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Review

Recent enrichment of megafauna in the north of Eurasia supports the concept of Pleistocene rewilding

Igor Popov

Department of Applied Ecology, Faculty of Biology, St. Petersburg State University, St. Petersburg, Russia

Correspondence: Igor Popov (i.y.popov@spbu.ru, igorioshapopov@mail.ru)

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'Pleistocene rewilding' refers to the concept of restoring ecosystems to their state during the Pleistocene epoch, by (re-)introducing species or their close relatives that were present during that time, in an effort to revive ecological processes that existed before human-driven extinctions. This concept is highly controversial for both ethical and ecological reasons. Here I review evidence of recent northward range expansions of various large land mammals in boreal Eurasia, and discuss whether this provides evidence that rewilding projects might be justified and feasible. Around 100 years ago, the native boreal fauna of Eurasia included five species of large land mammals: moose *Alces alces*, brown bear *Ursus arctos*, wolf *Canis lupus*, reindeer *Rangifer tarandus*, and snow sheep *Ovis nivicola*, but since then the list has expanded. This is due to the introduction of bison *Bison bonasus*, *Bison bison*, muskox *Ovibos moschatus*, non-native deer, and feral horses, as well as the northward expansion of wild boar *Sus scrofa*, roe deer *Capreolus capreolus*, *Capreolus pygargus*, and red deer *Cervus canadensis*. In addition, several southern species temporarily occurred in the north, including tiger *Panthera tigris*, sika deer *Cervus nippon*, and yak *Bos grunniens*. This ongoing enrichment of the boreal fauna is reminiscent to Pleistocene rewilding. However, so far, the abundance of expanding large mammals species remains low. Large-scale projects on Pleistocene rewilding are labor-intensive, expensive, and not popular enough to receive support, and therefore their realization is problematic

Keywords: boreal, large mammals, non-native species, northwards expansion, rewilding

Introduction

To enhance the diversity and richness of wildlife is a commonly emphasized goal in the new Millennium (Toledo et al. 2011, Deinet et al. 2013, Jepson 2016, Root-Bernstein et al. 2018). Given the long history of human pressure faced by many species, leading some to extinction, 'rewilding' efforts to revive ecological processes that existed before human-driven extinctions, may be ecologically and ethically justified. Some of the most prominent rewilding initiatives use the Pleistocene epoch as

a reference, i.e. ecosystems of the past containing numerous species of large mammals (Smit et al. 2015, Olofsson and Post 2018, Van Klink et al. 2020). Most of these became extinct around 10 000 BCE, and this event marks the Pleistocene–Holocene boundary (Pillans and Gibbard 2012). Advocates of Pleistocene rewilding argue that to counteract this loss, it is justified to increase the number and expand the range of surviving equivalents of extinct large mammals, such as elephants, camels, lions, etc. (Donlan et al. 2005, Wolverton 2010, Toledo et al. 2011, Lundgren et al. 2020). Opponents argue that this approach does not restore the natural state of the environment but rather creates new 'Frankenstein ecosystems' potentially leading to numerous unwanted and unpredictable consequences, representing a danger for the threatened native objects (Rubenstein et al. 2006, Oliveira-Santos and Fernandez 2010, Seddon et al. 2011). This issue is still under debate, and the number of publications is increasing (Gordon et al. 2021).

Pleistocene rewilding might be especially tempting in the boreal zone of Eurasia, because it is large, sparsely populated, and seems to be suitable for large-scale projects. Mammoth fauna once thrived in this region, comprising also rhinoceroses, wild cattle, deer, saigas, and other large mammal species. Conventionally, climate change is considered the most important factor leading to mammoth fauna extinction: as the environment became hotter and wetter, the arboreal vegetation expanded, suppressing grasslands, which meant habitat loss for mega-herbivores (Vereshagin 1979, Grayson and Meltzer 2003). However, the viewpoint that humans exterminated them also has support (Martin 1984, Haynes 2007, Svenning et al. 2016, Nagaoka et al. 2018). It is likely that both humans and climate change contributed to the transformations of the fauna (Johnson 2002, Wroe et al. 2004, Nogués-Bravo et al. 2008). If humans indeed played a role in the extinction of mammoth megafauna, increasing the number of large mammals in the boreal zone could trigger vegetation transformations, causing forests and mires to yield to grasslands, thus recreating the highly productive vegetation type known as the 'mammoth steppe'. This concept has been under experimental verification for some time. In 1997, Sergey Zimov and his colleagues established the 'Pleistocene Park' near the Arctic Circle in eastern Russia (Yakutia Republic) (Zimov 2005). The park comprises a roughly circular fenced area 4 km in diameter, housing various herbivores including bison *Bison bonasus, Bison bison*, muskoxen *Ovibos moschatus*, and numerous domestic ungulates of northern breeds: cattle *Bos taurus*, sheep *Ovis aries*, camels *Camelus bactrianus*, yaks *Bos grunniens*, horses *Equus ferus caballus*, and reindeer *Rangifer tarandus* (Pleistocene Park 2023). Carnivorous mammals were not introduced in the park, but native bears *Ursus arctos* and wolves *Canis lupus* access it occasionally. The management of the park aims to maximize the diversity of ungulates so that their community resembles that of the Pleistocene. It is expected that this will have various effects on the vegetation, continuously increasing the carrying capacity of the park, which over time will turn into something similar to the African savanna. The realization of the Pleistocene Park project addresses not only the enrichment of megafauna, but also global geophysical processes including permafrost melting, carbon dioxide and methane emissions. Today, mosses cover vast expanses of the boreal zone, which are covered by a thick layer of snow in winter. This acts as thermal insulation, meaning that the soil does not freeze deeply enough each winter, accelerating permafrost melting. Rapid melting of permafrost results in erosion of the terrain, and increases emission of carbon dioxide and methane from ancient soils. 'Mega-mammals', so the project's idea, would trample mosses and snow, increasing cold penetration and slowing the melting of permafrost (Zimov et al. 2012, Macias-Fauria et al. 2020, Zimov 2022). Ungulates survive in Pleistocene Park, but not independently. Supplemental feeding supports their existence, and there are no stable reproducing populations, necessitating regular replenishments. The plots of transformed vegetation occupy rather small areas (Popov 2020). The maintenance of the park is very labor-intensive, and the number of supporters is rather small. The park's current situation provoked the hypothesis that Pleistocene rewilding in the north is theoretically feasible but currently impractical due to technical limitations.

The park remains a small area with a small number of ungulates, limiting its ability to assess the prospects for transforming large areas. To evaluate the Pleistocene rewilding concept in general, and the Pleistocene Park concept in particular, it is worthwhile to analyze indications of recent enrichment of the megafauna of the Eurasian north. If any additional species of large mammals recently became established there either because of intentional releases or natural expansion, this would be evidence in favor of the Pleistocene Park concept. This paper therefore provides a systematic review of data on the recent enrichment of northern megafauna to provide evidence to support or refute the feasibility of Pleistocene rewilding in the north.

Material and methods

The situation that existed 100 years ago was considered as a baseline. At that time, the northern boundary of the native range of wild boar *Sus scrofa*, roe deer *Capreolus capreolus* and red deer *Cervus elaphus* was identified (Formozov 1946, Geptner 1961). The boundary nearly coincided among these species, but the roe deer was distributed a little farther northwards than the others in some places. Other southern 'mega-mammals' were distributed far to the south. In the west, the boundary occurred at 60°N, but it shifted from the Baltic Sea basin to the south-east up to the southern Urals (55°N), then it passed eastwards between 55–58°N. This boundary corresponds with the border of thick snow coverage, restricting the distribution of several species. In the 1920s, snow coverage at least 40 cm thick persisted there for five months (Formozov 1946). In the bioregion framework (Olson et al. 2001), it is the border between the zones of boreal (taiga) forests and temperate broad-leaved and mixed forests. It was used as the benchmark of north and South in this study. As

for the difference between 'mega-mammals' and others, the benchmark of 44 kg was used. It was suggested in the studies of megafauna as comparing animals' size to humans, 'mega-mammals' are those which are approximately of the same size or larger (Martin 1984), though other thresholds are also in use (Moleón et al. 2020). Native modern land fauna of northern Eurasia included five such species: moose *Alces alces*, reindeer *R. tarandus*, snow sheep *Ovis nivicola*, brown bear, and wolf (Geptner et al. 1961, 1967). All other species of large mammals can be considered non-native because they either never lived in northern Eurasia, or lived in a remote past – usually thousands of years ago, and only in small areas – several hundred years ago. In this study, the introductions or natural distribution of such non-native species of 'mega-mammals' to the north over the past 100 years were reviewed. The literature search aimed to elucidate which additional species penetrated the boreal zone, their current status and trends, and the causes behind their range expansions or contractions. Data on recent changes in distribution areas of native northern species was also analyzed. The information was collected using Google Scholar (2023), GBIF (2023) and the Russian Science Citation Index (2023). The search was carried out using the keywords 'invasions', 'alien species', 'introductions', names of species of large mammals, names of countries of northern Europe and parts of the Russian Federation. The list of species was compiled using GBIF and the IUCN Red List of Threatened Species (2023), and was refined as searches progressed. Search focused primary on review articles or monographs containing information on distribution and abundance of mammal species. In a case of need, information was updated using local sources such as websites of naturalists or relevant institutions.

Results

Introductions of non-native species

Twenty six sources on non-native large mammals in northern Eurasia were analyzed. They include 4 monographs, 16 journal articles, 4 articles of the collections of papers and 2 databases.

European bison *Bison bonasus*

Historically, the European bison inhabited the Caucasus and eastern Europe, but they became extinct in the wild in the 1920s (Plumb et al. 2020). Afterwards, the bison that survived in captivity were bred and reintroduced into various locations across eastern Europe and several populations were founded. Most of them are located within the native range, but northern areas were also involved in this process. In 1991, one male and two females were moved to Vologodskaya oblast (northwest Russia) (Table 1, Fig. 1). Initially they were kept in a corral, but they escaped soon after. They found a suitable location about 20 km away and settled there. Afterwards, new individuals were added from the breeding sites located in the reserves of central Russia from time to time, the European bison reproduced, and their numbers continuously increased.

Table 1. Introductions of non-native ungulates in the northern zone of Eurasia. Under 'Status', '+' indicates the continued existence of released individuals and their offspring in 2023.

Species	Location	Years of introduction	Status	Sources
European bison, *Bison bonasus*	60°N, 38°E	1991	+	Gusarov 2022
American bison *Bison bison*	61°N, 128°E	2006, 2011, 2013, 2020	+	Smetanin 2017, Argunov 2018, Smetanin and Safronov 2022
	68°N, 161°E	2019, 2021	+	Pleistocene Park 2023
Muskox *Ovibos moschatus*	62°N, 09°E	1946-1953	+	Lønø 1960
	74°N, 106°E	1974, 1975	+	Yakushkin 1998
	71°N, 179°E	1975	+	Yakushkin 1998
	73°N, 125°E	1996	+	Tsariov 2007
	73°N, 117°E	1997, 2000	+	Tsariov 2007
	67°N, 67°E	1998, 2003	+	Tsariov 2007
	74°N, 112°E	2001, 2002	+	Tsariov 2007
	71°N, 149°E	2000, 2009	+	Ovtsebyk 2023
	69°N, 159°E	2014	+	Ovtsebyk 2023
	63°N, 151°E	2007	+	Ovtsebyk 2023
	59°N, 150°E	2018, 2020	+	Ovtsebyk 2023
Sika deer *Cervus nippon*	60°N, 30°E	1958	Exterminated in 1990s	Pavlov 1974 Oral communications by locals
White-tailed deer *Odocoileus virginianus*	Southern Finland	1934, 1948	+	Nummi 2001
Fallow deer *Dama dama*	Southern Sweden	Since 1570	+	Kjellander et al. 2012
	Southern Finland	1930s, 1950s	+	Nummi 2001
Mouflon *Ovis musimon*	Southern Finland	1939, 1949	+	Nummi 2001
Feral horse	51°N, 156°E	?	+	Milchevsky and Filatova 2015
Equus ferus caballus	66°N, 36°E	1990s	+	Blokhina et al. 2021
Yak *Bos grunniens*	61°N, 127°E	1971, 1973, 1974	Exterminated in 1980s	Shadrina et al. 2022

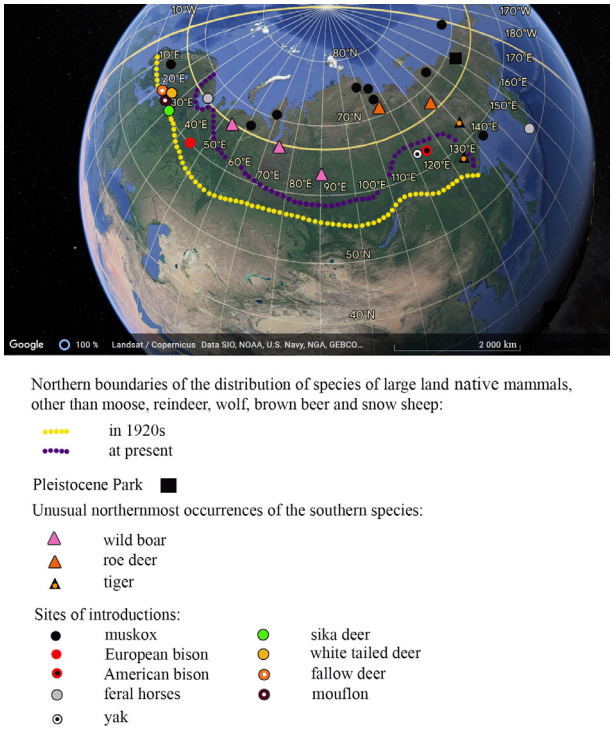

Figure 1. Enrichment of the megafauna in the north of Eurasia. Results of this review indicate that the distribution boundary of several species of large land mammals has moved north by several 100 km in the course of the last 100 years.

According to the recent census (2024), there are 173 individuals (Igor Gusarov, project coordinator European bison introduction to Vologodskaya oblast, pers. comm.). These bison have found suitable habitats comprising abandoned farmland and surrounding forests (Nikulnikov et al. 2016, Gusarov 2022), but receive supplemental feeding during winter. Consequently, their range remains limited, and their ability to sustain themselves independently is still uncertain. While sightings have been reported at distances of several tens of kilometers from the initial release point, during winter, they tend to congregate near feeding areas (Gusarov 2022). If several individuals overwinter in the other places, their number is insignificant.

The breeding of European bison takes place mainly in a framework of threatened species conservation. However, in the case of Vologodskaya oblast, other motives were also present. The first breeding was done through the initiative of local specialists dealing with cattle breeding. The European bison were discussed as a source of meat and potential genetic material to improve the local cattle (Tyapugin and Simonov 2009), although their importance in the context of ecology and conservation biology was also identified (Shumov et al. 2007).

American bison *Bison bison*

Bison similar to the American species existed in eastern Siberia into historical time, but disappeared about 1000 years ago (Lazarev 2008). In 2006, 30 American wood bison *Bison bison athabascae* were imported there. A special farm was arranged for them in a central Yakutia (Smetanin 2017, Argunov 2018). In 2011, 2013 and 2020, 30 additional bison were imported each year (Table 1, Fig. 1). They were kept in corrals, and a portion of them were released. Almost all bison survived and their reproduction was successful. In 2022, the total number was 310, of which 101 were in a natural environment. Several individuals traveled up to 200 km from the farm, but came back; most of the bison have not spread very far away. The present situation is considered an initial stage of acclimatization, which seems to be successful (Smetanin and Safronov 2022). It is considered a promising subject in terms of land use, meat production, threatened species conservation, and tourism (Smetanin 2017). However, it is questioned by some experts, because like in a case of European bison, the Yakutain ones receive supplemental feeding during winter, therefore they do not spread actively and their ability to survive by they own is still uncertain (Volpert et al. 2023).

Muskox *Ovibos moschatus*

The native range of muskox is in the extreme north of North America. In Eurasia, they became extinct about 2700 years ago (Lazarev 2008). A first attempt to introduce muskoxen to Eurasia took place in 1900, when a few of them were imported to Sweden, but they died soon after. In the 1920–1930s, 39 muskoxen were imported to Norway. A portion of them died soon after, but the rest were released at several sites. They settled on Svalbard and on the mainland, started to reproduce, but during the Second World War, they were almost exterminated. They survived only in Svalbard in small numbers. A second attempt occurred soon after the War (Lønø 1960, Table 1). It resulted in the formation of a population in southern Norway (Fig. 1). They spread around and came to occupy a small plot in Sweden. According to the recent census, there are 244 in Norway and 10 in Sweden (Cuyler et al. 2020). However, the muskoxen became extinct in Svalbard in the 1980s. This likely happened due to competition with reindeer (Klein and Staaland 1984), although some experts question this conclusion, because on other islands where both species coexist, it is the muskoxen that suppress the reindeer (Sheremetev et al. 2014). These authors believe that muskoxen died of pneumonia, which was provoked by humid climate and sources of infection originated from human settlements. However, it is not convincing as muskoxen lived in Svalbard over decades.

In 1974 and 1975, 50 muskoxen were imported from the USA and Canada to Russia. Thirty of them were released in the Taymyr Peninsula, and 20 on Wrangel Island (Table 1, Fig. 1). The former were kept in a corral for at least 5–6 years. When some of them escaped through holes in fences, they were caught and put back. Since 1979, groups of them were released, and in the 1980s they formed a stable population in the natural environment. Their number reached 415–435 individuals in 1990. Afterwards, a rapid increase took place. There were about 1600 individuals in 1996. Most of them

settled near the point of release. Rivers and mountains prevent their effective natural spread, but several young males walked several 100 km (Yakushkin 1998). On Wrangel Island, the introduction progressed slowly during the first years, but afterwards rapid growth in numbers occurred. They may have come to occupy all potential habitats, and currently there are several hundred individuals (Sipko et al. 2007).

These new populations of muskoxen were then used for introductions into several sites in Siberia (Table 1, Fig. 1). Occasional occurrences in European Russia were recorded (Ovtsebyk 2023). Recently, their total number was estimated between 9700 and 18 500 (in 2022) (ibid.), or 15 796 (in 2004–2018) (Cuyler et al. 2020). A reliable census is problematic because muskoxen are sparsely distributed over a huge area, but an upward population trend is evident, further expansion is likely as they have only occupied a small fraction of potential habitats (Shadrina et al. 2022), and some enthusiasts are eager to introduce them 'everywhere' in the north (Ovtsebyk 2023). The project of muskox introduction originated from a slogan about the enrichment of fauna, which was popularized in the past (Pavlov et al. 1974). Importing muskoxen was frequently discussed in the 1920s–1930s due to their potential for commercial use. Now in Taymyr, the muskox is already considered a game animal, although the price for the license is so high that it is rarely purchased (Ovtsebyk 2023). Poaching takes place instead. Recent activities on muskox spread are partly related to the idea of Pleistocene rewilding. In 1997, a protected area was established in the northern Urals, where the organization of a 'Park of the Glacial Age' was planned, analogous to Pleistocene Park, although not realized; today, only muskoxen are bred there (ibid.).

Sika deer *Cervus nippon*

The native range of sika deer occupies a relatively small area in the Far East. Since the 1920s they were actively spread over Eurasia, and one point of introduction was in the boreal zone. This took place near the shore of Lake Ladoga (Table 1, Fig. 1). Sika deer were imported there in 1958. They were kept in corrals and released in various locations several times. Supplemental feed was put in the forests for their use. The sika deer reproduced, and their numbers increased up to several hundred. They found suitable habitat in the wet shrubs and cane thickets at the coast of the lake, although it was believed that they could not survive on their own because of thick snow coverage (Vereshagin and Rusakov 1979). The circumstances of sika deer survival in this new habitat remained understudied, because all of them were killed by poachers in 1990s, as reported by locals (Popov et al. unpubl.). Recent reports on sika deer in this area were not found. Now a hunting ground exists there, but only with native game species (Sosnovskoe GOOH 2024). The introduction of sika deer aimed to improve the state of threatened and commercially important species (Pavlov et al. 1974). In addition to their value as game, sika deer are of interest in traditional Chinese 'medicine', where the antlers are a valued raw material (Gilbey and Perezgonzalez 2012).

White-tailed deer *Odocoileus virginianus*

The native range of the white-tailed deer occupies extensive areas in the Americas from Peru to Canada (Gallina and Lopez Arevalo 2016). In 1934 it was imported to southern Finland, where it bred successfully, increased in numbers and became a game species. Nowadays, there are about 109 000 white-tailed deer (Poutanen et al. 2023). With the growth in numbers, it spread over a larger area, but the northwards expansion is not significant. They are primarily kept within game reserves and effectively controlled in terms of distribution and abundance, thus limiting their ability to spread actively on their own. There is only one recorded instance of them venturing into neighboring areas of Russia (Gaginskaya 2006).

Fallow deer *Dama dama*

The native range of fallow deer in historical time was mainly in Turkey, but it was frequently imported to Europe (including northern lands) as a game or ornamental species. Fallow deer settled in Scandinavian countries in the natural environment and spread (Table 1, Fig. 1). However, its range in the boreal zone is insignificant. Like in a case of white-tailed deer, its distribution and abundance is controlled effectively.

European mouflon *Ovis musimon*

European mouflon is a species that originated from feral sheep in the islands of the Mediterranean Sea several thousand years ago (Poplin 1979). Like deer, it is a popular subject of introductions outside of its native range. Within the boreal zone, in was imported to some southern Finnish islands as a game species, where it settled. The local population is considered established, but it is small and its range is restricted (Nummi 2001, Ermala 2004).

Feral or near-feral domestic ungulates

Several domestic ungulates are adapted to the boreal environment and seem to be close to their wild state. This is especially true for Yakutian horses. They remain in open air all year round and are able to get food in winter by digging though snow cover (Alekseev 2017). In European Russia, similar horses are also known (Yurieva and Vdovina 2012), but Yakutian ones are much more numerous. Sometimes the horses go without owners and live in a natural environment for some time. Two reports about the long existence of groups of such feral horses are known in the north. One case happened in Kamchatka Peninsula. Tourists often observed feral horses there, but experts did not, and the details of their origin and existence remain unknown (Milchevsky and Filatova 2015). The other case is better known: Yakutian horses were imported to a village in the south of the Kola Peninsula; they were abandoned in the 1980s or 1990s, but survived (Blokhina et al. 2021) (Table 1, Fig. 1). They became a local curiosity; tourists and locals feed them sometimes, but neither tourists or locals are numerous, and some locals dislike them (as they trample their kitchen gardens), therefore the horses are forced to live on their own. Current state and trend of this population are not known.

Experts have often speculated on the origin of the Yakutian horse. One version is that it is a close relative or descendant of the local wild horses living during the Pleistocene (Lazarev 2008). According to another version, this is a race of common horse selected by Yakutians during their advent to the north. In spite of adaptation to extreme cold, the Yakutian horses still depend on humans, as supplemental feeding is needed during winter. The independent survival of young individuals is especially problematic, because during summer, they simultaneously have to grow and accumulate fat (Alekseev 2017). Feral horses were not reported in Yakutia thus far, but it is known that wild horses existed there for a long time after the Pleistocene; they lived almost up to the Common Era (Lazarev 2008).

In addition to horses, domestic yak was involved a little in the enrichment of boreal fauna, although with even less success than horses. Several tens of yaks were imported to central Yakutia for acclimatization in the 1970s. It was expected that this would contribute the effective use of local biological resources to intensify meat production, but the yaks did not fare well in this environment. The yak is a mountain species, but it was settled in a lowland area. During the summer, yaks suffered from heat and a large number of insects, while in winter, they struggled with prolonged periods of snow cover, necessitating special care. The project was considered unsuccessful, and all yaks were culled in the 1980s (Shadrina et al. 2022).

Northwards expansion of southern species

Twenty three sources were analyzed, including reviews containing the current northern borders of the distribution of wild boar (Markov et al. 2022), red deer (Stepanova and Okhlopkov 2009) and roe deer (Danilkin 1992, Argunov 2013a, 2018). Taken together, they provided the basis for outlining a new boundary for boreal megafauna (Fig. 1). Southern species sometimes cross it, but their stable existence northwards has not yet been confirmed.

Wild boar *Sus scrofa*

The native range of wild boar once included the whole southern part of Eurasia, but by the 1920s only a few refuges remained. In the countries of northern Europe, it was exterminated completely. However, after reaching a minimum, the spread rapidly progressed. This process was stimulated by releases, supplemental feeding, and protection. In Russia, government institutions dealt with restocking, but in Scandinavian countries the wild boars were reintroduced unofficially: initially they either escaped from farms or were released by unauthorized individuals in Sweden (Rosvold and Andersen 2008) and came to Finland from Russia (Erkinaro et al. 1982). Nowadays, wild boars have settled far north of their initial range, especially in Europe and western Siberia. The northern boundary of their distribution shifted several 100 km, approaching the Arctic Circle in the west. Sometimes they migrate far northwards from the new range (Fig. 1, Table 2). The northwards expansion in eastern Siberia is not as substantial (Danilkin 2002, Markov et al. 2022). The expansion of the wild boar has been well-tracked by a number of specialists for decades. However, the interpretation of its reasons is presented rather vaguely. Among the reasons mentioned were global warming, economic development of the territory, conservation measures, extermination of wolves and other processes, but not very confidently, because the wild boar very quickly overcame all previously known climatic restrictions. This is especially true for snow cover. Wild boars in the north occur mainly near settlements, farmland, and game grounds, therefore they are considered sometimes to be a completely synanthropic species in the north (Danilov and Panchenko 2012). But their occurrence in nature reserves, i.e. in a natural environment, has also been reported (Popov and Starikov 2023). Wild boars currently appear to be thriving within their expanded range. On one hand, efforts are being made to exterminate them due to the threat of African swine fever. On the other hand, their value as a game animal ensures they are supported through feeding programs on hunting farms, preventing their decline.

Table 2. Unusual northernmost records of southern species of large mammals over the last century in the northernzone of Eurasia.

Species	Co-ordinates	Years	Details of record	Sources
Wild boar *Sus scrofa*	65°N, 53°E	1980s	Observation of single individuals and small groups	Danilkin 2002
	63°N, 71°E	1980s	Observation of single individuals and small groups, hunting	Danilkin 2002
	62°N, 90°E	1996	One hunted individual	Zyryanov and Sapogov 2012
Siberian roe deer *Capreolus pygargus*	71°N, 117°E	1994	1 male	Argunov 2013a
	71°N, 117°E	1995	Female with a cub	Argunov 2013a
	67°N, 154°E	2003	Observation of two individuals	Argunov 2013a
	67°N, 154°E	2008	One hunted individual	Argunov 2013a
Tiger *Panthera tigris*	59°N, 131°E	1929	Footprints, remains of reindeer eaten by tiger	Argunov 2013b
	55°N, 127°E	1942	Frozen dead tiger without wound	Pesterev 2000, Argunov 2013b
	59°N, 131°E	1978	Attack to humans	Argunov 2013b
	60°N, 134°E	1979	Footprints	Argunov 2013b
	62°N, 138°E	2012	Footprints	Argunov 2013b
	58°N, 131°E	2021	Footprints	Volpert et al. 2023

Roe deer, *Capreolus pygargus* and *Capreolus capreolus*

In the past, roe deer had a continuous range from Europe to the Far East, but it became fragmented. About 100 years ago, there was a particularly large gap in the east of European Russia. This separation accentuated the differences between western and eastern populations. Initially, they were linked by a series of intermediate forms and fitted well into the classical concept of a polytypic biological species. Today, however, the prevailing view is that roe deer should be divided into a European and a Siberian species, the latter being considerably larger. If the definition of a 'mega-mammal' is strictly defined as weighing more than 44 kg, only the Siberian roe deer fit this description. A record weight of 59 kg was reported for the Siberian roe deer (Pavlov et al. 1974), but only 37.4 kg for the European roe deer (Randveer 1985). Today, both species have almost bridged the gap between their ranges and are likely to merge again. As with the wild boar, the northwards expansion of roe deer took place over the last century (Danilkin 1992). The Siberian one has been more successful in this regard. In western Siberia and the Urals, it ranges up to 64°N by the 1960s, but shifted back to south because of intensive hunting, before a new expansion began (Danilkin 1992, Gashev 2014). Throughout most of eastern Siberia roe deer reached 58–60°N by the 1970s, and in some areas up to 63°N (Danilkin 1992, Argunov 2013a, 2018). In the new millennium, they have settled steadily as far north as 62°N. The following range extension was slower, but several individuals were recorded even north of the Arctic Circle (Fig. 1, Table 2). Siberian roe deer have also expanded westward and can now be found in central European Russia, reaching as far as the Volga River. In contrast, European roe deer have spread extensively throughout Scandinavia (Haugerud 1989, Halkka 1994), but their expansion into European Russia has been more limited. They occur along the western border of Russia within the boreal zone up to the Arctic Circle, but have not significantly advanced eastward (Danilov 2009).

In Europe, the increase in roe deer populations has primarily been attributed to effective population management in more developed countries, while a lack of hunting control has led to population declines in less developed areas, such as southeastern Europe (Burbaitė and Csányi 2009). Additional factors reported as influencing roe deer populations both in Europe and eastern Russia include natural fluctuations, climate change, favorable human land use, and the species' adaptability to changing environments (Velichenko 2020, Demidovich 2022). The complexity of these dynamics is further compounded by the less comprehensive study of the species' historical status, leaving it unclear whether roe deer are simply reoccupying their historical range or expanding beyond it. Similar to the case of the wild boar, roe deer have been observed to surpass previously described climatic limitations. In Siberia, expansion was not directly correlated with changes in temperature and snow cover. Recently, fluctuations in population numbers and migrations have been reported, but the overarching trend leans towards an increase in both numbers and range (Argunov 2013a, Gashev 2014).

Red deer, *Cervus elaphus* and *Cervus canadensis*

In the past, red deer occurred along the whole boundary of the boreal zone of Eurasia, but its range became fragmented because of continuous overhunting (Danilkin 1999). An especially substantial gap was from 45° to 90°E. As in the case of roe deer, the eastern and western red deer were considered subspecies of one species in the past, but they are now considered different species (Brook et al. 2018). In the 1920s and 1930s, efforts to protect them led to an increase in their numbers and range. The northwards expansion of the red deer in the west (i.e. *Cervus elaphus*) was rather insignificant. The red deer increased in numbers near the Baltic Sea, and in the 1970s, they reached the Russian section of the Gulf of Finland. Almost all of them were killed soon after, either by locals or predators (Vereshagin and Rusakov 1979). However, in what follows, a replenishment was imported from central Russia (Pavlov 1999). The deer still live there and spread around. Recently an especially long migration was recorded: a red deer female was photographed close to the southern border of Saint Petersburg, more than 100 km away from its typical habitat (Novosti Lenoblasti 2023). They may approach the 'initial' northern borderline, but have not yet crossed it. 200 km northwards, red deer are kept on a farm; sometimes they have escaped and wandered around, but they have not formed a stable population (Danilov 2009). A similar situation exists in Scandinavia, where red deer populations have increased but mostly within their native range (Deinet 2013).

In contrast, eastern red deer *Cervus canadensis* have expanded noticeably northwards, particularly eastwards from Lake Baikal, shifting the border by up to 200 km over several decades. They have been hunted as far north as 62°N. The spread of red deer mirrors that of roe deer, with European populations primarily rebounding within historical ranges due to reduced hunting pressure, while they are effectively controlled. In Siberia, several additional factors such as fires, deforestation, and other environmental impacts have caused habitat shifts in various directions (Stepanova and Okhlopkov 2009). Currently, red deer likely inhabit the northern part of their range relatively stably. In European Russia and western Siberia, populations at the northern border inhabit small refuges surrounded by barely suitable habitats, hindering further spread. Similarly, natural expansion from the east is impeded by deforested areas in the northeastern section of the range.

Tiger *Panthera tigris*

Tigers visiting northern areas have been documented since 1827 in Yakutia. At present, 11 detailed accounts are known, 6 of them were made during the last century (Table 2). Most of the visits took place in the Aldan River valley (southern point in the Fig. 1). According to the communications of locals, tigers have occurred there even more often than well recorded cases indicate (Argunov 2013b). With the improvement of communication technologies, reports on tigers outside of their typical range have continuously grown over the last decade, but usually without enough evidence to be confirmed. Only one case that happened in 2021 was confirmed

by experts (Table 2). However, there are no doubts about the possibility of such events, because in the past all tigers coming to Yakutia were killed. A stuffed tiger is still kept in a local museum, and the battle between it and locals that took place in 1905 was described in detail (Pesterev 2000). These visits by tigers are believed to be the result of young males wandering in search of suitable territories. A stable presence north of their historical range is questioned due to insufficient numbers of ungulates (Volpert et al. 2023). Nonetheless, tigers remain rare animals, with the latest census in 2022 estimating a population of about 750 individuals (Amur tiger center 2024). It is believed that only now has some degree of habitat stabilization and restoration been achieved in the Amur basin. This suggests that conditions for overpopulation and potential expansion are just beginning to develop.

Changes in the range of native large northern mammals

Twenty sources summarizing the data on distribution of large mammals in the north were analyzed. They include 4 monographs, 10 journal articles and 6 articles from the databases of threatened species.

Wild reindeer *R. tarandus* suffered a decline, its range shrunk and became fragmented (Gunn 2016). It decreased in numbers because of hunting and competition from domestic analog. Several populations are listed in the Red Data Book of Russia (Panchenko et al. 2021). Wild reindeer are relatively numerous only in the center of the range, but they are declining there as well because of continuous overhunting (Perevalova 2022). Domestic reindeer often become feral, sometimes replacing the wild ones. Feral reindeer have been introduced multiple times to islands in the Arctic Ocean, the Bering Sea, and the Sea of Okhotsk to enrich the local fauna. These reindeer populations tend to fluctuate significantly. When their numbers increase, overabundance can occur, straining the food supply and leading to subsequent population decline, followed by either a gradual recovery or the complete disappearance of the reindeer (Vehov 2018).

The state of snow sheep *O. nivicola* is similar to that of wild reindeer. Some populations are listed in the Red Data Book of Russia (Sipko and Poyarkov 2021), some are approaching such status (Fil and Mosolov 2010), and some are understudied. In the 1980s, the total snow sheep population was estimated at 85 000–95 000, but recent estimates are not available (Harris and Tsytsulina 2008). Compared to other boreal 'mega-mammals', the number of snow sheep is relatively small for natural reasons. Their range consists of isolated areas in the northern part of the Russian Far East, with a small addition at the center of Siberia (Putorana Plateau). They inhabit highlands or rocky seashores where snow coverage is thin (Revin et al. 1988). The area of suitable habitats is relatively small, and continuous hunting is especially harmful to this species.

The range of the third species of native megafauna, the moose *A. alces*, has also changed. The number of moose increased, and the range expanded. The moose spread in all directions, including northwards. In the 1950s, the moose settled at the border of the tree line in the north and started to penetrate into tundra. In the 1980s they populated the whole boreal zone up to the coasts of the Arctic Ocean. In the tundra zone, they predominantly inhabit areas along rivers with some semblance of forests (Filonov 1983), although reports of their presence in true tundra have also been documented (Kopein and Olenev 1959). Causes of this expansion include hunting restrictions, an increase in the number of forest clearings, and natural fluctuations in population numbers, with an increase phase occurring currently (Danilov and Panchenko 2013, Panchenko et al. 2020). In addition to natural spread, moose have been involved in the artificial enrichment of fauna. They were introduced to Kamchatka, although the need for, and success of the effort were questionable (Ostanin et al. 1978). It was believed that Kamchatka is not suitable for them because of thick snow coverage (more than 1 m). However, from 1976 to 1982, 50 young moose were moved there, where they survived and reproduced. Now the moose steadily exist in Kamchatka as a game species (Fil and Gordienko 2009).

As for predators, the reports on the expansion in the north are known. The presence of brown bears *U. arctos* in tundra increased. In the past, it was believed that they only visit the tundra seasonally, but now they occur there steadily. The areas around river valleys are especially suitable for them. Increase in numbers in the north was reported both for Europe (Mineev 2007) and Siberia (Mamaev et al. 2019), attributed to changes in vegetation favoring bears due to global warming.

The wolf *C. lupus* population has also increased recently (Korolev 2016, Stepanova and Okhlopkov 2020, Rodríguez-Recio et al. 2022). In Europe, this increase is attributed to effective legal protection and rewilding projects aimed at increasing biodiversity, including predator populations (Boitani et al. 2022). In Russia, however, the increase in wolf numbers has been counteracted rather than encouraged. Shooting of wolves is often recommended and incentivized with bounties. However, fluctuations in hunting pressure occur due to varying prices and other circumstances. At present, the situation is relatively favorable for wolves in some regions, with increased ungulate populations, thinning of forests, and increasing habitat patchiness (Korolev 2016).

Discussion

The most noticeable recent enrichment of the fauna of the north occurred due to the gradual northward expansion of southern species. In some areas, roe deer have led the way, while in other places, wild boars have left them behind. These differences might be related to the local patterns of snow coverage, temperature, relief, and the availability of wetlands. Wild boars need wet food that they reach by digging into the soil, therefore they are more successful in northwards expansion when the cover of insulating snow is thick and the freezing of soil is relatively weak. Roe deer, on the contrary,

consume dry food during winter and cannot penetrate thick snow cover. Irrespective of these differences, both species are considered residents of the zone of deciduous forests or southern taiga, but have approached the tundra. Meanwhile, the tundra zone itself is changing. Its southern boundary tends to shift northward (Callaghan et al. 2004). Moreover, the 'greening' of the tundra is progressing: shrubs and grasses occupy more and more space compared to mosses and lichens (Berner et al. 2020). This change, obviously, is rather favorable for large herbivores, because it results in an increase in the potential food supply. It is likely that such a 'greened' tundra (Fig. 2) approaches the state of 'tundra-steppe'.

However, the tundra also faces challenges due to the presence of domestic ungulates, their owners, and other residents. This situation not only leads to the occupation of pastures but also contributes to the decline of wild animal populations. The inhabitants of the north have a long-standing relationship with nature, which often involves killing any observed animals, particularly those valuable for food or pelts. Reports on additional species in the north frequently mention the impact of hunting on these populations. The indicated locations of unusual occurrences of southern species in the extreme north were also often based on hunted individuals. When the locals see an unusual animal (like, for example, a roe deer or muskox) they do not miss the opportunity to kill it. At the same time, traditional land use is encouraged by the authorities in various ways. A number of international agreements and regional laws have been issued on this (for example, 'Declaration on the Rights of Indigenous Peoples' of the United Nations, 2007, or Decree of the Government of the Russian Federation of 4 February 2009 no. 132-r 'On the Concept of Sustainable Development of the Indigenous Minorities of the North, Siberia and the Far East of the Russian Federation'). When bans for harvesting some species are declared, exceptions are often made for locals. Moreover, since the locals are scarcely distributed over a vast area, their activity cannot be controlled. In such a situation, any 'mega-mammals' face a high risk of extermination. This negative impact may be reduced in the near future. Most of the Eurasian tundra zone is in Russia, but despite the efforts of the authorities, the number of people wishing to keep a traditional lifestyle is decreasing there (Rozanova 2019). Researchers consider the 'pessimistic scenario' likely (Koptseva 2017), i.e. an increasing number of indigenous reindeer herders and hunters will move to urban areas. At the same time, the urban population in the Russian Arctic is also decreasing (Popov 2022). From a megafauna and biodiversity conservation perspective, this is a positive trend. Therefore, it

Figure 2. 'Greened' tundra on Kildin Island (Barents Sea).

is possible that in the future, rewilding will progress and the potential of global warming will be realized.

In addition to warming, other factors might be involved in the northwards expansion of southern species. For example, the visits of tigers to the north took place irrespective of warming. These cases happened in cold years (1942), and some tigers visited such places, where it is still very cold. The northernmost point is remarkable for the fact that it is located relatively near the Oymiakon settlement (150 km), so-called 'Cold Pole'. The records below – 60°C happened there up to recent times (Obruchev 1938, Pogoda i klimat 2023). The 'neighboring' settlement of Verkhoyansk, 500 km from Oymiakon, has contested the title 'Cold Pole' as similar temperature records occurred there too. Tigers did not approach Verkhoyansk, but roe deer did. The author of the report about it (Argunov 2013a) considered this case an incident, but he himself noted that several decades ago the project of introduction of roe deer to Verkhoyansk was suggested. Based on relevant studies, this area was considered promising for such enrichment. It was assumed that roe deer could not reach the area naturally in big numbers because it was separated from the south by a wide band of dense coniferous forests. The fact that roe deer managed to overcome this barrier suggests that forestry activities may have thinned out this band of forests. This means that rather anthropogenic transformation of vegetation than global warming contributed northward migration of the roe deer.

Forestry intensification has been highlighted as a probable cause of the northward expansion of mammals in several of the aforementioned reports. Boreal forests have been subject to centuries of logging. This process continues today with inadequate control (Kuzmichev et al. 2018), and results in the creation of clearings, roads, and trails, transforming vast expanses of coniferous forests into a mosaic of diverse habitats containing a significant proportion of broad-leaved trees, shrubs, and herbs – essential food sources for ungulates (Fig. 3). Such transformed taiga zones become more conducive to migrations and settlements of 'mega-mammals,' thus likely facilitating further enrichment of the megafauna. The largest 'mega-mammals' are especially promising because they are 'keystone herbivores' that have essential influence on the vegetation. Their role in increasing the share of grasslands compared to woodlands is especially significant (Owen-Smith 1987). In the north, their role is similarly important with respect to snow coverage, which is a serious obstacle to the life of numerous ungulates; smaller ones are not able to dig through deep snow to find food, nor can they move rapidly to avoid predators. The 'keystone herbivores' make

Figure 3. 'Transformed taiga' in northwest Russia.

trails through the snow, which can be used by smaller 'mega-mammals'; therefore, the largest herbivores may provide access for smaller megafauna. While it remains speculative to imagine how these interrelationships functioned during the Pleistocene, similar dynamics can be readily observed today on a smaller scale, as exemplified by the case of wild boars. During winter, they gather in herds, which move in the form of a column lead by the largest individual. In this way, a trail appears. In the presence of large numbers of wild boars, a network of trails covers the forest, and this influences the other mammals. This is what enabled roe deer to expand northwards in the west of Russia (Danilov et al. 2017). It is likely that bison or horses have similar influence. The data on such phenomena are rather scarce. Only an increase in the number of 'mega-mammals' could provide grounds for the characterizing the ecological links between them and composition of their habitats. The same is true for the character of the transformation of vegetation in the north. At the moment, additional mega-herbivores are too scarce to transform taiga and tundra into tundra-steppe. They tend to seek suitable habitats in the available environment rather than transform it. Therefore, it is problematic to trace the global effect of rewilding in respect to permafrost melting, warming, methane, and carbon dioxide emission.

Although the spread of southern species is progressing, the number of 'mega-mammal' species among them is small. Apart from wild boars and roe deer, only red deer have noticeably moved north. A significant increase in diversity akin to the Pleistocene is possible through the introduction of non-native species, but progress in this area is very limited. The number of such examples is small, and they affect only a small part of the north. Only the muskox has settled relatively quickly over large areas and reached noticeable numbers, as it is well adapted to the northern environment. The others either became extinct or survive in small areas with human support. Introduction projects show that it is insufficient to simply release mammals of 'additional' species somewhere in the north. Even in the case of the muskox, the introduction required several years of work. First, it is necessary to find suitable habitats; cold resistance alone is not enough for success, as demonstrated by the example of the yak. Secondly, introduced animals need to be supported for some time through feeding and protection to ensure they reproduce and increase in numbers. If the released population is small, it may disappear due to natural fluctuations in numbers, among other threats such as predators, hunters, cold, or lack of food. As the example of the muskox showed, a new population may disappear for some unknown reason after decades of existence. The introduction of bison seems successful so far, but their numbers are still very low. Hopes that domestic analogues of Pleistocene animals would compensate for the low numbers of wild ones have not yet materialized. Only the wild reindeer has slightly expanded the range of megafauna.

Introduction work requires the enthusiasm of a large number of people, but at the moment, there is little evidence for the growth of enthusiasm for Pleistocene rewilding in the north of Eurasia. The benefits of this activity are not obvious either to the scientific community nor society at large. Although slogans regarding the enrichment of nature were popular in the past, the prevailing ideology changed to the opposite stance. Nowadays, any introductions are usually discouraged. The list of potential risks of such actions is very long as the introductions could influence landscapes, ecology, genetics, diseases, economy and politics (IUCN/SSC 2013). Especially active opponents of Pleistocene rewilding try to find all possible arguments up to the point that large animals can be dangerous for humans, and therefore there is no reason to work towards increasing their numbers (Shadrina et al. 2022). A neutral position is also expressed: additional 'mega-mammals' in the boreal zone is an introduction of alien species, but if similar ones existed there before, then this represents the restoration of the natural state of the environment – however, a lot of time has passed since their disappearance, the environment has changed, and therefore, this is no longer restoration, but still the introduction of alien species – and therefore the question remains open (Argunov 2018). Such a discussion took place in Sweden concerning the unauthorized restocking of wild boar. It resulted in a decision that it is restoration rather than an undesirable invasion (Magnusson 2020). As for the other additional mega-mammals, such discussions reaching a wide audience have not been organized. Typically, it is the concern of a small number of experts.

Both the criticism and the neutral position concerning Pleistocene rewilding in the boreal zone are not convincing because the valuable component of the ecosystem that would suffer from additional mega-mammals is not indicated. Moreover, the number of additional 'mega-mammals' is insignificant, and can decline to zero at any time. The history of hunting shows that large animals can be exterminated completely. In the north, 'mega-mammals' are especially vulnerable. During winter, they turn out to be defenseless against hunters. Their presence is easily identifiable by tracks, while at the same time, they cannot move quickly over long distances in deep snow, and therefore a hunter on skis or on a snowmobile can always reach them. However, ordinary people are usually afraid of large animals, and therefore have a negative attitude towards Pleistocene initiatives.

The observed situation with the enrichment of fauna supports the suggested hypothesis: the diversity and abundance of 'mega-mammals' in the north of Eurasia could be increased, but the realization of large-scale projects in this field is problematic. The same is true for Pleistocene rewilding in other parts of the globe, including the boreal areas. Increases in numbers and range expansion are progressing for several species of large mammals, both native and non-native: wild boar in North America (Snow et al. 2017), feral Asian buffalo *Bubalus bubalis* in South America (Hallett et al. 2021), feral camels in Australia (Saalfeld and Edwards 2010), deer in Europe (Deinet et al. 2013), etc. However, initiatives to significantly enrich the megafauna have not been realized, like, for example, an initiative to introduce the largest mega-mammals from the Old World to North America (Donlan et al. 2005). Something like this occurred by chance in South America when hippos *Hippopotamus amphibius*

from an abandoned zoo settled in the natural environment in Colombia, but there was more concern about how to remove the hippos rather than considering the potential benefits of such enrichment (Subalusky et al. 2023). An analogue of hippos (genus *Toxodon*) once existed in South America but became extinct about 12 000 years ago (MacFadden 2005), therefore this case aligns well with the Pleistocene rewilding concept, which was substantiated for South America (Galetti 2004). However, lack of support for this 'start' indicates that further progress is doubtful in a foreseeable future.

Conclusion

Over the past 100 years, the megafauna of the boreal zone in Eurasia has been enriched by the introduction of non-native species and the northward expansion of southern species. This development offers some insight into the concept of Pleistocene rewilding. However, the presence of these additional species remains very limited, both in terms of population size and available habitat. In addition to the ecological limitations, large-scale rewilding are labor-intensive, expensive, and not popular enough to attract significant support, therefore their realization is problematic at this time.

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Data availability statement

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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