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Distribution of the meadow lizard in Europe and its realized ecological niche model

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ABSTRACT

One of the most interesting but elusive members of the European herpetofauna is the meadow lizard (*Darevskia praticola*). It is a small, ground dwelling, predominantly forest living lacertid, for which many ecological and biological data are still missing. Moreover, at least for the western part of the species range (south-eastern Europe) its distribution and environmental associations are insufficiently known, likely due to difficulties in detection even with intensive field sampling. Here, we complemented the available literature records with our personal observations and explored the effects of environmental factors shaping the species ecological niche and distribution in Europe using the ecological niche modelling approach from Maxent software. The new records of the meadow lizard fill a gap in its known distribution. The most suitable habitats are in central and eastern Serbia, south-western Romania, and central, southern and south-western Bulgaria. Mean temperature of the coldest quarter, vegetation and slope had the strongest effect in defining the meadow lizard's ecological niche. Niche suitability increased with the increase in forest cover and slope, while the temperature showed a bell-shaped response with a rather narrow tolerance range for temperature. Contrary to expectations, precipitation seemed to have no contribution to the species occurrence. Ecological niche model performance increased with a higher resolution of predictor variables despite the lower number of available occurrence records, although the slope variable had a greater predictive power when calculated at a lower resolution. Interestingly, high resolution vegetation variables (30 m) were able to show some level of habitat fragmentation, which likely resulted from deforestation. Overall, our results epitomize the effects of limited sampling on the biogeography inference of elusive species while having significant repercussions on conservation priorities and management of the species.

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KEYWORDS
Darevskia praticola; species range; habitat suitability model; species distribution model; Maxent

Introduction

Species distribution is limited and shaped by various factors that are traditionally grouped into abiotic (e.g. temperature, humidity and precipitation) and biotic (e.g. competition,

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Supplemental material can be accessed here.

predation and mutualistic interactions) (Begon et al. 2006). Moreover, a species range can also be constrained by geographical barriers, historical conditions and its inability to disperse to suitable habitats outside the current range (Holt 2003; Sexton et al. 2009). It is important to note that abiotic factors may have a greater impact on some organisms (e.g. ectotherms) because of their specific biology. This is especially true for reptiles that are highly dependent on environmental temperature, as it affects all aspects of their biology, such as physiology, ecology and life-history traits, consequently influencing their distribution (Huey 1982; Adolph and Porter 1993; Vitt and Caldwell 2009). Additionally, many studies show that the habitat humidity is also an important factor (Daltry et al. 1998; Ferreira et al. 2016; Carneiro et al. 2017), and that its interaction with temperature is crucial for the activity patterns and the distribution of terrestrial reptiles (Sannolo et al. 2018). Recognizing these limiting factors helps in understanding the species distribution (Elith et al. 2006; Pearson et al. 2007; Kaliontzopoulou et al. 2008; Ananjeva et al. 2015), predicting the spread of invasive species (Peterson and Nakazawa 2008; Rödder et al. 2008; Rödder and Lötters 2010) and responses to climate change (Araújo et al. 2006; Sinervo et al. 2010; Meiri et al. 2013), as well as managing and conserving biodiversity (Santos et al. 2006; Lyet et al. 2013; Miró et al. 2017).

One rather elusive member of the European herpetofauna is the meadow lizard, *Darevskia praticola*, a small lacertid with a snout-to-vent length (SVL) usually less than 6.5 cm (Arnold 2004). Although the ecology and distribution of many European reptiles are relatively well studied, information is still scarce for the meadow lizard. Contrary to most members of its genus that are saxicolous, the meadow lizard is a ground dwelling species, found in and around broad-leaved woodlands or sometimes in meadows with lush vegetation (Arnold 2004; Agasyan et al. 2009). It is reported in association with oak tree woodlands (*Quercus* sp.), occasionally mixed with beech (*Fagus sylvatica*) (Radovanović 1951; Darevsky 1997; Arnold 2004). The forests that the meadow lizard predominantly inhabits are usually open, with a well-developed herbaceous vegetation understorey, and it seems to avoid dry forests (Strijbosch et al. 1989; Gherghel et al. 2011; Stojanov et al. 2011; Gaceu and Josan 2013). These forests often have a small surface water source (such as a stream) present and it has been observed that during the summer months the lizards migrate closer to these streams or damp forest valleys (Biserkov et al. 2007; Gherghel et al. 2011; Stojanov et al. 2011; Gaceu and Josan 2013). Also, in cases of deforestation and habitat loss, the meadow lizards can still be present at a certain locality, usually found in a vegetation belt surrounding streams or drainage canals that provide them with the grassy vegetation and the humidity they need (Covaciu-Marcov, Cicort-Lucaciu, Gaceu et al. 2009). Overall, the meadow lizard is a thermophilic species (Petrov 2007; Iftime et al. 2008; Covaciu-Marcov, Cicort-Lucaciu, Dobre et al. 2009) that is usually found in rather moist and shaded places in comparison with other small lacertids (Arnold 1987; Strijbosch et al. 1989; Darevsky 1997; Covaciu-Marcov, Cicort-Lucaciu, Gaceu et al. 2009). Moreover, its diurnal activity can be halted during particularly warm days, limiting the number of potential observations in the field (author's pers. obs.). The meadow lizard is currently listed as Near Threatened (NT) on the IUCN's European Red List of Reptiles (Cox and Temple 2009), but this assessment probably needs a revision (Freitas et al. 2016; Saberi-Pirooz et al. 2018). In addition, widespread habitat loss is observed in historical and contemporary cutting of oak forests, thus the species threat status should probably be upgraded (Covaciu-Marcov, Cicort-Lucaciu, Gaceu et al. 2009; Gherghel et al. 2011).

Successive additions to the distribution records in the last decades show that even the range of the meadow lizard is still insufficiently known (Naumov 2005; Petrov et al. 2006; Cogălniceanu et al. 2013; Gaceu and Josan 2013; Urošević et al. 2015; Freitas et al. 2016) and the known records are usually quite patchy (Beshkov and Nanev 2006; Cogălniceanu et al. 2013; Urošević et al. 2015). *Darevskia praticola sensu lato* is characterized by a disjunct distribution range divided into two parts: eastern (i.e. Caucasus) and western (i.e. eastern and south-eastern Europe) (Agasyan et al. 2009; Sillero et al. 2014). The two subranges are separated by the Black Sea, a 1000 km barrier between Europe and the Caucasus, and there are no species records either north or south of the Black Sea. This allows a clear definition of two geographically separate units. The geographic divergence likely happened due to a vicariance event associated with Plio-Pleistocene climatic and vegetation oscillations in the Black Sea region and a recent wide-ranging molecular study has estimated the divergence time between these two clades at approximately 2.5 million years (Freitas et al. 2016). Since this divergence is deep enough to promote considerable ecological separation (see for example the green lizards *Lacerta* sp. in the same area; Ahmadzadeh, Flecks et al. 2013), separate analysis of the ecological niche in these two subranges is recommended.

In this study we compiled published faunistic records and personal observations of the meadow lizard in the European part of the species range (the territory of Romania, Serbia, Bulgaria, north-eastern Greece and Turkish Thrace), as one of our aims was to update the distribution map of the species European lineage (*sensu* Freitas et al. 2016; Saberi-Pirooz et al. 2018). Having in mind the meadow lizard's preference for forested and humid habitats our hypothesis about its realized ecological niche (*sensu* Sillero 2011) was that the two main limiting factors are the presence of suitable forest habitats and the precipitation (that influences the habitat humidity). Hence, the aims of the study were: 1) to determine whether forest vegetation and precipitation have the main influence on the ecological niche of the meadow lizard; 2) to identify other important environmental factors that shape the ecological niche and could explain the habitat selection of the meadow lizard in Europe; 3) to recognize possibly overlooked parts of the species range and to show its potential habitats in Europe. We used ecological niche models (ENM) for these assessments.

Materials and methods

Distribution data

Geographic records were compiled from a large set of publications for: Romania (Cogălniceanu et al. 2013 and references therein; Gaceu and Josan 2013; Bogdan et al. 2014; Freitas et al. 2016), Bulgaria (Beshkov and Nanev 2006; Petrov et al. 2006; Stojanov et al. 2011; Lukanov and Tzankov 2016; Naumov et al. 2016; Tzankov and Slavchev 2016), Serbia (Urošević et al. 2015 and references therein; Freitas et al. 2016), Turkish Thrace and Greece (Eiselt 1970; Helmer et al. 1988; Ljubisavljević et al. 2006; Freitas et al. 2016) (see Supplemental material 1).

When not mentioned in the original literature the dates of observations were obtained through personal communication with the authors. All data points were georeferenced in QGIS, checked for errors and geographic position was corrected if needed. For example, one of the coordinates for Serbia in Freitas et al. (2016) was shifted from the original locality on Kopaonik Mt. to the vicinity of Blace due to a GPS error, while the locality for 'Savinac, DP81' in Urošević et al. (2015) was incorrectly georeferenced from the original paper of Crnobrnja and Rohalj (1988). Literature data were amended by field observations from 2010 to 2016, although our study was restricted to the borders of Serbia and Romania due to logistical reasons. Spatial precision of the coordinates was assessed for each literature record, while field locations were taken using GPS devices when the precision reached more than 5 m. Both literature and field records are given as Supplemental material 1, listing exact coordinates, coordinate precision, locality, date and data source.

The compiled database was used to fill a gap in the distribution map of the meadow lizard in Europe. The final map is given as a standard UTM MGRS grid of 10 × 10 km, which was previously used in most of the other publications from the study region.

Ecological niche modelling

Development of correlative modelling of species ecological niche significantly improved our ability to quickly and efficiently explore environmental limits of a species range (Franklin 2010). These techniques were especially helpful for studying rare and secretive species, where the lack of knowledge could be compensated using computer models (Pearson et al. 2007; Verovnik et al. 2014; Fois et al. 2015). In this study ecological niche was modelled using the Maxent approach proposed by Phillips et al. (2004). This algorithm is ranked among the best when absence data for the species are not available and seems to outperform other modelling methods in quality and predictive power when the number of geographic records is scarce (Elith et al. 2006; Phillips and Dudík 2008; Wisz et al. 2008). Maxent has successfully been used with other lizard species having scarce and fragmentary distribution records (de Pous et al. 2011; Ahmadzadeh, Carretero et al. 2013a). For a more comprehensive model construction and evaluation we ran Maxent 3.4.1 (Phillips et al. 2017) in R 3.3.3 statistical software (R Development Core Team 2008) equipped with dismo package. Raster calculations were performed in R using a raster package, while the final map layouts were prepared using QGIS 2.18.3 (QGIS Development Team 2009).

Maxent compares species occurrence data (presence points) against randomly sampled spatial coordinates from the studied region (background points). Here, species occurrences older than 20 years were discarded in the first step to get an ecological niche based on the contemporary distribution of the meadow lizard. The remaining data were cleaned by removing duplicated coordinates. Since species presence was not sampled evenly through the study area, the sampling bias had to be accounted for in the model (Phillips et al. 2009; Boria et al. 2014; Fourcade et al. 2014). For this purpose we used a subsampling method available in the package spThin (Aiello-Lammens et al. 2015), which removed presence points that were closer than the given distance and kept the remaining presences used to fit the model (the training presence points). Discarded presence points were further thinned to leave only a single presence per raster cell and were used as independent data to test the model performance (the test presence points). For background points, we used 10,000 randomly sampled spatial points restricted within the 50 km radius from the presence points.

Model complexity was controlled using the ENMeval package in R (Muscarella et al. 2014). The package creates a series of models using different regularization values and feature classes, compares them by AICc and allows one to select the best fitting model (as proposed by Warren and Seifert 2011). This procedure usually selects a model that is less complex than the default one assumed by Maxent. After AICc selection procedure, all training points were used to fit the model in dismo, while the test points were used for independent evaluation by calculating AUC_{Train} and AUC_{Test} metrics (Phillips and Dudík 2008). It should be noted that AUC is widely accepted for evaluation of ecological niche models, although this procedure is not without limitations (Lobo et al. 2008; Smith 2013).

We created two separate ecological niche models in order to make the most out of available records. The 'low resolution model' was fit using variables rescaled to the resolution of BioClim dataset (about 1 km) and presence records in resolution of up to 1 km (spThin distance = 10 km). The 'high resolution model' used variables rescaled to the resolution of the topographic layers (about 30 m) and the presence records with resolution of up to 30 m (spThin distance = 1 km). The low resolution model allowed the use of information from a larger set of presence points that would otherwise be discarded. On the other hand, the high resolution model could incorporate more details from the high resolution vegetation and topographic variables, but it could also significantly reduce the number of available presence points. It should be noted here that we were unable to run ENMeval on the high resolution model due to PC hardware constraints (CPU power and HDD space) and instead we used parameters suggested by AICc values from the low resolution model. In the final step, we used the D index (as proposed by Warren et al. 2008) to compare similarity between ecological niche models at different resolutions. Values range from '0' for completely different ecological niches to '1' for identical ecological niches.

We used three types of environmental layers referred to as climate, vegetation and topography in the text. A set of 1 km resolution BioClim variables was used to represent the climate envelope (Hijmans et al. 2005). Since forests have been mentioned as an important limiting factor in the meadow lizard distribution, we used a 30 m resolution Vegetation Continuous Fields (VCF) from 2015 to represent forest vegetation cover (Sexton et al. 2013). Topographic variables were represented by altitude, slope, aspect eastness and aspect northness, derived from a 30 m digital elevation raster (EEA 2013). Prior to the analysis original layers were reprojected to a EPSG:3035 projection.

To determine the variables which could explain species distribution we checked Maxent's contribution table and the output of the jackknife analysis. The most important variables contribute significantly to the model, have high values of permutational importance, score high gain in jackknife analysis if used on their own and significantly decrease model gain if excluded from the model. Finally, the shape of the species response to each environmental layer that contributed to the final model was determined using response curves.

Results

We gathered 786 georeferenced occurrence records for the meadow lizard in Europe (312 literature data and 474 personal field records) given as Supplemental material 1. Most of the records (except Stojanov et al. 2011) were precise enough to be shown on the UTM MGRS 10 × 10 km map (Figure 1). In total, the meadow lizard was recorded in 152 squares. It was reported for the first time in nine of UTM MGRS 10 × 10 km. Additionally, in two squares where the Danube River represents a natural borderline between Romania and Serbia (EQ82 and FQ04), and where the species presence was previously known only for the Romanian bank, we confirmed its occurrence also on the Serbian bank.

After a spThin subsampling procedure 45 occurrence records remained for the low resolution model and 36 occurrences remained for the high resolution model. In addition, 47 records remained for testing the low resolution model, while 144 points remained for testing the high resolution model performance. ENMeval package results (Supplemental material 2) suggested the usage of linear and quadratic features with a regularization multiplier of 3.5. Low resolution model reported AUC_{Train} value of 0.78 and AUC_{Test} value of 0.87. High resolution model performed better, with AUC_{Train} of 0.83 and AUC_{Test} of 0.86.

Both the observed distribution and modelled habitat suitability for the meadow lizard show that its distribution range is somewhat divided by high mountain ridges, agricultural plains and flatland areas along the major rivers (Figures 1 and 2). A detailed map of suitable habitats is also given in Supplemental material 3, to guide further search for this

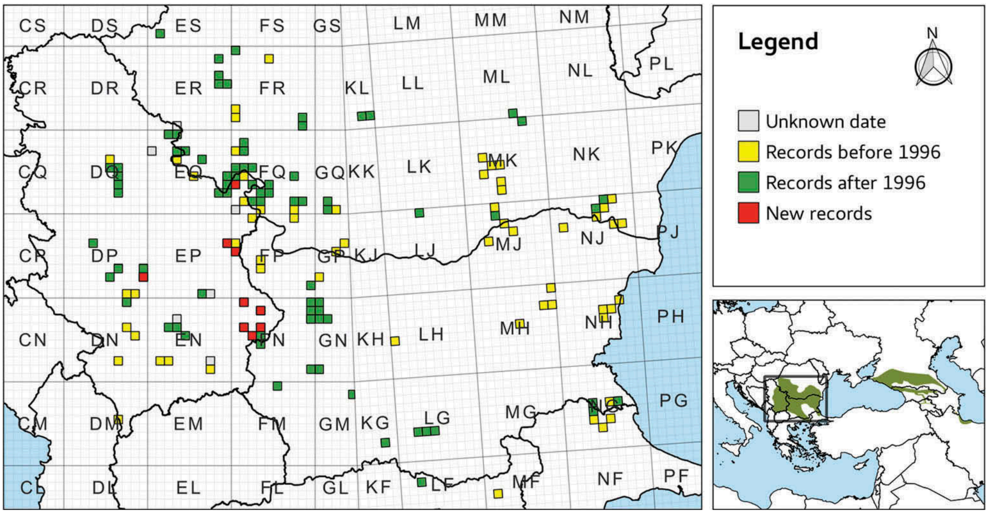

Figure 1. Distribution map of the meadow lizard (*Darevskia praticola*) in south-eastern Europe given on an MGRS UTM 10 × 10 km grid scale. A small overview map shows the study region and the two separate parts of the meadow lizard distribution – separate geographic units and evolutionary lineages of the species (modified from Agasyan et al. 2009). Letters on the distribution map refer to the names of larger (100 × 100 km) MGRS squares. Occurrence records were compiled from a large literature survey and our own data (see Supplemental material 1) and classified on the map according to the time frame of the findings.

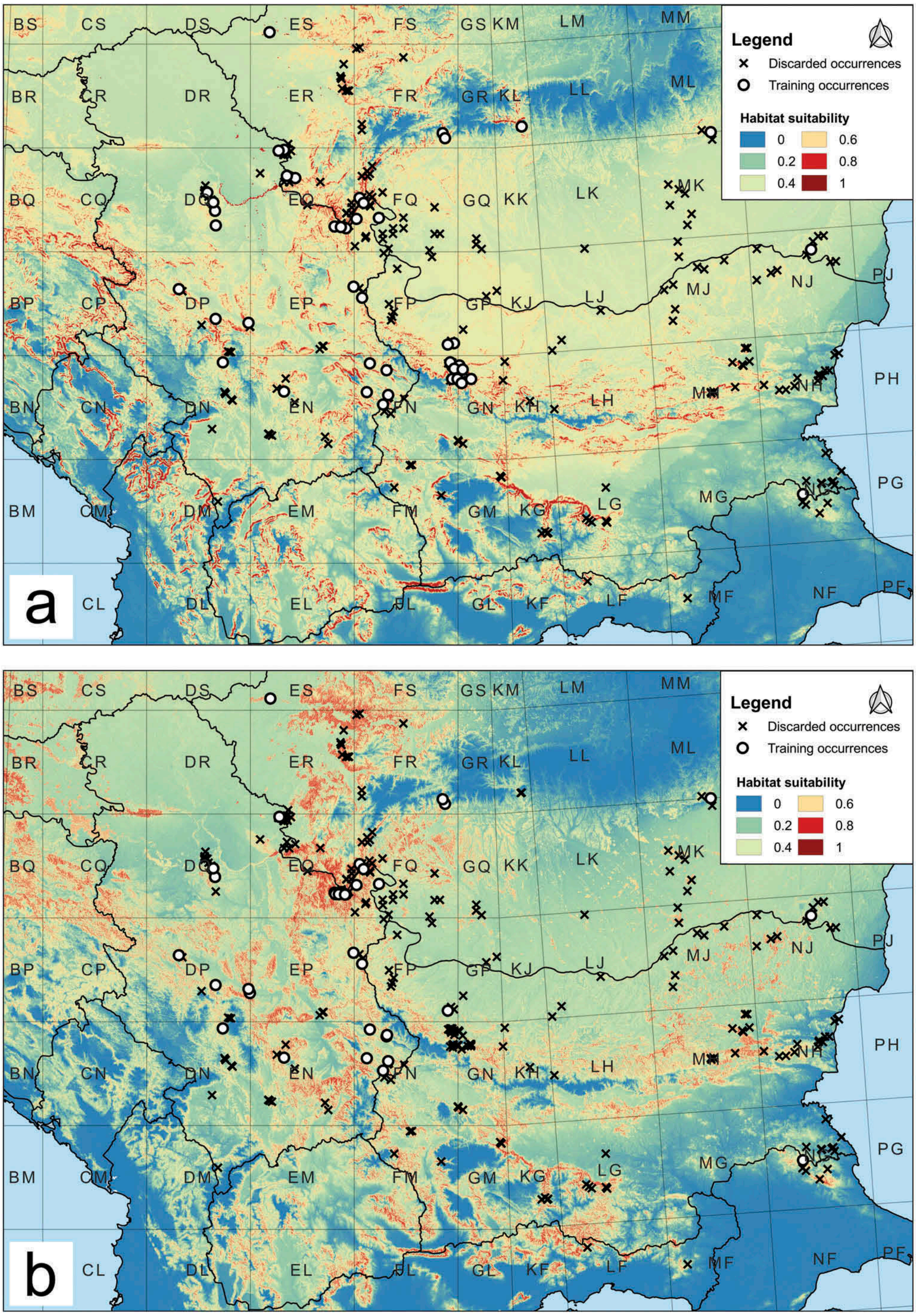

Figure 2. Habitat suitability maps for the meadow lizard (*Darevskia praticola*) in south-eastern Europe given separately for the low resolution (a) and the high resolution ecological niche model (b). Training points used for fitting the ecological niche models are represented with white dots, while the discarded occurrences are shown as '×' signs and placed for the overall visual representation of the model accuracy.

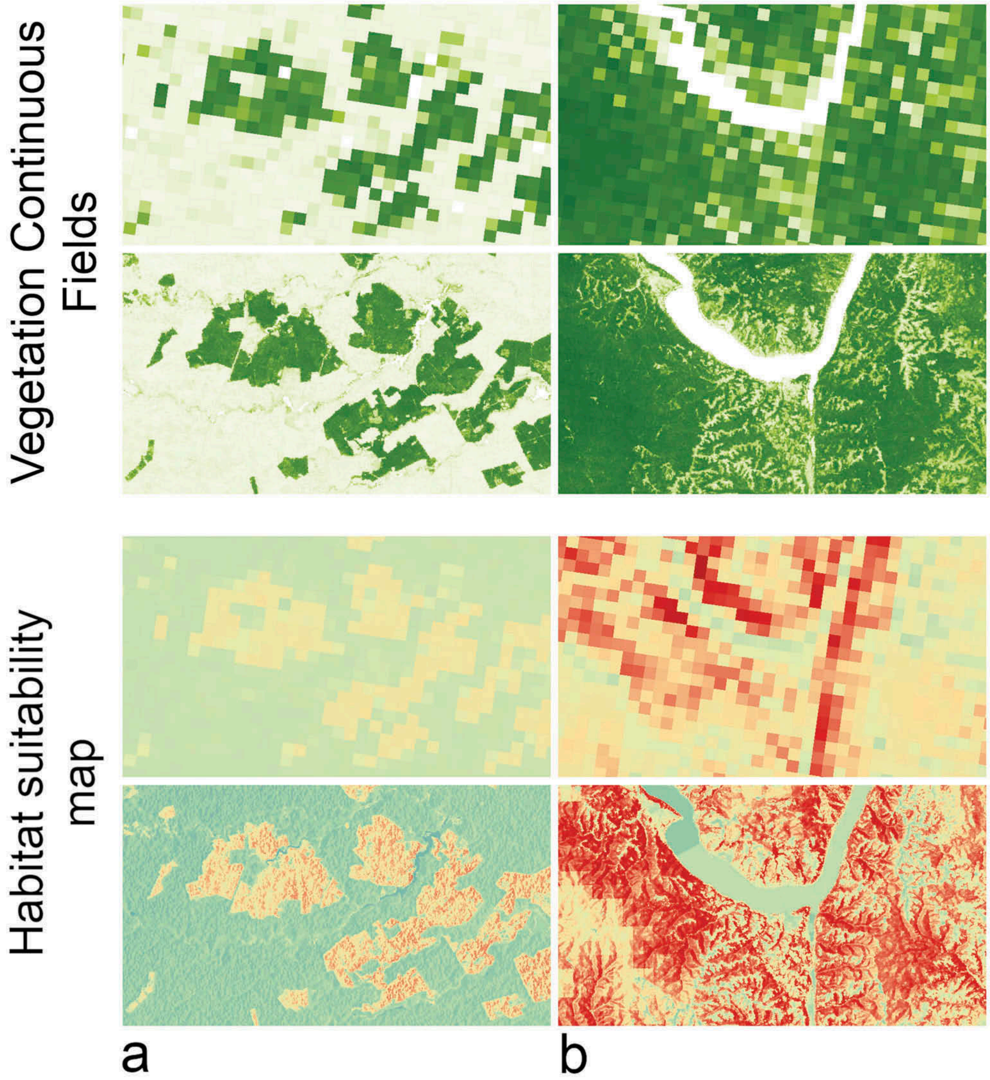

Figure 3. Examples showing details from the forest cover (Vegetation Continuous Fields layer) and the Maxent's habitat suitability map for the meadow lizard (*Darevskia praticola*). The maps show two localities: (a) a part of a fragmented forest area in southern Romania where the species occurs, and (b) an area near the Danube River along the border between Serbia and Romania, which is one of the places of greater habitat suitability for this species. The maps also show the difference between the low (upper images) and high (lower images) resolution of both the VCF layer and the habitat suitability.

elusive species. The most suitable habitats for the meadow lizard are located in central and eastern parts of Serbia, south-western Romania, across the Balkan Mountain Range in central Bulgaria and in the south and south-west of this country (Figure 2). Potential habitats also exist in the northern parts of Greece and in a small part of Turkish Thrace, where the species is also known from several records. The model shows suitable habitats for the meadow lizard present in the Former Yugoslav Republic of Macedonia, but the suitability decreases towards the Mediterranean region (i.e. in Montenegro and Albania).

Table 1. Variable contribution table given by Maxent ecological niche model for the meadow lizard (*Darevskia praticola*). Only the variables contributing to the model are shown in the table, while the most significant variables are shown in bold.

	High resolution model		Low resolution model	
Variable	Per cent contribution	Permutation importance	Per cent contribution	Permutation importance
Mean temperature of coldest quarter	43.2	28.8	33.5	18.8
Vegetation continuous fields	41.8	53.9	20.2	29.8
Slope	7	0	30.9	29
Altitude	0	0	8.4	15.4
Mean temperature of wettest quarter	0.1	0.2	6.3	1.6
Aspect eastness	4.6	3.8	0	0
Min temperature of coldest month	2.3	10.3	0	0
Precipitation of driest quarter	0.8	2.6	0	0
Mean temperature of driest quarter	0	0	0.8	5.5
Isothermality	0.1	0.2	0	0

Also, potential habitats are shown further west in Bosnia and Herzegovina and Croatia and to the north-west in Hungary.

Overall, habitat suitability maps created from the low resolution model (Figure 2(a)) and the high resolution model (Figure 2(b)) were very similar. The similarity index of ecological niches constructed at different resolutions was also exceptionally high (D = 0.96). However, the high resolution model was more precise, which can be observed by the closer inspection of the maps with the species' potential habitats (see Figure 3).

The low resolution model indicated that temperature, vegetation and slope had almost equal contributions to the ENM (Table 1, Supplemental material 4). The significance of temperature and especially of vegetation increased in the high resolution model, while the importance of slope variable decreased. Mean temperature of the coldest quarter was always the most important of all the temperature variables. None of the precipitation variables had substantial contribution to the models. Response curves of the most significant variables were similar for the high and the low resolution models (Supplemental material 5). According to the response curves, the ecological niche of the meadow lizard is located around 0°C of the mean temperature of the coldest quarter. The model showed that the habitat suitability for the species gradually and linearly increased with the increase in forest cover. The same was true for the relation with slope, where the suitability of the ecological niche linearly increased starting from the 0°. However, the line of the slope response curve was abrupt and its maximal values were reached at different points for the high and the low resolution models.

Discussion

Compiled records on the meadow lizard distribution in Europe show that the distribution data are still very limited. This is especially notable for the central and the eastern part of the study region (Figure 1). Field surveys resulted in finding several new localities, mainly in the eastern parts of Serbia. These new records filled the gap in the meadow lizards' distribution between Bulgaria, Danube region and central Serbia. Looking at the distribution map (Figure 1) there were no major changes between historical and recent distribution records on a larger scale (i.e. comparing occupancy of 10 × 10 km^2 squares). Observed lack of recent records from central Bulgaria, southern Romania and southern Serbia could be explained by insufficient field efforts. However, some of the historically known populations could also be extinct due to agriculture intensification and forest clear-cutting practice, which seems to be a plausible explanation for Romania (Covaciu-Marcov, Cicort-Lucaciu, Dobre et al. 2009a; Gherghel et al. 2011).

Most of the localities where the meadow lizard has been observed (Figure 1) fall well within the models' prediction of suitable habitats (Figure 2). In fact, the model predicted a wider distribution range, outside the already known suitable habitats where the meadow lizard had already been recorded (i.e. Romania, Serbia, Bulgaria, Greece and Turkey). As such, the model showed a presence of suitable habitats in the Former Yugoslav Republic of Macedonia. Although the meadow lizard was never recorded there (Sterijovski et al. 2014; Uhrin et al. 2016), its presence is quite plausible in the eastern part of the country, due to its close proximity to areas of known species presence in the neighbouring Bulgaria. These localities should be surveyed to corroborate predictive power of the model and to find previously unknown populations. A high suitability for the species in Fruška Gora Mountain (northern part of Serbia) and to the localities further west and north-west (Hungary, Croatia and Bosnia and Herzegovina) was not confirmed despite frequent visits. This could be associated either with geographic isolation and historical conditions or biological interactions that constrained species distribution to the now known area (e.g. Guisan et al. 2006; Elith and Leathwick 2009; Wiens 2011; Ahmadzadeh, Carretero et al. 2013a). It should be noted that in Figure 2 the species records that were not used to 'train' the model aligned with the places of intermediate and high habitat suitability. Along with high AUC scores, this suggested a high predictive power of the ENMs. Higher score of AUC_{Test} compared to $\text{AUC}_{\text{Train}}$ data was not expected and was likely the result of sampling bias that was still present in the test dataset (i.e. there were four times more test points than the train points for the high resolution model), while the spatial coverage of the test and the train datasets was similar (i.e. the datasets were not completely independent).

Both low and high resolution models generally produced similar habitat suitability maps (Figure 2(a), 2(b)), which was also confirmed by niche similarity index. Visible differences came from somewhat different contributions of variables in the final model, and from the more precise vegetation layers used in the high resolution model (Figure 3). Thus, the high resolution model prediction was more accurate, which was a direct result of incorporating more details about the forest cover in the study region. The high resolution layers enabled us to detect fragmentation in the forest habitats (Figure 3(a)) and correctly narrowed the range of suitable habitats (Figure 3(b)). In order to remove bias from the occurrence records, a significant proportion of the data was discarded, thus the train dataset was more limited and more restricted to Serbia in the high resolution model. However, there was no sign that reduced number of occurrence records downgraded the ENM prediction, nor that the significant bias was introduced. Previous modelling studies on lizards also suggested that increasing resolution is preferable over increasing the number of records with a coarser resolution (Kaliontzopoulou et al. 2008). In general, high resolution models perform better, but this is not always the case (see: Guisan et al. 2007). We recommend using precise occurrences when possible, as it allows the use of high resolution topographic or remote sensed variables, gives a more precise prediction and possible insights into microhabitat preferences. However, topographic variables calculated at a higher resolution may not always be the most suitable, since the contribution of slope variable in this study was more important when calculated over a coarse scale. A similar result was obtained when testing the effect of high resolution topographic variables on alpine plant species, where aspect performed better at a high resolution, while the slope shows most power at a coarser resolution (Lassueur et al. 2006). We tentatively interpret that slope may be a proxy of other terrain parameters (i.e. erosion or water retention), so it would affect species distribution on a wider scale.

Predicted ecological niche of the meadow lizard is in line with its known ecology. According to the literature, the meadow lizard is a predominantly forest dwelling species (Arnold 2004; Agasyan et al. 2009) and the model correctly selected these types of habitat as the most suitable (Table 1, Supplemental material 4, 5), confirming our hypothesis about the importance of forest habitats for its distribution. Inclusion of more detailed vegetation data (30 m resolution) shows fragmentary distribution of the meadow lizard habitats in some parts of the species range and this is easily observed in southern Romania where forest fragments are visible on the map as limited areas of greater habitat suitability (Figures 2(b) and 3(a)). In most of the species range its habitats are limited to small fragments created by human activities, through the clear-cutting of once continuous temperate deciduous forests (Pongratz et al. 2008; Kaplan et al. 2009). The species could still be absent due to habitat destruction and fragmentation despite climate suitability. In this situation, remote sensed vegetation cover gave us an interesting insight about the scale of the human impact on the distribution of the meadow lizard. High level of habitat fragmentation predicted for southern Romania is in fact true, since this part of the country is predominantly under agricultural use (Cogălniceanu et al. 2013). Gherghel et al. (2011) suggested that until recently the species inhabited the whole southern Romania, as this region was mostly covered by forests. About 50% reduction in forest cover happened during the last century (Giurescu 1975) and this could be the reason for the present patchy distribution of suitable habitats within the species range. Climatic parameters, especially temperature, were also important in explaining the species ecological niche (Table 1, Supplemental material 4, 5). The data suggest that the temperature in the winter period might be a crucial factor in shaping the species niche and that the niche is very narrow regarding temperature during the hibernation with allowed deviation of several degrees around 0°C (Supplemental material 5). Of all topographic variables, slope degree was the most important showing some preference of the species towards hilly areas. This could also be a result of forest cutting practices, where terrains more suitable for agriculture (flatlands) were cleared first, leaving forested areas on less accessible hilly terrains. Contrary to our initial hypothesis that the precipitation is an important limiting factor for this species, as the meadow lizard is considered to prefer more humid habitats (Arnold 1987; Strijbosch et al. 1989; Darevsky 1997; Covaciu-Marcov, Cicort-Lucaciu, Gaceu et al. 2009), it seems that this variable has almost no contribution to the species' ecological niche (Table 1, Supplemental material 4). However, these results do not completely deny our hypothesis and might be explained by the species preference towards the forest habitats. Forests buffer the effect of surrounding climate and create their own microclimate conditions (lower maximum temperatures, higher minimum temperatures and higher relative humidity in comparison to adjacent open habitats), enabling the forest living species to be less dependent on local climate patterns (Renaud et al. 2011; Gaudio et al. 2017).

Overall, this study systematized our knowledge on the distribution of the meadow lizard in the European part of the species range. The analysis confirmed the meadow lizard's close association with forest habitats and showed two important factors that limit its distribution – narrow climate tolerance and deforestation. This case shows that high resolution models are preferable, even at the price of discarding more occurrence records, but suggests that some topographic variables (i.e. slope) might be more useful if calculated at a lower resolution. The ENM was proven useful in predicting the distribution of an elusive lizard species and has helped to successfully overcome the challenges in data collection in the field. These additional findings confirmed the ENMs suitability for other taxa with similar obstacles in data collection. These results are valuable in aiding future surveys and could be used to orientate conservation and management actions to preserve the most important forest habitats of the meadow lizard. Results suggest that special attention should be given to small forest fragments that could be valuable in preserving the meadow lizard populations.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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Geolocation information

Study area (box): 47°00′N, 18°00′E to 41°00′N, 29°00′E

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