Mouane, A, et al. 2024. Amphibian and reptile diversity in natural landscapes and human-modified habitats of the Sahara Desert of Algeria: A better understanding of biodiversity to improve conservation. *Elem Sci Anth*, 12: 1. DOI: https://doi.org/10.1525/elementa.2022.00106

RESEARCH ARTICLE

Amphibian and reptile diversity in natural landscapes and human-modified habitats of the Sahara Desert of Algeria: A better understanding of biodiversity to improve conservation

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The spatial and seasonal variations in amphibian and reptile diversity were studied in different biotopes (lowlands, desert pavements "Reg," Sabkhas "salt lakes," date palm groves, wadis, and urban sites) at the Algerian Sahara Desert. No prior research has explored the connection between the distribution of reptiles and amphibians in Algeria's Sahara and the environmental diversity of biotopes and landscapes. This study aimed to address this significant knowledge gap by investigating the relationships between Saharan habitats and landscapes and their impact on herpetofaunal presence, abundance, and diversity. The diversity of amphibians and reptiles was assessed based on quantitative data of species captures using nonparametric diversity indices, species richness accumulation curves, and similarity analysis. At the Region of Oued Righ (Northern Sahara Desert), we identified 3 amphibians, 19 lizards, and 10 ophidian species. These 32 species (approximately 30% of the Algerian herpetofauna) were classified into 2 orders (Anura and Squamata), 15 families, and 23 different genera. The study area included 8 protected species in Algeria and 9 endemic species to the Mediterranean region, including 1 amphibian and 7 species of reptiles. *Acanthodactylus dumerilii* was the most abundant species (20.5% of the total), whereas *Chalcides ocellatus* occurred in 32.9% of specimens. The highest values of species richness were recorded in palm groves with 22 species and Shannon's diversity index (H') was 3.5, whereas the lowest values were obtained in Sabkhas (5 species) and urban sites (7 species). The number of individuals experienced significant variations between study biotopes and seasons. Overall, species richness estimators (Chao2 and Jackknife1) revealed that the current survey achieved 90% of inventory completeness. Estimates and interpolations of species richness showed higher values in urban sites, palm groves, desert pavements, and wadis compared to Sabkhas and lowlands where completeness ranged between 90% and 100%. The analysis of similarity indicated low similarity values (<50%) between biotopes studied. The highest similarities were noted between the mesic biotopes (Sabkhas, wadis, and palm groves), the xeric and undisturbed biotopes (desert pavements and lowlands), whereas urban sites showed a distinct herpetofaunal community that was completely different of that recorded in Sabkhas, wadis, and lowlands.

Keywords: Amphibians and reptiles, Biodiversity, Assemblage structure, Community similarity, Sahara Desert biotopes, Faunistics, Herpetofauna, Species richness estimates

1. Introduction

The Sahara Desert of Algeria has large geographical area (approximately 2 M km^2) with unique climatic conditions and a high variety of biotopes and landscapes. But there is a limited amount of research on the biodiversity of amphibians and reptiles in this area (see Box 1). The diversity of the Algerian herpetofauna is mainly dependent on factors related to geographical, climatic, and topographical features (Mouane, 2010; Rouag, 2012; Beddek, 2017). The existing literature are studies representing punctual observations and species listings, with some phylogenetic analyses for certain species (Le Berre, 1989; Schleich et al., 1996; Mouane, 2010; Dufresnes et al., 2019). In the region of Oued Righ (Septentrional Sahara), herpetological studies are very limited in space and most often site-specific. The most noteworthy research performed on amphibians and reptiles over last years treated mostly systematic and

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morphometric aspects of species (Ghennoum and Harrouchi, 2011; Laoufi, 2011) and/or inventory of herpetofauna (Mouane, 2010; Chenchouni, 2012a; Mebarki, 2012; Mouane et al., 2013). In fact, the scarcity of studies on amphibians and reptiles at the Sahara Desert of Algeria is due to the difficulty of terrain and environmental conditions. This complicates field works and also the danger in handling certain venomous species. Moreover, the difficult access to Algeria for foreign researchers due to security conditions of the country is among the causes that hindered herpetological studies in Algeria (most specifically in its Sahara). To this, we can add the relative rarity in local researchers in this research field.

Box 1. A short review on the state-of-the-art of herpetological studies in North Africa with a particular emphasis on Algeria

The herpetofauna of North Africa is well-known in Morocco and Tunisia with, among others, the work of Bons and Girot (1962), Nouira (1982, 1999), Nouira and Blanc (1993, 2003, 2004), Fahd (2001), Bons and Geniez (1996), Geniez et al. (2006), Kalboussi (2006), Beukema et al. (2013), and del Mármol et al. (2019). In Egypt, Libya, and Mauritania, reptiles and amphibians are fairly well explored (Padial and De La Riva, 2004; Baha El Din, 2006; Padial, 2006; Ibrahim, 2008; Bauer et al., 2017; Sow et al., 2017). However, in Algeria, studies related to this field are still undergoing where datasets regarding herpetofaunal geographic distribution are less complete compared to other neighboring countries. Among these previous studies, we can cite Gervais (1857) and Strauch (1862) describing some Ophidian species; Lallemant (1867) that represents a synoptic and analytical catalog of amphibians and reptiles; Boulenger (1891) describing the reptiles and batrachians of N. Africa "Barbary" (Morocco, Algeria, and Tunisia); Olivier (1894) that gave an update on the Algerian herpetofauna; Doumergue (1901) studied the herpetological fauna of Oran (western Algeria); Grenot and Vernet (1972) investigated reptiles of rocky deserts in the Western Sahara; Gauthier (1967) examined the ecology and ethology of reptiles in the region of Beni-Abbés (NW Sahara); Le Berre (1989) described the reptiles and amphibians of the Sahara; Schleich et al. (1996) on Amphibians and reptiles of North Africa; Chirio and Blanc (1997) on the status and distribution of reptiles in the Aurès Massif (NE Algeria); Cox et al. (2006) on the conservation status and distribution of reptiles and amphibians of the Mediterranean Basin, including Algeria; Mateao et al. (2013) and Escoriza and Ben Hassine (2019) represent the most comprehensive synthesis, so far, on diversity and conservation of amphibian assemblages in Algeria; and Beddek (2017) who focused on key information gaps that hinder the understanding of biodiversity and conservation biology of the Algerian herpetofauna. The synthesis of all these previous scientific works combined brings out a list of reptiles and amphibians of Algeria with 117 species. The order Squamata dominated with 78.6% of the total of species richness against 8.5% for Anura, 6% for Testudines, 3.4% for Ophidia, 2.6% for Caudata, and 0.9% for Crocodilia. Geographical, climatic, and topographical features of Algeria are the main drivers that control the diversity and distribution of herpetofauna (Mouane, 2010; Rouag, 2012; Beddek, 2017). These factors have also contributed to the isolation and diversification of several taxa, which allowed for the existence of several species specific to Algeria and/or the Sahara Desert (Rouag, 2012; Beddek, 2017).

To the best of our knowledge, no study has treated the distribution patterns of amphibians and reptiles in the Sahara Desert of Algerian in relation to environmental variability of biotopes and landscapes. This motivated us to examine the composition and estimate diversity of the amphibian and reptile communities in the main biotopes/landscapes of this region. The effects of spatial continuity and patchiness of habitats and landscapes should be considered when assessing and analyzing biodiversity patterns at regional and/or global scales (Böhm et al., 2013). Moreover, on a regional scale, species occurring within local communities depend on both environmental filters and biotic interactions within communities; thus the effect of each of these factors are strongly species specific and differ greatly among taxa (Wiens, 2011). Furthermore, discontinuous, isolated, and/or fragmented landscapes may have different spatial biodiversity patterns, both across and within different spatial zones (Kalboussi, 2006; Bensizerara et al., 2013).

Surveys dealing with the ecological factors that control the distribution and diversity of amphibians and reptiles highlighted specifically the climatic factors with their spatial and multiple temporal variations, vertical and horizontal vegetation structures of the habitat, water characteristics, topographic features, biotic interactions, and anthropogenic factors including urbanization, agriculture activities, and various disturbances (Fahd, 2001; Teixeira et al., 2001; Nouira and Blanc, 2003, 2004; Chenchouni, 2007; Hamer and Mcdonnell, 2010; Banville and Bateman, 2012; Mebarki, 2012). The understanding of relationships between species richness of a given biotope and its characteristics are helpful to assist decision-making of both species and habitat conservation planning at regional and large scale (Slimani, 1989; Cox et al., 2006; Rouag, 2012; Böhm et al., 2013; Beddek, 2017). This kind of information is further needed (especially in hot-arid regions) for guiding conservation actions to cover all species distribution ranges and making ecosystem planning more effective (Trape and Mane, 2006; Böhm et al., 2013; Mateo et al., 2013). The questions we ask here: What is the spatiotemporal amphibian and reptile assemblage composition in Sahara Desert? and What is the conservation status of each of the species found? These questions are part of the wider scientific research on the partitioning species ecological niches and biodiversity in relation to landscape structure and ecosystem functioning.

Our study investigated species richness and diversity parameters in various Saharan biotopes and during different seasons (desertic climate) to deepen our understanding on biodiversity patterns of amphibian and reptile communities of North Africa. This survey characterized amphibian and reptile species with several ecological statuses, including conservation status (globally, at the Mediterranean region and in Algeria), and it determined species chorological categories and diet profile. We hypothesize that amphibian and reptile diversity is biotope-specific and that biodiversity values vary between biotope and score higher in biotopes and seasons with favorable conditions (high moisture and vegetation cover with complex structure). Therefore, the scientific questions examined in this study were: (i) What is species composition of amphibian and reptile assemblages of the Sahara Desert of Algeria? (ii) What are the spatial and seasonal patterns of alpha biodiversity of these communities, (iii) How amphibian and reptile diversity is partitioned over Saharan biotopes? and (iv) What are the characteristic species and diversity similarities between these biotopes? For the former question, we are testing through a linear modeling approach how do these diversity parameters vary among Saharan biotopes and seasons.

2. Materials and methods

2.1. Study area

The region of Oued Righ located in the northern Sahara Desert. It is characterized by a vast set of oases and palm groves surrounded by large areas of sand dunes. It is located geographically in northeastern Algeria (latitudes ranged from 32°54'N to 39°09'N, and longitudes from 05°50'E to 05°75'E) and stretches over 150 km in length along the mainstream of Oued Righ, with a total area of 270 km^2 (Mouane, 2010; Chenchouni, 2012b). According to Chenchouni (2010), the Valley of Oued Righ is located between the Oriental Grand Erg in the east and the M'Zab Plateau in the west (**Figure 1**). The climate of the Oued Righ Valley is a hot arid desert climate (Köppen climate classification = BWh) characterized by very low precipitation (<150 mm/year), high temperatures, and low relative humidity (Bradai et al., 2015). De Martonne index is <4 indicating a hyper-arid climate where Budyko evaporation index is about 100% and the climatic net primary production is precipitation limited (Supplemental Table 1). Monthly maximum temperature exceeds 40°C during mid-hot season (June–July), whereas the lowest minimum temperature is about 3.2°C recorded in January. Monthly precipitation is less than 10 mm, with an annual effective rain = 63 mm that falls during 9 days throughout the year (Supplemental Table 2). The main agricultural activity in the region is the cultivation of date palm (*Phoenix dactylefera*) established in oases that have mesic and mild ecological conditions compared to the surrounding hot-arid desert (Idder-Ighili et al., 2015; Mihi et al., 2019). According to Mouane (2010), spontaneous plant species found in palm groves included green amaranth (*Amaranthus hybridus* L.), saltbush (*Atriplex dimorphostegia* Kar. & Kir.), cheeseweed (*Malva parviflora* L.), field bindweed (*Convolvulus arvensis* L.), shrubby seablight (*Suaeda fruticosa* Forssk. ex J.F.Gmel.), and scutch grass (*Cynodon dactylon* (L.) Pers.).

2.2. Biotopes and landscapes studied

To analyze the composition and diversity of amphibians and reptiles in the north-east of the Algerian Sahara, the study was carried out in 6 Saharan biotopes (**Figure 2**), which are (i) Lowlands, including Hamadas, are rocky plateaus with monotonous flat topography stretched over vast areas (Monod, 1992; Azizi et al., 2021); (ii) Wadis, including surrounding wadi beds, are watercourses and/or

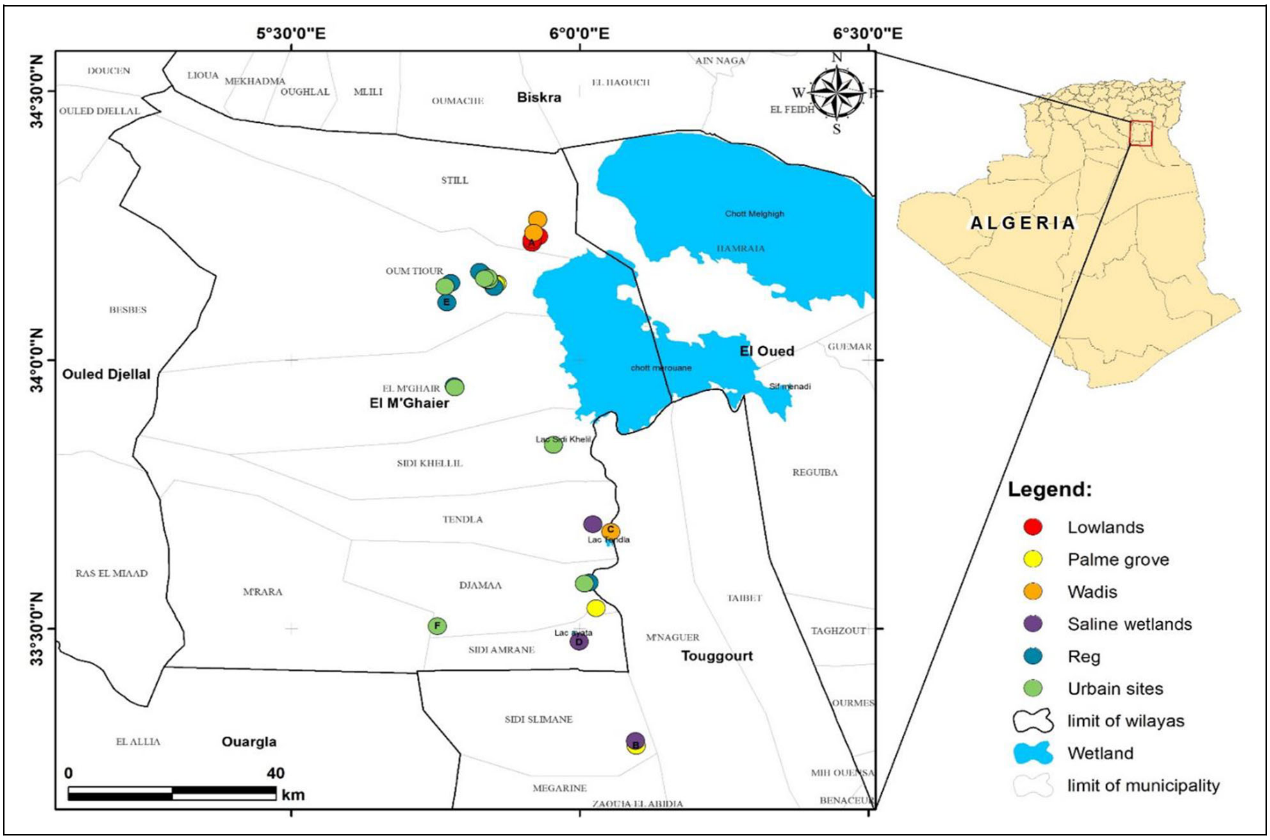

Figure 1. Location map of the region of Oued Righ (study area) in the Sahara Desert of Algeria. Letters in colored circles refer to the biotopes sampled and displayed in photographs of **Figure 2**.

Figure 2. Photos of different biotopes and landscapes studied in the Sahara Desert of Algeria, by Haroun Chenchouni and Aicha Mouane. (A) Lowlands of flat desert rangelands dominated by *Anabasis articulata* (Forssk.) Moq. (Amaranthaceae) and *Randonia africana* Coss. (Resedaceae), (B) A date palm grove "oasis" based on *Phoenix dactylifera* L. (Arecaceae), (C) Wadi invaded with *Phragmites communis* (Cav.) Trin. ex Steud. (Poaceae), (D) Sabkha "salt lake" with *Arthrocnemum macrostachyum* (Moric.) K.Koch (Chenopodiaceae) at the foreground and *Tamarix gallica* L. (Tamaricaceae) at the background near the lake waterbody (see Chenchouni, 2012b), (E) Desert pavement "Reg" dominated by *Limoniastrum guyonianum* Boiss. (Plumbaginaceae), (F) Urban site with an oasis of date palms at the background.

channels occupied permanently or temporarily with water; (iii) Palm groves are man-made ecosystems that characterize oases of hot drylands and have high plant and animal diversity. The palm grove represents a real forest creating local mesic climatic and edaphic conditions (i.e., soil moisture and air humidity) that attract a large number of life forms into these favorable environments (Guezoul et al., 2013; Mihi et al., 2019; Benras et al., 2023); (iv) Desert pavements known as "Reg," are plains of gravels and rock fragments that occupy large surfaces in the Sahara Desert (Monod, 1992; Bouallala et al., 2022; Bouallala et al., 2023); (v) Sabkhas, including also Chotts, represent salt lake wetlands with large expanses and low water levels (Chenchouni, 2017a). The crusty plates of various salts are deposited on the surface when the water evaporates under the effect of the heat (Monod, 1992); and (vi) Urban sites: characterized by the presence of human constructions and agglomerations with a relatively moderate density of inhabitants. The biotope types selected and considered are representative of the different biotopes/landscapes of the Sahara Desert in this study (Monod, 1992; Chehma, 2005; Chenchouni, 2010). The choice of these ecosystems aims at comparing amphibian and reptile communities between biotopes and thus analyzing diversity similarities "beta biodiversity."

2.3. Sampling and capture techniques

The study took place over a period of 5 consecutive years (from July 2011 to August 2015), with a total of about 150 expeditions in the Sahara. Every year, amphibians and reptiles were captured and sampled during the most favorable period that coincides with the seasons with warm temperatures (February–October). The total number of samples analyzed was 70 in all habitats, this included only samples with successful capture, that is, at least one individual captured. Sample size differed between biotopes, with 9 samples in lowlands, 15 in Regs, 11 in urban sites, 19 in palm groves, 9 in wadis, and 7 in Sabkhas. Field surveys were carried out monthly and each survey lasted from 4 to 11 hours with 8 hours on average, with the contribution of 4 participant persons on average. Depending on the month in which the field surveys were conducted, the samples were classified into 3 climatic seasons: (i) pre-hot season (February–March), (ii) hot season (April–August), and (iii) post-hot season (September–October). This sampling period, that is, "February–October" coincides with the activity of amphibians and reptiles in the study area (Mouane, 2010, 2020). Winter (November–January) was excluded from this study because of the nonactivity of most species.

The methods used in the current study were derived from those recommended in previous herpetological studies (Gruber, 1992; Fahd, 2001; Arnold and Ovenden, 2004; Miaud, 2005): namely (i) the technique of direct observation applied on sampling routes "transect method," and (ii) the systematic sampling of micro-biotopes where individuals were searched systematically. The catching process involved exploring areas likely to harbor amphibians and/or reptiles. Once an individual was spotted, we tried to trap it under vegetation tufts. Burrowing species were captured around/near their burrows, which are usually confined at the foot of vegetation. Lizards were hand captured, whereas snakes were captured using a herpetological catcher clip (snake grabber tongs). The capture of amphibians was done either by hand or by using a dip-net. Amphibian and reptile specimens captured were examined, measured, and photographed then released in the same site. Some specimens were preserved in solutions of 4% formalin or 75% ethanol and were deposited at the Faculty of Science and Nature (University of El Oued, Algeria). Species were identified based on morphological characteristics (e.g., scale structure and color) and using reptile and amphibian reference guides of the regions of Europe, North Africa, Sahara, and the Middle East (Cihar, 1979; Le Berre, 1989; Gruber, 1992; Bons and Geniez, 1996; Schleich et al., 1996; Arnold and Ovenden, 2004; Baha El Din, 2006; Geniez et al., 2006; Trape and Mane, 2006; Trape et al., 2012; Escoriza and Ben Hassine, 2019).

2.4. Data analysis

2.4.1. Conservation status, endemism, chorological categories, and diet profile

To characterize the ecology of identified amphibian and reptile species following to the ecological context of the study area, ecological statuses were assigned for each species, namely (i) conservation status: determined following the IUCN Red List categories of threatened species for the Mediterranean Region (Cox et al., 2006; www.iucnredlist.org); (ii) national protection status "NPS": defined based on the list of species protected by Decree No. 35 of June 10, 2012, relative to protected nondomestic animal species in Algeria (Official Journal of Algeria, 2012); (iii) endemism status that determines endemic species in the Mediterranean Region (Cox et al., 2006); (iv) chorological categories "CC": determined according to Schleich et al. (1996), Geniez et al. (2006), and Trape et al. (2012) that give the chorological type or biogeographic origin of reptiles and amphibians. Species were divided into five CC (Saharan, Mediterranean, Saharo-Mediterranean, Saharo-Sindian, and endemic to the Sahara); and (v) diet profile "DP": defined for each species based on the main diet during its life history and inferred from literature (Le Berre, 1989; Geniez et al., 2006; Trape and Mane, 2006); species were classified into 4 diet profiles: Carnivores "Car": reptile species feeding mainly on animals, including small vertebrates and invertebrates, Herbivores "Her": reptile species with most of their diet consisting of plant materials, Invertebrate feeders "Inv": amphibians with food spectrum dominated by aquatic invertebrates and/or seldom terrestrial arthropods, and Insectivores "Ins": reptiles feeding mainly on insects.

2.4.2. Diversity parameters

The following parameters were calculated per biotope and for the whole region for each inventoried species: (i) relative abundance "RA" which is the ratio of specific number of individuals "ni" to the total abundance "N," (ii) occurrence frequency "Occ" which represents the ratio between the number of samples containing the species in question and the total number of samples realized. Species were classified into 4 categories following occurrence percentage: (i) constant species "CN" are present in 50% or more of samples, (ii) common species "CM" are present in (25%–50%) of records, (iii) accidental species "AC" have occurrences varying between (10%–25%), and (iv) very accidental species "VA" have an occurrence less than 10% (Chenchouni, 2007).

Moreover, biodiversity of the amphibian and reptile assemblage was appraised per biotope using several parameters (Magurran, 2004; Chenchouni, 2017b): (i) species richness "S" that is defined as the total number of species found in a given biotope, (ii) mean species richness "S_m" referring to the number of samples conducted per biotope, (iii) ratio N/S that gives an average on the number of individuals per species per biotope, (iv) Shannon diversity index "H": $H = \Sigma(Pi \times \log_2 Pi)$, where Pi is the proportion of individuals of species i "n_i" on the total number of individuals "N," (v) evenness "E," where $E = H/H_{\max}$, with $H_{\max} = \log_2 S$ is the maximum diversity for the studied community of that biotope. Evenness values range between 1 indicating even proportions of species abundances and 0 revealing the dominance of a species, (vi) Simpson reciprocal index "SRI" ($1/D$), where $D = \Sigma n_i(n_i-1)/N(N-1)$, and (vii) ratio SRI/$S$.

2.4.3. Estimation of species richness

The asymptotic estimator Chao2 "$S_{(\text{Chao2})}$" and first order Jackknife's estimator "$S_{(\text{Jack1})}$" were used to estimate species richness of amphibians and reptiles in each biotope type and for the entire study region of Oued Righ. The formula of the first estimator is $S_{(\text{Chao2})} = S+((m-1)/m)(Q_1^2/2Q_2)$, whereas $S_{(\text{Jack1})} = S+Q_1((m-1)/m)$, with S: observed species richness, m: total number of samples, Q_1 and Q_2: the frequency of unique (species that occur in only one sample) and duplicate (species that occur in only two sample), respectively. Values of species richness estimates were expressed as mean ± standard deviation "SD" following a 100-randomization "runs." Estimates were carried out using the EstimateS program (Colwell, 2013). For each biotope, inventory completeness was calculated, to compare observed with estimated species richness, as a percentage of the observed species richness according to the corresponding species richness estimator, that is, $S_{(\text{Chao2})}$ and $S_{(\text{Jack1})}$.

2.4.4. Rarefaction and extrapolation

Species discovery curve or species accumulation curve displays the cumulative number of species recorded in a particular biotope as a function of the cumulative effort expended searching for them (number of samples in our case; Gotelli and Colwell, 2001; Chenchouni, 2017b). Thus, to determine whether the sampling effort applied in sampling each biotope correctly appraised species richness of that environment, rarefaction, and extrapolation curves were performed based on a set of appropriate statistical sampling models (Colwell, 2013; Chao et al., 2014). These curves help to obtain, based observed data, an estimate of the expected cumulative species richness as a function of the sampling effort provided. This method also has the advantage of comparing different datasets collected with different sampling efforts "number of samples." Species richness of a given biotope can be projected for a higher sample size with interpolation curves than the reference size (Colwell, 2013). This way, we managed to compare predicted species richness of different biotopes after having equalizing number of samples per biotope, which make comparison more accurate (Chenchouni, 2017b). The interpolations of species richness were assigned with the lower and upper bounds of 95% confidence interval and with SD values per sample point that was performed based on a 100-randomization (Colwell, 2013).

2.4.5. Similarities of communities between biotopes

To comparing beta-diversity of amphibians and reptiles between the 6 biotope/landscape types sampled in this study, similarities were computed using several qualitative (Jaccard and Sorenson similarity indices) and abundance-based indices. Quantitative indices included the raw and estimated indices of Chao-Jaccard and Chao-Sorenson, Bray-Curtis index, and Morisita-Horn index (Magurran, 2004; Chao et al., 2005; Colwell, 2013). Similarities were computed using the software EstimateS (Colwell, 2013). In addition, a Venn diagram was performed to plot common and biotope-specific amphibian and reptile species of each biotope (Heberle et al., 2015).

2.5. Statistical analysis

A multivariate analysis of variance "MANOVA" was performed in order to test differences in species abundances between the samples biotopes and studied seasons based on assemblage composition data. Values of diversity parameters (N, S, ratio N/S, H, $H_{\max}$, E, SRI, ratio SRI/S) were expressed as mean ± SD for biotopes and seasons and plotted as boxplots. Sample-based data were used to test the spatiotemporal variations of these parameters between study biotopes and seasons. The effects of "biotopes," "Seasons," and their interaction "Biotopes × Seasons" were incorporated in generalized linear model "GLM" with Poisson distribution error and log link function for N and S, Gaussian distribution, and Identity link for the ratio N/S, H, $H_{\max}$, and SRI, and quasibinomial distribution with logit link for E and the ratio SRI/S. All statistical analyses were conducted using the software R version 4.2.3 (R Core Team, 2023). In addition, relationships between diversity parameters of amphibian and reptile communities were tested using Pearson correlations and then the obtained correlation matrix was plotted using the package "corrplot" in R (Wei and Simko, 2017). The distribution of amphibian and reptilian species according to the different biotopes prospected was plotted using two-way cluster analysis. Clustering follows Ward's method using Bray-Curtis dissimilarity index based on total species abundances per biotope.

3. Results

3.1. Systematic list, species protection status, and endemism

In the 6 biotopes studied, a total of 32 species of amphibians and reptiles were identified based on the capture of 453 individuals. This fauna is classified into 2 classes, 2 orders (Anura and Squamata), 15 families, and 23 different genera; with 3 species of amphibians, 19 lizards, and 10 snakes (**Table 1**). Based on the IUCN Red List of Threatened Species, 31 species at the Oued Righ region are listed as "Least Concern," and 1 species North African spiny-tailed lizard (*Uromastyx acanthinurus*) as "Near Threatened" (Cox et al., 2006; www.iucnredlist.org). Seven species have a protection status in Algeria (*Trapelus mutabilis*, *Chamaeleo chamaeleon*, *Acanthodactylus dumerilii*, *Natrix natrix*, *Tarentola deserti*, *Chalcides ocellatus*, and *Scincus scincus*). The 8 species are endemic to the Mediterranean region (*Discoglossus pictus*, *Hemorrhois algirus*, *Acanthodactylus erythrurus*, *Acanthodactylus maculatus*, *Natrix maura*, *Tarentola deserti*, *Tarentola mauritanica*, and *Tarentola neglecta*). It is noteworthy to mention that previous inventories of Algeria's herpetofauna (Box 1; Rouag, 2012; Beddek, 2017) described a total of 117 species (Supplemental Table 3), with several subspecies, including 13 amphibians among which a new species the Carthaginian

Table 1. Systematic list and abundance of amphibian and reptile species of the Sahara Desert of Algeria, with their ecological statuses related to conservation "IUCN Red List," national protection, Mediterranean endemism, chorological categories, and diet profile

Order (Class)	Family	Species	IUCN Red List	NPS	End Med	CC	DP	Ni
Anura (Amphibia)	Bufonidae	*Bufotes boulengeri* (Lataste, 1879)	LC	No	No	Med	Inv	20
	Discoglossidae	*Discoglossus pictus* Otth, 1837	LC	No	Yes	Med	Inv	15
	Ranidae	*Pelophylax saharicus* (Boulenger in Hartert, 1913)	LC	No	No	Sah-Med	Inv	17
Squamata (Reptilia)	Agamidae	*Trapelus mutabilis* (Merrem, 1820)	LC	Yes	No	Sah	Ins	9
	Agamidae	*Uromastyx acanthinurus* Bell, 1825	NT	No	No	Sah	Her	1
	Chamaeleonidae	*Chamaeleo chamaeleon* (Linnaeus, 1758)	LC	Yes	No	Med	Ins	4
	Colubridae	*Hemorrhois algirus* (Jan, 1863)	LC	No	Yes	Sah-Med	Car	3
	Colubridae	*Spalerosophis diadema* (Schlegel, 1837)	LC	No	No	Sah-Sin	Car	16
	Colubridae	*Lytorhynchus diadema* (Duméril, Bibron & Duméril, 1854)	LC	No	No	Sah	Car	1
	Gekkonidae	*Stenodactylus petrii* Anderson, 1896	LC	No	No	Sah	Ins	7
	Gekkonidae	*Cyrtopodion scabrum* (Heyden, 1827)	LC	No	No	Med	Ins	6
	Lacertidae	*Acanthodactylus boskianus* (Daudin, 1802)	LC	No	No	Sah	Ins	18
	Lacertidae	*Acanthodactylus dumerilii* (Milne-edwards, 1829)	LC	Yes	No	Sah	Ins	93
	Lacertidae	*Acanthodactylus erythrurus* (Schinz, 1833)	LC	No	Yes	Med	Ins	1
	Lacertidae	*Acanthodactylus maculatus* (Gray, 1838)	LC	No	Yes	End Sah	Ins	11
	Lacertidae	*Acanthodactylus scutellatus* (Audouin, 1827)	LC	No	No	Sah-Sin	Ins	44
	Lacertidae	*Mesalina guttulata* (Lichtenstein, 1823)	LC	No	No	Sah	Ins	2
	Lacertidae	*Mesalina olivieri* (Audouin, 1829)	LC	No	No	Sah-Med	Ins	1
	Lamprophiidae	*Psammophis schokari* (Forskål, 1775)	LC	No	No	Sah-Sin	Car	27
	Lamprophiidae	*Rhagerhis moilensis* (Reuss, 1834)	LC	No	No	Sah-Sin	Car	2
	Natricidae	*Natrix maura* (Linnaeus, 1758)	LC	No	Yes	Med	Car	2
	Natricidae	*Natrix natrix* (Linnaeus, 1758)	LC	Yes	No	Med	Car	1
	Phyllodactylidae	*Tarentola deserti* Boulenger, 1891	LC	Yes	Yes	Sah	Ins	29
	Phyllodactylidae	*Tarentola mauritanica* (Linnaeus, 1758)	LC	No	Yes	Med	Ins	14
	Phyllodactylidae	*Tarentola neglecta* Strauch, 1887	LC	No	Yes	End Sah	Ins	8
	Psammophiidae	*Malpolon monspessulanus* (Hermann, 1804)	LC	No	No	Med	Car	3
	Scincidae	*Chalcides boulengeri* (Anderson, 1892)	LC	No	No	Sah	Ins	3

(continued)

Table 1. *(continued)*

Order (Class)	Family	Species	IUCN Red List	NPS	End Med	CC	DP	Ni
	Scincidae	*Chalcides ocellatus* (Forskål, 1775)	LC	Yes	No	Med	Ins	69
	Scincidae	*Scincus scincus* (Linnaeus, 1758)	LC	Yes	No	Sah	Ins	4
	Varanidae	*Varanus griseus* (Daudin, 1803)	LC	No	No	Sah-Sin	Car	4
	Viperidae	*Cerastes cerastes* (Linnaeus, 1758)	LC	No	No	Sah	Car	17
	Viperidae	*Echis leucogaster* Roman, 1972	LC	No	No	Sah	Car	1
Orders = 2	**Families = 15**	**Genera = 23, Species = 32**		**7**	**8**			***N* = 453**

IUCN Red List: Categories of threatened species of the IUCN Red List (www.iucnredlist.org) (NT: Near Threatened, LC: Least Concern), NPS: national protection status (Yes: protected nationally, No: nonprotected by the Algerian law), End Med: endemism status of species in the Mediterranean, CC: chorological categories (End Sah: endemic to the Sahara Desert, Med: Mediterranean, Sah: Saharan, Sah-Med: Saharo-Mediterranean, Sah-Sin: Saharo-Sindian), DP: diet profile (Car: carnivore, Her: herbivore, Ins: insectivore, Inv: invertebrate feeder), *Ni*: total number of individuals caught (i.e., all samples of biotopes pooled).

tree frog (*Hyla carthaginiensis*) was discovered recently (Dufresnes et al., 2019).

3.2. Diet profile and chorological categories

In all the biotopes studied, the category of insectivores comes first, either in terms of the number of individuals or species richness (17 species). Carnivores followed with 11 species (33.3%) (**Figure 3**). Amphibians were the most dominant invertebrate consumers "Inv" in Sabkhas where they accounted for 82.1% of the total species of this biotope. The Saharan and Mediterranean chorological types dominated in biotopes of Oued Righ Region, while the Saharan endemic CC were quite low. It was noted that the Mediterranean CC, either in terms of the number of individuals or species, dominated in palm groves, Sabkhas and wadis with 60.6%, 46.4%, and 28.6% of total species, respectively. The Saharan CC was the most dominant in urban sites (59.5%), the Reg (59.2%), and lowlands (45%). On the contrary, Saharan and Saharo-Mediterranean endemics were poorly represented in all the biotopes studied (**Figure 3**).

3.3. Spatial and seasonal patterns of abundance, occurrence, and diversity parameters

In terms of abundance, Duméril's fringe-fingered lizard (*Acanthodactylus dumerilii*) was the most abundant species in the lowlands, wadis, and Reg with RA = 35.9%, 10.7%, and 39.6%, respectively. At Sabkhas, Sahara frog (*Pelophylax saharicus*) was the most abundant with RA = 35.7%. The family Phyllodactylidae was the most abundant in urban sites with RA = 70.3% of total abundances (**Table 2**). The MANOVA indicated that abundance data of assemblage specific composition varied significantly among the biotopes (Pillai's test statistic = 3.327, approximate $F_{(5,\ 53)} = 1.62$, $P = 0.002$), whereas specific abundances showed no significant variation following seasons (Pillai = 1.195, approximate $F_{(3,\ 53)} = 1.068$, $P = 0.412$) and seasons at each biotopes "biotopes × seasons" (Pillai = 4.595, approximate $F_{(9,\ 53)} = 0.98$, $P = 0.575$). Species occurrence levels provide reliable information on characteristic species of a given habitat. In general, 3 species were constant (occurrence ≥ 50%) in lowlands, palm groves, and urban sites namely *Acanthodactylus dumerilii*, ocellated skink (*Chalcides ocellatus*), and Desert wall gecko (*Tarentola deserti*). On the other hand, the species considered as sporadic in the habitats studied of the Oued Righ Region were unique and duplicate, that is, those met only once or twice, respectively, in all the biotopes. In urban sites, *Tarentola deserti* was a very frequent species (occurrence = 90.9%). Similarly, *Chalcides ocellatus* has a constant occurrence (84.2%) in palm groves. *Discoglossus pictus* (42.9%), *Acanthodactylus boskianus* (44.4%), *Psammophis schokari* (33.3%), and *Trapelus mutabilis* (26.7%) were common in the study region, whereas most of other species were accidental with occurrences less than 25% (**Table 2**). In date palm groves, species were classified into 4 classes of occurrence: the most numerous were the constant species with 46 individuals but belonging to a single species (example *C. ocellatus*). In terms of species, the class of very rare (less frequent) species dominated with 13 species totaling 31 individuals. Three classes of occurrence were noted in Sabkhas and urban sites. In Sabkhas, common species dominated in terms of numbers (82%) and species (60%). While in urban sites, the class of constant species was dominant with 19 individuals, but all belonged to *T. deserti* (**Figure 3**).

The diversity of herpetofaunal communities has been characterized for both seasons and biotopes. The lowest abundances of species were recorded in wadis and urban sites with respectively 3.1 ± 3.2 and 3.4 ± 3.2 individuals/sample. The highest abundance was recorded during the hot season (April–August) with a total of 294 individuals caught. The highest species richness was recorded in palm groves with 22 species (average species richness = 3.2 ± 1.6 species/sample), whereas the lowest values were obtained in Sabkhas and urban sites with 1.9 ± 1.8 and 1.6 ± 1 species/sample. The hot season had higher values of total and average species richness with respectively 30 and 2.6 ± 1.9 species/sample compared to pre-hot and post-hot seasons (**Figure 4**).

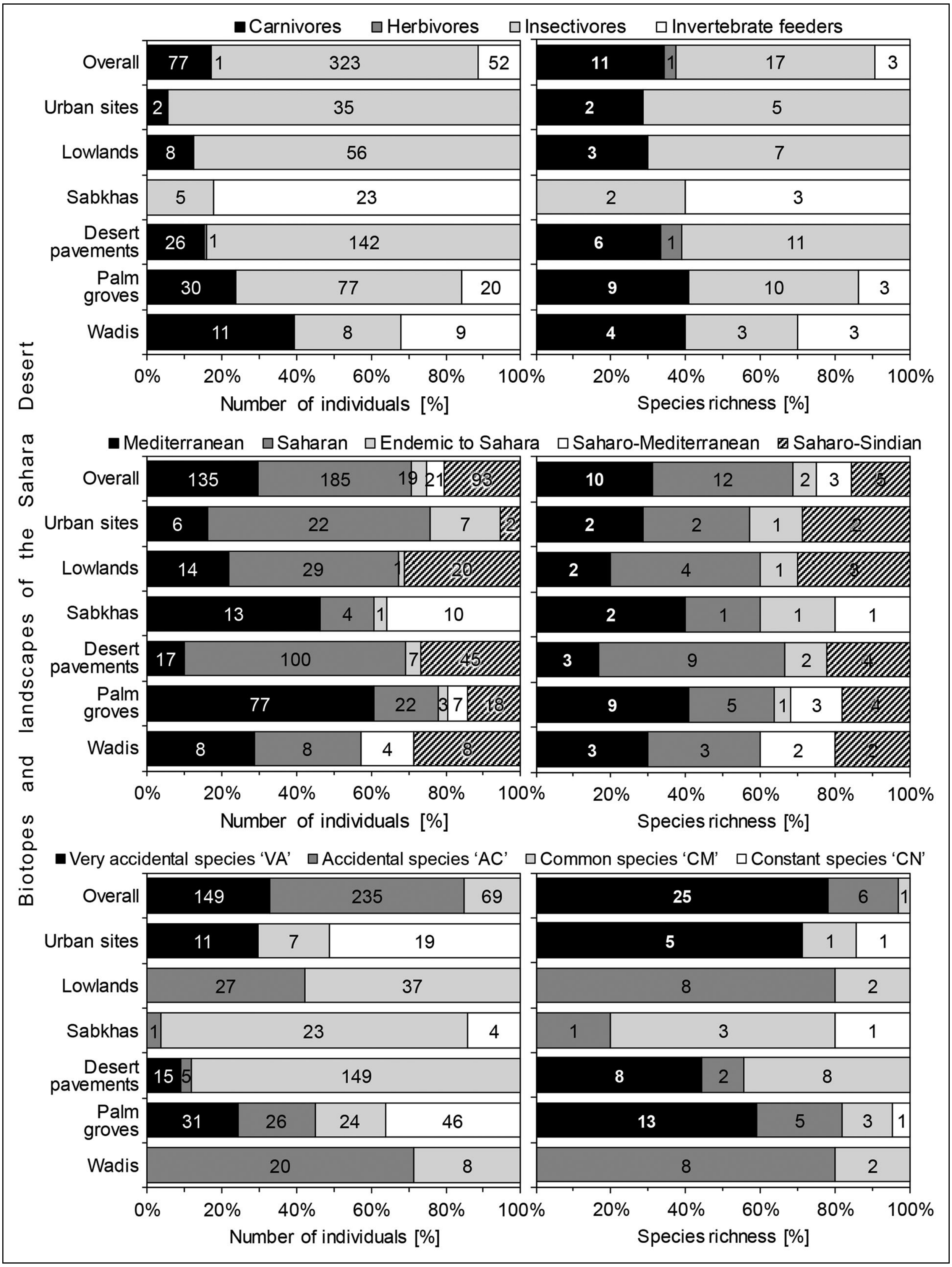

Figure 3. Distribution of biogeographic elements, trophic statuses, and categories and occurrences of amphibians and reptiles according to the different biotope types in the Oued Righ region (Sahara Desert of Algeria). The figures in the histograms represent the absolute abundances (*N*) and species richness (*S*) of each category.

Table 2. Relative abundances “RA,” frequencies of occurrence “Occc” (in %), and occurrence classes “OC” of amphibian and reptile species identified at different biotopes and landscapes in the region of Oued Righ Valley at the Sahara Desert of Algeria

	Lowlands			Wadis			Palm Groves			Reg			Urban Sites			Sabkha			Overall		
Amphibian and Reptile Species	**RA**	**Occ**	**OC**	**RA**	**Occ**	**OC**	**RA**	**Occ**	**OC**	**RA**	**Occ**	**OC**	**RA**	**Occ**	**OC**	**RA**	**Occ**	**OC**	**RA**	**Occ**	**OC**
Order: Anura																					
Bufotes boulengeri	–	–	–	14.2	11.1	AC	8.6	5.3	VA	–	–	–	–	–	–	17.9	28.6	CM	4.4.	5.7	VA
Discoglossus pictus	–	–	–	7.1	11.1	AC	3.9	5.3	VA	–	–	–	–	–	–	28.6	42.9	CM	3.3	7.1	VA
Pelophylax saharicus	–	–	–	10.7	11.1	AC	3.1	5.3	VA	–	–	–	–	–	–	35.7	42.9	CM	3.8	7.1	VA
Order: Squamata, Clade: Sauria																					
Trapelus mutabilis	–	–	–	–	–	–	0.8	5.3	VA	2.4	26.7	CM	–	–	–	14.3	57.1	CN	2.0	12.9	AC
Uromastyx acanthinurus	–	–	–	–	–	–	–	–	–	0.6	6.7	VA	–	–	–	–	–	–	0.2	1.4	VA
Chamaeleo chamaeleon	–	–	–	–	–	–	1.6	5.3	VA	1.2	13.3	AC	–	–	–	–	–	–	0.9	4.3	VA
Stenodactylus petrii	3.1	22.2	AC	–	–	–	–	–	–	1.2	6.7	VA	8.1	9.1	VA	–	–	–	1.5	5.7	VA
Cyrtopodion scabrum	–	–	–	–	–	–	0.8	5.3	VA	–	–	–	13.5	9.1	VA	–	–	–	1.3	2.9	VA
Acanthodactylus boskianus	–	–	–	7.1	22.2	AC	–	–	–	9.5	26.7	CM	–	–	–	–	–	–	4.0	8.6	VA
Acanthodactylus dumerilii	35.9	44.4	CM	10.7	11.1	AC	–	–	–	39.6	40.0	CM	–	–	–	–	–	–	20.5	15.7	AC
Acanthodactylus erythrurus	–	–	–	–	–	–	–	–	–	0.6	6.7	VA	–	–	–	–	–	–	0.2	1.4	VA
Acanthodactylus maculatus	1.6	11.1	AC	–	–	–	2.4	10.5	AC	3.6	6.7	VA	–	–	–	3.6	14.3	AC	2.4	7.1	VA
Acanthodactylus scutellatus	21.9	44.4	CM	10.7	11.1	AC	–	–	–	16.0	33.3	CM	–	–	–	–	–	–	9.7	14.3	AC
Mesalina guttulata	3.1	22.2	AC	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.4	2.9	VA
Mesalina olivieri	–	–	–	–	–	–	0.8	5.3	VA	–	–	–	–	–	–	–	–	–	0.2	1.4	VA
Tarentola deserti	–	–	–	–	–	–	7.9	26.3	CM	–	–	–	51.4	90.9	CN	–	–	–	6.4	21.4	AC
Tarentola mauritanica	9.4	11.1	AC	–	–	–	6.3	15.8	AC	–	–	–	–	–	–	–	–	–	3.1	5.7	VA
Tarentola neglecta	–	–	–	–	–	–	–	–	–	0.6	6.7	VA	18.9	27.3	CM	–	–	–	1.8	5.7	VA
Malpolon monspessulanus	–	–	–	7.1	22.2	AC	0.8	5.3	VA	–	–	–	–	–	–	–	–	–	0.7	4.3	VA
Chalcides boulengeri	–	–	–	–	–	–	0.8	5.3	VA	1.2	6.7	VA	–	–	–	–	–	–	0.7	2.9	VA
Chalcides ocellatus	12.5	11.1	AC	–	–	–	36.2	84.2	CN	8.3	33.3	CM	2.7	9.1	VA	–	–	–	15.2	32.9	CM
Scincus scincus	–	–	–	–	–	–	3.1	15.8	AC	–	–	–	–	–	–	–	–	–	0.9	4.3	VA

Order: Squamata, Clade: Ophidia																					
Hemorrhois algirus	–	–	–	3.6	11.1	AC	1.6	10.5	AC	–	–	–	–	–	–	–	–	–	0.7	4.3	VA
Spalerosophis diadema	1.6	11.1	AC	–	–	–	6.3	31.6	CM	3.6	26.7	CM	2.7	9.1	VA	–	–	–	3.5	17.1	AC
Lytorhynchus diadema	–	–	–	–	–	–	–	–	–	0.6	6.7	VA	–	–	–	–	–	–	0.2	1.4	VA
Natrix maura	–	–	–	–	–	–	1.6	5.3	VA	–	–	–	–	–	–	–	–	–	0.4	1.4	VA
Natrix natrix	–	–	–	–	–	–	0.8	5.3	VA	–	–	–	–	–	–	–	–	–	0.2	1.4	VA
Psammophis schokari	7.8	22.2	AC	17.9	33.3	CM	5.5	21.1	AC	5.3	40.0	CM	2.7	9.1	VA	–	–	–	6.0	22.9	AC
Rhagerhis moilensis	–	–	–	–	–	–	1.6	10.5	AC	–	–	–	–	–	–	–	–	–	0.4	2.9	VA
Varanus griseus	–	–	–	–	–	–	0.8	5.3	VA	1.8	13.3	AC	–	–	–	–	–	–	0.9	4.3	VA
Cerastes cerastes	3.1	22.2	AC	10.7	33.3	CM	4.7	26.3	CM	3.6	33.3	CM	–	–	–	–	–	–	3.8	21.4	AC
Echis leucogaster	–	–	–	–	–	–	–	–	–	0.6	6.7	VA	–	–	–	–	–	–	0.2	1.4	VA
Total	100			100			100			100			100			100			100		

RA: relative abundance, Occ: frequency of occurrence, OC: Occurrence categories, –: species absence, CN: constant species (Occ $\geq$ 50%), CM: common species (25% $\leq$ Occ < 50%), AC: accidental species (10% $\leq$ Occ < 25%), VA: very accidental species (Occ < 10%).

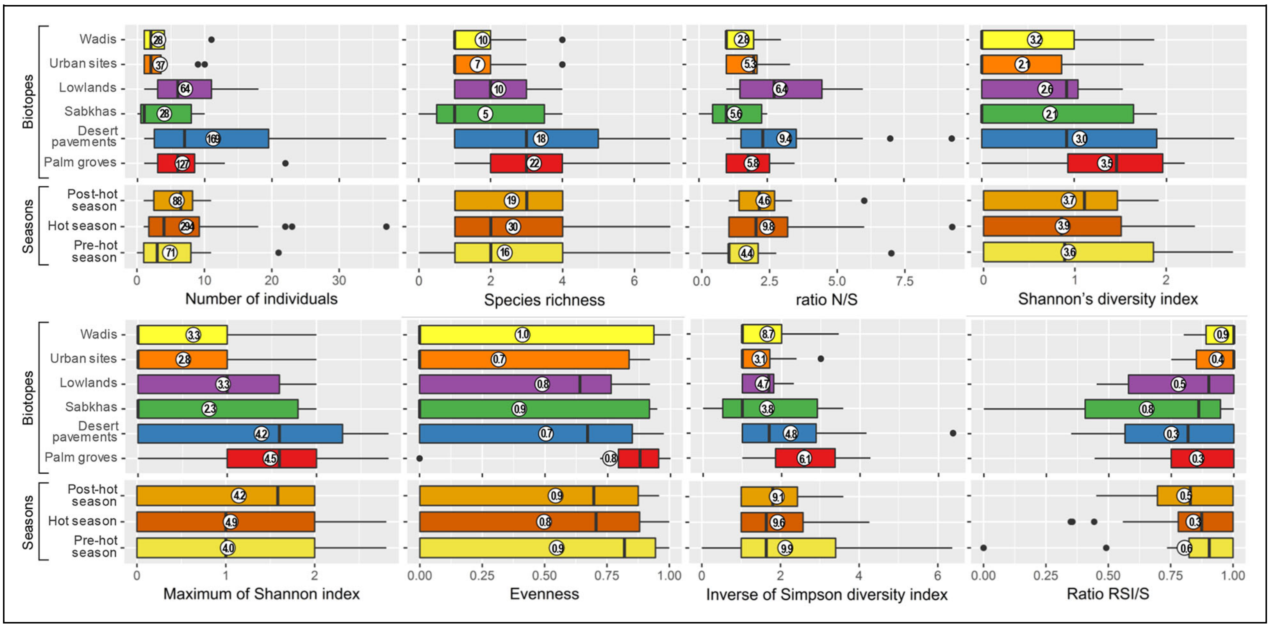

Figure 4. Diversity parameters of amphibian and reptile communities following seasons and type of biotopes in Sahara Desert of Algeria. White dots indicate the mean of observed data plotted in the boxplot (sample-based data), whereas the values displayed in white circles represent averaged estimates of each index for the pooled sample data per season or biotope. Solid black circle are outliers.

Table 3. Generalized linear models (GLMs) testing the variation of diversity parameters of amphibians and reptiles between biotopes and seasons in the Sahara Desert of Algeria

		N		*S*		*N/S*		*H*	
Variables	***df***	χ^2	***P* value**	χ^2	***P* value**	***F***	***P* value**	***F***	***P* value**
BT	5	92.23	<0.001	15.05	0.010	2.39	0.050	2.28	0.060
SN	2	13.69	<0.001	0.15	0.929	1.24	0.298	0.06	0.939
BT × SN	9	40.41	<0.001	6.57	0.682	0.52	0.852	0.46	0.893
		H_{max}		*E*		SRI		SRI/*S*	
Variables	***df***	***F***	***P* value**	***F***	***P* value**	***F***	***P* value**	***F***	***P* value**
BT	5	2.33	0.055	1.88	0.113	2.24	0.063	3.12	0.015
SN	2	0.02	0.981	0.19	0.825	0.46	0.632	0.39	0.679
BT × SN	9	0.54	0.842	0.76	0.649	0.45	0.901	1.13	0.359

Poisson (*type-II* likelihood ratio tests "χ^2"), Gaussian, and quasibinomial (type-II *F* tests) GLMs were implemented using sample-based data. BT = Biotopes; SN = Seasons.

Values of the *N/S* ratio were higher in the Reg (3.1 ± 2.5 individuals/species) and the lowest in Sabkhas (1.3 ± 1.1 individuals/species) during the pre-hot season (1.6 ± 1.5 individuals/species). Shannon's index revealed higher diversity in palm groves with $H = 3.5$, which was quite similar to diversity recorded in wadis ($H = 3.2$) during the hot season ($H = 3.9$). Moreover, the maximum diversity varied between 2.3 (in Sabkhas) and 4.5 (in palm groves). Evenness varied between 0.7 and 0.9 in study biotopes; and from 0.8 to 0.9 between the seasons. The SRI ranged between 1.4 ± 07 noted in urban sites and 2.6 ± 1.1 in palm groves. Overall, SRI averaged values that ranged between 1.9 ± 0.9 and 2.6 ± 1.1 (**Figure 4**).

According to the GLMs testing the spatio-seasonal variations of diversity parameters of amphibians and reptiles (**Table 3**), number of individuals "*N*" ($P < 0.001$), species richness "*S*" ($P = 0.010$), the ratio *N/S* ($P = 0.050$), and SRI/S ($P = 0.015$) varied significantly between study biotopes. Only *N* showed a significant variation between seasons ($P < 0.001$) and for the interaction "Biotopes × Seasons" ($P < 0.001$). For the rest of diversity parameters, there was no statistically significant difference ($P > 0.05$).

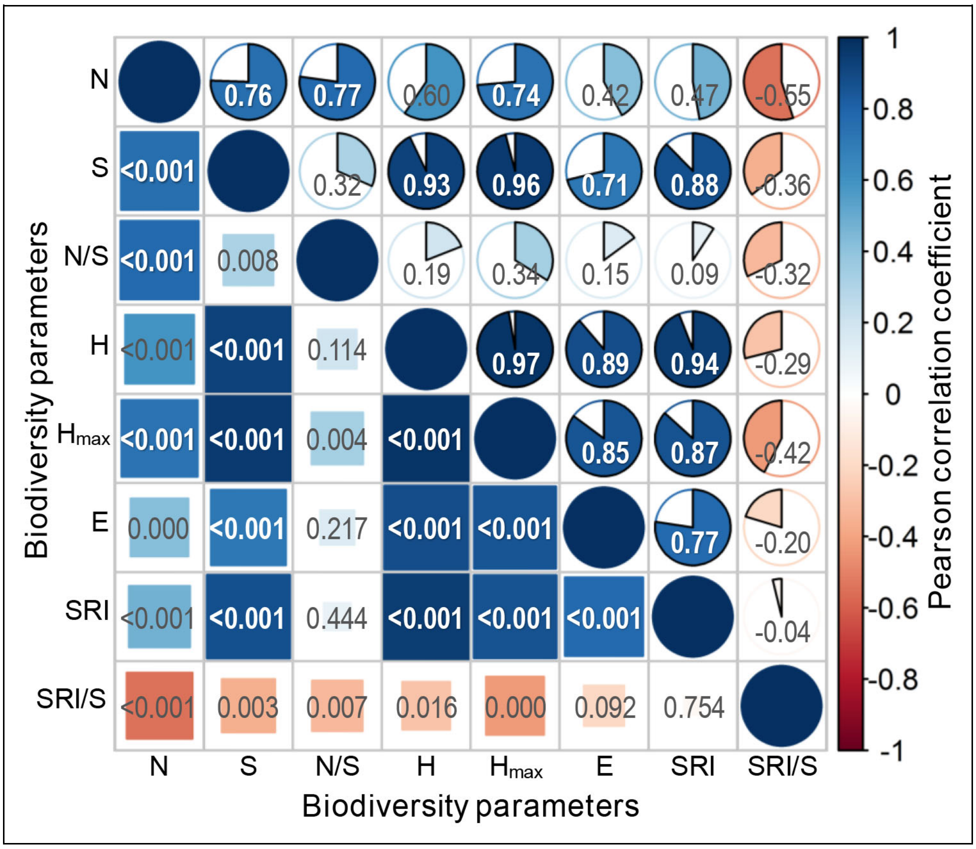

Figure 5. Matrix of correlations between diversity parameters of reptile and amphibian communities sampled in the Sahara Desert of Algeria (see the section "*2.4.2. Diversity parameters*" for abbreviations of biodiversity parameter). Pearson correlation tests are expressed as correlation coefficients (shown by color, intensity of shading in squares and pie charts, and values above diagonal) and *P* values (under diagonal).

All the interrelationships tested between diversity parameters showed positive correlations, except for those with the ratio SRI/*S* (**Figure 5**). Out of 28 correlation tests, 24 were statistically significant ($P \leq 0.05$), where 62% of the positive correlations showed strong corrections with Pearson coefficient values r >0.7. High correlation values (r > 0.5, P < 0.001) were observed between *N*, *S*, *H*, *E*, and between SRI and the rest of diversity parameters.

3.4. Species richness estimation and interpolation

The application of species richness asymptotic estimators Chao2 "$S_{(\text{Chao2})}$" and first-order Jackknife "$S_{(\text{Jack1})}$" showed that the expected species richness was higher than the observed richness in all biotopes studied and the whole region of Oued Righ (**Figure 6**). Estimates of species richness obtained using these 2 estimators showed much higher values in urban sites ($S_{(\text{Chao2})} = 11.5 \pm 6.4$ species, $S_{(\text{Jack1})} = 9.6 \pm 2$ species), palm groves ($S_{(\text{Chao2})} = 44.7 \pm 4.2$ species, $S_{(\text{Jack1})} = 33.4 \pm 3.4$species), Reg ($S_{(\text{Chao2})} = 26.7 \pm 8.3$ species, $S_{(\text{Jack1})} = 25.5 \pm 2.7$ species), and wadi ($S_{(\text{Chao2})} = 14.4 \pm 5$ species, $S_{(\text{Jack1})} = 15.3 \pm 3$ species) with respect to the slight increases of species richness expected in Sabkhas ($S_{(\text{Chao2})} = 5 \pm 0.2$ species, $S_{(\text{Jack1})} = 5.9 \pm 0.9$ species) and lowlands ($S_{(\text{Chao2})} = 11.1 \pm 1.7$ species, $S_{(\text{Jack1})} = 13.6 \pm 1.9$ species). Moreover, according to the Chao2 estimator, inventory completeness was 69.4% in wadis, 67.4% in Reg, 49.2% in palm groves, and 52.4% in urban sites. While the highest values of inventory completeness were 100% and 90.3% noted in Sabkhas and lowlands, respectively (Supplemental Table 4). According to the first-order Jackknife estimator, completeness was slightly lower in these latter 2 biotopes (85.3% and 73.7%, respectively) compared to Chao2, since the latter estimator takes into account duplicates in species richness estimates in addition to unique. The pattern of the estimated species richness obtained using the 2 estimators relative to the observed richness is similar and is due mainly to the frequency of appearance of unique and duplicate species with the increase of the sample size in the rarefaction curves. For the whole study area, the species richness is estimated at $S_{(\text{Chao2})} = 36.1 \pm 4.3$ species and $S_{(\text{Jack1})} = 38.9 \pm 2.9$ species, which indicated respectively an inventory completeness of 88.6% and 82.3% compared to the observed species richness ($S_{\text{est}} = 32 \pm 2.3$ species) (**Figure 6**, Supplemental Table 4).

Projected values of amphibian and reptile species richness "S_{est}" obtained with the extrapolation curves revealed that S_{est} substantially increased with the increase of number of samples in palm groves, desert pavement "Reg," wadis, and urban sites. At a size of 100 samples in each biotope, S_{est} was expected to increase by 110.5%, 78.8%, 80%, and 90.7% in palm groves, desert pavement "Reg," wadis, and urban sites, respectively, to reach up 46.3 ± 15.1, 32.2 ± 12.8, 18 ± 8.7, and 11.4 ± 5.7 species, with

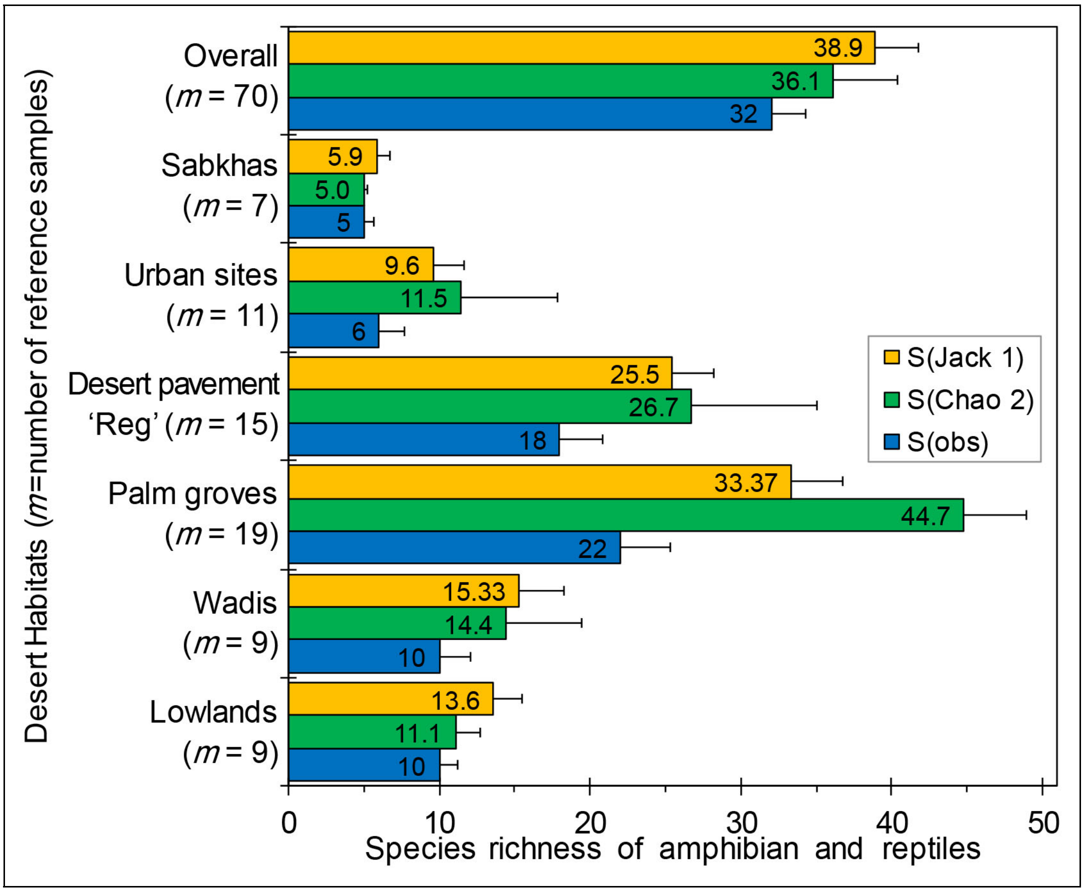

Figure 6. Observed "$S_{(obs)}$" and estimated species richness (using the asymptotic richness estimators: Chao2 "$S_{(Chao2)}$" and first-order Jackknife "$S_{(Jack1)}$") of amphibians and reptiles in different biotopes of the Sahara Desert of Algeria. Vertical bars represent standard deviations (SD).

total number of expected individuals of 668, 940, 311, 327.3 individuals, respectively (**Figure 7**). For 711 individuals expected in lowlands, S_{est} is predicted to record a moderate increase of 17.8%, resulting in a richness of 11.8 ± 2.4 species. Sabkhas were expected to have a species richness of 5.4 ± 1.1 species, a slight increase equivalent to 8.6% for a total of 400 individuals. For the entire region of Oued Righ, S_{est} was predicted to increase by 7.5% to reach 34.4 ± 2.6 species (CI: 29.2–39.5 species) with 647 individuals.

3.5. Spatial similarities of communities

The analysis of similarity revealed a difference in herpetological composition among the 6 biotopes surveyed (**Figure 8**). Large fluctuations in similarity values were noted, with the Jaccard qualitative index varying between 0% and 40%, while Sørensen qualitative index fluctuated between 0% and 57.1%. Overall, this indicates low similarities between the biotopes studied, since similarity values were higher than 50% in only 3.3% of the qualitative similarities comparisons and 13.3% of the quantitative similarities (**Table 4**). The highest quantitative similarity in species composition was recorded between lowlands and desert pavements (Morisita-Horn index = 93.2%), urban sites and palm groves (Chao-Sørensen index = 88.7%), desert pavements and wadis (Chao-Sørensen index = 64.5%), and between lowlands and wadis (Chao-Sørensen index = 57.9%). No similarity was detected between the herpetofauna of urban sites and Sabkhas, revealing completely different assemblages (**Table 4**, **Figure 8**). Quantitatively, the highest similarities were marked between lowlands and Regs, palm groves and urban sites; wadis and palm groves, and lowlands and wadis (**Table 4**).

The clustering analysis of species abundances based on Bray-Curtis distance confirmed the patterns of spatial similarity. It demonstrated that (i) the mesic biotopes, that is, Sabkhas, wadis, and palm groves have similar herpetofaunal community composition, where species of date palm groves and wadis within this cluster were closely similar; (ii) the xeric and natural biotopes that experience the least anthropogenic disturbance, that is, desert pavements and lowlands deserts were clustered as a group with homogenous herpetofaunal community; and (iii) highly disturbed and man-made biotopes namely urban sites had a unique composition of reptiles and amphibians (**Figure 9**). The main characteristic species of urban sites were *Stenodactylus petrii*, *Cyrtopodion scabrum*, *Tarentola deserti*, and *T. neglecta*. The species that characterized Sabkhas were *Bufotes boulengeri*, *Discoglossus pictus*, *Pelophylax saharicus*, and *Spalerosophis diadema*. In lowlands, *Acanthodactylus boskianus*, *A. dumerilii*, *A. maculatus*, *A. scutellatus*, *Psammophis schokari*, *Tarentola mauritanica*, *Chalcides ocellatus*, and *Cerastes cerastes* were the main typical species. Besides species of lowlands, the species *Uromastix*

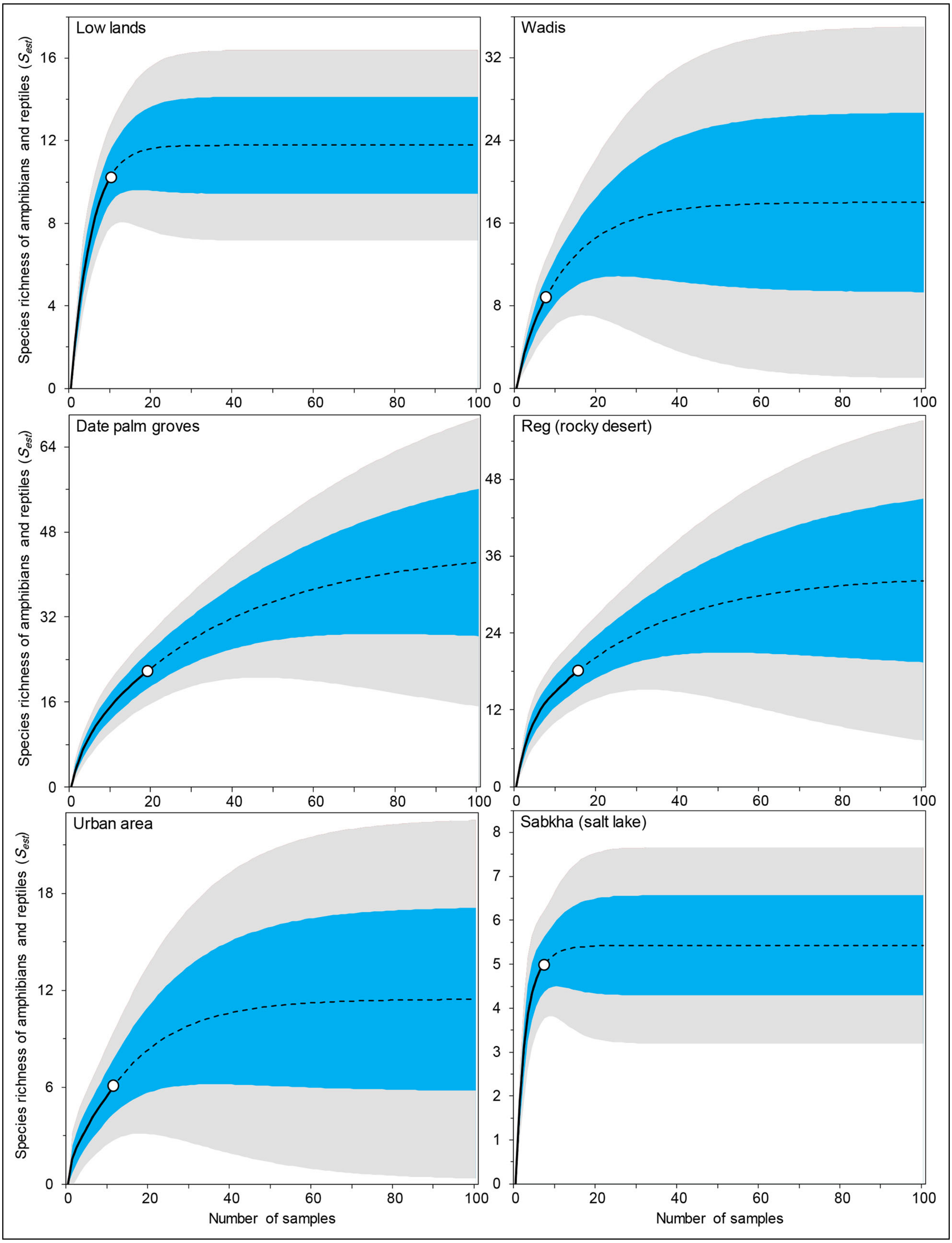

Figure 7. Sample-based rarefaction (solid line) and extrapolation (dashed line) curves of species richness estimated for amphibian and reptile communities living in the Sahara Desert of Algeria. White solid circles indicate $S_{(est)}$ obtained for the reference samples. Light grey shaded areas represent lower and upper bounds of 95% confidence interval for the $S_{(est)}$. Colored-shaded areas indicate ± SDs.

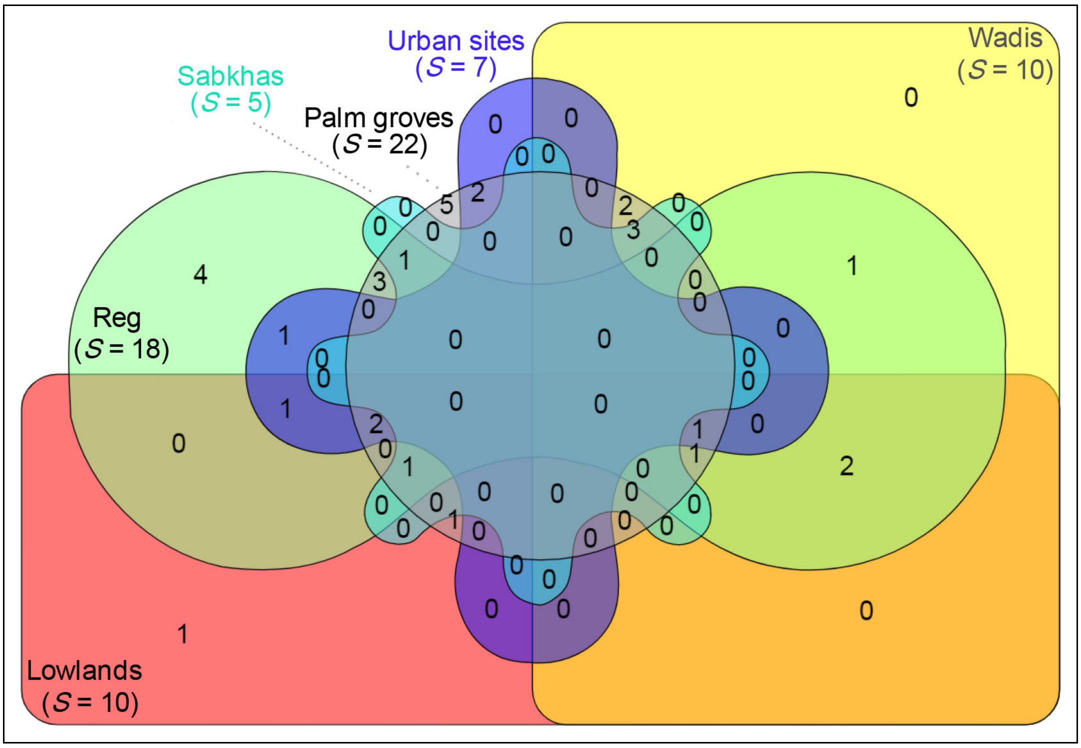

Figure 8. Six-set Venn diagram displaying amphibian and reptile species recorded in various biotopes of the Sahara Desert of Algeria.

Table 4. Qualitative and abundance-based similarities of amphibian and reptile communities between 6 study biotopes (LL: lowlands, WD: wadis, PG: palm groves, DP: desert pavements "Reg," US: urban sites, SK: Sabkhas) in the Sahara Desert of Algeria

	Similarity Estimates														
First Biotope	**LL**	**LL**	**LL**	**LL**	**LL**	**WD**	**WD**	**WD**	**WD**	**PG**	**PG**	**PG**	**DP**	**DP**	**US**
Similarity indices Second biotope	WD	PG	DP	US	SK	PG	DP	US	SK	DP	US	SK	US	SK	SK
Species richness observed in 1st biotope	10	10	10	10	10	10	10	10	10	22	22	22	18	18	7
Species richness observed in 2nd biotope	10	22	18	7	4	22	18	7	4	18	7	4	7	4	4
Shared species observed	4	6	8	4	1	7	5	1	2	9	5	4	5	2	0
Chao shared estimated	4.0	7.4	10.1	24.7	1.3	7.6	5.0	1.0	2.0	11.1	6.0	4.9	52.3	3.0	0.0
Jaccard qualitative index	25.0	23.1	40.0	30.8	7.7	28.0	21.7	6.3	16.7	29.0	20.8	18.2	25.0	10.0	0.0
Sørensen qualitative index	40.0	37.5	57.1	47.1	14.3	43.8	35.7	11.8	28.6	45.0	34.5	30.8	40.0	18.2	0.0
Chao-Jaccard-raw abundance-based	40.7	29.3	72.7	10.9	1.2	25.5	47.6	2.4	17.0	25.4	46.9	10.2	14.0	4.9	0.0
Chao-Jaccard-est. abundance-based	40.7	31.1	75.4	15.5	1.7	26.2	47.6	2.5	17.0	30.5	79.7	11.4	28.4	6.0	0.0
Chao-Sørensen-raw abundance-based	57.9	45.3	84.2	19.7	2.3	40.6	64.5	4.7	29.1	40.5	63.8	18.6	24.6	9.3	0.0
Chao-Sørensen-est. abundance-based	57.9	47.5	86.0	26.8	3.4	41.5	64.5	4.9	29.1	46.8	88.7	20.4	44.3	11.3	0.0
Morisita-Horn index	48.7	31.1	93.2	3.1	0.2	24.8	49.6	2.2	31.3	20.7	22.2	11.8	2.5	2.1	0.0
Bray-Curtis index	28.3	24.1	48.1	9.9	2.3	24.5	16.2	3.1	19.6	27.7	17.1	14.7	5.8	5.2	0.0

Chao-Jaccard and Chao-Sørensen indices are abundance-based indices (Chao et al., 2005).

acanthinurus, *Lytorhynchus diadema*, *Acanthodactylus erythrurus*, and *Echis leucogaster* were specific to desert pavements "Reg." The wadis included chiefly characteristic species of Sabkhas and lowlands. While the palm groves have common characteristic species with Sabkha, wadis, urban sites, Reg, and lowlands, in addition to *Bufotes*

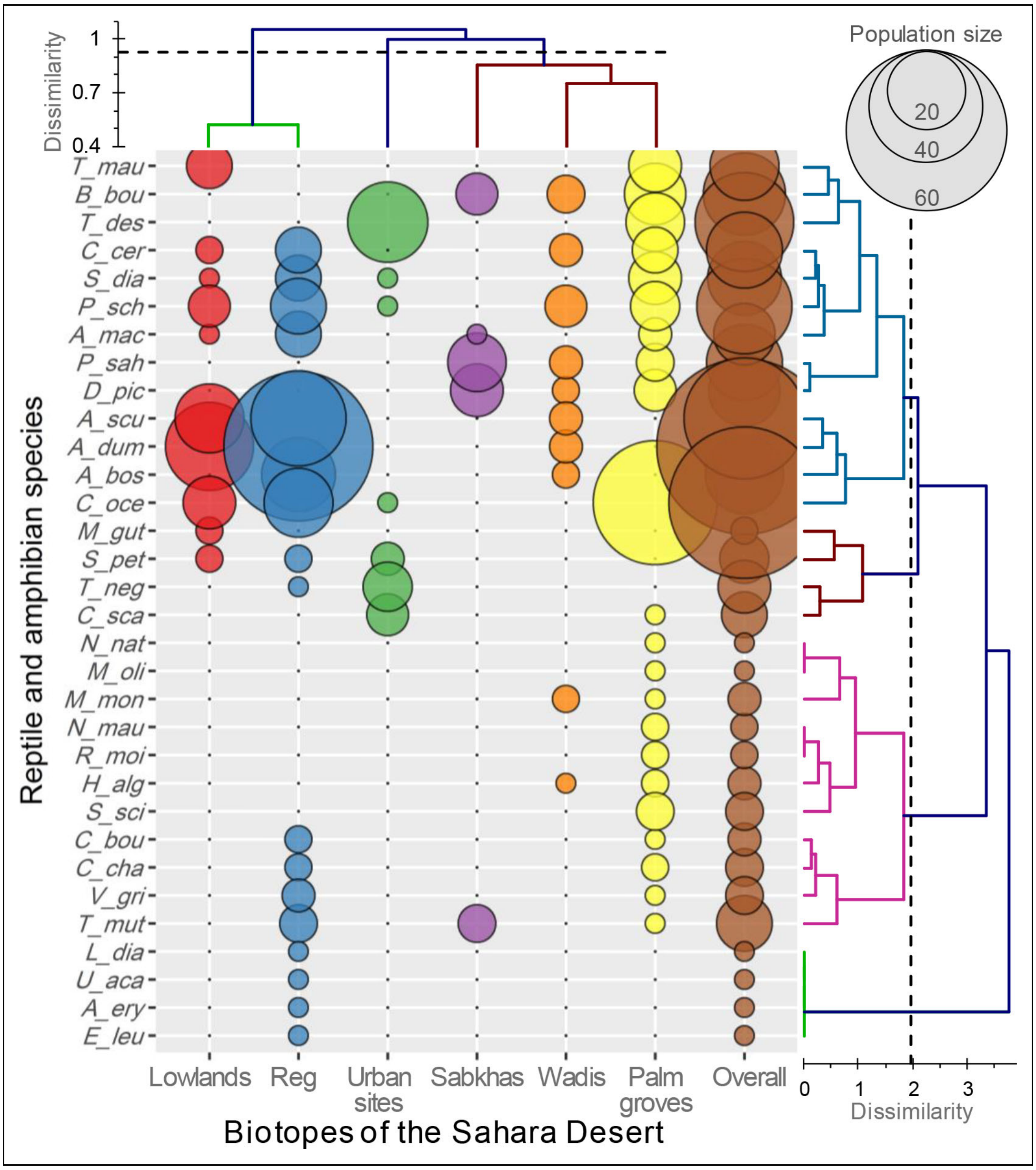

Figure 9. Two-way cluster analysis of amphibian and reptile assemblages in the Sahara Desert of Algeria. Clustering follows Ward's method using Bray-Curtis dissimilarity index based on species abundances which are proportional to circle sizes. Species abbreviations are given as first letter of genus followed by 3 first letter of species (full scientific names and specific relative abundances per biotope are provided in **Table 1** and **Table 2**, respectively).

boulengeri, *Trapelus mutabilis*, *Chamaeleo chamaeleon*, *Hemorrhois algirus*, *Mesalina olivieri*, *Rhagerhis moilensis*, *Natrix maura*, *N. natrix*, *Malpolon monspessulanus*, *Chalcides boulengeri*, *Scincus scincus*, and *Varanus griseus* which were clustered as a unique group on the vertical clustering analysis (**Figure 9**).

4. Discussion

Biogeographically, the dominance of the Saharan species in Oued Righ indicates that this region represents a transition between the Oriental Erg and the Saharan plateau, where the Oued Righ Valley is actually located. According to Chenchouni (2010), the Oued Righ Valley is located between the oriental Grand Erg in the east and the M'Zab Plateau in the west. This transition zone notably influences ecological connectivities and consequently the distribution of vertebrate species including amphibians and reptiles (Chenchouni, 2012a; Chaibi et al., 2015; Mouane, 2020; Chedad et al., 2021). The biogeographic distribution of animals depends strongly on the environmental parameters and presents in particular strong associations with climatic factors (Brito et al., 1999; Teixeira et al., 2001). Anthropogenic activities occasionally disrupt the biogeographic distribution of vertebrate species, altering ecological connectivities (Chaibi et al., 2012). From a biogeographic point of view, we note the dominance of Saharan and Saharo-Sindian CC with 45% and 35%, respectively (Mouane et al., 2013).

The Mediterranean CC are in second position, which indicates that the biogeographic position of the Oued Righ Region, although located within the Sahara Desert, is linked to the Mediterranean zone and more generally the Palearctic realm (Chenchouni, 2010). The abundance of Mediterranean CC is a good indicator of the specific ecological conditions prevailing in the palm groves of the region which constitute mosaic and scattered micro biotopes with a microclimate offering favorable ecological conditions for the establishment and adaptation of several nondesert species (Guezoul et al., 2013). According to Karmaoui (2015), the structure of vegetation within palm oases, especially the number of strata and vegetation complexity of each stratum, influences climatic factors. Thus, a dense palm grove with an upper stratum of date palms and a canopy with total cover and intermediate layers of trees and/or shrubs constitute an underlying mesoclimate that influences both the vegetation and animals of the palm grove (Guezoul et al., 2013; Mihi et al., 2019). Date palm trees and grove create good habitats, microhabitats, and microclimates for sheltering high number of both vertebrate and invertebrate preys of herpetofauna.

With the capture of 453 individuals belonging to 32 species (3 amphibians and 29 reptiles), the herpetofauna of the Septentrional Sahara is composed mainly of 19 Saurian species, of which 17 species are insectivorous. The majority of lizards feed on insects, mainly beetles, ants, termites, grasshoppers, and flies (Dipetra) (Le Berre, 1989; Schleich et al., 1996; Kalboussi, 2006). Carnivores ranked second with 11 species. Almost all species in this category belong to the Ophidian sub-order. These species feed primarily on lizards and small mammals especially rodents (Gruber, 1992; Trape and Mane, 2006). Among the reptiles reported in the different biotopes, the Ocellated Skink (*Chalcides ocellatus*) was the most abundant (RA = 36.2%) in the palm groves. According to Le Berre (1989), this species frequents a large variety of environments, including wadi beds and palm groves. Indeed, the species thrives in palm groves where it finds optimal ecological conditions (mainly adequate structure of understorey vegetation) for its survival and development.

With 3.4 and 3.2 species/sample, the highest values of mean species richness were observed in the Reg and palm groves, respectively, whereas the lowest value was recorded in urban sites with 1.6 species/sample. This explains why the date palm grove is the richest biotope in terms of species as it represents a favorable ecosystem for the life of reptiles and amphibians. On the other hand, urban sites are a less suitable environment for several species, especially amphibians. Vallan (2002) states that the richness of herpetofauna is connected to the intricate structure of the habitat. In a similar vein, palm groves stand out due to the existence of various elements like soil, crops, vegetation, and water, which combine to create a favorable ecological environment conducive to the establishment of diverse herpetofauna. Within these ecological conditions, there is an abundance of food, habitat structures that enhance predator avoidance, resting spots, and ample reproductive opportunities, among other factors (Srinivasulu and Das, 2008; Hamer and Mcdonnell, 2010; Banville and Bateman, 2012). According to the Shannon diversity index, palm groves have the most diversified herpetofaunal communities. The findings of this survey are in agreement with results of Mouane (2010) who indicated that the highest value of diversity belong to palm groves with Shannon index = 3.06 and evenness = 0.76; which implies that the organization and structure of the assemblage is balanced in this type of biotope.

In Sabkhas, the most abundant class is amphibians with 82.1% of total species, of which *Bufotes boulengeri* was the most abundant (35.7%). According to Le Berre (1989), this species prefers slightly salty waters. Almost the majority of species found in urban sites belong to the family Phyllodactylidae with 69.2% of total species. Species of this family are synanthropic and colonize in particular urban areas especially the old agglomerations. For example, the Desert wall gecko (*Tarentola deserti*) is frequent rocky cliffs, piles of stones, old walls, house ceilings, tree trunks, ruins, and woods (Le Berre, 1989; Schleich et al., 1996).

The highest species richness in the region of Oued Righ was noted in date palm groves, then in desert pavements "Reg," lowlands and wadis. According to Ouel El Hadj (2006), the palm grove represents a biotope with high diversity of flora and fauna. In addition, the presence of a diffuse plant cover in palm groves has a positive effect on the abundance of insects, which are the main food resource of several reptiles (Mouane, 2010; Mebarki, 2012). Urban sites come last in terms of species richness due to high human disturbances.

The highest values of similarity are reported between the lowlands and Regs and between wadis and palm groves. This can be explained by the relatively similar ecological conditions in these biotopes, in particular humidity, soil properties, vegetation, and so on. According to Chenchouni (2017a), all the physical and chemical properties of the soil come within the term of edaphic factors that influence various bioecological parameters of living beings, notably distribution and zonation along gradients of soil parameters. The common species between the 2 biotopes "lowlands and Regs" include *Acanthodactylus boskianus*, *Acanthodactylus maculatus*, *Acanthodactylus scutellatus*, *Cerastes cerastes*, *Chalcides ocellatus*, *Psammophis schokari*, *Spalerosophis diadema*, and *Stenodactylus petrii*. According to Gauthier (1967) and Le Berre (1989), *Acanthodactylus scutellatus* characterizes sandy habitats such as desert dunes, ergs, sandy beaches, and also frequents stony areas with diffuse vegetation. The species *Cerastes cerastes* frequents a wide variety of environments namely Hammada, Daya, Reg, rocky scree, wadi beds, and dunes. *Psammophis schokari* is found in different landscapes like Djebels, Dayas, Reg, Hammadas, and more rarely in Erg and dunes. *Spalerosophis diadema* occurrence is specific to stony and/or rocky arid biotopes.

This study reported the presence of the rough-tailed gecko (*Cyrtopodion scabrum*) in North and West Africa (except Egypt). See Mouane et al. (2021) for more details about the discovery of this species in Algeria. We speculate that the species might were introduced to Algeria through the transportation of some individuals as stowaways in vehicles as it is a synurbic species. During the last decade (personal observations: unpublished), we observed decline trends of *Tarentola* species in the study area and this may be related to the introduction of *C. scabrum*, hence, it should be closely monitored in future studies to assess its status as an invasive species in Algeria. Actually, the discovery of *C. scabrum* in Algeria might also be explained by the absence of exhaustive herpetological investigations devoted to the Sahara Desert. That is why it is necessary to explore other regions and habitats of this large ecoregion to understand community diversity and species distributional ranges (Chaibi et al., 2012; Mouane, 2020).

5. Conclusion

The study investigated the amphibian and reptile diversity in 6 biotopes of the Oued Righ region. It provided valuable information about the species composition, diversity, and distribution of amphibians and reptiles in the studied biotopes. A total of 32 species were identified, including 3 amphibians, 19 lizards, and 10 snakes. Most species were classified as "Least Concern" by the IUCN Red List, except for the North African spiny-tailed lizard, which was listed as "Near Threatened." Several species had protection status in Algeria, and 8 species were endemic to the Mediterranean region. Insectivores were the dominant dietary category, followed by carnivores. The spatial distribution of species varied across the biotopes, with the Mediterranean CC being dominant in some habitats. The abundance and occurrence frequencies of species differed among the biotopes, and the diversity parameters showed seasonal and spatial variations. Species richness estimators indicated higher expected richness than observed, and projected values suggested increased richness with larger sample sizes in specific biotopes. The similarities in species composition among the biotopes were generally low, except for certain pairs. The study highlights the presence of endemic and threatened species and provides insights into their ecological preferences and spatial patterns. Further research and conservation efforts are needed to better understand and protect the herpetofauna in the Sahara Desert.

Considering the protected and endemic statuses of certain species and the rarity of others, effective conservation measures and policy-making actions are required for amphibians and reptiles in the Septentrional Sahara region. It is imperative to establish strict regulations or outright bans on capturing, handling, exporting, and selling these animals. In the short term, the primary focus should be on diligently safeguarding the habitats that provide shelter to these species. Such habitat protection efforts necessitate collaboration with environmental protection organizations and active engagement with local communities. It is crucial to raise awareness among the local populations about the significance of biodiversity, even when it comes to reptiles and amphibians, as they are often perceived as unappreciated creatures.

Data accessibility statement

The raw dataset of total abundance, chorological categories, and diet profile of amphibian and reptile species identified at different biotopes and landscapes (lowlands, Wadis, palm groves, Reg, urban sites, and Sabkha) and seasons (pre-hot season, hot season, and post-hot season) in the region of Oued Righ Valley (Algeria) is available at https://doi.org/10.6084/m9.figshare.24993318.

Supplemental files

The supplemental files for this article can be found as follows:

See Tables S1–S4 attached as Supplementary Material.

Funding

This study was not funded by any source.

Competing interests

The authors declare that they have no competing interest.

Author contributions

Contributed to conception and design: AM, MS.

Contributed to acquisition of data: AM, AH, IG.

Contributed to analysis and interpretation of data: HC.

Drafted and/or revised the article: HC, AM.

Approved the submitted version for publication: AM, AH, IG, MS, HC.

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How to cite this article: Mouane, A, Harrouchi, A, Ghennoum, I, Sekour, M, Chenchouni, H. 2024. Amphibian and reptile diversity in natural landscapes and human-modified habitats of the Sahara Desert of Algeria: A better understanding of biodiversity to improve conservation. *Elementa: Science of the Anthropocene* 12(1). DOI: https://doi.org/10.1525/elementa.2022.00106

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Knowledge Domain: Ecology and Earth Systems

Published: March 06, 2024 **Accepted:** December 19, 2023 **Submitted:** August 17, 2022