

Niche conservatism and species richness patterns of squamate reptiles in eastern and southern Africa

IGNACIO MORALES-CASTILLA,^{1*} MIGUEL Á. OLALLA-TÁRRAGA,²
LUIS MAURICIO BINI,³ PAULO DE MARCO JR,³ BRADFORD A. HAWKINS⁴ AND
MIGUEL Á. RODRÍGUEZ¹

¹Department of Ecology, University of Alcalá, 28871 Alcalá de Henares, Madrid, Spain (Email: ignacio.morales@uah.es), ²Division of Biology, Imperial College London, Silwood Park Campus, Ascot, UK, ³Departamento de Biologia Geral, Instituto de Ciências Biológicas, Universidade Federal de Goiás, Goiania, GO, Brasil; and ⁴Department of Ecology and Evolutionary Biology, University of California, Irvine, California, USA

Abstract Niche conservatism has been proposed as a mechanism influencing large-scale patterns of taxonomic richness. We document the species richness patterns of five monophyletic squamate reptile groups (gekkonids, cordylids-scincids, lacertids, chameleons and alethinophidian snakes) in eastern and southern Africa, and explore if observed patterns reflect niche conservatism processes. We quantified richness and its relationships with current climatic conditions by gridding species' range maps at 110 × 110 km. Also, dated phylogenies and palaeoclimatic reconstructions, coupled with evidence from the fossil record, were used to approximate the areas and climate characteristics in which each group originated and/or radiated. Mean species richness and geographically corrected confidence intervals in current climate types were calculated for each group in order to establish their climatic preferences. On average, the species richness of older groups (gekkonids, cordylids-scincids and lacertids) was lower in equatorial climates and higher in arid and temperate conditions, whereas more recent groups (chameleons and alethinophidian snakes) were richer in equatorial and temperate climates and less rich in arid conditions. Across all groups, higher richness was associated with climatic characteristics similar to those prevailing at the time in which each group originated/radiated. The congruence of the current climates where reptile groups are richer and the past climates amidst which those groups originated is consistent with an explanation for their diversity gradients based on niche conservatism.

Key words: African biodiversity, diversity gradient, niche conservatism, palaeoclimate, reptile, richness patterns, Squamata.

INTRODUCTION

Broad-scale diversity gradients are the product of current climatic conditions, the location of centres of origin, and ecological and evolutionary responses to long-term environmental changes (Currie 1991; Ricklefs & Schluter 1993; Hawkins *et al.* 2003; Currie *et al.* 2004; Mittelbach *et al.* 2007; Wiens *et al.* 2007; Araújo *et al.* 2008; Hawkins 2008; Hortal *et al.* 2008). In particular, niche conservatism is becoming increasingly invoked to explain global diversity gradients (Hawkins 2008). This mechanism, also referred to as phylogenetic inertia, describes the conservation of biological and ecological traits among species as groups radiate, and with respect to climate tolerances it makes the testable prediction that extant species tend to be distributed in similar environments to those where their

group originated, because of difficulties in adapting to new climatic conditions (Peterson *et al.* 1999; Wiens & Donoghue 2004; Wiens & Graham 2005; Nogués-Bravo *et al.* 2008). Furthermore, clades will have occupied original habitats for longer than novel habitats; hence groups have had more time for species accumulation where they first appeared (Stephens & Wiens 2003; Hawkins 2008). These patterns have been found in turtles, birds and frogs (e.g. Stephens & Wiens 2003; Wiens *et al.* 2006; Hawkins *et al.* 2006, 2007).

Here we focus on eastern and southern Africa and document the species richness patterns of several clades of Squamata, the most species-rich order of living reptiles (Ricklefs *et al.* 2007). Africa represents a hot-spot of reptile diversity, and we selected these two disjunct areas because of the availability of detailed species distribution maps. These areas also include a representation of most of the climates found in Africa. The richness of several groups of reptiles has been shown to vary with climate in many parts of the world,

*Corresponding author.

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including Europe (Rodríguez *et al.* 2005; Olalla-Tárraga *et al.* 2006), the former USSR (Terent'ev 1963), North America (Schall & Pianka 1978; Olalla-Tárraga *et al.* 2006), Australia (Pianka & Schall 1981), the Kalahari Desert (Pianka 1971), Brazil (Costa *et al.* 2007) and globally (Terribile *et al.* 2009). In general, reptile richness is positively associated with temperature or solar radiation because reptiles are extreme solar ectotherms, which differentiates them from other vertebrate groups (see Whittaker *et al.* 2007). However, in tropical and subtropical latitudes, reptile richness generally has weaker relationships with energy variables (Pianka 1971; Pianka & Schall 1981; Costa *et al.* 2007; Ricklefs *et al.* 2007; Terribile *et al.* 2009).

Here we do not generate climate-richness models. Rather, we ask whether the richness of five squamate groups that originated at different times and in different macroclimatic conditions has preserved their ancestral climatic niches with respect to richness patterns. Specifically, for each lineage, we mapped its current species richness distribution in eastern and southern Africa and then examined if higher richness occurred in climates that are similar to those prevailing at the time (and, when possible, approximate place) of a group's origin. If so, this constitutes evidence that niche conservatism has influenced the current richness patterns of that clade and suggests that niche conservatism plays a significant role in the current diversity gradients of reptiles.

METHODS

Richness patterns

Range maps for native squamate reptiles were digitized from two field guides (Spawls *et al.* 1997; Branch 1998) covering 12 countries of southern and eastern Africa (i.e. Kenya, Tanzania, Rwanda, Burundi, Uganda, Namibia, Botswana, Zimbabwe, South Africa, Lesotho, Swaziland and southern Mozambique). Species range maps were then rasterized in ArcGIS in two equal-area grids, one comprising 456 cells of 110×110 km each that was used for analysis, and the other comprising of 8224 cells of 27.5×27.5 km that was used for mapping (richness maps also shown at 110×110 km resolution, see Appendix S3). Species richness for each cell was obtained by superimposing the individual species' range maps. Range maps are commonly used to study richness gradients, and the patterns they generate are very similar to those generated by other data sources at moderate to large scales (Hawkins *et al.* 2008; Hortal 2008). As our data sources were more than 10 years old, we also incorporated data from more recent sources (e.g. Mariaux & Tilbury 2006; Alexander & Marais 2007; Tolley & Burger 2007; Mariaux *et al.* 2008) to update distributions and incorporate newly described species.

Squamates were divided into five monophyletic lineages according to recent squamate molecular phylogenies (Kumazawa 2007; Vidal & Hedges 2009; Vidal *et al.* 2009):

gekkonids (Gekkonidae, 137 species); cordylids-scincids (Cordylidae and Scincidae, 144 species); lacertids (Lacertidae, 50 species); chameleons (Chamaeleonidae, 70 species); and alethinophidian or typical snakes (Viperidae, Boidae, Pythonidae, Colubridae, Natricidae, Lamprophiidae and Elapidae, hereafter snakes, 263 species). We excluded lineages with less than 20 species in the study region (Agamidae, Varanidae, Gerrhosauridae); the scolecophidian snakes (Typhlopidae and Leptotyphlopidae) were excluded because of both phylogenetic uncertainty regarding their origin and their fossorial nature. We used the taxonomy of Uetz (2009).

Data on past and current climates

For current climates we used the update of the Köppen–Geiger Climatic Classification (Köppen 1936) recently developed by Kottek *et al.* (2006), which defines climate types according to temperature and precipitation regimes. We digitized the eastern–southern African portion of Kottek *et al.*'s (2006) map, and each of our 456 analysis cells was assigned the dominant climate class within it. There are 14 Köppen–Geiger climate types in the study area (see Appendix S1), but we excluded two ('warm temperate climate with dry summer, warm' and 'warm temperate with dry summer, hot,' in Köppen–Geiger's terminology) because they covered very small areas in the study region and neither of them was the most representative climate of any cell. The 12 climate types used for analysis and both their total area and percentage area in eastern–southern Africa were summarized in Table 1.

Based on dated phylogenies (Kumazawa 2007; Vidal & Hedges 2009; Vidal *et al.* 2009), we focused on the distribution of palaeoclimates in three relevant periods for squamate evolution: (i) early to late Jurassic for the divergence of gekkonids, cordylids-scincids and lacertids; (ii) early to late Cretaceous as the divergence period for chameleons and alethinophidian snakes; and (iii) the Eocene to Miocene, when major radiations of snake families and chameleon clades occurred (see also Raxworthy *et al.* 2002; Tolley *et al.* 2008). Accordingly, we obtained palaeoclimatic maps corresponding to these periods (Upchurch *et al.* 1998; Scotese *et al.* 1999; Rees *et al.* 2000; Scotese 2002; Ziegler *et al.* 2003) and rasterized them to calculate the percentage area occupied by each climate in both Africa and the world at each period. As these maps are based on the basic Köppen–Geiger types of climates (e.g. see Upchurch *et al.* 1998 for details), they provide an approximation of the major climatic characteristics during each relevant evolutionary event that can be compared with the distribution of current climate types.

Analysis

For each lineage, climatic preferences were initially explored by averaging the species richness of the cells corresponding to each climate type and then constructing a histogram of the mean values. Higher mean richness per cell in a particular climate type would suggest a preference of the lineage for that climate type. Also, 95% confidence intervals for the mean richness values were obtained to compare mean richness among climate types. For this we took into account that our

Table 1. Major types and subtypes of Köppen–Geiger climates in eastern and southern Africa

Köppen–Geiger climate type and subtype	Kottek <i>et al.</i> 's code	Code used here	Area (km ²)	Area (%)
Arid	B	A	3 025 000	54.8
Desert cold	BWk	Ad1	290 400	5.3
Desert hot	BWh	Ad2	641 300	11.6
Steppe cold	BSk	As1	290 400	5.3
Steppe hot	BSh	As2	1 802 900	32.6
Warm temperate	C	T	769 598	13.9
Fully humid hot	Cfa	Th1	60 500	1.1
Fully humid warm	Cfb	Th2	181 500	3.3
Dry winter, hot	Cwa	Td1	193 600	3.5
Dry winter, warm	Cwb	Td2	314 600	5.7
Equatorial	A	E	1 730 300	31.3
Rainforest, fully humid	Af	Eh1	48 400	0.9
Moonson	Am	Eh2	48 400	0.9
Savanna with dry summer	As	Ed1	181 500	3.3
Savanna with dry winter	Aw	Ed2	1 452 000	26.3

Climate codes used by Kottek *et al.* (2006) are included, but English-based codes were used in this paper. The total and percentage areas covered by each climate type in the study region are provided. Two poorly represented warm temperate climate subtypes were excluded from the table (and from analysis) but were included to compute total and percentage areas. Fully humid climates are those lacking a dry season with constant precipitation rates along the year. All calculations were based on grid cells in which the dominant climate subtype was assigned (see *Methods*).

species richness data are strongly spatially autocorrelated (see below and Appendix S2), which causes degrees of freedom and standard errors to be overestimated and underestimated, respectively (Legendre 1993; Diniz-Filho *et al.* 2003). To resolve this we calculated an autoregressive parameter (ρ) for each lineage within each climate type using pure autoregressive models in SAM 3.0 (Rangel *et al.* 2006) and then estimated the geographically effective sample size following the method described in Griffith (2003) based upon a single mean response.

Because climate types differed strongly in terms of area in the study region (Table 1; see also Appendix S1), we generated an area-based rank of the climate types and then calculated, for each species group, its Spearman rank-order correlation with the mean richness obtained when ignoring area. High positive correlations would indicate an effect of area on patterns of mean species richness among the climate types.

RESULTS

Patterns of species richness differed among older and recent groups, although there were some similarities, particularly in mountainous areas where richness tended to be high (Fig. 1). However, Pearson correlations of richness with elevation were positive and weak for gekkonids ($r = 0.142$), cordylids-scincids ($r = 0.239$), snakes ($r = 0.200$) and chameleons ($r = 0.547$) but negative for lacertids ($r = -0.286$). Gekkonids, lacertids and cordylids-scincids (the older groups) were richer in southern Africa, particularly in the west and along the Great Escarpment (Fig. 1a–c). Lacertids were absent from some eastern Africa areas (Fig. 1b) as were chameleons, which were also absent from parts of

southern Africa (Fig. 1d). There were also few chameleons in southern Africa (Fig. 1d). Both chameleons and snakes (Fig. 1e) had high richness around Lake Victoria, and both groups were richest in the Albertine Rift Mountains. Snake richness was also high along the Great Escarpment. In general, the richness of all five groups had patterns of spatial autocorrelation characteristic of clines, with positive autocorrelations at shorter distances and most negative autocorrelations at larger distances (for details see Appendix S2).

Mean richness calculated for each Köppen–Geiger climate type (Fig. 2; for details see Appendix S4) indicated that the lineages were distributed differentially across current climate types. Gekkonids had higher mean richness in arid climates, and intermediate richness in temperate climates (Fig. 2a), with corrected 95% confidence intervals showing no overlap between the most arid climates (Ad1 and Ad2) and the most humid equatorial climates (Eh1 and Eh2). Similarly, for lacertids, higher and intermediate mean richness occurred in arid and temperate climates, respectively (Fig. 2b), but only the two most arid desert climates (Ad1, Ad2) significantly differed from every equatorial climate. Overall, these results indicated an association with arid conditions, and a secondary association with temperate climates for both gekkonids and lacertids. In contrast, cordylids-scincids were associated with temperate conditions (Fig. 2c). Even though this group was secondarily associated with arid climates, mean richness in these environments only differed significantly from equatorial savannas with dry winters (Ed2). Notably, associations with equatorial climates were weakest in gekkonids, lacertids and cordylids-scincids.

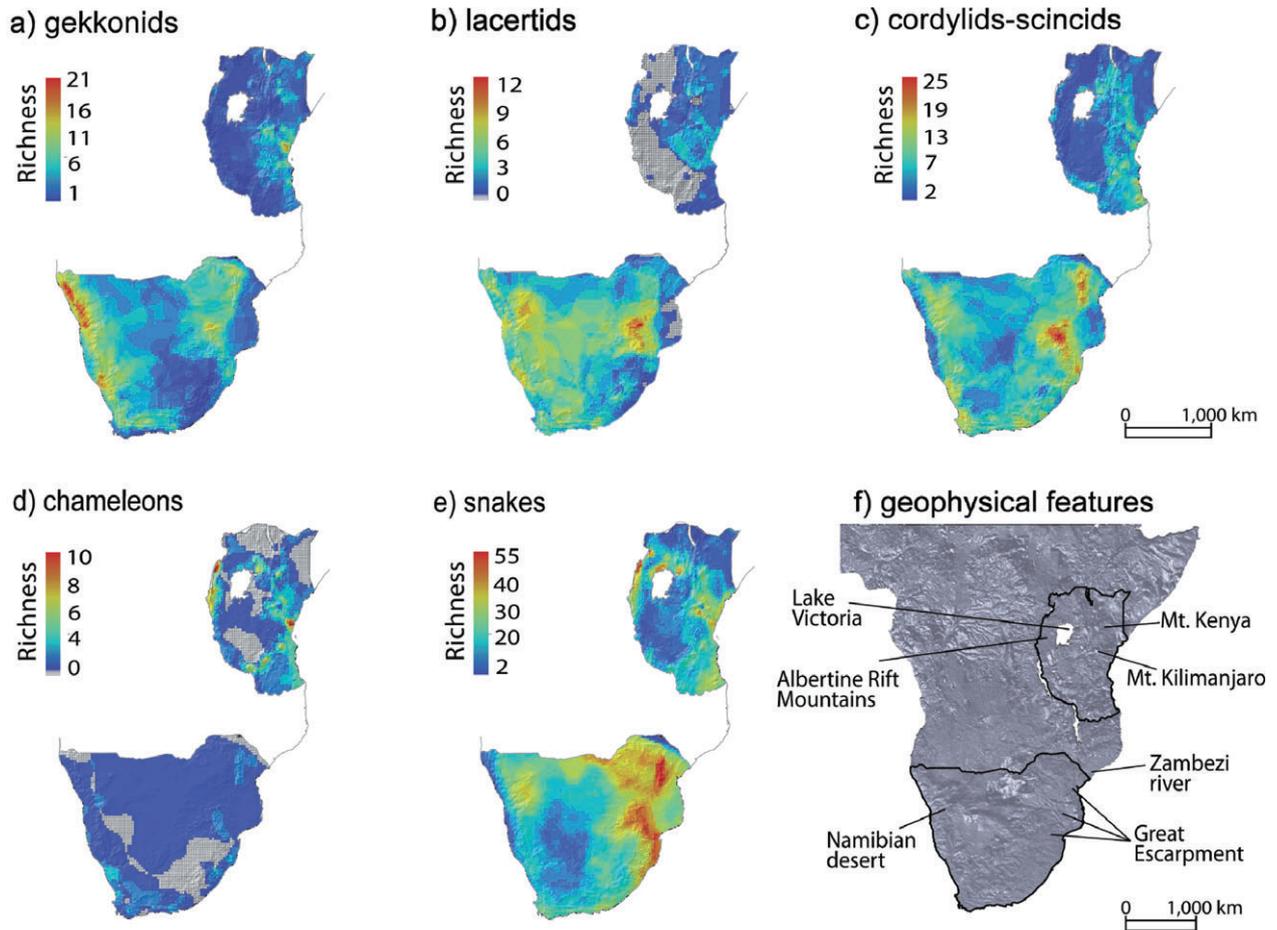


Fig. 1. Species richness patterns of five squamate reptile groups in eastern and southern Africa (a–e) at a 27.5-km scale. (f) Major geophysical features of Africa.

The climatic associations of chameleons and snakes (the more recent groups) were characterized by higher mean richness in equatorial climates and intermediate values in temperate ones, with no significant differences between both types of climates according to the 95% confidence intervals (Fig. 2d,e). For chameleons (Fig. 2d), mean richness in three equatorial climates (Eh1, Ed1 and Ed2) was significantly higher than in hot arid desert (Ad2) and in the two arid steppe climates (As1 and As2). For snakes, mean species richness was significantly higher in humid equatorial climates (Eh1 and Eh2) than in arid desert climates (Ad1 and Ad2). So, in contrast to the three older groups, chameleons and snakes showed a tendency to be preferentially associated with humid equatorial climates, while avoiding arid conditions.

Spearman rank-order correlations of mean richness against Köppen–Geiger climate type areas to test the influence of area on mean richness patterns were positive but not significant for gekkonids and cordylids-scincids ($r = 0.309$, $P = 0.328$; and $r = 0.049$, $P =$

0.879 , respectively), positive and significant for lacertids ($r = 0.622$, $P = 0.031$), and negative and significant for chameleons and snakes ($r = -0.727$, $P = 0.007$; $r = -0.654$, $P = 0.021$, respectively). Thus, a potential effect of area on the mean richness patterns can be rejected for all groups except for lacertids.

DISCUSSION

The different groups of squamate reptiles had dissimilar distributions of species across current climate types. The key question is: do these distributions reflect characteristics prevailing in the palaeoclimates in which each group originated and/or radiated? To address this, we used the divergence times estimated by recent molecular phylogenetic hypotheses (Kumazawa 2007; Vidal & Hedges 2009; Vidal *et al.* 2009) and reviewed the literature on palaeoclimates and fossil records to try to document when, where and under which environmental characteristics each group

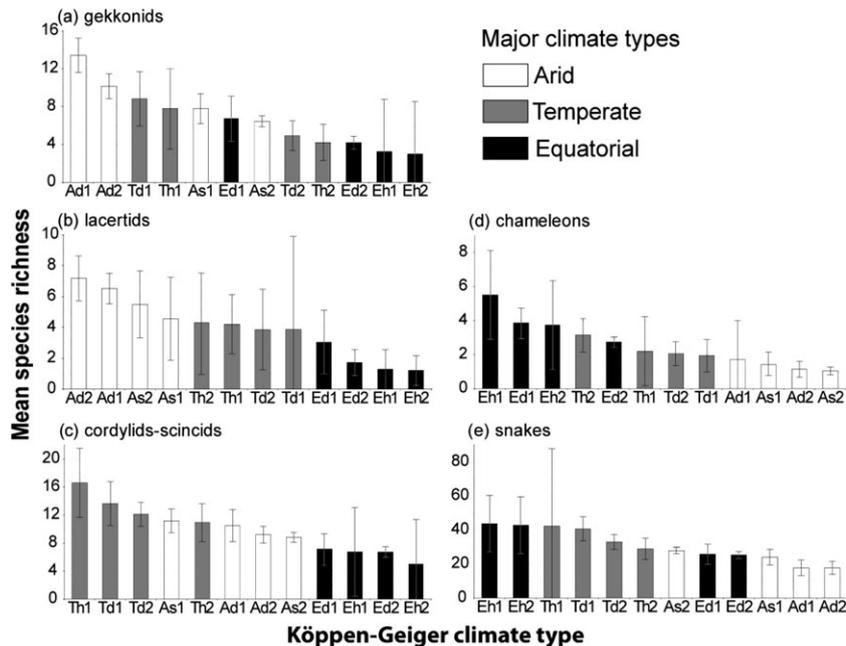


Fig. 2. Mean ($\pm 95\%$ confidence intervals) species richness of five squamate reptile groups in the 12 Köppen–Geiger climate types occurring in southern and eastern Africa (see Table 1 for climate codes). Major climate types are differentiated with a white to black scale. Confidence intervals were calculated taken into account geographically effective degrees of freedom (see *Methods*).

might have arisen and evolved. We assumed that similarities between species richness patterns across climate types and the characteristics of the palaeoclimates in which the groups might have evolved indicate an influence of ancestral niches on contemporary species richness patterns (see Wiens & Donoghue 2004; Wiens & Graham 2005).

The divergence of gekkonids, cordylids–scinoids and lacertids occurred during the Jurassic (about 196–145 Myr ago). According to palaeoclimatic reconstructions (Scotese *et al.* 1999; Rees *et al.* 2000; Ziegler *et al.* 2003), this period was predominantly arid in both the African portion of Gondwana (>80% of this area; see Table 1, Fig. 3) and across the planet (49%; see Table 1). The African Jurassic fossil record does not contain every lineage that diverged then. However, an African origin of cordylids has been suggested by Estes (1983), despite the lack of fossils in the early squamate fossil record of Gondwana (Evans 2003; Krause *et al.* 2003). A cosmopolitan distribution of early squamates across Gondwana has been proposed (Sampson *et al.* 1998) and is supported by several fossils (e.g. paramacellodid scincomorphs in Tanzania (Broschinski 1999); fragmentary reptile remains in Tanzania (Zils *et al.* 1995) and in India (Evans *et al.* 2002); remains of an early Jurassic lizard in South Africa (Kitching & Raath 1984); and squamate ancestors in the Karoo Basin of South Africa (Durand 2005; Rubidge 2005). So, if an African origin is accepted for gekkonids, cordylids–scinoids and lac-

ertids, they would have arisen during an arid Jurassic period deficient in warm humid (i.e. equatorial) conditions. The current distribution of the species of these groups indicates a propensity for arid and/or temperate climates in terms of species richness, with few species in equatorial climates. This is consistent with the hypothesis that niche conservatism has strongly influenced the richness gradients of these old groups.

For chameleons and snakes, the phylogenetic hypotheses (Kumazawa 2007; Vidal & Hedges 2009; Vidal *et al.* 2009) place the divergence of alethinophidian snakes and chameleons throughout the Cretaceous (about 145–65 Myr ago). During that period, arid climates contracted, and equatorial climates greatly expanded, covering a third of the African continent (Table 2, Fig. 3). Also, some simulations of Cretaceous palaeovegetation predict the existence of tropical rainforest in west-central Africa, tropical semi-deciduous forest in central Africa, and subtropical broad-leaved evergreen forests and woodlands in eastern and southern Africa (see Upchurch *et al.* 1998, their figure 2). Notably, the origin of chameleons has been placed in the Cretaceous in either eastern Africa or Madagascar (Hillenius 1959, 1986; Raxworthy *et al.* 2002); that is, coinciding with the areas that Upchurch *et al.* (1998) predicted to be occupied by tropical and subtropical forests. Along with this, several African snake fossils have been found in Cretaceous deposits (see Durand 2005) in Algeria (Rage

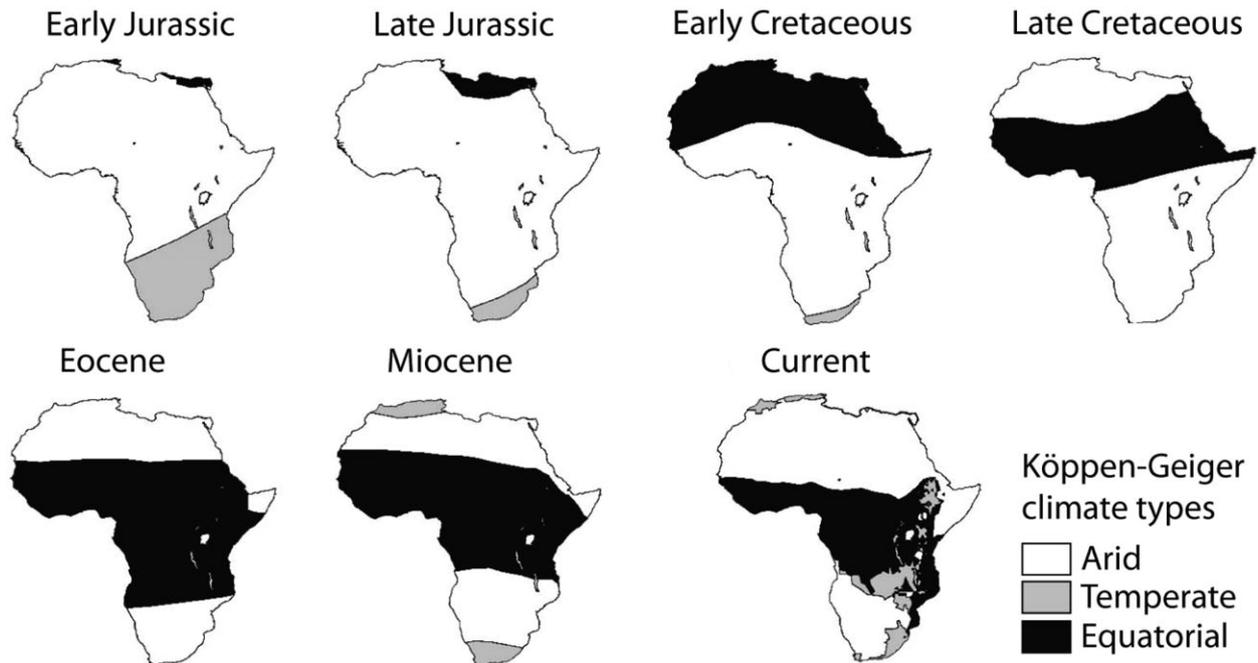


Fig. 3. The distribution of arid, equatorial and temperate Köppen–Geiger climates in relevant geological time periods for squamate reptile evolution in Africa. To facilitate comparisons among periods, the distribution of Paleoclimates (from Scotese 2002) has been adapted to the current shape of the African continent. The distribution of current climates is from Kottek *et al.* (2006).

Table 2. Major reptile radiation events (Rieppel *et al.* 1992; Evans *et al.* 2002; Raxworthy *et al.* 2002; Kumazawa 2007; Vidal & Hedges 2009) and their associated main Köppen–Geiger climate characteristics globally and in Africa as described in Scotese *et al.* (1999) and Scotese (2002)

Evolutionary event	Period	Myr ago	Region	Köppen–Geiger climate area (%)		
				Arid	Temperate	Equatorial
Divergence of gekkonids, cordylids–scincids and lacertids	Early–late Jurassic	199–145	Global	27.3–48.7	41.3–35.1	26.3–7.2
			Africa	80.9–92.6	17.9–3.3	1.0–4.1
Divergence of chameleons and snakes	Early–late Cretaceous	145–65	Global	32.2–28.2	28.7–38.9	23.3–20.4
			Africa	61.6–62.8	1.3–0	37.0–37.2
Major radiation of chameleons and snakes	Eocene–Miocene	55–18	Global	21.3–25.8	39.4–22.0	33.7–26.8
			Africa	39.4–41.3	0–4.9	60.6–53.7
Current	Present	0	Global	24.7	61.4	13.9
			Africa	54.8	13.9	31.3

All calculations considered two Köppen–Geiger major climate types (i.e. snow and polar), which were excluded from the table as they did not occur in Africa. Palaeoclimate reconstructions by Upchurch *et al.* (1998), Rees *et al.* (2000) and Ziegler *et al.* (2003) were also reviewed and found to be consistent in general with these data.

& Escuillié 2003), Morocco, Lybia and Egypt (Nessov *et al.* 1998; Rage & Cappetta 2002) and Sudan (Rage & Werner 1999). Those sites are believed to have had tropical climates at that time (Scotese *et al.* 1999). We found that, on average, the species richness of chameleons and snakes is currently lower in arid climates, and higher in equatorial and temperate climates. Accepting the imprecise nature of palaeoclimatic reconstructions and uncertainties in identifying where and when major clades arose, the predominately equatorial

characteristics of the areas in which each of these groups may have originated (see above) suggests that niche conservatism also influences the contemporary distribution of chameleons and snakes.

The Eocene–Miocene (about 55–18 Myr ago) represents another key period, as major radiations within vertebrate taxa during this time gave rise to many of the extant vertebrate groups (Clarke & Crame 2003; Vermeij 1987), including the chameleons and snakes (Kumazawa 2007; Sanders & Lee 2008; Vidal &

Hedges 2009; Vidal *et al.* 2009). This followed the Paleocene-Eocene thermal maximum and has been characterized by higher homogeneity of global temperatures and by the presence of equatorial rainforest as far as 45° North (Zachos *et al.* 2001). In Africa, equatorial climates occupied more than half of the continent, and arid climates more than one-third at the end of the period (Cerling *et al.* 1997) (Fig. 3). The African reptile fossil record during the Eocene-Miocene includes every lineage considered in this study (e.g. Pickford *et al.* 1996; Rage 2003). In particular, all records of chameleons and most records of snakes were in Kenya, Tanzania and Uganda (e.g. Pickford & Andrews 1981; Pickford *et al.* 1986; Rieppel *et al.* 1992), which were likely within the equatorial realm during the Eocene-Miocene (Fig. 3). Hence, the proliferation of species of chameleons and snakes would have occurred within equatorial climates, which is again consistent with the observed current patterns for equatorial and arid climates shown by both groups. This also identifies niche conservatism as a potential influence on the current distribution of the richness patterns of both groups.

Finally, it should be noted that the most humid Köppen-Geiger equatorial climates – rainforest, fully humid (Eh1) and Moonson (Eh2) climate types – are poorly represented in our study region, where they only cover 1.8% of the area. Both climate types contained the fewest species of the three older groups (gekkonids, lacertids and cordylids-scincids), but contained the richest assemblages of the more recent groups (chameleons and snakes) (see Fig. 2). The limited representation of equatorial climates in the study area may influence the power of statistical analyses, which found only a few cases of significant differences in mean species richness between climate types. Thus, it is possible that an extended database encompassing all of central Africa and its large equatorial band would render clearer positive and negative associations of the recent and older groups for these climates.

In sum, although exploratory analyses such as this one cannot be considered formal tests of explanations for biogeographical patterns (as discussed by Kerr *et al.* 2007), our data contain historical signals in the contemporary species richness gradients of African squamates that can be interpreted as the result of niche conservatism. Gaps of knowledge in the fossil record, and uncertainties regarding both the characteristics of past climates and the phylogenetic relationships among squamate groups (which are themselves hypotheses to be tested), require some caveats with respect to our interpretations of the patterns. Even so, until these gaps are filled, our results contribute to the growing evidence that niche conservatism strongly influences current species richness gradients.

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SUPPORTING INFORMATION

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

Appendix S1. Current distribution of Köppen–Geiger climates within the study area.

Appendix S2. Moran's *I* spatial correlograms for the species richness variation of five reptile groups.

Appendix S3. Richness maps at the 110 × 110 km. grid showing the 456 cells used for analysis of gekkonids (a), lacertids (b), cordylids-scincids (c), chameleons (d) and snakes (e). Panel (f) shows the 110 km analysis overlaying the map of Kottek *et al.*'s (2006) climatic regions.

Appendix S4. More detailed representation of Figure 2.