Diversity and Distributions, (Diversity Distrib.) (2016) 22, 371–384

A Journal of Conservation Biogeography
Diversity and Distributions

BIODIVERSITY RESEARCH

Conservation Biogeography of the Sahara-Sahel: additional protected areas are needed to secure unique biodiversity

José C. Brito[1,2*], Pedro Tarroso[1], Cândida G. Vale[1,2], Fernando Martínez-Freiría[1], Zbyszek Boratyński[1], João C. Campos[1,2], Sónia Ferreira[1,2], Raquel Godinho[1,2], Duarte V. Gonçalves[1,2], João V. Leite[1], Vanessa O. Lima[1], Paulo Pereira[1], Xavier Santos[1], Maria J. Ferreira da Silva[1,3,4], Teresa L. Silva[1,2], Guillermo Velo-Antón[1], Joana Veríssimo[1], Pierre-André Crochet[5], Juan M. Pleguezuelos[6] and Sílvia B. Carvalho[1]

[1]*CIBIO/InBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos da Universidade do Porto, R. Padre Armando Quintas, 4485-661 Vairão, Portugal,* [2]*Departamento de Biologia, Faculdade de Ciências, Universidade do Porto, Rua Campo Alegre, 4169-007 Porto, Portugal,* [3]*ONE (Organisms and Environment), School of Biosciences, Cardiff University, The Sir Martin Evans Building, Museum Avenue, Cardiff CF10 3AX, UK,* [4]*CAPP, School of Social and Political Sciences, Technical University of Lisbon, Rua Almerindo Lessa, 1300-663 Lisboa, Portugal,* [5]*CNRS-UMR 5175, Centre d'Ecologie Fonctionnelle et Evolutive, 1919 route de Mende, F-34293 Montpellier-Cedex 5, France,* [6]*Departamento de Zoología, Facultad de Ciencias, Universidad de Granada, E-18071 Granada, Spain*

*Correspondence: José Carlos Brito, CIBIO/InBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos da Universidade do Porto. R. Padre Armando Quintas, 4485-661 Vairão, Portugal.
E-mail: jcbrito@cibio.up.pt

ABSTRACT

Aim Identification of priority conservation areas and evaluation of coverage of the current protected areas are urgently needed to halt the biodiversity loss. Identifying regions combining similar environmental traits (climate regions) and species assemblages (biogroups) is needed for conserving the biodiversity patterns and processes. We identify climate regions and biogroups and map species diversity across the Sahara-Sahel, a large geographical area that exhibits wide environmental heterogeneity and multiple species groups with distinct biogeographical affinities, and evaluate the coverage level of current network of protected areas for biodiversity conservation.

Location Sahara-Sahel, Africa.

Methods We use spatially explicit climate data with the principal component analysis and model-based clustering techniques to identify climate regions. We use distributions of 1147 terrestrial vertebrates (and of 125 Sahara-Sahel endemics) and apply distance clustering methods to identify biogroups for both species groups. We apply reserve selection algorithms targeting 17% of species distribution, climate regions and biogroups to identify priority areas and gap analysis to assess their representation within the current protected areas.

Results Seven climate regions were identified, mostly arranged as latitudinal belts. Concentrations of high species richness were found in the Sahel, but the central Sahara gathers most endemic and threatened species. Ten biogroups (five for endemics) were identified. A wide range of biogroups tend to overlap in specific climate regions. Identified priority areas are inadequately represented in protected areas, and six new top conservation areas are needed to achieve conservation targets.

Main conclusions Biodiversity distribution in Sahara-Sahel is spatially structured and apparently related to environmental variation. Although the majority of priority conservation areas are located outside the areas of intense human activities, many cross multiple political borders and require internationally coordinated efforts for implementation and management. Optimized biodiversity conservation solutions at regional scale are needed. Our work contradicts the general idea that deserts are uniform areas and provide options for the conservation of endangered species.

DOI: 10.1111/ddi.12416
http://wileyonlinelibrary.com/journal/ddi

Keywords

Africa, biogeographical zones, conservation planning, desert diversity, environmental variation, gap analysis

INTRODUCTION

Motivated by the ever-increasing concerns about global biodiversity loss affecting world biomes (Butchart *et al.*, 2010; Cardinale *et al.*, 2012), the strategic goals of the Aichi Biodiversity Targets (CBD, 2010) listed global identification of priority areas for the conservation and evaluation of the effectiveness of current protected areas as key factors that need assessing to halt biodiversity loss by 2020. These objectives can be achieved under a systematic conservation planning approach (Margules & Pressey, 2000), which targets the conservation of the following: (1) current biodiversity patterns by protecting areas maximizing complementarity among the distribution of distinct species groups and (2) micro-evolutionary processes by preserving distinct populations occupying environmental gradients (Smith *et al.*, 2001; Pressey *et al.*, 2007). Regions combining similar climatic traits (climate regions) and species assemblages (biogroups, *sensu* biotic elements; Hausdorf, 2002) can be useful as coarse surrogates of biodiversity and eco-evolutionary processes when molecular data are not available or geographically comprehensive (Carvalho *et al.*, 2011). As such, conserving climate regions and biogroups assures both biodiversity persistence and evolution (Olson & Dinerstein, 1998).

Deserts and arid regions (defined by aridity index: < 0.20; Ward, 2009) represent about 18% of the world's land mass (Trabucco & Zomer, 2009). They are generally perceived as rather homogeneous and species poor, thus attracting less conservation concern in comparison with other regions (Durant *et al.*, 2012). However, they harbour about 25% of continental vertebrate species, including some of the most endangered species in the world (Mace *et al.*, 2005), and their communities are largely made up of highly adapted, specialized species that are found nowhere else.

The Sahara is the largest warm desert in the world and, together with the neighbouring arid Sahel, covers 11,230,000 km^2 and spans over 17 countries (Olson *et al.*, 2001) (Fig. 1). The diversity of Sahara-Sahel topographical features, its climatic heterogeneity and steep environmental gradients (Brito *et al.*, 2014) form distinct bioclimatic and phytogeographical regions (Quézel, 1978; Le Houérou, 1997; Sayre *et al.*, 2013), but their assessment using spatially explicit tools and multivariate integrative approaches is still missing. Moreover, the Sahara-Sahel faunal communities are composed of species with distinct biogeographical affinities, whose ranges have been shaped by multiple putative refugia and dispersal corridors linked to environmental variation (Brito *et al.*, 2014), but the composition and the number of biogroups remain unknown.

The Sahara-Sahel exhibits relatively low levels of anthropogenic change and low human population density in comparison with other biomes (CIESIN-FAO-CIAT, 2005; Ellis *et al.*, 2010). However, both regions have been affected by human activities (particularly over-hunting) that have driven many large-sized vertebrates to regional extinction and are endangering relict fauna associated with isolated mountain water pools and grassy habitats (Brito *et al.*, 2014; Durant *et al.*, 2014). Other pressures, such as overgrazing, wood collection, habitat conversion into farmland and exploitation of natural resources, are increasing and are considered serious threats to Sahara-Sahel biodiversity (Brito *et al.*, 2014; Duncan *et al.*, 2014). Several long-term conflicts (IEP, 2012) also hinder regional biodiversity research and hamper conservation funding (Durant *et al.*, 2012). Relatively large protected areas have been established (summing up to 7.4% of the Sahara-Sahel; Fig. 1) aimed mostly to conserve threatened large ungulates (e.g. Aïr-Ténéré and Tin Toumma, Niger) and wintering and migration bird areas of global importance (e.g. Banc d'Arguin, Mauritania). Nonetheless, biodiversity representation and persistence across climatic gradients, at regionally appropriate resolution to account for environmental variability and genetic diversity, remain unevaluated. Conservation planning scenarios identifying optimized conservation networks that maximize spatial representation of overall biodiversity patterns and processes, and minimize conflicts with human activities are needed to allocate the usually limited conservation funds (Waldron *et al.*, 2013). The Sahara-Sahel is an extreme region affected by devastating cyclic droughts (Brito *et al.*, 2014), where increased vulnerability to extinction of endemic functional groups has been associated with predicted climate changes (Vale & Brito, 2015). Thus, the Sahara-Sahel constitutes priority ecoregions (*sensu* Olson *et al.*, 2001) to apply conservation frameworks for the identification of optimized conservation networks.

We use spatially explicit climate data and distributional data of 1147 species of amphibians, reptiles, breeding birds and mammals to address the following questions: (1) How many regions with similar climatic features (climate regions) and species assemblage sharing similar distribution patterns (biogroups) can be defined within the Sahara-Sahel and how are they distributed? (2) Where are located the areas of highest species richness, particularly for endemic and threatened species? (3) Considering distinct conservation planning scenarios and data sets, where are priority conservation areas located? (4) Which is the level of coverage of the current protected area network for biodiversity conservation, as assessed by climate regions and biogroups? This study provides the first broad biogeographical classification of

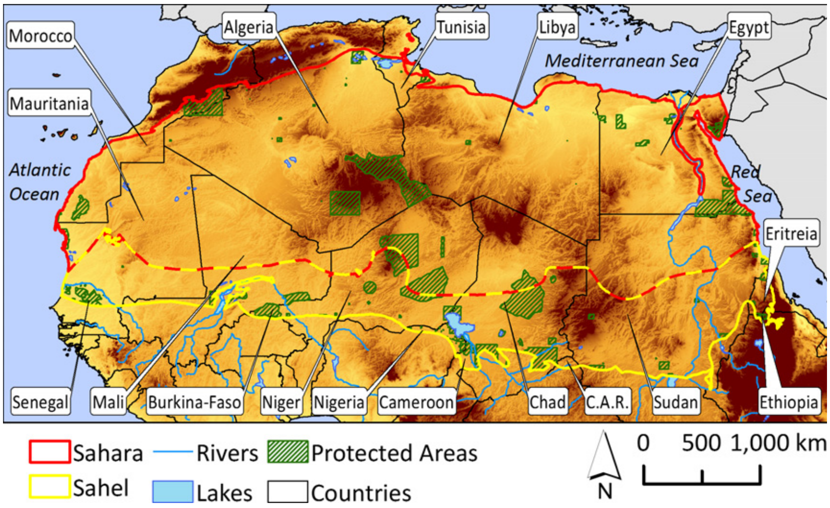

Figure 1 The Sahara-Sahel. Limits of the Sahara-Sahel (Olson *et al.*, 2001) and distribution of the main water bodies and protected areas. Elevation represented as a relief shading of brown gradient. C.A.R.: Central African Republic.

Sahara-Sahel vertebrate biodiversity, which serves to set up priorities for biodiversity conservation in this large and environmentally extreme region (see Fig. S1 for methodological overview).

METHODS

Study area

The study area covers a total of ≈11,200,000 km^2 and includes the Sahara (≈8,200,000 km^2) and Sahel (≈3,000,000 km^2) ecoregions (Fig. 1 and Fig. S2 in Supporting Information). The study area was divided into 4417 grid cells, using a grid of 0.5 degree resolution under the WGS84 coordinate reference system for all further analyses.

Climatic variables and identification of climate regions

Seven climatic variables, downloaded with 2.5-arc second spatial resolution (Hijmans *et al.*, 2005; Trabucco & Zomer, 2009), were upscaled to 0.5 degrees (≈50 km) using the average values. These variables are commonly used in climatic regionalization analyses (e.g. Rodrigues *et al.*, 2015) and included annual mean temperature (°C), maximum temperature of warmest month (°C), minimum temperature of coldest month (°C), temperature annual range (°C), annual precipitation (mm), precipitation of wettest month (mm), and potential evapotranspiration (mm). After data standardization, a principal components analysis (PCA) was performed to summarize the environmental data into three orthogonal components (PCs), accounting for 97.4% of the variability (Fig. S3). The PCs were then used in a model-based cluster analysis that allows determining the structure of the climate data without prior knowledge of the number of clusters (Fraley & Raftery, 2002). Using mixture models with multiple clustering schemes allows using model selection statistics, such as Bayesian information criterion (BIC), to identify the best clustering solution. Using the package 'MCLUST' in R (Fraley & Raftery, 2002), ten mixture models were tested with clustering schemes ranging from one to 20 clusters. The identified clusters represent different environmental states, designated hereafter as climate regions (see Appendix S1 for details).

Species distribution data and identification of biogroups

The list of continental terrestrial vertebrates that occurs in the Sahara-Sahel (derived primarily by expert elicitation) was retrieved from IUCN (2013) together with distribution polygons. It comprises 1147 species, including 53 amphibians, 198 reptiles, 586 breeding birds and 310 mammals (see Table S1). The current ranges were updated with data from the published atlases (Sindaco & Jeremcenko, 2008; Sindaco *et al.*, 2013). Historical distributions were built for 16 species that experienced recent range contraction based on reference works (Largen & Yalden, 1987; Ciofolo, 1995; Barnes, 1999; Emslie & Brooks, 1999; Manlius, 2000; Ostrowski *et al.*, 2001; Saleh *et al.*, 2001; Uphyrkina *et al.*, 2001; Rookmaaker, 2004; Beudels *et al.*, 2005; Haas *et al.*, 2005; Barnett *et al.*, 2006; Thiollay, 2006; Lagrot *et al.*, 2007; Bouché *et al.*, 2011; Brito *et al.*, 2011; Hekkala *et al.*, 2011). Historical range data were used to identify biogroups, while current range data were used for identifying priority areas for conservation. Species distribution polygons were intersected with a grid of 0.5 degree resolution to generate matrices of species presence/absence by grid cell (see Appendix S2 for details). Biogroups were defined as groups of species whose distributions are significantly more similar to each other than to those of species of other groups. Biogroups were identified using clustering methods implemented in the R package *prabclus* (Hennig & Hausdorf, 2008), based on the Kulczynski distance between each pair of species ranges (Hausdorf, 2002), for the total set of 1147 species (BTs) and for the 125 endemic species (BEs) separately (see Appendix S3 for details).

Identification of priority areas for conservation

The approach identified the minimum set of areas required to represent 17% (following Aichi Biodiversity Targets; CBD, 2010) of the distribution of each individual species and of all possible combinations of climate regions and biogroup distributions. The combination of climate regions and biogroup distributions is expected to act as a surrogate for the adaptive and neutral components of genetic diversity (Carvalho *et al.*, 2011). Neutral variation is mostly determined by vicariance events that probably have conditioned the genealogy and distribution of species in similar ways (Avise, 2009), while adaptive speciation is mediated by the environmental conditions and thus expected to differ among distinct environments (Doebeli & Dieckmann, 2003). Hence, the conservation of populations of a given species inhabiting distinct climate regions is expected to allow the preservation of adaptive processes along environmental transitions, while the conservation of populations occurring in distinct biogroups should allow preserving the neutral component of genetic diversity in areas where vicariance events played an important role in structuring biotas (Smith *et al.*, 2001; Pressey *et al.*, 2007; Carvalho *et al.*, 2011), such as the Sahara-Sahel (Brito *et al.*, 2014). Thus, conservation solutions ensure that 17% of the range of each species was covered and that complementarity of species representation is maximized, by selecting grid cells where both most endemic species occur and where several species co-occur.

Priority conservation areas were identified by running the software Marxan (Ball *et al.*, 2009) on two data sets (Total and Endemics) containing either all species (Total) or only endemic species (Endemics) and all respective combinations of climate regions and biogroups occurring in the study area in each case (see Appendix S4 for details). For each data set, priority areas for conservation were identified under two scenarios of grid cell availability (Fig. S4): i) *unlimited*, in which the algorithm was allowed to select areas from the overall study area without restrictions and ii) *limited*, in which the algorithm was forced to include in the solution all the grid cells currently categorized as protected area (IUCN & UNEP, 2013) and forced to exclude from the solution all the grid cells where gas, oil and mining exploitation occurs (for details on data availability see Brito *et al.*, 2014) or where human population density (CIESIN-FAO-CIAT, 2005) is above levels (> 50 inhabitants km^{-2}) known to cause biodiversity decline (Cincotta & Gorenflo, 2011). For each data set, the 'best solution' out of 1000 Marxan runs (i.e. the solution that retrieved the lowest score in the Marxan objective function; Ball *et al.*, 2009) and the frequency of selection of each grid cell were identified. The best solution was intersected with the distribution of protected areas and the occurrence of human activities. For all data sets and scenarios, it was quantified the number of prioritized grid cells with or without human activities and that occurred inside or outside the protected areas (IUCN & UNEP, 2013).

RESULTS

Distribution of climate regions

Seven clusters were retrieved as the most likely number of climate regions (Fig. S5). Five of them (CLIM1: 8.7% of the study area; CLIM2: 11.9%; CLIM5: 25.5%; CLIM6: 20.2%; and CLIM7: 13.0%) form latitudinally arranged belts (Fig. 2) across the continent following the temperature and precipitation gradients (Fig. S6). The CLIM3 (6.7%) and CLIM4 (13.8%) regions were in the centre of the study area and displayed the harshest climates in comparison with other climate regions (lowest rainfall levels in CLIM3–CLIM4 and highest temperatures in CLIM3; Fig. S6).

Less than 10% (1.1–9.6%) of the distribution of each climate region is represented in the current protected areas network, and the coverage of CLIM2–CLIM3 is particularly low (1.1% and 1.9%; Fig. S7).

Conservation status of terrestrial vertebrates

The majority of the 1147 taxa analysed (96.1%) are not classified as threatened according to IUCN criteria, but reptiles have a disproportionate number of species unassessed for extinction risk (Table 1). Mammals are the most threatened group (51.1% of the species within the categories of Vulnerable, Endangered or Critically Endangered; Table 1), particularly ungulates (17.8%; Table S1). On average, 11.5% of the distribution of species (14.7% for endemics) is covered by the current protected areas network (from 134 species with null inclusion to four species with full inclusion; 16 and 2 for endemics, respectively), and 84.4% of total species (76.8% for endemics) have < 17% of their range included inside the protected areas (Table S1).

Distribution of species richness, endemism and vulnerability to extinction

Species richness distribution of all 1147 terrestrial vertebrates is concentrated in the southern Sahel, followed by the north-western Sahara and the lower Nile valley (Fig. 3, Total).

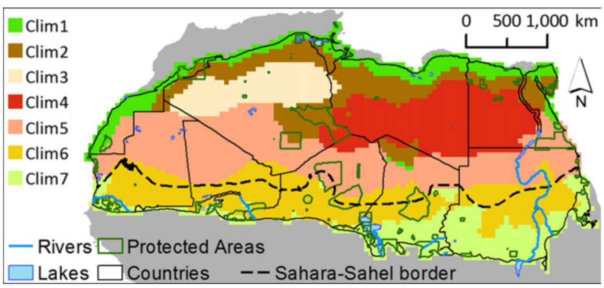

Figure 2 Main climate regions within the Sahara-Sahel. Climate regions defined by spatial principal components analyses (see Methods and Appendix S1 for details and Fig. S3) and model-based clustering algorithm at 0.5 degree resolution.

Table 1 Distribution of IUCN conservation status categories among amphibians, reptiles, breeding birds and mammals known to occur in the Sahara-Sahel. Total number (and percentage) of species is given for each taxonomic group and conservation category.

IUCN status	Amphibians	Reptiles	Birds	Mammals	Total *N* species
Extinct in the wild (EW)	–	–	–	1 (0.3)	1 (0.1)
Critically endangered (CR)	–	3 (1.5)	–	4 (1.3)	7 (0.6)
Endangered (EN)	–	1 (0.5)	4 (0.7)	4 (1.3)	9 (0.8)
Vulnerable (VU)	–	6 (3.0)	8 (1.4)	15 (4.8)	29 (2.5)
Near threatened (NT)	1 (1.9)	6 (3.0)	11 (1.9)	15 (4.8)	33 (2.9)
Least concern (LC)	50 (94.3)	84 (42.5)	563 (96.0)	250 (80.7)	947 (82.5)
Data deficient (DD)	2 (3.8)	10 (5.1)	–	21 (6.8)	33 (2.9)
Not evaluated (NE)	–	88 (44.4)	–	–	88 (7.7)
Total *N* species	53	198	586	310	1147

Consequently, in absolute values, the Sahel accumulates most of the threatened species and, together with the west and north-west Sahara and the Central Sahara Mountains, gathers also the highest richness of endemic species, and also the species with uncertain conservation category (Data Deficient or Not Evaluated by IUCN; Fig. S8). When considering species richness in relation to total species in a grid cell, the greatest proportion of endemic species, threatened species or species with uncertain conservation category is found in the Sahara (Fig. 3).

Distribution of biogroups

The clustering analysis retrieved a total of 10 biogroups as the solution that provides both the smallest number of biogroups and the greatest number of species classified into one of the biogroups (90.1% of species analysed). The distribution of the 10 biogroups is spatially aggregated and tends to follow a latitudinal gradient (Fig. 4). Analysis restricted to the 129 endemic species retrieved five biogroups that included 80% of endemics analysed (Fig. 5).

There was a general spatial similarity between the distribution of climate regions and particular biogroups (Fig. S9). For all species, the distribution of much of the diversity included in BT3 and BT6 (Fig. 4) overlaps the range of CLIM1 (Fig. 2), and the same pattern was found between BT1 and BT7-10 with CLIM7 (Fig. S9 right). For endemic species (Fig. 5), BE3 and partially BE1 broadly overlap with CLIM6 (Fig. 2), while BE4 broadly overlaps with CLIM1-2. The relatively range-restricted biogroups (BE2 and BE5) and biogroups ranging in peripheral regions (BT2) are distributed across multiple climate regions or do not fully cover any particular climate region. There was a general spatial similarity between the distribution of biogroups for endemics in relation to total species: BE1 overlaps with BT5, BE2 with BT6, BE3 with BT4 and BE4 with BT3 (Figs 4 & 5).

Less than 10% of the distribution of each biogroup (except BT8: 15%) is represented in the current protected areas network, and the coverage of BT6-7 and BE2 is particularly low (below 4% in all cases; Fig. S7).

Priority areas for conservation

Prioritized areas differed substantially between the conservation planning scenarios and whether total or endemics species data sets (and all combinations of climate regions and biogroups) were targeted, and ranged from 16.8% to 22.7% of the study area (Table 2). Larger area was required in the *limited* scenario relatively to the *unlimited*, regardless of the data set used and spatial aggregation levels of prioritized grid cells in the final solutions (Figs. 6 & S10).

Selected grid cells for conservation (best solution) and those that had a higher frequency of selection differed substantially between the *limited* and *unlimited* scenarios (Fig. 6). When availability was limited, solutions were fairly similar between total species and endemics data sets, and four main mega conservation areas connecting the current protected areas were identified: (1) a cluster from southern Morocco to western Mauritania, connecting the national parks of Dakhla and Banc d'Arguin; (2) a cluster in central Mali, linking the protected areas of Niger inland delta and Ansongo-Menaka; (3) a corridor from central Niger to south-eastern Chad, connecting the protected areas of Aïr-Ténéré, Termit-Tin Toumma, Lake Chad, Massenya and Balur Aouk et Salamat; and (4) a corridor along the Red Sea Mountains from southern Egypt to Ethiopia, linking the protected areas of Wadi El Gemal/Hamata and Shire. When the availability was unlimited, solutions were fairly different between total species and endemics data sets (Fig. 6).

Coverage of current protected areas network

Regardless of conservation scenarios and data sets analysed, the number of selected grid cells that are covered by protected areas was lower than the number presently outside (Table 2). In *limited* scenarios, prioritized grid cells outside the protected areas (targeting either all species or endemics) were located either away from the currently protected areas (e.g. Tademait-Grand Erg Occidental in Algeria, Libyan Desert across Libya to Egypt and the Nuba/White Nile in Sudan) or in the vicinity of protected areas, either expanding or connecting existing ones (e.g. protected areas in

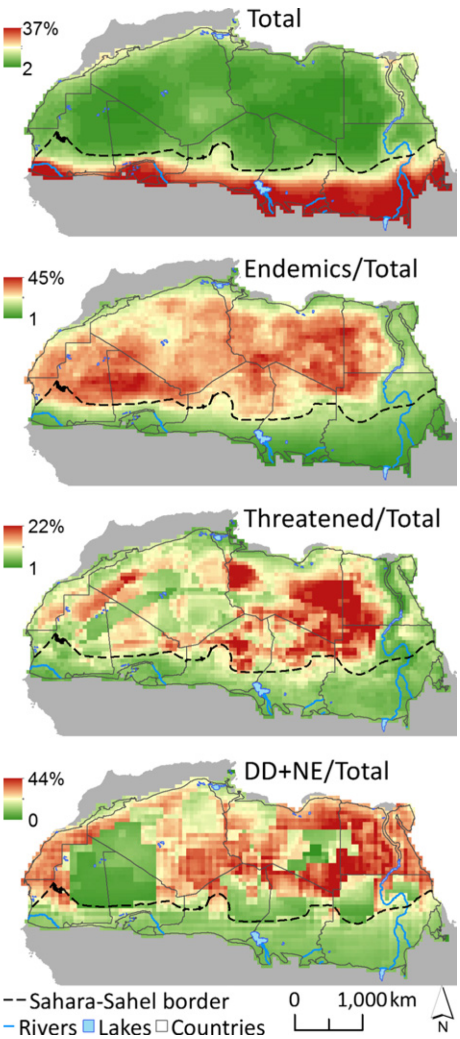

Figure 3 Distribution of combined species richness of amphibians, reptiles, breeding birds and mammals across the Sahara-Sahel. Total richness (1147 species) represented as percentage of species present in each grid cell of 0.5 degree resolution. Richness of endemic species (125 species), threatened species (45 species; categories Vulnerable, Endangered and Critically Endangered) and species considered Data Deficient (DD) or Not Evaluated (NE) (121 species) are given in relation to the total number of species per grid cell.

Morocco–Mauritania and Algeria–Niger–Chad) (Fig. S11). When considering *unlimited* scenarios, prioritized cells for both species data sets tended to form clusters within the presently unprotected areas. The proportion of selected grid cells that are affected by human activities was relatively low (< 12% in all scenarios) for both total species and endemics (Table 2; Fig. S11).

DISCUSSION

Our aim was to help identifying the conservation priorities for biodiversity in the Sahara-Sahel, a data deficient, large, remote and environmentally extreme region of the world. We first provide a comprehensive analysis of the spatial patterns of climatic and biological diversity and use it to identify areas that optimize their combined spatial representation.

Distribution of climate regions and biogroups

The general latitudinal distribution found of most climate regions and biogroups (Figs 2, 4 & 5) is concordant with other bioclimatic and phytogeographical classifications of the Sahara and of North Africa (Quézel, 1978; Le Houérou, 1997). However, the location of the Sahara-Sahel boundary and the distributions of climate regions and vertebrate biogroups identified here were not completely concordant with previous delimitations of ecoregions and ecosystems based on vegetation data (Olson *et al.*, 2001; Sayre *et al.*, 2013). The patterns of spatial overlap observed between some climate regions and biogroups distribution suggest biogeographical concordance and that Sahara-Sahel boundary may lie further north than is currently admitted (compare the present boundary with distribution of CLIM 6 in Fig. 2 and of BE1 in Fig. 5).

Climate regions located in the margins of the Sahara-Sahel tend to extend towards the central Sahara through the Atlantic and Red Sea coasts and the Central Sahara Mountains (Fig. 2). This pattern is in agreement with previous mapping of environmental variation and reconstruction of drainage basins, which have identified a series of putative corridors allowing past dispersal and contemporary gene flow across the Sahara-Sahel and that presently provide refugia for biodiversity (Drake *et al.*, 2011; Coulthard *et al.*, 2013; Brito *et al.*, 2014). Indeed, the distribution of biogroups BT1, 2 and 5 (Fig. 4) provides support for the role of the Atlantic Sahara, the mountains of the central Sahara and the Red Sea coast, and the Nile valley, as dispersal corridors for terrestrial vertebrates (Brito *et al.*, 2014). These regions also contain representatives from all biogroups identified for endemic species in the present study (Fig. 5), as well as a relatively high diversity of Afrotropical fishes and flora (Quézel, 1978; Lévêque, 1990; Anthelme *et al.*, 2011). The Sahara-Sahel mountains further disrupt the broad latitudinal distribution of climate regions and tend to form islands within particular climate regions. These mountains, as well as the Atlantic coast, constitute biogeographical crossroads where biogroups with northern distributions overlap with those with southern distributions.

While biogroups may reflect shared the historical patterns of vicariance and range expansion, climatic gradients shape current patterns of biodiversity and potential differentiation between populations (Belmaker & Jetz, 2012). The geographical concordance between the most wide-ranged climate regions and biogroups, derived from independent data sets, suggests that large-scale patterns of biodiversity distribution in the Sahara-Sahel are related to climatic variation (Le Houérou, 1997; Drake *et al.*, 2011). In contrast, the distribution of small-ranged biogroups appears detached from the

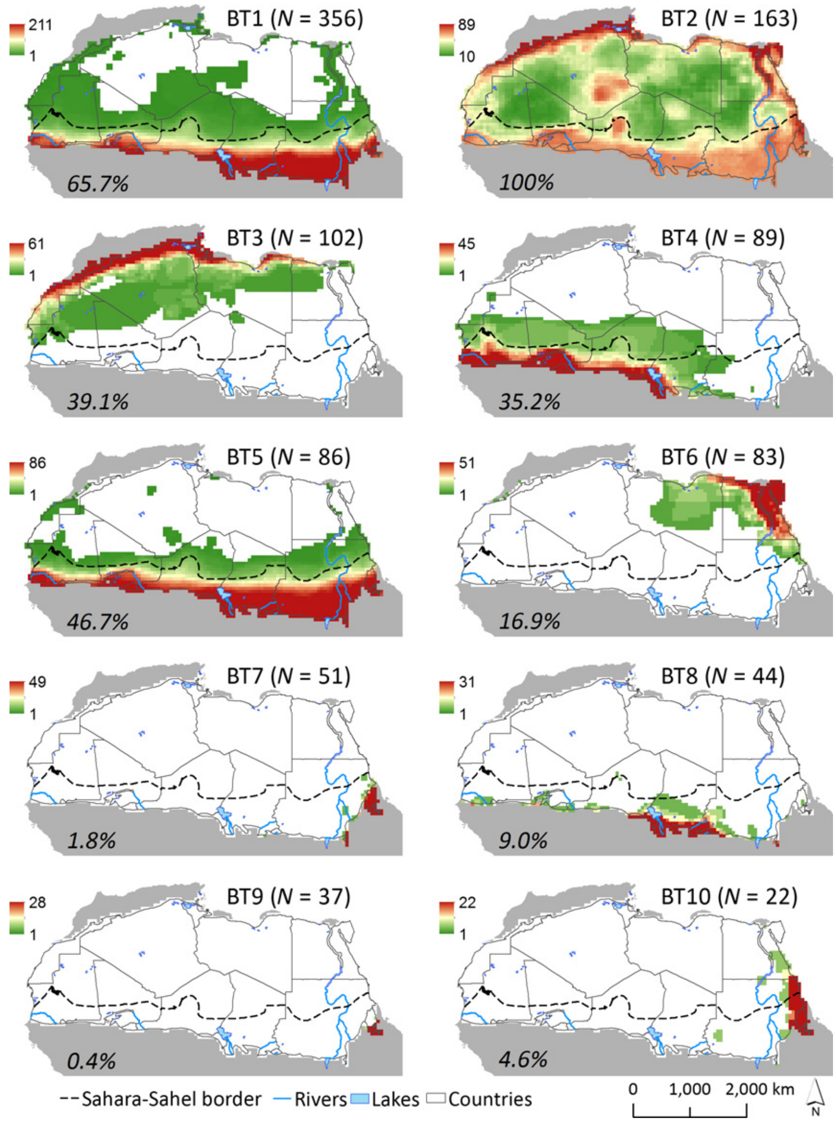

Figure 4 Main biogroups within the Sahara-Sahel based on the distribution of total species. Biogroups defined for a total of 1147 species of amphibians, reptiles, breeding birds and mammals, using distance-based parametric bootstrap tests (see Methods and Appendix S3 for details) at 0.5 degree resolution. The number of species included in each biogroup is presented (in brackets), the percentage of coverage of the Sahara-Sahel is displayed (italics), and the colour scale represents the number of species per grid cell.

climate data used to derive climate regions, suggesting alternative processes related to the origin and historical range of such biogroups.

Distribution of species richness and endemism

As expected, species richness is heterogeneously distributed across the Sahara-Sahel and exhibits highly distinct patterns when only endemics or when all species are considered (Fig. 3). While total species richness is mostly concentrated on the margins, in areas with maximum precipitation and primary productivity, the more arid central Sahara accumulates the highest relative endemic richness. Similarly, high species richness has been previously detected in the western and central Sahara-Sahel mountains and in the Nile valley in agreement with previous studies based on specific taxa (Patiny *et al.*, 2009; García *et al.*, 2010; Anthelme *et al.*, 2011; Brito *et al.*, 2011; Vale *et al.*, 2015). The few species found in the areas of the Sahara displaying the harshest climatic conditions comprise primarily endemics, which highlights the conservation value of extreme regions.

Vulnerability to extinction

The Sahel holds most threatened species as a result of the highest richness found in this area. Species with uncertain vulnerability (Data Deficient or Not Evaluated) also spread along the external limits of the Sahara, the Central Sahara Mountains and the Nile valley, the latter known also for accumulating threatened and Data Deficient freshwater biodiversity (García *et al.*, 2010). However, the Sahara concentrates the highest relative occurrence of threatened species, suggesting that the less numerous fauna of this area is proportionally more threatened than the fauna in the Sahel. Most threatened species correspond to ungulates and other large-sized mammals that have been mainly affected by overhunting and habitat loss (Durant *et al.*, 2014). Although the vast majority of species analysed were not classified as

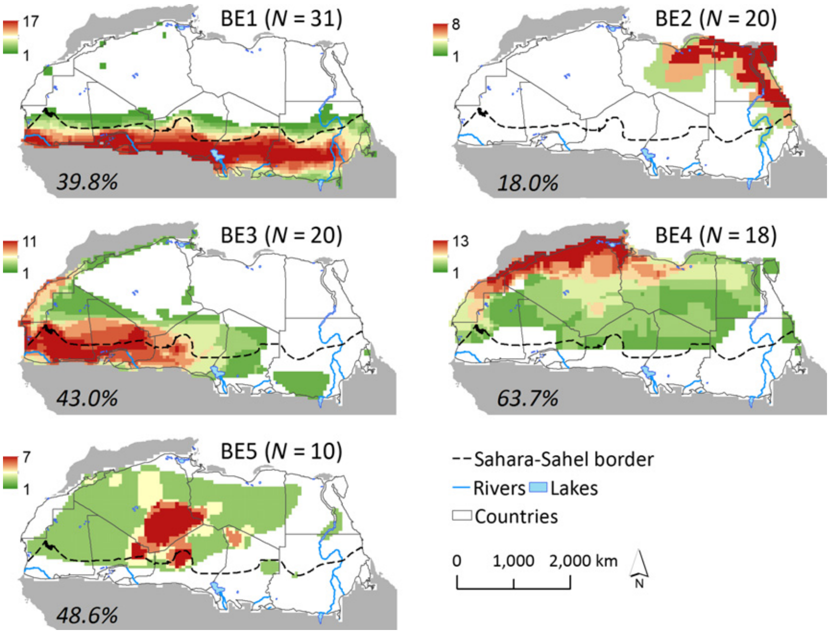

Figure 5 Main biogroups within the Sahara-Sahel based on the distribution of endemic species. Biogroups defined for a total of 125 endemic species of amphibians, reptiles, breeding birds and mammals, using distance-based parametric bootstrap tests (see methods and Appendix S3 for details) at 0.5 degree resolution. The number of species included in each biogroup is presented (in brackets), the percentage of coverage of the Sahara-Sahel is displayed (italics), and the colour scale represents the number of species per grid cell.

Table 2 Number of prioritized grid cells (in best Marxan solution) for conservation of vertebrate biodiversity in the Sahara-Sahel according to distinct conservation feature data sets and scenarios. Scenarios tested include limited and unlimited availability of grid cells (0.5 degree resolution) for conservation (see Fig. S4). Data sets are endemic species and total species and the respective combination of biogroups with climatic regions. For each scenario and data set, it is presented the number of prioritized cells (*N*) and percentage of the study area (in brackets) that are needed to achieve conservation targets (see Fig. 6 for spatial representation) and the number and percentage of prioritized cells that exhibit (With) or not (Without) relevant human activities and that are covered (Inside) or not (Outside) by current protected areas (see Fig. S11 for spatial representation).

		Human activities		Protected areas	
	N	With	Without	Inside	Outside
Endemic species					
Limited	933 (22.7)	60 (6.4)	873 (93.6)	254 (27.2)	679 (72.8)
Unlimited	693 (16.8)	79 (11.4)	614 (88.6)	91 (13.1)	602 (86.9)
Total species					
Limited	828 (20.1)	72 (8.7)	756 (91.3)	118 (14.3)	710 (85.7)
Unlimited	740 (18.0)	48 (6.5)	692 (93.5)	56 (7.6)	684 (92.4)

threatened, the lack of evaluation of nearly half of the reptiles (88 species) using IUCN criteria may be skewing such pattern (Bland *et al.*, 2015). Cryptic evolutionary lineages with narrow and fragmented ranges have been observed in many widespread taxa from multiple taxonomic groups (Brito *et al.*, 2014), suggesting that species-level diversity, and hence red listing of biodiversity, needs updating (particularly for reptiles).

Priority areas for conservation and coverage of current protection network

Despite the recent local conservation efforts, such as the creation of the largest African protected area in the Termit-Tin Toumma of Niger in 2012 or the establishment of breeding facilities for endangered birds and ungulates in several countries (see Brito *et al.*, 2014 for details), areas selected for biodiversity conservation in the Sahara-Sahel at present still lack optimization. Based on the current distribution of protected areas and human activities addressed, our study suggests that 73–86% of the selected grid cells required for achieving minimum representation goals for endemics and total species, respectively, are currently unprotected. While several protected areas have been designated in the central Sahara, the dispersal corridors identified along the Atlantic Sahara, Nile valley and the Red Sea Mountains remain understudied and poorly protected.

Priority areas identified when targeting all species or endemics based on the limited scenario include areas that have been considered a priority for African dragonflies or carnivores and mammals, at a global scale (Loyola *et al.*, 2009; Simaika *et al.*, 2013; Albuquerque & Beier, 2015). Conservation gaps for the global protection of evolutionary distinctiveness of birds have been also identified in many areas

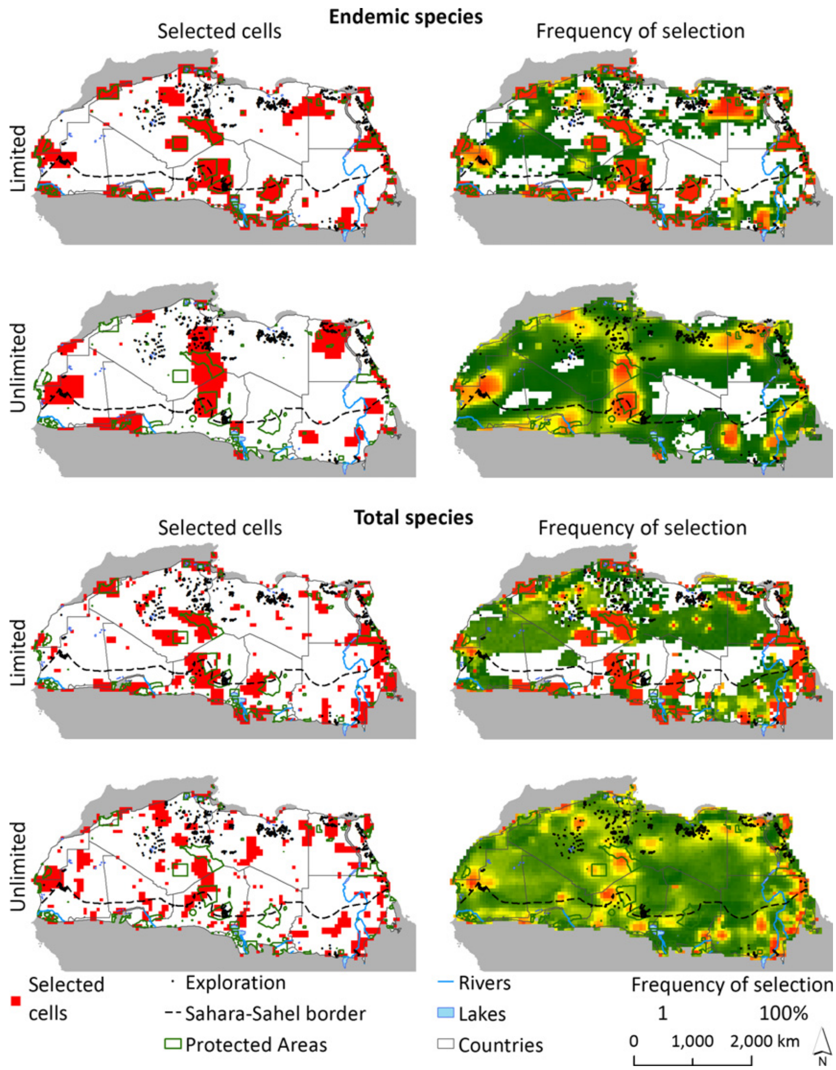

Figure 6 Priority conservation areas according to distinct conservation planning scenarios and data sets for the Sahara-Sahel. Selected cells (left column) depict 0.5 degree grid cells selected for conservation, and frequency of selection (right column) depicts the percentage of each cell being selected among 1000 simulations (see Methods and Appendix S4 for details). Data sets are endemic and total species richness. Scenarios tested include the following: 1) limited availability of cells for conservation (Fig. S4), which forced the inclusion of cells presently classified as protected areas and forced the exclusion of cells exhibiting human activities, and 2) unlimited availability of cells, which did not force exclusion or inclusion of any cells.

of the Sahel (Jetz *et al.*, 2014). Selected cells in scenarios considering the limited availability of grid cells suggested four main mega conservation areas and three new protected areas (Tademait-Grand Erg Occidental in Algeria, the Libyan Desert across Libya to Egypt and the Nuba/White Nile in Sudan). Alltogether, the seven prioritized areas represent about 53% of the selected cells for total species richness (11% of Sahara-Sahel) and would contribute to protect the Vulnerable *Acinonyx jubatus*, *Loxodonta africana* and *Panthera leo*, the Endangered *Gazella leptoceros* and *Kobus megaceros*, and the Critically Endangered *Acanthodactylus spinicauda*, *Addax nasomaculatus*, *Nanger dama* and *Philochortus zolii*, among others.

Conservation planning in the Sahara-Sahel

As predictions of human-induced climate change suggest that warming will increase in desert biomes at a high rate (Loarie *et al.*, 2009) and the potential for local adaptation to alleviate the impacts of climate change may be limited (Grigg & Buckley, 2013), future persistence of Sahara-Sahel biodiversity, especially endemics, seems uncertain. Population monitoring (e.g. Beudels *et al.*, 2005; Brito *et al.*, 2014; Duncan *et al.*, 2014; Vale *et al.*, 2015) and assessment of genetic diversity (e.g. Gonçalves *et al.*, 2012; Metallinou *et al.*, 2012; Kapli *et al.*, 2015) are being developed for particular taxa/regions. Nevertheless, they should be prioritized in areas concentrating large proportions of endemics and/or endangered taxa, to understand whether dispersal and plasticity and/or local adaptation may counteract global warming effects (Pauls *et al.*, 2013). Phylogenetic patterns highlighted the important areas of high average taxonomic diversity, evolutionary distinctiveness and phylogenetic richness, respectively, which are not observable in patterns of species richness (Davies & Buckley, 2011; Fritz & Rahbek, 2012; Jetz *et al.*, 2014). Phylogenetic hotspots in the Sahara-Sahel are thus also in need of identification, and molecular studies are warranted to derive integrative views on Sahara-Sahel biodiversity.

Although more than 90% of selected cells are outside the areas of intense human activities, regions, such as Termit-Tin Toumma and Gourma, suffer from ongoing armed conflict, civil unrest and human exploitation activities that need to be resolved, as they are endangering small-sized and isolated populations of vertebrates (e.g. Bouché *et al.*, 2011; Duncan *et al.*, 2014). Moreover, many selected areas transverse multiple political borders and require international coordination efforts for implementation and management of protected areas. Some countries have low human development and low economical resources to allocate to conservation planning (Niger and Chad with gross national income per capita around 1200 USD; UNDP, 2010), and six countries (Algeria, Eritrea, Mauritania, Morocco, Senegal and Sudan) are among the 40 most highly underfunded countries for biodiversity conservation (Waldron *et al.*, 2013). Greater regional investment is needed via resource allocation from major international funding institutions, such as the World Bank/Global Environmental Fund. The relatively low levels of anthropogenic habitat change and of human population density in the region (CIESIN-FAO-CIAT, 2005; Ellis *et al.*, 2010) offer a good opportunity for protecting biodiversity while minimizing conflicts with human activities. Biodiversity conservation and adequate network of protected areas offer potential economic inflow, via qualified ecotourism (Hosni, 2000), and stimulation of local economy and welfare (UNEP, 2006).

Conservation planning in extreme regions

Conservation planning is often faced with the challenge to identify optimized priority areas for conservation with few data available. Here, the paucity of species distribution data and socioeconomic data in the Sahara-Sahel constrained the accurate identification of conservation priorities and the testing of alternative prioritization scenarios.

The lack of detailed species distributions forced the use of occurrence polygons that probably inflated the rate of false presences (Graham & Hijmans, 2006; Rondinini *et al.*, 2006). In contrast, it is likely that the distribution of several species is underestimated, as areas such as the Atlantic Sahara and the Central Sahara Mountains are under-sampled because of their remoteness and long-term local conflicts (Brugière & Scholte, 2013; Ficetola *et al.*, 2013). When converting these polygons to a gridded data set, small grid sizes may provoke overestimation of species richness (Hurlbert & Jetz, 2007) and large grid cells may reduce efficiency in priority area selection (Warman *et al.*, 2004), both resulting in disconnections between the spatial scale of analyses and the scale at which conservation actions take place. A coarse spatial resolution was needed here as a compromise between the large extent of the study area, computational power and data availability.

Our aim was to identify priority areas for conservation based on species and climatic distributions, but we attempted to account for high economic value and human population density of some areas by excluding those areas in the limited scenarios. It is debatable whether these areas should be considered as of high priority for conservation given that they are highly threatened (Spring *et al.*, 2007). However, we did not consider the direct costs of preserving priority areas, such as management, acquisition and opportunity costs of protected areas (Adams *et al.*, 2010). Accounting for such factors in the Sahara-Sahel is impractical as a result of paucity of spatial data on economic activities and their income in the region, including pastoralism, hunting or land value (ECOWAS & SWAC-OCDE, 2006; Durant *et al.*, 2014; Rabeil *et al.*, 2014). Additionally, conflicts and social unrest are also frequent, spatially and temporally highly dynamic (Brito *et al.*, 2014), and are known to impact on protected areas management (Hanson *et al.*, 2009).

CONCLUSIONS

The identification of distinct climate regions and biogeographical groups presented here allows developing a first assessment of conservation priorities in the Sahara-Sahel. Regional analyses at finer scales will likely reveal additional or alternative areas where conservation efforts can be directed at (e.g. Sow *et al.*, 2014), but biodiversity assessments are needed beforehand to fill out current knowledge gaps in remote and hard-to-sample mountain areas. Even if the spatial resolution used constraints in real conservation measures, this study offers hints to direct future local research efforts and frameworks for regional conservation planning and uses integrative approaches that can be applied at finer-scale resolutions or in other extreme regions of the world with reduced data availability and subjected to marked environmental gradients.

ACKNOWLEDGEMENTS

Funding was provided by grants from the National Geographic Society (CRE-7629-04, CRE-8412-08, GEFNE-53-12), from Mohammed bin Zayed Species Conservation Fund (11052709, 11052707 and 11052499), from SYNTHESIS programs (BE-TAF-1796 and AT-TAF-1665), from Rufford Foundation (SG-15399-1), by Fundação para a Ciência e Tecnologia (FCT: PTDC/BIA-BEC/099934/2008, PTDC/BIA-BIC/118624/2010, PTDC/BIA-BIC/2903/2012), and by FEDER funds through the Operational Programme for Competitiveness Factors – COMPETE (FCOMP-01-0124-FEDER-008917/028276). Research conducted in the scope of the LIA known was ‘Biodiversity and Evolution’. Individual support was given by FCT (contracts IF/459/2013, 564/2012 and 1425/2014, and grants SFRH/BPD/69857/2010, 74423/2010, 73176/2010, 84822/2012, 88496/2012, 93473/2013, and SFRH/BD/65038/2009, 73680/2010, 72522/2010, 78402/2011, 87885/2012). Logistic support for fieldwork was given by Sahara Conservation Fund (Projet ASS, Niger), P.N. Banc d’Arguin and Fondation Internationale du Banc d’Arguin (Mauritania), Ministère de l’Environnement et du Développement Durable of Mauritania, and Faculty of Sciences and Technology (USTM; Mauritania).

REFERENCES

Adams, V.M., Pressey, R.L. & Naidoo, R. (2010) Opportunity costs: who really pays for conservation? *Biological Conservation*, **143**, 439–448.

Albuquerque, F. & Beier, P. (2015) Global patterns and environmental correlates of high-priority conservation areas for vertebrates. *Journal of Biogeography*, **42**, 1397–1405.

Anthelme, F., Abdoulkader, A. & Viane, R. (2011) Are ferns in arid environments underestimated? Contribution from the Saharan Mountains. *Journal of Arid Environments*, **75**, 516–523.

Avise, J.C. (2009) Phylogeography: retrospect and prospect. *Journal of Biogeography*, **36**, 3–15.

Ball, I.R., Possingham, H.P. & Watts, M.E. (2009) Marxan and relatives: software for spatial conservation prioritization. *Spatial conservation prioritization – quantitative methods and computational tools* (ed.by A. Moilanen, K.A. Wilson and H.P. Possingham), pp. 185–195. Oxford University Press, Oxford, UK.

Barnes, R.F.W. (1999) Is there a future for elephants in West Africa? *Mammal Review*, **29**, 175–199.

Barnett, R., Yamaguchi, N., Barnes, I. & Cooper, A. (2006) The origin, current diversity and future conservation of the modern lion (*Panthera leo*). *Proceedings of the Royal Society B: Biological Sciences*, **273**, 2119–2125.

Belmaker, J.C. & Jetz, W. (2012) Regional pools and environmental controls of vertebrate assemblages. *The American Naturalist*, **179**, 512–523.

Beudels, R.C., Devillers, P., Lafontaine, R.-M., Devillers-Terschuren, J. & Beudels, M.-O. (2005) *Sahelo-Saharan Antelopes. Status and Perspectives. Report on the conservation status of the six Sahelo-Saharan Antelopes*. CMS SSA Concerted Action, United Nations Environment Programme/ Convention on Migratory Species.

Bland, L.M., Collen, B., Orme, C.D.L. & Bielby, J. (2015) Predicting the conservation status of Data-Deficient species. *Conservation Biology*, **29**, 250–259.

Bouché, P., Douglas-Hamilton, I., Wittemyer, G., Nianogo, A., Doucet, J.-L., Lejeune, P. & Vermeulen, C. (2011) Will elephants soon disappear from West African savannahs? *PLoS ONE*, **6**, e20619.

Brito, J.C., Martínez-Freiría, F., Sierra, P., Sillero, N. & Tarroso, P. (2011) Crocodiles in the Sahara Desert: an update of distribution, habitats and population status for conservation planning in Mauritania. *PLoS ONE*, **6**, e14734.

Brito, J.C., Godinho, R., Martínez-Freiría, F. *et al.* (2014) Unravelling biodiversity, evolution and threats to conservation in the Sahara-Sahel. *Biological Reviews*, **89**, 215–231.

Brugière, D. & Scholte, P. (2013) Biodiversity gap analysis of the protected area system in poorly-documented Chad. *Journal for Nature Conservation*, **21**, 286–293.

Butchart, S.H.M., Walpole, M., Collen, B. *et al.* (2010) Global biodiversity: indicators of recent declines. *Science*, **328**, 1164–1168.

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace, G.M., Tilman, D., Wardle, D.A., Kinzig, A.P., Daily, G.C., Loreau, M., Grace, J.B., Larigauderie, A., Srivastava, D.S. & Naeem, S. (2012) Biodiversity loss and its impact on humanity. *Nature*, **486**, 59–67.

Carvalho, S.B., Brito, J.C., Crespo, E.J. & Possingham, H.P. (2011) Incorporating evolutionary processes into conservation planning using species distribution data: a case study with the Western Mediterranean herpetofauna. *Diversity and Distributions*, **17**, 408–421.

CBD (2010) *Strategic Plan for Biodiversity 2011-2020. Further information related to the technical rationale for the Aichi Biodiversity Targets, including potential indicators and milestones*. UNEP/CBD/COP/10/INF/12/Rev.1. Convention on Biological Diversity. Available at: http://www.cbd.int/doc/meetings/cop/cop-10/information/cop-10-inf-12-rev1-en.pdf (accessed 10 November 2012).

CIESIN-FAO-CIAT (2005) *Gridded population of the world: future estimates (GPWFE)*. Center for International Earth Science Information Network (CIESIN), Columbia University; United Nations Food and Agriculture Programme (FAO), and Centro Internacional de Agricultura Tropical (CIAT). Socioeconomic Data and Applications Center (SEDAC), Columbia University. Available at: http://sedac.ciesin.columbia.edu/gpw (accessed 12 July 2013).

Cincotta, R.P. & Gorenflo, L.J. (eds.) (2011) *Human population. Its influences on biological diversity*. Springer-Verlag, Berlin Heidelberg.

Ciofolo, I. (1995) West Africa's last giraffes: the conflict between development and conservation. *Journal of Tropical Ecology*, **1**, 577–588.

Coulthard, T.J., Ramirez, J.A., Barton, N., Rogerson, M. & Brücher, T. (2013) Were rivers flowing across the Sahara during the Last Interglacial? Implications for human migration through Africa. *PLoS ONE*, **8**, e74834.

Davies, T.J. & Buckley, L.B. (2011) Phylogenetic diversity as a window into the evolutionary and biogeographic histories of present-day richness gradients for mammals. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **366**, 2414–2425.

Doebeli, M. & Dieckmann, U. (2003) Speciation along environmental gradients. *Nature*, **421**, 259–264.

Drake, N.A., Blench, R.M., Armitage, S.J., Bristow, C.S. & White, K.H. (2011) Ancient watercourses and biogeography of the Sahara explain the peopling of the desert. *Proceedings of the National Academy of Sciences USA*, **108**, 458–462.

Duncan, C., Kretz, D., Wegmann, M., Rabeil, T. & Pettorelli, N. (2014) Oil in the Sahara: mapping anthropogenic threats to Saharan biodiversity from space. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **369**, 20130191.

Durant, S.M., Pettorelli, N., Bashir, S. *et al.* (2012) Forgotten biodiversity in desert ecosystems. *Science*, **336**, 1379–1380.

Durant, S.M., Wacher, T., Bashir, S. *et al.* (2014) Fiddling in biodiversity hotspots while deserts burn? Collapse of the Sahara's megafauna. *Diversity and Distributions*, **20**, 114–122.

ECOWAS & SWAC-OCDE (2006) The ecologically vulnerable zones of Sahelian countries. *Atlas on regional integration in West Africa*. ECOWAS and SWAC-OCDE. www.atlas-westafrica.org (accessed 14 October 2013).

Ellis, E.C., Goldewijk, K.K., Siebert, S., Lightman, D. & Ramankutty, N. (2010) Anthropogenic transformation of the biomes, 1700 to 2000. *Global Ecology and Biogeography*, **19**, 589–606.

Emslie, R. & Brooks, M. (1999) *African Rhino. Status survey and conservation action plan*. IUCN, Gland, Switzerland and Cambridge, UK.

Ficetola, G.F., Bonardi, A., Sindaco, R. & Padoa-Schioppa, E. (2013) Estimating patterns of reptile biodiversity in remote regions. *Journal of Biogeography*, **40**, 1202–1211.

Fraley, C. & Raftery, A.E. (2002) Model-based clustering, discriminant analysis and density estimation. *Journal of the American Statistical Association*, **97**, 611–631.

Fritz, S.A. & Rahbek, C. (2012) Global patterns of amphibian phylogenetic diversity. *Journal of Biogeography*, **39**, 1373–1382.

García, N., Cuttelod, A. & Abdul Malak, D. (2010) *The status and distribution of freshwater biodiversity in Northern Africa*. IUCN, Gland, Switzerland, Cambridge, UK, and Malaga, Spain.

Gonçalves, D.V., Brito, J.C., Crochet, P.-A., Geniez, P., Padial, J.M. & Harris, D.J. (2012) Phylogeny of North African *Agama* lizards (Reptilia: Agamidae) and the role of the Sahara desert in vertebrate speciation. *Molecular Phylogenetics and Evolution*, **64**, 582–591.

Graham, C.H. & Hijmans, R.J. (2006) A comparison of methods for mapping species ranges and species richness. *Global Ecology and Biogeography*, **15**, 578–587.

Grigg, J.W. & Buckley, L.B. (2013) Conservatism of lizard thermal tolerances and body temperatures across evolutionary history and geography. *Biology Letters*, **9**, 20121056.

Haas, S.K., Hayssen, V. & Krausman, P.R. (2005) *Panthera leo*. *Mammalian Species*, **762**, 1–11.

Hanson, T., Brooks, T.M., da Fonseca, G.A.B., Hoffmann, M., Lamoreux, J.F., Machlis, G., Mittermeier, C.G., Mittermeier, R.A. & Pilgrim, J.D. (2009) Warfare in biodiversity hotspots. *Conservation Biology*, **23**, 578–587.

Hausdorf, B. (2002) Units in biogeography. *Systematic Biology*, **51**, 648–652.

Hekkala, E., Shirley, M.H., Amato, G., Austin, J.D., Charter, S., Thorbjarnarson, J.B., Vliet, K.A., Houck, M.L., Desalle, R. & Blum, M.J. (2011) An ancient icon reveals new mysteries: mummy DNA resurrects a cryptic species within the Nile crocodile. *Molecular Ecology*, **20**, 4199–4215.

Hennig, C. & Hausdorf, B. (2008) prabclus*: functions for clustering of presence-absence and abundance data*. Available at: http://www.homepages.ucl.ac.uk/~ucakche (accessed 10 December 2011).

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**, 1965–1978.

Hosni, E. (2000) *Strategy for sustainable tourism development in the Sahara*. United Nations Educational, Scientific and Cultural Organization, Paris.

Hurlbert, A.H. & Jetz, W. (2007) Species richness, hotspots, and the scale dependence of range maps in ecology and conservation. *Proceedings of the National Academy of Sciences USA*, **104**, 13384–13389.

IEP (2012) *Global Terrorism Index: capturing the impact of terrorism for the last decade*. Institute for Economics and Peace, New York, NY, USA.

IUCN (2013) *The IUCN Red List of threatened species, 2013.1*. International Union for Conservation of Nature and Natural Resources. Available at: http://www.iucnredlist.org/ (accessed 9 July 2013).

IUCN & UNEP (2013) *The world database on protected areas (WDPA)*. UNEP-WCMC. Available at: http://protectedplanet.net/ (accessed 11 July 2013).

Jetz, W., Thomas, G.H., Joy, J.B., Redding, D.W., Hartmann, K. & Mooers, A.O. (2014) Global distribution and conservation of evolutionary distinctness in birds. *Current Biology*, **24**, 919–930.

Kapli, P., Lymberakis, P., Crochet, P.-A., Geniez, P., Brito, J.C., Almutairi, M., Ahmadzadeh, F., Schmitz, A., Wilms, T., Pouyani, N.R. & Poulakakis, N. (2015) Historical biogeography of the lacertid lizard *Mesalina* in North Africa and the Middle East. *Journal of Biogeography*, **42**, 267–279.

Lagrot, I., Lagrot, J.-F. & Bour, P. (2007) Probable extinction of the western black rhino, *Diceros bicornis longipes*: 2006 survey in northern Cameroon. *Pachyderm*, **43**, 19–28.

Largen, M.J. & Yalden, D.W. (1987) The decline of elephant and black rhinoceros in Ethiopia. *Oryx*, **2**, 103–106.

Le Houérou, H.N. (1997) Climate, flora and fauna changes in the Sahara over the past 500 million years. *Journal of Arid Environments*, **37**, 619–647.

Lévêque, C. (1990) Relict tropical fish fauna in Central Sahara. *Ichthyological Exploration of Freshwaters*, **1**, 39–48.

Loarie, S.R., Duffy, P.B., Hamilton, H., Asner, G.P., Field, C.B. & Ackerly, D.D. (2009) The velocity of climate change. *Nature*, **462**, 1052–1055.

Loyola, R.D., Oliveira-Santos, L.G.R., Almeida-Neto, M., Nogueira, D.M., Kubota, U., Diniz-Filho, J.A.F. & Lewinsohn, T.M. (2009) Integrating economic costs and biological traits into global conservation priorities for carnivores. *PLoS ONE*, **4**, e6807.

Mace, G.M., Masundire, H. & Baillie, J.E.M. (2005) Biodiversity. *Ecosystems and human-well being: current state and trends* (ed. by R.M. Hassan, R. Scholes and N. Ash), pp. 77–122. Island Press, Washington, DC.

Manlius, N. (2000) Historical ecology and biogeography of the Addax in Egypt. *Israel Journal of Zoology*, **46**, 261–271.

Margules, C.R. & Pressey, R.L. (2000) Systematic conservation planning. *Nature*, **405**, 243–253.

Metallinou, M., Arnold, E.N., Crochet, P.-A., Geniez, P., Brito, J.C., Lymberakis, P., Baha El Din, S.M., Sindaco, R., Robinson, M. & Carranza, S. (2012) Conquering the Sahara and Arabian deserts: systematics and biogeography of *Stenodactylus* geckos (Reptilia: Gekkonidae). *BMC Evolutionary Biology*, **12**, 258.

Olson, D.M. & Dinerstein, E. (1998) The Global 200: a representation approach to conserving the Earth's most biologically valuable ecoregions. *Conservation Biology*, **12**, 502–515.

Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C., D'Amico, J.A., Itoua, I., Strand, H.E., Morrison, J.C., Loucks, C.J., Allnutt, T.F., Ricketts, T.H., Kura, Y., Lamoreux, J.F., Wettengel, W.W., Hedao, P. & Kassem, K.R. (2001) Terrestrial ecoregions of the world: a new map of life on earth. *BioScience*, **51**, 933–938.

Ostrowski, S., Massalatchi, M. & Mamane, M. (2001) Evidence of a dramatic decline of the red-necked ostrich *Struthio camelus camelus* in the air and Ténéré National Nature Reserve, Niger. *Oryx*, **35**, 349–352.

Patiny, S., Michez, D., Kuhlmann, M., Pauly, A. & Barbier, Y. (2009) Factors limiting the species richness of bees in Saharan Africa. *Bulletin of Entomological Research*, **99**, 337–346.

Pauls, S.U., Nowak, C., Bálint, M. & Pfenninger, M. (2013) The impact of global climate change on genetic diversity within populations and species. *Molecular Ecology*, **22**, 925–946.

Pressey, R.L., Cabeza, M., Watts, M.E., Cowling, R.M. & Wilson, K.A. (2007) Conservation planning in a changing world. *Trends in Ecology and Evolution*, **22**, 583–592.

Quézel, P. (1978) Analysis of the flora of Mediterranean and Saharan Africa. *Annals of the Missouri Botanical Garden*, **65**, 479–534.

Rabeil, T., Newby, J.E. & Harouna, A. (2014) Innovation, traditional knowledge and awareness lead to good practices for avoiding biodiversity loss in the Sahara. *Biodiversity*, **15**, 185–191.

Rodrigues, P., Figueira, R., Pinto, P.V., Araújo, M.B. & Beja, P. (2015) A biogeographical regionalization of Angolan mammals. *Mammal Review*, **45**, 103–116.

Rondinini, C., Wilson, K.A., Boitani, L., Grantham, H. & Possingham, H.P. (2006) Tradeoffs of different types of species occurrence data for use in systematic conservation planning. *Ecology Letters*, **9**, 1136–1145.

Rookmaaker, L.C. (2004) Historical distribution of the black rhinoceros (*Diceros bicornis*) in West Africa. *African Zoology*, **39**, 63–70.

Saleh, M.A., Helmy, I. & Giegengack, R. (2001) The Cheetah, *Acinonyx jubatus* (Schreber, 1776) in Egypt (Felidae, Acinonychinae). *Mammalia*, **65**, 177–194.

Sayre, R., Comer, P., Hak, J. *et al.* (2013) *A new map of standardized terrestrial ecosystems of Africa*. Association of American Geographers, Washington, DC.

Simaika, J.P., Samways, M.J., Kipping, J., Suhling, F., Dijkstra, K.-D.B., Clausnitzer, V., Boudot, J.-P. & Domish, S. (2013) Continental-scale conservation prioritization of African dragonflies. *Biological Conservation*, **157**, 245–254.

Sindaco, R. & Jeremcenko, V.K. (2008) *The reptiles of the western palearctic, volume 1: annotated checklist and distributional atlas of the turtles, crocodiles, amphisbaenians and lizards of Europe, North Africa, Middle East and Central Asia*. Edizioni Belvedere, Latina.

Sindaco, R., Vench, A. & Grieco, C. (2013)*The reptiles of the western palearctic. 2. Annotated checklist and distributional atlas of the snakes of Europe, North Africa, Middle East and Central Asia*. Edizioni Belvedere, Latina.

Smith, T.B., Kark, S., Schneider, C.J. & Wayne, R.K. (2001) Biodiversity hotspots and beyond: the need for preserving environmental transitions. *Trends in Ecology and Evolution*, **16**, 431.

Sow, A.S., Martínez-Freiría, F., Dieng, H., Fahd, S. & Brito, J.C. (2014) Biogeographical analysis of the Atlantic Sahara reptiles: environmental correlates of species distribution and vulnerability to climate change. *Journal of Arid Environments*, **109**, 65–73.

Spring, D.A., Cacho, O., Mac Nally, R. & Sabbadin, R. (2007) Pre-emptive conservation versus "fire-fighting": a decision theoretic approach. *Biological Conservation*, **136**, 531–540.

Thiollay, J.M. (2006) Severe decline of large birds in the Northern Sahel of West Africa: a long term assessment. *Bird Conservation International*, **16**, 353–365.

Trabucco, A. & Zomer, R.J. (2009) *Global aridity index (global-aridity) and global potential evapo-transpiration (global-PET) geospatial database*. CGIAR Consortium for Spatial Information. Available at: http://www.csi.cgiar.org (accessed 23 June 2013).

UNDP (2010) *Human development report 2010.*, United Nations Development Programme, New York, NY, USA.

UNEP (2006) *Global deserts outlook*. United Nations Environment Programme, Kenya, Nairobi.

Uphyrkina, O., Johnson, W.E., Quigley, H., Miquelle, D., Marker, L., Bush, M. & O'Brien, S. (2001) Phylogenetics, genome diversity and origin of modern leopard, *Panthera pardus*. *Molecular Ecology*, **10**, 2617.

Vale, C.G. & Brito, J.C. (2015) Desert-adapted species are vulnerable to climate change: insights from the warmest region on earth. *Global Ecology and Conservation*, **4**, 369–379.

Vale, C.G., Pimm, S.L. & Brito, J.C. (2015) Overlooked mountain rock pools in deserts are critical local hotspots of biodiversity. *PLoS ONE*, **10**, e0118367.

Waldron, A., Mooers, A.O., Miller, D.C., Nibbelink, N., Redding, D., Kuhn, T.S., Roberts, J.T. & Gittleman, J.L. (2013) Targeting global conservation funding to limit immediate biodiversity declines. *Proceedings of the National Academy of Sciences USA*, **110**, 12144–12148.

Ward, D. (2009) *Biology of deserts*. Oxford University Press, Oxford.

Warman, L.D., Sinclair, A.R.E., Scudder, G.G.E., Klinkenberg, B. & Pressey, R.L. (2004) Sensitivity of systematic reserve selection to decisions about scale, biological data, and targets: case study from Southern British Columbia. *Conservation Biology*, **18**, 655–666.

SUPPORTING INFORMATION

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

Appendix S1 Identification of climate regions.

Appendix S2 Species distribution data.

Appendix S3 Identification of biogroups.

Appendix S4 Identification of priority areas for conservation.

Figure S1 Overview of analyses.

Figure S2 Main toponomies of the Sahara-Sahel.

Figure S3 Environmental variability in the Sahara-Sahel derived by Spatial Principal Components Analysis (SPCA).

Figure S4 Grid cells considered for the identification of priority conservation areas in the Sahara-Sahel.

Figure S5 Model-based clustering with Bayesian Information Criterion (BIC) for the identification of climate regions in the Sahara-Sahel.

Figure S6 Environmental characterization of climate regions of the Sahara-Sahel.

Figure S7 Representation of climate regions and biogroups for endemics and total species in the current protected areas network.

Figure S8 Distribution of combined species richness of amphibians, reptiles, birds, and mammals across the Sahara-Sahel.

Figure S9 Percentage of overlap in the distributions of biogroups and climate regions.

Figure S10 Relationships between aggregation levels and number of selected grid cells according to distinct conservation planning scenarios and data sets for the Sahara-Sahel.

Figure S11 Coverage of current protected areas network in relation to distinct conservation planning scenarios and data sets used for the Sahara-Sahel.

Table S1 Species analysed in the present study.

BIOSKETCH

The researchers involved in this analysis are the BIODESERTS research group at the CIBIO/University of Porto (http://cibio.up.pt/cibio.php?content=groups&menu=groups&group=biodesert). The group is focused on assessing biodiversity patterns and processes in deserts and arid regions.

Author contributions: J.C.B., P.T., C.G.V., F.M.F. and S.B.C. conceived the ideas, collected and analysed the data, and led the writing, to which all authors contributed.

Editor: Michael Bode