Acta Herpetologica 9(2): 203-217, 2014
DOI: 10.13128/Acta_Herpetol-12875

Factors determining Gekkotan (Reptilia, Sauria) distribution in Tunisia (North Africa)

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Submitted on 2013, 5th May; revised on 2014,2nd June; accepted on 2014, 3rd October
Editor: Ernesto Filippi

Abstract. Tunisian geckos count nine species (1 is insular relict, 1 is endemic, 2 are ubiquitous and 5 are enfeoffed). We aim to determine factors influencing their distributions. Surveys were founded on environmental divisions. Presence/absence data for 113 grids were analyzed using multivariate tools. 18 environmental variables were revealed and clustered into five factors to model species distributions. Established models were further projected on non-explored areas within Tunisian territory. The distribution of continental geckos follows an indirect bidirectional gradient; the South-northward one is physiologically stressful and the North-southward one is biologically stressful. Five biogeographic regions were established showing concordance with climatic and vegetation regionalization. The distribution of non-anthropophilic species is positively correlated to thermal amplitudes gradient. The distribution of anthropophilic taxa is positively correlated to agricultural land-use. Oasis, sebkhas and chotts are particular landscapes that disturb both distributions. Predicted areas follow the yielded distribution patterns despite some discrepancy for *S. sthenodactylus*. The niche characterizing shows that land use and altitude increase the probability of occurrence of *H. turcicus* and *T. mauritanica*. Alternatively, they decrease the probability of the presence of *T. deserti, T. neglecta, T. tripolitanus* and *S. petrii*. Models could also show that the absence of *S. sthenodactylus* in northern regions is attributed to high altitudes and cereal land-use. As to *T. fascicularis*, the displacement of the northern limits of its range is mostly attributed to an improvement of field investigations. Established model of its distribution shows a restricted area of probable occurrence in central Tunisia confirming its endemism.

Keywords. Gekkota, Tunisia, biogeography, clustering, UPGMA, ecological factors, principal component analysis, ecological niche modelling.

INTRODUCTION

Recent overviews of the distribution of some geckos occurring in Tunisia have been established (Nouira, 1997; Joger, 2003; Rufray et al., 2003; Delaugerre et al., 2011; Tlili et al., 2012 a, b). Reported data have marginally extended the known ranges of the two Phyllodactylidae *Tarentola fascicularis* and *Tarentola deserti* (Tlili et al., 2012 a). Most importantly, they have reported new record of *Stenodactylus sthenodactylus* in sub-humid regions (Tlili et al., 2012 b). These expansions may occur either because of variations in ecological factors or because of traits of the natural history of the species (MacArthur, 1972; Holt, 2003). Alternatively, it may be due to anthropogenic impact such as involuntary introduction accompanying human transport. Guisan et al. (1999) and Guisan and Zimmermann (2000) demonstrated that environmental variables usually replace a combination of dif-

ISSN 1827-9635 (print)
ISSN 1827-9643 (online)

www.fupress.com/ah

ferent resources and do not have direct physiological consequence for a species performance.

To shed light on the factors that shape species' ranges, scientists need to classify regional faunas into discrete groups (Guisan and Zimermann, 2000). In the case of Tunisia, this task is complicated by its location in the Mediterranean basin. Besides, it is a transition area between the Palearctic and the Afrotropical ecozones and thereby should be treated differently than the center of these two biogeographical regions (Kreft and Jetz, 2010). Moreover, located astride the Atlas domain and the old African continent, Tunisia might harbor species of many origins (Nouira, 1996). In such cases, several authors suggested to start by selecting appropriate environmental variables that might explain the observed distribution of species (e.g., Franklin et al., 2000; Guisan and Zimermann, 2000; Hirzel et al., 2002; Holt, 2003). Such studies have been already undertaken for several groups of reptiles in Tunisia including Lacertidae (Nouira, 1996) and Scincidae (Kalboussi, 2006). Parallel work for gekkotan fauna is lacking (Tlili et al., 2012 a, b) and questions relative to which factor influence the species distribution and how species will be distributed in time and space remain unanswerable (Heikinheimo et al., 2007). For instance, why did *S. sthenodactylus* (an arid species) extend its distribution only to a particular sub-humid region (Cape Bon Peninsula) among other similar regions in the extreme north of Tunisia (Tlili et al., 2012b)? Besides, why did some juxtaposed areas show variation concerning their biodiversity despite their proximal locations and similar abiotic characteristics (Tlili et al., 2012a)?

Given the above, this work has several aims: 1) to elaborate a map of biogeographical regions based on gekkotan species richness; 2) to extract the environmental variables constraining their distributions in Tunisia, 3) to identify areas of probable occurrence and 4) to assess their ecological niche (habitat).

MATERIAL AND METHODS

Study area

Located in the southern shore of the Mediterranean Sea, Tunisia is separated from Europe by the Channel of Sicily (140 km). Tunisian landscape is naturally regionalized into units with characteristic climate, landforms, soil and vegetation (Fakhfakh and Laclavère, 1979). The landscape is marked by a general low relief crossed by the Dorsal Mountain Chain (Fig. 1A). Within the Cap Bon and Medjerda lowland regions all the original woodlands and forests have been cleared for agriculture. Khroumirie and Mogod regions are areas in the north-west comprising mountainous Mediterranean forest and maquis. The central steppe region marks the transition zone between the Dorsal Mountain and the desert and harbors many salt lakes including 'chott El Jrid'. Jeffara and Dhahara regions are areas of subdesert, desert and Sahara landscapes where the stony ergs and the large sand-dunes of the Great Eastern Erg occur. The climate of Tunisia is mainly Mediterranean divided into 5 bioclimatic stages: Humid, Sub-humid, Semi-arid, Arid and Saharan (Emberger, 1950; Tlili et al., 2012b).

Sampling and mapping

Preliminary sampling took place in spring and summer seasons from 1996 to 2012 as described in Tlili et al. (2012 b). However, concentration of occurrence data was showed around locations of anthropophilic geckos' populations and differences in sampling efforts have been revealed from north (highly inventoried) to south (less inventoried). Thus, on the basis of distributions maps (Tlili et al., 2012 a, b), 0.3°×0.3° equal-area grids were chosen as a sampling unit to re-sample an equal number of replicates per environmental combination (Fig. 1B). Teams of work followed climatic gradient where each bioclimatic stage was surveyed by two observers in spring and summer seasons of 2011 and 2012 (Graham and Hijmans, 2006; Kreft and Jetz, 2010). Observers alternated between day and night attempting to seek for one specimen of each species for each grid (Guisan and Zimmermann, 2000). Maps were composed using QUANTUM-GIS software (Sillero and Tarroso, 2010).

Species distributions and regionalization

Absence/presence data were converted into a species per site incidence matrix in order to calculate species richness (S.R.) and grids similarities. A matrix of similarity coefficients between grids was established using Jaccard's index (Jaccard, 1908) suitable for binary data (Real and Vargas, 1996; Kreft and Jetz, 2010): $\jmath = c/N$ (c = number of attributes present in both operational taxonomic units OTUs, N = total number of attributes). The statistical significance of obtained pairs of OTUs was tested using the statistical table of probability values (Real, 1999). Herein, the probabilities associated with Jaccard's index depend only on the total number of attributes (N) present in either of the two OTUs being compared ($N = p + q - c$).

The 113 grids were clustered according to their species richness. A matrix of dissimilarities was established from Jaccard's distance ($D(j, k) = 1 - \jmath$). Obtained distances range from 0 to 1 (0 when both units have the same attributes, 1 when they share no attributes). The Unweighted Pair-Group Average (UPGMA (Sneath and Sokal, 1973)) was used as a linkage rule. The retained number of clusters was based on the number of bioclimatic stages (Guidi, et al., 2009).

Biogeographical patterns

Environmental variables were automatically selected by following environmental gradients detected from the clusters' structure (Guisan and Zimmerman, 2000; Hirzel et al., 2002).

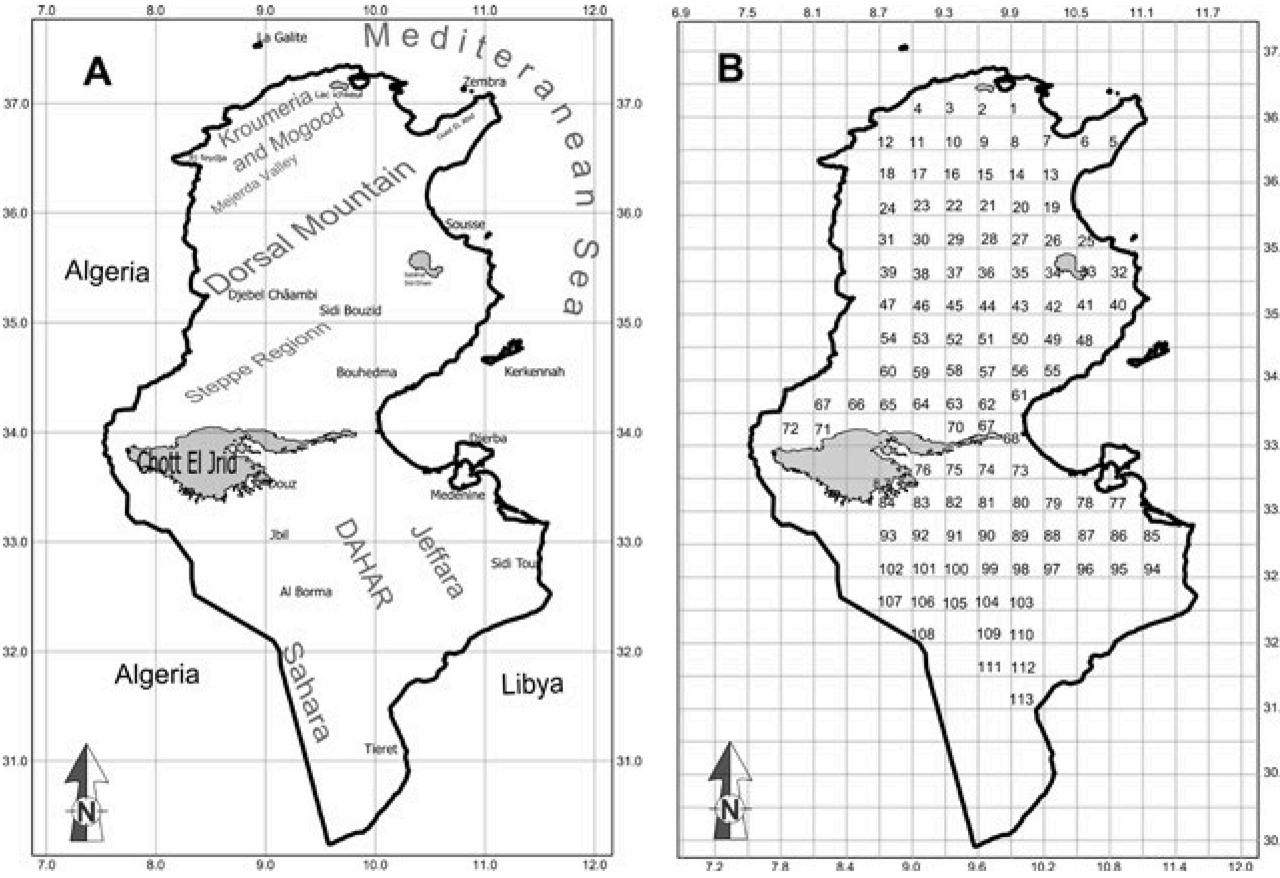

Fig. 1. Map of Tunisia. Geographic location and natural regions (A); sampling units numbers (B)

The 113 cells were characterized with variables relating to: 1) relief (the mean value), 2) Climate (Emberger coefficient, Thermal amplitudes (°C) and precipitation levels (mm)), 3) lithology (dominant type), 4) soil (dominant type), 5) water plan (presence of sebkhas, Chotts or lakes), 6) vegetation cover (woodland, degraded forest, steppe, subdesert, and desert), 7) Agriculture (cereal, olive, palm) and 7) urbanism (habitations, industrial, touristic and road densities). Spatial data were provided by the "Office Tunisien de la Cartographie" as printed maps and/or numerical data. Taking into account the strong correlations between most of these variables (Appendix 1), a linear transformation of correlated variables into uncorrelated variables was made via a Principal Component Analysis PCA (Kaplunovsky, 2005; Lawley et al., 2011). The extraction of principal components amounts to a variance maximizing (VARIMAX) rotation of the original variable space (Harrell et al., 1996; Guisan and Zimmermann, 2000; Clark et al., 2003; Kaplunovsky, 2005; Brito et al., 2011; Lawley et al., 2011). To confirm the orthogonal character of obtained factors, clusters of items and rotated axes were identified; then, correlations between those (oblique) factors were computed, and that correlation matrix of oblique factors is further factor-analyzed to yield a set of five orthogonal factors that divide the variability in the items into that due to common variance (secondary factors), and unique variance due to the clusters of similar items in the analysis (primary factors) (Appendix 2).

Species distribution modeling

Modeling of the distribution of the eight gekkotan species in Tunisia was assessed by means of Maxent 3.3.3 (Phillips et al., 2006, Philips and Dudik, 2008). The model for each of the eight gekkotan species expresses the suitability of each grid cell as a function of its environmental variables by mean of maximum entropy method. We considered variables extracted by factor analysis to produce "features" which constrain the probability distribution. For every cell occurring within Tunisian borders, Maxent produced a value of probability for the presence of a gecko species, ranging from 0 to 1. If p(x) is the raw output for environmental conditions x, the corresponding logistic value is c p(x) / (1 + c p(x)) for a particular value of c (namely, the exponential of the entropy of the raw distribution). For easier interpretation, cumulative probability values were transformed into three main distribution classes: 1) the 'out of range' area, 2) the 'suboptimal' area, and 3) the optimal area (Anadón et al., 2012). The importance of each environmental factor in explaining the observed distribution of geckos was evaluated by the percent of contribution (PC) and Permutation importance. Response curves obtained from Maxent were also used to discuss the niche of Tunisian Gekkota.

RESULTS

Taxonomic status and species richness

Tunisian geckos belong to three gekkotan families: Gekkonidae, Phyllodactylidae and Sphaerodactylidae (Table 1). Figure 2 illustrates the spatial variation of the species richness to latitudinal, climatic and geomorphological gradients. Beyond the latitude 36°, only two anthropophilic species *T. mauritanica* and *H. turcicus* occur (22.2% of the total gecko-diversity). Between latitude 35° and 36°, *S. sthenodactylus* occurs as well as the two anthropophilic species; it occupies 56.6% of the 113 grid cells. Between latitude 34° and 35°, five gekkotan species were found: *T. mauritanica*, *T. fascicularis*, *H. turcicus*, *T. tripolitanus* and *S. sthenodactylus*. Southward the latitude 34°, only species highly adapted to drastic Saharan conditions occurred: *S. sthenodactylus*, *S. petrii*, *T. deserti*, *T. neglecta* and *T. tripolitanus*.

Considering bioclimatic stages (Fig. 2A), species richness ranges from two to five species. Each stage contains only two gekkotan families. Only *Euleptes europaea* (relict of northern islands) occupies humid regions. Given its insular statute, it was not included in the following parts of analysis. The two anthropophilic species are widely distributed and occupy all bioclimatic stages. Six of the nine gekkotan species occur in arid environments.

According to lithology and vegetation (Fig. 2B), we note that the presence of geckos is heavily dependent on natural shelters availability such as rocky crevices, stones, sandy borrow or tree barks. Most importantly, we noticed that the aggregation of the non-anthropophilic geckos (in central and southern regions) is related to local variations of vegetal landscape. *T. fascicularis* is usually found in open steppe type in which *S. sthenodactylus* occupies either the bark of trees or small shrubs. *T. tripolitanus* is associated with burrows under rocks. In ergs, *S. sthenodactylus* and *S. petrii* are found exclusively at the base of the rare and dispersed plants.

Table 1. Taxonomic status of Tunisian Gekkota. S.I. species incidences.

Family	Genus	Species	Global distribution	S.I.	Statutes
Sphaerodactylidae	*Euleptes*	*europaea (*Gené, 1839)	Mainly restricted to Western Mediterranean island. Some small continental isolated populations have been reported in south of France and west of Italy (Salvidio and Delaugerre, 2003; Renet et al., 2008; Delaugerre et al., 2011; Salvidio et al., 2010).	---	Insular relict
Phyllodactylidae	*Tarentola*	*mauritanica* (Linnaeus, 1758)	It ranges from the Iberian Peninsula to Italy in the north of Mediterranean sea; and from Morocco to the Nile Delta in the south (Kluge, 2001)	59.3%	Ubiquitous
		neglecta Strauch, 1895	It is known with certainty in Algeria North-western Libya, Southern Tunisia and Chad (Schleich et al., 1996).	11.5%	Desert habitat
		deserti Boulenger, 1891	It is present in Morocco, Algeria and Tunisia (Schleich et al., 1996, Harris et al., 2006).	44.25%	Desert habitat
		fascicularis (Daudin, 1802)	This species was recently elevated to the specific rank by Joger and Bshaenia (2010).	13.3%	Endemic to central Tunisia
Gekkonidae	*Hemidactylus*	*turcicus* (Linnaeus, 1758)	A recent phylogeny assigned populations of North Africa to the Arid clade. This taxon has a large circum-Mediterranean distribution.	56.6%	Ubiquistous
	Stenodactylus	*petrii* Anderson, 1896	It is found in Africa, the Middle east and the southwest of Asia	23%	Desert habitat
		sthenodactylus (Lichtenstein, 1823)	It has been reported in Africa, the Middle East and Saudi Arabia (Schleich et al., 1996; Padial, 2006)	56.6%	Sandy areas
	Tropiocolotes	*tripolitanus* Peters, 1880	It ranges in North Africa, Middle East and parts of Asia. Populations of the Middle East have been transferred to the species *T. somalicus*. Those of Asia have been moved to *Asiocolotes* genera. Individuals from North Africa are now part of the species *T. tripolitanus* which is located in Tunisia, Libya and Egypt (Loveridge, 1974; Schleich et al., 1996)	41.6%	Desert habitat (Hamada)

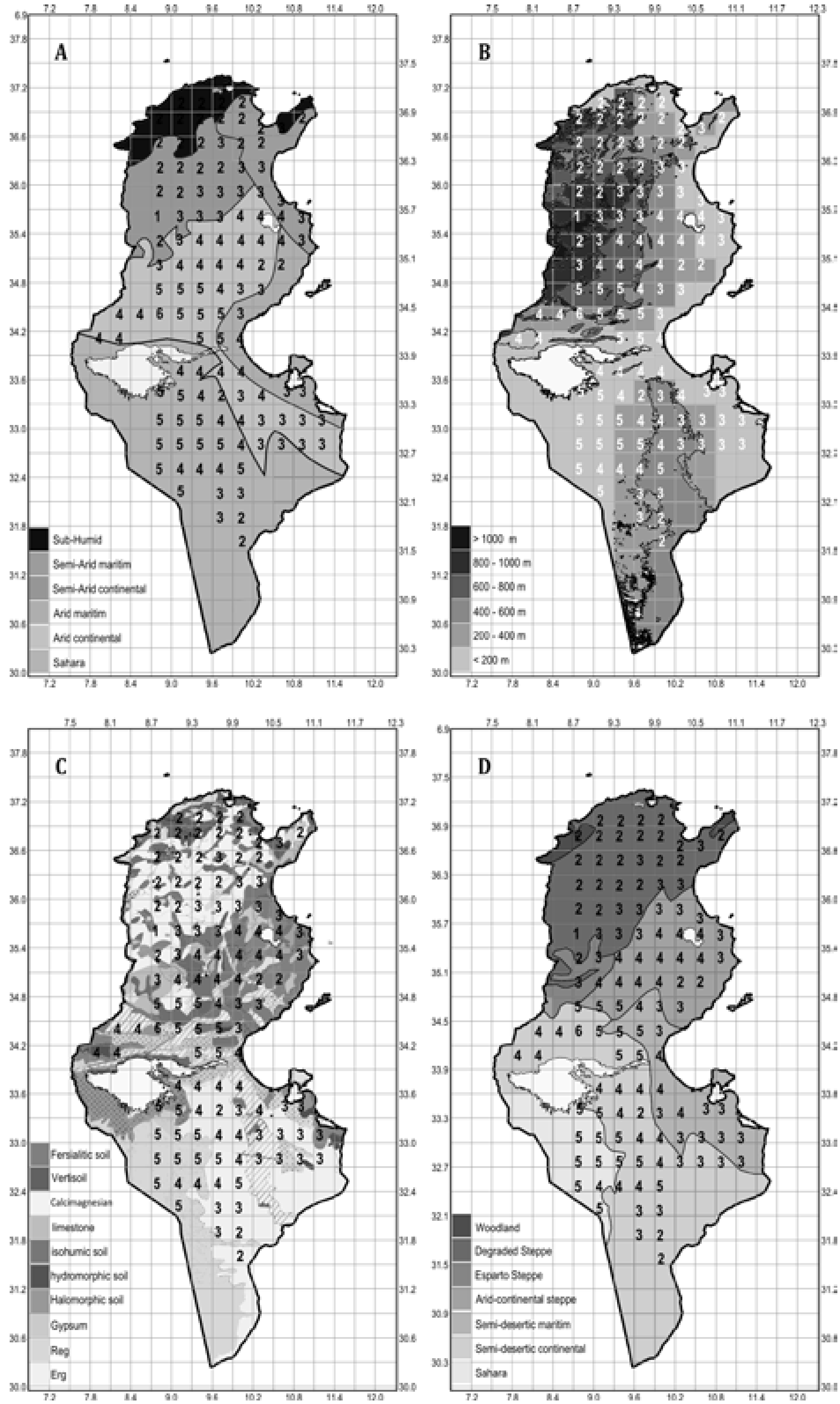

Fig. 2. Distribution of Gekkota species richness according to: bioclimatic stages (A), geomorphology (B), lithology (C) and vegetal cover. Maps were provided by the Office of the Ministry of Agriculture (Forestry Management Department) and further processed with QUANTUM-GIS software (Sillero and Tarroso, 2010).

Grids clustering and regionalization

Species richness varies from two to five species per grid cell. Calculated values of ȷ indices between the grids were all significant at the probability level 0.05. The dendrogram of Fig. 3A split at ȷ value of 0.6 to form two groups. The first group (yellow shades) assemblages grids occurring on Calci-magnesian and isohumic soils, under precipitation levels higher than 150 mm and with thermal amplitude lower than 20°C. This sub-branch contains two clusters: 1) Northern regions with the Sahel region (grids 49-56-57-61); and 2) Central region with Golf de Gabes region (grids 68-73-78-61). The second group (brown shades) gathers together the grids occurring on hydromorphic and poorly developed soils, under precipitation levels lower than 150 mm and with thermal amplitude higher than 20°C. It contains four clusters: 1) Chott El Jrid region (grids 65-66-70-73-74); 2) Tyaret region (grids 109-110-111-112-113); 3) Jbil region (grids 83-84-85-89-91-92-93-102-103-107-108) and 4) a cluster with no defined geographical area (grids 65, 66, 71 112, 113). A combination of corresponding colors was used to delineate regions according to cluster memberships (Fig. 3B).

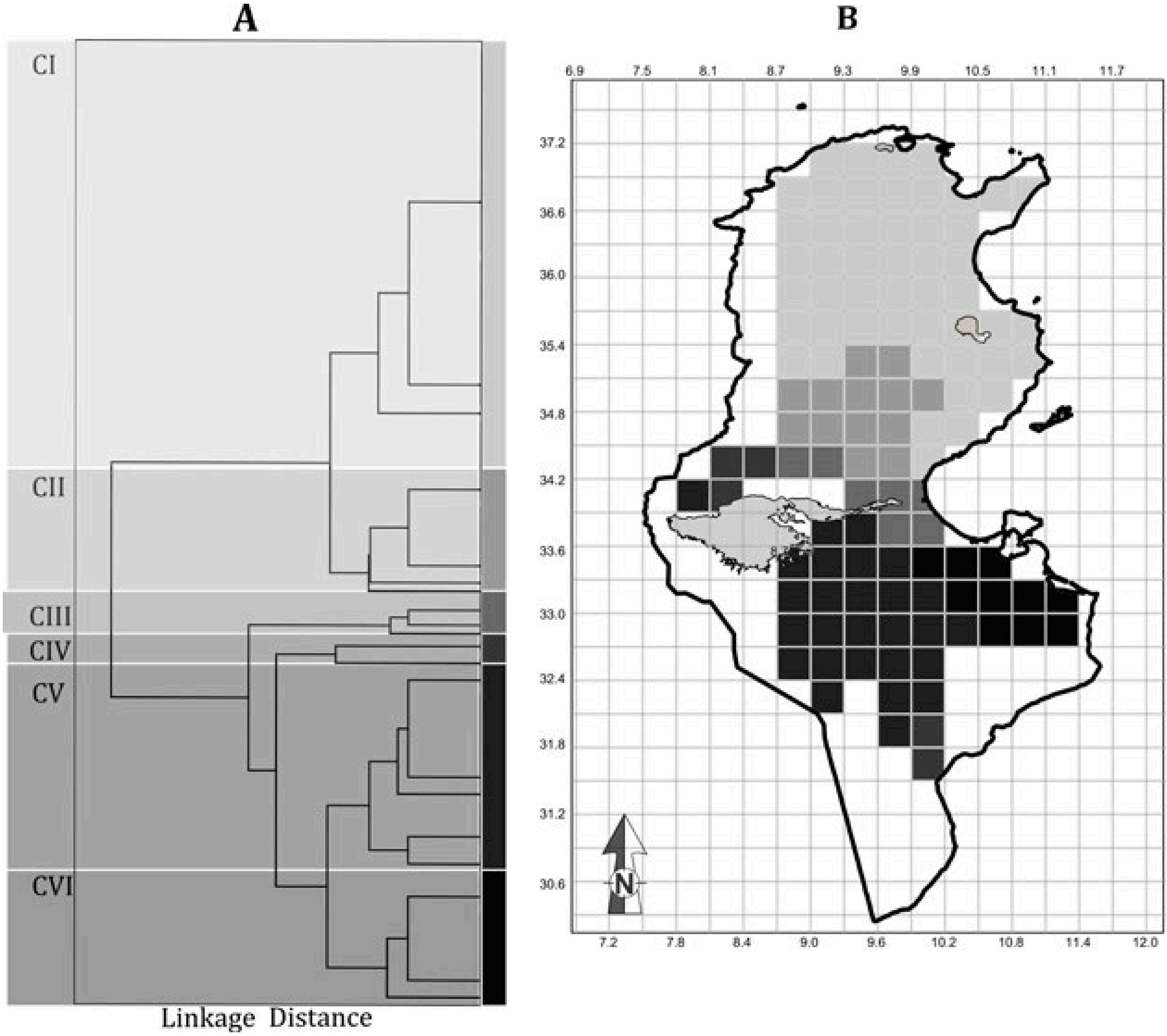

Fig. 3. Dendrogram (A) and map (B) resulting from UPGMA hierarchical clustering of grid cell assemblages of Gekkota based on Jaccard dissimilarity matrix at the species level. The six major biogeographical divisions are highlighted in the dendrogram with large colored rectangles.

Environmental factors

18 environmental variables were identified based on the hierarchical tree (Fig. 3A) and shared distribution patterns (Fig. 3). Most of these variables are highly correlated producing great redundancy. A linear transformation of correlated variables into uncorrelated variables via PCA retained five factors with Eigenvalues ≥ 1.0 (according to the Kaiser criterion). The total variance explained by all variables was 71.33% (Appendix 2). The orthogonal character of obtained factors was confirmed and clusters of items and rotated axes were identified (Table 2). Five orthogonal factors were yielded containing 11 environmental layers to develop gekkotan distribution models (Table 3).

Distribution model

The 11 environmental layers produced "features", which constrain the distribution of computed probabilities. In our case, the set of features depend on the number of presence records for the species. The receiver operating characteristic (ROC) curves show that models for all Phyllodactylidae (Appendix 3) and most of Gekkonidae (Appendix 4) will well perform in predicting occurrences compared to a random selection of points. In fact, AUC values are all higher than 0.7 except for *S. sthenodactylus* which is 0.578 (Table 4). Also, table 4 shows threshold models that permitted to identify suitable cells for each species. The analysis of variables' contributions

Table 2. Factor Loadings with VARIMAX as a rotation method. Underlined loadings are >0.6; Bold values are negative correlations. S.R. species richness.

	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5
Rain-thermal	**-0.895183**	0.006325	-0.048915	0.078812	0.127187
Precipitations	0.746916	0.350094	0.080001	0.105304	0.116798
Lithology	0.108549	-0.353286	0.17636	**-0.65443**	0.16875
Soil	0.745688	-0.035934	-0.069964	-0.020273	-0.053747
Accident	0.447775	-0.419113	0.322996	-0.214502	0.421146
Vegetation	0.874349	0.07004	0.136885	-0.045448	-0.140143
Cereal	0.884682	0.019462	0.048258	0.036604	-0.107117
Olive	0.26776	0.424258	-0.215968	0.250303	0.130972
Almond	0.27634	-0.052531	-0.188399	0.430077	-0.303976
Palm	-0.248537	0.132684	-0.045195	0.10083	0.839285
Water plan	0.045374	-0.040519	-0.03302	0.893364	0.145629
Coast	0.140236	0.887385	0.028427	-0.052517	0.032802
Altitude	0.581316	-0.466223	0.147382	-0.33244	0.023178
Urban	0.48289	0.551476	0.204528	0.190292	-0.02548
Tourism	0.131498	0.753782	0.056591	0.080994	0.147267
Species richness	0.049573	0.009893	**-0.961705**	0.101292	0.012076
Anthropophlic S.R.	0.858163	0.215614	-0.200664	0.148998	0.019184
Natural S.R.	**-0.665359**	-0.184663	**-0.650443**	-0.027808	-0.009454
Explained variance	5.67628	2.589464	1.711235	1.74057	1.129378
Proportion .Total	0.315349	0.143859	0.095069	0.096698	0.062743

Table 3. Extended Factor Loading Matrix: Correlations of variable clusters (oblique factors) with primary factors.

	Cluster 1	Cluster 2	Cluster 3	Cluster 4	Cluster 5
Secondary 1	0.242825	0.552793	-0.336319	0.545912	0.059906
Secondary 2	0.590997	0.220702	0.375875	-0.132976	-0.353716
Primary 1	0.769258	0.000000	0.000000	0.000000	0.000000
Primary 2	0.000000	0.803561	0.000000	0.000000	0.000000
Primary 3	0.000000	0.000000	0.863486	0.000000	0.000000
Primary 4	0.000000	0.000000	0.000000	0.827223	0.000000
Primary 5	0.000000	0.000000	0.000000	0.000000	0.933432

to each model (Table 5) shows that three to four variables are involved in controlling distributions of ubiquitous species (*H. turcicus, S. sthenodactylus, T. mauritanica, T. deserti* and *T. tripolitanus*). Only one variable contribute with more than 70% in modeling distributions of scarce and rare species (*T. neglecta and S. petrii*). Response curves (Fig. 4) show how the logistic prediction changes as each environmental variable is varied, keeping all other environmental variables at their average sample value. For instance, *S. sthenodactylus* does not show specific environmental requirement; however the probability of it occurrence decreases with increased cereal land use. The probability of occurrence of *T. neglecta* increases with thermal amplitudes. In fact, areas with thermal amplitudes higher than 19 are particularly favorable for *T. fascicularis*, *T. deserti*, *T. tripolitanus* and *S. petrii*. *T. fascicularis* showed very narrow environmental requirements; it occurs in area with 200 mm of precipitation, between 20 and 22 of thermal amplitudes, 200 to 400 m asl, less than 100 of population density and 200 quintal of cereal yielded per hectare. Variable jackknife showed that the environmental variable that decreases the gain the most when

Table 4. AUC (Area under curves), Cumulative threshold (C.T.), Logistic threshold (L.T.) and corresponding Fractional predicted Area (F.P.A.) for the MTP (Minimum training presences), MTSS (Maximum training sensitivity plus specificity) and EED (Equaled entropy of thresholded and original distributions). ***T.m.*** *Tarentola mauritanica,* ***T.n.*** *T. neglecta,* ***T.d.*** *T. deserti,* ***T.f*** *T. fascicularis,* ***H.t.*** *Hemidactylus turcicus,* ***S.p.*** *Stenodactylus petrii,* ***S.s.*** *S. sthenodactylus,* ***T.t.*** *Tropiocolotes tripolitanus.*

		H.t.	*S.p.*	*S.s.*	*T.d.*	*T.f.*	*T.m.*	*T.n.*	*T.t.*
A.U.C.		0.743	0.853	0.578	0.768	0.831	0.788	0.896	0.723
MTP	C.T.	3.197	5.835	1.902	4.437	9.081	3.108	3.161	4.648
	L.T.	0.166	0.277	0.280	0.223	0.215	0.226	0.338	0.247
	F.P.A.	0.623	0.362	0.931	0.499	0.442	0.524	0.290	0.643
MTSS	C.T.	6.55	13.186	12.861	4.434	17.655	8.489	17.017	12.569
	L.T.	0.28	0.394	0.452	0.223	0.366	0.72	0.390	0.411
	F.P.A.	0.587	0.303	0.779	0.499	0.326	0.463	0.216	0.512
EED	C.T.	3.197	2.595	1.121	2.331	50.819	2.429	3.161	3.185
	L.T.	0.166	0.235	0.236	0.152	0.141	0.221	0.338	0.208
	F.P.A.	0.653	0.401	0.954	0.548	0.524	0.537	0.290	0.679

Table 5. Analysis of variable contributions ***T.m.*** *Tarentola mauritanica,* ***T.n.*** *T. neglecta,* ***T.d.*** *T. deserti,* ***T.f.*** *T. fascicularis,* ***H.t.*** *Hemidactylus turcicus,* ***S.p.*** *Stenodactylus petrii,* ***S.s.*** *S. sthenodactylus,* ***T.t.*** *Tropiocolotes tripolitanus.*

Variable	Percent contribution								**Permutation importance**							
	H.t.	*S.p.*	*S.s.*	*T.d.*	*T.f.*	*T.m.*	*T.n.*	*T.t.*	***H.t.***	***S.p.***	***S.s.***	***T.d.***	***T.f.***	***T.m.***	***T.n.***	***T.t.***
Thermal amplitudes	43.6	0	10.4	0.2	0.1	13.3	3.8	1.2	**70.4**	**0**	**14.3**	**0.3**	**4.3**	**75.4**	**8.1**	**0**
Cereal	20.9	75.1	37.4	71.9	0.4	55.9	2.5	0.1	**12.3**	**41.8**	**17.5**	**32.8**	**25.5**	**15.4**	**0**	**4.3**
Precipitations	13.6	1.3	1.8	0	0	0.6	9.2	0	**0.8**	**14.3**	**2.4**	**0**	**0**	**2**	**76.2**	**0**
Urbanism	10.1	0	0.3	4.7	32.1	23.1	0	39.5	**13.8**	**0**	**11.8**	**9.9**	**2.5**	**5.6**	**0**	**39.6**
Emberger coefficient	5	0.3	17	0.6	20.1	0.3	78.2	0.2	**0**	**1.8**	**9**	**23.3**	**0**	**0**	**0**	**6.6**
Vegetation	3.8	0.3	12.9	17.6	22.4	6.7	0	49.5	**0**	**0**	**9**	**15.9**	**35**	**0**	**0**	**41.3**
Soil	1.7	4.4	8.6	3.1	12.5	0	1	2.6	**0**	**3.9**	**16.7**	**8.5**	**18.1**	**0**	**0.6**	**1.6**
Coast	0.6	0	0	0	1.7	0	0	1.4	**1.7**	**0**	**0**	**0**	**13.5**	**0**	**0**	**4.1**
Palm	0.5	0	0.1	0	1.4	0.1	0	0.1	**0.9**	**0**	**0**	**0**	**0.2**	**0.9**	**0**	**0**
Lithology	0.1	1.1	3.2	0.6	1.3	0	5.03	1.6	**0**	**4.4**	**4.5**	**0**	**1**	**0.7**	**14.4**	**0**
Waterplan	0	0	0.2	0	0	0	0	3.8	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**1.1**
Tourism	0	0	2.6	0.8	1.9	0	0	0	**0**	**0**	**9.6**	**8.1**	**0**	**0**	**0**	**1.2**
Olive	0	0.4	0	0	0	0	0	0	**0**	**1.6**	**0**	**0.1**	**0**	**0**	**0**	**0**
Altitude	0	1.7	1.6	0	2.6	0.1	0	0	**0**	**3.9**	**1.7**	**0**	**0**	**0**	**0**	**0**
Accident	0	3.2	0	0	0	0	0	0	**0**	**3.9**	**0**	**0**	**0**	**0**	**0**	**0**
Almond	0	0	3.8	0.4	0.5	0	0	0	**0**		**3.5**	**1.2**	**0**	**0**	0	0

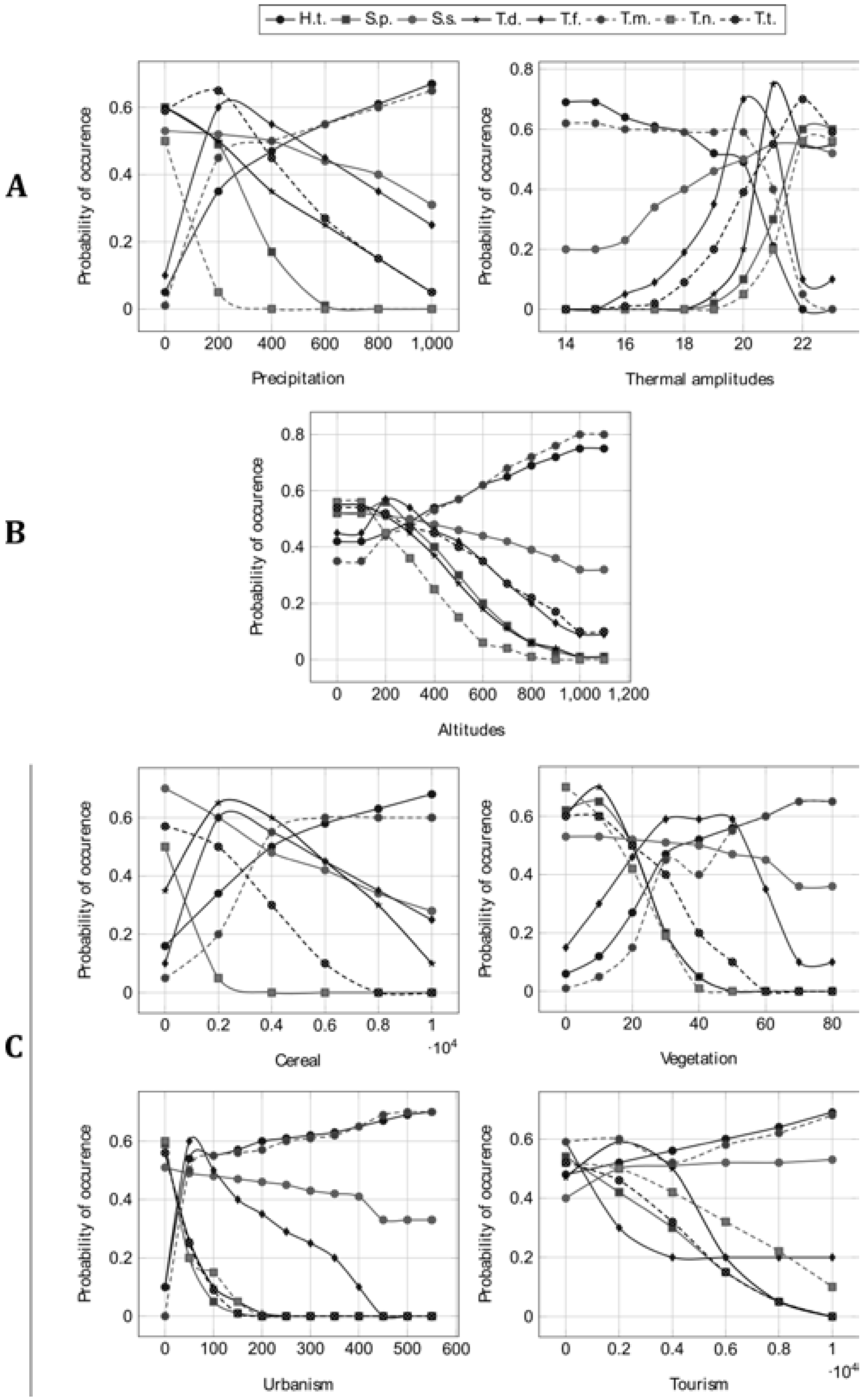

Fig. 4. Response curves explaining gekkotan niches. Climatic items (A), relief (B) and land-use-items (C).

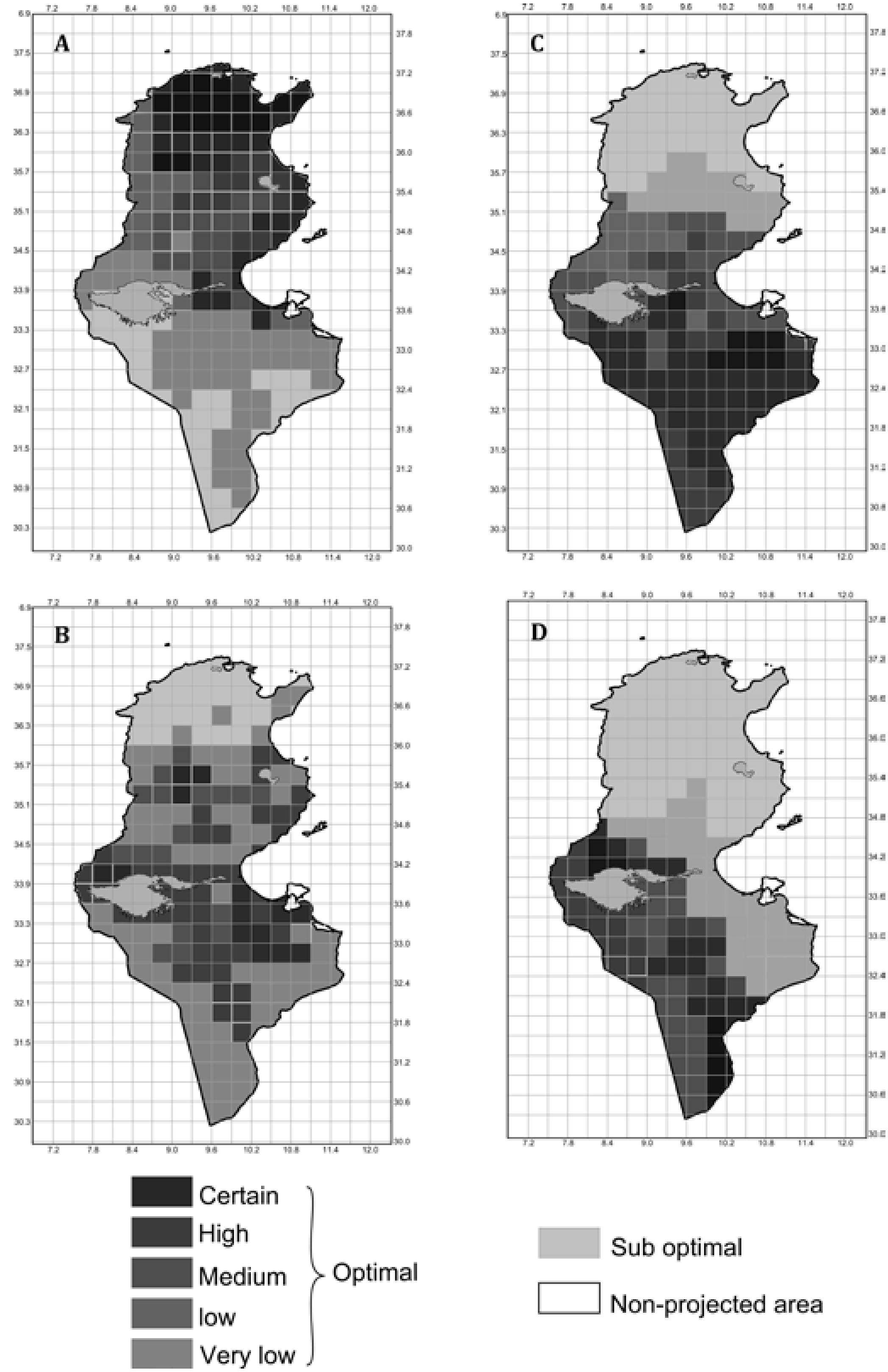

Fig. 5. Predicted probabilities of presence of Gekkonidae within Tunisian territory and habitat quality classes. *H. turcicus* (A), *S. sthenodactylus* (B), *S. petrii* (C) and *T. tripolitanus* (D).

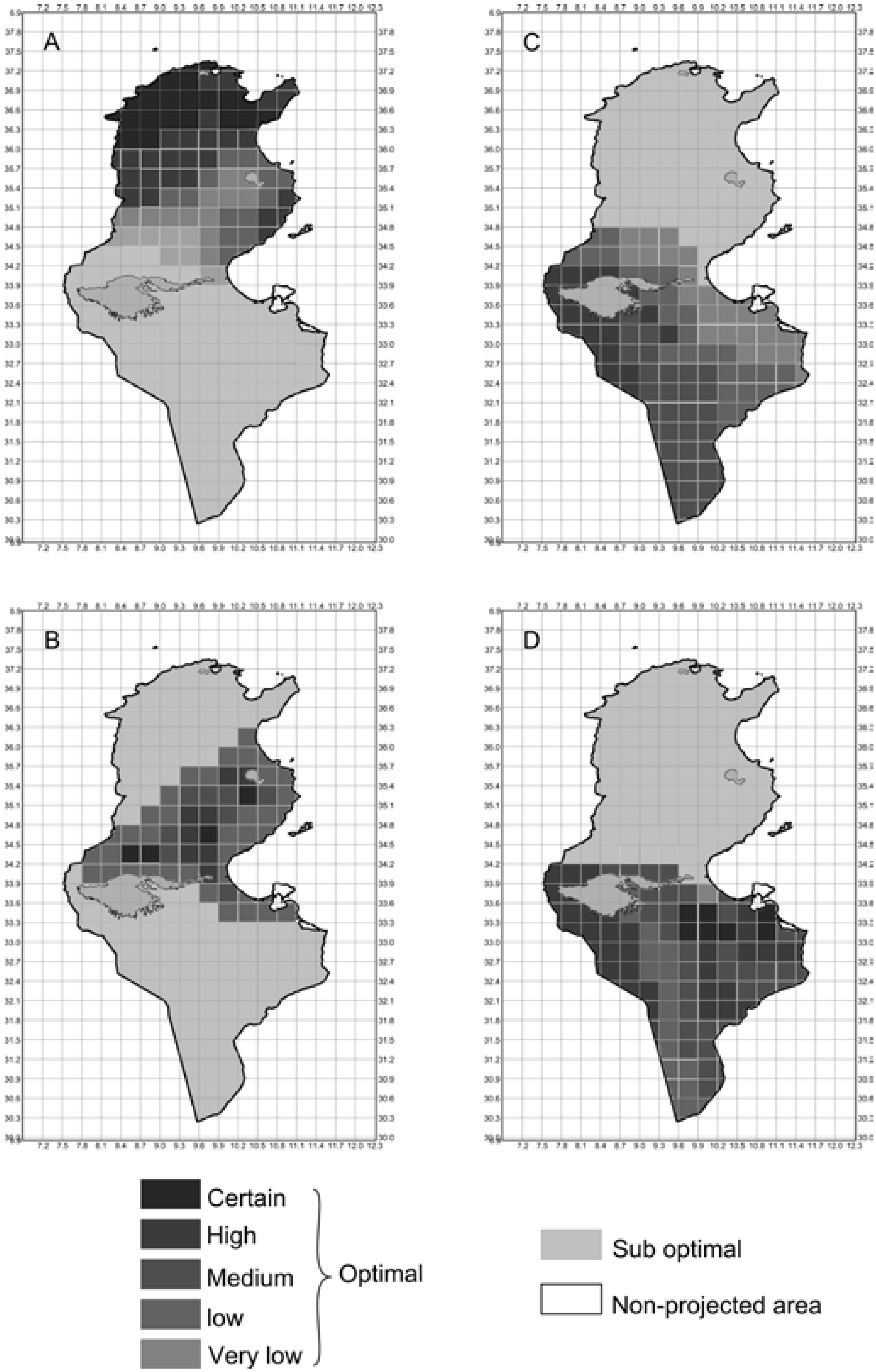

Fig. 6. Predicted probabilities of presence of Phyllodactylidae within Tunisian territory and habitat quality classes. *T. mauritanica* (A), *T. fascicularis* (B), *T. neglecta* (C) and *T. deserti* (D).

it is omitted is thermal amplitudes for *H. turcicus*, cereal for *Stenodactylus* genus, soil for *T. fascicularis*, thermal amplitudes for *T. mauritanica*, precipitations for *T. deserti*, and vegetation for *T. tripolitanus*. Figures 5 and 6 show the projection of the model to unexplored grids covering Tunisian territory.

DISCUSSION

Tunisian geckos count nine species showing expansions of their ranges (Tlili et al., 2012 a, b). They also presented distinct biogeographical affinities mostly concordant with the different habitat selection patterns (Fig. 3). This variation does not concern climatic affinities because 77.8% of Tunisian geckos are adapted to arid climate (unlike Tunisian Lacertidae) (Nouira, 1996; Nouira and Blanc, 2004) and Scincidae (Kalboussi, 2006). However, within this climatic frame, species of the same genus are latitudinally replaced to form several guilds according to vegetal and soil characteristics. The so far recognized distribution of gekkotan fauna shows that species distribution follows a bidirectional gradient. The South-North direction is physically stressful considering the increasing humidity and development of vegetal cover; these two parameters are constraining the species occurrences and only ubiquitous ones are present. The North-South direction is biologically stressful taking into account the increasing species richness (MacArthur, 1972; Real et al., 1997; Guisan and Zimmermann, 2000).

Assumptions yielded from field observations were confirmed and shared distribution patterns were determined (McLaughlin, 1992; Holt and Keitt, 2005; Heikinheimo et al., 2007; Escalante, 2009; Kreft and Jetz, 2010). Thereby, a biogeographical regionalization of Tunisia according to gekkotan species richness could be established yielding five regions (Fig. 3). Region I harbors Anthropophilic geckos widely distributed generally occupying habitats proximal to the sea (coastal line) or to an important water body (lagoon, lac …). The greatest parts of these lands are widely exploited for agricultural or industrial purposes. The south-western part of this region harbors Mediterranean taxa specific to North Africa; it represents the connecting point between Tunisia and southern neighboring countries and contains a large traffic network. Region II represents some culminant points in central Tunisia (Dorsal Mountain) and harbors endemic geckos in addition to anthropophilic ones. Region III harbors Saharo-sindian geckos which occupy area of arid steppe lands characterized by the continental influence and drastic conditions of life. As to region IV, it harbors Saharan geckos that occupy the Grand Erg Oriental. Finally region V harbors desert species that prefers rocky lands and small shrubs habitats.

The gecko-based regionalization observed in southern Tunisia coincides with that based on Lacertidae fauna (Nouira, 1996; 2004). For instance, Saharan and Saharo-sindian Lacertidae were reported in southern Tunisia; their differentiation was attributed to edaphic gradient and climatic conditions (Nouira and Blanc, 2003; 2004). While *Acathodactylus scutellatus* inhabits bordering regions of the Sahara, *A. dumerilli* occupies sandy habitats of barchans regions and *A. longipes* inhabits sandy Saharan biotopes of the grand erg oriental. The gecko-based regionalization is also concordant with our first assumptions yielded from field work. Nevertheless, we note the presence of a sixth cluster grouping spatially disjointed grids representing western and southern regions. Also, faunas of Northern regions are composed of two widespread cosmopolitan species which provide little useful biogeographical information. The question was then which of the environmental variables evidenced by clustering analysis is a more accurate representation of the distribution of geckos (Lawley et al., 2011; Strand, 2011).

It is known that for ectotherms, including lizards, climate has been proposed as a key factor of their distribution (e.g. Adolph and Porter, 1993; Doughty and Shine, 1995; Arad et al., 1997; Kaspari and Valone, 2002; Carretero, 2008; Salvidio and Oneto, 2008). Temperature and rainfall intervene indirectly by co-limiting primary production and physiologically limiting access to that production (Kaspari et al., 2000). Edaphic and relief characteristics take part in burrows selection (Zaady and Bouskila, 2002). Results provided herein suggest retaining five oblique factors to explain gekkotan distributions: 1) Environmental items, 2) coastal items, 3) biotic items, 4) sebkhas and chotts landscape items and 5) oasis landscape items. It also shows that gekkotan species richness is positively correlated to environmental items (climate and natural land-use). It is negatively correlated to coastal items (urban and touristic land-use) and geomorphology (altitudes and geological accidents). A strong relationship has been revealed between reptiles' occurrences and the orographic structures in Tunisia (Nouira, 1996). For instance, the Dorsal Mountain constitutes a barrier to the expansion of Saharan species toward the Palearctic domain and vice versa. So far, this is in accordance with our observations concerning the distribution of the species *S. sthenodactylus* being limited to the south-eastern limit of the Dorsal. The absence of the species in northern regions remains not explained by climate requirements alone; it could be related to geographical barriers and to their history of colonization and settlement. In fact, *S. sthenodactylus*, considered as Saharan, becomes related to widely Mediterranean species and expand its ecological niche to sub-humid regions. A better understanding of the niche of the species is shown in figure 4 where the probability of occurrence of the species decreases with high precipitations, low thermal amplitudes, altitudes higher than 250m, but most importantly, cereal land-use. Maps of the Fig. 2 show that these are the same characteristics of the extreme north of Tunisia which explains the absence of the species within this area. Map B of Fig. 5 shows that the suboptimal area of occurrence of *S. sthenodactylus* lays beyond the Dorsal Mountain and in the Cap Bon peninsula. However, area of very low probabilities of occurrence did appear in the map despite the certain presence of the species within this area.

For the other gekkotan species, predicted areas follow the general distribution patterns previously yielded. Besides, established models defined suitable habitats for each species and confirmed the latitudinal gradient of distribution. Land use and altitude increase the probability of occurrence of *H. turcicus* and *T. mauritanica*. Alternatively, they decrease the probability of the presence of *T. deserti, T. neglecta, T. tripolitanus* and *S. petrii*. *H. turcicus* occurs within area with high cereal land use; this is in accordance with field observations that revealed that the species inhabits preferentially hay fields. As to *T. fascicularis*, it showed a little displacement of the northern limit of its range towards semi-arid regions. Being a newly described species this displacement must be the result of better field explorations, however, modeling of its niche predicted areas of probable occurrence within the central arid steppe. High probabilities of occurrence of the species are restricted to domains characterized by less than 200 mm of precipitations, 22 to 21 thermal amplitudes, 200 m of altitudes and very low land use (Fig. 4).

ACKNOWLEDGMENTS

We thank the Office of the Ministry of Agriculture (Forestry Management Department) who provided necessary authorization for animal collecting (N° 902 and 1294). We also thank the officials from the meteorological stations and the Tunisia Wildlife Conservation Society TWCS who provided information and documents necessary to our work. Special thanks are addressed to Marc Cheylan, Claudia Corti and José D. Anadón for their helpful advices. Our gratitude is addressed to Doghri Moadha, Mrabet Kais, Doghri Ali, Khemiri Rajeh, and Doghri Aymen for material help.

SUPPLEMENTARY MATERIAL

Supplementary material associated with this article can be found at:
<http://www.unipv.it/webshi/appendix >
Manuscript number 12875. Appendix 1, Appendix 2, Appendix 3 A, Appendix 3 B.

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