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Global warming drives changes in carnivore communities in the North Sahara Desert

Yamna Karssene[1,2,*], Mohsen Chammem[2], Touhami Khorchani[2], Said Nouira[1], Fengqing Li[3,*,]**

[1]Département de Biologie, Faculté des Sciences de Tunis, Université de Tunis, El-Manar 2092, Tunisia
[2]Laboratoire d'Elevage et de la Faune Sauvage, Institut des Régions Arides de Médenine, 4119 Médenine, Tunisia
[3]Department of River Ecology and Conservation, Senckenberg Research Institute and Natural History Museum Frankfurt, 63571 Gelnhausen, Germany

ABSTRACT: Global warming is among the most serious environmental challenges facing ecosystems worldwide, due to rising temperatures and altered precipitation regimes. The North African Sahara Desert is considered to be one of the areas most affected by climate change, which will probably lead to the likely retraction of the Mediterranean ecosystem and an increase in desertification. We examined the effect of global warming on 3 carnivore species (*Canis anthus*, *Vulpes vulpes* and *V. zerda*) in the North African Sahara Desert in the 2000s, 2030s, 2050s and 2080s using species distribution models. Species occurrence records were collected from 175 sites, covering all of the arid and desertified areas of Tunisia between January 2014 and January 2016. Our results show that elevation and annual mean temperature are the most important factors associated with the distribution of *V. zerda*, while temperature and precipitation have major contributions in the distribution of *C. anthus* and *V. vulpes*. Future climate change in the North Sahara will reduce the spatial distribution of suitable habitats for *C. anthus* and *V. vulpes*; *V. zerda* will decrease in numbers around the 2030s and increase again thereafter. Our findings suggest that the ongoing warming effect will cause continued range shifts in carnivores; thus there is an urgent need for efficient conservation practices for carnivores to be implemented in this climatically vulnerable area.

KEY WORDS: Desert carnivores · Global warming · North Sahara Desert · Species distribution model · Predicted distribution

1. INTRODUCTION

Recent decades have seen great changes in global climate, with the average warming rate of the last 50 yr being nearly twice that of the last 100 yr (Pachauri et al. 2014, Xie et al. 2014). Such a rapid and abrupt warming trend is currently affecting all realms of ecosystems (Li et al. 2014, 2015, 2016, Niang et al. 2014, Baker et al. 2015). Indeed, global warming is expected to become one of the greatest drivers of biodiversity loss by the end of this century (Bellard et al. 2012). Adapting to new climatic conditions will be possible for widely distributed species, but many others will likely face local extinctions (Hoffmann & Sgrò 2011), especially protected endemic species (Midgley et al. 2003, Thuiller et al. 2005).

Loss of habitat is affecting carnivores worldwide, and their numbers have also been affected by overhunting, disease and population fragmentation (Gittleman et al. 2001, Turchin 2003). They are particularly vulnerable to global warming because of their low densities within relatively large distribution areas and because of their prey requirements. Three native medium-sized carnivores occur in North Africa: (1) the golden wolf *Canis anthus*, the first spe-

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*These authors contributed equally
**Corresponding author: qflee3@gmail.com

cies of wolf to be given official recognition in North Africa in recent times and different from Eurasian jackals (Koepfli et al. 2015); (2) the red fox *Vulpes vulpes* (Linnaeus, 1758), which is the most widely distributed species in the order Carnivora, although in Africa it is restricted to the North Sahara Desert; and (3) the fennec fox *V. zerda* (Zimmermann, 1780), the smallest carnivore in the world, which is widespread in sandy deserts and semi-deserts but whose pattern in habitat selection is unknown (Cuzin 2003). To date, our knowledge of the detailed distribution of these 3 carnivore species, and hence their responses to future global warming, remains inadequate. Thus there is an urgent need to evaluate the effects of global warming on the distribution of the carnivore species we surveyed; this is of the utmost importance if we are to design effective conservation strategies in this climatically vulnerable area (Bellard et al. 2012, Mantyka-Pringle et al. 2012).

In response to global warming, organisms are most likely to shift their distribution localities to suitable habitats (Parmesan et al. 1999, Colwell et al. 2008, Li et al. 2014). Compared to evolutionary adaptation, which commonly takes several hundred years for most species, migration is an efficient and practical way to maintain populations, and this is especially true over a relatively short period. Although the widely used species distribution models (SDMs) have been criticized for the unreliability of their predictions and their application to conservation (Wiens et al. 2009, Dawson et al. 2011), they remain useful tools for projecting with reasonable accuracy whether species' ranges will increase or decrease under global warming (Araújo et al. 2005, Green et al. 2008). Despite their limitations, SDMs are in continuous development and still constitute highly relevant models for dealing with important aspects of biodiversity vulnerability to climate change (Dawson et al. 2011, Bellard et al. 2012, Martínez-Freiría et al. 2016). Indeed, SDMs have been increasingly applied to many different climatic regions and various taxonomic groups (Luoto & Heikkinen 2008, Domisch et al. 2011, Meller et al. 2014, Thuiller et al. 2014, Li et al. 2015, 2016, Martínez-Freiría et al. 2016).

The North Sahara Desert was selected for our study because this region has multiple climatic types, and the great difference in climatic factors can increase the predicative accuracy of SDMs. The northern part of this region has a Mediterranean climate, which is considered to be highly responsive to climate change, whereas the southern part has a typically arid climate (Sanchez et al. 2004, Giorgi & Lionello 2008, Li et al. 2015). Climate predictions for this region indicate dramatic increases in temperature and decreases in precipitation, leading to a likely retraction of the Mediterranean ecosystem and an increase in desertification (Garcia et al. 2012).

In this study, we surveyed the distribution of the above 3 carnivore species in the North Sahara Desert of Tunisia. By means of SDMs, we attempted to (1) make a first estimate of the distribution areas of the 3 carnivores and (2) evaluate the abilities of carnivore species to shift their distribution ranges in response to future climate change.

2. MATERIALS AND METHODS

2.1. Study area

Our work was carried out in the southern zone of Tunisia, where arid and desert conditions are dominant (Le Houérou 1995) (Fig. 1). The climate is characterized by long dry seasons and extremely irregular spatiotemporal precipitation. Annual precipitation varies between 100 and 400 mm in southern Tunisia, while it does not exceed 100 mm in desert areas (Le Houérou 1995, 2001). Southern Tunisia is a region with unambiguously degraded vegetation and soil. The soils are characterized by an almost total absence of humus (Akrimi et al. 2000). Moreover, the lack of vegetation cover promotes wind and water erosion, leading to desertification. Favourable edaphic and topographic sites are dominated by steppe-like vegetation, including short perennial grasses and scattered dwarf shrubs (Akrimi et al. 2000). Such a fragile zone is suit-

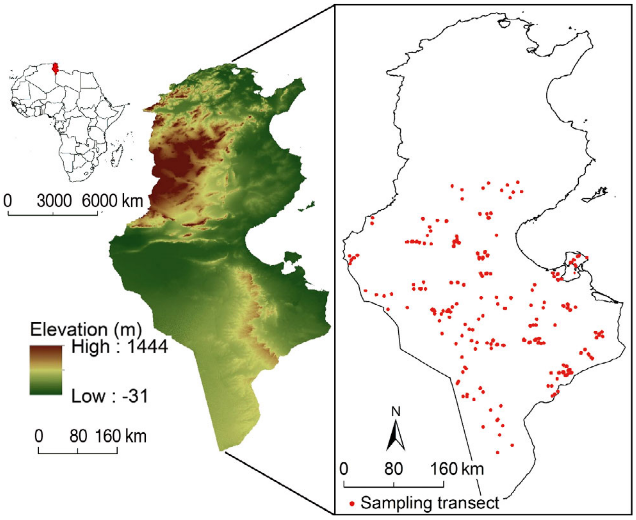

Fig. 1. Study area, showing the distribution of the sampling transects (red dots) in arid and desertified areas of Tunisia

able for designation as a critical habitat which requires special management considerations or full protection.

2.2. Field data collection

Sampling was conducted between January 2014 and January 2016. In total, 175 transects were surveyed by 3 observers, with each transect 2 km apart (Fig. 1). The transect size of a given species was defined based on the size of the estimated home range (Morrison 2013). The mean home range sizes of *Vulpes* spp. inhabiting arid or semiarid environments range from 6.97 km^2 for *V. pallida* (Sillero-Zubiri et al. 2016) to 10.2 km^2 for *V. rueppellii* (Lenain 2000) and 11 km^2 for *V. macrotis* (List & Macdonald 2003). Although no home range estimates are available for *Canis anthus*, it is assumed to have a larger home range than *Vulpes* spp., as home range size is positively related to body size in carnivores (Tucker et al. 2014). To obtain a uniform coverage within a major type of habitat and to reduce any bias that could result from the unequal distribution of transects, the transects were chosen so as to cover the whole study area. We used the transect approach to survey the presence of the 3 carnivores. In each transect, the occurrence of each species (tracks, scats, scratches, dens) was noted with a global positioning system (GPS). A total of 240, 470 and 104 occurrences were recorded for *C. anthus*, *V. vulpes* and *V. zerda*, respectively.

2.3. Environmental data

We used a total of 26 environmental variables, including 19 bioclimatic variables, 4 land use variables and 3 topographic variables (Table 1), to project the future distributions of each species. The 19 bioclimatic variables measured in baseline conditions (2000s, the average of 1960–2000) were obtained from the Worldclim database (www.worldclim.com). The future projections of bioclimatic variables for the 2030s, 2050s and 2080s were derived from the Canadian Centre for Climate Modelling and Analysis (CCCMA) under the IPCC 5th representative concentration pathway (RCP 4.5). The IPCC storylines describe the relationships between the forces driving greenhouse gas and aerosol emissions, such as demographic, social and environmental development (IPCC-TGICA 2007). The RCP 4.5 emission scenario was selected because it includes a balanced mix of all energy sources and closely matches the most likely realistic situation in terms of national energy sources (Li et al. 2016, Molinos et al. 2016). The land use data were extracted from the Global Land Cover 2000 project which has been carried out under the Fifth Framework Programme for Research of the European Commission (www.eea.europa.eu). For each site, 3 topographic variables (elevation, slope and aspect) were extracted from a digital elevation model at a resolution of 1 × 1 km (http://srtm.csi.cgiar.org). Since correlated variables

Table 1. Predictor variables used in species distribution models for 3 carnivores (*Canis anthus*, *Vulpes vulpes* and *V. zerda*) in Tunisia. The Worldclim database is available from www.worldclim.com. SRTM: shuttle radar topography mission (http://srtm.csi.cgiar.org), GLC: Global Land Cover 2000 (www.eea.europa.eu). The 7 climatic variables for which temporal patterns are shown in Fig. S1 in the Supplement are highlighted in **bold**

Category	Variable	Source
Climatic	**Bio 1 = annual mean temperature**	Worldclim
	Bio 2 = mean diurnal range (mean of monthly [max temp − min temp])	Worldclim
	Bio 3 = isothermality (Bio 2/Bio 7)	Worldclim
	Bio 4 = temperature seasonality (SD × 100)	Worldclim
	Bio 5 = max temperature of warmest month	Worldclim
	Bio 6 = min temperature of coldest month	Worldclim
	Bio 7 = temperature annual range (Bio 5−Bio 6)	Worldclim
	Bio 8 = mean temperature of wettest quarter	Worldclim
	Bio 9 = mean temperature of driest quarter	Worldclim
	Bio 10 = mean temperature of warmest quarter	Worldclim
	Bio 11 = mean temperature of coldest quarter	Worldclim
	Bio 12 = annual precipitation	Worldclim
	Bio 13 = precipitation of wettest month	Worldclim
	Bio 14 = precipitation of driest month	Worldclim
	Bio 15 = precipitation seasonality	Worldclim
	Bio 16 = precipitation of wettest quarter	Worldclim
	Bio 17 = precipitation of driest quarter	Worldclim
	Bio 18 = precipitation of warmest quarter	Worldclim
	Bio 19 = precipitation of coldest quarter	Worldclim
Topographic	Elevation	SRTM
	Slope	SRTM
	Aspect	SRTM
Land use	Bare	GLC
	Water	GLC
	Urban	GLC
	Shrub/grass	GLC

may cause over-parameterization and a reduced predictive power, we used Pearson's correlation analysis (Pearson's correlation coefficient < 0.75) to reduce the number of correlated climatic variables (Williams et al. 2003). From the total 26 variables, 13 variables with a slight correlation to each other (Pearson's correlation coefficient < 0.75) were used in the analysis. The temporal patterns of the 7 selected bioclimatic variables are shown in Fig. S1 in the Supplement at www.int-res.com/articles/suppl/c072p153_supp.pdf.

2.4. Baseline distribution area

We estimated the seasonal distribution area of each species using the 100 % minimum convex polygon (MCP) approach (Mohr 1947) and kernel density (KD) estimates (90 and 95 % fixed kernel) (Börger et al. 2006, Kie et al. 2010). MCP and KDs were conducted using the program Geospatial Modelling Environment (GME), version 0.7.3.0 (Beyer 2012) and the plugin bandwidth estimator algorithm in the '*ks*' package of R (Gitzen et al. 2006).

2.5. Species distribution model: baseline situation and future projections

SDMs were performed to examine the potential distributions of 3 carnivore species in the 2000s, 2030s, 2050s and 2080s using the BIOMOD2 package version 3.1.64 (Thuiller et al. 2015) in R (R Core Team 2015). The workflow scheme of the SDMs is shown in Fig. S2 in the Supplement. Six algorithms (ANN: artificial neural networks; CTA: classification tree analysis; GBM: generalized boosting model; MARS: multivariate adaptive regression splines; MAXENT: maximum entropy; RF: random forest) were used in the SDMs. These algorithms perform well with different sample sizes (e.g. Elith et al. 2006, Hernandez et al. 2006) and have been successfully applied in many climate change assessments (Carvalho et al. 2010, Lemes & Loyola 2013, Martínez-Freiría et al. 2013). Detailed descriptions of the algorithms can be found in Thuiller et al. (2015) and Phillips et al. (2006).

These modelling algorithms require distinct observational data: both presence and absence data in CTA, RF and MARS and presence-only data in ANN, GBM and MaxEnt (Phillips et al. 2006, Thuiller et al. 2009, 2012). As confirmed absences are difficult to obtain, especially for mobile and secretive species, and require higher levels of sampling effort (Mackenzie & Royle 2005), presence-only models have often been used to make up for the lack of absence data (Graham et al. 2004). However, presence/absence models tend to perform better than presence-only models (Elith et al. 2006). Thus, presence/absence models are increasingly used, by creating pseudo-absences when only presence data are available. Presence data were imported to BIOMOD2 where pseudo-absences were randomly created for each species. In total, 5000 pseudo-absences were employed in the SDMs. Each item of pseudo-absence data represented 10 times the number of presence data (Thuiller et al. 2009, 2012). The number of pseudo-absences was chosen to have the same weight as presence data in the calibration process of the models (i.e. prevalence = 0.5).

Prior to analysis, the occurrence of each species was randomly split into 2 sets: a training (80 %) and a testing set (20 %). In total, 10 replicates were run for the 6 algorithms. The training set was used to calibrate the model, and the testing set was used to validate the calibrated model. Models were evaluated using the true skill statistic (TSS) metric, which is highly effective for testing the performance of models (Allouche et al. 2006). TSS scores range from 0 to 1, where 0 describes a model no better than random while 1 describes absolute consistency between predictions and observations. Only models performing better than TSS ≥ 0.6 were chosen for the ensemble model to produce more robust predictions (Araújo & New 2007). Finally, the predicted suitability maps based on the ensemble model were converted into binary maps by applying a cut-off value which minimizes the difference between sensitivity (true positive prediction, i.e. presence) and specificity (true negative prediction, i.e. absence) (Nenzén & Araújo 2011).

3. RESULTS

3.1. Baseline distribution area

All 3 species exhibited distinct geographical affinities, which are reflected in the different habitat selection patterns. *Canis anthus* and *Vulpes vulpes* occurred in the arid climate where the areas concerned were drier than desert areas. *V. zerda* is mostly linked to the desert topoclimatic unit of the study area. The distribution areas based on the kernel method were 63 980, 49 476 and 42 191 km^2 for *C. anthus*, *V. vulpes* and *V. zerda*, respectively (Fig. 2). *C. anthus* was more generalized, *V. vulpes* was mainly found near urban areas, and *V. zerda* was mostly found in the sandy area of southwestern Tunisia.

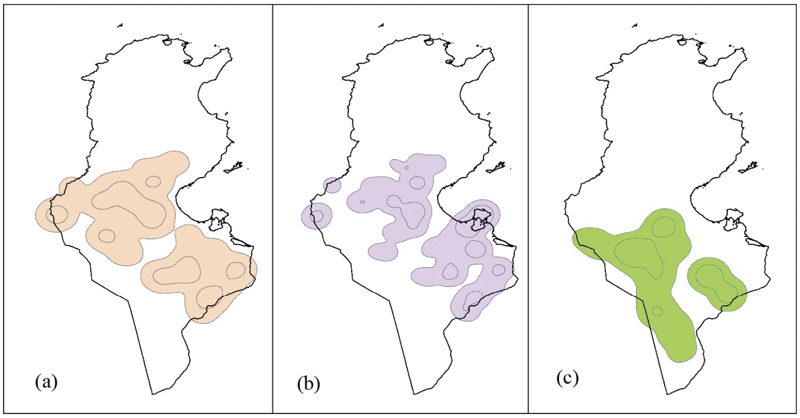

Fig. 2. Kernel distribution areas of (a) *Canis anthus*, (b) *Vulpes vulpes* and (c) *V. zerda* in arid and desertified areas of Tunisia. Shading indicates 95 % fixed kernel density (KD) estimates; lines indicate 90 % KD estimates

3.2. Model performances

The overall model performance (Fig. 3) was good for *C. anthus* (mean ± SE; TSS: 0.85 ± 0.01; specificity: 0.94 ± 0.00; sensitivity: 0.91 ± 0.01), *V. vulpes* (TSS: 0.88 ± 0.00; specificity: 0.96 ± 0.01; sensitivity: 0.92 ± 0.01) and *V. zerda* (TSS: 0.88 ± 0.01; specificity: 0.90 ± 0.00; sensitivity: 0.98 ± 0.01). The results of all the modelled species can therefore be used in the following analysis.

3.3. Importance of environmental variables

For all models, bioclimatic and topographic variables have important effects on the distribution of carnivores (Fig. 4). In the model of *C. anthus*, precipitation during the warmest quarter had the greatest influence (mean ± SE: 21 ± 2 %) followed by annual mean temperature, minimum temperature of the coldest month and maximum temperature of the warmest month (Fig. 4). In the model of *V. vulpes*, annual mean temperature made the largest contribution (20 ± 2 %), followed by maximum temperature of the warmest month and precipitation during the warmest quarter, with an average of 17 ± 1 % for each. The minimum temperature of the coldest month contributed 12 ± 2 % to the model of *V. vulpes*. The cumulative contributions of these factors reached values as high as 66 %. In the model of *V. zerda*, the 5 most influential variables were elevation (19 ± 2 %), annual mean temperature (15 ± 2 %), mean temperature of the wettest quarter (15 ± 1 %), maximum temperature of the warmest month (12 ± 2 %) and bare terrain (12 ± 1 %). Aspect and isothermality had a limited influence on the models of these 3 species, while no effect was observed for urban areas and the availability of water (Fig. 4).

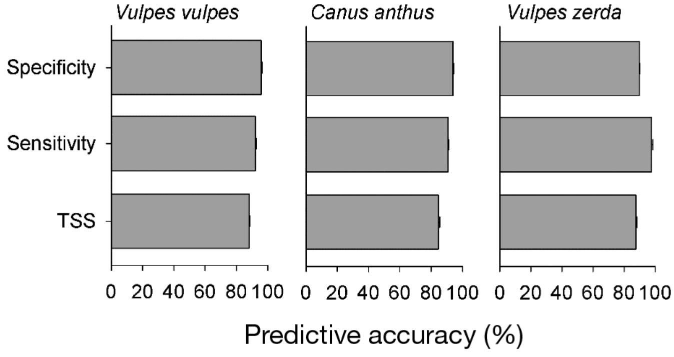

Fig. 3. Indicators of the predictive accuracy (%, mean ± SE) of species distribution models for *Canis anthus, Vulpes vulpes* and *V. zerda* in Tunisia. TSS: true skill statistic (scores range from 0 to 1, where 0 describes a model no better than random while 1 describes absolute consistency between predictions and observations)

3.4. Predicted habitat suitability in the event of future global warming

The predicted extension of suitable areas under future conditions was mostly variable (Fig. 5, Table 2). A general reduction in the spatial distribution of suitable environmental conditions was observed for the 3 species, with the most dramatic case being *C. anthus*, which is predicted to lose approximately 86 and 97 % of suitable areas by the 2030s and 2080s, respectively (Fig. 5, Table 2). Reductions ranging from 40 to 58 % of suitable space (Table 2) between the 2030s and 2080s were predicted for *V. vulpes* in the southeastern Tunisia and at the northern edge of the sandy area (Fig. 5), while in other regions it became fragmented. Loss of habitat areas which are currently suitable was predicted for sectors of southwestern Tunisia. Overall, a restricted range expansion of suitable habitat areas was observed for *V. vulpes*, which will migrate to a small part of southeastern Tunisia by the 2080s (Fig. 5). The most significant drop in suitable areas was observed in southwestern Tunisia for *V. zerda* (Fig. 5). Furthermore, areas with low values of suitable habitats were situated close to urban areas in the southeast and north of the country.

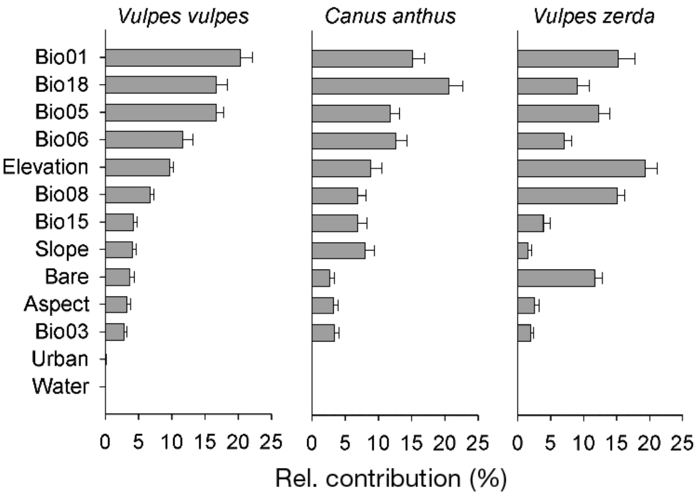

Fig. 4. Relative contributions (%, mean ± SE) of environmental predictors for determining the baseline distributions of carnivore species. The relative contributions of environmental predictors of all algorithms were averaged using identical weighting as for the ensemble models, and were then averaged for all species. Environmental predictors are defined in Table 1

Global warming is predicted to bring about major reductions (50%) in suitable areas for *V. zerda* by the 2030s, but it was predicted that suitable areas for this species would increase by the 2050s and 2080s. However, these areas are still smaller than its baseline distribution area (Fig. 5, Table 2).

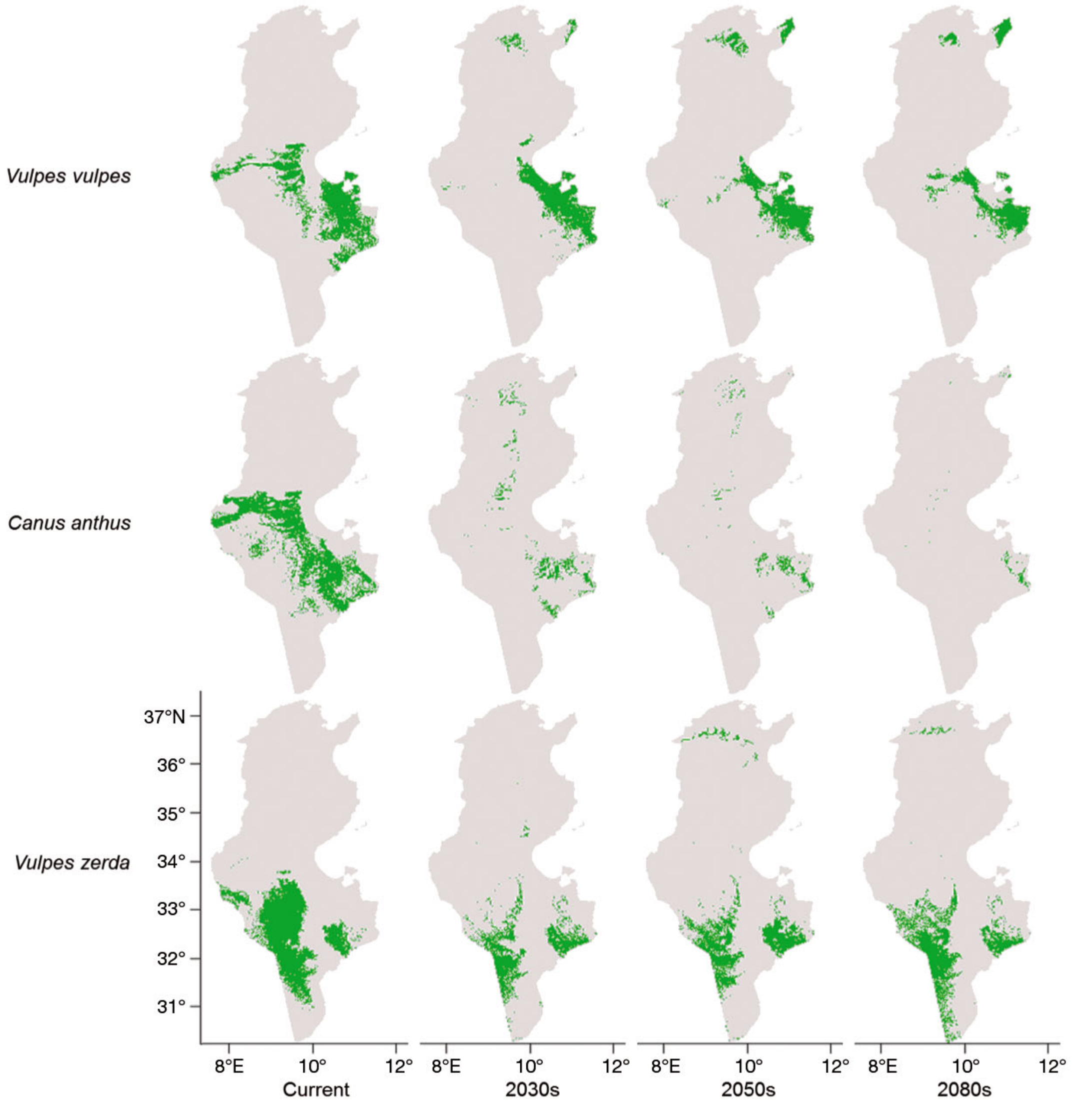

Fig. 5. Habitat suitability maps for *Canis anthus*, *Vulpes vulpes* and *V. zerda* based on species distribution models in Tunisia. Green and grey are suitable and unsuitable habitat, respectively

Table 2. Number of sites out of 10 000 random sites where species were expected to occur up until 2080. Values in parentheses indicate the % change in range, i.e. the reduction in suitable habitat relative to the current value

Species	Current	2030s	2050s	2080s
Canis anthus	2332	326 (−86)	193 (−92)	66 (−97)
Vulpes vulpes	1887	1129 (−40)	1014 (−46)	791 (−58)
Vulpes zerda	2346	1161 (−50)	1335 (−43)	1557 (−33)

4. DISCUSSION

Our study represents the first attempt to establish the observed and potential distribution areas of 3 carnivores (*Canis anthus*, *Vulpes vulpes* and *V. zerda*) in the North Sahara Desert. *C. anthus* and *V. vulpes* occurred in the most humid regions close to productive environments with water availability in the study area, while the distribution area of *V. zerda* was mostly related to the desertified topoclimatic unit in southwestern Tunisia. Due to recent settlements, the expansion of *V. vulpes* to southern Tunisia has spread along the major paved route of the region. Our current work successfully predicted the distribution of 3 carnivore species in the North Sahara, increasing our confidence that the models will be useful for future attempts to understand possible changes in species' ranges which are driven by climate change. In addition, our models used these relationships between climate change and species' distributions to provide a robust set of projected changes for native carnivores across the North Sahara Desert landscape between now and the end of the century. We performed a more detailed study on the suitable habitat of carnivores that will function as an important first step in developing strategies and managing carnivore conservation.

SDMs revealed that the most important variables related to species' distributions were the warmest quarter and annual mean temperature. Projections for future conditions reported reductions in suitable areas for almost all of the species. This work supports the prediction that the decrease in precipitation and increase in temperature will be the main factors affecting the presence of several species in North Africa (Martínez-Freiría et al. 2013, Li et al. 2015). These results are similar to those of Martínez-Freiría et al. (2013), who suggested that precipitation and temperature are the main factors affecting endemic reptiles in Morocco. These factors seem to reflect a progressive increase in aridity in the country over time, with a high impact in lowland and midland arid areas, but a more stable maintenance of climatic conditions close to the sea. Indeed, climate predictions for North Africa include drastic increases in temperature and decreases in precipitation, leading to the likely retraction of Mediterranean ecosystems and the expansion of arid habitats and desertification (Malcolm et al. 2006, Garcia et al. 2012, Niang et al. 2014). Variations in these climatic conditions were predicted to induce range shifts and reductions of suitable areas for carnivores, especially for *C. anthus* and *V. vulpes*.

Changes in spatial distribution as the climate changes by the 2080s are apparent, with more locations with unsuitable habitats and few suitable habitats continuing to exist. The predicted distribution of *C. anthus* indicates a substantial decrease in habitat suitability, which makes it highly vulnerable to extinction. This species should be targeted for monitoring programs to assess its population status and to ensure its survival over time. *V. zerda* seems to be associated with high temperatures in bare areas with a high elevation. This implies that it is a species associated with Saharan climate. Indeed, the sandy areas are characterized by a low density of vegetation and severe climatic conditions. It can be concluded that *V. zerda* tolerates higher temperatures than the other 2 species. In addition, increased desertification explains the continued survival of this species in southern Tunisia. In the northern Mediterranean region, the area of unproductive shrubland is expected to expand, while in North Africa and the Near East, most of the steppe rangeland could give way to desert by the 2050s or earlier. Elevation strongly influenced our *V. zerda* models, but had a minor influence on *C. anthus* and *V. vulpes*. The elevation of southwestern Tunisia is greater than that of the southeast, which reflects the importance of elevation in the distribution of *V. zerda*. As climatic conditions remain more stable in lowlands close to the sea, some suitable areas could maintain the presence of *V. vulpes* by the 2080s, thereby acting as refugia under climate change (Martínez-Freiría et al. 2013).

The importance of urban and water factors in our models must be interpreted with caution. Although our analysis shows that these factors had no influence on the outcome of the carnivore models, in reality, even though *C. anthus* and *V. vulpes* are found near human settlements (Cuzin, 2003, Sillero-Zubiri et al. 2004, Brito et al. 2009), this does not imply that these regions are suitable for the species. Many species worldwide are affected by human factors, but assessments of range dynamics according to climate change scenarios frequently disregard their effects

(Thuiller et al. 2006, Garcia et al. 2012). Nonetheless, in the case of African terrestrial vertebrates, about 18% of species evaluated by the IUCN are considered to be threatened as a consequence of habitat loss and fragmentation, or because of poaching. Indeed, irrespective of the major effect which climate change will have on future species' distributions, human activities are well known to have facilitated dramatic reductions in the distributional ranges of species (e.g. Ceballos & Ehrlich 2002, Midgley et al. 2003, Pimm et al. 2006, Martínez-Freiría et al. 2016), and continue to be an important factor when it comes to determining the range size of many taxa.

SDMs are being widely used to predict spatiotemporal variations in plant and animal populations (Koo et al. 2015). Many studies have shown similar patterns in the reduction of suitable areas under climate warming (e.g. Martínez-Freiría et al. 2013, 2016, Koo et al. 2015, Li et al. 2015). We found that, under future climatic conditions, the distribution of *C. anthus* and *V. vulpes* will decrease significantly. Although the distribution of *V. zerda* will decrease slightly at first, it will subsequently begin to increase. These trends are in line with those found in previous studies (Pedersen et al. 2014, Hu et al. 2015). The application of our modelling approach allows us to identify suitable areas where the implementation of some conservation measures is of huge importance to such carnivores. Carnivores play an important role in structuring communities (e.g. Ripple et al. 2010, Levi & Wilmers 2012); thus a decrease in the distribution of *C. anthus* and *V. vulpes* may significantly affect the relative abundance of their prey. In many circumstances, such impacts will help to maintain mammalian, avian, invertebrate and herpetofaunal abundance and richness (Ripple et al. 2014). Also, the decrease of the carnivores' distribution in general can affect plant communities indirectly through predation on seed predators and the consumption of fruits. The species we studied appeared to be closely connected to particular climatic conditions and habitats. This will allow managers to preserve suitable habitats in order to sustain their populations in the near future through field management practices (Kalle et al. 2013).

Our model predictions performed excellently based on TSS (>0.85). However, we are well aware that factors other than climate and land use define niche space, and that our consensus models may not accurately predict the impact of global warming on the distribution of North African desert carnivores. Such factors involve interactions between coexisting species and human activities (Martínez-Freiría et al. 2016). The interactions between a carnivore and its ecosystem have an important effect on its distribution, since the abundance of prey and competition between them can modify the existence of the species even in the presence of a suitable climatic environment (Kissling et al. 2012). The predictions are also affected by model uncertainty and the limitations of the measurement system (Koo et al. 2015), such as observation error, strategies of data collection (Rocchini et al. 2012) and different sampling dates between regions (Tonkin et al. 2015). We used a fine grid cell size (1 × 1 km), which should prevent the kind of underestimations related to the use of large grid cells for distributional data (Araújo et al. 2006, Carvalho et al. 2010). Secondly, uncertainties deriving from the statistical technique (Wiens et al. 2009, Barbet-Massin et al. 2012) were avoided through the use of 6 high-performing modelling algorithms (TSS > 0.6).

In conclusion, the models based on presence data for carnivores and environmental input data for 4 different time periods suggested that populations of *C. anthus* and *V. vulpes* will experience less favourable conditions in southern Tunisia in the future. The relative importance of climate, land use and topographic factors on carnivores varied considerably among the 3 studied species across southern Tunisia. Precipitation in the warmest quarter and annual mean temperature were the main factors affecting their future distribution. Studies for monitoring populations and managing and conserving habitats should be performed in Tunisia and should focus primarily on *C. anthus* and *V. vulpes*, as they are identified as being highly vulnerable to climate change. New conservation zones should be considered in those areas, since the refugia identified for these species are mainly in the lowlands close to the sea.

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