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Evolution, ecology and conservation—revisiting three decades of Arctic fox population genetic research

Karin Norén^a, Love Dalén^{a,b}, Øystein Flagstad^c, Dominique Berteaux^d, Johan Wallén^a & Anders Angerbjörn^a

^aDepartment of Zoology, Stockholm University, Stockholm, Sweden; ^bDepartment of Bioinformatics and Genetics, Swedish Museum of Natural History, Stockholm, Sweden; ^cNorwegian Institute for Nature Research, Trondheim, Norway; ^dCanada Research Chair on Northern Biodiversity and Centre for Northern Studies, Université du Québec à Rimouski, Rimouski, Canada

ABSTRACT

Three decades have passed since the Arctic fox (*Vulpes lagopus*) was first put into a population genetic perspective. With the aim of addressing how microevolution operates on different biological levels, we here review genetic processes in the Arctic fox at the level of species, populations and individuals. Historical and present dispersal patterns, especially in the presence of sea ice, are the most powerful factors that create a highly homogeneous genetic structure across the circumpolar distribution, with low detectable divergence between the coastal and lemming ecotypes. With dispersal less pronounced or absent, other processes emerge; populations that are currently isolated, for example, because of the lack of sea ice, are genetically divergent. Moreover, small populations generally display signatures of genetic drift, inbreeding, inbreeding depression and, under specific situations, hybridization with domestic fox breeds. Mating system and social organization in the Arctic fox appear to be determined by the ecological context, with complex mating patterns and social groups being more common under resource-rich conditions. In isolated populations, complex social groups and inbreeding avoidance have been documented. We emphasize the value of genetic data to decipher many previously unknown aspects of Arctic fox biology, while these data also raise numerous questions that remain unanswered. Pronounced intra-specific ecological variation makes the Arctic fox an ideal study organism for population genetic processes and the emergence of functional genomics will generate an even deeper understanding of evolution, ecology and conservation issues for several species.

KEYWORDS

Glaciations; microevolution; dispersal; adaptation; DNA; *Vulpes lagopus*

Introduction

The Arctic is characterized by low temperatures, seasonal resource limitations as well as historical and ongoing climate change (Callaghan et al. 2004). For Arctic species, these conditions put high demands on their capacity to respond to the environment (Berteaux et al. 2004; Gilg et al. 2012). Understanding the factors determining the amount and geographic distribution of evolutionary raw material is of particular importance for species in these extreme habitats (Gilg et al. 2012). Although only four microevolutionary processes (genetic drift, natural selection, mutations and dispersal with gene flow) shape the genetic composition of species, populations and individuals, these processes are in turn influenced by numerous historical and contemporary factors (Wright 1931; Hewitt 2001). Genetic drift contributes to stochastic loss of genetic variation and operates with a rate that is determined by the effective population size (N_e , i.e., the number of genetically effective individuals; Nei et al. 1975). Natural selection is the main driver underlying adaptation to the environment and individual fitness

(Roughgarden 1971). How selection operates is influenced by the ecological context, especially under fluctuating conditions, when trait-specific selection pressures vary considerably. Furthermore, in a small population, genetic drift usually exceeds the impact of natural selection (Wright 1931). Genetic drift and selection are, however, counteracted by dispersal and mutations (Wright 1931). Dispersal is the most powerful micro-evolutionary process and, even at low frequency, it promotes genetic similarity across regions, counteracts adaptation and increases genetic variation. A prerequisite for genetic contribution to future generations is that dispersal results in gene flow—that immigrants actually reproduce in the new area.

The emergence of genetic tools and the inclusion of population genetics in traditional and applied biological science have brought important theoretical and practical insights within the fields of ecology, evolution and conservation biology. For many well-studied species, however, population genetic efforts have focused on addressing questions related to evolution and ecology or have mainly been centred on conservation genetic aspects. An ideal model

organism would present pronounced intra-specific variation within these three frameworks, specifically with regards to abundance, demography and ecology.

The considerable intra-specific variation in abundance, demography and ecology makes the Arctic fox (*Vulpes lagopus*) an ideal model system addressing a broad range of scientific and applied questions using population genetics tools (Berteaux et al. 2017). Pioneering biologists used the Arctic fox to illustrate the process of selection and adaptation to extreme environments (Wallace 1885; Elton 1924). Although early interest regarding Arctic fox genetics mainly focused on fur colouring (Adalsteinsson et al. 1987) and its relation to climate, the species was first put into a traditional population genetics context when Wayne & O'Brien (1987) used allozyme electrophoresis to address the phylogenetic relationship in canids. Since then, more than 40 scientific papers and reports covering a wide range of genetic topics have been published, and it remains a remarkably active field in which new ideas and methods are constantly emerging (Fig. 1).

Here, we present the first extensive review of Arctic fox population genetics by revisiting the past three decades of genetic research, with emphasis on its relevance to Arctic fox ecology, evolution and conservation. We summarize findings at the species, population and individual levels by evaluating: (1) the role of past ecology and demography on Arctic fox speciation; (2) the role of past and present ecology and demography on the genetic structure and

conservation status of populations; and (3) the role of social organization and mating behaviour on the fine-scaled distribution of genetic variation within and between individuals.

Species

Speciation requires significant evolution over long time spans, a key process in which natural selection promotes local adaptations. Such evolution usually occurs under situations of limited or absent dispersal (Fig. 2a). Under situations of low effective population size (N_e), genetic drift can accelerate to genetic divergence from the ancestor population (Fig. 2b).

Speciation: isolation and selection

The first genetic studies of most species, including the Arctic fox, were conducted at the species level (Wayne & O'Brien 1987). The Arctic fox is a comparatively young species that likely traces its origin to the Middle Pleistocene or possibly the late stages of the Early Pleistocene (Sher 1986; Perini et al. 2010). The earliest remains of Arctic foxes in the fossil record are found in the Olyorian fauna of north-east Siberia, which suggests a Beringian origin, no later than 500 000 years before the present (Sher 1986). In contrast, the earliest fossil-record appearance of Arctic foxes in Europe dates to approximately 200 000 before the present (Kurtén 1968).

Because phylogenetic analyses show that the Arctic fox's closest extant relative is the North American swift fox (*Vulpes velox*), it has been suggested that the Arctic fox evolved from a temperate swift fox-like ancestor (Geffen et al. 1992; Mercure et al. 1993; Bardeleben et al. 2005). Stewart et al. (2010) proposed that the origin of Arctic species may have been catalysed by the isolation of ancestral temperate populations in a cryptic northern refugium during periods of decreasing global temperatures. A possible speciation scenario for the Arctic fox may therefore be that the distribution of its swift-fox-like ancestor extended far into northern North America during an interglacial in the Middle Pleistocene. As the climate shifted towards glacial conditions, a population may have become isolated in the north and subjected to strong selection pressures associated with cold conditions. A recent genomic study indicates that the Arctic fox adaptation to life in the Arctic environment was associated with strong positive selection on genes that regulate fatty-acid metabolism (Kumar et al. 2015). Periods of food scarcity in the Arctic ecosystem occurring with rodent population cycles and seasonal bird migrations make adaptations to withstand starvation crucial. An efficient metabolism (through, e.g., fatty-acid

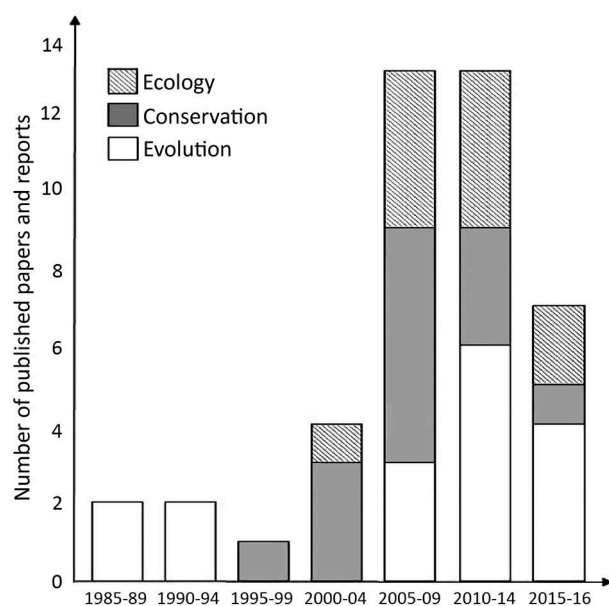


Figure 1. Timeline with number of published Arctic fox genetic studies within the fields of ecology, evolution and conservation (1985–2016). Data were assembled through authors' background knowledge in combination with literature searches in Google Scholar and Web of Science (search words: 'genetics', 'Arctic fox', '*Alopex lagopus*' and/or '*Vulpes lagopus*') for the given time periods.

regulation) could be a consequence of these large and seasonal fluctuations in food availability.

Population

On a population level, dispersal is a key process that can overshadow the signatures of other micro-evolutionary processes (Fig. 2a). Under low or absent dispersal, however, the relationship between effective population size (N_e) and the strength of the selection pressure for a specific trait will determine whether genetic drift or natural selection becomes most influential (Fig. 2b).

Historical processes: range shifts and demographic expansions

The genetic composition of populations is shaped by both past and present processes. For species in the Arctic, repeated glaciations during the Pleistocene have had a strong impact (Hewitt 2001). The Arctic fox has a relatively low neutral and functional genetic

diversity compared to many other species (Dalén et al. 2005; Kumar et al. 2015). This pattern is likely a consequence of repeated isolation in refugia during interglacial warm periods, when Arctic fox distribution was restricted to high-latitude regions. Analysis of mitochondrial DNA variation supports this scenario, since the distribution of pairwise mitochondrial DNA sequence differences among individuals is consistent with a demographic expansion starting approximately 118 000 years ago, coinciding with the end of the Eemian interglacial (Dalén et al. 2005). During the ensuing Late Pleistocene glaciation (ca. 117 000–10 000 years ago), Arctic foxes were widely distributed in continental Eurasia and North America (Kurtén 1968; Kurtén & Anderson 1980; Sommer & Benecke 2005). However, as temperatures started to increase at the start of the Holocene, Arctic fox distribution again contracted towards the north, until it reached its current circumpolar distribution (Audet et al. 2002). Several regions that had been glaciated during the last ice age, such as Scandinavia, most of Canada as well as several Arctic islands, were

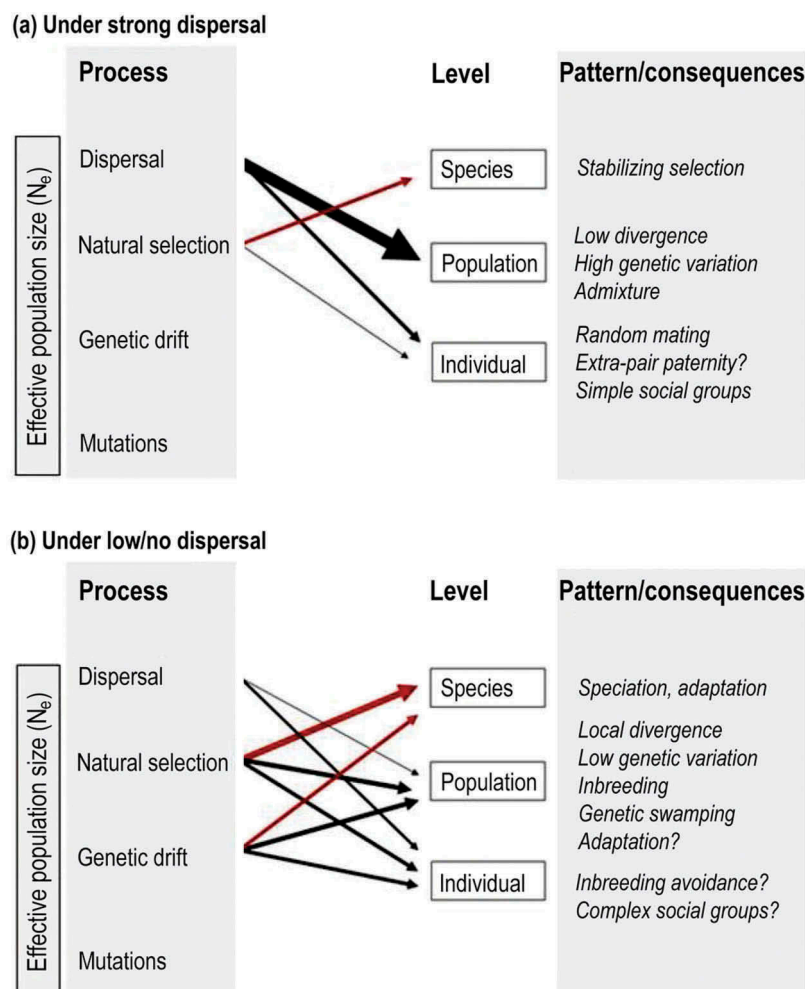


Figure 2. Conceptual model illustrating Arctic fox microevolution at the species, population and individual levels with recorded consequences under (a) strong dispersal and (b) no or low dispersal. The size of the arrow represents the relative strength of each process; red arrows correspond to long evolutionary timeframes whereas black arrows represent shorter timeframes. Under long timeframes, mutations may have a significant impact, but this has not been investigated.

colonized as the ice sheets contracted. There is low phylogeographic structure and a high level of shared ancestral haplotypes across the circumpolar range (Dalén et al. 2005), which means that the postglacial origin of populations in specific regions cannot be assessed. This could be due to high gene flow during the Holocene (Dalén et al. 2005) or because populations in previously glaciated regions all originate from a single Late Pleistocene source population in Beringia. A study based on ancient DNA from Late Pleistocene samples from mid-latitude Europe (i.e., south of the Arctic fox's current distribution) seems to support this later scenario since it suggested that Scandinavia was colonized through a westwards range expansion from Beringia, rather than from the south (Dalén, Nyström et al. 2007). These findings indicate that populations at the southern edge of the Arctic fox glacial distribution made little or no contribution to the modern-day gene pool. It should be noted that such local extinctions during range contractions could be a contributing factor to the comparatively low levels of genetic diversity in the Arctic fox today.

Large-scale genetic structure: dispersal across the sea ice

In addition to historical events, various ongoing population processes shape the distribution and abundance of genetic diversity within and between populations. For the Arctic fox, there are numerous records of long-distance dispersal across the sea ice (Fig. 3). Satellite tracking (Lai et al. 2015) and indigenous

knowledge (Gagnon & Berteaux 2009) show that Arctic foxes routinely use sea ice for both foraging and long-distance dispersal (Fig. 3b). Arctic foxes tracked in the Canadian Arctic can travel thousands of kilometres over land and sea ice. For example, one adult female and one adult male from Bylot Island (Nunavut, Canada) moved 4599 and 2193 km, respectively, from February to July 2009 (Tarroux et al. 2010). These individuals showed high and sustained travel rates reaching 90 km/day. Sea ice can therefore effectively connect terrestrial habitats separated by water bodies.

These long-distance movements are subsequently reflected in the genetic structure of populations (Fig. 3). The general pattern is low differentiation between regions connected by sea ice (Dalén et al. 2005; Carmichael, Krizan et al. 2007; Geffen et al. 2007; Norén, Carmichael, Dalén et al. 2011; Norén, Carmichael, Fuglei et al. 2011). This means that North America, Greenland, Svalbard and Siberia can more or less be considered as one homogeneous population (Dalén et al. 2005; Carmichael, Krizan et al. 2007; Geffen et al. 2007; Norén, Carmichael, Dalén et al. 2011; Norén, Carmichael, Fuglei et al. 2011), while regions without yearly access to sea ice, such as Scandinavia, Iceland, Pribilof Island and the Commander Islands, display higher levels of genetic divergence (Dalén et al. 2005; Geffen et al. 2007; Norén, Carmichael, Dalén et al. 2011). The presence of sea ice in the past is an additional determinant of the present genetic structure. A study of the Icelandic Arctic fox using ancient DNA indicated that the cold period of the Little Ice Age, ca. 15th–19th centuries, may have given access to sea ice, facilitating long-

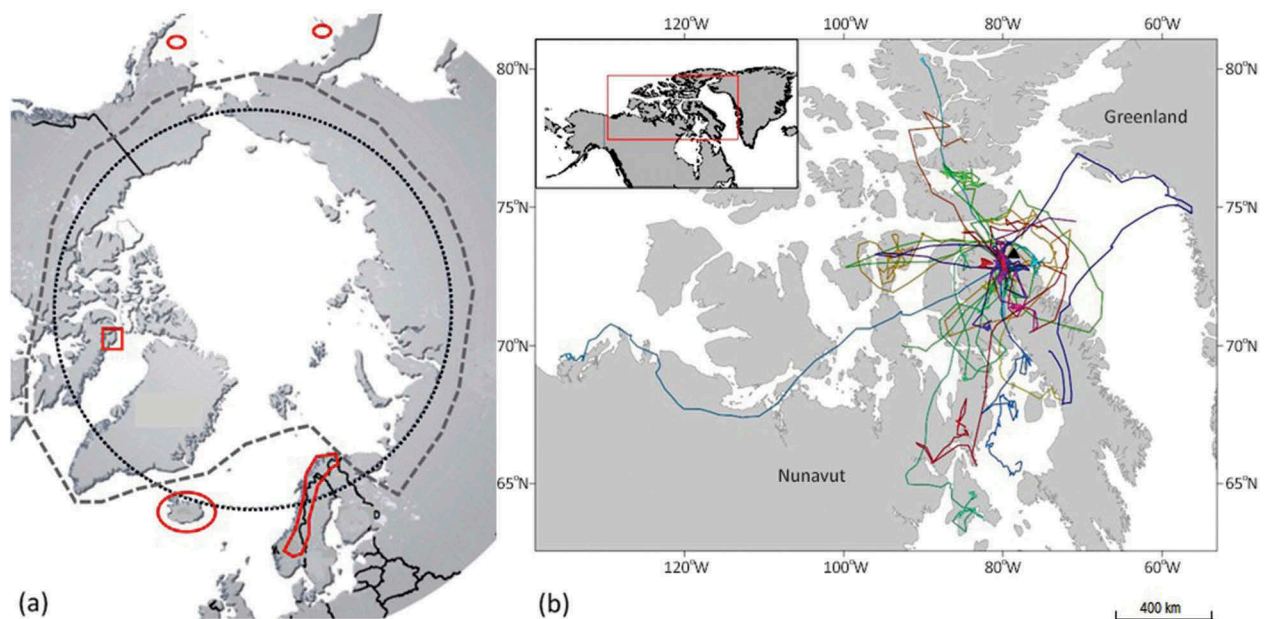


Figure 3. (a) Map showing the locations of genetically divergent populations in Iceland, Scandinavia and the Commander Islands and on Pribilof Island marked in red circles and genetically continuous populations connected by sea ice within the grey dashed line. Bylot Island (red square) and the Arctic Circle (black dotted line) are also indicated. (b) Large-scale movements of 31 Arctic foxes captured in 2007–2015 on Bylot Island (black triangle), Nunavut, Canada. Foxes were tracked with Argos satellite telemetry as they travelled throughout the Canadian Arctic Archipelago and Greenland (Lai et al. 2015).

distance dispersal and gene flow that decreased the Icelandic population's isolation to the extent that it is less genetically divergent and more variable than it was 1000 years ago (Mellows et al. 2012).

Large-scale genetic structure: dispersal and selection

The division of the species into two ecologically distinct ecotypes—the lemming fox and the coastal fox—is an intriguing aspect in Arctic fox biology. Since Braestrup (1941) described this partition it has been the subject of considerable research (Vibe 1967; Tannerfeldt & Angerbjörn 1998; Geffen et al. 2007; Norén, Carmichael, Dalén et al. 2011). The ecotype distinction is based on the contrasting stability and abundance of resources in relation to differences in reproductive strategies and behaviour (Tannerfeldt & Angerbjörn 1998). Based on this, several population genetic studies have focused on testing whether the ecologically distinct lifestyles have a genetic background (Meinke et al. 2001; Dalén et al. 2005; Carmichael, Krizan et al. 2007; Geffen et al. 2007; Norén, Carmichael, Dalén et al. 2011). Dalén et al. (2005) identified mitochondrial genetic divergence between the ecotypes and suggested that this was due to a higher gene flow between foxes belonging to the lemming ecotypes, which could be due to fitness differences. The same pattern is reflected in the higher occurrence of blue foxes in coastal habitats and white foxes in lemming habitats, which has been interpreted as a possible adaptation to the snow cover (Braestrup 1941; Vibe 1967). Since fur colour is determined by only three loci, with the blue allele dominant over the white one (Adalsteinsson et al. 1987; Våge et al. 2005), divergence may not be reflected in the overall genetic structure (e.g., Poelstra et al. 2014). In agreement with this, the main conclusions of other papers covering this theme have been that dispersal and gene flow is a more powerful process than selection in determining large-scale genetic structure (Dalén et al. 2005; Carmichael, Krizan et al. 2007; Geffen et al. 2007; Norén, Carmichael, Dalén et al. 2011). The fact that most populations belonging to the coastal ecotype, except in the archipelago of Svalbard and Greenland, are isolated by year-round open water suggests that the observed distinctiveness may arise from lack of immigration rather than selection.

The importance of dispersal across sea ice, in combination with the ecological differences between coastal and lemming fox habitats, was highlighted by Norén, Carmichael, Fuglei et al. (2011), who conducted a temporal genetic analysis of the coastal fox population in the High-Arctic islands of Svalbard. The results clearly demonstrated high levels of genetic admixture in Svalbard, where immigration

from the surrounding lemming fox populations, such as those in Siberia and North America, is common. In the same study, the genetic similarity between Svalbard and the surrounding lemming fox populations increased during the summer, which suggests that lemming fox immigrants do not establish a territory and reproduce (e.g., Dalén et al. 2005). This means that even though there is a high level of immigration into Svalbard, gene flow is low or absent. The immigrants either continue their migration route or, on account of lack of experience and/or local adaptations, are competitively inferior to native foxes (Norén, Carmichael, Fuglei et al. 2011).

Despite the pronounced ecological differences between coastal and inland habitats, genetic divergence between the two ecotypes is typically low or absent. It is possible that high gene flow overshadows the impact of selection (Fig. 2), but there are also other, not mutually exclusive, explanations. First, categorizing foxes into two separate ecotypes may be problematic: rather than two ecotypes, there may be a gradient with intermediate levels of adaptation. Second, it is possible that distinct ecotypes occur, but the limited number of genetic markers that have been applied cannot reflect the actual adaptations. Instead, selection may only operate on specific parts of the genome (Stapely et al. 2010; Poelstra et al. 2014). The finding of ongoing dispersal but lack of gene flow between the ecotypes in Svalbard, i.e., no or low reproduction for immigrant foxes (Norén, Carmichael, Fuglei et al. 2011), supports the idea of adaptation to contrasting ecosystem conditions. Third, it is possible that the distinct lifestyles associated with the coastal and inland habitats may be the outcome of phenotypic plasticity rather than selection and adaptation (Berteaux et al. 2004).

Local genetic structure: dispersal, genetic drift and selection

In contrast to large-scale genetic structure, which is determined by a limited number of factors, genetic structuring at the local scale is influenced by diverse factors and is highly context dependent. Dispersal (Meinke et al. 2001) or lack thereof (Strand et al. 1998; Dalén et al. 2002; Dalén et al. 2006; Norén, Angerbjörn et al. 2009) remains the key process, also at the local scale. This can be illustrated by the Icelandic Arctic fox population, where a narrow isthmus separates foxes living in the north-west from the rest of the population. This barrier prevented gene flow for a long time and resulted in genetic divergence of foxes in north-western Iceland (Norén, Angerbjörn et al. 2009). Apart from actual geographical barriers, there are additional factors that influence to what extent gene flow actually occurs. For instance, low population size in combination with a

fragmented landscape promotes isolation and causes stronger genetic divergence, as was recorded for the Scandinavian Arctic fox (Strand et al. 1998; Dalén et al. 2002; Dalén et al. 2006).

Even though dispersal is the most powerful process (Fig. 2a) at the local scale, subtle factors can influence dispersal patterns and shape genetic structure. For example, natal habitat biased dispersal may shape dispersal patterns (Pagh & Hersteinsson 2008). Such preferences can arise through local adaptations or imprinting from the natal habitat and can mediate dispersal into habitats with environmental conditions similar to the natal ones. The contrasting Icelandic habitats may have contributed to the observed genetic differences between the north-west and the rest of Iceland (Norén, Angerbjörn et al. 2009).

Another perspective of genetic structure is how diseases and parasites influence dispersal and adaptation. Norén, Carmichael, Fuglei et al. (2011) identified a temporal correspondence between inland habitat lemming crashes, genetic shifts and rabies outbreaks in Svalbard. Arctic rabies originates from Siberia and it is likely that emigration triggered by lemming crashes in Siberia is the cause underlying rabies outbreaks in Svalbard (Norén, Carmichael, Fuglei et al. 2011). In contrast to this, Goldsmith et al. (2016) identified divergence of Arctic foxes in a specific region of Alaska, where irregular access to sea ice reduces immigration. Interestingly, the observed genetic structure in this region corresponded to the occurrence of a genetically distinct rabies strain not present elsewhere. The authors suggested that rabid foxes most likely die before they can undertake long-distance movement and spread the virus to other regions.

Whether hosts can drive the evolution of diseases and parasites and whether hosts and pathogens have similar genetic patterns is another area of interest. Hanke et al. (2016) addressed this question with regard to Arctic foxes and rabies. Based on mitochondrial sequencing of Arctic foxes in Greenland, they recorded a fine-scaled spatial structure. This structure did not show any correspondence to the genetic divergence of rabies strains, which suggests that other factors than host dispersal patterns drive pathogen evolution.

Small population paradigm: genetic drift and inbreeding

Although abundant in many parts of the Arctic, the Arctic fox is threatened in Scandinavia and Mednyi Island, and is close to going extinct in Finland. The Arctic fox population in Fennoscandia went through a demographic bottleneck caused by hunting in the 19th century and irregular lemming cycles and red fox expansion has kept it small (Angerbjörn et al.

2013). On Mednyi Island, an outbreak of sarcoptic mange decimated the population and its present size is estimated at ca. 90 individuals (Goltsman, Kruchenkova, Sergeev, Johnson et al. 2005; Goltsman, Kruchenkova, Sergeev, Volodin et al. 2005). The processes operating in these well-studied populations can thus illustrate a number of key concepts of the small population paradigm (Caughley 1994).

Drastic population declines are associated with considerable loss of genetic variation through genetic drift (Fig. 2b; Nei et al. 1975). Comparing pre- and post-bottleneck samples in Scandinavia (Nyström et al. 2006) and Mednyi Island (Ploshnitsa et al. 2013) demonstrated that at least 25% of the historical level of neutral genetic variation (measured with microsatellites) was lost through these drastic population declines. An even higher loss of functional genetic variation was detected on Mednyi Island (Ploshnitsa et al. 2011) by sequencing immune system genes located in the major histocompatibility complex (379 bp). This study documented a loss of 80% of the alleles in the pre-bottleneck population. Although there were signatures of balancing selection, the authors concluded that, in such a small population, the strength of selection was not sufficient to overshadow the effect of genetic drift induced by the population bottleneck.

Population declines may also exert genetic consequences within the population through geographic and demographic fragmentation. Apart from the rapid loss of variation associated with population bottlenecks, genetic drift in combination with mutations and lack of immigration will over time increase genetic differentiation from surrounding populations. On a global scale, both Scandinavia and Mednyi Island are genetically unique (Dalén et al. 2005; Norén, Carmichael, Dalén et al. 2011; Geffen et al. 2007), which can be attributed to the combined effect of prevented dispersal due to the lack of sea ice and genetic drift caused by bottlenecks (Nyström et al. 2006; Ploshnitsa et al. 2011). On the long Scandinavian Peninsula, the Arctic fox population is fragmented into four genetically distinct subpopulations in which levels of genetic variation decrease with increasing distance to Russia (Dalén et al. 2006). Dispersal between the populations is currently low, but within-population genetic variation is still relatively high, which suggests recent population fragmentation within Scandinavia. Furthermore, the Scandinavian tundra is a naturally fragmented landscape that is intersected with boreal forests, which may strengthen this genetic substructure even more.

Another potential risk of low population size is inbreeding depression, which arises when matings between close relatives increase homozygosity of deleterious alleles and reduce individual fitness

(Frankham 1995). A recent pedigree analysis of the southernmost Swedish subpopulation revealed that, over the eight-year study period, the inbreeding level has risen from $F = 0$ to $F = 0.125$, a level that corresponds to half-sibling matings (Norén et al. 2016). The main events of inbreeding occurred as matings between cousins, but there were also records of full-sibling matings. These full-sibling matings were only recorded between siblings from different cohorts and not between littermates, which suggest that inbreeding avoidance mechanisms may be in play, although they are not preventing inbreeding completely (Godoy et al. unpubl. data). The study also demonstrated that inbreeding caused reductions in fitness by means of reduced first-year survival and reproduction (Norén et al. 2016). Inbreeding depression varied across phases of the lemming cycle: inbred individuals born at low rodent density exhibited reduced first-year survival whereas inbred individuals born at high rodent abundance instead displayed reduced chances of reproducing.

Genetic swamping, hybridization and introgression

For small populations, hybridization with closely related species may pose yet another threat (Allendorf et al. 2001). Introducing genetic material this way may be beneficial through increase in population genetic variation and individual fitness (heterosis), but hybridization has also caused extinction of natural populations and species through loss of local adaptations or disruption of co-adapted gene complexes (Rhymer & Simberloff 1996). Of particular concern is the introgression of domestic genes into natural populations by hybridization between wild species and their domestic counterparts. Such introgression has been documented in populations of various taxa (Rheindt & Edwards 2011; Perrier et al. 2013).

Arctic foxes have been farmed to produce fur for the clothing industry for approximately 100 years (Konnerup-Madsen & Hansen 1980). The founders of Scandinavian farm foxes were mainly imported from Alaska, Canada, Svalbard and Greenland, and have been exposed to intense selective breeding to optimize fur quality (Nordrum 1994). Although their origin is quite recent, escaped farm foxes may pose a serious threat to small natural populations through loss of local adaptations and genetic swamping. Hybridization between wild and farmed Arctic foxes was first documented in Iceland (Hersteinsson 1986) and more recently in Scandinavia (Norén et al. 2005; Norén, Kvaløy et al. 2009). In Iceland, where the Arctic fox population is quite large and robust, there is no known effects of the documented hybridization (Hersteinsson 1986). In sharp contrast, the

documented hybridization event in Scandinavia had severe demographic and genetic consequences (Norén, Kvaløy et al. 2009; Flagstad et al. unpubl. data) that ultimately led to the extirpation of one subpopulation.

Farmed foxes are genetically divergent from wild, Scandinavian Arctic foxes (Norén et al. 2005). Norén, Kvaløy et al. (2009) identified a farm fox specific mitochondrial haplotype (termed H9) in 25 out of 182 samples collected across Scandinavia. Of the foxes carrying haplotype H9, 21 had been collected within or near a subpopulation in south-western Norway. Analysis of microsatellite data implied that the free-ranging H9 individuals were farm foxes rather than wild Arctic foxes and that the entire subpopulation consisted of either farm foxes or putative hybrids. Genetic analyses of museum specimens collected in the area (1897–1975) demonstrated that the farm fox genotypes had been recently introduced to the area (Norén, Kvaløy et al. 2009). Flagstad et al. (unpubl. data) back-traced the origin of the introgression and found evidence for breeding and subsequent release of farmed foxes at a neighbouring tourist hut occurring over a 10–15-year period. The released foxes had hybridized with the indigenous foxes, resulting in complete swamping of the original gene pool. The last known pure wild fox in the area died in 2000. Norwegian management authorities removed the remaining population of farmed foxes and hybrids in 2009. To re-establish a natural population in the area, Arctic foxes of wild origin from the Norwegian Captive Breeding Programme have been released (Landa et al. 2017).

Genetic monitoring

The low temperatures on the mountain tundra provide excellent conditions for successfully analysing non-invasive samples such as faeces and snow tracks (Dalén, Elmhagen et al. 2004; Dalén, Götherström et al. 2004; Dalén, Götherström et al. 2007). Dalén, Götherström et al. (2004) demonstrated how mitochondrial analysis of faecal samples can be used to distinguish between Arctic and red (*Vulpes vulpes*) foxes as well as wolverines (*Gulo gulo*), and subsequently Dalén, Elmhagen et al. (2004) used this method to show that while red and Arctic foxes are sympatric in winter, Arctic foxes retreat to higher altitudes in summer, which most likely is due to the increased risk of red fox predation on Arctic fox cubs at lower altitudes. This method was later developed by Meijer et al. (2008), who used microsatellite genotyping of faecal samples to estimate population size and survival in the southernmost Swedish subpopulation. In total, 98 Arctic fox faecal samples were genotyped at nine microsatellite loci. Visual observations of ear-tagged individuals were recorded

simultaneously. The minimum number alive was 12 individuals using visual observations, 30 using molecular tracking and 36 by combining the data sets. A mark–recapture estimate of population size for visual observations was uninformative (95% confidence interval 6–212 individuals), while the same approach using the molecular tracking data set gave a far more precise population size estimate (95% confidence interval 36–55 individuals).

Molecular tracking can also be used to estimate other population parameters (Schwartz et al. 2007). Meijer et al. (2008) estimated the age-specific finite survival rate during one year (summer to summer) by combining molecular tracking with visual observations and matching the faecal genotypes to genotypes of known origin (collected as tissue samples during ear-tagging). Juveniles displayed a lower survival than the adults during autumn, whereas there was no evidence for age-specific survival difference during spring. On a yearly basis, juvenile survival was only 8% (95% confidence interval 0.02–0.18), while adults had a survival of 59% (95% confidence interval 0.39–0.82).

Molecular tracking is today an important and integrated part in the monitoring of Scandinavian Arctic foxes (e.g., Johansson et al. 2009; Rød-Eriksen et al. 2014; Eide et al. 2015). Norwegian authorities use molecular tracking to estimate population size, distribution and genetic variation on a yearly basis. Furthermore, genetic analyses are also used to continuously evaluate the establishment of Arctic foxes released from the Norwegian Arctic Fox Captive Breeding Programme, as well as to screen for farm foxes and hybrids in the wild.

Individual

How individuals distribute in time and space is dependent on a combination of dispersal and population inbreeding levels as well as the selective benefits of different spacing behaviours and social interactions in relation to the ecological context (Fig. 3).

Mating system: selection and dispersal

Arctic foxes have diverse breeding behaviours that make them valuable for testing hypotheses relating to mating systems and reproductive tactics. Surprisingly, however, published genetic appraisals informing on paternity, maternity and mate choice in Arctic fox populations are limited. Microsatellite genotyping allowed Carmichael, Szor et al. (2007) to provide the first genetic evidence of polyandry with multiple paternity in the Arctic fox on Bylot Island (Canada). Cameron et al. (2011) used larger sample sizes from the same population to demonstrate that although monogamy with bi-parental care was the

dominant social mating system, 31% of cubs with a known social father were born from extra-pair matings. Extra-pair paternity was more frequent at the centre of a large goose colony and decreased with increasing distance (Cameron et al. 2011).

The level of extra-pair paternity seems to differ considerably between populations. Norén et al. (2012) used microsatellite analysis to investigate mating system in four Arctic fox populations—Scandinavia, Iceland, Svalbard and the Canadian Arctic Archipelago—in contrasting ecological conditions. Social and genetic monogamy was the dominant mating system in all study populations and the level of extra-pair matings was considerably lower than on Bylot Island. This suggests that the high resource abundance on Bylot Island lowers the potential costs of engaging in extra-pair matings, while lower resource abundance in combination with intra- or inter-specific competition increases female cost for such behaviours. The costs are likely connected to the risk of losing male investment in the offspring, which can decrease cub survival under limited resource conditions and high predation pressure (Cameron et al. 2011; Norén et al. 2012).

Mate choice is another central aspect of reproduction and individual fitness. This choice can, for instance, be influenced by the presence of close relatives in the population. Geffen et al. (2011) examined whether mates were randomly selected outside natal groups and whether inbreeding was avoided inside natal groups. By comparing two inbred Arctic fox populations from Scandinavia (northern and southern Scandinavia) and one non-inbred population from north-western Iceland, the proportion of related and unrelated pairs was quantified through microsatellite analyses. Although the kin encounter rate was significantly higher in inbred populations, the proportion of related and unrelated breeding pairs did not differ significantly from random mating expectations. Geffen et al. (2011) concluded that relatedness did not influence mate selection outside natal groups. Based on a pedigree analysis of the southernmost Scandinavian subpopulation (Norén et al. 2016), Godoy et al. (unpubl. data) used simulations of random mating to demonstrate that the population development of inbreeding over time was lower than what is expected from random mating. This suggests that, even though the mechanism is not fully understood, there is a component of inbreeding avoidance involved in Arctic fox mating patterns.

Social organization: selection and dispersal

Arctic foxes are in general territorial and single breeding pairs are the norm (Angerbjörn et al. 2004). They tend to form smaller social units than other canids (Audet et al. 2002; Baker et al. 2004),

although increased social complexity is observed in isolated populations, where groups can contain multiple females and occasionally also multiple males (Goltsman, Kruchenkova, Sergeev, Johnson et al. 2005; Goltsman, Kruchenkova, Sergeev, Volodin et al. 2005; Elmhagen et al. 2014). In these isolated populations, multiple breeding females can live together at the same den (Strand et al. 2000; Angerbjörn et al. 2004; Kruchenkova et al. 2009; Elmhagen et al. 2014).

Through the inclusion of genetic analyses into studies of social organization, an even more complex social pattern has emerged. Relatedness analyses based on microsatellites have revealed non-reproductive adults providing for the cubs, the merging of up to three litters at the same den site, as well as the occurrence of plural breeding females more commonly than previously thought (Carmichael, Szor et al. 2007; Cameron et al. 2011; Norén et al. 2012). There was a considerable variation in social group composition in response to contrasting ecological conditions (measured as resource abundance and predation pressure) across four ecosystems (Scandinavia, Iceland, Svalbard and the Canadian Arctic Archipelago; Norén et al. 2012). Group structure was likely determined by an ecological trade-off in which a sufficient amount of food is a pre-requisite for forming complex groups but the more efficient guarding and predator defence related to a larger group can increase the benefits of social complexity: the Hersteinsson model (Norén et al. 2012).

Another aspect of social organization is how individuals space themselves in relation to each other. Ehrich et al. (2012) used microsatellite analysis to investigate how individuals of different age classes were distributed in the High-Arctic archipelago of Svalbard. Among more than 500 individuals, they found that littermates tended to associate close to each other during their first winter. This kin structure was more pronounced among juvenile females, which suggests that juvenile dispersal is male-biased. In complex social groups, non-reproducing individuals were always first-order relatives (such as yearling offspring or full-siblings) to one or both individuals in the breeding pair (Norén et al. 2012). The same goes for plural breeding females where the associated individuals were sisters or mother-offspring (Norén et al. 2012).

Discussion

Our overall aim here has been to disentangle micro-evolutionary processes at different levels in the Arctic fox. What distinguishes the Arctic fox from other species is the pronounced intra-specific variation. Neutral, stochastic and systematic processes can therefore be investigated both on a temporal and

spatial scale using the same study organism (Norén & Angerbjörn 2014). This makes the Arctic fox an ideal, higher-level model organism for addressing population genetic patterns and processes in light of evolution, ecology and conservation concerns.

The genetic consequences of previous ice ages and range contractions are apparent at both the species and population levels. Dispersal patterns in relation to the historical and contemporary presence or absence of ice exert strong impacts on the genetic composition (Fig. 3). Interestingly, even though the Arctic fox is a highly variable species in terms of life-history and ecology, it displays unusually low genetic divergence across its circumpolar distribution, with a limited number of factors determining the genetic patterns.

At the species level, the putatively recent divergence of the Arctic fox from a swift fox ancestor that became trapped in a cryptic northern refugium (Stewart et al. 2010 and references therein) highlights the role of climate adaptation and limited dispersal as central drivers of the speciation process. This illustrates how selection can have a significant impact in the absence of dispersal. In addition to this, genetic drift has likely contributed to the speciation process since the effective size (N_e) of a population becoming trapped in a refugium likely was small.

Dispersal is a powerful process that appears to overshadow other micro-evolutionary processes (Fig. 2a; Wright 1931). In addition to sea ice, population specific demography may influence the extent of dispersal. In cyclic Arctic fox populations, dispersal may be triggered by fluctuations in density, which can create pulses of emigrating foxes (Norén & Angerbjörn 2014) and temporal variation in levels of genetic connectivity would therefore be expected (e.g., Norén, Carmichael, Fuglei et al. 2011). In absence of dispersal, other microevolutionary processes become apparent (Fig. 2b). For example, a small and isolated population is strongly associated with genetic drift and (at least in Scandinavia) inbreeding depression (Norén et al. 2016). Another perspective worth emphasizing is the potential of small Arctic fox populations as useful model systems that illustrate the small population paradigm (Gilpin & Soulé 1986). In addition to intensified genetic drift following bottlenecks, genetic consequences from classical conservation genetic issues such as inbreeding depression and genetic swamping have been documented.

Assessing relationships among individuals has also highlighted how the ecological context can influence individual dispersal patterns and association during mating, rearing of cubs and in social groups. Also at this level, dispersal on a smaller scale, in combination with selection for the most beneficial strategies given the ecological context, were the most likely

underlying processes. In concordance with fundamental theories in behavioural ecology (e.g., Macdonald 1983), resource abundance is a central factor determining variation in social systems and subsequently the distribution of individual genetic variation. Presence of predators and close relatives may be additional factors. The findings illustrate the potential of genetic tools to resolve some important outstanding questions regarding behavioural ecology in the Arctic fox as well as other species. Although speculative, it is also possible that the potential for dispersal influences mating systems and social organization. Sea ice and long-distance migrations increase the probability of associating with potential partners, which may contribute to the higher level of extra-pair paternity observed on Bylot Island (Cameron et al. 2011). Furthermore, the low dispersal (and presence of close relatives) as a consequence of long-term small effective population size (N_e) within Scandinavia can contribute to high social complexity and tendencies for inbreeding avoidance in mating patterns (Godoy et al. unpubl. data; Norén et al. 2012). Furthermore, high intra-specific variability in breeding behaviour and ecological conditions clearly provides fertile ground for genetic studies of the Arctic fox that may also advance our understanding of mating and social systems in other mammals.

Viewing the publication rate and themes of Arctic fox genetics over a timeline, it is apparent that the focus has shifted over the years (Fig. 1). Although early interest in Arctic fox genetics mainly fell within the evolutionary framework, the more recent scientific focus has mainly been devoted to the fields of ecology and conservation (Table 1, Fig. 1). This can be attributed to the capacity of available genetic tools, but also the scientific trends and the ecological context (Table 1). For instance, in areas where the Arctic fox is abundant, a considerable part of the research has been focused on context-specific ecological processes related to dispersal and adaptation. In small and threatened populations, on the other hand, efforts have primarily concerned processes connected to the small population size and conservation. Given the emergence of next generation

sequencing technologies, we expect an accelerated interest in Arctic fox genetics/genomics and that the evolutionary framework will receive higher-level attention in the nearby future. These techniques typically require high-quality samples and is therefore a less useful tool in areas where samples are mainly collected non-invasively.

Research is not a linear process and, in pace with the development of novel genomic tools, we predict that the focus will shift back to the species level and traditional evolutionary key questions such as speciation and adaptation. It is noteworthy that early efforts in this field concerned the genetics underlying specific characters (e.g., fur colouring) and its adaptive value. Through emergence of functional genomics, we expect a return to those classical questions, as illustrated by recent accomplishments (e.g., Kumar et al. 2015). More specifically, genome sequencing will provide detailed insight into the timing of speciation in the Arctic fox, which genes have been under strong positive selection in the Arctic fox lineage and whether there are any functional genetic differences among the lemming and coastal ecotypes. In addition to this, the high-resolution data from small and threatened populations would be a very beneficial resource for the emerging field of conservation genomics, for example, through characterization of signatures of inbreeding at the genome level and identification of genomic regions introgressed from farm foxes into wild populations.

Classified as a flagship species by the International Union for Conservation of Nature (IUCN 2009), the Arctic fox lives in an ecosystem constantly undergoing environmental fluctuations as well as large-scale climatic changes. Predicting how climate change will influence the Arctic fox in the future is difficult, but learning from the past can contribute to our understanding about how the Arctic fox will respond to these changes. Dalén, Nyström et al. (2007) used ancient DNA analysis to demonstrate that the European Arctic fox was extirpated from its former distribution as a consequence of climate change. Whether this has occurred also in other regions that have been exposed to rapidly increasing temperatures in the past could be evaluated using similar approaches,

Table 1. Overview showing population status, demography and ecological context versus focus of population genetic studies for all regions. Data on population characteristics were collected from Norén, Carmichael, Dalén et al. (2011) and data on published papers are drawn from Fig. 1.

Region	Demography		Ecology		Population genetic research		
	Abundance	Demography	Ecotype	Sea ice	Evolution	Ecology	Conservation
North America	Common	Cyclic	Lemming	X	X	X	
Svalbard	Common	Non-cyclic	Coastal	X		X	
N, W, S Greenland	Common	Non-cyclic	Coastal	X		X	
E Greenland	Common	Cyclic	Lemming	X		X	
Iceland	Common	Non-cyclic	Coastal			X	
Scandinavia	Rare	Highly cyclic	Lemming			X	X
Siberia	Common	Highly cyclic	Lemming	X		X	
Commander Islands	Rare	Non-cyclic	Coastal		X		X
Pribilof Island	Rare	Non-cyclic	Coastal		X		X

as well as recent developments in palaeogenomic methods. The detailed understanding of genetic processes that will arise from future genomic analyses will likely enable better predictions about the future of the Arctic fox.

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