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Ecological niche differentiation and taxonomic distinction between *Eremias strauchi strauchi* and *Eremias strauchi kopetdaghica* (Squamata: Lacertidae) on the Iranian Plateau based on ecological niche modeling

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Abstract

Eremias strauchi strauchi and *Eremias strauchi kopetdaghica* are genetically and morphologically distinct and are distributed allopatrically in northeastern and northwestern Iran. *E. s. strauchi* is distinguishable by having green spots on lateral parts of the body, while *E. s. kopetdaghica* is characterized by white spots and irregular black dots on lateral parts of the body. Recent molecular studies have suggested that these are two distinct species, but other types of analyses leave their classification unclear. In this study, we evaluated their taxonomic status using additional data (including ecological niches) to confirm the hypothesis that they are two species. All known records of their occurrence were employed to predict and evaluate the suitable areas where they may be expected to be found in Iran. We then performed niche similarity tests (niche identity and background tests) and point-based analyses to compare their ecological niches and explain ecological differentiation. Niche models of *E. s. strauchi* and *E. s. kopetdaghica* had good results and powerful performance based on high area under the curve (AUC) values [*E. s. strauchi* = 0.992, standard deviation (SD) = ± 0.008; *E. s. kopetdaghica* = 0.978, SD = ± 0.032]. Ecological differentiation has been found across the entire range, indicating that ecological differentiation had an important role in species differentiation. Environmental conditions for the species diverged along environmental variables, as precipitation of coldest quarter for the "Strauch" subspecies and precipitation of warmest quarter for the "Kopet dagh" subspecies were most important in determining habitat suitability, respectively. These two factors are important in niche differentiation between the two species and influenced their genetic divergence. Finally, our results confirmed the niche differentiation between *E. s. strauchi* and *E. s. kopetdaghica* and added new insights into the taxonomic distinction between *E. s. strauchi* and *E. s. kopetdaghica*.

Keywords: *Ecological niche modeling,* E. s. kopetdaghica*,* E. s. strauchi*, MaxEnt, niche divergence*

Introduction

There are several criteria, such as morphological characters and DNA markers, which are used to diagnose and delimit species. Integrating these criteria can resolve many taxonomic uncertainties (Mayr 1942; Van Valen 1976; Coyne & Orr 2004; Futuyma 2005; De Queiroz 2007). In recent years, adding the ecological niche approach to previous criteria has been used to help us in species delimitation (Rissler & Apodaca 2007). In an ecological view of the species concept, environmental variables may help to delimit species with the assumption that each species has its own particular niche (Van Valen 1976). It has been shown that geographic isolation plays an important role in speciation (Wiens 2004). This might be influenced by climate change between two geographically isolated regions, resulting in the prevention of gene flow (Webb et al. 2002). Ecological conditions may reinforce speciation by changing the ecological similarities along the evolutionary time scale (Barraclough & Vogler 2000; Rundle et al. 2000; Turelli et al. 2001; Ogden & Thorpe 2002; Kozak & Wiens 2006).

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Species recognition is usually based on morphological character differences (Bauer et al. 2010) and, until recently, most biologists have used this traditional method as the primary evidence for species delimitation. However, as new methodological approaches for species delimitation become available (molecular and ecological), these approaches are employed in more integrative studies. Ecological divergence is an important stage in the speciation process and this may be identified by examining the ecological niches of the groups under study (Funk et al. 2006). Ecological niche-based models (ENM) may be used for very diverse aims, including conservation planning (Urbina-Cardona & Flores-Villela 2010), taxonomic decisions (Wiens & Graham 2005) and speciation mechanisms (Kozak & Wiens 2006). ENM is another technique that may help us in making taxonomic decisions and can predict the potential distribution of species by combining species occurrence records with environmental data (Elith et al. 2006; Kozak & Wiens 2006; Phillips et al. 2006; Kozak et al. 2008). Several studies have examined speciation mechanisms causing niche divergence, suggesting that this type of speciation is common among closely related species (Losos et al. 2003; Rice et al. 2003; Graham et al. 2004; Jakob et al. 2010). Niche conservatism is a process that occurs between two populations of species that are allopatric in regions with similar climatic conditions, but with unsuitable conditions in intervening regions that maintain their separation (Kozak & Wiens 2006). Allopatric speciation is a common mode for speciation. In allopatric speciation, new species appear when an event separates one (or more) population(s) from another population of a species. This event is defined as the appearance of natural barriers or physical limitations that divide the geographic range (Wiens 2004; Kozak & Wiens 2006).

Eremias strauchi is one of the species of the *Eremias* genus that is distributed on both sides of the Caspian Sea in northern Iran (Anderson 1999; Sindaco & Jeremčenko 2008). Two subspecies, *Eremias strauchi strauchi* and *Eremias strauchi kopetdaghica*, are distributed allopatrically in both northern corners of eastern and western Iran (Anderson 1999; Rastegar-Pouyani et al. 2007). The divergence time of *Eremias strauchi* was estimated as about 14–15 million years ago (Rastegar-Pouyani et al. 2012), which is apparently sufficient for ecological niche divergence (Raxworthy et al. 2007). The current distribution of *E. s. strauchi* is known to include regions in northwestern Iran (East and West Azerbaijan and Ardabil provinces; Ahmadzadeh et al. 2009), while *E. s. kopetdaghica* is distributed in northeastern Iran (Golestan, North and Razavi Khorasan provinces; Hosseinian Yousefkhani et al. 2013) (Figure 1a).

Ahmadzadeh et al. (2009) and Hosseinian Yousefkhani et al. (2013) analyzed morphologic traits in these two subspecies and, in contrast with other subspecies presented in the herpetological literature (Anderson 1999), the morphological variation between these two subspecies is limited to color pattern. The important visible difference is the presence of green coloration and lateral spots in the western subspecies (*E. s. strauchi*) that are absent or indistinct in eastern subspecies (*E. s. kopetdaghica*). Recently, Rastegar-Pouyani et al. (2015) studied these two subspecies using molecular markers, two mitochondrial markers, cyt *b* and 12S, and a nuclear gene (RAG1). According to their results, the taxonomic status of the two traditional subspecies of *Eremias strauchi* was upgraded to the species rank with about 16% of mtDNA uncorrected genetic distance. Using ENM methods, we can test whether ecological niches are identical or different between the two subspecies. Results from ENM can explain the relationships between ecological divergence, phenotypic variation, genetic divergence, environmental variables and speciation (Rissler & Apodaca 2007; Warren et al. 2008).

In this study, the geographic isolation of *E. s. strauchi* and *E. s. kopetdaghica* was examined. ENMs were used to predict the potential distribution of the two taxa and to examine ecological differentiation between them to further clarify their taxonomic status. We discuss important abiotic factors (temperature and precipitation) and how these factors can impact niche differentiation and geographic isolation.

Materials and methods

Occurrence records and environmental data

Georeferenced distribution records for the two taxa were collected from the literature, publications and museum records as precise coordinates (decimal degrees). In total, 51 records for *E. s. strauchi* and 23 records for *E. s. kopetdaghica* were obtained from these resources (Appendix I).

A total of 19 bioclimatic variables and the altitude in 30 arc-seconds (approximately 1 km^2) for the current time scale were downloaded from the WorldClim website (Hijmans et al. 2005; www.worldclim.org). In addition, we used a factor (i.e., slope) that represents the topographic effect on the species presence. Distribution points of both subspecies and climatic layers were employed by Openmodeller v. 1.0.7 (Muñoz et al. 2011) to reach the number of correlated variables. Bivariate-correlation Pearson coefficients

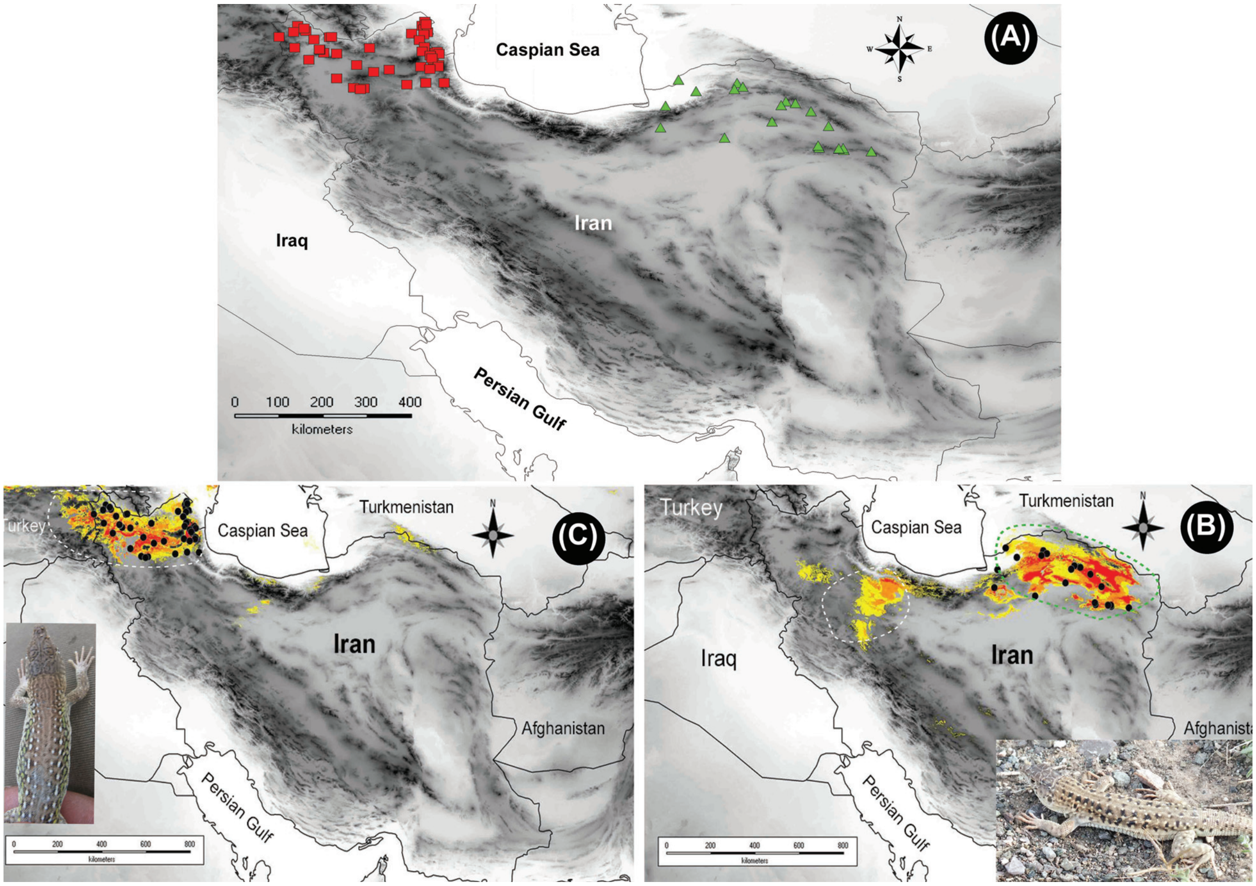

Figure 1. (A) Species sample localities for *Eremias strauchi strauchi* and *E. s. kopetdaghica*. Red squares represent *E. s. strauchi*, while green triangles represent *E. s. kopetdaghica*. (B, C) Predicted potential niche of *E. s. strauchi* and *E. s. kopetdaghica* generated by MaxEnt. Three main colors show habitat suitability in the map. Yellow color (in online version) represents suitability of less than 0.5, orange color represents suitability between 0.5 and 0.75, and red color represents suitability greater than 0.75. Azerbaijan territory is marked by dash line.

were used to identify variable pairs with correlations > 0.75, which were subsequently removed from the analysis. Finally, six variables with low correlation (< 0.75) were selected: BIO3 (isothermality); BIO8 (mean temperature of wettest quarter); BIO9 (mean temperature of driest quarter); BIO18 (precipitation of warmest quarter); BIO19 (precipitation of coldest quarter); and slope as the topographic variable.

ENM

MaxEnt 3.3.3e was employed to predict the species distribution patterns (Phillips et al. 2006). MaxEnt assessment employs environmental data as layers and presence-only records for each taxon (Elith et al. 2011).

Seventy percent of occurrence data were used for model training and 30% were used for model testing. We used default parameters as a maximum 500 iterations, convergence threshold 10^{-5}, regularization multiplier 1 and 10 replicates (Phillips et al. 2006). Model validation was conducted by calculating the area under the curve (AUC), which reflects the model's ability to distinguish between presence records and random background points (Hanley & McNeil 1982; Phillips et al. 2006). Normally, the AUC of the models is between 0.5 (the predicted model is not better than random points) and 1 (the predicted model is very good). However, an AUC value > 0.9 is very good, > 0.8 is good and > 0.7 is better than random prediction (Swets 1988). A jackknife test was run to evaluate the relative importance of the variables. The variable with the highest gain adds the most useful information to the model, while the variable with the lowest gain importance has little effect on the model. Finally, we extracted the environmental suitability index generated by the niche model and regressed it against latitude and longitude to evaluate their effects on niche differences (Wellenreuther et al. 2012).

Ecological niche divergence (niche identity and background) tests

The identity test is used to test habitat suitability scores for *E. s. strauchi* and *E. s. kopetdaghica* to assess significant niche differences generated by ENM (Warren et al. 2010). ENMTools was employed to calculate the niche overlap test to examine niche divergence between species. Schoener's *D* (Warren et al. 2008) and Hellinger's-based *I* (Schoener 1968) are two indices for 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 particular regions (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 *E. s. strauchi* and *E. s. kopetdaghica* 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 other (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).

Point-based analysis

Pixel values for each of the six environmental layers were extracted at each point site and employed to evaluate the niche differences between *E. s. strauchi* and *E. s. kopetdaghica*. Principal component analysis (PCA) was performed to obtain the principal components from six climate variables that can show the variability. Finally, to examine whether there was a significant difference between the ecological niches of *E. s. strauchi* and *E. s. kopetdaghica*, we conducted a multivariate analysis of variance (MANOVA) using SPSS 20.0.

Results

Ecological niches

Occurrence data of the two subspecies showed that their distribution ranges do not have any overlap (Figure 2). Ecological models for the two subspecies confirmed the occurrence of suitable areas for their presence in Iran (Figure 1b, c). Estimated training AUC values ± standard deviation (SD), 0.992 ± 0.008 (test AUC value ± SD = 0.995 ± 0.002) for *E. s. strauchi* and 0.978 ± 0.032 (test AUC value ± SD = 0.998 ± 0.001) for *E. s. kopetdaghica* indicated very good model results in comparison with random background points. Habitat suitability for *Eremias strauchi kopetdaghica* predicted its presence in northeastern Iran, in the Kopet Dagh-Hezar Masjed district, and also in the Qazvin province, the latter being an area outside of the current known range of the species (Figure 1b). *Eremias strauchi strauchi* was predicted to be present in northwestern Iran but restricted from inhabiting other parts of the country by unsuitable habitat in the Azerbaijan territory (Figure 1c).

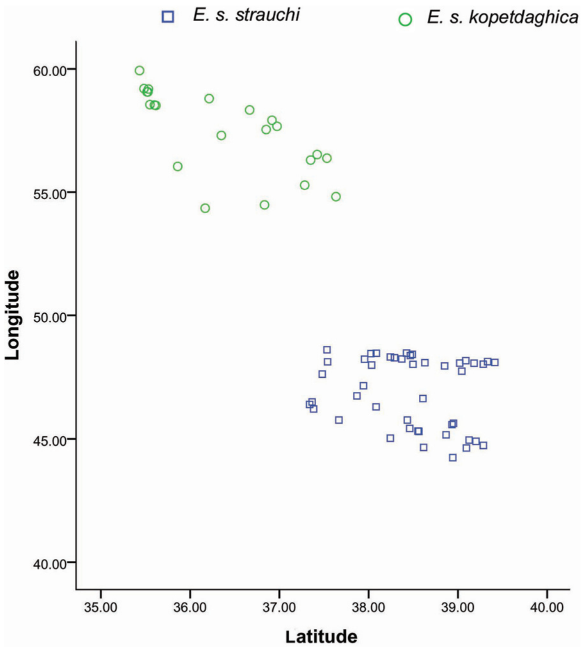

Figure 2. Pattern of species occurrence records with respect to latitude against longitude.

Minimum training presence values were extracted as an environmental suitability index from the average predicted distribution of each subspecies, separately. The index regressions against latitude and longitude were performed. Regression of environmental suitability against latitude was significant for *E. s. kopetdaghica* ($R^2 = 0.059$, $P < 0.05$, intercept = 0.426) and not significant for *E. s. strauchi* ($R^2 = 0.005$, $P > 0.05$, intercept = 0.059). Environmental suitability index was regressed against longitude and latitude and the results that were not significant for *E. s. kopetdaghica* ($R^2 = 0.109$, $P > 0.05$, intercept = 0.007) but that

Table I. Relative importance and percentage of contribution of variables used in MaxEnt model for *Eremias strauchi strauchi* and *E. s. kopetdaghica*.

Description of variables	Contribution of *E. s. strauchi* (%)	Contribution of *E. s. kopetdaghica* (%)
Isothermality	11.7	14.8
Average temperature of the wettest quarter of the year	7.8	4.6
Average temperature of the driest quarter of the year	14.7	7.8
Precipitation of the warmest quarter of the year	22.2	35.3
Precipitation of the coldest quarter of the year	34.4	31.8
Slope	9.2	5.9

were significant for *E. s. strauchi* ($R^2 = 0.007$, $P < 0.05$, intercept = 0.130). There was no longitudinal overlap of the two subspecies (*E. s. strauchi* and *E. s. kopetdaghica*). The percentage contribution of each bioclimatic variable showed that precipitation of coldest quarter for *E. s. strauchi* and precipitation of warmest quarter for *E. s. kopetdaghica* had the highest contribution to the models, respectively (Table I).

Niche similarity tests

ENMTools results indicated that niche overlap between *E. s. strauchi* and *E. s. kopetdaghica* was very low (Hellinger's-based $I = 0.402$ and Schoener's $D = 0.120$). The identity test indicated that our null hypothesis of niche overlap between the two species was rejected and overlap between the two subspecies was significantly different (*t*-test, df = 99, $P < 0.05$). The model indicated that estimated niche models for *E. s. strauchi* and *E. s. kopetdaghica* were completely separate and significantly distinct ($D_{H0} = 0.447 \pm 0.082$ vs. $D_{H1} = 0.120$ and $I_{H0} = 0.583 \pm 0.032$ vs. $I_{H1} = 0.402$) (Figure 3a). In the background test (Figure 3b), there was a non-significant divergence between the focal potential niche of both taxa and the random background points (*t*-test, df = 99, $P > 0.05$ for Schoener's *D;* *t*-test, df = 99, $P > 0.05$ for Hellinger's-based *I*).

Point-based analysis

A PCA analysis was performed on the pixel values for each variable. The first four principal components (PC) explain 94% of the variation, with the following order: 46.19%, 22.06%, 16.67% and 9.8% of all variation, respectively. PC1 interprets the variation of both precipitation variables from coldest and warmest quarters, but PC2 is correlated with the mean temperature of the wettest quarter. PC3 and 4 loaded mainly on both precipitation and temperature variables (Table II). Based on the MANOVA analysis, environmental conditions significantly differed between the two subspecies (Pillai's trace = 102.76; $P < 0.001$; Figure 4).

Discussion

ENM can provide additional information regarding taxonomic distinction and niche differentiation between sister species (Nakazato et al. 2010). This is the first study that used ENM to evaluate the ecological niche differentiation between *E. s. strauchi* and *E. s. kopetdaghica* in Iran. There is no geographical overlap between *E. s. strauchi* and *E. s. kopetdaghica* (Figure 1), showing that each subspecies has its own distribution range. Ecological niche differentiation, one of the factors for speciation, is confirmed by the niche identity test and background test because both tests supported the significant ecological niche divergence between two subspecies. The distinct lineages were previously explained by mitochondrial DNA data (Rastegar-Pouyani et al. 2015), and here we have added ecological niche differentiation to support this conclusion.

In addition to biotic factors (such as competitors or predictors), abiotic factors (such as environmental factors or microhabitat structures) are involved in species distribution and in determining occupied areas (Peterson et al. 1999). Abiotic factors such as climatic variables can promote adaptive divergence and speciation (Rissler & Apodaca 2007). Our results showed significant ecological niche differentiation between *E. s. strauchi* and *E. s. kopetdaghica* based on six climatic variables.

The distribution of both taxa appears to be highly dependent on winter and summer precipitation. However, winter precipitation is important for the *E. s. strauchi* model and summer precipitation is important for the *E. s. kopetdaghica* model (Table I). The predicted occurrence probability of each taxon does not cover areas that are predicted to be suitable for the other. Environmental variables were employed to demonstrate the variation of the two taxa in ecological space by PCA

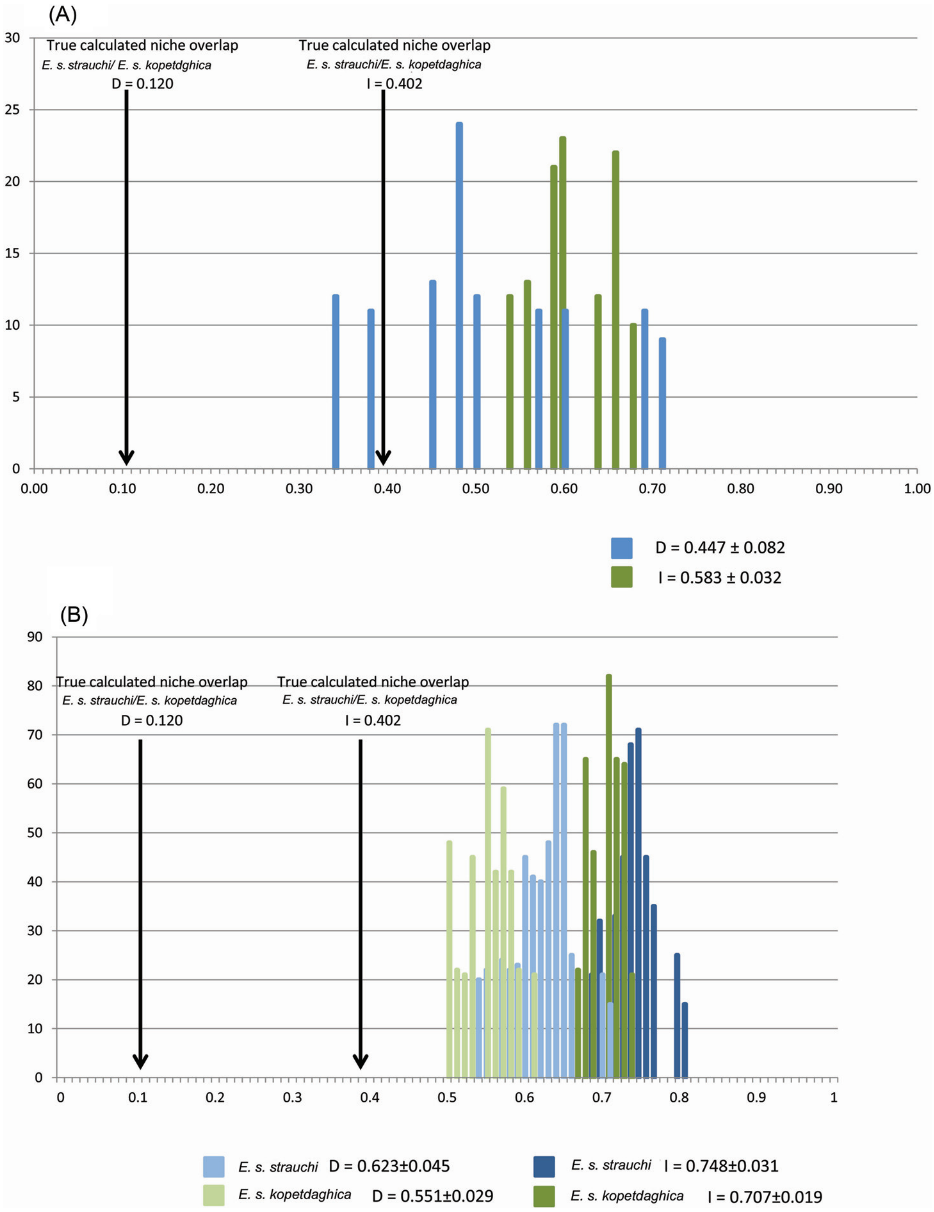

Figure 3. (A) Results of the identity test. Black arrows refer to the actual niche overlap as calculated by ENMTools (*D* and *I*). The green and blue columns are calculated by replicates with identity test mode (see online version for colors). (B) The background test considering each subspecies as a focal species and range of another subspecies as background (e.g. *Eremias strauchi strauchi* as focal species and *E. s. kopetdaghica* as background and vice versa). The x-axis indicates the value of *D* and *I*, whereas the y-axis refers to the number of randomization.

(Figure 4). If species adapt to special climatic conditions (or different local conditions), it leads to niche differentiation and consequently results in morphological variation because of the different adaptations needed to survive and reproduce (Nakazato et al. 2010; Khimoun et al. 2013). 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 *E. s. strauchi* and *E. s. kopetdaghica*. The identity test suggested their ecological niches were significantly different (Figure 3a). Additionally, the background test suggested that both ecological niches were more similar to the background from the range of *E. s. strauchi* than expected by chance, and were less similar to the range of *E. s. kopetdaghica* than expected by chance (Figure 3b).

Based on these results, there is significant niche differentiation between *E. s. strauchi* and *E. s. kopetdaghica*. Ecological niche divergence, in the present study, in an allopatric condition has been

Table II. Results of the principal component (PC) analysis of six environmental variables.

Environmental data		PC1	PC2	PC3	PC4
BIO3	Isothermality	−0.550	−0.719	0.164	0.345
BIO8	Average temperature of the wettest quarter of the year	−0.312	0.834	0.028	0.419
BIO9	Average temperature of the driest quarter of the year	−0.828	0.248	−0.101	−0.458
BIO18	Precipitation of the warmest quarter of the year	0.944	0.152	−0.067	0.085
BIO19	Precipitation of the coldest quarter of the year	0.884	−0.100	−0.037	−0.142
Slope	Slope	0.114	0.129	0.978	−0.117

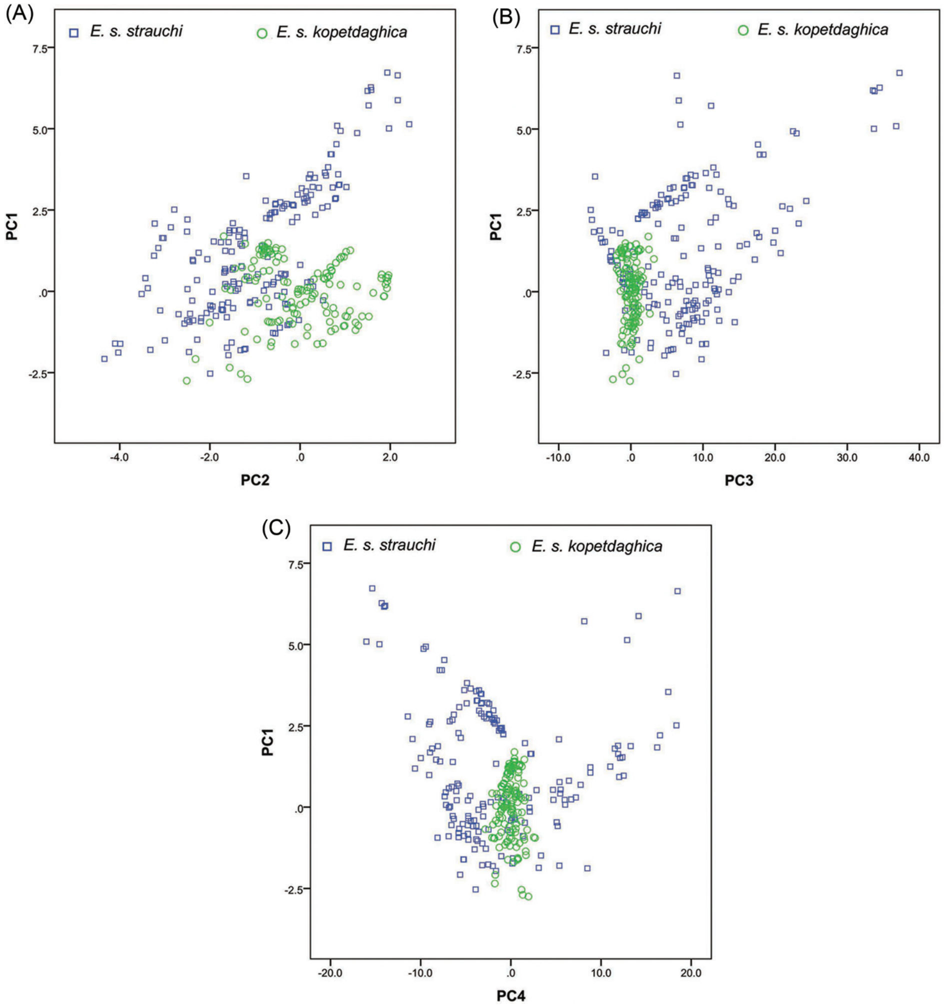

Figure 4. Principal component (PC) analysis of niche differentiation between *Eremias strauchi strauchi* and *E. s. kopetdaghica*. (A) The x-axis indicates PC2, and the y-axis indicates PC1. (B) The x-axis indicates PC3, and the y-axis indicates PC1. (C) The x-axis indicates PC4, and the y-axis indicates PC1.

inferred to represent ecological speciation (Rundle & Nosil 2005; Wellenreuther et al. 2012). Our results confirm the taxonomic suggestion of Rastegar-Pouyani et al. (2015) that both subspecies can be upgraded to the species level.

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Supplemental data

The supplemental material for this article can be accessed here: http://dx.doi.org/10.1080/11250003.2016.1209581

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