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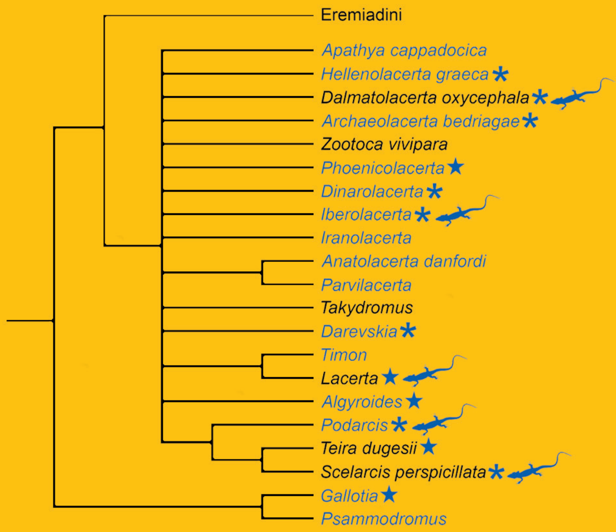

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Ecological niche modeling of two Afrotropical snakes: is the Sahara desert a true barrier for these species?

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Abstract: The Sahara desert is a major biogeographic barrier for the expansion of Afrotropical and Mediterranean faunas due to the extreme dry conditions of this region. However, groups of reptiles that are primarily distributed to the south of the Sahara have relictual distributions in climatically favorable regions of southern Morocco and along the Nile River, in Egypt. Hence, the objective of the present study was to determine the presence of corridors for two species of Sahelian snakes: *Dasypeltis scabra* and *Lamprophis fuliginosus,* that could link populations that are located to the north and south of the Sahara, using ecological niche modeling. Furthermore, we investigated whether the populations located to the north of the Sahara occupy a distinct niche from those located in sub-Saharan Africa. The results indicate the possible existence of discontinuity in the distribution of both species produced by the arid desert conditions, and that in both species there is not segregation in the ecological niche when comparing disjoint populations.
Key words: Afrotropical, biogeographical barrier, *Dasypeltis scabra*, *Lamprophis fuliginosus,* GIS.

Resumen: Modelización del nicho ecológico de dos serpientes Afrotropicales: ¿es el desierto del Sahara una auténtica barrera para estas especies? – Las condiciones de aridez extrema hacen que el desierto del Sahara constituya una barrera biogeográfica importante para la expansión de especies Afrotropicales y Mediterráneas. Un conjunto de especies de reptiles cuya distribución se localiza fundamentalmente al sur del Sahara presentan distribuciones relictuales en regiones climáticamente favorables del sur de Marruecos y a lo largo del curso del río Nilo, en Egipto. En el presente estudio se trata de determinar si existen corredores para dos especies de serpientes: *Dasypeltis scabra* y *Lamprophis fuliginosus* que permitan el contacto entre las poblaciones situadas al norte y al sur del Sahara, basándose en modelización del nicho ecológico. Del mismo modo se estudia si las poblaciones situadas al norte del Sahara ocupan un nicho ecológico diferenciado de las situadas al sur del Sahara. Los resultados indican la posible existencia de una discontinuidad importante en la distribución de ambas especies producida por el desierto del Sahara y que no existe una segregación en el nicho ecológico ocupado por ambas especies comparando las poblaciones aisladas por el desierto.
Palabras clave: Afrotropical, barrera biogeográfica, *Dasypeltis scabra*, *Lamprophis fuliginosus,* SIG.

INTRODUCTION

Northern Africa represents an area of contact between faunas of both Palaearctic and Afrotropical origin (SAMROUI *et al.,* 1998; GERAADS, 2008). Marginal populations of certain Afrotropical reptile species are found in favourable climatic regions in Morocco and Egypt (SOCHUREK, 1979; BAHA EL DIN & SALAMA, 1992; SCHLEICH *et al.,* 1996). The snake *Dasypeltis scabra* is one of such species, the northern limit of its distribution occuring in the Souss Valley of Morocco (BONS & GENIEZ, 1996) and in the lower Nile

Valley of Egypt (ANDERSON, 1898; BAHA EL DIN, 2006). The taxonomy of this species has been recently reviewed and it is possible that *D. scabra* proves to be a complex of species distributed in disjunct populations throughout the Sahel (TRAPÉ & MANÉ, 2006). In addition, *Lamprophis fuliginosus* is another species of snake of primarily sub-Saharan range, with its northern limit in southern Morocco, yet appears to be absent from the lower Nile Valley (BAHA EL DIN, 2006). Both species exhibit a nocturnal behavior (SEEBACHER & FRANKLIN, 2005; GROßMANN & STARCK, 2007) and are considered rare in the extreme northern limits of their range (SCHLEICH *et al.*, 1996; GENIEZ *et al.*, 2004). The Sahara desert appears to create discontinuity in the distribution of both species, yet the elusive nature of these two species may mean that some residual populations may remain undetected. One possible method to test the existence of a corridor that connect the populations situated to the north and south of the Sahara is by analyzing the existence of suitable environmental conditions based on bioclimatic layers (e.g. PETERSON, 2001; KOZAK *et al.,* 2008). In the present manuscript we describe several new locations of populations for these species in southern Morocco, which we combined with the records obtained from the GBIF database, in an attempt to test the hypotheses about whether (1) the Sahara causes real discontinuities for Afrotropical species and (2) populations located to the north of the Sahara occupy a different ecological niche to sub-Saharan populations.

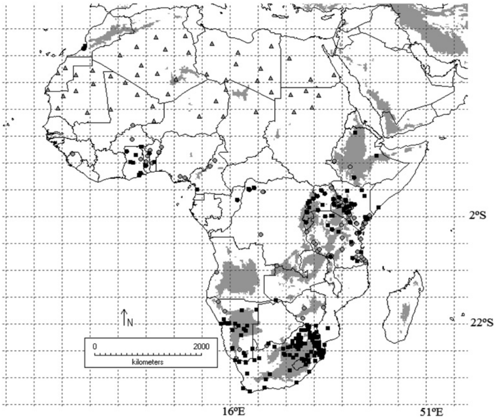

FIGURE 1. Localities included in the analysis. Squares: *D. scabra,* circles: *L. fuliginosus*, triangles: absences. In grey, mountain ranges.

FIGURA 1. Localidades incluidas en el análisis. Cuadrados: *D. scabra,* círculos: *L. fuliginosus*. triángulos: ausencias. En gris, cadenas montañosas.

MATERIALS AND METHODS

During the course of six surveys conducted from 2007 to 2009 three specimens of *D. scabra* and two of *L. fuliginosus* were found in the region of Sidi-Ifni (south-west Morocco). Individuals of *D. scabra* were found at 29.78° N, 9.84° W and at 29.23° N, 10.09° W and *L. fuliginosus* at 29.23° N, 10.09° W and 29.27° N, 10.24° W (Fig.1). These records confirm the presence of both species in previously unknown locations (BONS & GENIEZ, 1996; GENIEZ & GUILLOD, 2003). We used these locations, and those obtained from GBIF (GBIF DATAPORTAL, 2010), to model the probability of the presence of both species using the program Maxent version 3.3.2 (PHILIPS *et al.*, 2010). The GBIF database has been succesfully used to model the distribution of other species of vertebrates (e.g. COSTA *et al.,* 2008; THORN *et al.*, 2009) although it has the limitations of the databases from collections (GRAHAM *et al.,* 2004). In our case the GBIF database does not represent a complete sample of the known distribution of both species although it provides an adequate number of localities that can be considered representative of both species in sub-Saharan Africa (see BRANCH, 1998; BROADLEY *et al.*, 2003; LARGEN & SPAWLS, 2010).

The Maxent algorithm has proven useful in modeling species distributions, obtained only from known localities of presence (PHILIPS *et al.,* 2006). In the current study Maxent models were performed with the inclusion of four bioclimatic layers (i.e. temperature seasonality, maximum temperature of warmest month, minimum temperature of coldest month and annual precipitation) that were downloaded from the WorldClim database (WORLDCLIM, 2009). We have selected the bioclimatic variables that we considered relevant to the survival of the studied species (REBELO & JONES, 2009), in this case two species of subtropical snakes whose northernmost populations may be limited by temperature extremes (in southern Morocco) and precipitation (in the Sahara desert). Correlation among variables was tested by generating 1000 random points within the study area (PARRA *et al.,* 2004), extracting variable values for each point and computing the Pearson correlation coefficient. In this case none of the included variables has a correlation coefficient above 0.8. All environmental layers have been rescaled to a resolution of 0.1°.

From the GBIF database we included only those records separated by a minimum distance of 0.1°, in order to minimize spatial autocorrelation. In the case of *D. scabra,* the GBIF data indicated important prospection bias, given that of the 361 localities, 298 were situated to the south of latitude 23° S. As a result, we selected 10% of localities from this region at random. We performed 100 Maxent replications, using 70% random localities for calibration and 30% random localities as test data. The projection shown presents the average result of these 100 replications. The accuracy of the models has been evaluated by the area under curve (AUC) obtained from receiver operating characteristics plot (PHILIPS *et al.,* 2006). In order to determine areas showing the minimum suitable conditions for both species we selected two decision thresholds: the lowest presence threshold (LPT) (minimun predicted area maintaining zero omission error), and percentile 10 of predicted values (P10) (for detailed description of these thresholds see PEARSON *et al.,* 2007). The performance of each threshold was tested calculating Kappa statistic and false predictive rates.

The data obtained from bioclimatic layers and presence localities was also used to perform a principal component analysis (PCA), with the aim of classifying subsets of localities and to test whether differences between groups of localities are significant. For the PCA, we included only spatially independent localities, without discarding records that belonged to the prospection biased subset. In the PCA presence localities were grouped into two subsets, sub-Saharan Africa and Morocco. We also generated a third subset, including 50 random points excluding occurrence localities occupied by both species (CHEFAOUI & LOBO, 2008) and along the strip of land that separates the populations located north and south of the Sahara (Fig.1). These pseudo-absences were also used to test the accuracy of LPT and P10 thresholds. For the environmental analysis we extracted the values for altitude, 19 bioclimatic variables and the normalized vegetation difference index (NVDI) for the month of may (northern hemisphere) and october (southern hemisphere) for each locality using DIVA-GIS 7.7.1 (HIJMANS *et al.,* 2009). NVDI is a variable whose value is positively related to the density of vegetation and negatively to areas devoid of vegetation (MYNENI *et al.,* 1995). The NVDI layers were downloaded from EDIT GEOPLATFORM (2010). Axes with eigenvalues > 1 obtained by comparing Sahara and sub-Sahara groups were included in a MANOVA test in order to test if the observed differences are statistically significant. Moroccan localities have not been included in the MANOVA analysis due to insufficient sample. All statistical analyses were performed using Statistica version 8.

RESULTS

The projections obtained by Maxent provided an AUC value of 0.88 in the case of the *D. scabra* model, and 0.87 in the case of the *L. fuliginosus* model. These AUC values suggest that both models adequately fit the known distribution of both species (BEAUMONT *et al.,* 2009). The Kappa statistics obtained for the different thresholds indicate that both the LPT and the P10 provide a good level of agreement in both species (MONSERUD & LEEMANS, 1992) but the greater accuracy is obtained for LPT (Table 1). These results suggest the existence of large unsuitable areas for both species in the region that separates the southern Moroccan populations from those located in the Sahel (Figs. 2, 3). The result of comparing by MANOVA test PCA axes provides significant results ($p < 0.05$) when comparing groups of localities from Sahara and sub-Sahara in the case of both snakes. In the case of both snakes Moroccan

TABLE 1. Threshold dependent measures of accuracy. Fpos: false positive rate. Fneg: false negative rate, LPT: lowest presence threshold, P10: percentile 10 of predicted values.
TABLA 1. Valores de precisión dependientes del umbral. Fpos: tasa de falsos positivos. Fneg: tasa de falsos negativos, LPT: umbral de mínima presencia, P10: percentil 10 de los valores predichos.

Thresholds	Kappa	Fpos	Fneg
LPT *D. scabra*	0.96	0.06	0
LPT *L. fuliginosus*	0.97	0.04	0
P10 *D. scabra*	0.84	0	0.1
P10 *L. fuliginosus*	0.83	0	0.1

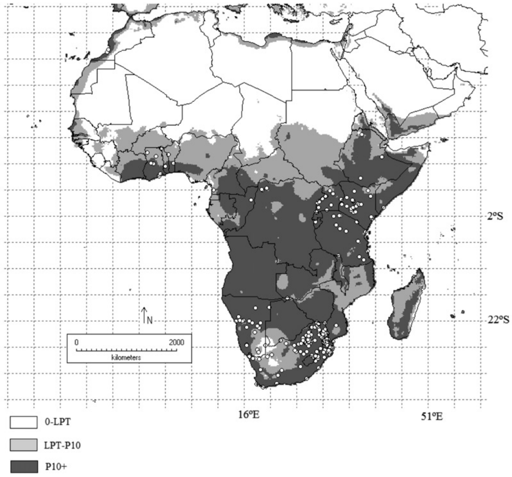

FIGURE 2. Maxent projection of *D. scabra*. LPT: lowest presence threshold, P10: percentile 10 of the predicted values. White circles represent locaties included in the study.
FIGURA 2. Proyección obtenida por Maxent de *D. scabra*. LPT: umbral de mínima presencia, P10: percentil 10 de los valores predichos. Los círculos blancos representan las localidades incluidas en el estudio.

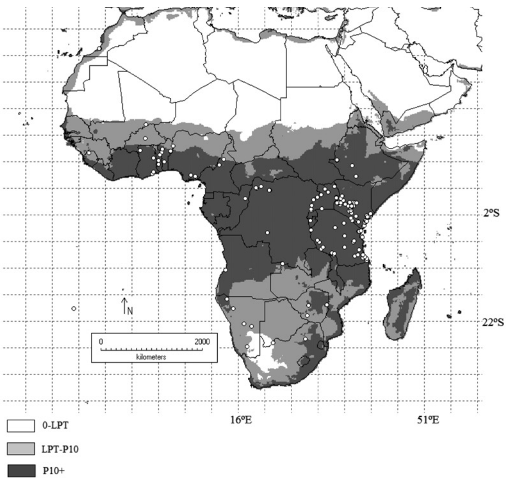

FIGURE 3. Maxent projection of *L. fuliginosus*. LPT: Lowest presence threshold, P10: percentile 10 of the predicted values. White circles represent locaties included in the study.
FIGURA 3. Proyección obtenida por Maxent de *L. fuliginosus*. LPT: umbral de mínima presencia, P10: percentil 10 de los valores predichos. Los círculos blancos representan las localidades incluidas en el estudio.

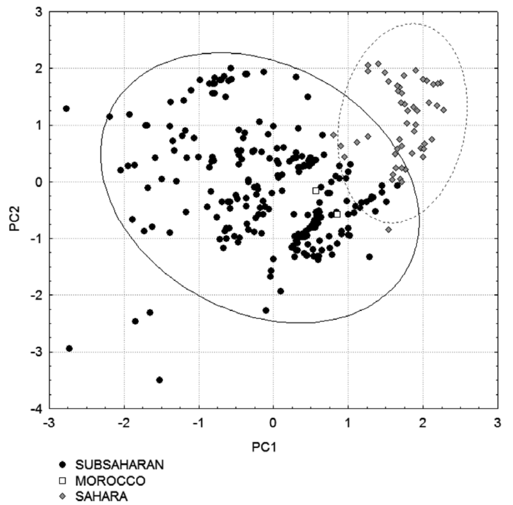

FIGURE 4. PCA scatterplot obtained from 21 environmental variables. Cases represent localities of *D. scabra*. PC1: 44%, PC2: 30%. Ellipses represent 95% confidence intervals.
FIGURA 4. Diagrama de dispersión obtenido mediante PCA de 21 variables ambientales. Los símbolos representan localidades de *D. scabra* (PC1: 44%, PC2: 30%) y las elipses los intervalos de confianza al 95%.

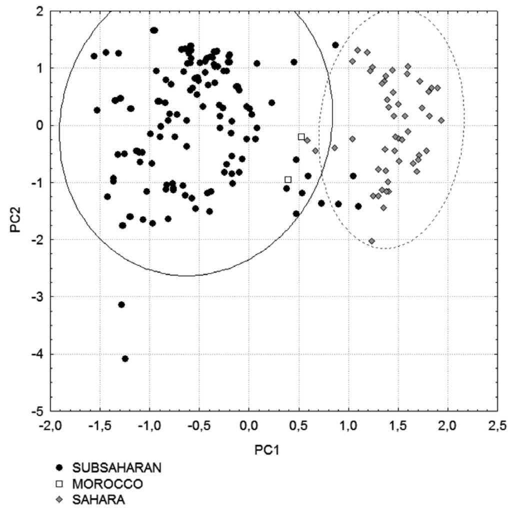

FIGURE 5. PCA scatterplot obtained from 21 environmental variables. Cases represent localities of *L. fuliginosus*. PC1: 49%, PC2: 23%. Ellipses represent 95% confidence intervals.
FIGURA 5. Diagrama de dispersión obtenido mediante PCA de 21 variables ambientales. Los símbolos representan localidades de *L. fuliginosus* (PC1: 49%, PC2: 23%) y las elipses los intervalos de confianza al 95%.

localities are within the 95% confidence interval (Fig.4) but in the *L. fuliginosus* one of the locaties is outside this confidence band (Fig.5), suggesting that the Moroccan populations are close to the ecological limits for this species.

DISCUSSION

These results suggest that the Sahara desert presents a real discontinuity in the distribution ranges of the two studied snake species. A similar distribution pattern has been observed in other Afrotropical species located to the north of the Sahara (BÖHME *et al.,* 1998; DE SMET, 1999; BAYLESS, 2002), suggesting that the Sahara desert is an important barrier, preventing current penetration further north by Afrotropical reptile species. In this sense, the presence of these snakes to the north of the Sahara may possibly be explained by a recent episode of expansion of their ranges due to more humid paleoclimatic conditions, possibly in the late Pleistocene or recent Holocene (OUAHBI *et al.,* 2003; MOULINE *et al.,* 2008). Alternatively the presence of *D. scabra* in Egypt may also be explained by the green corridor formed by the Nile valley. In this sense, the Maxent model indicates that *D. scabra* has a low probability of presence in the Egyptian locality, which was the Fayoum depression (north-west of the Nile valley). It may be inferred from this result that the persistence of this species in Egypt may be favoured by the milder conditions of the Nile valley, as has also been observed in other Afrotropical species occurring in Egypt (DIJKSTRA & BOUDOT, 2010). Interestingly both models predict the presence of these snakes in

Yemen, where both species are already recorded to occur (EGAN, 2007). In Morocco, the model indicate the presence of appropriate conditions for *D. Scabra* in the region of Dakhla (south-west of the Western Sahara). At this location, several amphibian and reptile species with Mediterranean, Macaronesian and Sahelo-Saharan origin have been already described (GENIEZ *et al.*, 2004). The low degree of niche differentiation between the populations on either side of the Sahara, especially in the case of *D. scabra*, suggests that these species have not evolved to occupy a differentiated niche in northern Africa, and the isolation that is observed under present climatic conditions possibly reflects the collapse of a continuous distribution in the recent past. Fragmentation of populations added to the small area they occupy in Morocco may predispose these snakes to stochastic extinction processes (DAVIES *et al.,* 2000; DRISCOLL, 2004). For this reason it would be desirable to determine the conservation status of populations that still remain in Morocco and improve the preservation of the habitats in which both species occur, at this time suffering from severe overgrazing.

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