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## Research Article

## Biogeography and conservation of mammals from the West Sahara-Sahel: an application of ecological niche-based models and GIS

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## Abstract

The West Sahara-Sahel is a remote region where knowledge gaps on mammal distribution have hampered accurate local biodiversity assessments and the development of optimised conservation planning in the region. Using a geographical information system and ecological niche-based modelling tools, this study combines high resolution presence data from 22 mammals and environmental factors from the West Sahara-Sahel to identify suitable areas for mammal occurrence, biogeographic affinities among taxa, and local hotspots of species richness. The maximum entropy approach was used to relate environmental factors with mammal distributions and to predict suitable areas of species' occurrence. Biogeographic groups were defined based on the spatial similarities of predicted distributions. Ecological niches of analysed taxa were summarized through Principal Components Analyses based on topoclimatic and habitat variables. Distributions of most mammals were related with climate and/or habitat features, and some were associated with topography. Suitable areas were predicted mostly within known distributions of mammalian taxa. Low values of niche breadth were estimated for all taxa, indicating a tendency for specialization in the study area. Shared distributional ranges among taxa allowed the identification of five groups with different biogeographic affinities. Most groups occurred in the ecoregions North Saharan steppe and woodlands and Sahelian Acacia savanna, reflecting their availability and stressing the importance of these ecoregions for local mammal conservation. Predicted suitable areas were poorly represented in the current network of protected areas, especially in Mauritania. The southern Mauritanian mountains contained suitable habitat for most of the studied mammals, but are largely unprotected. The fine scale ecological niche-based models built with high resolution data can be used to identify key-areas for conservation and management, and could be applied to other remote regions and taxonomic groups worldwide.

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## Introduction

Global biodiversity loss is a major concern for humanity, given its crucial role for ecosystem services (Butchart et al., 2010; Cardinale et al., 2012). The strategic goals of the Aichi Biodiversity Targets (CBD, 2010) listed key-targets to halt biodiversity loss by 2020. Among targets are the global identification of priority areas for conservation and the evaluation of the effectiveness of current protected areas. To achieve them, accurate knowledge about biodiversity distribution is needed and spatial mapping at high-resolution is particularly crucial to optimize conservation planning (Ferrier et al., 2002).

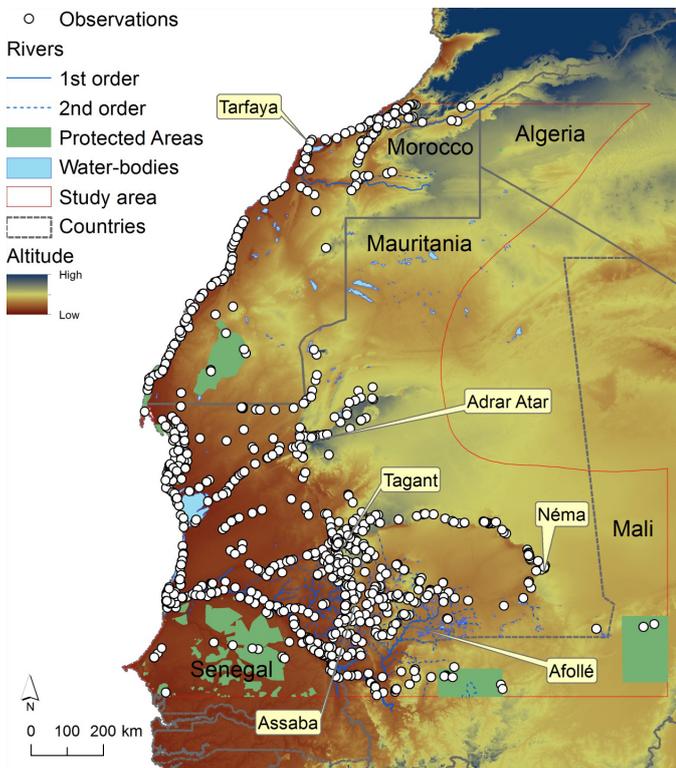
Deserts and arid regions (aridity index <0.20; Ward, 2009) are generally perceived as homogeneous and species-poor (Durant et al., 2014). However, they contain about 25% of terrestrial vertebrate species (Mace et al., 2005), provide local biodiversity hotspots, and harbour many endemic species with unique adaptations to extreme environmental conditions (Murphy et al., 2012; Wilson and Pitts, 2012). The West Sahara-Sahel of Africa covers twelve ecoregions (Olson et al., 2001) from coastal sandy beaches to inland mountain areas (Fig. 1).

The dramatic climatic oscillations affecting the region since the Pliocene (5.3 Mya) have caused multiple dry-wet cycles (Le Houérou, 1997) and are hypothesised to shape present-day biodiversity patterns (Brito et al., 2014). Local biodiversity hotspots have been identified in mountain rock pools (locally known as gueltas), where isolated refugial populations of Afro-tropical taxa are found (Vale et al., 2015a). Parts of the region have been identified as priority areas for the conservation of Sahara-Sahel endemics, but coverage by the current network of protected areas is low (Brito et al., 2016). In general, knowledge about biodiversity distribution in West Sahara-Sahel is scarce, in comparison with other regions (Brito et al., 2014; Durant et al., 2014). The history of conflicts since mid-1970s combined with general remoteness (Brito et al., 2014) have hampered biodiversity assessments and consequently, optimised conservation planning in the region is still underdeveloped.

Mammals are a diverse group of animals that show particular adaptations to arid environments (Ward, 2009). Although 105 mammals have been described in West Sahara-Sahel (IUCN, 2015), knowledge on their distribution is poor. Some regions have been relatively well sampled, such as the lower Drâa river valley (Cuzin, 2003; LeDauphin, 2005) or coastal Mauritania (Granjon et al., 1997, 2002), but available distribution data from inland and remote areas is scarce and displays

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**Figure 1** – Distribution of 1156 observations of mammals in the West Sahara-Sahel, used to develop ecological niche-based models.

coarse resolution (e.g. Sevenet, 1943; Dekeyser and Villiers, 1956; Poulet, 1970, 1974). Over the last decade, opportunistic data started to be collected mostly along coastal areas (Bergier et al., 2010, 2011; Chevalier et al., 2012; Moutinho et al., 2015) and in inland mountains of Mauritania (Padial and Tellería, 2009; Boratyński et al., 2013; Vale et al., 2015a). For Mauritania, comprehensive distribution data has been compiled (Padial and Ibáñez, 2005) and further complemented with recent observations (Brito et al., 2010). However, high spatial resolution distribution data (e.g.: 1×1 km) is mostly unavailable (but see Brito et al., 2010; Boratyński et al., 2013). The identification of environmental factors related to mammal distribution and the determination of biogeographic patterns derived from ecological niche-based models (ENM) have been performed solely for canids (Brito et al., 2009), an endemic gundi (Vale et al., 2012) and the Guinean baboon (Vale et al., 2015b). Mauritanian populations of patas monkeys and rock hyraxes were also accessed for ecological niche differences in comparison to global populations (Vale et al., 2014). These works highlighted the importance of using high-resolution distribution data in the development of local ENMs. Given that accurate spatial resolution improves future conservation planning, these approaches should be extended to other taxa in the region.

This work explored the usefulness of geographical information systems (GIS) and ENMs built with high resolution data to accurately derive data for the conservation of mammal biodiversity. It combined high precision observations from 22 mammals, which are representative of the West Sahara-Sahel ecoregions (including the endemic species, *Felovia vae*; Tab. 1), with a series of environmental factors to answer the following questions: 1) which environmental factors are most related with species occurrence? 2) Where are probable areas for species occurrence located? 3) How many biogeographic groups can be found and how wide is their ecological niche breadth? 4) Where are located hotspots of species richness? and 5) what is the level of coverage of species distribution by the current network of protected areas? This work aims to update the current knowledge on the distribution of selected mammals in West Sahara-Sahel and to improve their conservation. It is also aimed at providing a case-study for the application of

GIS and ENMs to the biogeography and conservation of mammals that can be applied in other regions of the world.

## Materials and methods

### Study area and fieldwork

The study area is located in the West Sahara-Sahel and comprises southern Morocco, Mauritania, northern Senegal, and south-western Mali (Fig. 1). Limits were set to include all observations and sampled ecoregions.

Sixteen overland expeditions to southern Morocco and Mauritania were performed between 2001 and 2015 for collecting species distribution data. The expeditions were carried out annually from September to December, except in 2009 (March-May) and 2015 (August-September), resulting in a total of 639 work/days, and about 130,000 km covered (Fig. S1). Sampling was performed by two to nine persons (average by expedition: 5.4 persons), using distinct types of field methods: 1) sampling along roads for run-over specimens; 2) random walks during the daytime and after sunset searching for presence signs (e.g. burrows, faces, howling, spines); 3) trapping for small-mammals, performed after 2011, (total 3527 trap-nights; 24.32 traps/night); 4) camera-trapping, performed after 2011, on 95 localities with an average of 4.52 cameras/locality (ranged from 1 to 9 cameras/night); and 5) opportunistic observations (e.g. along road while driving). Overall, sampling was biased towards paved roads and main trails, protected areas (PN Banc d'Arguin and PN Diawling in Mauritania), and inland water-bodies.

### Distribution data

A total of 1395 observations (84% after 2008) were collected from 22 taxa (Fig. 1; Tab. S2). Observations were geo-referenced (with a Global Positioning System on the WGS84 datum). The identification of 18% of the observations (254 samples of *Aterix*, *Canis*, *Gazella*, *Paraechinus*, and *Vulpes*) was confirmed by molecular markers under the context of molecular-based studies being developed in the region (e.g. Koepfli et al., 2015; Leite et al., 2015; authors, unpub. data). About 79% are original observations while 21% have already been published (Brito et al., 2009, 2010; Moutinho et al., 2015). Although other observations were available for some taxa in the bibliography (e.g. Bergier et al., 2010, 2011; Chevalier et al., 2012, and other references mentioned in introduction), they were not considered here due to their coarse spatial resolution.

Multiple observations falling within 1×1 km grid cells were collapsed to a single record with resulting in 1156 observations being retained for analysis (Tab. 1). Spatial biases in the sampling effort and distinct species' detectability can bias ecological models (see Merow et al., 2013). For this reason, the degree of data clustering was assessed with the Nearest Neighbour Index (NNI), implemented in the "Spatial Analyst" extension of ArcGIS 10.0 (ESRI, 2011). The index indicated random to dispersed distributions for *D. braueri*, *G. dorcas*, *G. genetta*, *M. capensis*, and *P. africanus* (NNI>1.14), and some degree of clustering for the remaining taxa (0.37<NNI<0.86). In each taxon with clustered distributions, observations were randomly removed from clusters of taxon occurrence according to NNI and two data sets were built for each taxon: one for training and testing models and other for validation (Tab. 1).

### Environmental variables

Two sets of environmental factors or ecogeographical variables (hereafter EGVs) were selected for the ecological niche-based modelling according to the degree of coverage in the study area and their likely importance for the ecology and distribution of the taxa (Brito et al., 2009; Vale et al., 2012, 2014, 2015b). The topoclimatic set included five climate grids (Hijmans et al., 2005; Tab. 2) and one topographic grid (USGS, 2006) used to derive topographic ruggedness index (TRI) using the package "Raster" in R (Hijmans et al., 2015). The habitat set included five distances to habitats categories derived from a land-cover grid for the years 2004–2006 (Bicheron et al., 2008), and

**Table 1** – Total number of observations of each taxon collected during fieldwork (N-T), number of observations after removing duplicates from grid cells (N-NoD), number used for training (N train) and testing (N test) ecological models, and number included in the data set for validation (N Val).

Code	Taxa	N-T	N-NoD	NNI	p-value	N train-test	N Val
Aalb	<i>Atelerix albiventris</i>	25	23	1.36	0.01	15–1	6
Cant	<i>Canis anthus</i>	133	117	0.88	0.08	46–15	34
Dbra	<i>Desmodelliscus braueri</i>	15	11	1.31	0.05	9–1	
Epat	<i>Erythrocebus patas</i>	23	19	1.27	0.06	12–1	6
Fsly	<i>Felis silvestris lybica</i>	33	30	0.99	0.93	18–2	10
Fvae	<i>Felovia vae</i>	219	147	0.88	0.067	45–14	32
Gdor	<i>Gazella dorcas</i>	12	12	1.14	0.37	10–1	
Ggen	<i>Genetta genetta</i>	18	17	1.41	0.00	15–1	
Gger	<i>Gerbillus gerbillus</i>	25	25	0.98	0.85	16–1	8
Hcri	<i>Hystrix cristata</i>	26	26	1.09	0.48	17–1	8
Jacu	<i>Jaculus</i> spp.	172	155	0.89	0.09	48–16	33
Lepu	<i>Lepus</i> sp.	80	78	0.90	0.18	39–12	18
Mcap	<i>Mellivora capensis</i>	12	12	1.44	0.00	10–1	
Ppap	<i>Papio papio</i>	117	54	0.86	0.12	26–8	13
Paet	<i>Paraechinus aethiopicus</i>	61	59	1.75	0.00	30–10	14
Pafr	<i>Phacochoerus africanus</i>	15	14	1.74	0.00	12–1	
Pcap	<i>Procavia capensis</i>	61	51	0.77	0.02	23–7	21
Pobe	<i>Psammomys obesus</i>	29	29	0.80	0.27	16–4	9
Vpal	<i>Vulpes pallida</i>	69	63	0.86	0.07	34–11	18
Vrue	<i>Vulpes rueppellii</i>	63	44	1.05	0.56	27–8	9
Vzer	<i>Vulpes zerda</i>	69	57	0.83	0.05	27–8	16
Xery	<i>Xerus erythropus</i>	118	113	1.50	0.05	38–12	32
	Total	1395	1156				

distances to mountain rock pools (locally known as *gueltas*) and to permanent rivers, both digitized from the IGN maps and ground-validated in Mauritania by fieldwork (Vale et al., 2014, 2015b; Tab. 2). To convert the original categorical habitat EGVs into continuous variables, a binary grid was created for each habitat type. The Euclidean distance of each grid cell to the closest habitat type cell was calculated using the “Euclidean distance” tool in ArcGIS 10.0. All EGVs had 30” pixel size (~1 km). Most EGVs had correlation coefficients below 0.75, but two exceptions were allowed between: Bio5 and Bio7 (0.84) and between distance to rock and bare areas (0.77), given their likely importance for the ecology and distribution of the target taxa in the study area (Brito et al., 2009; Vale et al., 2012, 2014).

### Environmental variability

Two Spatial Principal Components Analyses (SPCA) were independently performed to summarize the spatial topoclimatic (PCATc) and habitat variability (PCAha) of the study area (Brito et al., 2011, 2016). All environmental variables were previously centred and scaled due to different measurement units. The SPCAs were performed with the “Principal Components Analysis” extension of ArcGIS 10.0 (ESRI, 2011). The first three orthogonal components retained in PCATc and four in PCAha explained much of the environmental variability (see results) and thus, were used for modelling purposes (Tab. 2). The first two components were used to summarize the spatial topoclimatic and habitat range of each taxon. The values of each retained component of each SPCA were extracted for taxa observations using the tool “Extract multi values to points” in ArcGIS 10.0 (ESRI, 2011). The spatial topoclimatic and habitat variability of each taxon was then visually compared with the first two retained components of both PCATc and PCAha of the study area.

### Ecological niche-based modelling

The Maximum Entropy approach implemented in Maxent v.3.3.3 software (Phillips et al., 2006) was used to identify environmental variables related to the distribution of each taxon and to predict the relative occurrence rate (ROR) of each taxon. This technique requires only presence data as input and consistently performed well in comparison to other methods, even with low sample sizes (Elith et al., 2006; Hernandez et al., 2006). The Maximum Entropy approach is particularly suited for

the present study, given that study area was not sampled using standardized efforts and techniques, and several species exhibit low detectability and large home ranges. The first three and four retained orthogonal components of both PCATc and PCAha, respectively, were used as models inputs (Brito et al., 2011). Models were developed with replicates and a percentage of test data chosen by bootstrap with random seed, and raw output (Phillips et al., 2006). The regularization multiplier, feature type, number of replicates and percentage of data for testing were set according to the number of observations available for each taxon: linear and quadratic features with 0.5 of regularization multiplier, with 10 replicates and 10% of test data for taxa with less than 15 observations; and auto-features with 0.75 of regularization multiplier with 10 replicates and 10% of test data for taxa with 15 to 30 replicates and with 25 replicates and 25% testing for those with more than 30 observations. Both the regularization multiplier value and the features types were chosen after an initial evaluation of the performance of models built with different sample sizes and for species with different biogeographic affinities (Fig. S3). The best feature type and regularization multiplier was chosen based on comprise between the higher values of the area under the curve (AUC) of the receiver-operating characteristics (ROC) plot (Anderson and Gonzalez, 2011) and lower values of corrected Akaike information criteria (AICc, Fig. S3; Warren and Seifert, 2011). AICc was calculated using the software ENM tools (Warren et al., 2010). Area under the curve (AUC) of the receiver-operating characteristics (ROC) plot was then taken as a measure of all models fitness (Fielding and Bell, 1997). Additionally, for taxa with no validation data available (Tab. 1), a ‘leave-one-out’ procedure was implemented, as this cross-validation technique provides an unbiased assessment of model performance, even at small sample sizes (Olden and Jackson, 2000). For each taxon, observations were removed once from the training data and a model was built using the remaining  $n-1$  observations (Pearson et al., 2007). Thus, for a given taxa with  $n$  occurrences,  $n$  individual models were built. Agreement among each individual model was accessed throughout a pairwise comparison using a Pearson correlation of the relative occurrence rate models. Predictive performance was then assessed based on the ability of each model to predict the single occurrence excluded from the training data set. Finally, the replicates were averaged to generate a forecast of taxa presence probability, which is a robust procedure to derive consensus predictions of likelihood of pres-

ence (Marmion et al., 2009). Plots depicting standard deviation among replicates were also considered as a measure of models performance.

The importance of environmental variables for explaining the distribution of each taxon was determined from their average percentage of contribution, permutation importance and Jackknife analysis (Vale et al., 2014, 2015b). Relationships between the relative occurrence rate (ROR) of each taxon and environmental variables were determined by visual examination of response curves profiles from univariate models.

### Probable distributions and species richness hotspots

The ROR models of each taxon were reclassified to display grid cells of probable presence and absence, using “Reclassify” tool of ArcGIS 10.0 (ESRI, 2011). Given that less restrictive thresholds can be applied for conservation purposes (Liu et al., 2005), the minimum training presence threshold (MTP) was applied. This threshold forces all training observations to be considered as predicted. To calculate MTP for each taxon in each model, training observations were intersected with the average probability of occurrence models and the minimum probability value was taken as the MTP (Vale et al., 2014). The MTP was then used to classify average continuous probabilities models into binary maps. To identify local hotspots of richness, the binary maps for each taxon were added in ArcGIS, using the tool “Raster calculator” (ESRI, 2011). The binary maps for each taxon were further intersected with a shapefile of implemented protected areas (IUCN and UNEP, 2013) to quantify the percentage of formally protected suitable areas for each taxon.

### Biogeographic groups and ecological niche traits

To evaluate the number of biogeographic groups present in the study area and the taxa included in each group, three steps were followed. First, pairwise comparisons were performed between the binary predictions of taxa presence/absence. Spatial comparisons were performed in Map Comparison Kit software (Visser and Nijs, 2006) and the Kappa coefficient was taken as the measure of similarity of pairwise distributions (Cohen, 1960), which allowed grouping species according to their distributional ranges. Second, the binary predictions for each taxon were intersected with the ecoregions present in the study area (Olson et al., 2001) to measure the biogeographic affinities of each taxon to each ecoregion (Brito et al., 2011). Third, the ecological niche breadth of each taxon across the ecoregions was quantified using the Standardised Levin’s B measure of niche breadth:  $B_s = B - 1/n - 1$ , where B is the Levin’s index and n the total number of ecoregions in the study area. B is given by  $1/P(p^2)$ , where p is the proportion of suitable area in each ecoregion.

## Results

### Environmental variability

The first three and four axes of the Spatial Principal Components Analyses (SPCA) explained 89.8% and 87.3% of the topoclimatic (PCAtc) and habitat (PCAha) variances of the study area, respectively (Tab. 2). The first two principal components (TcPC1 and TcPC2) of the PCAtc accumulated most of the temperature variability, while the third component (TcPC3) retained the topographic variability (Tab. 2). The HaPC1 of the PCAha depicted the variation in distances to bare areas and rocky deserts, while the HaPC2 retained the variability in distance to rivers and vegetated areas. The HaPC3 accumulated the variance in distance to sandy areas and herbaceous vegetation, and HaPC4 depicted a negative correlation with distance to gueltas (Tab. 2).

### Ecological niche-based models

The ROC plots exhibited high average AUCs with low standard deviations (SD) for both training and test data sets and all taxa (Tab. S4). The average AUCs for training data sets ranged from 0.88 to 1.00 among taxa, whereas for the test data set they ranged from 0.81 to 0.98. Pairwise comparisons between individual ROR leave-one-out models showed high levels of agreement ( $r > 0.76$ ). Binary maps identified suitable cells for each taxon. The average percentage of correct classifica-

tion rate of the validation data set was 94.2% ( $66.7 < \%CCR < 100$ ; Tab. S4).

### Importance of environmental factors

The percentage contribution, the permutation importance and the Jackknife evaluation of the predicted models agreed in the most important EGVs for each taxon (Tab. 3 and Fig. S5). The distributions of taxa were mostly related with HaPC2, TcPC1 and HaPC1, with the exception of *Felovia vae*, *Hystrix cristata*, and *Procapra capensis* that were mostly related with TcPC3 (Tab. 3). The variation of ROR along the analysed environmental gradients revealed that most taxa tended to respond similarly to the same set of environmental conditions (Fig. 2). Comparing with the remaining taxa, the relative occurrence of *G. dorcas* was unimodal along HaPC2 variation (synthesising variation in distances to rivers and vegetated areas). *G. genetta*, *P. papio* and *V. pallida* showed unimodal responses at relative distances to rivers and vegetated areas, while the relative occurrence rate of *M. capensis* decreased with increasing distances to HaPC2. Latter pattern could be also observed along HaPC1 (synthesising variation in distances to bare and rocky areas), with some exception such *V. zerda*, which showed a unimodal response along HaPC1 variation. All taxa exhibited a unimodal response along TcPC3, although the relative occurrence of *P. papio* was higher in ruggedness areas.

### Probable distributions and species richness hotspots

Ecological models identified suitable cells for the occurrence of taxa mostly in areas where they were known to occur, but also in areas where they are unknown (Fig. 3 and S6). Hotspots of species richness were located mainly in Mauritanian mountains, which were predicted as suitable for at least 15 taxa (Fig. 3). Small and fragmented hotspots were also observed in the regions of Tarfaya and Néma. The suitable ranges of most taxa were mostly unprotected throughout the study area (average  $< 9.9\%$ , Tab. 3).

### Biogeographic groups and ecological niche traits

The analyses of the Kappa coefficients between pairwise comparisons of suitable areas for each taxon suggested consistent shared ranges in five groups of taxa, with the exception of *P. africanus* (Tab. S7). Taking into account the general distribution pattern of each taxon (Fig. 3) included in each group, they were named: 1) the Sahel group, which ranges mostly throughout the Sahel and it is composed by *A. albiventris*, *D. braueri*, *E. patas*, *G. genetta*, *M. capensis*, *P. africanus*, *V. pallida* and *X. erythropus*; 2) the Mountain group, which aggregates *F. vae*, *H. cristata*, *P. papio* and *P. capensis* and is mostly restricted to the Mauritanian mountains; 3) the Sahara-Sahel group, which is composed by *C. anthus*, *Lepus* sp., *Jaculus* sp., *F. s. lybica*, *G. gerbilus*, *P. aethiopicus* and *V. rueppellii*, and it is widely distributed throughout the Atlantic coast, the Sahara desert and the Sahel; 4) the Sahara group, which comprises *G. dorcas* and *V. zerda*, both ranging throughout the Sahara desert; and 5) the Coastal group with only one species, *P. obesus*, restricted to the ecoregion Atlantic coastal desert. There were significant differences ( $p < 0.0001$ ) in the proportions of predicted suitable areas for each taxon in each ecoregion (Fig. 4). Both Sahel and Mountain groups were more frequently predicted in the Sahelian Acacia savanna ecoregion. Large portions of suitable areas of taxa from the Sahara-Sahel group were predicted in the ecoregions Sahelian Acacia savanna and North Saharan steppe and woodlands. Both Sahara and Coastal groups were found in the North Saharan steppe and woodlands ecoregion. These groups tended to occupy distinct topoclimatic and habitat environmental spaces according to the first two axes of the PCAtc and PCAha, particularly in the topoclimatic space (Fig. S8).

The  $B_s$  measure of niche breadth was low for all taxa ( $B_s < 0.2$ ), indicating that they tended to be specialized in the study area, particularly *D. braueri*, *E. patas*, *G. genetta*, *H. cristata*, *M. capensis*, *P. papio*, *P. africanus* and *V. pallida* (Tab. 3).

**Table 2** – Code, description, range (minimum and maximum), and units of the topoclimatic and habitat variables used to characterize the environmental variability of the study area. Percentage of explanation of the first principal components (PC) and loading scores of the environmental variable derived from a Spatial Principal Components Analyses built with topoclimatic (Tc) and habitat (Ha) variables, independently.

Code	Description	Units	Range	TcPC1	TcPC2	TcPC3	HaPC1	HaPC2	HaPC3	HaPC4
Topoclimatic	% Variance explained			37.7	35.7	16.4				
Bio1	Annual Mean Temperature	°	16.3–30.8	-0.19	0.63	0.07				
Bio5	Max Temperature of Warmest Month	°	24.1–48.3	0.34	0.58	0.08				
Bio6	Min Temperature of Coldest Month	°	2.7–18.1	-0.58	0.28	-0.03				
Bio7	Temperature Annual Range (Bio5-Bio6)		10.9–42.8	0.58	0.32	0.08				
Bio12	Annual Precipitation	mm	13–901	-0.42	0.25	0.13				
TRI	Topographic ruggedness index		0–302.8	-0.02	-0.14	0.98				
Habitat	% Variance explained			33.9	28.2	14.4	10.8			
D_bare	Bare areas	°	0–1.58	0.57	0.04	0.04	0.35			
D_cohe	Closed to open (>15%) herbaceous vegetation	°	0–11.11	-0.28	0.2	0.83	-0.004			
D_rock	Consolidated bare areas (hardpans, gravels, bare rock, stones, boulders)	°	0–2.37	0.59	-0.12	0.09	0.22			
D_sand	Non-consolidated bare areas (sandy desert)	°	0–2.97	0.34	-0.41	0.42	-0.3			
D_spvq	Sparse (<15%) vegetation or grassland	°	0–3.07	0.08	0.59	0.22	0.45			
D_guel	Gueltas (mountain rock pools)	°	0–6.46	0.34	0.34	0.09	-0.68			
D_river	Permanent rivers	°	0–6.09	0.14	0.56	-0.25	-0.25			

## Discussion

Geographical information systems (GIS) and ecological niche-based models (ENMs) have prompted biodiversity conservation studies with robust analytical methods (Guisan and Zimmermann, 2000). Among several applications, ENMs have become increasingly popular in recent years for predicting and identifying suitable areas of species occurrence, particularly for rare species (e.g.: Gaubert et al., 2006), or over large and remote study areas (e.g.: Travaini et al., 2007), predicting climate change induced range shifts (e.g.: Thuiller et al., 2005; Martínez-Freiría et al., 2013), assessing the conservation status of poorly known species (e.g.: Vale et al., 2012), and identify priority areas for conservation (e.g.: Carvalho et al., 2011; Brito et al., 2016). This study illustrates how GIS and ENMs could be used to identify biogeographical patterns and important areas for conservation in remote and hard to sample areas.

### Methodological limitations and implications

High resolution distribution data were used to predict suitable areas for the occurrence of selected mammals in the West Sahara-Sahel. Despite the spatial precision in the occurrence data used in this study, uncertainties in ecological modelling may arise from multiple factors. These include sampling design, the environmental factors selection and modelling techniques applied (Araújo and Guisan, 2006; Wiens et al., 2009; Merow et al., 2013; Yackulic et al., 2013). Specifically in this study, ecological models were based in partial distributions, which have been shown to provide biased predictions of species–environment interactions, particularly for regions or time periods other than those where models were built (Thuiller et al., 2004; Martínez-Freiría et al., 2015). However, regional models built with precise data have been shown to provide more accurate identifications of suitable areas for peripheral populations at present conditions (Vale et al., 2014). Given that the West Sahara-Sahel corresponds to the range margin of most taxa analysed, the developed ecological models should provide accurate predictions of distribution areas.

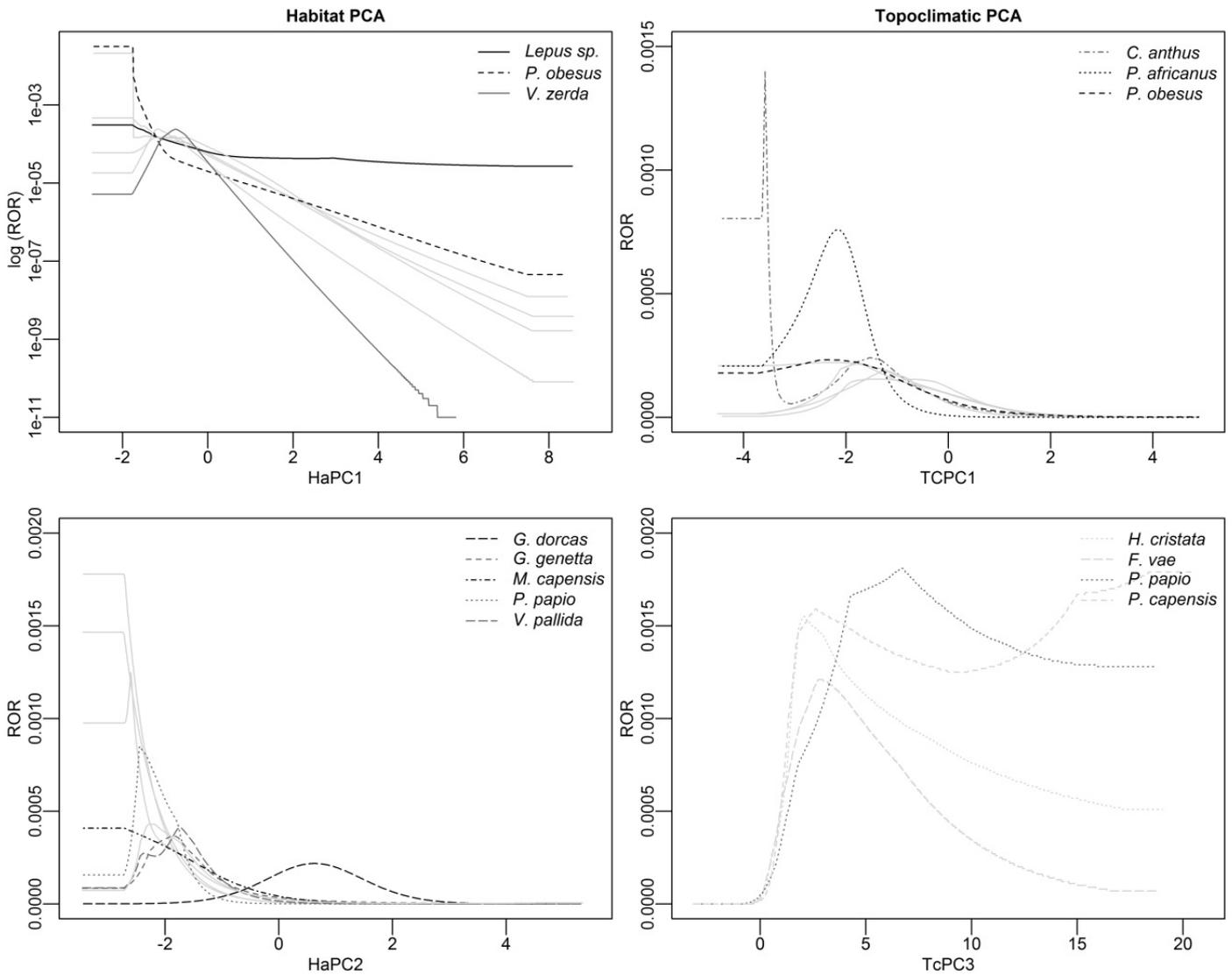
Secondly, sampling was mostly based in opportunistic observations and was concentrated along roads. Roadside sampling has been associated to lack of accuracy of ENMs, exacerbating statistical problems when models are based on small sample sizes (Kadmon et al., 2004; Wisz et al., 2008). However, if the range of environmental gradients available in the study area is covered, roadside sampling can be a valuable, unbiased source of information for ecological modelling (McCarthy et al., 2012). Given that all ecoregions were covered by sampling efforts, there is confidence in the robustness and accuracy of the predicted models. Also, we have spatially filtered the data while reducing

clustering, which has also been demonstrated as one of the best solutions to overcome sampling bias towards some regions (Kramer-Schadt et al., 2013).

Thirdly, for some taxa, there were few observations available for building ENMs. Low sample size for model building has been associated with poor model performance and accuracy (Stockwell and Peterson, 2002). To overcome this issue, models were built with Maxent, which has high performance with relatively low sample sizes when compared with other presence-background models (Elith et al., 2006; Hernandez et al., 2006). Despite the high performance of Maxent, the regularization multiplier value is known to influence models performance being related to sample size and independence of the data (Anderson and Gonzalez, 2011). As such, a previous evaluation of the feature types and value of the regularization multiplier was performed to further increase the performance of the models (even those built with low sample sizes). Moreover, the number of replicates and percentage of data assigned for testing was set according to the sample size, in order to avoid over-fitting of models. For taxa with no validation data and extremely low sample sizes, the “leave-one-out” procedure appeared to be a successful approach providing high correct classification rates and statistical significance (Pearson et al., 2007). Still, the suitable range of *P. africanus* was most likely underestimated, which is probably related with poor sampling south of Senegal River. Overall, measures of models performance (AUC), accuracy (% CCR) and agreement among individual model ( $r > 0.76$ ) were generally high, increasing confidence in predicted suitable areas.

### Environmental factors related with species occurrence

Ecological niche-based models allowed identifying relationships between the distributions of taxa and local eco-geographic gradients in the West Sahara-Sahel. Most distributions are related with climate (TcPC1: temperature) and/or with habitat features (HaPC1: distance to bare and rocky areas; HaPC2: distance to rivers and sparse vegetation). Exceptionally, the distributions of *Felovia vae*, *Hystrix cristata*, and *Procapra capensis* were yet related with topography (TcPC3: TRI). The importance of these environmental factors for explaining local taxa distribution was previously observed for diverse mammals (Cooper et al., 2006; Brito et al., 2009; Padial and Tellería, 2009; Vale et al., 2012, 2014, 2015b) and other local vertebrates (e.g. vipers, Brito et al., 2011), as well as in other regions (e.g.: Sillero-Zubiri et al., 2004). Additionally, most taxa tended to respond similarly to the same set of environmental conditions. These responses were concordant with those previously observed in other studies. For instance, relative occurrence rate of *V. zerda* decreased with increasing distances to rocky deserts (Brito et al., 2009), while *P. papio* is present in more ruggedness areas (Vale



**Figure 2** – Response curves for the habitat and topoclimatic factors most related to the distribution of analysed taxa. The HaPC1 and HaPC2 retain the variability in distance to bare and consolidated bare areas and in distance to rivers and vegetated areas and. The TCPC1 depict most of the variability in temperature while TCPC3 the variation in topographic ruggedness.

et al., 2015b). Previous studies have also highlighted the importance of gueltas, rocky areas, and slope which are mostly associated with water availability and mountainous areas (Vale et al., 2012, 2014, 2015a), and of temperature for taxa occurring in the driest areas (Brito et al., 2009). Altogether, the observed concordances among taxa in the most important environmental factors related to distribution patterns and the consistent responses to such environmental variation suggest that these specific environmental factors (topography, temperature and water related features) shape biodiversity distribution in the West Sahara-Sahel.

**Predicted taxa occurrence**

Fine-scaled ecological models allowed the definition of accurate suitable areas for selected mammals in the West Sahara-Sahel. Although areas of occurrence were predicted mostly within the general known distributions for most taxa (IUCN, 2015), they were also predicted for regions outside IUCN ranges. Suitable areas were identified to the north of the known ranges of *A. albiventris* and *H. cristata*, and to the south of the known range of *P. aethiopicus*. For *P. obesus* predicted suitable areas increased the potential range along coastal areas. Predicted areas were also supported by our observations, which suggest that IUCN ranges maps of these taxa should be updated in order to include areas here identified as suitable. Low values of ecological niche breadth were predicted for all taxa ( $B_s < 0.2$ ), indicating that these can be considered specialists within the West Sahara-Sahel. Since the study area is mostly located at the edge of the complete range of each

taxon (except for the endemic *F. vae*), the distribution of local populations may be restricted to patches of suboptimal and unique habitats (Braunisch et al., 2008; Vale et al., 2014). In fact, previous studies have observed that *E. patas* and *P. capensis* in the study area select marginal habitats and live in narrow ranges of environmental conditions, while *P. papio* becomes specialised most likely due to niche truncation (Vale et al., 2014, 2015b). Despite the overall low values of niche breadth, the magnitude of specialization differed among taxa. Such variation might be related with species adaptive capacities, such as high dispersal abilities. Another possible explanation is related with the geographic location of the range limits of each taxon. Given that the region exhibits strong latitudinal variation in climate (Brito et al., 2016), taxa exhibiting predominately latitudinal ranges should become more specialised close to the edges, in comparison to those with a longitudinal limit, as observed for instance when comparing *C. anthus* and *V. pallida* (lower in the latter taxon). Overall, this study suggests that niche truncation may be a common pattern within the mammals inhabiting the West Sahara-Sahel, and that populations of ecologically plastic species throughout their complete range tend to appear specialised in the study area.

**Biogeographic patterns**

Shared distributional ranges among the analysed taxa allowed defining biogeographic patterns for the West Sahara-Sahel mammals. Five groups of taxa sharing similar distributions (hereafter and for simpli-

**Table 3** – Percentage of contribution of environmental variables for ecological niche-based models for each taxon. Ecological models were derived with the first principal components of both topoclimatic and habitat PCAs: HaPC1, HaPC2, HaPC3 and HaPC4 - first, second, third and fourth components of habitat PCA, respectively; and TcPC1, TcPC2 and TcPC3 - first, second and third components of topoclimatic PCA, respectively. Standardised Levin's B measure of niche breadth (L-B). Percentage of suitable area for each taxon covered by protected areas in the study area (% PA).

Taxa	% of Contribution (Permutation rate)							L-B	%PA
	HaPC1	HaPC2	HaPC3	HaPC4	TcPC1	TcPC2	TcPC3		
Aalb	1.6 (2.2)	59.9 (41.7)	13.3 (25.8)	4.6 (17.1)	5.9 (1.9)	7.8 (6.0)	7.0 (5.3)	0.07	5.9
Cant	14.3 (28.9)	14.7 (16.0)	12.5 (12.6)	2.5 (4.9)	31.1 (21.7)	7.0 (8.8)	18.0 (7.0)	0.18	7.1
Dbra	9.6 (13.9)	57.6 (30.4)	6.3 (8.4)	3.3 (9.6)	3.2 (21.9)	15.3 (10.4)	4.6 (5.3)	0.04	5.8
Epat	13.5 (21.2)	62.5 (55.5)	11.1 (3.1)	0.7 (0.7)	5.9 (14.2)	1.3 (4.1)	5.0 (1.2)	0.04	2.3
Fsly	16.4 (9.8)	23.5 (18.0)	5.9 (8.5)	1.8 (6.0)	29.6 (51.1)	5.0 (3.2)	17.8 (3.5)	0.09	5.5
Fvae	2.2 (3.8)	14.2 (24.1)	18.0 (25.7)	2.0 (4.6)	1.2 (3.8)	1.7 (4.8)	60.6 (33.3)	0.09	1.3
Gdor	9.5 (15.6)	11.7 (15.3)	39.9 (46.2)	2.4 (2.3)	1.7 (4.3)	26.6 (13.4)	8.3 (2.9)	0.15	7.5
Ggen	11.6 (29.2)	42.5 (35.6)	23.9 (6.5)	1.9 (3.0)	6.2 (17.3)	8.5 (5.9)	5.4 (2.4)	0.02	3.4
Gger	25.4 (27.1)	9.4 (17.5)	21.7 (18.2)	13.5 (12.9)	11.4 (17.6)	12.1 (2.9)	6.6 (3.8)	0.16	3.5
Hcri	3.1 (4.7)	20.5 (40.1)	17.8 (23.3)	0.8 (4.7)	1.3 (3.4)	1.9 (3.0)	54.7 (20.8)	0.02	0.1
Jacu	37.3 (46.9)	3.5 (2.8)	7.8 (7.1)	4.7 (11.3)	27.2 (24.0)	11.0 (3.1)	8.5 (4.7)	0.15	3.4
Lepu	17.5 (16.4)	6.3 (7.8)	6.1 (9.8)	9.3 (17.4)	30.5 (29.9)	15.8 (9.6)	14.6 (9.2)	0.2	5.9
Mcap	17.3 (25.7)	42.6 (12.5)	22.8 (11.2)	3.5 (7.3)	7.8 (28.5)	3.9 (14.3)	2.2 (0.5)	0.00	1.2
Ppap	4.9 (7.9)	45.6 (83.2)	13.4 (1.6)	1.8 (2.6)	1.6 (1.3)	1.9 (2.1)	30.7 (1.2)	0.02	0.1
Paet	14.2 (20.7)	3.7 (7.5)	32.3 (24.0)	4.1 (5.2)	16.4 (19.2)	19.1 (16.8)	10.2 (6.6)	0.15	3.8
Pafr	13.9 (30.3)	8.3 (20.5)	15.2 (2.8)	7.2 (12.9)	30.9 (19.6)	21.8 (11.6)	2.6 (2.4)	0.03	8.8
Pcap	3.1 (5.6)	6.9 (19.8)	14.7 (24.8)	0.4 (0.8)	1.8 (2.4)	2.3 (1.8)	70.8 (44.7)	0.09	1.5
Pobe	18.4 (4.5)	3.0 (7.0)	7.3 (8.6)	0.5 (2.7)	8.1 (13.2)	58.2 (59.7)	4.5 (4.3)	0.16	4.1
Vpal	10.8 (20.3)	52.9 (42.1)	21.9 (15.9)	4.0 (9.0)	3.6 (8.7)	3.9 (2.4)	2.9 (1.7)	0.02	3.5
Vrue	26.1 (25.4)	2.1 (4.4)	39.1 (32.1)	5.3 (5.2)	8.0 (15.7)	7.0 (9.4)	12.3 (7.8)	0.16	3.4
Vzer	15.1 (19.6)	16.6 (18.6)	38.1 (37.4)	9.3 (6.8)	5.6 (8.9)	8.2 (5.4)	7.2 (3.2)	0.19	3.2
Xery	4.0 (5.3)	57.5 (48.8)	20.9 (21.0)	2.3 (5.9)	7.7 (13.0)	4.2 (3.5)	3.3 (2.5)	0.06	9.9

city, biogeographic groups) were identified at the regional level, which broadly matched with the biogroups identified in a broad-scale zoogeographical analysis of vertebrate distribution in the Sahara-Sahel (Brito et al., 2016). Concordance across scales provides robustness for derived biogeographic groups in the study area. The only exception was the mountain group, which was not detected in the broad-scale study. The ability to discriminate such group in the present study is most likely related with the use of high-precision observations (GPS coordinates vs. IUCN range polygons in Brito et al., 2016) and small pixel size (1 × 1 km vs. 50 × 50 km in Brito et al., 2016). These findings further emphasize the usefulness of using high precision observations in local assessments of biogeographic patterns.

### Conservation implications

This study updated the current knowledge on the distribution patterns for 21% of mammals occurring in the West Sahara-Sahel (IUCN, 2015). Data collected during fieldwork allowed the application of local and high resolution ENMs to build accurate species distribution maps, previously unavailable for most taxa. In the West Sahara-Sahel, mammal distributions can be aggregated into five groups with distinct biogeographic affinities. Most groups occurs in the ecoregions North Saharan steppe and woodlands and Sahelian Acacia savanna as result of their availability in the study area, stressing the importance of these ecoregions for the long term conservation of these mammals (Brito et al., 2016).

According to the predicted suitable areas, the analysed mammals are poorly represented in the current network of protected areas. Protected areas in the West Sahara-Sahel are mostly located along coastal regions, which provide a reasonable representation of *P. obesus* and other coastal mammals that were not analysed in this study. Further studies should try to include other marginal mammals to evaluate the effectiveness of the current protected area network for this biogeographic group. Nevertheless, the hotspots of the selected mammal richness identified for the mountains of Tagant, Assaba and Afollé in Mauritania remain poorly protected. The biological value of these mountains have been increasingly emphasised as they constitute suitable areas for several species from different taxonomic groups and biogeographic affinities (Brito et al., 2009, 2010, 2011; Padial and Tellería, 2009; Trape,

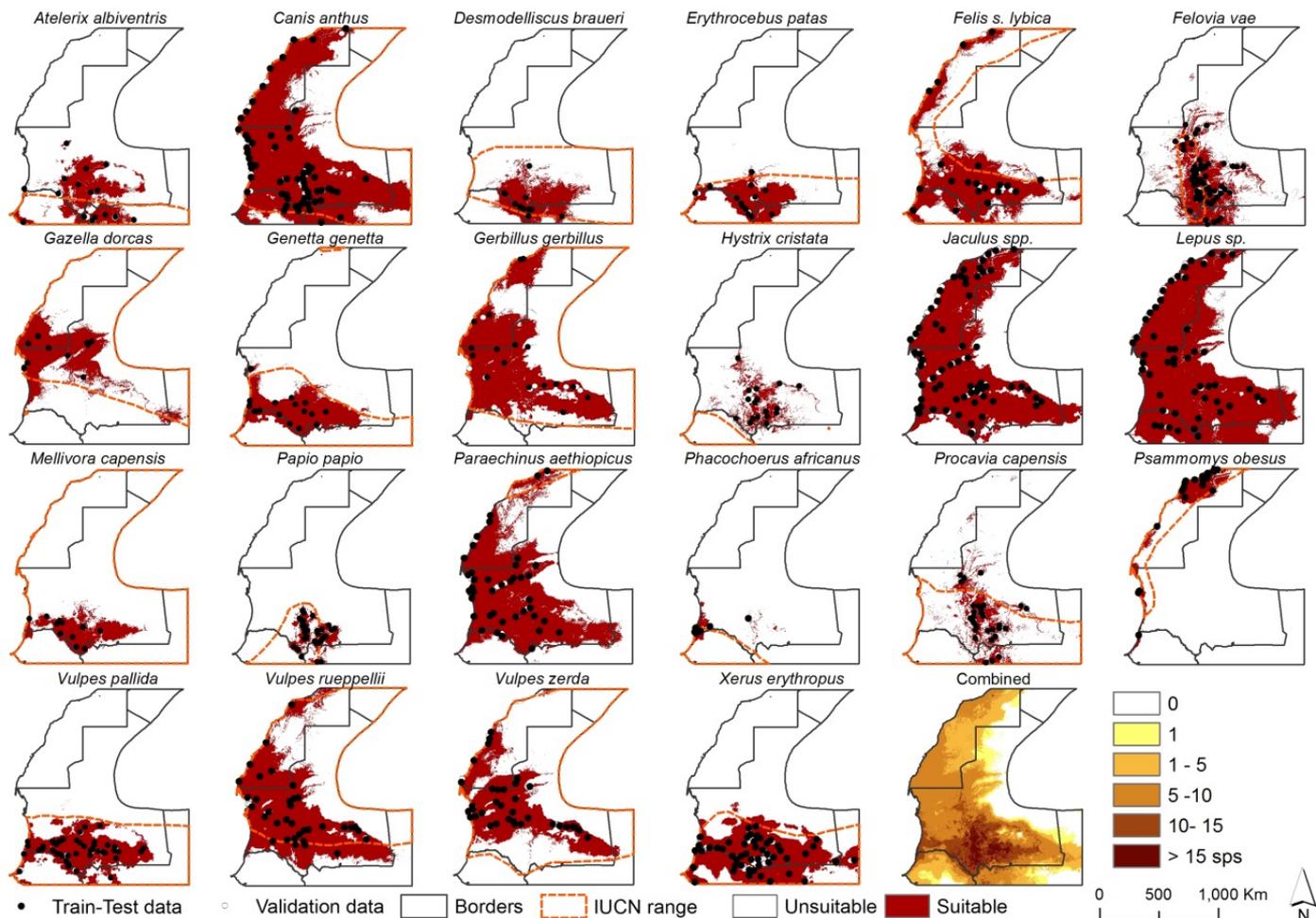
2009; Padial et al., 2013; Vale et al., 2012, 2014, 2015a,b). The present results further suggest that the designation of protected areas should be considered for these mountains.

### Conclusions

The biogeographic patterns observed in this study may provide useful prior information for assessing other mammals distributed along the West Sahara-Sahel. Ecological niche-based models built with high resolution data can be used to identify key-areas for conservation and management, and should be used to investigate range dynamics of rare and endangered taxa across the Sahara-Sahel (Durant et al., 2014). The methodological approach followed can be applied to other remote regions of the world and taxonomic groups. ☞

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**Figure 3** – Distribution of predicted suitable areas for the occurrence of each taxon and of predicted species richness (Combined). The total data set of observations available for each taxon is displayed. Dashed lines represent the respective IUCN polygon.

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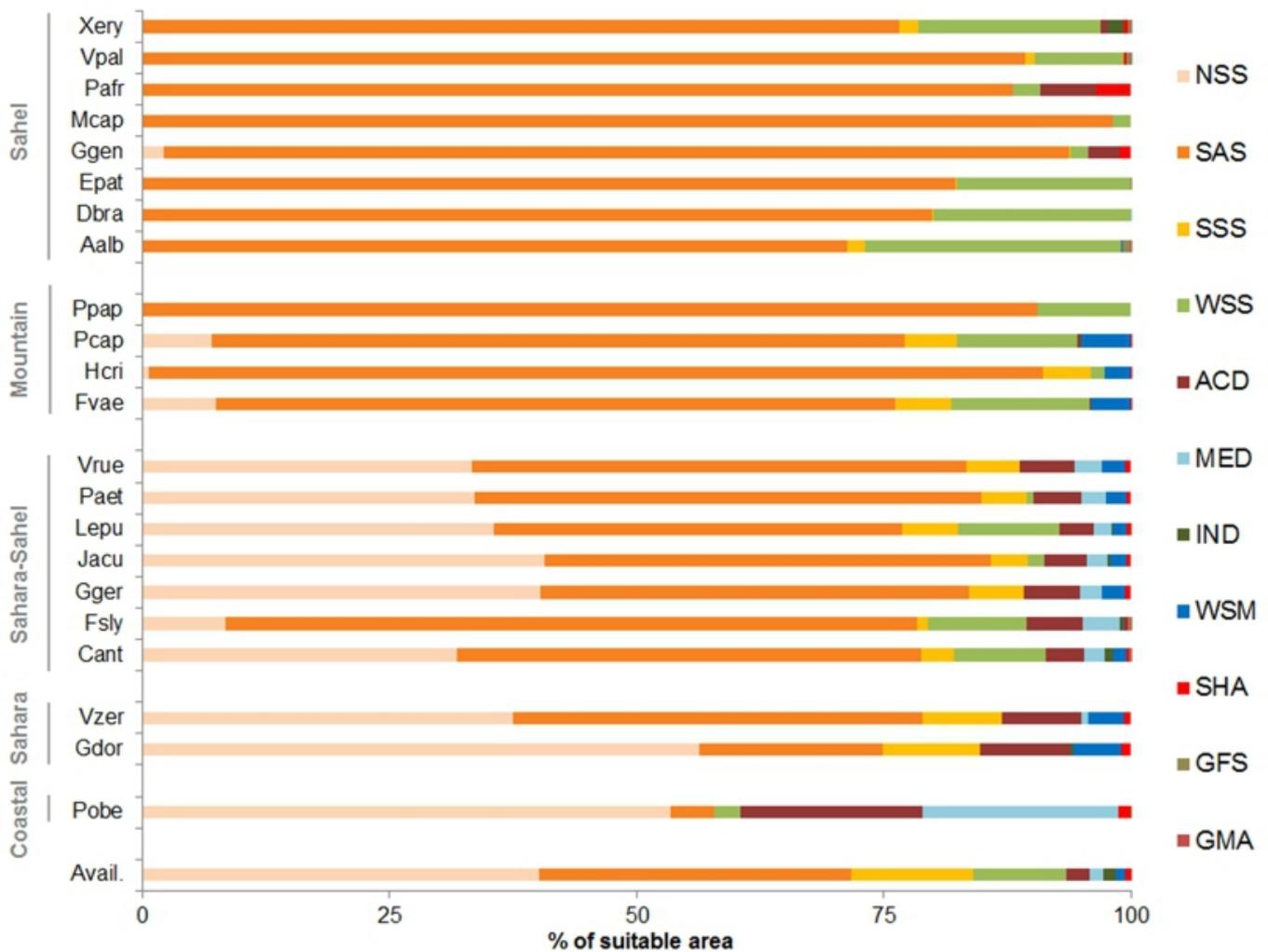
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**Figure 4** – Percentage of grid cells predicted as suitable for occurrence of each taxon in each ecoregion present in the study area and availability of each ecoregion. Ecoregions are: North Saharan steppe and woodland (40.1% of study area; NSS); Sahelian Acacia savanna (31.5%, SAS); South Saharan steppe and woodlands (12.4%, SSS); West Sudanian savanna (9.5%; WSS); Atlantic coastal desert (2.4%; ACD); Mediterranean Acacia-Argania dry woodlands and succulent thickets (1.4%; MED); Inner Niger Delta flooded savanna (1.2%; IND); West Saharan montane xeric woodlands (1.0%; WSM); Saharan halophytics (0.4%; SHA); Guinean forest-savanna mosaic (0.1%; GFS); and Guinean mangroves (0.01%; GMA). Taxon codes are given in Tab. 1. Taxa are organised according to range similarities in the Sahara-Sahel (see Tab. S7 for details).

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## Supplemental information

Additional Supplemental Information may be found in the online version of this article:

- Figure S1** Routes of the 16 field missions carried out between 2002 and 2015, distribution of ecoregions, and location of the study area in the African context.
- Table S2** Locations of observations of mammals in the West Sahara-Sahel.
- Figure S3** Evaluation of Maxent models.
- Table S4** Measures of the fit of ecological niche-based models for each taxon.
- Figure S5** Jackknife results for the environmental factors used in ecological niche-based models for each taxon.
- Figure S6** Mean relative occurrence rate (ROR) of each taxon in the study area.
- Table S7** Kappa coefficient measure of pairwise comparison between suitable areas of distinct taxa.
- Figure S8** Topoclimatic and habitat variability of the study area derived by a Spatial Principal Components Analysis and location of each taxa along the gradient.