

REVIEW

A biogeographical regionalization of Angolan mammals

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ABSTRACT

1. We developed a biogeographical regionalization of Angolan mammals based on data collected before major declines occurred during the civil war (1975–2002). In terms of its biodiversity, Angola is one of the least known of all African countries.
2. We used 9880 grid records of 140 species (rodents, ungulates and carnivores) collected mainly in 1930–80, at a quarter degree cell resolution. Biogeographical regions were identified by using cluster analysis, based on β_{sim} dissimilarity matrices and a hierarchical classification using Ward's method. An indicator value analysis was used to identify species characterizing each region. Distance-based redundancy analysis was used to investigate the environmental correlates of mammalian assemblages.
3. Four biogeographical subdivisions emerged from ungulate distributions, while rodent and carnivore data were largely uninformative. In the north, the Zaire-Lunda-Cuanza region was mainly characterized by ungulate species associated with Congolian forests. In the south, the Namibe and Cunene-Cuando Cubango regions were mainly characterized by ungulates widespread in south-western and southern Africa. In between these regions, the Central Plateau region was mainly

characterized by a few widespread ungulate species that are relatively common in dense miombo woodlands.

4. Biogeographical patterns were significantly associated with a dominant north-south gradient of decreasing humidity and increasing temperature, and with a concurrent gradient from dense forests and woodlands to open savannas, grasslands and deserts.

5. The biogeographical regions we identified in Angola were largely consistent with other biogeographical regionalizations developed using various taxonomic groups at larger spatial scales. Biogeographical patterns reflected the southward penetration of Congolian forest species in the north, and the northward penetration of southern African desert/grassland species in the south-west and of open savanna species in the south. These processes seem to be controlled by the distribution of vegetation types, which in turn are associated with climatic gradients and soil types. The stronger patterns observed for ungulates than for other mammals may reflect the close association of ungulates to specific vegetation types.

INTRODUCTION

Biogeographical regionalizations allow the definition of homogeneous regions in terms of species assemblages, and the identification of factors potentially shaping the spatial distribution of such assemblages. Therefore, they are increasingly regarded as a preliminary step towards the planning of conservation efforts (Ladle & Whittaker 2011). Despite their value, development of accurate biogeographical regionalizations is limited by the shortage of information on species' distributions, particularly in poorly explored regions of the world. In such areas, species' distribution data often reflect the distribution of researchers' interests rather than that of species, creating a number of spatial biases that may confound biological patterns (Pyke & Ehrlich 2010). Furthermore, the time frame for data collection may be considerably different from the time frame of the analysis, thus bringing in additional inaccuracies with regard to the current situation (Pyke & Ehrlich 2010). The practical application of these studies may also be limited because data resolution may be too coarse to delineate accurately the boundaries between adjacent regions. Development of biogeographical regionalizations in poorly known areas thus remains a theme of major applied value, which may help to validate studies conducted at larger spatial scales and contribute towards refining the prioritization of conservation action.

Efforts to develop comprehensive biogeographical regionalizations for Africa have a long history. Early researchers investigated the biogeographical patterns of the plants (Lebrun 1947, Monod 1957, White 1965), butterflies (Carcasson 1964), amphibians (Poynton 1964) and birds (Chapin 1932) of Sub-Saharan and Southern Africa. Research on this topic has proceeded during the past two decades, and biogeographical regionalizations have been proposed for

amphibians (Penner et al. 2011), birds (de Klerk et al. 2002, Muñoz et al. 2003) and mammals (Gelderblom et al. 1995, Rowe-Rowe & Taylor 1996, Grubb et al. 2000). Researchers analysing both plant and animal distributions proposed the division of Sub-Saharan Africa into the Saharan, Sudanian, Ethiopian, Somalian, Congolian, Zambebian and Southern African regions (Linder et al. 2012). These broad biogeographical regions, however, were recognized as containing substantial internal structure, corresponding to sub-regions characterized, for instance, by particular environmental conditions or by the presence of centres of endemism and islands of high diversity (Linder et al. 2012). Accurate identification of sub-regions would require analyses conducted at finer resolution than typically carried out; such analyses could strongly contribute to improving our knowledge of African biogeography.

In this study, we undertake a biogeographical regionalization of Angola based on previously unavailable data on the historical distribution of mammalian species. Angola is a large and biodiverse country in south-western Africa, which includes areas of global conservation importance such as the coastal escarpment, but where biodiversity research is largely lacking (Myers et al. 2000, Figueiredo et al. 2009, Mills 2010, Romeiras et al. 2014). Linder et al. (2012) classified most of the country as falling into the Zambebian region, with a transition fringe in the Congolian biogeographical unit in the north (Shaba), and transition fringes in the South African unit in the south-west (south-western Angola) and in the south (Kalahari). The boundaries between units, however, were highly sketchy and varied to some extent depending on the taxonomic group (Linder et al. 2012). Furthermore, within the large Zambebian region, there is probably much biotic heterogeneity, as suggested for instance by the identification of several vegetation units in early phytogeographic research (Barbosa 1970) and

by high levels of species turnover (Linder et al. 2012). The analysis of mammalian data could contribute towards resolving these uncertainties, as mammals are a relatively specious group for which a wealth of information exists from colonial times (mainly from the 20th century; Linder et al. 2012). Although humans have a strong impact on mammalian distributions, particularly on those of large carnivores and ungulates, most of the data we used were collected before the civil war (1975–2002) when widespread poaching strongly affected a range of species (Crawford-Cabral & Verissimo 2005, Chase & Griffin 2011).

The aims of this study were to: (1) review and compile in a digital format the data on mammalian species' distributions for Angola; (2) use the data to identify biogeographical units or regions, based on repeatable statistical procedures; (3) identify 'indicator' species that discriminate the different regions; and (4) identify the environmental correlates of the biogeographical patterns uncovered. Results were interpreted in the light of current understanding of the biogeography of this region of Africa.

METHODS

Study area

Angola is a large country ($1.25 \times 10^6 \text{ km}^2$) located on the south-western coast of Africa ($4^{\circ}22'S$, $18^{\circ}03'S$; Fig. 1). Elevation varies from 0 to 2620 m above sea level; the littoral plains are separated from the inland plateau by a north-south escarpment running parallel to the coast. Climate ranges from tropical wet/humid in the north to extremely arid in the south-west. Angola has a diverse array of ecosystems and is biologically mega-diverse, encompassing 15 World Wildlife Fund (WWF) Ecoregions (Olson et al. 2001; Fig. 1). In the north and north-west, there are Congolian forest-savanna mosaics and the scarp savannas and woodlands. The south-western coastal plain is occupied by the Kaokoveld desert and Namibian dry savanna woodlands. The most widespread vegetation is the miombo woodland occupying the Central Plateau. In the southern borders, the miombo is replaced by mopane *Colophospermum mopane* and baikiaea *Baikiaea plurijuga* woodlands. The terrestrial mammalian fauna comprises 274 species, 13 of which are endemic and 19 are globally threatened (Wilson & Reeder 2005, Anonymous 2013). During the civil war, there was uncontrolled poaching of large mammals, so their current status is largely unknown (Crawford-Cabral & Verissimo 2005, Pitra et al. 2006, Chase & Griffin 2011).

Species data

Based on data available in the literature (Crawford-Cabral & Simões 1987, 1988, Crawford-Cabral 1998, Crawford-

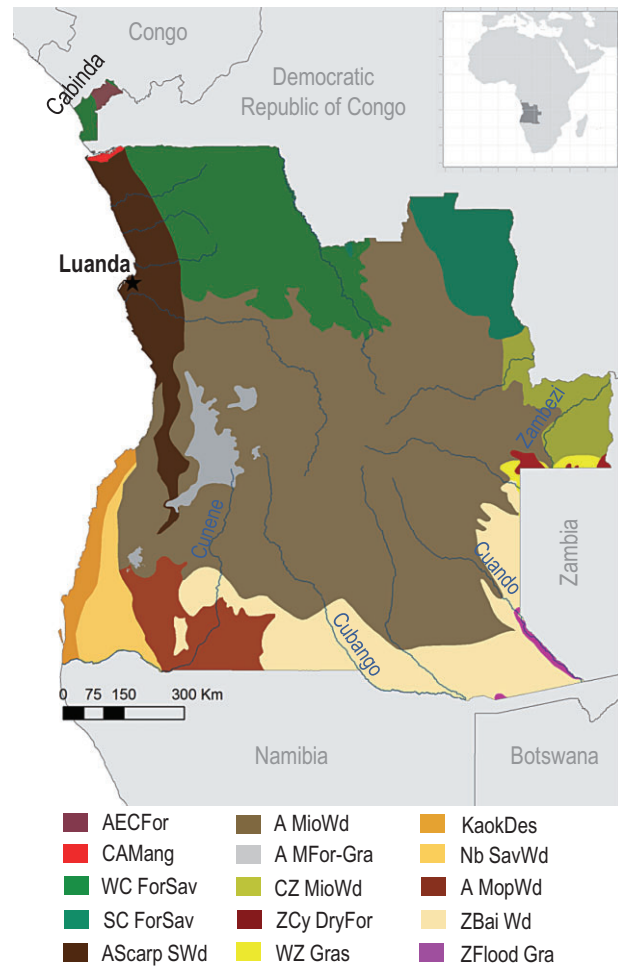


Fig. 1. Geographical location of Angola, Africa, showing its major rivers and WWF Ecoregions: AECFor, Atlantic Equatorial Coastal Forest; CAMang, Central African Mangroves; WCForSav, Western Congolian Forest-Savanna Mosaic; SCForSav, Southern Congolian Forest-Savanna Mosaic; AScarpSWd, Angolan Scarp Savanna and Woodlands; AMioWd, Angolan Miombo Woodlands; AMFor-Gra, Angolan Montane Forest-Grassland Mosaic; CZMioWd, Central Zambebian Miombo woodlands; ZCyDryFor, Zambebian Cryptosepalum Dry Forests; WZGras, western Zambebian Grasslands; KaokDes, Kaokoveld Desert; NbSavWd, Namibian Savanna Woodlands; AMopWd, Angolan Mopane Woodlands; ZBaiWd, Zambebian Baikiaea Woodlands; ZFloodGra, Zambebian Flooded Grasslands.

Cabral & Verissimo 2005), we compiled and georeferenced, at a resolution of quarter degree grid cell (approximately $25 \times 25 \text{ km}$), a total of 9880 occurrence records of 140 rodent, ungulate and carnivore species (Fig. S1 and Table S1 in Appendix S1). The data set is available for download at <http://www.gbif.org/dataset/2fea4042-5aba-4cda-bab9-adcf-a2bbe97d>. Most information was collected from 1930 to 1980, but the oldest records date back to 1860 (Fig. S2 in Appendix S1). The north-western enclave of Cabinda was

excluded from analysis because this small area is disjointed from the rest of the country and has very distinct environmental conditions (Barbosa 1970). Therefore, the bushpig *Potamochoerus porcus*, occurring only in Cabinda, was excluded from analysis. The African manatee *Trichechus senegalensis* was also excluded because it is exclusively aquatic. The subspecies considered in the original publications were maintained because they correspond to taxa that could be easily recognized by field observers. In common with other biogeographical and phylogeographical studies (e.g. Lorenzen et al. 2012), we used the term ungulate in a descriptive sense to refer to hooved mammals, though it does not correspond to a well-defined taxonomic unit. Nomenclature follows Wilson and Reeder (2005), unless indicated otherwise (Table S1 in Appendix S1).

Environmental data set

Relationships between species assemblages and environmental conditions were explored by using climate, soil, landform and vegetation variables (Tables S2 and S3 in Appendix S1). Climate data were obtained from WorldClim (version 1.4) at a resolution of 2.5 arc-min, using the 19 variables describing aspects of temperature and precipitation (Hijmans et al. 2005), and elevation. They encompassed the period from 1950 to 2000 and were resampled to mirror species data resolution. A principal component analysis was performed to investigate multicollinearity and reduce dimensionality (Dormann et al. 2013). The four most uncorrelated climate variables were carried on to subsequent analysis (Table S2 in Appendix S1). The dominant soil type and landform of each grid cell were extracted from the Soil and Terrain Digital Database for Southern Africa v. 1.0 (SOTERSAF, available at <http://www.isric.org/data/soil-and-terrain-database-southern-africa-ver-10-sotersaf>). Soil categories were placed in major groups according to the World Reference Base for Soil Resources (Anonymous 2006). The dominant vegetation type was extracted from the phytogeographic map of Angola (Barbosa 1970). The total number of species records per grid cell was included to account for the possibility of sampling effort influencing perceived variation in species assemblage patterns (Barbosa et al. 2010).

Data analysis

IDENTIFICATION OF BIOGEOGRAPHICAL REGIONS

Data analysis was designed to identify biogeographical regions, corresponding to sets of grid cells that are more similar in species composition to each other than to any other set of grid cells. Separate analyses were carried out for the overall data set, and for the rodent, carnivore and ungu-

late data sets, in order to check whether the different groups presented similar patterns. Cells with fewer than five species were excluded because preliminary analysis suggested that this cut-off represented a good compromise between eliminating potential biases and the artefacts created by few records per cell, and the need to retain a sufficiently large number of cells to obtain meaningful spatial patterns (Heikinheimo et al. 2007, Kreft & Jetz 2010). Dissimilarity between each pair of cells was estimated using the Simpson dissimilarity index (β_{sim}) because it is independent of species richness gradients and does not take double absences into account (Koleff et al. 2003, Kreft & Jetz 2010). The cells were then clustered by applying Ward's minimum variance clustering method to the β_{sim} dissimilarity matrix (Borcard et al. 2011). To determine the optimal number of clusters, we examined fusion level plots of the merging height of nodes in the dendrogram against the number of clusters and applied the L-method (Salvador & Chan 2004). We evaluated the validity of cluster results by using the cophenetic correlation coefficient (Legendre & Legendre 1998, Kreft & Jetz 2010). We also mapped the spatial distribution of the groups to check for spatial coherence (i.e. the association of a group with a well-defined spatial region). When groups were not associated with well-defined regions, we reduced the number of groups to maximize spatial interpretability (Legendre & Legendre 1998). Analyses were implemented in R v.3.0.1 (Anonymous 2005) using the 'cluster' (Maechler et al. 2014) and 'vegan' (Oksanen et al. 2013) packages.

To visualize the spatial pattern of biogeographical regions obtained for carnivores, ungulates and rodents at each level of cluster analyses, we converted grid cells into a network of Thiessen polygons (Schulman et al. 2007, Vale & Jenkins 2012). Each Thiessen polygon contained the centre of a single grid cell with species occurrence records (anchor point), and delimited the area within which any locality is closer to its anchor point than to the anchor point of all other Thiessen polygons (Lo & Yeung 2002). Thiessen networks provide a simple method to visualize spatial variation in collection intensity because polygons tend to be larger where sampling was sparser (Schulman et al. 2007, Vale & Jenkins 2012). The average area of Thiessen polygons thus provided a surrogate of sampling effort in different biogeographical regions (Schulman et al. 2007, Vale & Jenkins 2012).

INDICATOR SPECIES

Indicator species analysis was used to explore the composition of mammal assemblages in the biogeographic regions and to identify which species discriminate the different regions well and can thus be interpreted as being characteristic of them (Dufrene & Legendre 1997, Procheş & Ramdhani 2012). An indicator value (IndVal) was estimated

for each species, as the product of the relative frequency of the species in the target site group divided by the sum of relative frequencies over all groups, and the relative frequency of occurrence of the species inside the target site group. The maximum value ($\text{IndVal} = 1$) is given to a species when it is found in all sites of a group (maximum specificity) and exclusively in that group (maximum fidelity). We considered a species to be an indicator when its $\text{IndVal} > 0.50$ for a $P < 0.05$. The statistical significance of each IndVal was assessed through a randomization procedure with 999 permutations. Analysis was performed using the function 'multipatt' from the R package 'indicpecies' (De Cáceres & Legendre 2009).

ENVIRONMENTAL RELATIONSHIPS

Distance-based redundancy analysis (dbRDA) was used to investigate the influences of environmental variables on the species composition of mammalian assemblages, thus contributing to our interpretation of the results of the cluster analysis. The dbRDA technique uses redundancy analysis but allows the analysis to be based on a range of ecologically meaningful measures of dissimilarity, through the use of principal coordinate analysis (Legendre & Anderson 1999). Dissimilarity was based on β_{sim} to maintain consistency with the cluster analysis, but values were square-root transformed to eliminate negative eigenvalues from the principal coordinate analysis (Legendre & Anderson 1999). We started analysis by building a full model including the seven environmental variables and the surrogate of sampling effort. A backward elimination procedure was then used to remove the variables least related to variation in mammalian assemblage. We eliminated all variables with $P > 0.05$, as judged from Monte Carlo permutation tests (1000 permutations). The overall significance of the reduced model and that of individual axes was also assessed with permutation tests. All analyses were performed in R using 'vegan' (Oksanen et al. 2013).

RESULTS

Biogeographical regions

Dendrograms produced in cluster analysis retained about 40–50% of pairwise dissimilarity between grid cells, considering either the overall data set or each of the three species groups (carnivores, ungulates and rodents; Table S4 in Appendix S2). The numbers of clusters identified by the L-method were five for carnivores, 11 for ungulates, and 12 for rodents and the overall data set (Fig. S3 in Appendix S2). However, visual inspection of maps suggested that the number of subdivisions identified was overly large as there was no clear matching between clusters of grids and

coherent geographical regions. Maps produced using smaller numbers of clusters suggested that maximum spatial interpretability was reached for subdivisions in three or four clusters (Fig. 2).

For the overall data set, the first split retrieved two well-defined regions, one in northern and central Angola, and another in the south and extreme east of the country (Fig. 2a). The second split (three clusters) largely retained the north-central region, while in the south, it separated the Namibe region, roughly corresponding to the Kaokoveld desert and the Namibian dry savanna woodlands of the south-western coastal plain, and the Cunene-Cuando Cubango region, mainly encompassing the Mopane and baikiaea woodlands along the border with Namibia. Spatial coherence was largely lost in the third and fourth splits, though the Namibe and Cunene-Cuando Cubango regions retained their identity. The Central Plateau was divided into two or three loosely defined regions, which strongly intergraded into each other.

Clusters identified using the ungulates shared some similarities to those obtained with the overall data set, though with some differences (Fig. 2b). The first split also separated the northern from the southern regions, but in contrast to the global analysis, part of the Central Plateau was assigned to the southern region. The second split separated the Namibe region from the rest of the southern region. The third split further subdivided the southern region, separating the Cunene-Cuando Cubango region from the southern part of the Central Plateau. The northern-central region was subdivided in the fourth split, largely separating the Congolian woodland-savanna mosaics of the north and north-west, from the southern miombo woodlands of the Central Plateau. However, the two subregions did not show well-defined boundaries, intergrading to some extent into each other.

Clustering for rodents and carnivores showed weak spatial patterns (Fig. 2c, d). Nevertheless, the Namibe region was clearly identified from the carnivore data set, which also showed some separation between the northern and southern regions of Angola (Fig. 2d).

Indicator species

For the overall data set and considering the division in three broad regions (Fig. 2a), a total of 18 species (all ungulates) showed an $\text{IndVal} > 0.50$ for a $P < 0.05$ and were thus identified as indicators (Fig. 3a; Table S5 in Appendix S2). The northern-central region was mostly associated with the presence of African forest buffalo *Syncerus caffer nanus*, bushbuck *Tragelaphus scriptus*, bushpig *Potamochoerus larvatus* and hippopotamus *Hippopotamus amphibius*. The Namibe region was characterized primarily by the presence of springbok *Antidorcas marsupialis*, Kirk's dik-dik

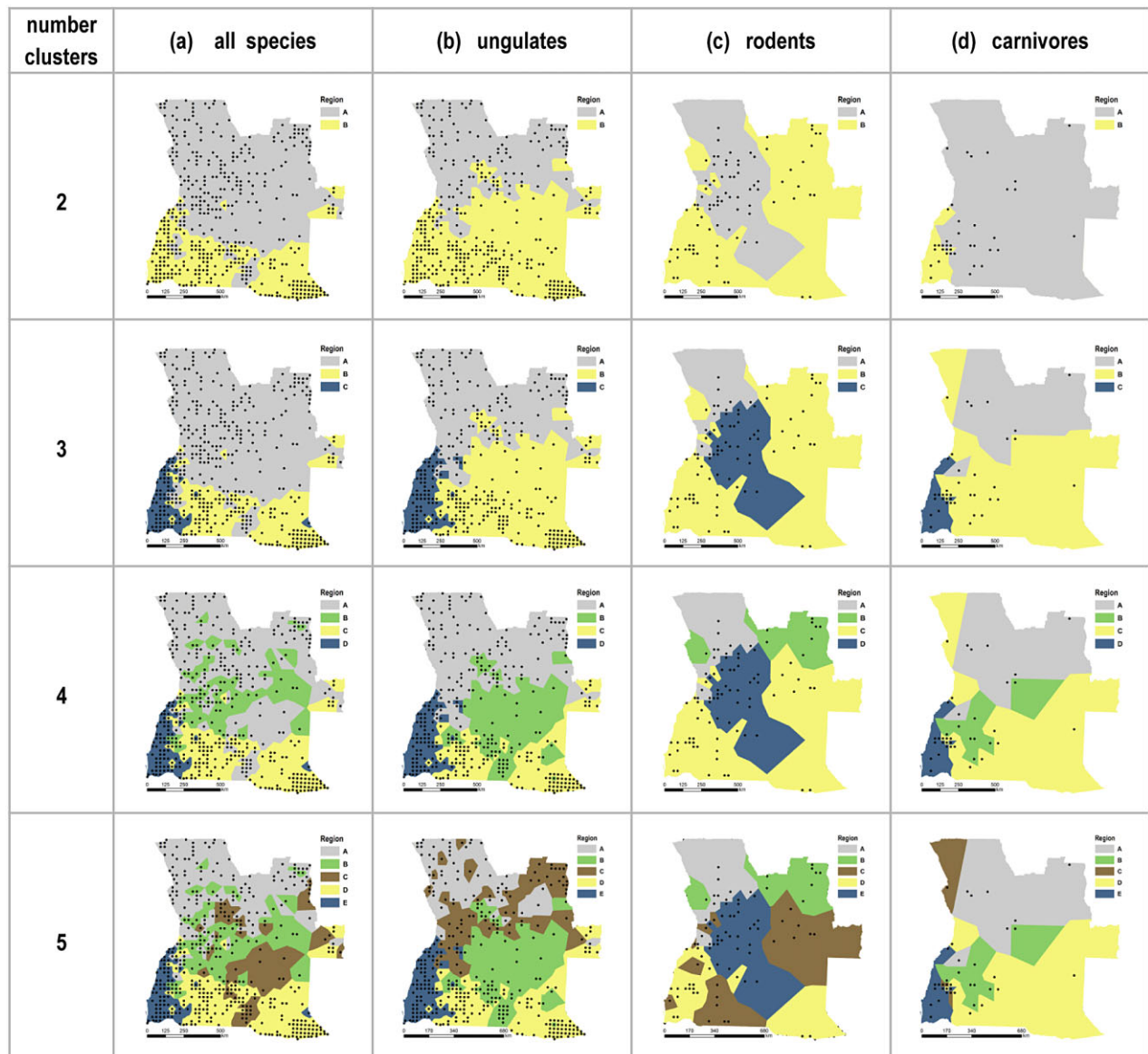


Fig. 2. Sequence of clustering of the mammal data cells for the first four splits of the cluster analysis and for each data set: (a) all species; (b) ungulates; (c) rodents; (d) carnivores. Colours are used to differentiate clusters within each image and do not imply one-to-one matches between images of the same data set.

Madoqua kirkii, klipspringer *Oreotragus oreotragus*, gemsbok *Oryx gazella*, mountain zebra *Equus zebra*, greater kudu *Tragelaphus strepsiceros*, steenbok *Raphicerus campestris* and Burchell's zebra *Equus burchellii*. The Cunene-Cuando Cubango region was associated with blue wildebeest *Connochaetes taurinus*, roan antelope *Hippotragus equinus*, elephant *Loxodonta* spp., buffalo *Syncerus caffer caffer*, common tsessebee *Damaliscus lunatus* and sable antelope *Hippotragus niger niger*. Albeit with much lower IndVals, there were some rodents and carnivores associated with the three regions, including for instance in the north-central region: *Mastomys angolae* (0.44), Southern savanna gerbil

Gerbilliscus validus (0.39) and Griselda's Lemniscomys *Lemniscomys griselda* (0.38); Cunene-Cuando Cubango region: highveld gerbil *Gerbilliscus brantsii* (0.30), black-tailed Thallomys *Thallomys nigricauda* and spotted hyena *Crocuta crocuta*; Namibe region: Cape fox *Vulpes chama* (0.44), Namaqua rock rat *Aethomys namaquensis* (0.44) and rock hyrax *Procavia (capensis) welwitschii* (0.42).

Considering the four broad regions identified for ungulates (Fig. 2b), the species with strong IndVals for the Namibe region were the same as those identified in the overall analysis, though there were some differences in their relative importance (Fig. 3b, Table S6 in Appendix S2).

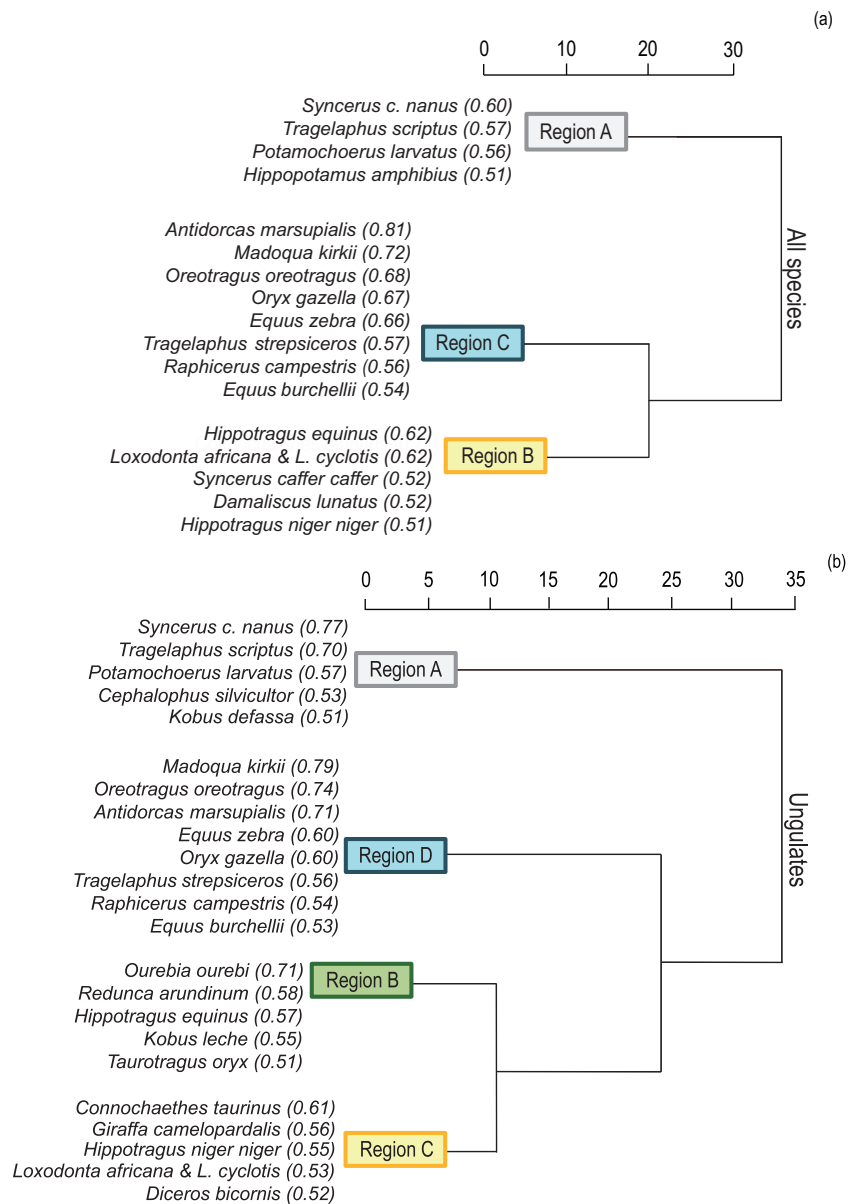


Fig. 3. Dendrograms of the dissimilarity for the overall dataset (all species; a) and for the ungulate species dataset (b), and the biotic regions, built with Ward's Minimum Variance clustering with β sim index of dissimilarity. Indicator species are shown for each biotic region, and their IndVal for each biotic region is given in parentheses. The top horizontal axis represents β sim dissimilarity values.

There were also similarities between analyses for the Cunene-Cuando Cubango, though there was increasing IndVal of the giraffe *Giraffa camelopardalis* and black rhino *Diceros bicornis*, while the roan antelope became one of the indicator species of the Central Plateau region. Other indicator species of the Central Plateau were oribi *Ourebia ourebi*, southern reedbuck *Redunca arundinum*, southern lechwe *Kobus leche* and common eland *Taurotragus oryx*. In the northern region, the main indicator species were forest buffalo, bushbuck, bushpig, yellow-backed duiker *Cephalophus silvicultor* and defassa waterbuck *Kobus ellipsiprymnus defassa*. For rodent and carnivore data sets, no indicator analysis was performed given the weak results obtained in the cluster analysis.

Environmental factors

The dBRDA revealed a significant effect of environmental variables on assemblage patterns, which accounted for about 24% of total variation in the dissimilarity matrix for the overall mammalian data set (Fig. 4a, Table S7 in Appendix S2). The first axis was significant ($F = 50.24, P < 0.005$; 9% of total variation; 37% of constrained species-environment variation), and it largely reflected a climatic gradient of increasing mean temperature and precipitation, more densely forested vegetation types, and soils associated with more humid and forested conditions (ferralsols and luvisols). The axis largely separated the drier and more open Namibe and Cunene-Cuando Cubango regions from the

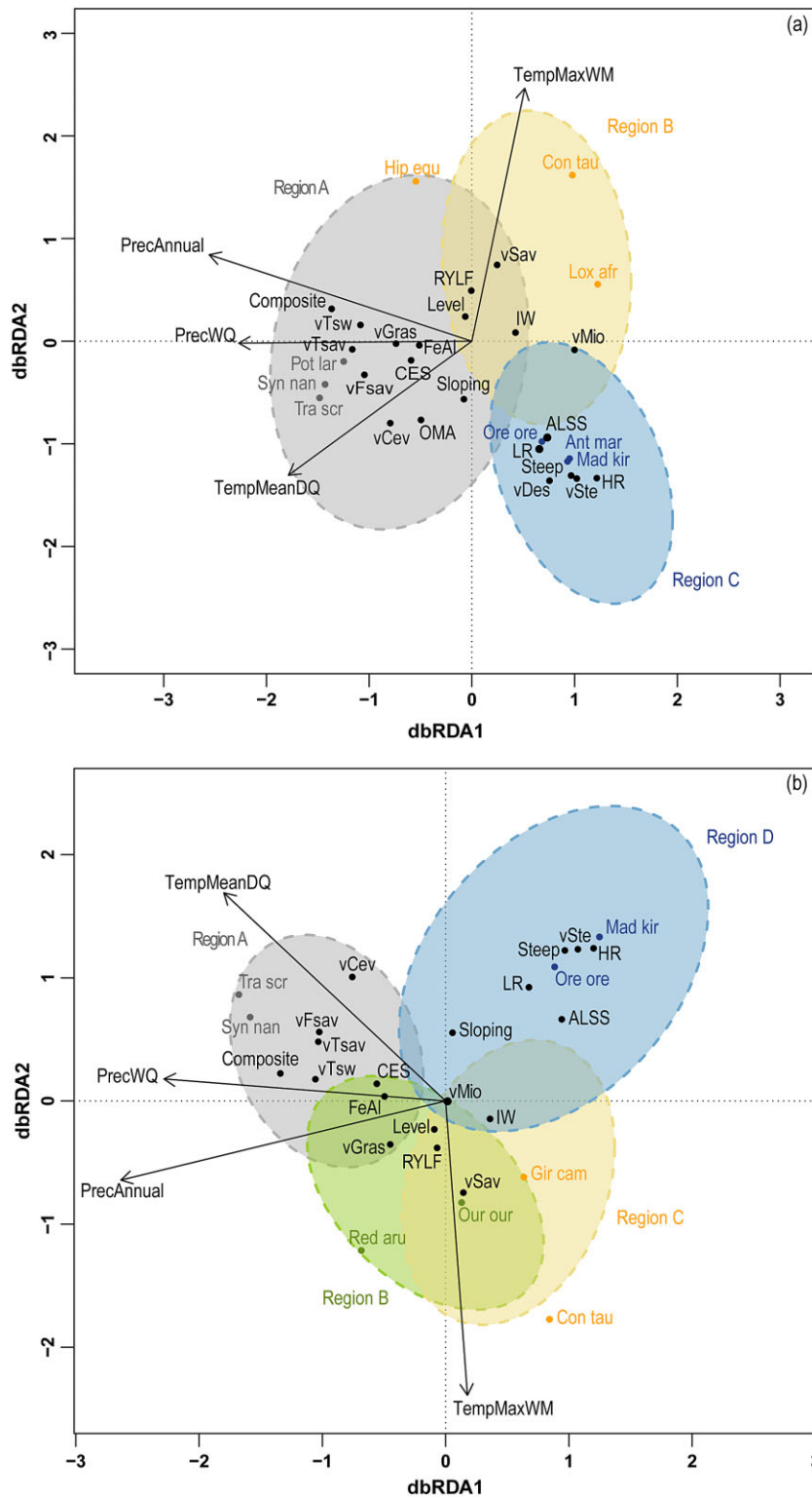


Fig. 4. Triplots of distance-based redundancy analysis (dbRDA) for the overall dataset (all species; a) and for the ungulate species dataset (b). Ellipses represent the 95% confidence intervals of biogeographical regions identified in cluster analysis. Arrows indicate the gradients of quantitative environmental variables (TempMaxWM: maximum temperature of the warmest month; TempMeanDQ: mean temperature of driest quarter; PrecAnnual: annual precipitation; PrecWQ: precipitation of warmest quarter). Qualitative variables are represented by their centroids (codes in Appendix S1). Only the first three (for all species) and two (for ungulates) indicator species of each group are represented (species codes in Appendix S1).

moister and more forested northern-central region. The second axis was also significant ($F = 32.8$, $P < 0.005$; 6% of total variation; 24% of constrained variation), and it mainly corresponded to a gradient of increasing maximum temperature of the warmest month. Along this axis, there was a separation of the two drier biogeographical regions. The Namibe region was associated with desert and steppe vegetation, hard rock, shallow and stony soils (leptosols), or arid zone soils (calciols), and steep landforms. In contrast, the Cunene-Cuando Cubango region was associated with higher temperature in the warmest months, and shrub and tree savanna vegetation.

The species–environment relationships extracted by the dbRDA for ungulates were also significant, accounting for about 32% of total variation in the dissimilarity matrix for the ungulate data set (Fig. 4b, Table S8 in Appendix S2). The first axis was significant ($F = 68.6$, $P < 0.005$; 14% of total variation; 43% of constrained species–environment variation), and it also highlighted a gradient stretching from the drier Namibe and Cunene-Cuando Cubango regions to the moister and more forested northern region. The Central Plateau had an intermediate position along this axes, reflecting smooth north–south transitions rather than sharp discontinuities between regions. The second axis was also significant ($F = 40.89$, $P < 0.005$; 8% of total variation; 26% of constrained variation); it mainly separated the Namibe region from the Cunene-Cuando Cubango region and was also defined by the gradient of increasing temperature in the warmest months identified for the overall assemblage.

DISCUSSION

We identified four main biogeographical units in Angola: one northern region (Zaire-Lunda-Cuanza), one central region (Central Plateau) and two regions in the south (Namibe and Cunene-Cuando Cubango). Although these regions emerged clearly when we considered ungulate distributions, the results for rodents and carnivores were largely inconclusive. The biogeographical patterns identified were associated with a marked environmental gradient, from more humid and forested areas in the north and north-west, to drier and more open woodlands and savannas in the south and south-east. Overall, our results are in line with the recent biogeographical regionalization of Africa proposed by Linder et al. (2012), though we suggest some refinements to the boundaries between regions and add detail to regions previously recognized as largely homogeneous. Our results also agree with a recent worldwide analysis that places northern Angola in the transition between Guineo-Congolian and South African regions, though it does not recognize the three regions identified by our study within the latter region (Holt et al. 2013).

Limitations and potential shortcomings

Although our study has some limitations and potential shortcomings, these are unlikely to affect our key conclusions. In common with other studies based on biological surveys in remote regions (Ponder et al. 2001, Pyke & Ehrlich 2010), our study was affected by the concentration of records in National Parks and Game Reserves, along roads and railway lines, near human settlements and farms, and in otherwise more visited areas (Crawford-Cabral & Mesquitela 1989). Also, observers ranged from professional zoologists to inexperienced travellers and hunters, which may have biased the data in less explored regions towards the most conspicuous species. This might have contributed towards enhancing the identification of biogeographical regions for which more data were available, particularly the Namibe and the Cunene-Cuando Cubango regions. However, these regions are unlikely to be artefacts because they are associated with very particular environmental conditions and with a set of mammalian species that are rare or absent elsewhere in Angola (Crawford-Cabral & Verissimo 2005). Moreover, the north–south division into two or three biogeographical regions is unlikely to be a product of biased data, because it was associated with marked environmental gradients that are expected to influence the distributions of mammalian species. Including the number of records of mammals per cell as a surrogate of sampling effort did not affect the results of dbRDA, further suggesting that sampling bias did not contribute significantly to the main patterns we observed.

Another potential problem was that the overall data set was dominated by ungulate data; far fewer records were available for rodents and carnivores. This probably explains the similarity of the results obtained in the overall analysis and those obtained from the ungulate data sets, though the latter provided more detailed geographical patterns. It cannot be ruled out, however, that the stronger associations observed for ungulates resulted from their closer association to specific vegetation types than rodents and carnivores, though further information would be needed to support this view. Overall, biogeographical regions should be identified by considering the ungulate data, pending further information to assess whether the results for ungulates apply generally to mammalian groups.

Biogeographical units

Based on the results for ungulates (Fig. 4b), we suggest that Angola can be divided into four biogeographical regions, each characterized by a set of indicator species and associated with particular environmental conditions and vegetation types.

ZAIRE-LUNDA-CUANZA

The Zaire-Lunda-Cuanza region corresponds to a rough triangle with vertices in the provinces of Zaire, Lunda Norte and Cuanza Sul, located in north and north-west Angola. It emerged from the analysis of ungulates, while in the overall analysis, it was lumped with the Central Plateau. The region matches the Angolan portion of the Shaba region identified by Linder et al. (2012), which represents the transition between Guineo-Congolian rain forests and the Zambebian region. It matches reasonably well to WWF Ecoregions, encompassing the blend of humid evergreen and semi-deciduous forests, woodlands, shrublands and grasslands characterizing the western Congolian forest-savanna mosaic (Olson et al. 2001, Fig. 1). Along the coastal belt, it includes most of the Angolan scarp savanna and woodlands. The region also encompasses the northern part of the deciduous broadleaf savannas and woodlands characterizing the Angolan miombo woodlands. Two key indicator species were the forest buffalo and the yellow-backed duiker, which have their core range within the Congo Basin forests, reaching their southern limit in Angola. Other indicators show much the same pattern, including blue duiker *Philantomba monticola*, black-fronted duiker *Cephalophus nigrifrons* and bay duiker *Cephalophus dorsalis*. The other species with high IndVal were bushpig, bushbuck and defassa waterbuck, which have a relatively wide distribution both in Sub-Saharan Africa and Angola, but which, in this region, occupy a band below the southern limit of the Congo Basin forest, spreading from the coast into Zambia. These species tend to be rare or absent in southern Angola.

CENTRAL PLATEAU

The Central Plateau region corresponds to the south and south-eastern parts of the central plateau of Angola. It intergrades to some extent with the Zaire-Lunda-Cuanza region, suggesting that there is a north-south gradient in mammalian assemblages, rather than two well-defined regions. This view is supported by the lumping of the two regions in the analysis using the overall data set. The Central Plateau is included in the Zambebian region of Linder et al. (2012) and encompasses to a large extent the WWF Ecoregion of the Angolan miombo woodlands (Olson et al. 2001). It comprises moist, deciduous broadleaf savannas and woodlands dominated by the genera *Brachystegia*, *Julbernardia* and *Isobertinia*, interspersed with grassland areas. The main indicator species are widespread in Africa, occurring in the belt of woodlands and savannas surrounding the Guineo-Congolian region: oribi, roan antelope, elande, common warthog *Phacochoerus africanus* and bush duiker *Sylvicapra grimmia*. Also characterizing this region is the local endemic giant sable antelope *Hippotragus niger variani*. The southern

lechwe and the southern reedbuck also showed a high IndVal for this region, though they are widespread elsewhere in Angola.

CUNENE-CUANDO CUBANGO

The Cunene-Cuando Cubango region was clearly identified in the analyses of both the overall and the ungulate data sets. It encompasses a band running along the southern border of Angola with Namibia, eastward of the Namibe region and continuing farther north along the border with Zambia. The region is interrupted by a strip running along the Cubango River and showing affinities with the Central Plateau. Although the overall biogeographical regionalization of Linder et al. (2012) includes the entire Cunene-Cuando Cubango region within the Zambebian region, in the partial analysis for mammals, it is included to a considerable extent within the South African/Kalahari region. The Cunene-Cuando Cubango region therefore probably corresponds to the northern limit of the Kalahari sub-region (Linder et al. 2012). In terms of WWF Ecoregions, most of the Cunene-Cuando Cubango region is included in the Zambebian baikiaea woodlands, though in the border with the Namibe region, it encompasses the Angolan mopane woodlands. Most indicator species have a large natural distribution in savannahs of southern and eastern Africa, but they have a restricted distribution elsewhere in Angola: wildebeest, giraffe, sable antelope, black rhino, common tsessebee, buffalo, hartebeest *Alcelaphus buselaphus* and impala *Aepyceros melampus melampus*. Elephants in Angola are mostly associated with the Cunene-Cuando Cubango region and are largely absent from the miombo woodlands, though they also occur in the Congolian forest-savanna mosaics (Crawford-Cabral & Veríssimo 2005).

NAMIBE

The Namibe region was identified by both the overall and the ungulate data sets, and encompasses south-western Angola. It matches closely the south-western Angola region defined by Linder et al. (2012), which is part of the large Southern Africa Region. It has also a strong correspondence with the WWF Ecoregions of the Kaokoveld desert, representing the northern part of the vast Namib Desert, and the Namibian savanna woodlands. Rock hyrax *Procavia capensis welwitschii* and black-faced impala *Aepyceros melampus petersi* are characteristic of the region, being endemic to south-western Angola and north-western Namibia. Yellow-spotted rock hyrax *Heterohyrax brucei*, Kirk's dik-dik and, to a lesser extent, klipspringer also have a restricted distribution, though they also occur in arid and semi-arid habitats in disjointed areas of north-eastern and eastern Africa. Other indicators such as springbok, gemsbok

and mountain zebra are associated with dry grasslands, bushland and/or shrubland of south-western and southern Africa, showing a marginal extension into south-western Angola. Steenbok, greater kudu and Burchell's zebra are widespread in eastern and southern Africa, but in Angola, they occur primarily in the south and south-west.

Environmental influences on biotic regionalization

The results of dbRDA revealed a north–south sequence of intergrading biogeographical regions which follows the dominant climate gradients in this region of Africa (Le Houérou 2009), and the associated variation in soil and vegetation types. This sequence also matches closely a strong north–south gradient in closed canopy forest cover (Hansen et al. 2013) with a progressive southwards transition to savannahs (Murphy & Bowman 2012). In the north and north-west, the climate is predominantly humid equatorial, with high precipitation following a bimodal pattern, rain concentrated in summer and temperature with low annual amplitude (Le Houérou 2009). These conditions are associated with dense evergreen forest and woodland mosaics (Hansen et al. 2013), which allow the penetration of Congolian elements into the Zaire-Lunda-Cuanza region. The southern penetration of Congolian species seems to be favoured also by the presence of dense gallery forests, which may provide suitable habitat conditions for them in otherwise drier forest areas (Crawford-Cabral & Veríssimo 2005). Southward, the climate progressively ranges from tropical humid to semi-arid, with declining annual precipitation, and increases in the annual amplitude of temperature and in the temperature of the warmest month (Le Houérou 2009). Except for the desert region of Namibe, the driest extreme of the climate gradient is found in the Cunene-Cuando Cubango region, which is occupied by dry-deciduous savannahs and allows the northward penetration of many species widespread elsewhere in southern Africa.

The Central Plateau occupies an intermediate position in the north–south gradient, showing a set of a few characteristic species that are widespread in southern and eastern Africa, and also occur elsewhere in other regions of Angola. The only exception is the endemic giant sable antelope, which has a very small natural range covering only a small proportion of the region. Therefore, the Central Plateau appears to be separated from the other regions, mainly because it is occupied at relatively low density by a few widespread species (Huntley 1974), rather than being characterized by a particular set of unique species. This may be a consequence, at least partly, of the poor browsing conditions provided by the dry miombo woodlands covering this region: there is a shortage of browse in the dry season, the quality of leaf matter is low, and the canopies of most trees

are high and inaccessible (Frost 1996). Furthermore, many savanna herbivores prefer areas of low tree density (Riginos & Grace 2008), which contributes to the absence of many species in dense miombo woodland. The region thus probably represents a barrier that prevented the penetration southwards of Congolian species, and the penetration northwards of species from southern Africa.

The coastal Namibe region seems to be somewhat eccentric to the dominant north–south climate gradient (Le Houérou 2009): it is an arid to hyper-arid tropical region with relatively low temperature and little annual variation in temperature, which is shaped by the local effects of the cold Benguela current. The region shares with western Namibia a range of unique mammalian species adapted to desert conditions and favours also the occurrence of other dry grassland and open savanna species. Recent phylogeographic studies suggest that this region was a Pleistocene refugium for a number of species, some of which show genetic divergence from populations elsewhere in Africa (Lorenzen et al. 2012).

Although human activities are known to affect African mammals strongly (Ceballos & Ehrlich 2002, Craigie et al. 2010), it is unlikely that humans have shaped to a significant extent the large-scale biogeographical patterns observed in this study. This is because the study was based on data collected from a long period before intense poaching resulted in major population declines and local extirpation of large ungulates and carnivores in Angola (Crawford-Cabral & Veríssimo 2005, Pitra et al. 2006, Chase & Griffin 2011). Therefore, the data set probably reflects the natural distribution of most species, as suggested for instance by the relatively large ranges observed for sensitive species such as elephants and black rhinos (Crawford-Cabral & Veríssimo 2005). Also, there is no evidence that the data set included occurrences of species that had been translocated outside their natural ranges, although translocation is known to have occurred in other regions of Africa (Spear & Chown 2009). Finally, it is unlikely that anthropogenic fires influenced our results significantly, though they are widespread in African ecosystems and are known to affect African mammals strongly at the local and landscape scales (e.g. Bond & Archibald 2003). This view is supported by recent research suggesting that the large-scale distribution of forests and savannahs is mostly determined by climatic and edaphic controls (Murphy & Bowman 2012, Zeng et al. 2014), despite the influence of fire on local vegetation structure (e.g. Ryan & Williams 2011). Therefore, we believe that the Angolan biogeographical regionalization described here largely reflects the operation of natural rather than anthropogenic processes and thus, it provides a baseline for assessing changes induced by relatively recent impacts such as poaching (Crawford-Cabral & Veríssimo 2005) and deforestation (Hansen et al. 2013).

Overall, our results suggest that the biogeographical patterns observed in this study are shaped to a large extent by the position of the country at the crossroads between the humid, evergreen forests of the Congolian Basin, the desert and arid savannas of south-western Africa, and the dry deciduous woodlands and savannahs of southern and eastern Africa (Le Houérou 2009). Each of these habitat types is associated with a characteristic set of mammalian species that penetrate into Angola and intergrade into each other to a variable extent, probably depending on the dominant vegetation types, which in turn are shaped by climate and edaphic factors. It is likely that the same gradients also affect mammalian groups not analysed here, as well as other plant and animal groups (Linder et al. 2012). Analysing the consistency of the patterns observed for a wide range of species would be a valuable subject for further research. Such research could contribute greatly towards conservation planning in Angola and towards our understanding of African biogeography.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1. Supplementary materials and methods – lists of species and environmental correlates.

Appendix S2. Supplementary results.