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Prospects for the dispersion of European bison, *Bison bonasus*, in the North

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ABSTRACT

The European bison continues to be a conservation dependent species, as it inhabits small reserve areas that require strict management. To ensure the species' long-term viability, it is imperative to expand both its population size and geographical range. However, achieving this expansion within its historical range poses challenges due to intensive land use and dense human populations. The objective of this study was to model the potential distribution of the European bison beyond its historical range, specifically in the boreal zone of Europe. Utilizing the maximum entropy method alongside bioclimatic variables and land use analysis, the research revealed a significant expanse of suitable territory. This suggests the feasibility of establishing a contiguous habitat capable of supporting a substantial European bison population. Factors such as ongoing global warming, deforestation, and agricultural decline are further enhancing the creation of favorable habitats for the species.

1. Introduction

Around a century ago, the European bison, *Bison bonasus,* teetered on the brink of extinction, with only a handful surviving in captivity after being wiped out in the wild. Through breeding programs they were saved from extinction. Presently, their population has rebounded to several thousand, but they remain conservation dependent (Plumb et al., 2020). Additional feeding is employed to prevent damage to their populations, even in areas considered as close to their natural habitat as possible (Pucek et al., 2004; Bramorska et al., 2023) and even in these areas the farm crops depredation by European Bison still occurs (Hofman-Kamińska, Kowalczyk, 2012); this means that they cannot survive independently in a natural or near-natural environment. They inhabit small reserves, necessitating regular transport between them and measures to bolster their numbers to prevent inbreeding depression. The European bison is characterized as a refugee species: originally inhabiting the open areas, human activity drove them into forests, resulting in suboptimal habitats (Kerley et al., 2020). Nowadays, various habitats are "offered" to them, including abandoned agricultural lands (Kuemmerle et al., 2020). The future of the European bison has been actively discussed recently (Plumb, 2022). Previously, the goal of experts was to save the species, which has now been achieved. The current discussion focuses on the specifics of their future existence. Solving the question of how to coexist with European bison on a densely populated continent involves numerous ecological, social, and political challenges (Tusznio et al., 2024). Ideally, European bison would thrive autonomously like other ungulates in the boreal zone, like, for example, wild boar (*Sus scrofa*) or moose (*Alces alces*). However, suitable space within their historical range is limited, with potential areas for introduction being small and isolated from each other (Kuemmerle et al., 2011; Bleyhl et al., 2015; Perzanowski et al., 2019). The formation of corridors between shelters is possible only in certain areas, and has not been fully implemented (Olech and Perzanowski, 2022). Even if these areas were fully utilized, establishing large, stable populations would remain challenging. Translocation or introduction beyond the historical range presents a potential solution (Seddon, 2010). In this case, more northern territories seems to be promising because of sparse human population and changing climates due to warming trends. Moreover, the bison were found there in prehistoric times, therefore now the introduction cannot be unambiguously regarded as the introduction of an alien species. One small population of the European bison already exist beyond the historical range in the North-West Russia, Vologodskaya oblast (Gusarov, 2019). Additionally, a small number are kept in similar climatic conditions on fenced farms near St. Petersburg (Vyborgsky raion, 2021; Zubrovnik, 2024).

Maxent modeling based on bioclimatic variables and "present-

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natural" distribution shows that European bison habitat north of the historical range is possible (Jarvie and Svenning, 2018). "Present-natural" means the estimated distributions for the present day (notably current climate) in the complete absence of past and present human impacts. This "pseudo-presence" modeling resulted in a very large potential European bison range, part of which is likely unsuitable due to a lack of appropriate habitats. We decided to look into this: to refine the modeling based on actual distribution and find out how much of the potential new range in the North is actually suitable for European bison in the near future, as well as the likely population size. The hypothesis is that habitation is possible, but the suitable area is rather small comparing to the whole area northwards from historical range of European bison. It was spurred by observations in the Vologodskaya oblast (Fig. 1), where European bison have resided for over four decades but have only slowly expanded their territory.

2. Materials and Methods

We used Maxent software version 3.4.4 (Phillips et al., 2023) with initial presence points from the recent review on the European bison status (Olech and Perzanowski, 2022). Only 49 points marking the locations of free herds were included in the analysis (Fig. 2, Supplement 1). Co-ordinates were specified using Google Earth program. Nineteen bioclimatic variables (Bio1-Bio19) corresponding to recent environmental conditions (1970–2000) were taken from the WorldClim database (2024), with a spatial resolution of 2.5 arc-minutes. It was used for choice of variables and testing the model. Additionally, we used vegetation cover data. For this purpose, land cover layers (LCL) were selected from the Land Cover Classification System (LCCS) developed by the United Nations (UN) Food and Agriculture Organization (FAO), corresponding to the points of presence (Buchhorn et al., 2020). To predict the possible distribution of *Bison bonasus* in 2050 (2041–2060) and 2070 (2061–2080), we loaded bioclimatic variables (Bio1-Bio19) from two general circulation model (GCMs): Climate Model of the Institute of Numerical Mathematics of the Russian Academy of Sciences (fifth generation) – INM-CM5-0 (Volodin et al., 2019), and Earth System Model of the Euro-Mediterranean Center on Climate Change (second generation) – CMCC-ESM2 (Lovato et al., 2021). Both climate models are part of the Coupled Model Intercomparison Project, Phase 6 (CMIP6, 2024). Four shared socioeconomic pathways (SSPs) were used: SSP1-2.6 (a sustainable development scenario with low greenhouse gas emissions and a commitment to sustainable development and reduced inequality); SSP2-4.5 (a middle of the road scenario with moderate greenhouse gas emissions, in which social, economic, and technological trends do not change significantly from historical patterns); SSP3-7.0 (a scenario of a fragmented world with high greenhouse gas emissions, strong competition between countries and slow technological progress); SSP5-8.5 (a fossil-fuel intensive scenario with very high greenhouse gas emissions and rapid economic and social growth driven by globalization and market forces) (Riahi et al., 2017; Masson-Delmotte et al., 2021). The dataset was also downloaded from the WorldClim website with a spatial resolution of 2.5 arc-minutes. Land cover layers are assumed to be highly dynamic and were not included in the modeling of potential future spread. To avoid the influence of multicollinearity, cross-sectional correlations (Pearson correlation analysis) were carried out for bioclimatic variables in SPSS 23.0. Variables with a Pearson

Fig. 1. European bison in a boreal forest, Vologodskaya oblast (2024).

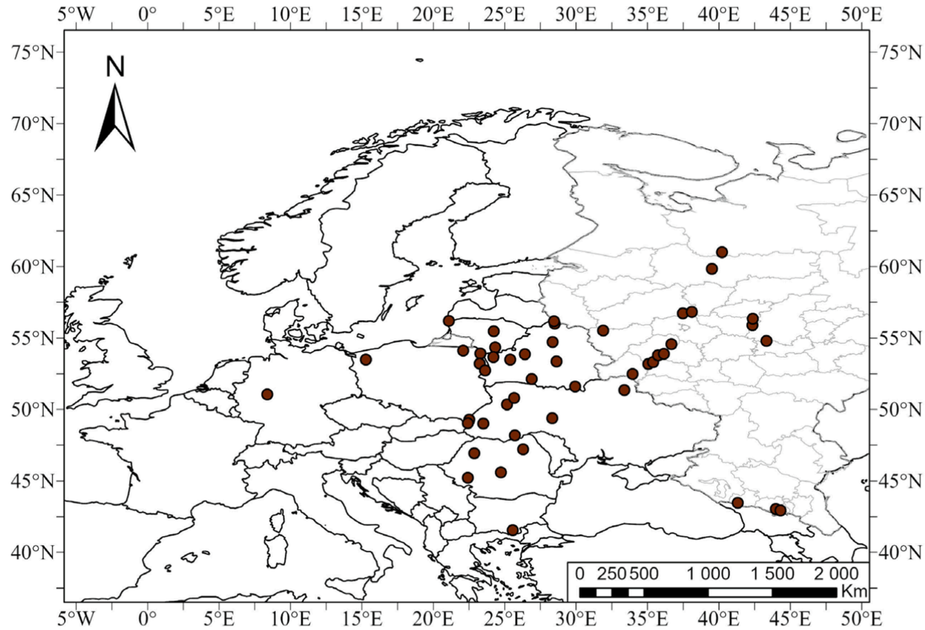

Fig. 2. Actual distribution of the free herds of European bison (Olech and Perzanowski, 2022).

correlation coefficient |r| >0.8 were excluded from further analysis, provided that such variables were not important for the species ecology (Yi et al., 2018) (Supplement 2). After the test modeling, variables with zero variable contributions were also removed. Seventy-five percent of the species occurrence data were used to train the model, with the remaining 25 % allocated as test data to check the model's quality. The "Default prevalence" value was changed to 0.2 due to the relative rarity of the species being studied. Additionally, a jackknife test was chosen to measure variable importance. To confirm the model's reliability, receiver operating characteristic (ROC) analysis was used. The area under the ROC curve (AUC) is analyzed, with values varying from 0 to 1. A value of 0.5–0.6 indicates unsuccessful simulation, 0.6–0.7 is considered bad, 0.7–0.8 satisfactory, 0.8–0.9 good, and values greater than 0.9 excellent (Araujo et al., 2005). The simulation results were loaded into ArcGIS Pro for further analysis. We used the "Natural Breaks (Jenks)" method to divide the data into four classes of potential species distribution areas: $\leq$ 0.09 unsuitable habitat, $\leq$ 0.3 poorly suitable habitat, $\leq$ 0.6 moderately suitable habitat, $\leq$ 1 highly suitable habitat (Duan et al., 2022).

Areas where the natural existence of European bison is problematic were excluded from the potential distribution area obtained from the modeling. These include areas with high population densities, predominated by farmland and settlements, and lacking sufficiently large wildlife areas. To assess sufficiency, we used information about the minimum population size and the area required for one European bison to live. According to recent estimates, at least 50 individuals are required for minimizing the effects of stochastic gene loss in small isolated populations, although the bigger number is desirable (Pucek et al., 2004). For estimating the area, figures of about 1 individual per 200 ha are usually given (Minprirody of Russia, 2021). This aligns with the area of the smallest reserves where European bison live, such as the Bryansk Forest (12280 ha) and the Turmonsky Nature Reserve (12,600 ha) (Minprirody of Russia, 2021). However, this applies to the historical range of the European bison, not the North. For the northern habitats of the analogue of the European bison, the American wood bison (Bison bison *athabascae*), this is regarded as the maximum, while it can be 10 times less, and 1 per 500 ha is the most realistic number (Steenweg et al., 2016). This means that an effective population requires at least 25,000 ha. For a significant increase in numbers, we considered areas suitable only if they were not isolated from the main habitat. Swamps and other damp areas are unsuitable for European bison, so regions with low relief and no relatively dry forests of the specified area were excluded. To exclude all these unsuitable areas, we used the Land Cover Classification System (Buchhorn et al., 2020), excluding lands with a permanent mixture of water and vegetation, lands with moss and lichen, and areas covered by buildings and other man-made structures. Bodies of water were also excluded. We did not consider the territory beyond the Urals, as it is generally accepted that bison in historical times there were closer to the American wood bison than the European one. Recently, efforts have been made to introduce American bison to Siberia (Smetanin and Safronof, 2022).

We used the bioregion framework (Olson et al., 2001) to define the north–south boundary. The border of the zones of boreal forests and mixed forests approximately corresponds to estimates of the northern border of the historical range of European bison (Minprirody of Russia, 2021; Shevchenko, 2016). In the past, it was considered the boundary of thick snow cover, which limited the distribution of several mammal species (Formozov, 1946). It runs approximately along the 60th parallel in Scandinavia, but east of the Gulf of Finland and Lake Ladoga, it gradually shifts south towards the southern Urals to the 57th parallel.

3. Results

The training and test values were 0.991 and 0.988, respectively, indicating that the simulation is "excellent," and the prediction results of the Maxent model in this study have high accuracy (Fig. 3) (Araujo et al., 2005). Among the 15 environmental variables, the following factors are of primary importance for the potential distribution of European bison: Precipitation of Coldest Quarter (Bio19) – 23.7 %, Precipitation of Warmest Quarter (Bio18) – 20.3 %, Annual Mean Temperature (Bio1) – 16.8 %, Closed forest, deciduous broadleaf (UN-LCCS_114) – 15.2 % and Temperature Annual Range (Bio7) – 7.3 %, (Table 1). The total contribution of other variables was 16.7 %. According to the jackknife test, Annual Mean Temperature (Bio1), Mean Temperature of Warmest Quarter (Bio10), and Precipitation of Coldest Quarter (Bio19) were the top three factors during training and testing (Fig. 4).

Modeling showed that it is possible to form European bison habitat north of the historical range up to parts of the coast of the Barents and White Seas. However, in the central part of the potential range, areas with high population density and a high degree of development are

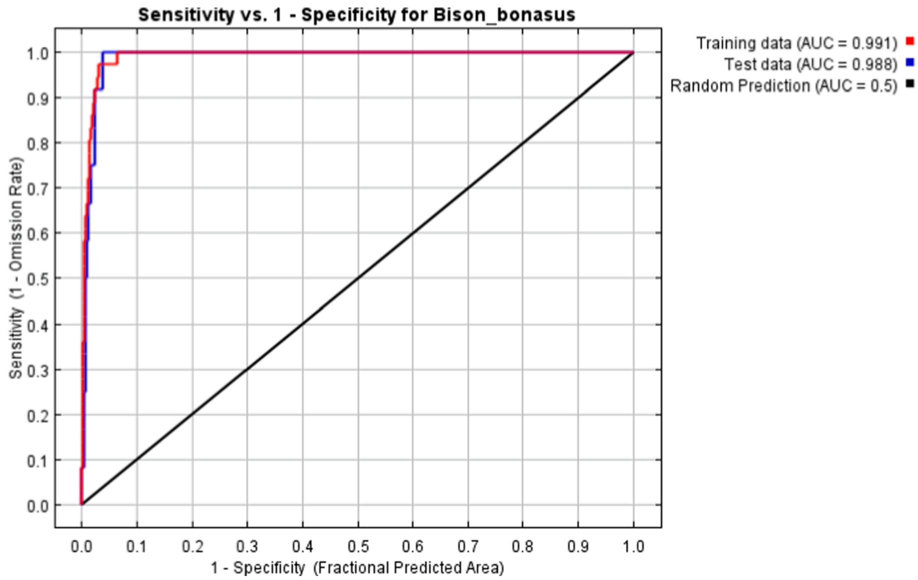

Fig. 3. Receiver operating characteristic (ROC) curve and the area under the subject curve (AUC) of the Maxent model. The red curve indicates training data, the blue curve indicates test data, and the black line indicates random prediction. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Environmental variables and their percent contribution and permutation importance in the Maxent prediction model.

Variable	Description	Percent contribution, %	Permutation importance, %
Bio19	Precipitation of Coldest Quarter	23.7	3
Bio18	Precipitation of Warmest Quarter	20.3	2.2
Bio1	Annual Mean Temperature	16.8	76.1
UN-LCCS_114	Closed forest, deciduous broad leaf. tree canopy > 70 %, consists of seasonal broadleaf tree communities with an annual cycle of leaf-on and leaf-off periods	15.2	1.3
Bio7	Temperature Annual Range (Bio5-Bio6)	7.3	7.1
UN-LCCS_111	Closed forest, evergreen needle leaf. tree canopy > 70 %, almost all needle leaf trees remain green all year. Canopy is never without green foliage	5.1	0.8
UN-LCCS_40	Cultivated and managed vegetation/agriculture (cropland). Lands covered with temporary crops followed by harvest and a bare soil period (e.g., single and multiple cropping systems). Note that perennial woody crops will be classified as the appropriate forest or shrub land cover type	3.5	0.8
UN-LCCS_115	Closed forest, mixed. Closed forest, mix of types	2.4	0.5
Bio15	Precipitation Seasonality (Coefficient of Variation)	1.8	1.7
UN-LCCS_30	Herbaceous vegetation. Plants without persistent stem or shoots above ground and lacking definite firm structure. Tree and shrub cover is less than 10 %	1.1	0.4
UN-LCCS_90	Herbaceous wetland. Lands with a permanent mixture of water and herbaceous or woody vegetation. The vegetation can be present in either salt, brackish, or fresh water	0.9	0.1
Bio10	Mean Temperature of Warmest Quarter	0.8	0.5
UN-LCCS_126	Open forest, unknown. Open forest, not matching any of the other definitions	0.7	0.1
Bio3	Isothermality (Bio2/Bio7) (×100)	0.3	5.5
Bio2	Mean Diurnal Range (Mean of monthly (max temp − min temp))	0.1	0

availble, which are hardly suitable for the big numbers of them. In the North, near the shore of the White Sea, there is also a poorly suitable area due to extensive swamps (Fig. 5). If to exclude these areas, the total area of the European bison habitat predicted north of the historical range boundary would be either 1699600, or 1775000 km^2 (Table 2). Modeling of future distribution shows that this area could either decrease by several hundred thousand square kilometers, or increase, or remain approximately the same (Table 3). Various scenarios resulted in numbers from 1051548 km^2 to 1890016 km^2.

4. Discussion

Ecological modeling suggests that European bison may be present in the boreal zone, potentially establishing a big unfragmented range. Alternative climatic scenarios resulted in the numbers 1–1.9 mln sq. km for its area, i. e. about 10–20 % of the total area of Europe northwards from historical range of European bison. Based on the above mentioned estimated potential density (1 bison per 500 ha), the total number of European bison in this area can be at least several hundred thousand. Despite the warming trend, some reduction in the potential range in the future cannot be ruled out. This can be explained by the fact that due to warming, evaporation from the ocean increases, the amount of precipitation increases, and in winter this leads to an increase in snow cover. Winter precipitation, as modeling has shown, is the main climatic factor affecting European bison. However, at the same time, the impact of warming may have a positive effect as well due to changes in vegetation and increased productivity. Recently, there has been a progressive greening of the tundra and a shift in the forest boundary to the north (Berner et al., 2020). These changes obviously have a positive effect on the expansion of southern species to the north. Moreover, the identified

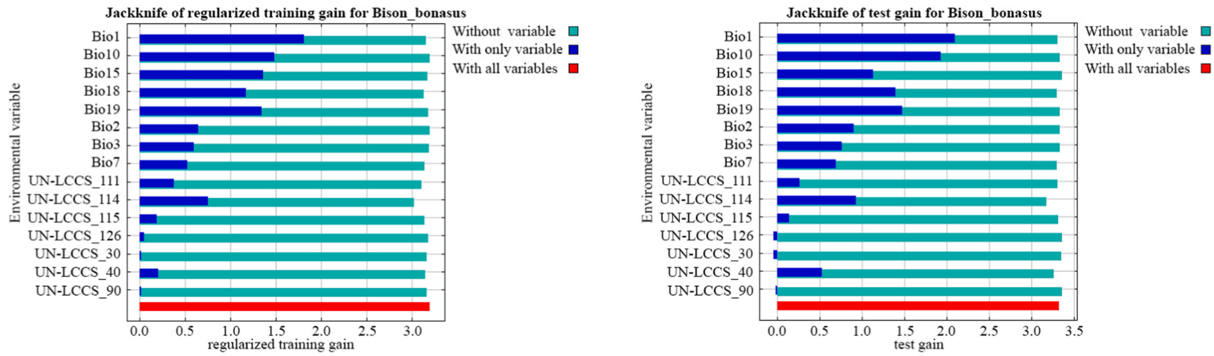

Fig. 4. The results of the jackknife test of variable importance. The dark blue bands indicate the gain from using each variable in isolation, the green bands indicate the gain lost by removing a single variable from the full model, and the red band indicates the gain using all variables. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

area has recently undergone other changes likely to contribute to the formation of suitable habitats especially in the Russian part. Deforestation is advancing, resulting in the creation of numerous clearings, precisely the environment needed for ungulates, including European bison, instead of vast tracts of coniferous forests. Loggers have already reached remote territories, such as the central Arkhangelskaya oblast, where pristine taiga has long persisted (Fig. 6). Old-growth forests in the European part of Russia occupy a negligibly small area (Kobyakov and Jakovlev, 2013). Meanwhile, unlike Europe, the maintenance of tree monoculture develops slowly; usually the forests renovate by themselves, therefore the clearings demonstrate a mosaic of various coniferous and broad-leaved trees. Such habitats are favorable for ungulates. Additionally, suitable habitats are evolving in abandoned settlements and surrounding farmland. Overgrown meadows and shrubs are emerging, serving as suitable feeding grounds. The northernmost European bison population thrives in such conditions, and the extent of such areas has been steadily increasing over last decades. In the 1960 s, a policy of consolidating rural settlements was initiated in the USSR, gradually accelerating over time. Small villages were deemed “unpromising”, leading to their abandonment and disappearance (Mazur, 2005; Siminchenko, 2023). The collapse of the Soviet Union affected not only small settlements but also larger ones, resulting in thousands of deserted villages in the boreal zone and ongoing depopulation of rural areas, and this process still continues (Rumjancev et al., 2019).

The suitability of the boreal zone for European bison is indirectly supported by the data on the American one. American wood bison was successfully introduced in Canada and Alaska in places where they were exterminated in the distant past (U.S. Fish and Wildlife Service, 2021; Bath et al., 2022). The northernmost populations of American bison live in the same climatic zone as the area identified in this work. Genetic similarities between American and European bison suggest potential adaptation of the latter to northern conditions over time. The other indirect evidence on the prospects for the spread of European bison over boreal lands is the recent expansions of southern species northward. These facts are known for a large number of animals (Loarie et al. 2009). Ungulates also follow this “rule”. In Europe, this applies to roe deer (*Capreolus capreolus*), wild boar and moose (Filonov, 1983; Danilkin 1992, 2002; Markov et al., 2022). They have spread to the Arctic Circle and even further north over the past few decades. This is due not only to warming, but also to the anthropogenic transformation of the territory, which was mentioned above. This circumstance is especially clearly seen in the case of wild boars. They are usually found in the North near farmland, and the peak of their expansion occurred in the 1990 s, when large areas of abandoned fields appeared (Danilov and Panchenko, 2012).

There are opportunities for European bison to extend their habitat northward. However, their ability to expand autonomously in the near future is unlikely. The population of European bison in the North is currently small. They are traditionally fed and therefore show reluctance to settle independently. Additionally, their reproduction rate is slow. Significant human efforts are required to increase their population and range. This involves active management, including feeding, genetic monitoring, protection, and more. While the topic may gain popularity, there is also expected opposition and criticism. For instance, the bison reintroduction project in Yakutia faced objections, including concerns about the potential danger posed by large animals to humans and the undesirability of increasing their numbers (Shadrina et al., 2022). This is despite Yakutia having an extremely low population density, which hardly tends to increase significantly. This area is even not connected by roads or railways to the rest of the world.

The introduction of European bison is of interest not only in terms of preserving charismatic and conservation dependent species but also in the implementation of Pleistocene rewilding projects. Proponents believe there is every reason to try to restore the semblance of Pleistocene ecosystems containing many large animals (Donlan et al., 2005). In relation to the boreal zone, this concept has recently been developed and tested experimentally by Sergey Zimov, who created the “Pleistocene Park” in Yakutia (Zimov, 2005). This is a fenced area of about 20 square kilometers, into which various ungulates have been imported over time – bison (*Bison bonasus, Bison bison*), camels (*Camelus bactrianus*), horses (*Equus ferus caballus*), yaks (*Bos grunniens*), etc. It is expected that they will transform the environment: instead of trees and bushes, grasses will predominate in the vegetation, and tundra-steppe will again form in the Park – a highly productive community reminiscent of the African savannah that existed there in the past (finds of prehistoric bison and other large mammals in the Park and its environs are a constant reminder of this). The assessments of both the concept and the Park are contradictory. Despite the enthusiasm of a number of experts, such initiatives are criticized. According to critics, since much time has passed since the Pleistocene, this is no longer restoration but the creation of something new and potentially undesirable; it is better to focus efforts on protecting what exists (Rubinstein et al., 2006; Oliveira-Santos and Fernandez, 2010). At least in the case of the boreal zone of Europe and European bison, this objection is not very convincing, because it is unclear what is so especially valuable in it that bison can destroy. Excessive overgrowth of the territory with boreal forest leads to an impoverishment of the fauna and a decrease in conservation value. This was analyzed for a small area recently (an abandoned island in the Baltic Sea (Popov et al., 2023)), but it is likely that the same applies to a larger area. The boreal flora and fauna are rather poor. There are few particularly rare species on a global scale, and those that exist would hardly suffer from the presence of the European bison. There is only one ungulate species among them, which is wild reindeer *Rangifer tarandus* (Gunn, 2016); but the ecological overlap between wild reindeer and European bison is insignificant. The other threatened or near-threatened animal species of northern Europe include noble crayfish (*Astacus*

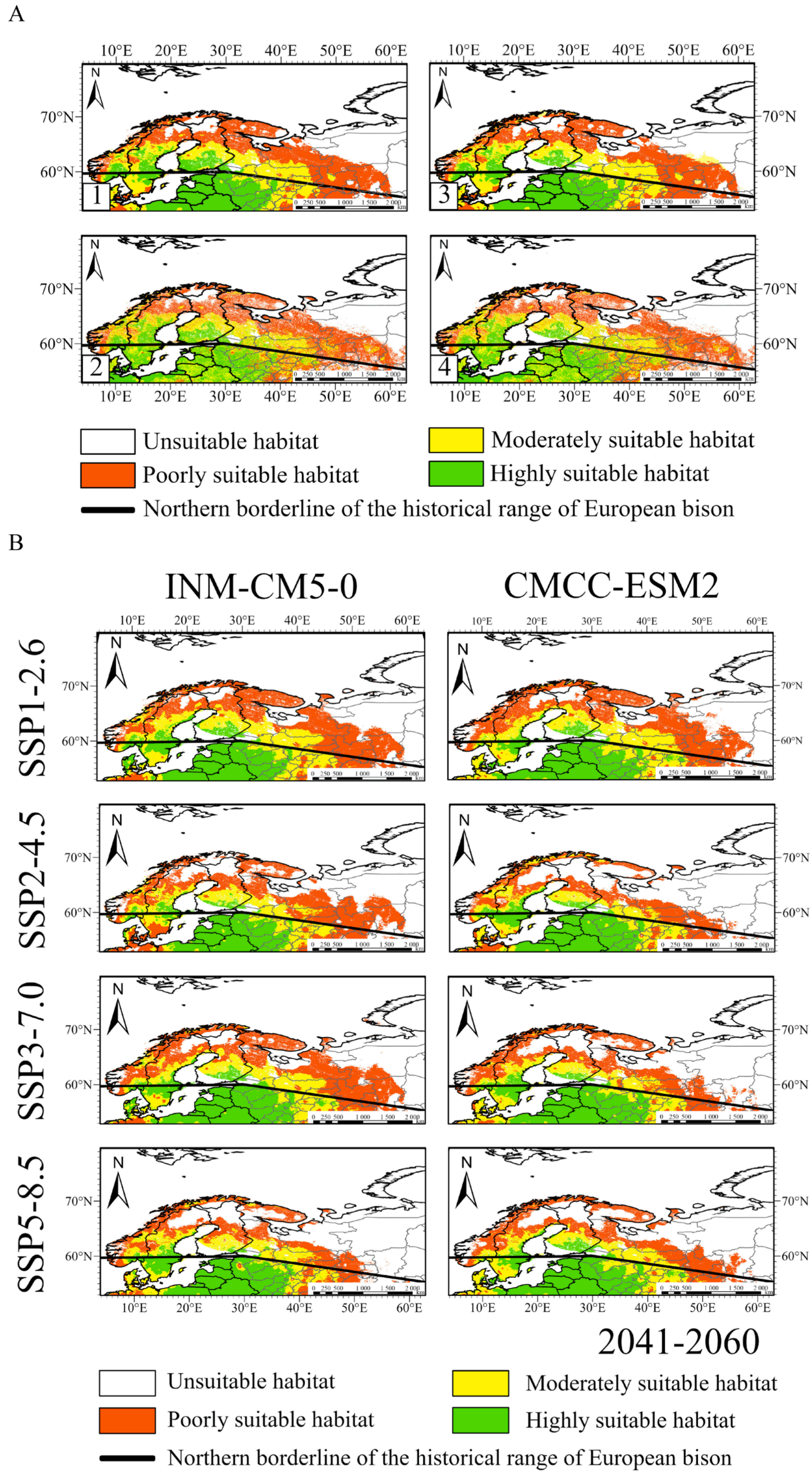

Fig. 5. Prediction of potential habitat areas of *Bison bonasus*: A. Prediction under current climate scenario. Models driven by (1) bioclimatic variables and (2) bioclimatic and land cover variables, (3) and (4) with excluded areas respectively. B. Prediction under two General Circulation models (INM-CM5-0, CMCC-ESM2) and four shared socioeconomic pathways (SSP1-2.6, SSP2-4.5, SSP3-7.0, SSP5-8.5) in 2041–2060. C. Prediction under two General Circulation models (INM-CM5-0, CMCC-ESM2) and four shared socioeconomic pathways (SSP1-2.6, SSP2-4.5, SSP3-7.0, SSP5-8.5) in 2061–2080.

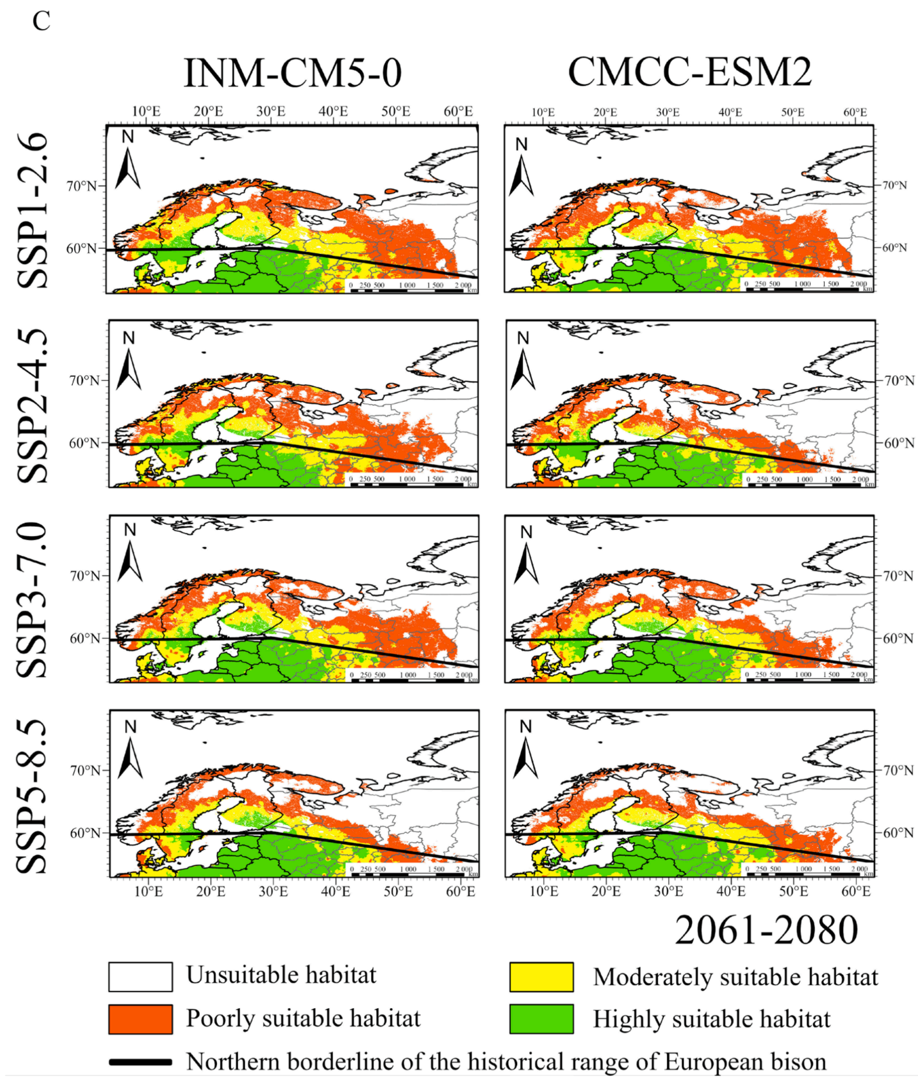

Fig. 5. (*continued*).

Table 2
Potential habitat area of *Bison bonasus* under current climate scenario.

Variable	Habitat area, km^2			
	Poorly suitable habitat	Moderately suitable habitat	Highly suitable habitat	Total suitable habitat
Bio	996,295	535,386	167,899	1,699,580
Bio and UN-LCCS	1,024,181	541,563	209,467	1,775,211

astacus), several waterbirds (curlew *Numenius arquata*, black-tailed godwit *Limosa limosa*, northern lapwing *Vanellus vanellus*, Eurasian oystercatcher *Haematopus ostralegus*, velvet scoter *Melanitta fusca*, black-legged kittiwake *Rissa tridactyla*), two species of freshwater bivalves (pearl mussel *Margaritifera margaritifera*, thick-shelled river mussel *Unio crassus*), pond bat (*Myotis dasycneme*), European mink (*Mustela lutreola*) (the last one is almost extinct) (Popov, 2021). This list is not constant and tends to increase, but it illustrates the main animals groups requiring attention. The European bison cannot affect most of them. It could affect only the waders, but rather positively. These birds require open areas for nesting, while ungulates support the existence of them. The possible impact of European bison on boreal ecosystems requires further research, but it is clear that there is at least some potential for its habitation in the North, and it is worth exploiting it, given the challenges within the historical range.

5. Conclusion

It is feasible for European bison to inhabit areas north of their historical range in Europe. Factors such as global warming, deforestation, and agricultural decline in the taiga zone of Russia create favorable conditions for European bison to expand northward across a vast territory. Encouraging this process could be a promising approach to bolster their population, thereby contributing to species conservation efforts and partially realizing rewilding projects.

CRediT authorship contribution statement

Igor Popov: Writing – review & editing, Investigation, Formal analysis, Data curation, Conceptualization. **Diana Smolina:** Writing – review & editing, Writing – original draft, Visualization, Formal analysis, Data curation, Conceptualization. **Igor Gusarov:** Writing – review & editing, Investigation, Formal analysis, Data curation, Conceptualization.

Table 3
Spatial changes of potential habitat area of *Bison bonasus* under different future climate scenarios.

Model	Periods	Scenarios	Habitat area, km^2 Poorly suitable habitat	Moderately suitable habitat	Highly suitable habitat	Total suitable habitat
INM-CM5-0	2041–2060	SSP1-2.6	1,110,520	506,354	135,791	1,752,665
		SSP2-4.5	1,020,361	386,247	82,132	1,488,740
		SSP3-7.0	1,125,857	479,427	114,881	1,720,165
		SSP5-8.5	1,091,435	495,571	100,652	1,687,658
	2061–2080	SSP1-2.6	1,120,566	618,318	151,132	1,890,016
		SSP2-4.5	1,088,016	450,971	119,779	1,658,766
		SSP3-7.0	1,109,842	462,907	124,082	1,696,831
		SSP5-8.5	1,144,813	483,090	93,668	1,721,571
CMCC-ESM2	2041–2060	SSP1-2.6	667,257	311,637	114,046	1,092,940
		SSP2-4.5	709,792	402,166	73,361	1,185,319
		SSP3-7.0	806,772	325,952	98,237	1,230,961
		SSP5-8.5	804,679	348,891	114,655	1,268,225
	2061–2080	SSP1-2.6	750,880	290,095	56,984	1,097,959
		SSP2-4.5	626,776	328,177	96,595	1,051,548
		SSP3-7.0	782,073	396,794	131,940	1,310,807
		SSP5-8.5	703,257	397,737	60,621	1,161,615

Fig. 6. Former pristine taiga at the Pinega River: pictures by Igor Shpilenok, 2019, (reproduced with permission) and aerial picture.

Declaration of competing interest

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

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jnc.2024.126711.

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