



## Where winter rules: Modeling wild boar distribution in its north-eastern range

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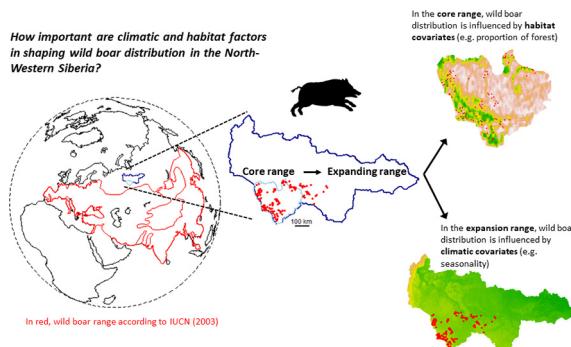
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### HIGHLIGHTS

- Wild boar continues expanding in north-western Asia.
- In areas permanently inhabited by wild boar, habitat covariates play a marked role.
- At the edge of distribution, mostly climatic variables contribute.
- Results highlight the risk of further wild boar expansion under climate change.

### GRAPHICAL ABSTRACT



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### ABSTRACT

Wild boars are distributed almost all over the Earth. Though, Northern Asia remained not inhabited by the species until the end of the 20th century. In the last two decades slowly but surely the wild boar has expanded the north-eastern edge of its range to the northern border of the taiga. Investigating environmental factors that underlie range expansions is crucial for understanding its mechanism and predict future changes in species distribution and biodiversity. Here we investigated the distribution of wild boar in its northeastern range, comparing the role of habitat and climate variables at three spatial scales: the permanently occupied area, the area of potential expansion and the total area.

We have shown that along the gradient of wild boar occupancy (from permanently to sporadically occupied to presently unoccupied) the importance of habitat variables decreases while importance of climatic variables increases. Our analysis suggests that the potential range increase of the species results from the combined effect of habitat and climatic variables. A possibility for future expansion, however, is rather related to climate change (particularly to the increase of temperature at high latitudes) than to the alteration of habitat or shifts in resource use.

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### 1. Introduction

Understanding niche dynamics is a prerequisite to predicting patterns of species distribution in relation to climate change and biological

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invasions (Pearman et al., 2008). Presently, there are many examples of fast expansions of species ranges resulting from both natural expansion and intentional introduction. The following three hypotheses could explain such phenomena (Broennimann et al., 2007; Pearman et al., 2008): i) the environmental conditions changed in such a way that the factors (abiotic and/or biotic) limiting species distribution have disappeared (e.g. climatic barrier modified by global warming (Chen et al., 2011), ii) the species had potential to expand due to its wide fundamental niche parameters (e.g. species presenting wide behavioral and/or feeding plasticity), iii) the species was able to shift or expand its ecological niche while adapting to a new environment (e.g. by climatic niche shift or release from natural enemies).

A number of studies (Peterson, 2011 and references therein) argue that the presence of species in a given environment depends on the species' physical ability to access this environment rather than on parameters of the species' fundamental (particularly, climatic) niche. It is worth to mention that a lack of the species' ability to disperse is in most cases related to the effect of some biotic or abiotic factors and could be treated as a special case of the first hypothesis. In fact, both the first and second hypothesis address the parameters of species fundamental niche and the concept of niche conservatism (Holt, 2009; Peterson, 2011). The third hypothesis is the most interesting from the point of view of micro-evolution since it demonstrates that organisms are able to adapt to rapid changes of environmental conditions (Broennimann et al., 2007; Hill et al., 2013; Lancaster et al., 2015). All three hypotheses must be considered when investigating the causes and consequences of species expansions to new regions, especially when a species is of economic importance and could be treated as a pest or an ecological engineer (Crooks, 2002; Cuddington and Hastings, 2004).

Species distribution models (SDMs) or ecological niche models (ENMs) are powerful instruments to compare a species' historical range and recently settled areas (Elith et al., 2006; Phillips and Dudík, 2008). Initially, SDMs were mainly based and developed on the concept of niche conservatism (Hill et al., 2013). Recent studies have however demonstrated that ecological requirements that species show in the core part of their distribution range cannot be directly used for predicting its occurrence in unoccupied or newly settled territories (Broennimann et al., 2007; Lancaster et al., 2015; Pearman et al., 2008). Theoretically, in recently settled areas, a species can adapt its needs to the resources at disposal when habitats in a newly occupied territory are very different from those in the historical range (Mainali et al., 2015). That is why it is important to study the resources used by species in its area of expansion (or distribution edge) prior to project its distribution in unoccupied or newly settled territories. Presence-only models are of particular interest to investigate such question since species at the edges of their geographical range are typically rare, thus have low abundance and unstable population dynamics (Brown et al., 1995; Williams et al., 2003). SDMs are not only tools enabling to predict species distribution in unoccupied areas, but they also provide information on the relative importance of the environmental factors used to build these models.

The wild boar (*Sus scrofa* L., 1758) is one of the species whose geographical range has expanded far beyond its native range, both naturally (Morelle et al., 2016) and following human introduction e.g. into North and South America and Australia (Barrios-Garcia and Ballari, 2012; Bengsen et al., 2018; Meyer, 2018; Salvador and Fernandez, 2018). Today the species has become the second most abundant ungulate in Europe and it is considered a pest in many areas (Massei et al., 2015; Massei and Genov, 2004). In its native range, wild boar suffered a strong contraction of its geographical range until the early 20th century due to persecution and intensive hunting (Danilkin, 2002). Then wild boar progressively re-established its native range and in Eastern Europe, particularly in Russia, the species expanded to several north-eastern regions where it had not previously been reported (Danilkin, 2002; Danilov and Panchenko, 2012; Markov, 1997). This expansion was partly due to intentional releases of individuals (Danilkin, 2002) but in

great extent it was a natural dispersion of animals in the north-eastern direction (Danilov and Panchenko, 2012).

While wild boar was previously suggested to be limited in its distribution by the isoline of snowdepth of 30–40 cm (Formozov, 1990), in the second half of the 20th century the species has been detected in areas where the average snowdepth exceeds 50–70 cm and where the average winter temperatures are below  $-30^{\circ}\text{C}$ . Wild boar records were even made close to the Arctic circle (Markov et al., 2004). These data suggest that the ecological plasticity of wild boar has previously been underestimated or the species' ecological niche has shifted to adapt to new environment. Wild boar is considered an ecosystem engineer because it modifies the structure and composition of soil and plant communities through soil rooting and nest building behavior (Cuevas et al., 2010). This behaviour is especially pronounced in recently invaded areas (Barrios-Garcia and Ballari, 2012). Thus, understanding mechanisms of its expansion to new areas is important for conservation of biodiversity in northern ecosystems (Pauchard et al., 2016).

In this study, using SDM, we investigated the environmental and climatic factors influencing the spatial distribution of wild boar in the northern edge of its native range (north of Western Siberia). Both the climatic and habitat conditions of this area are markedly different from those in the core part of the species geographical range, which raises the question about the changes in the spectrum of resources used by the wild boar and the ways the species exploits it.

We hypothesize that along the core-edge range, the distribution of wild boar is increasingly influenced by climatic factors. Thus, the distribution of wild boar in the core area is predicted to be influenced by habitat factors while at the edge of the distribution of wild boar, climatic variables are most influencing.

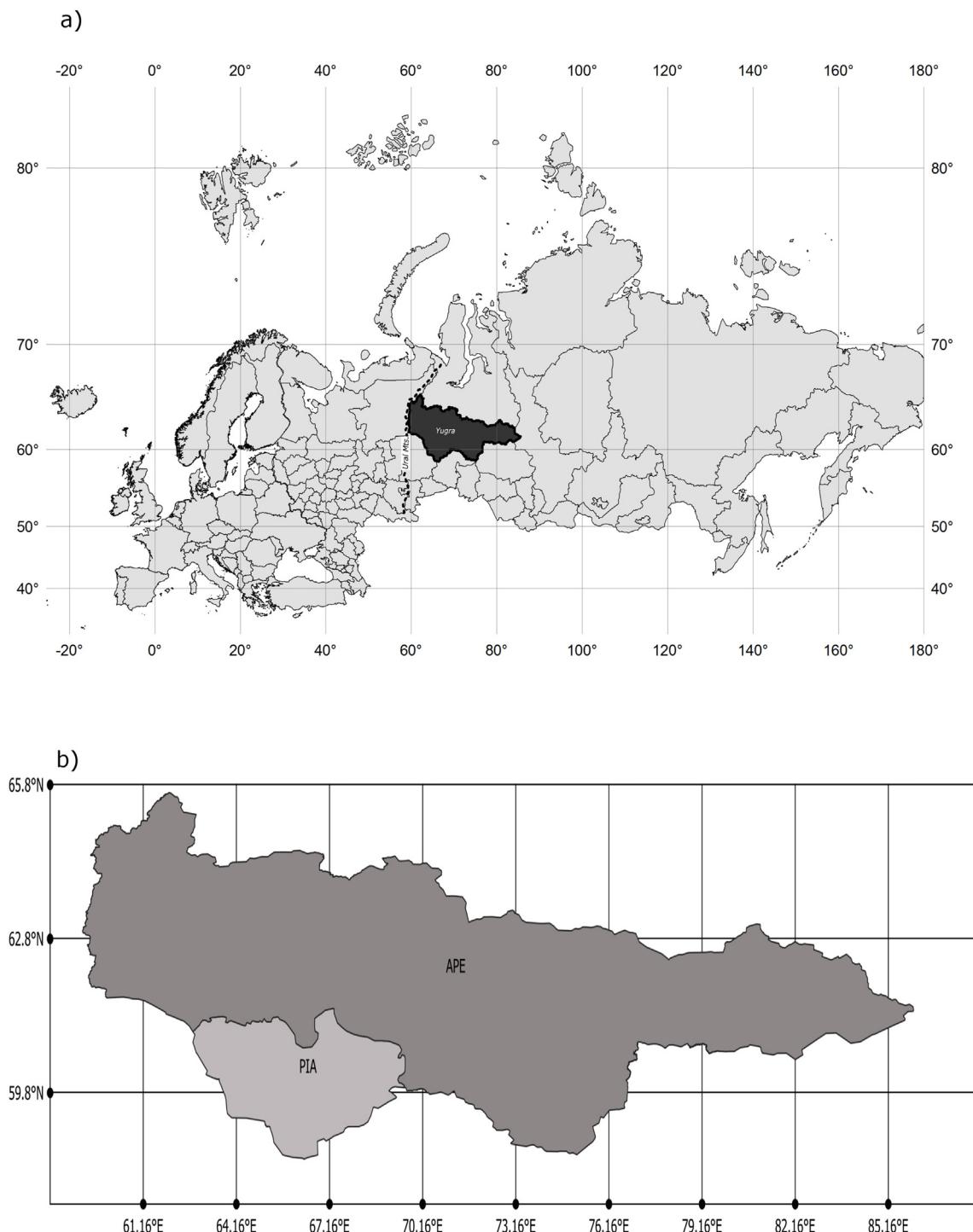
## 2. Methods

### 2.1. Study area

Khanty-Mansy Autonomous okrug –Yugra occupies the central part of the West Siberian Plain (Fig. 1a). It stretches in the east-west direction for 1400 km (from Ural mountains to Ob'-Yenisey watershed, between  $60^{\circ}$  and  $86^{\circ}$  E) and in the north-south direction for approximately 800 km, situated between  $58^{\circ}30'$  and  $65^{\circ}30'$  N. The terrain is primarily a lightly dissected plain with an elevation of no  $>200\text{ m}$  above sea level; however, the mountain ridges of the Northern and Polar Ural are present in the western part of the region. The highest point is Narodnaya Mountain (1895 m above sea level). The main river is Ob', which flows in the south-north direction and divides the territory of Yugra into its western (situated closer to the Ural mountains) and eastern (West Siberian) parts. Irtysh is another large river that flows from east to west and divides the eastern Yugra into its northern and southern parts.

The climate is moderately continental. The average temperature in January varies within the region from  $-18^{\circ}\text{C}$  to  $-24^{\circ}\text{C}$ . Winter begins in the end of October and lasts until the end of April. The number of days with stable snow cover is 180–200 (during 40% of which the temperature is below  $-20^{\circ}\text{C}$ ), and the average depth of snow varies from 50 to 60 cm in the southern part of region to approximately 80 cm in its northern area. The average temperature in July rises to 15–18 °C.

According to Moskvina and Kozin (2001 with changes) the territory of Yugra region is divided into 16 landscape provinces, which are territories with one or several similar types of landscape, similar orographic, lithological and vegetation characteristics, situated typically within one natural zone (Suppl. A for a brief description of the provinces). The western-most province is the Ural Mountains. The southwestern part of the region is primarily lowland with a very high (up to 80%) proportion of bog, marshes and lakes. Upland plains lie in the northern and northeastern parts of the region. The main tree species are spruce



**Fig. 1.** a) geographical position of Yugra region on the map of Eurasia; b) map of the total study area with area permanently inhabited by the wild boar (PIA) and area of potential expansion (APE).

(*Picea sp.*), Scotch pine (*Pinus sylvestris*) and Siberian pine (*Pinus sibirica*), with larch (*Larix siberica*) in the northern parts of the region (Moskvina and Kozin, 2001 with changes). In most forest types, lichen and green moss dominate the herbaceous layer.

In this area, wild boar have naturally expanded to this region in the end of 1980-s, and stable populations were established in the beginning of the 21st century. Currently wild boar is known to inhabit the southern part of the region approximately up to 62° n. l. but records of this species were made much further to the north (Markov et al., 2019). Presently wild boar is in the list of game species in the study area, hunting is allowed from mid-June to the end of February.

Other ungulate species present in the study area are moose (*Alces alces*) and reindeer (*Rangifer tarandus*). Most common species of carnivores are brown bear (*Ursus arctos*) and wolverine (*Gulo gulo*), while the wolf (*Canis lupus*) is relatively rare (Plotnikov, 1997). Though ungulates could constitute important part of the brown bear and wolverine diets (Dahle et al., 2018; Tirronen et al., 2016; van Dijk et al., 2007) they cannot be treated as significant factors of ungulates' mortality (Bolshakov et al., 2009).

The human population density is extremely low and does not exceed 3.1 persons per square kilometer. The regional economy is based on forestry, oil and gas production, with almost no agriculture.

## 2.2. Data

We used wild boar presence points in Yugra region made in 2001–2016 when the species has been recorded annually in the study area. This period of 15 years allowed us to take into accounts possible temporal changes in the animals' distribution. Most records (approximately 66%) were made in winter during the regular census of animals, based on snow track counts (Stephens et al., 2006). Roughly 28% of the records were made in the snow-free season or seasons with little snow cover (spring–autumn). The types of records were mainly footprints (69.9%), direct observations (7.8%), and hunted animals (3.6%). These records were located in a variety of habitat types. The final dataset included 178 records.

## 2.3. Covariates

We modeled wild boar distribution with a set of climatic and habitat variables (Table 1). Data on climate were obtained from the WorldClim 2.0 database (Fick and Hijmans, 2017). From the monthly temperature and rainfall values we derived bioclimatic variables that represent annual or quarterly trends (e.g. mean annual temperature, annual precipitation, or temperature of the coldest quarter), seasonality (e.g. annual range in temperature and precipitation) and extreme or limiting environmental factors e.g., temperature of the coldest and warmest month, and precipitation of the wet and dry quarters). Globcover (<https://esa-landcover-cci.org>) raster maps of vegetation were used for classification of habitat. Initial types of vegetation presented on the Globcover maps (Bontemps et al., 2011) were reclassified to present the following main types of habitat: forest (including deciduous, coniferous and mixed forest), mosaic habitat (mosaic forest or shrubland (20–70%) / grassland (20–70%)), swamped habitat, (semi-)open habitat

(sparse (<15%) vegetation) and water bodies (rivers and lakes). We also calculated raster maps of the proportion (percentage) and fragmentation of the habitat types (forest, mosaic, open, bogs), the number and the diversity of habitat types. These raster maps were calculated following Riitters et al. (2013) using the tools fragmentation and diversity in SAGA GIS (Conrad et al., 2015). The values were calculated for each pixel in a  $6 \times 6$  km moving window in order to fit the home range size of wild boar (Markov et al., 2019; Keuling et al., 2018).

## 2.4. Modeling approach

Range-shifting species violate the assumption of equilibrium between the species and the environment (Elith et al., 2010). Particularly, in the areas where species has established more or less stable populations its' relationships with the environment may differ from those in the areas where only single records were observed. To take into account this risk, we weighted our data to the constancy of species presence in the different parts of the study area Elith et al. (2010) by defining three scales of analysis. The first scale of investigation is the Permanently Inhabited Area (further PIA). It corresponds to the core distribution of wild boar in the study area. For this analysis, we used records from the province of Konda-Tavda which covers most part of the area permanently inhabited by the species (see Fig. 1b and Suppl. A). The second scale of analysis was the Area of Potential Expansion (further APE) or the edge of distribution. For this scale, we used wild boar records from the territory of Yugra, excluding the set of points used for the PIA analysis where wild boar was periodically present or vagrant. The third scale of analysis is the Total Study Area (further TSA) combining both PIA and APE.

We modeled the current distribution of wild boar in the study area with MaxEnt software v. 3.4.1 in a series of hierarchical models (Table 2). We choosed MaxEnt against others modeling approaches, such as GLM and random forest, because MaxEnt has a proven efficiency to deal with small sample size and has demonstrated strong performance when compared to other modeling approaches (Elith et al., 2011). The idea of the first modeling stage was to use all possible predictors without building a-priori hypotheses. The reasons for these were that i) wild boar is a generalist species and in different parts of its geographical range its distribution and abundance could be affected by various climatic and habitat factors, like high and lows temperature, summer or winter precipitation or habitat diversity (Lewis et al., 2017; McClure et al., 2015; Melis et al., 2006; Oja et al., 2014; Vetter et al., 2015 and references therein) and ii) possible biotic and abiotic interactions in the newly settled areas are unknown and any predictor could potentially be important for the species. After the first stage of modeling (Model 1 and 2) we selected the variables with the highest contribution to the model based on results of gain and permutation tests, jackknife test for test subsample and AUC. These variables were checked for cross-correlation and from the pairs of variables with correlation coefficient higher than 0.7 one variable was chosen for further analysis.

Variables selected from Models 1 and 2 were used in Model 3. In this model the results of the gain test, the permutation test, the jackknife tests for test gain and the AUC for test data were used as indicators of predictor variables' contribution to the model. To assess the effect of each variable on the probability of wild boar presence we used the response curves representing a MaxEnt model created using only the corresponding variable.

As records sampling was biased towards roads and such bias is known to greatly impact MaxEnt outcomes (Kramer-Schadt et al., 2013), we used the inverted map of distance to roads as a bias raster in our analysis. This bias raster was used to generate 10,000 background points weighted by the distance to road (higher probability of background points close to roads). The distances to roads were calculated using the Euclidian distance tool in ArcGIS 10.4. The resolution of all maps was about 1x1km.

**Table 1**  
Covariates used for modeling the wild boar presence in the north-western Siberia.

Class	Name	Subject	Type
Climatic	bio 1	Annual Mean Temperature	Continuous
	bio2	Mean Diurnal Range (Mean of monthly (max temp - min temp))	Continuous
	bio 3	Isothermality (BIO2/BIO7) (* 100)	Continuous
	bio 4	Temperature Seasonality (standard deviation *100)	Continuous
	bio 5	Max Temperature of Warmest Month	Continuous
	bio 6	Min Temperature of Coldest Month	Continuous
	bio 7	Temperature Annual Range (BIO5-BIO6)	Continuous
	bio 8	Mean Temperature of Wettest Quarter	Continuous
	bio 9	Mean Temperature of Driest Quarter	Continuous
	bio 10	Mean Temperature of Warmest Quarter	Continuous
	bio 11	Mean Temperature of Coldest Quarter	Continuous
	bio 12	Annual Precipitation	Continuous
	bio 13	Precipitation of Wettest Month	Continuous
	bio 14	Precipitation of Driest Month	Continuous
	bio 15	Precipitation Seasonality (Coefficient of Variation)	Continuous
	bio 16	Precipitation of Wettest Quarter	Continuous
	bio 17	Precipitation of Driest Quarter	Continuous
	bio 18	Precipitation of Warmest Quarter	Continuous
	bio 19	Precipitation of Coldest Quarter	Continuous
Habitat	hab	Reclassified LandCover Map	Categorical
	db	Proportion of bogs within 6 km around the point	Continuous
	df	Proportion of forest within 6 km around the point	Continuous
	dm	Proportion of mozaic habitat within 6 km around the point	Continuous
	do	Proportion of open habitat within 6 km around the point	Continuous
	dw	Proportion of water bodies within 6 km around the point	Continuous
Bias	div	Number of habitat categories within 6 km around the point	Continuous
	DistRoad	Disntace to roads, inverted	Continuous

**Table 2**

Scheme of the process of modeling the effect of climatic and habitat variables on the wild boar distribution in north-western Siberia.

Model #	Covariates	Source of data	Result
1	All climatic variables	WorldClim 2.0	Selection of variables with highest contribution to the model
2	All habitat variables	European space agency	Selection of variables with highest contribution to the model
3	Selected climatic+habitat variables		Final model

We run each model (PIA, APE, TSA) 50 times using bootstrapping (1000 replicates) with 75% of the presence records used for training the model and 25% used for testing it. Only linear and quadratic transformations of variables were used to avoid non-linear effects and provide more easier and more clear interpretation of the results. Models 1 and 2 (Table 2) were run with regularization multipliers (RM) 2, 1 and 0.5 and the RM = 0.5 provided the highest AUC values. Thus Model 3 was run only using RM = 0.5. The quality of all models was assessed using two metrics: i) the Receiver Operating Characteristic, i.e. the ROC curve or Area under the Curve (AUC), ranging between 0.5 (a model with no predictive ability) and 1 (a highly predictive model) (Hanley and McNeil, 1982) and ii) the true skill statistic (TSS), a threshold-dependent metric ranging from −1 to 1, where TSS = 0 corresponds to models with no skill to differentiate between the presence and absence of wild boar carcasses in a grid cell (Allouche et al., 2006).

### 3. Results

#### 3.1. Models performance

The MaxEnt model outcomes were shown to be robust and showed little variation measured in terms of the standard error of the AUC and TSS (Fig. 2). According to the AUC-TSS plot, the broader scale models, APE (mean AUC = 0.80, mean TSS = 0.44) and TSA (AUC = 0.81, TSS = 0.43) performed best, followed by the PIA model (AUC = 0.72, TSS = 0.27).

#### 3.2. Factors affecting wild boar distribution in the permanent inhabited area (PIA scale)

At the PIA scale, the climatic variables included in the final model (#3 in Table 2) were mean annual temperature (*bio1*), temperature seasonality (standard deviation \*100) (*bio4*) and the mean temperature of the driest quarter (*bio9*). Habitat variables included in the model were proportion of forests (*df*), water bodies (*dw*) and bogs (*db*) and the number of habitat categories in 6 square km around the pixel (See Suppl. B for details). The best performance for the model #3 was obtained using the regularization multiplier 0.5 (AUC for test dataset was  $0.72 \pm 0.05$ ) (Fig. 2, data for PIA scale).

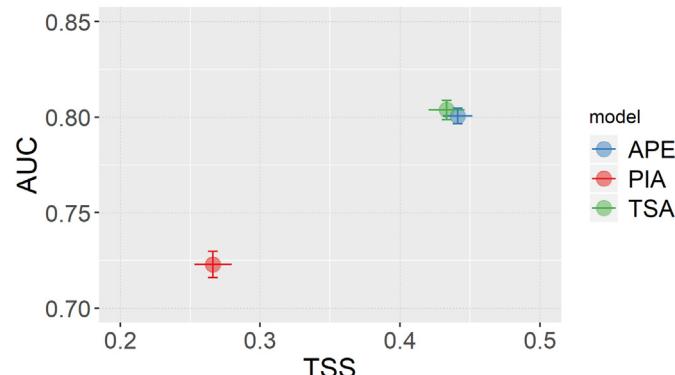


Fig. 2. Model performance at different spatial scales basing on Receiver Operative Characteristic/Area under Curve (AUC) and True Skill Statistics (TSS).

Three variables contributed most to the probability of wild boar presence: temperature seasonality (*bio4*), mean annual temperature (*bio1*) and proportion of forests (*df*) (Fig. 3, data for PIA scale). The response curves (see here and further Fig. 4, data for PIA scale) showed a linear decrease of the probability of occurrence with the temperature seasonality, while it increased with the mean annual temperature. The effect of the proportion of forest presented a bell-shaped response, with highest probability of occurrence between 50% and 60% of forest cover.

The generated map of the relative probability of wild boar presence in the southern part of Yugra (Fig. 5a) shows the mosaic of highly suitable habitat in the south-western part of this area. Habitats with medium suitability are situated along the river valleys in the central part of the study area, while the probability of wild boar presence in the eastern part of it was estimated as close to zero.

#### 3.3. Factors affecting wild boar distribution in the area of potential expansion (APE scale)

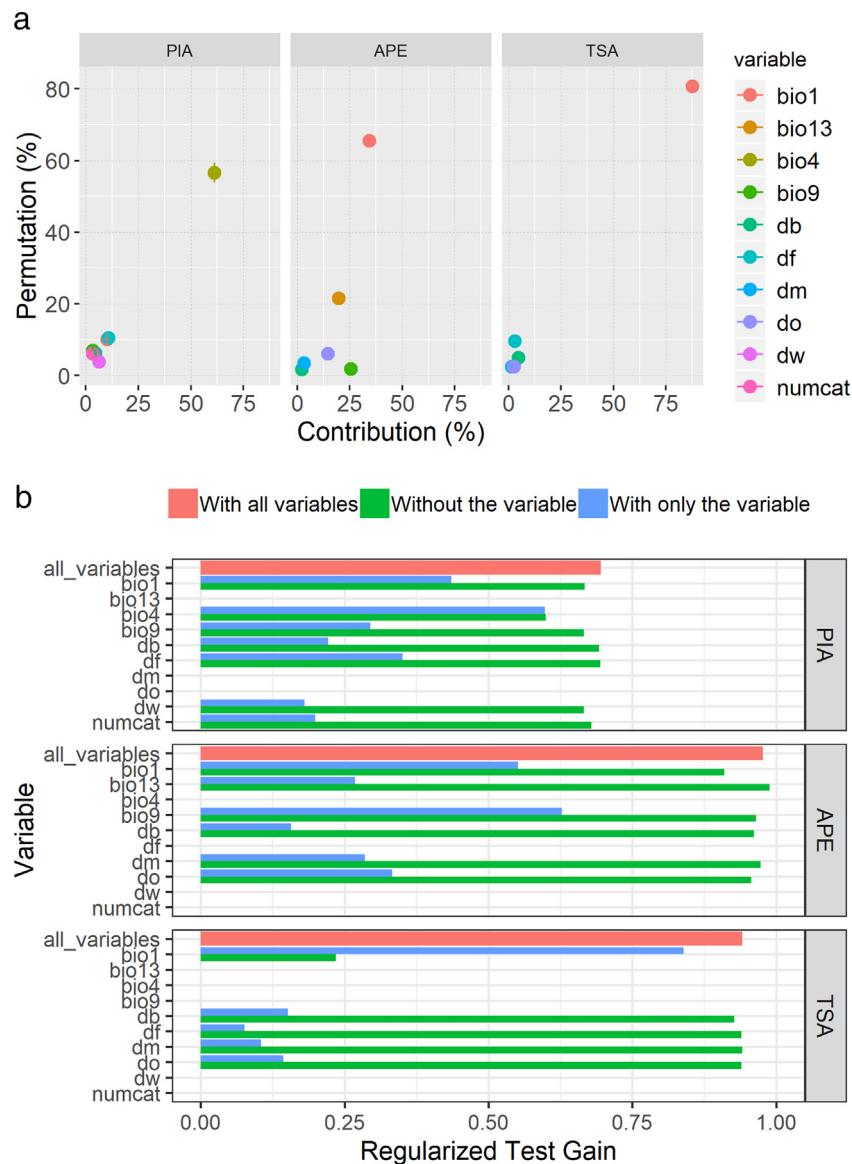
For the region of Yugra outside the Konda-Tavda landscape province the climatic variables included in the final model were the mean annual temperature (*bio1*), minimum temperature of driest quarter (*bio9*) and the precipitation of wettest month (*bio13*). Habitat variables included in the model were proportions of bogs (*db*), mosaic (*dm*) and open habitat (*do*) (See Suppl. C for details). The average value of AUC for this model was obtained using the regularization multiplier 0.5 and it was  $0.80 \pm 0.04$  (Fig. 2, data for APE scale).

The main contributing covariate in the wild boar presence in the area of potential expansion was the mean annual temperature (*bio1*) (Fig. 3, data for APE scale). The probability of wild boar presence was positively correlated with *bio1* (see here and further Fig. 4, data for APE scale). It was close to zero in the areas where mean annual temperature is below  $-4^{\circ}\text{C}$ , and exponentially increased in the areas with higher values. Other variable that contributed significantly to the model was the precipitation of the wettest month (*bio13*). Wild boar presence probability dropped strongly in the areas where this index was above 70 mm and went below 0.1 at the values above 90 mm.

The modeled average relative probability of wild boar presence at the APE scale (Fig. 5b) was close to one in the southern part of the area under consideration up to approximately  $61^{\circ}\text{ n. l.}$  (the river Ob'). In the northern parts of the study area the probability of species occurrence was zero or close to zero. The medium probability of occurrence at about 0.5–0.6 was observed for the river valleys in the central and western parts of the study area.

#### 3.4. Factors affecting wild boar distribution in the total study area (TSA scale)

For the whole region of Yugra the only climatic variable included in the final model was the mean annual temperature (*bio1*). Habitat variables included in the model were the proportions of mosaic (*dm*) and open habitat (*do*) (See Suppl. D for details). The average value of AUC for this model was obtained using the regularization multiplier 0.5 and it was  $0.80 \pm 0.03$  (Fig. 2, data for TSA scale). The contribution of *bio1* was about 90% making the input of habitat variables to the model negligible (Fig. 3, data for TSA scale). As expected, the probability of wild boar presence increased with increase of the mean annual temperature in the same way as for APE scale (Fig. 4, data for TSA scale).



**Fig. 3.** Contribution of habitat and climatic covariates in the three models developed: a) contribution in gain test vs permutation test; b) Results of the jackknife test of regularized test gain for the habitat and climatic covariates.

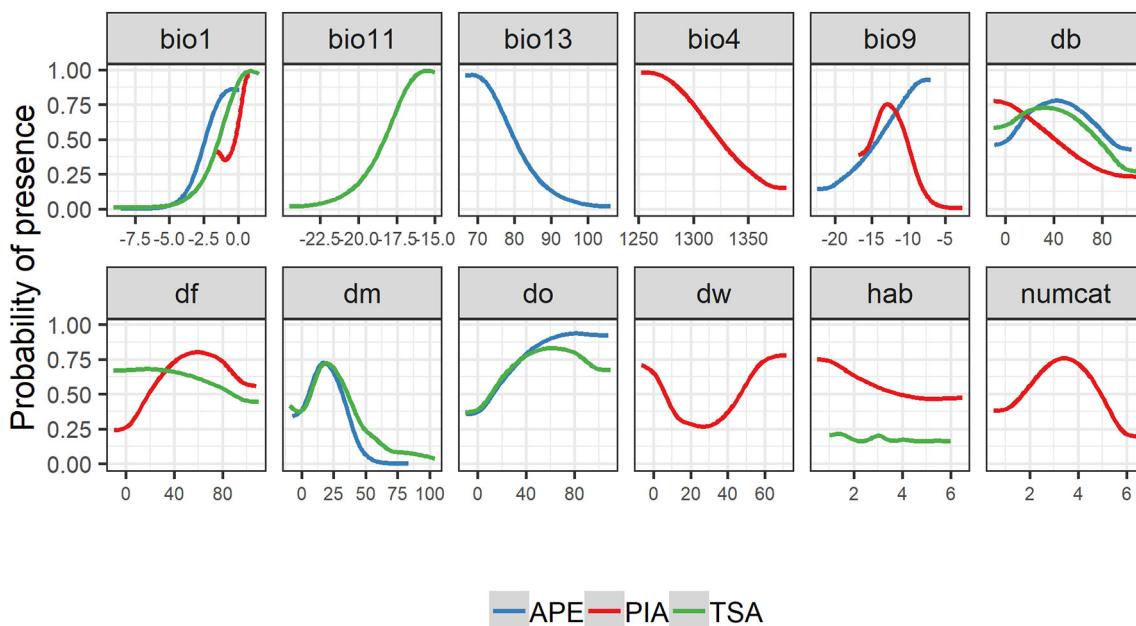
The average relative probability of wild boar presence in the whole region of Yugra (Fig. 5c) was not <0.5 to the south from approximately 61° n. l. (south from the river Ob'). The geographical limits of the area with the probability of occurrence >0.5 did not differ substantially for the mean, maximum and minimum estimates. In all scenarios western mountainous and eastern upland parts of the regions were predicted to have very low (close to zero) probability of occurrence.

#### 4. Discussion

Our results revealed the differences in the effect of climatic and habitat variables on wild boar distribution at various scales of analysis. At PIA scale, both the habitat and climate components strongly affect the probability of wild boar presence. We observed that probability of presence in the PIA region depended on the combined effect of climate stability and the availability of forest cover. It has been reported that the abiotic environment often indirectly influences the effects of biotic interactions (Godsøe et al., 2017). In this case we propose that the strong effect of temperature variation (*bio4*) and weaker effect of the proportion of forest (*df*) were linked and both effects demonstrate the importance of forest habitat for wild boar in the recently settled area at the

northern edge. It is known that providing climate stability is one of the key forest functions (Alkama and Cescatti, 2014; Suggitt et al., 2011). Thus, sufficient forest cover probably enables wild boar to counteract the strong temperature seasonality at this extreme northern edge of its distribution. Most of the studies of wild boar ecology both on the local (Keuling et al., 2018 and references therein) and global (Bosch et al., 2017) scale report the preference of different types of forest as main habitat. However, the 100% forested areas provide less probability of occurrence than areas with medium levels of forestation. This could be related to the higher natural productivity of forest edges in comparison with center parts of a forest due to the effect of ecotone (Kark, 2012). Also, this could be related to the observation bias, since the points within the continuous undisturbed woodland could be visited more rarely in comparison with partly transformed habitat where road networks exist. In any case, the occurrence of wild boar at the northern edge of its distribution is closely related to forested areas like in the other parts of the species' geographical range.

The part of the PIA where the relative probability of wild boar occurrence is close or equal to zero is presumably covered with open bog with very harsh climatic conditions (Plotnikov, 1997) (Fig. 5a). Thus, despite the high contribution of the *bio4* and *bio1* variables to the model at the



**Fig. 4.** Response curves for the climatic and habitat covariates.

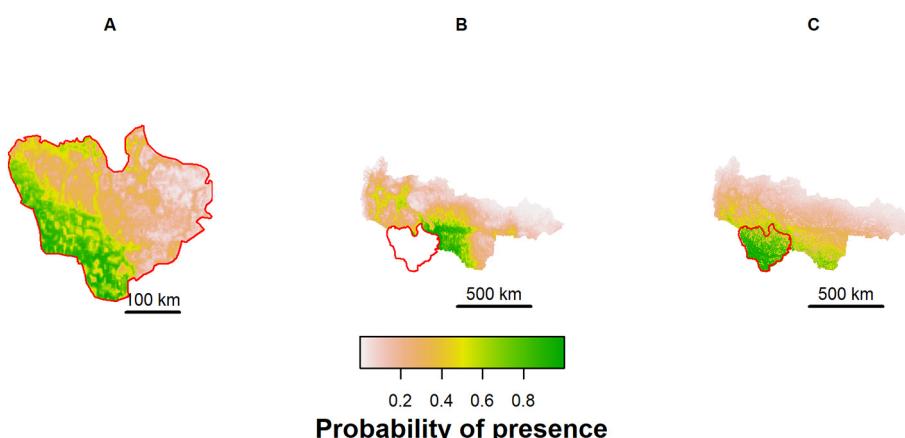
PIA scale, we suggest that the effect of climatic variables is indirect and the occurrence of wild boar in the southern part of the study area depends primarily on the distribution of forest.

At larger scales (both APE and TSA) the effect of climate dominates over the effect of habitat. The contribution of all habitat variables is negligible. When comparing the contribution of only habitat variables (Model 2) the most significant were proportions of mosaic (*dm*) and open (*do*) habitat, but not the proportion of forest (*df*) like at the PIA scale. This could be related to the lower proportion of forest cover at larger scale. Small sample size from the areas outside PIA suggests the possible effect of habitat variables could be underestimated due to low sampling effort in the northern part of the region.

Mean annual temperature was the most important factor predicting wild boar presence at the APE and the TSA scales, and the model predicted higher probability in the warmer areas. This result may look trivial, however a number of studies report presumably indirect role of climate on wild boar abundance and distribution. The direct effect of climate on wild boar consists in higher winter mortality (Jędrzejewski et al., 1992). Vetter et al. (2015) reported the dependence of wild boar population growth on winter temperatures even in southern regions of Europe but mentioned that the effect of climate could be

compensated with high amount of food. The indirect effect of climate on the availability of food and shelters has been reported in the northern edge of wild boar distribution in Norway (Rosvold and Andersen, 2008). Bergqvist et al. (2018) did not observe any effect of climate on the reproduction rate of wild boar population close to northern edge of geographical range in Sweden. Oja et al. (2014) reported an effect of the mean January temperature on wild boar population density in Estonia, but they concluded that the effect of food availability was more pronounced than the effect of climate. It is important to notice though that winter conditions reported in northern populations of Europe (average January temperature between  $-4$  and  $-20$  °C) are much milder than in Western Siberia (average January temperature between  $-23$  and  $-31$  °C).

In a European-wide scale analysis, Melis et al. (2006) reported strong effect of average January temperature on wild boar population density. The authors addressed the abundance of animals (not distribution) and this effect was interpreted in demographical terms and explained with increased winter mortality at low temperatures due to the low availability of food. Such density-independent mortality has been shown by a number of studies (see references in Melis et al., 2006) but it showed the effect of climate on the wild boar abundance rather than on its distribution.



**Fig. 5.** Map of the probability of occurrence of wild boar at the three scale of analysis: a) permanent inhabited area (PIA), b) area of potential expansion (APE), c) total study area (TSA).

Twenty years ago analyzing the newly established wild boar population in Sverdlovsk oblast' we demonstrated that wild boar abundance is more affected more by autumn mean temperature than winter conditions, while winter conditions (temperature, depth of snow and number of snow days) mostly conditioned the spatial distribution of wild boar in that study area (Markov, 1997). The results of the present study suggests similar mechanisms for north-western Siberia, with distribution of wild boar at the regional scale depending much more on climatic than on habitat factors. Such effect of winter temperatures suggests the absence of wild boar north to approximately 62° n. l.

We suggest two hypotheses explaining this absence of the species in the coldest parts of northwestern Siberia. First, it is possible, that wild boar can find shelters and food in the northern part of the region, but this food and shelters do not compensate energy expenses for standing the low temperatures. This hypothesis is supported by a number of reports of animals' presence in the snow-free periods. Only few records made in winter reported wild boar in human transformed habitat (gas pipeline) and in the patch of Siberian pine forest where they could get high-energy food (Siberian pine nuts) (Vorobjev, 2015).

The second hypothesis relates to the adaptation of wild boar to low temperatures, suggesting the species would be able to slowly evolve to shift their behavior and food habits and establish small but stable populations in areas with very low temperatures. This hypothesis is supported by a recent study demonstrating the genomic adaptation of wild boar to lower temperatures (Chen et al., 2018). Further, wild boar have developed morphological and behavioral mechanisms to compensate for low temperatures including dense winter fur (Foley et al., 1971) and the construction of farrowing nests in which temperatures can reach 20 °C (Algers and Jensen, 1990). The other support for this hypothesis is that at least some wild boar in the southern part of the study area successfully survived temperature minimum as low as −50 °C (pers. observation). In the south of Yugra wild boars build nests of dry grass and sphagnum moss, but in other areas of taiga zone they use branches of coniferous trees and other material. So, we suppose that if the wild boar will find material for building nests they will be able to survive and increase their presence in northern areas.

An important consequence of the dependence of wild boar distribution on winter temperatures is the possible effect of climate change. Melis et al. (2006) predicted that wild boar will respond to climate warming by an increase in local population densities and an expansion of the geographical range north and north-eastwards. This is indeed the case of wild boar expansion to the northwestern Siberia. In the end of the 20th century the increase in mean annual temperature for Siberia was about 0.34 °C/10 years, the duration of no-frost period in Western Siberia increased 2.3 days/10 years and the precipitation decreased in cold period of the year (Ippolitov et al., 2008). According to the response curves (Fig. 5), the exponential increase of wild boar presence was observed when the mean annual temperature increased from −9 °C to −4 °C. If the rate of the temperature increase will stay at the reported level the natural increase of wild boar presence in the northern part of Yugra region would happen in about 150 years. At the same time, high adaptability of species to northern conditions, as previously discussed, let suggest that this could happen faster. This suggestion is supported with the conclusions by Vetter et al. (2015) that wild boar populations in cooler regions are more sensitive to an increase in annual winter temperature than populations in warmer regions, i.e. northern populations began to grow at much lower winter temperatures in cooler regions compared to warmer areas.

It is worth to note that our results could be partly affected by the small sample size, especially at the APE scale. Though MaxEnt approach is known to be generally robust to small sample size (Graham et al., 2008), it is still possible that small number of observations could result in underestimation of probability of species occurrence in the some areas. At the same time, we aimed to model rather current than potential distribution, thus we have reasons to state that our results present the correct interpretation of the existing data. Special sampling of

northern areas as well as collection of data on habitat preferences at the scale of home range of single animals could improve the reliability of future models.

## 5. Conclusion

The present study demonstrates the marked role of climatic conditions in explaining the northeastern edge distribution of wild boar population. We did not observe marked differences of resource use by wild boar in northwestern Siberia in compare with other regions. Like in other parts of geographical range Siberian wild boar prefer forests and avoid areas with low winter temperatures and harsh weather conditions. Possibly, the expansion of wild boar to the north is promoted not by shifts in resource use, but by some behavioral adaptations of animals and by climate change.

Our results support the hypothesis that species niches based on species ecological requirements in the core parts of the geographical range are often underestimated (Peterson, 2011). In case of wild boar the species was able to expand far to the north without strong shift in resource use at least at the regional level. Strong effect of climate on species distribution indicates the importance of mechanistic approaches for predicting the species ranges and possible impact of climate change to biodiversity (Buckley et al., 2018). In fact, the severe climate still protects vulnerable northern ecosystems from intrusion of wild boar as a pest species.

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## CRediT authorship contribution statement

**Nickolay Markov:** Conceptualization, Methodology, Formal analysis, Writing - original draft, Project administration. **Nadezhda Pankova:** Conceptualization, Investigation, Resources. **Kevin Morelle:** Methodology, Formal analysis, Writing - original draft, Visualization.

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