Patterns of distribution and current protection status of the Carnivora, Chiroptera and Insectivora in South Africa

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Geographic patterns of species richness and endemism in three mammalian orders (Chiroptera, Insectivora and Carnivora) were studied in relation to the biomes and existing protected areas of greater South Africa (including Lesotho and Swaziland). Locality data for 21 500 specimens representing 124 species were analysed with a geographical information system. Species richness of Chiroptera is high in the savanna biome, particularly in the north-east of the country, owing to the marginal intrusion of 14 tropical species. Endemism in Chiroptera is low, however, with only two endemic species in the fynbos and Karoo biomes. The Carnivora display less biome specificity and endemism than the Chiroptera. Whereas the north-eastern savannas have the highest species richness, the transition between the Nama-Karoo and grassland biomes is an important southern African centre of endemism for the Carnivora, particularly the smaller species. In addition to being an important centre for species richness in the Carnivora and Chiroptera, the Kruger National Park is also particularly important for Red Data Book species in both orders. The Insectivora display both high species richness and endemism. Species richness of the Insectivora is greatest in the mesic south-east of the country, whereas endemism is most pronounced in the forest and grassland biomes. Differences in biome specificity and endemism between these orders reflect not only phylogenetic divergence, but also variation in body size, vagility and life-history strategies. Most of South Africa's endemics are small mammals and many of them are listed in the Red Data Book. Distributions, life-history strategies and trends in man-induced habitat degradation were used to re-evaluate the protection status of the 124 species. We conclude that at least 11 endemic species are not adequately protected by existing publicly owned protected areas and consequently identify several areas which need to be added to the existing protected area system.

Die geografiese patrone van spesiesverskeidenheid en endemisme in drie soogdier ordes (Chiroptera, Insectivora en Carnivora) is bestudeer in verhouding tot die biome en bestaande beskermde areas van groter Suid-Afrika (insluitend Lesotho en Swaziland). Lokaliteitdata vir 21 500 eksemplare verteenwoordigend van 124 spesies is geanaliseer met behulp van 'n geografiese informasiesisteem. Spesiesverskeidenheid van Chiroptera is die hoogste in die savanna-bioom, veral in die noord-oostelike dele van die land as gevolg van die marginale indringing van 14 tropiese spesies. Endemisme in Chiroptera is laag, met slegs twee endemiese spesies, een elk in die fynbos- en Karoo-biome. Die Carnivora vertoon minder bioomspesifisiteit en laer endemisme as die Chiroptera. Terwyl die noord-oostelike savannas die hoogste Carnivora spesiesverskeidenheid het, is die oorgang tussen die Nama-Karoo- en grasland-biome belangrik vir die endemiese Carnivora van suidelike Afrika, veral wat betref die kleiner spesies. Die Nasionale Kruger Wildtuin is nie net 'n belangrike sentrum vir spesiesverskeidenheid wat betref die Carnivora en Chiroptera, maar ook vir Rooi Data Boek-spesies van die twee ordes. Die Insectivora vertoon beide hoë spesiesverskeidenheid en endemisme, met die hoogste spesiesverskeidenheid in die mesiese suid-oostelike dele van die land, terwyl endemisme meer algemeen voorkom in die woud- en grasland-biome. Hierdie verskil in bioomspesifisiteit en endemisme reflekteer nie slegs filogenetiese divergensie tussen die ordes nie, maar ook variasie in liggaamsgrootte, verspreidingsvermoë en historiese lewensstragtegieë. Meeste van die Suid-Afrikaanse inheemse fauna is klein soogdiere en baie van hulle is gelys in die Rooi Data Boek. Die bewaringstatus van 124 spesies is geherevalueer met inagneming van verspreidings, lewensgeskiedenis- strategieë en verskynsels soos habitats wat deur die mens gedegradeer is. Ons gevolgtrekking is dus dat ten minste 11 van die endemiese spesies nie genoegsaam deur die bestaande reservaate beskerm word nie. Gevolglik het ons verskeie gebiede geïdentifiseer wat by die bestaande reservaatsisteem gevoeg moet word.

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Introduction

South Africa's commitment to the Convention on Biological Diversity needs to include a strategic plan for the preservation of its biodiversity. Mapping our biodiversity is a first step towards this, and facilitates research relevant to policy makers. Hockey, Lombard & Siegfried (1994) argued that, given time and financial constraints, it seems logical to develop such a national plan using well-documented taxocenes. They also concluded that species should be considered the units of biodiversity. Given the patchiness of many species distributions, effective biodiversity mapping should use a relatively fine scale of resolution.

Despite the demonstrable need for a central, easily accessible database of species distributions in South Africa, no such database is yet available. Recent studies on patterns of species richness and endemism among mammals (Siegfried & Brown 1992; Gelderblom 1993; Turpie & Crowe 1994) therefore had to rely on range maps from general texts. Furthermore, many of these studies had the following limitations: they used a one-degree or coarser grid scale for mapping; they relied on outdated taxonomy (Smithers 1983); or they ignored bats, the Insectivora and/or rodents, which comprise over 50% of local mammal species. Their results can thus be regarded as preliminary.

This study re-assesses the protection status of species included in three mammalian orders, and identifies areas of importance ('hotspots') or inadequately protected taxa, based on spatial analyses of point distribution data extracted from museum records and regional texts. We targeted bats (Chiroptera) as they are speciose and have been omitted from many previous studies (Siegfried & Brown 1992), and insectivores (Insectivora) as they comprise the majority of South African endemics. Carnivores (Carnivora) were also afforded priority, since many species are directly threatened by humans.

Methods

Distribution data (locality coordinates, or quarter degree squares 15' × 15' = QDS) for 21500 specimens in five natural history museums (Transvaal, Natal, Durban Natural Science, Carnegie, Smithsonian) were collated, and supplemented with literature records from major regional texts (Stuart 1981; Rautenbach 1982; Lynch 1983, 1989, 1994; Rowe-Rowe 1992). Only data for indigenous, terrestrial species found in the greater South Africa (including Lesotho and Swaziland) were considered. The baseline taxonomy used was that of Meester, Rautenbach, Dippenaar & Baker (1986), but with changes in accordance with more recent publications (Bronner, Taylor, Dippenaar, Watson, Robinson & Meester 1992; Wilson & Reeder 1993). In contrast to Wilson & Reeder (1993), we treated *Myosorex tenuis* as synonymous with *M. cafer,* since the specific rank of the former has not been conclusively demonstrated. For the same reason, *Eptesicus melckorum* was included in the widespread species *E. capensis* (Rautenbach, Bronner & Schlitter 1993).

The data used included information only from areas where species are confirmed present. Many regions, particularly in the arid interior, are inadequately sampled. In contrast, areas such as Gauteng, the Cape Peninsula and many of the protected areas are intensively sampled. The data are therefore affected by a bias in sampling intensity which must be taken into consideration when reviewing the results.

At each museum, data for each species were assembled and checked, before collation at the FitzPatrick Institute. The data were then overlaid with spatial information for publicly owned protected areas and the biomes (*sensu* Rutherford & Westfall 1986) using an ARC/INFO GIS as described in the introductory paper in this volume (Lombard 1995). The forests were not analysed because they occur at too fine a scale for effective analysis with QDS resolution data. The reserve database used was that of publicly owned protected area boundaries (Lombard 1995).

Four sets of analyses were performed on data for each of the three orders to determine: (i) patterns of species richness; (ii) patterns of RDB species richness of threatened taxa (species included in the endangered, vulnerable, rare and indeterminate categories of the most recent Red Data Book) (iii) patterns of endemism; and (iv) patterns of distribution and dispersion among the biomes *sensu* Rutherford & Westfall (1986). We defined hotspots as the top 5% of all data-containing QDSs in terms of species richness, RDB richness or endemism (Prendergast, Quinn, Lawton, Eversham & Gibbons 1993). Endemics were defined as species with more than 90% of their range in greater South Africa. Species were deemed to be adequately protected if >5% of their records fell within protected areas. Exclusive species were defined as being entirely restricted to a particular biome.

The three orders of mammals examined in this study were further subdivided for the first three analyses. Within the Insectivora, the families Chrysochloridae (golden moles) and Soricidae (shrews) were examined separately, as each occupy a distinct ecological niche. The Megachiroptera (frugivorous bats) and Microchiroptera (insectivorous bats) were also analysed separately, in view of their divergent habits and potentially divergent evolutionary histories (Goodman 1991). Small carnivores were examined separately, as the distributions of the large carnivores are determined almost entirely by the protected areas, which biases biogeographical patterns in this order.

Patterns of distribution and dispersion among the biomes of Rutherford & Westfall (1986) were identified by cluster analysis (UPGMA), for all species combined, and also for each order separately. Distribution data were quantified by weighting the presence of each species within each biome according to the number of QDSs in which it was recorded. Three measures of association were used. Duellman's (1965) faunal resemblance factor (FRF), which places emphasis on the presence or absence of taxa, was employed to assess taxonomic resemblance between biomes. As the FRF does not adequately compensate for differences in species density between biomes, Bray-Curtis (BC) and euclidean distance coefficients (ED) were used to identify patterns of hierarchic similarity among the biomes, based on both taxonomic affinity and variation in the size and dispersion of the zonal faunas. All multivariate analyses were performed using BIOΣTAT II (Pimenter & Smith 1986) on a 80386 microcomputer.

Results

Carnivora

Species richness

Species richness of the carnivores is greatest in the mesic, eastern parts of South Africa, particularly in the savanna and grassland biomes (see Table 1, Figure 1, Figure 2a). Species richness is much lower in the drier, western parts of the country, especially the Succulent Karoo (Table 1). There is a very clear centre of species richness in the Kruger National Park (Figure 2a). The savanna biome contains the most species records and the only exclusive species, *Panthera leo, Civettictus civetta* and *Paracynictis selousi.* The civet and Selous

Table 1 Summary of biome species richness, Red Data Book richness, endemicity and exclusivity for the Carnivora, Chiroptera and Insectivora in South Africa

Biome	Records[1]	Species[2]	RDB[3]	Endemics[4]	Exclusives[5]
Carnivora					
Fynbos	8,3	20	7 (0,35)	4 (0,20)	0
Grassland	38,1	31	10 (0,32)	4 (0,13)	0
Nama-Karoo	12,6	26	9 (0,35)	4 (0,15)	0
Succulent Karoo	4,0	18	6 (0,33)	4 (0,22)	0
Savanna	36,9	34	12 (0,35)	4 (0,12)	3
Chiroptera					
Fynbos	11,8	18	3 (0,17)	2 (0,11)	1
Grassland	16,6	31	7 (0,23)	1 (0,03)	0
Nama-Karoo	4,8	17	3 (0,18)	2 (0,12)	1
Succulent Karoo	3,4	12	0 (0, 0)	1 (0,08)	0
Savanna	63,4	51	23 (0,45)	1 (0,02)	15
Insectivora					
Fynbos	10,3	9	4 (0,44)	6 (0,67)	0
Grassland	41,3	23	13 (0,57)	12 (0,52)	1
Nama-Karoo	3,9	9	2 (0,22)	5 (0,56)	0
Succulent Karoo	3,7	9	4 (0,44)	6 (0,67)	3
Savanna	40,9	24	14 (0,58)	12 (0,50)	2

[1] % Records: Percentage of the total number of carnivore records found in that biome. [2] Species: Number of species [3] RDB: Number of Red Data Book species, followed by the proportion of species in the biome that are listed in the RDB. [4] Endemics: Number of endemic species, followed by the proportion of species in the biome that are endemic. Note that for carnivores there are no South African endemics and the calculations are based on southern African endemics. For the Chiroptera and Insectivora the endemics are defined as having 90% of their range within South Africa. [5] Exclusives: Species recorded exclusively in one biome.

mongoose are further restricted to savanna woodland. Only 20% of species occur in under three biomes (Table 2), confirming that carnivores exhibit little habitat specificity.

The transition zone between the Nama-Karoo and the grasslands in the southern Free State is a region of high species richness for the small carnivores. They also exhibit higher species richness in the eastern parts of South Africa, but the concentration of species in the Kruger National Park is less pronounced.

Red Data Book richness

The pattern of RDB richness follows that of species richness, with an even more pronounced concentration of species in the Kruger National Park (Figure 2b). The Kwazulu-Natal Drakensberg is also an important area. The lower portion of the Nama-Karoo-grassland transition in the Eastern Cape appears to be important for the smaller RDB carnivores.

Endemics

The only possible South African endemic is *Galerella swinnyi* from Port St Johns, the status of which is dubious, therefore it was treated as a subspecies of *G. sanguinea*, the slender mongoose. Although there are no South African endemics, the drier 'South-West Arid' biome (*sensu* Meester 1965 = Nama-Karoo, arid savanna and Succulent Karoo) has six southern African endemics (*Hyaena brunnea, Felis nigripes, Vulpes chama, Suricata suricatta, Cynictis penicillata, Galerella pulverulenta,* and two endemic subspecies *Galerella s. swinnyi* and *Galerella s. nigrata*). (Southern Africa was defined as that portion of mainland Africa south of the Cunene and Zambezi rivers.)

There is a concentration of southern African endemics in the transition between the grassland and Nama-Karoo biomes (Figure 2c). This area extends from the southern Free State

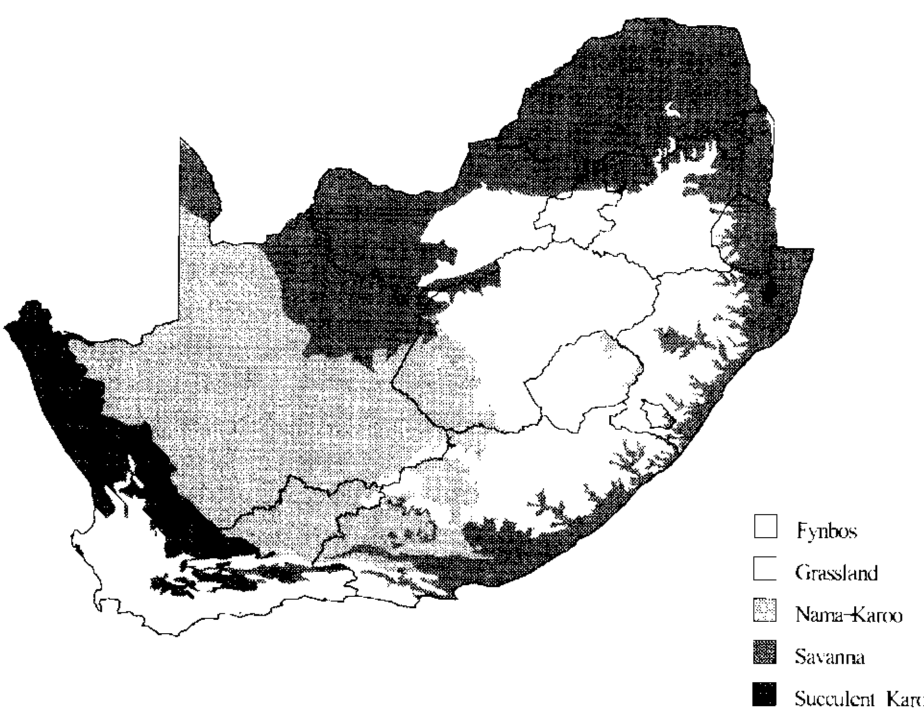

Figure 1 Distribution of the biomes and political boundaries in greater South Africa. (Biomes after Rutherford & Westfall 1986).

Figure 2 Patterns of species richness (a), RDB richness (b) and endemism (c) for the Carnivora in greater South Africa. The keys indicate the number of carnivore species per QDS. The highest category (black) indicates the hotspots.

Table 2 Biome specificity in the Carnivora, Chiroptera and Insectivora of South Africa, as indicated by the number of species occurring in one or more biomes

Carnivora		Chiroptera		Insectivora	
No. species	No. biomes	No. species	No. biomes	No. species	No. biomes
3	1	17	1	6	1
4	2	15	2	17	2
6	3	9	3	5	3
6	4	6	4	1	4
15	5	6	5	3	5

down to the coastal plain near Grahamstown. A smaller centre of endemism exists at the interface of the fynbos and Succulent Karoo in the Western Cape Province.

Protection of hotspots and priority species

Hotspots of species richness are relatively well protected, but at least 10 areas, chiefly in the southern Free State, deserve further attention. Similarly, only four RDB hotspots, three on the border with Botswana, and one in southern Free State, are not protected (Figure 3). The inadequately protected southern Free State is also important in terms of high endemism (Figure 3). Only *Rhynchogale melleri* (Meller's mongoose) is not represented in a publicly owned protected area in this dataset. *Felis nigripes* (the small spotted cat) has only one data point (out of 74) in a protected area, but may also occur at Barberspan Nature Reserve in the North West Province.

Chiroptera

Species richness

Species richness is greatest in savannas (63,4% of all records, 51 species; Table 1), particularly in the woodland savanna of the Northern Province and North West Province. The Kruger National Park is important, with exceptionally high species richness in the Pafuri region (Figure 4a). There are also smaller areas of high species richness in Kwazulu-Natal, Gauteng and the Eastern Cape. All the hotspots for species richness fall within the savanna biome. The grassland is the next most important biome (16,6% of records, 31 species). As in the carnivores, species richness in the fynbos and Karoo biomes is much lower.

The savanna contains 15 exclusive species (Table 1), 14 of which are restricted to savanna woodland. Biome specificity is pronounced as more than 75% of species occur in three or fewer biomes (Table 2), and 17 species are found exclusively in one biome.

The Megachiroptera have fewer records and lower species diversity (8/51 = 16% of bats). The hotspots of Megachiropteran species richness occur exclusively within the Northern Province, whereas the Microchiroptera have additional hotspots in northern Kwazulu-Natal, Gauteng and the Eastern Cape.

Red Data Book richness

The concentration of species in the savannas of the Northern Province and northern Kwazulu-Natal is even more pronounced for threatened taxa (Figure 4b).

Figure 3 Unprotected hotspots of species richness, Red Data Book richness and endemism for Carnivora overlaid with the existing publicly owned protected areas.

Endemics

Despite their low species richness, the fynbos and Karoo biomes are the only regions with endemics (Figure 4c). Two Microchiroptera, *Rhinolophus capensis* and *Myotis lesueuri*, occur in these biomes with only marginal intrusions into savanna or grassland.

Protection of hotspots and priority species

Of the species richness hotspots, only the Amatola region of Eastern Cape is not protected (Figure 5). All hotspots coincide with protected areas, as although the Waterberg, which is a hotspot of species richness and RDB species, is not protected by any publicly owned protected areas, it is covered by private reserves. Similarly the QDSs with both endemic species also contain protected areas.

Although *Eidolon helvum* (the straw-coloured fruit bat) has <5% of its records in protected areas, it is widespread and migrates over large distances and thus does not warrant priority status. *Myotis lesueuri* (Lesueur's hairy bat) also has <5% of its records in protected areas. As this endemic species has a karyotype which is thought to be ancestral to vespertilionid bats (Rautenbach, *et al.* 1993), and has a few, scattered populations in the drier parts of the country, its Red Data Book status should be changed from Indeterminate to Rare (Smithers 1986: pp. 6), and its conservation status improved. *Otomops martiensseni* (the large-eared free-tailed bat) also has <5% of its records in protected areas, but probably does occur in several Durban municipal reserves. It is represented in southern Africa by the endemic subspecies *O. m. icarus* which has a limited distribution. As it is a roof-dweller which is increasingly being subjected to eradication by pest-control companies, it must be considered a species of conservation concern; we thus recommend that it be afforded priority status. *Rhinolophus denti* (Dent's horseshoe bat) also has few records in existing protected areas but is not a high priority species, as it is probably only a subspecies of *R. swinnyi* (Swinny's horseshoe bat) (Rautenbach 1986).

Insectivora

Species richness

Species richness is concentrated in the eastern, mesic parts of South Africa, and is particularly rich at the boundary of the grassland (41% of records, 23 species, Table 1) and savanna (41% of records, 24 species, Table 1) biomes. Species richness is high in the north and east, and coincides largely with mountainous regions and forests receiving high precipitation (Figure 6a).

Two species occur exclusively in the savanna: *Amblysomus julianae* and *Calcochloris obtusirostris*. A further nine species are found only in grassland and savanna. Three species are found exclusively in the Succulent Karoo: *Cryptochloris wintoni, C. zyli*, and *Eremitalpa granti*. If forests were analysed separately, they would have two exclusives (*C. trevelyani* and *C. duthieae;* G.N. Bronner pers. obs.). Over 71% of species are found in under three biomes (Table 2). Biome specificity is thus pronounced, as in bats.

Chrysochlorid (golden mole) species richness is concentrated in the savannas and grasslands of Gauteng and Mpumalanga, and in a broad band around the coast. They do not extend far into the arid interior of the country and are entirely absent in the arid savanna of the Northern Cape.

The soricids (shrews) also exhibit high species richness in the mesic savanna woodlands in the north-east of the country. However, they extend further into the western parts of the grasslands and the and savanna than is the case with chrysochlorids.

Red Data Book richness

RDB richness is also concentrated in the savanna and grass-

(a)

(b)

(c)

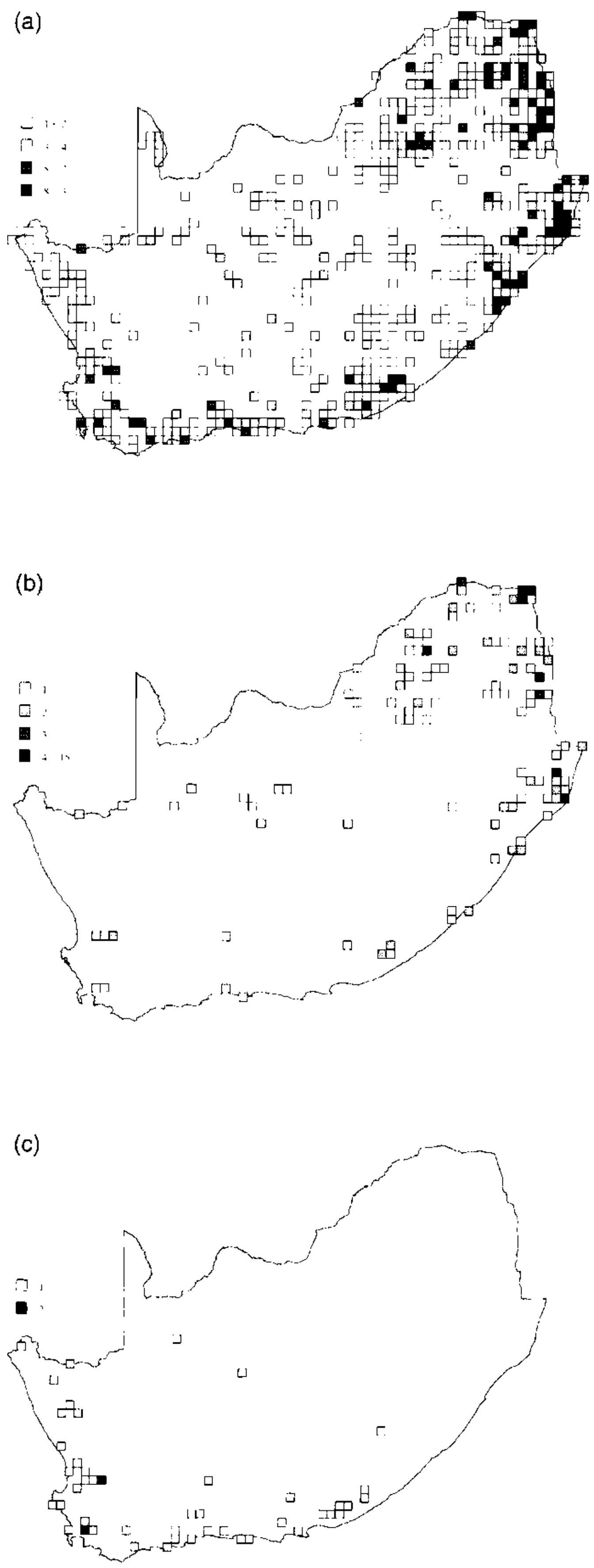

Figure 4 Patterns of species richness (a), RDB richness (b) and endemism (c) for the Chiroptera in greater South Africa. The keys indicate the number of bat species per QDS. The highest category (black) indicates the hotspots.

land biomes of the northern and eastern parts of South Africa particularly on the Free State-Gauteng, and Free State-Mpumalanga boundaries, as well as in south-eastern Kwazulu-Natal (Figure 6b, Table 1). The southern coast is also important for RDB species, particularly the forests of the Knysna-Tsitsikamma region.

Endemics

The insectivores comprise 46% of all South African endemic mammals. Of the 20 insectivore endemics, 16 (80%) are chrysochlorids. Endemism is concentrated in the NE savanna and grassland, and along the SE coast, which are also the areas of highest species richness (Figure 6c). Nevertheless, the SW regions still have a higher percentage of endemics (Table 1).

Protection of hotspots and priority species

Almost all the QDSs with high species richness correspond with existing protected areas in the savanna and grasslands of KwaZulu-Natal and Mpumalanga. The unprotected hotspots are: Wakkerstroom in Mpumalanga; the NE Kwazulu-Natal mist forests; Port St Johns in the Eastern Cape; and Lamberts Bay in the Western Cape (Figure 7). Wakkerstroom contains three sympatric golden moles (*Chrysospalax villosus, Amblysomus septentrionalis* and *Chlorotalpa sclateri*; see Bronner, in press), which contribute to its hotspot status. The Port St Johns hotspot also contains three chrysochlorids (*Chrysospalax villosus, Chrysospalax trevel-yani* and *Amblysomus hottentotus*). Similarly, the hotspot status of the Lamberts Bay QDS is due to the sympatric presence of three golden mole species: *Cryptochloris zyli* (which is known from only this locality), *Eremitalpa granti* and *Chry-sochloris asiatica.*

Of the four RDB hotspots, three overlap with existing protected areas, thus only Wakkerstroom is not protected (Figure 7). The hotspot in the Knysna-Tsitsikamma forest is conspicuous, and is due to the presence of *Myosorex longicaudatus* (the long-tailed forest shrew) which is known from only this area, as well as two golden mole species with limited distributions.

With regard to hotspots of endemism, both Wakkerstroom and Port St Johns are not adequately protected (Figure 7).

The following species have <5% of their records within protected areas: *Atelerix frontalis* (the South African hedgehog); and the golden moles *Chrysospalax trevelyani, Cryptochloris wintoni, Cryptochloris zyli, Chrysochloris visagiei, Chlorotalpa sclateri, Eremitalpa granti, Amblysomus septentrionalis,* and *Amblysomus marleyi. C. trevelyani* (the giant golden mole) is restricted to forests with deep soils, leaf litter and dense shrubs, a habitat which is increasingly threatened. Although protected in state forests, giant golden moles are preyed upon by feral dogs (Nicoll & Rathbun 1990). More forest protected areas and anti-predation measures are thus needed to ensure adequate levels of protection for this species.

E. granti is protected in Namibia. However, the moles there represent a distinct subspecies (*E. g. namibensis*). For this reason, additional protection of *E. g. granti* within South Africa is recommended. *C. sclateri* is widespread, coexists well with man, and is thus probably not in any danger. It has also recently been recorded from Garden Castle Nature

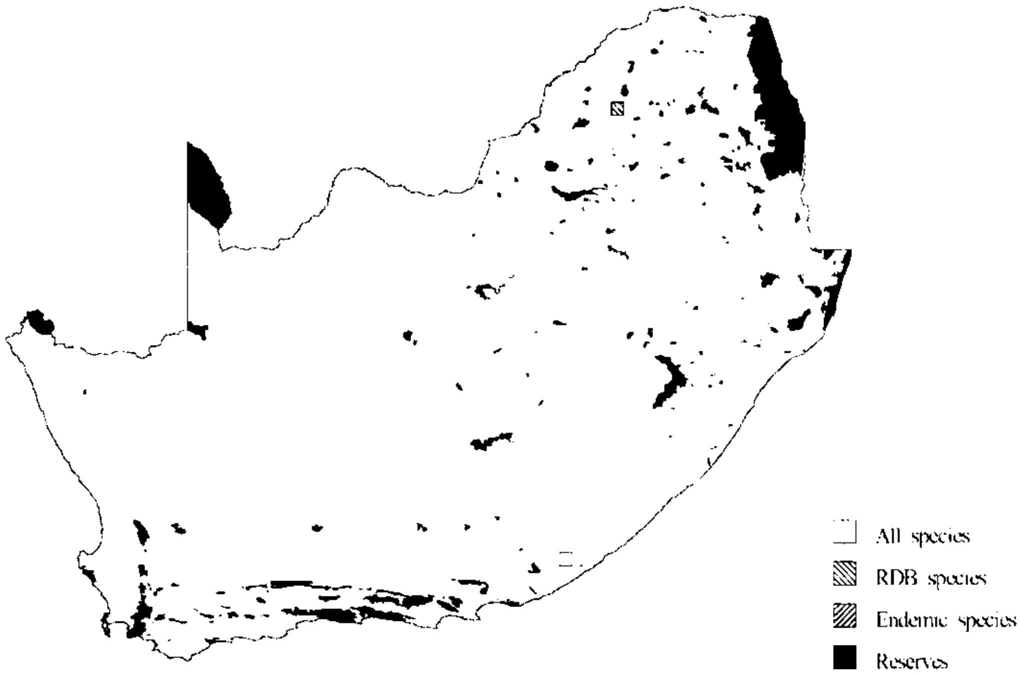

Figure 5 Unprotected hotspots of species richness, Red Data Book richness and endemism for Chiroptera overlaid with the existing publicly owned protected areas.

Reserve in Kwazulu-Natal. *Chrysochloris visagiei* is probably only an aberrant *C. asiatica* (Meester *et al.* 1986, G.N. Bronner pers. obs.), and thus is not suitable for conservation prioritization. *Amblysomus septentrionalis* (a cryptic species formerly included in *A. hottentotus*; Bronner in press) has not yet been recorded in a national or provincial protected area, but does occur in the Ermelo municipal reserve. Since this species is adaptable and coexists with man (G.N. Bronner pers. obs.), its conservation status is probably satisfactory.

A. marleyi, however, has a very restricted distribution on the eastern slopes of the Lebombo mountains in N. Kwazulu-Natal, and does not occur in any publicly owned protected areas. This species should be afforded priority status, and satisfies the Red Data Book criteria for classification as Rare (Smithers 1986: pp. 6). Similarly, *C. wintoni* and *C. zyli* are known from only scattered localities on the sandy Namaqualand plain in the Succulent Karoo, a habitat that is being degraded by strip mining. Their assignment to the IUCN status of Rare (*cf.* Indeterminate) thus seems justified, as recommended by Meester (1976).

Intensity of sampling and range size

Most carnivores were recorded from 10 or more QDSs, implying that they are relatively well sampled and occur over fairly wide ranges (Table 3). Conversely, over 40% of bat and insectivore species occurred in <10 QDSs, which indicates the low intensity of sampling in these groups. The Nama-Karoo has the lowest number of species and records; this is partly a consequence of inadequate sampling, and as a result no data are available for numerous QDSs.

Patterns of distribution and dispersion among the biomes (*sensu* Rutherford & Westfall 1986)

Faunal resemblance factors (FRF) computed from combined data for the three orders are mostly above 0,5 (Table 4), indicating that more than half of the species occurring in each biome are shared with another biome. Relatively high FRF indices are also evident when data for the carnivores are analysed separately. However, FRF values computed from data for bats and insectivores independently are considerably lower than either the combined values, or those of carnivores.

A phenogram based on the combined FRF values (Figure 8) separates the five biomes into two groups. One group comprises fynbos, Nama- and Succulent Karoo, which diverge at relatively low FRFs. The other includes grassland and savanna, which are linked by a much higher FRF of 0,856, suggesting a close faunal resemblance between them. However, in phenograms based on Euclidean distance and Bray-Curtis coefficients, grassland clusters well apart from savanna, grouping most closely with fynbos. This pattern is also evident when data for the three orders are analysed independently (Figure 9).

Linkage orders and zonal inter-relationships for carnivores, bats and insectivores differ, but some trends are evident. The FRF phenograms indicate that carnivores show closer taxonomic affinity between biomes than either bats or insectivores. The savanna and Karoo biomes are closely linked in the carnivore phenograms, whereas, these zones plot well apart in the bats and insectivores. The wide separation of savanna from the other biomes in the ED phenogram for bats emphasizes the remarkable species richness of the savanna bat fauna.

Discussion

Knowledge of species distributions and the processes which drive them facilitates conservation. Crowe (1990) suggested that in South Africa these patterns are largely determined by rainfall as mediated by vegetation. Endemism in isolated biomes, such as fynbos, is higher than that found in extensive biomes such as savanna. Many tropical species found in these

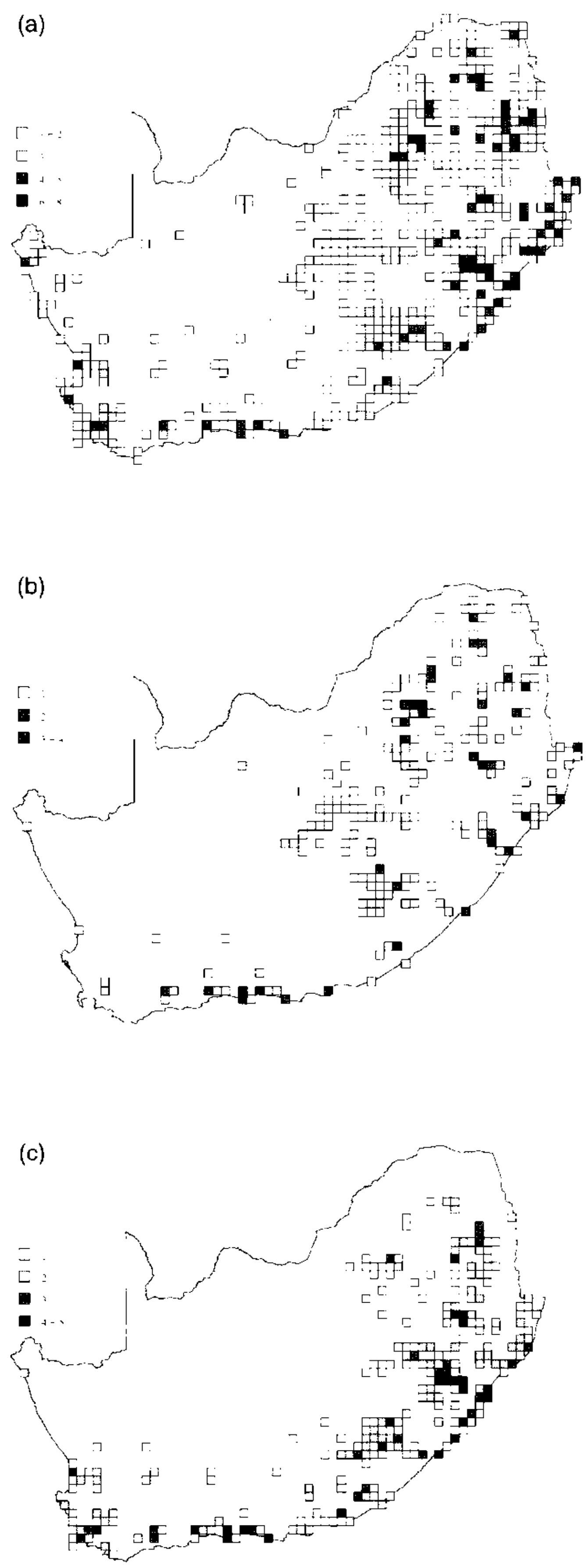

Figure 6 Patterns of species richness (a), RDB richness (b) and endemism (c) for the Insectivora in South Africa. The keys indicate the number of carnivore species per QDS. The highest category (black) indicates the hotspots.

large biomes extend marginally into South Africa, giving rise to high species richness on the northern borders. This phenomenon is termed the subtropical subtraction syndrome, and is evident in the Chiroptera and to a lesser extent in the Carnivora. In the Insectivora, this phenomenon is also evident in the Soricomorpha (shrews), but not in the Chrysochloromorpha (golden moles) which have a markedly southern African centre of diversity.

Carnivora

The high diversity of carnivores in the NE savanna is promoted by the extensive Kruger National Park which supports species with large area requirements, particularly RDB species that do not coexist well with man.

This study, like previous work (Skinner & Smithers 1990; Turpie & Crowe 1994), indicates that most carnivores have large, pan-African distributions with low biome specificity. This can be attributed to their generalized habitat requirements, relatively larger size and consequent greater vagility.

The unprotected hotspot in the southern Free State contains high species richness, endemics and RDB species, and is thus a conservation priority for carnivores in South Africa. Augmentation of the protected area network in this region would improve the protection of a maximum number of species with a minimum of land. However this hotspot coincides with a transition zone where species adapted to different vegetation types coexist at the extremes of their ranges. Conservation of hotspots closer to the centre of the respective vegetation types, in this case the Karoo savanna and grassland biomes, would be more effective, but less economical in terms of the land area required.

The hotspot of southern African carnivore endemics in the SW arid region of South Africa is notable in view of Turpie & Crowe's (1994) definition of a SW biogeographical province of endemism for carnivores in Africa. The boundaries of this area agree with the SW Arid region of Meester (1965) and Rautenbach (1978), but not Rutherford & Westfall's (1986) re-defined limits of biomes. Turpie & Crowe (1994) also noted a trend towards increasing species richness of carnivores as one approaches the equator, hence the northerly concentration of species richness in South Africa.

Chiroptera

The importance of the savannas for bats is evident in terms of species richness and RDB species and has been noted by other authors (Rautenbach 1978). It has also been noted that the positive correlation between rainfall and species richness on a latitudinal basis, which is shown by most mammalian taxa in South Africa, is particularly marked in the bats (Nel 1975).

High species richness in NE woodland savanna may be attributed to the marginal intrusion of 14 tropical species that have their centres of distribution further north in Africa. Many of these subtropical species are listed in the RDB as a result of their limited distribution in South Africa. Sampling bias is also implicated in the concentration of species in the Kruger National Park, as the Transvaal Museum has sampled the Pafuri region intensively for over 15 years.

Bats exhibit higher biome specificity than carnivores as a result of greater specialization to particular habitats (espe-

Figure 7 Unprotected hotspots of species richness, Red Data Book richness and endemism for Insectivora overlaid with the existing publicly owned protected areas.

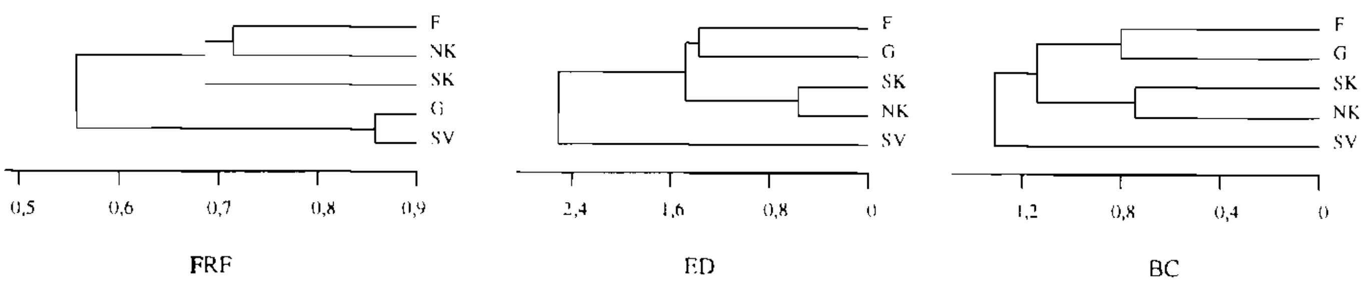

Figure 8 Faunal affinities of the biomes in South Africa, as indicated by UPGMA cluster analysis of Faunal Resemblance Factors (FRF), Euclidean distances (ED) and Bray-Curtis (BC) coefficients computed from the combined data for 124 species of Carnivora, Chiroptera and Insectivora. Biome abbreviations are: F = fynbos; NK = Nama-Karoo; SK = Succulent Karoo; G = grassland; SV = savanna. The resolution of our data prevented the analysis of the Forest biome, which is highly-fragmented and relatively small in area, as a distinct zoogeographic zone. Data for the forest biome are thus apportioned among adjoining fynbos, grassland and savanna biomes.

Table 3 Level of sampling and range size

Cumulative No. species	Cumulative percentage	No. QDS
Carnivora		
0	(0%)	< 5
2	(6%)	< 10
12	(35%)	< 100
Chiroptera		
15	(28%)	< 5
23	(48%)	< 10
50	(94%)	< 100
Insectivora		
8	(25%)	< 5
14	(44%)	< 10
30	(94%)	< 100

cially woodland). They are, however, less specific than the Insectivora, and show remarkably low endemism. This is probably a consequence of the relatively high vagility concomitant with flight, and their migratory tendencies.

Insectivora

The mesic eastern savanna and grassland is important for the insectivores. A finer scale of analysis will undoubtedly reveal the importance of the forests for this taxon. Again, inequitable geographic sampling may have biased results, especially for the golden moles which are notoriously difficult to catch. Scarcity in the drier, western parts of the country is, however, real, as most local species are mesic-adapted (Skinner & Smithers 1990).

Unlike many vertebrates, in the insectivores the areas of highest endemism and highest species richness coincide. The high endemism of the insectivores reflects the low vagility of most species (especially fossorial golden moles), their small size, and their specialized habitat requirements. The particu-

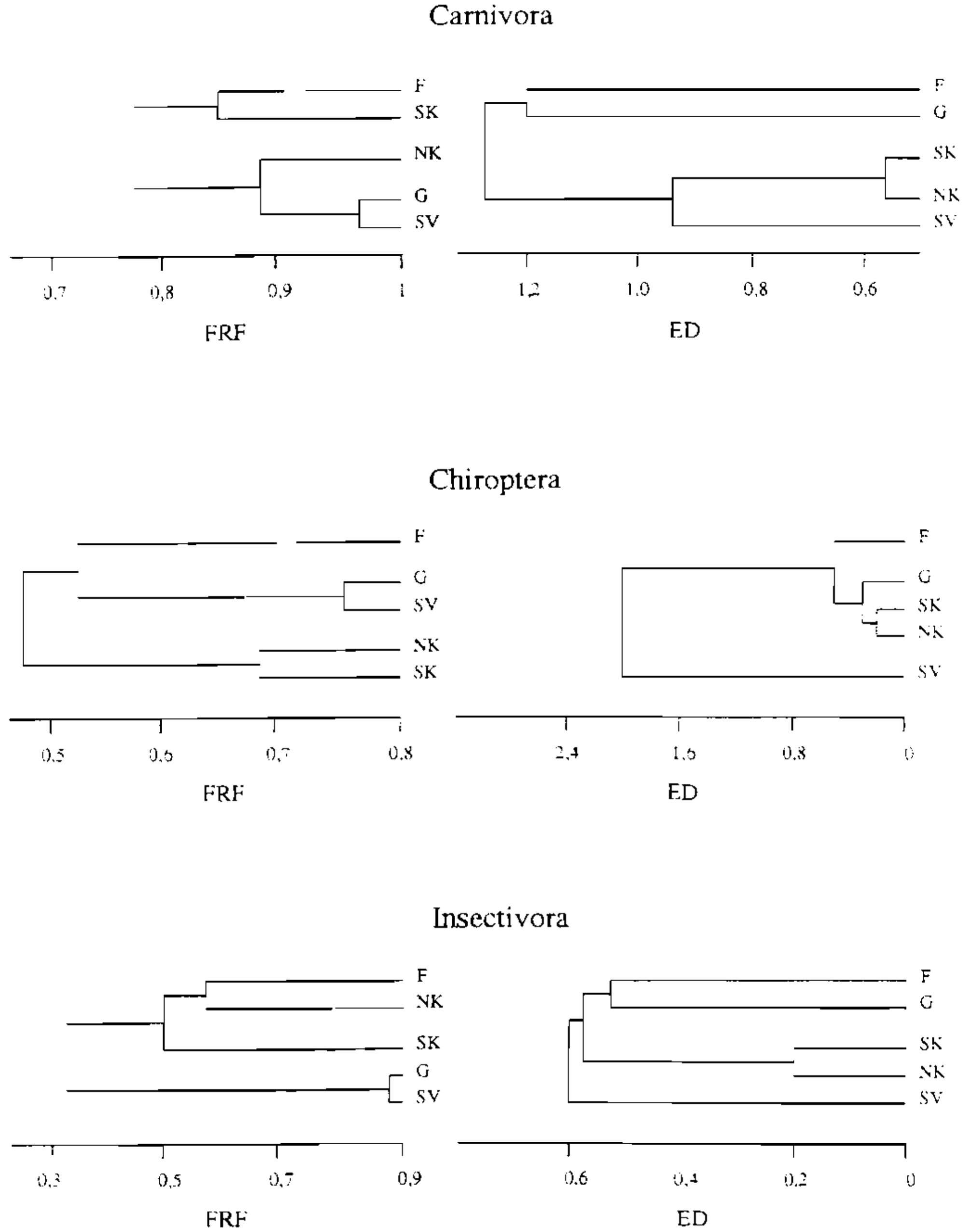

Figure 9 Phenograms produced from UPGMA clustering of Faunal Resemblance Factors (FRF) and Euclidean distances (ED) among the biomes, based on independent analysis of data for the Carnivora, Chiroptera and Insectivora. Biome abbreviations are: F = fynbos; NK = Nama-Karoo; SK = Succulent Karoo; G = grassland; SV = savanna.

larly high endemism in the golden moles is thought to indicate local speciation as they are unique amongst the insectivores in having a markedly southern African centre of distribution (Nicoll & Rathbun 1990).

The very low vagility of the Chrysochloridae is characteristic of subterranean mammals, and appears to be a predictor of high endemism, and indeed, high differentiation within populations. This emphasizes the need to protect these species throughout their ranges, especially in view of cryptic species which have recently been identified (Bronner in press). Siegfried & Brooke (1994) also highlight the importance of protecting under-recognized taxa (which they define as subspecies which are deserving of full specific status) such as *Eremitalpa granti*. The recognition and protection of cryptic and under-recognized species is important as they are frequently endemic (Siegfried & Brooke 1994).

The level of endemism is highest in the insectivores. Furthermore, many insectivores are listed in the Red Data Book. This combination is of concern, and indicates that they should be a priority taxon for conservation action. The Wakkerstroom and Port St Johns regions are both home to several endemics, but do not contain any protected areas. Protection of these areas is particularly important in view of the RDB status of many of the resident endemic insectivores.

General trends

The influence of biomes and their size

In all orders, the savannas followed by the grasslands emerge as the most important biomes in terms of percentage of

Table 4 Resemblance of the insectivore, bat and carnivore faunas of five biomes in South Africa. (a) FRF indices for all species combined (above diagonal), and for insectivores only (below diagonal). (b) FRF indices for carnivores (above diagonal) and bats (below diagonal)

	Fynbos	Nama-Karoo	Succulent Karoo	Grassland	Savanna
(a) Insectivora\All taxa					
Fynbos	–	0,708	0,698	0,575	0,552
Nama-Karoo	0,556	–	0,704	0,672	0,608
Succulent Karoo	0,556	0,444	–	0,516	0,446
Grassland	0,312	0,500	0,180	–	0,856
Savanna	0,364	0,424	0,180	0,894	–
(b) Chiroptera\Carnivora					
Fynbos	–	0,826	0,842	0,784	0,740
Nama-Karoo	0,572	–	0,818	0,912	0,860
Succulent Karoo	0,400	0,690	–	0,734	0,692
Grassland	0,530	0,500	0,512	–	0,952
Savanna	0,492	0,756	0,380	0,756	–

records, the number of species and the number of endemics represented. High mammalian species richness in savannas has been noted by several authors and is suggested to be a result of the high diversity of habitats (Rautenbach 1978; Siegfried & Brown 1992).

These two biomes are, however, very large. When one considers biome area, the fynbos followed by the Succulent Karoo become the most important in terms of density of species and endemics.

Savanna, followed by grassland, also has the highest number of RDB species per unit area. In view of the pressures from agricultural and pastoral development in these two biomes, these RDB species are of concern (Coe 1989). Flagship species are large, charismatic species, the protection of which is assumed to provide an umbrella of protection for the smaller components of biodiversity. Although the numerous protected areas in these biomes protect these flagship species, this analysis reveals that the smaller sized taxa, particularly insectivores, are not adequately protected by this approach. Other biomes, such as the Karoo, have fewer flagship species and are even less protected by existing protected areas, despite the numerous endemic and Red Data Book species they contain (Hilton-Taylor & Le Roux 1989).

Patterns of distribution among the different biomes

The FRF values computed from data for all species combined are well above those reported for southern African mammals in general by Rautenbach (1978), and would seem to indicate that the mammal faunas of the different biomes are too similar to warrant their recognition as distinct zoogeographic zones. However, the relatively high FRF indices for all species combined appear to be influenced largely by the inclusion of the carnivores, which, as discussed earlier, have low biome specificity. The smaller-sized bats and insectivores show greater biome specificity, and consequently also low FRF indices. For these orders, the FRF values are low enough to warrant the consideration of fynbos, Nama- and Succulent Karoo as defined by Rutherford & Westfall (1986) on a botanical basis as valid zoogeographic zones, with relatively distinctive faunas.

Conversely, the tendency for grassland and savanna biomes to fall in the same subclusters in FRF phenograms for all three orders (Figure 9) indicates that the faunas of these zones are taxonomically too similar to warrant distinction between them. This agrees with Meester's (1965) relegation of grassland to a subzone of southern savanna. However, the wide separation between grassland and savanna in ED and Bray-Curtis phenograms indicates that when both taxonomic similarity and the disproportionate sizes and densities of the faunas are considered, grassland must be considered a distinct biome with closer affinity to fynbos than savanna. This agrees with the findings of Rautenbach (1978), which were based on analyses of southern African mammals.

Our results do not, however, fully support Rautenbach's (1978) conclusion that savanna is faunistically most closely related to the arid biotic zones further to the west in South Africa, as this biome is well differentiated from others in euclidean distance phenograms for bats and insectivores (Figure 9).

Intensity of sampling

The Succulent and Nama-Karoo together with the arid savanna comprise the SW Arid region. Despite the importance of their unique fauna (Moreau 1952; Balinsky 1962; Bigalke 1972; Meester 1965), these areas are severely undersampled. Many species are inadequately sampled, especially the small, cryptic mammals which are difficult to trap. This indicates a pressing need for further work on the distribution of South African mammalian taxa.

Conclusions

Our analysis of the distributions of carnivores, bats and insectivores in South Africa reveals several interesting patterns. Vegetation appears to have an important influence on the distributions of the Chiroptera and Insectivora, and cluster analyses indicate that the botanically defined biomes of Rutherford & Westfall (1986) are valid for these orders. These biomes are not, however, clearly differentiated in the more euryoecious carnivores. Our results support Rautenbach's (1978) separation of savanna and grassland, but not the close affinity of the savanna and the and western biomes which he proposed.

Species richness is highest in the northern savannas, with the south-western biomes exhibiting higher endemism. Within the savanna, the Kruger National Park is particularly important in terms of both species richness and RDB species for bats and carnivores. Both of these orders exhibit low endemism and a pronounced subtropical subtraction syndrome. The insectivores, on the other hand, have very high levels of endemism focused in the coastal forests of the Eastern and Western Cape Province and the grasslands of the Wakkerstoom area of Mpumalanga.

The Wakkerstroom and Port St. Johns insectivore hotspots are inadequately protected as is the southern Free State which is important for carnivores in terms of species richness, southern African endemics and RDB species. The bat hotspots are, however, fairly well protected.

Amongst the carnivores, species which require additional protection include *Rynchogale melleri* and *Felis nigripes*. Bats which require additional protection include *Myotis lesueuri* and *Otomops martiensseni*. Seven insectivore species require improved protection. They include *Atelerix frontalis* and six chrysochlorids: *Chrysospalax trevelyani, Cryptochloris wintoni, Cryptochloris zyli, Eremitalpa granti, Amblysomus septentrionalis* and *Amblysomus marleyi*.

This analysis thus reveals that the existing protected area system needs to be supplemented with additional protected areas in the southern Free State, Wakkerstroom and Port St Johns areas if all Insectivora, Chiroptera and Carnivora are to be adequately protected. It also indicates the pressing need for more intensive sampling of the cryptic small mammals, particularly in the arid interior of South Africa.

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