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Desert-adapted species are vulnerable to climate change: Insights from the warmest region on Earth



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ABSTRACT

Climate change is eroding biodiversity and conservation efforts have focused on species' potential responses to those changes. Biological traits associated with sensitivity and adaptive capacities may contribute in identifying a species vulnerability to climate change. Desert-living species could be particularly vulnerable to climate change as they may already live at their physiological limits. This work aims to identify functional groups in Sahara-Sahel endemics, to determine their spatial distribution and to evaluate how the predicted magnitude and velocity of climate change in the region might affect them. We collated biological traits data for all Sahara-Sahel endemics. We then summarized the functional strategy of each species into functional groups with different sensitivities and adaptive capacities to climate change. Future climate scenarios were reclassified to identify areas where predicted temperature and precipitation approach the physiological limits of each group. We calculated the velocity of temperature and precipitation change as the ratio of the temporal gradient to the spatial gradient. Specific magnitudes and velocities of environmental change threaten our seven function groups differently according to their level of exposure and geographical distributions. Groups are more exposed to precipitation than to temperature changes. The more exposed functional groups lived mostly in flat areas, where the predicted magnitude and velocities of change were also the highest. Some functional groups with high adaptive capacities (e.g. volant species) may be able to colonize distinct areas. Other groups with low sensitivity and adaptive capacity (e.g.: ectotherms with small home ranges) may be vulnerable to climate change. Different biological traits contributed to the extent to which climate change harms species. The desert-adapted species may be the most vulnerable ones. The vulnerability patterns of Sahara-Sahel functional groups provide indications of combinations of biological traits and biodiversity's exposure to climate change in other warm deserts of the world.

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1. Introduction

Climate change is widely accepted as a major threat to biodiversity, with potential to accelerate the pace of its loss (Bellard et al., 2014). We need accurate forecasts of climate change effects on biodiversity to design the most proactive conservation strategies. Most current assessments of its potential impacts are focused either on changes in the geographical extent of

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species' climate space or changes in the exposure of areas to different dimensions of climate change. Yet, models focused on changes in the species' distribution fail to explicitly reflect the broad range of climate-induced stress affecting populations' ecology and species' physiology (Foden et al., 2013; Willis et al., 2015). Studies rarely appreciate the quantifications of areas exposed to the different dimensions of climate change in combination, despite their different implications for biodiversity (Garcia et al., 2014). For instance, decreasing local climate suitability (magnitude) may threaten species living close to their upper climatic tolerance limits, and high velocities of climate change may affect the ability of species to track suitable climatic conditions, particularly those with low dispersal abilities (Garcia et al., 2014). As such, climate change' assessments and identification of the most vulnerable species would profit from the incorporation of biological traits and combined analyse of the effects of different dimensions of climate change.

Rapidly changing climate will likely alter the selective pressures acting on species. Species vulnerability to these changes will yet depend on their level of exposure. That is, to what extent will their geographical environment space change their sensitivity, i.e. the lack of potential for a species to persist *in situ*. And how will it affect their adaptive capacity, i.e. the species' inability to avoid the harmful impacts of climate change through dispersal or micro-evolutionary change (Foden et al., 2013; Moritz and Agudo, 2013; Willis et al., 2015). Among other biological traits correlated with species extinction risk, those related with sensitivity include thermoregulation, activity, habitat specialisation, reproduction, and ecological plasticity. Those related with adaptive capacity include dispersal ability and body size (Brook et al., 2008; Kearney, 2013; Pincheira-Donoso et al., 2013; Bennie et al., 2014; McCain and King, 2014; Buckley et al., 2015). For instance, diurnal ectotherms may be particularly sensitive to temperature changes, as they regulate body temperature directly from external sources and simultaneously present low adaptive capacity due to relatively sedentary behaviour and small home ranges (Barrows, 2011). Increasing body size and activity time in mammals strongly relate to local extirpations, range contractions, and population declines (McCain and King, 2014). Beside species' evolutionary history (e.g.: its exposure to past climate fluctuations) and physiological plasticity or acclimation increase their resilience to environmental fluctuations; the magnitude of future climate change may outstrip species' sensitivity and adaptive capacity (Seebacher et al., 2014). Moreover, species living in flat areas are potentially more exposed to climate change as high change velocities are higher there (Loarie et al., 2009). For species to persist they will need to keep pace with the moving climate, and exhibit high adaptive capacities, such as dispersal (Walther et al., 2002; Massot et al., 2008). As such, the magnitude and velocity climate change will have fundamentally different impacts depending on the species sensitivity and adaptive capacities.

Deserts and arid regions harbour unexpectedly high diversity of species subject to a strong climatic control (Ward, 2009). Due to convergent evolution of biological traits and/or adaptive processes, desert species exhibit unique morphological, physiological and/or behavioural adaptations to climatic extremes (Murphy et al., 2012, 2013; Wilson and Pitts, 2012; Brito et al., 2014). Despite of this, they may be sensitive to increasing temperature, due to physiological limits constraining the evolution of species' tolerances to high temperatures (Araújo et al., 2013). Furthermore, in arid environments, changes in precipitation might have even more dramatic impacts on biodiversity in comparison to other ecosystems. Precipitation changes affects species as it promotes germination and food and water supply (Beatley, 1969; Pianka, 1970; Brown and Ernest, 2002). Moreover, in warming areas, rainfall fluctuations stimulate evaporation or soil warming, promoting aridity (Ward, 2009; Sherwood and Fu, 2014). Indeed, the impact of the progressive aridity conditions on arid adapted species have been already observed by negative population trends, extinctions and range shifts in the Sahara-Sahel (Trape, 2009; Brito et al., 2014). The region displays high topographical and climatic heterogeneity and has experienced recent and strong climatic oscillations (Wang et al., 2008; Claussen, 2009; Brito et al., 2014). Such fluctuations have greatly shaped land-cover and biodiversity distribution (Dumont, 1982; Le Houérou, 1992, 1997; Drake et al., 2011), suggesting that the predicted strong and fast climate changes for the region (IPCC, 2013; Loarie et al., 2009) will threaten its biodiversity. Although, Sahara-Sahel endemics are arid-adapted species, they might be sensitive to temperature and precipitation changes, or have a capacity to handle to the predicted changes. Thus, we should identify the groups of species that combine biological traits related to vulnerability to different dimensions of climatic change. Their identification will allow designing future conservation plans for Sahara-Sahel biodiversity under climate change.

Our main goal is to identify the most vulnerable functional groups in the Sahara-Sahel under future climate changes, by addressing four questions: (i) which functional groups are more vulnerable to magnitude of climate change; (ii) which functional groups will likely be able to keep pace with predicted velocity of climate change; (iii) where are located the potentially most vulnerable areas? and (iv) how are the most vulnerable functional groups represented within the current protected areas network? We hypothesise that functional groups comprising diurnal ectotherms with low adaptive capacities (e.g.: small home range and body size) should be most vulnerable to changes in the magnitude and velocity of temperature while groups containing endotherms with low adaptive capacity (low dispersal ability) should be most vulnerable to changes in precipitation. Functional groups harbouring taxa simultaneously sensitive and with low adaptive capacity and living in flat areas are expected to be more vulnerable to the velocity of climate change. The identification of functional groups and their potential vulnerability to climate change are essential to design proactive conservation plans for Sahara-Sahel biodiversity.

2. Material and methods

Our study area covers a total of $\approx 11,200,000$ km² and includes the Sahara ($\approx 8,200,000$ km²) and Sahel ($\approx 3,000,000$ km²), as defined by Olson et al. (2001) (Fig. 1). We have divided the study area into 4417 grid cells, using a grid of ~ 54 km ($\sim 0.5^\circ$) resolution projected to Africa Albers Equal Area Conic projection.

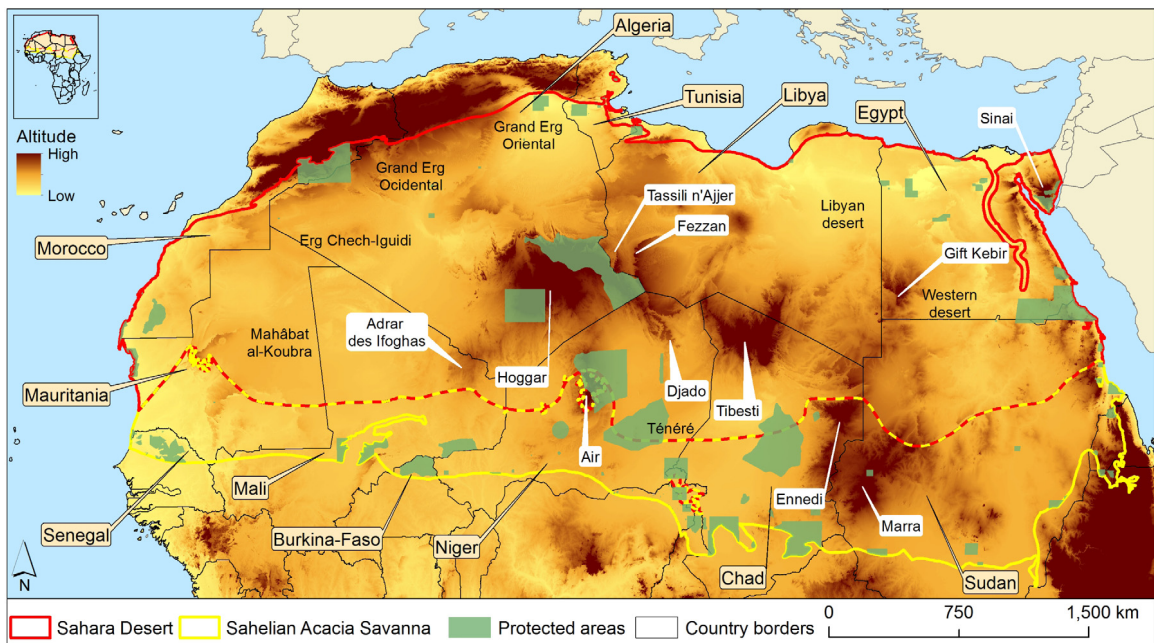


Fig. 1. The Sahara-Sahel study area. Limits of the Sahara-Sahel (Olson et al., 2001) and distribution of protected areas (green). Countries names are in pink balloons. Main mountain names (white balloons) and empty quarters of the Sahara-Sahel used in the text. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2.1. Distribution data and biological traits

The total list of endemics vertebrates (125 species) occurring in the Sahara-Sahel was retrieved from IUCN (2013) and BirdLife International & NatureServe (2011) databases (97 terrestrial amphibians, reptiles and mammals and birds) and further supplemented with local distribution data from published atlases (28 reptiles; Sindaco and Jeremčenko, 2008; Sindaco et al., 2013). We have considered species with at least 75% of their range overlapping the study area as endemics or nearly endemic species of the Sahara-Sahel. Polygons of species distribution were intersected with a grid of grid of ~ 54 km ($\sim 0.5^\circ$) degree resolution to generate matrices of species presence/absence by grid cell.

We described the functional strategy of each species using two main categories: sensitivity and adaptive capacity. These are thought to be mostly closely related with responses to climate change (Foden et al., 2013). Given that there is no information about physiological traits for Sahara-Sahel endemics, we used surrogate biological traits related with species extinction risk (Brook et al., 2008; Kearney, 2013; Pincheira-Donoso et al., 2013; Bennie et al., 2014; McCain and King, 2014; Buckley et al., 2015). We collated information for each species biological trait from bibliography, public databases and expert knowledge (List A.1). Sensitivity was described using seven categorical traits: (1) Thermoregulation, coded as ectothermic or endothermic; (2) Water dependency in some stage of life cycle, coded as yes or no; (3) Habitat selection, coded as presence/absence in vegetated areas, bare areas, rocky outcrops, and/or sandy areas; (4) Activity, coded for simplicity as nocturnal or diurnal; (5) Reproduction, coded as oviparity or viviparity; (6) Diet, coded as omnivorous, carnivorous, insectivorous or herbivorous; and (7) Ecological plasticity, given by the number of ecoregions where the species were present, ranging from one to seven. Adaptive capacity was described using three biological traits: (1) home range size, coded using categories: <1 km²; 1–5; 5–10; 10–20; 20–40; and >40 km²; (2) Body size (cm), which was a continuous variable; and (3) Volant, coded as yes or no.

To estimate the level of redundancy among biological traits, we used a correlation test to each pair of biological traits. We first created a distance matrix for each biological trait, using Gower distance, as most of the variables are nominal (Gower, 1971; Podani, 1999). We performed a Mantel test with the Spearman rank correlation method between every possible pair of distance matrices, using the package Vegan implemented in R. All biological traits had correlations values below 0.432, with the only exception of Thermoregulation and Reproduction ($\rho = 0.677$; Table A.1).

2.2. Identification of functional groups

We have computed a pairwise differences matrix between species using Gower distance, which allows mixing different types of variables (Gower, 1971; Podani, 1999). Given that the importance of each biological trait is unknown *a priori*, we gave equal weights to each. As habitat selection is a qualitative biological trait for which a species could have more than one attribute (e.g. they could occur both in bare and rocky areas) different weights are required (Laliberté and Legendre, 2010).

We have assumed a weight $w_i = x_i/b_i$ to each binary variable (e.g. presence/absence in bare areas) required to reclassify the main trait (Habitat selection), where x_i is the original weight given to the main biological trait i and b_i is the number of binary variables required to re-code trait i (Laliberté and Legendre, 2010). We used the “ k -means” method and the Simple Structure index (SSI) to estimate the number of functional groups and functional group richness. To estimate the independent contributions of each biological trait to the global Gower’s distance, we correlated squared distance matrices for each trait with the global squared distance (Pavoine et al., 2009). A Principal Coordinates Analysis (PCoA) using Gower distance matrix was calculated to locate each functional group in the multidimensional trait space. The resulting PCoA axes were taken as new “traits” to calculate the volume of the multidimensional trait space occupied by species within the functional space. The multidimensional trait space of each functional group was the minimum convex hull that includes all species from each functional group (Villéger et al., 2008). As negative PCoA cannot be represented in a Euclidean space, we have applied a Cailliez correction (Cailliez, 1983). As dimension reduction was required, only two PCoA axes were used to define the minimum convex hull for all. All analysis were performed within R environment (version 3.1.1), with the FD package, version 1.0–12 (Laliberté et al., 2014).

To test if the number of functional groups differs from what we expect if we selected species at random, we performed a simulation approach to create null distributions of Functional Group Richness (FGR) for a given species richness value. We randomly selected species from the total number of species richness, and performed 999 replicates to produce a final median null distribution of the FGR values. Based on the null distributions, we calculated the standard effective size (SES) for each pixel ($\sim 0.5^\circ$) to measure the deviation of the observed value from the mean of the null distribution, but removing the directional bias associated with the decrease in variance in the expected values with increasing species richness (Swenson, 2014). P -values were calculated to test our null hypothesis: the number of functional groups in each pixel does not differ from what one expects by chance. For negative values of SES, FGR is lower than expected by chance and positive SES, the opposite. We used the same simulation approach to test if the patterns of each functional group are constant if we selected species at random.

Each observed group richness was converted into percentage of group richness in relation to the total species richness by pixel. This was done to access presentation of each group by pixel. To access the current extent of each group we reclassified latter maps, in order to ensure 50% of representativeness of each group by pixel. For groups with distribution skewed to the low values, we retained 75% as the distribution of the values.

2.3. Climate data and analysis

For current and future climate data we used 30-arcsecWorldClim Annual Mean Temperature and Total Annual Precipitation bioclimatic variables (<http://www.worldclim.org/>). Future variables were download for two time periods available 2041–2060 and 2061–2081 (hereafter referred as: 2050s and 2080s, respectively), based on two greenhouse gas concentration trajectories or representative concentration pathways (RCP4.5 and RCP 8.5) implemented by ten general circulation models (GCMs) of the Coupled Model Intercomparison Project Phase 5 (CMIP5) multi model dataset: CCSM4, HadGEM2-AO, HadGEM2-ES, IPSL-CM5A-LR, MIROC-ESM-CHEM, MIROC-ESM, MIROC5, MRI-CGCM3 and NorESM1-M adopted by the IPCC for its fifth Assessment Report (AR5) (IPCC, 2013). We excluded GCMs for which all RCPs were not available, with the exception of BCC-CSM1-1 that was excluded due to artefacts detected in one of the variables. Representative Concentration Pathways (RCPs) are four greenhouse gas concentration and we used only the RCP 4.5 and RCP 8.5 in order to test two extreme scenarios. All variables for all time periods were projected to Africa Albers Equal Area Conic and upscale to ~ 54 km ($\sim 0.5^\circ$).

We summarize the 10 GCMs, into mean, upper and lower projection by calculating the mean and the mean \pm s.d. of the 10 GCMs for 2080s and for each pathway (Fig. A.1). To identify areas where each functional group might be more exposed to climate change, we reclassified the mean, upper and lower projections and overlapped them with each functional group extent. To reclassify the temperature projections, we applied lower critical temperatures observed for reptiles, mammals, and birds as threshold and according to each functional group (mean–s.d., according to Araújo et al., 2013). We applied the lower values, as the maximum of the annual mean temperature predicted for the study area is lower than the mean critical values. To reclassify the precipitation projections, we used the value for classifying arid environments (200 mm; Greve et al., 2011). Latter reclassifications have resulted in binary maps for each functional group classifying areas above and below critical temperatures and precipitations. The range of each functional group was intercepted with current protected areas network.

We have computed the velocity of climate change for both mean annual temperature ($^\circ\text{C}$) and total annual precipitation (mm) as the ratio of the temporal gradient to the spatial gradient (Loarie et al., 2009). To compute temporal gradients, we first calculate separate slopes for each pixel from each of the 10 separate GCMs time series and for the two pathways, using linear regression. To calculate the spatial gradient, from the current climate maps, we calculated spatial gradients from a 3×3 grid cell neighbourhood using the average maximum technique. We calculated the velocity of climate change for each pathway and for the 10 separate GCMs, and summarized into the mean velocity of climate change. We plotted the histograms of the velocity of climate change for each functional group extent of occupancy and compared with the mean velocity of climate change of each group.

3. Results

We identified seven functional groups in the Sahara-Sahel based on the Gower distance matrix between species traits (Fig. 2; Table A.2) and reproduction and thermoregulation were the biological traits with higher independent contribution

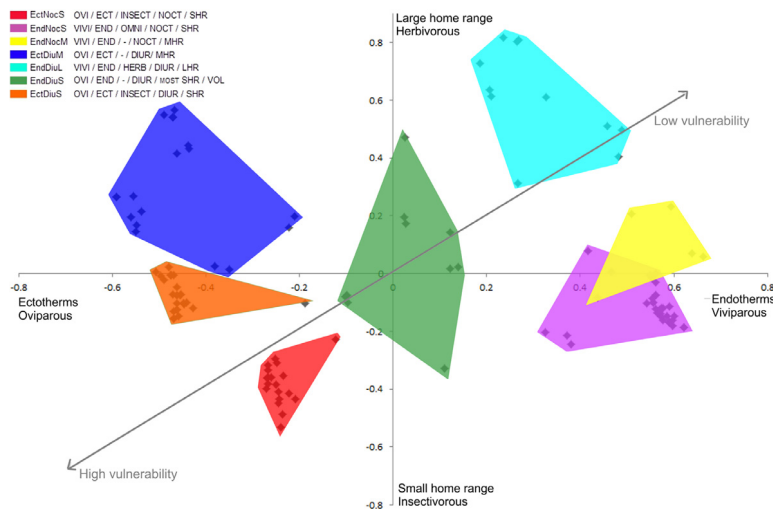


Fig. 2. Minimum convex hull of Sahara-Sahel functional group derived from a pairwise distance matrix between species traits and summarized in the first two axes of a PCoA. Groups characterised by the traits: OVI—oviparous; VIVI—viviparous; END—endotherms; ECT—ectotherms; INSECT—mostly insectivorous; OMNI—mostly omnivorous; HERB—herbivorous; NOCT—nocturnal; DIUR—diurnal; SHR—small home range; LHR—large home range; VOL—volant.

to the global mean distance (0.69 and 0.68, respectively, Table A.3): EctNocS is mostly nocturnal ectotherms, mostly insectivorous with small home ranges; EndNocS grouped small mammals, mostly nocturnal and omnivorous, with small home ranges; EndNocM grouped nocturnal endotherms with medium to high home ranges; EctDiuM had diurnal reptiles with medium home ranges; EndDiuL grouped diurnal endotherms, herbivorous and with moderate to high home ranges; EndDiuS included birds with small home ranges; and EctDiuS is mostly constituted of lizards, which are diurnal ectotherms with small home ranges (Fig. 2; Table A.2).

Functional group richness was a function of species richness. It does not significantly differ from what one expects from species richness (Fig. A.2). The observed number of function groups in each pixel was not significantly different than averaged expected by chance ($\max = 8$, $p > 0.5$ Fig. A.2). The same was observed for the pattern of each group, as species consistently grouped with the same species ($p > 0.05$, Fig. A.3).

Functional groups exhibited different distribution patterns across the Sahara-Sahel (Fig. 3): (i) from wide distribution covering both Sahara and Sahel ecoregions (EctNocS; EndNocS; EndNocM; EctDiuM and EndDiuL) to restricted to one of the ecoregions (EndDiuS to the Sahel and EctDiuS to the Sahara); and (ii) from distribution across the lowland areas (EndNocS and EctDiuS) to restricted to mountain ranges (EndNocM and EndDiuL). Groups were potentially exposed to distinct magnitudes of temperature and precipitation changes according to their range (Fig. 4): (i) most groups were affected principally by changes in precipitation rather than by temperature (EctNocS, EctDiuM, EndDiuL and EctDiuS). EndDiuS was most susceptible to temperature changes (Fig. 4; Fig. A.1; Table A.4). (ii) Two groups (EndNocS and EndNocM) were affected by both precipitation and temperature changes in almost the same proportions (Fig. 4; Fig. A.1; Table A.4). (iii) There were groups (EndNocS, EctDiuM, EndDiuL and EctDiuS) that were exposed in all their extent of occurrence, while other groups (EctNocS, EndNocM and EndDiuS) were only sensible in parts of their extent (Table A.4). (iv) Areas of exposure to both precipitation and temperature changes were in the transition between Sahara-Sahel (affecting EndNocS, EndNocM, EndDiuS and EctDiuS).

Groups were more exposed to velocity of change in precipitation according to their range in comparison to temperature velocity (Fig. 5). The overall distribution of values of velocity of temperature change in each group range was below the mean values of velocity for each group. In contrast, the values of velocity of precipitation change in EndNocS, EndNocM, EndDiuS and EctDiuS was skewed suggesting vulnerability to precipitation change.

From the total range of each functional group only less than 11% is located in currently protected areas (Table A.4). Overall, less than 8% of the potentially vulnerable areas were located in protected areas. No more than 1% of the exposed ranges of groups EctNocS, EndNocS, EctDiuM, and EctDiuS to temperature change are currently protected, and less than 3% of the exposure areas of groups EctNocS, EndNocM and EndDiuS to precipitation changes are located within protected areas. Less than 3.4% of the range of groups potentially not exposed to climate change is located in current protected areas.

4. Discussion

4.1. Uncertainties in functional groups and climate change analyses

Different dimensions of climate change have different implications for biodiversity depending on the degree of a species' exposure, plus its sensitivity to the new conditions and its adaptive capacity to track shifting habitats. We developed a framework for identifying the Sahara-Sahel endemics most vulnerable to the magnitude and velocity of climate change. We

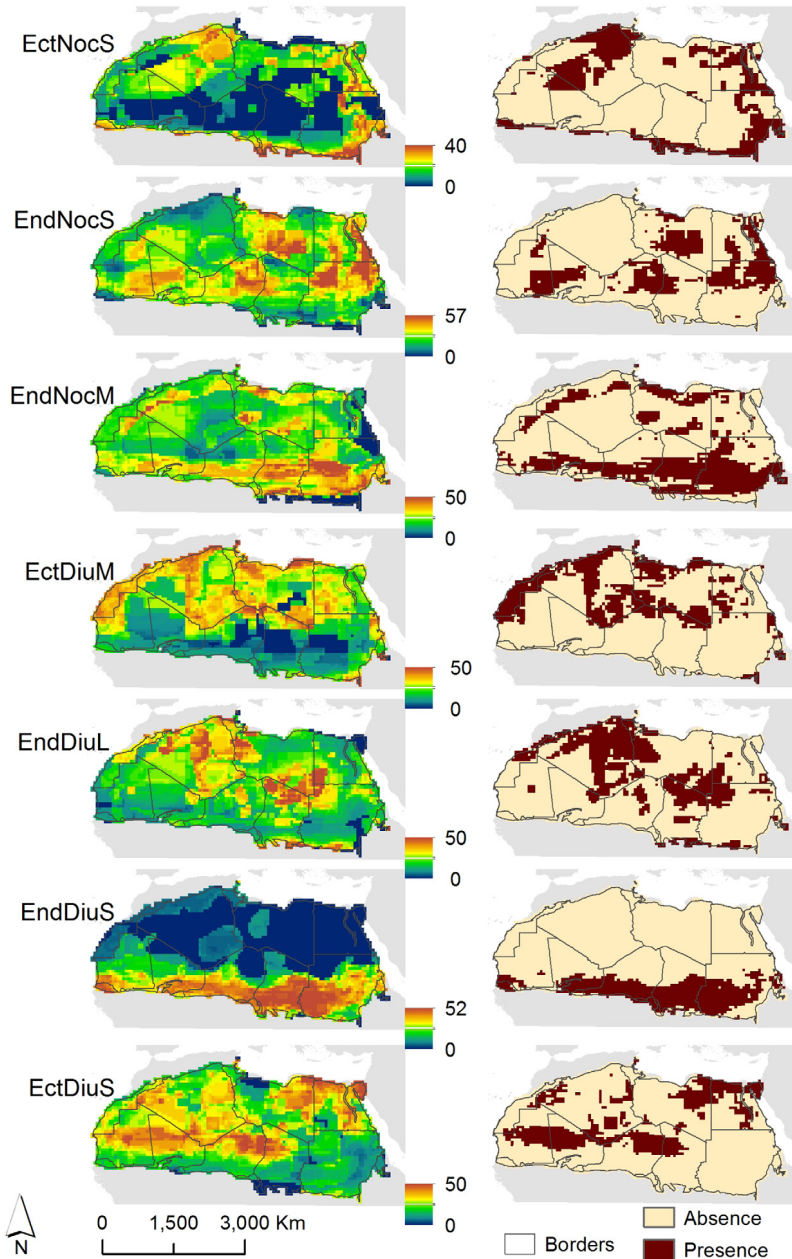


Fig. 3. Distribution patterns of functional groups in the Sahara-Sahel. The left column depicts species richness of each group, expressed as percentage of species of each group in relation to the total number of species per grid cell. The right column depicts the area of occupancy of each functional group.

did this by measuring their level of exposure and simultaneously using functional groups as proxies for testing sensitivity and adaptive capacities. Despite being challenging, assessments of climate change impacts on biodiversity can benefit from enhanced capacity to represent species by their biological traits (Dawson et al., 2011; Araújo et al., 2013). Due to the lack of information on species' physiological traits, we recognize the susceptibility of the identified functional groups. The inclusion of quantitative traits (e.g.: water balance, metabolic rate, body temperature, thermal limits, evapo-transpiration, reproduction rates, dispersal capacity) would probably yield more accurate results. To overcome the lack of ecophysiological parameters data, we have increased the number of the biological traits used and have set an upper limited of groups to be created, avoiding a large number of groups characterized by few biological traits.

The Sahara-Sahel region's long-term local conflicts and remoteness hamper biodiversity assessments (Brito et al., 2014). As such, there are regional sampling gaps that cause generalised lack of high resolution observational data (e.g.: GPS points) for the taxa addressed in the current study. Consequently, we based the analyses developed on the extent of occurrence from IUCN, Birdlife and published distribution atlases. Using range polygons forced means we developed analyses with

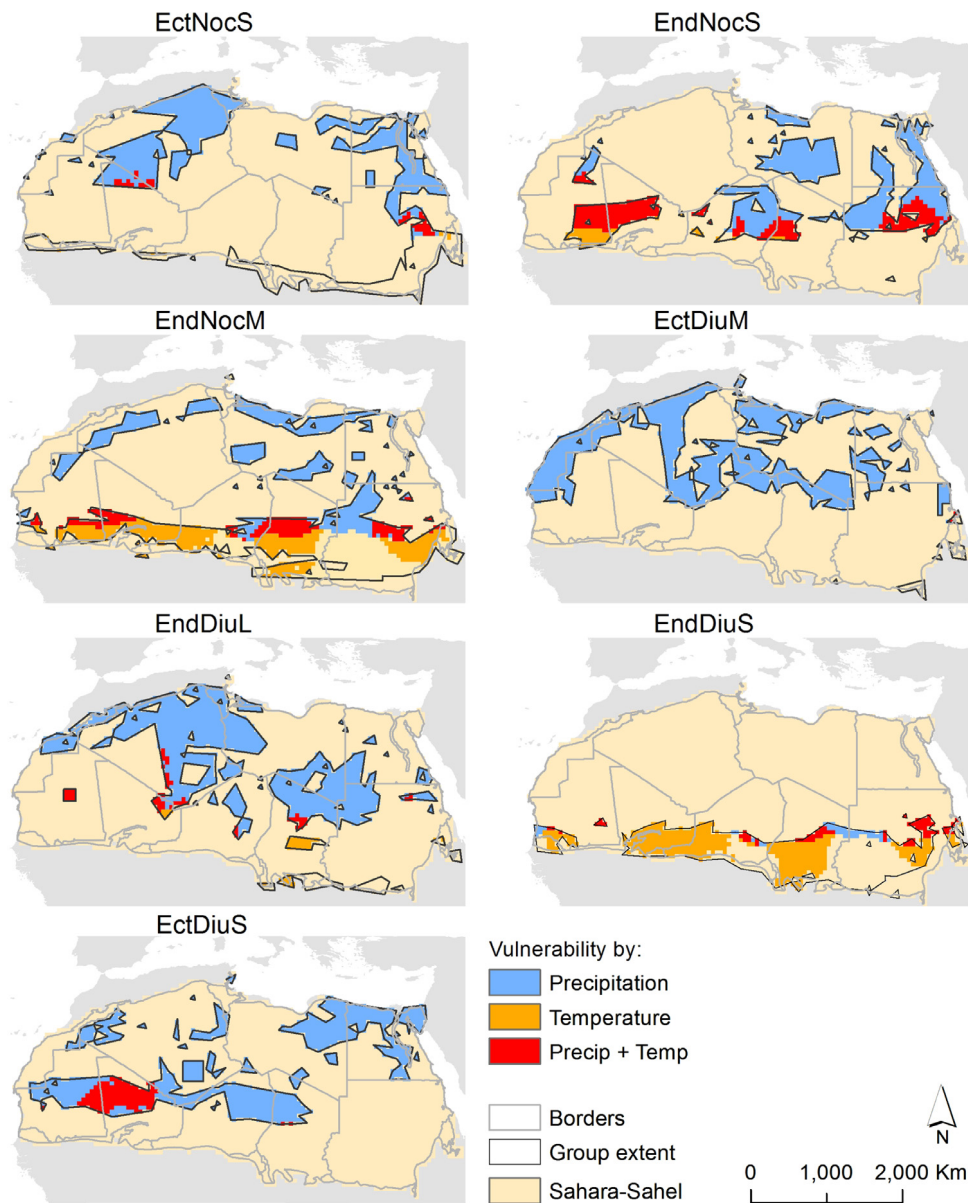


Fig. 4. Vulnerability scenarios for each functional group in 2080. Vulnerability identified by magnitude of change in mean annual precipitation (mean of GCM's), in upper annual mean temperature (mean of GCMs + sd), and in both factors (Precip + Temp) by 2080 in comparison to present time. Thresholds to identify vulnerability areas for each functional group were the lower critical temperature (mean of critical temperatures – sd) and 200 mm of precipitation. Extent of occurrence of each functional group is presented (black polygons).

a low spatial resolution (half-degree cells). This hampered the application of ecological niche modelling algorithms for assessing gains and losses of climatically suitable areas. Although range polygons might overestimate areas of exposure, they allow including species with small and narrow ranges for which there is insufficient observational data to derive accurate ecological niche models. The approach here used allows us to analyse the entire species dataset without restrictions.

The low resolution of species distribution data forced climate change analyses to be performed also with coarse spatial resolution. Despite diluting the spatial distribution of climate, uncertainties are more likely to arise from the climate projections used to drive climate models. In fact, GCMs exhibited considerable variation among models, which can affect the accuracy of biodiversity impact assessments under climate change (Buisson et al., 2010). Given those variations, we have applied a multi-model ensemble average forecast technique (Loarie et al., 2009; Fordham et al., 2011). We summarized uncertainty by mapping the upper and lower values of changes in the magnitude of climate change. Yet, to retain the differences among them, we calculated the individual velocity of climate change for each GCMs. Finally, we calculated a mean of the velocity of climate change and its standard deviation of each GCM and pathway, to account for their differences.

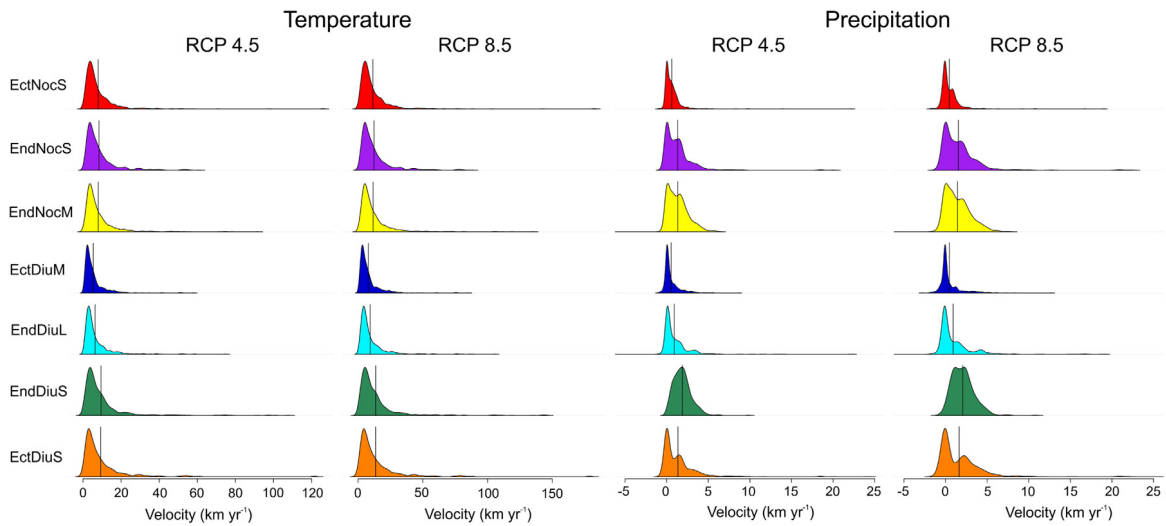


Fig. 5. Predicted velocity of climate change within the extent of occurrence of each functional group. Velocity of annual mean temperature (temperature) and annual mean precipitation (precipitation) change calculated for two pathways (RCP 4.5; RCP 8.5). Vertical bars indicate the mean velocity for each group.

We identified the level of exposure of each functional group, by intersecting their range with the distribution of the magnitude and velocity of climate change. We then applied a threshold (minimum critical thermal limit) according to the observed values for endotherms and ectotherms reported in the bibliography (Araújo et al., 2013). As we have applied the minimum critical thermal (mean critical temperature—s.d. of the mean critical temperature), the identified areas of exposure to temperature are conservative and probably overestimated. However, we did this because the mean critical thermal limits described in the literature were higher than the expected maximum temperature for the region for 2080 (Araújo et al., 2013; IPCC, 2013).

4.2. Functional groups and vulnerability to climate change

Functional group and species richness followed similar distribution patterns. The observed strong relation might be due to the extreme environments of the Sahara-Sahel. Species adapted to extreme conditions are likely to converge in physiological traits due to organism's limitations to adapt to harsh conditions (Bickford et al., 2006). As such, areas harbouring more species are expected to present a higher number of functional groups. Yet, this spatial match does not prevent or even preclude assessing the number of functional groups and their vulnerability to the predicted climate changes.

We summarized the functional strategy of the Sahara-Sahel endemics into seven functional groups with different sensitivity and adaptive capacities as well as distribution patterns. Functional groups in the Sahara-Sahel were vulnerable to distinct magnitudes and velocities of climate changes. As expected, they were particularly exposed to changes in precipitation. A lack of precipitation defines deserts (Ward, 2009), so we expect their species to be more vulnerable to precipitation fluctuations, either by the degree of exposure or by sensitivity and adaptive capacities. Both nocturnal and diurnal mammals (EndNocM and EndDiuL, respectively) and birds (EndDiuS) range in areas of decreasing precipitation and/or increasing temperature in the future. Despite being exposed, they might be able to overcome these changes by physiological plasticity. Under extreme temperatures and limited water availability, these species may be able to survive. They present physiological, morphological, and behavioural mechanisms developed to either avoid or tolerate harsh environmental conditions (Holl, 1985; Gouat, 1993; Williams and Tieleman, 2005; Cain III et al. (2006); Vale et al., 2012). Moreover, they might have the capacity for colonizing other suitable areas. As an example, despite having small home ranges, birds (EndDiuS) exhibit reduced metabolism rates, small clutch sizes, and slow nestling developments (Williams and Tieleman, 2005). As such, they have the capacity to forage food at large distances and/or colonize other suitable areas. Although the combination of sensitivity and adaptive capacity related traits might favour these groups, they include some of the most threatened species inhabiting the Sahara-Sahel (e.g.: *Addax nasomaculatus* and *Nanger dama*). These species have experienced extreme range reductions due to human activities (e.g.: direct persecution, harassment, poaching, and land transformation; Wachter et al., 2004). Currently, only around 8.5% of their exposed extent of occurrence is protected. As human's activities might constitute barrier to these species dispersal (Duncan et al., 2014), further studies should identify suitable corridors through which species might disperse without human pressure.

The most vulnerable functional groups in the Sahara-Sahel are small mammals and lizards (EndNocS and EctDiuS). They were potentially exposed to changes in the magnitude and velocity of precipitation and also locally exposed to temperature changes. Despite being arid-adapted species, they might be living close to their upper thermal limits. As tolerance to heat is largely conserved across lineages, latter species will unlikely evolve physiological tolerances to increasing heat (Araújo

et al., 2013). Lizards (EctDiuS) are directly sensitive to temperature changes due to their thermoregulation mechanisms (e.g. Cowles and Bogert, 1944; Pianka, 1970; Hoffmann et al., 2013; Ferri-Yáñez and Araújo, 2015). They also have small home ranges and body size and thus low adaptive capacity. Additionally, their dispersal is strongly affected by rising temperatures (Massot et al., 2008). On the contrary, small mammals (EndNocS) are known to tolerate high body temperatures and/or high environmental temperatures (Boyles et al., 2011). They might be able to cope with warming trend, despite overspending energy and potentially compromising the reproduction success and dispersal capacity (Beatley, 1969; Boyles et al., 2011). Moreover, the reproduction success and abundance of both groups has still been associated to rainfall and food availability (Beatley, 1969; Pianka, 1970). The level of exposure, associated with a combination of intrinsic and extrinsic traits makes both small mammals and lizards the most vulnerable groups in the Sahara-Sahel. Yet their sensitive and adaptive capacity depends on several of other intrinsic factors such as genetic diversity; phenotypic plasticity, evolutionary rates and life history traits (Dawson et al., 2011). In addition, other dimensions of climate change might differently affect these groups. For instance, lizards might be affected by changes in climate extremes, and in distance and direction of change of the analogous climates, due to their low adaptive capacity, particularly low dispersal ability. Further investigation on other dimensions of climate change is needed for the functional groups here identified. Moreover, climate change is more than changes in temperature and rainfall. There are also changes in surface temperature, evaporation and wind, for instance. Further ecological, genetic and physiological studies should be combined to confirm if these groups are able to adapt by ecological plasticity or dispersal to other suitable areas.

4.3. Vulnerable areas and status of protection

The flat and arid Sahara-Sahel regions harbour the most vulnerable functional groups. They are predicted to be highly exposed to climate change (Loarie et al., 2009). Parts of the ranges of small mammals (EndNocS) and lizards (EctDiuS) were located in the most arid and flat areas of the Sahara-Sahel. These functional groups have been exposed to past climate fluctuations, as the region has experienced multiple dry-wet cycles since the Pliocene (5.3 to 2.5 Mya), which have shaped local biodiversity distribution (Brito et al., 2014). While past exposure to climate fluctuations may provide indications on the ability of the functional groups to persist, it is unknown if species will be able to keep pace with future climate changes through behavioural shifts or dispersal. As a result of ongoing climate warming, it has been observed up-slope movements to higher elevations and latitudes (Parmesan, 2006; Guralnick and Pearman, 2010). During the past climatic oscillations, Sahara-Sahel Mountains were refugia for several species (Trape, 2009; Brito et al., 2014). However, their role under future climate changes for most vulnerable functional groups is unknown. Even if mountains hold suitable habitats in the future, the capacity of small mammals and lizards to track rapid climate change is uncertain. At leading-edges, colonization rates are determined jointly by rates of reproduction and dispersal associated with the availability of suitable resources in novel habitats (Angert et al., 2011). On the other hand, the vast empty-quarters, where the magnitude and velocities of climate change will be higher, hold some of the most threatened functional groups. Currently, they are crucial refugia for threatened species (e.g.: *Chlamydotis undulate*, *Addax nasomaculatus* and *Acinonyx jubatus*; Saleh et al., 2001; Beudels et al., 2005; Chammem et al., 2012). The location of the threatened functional groups and the lack of formerly protection (Table S3) reinforce their vulnerability to future climate changes. Increasing the size of current protected areas through habitat corridors and the establishment of new reserves has been suggested to try to carry the moving climates and ecosystems (Hannah et al., 2008; Loarie et al., 2009). As both mountains and lowlands are potential refugia in the Sahara-Sahel, a network of protected areas should create connectivity between them. Monitoring programs of biodiversity status and trends should be design to the most threatened species and potentially vulnerable functional groups, as well as to particularly local hotspots, such as small sized mountain inland waters (Vale et al., 2015) that may be crucial for local persistence of water-dependent species.

5. Conclusions

The combination of different biological traits contributed to the extent to which species are exposed to climate change. Desert-adapted species with low adaptive capacity constituted the most vulnerable functional groups in the Sahara-Sahel. They are also present in other warm deserts in the world, so they might be equally vulnerable to future climatic changes. Indeed, the sensitivity to climate change for desert's tortoises was already observed in the Mojave-Sonora Desert (Barrows, 2011). Our study is a preliminary assessment of the most vulnerable functional groups in the Sahara-Sahel, but further studies should incorporate genetic diversity and evolutionary rates. This study provides indications on level of exposure to climate change and combination of biological traits related with sensitivity and adaptive capacity that may endanger biodiversity in warm deserts worldwide. The methodological framework here implemented could be applied to other warm deserts as well as to other biomes.

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Appendix A. Supplementary data

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