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Patterns of distribution, diversity and endemism of larger African mammals

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Patterns of distribution and diversity (= species richness) of larger African mammals, and three subsets thereof (ungulates, carnivores and primates), are identified and analysed quantitatively. Distributional patterns generally correspond well with those of present-day vegetation types and of resident non-aquatic birds. However, the precise locations of zonal boundaries and the degree of zonation differ between groups, primarily reflecting their different ecological requirements. Large mammal diversity increases towards the equator, but diversity patterns differ substantially between the groups. Diversity is positively correlated with vegetation type diversity, and vegetation types analysed as separate units explain over 85% of the variance in the diversity of the mammal groups investigated. In addition, both distributional and diversity patterns appear to have been affected by past environmental factors.

Diversiteits- en verspreidingspatrone van groot Afrika soogdiere, en die van drie groepe (hoefdiere, vleisvreters en primate), word geïdentifiseer en kwantitatief geanaliseer. Alhoewel die verspreidingspatrone goed ooreenstem met die van huidige plantsoorte en plaaslike nie-akwatiese voëls, verskil verspreidingsgrense en die graad van verskeidenheid tussen groepe, wat verskillende ekologiese behoeftes weerspieël. Terwyl die verskeidenheid van groot soogdiere nader aan die ewenaar vermeerder, verskil die patrone van verskeidenheid tot 'n groot mate tussen groepe. Daar is 'n positiewe korrelasie tussen soogdierdiversiteit en plantegroeidiversiteit, en plantegroei-soorte wat as afsonderlike eenhede ge-analiseer is, verklaar meer as 85% van die variasie in die soogdiergroepe wat ondersoek is. Verder blyk dit asof beide verspreidings- en verskeidenheidspatrone beïnvloed was deur omgewingsfaktore wat in die verlede geheers het.

Any study of biotic distribution, diversity and endemism requires the identification of pattern before an understanding of the underlying causal processes can be achieved (Nelson & Platnick 1981). In this study, we attempt to identify and interpret patterns of distribution, diversity and endemism for larger African mammals, and focus also on three main subsets thereof: ungulates, carnivores and primates. These patterns are then interpreted in the light of past and present distribution and diversity of vegetation. The use of vegetation as the primary factor which influences distribution/diversity patterns can be justified as being '...the most meaningful ecological summary of the influences of soil, climate, topography and other static and dynamic environmental factors' (Davis 1962).

Methods

Raw data

Distributional information for larger mammals which occur in southern Africa was extracted from Smithers (1983). Supplementary information for the remainder of the continent was obtained from Dorst & Dandelot (1970) and Haltenorth & Diller (1977). This study is based on ideal broad distributions of mammals in Africa, i.e. not taking into account changes brought about by human settlement and associated vegetation changes. Major contractions in faunal ranges, however, such as the disappearance of many large mammal species from the south-western Cape (Skead 1980) are reflected in the distribution maps analysed (Smithers 1983).

In all, 211 species were studied (Appendix 1). Insectivores, rodents and bats were not included in this study, owing to the lack of distributional information for species which occur outside of southern Africa. A 160-quadrat grid (Figure 1), was used to extract the distributional information for each species for each quadrat, using a scoring system of 0–10 (0 = absent; 10 = occurring throughout quadrat). The quadrat size was chosen on the basis of software limitations and was smaller in area than all but 4% of the species' ranges. Four mammal data sets were prepared for analysis: all species studied; ungulates (89 species); carnivores (60 species) and primates (45 species).

Vegetational information was extracted from White's (1983) vegetation map of Africa. His 80 vegetation types (including sub-categories) were grouped into 49 broader categories, though still adhering to the 17 major groups described by the author (Appendix 2). For each quadrat, the percentage cover of each vegetation type and the number of vegetation types present were recorded.

Numerical and statistical methods

Patterns of distribution and diversity were determined for each of the four data sets (all large mammals, ungulates, carnivores and primates) using multivariate quantitative analyses, following the approach employed by Crowe & Crowe (1982) and discussed in detail by Field, Clarke & Warwick (1982). Cluster analysis, non-metric multidimensional scaling and information statistic tests were performed on the quadrat distributional data in order to identify major mammalian zones. The Bray-Curtis measure of similarity (Bray & Curtis 1957) and the unweighted pair-group method (Sneath & Sokal 1973) were used in cluster analyses to identify any hierarchic similarity among groups of quadrats. This approach excludes negative matches as evidence of similarity and takes variation in abundance into account,

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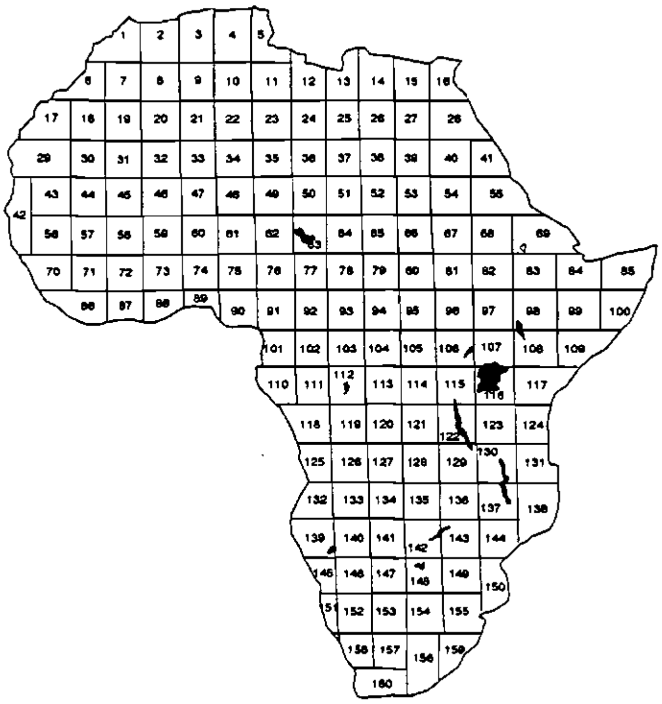

Figure 1 The grid quadrat system used to extract data from the mammal distribution maps. Superimposed on the grid are the positions of the major lakes and pans in Africa in the following grid squares: 63. Lake Chad; 69. Lake Tana; 98. Lake Rudolf, 106. Lake Albert; 112. Lake Leopold II; 116. Lake Victoria; 122. Lake Tanzania; 130. Lake Malawi; 139. Etosha Pan; 142. Lake Kariba; 148. Makgadikgadi Pan.

as opposed to the alternative Jaccard coefficient which is sensitive to both presence or absence of species and does not consider variation in relative abundance (Field & MacFarlane 1968). The validity of quadrat grouping recognized by the cluster analyses was assessed by producing a two-dimensional ordination for each of the four data sets, using non-metric multidimensional scaling (MDS). MDS is a less constraining approach than cluster analysis, since a hierarchic pattern of quadrat similarity is not forced onto the data (Crowe & Crowe 1982; see Shepard 1980). Once the zones (groups of quadrats) were identified, the Information Statistic test (I-test; Field 1969) was used *a posteriori* to determine the characteristic species of each zone. The recognition of distributional zones was dependent on the quadrat groups being distinct in both cluster analysis and MDS, and characterized by the presence of several species. The distributional boundaries of the most characteristic species of each zone (those restricted to and widespread within the zone) were then used to express the results of the cluster analyses and MDS cartographically. In exceptional cases, zones were allowed to be delimited by default, i.e. by the boundaries of adjacent zones.

Zonal endemics were recognized as those species having more than 85% of their range confined to a particular zone. The percentage of endemic species out of the total number of mammals in each subset was calculated, and relative endemism was calculated as percentage endemism as a function of zone area (number of quadrats within that zone), and provides a useful means of comparison, within and between mammal zones.

A correlation analysis was used to determine the relation between species diversity for the four data sets (number of species per quadrat) and the number of vegetation types present. Stepwise multiple linear regression (Allen 1973) was used to relate species diversity to a combination of vegetation types weighted by their percentage cover of each quadrat. Residual plots (deviations from the value predicted by the regression) were used to recognize areas which deviate substantially from the general trends. In these analyses, those quadrats which had unexpectedly high species diversity were considered as possible palaeoecological 'refugia' (*sensu* Haffer 1969) and, where endemism was also high, these refugia were considered to be centres of speciation (i.e. Type II refugia, *sensu* Crowe & Crowe 1982).

Results

The results for the cluster analyses and MDS for all mammals studied, and each subset thereof, are summarized in Figures 2 and 3 respectively, and the zones of mammal distribution supported by cluster analysis, MDS and I-tests are depicted in Figure 4. These zones are listed in Tables 1–4, together with information on species diversity, endemism and characteristic species. Patterns of African mammal diversity are depicted in Figure 5. Table 5 lists the correlation coefficients between mammal diversity and the number of vegetation types, and results of the multiple regression analyses between mammal diversity and the different vegetation types are shown in Table 6. The residual plots from the correlation between mammal diversity and vegetation diversity are shown in Figures 6 and 7.

Discussion

Patterns of distribution

The subregional boundaries of large mammals correspond well with boundaries between major African vegetation types (i.e., forest, savanna and arid zones; Figure 4a). The provincial division of the Saharan Subregion represents the northernmost limit for some species (e.g. *Addax nasomaculatis, Crocuta crocuta)*. However, few species are endemic to this subregion and none are endemic to its Northern Province (Table 1). The division of the Forest Subregion is influenced by carnivore and primate distributions, and its Western Province has the highest relative endemism of larger African mammals. The Savanna Subregion contains 60% of African mammals (Table 1) and its subdivision is influenced primarily by ungulate distributions. There is marked variation in the degree of biogeographical zonation (though not in the placement of boundaries) between ungulates, carnivores and primates (Figure 4).

The extensive radiation of ungulates in Africa is reflected in the highly fragmented zonation found for this group (Figure 4b). Most ungulate species are found in the Northern Savanna, Southern Savanna and Somali Arid Subregions, of which the latter has the highest level of absolute as well as relative endemism (Table 2). Savannas include a variety of vegetation types including bushland, thickets, woodlands and vegetational mosaics, and the Somali Arid Subregion is particularly diverse in topography and vegetation, ranging from semi-arid lowlands to montane forests and woodlands.

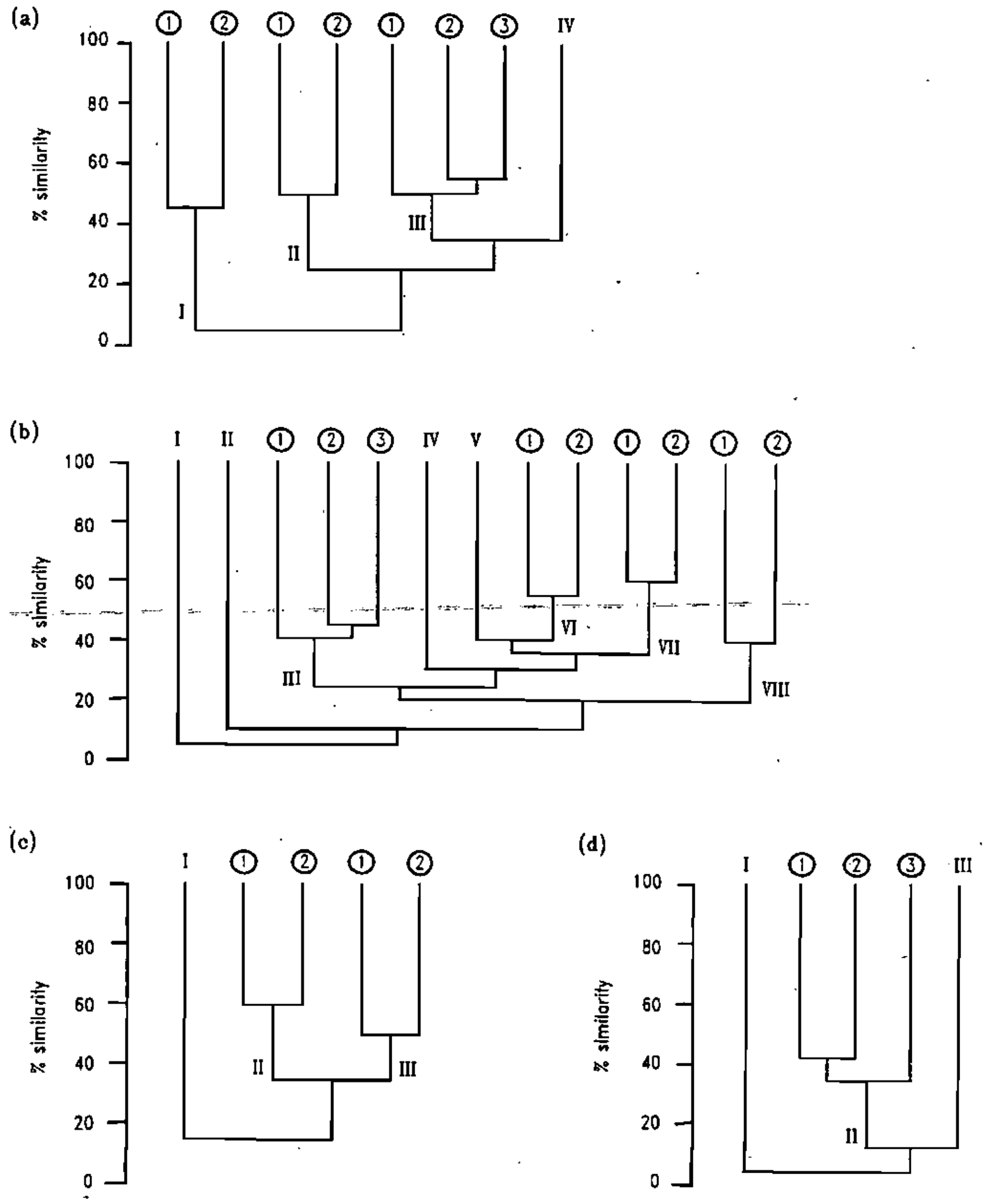

Figure 2 Large mammal (a), ungulate (b), carnivore (c) and primate (d) distribution zones suggested by cluster analysis. Roman numerals denote subregions and circled numbers represent subregion provinces.

Only a few smaller species are forest-adapted, e.g. the cephalophines (Bigalke 1972). The incorporation of forest-savanna mosaics into the Lowland Forest Subregion (Figure 4b, zone VI.2) is due both to its lack of penetration by many savanna species and to its use by lowland forest species (e.g. *Cephalophus silvicultor*), and implies a greater sensitivity to the presence of forest than for other groups. No species, however, is confined to this zone.

Many carnivores have widespread distributions reflecting generalized habitat requirements and, consequently, this group has fewer distribution zones than ungulates (Figure 4c). With the exception of the fennec (*Fennecus zerda*) and sand cat (*Felis margarita*) all carnivores occur in the Savanna Subregion (Table 3), and about half are found in the remaining areas, with relatively few species endemic to any particular zone. There is some extension of the ranges of certain carnivores along the Mediterranean borders of the Sahara, either up the western side (e.g. *Mellivora capensis*, *Genetta genetta*) or through most of the area (e.g. *Felis libyca*, *Herpestes ichneumon*). This is partly due to the fact that many of the species occur (e.g. *Felis libyca*) or occurred in Europe and/or Asia. The penetration of carnivores into desertic areas, the comparatively lower distinction of their Southwest Arid zone and the absence of a Somali Arid zone all imply a greater ability than ungulates to exploit arid areas, and this is probably facilitated by their diet and physiology (Bigalke 1978).

Primates are largely restricted in range to the Lowland Forest Subregion, and none occur in the Saharan Subregion (Figure 4d, Table 4). In the Lowland Forest Subregion primates are either distributed throughout the zone (e.g. *Cercopithecus mona*, *Pan troglodytes*), confined to one of the three provinces [e.g. *Cercopithecus diana* (1); *Cercopithecus cephus* (2); *Cercocebus aterrimus* (3)], or in two adjacent provinces [e.g. *Cercocebus torquatus* (1,2); *Cercocebus albigena* (2,3)]. The remaining species, mainly

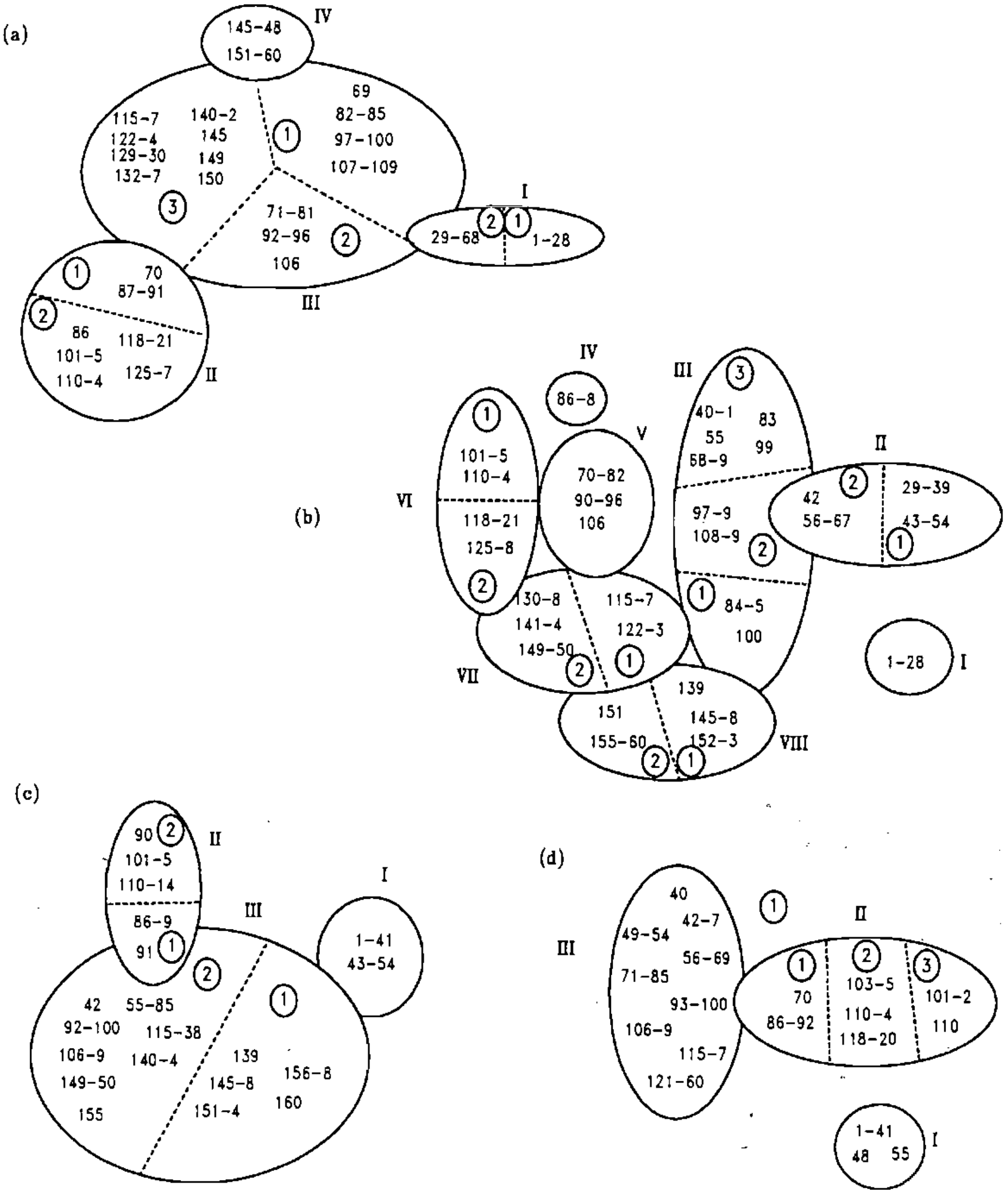

Figure 3 Large mammal (a), ungulate (b), carnivore (c) and primate (d) distribution zones suggested by multidimensional scaling. Zonal symbols as in Figure 2.

baboons, have extensive distributions, but only three species (*Papio ursinus*, *Cercopithecus aethiops* and *Galago senegalensis*) have penetrated the Southwest Arid area.

As with the zonation patterns of African birds (Chapin 1932; Moreau 1952; Crowe & Crowe 1982) and small mammals (Davis 1962), the major zonational boundaries of larger African mammals closely follow those of the major vegetation types. The more intricate zonation of Africa by ungulates corresponds most closely to that for African non-aquatic birds (Crowe & Crowe 1982). We believe that this relatively fine partitioning of Africa is due to the fact that both groups have specialists which evolved allopatrically in the same ecological 'islands' of isolated biotopes during periods of marked expansion and contraction of forest and savannas. There are, however, some notable differences in zonation between large mammals and other groups. A Southwestern Cape Fynbos zone is recognized as a centre of endemism for birds, amphibians and mammals (Bibby *et al.* 1992; Groombridge 1992), but is not defined by large mammal distributions, and no large mammals are confined to this area. Similarly, a Montane zone is recognized as a centre of endemism for birds (Dowsett 1980, 1986; Bibby *et al.* 1992), but with the exception of two monkeys (*Cercopithecus l'hoesti* and *C. hamlyni*) restricted to the montane forests of central Africa, no large mammals are confined to a montane zone. The Dahomey Gap, a break in the lowland forest belt, is reputed to have been an important zoogeographical barrier for forest birds (Moreau 1966). However, it is

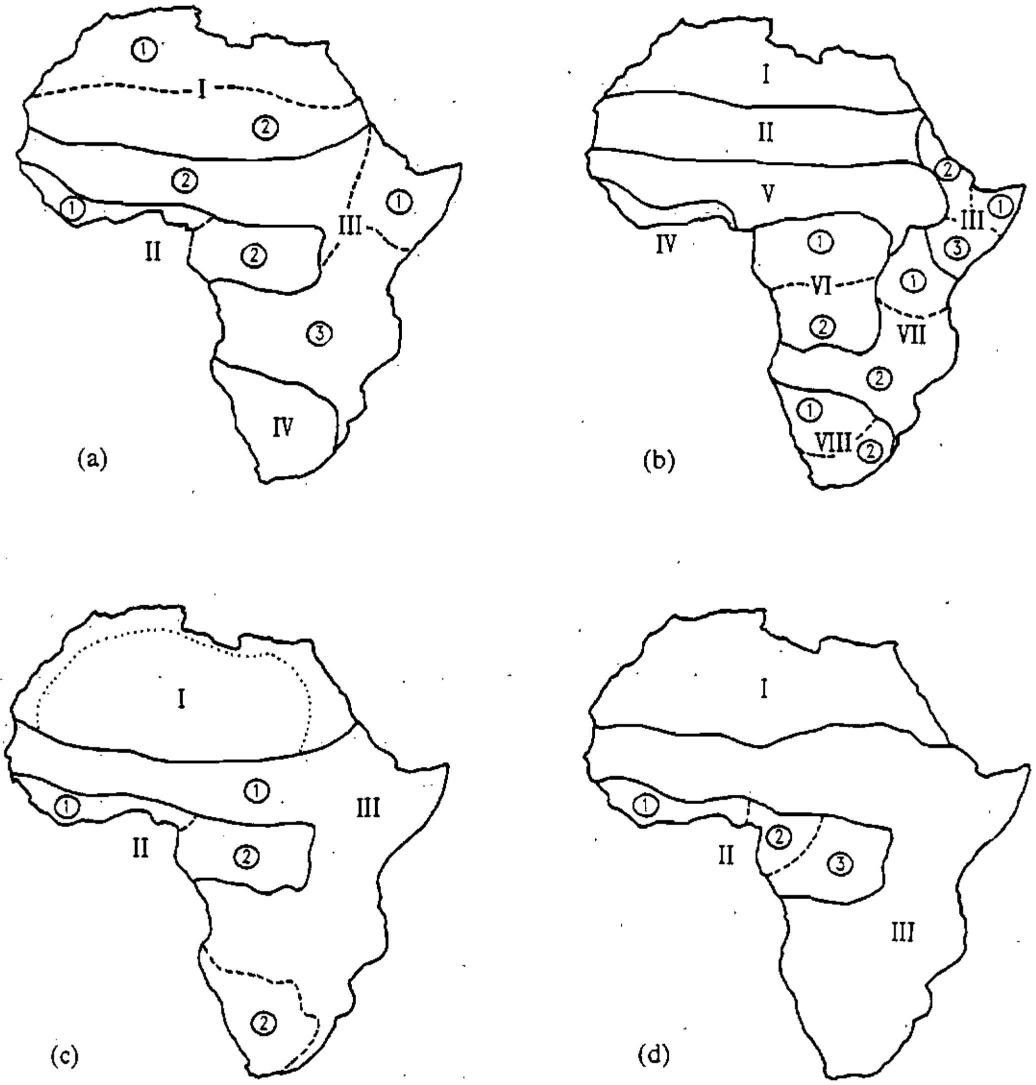

Figure 4 Large mammal (a), ungulate (b), carnivore (c) and primate (d) subregional (roman numerals) and provincial (circled numbers) boundaries suggested by the distributions of the most characteristic species.

not significant for larger mammals in general, although it limits the range of certain western forest primates. Within the Lowland Forest zone, the Cameroon mountain and highlands system acts as a boundary for all the mammalian groups analysed, as well as in avifaunal studies (Crowe & Crowe 1982). This feature is evidently an effective barrier within the forest region, and probably played a role in allopatric speciation. Finally, a greater proportion of African large mammals (14/211) than Afrotropical birds (33/1481; Moreau 1966) have ranges extending beyond the traditional northern boundary of the Afrotropical Region, into Mediterranean Africa.

It has been suggested that zonal boundaries which cannot be explained by existing physical or environmental barriers are related to past environmental conditions, and resulting speciation events (Balinsky 1962; Udvardy 1969; Bigalke 1972; Crowe & Crowe 1982; Brain 1985). Historical influence on present day distribution of mammals is evident. Crowe (1978) illustrated hypothetical vegetation patterns that could have existed during past wet and dry climatic phases. A noteworthy change occurred in the Congo River basin within the present Lowland Forest zone, in which the development of a lake, where present mesic forest vegetation exists, served to separate areas to the east and west, which during dry phases, became isolated patches. Crowe & Crowe (1982) proposed that these areas provided *refugia* (centres of speciation) for forest-dwelling birds. That this may have also resulted in primate speciation is evident from the boundary dividing the central forest region.

Also related to past dry periods is Balinsky's (1962) proposed arid 'corridor' which linked the arid areas of the north-east and south-west. Free migration of animals along this corridor would have occurred during relatively arid phases, but during the wetter periods it is postulated that the eastward extension of the rainforest across the corridor separated animals to the north-east and south-west. This would account for the many disjunct distributions of mammals (e.g. *Madoqua kirkii, Oryx gazelle, Genetta genetta*) which have populations in the two arid zones, separated by areas of moister savanna, as well as the fairly high endemism found at these extremities. There are also congeneric species which are separated in this way (e.g. *Equus zebra* and *E. grevyi*), supporting the fact that this process has significance as a means of speciation. Moreover, the exist-

Table 1 Large mammal zonal diversity, (D), endemism (E), percentage endemism (%E), relative endemism (R), and characteristic species. Zone numbers are those in Figure 4a

Zone name	D	E	%E	R	Characteristic mammals
I Saharan Subregion	24	11	5	0,09	*Gazella dorcas* *Gazella leptoceros* *Poecilictus libyca*
1. Northern Province	14	0	0	0	
2. Southern Province	24	6	3	0,12	*Oryx dammah* *Gazella dama* *Felis margarita*
II Lowland Forest Subregion	84	41	19	1,12	*Perodictus potto* *Galagoides demidovi* *Cercopithecus mona*
1. Western Province	46	16	8	1,14	*Genetta pardina* *Mungos gambianus* *Colobus polykomos*
2. Eastern Province	65	15	7	0,70	*Cephalophus nigrifons* *Cephalophus callipygus* *Cercocebus albigena*
III Savanna Subregion	125	54	26	0,35	*Crocuta crocuta* *Panthera leo* *Felis serval*
1. Somali Arid Province	70	15	7	0,58	*Oryx beisa* *Litocranius walleri* *Gazella soemmeringi*
2. Northern Savanna Province	58	8	4	0,13	*Papio anubis* *Gazella rufifrons* *Cephalophus rufilatus*
3. Southern Savanna Province	95	16	8	0,26	*Helogale parvula* *Hippotragus niger* *Aepyceros melampus*
IV Southwest Arid Subregion	52	16	8	0,53	*Cynictus penicillata* *Vulpes chama* *Antidorcas marsupialis*

Table 2 Ungulate zonal diversity (D), endemism (E), percentage endemism (%E), relative endemism (R), and characteristic species. Zone numbers are those in Figure 4b

Zone name	D	E	%E	R	Characteristic ungulates
I Saharan Subregion	2	1	1	0,04	*Gazella leptoceros* *Gazella dorcas*
II Sudanese Arid Subregion	10	4	4	0,16	*Oryx dammah* *Gazella dorcas* *Addax nasomaculatis*
III Somali Arid Subregion	35	16	18	1,38	*Oryx beisa* *Rhyncotragus guentheri* *Litocranius walleri*
1. Arid Province	17	4	4	1,33	*Gazella spekei* *Ammodorcas clarkei* *Dorcotragus megalotis*
2. Highland Province	15	3	3	0,75	*Capra ibex* *Tragelaphus buxtoni* *Equus asinus*
3. Grass Steppe Province	24	3	3	0,50	*Gazella granti* *Damaliscus hunteri* *Tragelaphus imberbis*
IV Western Forest Subregion	17	6	7	1,75	*Cephalophus niger* *Neotragus pygmaeus* *Cephalophus zebra*
V Northern Savanna Subregion	28	6	7	0,20	*Kobus kob* *Cephalophus rufilatus* *Taurotragus derbianus*
VI Central Forest Subregion	31	6	7	0,01	*Cephalophus monticola* *Cephalophus sylvicultor* *Cephalophus nigrifrons*
1. Northern Province	21	4	4	0,40	*Cephalophus callypigus* *Cephalophus leucogaster* *Cephalophus dorsalis*
2. Southern Province	23	0	0	0.00	
VII Southern Savanna Subregion	40	12	13	0,57	*Equus burchelli* *Taurotragus oryx* *Aepyceros melampus*
1. East African Province	37	0	0	0	
2. Temperate Province	32	4	4	0,25	*Raphicerus sharpei* *Hippotragus niger* *Alcelaphus lichtensteini*
VII Southwest Arid Subregion	25	8	9	0,60	*Antidorcas marsupialis* *Oryx gazella* *Pelea capreolus*
1. Kalahari Province	12	2	2	0,29	*Oryx gazella* *Alcelaphus caama*
2. Karoo-grassland Province	17	4	4	0,50	*Pelea capreolus* *Damaliscus dorcas* *Raphicerus melanotis*

ing forest vegetation associated with the montane belt forms an equatorial division of the savanna for all groups except the carnivores.

Fewer carnivores have disjunct distributions, however, and these are separated by a narrower gap (e.g. *Otocyon megalotis*) and no sister species are separated in this way. This is probably because arid/mesic gradients are not as effective as barriers for carnivores.

Patterns of diversity

Larger African mammals increase in diversity towards the equator (Figure 5a). This trend has been found for vertebrate faunas in North America (Klopfer & MacArthur 1960; Wilson 1974), the former Soviet Union (Terent'ev 1963), Australia (Schall & Pianka 1978) and for non-aquatic African birds (Crowe & Crowe 1982). Even coastal marine invertebrates and algae follow this pattern (Fischer 1960), with the exception of burrowing faunas (Thorson 1957) which are sheltered from climatic effects. Several workers have attempted to explain this global phenomenon in terms of a universal causal factor, and at least six major hypotheses have been proposed (summarized in Pianka 1966).

The increase in diversity towards the equator for North American mammals is mainly due to the steep increase in bats (Wilson 1974). Without this group, quadrupedal mammal diversity decreases northwards only slightly until

Table 3 Carnivore zonal diversity (D), endemism (E), percentage endemism (%E), relative endemism (R), and characteristic species. Zone numbers are those in Figure 4c

Zone name	D	E	%E	R	Characteristic carnivores
I Saharan Subregion	15	0	0	0	
II Lowland Forest Subregion	24	13	22	1,29	*Felis aurata* *Crossarchus obscurus* *Poiana richardsoni*
1. Western Province	18	3	5	0,71	*Genetta pardina* *Mungos gambianus* *Genetta villiersi*
2. Eastern Province	19	7	12	1,20	*Aonyx congica* *Genetta victoriae* *Genetta servalina*
III Savanna Subregion	57	28	47	0,63	*Ictonyx striatus* *Genetta genetta* *Lycaon pictus*
1. Savanna Province	35	4	7	0,12	*Canis adustus* *Helogale parvula* *Mungos mungo*
2. Southwest Arid Province	19	6	10	0,67	*Vulpes chama* *Cynictus penicillata* *Suricata suricatta*

Table 4 Primate zonal diversity (D), endemism (E), percentage endemism (%E), relative endemism (R), and characteristic species. Zone numbers are those in Figure 4d

Zone name	D	E	%E	R	Characteristic primates
I Saharan Subregion	0	0	0	0	
II Lowland Forest Subregion	35	29	66	3,14	*Galagoides demidovi* *Cercopithecus mona* *Perodicticus potto*
1. Western Province	22	5	11	1,83	*Colobus polykomos* *Cercopithecus petaurista* *Colobus verus*
2. Central Province	26	10	23	4,60	*Euoticus elegantulus* *Galago alleni* *Arctocebus calabarensis*
3. Eastern Province	28	3	7	0,70	*Colobus angolensis* *Cercopithecus ascanius* *Colobus pennanti*
III Savanna Subregion	8	5	11	0,22	*Galago senegalensis* *Cercopithecus aethiops* *Cercopithecus mitis*

Table 5 Correlations between mammal diversity and number of vegetation types

Mammal groups	*r*	*p*
ALL	0,50	< 0,001
UNG	0,49	< 0,001
CAR	0,52	< 0,001
PRI	0,20	< 0,011

extreme conditions north of 50°N are encountered. In comparison, the increase of larger African mammal diversity towards the equator is steeper, but there are factors specific to each major group which can probably account for much of this gradient.

The region of greatest diversity for each mammal group in Africa is not distributed across the whole equatorial region, but is restricted to the vegetation type to which each group is historically, and thus generally, most adapted. Ungulate species diversity is greatest in the savanna-woodland areas of the eastern tropical belt (Figure 5b). The mosaic structure of this vegetation group, as well as the fine dietary niche separation amongst ungulates, allows the coexistence of several species in an area (Lamprey 1963; Murray & Brown 1993), and the region is topographically highly diverse (Kingdon 1971), incorporating the Ethiopian Highlands and African Rift Valley. In addition, it contains the junction of three zones, the sympatry of component taxa of which could have been overemphasized by the relatively coarse scale of data collection. Primate diversity is highest in the tropical lowland forest (Figure 5d), requiring no further explanation than the presence of their preferred habitat, together with the refugium hypothesis offered earlier. Carnivore diversity is relatively evenly spread throughout the continent, with the exception of the Sahara, having peaks in the equatorial savanna and the south (Figure 5c). The southern peak corresponds to the boundary between two zones and may either be an artifact of data collection or a real area of overlap. Carnivores are not species-specific in their prey choice, although they may be limited to a certain prey size range (Smithers 1983). Within a biome, habitat is thus probably important only inasmuch as it affects prey availability, and global trends in diversity do not, of course, apply to population numbers.

Crowe & Crowe (1982) attempted to explain patterns of bird diversity in terms of vegetation diversity (number of vegetation types). Analyses of this kind in the case of mammals revealed even weaker correlations than found for birds (Table 5). However, vegetation types analysed as separate units in multiple regression analyses were able to explain over 85% of the variance in mammal diversity in all cases (Table 6). The importance of desert as an inhibitory factor is emphasized, but the apparent negative effect of Mediterranean sclerophyll forest may be due to its inaccessibility. Tropical vegetation types are an important correlate of species diversity, and the major positive influences for each mammal subset are the vegetation types associated with their ecological requirements. Thus, it follows that most variance in primate diversity is associated with the least amount of vegetation types, and deserts are only of secondary importance to carnivores.

Much of the deviation in diversity trends (Figures 6 and 7) can be explained by the presence of landscape features such as water bodies and mountains. In all the groups studied, lower than expected diversity is found in the Marra mountain area of Sudan and, except for primates, in the Ethiopian and Somali lowlands. Low diversity associated

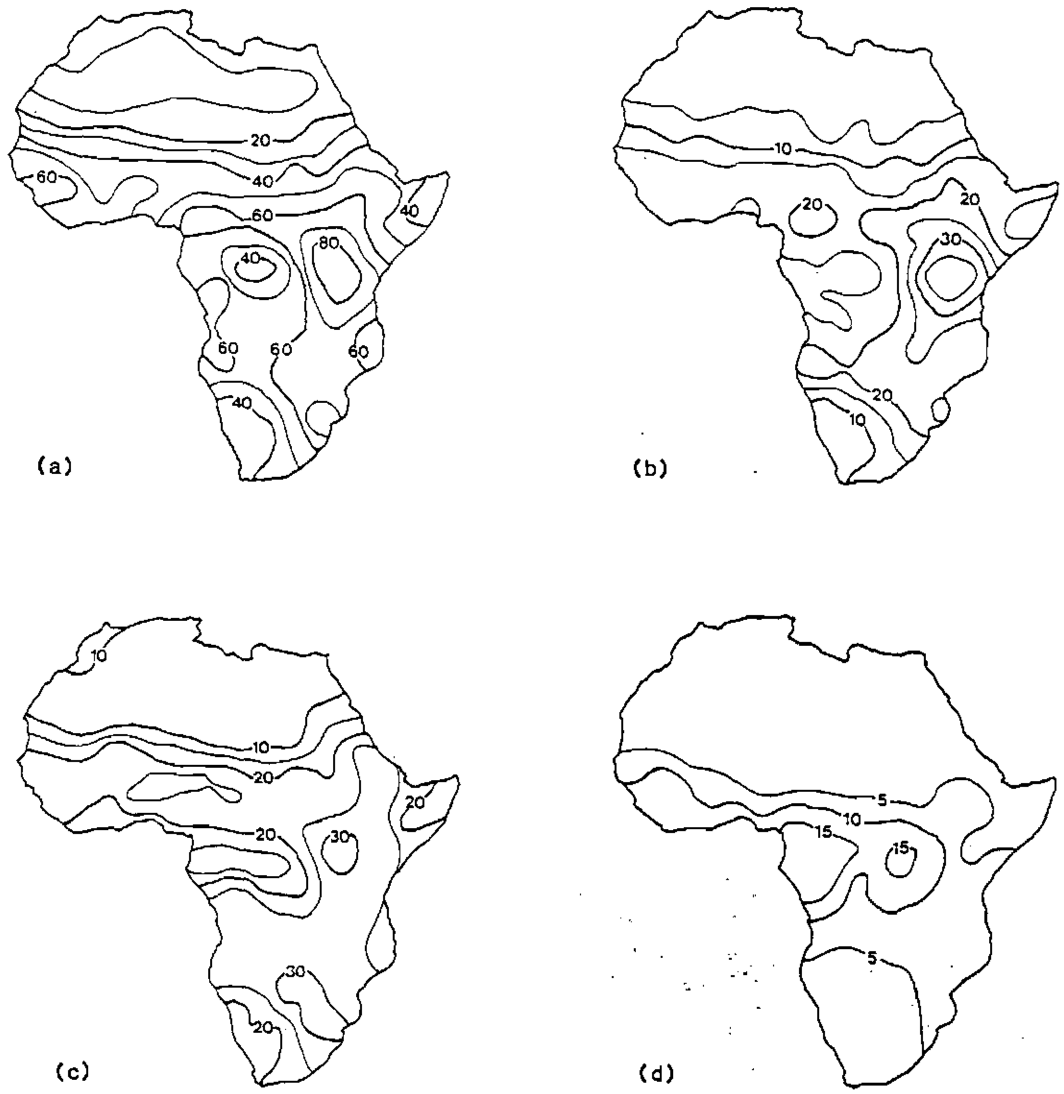

Figure 5 Geographical variation in diversity of the larger African mammals (a), ungulates (b), carnivores (c) and primates (d).

with Lake Victoria is probably due to the corresponding gap on the distribution maps created by the lake. Carnivores also have lower than expected diversity in the Atlas Mountains of Algeria, the Guinea highlands and Cameroon Highlands.

Higher than expected diversity, in all groups except primates, is associated with rivers or lakes in arid areas: Lakes Chad, Tana, Tanganyika, and the East African lakes; the Nile River, the Niger River and associated wetlands in central Mali, and the Okavango River. Higher than expected diversity for all groups except primates is also found in the vegetational mosaics south of the lowland forest, in the mountainous area around Swaziland, and in Namaqualand.

Primates have lower than expected diversity in the central lowland forest, in the region of the Congo River and associated marshlands and lakes, and higher than expected diversity in the lowland forest immediately to the west of this area. These patterns further support the idea of a central forest barrier and adjacent refugia. Higher than expected primate diversity is also associated with highlands in Guinea, Cameroon, and east Africa.

Implications for conservation

Centres of endemism and diversity are two criteria used to identify areas of importance for the conservation of biotic diversity. Thus, in the lowland forest, the central province is the centre of highest primate endemism, and the western province is important for all of the three subgroups. The Somali Arid Subregion is the area of highest ungulate endemism and carnivore endemism is fairly high in the Southwest Arid Province. The areas richest for endemic mammals (including small mammals) identified by Bibby *et al.* (1992) include these above-mentioned areas as well as montane and Cape fynbos areas. However, although this endemism-based approach has been used by Bibby *et al.* (1992) and others to identify and prioritize areas for conservation, these areas do not coincide with the areas of highest diversity for larger mammals, which occur in the savanna regions, except in the case of primates. As an additional criterion, the degree of zonation within each group serves as a guide to the variety of areas that need to be conserved in order to preserve maximum diversity, and it is further necessary to identify areas of high endemism and richness within these particular biogeographical regions (Rebelo & Siegfried 1992). Thus, the conservation of representative taxa for each subregion is a minimum requirement, and within each biogeographical province, an ideal goal.

Table 6 Summary of results of stepwise multiple regression analyses of mammal diversity *vs* vegetation diversity (VEG). The ten best correlated vegetation types and their contribution to the total multiple coefficient of determination (R^2) are listed for each group

All species			Ungulates			Carnivores			Primates		
VEG *	R^2	Sign of r	VEG	R^2	Sign of r	VEG	R^2	Sign of r	VEG	R^2	Sign of r
70	0,36	–	70	0,31	–	25	0,32	+	1	0,42	+
67	0,19	–	67	0,12	–	10	0,14	–	11	0,20	+
45	0,05	+	45	0,09	+	67	0,13	–	25	0,10	+
25	0,04	+	25	0,06	+	19	0,05	+	8	0,06	+
42	0,04	+	42	0,07	+	42	0,04	+	19	0,06	+
11	0,03	+	19	0,03	+	22	0,03	+	42	0,03	+
19	0,03	+	10	0,03	–	34	0,02	+	15	0,01	+
10	0,02	–	1	0,02	+	10	0,02	–	35	0,01	+
35	0,02	+	35	0,02	+	58	0,01	+	45	0,01	+
1	0,02	+	38	0,02	+	11	0,01	+	40	0,01	+
Tot. R^2 = 0,90			Tot. R^2 = 0,86			Tot. R^2 = 0,86			Tot. R^2 = 0,89		

* 1 = Lowland rain forest; 8 = Swamp forest; 10 = Mediterranean scleryphyllous forest; 11 = Lowland forest/Secondary grassland mosaic; 15 = West African coastal mosaic; 19 = Montane vegetation; 22 = Forest / secondary grassland / woodland mosaic; 25 = Woodland; 34 = S.A. scrub woodland / Highveld grassland mosaic; 35 = Woodland / bush-land / grassland transition; 38 = Evergreen bushland and thicket; 40 = Itigi deciduous thicket; 42 = Somalia-Masai deciduous bushland and thicket; 45 = Evergreen bushland / wooded grassland mosaic; 58 = Highveld grassland; 67 = Absolute desert; 70 = Semi-desert.

Conclusions

Patterns of distribution vary amongst the main groups of the larger African mammals. Distributional boundaries tend to be physical or ecological barriers which, in most cases, closely follow the limits of major vegetation types. Where vegetation forms a gradient of gradual change from one type to another (e.g. savanna to lowland forest), boundary limits, as dictated by the ecological requirements of the group, are 'flexible' to a degree which depends on the steepness of the gradient.

Although the zones identified correspond to a certain extent to the major biotic zones that have been identified by other biogeographical studies, it has become evident that to attempt to define these boundaries as a steadfast rule is unrealistic. The heterogeneity of the various faunal components determines some major differences, and even within the mammals, there are major differences between groups. Patterns that cannot be explained solely by existing environmental features can mostly be attributed to vegetational changes that have occurred in the past. The patterns of diversity and endemism observed substantiate much of the evidence for these evolutionary events.

Reasons for the equator-ward increase in diversity become clearer when separate mammal groups are observed. This trend is largely due to the concentration of primates in the equatorial lowland forest, and to the radiation of ungulates in the vegetationally and topographically diverse regions of East Africa.

Finally, the discrepancies in areas of high endemism and diversity between and within the different subsets complicate the identification of conservation 'hotspots' for large mammals, but the degree of zonation within each group provides a guideline as to the complexity of reserve networks required for the conservation of maximum diversity.

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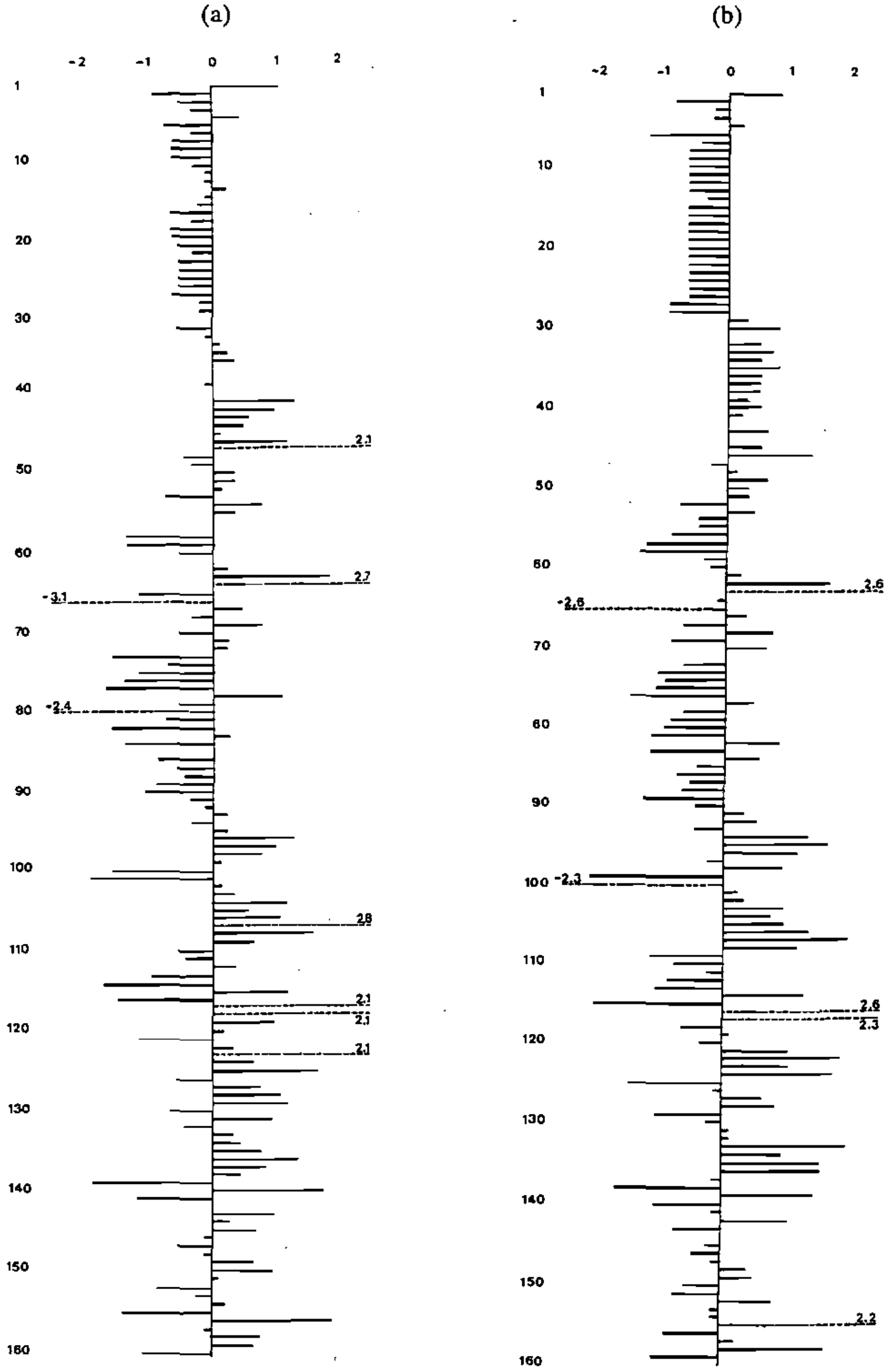

Figure 6 Standardized residuals (Allen 1973) for each sampling quadrat for large mammal (a) and ungulate (b) diversity *vs* vegetation diversity regressions.

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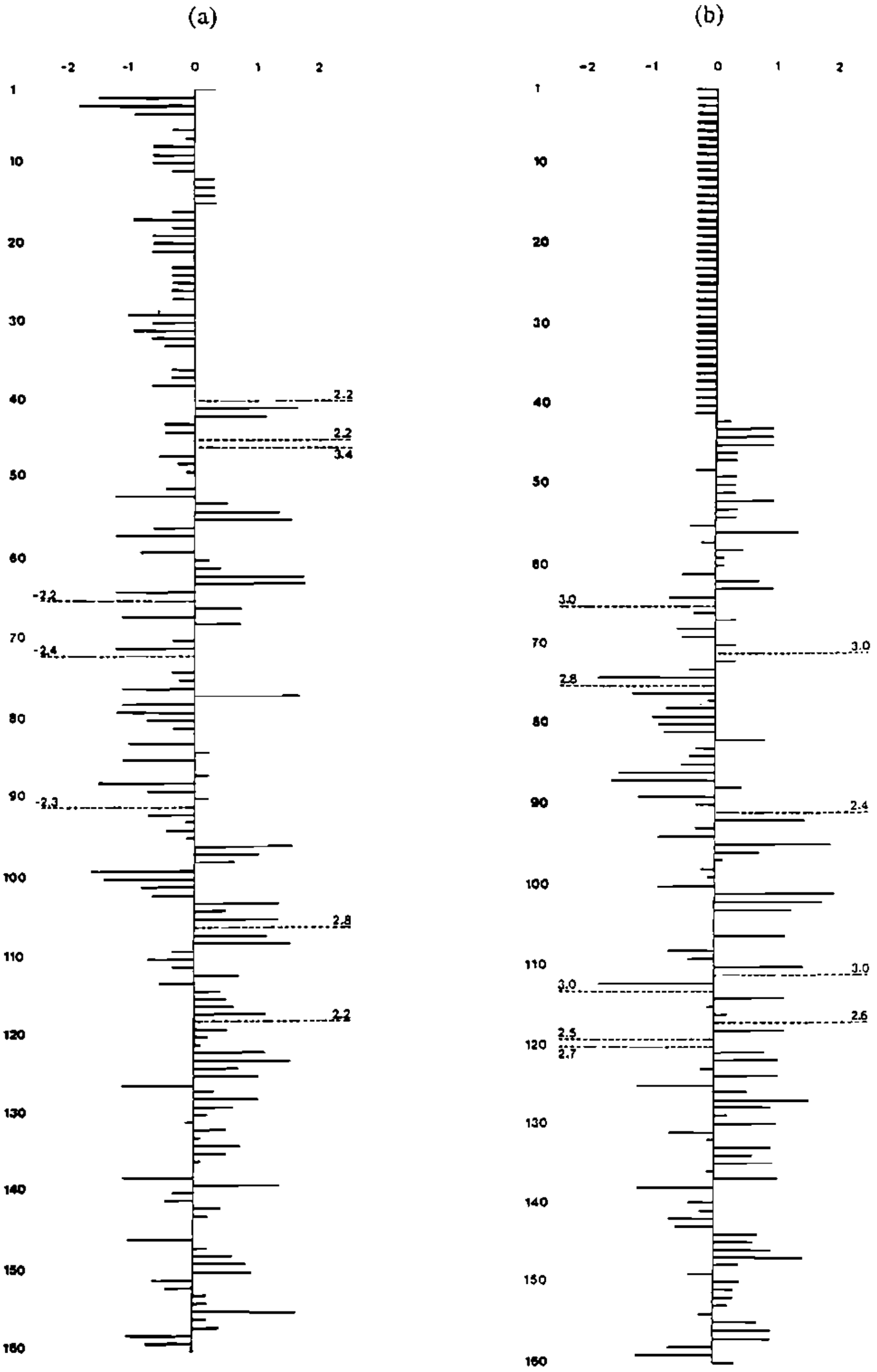

Figure 7 Standardized residuals (Allen 1973) for each sampling quadrat for carnivore (a) and primate (b) diversity *vs* vegetation diversity regressions.

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Appendix 1 African mammal species used in this study

PRIMATA

Perodicticus potto
Artocebus calabarensis
Galago alleni
Galago crassicaudatus
Galago senegalensis
Euoticus elegantulus
Galagoides demidovi
Papio hamadryas
Papio papio
Papio anubis
Papio gelada
Papio sphinx
Papio leucophaeus
Papio ursinus
Papio cynocephalus
Cercocebus torquatus
Cercocebus galeritus
Cercocebus aterrimus
Cercocebus albigena
Allenopithecus nigroviridis
Miopithecus talapoin
Cercopithecus cephus
Cercopithecus erythrotus
Cercopithecus erythrogaster
Cercopithecus ascanius
Cercopithecus petaurista
Cercopithecus nictitans
Cercopithecus mitis
Cercopithecus mona
Cercopithecus diana
Cercopithecus neglectus
Cercopithecus l'hoesti
Cercopithecus hamlyni
Cercopithecus pygerythrus
Cercopithecus albogularis
Erythrocebus patas
Colobus verus
Colobus badius
Colobus pennanti
Colobus polykomos
Colobus angolensis
Colobus abyssinicus
Colobus satanas
Gorilla gorilla
Pan troglodytes

PHOLIDOTA

Manis temmincki
Manis (Smutsia) gigantia
Manis (Phatoginus) tricuspis
Manis (Uromanis) tetradactyla

LAGOMORPHA

Pronolagus rupestris
Pronolagus crassicaudatus
Pronolagus randensis
Bunolagus monticularis
Lepus capensis
Lepus saxatilis
Lepus crawshayi
Poelagus marjorita

CARNIVORA

Proteles cristatus
Hyaena brunnea
Hyaena hyaena
Crocuta crocuta
Acinonyx jubatus
Panthera pardus
Panthera leo
Felis caracal
Felis libyca
Felis nigripes
Felis serval
Felis margarita
Felis aurata
Felis chaus
Otocyon megalotis
Lycaon pictus
Vulpes chama
Vulpes vulpes
Vulpes ruppelli
Vulpes pallida
Canis adustus
Canis mesomelas
Canis aureus
Canis simensis
Aonyx capensis
Aonyx congica
Lutra maculicollis
Mellivora capensis
Poecilogale albinucha
Ictonyx striatus
Nandinia binotata
Civettictis civetta
Genetta genetta
Genetta tigrina
Genetta pardina
Genetta victoriae
Genetta abyssinica
Genetta villiersi
Genetta servalina
Suricata suricatta
Paracynictus selousi
Cynictus penicillata
Herpestes ichneumon
Herpestes naso
Galerella sanguinea
Galerella pulverulenta
Rhynchogale melleri
Ichneumia albicauda
Atilax paludinosus
Mungos mungo
Mungos gambianus
Helogale parvula
Fennecus zerda
Poecilictus libyca
Poiana richardsoni
Osbornictus piscivora
Bdeodale crassicaudata
Bdeogale nigripes
Dologale dybowskii
Crossarchus obscurus

TUBULIDENTATA

Orycteropus afer

Appendix 1 Continued

PROBOSCIDEA

Loxodonta africana

HYRACOIDEA

Procavia capensis
Heterohyrax brucei
Dendrohyrax arboreus

UNGULATA

Ceratotherium simum
Diceros bicornis
Equus zebra
Equus burchelli
Equus (Asinus) asinus
Equus (Dolichohippus) grevyi
Choeropsis liberiensis
Sus scrofa
Phacochoerus aethiopicus
Potamochoerus porcus
Hippopotamus amphibius
Hyemoschus aquaticus
Giraffa camelopardalis
Connochaetes gnou
Connochaetes taurinus
Alcelaphus lichtensteinii
Alcelaphus busephalus
Damaliscus dorcas
Damaliscus lunatus
Damaliscus korrigum
Damaliscus hunteri
Cephalophus monticola
Cephalophus natalensis
Cephalophus sylvicultor
Cephalophus jentinki
Cephalophus spadix
Cephalophus niger
Cephalophus rufilatus
Cephalophus zebra
Cephalophus callipygus
Cephalophus dorsalis
Cephalophus leucogaster
Cephalophus olgibyi
Cephalophus nigrifrons
Sylvicapra grimmia
Antidorcas marsupialis
Oreotragus oreotragus
Madoqua kirkii
Ourebia ourebi
Raphicerus campestris

Appendix 1 Continued

Raphicerus melanotis
Raphicerus sharpei
Neotragus moschatus
Neotragus pygmaeus
Neotragus batesi
Aepyceros melampus
Pelea capreolus
Hippotragus equinus
Hippotragus niger
Oryx gazella
Oryx dammah
Oryx beisa
Syncerus caffer
Tragelaphus strepsiceros
Tragelaphus spekei
Tragelaphus angasii
Tragelaphus scriptus
Tragelaphus imberbis
Tragelaphus buxtoni
Taurotragus oryx
Taurotragus derbianus
Redunca arundinum
Redunca fulvorufula
Redunca redunca
Kobus ellipsiprymnus
Kobus leche
Kobus vardonii
Kobus defassa
Kobus megaceros
Hylochoerus meinertzhageni
Ammotragus lervia
Okapia johnstoni
Boocerus euryceros
Addax nasomaculatus
Litocranius walleri
Ammodorcas clarkei
Gazella dama
Gazella soemeringi
Gazella granti
Gazella dorcas
Gazella pelzelni
Gazella spekei
Gazella rufifrons
Gazella thomsoni
Gazella leptoceros
Dorcotragus megalotis
Rhyncotragus guentheri
Madoqua saltiana
Capra ibex

Appendix 2 Grouping of White's vegetation types and description of each group

Major type	White's map units	Description
Forest	1-3	Lowland rainforest
	4	Transitional rainforest
	6	Zambezian dry evergreen forest
Forest transitions and mosaics	11–14	Lowland rainforest and secondary grasslands
	15,16	Coastal mosaics
	17	Cultivation and secondary grassland replacing upland and montane forest
	19	Montane vegetation
	20	Transition from Afromontane scrub forest to Highveld grassland
	21	Mosaic of Zambesian dry evergreen forest and wetter miombo woodland
	22	Mosaic of dry deciduous forest and secondary and wooded grassland
	23	Mosaic of Mediterranean montane forest and altimontane shrubland
	24	Mosaic of Afromontane scrub forest, Zambezian scrub woodland and secondary grassland
Woodland	25–30	Woodlands
Woodland mosaics and transitions	31	Mosaic of wetter Zambezian woodland and secondary grassland
	32,33	Jos and Mandara Plateau mosaics
	34	Transition from South African scrub woodland to Highveld grassland
	35	Woodland transition to *Acacia* deciduous bushland and wooded grassland
	36	Transition from *Colophospermum mopane* scrub woodland to Karoo-Namib shrubland
Secondary wooded grassland	37	*Acacia polyacantha* secondary wooded grassland
Bushland and thicket	38,39	Evergreen and semi-evergreen bushland and thicket
	40	Itigi deciduous thicket
	42	Somalia-Masai deciduous bushland and thicket
	43,44	Deciduous wooded grassland and bushland
Bushland and thicket mosaics	45	Mosaic of East African evergreen bushland and secondary *Acacia* wooded grassland
	47	Mosaic of *Brachystegia bakerana* thicket and edaphic grassland

Appendix 2 Continued

Major type	White's map units	Description
Traditional scrubland	48	Tugela basin wooded bushland
	49	Transition from Mediterranean *Argania* scrubland to succulent semi-desert shrubland
Cape shrubland	50	Fynbos
Semi-desert vegetation	51	Bushy Karoo-Namib shrubland
	52	Succulent Karoo shrubland
	53	Dwarf Karoo shrubland
	54,55	Semi-desert grassland and shrubland
	56	The Kalahari/Karoo-Namib transition
Grassy shrubland	57	Grassy shrubland
Grassland	58	Highveld grassland
	59–61	Edaphic grassland
Edaphic grassland mosaics	62	Mosaic with *Acacia* wooded grassland
	63	Mosaic with communities of *Acacia* and broad-leaved trees
	64	Mosaic with semi-aquatic vegetation
Altimontane	65,66	Altimontane vegetation
Desert	67–69,74	Vegetationless deserts
	70–72	Deserts with vegetation
Azonal	75	Herbaceous swamp and aquatic vegetation
	76	Halophytic vegetation
	77	Mangrove
	78–80	Anthropic landscapes