

Research Article

Ensemble modelling for smart conservation strategies for forest reptile species at their range edges in Europe amidst climate change

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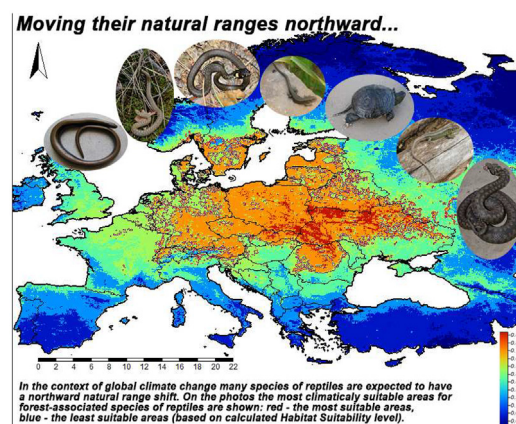
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HIGHLIGHTS

- Forest herpetofauna will likely face a northward distribution shift in the near-decades.
- Forests of Northern Europe tend to become sanctuaries for herpetofauna diversity.
- By 2050 the greatest reduction in range is expected for *Z. vivipara* and *V. berus*.

GRAPHICAL ABSTRACT



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ABSTRACT

Reptile fauna should be considered a conservation objective, especially in respect of the impacts of climate change on their distribution and range's dynamics. Investigating the environmental drivers of reptile species richness and identifying their suitable habitats is a fundamental prerequisite to setting efficient long-term conservation measures. This study focused on geographical patterns and estimations of species richness for herpetofauna widely spread *Z. vivipara*, *N. natrix*, *V. berus*, *A. colchica*, and protected in Latvia *C. austriaca*, *E. orbicularis*, *L. agilis* inhabiting northern (model territory Latvia) and southern (model territory Ukraine) part of their European range. The ultimate goal was to designate a conservation network that will meet long-term goals for survival of the target species in the context of climate change. We used stacked species distribution models for creating maps depicting the distribution of species richness under current and future (by 2050) climates for marginal reptile populations. Using cluster analysis, we showed that this herpeto-complex can be divided into "widespread species" and "forest species". For all forest species we predicted a climate-driven reduction in their distribution range both North (Latvia) and South (Ukraine). The most vulnerable populations of "forest species" tend to be located in the South of their range, as a consequence of northward shifts by 2050. By 2050 the greatest reduction in range is predicted for currently widely spread *Z. vivipara* (by 1.4 times) and *V. berus* (by 2.2 times). In terms of designing

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an effective protected-area network, these results permit to identify priority conservation areas where the full ensemble of selected reptile species can be found, and confirms the relevance of abiotic multi-factor GIS-modelling for achieving this goal.

1. Introduction

Among all terrestrial vertebrates, reptiles emerge as the most vulnerable and significantly impacted by the escalating effects of climate change (Winter et al., 2016; Mi et al., 2023). It is roughly estimated that 21%–27% of the world's reptiles are threatened (Kuybida et al., 2019; Di Marco, 2022). In the context of climate change, many species face additional challenges such as habitat destruction due to anthropogenic impacts, including fragmentation and cultivation of landscapes, particularly deforestation and drainage of wetlands (Cochard, 2011; Suislepp et al., 2011). Such changes affect the preferable climatic conditions essential for reptiles of the Palearctic: seasonal temperature changes (e.g., winter temperature drops enable activity pause, correct development of sex cells and proper breeding behavior), daily temperature changes (enabling basking and resting periods), suitable temperature and moisture regimes needed for proper egg incubation, sufficient habitat humidity providing appropriate water, nutrients, food and hides (Araujo et al., 2006; Böhm et al., 2013; Mantyka-Pringle et al., 2012). This vulnerability is particularly evident in Europe, where a variety of reptiles that inhabit forest environments are on the brink of their European habitat. Understanding the profound implications of climate change for these forest reptiles at the edge of their range is crucial for formulating effective conservation strategies (Hardie and Hutchings, 2010). So, the northern edge of the reptile range distribution is an ecologically and evolutionarily sensitive area where populations face unique challenges due to the harsh climatic conditions and limited resources. In the south of their range distribution, reptiles face massive competition and habitat degradation (Nekrasova, 2023; Nekrasova et al., 2018, 2019a, 2019b, 2021, 2022; Nekrasova and Tytar, 2014; Vasyliuk et al., 2015). This habitat loss reduces the availability of suitable sites, leading to declines in population size and changes in range dynamics. This is due to a number of factors including: rising temperatures and aridity, competition with more thermophilic invasive species, increased urbanization and agriculture. Edge effects, which are the changes in environmental conditions that occur at the boundaries between habitats, can further exacerbate these challenges and threaten reptile populations (Nekrasova, 2018; Nekrasova et al., 2019b; Nekrasova and Kostushyn, 2016; Nekrasova and Marushchak, 2023; Pupins, 2007; Pupins et al., 2017). Not all reptiles can withstand increasing temperatures, which make them more vulnerable to environmental changes, competition with new, better-adapted invasive species, habitat fragmentation and human pressures (Huey, 1982; IPCC, 2013; Mi et al., 2022).

Climate change is causing reptile habitats to shift north due to altered temperatures and precipitation regimes (Nekrasova et al., 2013; Nekrasova and Tytar, 2014, 2019). As a result of such changes, distribution ranges' shifts have been predicted and in particular cases already verified across a wide array of European taxa, with the majority of species moving their distribution edges towards higher latitudes and altitudes (Brandon et al., 2005; Chen et al., 2011; Nekrasova et al., 2013; IPCC, 2013; Pupina et al., 2018; Nekrasova et al., 2019).

Understanding the patterns of formation and distribution of biodiversity wealth is crucial for effective biodiversity conservation efforts in our time (Global Biodiversity Convention, 1993; Pecl et al., 2017). Herpetofauna, as an important part of biodiversity, plays a key role in ecosystems, serving as a necessary element in trophic and bioenergetic connections. However, despite their significance, many reptile species are threatened with extinction due to habitat loss, climate change, and anthropogenic impacts. Protecting reptile habitats is a critical aspect of biodiversity conservation efforts. In Europe, reptiles such as the European pond turtle (*Emys orbicularis* (Linnaeus, 1758)) are protected by the

Bern Convention (Resolution 6) and are included in the Natura 2000 network. In Eastern European countries, including Ukraine, they are also protected under the Emerald Network (Marushchak et al., 2019; Nekrasova et al., 2021). A crucial aspect of preserving biodiversity is the protection of various species' habitats. This includes the prominent umbrella species, which are used to create standard distribution models (SDMs), and the intricate web of other species, known as ensemble species (ESDM), that play a crucial role in maintaining ecological balance. These species are not just part of the ecosystem, they are the backbone of it, and their protection is essential for the survival of all associated species (Nekrasova and Tytar, 2014; Tytar et al., 2018; Nekrasova et al., 2019).

Conservation efforts must take into account both umbrella and ensemble species, as well as the complex interactions between different species and their habitats. This requires a holistic approach to biodiversity conservation that considers selection of keystone species representing key processes or functions in the local ecosystem, which is the main goal to achieve. In a changing climate, this approach becomes even more important as habitats and species distribution shift. Understanding the contribution of climate as a whole and its separate components in determining of species spatial distribution and how its possible changes is at long-term scale using the tools of GIS-modelling and building SDM is a critical technique for investigating a variety of conservation and management issues, increasing their effectiveness (Hawkins et al., 2003). A SDM uses correlative modelling that is based on geographical information system applied to find associations between defined environmental variables and occurrence records of the species studied (Tytar et al., 2015). The mentioned variables typically represent abiotic factors (Van Echelpoel et al., 2015; Peterson and Vieglais, 2001). Biotic factors, which are challenging to model explicitly, may be implicitly represented in the model as they strongly correlate with abiotic ones (Soberón and Nakamura, 2009; Tytar, 2011). Therefore, it is assumed that biotic processes leading to the species realized ecological niche and distribution may be captured by the relationship between the environmental predictor variables of abiotic character and the modelled species' occurrence patterns. The generated resulting model creates a so-called bioclimatic envelope illustrating the potential species niche (Elith et al., 2011). This niche model is used to examine the geographic space and highlights areas where the studied species is likely to occur under the given predicted environmental factors and scenarios (Van Echelpoel et al., 2015; Zeng et al., 2016). Many different algorithms are used in species distribution modelling depending of each particular situation, and the predicted distributions can vary between algorithms (Elith et al., 2011; Marmion et al., 2009). Because of this variability, ESDM based on a weighted average of individual SDMs have become widely used to account for potential error associated with each algorithm (Araujo and New, 2007). Overall, stacked species distribution models (SSDMs) represent a promising approach for improving the accuracy and reliability of species distribution models in the face of climate change.

We used this approach to create SSDMs based on several modelling approaches and multiple species at the same time. The goal of our work was to analyse the patterns and prospects for the distribution of seven species of reptiles (protected by the Bern Convention) that are found in Northern Europe and the drivers of their range dynamics in the context of climate change. In order to exclude geographical and genetic variability of these seven species, we focused on Eastern Europe, where environmental conditions are particularly different for some species compared to the entire range (e.g., *Anguis* genus). Afterwards, using habitat suitability mapping it was possible to identify priority conservation

areas in terms of both restoration and/or preservation (Gibson et al., 2004) and guide conservation plans with deeper understanding of the species' needs in future according to the modelled picture (Gaston and Williams, 1996). With a focus on areas situated at the periphery of their European habitat range, our research endeavors to unravel the intricate dynamics between climate change and the habitats of these reptile populations. Additionally, studying the patterns of change in reptile species richness can contribute to understanding of broader ecological and evolutionary processes.

Therefore, the goals of this article were to: 1) analyse the spatial patterns of current distribution of seven reptile species in Eastern Europe; 2) assess the dynamics of their ranges under climate change; 3) identify the drivers of their range dynamics under climate change; and 4) identify the long-term priority conservation areas of these species to preserve reptile species richness in the context of climate change.

Nevertheless, for the effective implementation of conservation initiatives, a deep understanding of the ecology and biology of reptiles, as well as the environmental contexts especially taking into account the complexes of abiotic factors (through short- and long-term modelling) affecting their survival and distribution, is necessary. Research in this area can contribute to the development of more effective long term conservation strategies that take into account both global and local characteristics. In this article, we examined concurrent approaches to the study and conservation of reptiles and proposed new methods that can be used to enhance their present and future protection.

2. Materials and methods

For the study, the Ensemble Modelling was applied using the following set of steps: 1) collection of species occurrence data; 2) collection and processing of ecological data; 3) construction of species distribution models (individual SDM, ensemble SDM (ESDM), and stacked SDM (SSDM)); 4) assessment of variable importance; 5) testing the significance of SSDM; 6) analysis of models using multiple regression analysis (SAGA GIS); 7) statistical testing; 8) interpretation of results; 9) field verification of results in natural conditions (Nekrasova et al., 2019; Zurell et al., 2020).

2.1. Occurrence data

The seven species chosen for this study were in one hand the widely spread legless lizards of *Anguis fragilis* complex (*Anguis colchica* (Nordmann, 1840), thereafter referred as “*Anguis colchica*” (Linnaeus, 1758), lizard *Zootoca vivipara* (Jacquin, 1787), snakes *Natrix natrix* (Linnaeus, 1758), *Vipera berus* (Linnaeus, 1758) and in the other hand pan-Europe protected snake *Coronella austriaca* (Laurenti, 1768), pond turtle *E. orbicularis* (Linnaeus, 1758), and lizard *Lacerta agilis* (Linnaeus, 1758)). The species were chosen based on their ecological preferences and their dependance on forest biotopes and habitats, whose degradation leads significant decline in their numbers if they are eurybiontic, or even to local disappearance. All species tend to inhabit northern part of Europe, being to some extent associated with forest massifs of the north. This results in their wide spreading on the territories that experience considerable changes in temperature and other climatic factors throughout the year. The studied species make extensive use of both wetland and upland habitats and have been negatively impacted by habitat loss and degradation resulting from wetland drainage, agriculture, and urbanization. As a consequence, over much of their range and especially at the edge of the range, they persist in small populations isolated from conspecifics by habitat fragmentation.

A total of 7,900 georeferenced occurrence points across Europe were compiled from the literature (Sillero et al., 2014), GBIF databases (Nekrasova, 2023; GBIF.org, 2021) and unpublished field reports. These reports covered the north of European range (model territory Latvia) provided by M. Pupins and A. Čeirāns (<http://www.dabasdati.lv>) and the southern European range (model territory Ukraine) provided by

Table 1

Environmental variables (factors) selected after using of ‘virtualspecies’ package in R to avoid autocorrelation between initial 35 variables from the CliMond database.

Number	Abbreviation	Variable
1	bio01	Annual mean temperature (°C)
2	bio02	Mean diurnal temperature range (mean (period max-min)) (°C)
3	bio03	Isothermality (bio02/bio07)
4	bio04	Temperature seasonality
5	bio06	Min temperature of coldest week (°C)
6	bio07	Temperature annual range (bio05-bio06) (°C)
7	bio08	Mean temperature of wettest quarter (°C)
8	bio10	Mean temperature of warmest quarter (°C)
9	bio11	Mean temperature of coldest quarter (°C)
10	bio12	Annual precipitation (mm)
11	bio14	Precipitation of driest week (mm)
12	bio15	Precipitation seasonality
13	bio17	Precipitation of driest quarter (mm)
14	bio25	Radiation of driest quarter (W m ⁻²)
15	bio30	Lowest weekly moisture index
16	bio34	Mean moisture index of warmest quarter

O. Nekrasova. The data were gathered for the seven species: widely spread *Anguis fragilis* complex ($n = 1,399$ occurrence data), *Zootoca vivipara* ($n = 1,133$), *Natrix natrix* ($n = 1,655$), *Vipera berus* ($n = 994$) and protected in Europe *Coronella austriaca* ($n = 1,045$), *E. orbicularis* ($n = 821$), and *Lacerta agilis* ($n = 853$). Sources for taxonomy are from the IUCN Red List of Threatened Species, version 2014.3 (<http://www.iucnredlist.org>). Using the ‘GeoRes’ option to thin occurrences resulted in a substantial reduction of the original dataset to 1888 georeferenced records subsequently employed for building the SSDMs. All records were non-duplicate. None of the protected species were handled. The study was performed in accordance with all relevant guidelines and regulations of related legislation in all countries. Under the Ukrainian law “On the protection of animals from cruel treatment” and Latvian law “On the protection of species and habitats” the species were handled by experts (our co-authors) who are permitted to capture for scientific purposes without any additional specific certification.

2.2. Environmental data collection and processing

To understand the role of environmental conditions, gradients and their significance in shaping the current distribution of every species, we used a set of 35 bioclimatic variables exported from the CliMond database for the period 1970–2000 (Kriticos et al., 2012; Madden and Williams, 1978; <https://climond.org/>, accessed 27 December 2020, A1B). We used the CliMond database for modelling at European scale, and from the resulting models we only selected the East European area to study the possibilities of dispersal of exotic species.

From the initial number of registrations downloaded, those marked as “absence”, lacking information on data, coordinates, associated with zoo or private collections (therefore with high chance of being supported by humans) and indicated as a result of machine observation, were removed in order to minimize the data of false presence in the introduced state. Duplications of coordinates were removed as well. To account for sampling bias, we used the nearest neighbor distance method (‘ntbox’ package in R; Osorio-Olvera et al., 2020) for clearing the data in order to avoid autocorrelation. Occurrence points that were ≤ 0.1 units (10 arcminutes) away from each other were removed. Then the ‘random selection’ module in QGIS was applied allowing to avoid errors due to spatial autocorrelation.

In order to avoid autocorrelation between the variables (Braunisch et al., 2013; Burnham and Anderson, 1998; Merow et al., 2014), highly cross-correlated (> 0.7) ones were removed using the ‘virtualspecies’ package in R, resulting in a selection of only 16 variables (Table 1).

Table 2

Environmental variables (factors) selected after using of ‘virtualspecies’ package in R to avoid autocorrelation between initial variables from the GAEZ and GlobCover databases.

Number	Variable
1	Accessibility
2	Agro-ecological zone
3	Air frost number
4	Annual precipitation
5	Annual P_PET ratio
6	Annual temperature range
7	Dominant soil
8	Dominant land cover pattern
9	Forest land
10	Frost-free period
11	Globcover, 2009
12	Mean annual temperature
13	Median altitude
14	Quarterly P_PET ratio (April to June)
15	Reference evapotranspiration
16	Reference length of growing period
17	Terrain slope index
18	Temperature growing period
19	Thermal climates

Table 3

Statistical methods used to fit the species distributions models.

Algorithm	Abbreviation	References
Random Forest	RF	Breiman, 2001
Support Vector Machines	SVM	Cortes and Vapnik, 1995
Generalized Linear Models	GLM	McCullagh and Nelder, 1989
Maximum Entropy Modelling	MaxEnt	Phillips et al., 2006

To study the specific features of each species, we employed bioclimatic, agro-ecological and landscape factors from the Global Agro-ecological Zones (GAEZ) Database (IIASA/FAO, 2012; Global Agro-ecological Zones v3.0, <http://www.fao.org>; Fischer et al., 2012) and GlobCover (22 classes: tree cover, shrub cover, herbaceous cover, cropland, other natural vegetation, 2009, http://due.esrin.esa.int/page_globcover.php, accessed on 5 March 2021; Arino et al., 2012). Highly correlated (> 0.7) predictors were removed using the ‘virtualspecies’ package in R (Dupin et al., 2011; Hijmans et al., 2015), resulting in a selection of 19 variables (Table 2).

2.3. Fitting species distribution models

Although it could be assumed that interspecific interactions (biotic factors) provide a more accurate depiction of the species’ realized ecological niche and distribution, this study focuses on the relationship between abiotic environmental predictor variables and the modelled occurrence patterns of species. We considered the SDMs as representing the environmental aspect of the ecological niche (potential niche), rather than offering a comprehensive representation of whole ecological niche. Created maps illustrate the habitat suitability (HS) predicted according to the used registration points for each species and variables of different abiotic factors (Tables 1, 2) which reflects the potentially suitable biotopes (habitats). Here we understand potentially suitable habitat in the same way as predicted suitable habitat: habitat suitability is a quantitative measure of the predicted suitable habitat or potentially suitable habitat.

The species distribution models for 7 species were built by assembling 4 widely-used modelling algorithms (Table 3): two machine learning methods (Random Forest (RF) and Support Vector Machines (SVM)), one regression method (Generalized Linear Models (GLM)), and one Maximum Entropy Modelling (MaxEnt). Three types of models were created: individual SDMs; ensemble SDMs (ESDMs, using different modelling algorithms); stacked SDMs (SSDMs) combining several SDMs or

ESDMs outputs to model species assemblages and computed species diversity and species richness (Allouche et al., 2006). As different sets of data were used for calibrating the model, to account for within-algorithm model variation, distribution models for each species were computed using ten model repetitions. To evaluate the predictive performance of each algorithm, we used a random subset of 70 % of the data to calibrate the model, and the remaining 30 % for evaluation, using the area under the relative operating characteristic curve (AUC). The AUC’s threshold and prevalence independent nature were used as effective model accuracy metric. AUC values > 0.5 were considered to represent good classification results (the model performs better than random). Predictions from models with moderate fit ($AUC > 0.6$) were included in the final ensemble, and the weighting of each algorithm prediction was based on the sensitivity-specificity equality (SES) (Liu et al., 2013). Default parameters of the dependent R package of each algorithm were conserved. The ‘GeoRes’ option was used to thin the point data. Thinning removes unnecessary records, reducing the effect of sampling bias while retaining the greatest amount of information. The outputs of the different species were aggregated in SSDM maps of local species richness and averaged habitat suitability probabilities.

The average contribution of each environmental variable across all selected models was calculated using Pearson’s correlation coefficient between fitted values and predictions, with each variable permuted via a randomisation procedure. In this method, low coefficients correspond to high variable importance (Thuiller et al., 2009). All analyses were done in the R statistical environment version 3.5.1 (R Core Team, 2020) using the SSDM package (Schmitt et al., 2017).

To test the significance of staked models, we also used MaxEnt v3.3.3k software with 25 replicates (Phillips et al., 2006), according to the published methods following the standard protocol (Zurell et al., 2020). At the same time, models were built both for the distribution of each species and for the complex of species for the current and future scenarios (SAGA GIS, QGIS). Reliability of the obtained models was assessed using Multiple Regression Analysis in SAGA GIS. This tool is used to analyze the relationships between several independent variables (predictors) and one dependent variable. Additionally, this method helps evaluate the similarity of the obtained models by analyzing the coefficient of determination (R^2), integrating joint ranges, and analyzing residuals (Bahrenberg et al., 2017). In SAGA GIS it is possible to create maps showing how predicted values from a multi-regression model vary across a geographic area and visualize identified clusters through cluster analysis. By combining these methods one can gain deeper insights from spatial data (Nekrasova et al., 2019). Statistical processing of the obtained data was carried out in Statistica v 10.0.

3. Results

All seven studied species of reptiles have their own biotope specialization and are unevenly distributed over the study area. To understand the trends associated with climate change, we analysed the modelling results and the building of the ESDM model for each of the species. Therefore, we separately analysed the distribution of these 7 species using landscape, agro-ecological and bioclimatic predictors (International Institute for Applied Systems Analysis (IIASA) / Food and Agriculture Organization of the United Nations (FAO), Global Agro-Ecological Zoning (GAEZ) and GlobCover factors, www.fs.usda.gov/ccrc/topics/wildlife/reptiles/), based on our original data collected in the field.

3.1. Ensemble modelling of species richness

The weighted average area under the curve (AUC) across the four models of species diversity was ~ 0.65 , comprising a RFs model ($AUC = 0.63$), GLM ($AUC = 0.64$), SVM model ($AUC = 0.66$), and a MaxEnt model ($AUC = 0.67$).

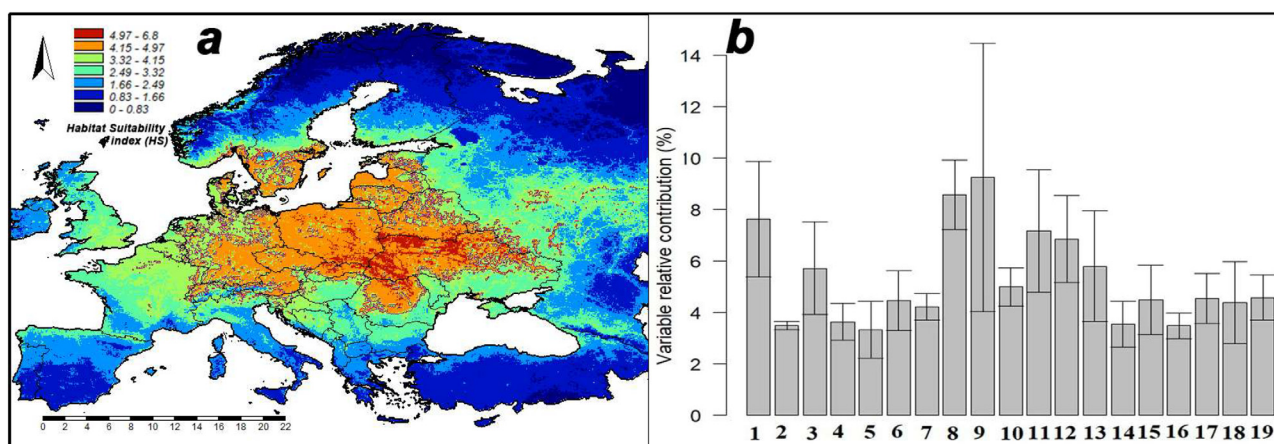


Fig. 1. Mean species richness of seven reptile species in Eastern Europe and adjacent areas: (a) under current climate, using bioclimatic, agro-ecological and landscape factors from the Global Agro-ecological Zones GAEZ & GlobCover; (b) histogram of variable relative contributions evaluated with Pearson's coefficient (x-axis labels refer to environmental variables in Table 2).

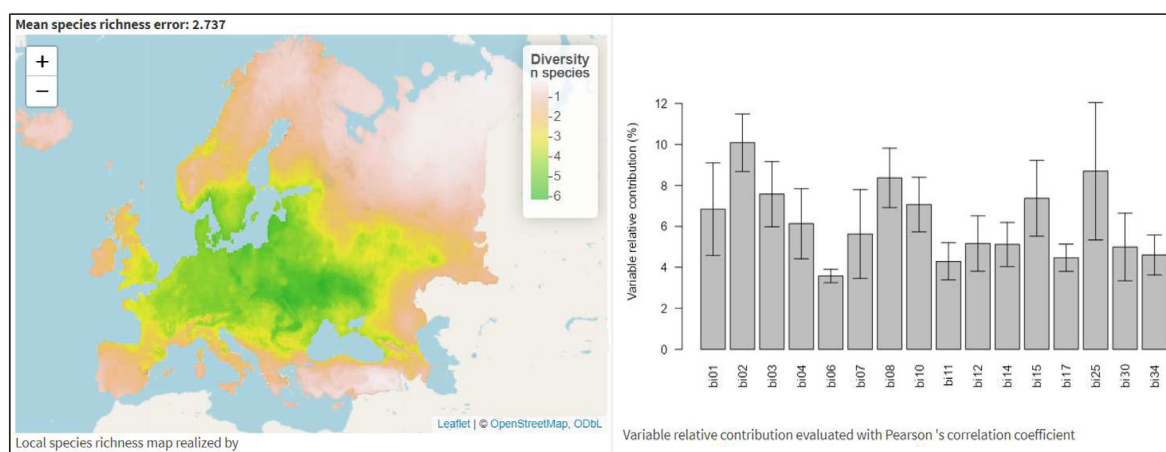


Fig. 2. Mean species richness of seven reptile species in Eastern Europe and adjacent areas: (a) under current climate, CliMond; (b) histogram of variable relative contributions evaluated with Pearson's coefficient (x-axis labels refer to environmental variables in Table 1).

The number of species was maximum (up to seven species, i.e. all study species) in the central part of the range, and decreased towards the edges of the range, up to four species at the north, and three at the south of the distribution range, illustrating an edge effect (Fig. 1).

According to the modelling results using GAEZ and GlobCover databases, the biggest contribution (> 5 %) to the species richness model, and therefore the spreading of these species within the studied area, was made by seven variables: Accessibility; Air frost number; Dominant land cover pattern; Forest cover; Globcover, 2009; Mean annual temperature and Median altitude. The same modelling using variables from CliMond database showed similar picture, but with less rapid differences between variables, ten of which had high contribution to the built model (> 5 %). Among these variables, bio02 (Mean diurnal temperature range), bio08 (Mean temperature of wettest quarter) and bio25 (Radiation of driest quarter) had the highest contributions to the model. These factors are crucial for the reptile species, as they limit their ability to survive during the winter period and breed during the summer period in a continental climate (Fig. 2). Therefore, we applied further cluster analysis with the chosen GAEZ and GlobCover variables.

According to this consensus approach and analyzing the influence of CliMond factors, local species richness of study reptile species across Europe under current climate was primarily associated with temperature-related factors (bio1 and bio2, more than 10%), and to a lesser extent with bio15 (Precipitation seasonality) (Fig. 2b).

3.2. Environmental factors defining forest species

We have statistically confirmed that the studied herpetofauna can be divided into two herpetological complexes according to contributions of predictors from the GAEZ dataset and GlobCover. So, using cluster analysis (Ward's method and Pearson correlation distance), they can be divided into two clades – “forest species” and “widespread species” (Fig. 3).

Following the Cluster analysis, it can be seen that factors such as “Dominant land cover pattern”, “Forest land” and “Air frost number” tend to be the most contributive to modelling of the cluster of “forest species” – *A. colchica*, *V. berus* and *Z. vivipara*. Meanwhile, other species, clustered to other groups tend to have other variables with greatest contribution to their models: “Accessibility” for *L. agilis*, “Globcover” for *N. natrix*, “Mean annual temperature” and “Median altitude” for *E. orbicularis*. For *C. austriaca* none of the used variables showed clearly highest contribution to the model (Fig. 3).

To understand the climatic preferences of reptiles, we examined both the SDM models of each species and the ESDM models of 2 groups of species with different specializations in different regions and different habitats: so-called “forest species” (northern part of Eastern Europe) and “widespread species” (from the Black Sea – Ukraine to the Baltic Sea – Latvia).

The species-specific general models predicted a northward shift for all species. To illustrate, the potentially suitable territory, based on the

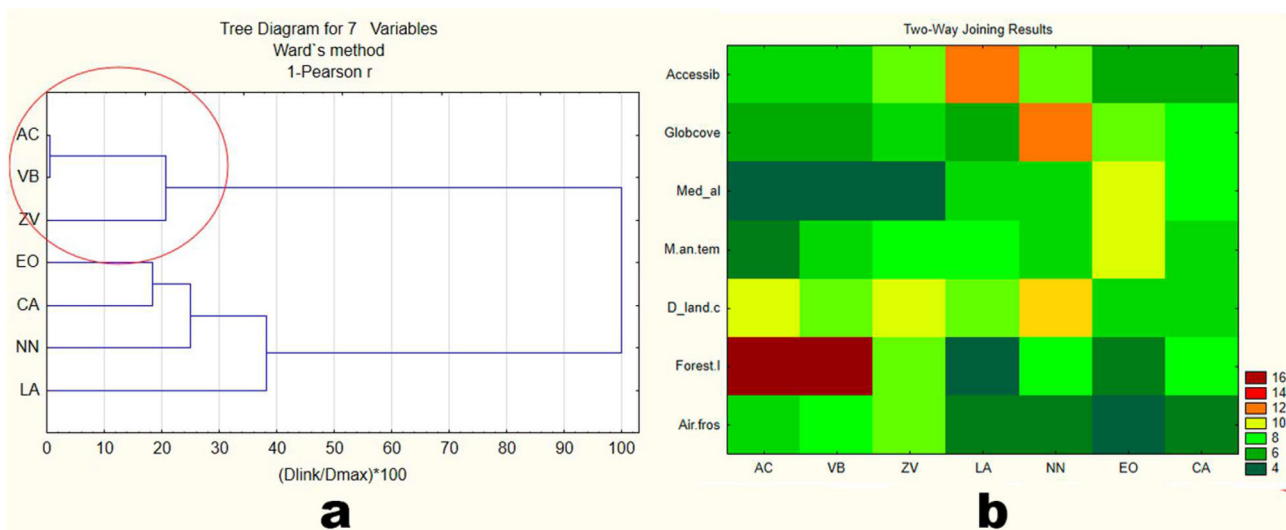


Fig. 3. Results of cluster analysis using the most contributing predictors [(Accessib. – “Accessibility”; D_land.c – “Dominant land cover pattern”; Forest.l – “Forest land”; Globcove – “Globcover”; M.an.tem – “Mean annual temperature”; Med_al – “Median altitude”; Air.fros – “Air frost number”)], distinguished when building ESDMs for each species [AC – *A. colchica*; VB – *V. berus*; ZV – *Z. vivipara*; EO – *E. orbicularis*; CA – *C. austriaca*; NN – *N. natrix*; LA – *L. agilis*]: (a) tree diagram for the 7 species in Eastern Europe, and (b) two-way joining results (with the scale representing the contribution of each variable (%) chosen from the initial modelling and used for the analysis).

Table 4

Percentage of potentially highly suitable area (according to modelled habitat suitability (HS)) for 7 species in Eastern Europe, and change in available HS between current and 2050 climates; those species considered to be “forest species” according to the cluster analysis are marked with *.

Species		Percentage of potentially suitable habitats (according to modelled HS) in Eastern Europe (%)		Change (%)
		Current	2050	
“widespread species”	<i>E. orbicularis</i>	30	48	+60
	<i>L. agilis</i>	36	41	+14
	<i>N. natrix</i>	39	43	+10
	<i>C. austriaca</i>	22	24	+9
“forest species”	<i>A. colchica</i> *	26	29	+12
	<i>Z. vivipara</i> *	28	20	–29
	<i>V. berus</i> *	21	10	–52

predicted habitat suitability (HS), for the “widespread species” (*E. orbicularis*, *L. agilis*, *N. natrix*) covers between 30% and 39% of Eastern Europe (Fig. 4). At the same time for these species, despite the northward shift of their range and the reduction of the range in the south, a slight increase in the area of suitable habitat is expected by 2050.

Contrary, for the “forest species”, a reduction (by 1.4–2.2 times) in territories is predicted in the 2050, especially for *Z. vivipara* (from 28% to 20%) and *V. berus* (from 21% to 10%). For *A. colchica* the suitable habitat range area, even taking into account the mentioned northward shift, will increase from 26% to 29% (Table 4).

4. Discussion

Based on the modelling results, it was found out that although the focal reptile species have different specializations and occupy different micro-habitats, they face the same prospects in the future—reduction in the area of suitable habitat in the south of the range with its northward shift. The results of our modelling show that the greatest richness of reptile species is observed in the central part of their shared range (up to 7 species). As we move towards the edges of the area occupied by these reptile species, the number of species decreases (Marmion et al.,

2009). The situation is worsened not only due to the recent intensification of agricultural processes in the southern areas and global climate change, but also as a result of military actions and accompanying anthropogenic transformations of nature since 2014. For example, taking part in Ukraine for more than 10 years now, military conflicts led to the destruction of the remnants of forested biotopes leaving no place to survive for forest-associated reptile species. These transformations include: increasing the agricultural lands by plowing the river valleys, conducting construction works, creating trenches, dugouts and other military constructions in terms of self-defense from the aggression, digging channels, planting invasive species of plants, and changing of hydrological regimes (Marushchak et al., 2019; Nekrasova et al., 2021, 2022). Therefore, reptile populations in the southern part of their range face significant pressure, as not all species have time to adapt to rapidly changing climatic conditions and anthropogenic pressure (Pecl et al., 2017; Mi et al., 2022).

In the study, SDMs and SSDMs were built for seven species using four modeling algorithms (Table 3). It should be noted that these models provide the potential ecological niche of a species based on climatic and other abiotic factors presented in Tables 1 and 2. This study does not account for biotic interactions, such as competition and predation, which can restrict a species’ realized niche. Therefore, the resulting models should be interpreted as a prediction of potential, rather than actual, species distributions.

Species that prefer “forest and wet biotopes” include *A. colchica*, *Z. vivipara*, *V. berus* which are found in the northern part of Eastern Europe (Fig. 5). Similarities between the SDMs of these species were identified, with a R^2 (or coefficient of determination) reaching 81%. These species also have their own special breeding strategy—ovoviviparity and do not depend on warm climates. We found that the important predictors for modelling the distribution of these 3 species are precisely the features of the land cover—“Forest land” and “Dominant land cover pattern”, as well as the “Air frost number” associated with the characteristics of wintering. While these species can be considered as mainly forest zone species, in the northern parts of their ranges they show clear preferences for disturbed sites with canopy gaps or/and more open and well-lit forest types (Čeirāns, 2004, 2007).

Species in the category “widespread” have a multidirectional specialization, and, at the same time, they are eurybiontic and can occupy

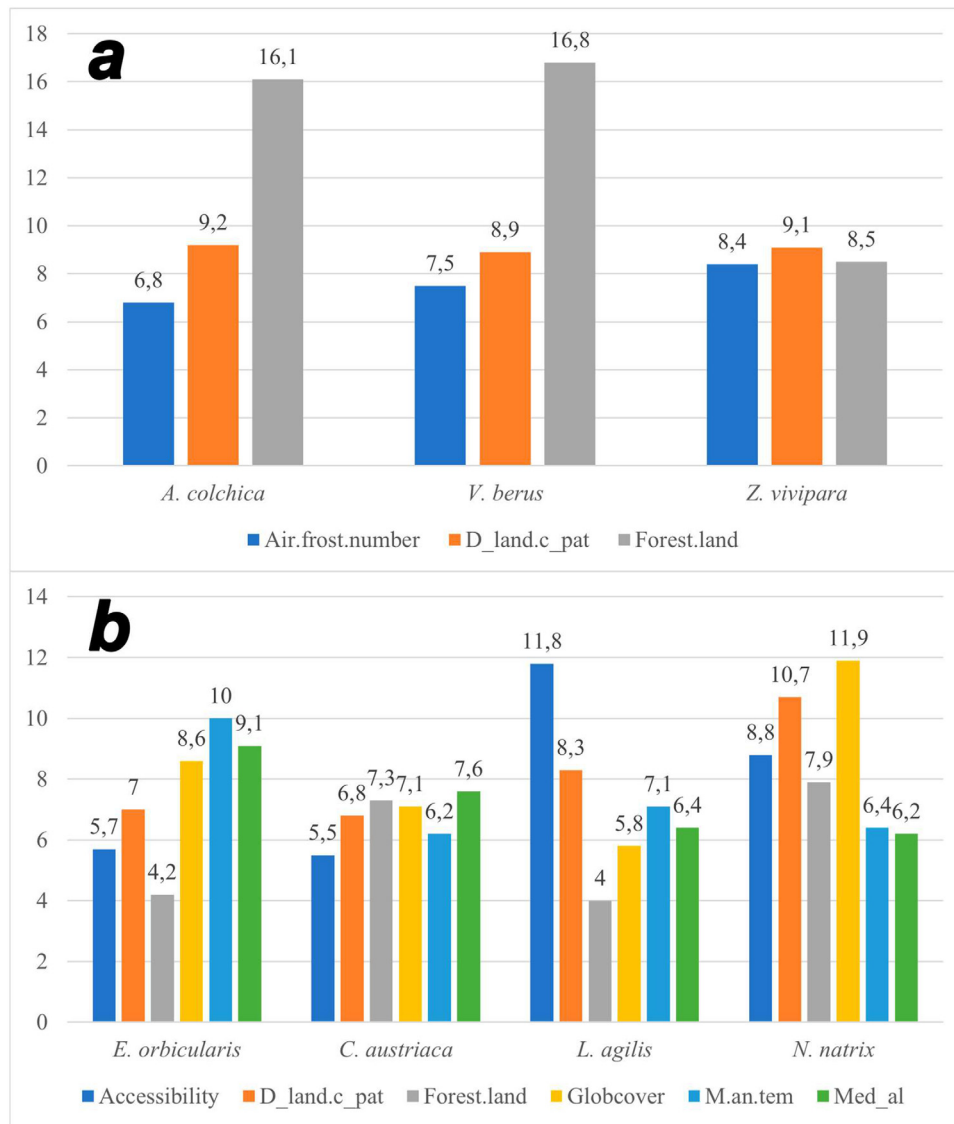


Fig. 4. Graph of most contributing predictors (factors, see Environmental data collection and processing section of Materials and Methods, Table 2) (Air.frost.number – Air frost number; D_land.c_pat – Dominant land cover pattern; Forest.land – Forest land; Accessibility – Accessibility; Globcover – Globcover, 2009; M.an.tem. – Mean annual temperature; Med_al – Median altitude) evaluated with Pearson (% see Fig. 3) for building ESDMs involving 7 species of Eastern Europe: (a) “forest species” and (b) “widespread species”.

a wide variety of biotopes and even tend to synanthropization, especially in the south of the range, except for *C. austriaca* (a rare species protected in all studied area (Akimov, 2009; Nekrasova et al., 2013)). For *C. austriaca*, “Median altitude” is the first amongst the predictors, and then only “Forest land”. This is quite understandable, since this species prefer transitional, semi-open habitats on the northern periphery of the species range in Latvia (Čeirāns and Nikolajeva, 2017), and is also found in complex gulch systems in the steppe region.

For the widespread eurybiontic lizard *L. agilis*, the semi-aquatic species snake *N. natrix* and pond turtle *E. orbicularis*, habitat is associated to water bodies and rivers throughout Eastern Europe (similarities between the SDMs of these species were found at R^2 around 60%). For *E. orbicularis* the limiting factor (GAEZ), in addition to the “Mean annual temperature”, is a relief feature—“Median altitude”, because this turtle species prefers lowlands (river floods and non-freezing water bodies) and does not actually occur in the mountain areas. In the steppe zone, where there are few lakes, it survives in anthropogenic water bodies and tendencies towards synanthropization are also noted (Marushchak et al., 2019; Nekrasova et al., 2021). Sometimes, pond turtles occur together with invasive *T. scripta* (Nekrasova et al., 2022, 2024) in the south of Eastern Europe and competition is possible. The study of the influence of bioclimatic factors allowed to conclude that over time changes to the

pond turtle’s home range are possible: an increase in suitable areas by 2050, with a shift in a north-east direction and significant fragmentation of potentially suitable habitats in the south, and then their reduction by 2090 (Pupina et al., 2018). Interestingly, in the north of their range, European pond turtles are characterized by particular morphological features, e.g., their body size has been reported to relate to climatic and geographical gradients (Joos et al., 2017) as confirmed by our field observations (Nekrasova et al., 2020; Pupins et al., 2020).

There are also noted morphological features in other species of reptiles, associated with climatic factors such as “humidity” and ecological and landscape features in the continental biogeographic zone of Ukraine. Thus, in the most widespread reptiles of Ukraine *L. agilis* and *N. natrix*, which are found in a wide variety of biotopes (important predictors are “Dominant land cover pattern” and “Accessibility” (similarity between the SDMs of these species reached R^2 around 70%). The emergence of new and rare morphotypes in certain specific biotopes has been recorded. For example, individuals with a rare coloration *L. agilis* var. *erythro-(viridi)-nota* (Fig. 6b) are more associated with forest and humid biotopes. Moreover, they are often found in conjunction with *Z. vivipara* and are very similar in colour. Recently, a large number of *N. natrix* melanistic individuals (without yellow “ears”, Fig. 6d) have also appeared in the north of the range.

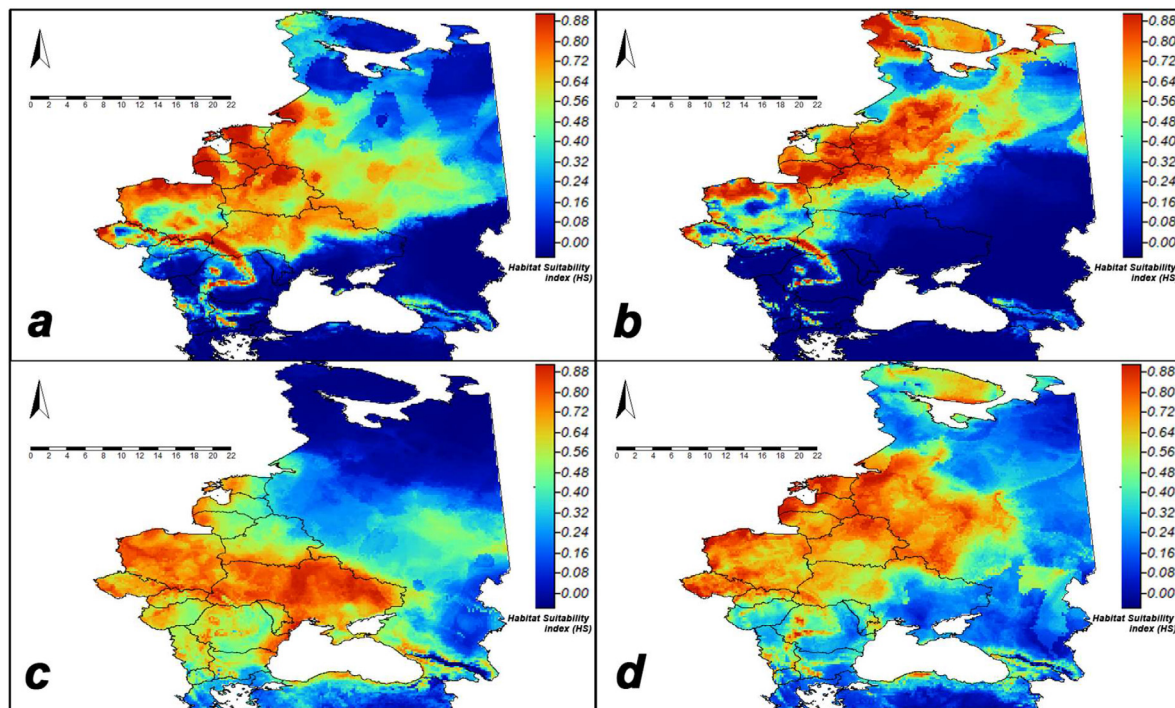


Fig. 5. As a result of Multiple regression analysis, the following models were created to represent the area of intersection of current suitable habitats for the “forest species” *V. berus*, *A. colchica* and *Z. vivipara*, under current (a) and 2050 conditions (b) and for four “widespread species”, namely *N. natrix*, *E. orbicularis*, *L. agilis*, *C. austriaca*, under current (c) and for 2050 conditions (d).

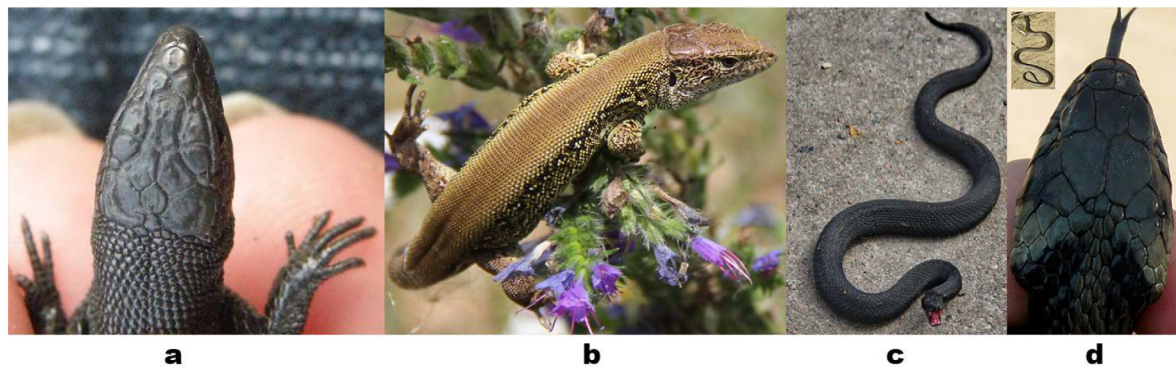


Fig. 6. Morphological features in four species of reptiles of Ukraine, associated with climatic factors: (a) *Z. vivipara* var. *nigra*; (b) *L. agilis* var. *erythro-(viridi-)nota* (Nekrasova et al., 2018) (c) *V. berus nikolskii*; (d) *N. natrix melanist* (photo Nekrasova O.).

In a study of the distribution of melanistic lizards, rare for Ukraine, *Z. vivipara* var. *nigra* (Fig. 6a), a correlation was found with factors such as Bio24 “Radiation of wettest quarter” (50.4%) and Bio35 “Mean moisture index of coldest quarter” (18.9%). Black lizards are also more common in more humid forest biotopes, sometimes together with the black viper *V. berus nikolskii* Vedmederja, Grubant et Rudaeva, 1986 (MaxEnt, CliMond, Fig. 6c). It is expected that the emergence of melanistic morphotypes allows the melanistic individuals to absorb heat more rapidly, allowing them to accommodate energy resources faster than their relatives of normal coloration. Also, melanistic individuals have benefits from more effective camouflaging against dark background (Mader et al., 2022).

Thus, forested wetland biotopes and wetlands play a significant role in preserving not only reptile species richness but also the wide variety of reptile morphotypes. In Ukraine, some “forest species” may face the brink of extinction in the future (especially in the south) (Fig. 4; Marushchak et al., 2019). Therefore, we used this new knowledge based

on such modelling to develop protected networks such as the Emerald Network in Ukraine. At current stage of the creation of objects of the Emerald Network, it is worth stating the increase in the area of such objects for the preservation of one of its key species of herpetofauna—the European pond turtle *E. orbicularis*. As of 2016, the total area of Emerald Network objects for *E. orbicularis* was 4,065,442 ha, which increased to 5,270,771 ha (+30%) after the addition of new sites approved by Secretariate of the Bern Convention. Several additional sites, created in part to protect *E. orbicularis* and covering a total area of 1,662,490 ha, have been awaiting inclusion in the Emerald Network since 2021 (Marushchak et al., 2019; Vasyliuk and Marushchak, 2020). This inclusion would triple the total area dedicated to species within the Emerald Network. At the biogeographical seminar held in Minsk (Belarus) on June 18–19, 2019, international experts assessed the adequacy of the Emerald Network’s development within existing biogeographical regions. The conclusions, outlined in the draft document Emerald Second Biogeographical Seminar BY, MD and UA 18–19 June 2019—Draft

Conclusions, evaluated the representation of animal species listed in Res. No. 6 (1998) of the Bern Convention within proposed Emerald Network Sites in Belarus, the Republic of Moldova and Ukraine (Alpine, Boreal, Continental, Pannonian and Steppic). Using a GIS-approach, the Emerald Network for *E. orbicularis* in Continental biogeographic region was classified as “IN MIN”, meaning habitats / species must be added to the database in existing network areas, but without the need to add new areas. These international and regional initiatives emphasize the need for coordinated cross-bordering actions to conserve reptiles and their natural habitats.

In terms of practicality, the results we obtained can help to capture the full suite of selected reptile species richness within regions in the north and south of the range for designing an effective protected-areas network that will simultaneously meet goals for both ecological representation and persistence in the face of climate change. In this respect, long-term nature conservation goals in Latvia could be reached in the areas outlined by the SSDMs in Kurzeme, Riga, and Zemgale provinces. In Ukraine, long-term stability is expected in the western part of the country, namely in Transcarpathia, Lviv, Ternopil, and Ivano-Frankivsk regions, as well as in the southern portion of Volyn region.

To effectively protect reptile populations in North-Eastern Europe, a comprehensive approach is needed to address the various threats they face. These include:

- protecting and restoring suitable reptile habitats: this involves conserving natural areas, such as forests, wetlands, and grasslands, which provide essential conditions for breeding and shelter;
- managing invasive species: this involves implementing effective control and eradication programs for invasive species that pose threats to native reptile populations;
- reducing habitat fragmentation: this involves minimizing human activities that fragment habitats, such as urbanization and infrastructure development;
- promoting public education and awareness: this involves raising public understanding of the importance of reptile populations and the threats they face, fostering community support for conservation efforts.

It is by implementing the strategies, that take into account the results of short- and long-term bioclimatic modelling, we can safeguard the future of reptile populations in North-Eastern Europe and ensure the continued health and resilience of these ecosystems. It would be interesting to continue such studies in other regions of the European range to preserve the most vulnerable protected species of reptiles (protected by the Bern Convention).

5. Conclusions

The ensemble modeling of local reptile species richness in Eastern Europe has revealed data on the spatial structure and future prospects of widely spread and protected species population distribution. The results showed that the seven studied reptile species exhibit different biotope specializations and are unevenly distributed across the region. Particularly high species richness is observed in the central part of Eastern Europe, with a gradual decrease towards the edges, highlighting the edge effect. Importantly, we showed that local species richness of reptiles primarily depends on temperature and precipitation seasonality, leading to a predicted northward shift in the distribution of these species as climate change progresses. For widespread species such as pond turtle *E. orbicularis*, snake *N. natrix* and lizard *L. agilis*, a slight increase in suitable habitat is anticipated by 2050, despite a reduction in their range in the south. Through cluster analysis, we also could distinguish above mentioned “widespread species” “forest species” based on their habitat preferences and ecological requirements. This classification emphasizes the need for targeted and smart conservation strategies tailored to the specific needs of each group. The most vulnerable populations of “forest reptiles”, namely common adder and viviparous lizard, in terms of

climate change and complex impact of many other factors tend to be located in the south of their range. By 2050 the greatest reduction in range is expected for the lizard species *Z. vivipara* (by 1.4 times) and snake *V. berus* (by 2.2 times). This is also due to the fact that their habitats have been recently actively anthropogenically transformed in the south of their range which greatly limits their ability to adapt to changing climate. In present times, beside climate drivers, military conflicts may heavily contribute to the risks of extinction of these species (and others as well). Therefore, these two species should be granted the first priority in providing measures for saving their key habitats in the areas where the most suitable (in terms of climatic modelling) territories are situated.

Abbreviations

SDM - standard distribution model
 ESDM - ensemble species distribution model
 GIS-modelling – geographic information system modelling
 SSDM - stacked species distribution model
 RF - Random Forest
 SVM - Support Vector Machines
 GLM - Generalized Linear Models
 MaxEnt - Maximum Entropy Modelling
 AUC - area under the relative operating characteristic curve
 SES - sensitivity-specificity equality

Declaration of competing interests

The authors declare that there are no known competing financial interests or personal relationships that influenced the work reported in this paper.

CRediT authorship contribution statement

Oksana Nekrasova: Writing – original draft, Visualization, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Mihails Pupins:** Writing – review & editing, Supervision, Resources, Project administration, Funding acquisition, Formal analysis, Conceptualization. **Volodymyr Tytar:** Writing – review & editing, Validation, Software, Investigation, Formal analysis, Data curation. **Andris Čeirāns:** Writing – review & editing, Supervision, Project administration, Funding acquisition, Conceptualization. **Oleksii Marushchak:** Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Formal analysis, Conceptualization. **Arturs Škute:** Writing – review & editing, Funding acquisition, Data curation, Conceptualization. **Kathrin Theissinger:** Writing – review & editing, Validation, Supervision, Resources. **Jean-Yves Georges:** Writing – review & editing, Validation, Supervision, Resources, Methodology, Funding acquisition, Conceptualization.

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