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# Patterns of species richness, endemism and environmental gradients of African reptiles

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## ABSTRACT

**Aim** To map and assess the richness patterns of reptiles (and included groups: amphisbaenians, crocodiles, lizards, snakes and turtles) in Africa, quantify the overlap in species richness of reptiles (and included groups) with the other terrestrial vertebrate classes, investigate the environmental correlates underlying these patterns, and evaluate the role of range size on richness patterns.

**Location** Africa.

**Methods** We assembled a data set of distributions of all African reptile species. We tested the spatial congruence of reptile richness with that of amphibians, birds and mammals. We further tested the relative importance of temperature, precipitation, elevation range and net primary productivity for species richness over two spatial scales (ecoregions and 1° grids). We arranged reptile and vertebrate groups into range-size quartiles in order to evaluate the role of range size in producing richness patterns.

**Results** Reptile, amphibian, bird and mammal richness are largely congruent ( $r = 0.79–0.86$ ) and respond similarly to environmental variables (mainly productivity and precipitation). Ecoregion size accounts for more variation in the richness of reptiles than in that of other groups. Lizard distributions are distinct with several areas of high species richness where other vertebrate groups (including snakes) are species-poor, especially in arid ecoregions. Habitat heterogeneity is the best predictor of narrow-ranging species, but remains relatively important in explaining lizard richness even for species with large range sizes.

**Main conclusions** Reptile richness varies with similar environmental variables as the other vertebrates in Africa, reflecting the disproportionate influence of snakes on reptile richness, a result of their large ranges. Richness gradients of narrow-ranged vertebrates differ from those of widespread taxa, which may demonstrate different centres of endemism for reptile subclades in Africa. Lizard richness varies mostly with habitat heterogeneity independent of range size, which suggests that the difference in response of lizards is due to their ecological characteristics. These results, over two spatial scales and multiple range-size quartiles, allow us to reliably interpret the influence of environmental variables on patterns of reptile richness and congruency.

## Keywords

climatic variables, cross-taxon congruence, ecoregions, endemism, lizards, range-size quartiles, reptiles, snakes, species richness

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## INTRODUCTION

Patterns of species richness have been described across many taxa and over multiple scales (e.g. Currie, 1991; Hawkins *et al.*, 2003; Field *et al.*, 2009; Belmaker & Jetz, 2011). Richness gradients have generally been attributed to environmental constraints such as temperature (ambient energy), water availability (Currie, 1991), habitat heterogeneity (Kerr & Packer, 1997; Hortal *et al.*, 2013), and productive energy (Evans *et al.*, 2005). The distributions of amphibians, mammals and birds are now mapped to the species level, and their richness patterns are widely studied (e.g. Grenyer *et al.*, 2006), whereas reptile distributions are largely unmapped, and remain the least studied among terrestrial vertebrates (McCain, 2010). Of studies which have examined patterns of reptile species richness gradients, few have distinguished between the distinct reptile lineages – amphisbaenians, crocodiles, lizards, snakes and turtles (e.g. Currie, 1991; Qian *et al.*, 2007; Powney *et al.*, 2010). A biogeographical bias is also evident – reptile richness has been studied in North America, Europe, Australia and China (Currie, 1991; Rodriguez *et al.*, 2005; Qian *et al.*, 2007; Powney *et al.*, 2010), but few studies have investigated their diversity elsewhere, especially in Africa (Deikumah *et al.*, 2014; Meiri, 2016). Examining the environmental effects on species richness on a per region basis is important, as non-stationarity has been shown across multiple geographical regions (Schall & Pianka, 1978; Davies *et al.*, 2007; Powney *et al.*, 2010; Buschke *et al.*, 2015).

Reptiles will soon emerge as the richest class of terrestrial vertebrates at current levels of species description (Pincheiro-Dinoso *et al.*, 2013; Meiri & Chapple, 2016). Understanding reptile richness is particularly important, as they are ecologically distinct from other terrestrial vertebrate taxa. As ectothermic amniotes, their species richness patterns are thought to be mostly associated with measures of ambient energy, in contrast to endotherms and amphibians, which are more reliant on water and productivity (Hawkins *et al.*, 2003; Rodriguez *et al.*, 2005; Qian *et al.*, 2007).

Distinct reptile groups are likely to respond differently to environmental variables. For example, snake species richness gradients suggest that they are closely related to both energy and water availability (Hawkins *et al.*, 2003; Terribile *et al.*, 2009). Turtle species richness is usually found to increase with both temperature and precipitation (Schall & Pianka, 1978; Iverson, 1992). However, while just over half of the turtle species (and all crocodile species) in Africa are aquatic (Trape *et al.*, 2012), a significant number of turtle species are also adapted to semi-arid regions. Similarly, lizards are known to inhabit diverse ecoregions ranging from desert to tropical (e.g. in Australia; Powney *et al.*, 2010). Previous studies of lizard species richness gradients suggest that they are most closely related to temperature (Hawkins *et al.*, 2003; Rodriguez *et al.*, 2005; McCain, 2010). This is because lizards are ectothermic amniotes, requiring heat for

metabolic activities, but are able to do with very little water (Schall & Pianka, 1978). Amphisbaenians are a small (195 species, 74 of which inhabit Africa; Uetz, 2015) and poorly studied group. Because of their fossorial nature we predict their distributions to be less affected by climate.

Different environmental variables may constrain the species richness of vertebrate groups with different geographical ranges and dispersal ability. Heterogeneity measures often become more important relative to climatic variables in explaining narrow-ranged species richness (Szabo *et al.*, 2009; Belmaker & Jetz, 2011). Habitat complexity may provide more unique niches for habitat specialists, and complex habitats may inhibit movement of species with poor dispersal ability – but affect highly vagile species with wide physiological tolerance to a lesser extent.

We assembled a comprehensive geographical distribution map of all African reptile species in order to: (1) assess the species richness patterns of reptile (and included groups: amphisbaenians, crocodiles, lizards, snakes and turtles) distributions in Africa, (2) quantify the overlap in species richness of reptile (and included groups) with the other vertebrate classes, (3) investigate the environmental correlates underlying these patterns and (4) evaluate the role of range size on the species richness patterns of reptiles and vertebrate groups.

## METHODS

We obtained data on the distribution of reptile species in mainland Africa from a variety of published sources, including field-guides and atlases (especially Bates *et al.*, 2014; Branch, 1998, 2014; Carranza *et al.*, 2008; Chippaux, 2006; Chirio & LeBreton, 2007; Gans, 1987; Largen & Spawls, 2010; Pauwels & Vande Weghe, 2008; Sindaco & Jeremcenko, 2008; Spawls *et al.*, 2002; Tilbury, 2010; Trape & Mane, 2006; Trape *et al.*, 2012), museum databases, the primary literature and IUCN assessments (see Appendix S1 in Supporting Information). Where published maps and data were unavailable, those of us with much experience in studying African reptiles in the field and in natural history collections (DGB, AMB, LC, ML, DM, ZTN and JFT) drew expert-ranges based on collection localities, their own observations and intimate knowledge of habitats in the region, and on specimens from known localities. The distributions of 71 amphisbaenian, four crocodile, 928 lizard (suborder Sauria), 551 snake (suborder Serpentes) and 47 turtle (order Testudines) species inhabiting Africa (Uetz, 2015) were digitized using ArcGIS 10.0. We obtained digital maps for the 1905 breeding bird species in the region from BirdLife International & NatureServe (2013), and digital maps for the 1113 mammal and 769 amphibian species inhabiting the region from the IUCN (2014). Marine taxa were omitted. Point locality data were converted to polygons buffered by a 1 km radius in order to calculate range size. Digitized maps were overlaid at two different spatial scales to determine species

richness: (1) WWF ecoregions (herein referred to as *ecoregion scale*), consisting of 107 regions in Africa (excluding the 'Lake' ecoregion; data from Olson *et al.*, 2001), and (2) An equal-area Behrmann projection grid at a resolution of  $\sim 1^\circ$  (herein referred to as *1° scale*), comprising 3146 cells. Species richness (henceforth '*richness*') is the number of species present in each ecoregion they intersect. The advantage of using ecoregions is that they are ecologically distinct units that allow us to directly evaluate the influence of environmental measures without positively biasing habitats that cover large areas (e.g. the Sahara desert will be counted only once and not multiple times as in grid-based analyses) or wide-ranging species found in multiple grid cells, thus reducing pseudoreplication and spatial-autocorrelation (Jetz & Fine, 2012; Belmaker & Jetz, 2015; Buschke *et al.*, 2015). We retain the grid-based analyses to assess the scale-dependence of the results and to assure the results are not contingent on the spatial scale over which richness was estimated.

### Environmental correlates of species richness

Richness was related to four variables to test climatic, ecological and energetic determinants explaining diversity gradients: (1) mean annual temperature ( $^\circ\text{C}$ ,  $0.16^\circ$  resolution; data from Hijmans *et al.*, 2005; BIO1 2014), representing ambient energy, (2) mean annual precipitation (mm,  $0.16^\circ$  resolution; from Hijmans *et al.*, 2005; BIO12 2014), representing water availability, (3) elevation range (m,  $0.16^\circ$  resolution; from Hijmans *et al.*, 2005), representing habitat heterogeneity, and (4) net primary productivity (NPP) ( $\text{g C year}^{-1}$ ,  $0.25^\circ$  resolution; from Imhoff *et al.*, 2004), representing productive energy. We included ecoregion area as a predictor to account for the variation in size among ecoregions (ranging in Africa from  $\sim 16 \text{ km}^2$  to 4.7 million  $\text{km}^2$ ). Areas were log-transformed, and mean precipitation and elevation range were square-root transformed to reduce heteroscedasticity and normalize model residuals. We standardized each predictor variable to provide comparable regression coefficients. All variables were tested for collinearity using variance inflation factors (VIF), and selected due to their presumed effect on richness gradients. We excluded additional variables that

were collinear with other variables we examined (VIF scores  $> 5$ , see Craney & Surlles, 2002; O'Brien, 2007). These included: minimum elevation, seasonality in temperature, seasonality in precipitation, minimum temperature and maximum temperature (data from Hijmans *et al.*, 2005).

### Range-size quartiles

In order to analyse the response of different range-sized groups to environmental correlates, we calculated the geographical range extent ( $\text{km}^2$ ) of species using the best resolution maps. We divided the overall reptile class into four groups based on range size from first quartile (narrow-ranging species) to fourth quartile (wide-ranging species). We then assigned lizard, snake, amphibian, bird and mammal species to these range-size quartiles, so that equivalent quartiles contained only species with comparable range sizes (Table 1; Appendix S2).

Reptile species richness and environmental data within ecoregions are presented in Appendix S3. Reptile species' range size, quartile and number of ecoregions occupied are presented in Appendix S4.

### Statistical analyses

Pearson's correlation was used to measure the degree of congruence between reptile groups and across vertebrate classes. We corrected the degrees of freedom to account for spatial autocorrelation using a modified *t*-test using the Clifford correction (Clifford *et al.*, 1989). To measure the correlations between overall reptile richness and that of each reptile subgroup we subtracted the number of species in the corresponding subgroup from the overall reptile numbers. We used hierarchical partitioning to assess the average contribution of each predictor to the variance in richness for each taxon, based on the independent contributions of each predictor (Murray & Conner, 2009). Total  $R^2$ -values for each model were calculated from fitting generalized linear models with Gaussian distributions. All statistical analyses were performed using R version 3.2.0 (R Development Core Team, 2014), and the packages 'hier.part' and 'SpatialPack'.

**Table 1** Vertebrate range-size quartiles. Quartiles are based on reptile range sizes. Values are the number of species in each range-size quartile (in parentheses: the proportion of all species in that taxon).

Taxon	1st quartile Range area ( $\text{km}^2$ ): 0–12,207	2nd quartile Range area ( $\text{km}^2$ ): 12,208–102,968	3rd quartile Range area ( $\text{km}^2$ ): 102,969–734,587	4th quartile Range area ( $\text{km}^2$ ): 734,588–19,078,943	Median range size of taxon ( $\text{km}^2$ )
Reptiles	400 (25%)	400 (25%)	400 (25%)	401 (25%)	105,025
Amphisbaenians	32 (45%)	18 (25%)	16 (23%)	5 (7%)	18,993
Lizards	254 (27%)	295 (32%)	231 (25%)	148 (16%)	59,407
Snakes	113 (21%)	83 (15%)	138 (25%)	217 (39%)	387,884
Turtles	1 (2%)	5 (11%)	15 (32%)	26 (55%)	989,462
Amphibians	354 (46%)	118 (15%)	144 (19%)	153 (20%)	18,317
Birds	144 (7.5%)	186 (10%)	506 (27%)	1,063 (55.5%)	1,037,354
Mammals	181 (16%)	170 (15%)	312 (28%)	447 (40%)	434,019

## RESULTS

### Patterns of species richness and cross-taxon congruence

Reptile richness at the ecoregion scale (Fig. 1) is largely congruent with amphibian, bird and mammal richness ( $r$  values between 0.79–0.86; Table 2). All groups show classic latitudinal gradients, but reptile hotspots extend further into arid ecoregions. Amphibians are distinct in being nearly absent from arid regions. Overall reptile richness is mostly influenced by snake richness, which is the most congruent of the reptile groups to the other classes ( $r$  values between 0.85–0.89). Turtle richness is also congruent with the other classes ( $r$  values between 0.80–0.83). In contrast, amphisbaenian and lizard richness are considerably less congruent with all other groups ( $r$  values between 0.35–0.56; Fig. 1).

Patterns of cross-taxon congruence are consistent at the 1° scale (Table 3), with amphisbaenian and lizard richness having non-significant relationships after correcting the numbers of degrees of freedom.

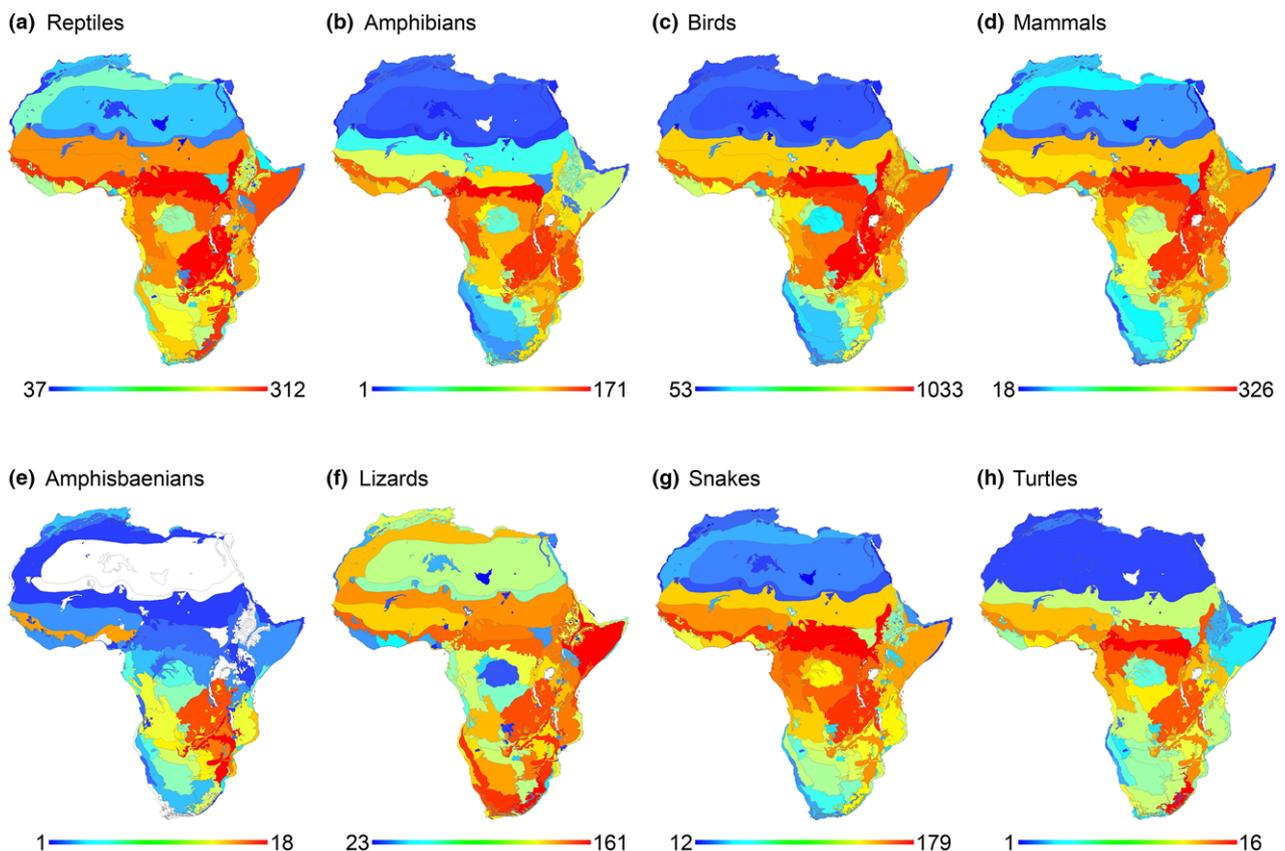
The disparity between the richness of reptiles and other classes is mostly attributed to the influence of lizard distribution, which is qualitatively very different from the other reptile and non-reptile groups. Lizard richness hotspots are widely dispersed and distinct. Ecoregions with high diversity

of lizards include arid regions such as the Namibian savanna woodlands, Nama Karoo, North Saharan steppe, Mediterranean woodlands and forests, as well as the mountainous ecoregion of the Drakensberg (Fig. 1; see Appendix S5 for list of richest ecoregions per taxon). The richness of other reptile groups and of the other classes is relatively low in these ecoregions. Amphisbaenian richness is centred in the woodland ecoregions of southern and central Africa (as well as the Guinean forest-savanna mosaic), and is the most restricted of all groups, markedly absent from desert areas. Turtle richness resembles snake richness, but turtles do not range as far into arid ecoregions (see Appendix S6 for an ecoregion map of crocodile richness with  $n = 4$  species).

Patterns of reptile species richness are consistent at the 1° scale (Fig. 2). Overall reptile richness patterns most strongly resemble snake richness. Lizard richness hotspots are more distinct and disparate at this resolution, such as in areas of West Africa, the Sahara and North Africa. Amphisbaenian and turtle richness patterns are most restricted and significantly absent from arid regions.

### Environmental correlates of species richness

We used hierarchical partitioning to assess the average independent contribution of each predictor to the variance in richness (Fig. 3). The total amount of explained variation is



**Figure 1** Species richness of vertebrate classes (a–d) and reptile groups (e–h) within African ecoregions. Colour codes correspond to species numbers in ecoregion from low (blue) to high (red). White denotes no species.

**Table 2** Ecoregion cross-taxon congruence of vertebrate species richness (Pearson's correlation). *P*-values are < 0.001 for all correlations, number of ecoregions is 107, (*r*-value above the diagonal, numbers of degrees of freedom corrected for spatial-autocorrelation below the diagonal).

Taxon	Amphibians	Birds	Mammals	Reptiles	Amphisbaenians	Lizards	Snakes	Turtles
Amphibians	—	0.81	0.83	0.79	0.45	0.45	0.85	0.83
Birds	94.02	—	0.94	0.83	0.35	0.52	0.88	0.82
Mammals	91.91	92.43	—	0.86	0.39	0.56	0.89	0.80
Reptiles	95.95	95.41	94.62	—	−0.49	−0.53	0.62	−0.87
Amphisbaenians	93.92	99.17	94.57	102.57	—	0.41	0.44	0.47
Lizards	98.91	97.48	96.14	98.34	101.37	—	0.51	0.56
Snakes	94.80	94.17	93.65	98.04	99.85	98.45	—	0.90
Turtles	99.44	97.84	97.72	97.56	106.12	100.19	97.55	—

**Table 3** Behrmann grid (1° scale) cross-taxon congruence of vertebrate species richness (Pearson's correlation). Number of grid cells is 3108, (*r*-value above the diagonal, *P*-value in parentheses, numbers of degrees of freedom corrected for spatial-autocorrelation below the diagonal).

Taxon	Amphibians	Birds	Mammals	Reptiles	Amphisbaenians	Lizards	Snakes	Turtles
Amphibians	—	0.84 (0.002)	0.87 (< 0.001)	0.85 (< 0.001)	0.31 (0.287)	0.35 (0.049)	0.84 (< 0.001)	0.79 (0.001)
Birds	8.48	—	0.95 (< 0.001)	0.83 (0.001)	0.32 (0.328)	0.38 (0.072)	0.80 (0.003)	0.85 (0.001)
Mammals	8.76	6.91	—	0.87 (< 0.001)	0.28 (0.380)	0.36 (0.071)	0.85 (0.001)	0.83 (0.001)
Reptiles	10.76	8.68	9.75	—	0.28 (0.318)	0.27 (0.120)	0.51 (0.013)	0.83 (< 0.001)
Amphisbaenians	11.94	9.17	9.00	12.63	—	0.31 (0.097)	0.21 (0.459)	0.27 (0.337)
Lizards	29.71	21.08	23.91	32.50	28.73	—	0.25 (0.134)	0.34 (0.070)
Snakes	10.23	8.94	8.78	20.71	12.29	35.43	—	0.81 (< 0.001)
Turtles	10.99	8.63	9.12	11.32	12.31	26.75	11.16	—

considerably lower for amphisbaenian and lizard richness ( $R^2$  values = 0.28 and 0.46 respectively), compared to the other reptile and vertebrate groups ( $R^2$  values between 0.63–0.75).

Net primary productivity and precipitation explain most of the variation in richness of amphibians, mammals and birds, as well as that of snakes and turtles – but are unrelated to lizard richness. In lizards, richness is most strongly correlated with ecoregion area and elevation range, and amphisbaenian richness is most strongly correlated with area and NPP. Reptile groups (especially lizards) are unique in that ecoregion area accounts for a substantial proportion of variation in their richness. Temperature explains relatively little of the variation in the richness of all groups, including lizards, and of reptile richness in general.

Environmental correlates of species richness are consistent at the 1° scale (Appendix S7). Net primary productivity and precipitation explain most of the variation in richness of all groups except lizards, in which richness is most strongly correlated with elevation range.

### Effects of range size

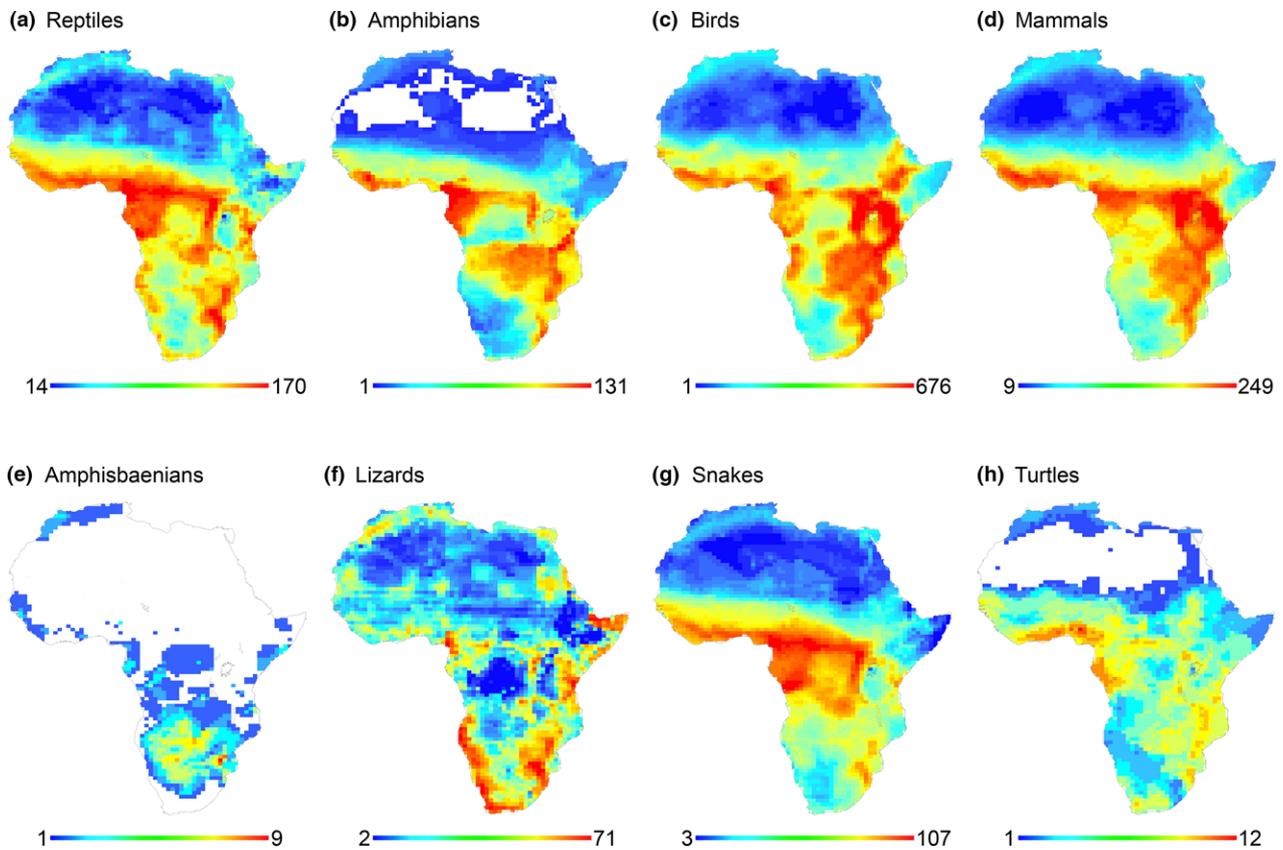
Elevation range is the most important variable explaining the richness variation of narrow-ranging lizards, snakes and reptiles in general (Fig. 4). The effect of elevation on richness is reduced for wide-ranging species, but remains relatively important in explaining lizard richness even at larger range

sizes. Similarly, elevation range is the most significant predictor of richness variation in narrow-ranging amphibian, bird and mammal species (Fig. 5), but is reduced for wide-ranging species, and replaced by NPP and precipitation, which have no effect on the richness of even the large-ranged lizards.

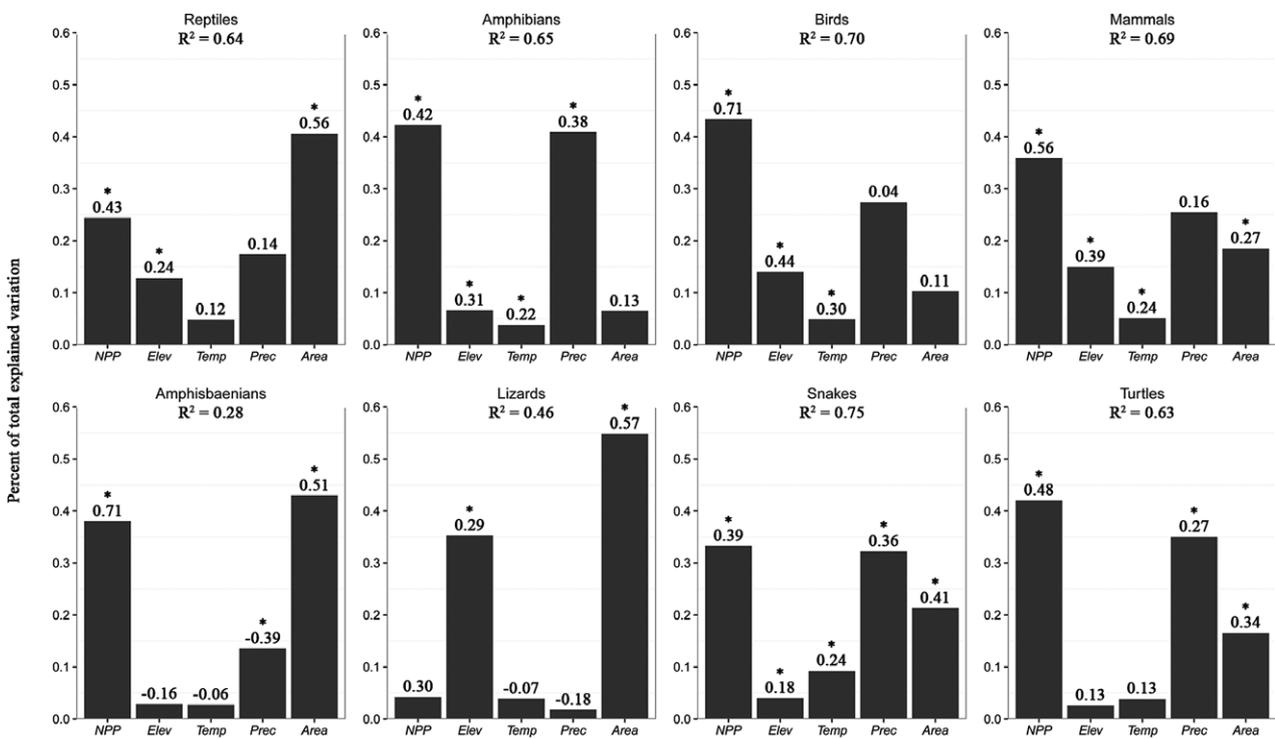
### DISCUSSION

We present the first comprehensive reptile richness maps for all of Africa. Overall reptile richness is largely congruent with that of other vertebrates. Different reptile groups and range-sized quartile groups, however, have different patterns of richness. In particular, patterns of lizard richness emerge as distinct from the other reptile and vertebrate groups by responding differently to richness predictors, which may in-turn influence their patterns of congruency.

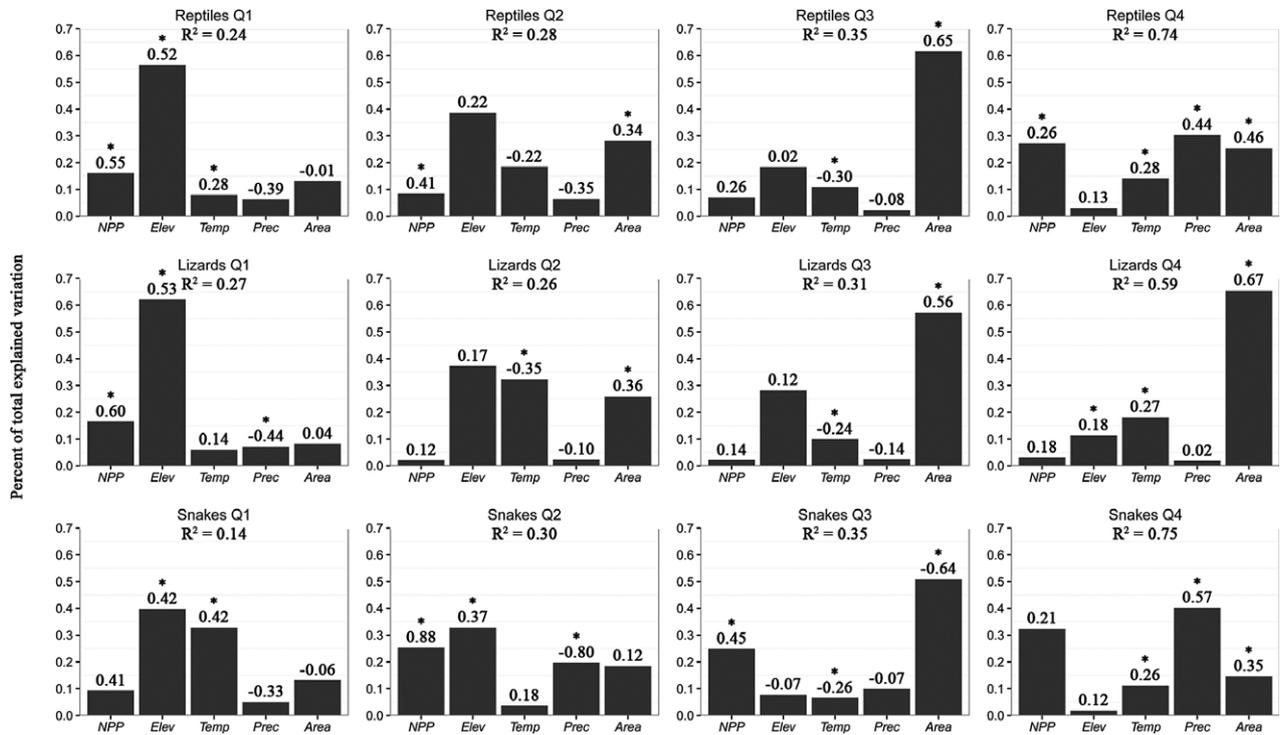
Net primary productivity is the strongest predictor of species richness in all classes and the clear latitudinal pattern seen in our richness maps (Figs 1 & 2) reflects a strong correlation with NPP as one moves closer to the equator (Gillman *et al.*, 2015). We find a stronger effect of NPP at the spatially finer 1° scale (Appendix S7) showing that constraints on richness by energy availability are more likely to operate over finer scales (Belmaker & Jetz, 2015). Only lizards have richness hotspots in arid ecoregions, as we predicted, and similar to findings elsewhere (Schall & Pianka,



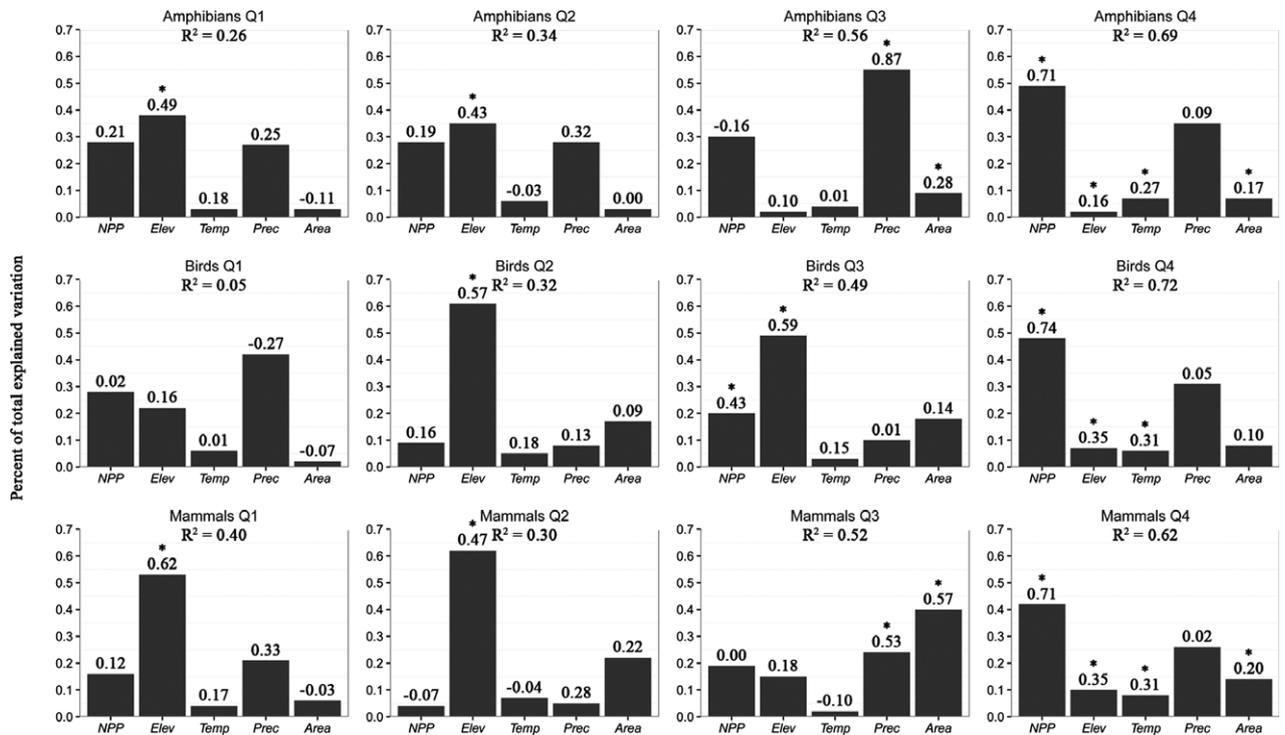
**Figure 2** Behrmann grid (1° scale) species richness of vertebrate classes (a–d) and reptile groups (e–h) in Africa. Colour codes correspond to species numbers in grid cells from low (blue) to high (red). White denotes no species.



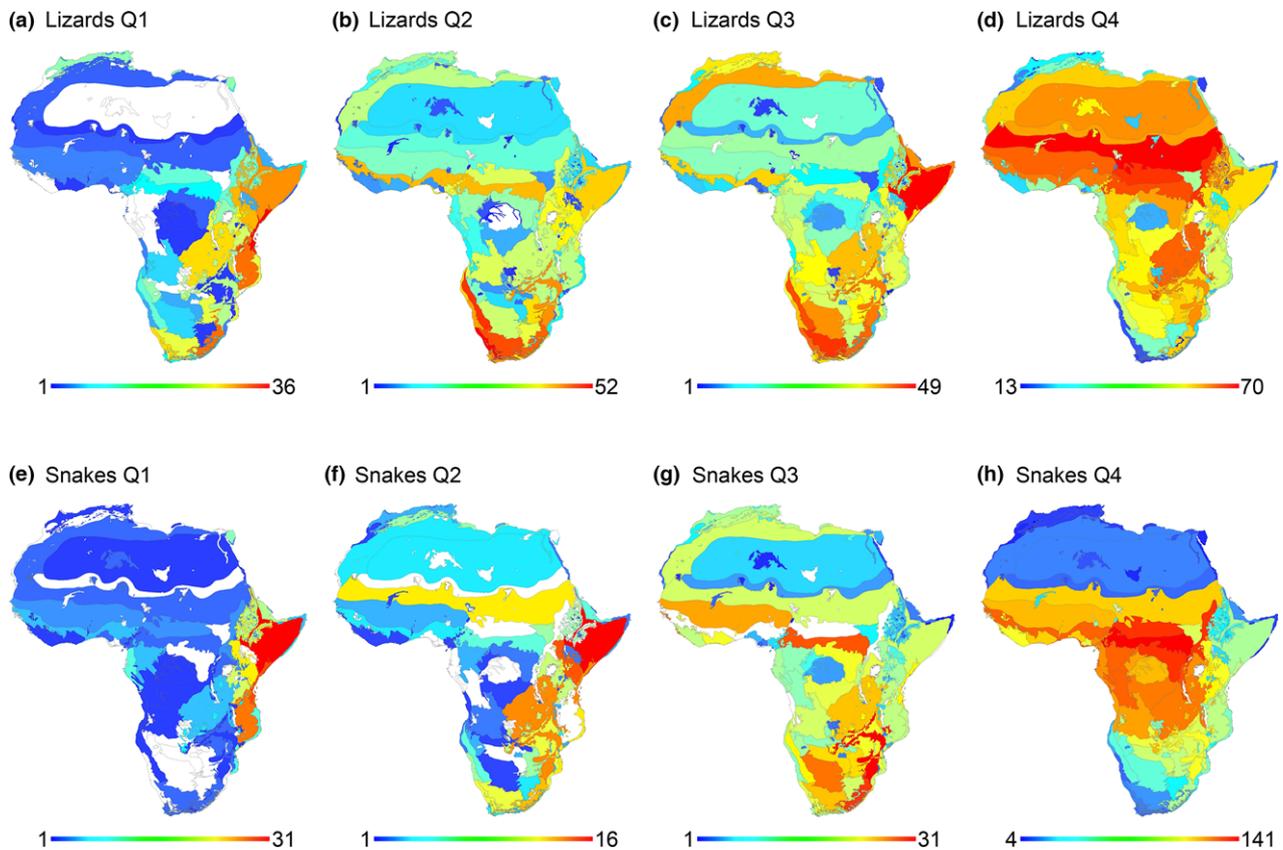
**Figure 3** Relative importance of species richness predictors ( $N = 107$  ecoregions). Numbers above bins are regression coefficients as single predictors, \*Significant  $P$ -values for variable as single predictor.



**Figure 4** Relative importance of species richness predictors ( $N = 107$  ecoregions) of narrow- and wide-ranging reptile groups. Q1–4 = quartiles 1 (narrow) to 4 (wide), numbers above bins are regression coefficients as single predictors, \*Significant  $P$ -values for variable as single predictor.



**Figure 5** Relative importance of species richness predictors ( $N = 107$  ecoregions) of narrow- and wide-ranging vertebrate classes. Q1–4 = quartiles 1 (narrow) to 4 (wide), numbers above bins are regression coefficients as single predictors, \*Significant  $P$ -values for variable as single predictor.



**Figure 6** Species richness of narrow- and wide-ranging lizard and snake groups within African ecoregions. Q1–4 = quartiles 1 (narrow) to 4 (wide). Colour codes correspond to species numbers in ecoregion from low (blue) to high (red). White denotes no species.

1978; Powney *et al.*, 2010). Lizards are well adapted to the harsh conditions of the desert (Rabosky *et al.*, 2007), which is confirmed by the relatively low correlation of lizard species richness with NPP.

That variation in reptile richness is only weakly explained by temperature is surprising, as richness in reptiles, and especially in lizards, is thought to respond almost exclusively to ambient energy (Schall & Pianka, 1978; Hawkins *et al.*, 2003). In fact, temperature explains very little of the variation in richness of African vertebrate groups. This is consistent with previous studies that show either no relationship or a negative relationship with ambient energy at warm regions (Currie, 1991; Hawkins *et al.*, 2003). Kerr & Packer (1997) proposed that below 45° latitude, ambient energy no longer relates to mammal richness. This may be true also for reptile richness in Africa, a generally hot, equatorial continent. Studies that do show a positive relationship between reptile richness and ambient energy in North America (Currie, 1991), Europe (Rodriguez *et al.*, 2005), and China (Qian *et al.*, 2007) are all set in higher latitudes than Africa.

An exception is Australia, a high-energy zone in which lizard richness does correspond (albeit weakly) to temperature (Powney *et al.*, 2010). However, this may be an underlying consequence of the preponderance of large and homogeneous arid-zones in Australia. This homogeneity allows for species' ranges to overlap more (James & Shine, 2000).

Ecoregion size explains a substantial proportion of variation in richness of reptiles, especially lizards. Some of the arid ecoregions in which lizard richness is relatively high – the Sahara Desert, Sahelian *Acacia* savanna, and North Saharan steppe and woodlands, are the three largest ecoregions in Africa. Thus, lizards which are uniquely adapted to these arid regions, benefit additionally by the large size of these regions, in which speciation dynamics may be enhanced (Rabosky *et al.*, 2007; Kisel *et al.*, 2011).

There are distinct richness hotspots for different lizard families (Appendix S8): agamas, lacertids and geckoes are most prevalent in deserts (but note that agamas ( $n = 77$ ) are richest in the Sahel, lacertids ( $n = 123$ ) in the Sahara, and geckos ( $n = 269$ ) in the Namib), and chameleons ( $n = 110$ ) most widespread in tropical forests. Skinks ( $n = 233$ ) are widespread and prevalent in large areas of Africa. This provides support for a possible mechanism explaining lizard species richness – different ecoregions act as centres of lizard diversification. This is corroborated by the weak spatial correlation at the ecoregion scale, as evident in the fact that numbers of degrees of freedom corrected for spatial-autocorrelation using the Clifford method are similar to the non-corrected numbers (Table 2; note that this is not the case at the 1° scale, Table 3). Snakes and turtles also display distinct high richness areas based on subclade (Appendices S9 & S10) further supporting the role of diversification and area in

shaping reptile richness patterns. Additionally, richness maps of lizards and snakes in different range-size quartiles (Fig. 6) demonstrate diverse richness peaks according to range size.

Similar to previous studies (see also Szabo *et al.*, 2009; Belmaker & Jetz, 2011), narrow-ranged species switch to a high relative importance of habitat heterogeneity, which is reduced for wide-ranging species and replaced by NPP. However, habitat complexity remains a relatively strong predictor of variation in lizard richness even at large range sizes, reflecting their ability to specialize in diverse ecoregions. This, coupled with the lack of relationship between lizard richness and NPP, implies that the difference in response of lizards and the other vertebrate groups to environmental variables is due to underlying differences in their ecological characteristics and physiology independent of their narrower average range size.

Differences in range size may reflect underlying ecological dissimilarities in dispersal ability and body size (Gaston & Blackburn, 1996; Lester *et al.*, 2007). The relatively large range sizes of snakes are perhaps related to their large body size and generally higher trophic level (Anderson, 1984). The strong correlation between snake and reptile richness (Tables 2 & 3; Figs 1 & 2) is a consequence of the formers' large ranges leading to higher snake range overlap on sampling units. This results in the disproportionate influence of snakes (and wide-ranging species) on patterns of reptile richness, and further emphasizes the value of analysing taxonomic groups separately in order to assess true patterns of richness.

We hypothesize that the weak relationship between the climatic variables and lizard richness results from lizard species' narrow and irregular distributions reflecting their ability to specialize in specific niches. The weak relationship between amphisbaenian richness and the climatic variables may be due to their very restrictive ecological requirements and limited overall distribution within Africa, as well as dispersal limitations imposed by their subterranean lifestyle. The higher amount of explained variation for wide-ranging species may be due in part to the underlying spatial-autocorrelation of their large ranges overlapping with the environmental gradients, and not necessarily because these are more important for wide-ranging species (Szabo *et al.*, 2009; Buschke *et al.*, 2015).

In conclusion, reptile species richness in Africa is largely congruent with the richness of amphibians, birds and mammals, perhaps as a result of similar responses to similar environmental variables. Richness gradients of narrow-ranged reptiles and vertebrate groups differ from those of wide-spread taxa, which may reflect evolutionary centres of diversification and endemism. Patterns of amphisbaenian and especially lizard species richness stand distinct from those of the other reptile groups. Lizards have several richness hot-spots, particularly in arid ecoregions. Coupled with the small range size of most lizard species this may have considerable bearing on any attempts to employ large-scale conservation efforts based on surrogacy.

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## SUPPORTING INFORMATION

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

**Appendix S1** Sources used to compile species distribution data: (a) African amphisbaenian species distribution data.

(b) African crocodile species distribution data. (c) African lizard species distribution data. (d) African snake species distribution data. (e) African turtle species distribution data. (f) Reference list for the sources of distribution data of all reptile taxa.

**Appendix S2** Histograms of range size of (a) reptile, lizard and snake quartiles, and (b) amphibian, bird and mammal quartiles.

**Appendix S3** African ecoregion reptile species richness and environmental data.

**Appendix S4** Range size, quartile and number of occupied ecoregions of reptile species in Africa.

**Appendix S5** Percentage of species present in top ten richest ecoregions of vertebrate classes (a–d) and reptile groups (e–h).

**Appendix S6** Species richness of crocodiles within African ecoregions. Colour codes correspond to species numbers in ecoregion from low (blue) to high (red).

**Appendix S7** Relative importance of species richness predictors at Behrmann Grid (1° scale). Numbers above bins are regression coefficients as single predictors, \*Significant *P*-values for variable as single predictor. (3,108 DF.)

**Appendix S8** Lizard family species richness within African ecoregions (only richest families displayed). Colour codes correspond to species numbers in ecoregion from low (blue) to high (red). White denotes no species.

**Appendix S9** Snake family species richness within African ecoregions (only richest families displayed). Colour codes correspond to species numbers in ecoregion from low (blue) to high (red). White denotes no species.

**Appendix S10** Turtle family species richness within African ecoregions (only richest families displayed). Colour codes correspond to species numbers in ecoregion from low (blue) to high (red). White denotes no species.

## BIOSKETCH

**Amir Lewin** is a PhD student studying the impact evaluation of protected areas. He is interested in the ecology and conservation of vertebrates.

Author contributions: A.L. digitized lizard ranges, ran the analyses and wrote the paper. A.F. digitized snake ranges. Y.I. digitized turtle and crocodile ranges. M.N., E.M., E.V. and O.T. helped with GIS and statistical analyses. D.G.B., A.M.B., L.C., A.L., M.L., S.M., D.M., M.N., Z.T.N., U.R. and J.F.T. derived the data and ran quality control for them. J.B. and S.M. helped with the study design and writing. S.M. initiated the project and digitized amphisbaenian ranges.

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