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Global warming and effects on the arctic fox

EVA FUGLEI and ROLF ANKER IMS

ABSTRACT

We predict the effect of global warming on the arctic fox, the only endemic terrestrial predatory mammals in the arctic region. We emphasize the difference between coastal and inland arctic fox populations. Inland foxes rely on peak abundance of lemming prey to sustain viable populations. In the short-term, warmer winters result in missed lemming peak years and reduced opportunities for successful arctic fox breeding. In the long-term, however, warmer climate will increase plant productivity and more herbivore prey for competitive dominant predators moving in from the south. The red fox has already intruded the arctic region and caused a retreat of the southern limit of arctic fox distribution range.

Coastal arctic foxes, which rely on the richer and temporally stable marine subsidies, will be less prone to climate-induced resource limitations. Indeed, arctic islands, becoming protected from southern species invasions as the extent of sea ice is decreasing, may become the last refuges for coastal populations of arctic foxes.

Keywords: *arctic fox,* Alopex lagopus*,* Vulpes lagopus*, global warming, climate change, Arctic, tundra ecosystems, missed lemming cycles, predators, sea ice*

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Introduction

It is now documented that global warming strongly will affect the distribution and abundance of both plants and animals. It is also recognized that the Arctic is especially vulnerable to climate change because global warming is most pronounced at high latitudes[1]. The terrestrial Arctic is dominated by tundra (Table 1); that is land areas north of the latitudinal tree line. The arctic tundra constitutes about 10% of the land area on earth and is situated as a circumpolar, relatively narrow zone delineated by the boreal forest in south and the Arctic Ocean in the north (Figure 1). The arctic tundra is predicted to shrink under global warming as the boreal forest zone will be moving to the north (Figure 1). However, ecological processes and characteristic species within the tundra ecosystem are likely to be affected long before the open tundra becomes forested.

The arctic fox (*Vulpes lagopus*) is one of the most characteristic species of the tundra. In this article, we discuss how the anticipated warmer climate is likely to affect the arctic fox and the wider ecological relations involving the arctic fox.

Table 1 *Definitions of concepts or terms associated with arctic fox ecology*

Concept/term	Definitions
Arctic tundra	Areas with vegetation north of the arctic tree-line
Population cycles	Multi-annual fluctuations in population density with a fairly constant periodicity
Food web	The web of feeding relations in an ecosystem
Trophic level	Different feeding levels in the food web, *i.e.* plants, herbivores and predators
Trophic interactions	Interaction between different (trophic) levels in the food web due to feeding relation; *e.g.* plant-herbivore and predator-prey relations
Trophic cascade	An external influence that initially impacts the top or the bottom of a food web that subsequently propagates upwards or downwards through all the trophic levels
Gene flow	Exchange of genes between different parts of a species geographic range due to movements of individuals
Panmictic	The part of a species range that are connected by substantial gene flow
Dispersal	Movement of individuals away from their natal site
Biome	A biome is a major class of ecologically similar *communities* of *plants*, *animals*, and *soil organisms*; examples: Arctic tundra, boreal coniferous forest

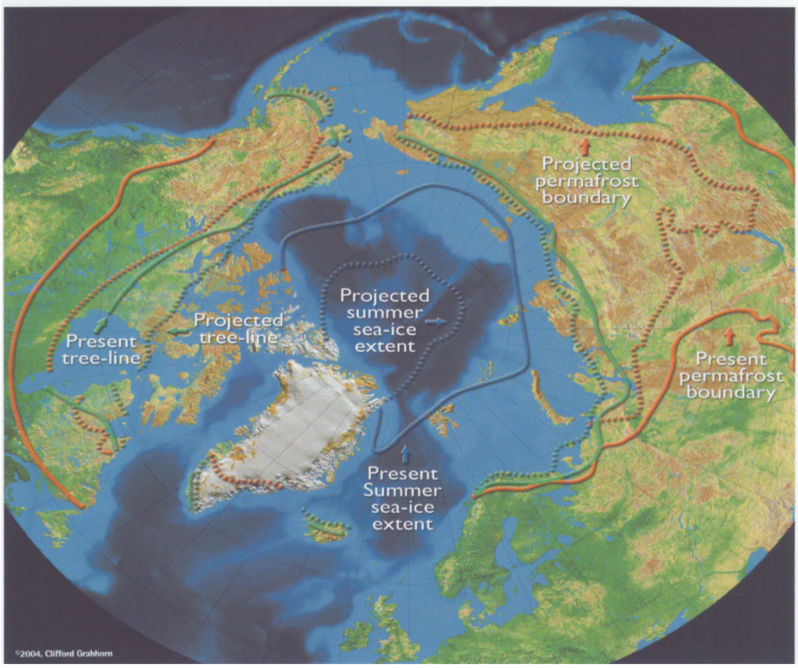

Fig. 1. *The current delineation of the tundra biome (*i.e. *areas north of the current northern tree-line) and projection from ACIA*[1] *of changes in the tree-line and the extent of summer sea ice by the end of the century, and the extent of permafrost beyond the 21st century.*

Biological characteristics of the arctic fox

Morphology and physiology

The arctic fox, which long was classified as the only species in the genus *Alopex*, has recently been placed in the genus *Vulpes*, to which most other fox species also belong. The arctic fox is among the smallest species in the dog family (*Canidae*), normally weighing between 2.5 and 4.0 kg. It is found in two colour types (morphs), white and blue. White foxes have a pure white winter coat, which in summer turns brownish-grey on the dorsal side and white on the belly. The blue morph remains dark or charcoal coloured all year round, but becomes somewhat lighter in winter. Blue foxes are most frequently found in coastal areas without sea ice and with little snow in the winter and the dark colour may serve as a camouflage in such habitats[2]. On the snow-covered inland tundra and on sea ice a white winter fur is clearly the most cryptic colouration (Figure 2).

Fig. 2. *Arctic fox of the white colour morph (summer upper left, winter lower left) and the blue colour (summer upper right, winter lower right). Photo by Jason Roberts (winter white and blue) and by Eva Fuglei (summer white and blue).*

Arctic foxes are very well adapted to a life in some of the coldest areas on earth. They have a short snout and short rounded ears which minimizes the heat loss through these parts of the body. In winter, they are equipped with an excellent insulating winter fur, which is extremely thick with dense under-fur and long guard hairs[3]. Even the paws are covered by fur. The excellent winter fur has made the arctic fox a very valued fur bearer, and it is still harvested in many places in the Arctic. In addition to the winter fur, a thick fat layer under the skin contributes to the thermal insulation of the inner parts of the body. The energy contained in this fat layer make the fox endure periods with little food even in extremely cold weather. Moreover, the arctic fox can sustain periods of starvation by lowering their metabolic rate[4,5]. The shedding of winter fur starts in May and the much shorter summer fur is in place in July[3]. Thus, a warmer summer climate will most likely not represent any physiological tress for the arctic fox.

Geographic distribution and genetics

Arctic foxes have a circumpolar distribution and are found in all kinds of tundra habitats, from the sub-arctic mountain tundra in central Fennoscandia, through the vast arctic tundra of Eurasia and North America, and on all the large Arctic and sub-arctic islands such as Greenland, Iceland and Svalbard, and arctic archipelagos of Siberia, Canada and the Bering Strait[6].

Apart from some isolated islands in the Bering Strait such as the Commander Islands (Mednyi and Bering Islands, Russia) and the Pribilof Islands (St. George and St. Paul Islands, USA), where local arctic fox populations have been isolated for a long time[7,8], there is little genetic differentiation across its vast geographic range[8–10]. Evidently fox individuals can migrate over long distances and thereby cause substantial gene flow (Table 1). In fact, Arctic island populations are not isolated as long as they occasionally can be connected to other islands or the mainland by sea ice. Consequently, sea ice occurrence can explain 40–60% of the variance in genetic distance between arctic fox populations on different continents or islands[8]. Typically, an island like Iceland that only in exceptionally cold winters is connected by sea ice to other parts of the Arctic harbour a fox population with relatively low genetic diversity[8,9].

Quite a lot is known about the historical geographic distribution of the arctic fox based on fossil and archaeological material. Like other polar-adapted species the arctic fox has shown distinct geographic range dynamics during the most recent climatic cycle[9,11]. Polar species typically expand their range during ice ages and contract it during the interglacials. Specifically, the arctic fox experienced an extensive range expansion during the last glaciation (9,000–15,000 BC) in which they were widely distributed across southern Europe (*e.g.*, south France and Ukraine) and throughout large areas of the Palaearctic region[12,13]. During the current interglacial, arctic foxes have retreated following the arctic tundra northward[14].

Habitat, diets and life history characteristics

Arctic foxes live in two main tundra types, *i.e.* inland and coastal tundra. These two habitat types, being different in the availability of food resources, give rise to differences in arctic fox diets and life history characteristics[15]. In most inland tundra areas, lemmings and other small rodents constitute the main node between plants and predators in the food web (Table 1), in the sense that these small herbivores are temporally the most abundant prey[16]. Lemming populations exhibit strong cyclic fluctuations in abundance with a periodicity of 3–5 years[17]. At lemming peak abundance arctic foxes experience a bonanza in food resources and they produce litters with up to 19 young. However, in lemming-low years foxes normally do not breed at all, but subsist on a diet of other terrestrial food sources such as ptarmigan, geese and carrion of reindeer and musk ox. Although arctic foxes have been reported to reach an age of 13 years in the wild, most foxes do not live more than 3–4 years[18]. So an inland arctic fox cannot expect to experience more than one lemming peak year and one good breeding season in their lifetime.

Coastal foxes in regions without lemmings like Iceland, West Greenland and Svalbard often rely on food resources from the marine food web. In particular, seabirds, including their eggs and young, make up a substantial proportion of their diets, especially in the summer[19,20]. However, the arctic fox is known to prey on other marine animals as well. For instance, they hunt ringed seal pups on the sea ice[21], and some foxes may follow Polar bears on the sea ice in the winter so as to scavenge on remains of their kills[22]. Under other circumstances, a substantial fraction of coastal arctic fox food may consist of marine invertebrates that are found along the shore[19]. In contrast to the inland situation with strong inter-annual variation in the abundance of lemming prey, the marine food web provides a more stable food base for the arctic fox. Thus foxes can breed most years and their litter sizes are less variable with normally 4–6 cubs per litter[18,23]. To further enhance the stability of food resources throughout the year the arctic fox stores excess food during spring and summer, for use in late autumn and winter[24].

In some areas, the arctic fox does not fall distinctly into either a coastal or inland ecological niche. For instance, in coastal tundra areas which harbour cyclic lemming populations, arctic foxes typically switch between terrestrial (*i.e.* lemmings) and marine resources depending on what is most profitable in a given year[25]. Indeed, the arctic fox is a true opportunist that makes the best out of the ecological circumstances as they vary in time and space.

Population ecology

The home ranges of arctic fox in the breeding season vary in sizes from 4 to 60 km^2 depending on the availability of food resources[26–29]. Thus resource rich areas and years can sustain dense arctic fox populations. The strong cyclic pulses in lemming abundance followed by boosts in reproduction of inland arctic fox give rise to distinct fox population cycles[30] (Table 1). Such cycles are very evident in harvest statistics (Figure 3). In tundra areas without lemmings such as on Iceland, Svalbard and western Greenland fox

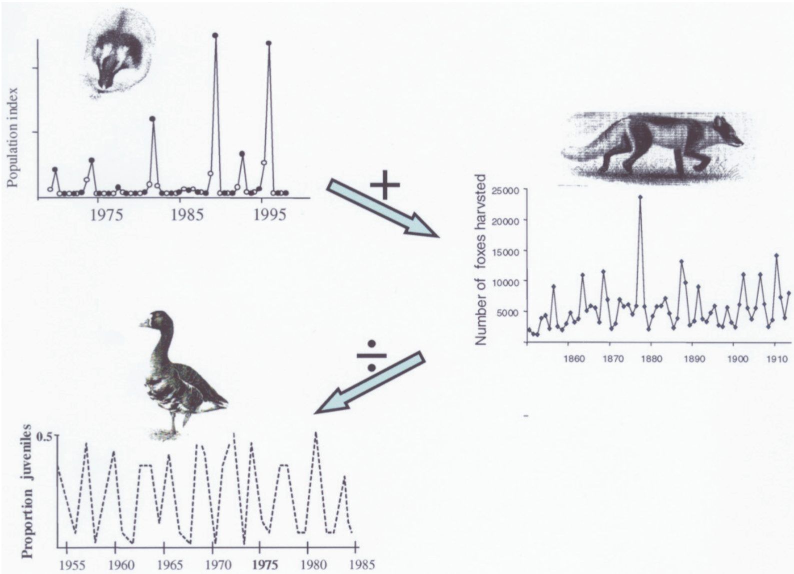

Fig. 3. *Cyclic ecosystem impact of the arctic fox through the "alternative prey mechanism" in inland tundra. Cyclic lemming populations, being primary prey for arctic foxes, drive an equivalent fox population cycle, which in turn drives a demographic cycle in arctic geese, serving alternative prey for foxes. The population curves represents trapping data on Norwegian lemmings in mountain tundra[67], harvest statistics of arctic fox from the Canadian Arctic[30] and arctic geese from Taimyr[11].*

population dynamics do not show any signs of cyclicity[18,23]. As can be expected coastal arctic foxes maintain more stable populations than inland foxes. However, locally quite pronounced fluctuations may still occur[31].

While breeding, an arctic fox pair is resident in the summer, and defends its home range against other foxes; the pair can switch to a more nomadic behaviour during winter, presumably in search for food when such is scarce[27]. Mass migration of the arctic foxes may, after peaks and subsequent crashes in lemming abundance, sometimes extend deep into the boreal forest[32]. However, the arctic fox never establish breeding populations outside the tundra.

The total population size of arctic foxes is uncertain or unknown for most arctic regions. One of the best population estimates is from Iceland that houses an increasing population of more than 6000 individuals[18]. The vast Russian tundra with plenty of excellent lemming habitat houses most arctic foxes globally, and the total population size there may be of the order of 200,000–800,000 individuals[33]. Little information is available from Bering Island

(Russia), Canada, USA (coastal Alaska), Greenland and Svalbard (Norway), but the population sizes are presently regarded as large and stable. The only areas that house small and declining arctic fox populations are Mednyi Island (Russia) and Fennoscandia (Finland, mainland Norway and Sweden)[7,34]. On the Mednyi Island there is presently only about 90 foxes[7], while in Fennoscandia the breeding population is probably in the range of 50–100 individuals[34].

Role in the ecosystem

The high population density sometimes attained by the arctic fox indicates that this predatory mammal can have large impacts on the structure and dynamics of the relatively simple arctic food webs. Coastal foxes prey intensively on sea birds when they have access to their breeding colonies. Arctic foxes introduced to the Aleutian archipelago dramatically reduced the breeding populations of sea birds[35]. This in turn had strong impacts that cascaded down to the base of the food web so as to shift the vegetation from lush grassland to unproductive shrub and moss dominated tundra (Figure 4). The cascading effect was mediated by obstructed nutrient transport by seabirds from sea to land.

Although it has often been claimed that lemming population cycles may originate from predator–prey interaction[36], it has yet to be shown that the arctic fox can drive lemming cycles. However, what is clear is that the arctic fox can provide a dynamical link between the lemming cycle and other components of the food web. One such link is due to the so-called *alternative prey mechanisms*. In crash years of the lemming cycle, foxes turn to alternative prey, such as eggs and chicks of geese[37,38] and shore-birds[39]. This causes demographic cycles in the populations of such birds that perfectly mirror the lemming cycle (Figure 3).

Another ‘‘spill over effect’’ that may have its origin in the lemming cycle is arctic fox born zoonoses. Zoonoses are wildlife diseases that may spill over to humans. The most notable zoonose in the case of the arctic fox is rabies. Arctic rabies is often most prevalent in peak density arctic fox populations following lemming years[40]. Arctic rabies is spread from continents to islands by dispersing arctic foxes on the sea ice[41] and such dispersal movements (Table 1) are most likely following lemming years. Arctic foxes are also responsible for the transmission of the tapeworm *Echinococcus multilocularis* which causes fatal liver infection in humans[42].

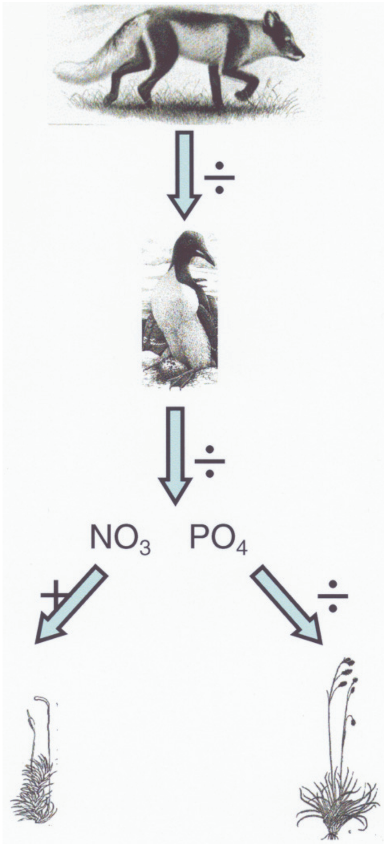

Fig. 4. *How introduced arctic foxes on arctic islands with sea bird colonies can bring about a top-down trophic cascade (Table 1). Arctic foxes can severely reduce the size of the breeding colonies of seabirds and thereby obstruct the transportation of nutrient from ocean to land. The reduced nutrient inputs change the vegetation from productive grassland to unproductive moss tundra.*

Climate change and the arctic fox

The ultimate climate threat to the arctic fox, and all other tundra-dwelling organisms, is the retreat of the entire tundra biome (Table 1) as boreal forest expands northward (Figure 1). According to prevailing climate change scenarios[43] the forest will finally extend north to the coast of the Arctic oceans both on the Eurasian and the American continent. So superficially it may seem as a trivial task to predict the ultimate fate of species like the arctic fox that cannot live their lives in the forest. However, the spread of forest is a relatively slow and spatially uneven process. In fact, some presently forested areas in the Arctic may experience a temporal retraction of the northern forest borders due to melting permafrost and human interference[43]. Below we highlight changes in the tundra ecosystem that may affect the arctic fox long before the boreal forest eventually closes the era of the arctic tundra.

Changed food resource dynamics

As explained above the population cycle of lemming and voles is a key-stone process in the functioning of tundra ecosystems. In inland tundra, where the strong cyclic boosts and busts of small rodent biomass completely dominate the resource dynamics, resident predators possess particular life adaptations to cope with the vagrancy in the amount of prey. In particular, a high reproductive output at lemming peak densities, for instance in terms of large fox litters, is necessary to sustain a predator population until the next lemming peak. If lemming peaks for some reason are missed, in otherwise resource-poor tundra, the population of relatively short-lived predators such as the arctic fox will rapidly decline.

Missed lemming and vole peak years appear to be exactly one of the problems of the declining arctic fox populations in mountain tundra of Fennoscandia[16,44]. After some high lemming peaks during the 1970s and early 1980s, proper peak years were missing in the period 1985–2000, and consequently, the arctic fox population experienced a pronounced decline[34]. In the 2000s, the high amplitude lemming cycle reappeared in the central part of the Scandinavian mountain chain and the arctic fox population here appears now to be in a phase of recovery (A. Angerbjörn, personal communication).

There is, however, reason to believe that the population cycles of lemmings and voles will become increasingly more unstable and faint as climate becomes warmer[16,45]. This is because such population cycles appear to be dependent on long, cold and stable winters[45]. The recent tendency for warmer and more unstable winters with repeated freeze-thaw events are likely to be devastating for small mammals that must find food plants in the snow pack[46,47]. Freeze-thaw events result in the formation of ice crust that makes the food plants less accessible. Among the herbivorous small mammals, lemming species of the genus *Lemmus* are likely to be most vulnerable to such ice-crusting since they depend on moss at the ground, which is the first vegetation to become encapsulated by ice. Voles that forage on erect shrubs that often will protrude the ice crust can be predicted to be less vulnerable.

On the other hand, winter thaw-freeze cycles associated with global warming may also benefit some arctic fox populations, at least temporarily. Similar to the case of small mammal herbivores, the formation of ice crust on the tundra may also severely limit the forage availability for large herbivores. Dramatic population crashes in reindeer and musk ox following ice-crusting and ‘‘locked’’ pastures have been reported from different locations in the Arctic[48,49]. The increased supply of carrion resulting from such catastrophic winters for resident arctic reindeer populations has been reported to result in increased breeding success of arctic foxes on Svalbard[31]. Whether such events will benefit arctic foxes on the long term is, however, uncertain. If the increasingly more difficult winters results in generally smaller populations of truly arctic herbivores this will clearly also harm the arctic fox.

The negative effects of climate change on biomass of herbivores in arctic areas are, however, only expected to be temporary. In the long-term, a warmer climate means longer growth seasons for plants and more plant biomass for herbivores to consume. One example of increasing plant biomass on tundra is the rapid expansion of shrubs such as willows and dwarf birch which is now reported in the Alaskan tundra[50,51]. The process of ‘‘shrub encroachment’’ of the tundra is much faster than the expansion of trees and forest, since these shrubs are already in place on the tundra. An increased biomass of shrubs provides subsistence for other herbivores than lemmings and reindeer. Increased populations of typically shrub-browsing herbivores such as hare, grouse, voles and moose is likely to increase the overall biomass, diversity and stability of herbivore prey for carnivores. If left alone this could have benefited the arctic fox. The problem for the arctic fox under such circumstances is that it will not be ‘‘left alone’’.

Competition and predation

The arctic fox is a small-sized predator that is an inferior competitor, and may even serve as a prey to many other carnivores. Increased ecosystem productivity, due to shrub encroachment on the tundra, will lead to invasion of more southerly-distributed species acting as competitors and predators of the arctic fox. Most important in this context is the red fox. Arctic and red foxes are sympatric (inhabit the same geographic region) in a narrow overlap zone in the low Arctic[52]. However, the red fox is a dominant competitor and predator both for juvenile and adult arctic foxes[44,53]. A recent northward expansion of the red fox is well documented[52].

Already Skrobov[54] noted a general northward advance of red fox with the resulting replacement of the arctic fox in arctic Russia. In Fennoscandia, the arctic fox has retreated to higher altitudes in the mountain tundra probably due to increased competition with the red fox at lower altitudes[44,55,56]. In southern arctic tundra in northern Norway the retreat of the arctic fox was most prevalent on the shrubbiest parts of the tundra[57], which is consistent with the hypothesis that the problem for the arctic fox is ultimately related to a climate change induced increase in ecosystem productivity.

Arctic fox island populations and the decreased extent of the Polar sea ice

Most of the islands located in the Arctic Ocean are populated by arctic foxes. Some of these are the most northern terrestrial environments on earth and therefore will be the last to be warmed up to the extent that arctic fox habitats are lost. Another aspect that is likely to increase the role of arctic islands as the last refuges for terrestrial arctic fauna and flora is the rapidly decreasing extent of the sea ice[58,59]. In a few decades the ice connection between the continents at the arctic islands may be permanently lost meaning the island ecosystems will be protected from invasions of such southern species like the red fox. However, the lost sea ice connection between arctic islands and continents will also mean that the present connectivity and gene flow of the currently large panmictic (Table 1), circumpolar arctic fox population[8–10], will be lost. As a consequence genetic differentiation among separate populations can be predicted to increase in the future. Moreover, some island populations of restricted size are likely to lose genetic variation[60]. Finally, small island populations, which are prone to go extinct for other reasons[61], will not become re-colonized.

The last point is nicely illustrated with the recent history of two arctic fox populations on the Norwegian islands, Bear Island and Jan Mayen. On Bear Island, which is located between Spitsbergen and the Norwegian mainland, the arctic fox population was hunted to extinction during the Second World War. In winters, when extensive sea ice connected Bear Island with Spitsbergen, arctic foxes re-colonized Bear Island as to establish a reproducing population (Strøm and Fuglei unpublished data). On Jan Mayen, which is located further south between Greenland and the mainland of Norway, records from Dutch whalers specifically stated that this island lacked arctic foxes in the 1600s[62]. During severe ice conditions in late 1800s the arctic fox population were established on the island, but was eradicated by over harvesting during the first part of the 1900s[63]. The recent absence of sea ice in the Greenland Sea and the Norwegian Sea has prevented the arctic fox from recolonizing Jan Mayen and thus this population may be permanently extinct.

For coastal arctic foxes the reduction of the pack ice may also have several effects on their feeding relations to the marine ecosystem. Sea ice dependent seal species and the polar bear will clearly be severely affected by the loss of sea ice[64,65]. Thus hunting ringed seal pups and scavenging on the remains of polar bear kills may soon no longer be possible for the arctic fox. However, the fact that the arctic fox maintains large and highly viable populations along the completely ice-free coasts of Iceland[19] indicates that a future for the arctic fox on arctic islands not surrounded by sea ice might be unproblematic.

Conclusions and perspectives

Like many other species adapted to a life in a polar environment the arctic fox will come under pressure as the globe is warming up. Ultimately, the arctic fox depend on open tundra habitats, and if this habitat eventually becomes closed by a northwards expanding forest, also the history of arctic fox as an extant species will be closed. Of most immediate concern, however, are the more rapidly occurring ecological changes presently taking place within the tundra ecosystem, which may exclude the arctic fox from large parts of the circumpolar tundra biome in the course of a few decades. Locally, the arctic fox population can be conserved with specific management actions, for instance, with control of red fox populations as now is attempted in Fennoscandia[34,66]. However, the best hope for future persistence of the arctic fox is high Arctic islands, which may represent the safest refuges for arctic fauna and flora on a warmer globe.

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