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Land snails *Brephulopsis cylindrica* and *Xeropicta derbentina* (Gastropoda: Stylommatophora): case study of invasive species distribution modelling

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ABSTRACT. The terrestrial snails *Brephulopsis cylindrica* and *Xeropicta derbentina* are native to steppes of the Northern Black Sea region; *X. derbentina* has also initially inhabited Eastern Mediterranean, the Caucasus, and Anatolia. However, in last decades the species are increasingly reported outside of their natural range which renders them as likely invasive. The paper aims to assess the ecological suitability of adjacent habitats in terms of the molluscs invasion. We address this using species distribution modelling (SDM). The selected environment predictors for SDM included 22 environment factors such as land cover, enhanced vegetation index (EVI), altitude, and 19 bioclimatic parameters. The resulted model suggests that the area with maximum suitability extends from the natural range to the Central Danube lowland in the West and up to the Volga Upland in the Northeast. These regions have similar EVI and are largely croplands. Among the predictors, the minimum temperature of the coldest month has the greatest impact on the modelling results, which agrees with the variable being the limiting factor for the distribution of subtropical invertebrates. The study reinforces the notions that *X. derbentina* and *B. cylindrica* are likely to further expand the boundaries of their range thus posing threats to native ecosystems.

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Моделирование распространения наземных моллюсков-вселенцев *Brephulopsis cylindrica* and *Xeropicta derbentina* (Gastropoda: Stylommatophora)

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РЕЗЮМЕ. Наземные моллюски *Brephulopsis cylindrica* и *Xeropicta derbentina* исконно населяют степные биотопы Северного Причерноморья. Для *X. derbentina* нативный ареал также включает Восточное Средиземноморье, Кавказ, Малую Азию. В последние десятилетия увеличилось количество находок этих видов за пределами естественного ареала, что указывает на их инвазивный потенциал. Это обусловило необходимость оценки пригодности территорий, окружающих естественный ареал видов, и потенциально уязвимых для их инвазий. Для решения этой задачи были применены методы моделирования распространения видов (SDM). В качестве предикторов для SDM были выбраны 22 фактора окружающей среды, такие как тип земельных угодий (land cover), расширенный вегетационный индекс (EVI), высота над уровнем моря и 19 климатических параметров. Результаты моделирования показали, что зона, наиболее пригодная для обитания исследуемых видов, простирается от естественного ареала до Среднедунайской низменности на западе и до Приволжской возвышенности на северо-востоке. Эти территории имеют схожие значения EVI и преимущественно являются землями сельскохозяйственного назначения. Среди предикторов наибольшее влияние на результаты моделирования оказывает минимальная температура самого холодного месяца, что согласуется с тем, что этот фактор является лимитирующим для распространения субтропических беспозвоночных. Исследование подтверждает представления о том, что *X. derbentina* и *B. cylindrica*, вероятно, еще больше расширят границы своего ареала, создавая тем самым угрозу местным экосистемам.

Introduction

Many species, both animals and plants, of the Ponto-Caspian, in particular the northern Black Sea region and the Caucasus, are well known as expanding their ranges across Europe [Hulme, 2007; Keller *et al.*, 2011; Wagner *et al.*, 2017]. Many of these invaders have had dramatic consequences for native flora and fauna [Jahodová *et al.*, 2007; Berezina, 2007; Hohenadler *et al.*, 2019; Ward, Ricciardi, 2007]. Moreover, certain species originating in the Ponto-Caspian region are currently marked as potential invaders threatening Europe [Gallardo, Aldridge, 2013]. This situation necessitates research regarding the possible expansion of such alien species to new territories. In recent decades, species distribution modelling (SDM) has become a major tool for assessing the suitability of habitats for potential range expansion of invasive species [Gallien *et al.*, 2010; Goldsmit *et al.*, 2020; Srivastava, 2019; Pěknicová, Berchová-Bímová, 2016; Uden *et al.*, 2015]. Being a versatile technique, SDM is easily modified for the purpose of the particular analysis. For example, SDM predictions combined with genetic structure analysis can enable reconstruction of the history of founder invasion [Sherpa *et al.*, 2020]. Its ability to include a multiplicity of environmental factors also expands the list of SDM applications. The traditional approach generally focused on climatic predictors as key variables permitting successful invasion, especially under global climate change [Reside *et al.*, 2019; Journé *et al.*, 2020; Zhang *et al.*, 2019]. However, climatic data by themselves are not sufficient to model the potential distribution of invasive species [Barbet-Massin *et al.*, 2018]. Other features of habitat are important as well. For example, in the case of aquatic species SDM one can also consider water chemistry and proximity to man-made objects, etc. [Gallardo *et al.*, 2020; Rodríguez-Rey *et al.*, 2019]. In the case of terrestrial species, incorporating vegetation indices and land cover type as covariates can improve SDM predictions [Cord *et al.*, 2014; Feilhauer *et al.*, 2012; Wen *et al.*, 2015; Wilson *et al.*, 2013].

Our research focuses on alien molluscs. This phylum not only includes numerous invaders, but several species known as among “100 of the world’s worst invasive alien species” [Lowe *et al.*, 2000]. In addition, invertebrate invaders have many ways to be introduced to new areas and thus can easily spread throughout the world [Cowie, Robinson, 2003]. Unsurprisingly, these species often become SDM study objects. Prediction of their dispersal helps to pinpoint potential hotspots of an invasion and possibly manage it. Such predictions are important both at global and regional scales, as seen from numerous examples. Predicted shifts of environmental suitability for native and invasive molluscs of the order Unionida in water bodies of Southeast Asia further enabled the monitoring of the conservation status of freshwater biodiversity [Gallardo *et al.*, 2018]. Combining SDM and molecular genetic analyses allowed both reconstruction of introduction history and prediction of new invasions by slugs in the genus *Arion* across different continents [Zemanova *et al.*, 2018]. Based on dispersal-related factors, distribution overlaps between *Dreissena polymorpha* (Pallas, 1771) and *D. rostriformis bugensis* (Andrusov, 1897) were predicted at the global scale [Quinn *et al.*, 2014]. Invasive potential of *D. polymorpha* was assessed using the MaxEnt algorithm, and the vulnerability of certain Italian water bodies to invasion by these bivalves was demonstrated [Bosso *et al.*, 2017]. Predicting the distribution of the well-known invasive snail *Potamopyrgus antipodarum* (Gray, 1843) has demonstrated the potential susceptibility of protected areas in South America to invasion by this species [Alexandre da Silva *et al.*, 2019]. According to SDM that used 19 climatic predictors, the distribution of another invasive freshwater mollusc *Pomacea canaliculata* (Lamarck, 1819) is possible on all six continents [Lei *et al.*, 2017]. The same algorithm was used to predict the potential distribution of another commonly recognised invader, *Lissachatina fulica* (Bowdich, 1822), in Nepal [Adhikari *et al.*, 2020]. The predatory land snail *Oxychilus alliarius* (Miller, 1822) was shown to have spread across the Hawaiian Islands to all suitable areas and to have the potential to establish on other oceanic islands based on SDM modeling [Curry *et al.*, 2020].

In recent decades, the terrestrial molluscs *Xeropicta derbentina* (Krynicki, 1836) and *Brephulopsis cylindrica* (Menke, 1828) have expanded the northwestern boundaries of their ranges. Both species are native to the northern Black Sea region, and the native range of *X. derbentina* also includes the Caucasus and Anatolia [Schileyko, 1978]. Records of this species in Western Europe (France) are known as early as the middle of the twentieth century [Van Regteren Altena, 1960]. The species have successfully adapted to their new habitats and formed established populations [Aubry *et al.*, 2005; Kiss *et al.*, 2005]. During the last decade, many new records of *X. derbentina* across Ukraine, including western Transcarpathia, were published [Gural-Sverlova, Gural, 2017; Balashov *et al.*, 2018b]. Since 2014, a population of this species has been known in southwestern Russia [Adamova *et al.*, 2019]. Around this time, *B. cylindrica* was also found to be invasive [Snegin *et al.*, 2017]. The native range of *B. cylindrica* is the Crimean Peninsula, but in recent decades, it has become established across the northern Black Sea region and the steppe region of Ukraine [Kramarenko, Sverlova, 2001; Vitchalkovskaya, 2008; Zhukov *et al.*, 2019; Balashov *et al.*, 2018b]. In addition, one occurrence of *B. cylindrica* has been confirmed in Belarus, which is currently the westernmost point that this species has reached [Rabchuk, Zemoglyadchuk, 2011]. In their native ranges, both species inhabit open steppe areas where their populations are numerous. Both are typical xerophilous species having various adaptations to arid environments [Di Lellis *et al.*, 2012; Troschinski *et al.*, 2014; Dieterich *et al.*, 2015; Kramarenko, 2016]. Studies of dispersal and locomotor activity of *X. derbentina* indicate its ability for successful geographical spread [Popov, Kramarenko, 2004; Aubry *et al.*, 2006].

In this study, we quantify habitat suitability of the areas surrounding the native range of *X. derbentina* and *B. cylindrica*. To do so, we use climatic parameters, altitude, enhanced vegetation index (EVI), and land cover type as predictors. Our research focuses on identifying potential habitats that are currently vulnerable to invasion by these two species beyond their native ranges.

Material and methods

Study regions, Species occurrence data, and Predictors

Actual localities, i.e., places where *X. derbentina* and *B. cylindrica* had been reported, came from three sources: field collection data of the authors (29 sites for *X. derbentina* and 23 for *B. cylindrica*), published records (59 and 45 sites) [Balashov, Baidashnikov 2012; Balashov *et al.,* 2018a; Balashov *et al.,* 2018b; Rabchuk, Zemoglyadchuk 2011; Gural-Sverlova, Gural 2007; Vitchalkovskaya 2008; Kramarenko, Sverlova 2001; Gural-Sverlova, Gural 2017; Gural-Sverlova *et al.,* 2018; Kramarenko, Dovgal 2014; Kovalenko 2019; Zhukov *et al.,* 2019;], and data in the GBIF database that also include iNaturalist data (gbif.org) (62 and 83 sites); all localities are shown in Fig. 1, with data in Supplementary Material Tables 1-4. In total, 150 sites for *X. derbentina* and 151 for *B. cylindrica* were used as primary data. Randomly selected background points served as "pseudo-absence" points.

The study region lies within a rectangle between 12°E to 47°E and 37°N to 55°N. It spans the natural range of the species (the Eastern Mediterranean and the Black Sea region, including the Crimean Peninsula, the Western Caucasus, and Anatolia) as well as the surrounding areas (most importantly, Eastern Europe), into which, according to numerous records over recent decades, the species are expanding. The population of *X. derbentina* that settled in South France was intentionally excluded from our work as highly isolated from the major distribution area. To reduce sampling bias we performed spatial thinning: if two or more records occurred within a 5 km radius, only one was preserved [Aiello-Lammens *et al.*, 2015]. The distance was selected after evaluation of thinning with 1,2, … 20 km radius as the most suitable, it allows to preserve a substantial number of observations that still are not too close to each other. Sampling bias is a common obstacle to a successful SDM; it is caused by uneven coverage of the area by localities. This was essential for our particular work given that most observations came from a well-studied yet limited geographical area.

The initial set of predictors comprised: 1) 19 bioclimatic parameters taken from the WorldClim.org database; 2) altitude (WorldClim.org); 3) land cover (MODIS / Terra + Aqua Land Cover Type Yearly L3 Global 500 m SIN Grid), and 4) the enhanced vegetation index (EVI). Satellite data (land cover, EVI) were taken from the Moderate Resolution Imaging Spectroradiometer (MODIS). We used the maximum EVI values for the year.

From WorldClim database we initially used all 19 bioclimatic variables: BIO1 = Annual Mean Temperature; BIO2 = Mean Diurnal Range (Mean of monthly (max temp - min temp)); BIO3 = Isothermality (BIO2/BIO7) (×100); BIO4 = Temperature Seasonality (standard deviation ×100); BIO5 = Max Temperature of Warmest Month; BIO6 = Min Temperature of Coldest Month; BIO7 = Temperature Annual Range (BIO5-BIO6); BIO8 = Mean Temperature of Wettest Quarter; BIO9 = Mean Temperature of Driest Quarter; BIO10 = Mean Temperature of Warmest Quarter; BIO11 = Mean Temperature of Coldest Quarter; BIO12 = Annual Precipitation; BIO13 = Precipitation of Wettest Month; BIO14 = Precipitation of Driest Month; BIO15 = Precipitation Seasonality (Coefficient of Variation); BIO16 = Precipitation of Wettest Quarter; BIO17 = Precipitation of Driest Quarter; BIO18 = Precipitation of Warmest Quarter; BIO19 = Precipitation of Coldest Quarter.

A hierarchical cluster analysis of the initial dataset using Ward's method suggested six clusters that roughly corresponded to the natural zoning of the study area (Fig. 2). Ward's clusterization is a commonly used technique that produces compact and robust clusters in multivariate data. It provides a dendrogram structure that describes hierarchical, i.e. tree-like structure and enables a practitioner to visually assess the number of clusters. To obtain a more valid estimation and avoid multicollinearity among the predictors, we used exploratory data analysis. Pearson correlation coefficient and principal component analysis (PCA, Fig. 3) suggested reducing the the initial set of predictors to 11 variables which were least correlated and hold more variance: land cover type, EVI, altitude, and 8 of WorldClim layers, namely BIO5 (Max Temperature of Warmest Month), BIO6 (Min Temperature of Coldest Month), BIO7 (Temperature Annual Range), BIO9 (Mean Temperature of Driest Quarter), BIO12 (Annual Precipitation), BIO13 (Precipitation of Wettest Month), BIO14 (Precipitation of Driest Month),

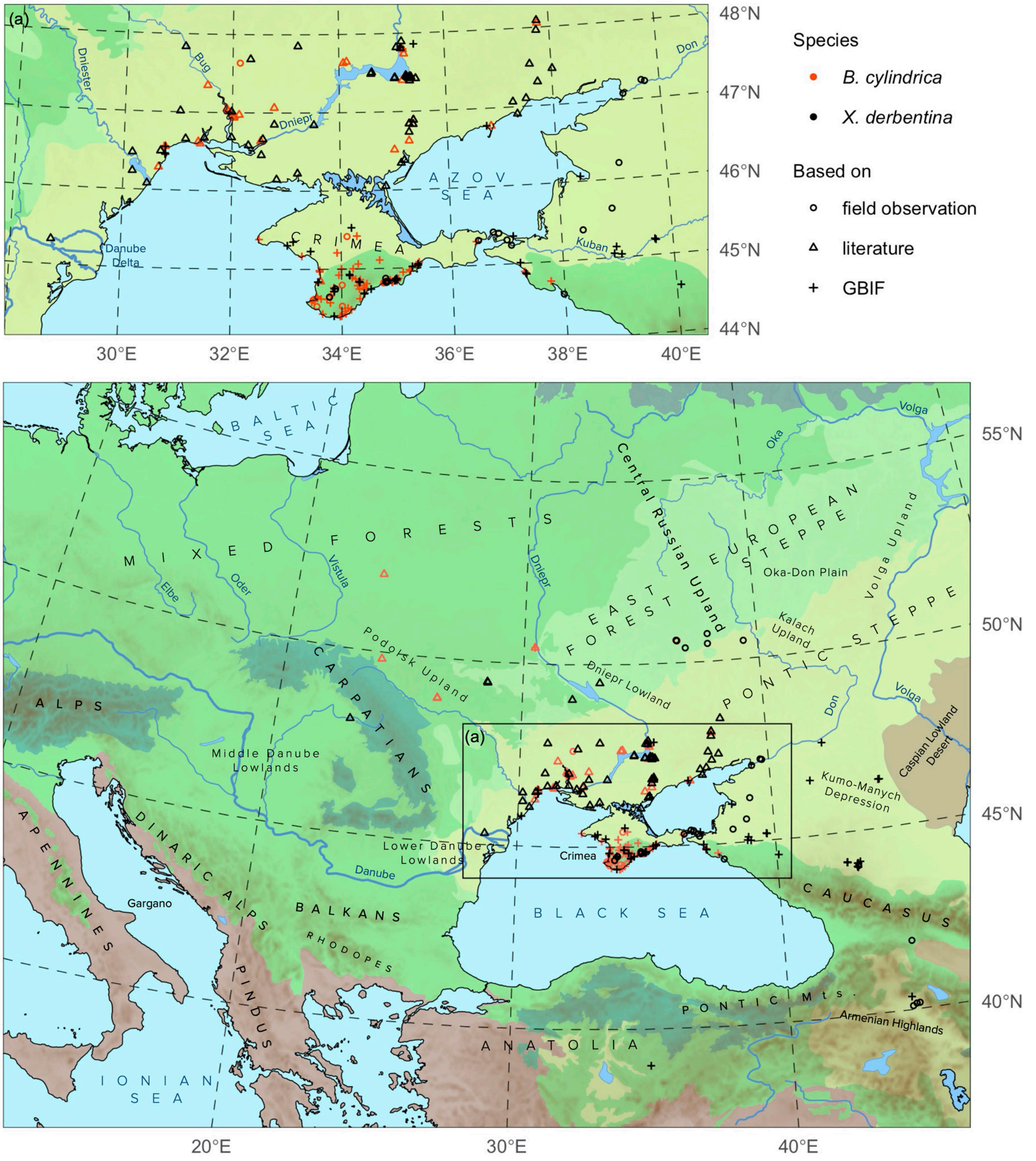

FIG. 1. Known localities of *B. cylindrica* and *X. derbentina* in the study area. Basemap: coastline, rivers – Natural Earth @ naturalearthdata.com; Terrain Tiles – @ registry.opendata.aws/terrain-tiles; ecoregions after Dinerstein E. *et al*. [2017].

РИС. 1. Точки находок видов на исследуемой территории. Базовая карта: береговая линия, речная сеть – Natural Earth @ naturalearthdata.com; рельеф – Terrain Tiles @ registry.opendata.aws/terrain-tiles; экорегионы по Dinerstein E. *et al*. [2017].

BIO19 (Precipitation of Coldest Quarter). The BIO8 (Mean Temperature of Wettest Quarter) layer had many values close to zero in the eastern part of the study area, so we also excluded it from the set of predictors. Since the studied species are xerophilous and inhabit open steppe biotopes, we also kept the vegetation index, land cover, and minimum temperature of the coldest month. The vegetation index and land cover type stress the importance of anthropogenically transformed landscapes for the introduction of alien terrestrial molluscs into the new areas while the minimum temperature of the coldest month represents a limiting factor for invertebrates naturally living in a subtropical climate.

Species distribution modelling

The model exploited four different algorithms and cross-validation by fivefold subsampling that resulted in 20 implementations for each species. For further work, implementations were selected that

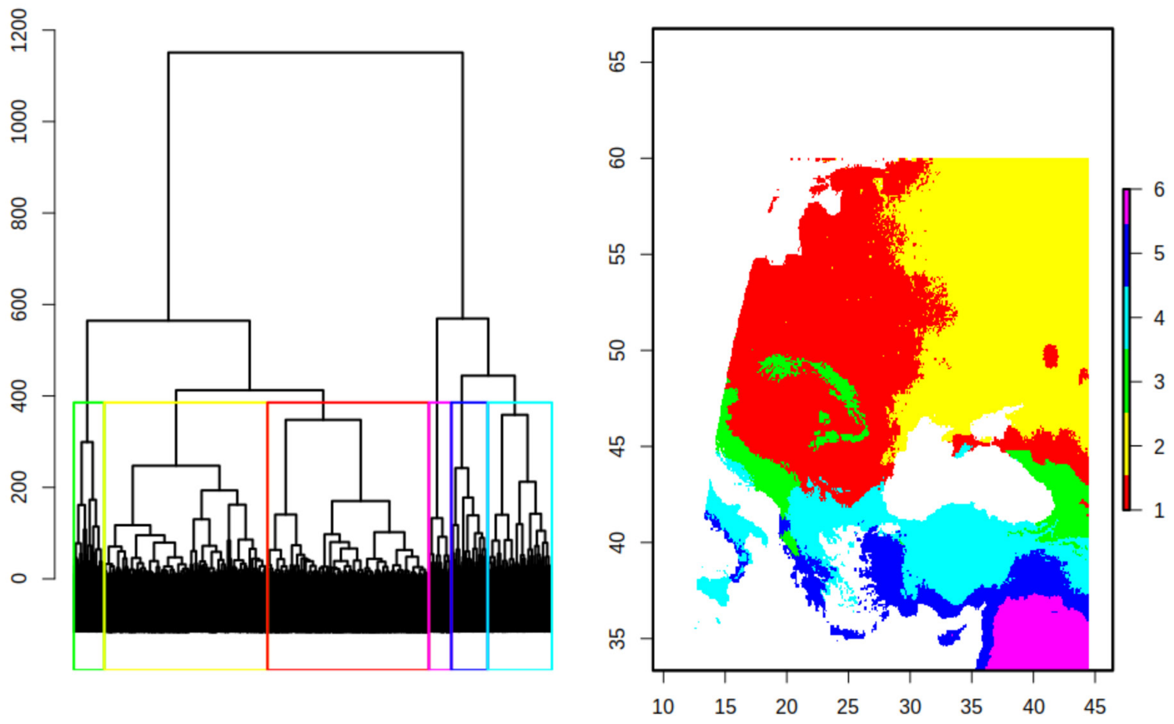

FIG. 2. Cluster analysis using Ward’s method: dendrogram and clusters on the mapColors highlight clusters 1 to 6.

РИС. 2. Результаты кластерного анализа по методу Уорда: дендрограмма и кластеры на карте. Цветами выделены кластеры с 1 по 6.

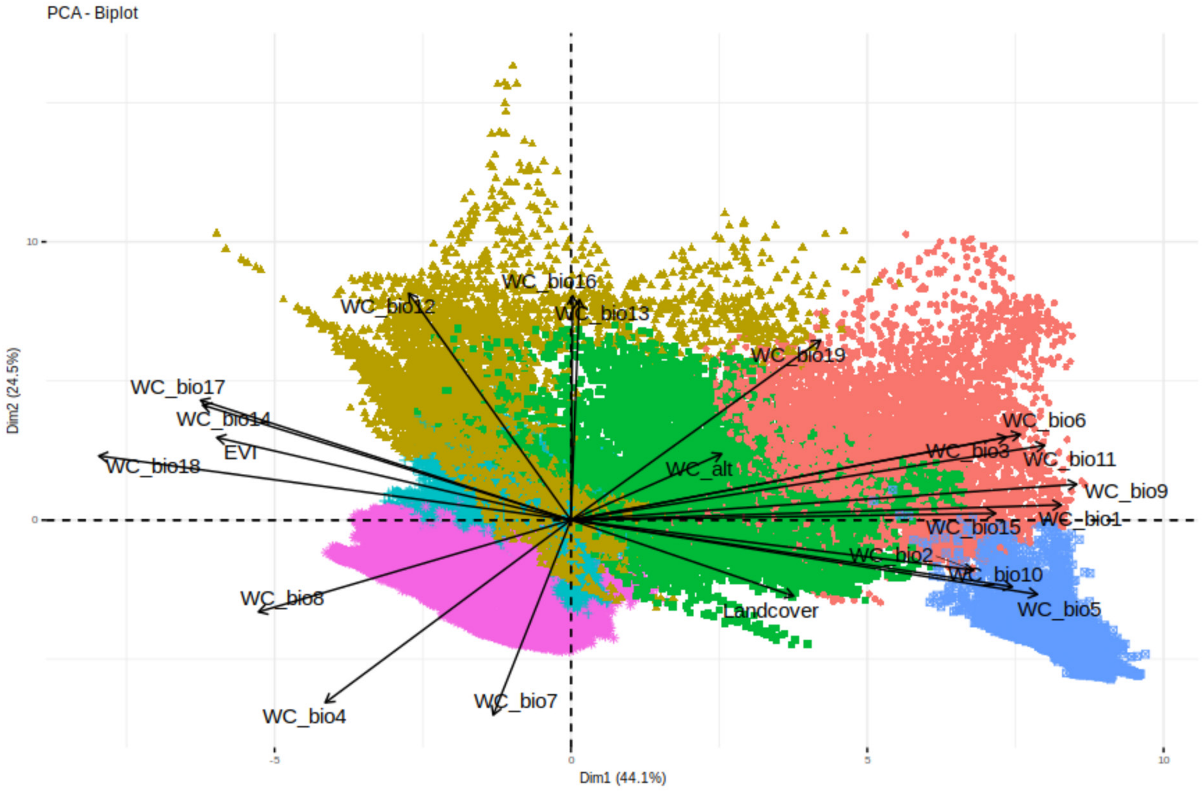

FIG. 3. Principal component analysis (PCA). The dimensionality reduction technique represents multivariate data on the 2D plane thus showing their structure. Datapoint colors are the same as in Fig. 2.

РИС. 3. Результаты анализа главных компонент (PCA). Методика снижения размерности представляет многомерные данные на двумерной плоскости, тем самым показывая их структуру. Цвета точек данных такие же, как на Рис. 2.

Table 1. Model statistics.
Modelling algorithms: GLM – generalized linear model, RF – random forests, BRT – boosted regression trees, FDA – flexible discriminant analysis.
Statistics indexes: AUC – area under the ROC-curve, COR – crude odds ratio, TSS – true skill statistic.

Табл. 1. Статистические характеристики моделей.
Алгоритмы: GLM – обобщенная линейная модель, RF – модель случайного леса, BRT – усиленные регрессионные деревья, FDA – гибкий дискриминантный анализ.
Статистические показатели: AUC – площадь под ROC-кривой, COR – отношение шансов, TSS – TSS-статистика

	Algorithms	AUC	COR	TSS	Deviance
X. derbentina	glm	0.89	0.69	0.72	0.99
	rf	0.92	0.75	0.75	0.68
	brt	0.89	0.67	0.69	0.96
	fda	0.87	0.69	0.73	1.04
B. cylindrica	glm	0.97	0.83	0.89	0.59
	rf	0.96	0.83	0.88	0.53
	brt	0.95	0.78	0.83	0.84
	fda	0.97	0.83	0.89	0.50

had the maximum values of performance indicators (Table 1) and accordingly four models were chosen for each species. Finally, we derived one ensemble prediction for each species that took advantage of all the trained models while reducing their bias. We evaluated the suitability scores of habitat on a scale from 0 to 1.

Data analysis and modelling were performed in R version 3.6.3 [R Core Team 2020] using packages sdm [Naimi, Araújo 2016]. The complete script is deposited on the GitHub repository (https://github.com/FVortex/Snail-SDMs).

Results

The four models having the highest area under ROC-curve values for each species were selected (Fig. 4). Additional criteria were the highest threshold-dependent statistics (e.g. TSS) and threshold-independent statistics (e.g. AUC, COR) (Table 1). Each of the four algorithms was implemented 5 times using cross-validation by subsampling (Figs 5 and 6). The predictions obtained varied substantially. The generalized linear model (glm) algorithm suggested a larger suitable area for both species. Other algorithms differed in the size of the zone with a high probability of habitat for *X. derbentina* in Anatolia. For *B. cylindrica*, three of the algorithms (RF - random forest, BRT - boosted regression trees, FDA - flexible discriminant analysis) pointed to larger territory with 0.4-0.6 suitability scores of habitat. For each species, we derived one ensemble prediction that combines results of different models (GLM, RF, BRT, FDA) and is likely to have produced a more reliable result (Figs 7 and 8) [Hao *et al.*, 2019; Araujo, New, 2007].

The estimated potential ranges of the two species largely overlap. The potential range of *X. derbentina* is wider, which agrees with its wider natural range. However, in the case of the Caucasus and Anatolia, our estimation for *X. derbentina* was biased because of the lack of localities there. This caused the estimated potential range to extend from only part of the native range.

A significant part of the potential range of *X. derbentina* extends beyond the eastern boundaries of the current non-native range as far as Volgograd (48.705°N, 44.495°E) and the Tambov region (51.983°N, 42.2610°E). Thus, the southeastern region of the East European Plain appears to be potentially suitable for these two species. The potential range includes the southern part of the Central Russian Upland but also the Kalach Upland as well as the southern part of the Oka-Don Plain, namely the Khopersko-Buzuluk Plain. Smaller areas with a 0.45-0.6 suitability for *X. derbentina* are located on the Volga Upland. The north-easternmost site with a suitability ≥ 0.5 for this species is Kamenka (53.186°N, 44.047°E). In addition, the model showed high suitability of some areas in the Middle and Lower Danube lowlands, the Balkans, and eastern Apennines for *X. derbentina*.

To sum up the results, our model suggests that the entire steppe zone of Eastern Europe can potentially be inhabited by *X. derbentina*.

The potential range of *B. cylindrica* is mainly located within that of *X. derbentina* with only minor differences. For example, the Crimean Mountains represent a highly suitable region for *B. cylindrica* while, for *X. derbentina,* the model suggested this territory to be less suitable.

According to the models, the potential range of

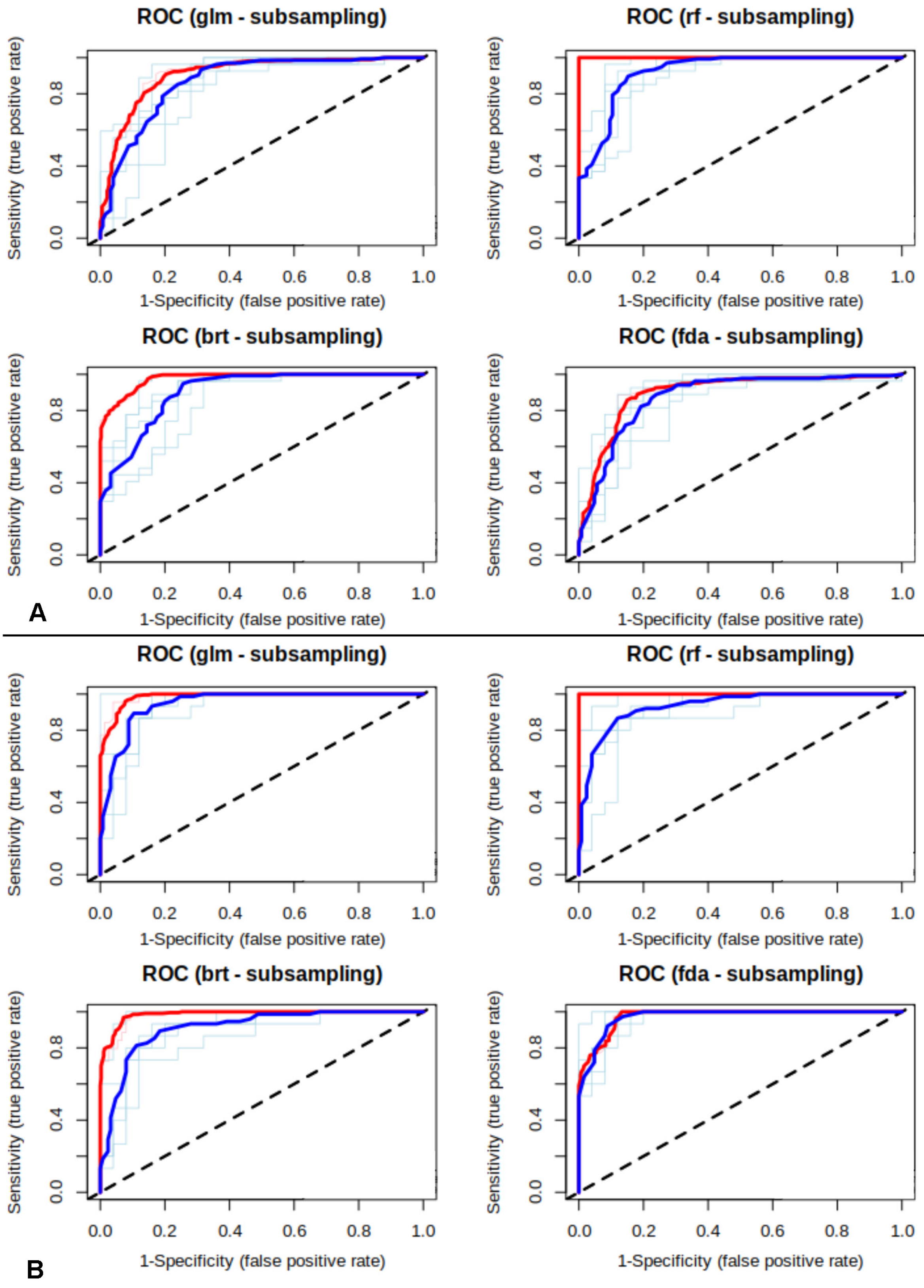

FIG. 4. Receiver operator curves (ROC) and area under curve (AUC) values for different models. **A.** Results for *Xeropicta derbentina*. **B.** Results for *Brephulopsis cylindrica*. Red curve represents the model performance for a training set, pale blue lines — for testing sets and separate models, thick blue line — overall performance among all models.

РИС. 4. ROC-кривые и площадь под ROC-кривой (AUC) для разных моделей. **A.** Результаты для *Xeropicta derbentina*. **B.** Результаты для *Brephulopsis cylindrica*. Красная кривая иллюстрирует показатели модели для обучающего набора, бледно-голубые линии — для тестовых наборов и отдельных моделей, толстая синяя линия — общие показатели всех моделей.

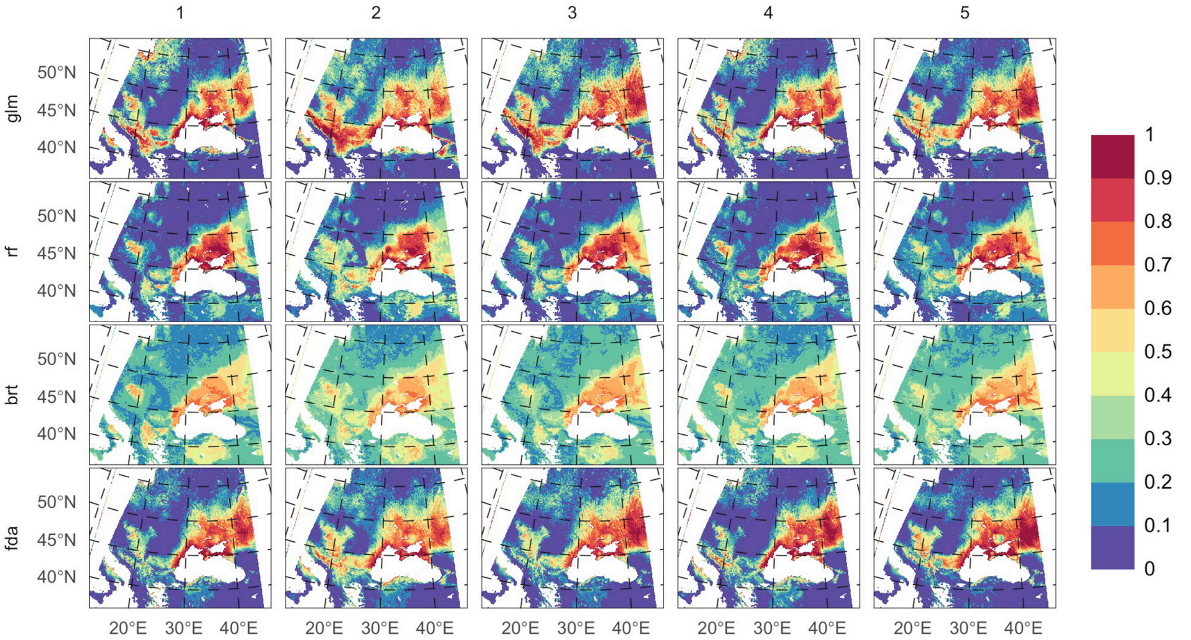

FIG. 5. *Xeropicta derbentina* habitat suitability according to tested four model types. Column names indicate sample numbers.

РИС. 5. Пригодность местообитаний для *Xeropicta derbentina* согласно протестированным моделям четырех типов. Имя колонки обозначает номер выборки.

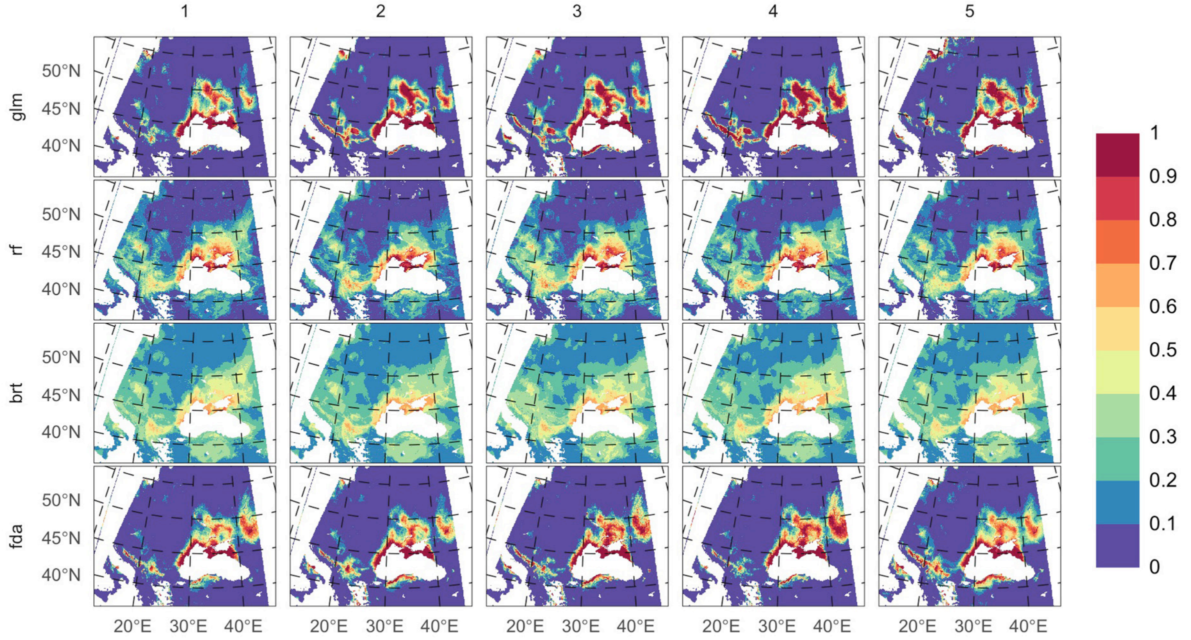

FIG. 6. *Brephulopsis cylindrica* habitat suitability according to tested four model types. Column names indicate sample numbers.

РИС. 6. Пригодность местообитанийдля *Brephulopsis cylindrica* согласно протестированным моделям четырех типов. Имя колонки обозначает номер выборки.

B. cylindrica is bounded in the east by the southern part of the Volga Lowland and partly by the Kumo-Manych depression. In the north, the spread of *B. cylindrica* from the Crimean Peninsula is possible along the Dnieper valley. Notably, similarly to *X. derbentina*, the areas of lesser suitability for *B. cylindrica* are the Middle and Lower Danube lowlands, the Balkans, and the east side of the Apennines.

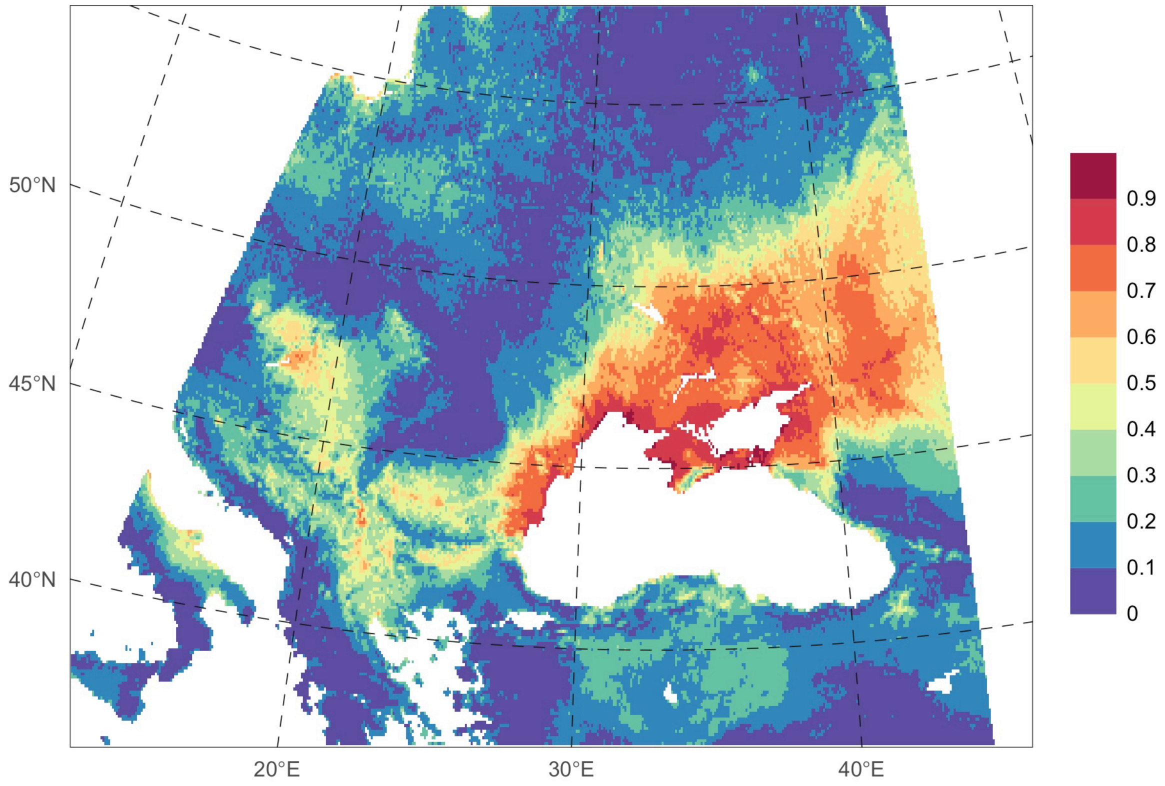

FIG. 7. *Xeropicta derbentina* habitat suitability according to the ensemble model.

РИС. 7. Пригодность местообитаний для *Xeropicta derbentina* согласно ансамблевой модели.

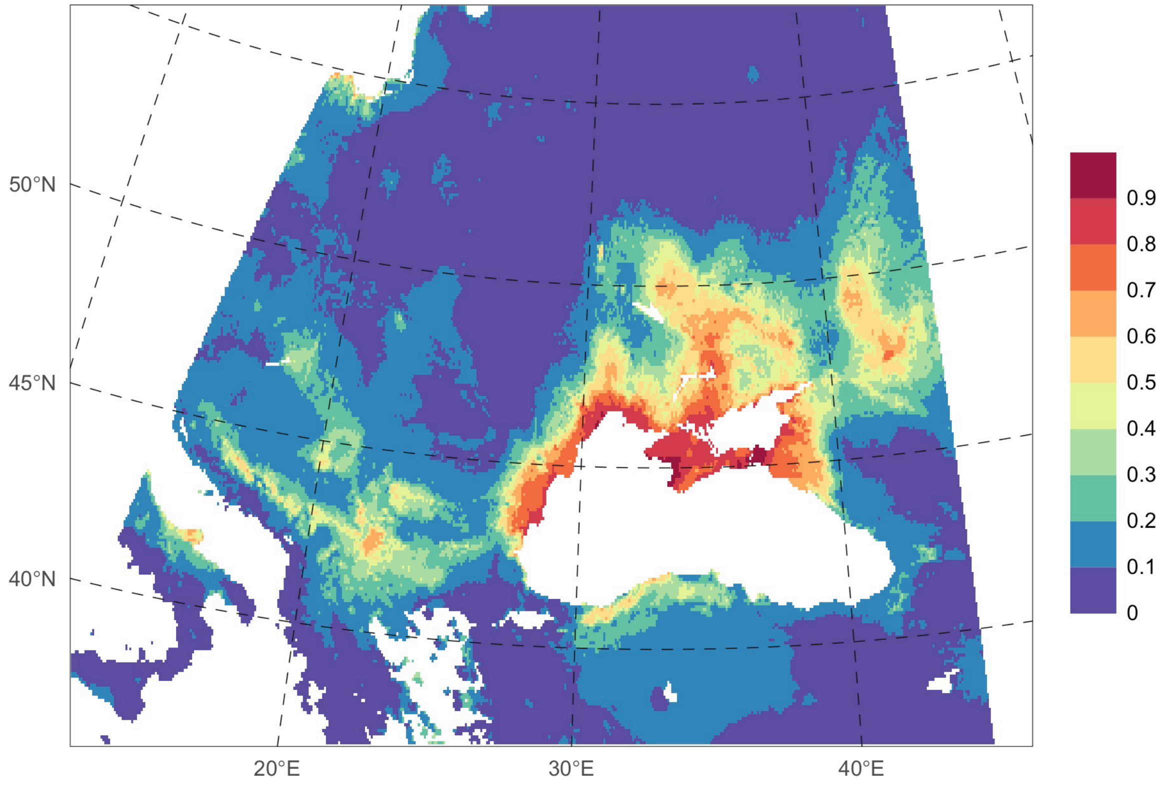

FIG. 8. *Brephulopsis cylindrica* habitat suitability according to the ensemble model.

РИС. 8. Пригодность местообитаний для *Brephulopsis cylindrica* согласно ансамблевой модели.

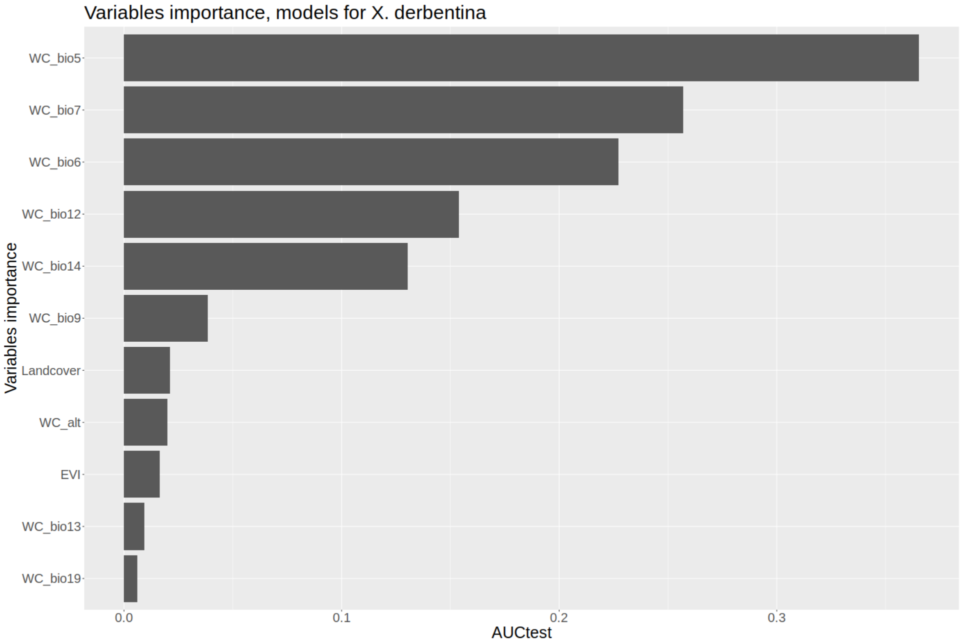

Fig. 9. Relative importance of SDM variables for *Xeropicta derbentina.*

РИС. 9. Относительная важность предикторов для моделей распространения *Xeropicta derbentina.*

As for Anatolia, a few sites along the southern coast of the Black Sea and in the mountains appeared suitable for both *B. cylindrica* and *X. derbentina*. For *X. derbentina,* potential habitats were predicted in the East Pontic Mountains (Lazistan Range) as well as between the Kure and Koroglu ranges, the main part of the Pontic Mountains. High suitability for *B. cylindrica* was evidenced in the Sakarya River valley in northwestern Anatolia.

Rather surprisingly, several models pointed to some parts of the eastern Baltic coast and certain islands in the Baltic Sea, including Gotland island, as potentially suitable for both species. However, the ensemble prediction showed most of the East European Plain northwest of the Dnieper and Don valleys to be negligibly suitable for them.

Variable importance estimates were calculated using variance inflation factor (VIF) which is the ratio of the variance of estimating some parameter in a model. They indicated the differences between the contributions of the predictors (Figs 9 and 10) to the SDM build. The climatic factors BIO 5 (Max Temperature of Warmest Month), BIO6 (Min Temperature of Coldest Month), BIO7 (Temperature Annual Range) and BIO12 (Annual Precipitation) were highly impactful to the models for both species.

The climatic parameters characterizing precipitation were found to be more important in the case of *B. cylindrica*. In addition to annual precipitation, a significant contribution was for precipitation of the driest month, which is limiting for xerophilous species.

As can be seen from the figures, the vegetation index and land cover type did not make such a significant contribution to the forecast results but also influenced the result, but this predictor is more important for *X. derbentina* than for *B. cylindrica.*

Discussion

As expected, the predicted susceptible habitat areas that are suitable for *B. cylindrica* and *X. derbentina* cover the natural ranges of the species. The area with the highest suitability (especially for *X. derbentina*) encircles the northern part of the Black Sea and Azov Sea regions. The belt of suitable areas begins from the Taman and Crimean Peninsulas and extends to the western part of the Black Sea region (43.243°N, 27.823°E, Varna, Bulgaria) and partly to the eastern Balkans. Separate suitable habitats (0.45-0.7 suitability scores) were identified for *X. derbentina* in the Rhodope Mountains, on the Middle and Lower Danube lowlands. For *B. cylindrica*, the main part of the Balkans had habitat suitability ≤ 0.3.

Notably, the territory of the northern part of the Black Sea region is inhabited not just by the studied species but also by their close relatives *X. krynickii* and *B. bidens*. However, there are very few records of these species beyond their native range. According to Gural-Sverlova and Gural [2017], the distribution

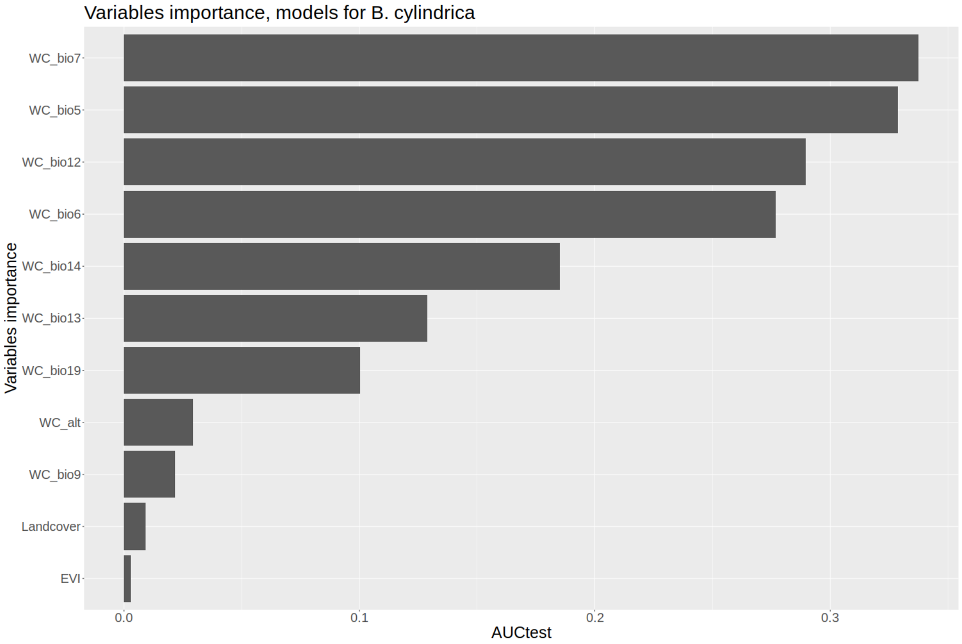

FIG. 10. Relative importance of SDM variables for B*rephulopsis.cylindrica.*

РИС. 10. Относительная важность предикторов для моделей распространения *Brephulopsis.cylindrica* .

of *X. krynickii* is confined to the sea coast that limits the spread of this species to the north.

The SDM results were probably biased in part because of the limited records available on GBIF and iNaturalist. This kind of bias is typically caused by having limited field surveys of a region [Lissovsky *et al*., 2020]. In the case of *X. derbentina,* the records densely cover the Crimean Peninsula and the northern part of the Black Sea region while the eastern and southern Black Sea region remains understudied (see Fig. 1). Despite spatial thinning, the uneven geographic coverage of data probably hampered the prediction. This explains the predicted high suitability for *X. derbentina* of the Azov region, the territory of the Donetsk ridge, the Dnieper Lowland, and the Dnieper Upland where most of the records occurred, while the Armenian Highlands and the Kura-Aras Lowland, where this species was also recorded, but in small numbers, were noted as potentially suitable areas only by a few of the individual models, but not by the ensemble model. In the case of *B. cylindrica,* the uneven geographic coverage of the data explains a gap in suitable areas from the southeast of the Central Russian Upland (Belgorod Region, Alekseevka) to the northeast of the Kumo-Manych depression (Tikhoretsk and Salsk).

The belt of high suitability areas falls within a steppe and forest-steppe zone of Eastern Europe with feather grass-fescue and thyme vegetation. It is a flat terrain, inhabited by xerophilous and xeromesophilic snail species. The terrestrial mollusc fauna of the steppe has been described in detail for Ukraine [Balashov, 2016; Balashov, Krivohizhaya, 2015; Balashov *et al*., 2013; Balashov *et al*., 2018a; Balashov *et al*., 2018b; Gural-Sverlova, 2018]. The most widespread native snail species of this region are *Chondrula tridens* (Müller, 1774), *Helicopsis* sp and *Pupilla* sp. These species are also indigenous to other parts of the predicted range of *X. derbentina* and *B. cylindrica*, namely, the South of the Central Russian Upland, South of the Oka-Don Plain, and adjacent steppe territories to the north and east [Nikolaev, 1973]. Interestingly, the supposedly highly suitable territory for *X. derbentina* and *B. cylindrica* is characterised by chalk outcrops. Calcium-rich soils here may favour colonization of the biotopes by new species of terrestrial molluscs [Juřičková *et al*., 2008]. Similar biotopes and soils are also typical of the Volga Upland, where the steppe mollusc communities are mainly composed of the same native species [Stoiko *et al*., 2014].

Somewhat high suitability was predicted for the Middle and Lower Danube lowlands (from 0.45 to 0.7). These are also open steppes and forest-steppes (e.g. the Pannonian Steppe), where the native malacofauna includes mostly the same xerophilous species [Bába, 1989; Balashov *et al*., 2020]. In addition, these open steppe biotopes are inhabited by certain Balkan species, for example, *Xerolenta obvia*

(Menke, 1828), the range of which extends to the Podolsk Upland [Balashov, 2016].

Higher suitability sites in the Balkans (Montenegro) are interesting because of the finding of a *X. derbentina* population nearby in the last decade [De Mattia, Pešić, 2014]. This reinforces the validity of the SDM prediction.

The majority of the eastern Apennines coast had lower predicted suitability for *X. derbentina* and *B. cylindrica*. However, the area with estimated suitability of 0.45-0.6 extends to the Gargano Peninsula, and given close location of Gargano National Park (Provincia di Foggia, Italy), this area requires further attention. Currently, *X. derbentina* has been found in northeastern Italy [De Mattia, 2007].

Three thermal factors, Max Temperature of Warmest Month, Min Temperature of Coldest Month, and their difference (Temperature Annual Range) contributed the most to the models for both species. In addition to the listed temperature factors, the Annual Precipitation also made a significant contribution to the forecasts.

High importance of the minimum temperature of the colder months was somewhat expected for the Black Sea species as it is related to the limiting factor which restrains the spread of species to northern territories. Biological invasions are strongly influenced by climate change [Thomas, 2010; Hulme, 2017]. For example, the diversity of non-native species of molluscs in European cities is related to January temperature: in European cities in warmer regions the diversity of non-native species was higher [Horsák *et al.*, 2016]. This once again supports the validity of our models. Together with changing Temperature Annual Range, the minimum temperature of the colder months might explain the probability of the rather unexpected predicted dispersal of both species in the areas of the Baltic coast and on the island of Gotland. Another group of climatic predictors related to precipitation, notably Precipitation of Wettest Month, appeared critical for *X. derbentina.*

Even though the exploratory analysis pointed to landcover and EVI as least important for further analysis (Figs. 9 and 10) there is an agreement between their spatial distribution and the SDM prediction. Similar EVI values are observed in areas corresponding to high suitability for both species. The vegetation index describes the type of vegetation, which in turn largely determines the terrestrial mollusc community structure [Lososová *et al.*, 2011]. Land Cover Type as a covariate highlights croplands as highly suitable regions. Anthropogenically transformed ecosystems are well known for their high risk of biological invasion; various agricultural ecosystems, including croplands, are also amenable to colonisation by alien snails, as is evidenced by the many snail and slug species that are pests of crops [Guiller *et al.*,2012; Thiengo *et al.*, 2007; Thunnissen *et al.*, 2021].

The next point is that habitats suitable for *X. derbentina* and *B. cylindrica* are confined to densely populated areas. First, certain features of the colonization process itself are important. The introduction of land snails is influenced by various anthropogenic features such as roads and railways, and human activities such as transport of horticultural and general agricultural products [Cowie, Robinson, 2003; Bergey *et al.*, 2014]. This enables the introduction of molluscs into urban and agricultural ecosystems. Because of reduced biodiversity, weak competition and interspecies interactions, these ecosystems are vulnerable to successful expansion of invaders [Santana Marques *et al.*, 2020]. This, for example, was described in Ukrainian cities for alien land snails, including *X. derbentina* and *B. cylindrica* [Son, 2010]. Second, these snail species inhabit steppe biotopes, but in Europe most of the steppe landscapes have been anthropogenically transformed. Remaining areas of steppe vegetation are mainly near settlements and their surroundings or agricultural land. These changes in biotopes also apply to a part of the natural range of species in the Black Sea region. We assume that these points make these species preadapted to the conditions in the new regions. This pre-adaptation of alien species increases the success of invasion [Facon et al., 2006].

High suitability of the steppe and forest-steppe zone of Eastern Europe for alien xerophilous snails represents a risk for native faunas. The negative impact of *B. cylindrica* on the diversity of the steppe ecosystem has already been shown by Balashov *et al.* [2018a] in Podolski Tovtry National Nature Park (western Ukraine). In this regard, the SDM approach identifies areas where alien and native (including endangered) species compete [Vicente *et al.*, 2011], which is especially important for protected areas [Pěknicová, Berchová-Bímová, 2016]. Unfortunately, because of the lack of data on native land molluscs in areas of the Central Russian Upland and the Oka-Don Plain, we cannot estimate how devastating the impact of *X. derbentina* and *B. cylindrica* on local ecosystems may have been. However, our results highlight areas where such studies could be conducted in the future.

To sum up, our SDM modelling suggests that *X. derbentina* and *B. cylindrica* are likely to expand their range. This requires a transport vector as a means of spread. Given that the highly suitable regions are mostly urbanised with well-developed transport systems, their colonisation appears likely. Our result confirmed that the steppe biotopes, especially croplands, in Eastern Europe are potentially suitable for these xerophilous snails. The prediction obtained using SDM provides a guide for management of *X. derbentina* and *B. cylindrica* invasion in highly susceptible areas.

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