPhase	Rodent Phase 1	-0.054 ± 0.074	-1.846	0.074	6.639	3	0.084
			Rodent Phase 2	0.067 ± 0.038	1.773	0.085			
			Rodent Phase 3	-0.018 ± 0.026	-0.680	0.501			
			Rodent Phase 4	-0.009 ± 0.031	-0.276	0.784			
	3	RedShot	Red Shot	-0.000 ± 0.000	-0.623	0.537	0.407	1	0.523
(d) I_{MLH}	*2*	RodentPhase	Rodent Phase 1	-0.053 ± 0.030	-1.758	0.088	6.108	3	0.107
			Rodent Phase 2	0.066 ± 0.039	1.699	0.098			
			Rodent Phase 3	-0.018 ± 0.026	-0.674	0.505			
			Rodent Phase 4	-0.011 ± 0.032	-0.359	0.722			

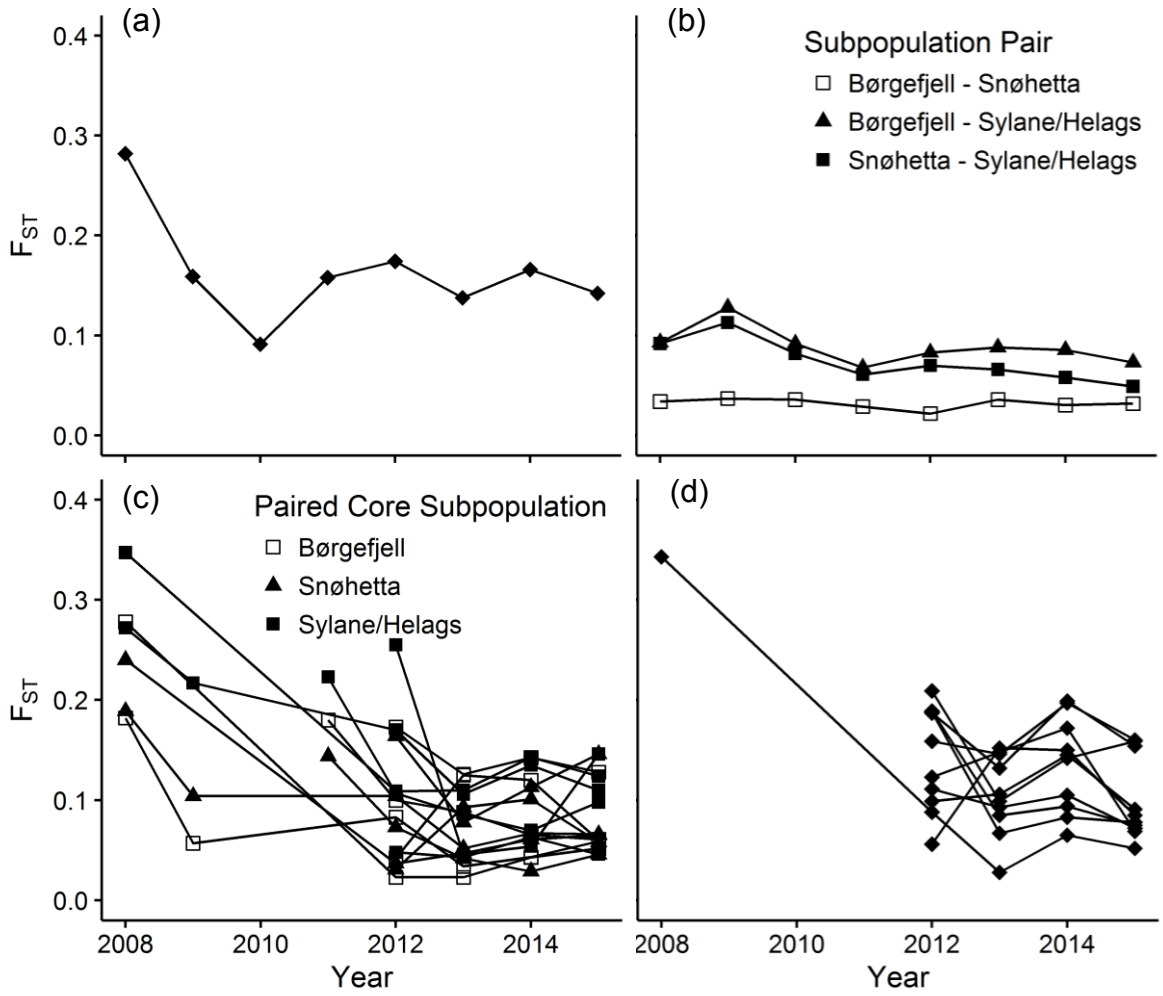

Figure 5. Annual changes in genetic differentiation (F_{ST}) between arctic fox subpopulations in mid-Scandinavia between 2008 and 2015 measured as (a) global metapopulation differentiation, (b) pairwise differentiation between core subpopulations, (c) pairwise differentiation between core and stepping stone subpopulations (Knutshø, Forollhogna, Kjølifjellet, Blåfjellet/Skjækerfjellet, and Hestkjølen), and (d) pairwise differentiation between stepping stone subpopulations.

After employing the Evanno method (Evanno et al. 2005), results of the STRUCTURE analyses suggested that the most appropriate number of genetic clusters was $K = 2$ for all years. The majority of samples from Børgefjell/Borgafjäll and Snøhetta assigned consistently to one cluster while samples from Sylane/Helags assigned predominantly to the other (Fig. 6). The results of the principal component analysis (PCA) complemented the STRUCTURE results, confirming the aforementioned clustering pattern, and revealing a clear genetic distinction between the Børgefjell/Borgafjäll-Snøhetta cluster and the Sylane/Helags cluster in 2008 and up until 2010 (Fig. 7). For the stepping stone subpopulations, assignment and association patterns varied over time providing insight into the origin of founders

and migrants to these populations. Samples from Blåfjellet/Skjækerfjellet, Hestkjølen, and Knutshø assigned mainly to the Børgefjell/Borgafjäll-Snøhetta cluster (Fig. 6), and the PCA confirmed the close genetic associations between these populations (Fig. 7). Samples from Kjølifjellet and Forollhogna, on the other hand, showed greater assignment and association to the Sylane/Helags cluster (Fig. 6; Fig. 7). In contrast to the homogenous assignment patterns observed at Blåfjellet/Skjækerfjellet and Hestkjølen, the stepping stone subpopulations between Snøhetta and Sylane/Helags (Knutshø, Forollhogna, and Kjølifjellet) showed relatively high temporal variation in assignment, particularly in the initial years after recolonization (Fig. 6). By 2014/2015 however, these subpopulations assigned more consistently to one of the two main clusters. The PCA revealed a substantial decrease in metapopulation differentiation over the course of the study, illustrated by the gradual increase in association between the subpopulation clusters (Fig. 7). A similar pattern was confirmed by the STRUCTURE analyses which shows a gradual increase in assignment heterogeneity over time, particularly in the core subpopulations (Fig. 6).

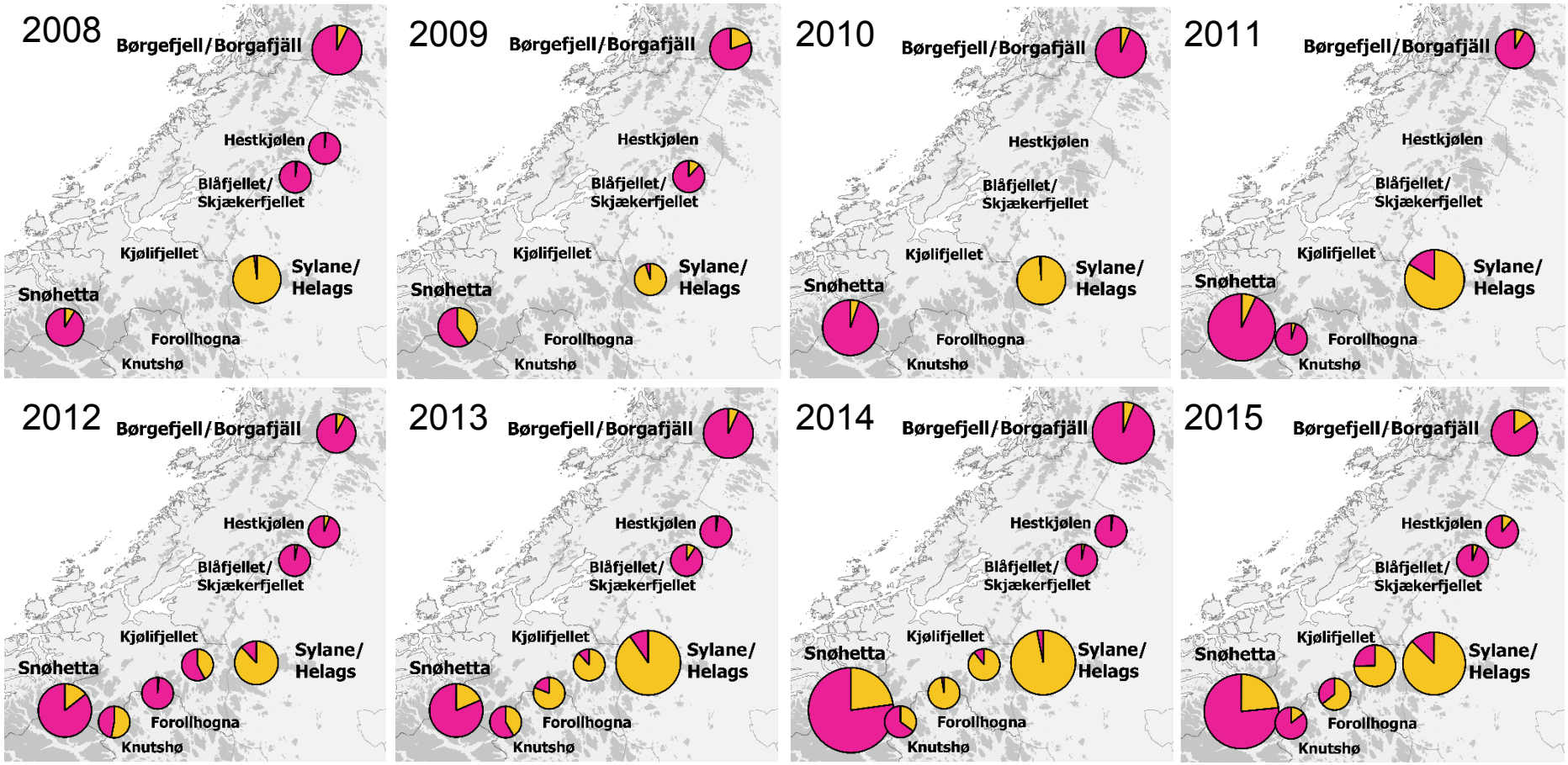

Figure 6. Maps showing population level assignment of eight mid-Scandinavian arctic fox populations to $K = 2$ genetic clusters, as inferred by STRUCTURE analyses each year from 2008 to 2015. The first cluster is indicated in yellow and the second cluster is indicated in violet. Cases where populations show partial assignment to both clusters indicate immigration and admixture. Assignment pies are scaled based on population size. The smallest pies represent $n \leq 15$, while the largest pies represent $n \geq 75$.

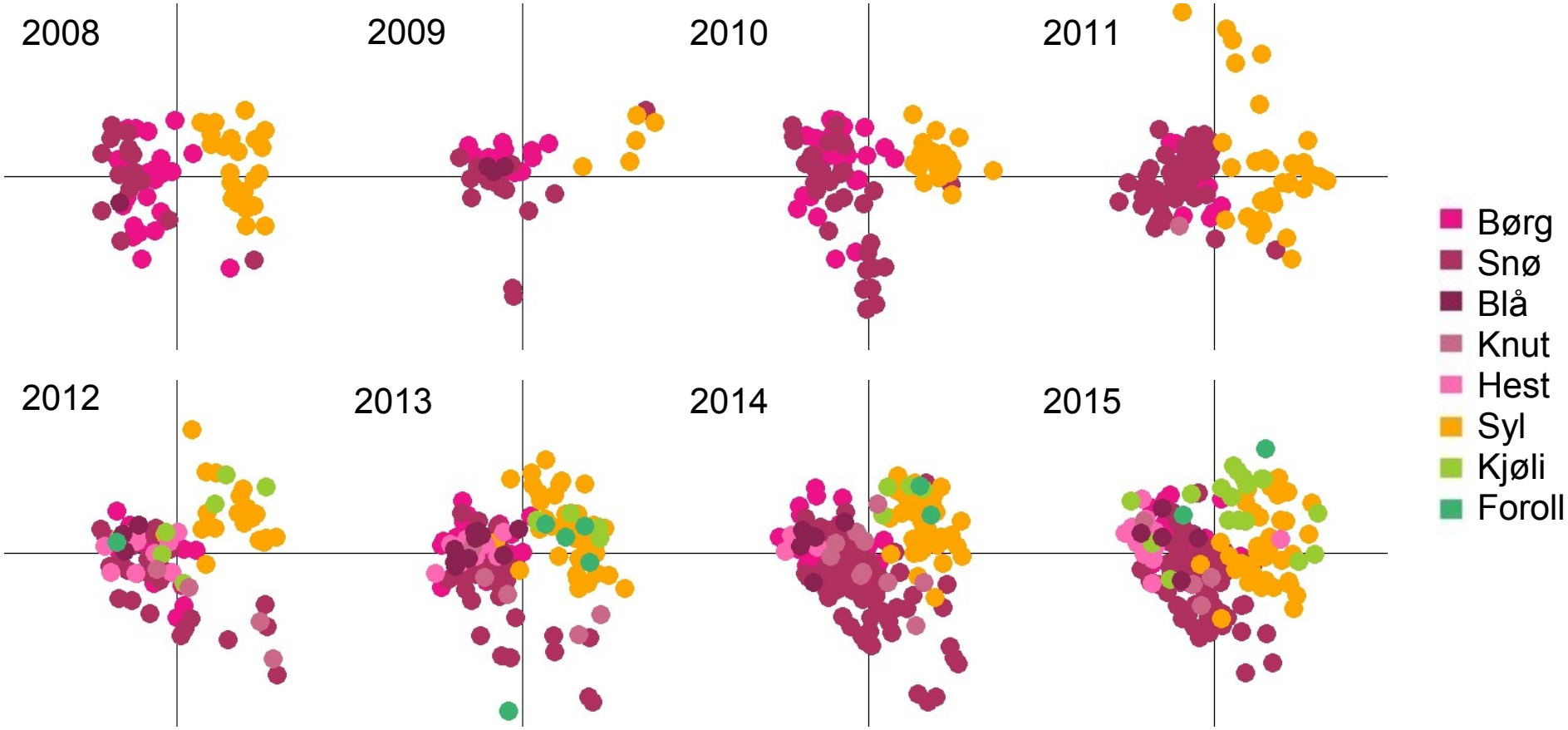

Figure 7. Principal component analysis (PCA) showing the genetic clustering of eight arctic fox subpopulations in mid-Scandinavia each year from 2008 to 2015. The eight subpopulations include Børgefjell/Borgafjäll (Børg), Snøhetta (Snø), Blåfjellet/Skjækerfjellet (Blå), Knutshø (Knut), Hestkjølen (Hest), Sylane/Helags (Syl), Kjølifjellet (Kjøli), and Forollhogna (Foroll). The x-axis represents the first principal component (PC1), and the y-axis represents the second principal component (PC2). Across years, PC1 explained an average of 11.44% of the variance (min = 9.05, max = 14.55), while PC2 explained an average of 8.31% of the variance (min = 7.28, max = 10.86).

Temporal changes in immigration

Dispersal between the Sylane/Helags area (including Kjølifjellet and Forollhogna), Børgefjell/Borgafjäll area (including Hestkjølen and Blåfjellet/Skjækerfjellet), and Snøhetta area (including Knutshø) as inferred by assignment tests in ONCOR, showed an overall increase throughout the study period (Fig. 8). In 2009 and 2010 no immigrant recruits were detected, and in both years, only a single individual (sampled at Børgefjell) showed mixed assignment. Starting in 2011, a marked increase in immigration to Sylane/Helags was observed. In 2011, seven recruits at Sylane/Helags assigned genetically to the Børgefjell/Borgafjäll–Snøhetta cluster, and in 2012 eight recruits at Sylane/Helags assigned genetically to the Børgefjell/Borgafjäll–Snøhetta cluster, comprising 20% and 31% of the new recruits for each respective year. The first immigrants to Børgefjell/Borgafjäll were detected in 2013, where three sampled recruits assigned to the Sylane/Helags cluster, and the first migrant to Snøhetta was detected in 2014. In 2015, immigrant recruits were detected in all three areas, with particularly high immigration to Sylane/Helags where 14 % of the new recruits assigned to the Børgefjell/Borgafjäll-Snøhetta cluster. In parallel with the increase in detected dispersers, the proportion of individuals not clearly assigning to any one cluster also increases over the study period, likely reflecting offspring of reproducing immigrants and native foxes.

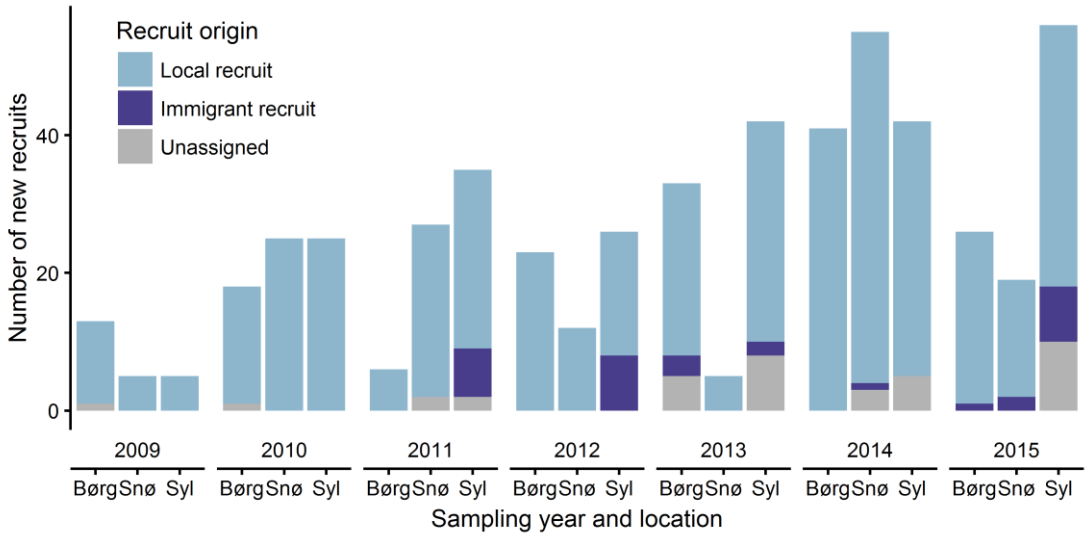

Figure 8. Origin of annual recruits (local or immigrant, see text for details) in the Børgefjell/Borgafjäll area (Børg; including Børgefjell/Borgafjäll, Hestkjølen and Blåfjellet/Skjækerfjellet), Snøhetta area (Snø; including Snøhetta and Knutshø), and Sylane/Helags area (Syl; including Sylane/Helags, Kjølifjellet and Forollhogna).

Discussion

Over the past decade, the arctic fox population in mid-Scandinavia has more than doubled in size, dispersal between subpopulations has increased, and a number of historical subpopulations have been recolonized. In parallel with these demographic changes, my results show that genetic diversity within subpopulations has increased, while genetic structuring and differentiation between subpopulations have decreased. The implementation of conservation efforts aimed at supporting the endangered arctic fox population has likely influenced these genetic changes both directly and indirectly, by reducing environmental resistance, facilitating increased reproduction, and promoting density-dependent dispersal.

In general, genetic diversity increased in all subpopulations during the course of the study. Notably, my estimates of genetic diversity from 2008/2009 show similar levels of average expected and observed heterozygosity at Børgefjell/Borgafjäll and Sylane/Helags, compared with diversity levels reported by Dalén et al. (2006) for the same populations and loci up to a decade before. This suggests that the observed increase in genetic diversity did not occur immediately following the initial implementation of conservation actions, including red fox culling and supplementary feeding between 1998 and 2008 (Appendix, Table A2). Rather, genetic changes seem to have occurred as a delayed response to these actions and/or as a result of the release of individuals from the captive breeding program, and the additional implementation of red fox culling and supplementary feeding in the stepping stone areas between 2007 and 2015.

While genetic diversity showed a general increase in all subpopulations, the observed changes were most pronounced at Sylane/Helags, where average allelic diversity increased by 50% between 2008/2009 and 2014/2015 (Fig. 3a). Multiple studies indicate that outcrossing by just a few individuals into a small and inbred population may replenish genetic variation, thereby preventing inbreeding depression (Spielman and Frankham 1992; Ebert et al. 2002) and increasing fitness (Westemeier et al. 1998; Madsen et al. 1999; Hogg et al. 2006; Johnson et al. 2010; Heber et al. 2013; Frankham 2016) in a process known as “genetic rescue” (Ingvarsson 2001; Tallmon et al. 2004; Whiteley et al. 2015). This was exemplified

in the severely bottlenecked grey wolf (*Canis lupus*) population in Scandinavia in the early 1990s, where the arrival of a single immigrant resulted in increased heterozygosity, the rapid spread of new alleles, exponential population growth, and significant outbreeding (Vila et al. 2003).

Norén et al. (2016) showed that the arctic fox population at Helags originated from only five founders, and reported significant inbreeding depression in both reproduction and survival at Helags between 2000 and 2009. The increase in genetic diversity at Sylane/Helags from 2011 onwards thus suggests that the arrival and successful reproduction of one or more immigrants in 2010 may have prompted a genetic "rescue" effect. While the ONCOR analyses did not directly identify any migrants to Sylane/Helags in 2010 (Fig. 8), Hasselgren (2017) report the arrival and successful reproduction of two male arctic foxes at Helags in 2009/2010. It appears that these two males and their offspring had an enormous genetic impact in this population, contributing to the 50% increase in average allelic diversity.

Despite the significant increase in average allelic diversity during the study period, no significant change was detected in average heterozygosity (Table 1). One explanation for this discrepancy could be that the temporal scale of our study was not long enough to capture changes in average expected and observed heterozygosity. In the case of the Florida panther, the release of eight captive-bred individuals into a highly inbred population resulted in a substantial increase in heterozygosity over a 10-year period. However, it took more than four years before a detectable response in heterozygosity was observed (Johnson et al. 2010). It is also worth pointing out that despite small population sizes, at which high rates of genetic drift and inbreeding are expected (Wright 1931; Hanski 1998), no decrease in either average observed or expected heterozygosity was detected. This result suggests that although there was no significant increase in heterozygosity, the management actions (and dispersal) did at least maintain genetic variation in the subpopulations.

Throughout the course of the study, Snøhetta showed consistently higher levels of average expected and observed heterozygosity compared to both Sylane and Børgefjell/Borgafjäll (Fig. 4a, Fig. 5a). The high levels of variation at Snøhetta may be explained by the diverse background of the captive-bred individuals that were

released at Snøhetta between 2007 and 2010 (Appendix, Table A1), amplified by cross-breeding between the diverse genetic lineages present in the captive breeding program. Genetic analysis of two reintroduced populations of rocky mountain wolves produced similar results, with founder individuals (originating from multiple source populations) showing higher expected heterozygosity compared to either of their source populations (Forbes and Boyd 1997).

Despite the growing popularity of reintroduction and supplementation programs, however, very few other studies have demonstrated comparable results in terms of both population growth, and maintenance of genetic diversity post reintroduction (Griffith et al. 1989; Wolf et al. 1996; Fischer and Lindenmayer 2000). On the contrary, many studies examining isolated reintroduced populations have reported significant reductions in genetic variability after reintroduction (Broders et al. 1999; Williams et al. 2000; Hedrick et al. 2001). One particularly common cause of genetic variability loss in reintroduced populations is insufficient founding group size (Nei et al. 1975; Berry 1986; Maudet et al. 2002). Additionally, the use of captive breeding in reintroduction programs is associated with substantial risk, as the captive environment may erode the genetic basis for important morphological, physiological, and behavioral traits via artificial selection (Miller et al. 1999; Christie et al. 2012). If this occurs, individuals may exhibit reduced fitness and be left unsuited for life in the wild (McPhee 2004; Araki et al. 2007).

The captive breeding program took into account both disease risk and genetic background when capturing foxes from the wild remnant populations to form the breeding pool (Landa et al. 2017). To minimize adaptation to captivity, appropriate replacement protocols were established so that no single founder line would exceed three generations in captivity (Landa et al. 2017). Additionally, a substantial number of individuals were released at Snøhetta (n = 67) in four separate release events to avoid loss of genetic variation due to founder effects (Landa et al. 2017). Curiously, while gene flow has been suggested to play an important role in maintaining genetic variability in reintroduced populations (Hicks et al. 2007), my results did not detect any immigrants to Snøhetta before 2014 (Fig. 8). On the contrary, many dispersers from Snøhetta emigrated to Sylane/Helags and adjacent mountain fragments throughout the study. This suggests that the reintroduction at Snøhetta not only led

to the re-establishment of a genetically viable population, but additionally that the population seems to have contributed to the observed increase in dispersal, acting as a "source" population (Pulliam 1988).

In parallel with the changes in genetic diversity, changes in the genetic structure of the mid-Scandinavian arctic fox population were also detected. My results indicate a considerable decrease in genetic differentiation between subpopulations over the course of the study, as is expected as a result of increased connectivity and inter-population dispersal (Slatkin 1987; Wade and McCauley 1988; Hale et al. 2001). The decrease was most pronounced at the metapopulation level, where genetic differentiation decreased by 49%, and for pairwise estimates between core and stepping stone populations which showed a 68% reduction in differentiation (Fig. 5a, c). The high level of differentiation observed during the first half of the study period is likely the result of founder effects during recolonization events (Mayr 1954; Wright 1984; Wade and McCauley 1988), which became less pronounced over time as the size of the recolonized populations grew, and their genetic composition became more similar to that of their source populations.

In the last year of the study, 2015, the level of differentiation between subpopulations at the metapopulation level was still fairly high (0.12), reflecting the stochastic genetic composition in the recolonized populations (Mayr 1954; Wright 1984; Wade and McCauley 1988). Average pairwise differentiation between core populations at the end of the study period was much lower (0.05). This amount of differentiation is moderate for natural populations of animals (Nei 1987; Hartl et al. 2007), and theoretically indicates a sufficient level of gene flow to avoid the harmful effects of local inbreeding (Lowe and Allendorf 2010). The lower average pairwise differentiation between the core populations was clearly accentuated by the extremely low pairwise differentiation between Børgefjell/Borgafjäll and Snøhetta throughout the study (Fig. 5b), which was expected given that many of the Snøhetta founders had a genetic background from Børgefjell/Borgafjäll (Appendix, Table A1) (Williams et al. 2000; Latch and Rhodes 2005).

Despite a substantial reduction in genetic differentiation, the mid-Scandinavian arctic fox population grouped consistently into two genetic clusters throughout the

course of the study. Across years, individuals from Børgefjell/Borgafjäll and the re-established Snøhetta population assigned to the first cluster, while individuals from Sylane/Helags assigned to the other. This overall clustering pattern reflects the historical and more recent population bottleneck events described by Dalén et al. (2006) and Nyström et al. (2006) and the fact that the population at Sylane/Helags was founded by only five individuals (Norén et al. 2016). At the population level, assignment to the two clusters varied between years, showing a general increase in assignment heterogeneity over time. This is in accordance with the observed increase in dispersal and decrease in population differentiation over the course of the study (Fig. 8; Fig. 5).

Many of the recolonized stepping stone populations showed high inter-annual variation in assignment, highlighting the profound influence of immigrants on the genetic composition of these small subpopulations. For Blåfjellet/Skjækerfjellet and Hestkjølen, patterns of assignment clearly reflected their geographic proximity to Børgefjell/Borgafjäll. The patterns of assignment for the stepping stone populations between Snøhetta and Sylane/Helags, while varying considerably more throughout the study period, also seemed to develop towards an assignment equilibrium reflecting their geographical proximity to the core populations surrounding them. Given the high intrinsic dispersal capacity of the arctic fox (Eberhardt and Hansson 1978; Garrott and Eberhardt 1987; Strand et al. 2000), this finding suggests that realized patterns of dispersal (and resultant genetic structure) may not only be limited by geographical distance, but also by behavioural and/or ecological factors (Rueness, Jorde, et al. 2003; Pilot et al. 2006). For instance, territorial behaviour and female natal philopatry have been confirmed in the arctic fox (Eberhardt et al. 1982; Hersteinsson and Macdonald 1992; Kullberg and Angerbjörn 1992; Strand et al. 2000), and both of these behaviours have been suggested to promote genetic structure (Sugg et al. 1996; Piertney et al. 1998).

Like the changes in genetic diversity, the recolonization of stepping stone regions seemed to correspond with the first release of captive-bred foxes from the captive breeding program, and the implementation of conservation efforts in the stepping stone areas (Fig. 2; Appendix, Table A2). These changes, along with the marked increase in dispersal, suggest a substantial shift in the dynamics of the mid-

Scandinavian arctic fox population around 2010/2011. A number of empirical studies have revealed similar patterns, reporting both recolonization and range expansion following demographic recovery (Lubina and Levin 1988; Bales et al. 2005). According to theory, the optimal emigration strategy is often to remain in the natal patch until a threshold density, close to the local carrying capacity (Hovestadt et al. 2010; Clobert 2012). Above this threshold, a gradual increase in emigration rate is expected. Assuming that the arctic fox exhibits density-dependent dispersal, the observed increase in dispersal could be the result of demographic growth towards threshold density, leading to the re-establishment of density-dependent dispersal and healthy metapopulation dynamics. While density-dependant dispersal was not directly tested, Eide et al. (2015) made a similar connection, suggesting that the observed demographic growth seemed to have a self-reenforcing effect leading to restoration of the natural metapopulation dynamics of the system. Furthermore, emigration rate should increase as mortality costs associated with dispersal decrease (Hovestadt et al. 2010). If the implementation of supplementary feeding and red fox culling in stepping stone areas reduced the risk of dispersal mortality, these strategies may also have influenced the marked shift in dispersal and metapopulation dynamics.

These results emphasize the role of dispersal as the underlying mechanism influencing changes in genetic diversity and differentiation, and suggest a connection between the observed genetic changes and the implementation of conservation actions. Despite this apparent connection, however, the generalized linear model (GLM) approach assessing the relationship between conservation efforts, rodent abundance, and genetic diversity, showed mixed results and explained minimal variance in the respective diversity parameters. One explanation for this could be that relatively low samples sizes and oversimplification in the modeling process compromised my ability to detect the biologically relevant relationships (Burnham and Anderson 1992; Steidl et al. 1997; Bourne et al. 2007). In constructing the GLMs, only the main effects of the explanatory variables (supplementary feeding, red fox culling, captive release, and rodent phase) were considered, however some of these factors may interact, and do show a degree of correlation (Appendix, Table A6). Furthermore, the models assumed a direct inter-

annual relationship between conservation, rodent phase, and genetic diversity. However, as discussed previously, different diversity parameters may differ in their response time. In order to truly determine the influence of conservation and rodent abundance on genetic diversity, models may need to take into account these complex interactions and sources of variation.

Implications for conservation management

The current level of genetic diversity in the mid-Scandinavian arctic fox population is quite high, especially considering the recent bottleneck suggested by Nyström et al. (2006). The substantial increase in genetic diversity within populations, decrease in differentiation among populations, and the general increase in dispersal throughout the study period, suggest that a degree of connectivity has been re-established. As connectivity is essential for both local and global population persistence in metapopulations (Hanski and Gilpin 1997; Hanski 1998; Hanski and Gaggiotti 2004), these changes suggest an increase in the long-term viability of the Scandinavian arctic fox population.

As clearly demonstrated, dispersal is the central process influencing genetic structure and subpopulation level genetic diversity. Indeed, for species like the Scandinavian arctic fox, living in fragmented habitats and relying on fluctuating prey resources, dispersal and settlement of immigrants may be the key to population persistence (Loison et al. 2001). In order to better understand the role of dispersal and the influence of conservation measures on dispersal and diversity, future studies should address both the factors that trigger dispersal and recolonization, as well as the factors that hinder movement, increase environmental resistance, and reduce connectivity.

The notable shift in metapopulation dynamics that occurred during the course of the last decade has had a profound effect on genetic diversity and differentiation in the arctic fox in mid-Scandinavia. For planning and evaluating conservation management, the possible existence of a threshold population size for healthy metapopulation dynamics should be explored in future studies. Furthermore, a better understanding of density-dependent dynamics and threshold population

sizes would also be beneficial for future research and conservation of other endangered species exhibiting similar population dynamics and biology.

My results confirm the genetic success of reintroductions from the Norwegian Arctic Fox Captive Breeding Program, highlighting the importance of founder population size and careful genetic planning for maintaining genetic diversity post re-introduction. It appears that the release of foxes over a four-year period stimulated the restoration of metapopulation dynamics, and even though there has been no release of foxes in the study area since 2011, dispersal rates and metapopulation size is still increasing. The success of the captive breeding program may be useful as a model on which to base future conservation management and reintroduction programs.

In conclusion, the evidence of increased dispersal, increased genetic diversity, and decreased differentiation in the mid-Scandinavian arctic fox population during the last decade indicate restoration of metapopulation connectivity and an increase in long-term population viability. While a direct relationship between conservation actions and genetic diversity was not revealed, the implementation of conservation efforts has undoubtedly influenced the observed genetic changes. Finally, considering the four-year generation time of the arctic fox and the relatively short temporal scale of this study, the genetic and demographic responses documented in this study occurred surprisingly rapidly. Indeed, in light of these rapid changes, and given sufficiently stable rodent dynamics, it is not inconceivable that the arctic fox population in Scandinavia may be able to persist without intervention in the not so distant future.

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Appendix

Table A1. Overview of the genetic/geographic background of all captive bred arctic foxes released into the wild in mid-Scandinavia (n = 90), spanning from 2007 (the first release in mid-Scandinavia) to 2011 (the most recent release in mid-Scandinavia).

Release Population	Release Year	Fox ID	Sire	Dam
Knutshø	2008	AF0061	Dividalen	Børgefjell
		AF0065	Dividalen	Børgefjell
		AF0079	Finnmark/Saltfjellet*	(Dividalen/Børgefjell)**/Porsanger vest*
		AF0087	Finnmark/Saltfjellet*	(Dividalen/Børgefjell)**/Porsanger vest*
	2011	AF0207	Finnmark/Saltfjellet*	Helags
		AF0209	Finnmark/Saltfjellet*	Helags
		AF0210	Finnmark/Saltfjellet*	Helags
		AF0211	Finnmark/Saltfjellet*	Helags
		AF0212	Finnmark/Saltfjellet*	Helags
		AF0213	Finnmark/Saltfjellet*	Helags
		AF0214	Finnmark/Saltfjellet*	Helags
		AF0215	Finnmark/Saltfjellet*	Helags
		AF0231	Porsanger Vest	Finnmark/Saltfjellet*
		AF0232	Porsanger Vest	Finnmark/Saltfjellet*
		AF0233	Porsanger Vest	Finnmark/Saltfjellet*
		AF0234	Porsanger Vest	Finnmark/Saltfjellet*
		AF0235	Porsanger Vest	Finnmark/Saltfjellet*
		AF0236	Porsanger Vest	Finnmark/Saltfjellet*
Snøhetta	2007	AF0036	Dividalen	Børgefjell
		AF0037	Dividalen	Børgefjell
		AF0040	Dividalen	Børgefjell
		AF0047	Dividalen/Børgefjell*	Blåfjellet
		AF0053	Dividalen	Børgefjell
		AF0035	Dividalen	Børgefjell
		AF0043	Børgefjell	Dividalen/Børgefjell*
		AF0050	Dividalen/Børgefjell*	Blåfjellet
		AF0051	Dividalen/Børgefjell*	Blåfjellet
		AF0004	Unknown	Unknown
		AF0020	Unknown	Unknown
		AF0030	Dividalen	Børgefjell
		AF0039	Dividalen	Børgefjell
		AF0042	Dividalen	Børgefjell
		AF0044	Børgefjell	Dividalen/Børgefjell*
		AF0038	Dividalen	Børgefjell
	2008	AF0058	Dividalen	Børgefjell
		AF0063	Dividalen	Børgefjell
		AF0081	Finnmark/Saltfjellet*	(Dividalen/Børgefjell)**/Porsanger vest*
		AF0088	Finnmark/Saltfjellet*	(Dividalen/Børgefjell)**/Porsanger vest*
		AF0029	Dividalen	Børgefjell
		AF0059	Dividalen	Børgefjell
		AF0062	Dividalen	Børgefjell
		AF0071	Børgefjell	Dividalen/Børgefjell*
		AF0072	Børgefjell	Dividalen/Børgefjell*
		AF0077	Børgefjell	Dividalen/Børgefjell*
		AF0078	Børgefjell	Dividalen/Børgefjell*
		AF0080	Finnmark/Saltfjellet*	(Dividalen/Børgefjell)**/Porsanger vest*
	2009	AF0086	Finnmark/Saltfjellet*	(Dividalen/Børgefjell)**/Porsanger vest*
		AF0089	Finnmark/Saltfjellet*	(Dividalen/Børgefjell)**/Porsanger vest*
		AF0090	Finnmark/Saltfjellet*	(Dividalen/Børgefjell)**/Porsanger vest*

		AF0091	Finnmark/Saltfjellet*	(Dividalen/Børgefjell)**/Porsanger vest*
		AF0092	Finnmark/Saltfjellet*	(Dividalen/Børgefjell)**/Porsanger vest*
		AF0094	Finnmark/Saltfjellet*	(Dividalen/Børgefjell)**/Porsanger vest*
		AF0095	Finnmark/Saltfjellet*	(Dividalen/Børgefjell)**/Porsanger vest*
		AF0110	Saltfjellet	Reisa Nord
		AF0111	Saltfjellet	Reisa Nord
		AF0112	Saltfjellet	Reisa Nord
		AF0118	Saltfjellet	Reisa Nord
		AF0119	Saltfjellet	Reisa Nord
		AF0120	Saltfjellet	Reisa Nord
		AF0121	Saltfjellet	Reisa Nord
		AF0122	Saltfjellet	Reisa Nord
	2010	AF0139	Børgefjell	Dividalen/Børgefjell*
		AF0142	Børgefjell	Dividalen/Børgefjell*
		AF0143	Børgefjell	Dividalen/Børgefjell*
		AF0146	Børgefjell	Dividalen/Børgefjell*
		AF0148	Børgefjell	Dividalen/Børgefjell*
		AF0150	Børgefjell	Dividalen/Børgefjell*
		AF0151	Børgefjell	Dividalen/Børgefjell*
		AF0187	Finnmark/Saltfjellet*	Helags
		AF0188	Finnmark/Saltfjellet*	Helags
		AF0189	Finnmark/Saltfjellet*	Helags
		AF0190	Finnmark/Saltfjellet*	Helags
		AF0191	Finnmark/Saltfjellet*	Helags
		AF0192	Finnmark/Saltfjellet*	Helags
		AF0141	Børgefjell	Dividalen/Børgefjell*
		AF0144	Børgefjell	Dividalen/Børgefjell*
		AF0145	Børgefjell	Dividalen/Børgefjell*
		AF0147	Børgefjell	Dividalen/Børgefjell*
		AF0149	Børgefjell	Dividalen/Børgefjell*
		AF0152	Børgefjell	Dividalen/Børgefjell*
		AF0180	Finnmark/Saltfjellet*	(Dividalen/Børgefjell)**/Porsanger vest*
		AF0181	Finnmark/Saltfjellet*	(Dividalen/Børgefjell)**/Porsanger vest*
		AF0182	Finnmark/Saltfjellet*	(Dividalen/Børgefjell)**/Porsanger vest*
		AF0183	Finnmark/Saltfjellet*	(Dividalen/Børgefjell)**/Porsanger vest*
		AF0184	Finnmark/Saltfjellet*	(Dividalen/Børgefjell)**/Porsanger vest*
Sylane/ Helags	2008	AF0060	Dividalen	Børgefjell
		AF0067	Dividalen	Børgefjell
		AF0069	Børgefjell	Dividalen/Børgefjell*
		AF0073	Børgefjell	Dividalen/Børgefjell*
		AF0076	Børgefjell	Dividalen/Børgefjell*

* Sire or Dam born in captivity (Maternal Grand Sire/Maternal Grand Dam)

** Sire/Dam and Grand Sire/ Grand Dam born in captivity (Maternal Grand Grand Sire/Maternal Grand Grand Dam)

Table A2. The intensity of conservation actions implemented, and annual records of the rodent phase (low, increasing, peak, declining) in eight mid-Scandinavian subpopulations between 1999 and 2015. Annual conservation intensity in each subpopulation is measured as the number of dens fed, the number of red foxes culled, and the number of captive-bred foxes released each year between 1999 and 2015. Years included in this study are indicated in bold.

Population	Year	# Dens fed	# Red foxes culled	# Captive bred foxes released	Rodent phase
Blåfjellet/	1999	0	0	0	1
Skjækerfjellet	2000	0	0	0	2
	2001	0	0	0	3
	2002	0	0	0	1
	2003	0	0	0	1
	2004	0	0	0	3
	2005	0	0	0	4
	2006	0	0	0	1
	2007	0	0	0	3
	2008	**0**	**0**	**0**	**4**
	2009	**0**	**0**	**0**	**1**
	2010	**0**	**0**	**0**	**3**
	2011	**6**	**3**	**0**	**3**
	2012	**7**	**199**	**0**	**1**
	2013	**9**	**84**	**0**	**2**
	2014	**9**	**25**	**0**	**3**
	2015	**9**	**72**	**0**	**4**
Børgefjell/	1999	0	0	0	1
Borgafjäll	2000	4	4	0	1
	2001	4	0	0	3
	2002	3	4	0	1
	2003	5	4	0	1
	2004	12	18	0	3
	2005	7	32	0	4
	2006	12	27	0	1
	2007	9	14	0	3
	2008	**19**	**28**	**0**	**4**
	2009	**21**	**32**	**0**	**1**
	2010	**22**	**27**	**0**	**3**
	2011	**22**	**17**	**0**	**3**
	2012	**22**	**38**	**0**	**1**
	2013	**23**	**13**	**0**	**2**
	2014	**24**	**14**	**0**	**3**
	2015	**24**	**15**	**0**	**4**
Forollhogna	1999	0	0	0	2
	2000	0	0	0	3
	2001	0	0	0	4
	2002	0	0	0	1
	2003	0	0	0	3
	2004	0	0	0	4
	2005	0	0	0	1
	2006	0	0	0	2
	2007	0	0	0	3
	2008	**0**	**0**	**0**	**4**

	2009	**0**	**0**	**0**	**2**
	2010	**0**	**0**	**0**	**3**
	2011	**0**	**0**	**0**	**4**
	2012	**2**	**0**	**0**	**1**
	2013	**2**	**0**	**0**	**3**
	2014	**2**	**0**	**0**	**4**
	2015	**2**	**0**	**0**	**1**
Hestkjølen	1999	0	0	0	1
	2000	0	0	0	2
	2001	0	0	0	3
	2002	0	0	0	1
	2003	0	0	0	1
	2004	0	0	0	3
	2005	0	0	0	4
	2006	0	0	0	1
	2007	0	0	0	3
	2008	**0**	**0**	**0**	**4**
	2009	**0**	**0**	**0**	**1**
	2010	**0**	**0**	**0**	**3**
	2011	**3**	**0**	**0**	**3**
	2012	**5**	**57**	**0**	**1**
	2013	**5**	**12**	**0**	**2**
	2014	**5**	**5**	**0**	**3**
	2015	**5**	**28**	**0**	**4**
Kjølifjellet	1999	0	0	0	1
	2000	0	0	0	2
	2001	0	0	0	3
	2002	0	0	0	4
	2003	0	0	0	1
	2004	0	0	0	2
	2005	0	0	0	3
	2006	0	33	0	1
	2007	0	22	0	3
	2008	**0**	**26**	**0**	**4**
	2009	**0**	**29**	**0**	**1**
	2010	**0**	**12**	**0**	**3**
	2011	**4**	**13**	**0**	**3**
	2012	**5**	**14**	**0**	**1**
	2013	**5**	**7**	**0**	**2**
	2014	**5**	**14**	**0**	**3**
	2015	**5**	**10**	**0**	**4**
Knutshø	1999	0	0	0	2
	2000	0	0	0	3
	2001	0	0	0	4
	2002	0	0	0	1
	2003	0	0	0	3
	2004	0	0	0	4
	2005	0	0	0	1
	2006	0	0	0	2
	2007	0	0	0	3

	2008	**1**	**0**	**4**	**4**
	2009	**1**	**0**	**0**	**2**
	2010	**1**	**0**	**0**	**3**
	2011	**2**	**0**	**14**	**4**
	2012	**3**	**0**	**0**	**1**
	2013	**3**	**0**	**0**	**3**
	2014	**3**	**5**	**0**	**4**
	2015	**4**	**0**	**0**	**1**
Snøhetta	1999	0	0	0	2
	2000	0	0	0	3
	2001	0	0	0	4
	2002	0	0	0	1
	2003	0	0	0	3
	2004	0	0	0	4
	2005	0	0	0	1
	2006	0	0	0	2
	2007	0	0	16	3
	2008	**8**	**0**	**12**	**4**
	2009	**9**	**0**	**15**	**2**
	2010	**16**	**0**	**24**	**3**
	2011	**18**	**0**	**0**	**4**
	2012	**18**	**0**	**0**	**1**
	2013	**19**	**0**	**0**	**3**
	2014	**18**	**0**	**0**	**4**
	2015	**20**	**0**	**0**	**1**
Sylane/Helags	1999	10	0	0	1
	2000	7	2	0	2
	2001	12	32	0	3
	2002	7	27	0	4
	2003	5	15	0	1
	2004	8	8	0	2
	2005	9	86	0	3
	2006	20	81	0	1
	2007	10	58	0	3
	2008	**24**	**107**	**5**	**4**
	2009	**25**	**56**	**0**	**1**
	2010	**29**	**34**	**0**	**3**
	2011	**37**	**57**	**0**	**3**
	2012	**39**	**51**	**0**	**1**
	2013	**40**	**37**	**0**	**2**
	2014	**42**	**18**	**0**	**3**
	2015	**46**	**23**	**0**	**4**

Table A3. Minimum population size estimated from eight mid-Scandinavian arctic fox subpopulations from 2008 to 2015 based on DNA analysis of fecal, hair, and tissue samples. See Methods for further information on how samples were obtained in each of the subpopulations.

Population	2008	2009	2010	2011	2012	2013	2014	2015
Børgefjell/Borgafjäll	26	18	27	16	16	26	40	22
Snøhetta	15	16	33	47	30	30	76	58
Sylane/Helags	24	5	25	37	20	44	44	41
Hestkjølen	1				10	8	5	11
Kjølifjellet					8	5	4	18
Knutshø				1	4	5	10	4
Blåfjellet/Skjækerfjellet	1	3			3	10	6	5
Forollhogna					1	5	2	2
Total	67	42	85	101	92	133	187	161

Table A4. Deviations from Hardy-Weinberg equilibrium (HWE) at eight loci in samples collected in eight mid-Scandinavian arctic fox populations between 2008 and 2015. Deviations are calculated per locus per population based on a reduced dataset containing all unique individuals identified during the study. The critical *p*-value after Bonferroni correction (0.05/64) was 0.008. Significant deviations from HWE based on the Bonferroni corrected critical *p*-value are shown in bold.

Population	Locus	HWE *p*-value	Population	Locus	HWE *p*-value
Blåfjellet/Skjækerfjellet	3	0.0067	Kjølifjellet	3	0.0043
	9	0.1209		9	0.2814
	140	0.8777		140	0.0039
	173	0.4197		173	0.3533
	250	0.7449		250	0.0125
	377	0.9370		377	0.6764
	758	0.0623		758	0.2335
	771	0.3374		771	0.1492
Børgefjell/Borgafjäll	3	0.1279	Knutshø	3	0.9293
	9	0.1719		9	0.0992
	140	0.7748		140	0.6613
	173	0.5328		173	**0.0000**
	250	0.0875		250	0.3083
	377	0.2789		377	0.8735
	758	0.0088		758	0.0651
	771	0.0412		771	0.6941
Forollhogna	3	0.0131	Snøhetta	3	0.0984
	9	**0.0000**		9	0.1597
	140	0.1053		140	0.9587
	173	0.5843		173	0.0941
	250	0.0212		250	0.0078
	377	0.5149		377	0.3359
	758	0.0043		758	0.0108
	771	0.1691		771	0.7747
Hestkjølen	3	0.0753	Sylane/Helags	3	0.0062
	9	0.2013		9	**0,0000**
	140	0.9057		140	0.3147
	173	0.2329		173	0.4782
	250	0.9620		250	0.3643
	377	0.0101		377	**0.0002**
	758	0.1955		758	0.0786
	771	0.6379		771	0.1245

Table A5. Linkage disequilibrium (LD) measured for all loci pairs based on sampled collected in 8 mid-Scandinavian arctic fox populations between 2008 and 2015. Deviations are calculated per locus pair per population based on a reduced dataset containing all unique individuals identified during the study. The critical *p*-value after Bonferroni correction (0.05/224) was 0.0002. Significant deviations from LD based on the Bonferroni corrected critical *p*-value are shown in bold.

Population	Locus Pair		LD p-value	Population	Locus Pair		LD p-value
Blåfjellet/	140	173	0.509	Kjølifjellet	140	173	0.235
Skjækerfjellet	140	250	0.129		140	250	0.000
	140	377	0.297		140	377	0.160
	140	758	0.299		140	758	0.182
	140	771	0.113		140	771	0.976
	173	250	0.488		173	250	0.004
	173	377	0.471		173	377	0.425
	173	758	0.388		173	758	0.156
	173	771	0.406		173	771	0.167
	250	377	0.602		250	377	0.061
	250	758	0.371		250	758	0.155
	250	771	0.060		250	771	0.827
	3	140	0.001		3	140	**0.000**
	3	173	0.208		3	173	0.006
	3	250	0.071		3	250	0.004
	3	377	0.239		3	377	0.300
	3	758	0.315		3	758	0.149
	3	771	0.047		3	771	0.338
	3	9	0.121		3	9	0.152
	377	758	0.684		377	758	0.266
	377	771	0.137		377	771	0.157
	758	771	0.043		758	771	0.244
	9	140	0.233		9	140	0.515
	9	173	0.802		9	173	0.427
	9	250	0.344		9	250	0.040
	9	377	0.399		9	377	0.331
	9	758	0.130		9	758	0.722
	9	771	0.024		9	771	0.164
Børgefjell/	140	173	0.041	Knutshø	140	173	0.533
Borgafjäll	140	250	0.004		140	250	0.302
	140	377	0.018		140	377	0.465
	140	758	0.197		140	758	0.199
	140	771	0.079		140	771	0.136
	173	250	0.001		173	250	0.025
	173	377	0.677		173	377	0.564
	173	758	0.003		173	758	0.664
	173	771	0.099		173	771	0.912
	250	377	0.061		250	377	0.207
	250	758	**0.000**		250	758	0.068
	250	771	0.093		250	771	0.509
	3	140	**0.000**		3	140	0.874
	3	173	0.058		3	173	0.533
	3	250	0.002		3	250	0.392
	3	377	0.001		3	377	0.041
	3	758	**0.000**		3	758	0.698
	3	771	0.001		3	771	1.000
	3	9	0.318		3	9	0.085
	377	758	0.263		377	758	0.172
	377	771	**0.000**		377	771	1.000
	758	771	0.820		758	771	1.000
	9	140	0.002		9	140	0.183
	9	173	0.091		9	173	0.769

	9	250	0.024		9	250	0.980
	9	377	0.392		9	377	0.667
	9	758	0.738		9	758	0.680
	9	771	0.142		9	771	0.786
Forollhogna	140	173	1.000	Snøhetta	140	173	**0.000**
	140	250	0.400		140	250	**0.000**
	140	377	1.000		140	377	0.000
	140	758	1.000		140	758	**0.000**
	140	771	0.134		140	771	**0.000**
	173	250	1.000		173	250	**0.000**
	173	377	1.000		173	377	**0.000**
	173	758	1.000		173	758	**0.000**
	173	771	1.000		173	771	0.002
	250	377	0.699		250	377	0.004
	250	758	1.000		250	758	**0.000**
	250	771	0.200		250	771	**0.000**
	3	140	0.133		3	140	**0.000**
	3	173	1.000		3	173	**0.000**
	3	250	0.199		3	250	**0.000**
	3	377	1.000		3	377	**0.000**
	3	758	1.000		3	758	**0.000**
	3	771	0.066		3	771	0.000
	3	9	1.000		3	9	**0.000**
	377	758	0.467		377	758	0.020
	377	771	1.000		377	771	**0.000**
	758	771	1.000		758	771	0.037
	9	140	0.467		9	140	**0.000**
	9	173	1.000		9	173	0.875
	9	250	1.000		9	250	0.007
	9	377	0.800		9	377	0.757
	9	758	0.467		9	758	0.052
	9	771	1.000		9	771	0.001
Hestkjølen	140	173	0.150	Sylane/	140	173	0.094
	140	250	0.852	Helags	140	250	**0.000**
	140	377	0.183		140	377	0.030
	140	758	0.130		140	758	0.068
	140	771	0.174		140	771	**0.000**
	173	250	0.889		173	250	**0.000**
	173	377	0.045		173	377	0.026
	173	758	0.511		173	758	**0.000**
	173	771	0.479		173	771	0.317
	250	377	0.476		250	377	0.047
	250	758	0.731		250	758	**0.000**
	250	771	0.937		250	771	**0.000**
	3	140	0.068		3	140	**0.000**
	3	173	0.288		3	173	0.158
	3	250	0.055		3	250	0.002
	3	377	0.602		3	377	0.581
	3	758	0.329		3	758	0.017
	3	771	0.414		3	771	0.002
	3	9	0.900		3	9	0.020
	377	758	0.129		377	758	0.022
	377	771	0.203		377	771	**0.000**
	758	771	0.394		758	771	0.162
	9	140	0.754		9	140	**0.000**
	9	173	0.317		9	173	0.565
	9	250	0.034		9	250	0.009
	9	377	0.393		9	377	0.573
	9	758	0.547		9	758	0.002
	9	771	0.687		9	771	0.008

Table A6. Pearson correlations between explanatory continuous variables used to model the effects of conservation efforts on inter-annual change in genetic diversity. Explanatory variables include the number of dens fed (DensFed), the number of red foxes culles (RedCulled), and the number of captive-bred foxes released from the Norwegian Captive Breeding Program (ReleasedFoxes). Significant *p*-values are indicated in bold.

Variables	N	Correlation	*p*-value
DensFed – RedCulled	64	0.292	**0.019**
DensFed – ReleasedFoxes	64	-0.012	0.922
RedCulled – ReleasedFoxes	64	-0.098	0.442