Evolutionary Ecology (2005) 19:199–219
DOI: 10.1007/s10682-004-8152-7

Research article

Macroevolutionary processes and biomic specialization: testing the resource-use hypothesis

MANUEL HERNÁNDEZ FERNÁNDEZ[1,2,3,*] and ELISABETH S. VRBA[1]

[1]*Department of Geology and Geophysics, Kline Geology Laboratory, Yale University, P.O. Box 208109, New Haven, CT 06520-8109, USA;* [2]*Departamento de Paleobiología, Museo Nacional de Ciencias Naturales, Consejo Superior de Investigaciones Científicas, C/ José Gutiérrez Abascal 2, 28006, Madrid;* [3]*Departamento de Paleontología, Facultad de Ciencias Geológicas, Universidad Complutense de Madrid, Ciudad Universitaria, 28040, Madrid, Spain*
*(*author for correspondence, fax: +34-91-5644740; e-mail: hdezfdez@geo.ucm.es)*

Received 3 June 2004; Accepted 21 December 2004

Co-ordinating editor: N. Chr. Stenseth

Abstract. The resource-use hypothesis predicts that generalist species have lower speciation and extinction rates than specialists. In this work we test several subsidiary predictions of the resource-use hypothesis using the biomic specialization index (BSI) for each African large mammal species, which is based on its geographical range within different climate zones. This index can be used globally allowing intercontinental and intertaxa comparisons. Our results are consistent with the axioms of the resource-use hypothesis theory, which predicts (1) a high frequency of stenobiomic species, (2) carnivores are more eurybiomic than herbivore clades (particularly, Artiodactyla and Primates), (3) the higher incidence of these biomic specialists in the tropical rainforest and desert biomes, and (4) the fact that certain combinations of inhabited biomes occur more frequently among species than do others. We also found that the tropical deciduous woodland is an important source of new species, and that there is a macroevolutionary segregation between extreme eurybiomic species (inhabitants of five or more biomes) and 'semi-eurybiomic' species (inhabitants of 2–5 biomes). These results can also be explained within the premises of the resource-use hypothesis. Finally, we discuss the relevance of our results to the understanding of the latitudinal gradient in species richness.

Key words: Africa, bioclimatology, ecological specialization, macroecology, macroevolution, Mammalia, speciation

Introduction

The role of the degree of resource specialization has long featured in macroevolutionary hypotheses on why clades differ in speciation (S) and extinction (E) rates. Workers on different organismal groups have shown evidence that lineages of specialists are more speciose than lineages of generalists, and proposed hypotheses that imply such a prediction (Stebbins, 1950, on plants; Simpson, 1953, on mammals; Rensch, 1959; Eldredge, 1979; Eldredge and Cracraft, 1980; Vrba, 1980a, 1987, 1992). However these hypotheses differ in the processes they invoke. For instance, Eldredge and Cracraft (1980) followed earlier writings in arguing for biotic interactions as primary causes of differing species richness among clades. In their view S may be similar in generalist and specialist lineages, but the overlapping resource bases of incipient or new generalist species results in a greater incidence of competitive exclusion to extinction, and thus in a less speciose record. This is a view ‘through the glasses of extinction’ of differential species richness.

In contrast Vrba’s resource-use hypothesis (Vrba, 1980a, 1987) stressed the selection pressures associated with physical environmental changes as the direct promoters of vicariance (fragmentation of species’ geographic distributions) and therefore of speciation: generalists are less susceptible to withdrawal of their resources, to strong directional selection and to vicariance as environments change. Thus generalist species have lower S and E. Specialists are converse in all these respects. This hypothesis further differs from others in that it singles out a particular kind of specialist–generalist contrast as the most important to species turnover rates: that between biome specialists and generalists, or stenobiomic and eurybiomic species (Vrba, 1987). Terrestrial biomes are characterized by gross vegetational physiognomy. Thus a stenobiomic species is restricted to a particular biome, or narrow range of vegetation physiognomy, and its lineage is predicted to have high S in the face of recurrent environmental change, while a eurybiomic species can use resources in more than one biome with predicted lower S. Under this hypothesis the set of species-specific adaptations produced by speciation events in a clade is essentially random with respect to the direction of evolutionary trends, and with respect to the eurytopic-stenotopic spectrum. But because the more stenobiomic subset of species tend to speciate at a faster rate than other species (Vrba, 1980a), over long time period, there will be an average bias towards greater representation of biomic specialist species in clades and ecosystems (Vrba, 1987, 1989).

Vrba (1987) tested several evolutionary hypotheses related to the gradient in specialization. Her results supported the resource-use hypothesis, which has been included as a major part of a larger macroevolutionary theory, the habitat-theory (Vrba, 1992, 1995). Vrba used the abundant information on the fossil record of some African clades of large mammals to test the resource-use hypothesis. But information on the fossil record of other continents or biological groups is far from complete. In this paper, using the complete fauna of African large mammals, we test several additional predictions of the resource-use hypothesis that are based in the ecology of the extant species, and, therefore, information on the fossil record is not needed. These predictions include the following:

(1) Since clades of biomic specialist species generally have had a high incidence of vicariance, speciation and extinction, biomic specialist species should be clearly more numerous than eurybiomic species.

(2) When studied separately, some mammalian clades should be more generalist than other groups because the resources they need to survive may be found in environments which differ vastly in climate. For example, while carnivores are not species-specific feeders, most herbivores are adapted to particular vegetation types, and even particular plant species (Vrba, 1980a, b). So, in broad overview, we would expect carnivores as a whole to be displaced more towards the eurytopic extreme of the eurybiomic–stenobiomic sliding scale than herbivores
(3) Biomes that underwent a high degree of fragmentation during the recurrent environmental extremes of the astronomical cycles (also called Milankovitch cycles) should have a higher proportion of stenobiomic species than those that have not undergone extensive fragmentation. In the present context the biomes corresponding to the extremes of the climatic cycles are the tropical rainforest and the desert (Adams *et al.*, 1990; Prentice *et al.*, 1993).
(4) From the previous predictions, it should be expected that certain combinations of inhabited biomes occur more frequently among species than do others. These combinations must be those that include few biomes.

Testing these predictions 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 and Foley, 1999; Harcourt, 2000). However, rare taxa, precisely because they are rare, are likely to be less studied with respect to such measures than are common taxa. This results in less knowledge about species variation in behavior and ecology in these rare taxa (Cotgreave and Pagel, 1997). If this is the case, information of this kind on rare taxa could be strongly biased (Doherty and Harcourt, 2004). Also, some of these measures are difficult to apply to continent-wide, intercontinental and global comparisons as well as to highly dissimilar taxa. Therefore, one needs to use ecological categories of specialization that are sufficiently general to address these problems. In this paper, we single out biomic specialization as of especial relevance (following Vrba, 1987) and propose a new measure of biomic specialization (or adaptability) that can be used at global scale and with disparate taxa (following Hernández Fernández, 2001).

Materials and 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 (Primates, Carnivora, Proboscidea, Perissodactyla, Hyracoidea, Tubulidentata, Artiodactyla and Pholidota). 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 and Reeder (1993).

Information on the African geographic distributions of mammal species was obtained from Dorst and Dandelot (1969), Kingdon (1971–1982), Skinner and Smithers (1990), Wilson and Reeder (1992) and Kingdon (1997). We have also used Corbet (1978), Hall (1981) and Corbet and Hill (1992) for species with geographical ranges that extend beyond 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 and Salanon, 1973; Lieth, 1975; Strahler and Strahler, 1987), termed zonobiomes by Walter (1970). In this paper, we effectively use the terms biome and zonobiome synonymously, and we recognize that there is a one-to-one correspondence between these and the climate zones (Table 1). Climatic zones I–V exist in Africa today.

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 climate zone only. For instance, in the present case, the Zaire basin is a climatic dominion of the equatorial climate zone and it is geographically separated from the Ivory Coast, the other African climatic dominion of the equatorial climate zone. The only exception to the geographic separation between climatic dominions within a climatic zone occurs in the climate zone II. Although the Sudano-Guinean woodlands and Angolo-Zambezian woodlands have overlapping boundaries, we treat them as different climatic dominions since the overlap zone is very narrow. A map of the present African climate dominions is presented in Figure 1.

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

Table 1. Climatic typology used in this paper and its correspondence with world vegetation types

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

Modified from Walter (1970); Walter considers II/III as a zonoecotone between tropical forests and deserts, but we consider it as a zonobiome.

Table 2. African climatic dominions

Abbr.	Name	Climate zone
I (W)	Ivory Coast rainforest	I
I (Ce)	Zaire Basin rainforest	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

Based in map by Allué Andrade (1990); see Figure 1.

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 climate zones (biomes) inhabited by it. Thus BSI equals 1 for most specialized species whereas for generalist species it could be as high as 10. The decision on the number of climate zones inhabited by a species was based on the following. If 15% or more of the geographical range of a species is situated within a climate zone, the species was recorded as present in that climate zone. Since 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 climate zone if it inhabits 50% or more of one climatic dominion (Hernández Fernández, 2001).

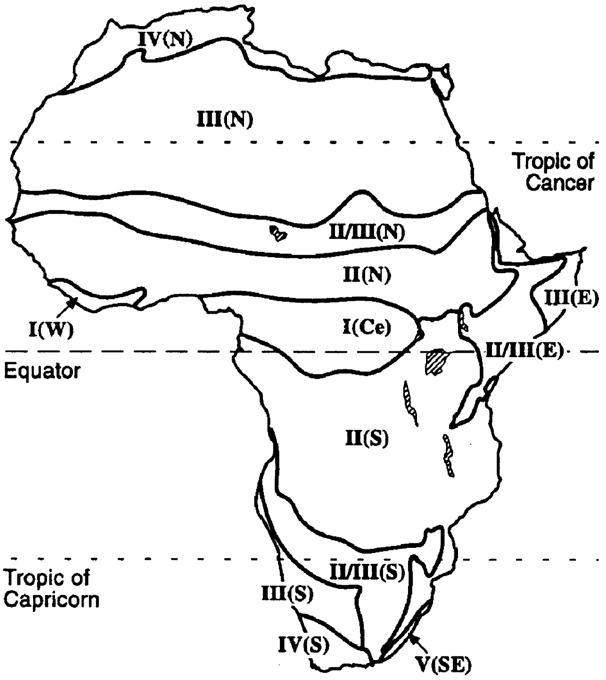

Figure 1. Map of African climatic dominions. Abbreviations as in Table 2.

The presence in a mountain vegetation belt was also recorded as presence in the corresponding analogous climate zone.

We define biomic specialists, or stenobiomic species, as those with a BSI = 1. Thus generalist species are those with a BSI > 1. This category may be subdivided in two groups. We will use the term 'semi-eurybiomic species' for those species with 1 < BSI < 5. Extreme eurybiomic species are those with BSI ≥ 5. We have chosen BSI = 5 as the limit between semi-eurybiomic and extreme eurybiomic species because those species that are able to inhabit five or more different biomes must confront very different environmental conditions both in terms of temperature (e.g., from tropical rainforest to temperate evergreen forest) and rainfall (e.g., from rainforest to desert). This classification, in principle, also applies beyond Africa, namely in temperate regions.

Analyses

Monte Carlo

Our data-set forms the entire population of interest (all the African large mammal species). Therefore, randomization is a suitable statistical method to test the hypothesis that a non-random process has generated significantly more biomic specialist species than eurybiomic species. So, this prediction of the resource-use hypothesis was tested using Monte Carlo simulations. We set up a null hypothesis, which assumes that the observed presences/absences of each species are randomly placed among biomes. Thus, our null hypothesis states that any difference between the proportions of African species with different values of BSI could have been obtained purely due to chance. Nevertheless, biogeographical and ecological features (e.g. biome size, climatic conditions, habitat heterogeneity, biological interactions, etc. ...) have an effect on species richness and are specific for each climate zone. Thus, there is no reason to believe that all the biomes must have the same number of species. Therefore, the hypothesis that all species are equally likely to occur on any biome is almost certainly false, and is not a useful null hypothesis. For this reason, we conduct a simulation procedure that places species in biomes randomly with the constraint of preserving the observed species richness in each biome. Then samples of BSI incidence are obtained, as when the actual data are examined. The randomization process is repeated 1,000 times to obtain null distributions of the frequency estimates for the percentage of species at each BSI from the total number of species. The probability (*p*-value) that a BSI value could obtain by chance a percentage greater than the observed is obtained from the proportion of null values that are greater than the observed percentage; alternatively, the fraction of null values less than the observed is the probability of obtaining a percentage of species less than the observed value (Gotelli and Graves, 1996; Manly, 1997).

To test whether tropical rainforest and desert biomes have a higher proportion of biomic specialist species than the rest of the African biomes we employ the Monte Carlo simulations performed for the previous test. In this case, the null hypothesis is that any differences between the proportions of African stenobiomic species ($BSI = 1$) in each biome could have been resulted by chance. The null distribution of the frequency estimates resulted from 1,000 random samples of proportions of biomic specialist species in each biome. The *p*-values are calculated as in the previous test.

Climatic combinations

We studied the different combinations of biomes that are today inhabited by the African large mammals and recorded which of these combinations include higher or lower numbers of species. The potential total number of climatic combinations (PTCC) that could be expected in the present world with 10 climate zones can be calculated with the formula:

$$\begin{aligned}\mathrm{PTCC} = {}& {}_{10}C_{10} + {}_{10}C_{9} + {}_{10}C_{8} + {}_{10}C_{7} + {}_{10}C_{6} + {}_{10}C_{5} + {}_{10}C_{4} + {}_{10}C_{3} \\ & + {}_{10}C_{2} + {}_{10}C_{1}\end{aligned}$$

$$\mathrm{PTCC} = 1 + 10 + 45 + 120 + 210 + 252 + 210 + 120 + 45 + 10 = 1023$$

If we deleted the combinations that include only the four climate zones without extensive (non-mountainous) climatic dominions in Africa (VI–IX) then we obtain a potential African number of climatic combinations (PACC):

$$\text{PACC} = \text{PTCC} - ({}_4C_4 + {}_4C_3 + {}_4C_2 + {}_4C_1)$$

$$\text{PACC} = 1023 - (1 + 4 + 6 + 4) = 1008$$

Since, the difference between PTCC and PACC is so small and the montane biomes are also included in the bioclimatic characterization of the species, we used PTCC in the subsequent analyses.

Results and discussion

Distribution of the biomic specialization index (BSI) in Africa

The frequency distribution of BSI is strongly right-skewed (Fig. 2). Mean BSI is 2.4. Approximately 70% of the large mammalian species in Africa inhabit only one or two biomes. At the other extreme, only a little more than 5% of the species inhabits five or more biomes. The most eurybiomic species is the ratel

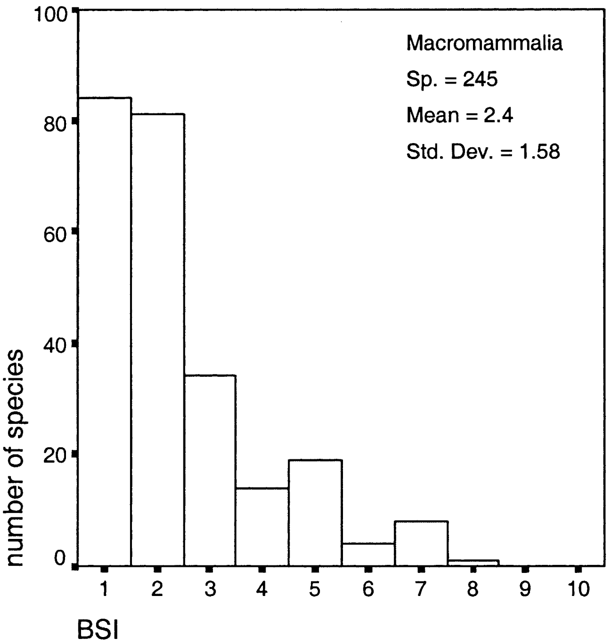

Figure 2. Frequency distribution of biomic specialization index (BSI) for African large mammals. See text for the method used to measure BSI.

(*Mellivora capensis*), which inhabits eight climate zones due to its ecological versatility that results in its presence in southern Asia, most of Africa and all the vegetation belts of its tropical mountains (Kingdon, 1997). Thus, most African large mammalian species live in a narrow range of ecological conditions, here represented by biomes. Only a few species inhabit more than five biomes, and none is generalist enough to occupy all biomes. This is in agreement with Pagel *et al.*'s (1991) results for North American mammals. Perhaps the degree of specialization required to be able to survive at biomic extremes prevents occupation of all biomes.

Table 3 and Figure 3 show the results of the Monte Carlo simulation. There is a significantly higher proportion of biomic specialist species (BSI $= 1$) in the African assemblage of large mammals than expected by chance. The proportion of species with BSI $= 2$ is not different from that expected from the modeled random distribution of species in biomes. Nevertheless, the proportion of other semi-eurybiomic species is significantly lower than estimated by the Monte Carlo model. The proportions of extreme-eurybiomic species (BSI $= 5$–8; there are no African mammals with BSI $= 9$–10) are significantly (or nearly significantly for BSI $= 6$) higher than expected from the null hypothesis.

These results are broadly consistent with the resource use hypothesis. Nevertheless, an unexpected result of our analysis is the fact that the proportions of extreme eurybiomic species are higher than expected by a random model. Two possibilities may apply. First, the resource-use hypothesis predictions may be relevant to an 'equilibrium' situation; the modern situation may have been moved away from equilibrium by recent extinction events. The last important extinction event in the African continent was, however, around 1.0–0.5 million

Table 3. Proportion of African large mammal species in each BSI (%; total number of species = 245), and comparison with the Monte Carlo simulations (N = 1,000)

BSI	Africa %	Monte Carlo analysis			
		Mean%	Std. dev.	Range	*p*
1	34.29	19.91	2.11	13.22–27.50	< 0.001
2	33.06	33.02	3.02	23.01–42.55	0.489
3	13.88	28.33	2.90	18.97–36.68	*< 0.001*
4	5.71	13.93	2.05	7.46–21.59	*< 0.001*
5	7.76	4.06	1.18	1.28–7.79	0.001
6	1.63	0.69	0.54	0.00–3.04	0.080
7	3.27	0.06	0.16	0.00–0.86	< 0.001
8	0.41	0.00	0.03	0.00–0.44	0.004
9	0.0	0.0	0.0	0.0–0.0	1.000
10	0.0	0.0	0.0	0.0–0.0	1.000

p, probability of the proportion of species being greater than or equal to (plain) or lower than or equal to (italics) the observed proportion in the African large mammal fauna.

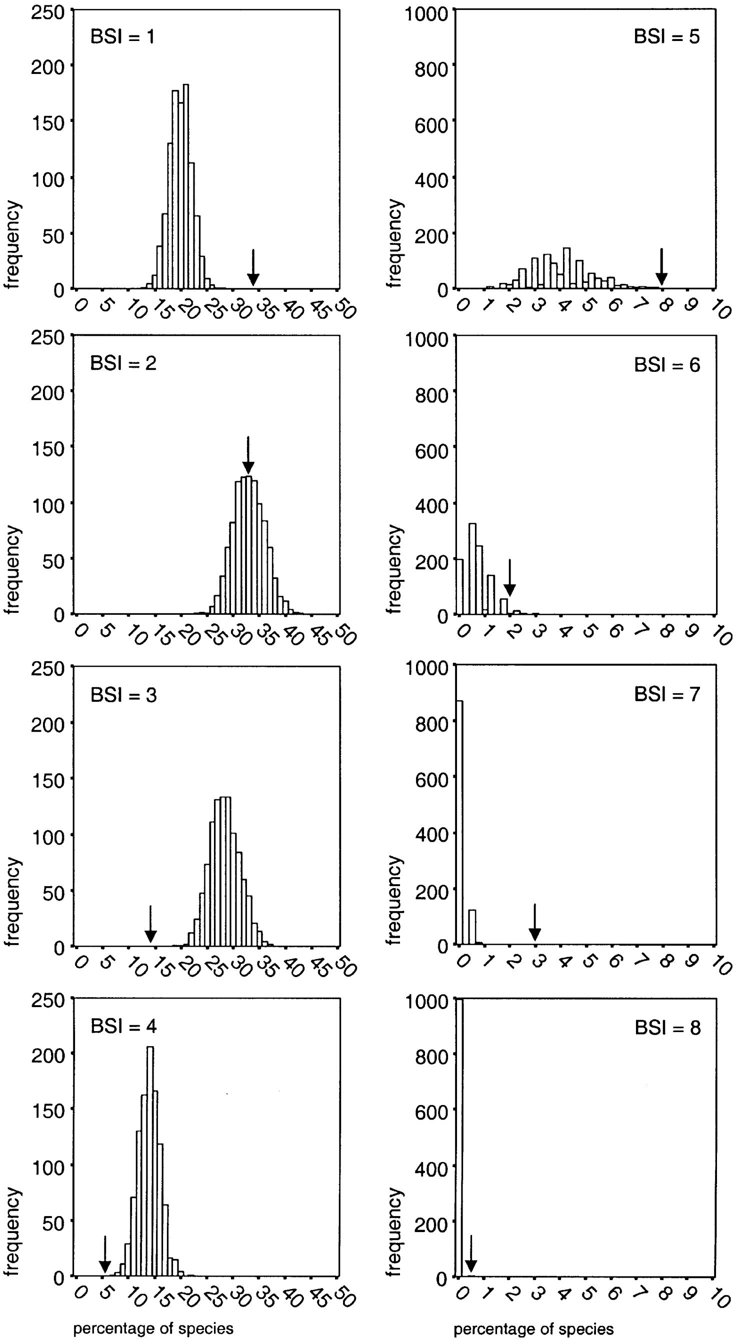

Figure 3. Distribution of the proportion of species with different BSI, calculated on 1,000 Monte Carlo simulations run on the data from African large mammals (see text). The arrows show the observed values in the African fauna. Note the change in scales in the figures on the right side.

years ago (Vrba, 2000, 2004). Therefore, in our opinion, the African mammal fauna has had sufficient time to recover from the most recent extinction event. Second possibility; since these extreme eurybiomic species can usually survive in the biomes at both climatic extremes of the Milankovitch cycles, they were not affected by even the strongest climatic changes of the Late Neogene. The effect of this is that, although they have lower rates of vicariance and speciation, the extinction rates may be much lower than in semi-eurybiomic species. Therefore, the extreme eurybiomic species may have experienced a net increase in species over time.

Distribution of BSI in mammalian clades

Figure 4 compares the BSI histograms among taxonomic groups (Tubulidentata and Proboscidea are not shown because each has only one species in Africa). Those distributions are broadly similar to that of the whole macromammalian assemblage, except for Carnivora and possibly Hyracoidea. There are proportionally more carnivore and hyrax species inhabiting a greater number of biomes (higher BSI) than is the case in, for example, Primates or Artiodactyla. This is reflected in the mean BSI for each order (Table 4).

Therefore, the separate results for orders indicate that Carnivora are more eurybiomic than are artiodactyls and primates, as suggested by the resource-use hypothesis. Vrba (1987) argued that the larger carnivores are eurybiomic and showed that their lineages in Africa had lower speciation rates than did most other mammalian clades. Because they are not species-specific, but rather size-specific, feeders (see also Vrba, 1980b), any one species may be found in environments which differ vastly in climate, vegetation and herbivore species. In spite of their generally wide geographical distributions (Rapoport, 1975; Pagel *et al.,* 1991; Letcher and Harvey, 1994; Ruggiero, 1994), such carnivore species do not encounter 'new food environments' readily. Most herbivores of broadly comparable body size, in contrast, are adapted to particular vegetation types, and even particular plant species and plant parts (Vrba, 1980a).

Similarly, the relatively high mean BSI for the species-poor and generalist Hyracoidea (Table 4) is as expected under the resource use hypothesis. The extant Hyracoidea comprises the single family Procaviidae, which had limited diversification since its Middle Eocene origin and contains its maximum number of genera today (Maglio, 1978; Meyer, 1978; Nowak, 1991). Hyraxes have a relatively high mean BSI, consistent with the fact that they are marked generalists. They feed mainly on vegetation but they are both grazers and browsers. Three of the five species feed on the ground as well as in trees. Finally, these animals are not limited in their distribution by a lack of water (Nowak, 1991).

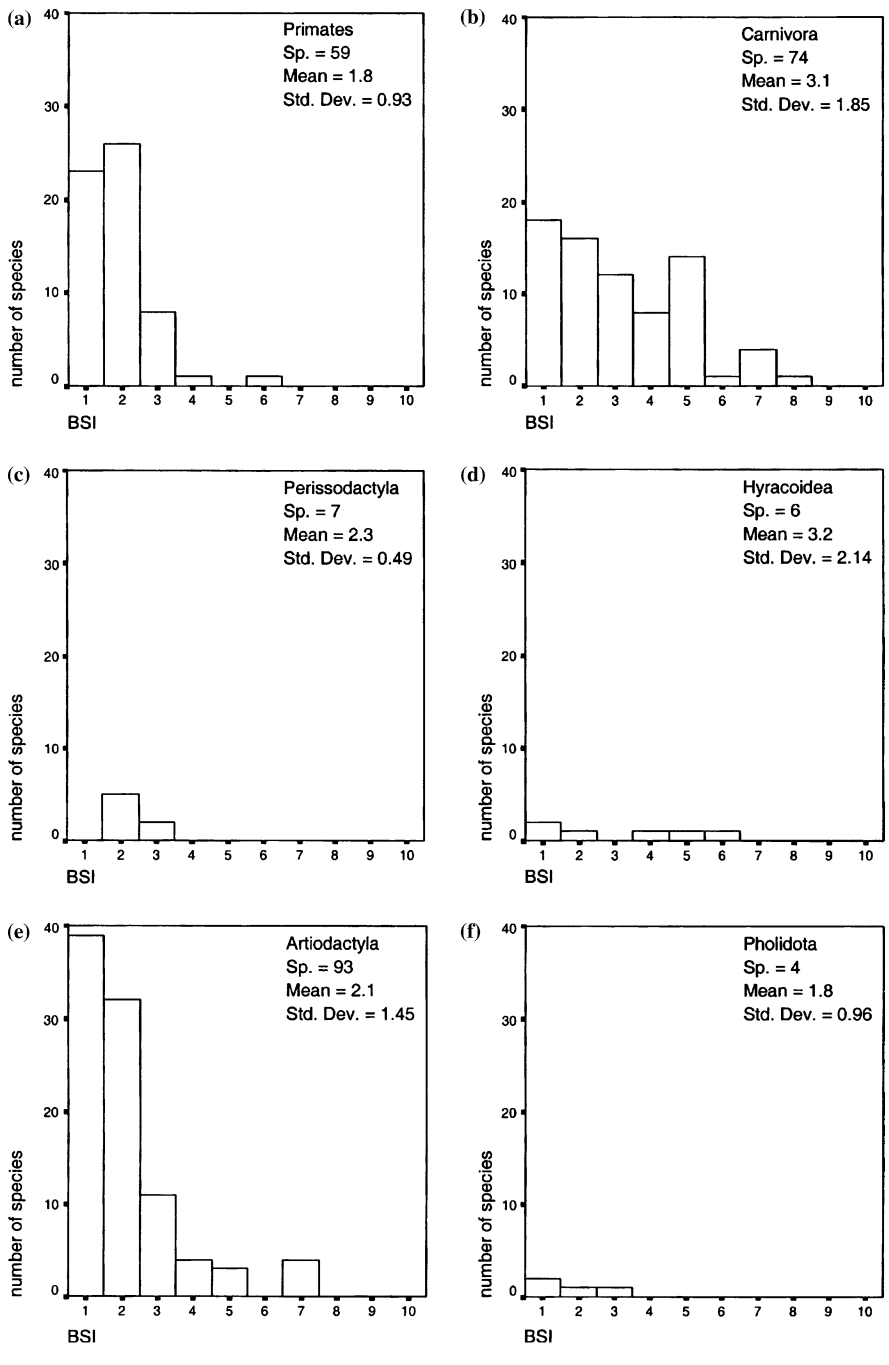

Figure 4. Histograms as in Figure 2 for mammalian orders: (a) Primates, (b) Carnivora, (c) Perissodactyla, (d) Hyracoidea, (e) Artiodactyla, (f) Pholidota. Sp., number of species.

Table 4. Differences among African mammalian species in average value of species' BSI

Order	Species number	BSI	
Primates	59	1.85	(0.925)
Carnivora	74	3.11	(1.847)
Proboscidea	1	6.00	(–)
Perissodactyla	7	2.29	(0.488)
Hyracoidea	6	3.17	(2.137)
Tubulidentata	1	5.00	(–)
Artiodactyla	93	2.10	(1.445)
Pholidota	4	1.75	(0.957)
Total	245	2.40	(1.577)

Table values, except for species number, are means and, in parentheses, SDs.

Proportion of biomic specialists in the African biomes

As predicted, the proportion of stenobiomic species (BSI = 1) is significantly higher than expected by chance in the tropical rainforest and subtropical desert biomes. Table 5 shows that, of all species in the rainforest biome, 33.0% are restricted to it (rainforest specialists with BSI = 1). This analogous percentage is 13.9% in the subtropical desert biome.

Causes that contributed to the relatively low proportions of specialists in the desert biome (Table 5) may include the following. Among the biome-specific factors expected to increase the probability of speciation through long time is a high incidence of vicariance, which results in small and decisively separated populations. We suggest that, during the past 2.5 million years of the Modern Ice Age, the rainforest biome underwent more reduction into small populations than did adjacent biomes (Vrba, 1992), and also that the transition from

Table 5. Number of stenobiomic species (BSI = 1) In African biomes and comparison with the Monte Carlo simulations (N = 1,000)

Biome	Africa			Monte Carlo analysis			
	sp.	sp. (BSI = 1)	%	Mean %	Std. dev.	Range	p
I	103	34	33.0	7.90	2.41	0.97–16.50	< 0.001
II	146	29	19.9	11.43	2.37	3.42–19.18	< 0.001
II/III	94	6	6.4	7.43	2.55	1.06–17.02	*0.444*
III	72	10	13.9	6.58	2.81	0.00–15.28	0.004
IV	57	3	5.3	5.94	3.06	0.00–15.79	*0.545*
V	65	0	0.0	6.32	2.93	0.00–16.92	*0.017*

Sp, number of species. %, proportion of species with BSI = 1 in relation to total number of species. p, probability in each biome of the proportion of species with BSI = 1 being greater than or equal to (plain) or lower than or equal to (italics) the observed proportion; n the African large mammal faunas.

vicariant rainforest islands to surrounding tropical deciduous woodland were relatively sharply demarcated (as they are today) by qualitative change from absence to presence of a dry season. In contrast, the desert biome may have had a lower incidence of small vicariated populations of resident species and, therefore, of allopatric speciation. In addition, for the desert biome the transitions to neighboring biomes are more ‘fuzzy’, being due to quantitative changes in the duration of the dry period. These quantitative changes are gradual and may allow the presence in transitional areas of more generalist species in common with bordering biomes. Also, deserts support few large mammal species in low abundances, and the evolutionary transition to a restricted desert inhabitant requires a high degree of specialization in morphology, physiology and behavior, and may be rare in evolution (e.g. Maloiy, 1972). These hypotheses are not mutually exclusive and some combination of them may be necessary to account for the observed patterns.

On the other hand, the proportion of biomic specialists is also significantly higher than expected in the tropical deciduous woodland (19.9%). This result is broadly consistent with the predictions of the habitat theory and resource-use hypothesis (Vrba, 1987, 1992, 1995, 1999) of an Equator-ward gradient in proportions of specialist species, with highest proportions in the biome that is the best represented on and around the equator, namely the rainforest biome. It also predicts the presence of higher proportions of stenobiomic species in the biomes with more expansion-reduction during the glacial–interglacial cycle. An explanation based on the size of the tropical deciduous woodland biome may be suggested for the relatively high percentage of specialist species in this biome. This biome is very large and, although this biome is not a climatic extreme, shifts due to climatic change could be associated with area retraction. Therefore, a number of refuges could be isolated from this biome during the glacial epochs (Adams *et al.*, 1990), promoting speciation and associated specialization.

Finally, the proportion of stenobiomic species in the temperate evergreen forest biome is significantly lower than expected (0.0%). This seems to suggest that this biome tends to disappear completely in Africa during the dry extreme of the glacial–interglacial cycles, or at least it is reduced enough to not allow the persistence of endemic large mammal populations.

Climatic combinations

There is a substantial difference between the number and distribution of potential climatic combinations (Fig. 5a) and the actual climatic combinations present in the African large mammals today (Fig. 5b). The African large mammals include only 48, or 4.7%, combinations of the 1023 potential climatic combinations. It is obvious that there are significantly more combinations of few biomes than expected in a random sample from the potential combinations.

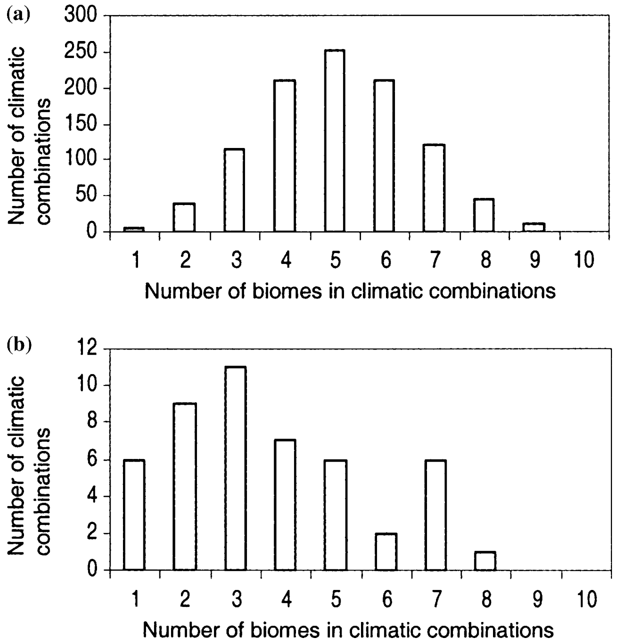

Figure 5. Frequencies of climatic combinations, in terms of numbers of biomes inhabited by species, in living African large mammals: (a) potential (b) observed.

Table 6 shows the number of species for every climatic combination. The most frequent combinations are I–II (36 species), I (34) and II (29). Other frequent combinations are II/III–III (17 species), I–II–V (13), II–II/III (12), II–II/III–III–IV–V (11) and III (10). Thus some of the climatic combinations implying few biomes are the most frequent among large African mammal species, and certainly those biomes that have suffered most fragmentation during the Milankovitch cycle are strongly represented in these combinations. This result supports the third prediction of the resource-use hypothesis analyzed in this work.

Given the previous analysis, the high frequency of stenobiomic species that inhabit either the biome I or II is not surprising. Similarly, there is a high proportion of species that exclusively inhabit biomes I and II (Table 6), as might be expected if the interface between these two biomes has had a particularly high incidence of vicariance and speciation. Relevant here are recent arguments that there may have been higher speciation rate in zonoecotone I/II than in the adjacent biomes (Enserink, 1997; Smith *et al.*, 1997; Schneider *et al.*, 1999), and that a similar effect may characterize other ecotones (Blondel *et al.*, 1999). This might explain the relatively high number of species restricted to two biomes. Nevertheless, one should note that under the modeled null hypothesis this result may be expected.

Table 6. Climatic combinations in African large mammals nowadays

Climatic combinations	N. biomes	Sp.
I	1	34
I–II	2	36
I–II – II/III	3	1
I–II–II/III– III–IV	5	2
I–II–II/III–III–IV– V	6	3
I–II–II/III–III–IV– V– VI	7	1
I–II–II/III–III–IV–V–VII–VIII	8	1
I–II–II/III–III– V	5	1
I–II–II/III–IV–V	5	3
I–II–II/III–IV– V – VI–VII	7	1
I–II–II/III–V	4	3
I–II–IV–V–VI–VII–VIII	7	1
I–II–V	3	13
I–V	2	1
I–V–VIII	3	2
II	1	29
II–II/III	2	12
II–II/III–III	3	2
II–II/III–III–IV	4	3
II–II/III–III–IV– V	5	11
II–II/III–III–IV–V–VI–VII	7	1
II–II/III–III–IV–V–VII–VIII	7	3
II–II/III–III–V	4	4
II–II/III–III–V–VII–VIII	6	1
II–II/III–IV	3	1
II–II/III–IV–V	4	1
II–II/III–V	3	4
II–II/III–V–VII–VIII	5	1
II–IV–V–VIII	4	1
II-V	2	5
II–V–VII–VIII	4	1
II/III	1	6
II/III–III	2	17
II/III–III–IV	3	7
II/III–IV	2	3
II/III–IV–V	3	1
III	1	10
III–IV	2	3
III–IV–V–VI–VII–VIII–IX	7	1
III–IV–VII	3	1
IV	1	3
IV–VI	2	1
IV–VI–VII	3	1
IV–VI–VII–VIII	4	1
IV–VI–VII–VIII–IX	5	1
IV–VI–VIII	3	1
VII	1	2
VII–VIII	2	3
Total species		245

N, biomes, number of inhabited biomes, Sp., number of species.

Most of the eurybiomic species are grouped in the same climatic combination (II–II/III–III–IV–V); namely, they inhabit all African biomes except the tropical rainforest. The few extreme eurybiomic species (BSI ≥ 5) that inhabit the tropical rainforest (13 species) are distributed among several climatic combinations none of which includes more than three species. Table 7 shows that the zonobiome I has a lower number of eurybiomic species per climatic combination than other biomes. It suggests that among those biome generalists present in the rainforest biome there is less ecological overlapping (as expressed by their bioclimatic characterization) than among the generalist inhabitants in other biomes.

Implications for the latitudinal gradient in species richness

One of the most debated patterns in ecology is the latitudinal gradient in species richness; namely, the observation that the number of species increases from the poles to the Equator. Multiple hypotheses have been proposed to explain spatial variability in species richness (Palmer, 1994; Willig *et al.*, 2003). The focus on vicariance as an agent of speciation, and on differing susceptibilities to vicariance as causal of differential speciation rates, offers an additional possible explanation for the gradient in latitudinal species richness. On an Earth with polar ice, the high latitudes are less likely than the tropics to be centers of biotic vicariance that leads to speciation (Vrba, 1985). Although alternative environments come and go at high latitudes with the astronomical climatic cycles, only the interglacial alternative offers areas that are inhabitable for organisms, while the glacial extreme causes mainly extinction. In contrast, in the tropics vicariance involving inhabitable environments – and therefore potential speciation – occurs during during both climatic excursions. The present polar ice phase started in the Oligocene with Antarctic glaciation, and progressive intensification of Antarctic ice build-up occurred during the Miocene (Kennet, 1995). At about 2.5 million years ago the first extensive Arctic glaciation, and the start of sustained glacial–interglacial cycles, marked the onset of the so-called Modern Ice Age which continues to the present day

Table 7. Number of extreme eurybiomic species (BSI ≥ 5) in African biomes

Biome	Sp. (BSI ≥ 5)	N.cc. (BSI ≥ 5)	Sp./n.cc.
I	13	8	1.625
II	30	12	2.500
II/III	29	11	2.636
III	25	9	2.778
IV	29	11	2.636
V	29	12	2.417

Sp., number of species with BSI ≥ 5, N.cc., number of climatic combinations with BSI ≥ 5, Sp./n.cc., number of species per combination.

(Shackleton, 1995). De Menocal and Bloemendal (1995) showed that throughout the Modern Ice Age Africa tropical climate has been dependent on high latitude climatic change, with major tropical vegetation changes in response to the glacial–interglacial cycles (see for example Dupont and Leroy's (1995) documentation of large scale expansions and contractions of the Sahara desert and adjacent vegetation zones since about 2.7 million years ago). If vicariance followed by speciation has been more prevalent in the tropics over the past polar ice phase, and also more prevalent in specialist lineages, then the tropics should today be relatively enriched in species and specially in specialist species; and the rainforest biome is expected to have undergone the highest incidence of reduction in area and species' vicariance (Vrba, 1992). In sum, the resource use hypothesis predicts that today there should be an Equator-ward gradient towards increasing species richness and particularly towards higher proportions of specialist species. Although there seems to be little reason to believe that a single factor will be found to explain this pattern, our study supports the assumption that historical factors plaid a role in elevating the diversity of non-volant mammals in some tropical biomes, specially the tropical rain forest.

Conclusions

The resource use hypothesis and related habitat theory (Vrba, 1992, 1995, 1999) suggests that the key to present-day macroecological patterns is found in the past: in the long term history of turnover (speciation, extinction) of clades, and in the palaeoclimatic and other geological changes of the areas in which the clades evolved. It argues that the initiating causes of modern phylogenetic, biogeographic, and macroecological patterns in species richness should be sought in those long-term historical factors that have over the past few millions of years affected rates of species' vicariance, of speciation and of net rates of species increase in clades. The predictions of the resource use hypothesis include generally higher rates of vicariance and speciation over the past few millions of years in the rainforest and desert biomes. This hypothesis also predicts that biome specialists have had higher rates of vicariance and speciation than have biome generalists. Therefore today there should be an Equator-ward gradient towards increasing species richness and particularly towards higher proportions of specialist species with highest proportions in the biome that is best represented on and around the equator, namely the rainforest biome. Our results for Africa appear to be consistent with each of these predictions. Therefore, the analyses presented here offer support to the resource-use hypothesis and we hope they will stimulate additional research in other biogeographical areas or taxonomical groups. Similarly, in those regions with a good paleontological record, a stronger test would result from investigation whether past combinations of particular taxa, areas, and time periods with their global climatic characteristics – combinations which were unlike anything today and which therefore imply their own predictions under the resource use hypothesis – do or do not support the hypothesis.

Acknowledgements

We thank B. Luna (Castilla-La Mancha University, Toledo) for the useful comments she provided on an earlier version of this work. S. Hochgraf is responsible for the artwork on the Figure 1. This study was supported by the Spanish Interministerial Commission of Science and Technology (PB98-0691-C03-02) and the Ministry of Science and Technology (BTE2002-00410). One of the authors (M.H.F.) has been funded by postdoctoral grants from the Fulbright Visiting Scholar Program, with the financial sponsorship of the Spanish Ministry of Education, Culture and Sport.

References

Adams, J.M., Faure, H., Faure-Denard, L., McGlade, J.M. and Woodward, F.I. (1990) Increases in terrestrial carbon storage from the Last Glacial Maximum to the present. *Nature* **348**, 711–714.

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

Blondel, J., Dias, P.C., Perret, P., Maistre, M. and Lambrechts, M.M. (1999) Selection-based biodiversity at a small spatial scale in a low-dispersing insular bird. *Science* **285**, 1399–1402.

Corbet, G.B. (1978) *The Mammals of the Palaearctic Region: A Taxonomic Review*. Cornell University Press, London.

Corbet, G.B. and Hill, J.E. (1992) *The Mammals of the Indomalayan Region: A Systematic Review*. Oxford University Press, Oxford.

Cotgreave, P. and Pagel, M. (1997) Predicting and understanding rarity: the comparative approach. In W.E. Kunin and K.J. Gaston (eds.), *The Biology of Rarity*, Chapman & Hall, London, pp. 237–261.

De Menocal, P.B. and Bloemendal, J. (1995) Plio-Pleistocene climatic variability in Subtropical Africa and the paleoenvironment of hominid evolution: a combined data-model approach. In E.S. Vrba, G.H. Denton, T.C. Partridge, and L.H. Burckle (eds.), *Paleoclimate and Evolution, with Emphasis of Human Origins*, Yale University Press, New Haven, pp. 262–288.

Doherty, D.A. and Harcourt, A.H. (2004) Are rare primate taxa specialists or simply less studied? *J. Biogeogr*. **31**, 57–61.

Dorst, J. and Dandelot, P. (1969) *A Field Guide to the Larger Mammals of Africa*. Houghton Mifflin, Boston.

Dupont, L.M. and Leroy, S.A.G. (1995) Steps toward drier climatic conditions in northwestern Africa during the Upper Pliocene. In E.S. Vrba, G.H. Denton, T.C. Partridge and L.H. Burckle (eds.), *Paleoclimate and Evolution, with Emphasis of Human Origins*, Yale University Press, New Haven, pp. 289–298.

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

Eldredge, N. (1979) Alternative approach to evolutionary theory. *Bulletin of the Carnegie Museum of Natural History* **13**, 7–19.

Eldredge, N. and Cracraft, J. (1980) *Phylogenetic Patterns and the Evolutionary Process*. Columbia University Press, New York.

Enserink, M. (1997) Life on the edge: rainforest margins may spawn species. *Science* **276**, 5320.

Gotelli, N.J. and Graves, G.R. (1996) *Null Models in Ecology*. Smithsonian Institution Press, Washington, DC.

Hall, E.R. (1981) The *Mammals of North America, Vols I-II*. John Wiley and Sons, New York.

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

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

Kennet, J.P. (1995) A review of polar climatic evolution during the Neogene, based on the marine sediment record. In E.S. Vrba, G.H. Denton, T.C. Partridge and L.H. Burckle (eds.), *Paleoclimate and Evolution, with Emphasis of Human Origins,* Yale Univ. Press, New Haven, pp. 49–64.

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.

Lacoste, A. and Salanon, R (1973) *Éléments de Biogéographie*. Fernand Nathan, Paris.

Letcher, A.J. and Harvey, P.H. (1994) *Variation in Geographical Range Size among Mammals of the Palearctic*. *Am. Nat*. **144,** 30–42.

Lieth, H. (1975) Primary productivity of the major vegetation units of the world. In H. Lieth and R.H. Whittaker (eds.), *Primary Productivity of the Biosphere*, Springer, Berlin, pp. 203–215.

Maglio, V.J. (1978) Patterns of faunal evolution. In V.J. Maglio and H.B.S. Cooke (eds.), *Evolution of African Mammals*, Harvard University Press, Cambridge, pp. 603–619.

Maloiy, G.M.O. (ed.) (1972) *Comparative Physiology of Desert Animals*. Academic Press, London.

Manly, B.F.J. (1997) *Randomization, Bootstrap and Monte Carlo Methods in Biology*. Chapman & Hall, London.

Meyer, G.E. (1978) Hyracoidea. In V.J. Maglio and H.B.S. Cooke (eds.), *Evolution of African Mammals,* Harvard University Press, Cambridge, pp. 284–314.

Nowak, R.M. (1991) *Walker's Mammals of the World*. The Johns Hopkins University Press, Baltimore.

Odum, E.P. (1971) *Fundamentals of Ecology*. Saunders, Philadelphia.

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

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

Prentice, I.C., Sykes, M.T., Lautenschlager, M., Harrison, S.P., Denissenko, O. and Bartlein, P.J. (1993) Modelling global vegetation patterns and terrestrial carbon storage at the last glacial maximum. *Global Ecol. Biogeogr. Letters* **3**, 67–76.

Rapoport, E.H. (1975) *Areografía: Estrategias Geográficas de las Especies*. Fondo de Cultura Económica, Mexico.

Rensch, B. (1959) *Evolution above the Species Level*. Methuen and Company, London.

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

Schneider, C.J., Smith, T.B., Larison, B. and Moritz, C. (1999) A test of alternative models of diversification in tropical rainforests: ecological gradient vs. rainforest refugia. *Proc. Natl. Acad. Sci. USA* **96**, 13869–13873.

Shackleton, N.J. (1995) New data on the evolution of Pliocene climatic variability. In E.S. Vrba, G.H. Denton, T.C. Partridge and L.H. Burckle (eds.), *Paleoclimate and Evolution, with Emphasis of Human Origins*, Yale University Press, New Haven, pp. 242–248.

Simpson, G.G. (1953) *The Major Features of Evolution*. Columbia University Press, New York.

Skinner, J.D. and Smithers, R.H.N. (1990) *The Mammals of the Southern African Subregion*. University of Pretoria, Pretoria.

Smith, T.B., Wayne, R.K., Girman, D.J. and Bruford., M.W. (1997) A role for ecotones in generating rainforest biodiversity. Sc*ience* **276**, 1855–1857.

Stebbins, L (1950) *Variation and Evolution in Plants*. Columbia University Press, New York.

Trahler, A.N. and Strahler, A.H. (1987) *Modern Physical Geography*. John Wiley and Sons, New York.

Vrba, E.S. (1980a) Evolution, species and fossils: how does life evolve? *S. Afr. J. Sci.* **76**, 61–84.

Vrba, E.S. (1980b) The significance of bovid remains as indicators of environment and predation patterns. In A.K. Behrensmenyer and A.P. Hill, (eds.), *Fossils in the Making,* University of Chicago Press, Chicago, pp. 247–271.

Vrba, E.S. (1985) Environment and evolution: alternative causes of the temporal distribution of evolutionary events. *S.* A*fr. J. Sci.* **81**, 229–236.

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

Vrba, E.S. (1989) What are the biotic hierarchies of integration and linkage? In D.B. Wake G. and Roth, (eds.) *Complex Organismal Functions: Integration and Evolution in Vertebrates,* John Wiley and Sons, New York, pp. 379–401.

Vrba, E.S. (1992) Mammals as a key to evolutionary theory. *J. Mammal.* **73**, 1–28.

Vrba, E.S. (1995) On the connections between paleoclimate and evolution. In E.S. Vrba, G.H. Denton, T.C. Partridge and L.H. Burckle (eds.), *Paleoclimate and Evolution, with Emphasis of Human Origins,* Yale University Press, New Haven, pp. 24–45.

Vrba, E.S. (1999) Habitat theory in relation to the evolution in African Neogene biota and hominids. In T.G. Bromage and F. Schrenk (eds.), *African Biogeography, Climate Change, and Human Evolution,* Oxford University Press, New York, pp. 19–39.

Vrba, E.S. (2000) Major features of Neogene mammalian evolution in Africa. In T.C. Partridge and R.R. Maud (eds.), *The Cenozoic of Southern Africa,* Oxford University Press, Oxford, pp. 277–304.

Vrba, E.S. (2004) Mass turnover and heterochrony events in response to physical change. *Paleobiology*.

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

Walter, H. and Breckle, S.-W. (1986) *Ecological Systems of the Geobiosphere. Vol.* 2 *Tropical and Subtropical Zonobiomes*. Springer, Berlin.

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

Willig, M.R., Kaufman, D.M. and Stevens, R.D. (2003) Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. *Annu. Rev. Ecol. Evol. Syst.* **34**, 273–309.

Wilson, D.E. and Reeder, D.M. (1993) *Mammal Species of the World: A Taxonomic and Geographic Reference*. Smithsonian Institution Press, Washington.