



HISTORICAL DETERMINANTS OF MAMMAL DIVERSITY IN AFRICA: EVOLUTION OF MAMMALIAN BODY MASS DISTRIBUTION IN AFRICA AND SOUTH AMERICA DURING NEOGENE AND QUATERNARY TIMES

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Abstract: Local mammalian communities in Africa present the highest species richness in the world, only paralleled by some communities in the Oriental biogeographic region. Differences in mammalian species richness are especially outstanding when compared with South American communities, despite their similar latitudinal position and regional species richness. Recent study has shown that these differences are not only related to contemporary determinants but also to biogeographic-historic factors, which acted on the composition of the regional pool of species. One of the main differences in composition between the two regions relates to the high diversification of large mammals in Africa, which greatly contributes to the high values of local community richness in this region. The absence of extant large mammals in the South American region has been proposed to result from Pleistocene-Holocene extinctions, which affected large mammals all over the world. However, a gradual pattern of decrease in the abundance of large mammal species can be appreciated in almost all regions except Africa since the late Miocene and through the Pliocene. To test these hypotheses we compare the patterns of macromammal body mass distribution - at regional and local scales - in the two regions over the past 20 million years and relate the observed changes to major geological events.

Key words: Mammals; communities; species richness; body mass; Neogene; Quaternary; Africa; South America

1. INTRODUCTION

Most of the richest mammal communities in the world are found in Africa south of the Sahara desert. Moreover, on average African mammal communities are richer than those of any other biogeographic region (*sensu* Cox, 2001) except the Oriental one (see Fig. 1). Such differences in species richness are especially striking when African communities are compared to South American ones, despite their similar area, latitudinal position, landscapes (see Vivo and Carmignotto, 2004 and references therein) or richness of their regional pool (Africa: 861 species; South America: 777; data from Nowak, 1999). These differences have been related to differences in the abundance of medium and large mammal species (see Cristoffer and Peres, 2003; Vivo and Carmignotto, 2004), that is, to differences in the composition of their regional pools. While Africa has an abundant fauna of large mammals, such species are almost absent from South America. Several hypotheses based on historical processes have been proposed to explain these differences. Most of them establish that the differences are due to the disappearance of the large mammals in South America either during the Great American Biotic Interchange, the megafaunal extinctions of the Pleistocene, or even as late as the middle Holocene. Other authors have reported that a pattern of decrease in the abundance of large mammal species since the late Miocene can be observed throughout all continents except Africa, making this continent a refuge of high large mammal diversity and posing the question of what makes Africa so special.

In the present contribution we will compare the evolution of mammal sizes in Africa and South America during the last 20 million years. Our aim is to describe the pattern of change in body size in the mammal faunas in the two continents and to find out if the available data support any of the previous hypotheses. Before analyzing the fossil data, we test the premises about the recent faunas on which they are based on. That is, we test whether differences in the abundance of large mammals are responsible for the differences in local richness between continents, and particularly between Africa and South America. We also test whether these differences are related to historical causes or if they can be explained by ecological, contemporary causes such as climate, productivity or others. Both analyses of recent fauna are preliminary since our intention is simply to confirm that these conditions are met and that the fossil record can help to understand the recent patterns of species richness distribution. Concerning the fossil record, we first compare the size distribution of the regional pools of South America and

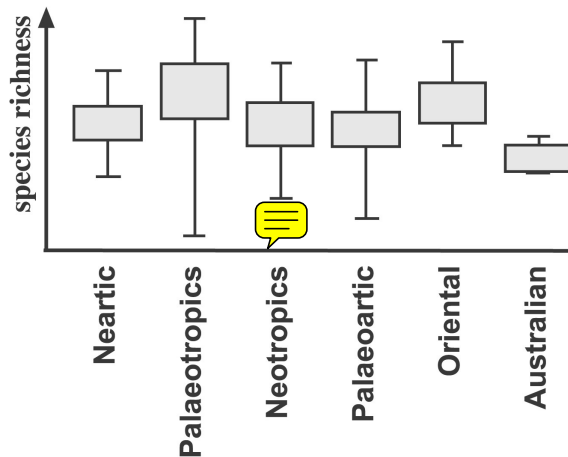


Figure 1. Box & Whisker plot of the local mammal richness (number of species) in the different biogeographic regions. Total number of localities=236; Palaeotropics=26; Neotropics=27; Oriental=10; Australian=8; Nearctic=92; Palaeoartic=73. Locality data obtained from the bibliography.

Africa to determine their similarities and differences and the period when today's differences were established. We finally explore how variations in the regional pool of the different body sizes affect the species richness of local faunas in Africa.

2. MATERIALS AND METHODS

Recent data were compiled from the bibliography and existing databases. Lists of species for the different localities were obtained from the bibliography following criteria specified in Rodríguez (2001). Body mass data for recent species were obtained mainly from Nowak (1999) and to a lesser degree from other bibliographic sources. Fossil data was reduced to two subregions, East Africa in Africa and South America south of the Equator, where enough information and detailed reviews were available. Data on the generic diversity in East Africa is taken from Pickford and Morales (1994) and in Southern South America from Pascual et al. (1996). There are marked differences in the time intervals as well as in the taxonomy and sampling units used in both continents, however we feel that they will not substantially affect the obtained patterns of change though it would clearly affect absolute numbers. Body mass data comes from the bibliography and anatomical comparisons. Only macromammal species, i.e. over 1 kg, were considered. Body masses were assigned to the following

categories modified from Andrews et al. (1979): C=1-10 kg; D=11-45 kg; E=46-90 kg; F=91-180 kg; G=181-360 kg; H=361-1000 kg; and I>1000 kg (A and B correspond to masses <1 kg). Each genus was assigned to one or several categories according to the body masses of its species. Data from individual African localities were obtained from faunal lists of localities in Pickford (1986) and other bibliographic sources.

Today's differences in local species richness of large and small mammals between continents were assessed by means of ANOVA tests. Analyses were replicated for species ≥ 45 kg and < 45 kg using as the dependent variable \log_{10} of local richness of species below and over 45 kg; as factor, the biogeographic region; and locality area as a covariate. The Tuckey honest test was used as a post-hoc test to look for significant differences between continents.

The analyses of the effects of contemporary-ecologic factors and biogeographic-historic factors on local species richness of large and small mammals were performed by means of partial regressions using GLM (see Legendre and Legendre, 1998). Mammal data comes from checklists of 86 localities (36 from Africa and 50 from South America; see Rodríguez, 2001). Environment was measured as the 6 axis extracted from monthly values of Cloudiness, Precipitation and Temperature ($12 \times 3 = 36$ variables; Leemans and Cramer, 1991), and annual ETP (Deichman and Eklundh, 1991; GIS database from <http://www.grid.unep.ch/data/grid/>). Analyses were performed for local species richness of mammals over and under 45 kg and for all mammal species in the communities.

Patterns of body mass distribution during the last 20 Ma were estimated from the body mass of all genera present in each of the considered times periods in South America and Africa. For genera with body masses in more than one category, the value for each category was calculated as the correspondent fraction (i.e. if three categories are present in a genus, each category is assigned a value of 0.33 for that genus). Genus values for each category in a time period are added and the obtained value is used as a proxy of the richness of that category during that time lapse. Body mass values for the different categories are plotted against time. Millions of years in Africa and local biochronologic units (SALMAs) in South America (according to Pascual et al., 1996) were used as time units.

Kendall's Tau was used to analyze the correlation between regional pool and local richness of the different body mass categories in Africa. Regional richness was estimated at the generic level, while local richness was measured at the species level to maximize the information of each locality.

Table 1. Tukey HSD test (post-hoc test) for species both over and under (<) 45 kg. PAR: Palaeoartica; OR: Oriental; NTR: Neotropics; NAR: Neartica; AUS: Australian; PTR: Palaeotropics. Significant differences between regions in bold type ($p < 0.05$). Dependent variable: Log_{10} of local richness of species below and over 45 kg. Factor: biogeographic region. Locality area included as a covariate

		Species \geq 45 kg				
	PAR	OR	NTR	NAR	AUS	
PAR						
OR	.231					
NTR	.108	.001				
NAR	.688	.671	.004			
AUS	.088	.004	.415	.037		
PTR	.000	.187	.000	.000	.000	

		Species < 45 kg				
	PAR	OR	NTR	NAR	AUS	
PAR						
OR	.655					
NTR	.997	.842				
NAR	.999	.606	.991			
AUS	.686	.113	.535	.719		
PTR	.003	.862	.015	.002	.011	

3. RESULTS

ANOVA analyses verify that large mammal richness plays a relevant role in the differences in local richness between continents ($F=20.54$; $p < 0.001$). ANOVA analysis also detects significant differences for the species under 45 kg ($F=6.542$; $p < 0.001$). However, differences between paleotropical and neotropical regions are highly significant for richness of species over 45 kg (Tukey test, $p < 0.001$) while only marginally significant for sizes under this body mass ($p=0.015$; see Table 1).

Concerning the factors affecting species richness, variation partitioning analysis shows the important role of biogeographic factors related to the history and topography of each region in determining local richness of large mammals (Fig. 2). While the effect of Environment was higher when considering all mammal species or those under 45 kg, the effect of Region (Paleotropical vs Neotropical), as well as the region-mediated environmental influence, were prominent for species over 45 kg. In fact, the results confirm that biogeographic factors including history can be considered more relevant than environment in determining the differences in local richness of large mammal species in South America and Africa.

The evolution of the body mass composition in the regional pool in South America and Africa are presented in Figure 3. Both continents reveal an

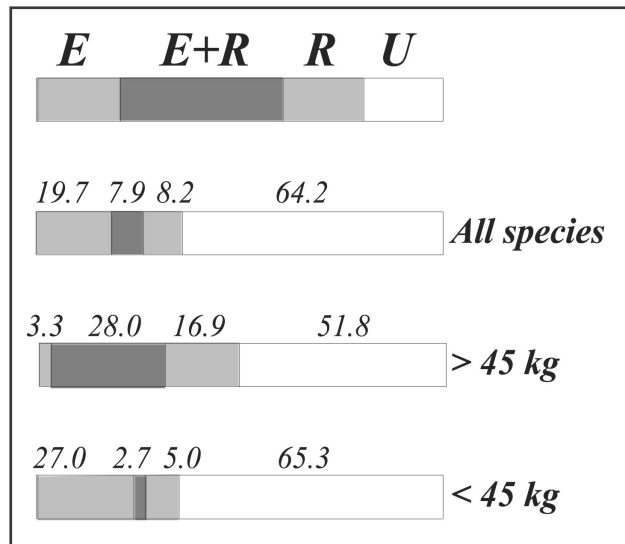


Figure 2. Bars represent the separate influence over local species richness of Environment (E), Region (R), their joint effects (E+R), and the unexplained variation (U). While the effect of Environment was higher when considering either all mammal species, or only those below 45 kg, the effect of Region (Paleotropical vs Neotropical), as well as the region-mediated environmental influence, were much higher when only species of equal or more than 45 kg were considered.

increase of large mammal species richness until ca 7 Ma. Later, South America suffered a dramatic reduction of richness during the late Miocene and Pliocene and, after a partial recovery, almost all genera over 200 kg became extinct during the Pleistocene extinctions. Meanwhile, Africa suffered a decrease in proboscidean abundance, compensated by an increase in genera between 90 and 1000 kg. Thus, present regional differences in body mass composition may be linked to the Pleistocene megafaunal extinction suffered by South America, but also to a long-term increase of large mammals in Africa (between 90 to 1000 kg).

Lastly, Kendall's Tau analysis of the relationship between regional pool and local richness in the different body mass categories in Africa shows that local richness of mammals under 100 kg (categories C, D and E; see Table 2) is not correlated with their regional pool, while mammals over 100 kg (categories F, G, and I) do present a significant correlation between richness at both scales.

Category H does not show correlation, probably due to scarcity of taxa in the African record. Similar results have been obtained analyzing recent faunas (data not shown) pointing out that changes in the regional pool of

Table 2. Kendall's Tau analyses of the correlation between regional pool and local richness in Africa. Data on regional richness of genera from Pickford & Morales (1994); local richness of species taken from faunal lists of localities in Pickford (1986) and other bibliographic sources. Cat.=body mass category; N=number of comparisons. Significant correlations marked in bold type ($p < 0,01$)

Cat.	N	Kendall's Tau	Z	p-level
C	20	0,00559	0,0345	0,973
D	20	-0,24809	-1,5294	0,126
E	20	0,34464	2,1245	0,034
F	20	0,47363	2,9196	0,004
G	20	0,49373	3,0436	0,002
H	20	-0,22636	-1,3954	0,163
I	20	0,49303	3,0392	0,002

large mammals have major effects on local richness while these effects are more restricted when they affect medium and small sized taxa.

4. DISCUSSION AND CONCLUSIONS

In agreement with previous authors (see Vivo and Carmignotto, 2004 and references therein), we have shown that biogeographic differences in the regional pool of large species of Africa and South America may underlie the higher richness of African mammal communities. Our results also agree with previous authors (see *op. cit.*) in the leading role of historical factors in determining the differences in large species abundance. In this sense, we have shown that while the abundance of "small" mammals (below 45 kg) in a community depend on environmental factors, the richness of "large" species mainly depends on biogeographical factors.

Concerning the fossil record of the body mass distribution from Africa and South America, our results do not allow us to fully accept or deny any of the hypotheses proposed. Trends of diversification and extinction are apparent since the late Miocene in both continents, although the Pliocene climatic-environmental changes due to the Andean Diaguaita diastrophic phase and Pleistocene extinctions meant major events in South America. However, the main differences can be observed in the generic richness of the body mass categories. That is, while Pliocene and mainly Pleistocene extinctions caused the disappearance of all mammals over 200 kg in South America, it was restricted to mammals over 1000 kg in Africa and was coupled with an increase in the richness of the rest of the large mammals. The effects of these regional differences on local richness depend on the body mass category affected (at least in Africa; see Fig. 3). Local richness of large species (species over 100 kg) is correlated to regional

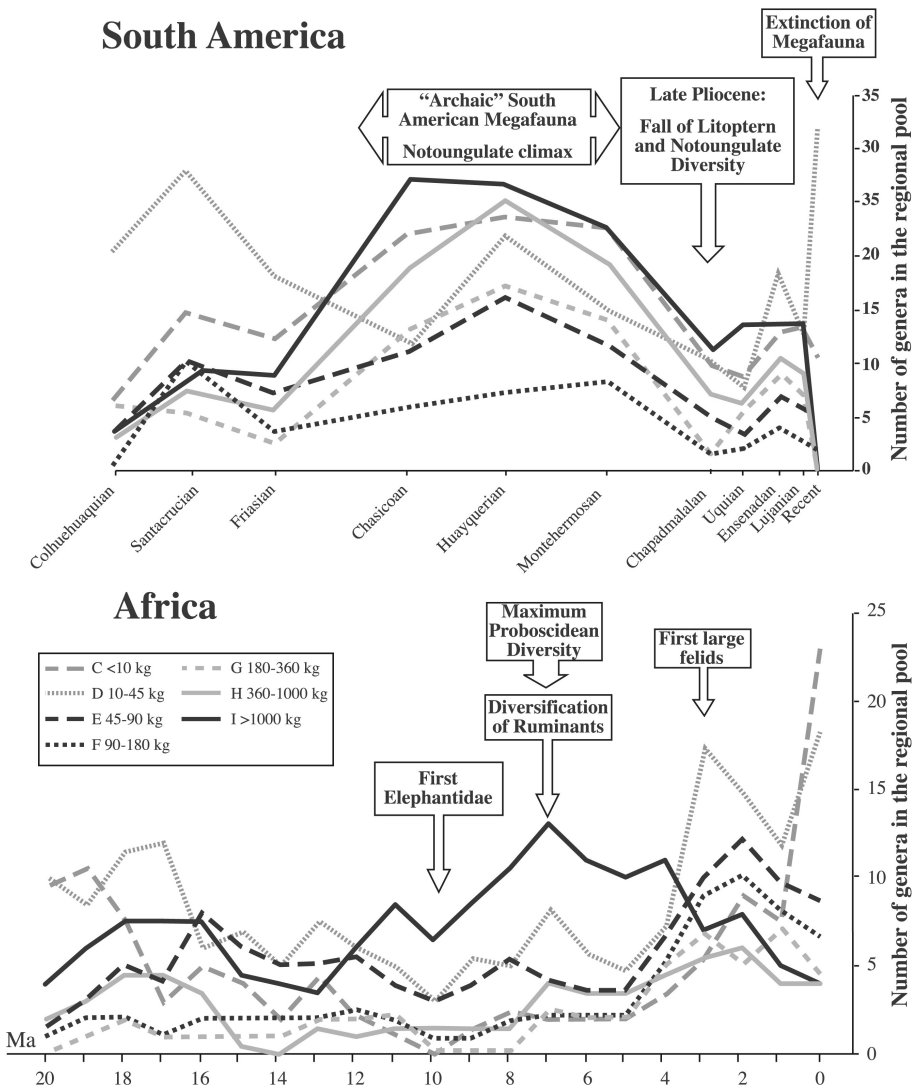


Figure 3. Numbers of genera in the considered body mass categories in East Africa and Southern South America during the last 20 million years. Time units: millions of years in Africa and local biostratigraphic units (SALMAs) in South America (dating of the different SALMAs according to Pascual et al., 1996). Codes for body mass categories detailed in the graph.

richness, while the local richness of small mammals seems to be independent of the regional pool. Thus, processes affecting the regional pool of large species have a deep effect on local communities through time.

In summary, our results show that African high local richness is related to a restricted megafaunal extinction (only species over 1000 kg) and to a unique history of diversification of large mammals (between 200-1000 kg).

The effects of these processes are specially relevant due to strong correlation between Local and Regional Richness in species over 100 kg.

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REFERENCES

- Andrews, P., Lord, J. M., and Evans, E. M. N., 1979, Patterns of ecological diversity in fossil and modern mammalian faunas, *Biol. J. Linn. Soc.* **11**:177-205.
- Cox, C. B., 2001, The biogeographic regions reconsidered, *J. Biogeogr.* **26**:511-523.
- Cristoffer, C., and C. A. Peres., 2003, Elephants vs. Butterflies: the ecological role of large herbivores in the evolutionary history of two tropical worlds, *J. Biogeogr.* **30**:1357-1380.
- Deichmann, U., and Eklundh, L., 1991, *Global Digital Data Sets for Land Degradation Studies: a GIS Approach*, UNEP/GEMS and GRID, Nairobi, Kenya.
- Leemans, R., and Cramer, W. P., 1991, *The IIASA Database for Mean Monthly Values of Temperature, Precipitation and Cloudiness of a Global Terrestrial Grid*, IIASA, Laxenburg, Austria.
- Legendre, P., and Legendre, L., 1998, *Numerical Ecology*, 2nd English ed., Elsevier, Amsterdam.
- Nowak, R. M., 1999, *Walker's Mammals of the World*, Johns Hopkins Univ. Princeton, USA.
- Pascual, R., Ortiz-Jaureguizar, E., and Prado, J. L., 1996, Land Mammals: Paradigm for Cenozoic South American Geobiotic Evolution, *Münch. Geowiss Abh.* **30**:265-319.
- Pickford, M., 1986, Cainozoic palaeontological sites of western Kenya, *Münch. Geowiss Abh.* **8**:1-151.
- Pickford, M., and Morales, J., 1994, Biostratigraphy and palaeobiology of East Africa and the Iberian Peninsula, *Palaeogeogr. Palaeoclimat. Palaeoecol.* **112**:297-322.
- Rodríguez, J., 2001, Structure de la communauté de mammifères pléistocènes de Gran Dolina (Sierra de Atapuerca, Burgos, Espagne), *L'Anthropologie* **105**:131-157.
- Vivo, M., and Carmignotto, A. P., 2004, Holocene vegetation change and the mammal faunas of South America and Africa, *J. Biogeogr.* **31**:943-957.

Editors Note: In Figure 1 – Nearctic and Palaearctic are misspelled