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BIRD AND DUNG BEETLE ASSEMBLAGE STRUCTURE IN THE
MAPUTALAND CENTRE: AN ANALYSIS OF CONGRUENCE

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Centre: An analysis of congruence**

by

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ABSTRACT

In southern Africa, the Maputaland Centre (MC) forms one of the most significant centres of endemism and diversity. Its characteristic Sand Forest habitat contains the highest number of endemic plant species in the MC, and shows a weak biogeographic affiliation to Afromontane forest. Despite suggestions that endemic fauna are also restricted to Sand Forest, habitat selection (i.e. habitat-associated heterogeneity in assemblages) has not been investigated for these taxa, and their biogeographic affiliations have not been adequately resolved. Such information is important due to the current threats to Sand Forest habitat both within and outside formal conservation areas. In this study I examine variation in bird and dung beetle assemblages between habitats (Sand Forest and the Mixed Woodland matrix within which it is embedded), and between reserves (Tembe Elephant Park, Sileza Nature Reserve), in the MC, and the regional biogeographic affinities of the birds. Both bird and dung beetle assemblages were homogenous within habitat types within reserves, but differed between habitat types, and between reserves within the same habitat type. Endemic bird species were most abundant and tended to be restricted to Sand Forest habitats, but often in only one of the two reserves sampled. These birds, which have previously been considered rare, were found to achieve reasonably high abundances in Sand Forest (i.e. rarity tends to be diffusive).

None of the rare or common dung beetle species studied here were endemic to a reserve or to the MC. These results extend previous demonstrations of significant between-reserve heterogeneity in plant assemblages, to animal assemblages, and suggest that a broad conservation goal of conserving 10% of a given vegetation type does not translate into effective reserve design at a local scale in the MC. In addition, dung beetle detector species were identified that can be used to monitor change in Sand Forest patches, especially in Tembe where Sand Forests are under threat from elephants. The species occupancy frequency distributions for all three assemblages were largely similar at all spatial scales examined (i.e. local habitat reserve, reserve, habitat and regional scales). No evidence was thus found of organismal scaling. In contrast, the species occupancy frequency distributions for all three assemblages changed from bimodal at the smallest scale to unimodal at the largest scale (distance scaling). The patchiness of the Mixed Woodland – Sand Forest system and associated metapopulation dynamics may be generating this bimodality at the local habitat scale. At a more regional scale the avian assemblages of both Sand Forests and Mixed Woodlands have close affinities to those of Afromontane forests. In light of palynological, and other biogeographic studies of the region, these results suggest that avian assemblages of especially Sand Forest habitats were derived from Afromontane faunas that have subsequently evolved *in situ*.

OPSOMMING

Die Maputaland Sentrum (MS) vorm een van die mees betekenisvolle sentrums vir endemisme en diversiteit in suidelike Afrika. Die kenmerkende Sandwoudhabitat besit die hoogste aantal endemiese plant spesies in die MS, en toon 'n klein mate van biogeografiese affiliasie met die Afromontaan-woude. Ondanks aanduidings dat die endemiese fauna ook beperk is tot die Sandwoude, is hul habitat seleksie (m.a.w. habitat geassosieerde heterogeniteit in gemeenskappe) nog nie ondersoek nie, en hul biogeografiese affiliasies nog nie voldoende opgelos nie. Sulke inligting is belangrik weens bedreiging vir die Sandwoudhabitat beide binne en buite formele bewaringsareas. In hierdie studie is die variasie in voël- en muskruiergemeenskappe tussen habitate (Sandwoude- en die Gemengde Bosveldmatriks waarin dit geleë is), en tussen reservate (Tembe Olifantpark, Sileza Natuurreservaat), in die MS bestudeer, sowel as die streek se biogeografiese verwantskappe van die voëls. Beide voël- en muskruiergemeenskappe was homogenies binne 'n habitat tipe binne die reservate, maar het verskil tussen habitat soorte, en ook tussen reservate ten opsigte van dieselfde habitat soort. Endemiese voël spesies was die volopste, asook beperk tot die Sandwoudhabitat, maar meestal slegs in een van die twee reservate waar versamel is. Hierdie voëls wat voorheen as skaars beskou is, het redelike hoë getalle in die Sandwoude getoon (m.a.w. skaarsheid neig om nie deurlopend te wees nie). Geen van die skaars of algemene muskruier spesies van hierdie studie was endemies tot 'n reservaat of tot die MS nie. Hierdie resultate verbreed vorige demonstrasies van betekenisvolle tussen-reservaat heterogeniteit in plantgemeenskappe na diergemeenskappe, en stel voor dat 'n breë bewaringsdoelwit van 10% van 'n gegewe plantegroei nie as 'n effektiewe reservaatbeplanningmaatstaf op 'n plaaslike skaal in die MS gebruik kan word nie. Hierby was muskruier aanwyser spesies geïdentifiseer wat gebruik kan word om versteuring in Sandwoud kolle te monitor, veral in Tembe waar Sandwoude bedreig word deur olifante. Die spesiesbesetting verspreidingsfrekwensies vir al drie gemeenskappe was grootliks dieselfde vir al die ruimtelike skale bestudeer (m.a.w. plaaslike reservaat habitat, reservaat, habitat en streek skale). Geen tekens van organismiese-skaling ("organismal scaling") was dus gevind nie. In kontras hiermee, het die spesiesbesetting verspreidingsfrekwensies vir al drie gemeenskappe vanaf bi-modaal by die kleinste skaal na uni-modaal ("unimodal") by die grootste skaal verander (afstand-

skaling) (“distance scaling”). Die gefragmenteerde Gemengde Bosveld - Sandwoud sisteem tesame met die geassosieëerde metapopulasie dinamiek kan moontlik die dryfveer agter die bi-modaliteit by die plaaslike habitat skaal wees. Op ‘n meer plaaslike skaal het die voëlgemeenskappe van beide Sandwoude en Gemengde Bosveld ‘n noue verwantskap met Afromontaan-woude getoon. Aan die hand van palinologiese en ander biogeografiese studies van die area, stel dié resultate voor dat voëlgemeenskappe van veral Sandwoudhabitate ontstaan het vanuit Afromontaan faunas wat daaropvolgend *in situ* evolusionêre verandering ondergaan het.

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CHAPTER 1 – INTRODUCTION

Rationale and background

Projected biodiversity losses (Margules and Austin 1991, Smith *et al.* 1993, Thirgood and Heath 1994, Flather *et al.* 1997, Collins and Glenn 1997, Soulé and Sanjayan 1998), have shifted modern conservation approaches from focussing on a few large, charismatic and threatened animals, to the protection of ecosystems and the ecological processes which maintain them (Lovejoy 1995, May 1995, van Jaarsveld and Chown 1996). To attain these goals, conservation practitioners must make use of conservation networks to identify areas most suited for biodiversity conservation (see Lombard *et al.* 1996, Flather *et al.* 1997, Lawton *et al.* 1998, van Jaarsveld *et al.* 1998). However, priority conservation areas identified at broad global or regional scales (e.g. priority grids identified by selection algorithms) are heterogeneous and cannot be summarily translated into effectively designed local conservation areas without reference to local landscape and species distribution patterns. The scientific framework within which the present study was conducted is that of local habitat-associated heterogeneity in assemblages. This local heterogeneity can be pervasive across scales and may significantly complicate the development of effective regional conservation strategies (Noss 1990, Flather *et al.* 1997). A case in point is the Maputaland-Pondoland Regional Mosaic in southern Africa (White 1983).

The southern African subcontinent contains a diversity of habitats unsurpassed by any other region of comparable size (Allan *et al.* 1997), and South Africa is one of Africa's most biologically diverse countries (Davis *et al.* 1994, Lombard 1995). A recent analysis identified 68 vegetation types in South Africa, Lesotho and Swaziland alone (Low and Rebelo 1996). In terms of floral endemism and diversity, the Cape floristic region is well known (Bond and Goldblatt 1984, Cowling *et al.* 1997). However, a number of additional centres of plant endemism exist within southern Africa (van Wyk 1990, Davis *et al.* 1994).

The Maputaland-Pondoland Regional Mosaic (White 1983), is the most significant of these (confirmed in Bykov 1983). The northernmost region of this Mosaic, the region where this study was conducted, is termed the Maputaland Centre (MC) (Fig. 1). It corresponds with the southern part of the South-east African coast Endemic Bird

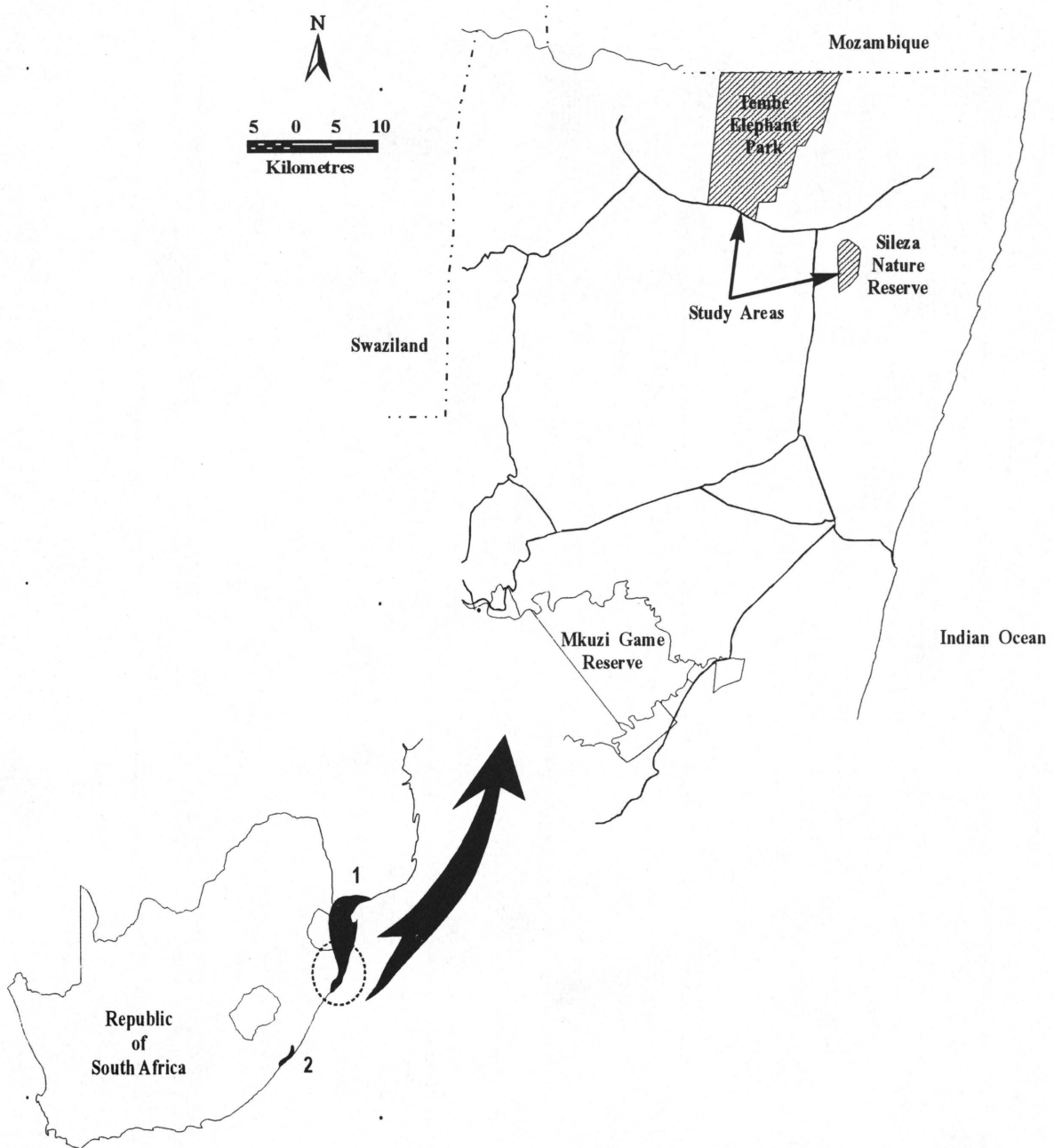


Fig. 1. Map of South Africa showing the location of (1) the Maputaland Centre, (2) the Pondoland Centre and the study areas within the Maputaland Centre.

Area (ICBP 1992, Thirgood and Heath 1994), and marks the southern limit of subtropical environmental conditions along the African east-coast.

The core area of the Centre (c. 26 734 km²) has been defined by van Wyk (1994) as that part of southern Mozambique and north-eastern KwaZulu-Natal which is bounded in the north by the Inkomati-Limpopo River, in the east by the Indian Ocean, in the west by the western foothills of the Lebombo Mountains and in the south by the St. Lucia Estuary, from where it extends further along the coast down to near Mtunzini (including the transitional Ngoye Range). Except in the north where the line appears more arbitrary, the boundaries of the MC are biogeographically clearly defined (van Wyk 1994).

Sand Forest habitat

The MC can be divided into a number of major habitat types (see Moll 1977, 1980), of which the characteristic Sand Forest habitat, with a biogeographic affiliation to Afromontane forest (White 1978, Low and Rebelo 1996), has the highest plant diversity and a significant number of endemic plant species (15% - W. S. Matthews, pers. comm., van Wyk 1996). A number of studies using broad scale analysis, either for atlasing or conservation planning purposes, have also found that the MC is an area of unusually high species richness and endemism for mammals and birds (Gelderblom *et al.* 1995, Clancy 1996, Allan *et al.* 1997), although the biogeographic affinities of this fauna has not been well studied.

On the basis of palynological studies, it has been argued that a combination of the presence of *Podocarpus* (Podocarpaceae) tree species, fynbos elements, and grassland in the Maputaland region, and the absence of mangroves (Botha *et al.* 1992, Scott *et al.* 1992), suggest an Afromontane forest biogeographic affiliation for Sand Forests, 11 000 - 5 000 years BP. However, broad scale avian studies suggest little affiliation with Afromontane forest and align the avifauna of Sand Forest with an complex East Coast Littoral vegetation unit (Allan *et al.* 1997). This unit included Coastal Forest, Sand Forest, Coastal Thicket, Coastal Grasslands and Mangroves with no strong ties to the Afromontane forest (Allan *et al.* 1997).

To date, however, few local scale studies have investigated the faunas of Sand Forest habitat patches, and the surrounding savanna-like Mixed Woodland matrix within

which they are embedded (van Wyk 1990, 1994, 1996). Thus, the faunal affinities of the most significant habitats of the MC remain poorly understood, as does the level of habitat-associated heterogeneity and spatial congruence in animal assemblages at these scales.

Birds and dung beetles (Coleoptera: Scarabaeidae) were selected as focal taxa for this study because they are ecologically unrelated so patterns of autocorrelation between them are not expected. Moreover, they are systematically well-known in southern Africa (Allan *et al.* 1997, Davis 1997), reasonably straightforward to sample quantitatively (Buckland *et al.* 1994, MacNally 1997), and dung beetles are known to play important roles in ecosystem functioning in tropical African savannas (Hanski and Cambefort 1991).

Objectives

The initial objective of this study was to develop a better understanding of bird and dung beetle assemblage heterogeneity in these broad habitat types. I therefore complimented existing plant and vertebrate data sets by examining habitat-associated heterogeneity and endemism of dung beetle and bird assemblages in Sand Forest patches, and the Mixed Woodland matrix, in two game reserves (Tembe Elephant Park, 27°01'S 32°24'E (hereafter Tembe) and Sileza Nature Reserve, 27°06'S 32°36'E (hereafter Sileza)) from the MC. Groups of species from each of the two taxa, characteristic of each habitat type and reserve, as well as dung beetle species that may be used to monitor changes in Sand Forest habitats, were identified. Lastly, the broader scale biogeographic affiliations of Sand Forest bird assemblages were examined by comparing these data with information published in the Atlas of Southern African birds (Harrison *et al.* 1997).

Study area

The stratigraphy of the Mozambique Coastal Plain consists of a multi-layered sequence of aeolian deposits on a eastward sloping cretaceous siltstone floor (SACS 1980). The prominent north-south dune ridges, which are a conspicuous topographical feature of the coastal plain, were deposited on the ancient shoreline which prograded in an easterly direction over the past 1.8 myr. Consequently, the dunes increase in age from the coast

inland (Davis 1976). Three dune ages can be recognized. The oldest ridge is of Early Pleistocene origin (1.8 million - 30 000 years old), a younger deposit is of Late Pleistocene (30 000 - 10 000 years old) origin, and recent deposits (< 10 000 years old) are found on the coast (Davis 1976, Hobday 1979).

With the exception of the narrow Lebombo Range that rises to an elevation of some 600 m, the region is a flat, low-lying coastal plain with a maximum elevation of approximately 150 m above sea level. The high coastal dune ridge along the shoreline rises to almost 200 m above sea level in places in KwaZulu-Natal, and is said to be amongst the tallest vegetated dunes in the world (Fig. 2 - van Wyk 1996). Both Tembe and Sileza contain undulating sand ridges (linear north-south trending dunes) interspersed with depressions. If soil clay content is high, these depressions may form pans or high water-table areas (W. S. Matthews, pers. comm.).

In Tembe, the water table varies from the surface (e.g. Muzi swamp and high water table grassland) to depths of 60 or more meters below the surface. The only surface water in the reserve which is present during most years is the Muzi swamp in the east of the reserve which flows north into Mozambique. Several seasonal pans are found on the duplex soils. In Sileza, a shallow water table exists that supports all the marshes and pans. It varies from the surface to depths of between 7 - 10 m below the surface (W. S. Matthews, pers. comm.).

The soils in both study areas are homogeneous, grey, siliceous, aeolian sands which are highly leached (dystrophic) and relatively acidic (water pH \approx 6.1) - (W. S. Matthews, pers. comm.), (soil nomenclature follows the FAO Soil classification system (FAO 1974) and the Soil Classification working group (1991)).

The region generally has a warm to hot humid sub-tropical climate (Schultze 1982). The mean annual rainfall is approximately 1100 mm along the coast, but declines progressively inland to 500-600 mm on the western plains. The crest of the Lebombo Range receives about 800-1000 mm per year (Bruton and Cooper 1980, Schulze 1982). Average humidities are high even in the drier inland parts of the region. Winters are drier than summers, although rain is received throughout the year. There is no frost in winter. During the dry seasons morning mist is not uncommon (Bruton and Cooper 1980). Rainfall, temperature and humidity data for the two specific stations relevant to the study

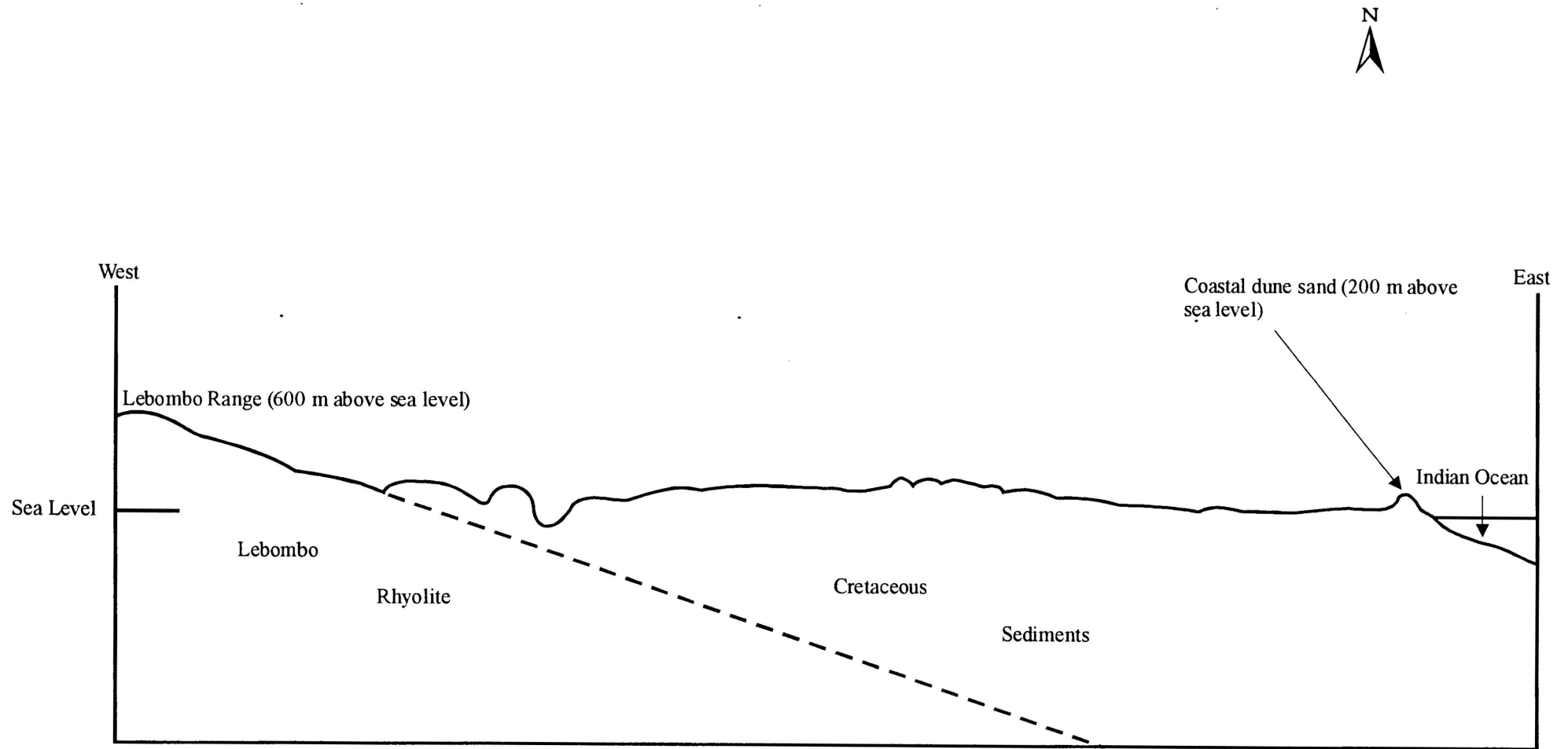


Fig. 2. Schematic cross-section of the Maputaland region (not to scale).

areas (Phelendaba bordering Sileza and Sihangwana in Tembe) are provided in Table 1.

Vegetation

The total number of vascular plant species in the Maputaland Centre is at least 2500, but may be as high as 3000. Of these at least 203 species/ infraspecific taxa and three genera are endemic to the centre (*Brachychloa*, *Galpinia* and *Helichrysopsis*). No families are endemic to the centre (van Wyk 1996).

The centre consists of a mosaic of extensive savanna communities arranged in complex patterns, forests (mainly on recent and ancient coastal dunes and the Lebombo Mountains) and, grasslands and swamps which are largely located by edaphic conditions. Two vegetation types occur in Tembe and Sileza, which are recognized as Sand Forest and Mixed Woodland (Figs. 3 and 4). Sand Forest which is confined to the tropical and subtropical coastal belt of KwaZulu-Natal, comprises a mosaic of patches within a matrix of open and closed Mixed Woodland (Fig. 5). Sand Forest is characterized by tree species such as *Dialium schlechteri* and *Erythrophleum lasianthum* (Caesalpinioideae) (Moll 1977, van Wyk 1996) with a poorly developed understory. The surrounding, more open, Mixed Woodland is characterized by common, woody savanna species such as *Acacia burkei* Benth, *Albizia versicolor* and *A. adianthifolia* (Mimosoideae). It has a well developed grass understory represented by *Aristida*, *Pogonarthria* and *Perotis* species (Moll 1977, 1980).

Fauna

Of the more than 472 species of birds recorded in the Centre (almost 60 percent of South Africa's total - van Wyk 1996), 4 species and about 19 subspecies are endemic to the Centre (Table 2 – Clancey *et al.* 1991, Clancey 1996).

The region is of exceptional vertebrate and invertebrate interest because of the distinct biogeographic transformation in the region (Poynton 1961). There is theoretical and empirical evidence that a hotspot of mammalian species richness exists in the centre, with some 102 species reportedly being indigenous to the Centre (Gelderblom and Bronner 1995, Mugo *et al.* 1995, van Wyk 1996). This is attributed to the wide variety of microhabitats and exploitable niches associated with the mosaic of vegetation types

Table 1. Monthly rainfall, temperatures and humidity for Tembe and Sileza during May 1995 and April 1996 (Weather Bureau).

Month	Tembe				Sileza						
	Temperature (°C)			Rainfall (mm)	Temperature (°C)			Rainfall (mm)	Humidity		
	Min	Max	Mean		Min	Max	Mean		Mean	14h00	20h00
May	13.90	25.70	19.80	68.10	13.20	25.60	19.40	69.50	56	85	70.50
June	9.90	24.20	17.10	23.60	9.20	24.00	16.60	21.40	50	85	67.50
July	10.60	24.70	17.70	0.00	9.90	24.90	17.40	0.00	49	84	66.50
August	12.20	26.30	19.30	50.20	11.80	25.90	18.90	23.00	44	72	58.00
September	15.60	30.00	22.80	0.00	15.80	29.30	22.60	0.00	46	77	61.50
October	18.00	30.50	24.30	83.20	18.10	29.10	23.60	88.40	55	80	67.50
November	19.00	30.10	24.60	87.00	18.40	28.80	23.60	75.00	62	82	72.00
December	18.90	29.25	24.10	313.40	18.80	28.70	23.80	288.10	63	84	73.50
January	21.60	31.20	26.40	90.40	21.00	30.60	25.80	161.00	66	82	74.00
February	20.80	31.70	26.30	119.00	20.30	30.30	25.30	110.30	67	86	76.50
March	18.40	30.00	24.20	38.60	17.40	28.60	23.00	30.00	62	87	74.50
April	16.00	29.00	22.50	41.00	14.80	26.80	20.80	41.00	60	88	74.00
				914.50				907.70			

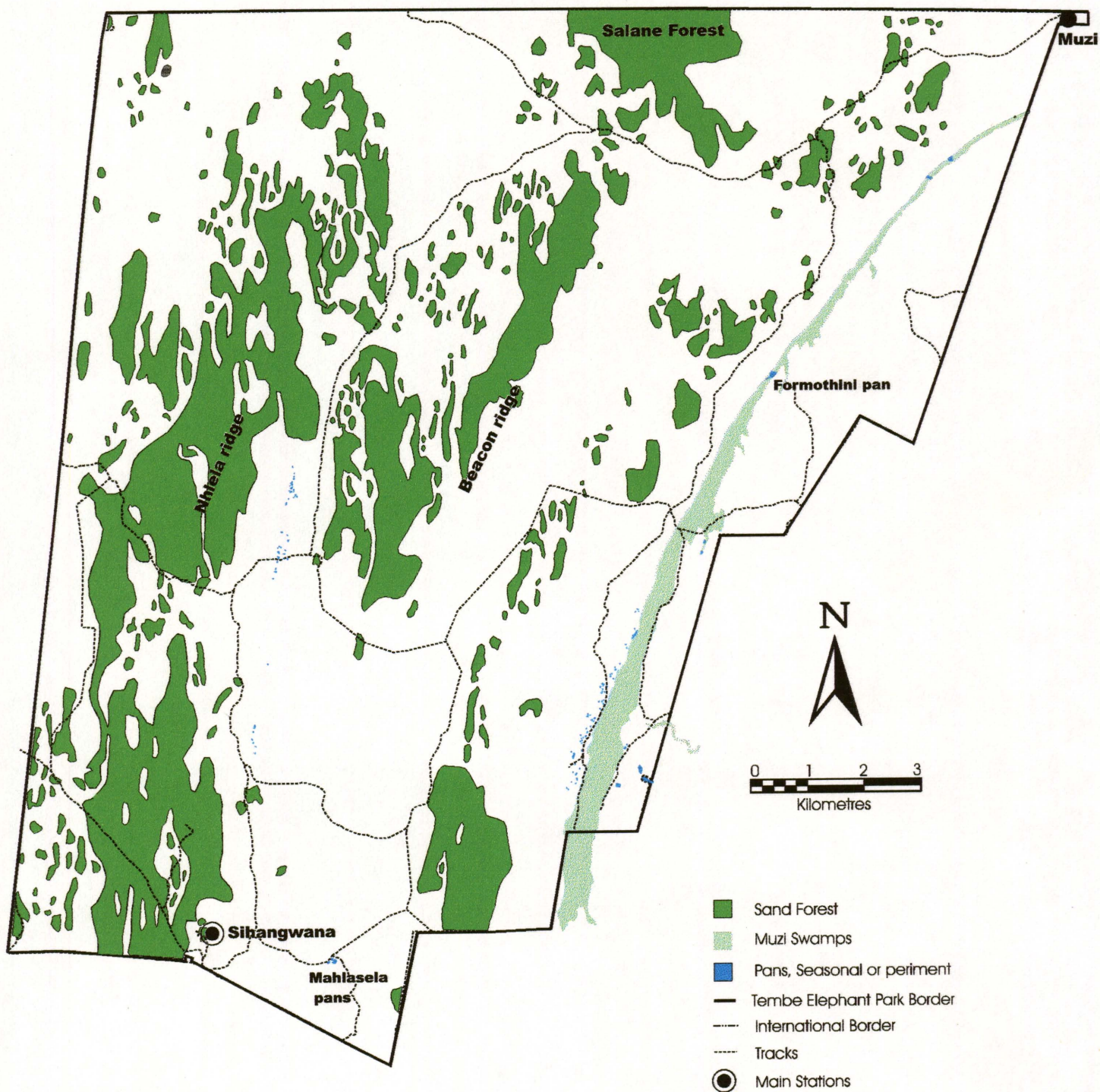


Fig. 3. Tembe Elephant Park vegetation map.

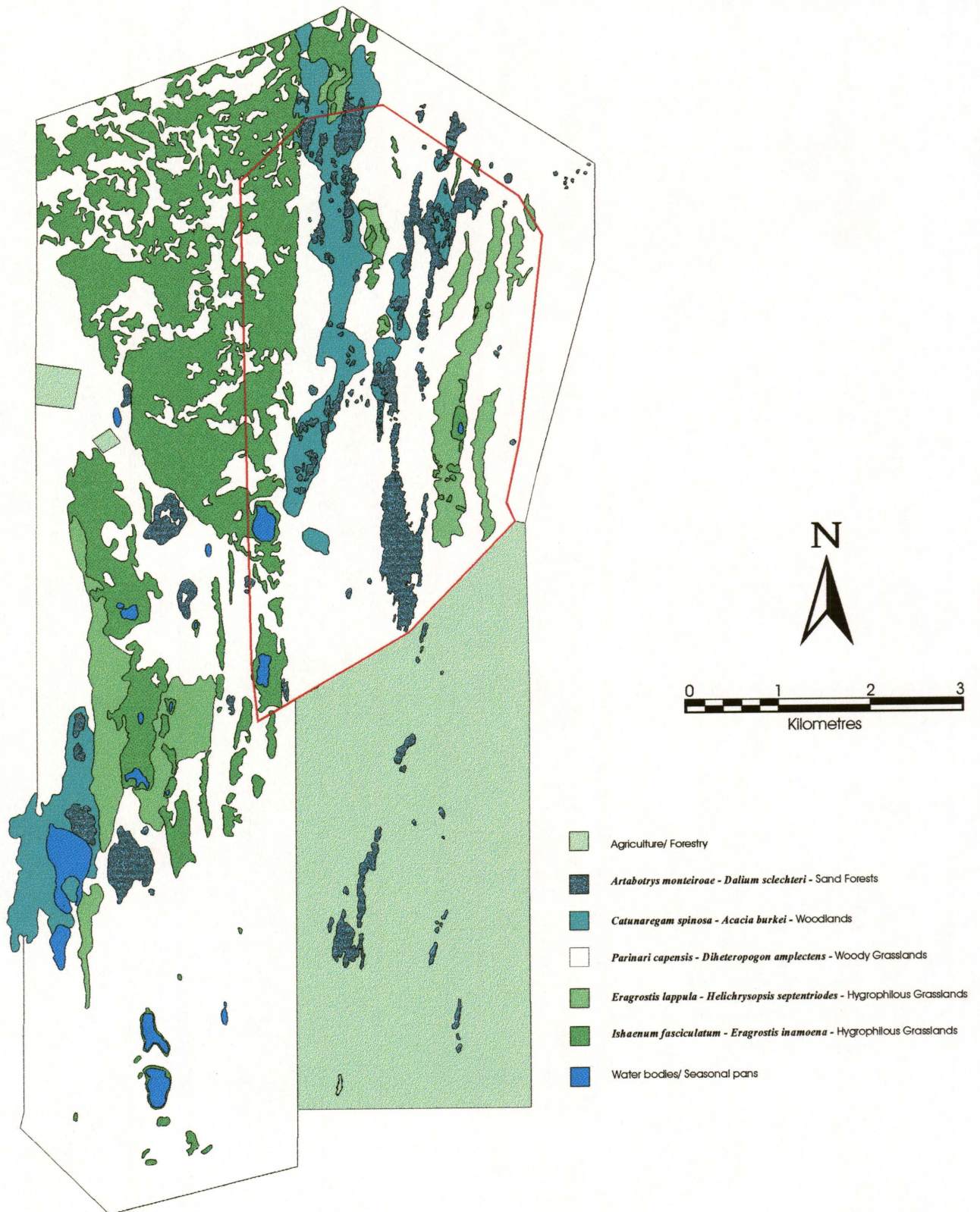


Fig. 4. Sileza Nature Reserve vegetation map.



Fig. 5. Vegetation photographs showing (a) Sand Forest habitat, (b) open Mixed Woodland habitat, and (c) closed Mixed Woodland habitat.

Table 2. Bird species and subspecies endemic to the Maputaland Centre.

Species and subspecies	Species common name	Family
<i>Anthus caffer traylori</i>	Bushveld Pipit	MOTACILLIDAE
<i>Apalis melanocephala addenda</i>	Blackheaded Apalis	SYLVIIDAE
<i>Apalis ruddi</i>	Rudd's Apalis	SYLVIIDAE
<i>Apalis thoracica lebomboensis</i>	Barthroated Apalis	SYLVIIDAE
<i>Batis fratrum</i>	Woodward's Batis	MUSCICAPIDAE
<i>Calandrella cinerea alluvia</i>	Redcapped Lark	ALAUDIDAE
<i>Cisticola fulvicapillus lebombo</i>	Neddicky	SYLVIIDAE
<i>Cisticola textrix marleyi</i>	Cloud Cisticola	SYLVIIDAE
<i>Erythropygia leucophrys simulator</i>	Whitebrowed Scrub Robin	TURDIDAE
<i>Erythropygia quadrivirgata wilsoni</i>	Bearded Scrub Robin	TURDIDAE
<i>Erythropygia signata tongensis</i>	Brown Scrub Robin	TURDIDAE
<i>Hypargos margaritatus</i>	Pinkthroated Twinspot	ESTRILDIDAE
<i>Laniarius ferrugineus tongensis</i>	Southern Boubou Shrike	MALACONOTIDAE
<i>Macronyx ameliae ameliae</i>	Pinkthroated Longclaw	MOTACILLIDAE
<i>Malaconotus olivaceus vitorum</i>	Olive Bush Shrike	MALACONOTIDAE
<i>Melaenornis pallidus sibilans</i>	Mousecoloured Flycatcher	MUSCICAPIDAE
<i>Nectarinia neergaardi</i>	Neergaard's Sunbird	NECTARINIIDAE
<i>Ploceus bicolor sclateri</i>	Forest Weaver	PLOCEIDAE
<i>Ploceus subaureus tongensis</i>	Yellow Weaver	PLOCEIDAE
<i>Pogoniulus pusillus niethammeri</i>	Redfronted Tinker Barbet	CAPITONIDAE
<i>Poicephalus cryptoxanthus cryptoxanthus</i>	Brownheaded Parrot	PSITTACIDAE
<i>Uraeginthus granatinus retusus</i>	Violeteared Waxbill	ESTRILDIDAE
<i>Vidua regia woltersi</i>	Shaft-tailed Whydah	VIDUIDAE

found in the region (Rautenbach *et al.* 1980). Taxa endemic to the Centre include 14 mammal subspecies, (Gelderblom and Bronner 1995, Mugo *et al.* 1995), 23 reptiles (about 112 indigenous species/ subspecies), 3 frogs (45 indigenous species/ subspecies) and 8 fresh water fishes (67 indigenous species) (see van Wyk 1996). Moreover, the beaches along the coast of the region are a major nesting ground for marine turtles.

The structure of the thesis

Following this Introduction, Chapter 2 concentrates on the variation of Sand Forest dung beetle assemblages, and how this variation compares with that found in plants from the same region. In addition, characteristic dung beetle species (endemic or specialist faunas) for each habitat were identified together with detector species that can be used to monitor changes in Sand Forests (e.g. elephant impact). In Chapter 3 the same habitat-associated heterogeneity in avifauna assemblages, together with their biogeographic affinities, were examined. The local scale conservation implications of these results were then assessed. Chapter 4 examined patterns of species occupancy frequency distributions for plants, dung beetles and birds at four spatial scales in Tembe and Sileza. Chapter 5 provides a summary of the results from Chapters 2, 3 and 4 with reference to their conservation and management implications for the region (and especially for the Sand Forest habitat in Tembe). In addition, some thoughts on future research topics are provided.

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CHAPTER 2

Conservation of heterogeneity among dung beetles in the Maputaland Centre of Endemism, South Africa

Introduction

Priority conservation areas identified at broad global or regional scales (e.g. priority grids identified by selection algorithms) are heterogeneous and cannot be translated into effective local conservation strategies without reference to local landscape and species distribution patterns. This local heterogeneity can be pervasive across scales and may significantly complicate the development of effective regional conservation strategies (Wiens 1989, Noss 1990, Flather *et al.* 1997). A case in point is the Maputaland-Pondoland Regional Mosaic, previously known as the Tongaland-Pondoland Regional Mosaic in southern Africa (White 1983). In this centre of endemism there are at least two clear foci of high floristic endemism (van Wyk 1990, 1994), of which the northernmost is termed the Maputaland Centre (Fig. 1).

The Centre constitutes the southernmost end of the tropics in eastern Africa, and many tropical plant and animal species reach their southernmost distributional limits here (Poynton 1961, van Wyk 1996). The region, which is invariably included in South African area selection analysis (Cowling and Hilton-Taylor 1994, Lombard 1995) can be divided into a number of major habitat types (see Moll 1977, 1980) of which the Sand Forest habitat has the highest plant diversity and a significant number of endemic plant species. It appears that many of the Maputaland Centre's endemic vertebrate species and subspecies are also restricted to Sand Forest (van Wyk 1996). Moreover, there are significant differences in the plant communities of Sand Forest between the Tembe and Sileza reserves (W. S. Matthews, pers. comm.).

The invertebrate fauna of this heterogeneous landscape is poorly studied. It is not known, for example, whether invertebrate assemblages in the region are similarly heterogeneous, or the extent to which the two major habitat types (Sand Forest and Mixed Woodland) are characterized by endemic or specialist faunas. Dung beetles (Coleoptera:

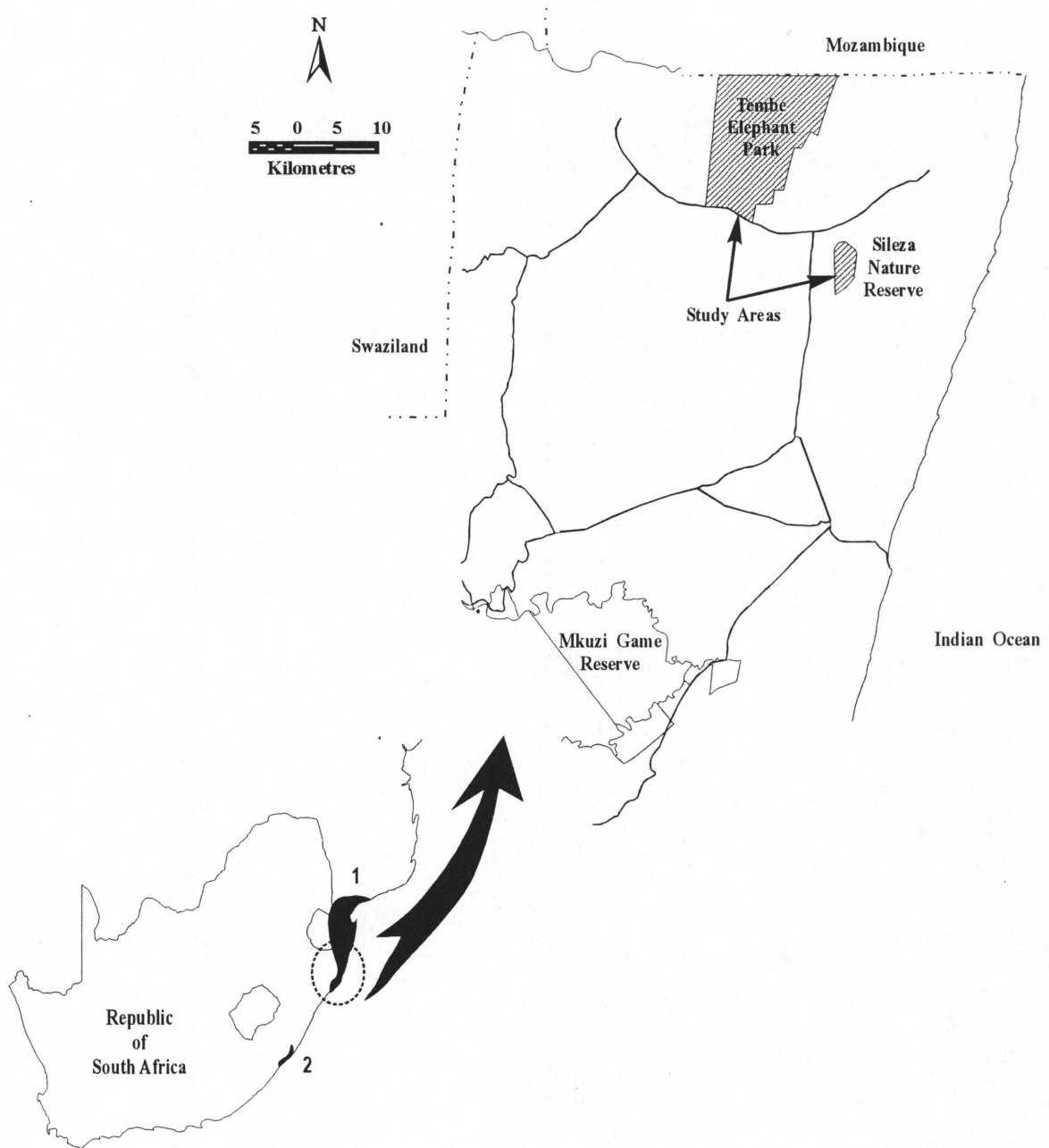


Fig. 1. Map of South Africa showing the location of (1) the Maputaland Centre, (2) the Pondoland Centre and the study areas within the Maputaland Centre.

Scarabaeidae) were chosen as the target group of this study to establish the extent to which an invertebrate assemblage in the Centre matches the high level of floral and vertebrate diversity and endemism. Dung beetles were chosen because they are systematically well-known in southern Africa (see Davis 1997), and play important roles in ecosystem functioning in tropical African savannas (Hanski and Cambefort 1991). They are also known to be sensitive to alterations in habitat structure (Klein 1989, Chown and Steenkamp 1996), and it may therefore be possible to use them to characterize, and to monitor changes in, habitat types (see McGeoch 1998 for further discussion of the selection of “indicator” species). This has been successfully achieved with other well known groups of Coleoptera (see Dufrêne and Legendre 1997).

Furthermore, patches of Sand Forest, embedded within a matrix of open and closed Mixed Woodland, are under considerable threat. In both South Africa and Mozambique extensive commercial afforestation, local use of fuelwood, and clearance for agriculture are taking place within this habitat type (Davis *et al.* 1994, Cole and Landres 1996). Only small portions of Sand Forest are presently protected in four conservation areas in South Africa (3 020 ha in Tembe Elephant Park out of a total of 30 079 ha; 25 ha out of 2 500 ha in Sileza Nature Reserve; 1 500 ha out of 29 000 ha in Mkuzi Game Reserve, and a few patches in Falsebay Park). A conservation conflict is, however, developing within the largest of these protected areas (Tembe Elephant Park - Fig. 1). The rationale for the declaration of this park was Sand Forest conservation, as well as the conservation of the elephant *Loxodonta africana* in northern KwaZulu-Natal. Although elephants prefer plant species growing in non-Sand Forest habitats, they are increasingly using Sand Forests because of the relatively small size of the Tembe Elephant Park, with marked effects. Elephants are not present in Sileza Nature Reserve and the Sand Forest patches here are therefore not under similar threat. However, these reserves are unlikely to adequately represent regional Sand Forest diversity if there is substantial between-patch heterogeneity in animal and plant diversity within and among them.

The aims of the present study were therefore to complement existing plant and vertebrate data sets by examining habitat specificity of dung beetles and variation in

assemblages between habitats (Sand Forest and Mixed Woodland), and between reserves (Tembe Elephant park and Sileza Nature Reserve). In addition, groups of species characteristic of each habitat type and reserve, as well as species that may be used to monitor changes in Sand Forest habitat, are identified.

Material and methods

Study area

Field work was undertaken in Tembe Elephant Park (27°01'S 32°24'E) and Sileza Nature Reserve (27°06'S 32°36'E), on the southern Mozambique Coastal Plain of Northern KwaZulu-Natal, South Africa. Sand Forest is characterized by tree species such as *Dialium schlechteri* Harms and *Erythrophleum lasianthum* Corbishley (Caesalpinioideae) (Moll 1977, van Wyk 1996) with a poorly developed understory. The surrounding, more open, Mixed Woodland is characterized by common, woody savanna species such as *Acacia burkei* Benth, *Albizia versicolor* Welw. ex Oliver and *A. adianthifolia* (Schumacher) W.F. Wight (Mimosoideae). It has a well developed grass understory represented by *Aristida*, *Pogonarthria* and *Perotis* species (Moll 1977, 1980). The soils in both study areas are homogeneous, grey, siliceous, aeolian sands which are highly leached (dystrophic) and relatively acidic (water pH \approx 6.1) - (W. S. Matthews, pers. comm.).

Sampling and species identification

Replicated sampling sites in these reserves were selected from within standardised vegetation communities (Sand Forest and Mixed Woodland - van Wyk 1996). Two Sand Forest sites and two Mixed Woodland sites were sampled in each reserve, i.e. eight sampling sites, grouped into four reserve-habitat combinations (Tembe Sand Forest, Tembe Mixed Woodland, Sileza Sand Forest, Sileza Mixed Woodland). At each sampling site, 30 pitfall traps were set out in groups of six on a 2 m x 2 m grid. Distances between the five grids within a site, between sites, and between the areas sampled in the two reserves were, respectively, 200 m, 1.3 – 3.1 km and c. 18 km (Fig. 2).

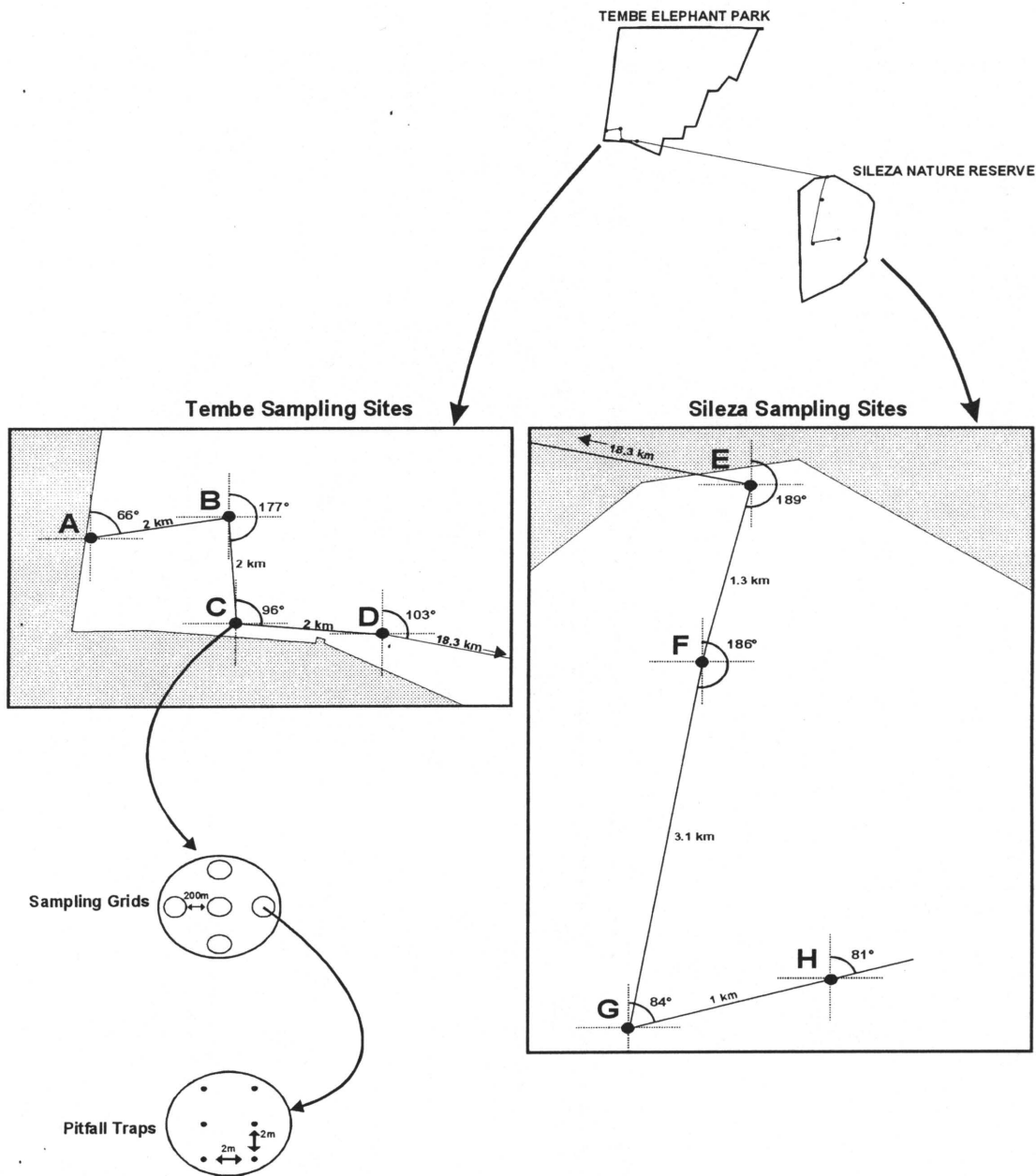


Fig. 2. Schematic diagram showing the two reserves (Tembe Elephant Park and Sileza Nature Reserve), and illustrating the relative positions of the two habitat types (Sand Forest and Mixed Woodland), eight sites, five grids within a site, and six pitfall traps within a grid, for each of the reserves: (A) Tembe Mixed Woodland 2; (B) Tembe Sand Forest 2; (C) Tembe Sand Forest 1; (D) Tembe Mixed Woodland 1; (E) Sileza Sand Forest 1; (F) Sileza Mixed Woodland 1; (G) Sileza Mixed Woodland 2; (H) Sileza Sand Forest 2.

Beetles were sampled bimonthly between May 1995 and April 1996, at all four sites in a reserve (the two reserves were sampled in alternative months), using pitfall traps baited with 50 g elephant dung. During one month, the pitfalls were set once for 48 hours, with rebaiting and the first collection taking place at 24 h, and the second collection at 48 h. Traps were then closed and left *in situ* until the following sampling month. Specimens were identified by comparing them to identified specimens in the collections of the South African National Insect Collection.

Data analysis

The number of individuals of each species trapped over the course of the study period were summed for each sampling grid and each site. Multivariate community analysis of the absolute dung beetle abundance data were made using PRIMER v4.0 1994 (Clarke and Warwick 1994). Cluster analysis, using group averaging and Bray Curtis similarity measures (Bray and Curtis 1957) were used to examine relationships between sampling grids, sites, and habitat types both within and between reserves. The data were double square-root transformed prior to analysis (to weight common and rare species equally) (Clarke and Warwick 1994). Analysis of similarity (ANOSIM – Clarke 1993), was used to establish the significance of differences between habitats and sampling units; this is a non-parametric permutation procedure applied to rank similarity matrices underlying sample ordinations (Clarke 1993), in which a significant global *R*-statistic of close to one indicates distinct differences between the assemblages/ habitats compared. Non-metric multi-dimensional scaling (MDS) was used to display the relationships between the sites in an ordination analysis.

Characteristic dung beetle species (indicator species) were identified for each habitat type using the Indicator Value Method (Dufrêne and Legendre 1997). This assesses the degree (expressed as a percentage) to which each species fulfils the criteria of specificity (uniqueness to a particular site) and fidelity (frequency within that habitat type) for each habitat cluster compared with all other habitats. The higher the percentage IndVal (indicator value) obtained, the higher the specificity and fidelity values for that species, and the more representative the species is of that particular habitat. Species with

high IndVals thus make reliable indicator species not only because they are specific to a locality, but also because they have a high probability of being sampled in that locality during monitoring and assessment (McGeoch and Chown 1998). The species abundance matrix from each site was used to identify indicator species. The following comparisons were made: Tembe Sand Forest vs. Tembe Mixed Woodland, Sileza Sand Forest vs. Sileza Mixed Woodland, and overall Sand Forest vs. Mixed Woodland. Dufrêne and Legendre's (1997) random reallocation procedure of sites among site groups was used to test the significance of the IndVal measures for each species. Those species with significant IndVals > 70% (subjective benchmark) were then regarded as indicator species for the habitat in question.

The closed Sand Forest habitats are thought to represent the older landscape elements on the Maputaland coastal plain (van Wyk 1996). Disturbance to these, e.g. by elephant foraging, usually results in an opening up of the habitat and conversion to Mixed Woodland, the matrix habitat type. To date, no reversion to the original habitat structure has been recorded for disturbed Sand Forest patches (W. S. Matthews, pers. comm.). Therefore IndVal scores were also used to identify 'detector' species (see McGeoch 1998) for such change. These were chosen as those that had significant IndVals of 50-70% for Mixed Woodland *and* 5-50% for Sand Forest. The rationale for selecting potential detector species in this way, is that first, reliable indicator species (i.e. those with high specificity and fidelity, and as used here with significant IndVals of > 70%) are unlikely to move from their preferred habitat to adjacent habitats, even under changing habitat conditions. Populations of these species need only be monitored within their preferred habitat. Second, generalist species are also unlikely to respond very rapidly to changing habitat conditions. On the other hand, those species with some degree of habitat preferences (as used here those with significant IndVal measures of between 50 and 70%) are likely to move to adjacent habitats more rapidly under changing habitat conditions than either of the previous two categories. These detector species would thus be most likely to invade Sand Forest in the early stages of their change to a Mixed Woodland-like habitat (McGeoch, unpublished). Detector species were thus selected from Tembe Mixed

Woodland and Sileza Mixed Woodland separately, and then from the overall Mixed Woodland data set.

Rare species were also identified for each habitat type and for each reserve. Following Gaston (1994) I defined these as the 25% least abundant species in my samples (proportion of species method).

Results

Sixty six dung beetle species (42 611 individuals), were collected in pitfall traps from the two habitats in Tembe and Sileza (Appendix 1). The total number of dung beetles recorded for each sampling grid within each month can be seen in Appendices 2.1 – 2.6 and 3.1 – 3.6. An additional seven species were collected by hand within the study area, but were never found in the pitfalls.

Rank-abundance curves for each of the habitat types in each of the reserves are shown in Fig. 3. Dominance by specific species in samples was less marked in the Tembe sites than in those at Sileza. Likewise, dominance was lower in Mixed Woodland than in Sand Forest (Fig. 3), and total dung beetle abundance and species richness was higher in the Mixed Woodland ($n = 26\ 533$, $S = 68$) than in Sand Forest ($n = 16\ 078$, $S = 53$) (Appendix 1). *Proagoderus dives* was the most abundant species in Mixed Woodland in both Sileza and Tembe (Appendix 1), whereas *Proagoderus aciculatus* dominated Sand Forest in both Sileza and Tembe (51% and 33%, respectively).

Analysis of similarity indicated no significant differences among sampling grids within sites ($p > 0.05$). Likewise, after pooling grid data for each site, analysis of similarity showed no significant differences between sites, within habitat types for each reserve (Fig. 4). However, beetle assemblages differed considerably both between habitat types in a given reserve, and between similar habitat types in the two reserves (Fig. 4). In addition, it is clear from Figure 3 that the Sand Forest faunas in the two reserves were less alike than were the two Mixed Woodland faunas.

Mixed Woodland had a more even distribution of indicator values, as well as higher absolute indicator species values, than Sand Forest (Fig. 5(a), Table 1). Mixed Woodland thus had a larger complex of more characteristic dung beetle species than Sand

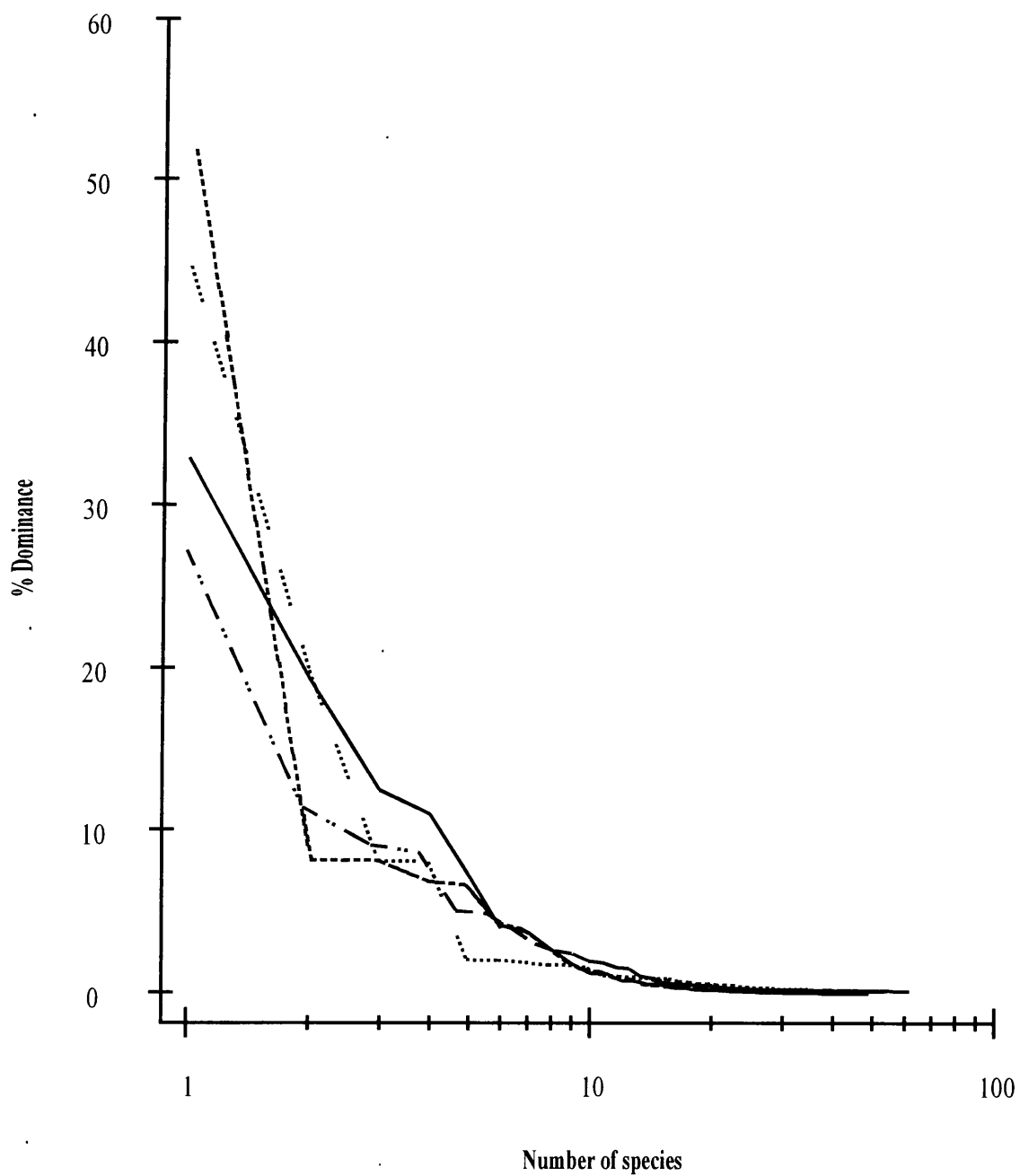


Fig. 3. Rank-abundance curves showing dung beetle assemblage dominance in the different habitat types: (____) Tembe Sand Forest; (.....) Sileza Sand Forest; (_ .. _) Tembe Mixed Woodland; (..... ..) Sileza Mixed Woodland.

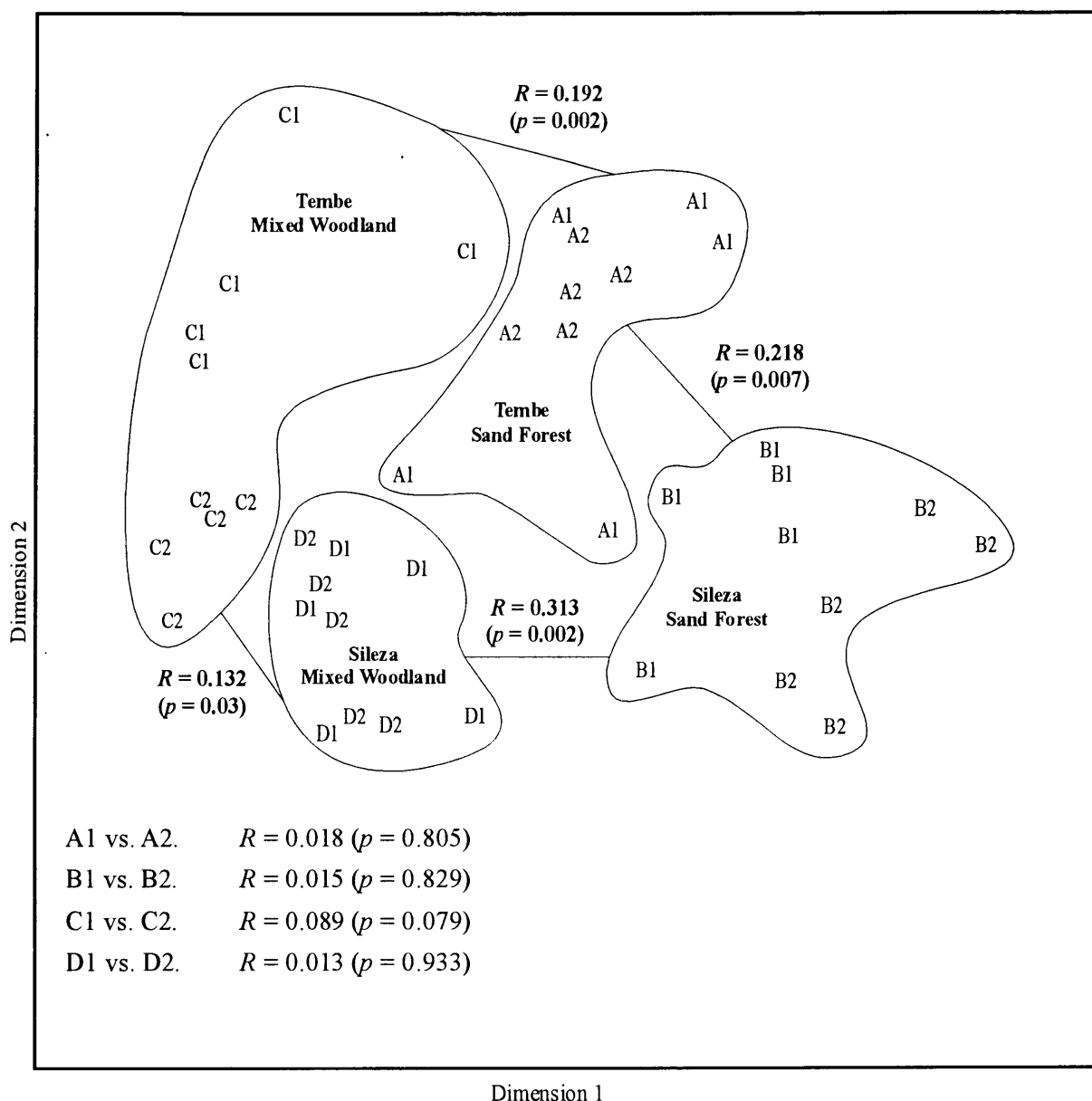
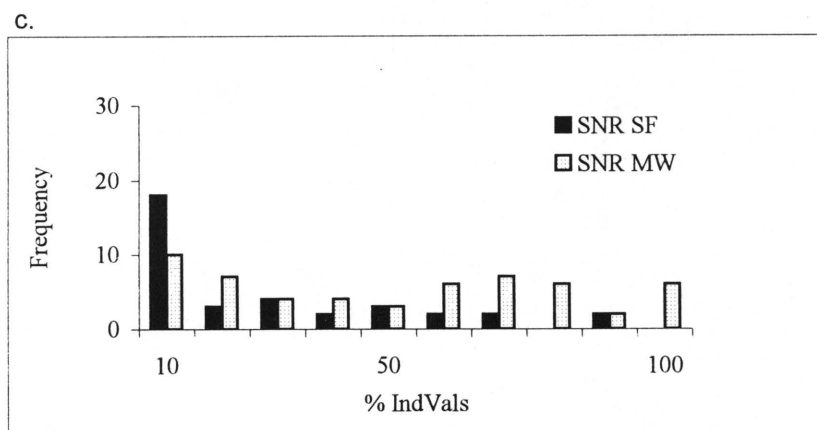
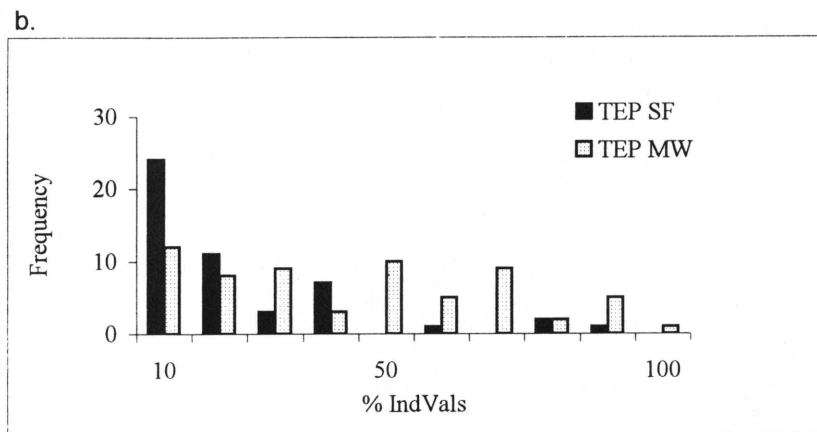
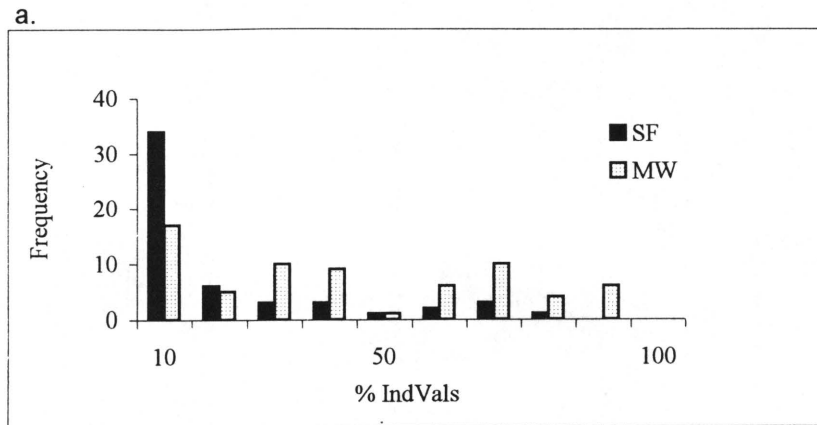


Fig. 4. Non-metric multi-dimensional scaling ordination of the abundances of species in the dung beetle assemblages at the four pairs of habitat sites (and 40 grid sites). The absolute distance between every pair of points on the ordination is a relative measure of their similarity. The R -statistic is a measure of the similarity of assemblages. If R is significantly different from zero, then there are significant differences between assemblages.



Figs. 5. (a)-(c). Dung beetle indicator species value distributions for the different habitat type comparisons: (TEP) Tembe Elephant Park; (SNR) Sileza Nature Reserve; (SF) Sand Forest; (MW) Mixed Woodland.

Table 1. Percentage indicator values (IndVal > 70%) of Scarabaeidae species for three different habitat comparisons. Bold species names and %IndVals denote maximum absolute % indicator values across all habitat type comparisons for that species.

Tembe	% IndVal	Sileza	% IndVal	Combined	% IndVal
Sand Forest					
<i>Sisyphus</i> sp.Y sensu Paschalidis	86.32	<i>Gareta azureus</i>	90.00	<i>Onthophagus lacustris</i>	71.36
<i>Onthophagus lacustris</i>	75.54	<i>Sisyphus bornemisszanus</i>	89.92	<i>Sisyphus bornemisszanus</i>	70.01
<i>Proagoderus aciculatus</i>	70.64				
Mixed Woodland					
<i>Sisyphus sordidus</i>	97.23	<i>Copris puncticollis</i>	100.00	<i>Sisyphus sordidus</i>	88.03
<i>Metacatharsius pseudoopacus</i>	87.61	<i>Onthophagus signatus</i>	100.00	<i>Pedaria</i> prob. sp.IV sensu Davis	84.74
<i>Pedaria</i> sp.III sensu Davis	87.24	<i>Proagoderus bicallosus</i>	100.00	<i>Onthophagus</i> cf. <i>fimetarius</i>	83.28
<i>Copris inhalatus</i> prob. <i>sanctaeluciae</i>	84.26	<i>Onthophagus</i> cf. <i>fimetarius</i>	99.17	<i>Metacatharsius pseudoopacus</i>	83.07
<i>Pedaria</i> prob. sp.IV sensu Davis	83.32	<i>Proagoderus dives</i>	92.46	<i>Pedaria</i> sp.III sensu Davis	82.90

Table 1 (continued).

Tembe	% IndVal	Sileza	% IndVal	Combined	% IndVal
<i>Kheper lamarcki</i>	82.86	<i>Catharsius</i> sp. near <i>pandion</i>	92.39	<i>Proagoderus dives</i>	81.89
<i>Onthophagus ursinus</i>	75.62	<i>Pedaria</i> prob. sp.IV <i>sensu</i> Davis	89.17	<i>Copris puncticollis</i>	79.12
<i>Euonthophagus carbonarius</i>	71.08	<i>Neosisyphus rubrus</i>	85.91	<i>Onthophagus signatus</i>	76.75
		<i>Metacatharsius pseudoopacus</i>	80.00	<i>Proagoderus bicallosus</i>	75.34
		<i>Pedaria</i> sp.III <i>sensu</i> Davis	80.00	<i>Kheper lamarcki</i>	74.11
		<i>Pedaria</i> prob. sp.I <i>sensu</i> Davis	80.00	<i>Onthophagus ursinus</i>	70.47
		<i>Caccobius viridicollis</i>	78.49	<i>Onthophagus</i> spp.	70.29
		<i>Onthophagus</i> spp.	77.94		
		<i>Onthophagus</i> cf. <i>sugillatus</i> sp.A	75.29		

Forest. A comparison of the species indicator value distributions for Sand Forest and Mixed Woodland within each of the reserves showed similar trends (Figs. 5(b) and 5(c)). In both reserves, the characteristic species for Mixed Woodland tended to have higher IndVals than those in Sand Forest (Table 1). Species reached their maximum IndVals in the within-reserve comparisons (Table 1). For example, *Sisyphus sordidus* had the highest indicator value for Tembe Mixed Woodland when comparing this habitat type to Tembe Sand Forest. Therefore indicator species did not show high habitat specificity and fidelity at the overall, Mixed Woodland vs. Sand Forest level.

Thirteen detector species of potential changes in Sand Forest habitats for the two reserves, and for Sand Forest as a whole were recognised from the Mixed Woodland habitats (Table 2). Only *Pachylomerus femoralis* occurred in two of the lists, i.e. the lists were quite distinctive, making these detector species sets reserve specific.

The number of rare species recorded within each habitat type in each reserve varied from eight to sixteen (Table 3), and a total of 36 of the 66 species sampled were considered rare in at least one of the four habitat localities (Appendix 1). Of these 36 rare species, only two (*Euoniticellus spinipes* and *Onthophagus aeruginosus*) were considered rare in at least three habitat types, and in the fourth habitat type (Tembe Mixed Woodland) they were slightly more abundant. Of the 11 species that were considered rare in at least two habitat types, eight were not classed as rare in the other habitat types and three were absent elsewhere. Similarly, of the 23 species that were rare in one habitat type only, ten occurred in no other habitat types, whereas 13 were not classified as rare in at least one of the other habitat types. Amongst the 30 species not classified as rare, only three showed any form of habitat and/ or reserve specificity: *Catharsius heros* and *Onthophagus obtusicornis* were restricted to Tembe Mixed Woodlands, and *Onthophagus plebejus* was restricted to Tembe (Appendix 1).

Discussion

Rarity and endemism

Based on comparisons with collected material in the South African National Collection of Insects, it appears that none of the rare or common species in the dung beetle assemblages

Table 2. Dung beetle species as detectors for changes in Sand Forest. Indicator values for Mixed Woodland (MW) and Sand Forest (SF).

Habitat	Species	% IndVal	
		MW	SF
Tembe Mixed Woodland	<i>Proagoderus dives</i>	68.37	31.63
	<i>Onthophagus cf. fimetarius</i>	61.89	6.79
Sileza Mixed Woodland	<i>Sisyphus sordidus</i>	69.28	24.58
	<i>Euonthophagus carbonarius</i>	66.67	6.67
	<i>Pachylomerus femoralis</i>	63.98	36.02
	<i>Oniticellus formosus</i>	57.50	5.36
Overall Mixed Woodland	<i>Onthophagus cf. sugillatus</i> sp.A	67.58	27.56
	<i>Euonthophagus carbonarius</i>	67.48	9.28
	<i>Onthophagus cf. vinctus</i>	63.05	36.95
	<i>Pachylomerus femoralis</i>	61.74	35.01
	<i>Catharsius tricornutus</i>	54.47	11.17
	<i>Caccobius viridicollis</i>	54.17	5.56
	<i>Copris urus</i>	51.58	9.21

Table 3. Total numbers of species of rare dung beetles, and numbers of dung beetle species recorded as rare in a single locality only, recorded in the separate Sand Forest and Mixed Woodland habitats at Tembe (T) and Sileza (S) reserves and in the reserves as a whole.

	Sand Forest			Mixed Woodland			Tembe	Sileza
	T	S	T+S	T	S	T+S		
Total	12	8	17	15	16	29	24	21
Restricted	3	3	7	9	8	19	15	12

studied here are endemic to Tembe, Sileza or the Maputaland Centre. However, *Onthophagus* (*fimetarius* group) was not present in the National Collection of Insects, and *Scarabaeus* cf. *xavieri* is probably an undescribed species. Fourteen of the species found in this study can, however, be treated as coastal endemics (A .L. V. Davis, pers. comm.) and 26 species recorded in the Sand Forest and Mixed Woodland habitats of Tembe and Sileza were not recorded in Mkuzi Game Reserve by Doube (1991) (Appendix 1).

None of these species was consistently rare in the present study. Thus, no species considered rare in this study is endemic to the study area or is thought to be geographically rare in southern Africa. Such diffusive rarity is not uncommon in relatively small-scale studies (Gaston 1994), and species identified as rare may be those that are at the edge of their ranges (see Brown 1988, Brown *et al.* 1996), are in habitats that are not entirely suitable for them, or are transient (Gaston *et al.* 1993). Therefore it appears that the identification of rare species at a local scale (using any of the abundance criteria suggested by Gaston 1994), is unlikely to provide insight into the conservation requirements of the species involved unless information on their regional distributions and abundances elsewhere is taken into account (Heikkinen 1998).

Although such a statement is almost a platitude with regard to the conservation of better known groups such as birds (MacNally 1997), this is not so in the case of less well-known taxa such as invertebrates. Such lack of congruence in rarity (i.e. species may be rare or common depending on where they are sampled) has been documented for other taxa (see Gaston 1994, McGeoch and Chown 1997), and suggests that an important requirement for insect conservation is the mapping of insect distributions at larger scales (Freitag and Mansell 1997, Muller *et al.* 1997).

Reserve and habitat comparisons

Dung beetle assemblages in both Tembe Elephant Park and Sileza Nature Reserve were homogenous within particular habitat types, although they differed considerably between habitat types in a given reserve, and between reserves for a given habitat type. Soil type plays an important role in determining dung beetle distribution (Endrody-Younga 1982,

Doube 1983, Fay 1986, Davis 1987), and may indeed account for the low species richness at Tembe compared to a reserve such as Mkuzi (with 120 species, and which lies slightly further south and includes sandy and clay soils (see Tribe 1976, Doube 1991)). However, there is very little soil type variation in the study area. The two habitat types do have rather different vegetation structures, and such differences are known to have a pronounced effect on dung beetle assemblages (Doube 1983, Klein 1989, Steenkamp and Chown 1996). The differences found among the samples of dung beetles in this study may be partly due to differences in the light intensity and microclimate produced by the vegetation (see Lewis and Taylor 1965, Houston and McIntyre 1985) and partly to differences in food resources between habitats and between reserves (see e.g. Doube 1991).

Indicator and detector species

Although there are clear differences between the Sand Forest and Mixed Woodland habitats as a whole, no species could reliably be considered indicators of Mixed Woodland or Sand Forest at this scale. Where Sand Forest and Mixed Woodland habitats were compared including the data from all of the sites, none of the indicator species that were identified reached their maximum indicator value. However, within reserves, at least one species was a useful indicator for a given habitat. For example, *Gareta azureus* was a reliable indicator species for distinguishing Sileza Sand Forests from Sileza Mixed Woodlands. In general, Sand Forest habitats (in both reserves) tended to have fewer characteristic species, showing high abundance and high habitat fidelity, than the Mixed Woodland habitats.

However, the detector species for Sand Forests (i.e. Mixed Woodland species with intermediate IndVals) can also be used to monitor impacts on them. Not only do these detector species tend to be uncommon in Sand Forest (and generally widespread in Mixed Woodland), but detecting a new species presence (and an increase in its frequency and abundance) in Sand Forest is likely to be far more reliably undertaken than detecting the absence of a species with a high IndVal for Sand Forest (see Underwood 1997). Thus, the most useful species for indicating change in Sand Forest habitats within a particular

reserve are both those with a high IndVal for Sand Forest (for that reserve) (i.e. indicator species), and those Mixed Woodland species identified as detector species for the reserve in question (McGeoch, unpublished).

Conservation implications

Heterogeneity in dung beetle assemblages has profound implications, particularly for the conservation of Sand Forest in the Maputaland Centre. Since there are significant differences in both dung beetles and plants between the Sand Forests located in Tembe and those in Sileza, it is clear that representative patches of these forests should be conserved in both reserves. Monitoring of the impact of large herbivores on these forests in Tembe is currently being undertaken (W. S. Matthews, pers. comm.), and should be continued. Heavy utilization of Sand Forests by elephants is thought to lead to opening up of these habitats, and the subsequent development of a structure more like Mixed Woodland. Quantifying this change by botanical surveys is an essential first step in informing conservation decisions. However, a 48 hr survey of the dung beetles present during the peak summer season could provide an additional indication of the extent to which a Sand Forest patch is changing within a particular reserve, if this survey is continued as a monitoring programme over a number of years. Such monitoring could assist with the difficult and contentious conservation decisions that surround the manipulation of a large herbivore population in a reserve that was proclaimed with more than a single conservation goal in mind.

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Appendix 1. The total number of dung beetles recorded in the Tembe (T) and Sileza (S) Sand Forest and Mixed Woodland habitats. Bold values denote rare species defined as the 25% least abundant species in each of the four habitat types.

Species	Sand Forest		Mixed Woodland		Species	Sand Forest		Mixed Woodland	
	T	S	T	S		T	S	T	S
<i>Allogymnopleurus consocius</i>	0	0	1	0	<i>Cyptochirus ambiguus</i>	1	0	5	0
<i>Anachalcos convexus</i>	31	96	19	107	<i>Drepanocerus impressicollis</i>	0	0	3	0
<i>Caccobius</i> spp.	22	9	40	74	<i>Drepanocerus kirbyi</i>	0	0	8	5
<i>Caccobius viridicollis</i>	49	1	78	52	<i>Euoniticellus spinipes</i> ^a	2	3	11	1
<i>Catharsius harpagus</i> ^a	1	3	9	7	<i>Euonthophagus carbonarius</i>	62	5	240	25
<i>Catharsius heros</i> ^a	0	0	8	0	<i>Garetta azureus</i> ^a	6	290	2	0
<i>Catharsius</i> sp. near <i>pandion</i>	4	61	5	85	<i>Heliocopris japedus</i> ^a	0	0	1	0
<i>Catharsius tricornutus</i>	12	4	30	11	<i>Hyalonthopagus alcyonides</i>	0	0	10	1
<i>Copris inhalatus</i> prob. <i>sanctaeluciae</i> ^a	3	4	44	42	<i>Kheper lamarcki</i>	18	13	87	23
<i>Copris mesacanthus</i>	10	0	16	5	<i>Liatongus militaris</i>	0	0	2	0
<i>Copris puncticollis</i>	16	0	67	120	<i>Metacatharsius exiguus</i> ^a	1	0	12	15
<i>Copris urus</i> ^a	6	4	19	11	<i>Metacatharsius pseudoopacus</i>	3	0	110	19

Appendix 1 (continued). Species	Sand Forest		Mixed Woodland		Species	Sand Forest		Mixed Woodland	
	T	S	T	S		T	S	T	S
<i>Metacatharsius</i> sp.1 ^a	1	0	0	0	<i>Onthophagus</i> cf. <i>vinctus</i>	924	607	1535	1079
<i>Metacatharsius</i> sp.2 ^a	1	0	0	3	<i>Onthophagus lacustris</i>	1047	142	339	55
<i>Neosisyphus fortuitus</i>	2	29	1	19	<i>Onthophagus obtusicornis</i>	0	0	75	0
<i>Neosisyphus mirabilis</i>	64	511	200	261	<i>Onthophagus plebejus</i>	5	0	15	0
<i>Neosisyphus rubrus</i>	4	3	3	63	<i>Onthophagus signatus</i>	13	0	49	258
<i>Oniticellus egregius</i>	0	0	0	2	<i>Onthophagus</i> sp.(<i>fimetarius</i> group) ^a	0	30	2	0
<i>Oniticellus formosus</i>	0	5	91	23	<i>Onthophagus</i> spp. ^a	198	62	396	219
<i>Oniticellus planatus</i>	1	0	24	6	<i>Onthophagus stigmosus</i>	607	210	1220	198
<i>Onitis caffer</i> ^a	0	0	14	1	<i>Onthophagus ursinus</i> ^a	11	3	190	28
<i>Onitis</i> spp. ^a	0	0	1	1	<i>Pachylomerus femoralis</i>	249	612	517	1087
<i>Onitis tortuosus</i> ^a	0	0	2	0	<i>Pedaria</i> sp.III <i>sensu</i> Davis	8	0	253	63
<i>Onthophagus aeruginosus</i>	1	1	77	1	<i>Proagoderus aciculatus</i>	2762	3934	1158	2693
<i>Onthophagus</i> cf. <i>fimetarius</i> ^a	24	2	83	240	<i>Proagoderus bicallosus</i> ^a	5	0	9	30
<i>Onthophagus</i> cf. <i>juvencus</i> ^a	5	0	6	5	<i>Proagoderus brucei</i> ^a	0	0	0	1
<i>Onthophagus</i> cf. <i>sugillatus</i> sp.A	335	43	671	131	<i>Proagoderus dives</i>	1624	496	3689	6078
<i>Onthophagus</i> cf. <i>sugillatus</i> sp.C	55	5	128	125	<i>Scarabaeus</i> cf. <i>xavieri</i> ^a	2	0	16	3

Appendix 1 (continued). Species	Sand Forest		Mixed Woodland		Species	Sand Forest		Mixed Woodland	
	T	S	T	S		T	S	T	S
<i>Scarabaeus galenus</i>	0	2	15	5	<i>Tropidonitis paradoxus</i> ^a	0	0	0	1
<i>Scarabaeus goryi</i>	7	21	7	50	Unidentified sp.A ^a	0	6	3	3
<i>Scarabaeus zambesianus</i>	2	0	15	1	Unidentified sp.B ^a	1	0	1	0
<i>Sisyphus bornemisszanus</i> ^a	28	321	14	36					
<i>Sisyphus sordidus</i>	18	98	646	221	Species richness	49	36	55	64
<i>Sisyphus</i> sp.Y <i>sensu</i> Paschalidis ^a	82	43	13	16	Total individuals	8398	7680	12702	13831
<i>Tragiscus dimidiatus</i>	0	0	1	0					

^aSpecies not recorded in Mkuzi Game Reserve by Doube (1991).

Appendix 2.1 - 2.6. The total number of dung beetles recorded in the Tembe (TEP) Sand Forest (SF) and Mixed Woodland (MW) habitats between May 1995 and April 1996 for each sampling grid.

2.1. May 1995.		TEP SF 1					TEP SF 2					TEP MW 1					TEP MW 2				
Species	Sites Grids																				
		A	B	C	D	E	A	B	C	D	E	A	B	C	D	E	A	B	C	D	E
<i>Allogymnopleurus consocius</i>																					1
<i>Anachalcos convexus</i>												1									
<i>Caccobius viridicollis</i>									34												
<i>Catharsius heros</i>												2									
<i>Catharsius tricornutus</i>	2											3								1	
<i>Copris inhalatus</i> prob. <i>sanctaeluciae</i>														4						1	
<i>Copris mesacanthus</i>							1				1				1						
<i>Copris puncticollis</i>																					1
<i>Copris urus</i>											1	1		5							
<i>Drepanocerus kirbyi</i>													1								
<i>Euonthophagus carbonarius</i>				11			7					11		32	44	28				5	
<i>Gareta azureus</i>						1															
<i>Hyalonthopagus alcyonides</i>																				2	
<i>Kheper lamarcki</i>													1					1	1	1	
<i>Metacatharsius pseudoopacus</i>	2						1														
<i>Neosisyphus mirabilis</i>							1					9	2	4	10	7					
<i>Neosisyphus rubrus</i>												1			1						
<i>Oniticellus formosus</i>														44		1					
<i>Oniticellus planatus</i>														20					3		
<i>Onthophagus aeruginosus</i>									1				3			1					
<i>Onthophagus</i> cf. <i>fimetarius</i>														8	2		2				
<i>Onthophagus</i> cf. <i>juvencus</i>					5									4		1		1			
<i>Onthophagus</i> cf. <i>sugillatus</i> sp.A	10	3	1	1	2		2	15	17	12	1	32	95	84	34	32	6	1			
<i>Onthophagus</i> cf. <i>sugillatus</i> sp.C		5						2		2	1	3		4	6	20					6
<i>Onthophagus</i> cf. <i>vinctus</i>	23	11	13	18	15			7	32	41	17	93	68	64	83	14	5	14	30	15	
<i>Onthophagus lacustris</i>	72	11	49	11	6		18	13	11	11	5	12	23		31	10	1				
<i>Onthophagus obtusicornis</i>																1					
<i>Onthophagus plebejus</i>		1							2	2			2	2	3						
<i>Onthophagus signatus</i>																				4	
<i>Onthophagus</i> spp.	4	4							7				35	8		10		2	6		
<i>Onthophagus stigmatosus</i>	1	5		5			1	2	25	37	1	3	24	16	8	4					1
<i>Onthophagus ursinus</i>		2																			
<i>Pachylomerus femoralis</i>	1	2		3	2		1		2	7	3	6	2	2	4		13	14	15	15	16
<i>Pedaria</i> prob. sp.I <i>sensu</i> Davis		1																			
<i>Pedaria</i> prob. sp.IV <i>sensu</i> Davis											1										
<i>Proagoderus aciculatus</i>	34	35	25	40	29		1	5	14	20	1	9	5	8	5	7	5	5	5	8	4
<i>Proagoderus dives</i>	3	7	5	8	4						5	8	25	21	34	28	68	70	118	41	136
<i>Sisyphus bornemisszanus</i>												1		1							
<i>Sisyphus sordidus</i>			1					3	1				6	1	13	9		5	2		
<i>Sisyphus</i> sp.Y <i>sensu</i> Paschalidis	1		3				3		3	1							1			1	

2.2. July 1995.		TEP SF 1					TEP SF 2					TEP MW 1					TEP MW 2				
Species	Sites																				
	Grids	A	B	C	D	E	A	B	C	D	E	A	B	C	D	E	A	B	C	D	E
<i>Caccobius viridicollis</i>											1										
<i>Catharsius harpagus</i>											1	1				1	4			2	
<i>Catharsius</i> sp. near <i>pandion</i>										1							1				
<i>Catharsius tricornutus</i>																			2		1
<i>Copris inhalatus</i> prob. <i>sanctaelucia</i>																			2		
<i>Copris mesacanthus</i>															1						
<i>Copris urus</i>																	1	1			1
<i>Euonthophagus carbonarius</i>														3		6					
<i>Neosisyphus mirabilis</i>												9		1	6	2					
<i>Oniticellus formosus</i>																1					
<i>Onthophagus aeruginosus</i>												3	2	1	4	4	2				
<i>Onthophagus</i> cf. <i>fimetarius</i>													11				5				3
<i>Onthophagus</i> cf. <i>sugillatus</i> sp.A		1					6		5	3		7		14	3	5	6	23	3	4	2
<i>Onthophagus</i> cf. <i>sugillatus</i> sp.C							6				2					1				11	1
<i>Onthophagus</i> cf. <i>vinctus</i>		1									1	7	14	2	5		18	24	8	5	3
<i>Onthophagus lacustris</i>		81	15	73	40	46	9	31	16	29	125	16	8	5	20	10	2	1	1		3
<i>Onthophagus obtusicornis</i>												4	4	1		1					
<i>Onthophagus</i> spp.										2	4	9		1	22	13	1	12			8
<i>Onthophagus stigmatosus</i>				2					1			2				13					
<i>Pachylomerus femoralis</i>				1								2		5	2		12	5	9	9	9
<i>Pedaria</i> prob. sp.IV <i>sensu</i> Davis			1											2	3			2		1	4
<i>Proagoderus aciculatus</i>			2				1	5	3		1	2	3	3	3		2	2			
<i>Proagoderus dives</i>		3	5	5	6	2	1		1	3	4	24	6	4	16	6	21	20	17	14	12
<i>Scarabaeus goryi</i>															2						
<i>Sisyphus bornemisszanus</i>												3	1					3			
<i>Sisyphus sordidus</i>													1		1	1	5	12	1	14	7
<i>Sisyphus</i> sp.Y <i>sensu</i> Paschalidis		4	1	3	1	4	9		5	3		3				1					

2.3. September 1995.

Species	TEP SF 1					TEP SF 2					TEP MW 1					TEP MW 2					
	A	B	C	D	E	A	B	C	D	E	A	B	C	D	E	A	B	C	D	E	
<i>Caccobius</i> sp.													1							4	
<i>Caccobius viridicollis</i>													12								
<i>Catharsius</i> sp. near <i>pandion</i>			1																		
<i>Catharsius tricornutus</i>															1	1		1	1	1	
<i>Copris inhalatus</i> prob. <i>sanctaeluciae</i>												1	1	1							
<i>Copris puncticollis</i>														1							
<i>Copris urus</i>																					1
<i>Euonthophagus carbonarius</i>											6	3	11	3	35						
<i>Kheper lamarcki</i>											1		1								
<i>Metacatharsius pseudoopacus</i>													1	3	1						
<i>Neosisyphus mirabilis</i>															3						
<i>Onthophagus aeruginosus</i>											1		2	1							
<i>Onthophagus</i> cf. <i>sugillatus</i> sp.A															9						
<i>Onthophagus</i> cf. <i>sugillatus</i> sp.C														6	3						
<i>Onthophagus</i> cf. <i>vinctus</i>			1		1									2	11		1				
<i>Onthophagus lacustris</i>	32	2	60	15	17		1			1					1	1					
<i>Onthophagus</i> spp.	1											2	7	7					1	1	
<i>Onthophagus ursinus</i>															4						
<i>Pachylomerus femoralis</i>	1						3		1		1	1	1	5			2	8	3	4	
<i>Pedaria</i> sp.III <i>sensu</i> Davis		1									1	3	5	27				1			
<i>Pedaria</i> prob. sp.I <i>sensu</i> Davis													2	8						2	2
<i>Pedaria</i> prob. sp.IV <i>sensu</i> Davis														6	13						
<i>Proagoderus aciculatus</i>	2	2				2	1			1	1	1	2	2			4	5		1	1
<i>Proagoderus dives</i>											1		1				14	3	22	7	14
<i>Sisyphus sordidus</i>																				1	
<i>Sisyphus</i> sp.Y <i>sensu</i> Paschalidis		1	3		1																

2.4. November 1995.

Species	TEP SF 1					TEP SF 2					TEP MW 1					TEP MW 2								
	Sites Grids	A	B	C	D	E	A	B	C	D	E	A	B	C	D	E	A	B	C	D	E			
<i>Anachalcos convexus</i>		2	1		10	2		1		2			1									2		
<i>Caccobius</i> sp.			5											17					13					
<i>Caccobius viridicollis</i>													11	7			12	6	16	1	2			
<i>Copris inhalatus</i> prob. <i>sanctaelucia</i>																			1					
<i>Copris puncticollis</i>																			1					
<i>Copris urus</i>			1																			1		
<i>Cyptochirus ambiguus</i>																						1		
<i>Drepanocerus kirbyi</i>																						2		
<i>Euoniticellus spinipes</i>																						1		
<i>Euonthophagus carbonarius</i>				1															1	3	1	1		
<i>Gareta azureus</i>		1																				2		
<i>Hyalonthopagus alcyonides</i>																				1	3	3	1	
<i>Kheper lamarcki</i>			1				1	1						1						5	1	2	4	
<i>Liatongus militaris</i>																						1		
<i>Metacatharsius pseudoopacus</i>														2						1		2		
<i>Neosisyphus fortuitus</i>					1																			
<i>Neosisyphus mirabilis</i>			4	1	5			1	1	1	2	13	2	7	4	7	2				1	3		
<i>Oniticellus formosus</i>																				3	29			
<i>Oniticellus planatus</i>																						1		
<i>Onthophagus aeruginosus</i>														1										
<i>Onthophagus</i> cf. <i>fimetarius</i>			15						1											9	6		14	4
<i>Onthophagus</i> cf. <i>sugillatus</i> sp.A		2	2	5		5	5	12	16	8	35	9			9					3	11	9		
<i>Onthophagus</i> cf. <i>sugillatus</i> sp.C					3			1							2	7								
<i>Onthophagus</i> cf. <i>vinctus</i>		26	19	4	28	4	5	2	5	20	11	38	4	6	13	84	25	13	15	2	17			
<i>Onthophagus lacustris</i>			1	6	2		1	1	1		1	3	1			2	5					4		
<i>Onthophagus obtusicornis</i>												9		3	1	1								
<i>Onthophagus plebejus</i>																	2			4		2		
<i>Onthophagus signatus</i>														1						5		20		
<i>Onthophagus</i> spp.		2	2	1	5		1		2		10	13	16	57	31		1							
<i>Onthophagus stigmatosus</i>		13			15	14	21	3	16	58	5	103	52	117		58	2	12	3		8			
<i>Onthophagus ursinus</i>			1										13	7			3	5	6		13			
<i>Pachylomerus femoralis</i>		2	1		23					3	3	1		1	4		13	4	5	3		6		
<i>Pedaria</i> sp.III sensu Davis			1													19				1				
<i>Pedaria</i> prob. sp.IV sensu Davis					3	1								1		32	2	1			3	1		
<i>Phalops boschas</i>												1	1											
<i>Proagoderus aciculatus</i>		30	28	20	89	15	65	37	56	44	87	31	7	104	2	42	20	19	8	10		4		
<i>Proagoderus bicallousus</i>		2									1						1			1		1		
<i>Proagoderus dives</i>		11	44	1	131	15	84	60	75	35	80	42	27	14	14		195	114	67	87	23			
<i>Scarabaeus</i> cf. <i>xavieri</i>																								
<i>Scarabaeus galenus</i>														4										
<i>Scarabaeus goryi</i>					3																		1	
<i>Sisyphus bornemisszanus</i>							4		1	1	3				3									
<i>Sisyphus sordidus</i>							2		2	1	2	11	12		7	6	43	23	24	14	11			
<i>Sisyphus</i> sp.Y sensu Paschalidis		1	1	3			5	2		3		1												
Unidentified														1		1						1		

2.5. January 1996.

Species	TEP SF 1					TEP SF 2					TEP MW 1					TEP MW 2					
	A	B	C	D	E	A	B	C	D	E	A	B	C	D	E	A	B	C	D	E	
<i>Anachalcos convexus</i>		1		1		3				2	3	2			2					2	1
<i>Caccobius</i> sp.		15				2						5									
<i>Caccobius viridicollis</i>								8				11									
<i>Catharsius</i> sp. near <i>pandion</i>														1				1		1	
<i>Catharsius tricornutus</i>																1	1				2
<i>Copris inhalatus</i> prob. <i>sanctaeluciae</i>			1		1	1						1		1		1	4	1	2	16	
<i>Copris mesacanthus</i>	1		2									7		1			3		1	1	
<i>Copris puncticollis</i>						1	5			1		2				1					1
<i>Copris urus</i>																				1	
<i>Cyptochirus ambiguus</i>				1								1		1	1						
<i>Drepanocerus impressicollis</i>												3									
<i>Drepanocerus kirbyi</i>												5									
<i>Euoniticellus spinipes</i>							2				1	7	1					1			
<i>Euonthophagus carbonarius</i>					2				8			19	1				3				8
<i>Gareta azureus</i>						2															
<i>Kheper lamarcki</i>	1	1		7								2	5	5	1	1	2	4			8
<i>Liatongus militaris</i>														1							
<i>Metacatharsius exiguus</i>		1																			12
<i>Metacatharsius pseudoopacus</i>												15	9	28			1	18			27
<i>Metacatharsius</i> sp.		1																			
<i>Metacatharsius</i> sp.		1																			
<i>Neosisyphus fortuitus</i>							1							1							
<i>Neosisyphus mirabilis</i>		1				1	3				27	18	4	33	21						
<i>Neosisyphus rubrus</i>							3							1							
<i>Oniticellus formosus</i>															11						1
<i>Oniticellus planatus</i>									1												
<i>Onitis caffer</i>											1			1		2	2	7			
<i>Onitis</i> sp.																					1
<i>Onitis tortuosus</i>																					2
<i>Onthophagus aeruginosus</i>											3	31	1	1							
<i>Onthophagus</i> cf. <i>fimetarius</i>																	5	7			
<i>Onthophagus</i> cf. <i>sugillatus</i> sp.A	6		16		13	19	1		3	27	20	14	59	3		5	2	13	1	33	
<i>Onthophagus</i> cf. <i>sugillatus</i> sp.C	2				1	3	8		2	2	4	15						1			
<i>Onthophagus</i> cf. <i>vinctus</i>	27	77	7	47	32	25	24	31	10	17	16	136	128	177	54	9	13	11	28	46	
<i>Onthophagus lacustris</i>	6	1	8	4	6		3	5	1	4	19	5	5			1		5		19	
<i>Onthophagus obtusicornis</i>											2	36		1							
<i>Onthophagus signatus</i>		13										7	1								11
<i>Onthophagus</i> sp.(<i>fimetarius</i> group)												2									
<i>Onthophagus</i> spp.	1				3	6	17			1	7	32			18		3				
<i>Onthophagus stigmosus</i>	12	36	13	17	1	42	18	40	7	34	72	174	132	98	303						1
<i>Onthophagus ursinus</i>								5				36	51	48							
<i>Pachylomerus femoralis</i>	16	38	7	46	18					1		14	36	15		35	29	42	14	39	
<i>Pedaria</i> sp.III sensu Davis		5							1			3	1								62

Appendix 2.5 (continued). Species	Sites TEP SF 1					Sites TEP SF 2					Sites TEP MW 1					Sites TEP MW 2				
	Grids					Grids					Grids					Grids				
	A	B	C	D	E	A	B	C	D	E	A	B	C	D	E	A	B	C	D	E
<i>Pedaria</i> prob. sp.I <i>sensu</i> Davis		1										2								13
<i>Pedaria</i> prob. sp.IV <i>sensu</i> Davis												3	34		8	23		31	28	66
<i>Phalops boschas</i>												1								
<i>Proagoderus aciculatus</i>	40	115	120	164	49	110	67	87	30	25	118	227	91	203	40	1	4	5	2	14
<i>Proagoderus bicallosus</i>							1	1				1	1	3	1					
<i>Proagoderus dives</i>	109	215	22	173	57	40	35	22	1	15	103	296	319	415	139	40	38	103	56	267
<i>Scarabaeus</i> cf. <i>xavieri</i>	1	1											2	2		4		1		5
<i>Scarabaeus galenus</i>												2		2		2		3		1
<i>Scarabaeus goryi</i>					1							2						1	1	
<i>Scarabaeus zambesianus</i>		1		1									2			3		2	1	1
<i>Sisyphus bornemisszanus</i>		1		12					1											
<i>Sisyphus sordidus</i>		1					1				17	30	20	42	23	19	18	48	43	83
<i>Sisyphus</i> sp.Y <i>sensu</i> Paschalidis	2			1		3	3				1	3	1							
<i>Tragiscus dimidiatus</i>														1						
Unidentified		1												1						

2.6. March 1996.

Species	TEP SF 1					TEP SF 2					TEP MW 1					TEP MW 2				
	A	B	C	D	E	A	B	C	D	E	A	B	C	D	E	A	B	C	D	E
<i>Anachalcos convexus</i>		3	1	2								3					1			1
<i>Caccobius viridicollis</i>										6										
<i>Catharsius harpagus</i>													1							
<i>Catharsius heros</i>												2		4						
<i>Catharsius sp. near pandion</i>				1	1															1
<i>Catharsius tricornutus</i>	1					3			1	4	1					7	1		1	2
<i>Copris inhalatus</i> prob. <i>sanctaeluciae</i>											1		1	1			1	2		1
<i>Copris mesacanthus</i>						2	3						1							
<i>Copris puncticollis</i>	1	2	1			2							2			14	1	11	5	26
<i>Copris urus</i>	2					2							3			2		1	1	
<i>Euonthophagus carbonarius</i>						25	8						4			7		1	4	
<i>Gareta azureus</i>						2														
<i>Heliocopris japedus</i>														1						
<i>Kheper lamarcki</i>				3	1	2					2	5	16	11	4		1			1
<i>Metacatharsius pseudoopacus</i>											1									
<i>Neosisyphus mirabilis</i>	1	2				18	6	11	3	2	1	1	1		2					
<i>Neosisyphus rubrus</i>				1																
<i>Onitis caffer</i>											1									
<i>Onthophagus aeruginosus</i>											3	2	1	3	7					
<i>Onthophagus cf. fimetarius</i>						8					6					1				
<i>Onthophagus cf. sugillatus</i> sp.A	2		10		1	50	8	3	2	35	3	2	1	18	32	16		1	8	4
<i>Onthophagus cf. sugillatus</i> sp.C								6	1	8	1				31	2		1	1	2
<i>Onthophagus cf. vinctus</i>	7	22	24	29	34	120	28	42	8	8	18	24	7	18	42	10	6	30	51	8
<i>Onthophagus lacustris</i>	13	4	17	2	7	25	30	35	15	48	33	31	1	18	28		3	1	2	8
<i>Onthophagus obtusicornis</i>											1	5			5					
<i>Onthophagus</i> spp.		4	2			45	25	39		10	5	59	1				8			
<i>Onthophagus stigmaticus</i>	1	6	1	4	9	2	54	58	12	15	4	5								5
<i>Onthophagus ursinus</i>			1	2											1		3			
<i>Pachylomerus femoralis</i>	2	9	2	39	3	7	2						34	7		10	1	7	4	28
<i>Pedaria</i> sp.III sensu Davis															33			44		53
<i>Pedaria</i> prob. sp.I sensu Davis						38										48	2			
<i>Pedaria</i> prob. sp.IV sensu Davis	4	5		8				2				40	8			2				
<i>Proagoderus aciculatus</i>	6	59	23	110	17	499	323	114	74	35	46	6	4	13	26	10	3		2	3
<i>Proagoderus dives</i>	1	40	9	110	8	124	34	10	1		10		81	39	35	180	24	43	70	97
<i>Scarabaeus cf. xavieri</i>																		1		
<i>Scarabaeus galenus</i>														1						
<i>Scarabaeus goryi</i>								3												
<i>Scarabaeus zambesianus</i>																4				2
<i>Sisyphus bornemisszanus</i>						5					1				1					
<i>Sisyphus sordidus</i>		1					1	1	1		1	1	4	2		14	9	5	15	22
<i>Sisyphus</i> sp.Y sensu Paschalidis						10	1			1	1									

Appendix 3.1 - 3.6. The total number of dung beetles recorded in the Sileza (SNR) Sand Forest (SF) and Mixed Woodland (MW) habitats between May 1995 and April 1996 for each sampling grid.

3.1. June 1995.		SNR SF 1					SNR SF 2					SNR MW 1					SNR MW 2				
Species	Sites	A	B	C	D	E	A	B	C	D	E	A	B	C	D	E	A	B	C	D	E
	Grids																				
<i>Anachalcos convexus</i>							1														
<i>Copris inhalatus</i> prob. <i>sanctaeluciae</i>												1	2								
<i>Copris puncticollis</i>												2	9	2		4					1
<i>Copris urus</i>												1									
<i>Euonthophagus carbonarius</i>					1		1										1	2		1	
<i>Gareta azureus</i>									1												
<i>Metacatharsius exiguus</i>												1									
<i>Neosisyphus mirabilis</i>		3	2		1	3								1			8				
<i>Neosisyphus rubrus</i>												1									
<i>Onitis caffer</i>																				1	
<i>Onthophagus</i> cf. <i>fimetarius</i>												7			4					1	1
<i>Onthophagus</i> cf. <i>juvencus</i>																1					
<i>Onthophagus</i> cf. <i>sugillatus</i> sp.A												2		1		2		1			1
<i>Onthophagus</i> cf. <i>vinctus</i>		3					4					8	4	8	2	6	3	4	2	3	2
<i>Onthophagus lacustris</i>							1	2	1						1						
<i>Onthophagus signatus</i>												1									
<i>Onthophagus</i> spp.												4			2	2					
<i>Onthophagus stigmaticus</i>						2										1					1
<i>Pachylomerus femoralis</i>		11	7	2	21	14						4	3		14	12	3	11	10	14	11
<i>Phalops boschas</i>																					2
<i>Proagoderus aciculatus</i>		3	1		3	2			1	1				2	1	1	2	2		9	3
<i>Proagoderus dives</i>							1			2		1	12	3	21	17	1	13	23	2	3
<i>Sisyphus</i> sp.Y <i>sensu</i> Paschalidis																					1

3.2. August 1995.

Species	Sites Grids	SNR SF 1					SNR SF 2					SNR MW 1					SNR MW 2				
		A	B	C	D	E	A	B	C	D	E	A	B	C	D	E	A	B	C	D	E
<i>Anachalcos convexus</i>																	2				
<i>Catharsius harpagus</i>																				1	
<i>Catharsius</i> sp. near <i>pandion</i>		1																			
<i>Catharsius tricornutus</i>																	1				2
<i>Copris inhalatus</i> prob. <i>sanctaeluciae</i>													2	1	1	1					
<i>Copris puncticollis</i>												7					7	4			2
<i>Neosisyphus mirabilis</i>							1					1									
<i>Onthophagus</i> cf. <i>fimetarius</i>												1		7						5	
<i>Onthophagus</i> cf. <i>vinctus</i>				1		1			1			3	4	4	10	3		1		1	
<i>Onthophagus lacustris</i>	1																				2
<i>Onthophagus</i> spp.																				1	
<i>Onthophagus stigmatosus</i>							1						1		1	2	13	1	1		
<i>Pachylomerus femoralis</i>				1		2				1	2	3		4	8	2	5	1	2	2	
<i>Pedaria</i> prob. sp. IV sensu Davis												2		3		1	3				
<i>Proagoderus aciculatus</i>		1		1		6		4	2			10	5	1	4						
<i>Proagoderus dives</i>		1	4	1			1	2	1	3	1			2	1	1	7	6	3	2	4
<i>Sisyphus sordidus</i>													1								
<i>Sisyphus</i> sp. Y sensu Paschalidis		1																			

3.3. October 1995.

Species	Sites Grids	SNR SF 1					SNR SF 2					SNR MW 1					SNR MW 2				
		A	B	C	D	E	A	B	C	D	E	A	B	C	D	E	A	B	C	D	E
<i>Anachalcos convexus</i>		2					2					4		2	10	3	1	1	4		
<i>Caccobius</i> sp.															1		7	13	7	5	8
<i>Caccobius viridicollis</i>							1					18	9	1		4		8	1		5
<i>Catharsius</i> sp. near <i>pandion</i>		1										14		4	2			2			
<i>Catharsius tricornutus</i>											1			2	1			1			
<i>Copris inhalatus</i> prob. <i>sanctaeluciae</i>									1												
<i>Copris puncticollis</i>																	1		2	1	3
<i>Copris urus</i>										1							1				1
<i>Drepanocerus kirbyi</i>																		1	3		
<i>Euonthophagus carbonarius</i>	1																				
<i>Gareta azureus</i>	15	22	8	20	5		1	7													
<i>Kheper lamarcki</i>												3				1	1				1
<i>Metacatharsius exiguus</i>													3		2		1				
<i>Metacatharsius pseudoopacus</i>															2			5			1
<i>Neosisyphus fortuitus</i>		5					5	17				1									3
<i>Neosisyphus mirabilis</i>	14	12	4	15	4		23	111	16	33	16				5	12	6	17	2	7	
<i>Neosisyphus rubrus</i>																	1			1	1
<i>Oniticellus planatus</i>																				1	1
<i>Onthophagus aeruginosus</i>																		1			
<i>Onthophagus</i> cf. <i>fimetarius</i>												5			1		2		1	1	1
<i>Onthophagus</i> cf. <i>sugillatus</i> sp.A	4				1	1	9	4			3	4	1			3				1	
<i>Onthophagus</i> cf. <i>sugillatus</i> sp.C							1		1		4			2			1			1	
<i>Onthophagus</i> cf. <i>vinctus</i>	35	24	9	22	4	13	30	28	6	14	62	6	12	10	3	14	33	8	9	56	
<i>Onthophagus lacustris</i>	4	1	4		7			2													
<i>Onthophagus signatus</i>												62	2	3	15	23	13	46	13	8	35
<i>Onthophagus</i> sp.(<i>fimetarius</i> group)						12	2	3	4	9											
<i>Onthophagus</i> spp.	2	3	7	15	7					5				11	9	13	2	14	2	4	
<i>Onthophagus stigmatosus</i>									1		2									5	
<i>Onthophagus ursinus</i>							1	1		1		9	3	1	1		9		2		
<i>Pachylomerus femoralis</i>	3	17	7	6	14	1	2	4	4	1	32	7	10	25	19	32	25	28	30	28	
<i>Pedaria</i> sp.III sensu Davis												3	1	3	4	4	9				
<i>Pedaria</i> prob. sp.I sensu Davis												1	1		2	5	10	5	3	13	
<i>Pedaria</i> prob. sp.IV sensu Davis														1	1	2			2	2	
<i>Proagoderus aciculatus</i>	80	88	33	175	91	79	46	77	148	74	129	24	22	20	33	32	34	28	35	35	
<i>Proagoderus bicallosus</i>																	1		1	1	
<i>Proagoderus brucei</i>																1					
<i>Proagoderus dives</i>			1	3	6		3	6	7		65	9	27	65	53	216	219	83	124	172	
<i>Scarabaeus goryi</i>	1			2				1			11	1	3								
<i>Sisyphus bornemisszanus</i>	5	3	2	1		39	19	45	23	4	7	2			2	2	9				
<i>Sisyphus sordidus</i>						3	4	7			3	7		21	9	11	13	11	6	14	
<i>Sisyphus</i> sp.Y sensu Paschalidis	13	3	3		7	1				1				1	2	1	3				

3.4. December 1995.		SNR SF 1					SNR SF 2					SNR MW 1					SNR MW 2				
Species	Sites	A	B	C	D	E	A	B	C	D	E	A	B	C	D	E	A	B	C	D	E
	Grids																				
<i>Anachalcos convexus</i>			1	3	2	2						3	2	12	2	3		2	3	4	3
<i>Caccobius</i> sp.			9											33							
<i>Caccobius viridicollis</i>																			2		
<i>Catharsius harpagus</i>								3					2							2	2
<i>Catharsius</i> sp. near <i>pandion</i>													2	24		15				2	2
<i>Catharsius tricornutus</i>													2								
<i>Copris inhalatus</i> prob. <i>sanctaeluciaae</i>													6	12		2					4
<i>Copris mesacanthus</i>																	2	3			
<i>Copris puncticollis</i>													3			2		4	2	4	6
<i>Copris urus</i>				2												1					
<i>Euoniticellus spinipes</i>			1	1			1														
<i>Euonthophagus carbonarius</i>										2		3				2			4		3
<i>Gareta azureus</i>		2	109		1	10			4	6											
<i>Hyalonthophagus alcyonides</i>																1					
<i>Kheper lamarcki</i>					4				2					3			3			3	
<i>Metacatharsius exiguus</i>													2	6							
<i>Metacatharsius pseudoopacus</i>													1	3			2				
<i>Metacatharsius</i> sp.													1								
<i>Neosisyphus fortuitus</i>			1										2	3	3						
<i>Neosisyphus mirabilis</i>			13		4	6	22	7	10	19		51	25	21		5		2	6	2	4
<i>Neosisyphus rubrus</i>			3									12	3			6	2				3
<i>Oniticellus formosus</i>					1					3			1			1	2		3	3	3
<i>Oniticellus planatus</i>																1					
<i>Onthophagus aeruginosus</i>							1														
<i>Onthophagus</i> cf. <i>fimetarius</i>												3	18	18		7		46			
<i>Onthophagus</i> cf. <i>sugillatus</i> sp.A					8			2					36		3	14		10		2	10
<i>Onthophagus</i> cf. <i>sugillatus</i> sp.C					1									114							
<i>Onthophagus</i> cf. <i>vinctus</i>		37	146	19	29	40	7	6	4	2	63	84	84	124	34	53	22		4	5	72
<i>Onthophagus lacustris</i>		6	3	8	8	55	1	3			18	24				2				2	5
<i>Onthophagus signatus</i>															31						
<i>Onthophagus</i> spp.		5	6		4		1					3		18		21		3			
<i>Onthophagus stigmosus</i>		4	70	32	56	12				3			17	1	39	22	9				
<i>Onthophagus ursinus</i>																1					
<i>Pachylomerus femoralis</i>		62	33	14	27	42	9	54	39	25	22	18	4	15	43	45	42	40	45	36	25
<i>Pedaria</i> sp.III sensu Davis															6						
<i>Pedaria</i> prob. sp.I sensu Davis															3				2		
<i>Pedaria</i> prob. sp.IV sensu Davis														25		24		4			
<i>Proagoderus aciculatus</i>		66	249		124	181	100	66	43	138		633	169	148	15	56	6	4	6	13	18
<i>Proagoderus bicallosus</i>													6	1	5	3	2			2	
<i>Proagoderus dives</i>		1	210		16	55		6	7	16		1065	344	142	120	192	45	91	81	55	166
<i>Scarabaeus</i> cf. <i>xavieri</i>																1	2				
<i>Scarabaeus galenus</i>									2									2		2	
<i>Scarabaeus goryi</i>		4		2	1			2		1		9	3	10					3	2	
<i>Sisyphus bornemisszanus</i>		15	18		5	13	29	12	13	13				3	1			2			
<i>Sisyphus sordidus</i>			33		7	3						27	13	16		20	4	2	10	9	4
<i>Sisyphus</i> sp.Y sensu Paschalidis			4											1	4						2
Unidentified			6									3									

3.5. February 1996.

Species	Sites Grids					SNR SF 2					SNR MW 1					SNR MW 2				
	A	B	C	D	E	A	B	C	D	E	A	B	C	D	E	A	B	C	D	E
<i>Anachalcos convexus</i>	5	2	8	8	1				2	1	1	1	17	6		5	7	5	1	
<i>Caccobius viridicollis</i>																4				
<i>Catharsius</i> sp. near <i>pandion</i>			1	2								2	7	3	2	1	1	1		
<i>Catharsius tricornutus</i>			1															1	1	
<i>Copris inhalatus</i> prob. <i>sanctaeluciae</i>			2	1								1	2	2	2					
<i>Copris puncticollis</i>												2		1	4	4	17	13	4	
<i>Copris urus</i>															1	2	2			
<i>Drepanocerus kirbyi</i>														1						
<i>Euoniticellus spinipes</i>																	1			
<i>Euonthophagus carbonarius</i>											1			4		2			1	
<i>Gareta azureus</i>	2	2	5	8	8		1	8	8											
<i>Kheper lamarcki</i>	3			4								1	3				2	1	1	
<i>Metacatharsius pseudoopacus</i>														2				1		
<i>Metacatharsius</i> sp.																2				
<i>Neosisyphus fortuitus</i>							1					2		2	1	1				
<i>Neosisyphus mirabilis</i>	3	2	2		4	8	7	16	67	7	2	7	3	8	3			7	6	
<i>Neosisyphus rubrus</i>											6	6	1	1	4	6		3	2	
<i>Oniticellus egregius</i>																	1		1	
<i>Oniticellus formosus</i>		1										5							1	
<i>Oniticellus planatus</i>												1	1				1			
<i>Onitis</i> sp.											1									
<i>Onthophagus</i> cf. <i>fimetarius</i>												1	58	6		4	41			
<i>Onthophagus</i> cf. <i>juvencus</i>												1								3
<i>Onthophagus</i> cf. <i>sugillatus</i> sp.A	2						9				1	2	2			1	1	5		
<i>Onthophagus</i> cf. <i>sugillatus</i> sp.C							2								2					
<i>Onthophagus</i> cf. <i>vincitus</i>	2	3	3	2	1	1	4	1		3	14	2	124		23	18	28	16		
<i>Onthophagus lacustris</i>	3	1	2	1						1		5		7	2		2	3		
<i>Onthophagus signatus</i>													3							3
<i>Onthophagus</i> spp.												3	42			10				
<i>Onthophagus stigmatosus</i>						2		2	22		2		16		1	11	31			
<i>Pachylomerus femoralis</i>	30	34	13	1	39	2	5	5	4	5	28	31	38	33	16	35	25	36	11	21
<i>Pedaria</i> sp.III sensu Davis												12		14					3	4
<i>Pedaria</i> prob. sp.I sensu Davis													3		37	7		11	3	2
<i>Pedaria</i> prob. sp.IV sensu Davis				1							1		10	1			13			4
<i>Phalops boschas</i>													5							
<i>Proagoderus aciculatus</i>	168	181	124	82	100	154	52	144	254	292	157	55	108	127	110	113	66	133	35	15
<i>Proagoderus bicallosus</i>																	1	3	1	
<i>Proagoderus dives</i>	3	23	13		11	9	2	8	16		34	125	70	113	110	183	231	344	150	144
<i>Scarabaeus galenus</i>																	1			
<i>Scarabaeus goryi</i>	3	2	2										1					5		
<i>Scarabaeus zambesianus</i>																				2
<i>Sisyphus bornemisszanus</i>	13	5		1					33					3						
<i>Sisyphus sordidus</i>		6	1	1		7		15		11			3		1	4		3		
<i>Sisyphus</i> sp.Y sensu Paschalidis				10									1							
<i>Tropidonitis paradoxus</i>														1						

3.6. April 1996.

Species	Sites Grids					SNR SF 2					SNR MW 1					SNR MW 2						
	A	B	C	D	E	A	B	C	D	E	A	B	C	D	E	A	B	C	D	E		
<i>Anachalcos convexus</i>	1	10	16	1	28								1		1				1			
<i>Catharsius</i> sp. near <i>pandion</i>				2									1									
<i>Catharsius tricornutus</i>		1	1																			
<i>Copris inhalatus</i> prob. <i>sanctaeluciae</i>																		3				
<i>Copris puncticollis</i>												1						2			4	
<i>Copris urus</i>		1																1		1		
<i>Euonthophagus carbonarius</i>																			1			
<i>Gareta azureus</i>				5	3	29																
<i>Metacatharsius pseudoopacus</i>																		1	1			
<i>Neosisyphus fortuitus</i>																					1	
<i>Neosisyphus mirabilis</i>	2	6	9	3	2		26	17	4	3		1	2		1	7	1	8	11		3	
<i>Neosisyphus rubrus</i>																1		2		1		
<i>Oniticellus formosus</i>																		2				
<i>Onthophagus</i> cf. <i>fimetiarius</i>	1									1		1										
<i>Onthophagus</i> cf. <i>sugillatus</i> sp.A		3																8		7	2	8
<i>Onthophagus</i> cf. <i>sugillatus</i> sp.C																1						
<i>Onthophagus</i> cf. <i>vinctus</i>		8	17	1		1	6	5	1		2	4	7	4	13	8	27	15		11		
<i>Onthophagus lacustris</i>			8	1																		
<i>Onthophagus</i> spp.					2		2	1	2			3		1	17		18	5			11	
<i>Onthophagus stigmosus</i>	1				1	1									1	6		4	5	5		
<i>Onthophagus ursinus</i>																2						
<i>Pachylomerus femoralis</i>	2	1	10	1	9		3			1	19	15	60	13	14	6	12	2	10		4	
<i>Pedaria</i> prob. sp.IV sensu Davis												1	1		1	2	3					
<i>Proagoderus aciculatus</i>	24	170	186	39	3	19	5	27	24	3	1	15	92		44	23	84	15				
<i>Proagoderus bicallosus</i>																					1	
<i>Proagoderus dives</i>	4	13	13			7	20				2	138	134		181	87	132	123	218	103		
<i>Scarabaeus goryi</i>													1						1			
<i>Sisyphus bornemisszanus</i>	4	3						3							1						4	
<i>Sisyphus sordidus</i>												1	3	1			3	1				

CHAPTER 3

Habitat-associated heterogeneity, endemism, and biogeographic affiliations of Sand Forest avian assemblages in South Africa: Conservation implications

Introduction

The Maputaland Centre in South Africa (MC) (Fig. 1), is recognised as a region of considerable biological importance and invariably emerges as an important conservation area for the region (Cowling and Hilton-Taylor 1994, Lombard 1995). It forms the northernmost focal area of floristic endemism of the regional Maputaland-Pondoland Mosaic (White 1983, van Wyk 1990, 1994, Davis *et al.* 1994), and is part of a complex biogeographic region where Afromontane and lowland tropical elements intermingle (White 1978, Poynton and Boycott 1996). Second only to the greater Cape Flora (see Bond and Goldblatt 1984, Cowling *et al.* 1997, Cowling *et al.* 1998), the MC forms one of southern Africa's most important centres of floristic diversity and endemism (van Wyk 1996), and is also recognised as an important centre of vertebrate species richness and endemism (Poynton 1961, ICBP 1992, Thirgood and Heath 1994, Gelderblom *et al.* 1995, Clancey 1996, Poynton and Boycott 1996, Allan *et al.* 1997).

The Sand Forest habitat type, which is considered a true forest vegetation type with a biogeographic affiliation to Afromontane forest (White 1978, Low and Rebelo 1996), has the highest plant diversity and harbours the highest proportion of endemic plant species of all the habitat types in the MC (W. S. Matthews, pers. comm., van Wyk 1996). Based on qualitative evidence, it has also been suggested that most of the endemic vertebrate species from the region are restricted to Sand Forests (van Wyk 1996), although the biogeographic affinities of this fauna have not been well studied. On the basis of broad scale studies, Poynton (e.g., 1961, Poynton and Boycott 1996) emphasized the co-occurrence of Afromontane and lowland tropical amphibian faunas, but concluded that vegetation type played little role in the distribution of frog species. Likewise, on the grounds of similar broad scale studies, Allan *et al.* (1997) suggested that the avifauna of Sand Forests was part of a complex East Coast Littoral biome rather than an Afromontane one. To date, however, few local scale studies have investigated the faunas

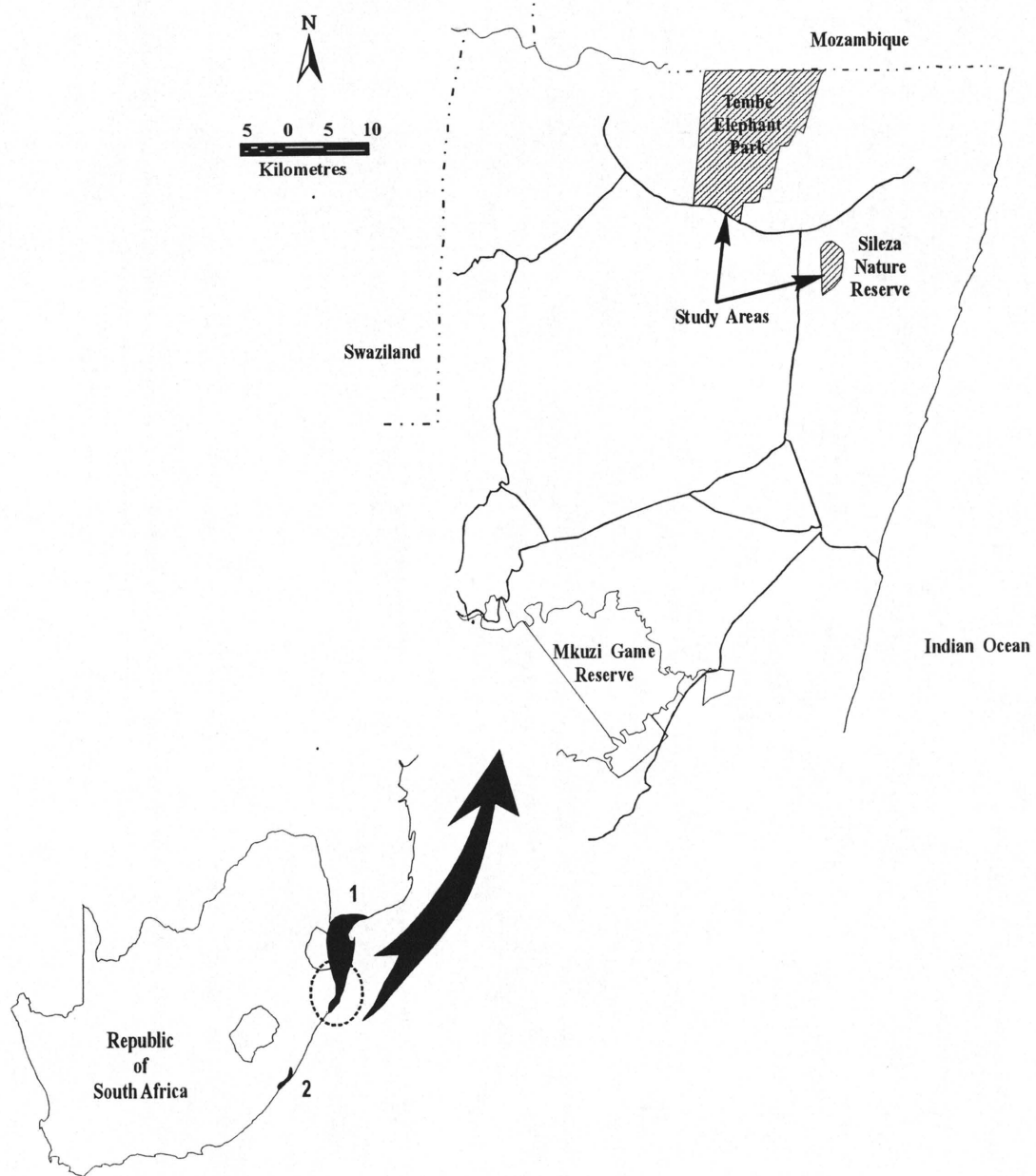


Fig. 1. Map of South Africa showing the location of (1) the Maputaland Centre, (2) the Pondoland Centre and the study areas within the Maputaland Centre.

of Sand Forest habitat patches, and the surrounding savanna-like Mixed Woodland matrix within which they are embedded (van Wyk 1990, 1994, 1996). Thus the faunal affinities of the most significant habitats of the MC remain poorly understood, as does the level of habitat-associated heterogeneity in animal assemblages at these scales (but see van Rensburg *et al.* in press, Chapter 2 for information on invertebrates).

Understanding the affinities of the Sand Forest faunas and determining their spatial heterogeneity at small spatial scales is especially important in the context of regional and local conservation priorities in southern Africa. Despite emerging as an important area in regional conservation goal setting (see above), it is not known to what extent the various habitats of the MC contribute to selection of the area as a conservation priority. Without reference to such local landscape and species distribution patterns, priority conservation areas identified at broad global or regional scales (e.g. priority grids identified by selection algorithms) cannot be translated into effectively designed local conservation areas (see Murphy 1989, Wiens 1989, Noss 1990, Flather *et al.* 1997 for rationale and discussion). This is of particular importance given that Sand Forest patches in the MC are under considerable threat. In both South Africa and Mozambique extensive commercial afforestation, local use of fuelwood, and clearance for agriculture are taking place within this habitat type (Davis *et al.* 1994, Cole and Landres 1996). Only small portions of Sand Forest are presently protected in four conservation areas in South Africa (3 020 ha in Tembe Elephant Park out of a total of 30 079 ha; 25 ha out of 2 500 ha in Sileza Nature Reserve; 1 500 ha out of 29 000 ha in Mkuzi Game Reserve, and a few patches in Falsebay Park), and a conservation conflict is developing within the largest of these (Tembe Elephant Park - Fig. 1, see van Rensburg *et al.* in press, Chapter 2). The rationale for the declaration of this park was Sand Forest conservation, as well as the conservation of the elephant *Loxodonta africana* in northern KwaZulu-Natal. Although elephants prefer plant species growing in non-Sand Forest habitats, they are increasingly using Sand Forests because of the relatively small size of the Tembe Elephant Park, with marked effects. Elephants are not present in at least two of the other reserves (Sileza Nature Reserve and Falsebay Park), and the Sand Forest patches here are therefore not under similar threat. However, relying on these two reserves to adequately represent regional Sand Forest diversity is unlikely to be an effective conservation strategy if there

is substantial heterogeneity in animal and plant assemblages among reserves. Such heterogeneity has been demonstrated for plants (W. S. Matthews, pers. comm.) and for invertebrates (van Rensburg *et al.* in press, Chapter 2), but spatial heterogeneity in vertebrate assemblages at the local scale has not been examined.

In this study, I therefore investigate habitat-associated heterogeneity and endemism of avian assemblages in Sand Forest patches, and the Mixed Woodland matrix, in two game reserves in the Maputaland Centre. In addition, using information published in the Atlas of Southern African birds (Harrison *et al.* 1997) I investigate the biogeographic affinities of these assemblages. I have selected birds as my focal taxon because the MC hosts almost 60% of the 800 bird species recorded in South Africa on only 2.19% of its land surface area (van Wyk 1996, Harrison *et al.* 1997), because they are systematically well known, well surveyed (Allan *et al.* 1997) and relatively straightforward to sample quantitatively (Buckland *et al.* 1994, MacNally 1997), and because the region harbours numerous endemic species and subspecies (ICBP 1992, Clancy 1996, van Wyk 1996, Allan *et al.* 1997).

Material and methods

Study area

Field work was undertaken in Tembe Elephant Park (27°01'S 32°24'E) (hereafter Tembe) and Sileza Nature Reserve (27°06'S 32°36'E) (hereafter Sileza), on the southern Mozambique Coastal Plain of Northern KwaZulu-Natal, South Africa. Sand Forest is characterized by tree species such as *Dialium schlechteri* and *Erythrophleum lasianthum* (Caesalpinioideae) (Moll 1977, van Wyk 1996) with a poorly developed understory. The more open, Mixed Woodland matrix is characterized by common, woody savanna species such as *Acacia burkei*, *Albizia versicolor* and *A. adianthifolia* (Mimosoideae). It has a well developed grass understory represented by *Aristida*, *Pogonarthria* and *Perotis* species (Moll 1977, 1980). The soils in both study areas are homogeneous, grey, siliceous, aeolian sands which are highly leached (dystrophic) and relatively acidic (water pH \approx 6.1) - (W. S. Matthews, pers. comm.).

Local sampling procedures and construction of regional assemblages

Replicated survey areas in the reserves were selected from within standardised vegetation communities (Sand Forest and Mixed Woodland - van Wyk 1996). Two Sand Forest sites and two Mixed Woodland sites were surveyed in each reserve, i.e. eight survey sites, grouped into four reserve-habitat combinations (Tembe Sand Forest, Tembe Mixed Woodland, Sileza Sand Forest, Sileza Mixed Woodland). Each survey site comprised sixteen fixed survey points. Following Buckland *et al.* (1994), the appropriate number of survey points for these assemblages was determined from a pilot study. Distances between the sixteen points within a site, between sites, and between the areas sampled in the two reserves were, respectively, 150 m, 1.3 – 3.1 km, and *c.* 18 km (Fig. 2). These distances minimised the probability of double detection, ensuring data independence, and provided suitable replicates for the study. Because of terrain difficulties, particularly in the Sand Forest, sampling points were placed along game and elephant paths. Although sampling bias could potentially result, this is unlikely where mobile animals such as birds are surveyed (S. T. Buckland, pers. comm.). Survey points were, however, identified without prior knowledge of bird distributions, and care was taken to ensure that sampling points did not follow more prominent natural features (e.g., forest edges - see Guthery 1988).

Visual and auditory bird surveys were conducted bimonthly between May 1995 and April 1996, at all four sites in a reserve (the two reserves were surveyed in alternative months), using point sampling (see Buckland *et al.* 1994 for a discussion of the advantages and disadvantages of this method). During one month, each of the four sites was surveyed four times. The 16 sampling points from a single site were surveyed in one morning (10 minutes per sampling point). Three minutes were spent at each survey point prior to data collection to allow the birds time to adjust to the disturbance caused by the observer. Survey periods were limited to reduce the risk of multiple detection resulting from birds moving out of and back into an observation area, which could lead to substantial density overestimation (Buckland *et al.* 1994). Thus a compromise between maximization of the probability that individuals in a survey point would be detected (e.g. interval-based bird calls), and minimization of the probability of multiple detection, or of attracting curious species (e.g. Southern Boubou Shrike, *Laniarius ferrugineus*

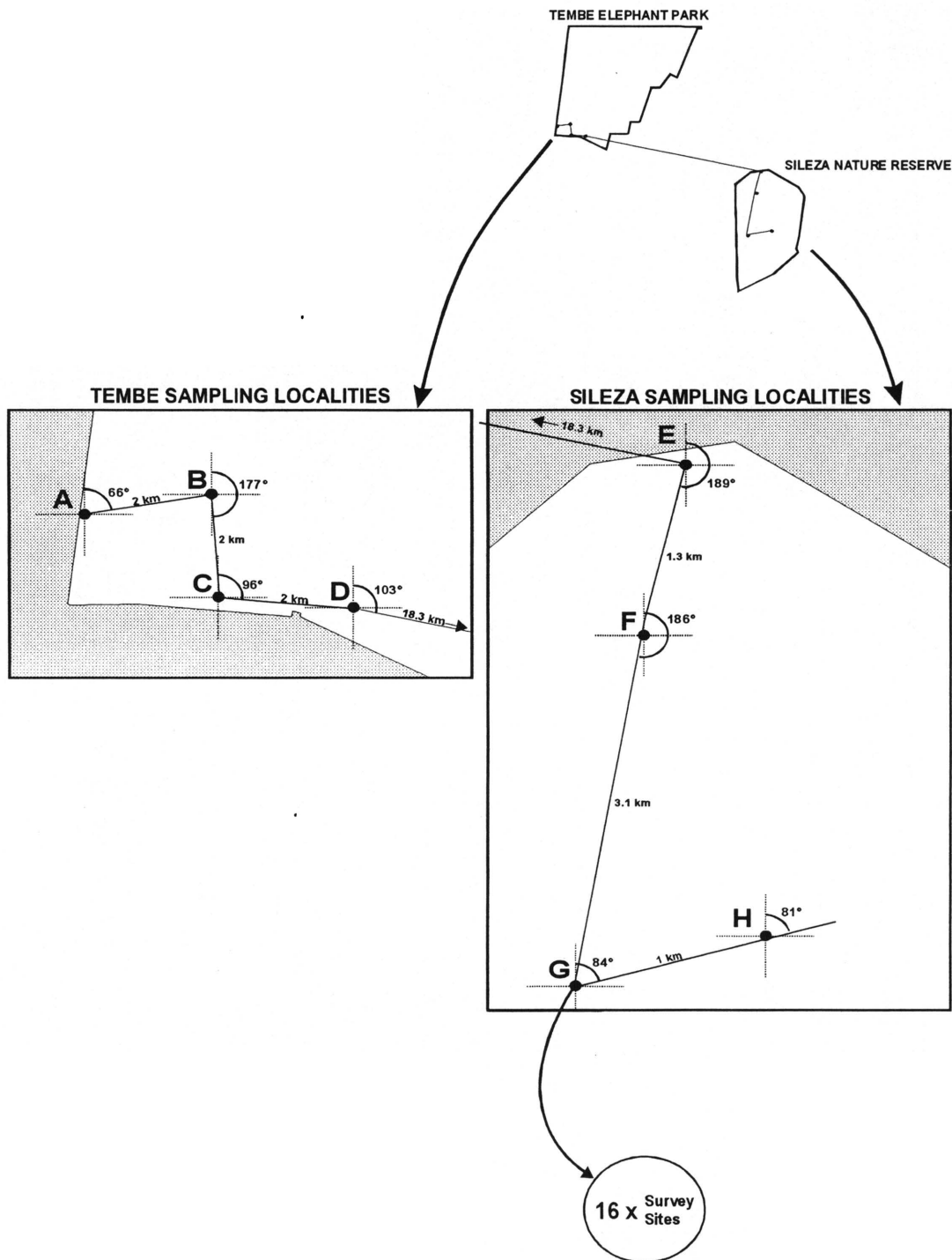


Fig. 2. Schematic diagram showing the two reserves (Tembe Elephant Park and Sileza Nature Reserve), and illustrating the relative positions of the two habitat types (Sand Forest and Mixed Woodland), eight sites, and sixteen survey points within a site, for each of the reserves: (A) Tembe Mixed Woodland 2; (B) Tembe Sand Forest 2; (C) Tembe Sand Forest 1; (D) Tembe Mixed Woodland 1; (E) Sileza Sand Forest 1; (F) Sileza Mixed Woodland 1; (G) Sileza Mixed Woodland 2; (H) Sileza Sand Forest 2.

tongensis), was sought.

On initial detection, birds were placed into distance categories, demarcated by fixed markers placed at known distances from the observation point (0 - 4; 5 - 9; 10 - 15; 16 - 30 and 31 - 50 m) before the study commenced. Although determination of the exact distance at which each bird was detected would have been desirable, this was not practicable when many birds were heard and not observed (Buckland *et al.* 1994). In addition, estimation of exact distances when large numbers of birds are seen over a short period may lead to observational difficulties and a reduction in survey accuracy (Bibby *et al.* 1985). The distance to a bird in the tree canopy was taken as the distance from the observer to a point directly below the bird on the ground. All birds within 50 m of the survey point, including birds involved in territorial displays, were recorded. Birds flying over the study area were excluded. Records were also categorised as reliable sightings, or as bird call records. Unreliable sightings were not included in the database.

For an analysis of biogeographic affinity of the avian assemblages, a species presence/absence matrix was constructed for the combined survey results for Sand Forest, and those for Mixed Woodland. In addition, presence/absence matrices were generated for avian assemblages in the southern African biomes delimited by Low and Rebelo (1996) (see also Rutherford and Westfall 1994), and the biomes delimited by Allan *et al.* (1997), using the quarter degree grid square data provided in the South African Bird Atlas (Harrison *et al.* 1997).

Data analysis

Sample sizes from specific localities were sufficient to allow the calculation of absolute bird abundances ($n = 64$ survey points per month per habitat, coefficient of variation = 12%, see Buckland *et al.* 1994). The number of individuals of each species observed over the course of the study period was summed for each survey point (survey points within a site were reduced from 16 to four by randomly pooling sets of four data points), within each site. Relative bird densities in the different sites were estimated using the DISTANCE software package (see Buckland *et al.* 1994).

Multivariate community analysis was undertaken using PRIMER v4.0 1994 (Clarke and Warwick 1994). Cluster analysis, using group averaging and Bray Curtis

similarity measures (Bray and Curtis 1957) was used to examine abundance relationships between survey points, sites and habitat types both within and between reserves. These data were double square-root transformed prior to analysis (to weight common and rare species equally) (Clarke and Warwick 1994). Analysis of similarity (ANOSIM - Clarke 1993) was used to establish the significance of differences between habitats and survey units; this is a non-parametric permutation procedure applied to rank similarity matrices underlying sample ordinations (Clarke 1993), in which a significant global *R*-statistic of close to one indicates distinct differences between the assemblages/ habitats compared. Non-metric multi-dimensional scaling (MDS) was used to display the relationships between the sites in an ordination.

Characteristic bird species (which can be considered indicator species) were identified for each habitat type using the species abundance matrix from each site as input to the Indicator Value Method (Duf rene and Legendre 1997). This method assesses the degree (expressed as a percentage) to which each species fulfils the criteria of specificity (uniqueness to a particular site) and fidelity (frequency within that habitat type) for each habitat cluster compared with all other habitats. The higher the percentage IndVal (indicator value) obtained, the higher the specificity and fidelity values for that species, and the more representative the species is of that particular habitat. Species with high IndVals thus make reliable indicator species not only because they are specific to a habitat, but also because they have a high probability of being surveyed in that habitat during monitoring and assessment (McGeoch and Chown 1998). The following comparisons were used for assessment of indicator species: Tembe Sand Forest vs. Tembe Mixed Woodland, Sileza Sand Forest vs. Sileza Mixed Woodland, and all Sand Forest habitats vs. all Mixed Woodland habitats. Duf rene and Legendre's (1997) random reallocation procedure of sites among site groups was used to test the significance of the IndVal measures for each species. Those species with significant IndVals > 70% (subjective benchmark) were then regarded as indicator species for the habitat in question.

Rare species were also identified for each habitat type and for each reserve. Following Gaston (1994) I defined these as the 25% least abundant species in my samples (proportion of species method).

For determining biogeographic affinities, cluster analysis, using group averaging and Bray Curtis similarity measures (Bray and Curtis 1957), was used to examine relationships between the assemblages of the Sand Forest and from Mixed Woodland habitats, and those of the southern African biomes identified by Low and Rebelo (1996), and Allan *et al.* (1997).

Results

Out of a total of 5 556 bird records, 112 species, representing 36 families, were recorded from the two habitats in Tembe and Sileza. Both abundance (n) and species richness (S) were higher in Tembe ($n = 2\ 976$, $S = 96$) than in Sileza ($n = 2\ 580$, $S = 90$) (see Appendix 1). Blackeyed Bulbul, *Pycnonotus barbatus* was the most abundant species in Sileza Mixed Woodlands, whereas Rattling Cisticola, *Cisticola chiniana* dominated the Tembe Mixed Woodlands. In contrast, Sombre Bulbul, *Andropadus importunus* was the most abundant species in Sileza Sand Forests, whereas Yellowbellied Bulbul, *Chlorocichla flaviventris* was dominant in Tembe Sand Forests (see Appendix 1).

Analysis of similarity indicated no significant differences among the four pooled survey points within sites ($p > 0.05$). Likewise, after pooling point data for each site, analysis of similarity showed no significant differences between sites, within habitat types for each reserve (Fig. 3). However, bird assemblages differed both between habitat types in a given reserve, and between reserves for a given habitat type (Fig. 3).

Twenty five species were found to occur consistently within a particular habitat in a given reserve, thus achieving high and significant IndVals (Table 1). Of the four species and 19 subspecies endemic to the MC (Clancey *et al.* 1991, Clancey 1996), four species and six subspecies were included amongst these, and two additional endemic subspecies were recorded in the study area, though less consistently (Table 1, Appendix 1). Of the four endemic species, Neegaard's Sunbird, *Nectarinia neergaardi* was restricted to and abundant in Tembe Sand Forest (Table 1), Rudd's Apalis, *Apalis ruddi* occurred in all four habitats, but was consistently recorded and abundant in Sileza Sand Forest only (Appendix 1, Table 1), and Woodward's Batis, *Batis fratrum* was consistently recorded in reasonably high densities in both Tembe and Sileza Sand Forests (indicated by its high IndVal), although a few individuals were also recorded in Tembe Mixed Woodland. In

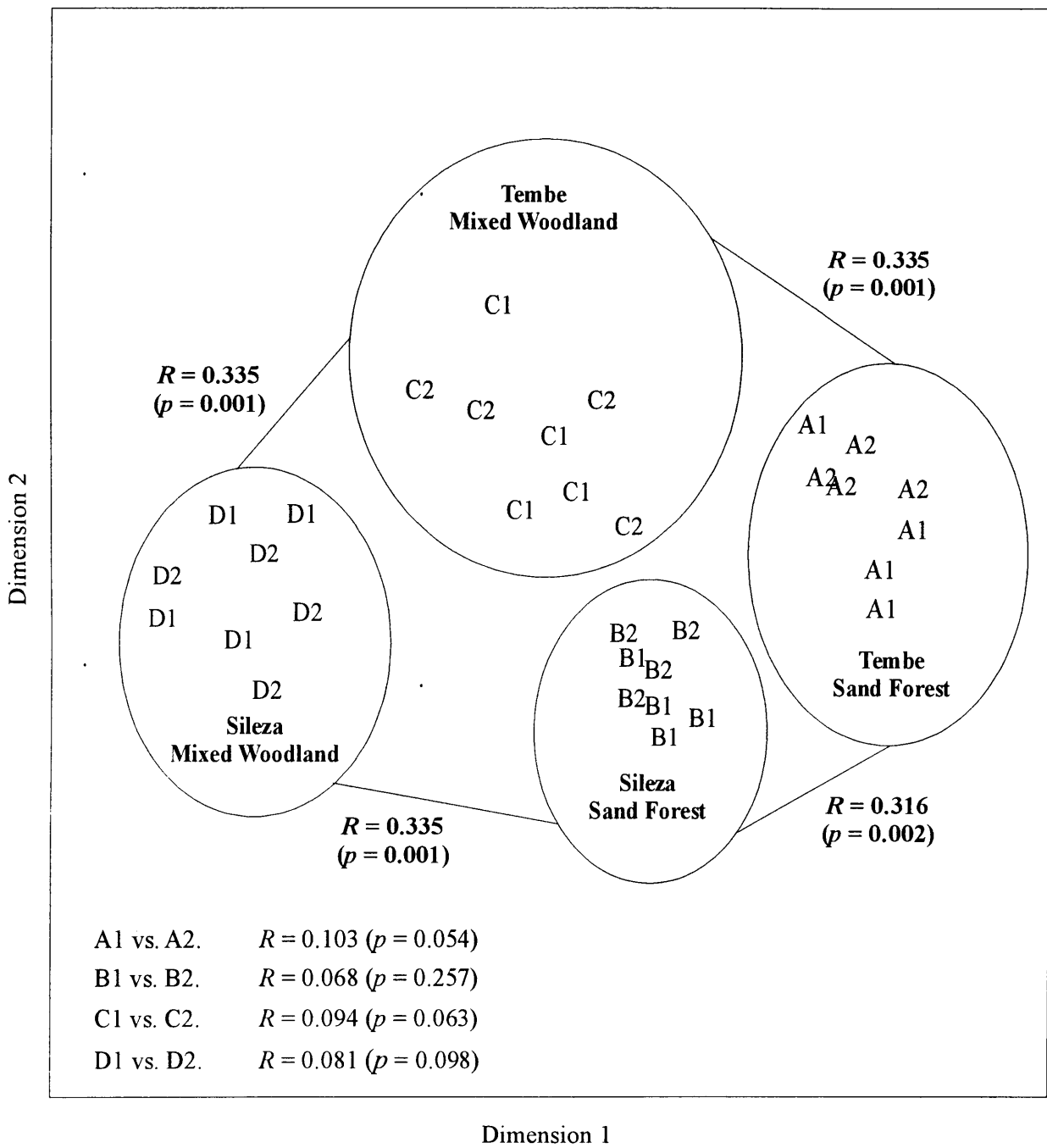


Fig. 3. Non-metric multi-dimensional scaling ordination of the abundances of species in the bird assemblages at the four pairs of habitat sites (and survey sites). The absolute distance between every pair of points on the ordination is a relative measure of their similarity. The R -statistic is a measure of the similarity of assemblages. If R is significantly different from zero, then there are significant differences between assemblages.

Table 1. Percentage indicator values (IndVal > 70%) of bird species for two different habitat comparisons. The total individuals for the opposite habitat are given in parentheses (*n*). * = Species and subspecies endemic to the Maputaland Centre.

Tembe Sand Forest	%	Sileza Sand Forest	%	Tembe Mixed Woodland	%	Sileza Mixed Woodland	%
	IndVal		IndVal		IndVal		IndVal
Neergaard's Sunbird*	98 (0)	Bluemantled Flycatcher	100 (0)	Tawnyflanked Prinia	96 (1)	Longbilled Crombec	100 (0)
Brown Scrub Robin*	97 (3)	Yellowbellied Bulbul	100 (0)	Chinspot Batis	95 (3)	Threestreaked Tchagra	100 (0)
Southern Boubou Shrike*	92 (5)	Forest Weaver*	98 (1)	Blackeyed Bulbul	91 (8)	Yelloweyed Canary	100 (0)
Woodwards' Batis*	90 (5)	Blackbellied Glossy Starling	93 (3)	Pinkthroated Twinspot*	86 (6)	Rattling Cisticola	99 (0)
Bluemantled Flycatcher	89 (6)	Rudd's Apalis*	90 (5)	Orangebreasted Bush Shrike	82 (1)	Neddicky*	97 (1)
African Broadbill	88 (0)	Redchested cuckoo	88 (0)	Whitebrowed Scrub Robin*	80 (8)	Chinspot Batis	92 (7)
Yellowspotted Nicator	88 (4)	Southern Boubou Shrike*	84 (12)	Blue Waxbill	75 (0)	Mousecoloured Flycatcher*	88 (0)
Gorgeous Bush Shrike	77 (3)	Squaretailed Drongo	84 (18)	Blackcrowned Tchagra	72(1)	Redfaced Mousebird	81 (1)
Blackbellied Glossy Starling	74 (29)	Greenbacked Bleating Warbler	83 (22)	Southern Black Tit	71 (2)	Sabota Lark	75 (0)
Yellowbellied Bulbul	70 (58)	Terrestrial Bulbul	83 (15)			Southern Black Tit	75 (0)
		Grey Sunbird	82 (13)			Blackeyed Bulbul	70 (70)
		Little Purplebanded Sunbird	76 (7)				
		Brown Scrub Robin*	75 (0)				
		Woodward's Batis*	75 (0)				
		Pinkthroated Twinspot*	71 (17)				

contrast, Pink-Throated Twinspot, *Hypargos margaritatus* occurred in all four habitats and was consistently recorded in relatively high densities in both Tembe Mixed Woodland and Sileza Sand Forest. Thus of the endemic species, three consistently preferred Sand Forest habitats and one was restricted mostly to Mixed Woodland. None of these endemic species were classed as rare in their respective assemblages (Appendix 1). Indeed, they were ranked amongst the ten (Neergaard's Sunbird and Rudd's Apalis) or twelve (Pink-Throated Twinspot and Woodward's Batis) most abundant species in those habitats where they achieved their highest abundances.

Of the endemic subspecies that were consistently present in at least one of the habitats, those of Southern Boubou Shrike, *Laniarius ferrugineus tongensis*, Forest Weaver, *Ploceus bicolor sclateri* and Brown Scrub Robin, *Erythropygia signata tongensis* were associated predominantly with Sand Forest, while those of Whitebrowed Scrub Robin, *Erythropygia leucophrys simulator*, Neddicky, *Cisticola fulvicapillus leboombo* and Mousecoloured Flycatcher, *Melaenornis pallidus sibilans* occurred predominantly in Mixed Woodland (Table 1). The endemic subspecies of Bearded Scrub Robin, *Erythropygia quadrivirgata wilsoni* were not common in any of the study sites (Appendix 1).

The number of rare species recorded within each habitat type in each reserve varied from sixteen to twenty-eight, and a total of 65 from 112 species sampled were considered rare in at least one of the four habitat localities (Appendix 1). However, this rarity was generally diffusive. Of the 16 species considered rare in at least two habitat types, eight were not classed as rare in at least one of the other habitat types (Appendix 1), and of the 49 species that were rare in one habitat type only, 38 were not classified as rare in at least one other habitat type. At a broader scale, only nine species considered rare in this study are also considered rare in South Africa (see Harrison *et al.* (1997), Clancey *et al.* (1991) and Clancey (1996)).

In the biogeographic analysis, both the Sand Forest and the Mixed Woodland assemblages were most similar to assemblages found in the forest biome of Low and Rebelo (1996) (Fig. 4(a)), and the Afromontane forest biome of Allan *et al.* (1997) (Fig. 4(b)).

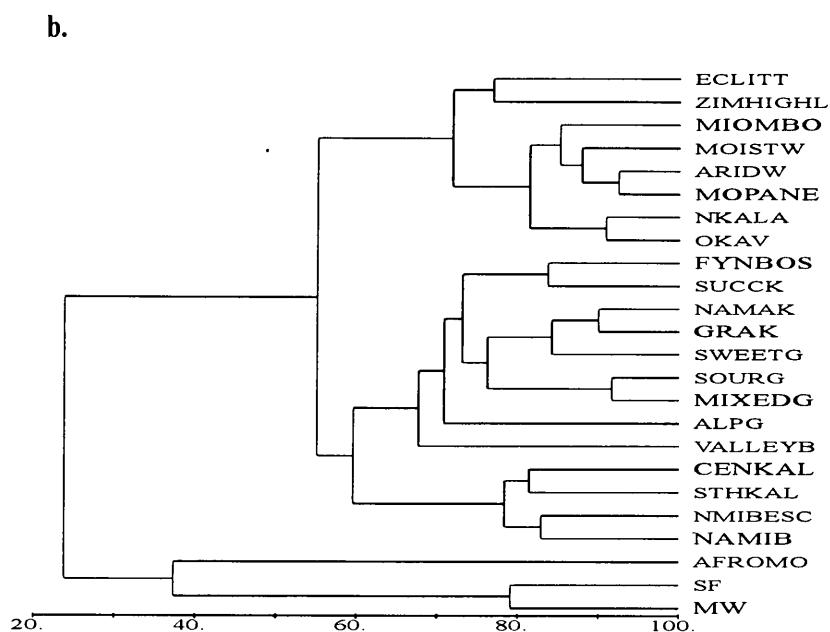
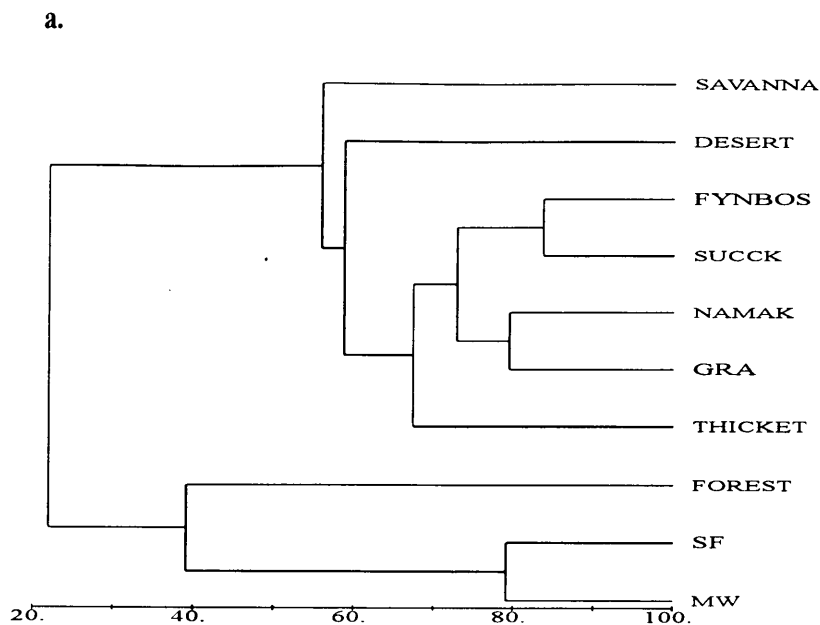


Fig. 4.(a) and (b). Cluster analysis were used to examine relationships between the overall Sand Forest (SF) and Mixed Woodland (MW) habitats vs. the combined Rutherford and Westfall's (1994) and Low and Rebelo's (1996) biomes (Forest, Thicket, Savanna, Grassland - Gra, Nama Karoo - Namak), Succulent Karoo - Succk, Fynbos and Desert), and also vs. Harrison *et al.*'s (1997) vegetation types (Central Kalahari - Cenkal, Southern Kalahari - Sthkal, Northern Kalahari - Nkala, Alpine Grasslands - Alpg, Sweet Grasslands - Sweetg, Mixed Grasslands - Mixedg, Sour Grasslands - Sourg, Namibian Escarpment - Nmibesc, Grassy Karoo - Grak, Nama Karoo - Namak, Succulent Karoo - Succk, Moist Woodland - Moistw, Arid Woodland - Aridw, Namib, Mopane, Okavango - Okav, Fynbos, Valley Bushveld - Valleyb, Miombo, East Zimbabwe Highlands - Zimhighl, East Coast Littoral - Eclitt and Afromontane Forest - Afromo).

Discussion

Although Allan *et al.* (1997) consider the avifauna of the MC to be part of a regional, East Coast Littoral mosaic with no clear affinities to other southern African biomes, the analysis undertaken here indicates that the bird assemblages of both Sand Forest and Mixed Woodland have their closest affinities with those of the Afromontane forests. Floristically, the Sand Forest vegetation type is included in a broader Forest Biome by Low and Rebelo (1996). In addition, it appears *Podocarpus* (Podocarpaceae) tree species, which are characteristic of these forests, were once more widespread along the Maputaland coast, but have retreated northwards as a consequence of climatic change since the Pleistocene (Botha *et al.* 1992, Scott *et al.* 1992). Currently, Afromontane forests and their faunas still reach the African coastline, but further to the south (see White 1978, Winterbottom 1978, Low and Rebelo 1996, Poynton and Boycott 1996) than was the case previously. Therefore from an avian assemblage perspective, and despite the subtropical climatic conditions of the Mozambique Plain, it appears that Sand Forest can be considered an Afromontane forest remnant, that has continued to evolve *in situ*.

Nonetheless, van Wyk (1996) has argued that although detailed studies of the affinities of the MC flora have not been undertaken, plant species linking the MC and Afromontane forests are uncommon. These contrasting findings of van Wyk (1996) and of the current avian study lend further support to both White (1978) and Poynton's (1961, Poynton and Boycott 1996) suggestions that the MC is a biogeographically complex region that requires additional biogeographic investigation.

However, it seems unlikely that further, assemblage-level analyses will resolve the origins of the biota of the region. Rather, phylogeographic analyses (see Moritz and Faith 1998, Templeton 1998), at both the population and species levels, are now required to resolve area relationships of the MC and its major habitat components. Such analyses would be especially insightful with regard to the southern limit of the MC, and the significant biogeographic barrier posed by the Limpopo basin (Poynton 1961, Winterbottom 1978, Clancey 1994, Poynton and Boycott 1996, van Wyk 1996).

Somewhat more surprising is the clear affinity shown between the avifauna of the more savanna-like Mixed Woodland (see van Wyk 1990, 1994, 1996) and that of Afromontane forests. However, this association does lend credence to the idea that

current vegetation change is generally from a Sand Forest structure to a more open, Mixed Woodland one, but that the reverse does not take place (van Rensburg *et al.* in press, Chapter 2). If Mixed Woodland did not develop *in situ*, closer relationships between the avifaunas of this savanna-like vegetation type and those of the true savannas, to the south and north west (see Low and Rebelo 1996, Allan *et al.* 1997), might be expected.

This directional change in vegetation structure has important conservation consequences, especially given current changes to Sand Forests (see Introduction). Not only are a variety of endemic plant species likely to be threatened by conversion of Sand Forests to Mixed Woodland (van Wyk 1996), but it appears that the majority of bird species (and at least some of the subspecies) endemic to the MC are either restricted to the Sand Forest habitats or achieve their greatest abundances within them, as was suspected by van Wyk (1996). In consequence, conversion of Sand Forest habitats is likely to have a direct, adverse effect on these species. That such habitat change is being precipitated by an increasing elephant population in Tembe Elephant Park is of particular concern. Not only is it clear that there are considerable differences between the Sand Forest and Mixed Woodland avifaunas, but this study also demonstrated significant heterogeneity in assemblages inhabiting the same habitat in Tembe and Sileza. Such habitat-associated and spatial heterogeneity is not uncommon in avian assemblages (e.g., Cody 1975, Gentilli 1992, Blondel and Vigne 1993, Cody 1993, MacNally 1997, Wiebe and Martin 1998), and has been demonstrated for both plants (W. S. Matthews, pers. comm.) and dung beetles (van Rensburg *et al.* in press, Chapter 2) in the present study area. However, it has profound consequences for the conservation of these assemblages, and especially for the endemic species that form part of them. For example, Neergaard's Sunbird was not recorded in Sand Forest in Sileza, but was abundant in Tembe, while Woodward's Batis was most abundant in Tembe Sand Forests. Clearly, an assumption that all Sand Forest bird species could be conserved in Sileza, because the Sand Forest habitat is well represented in this reserve, would be misleading. This spatial heterogeneity in the Sand Forest (and Mixed Woodland) assemblages suggests that these habitat types require conservation in more than a single reserve. The same conclusion for dung beetles was reached by van Rensburg *et al.* (in press), Chapter 2.

More generally, these findings suggest that a broad conservation goal of conserving 10% of each vegetation type (Low and Rebelo 1996) does not translate into effective reserve design at a local scale (see IUCN 1993, also van Jaarsveld and Chown 1996). Rather, it is clear that the spatial scale of heterogeneity within vegetation types must first be identified, and conservation areas then designed to incorporate the representation of this heterogeneity (see also Margules and Austin 1995, Lombard *et al.* 1996, Burnett *et al.* 1998, Wessels *et al.* in press). Thus using broad scale vegetation types as surrogates for species-level conservation seems unlikely to prove effective, especially if the 10% target is apportioned among areas in an arbitrary way at local scales (for further critical comment on the use of surrogates and the 10% approach, see Lawton *et al.* 1998, van Jaarsveld *et al.* 1998, Soulé and Sanjayan 1998).

The local scale studies undertaken here also demonstrated that at this scale, rarity is diffusive. Species rare in one habitat, or in a given habitat in a reserve, are not necessarily rare in another habitat or in the same habitat elsewhere. Such diffusive rarity at local scales has been documented elsewhere, is generally thought to be the consequence of either habitat selection by species, species reaching the edge of their range, or species being transient to a given area (Brown 1988, Brown *et al.* 1996, Gaston *et al.* 1993, Gaston 1994), and has important conservation implications, as I have shown above. However, diffusive rarity at broader spatial scales, a feature apparently characteristic of species endemic to the MC is also of considerable importance. For example, although Neergaard's Sunbird is regarded as uncommon and is included in the South African Red Data book as 'rare' (Brooke 1984), it was locally abundant in the present study. Likewise, Woodward's Batis is included in the South African Red Data Book on birds because it is rare and restricted (Brooke 1984), yet it achieved a reasonably high abundance in Sand Forest in Tembe Elephant Park. This provides further support for the idea that regional conservation assessments should seek to incorporate information on population sizes where this can be done (Nicholls in press, Williams in press), and, where possible, should be refined to take heterogeneity at smaller spatial scales into account (see also Noss 1990).

In sum, I have shown that the avifauna of Sand Forest and Mixed Woodland habitat types in the MC have their closest affinities with those of Afromontane forest, that

species considered geographically rare in southern Africa may achieve high abundances in these habitats, and that within a given habitat type there may be significant spatial heterogeneity in the avian assemblages and their component species. These findings suggest that if the evolution of faunas in this region is to be understood and if conservation actions are to be successful, the biogeography of the MC (and especially Sand Forest species) must be revisited using modern analytical techniques, and relict Sand Forests should be retained in as many reserves as possible (but especially in Tembe). Most significantly, however, my study suggests that capturing 10% of a broad scale surrogate such as vegetation type in protected (or specially managed) areas requires considerable refinement as to translate to effective reserve design at a local scale.

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Appendix 1. The total number of bird species recorded in the Tembe (T) and Sileza (S) Sand Forest and Mixed Woodland habitats. Bold values denote rare species defined as the 25% least abundant species in each of the four habitat types. SUM r = sum of the habitat types in which a species was classified as rare.

Species common name	Species	SUM r	Sand Forest		Mixed Woodland	
			T	S	T	S
Taxa rare in one or more habitats						
Bearded Scrub Robin	<i>Erythropygia quadrivirgata wilsoni</i> ^a	1	3	7	3	3
Black Flycatcher	<i>Melaenornis pammelaina</i>	2	0	1	3	0
Black Sunbird	<i>Nectarinia amethystina</i>	2	0	3	1	2
Blackbacked Cisticola	<i>Cisticola galactotes</i>	2	0	0	3	2
Blackcollared Barbet	<i>Lybius torquatus</i>	1	0	1	0	7
Blackcrowned Tchagra	<i>Tchagra senegala</i>	1	1	6	26	16
Blackheaded Oriole	<i>Oriolus larvatus</i>	1	14	0	14	1
Blue Waxbill	<i>Uraeginthus angolensis</i>	1	0	1	36	4
Bluegrey Flycatcher	<i>Muscicapa caeruleascens</i>	2	1	0	2	0
Bluethroated Sunbird	<i>Anthreptes reichenowi</i>	1	1	0	0	0
Brown Scrub Robin	<i>Erythropygia signata tongensis</i> ^a	1	90	11	3	0
Brownhooded Kingfisher	<i>Halcyon albiventris</i>	1	1	7	11	4
Brubru	<i>Nilaus afer</i>	2	1	0	1	0
Bully Canary	<i>Serinus sulphuratus</i>	1	0	1	0	0
Cardinal Woodpecker	<i>Dendropicos fuscescens</i>	1	1	0	9	6
Crested Barbet	<i>Trachyphonus vaillantii</i>	2	0	1	0	1
Crested Francolin	<i>Dendroperdix sephaena</i>	2	1	0	4	1
Crested Guineafowl	<i>Guttera edouardi</i>	1	7	0	2	0
Croaking Cisticola	<i>Cisticola natalensis</i>	1	0	0	4	1
Crowned Hornbill	<i>Tockus alboterminatus</i>	1	14	1	20	3
Dusky Flycatcher	<i>Muscicapa adusta</i>	1	0	1	5	3
Fantailed Cisticola	<i>Cisticola juncidis</i>	1	1	0	5	3
Fiscal Flycatcher	<i>Sigelus silens</i>	2	2	0	2	1
Forest Weaver	<i>Ploceus bicolor sclateri</i> ^a	1	70	43	35	1
Forktailed Drongo	<i>Dicrurus adsimilis</i>	1	0	4	2	4
Goldenbreasted Bunting	<i>Emberiza flaviventris</i>	1	0	1	21	3
Goldenrumped Tinker Barbet	<i>Pogoniulus bilineatus</i>	1	2	0	4	1
Goldtailed Woodpecker	<i>Campethera abingoni</i>	1	8	2	4	2
Gorgeous Bush Shrike	<i>Telophorus quadricolor</i>	1	23	17	3	4
Green Twinspot	<i>Mandingoa nitidula</i>	1	0	0	1	0
Grey Waxbill	<i>Estrilda perreini</i>	1	0	0	0	2
Greyheaded Bush Shrike	<i>Malaconotus blanchoti</i>	2	4	1	1	0
Hadedda Ibis	<i>Bostrychia hagedash</i>	1	1	0	0	0
Jameson's Firefinch	<i>Lagonosticta rhodopareia</i>	1	0	1	4	0
Lemonbreasted Canary	<i>Serinus citrinipectus</i>	1	0	1	0	26
Lilacbreasted Roller	<i>Coracias caudata</i>	1	0	0	1	0
Melba Finch	<i>Pytilia melba</i>	1	0	0	3	0
Mousecoloured Flycatcher	<i>Melaenornis pallidus sibilans</i> ^a	1	0	0	3	9
Narina Trogon	<i>Apaloderma narina</i>	1	14	0	3	0
Neddicky	<i>Cisticola fulvicapillus lebombo</i> ^a	1	0	1	29	38
Olive Sunbird	<i>Nectarinia olivacea</i>	2	0	3	1	1

Appendix 1 (continued).		SUM r	Sand Forest		Mixed Woodland	
Species common name	Species		T	S	T	S
Orangebreasted Bush Shrike	<i>Malaconotus sulfureopectus</i>	1	1	26	16	12
Paradise Flycatcher	<i>Terpsiphone viridis</i>	2	1	2	2	0
Pied Crow	<i>Corvus albus</i>	1	0	0	0	2
Pintailed Whydah	<i>Vidua macroura</i>	1	0	0	0	2
Purplecrested Lourie	<i>Tauraco porphyreolophus</i>	1	1	16	9	6
Rattling Cisticola	<i>Cisticola chiniana</i>	1	0	1	112	101
Redeyed Dove	<i>Streptopelia semitorquata</i>	1	3	5	1	6
Redfaced Cisticola	<i>Cisticola erythrops</i>	2	0	0	2	1
Redfaced Mousebird	<i>Urocolius indicus</i>	1	0	1	0	13
Redfronted Tinker Barbet	<i>Pogoniulus pusillus niethammeri</i> ^a	2	0	1	1	0
Rufousnaped Lark	<i>Mirafra africana</i>	1	0	0	3	5
Sabota Lark	<i>Mirafra sabota</i>	1	1	0	9	11
Scalythroated Honeyguide	<i>Indicator variegatus</i>	1	18	0	0	1
Scarletched Sunbird	<i>Nectarinia senegalensis</i>	1	0	1	0	0
Shelley's Francolin	<i>Francolinus shelleyi</i>	1	0	0	0	1
Spotted Flycatcher	<i>Muscicapa striata</i>	1	0	0	0	2
Starred Robin	<i>Pogonocichla stellata</i>	2	1	0	1	0
Striped Crested Cuckoo	<i>Clamator levaillantii</i>	1	1	0	0	0
Striped Kingfisher	<i>Halcyon chelicuti</i>	1	0	0	1	0
Tawnyflanked Prinia	<i>Prinia subflava</i>	2	1	8	22	1
Whitethroated Robin	<i>Cossypha humeralis</i>	2	1	16	2	5
Yellow White-eye	<i>Zosterops senegalensis</i>	1	0	0	2	0
Yellowbellied Eremomela	<i>Eremomela icteropygialis</i>	1	0	0	1	0
Yellowspotted Nicator	<i>Nicator gularis</i>	1	28	6	4	2
Taxa common in all habitats						
African Broadbill	<i>Smithornis capensis</i>		22	12	0	0
Black Cuckooshrike	<i>Campephaga flava</i>		4	2	0	0
Blackbellied Glossy Starling	<i>Lamprotornis corruscus</i>		82	40	29	3
Blackeyed Bulbul	<i>Pycnonotus barbatus</i>		8	70	83	163
Bluemantled Flycatcher	<i>Trochocercus cyanomelas</i>		50	24	6	0
Bronze Mannikin	<i>Spermestes cucullatus</i>		0	0	0	3
Cape Turtle Dove	<i>Streptopelia capicola</i>		21	13	18	4
Cape White-eye	<i>Zosterops pallidus</i>		2	0	0	0
Chinspot Batis	<i>Batis molitor molitor</i>		3	7	55	80
Collared Sunbird	<i>Anthreptes collaris</i>		5	23	15	15
Emeraldspotted Wood Dove	<i>Turtur chalcospilos</i>		40	16	67	14
Fantailed Flycatcher	<i>Myioparus plumbeus</i>		0	2	7	5
Flappet Lark	<i>Mirafra rufocinnamomea</i>		0	0	8	5
Greater Honeyguide	<i>Indicator indicator</i>		0	0	4	3
Green Pigeon	<i>Treron australis</i>		0	3	6	9
Greenbacked Bleating Warbler	<i>Cameroptera brachyura</i>		45	108	53	22
Grey Sunbird	<i>Nectarinia veroxii</i>		38	58	17	13
Heuglin's Robin	<i>Cossypha heuglini</i>		3	0	0	0
Klaas's Cuckoo	<i>Chrysococcyx klaas</i>		0	2	0	0
Kurrichane Thrush	<i>Turdus libonyana</i>		4	0	0	0
Little Purplebanded Sunbird	<i>Nectarinia bifasciata</i>		21	22	18	7
Longbilled Crombec	<i>Sylvietta rufescens</i>		0	0	6	23

Appendix 1 (continued).		Sand Forest		Mixed Woodland	
Species common name	Species	T	S	T	S
Natal Robin	<i>Cossypha natalensis</i>	11	13	8	4
Neergaard's Sunbird	<i>Nectarinia neergaardi</i> ^a	82	0	0	0
Pinkthroated Twinspot	<i>Hypargos margaritatus</i> ^a	6	41	38	17
Puffback Shrike	<i>Dryoscopus cubla</i>	78	57	80	47
Redbilled Helmetshrike	<i>Prionops retzii</i>	11	0	9	0
Redbilled Woodhoopoe	<i>Phoeniculus purpureus</i>	4	0	4	0
Redchested cuckoo	<i>Cuculus solitarius</i>	18	15	5	0
Rudd's Apalis	<i>Apalis ruddi</i> ^a	2	46	10	5
Sombre Bulbul	<i>Andropadus importunus</i>	40	212	67	102
Southern Black Tit	<i>Parus niger</i>	2	0	31	19
Southern Boubou Shrike	<i>Laniarius ferrugineus tongensis</i> ^a	60	63	5	12
Speckled mousebird	<i>Colius striatus</i>	0	9	0	15
Spectacled Weaver	<i>Ploceus ocularis</i>	0	0	0	9
Squaretailed Drongo	<i>Dicrurus ludwigii</i>	109	94	71	18
Tambourine Dove	<i>Turtur tympanistria</i>	15	2	0	0
Terrestrial Bulbul	<i>Phyllastrephus terrestris</i>	62	74	57	15
Threestreaked Tchagra	<i>Tchagra australis</i>	3	0	31	14
White Helmetshrike	<i>Prionops plumata</i>	0	0	5	0
Whitebellied Sunbird	<i>Nectarinia talatala</i>	0	46	8	94
Whitebrowed Scrub Robin	<i>Erythropygia leucophrys simulator</i> ^a	8	11	32	28
Woodwards' Batis	<i>Batis fratrum</i> ^a	46	16	5	0
Yellowbellied Bulbul	<i>Chlorocichla flaviventris</i>	132	31	58	0
Yellowbreasted Apalis	<i>Apalis flavida</i>	129	84	101	51
Yelloweyed Canary	<i>Serinus mozambicus</i>	0	0	18	17
Yellowthroated Longclaw	<i>Macronyx croceus</i>	0	0	0	10
Species richness		66	64	85	76
Total individuals		1 484	1 414	1 492	1 166
Density		27.42	31.48	26.71	15.87
% Coefficient of variation		11.04	9.46	13.09	9.78

^aSpecies and subspecies endemic to the Maputaland Centre.

CHAPTER 4

Organismal and distance scaling patterns of taxa in the Maputaland Centre of Endemism, South Africa: Possible generalities

Introduction

Hanski's (1982) core-satellite hypothesis focused much attention on the incidence of bimodality in the distribution of species occupancy frequency distributions (SOFD's). The dynamic metapopulation models developed by Hanski (1982) and Hanski and Gyllenberg (1993) predict bimodal species occupancy frequency distributions. In other words, the extent of occurrence (or range) of species in these distributions is divided into 10% occupancy classes. Species occupying > 90% of sites are then termed core species, and species occupying < 10% of sites are termed satellite species. Bimodal distributions with modes in these two classes are termed core-satellite distributions. The key mechanism of metapopulation models that predict core-satellite distributions is that these distributions are associated with a strong rescue effect (Hanski and Gyllenberg 1993). The bimodality thus arises as a result of two processes, i.e. an increase in the immigration rate with an increasing proportion of occupied sites, and a decrease in the extinction rate with an increasing immigration rate (Hanski and Gyllenberg 1993). Hanski and Gyllenberg (1993) showed that over the long-term, the distribution of occupancy values resulting from these colonisation-extinction properties of the rescue effect and from interspecific variation in these extinction-colonisation ratios, is bimodal. Therefore, when core-satellite distributions appear in empirical data for particular species assemblages, Hanski's (1982) and Hanski and Gyllenberg's (1993) interpretations suggest a metapopulation structure and the presence of a strong rescue effect in those assemblages.

There have, however, been many other, non-metapopulation based, interpretations of core-satellite distributions (see also response to some of these by Hanski (1991)): (i) it has been suggested that bimodality is an artefact because occupancy is constrained to lie between zero and one (Raunkiaer 1934, Williams 1950); (ii) the ecological relevance of bimodality has been questioned because it may arise from sampling biases when rare species are less likely to be observed or sampled (Nee *et al.* 1991); (iii) the presence or

absence of bimodality is sensitive to the spatial scale of observation (Brown 1984); (iv) Williams (1964) showed that the larger the number of sample sites, the greater the proportion of satellite species and the smaller the proportion of core species; (v) bimodality has been shown to arise as a direct consequence of underlying lognormal or logarithmic rank abundance curves (Papp 1997); (vi) Brown (1984) proposed that bimodal SOFD's result because species are either specialists or generalists and thus occupy either a few or most habitat patches; (vii) Maurer (1990) suggested that SOFD's are determined by the productivity of landscapes and the degree of dominance of species in them (he predicted that bimodality is most likely to be found in lower productivity landscapes where a few species dominate resource use); (viii) tourist species bring about an inflation in the satellite mode (Nee *et al.* 1991), and (ix) better dispersing taxa cause an inflation in the core mode (Collins and Glenn 1997); (x) in addition, bimodality has also been the subject of debate because it is statistically difficult to verify (Tokeshi 1992). Interpretation of the presence of bimodality in SOFD's therefore faces problems associated not only with the quantification of bimodality, but also, and perhaps more importantly, with the identification of the mechanisms underlying that bimodality. That is, the pattern may have either an artefactual or biological origin, and if biological, the mechanism may, or may not, involve metapopulation dynamics.

In an attempt to achieve some clarity on the shape of SOFD's and the mechanisms that generate them, it is helpful to consider the closely related interspecific abundance range-size relationship (ARSR). It has been widely documented that abundant species commonly have wider ranges than locally rare species, although the proportion of variation explained is generally low (Gaston *et al.* 1997). However, Gaston *et al.* (1997) show that positive ARSR's may be generated by any of eight principal mechanisms (including both artefactual and biological, of which one is metapopulation based). They also show that none of these mechanisms has unequivocal support, and that each are likely to contribute to the relationship to different degrees under different circumstances. Although far less attention has been paid to understanding SOFD's than has been the case for ARSR's, it appears likely that SOFD's are likewise not generated by any single or simple combination of mechanisms.

Regardless of the mechanisms involved, bimodal SOFD's regularly appear in

studies of a variety of taxa at a variety of spatial scales (e.g. Gotelli and Simberloff 1987, Collins and Glenn 1990, Pirintsos *et al.* 1996, Collins and Glenn 1997). In the face of the numerous explanations that have been proposed to explain them, further consideration of bimodality patterns is thus needed. If it is possible to infer any biological process (as suggested by Hanski (1982) and Hanski and Gyllenberg (1993)), or any assemblage characteristic (such as the spread of specialist and generalist species, Brown 1984), from the shape of a SOFD, then these would become valuable tools for assessing and monitoring the *status quo* and changes in communities and habitats. It is therefore necessary not only to distinguish between underlying mechanisms, but also to quantify the spatial and organismal dependence of these (Nee *et al.* 1991, Collins and Glenn 1997, Gaston and Lawton 1990, Nieminen and Hanski 1998, With 1995). One approach is to conduct studies on a variety of taxa at a variety of spatial scales, quantifying and comparing the shapes of the SOFD's found. Should generalities in the incidence of core-satellite species distributions be found from these studies, tests can then be conducted to investigate the mechanisms (be they biological, including metapopulation-based, or artefactual) that generate them.

Adopting the approach described above, Collins and Glenn (1997) focused on the distribution pattern predicted by the core-satellite hypothesis, and examined to what extent bimodality was a function of distance and organismal scaling. They argued that given an increase in environmental heterogeneity with increasing spatial scale, patterns of regional species distribution will change accordingly with an increase in regionally rare species and a decrease in regionally abundant species with an increase in the size of an area sampled (i.e. spatial scaling). Considering organismal scaling, they proposed that within a particular spatial scale, taxa with greater dispersal abilities may be expected to have more core (widespread) species than taxa with poorer dispersal abilities. After empirically testing both of these predictions, they found that bimodality patterns across two spatial scales did indeed change as predicted. In contrast, the organismal scaling prediction did not hold. Although patterns of bimodality did vary between taxa, the proportion of regionally widespread and rare species did not differ following the rank order of the dispersal ability of the taxa tested.

Following on from this first attempt at generality by Collins and Glenn (1997), the

aim of the study presented here was thus to test the predictions of Collins and Glenn (1997) in a different geographic region, at different scales, and (in part) on comparable groups of taxa, namely plants, birds and dung beetles. First I examine the relationship between distribution and abundance because positive abundance range size relationships are fundamental to most regional metapopulation models (Hanski 1982, 1991, Brown 1984, Kolasa 1989, Collins and Glenn 1997), and metapopulation dynamics is one of the mechanisms proposed to explain bimodality. I then test, for all taxa, the prediction of increasing numbers of satellite species, and decreasing numbers of core species, with increasing spatial extent. I also compare the species occupancy distributions of taxa within each of the spatial scales on the assumption that their rank-order dispersal ability is birds > dung beetles > plants. Here I predict, based on Collins and Glenn's (1997) rationale, that the better dispersing taxa will have more core species than the poorer dispersing taxa. Finally I evaluate our findings in light of the various mechanisms proposed to generate bimodality in species occupancy frequency distributions.

Material and methods

Study area

Field work was undertaken in Tembe Elephant Park (27°01'S 32°24'E) and Sileza Nature Reserve (27°06'S 32°36'E), on the southern Mozambique Coastal Plain of Northern KwaZulu-Natal, South Africa. The two distinct habitat types in these reserves are Sand Forest and Mixed Woodland, where smaller Sand Forest patches tend to be embedded within a larger matrix of Mixed Woodland (van Wyk 1996). Sand Forest is characterized by tree species such as *Dialium schlechteri* and *Erythrophleum lasianthum* (Caesalpinioideae) (Moll 1977, van Wyk 1996) with a poorly developed understory. The surrounding, more open, Mixed Woodland is characterized by common, woody savanna species such as *Acacia burkei*, *Albizia versicolor* and *A. adianthifolia* (Mimosoideae). It has a well developed grass understory represented by *Aristida*, *Pogonarthria* and *Perotis* species (Moll 1977, 1980). The soils in both study areas are homogeneous, grey, siliceous, aerolian sands which are highly leached (dystrophic) and relatively acidic (water pH \approx 6.1) - (W. S. Matthews, pers. comm.).

Sampling

Replicated sampling sites in these reserves were selected from within standardised vegetation communities (Sand Forest and Mixed Woodland - van Wyk 1996). Two Sand Forest sites and two Mixed Woodland sites were sampled in each reserve, i.e. eight sampling sites, grouped into four reserve-habitat combinations (Tembe Sand Forest, Tembe Mixed Woodland, Sileza Sand Forest, Sileza Mixed Woodland). Distances between sites, and between the areas sampled in the two reserves were, respectively, 1.3 – 3.1 km and *c.* 18 km.

Bird surveys

Each survey site comprised sixteen fixed survey points. The appropriate number of survey points for these assemblages was determined from a pilot study following the method advocated by Buckland *et al.* (1994). Distances between the sixteen points within a site were 150 m. These distances minimised the probability of double detection, ensuring data independence, and provided suitable replicates for the study. Because of terrain difficulties, particularly in the Sand Forest, sampling points were placed along game and elephant paths. Although this could potentially bias the results, this is unlikely where mobile animals such as birds are surveyed (S. T. Buckland, pers. comm.). Survey points were, however, identified without prior knowledge of bird distributions, and care was taken to ensure that sampling points did not follow more prominent natural features (e.g. forest edges - see Guthery 1988).

Visual and auditory bird surveys were conducted bimonthly between May 1995 and April 1996, at all four sites in a reserve (the two reserves were surveyed in alternative months), using point sampling (see Buckland *et al.* 1994). During one month, each of the four sites was surveyed four times. The 16 sampling points from a single site were surveyed in one morning (10 minutes per sampling point). Three minutes were spent at each survey point prior to data collection to allow the birds time to adjust to the disturbance caused by the observer. Survey periods were limited to reduce the risk of multiple detection resulting from birds moving out of and back into an observation area, which could lead to substantial density overestimation (Buckland *et al.* 1994). Thus a compromise between maximisation of the probability that individuals in a survey point

would be detected (e.g. interval-based bird calls), and minimisation of the probability of multiple detection, or of attracting curious species (e.g. Southern Boubou Shrike *Laniarius ferrugineus*), was sought.

On initial detection, birds were placed into distance categories, demarcated by fixed markers placed at known distances from the observation point (0 - 4; 5 - 9; 10 - 15; 16 - 30 and 31 - 50 m) before the study commenced. Although determination of the exact distance at which each bird was detected would have been desirable, this was not practical when many birds were heard and not observed (Buckland *et al.* 1994). In addition, estimation of exact distances when large numbers of birds are seen over a short period, may lead to observational difficulties and a reduction in survey accuracy (Bibby *et al.* 1985). The distance to a bird in the tree canopy was taken as the distance from the observer to a point directly below the bird on the ground. All birds within 50 m of the survey point, including birds involved in territorial displays, were recorded. Birds flying over the study area were excluded. Records were also categorised as reliable sightings, or as bird call records. Unreliable sightings were not included in the database. The number of individuals of each species observed over the course of the study period were summed for each survey point (survey points within a site were reduced from 16 to four by randomly pooling sets of four data points), within each site.

Beetle sampling

At each sampling site, 30 pitfall traps were set out in groups of six on a 2 m x 2 m grid. Distances between the five grids within a site were 200 m. Beetles were sampled bimonthly between May 1995 and April 1996, at all four sites in a reserve (the two reserves were sampled in alternative months), using pitfall traps baited with 50 g elephant dung. During one month, the pitfalls were set once for 48 hours, with rebaiting and the first collection taking place at 24 h, and the second collection at 48 h. Traps were then closed and left *in situ* until the following sampling month. Specimens were identified by comparing them to identified specimens in the collections of the South African National Insect Collection. The number of individuals of each species trapped over the course of the study period was summed for each sampling grid and each site.

Plant sampling

Twenty 100 m² sample plots (10 m x 10 m) were distributed in a stratified manner throughout the sampling sites. Sampling was carried out by W. S. Matthews from January to May 1993. The total floristic composition, as well as a cover-abundance value for each species, was recorded by using the Braun-Blanquet cover-abundance scale as described by Mueller-Dombois and Ellenberg (1974): R = rare, + = < 1%, 1 = 1 - 5%, 2A = > 5 - 12%, 2B = > 12 - 25%, 3 = > 25 - 50%, 4 = > 50 - 75% and 5 = > 75% (Matthews *et al.*, unpublished, and Matthews and Page, unpublished, for further details of sampling and plant community dynamics on Tembe and Sileza).

Data analysis

Four spatial scales were considered in the analyses; local (each reserve-habitat combination, between 2 to 4.5 km²), reserve (Tembe and Sileza - 4 to 6 km²), habitat (all Sand Forest and all Mixed Woodland, between 22 to 24 km²), and regional (where regional indicates purely the full extent of the area sampled; i.e. all sampled sites, approx. 26 km²).

Linear regression was used on each taxon at each of four spatial scales sampled in the region to establish whether positive interspecific abundance-range size relationships existed (calculated for occupied sites only). Patterns in the regional distribution of species were examined by plotting the number of species occurring in 1, 2, 3.. to n sites for each taxon (birds, dung beetles and plants). In all cases the number of sites sampled, and in which species were recorded, was ≥ 10 , thus, distribution was expressed as proportion of sites occupied.

Tokeshi's (1992) method of determining the exact probability of obtaining an observed frequency value (p_c) for the left- and right-most classes under the null hypothesis of random occurrence of species in a region was used to quantify modality patterns (see also Collins and Glenn 1997). The probability of obtaining the observed frequency for the left (p_l)- or right (p_r)- most class can also be calculated separately under the same null hypothesis (Tokeshi 1992): if $p < 0.05$ for both the left- and right-extreme frequency classes then the distribution is bimodal, whereas if $p < 0.05$ for only one of the classes then the distribution is unimodal. This method was used for each taxon at each

spatial scale. The frequency distributions of each taxon within each spatial scale were compared using Kolmogorov-Smirnov two-sample tests (Siegel 1956).

Distance scaling was assessed by examining each taxon across the three spatial scales, whereas organismal scaling was assessed by comparing the taxa within each spatial scale.

Results

The number of species recorded in each taxon across scales ranged between 64 and 113 for birds, 36 and 69 for dung beetles and 96 to 502 for plants (Table 1). The relationship between number of sites occupied and average abundance was positive for all, and significant for 24 of the 27 taxon-spatial scale combinations (Table 1). The three non-significant relationships were all at a local scale. Nonetheless, the metapopulation assumption (Hanski 1982), or prediction (Hanski and Gyllenberg 1993), of a positive relationship between distribution and abundance was largely met.

Distance scaling

Significant bimodality was detected in a number of taxon-spatial scale combinations (Table 2). However there was a clear tendency for decreasing frequency of bimodality with increasing spatial scale (Table 2). Evidence of distance scaling was also stronger for within, rather than across, habitat types (Table 2). Moving from within habitat types at the local scale, directly to the same habitat type at the broader habitat scale (skipping the reserve scale), the switch from bimodal to unimodal is clearer than when including the intermediate reserve scale which combines data for both habitat types (Table 2).

Within each of the three taxa examined there were fewer species in the core mode at habitat and regional (larger) scales than at local and reserve (smaller) scales (Figs. 1.(a)-(c), Table 3). The number of satellite species, in contrast, increased from local to regional scales for dung beetles. The increase was less clear for birds, and neither an increase or a decrease in number of species with increasing spatial scale was evident for plants (Table 3). Distance scaling was thus clear for core, but not satellite, species in each of the three taxa tested.

Table 1. Relationship between number of sites occupied and average abundance for each taxon group at each spatial scale based on linear regression (all were positive). Average abundances were calculated from the number of occupied sites (given here) rather than the total number of sites; * - indicates significance at the “table-wide” α level for birds, dung beetles and plants using the sequential Bonferroni technique (Rice 1988).

Spatial scale	Taxon group	No. species	No. sites	R^2	p – value	
Local scale						
Tembe Sand Forest	Birds	66	15	0.81	<0.001	*
	Dung beetles	49	10	0.31	0.089	ns
	Plants	96	10	0.87	<0.001	*
Sileza Sand Forest	Birds	64	16	0.75	<0.001	*
	Dung beetles	36	10	0.54	0.014	*
	Plants	108	10	0.77	0.053	ns
Tembe Mixed Woodland	Birds	86	16	0.76	<0.001	*
	Dung beetles	55	10	0.45	0.035	*
	Plants	293	20	0.39	<0.01	*
Sileza Mixed Woodland	Birds	75	15	0.65	<0.001	*
	Dung beetles	64	10	0.34	0.074	ns
	Plants	157	17	0.43	<0.01	*
Reserve scale						
Tembe	Birds	95	25	0.76	<0.001	*
	Dung beetles	66	20	0.35	<0.01	*
	Plants	231	28	0.59	<0.01	*
Sileza	Birds	91	27	0.71	<0.01	*
	Dung beetles	57	16	0.28	0.036	*
	Plants	198	20	0.56	<0.01	*

Table 1 (continued).

Spatial scale	Taxon group	No. species	No. sites	R^2	p – value	
Habitat scale						
Sand Forest	Birds	88	27	0.74	<0.001	*
	Dung beetles	53	15	0.41	0.0101	*
	Plants	160	14	0.48	<0.01	*
Mixed Woodland	Birds	100	29	0.72	<0.001	*
	Dung beetles	69	20	0.30	0.0126	*
	Plants	344	40	0.47	0.0279	*
Regional scale						
	Birds	112	43	0.70	<0.001	*
	Dung beetles	69	29	0.28	<0.01	*
	Plants	502	54	0.56	0.0122	*

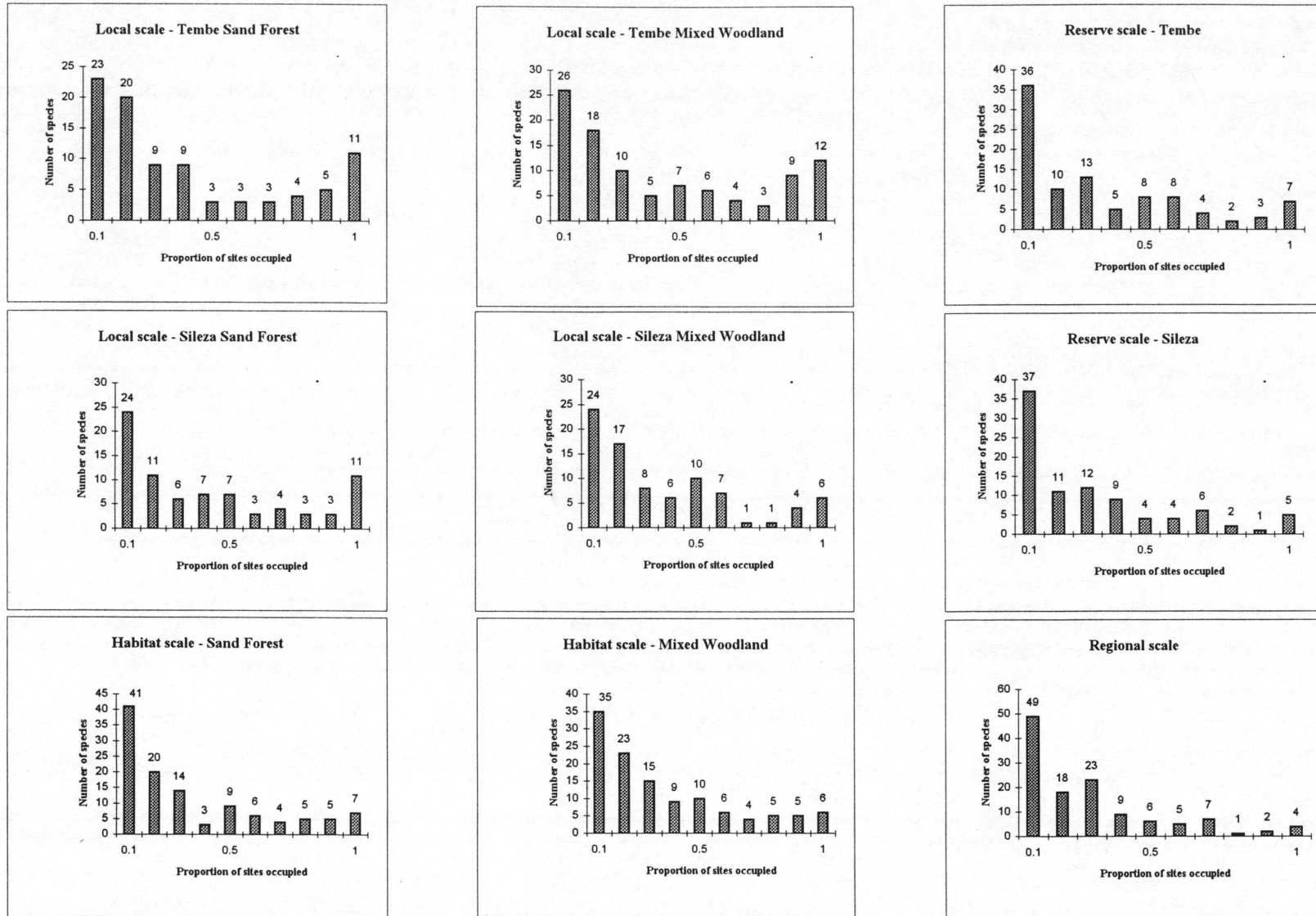
Table 2. Classification of frequency distribution functions for each taxon group at each spatial scale, and for dung beetle functional groups at a regional scale. Overall distribution (p_c), left-most mode (p_l), right-most mode (p_r). Not significant (ns).

Spatial scale	Taxon group	p_c	p_l	p_r	Diagnosis
Local scale					
Tembe Sand Forest	Birds	<0.0001	<0.0001	0.02	Bimodal
	Dung beetles	0.0002	0.002	0.02	Bimodal
	Plants	<0.0001	<0.0001	0.02	Bimodal
Sileza Sand Forest	Birds	<0.0001	<0.0001	0.02	Bimodal
	Dung beetles	0.0007	0.01	0.03	Bimodal
	Plants	<0.0001	<0.0001	0.02	Bimodal
Tembe Mixed Woodland	Birds	<0.0001	<0.0001	0.04	Bimodal
	Dung beetles	0.0001	0.002	0.02	Bimodal
	Plants	<0.0001	<0.0001	0.04	Bimodal
Sileza Mixed Woodland	Birds	<0.0001	<0.0001	ns	Unimodal
	Dung beetles	0.0002	0.0009	0.04	Bimodal
	Plants	<0.0001	<0.0001	ns	Unimodal
Reserve scale					
Tembe	Birds	<0.0001	<0.0001	ns	Unimodal
	Dung beetles	0.0001	0.0004	0.04	Bimodal
	Plants	<0.0001	<0.0001	0.04	Bimodal
Sileza	Birds	<0.0001	<0.0001	ns	Unimodal
	Dung beetles	0.0002	0.0009	0.04	Bimodal
	Plants	<0.0001	<0.0001	ns	Unimodal
Habitat scale					
Sand Forest	Birds	<0.0001	<0.0001	ns	Unimodal
	Dung beetles	<0.0001	<0.0001	ns	Unimodal
	Plants	<0.0001	<0.0001	ns	Unimodal

Table 2 (continued).

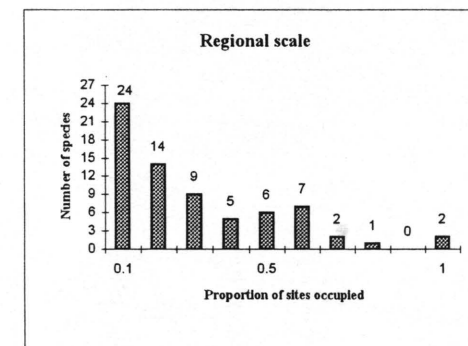
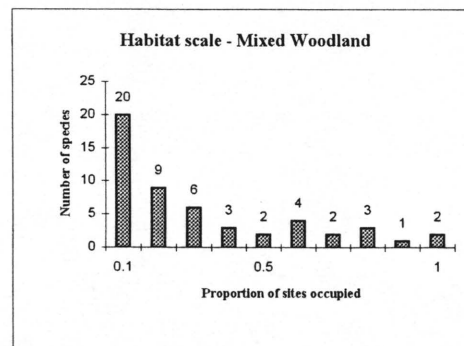
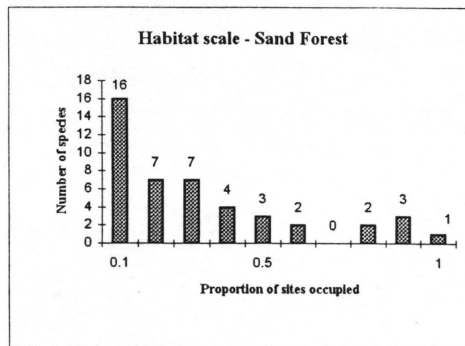
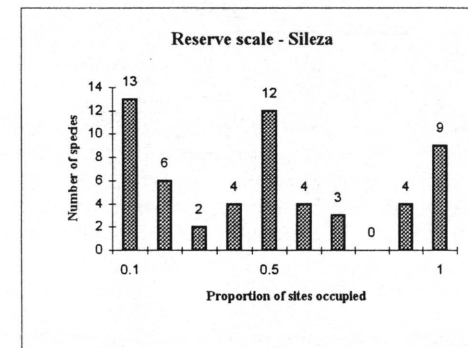
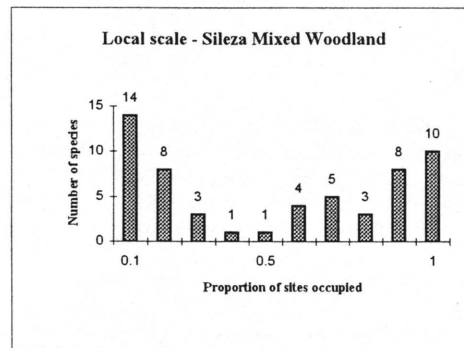
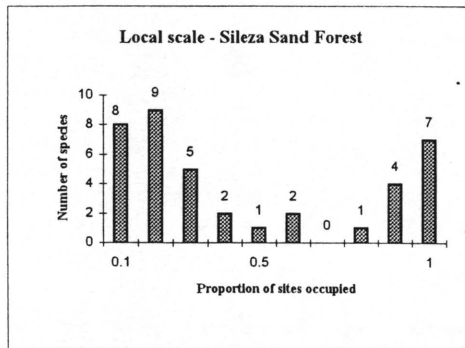
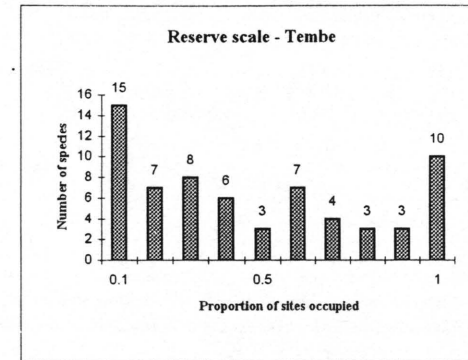
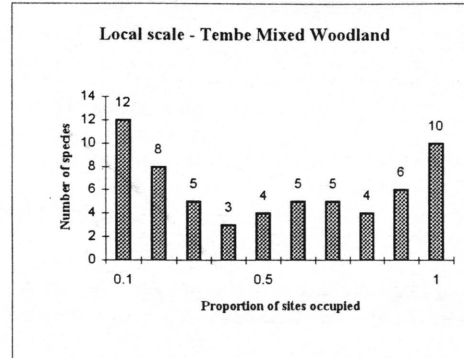
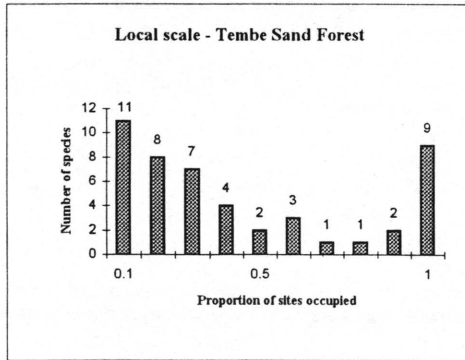
Spatial scale	Taxon group	p_c	p_l	p_r	Diagnosis
Mixed Woodland	Birds	<0.0001	<0.0001	ns	Unimodal
	Dung beetles	<0.0001	<0.0001	ns	Unimodal
	Plants	<0.0001	<0.0001	ns	Unimodal
Regional scale					
	Birds	<0.0001	<0.0001	ns	Unimodal
	Dung beetles	<0.0001	<0.0001	ns	Unimodal
	Plants	<0.0001	<0.0001	ns	Unimodal

a. Birds.



Figs. 1. (a)-(c). Effects of increasing spatial scale on distribution functions of birds, dung beetles and plants. As spatial scale increases, the proportion of species in the core mode (found at > 90% of sites) decreases, and the proportion of species in the satellite mode (at $\leq 10\%$ of sites) increases.

b. Dung
beetles.



c. Plants.

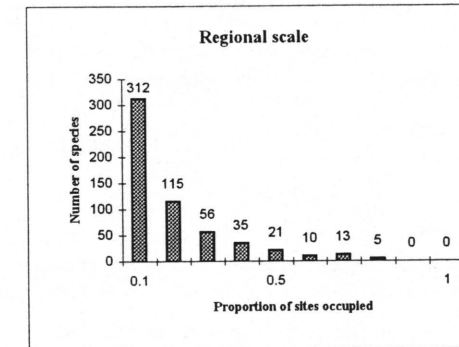
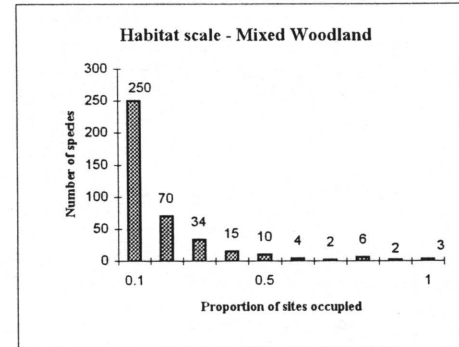
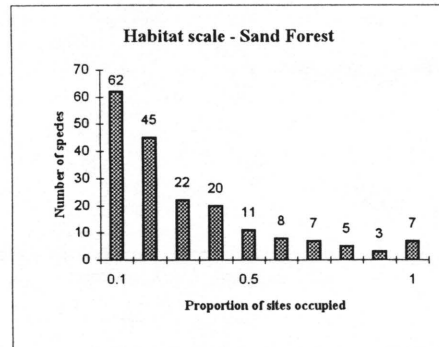
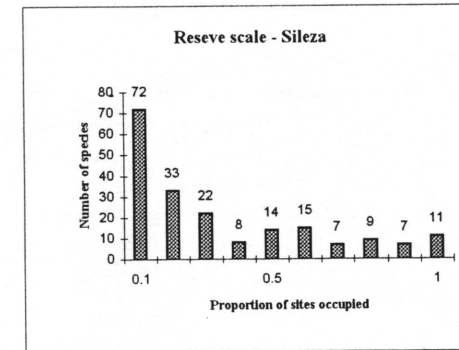
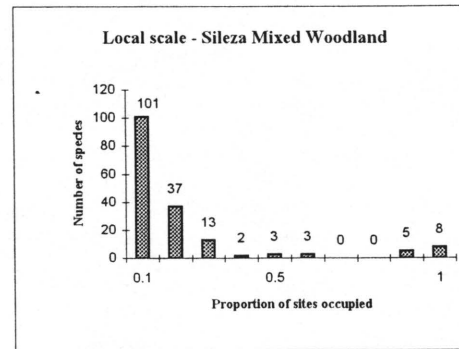
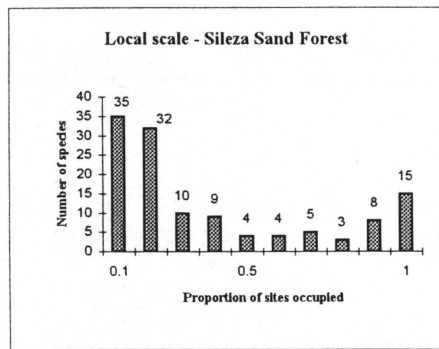
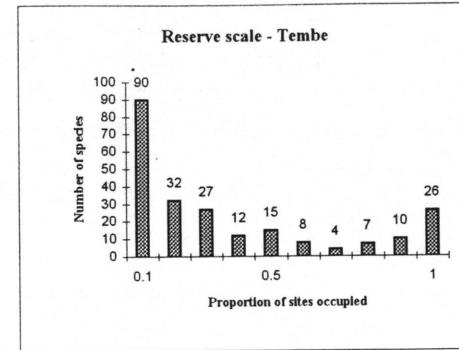
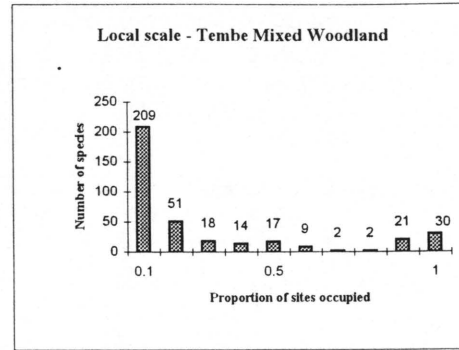
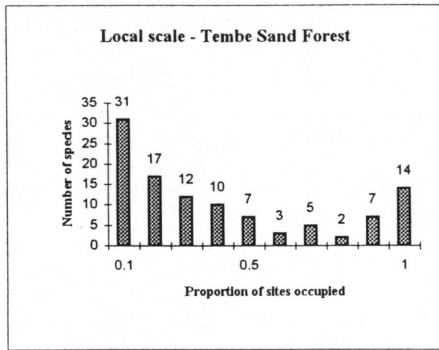


Table 3. Percentage core and satellite mode for each taxon at the different spatial scales (distance scaling). Spatial scales are ranked from smallest to largest.

Taxon	Scale	Proportion of sites Occupied	
		Satellite mode 0 - 10%	Core mode 90 - 100%
Dung beetles	Local – Tembe Sand Forest	22	18
	Local – Sileza Sand Forest	22	19
	Local – Tembe Mixed Woodland	22	18
	Local – Sileza Mixed Woodland	22	16
	Reserve – Sileza	23	16
	Reserve – Tembe	23	15
	Habitat – Sand Forest	30	2
	Habitat – Mixed Woodland	29	3
	Regional	35	3
Plants	Local – Tembe Sand Forest	32	15
	Local – Sileza Sand Forest	32	14
	Local – Tembe Mixed Woodland	71	10
	Local – Sileza Mixed Woodland	64	5
	Reserve - Sileza	36	6
	Reserve – Tembe	39	11
	Habitat – Sand Forest	39	4
	Habitat – Mixed Woodland	73	1
	Regional	62	0
Birds	Local – Tembe Sand Forest	35	17
	Local – Sileza Sand Forest	38	17
	Local – Tembe Mixed Woodland	30	14
	Local – Sileza Mixed Woodland	32	8

Table 3 (continued).		Proportion of sites Occupied	
		Satellite mode	Core mode
Taxon	Scale	0 - 10%	90 - 100%
	Reserve - Sileza	41	5
	Reserve – Tembe	38	7
	Habitat – Sand Forest	47	8
	Habitat – Mixed Woodland	35	6
	Regional	44	4

Organismal scaling

Only two of the comparisons between frequency distributions of taxa within spatial scales were significant (Table 4). The distributions of the three taxa were therefore almost exclusively similar within the scales examined, and there was thus very little difference in the proportion of species in core and satellite modes between taxa within scales. There was also very little evidence of organismal scaling (larger core modes for better dispersing taxa) according to the proposed rank dispersal ability of the three taxa examined (i.e. birds > dung beetles > plants) (Table 5). Dung beetles had the largest core mode percentages at all local and reserve scales. At the larger habitat and regional scales birds did have higher core percentages than the other two taxa (Table 5). These results thus provide little evidence of organismal scaling.

To further test Collins and Glenn's (1997) organismal scaling prediction of better dispersing taxa (i.e. those with larger ranges) in the core mode, I used the bird data collected here, and examined the broader southern African distributions (% of 25 km² grid cells in which species has been recorded in southern Africa, extracted from Harrison *et al.* 1997) of those species in the core and satellite categories of the distributions generated by this study (Figs. 1.(a)-(c)). Species in each of the core and satellite categories in this study included species with both narrow and wide ranges in southern African (Fig. 2). This was true of core and satellite categories at local, habitat and regional scales. For example, at the Sand Forest habitat scale satellite species included species that occur from between 0.04% to 70% of the grid cells in southern Africa. Within the core category in the same habitat there were species that are found in between 2.2% to 32.7% of the quarter degree grid cells in southern Africa. Therefore, neither core nor satellite modes contained species with either exclusively narrow or wide distribution ranges in southern Africa.

Discussion

Distance scaling

As found in numerous, similar empirical studies to date (e.g. Gotelli and Simberloff 1987, Collins and Glenn 1990, Pirintsos *et al.* 1996, Collins and Glenn 1997), the incidence of bimodality in the frequency distributions in this study was high (50%).

Table 4. Differences in frequency distribution functions among taxa at each spatial scale. Values are statistical probabilities based on pairwise Kolmogorov Smirnov two-sample tests.

Spatial scale	Taxon group	Taxon group	
		Plants	Birds
Local scale			
Tembe Sand Forest	Birds	ns	
	Dung beetles	ns	ns
Sileza Sand Forest	Birds	ns	
	Dung beetles	ns	ns
Tembe Mixed Woodland	Birds	ns	
	Dung beetles	<0.05	ns
Sileza Mixed Woodland	Birds	ns	
	Dung beetles	ns	ns
Reserve scale			
Tembe	Birds	ns	
	Dung beetles	ns	ns
Sileza	Birds	ns	
	Dung beetles	<0.05	ns
Habitat scale			
Sand Forest	Birds	ns	
	Dung beetles	ns	ns
Mixed Woodland	Birds	ns	
	Dung beetles	ns	ns
Regional scale			
	Birds	ns	
	Dung beetles	ns	ns

Table 5. Percentage core mode (> 90% of sites occupied) for the different taxa at each spatial scale (organismal scaling). Tembe (T), Sileza (S), Sand Forest (SF) and Mixed Woodland (MW).

Scale	Taxon	Percentage core mode in each site			
		TSF	SSF	TMW	SMW
Local	Plants	15	14	10	5
	Dung beetles	18	19	18	16
	Birds	17	17	14	8
Reserve	Plants	T 11	S 6		
	Dung beetles	15	16		
	Birds	7	5		
Habitat	Plants	SF 4	MW 1		
	Dung beetles	2	3		
	Birds	8	6		
Regional	Plants	Regional 0			
	Dung beetles	3			
	Birds	4			

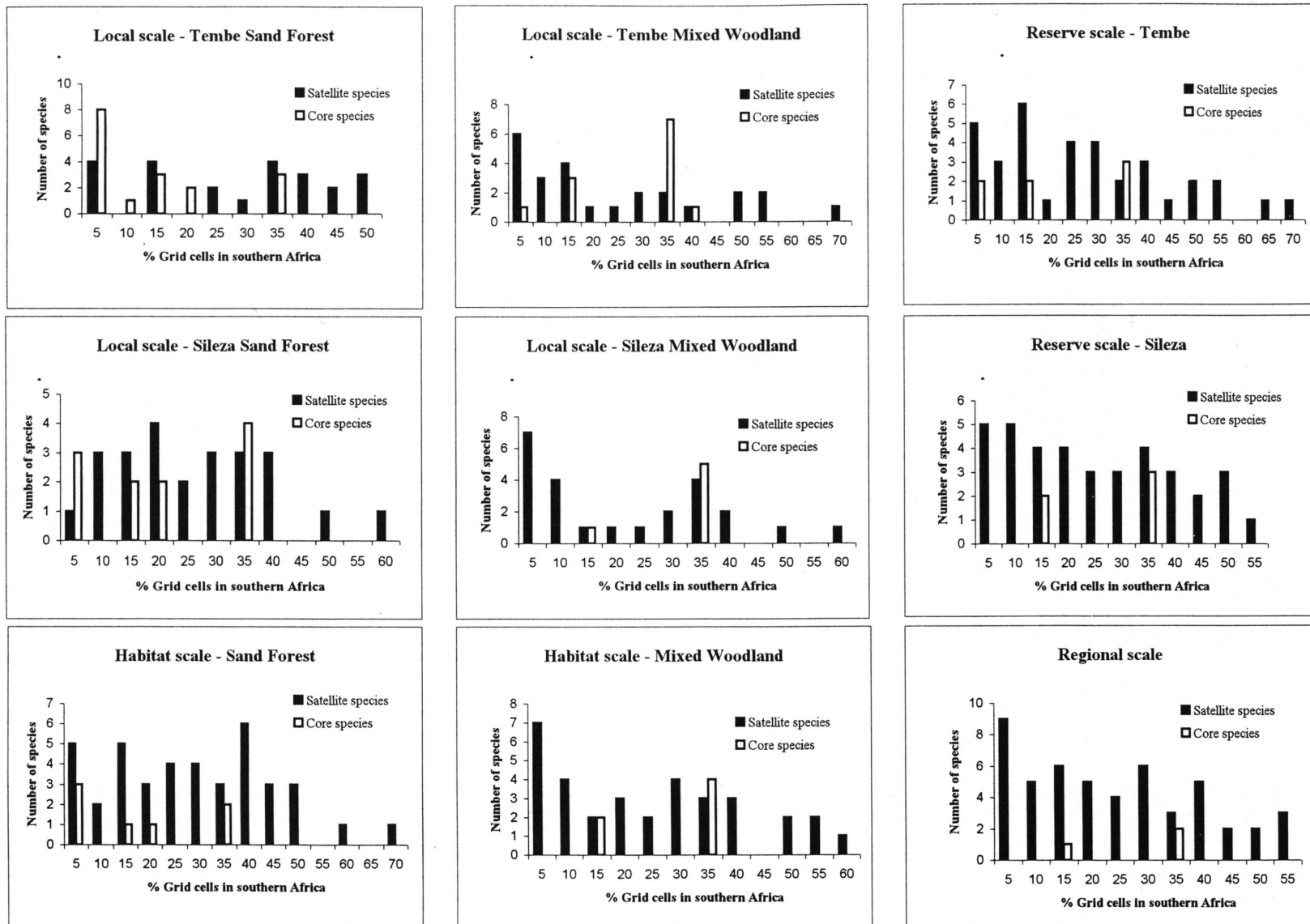


Fig. 2. Percentage of quarter degree (25 km²) grid cells in which the core and satellite bird species identified, at four spatial scales, in the present study are found in southern Africa.

However, unlike other studies, across taxa I found a decreasing incidence of bimodality with an increase in the spatial extent covered. Although Collins and Glenn (1997) found a similar change across two scales, their small scale (36 km²) was somewhat larger than the regional scale (26 km²) in this study. The larger scale Collins and Glenn (1997) examined also included a different geographic area to the smaller scale they examined, with variable spatial extents, for each taxon (they do not provide areas of coverage). Therefore, within each taxon the species set at the smaller scale was not a geographic subset of the assemblage at the larger scale, and it is unclear to what extent, if any, the species composition of the assemblages at the two scales overlap. This study, in contrast, examines true distance scaling where each smaller spatial scale is a geographic subset of the one above it. Nonetheless I too find a decrease in the frequency of bimodality with increasing spatial extent, although across four rather than two spatial scales. Furthermore, I find that this pattern is stronger within (from almost exclusively bimodal at local habitat scale (2 - 4 km²) to exclusively unimodal at the larger habitat scale (22 - 24 km²)), than across, habitat types (see also Raunkiaer 1934, Gotelli and Simberloff 1987). Bimodal and unimodal distributions were equally frequent at the smaller (across habitat) reserve scale (4 - 6 km², including two habitat types) becoming unimodal at the regional (26 km²) scale. Other studies of Tembe Elephant Park and Sileza Nature Reserve show significant differences in the bird (van Rensburg *et al.*, unpublished, Chapter 3) and dung beetle (van Rensburg *et al.* in press, Chapter 2) assemblages of the two habitats (Sand Forest and Mixed Woodland). This may explain the incidence of unimodality at smaller, across habitat (i.e. reserve) scales, where inclusion of a new habitat type and different species assemblage leads to a more rapid increase in species in the satellite mode, than would the addition of a patch of the original habitat type. Because the core-satellite hypothesis attempts to explain the distribution of species that can potentially occupy all sites (i.e. considers SOFD's within homogenous sets of patches) (Hanski and Gyllenberg 1993), it is therefore important to consider the possible effects of including different habitats on the shape of SOFD's (see also Raunkiaer 1934, Gotelli and Simberloff 1987). It is thus critical to have information on the heterogeneity of an area before attempting to quantify SOFD's. In spite of SOFD's being examined across habitat types for part of the analyses presented here, bimodality remained more frequent at smaller than larger

scales for this part of the analysis.

Organismal scaling

The prediction of higher proportions of core species for taxa with better dispersal abilities, based on the assumption that birds are better dispersers than dung beetles and dung beetles better than plants, was not realised in this study. On further consideration it appears unlikely that any conclusions can be made about the dispersal abilities of species in core and satellite modes when sampling is conducted as it was in both this study and by Collins and Glenn (1997). When representative samples are taken of an assemblage from a local patch, habitat or region (as was the case here), the occurrence of a species at a certain number of sites represents the distribution of that species in the area sampled. Given that over evolutionary time most species have had the opportunity to colonise and occupy all suitable patches (and this is a reasonable assumption in the areas sampled here), then the occupancy distributions represent snapshots of accumulated distributions over evolutionary time. In this instance better dispersers may not necessarily be expected to occur at more sites than poorly dispersing species. However, if the actual colonisation of an area, particularly an island, is being monitored over time (such as is the case in the study by Nieminen and Hanski 1998), it is likely that better dispersing species will shift more rapidly from the satellite to core mode of SOFD's than species with poorer dispersal abilities. This may also of course be true of highly fragmented or very patchy habitats (With and Crist 1995). Given sufficient time in comparatively unfragmented habitats, however, the core-satellite distribution will again represent only those species that are either locally or regionally rare or abundant, without encompassing any information on the dispersal abilities of the species concerned. This argument is supported by the occurrence of both widely and narrowly distributed bird species in southern Africa in each of the core and satellite modes of the SOFD's generated by sampling Sand Forest and Mixed Woodland in Tembe and Sileza. Assumptions of the relative dispersal abilities of higher-level taxonomic groups is also problematic. For example, it has recently been shown that rate of spread of tree species may be far more rapid than previously thought (Clark 1998). It is thus clear that the species in core categories do not exclusively demonstrate greater 'dispersal abilities', if one uses, as

suggested by Collins and Glenn (1997), the number of sites at which a species is present as an indication of its dispersal ability.

Mechanisms

Returning to the mechanisms outlined in the Introduction that have been proposed to explain bimodality and the variability in its incidence, a number appear invalid or inapplicable when one considers the patterns found here and the way in which this study was conducted. (i) If bimodality occurs because occupancy is constrained to lie between zero and one (Raunkiaer 1934, Williams 1950), then this mechanism should apply equally to all spatial scales. This was not the case here. (ii) Considering sampling representivity and the possible effect of undersampling rare species on SOFD's, the assemblages of the three taxa sampled in this study are based on data accumulated over 12 months and were highly representative of the area. Although representative, it is possible that rare species in these assemblages were sampled at fewer sites than at which they actually occur, bringing about an inflation in satellite modes. Nonetheless, it is the disappearance of the core mode at larger scales, rather than the change in the satellite mode, that converts the SOFD from bimodal at small scales to unimodal at larger scales. (iii) I do find that SOFD's are sensitive to spatial scale of observation, and furthermore that there appears to be a systematic pattern to this sensitivity. SOFD's are bimodal at smaller spatial scales, becoming unimodal at larger spatial scales. (iv) This decrease in the fraction of species in the core mode with increasing spatial scale could be attributed to Williams' (1964) demonstration that the more sites sampled, the lower the fraction of species present in the core mode. However, I think that this is not the case. First, there is some overlap in the number of occupied sites (from which the SOFD's were generated) between spatial scales. Second, Gotelli and Simberloff (1987) show that the predicted reduction in the proportion of core species across an increase of 100 sampled quadrates was only approximately 2 - 3 %. The observed reduction in core species across 100 quadrates, in contrast, was approximately 16% (see Fig. 6. Gotelli and Simberloff 1987). Similarly, in this study there was a reduction of 13 – 15% in core species between smallest to largest scales, with an average increase of only 40 sample sites (see Tables 1 and 3). The reduction in percentage core species therefore appears far greater than may

be expected to result purely from an increase in sample size. (v) The bimodal SOFD's may arise from underlying lognormal or logarithmic series rank abundance distributions (Papp 1997). This does not necessarily invalidate any of the biological mechanisms listed here (vii – xi). Also, although Papp (1997) shows that these distributions generate bimodal SOFD's, he does not consider possible alternative mechanisms that may also generate bimodality, nor does he suggest which form of rank abundance distribution underlies unimodal SOFD's. (vi) As outlined by Hanski and Gyllenberg (1993), Brown's (1984) specialist-generalist explanation for bimodality does not hold within patches of similar habitat, because all species can potentially occupy all sites. In this study bimodality is predominant within homogenous sets of patches (i.e. at the local habitat scale) and the assumption that all species could occupy all patches within these sites appears sound. In addition, the bird species in the core and satellite models in this study do not qualify as generalist or specialist species respectively, either in terms of their diets or in terms of their habitat affinities (e.g. widespread scavenger species in the satellite mode, and species with extremely narrow distributions in the core mode) (vii) Commenting on the core mode, Maurer (1990) predicted that bimodality is associated with high dominance in assemblages in low productivity habitats. Although I cannot comment on the productivity of the habitats sampled, at the local habitat scale the dung beetle and bird assemblages of Sileza Sand Forest had the highest percentage dominance (52%), and Tembe Mixed Woodland the lowest dominance (28%) (van Rensburg *et al.* in press, Chapter 2, van Rensburg, unpublished). In spite of this 24% change and comparatively low degree of assemblage dominance, the SOFD's for both taxa in both of these local habitats were bimodal. (viii) Tourist species may indeed bring about an inflation in the satellite mode, but again it is the presence or absence of a core rather than the satellite mode, that identifies the SOFD's as either bi- or unimodal. (ix) Little evidence of organismal effect on the shape of SOFD's was found here and, as outlined above, such an effect is unlikely in this type of study (i.e. partial analysis, *sensu* Gaston and Blackburn 1996, and a snapshot of species distributions that have accumulated over time). (x) Although there has been debate on the difficulty of statistically identifying bimodality, Tokeshi's (1992) method, that gives an exact probability of obtaining an observed frequency for the core and satellite modes, does provide a quantitative means of

assessing bimodality. The final mechanism (xi) proposed to explain bimodality is of course a rescue effect associated with metapopulation dynamics. If there is no bimodality there should be no rescue effect, and I could therefore state that metapopulation dynamic processes are not generating the SOFD's at larger scales (22 – 26 km²) for the three taxa I examined. Bimodality at the local habitat level on the other hand was pervasive. Therefore, in the apparent absence of artefactual and other biological mechanisms (see above), the presence of a strong, metapopulation dynamics associated rescue effect may be predicted for dung beetles, birds and plants within scales of 2 – 4.5 km² in Tembe and Sileza. Very little evidence exists in the literature in support of plant or vertebrates exhibiting metapopulation dynamics (Gotelli and Kelley 1993, Harrison *et al.* 1995, Gaston *et al.* 1997, Scheiner and Rey-Benayas 1997, Pfister 1988), and only some evidence has been found for insect species (e.g. Harrison *et al.* 1988, Kindvall and Ahlén 1992, Hanski 1994). Birds, for example, appear unlikely to exhibit metapopulation dynamics because the dispersal abilities of the vast majority of species are so large (Blackburn *et al.* 1997). Nonetheless, in this study both bird and dung beetle assemblages were found to differ significantly between Mixed Woodland and Sand Forest habitats, and Sand Forest characteristically exists as distinct patches of varying sizes within a matrix of Mixed Woodland (van Wyk 1996, van Rensburg *et al.* in press, Chapter 2). At the local habitat scale bimodality was found for all Sand Forest assemblages, whereas the two unimodal SOFD's at this scale were associated with Mixed Woodland. The patchiness of the Mixed Woodland – Sand Forest system may therefore be playing a role in generating the bimodality found.

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CHAPTER 5 - CONCLUSION

Previous assessments of large herbivore impacts in Tembe showed that *Albizia versicolor* and *A. adianthifolia* trees which are characteristic of Mixed Woodlands, attained the highest percentage elephant utilization when compared to tree species characteristic of Sand Forests (*Dialium schlechteri* and *Erythrophleum lasianthum* - W. S. Matthews, pers. comm). However, more recent results suggest that the percentage elephant utilization of Sand Forest tree species is increasing. This is a direct result of the northern border of Tembe being closed in 1989 to prevent poaching, restricting natural movement patterns of elephants into southern Mozambique. Because Tembe consists mostly of leached sands of low fertility the quality of forage for elephants and other game is generally poor. On the other hand the alluvial soil floodplains, with their higher nutritional levels, found in southern Mozambique provided higher quality food sources. Thus, after 1989 the size of Tembe (in which the largest proportion of Sand Forest habitat is currently protected) became small, together with a restriction to natural movement patterns of elephants. This caused a forage shortage, which led to opening up these Sand Forests, and the subsequent development of a structure more like Mixed Woodland. To date there is no evidence that Mixed Woodlands recreates to Sand Forests.

Because the Mixed Woodland bird assemblages show similar affinities to those of the Sand Forests, both of which are Afrotropical it appears that this trend of changes from Sand Forest to Mixed Woodland has been ongoing for some time. Given this situation and the overall concern for regional conservation of Sand Forest, the initial reasons for undertaking this study seem justified. That is, it is important to identify which species are restricted to Sand Forests, how assemblages differ between this habitat in different reserves, and which species can be used as indicators and potential detectors. Detector species were only identified for the dung beetle taxon and not for the birds, because a much larger proportion of the total number of species within a particular habitat can be sampled for dung beetles within a short period of time (e.g. 48 hr survey), which makes the dung beetles more practical when costs are taken into account.

This study showed that there is considerable between reserve heterogeneity in both birds and dung beetles and conservation of Sand Forest in as many sites as possible

is important. In addition, this finding adds strength to the argument that problems associated with elephant-induced damage to Sand Forests in Tembe must be addressed. If this is not done, a number of endemic bird species, which are abundant in the Sand Forests in Tembe, will face increasing threat within this conservation area. Thus the botanical surveys of elephant damage should be continued and perhaps supplemented with the monitoring of dung beetle indicator and detector species identified here.

To insure that conservation decisions based on the outcome of this study can be taken with greater certainty the following additional research should be addressed.

Suggested future research topics:

- The indicator and detector species analyses should be repeated in other Sand Forest regions to determine whether these species are useful in this regard elsewhere. This will also provide additional insight into the utility of this concept for future work of this nature.
- The time span over which these detector species react to changes in the Sand Forest habitat patches should be determined, perhaps outside of the Tembe Elephant Park where Sand Forests are being modified at a rapid rate.
- How does the variation in the size of a Sand Forest patch influence the assemblage composition of taxa. For example, what is the smallest Sand Forest patch size that will maintain a viable avian assemblage? Such information will have important conservation consequences for Sand Forests and their biota, given that this biological important habitat is currently under threat both within and outside formal conservation areas.
- Although Allan *et al.* (1997) consider the avifauna of the MC to be part of a regional, East Coast Littoral mosaic with no clear affinities to other southern African biomes, the analysis undertaken here indicates that the bird assemblages of both Sand Forest and Mixed Woodland have their closest affinities with those of the Afromontane forests. However, it seems unlikely that further, assemblage-level analyses will resolve the origins of the biota of the region. Rather, phylogeographic analyses, at both the population and species levels, are now required to resolve area relationships of the MC and its major habitat components. Such analyses would be especially

insightful with regard to the southern limit of the MC, and the significant biogeographic barrier posed by the Limpopo basin.

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