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Modeling the Potential Spread of Alien Terrestrial Snails in Eastern Europe

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Abstract—The paper presents a prediction of the spread of nine alien land snail species (Mollusca, Gastropoda, Stylommatophora) in the European part of Russia and adjacent territories. Climate variables, land use type, and extended vegetation index were selected as predictors. The potential spread of each species was modeled. The habitat suitability for different numbers of alien species was identified on the study area. An analysis of the potential overlap of ranges has shown which species can co-colonize new territories for them. In general, the most favorable habitat conditions for the studied species are determined in the Black Sea region, the Azov region, the Caucasus, the Podolsk Upland, and the Middle Danube and Lower Danube lowlands. The association of alien land snail species with anthropogenically changed landscapes has been confirmed.

Keywords: potential range, SDM, ecological modeling, European territory of Russia

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INTRODUCTION

In recent decades, new cases of the invasion of alien species of terrestrial mollusks into Eastern Europe, in particular, into the European territory of Russia (ETR) and adjacent territories, have been observed quite frequently (Egorov, 2015, 2021; Kramarenko, 2016; Gural-Sverlova, and Gural, 2017; Adamova, 2021; Adamova et al., 2022b). Often, alien mollusks form stable populations and continue to spread. The expansion of alien terrestrial mollusks occurs in the following directions: from south to north (Caucasian, Crimean, southern European species), from west and northwest to east (central European and western European species) (Shikov, 2016). Naturally, questions arise: How widely can a particular alien mollusk spread and what territories are most vulnerable to the expansion of different species of alien mollusk? Ecological modeling methods are successfully used to find answers to such questions. In particular, species distribution modeling (SDM) methods are widely used to identify suitable habitats and areas of potential distribution of alien species (Uden et al., 2015; Pěknicová and Berchová-Bímová, 2016; Srivastava et al., 2019). In view of their ecological and often economic importance, mollusks are becoming the objects of such research. However, at present, there is virtually no work to assess the potential expansion of terrestrial mollusks in the European part of Russia and adjacent territories. An exception is work on modeling the propagation of *Arianta arbustorum* Linnaeus, 1758 (Bondareva et al., 2020), *Brephulopsis cylindrica* Menke, 1828, and *Xeropicta derbentina* Krynicki, 1836 (Adamova et al., 2022a). However the aforementioned works have significant shortcomings. So, when modeling *A. arbustorum*, the authors used only climatic factors as predictors, without any selection of variables; no preliminary analysis of the locations was performed to reduce spatial autocorrelation, and no threshold was defined for assessing the suitability of the area. In addition, the study region in this work does not include the eastern part of the potential range (Bondareva et al., 2020). In a published paper on modeling the potential range of *B. cylindrica* and *X. derbentina*, the threshold for dividing a territory into habitable and uninhabitable was not determined, and the overlap of species ranges was not assessed. It is clearly possible to create improved models of the potential range of these alien species, taking into account the important methodological recommendations presented in the literature (Guisan et al., 2017; Petrosyan et al., 2023).

Nine species of terrestrial mollusks that are known as invaders in different regions of the European part of Russia and neighboring countries were selected as objects of this study, namely: *Arianta arbustorum* Linnaeus, 1758; *Brephulopsis cylindrica* Menke, 1828; *Caucasotachea vindobonensis* C. Pfeiffer, 1828; *Harmozica ravergiensis* Férussac, 1835; *Helix lucorum* Linnaeus, 1758; *Helix pomatia* Linnaeus, 1758; *Monacha cartusiana* O.F. Müller, 1774; *Xeropicta derbentina*

Krynicki, 1836; *Xeropicta krynickii* Krynicki, 1833. Some of the listed species (*A. arbustorum*, *C. vindobonensis*, *H. pomatia*) penetrated into the ETR quite a long time ago; the settlement of others has been noticed in recent decades (*B. cylindrica*, *X. derbentina*, *X. krynickii*, *H. ravergiensis*, *H. lucorum*, *M. cartusiana*). The choice of alien mollusks for modeling was determined by the results of the author's field observations during the survey of the territory of a number of regions of the ETR and the identified new finds of alien populations.

The studied species of mollusks not only have different regions of origin (Table 1) but also belong to different ecological groups (Geyer, 1927; Shileiko, 1978). Naturally, they exhibit different preferences for habitats and environmental variables. *B. cylindrica*, *X. derbentina*, and *X. krynickii* are confined to open steppe biotopes. These are xerophilic mollusks with various adaptations to conditions of drought, increased insolation, and high temperatures (Kramarenko, 1997; Di Lellis et al., 2012; Troschinski et al., 2014). Three more species (*H. ravergiensis*, *H. lucorum*, *M. cartusiana*) can be classified as xeromesophilic. These mollusks also inhabit open biotopes, but can also live in shaded biotopes with tree and shrub cover. Finally, *A. arbustorum* and *H. pomatia* are confined to shaded, humid forest biotopes.

The species of land mollusks that were chosen as the object of this study are known to be alien not only in Russia but also in countries the near and far abroad. Species *X. derbentina* and *X. krynickii* in recent decades have spread north and northwest from their natural range: in particular, populations have been studied in Serbia, Croatia, Montenegro, Italy, and France (Aubry et al., 2005; De Mattia, 2007; De Mattia and Pešić, 2014; Wagner and Bertrand, 2021). Populations of these invaders were found in Belgorod region of Russia and in a number of regions of Ukraine (Gural-Sverlova and Gural, 2017; Adamova et al., 2019). Alien populations of *B. cylindrica* are known on the territory of Russia, Ukraine, and Belarus (Rabchuk and Zemoglyadchuk, 2011; Snegin et al., 2017; Balashov et al., 2018a). *A. arbustorum* spreads across the territory of the Russian Plain from the northwest to the east and south (Shikov, 2016; Bondareva et al., 2020; Egorov, 2021). *C. vindobonensis* spreads northward across the Russian Plain (Shikov, 2016; Egorov, 2018). Populations of the Caucasian species *H. ravergiensis* were discovered and studied on the territory of the Russian Plain, including the Central Russian Upland, the Dnieper Upland, and Dnieper Lowland (Balashov et al., 2013, 2018b; Shikov, 2016; Adamova, 2021; Ostrovsky, 2022). The distribution of two species of the genus *Helix* (*H. pomatia* and *H. lucorum*) was noted in the center and south of the Russian Plain (Balashov et al., 2013; Egorov, 2015). On these same territories, as well as in the southwest of the Russian Plain, alien populations of *M. cartusiana* are known (Shikov, 2016; Gural-Sverlova and Gural, 2022).

The aim of the study is to create models of the spatial distribution of alien species of terrestrial mollusks in Eastern Europe under current climate conditions. To achieve the goal, the following tasks were solved in the work: (1) assessment of the risk of dispersal of the species of mollusks under study in the designated area using ecological modeling methods (SDM); (2) assessment of the degree of overlap of potential ranges within the study region; (3) assessment of the suitability of territories for cohabitation of different species.

MATERIALS AND METHODS

The sources of data on the species finds were the author's field collections; the malacological collection of the Zoological Institute of the Russian Academy of Sciences and the Zoological Museum of Moscow State University; the catalog of the State Natural History Museum of the National Academy of Sciences of Ukraine (Gural-Sverlova and Gural, 2020); published sources (see Table 1); and datasets hosted by GBIF—Global Biodiversity Information Facility (DOI: 10.15468/qxy4mc; 10.15468/kllkyl; 10.15468/bmk3ab; 10.15468/qn6223; 10.15468/pnkuwh; 10.15468/fsreqb; 10.15468/4f0bmt).

Since the data were obtained from different sources, in some cases, owing to the close location of the points of finds, the distribution of the data may be distorted because of the unevenness of their collection (Guisan and Zimmermann, 2000). To avoid this, a procedure of spatial rarefaction of the points of discovery of each species was carried out using the spThin package in the R environment (Aiello-Lammens et al., 2015). Depending on the initial distribution of points, the thinning distance was 5–10 km (Petrosyan et al., 2023). Random background points, so-called pseudo-absence points in the model training domain, were generated as absence points (Guisan et al., 2017; Petrosyan et al., 2023). The study area included the European part of Russia and adjacent territories from 66° N to 40° N, from 20° E to 60° E, including native ranges of mollusks.

The initial set of predictors included 19 bioclimatic variables from the WorldClim set 2.1 with a resolution of 2.5 arcmin (WorldClim.org) (Fick and Hijman, 2017), land cover/land use type, and enhanced vegetation index (EVI). Land cover type (land use) and EVI data are taken from the public domain earthexplorer.usgs.gov and are raster layers created from MODIS (Moderate Resolution Imaging Spectroradiometer) satellite images. Land cover types are identified in accordance with the classification of the International Geosphere-Biosphere Programme (Friedl et al., 2010).

The selection of predictors for the models took place in two stages. Initially, on the basis of the calculation of the VIF (variance inflation factor) from the initial set of bioclimatic, eight variables were selected

Table 1. Number of points of finds with indication of native range of species

Species and its native range	Number of points in the dataset						Published sources and DOI of GBIF datasets
	author's collections	literature	collection of the Museum of Moscow State University	collection of ZIN RAS	GBIF	total	
A. arbustorum NW, C Europe	3	47	6	17	177	250	Balashev and Baidashnikov, 2012; Kotsur, 2013; Ostrovsky, 2016; Mukhanov and Lisitsyn, 2017; Bondareva et al., 2020; Gural-Sverlova and Gural, 2020; Zemoglyadchuk, 2020; Egorov, 2021; 10.15468/qxy4mc; 10.15468/kllkyl; 10.15468/bmk3ab; 10.15468/qn6223
B. cylindrica Crimea	30	45	8	15	4	102	Kramarenko and Sverlova, 2001; Sverlova and Gural, 2007; Vychalkovskaya, 2008; Rabchuk and Zemoglyadchuk, 2011; Kramarenko and Dovgal, 2014; Balashov et al., 2018a; Gural-Sverlova et al., 2018; Khailenko, 2018; Zhukov et al., 2019; Kovalenko, 2019; 10.15468/pnkuwh
C. vindobonensis C, SE Europe, Caucasus, Crimea	18	121	10	68	2	219	Gural-Sverlova and Gural, 2020; Shikov, 2023; 10.15468/fsreqb
H. ravergiensis Caucasus	33	9	8	80	0	130	Gural-Sverlova and Timoshenko, 2012; Balashov et al., 2018b; Gural-Sverlova and Gural, 2020; Ostrovsky, 2022
H. lucorum S Europe, Crimea, Caucasus	15	19	15	39	0	88	Gural-Sverlova and Gural, 2020
H. pomatia C, SE Europe	16	91	14	25	16	162	Stoyko and Bulavkina, 2008; Sachkova, 2009; Balashev and Baidashnikov, 2010; Balashev et al., 2013; Kotsur, 2013, 2015; Shikov, 2016; Snegin and Artemchuk, 2017; Aleksanov et al., 2019; Gural-Sverlova and Gural, 2020; 10.15468/qxy4mc; 10.15468/bmk3ab; 10.15468/kllkyl; 10.15468/4f0bmt
M. cartusiana S Europe, Crimea, Caucasus	14	41	13	27	0	95	Gural-Sverlova and Gural, 2020
X. derbentina Caucasus, Crimea, Asia Minor	59	107	25	142	1	334	Balashev and Baidashnikov, 2012; Gural-Sverlova and Gural, 2017; Balashov et al., 2018a; Gural-Sverlova et al., 2018; Gural-Sverlova and Gural, 2020; 10.15468/pnkuwh
X. krynickii Caucasus, Crimea, Asia Minor	8	35	12	23	2	80	Gural-Sverlova and Gural, 2020; 10.15468/pnkuwh

Table 2. Variables included in the final predictor sets

Variable	Description, VIF value for bioclimatic variables
BIO1	Average annual temperature, VIF = 4.73
BIO2	Average daily temperature range, VIF = 1.94
BIO4	Seasonal temperature, VIF = 3.14
BIO8	Average temperature of the wettest quarter, VIF = 1.49
BIO9	Average temperature of the driest quarter, VIF = 4.45
BIO15	Variation coefficient of precipitation, VIF = 1.64
BIO18	Precipitation of the warmest quarter, VIF = 5.42
BIO19	Precipitation of the coldest quarter, VIF = 2.27
EVI	Extended Vegetation Index
LU1	Evergreen coniferous forest. Evergreen coniferous trees predominate (forest canopy >2 m). Tree cover >60%
LU4	Broad-leaved forests. Broad-leaved trees predominate (forest canopy >2 m). Tree cover >60%
LU5	Mixed forests. There is no predominance of either deciduous or evergreen conifers (40–60% of each tree type, forest canopy >2 m, tree cover >60%)
LU8	Tree cover 30–60% (canopy >2 m)
LU9	Tree cover 10–30% (canopy >2 m)
LU10	Herbaceous annuals predominate (<2 m)
LU11	Permanently flooded lands with 30–60% water cover and >10% vegetation cover
LU12	At least 60% of the area is occupied by arable land
LU13	At least 30% of the area of impervious surface, including building materials, asphalt, and vehicles
LU14	Mosaic of small household plots with 40–60% woody, shrubby, or herbaceous vegetation
LU16	At least 60% without vegetation (sand, rocks, soil), areas with vegetation less than 10%

for modeling (Table 2). Bioclimatic variables were excluded using a VIF threshold of 10.

Next, the relative contribution of each variable was assessed on the basis of the results of the correlation analysis using Pearson's coefficient (Thuiller et al., 2009). This procedure was carried out on a set of 8 bioclimatic predictors, EVI, and 16 land cover types. As a result, a final set of predictors was formed for each species, each of which had a significant contribution to the model. Of the 16 land cover types, 11 variables were included in the final sets of predictors (see Table 2). The relative contribution of variables from the final sets was calculated by averaging over all models.

Three methods were used for modeling: Generalized Linear Model (GLM), Random Forest (RF), and Maximum Entropy (MaxEnt). In constructing the models, spatial cross-validation of the sample by the regrouping method (k-fold cross validation) was used to obtain independent training data sets and test the suitability of the models. The original sample was divided into training (75%) and test (25%). The quality of fitness of the models was assessed using the area-under-the-curve (AUC) and TSS statistics. On the basis of the models obtained, an ensemble forecast was created according to the weighted results based on the models (GLM, RF, MaxEnt).

For each species, the entire study area was divided into habitable and uninhabitable areas. The threshold value of area suitability was calculated for each species using the method of maximizing the sum of sensitivity and specificity (maxSSS) (Liu et al., 2016; Guisan et al., 2017; Petrosyan et al., 2023). As a result, binary maps of potential ranges were obtained with the division of the territory into two values: territory suitable for habitation (1) and unsuitable (0).

In addition to obtaining predictions for each species individually, sections of the study area that were potentially suitable for the joint settlement of several

Table 3. Evaluation of the quality of model forecasts

	GLM		RF		MaxEnt		Ensemble		
	AUC	TSS	AUC	TSS	AUC	TSS	AUC	TSS	threshold
A. arbustorum	0.92	0.77	0.97	0.84	0.95	0.82	0.94	0.81	0.31
B. cylindrica	0.85	0.70	0.99	0.92	0.98	0.91	0.94	0.84	0.63
C. vindobonensis	0.92	0.75	0.95	0.80	0.93	0.75	0.93	0.77	0.42
H. ravergiensis	0.92	0.78	0.93	0.77	0.92	0.77	0.92	0.77	0.42
H. lucorum	0.94	0.80	0.96	0.84	0.95	0.84	0.95	0.82	0.39
H. pomatia	0.90	0.72	0.93	0.76	0.92	0.73	0.92	0.72	0.35
M. cartusiana	0.92	0.78	0.95	0.82	0.93	0.82	0.93	0.81	0.31
X. derbentina	0.93	0.76	0.96	0.81	0.95	0.82	0.94	0.80	0.42
X. krynickii	0.94	0.82	0.97	0.92	0.97	0.91	0.96	0.88	0.39

species were also identified. That is, these are places that are most suitable not only for one alien species, but for several at once. To do this, a map was obtained by summing binary rasters, reflecting the number of species potentially capable of populating the study area.

The similarity of suitable areas of the studied species was assessed on the basis of the I-statistics (index) (Warren et al., 2008) in the R package dismo (Hijmans et al., 2022). The index value ranges from 0 (no overlap at all) to 1 (complete overlap). The rasters obtained as a result of the simulation were used to calculate the I-statistics. For species with a pairwise range overlap value ≥0.5, maps of the potential distribution of a pair of alien species in the study area were created.

Modeling, the main part of the preparatory work with data, and assessment of the quality of predictive models were carried out in the R environment version 4.1.2 (R Core Team, 2021) using the following packages: sdm (Naimi and Araújo, 2016), usdm (Naimi et al., 2014), dismo (Hijmans et al., 2022), sp (Pebesma and Bivand, 2005; Bivand et al., 2013), raster (Hijmans, 2022), rgdal (Bivand et al., 2022), rgeos (Bivand and Rundel, 2021). Processing of raster images and summarization of rasters, as well as preparation of final maps and calculation of area of territories, were performed in ArcGIS version 10.7 (https://www.esri.com).

RESULTS

The models obtained, including ensemble ones, are characterized by high predictive ability, as evidenced by the AUC and TSS values (Table 3).

The final sets of predictors that were used for modeling included from 14 (for *M. cartusiana*, *X. krynickii*) to 7 variables (for *X. derbentina*). The relative contribution of each predictor is presented in Table 4. For all mollusk species, the average annual temperature (bio 1) was found to be significant. Moreover, for xerophilic mollusks of the genus *Xeropicta* and xeromesophilic species *C. vindobonensis*, the contribution of this variable to the forecast was the highest. And for the meso-hygrophilic species *A. arbustorum*, the most significant were the average daily temperature range (bio 2) and seasonal temperature (bio 4). This species differs from others in the absence of significant predictors characterizing precipitation. But the average temperature of the driest quarter (bio 9) makes some contribution to the forecast; that is, the species depends on a certain combination of temperature and humidity.

For the remaining mollusks, precipitation from the warmest quarter (bio 18) and, in some cases, precipitation from the coldest quarter (bio 19) were included in the predictor sets on the basis of their significant contribution to the prediction. Among the land use types, mixed forests (LU5) and urbanized areas (LU13) turned out to be significant for almost all species. The vegetation index EVI was found to be significant only for three species: *B. cylindrica*, *H. ravergiensis*, and *H. lucorum*. The remaining predictors contributed relatively equally to the prediction.

The results of the modeling are presented in the form of maps of potentially habitable areas (Fig. 1). Within the boundaries of the region of study, the distribution of mollusks is possible in areas adjacent to native ranges, as well as in individual areas scattered throughout the study area.

From the estimates obtained, it follows that mollusks with a wider natural range have a larger area of potential distribution (Table 5). These species include

Table 4. Relative contribution of variables (%) based on correlation metrics

	A. arbustorum	*B. cylindrica*	*C. vindobonensis*	*H. ravergiensis*	*H. lucorum*	*H. pomatia*	*M. cartusiana*	*X. derbentina*	*X. krynickii*
bio1	4.5*	16.8*	27.9*	9.3*	10.8*	16.1*	10.8*	33.7*	34.1*
bio2	29.7*	14.4*	10.8*		0.6	9.8*	4.2*		2.6
bio4	27.8*	3.7*		3	11.6*		2.8	8.7*	1.8
bio8			7.0*		10.1*		2.4*		
bio9	4.7*	8.5*			6.5*		5.4*		3.5*
bio15	1.3	3.4*		1.4			1.6		6.7*
bio18		6.6*	9.5*	6.2*	5.1*	8.5*	4.9*	9.9*	3.4*
bio19		7.9*		5*			0.8		2.2*
EVI	0.6	3.6*		5.1*	3.1*		0.8		
LU1				7.2*	7.8*		8.7*		
LU4	2*		1.4						
LU5	4	9.9*	12*	16.5*	6.1*	5.4*	3.7*	16.4*	13.7*
LU8	2.6	0.9						0.5	2.2*
LU9						4.1*			
LU10		1.8*		4.8*			0.7	2.9	2.4*
LU11		1.8*				0.6			1.5
LU12	2.9		3.2*		2.9*	2*	0.7		6.3*
LU13	14.0*	11.5*	11.8*	21.2*	18.2*	16.8*	12.2*	10.8*	
LU14	0.8	3.3*							
LU16									0.8

H. pomatia, *A. arbustorum*, *X. derbentina*, *C. vindobonensis*, and *M. cartusiana*.

The potential ranges of species overlap to varying degrees (Table 6). Maps of overlapping potential ranges of species (I ≥ 0.45) are presented in the Appendix. Propagation of *A. arbustorum* goes from the northwest to the south. *H. pomatia* spreads from west to east. From the Baltics to the Podolsk Upland, the ranges of species overlap significantly. Overlap of *A. arbustorum* with other species is not so significant. *H. pomatia* has a range overlap with the southern European species *C. vindobonensis*. In addition to the western part of the region of study, these species have common areas of potential distribution from the Azov region to the Central Russian Upland.

Table 5. Area of potentially habitable territory

Species	Area, sq. km
A. arbustorum	1 170 865
B. cylindrica	210 956
C. vindobonensis	982 045
H. ravergiensis	645 009
H. lucorum	628 528
H. pomatia	1 383 689
M. cartusiana	946 436
X. derbentina	988 462
X. krynickii	559 092

All other species are distributed from south to north. The overlap of potential ranges among these species is expressed to a greater extent. This is expected given their common native ranges (the Caucasus, the Black Sea region, southern Europe, Asia Minor). In particular, the greatest number of pairwise "coincidences" with other mollusks was found in *C. vindobonensis*, *M. cartusiana*, *X. derbentina*, and *X. krynickii*. Areas of overlapping potential ranges are mainly located in the Caucasus and the Black Sea region, as

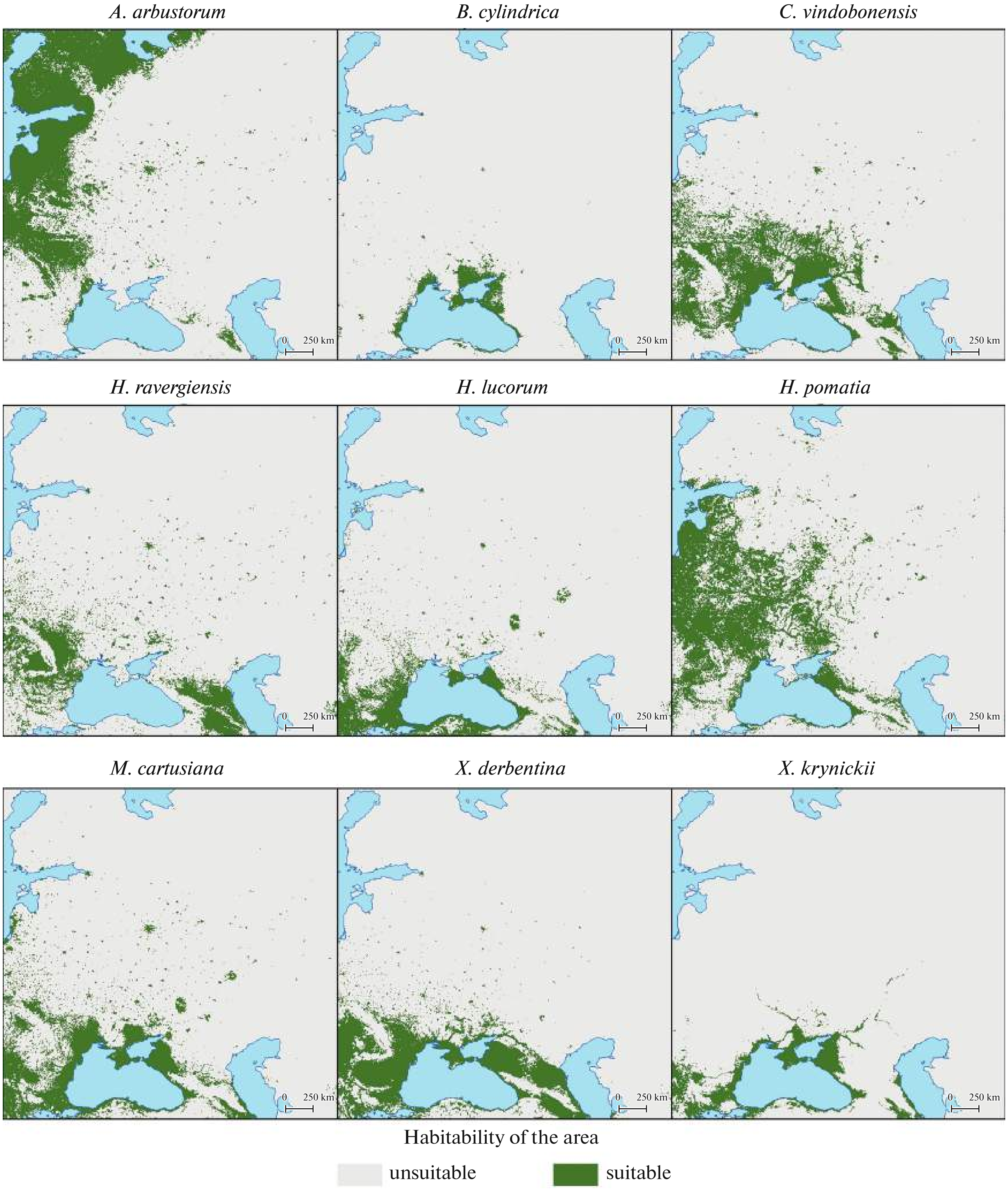

Fig. 1. Suitability of the territory for habitation of the mollusk species under study.

Table 6. Values of I-statistics for assessing range overlap

	A. arbustorum	*B. cylindrica*	*C. vindobonensis*	*H. ravergiensis*	*H. lucorum*	*H. pomatia*	*M. cartusiana*	*X. derbentina*	*X. krynickii*
A. arbustorum	1								
B. cylindrica	0.08	1							
C. vindobonensis	0.24	0.35	1						
H. ravergiensis	0.20	0.15	0.52	1					
H. lucorum	0.08	0.35	0.30	0.34	1				
H. pomatia	0.48	0.25	0.57	0.39	0.25	1			
M. cartusiana	0.17	0.45	0.56	0.46	0.67	0.41	1		
X. derbentina	0.10	0.40	0.56	0.62	0.59	0.37	0.69	1	
X. krynickii	0.02	0.51	0.31	0.20	0.50	0.23	0.61	0.53	1

well as in the Lower Danube Lowland and the Balkans.

The smallest area of potential distribution was found for the endemic species of Crimea and the Northern Black Sea region, *B. cylindrica*. This species has an overlapping range with *M. cartusiana* and *X. krynickii*.

In the study area, sections suitable for habitation of different numbers of species were identified (Fig. 2).

Figure 2 shows that the study area is dominated by areas suitable for the habitation of one or two species of mollusks. A significant portion of this territory is located in the northwest of the region of study. This is a range of *A. arbustorum*, which overlaps the least with the ranges of the other species studied. The areas suitable for the habitation of the maximum number of species are located in the Black Sea region, the Azov region, the Caucasus, the Podolsk Upland, and the Middle Danube and Lower Danube Lowlands, and are also scattered in the form of small areas confined to the lands of populated areas. At the same time, for all species, the eastern part of the region of study turned out to be less suitable or completely unsuitable for habitation.

DISCUSSION

The temperature and humidity of the environment are key ecological factors for terrestrial mollusks (Riddle, 1983; Likharev and Rammelmeyer, 1952). A study of the diversity of mollusk communities across a latitudinal gradient in northeastern Russia showed that climatic variables are the main factors influencing the suitability of a territory for terrestrial mollusks in the boreal zone (Horsák et al., 2013).

This study examines the potential spread of the southern species northward and the spread of the northwestern species (*A. arbustorum*) to the south. It can be expected that the distribution of terrestrial mollusks from one climatic zone to another is primarily limited by climatic conditions. The modeling results indicate that climate variables such as temperature and precipitation made a significant contribution to the forecast. The studied species of mollusks can be divided into three ecological groups depending on their relationship to the temperature and humidity of the habitat. In one combination or another, all sets of predictors contain variables that characterize exclusively temperature variables of the environment (bio1, bio2, bio4). Their contribution exceeds the contribution of all other variables for all species. At the same time, for the northwestern mesohygrophilic mollusk *A. arbustorum*, the main contribution to the forecast was made by variables characterizing temperature fluctuations, and not by the average annual temperature, as for the other species. Most of the studied mollusks are distributed from southern regions and are adapted to arid conditions (Kramarenko, 1997; Staikou, 1999; Dittbrenner et al., 2009). Adaptations of xerophilic and xeromesophilic mollusks allow them to accumulate moisture and withstand high insolation and overheating (Staikou et al., 2024). It can be assumed that lower temperatures will have a negative impact on such species. This may be explained to some extent by the presence of cryoprotective compounds in the tissues of mollusks, as shown in a study of the biochemical composition of the hemolymph of a mesophilic mollusk *H. pomatia* in a state of hibernation (Nicolai et al., 2011). Interestingly, this species,

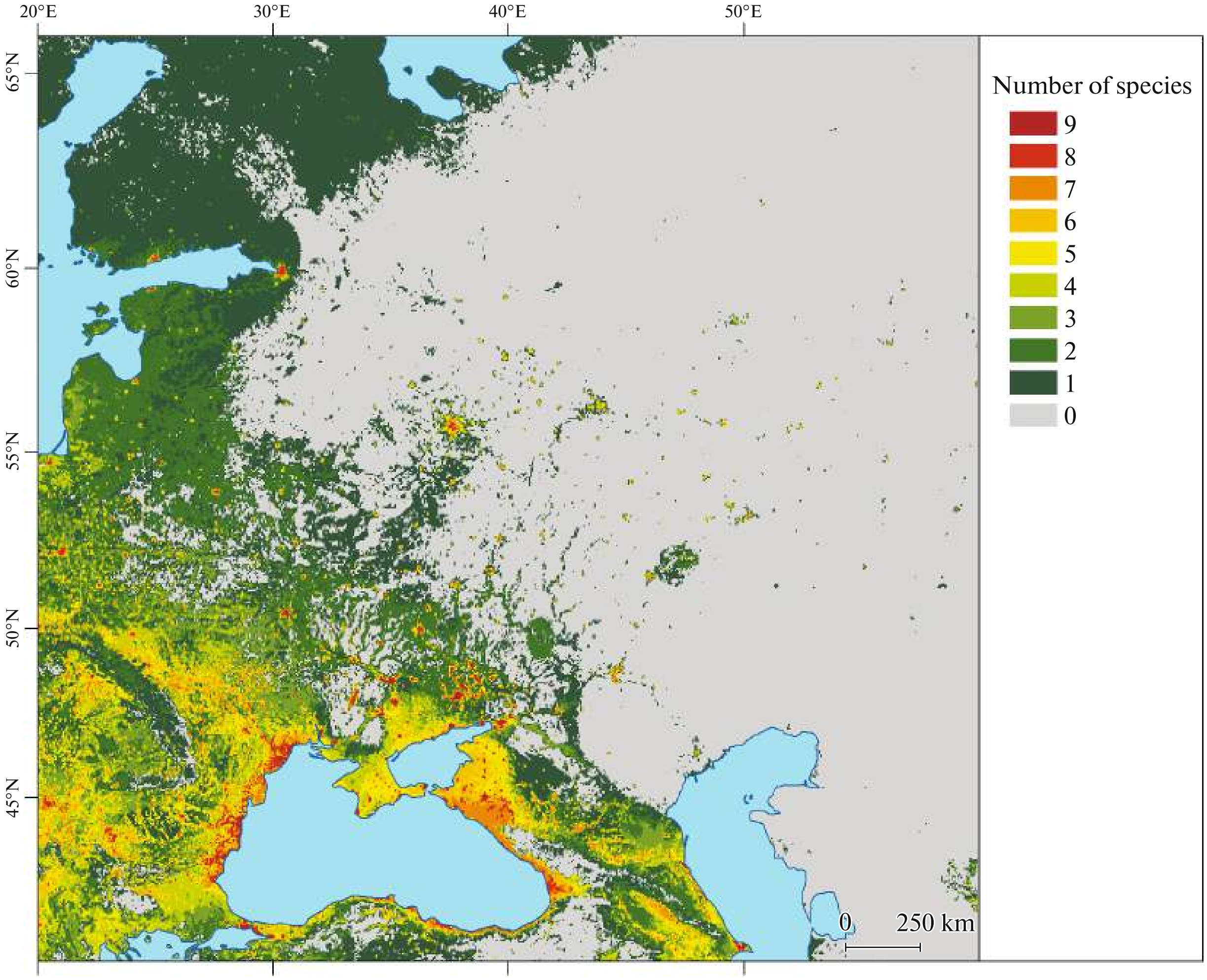

Fig. 2. Suitability of the territory for habitation of different numbers of species under study.

according to the forecast obtained, has the largest area of potential distribution.

Total annual precipitation (bio12) had no effect on species distribution. But variables that reflect the relationship between temperature and humidity (bio9, bio18, bio19) were found to be important. For all species except *A. arbustorum*, a significant contribution to the forecast was made by the bio18 variable—precipitation of the warmest quarter, which can be explained by the origin of these species from southern climatic zones.

In addition to climatic factors, variables characterizing the type of land cover were used as predictors. These variables were represented as raster binary layers. The data contained in the pixel values of such a layer reflect the result of the classification of the earth's surface, which took into account the main recognizable land surfaces (Sulla-Menashe et al., 2019). The original names of land cover types (Friedl et al., 2010) do not literally mean one or another type of biome. Thus, variables LU8 and LU9 are designated in the original classification as "Woody savanna" and "Savanna," but more accurately these land cover types can be designated as sparse forest (see Table 2). Moreover, areas with this type of cover are present in different climatic zones. Relatively high contributions to most models were made by variables containing data on the distribution of anthropogenically modified areas (LU13) and mixed woody vegetation (LU5). The contribution of the variable "mixed forest" is higher for steppe species: their distribution is associated with the absence of forest cover. The association of the grape snail with forest biotopes also affected the forecast: forested areas in the forest steppe were shown to be suitable for the habitation of the species.

Anthropogenically modified territories are suitable for habitation of all the studied invaders, which should be discussed separately. Often, owing to an unevenly surveyed territory, the points of discovery that are used to model the range are concentrated around populated areas, roads, and other similar objects (Lisovsky et al., 2020). However, in the present study, this circumstance was taken into account: at the stage of data preparation, spatial rarefaction of points was carried out. In the case of the species under study, their association with anthropogenically altered areas is apparently an ecological feature. It is known that alien species primarily successfully colonize urbanized landscapes, which can become a springboard for further expansion (Cadotte et al., 2017; Marques et al., 2020; Borden and Flory, 2021). Using the example of Central Europe, it has been shown that the malacofauna of cities has a significant invasive component (Horsák et al., 2016). It is important to note that all the species under study are common in their native ranges, which has long been known (Geyer, 1927; Likharev and Rammelmeyer, 1952; Shileiko, 1978). In their natural ranges, all the studied mollusks successfully colonized, in addition to natural biotopes, anthropogenically altered territories. Perhaps the most famous example is the grape snail. D. Geyer described the typical habitats of the species: gardens, parks, cemeteries, etc. It was also noted that the distribution of *H. pomatia* in Eastern Europe is associated with the introduction and cultivation of the species (Geyer, 1927). In this case, for *H. pomatia* and *C. vindobonensis*, a natural distribution in Europe from the Last Glacial Maximum refugium, presumably from the southeastern Carpathians, is shown (Korábek et al., 2022). However, our work considers only the distribution of species under current climate conditions.

Anthropochory and association with anthropogenically altered areas are described for *B. cylindrica*, *H. ravergiensis*, *M. cartusiana*, *X. derbentina*, and *X. krynickii* on the territory of Ukraine (Son, 2010; Gural-Sverlova and Gural, 2017, 2022; Zhukov et al., 2019). The distribution of Turkish snail *H. lucorum* in Central and Western Europe in the last decade has been limited to urbanized areas (Doležal, 2021). European species *A. arbustorum* in its native range it inhabits both flat and mountainous areas, and the mollusk exhibits wide morphological variability (Kleewein, 1999). Typical habitats in Central Europe for this species are ravines, meadows, and other moist biotopes, mainly with large-leaved vegetation (Geyer, 1927). On the territory of the secondary range, confinement of *A. arbustorum* to anthropogenically modified biotopes and gradual spread in populated areas, including large cities, were revealed (Shikov, 2016; Mukhanov and Lisitsyn, 2017; Egorov, 2021).

The overlapping zones of potential ranges, mostly include territories of natural ranges. Within the potential distribution, overlap is observed in the same areas that are most suitable for habitation by most of the studied invaders.

Considering the region of study as a whole (see Fig. 2), we can conclude that the more continental the climate on the territory, the fewer the number of mollusk species studied for which it is most suitable. This explains the “gray area” on the map in the eastern part. The territories that turned out to be suitable for habitation of all species are mainly located in the Black Sea region, the Azov region, the Caucasus, the Podolsk Upland, and the Middle Danube and Lower Danube lowlands. The Caucasus and the Black Sea region are characterized by high biodiversity, including the diversity of malacofauna (Likharev and Rammelmeyer, 1952; Walther et al., 2014). For most of the species under study, this area is part of the native range, but for *A. arbustorum* and *H. pomatia*, this is a potentially habitable area. In addition, owing to the confinement of the invaders to anthropogenic biotopes, the territories of populated areas are also suitable for habitation of most of the studied mollusks. Thus, in the northern and northeastern part of the potential range of *H. ravergiensis*, habitable areas are scattered pointwise owing to their proximity to populated areas. Overlapping potential ranges between pairs of these species occurs mainly either within the native ranges or in areas suitable for habitation by all species.

As an assumption, it can be noted that, when the species under study populate anthropogenically modified territories, in particular, the territories of populated areas, a negative effect on the local flora and fauna is unlikely. This assumption is due to the fact that the invaders, apparently, fill a certain “vacuum” in disturbed ecosystems (Alimov and Bogutskaya, 2004). The distribution of these species in natural ecosystems is also determined by biotic factors. For this reason, it is possible to propose stricter control over potential invaders on the territories shown in this work as the most suitable for their expansion. However, the assessment of the potential impact of alien species on the native biota requires additional research.

CONCLUSIONS

All species of terrestrial mollusks under study have the potential for further expansion to new territories under the current climate conditions. Modeling results confirmed the role of climate in the spread of alien terrestrial mollusks. In the eastern part of the region of study, current climatic conditions are not suitable for the habitat of the species under consideration. The confinement of alien mollusks to anthropogenic biotopes was quite clearly reflected in the modeling results. However, it is important to note that, although populated areas may serve as springboards for further invasion, the spread of the species into natural ecosystems in areas that do not have suitable climatic conditions is unlikely.

APPENDIX

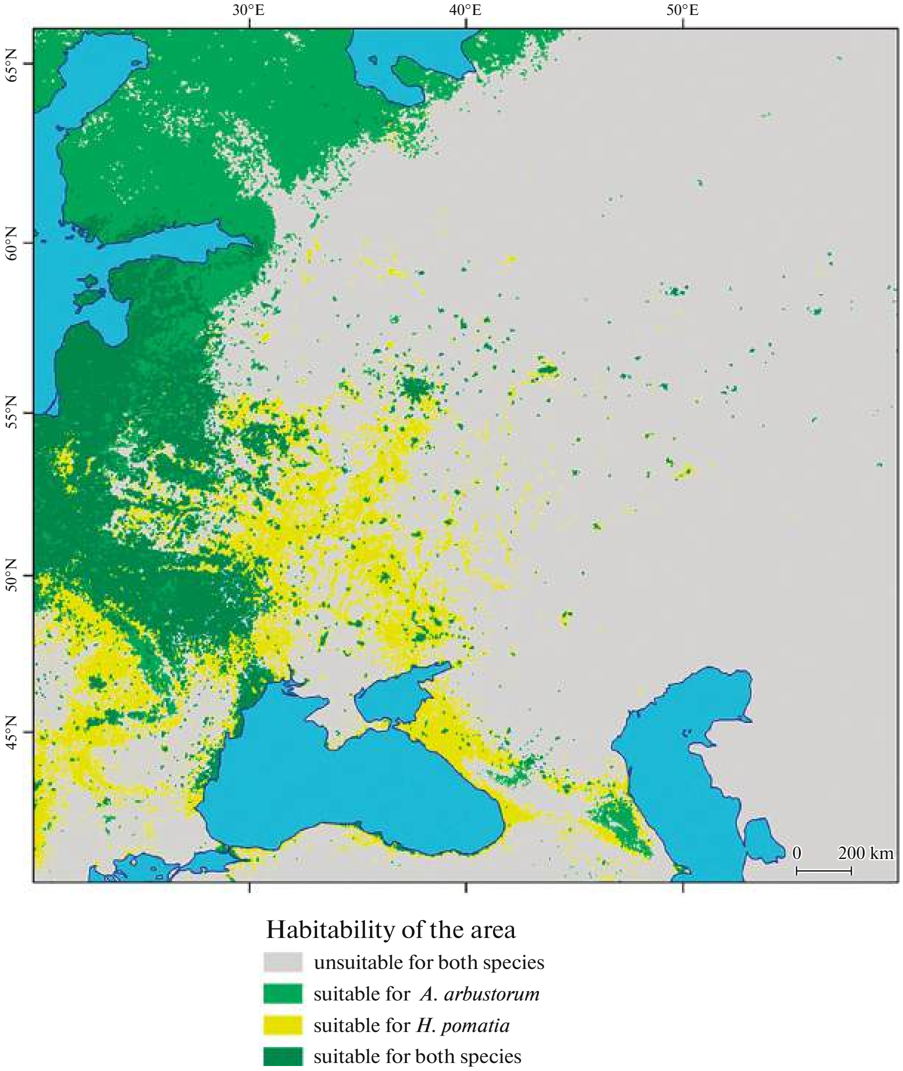

Fig. A1. Overlapping potential habitats of *H. pomatia* and *A. arbustorum*.

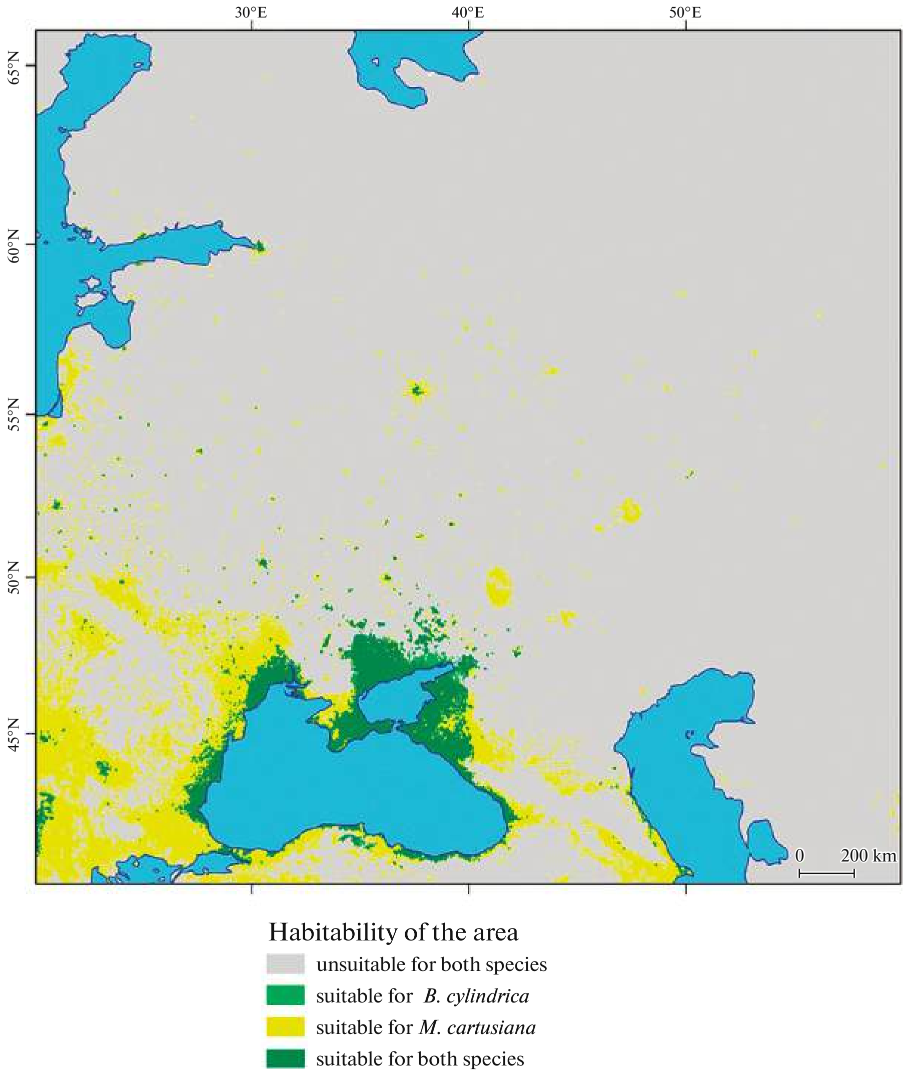

Fig. A2. Overlapping potential habitats of *B. cylindrica* and *M. cartusiana*.

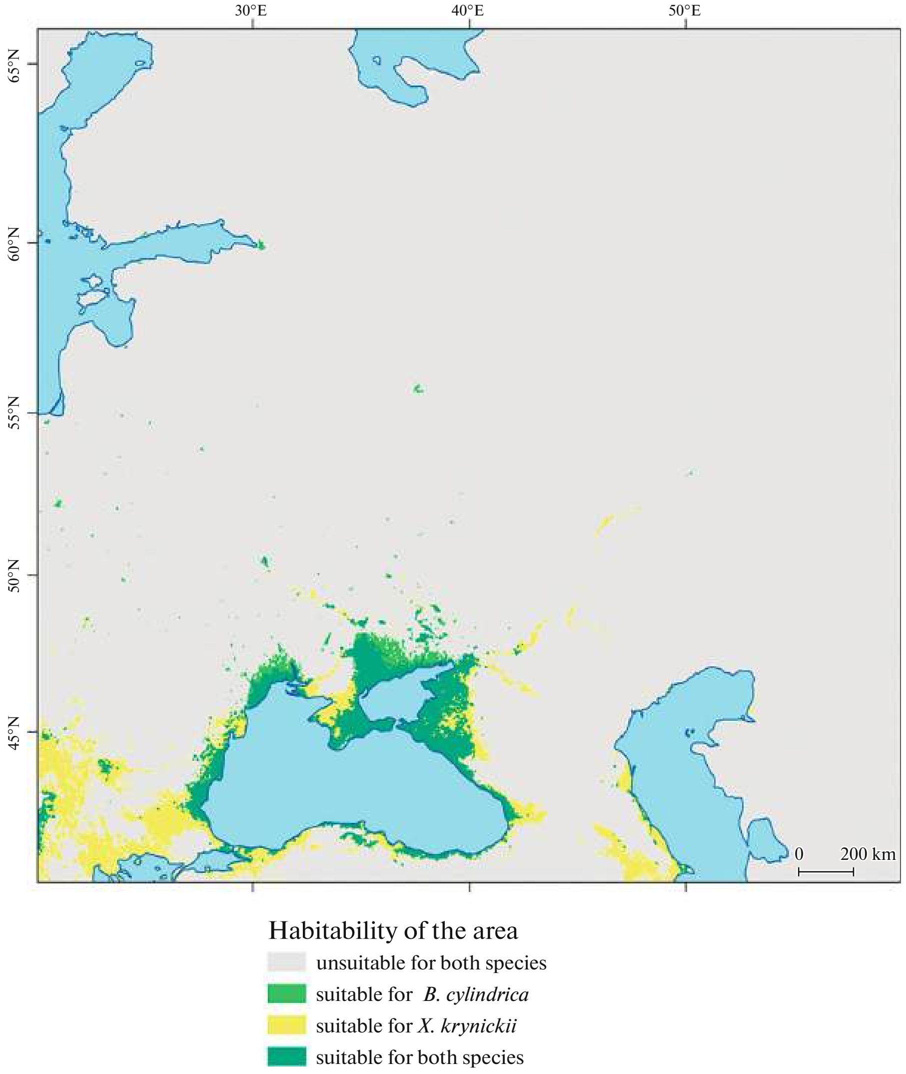

Fig. A3. Overlapping potential habitats of *B. cylindrica* and *X. krynickii*.

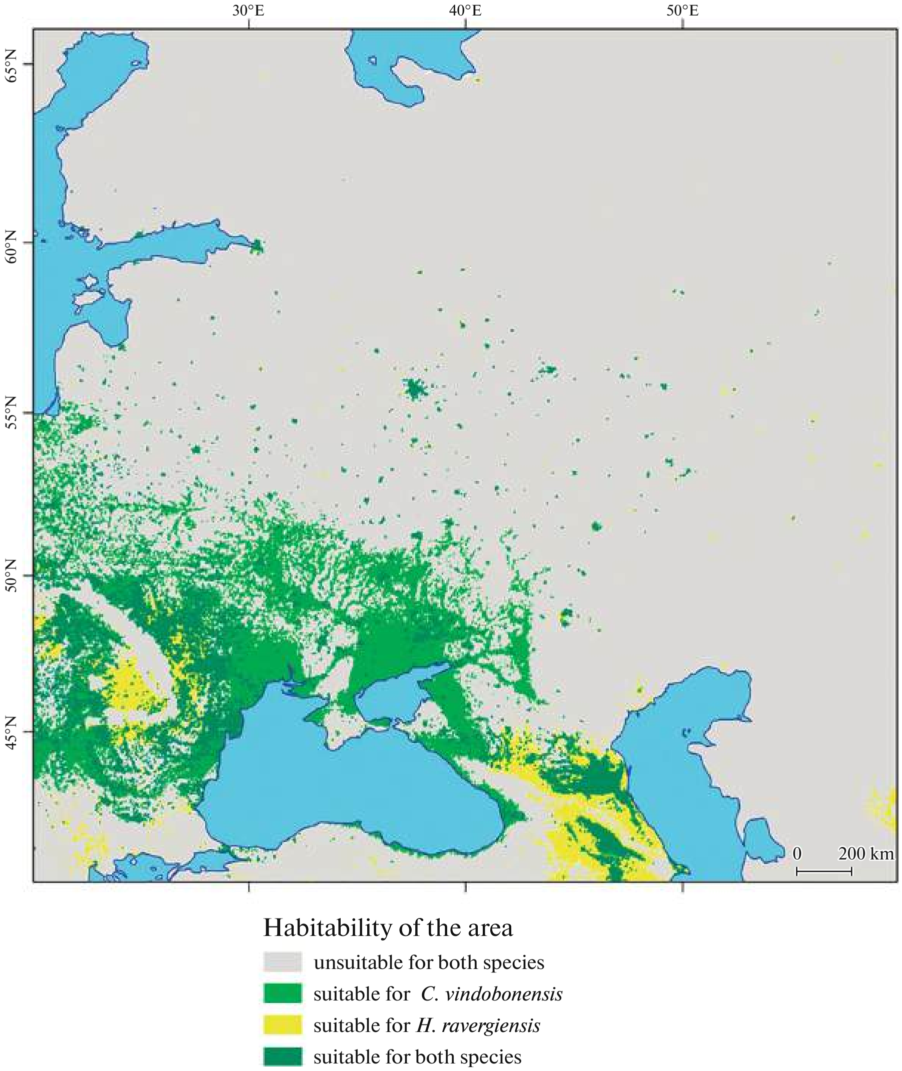

Fig. A4. Overlapping potential habitats of *C. vindobonensis* and *H. ravergiensis.*

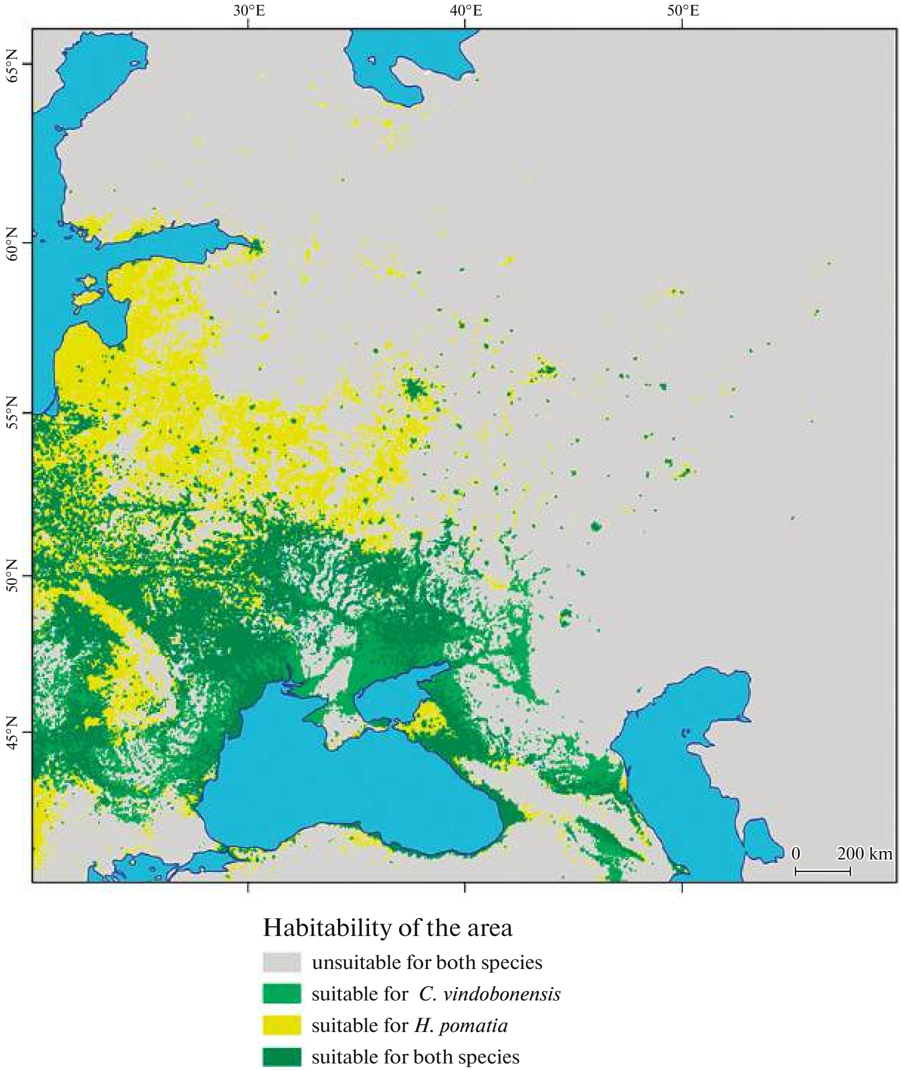

Fig. A5. Overlapping potential habitats of *C. vindobonensis* and *H. pomatia*.

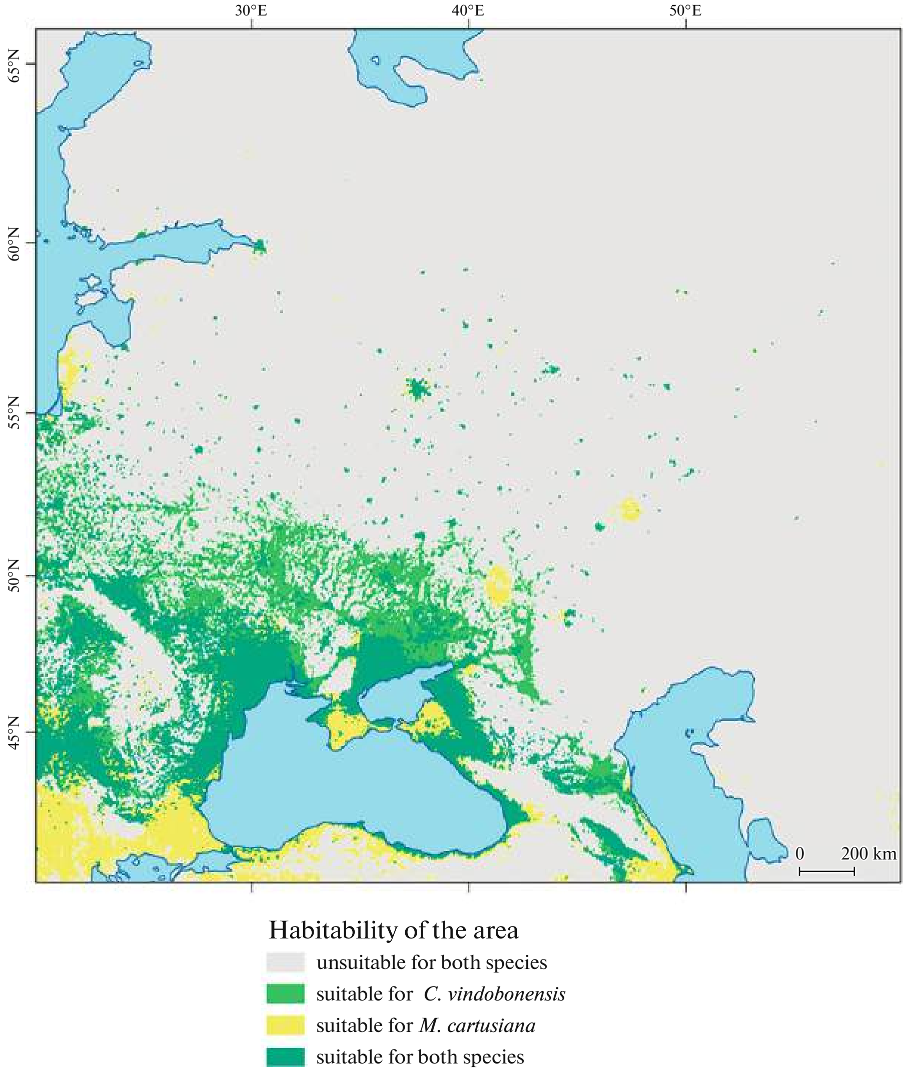

Fig. A6. Overlapping potential habitats of *C. vindobonensis* and *M. cartusiana*.

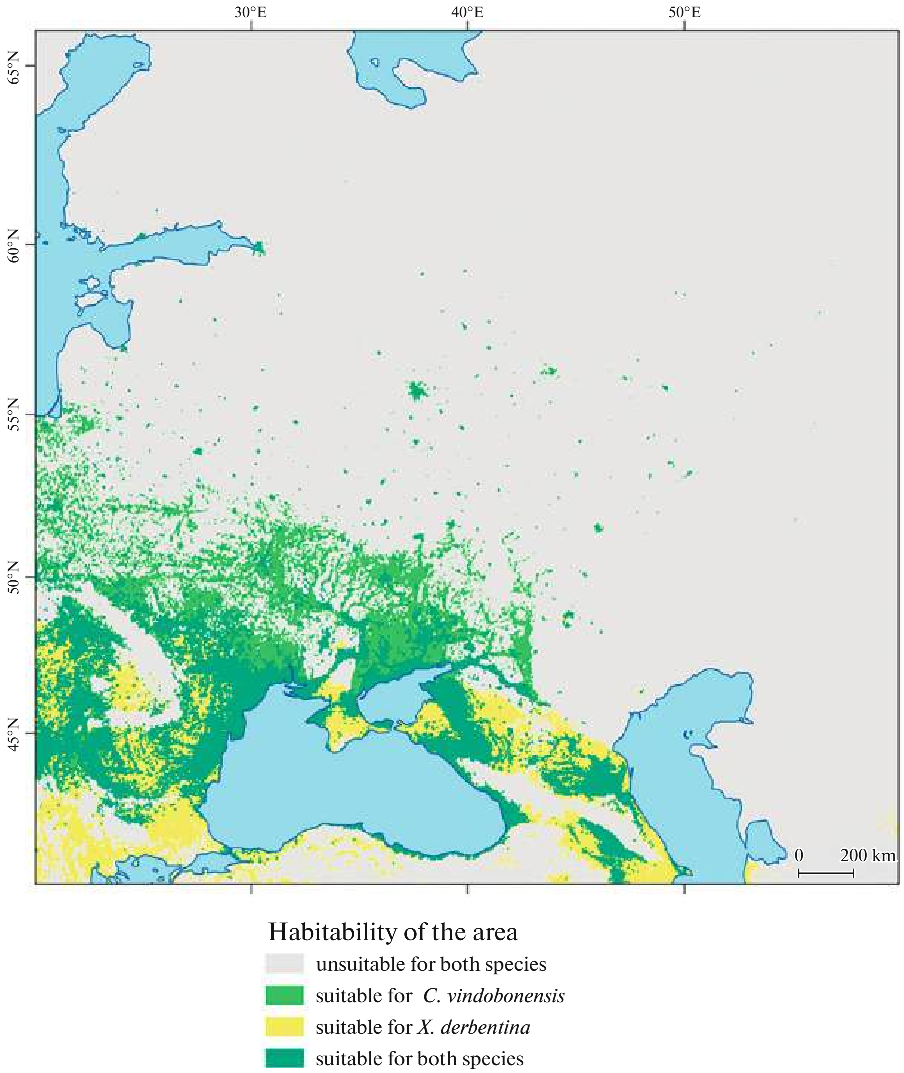

Fig. A7. Overlapping potential habitats of *C. vindobonensis* and *X. derbentina*.

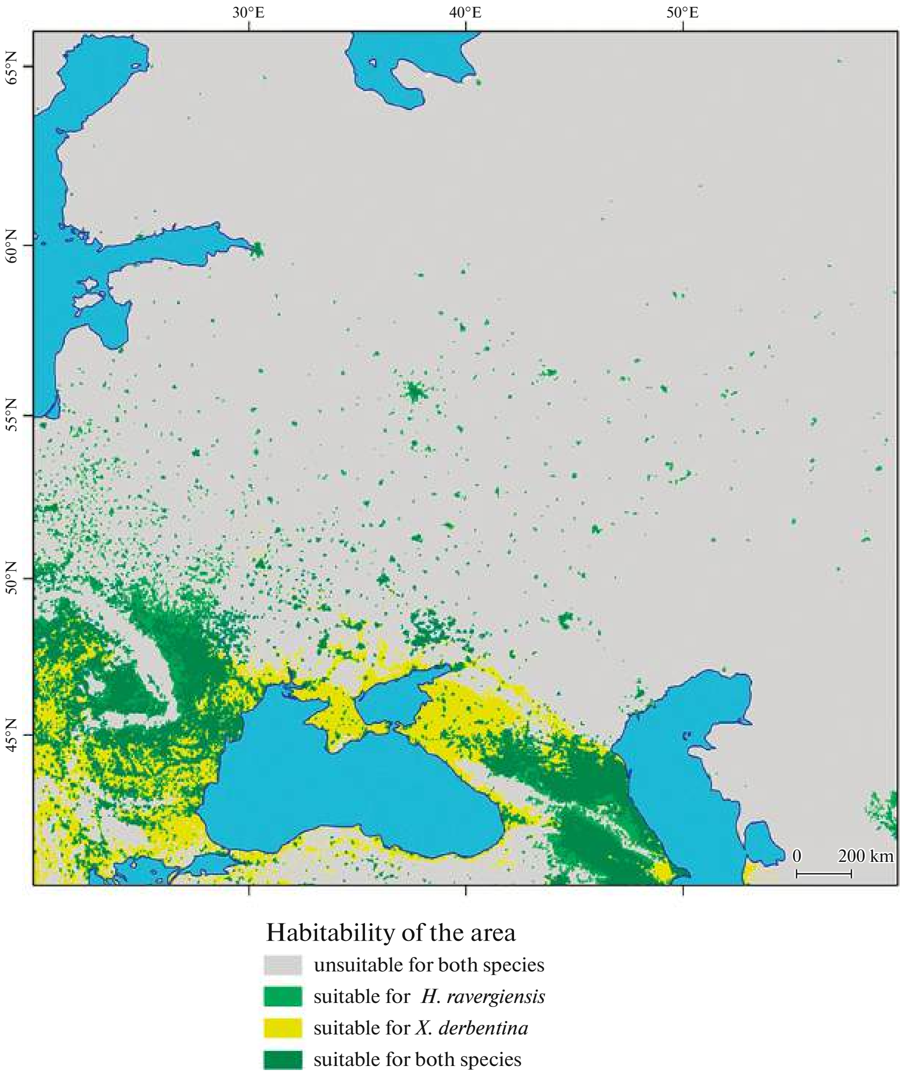

Fig. A8. Overlapping potential habitats of *H. ravergiensis* and *X. derbentina*.

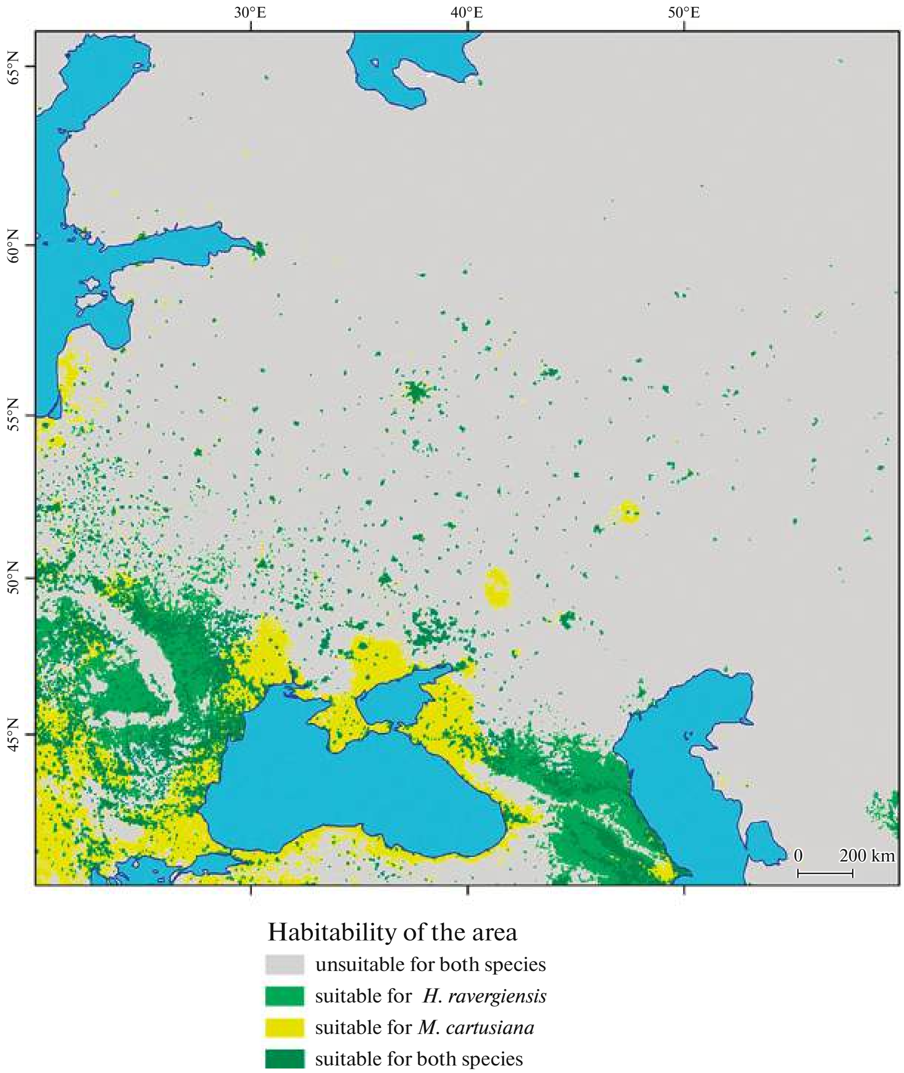

Fig. A9. Overlapping potential habitats of *H. ravergiensis* and *M. cartusiana*.

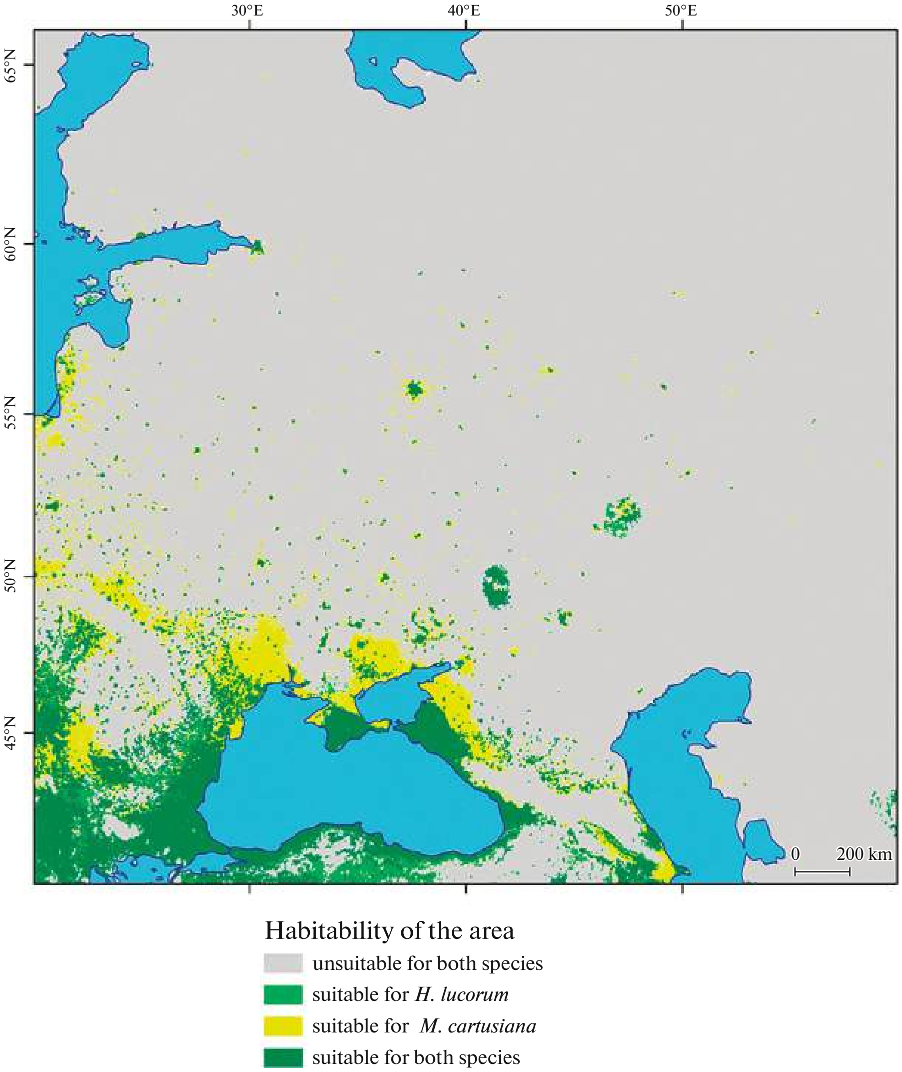

Fig. A10. Overlapping potential habitats of *M. cartusiana* and *H. lucorum*.

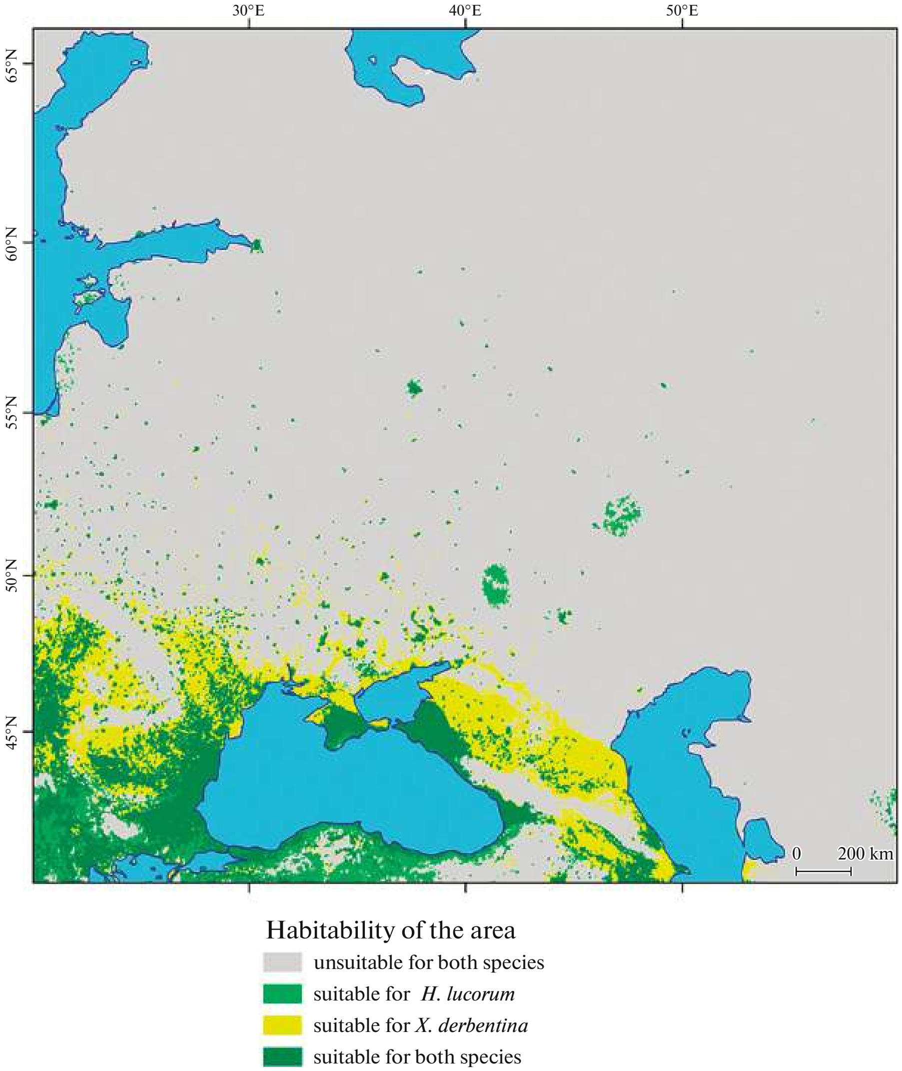

Fig. A11. Overlapping potential habitats of *X. derbentina* and *H. lucorum*.

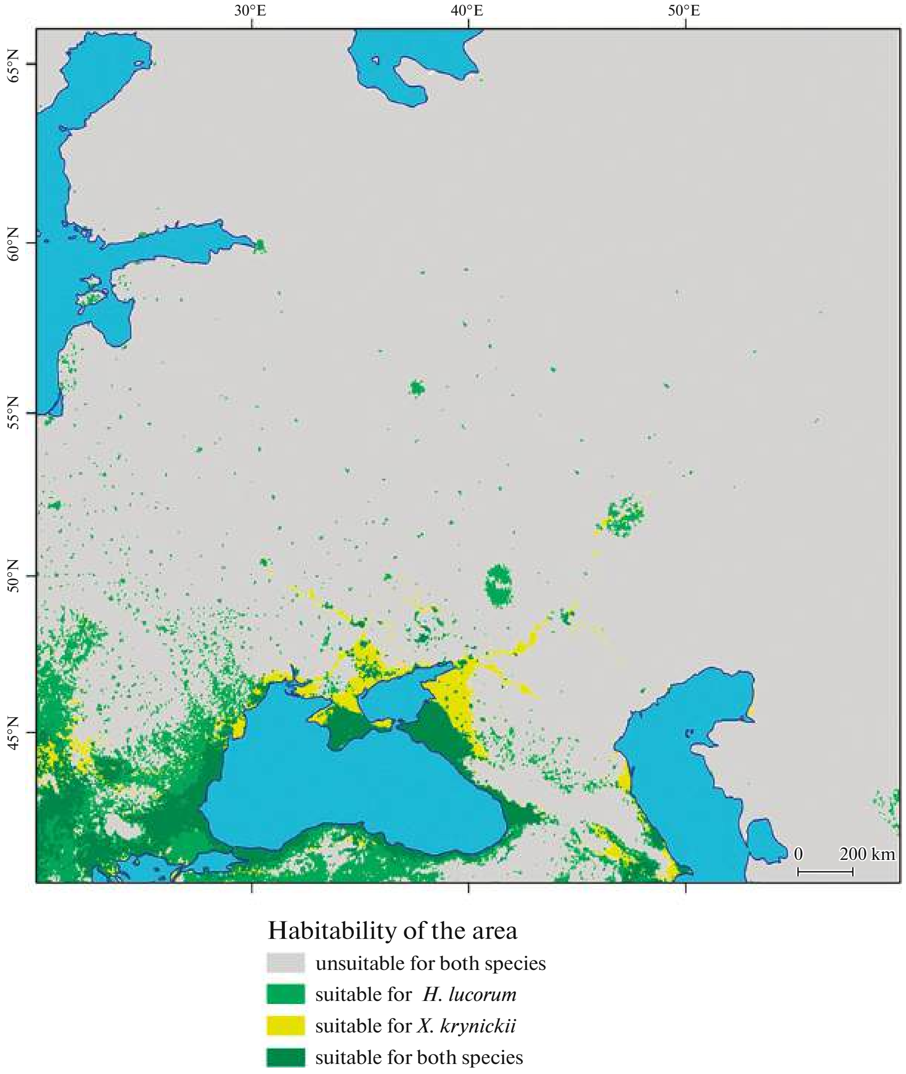

Fig. A12. Overlapping potential habitats of *X. krynickii* and *H. lucorum*.

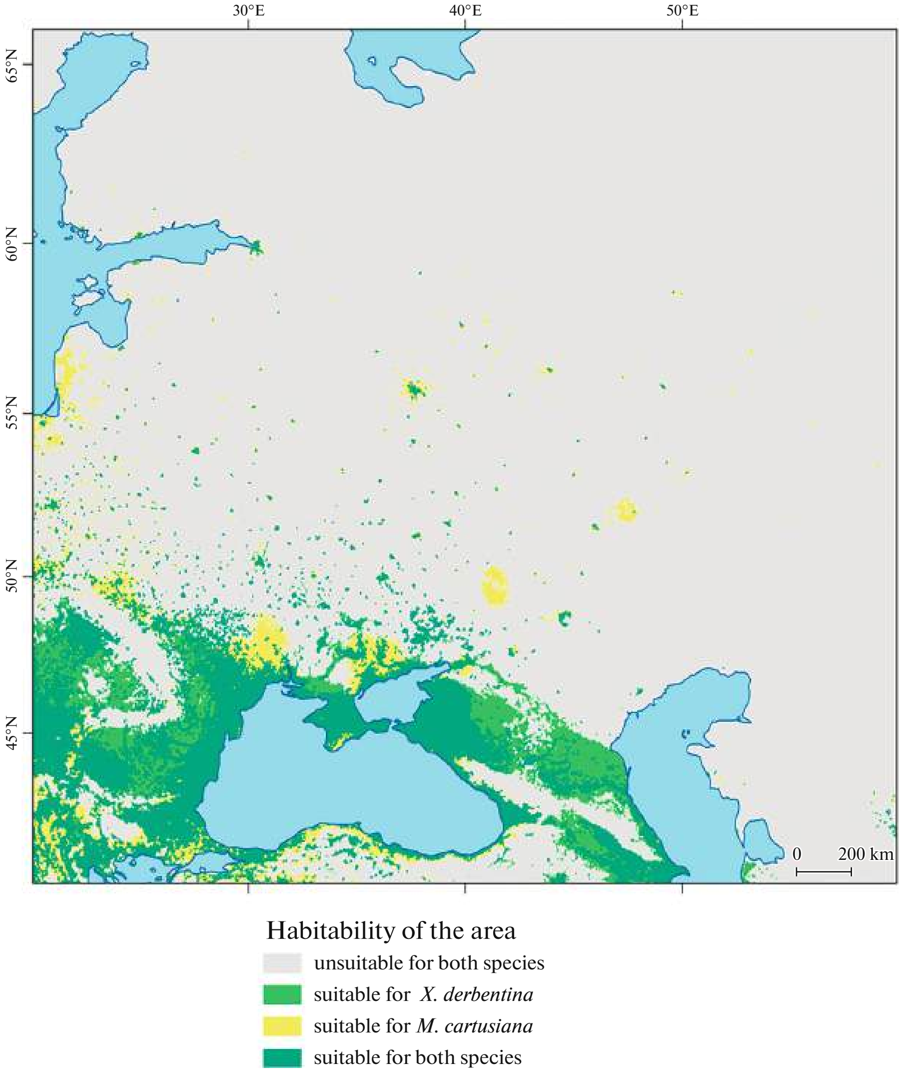

Fig. A13. Overlapping potential habitats of *M. cartusiana* and *X. derbentina*.

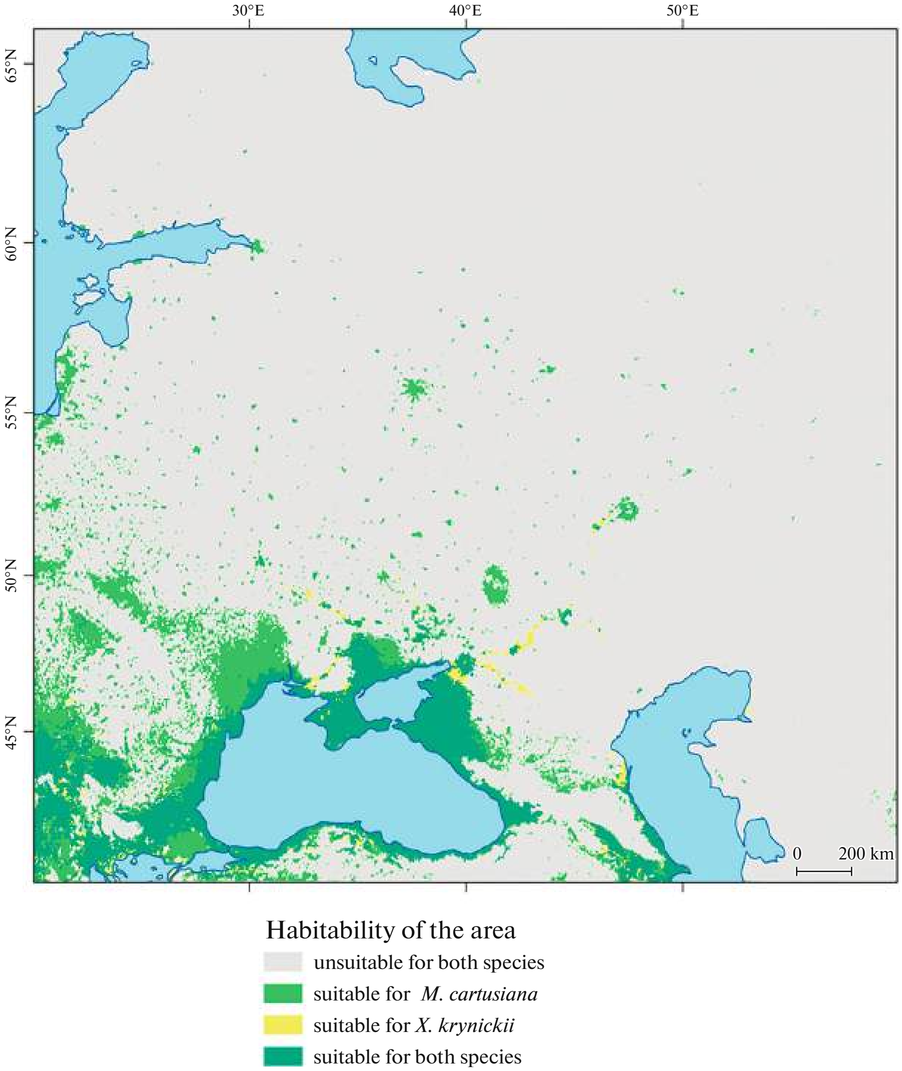

Fig. A14. Overlapping potential habitats of *M. cartusiana* and *X. krynickii*.

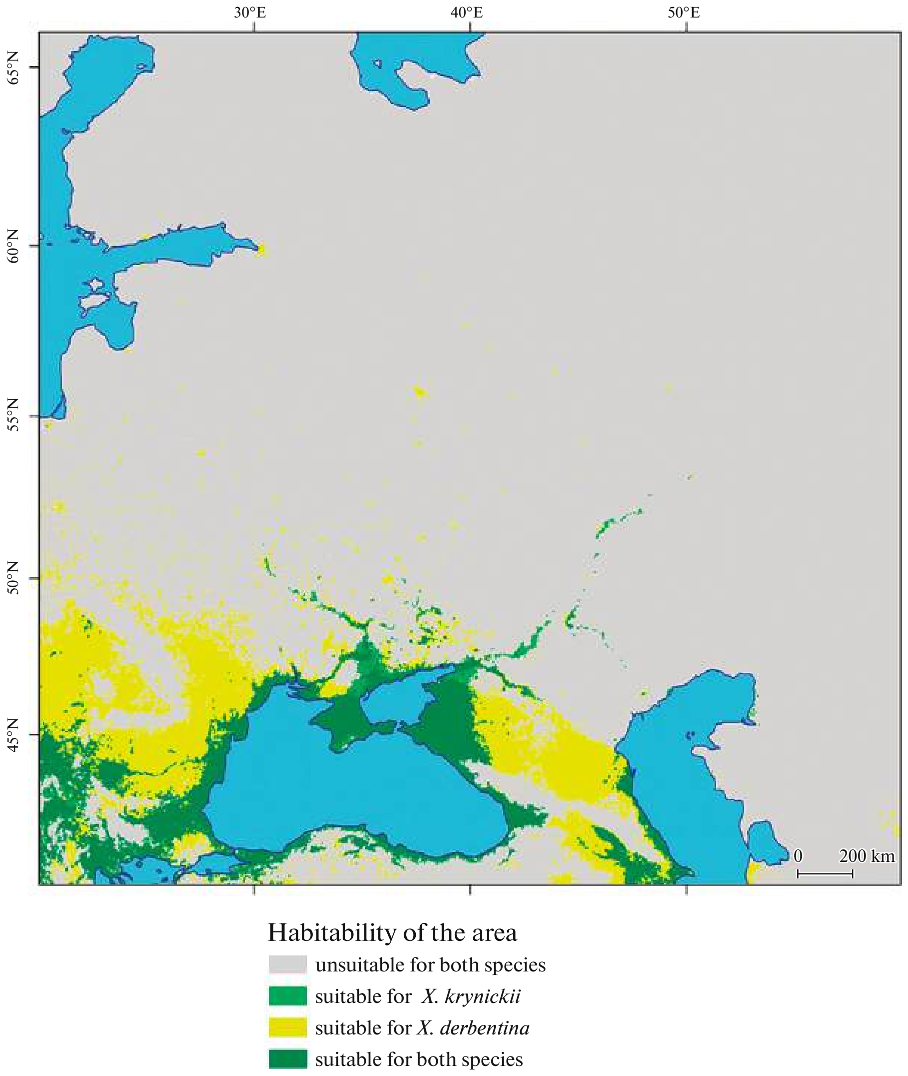

Fig. A15. Overlapping potential habitats of *X. derbentina* and *X. krynickii.*

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ETHICS APPROVAL AND CONSENT TO PARTICIPATE

This work does not contain any studies involving human and animal subjects.

CONFLICT OF INTEREST

The author of this work declares that she has no conflicts of interest.

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