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Ecological modeling of the Grass snake (*Natrix natrix*) and Dice snake (*N. tessellata*) in Bulgaria confirms their wide-ranging distribution

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Abstract. We developed Environmental Niche Models (ENMs) for the two species of semi-aquatic snakes from the genus *Natrix* occurring in Bulgaria (*N. natrix*, *N. tessellata*). The Maxent-generated ENMs had high AUC values (>0.86). Three variables common between the two models contributed 73.7% for *N. natrix* and 70.6% for *N. tessellata*: 'distance to (the nearest natural) flowing water' (28.1% for *N. natrix* and 32% for *N. tessellata*), 'distance to (the nearest) standing water' (25.5% and 14.4%), and 'elevation' (20.1% and 24.2%). *Natrix natrix* has a wider ecological niche, potentially comprising 15% of Bulgaria, compared to 8% for *N. tessellata*; the niches overlap to a large extent (Shoener's D = 0.708). These ENMs are especially helpful for guiding future surveys, especially in under-sampled areas.

Keywords: Maxent, modeling, species distribution models, niche, surveying.

Introduction

The Common grass snake *Natrix natrix* (Linnaeus, 1758) and the Dice snake *N. tessellata* (Laurenti, 1768) are widely distributed across the Palearctic, where they inhabit a range of terrestrial and aquatic habitats, and can be easily observable, also due to their often high local densities (Speybroeck et al. 2016). In Bulgaria (SE Europe), these two natricine semi-aquatic snakes are common, abundant, and occur throughout at elevations from the sea level up to 2,000 m for *N. natrix* and 1,420 m for *N. tessellata*, although observations are typically below 1,000 m (Tzankov et al. 2014). They are associated with lotic and lentic aquatic habitats ranging from freshwater small semi-temporary waters to rivers and the sea coast, with *N. natrix* also occurring in gardens, open woodlands, rough grasslands (Speybroeck et al. 2016). *Natrix natrix* has a diverse diet often connected to prey items linked to aquatic habitats and consisting predominantly of amphibians and fish, with subadults also consuming invertebrates, while *N. tessellata* is a fish specialist (Šukalo et al. 2014, Speybroeck et al. 2016). *Natrix tessellata* can also attain potentially high densities locally (>5,800 individuals/~18 ha island) and have a number of avian and mammalian predators (Ajtić et al. 2013); some predators might be of conservation importance. Ecologically, coupled with their ectothermic biology, these characteristics make them an important component of the food web and the transfer of energy from aquatic to terrestrial environments.

The genus *Natrix* is extensively studied in many parts of its range. However, at least in Bulgaria, the limited financial and man-power resources have hindered research on their biology, including their distribution and ecological requirements. This can be ameliorated by prioritizing both general and specific sampling areas, based on increased understanding of the eco-physiological drivers of their distribution. Environmental niche modeling (ENM) based on real observations is one such solution (Mizsei et al. 2016). Locally, models using a similar method as the one we apply here were generated for both *Natrix* species for the Vitosha Mountain (Tzankov et al. 2014).

The main aim of this study was to generate the first models of the potential distribution of the two *Natrix* species in Bulgaria, which would be among the few for the genus overall. We set ourselves the following tasks: 1) Create robust ENMs representing the potential for their distribution; 2) Identify and compare major eco-geographical factors contributing to the ENMs; 3) Identify understudied areas; 4) Estimate the niche overlap between the two species, to confirm/refute if the models produce the expected differences between the ecological niches based on our expert knowledge.

Materials and methods

Study species

Natrix natrix has a ubiquitous distribution, predominantly at lower elevations but even up to 2,000 m a.s.l. (Buresch & Zonkow 1934, Naumov & Tomović 2005). It inhabits all types of freshwater wetlands (e.g. streams and river courses, temporary and permanent ponds, spills, natural and artificial lakes, reservoirs, marshes, canals), but also may be observed in brackish waters, such as river mouths at the Black Sea (Tzankov et al. 2014). *Natrix natrix* can move up to 2 km from its active season habitats to reach wintering dens or up to several kilometers in search of suitable egg laying sites (Biserkov & Naumov 2007b, Tzankov et al. 2014, Speybroeck et al. 2016). The diet consists of adult amphibians and their larvae (predominantly anurans, but also urodelans) and fish, occasionally small mammals, birds, and lizards.

Natrix tessellata is widespread in diverse water bodies throughout Bulgaria. About 85% of the known localities are at 0–500 m, with only two records above 1,100 m, with the highest being at 1,420 m from Rila Mountain (Naumov et al. 2011, Tzankov et al. 2011). It withstands highly elevated blood plasma sodium levels (Brischoux & Kornilev 2014, Brischoux et al. 2017), partially explaining why it is very common along the Black Sea and in brackish waters. It feeds predominantly on fish, but its diet includes frogs and their larvae, newts, and small rodents (Beshkov 1978, Beshkov & Nanev 2002). While it could venture up to 5 km from the shore within shallower waterbodies, on land it is usually located within 20 m of water (Biserkov & Naumov 2007a).

Study site

The territory of Bulgaria covers ca. 111,000 km² and encompasses diverse eco-physiographic conditions and habitats. Elevation ranges from 0 to 2,925 m a.s.l., with highly diverse relief, stretching from extensive plains and lowlands to subalpine and alpine mountains. Five hypsometric belts consist of lowlands (0–200 m, 31.4% of the territory), hills (200–600 m, 41.0%), low mountains (600–1,000 m, 15.3%), mountains of average height (1,000–1,600 m, 9.8%) and high mountains (> 1,600 m, 2.5%) (Simeonov & Totzev 1997). The climate is dominated by Mediterranean, Oceanic and Continental influences, combining 12 Köppen-Geiger climate classes (Beck et al. 2018).

Within the hydrographic resources of Bulgaria, rivers represent the highest volume and are most widely distributed throughout the country; overall, over 1,200 rivers run for about 19,700 km, but most of these are small and many dry annually (Varbanov 2002). The small area and the diverse relief limit the number of large internal rivers – only 30 rivers are longer than 100 km (Varbanov 2002).

Ecological niche modeling

For manipulation, visualization, and analysis of the digital layers and the observations data we used ArcGIS v.10.3 (ESRI, Redlands, CA, USA). We generated the model using the software Maxent v.3.4.4 (Phillips et al. 2006, 2017), which uses a machine-learning technique called maximum entropy modeling and is based on species presence. We used a similar methodology to model on a national level other semi-aquatic species in Bulgaria: the Alpine newt *Ichthyosaura alpestris* (Naumov et al. 2020), the European pond turtle (*Emys orbicularis*) and the Balkan terrapin (*Mauremys rivulata*) (Kornilev et al. 2017), and locally the herpetofauna of Vitosha Mountain (Tzankov et al. 2014).

The modeling was based on actual observations due to the practical impossibility of proving absences. Using published literature and personal unpublished observations provided by users of the data collection system SmartBirds.org with the integrated SmartBirds Pro Android application, we compiled into a Geographic Information System (GIS) database over 2,150 observations (1,520 with coordinates, post-2000) for *N. natrix* and 1,690 (1,042) for *N. tessellata*; overall, data were collected mostly opportunistically by multiple observers until 2022. About 90% of records are post-2010. This temporal distribution should reflect more accurately correlations with the available climatic and habitat data and should improve the accuracy of the localities due to the increased use of handheld Global Positioning System (GPS) units and Android devices with precise geolocation capabilities.

To minimize spatial autocorrelation, we subsampled the observations to be used for modeling by using a randomly generated sample where the minimum distance between adjacent locations was 200 m. This distance was based on recorded mean movements for the more mobile species *N. natrix* (Madsen 1984). This also reduces sampling bias through the use of systematic sampling, showing better results than other methods especially in cases where bias is unknown (Fourcade et al. 2014). The data distribution covers the whole country, thus it likely includes the range of environmental factors (e.g. elevation, temperatures) experienced by the species.

To avoid selecting unrealistic background locations, we used a mask to exclude areas above the maximum known elevations where it is unlikely to find the species and added a buffer of 100 m (thus, 2,100 m for *N. natrix* and 1,520 m for *N. tessellata*).

Given the mobility of the species, the error of specialized handheld and mobile GPS sensors (min. 3 m, but can be as high as 15 including due to human error), the resolution of the existing layers (40 m for DEMs, ~1 km for climatic variables), and the size of the water bodies, we modeled with a pixel size of 40 m. Layers with original pixel size greater than 40 m (WorldClim, Global Aridity Index & Global Potential Evapotranspiration) were unified to 40 m resolution by "cubic convolution". Such resolution matches the recommendation to fit models with the finest possible analysis grain that is also closely related to the response grain even if occurrence data suffer from some minor positional errors (Gábor et al. 2022). Layers with categorical data were converted to continuous using the Euclidean distance of each grid cell to the closest type cell using the "Euclidean distance" tool in ArcGIS (Vale et al. 2016).

The following set of continuous environmental factors (layers) were used: 1) the 19 climate variables from WorldClim v.2 (averaged over 1970–2000) (Fick & Hijmans 2017); 2) Global Aridity Index & Global Potential Evapotranspiration (CGIAR-CSI Global-Aridity and Global-PET Geospatial Database) (Trabucco & Zomer 2009); 3) elevation (40-m Digital Elevation Model) and derived from it aspect, slope, and annual solar radiation; 4) the Euclidean distance to three types of water bodies: standing water bodies (e.g. dams, ponds, lakes), natural flowing water courses (e.g. rivers, streams, creeks) and artificial canals mostly used for irrigation. The layers with types of water bodies were based on data and categories from the GIS databases of OpenStreetMap and the study on integrated water management (MoEW, JICA). Canals may be locally abundant in many parts of the country and were separated from the natural waters because they are managed for agricultural purposes, resulting in different habitats.

We used the same method and settings to generate all ENMs. The following settings were used in Maxent: replicates with "cross-validate" resampling, 25% of observations used for verification in each replicate, 100,000 background points, logistic output, regularization multiplier = 1.

To minimize collinearity we used the "Absolute value of correlation coefficients ($|r|$)" method (Dormann et al. 2013). For this purpose, 100,000 random geographic points (falling within the modeled territory, excluding the high elevations, and with a minimum distance of 200 m from each other) were assigned the corresponding values of all variables. Spearman Rank Order Correlations were calculated using Statistica v.10 (StatSoft, Tulsa, OK, USA) for the environmental factors, with $|r| = 0.7$ being the cutoff value for correlation. A preliminary model was run with 10 replicates and all environmental factors included. For the final model, environmental factors were retained or removed according to the following scheme: the factor with the highest percent contribution (PC) was retained and all correlated factors were removed; of the remaining factors, the one with the second highest PC was retained and all factors correlated with it were removed, and so on.

The final ENMs were generated with the remaining factors determined from the previous step, through 100 iterations. Pixels with values below those calculated by Maxent for the "Maximum test sensitivity plus specificity logistic threshold" (maxSSS, as one of the best methods; Liu et al. 2005, 2016) were excluded from the ENM. For visualization and analysis purposes, the remaining pixels were classified as "Low", "Medium", and "High" suitability using Jenks Natural Breaks in ArcGIS.

To further assess the real-world predictive power of the produced ENMs, we used previously unused observations from SmartBirds.org (from 2022) and from GBIF (with accuracy ≤40 m; GBIF 2023a,b).

To compare the ecological niche overlap, we used Schoener's D (Schoener 1968), I statistic (Warren et al. 2008), and relative rank (RR; Warren & Seifert 2011), calculated using the Niche Overlap tool of ENMTools 1.4.4.

Results

We produced robust ENMs for *Natrix natrix* and *N. tessellata* for the territory of Bulgaria (Fig. 1). The ENMs have a high degree of predictability, based on the high AUC values (>0.86). The ENMs for *N. natrix* and *N. tessellata* were generated based on 12 and 13 variables, respectively, partially overlapping for both species (Table 1). Variables linked to the presence of aquatic habitats contributed extensively to both ENMs. Three variables explained a total

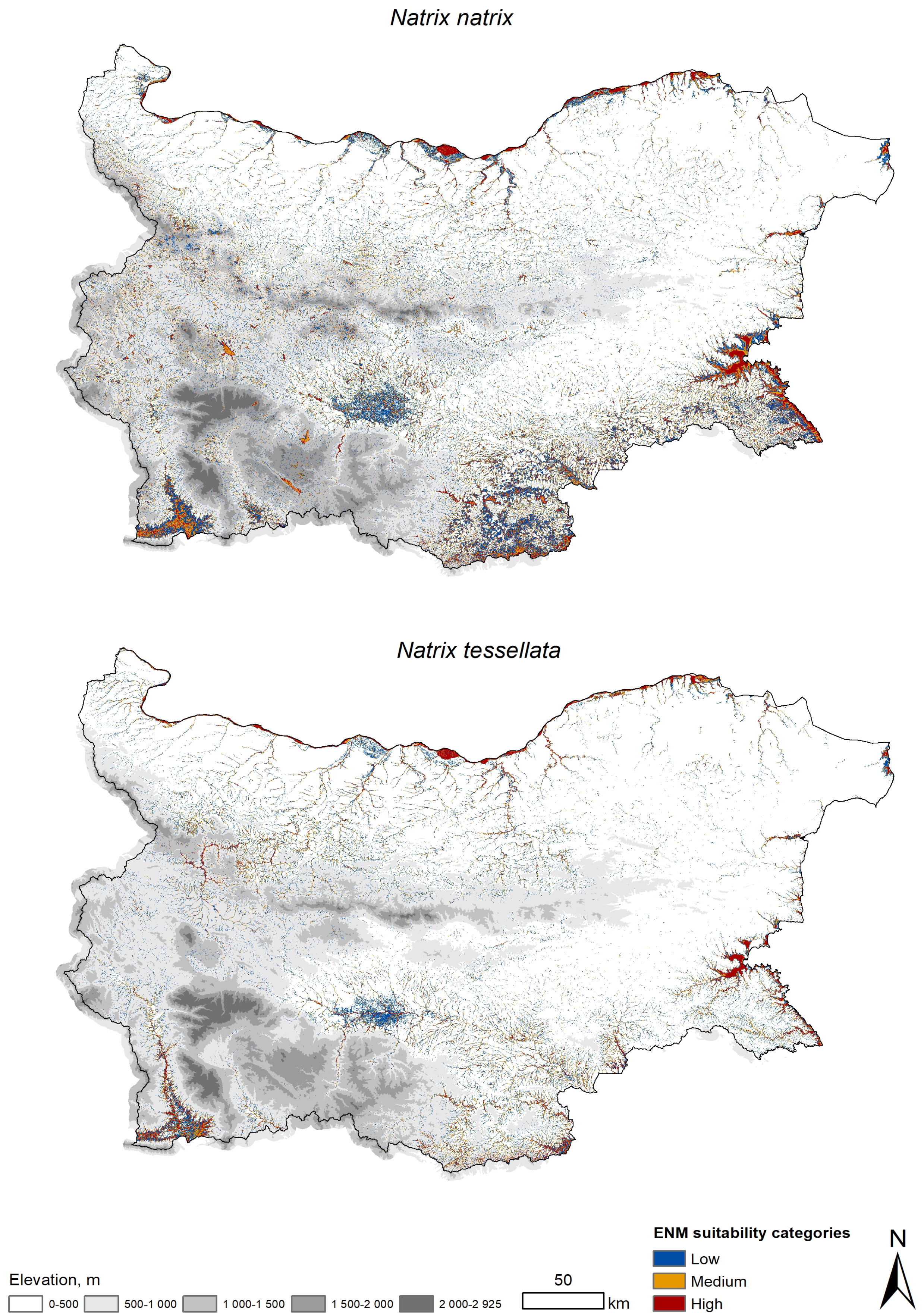

Figure 1. Maxent average Ecological Niche Models for *Natrix natrix* and *Natrix tessellata* in Bulgaria. Original model predictions were categorized into three suitability categories: Low, Medium, and High (0.316–0.453, 0.453–0.640, 0.064–1 for *N. natrix* and 0.254–0.407, 0.407–0.618, 0.618–1 for *N. tessellata*).

of 73.7% for *N. natrix* and 70.6% for *N. tessellata*: 'distance to (the nearest natural) flowing water' (28.1% for *N. natrix* and 32% for *N. tessellata*), 'distance to (the nearest) standing water' (25.5% and 14.4%), and 'elevation' (20.1% and 24.2%). The next variables in terms of their percent contribution were the 'warmest quarter' (Bio18; 8.4%) for *N. natrix* and 'driest quarter' (Bio17; 10.9%) for *N. tessellata*. The remaining variables had very low contributions to the ENMs.

The importance of these variables for our ENMs were corroborated by the jackknife results, specifically the differences in average training and test gain and area under the curve (AUC) on test data between models built *without* and *only with* a given variable (Fig. 2). Differences closer to zero denote variables that contribute more to the ENMs – for both species these include 'distance to flowing water', 'distance to standing water', and 'elevation'.

Expectedly, both ENMs predict suitable habitats throughout the country, linked to the presence of water bodies. Common major areas with suitable habitat include the proximity to the Danube River and its tributaries in the Danube plain, Struma River in the SW, the Thracian plain around Plovdiv city, Eastern Rhodopes Mountains, Strandzha Mountain, and the Black Sea coast (but see discussion) (Fig. 1). However, *N. natrix* has a wider ecological niche, considering the potentially larger suitable territory predicted by the ENMs – 15% of Bulgaria, compared to 8% for *N. tessellata* (Table 2). The two species have similar niches (0, no overlap; 1, complete overlap) based on two indexes we calculated: Shoener's D (0.708), Warren's I (0.928); the third index (Relative rank = 0.785) suggests that wherever the two species are likely to co-occur their niches are similar.

Based on the major changes in curvature of the marginal response curves, the predicted probability of presence for *N. natrix* remains high up to 2.5 km from flowing waters, while it drops off much faster for *N. tessellata* shortly after the zero (Fig. 3). Similarly, *N. natrix* is more likely than *N. tessellata* to be further away from standing waters (up to 1 km) and is likely to be found at much higher elevations, while *N. tessellata* is unlikely to be found above 500 m.

To assess the real-world predictive power of the ENMs, we obtained 507 observations not used in generating the ENMs (*N. natrix*: 112 from GBIF, 178 from SmartBirds.org; *N. tessellata*: 101 from GBIF, 116 from SmartBirds.org) (Fig. 4). Overall, only 16.6% of the new observations for *N. natrix* and 13.4% for *N. tessellata* were outside of the predicted suitable territories; within the low, medium, and high suitability categories were 14.8%, 16.6%, and 52.1% of the records for *N. natrix* and 12.9%, 13.4%, and 60.4% for *N. tessellata*, respectively.

Table 1. Average Percent contribution (%) and Permutation importance (PI) of uncorrelated variables, estimated by Maxent in Ecological Niche Models (ENMs) for *Natrix natrix* and *N. tessellata* in Bulgaria. The average test Area Under Curve (AUC) is presented with the Standard Deviation (SD) following the species names. Models were based on 1,040 and 548 training samples, respectively.

	Natrix natrix				*Natrix tessellata*			
AUC (SD)	0.86 (0.05)				0.93 (0.03)			
Variable	**%**	**min–max**	**PI**	**min–max**	**%**	**min–max**	**PI**	**min–max**
Aspect	0.5	0.2–1.9	0.5	0.2–0.8	1.2	0.2–1.7	0.2	0–0.5
Slope	4.3	2.7–5.1	5.2	3.7–6.3	3.4	2.4–5.2	6	5–7
Elevation	20.1	17–21.5	17.9	16.1–20.1	24.2	22.1–26.8	21.8	19.3–24.7
Canals, distance to	3.3	2.9–3.7	3.2	2.4–3.7	1.1	0.9–1.5	2.3	1.6–2.8
Standing water, distance to	25.5	24.6–26.8	11.8	10.2–13.1	14.4	12.3–16.2	4.4	3.9–5
Flowing water, distance to	28.1	27.2–29.7	27.2	25.2–28.9	32.0	30.9–33.6	25.1	23.4–27
Pot. evapotranspiration	–	–	–	–	3.4	2–4.9	3	1.7–4.8
Solar radiation	–	–	–	–	2.6	2.1–3.4	12.8	11.4–14.2
Temperature (BioX)								
Mean diurnal range (02)	–	–	–	–	1.0	0.7–1.5	1.1	0.6–1.9
Isothermality (03)	1.4	1.1–1.8	5.7	4.4–7.3	–	–	–	–
Min., coldest month (06)	–	–	–	–	1.1	0.7–1.6	0.8	0.5–1.4
Annual Range (07)	0.5	0.3–0.8	7.8	6.4–9.6	–	–	–	–
Precipitation (BioX)								
Seasonality (15)	3.6	2.6–4.1	7.8	5.7–10.2	2.1	1.4–3.2	4.5	3.2–5.5
Driest quarter (17)	3.2	2.4–4.4	3.5	2.3–5.6	10.9	9.7–12.5	15.5	13.1–17.8
Warmest quarter (18)	8.4	7.6–9.9	6.1	4.8–8.2	–	–	–	–
Coldest quarter (19)	1.2	0.8–1.6	3.2	2.3–4.6	2.5	1.8–3.5	2.5	1.9–3.4

Discussion

We developed the first robust ENMs for *N. natrix* and *N. tessellata* in Bulgaria. Overall, we chose settings for the ENMs that should result in models that do not over- or underestimate the niche breadth. This provides the background for two future steps in increasing our understanding of the biology of *Natrix* in Bulgaria. First, we identified broad areas of potentially suitable habitat, where more sampling should be carried out. Second, we identified major ecological and physico-geographical variables that predict the occurrence of the species that should be the focus of further targeted studies. The marginal response curves matched what we know about the biology of the species, especially in relation to their dependence on water bodies and limits in their altitudinal distribution.

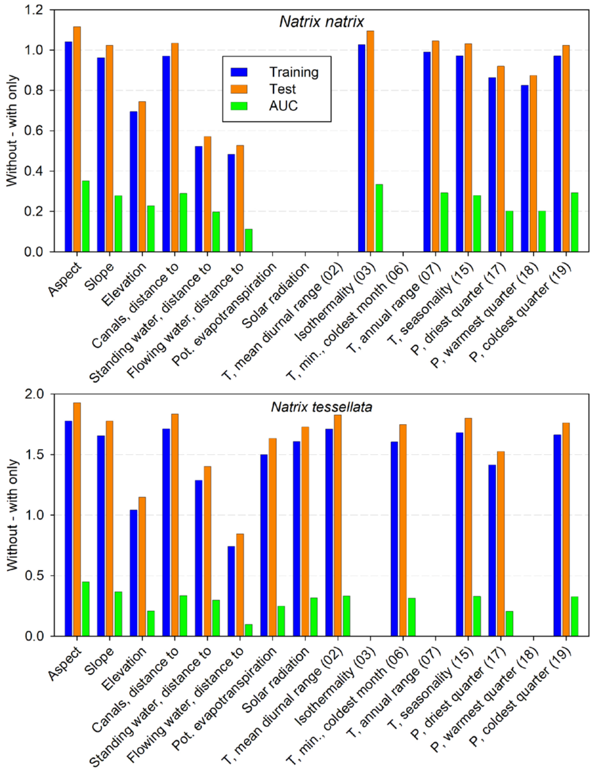

Figure 2. Jackknife results for Maxent ENMs for *Natrix natrix* and *Natrix tessellata* in Bulgaria. Differences are shown in average training, test gain and area under the curve (AUC) on test data between models built *without* and *only with* a given variable. Values closer to 0 denote variables more strongly related to the distribution of each species.

Table 2. Area (in km²) of three classes of suitability, based on Maxent Ecological Niche Models for *Natrix natrix* and *Natrix tessellata* for Bulgaria (110,878.9 km²).

	N. natrix		*N. tessellata*	
Low	8,810.0	7.9%	4,808.6	4.3%
Medium	5,254.9	4.7%	2,672.4	2.4%
High	2,529.7	2.3%	1,459.9	1.3%

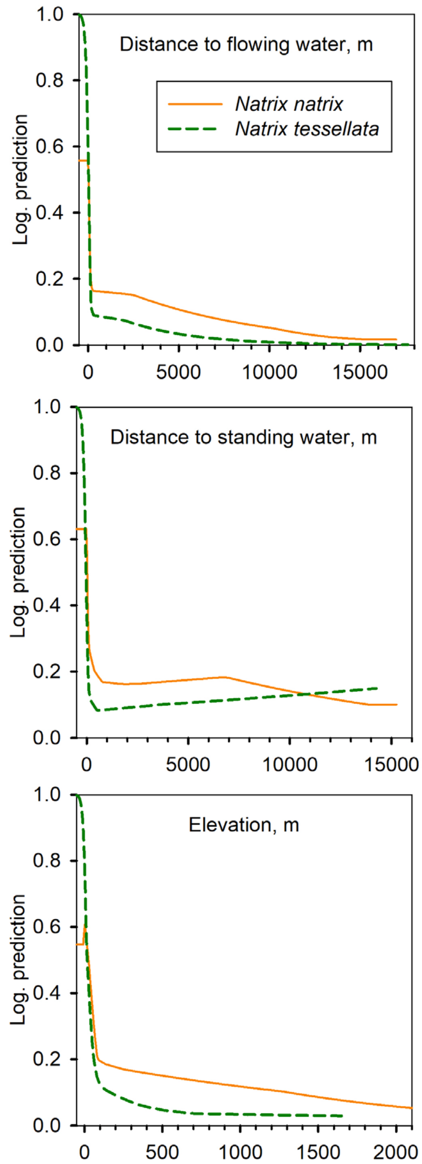

Figure 3. Response curves of major variables contributing to the ENMs for both *Natrix natrix* (–) and *N. tessellata* (- -).

Areas requiring further field sampling

Clear sampling bias is observable, focused around areas with active herpetologists or ones that are of higher interest due to their higher overall diversity (e.g. Vitosha Mountain near the capital Sofia, Plovdiv and Burgas cities; Struma Valley in the SW, Eastern Rhodopes and Strandzha Mountains in the SE, the Black Sea Coast). Although the observations obtained after the generation of the ENMs fell mostly within the predicted suitable territories, subsequent acquisition of observations, especially from areas that are either with presumed absence or high suitability, could further improve updates of the models and aid in filling out missing atlas-level data, especially at grids <10×10 km. Some specific areas that warrant more extensive surveying for both species include most of the tributaries of the Danube in the Danubian lowlands, Dobrudzha and Ludogorie in the NE, and the lowlands between Stara Zagora and Burgas in the SE. The NE is particularly interesting, as it remains among the least sampled herpetological lowland regions in the country. Few observations for both species have been made there. Although no national mapping has been published for *N. natrix* so far, no records for *N. tessellata* were published for the NE in its latest mapping (Naumov et al. 2011). Lack of sampling and limited rivers to serve as dispersal corridors between the existing numerous small ponds (often man-made and used for watering livestock) were identified as likely reasons for these results (Naumov et al. 2011).

ENMs and model contributing factors

The results support our understanding of the closer association of both species to aquatic habitats and their importance. Interestingly, canals seem to have a lower importance for both species (3.3% and 1.1%). We presume this is based on the deteriorated canal irrigation system post-1990 (Varbanov 2002) combined with the fact that typically water is released in the canals only temporarily.

Since most water bodies (especially the standing ones and flowing ones at lower elevations) are situated on mostly flat terrains, the aspect and slope had low contribution. Variables related to temperature (Bio2–7, solar radiation, potential evapotranspiration) likely correlate with elevation and were thus weaker predictors. Also, within the study area elevation seems to account for most of the variation in the climatic conditions suitable to the ecology of the study species. Therefore, variables related to temperature and precipitation contribute so little to ENMs, similar to the results we obtained for two semi-aquatic turtles within Bulgaria (*Emys orbicularis* and *Mauremys rivulata*) (Kornilev et al. 2017).

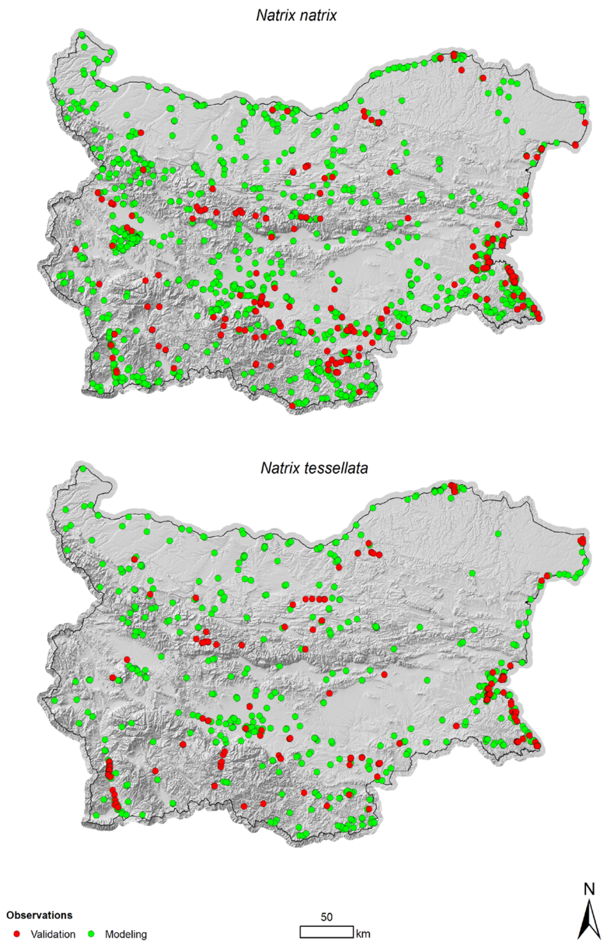

Figure 4. Indicative distribution of observations used in the generation and the subsequent validation of the Ecological Niche Models of *Natrix natrix* and *Natrix tessellata* in Bulgaria.

Especially for *N. tessellata*, the ENM likely underestimates the potential habitats situated along the coast of the Black Sea. Based on personal observations and published studies (Brischoux & Kornilev 2014, Brischoux et al. 2017), likely major part of the immediate coastline could be suitable, if there is a source of freshwater nearby. However, some of the layers (e.g. Bioclim) do not cover completely the whole coastline and thus, this area could not be properly included in the model.

The local ENMs for Vitosha mountain presented in Tzankov et al. (2014) were created using a similar method, the major difference being the use of land cover instead of distance to water. For *N. natrix*, land cover contributed 60.3%, precipitation of the driest month (Bio14) –7.6%, elevation – 6.4%, and solar radiation – 6.3%; for *N. tessellata*, land cover was 44.2%, elevation was 24.4%, precipitation of the driest month (Bio14) was 19.7%, and aspect was 5.4%.

We identified three studies that produced ENMs for *Natrix* species. A study on *N. natrix* covered Europe at a resolution of 50-km cell and combined models including both biotic and abiotic factors; temperature and isothermality were significant predictors, but prey species richness was the most important when included in models (Michailidou et al. 2021). A study on *N. natrix cypriaca*, a subspecies limited to small areas on the island of Cyprus, was done at 250-m and 1-km resolutions using a comparable method and environmental variables (Zotos et al. 2022). In their combined envelope Maxent model, distance to main rivers had the highest importance (33%), followed by distance from wetlands (16%), very similar to our results. Their response curve for distance to main river shows a 50% reduction after 450 m and a near zero probability after 5 km, also similar to our results. A Maxent ENM for *N. tessellata* across Ukraine was created at a 10′ or 30′ resolution based on CliMond bioclimatic variables, where 'Annual mean temperature' (19.1%; Bio01), 'Mean diurnal range' (13.8%; Bio02), and 'Radiation of warmest quarter' (12.7%) contributed the most to the model (Nekrasova & Tytar 2014); however, potentially autocorrelation between the 35 variables was not considered.

<u>Future directions for modeling</u>

We have aimed at creating more conservative models on a national level that should be most useful in identifying broad eco-geographical characteristics for the potential distribution of the studied species. Although Bulgaria provides diverse eco-physico-geographic conditions, our results need to be treated carefully, considering the ENMs cover small parts of the extensive distribution of species with high plasticity, whose true niches are broader. Comparisons with ENMs from other territories may suggest different local drivers for their distribution. Future modeling, especially of smaller territories, could benefit from improved characterization of waters, including parameters such as flow speed, contamination, presence and type of aquatic and riparian vegetation. Another key component for future modeling should include the abundance of prey, especially amphibians and fish, used by Michailidou et al. (2021) and suggested as an important factor by Zotos et al. (2022).

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