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ORIGINAL ARTICLE

Ecological niche divergence between *Darevskia rudis* and *D. bithynica* (Lacertidae) in Turkey

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Abstract

Darevskia rudis (Bedriaga, 1886) and *D. bithynica* (Méhely, 1909) are morphologically different species, but they are phylogenetically same species in the *D. rudis* complex. These species are distributed in northern of Turkey. In the present study, we have evaluated taxonomic status of *D. rudis* and *D. bithynica* using ecological niche differentiation. All occurrence data of these species were used to predict and evaluate the suitable areas where they may be expected to be found in Turkey. In order to compare their ecological niches and explain ecological differentiation, niche similarity tests (niche identity and background tests) and point-based analyses were performed. According to results of ecological niche modeling, we found niche differentiation between *D. rudis* and *D bithynica*. Ecological niches for the two species differentiated along environmental variables, as precipitation of driest quarter for the two species were most important in determining habitat suitability. This factor is important in niche differentiation between the two species. Finally, our results confirmed the niche differentiation between *D. rudis* and *D. bithynica* and added new insights into the taxonomic distinction between *D. rudis* and *D. bithynica* that they are two species.

Keywords *Darevskia* · Lacertidae · Turkey · Niche differentiation · Reptiles

Introduction

The preservation of the niche is a phenomenon that conserves the general ancestral characteristics among different species (Wiens and Graham 2005). Therefore, ecological niche is very important to separate a species from another species, and according to the ecological species criterion, all the species have a special niche in their living area (Van Valen 1976). Geography has an important role to differentiate niche among the species, and isolation zones do not only distinguish between species but can also lead to differentiation of their ecological requirements (Kurnaz et al. 2019). Ecological niche modeling is a prime method trying to estimate the habitat suitability of species in other potential areas using locality records of species and bioclimatic layers (Graham et al. 2004; Hosseinian Yousefkhani et al. 2013). This method uses to examine the effects of environmental conditions on species distribution, and also there are many studies showing that bioclimatic variables are effective on the ecological niche modeling of species (Litvinchuk et al. 2010; Doronin 2012; Fattahi et al. 2014; Hosseinian Yousefkhani et al. 2013; Kurnaz et al. 2019; Hosseinian Yousefkhani 2019).

Darevskia rudis (Bedriaga, 1886) and *D. bithynica* (Méhely, 1909) are morphologically two separate species; they have a geographically allopatric distribution in northern Turkey (Arribas et al. 2013). However, recent molecular study based on the nuclear and mitochondrial markers indicated that these species were not separate (Koç et al. 2017). Also, Koç et al. (2017) reported that *D. rudis* complex is still ongoing, and gene exchange between species continues. These two species showed molecular and morphological discordance. In the present study, we employed both occurrence records of the species in Turkey and environmental layers to predict the potential distribution model and compared the results to calculate the level of ecological niche overlap. The main purposes of this study are: 1) to predict highly suitable areas for

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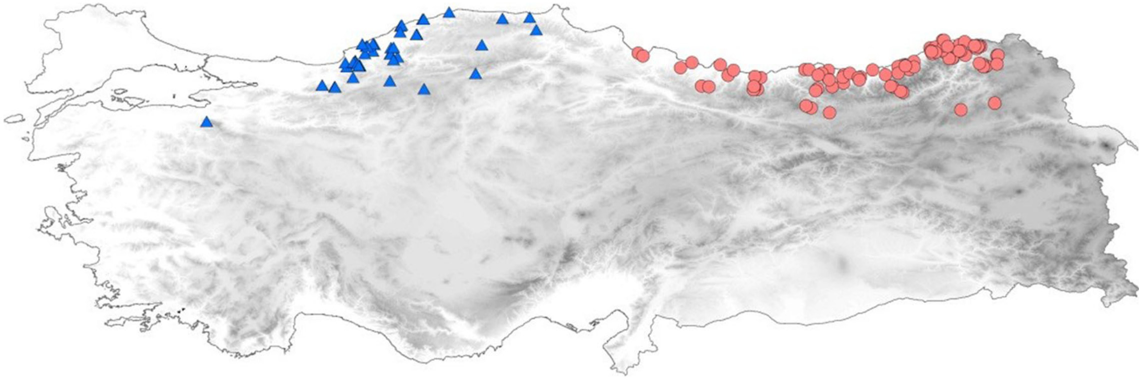

Fig. 1 Map of Turkey and distribution range of *D. rudis* (red circles) and *D. bithynica* (blue triangles). Their distribution range does not have any overlap

D. rudis and *D. bithynica* distribution and determine which environmental factors are important for species distribution; and 2) to measure and compare niche divergence between two species showing discordance based on molecular and morphological data.

Materials and methods

A total of 133 occurrence data was collected from field studies and published literatures (Budak and Böhme 1978; Kumlutaş et al. 1998; Arribas et al. 2013; Gül et al. 2014; Roca et al. 2015; Göçmen et al. 2016; Koç et al. 2017). Eighty-eight of these localities are represented with *D. rudis*, 45 of them are represented with *D. bithynica*. The map of current distribution for these two species is shown in Fig. 1. Also, the geographical discrimination of the two species is given in Fig. 2 as plotted using SPSS software program.

Nineteen bioclimatic variables were downloaded from Global Climate Data to construct species distribution modeling (Hijmans et al. 2005; available at www.worldclim.org). These data were generated from global ESRI grids in the highest resolution [30″ (~1 km)] for current conditions (~1950–2000). Each bioclimatic variable was limited to the land border of Turkey using by Arc Toolbox (extract by mask) in ArcGIS ver. 10.3 software. In order to eliminate the negative effect resulting from other environmental variables, Pearson correlation coefficient ($0.75 < r < -0.75$) was calculated using ENMTools 1.3 (Warren et al. 2010) for all variables, and then highly correlated variables were left out

Fig. 2 Pattern of species occurrence records with respect to latitude against longitude

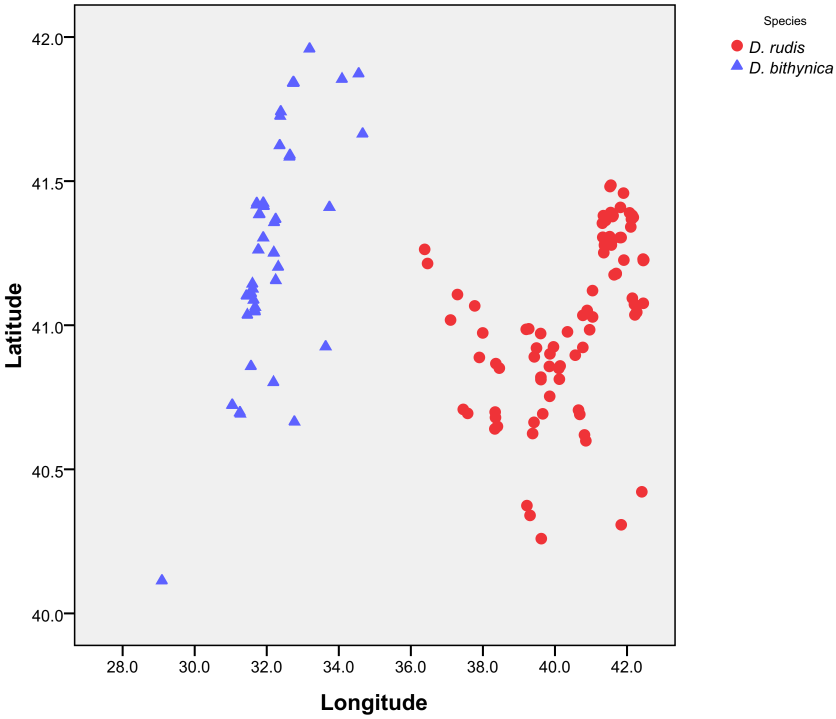

Table 1 Percentage contribution of all examined layers in species distribution modeling of *D. rudis* and *D. bithynica*

Environmental layer	*D. bithynica*	*D. rudis*
BIO 6	5.2%	2.8%
BIO 8	1.7%	7.7%
BIO 9	5.9%	4.2%
BIO 11	16%	1.8%
BIO 17	**71.3%**	**83.5%**

from distribution modeling of *D. rudis* and *D. bithynica* (Appendix: Table 2).

After the correlation analysis, Maxent 3.3.3e (Phillips et al. 2006) software was used to perform species distribution modeling. To develop the model, 133 occurrence data based on literature and field studies were used. A quarter (25%) of the occurrence data was set aside as test points, and 10,000 background points were used to determine the distribution. Additionally, the regularization multiplier = 0.5, maximum iterations = 500, and convergence threshold = 10^{-5} were chosen in Maxent. In order to test the variable importance, the jackknife test of variable importance was chosen in Maxent, and the model was run as ten replicates. The result of the receiver operating characteristic (ROC) curve is important for model sensitization and the value of the area under the curve (AUC) closest to 1 indicated the excellent model performance. A value near 0.5 suggests that the result is not better than random (Raes and ter Steege 2007; Gallien et al. 2012).

The identity test is used to test habitat suitability scores for two species to assess significant niche differences generated by ENM (Warren et al. 2010). ENMTools was employed to calculate the niche overlap test between the species. Schoener's *D* (Warren et al. 2008) and Hellinger's-based *I* (Schoener and Gorman 1968) are two indices for the niche identity and were calculated based on the habitat suitability comparison from ENM. Schoener's *D* calculates the suitable range for a given species based on probability distributions for inhabiting a particular region (cells), calculating niche overlap based upon species abundance in those locations. Hellinger's-based *I* is based purely on probability distributions without the assumptions of Schoener's *D*. (Warren et al. 2010). Both indices range from 0 (complete divergence/no overlap) to 1 (high similarity/complete overlap). Background tests were performed to evaluate whether the ecological niches of two species are different from each other beyond expected differences based upon the environmental conditions that they require (Warren et al. 2008). We compared the niche models of potential habitat for each species with a series of 100 pseudoreplicate models generated using data from the others (Warren et al. 2008). The Schoener's *D* and Hellinger's-based *I* of the true calculated niche were compared to the null distribution of 100 replicates (Warren et al. 2008).

Results

Because of low correlation, we chose a total of five variables to use ecological niche modeling for *D. rudis* and *D. bithynica*, and these variables were used in the present study. Bio-6 (Min Temperature of Coldest Month), Bio-8 (Mean Temperature of Wettest Quarter), Bio-9 (Mean Temperature of Driest Quarter), Bio-11 (Mean Temperature of Coldest Quarter), Bio-17 (Precipitation of Driest Quarter) were chosen for distribution model. The contributions of the variables are given in Table 1.

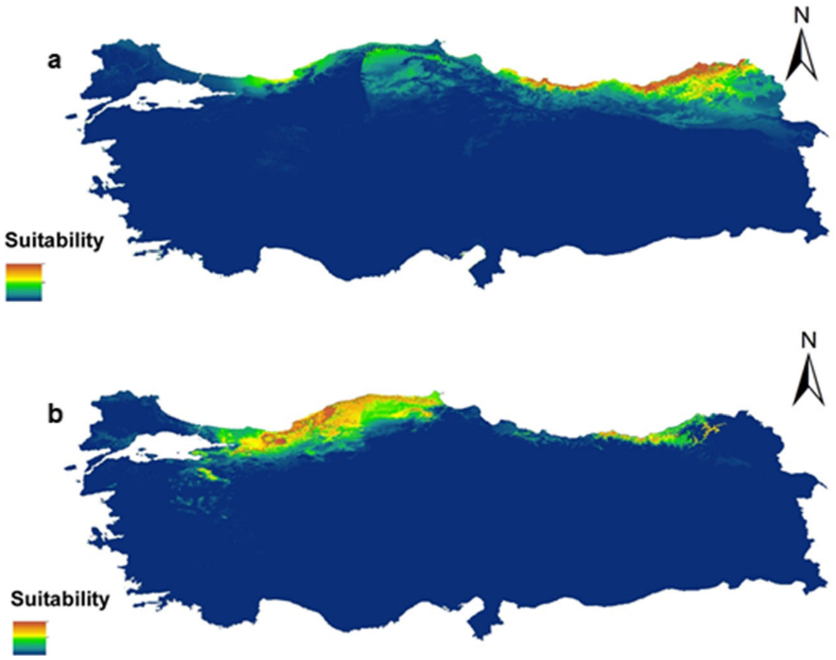

Fig. 3 Habitat suitability prediction of **a** *D. rudis* and **b** *D. bithynica* in Turkey. Warmer color refers to the high suitability degree for species presence

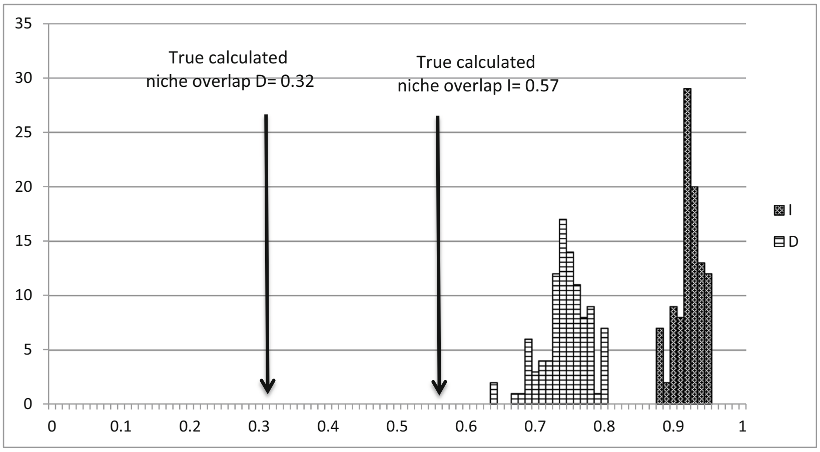

Fig. 4 Identity test between *D. rudis* and *D. bithynica* in northeastern Turkey. The expected niche area is significantly out of the observed niche between them

Based on the results, BIO 17 is the most contributing variable for both species presence with more than 70% of the contribution.

Geographical records of two species have no overlap in their distribution ranges (Fig. 1). Similarly, the distribution range of both species was plotted and shows no overlap between them (Fig. 2). Ecological models of *D. rudis* and *D. bithynica* confirmed the occurrence of suitable areas for their presence in Turkey (Fig. 3). Estimated training AUC values ± standard deviation (SD), 0.971 ± 0.014 for *D. rudis* and 0.979 ± 0.012 *D. bithynica* indicated very good model results in comparison with random background points. The habitat suitability for *D. rudis* was predicted to be in northern Turkey, especially in the central and eastern Black Sea region, while the predicted habitat suitability for *D. bithynica* was shown in the western Black Sea region (Fig. 3).

Ecological niche modeling results showed that there is no niche overlap between two species (Hellinger's-based $I = 0.58$ and Schoener's $D = 0.33$ for *D. rudis*/*D. bithynica*). The identity test indicated that our null hypothesis of niche overlap between *D. rudis* and *D. bithynica* was rejected and overlap between two species was significantly different (t-test, $df = 99$, $P < 0.05$). The model indicated that estimated niche model for *D. rudis*/*D. bithynica* ($D_{H0} = 0.75 \pm 0.03$ vs. $D_{H1} = 0.33$ and $I_{H0} = 0.93 \pm 0.02$ vs. $I_{H1} = 0.58$ were completely separated and significantly different (Fig. 4). The identity test indicated that the overlap between the two species was significantly different. The model indicated that estimated niche models for the two species were completely separated and significantly distinct (Fig. 4). According to niche results, because these two species have a different ecological niche, it can be stated that these groups are separate species. Because of the allopatric distribution of both species, we don't run the background test. It is necessary when two species have parapatric distribution.

Discussion

Ecological niche modeling may supply important information to solve taxonomic distinction and niche differentiation among the close species groups (Nakazato et al. 2010; Hosseinian Yousefkani et al. 2016). Also, niche separation is very important for each species because each of them has a different niche according to ecological knowledge (Kurnaz et al. 2019). This situation shows that they need different requirements in their habitats. This is the first study that used ENM to evaluate the ecological niche differentiation between *D. rudis* and *D. bithynica* in Turkey. There is no geographical overlap between *D. rudis* and *D. bithynica* (Fig. 1), showing that each species has its own distribution range. Ecological niche differentiation, one of the factors for the speciation, is confirmed by the niche identity test because the test supported the significant ecological niche divergence between two species groups in the present study. The differentiation between *D. rudis* and *D. bithynica* on the species level was previously explained by morphology (Arribas et al. 2013). However, they did not separate based on molecular study (Koç et al. 2017). Our results were congruent with the study of Arribas et al. (2013).

Species distribution has also been affected many factors, including biotic factors including competitors or predictors and abiotic factors such as environmental factors or microhabitat structures (Peterson et al. 1999). Abiotic factors such as climatic variables can promote adaptive divergence and speciation (Rissler and Apodaca 2007). Our results showed significant ecological niche differentiation between *D. rudis* and *D. bithynica* based on five climatic variables.

Three different approaches concluded that there are significant niche differences between the species. According to the niche similarity test, there is significant ecological differentiation between *D. rudis* and *D. bithynica*. The identity test suggested their ecological niches were significantly different (Fig. 4). Based on these results, there is significant niche differentiation between *D. rudis* and *D. bithynica*. Ecological niche divergence, in the present study, in an allopatric condition has been inferred

Table 2 Pearson correlation table that shows high correlated variables (more than 0.75)

Variables	bio19	bio1	bio2	bio3	bio4	bio5	bio6	bio7	bio8	bio9	bio10	bio11	bio12	bio13	bio14	bio15	bio16	bio17	bio18
bio19		0.75	0.99	0.99	0.88	0.99	−0.01	0.99	0.13	0.20	0.99	0.01	0.99	0.99	0.99	0.99	0.99	0.99	0.99
bio1			0.75	0.75	0.67	0.75	0.01	0.75	0.10	0.20	0.75	0.01	0.75	0.75	0.75	0.75	0.75	0.75	0.75
bio2				0.99	0.89	0.99	0.,01	0.99	0.12	0.20	0.99	0.01	0.99	0.99	0.99	0.99	0.99	0.99	0.99
bio3					0.88	0.99	0.01	0.99	0.12	0.20	0.99	0.01	0.99	0.99	0.99	0.99	0.99	0.99	0.99
bio4						0.89	0.16	0.89	0.12	0.23	0.89	0.08	0.88	0.88	0.88	0.89	0.88	0.88	0.88
bio5							−0.01	0.99	0.12	0.20	0.99	0.01	0.99	0.99	0.99	0.99	0.99	0.99	0.99
bio6								0.01	0.13	0.08	−0.01	−0.01	−0.01	−0.01	0.01	0.01	−0.01	0.01	0.01
bio7									0.12	0.21	0.99	0.01	0.99	0.99	0.99	0.99	0.99	0.99	0.99
bio8										−0.01	0.12	−0.11	0.13	0.12	0.12	0.12	0.12	0.12	0.12
bio9											0.20	0.11	0.20	0.20	0.21	0.20	0.21	0.21	0.21
bio10												0.01	0.99	0.99	0.99	0.99	0.99	0.99	0.99
bio11													0.01	0.01	0.01	0.01	0.01	0.01	0.01
bio12														0.99	0.99	0.99	0.99	0.99	0.99
bio13															0.99	0.99	0.99	0.99	0.99
bio14																0.99	0.99	0.99	0.99
bio15																	0.99	0.99	0.99
bio16																		0.99	0.99
bio17																			0.99

to represent ecological speciation (Rundle and Nosil 2005; Wellenreuther et al. 2012). Our results confirm the taxonomic suggestion of Arribas et al. (2013) that both species can be upgraded to the species level in terms of ecological niche.

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Compliance with ethical standards

Conflict of interest The authors have no conflict of interest.

Appendix

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