

Ecological niche differentiation in the Anatolian rock lizards (Genus: *Anatololacerta*) (Reptilia: Lacertidae) of the Anatolian Peninsula and Aegean Islands

MEHMET KÜRŞAT ŞAHİN^{1,*}, KAMIL CANDAN^{2,3}, DANA KARAKASI⁴, PETROS LYMBERAKIS⁴, NIKOS POULAKAKIS^{4,5,6}, YUSUF KURLUTAŞ^{2,3}, ELIF YILDIRIM^{2,3}, ÇETİN ILGAZ^{2,3}

¹ Department of Biology, Kamil Özdağ Faculty of Science, Karamanoglu Mehmetbey University, Karaman, Turkey

² Department of Biology, Faculty of Science, Dokuz Eylül University, Buca, İzmir, Turkey

³ Research and Application Center for Fauna Flora, Dokuz Eylül University, Buca, İzmir, Turkey

⁴ Natural History Museum of Crete, School of Sciences and Engineering, University of Crete, Knossos Av, 71409 Irakleio, Greece

⁵ Department of Biology, School of Sciences and Engineering, University of Crete, Vassilika Vouton, 70013, Irakleio, Greece

⁶ Institute of Molecular Biology and Biotechnology (IMBB), Foundation for Research and Technology – Hellas (FORTH), N. Plastira 100, Vassilika Vouton, GR-70013 Irakleio, Greece

*Corresponding author. Email: yasambilimci.kursat@gmail.com

Submitted on: 2022, 9th May; revised on: 2022, 8th June; accepted on: 2022, 27th June
Editor: Mattia Falaschi

Abstract. The genus *Anatololacerta* is distributed in the eastern Mediterranean region including Asia Minor and some east Aegean islands. Recent phylogenetic studies suggested that this genus displayed cryptic diversity and was divided into five species: *A. anatolica*, *A. pelasgiana*, *A. ibrahimi*, *A. finikensis* and *A. danfordi*. The ecological niche differentiations of these species have not been studied so far. Our aims for this study were to predict the potential suitable habitats for the species nested in genus *Anatololacerta*, and to examine the niche overlaps and differentiations via identity and background tests. The occurrence data were obtained from literature and our own field surveys. Occurrence records were rarefied and assessed in a 30 arc-second resolution layer, compatible with several bioclimatic and topographic variables. Species distribution analyses were performed using maximum entropy approach and pairwise niche comparisons were evaluated by identity and background tests. Our results demonstrated that the species delimitation among this genus was not only affected by geographic isolation but also that precipitation and temperature influenced the habitat suitability for these species. Predicted suitability usually well matched the actual species distributions. Moreover, the niche overlap (identity test) analyses verified that allopatric *Anatololacerta* species show clear ecological differentiations. However, a niche overlap between parapatric species *A. pelasgiana* and *A. finikensis*, was confirmed by identity and background tests. It has been suggested that these parapatric species could be more affected by microclimatological parameters than the others. The results of our study are in agreement with the latest phylogenetic study within this genus.

Keywords. Squamata, *Anatololacerta*, niche overlap, precipitation, temperature, MaxEnt, Anatolia.

INTRODUCTION

Ecological factors, e.g., climatic factors, significantly affect the distribution of organisms and may lead to for-

mation of new species (Zhao et al., 2019). Each species often has unique ecological niche characteristics and as a result of it, ecological needs differ even for sympatric or sister species (Soberon and Peterson, 2005). Quantifying

and visualizing the effects of spatial and temporal ecological patterns on speciation processes have contributed to our knowledge of interactions between species and their environments (Jezkova and Wiens, 2018; Kurnaz et al., 2019; Şahin et al., 2021). In the last two decades, Ecological Niche Modeling (ENM) was frequently used to better understand these processes. ENM is a method used to predict the habitat suitability of species across space by using occurrence records and bioclimatic and topographic variables (Barve et al., 2011; Kass et al., 2018; Hosseiniian Yousefkhani et al., 2019). Moreover, ENM is a very beneficial approach to better understand aspects of conservation, ecology, distribution, and evolutionary history of the species (Guisan and Zimmermann, 2000; Araújo et al., 2006; Phillips et al., 2006). Latest tool developments in modeling studies such as *ENMTools* (Warren et al., 2021), *ENMeval* (Muscarella et al., 2014) and *kuenm* (Cobos et al., 2019) provide frameworks able not only to generate maps but also to assess the niche overlap and the possible degree of differentiation among multiple species.

The complex geological history of Western Asia has shaped the Anatolian Peninsula, the Caucasus Mountains, and the Iranian steppes, resulting in high variations in vegetation covers and topographic patterns in these regions (Rajabizadeh et al., 2016). In addition, many environmental dynamics, like atmospheric concentrations of greenhouse gases, precipitation and temperature fluctuations, alterations in land use and cover have influence on ecosystem and biodiversity structure in Mediterranean Basin (Klausmeyer and Shaw, 2009). Despite some parts of the Anatolian Peninsula and its close areas have been studied in terms of ENM species distribution analysis for several herptile species (Gül et al., 2015, 2016, 2018; Hosseiniian Yousefkhani et al., 2016, 2019; Heidari, 2019; Candan et al., 2021; Kurnaz and Şahin, 2021a), the western part of the peninsula and/or with Aegean Islands and Cyprus has still been less represented (Kıraç et al., 2022).

The herpetofauna in the Anatolian Peninsula and Aegean Islands is rich (180 species) (Kurnaz, 2020; Baran et al., 2021; Yaşar et al., 2021), almost as the 60 % of whole European continent (301 species) (Speybroeck et al., 2020). Besides, recent discoveries of the new species have been making the herpetofauna richer (Tuniyev et al., 2018; Jablonski et al., 2019; Yılmaz et al., 2021; Kurnaz and Şahin, 2021b; Arribas et al., 2022; Kurnaz et al., 2022). However, even though this region has been investigated in several biogeographic or phylogeographic studies (Kornilios et al., 2012; Skourtanioti et al., 2016; Kotsakiozi et al., 2018; Bozkurt and Olgun, 2020), the effects of environmental conditions on the distribution of reptile species or subpopulations are being studied only in the

last decade (Fattahi et al., 2014; Gül et al., 2015; Hosseiniian Yousefkhani et al., 2019; Kurnaz and Hosseiniian Yousefkhani, 2020, 2021).

Anatololacerta Arnold, Arribas & Carranza, 2007 is an Eastern Mediterranean lacertid genus that is distributed along the western and southern parts of Anatolia and some Aegean islands (Karakasi et al., 2021). However, taxonomic debates on some populations of this genus have been historically controversial. Species of this genus represent an example of cryptic diversity (Bellati et al., 2015; Candan et al., 2016), a common phenomenon among lacertids (Kaliontzopoulou et al., 2012; Barata et al., 2012; Tamar et al., 2015; Freitas et al., 2016; Psonis et al., 2017; Šmíd et al., 2017; Mendes et al., 2018). The recent study on the phylogenetic relationships of *Anatololacerta* clades (Karakasi et al., 2021) classified them into five species: i) *Anatololacerta anatolica* (Werner, 1900) distributed in northwestern Anatolia, Icaria and Samos islands ii) *Anatololacerta pelasgiana* (Mertens, 1959) in southwestern Anatolia, Symi and Rodos islands iii) *Anatololacerta finikensis* (Eiselt & Schmidtler, 1987) in western part of Mediterranean region and Psomi island iv) *Anatololacerta ibrahimi* (Eiselt & Schmidtler, 1987) central part of Mediterranean region v) *Anatololacerta danfordi* (Günther, 1876) in eastern Mediterranean region. Therefore, the cryptic diversity within this genus inspired us to test if the species delimitations can be affected by bioclimatological and/or topographic factors. That's why the objectives of the present study are i) to predict highly suitable areas for each *Anatololacerta* species distribution and determine which environmental factors are important; ii) to measure and compare the niche divergence within the genus *Anatololacerta*, as a case study for cryptic species.

MATERIALS AND METHODS

Study area and input data

This study was conducted within 25-37° East Longitude and 34.5-41° North Latitude, covering the western and southern parts of Anatolia and Aegean islands (Fig. 1). A total of 159 occurrence data (31 for *A. anatolica*, 46 for *A. pelasgiana*, 22 for *A. finikensis*, 37 for *A. ibrahimi*, and 23 for *A. danfordi*) were obtained from field surveys and literature (Eiselt and Schmidtler, 1986; Mulder, 1995; Baran and Kumlutaş, 1999; Kumlutaş et al., 2015; Yakın and Tok, 2015; Beşer, 2015; Bellati et al., 2015; Candan et al., 2016; Sarıkaya et al., 2017; Beşer et al., 2020; Karakasi et al., 2021). The raw input data for localities are given in Table S1. Data for these species were error-checked and improved to meet appropriate standards for ecological

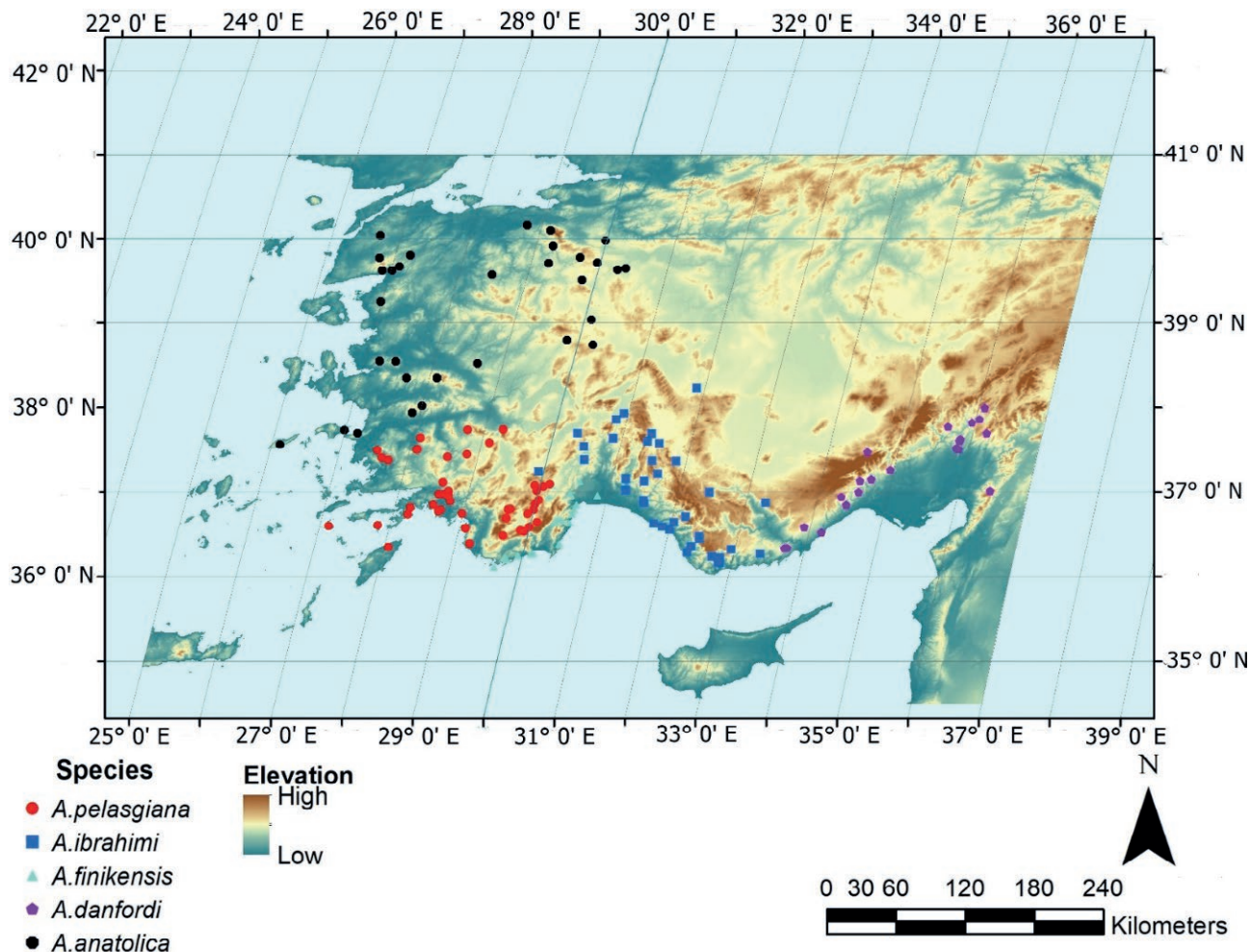


Fig. 1. Species occurrence records for genus *Anotolacerta* in the Anatolian Peninsula and Aegean Islands.

niche modeling in two steps. Firstly, georeferenced data were checked for error and data consistency for geographic coordinates (Chapman, 2005). Secondly, in order to avoid spatial sampling biases and misinterpretation of the habitat suitability analysis and niche overlap tests, the occurrence records for each species were spatially rarefied with keeping one locality in each 2 km by SDM Toolbox 2.0 (Brown, 2014).

Nineteen bioclimatic and one topographic variables were downloaded from WorldClim version 2.1 (Fick and Hijmans, 2017). The bioclimatic data were generated from global ESRI grids for current conditions (~1970-2000). Additionally, three topographic variables were obtained from the studies of Gavashelishvili and Tarkhishvili (2016), and Gavashelishvili et al. (2018). All these environmental variables were at 30 arc-second resolution (~1 km) (Table S2) and each layer was clipped for the study area in ArcGIS 10.6.1 (ESRI, California, CA, USA)

for the whole study area. Pearson Correlations between variables were calculated in R v4.1.3 (R Core Team, 2020) and highly correlated variables were eliminated ($r \geq |0.8|$) (Fig. S1).

Ecological niche modeling

Due to its robustness and dependence on presence and pseudo-absence data, maximum entropy approach was used for niche modelling. The maximum entropy algorithm, which generates the probability of presence of a given species that varies between 0 to 1, provides predictions from presence and pseudo-absence data (Phillips et al., 2009). A total of 2000 background points for each species were randomly sampled across the study area. The potential habitat suitability was modeled by using the *kuenm* package in R for the implementation of Max-

Table 1. Percentage contribution of the environmental layers used in species distribution modeling of *Anatololacerta* species.

Species	Bio 3	Bio 5	Bio 7	Bio 17	River_dist	Lai
<i>A. anatolica</i>	3.1	11.1	35.4	29.5	5.9	15.1
<i>A. danfordi</i>	13.5	1.5	17.8	19.9	3.6	43.7
<i>A. finikensis</i>	19.7	27.3	5.5	35.7	6.5	5.3
<i>A. ibrahimi</i>	0.9	8	7.2	36.6	36.9	10.4
<i>A. pelasgiana</i>	7.3	26	19.6	23	10.7	13.3

Ent 3.4.1 (Phillips et al., 2017; Cobos et al., 2019). To create the models for each *Anatololacerta* species, 80 % of the occurrences were used for the creation of candidate models and the remaining 20 % for independent presence as test data. The bioclimatic and topographic envelopes, derived from environmental variables, were constructed as set for each species (Table 1).

Model selection

To optimize model complexity for all 5 species, 31 combinations of MaxEnt's 5 feature classes [hinge (h), threshold (t), product (p), quadratic (q) and linear (l)] along with 17 regulation multiplier values (0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9, 1, 2, 3, 4, 5, 6, 8, 10) were evaluated. Using these combinations allowed us an optimal approach for generating diverse candidate models in order to select the models that explain our data best (Muscarella et al., 2014; Cobos et al., 2019). After that, candidate models were evaluated and best models were selected using not only AUC values (with the highest values), but also Akaike Information Criterion corrected for small sample sizes (AICc) (with the lowest values) (Hurvich and Tsai, 1989). Significance tests were performed using partial ROC (Peterson et al., 2008), and predictive power with a 5% omission rate (Anderson et al., 2003). Model AUC scores are evaluated as follows: AUC = 0.5: a performance equivalent to random, AUC > 0.7: useful performance, AUC > 0.8: good performance, AUC > 0.9: excellent (Manel et al., 2001). Finally, all model inputs were transformed into binary predictions using minimum training presence as the threshold to distinguish unsuitable from suitable areas (Pearson et al., 2007; Rodríguez-Ruiz et al., 2020).

Niche equivalency

In order to assess the niche overlap among *Anatololacerta* species, ENMTools (Warren et al., 2021) was applied to calculate Schoener's *D* (Schoener, 1968) and

Hellinger's-based *I* (Warren et al., 2008) niche similarity metrics for niche overlap test due to their simplicity, long usage time and effective method to measure niche similarities (Warren et al., 2008). These indices ranged from 0 (no overlap) to 1 (identical niches).

The significance of the niche difference was assessed by pooling the occurrences from each taxon, and generating 100 pseudo-replicates. Afterwards, one-sided test and an α level of 0.05 was applied to compare the true calculated overlap to the null distribution of niche overlap. This means that the ENM of two species is not equivalent when the overlap value is smaller than 5% of the null distribution.

Background test

Background test was conducted in order to determine the differential availability of habitat for examined species (Warren et al., 2008). The running conditions of the background test were similar to the niche overlap tests (identity test).

RESULTS

Ecological niche models and the contribution of environmental variables

On the basis of minimum training presence threshold, ecological niche modeling predictions for each *Anatololacerta* species were reliable enough to result in realistic maps, and these predictions were separately conducted for each species with lowest AICc values.

A total of 4 bioclimatic and 2 topographic variables contributed to map the predicted distribution of each species (Table 1). The ultimate models were selected based on the lowest AICc from evaluation metric results (Table 2). The MaxEnt models demonstrated a significant ability to generate ecological niche models for *Anatololacerta* species with average test AUC of models as follows: 0.818 ± 0.093 for *A. anatolica*, 0.818 ± 0.083 for *A. pelasgiana*, 0.927 ± 0.045 for *A. finikensis*, 0.830 ± 0.083 for *A. ibrahimi* and 0.895 ± 0.104 for *A. danfordi*.

Based on these results, most of the suitable predicted areas were relatively wider than the present distributions of each species. The potential distribution of all *Anatololacerta* species are shown in Fig. 2 a-e. Although the bioclimatic and topographic variables that contributed to species distribution were the same, their contribution percentiles were different. The distribution of *A. anatolica* is highly associated with the temperature annual range - Bio 7 - (35.4 %), while that of *A. danfordi* with the Mean Leaf Area Index

Table 2. Summary statistics for the best models selected for species distribution maps of *Anatololacerta* species via *kuenm* package. AICc: a corrected AIC score, used for a small sample size by increasing the cost for each parameter; wAICc: the model weight is the relative likelihood for each model, divided by the total relative likelihood for all models that were considered; Δ AICc: the difference between the model with the lowest score (the “best” model) and the AICc score for each model; AUC: area under the curve is a measure of the accuracy of the model; mean AUC ratio ≥ 1.00 , $p < 0.05$ means predictions are significantly better than a random model.

Species	Best MaxEnt features	AICc	wAICc	Δ AICc	AUC	Mean AUC ratio
<i>A. anatolica</i>	hinge	765.536	0.191	0.134	0.818 \pm 0.093	1.672 (p = 0.03)
<i>A. danfordi</i>	threshold	583.369	0.584	1.881	0.895 \pm 0.104	1.000 (p = 0.02)
<i>A. finikensis</i>	quadratic	394.171	0.182	0.395	0.927 \pm 0.045	1.619 (p = 0.03)
<i>A. ibrahimi</i>	threshold	908.851	1.000	0.143	0.830 \pm 0.083	1.353 (p = 0.01)
<i>A. pelasgiana</i>	product	993.837	1.000	0.111	0.818 \pm 0.083	1.720 (p = 0.02)

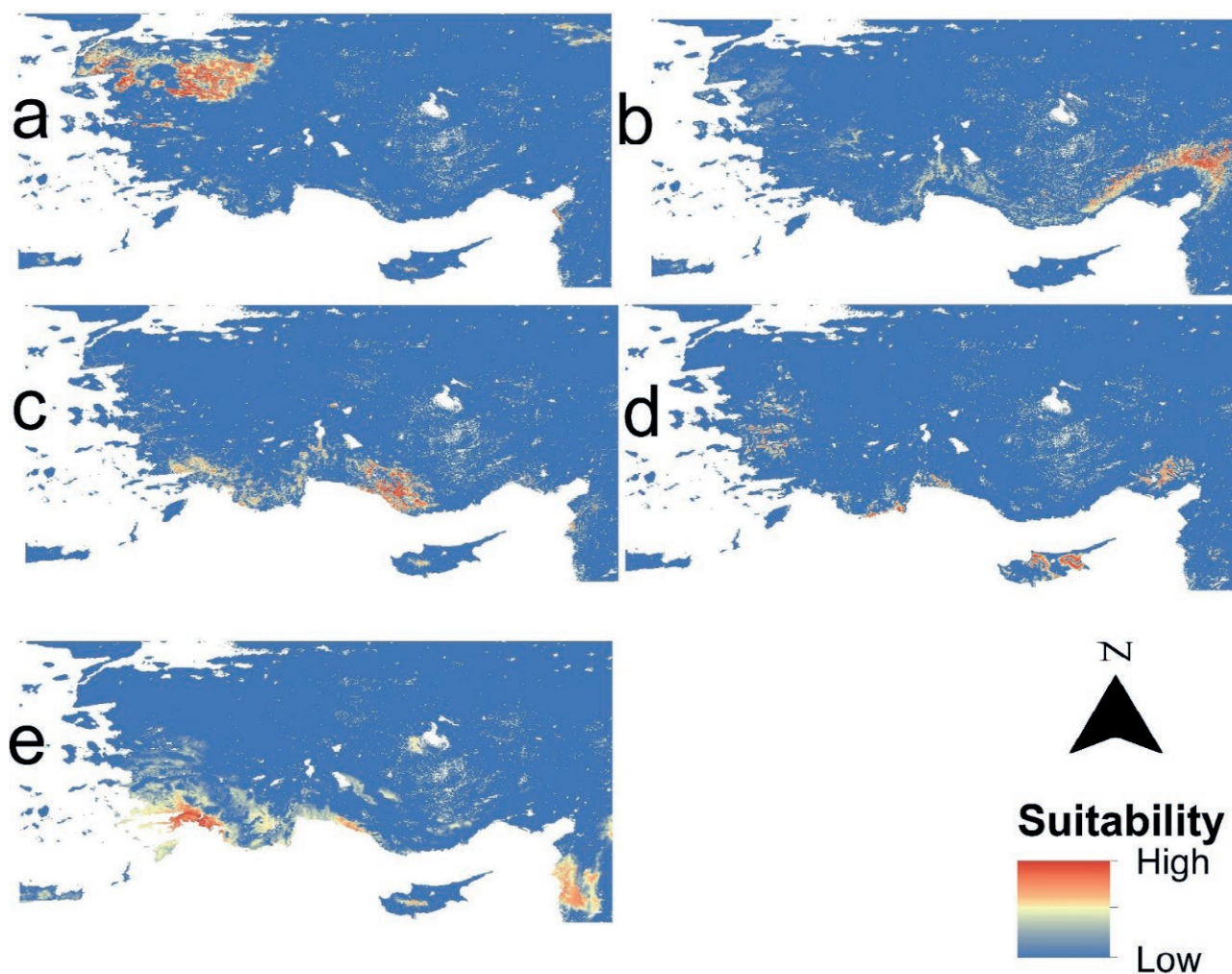


Fig. 2. Habitat suitability predictions of a. *A. anatolica*, b. *A. danfordi*, c. *A. ibrahimi*, d. *A. finikensis*, e. *A. pelasgiana* in the Anatolian Peninsula and Aegean Islands (Warmer colors refer to high suitability).

(43.7 %), and that of *A. finikensis* with the precipitation of driest quarter - Bio 17 - (35.7 %). The distribution of the remaining two species was highly determined by the envi-

ronmental variables as follows: distance to the river (36.9 %) for *A. ibrahimi* and maximum temperature of the warmest period - Bio 5 - (26 %) for *A. pelasgiana*.

Table 3. Niche overlap analyses among *Anatololacerta* species in the Anatolian Peninsula and Aegean islands.

Comparisons <i>Anatololacerta</i> sp.	Measured Niche Overlap		Identity Test		Background Test**	
	Schoener's <i>D</i>	Hellinger's based <i>I</i>	Schoener's <i>D</i>	Hellinger's based <i>I</i>	Schoener's <i>D</i>	Hellinger's based <i>I</i>
<i>pelasgiana</i> vs. <i>anatolica</i>	0.418	0.712	0.679*	0.896*	0.362	0.648
<i>pelasgiana</i> vs. <i>danfordi</i>	0.529	0.803	0.639*	0.867*	0.307	0.586
<i>pelasgiana</i> vs. <i>finikensis</i>	0.666	0.888	0.633	0.862*	0.342	0.610
<i>pelasgiana</i> vs. <i>ibrahimi</i>	0.641	0.879	0.693*	0.910*	0.346	0.623
<i>anatolica</i> vs. <i>danfordi</i>	0.389	0.669	0.693*	0.909*	0.347	0.625
<i>anatolica</i> vs. <i>finikensis</i>	0.341	0.688	0.592*	0.851*	0.328	0.606
<i>anatolica</i> vs. <i>ibrahimi</i>	0.453	0.740	0.646*	0.883*	0.305	0.577
<i>danfordi</i> vs. <i>finikensis</i>	0.472	0.748	0.582*	0.835*	0.292	0.569
<i>danfordi</i> vs. <i>ibrahimi</i>	0.593	0.847	0.649*	0.884*	0.294	0.574
<i>finikensis</i> vs. <i>ibrahimi</i>	0.547	0.822	0.655*	0.895*	0.313	0.559

* Identity test showed significant niche differentiation (all p-value < 0.05).

** No background test showed significant overlap (all p-values > 0.05).

On the other hand, even though ENM in geographic space was generally suited to determine geographic isolation between the cryptic species, discussions on species delimitation have been continuing for the last two decades (Raxworthy et al., 2007; Fišer et al., 2018). Therefore, over-predicted areas were discarded from our final discussion.

Niche overlap tests

The measured niche overlaps among all species are presented in Table 3. The null hypothesis of niche overlap between *Anatololacerta* species (except *pelasgiana* vs *finikensis*) were rejected because empirical values for Schoener's *D* and Hellinger's based *I* test statistics were significantly different than the null distribution of overlap test for each species comparisons (Fig. S2 a-j) (*t* test, *df* = 99, *P* < 0.05). In other words, the ecological niche models of most of these species were nonequivalent. Background test for the parapatric *A. pelasgiana* and *A. finikensis* confirmed the niche overlap between these species in terms of global bioclimatic and selected topographic variables (Fig. S2 k). On the other hand, background tests for species that represent allopatric diversification patterns demonstrated that empirical values for Schoener's *D* and Hellinger's based *I* test statistics did not significantly differ from the null distribution (Fig. S2 l-t).

DISCUSSION

ENM on environmental layers has revealed not only additional insights into evolutionary lineages (Rissler and

Apodaca, 2007) but also niche distinctiveness of species (Nakazato et al., 2010). Climatic niche has a remarkable effect on the area where species occur and each species requires a unique niche according to its ecological needs (Gewin, 2006; Rissler and Apodaca, 2007; Gül, 2019). There has been no study on the ecological niche of all Anatolian rock lizards so far. In this study, we have modeled environmental niches of all *Anatololacerta* species on the Anatolian Peninsula and the Aegean islands. Our results suggested that the niche divergence among the genus was confirmed for allopatric species (Fig. S2 a-j). However, the results for *A. pelasgiana* and *A. finikensis* showed that there is a niche overlap between these species (Fig. S2 k).

The present study showed the differentiation in the requirements of the ecological conditions among the *Anatololacerta* species (Fig. 2 a-e, Table 1). In other words, we assessed ecological niche differentiation to examine the phylogenetic-based taxonomic outputs for this genus. The speciation process within this genus was so far explained only by the geological factors and physical barriers (Schmidtler, 1998; Bellati et al., 2015). Based on the given results, we could assume that the differentiation within the genus and their present allopatric distribution on the Anatolian Peninsula and the Aegean islands is associated with ecological factors as well. The bioclimatological and topographical conditions provided remarkable contributions to the genetic diversity among this genus in terms of allopatric speciation. Even though ENM for each *Anatololacerta* species were generated using the same bioclimatic and topographic layers, the contribution percentiles of these variables were different. For instance, the dominant contributing variable for each *Anatololacerta* species is different: temperature annual

range for *A. anatolica*, mean leaf area index for *A. danfordi*, distance to river for *A. ibrahimi*, precipitation of driest quarter for *A. finikensis*, and maximum temperature of the warmest period for *A. pelasgiana*.

On the other hand, allopatric speciation dynamics were not only supported climatologically but also geographically (Eiselt and Schmidtler, 1986; Bellati et al., 2015). For example, separation between *A. anatolica* and the rest of the genus was highly related to the occurrence of the Great Menderes River. Additionally, *A. danfordi* was isolated from the rest of the genus by Central Taurus Mountains and located in the eastern part of Mediterranean region. Lastly, *A. ibrahimi* was only distributed in the northern and southern slopes of Central Taurus Mountains.

When it comes to parapatric speciation, the niche overlap case, that was demonstrated in the comparison between *A. pelasgiana* and *A. finikensis*, was needed to be discussed in another way, because distribution of both species was limited to only southwestern Anatolia and some Aegean islands. The actual utilization of the niche is significantly influenced by ecological interactions of various sorts. Thus, it could be helpful to use data on different selective regimes to examine the speciation dynamics of these parapatric species (Gavrilets et al., 2000; Mammola et al., 2018).

In order to discuss these speciation dynamics among this genus, it might be also beneficial to have evaluations on climate based historical perspective. Karakasi et al. (2021) revealed that the first split in *Anatololacerta* occurred in Early Pleistocene approximately 1.62 Mya with the separation of *A. anatolica* and the recent one was between *A. pelasgiana* and *A. ibrahimi* (0.56 Mya). The latter split matches the Mindel glacial period. According to the literature, 16 glacial periods have occurred during the last 2.4 million years in the Pleistocene (Webb and Bartlein, 1992; Hewitt 1996, 2000). Moreover, it was highly thought that the last four glacial periods in Pleistocene had a remarkable impact on faunal composition of Anatolia and related areas (Çıplak, 2004). Fluctuations in the temperature during these periods not only affected the movements of old Anatolian populations (Çıplak, 2004) but also shaped the vegetation dynamics with important changes (Jiménez-Moreno et al., 2015). In addition, the precipitation and temperature dynamics for a long time might have an impact on the vegetation patterns along western and southern parts of Anatolian Peninsula (Şahin et al., 2021).

On the other hand, the comparisons among allopatric *Anatololacerta* species revealed that, while their niches are not more similar than expected by chance (Fig. S2 a-j), their niches are not equivalent (Fig. S2 l-u). Studies

on allopatric *Neurergus* species in Anatolia (Gül, 2019), speciation dynamics of endemic lizards in Madagascar (Nunes et al., 2022) and diversification of shrews in island dispersal events (Esselstyn et al., 2011) demonstrated that differences between their climatic niches are compatible with the abiotic environmental conditions between the geographical regions where allopatric species have been inhabiting. In fact, although this situation shows that allopatric *Anatololacerta* species living in the same geography have different niche requirements, the isolation areas between the inhabiting zones do not have an effect on the differentiation of environmental characteristics.

If species fit to particular climatic conditions (or various local conditions), it brings to niche differentiation because of the unique adaptations needed to survive and breed (Nakazato et al., 2010). In the present study, ecological niche divergence has been inferred to display ecological speciation of species with allopatric distributions. Our results are compatible with the taxonomic suggestion of the work of Karakasi et al. (2021) that discerns each allopatric clade at the species level.

ACKNOWLEDGEMENTS

The field surveys were carried out with the permission of Republic of Turkey Ministry of Agriculture and Forestry (Permission Number: B.23.0.D MP.0.15.01-510.02-2943). We appreciate the editor and anonymous reviewers for helpful comments on the improving of the manuscript. We also would like to thank Leona Walter for proofreading.

SUPPLEMENTARY MATERIALS

Supplementary material associated with this article can be found at <<http://www-9.unipv.it/webshi/appendix/index.html>> manuscript number 13089

REFERENCES

- Anderson, R.P., Lew, D., Peterson, A.T. (2003): Evaluating predictive models of species' distributions: Criteria for selecting optimal models. *Ecol. Modell.* **162**: 211-232.
- Araújo, M.B., Thuiller, W., Pearson, R.G. (2006): Climate warming and the decline of amphibians and reptiles in Europe. *J. Biogeogr.* **33**: 1712-1728.
- Arribas, O., Candan, K., Kurnaz, M., Kumlutaş, Y., Caynak, E.Y., Ilgaz, Ç. (2022): A new cryptic species

- of the *Darevskia parvula* group from NE Anatolia (Squamata, Lacertidae). *Org. Divers. Evol.* **22**: 475-490.
- Baran, İ., Avcı, A., Kumlutaş, Y., Olgun, K., Ilgaz, Ç. (2021): Türkiye Amfibi ve Sürüngenleri. Palme Yayınevi, İzmir.
- Baran, İ., Kumlutaş, Y. (1999): On *Lacerta danfordi* (Reptilia: Lacertidae) population of the Köyceğiz Specially Protected Area. *Turk. J. Zool.* **23**: 7-14.
- Barata, M., Carranza, S., Harris, D.J. (2012): Extreme genetic diversity in the lizard *Atlantolacerta andreanaskyi* (Werner, 1929): A montane cryptic species complex. *BMC Evol. Biol.* **12**: 167.
- Barve, N., Barve, V., Jiménez-Valverde, A., Lira-Noriega, A., Maher, S.P., Peterson, A.T., Soberón, J., Villalobos, F. (2011): The crucial role of the accessible area in ecological niche modeling and species distribution modeling. *Ecol. Model.* **222**: 1810-1819.
- Bellati, A., Carranza, S., Garcia-Porta, J., Fasola, M., Sindaco, R. (2015): Cryptic diversity within the *Anatololacerta* species complex (Squamata: Lacertidae) in the Anatolian Peninsula: Evidence from a multi-locus approach. *Mol. Phylogenet. Evol.* **82**: 219-233.
- Beşer, N. (2015): Adana ilinin kuzeyinde yayılış gösteren *Anatololacerta danfordi* (Günther, 1876) popülasyonlarında yaş tayini ve bazı büyüme parametrelerinin belirlenmesi. Master's Thesis, Adnan Menderes University.
- Beşer, N., Ilgaz, Ç., Kumlutaş, Y., Candan, K., Güçlü, Ö., Üzümlü, N. (2020): Age and growth in two populations of Danford's lizard, *Anatololacerta danfordi* (Günther, 1876), from the eastern Mediterranean. *Turk. J. Zool.* **44**: 173-180.
- Bozkurt, E., Olgun, K. (2020): Taxonomic investigation of the genus *Ablepharus* (Sauria: Scincidae) with molecular and morphological methods in Anatolian populations. *Turk. J. Zool.* **44**: 134-145.
- Brown, J.L. (2014): SDM toolbox: A python-based GIS toolkit for landscape genetic, biogeographic and species distribution model analyses. *Methods Ecol. Evol.* **5**: 694-700.
- Candan, K., Kankılıç, T., Güçlü, Ö., Kumlutaş, Y., Durmuş, S. H., Lymberakis, P., Poulakakis, N., Ilgaz, Ç. (2016): First assessment on the molecular phylogeny of *Anatololacerta* (Squamata, Lacertidae) distributed in Southern Anatolia: Insights from mtDNA and nDNA markers. *Mitochondrial DNA* **27**: 2285-2292.
- Candan, K., Gül, S., Ilgaz, Ç., Kumlutaş, Y. (2021): An overview of historical distribution patterns of *Chalcides ocellatus* (Forsskål, 1775) using ecological niche modelling: Taurus Mountains as a refugium. *Russ. J. Herpetol.* **28**: 319-326.
- Chapman, A.D. (2005): Principles and Methods of Data Cleaning: Primary Species and Species-Occurrence Data. GBIF. URL <https://www.gbif.org/document/80528/principles-and-methods-of-data-cleaning-primary-species-and-species-occurrence-data>. Date accessed: 01/08/2022.
- Çıplak, B. (2004): Biogeography of Anatolia: The marker group Orthoptera. *Mem. Soc. Entomol. Ital.* **82**: 357-372.
- Cobos, M.E., Peterson, A.T., Barve, N., Osorio-Olvera, L. (2019): *kuenm*: An R package for detailed development of ecological niche models using Maxent. *PeerJ.* **7**: e6281.
- Eiselt, J., Schmidtler, J.F. (1986): Der *Lacerta danfordi*-Komplex (Reptilia: Lacertidae). *Spixiana* **9**: 289-328.
- Esselstyn, J.A., Maher, S.P., Brown, R.M. (2011): Species interactions during diversification and community assembly in an island radiation of shrews. *PLoS One.* **6**: e21885.
- Fattahi, R., Ficetola, G.F., Rastegar-Pouyani, N., Avcı, A., Kumlutaş, Y., Ilgaz, Ç., Hosseinian Yousefkhani, S.S. (2014): Modelling the potential distribution of the Bridled Skink, *Trachylepis vittata* (Olivier, 1804), in the Middle East. *Zool. Middle East* **60**: 208-216.
- Fick, S.E., Hijmans, R.J. (2017): WorldClim 2: New 1km spatial resolution climate surfaces for global land areas. *Int. J. Climatol.* **37**: 4302-4315.
- Fişer, C., Robinson, C.T., Malard, F. (2018): Cryptic species as a window into the paradigm shift of the species concept. *Mol. Ecol.* **27**: 613-635.
- Freitas, S., Vavakou, A., Arakelyan, M., Drovetski, S.V., Crnobrnja-Isailović, J., Kidov, A.A., Cogălniceanu, D., Corti, C., Lymberakis, P., Harris, D.J. (2016): Cryptic diversity and unexpected evolutionary patterns in the meadow lizard, *Darevskia praticola* (Eversmann, 1834). *System. Biodivers.* **14**: 184-197.
- Gavashelishvili, A., Tarkhnishvili, D. (2016): Biomes and human distribution during the last ice age. *Glob. Ecol. Biogeogr.* **25**: 563-574.
- Gavashelishvili, A., Yarovenko, Y.A., Babayev, E.A., Mikladze, G., Gurielidze, Z., Dekanoidze, D., Kerdikoshvili, N., Ninua, L., Paposhvili, N. (2018): Modeling the distribution and abundance of eastern tur (*Capra cylindricornis*) in the Caucasus. *J. Mammal.* **99**: 885-897.
- Gavrilets, S., Li, H., Vose, M.D. (2000): Patterns of parapatric speciation. *Evolution* **54**: 1126-1134.
- Gewin, V. (2006): Beyond neutrality-Ecology finds its niche. *PLoS Biol.* **4**: e278.
- Guisan, A., Zimmermann, N.E. (2000): Predictive habitat distribution models in ecology. *Ecol. Modell.* **135**: 147-186.

- Gül, S. (2019): Is there an ecological barrier between allopatric spotted newts (*Neurergus strauchii* and *Neurergus crocatus*) in Turkey? A view to the glacier mountains of Hakkari. In Salamander: Habitat, Behavior and Evolution, pp. 63-85. Gerasimov, R., Ed, Nova Science Publishers, New York.
- Gül, S., Kumlutaş, Y., Ilgaz, Ç. (2015): Climatic preferences and distribution of 6 evolutionary lineages of *Typhlops vermicularis* Merrem, 1820 in Turkey using ecological niche modeling. Turk. J. Zool. **39**: 235-243.
- Gül, S., Kumlutaş, Y., Ilgaz, Ç. (2016): Predicted distribution pattern of *Pelias kaznakovi* (Nikolsky, 1909) in the Caucasus hotspot with a new locality record from Turkey. Russ. J. Herpetol. **23**: 224-230.
- Gül, S., Kumlutaş, Y., Ilgaz, Ç. (2018): Potential distribution under different climatic scenarios of climate change of the vulnerable Caucasian salamander [*Mertensiella caucasica* (Waga, 1876)]: A case study of the Caucasus Hotspot. Biologia **73**: 175-184.
- Heidari, N. (2019): Ecological niche differentiation between *Acanthodactylus micropholis* and *A. khamiensis* (Sauria: Lacertidae) in southern Iran. Zoologia **36**: e27357.
- Hewitt, G.M. (1996): Some genetic consequences of ice ages, and their role in divergence and speciation. Biol. J. Linn. Soc. **58**: 247-276.
- Hewitt, G. (2000): The genetic legacy of the Quaternary ice ages. Nature **405**: 907-913.
- Hosseinian Yousefkhani, S.S., Mirshamsi, O., Ilgaz, Ç., Kumlutaş, Y., Avcı, A. (2016): Ecological Niche Divergence between *Trapelus ruderatus* (Olivier, 1807) and *T. persicus* (Blanford, 1881) (Sauria: Agamidae) in the Middle East. Asian Herpetol. Res. **7**: 96-102.
- Hosseinian Yousefkhani, S.S., Rastegar-Pouyani, E., Ilgaz, Ç., Kumlutaş, Y., Avcı, A., Wink, M. (2019): Evidences for ecological niche differentiation on the Anatolian lizard (*Apathya cappadocica* ssp.) (Reptilia: Lacertidae) in western Asia. Biologia **74**: 1661-1667.
- Hurvich, C.M., Tsai, C.L. (1989): Regression and time series model selection in small samples. Biometrika **76**: 297-307.
- Jablonski, D., Kukushkin, O.V., Avcı, A., Bunyatova, S., Kumlutaş, Y., Ilgaz, Ç., Polyakova, E., Shiryayev, K., Tuniyev, B., Jandzik, D. (2019): The biogeography of *Elaphe sauromates* (Pallas, 1814), with a description of a new rat snake species. PeerJ **7**: e6944.
- Jezkova, T., Wiens, J.J. (2018): Testing the role of climate in speciation: New methods and applications to squamate reptiles (lizards and snakes). Mol. Ecol. **27**: 2754-2769.
- Jiménez-Moreno, G., Alçiçek, H., Alçiçek, M.C., van den Hoek Ostende, L., Wesselingh, F.P. (2015): Vegetation and climate changes during the late Pliocene and early Pleistocene in SW Anatolia, Turkey. Quat. Res. **84**: 448-456.
- Kalioztopoulou, A., Carretero, M.A., Llorente, G.A. (2012): Morphology of the *Podarcis* wall lizards (Squamata: Lacertidae) from the Iberian Peninsula and North Africa: Patterns of variation in a putative cryptic species complex. Zool. J. Linn. Soc. **164**: 173-193.
- Karakasi, D., Ilgaz, Ç., Kumlutaş, Y., Candan, K., Güçlü, Ö., Kankılıç, T., Beşer, N., Sindaco, R., Lymberakis, P., Poulakakis, N. (2021): More evidence of cryptic diversity in *Anatololacerta* species complex Arnold, Arribas and Carranza, 2007 (Squamata: Lacertidae) and re-evaluation of its current taxonomy. Amphibia-Reptilia **42**: 201-216.
- Kass, J.M., Vilela, B., Aiello-Lammens, M.E., Muscarella, R., Merow, C., Anderson, R.P. (2018): Wallace: A flexible platform for reproducible modeling of species niches and distributions built for community expansion. Methods Ecol. Evol. **9**: 1151-1156.
- Kıraç, A., Gidiş, M., Mert, A., Başkale, E. (2022): Climate change and the fate of endemic Beyşehir Frog, *Pelophylax caralitanus*. Amphib. Reptile Conse. **16**: 76-85.
- Klausmeyer, K.R., Shaw, M.R. (2009): Climate change, habitat loss, protected areas and the climate adaptation potential of species in Mediterranean ecosystems worldwide. PloS One **4**: e6392.
- Kornilios, P., Ilgaz, Ç., Kumlutaş, Y., Lymberakis, P., Moravec, J., Sindaco, R., Rastegar-Pouyani, N., Afroosheh, M., Giokas, S., Fragedakis-Tsolis, S. (2012): Neogene climatic oscillations shape the biogeography and evolutionary history of the Eurasian blindsnake. Mol. Phylogenet. Evol. **62**: 856-873.
- Kotsakiozi, P., Jablonski, D., Ilgaz, Ç., Kumlutaş, Y., Avcı, A., Meiri, S., Itescu, Y., Kukushkin, O., Gvoždík, V., Scillitani, G. (2018): Multilocus phylogeny and coalescent species delimitation in Kotschy's gecko, *Mediodactylus kotschyi*: Hidden diversity and cryptic species. Mol. Phylogenet. Evol. **125**: 177-187.
- Kumlutaş, Y., Ilgaz, Ç., Candan, K. (2015): Fethiye-Göcek (Muğla) Özel Çevre Koruma Bölgesi'nin herpetofaunik çeşitliliği. Anadolu Doğa Bilimleri Dergisi **2**: 155-162.
- Kurnaz, M. (2020): Species list of Amphibians and Reptiles from Turkey. J. Anim. Divers. **2**: 10-32.
- Kurnaz, M., Hosseinian Yousefkhani, S.S. (2020): Ecological niche divergence between *Darevskia rudis* and *D. bithynica* (Lacertidae) in Turkey. Biologia **75**: 1307-1312.
- Kurnaz, M., Hosseinian Yousefkhani, S.S. (2021): A Contribution to the biogeography of *Ablepharus anatolicus*

- and *A. budaki* (Squamata: Scincidae) using ecological niche modeling in Turkey. *Folia Biol. (Kraków)*. **69**: 159-166.
- Kurnaz, M., Kutrup, B., Hosseinian Yousefkhani, S.S., Koç, H., Bülbül, U., Eroğlu, A.İ. (2019): Phylogeography of the red-bellied lizard, *Darevskia parvula* in Turkey. *Mitochondr. DNA A* **30**: 556-566.
- Kurnaz, M., Şahin, M.K. (2021a): A contribution to the biogeography and taxonomy of two Anatolian mountain brook newts, *Neurergus barani* and *N. strauchii* (Amphibia: Salamandridae) using ecological niche modeling. *Turk. J. Zool.* **45**: 54-64.
- Kurnaz, M., Şahin, M.K. (2021b): Contribution to the taxonomic knowledge of *Acanthodactylus* (Squamata, Lacertidae): Description of a new lacertid lizard species from Eastern Anatolia, Turkey. *J. Wildl. Biodivers.* **5**: 100-119.
- Kurnaz M., Şahin, M.K., Eroğlu, A.İ. (2022): Hidden diversity in a narrow valley: Description of new endemic Palearctic rock lizard *Darevskia* (Squamata: Lacertidae) species from northeastern Turkey. *Zool. Stud.* **61**: 44.
- Mammola, S., Arnedo, M.A., Pantini, P., Piano, E., Chiappetta, N., Isaia, M. (2018): Ecological speciation in darkness? Spatial niche partitioning in sibling subterranean spiders (Araneae: Linyphiidae: *Troglohyphantes*). *Invertebr. Syst.* **32**, 1069-1082.
- Manel, S., Williams, H.C., Ormerod, S.J. (2001): Evaluating presence-absence models in ecology: the need to account for prevalence. *J. Appl. Ecol.* **38**: 921-931.
- Mendes, J., Salvi, D., Harris, D.J., Els, J., Carranza, S. (2018): Hidden in the Arabian Mountains: Multilocus phylogeny reveals cryptic diversity in the endemic *Omanosaura* lizards. *J. Zoolog. Syst. Evol.* **56**: 395-407.
- Mulder, J. (1995): Herpetological observations in Turkey (1987-1995). *Deinsea* **2**: 51-66.
- Muscarella, R., Galante, P.J., Soley-Guardia, M., Boria, R.A., Kass, J.M., Uriarte, M., Anderson, R.P. (2014): *ENMeval*: An R package for conducting spatially independent evaluations and estimating optimal model complexity for Maxent ecological niche models. *Methods Ecol. Evol.* **5**: 1198-1205.
- Nakazato, T., Warren, D.L., Moyle, L.C. (2010): Ecological and geographic modes of species divergence in wild tomatoes. *Am. J. Bot.* **97**: 680-693.
- Nunes, L.A., Raxworthy, C.J., Pearson, R.G. (2022): Evidence for ecological processes driving speciation among endemic lizards of Madagascar. *Evolution* **76**, 58-69.
- Pearson, R.G., Raxworthy, C.J., Nakamura, M., Townsend Peterson, A. (2007): Predicting species distributions from small numbers of occurrence records: A test case using cryptic geckos in Madagascar. *J. Biogeogr.* **34**: 102-117.
- Peterson, A.T., Papeş, M., Soberón, J. (2008): Rethinking receiver operating characteristic analysis applications in ecological niche modeling. *Ecol. Modell.* **213**: 63-72.
- Phillips, S.J., Anderson, R.P., Schapire, R.E. (2006): Maximum entropy modeling of species geographic distributions. *Ecol. Modell.* **190**: 231-259.
- Phillips, S.J., Dudík, M., Elith, J., Graham, C.H., Lehmann, A., Leathwick, J., Ferrier, S. (2009): Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. *Ecol. Appl.* **19**: 181-97.
- Phillips, S.J., Dudík, M., Schapire, R.E. (2017): Maxent software for modeling species niches and distributions (Version 3.4.1). URL http://biodiversityinformatics.amhn.org/open_source/maxent/. [accessed on 1 August 2022]
- Psonis, N., Antoniou, A., Kukushkin, O., Jablonski, D., Petrov, B., Crnobrnja-Isailović, J., Sotiropoulos, K., Gherghel, I., Lymberakis, P., Poulakakis, N. (2017): Hidden diversity in the *Podarcis tauricus* (Sauria, Lacertidae) species subgroup in the light of multilocus phylogeny and species delimitation. *Mol. Phylogenet. Evol.* **106**: 6-17.
- Rajabizadeh, M., Nagy, Z.T., Adriaens, D., Avci, A., Masroor, R., Schmidtler, J., Nazarov, R., Esmaeili, H.R., Christiaens, J. (2016): Alpine-Himalayan orogeny drove correlated morphological, molecular, and ecological diversification in the Persian dwarf snake (Squamata: Serpentes: *Eirenis persicus*). *Zool. J. Linn. Soc.* **176**: 878-913.
- Raxworthy, C.J., Ingram, C.M., Rabibisoa, N., Pearson, R.G. (2007): Applications of ecological niche modeling for species delimitation: A review and empirical evaluation using day geckos (*Phelsuma*) from Madagascar. *Syst. Biol.* **56**: 907-923.
- Rissler, L.J., Apodaca, J.J. (2007): Adding more ecology into species delimitation: Ecological niche models and phylogeography help define cryptic species in the black salamander (*Aneides flavipunctatus*). *Syst. Biol.* **56**: 924-942.
- Rodríguez-Ruiz, R., Juárez-Agis, A., García-Sánchez, S., Olivier-Salome, B., Zeferino-Torres, J., Rivas-González, M. (2020): Modelling the current and future potential distribution of *Maconellicoccus hirsutus* (Green, 1908) a pest of importance for Mexico. *AgroProductividad* **13**: 47-52.
- R Core Team (2020): R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria.

- Şahin, M.K., Candan, K., Caynak, E.Y., Kumlutaş, Y., Ilgaz, Ç. (2021): Ecological niche divergence contributes species differentiation in worm lizards (*Blanus* sp.) (Squamata: Amphisbaenia: Blanidae) in Mediterranean part of Anatolian peninsula and the Levantine region. *Biologia* **76**: 525-532.
- Sarıkaya, B., Yıldız, M.Z., Sezen, G. (2017): Adana ilinin herpetofaunası. *Kommagene Biyoloji Dergisi* **1**: 1-11.
- Soberon, J., Peterson A.T. (2005): Interpretation of models of fundamental ecological niches and species' distributional areas. *Biodivers. Inform.* **2**: 1-10.
- Schmidtler, J.F. (1998): Verbreitungsstrukturen der Herpetofauna im Taurus-Gebirge, Türkei (Amphibia; Reptilia). *Faunistische Abhandlungen, Staatliches Museum Für Tierkunde in Dresden* **21**: 133-148.
- Schoener, T.W. (1968): The *Anolis* lizards of Bimini: Resource partitioning in a complex fauna. *Ecology* **49**: 704-726.
- Skourtanioti, E., Kapli, P., Ilgaz, Ç., Kumlutaş, Y., Avcı, A., Ahmadzadeh, F., Crnobrnja-Isailović, J., Gherghel, I., Lymberakis, P., Poulakakis, N. (2016): A reinvestigation of phylogeny and divergence times of the *Ablepharus kitaibelii* species complex (Sauria, Scincidae) based on mtDNA and nuDNA genes. *Mol. Phylogenet. Evol.* **103**: 199-214.
- Šmíd, J., Moravec, J., Gvoždík, V., Štundl, J., Frynta, D., Lymberakis, P., Kapli, P., Wilms, T., Schmitz, A., Shobrak, M. (2017): Cutting the Gordian Knot: Phylogenetic and ecological diversification of the *Mesalina breviostris* species complex (Squamata, Lacertidae). *Zool. Scr.* **46**: 649-664.
- Speybroeck, J., Beukema, W., Dufresnes, C., Fritz, U., Jablonski, D., Lymberakis, P., Martínez-Solano, I., Razzetti, E., Vamberger, M., Vences, M., Vörös, J., Crochet, P. (2020): Species list of the European herpetofauna – 2020 update by the Taxonomic Committee of the Societas Europaea Herpetologica Amphibia-Reptilia **41**: 139-189.
- Tamar, K., Carranza, S., In den Bosch, H., Sindaco, R., Moravec, J., Meiri, S. (2015): Hidden relationships and genetic diversity: Molecular phylogeny and phylogeography of the Levantine lizards of the genus *Phoenicolacerta* (Squamata: Lacertidae). *Mol. Phylogenet. Evol.* **91**: 86-97.
- Tuniyev, B.S., Avcı, A., Ilgaz, Ç., Olgun, K., Petrova, T.V., Bodrov, S.Y., Geniez, P., Teynié, A. (2018): On taxonomic status of shield-head vipers from Turkish Lesser Caucasus and East Anatolia. *Proceedings of the Zoological Institute RAS* **322**: 3-44.
- Warren, D.L., Glor, R.E., Turelli, M. (2008): Environmental niche equivalency versus conservatism: Quantitative approaches to niche evolution. *Evolution: International Journal of Organic Evolution* **62**: 2868-2883.
- Warren, D.L., Matzke, N.J., Cardillo, M., Baumgartner, J.B., Beaumont, L.J., Turelli, M., Glor, R.E., Huron, N.A., Simões, M., Iglesias, T.L. (2021): *ENMTools* 1.0: An R package for comparative ecological biogeography. *Ecography* **44**: 504-511
- Webb III, T., Bartlein, P.J. (1992): Global changes during the last 3 million years: Climatic controls and biotic responses. *Annu. Rev.Ecol. Syst.* **23**: 141-173.
- Yakın, B.Y., Tok, C.V. (2015): Age estimation of *Anatololacerta anatolica* (Werner, 1902) in the vicinity of Çanakkale by skeletochronology. *Turk. J. Zool.* **39**: 66-73.
- Yaşar, Ç., Çiçek, K., Mulder, J., Tok, C.V. (2021): The distribution and biogeography of amphibians and reptiles in Turkey. *North West J. Zool.* **17**: 232-275.
- Yılmaz, C., Ilgaz, Ç., Üzüm, N., Avcı, A. (2021): First record of Jan's Cliff Racer, *Platyceps rhodorachis* (Jan, 1863) (Serpentes: Colubridae) in Turkey. *Zool. Middle East* **67**: 92-94.
- Zhao, Q., Zhang, H., Wei, J. (2019): Climatic niche comparison across a cryptic species complex. *PeerJ* **7**: e7042.