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ORIGINAL ARTICLE

Rapoport effect and biomic specialization in African mammals: revisiting the climatic variability hypothesis

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ABSTRACT

Aim One of the mechanisms proposed to explain the tendency for geographical range size to increase from the equator to the poles, known as the Rapoport effect, is the climatic variability hypothesis. It states that, towards higher latitudes, greater seasonal climatic variability is the most important pressure that selectively promotes greater general climatic tolerance of species, and therefore also more extensive species ranges. In order to test this hypothesis, we explore the influence of climate, area and biome diversity on the latitudinal gradient of climatic specialization.

Location The study used the large mammal assemblage from Africa.

Methods The degree of climatic specialization of African large mammals (Primates, Carnivora, Proboscidea, Perissodactyla, Hyracoidea, Tubulidentata, Artiodactyla and Pholidota) is investigated using the biomic specialization index (BSI) for each mammal species, based on the number of biomes it inhabits. We studied the influence of 11 climatic and biogeographical predictors in the latitudinal pattern of biomic specialization. Stepwise multiple regressions were used to identify the strongest predictors of biomic specialization in Africa and, separately, in both continental hemispheres. We also studied differences among taxonomical groups (primates, carnivores and artiodactyls). We used correlograms generated using Moran's I coefficients to control for spatial autocorrelation in all these analyses.

Results Average BSI values for successive 1°-latitude bands generally decline towards the equator and temperature variability emerged as the most predictive factor in the regression model for the whole continent, thus supporting the climatic variability hypothesis. Nevertheless, there are differences between hemispheres and among taxa. While temperature variability is the most important predictor of latitudinal variability in biomic specialization in most of the regression models for the northern hemisphere, continental area for each latitudinal band is the best predictor in all the regression models in the southern hemisphere.

Main conclusions It appears that similar patterns in latitudinal variation in average BSI may be caused by different factors in the two hemispheres. We suggest that the strong north–south geographical asymmetry of Africa, which influences its biogeographical structure, and the presence of land connections with Eurasia in the northern hemisphere are responsible for the observed patterns. Our data illustrate the influence of continental biogeographical structure and history on macroecological patterns.

Keywords

Artiodactyla, bioclimatology, biogeography, biome, Carnivora, ecological pattern, ecological specialization, macroecology, Mammalia, Primates.

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INTRODUCTION

Since more than two centuries ago (Forster, 1768; von Humboldt, 1808; Wallace, 1878), it has been reported that species richness increases with decreasing latitude. The reasons for this remain poorly understood in spite of the large associated literature. Many different explanations have been suggested (Stevens, 1989; Pagel *et al.*, 1991; Palmer, 1994; Willig *et al.*, 2003), highlighting factors such as productivity, geographical area, habitat size and heterogeneity, interspecific competition, palaeoclimate history, and present climatic variation and disturbance regimes (Pianka, 1966; MacArthur, 1972; Rapoport, 1975; Rosenzweig, 1975; Anderson & Koopman, 1981; Myers & Giller, 1988; Brown & Nicoletto, 1991; Rohde, 1992; Huston, 1994; Ruggiero, 1994; Rosenzweig, 1995; Gaston, 1996). Much of the literature on continental variation in the number, density and geographical patterns of mammalian species has dealt, implicitly or explicitly, with Rapoport's rule (Simpson, 1964; Wilson, 1974; Rapoport, 1975; Schall & Pianka, 1978; McCoy & Connor, 1980; Brown & Maurer, 1989; Stevens, 1989; Pagel *et al.*, 1991; Letcher & Harvey, 1994; Ruggiero, 1994; Smith *et al.*, 1994; Brown, 1995; Cowlishaw & Hacker, 1997; Lyons & Willig, 1997; Ruggiero *et al.*, 1998; Eeley & Foley, 1999; Harcourt, 2000; Lyons & Willig, 2002). This second macroecological question concerns the tendency for geographical range size to increase from the equator to the poles, named Rapoport's rule (Stevens, 1989) after Rapoport's (1975, 1982) observations on the geographical distributions of subspecies.

Rapoport's rule and the latitudinal species richness gradient may share a common cause, and an understanding of the former may shed light on the latter (Stevens, 1989). This topic has been recently debated vigorously (Rohde, 1996; Stevens, 1996; Cowlishaw & Hacker, 1998; Gaston *et al.*, 1998a,b; Kolasa *et al.*, 1998; Gaston & Chown, 1999; Kerr, 1999; Taylor & Gaines, 1999; Ashton, 2001). As the applicability of Rapoport's rule has been claimed to vary among taxa and continents (see e.g. Ruggiero, 1994; Blackburn & Gaston, 1996a; Harcourt, 2000), we follow Blackburn & Gaston (1996a) in using the more neutral term Rapoport effect.

The Rapoport effect and the significance of climatic specialists and generalists

One proposed explanation for the Rapoport effect, the climatic variability hypothesis (Allee *et al.*, 1949; Dobzhansky, 1950; Stevens, 1989), involves the distinction between ecological specialists and generalists, namely the variation among organisms and species in breadth of resource use and tolerance of environmental variability. It posits that, because higher latitudes have greater climatic variation on seasonal and longer time scales than have the tropics, natural selection should promote a more generalist climatic tolerance (or broader climatic adaptability) at higher than lower latitudes. As a consequence, high latitude forms are likely to be less restricted and more generalized in their habitat use, with concomitant greater latitudinal extent of species distributions than is the case at low latitudes (Stevens, 1989). This effect also influences the latitudinal gradient in species richness because the greater niche overlap among generalists is expected to result in competitive exclusion and therefore a reduction in species diversity nearer the poles.

Supporting evidence for this hypothesis has been found in the case of some continents and mammal groups (Pagel *et al.*, 1991; Ruggiero, 1994; Cowlishaw & Hacker, 1997; Eeley & Foley, 1999; Harcourt, 2000). Greater annual climatic variability at higher latitudes has been reported for Africa (in precipitation; Cowlishaw & Hacker, 1997), South America (in temperature; Ruggiero, 1994) and within the Palearctic (in temperature variability, although other measures of climatic variability offered contradictory results; Letcher & Harvey, 1994). However, the climatic variability hypothesis does not appear to apply in other cases (Ruggiero, 1994). Although climate must set the absolute limits of a species' distribution, other aspects of the habitat must also be important, as there are marked discontinuities in species assemblages between biomes (Letcher & Harvey, 1994; Ruggiero, 1994; Smith *et al.*, 1994). Similarly, the topographic diversity of the continent (in particular the position and orientation of mountain ranges) may be very important in determining the size and shape of geographical ranges (Brown & Maurer, 1989; Pagel *et al.*, 1991; Letcher & Harvey, 1994; Ruggiero, 1994; Smith *et al.*, 1994; Ruggiero *et al.*, 1998). Furthermore, while sometimes the Rapoport effect is associated with greater adaptability of high-latitude taxa, cases of differential adaptability in the absence of the Rapoport effect are known (Harcourt, 2000).

Therefore, initial acceptance that the latitudinal gradient in geographical range size is a consequence of climatic variability and degree of species climatic specialization is increasingly being challenged. Evidence is growing that no single explanation may be adequate. Several hypotheses other than greater adaptability of higher latitude taxa exist for the Rapoport effect (Brown, 1995; Gaston *et al.*, 1998a). It is not obvious that either the adaptability hypothesis, or any one of the other hypotheses, can on its own explain all the observed continental variation. Some combination of two or more of the implied processes may be necessary to account for the Rapoport effect (Brown, 1995), although the evidence for some is stronger than it is for others (Gaston *et al.*, 1998a).

Objectives

The aim of this work is to determine if the climatic variability hypothesis is supported by the pattern observed in the assemblage of African large mammals. Testing this hypothesis requires measures of specialization and generalization (or lesser vs. greater adaptability). Several indices of this kind have been proposed: number of habitat types occupied by a taxon, number of food types used, body mass and number of subtaxa per taxon (Pagel *et al.*, 1991; Eeley & Foley, 1999; Harcourt, 2000). But some of these measures are difficult to apply to continent-wide, intercontinental and global comparisons as well as to highly dissimilar taxa. Therefore, it is necessary to use ecological categories of specialization that are sufficiently broad to solve these problems. In this paper, we single out biomic specialization as of special relevance (following Vrba, 1987) and propose a new measure of biomic specialization (or adaptability) that can be applied to different groups at the global scale (following Hernández Fernández, 2001).

METHODS

Data

The study area is the African continent. It excludes Madagascar and all offshore islands. The data represent the geographical distributions of all the 245 terrestrial large mammal species occurring within Africa. Here, we define large mammals as those included in a series of orders, which are characterized on average by medium–large body size (Primates, Carnivora, Proboscidea, Perissodactyla, Hyracoidea, Tubulidentata, Artiodactyla and Pholidota). It excludes Chiroptera, Insectivora, Lagomorpha, Macroscelidea and Rodentia. The list also contains species that became extinct during the last two centuries. Species introduced by humans are omitted. For taxonomic consistency, we have followed the species-level taxonomy of Wilson & Reeder (1993).

Information on the African geographical distributions of mammal species was obtained from Dorst & Dandelot (1969), Kingdon (1971, 1977, 1979, 1982a,b), Skinner & Smithers (1990), Nowak (1991), Wilson & Reeder (1993) and Kingdon (1997). We have also used Corbet (1978), Hall (1981) and Corbet & Hill (1992) for species with geographical ranges falling outside Africa.

Climatic typology

We use the climatic classification of Walter (1970), summarized in Table 1, and mapped in Allué Andrade (1990). This typology has been selected because it has a simple nomenclature and coincides with traditional biomes (Odum, 1971; Lacoste & Salanon, 1973; Lieth, 1975; Strahler & Strahler, 1987), termed zonobiomes by Walter (1970). Climatic zones I–V exist in Africa today. In this paper, the term biome, zonobiome and climate zone are used synonymously (Table 1) and henceforth we only use biome in order to facilitate comprehension.

Thirteen climatic dominions have been determined for the African continent (Table 2). A climatic dominion was defined by Hernández Fernández (2001) as a continuous terrestrial area within one biome only. For instance, in the present case, the Zaire basin is a climatic dominion of the tropical rain forest biome and it is geographically separated from the Ivory Coast, the other African climatic dominion of the tropical rain forest biome. The only exception to the geographical separation between climatic dominions within a biome occurs in the biome II. Although the Sudano-Guinean woodlands and Angolo-Zambezian woodlands have overlapping boundaries, we treat them as different climatic dominions as the overlap zone is very narrow. A map of the present African climatic dominions is presented in Fig. 1.

Table 1 Climatic typology used in this paper and its correspondence with world vegetation types. Zonobiome, *sensu* Walter (1970), mainly vegetation type and synonymous to biome. Modified from Walter (1970); Walter considers II/III as a zonoecotone between tropical forests and deserts, but we consider it as a zonobiome

Zone	Climate zone	Zonobiome
I	Equatorial	Evergreen tropical rain forest
II	Tropical with summer rains	Tropical deciduous woodland
II/III	Transition tropical semiarid	Savanna
III	Subtropical arid	Subtropical desert
IV	Winter rain and summer drought	Sclerophyllous woodland–scrubland
V	Warm-temperate	Temperate evergreen forest
VI	Typical temperate	Nemoral broadleaf-deciduous forest
VII	Arid-temperate	Steppe to cold desert
VIII	Cold-temperate (boreal)	Boreal coniferous forest (taiga)
IX	Artic	Tundra

Table 2 African climatic dominions. Based on map by Allué Andrade (1990); see Fig. 1

Abbr.	Name	Climate zone
I (W)	Ivory Coast rain forest	I
I (Ce)	Zaire Basin rain forest	I
II (N)	Sudano-Guinean woodland	II
II (S)	Angolo-Zambezian woodland	II
II/III (N)	Sahelian savanna	II/III
II/III (E)	East African savanna	II/III
II/III (S)	Kalahari-Highveld savanna	II/III
III (N)	Sahara desert	III
III (E)	Somali desert	III
III (S)	Namib-Karoo desert	III
IV (N)	Mediterranean Maghreb	IV
IV (S)	Cape fynbos	IV
V (SE)	Natalian forest	V

Vegetation belts in mountains must also be taken into account. The altitudinal gradient represents a habitat series analogous to that of biomes in a latitudinal gradient (Walter, 1970; Walter & Breckle, 1986). We can recognize several vegetation belts in the Subsaharan mountains (Walter & Breckle, 1986; Kingdon, 1997): lowlands belt, montane forest belt (analogous to biome V), subalpine forest-ericacean belt (analogous to biome VIII) and afroalpine belt (analogous to biome VII). In the Atlas mountains the recognized vegetation belts are (Walter, 1970; Walter & Breckle, 1991): lowlands belt, montane deciduous forest belt (analogous to biome VI), subalpine forest belt (analogous to biome VIII) and alpine belt (analogous to biome VII).

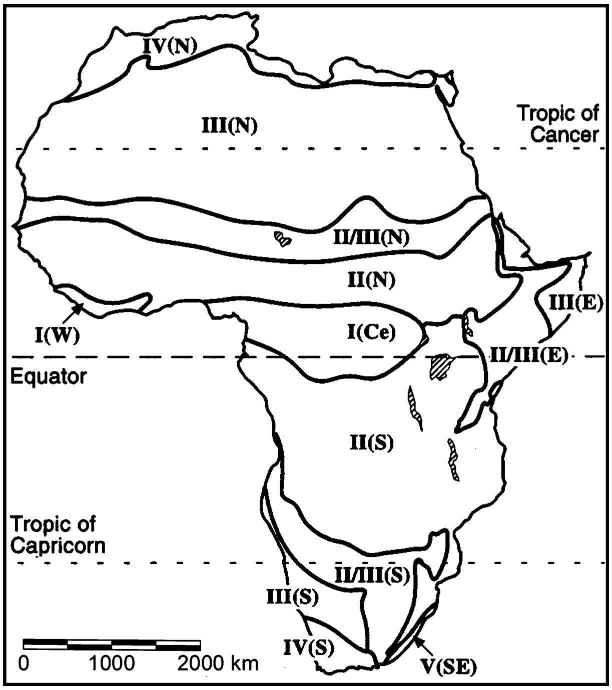

Figure 1 Map of African climatic dominions. Abbreviations as in Table 2.

Bioclimatic characterization of species

We applied the methodology developed by Hernández Fernández (2001) to the African large mammals: for each species we computed the biomic specialization index (BSI), which is the number of biomes inhabited by it. Thus BSI equals 1 for most specialized species (stenobiomic species) whereas for generalist species (eurybiomic species) it could be as high as 10. The decision on the number of biomes inhabited by a species was based on the following. If 15% or more of the geographical range of a species is situated within a biome, the species was recorded as present in that biome. As some climatic dominions are small enough to comprise less than 15% of the total distribution ranges of species with large range sizes, a species was also recorded as present in a specific biome if it inhabits 50% or more of one climatic dominion (Hernández Fernández, 2001). The presence in a mountain vegetation belt was also recorded as presence in the corresponding analogous biome.

Latitudinal distributions

In analyses of latitudinal patterns, all latitudes in the southern hemisphere were arbitrarily assigned negative values. Latitudinal patterns in BSI were analysed using two different methods.

Across-species method

We examined latitudinal patterns in BSI comparing latitudinal midpoint and BSI across species, using all species as separate data points in the analysis. The latitudinal midpoint of the range (L_M) was calculated as:

$$L_M = (L_N + L_S)/2$$

where L_N is the latitude of the northernmost extant limit and L_S the latitude of the southernmost extant limit of the species geographical range. In cases of species with disjunct range areas, the latitudinal midpoint may fall at a latitude at which the species does not occur, but this is not a common situation in the present assemblage.

A potential problem is non-independence of species data as a result of their common ancestry and shared phylogenetic constraints (Harvey & Pagel, 1991). Nonetheless, we did not use a phylogenetic comparative method because there is no body of relevant phylogenetic information for the African larger mammals, and the potential influence of phylogeny should be considered in evaluating our results. Although formal comparative methods have been used previously to examine the effects of phylogeny on geographical patterns in species range size (Pagel *et al.*, 1991; Letcher & Harvey, 1994; Blackburn & Gaston, 1996a; Cowlishaw & Hacker, 1997; Eeley & Foley, 1999; Harcourt, 2000), most of the studies that have investigated the problem both with and without the use of a formal phylogenetic comparative method to control for the effects of phylogeny, have observed a similar relationship under the two approaches (Gaston *et al.*, 1998a).

Average method

For each 1°-latitude band, we estimated the average BSI for all species whose ranges fall within that latitudinal band. We then tested for latitudinal variation in the average BSI values. This method has frequently been used to examine latitudinal gradients in range size (Stevens, 1989; Pagel *et al.*, 1991; Letcher & Harvey, 1994; Blackburn & Gaston, 1996a). Although this method suffers from several problems, such as statistically non-independence of latitudinal means due to the fact that each species contributes to the BSI averages at more than one latitude (see Pagel *et al.*, 1991), it is used here because it is unique in incorporating information on all species occurring at each latitude (Blackburn & Gaston, 1996a).

Climatic variability in relation to the BSI

In order to test the climatic variability hypothesis, climatic data were obtained from the literature (Meteorological Office, 1983) for 525 African meteorological stations, and a stepwise multiple regression was used to determine which variables explain most of the variance in average BSI.

Temperature variability (T.var.) was quantified as the mean annual temperature range by calculating the difference (in °C) between the mean temperature of the warmest month and the mean temperature of the coldest month. Precipitation variability (P.var.) is expressed as the difference (in mm) between the maximum and minimum monthly precipitation divided by the total annual rainfall. In addition, the following climatic variables were entered into the regression: mean annual temperature (T), coldest month mean temperature (Tmin), total annual rainfall (P) and Lang's moisture factor (P/T), which describes the interaction of rainfall and temperature (American Meteorological Society, 2000). Because each latitudinal band may encompass a wide variety of temperatures and rainfall, values were averaged for each 1° of latitude. Finally, latitudinal area (Area, in km^2; continental area included in each latitudinal band), number of lowland biomes (LB.num.), number of montane biomes (MB.num.; altitudinal vegetation belts in the mountains across each latitudinal band), lowland biomes density (LB.dens.; LB.num./km$^2 \times 1000$), and montane biomes density (MB.dens.; MB.num./km$^2 \times 1000$) in each latitudinal band were included into the regression to determine whether increasing BSI was simply a function of increasing area or biome availability. In this manner we correct for differences in area or biome diversity among latitudinal bands. The larger lakes in the Rift Valley and the Lake Chad were not included in the calculus of latitudinal area. The values of these variables in each latitudinal band are shown in Appendix S1 (see Supplementary material).

Separate stepwise multiple regressions were performed for all larger mammal species from all of Africa, for all species from each of northern and southern hemispheres of Africa, and for each of Primates, Carnivora and Artiodactyla, in all of Africa, and separately in northern and southern Africa. The analyses for Primates in all Africa, and in northern Africa, were repeated after deleting the records north of the Sahara. This was performed because our analysis of the general latitudinal pattern in average BSI indicated that the presence of the Barbary macaque (*Macaca sylvanus*), a representative of a very different biogeographical group of primates with an Asian origin, in the Mediterranean Maghreb modifies the general latitudinal pattern in average BSI (see results for Primates below).

Many characteristics of macroecological data bases, such as collinearity and spatial autocorrelation in latitudinal gradients, are problematic in regression analyses and can lead to biased estimators and spurious biological conclusions. For this reason, simple linear correlation among environmental predictors was used to evaluate the potential effects of collinearity on the performance of the stepwise multiple regressions. Additionally, we followed the stepwise regression models with ordinary least squares multiple regression models to assess changes in the coefficients of determination. The pattern of spatial autocorrelation in the BSI was evaluated by comparing the spatial autocorrelation in the original BSI data with that of the residuals of the regression models, based on Moran's *I* coefficients (Moran, 1950; Cliff & Ord, 1981; Diniz-Filho *et al.*, 2003). Correlograms of the raw biomic specialization data were generated using SAAP 4.3 (Wartenberg, 1989) for each data set, using 10 distance classes. This quantified the patterns of autocorrelation in the dependent variable at various spatial scales. The regression models were then fitted and Moran's *I*s on the residuals were recalculated. We followed the Bonferroni criterion to assess the significance of the correlogram as a whole (Oden, 1984; Diniz-Filho *et al.*, 2003).

Finally, following Rahbek & Graves (2001), we emphasize the relative ranking of variables in regression models rather than *P*-values. The performance of models was compared in terms of r^2 values. Further, the primary interest is in identifying the strongest predictors of mammalian biomic specialization rather than identifying all factors that may show a statistical association with specialization, however weak. Thus, the minor variables likely to be influenced by spatial autocorrelation are not interpreted.

RESULTS

Latitudinal patterns in BSI

The results of the across-species method show a large concentration of biome specialist species between 5° S and 10° N (Fig. 2). Sixty-three per cent of the species with BSI = 1 have their latitudinal midpoints within this latitudinal range. There are strong differences between the northern and southern hemispheres, with a decrease in maximum BSI with latitude south of the equator. These differences were tested by means of linear correlations. While the correlation between BSI and latitudinal midpoint is not significant in the south ($r = -0.003$, $P = 0.978$, $n = 126$), it is significant in the north ($r = 0.252$, $P = 0.004$, $n = 127$).

The average method reveals a clear pattern (Fig. 3). The smallest average BSI occurs between *c.* 4° S and 5° N. The relationship between average value of species BSI and latitude is noteworthy in both northern and southern hemispheres. That is, average BSI values are much larger

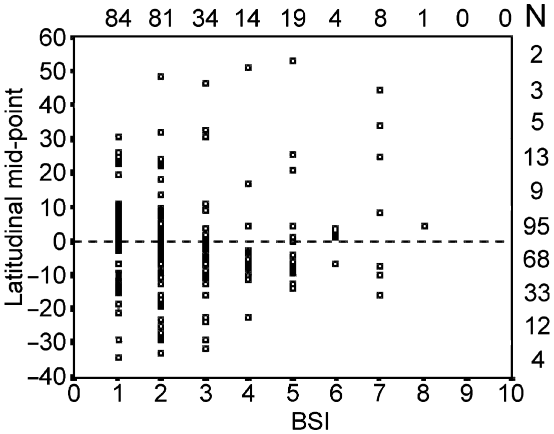

Figure 2 The relationship between biomic specialization index (BSI) and the latitudinal midpoint of a species geographical range for African large mammals (the 'across-species' method, see text). Horizontal dashed line, equator; negative latitudes are south of the equator. N, number of species in each BSI grade (above), and number of species with their mid-latitudinal point within each 10° latitudinal band (right).

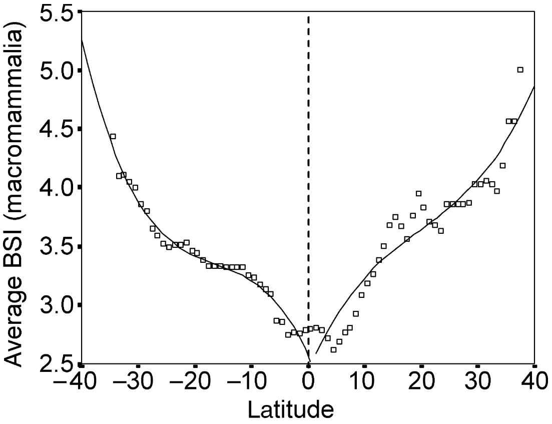

Figure 3 Relationship between latitude and average BSI of species for each 1° latitude row of all species present at that latitude. The cubic regression curves for northern and southern hemispheres are shown. Negative latitudes are in the southern hemisphere. Vertical dashed line, equator.

(implying a lower proportion of biome specialists) in African temperate and subtropical latitudes than in tropical ones. Yet the southern pattern differs from the northern one: the mean BSI values of the inflection points obtained when the data are fitted by a third-order polynomial (Fig. 3) and the latitudinal extents of the 'plateaus' defined around them differ between the southern and northern curves (mean BSI = 3.3–3.5, 11°–26° S; mean BSI = 3.6–4.0, 14°–33° N, respectively) and the northern hemisphere plateau is less well defined.

Primates

Using the across-species method, there is no correlation in Primates between BSI and latitudinal midpoint, either in the northern ($r = 0.251$, $P = 0.165$, $n = 32$) or the southern hemisphere ($r = -0.005$, $P = 0.977$, $n = 31$).

The average method shows a pattern for Primates that differs from that for all large mammals (Fig. 4a). The smallest average BSI is attained between *c.* 7° S and 6° N. There is a considerable relationship between average value of species BSI and latitude for the southern hemisphere; but for the northern hemisphere this relationship is weak, albeit statistically significant. The general pattern in the southern hemisphere is similar to the pattern of all large mammals, although the plateau is shifted towards the equator (Fig. 4a). In the northern hemisphere, however, the pattern is completely different, probably due to the existence of the Sahara desert and the presence of the Barbary macaque (*Macaca sylvanus*) in the Mediterranean Maghreb. This species is a representative of a very different biogeographical group of primates with an Asian origin. The relationship between average BSI value of Primate species and latitude in the northern hemisphere is considerably improved if the records north of the Sahara are deleted. Then the northern plateau appears again although it is shifted to the equator (Fig. 4a; dotted line), as in the southern hemisphere.

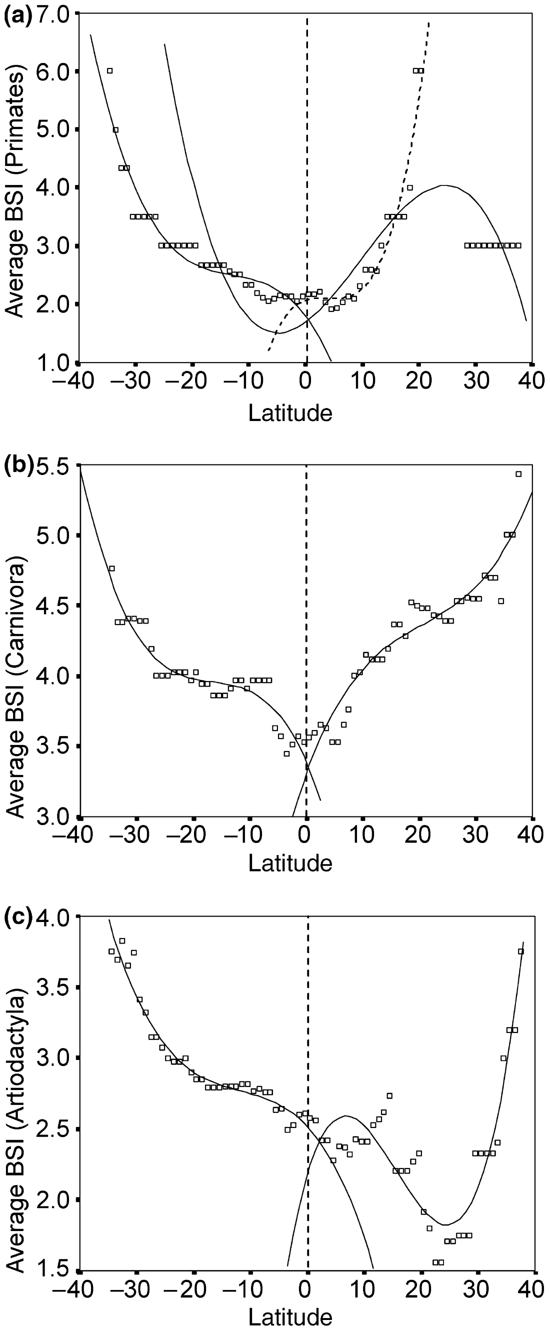

Figure 4 As in Fig. 3, but for mammalian orders: (a) Primates (dotted line, cubic regression curve for northern hemisphere omitting *Macaca*), (b) Carnivora and (c) Artiodactyla.

Carnivora

There is no correlation between BSI and latitudinal midpoint in Carnivora, neither in the northern hemisphere ($r = 0.204$, $P = 0.214$, $n = 39$) nor southern hemisphere ($r = 0.070$, $P = 0.675$, $n = 38$).

The carnivoran pattern obtained by the average method is closely similar to that for the all African large mammals (Fig. 4b). The smallest average BSI is attained approximately between 5° S and 5° N. There is an important relationship between average value of species BSI and latitude. As in the case of all large mammals, there is a plateau in the relationship between mean BSI and latitude in both hemispheres. But the mean BSI value at these plateaus and their latitudinal extent differ in southern and northern hemispheres (mean BSI *c.* 3.9, 6°–27° S; mean BSI = 4.4–4.6, 15°–31° N, respectively) and the northern hemisphere terrace is again not as well defined as the southern one.

Artiodactyla

Using the across-species method, the correlation between BSI and latitudinal midpoint for Artiodactyla species is significant for the northern hemisphere ($r = 0.292$, $P = 0.049$, $n = 46$) but not for the southern hemisphere ($r = 0.071$, $P = 0.634$, $n = 47$).

The artiodactyl pattern obtained by the average method differs considerably from that for all large mammals (Fig. 4c). The smallest average BSI is attained at around the Tropic of Cancer. There is a striking relationship between average value of species BSI and latitude for both hemispheres. The general pattern in the southern hemisphere is very similar to the pattern for all large mammals, with the plateau placed between 6 and 18° S (mean BSI *c.* 2.8). In the northern hemisphere, however, the pattern is completely different.

Climatic variability in relation to BSI

Appendix S2 (see Supplementary Material) shows the correlations between the 11 environmental variables to investigate the patterns of collinearity among them. Strong correlation ($r > 0.85$) was found only in the relationships between total annual rainfall and Lang's moisture factor ($r = 0.973$), between temperature variability and total annual rainfall ($r = -0.897$) and between mean annual temperature and mean temperature of the coldest month ($r = 0.859$).

Tables 3 and 4 summarize the results of the stepwise and ordinary least squares multiple regressions to determine which climatic and biome variables explain most of the variance in average BSI. The ordinary least squares regression models always present higher coefficients of determination than the stepwise models, but the additional explained variance is only *c.* 7% on average (the range is from 0.1% to 25.7%). If we do not take into account the Primate models that include *Macaca* the average additionally explained variance rises only 5% (0.1–11.3%). Appendix S3 (see Supplementary Material) shows the regression coefficients for the environmental variables included in the stepwise models, as well as their coefficients in the ordinary least squares models. No remarkable changes are perceived, which indicates that the performance of the stepwise regressions has

Table 3 Results of the stepwise and ordinary least squares (OLS) regressions where average BSI for all African large mammals in each latitudinal band is the dependent variable. Shown for all Africa and for each hemisphere

	Africa			Northern hemisphere			Southern hemisphere		
Taxa	Step	r^2	Variable	Step	r^2	Variable	Step	r^2	Variable
Macromammalia	1	0.699	T.var.	1	0.774	T.var.	1	0.862	Area
	2	0.792	T.var. LB.dens.	2	0.849	T.var. LB.dens.	2	0.906	Area Tmin
	3	0.832	T.var. LB.dens. Area	3	0.888	T.var. LB.dens. P.var.	3	0.928	Area Tmin P.var.
	4	0.851	T.var. LB.dens. Area P.var.	4	0.905	T.var. LB.dens. P.var. MB.dens.			
	5	0.861	T.var. LB.dens. Area P.var. T	5	0.924	T.var. LB.dens. P.var. MB.dens. LB.num.			
	6	0.886	T.var. LB.dens. Area P.var. T Tmin						
	OLS	0.887	All variables	OLS	0.970	All variables	OLS	0.972	All variables

Area, area in each latitudinal band; LB.den., lowland biomes density in each latitudinal band; LB.num., number of lowland biomes in each latitudinal band; MB.den., montane biomes density in each latitudinal band; P, average total annual precipitation in each latitudinal band; P.var., average precipitation variability in each latitudinal band; T, average mean annual temperature in each latitudinal band; Tmin, average coldest month mean temperature in each latitudinal band; T.var., average temperature variability in each latitudinal band.

Table 4 Results of the stepwise and ordinary least squares (OLS) regressions where average BSI (for different taxa) in each latitudinal band is the dependent variable. Shown for all Africa and for each hemisphere

	Africa			Northern hemisphere			Southern hemisphere		
Taxa	Step	r^2	Variable	Step	r^2	variable	Step	r^2	Variable
Primates	1	0.500	P	1	0.551	P/T	1	0.904	Area
	2	0.639	P LB.dens.				2	0.921	Area LB.dens.
							3	0.931	Area LB.dens. Tmin
	OLS	0.766	All variables	OLS	0.808	All variables	OLS	0.942	All variables
Primates without *Macaca*	1	0.636	P	1	0.770	T.var.			
	2	0.738	P LB.dens	2	0.850	T.var. T.			
	OLS	0.833	All variables	OLS	0.924	All variables			
Carnivora	1	0.708	T.var.	1	0.759	T.var.	1	0.813	Area
	2	0.766	T.var. LB.dens.	2	0.815	T.var. LB.dens.	2	0.853	Area P.var.
				3	0.851	T.var. LB.dens. P.var.			
				4	0.875	T.var. LB.dens. P.var. LB.num.			
				5	0.891	T.var. LB.dens. P.var. LB.num. MB.num.			
	OLS	0.846	All variables	OLS	0.940	All variables	OLS	0.884	All variables
Artiodactyla	1	0.622	Area	1	0.583	LB.dens.	1	0.905	Area
	2	0.729	Area LB.num.	2	0.685	LB.dens. MB.dens.	2	0.927	Area Tmin
	3	0.752	Area LB.num. LB.dens.	3	0.765	LB.dens. MB.dens. P.var.			
	4	0.769	Area LB.num. LB.dens. P.var.						
	5	0.786	Area LB.num. LB.dens. P.var. P/T.						
	6	0.800	Area LB.num. LB.dens. P.var. P/T. T.var.						
	OLS	0.821	All variables	OLS	0.878	All variables	OLS	0.944	All variables

Area, area in each latitudinal band; LB.den., lowland biomes density in each latitudinal band; LB.num., number of lowland biomes in each latitudinal band; MB.den., montane biomes density in each latitudinal band; MB.num, number of montane biomes in each latitudinal band; P, average total annual precipitation in each latitudinal band; P.var., average precipitation variability in each latitudinal band; P/T, average Lang's moisture factor in each latitudinal band; T, average mean annual temperature in each latitudinal band; Tmin, average coldest month mean temperature in each latitudinal band; T.var., average temperature variability in each latitudinal band.

not been appreciably affected by collinearity among the predictor variables.

Correlograms in Appendix S4 (see Supplementary Material) show that fitting the variables included in the stepwise regression models were not able to remove all spatial autocorrelation in the continental data set, although autocorrelation was considerably reduced in all distance classes. The analyses for the hemispheric data sets show a different outcome. The northern hemisphere data set shows that autocorrelation has been successfully removed by the stepwise regression models (excepting the analysis for Primates including *Macaca*). On the contrary, a significant amount of spatial autocorrelation remains in the southern hemisphere data sets. This indicates that whereas the analysed environmental variables can account for the spatial pattern in biomic specialization very well in the northern hemisphere, additional factors not included in this analysis are needed to fully account for spatial variation in mammalian biomic specialization in the southern hemisphere. We believe that historical factors may significantly contribute to the specialization pattern, as we clarify in the next section.

For all the larger mammals, there were six steps with six of the 11 studied variables included at the final step (Table 3). The single most important climatic variable is temperature variability (mean annual temperature range), which has a positive relationship with average BSI and accounts for 69.9% of the variance, thus supporting the climatic variability hypothesis. The next two variables are both geographical measures (lowland biome density and area). The remaining variables included in the regression are precipitation variability, mean annual temperature and mean temperature of the coldest month. Five variables are not included in the regression. The latitudinal average BSI remains unaffected by annual precipitation, moisture, montane biome density and number of biomes.

The results for the separate stepwise regression for the northern hemisphere were very similar to those for all larger mammals. The single most important climatic variable is temperature variability, accounting for 77.4% of the variance on average BSI. However, the results for the southern hemisphere differ in that the most important variable is latitudinal area ($r^2 = 86.2$). Two additional variables explain only 4.4% (mean temperature of the coldest month) and 2.2% (precipitation variability) of the variance. Thus latitudinal area is by far the most important variable explaining the macromammalian latitudinal average BSI in the southern hemisphere.

The stepwise regression results for Primates, Carnivora and Artiodactyla are summarized in Table 4. In the primate analysis of all Africa, the most important climatic variable is total annual precipitation, accounting for 50% of the variance in latitudinal average BSI. The second most important variable is lowland biomes density (13.9% of the variance). If *Macaca* records are deleted the result is very similar, although the explained variance increases. The analysis of the northern hemisphere shows that the most important variable is the Lang's moisture factor (55%). When *Macaca* records are deleted, the single most important variable is temperature variability, accounting for 77% of the variance. The most important variable in the southern hemisphere is the latitudinal area (90%), as in the analysis of all large African mammals.

The results for Carnivora were very similar to those for all the large mammal species and Primates and we will not make further comments here.

The analogous results for Artiodactyla differ from those of the other orders, as might be expected from the very different latitudinal pattern in average BSI. The result for all Africa indicated that the most important variable is latitudinal area, accounting for 62% of the variance. Only in the fourth step was a climatic variable introduced; precipitation variability which accounts for only an additional 1.7% of the variance. The analysis of the northern hemisphere shows that the most important variables are lowland biomes density (58%), montane biomes density (10%) and precipitation variability (8%). The most important variable in the southern hemisphere is again latitudinal area, which explains for 90% of the variance. Thus, while the results for artiodactyls show the same relationship with latitudinal area as was found in the other groups in the south, they differ in the analysis of northern Africa. In this latter case, average BSI and biome density (lowland and montane) increase together. Namely, a lesser biome diversity produces an increase in the frequency of stenobiomic species.

DISCUSSION

Relations among BSI, latitude and biogeography

The patterns of BSI across latitudes remain broadly similar when analysed using different methods. Across-species and average methods indicate that minimum BSI is generally attained by species at near the equator, although the results of the two methods differ in some respects.

Across-species method

The result that BSI and latitudinal midpoint for all large mammals show a significant positive correlation in northern but not southern Africa must be due in part to differences in between north and south in continental shape and intercontinental geographical connections. Northern Africa not only has a larger area, but also has provided access for species to (or from) temperate biomes on neighbouring continents. In contrast, southern African species are confined to a smaller tropical and subtropical area that narrows towards the south. It seems that this difference, to which we will refer as the 'north–south geographical asymmetry', has influenced the pattern of species BSI values in the southern hemisphere (Fig. 5).

In the south, for the species with latitudinal midpoints falling in latitudinal bands with large areas, the variation in the BSI values is often large. But the species with latitudinal midpoints falling in latitudinal bands with small areas have only lower BSI values. This relationship does not exist in the African north.

When the across-species method is applied to mammal orders, the relationship between BSI and latitudinal midpoint

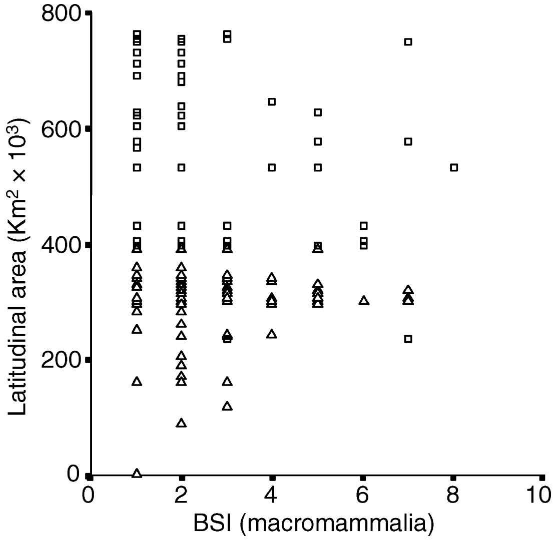

Figure 5 Relationship between species BSI and latitudinal area in their latitudinal midpoint. Squares, species with northern hemisphere midpoints; triangles, species with southern hemisphere midpoints.

is not significant except for Artiodactyla in the northern hemisphere. Neither is the relationship between species BSI on the one hand, and latitudinal area in their latitudinal midpoint on the other hand, significant for Primates and Carnivora (Fig. 6). Only Artiodactyla shows the same relationship as in all large mammals: species with southern latitudinal midpoints falling in latitudinal bands with smaller areas have generally lower BSI values. It appears that the north–south geographical asymmetry may affect the geographical distributions of only some taxa in the African southern hemisphere.

Average method

The result that average BSI per latitude row is highly positively correlated with latitude indicates a much higher proportion of specialist species in equatorial areas. The relationship appears to have a sigmoidal shape (Fig. 3). The rate of increase in the average BSI from low to middle to higher latitudes changes from high to low and back to high. These changes in the average BSI increase are more marked in the southern hemisphere, which is probably related to the presence of the large climatic dominion II (S). This result for average BSI cannot be taken as indicative of that which would be found for individual species. The across-species and average methods are not simply different methods of quantifying the same relationship; the former relates latitudinal variation in range size to the latitudinal midpoint of species distributions, whereas the latter shows variation in the mean range size of all species present at a latitude (Gaston *et al.*, 1998a). The much weaker relationship, with substantial variation, in the across-species results (Fig. 2) may reflect the African north–south geographical asymmetry. The relationship between average BSI and latitude (Fig. 3) is useful in its own right because it highlights a very general and strong trend that is probably important for interpreting latitudinal gradients in geographical range sizes and species richness.

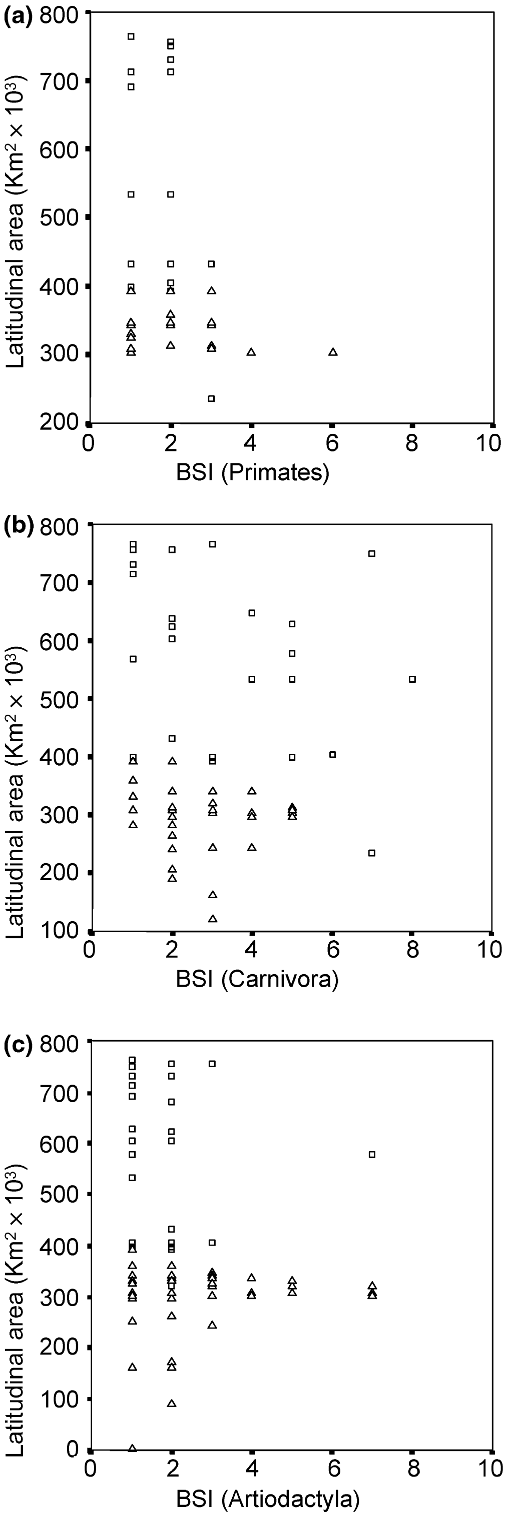

Figure 6 As in Fig. 5, but for mammalian orders: (a) Primates, (b) Carnivora and (c) Artiodactyla.

In each of the separate results for Primates or Carnivora, average BSI is lowest near the equator and displays a general increase with increasing latitude (Fig. 4). Differences between these taxa include the following. Primates have lower average BSI values than Carnivora across most of the latitudinal spectrum. These values are higher than those of Carnivora only in the extreme south and at the southern boundary of the Sahara, where the only one primate species present is the baboon (*Papio hamadryas*). Primates have a very slow rate of increase in the average BSI in the lower latitudes of the southern hemisphere, and at *c.* 25° S this increases suddenly. Once more, this may be related with the large Angolo-Zambezian climatic dominion, II (S). On the contrary, in the northern hemisphere the rate of increase is very fast, probably due to an intensified environmental gradient between the Tropic of Cancer and the equator, which is provoked by the presence of the Sahara desert. The average BSI of Carnivora shows a faster rate of increase in the northern than the southern hemisphere, but this process is not as marked as in Primates and the Sahara desert does not interrupt this tendency in carnivores.

The pattern in Primates may result from the fact that most of them are adapted to the more stable temperature conditions in the tropics (Janzen, 1967; Stevens, 1989). Results very similar to ours have been presented by Eeley & Foley (1999). They found a general latitudinal increase in mean habitat niche breadth. This supports Stevens' (1989) climatic variability hypothesis, which implies that niche breadth is strongly correlated with latitude and range size. Cowlishaw & Hacker (1997) and Harcourt (2000) present convincing evidence that the range size of African primates reflects climatic variation, in particular in seasonality of rainfall.

The pattern in Artiodactyla differs substantially from the previous ones. The latitudinal pattern in the south is broadly similar to the general one but with lower average BSI values. The greatest difference from the general pattern can be observed in the northern hemisphere. In this order the lowest values of average BSI occur in the area of the Sahara desert. In this case, it seems that the latitudinal plateau, which is present in the general pattern and in other orders, has subsided into a valley because of the high degree of specialization needed by a herbivore to survive in a large desert. It appears that the 'typical' pattern (that of the all large mammals) has been distorted by the presence of this large desert.

Does the climatic variability hypothesis apply to African larger mammals?

Our results for African large mammals are relevant to hypotheses that seek to explain the Rapoport effect, namely the tendency for geographical range size to increase from the equator to the poles. As it was said above, the most often cited explanation is the climatic variability hypothesis (Stevens, 1989): that the greater seasonal variation in higher latitudes favours species that can tolerate a wider range of climatic conditions and habitats, which consequently attain larger geographical distributions (Allee *et al.*, 1949; Janzen, 1967; Stevens, 1989). Stevens (1989), based primarily on North American data, cited evidence for the expected latitudinal variation in climatic variability and concluded that it does indeed play a primary causal role in promoting the Rapoport effect. Pagel *et al.* (1991), again based on North American data, found the degree of habitat diversity to be an important determinant of geographical range size and species richness. The present results for Africa offer a comparison with these conclusions for North America. Africa has a different latitudinal extent and its own strong north–south geographical asymmetry which, as already mentioned, appears to correlate with African latitudinal patterns in BSI.

The results of stepwise multiple regression, of average BSI values for all African large mammals in each latitudinal band on eleven climatic and geographical variables (Table 3), suggest that temperature variability accounts for *c.* 70% of the variance. Thus the result for the entire African pattern appears to support the climatic variability hypothesis.

However, the separate analysis for northern and southern Africa (Table 3) gave more complex results. Those for the north are very similar to those of the all-African analysis. But for the southern data set, the most important climatic variable is latitudinal area ($r^2 = 86.2\%$), while mean temperature of the coldest month and precipitation variability explain only an additional 4.4% and 2.2% of the variance, respectively. This finding does not support the climatic variability hypothesis. It suggests that a similar pattern in latitudinal variation in average BSI was caused by different factors in the two hemispheres. In the north, increasing temperature variability towards higher latitudes appears to have influenced increasing biomic generalization. In addition, the northern connections with Eurasia have facilitated the entry of Eurasian immigrants into Africa, and mostly into northern Africa (more than half of the 23 species of African large mammals that also occur out of Africa do not inhabit south of the equator). Such species are generally eurybiomic. In the south, continental narrowing (or decreasing latitudinal area) towards higher latitudes had a major influence on southward increase in average BSI, that is, in the proportion of biome generalists, according to our results. A possible explanation draws on the observations that the narrow southern extreme of Africa includes several small climatic dominions of different biomes, and that mammalian population density decreases with increasing body size (Brown, 1995); for the geographical ranges of large mammal species to be large enough to sustain genetically viable populations, perhaps many of these ranges need to span several biomes in southern Africa. The probability of extinction is greatly increased at small population sizes (MacArthur & Wilson, 1967; Goel & Richter-Dyn, 1974; Goodman, 1986) and it may be additionally increased by restriction to a small area where the entire species could be eliminated by a regional abiotic or biotic catastrophe (Brown, 1995). Additionally, some of the smallest climatic dominions were substantially reduced in area during the recurrent Pleistocene climatic changes. Thus, perhaps the species we see today at the higher latitudes of southern Africa are mostly those that could evolve to inhabit several of the small southern climatic dominions and thereby maintain long-term viable population sizes and avoid extinction.

Such an extinction process has been proposed to explain the current situation of the Iberian lynx (*Lynx pardinus*) and the Spanish imperial eagle (*Aquila adalberti*), two very endangered stenobiomic species (Ferrer & Negro, 2004). It has also been alleged in order to elucidate the extinction of the Pleistocene European jaguar (*Panthera gombaszoegensis*); the geographical distribution of this big felid during the glacial periods was restricted to the Mediterranean peninsulas, whose areas were unable to guarantee the survival of a sustainable population for a period of 1000 years, which illustrates the role of chance in survival in such refugia (O'Regan *et al.*, 2002). Within the African context, an example of this extinction process might be symbolized by the blue buck (*Hippotragus leucophaeus*). Although the fossil record of this species suggests a wider distribution at the beginning of the Holocene, ecological change seems to have been responsible for the initial reduction of the range in this stenobiomic species. By the time of European settlement at the Cape Province, the blue antelope's distribution and population were reported to be extremely limited (Robinson *et al.*, 1996), probably far beyond the point where genetic impoverishment depresses the species viability to a point from which it could not recover. It was the first African mammal to have become extinct in historic times (*c.* 1799–1800).

The stepwise regression results for Primates, Carnivora and Artiodactyla (Table 4) all agree with respect to southern Africa: in each case latitudinal area emerged as the most important variable correlating with average BSI. This resembles the result obtained for all southern African large mammals and we suggest that the explanation invoking the north–south geographical asymmetries of Africa, which was outlined above for the case of all southern taxa, may apply also to each of the separate southern African cases of primates, carnivores and artiodactyls. The separate results for Carnivora and Primates in northern Africa (with the Maghreb species *Macaca sylvanus* omitted in the case of Primates), that the single most important variable in each case is temperature variability (Table 4), support the climatic variability hypothesis. But this hypothesis is rejected by the result for Artiodactyla in northern Africa, for which the most important variable is biome density (lowland and montane). In this case, average BSI increases when biome density increases. That is to say, a lesser biome density produces an increase in the frequency of stenobiomic species. We suggest that the same explanation as the one suggested above, for the unique artiodactyl latitudinal pattern in BSI, applies here as well. Namely, the result reflects the influence of the Sahara desert.

Importance of biogeographical structure in latitudinal gradients

The geographical patterns of large mammal species are broadly explicable by parallel patterns of habitat diversity in Africa, or what Simpson (1964) called macrospatial heterogeneity. We suggest that the distinct latitudinal pattern in BSI of different African large mammal orders could be the consequence of the biomes distribution in Africa and of the differences in how distinct orders respond to these different environments. For example, in the present study it is shown that the Sahara desert has great influence on the latitudinal pattern of average BSI for Artiodactyla. This could be due to its large size. The potential importance of biogeographical structure in determining patterns in range size has been suggested previously by Pagel *et al.* (1991), Roy *et al.* (1994), Blackburn & Gaston (1996a,b,c) and Ruggiero *et al.* (1998). Our results indicate that it is also influential for the pattern in biomic specialization.

Biogeographical history has been recognized as one of the key processes driving most macroecological patterns in relatively recent times (Ricklefs & Schluter, 1993; Ruggiero *et al.*, 1998). Differences in the history of the regions and their fauna could generate substantial changes at the boundary between the main biogeographical regions and subregions. Thus, biogeographical structure of the continents generates major constraints on local ecological patterns and processes. This stresses the importance of taking into account the effect of biogeographical structure in analyses of geographical gradients in macroecological patterns (Roy *et al.*, 1994; Blackburn & Gaston, 1996a; Ruggiero *et al.*, 1998).

CONCLUSIONS

Stevens' (1989) arguments for key causal elements focus on recent and present-day ecological processes, and on latitudinal differences in climatic variability rather than on differences between taxa or biogeographical history of areas. His hypothesis is that, towards higher latitudes, greater seasonal climatic variability is the most important influence that selectively promotes more generalistic climatic tolerance of organisms and species, and therefore also latitudinally more extensive species geographical ranges. In our test of this hypothesis, using stepwise regressions of degree of biome specificity (BSI) on various climatic and biome variables, the patterns and most important causal influences seem to differ variously between northern and southern Africa, and between mammalian orders. Thus, the climatic variability hypothesis does not appear to provide a general explanation for the African case. But our test results do support the notion that temperature variability is an important causal element in the latitudinal pattern of average BSI for some African large mammals groups. After comparing patterns in geographical range size of six animal groups representing higher taxonomic levels, France (1992) suggested that this latitudinal pattern may have a unique shape for each taxon. He pointed out that a number of taxon-specific factors (e.g. dispersion capabilities, ecophysiological properties) can account for such different patterns. Ruggiero (1994) suggests that similar forces might account for differences in the magnitude of Rapoport effect at different taxonomic levels after her analysis of South American mammals. Given the evidence obtained from the present analysis, we can suggest that these taxon-specific factors are coupled with area-specific factors (e.g. size, biogeographical history, climatic factors, vegetation cover and composition, etc.) to produce very complex patterns which vary depending on the taxon and geographical area studied.

Nevertheless, we think that these differences among taxa can be broadly framed inside a general pattern. Begon *et al.* (1986) have suggested that a small extrinsic force could ultimately determine the latitudinal gradients and also promote a cascade of other factors (such as differences in productivity, competition and predation) that reinforce the initial pattern. Our results suggest that annual temperature variability could be such a subtle force in the evolution of mammalian communities, in agreement with Letcher & Harvey (1994) and Hernández Fernández *et al.* (2003).

In sum, although the climatic variability hypothesis appears to apply substantially to aspects of the African latitudinal pattern, we conclude that its failure to provide a general explanation is due to the fact that it does not consider the influence of the special characteristics of particular taxa, areas and past climatic history. In Africa, among major and peculiarly northern causal influences on the distribution of biome specialization and other patterns, are the enormous Sahara desert (which started to spread *c.* 2.7 Ma; Dupont & Leroy, 1995) and the extensive intercontinental connections with Eurasia, which have been available intermittently since *c.* 20 Ma. In southern Africa, continental narrowing towards the south and biogeographical structure, including the absence of continental connection with temperate latitudes, emerged as likely major causes. In addition, the separately analysed patterns for mammal orders variously indicate different causal processes.

It follows that comparison of any one set of results, such as ours for African large mammals, with others should be done with caution. Our latitudinal analysis of the variation in BSI does not encompass the entire range of possible latitudes. There is no evidence to date that the pattern of variation observed here can be extrapolated from the African latitudinal range to higher latitudes, nor even to other tropical regions of the world. In fact, the results in this paper indicate that the particulars of continental biogeography are very important causal factors of macroecological patterns and additional studies in other continents and faunal groups must be done.

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SUPPLEMENTARY MATERIAL

The following material is available from http://www.blackwellpublishing.com/products/journals/suppmat/JBI/JBI1188/JBI88sm.htm

Appendix S1 Data on average BSI, climate and biogeographical structure for the African latitudinal bands.

Appendix S2 Correlations between the 11 environmental variables studied in this work.

Appendix S3 Regression coefficients for the environmental variables included in the stepwise regression models.

Appendix S4 Correlograms for each studied data set and the corresponding stepwise regression model.

REFERENCES

Allee, W.C., Emerson, A.E., Park, O., Park, T. & Schmidt, K.P. (1949) *Principles of animal ecology*. Saunders, Philadelphia.

Allué Andrade, J.L. (1990) Atlas fitoclimático de España. *Monografías del Instituto Nacional de Investigaciones Agrarias*, **69,** 1–223.

American Meteorological Society (2000) *Glossary of meteorology*. American Meteorological Society, Boston, MA.

Anderson, S. & Koopman, K.F. (1981) Does interspecific competition limit the sizes of ranges of species? *American Museum Novitates*, **2716,** 1–10.

Ashton, K.G. (2001) Are ecological and evolutionary rules being dismissed prematurely? *Diversity and Distributions*, **7,** 289–295.

Begon, M.J., Harper, J.F. & Townsend, C.R. (1986) *Ecology*. Blackwell Scientific, Oxford.

Blackburn, T.M. & Gaston, K.J. (1996a) Spatial patterns in the geographic range sizes of bird species in the New World. *Philosophical Transactions of the Royal Society of London B, Biological Sciences*, **351,** 897–912.

Blackburn, T.M. & Gaston, K.J. (1996b) Spatial patterns in the species richness of bird species in the New World. *Ecography*, **19,** 369–376.

Blackburn, T.M. & Gaston, K.J. (1996c) A sideways look at patterns in species richness, or why there are so few species outside the tropics. *Biodiversity Letters*, **3,** 44–53.

Brown, J.H. (1995) *Macroecology*. University of Chicago Press, Chicago, IL.

Brown, J.H. & Maurer, B.A. (1989) Macroecology: the division of food and space among species on continents. *Science*, **243,** 1145–1150.

Brown, J.H. & Nicoletto, P.F. (1991) Spatial scaling of species composition: body masses of North American land mammals. *The American Naturalist*, **138,** 1478–1512.

Cliff, A.D. & Ord, J.K. (1981) *Spatial processes: models and applications*. Pion Ltd, London.

Corbet, G.B. (1978) *The mammals of the Palaearctic region: a taxonomic review*. Cornell University Press, London.

Corbet, G.B. & Hill, J.E. (1992) *The mammals of the Indomalayan region: a systematic review*. Oxford University Press, Oxford.

Cowlishaw, G. & Hacker, J.E. (1997) Distribution, diversity, and latitude in African primates. *The American Naturalist*, **150,** 505–512.

Cowlishaw, G. & Hacker, J.E. (1998) Too much latitude for Rapoport's rule? *Trends in Ecology and Evolution*, **13,** 241–242.

Diniz-Filho, J.A.F., Bini, L.M. & Hawkins, B.A. (2003) Spatial autocorrelation and red herrings in geographical ecology. *Global Ecology and Biogeography*, **12,** 53–64.

Dobzhansky, T. (1950) Evolution in the tropics. *American Scientist*, **38,** 209–221.

Dorst, J. & Dandelot, P. (1969) *A field guide to the larger mammals of Africa*. Houghton Mifflin, Boston, MA.

Dupont, L.M. & Leroy, S.A.G. (1995) Steps toward drier climatic conditions in northwestern Africa during the Upper Pliocene. *Paleoclimate and evolution, with emphasis of human origins* (ed. by E.S. Vrba, G.H. Denon, T.C. Partridge and L.H. Burckle), pp. 289–298. Yale University Press, New Haven, CT.

Eeley, H.A.C. & Foley, R.A. (1999) Species richness, species range size and ecological specialization among African primates: geographical patterns and conservation implications. *Biodiversity and Conservation*, **8,** 1033–1056.

Ferrer, M. & Negro, J.J. (2004) The near extinction of two large European predators: super specialists pay a price. *Conservation Biology*, **18,** 344–349.

Forster, J.R. (1768) *Observations made during a voyage round the world, on physical geography, natural history, and ethic philosophy*. G. Robinson, London.

France, R. (1992) The North American latitudinal gradient in species richness and geographic range of freshwater crayfish and amphipods. *The American Naturalist*, **139,** 342–354.

Gaston, K.J. (ed.) (1996) *Biodiversity: a biology of numbers and difference*. Blackwell Science, Oxford.

Gaston, K.J. & Chown, S.L. (1999) Why Rapoport's rule does not generalize? *Oikos*, **84,** 309–312.

Gaston, K.J., Blackburn, T.M. & Spicer, J.I. (1998a) Rapoport's rule: time for an epitaph? *Trends in Ecology and Evolution*, **13,** 70–74.

Gaston, K.J., Blackburn, T.M. & Spicer, J.I. (1998b) Reply. *Trends in Ecology and Evolution*, **13,** 242.

Goel, N.S. & Richter-Dyn, N. (1974) *Stochastic models in biology*. Academic Press, New York.

Goodman, D. (1986) The demography of chance extinction. *Viable populations* (ed. by M.E. Soulé), pp. 11–34. Cambridge University Press, Cambridge.

Hall, E.R. (1981) *The mammals of North America*, Vols I–II. John Wiley & Sons, New York.

Harcourt, A.H. (2000) Latitude and latitudinal extent: a global analysis of the Rapoport effect in a tropical mammalian taxon: primates. *Journal of Biogeography*, **27,** 1169–1182.

Harvey, P.H. & Pagel, M.D. (1991) *The comparative method in evolutionary biology*. Oxford University Press, Oxford.

Hernández Fernández, M. (2001) Bioclimatic discriminant capacity of terrestrial mammal faunas. *Global Ecology and Biogeography*, **10,** 189–204.

Hernández Fernández, M., Salesa, M.J., Sánchez, I.M. & Morales, J. (2003) Paleoecología del género *Anchitherium* von Meyer, 1834 (Equidae, Perissodactyla, Mammalia) en España: evidencias a partir de las faunas de macromamíferos. *Coloquios de Paleontología, Volumen Extraordinario*, **1,** 253–280.

von Humboldt, A. (1808) *Ansichten der Natur mit wissenschaftlichen Erlauterungen*. J.G. Cotta, Tübingen.

Huston, M.A. (1994) *Biological diversity: the co-existence of species on changing landscapes*. Cambridge University Press, Cambridge.

Janzen, D.H. (1967) Why mountain passes are higher in the tropics. *The American Naturalist*, **101,** 233–249.

Kerr, J.T. (1999) Weak links: 'Rapoport's rule' and large-scale species richness patterns. *Global Ecology and Biogeography*, **8,** 47–54.

Kingdon, J. (1971) *East African mammals. An atlas of evolution in Africa*, Vol. I. Academic Press, London.

Kingdon, J. (1977) *East African mammals. An atlas of evolution in Africa*, Vol. III. Part A (carnivores). Academic Press, London.

Kingdon, J. (1979) *East African mammals. An atlas of evolution in Africa*, Vol. III. Part B (large mammals). Academic Press, London.

Kingdon, J. (1982a) *East African mammals. An atlas of evolution in Africa*, Vol. III. Part C (bovids). Academic Press, London.

Kingdon, J. (1982b) *East African mammals. An atlas of evolution in Africa*, Vol. III. Part D (bovids). Academic Press, London.

Kingdon, J. (1997) *The Kingdon field guide to African mammals*. Academic Press, London.

Kolasa, J., Hewitt, C.L. & Drake, J.A. (1998) Rapoport's rule: an explanation or a byproduct of the latitudinal gradient in species richness? *Biodiversity and Conservation*, **7,** 1447–1455.

Lacoste, A. & Salanon, R. (1973) *Éléments de biogéographie*. Fernand Nathan, Paris.

Letcher, A.J. & Harvey, P.H. (1994) Variation in geographical range size among mammals of the Palearctic. *The American Naturalist*, **144,** 30–42.

Lieth, H. (1975) Primary productivity of the major vegetation units of the world. *Primary productivity of the biosphere* (ed. by H. Lieth and R.H. Whittaker), pp. 203–215. Springer-Verlag, Berlin.

Lyons, S.K. & Willig, M.R. (1997) Latitudinal patterns of range size: methodological concerns and empirical evaluations for New World bats and marsupials. *Oikos*, **79,** 568–580.

Lyons, S.K. & Willig, M.R. (2002) Species richness, latitude, and scale-sensitivity. *Ecology*, **83,** 47–58.

MacArthur, R.H. (1972) *Geographical ecology: patterns in the distribution of species*. Harper and Row, New York.

MacArthur, R.H. & Wilson, E.O. (1967) *The theory of island biogeography*. Princeton University Press, Princeton, NJ.

McCoy, E.D. & Connor, E.F. (1980) Latitudinal gradients in the species diversity of North American mammals. *Evolution*, **34,** 193–203.

Meteorological Office (1983) *Tables of temperature, relative humidity, precipitation and sunshine for the world. Part IV. Africa, the Atlantic Ocean South of 35°* N and the Indian Ocean. Her Majesty's Stationery Office, London.

Moran, P.A.P. (1950) Notes on continuous stochastic phenomena. *Biometrika*, **37,** 17–23.

Myers, A.A. & Giller, P.S. (1988) *Analytical biogeography: an integrated approach to the study of animal and plant distributions*. Chapman & Hall, London.

Nowak, R.M. (1991) *Walker's mammals of the world*, 5th edn. The Johns Hopkins University Press, Baltimore, MD.

O'Regan, H.J., Turner, A. & Wilkinson, D.M. (2002) European Quaternary refugia: a factor in large carnivore extinction? *Journal of Quaternary Science*, **17,** 789–795.

Oden, N.L. (1984) Assessing the significance of a spatial correlogram. *Geographical Analysis*, **16,** 1–16.

Odum, E.P. (1971) *Fundamentals of ecology*, 3rd edn. Saunders Company, Philadelphia.

Pagel, M.D., May, R.M. & Collie, A.R. (1991) Ecological aspects of the geographical distribution and diversity of mammalian species. *The American Naturalist*, **137,** 791–815.

Palmer, M.W. (1994) Variation in species richness: towards a unification of hypotheses. *Folia Geobotanica Phytotaxonomica*, **29,** 511–530.

Pianka, E.R. (1966) Latitudinal gradients in species diversity: a review of concepts. *The American Naturalist*, **100,** 33–46.

Rahbek, C. & Graves, G.R. (2001) Multiscale assessment of patterns of avian species richness. *Proceedings of the National Academy of Sciences of the USA*, **98,** 4534–4539.

Rapoport, E.H. (1975) *Areografía: estrategias geográficas de las especies*. Fondo de Cultura Económica, Mexico.

Rapoport, E.H. (1982) *Areography: geographical strategies of species*. Pergamon Press, Oxford.

Ricklefs, R.E. & Schluter, D. (1993) *Species diversity in ecological communities*. University of Chicago Press, Chicago, IL.

Robinson, T.J., Bastos, A.D., Halanych, K.M. & Herzig, B. (1996) Mitochondrial DNA sequence relationships of the extinct blue antelope *Hippotragus leucophaeus*. *Naturwissenschaften*, **83,** 178–182.

Rohde, K. (1992) Latitudinal gradients in species diversity: the search for the primary cause. *Oikos*, **65,** 514–527.

Rohde, K. (1996) Rapoport's rule is a local phenomenon and cannot explain latitudinal gradients in species diversity. *Biodiversity Letters*, **3,** 10–13.

Rosenzweig, M.L. (1975) On continental steady states of species. *Ecology and evolution of communities* (ed. by M.L. Cody and J.M. Diamond), pp. 121–140. Belknap Press, Cambridge.

Rosenzweig, M.L. (1995) *Species diversity in space and time*. Cambridge University Press, Cambridge.

Roy, K., Jablonski, D. & Valentine, J.W. (1994) Eastern Pacific molluscan provinces and latitudinal diversity gradient: no evidence for 'Rapoport's rule'. *Proceedings of the National Academy of Sciences of the USA*, **91,** 8871–8874.

Ruggiero, A. (1994) Latitudinal correlates of the sizes of mammalian geographical ranges in South America. *Journal of Biogeography*, **21,** 545–559.

Ruggiero, A., Lawton, J.H. & Blackburn, T.M. (1998) The geographic ranges of mammalian species in South America: spatial patterns in environmental resistance and anisotropy. *Journal of Biogeography*, **25,** 1093–1103.

Schall, J.J. & Pianka, E.R. (1978) Geographical trends in numbers of species. *Science*, **201,** 679–686.

Simpson, G.G. (1964) Species density of North American recent mammals. *Systematic Zoology*, **13,** 57–73.

Skinner, J.D. & Smithers, R.H.N. (1990) *The mammals of the southern African subregion*, 2nd edn. University of Pretoria, Pretoria.

Smith, F.D.M., May, R.M. & Harvey, P.H. (1994) Geographical ranges of Australian mammals. *Journal of Animal Ecology*, **63,** 441–450.

Stevens, G.C. (1989) The latitudinal gradient in geographical range: how so many species coexist in the tropics? *The American Naturalist*, **133,** 240–256.

Stevens, G.C. (1996) Extending Rapoport's rule to Pacific marine fishes. *Journal of Biogeography*, **23,** 149–154.

Strahler, A.N. & Strahler, A.H. (1987) *Modern physical geography*. John Wiley & sons, New York.

Taylor, P.H. & Gaines, S.D. (1999) Can Rapoport's rule be rescued? Modelling causes of the latitudinal gradient in species richness. *Ecology*, **80,** 2474–3482.

Vrba, E.S. (1987) Ecology in relation to speciation rates: some case histories of Miocene-Recent mammal clades. *Evolutionary Ecology*, **1,** 283–300.

Wallace, A.R. (1878) *Tropical nature and other essays*. Macmillan, London.

Walter, H. (1970) *Vegetationszonen und Klima*. Eugen Ulmer, Stuttgart.

Walter, H. & Breckle, S.-W. (1986) *Ecological systems of the geobiosphere. Vol. 2. Tropical and subtropical zonobiomes*. Springer-Verlag, Berlin.

Walter, H. & Breckle, S.-W. (1991) *Ökologie der Erde*, Vol. 4. Gustav Fischer, Stuttgart.

Wartenberg, D. (1989) *SAAP 4.3: spatial autocorrelation analysis program*. Exeter Software, Setauker.

Willig, M.R., Kaufman, D.M. & Stevens, R.D. (2003) Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. *Annual Review on Ecology, Evolution, and Systematics*, **34,** 273–309.

Wilson, J.W. III (1974) Analytical zoogeography of North American mammals. *Evolution*, **28,** 124–140.

Wilson, D.E. & Reeder, D.M. (1993) *Mammal species of the world: a taxonomic and geographic reference*, 2nd edn. Smithsonian Institution Press, Washington, DC.

BIOSKETCHES

Manuel Hernández Fernández has a broad interest in evolutionary ecology, encompassing a wide variety of problems related to the biological and climatic evolution of the Neogene-Quaternary Earth. He is particularly interested in the interface between macroecology and palaeoclimatology. Further information is available at http://www.ucm.es/info/paleo/personal/hdezfdez.htm.

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Editor: Philip Stott

Appendix S1. Data on average BSI, climate and biogeographic structure for the African latitudinal bands. S, species richness; BSI, biomic specialization index; T.var., temperature variability; P.var., precipitation variability; T, mean annual temperature; Tmin, mean temperature of the coldest month; P, annual rainfall; P/T, Lang's moisture coefficient; LB.num.; lowland biome number; MB.num.; montane biome number; LB.dens.; lowland biome density; MB.dens.; montane biome density.

latitudinal band	S	average BSI Macromammalia	average BSI Primates	average BSI Carnivora	average BSI Artiodactyla	T.var.	P.var.	T (°C)	Tmin (°C)	P (mm)	P/T	area (Km2)	LB. num.	MB. num.	LB. dens.	MB. dens.
37.5 N	20	5.00	3.00	5.43	3.75	14.90	0.19	17.95	11.00	682.00	37.99	55000	1	0	0.018	0.000
36.5 N	23	4.57	3.00	5.00	3.20	15.18	0.17	17.18	10.61	584.25	34.02	122834	1	1	0.008	0.008
35.5 N	23	4.57	3.00	5.00	3.20	15.45	0.17	17.77	10.37	436.80	24.72	173459	1	2	0.006	0.012
34.5 N	27	4.19	3.00	4.53	3.00	17.34	0.17	17.01	8.76	483.25	33.22	190334	2	1	0.011	0.005
33.5 N	32	3.97	3.00	4.70	2.40	16.58	0.20	17.90	9.74	396.00	28.37	235334	2	2	0.008	0.008
32.5 N	32	4.03	3.00	4.70	2.33	16.68	0.22	20.08	10.75	247.08	12.71	319709	2	2	0.006	0.006
31.5 N	33	4.06	3.00	4.71	2.33	15.97	0.19	20.19	12.11	142.80	7.30	398459	2	0	0.005	0.000
30.5 N	35	4.03	3.00	4.55	2.33	15.38	0.22	19.00	11.13	144.60	8.07	499709	2	2	0.004	0.004
29.5 N	35	4.03	3.00	4.55	2.33	16.69	0.24	21.57	12.76	46.57	2.30	522209	2	2	0.004	0.004
28.5 N	30	3.87	3.00	4.56	1.75	15.44	0.35	21.83	13.48	34.00	1.69	539084	2	0	0.004	0.000
27.5 N	28	3.86	-	4.53	1.75	18.44	0.27	23.48	14.01	25.00	1.13	553146	1	0	0.002	0.000
26.5 N	28	3.86	-	4.53	1.75	15.50	0.23	23.83	15.60	52.00	2.29	567209	1	0	0.002	0.000
25.5 N	28	3.86	-	4.39	1.71	17.15	0.27	23.82	14.53	16.33	0.68	578459	1	0	0.002	0.000
24.5 N	28	3.86	-	4.39	1.71	16.12	0.22	25.88	17.15	18.00	0.71	589709	1	0	0.002	0.000
23.5 N	32	3.63	-	4.42	1.56	11.65	0.36	23.33	16.78	19.00	0.93	603771	1	0	0.002	0.000
22.5 N	34	3.68	-	4.43	1.56	15.80	0.22	21.45	12.60	54.00	2.52	623459	1	0	0.002	0.000
21.5 N	35	3.71	-	4.48	1.80	17.05	0.25	26.40	16.60	3.00	0.11	634709	1	0	0.002	0.000
20.5 N	35	3.83	6.00	4.48	1.91	12.17	0.34	26.10	19.57	81.33	3.01	629084	1	0	0.002	0.000
19.5 N	38	3.95	6.00	4.50	2.33	13.78	0.44	28.32	21.18	79.67	2.79	629084	1	0	0.002	0.000
18.5 N	45	3.76	4.00	4.52	2.27	13.14	0.41	27.63	19.96	101.60	3.71	637521	1	0	0.002	0.000
17.5 N	52	3.56	3.50	4.28	2.20	11.20	0.37	29.10	22.73	136.50	4.75	645959	2	1	0.003	0.002
16.5 N	57	3.67	3.50	4.37	2.20	10.92	0.41	28.34	22.24	256.60	9.12	651584	2	1	0.003	0.002
15.5 N	57	3.75	3.50	4.37	2.20	9.38	0.36	27.75	22.87	383.67	14.64	657209	3	1	0.005	0.002
14.5 N	62	3.68	3.50	4.19	2.73	8.91	0.36	27.69	23.10	573.43	20.70	679709	3	2	0.004	0.003
13.5 N	70	3.50	3.00	4.12	2.62	7.94	0.36	27.30	23.44	681.84	25.40	679709	3	3	0.004	0.004
12.5 N	76	3.38	2.56	4.12	2.57	7.92	0.33	27.64	23.96	912.67	33.12	685334	3	3	0.004	0.004
11.5 N	84	3.26	2.58	4.12	2.53	7.00	0.29	25.91	22.77	1016.44	41.13	719084	3	3	0.004	0.004
10.5 N	88	3.19	2.58	4.15	2.41	6.23	0.24	26.88	24.31	1286.93	48.89	764084	3	3	0.004	0.004
9.5 N	95	3.09	2.31	4.03	2.41	5.21	0.24	25.32	23.02	1282.94	50.98	755646	3	2	0.004	0.003
8.5 N	111	2.93	2.09	4.00	2.43	4.75	0.21	25.61	23.54	1509.10	61.32	750021	3	2	0.004	0.003
7.5 N	120	2.81	2.14	3.76	2.32	3.75	0.17	25.28	23.55	1534.73	61.63	730334	4	3	0.005	0.004
6.5 N	126	2.77	2.04	3.65	2.37	3.27	0.15	26.15	24.61	1555.13	60.07	713459	4	3	0.006	0.004
5.5 N	137	2.69	1.94	3.53	2.38	2.82	0.22	24.64	22.98	1516.55	61.51	690959	4	2	0.006	0.003
4.5 N	146	2.62	1.92	3.53	2.28	2.83	0.19	26.01	24.60	1711.75	66.25	533459	4	1	0.007	0.002

3.5	N	139	2.72	2.03	3.63	2.42	2.63	0.14	24.23	22.95	1341.00	56.48	432209	4	2	0.009	0.005
2.5	N	133	2.79	2.22	3.65	2.42	2.61	0.14	23.78	22.46	1470.11	64.80	404084	4	1	0.010	0.002
1.5	N	135	2.81	2.18	3.60	2.56	2.41	0.13	23.89	22.73	1389.29	59.07	398459	3	3	0.008	0.008
0.5	N	141	2.80	2.17	3.56	2.58	2.24	0.14	21.68	20.42	1595.00	72.13	392834	3	3	0.008	0.008
-0.5	S	140	2.79	2.14	3.53	2.61	2.24	0.09	24.16	22.74	1406.38	58.14	359084	3	3	0.008	0.008
-1.5	S	143	2.76	2.05	3.57	2.60	2.22	0.15	23.18	21.89	1377.30	59.82	347834	3	2	0.009	0.006
-2.5	S	141	2.77	2.14	3.51	2.53	2.47	0.18	23.50	22.17	1184.67	50.45	342209	3	3	0.009	0.009
-3.5	S	144	2.75	2.14	3.45	2.49	4.03	0.21	23.22	20.86	1158.22	50.00	336584	3	3	0.009	0.009
-4.5	S	132	2.86	2.16	3.57	2.64	4.25	0.17	24.48	21.93	1104.11	44.80	314084	2	1	0.006	0.003
-5.5	S	127	2.87	2.10	3.63	2.63	3.58	0.20	24.58	22.58	1387.70	57.20	308459	2	0	0.006	0.000
-6.5	S	105	3.10	2.05	3.97	2.76	4.68	0.23	24.84	22.10	988.00	39.49	297209	2	1	0.007	0.003
-7.5	S	103	3.14	2.11	3.97	2.76	2.65	0.19	24.83	23.19	1334.67	53.56	302834	2	1	0.007	0.003
-8.5	S	97	3.18	2.19	3.97	2.78	3.94	0.20	22.31	20.10	1093.43	50.27	302834	2	1	0.007	0.003
-9.5	S	91	3.24	2.33	3.97	2.77	4.54	0.22	20.38	17.59	1235.50	64.99	308459	2	1	0.006	0.003
-10.5	S	91	3.25	2.33	3.91	2.82	4.47	0.20	22.21	19.69	1148.29	52.47	308459	2	1	0.006	0.003
-11.5	S	87	3.32	2.50	3.97	2.82	6.21	0.22	24.07	18.29	1153.22	50.62	302834	2	0	0.007	0.000
-12.5	S	87	3.32	2.50	3.97	2.80	5.59	0.21	21.48	18.11	1214.25	58.43	319709	2	1	0.006	0.003
-13.5	S	87	3.32	2.57	3.91	2.80	7.13	0.24	20.60	16.43	1078.78	52.58	325334	2	1	0.006	0.003
-14.5	S	87	3.32	2.67	3.86	2.80	7.48	0.23	21.67	17.46	970.29	45.09	330959	2	1	0.006	0.003
-15.5	S	86	3.33	2.67	3.86	2.79	8.49	0.24	22.47	17.76	771.14	34.77	330959	3	1	0.009	0.003
-16.5	S	86	3.33	2.67	3.86	2.79	7.93	0.21	27.18	20.05	946.83	36.05	319709	3	0	0.009	0.000
-17.5	S	85	3.33	2.67	3.94	2.79	7.32	0.23	24.09	18.66	785.75	32.95	297209	3	0	0.010	0.000
-18.5	S	84	3.38	2.67	3.94	2.85	8.55	0.22	21.03	15.94	854.75	40.61	283146	3	1	0.011	0.004
-19.5	S	82	3.44	3.00	4.03	2.85	8.60	0.21	22.61	17.40	904.25	39.46	263459	3	1	0.011	0.004
-20.5	S	81	3.46	3.00	3.97	2.90	7.99	0.21	20.77	15.89	795.40	38.46	263459	3	0	0.011	0.000
-21.5	S	78	3.53	3.00	4.03	3.00	11.18	0.21	21.10	14.25	427.00	20.24	252209	3	0	0.012	0.000
-22.5	S	79	3.51	3.00	4.03	2.97	8.04	0.21	21.26	15.92	405.00	18.12	243771	3	1	0.012	0.004
-23.5	S	79	3.51	3.00	4.03	2.97	9.42	0.16	20.83	15.25	620.67	29.09	240959	3	0	0.012	0.000
-24.5	S	78	3.49	3.00	4.00	3.00	11.38	0.17	21.89	15.38	510.20	22.95	232521	3	0	0.013	0.000
-25.5	S	77	3.52	3.00	4.00	3.07	9.89	0.17	18.80	13.03	683.50	36.70	207209	3	1	0.014	0.005
-26.5	S	75	3.59	3.50	4.00	3.15	10.74	0.16	17.98	11.88	525.00	30.64	207209	3	0	0.014	0.000
-27.5	S	72	3.65	3.50	4.19	3.15	13.20	0.15	17.23	9.75	648.00	37.57	190334	4	0	0.021	0.000
-28.5	S	66	3.80	3.50	4.39	3.32	12.44	0.13	18.29	11.68	664.80	36.40	173459	4	1	0.023	0.006
-29.5	S	63	3.86	3.50	4.39	3.41	11.72	0.13	17.34	11.00	449.50	25.35	162209	5	1	0.031	0.006
-30.5	S	58	4.00	3.50	4.41	3.74	12.54	0.14	17.25	10.63	531.57	31.21	150959	5	0	0.033	0.000
-31.5	S	57	4.05	4.33	4.41	3.65	11.56	0.13	16.70	10.66	509.20	29.11	120021	5	0	0.042	0.000
-32.5	S	54	4.11	4.33	4.38	3.83	10.30	0.14	14.62	9.27	271.33	18.70	111584	4	1	0.036	0.009
-33.5	S	51	4.10	5.00	4.38	3.69	8.53	0.11	16.64	12.36	749.50	48.62	89084	3	0	0.034	0.000
-34.5	S	39	4.44	6.00	4.76	3.75	6.63	0.07	17.35	14.23	440.00	25.44	2250	1	0	0.444	0.000

Appendix S2 Correlations between the eleven environmental variables studied in this work. Values above the diagonal are correlation coefficients (r) while those below are significance values (p). Bold, correlations in which r is higher than 0.850; italics, non significant correlations.

	T	T.var.	Tmin	P	P.var.	P/T	Area	LB.num.	MB.num.	LB.dens.	MB.dens.
		-0.305	**0.859**	*0.175*	0.639	*-0.021*	0.808	*-0.145*	0.241	-0.283	*-0.191*
.var.	0.009		-0.734	**-0.897**	0.270	-0.843	*-0.042*	-0.444	-0.467	*-0.058*	-0.244
min	<0.001	<0.001		0.604	0.309	0.438	0.620	*0.123*	0.471	*-0.160*	*0.038*
	0.139	<0.001	<0.001		-0.415	**0.973**	*-0.003*	0.475	0.533	*-0.070*	0.327
.var.	<0.001	0.021	0.008	<0.001		-0.524	0.653	-0.411	*-0.078*	-0.309	-0.294
/T	0.857	<0.001	<0.001	<0.001	<0.001		*-0.178*	0.484	0.468	*-0.023*	0.355
rea	<0.001	0.723	<0.001	0.980	<0.001	0.131		*-0.135*	0.334	-0.336	*-0.146*
.B.num.	0.220	<0.001	0.300	<0.001	<0.001	<0.001	0.255		0.314	*-0.070*	0.203
IB.num.	0.040	<0.001	<0.001	<0.001	0.511	<0.001	0.004	0.007		*-0.153*	0.762
.B.dens.	0.015	0.623	0.176	0.554	0.008	0.848	0.004	0.555	0.197		*-0.108*
IB.dens.	0.105	0.038	0.749	0.005	0.012	0.002	0.217	0.086	<0.001	0.364	

Appendix S3 Regression coefficients for the environmental variables included in the stepwise regression models developed in this work (see Tables 3 and 4). Statistics for the stepwise and ordinary least squares regression models are showed for comparison.

Model	factor	stepwise				ordinary least squares			
		b	SE	t	sig	b	SE	t	sig
Macromammalia	T.var.	0.151	0.021	7.084	<0.001	0.151	0.025	6.097	<0.001
Africa	LB.dens.	2.221	0.447	4.965	<0.001	2.045	0.583	3.510	0.001
	Area	0.000	0.000	-4.309	<0.001	0.000	0.000	-3.501	0.001
	P.var.	1.895	0.462	4.098	<0.001	1.782	0.587	3.037	0.004
	T	-0.154	0.035	-4.450	<0.001	-0.155	0.045	-3.450	0.001
	Tmin	0.144	0.038	3.818	<0.001	0.148	0.045	3.263	0.002
Macromammalia	T.var.	0.072	0.010	6.979	<0.001	0.197	0.030	6.488	<0.001
Northern hemisphere	LB.dens.	72.440	10.783	6.718	<0.001	124.077	24.691	5.025	<0.001
	P.var.	1.848	0.429	4.304	<0.001	1.065	0.492	2.166	0.040
	MB.dens.	31.985	11.170	2.864	0.007	72.741	27.620	2.634	0.014
	LB.num.	-0.152	0.054	-2.827	0.008	-0.194	0.046	-4.204	<0.001
Macromammalia	Area	0.000	0.000	-8.027	<0.001	0.000	0.000	-2.315	0.030
Southern hemisphere	Tmin	-0.027	0.008	-3.132	0.004	-0.048	0.053	-0.919	0.367
	P.var.	2.008	0.664	3.025	0.005	1.092	0.970	1.126	0.272
Primates	P	-0.001	0.000	-8.651	<0.001	-0.006	0.001	-4.528	<0.001
Africa	LB.dens.	6.413	1.303	4.921	<0.001	6.689	1.561	4.285	<0.001
Primates	P/T	-0.030	0.005	-5.967	<0.001	0.081	0.057	1.436	0.167
Northern hemisphere									
Primates	Area	0.000	0.000	-5.050	<0.001	0.000	0.000	-2.869	0.009
Southern hemisphere	LB.dens.	3.168	0.913	3.471	0.002	2.609	1.401	1.862	0.075
	Tmin	-0.044	0.021	-2.065	0.047	-0.135	0.115	-1.176	0.251
Primates without *Macaca*	P	-0.002	0.000	-10.300	<0.001	-0.004	0.001	-2.945	0.005
Africa	LB.dens.	5.557	1.226	4.534	<0.001	5.423	1.585	3.421	0.001
Primates without *Macaca*	T.var.	0.389	0.048	8.150	<0.001	0.796	0.411	1.937	0.085
Northern hemisphere	T	-0.313	0.101	-3.097	0.006	-1.317	0.531	-2.478	0.035
Carnivora	T.var.	0.071	0.005	14.781	<0.001	0.148	0.023	6.442	<0.001
Africa	LB.dens.	1.898	0.457	4.155	<0.001	1.735	0.540	3.213	0.002
Carnivora	T.var.	0.051	0.010	5.371	<0.001	0.197	0.068	2.925	0.007
Northern hemisphere	LB.dens.	54.711	9.873	5.542	<0.001	103.250	26.792	3.854	0.001
	P.var.	1.163	0.378	3.075	0.004	1.068	0.534	2.001	0.056
	LB.num.	-0.179	0.054	-3.314	0.002	-0.199	0.050	-3.978	<0.001
	MB.num.	0.070	0.032	2.168	0.038	-0.086	0.070	-1.237	0.227
Carnivora	Area	0.000	0.000	-11.690	<0.001	0.000	0.000	-2.056	0.051
Southern hemisphere	P.var.	1.830	0.620	2.950	0.006	1.271	0.986	1.289	0.210
Artiodactyla	Area	0.000	0.000	-10.160	<0.001	0.000	0.000	-6.834	<0.001
Africa	LB.num.	0.200	0.033	5.980	<0.001	0.189	0.036	5.190	<0.001
	LB.dens.	2.745	0.680	4.035	<0.001	1.980	0.760	2.604	0.012
	P.var.	2.419	0.659	3.671	<0.001	2.349	0.766	3.067	0.003
	P/T	0.011	0.003	3.044	0.003	0.008	0.013	0.586	0.560
	T.var.	0.028	0.013	2.113	0.038	0.076	0.032	2.348	0.022
Artiodactyla	LB.dens.	113.436	14.535	7.805	<0.001	128.971	39.597	3.257	0.003
Northern hemisphere	MB.dens.	71.776	14.958	4.799	<0.001	69.356	44.296	1.566	0.129
	P.var.	1.972	0.576	3.423	0.002	1.705	0.789	2.162	0.040
Artiodactyla	Area	0.000	0.000	-9.434	<0.001	0.000	0.000	-2.897	0.008
Southern hemisphere	Tmin	-0.022	0.007	-3.056	0.005	-0.012	0.047	-0.263	0.795

Appendix S4 Correlograms for raw average biomic specialization data (black squares) and for residuals after fitting the environmental variables included in the stepwise regression models developed in this work (white circles) (see Tables 3 and 4). Although extreme values of autocorrelation in the raw data have been usually detected for the largest distance class, Moran's I (vertical axis) has been scaled from 1 to -1 for clarity. There is no data on the two largest distance classes for Primates without *Macaca* in the northern hemisphere because there are no species north of the southern limit of the Sahara desert. Significance levels of the correlograms after a Bonferroni correction are shown for both, raw data (regular) and residuals (cursive).