

The correspondence between environmental similarity and geographical sympatry in *Uromastyx* species

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Abstract. Estimating the realized and potential distribution of species has become a very active field of research with capacity to propose likely speciation mechanisms. Here, environmental variables and point locality data derived from several sources were used to examine the concordance between geographical distributions and environmental niches derived from occurrences for eleven species of the genus *Uromastyx* (Reptilia, Agamidae). Our results indicate that the degree of geographical overlap is definitively and statistically lower than the degree of environmental similarity. This reinforces the hypothesis that speciation process within the genus *Uromastyx* will be mainly based on geographical isolation. However, the environmental divergence among some groups of species cannot be excluded; high environmental distances can be obtained for some related species and the environmental gradient represented by two unique climatic variables allows discriminating some species among which an ecological or environmental segregation would be a plausible explanation.

Keywords: distribution models, ecological speciation, environmental niches, geographical distributions, sympatry.

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Understanding the geographical distribution of species or clades as well as the environmental characteristics of their inhabited locations is essential for biogeographic or macroecological purposes. When jointly examined between related taxa, these two types of data may help to suggest the mode of speciation acting on the diversification of a clade (Mayr, 1970). Thus, the degree of geographical co-occurrence of closely related species and their correspondence with environmental conditions allows to disentangle the comparative role played by ecological processes and dispersal limitations on speciation processes and biodiversity patterns (Coyne and Orr, 2004; Graham et al., 2004; Hua and Wiens, 2013; Anacker and Strauss, 2014; Pyron et al., 2015). The probability of discrepancy in the environmental conditions experienced by the species of a clade should be higher when parapatric or allopatric speciation processes have taken place. Although these environmental-geographical comparisons will not be uncontroversial (Crisp and Cook, 2012; Boucher et al., 2014; Warren et al., 2014) they can be considered a first and provisional effort to reveal the probable evolutionary forces acting on a clade when more detailed phylogenetic information is lacking.

When the only available source of information is a more or less complete knowledge about species distributions, these locations can be used to infer both the probable realized distributions of species and their environmental preferences and potential distributions (Lobo, 2016). The joint use of these two inferences (realized distributions and “niches”) derived from observed occurrences allow us to quantify similarities and differences in niche characteristics among sister species and their

relationships with geographical distributions (Warren et al., 2008).

Uromastix species are medium size to large lizards distributed in deserts and semi-deserts areas of Saharo-Arabian region from North Africa to the Middle East (Wilms, 2005; Sindaco and Jeremčenko, 2008; Wilms et al., 2009a). They occupy various habitats such as dry compacted soils, gravelly to rocky surfaces, and areas with rocky slopes in mountain valleys (Nouira and Blanc, 1993; Peyre, 2006; Wilms and Böhme, 2007). This lizard lives alone in burrows with only one entrance/exit (Wilms et al., 2010). Several authors (Dubuis et al., 1971; Grenot, 1976; Grenot and Loirat, 1976) considered *Uromastix* species as largely herbivorous, consuming predominantly plant material during their active seasons, although other authors describe these lizards as omnivorous (Bartlet, 2003; Wilms, 2007). The recent phylogenetic and taxonomic revisions of the genus *Uromastix* (Amer and Kumazawa, 2005; Wilms et al., 2009; Tamar et al., 2018) have contributed greatly to our understanding of the intra-and interspecific relationships within this genus. To date, the genus can be considered monophyletic and the established species are phylogenetically well supported recognizing the existence of five distinct taxonomic groups (Tamar et al., 2018).

In this study, we examine the concordance between geographical distributions and environmental niches derived from occurrences for eleven of the fifteen recognized species of the genus *Uromastix* Merrem, 1820. Using a recently proposed methodology (García-Roselló et al., 2019) the aim of this manuscript is to describe and quantify the probable geographical and niche overlap among *Uromastix* species in order to assist in explaining the process of speciation among the genus.

The *Uromastix* genus comprises fifteen recognized species (Roskov et al., 2016), which were clustered into five phylogenetic groups (Tamar et al., 2018): *U. acanthinura* (Bell, 1825), *U. aegyptia* (Forskål, 1775), *U. alfredschmidti* (Wilms and Böhme, 2000), *U. benti* (Anderson, 1894), *U. dispar* (Heyden, 1827), *U. geyri* (Müller, 1922), *U. macfadyeni* (Parker, 1932), *U. occidentalis* (Mateo et al., 1998), *U. ocellata* (Lichtenstein, 1823), *U. ornata* (Heyden, 1827), *U. princeps* (O'Shaughnessy, 1880), *U. thomasi* (Parker, 1930), *U. shobraki* (Wilms and Schmitz, 2007), *U. yemenensis* (Wilms and Schmitz, 2007) and *U. nigriventris* (Rothschild and Hartert, 1912). These species are distributed throughout various desert and semi-desert arid regions of North Africa, the Horn of Africa (Ethiopia, Eritrea, Djibouti and Somalia), the Arabian Peninsula and part of the Middle East (Israel, Jordan, Syria, Iraq and west Iran), corresponding to an area located between 5° and 35°N in latitude (Gusten et al., 2003; Wilms and Böhme, 2007; Wilms et al., 2009a). Georeferenced occurrence data for the 15 species of this genus were downloaded from the Global Biodiversity Information Facility, using the 'gbif' function in the ModestR package (García-Roselló et al., 2014), but mainly by incorporating the occurrence localities available in the scientific publications reporting the presence of this genus (Arnold, 1980a, b; Leviton et al., 1992; Wilms and Böhme, 2000; Amer and Kumazawa, 2005; Wilms and Schmitz, 2007; Wilms and Böhme, 2007; Wilms et al., 2009a, b; Wilms et al., 2010; Castilla et

al., 2011; Metallinou et al., 2012; Trape et al., 2012; Mazuch, 2013; Pyron et al., 2013; Tamar et al., 2018), as well as from our own surveys carried out in Tunisia for *U. acanthinura*.

A total of 27 environmental variables at a resolution of 5¹ (approximately 10 × 10 km) were used as predictors: 5 topographic (altitude, altitude diversity, slope, slope diversity and aspect diversity), one edaphic (edaphic diversity), and 21 climatic. Altitude come from a digital elevation model (DEM) downloaded from the USGS EROS Data Center (<http://eros.usgs.gov/>). This DEM has been used to calculate both a slope and an aspect map, also estimating the diversity of slopes and aspects in a 7 × 7pixel windows using the classical Shannon diversity index. We used the world map of soil orders coming from the U.S. Natural Resource Conservation Service (www.nrcs.usda.gov/wps/portal/nrcs/detail/soils/use/) to calculate the diversity of soils in the same way that in the case of topographic variables. Finally, the 19 bioclimatic variables of WorldClim were also used (see <http://www.worldclim.org>; Hijmans et al., 2005) adding aridity and continentality as calculated by Valencia-Barrera et al. (2002).

The modelling procedure is directed to provide a geographical representation of the suitable and accessible areas with environmental conditions similar to those existing in the observed occurrence areas. To do that a simple protocol has been followed (Lobo, 2016), avoiding the use of the so called background absences and complex modelling techniques. The complete procedure is fully described in García-Roselló et al. (2019) but can be summarized in three steps. Firstly, the distributional extent of the genus was delimited as the one composed by the main river basins of level 0 with presence *Uromastyx* observations for all the compiled occurrences of the genus. Watershed information provided by the WaterBase project (www.waterbase.org) is used for this purpose. Subsequently, most relevant predictor variables within this area are selected eliminating sequentially those with a Variance Inflation Factor lower than 5, and submitting the remaining predictors to an analysis able to select the variables with a high capacity of discriminating the occurrence cells in the selected region (Guisande et al., 2017). In our case, these analyses allows to eliminate 18 variables thus selecting as the most relevant three topographic variables (altitude diversity, slope and slope diversity) and six climatic ones mainly related with precipitation values (mean diurnal range of temperature, mean temperature of the driest quarter, precipitation of the driest month, precipitation of the coldest quarter, precipitation of the warmest quarter and precipitation of the wettest month). The values of these nine variables were subsequently used to derive a potential distribution map for each one of the species with more than 10 records (without duplicates) following a multidimensional enveloping procedure (see Boothet al., 2014). Thus, a binary suitability map was finally generated for all the species except for *U. macfadyeni* (6 records), *U. occidentalis* (5 records), *U. shobraki* (9 records) and *U. yemenensis* (6 records) (supplementary fig. S1). This binary suitability map was carried out estimating the maximum and minimum environmental values of each selected environmental variable for the occurrence

observations following a generalized intersection procedure (Jiménez-Valverde et al., 2011; Lobo, 2016). This map would show all the localities with similar environmental conditions to those existing in the observed occurrences, assuming that each species may inhabit under those environmental conditions limited by the extreme conditions at which occurrences have been observed.

Table 1. Number of occurrences used in the modelling process for each one of the *Uromastix* species (Oc), area in $\text{km}^2 \times 1000$ of the obtained potential distribution, mean percentage of overlap of each species with regards to all the other species in their realized distributions (OvRD), mean percentage of range overlap in the potential distributions (OvPD) and Mahalanobis distance (MD) of the occurrences (mean \pm SE) to the centroid of the environmental conditions in the space delimited by the values of the nine selected environmental variables for all the occurrence *Uromastix* data. The five species groups recognized by Tamar et al. (2018) are indicated by squares with dashed lines.

Species	Oc	Area	OvRD	OvPD	MD
<i>U. acanthinura</i>	91	2635	1.1	27.3	8.82 \pm 2.72
<i>U. alfredschmidti</i>	20	29	12.8	36.8	4.59 \pm 0.56
<i>U. dispar</i>	123	7342	1.8	21.7	9.14 \pm 0.61
<i>U. geyri</i>	53	1791	9.8	31.5	10.30 \pm 0.72
<i>U. nigriventris</i>	46	2237	1.6	24.3	13.00 \pm 1.23
<i>U. bentii</i>	20	419	2.2	32.8	23.02 \pm 4.95
<i>U. ocellata</i>	25	11 970	0.6	18.5	40.50 \pm 7.72
<i>U. ornata</i>	52	2504	8.8	28.5	13.29 \pm 2.25
<i>U. princeps</i>	22	338	0.0	38.2	12.89 \pm 2.63
<i>U. aegyptia</i>	299	13 874	1.0	18.0	11.21 \pm 1.19
<i>U. thomasi</i>	27	76	0.1	24.3	13.37 \pm 1.96

Table 2. General Linear Models representing the explanatory capacity of each one of the nine selected environmental variables to discriminate the occurrences of *Uromastix* species. (%) is the percentage of statistically significant pairwise comparison on the total possible comparisons ($n = 55$) using a post-hoc Unequal N-HSD test.

Environmental variables	$F_{(10,567)}$	Adj $R^2 \times 100$	(%)
Altitude diversity	7.11	9.57	16
Mean diurnal range of temperature	35.99	37.74	56
Mean temperature driest quarter	31.45	34.54	40
Precipitation coldest quarter	24.87	29.27	35
Precipitation driest month	16.23	20.88	31
Precipitation warmest quarter	38.56	39.43	44
Precipitation wettest month	9.33	12.62	20
Slope	8.85	13.50	15
Slope diversity	16.48	22.52	33

The so obtained potential distribution maps can be considered geographical representations of the *Uromastix* environmental space occupied by each studied species. Subsequently, we estimate all pairwise percentages of geographical overlap values between the potential distributions of all the species within the area in which these occurrences appear (from 0° to 42° in latitude and from -20° to 65° in longitude). The mean overlap of each species with all the other species is used to measure the degree of similarity that a species can attain in their environmental niche. Realized distributions were approximated by simply delimiting the smallest convex polygon enclosing all occurrences or convex-hull, also calculating the mean overlap of these distributions for each species. Taking into account the nine selected predictor variables, the centroid of the environmental conditions for all *Uromastix* occurrence data is also calculated and the scale-invariant Mahalanobis distance (MD) used to measure the distance from this centroid to the occurrence observations of each one of the species. The average value of MD for each species can be considered a measure of the degree of similarity of the environmental space occupied by each species with respect to the general *Uromastix* environmental space. The upper quartile MD value when all *Uromastix* occurrence data are considered (MD = 12.58) has been taken as the cut-off value to discriminate the species living under the most dissimilar environmental conditions.

General Linear Models (one-way ANOVA) were used to estimate the comparative capacity of each one of the selected predictor variables to discriminate the occurrence of the different *Uromastix* species, estimating by a post-hoc Unequal N-HSD test those statistically significant differences between species pairs. All the analyses have been made using ModestR (García-Roselló et al., 2103, 2014; see www.ipez.es/ModestR) and STATISTICA packages (StatSoft Inc., v12.0).

The mean percentage of between species overlap in the potential distribution is moderately high (27.4%) being high in *U. alfredchmidti*, *U. geyri*, *U. benti* and *U. princeps* and low in *U. aegyptia* or *U. ocellata* (table 1). In any case, this percentage of between species overlap in the potential distributions is significantly higher than the one obtained for realized distributions (mean = 3.6%; t-test for dependent samples; $t = 12.85$, $df = 10$; $p = <0.0001$). Both overlap measurements are also uncorrelated (Pearson $r = 0.48$; $p = 0.14$). These results suggest that the degree of geographical overlap is lower than the degree of environmental sharing; a pattern reinforcing the hypothesis of a speciation process mainly based on geographical isolation processes (Gonçalves et al., 2018; Tamar et al., 2018).

Mahalanobis distance values (MD) for each species to the centroid of the environmental conditions estimated for all *Uromastix* occurrence data indicate that, in six of the eleven species, the mean MD values are higher than the upper quartile MD value for all the *Uromastix* occurrences (MD = 12.58;

table 1). Interestingly, the three studied species included in the *ocellata* group show higher MD values suggesting that environmental segregation could have played an important role in the speciation processes of this group inhabiting the Arabian Peninsula and the Red Sea. The environmental gradient represented by the two environmental variables with a higher explanatory capacity (table 2) allows to visualize the general environmental overlap of the studied species, as well as the environmental segregation of the species of the *ocellata* group (supplementary fig. S2). The species of the *acanthinura* group would be characterized by inhabiting under more similar environmental conditions. According to several studies (Amer and Kumazawa, 2005; Wilms et al., 2009; Tamar et al., 2018), this group of species would have diversified more recently (Pliocene-Pleistocene) colonizing the arid and continental conditions of North of Africa. We suggest that dispersal limitations may have been the main processes able to explain current the current distribution of the species of the *acanthinura* group.

In conclusion, the provided results indicate that speciation processes within the genus *Uromastyx* will be caused by geographical isolation, especially in the case of the most recent clades, while ecological or environmental niche segregation would be a more plausible explanation for some groups of species dating from Miocene.

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Figure S1. Available occurrences for each one of the *Uromastix* species and for the genera (green points), and potential distributions according to the followed procedure within the considered area. The black square in the map of *U. acanthinura* represents a 1° cell.

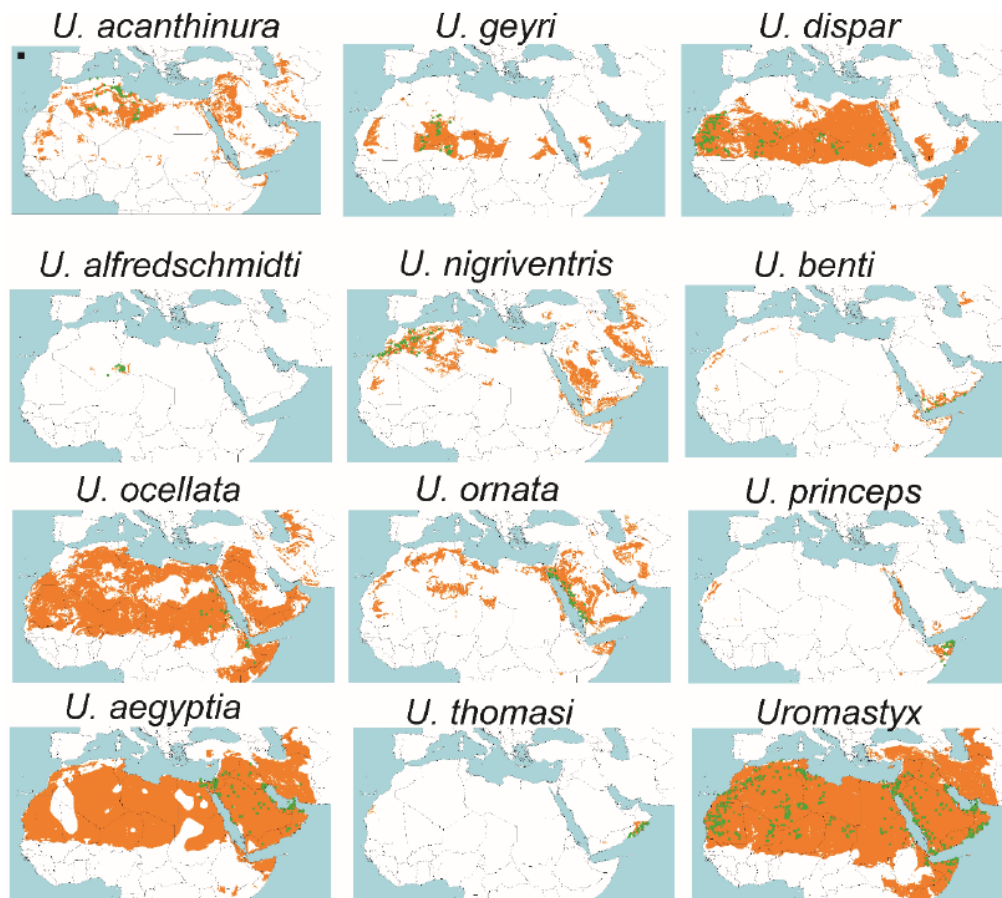


Figure S2. Distribution of all *Uromastyx* occurrences (open circles) in the gradient represented by the two environmental variables with a higher discriminatory capacity (see table 2), and location in this gradient of the species of the *ocellata* group (ellipses with red dashed line). *U. princeps*, *U. aegyptia* and *U. thomasi* are represented by green, violet and blue ellipses with dashed lines, while black lines are those of the species belonging to the *acanthinura* group. The centre of each circle represents mean environmental values of species occurrences while the size of the circles is proportional to the standard deviation of these values. The different colours represent the five recognized phylogenetic groups of species according to Tamar et al. (2018).

