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Ecological Niche Divergence between Two Subspecies of Large-scaled Agama, *Laudakia nupta* (De Filippi, 1843) (Sauria: Agamidae), in Iran

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Abstract: The ecological niche divergence between the subspecies *Laudakia nupta nupta* and *L. nupta fusca* was examined on the basis of the analysis of five environmental variables, i.e. annual daily temperature difference, temperature seasonality, average annual precipitation, precipitation of the driest month and precipitation of the driest quarter of the year. Ecological niche modelling was employed to determine the geographically isolated subspecies of *L. nupta* and the effect of the Zagros Mountains on their distribution pattern. Performance of the models was evaluated in good shape and the AUC ±SD values were obtained as 0.908±0.012 for *L. n. nupta* and 0.937±0.005 for *L. n. fusca*. Statistical analyses of environmental values (presence records) indicate that there is no overlap in their predicted ranges based on climate data. It is important to continue this work by examining the molecular markers of *L. n. nupta* and *L. n. fusca* and explaining the genetic differentiation between them.

Key words: climate requirements, ecological preferences, *Laudakia nupta*, Species distribution modelling (SDM)

Introduction

Ecological niche modelling (ENM) is a useful tool to predict the divergence between lineages or subspecies of a given species. Allopatric speciation is a common mode of speciation that is considered when clades are geographically isolated (Turelli *et al.* 2000; Coyne, Orr 2004). If two sets of populations exist in different environmental conditions across a geographic space, it could be speculated that the population might be diverging from the ancestral clade and this may be occurring during rapid adaptation to new ecological conditions (Wiens 2004). Additionally, several hypotheses have been developed to explain speciation under genetic differentiation and ecological niche divergence when there are differences in geographic distribution (Graham *et al.* 2004). ENM can produce a predicted distribution map for the species according to environmental variables recorded in locations where the species is found (Guisan, Thuiller 2005).

From a zoogeographic point of view, Iran has an important role in the biodiversity of the Middle East as the country is located between three different zoogeographic realms, i.e. Palaearctic, Afrotropical (Ethiopian) and Oriental (Kreft, Jetz 2013). This suggests that Iran has a richer herpetofauna than the adjacent countries. Several mountain chains occur in Iran and the country is bordered by natural barriers including the Zagros Mountains in the west, the Alborz and Kopet Dagh Mountains in north and north-east, and the Makran Basin in South-eastern Iran. These features distinguish Iran from adjacent lowland regions (Fisher 1968). These parts of Iran acted as a refuge during the glaciation periods. Areas in these regions that are used as refuges are important for the adaptive radiation and diversification of reptile's lineages because of the presence of many endemic species of reptiles in Iran (Smid *et al.* 2014).

Laudakia nupta (De Filippi, 1843) is an agamid lizard distributed in most parts of the country that has two subspecies with precise records in Iran, i.e. the nominotypical *L. n. nupta*(De Filippi, 1843) and *L. n. fusca* (Blanford, 1876). Minton (1966) examined the vegetation in the habitats of both subspecies in Iran and indicated that *L. n. nupta* occurs in relatively dense shrubs dominated by *Quercus brantii* Lindl. while *L. n. fusca* occurs in steppe-like habitats with scattered trees. This substantial difference between the habitats of these subspecies suggests the possibility of niche divergence. These subspecies show high genetic differentiation based on a mtDNA marker (unpublished data), suggesting that it would be worthwhile to use ecological niche modelling on them to test this hypothesis. The present study addresses the question of whether ecological niche divergence can support the molecular data and genetic differentiation between these subspecies using Maxent statistical analysis.

Materials and Methods

I obtained 212 records for *L. n. fusca* and *L. n. nupta*, with eight (unique) records for *L. n. fusca* and 204 records (129 unique records) for *L. n. nupta* (Fig. 1A, B). All records were obtained from the literature, Herpnet, museums and published papers prior to 2014 (Smid *et al*. 2014). Environmental layers were downloaded in resolution 30 arc-second from the worldclim website (Hijmans *et al*. 2005; www.worldclim.org) and were extracted using ArcGIS 9.2 for the territory within Iran. All 19 environmental variables were categorised into two groups as temperature and precipitation variables within this area.

Maxent (3.3.3e) was employed to generate the ENM for species habitat modelling (Philips *et al*. 2006; Elith *et al*. 2011). This method does not require absence data for the analysis and can be used with a low number of presence points (Tarkhnishvili *et al*. 2008). Niche models were built for the two subspecies separately. Five low-correlated environmental variables were examined for known distributional records: annual daily temperature difference (BIO2), temperature seasonality (BIO4), average annual precipitation (BIO12), precipitation of the driest month (BIO14) and precipitation of the driest quarter of the year (BIO17). The values belonging to five layers for the two subspecies were extracted by ModEco v. 1.0 and were used to show differences using two-tailed Mann-Whitney U-test conducted using SPSS 20.0. Model accuracy was evaluated using area under the curve (AUC) value related to receiver operator characteristics (ROC). Models with AUC = 0.5 indicate a performance equivalent to random; those with AUC > 0.7 indicate useful performance, those with AUC > 0.8 indicate good performance, and those with AUC ≥ 0.9 indicate excellent performance (Swets 1988; Engler *et al*. 2004).

Results

Environmental variables of the habitats of the two subspecies were compared and showed significant differences between *L. n. nupta* and *L. n. fusca*. Five bioclimatic variables had different mean values between the subspecies and all of them showed significant *P* values (annual daily temperature difference, $U = 2.84$, $P < 0.05$; temperature seasonality, $U = 3.90$, $P < 0.05$; average annual precipitation, $U = 2.31$, $P < 0.05$; precipitation of the driest month, $U = 3.14$, $P < 0.05$; precipitation of the driest quarter of the year, $U = 2.27$, $P < 0.05$). A brief list of relevant values of differences between the two subspecies is presented in Table 1 as mean values, SD and significance level.

Annual daily temperature difference, temperature seasonality and average annual precipitation were higher for *L. n. nupta* than for *L. n. fusca*. Precipitation of the driest month and precipitation of the driest quarter of the year had higher values for *L. n. fusca*. This evidence suggests that *L. n. nupta* inhabits warmer and drier areas while *L. n. fusca* is commonly found in wetter and relatively warmer regions. Two models (Maximum Entropy models) were performed independently for both subspecies using the five described variables. AUC performance criteria were obtained for both subspecies with the high values (Mean±SD) as 0.908 (±0.012) for *L. n. nupta* and 0.937 (±0.005) for *L. n. fusca*. On two separated maps, the potential distribution areas for both subspecies showed that two groups had separate and complementary distribution (Fig. 1A, B).

Discussion

Ecological niche divergence between two lineages of a given species with genetic differentiation shows ancient divergence between them and indicates that different ecological conditions have promoted the reproductive isolation between them. On the other hand, phylogeographic studies can help to explain the genetic population structure in comparison with different geographical conditions (Avise 2000).

In previous years, there was no strong molecular or morphological data for this widely distributed species on the Iranian Plateau. Based on molecular data (unpublished data), the species (formerly considered

Table 1. Comparison between environmental variables for two subspecies. Data were extracted using Modeco and analysed using a Mann-Whitney *U* test

Environmental variable	*U*	*L. n. nupta*	*L. n. fusca*	*P* value
		Mean±SD (N=129)	Mean±SD (N=8)	
BIO2	2.84	147.45±17.90	127.00±28.68	0.034
BIO4	3.90	8163±879.04	6827.57±919.42	0.001
BIO12	2.31	256.51±126.48	145.14±56.53	0.018
BIO14	3.14	0.16±0.43	0.71±0.75	0.003
BIO17	2.27	1.69±2.51	4.00±4.24	0.009

to have two subspecies as *L. n. nupta* and *L. n. fusca*) can be split into two species. The Zagros Mountains has an important role in the diversification of reptiles in Iran, because many endemic reptiles (lizards and snakes) are found in restricted areas on these mountains (Ahmadzadeh *et al*. 2012; Rajabizadeh *et al*. 2012; Smid, Frynta 2012). This natural barrier split the central part of the Iranian plateau from the adjacent low-lands as the Persian Gulf coastal regions in the south and the Mesopotamian plain in the west. Zagros contains two main areas uplands or high-elevated mountainous regions and low-elevated foothills areas and each of them has a specific climate. The hills and foothills of Zagros have warmer and drier climate than other high-elevated regions in the area (Anderson 1999). According to my model, these elevated regions are the best habitat for *L. n. nupta* (Figure 1B). *L. n. fusca* is another subspecies or lineage found in South-eastern Iran or in the Makran basin. This region is completely different from the Zagros foothills and has unique climatic conditions, also according to the zoogeographic regions as this part of Iran is located in Oriental Realm (Kreft, Jetz 2013). The predicted suitable habitat map shows suitable regions for *L. n. fusca* in the coastal areas of the Oman Sea (Fig. 1B).

On the other hand, favourable areas of habitat for *L. n. nupta* are found in western Zagros. High suitable regions are located in the Lorestan, Khuzestan, Kermanshah, Fars (Persepolis), Kurdistan and Ilam provinces, but there are several records of the subspecies in central plateau of Iran (including records from Qom, Khorasan, Yazd, and the northern part of Sistan-Baluchestan provinces). The distribution pattern of the eastern population based on presence records in Eastern and NE Iran in an unsuitable region promoted me to hypothesise that this subspecies may be split into two groups (a western clade and an eastern clade).

Differences in climatic conditions between the areas where the subspecies are found indicate that each has its own micro-climate preferences and that

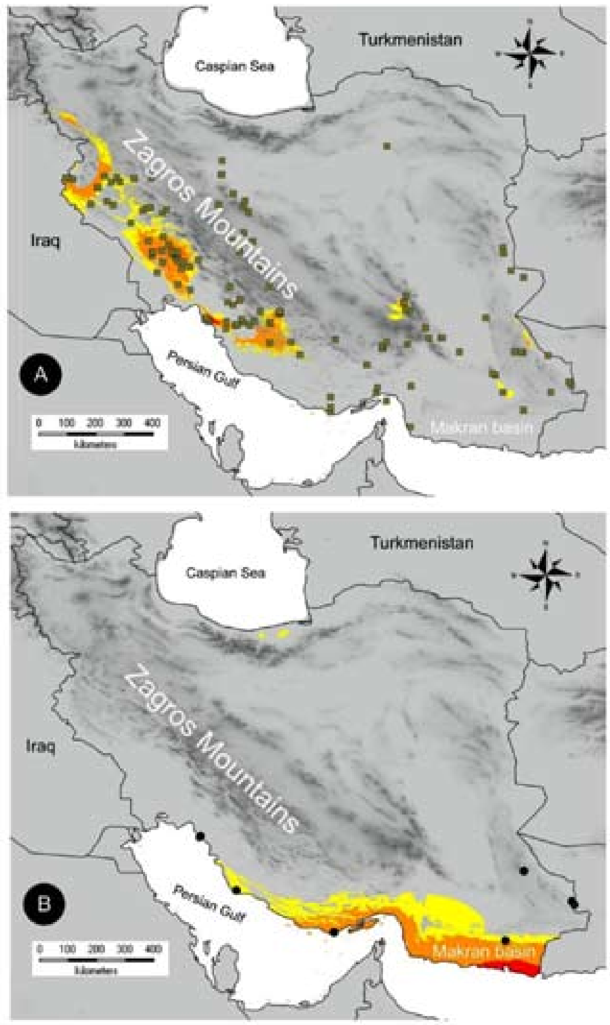

Fig. 1. Predicted potential niches of *L. n. nupta* (A) and *L. n. fusca* (B) as generated in Maxent. The colour change from red to yellow indicates decreasing habitat suitability.

they are restricted to specific areas. Population expansion requires similar environmental gradients. Because of these differences, further dispersion of both subspecies along the environmental gradient may be prevented (Costa *et al*. 2008).

Finally, the predicted distribution pattern for each subspecies is similar to the range occupied by each subspecies (Fig. 1). As the models clearly show, Zagros is an important genetic and geographic barrier between the subspecies of *L. nupta* and also demonstrates the different microhabitat preferences of the subspecies. I highly suggest taking into account morphological and molecular data to resolve the remaining questions. Including all available data will provide a clearer picture of the status of this species in Iran.

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