

**Heterogeneity of dung beetle (Coleoptera: Scarabaeidae)
assemblages in northern KwaZulu-Natal, South Africa:
Conservation implications**

by

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ABSTRACT

Investigating the extent of local scale heterogeneity in assemblages is necessary to achieve a sound understanding of the processes giving rise to local assemblage patterns and the variation between them. Moreover, a clear understanding of local scale heterogeneity of assemblages is imperative in the development of effective regional conservation strategies. Previous studies examined the local scale heterogeneity in dung beetle assemblages between mixed woodland and sand forest habitats in Tembe Elephant Park, KwaZulu-Natal. Sand forest is an endangered habitat type in southern Africa which, when disturbed, opens up and changes towards mixed woodland. Reversion to the original sand forest structure after disturbance has never been recorded. Dung beetle assemblages were found to be homogenous within, but significantly heterogenous between, habitat types. It was therefore suggested that disturbance of sand forest (elephant foraging inside, and human occupation outside the Park) was likely to affect the assemblage structure of dung beetles in sand forest. Therefore, the aim of this study was to determine the effect of human- and elephant-induced disturbance on dung beetle assemblages in sand forest. Furthermore, disturbed sand forest dung beetle assemblages were predicted to be more similar to mixed woodland than to undisturbed sand forest assemblages. Disturbance by elephants causes sand forest vegetation structure to change to that of mixed woodland and this resulted in elephant-disturbed sand forest dung beetle assemblages becoming more similar to mixed woodland assemblages. Assemblages in human disturbed sand forest were unique and associated with human-related activities. The reliability and predictability of dung beetle indicator (species specific to a particular habitat type) and detector species (species indicative of the direction of habitat change) identified for Tembe in a previous study were tested. The results of this study largely supported the suite of bioindicator species first identified. Detector species were found to provide information complimentary to the indicator species and vegetation data available for sand forest. In addition, an identification key for the dung beetle species collected in Tembe Elephant Park to date was compiled. This key facilitates the use of dung beetle assemblages in indicator and monitoring systems in this reserve by providing a rapid and effective means of identifying the dung beetle species. The abundance-body size

relationships of the dung beetle assemblages in mixed woodland, undisturbed and disturbed sand forests were also determined. Four hypotheses that account for the relationship between body size and abundance or its variants, were tested here, namely the energy equivalence rule, interspecific competition, differential extinction, and the biomass frequency distribution hypothesis. The disturbed sand forest assemblages were used to test whether disturbance alters the relationships between the macroecological variables (i.e. body size, abundance and biomass) and their interrelationships. This study provided some support for the biomass hypothesis. The major relationship between body size and abundance held despite human- and elephant-induced disturbance. Nonetheless, this study indicates that human- and elephant-induced disturbance alter sand forest dung beetle assemblages and may have significant implications for other taxa that occupy this endangered habitat type. Monitoring of the impacts of large herbivores on sand forest in reserves should thus be continued, and dung beetles provide one effective means by which this can be achieved.

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GENERAL INTRODUCTION

Investigating the extent of local scale heterogeneity in assemblages is necessary to achieve a sound understanding of the processes giving rise to local assemblage patterns and the variation between them (Ricklefs & Schluter 1993; Lawton 1999; Gaston 2000). Such investigations are important within a modern conservation-planning context where the approach shifted from focussing on charismatic and threatened animals to the protection of ecosystems and the processes maintaining them (May 1995; Van Jaarsveld & Chown 1996). It has been shown that priority conservation areas identified at broad, regional scales cannot be translated into effectively designed local conservation areas without reference to local heterogeneity in species distribution patterns (Noss 1990; Rodrigues *et al.* 1999). Therefore, a clear understanding of local scale heterogeneity of assemblages is imperative in the development of effective regional conservation strategies (Noss 1990; Flather *et al.* 1997). However, local habitat-associated heterogeneity in assemblages can be pervasive across scales and may complicate conservation strategy development (Noss 1990; Flather *et al.* 1997). The Maputland Centre of Endemism (MC) is just such an area where habitat-associated heterogeneity in assemblages exists (Van Rensburg *et al.* 1999, 2000).

The MC comprises the southernmost end of the tropics in eastern Africa (Fig. 1) and has a high faunistic and floristic diversity (Van Wyk 1996). Within the MC sand forest exists as patches in a matrix of mixed woodland (Fig. 2) and is considered to be the oldest habitat type in this region (Van Wyk 1996). This habitat type is confined to the tropical and subtropical coastal belt of KwaZulu-Natal and is only extensive in the north-eastern areas of this province in South Africa (McKenzie 1996). Within the MC, sand forest harbors the largest proportion of endemic plant and vertebrate species. This habitat is however under considerable threat of deforestation (Davis *et al.* 1994; Matthews *et al.* 1999). Approximately 3,542 km² of sand forest exists in the MC (McKenzie 1996) of which approximately 45 % are transformed as a result of clearing for agriculture and firewood (Davis *et al.* 1994; Cole & Landres 1996). Approximately 44.62 % of sand forest is conserved within four reserves (McKenzie 1996): Tembe Elephant Park (3,020 ha out of a total of 30,079 ha), Sileza Nature Reserve (25 ha out of 2,500 ha), Mkuzi

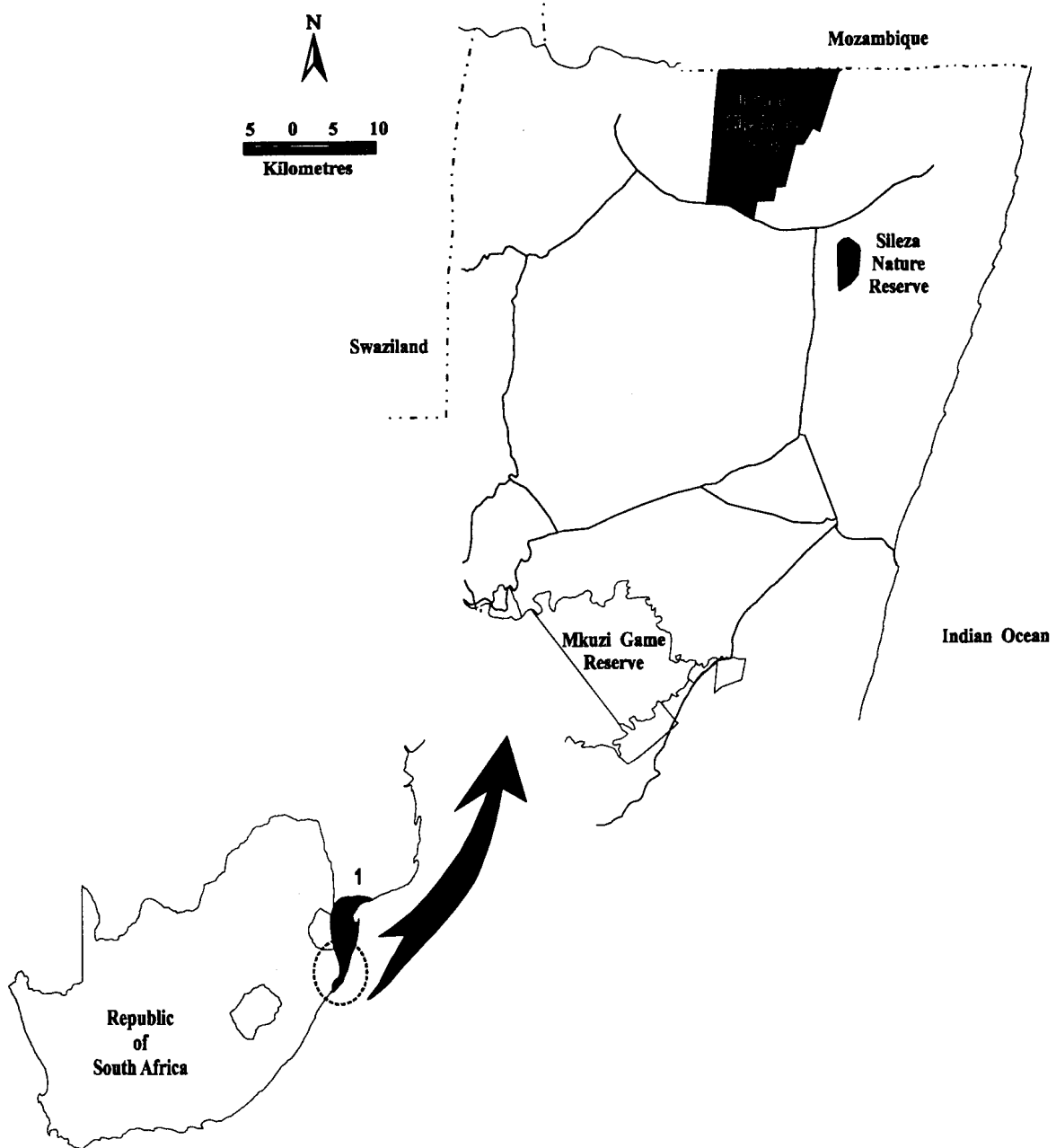


Fig. 1. Map of South Africa showing the location of 1) the Maputland Centre of Endemism (MC) and of Tembe Elephant Park within the MC.

Game Reserve (1,500 out of 29,000 ha) and a few patches in Falsebay Park (Van Rensburg *et al.* 1999). However, an apparent conservation conflict is arising in the largest of these reserves, Tembe Elephant Park. In this reserve elephants are increasingly utilizing sand forest as a result of the high densities at which these animals occur. Sand forest is thus endangered both inside and outside protected areas.

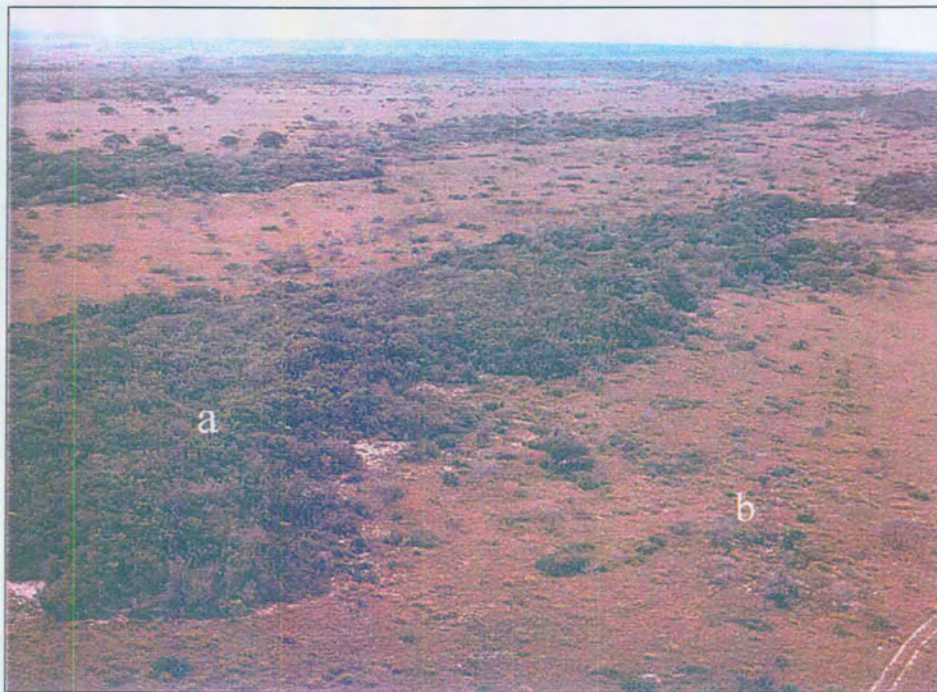


Fig. 2. Aerial photo of Tembe Elephant Park showing the dense sand forest (a) in the mixed woodland matrix (b).

Objectives and structure of the thesis

This study investigated the effects of human and elephant disturbance on sand forest using dung beetle assemblages in and adjacent to Tembe Elephant Park. Dung beetles were chosen because they are systematically well known in southern Africa (Davis 1997). Southern Africa has 780 dung beetle species in the family Scarabaeidae, of

which up to 150 species may be found in one locality (Scholtz & de Villiers 1983). Dung beetles are also important components of most habitat types (Hanski & Cambefort 1991). They play important roles in ecosystem functioning and are involved in nutrient cycling, seed dispersal and in the control of vertebrate endoparasites by removal of the source of infection (dung) (e.g. Gibbs & Stanton 2001). Dung beetles are also easy to sample quantitatively (Buckland *et al.* 1994) and the environmental and habitat associated factors influencing dung beetle assemblage structure at local scales are comparatively well known (Nealis 1977; Doube 1983; Hanski & Cambefort 1991). For example, the local distribution of dung beetles is strongly influenced by vegetation structure and soil type (Nealis 1977; Doube 1983; Klein 1989). Dung beetle assemblage structure is therefore expected to mirror changes in habitat structure.

A previous study conducted by Van Rensburg *et al.* (1999) on dung beetle assemblages in sand forest and mixed woodland habitat types in Tembe elephant Park and Sileza Nature Reserve found dung beetle assemblages to be homogenous within, but significantly heterogenous between, habitat types. It was therefore suggested that disturbance of sand forest (elephant foraging inside, and human occupation outside the Park) was likely to affect the community structure of dung beetles in sand forest (Van Rensburg *et al.* 1999).

Van Rensburg *et al.* (1999) hypothesized that, because sand forest vegetation structure changes to that of mixed woodland when disturbed (Van Rensburg *et al.* 1999), dung beetle assemblages in sand forest will also change to mixed woodland assemblages. The first objective of this study was therefore to test this hypothesis (Chapter 1).

Thereafter, Chapter 2 tested the reliability and predictability of dung beetle indicator species (species characteristic of mixed woodland and sand forest habitats), as well as species predicted to indicate changes in sand forest vegetation structure due to disturbance (such as deforestation by humans or elephant foraging), identified by Van Rensburg *et al.* (1999) for Tembe Elephant Park. In addition, an identification key for the dung beetle species collected in Tembe Elephant Park to date was compiled (Chapter 3). This is an accessible and easily used key for the non-taxonomist and will assist in monitoring programs where the dung beetle indicator species are implemented. A CD-ROM based version of the key is also included in this thesis. Chapter 4 determined the

relationships between the macroecological variables (abundance, body size and biomass) in the dung beetle assemblages in mixed woodland and sand forest in Tembe Elephant Park, as well as the mechanisms responsible for generating the observed patterns in these relationships. The effect of human- and elephant-induced disturbance on the relationships between the macroecological variables of dung beetle assemblages in sand forest was also determined.

Each of these chapters was written as an individual research paper and there is thus some overlap in the introductions and research methods of each. The general conclusion provides a summary of the results from Chapters 1, 2, 3 and 4 and discusses the conservation and management implications of these for sand forest inside and outside of Tembe Elephant Park.

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**Human and elephant induced changes to dung beetle (Coleoptera:
Scarabaeidae) assemblages in and adjacent to Tembe Elephant Park
(KwaZulu-Natal, South Africa)**

INTRODUCTION

The spatial distributions of dung beetles are known to be influenced by a combination of climate (Davis & Dewhurst 1993), soil type (Nealis 1977; Cambefort 1991; Doube 1991), vegetation structure (Nealis 1977; Doube 1983; Klein 1989; Steenkamp & Chown 1996; Van Rensburg *et al.* 1999), dung type and the availability (dung quantity) thereof (Davis 1994a, b; Hanski & Cambefort 1991; Lumaret *et al.* 1992). These factors result in specialized biogeographical associations of dung beetles, and several species tend to be endemic to particular habitat types in specific climatic regions (Davis 1997). However, local scale heterogeneity of dung beetle assemblages may be pronounced (Hanski & Cambefort 1991; Finn *et al.* 1999; Van Rensburg *et al.* 1999). Dung beetles are very sensitive to habitat changes (Klein 1989), and disturbance can have significant effects on the structure of dung beetle assemblages, for example species diversity, abundance, biomass and dominance (Peck & Forsyth 1982; Steenkamp & Chown 1996; Gibbs & Stanton 2001; Lobo 2001; Roslin & Koivunen 2001).

Dung beetle species richness in an area is also closely linked to mammal species richness and a large and diverse mammal fauna is important for the maintenance of a large and diverse dung beetle fauna (Peck & Forsyth 1982; Klein 1989; Hanski & Cambefort 1991). When habitats are cleared and domestic animals introduced changes in both habitat structure and dung type availability occur (Peck & Forsyth 1982). For example, Peck & Forsyth (1982) showed that the clearing of rain forests eliminated native forest dung beetle fauna therein and a different, smaller assemblage of species associated with human activities became established. Similar habitat changes have been predicted to

be altering the structure of dung beetle assemblages in the Maputuland Centre of Endemism in KwaZulu Natal, South Africa.

Van Rensburg *et al.* (1999) examined the variation in dung beetle assemblages in the two dominant vegetation types (mixed woodland and sand forest) in this region. Dung beetle assemblages were found to be homogenous within sand forest and mixed woodland habitats in Tembe Elephant Park (hereafter Tembe), although pronounced heterogeneity was found both between habitat types and nature reserves in the area (Van Rensburg *et al.* 1999). Van Rensburg *et al.* (1999) also predicted that disturbance, in the form of over-utilization of sand forest by elephants inside Tembe Elephant Park and clearing of sand forest by human communities outside the Park, would alter dung beetle assemblage structure. Specifically they predicted that opening of the sand forest canopy (by elephant browsing or clearing by humans) would result in the sand forest dung beetle assemblage becoming more similar to the dung beetle assemblage in mixed woodland. This prediction was based on the fact that when sand forest is disturbed, the canopy opens and the plant community converts to mixed woodland habitat. Sand forest is the oldest habitat type on the Maputuland coastal plain and at present is an endangered habitat type (Van Wyk 1996). Reversion to the original sand forest structure after disturbance has never been recorded (Van Rensburg *et al.* 1999).

This study, therefore, tested the hypothesis that dung beetle assemblages in elephant- and human-disturbed sand forests are more similar to mixed woodland assemblages than to those of undisturbed sand forest. The key questions addressed were: 1) are there differences in dung beetle community structure between undisturbed sand forest and human-disturbed sand forest, and between undisturbed sand forest and elephant-disturbed sand forest, and 2) are dung beetle assemblages in human- and elephant-disturbed sand forests more similar to those in mixed woodland than to those in undisturbed sand forest?

MATERIAL AND METHODS

Study area

Sampling was done in and adjacent to Tembe Elephant Park (27°01'S 32°24'E) on the southern Mozambique Coastal Plain of Northern KwaZulu-Natal, South Africa. In this reserve sand forest (Fig. 1.1a) exists as patches in a matrix of mixed woodland (Fig. 1.1b). The closing of the northern border of the reserve in 1989 restricted the natural movement of elephants into southern Mozambique. Because of the high densities of elephants within the reserve (130 – 140 animals in 30,079 ha; Matthews, pers. comm.) and the restriction on their movement between Tembe and southern Mozambique, the percentage utilization of the endemic-rich sand forest is increasing rapidly. As the elephants foraging in, and move through the sand forest the closed canopy of this vegetation type is opened up (Fig. 1.2a, b). To protect sand forest patches from elephant damage, a 750 ha (c. 2.5 % of the reserve) area within the south of the reserve has been fenced off from the remainder of the Park to exclude elephants (i.e. the botanical reserve). Outside and adjacent to Tembe, human communities inhabit the area at moderate to high densities. A mean population size of c. 28,000 humans was calculated for the four quarter-degree cells bordering on Tembe (Statistics South Africa 1996). Disturbance to sand forest in these areas occurs as a result of clearing for firewood and living areas, and grazing by livestock, especially cattle (Davis *et al.* 1994; Cole & Landres 1996) (Fig. 1.2c, d).

Sampling and species identification

Sampling was done during December 1998 and January 2000, a period of high dung beetle activity (during mid summer after periods of rainfall, see Doube 1987) following the same sampling regime as Van Rensburg *et al.* (1999). During both sampling periods two mixed woodland and two sand forest areas were sampled. Different sites were used for each of the sampling periods. During December 1998, closed canopy sand forest areas were sampled which represented undisturbed sand forest. Two human-disturbed sand forest areas adjacent to the reserve were also sampled (Fig. 1.3).

a)



b)



Fig. 1.1. Vegetation in Tembe Elephant Park showing a) sand forest and b) mixed woodland.

a)



b)



c)



d)



Fig. 1.2. Vegetation in and adjacent to Tembe Elephant Park showing elephant-disturbed sand forest (a, b) and human-disturbed sand forest (c, d).

During January 2000 two sand forest areas were sampled inside the botanical reserve to exclude disturbance caused by elephants, and two elephant-disturbed sand forest areas were sampled inside the reserve (Fig. 1.3). Elephant-disturbed sand forest was identified as areas that showed evidence of recent elephant activity such as large trees that were removed by these large herbivores and therefore opening up the sand forest canopy.

During each of the sampling periods five grids of six pitfall traps each were placed in each area. The pitfalls were placed in a 2 x 3 design on a 2 m x 4 m grid. The traps were baited using 50 g elephant dung and set out for 24 hours. Sampling grids were placed a minimum of 200 m apart in each area to maintain sampling independence. The dung beetles collected were identified by comparison with identified specimens in the South African National Insect Collection and with the help of Dr A. Davis (pers. comm.).

Data analysis

Total species richness and abundance were determined for each habitat type (i.e. mixed woodland, undisturbed sand forest, human-disturbed and elephant-disturbed sand forest). The number of individuals sampled was summed for each sampling grid (six pitfalls) in each sampling period and the mean species richness and abundance was calculated across grids. Mean species richness and abundance were compared between habitat types within and across the two sampling periods using Analysis of Variance. Tukey HSD tests were used to determine which dung beetle assemblages were significant different from each other in terms of these measures.

Species accumulation curves were compiled for each habitat type in each sampling period to determine the degree of sampling representivity. Grids were randomly and sequentially selected without replacement until all grids were selected within each habitat type in each sampling period. This procedure was repeated ten times. The mean number of species across the ten replicates for each grid was then used to compile species accumulation curves.

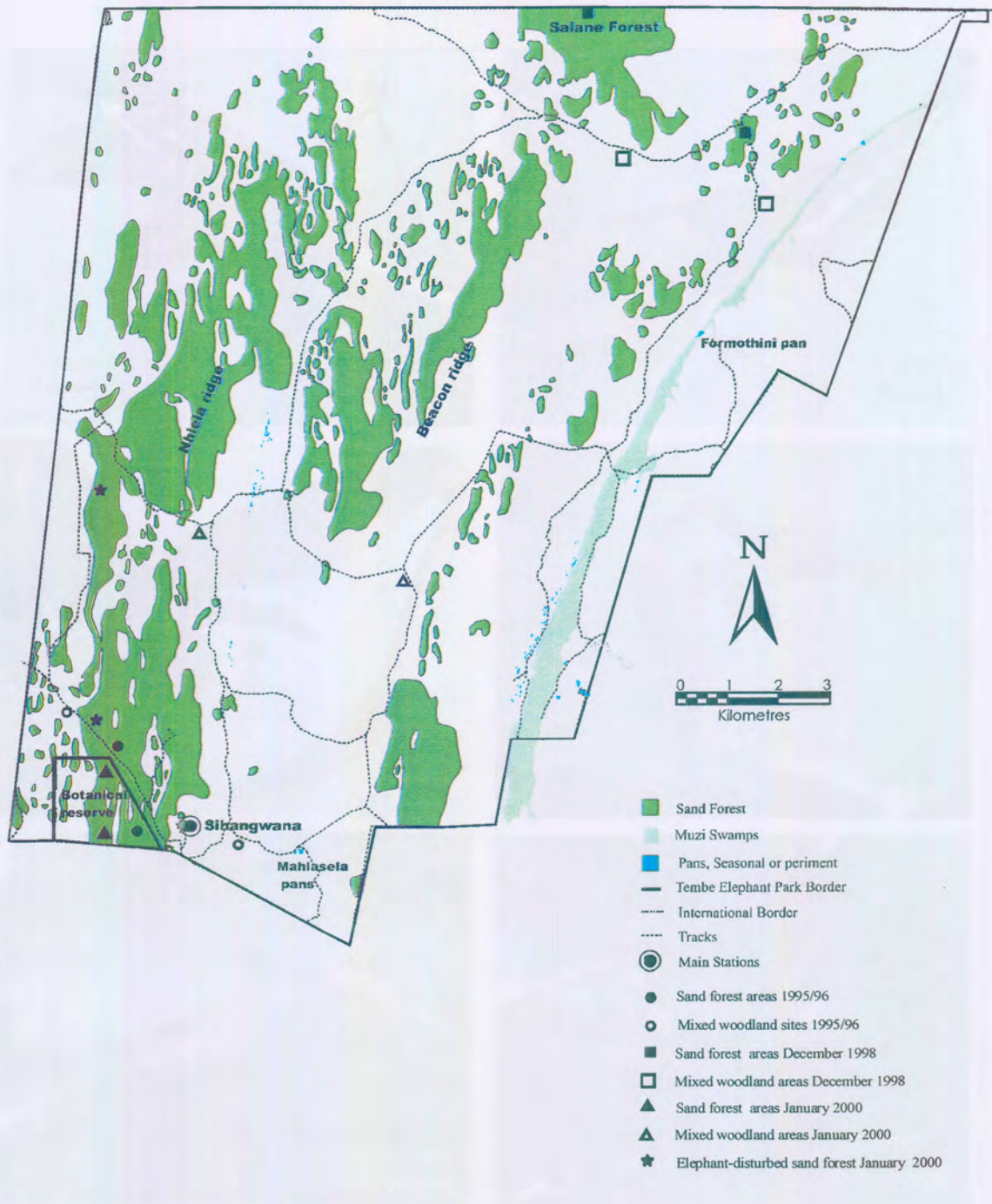


Fig. 1.3. Vegetation map of Tembe Elephant Park showing the areas sampled during 1995/96 (Van Rensburg *et al.* 1999), December 1998 and January 2000. Two human-disturbed sand forest sites were sampled in December 1998 approximately 5 km to the west of the Park.

Species specific to each habitat type were identified (i.e. species sampled only in one particular habitat type over both sampling periods) to determine whether certain species were restricted to a particular habitat type, and whether disturbed areas had unique species (species unique to a dung beetle assemblage disturbed either by human activities or by elephants). The proportion of species shared between habitat types was also determined within sampling periods to determine how similar the species composition of the different habitat types were.

The dung preference of each dung beetle species sampled was determined (Hanski & Cambefort 1991; Davis 1994b) to investigate if the presence of human (omnivore) dung influenced the community membership of dung beetle assemblages in human-disturbed sand forest sites. The abundances of species sampled in human-disturbed sand forest were compared with those in undisturbed sand forest, as well as between the elephant-disturbed and undisturbed sand forests sampled in January 2000, using a Mann-Whitney U-test. The objective here was to determine if the abundance of omnivore dung-preferring species increased as a result of the presence of human dung in the disturbed habitats adjacent to Tembe.

Dung beetle assemblage structure of the habitat types was compared using non-metric multi-dimensional scaling (MDS) and analysis of similarity (PRIMER v5.0 1994) (Clarke & Warwick 1994). Bray Curtis similarity measures (Bray & Curtis 1957) were used to determine whether habitat and disturbance types differed in dung beetle community structure. Common and rare species were weighted equally by double-root transformation of the data before analysis (Clarke & Warwick 1994). The significance of the differences between habitat and disturbance types within each sampling period was established using analysis of similarity (ANOSIM – Clarke 1993). This is a non-parametric permutation procedure applied to rank similarity matrices underlying sample ordinations (Clarke 1993). A global R -statistic is generated and the closer a significant global R is to one, the more distinct the differences between assemblages are (Clarke 1993). The relative differences between R -values were used to determine how similar dung beetle assemblages were between habitat types within and between sampling periods. The relationships between habitat types within and between sampling periods were displayed using non-metric multi-dimensional scaling (MDS) ordinations.

RESULTS

A total of 77 dung beetle species representing 24 genera (31,055 individuals) were collected during the 1998 sampling period, compared to 52 species representing 18 genera (9,618 individuals) during the 2000 sampling period (Appendix A). Mean species richness and abundance were significantly different between habitat types across sampling periods (Table 1.1). In December 1998 mixed woodland had a significantly higher species richness and abundance of dung beetles than undisturbed and human-disturbed sand forests (Table 1.1). In January 2000 no significant differences in species richness were found between habitat types, but dung beetles were significantly more abundant in mixed woodland than in undisturbed sand forest (Table 1.1).

Table 1.1. Species richness and abundance of dung beetles collected in mixed woodland and sand forest during each sampling period. *n* = number of sampling grids, *S* = total richness, *N* = total abundance.

Habitat and sampling period	Richness Mean ± S.E.	Abundance Mean ± S.E.	<i>n</i>	<i>S</i>	<i>N</i>
December 1998	($F_{2,27} = 31.711$, $P < 0.01$)	($F_{2,27} = 14.452$, $P < 0.01$)			
Sand forest	22.40 ± 1.69 a	675.90 ± 110.04 a	10	39	6759
Human-disturbed sand forest	19.60 ± 1.39 a	543.20 ± 187.73 a	10	45	5432
Mixed woodland	39.60 ± 2.35 b	1886.80 ± 257.70 b	10	65	18863
January 2000	($F_{2,27} = 2.903$, $P = 0.119$)	($F_{2,27} = 4.860$, $P = 0.016$)			
Sand forest	18.60 ± 0.95	222.70 ± 25.70 a	10	37	2227
Elephant-disturbed sand forest	21.30 ± 1.37	317.80 ± 58.02 ab	10	39	3178
Mixed woodland	21.90 ± 1.12	421.30 ± 45.42 b	10	44	4213

Species accumulation curves of undisturbed- and human-disturbed sand forests for 1998 showed very similar patterns (Fig. 1.4a), and the same was true for mixed woodland and elephant-disturbed sand forest during 2000 (Fig. 1.4b). Species were thus sampled at approximately the same rate in undisturbed and human-disturbed sand forest during 1998, and in mixed woodland and elephant-disturbed sand forest during the 2000 sample. Although the species accumulation curves did not reach a species richness asymptote, the dung beetle assemblages in the mixed woodland and sand forest areas sampled in January 2000, and the sand forest sampled in December 1998, each contained 80 % of the species sampled by Van Rensburg *et al.* (1999) for Tembe from May 1995 - April 1996. In December 1998, 15 % more species were sampled in mixed woodland compared to the number of species collected by Van Rensburg *et al.* (1999).

However, the sampling effort in this study constituted one twelfth of the sampling effort of Van Rensburg *et al.*'s (1999) study. They sampled bimonthly over a period of twelve months and pitfall traps were set for 48 hours. During the December 1998 and January 2000 sampling periods a single sample was taken over 24 hours. Therefore, the likely reason why a species richness asymptote was not reached during the 1998 and 2000 sampling periods is that the sampling effort was too low (i.e. 24 hours in contrast to the 48 hour period during 1995/96, see Van Rensburg *et al.* 1999).

The number of mixed woodland-specific species was high compared to sand forest-specific species (Table 1.2). This is however not surprising given that species richness is higher in mixed woodland than in sand forest. Only one species (*Drepanocerus impressicollis*) was sampled in mixed woodland over both sampling periods while no such species were found in sand forest (Table 1.2). No habitat-specific species were found in the sand forests sampled in 1998 or in the elephant-disturbed sand forest, while four species were sampled that were unique to human-disturbed sand forest (Table 1.2). These species were all omnivore dung specialists (Appendix B).

In total, 19 species (35 % of the total number of species) had significantly different abundances between undisturbed and human-disturbed sand forest (Table 1.3) in December 1998. Three of these species were herbivore dung preferring species, of which two species did not occur in human-disturbed sand forest and one had a higher abundance in undisturbed sand forest (Table 1.3). Six omnivore dung specialist species had higher abundances in the human-disturbed areas (Table 1.3). The presence of omnivore dung in

human-disturbed sand forest did thus only increase the abundance of a very small proportion of omnivore dung specialist species in this habitat type. In January 2000 nine species (21 % of the total number of species) had significantly different abundances in undisturbed and elephant-disturbed areas. The abundance of five of these species was higher in elephant-disturbed sand forest (Table 1.3).

The undisturbed and disturbed sand forest areas shared the highest proportion of species in both sampling periods (Table 1.4). Elephant-disturbed sand forest shared a higher proportion of species than human-disturbed sand forest with mixed woodland and undisturbed sand forest respectively (Table 1.4). The lowest proportion of species was shared between mixed woodland and sand forest assemblages in both sampling periods. Therefore, in terms of assemblage membership, disturbed sand forest remained more similar to undisturbed sand forest than to mixed woodland.

There were significant differences between dung beetle assemblages in the different habitat types within each sampling period, as well as across sampling periods (across habitats and sampling periods: Global $R = 0.892$, $P < 0.001$; December 1998: Global $R = 0.925$, $P < 0.001$; January 2000: Global $R = 0.911$, $P < 0.001$). Although all the habitats sampled were significantly different from each other (Table 1.5, Fig. 1.5), undisturbed sand forest areas sampled in the different sampling periods were overall more similar to each other than to mixed woodland areas. Differences between R -values were small between habitat types within the two sampling periods (Fig. 1.6). During both sampling periods the assemblage structure of dung beetles in mixed woodland and sand forest were the least similar (Fig. 1.6). Human-disturbed sand forest was marginally more similar to undisturbed sand forest than to mixed woodland (Fig. 1.6a), while elephant-disturbed sand forest was marginally more similar to mixed woodland (Fig. 1.6b). Therefore, unique dung beetle assemblages resulted from both human and elephant disturbance of sand forest.

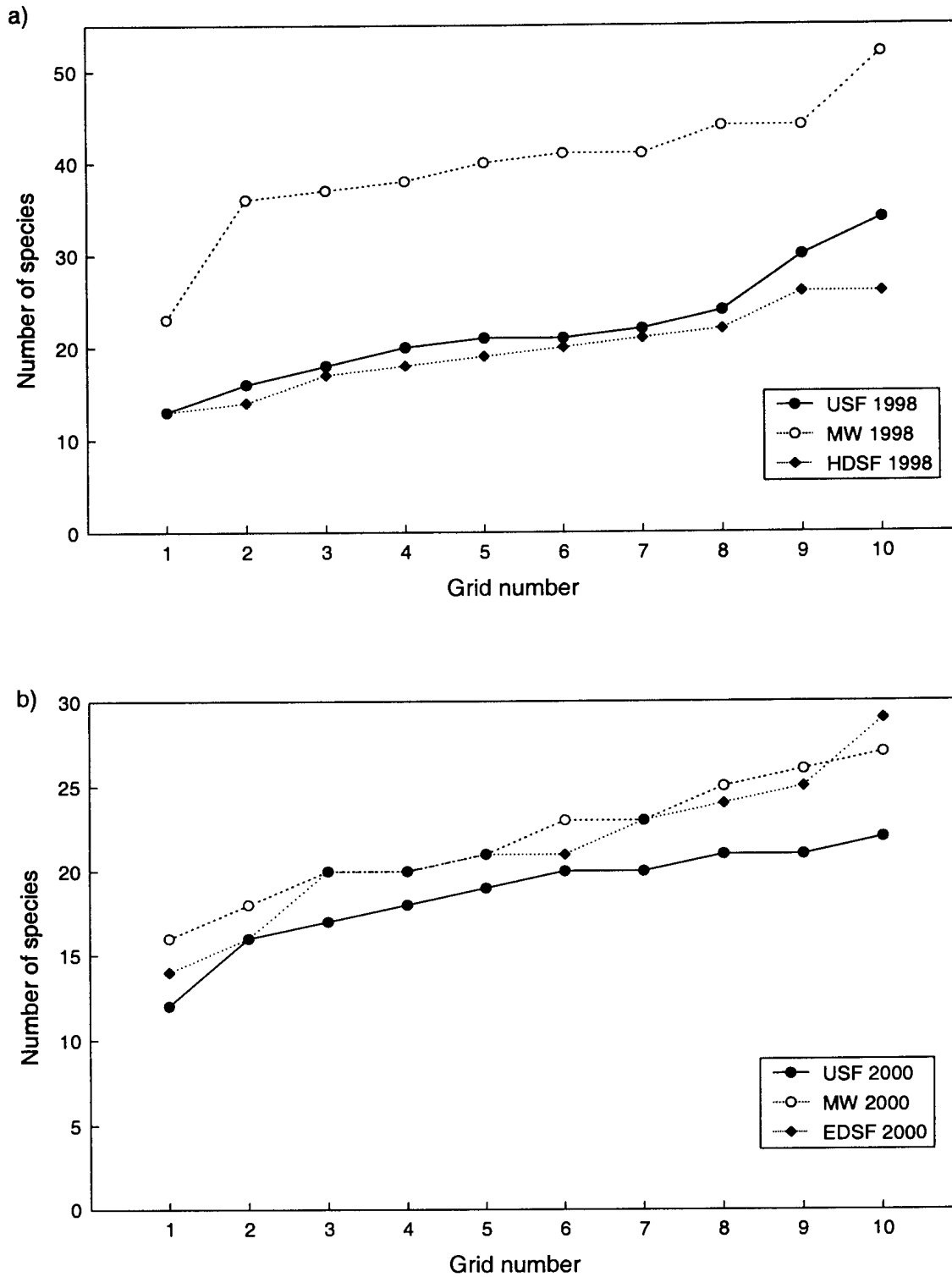


Fig. 1.4. Species accumulation curves of a) December 1998 and b) January 2000. USF = undisturbed sand forest, MW = mixed woodland, HDSF = human-disturbed sand forest, EDSF = elephant-disturbed sand forest.

Table 1.2. Dung beetle species unique to specific habitat types or sampling periods.

HDSF = human-disturbed sand forest, EDSF = elephant-disturbed sand forest.

Species	SF	HDSF	MW	SF	EDSF	MW
	1998	1998	1998	2000	2000	2000
<i>Pedaria</i> sp. IV sensu Davis				X		
<i>Copris denticulatus</i>		X				
<i>Copris</i> sp. 1		X				
<i>Onthophagus lamelliger</i>		X				
<i>Proagoderus brucei</i>		X				
<i>Catharsius harpagus</i>						X
<i>Catharsius heros</i>						X
<i>Copris urus</i> (small)						X
<i>Cyptochirus ambiguus</i>						X
<i>Drepanocerus kirbyi</i>						X
<i>Hyalonthophagus alcyonides</i>						X
<i>Neosisyphus rubrus</i>						X
<i>Proagoderus bicallosus</i>						X
<i>Scarabaeus zambesianus</i>						X
<i>Drepanocerus impressicollis</i>			X			X
<i>Gymnopleurus virens</i>			X			
<i>Liatongus militaris</i>			X			
<i>Oniticellus formosus</i>			X			
<i>Onitis deceptor</i>			X			
<i>Onitis</i> sp. 1			X			
<i>Onthophagus bicavifrons</i>			X			
<i>Onthophagus rasipennis</i>			X			
<i>Phalops flavocinctus</i>			X			
<i>Scarabaeus galenus</i>			X			

Table 1.3. Significant differences in dung beetle abundance between disturbed and undisturbed sand forest. D = dung preference, O = omnivore dung, H = herbivore dung, *U* = Mann-Whitney U test, USF = undisturbed sand forest, HDSF = human-disturbed sand forest, EDSF = elephant-disturbed sand forest. *P* is significant at the table wide α -level of 0.05 using the sequential Bonferroni technique (Rice 1989).

Species	D	Abundance		<i>U</i>	<i>P</i>	n
		mean \pm S.E.				
December 1998		USF	HDSF			
<i>Caccobius cavatus</i>	O	46.60 \pm 19.54	3.70 \pm 1.81	15.0	0.008	10
<i>Caccobius nigrutilus</i>	O	-	9.50 \pm 6.32	5.0	0.000	10
<i>Caccobius</i> sp. 1	O	61.8 \pm 22.80	1.70 \pm 1.27	6.0	0.001	10
<i>Caccobius</i> sp. 3	O	15.40 \pm 4.82	0.40 \pm 0.22	2.0	0.000	10
<i>Euonthophagus carbonarius</i>	O	0.20 \pm 0.20	8.60 \pm 4.19	8.5	0.001	10
<i>Neosisyphus fortuitus</i>	H	2.70 \pm 1.27	-	15.0	0.002	10
<i>Neosisyphus mirabilis</i>	H	6.50 \pm 2.53	-	5.0	0.000	10
<i>Oniticellus planatus</i>	H	2.40 \pm 0.93	0.50 \pm 0.40	20.0	0.015	10
<i>Onthophagus lacustris</i>	O	30.20 \pm 5.53	0.70 \pm 0.60	6.0	0.000	10
<i>Onthophagus pullus</i>	O	8.20 \pm 5.17	52.90 \pm 15.71	15.5	0.008	10
<i>Onthophagus stigmosus</i>	O	40.30 \pm 11.68	3.10 \pm 2.15	10.0	0.002	10
<i>Onthophagus sugillatus</i> sp. A	O	3.70 \pm 2.00	161.50 \pm 62.13	5.0	0.001	10
<i>Onthophagus ursinus</i>	O	6.90 \pm 4.32	26.60 \pm 7.20	18.5	0.016	10
<i>Onthophagus vinctus</i>	O	0.30 \pm 0.30	39.30 \pm 29.16	11.5	0.001	10
<i>Pachylomerus femoralis</i>	O	7.20 \pm 1.43	1.20 \pm 0.44	9.0	0.002	10
<i>Proagoderus aciculatus</i>	O	227.80 \pm 56.22	4.00 \pm 1.67	0.0	0.000	10
<i>Proagoderus dives</i>	O	91.80 \pm 23.75	11.90 \pm 3.02	14.0	0.006	10
<i>Sisyphus sordidus</i>	O	3.40 \pm 1.69	-	15.0	0.002	10
<i>Sisyphus</i> sp Y <i>sensu</i> Paschalides	O	55.80 \pm 23.86	20.70 \pm 10.99	22.5	0.037	10



Table 1.3. (continued)

January 2000		USF	HDSF			
<i>Caccobius</i> sp. 1	O	24.80 ± 5.68	2.80 ± 1.40	5.5	0.001	10
<i>Caccobius</i> sp. 3	O	1.20 ± 0.50	60.70 ± 18.44	0.0	0.000	10
<i>Euonthophagus carbonarius</i>	O	-	2.60 ± 0.88	10.0	0.001	10
<i>Neosisyphus fortuitus</i>	H	0.10 ± 0.10	3.40 ± 1.70	18.0	0.006	10
<i>Onthophagus lacustris</i>	O	38.70 ± 5.54	3.80 ± 1.34	0.0	0.001	10
<i>Onthophagus sugillatus</i> sp. B	O	15.90 ± 3.06	2.60 ± 0.99	3.5	0.001	10
<i>Onthophagus sugillatus</i> sp. C	O	5.10 ± 1.39	0.50 ± 0.22	10.0	0.002	10
<i>Proagoderus dives</i>	O	18.00 ± 4.26	76.50 ± 13.46	6.0	0.001	10
<i>Sisyphus sordidus</i>	O	1.40 ± 0.70	9.20 ± 2.03	7.5	0.001	10

Table 1.4. Number of dung beetle species shared between habitat types within sampling periods. USF = undisturbed sand forest, MW = mixed woodland, HDSF = human-disturbed sand forest, EDSF = elephant-disturbed sand forest.

Habitat	No. of species	No. shared species	% species shared
December 1998			
USF and HDSF	52	32	61.54
MW and HDSF	71	39	54.93
USF and MW	36	68	52.94
USF, MW and HDSF	77	31	40.26
January 2000			
USF and EDSF	44	32	72.73
MW and EDSF	49	34	69.39
USF and MW	54	27	50.00
USF, MW and HDSF	52	26	50.00

Table 1.5. Analysis of similarity between the different habitat types across sampling periods. *R* = Global *R*-statistic (Clarke 1993), USF = undisturbed sand forest, MW = mixed woodland, HDSF = human-disturbed sand forest and EDSF = elephant-disturbed sand forest. *P* is significant at the table wide α -level of 0.05 using the sequential Bonferroni technique (Rice 1989).

Habitats	<i>R</i>	<i>P</i> <
MW 1998 vs. MW 2000	0.997	0.001
MW 1998 vs. USF 2000	1.000	0.001
MW 1998 vs. EDSF 2000	0.994	0.001
USF 1998 vs. MW 2000	0.987	0.001
USF 1998 vs. USF 2000	0.676	0.001
USF 1998 vs. EDSF 2000	0.904	0.001
HDSF 1998 vs. MW 2000	0.952	0.001
HDSF 1998 vs. USF 2000	0.891	0.001
HDSF 1998 vs. EDSF 2000	0.921	0.001

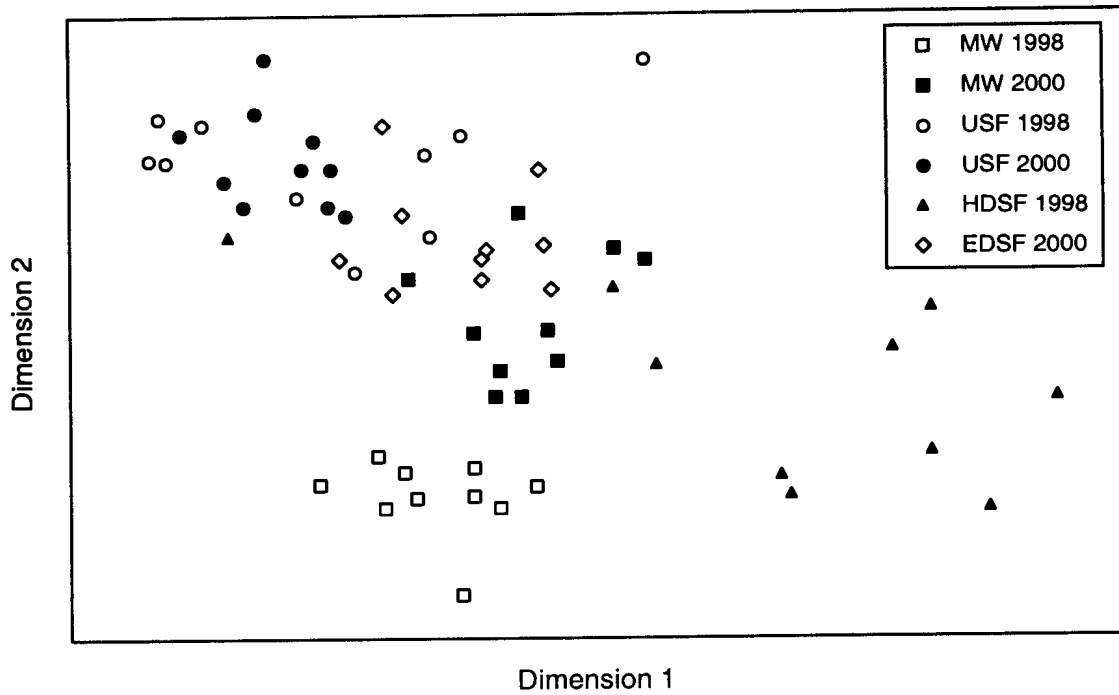


Fig. 1.5. Non-metric MDS ordination of dung beetle assemblages sampled during December 1998 and January 2000. MW = mixed woodland, USF = undisturbed sand forest, HDSF = human-disturbed sand forest, EDSF = elephant-disturbed sand forest.

DISCUSSION

This study confirmed that dung beetle assemblages in sand forest and mixed woodland differ considerably. Van Rensburg *et al.* (1999) first quantified this heterogeneity between dung beetle assemblages in the two habitat types and attributed it to differences in vegetation structure between the habitat types (see Van Rensburg *et al.* 2000). Vegetation structure can have pronounced effects on dung beetle assemblage structure and the dense vegetation of the sand forest may impede flight maneuverability and searching success of dung beetles (Nealis 1977; Doube 1983; Klein 1989; Steenkamp & Chown 1996). Dung beetles also show preference for habitats with particular light intensities (Doube 1983). The light intensity in the dense sand forest is lower than in the more open mixed woodland. It is thus not surprising that species richness and abundance was lower in sand forest than in the more open mixed woodland, or that the mixed woodland supported more habitat-specific species.

Thirty-two percent fewer species (25 % reduction in number of genera) and 69 % fewer individuals were collected in January 2000 than in December 1998. This difference in species richness and abundance between sampling periods is likely to be a result of differences in weather conditions during sampling periods. In December 1998 sampling was conducted during a period when dung beetle activity was high, i.e. shortly after rainfall during mid-summer (see Doube 1987). In January 2000 sampling was conducted on dry, semi-overcast days and during a period of high rainfall. Nonetheless, within sample period comparisons remain valid. In addition, in spite of differences between sampling periods, dung beetle assemblages in sand forest of the two periods remained more similar to each other than to the other habitat types.

Dung beetle assemblages were different in all the habitat types and disturbance caused by humans and elephants resulted in dung beetle assemblages being unique in these disturbed habitats. Dung beetle assemblages in human-disturbed sand forest were marginally more similar to those in undisturbed sand forest, but clear differences in assemblage structure still existed. Although most dung beetle species are able to utilize a wide variety of resource types (Gordon & Cartwright 1974), differences in dung beetle assemblage structure between human-disturbed and undisturbed sand forests may be attributed to differences in the dung type available and the distribution thereof in these

habitats. Within Tembe large herbivores can move freely through the reserve and dung is distributed more randomly than in the disturbed areas, while humans and their livestock occur in medium to high concentrations in the disturbed sand forest. This causes increased resource quantity, especially of omnivore (human) dung, within human-disturbed areas. An increase in resource availability can cause dung beetle assemblage structure to change by either increased abundances of the species within the assemblage or by an increase in species richness (Hanski & Cambefort 1991; Lumaret *et al.* 1992). Similar to the results found here Peck and Forsyth (1982) found that a different, smaller and less species rich dung beetle assemblage associated with human activities becomes established with the introduction of humans and their livestock into an area. The presence of human dung in disturbed sand forest increased the species richness of dung beetles preferring omnivore dung. However, the abundance of only a small proportion (18 %) of these omnivore specialist species increased. Nonetheless, the combined effect of higher resource availability and the presence of human dung in the disturbed sand forest may explain the differences in the dung beetle assemblage structure between the undisturbed and human-disturbed habitats.

Within Tembe, elephant-induced disturbance to sand forest also resulted in a change in dung beetle assemblage structure. Dung beetle assemblages in the elephant-disturbed sand forest were more similar to mixed woodland assemblages than to those in undisturbed sand forest. As previously mentioned, the dense sand forest vegetation may impede flight maneuverability and searching success of dung beetles (Nealis 1977; Doube 1983; Klein 1989; Steenkamp & Chown 1996). The sand forest vegetation opens and the light intensity increases as a result of elephants foraging and moving through this habitat type (Van Rensburg *et al.* 1999). Dung beetles will thus be able to move more freely through the elephant-disturbed areas and will have a higher success in finding resources because the vegetation within disturbed areas will be less dense than in undisturbed areas. Resource availability and quantity will also increase in elephant-disturbed areas compared to undisturbed sand forest because of the presence of these large herbivores in the habitat. Therefore, the abundances of dung beetles may increase because of this higher resource availability in elephant-disturbed areas (Hanski & Cambefort 1991; Lumaret *et al.* 1992) and this may contribute to the assemblages in elephant-disturbed sand forest being more similar to mixed woodland assemblages than to those in undisturbed sand forest.

Although significant differences existed between undisturbed- and disturbed sand forest sites these habitats shared the highest proportion of species during both sampling periods. This is likely to be a result of remaining similarities in habitat structures of undisturbed and disturbed sand forests. Humans and elephants alter the sand forest vegetation structure, but areas of intact sand forest still exist and the habitat structure will thus predominantly be that of sand forest. Also, disturbed sand forest remains recognizable as sand forest by its plant species composition and broader scale patch structure. A higher proportion of dung beetle species was shared between habitat types in January 2000 than in December 1998. This may be a result of a higher proportion of rare and transient species sampled in December 1998 (because of the much higher species richness during this sampling period), which could result in a lower proportion of species shared between habitats.

In conclusion, this study indicates that the impact of human- and elephant-induced disturbance on sand forest dung beetle assemblages may have significant implications for other taxa that occupy this endangered habitat type. Sand forest has the highest plant diversity, as well as the highest proportion of endemic plant species in the Maputland Centre of Endemism (MC), and many of the MC's endemic vertebrate species are also restricted to this habitat type (Van Wyk 1996). Given the unidirectional change of sand forest vegetation structure to that of mixed woodland (Van Rensburg *et al.* 1999) and the severe impacts of human- and elephant-induced disturbance on dung beetle assemblage structure in sand forest, it is likely that these endemic taxa may also be threatened. Monitoring of the impacts of large herbivores, like elephants, on sand forest are currently being undertaken in Tembe (Matthews pers. comm.) and it is imperative that it should be continued. Such monitoring could assist in the difficult conservation decisions surrounding the manipulation of elephant population size in this reserve where a conservation conflict is developing.

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CHAPTER 2

Testing an ecological bioindicator system using dung beetle (Coleoptera: Scarabaeidae) assemblages in northern KwaZulu-Natal, South Africa.

INTRODUCTION

A biological indicator (or bioindicator) is defined as a species, or a group of species, which reflects the state of the environment and the impact of environmental change on a habitat, ecosystem or a community (McGeoch 1998). Aquatic macroinvertebrate assemblage structure and composition has long and successfully been used as bioindicators for monitoring the ecological state of ecosystems (Hellawell 1978; Savage 1982; Weatherley & Ormerod 1990; Spellerberg 1991; Chessman 1995; Learner & Chawner 1998). For example, in South Africa, dragonflies have been used to monitor biotope quality and the effects of anthropogenic disturbance on river systems (Clark & Samways 1996; Samways & Steytler 1996; Stewart & Samways 1998). However, the use of terrestrial invertebrates as bioindicators is faced with a number of difficulties. Terrestrial ecosystems are much more variable and more complex with a higher species richness than aquatic ecosystems and it is more difficult to quantify abiotic factors, such as air pollution, in terrestrial systems (Steele 1991; Lawton & Gaston 2001). Nonetheless, a diverse array of terrestrial invertebrate taxa have been used as bioindicators. Examples of these include spiders (Klimes 1987; Churchill 1997), springtails (Greenslade & Greenslade 1987; Van Straalen & Verhoef 1997), cicadas (Milton & Dean 1992), flies (Parsons 1991), grasshoppers (Fisher *et al.* 1997; Samways 1997), butterflies (Brown 1991; Kremen 1992; Pollard & Yates 1993; Hill 1999), moths (McGeoch & Chown 1997; Kitching *et al.* 2000), beetles (Stork 1990; Halffter & Favila 1993; Rodríguez *et al.* 1998; Van Rensburg *et al.* 1999), ants (Majer 1983; Andersen 1997a, b; Majer & Nichols 1998) and bees (Tschamtkke *et al.* 1998).

All of the above mentioned taxa have been argued to be good bioindicators, although such claims are questioned on the basis that the robustness of the proposed bioindicators were not tested (Landres *et al.* 1988; New 1993; Lawton *et al.* 1998; McGeoch 1998; Hilty & Merenlender 2000). Specific criteria for the selection of indicator species or taxon groups listed and discussed in the literature (Noss 1990; Pearson & Cassola 1992; Pearson 1994; McGeoch 1998; Hilty & Merenlender 2000) are met in these studies. However, indicator taxon responses (changes in species abundance, richness and composition in relation to disturbance such as land-use) must also be interpreted correctly (Andersen 1999). It is thus important to distinguish between natural variability in assemblage structure and responses to anthropogenic disturbance (Hellawell 1991; Welsh & Ollivier 1998). The robustness of selected bioindicator species must be tested using independent data sets collected in the same environment at multiple temporal and spatial scales to determine the reliability with which these species can be implemented in monitoring programs (Weaver 1995; Majer & Nichols 1998; McGeoch 1998; Lawton & Gaston 2001). To date, few studies have tested the adequacy of bioindicators in this way (e.g. Rodríguez *et al.* 1998; Jones & Eggleton 2000; Rösch *et al.* 2001).

Therefore, the aim of this study was to test a suite of dung beetle indicator species identified in a previous study by Van Rensburg *et al.* (1999). These indicator species are representative of sand forest or mixed woodland habitats in Tembe Elephant Park, South Africa and should thus have high specificity (uniqueness to a particular habitat type) and fidelity (frequency within that habitat type) for the habitat type it is representative of. Sand forest is an endangered habitat type that contains a large proportion of endemic plant and vertebrate species (Van Wyk 1996; Van Rensburg *et al.* 2000a). However, only a small proportion of sand forest is protected in four reserves in South Africa, namely Tembe Elephant Park (3,020 ha out of 30,079), Sileza Nature Reserve (25 ha out of 2,500), Mkuzi Game Reserve (1,500 ha out of 29,000) and a few patches in Falsebay Park. Outside of these protected areas sand forest is under threat due to extensive deforestation, clearing for agriculture and use for firewood (Davis *et al.* 1994; Cole & Landres 1996; Matthews *et al.* 1999). When disturbed, the sand forest vegetation structure

opens up and changes to that of mixed woodland. No reversion to the original sand forest structure has been recorded to date (Van Rensburg *et al.* 1999).

In addition to indicator species, Van Rensburg *et al.* (1999) therefore also identified 'detector species', i.e. species that can be used to monitor changes in sand forest. These detector species are dung beetle species with a lower degree of habitat specificity than the highly specific indicator species. They argued that these species would move to adjacent habitats more rapidly under changing habitat conditions than highly habitat specific or generalist species. These detector species would invade sand forest in the early stages of its conversion to mixed woodland (Van Rensburg *et al.* 1999). Detector species will thus be useful in monitoring sand forest for disturbance and act as detectors of change in habitat state from sand forest to mixed woodland (McGeoch *et al.* in press).

The dung beetle assemblage data set collected by Van Rensburg *et al.* (1999) was not biased by inter-seasonal abundance changes because it included data collected across the full seasonal spectrum. The selection of the initial set of dung beetle indicator species was thus based on temporally representative data and are more likely to be robust indicators of a particular habitat type (McGeoch *et al.* in press). However, assemblage data collected within a particular season may be less reliable. It has been shown that dung beetles are sensitive to changes in weather conditions within a season and that significant fluctuations in their abundances occur between seasons (Doube 1987). It is thus important that the collection of dung beetle assemblage data for bioindication must take place during periods of high abundance and activity because the indicator value of species could be misinterpreted due to intra-seasonal species activity and abundance changes.

McGeoch *et al.* (in press) tested the dung beetle indicator and detector species identified by van Rensburg *et al.* (1999) on an independent data set collected in Tembe. Their results largely supported the suite of 11 dung beetle indicator species of which three species were indicators of sand forest and eight of mixed woodland. Two of these species (one each in mixed woodland and sand forest) were discarded as indicators and the suite of indicator species was thus refined. They also tested the responses of the detector species to habitat disturbance by including data collected from a human-

disturbed sand forest adjacent to the reserve. One third of the detector species (four species out of a total of 11 species) responded as predicted, i.e. these species were better indicators of disturbed than undisturbed sand forest. Two of the detector species identified by Van Rensburg *et al.* (1999) were also characteristic (indicator) species of disturbed sand forest.

The consistency and reliability of the dung beetle indicator and detector species identified by Van Rensburg *et al.* (1999), and tested by McGeoch *et al.* (in press) was tested once more in this study. Such repeated testing has been advocated to test the reliability with which indicator taxa can be implemented in monitoring programs (Weaver 1995; Majer & Nichols 1998; McGeoch 1998; Lawton & Gaston 2001). Confidence intervals for the indicator values of each species were calculated whereby the reliability of these species was established. The effect of dung beetle abundance differences between sampling periods on the specificity of the species to a habitat type, and fidelity (frequency of occurrence within a specific habitat) of the species was also examined.

The data set used here to test these indicator and detector species included data collected from elephant-disturbed sand forest inside of the reserve. Elephants tend to prefer plant species growing in mixed woodland, but the high densities of these animals in the reserve are resulting in increased utilization of sand forest (Van Rensburg *et al.* 1999). The aim here was to test the responses of the detector species identified by Van Rensburg *et al.* (1999) to elephant disturbance in sand forest. It was also determined whether the same species respond as predicted (i.e. are better indicators of disturbed than of undisturbed sand forest) to elephant disturbance in sand forest than those detectors that responded to human-disturbed sand forest (McGeoch *et al.* in press). Several questions were addressed to test the robustness of the species predicted to act as indicators of sand forest and mixed woodland in Tembe Elephant Park and detectors of habitat change from sand forest to mixed woodland. First, are the indicator species identified for sand forest and mixed woodland habitats (Van Rensburg *et al.* 1999) reliable and consistent between sampling periods? Second, is the specificity and fidelity of species to a particular habitat type affected by differences in species abundance between sampling periods? Third, do the species predicted to indicate habitat change in sand forest respond as predicted, and

do the same species respond to elephant disturbance than to human disturbance in sand forest?

MATERIAL AND METHODS

Sampling and species identification

Dung beetles were sampled during January 2000 (a period of high dung beetle activity, see Doube 1987), in Tembe Elephant Park (27°01'S 32°24'E) (hereafter Tembe) in Northern KwaZulu-Natal, South Africa on the southern Mozambique Coastal Plain. The same sampling regime as that of Van Rensburg *et al.* (1999) and McGeoch *et al.* (in press) was used, but different areas of the Park were sampled (see Fig. 1.3). The dung beetles were sampled during a period when beetle activity is known to be high (early to mid summer, shortly after rainfall; see Doube 1987). Two undisturbed sand forest and two mixed woodland sites were sampled inside of Tembe. The undisturbed sand forest areas were sampled inside the botanical reserve to exclude disturbance caused by elephants. Two elephant-disturbed sand forest areas were sampled additionally inside of the reserve. Elephant-disturbed sand forest was identified as areas that showed evidence of elephant activity such as trees and shrubs that were removed by these large herbivores and the sand forest canopy was opened up.

Five grids of six pitfall traps each were placed in each area. The pitfalls were placed in a 2 x 3 design on a 2 m x 4 m grid. The traps were baited using 50 g elephant dung and set out for 24 hours. Sampling grids were placed a minimum of 200 m apart in each area to maintain sampling independence. The dung beetles collected were identified by comparison with identified specimens in the South African National Insect Collection and with the help of Dr A. Davis (pers. comm.).

The sampling effort in this study was the same as in the 1998 sampling period (McGeoch *et al.* in press), but only one twelfth of the 1995/96 sampling period (Van Rensburg *et al.* 1999). The study areas used during the latter sampling period (two sand forest and two mixed woodland areas) were sampled bimonthly over a period of twelve months. Each site was thus sampled six times over the twelve-month period. Pitfall traps

were set for 48 h and rebaited with the first collection after 24 hours and the second collection at 48 hours. The 1995/96 data set can therefore be regarded as a reference data set for the selection of indicator species because species richness reached an asymptote during this yearlong sampling period (see Van Rensburg *et al.* 2000b). Although the sampling effort was only one twelfth of that of the 1995/96 sampling period, McGeoch *et al.* (in press) argued that a single sample taken during peak dung beetle abundance was sufficient to test the dung beetle indicator species because the majority of species are active and present in sufficient numbers during these periods (see Doube 1983).

Data analysis

The number of individuals of each species sampled was summed for each sampling grid. The mean species richness and abundance of the dung beetles were calculated across sampling grids for each of the habitat types (mixed woodland, undisturbed and elephant-sand forest) and compared to that found by Van Rensburg *et al.* (1999) and McGeoch *et al.* (in press) using Analysis of Variance. Tukey HSD tests were used to determine which of the dung beetle assemblages were significantly different from each other in terms of their mean species richness and abundance.

Indicator values and species

Dufrêne and Legendre's (1997) Indicator Value Method was used to identify characteristic dung beetle species (i.e. indicator species) for each habitat type (see McGeoch & Chown 1998 for evaluation of this method). Using this method, measures of specificity (uniqueness to a particular habitat) and fidelity (frequency within that particular habitat type) are combined independently for each dung beetle species. An *Indicator Value (IndVal)* is then provided, as a percentage, for each species. The specificity measure can be calculated as:

$$A_{ij} = N_{individuals_{ij}}/N_{individuals_i}$$

where $N_{individuals_{ij}}$ is the mean number of species i across sites of group j , and $N_{individuals_i}$ is the sum of the mean numbers of individuals of species i over all groups.

The fidelity measure is calculated as:

$$B_{ij} = N_{sites_{ij}}/N_{sites_j}$$

where $N_{sites_{ij}}$ is the number of sites in habitat j where species i is present, and N_{sites_j} is the total number of sites in that habitat. The indicator value for species i in habitat j is then calculated as the product of the specificity and fidelity measures:

$$IndVal_{ij} = A_{ij} \times B_{ij} \times 100$$

IndVal analyses were conducted for the mixed woodland versus sand forest habitats sampled in January 2000 and the significance of the *IndVal* measures for each species were tested using a random reallocation procedure of sites among site groups (Duf rene & Legendre 1997). Species with significant *IndVals* of greater than 70 % (subjective benchmark, see Van Rensburg *et al.* 1999; McGeoch *et al.* in press) were then regarded as indicator species for that particular habitat.

The number and identity of indicator species found in this study were then compared to that found by Van Rensburg *et al.* (1999) because they selected indicator species based on a temporally representative data set. Dung beetle abundance is sensitive to inter-seasonal fluctuations in weather conditions (Doubt 1987) and by using a data set collected across the full seasonal spectrum, the selection of indicator species was not biased by fluctuations in species abundance caused by inter-seasonal changes (Davis 1997). An asymptote to species richness was also reached over the year long sampling period (Van Rensburg *et al.* 2000b) and this data set can thus be regarded as representative for the area. Only species collected during all three sampling periods (May 1995 – April 1996, Van Rensburg *et al.* (1999); December 1998, McGeoch *et al.* (in press); January 2000) were included in the following analyses. To determine which of the species had mean *IndVals* significantly greater than 70 % (subjective benchmark, see Van

Rensburg *et al.* 1999; McGeoch *et al.* in press) across all three sampling periods, t-tests were used (Bulmer 1979). Confidence intervals were also calculated for each of the indicator species. Simple linear regressions (with arcsine transformation of values, see Collett 1991; Crawley 1993) were used to determine the relationship between the *IndVals* of species in sand forest and mixed woodland in the three sampling periods, as well as between the *IndVals* of species and the change in their *IndVals* between sampling periods. Simple linear regression was also used to examine the relationship between means and variances of the *IndVals*, which was calculated for each species from their *IndVals* for the three sampling periods ($n = 3$). These analyses were conducted to determine how consistent the *IndVals* of the species were across sampling periods and the predictability of the *IndVal* of a species was therefore determined.

Thereafter the relationships between the fidelity and specificity components of the *IndVals* of all the species collected in the different habitats (i.e. human-disturbed sand forest December 1998, elephant-disturbed sand forest January 2000, and undisturbed sand forest and mixed woodland areas sampled in all three sampling periods) and their abundances were examined across habitat types and sampling periods using generalized linear models (McCullagh & Nelder 1989; Collett 1991). This was done to determine whether the fidelity and specificity of a species to a particular habitat type, and therefore the *IndVal* of the species in that habitat type, will be affected by fluctuations in its abundance.

Detector species

Detector species (i.e. species predicted to act as detectors of a change in habitat from sand forest to mixed woodland) were identified as species with *IndVals* between 5 % and < 50 % for sand forest and between 50 % and < 70 % for mixed woodland (see Van Rensburg *et al.* 1999; McGeoch *et al.* in press). Van Rensburg *et al.* (1999) argued that the selection of potential detector species in this way is warranted for two reasons. First, habitat specific species (i.e. species with *IndVals* > 70 %) are unlikely to move to other habitat types under changing conditions within their preferred habitat. These habitat specific species need thus only be monitored in the habitat to which they are specific.

Second, species with low specificity to a habitat type (generalists) are unlikely to respond rapidly to changes in the habitat they occur in. Therefore, species with some degree of habitat preference (i.e. species with *IndVals* of between 50 and 70 % in mixed woodland and between 5 and 50 % in sand forest) are selected as potential detector species because they are more likely to invade sand forest in its early stages of change to mixed woodland. The reliability of these detector species as indicators of the change from sand forest to mixed woodland as a result of elephant disturbance was tested by conducting habitat comparisons using *IndVals* calculated from 1) mixed woodland and sand forest 1995/96 and elephant-disturbed sand forest 2000, and 2) mixed woodland, sand forest and elephant-disturbed sand forest 2000. As predicted by McGeoch *et al.* (in press), these detector species would, first, be better indicators of disturbed than of undisturbed sand forest, and second, their *IndVals* for elephant-disturbed sand forest would be larger than for undisturbed sand forest in the combined analyses above.

RESULTS

A total of 52 species representing 18 genera were collected during January 2000 in Tembe. During the latter sampling period, 31 % fewer species were collected in mixed woodland and 25 % fewer species in sand forest compared to the 1995/96 sampling period of Van Rensburg *et al.* (1999). The total number of individuals collected during January 2000 was 74 % less in sand forest and 66 % less in mixed woodland compared to the number of individuals collected during the 1995/96 sampling period (Table 2.1). Mean species richness was significantly higher in mixed woodland in the 1995/96 and 1998 sampling periods than in the rest of the habitats and sampling periods (Table 2.1). No significant differences existed in mean species richness between undisturbed and disturbed sand forest areas (Table 2.1). Mean dung beetle abundance was significantly highest in the mixed woodland habitat sampled in 1998 (Table 2.1). Mean abundance also differed significantly between the sand forest areas sampled in 1995/96 and 1998 (Table 2.1). Disturbed and undisturbed sand forest areas did not differ significantly in mean beetle abundance within sampling periods (Table 2.1).

In January 2000, only one species was collected in sand forest that had not been collected in previous sampling periods in this habitat type (1995/96, Van Rensburg *et al.* 1999; December 1998, McGeoch *et al.* 1998), namely *Pedaria* sp. IV *sensu* Davis. Ten such species were collected in mixed woodland. No species specific to elephant-disturbed sand forest were collected. One species specific to mixed woodland (*Drepanocerus impressicollis*) was collected. This species occurred only in mixed woodland and was sampled across all three sampling periods. No such species were collected for sand forest.

Table 2.1. Species richness and abundance of dung beetles collected from each habitat and sampling period. *n* = number of sample grids, *S* = total richness, *N* = total abundance. Different letters associated with each mean in each column denote significant differences between means of $P < 0.05$.

Habitat and sample	Richness Mean ± S.E. $F_{7,72} = 24.75$ $P < 0.001$	Abundance Mean ± S.E. $F_{7,72} = 16.16$ $P < 0.001$	<i>n</i>	<i>S</i>	<i>N</i>
Mixed woodland					
1995/96	35.10 ± 1.73 a	1239.00 ± 148.88 b	10	64	12390
December 1998	39.60 ± 2.35 a	1886.80 ± 257.70 a	10	65	18863
January 2000	21.90 ± 1.12 b	421.30 ± 45.42 cd	10	44	4213
Sand forest					
1995/96	22.10 ± 1.14 b	839.40 ± 102.75 c	10	49	8394
December 1998	22.40 ± 1.69 b	675.90 ± 110.04 bcd	10	39	6759
January 2000	18.60 ± 0.95 b	222.70 ± 25.70 d	10	37	2227
Disturbed sand forest					
December 1998 (human-disturbed)	19.60 ± 1.39 b	543.20 ± 187.73 cd	10	45	5432
January 2000 (elephant-disturbed)	21.30 ± 1.37 b	317.80 ± 58.02 cd	10	39	3178

Indicator values and species

Twenty-four dung beetle species were collected in sand forest and 31 species in mixed woodland that occurred in all three sampling periods (i.e. 1995/96, December 1998 and January 2000). This constitutes 35 % and 40 % respectively of the total number of species collected within each habitat type across the three sampling periods. More species had *IndVals* of > 70 % in the sand forest (Fig. 2.1a) and mixed woodland (Fig. 2.1b) sampled in 1998 and 2000 than in those habitats sampled in 1995/96. Significant positive relationships existed between the *IndVals* of the dung beetle species sampled in 1995/96 and 2000 (sand forest: $F_{1,22} = 10.149$, $P < 0.004$, $R^2 = 0.316$; mixed woodland: $F_{1,29} = 5.196$, $P < 0.030$, $R^2 = 0.152$). However, only between 15 and 32 % of the variance in the *IndVals* of the species was explained by these relationships, and the *IndVal* of a species in 1995/95 was thus a poor predictor of its *IndVal* in the 2000 sampling period.

The relationship between the *IndVals* of the species in January 2000 and the change in *IndVal* between 1995/96 and 2000 was not significant in sand forest (Fig. 2.2a). However, the *IndVals* of the species in January 2000 and the change in *IndVal* between the 1998 and 2000 sampling periods showed a significant positive relationship in this habitat type (Fig. 2.2a). No significant relationships were found between the *IndVals* of species in January 2000 and the *IndVal* changes between the 1995/96 and 2000 sampling periods in mixed woodland (Fig. 2.3a), nor between the *IndVals* of species in January 2000 and the *IndVal* changes between the 1998 and 2000 sampling periods (Fig. 2.3b). The relationship between the mean *IndVals* of species and their variances were not significant for sand forest (Fig. 2.4a) or mixed woodland (Fig. 2.4b) assemblages. In both habitats *IndVals* between approximately 20 and 70 % were more variable than very low and high *IndVals* (Fig. 2.4 a, b).

Most of the species identified as indicators by Van Rensburg *et al.* (1999) in 1995/96 reappeared as indicators in January 2000 (Table 2.2). Four species had mean *IndVals* of less than 70 % across the three sampling periods in mixed woodland (Table 2.2). These species were *Proagoderus aciculatus* in sand forest, and *Metacatharsius pseudoopacus*, *Copris inhalatus* spp. *sanctaluciaae* and *Pedaria* sp. IV *sensu* Davis in

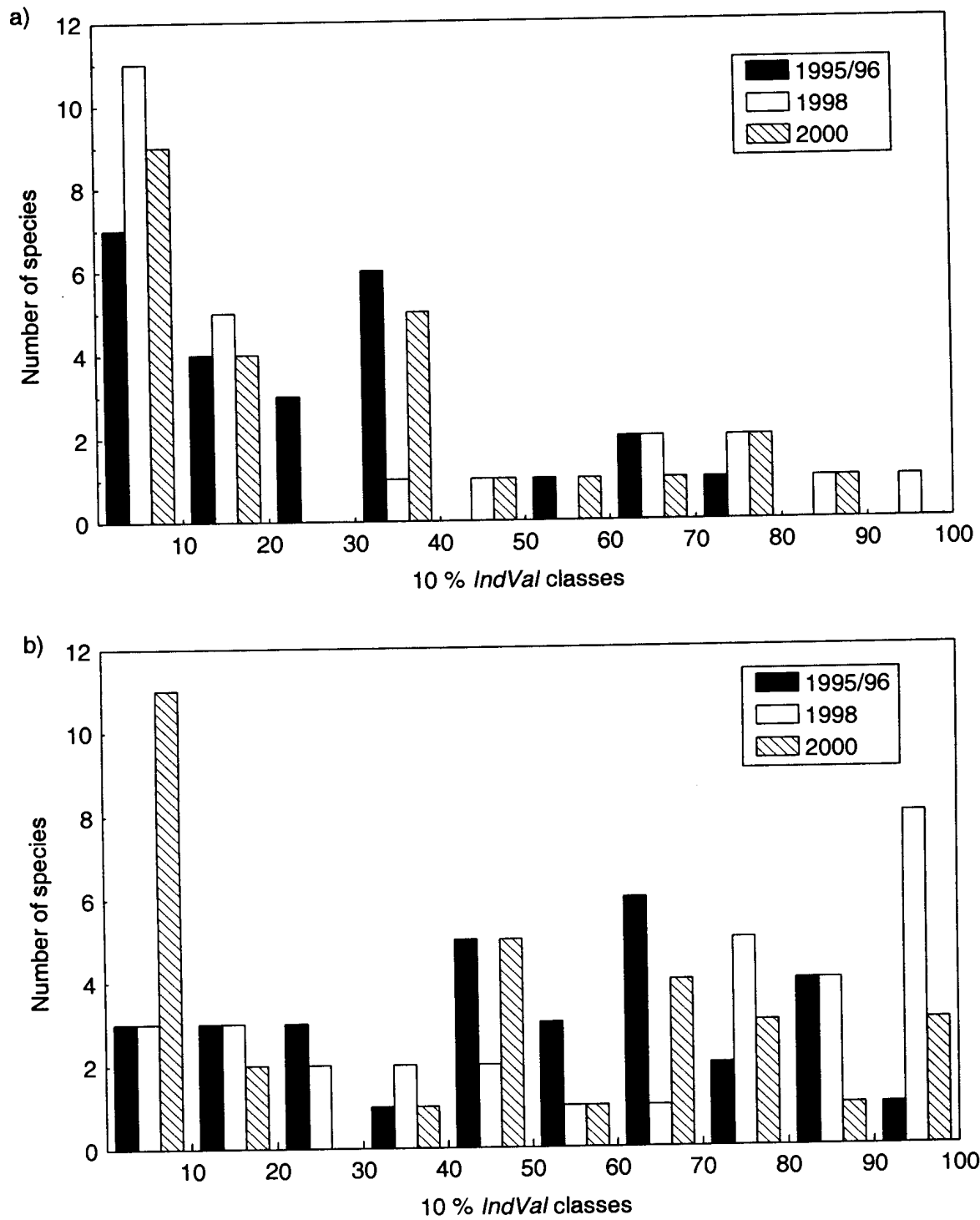


Fig. 2.1. The number of species in a) sand forest and b) mixed woodland within 10 % Indicator Value (% *IndVal*) classes. Only species sampled during all three study periods within each habitat type were included.

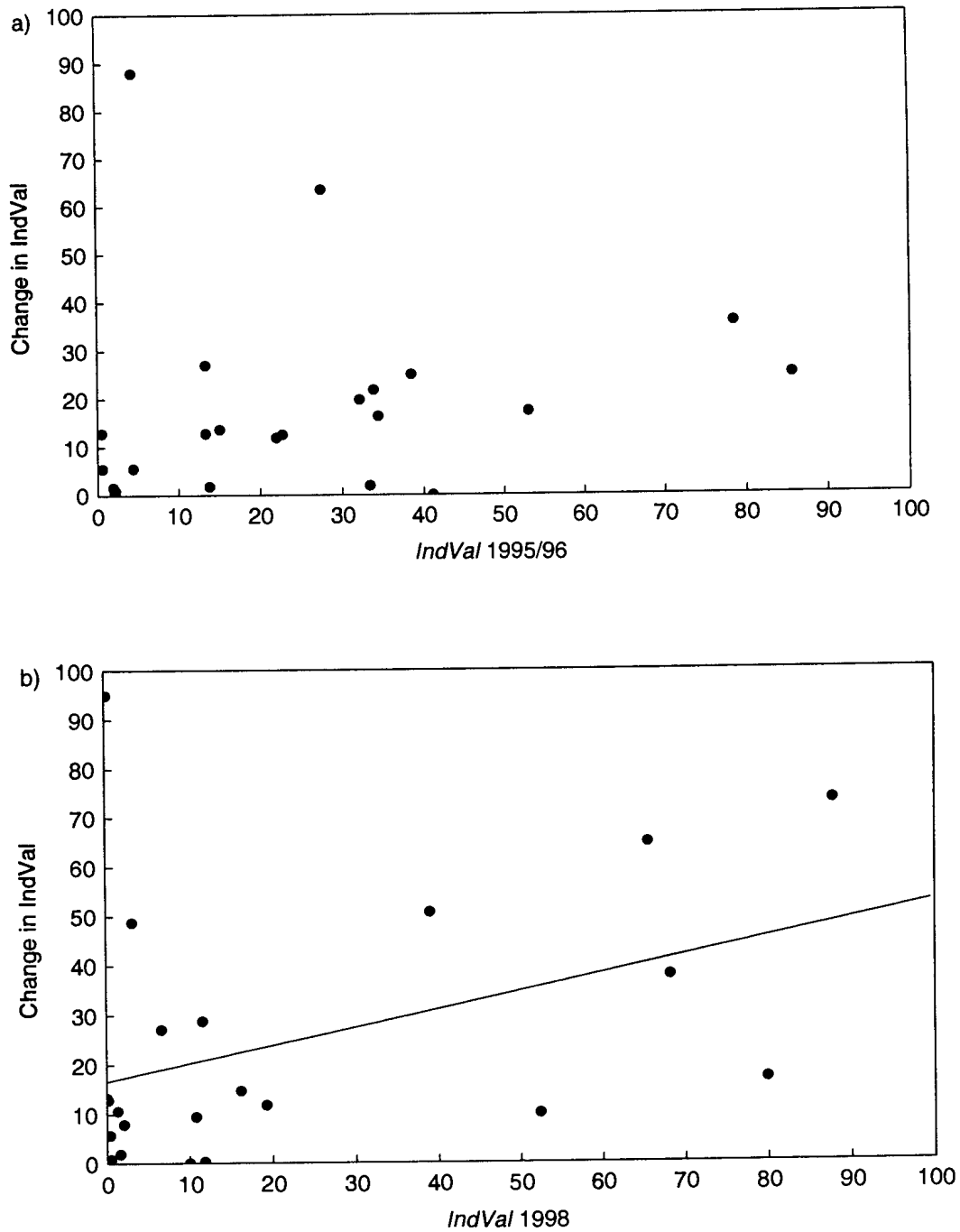


Fig. 2.2. The relationship between Indicator Values (% *IndVal*) and the change in Indicator Values of dung beetles in sand forest between years: a) 1995/96 to 2000 ($F_{1,22} = 0.532$, $P < 0.473$, $R^2 = 0.024$), b) 1998 to 2000 ($F_{1,22} = 4.328$, $P < 0.049$, $R^2 = 0.164$).

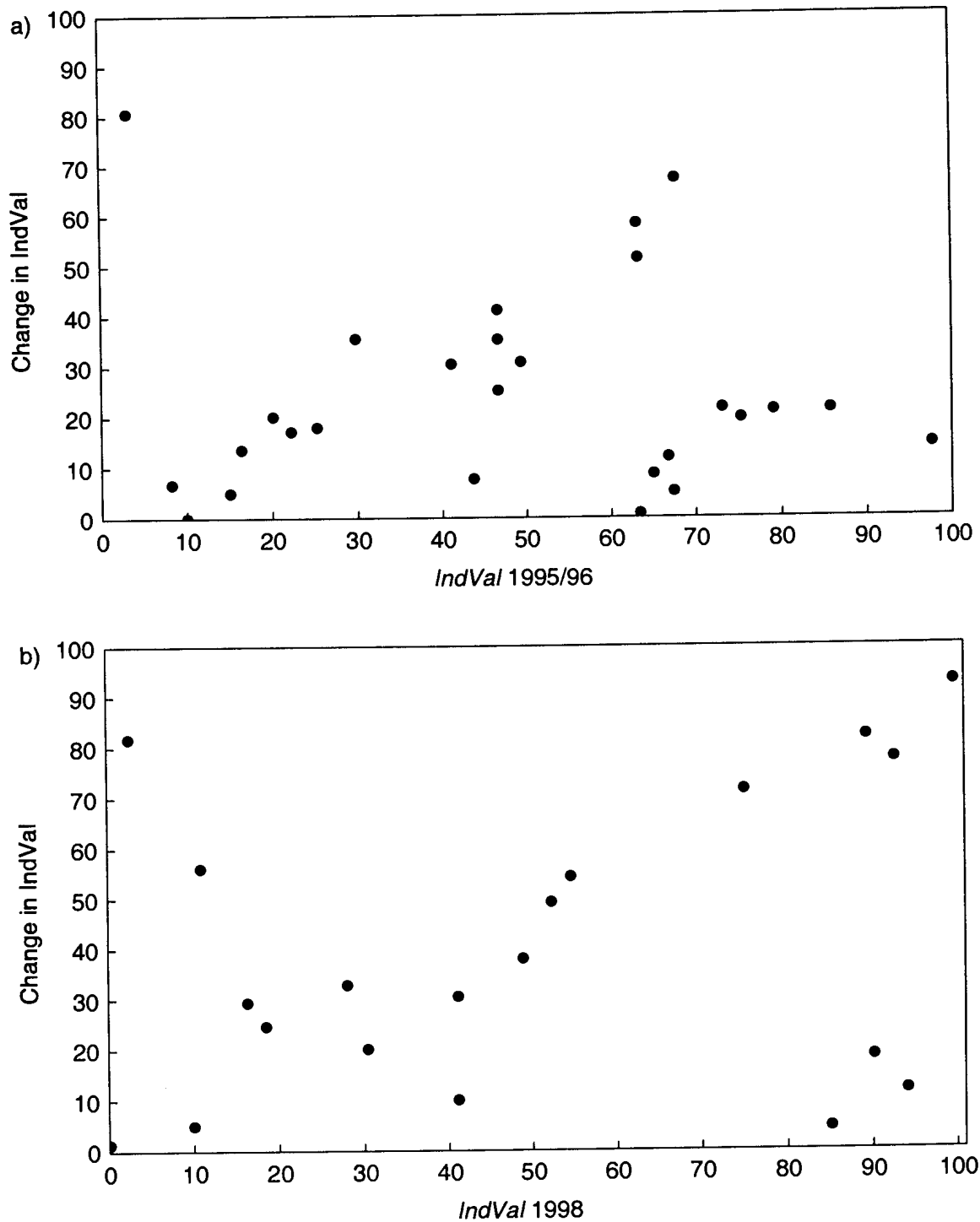


Fig. 2.3. The relationship between Indicator Values (% *IndVal*) and the change in Indicator Values of dung beetles in mixed woodland between years: a) 1995/96 to 2000 ($F_{1,29} = 1.064$, $P < 0.311$, $R^2 = 0.035$), b) 1998 to 2000 ($F_{1,29} = 2.726$, $P < 0.110$, $R^2 = 0.086$).

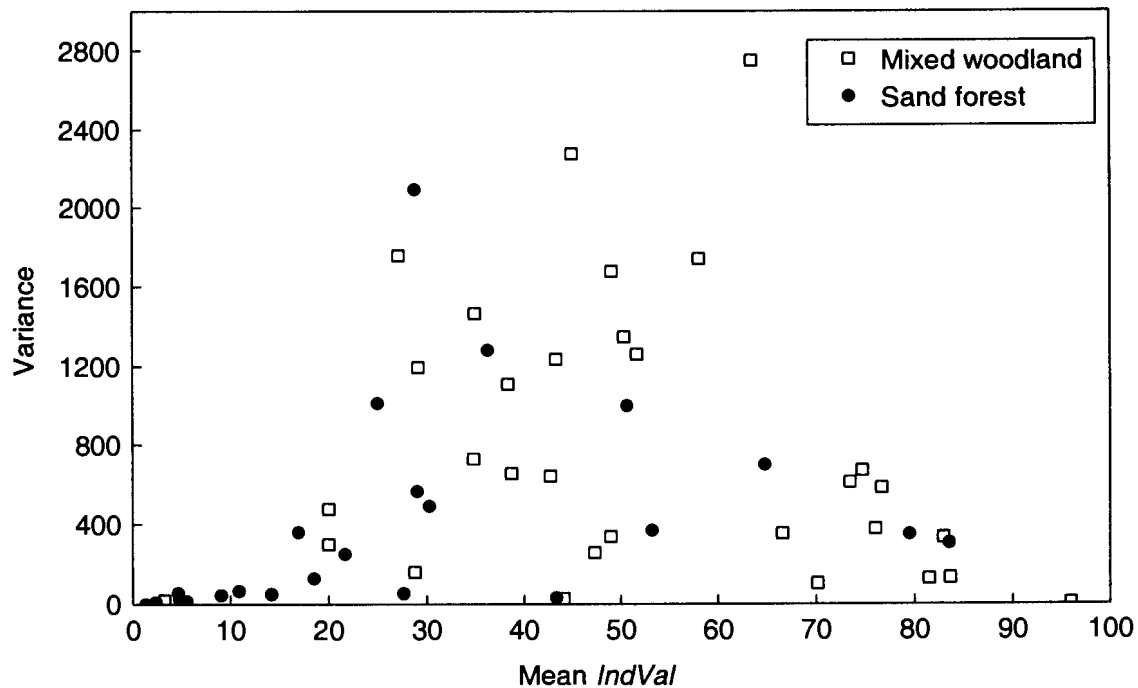


Fig. 2.4. The relationship between mean indicator values (*IndVals*) and their variances across the three sampling periods for sand forest ($F_{1,22} = 2.771$, $P < 0.110$, $R^2 = 0.112$) and mixed woodland ($F_{1,29} = 0.751$, $P < 0.393$, $R^2 = 0.025$).

mixed woodland (Table 2.2). The most reliable indicator species across the three sampling periods was *Sisyphus sordidus* in mixed woodland, which had the highest mean *IndVal* across the sampling periods and the lowest standard error of the mean (Table 2.2). This was also the only indicator species with an *IndVal* > 70 % when confidence limits are applied (Table 2.2).

A significant positive relationship was found between species abundance and the fidelity components of the species' *IndVals* ($df = 298$, deviance = 32.00; abundance: $df = 1$, $\chi^2 = 26.857$, $P < 0.001$) (Fig. 2.5a; Table 2.3). The fidelity value first reached a maximum of 1.0 for species with abundances of approximately 32 individuals (log abundance = 1.5) and all species with approximately 630 individuals (log abundance = 2.8) reached the maximum fidelity value of 1.0 (Fig. 2.5a). The relationship between species abundance and the *IndVals*' specificity component was not significant ($df = 298$, deviance = 38.316; abundance: $df = 1$, $\chi^2 = 1.765$, $P = 0.184$) (Fig. 2.5b; Table 2.3).

Table 2.2. Percentage indicator values of dung beetle species in the three sampling periods. 70% criterion: >, species with a mean *IndVal* significantly greater than 70% across the three sampling periods (*t* test, *df* = 2, *P* < 0.05); unmarked species had a mean *IndVal* across the three sampling periods of < 70%. 95 % confidence intervals are given in parenthesis.

Indicator species	% <i>IndVal</i>			Mean % <i>IndVal</i> ± S.E.	70% criterion
	1995/96	1998	2000		
Sand forest					
<i>Sisyphus</i> sp.Y <i>sensu</i> Paschalidis	86.32	99.47	64.81	83.53 ± 10.10 (40.07, 127.00)	>
<i>Onthophagus lacustris</i>	75.54	63.06	100	79.53 ± 10.85 (32.85, 126.21)	>
<i>Proagoderus aciculatus</i>	70.64	87.82	35.85	64.77 ± 15.29 (-1.00, 130.54)	
Mixed woodland					
<i>Sisyphus sordidus</i>	97.23	97.66	92.93	95.94 ± 1.51 (89.44, 102.44)	>
<i>Metacatharsius pseudoopacus</i>	87.61	99.50	3.33	63.48 ± 30.27 (-66.76, 193.72)	
<i>Pedaria</i> sp. III <i>sensu</i> Davis	87.24	98.73	62.88	82.95 ± 10.57 (37.48, 128.43)	>
<i>Copris inhalatus</i> spp. <i>sanctaeluciae</i>	84.26	80.00	10.00	58.09 ± 24.07 (-45.50, 161.67)	
<i>Pedaria</i> sp. IV <i>sensu</i> Davis	83.32	89.75	0.00	57.69 ± 28.90 (-66.68, 182.06)	
<i>Kheper lamarcki</i>	82.86	50.00	97.22	76.69 ± 13.98 (16.56, 136.83)	>
<i>Onthophagus ursinus</i>	75.62	78.43	96.79	83.61 ± 6.64 (55.05, 112.18)	>
<i>Euonthophagus carbonarius</i>	71.08	99.32	50	73.47 ± 14.29 (11.99, 134.94)	>

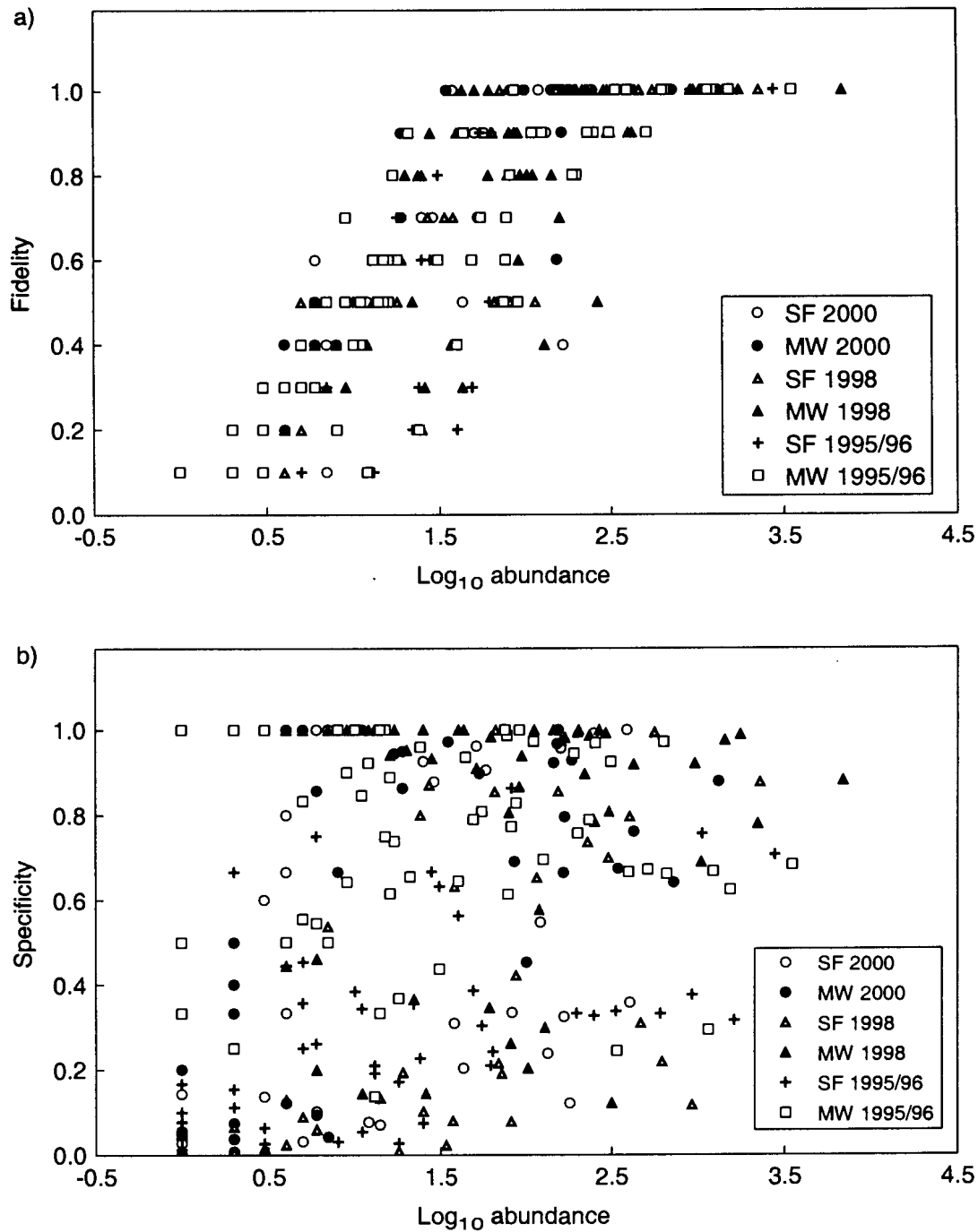


Fig. 2.5. The relationship between a) the fidelity and b) specificity of the indicator values and the abundance of the dung beetle species in sand forest and mixed woodland across sampling periods. MW = mixed woodland, SF = sand forest. Mean fidelity and specificity values are given in Table 2.3.

Table 2.3. The mean fidelity and specificity of the indicator values of the dung beetle species in sand forest and mixed woodland.

Habitat and sampling period	Fidelity (Mean \pm S.E.)	Specificity (Mean \pm S.E.)
Sand forest 1995/96	0.46 \pm 0.05	0.35 \pm 0.04
Sand forest 1998	0.38 \pm 0.06	0.38 \pm 0.06
Sand forest 2000	0.50 \pm 0.06	0.54 \pm 0.06
Mixed woodland 1995/96	0.61 \pm 0.04	0.77 \pm 0.03
Mixed woodland 1998	0.66 \pm 0.05	0.81 \pm 0.04
Mixed woodland 2000	0.50 \pm 0.06	0.72 \pm 0.05

Detector species

Seven of the 11 detector species identified by Van Rensburg *et al.* (1999) (Table 2.4A) responded as predicted, but only one species did so consistently across the two tests i.e. *Catharsius tricornutus* (Table 2.4B and C). None of the detector species were indicators of elephant-disturbed sand forest. An additional species met the criteria of being a detector species in January 2000, i.e. *Onthophagus pullus* (*IndVal*: mixed woodland 57.53, sand forest 7.36, elephant-disturbed sand forest 22.19).

When the indicator values of the dung beetle species sampled in sand forest and mixed woodland in 1995/96 were compared with the indicator values of the species collected in the elephant-disturbed sand forest areas (January 2000), three species emerged as indicators of elephant-disturbed sand forest. These species were *Caccobius* sp. 2 (*IndVal*: mixed woodland 0.0, sand forest 0.0, elephant-disturbed sand forest 100.0), *Caccobius* sp. 3 (*IndVal*: mixed woodland 0.0, sand forest 0.0, elephant-disturbed sand forest 100.0) and *Onthophagus pullus* (*IndVal*: mixed woodland 0.0, sand forest 0.0, elephant-disturbed sand forest 80.0). These species were however only sampled in the 1998 and 2000 sampling periods. When the *IndVals* of the three species in elephant-

disturbed sand forest were compared to their *IndVals* in sand forest and mixed woodland sampled in January 2000, only *Caccobius* sp. 3 emerged as an indicator of elephant-disturbed sand forest (*IndVal*: mixed woodland 18.87, sand forest 0.79, elephant-disturbed sand forest 79.55).

Table 2.4. Indicator values (*IndVal* %) for dung beetle species predicted to be detectors. Predictions were based on *IndVals* from A: mixed woodland: $50 \leq IndVal < 70$, sand forest: $5 \leq IndVal < 50$, and tested using *IndVals* in B. and C.

Species	Mixed woodland	Sand forest	Disturbed sand forest	Difference in <i>IndVal</i> ‡
A. Mixed woodland and sand forest data from 1995/6				
1. <i>Catharsius tricornutus</i>	59.06*	13.75		
2. <i>Onthophagus fimetarius</i>	61.89*	6.79		
3. <i>Onthophagus vinctus</i>	62.39*	37.61		
4. <i>Proagoderus dives</i>	68.37*	31.63		
5. <i>Onthophagus sugillatus</i> sp. A	66.23	33.77		
6. <i>Onthophagus sugilatus</i> sp. C	62.65	27.35		
7. <i>Onthophagus stigmatosus</i>	66.78	33.22		
8. <i>Neosisyphus mirabilis</i>	60.61	21.82		
9. <i>Pachylomerus femoralis</i>	60.51	32.76		
10. <i>Copris puncticollis</i>	56.62	11.47		
11. <i>Copris urus</i>	59.13	10.44		

Table 2.4. (continued)

B. Mixed woodland and undisturbed sand forest data from 1995/6 and elephant-disturbed sand forest data from 2000

1. <i>Catharsius tricornutus</i> †	46.10	10.73	15.37	+ 4.64
2. <i>Onthophagus fimetarius</i>	60.74	6.67	0.19	- 6.48
3. <i>Onthophagus vinctus</i>	59.17	35.66	2.59	- 33.07
4. <i>Proagoderus dives</i>	59.50	27.53	12.97	- 14.56
5. <i>Onthophagus sugillatus</i> sp. A	65.83	33.57	0.18	- 33.39
6. <i>Onthophagus sugillatus</i> sp. C	60.97	26.61	1.08	- 25.53
7. <i>Onthophagus stigmosus</i>	62.02	30.86	7.12	- 23.74
8. <i>Neosisyphus mirabilis</i>	60.61	21.82	0.00	- 21.82
9. <i>Pachylomerus femoralis</i>	56.78	30.74	4.94	- 25.80
10. <i>Copris puncticollis</i>	56.62	11.47	0.00	- 11.47
11. <i>Copris urus</i>	52.31	9.23	2.31	- 6.92

C. Mixed woodland, sand forest and elephant disturbed sand forest data from 2000

1. <i>Catharsius tricornutus</i> †	1.43	4.29	45.00*	+ 40.71
2. <i>Onthophagus fimetarius</i> †	44.12	0.00	1.18	+ 1.18
3. <i>Onthophagus vinctus</i> †	53.42	10.31	10.40	+ 0.09
4. <i>Proagoderus dives</i> †	58.04	7.99	33.97	+ 25.98
5. <i>Onthophagus sugillatus</i> sp. A	0.00	35.71	8.57	- 27.14
6. <i>Onthophagus sugillatus</i> sp. C	0.34	79.14*	3.45	- 75.69
7. <i>Onthophagus stigmosus</i> †	27.70	33.52	38.78	+ 5.26
8. <i>Neosisyphus mirabilis</i>	0.00	10.00	0.00	- 10.00
9. <i>Pachylomerus femoralis</i> †	49.13	21.97	23.12	+ 1.15
10. <i>Copris puncticollis</i>	0.00	0.00	0.00	0.00
11. <i>Copris urus</i> †	2.50	0.00	15.00	+ 15.00

* Indicator values (*IndVals*) significant at $P < 0.05$. † Species who's Indicator Values behaved as predicted. ‡ The % to which the species is a better (+) or worse (-) indicator of disturbed than undisturbed sand forest. Species with *IndVals* of 0 have no indicator value in the context of the three habitats being compared.

DISCUSSION

The suite of dung beetle species predicted to be bioindicators was tested and refined in this study using an independent data set collected 43 months after the initial study by Van Rensburg *et al.* (1999). Most of the indicator species were found to be robust indicators of the habitats to which they are specific. Previous studies have shown that dung beetles are sensitive to changes in habitat structure (Howden & Nealis 1975; Klein 1989; Nummelin & Hanski 1989; Halfpeter *et al.* 1992; Hill 1995; Davis & Sutton 1998; Davis *et al.* 2001). Dung beetles are thus useful as indicators because they reflect structural differences in habitats (Davis *et al.* 2001) such as difference between undisturbed and disturbed sand forests.

The list of 11 potential indicator species was reduced to seven reliable indicators, of which two were indicators of sand forest and five of mixed woodland. The two species discarded as indicators in a previous study by McGeoch *et al.* (in press) (*Onthophagus lacustris* in sand forest and *Kheper lamarcki* in mixed woodland) had mean *IndVals* > 70 % across the three sampling periods and were thus reinstated in the refined bioindicator suite of this study. Confidence intervals could also be determined for the *IndVals* of the species, which improved the reliability with which these species can now be used in monitoring systems. Nonetheless, these confidence limits were large and only one species proved to be a reliable indicator. The confidence intervals were however calculated using a very small sample size ($n = 3$). If these intervals were calculated using a larger sample size (more than three sample periods), the confidence intervals may decrease and the *IndVals* of the species may become more reliable. Continued long-term monitoring of these assemblages is thus recommended.

The change in the *IndVals* of the species with *IndVals* > 70 % was small between the 1995/96 and 2000 sampling periods compared to the change between the 1998 and 2000 sampling periods. The relationship between *IndVals* and their change between sampling periods was, however, only significant when the sand forest data collected in December 1998 and January 2000 were compared. Nonetheless, the huge change in *IndVals* between these two sampling periods compared to the smaller change in *IndVals* between 1995/96 and January 2000 indicated the importance of comparing a single

sample taken over a short period of time, with a well established baseline data set when testing indicator species.

The fidelity of species to a specific habitat type was shown to be sensitive to dung beetle abundance. However, even though the abundance of beetles was much lower in the 2000 sampling period than in the 1995/96 and 1998 sampling periods, most of the species identified as characteristic of sand forest or mixed woodland in 1995/96 remained so. McGeoch *et al.* (in press) gave three reasons why this might be the case. First, the fidelity of a species will not be affected if the abundance of a species change in the same direction in mixed woodland and sand forest. This is because the fidelity of a species is calculated from relative, rather than absolute differences in the frequency of occurrence of species across habitats. The abundances of the species in this study was lower in both mixed woodland and sand forest compared to previous sampling periods (1995/96 and 1998). This may explain why most of the indicator species remained indicators across the different studies. Second, abundance is logarithmically transformed in the relationship between fidelity and species abundance. Thus, a substantial change in abundance may not result in a change in the fidelity of a species. Third, if the fidelity of a species decreases as a result of a decrease in abundance, the specificity of the species might increase. As the abundance of a species decreases, the frequency of occurrence (fidelity) of that species will also decrease because abundance and fidelity are positively correlated. The species will thus become apparently more habitat specific by disappearing from non-preferred habitats. According to McGeoch *et al.* (in press) a cross-compensation might thus exist between a species' fidelity and specificity to a particular habitat because a decrease in fidelity and an increase in specificity will result in little or no change in the *IndVal* of a species. Based on the results of this study, all three reasons are valid.

McGeoch *et al.* (in press) confirmed that four of the 11 species predicted by Van Rensburg *et al.* (1999) acted as detectors of change in habitat from sand forest to mixed woodland, responded as predicted, i.e. they had higher *IndVals* in the disturbed sand forest than in undisturbed sand forest. According to them, these detector species also indicated the direction of change because their prevalence increased as the habitat changed from the less preferred undisturbed sand forest to the more preferred human-disturbed sand forest. The species were *Catharsius tricornutus*, *Onthophagus fimetarius*,

Onthophagus sugillatus sp. A and *O. sugillatus* sp. B. Two of these detector species were found to be indicators of human-disturbed sand forest in the study by McGeoch *et al.* (in press). These are species that prefer omnivore dung (Davis 1994, Appendix B) and the presence of human dung in the disturbed sand forest might have resulted in these species preferring this habitat above undisturbed sand forest. In contrast, only one of these species, *Catharsius tricornutus*, acted consistently as a detector species in this study. None of the detector species were indicative of elephant-disturbed sand forest but an additional species that was not in the original detector species list was identified as such (*Caccobius* sp. 3). McGeoch *et al.* (in press) have argued that detector species should not be selected based on average *IndVals* calculated across a number of sampling periods because of the shape of the relationship between mean *IndVals* and their variances. The *IndVals* of species are bounded between 0 and 100 %. Mean *IndVals* will thus lie closer to an intermediate *IndVal* (50 %) than the minimum and maximum *IndVals* from which it was calculated. Mean *IndVals* will have high variances when calculated from very dissimilar values. The same is found in other bounded systems (Lyons & Willig 1997; Colwell & Lees 2000). McGeoch *et al.* (in press) therefore suggested that detector species must be selected from those species with the necessary *IndVal* range, but with low variances. Only *Catharsius tricornutus* met these requirements across the three sampling periods. Species with *IndVals* within the necessary limits tend to have low variances in one habitat and high variances in the other.

This study and another by McGeoch *et al.* (in press) have shown that dung beetle indicator species selected from a temporally representative data set (i.e. the 1995/96 data set) are reliable and can be implemented in the monitoring of sand forest. A single, 24 hour long sampling period during periods of peak dung beetle abundance and activity will present representative data on the ecological state of sand forest. This approach is likely to be more feasible than monitoring the assemblages continuously across all seasons in terms of the financial cost and time associated with long-term monitoring programs (Noss 1990; Spector & Forsyth 1998, Lawton & Gaston 2001).

A very important criterion for the selection of reliable bioindicators is met in this study by testing the robustness of the bioindicator species using independent data sets collected in the same environment using three temporal and spatial replicates. The use of

these dung beetles as indicators will compliment existing botanical information on sand forest and the effects of disturbance on this habitat type (Van Wyk 1996; Van Rensburg *et al.* 1999). It is important to monitor sand forest not only outside of conservation areas, but also inside of these areas to determine the effect of large herbivores on this endangered habitat type. Continuous monitoring is necessary to assess the extent to which sand forest patches inside of reserves are changing. Important conservation decisions can be based on such information, which is imperative for the continued existence of sand forest.

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CHAPTER 3

Identification of dung beetles (Coleoptera: Scarabaeinae) in sand forest and mixed woodland assemblages in northern KwaZulu-Natal, South Africa.

INTRODUCTION

The Maputuland Centre of Endemism (MC) constitutes the southernmost end of the tropics in eastern Africa and is one of the most significant centers of biotic endemism in southern Africa (Van Wyk 1996). Two major habitat types can be identified in the MC, namely sand forest and mixed woodland. Sand forest has the highest plant diversity, as well as the highest proportion of endemic plant species in the MC, and many of the MC's endemic vertebrate species are also restricted to this habitat type (Van Wyk 1996).

In contrast to the well-known flora and vertebrate fauna of the MC, the invertebrates of this heterogenous landscape are poorly known (Van Rensburg *et al.* 1999). In an attempt to establish the extent to which invertebrate assemblages in the MC match the high level of floral and vertebrate diversity and endemism (Van Wyk 1996), and local scale heterogeneity (Poynton 1961), Van Rensburg *et al.* (1999) examined the variation in dung beetle assemblages between mixed woodland and sand forest in Tembe Elephant Park and Sileza Nature Reserve. The latter are two designated conservation areas in the MC in South Africa. Dung beetle assemblages were found to be homogenous within sand forest and mixed woodland habitats, although pronounced heterogeneity was found both between habitat types and nature reserves (Van Rensburg *et al.* 1999 and this study, see Chapter 1). No endemic species were identified (Van Rensburg *et al.* 1999).

Dung beetle indicator species have been identified that are specific to sand forest and mixed woodland in each reserve, and detector species that can be used to monitor changes in sand forest due to disturbance (e.g. through deforestation, Matthews *et al.*

1999) (Van Rensburg *et al.* 1999 and this study, Chapter 2). Sand forest is the oldest habitat type on the Maputoland coastal plain (Van Wyk 1996) and at present is endangered both inside and outside protected areas (i.e. Tembe Elephant Park, Sileza Nature Reserve, Mkuzi Game Reserve and Falsebay Park) (Matthews *et al.* 1999, Van Rensburg *et al.* 1999, Van Rensburg *et al.* 2000a). When sand forest is disturbed, the canopy opens up and the vegetation structure changes to that of mixed woodland. Reversion to the original sand forest structure after disturbance has not yet been recorded (Van Rensburg *et al.* 1999). Outside of the protected areas disturbance to sand forest occurs as a result of clearing for firewood and human occupation, as well as movement and grazing by domestic livestock, especially cattle (Davis *et al.* 1994; Cole & Landres 1996).

The increasing level of elephant disturbance in sand forest in Tembe is also of great concern, and has resulted in an apparent conservation conflict (Van Rensburg *et al.* 1999, 2000a). Although elephants prefer to forage in mixed woodland, they are increasingly utilizing sand forest as a result of their high density in Tembe (130 – 140 animals in 30,079 ha, Matthews, pers. comm.) (Van Rensburg *et al.* 1999). To protect sand forest patches from elephant damage, an area in the south of Tembe has been fenced off from the remainder of the Park to exclude elephants (approximately 750 ha, i.e. 2.5 % of the reserve). It is thus imperative that continuous monitoring systems are implemented in sand forest to quantify the impact of the heavy utilization of sand forest by large herbivores in Tembe. The impact of humans on unprotected sand forest areas must also be monitored to understand the impact of further deforestation on this endangered habitat type and its fauna. Here, a key is provided to the dung beetle species that have been collected in Tembe to date, as well as in human-disturbed areas adjacent to the reserve. The objective of this key is to facilitate the use of dung beetle assemblages in indicator and monitoring systems in this reserve by providing a rapid and effective means of identifying the dung beetle species.

MATERIAL AND METHODS

Sampling was done in and adjacent to Tembe Elephant Park (27°01'S 32°24'E) on the southern Mozambique Coastal Plain of Northern KwaZulu-Natal, South Africa during May 1995 to April 1996, December 1998 and January 2000 (see Fig. 1.3). Two mixed woodland and two sand forest sites were sampled during each sampling period. Different sites were used for each of the sampling periods. During December 1998, closed canopy sand forest areas were sampled which represented undisturbed sand forest. In addition, two human-disturbed sand forest areas adjacent to the reserve were also sampled. During January 2000 two sand forest areas were sampled inside the botanical reserve to exclude disturbance caused by elephants, and two elephant-disturbed sand forest areas (as areas that showed evidence of elephant activity such as large trees that were removed) were sampled inside the reserve.

During each of the sampling periods five grids of six pitfall traps each were placed at each site. The pitfalls were placed in a 2 x 3 design on a 2 m x 4 m grid. The traps were baited using 50 g elephant dung and set out for 24 hours in 1998 and 2000, and for 48 hours during the 1995/96 sampling period. During the 1995/96 sampling period the pitfall traps were re-baited after 24 hours and the dung beetles in the traps were collected. A second collection took place after another 24 hours. Sampling grids were placed a minimum of 200 m apart in each area to maintain sampling independence. The dung beetles collected were identified by comparison with identified specimens in the South African National Insect Collection and identification continued by Dr A. Davis.

A key, identifying all the dung beetle species collected during the three sampling periods to tribe and genus level, was collated from keys compiled by other authors (see the different sections of the key for references). Thereafter the key was compiled up to species level using a number of species specific characteristics.

RESULTS AND DISCUSSION

A total of 78 species in 28 genera and nine tribes were collected over the three sampling periods. Twenty-three mixed woodland-specific species and only three species

specific to undisturbed sand forest were collected over the three sampling periods (Table 3.1). During December 1998 four species specific to human-disturbed sand forest were collected, while no elephant-disturbed sand forest-specific species were sampled in January 2000 (Table 3.1).

This study provides an easily accessible, illustrated key for the identification of the dung beetle species collected in Tembe to date. It is, however, unlikely that all the dung beetle species present in Tembe and the surrounding human-disturbed area were collected during the three sampling periods (Davis pers. comm.). During the 1995/96 sampling period a species richness asymptote was reached for the dung beetles in Tembe (Van Rensburg *et al.* 2000b). However this was not the case in the 1998 and 2000 sampling periods (Chapter 1). Nonetheless, the structure of the key (i.e. identification first to tribe, then to genus, and finally to species-level) allows for the easy inclusion of species into the key should new species for the area be collected in the future.

The key uses a number of tribe- and genus-specific characters as well as other additional characters to identify beetles to species level. The taxonomy of nine dung beetles is still unclear, but these species were collected in sufficient numbers not to exclude them from the key, i.e. *Copris* sp. 1, *Metacatharsius* sp. 1, *Onitis* sp. 1, *Caccobius* spp. 1 – 3 and *Pedaria* spp. I, III and IV *sensu* Davis. One species, *Scarabaeus* cf. *xavieri*, may still be undescribed (Davis, pers. comm.). Twelve species were sampled in only one sampling period and one habitat type. These species were: *Tragiscus dimidiatus* and *Onitis caffer* (mixed woodland 1995/96); *Metacatharsius* sp. 1 (sand forest 1995/96); *Copris denticulatus*, *Copris* sp. 1, *Onthophagus lamelliger* and *Proagoderus brucei* (human disturbed sand forest 1998); *Onitis deceptor*, *Gymnopleurus virens*, *Onthophagus bicavifrons*, *Onthophagus rasipennis* and *Phalops flavocinctus* (mixed woodland 1998).

Beetles with very low abundances were included in the key although it was not specifically determined whether the species were rare or transient. The inclusion of these species increases the value of the key because they will assist in the monitoring of species turnover in sand forest and mixed woodland assemblages. The effects of disturbance caused by elephants in Tembe, and by humans outside of the reserve, can now effectively

be monitored using the dung beetle indicator and detector species identified by Van Rensburg *et al.* (1999) and tested in this study (Chapter 2) in conjunction with this key.

Table 3.1. Scarabaeidae species and tribes sampled in Tembe Elephant Park (T), Sileza Nature Reserve (S) and in human-disturbed sand forest (HDSF) adjacent to Tembe to date. SF = Sand forest, MW = mixed woodland, EDSF = elephant-disturbed sand forest.

Tribe and species	Author	Habitat			
		SF	MW	HDSF	EDSF
Canthonini					
<i>Anachalcos convexus</i>	Boheman, 1857	T/S	T/S	T	T
Coprini					
<i>Catharsius harpagus</i>	Harold, 1877	T/S	T/S		T
<i>Catharsius heros</i>	Boheman, 1960		T/S		T
<i>Catharsius</i> sp. near <i>pandion</i>	Harold, 1877	T/S	T/S	T	
<i>Catharsius tricornutus</i>	(DeGeer, 1778)	T/S	T/S	T	T
<i>Copris denticulatus</i>	Nguyen-Phung, 1988			T	
<i>Copris fidius</i>	(Olivier, 1789)	T	T		T
<i>Copris inhalatus</i> spp. <i>sanctaeluciae</i>	Nguyen-Phung & Cambefort, 1986	T/S	T/S	T	T
<i>Copris mesacanthus</i>	Harold, 1878	T	T/S	T	T
<i>Copris puncticollis</i>	Boheman, 1857	T	T/S	T	
<i>Copris</i> sp. 1				T	
<i>Copris urus</i>	Boheman, 1857	T/S	T/S	T	T
<i>Metacatharsius exiguus</i>	(Boheman, 1860)	T	T/S	T	T
<i>Metacatharsius pseudoopacus</i>	(Ferreira, 1965)	T	T/S	T	T
<i>Metacatharsius</i> sp. 1		T			
Dichotomiini					
<i>Heliocopris japetus</i>	Klug, 1855	T	T		T
<i>Pedaria</i> sp. I <i>sensu</i> Davis		T	T		
<i>Pedaria</i> sp. III <i>sensu</i> Davis		T	T/S		T
<i>Pedaria</i> sp. IV <i>sensu</i> Davis		T	T	T	T
Gymnopleurini					
<i>Allogymnopleurus consocius</i>	(Péringuey, 1900)		T	T	



Table 3.1. (continued)

<i>Garetta azureus</i>	(Fabricius, 1801)	T/S	T		T
<i>Gymnopleurus virens</i>	Erichson, 1843			T	
Oniticellini					
<i>Cyptochirus ambiguus</i>	(Kirby, 1828)	T	T		T
<i>Drepanocerus impressicollis</i>	Boheman, 1857		T		T
<i>Drepanocerus kirbyi</i>	Kirby, 1828	T	T/S	T	T
<i>Tiniocellus spinipes</i>	(Roth, 1851)	T/S	T/S		
<i>Liatongus militaris</i>	(Castelnau, 1840)		T		
<i>Oniticellus formosus</i>	Chevrolat, 1830	S	T/S		
<i>Oniticellus planatus</i>	Castelnau, 1840	T	T/S	T	
<i>Tragiscus dimidiatus</i>	Klug, 1855		T		
Onitini					
<i>Onitis caffer</i>	Boheman, 1857		T/S		
<i>Onitis deceptor</i>	Péringuey, 1900		T		
<i>Onitis</i> sp. 1			T/S		
<i>Onitis tortuosus</i>	Houston, 1983	T	T		
Onthophagini					
<i>Caccobius cavatus</i>	(d'Orbigny, 1908)	T	T	T	
<i>Caccobius nigrifulus</i>	Klug, 1855		T	T	
<i>Caccobius</i> sp. 1		T/S	T/S	T	
<i>Caccobius</i> sp. 2		T	T		T
<i>Caccobius</i> sp. 3		T	T		T
<i>Cleptoaccobius viridicollis</i>	(Fåhraeus, 1857)	T/S	T/S		T
<i>Euonthophagus carbonarius</i>	(Klug, 1855)	T/S	T/S	T	T
<i>Hyalonthopagus alcyonides</i>	(d'Orbigny, 1913)		T/S		T
<i>Onthophagus acquepubens</i>	d'Orbigny, 1905	T/S	T/S	T	
<i>Onthophagus aeruginosus</i>	Roth, 1851	T/S	T/S	T	T
<i>Onthophagus bicavifrons</i>	d'Orbigny, 1902		T		
<i>Onthophagus fimetarius</i>	Roth, 1951	T/S	T/S	T	T
<i>Onthophagus flavolimbatus</i>	Klug, 1855		T	T	
<i>Onthophagus juvenicus</i>	Klug, 1853	T	T/S	T	T
<i>Onthophagus lacustris</i>	Harold, 1877	T/S	T/S	T	



Table 3.1. (continued)

<i>Onthophagus lamelliger</i>	Gerstaecker, 1871				T
<i>Onthophagus obtusicornis</i>	Fåhraeus, 1857	T	T		T
<i>Onthophagus plebejus</i>	Klug, 1855	T			T
<i>Onthophagus pullus</i>	Roth, 1851	T	T	T	T
<i>Onthophagus rasipennis</i>	d'Origny, 1905		T		
<i>Onthophagus signatus</i>	Fåhraeus, 1857	T	T/S	T	T
<i>Onthophagus stigmaticus</i>	(d'Origny, 1902)	T/S	T/S	T	T
<i>Onthophagus sugillatus</i>	Klug, 1855	T/S	T/S	T	T
<i>Onthophagus ursinus</i>	(d'Origny, 1902)	T/S	T/S	T	T
<i>Onthophagus vinctus</i>	Erichson, 1843	T/S	T/S	T	T
<i>Phalops boschas</i>	Klug, 1855		T	T	
<i>Phalops flavocinctus</i>	Klug, 1855		T		
<i>Proagoderus aciculatus</i>	(Fåhraeus, 1857)	T/S	T/S	T	T
<i>Proagoderus bicallosus</i>	(Klug, 1855)	T	T/S		T
<i>Proagoderus brucei</i>	(Reiche, 1849)			T	
<i>Proagoderus dives</i>	(Harold, 1877)	T/S	T/S	T	T
Scarabaeini					
<i>Kheper lamarcki</i>	(MacLeay, 1821)	T/S	T/S		T
<i>Pachylomerus femoralis</i>	(Kirby, 1828)	T/S	T/S	T	T
<i>Scarabaeus galenus</i>	(Westwood, 1847)	T/S	T/S		
<i>Scarabaeus goryi</i>	Castelnau, 1840	T/S	T/S		T
<i>Scarabaeus cf. xavieri</i>		T	T/S		
<i>Scarabaeus zambesianus</i>	Péringuey, 1900	T	T/S		T
Sisyphini					
<i>Neosisyphus fortuitus</i>	Péringuey, 1900	T/S	T/S		T
<i>Neosisyphus mirabilis</i>	Arrow, 1927	T/S	T/S		
<i>Neosisyphus rubrus</i>	Paschalidis, 1974	T/S	T/S		T
<i>Sisyphus bornemisszanus</i>	Endrödi, 1983	T/S	T/S	T	
<i>Sisyphus sordidus</i>	Boheman, 1857	T/S	T/S	T	T
<i>Sisyphus sp. Y sensu Paschalidis</i>		T/S	T/S	T	T
<i>Sisyphus spinipes</i>	Thunberg, 1818	T	T		

The use of this key is however not restricted to sand forest and mixed woodland dung beetle assemblages of Tembe alone. All the species collected by Van Rensburg *et al.* (1999) in Sileza Nature Reserve (27°06'S 32°36'S) are also included in the species list for Tembe (see Table 3.1). It is thus possible to also use the key for dung beetle assemblages in the sand forest and mixed woodland of Sileza. Although the dung beetles sampled in Tembe and Sileza constitute the only record of sand forest dung beetles in the MC to date (Davis pers. comm.), the possibility exists that the key can be used to identify dung beetle species in unsurveyed sand forest habitats, similar to those in the two reserves. This has important conservation implications for sand forest. Van Rensburg *et al.* (1999) has shown that significant differences exist between sand forests in different areas and it is thus necessary to conserve more than a single sand forest area for the habitat and its biota to persist (Van Rensburg *et al.* 1999). This key will facilitate the identification of sand forest dung beetle assemblages similar to those in Tembe and Sileza for future conservation, as well as assemblages affected by human or elephant disturbance.

**Key to the dung beetles (Coleoptera: Scarabaeinae) of Tembe Elephant Park
(KwaZulu Natal, South Africa)**

1. Meso- and metatibiae long and thin, not broadening towards the tip; protibia with a terminal spur (Fig. 3.1a); each meso- and metatarsus of uniform width; dorsum generally flat (in Canthonini [*Anachalcos*] strongly convex).....2
- 1'. Meso- and metatibiae short and broad, broadening greatly towards the distal end; terminal spur of the protibiae sometimes absent; each meso- and metatarsus triangular (Fig. 3.2), broadening towards the distal end; dorsum highly convex (Coprini, Dichotomiini, Onthophagini) or rather flat (Oniticellini, Onitini, Onthophagini).....5

2. Sides of body, especially the pronotum, laterally compressed and flattened; elytra broad proximally, attenuating posteriorly; middle and hind legs extremely elongate; maximum body length 15 mm.....**Sisyphini**
- 2'. Sides of body not laterally compressed and flattened; middle and hind legs not extremely elongate.....3

Sisyphini (after Ferreira 1966)

- a. Lateral ridge of pronotum complete, running from distal to lateral margin.....**Sisyphus**
- a'. Lateral ridge of pronotum incomplete, effaced posteriorly.....**Neosisyphus**

Sisyphus

- i. Setae on odd-numbered interstriae of elytra are black bristles arranged in tufts.....**Sisyphus bornemisszanus**
- i'. Setae on elytra not arranged in discrete black tufts.....ii
- ii. Setae on elytra and pronotum yellowish brown and thick.....**Sisyphus sordidus**
- ii'. Setae on elytra and pronotum pale brown and thin.....**Sisyphus sp. Y sensu Paschalidis**

Neosisyphus

- i. Body brown to light orange-brown or yellow-brown; legs of lighter color than pronotum; anteromedian cleft of clypeus deep and angled.....***Neosisyphus rubrus***
- i'. Body entirely brown to dark brown or black; anteromedian cleft of clypeus shallow.....ii
- ii. Hind trochanter very large, its length more than half the length of metafemur (Fig. 3.3).....***Neosisyphus fortuitus***
- ii'. Hind trochanter shorter than half the length of the metafemur.....iii
- iii. Posterior margin of mesofemur with pronounced spine-like projection (Fig. 3.4).....***Neosisyphus mirabilis***
- iii'. No pronounced spine-like projection on posterior margin of mesofemur; metafemur of male with spine on posterior margin.....
.....***Neosisyphus spinipes***
- 3. Elytra emarginated laterally (Fig. 3.5); protarsi present.....**Gymnopleurini**
- 3'. Lateral margin of elytra entire, not emarginated; protarsi absent.....4

Gymnopleurini (after Ferreira 1962)

- a. Metasternal epimeron fused with the first abdominal sternite in the emarginated region of the elytra (Fig. 3.6); edges of epimeron not distinguishable from above; mesotibiae with a single terminal spur; clypeus bidentate; glossy metallic blue, green or maroon.....***Gymnopleurus virens***

- a'. Suture between metasternal epimeron and first abdominal sternite clearly visible in region of elytral emargination (Fig. 3.7); mesotibiae with one or two terminal spurs; clypeus quadridentate; matt metallic colouration.....b
- b. Mesotibiae with two terminal spurs, one large and immovable, the second smaller and articulated; matt metallic green.....*Garreta azureus*
- b'. Mesotibiae with a single terminal spur; matt metallic brown.....
.....*Allogymnopleurus consocius*
4. External edge of protibiae tridentate; whole body globularly convex; color matt maroon.....(**Canthonini**) *Anachalcos convexus*
- 4'. External edge of protibiae quadridentate (proximal tooth may be vestigial); body not globularly convex.....**Scarabaeini**

Scarabaeini (after Janssens 1938; Ferreira 1962, 1966; Mostert & Scholtz 1986; Scholtz & Howden 1987)

- a. Tarsi with a single claw.....*Kheper lamarcki*
- a'. Tarsi with two claws.....b
- b. Procoxae and profemora enlarged, obscuring prothorax ventrally (Fig. 3.8); metatarsal claws recessed and unevenly reduced (Fig. 3.9).....
.....*Pachylomerus femoralis*
- b'. Procoxae and profemora not enlarged; metatarsal claws not recessed.....
.....*Scarabaeus*

Scarabaeus

- i. Curved, anterior pointing spine on anterior apical border of profemur (Fig. 3.10).....***Scarabaeus galenus***
- i'. Profemur without curved, anterior pointing spine on anterior border.....ii
- ii. Internal margin of protibiae with two spines (Fig. 3.1b).....***Scarabaeus goryi***
- ii'. Internal margin of protibiae without spines.....iii
- iii. Small protuberance on mentum (Fig. 3.11)....***Scarabaeus zambesianus***
- iii'. No protuberance on mentum.....***Scarabaeus xavieri***

- 5. Second article of the labial palps shorter than the first; third article always clearly visible.....6
- 5'. Second article of the labial palps longer than the first; third article reduced, small, elongate and thin.....7
- 6. External ridge present on at least the metatibiae, often very short but in dorsal view clearly visible as a tooth-like structure.....***Coprini***
- 6'. External ridges of meso- and metatibiae absent.....***Dichotomiini***

Coprini (after Janssens 1939; Ferreira 1962, 1966; Balthasar 1963a, b)

- a. Elytra with a single lateral ridge.....*Copris*
- a'. Elytra with two lateral ridges, one sometimes incomplete.....b
- b. Large bodied (25 – 43 mm); ventral surface of protibiae with three long, oblique ridges (Fig. 3.12).....*Catharsius*
- b'. Small bodied (8 – 14 mm); external edge of ventral surface of protibiae bordered with ridge, lacking oblique ridges.....*Metacatharsius*

Copris

- i. Clypeus adentate.....*Copris inhalatus spp. sanctaluciae*
- i'. Clypeus bidentate or with an anteromedian cleft.....ii
- ii. Clypeus adentate with an anteromedian cleft.....iii
- ii'. Clypeus bidentate, anteromedian cleft of clypeus angled.....iv
- iii. Large-bodied, body length 20 mm; cephalic horn of clypeus basally widened in males.....*Copris urus*
- iii'. Small-bodied, body length 12 mm; cephalic horn of clypeus not basally widened in males.....*Copris puncticollis*
- iv. Median carina and two lateral carinae on pronotum.....
.....*Copris denticulatus*



- iv'. Either median pronotal carina or two or no lateral pronotal carinae present.....v
- v. Median pronotal carina present, no dorso-lateral pronotal carinae.....
*Copris sp. 1*
- v'. Two parallel dorso-lateral carinae present on pronotum.....iv
- vi. Pronotal disc surrounded by two lateral carinae so that pronotal disc seems depressed (Fig. 3.13); cephalic horn of clypeus longer than protibia, small spine at posterior base of horn in males....*Copris fidius*
- vi'. Two small lateral pronotal carinae present in males, cephalic horn of clypeus shorter than protibia, small spine in middle of posterior edge of horn in males.....*Copris mesacanthus*

Catharsius

- i. Clypeus bidentate.....*Catharsius sp. near pandion*
- i'. Clypeus adentate.....ii
- ii. Two large and conspicuous pronotal protuberances (horns) present in males.....*Catharsius tricornutus*
- ii'. Lateral pronotal crest present.....iii
- iii. Lateral pronotal crest shorter than base of vertex.....
*Catharsius harpagus*

iii'. Lateral pronotal crest longer than base of vertex.....*Catharsius heros*

Metacatharsius

i. Matt black; protuberance on mentum....*Metacatharsius pseudoopacus*

i'. Glossy black or brown; no protuberance on mentum.....ii

ii. Body length 15 mm; glossy black.....*Metacatharsius exiguus*

ii'. Body length 8 mm; brown to black.....*Metacatharsius sp. 1*

Dichotomiini (after Janssens 1939; Ferreira 1962, 1966)

a. Large bodied with length greater than 30 mm; abdominal sternites not fused.....*Heliocopris japetus*

a'. Small bodied; abdominal sternites fused.....*Pedaria*

Pedaria

i. Base of pronotum with no punctation (Fig. 3.14).....
.....*Pedaria sp. I sensu Davis*

i'. Base of pronotum with punctation.....ii

ii. Primary interval of elytra with two rows of punctation.....
.....*Pedaria sp. III sensu Davis*

ii'. Primary interval of elytra with three rows of punctation.....
.....*Pedaria sp. IV sensu Davis*

7. Scutellum not visible; body usually short and convex.....**Onthophagini**
- 7'. Scutellum small but visible; body somewhat flattened and elongate, square-shaped.....8

Onthophagini (Balthasar 1963b; Ferreira 1966; Cambefort 1979; Branco 1992)

- a. Apex of protibiae straight and right-angled; apical tooth at right angle to apex of protibiae.....b
- a'. Apex of protibiae strongly oblique.....c
- b. Square or rectangular apical tooth of tibial dentition pointing ventrally in males; antennae with 8 articles; small-bodied (2.5 – 3.5 mm); clypeus bidentate; head without sculpture.....*Cleptocaccobius viridicollis*
- b'. Combinations of characters different.....*Caccobius*

Caccobius

- i. Clypeus adentate.....ii
- i'. Clypeus bidentate.....iv
- ii. Punctuation on pronotum and elytra fine, few fine setae; frontal carina present on clypeus.....*Caccobius nigrutilus*
- ii'. Punctuation on pronotum and elytra prominent, very setose; frontal carina absent from clypeus.....iii



- iii. Frontogenal suture carinate.....*Caccobius* sp. 2
- iii'. Frontogenal suture not carinate.....*Caccobius* sp. 3
- iv. Body length 2 – 3 mm; brown with light brown legs.....
.....*Caccobius cavatus*
- iv'. Body length 3.5 – 4.5 mm; black with brown legs.....*Caccobius* sp. 1
- c. Meso- and metatarsi more or less flat, broadening slightly, second to fourth articles of uniform length; lateral interstriae of elytra with incomplete pseudostriae on the posterior half; pronotum large relative to elytra.....*Phalops*
- c'. Meso- and metatarsi unmodified, length of second to fourth articles clearly different; lateral interstriae of elytra without pseudostriae; proportions of pronotum relative to elytra unmodified.....d

Phalops

- i. Genae distinctly rounded and projecting past posterior angle of clypeus (Fig. 3.15); frontal carina of clypeus distinct, no basal lamina present on vertex.....*Phalops boschas*
- i'. Gena not rounded and projecting past posterior angle of clypeus; frontal carina of clypeus absent, vertex with distinct basal lamina (Fig. 3.16).....*Phalops flavocinctus*
- d. Posterior margin of pronotal disc with median apex; metallic colouration.....
.....*Proagoderus*

d'. Posterior margin of pronotal disc arcuate, without median apex.....
.....*Onthophagus*

Proagoderus

i. Metallic maroon; two distinct unpunctured carinae on pronotum,
stretching from the basal to the anterior margin (Fig. 3.17).....
.....*Proagoderus bicallosus*

i'. Metallic green, blue or red.....ii

ii. Pronotal disc sparsely and finely punctulate.....*Proagoderus dives*

ii'. Thin, unpunctured strip stretching from the median point of the
pronotal disc to the anterior pronotal margin.....iii

iii. Median pronotal carina distinct, not punctate.....
.....*Proagoderus brucei*

iii'. Median pronotal carina absent.....*Proagoderus aciculatus*

Onthophagus (including *Hyalonthophagus* and *Euonthophagus*)

i. Metallic colouration.....ii

i'. Non-metallic colouration.....vi

ii. Pronotum not punctured; shiny metallic blue or green.....
.....*Hyalonthophagus alcyonides*

- ii' Pronotum punctulate, matt metallic colouration.....iii
- iii. Clypeus bidentate; clypeus, pronotum and elytra metallic maroon, elytra with yellow markings on lateral edges and apex.....
.....*Onthophagus bicavifrons*
- iii'. Clypeus adentate.....iv
- iv. Pronotum and clypeus metallic green (can be maroon), elytra light brown with black puncture marks; male with two slight protuberances on pronotum.....*Onthophagus plebejus*
- iv'. Clypeus, pronotum and elytra metallic.....v
- v. Pronotum with four protuberances.....*Onthophagus fimetarius*
- v'. Median pronotal carina present in females, no pronotal protuberances in males; males with two cephalic horns on clypeus.....*Onthophagus aeruginosus*
- vi. Clypeus, pronotum and elytra black with no markings.....vii
- vi'. Elytra with brown patterning.....xi
- vii. Clypeus bidentate.....viii
- vii'. Clypeus adentate.....x
- viii. Interstriae of elytra extremely dense and finely punctulate, granules present on interstriae; pronotum granulate.....
.....*Onthophagus obtusicornis*



- viii'. Punctures in interstriae not extremely dense and fine, pronotum punctulateix
- ix. Pronotum glossy black with no setae.....
.....*Euonthophagus carbonarius*
- ix'. Pronotum setose.....*Onthophagus acquepubens*
- x. Frontal and vertex carinae absent; protibial spur curved, pointing ventrally.....*Onthophagus lacustris*
- x'. Frontal and vertex carinae present, protibial spur not ventrally curved.....*Onthophagus juvenicus*
- xi. Elytra brown with black patterning.....xii
- xi'. Elytra black with brown patterning.....xv
- xii. Elytra transparent, first interval black.....*Onthophagus rasipennis*
- xii'. Elytra not transparent, first interval black.....xiii
- xiii. Elytra glossy yellow-brown with distinct dark brown marking (like correction mark), pronotum glossy black (Fig. 3.18).....
.....*Onthophagus flavolimbatus*
- xiii'. Elytra reddish brown.....xiv
- xiv. Clypeus bidentate.....*Onthophagus pullus*

- xiv'. Clypeus adentate.....*Onthophagus ursinus*
- xv. Clypeus adentate.....*Onthophagus stigmaticus*
- xv'. Clypeus bidentate.....xvi
- xvi. Anteromedian cleft of clypeus deep and not angled.....
.....*Onthophagus vinctus*
- xvi'. Anteromedian cleft of clypeus angled.....xvii
- xvii. Median pronotal carina present..... *Onthophagus lamelliger*
- xvii'. No median pronotal carina present.....xviii
- xviii. Pro-, meso- and metafemuræ light brown.....
.....*Onthophagus signatus*
- xviii'. Pro-, meso- and metafemuræ black.....*Onthophagus sugillatus*
8. Antennae with 9 articles.....**Onitini**
- 8'. Antennae with 8 articles.....**Oniticellini**

Onitini (after Cambefort 1975; Balthasar 1963b)

- a. Metallic green colouration.....*Onitis tortuosis*
- a'. Black colouration.....b

- b. Vertex tubercle absent; ventral carina of protibiae with spine, anterior inferior margin of profemora with spine (Fig. 3.19).....*Onitis deceptor*
- b'. Vertex tubercle present; no spines on profemora or protibiae.....c
- c. Clypeus bidentate; frontal carina not curved; vertex tubercle nearest to basal carina of vertex (Fig. 3.20).....*Onitis caffer*
- c'. Clypeus acuminate; frontal carina curve towards vertex tubercle; vertex tubercle nearest to frontal carina.....*Onitis sp. 1*

Oniticellini (after Janssens 1953)

- a. Ridge at base of pygidium; pronotum and elytra highly sculptured, ridges on elytra.....*Cytochirus and Drepanocerus*
- a'. No ridge at base of pygidium; pronotum and elytra not sculptured.....b

Cytochirus and Drepanocerus

- i. Elytra patterned in white, light brown and dark brown setae, whole elytra covered in dense setae except in interstitial punctures, primary interstriae well defined ridges (Fig. 3.21).....*Cytochirus ambiguus*
- i'. Setae on elytra white, only on ridges.....ii
- ii. Elytra dark brown with light brown patches, setae on ridges single and in large tufts, shallowly punctulate (Fig. 3.22).....*Drepanocerus kirbyi*
- ii'. Elytra black with deep punctures, setae in small tufts (Fig. 3.23).....
.....*Drepanocerus impressicollis*

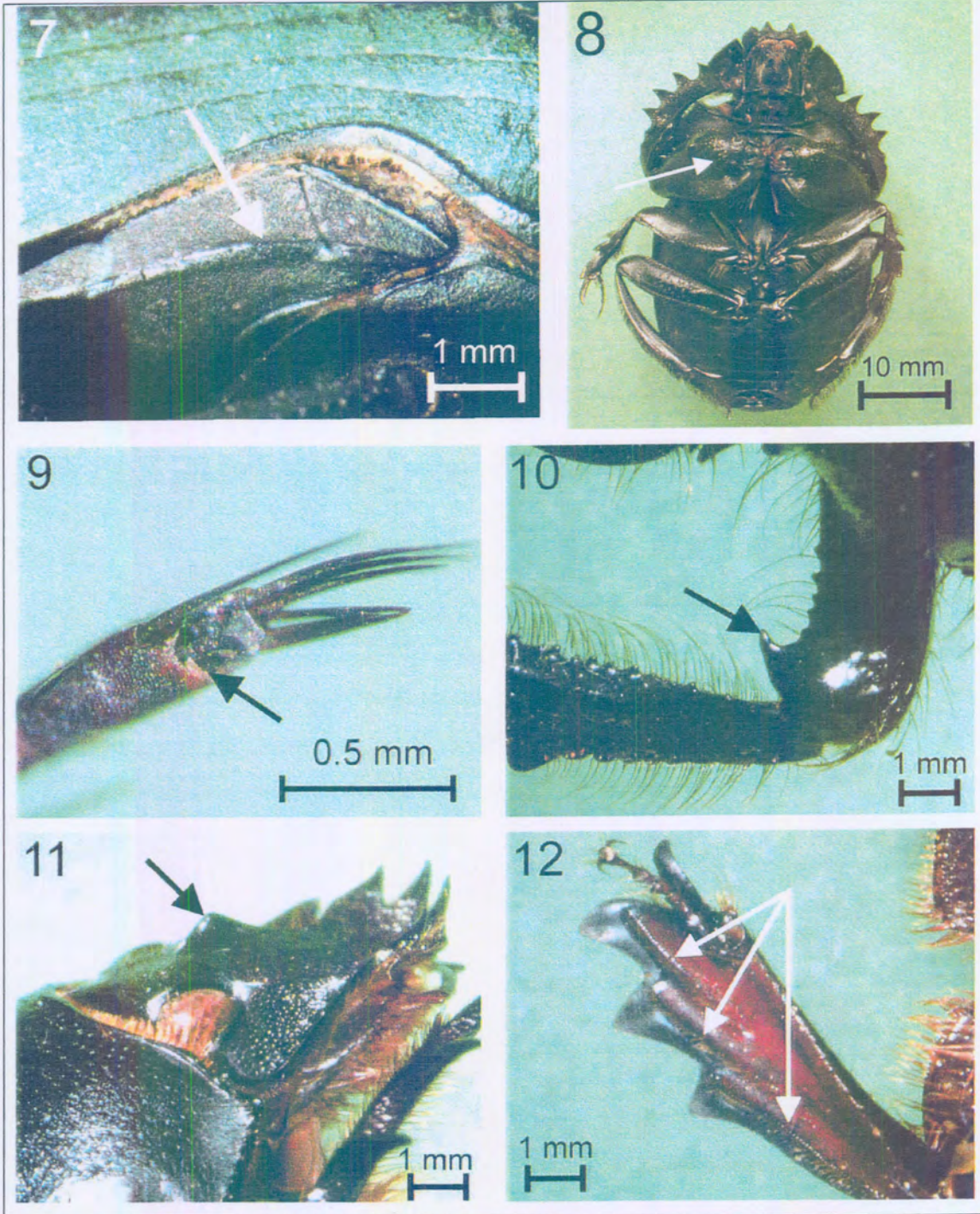


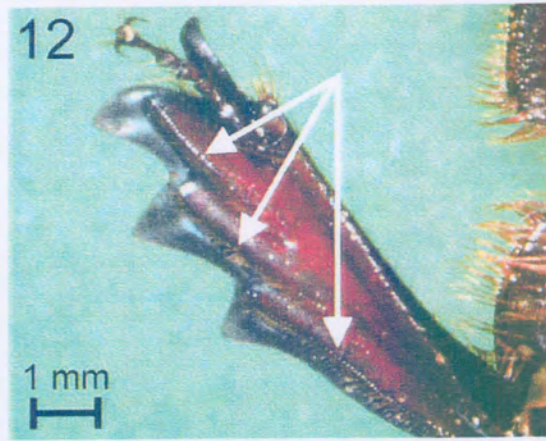
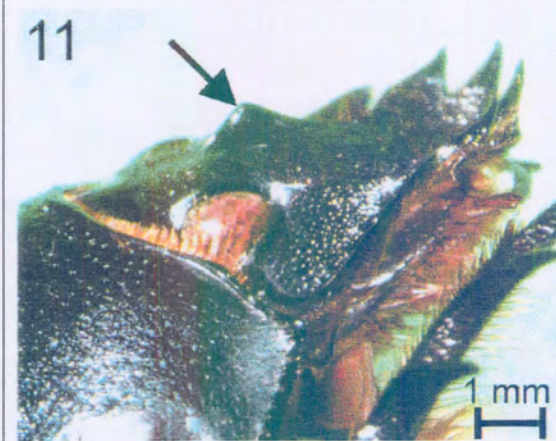
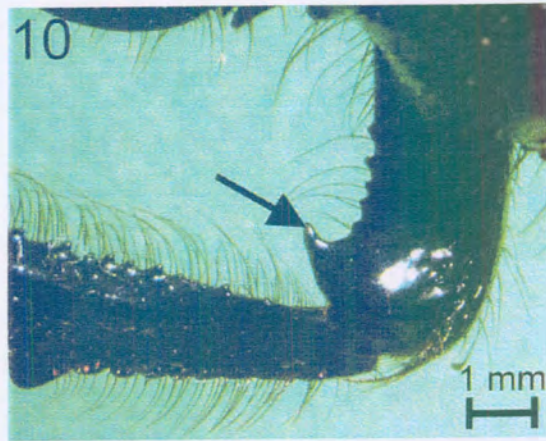
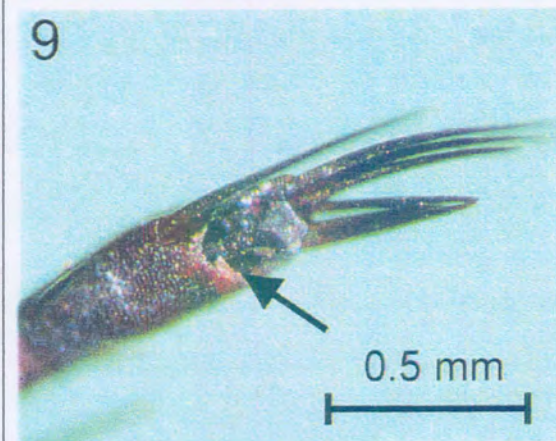
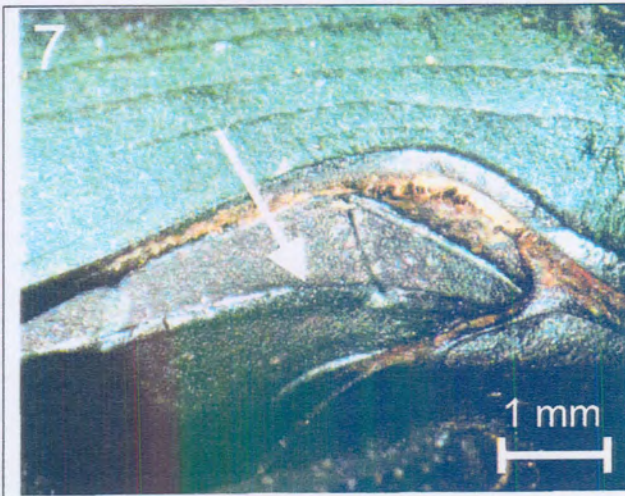
- b. First metatarsal article strongly flattened and broadened, longer than combined length of all other articles (Fig. 3.24); anterior half of metasternum with two median keels.....*Tragiscus dimidiatus*
- b'. First metatarsal article only weakly broadened, no longer than combined length of all other articles; metasternum lacking keels.....c
- c. Lateral margins of head angular and indented between clypeus and genae, genae prominent; apex of elytra with row of erect setae (Fig. 3.25); pronotal disc unmodified; patterned in brown and yellow.....*Tiniocellus spinipes*
- c'. Genae rounded with no more than weak indentation of margin between clypeus and genae.....d
- d. In lateral view sides of pronotal disc concave proximally to posterior angles; head and pronotal disc sculptured.....*Liatongus militaris*
- d'. In lateral view sides of pronotal disc straight or convex to posterior angles; head and pronotal disc only sculptured in large taxa; dorsum at least partly shiny.....*Oniticellus*

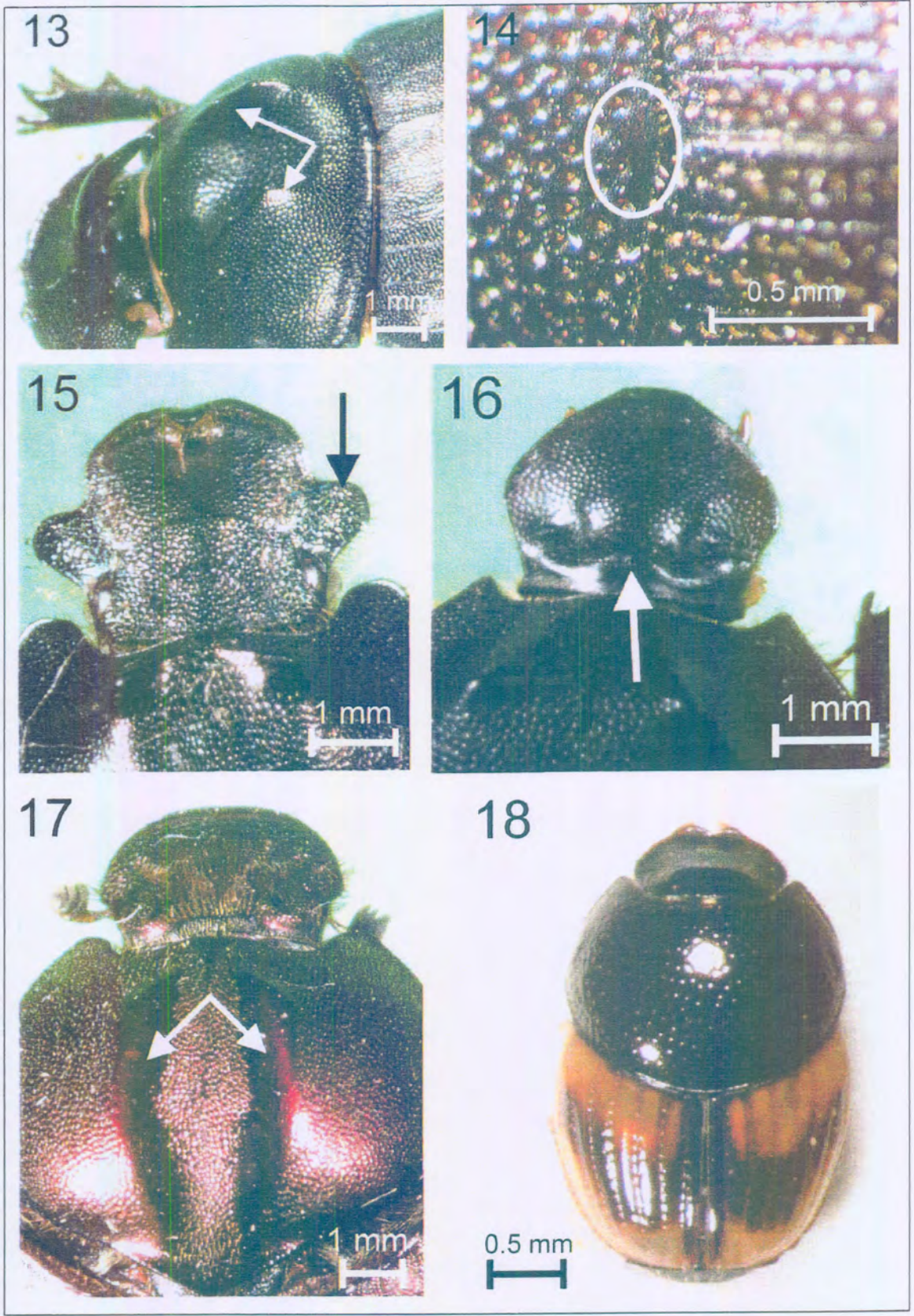
Oniticellus

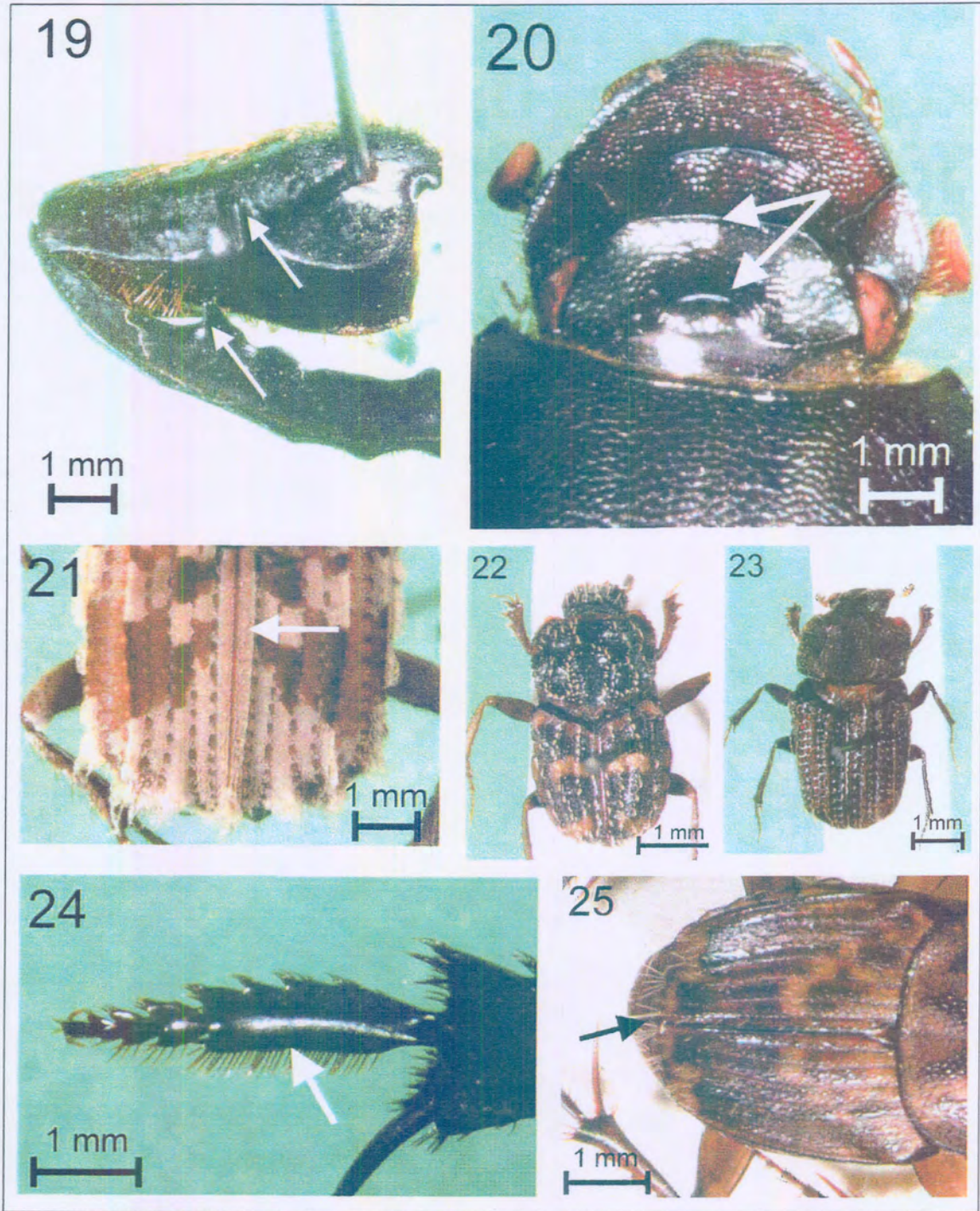
- i. Clypeus, pronotum and elytra black and brown patterned with brown legs; clypeus quadridentate.....*Oniticellus formosus*
- i'. Clypeus, pronotum and elytra black, clypeus bidentate.....
.....*Oniticellus planatus*

Fig. 3.1 (1-25). 1. Protibia of *Scarabaeus goryi* with **a.** terminal spur and **b.** two spines on the internal margin; 2. Tarsus of *Copris urus*; 3. Hind trochanter of *Neosisyphus fortuitus*; 4. Spine-like projection on mesofemur of *Neosisyphus mirabilis*; 5. Emarginated elytra of the Gymnopleurini; 6. Lateral view of *Gymnopleurus virens* showing the fused metasternal epimeron and first abdominal sternite; 7. Lateral view of *Garreta azureus* showing the suture between the metasternal epimeron and first abdominal sternite; 8. Ventral view of *Pachylomerus femoralis* showing the enlarged procoxae and -femorae; 9. Recessed metatarsal claws of *P. femoralis*; 10. Spine on profemur of *Scarabaeus galenus*; 11. Protuberance on mentum of *Scarabaeus zambesianus*; 12. Oblique ridges on ventral surface of the protibia of *Catharsius harpagus*; 13. Pronotal carinae of *Copris fidius*; 14. Base of pronotum of *Pedaria* sp. *I sensu* Davis; 15. Head of *Phalops boschas*; 16. Vertex of *Phalops flavocinctus* with basal lamina; 17. Pronotum of *Proagoderus bicallosus*; 18. *Onthophagus flavolimbatus*; 19. Profemur and -tibia of *Onitis deceptor*; 20. Head of *Onitis caffer*; 21. Elytra of *Cyptochirus ambiguus*; 22. *Drepanocerus kirbyi*; 23. *Drepanocerus impressicollis*; 24. Metatarsus of *Tragiscus dimidiatus*; 25. Apex of the elytra of *Tiniocellus spinipes* with erect setae.









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Abundance-body size relationships in a dung beetle assemblage: patterns, mechanisms and the effect of disturbance.

INTRODUCTION

Body size and abundance are two of the three fundamental macroecological variables that can be used to quantify animal assemblages. According to Gaston *et al.* (1993b) the following patterns have received the most attention in previous studies of these variables: (1) the species abundance distribution (number of species in different abundance classes), (2) the species body size distribution (number of species of different body-sizes), (3) the abundance-body size relationship (abundance of a species as a function of its body size), and (4) the total abundance:body size relationship (i.e. the total number of individuals, irrespective of species, as a function of body size). Although these four patterns are interrelated (Gaston *et al.* 1993b), to date the body size-abundance relationship (3 and 4 above) has been most extensively examined. A large body of literature exists that examine this relationship but the most comprehensive studies linking patterns and processes in macroecology are those of Blackburn and Gaston (e.g. Blackburn & Gaston 1999, 2001).

Two different patterns have emerged from the literature on abundance-body size relationships. Some studies have shown that smaller species tend to be more abundant than larger species (Damuth 1981; Lawton 1989; Pagel *et al.* 1991; Blackburn *et al.* 1993a; Blackburn & Gaston 1994; Cotgreave 1993; Currie 1993; Gaston *et al.* 1993b; Cambefort 1994; Loder 1997), while others have shown that species of intermediate size are most abundant (Blackburn *et al.* 1990; Gaston *et al.* 1993b; Stork & Blackburn 1993; Blackburn & Gaston 1994). These two patterns in the relationship between body size and abundance are usually explained by energetic constraints, i.e. that the abundance and body size of species in a population is determined by the amount of available energy in

the habitat. Damuth (1981) found that when the abundance and body mass of a given species are plotted logarithmically, a linear relationship with a slope of -0.75 exists. He also found that metabolic rate scales as $W^{+0.75}$, where W is body mass. Several studies of both insects and other taxa have supported these findings (Blackburn *et al.* 1993a, Cambefort 1994; Chown & Steenkamp 1996). Damuth (1981) further proposed that the energy used by a population of a given species is equal to the metabolic rate (R) multiplied by the population density (D). The relationship between $R \times D$ and the body mass (W) is $DR \propto W^{-0.75} \times W^{+0.75}$, which equals W^0 . The energy use of a species is thus independent of its body size, and all species in an assemblage therefore use equal amounts of energy because small-bodied species tend to be more abundant than large-bodied species. This was named the 'energetic equivalence rule' (Nee *et al.* 1991) (here referred to as hypothesis 1).

Six other hypotheses have however also been proposed to explain the negative relationship between body size and abundance (Blackburn & Gaston 1999). The first of these is the census area mechanism (hypothesis 2), which applies to the abundance-body size relationship only when abundance is a density measure (e.g. the number of individuals in a fixed sample area). A negative interspecific body size-density relationship is found when this mechanism applies because of variance in census area: small-bodied species are censused across smaller areas than large-bodied species (Blackburn & Gaston 1999; Gaston & Blackburn 2000). This means that a strong positive relationship between body mass of species and the area over which its density is censused exists (Blackburn & Gaston 1996, 1997; Gaston & Blackburn 2000). Therefore, sampling areas must be large enough for sufficient numbers of small and large individuals to occur in them, but small enough to ensure ease of sampling and replication. If the sampling area is too small, large bodied species will be sampled at very low abundances, which will result in a negative abundance-body size relationship. Different-sized census areas for different-sized species may result in this census-area effect (Blackburn & Gaston 1996, 1999).

The third hypothesis concerns latitudinal gradients in body size and abundance. Variation in body size and abundance are often found for species across different latitudes (Currie & Fritz 1993; Cushman *et al.* 1993; Taylor & Gotelli 1994; Hawkins & Lawton 1995; Blackburn & Gaston 1996; Gaston & Blackburn 1996). A negative body size-abundance relationship will exist if species occurring at high latitudes had lower

abundances than those at low latitudes (Blackburn & Gaston 1999; Gaston & Blackburn 2000). However, according to Blackburn and Gaston (1999) the latitudinal gradient mechanism will not result in a negative abundance-body size relationship because species at low latitudes tend to be smaller-bodied and less abundant than those at high latitudes. According to them, a negative abundance-body size relationship can result because small-bodied, rare species tend not to be sampled if a high proportion of these species are tropical (Lawton 1989). A disproportionate number of large-bodied tropical species are thus included in the analyses, resulting in a negative relationship between abundance and body size.

A negative relationship between abundance and body size may also be the result of a correlation between the latitude at which a species occurs and the species' position in the abundance-body size relationship. If species occurring at high latitudes fall below the abundance versus body size regression line, and species occurring at low latitudes fall above this regression line, abundance and body size will tend to increase with latitude (Blackburn & Gaston 1999; Gaston & Blackburn 2000). A negative abundance-body size relationship can thus be the consequence of compiling data from different latitudes (e.g. Currie & Fritz 1993).

Another hypothesis (4) proposed to explain the relationship between body size and abundance concerns concatenation of the underlying abundance and body size frequency distributions (Blackburn *et al.* 1993a; Blackburn & Gaston 1999). Here, random sampling from each of the abundance and body size frequency distributions is thought to result in a negative relationship between the two variables (also see Blackburn *et al.* 1990, Blackburn *et al.* 1993a, Currie 1993). This hypothesis is based on the assumption that the shape of the abundance frequency distribution is log-normal (Sugihara 1980; Tokeshi 1990; Nee *et al.* 1991; Gregory 1994). Taxa usually have more small-bodied than large-bodied species (Blackburn & Gaston 1994, Brown 1995). This results in small-bodied species representing a larger proportion of the underlying abundance frequency distribution. Small-bodied species will thus have higher maximum abundances (total number of individuals irrespective of species) than large-bodied species (Blackburn *et al.* 1993a). If this model were coupled with a minimum viable abundance constraint, where small-bodied species had higher minimum viable abundances than large-bodied species, a linear negative abundance-body size relationship would be

expected (Blackburn & Gaston 1999). Blackburn and Gaston (1999) stated that, for this hypothesis to hold, abundances must be random samples from a potential log-normal distribution. The random sample will however not sample species with abundances below a certain threshold, i.e. species that are not sampled because their abundances are too low to be detected by the sampling effort (Blackburn *et al.* 1993b). The 'random sample' taken from the abundance frequency distribution will thus in fact not really be taken randomly because these small-bodied, rare species with abundances below the minimum viable abundance threshold will never be sampled (Blackburn *et al.* 1993b; Blackburn & Gaston 1999). According to Blackburn and Gaston (1999) these arguments suggest that the concatenation hypothesis is not sufficient to explain the negative abundance-body size relationship and hence an additional explanation is required.

Interspecific competition has never been used to explain the relationship between body size and abundance (Blackburn and Gaston 1999). Competition does, however, explain some of the patterns observed within taxa (hypothesis 5). Positive abundance-body size relationships are expected when species in the same guild are compared where large body size is an advantage in interspecific competition (e.g. Cotgreave & Harvey 1991; Nee *et al.* 1991; Cotgreave 1994). This is because phylogenetically distinct tribes tend to form complete guilds (Nee *et al.* 1991). Interspecific competition will therefore be intense in a guild and if large bodied species are able to apportion a larger amount of the available resources, a positive abundance-body size relationship will result (Cotgreave 1993).

The differential extinction mechanism (hypothesis 6) has also been proposed to explain the relationship between abundance and body size patterns within taxa (Blackburn & Gaston 1999). This hypothesis states that positive abundance-body size relationships across species within tribes are the result of extinction patterns (Blackburn *et al.* 1994). Within taxa, large-bodied species are more susceptible to extinction than small-bodied species (Gaston & Blackburn 1995). Rare, large-bodied species may thus differentially go extinct within tribes, but not small-bodied species of the same abundance (Blackburn & Gaston 1999). Therefore, the probability that rare, large-bodied species will have been lost due to extinction within a tribe will become greater the older the tribe. Older tribes will thus have positive abundance-body size relationships because they

consist of rare and common small-bodied species, but only out of common large-bodied species (Blackburn & Gaston 1999).

Because biomass, body size and abundance are linked, Blackburn and Gaston (1999) suggested an additional model (hypothesis 7) where the biomass frequency distribution and a constraint on minimum viable abundance result in a negative abundance-body size relationship. They suggested that patterns in abundance and body size distributions, and the relationship between them, could to a large extent be derived from the biomass frequency distribution. In this model Blackburn and Gaston (1999) made three key assumptions: (1) the amount of biomass maintainable in a habitat is dependent on, and proportional to, the amount of energy available in that habitat; (2) this biomass is divided among species in such a way that a log-normal biomass frequency distribution is produced; (3) a minimum viable population abundance exists below which populations become extinct.

Blackburn and Gaston (1999) argued that for a given size, species with lower biomass will have fewer individuals, but for a given biomass small-bodied species will have more individuals. However, biomass cannot be divided too finely because a lower limit exists to the amount of biomass a species requires (Hutchinson 1959; Lawton 1990). This means that for a minimum biomass there will be fewer large or more small individuals. This will cause a negative abundance-body size relationship where maximum achievable abundance will decrease with increasing body size (Blackburn & Gaston 1999).

In spite of these various proposed explanations Gaston and Blackburn (2000) consider only two of the first six hypotheses to explain the body size-abundance relationship within British bird assemblages. These are the census area and the latitudinal gradient mechanisms. This study empirically tests four of the seven hypotheses using dung beetle assemblage data for Tembe Elephant Park, i.e. the energetic equivalence rule (hypothesis 1), interspecific competition (hypothesis 5), differential extinction (hypothesis 6) and the biomass frequency distribution hypothesis (hypothesis 7). Two of the remaining hypotheses are not applicable to this study (census area (hypothesis 2) and the latitudinal gradient (hypothesis 3) mechanisms) because sampling took place at one latitude and in the same area. The concatenation hypothesis (hypothesis 4) was also not tested because dung beetle assemblages were sampled from actual body size and

abundance distributions and not from a potential log normal abundance distribution. No assumptions were made about the normality of the abundance and body size distributions.

Previous studies of dung beetle assemblages in Tembe Elephant Park showed that assemblages are homogenous within sand forest and mixed woodland habitats (the two dominant habitat types in Tembe), although pronounced heterogeneity was found between habitat types (Van Rensburg *et al.* 1999; and this study, Chapter 1). Also, disturbance, in the form of over-utilization of sand forest by elephants inside Tembe and clearing of sand forest by human communities outside the Park, altered dung beetle assemblage structure (Chapter 1). Therefore it was also tested whether the relationships between the macroecological variables (abundance, body size and biomass) differed between assemblages in mixed woodland, undisturbed and disturbed sand forest. When the dense sand forest vegetation is disturbed, the canopy opens and the plant community converts to a more open mixed woodland habitat. Dense vegetation has been shown to impede flight maneuverability and searching success of large dung beetles (Nealis 1977) and it was thus expected that mixed woodland and disturbed sand forest would have more large-bodied species than undisturbed sand forest.

MATERIAL AND METHODS

Dung beetles were sampled during December 1998 and January 2000 in Tembe Elephant Park (27°01'S 32°24'E), South Africa on the southern Mozambique Coastal Plain of northern KwaZulu Natal. Different areas were used for each of the sampling periods. Two mixed woodland and two undisturbed sand forest areas were sampled in each sampling period. During December 1998, closed canopy sand forest areas were sampled which represented undisturbed sand forest. Two human-disturbed sand forest areas adjacent to the reserve were also sampled. During January 2000 two sand forest areas were sampled inside the botanical reserve to exclude disturbance caused by elephants, and two elephant-disturbed sand forest areas were sampled inside the reserve. Elephant-disturbed sand forest was identified as areas that showed evidence of elephant activity such as large trees that were removed by these large herbivores. Therefore, the dung beetle assemblage sampled was representative of that of the habitats and disturbance states in Tembe Elephant Park.

During each of the sampling periods five grids of six pitfall traps each were placed in each area. The pitfalls were placed in a 2 x 3 design on a 2 m x 4 m grid. The traps were baited using 50 g elephant dung and set out for 24 hours. Sampling grids were placed a minimum of 200 m apart in each area to maintain sampling independence. The dung beetles collected were identified by comparison with identified specimens in the South African National Insect Collection and with the help of Dr A. Davis (pers. comm.).

Twenty individuals of each of the species collected were measured and the mean length of each species was used to calculate the body mass of the species using a length-mass regression equation. This equation was derived from the means of length (mm) and mass (g) taken previously from dung beetles from Tembe Elephant Park by Chown and Scholtz (in prep.): $\log_{10} \text{ body mass (g)} = 2.54301 \times \log_{10} \text{ body length (mm)} - 3.41734$ ($n = 211$, $P < 0.001$, $R^2 = 0.988$). The body mass frequency distributions, with body mass (g) logarithmically transformed, were then determined for each habitat type in each sampling period. Ten size classes were used (see Loder 1997 for discussion and recommendation). These distributions were compared between habitat types within sampling periods using Kendall's coefficient of concordance (Zar 1996). A Kolmogorov-Smirnov one sample test was used to test if the body mass frequency distributions differed significantly from a log-normal distribution.

The abundance of each species was determined within each of the habitat types for each sampling period. Abundance frequency distributions were compiled for the habitats (undisturbed sand forest, human- and elephant-disturbed sand forest and mixed woodland) using logarithmic abundance classes (Cotgreave 1993; Gaston *et al.* 1993b). These distributions were used to determine whether abundances changed between habitat types within sampling periods and were again compared using Kendall's coefficient of concordance (Zar 1996).

Energetic constraint (hypothesis 1)

Ordinary least squares (OLS) regression was used to determine the relationships between log body mass and log abundance for the study habitats in each sampling period (Gregory & Blackburn 1995). Blackburn *et al.*'s (1992) method was used to determine the negative upper bound slopes (NUBS) using eight size classes. A t-test was used to

determine if these negative upper bound slopes differed significantly from -0.75 (Zar 1996). Metabolic rate of the dung beetles was estimated using a consensus equation for arthropods provided by Lighton and Fielden (1995): $SMR = 906 BM^{0.825}$, where SMR is the standard metabolic rate in microwatts at 25°C and BM the body mass in grams. Dung beetles appear to fit well within this equation's limits (Davis *et al.* 1999). The energy use of the dung beetles in each of the habitat types during each sampling period was calculated from the metabolic rate of the different species and was then plotted against log body mass (g). The same body size classes were used as in the body mass frequency distributions and differences between the distributions within sampling periods were determined using Kendall's coefficient of concordance (Zar 1996). OLS regression was used to determine the relationship between the residual variation in the abundance-body size relationship and metabolic rate to test whether the energetic equivalence rule explained the relationship between abundance and body mass (Blackburn *et al.* 1996; Blackburn & Gaston 1999). The energetic constraint hypothesis will be refuted if a significant relationship exists between the residual variation of the abundance-body size relationship and energy use of the dung beetles (see Blackburn *et al.* 1996; Blackburn & Gaston 1999).

Interspecific competition (hypothesis 5) and differential extinction (hypothesis 6)

To examine the interspecific competition and differential extinction hypotheses, each dung beetle species was assigned to a functional group (according to Doube 1990) and tribe (Davis pers. comm.). The relationship between abundance and body size within each tribe was examined using OLS regression for each habitat type in each sampling period. The data for determining abundance-body size relationships were combined for functional groups I and II (all rollers) and for functional groups III, IV, V and VII (all non-rollers). Functional group VI was not included because this group breeds in dung buried by other beetles and does not compete for resources with other functional groups (Doube 1990). OLS was used to examine the body size-abundance relationships within the two groupings (FG I and II, and FG III, IV, V and VII) in each of the habitat types during each sampling period. The interspecific competition hypothesis will not be refuted if significant positive relationships exist between abundance and body size within the

rollers (FG I & II) and non-rollers (FG III, IV, V & VII). The differential extinction hypothesis will be refuted if the abundance-body size relationships (within the rollers and non-rollers, and within tribes) are not positive and do not differ significantly between the undisturbed and disturbed sand forest areas.

Biomass (hypothesis 7)

Comparative absolute biomass of the dung beetles in each habitat type and sampling period was estimated by multiplying the mean body mass and abundance of each species (Pagel *et al.* 1991). The biomass frequency distributions were determined for the three study habitats (mixed woodland, undisturbed and disturbed sand forest) within each sampling period by plotting the number of species against log biomass. These distributions were compared using Kendall's coefficient of concordance (Zar 1996). A Kolmogorov-Smirnov one sample test was used to test if the biomass frequency distributions differed significantly from a log-normal distribution. Gaston and Blackburn's (1999) biomass hypothesis will be refuted if the biomass frequency distributions differed significantly from log-normal. The total biomass within each of the size classes (the same size classes used to determine the body mass frequency distributions) was also determined. Frequency distributions of biomass versus body mass were determined for each habitat type within each sampling period to determine how biomass changed with body size in the three habitat types. Kendall's coefficient of concordance (Zar 1996) was used to test whether these distributions differed between habitat types within sampling periods.

RESULTS

A total of 76 species in 25 genera were collected over the two sampling periods (Appendix A). Total species richness and abundance of dung beetles were highest in mixed woodland (Table 4.1). Mixed woodland assemblages had significantly higher mean species richness and mean abundance in December 1998 (Table 4.1). In January 2000 no significant differences were found in mean species richness between habitat types, but mean dung beetle abundance in mixed woodland was significantly higher than

that of undisturbed sand forest (Table 4.1). Mean body mass (g) (Appendix B) and body length (mm) was not significantly different between habitats within sampling periods, but mean dung beetle biomass (g) was significantly lower in human-disturbed sand forest in December 1998 than in the undisturbed sand forest and mixed woodland (Table 4.2).

Table 4.1. Species richness and abundance of dung beetles collected in mixed woodland and sand forest during each sampling period. n = number of sampling grids, S = total richness, N = total abundance, Tembe = undisturbed sand forest and mixed woodland combined. No letters in common denote significant differences at the table-wide α level of $p < 0.05$.

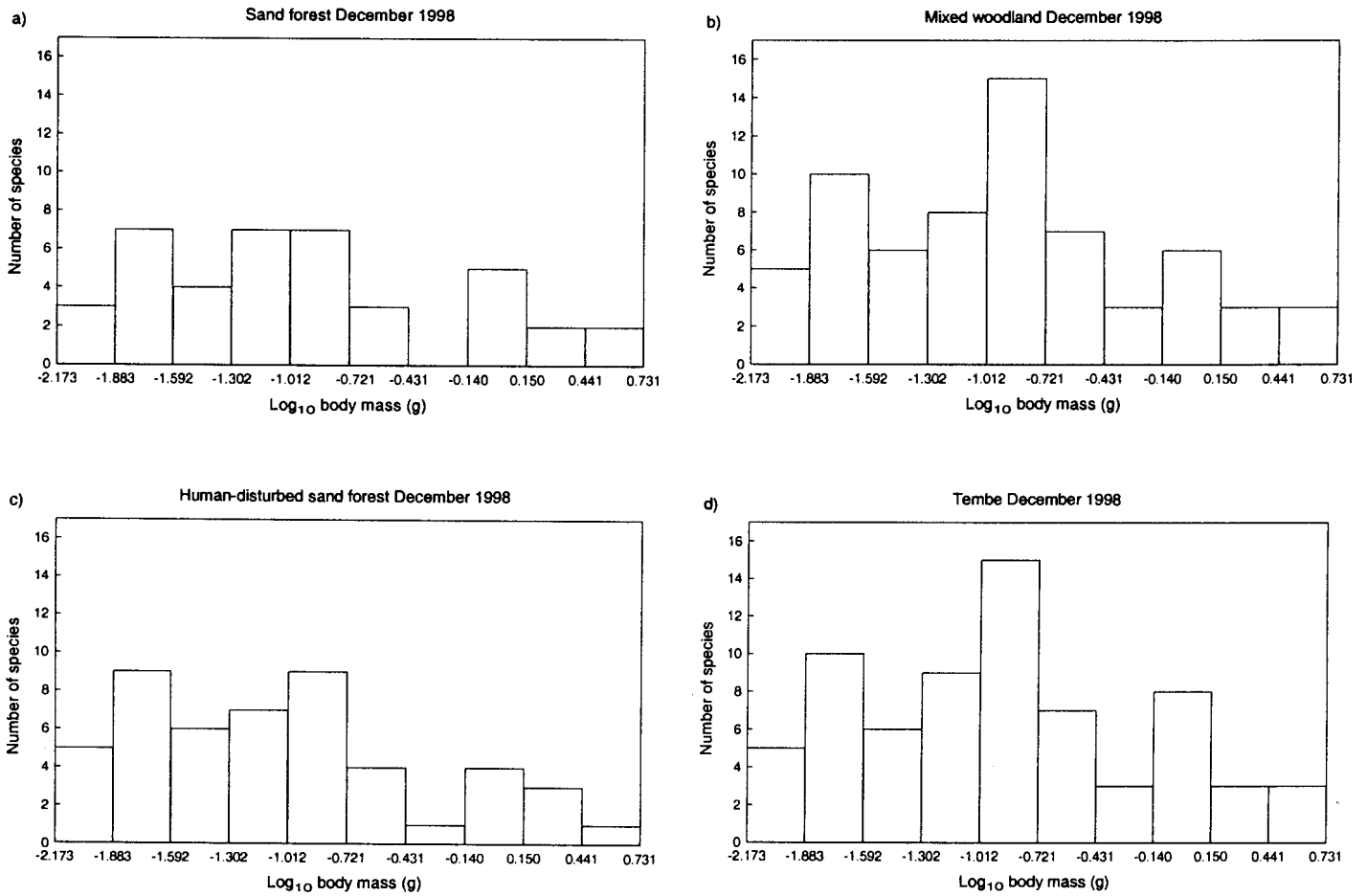
Habitat and sampling period	Richness mean \pm S.E.	Abundance mean \pm S.E.	n	S	N
December 1998	($F_{3,46} = 0.954$, $P < 0.01$)	($F_{3,46} = 7.275$, $P < 0.01$)			
Sand forest	22.40 \pm 1.69 a	675.90 \pm 110.04 ab	10	39	6759
Human-disturbed sand forest	19.60 \pm 1.39 a	543.20 \pm 187.73 b	10	48	5432
Mixed woodland	39.60 \pm 2.35 b	1886.80 \pm 257.70 c	10	65	18863
Tembe	30.95 \pm 2.61 ab	1281.10 \pm 194.58 ac	20	69	25622
January 2000	($F_{3,46} = 1.593$, $P = 0.204$)	($F_{3,46} = 3.055$, $P = 0.038$)			
Sand forest	18.60 \pm 0.95	222.70 \pm 25.70 a	10	37	2227
Elephant-disturbed sand forest	21.30 \pm 1.37	317.80 \pm 58.03 ba	10	39	3178
Mixed woodland	21.90 \pm 1.12	421.30 \pm 45.42 c	10	44	4213
Tembe	20.25 \pm 0.81	322.00 \pm 34.12 abc	20	52	6440

Table 4.2. Mean body size and biomass per dung beetle species collected in mixed woodland and sand forest during each sampling period. Biomass was compared between habitats within sampling periods using Kruskal-Wallis ANOVA by ranks. No letters in common denote significant differences at the table-wide α level of $p < 0.05$. N = number of sampling grids, Tembe = undisturbed sand forest and mixed woodland combined.

Habitat and sampling period	Body length (mm) mean \pm S.E.	Body mass (g) mean \pm S.E.	Biomass (g) Mean \pm S.E.
December 1998	($F_{3,217} = 0.444$, $P = 0.722$)	($F_{3,217} = 0.214$, $P = 0.887$)	($H_{3,221} = 17.457$, $P < 0.001$)
Sand forest	11.40 \pm 1.41	0.44 \pm 0.15	28.97 \pm 14.04 ac
Human-disturbed sand forest	10.58 \pm 1.17	0.36 \pm 0.12	5.21 \pm 1.55 ab
Mixed woodland	11.98 \pm 1.10	0.48 \pm 0.12	57.34 \pm 28.80 c
Tembe	12.38 \pm 1.07	0.50 \pm 0.12	70.16 \pm 32.98 c
January 2000	($F_{3,168} = 0.004$, $P = 0.999$)	($F_{3,168} = 0.004$, $P = 0.999$)	($H_{3,172} = 1.617$, $P = 0.656$)
Sand forest	13.29 \pm 1.82	0.70 \pm 0.21	11.26 \pm 5.28
Elephant-disturbed sand forest	13.14 \pm 1.73	0.68 \pm 0.20	17.09 \pm 7.18
Mixed woodland	13.37 \pm 1.63	0.67 \pm 0.20	25.07 \pm 11.34
Tembe	13.38 \pm 1.48	0.68 \pm 0.18	29.25 \pm 13.08

The body size frequency distributions (Fig. 4.1) were significantly different between habitat types within the December 1998 sampling period ($W = 0.788$, $\chi^2 = 23.634$, $n = 10$; Fig. 4.1a-c), but not within January 2000 ($W = 0.154$, $\chi^2 = 4.619$, $n = 10$; Fig. 4.1e-g). In December 1998 mixed woodland had the most species in the intermediate size classes (Fig. 4.1b) and the undisturbed and human-disturbed sand forests had most species in the small body size classes (Fig. 4.1 a, c). In January 2000 all habitat types (mixed woodland, undisturbed and elephant-disturbed sand forest) had the most species in the small body size classes (Fig. 4.1e-g). The two undisturbed sand forests (Fig. 4.1a, e) had no species in the seventh size class (0.371 – 0.724 g), while the human- (Fig. 4.1c) and elephant-disturbed sand forests (Fig. 4.1g) had only one species each in this size class, namely *Copris inhalatus* spp. *sanctaluciaae*. Also, seven species more were present in the fifth size class (0.097 – 0.190 g) in Tembe 2000 (Fig. 4.1h) compared to Tembe 1998 (Fig. 4.1d). None of the body mass frequency distributions were significantly different from a log-normal distribution (Table 4.3).

The abundance frequency distributions (Fig. 4.2) were also significantly different between habitats within the December 1998 sampling period ($W = 0.214$, $\chi^2 = 8.344$, $n = 10$; Fig. 4.2a-c) and not within January 2000 ($W = 0.136$, $\chi^2 = 5.315$, $n = 10$; Fig. 4.2e-g). In December 1998 the human-disturbed sand forest (Fig. 4.2c) had most species in the low abundance classes while the undisturbed sand forest (Fig. 4.2a) and mixed woodland (Fig. 4.2b) had more species of intermediate abundance. In January 2000 all three habitat types (mixed woodland, undisturbed and elephant-disturbed sand forest) had most species in the low abundance classes (Fig. 4.2e-g). When the total abundance of the beetles in the different habitat types was plotted against the same body mass classes used in determining the body size frequency distributions, the resulting frequency distributions (Fig. 4.3) of the three habitat types were significantly different from each other in both sampling periods (December 1998: $W = 0.658$, $\chi^2 = 19.727$, $n = 10$, Fig. 4.3a-c; January 2000: $W = 0.512$, $\chi^2 = 15.367$, $n = 10$, Fig. 4.3e-g). In December 1998, the three size classes ranging from 0.050 – 0.371 g had higher abundances in undisturbed (Fig. 4.3a) than in human-disturbed sand forest (Fig. 4.3c), even though human-disturbed sand forest had three species more in these size classes than the undisturbed areas (see Fig. 4.1).



(Fig. 4.1. a-d)

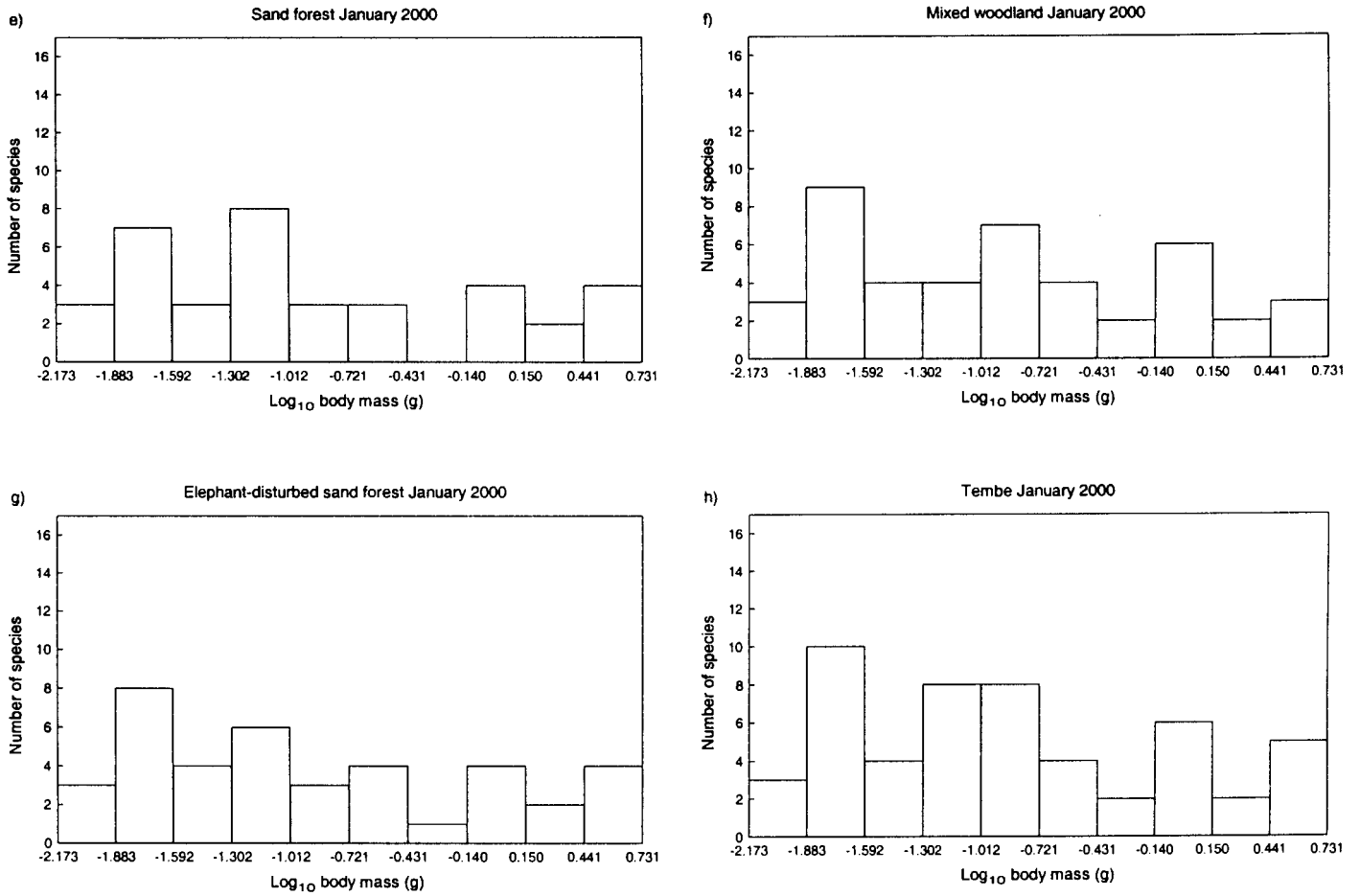
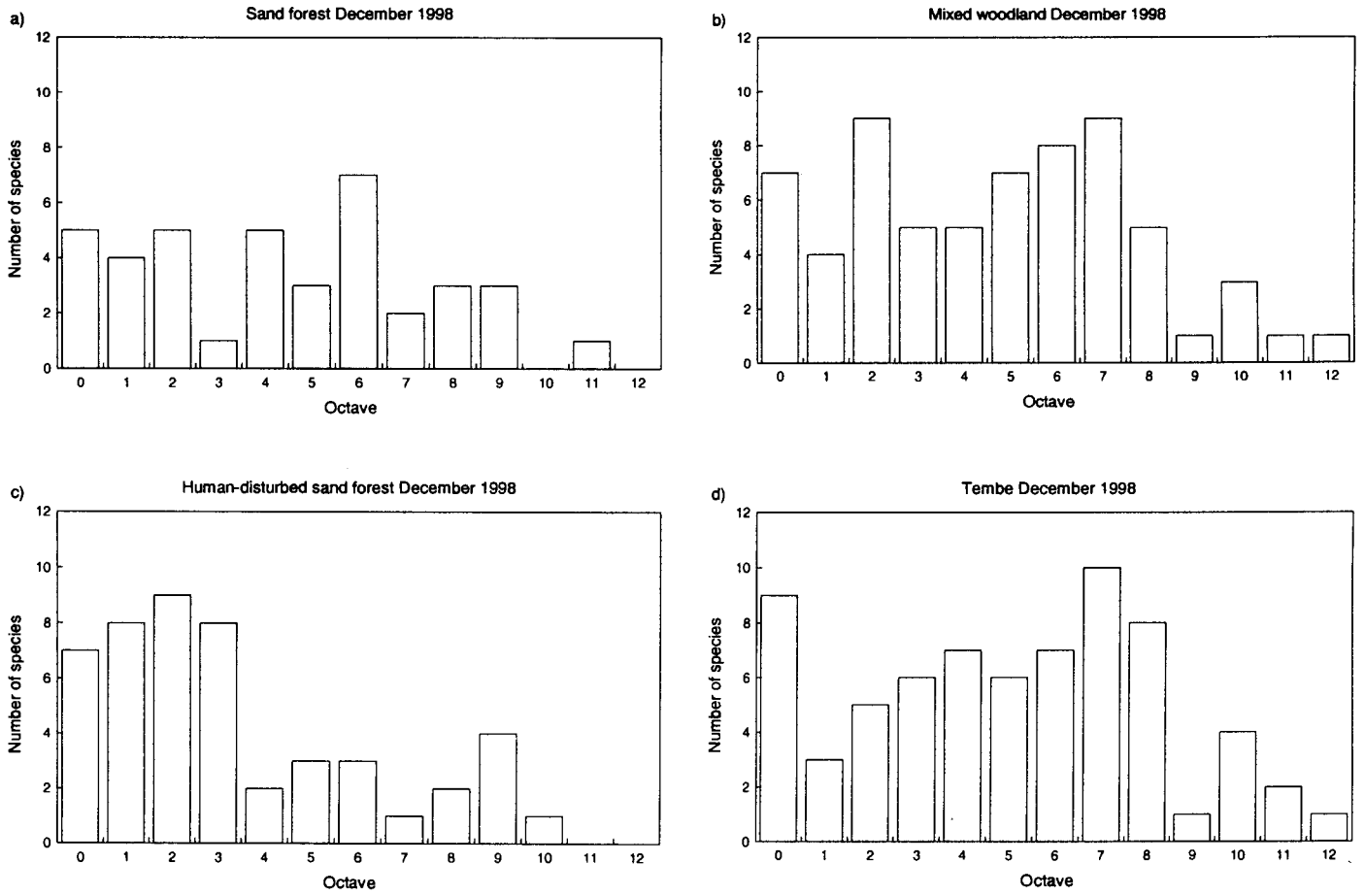


Fig. 4.1. a – h. Body mass frequency distributions for dung beetles in undisturbed sand forest, human- and elephant-disturbed sand forest, mixed woodland and in total for Tembe Elephant Park (undisturbed sand forest and mixed woodland). Each mass class equals 2.622 g.

Table 4.3. Results of Kolmogorov-Smirnov one sample test for a log-normal fit of body size (g) and biomass (g) frequency distributions of the dung beetles in the different habitat types within each of the sampling periods. d = K-S one sample test statistic, Tembe = undisturbed sand forest and mixed woodland combined.

Habitat	Body mass (g)		Biomass (g)	
	d	P	d	P
December 1998				
Sand forest	0.099	> 0.2	0.062	> 0.2
Human-disturbed sand forest	0.077	> 0.2	0.071	> 0.2
Mixed woodland	0.081	> 0.2	0.074	> 0.2
Tembe	0.078	> 0.2	0.118	> 0.2
January 2000				
Sand forest	0.152	> 0.2	0.071	> 0.2
Elephant-disturbed sand forest	0.122	> 0.2	0.080	> 0.2
Mixed woodland	0.093	> 0.2	0.065	> 0.2
Tembe	0.099	> 0.2	0.078	> 0.2



(Fig. 4.2. a –d)

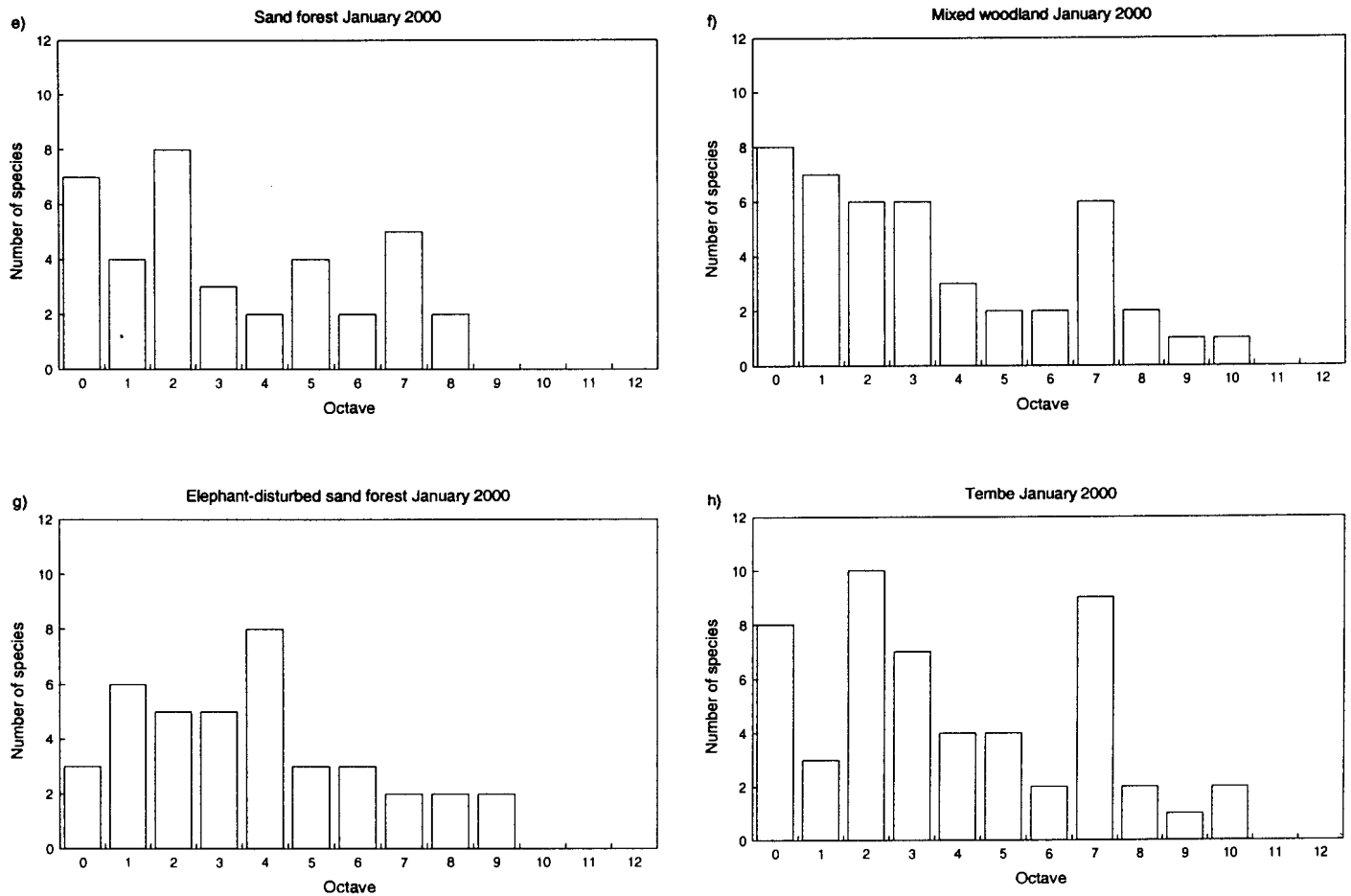
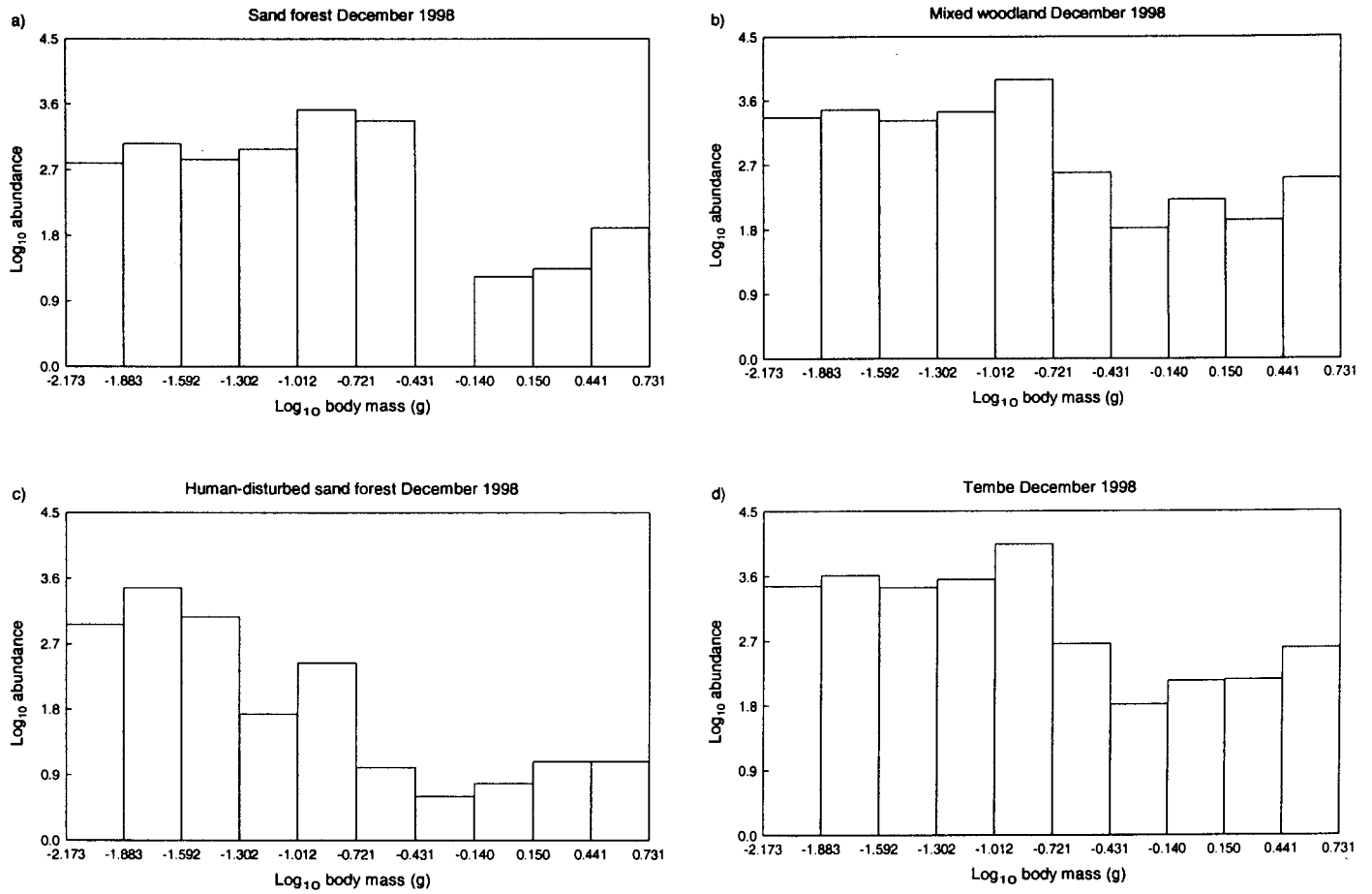


Fig. 4.2. a – h. Abundance frequency distributions for dung beetles in undisturbed sand forest, human- and elephant-disturbed sand forest, mixed woodland and in total for Tembe Elephant Park (undisturbed sand forest and mixed woodland). Each octave is a logarithmic abundance class with octave n containing all the species represented by at least 2^n individuals but fewer than 2^{n+1} . Thus octave 0 contains the species represented by 1 individual, octave 2, those with 3 - 4 individuals, octave 3, those with 5 – 8 individuals, etc.



(Fig. 4.3 a – d)

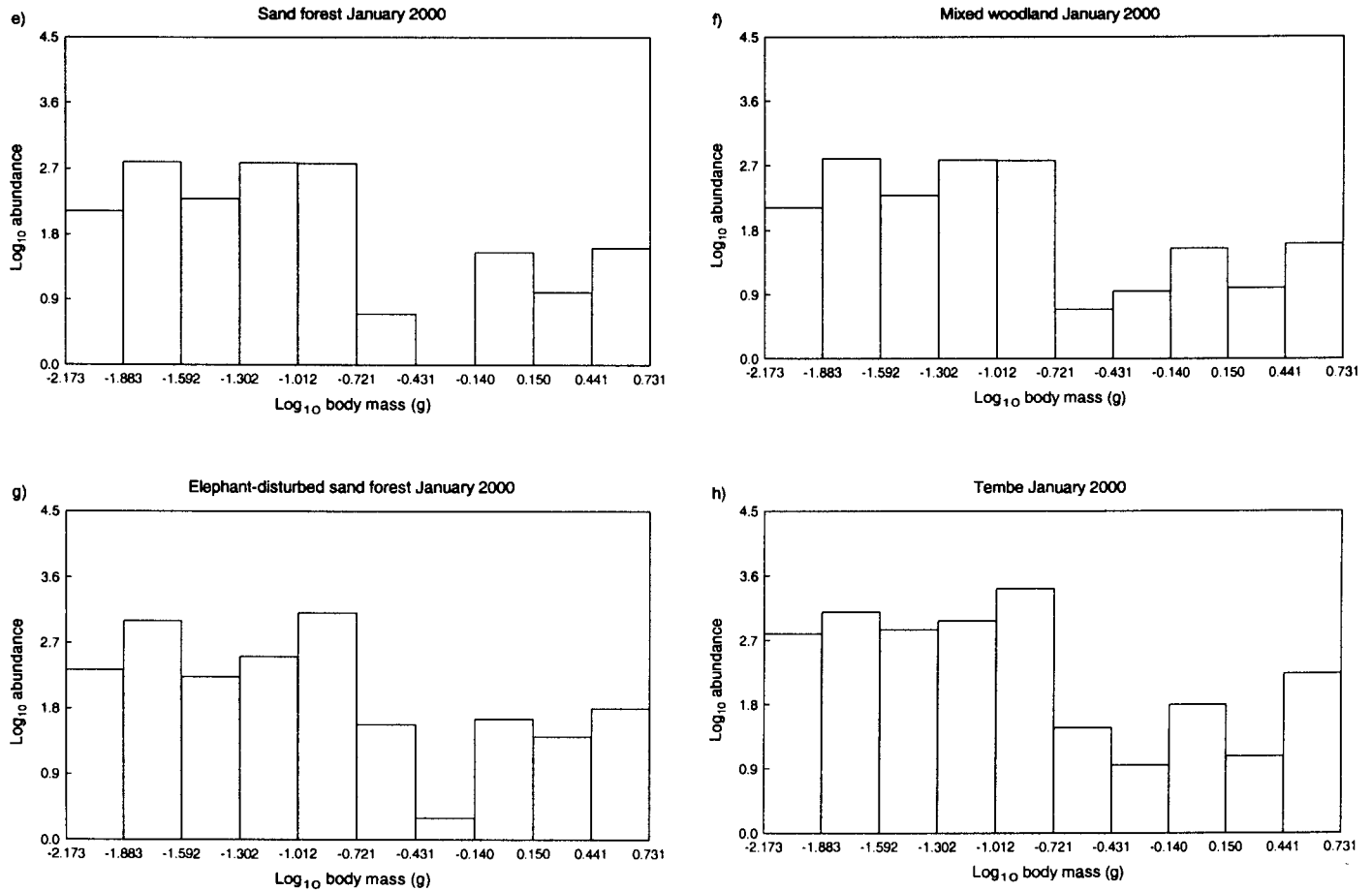


Fig. 4.3. a – h. The frequency distributions of log total abundance against log body mass (g) for dung beetles in undisturbed sand forest, human- and elephant-disturbed sand forest, mixed woodland and in total for Tembe Elephant Park (undisturbed sand forest and mixed woodland). Each mass class equals 2.622 g.

Energetic constraint (hypothesis 1)

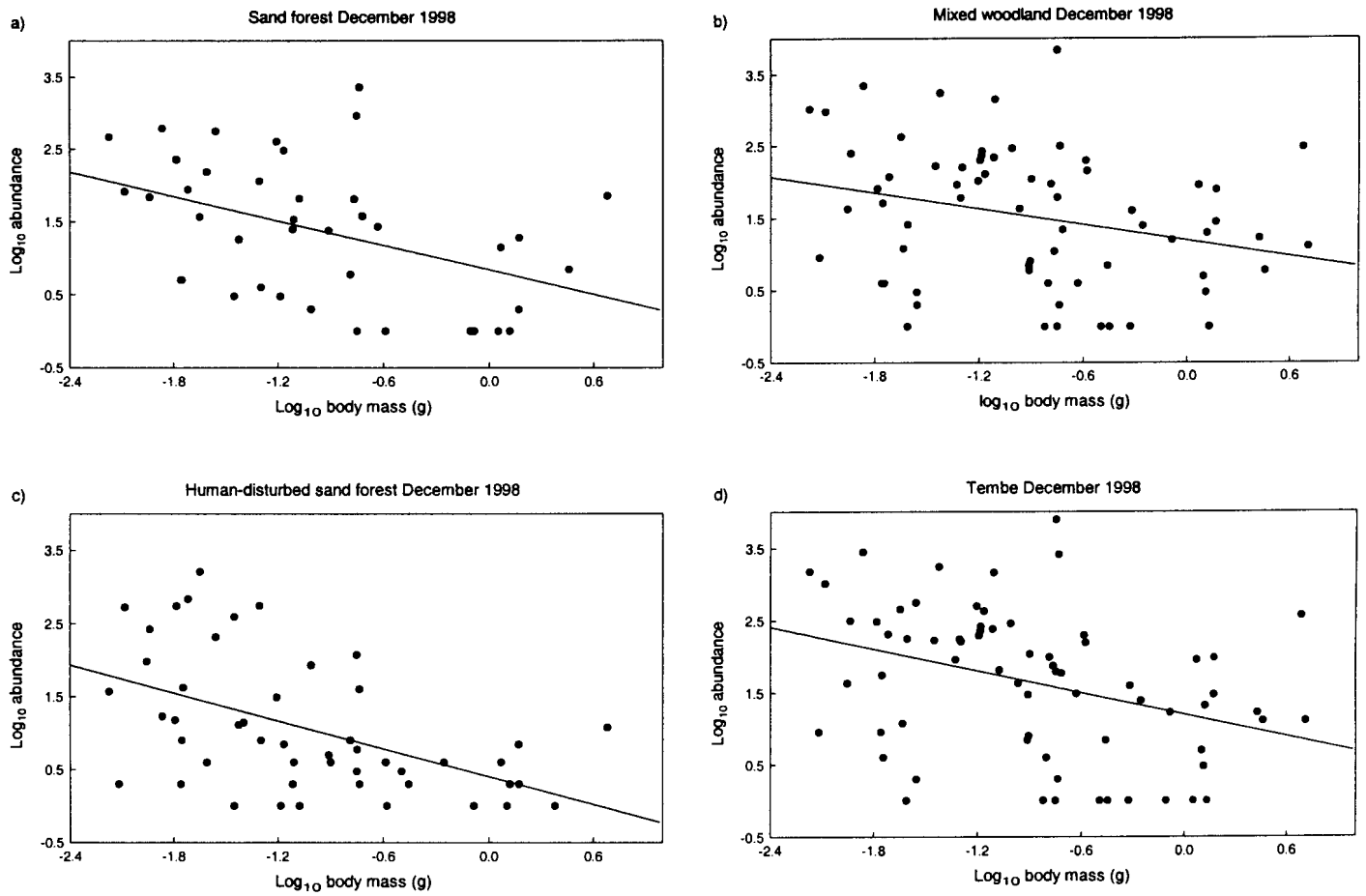
A significant negative relationship was found between body size and abundance in all habitat types (Table 4.4) and the shapes of these relationships were polygonal (i.e. maximum abundance peaks at intermediate body size while minimum abundance remains constant for all body sizes, e.g. Gaston & Blackburn 2000) (Fig. 4.4). Only the negative upper bound slope of the combined mixed woodland and undisturbed sand forest sampled during January 2000 (Fig. 4.4h) was significantly different from -0.75 even though these slopes ranged from -0.405 to -0.901 (Table 4.4). The energy use frequency distributions (Fig. 4.5) were also significantly different between habitat types within sampling periods (December 1998: $W = 0.483$, $\chi^2 = 14.500$, $n = 10$, Fig. 4.5a-c; January 2000: $W = 0.434$, $\chi^2 = 13.025$, $n = 10$, Fig. 4.5e-g). In all habitat types large-bodied species apportioned more energy than small-bodied species (Fig. 4.5). However, no significant relationships were found between the residual variation in the abundance-body size relationship and metabolic rate (Table 4.5). Therefore the energetic equivalence hypothesis was refuted.

Interspecific competition (hypothesis 5) and differential extinction (hypothesis 6)

After assigning species to tribes (Appendix A) and functional groups (Appendix B), the only significant relationships between body size and abundance were found in the Coprini in the elephant-disturbed sand forest (January 2000) and in the Sisyphini in the undisturbed sand forest areas sampled in both sampling periods (Table 4.6). In the Coprini this relationship was positive, while the relationship was negative in the Sisyphini (Table 4.6). Within functional groups, the overall relationship between body size and abundance was negative (Table 4.7). This negative abundance-body size relationship was significant within the non-rollers (Functional groups III, IV, V and VI combined), except in the undisturbed and elephant-disturbed sand forests (January 2000) (Table 4.7). No evidence was found that differences in body size-abundance relationships, within tribes (Table 4.6) and functional groups (Table 4.7), existed between undisturbed and disturbed sand forest areas. The interspecific competition and differential extinction hypotheses were thus also refuted.

Table 4.4. Slopes of the regressions of the relationships between log abundance and log body mass (g) for undisturbed sand forest, human- and elephant-disturbed sand forests, mixed woodland and in total for Tembe Elephant Park (i.e. sand forest and mixed woodland, Tembe), for each sampling period, using ordinary least squares: N = number of species, b = slope, NUBS = negative upper bound slope. Values in parentheses are 95 % confidence intervals for the slopes. Asterisks indicate negative upper bound slope significantly different from -0.75 .

Habitat type	N	R ²	P <	b	NUBS
December 1998					
Sand forest	39	0.191	0.005	-0.562 (-0.752, -0.372)	-0.750 (-1.164, -0.336)
Human disturbed sand forest	48	0.260	0.001	-0.637 (-0.794, -0.480)	-0.901 (-1.110, -0.692)
Mixed woodland	65	0.078	0.024	-0.365 (-0.522, -0.208)	-0.446 (-0.738, -0.154)
Tembe	69	0.132	0.002	-0.506 (-0.664, -0.348)	-0.474 (-0.781, -0.167)
January 2000					
Sand forest	37	0.223	0.003	-0.469 (-0.617, -0.321)	-0.414 (-0.716, -0.112)
Elephant disturbed sand forest	39	0.106	0.043	-0.306 (-0.452, -0.161)	-0.452 (-0.737, -0.167)
Mixed woodland	44	0.089	0.049	-0.330 (-0.492, -0.168)	-0.449 (-0.751, -0.147)
Tembe	52	0.171	0.002	-0.463 (-0.607, -0.319)	-0.405* (-0.704, -0.106)



(Fig. 4.4 a – d)

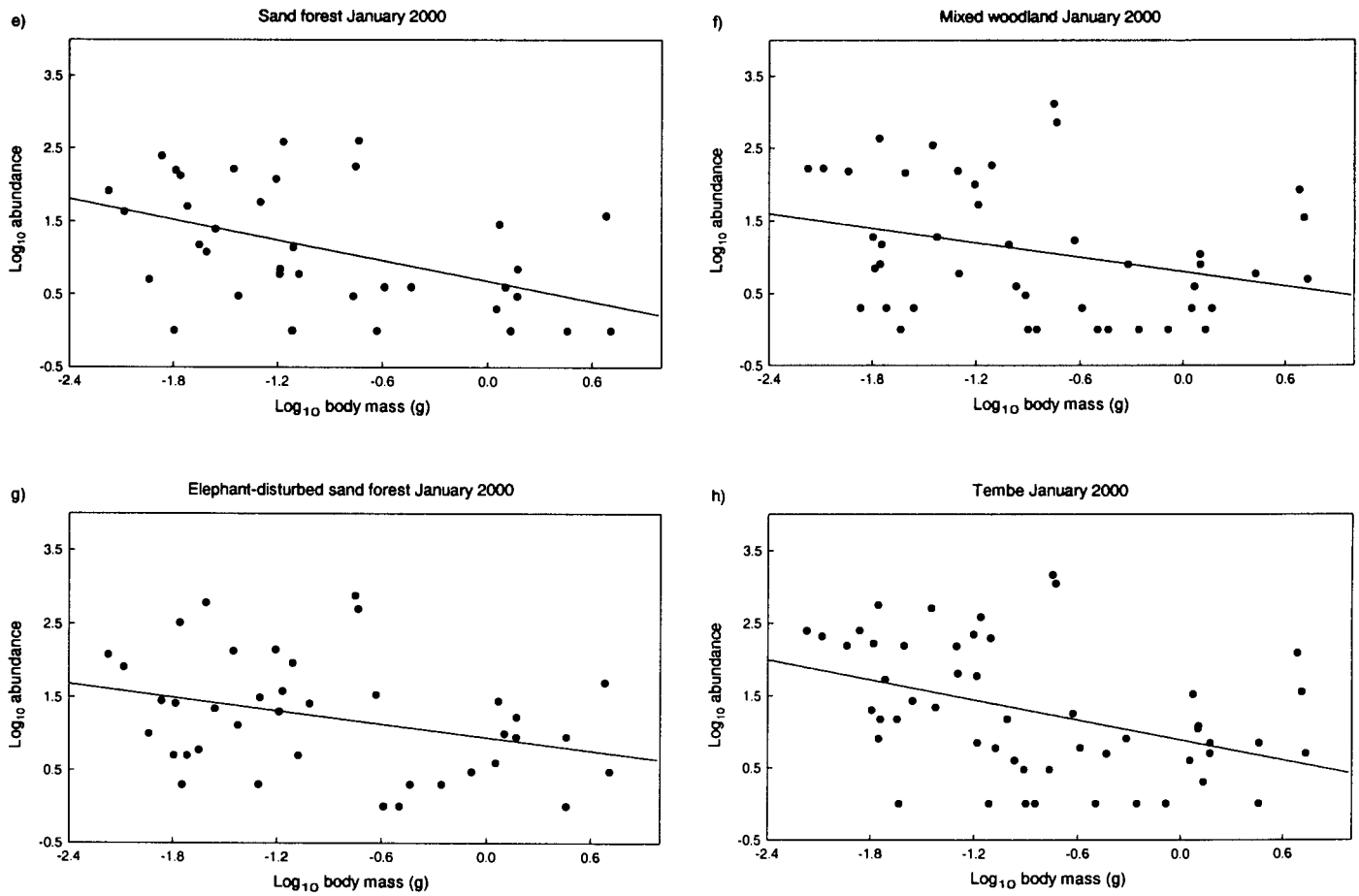
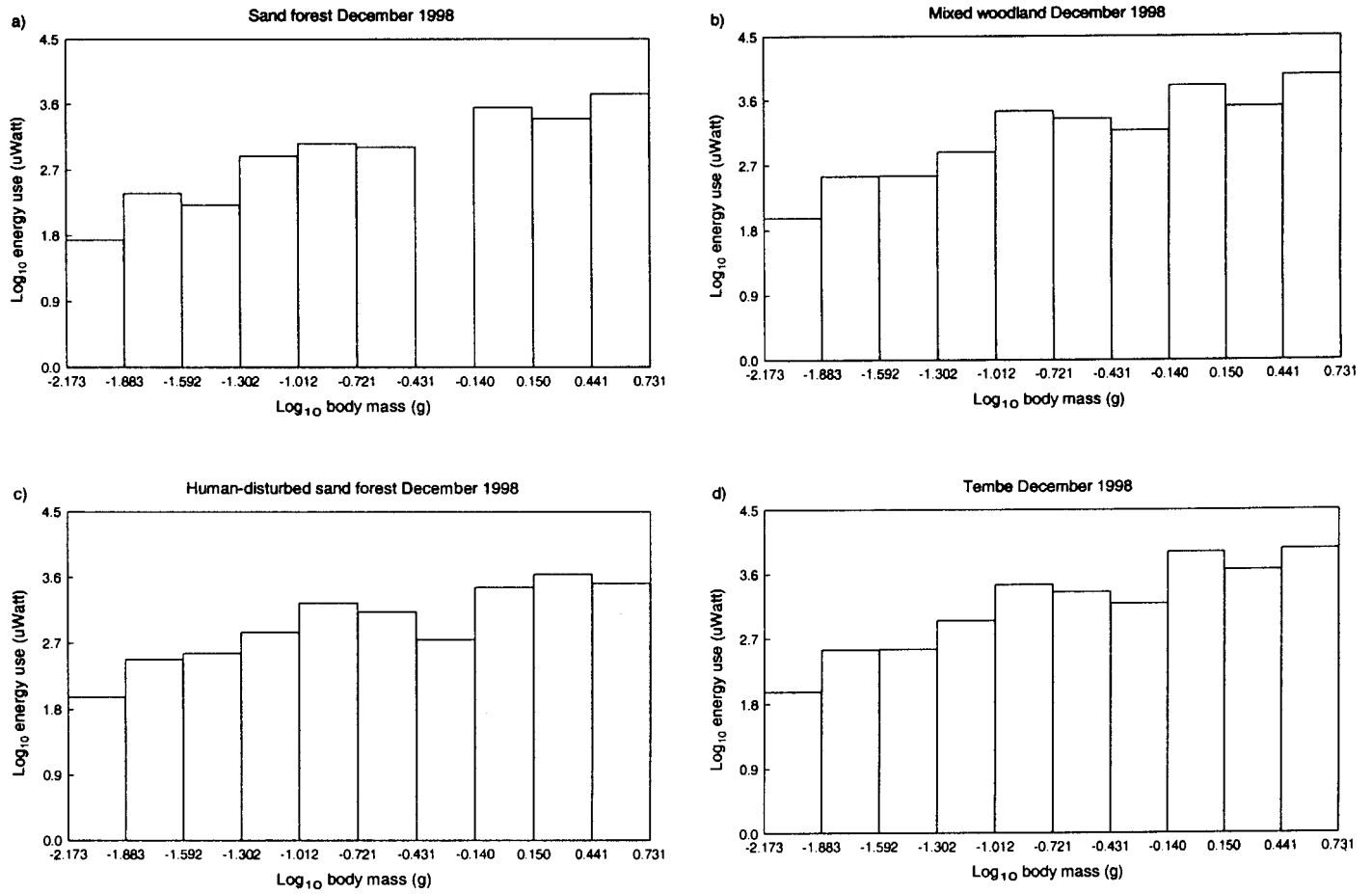


Fig. 4.4. a – h. The relationship between body size and abundance for dung beetles in undisturbed sand forest, human- and elephant-disturbed sand forest, mixed woodland and in total for Tembe Elephant Park (undisturbed sand forest and mixed woodland).



(Fig. 4.5 a – d)

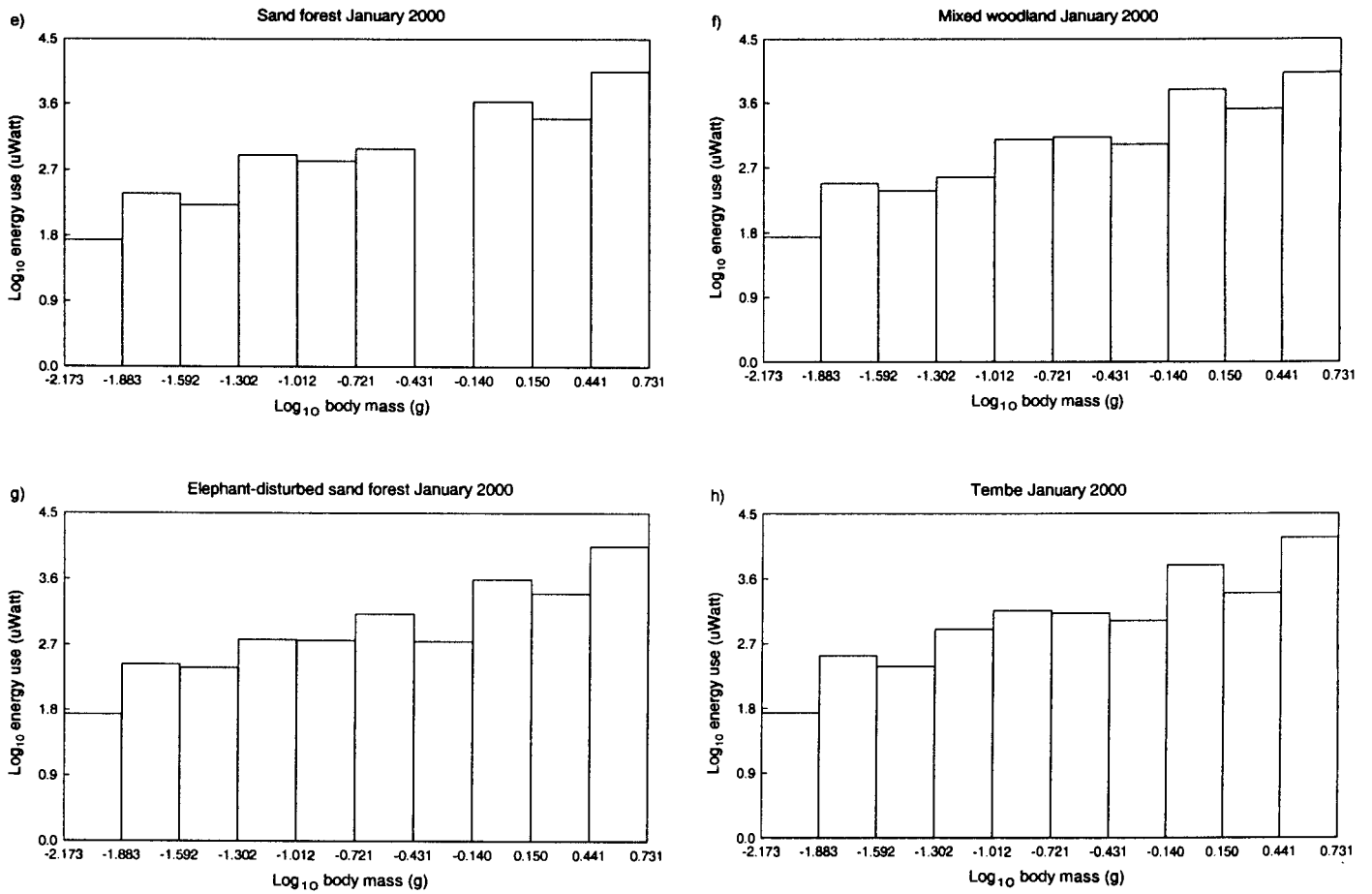


Fig. 4.5. a – h. Energy use:body mass distribution for dung beetles in undisturbed sand forest, human- and elephant-disturbed sand forest, mixed woodland and in total for Tembe Elephant Park (undisturbed sand forest and mixed woodland). Each mass class equals 2.622 g.

Table 4.5. Relationship between the residual variation in the abundance-body size relationship and metabolic rate of dung beetles in the undisturbed sand forest, human- and elephant-disturbed sand forests, mixed woodland and in total for Tembe Elephant Park (i.e. sand forest and mixed woodland, Tembe), for each sampling period.

Habitat	Energy Use (μ Watt)			
	N	df	F	P
December 1998				
Sand forest	39	37	0.117	0.734
Human disturbed sand forest	48	46	1.259	0.268
Mixed woodland	65	63	0.338	0.563
Tembe	69	67	0.333	0.566
January 2000				
Sand forest	37	35	0.019	0.891
Elephant disturbed sand forest	39	37	0.030	0.863
Mixed woodland	44	42	1.067	0.307
Tembe	52	50	1.425	0.238

Table 4.6. Regression results of log abundance against log body mass (g) within tribes for each habitat and sampling period. Tembe = undisturbed sand forest and mixed woodland combined. *P*-values are significant at the table-wide α -level of 0.05 using the sequential Bonferroni technique (Rice 1989).

Tribe	F(df)	R ²	B	<i>P</i> <
Coprini				
Sand forest 1998	3.025(1,3)	0.502	0.545	0.180
Human disturbed sand forest 1998	2.024(1,8)	0.202	-0.506	0.193
Mixed woodland 1998	0.179(1,6)	0.029	-0.103	0.687
Tembe 1998	0.265(1,7)	0.036	-0.121	0.623
Sand forest 2000	0.162(1,4)	0.039	-0.239	0.708
Elephant disturbed sand forest 2000	68.729(1,6)	0.920	0.628	0.001
Mixed woodland 2000	1.046(1,8)	0.116	0.483	0.336
Tembe 2000	0.709(1,9)	0.073	0.327	0.421
Oniticellini				
Mixed woodland 1998	1.387(1,4)	0.257	-0.317	0.304
Tembe 1998	0.713(1,4)	0.151	-0.255	0.446
Mixed woodland 2000	0.565(1,1)	0.361	-0.567	0.590
Tembe 2000	0.565(1,1)	0.361	-0.567	0.590
Onthophagini				
Sand forest 1998	0.013(1,17)	0.001	-0.013	0.910
Human disturbed sand forest 1998	2.391(1,27)	0.081	-0.137	0.134
Mixed woodland 1998	0.622(1,29)	0.021	-0.070	0.437
Tembe 1998	0.583(1,29)	0.020	-0.064	0.451



Table 4.6. (continued)

Sand forest 2000	1.614(1,16)	0.092	0.163	0.222
Elephant disturbed sand forest 2000	1.998(1,18)	0.100	0.160	0.175
Mixed woodland 2000	0.001(1,18)	0.001	-0.001	0.998
Tembe 2000	0.739(1,21)	0.034	-0.109	0.400
Scarabaeini				
Mixed woodland 1998	0.363(1,4)	0.083	0.191	0.579
Tembe 1998	1.911(1,4)	0.323	0.372	0.239
Sand forest 2000	0.688(1,2)	0.256	0.088	0.494
Elephant disturbed sand forest 2000	0.445(1,2)	0.182	0.081	0.573
Mixed woodland 2000	2.003(1,2)	0.500	0.389	0.293
Tembe 2000	0.818(1,3)	0.214	0.144	0.432
Sisyphini				
Sand forest 1998	9.846(1,4)	0.711	-0.607	0.035
Human disturbed sand forest 1998	26.066(1,1)	0.963	-0.220	0.123
Mixed woodland 1998	0.005(1,4)	0.001	-0.012	0.948
Tembe 1998	4.847(1,5)	0.492	-0.352	0.079
Sand forest 2000	23.912(1,3)	0.889	-0.615	0.016
Elephant disturbed sand forest 2000	0.026(1,2)	0.013	0.081	0.888
Mixed woodland 2000	0.282(1,2)	0.123	0.156	0.649
Tembe 2000	0.585(1,4)	0.128	-0.170	0.487

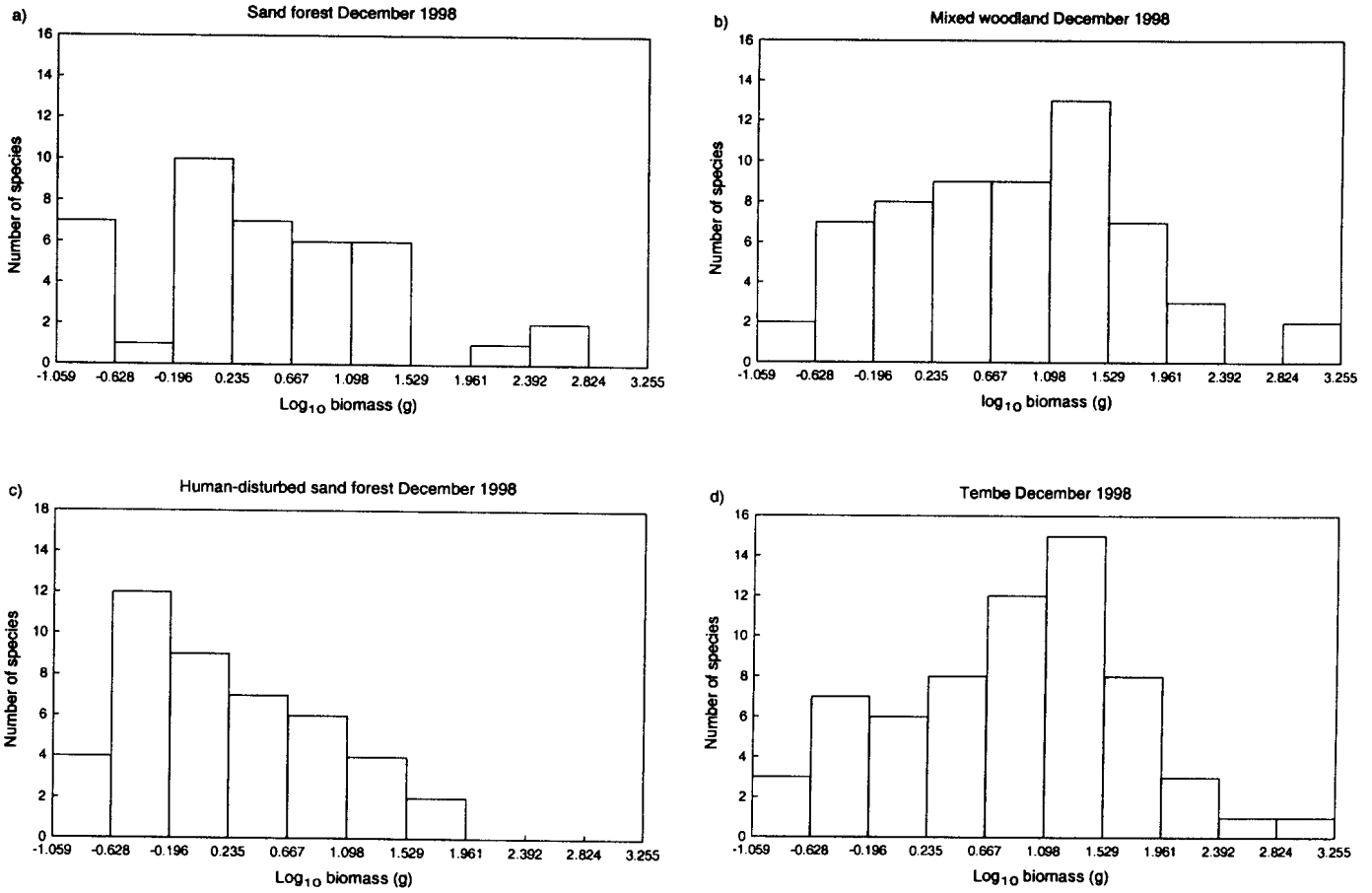
Table 4.7. Results of regression of log abundance against log body mass within functional groups in sand forest, undisturbed sand forest, human- and elephant-disturbed sand forests, mixed woodland and in total for Tembe Elephant Park (i.e. sand forest and mixed woodland, Tembe). *P* is significant at the table wide α -level of 0.05 using the sequential Bonferroni technique (Rice 1989).

Functional groups and habitat	F(df)	R ²	B	<i>P</i> <
Functional group I and II				
Sand forest 1998	4.339(1,8)	0.352	-0.604	0.071
Human disturbed sand forest 1998	0.187(1,4)	0.045	-0.204	0.688
Mixed woodland 1998	0.012(1,13)	0.001	0.026	0.913
Tembe 1998	2.136(1,15)	0.125	-0.275	0.165
Sand forest 2000	1.064(1,9)	0.106	-0.406	0.329
Elephant disturbed sand forest 2000	1.471(1,8)	0.155	-0.526	0.260
Mixed woodland 2000	0.304(1,8)	0.037	0.224	0.596
Tembe 2000	0.013(1,11)	0.001	-0.040	0.912
Functional group III, IV, V and VII				
Sand forest 1998	5.943(1,26)	0.186	-0.276	0.022
Human disturbed sand forest 1998	14.381(1,39)	0.269	-0.386	0.001
Mixed woodland 1998	5.830(1,44)	0.117	-0.227	0.020
Tembe 1998	7.952(1,48)	0.142	-0.238	0.007
Sand forest 2000	4.169(1,24)	0.148	-0.325	0.052
Elephant disturbed sand forest 2000	2.623(1,27)	0.089	-0.250	0.117
Mixed woodland 2000	6.920(1,31)	0.182	-0.332	0.013
Tembe 2000	12.100(1,36)	0.252	-0.386	0.001

Biomass (hypothesis 7)

The biomass frequency distributions of the dung beetle assemblages (Fig. 4.6) were not significantly different from each other within sampling periods (December 1998: $W = 0.133$, $\chi^2 = 3.989$, $n = 10$, Fig. 4.6a-c; January 2000: $W = 0.157$, $\chi^2 = 4.704$, $n = 10$, Fig. 4.6e-g). These distributions were also not significantly different from log-normal (Table 4.3). In December 1998 human-disturbed sand forest (Fig. 4.6c) had 11 species more in the second biomass class (0.236 – 0.637 g) than undisturbed sand forest (Fig. 4.6a), and no species in the eighth and ninth biomass classes (91.411 – 668.807 g).

The distributions of log total biomass against log body mass (g) (using the same mass classes used to determine the body size frequency distributions) (Fig. 4.7) were significantly different between habitat types within sampling periods (December 1998: $W = 0.658$, $\chi^2 = 19.727$, $n = 10$, Fig. 4.7a-c; January 2000: $W = 0.478$, $\chi^2 = 14.333$, $n = 10$, Fig. 4.7e-g). In December 1998 dung beetles in undisturbed sand forest (Fig. 4.7a) and mixed woodland (Fig. 4.7b) had high biomass in intermediate and large body size classes while human-disturbed sand forest (Fig. 4.7c) dung beetles had high biomass in smaller size classes. In January 2000 dung beetle assemblages in all three habitat types had high biomass in the intermediate and large body mass classes (Fig. 4.7e-g).



(Fig. 4.6. a – d)

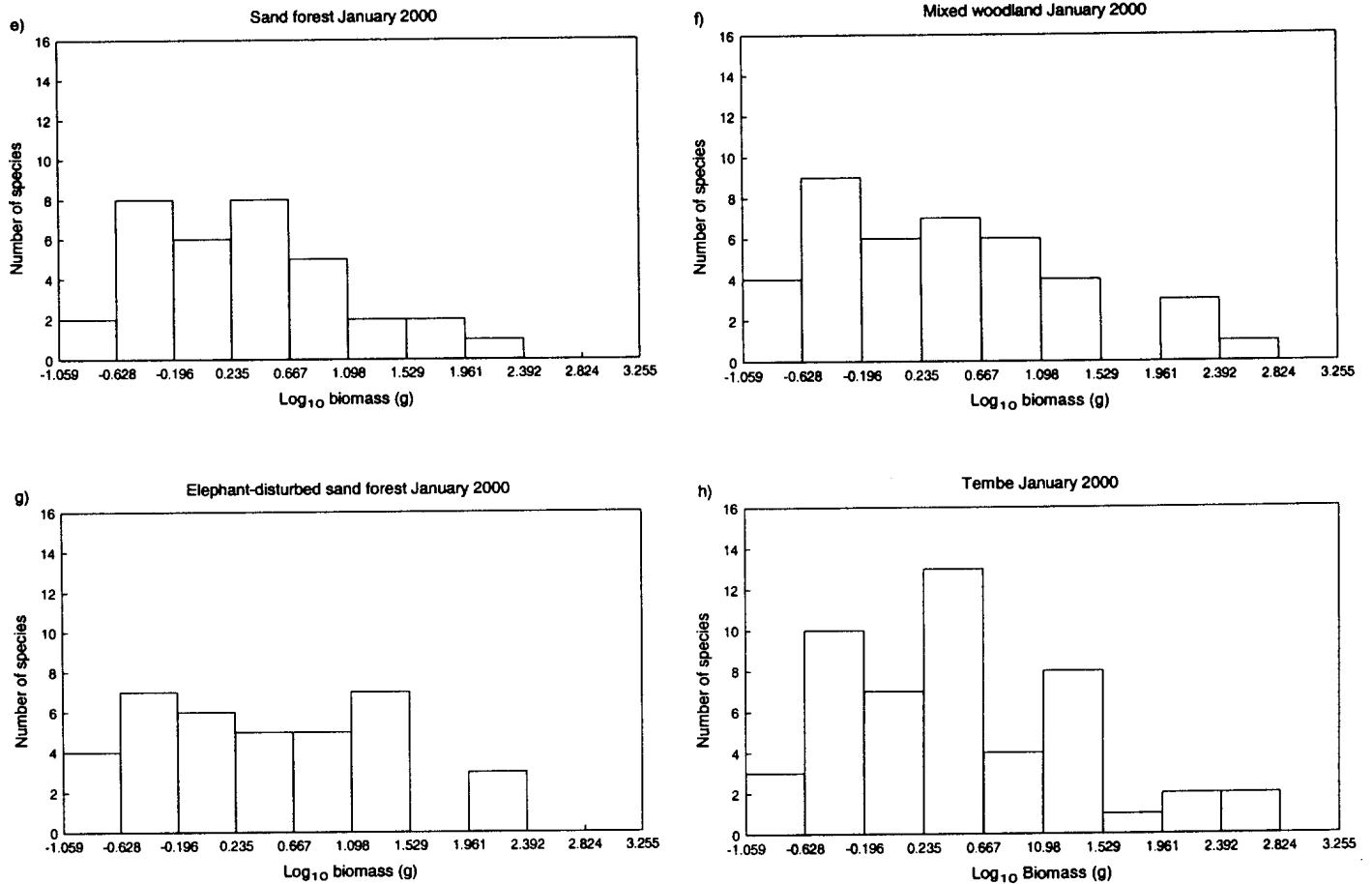
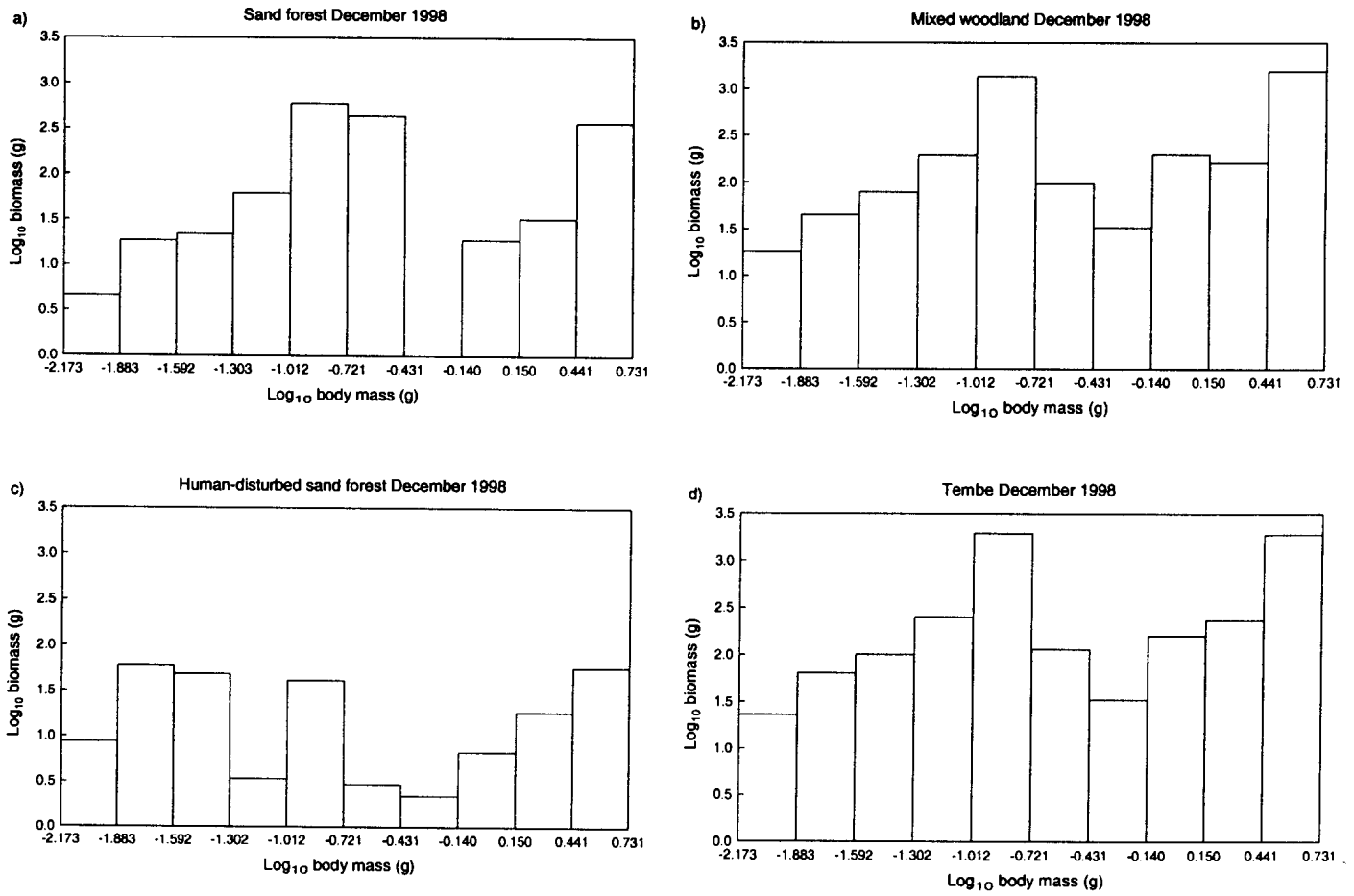


Fig. 4.6. a – h. The biomass frequency distributions for dung beetles in undisturbed sand forest, human- and elephant-disturbed sand forest, mixed woodland and in total for Tembe Elephant Park (undisturbed sand forest and mixed woodland).



(Fig. 4.7. a – d)

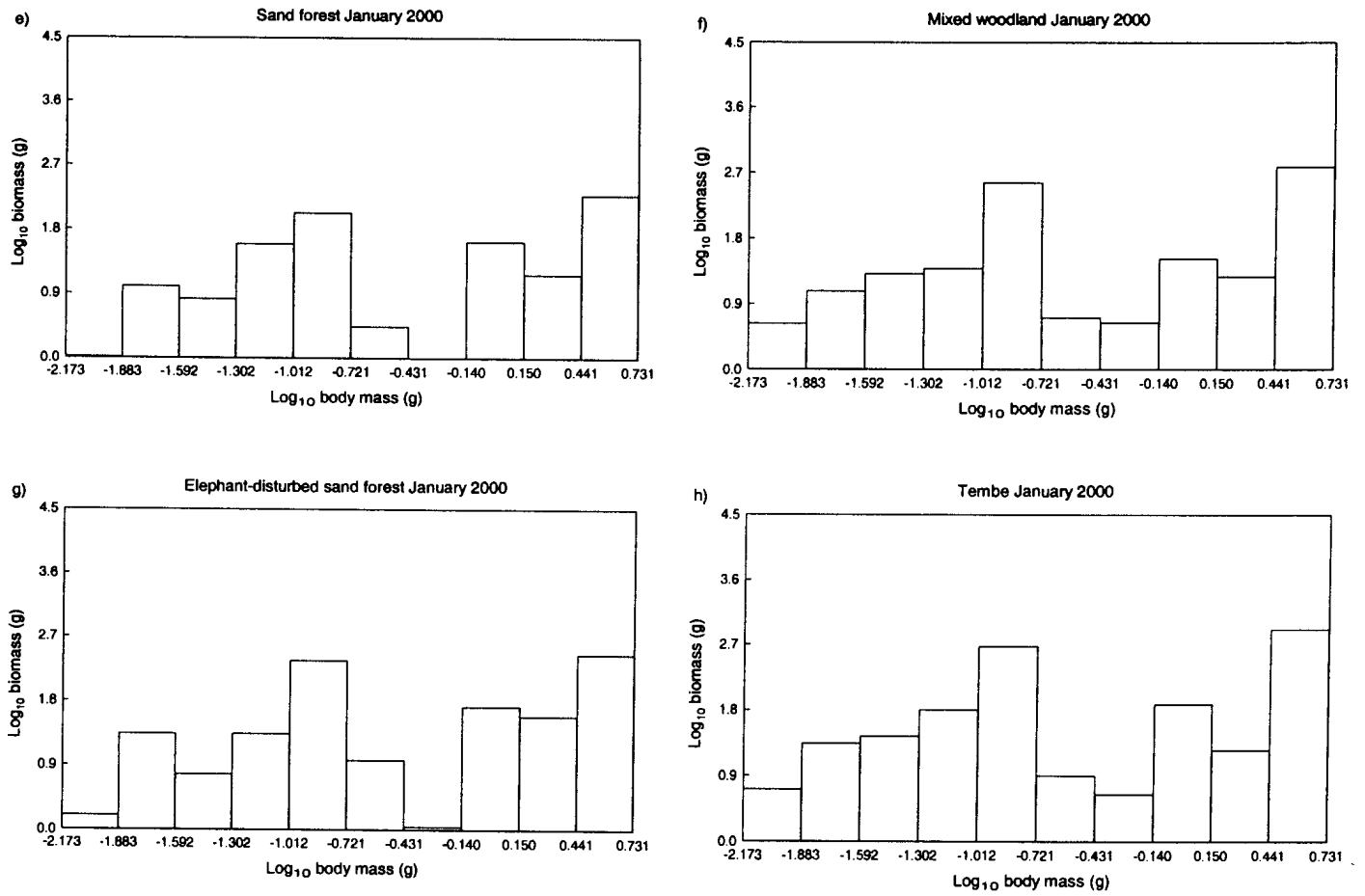


Fig. 4.7. a – h. Total biomass within each of the body mass classes of the dung beetles in undisturbed sand forest, human- and elephant-disturbed sand forest, mixed woodland and in total for Tembe Elephant Park (undisturbed sand forest and mixed woodland). Each mass class equals 2.622 g.

DISCUSSION

The body mass frequency distributions for all the dung beetle assemblages in this study fitted a log-normal distribution. This relationship has commonly been found for dung beetles in other areas (Chown & Steenkamp 1996; Gaston *et al.* 1993b). Blackburn and Gaston (1994), however, predicted a uniform distribution for assemblages in local habitats. Other studies reported species-body size distribution patterns ranging from being log-normal (Eadie *et al.* 1987; Morse *et al.* 1988) to significantly different from a log-normal distribution at local scales (Schoener & Janzen 1968; Basset & Kitching 1991; Gaston & Blackburn 2000). Gaston & Blackburn (2000) argued that species-body size distributions at local scales are random samples from the right-skewed distribution found at large (global and continental) scales, and this random sampling causes the variable species-body size patterns found at local scales.

Because this study was conducted at a local scale, less robust relationships between the parameters used to quantify animal assemblages (body size, abundance, biomass and energy use) are expected. Lawton (1989, 1990) gave three reasons why local and global relationships may differ. First, body size varies by many orders of magnitude in global relationships, while the variation is much smaller in local relationships. Second, rare species may be underrepresented in global studies because these studies are biased since data are compiled from the literature (Lawton 1989). In local studies rarity may be overestimated because transient individuals are included in samples (Lawton 1989, Blackburn *et al.* 1993a, Chown & Steenkamp 1996). Third, the inconsistent ways in which global data sets are compiled has an influence on slope estimates (Lawton 1989, 1990). Currie (1993) suggested that global and local patterns in relationships are different because local assemblages are truncated sub-samples of global assemblages. Chown and Steenkamp's (1996) study of southern African dung beetles supported this statement by Currie (1993) and it seems likely for the dung beetle assemblages in Tembe.

In an earlier study on dung beetle assemblages in Tembe, Van Rensburg *et al.* (1999) showed that sand forest and mixed woodland are quite different in vegetation structure, and that this has a pronounced influence on their dung beetle assemblages. They found that dung beetle assemblages were homogeneous within habitat types but differed between habitat types in Tembe, and that mixed woodland had a larger complex

of more characteristic species than the sand forest. Similar results were found in this study involving shorter periods of sampling during peak dung beetle activity periods. These differences between habitats may well be due to the fact that dense vegetation impedes flight manoeuvrability and searching success of large dung beetle species (Nealis 1977). The undisturbed sand forest is characterized by very dense vegetation compared to mixed woodland. Large dung beetles will thus be able to disperse more easily and will have a higher success rate at finding resources in the mixed woodland because it is more open (Nealis 1977; Cambefort 1994). Fewer large-bodied dung beetle species are thus expected in sand forest compared to mixed woodland. Similarly, disturbed sand forest is expected to have more large-bodied species than undisturbed sand forest because the vegetation structures of the disturbed areas are more open. However, contrary to expected all the habitat types had, however, a similar number of large-bodied species.

The abundance frequency distributions found in this study had the same bimodal appearance than those found in other local dung beetle assemblages, with peaks in the low and intermediate abundance classes (Hanski & Cambefort 1991, Chown & Steenkamp 1996). According to Hanski and Cambefort (1991) many rare species may be dispersers from other areas and more abundant species resident, which could result in the bimodal species-abundance relationship. Chown and Steenkamp (1996) tested this hypothesis by excluding transient species from their data. This did not alter the bimodal shape of the abundance frequency distribution, which suggests that tourists did not contribute to the bimodal shape. No species were thus excluded from the Tembe dung beetle data in determining the species-abundance relationships of the beetles in the different habitat types.

The abundance of large-bodied species was also expected to be higher within mixed woodland than in undisturbed sand forest, and higher in undisturbed sand forest than in disturbed areas, because of the differences in the vegetation structures of the different habitat types, as previously mentioned. Although large beetles were more abundant in mixed woodland compared to undisturbed sand forest, the abundance of intermediate to large species declined in human-disturbed sand forest compared to undisturbed areas. However, dung beetle assemblages in human disturbed sand forest are unique and associated with human activities (Chapter 1) and it is thus not surprising that

the observed pattern differs from the expected. The abundance of large-bodied species increased in elephant disturbed sand forest, as expected.

A polygonal abundance-body size relationship was found for the dung beetle assemblages in mixed woodland, undisturbed and disturbed sand forest. Blackburn and Gaston (1997) argued that the scale at which a study is executed would influence the abundance-body size relationship. According to them a negative linear relationship is found at global scales, where as a polygonal relationship is found at local scales. For example, studies conducted on local dung beetle assemblages have revealed polygonal relationships between abundance and body size (Blackburn *et al.* 1993a, Cambefort 1994, Chown & Steenkamp 1996). However, Blackburn *et al.* (1993a) suggested that polygonal abundance-body size relationships might be artefactual because sampling may be inadequate to determine the abundance of rare species. While this may have been the case for the technique used to sample dung beetles in Tembe, it is worth noting that abundances found in this study were generally much higher than those reported by Van Rensburg *et al.* (1999), especially for the December 1998 data. Nonetheless, there may still have been a sampling effect that could not be adequately accounted for.

According to Gaston *et al.* (1993a) tourists may increase the number of rare species sampled in a given area. Although the slope of the relationship between abundance and body size may be flattened if tourists are included, they found that tourist species in their study did not affect the abundance-body size relationship. Blackburn and Gaston (1997) stated that it is unlikely that tourist species will influence this relationship because these species are a minor component of species assemblages. In contrast with this, Chown and Steenkamp (1996) found that tourist species had an effect on the abundance-body size relationship of the dung beetle assemblage they studied. However, no species were excluded in this study because of the possibility that they could be tourists, but based on the arguments by Gaston *et al.* (1993a) and Blackburn and Gaston (1997) the inclusion of transient species will not significantly affect the abundance-body size relationship.

Body size explained a very small proportion (less than 30 %) of the variance in abundance of dung beetles in all habitat types in Tembe. Previous studies on dung beetle assemblages also showed body size to be a poor predictor of abundance (Blackburn *et al.* 1993a, Cambefort 1994). According to Gaston and Blackburn (2000) polygonal body

size-abundance relationships are generally characterized by such a low correlation between body mass and abundance. Cambefort (1994) stated that body size is a poor predictor of abundance for dung beetles because they are abundant and, on average, large in localities where mammals are abundant.

The dung beetles in this study showed the same trends in the different habitat types, i.e. small-bodied dung beetle species were on average more abundant, but large dung beetles appropriated larger amounts of energy. The large-bodied species also had higher total biomass than small-bodied species. Cambefort (1994) found that small-bodied dung beetle species are more abundant than large-bodied species at regional scales. Large-bodied species, however, have a higher total biomass and use a larger amount of the available resources. Thus, while it may be appealing to explain the relationship between abundance and body size with the idea that approximately equal amounts of energy are appropriated by all species in the environment (hypothesis 1) this idea was not supported here. In particular, the absence of a relationship between the residual variation in the abundance-body size relationship and metabolic rate is significant, constituting the most robust test of this idea (Blackburn *et al.* 1996; Blackburn & Gaston 1999). According to Blackburn and Lawton (1994) focussing on the value of the slope ignores the variance around the regression slope of the abundance-body size relationship. The variance around the slope could be high even when the relationship is strong because the slope is derived using logarithmically transformed data. Similarly different metabolic rates are predicted by the energetic equivalence rule for species of equal body mass that differ in abundance by three orders of magnitude (see Blackburn & Gaston 1999). These species' population energy use would also show three orders of magnitude difference if their metabolic rates were the same. Thus, if metabolic rate differences explain residual variation in the abundance-body size relationship, the energetic equivalence rule will explain the relationship between body size and abundance (Blackburn & Gaston 1999).

The energetic equivalence rule was criticized by Ebenman *et al.* (1995) who pointed out that the theory of energy constraint would only apply to maximum densities of animals. They stated that the overall relationship between body size and abundance would depend on the entire body size distribution of species (maximum and minimum densities). Blackburn *et al.* (1993) also criticized the energetic equivalence rule because

Damuth (1981), and many previous studies (e.g. Blackburn *et al.* 1990, 1992; Lawton 1990), used data compiled from the literature and not samples from whole communities. The number of rare and small-bodied species is so underestimated (Brown & Maurer 1987, Lawton 1991; Blackburn *et al.* 1993b). Gaston and Blackburn (2000) recently criticized the energetic equivalence rule for two reasons. First, the energy equivalence rule assumes that body size scales with metabolic rate with an exponent of -0.75 , which has been found not to be the case in several taxa (see Blackburn & Gaston 1997), and second, because of the lack of evidence that populations are energy limited. According to them this rule is correct to the extent that a negative body size-abundance relationship is a consequence of variation in the energetic requirements of individuals of species with different mean body mass, and energy use is the consequence of population limitation, rather than the cause (Gaston & Blackburn 2000).

Blackburn & Gaston (2001) further argued that the energetic equivalence rule would only apply to situations where the available energy is constant. They gave three reasons why observed and expected allometric relationships differ. First, energy may not be divided equally in assemblages. Second, the energy appropriated by a species and where the species lie along the abundance-body size relationship's slope may not be independent of each other. Third, a limited range in abundance or body size may be displayed by a species. Dung is an ephemeral and highly variable resource and competition for it can be fierce within dung beetle assemblages (Hanski & Cambefort 1991). Therefore, the available energy in Tembe for the beetles is not constant and the energetic equivalence rule can not apply to the abundance-body size relationships within the dung beetle assemblages. An interspecific allometric relationship of -0.75 for the body size-abundance relationship means that the allometric exponent of metabolic rate is 0.75 and does not mean that the population is limited by energetic constraints (Gaston & Blackburn 2000; Blackburn & Gaston 2001).

Although interspecific competition (hypothesis 5) has been shown to play an important role in structuring dung beetle communities (Giller & Doube 1989, 1994; Doube, 1990, 1991), and large body size is an advantage in interspecific competition between dung beetle species (Doube 1990), it did not explain the abundance-body size relationship of the dung beetle assemblages in the different habitat types in this study. A positive abundance-body size relationship is predicted within the rollers (FG I and II) and

non-rollers (FG III – V & VII), because the dung beetles within each of these two groupings all occupy the same guilds (Nee *et al.* 1991; Blackburn & Gaston 1999). However, within the rollers no significant relationships were found, and a significant negative abundance-body size relationship was found in the non-rollers. Also, positive abundance-body size relationships are expected within tribes with high niche overlap if the interspecific competition hypothesis explains the abundance-body size relationship (Blackburn & Gaston 1999). Only the Coprini sampled in the elephant-disturbed sand forest (January 2000) showed a significant positive abundance-body size relationship. The other significant relationships between abundance and body size were in undisturbed sand forest (December 1998 and January 2000) in the Sisyphini. The latter two relationships were both negative. No consistent evidence was thus found for the interspecific competition hypothesis.

The differential extinction hypothesis (hypothesis 6) was also rejected in this study because no evidence for differences in abundance-body size relationships, within tribes and functional groups, were found between the disturbed and undisturbed sand forest areas sampled in both sampling periods. Large-bodied species are more prone to extinction than small-bodied species (Gaston & Blackburn 1995); i.e. large-bodied species would go extinct first if their habitat were disturbed. It is thus expected that the abundance-body size relationships in disturbed and undisturbed sand forests would differ. But this is confounded by the prediction that because of flight manoeuvrability there will be more large bodied species in mixed woodland. However, within tribes, non-significant relationships were found between abundance and body size except in the Sisyphini in undisturbed sand forest. Within functional groups, this hypothesis could only be tested in the non-rollers. Dung beetle assemblages in both disturbed and undisturbed sand forests showed significant negative abundance-body size relationships. These results thus support Blackburn and Gaston's (1999) statement that little evidence exists for the differential extinction hypothesis.

Because log-normal frequency distributions of biomass were found in all habitat types within the different sampling periods, this study provides some support for Blackburn & Gaston's (1999) biomass hypothesis. At least one of the three assumptions of Blackburn & Gaston's (1999) model is met in this study, i.e. that the biomass of the dung beetles in the assemblages is divided among these beetles to produce a log-normal

biomass frequency distribution. Blackburn & Gaston (1999) suggested that Sugihara's (1980) sequential niche breakage model could produce a log-normal biomass distribution. This model states that successive species invading an environment will randomly acquire a proportion of the resources utilised by one of the species already present, which will result in a log-normal distribution of resources in the final assemblage of species. This process of resource division might exist within dung beetle assemblages because they utilise the same resource and assemblages are structured by competition within and between species (Doubé 1990, 1991; Giller & Doubé 1989, 1994; Hanski & Cambefort 1991). The assumption that the amount of maintainable biomass in an area depends on the available energy in that region has been shown to be valid across terrestrial and aquatic systems for herbivores (McNaughton *et al.* 1989; Cyr & Pace 1993) and this assumption thus seems reasonable for Tembe. The third assumption, that there is an abundance below which a species cannot persist, is according to Blackburn & Gaston (1999) true. Therefore, the biomass hypothesis proposed by Blackburn and Gaston (1999) to explain a negative abundance-body size relationship is supported by the dung beetle assemblages in mixed woodland, undisturbed and disturbed sand forests in Tembe Elephant Park.

This study provides strong evidence against the energy equivalence rule as an explanation for the negative abundance-body size relationship, and support for Blackburn & Gaston's (1999) biomass hypothesis. Given that much of the macroecological literature is based on studies in human-influenced landscapes, and is implicitly criticized because its relevance to more natural systems is unknown, this study is important. It shows that the major relationships between macroecological variables hold up despite disturbance. In this study disturbance did not alter the patterns and processes that drive macroecological patterns, or influence the factors generating these patterns.

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GENERAL CONCLUSION

The unidirectional alteration of sand forest vegetation structure to that of mixed woodland has important conservation implications. A large number of endemic plant and animal species are under considerable threat given the destruction of sand forest both inside and outside conservation areas (Davis *et al.* 1994; Matthews *et al.* 1999; Van Rensburg *et al.* 1999, 2000). Moreover, previous studies found that dung beetle (Van Rensburg *et al.* 1999), avian (Van Rensburg *et al.* 2000) and plant (Matthews *et al.* 1999) assemblage structures differ considerably between sand forest habitats in different reserves. These studies indicate that the conservation of sand forest habitats in a variety of areas is necessary for the persistence of this habitat and its biota. This study complemented the previous investigations of dung beetle assemblages in Tembe Elephant Park (Van Rensburg *et al.* 1999). The results indicated that human and elephant induced impacts have very different effects on dung beetle assemblages in sand forests. Elephant disturbance to sand forest results in dung beetle assemblages becoming more similar to mixed woodland assemblages. On the other hand, assemblages in human-disturbed sand forest were unique and were associated with human-related activities. However, neither human- nor elephant-induced disturbances altered the nature of the macroecological variables (i.e. body size, abundance and biomass) and their interrelationships within sand forest dung beetle assemblages.

Within Tembe Elephant Park, utilisation of sand forest by elephants has increased at an alarming rate since 1989 when the northern border of Tembe was closed in an attempt to prevent poaching within the reserve. The closing of the border restricted the natural movement of elephants into southern Mozambique, causing a forage shortage for the animals. Because of the high densities of elephants within the reserve (130 – 140 animals within the 30,079 ha of Tembe; Matthews, pers. comm.) and the restriction on their movement between Tembe and southern Mozambique, the percentage utilisation of the endemic-rich sand forest is increasing rapidly (Matthews pers. Comm.; Van Rensburg pers. comm.). Tembe contains the largest stands of well-preserved sand forest compared to all the other sand forest areas under conservation (Matthews *et al.* 1999), necessitating that the problem of elephant-induced damage to this habitat must be addressed.

The implementation of long-term monitoring programs of sand forest inside of reserves are thus important to assess the extent of the effects of large herbivores, such as elephants, on this endangered habitat type. The suite of dung beetle indicator and detector species previously identified for Tembe Elephant Park (Van Rensburg *et al.* 1999) was largely supported by the results of this study. These species can therefore be implemented in monitoring programs in Tembe in conjunction with the identification key for dung beetles in this reserve provided in this study. A 24 hour survey of dung beetles during the peak of summer will compliment existing botanical surveys in Tembe to assess the effects of elephant-induced damage to sand forest (Van Wyk 1996; Van Rensburg *et al.* 1999; Matthews, in press). Nonetheless, it is important to test the suite of bioindicators further in other sand forest patches within the reserve to increase the reliability with which confidence intervals of the indicator values for these species can be determined.

Furthermore, the effect of sand forest patch size, and the distance between these patches, on assemblage structures of taxa must be determined. It is especially important to determine what the smallest patch size is that will maintain viable assemblages of endemic taxa. Such information will have substantial conservation implications for sand forest and its biota. Outside of protected areas the biggest threat to sand forest is uncontrolled cattle grazing and fires (Matthews *et al.* 1999). However, human-induced disturbance, such as clearing for firewood and living areas, is highly concentrated and localized in certain areas. Consequently, the habitat structure in those areas is still predominantly that of sand forest. Conservation of areas outside reserves is advantageous for a host of reasons (Samways 1994). For example, the risk of local extinction is distributed between the different areas, promoting the persistence of species with metapopulation dynamics being the most important (Samways 1994). Knowledge of sand forest patch size, and distances between these patches required to maintain viable plant and animal assemblages can assist in managing and conserving the endangered habitat type in currently unprotected areas. The management of sand forest must be improved both inside and outside reserves to ensure that this endangered habitat type, and the endemic species restricted to it, is not irreversibly lost.

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Tribe classification and total abundance of the dung beetles recorded in Tembe Elephant Park sand forest and mixed woodland habitats, in the elephant-disturbed sand forest in Tembe and in the human-disturbed sand forest adjacent to Tembe, for the three sampling periods separately. USF = undisturbed sand forest, HDSF = human-disturbed sand forest, EDSF = elephant-disturbed sand forest.

Tribe and species	Author	Sand forest				Mixed woodland	
		1998	1998	2000	2000	1998	2000
		USF	HDSF	USF	EDSF		
Canthonini							
<i>Anachalcos convexus</i>	Boheman, 1857	14	4	29	28	91	4
Coprini							
<i>Catharsius harpagus</i>	Harold, 1877	0	0	1	0	1	1
<i>Catharsius heros</i>	Boheman, 1960	0	0	0	0	0	5
<i>Catharsius</i> sp. near <i>pandion</i>	Harold, 1877	19	2	17	0	79	0
<i>Catharsius tricornutus</i>	(DeGeer, 1778)	2	7	3	9	28	3
<i>Copris denticulatus</i>	Nguyen-Phung, 1988	0	1	0	0	0	0
<i>Copris fidius</i>	(Olivier, 1789)	0	0	4	2	0	1
<i>Copris inhalatus</i> spp. <i>sanctaeluciae</i>	Nguyen-Phung & Cambefort, 1986	0	4	0	2	25	1
<i>Copris mesacanthus</i>	Harold, 1878	0	1	4	10	0	8
<i>Copris puncticollis</i>	Boheman, 1857	1	6	0	0	62	0
<i>Copris</i> sp. 1		0	2	0	0	0	0
<i>Copris urus</i>	Boheman, 1857	1	1	0	3	23	4
<i>Metacatharsius exiguus</i>	(Boheman, 1860)	0	3	0	1	0	1
<i>Metacatharsius pseudoopacus</i>	(Ferreira, 1965)	1	4	4	1	199	2
Dichotomiini							
<i>Heliocopris japetus</i>	Klug, 1855	0	0	2	4	0	2
<i>Pedaria</i> sp. III <i>sensu</i> Davis		3	0	6	20	234	53
<i>Pedaria</i> sp. IV <i>sensu</i> Davis		25	2	1	0	219	0



Gymnopleurini

<i>Allogymnopleurus consocius</i>	(Péringuey, 1900)	0	1	0	0	144	0
<i>Garettia azureus</i>	(Fabricius, 1801)	1	0	2	4	0	2
<i>Gymnopleurus virens</i>	Erichson, 1843	0	0	0	0	1	0

Oniticellini

<i>Cyptochirus ambiguus</i>	(Kirby, 1828)	0	0	0	0	0	1
<i>Drepanocerus impressicollis</i>	Boheman, 1857	0	0	0	0	12	1
<i>Drepanocerus kirbyi</i>	Kirby, 1828	5	8	0	0	51	8
<i>Tiniocellus spinipes</i>	(Roth, 1851)	0	0	0	0	202	0
<i>Liatongus militaris</i>	(Castelnau, 1840)	0	0	0	0	8	0
<i>Oniticellus formosus</i>	Chevrolat, 1830	0	0	0	0	4	0
<i>Oniticellus planatus</i>	Castelnau, 1840	24	5	0	0	6	0

Onitini

<i>Onitis caffer</i>	Boheman, 1857	0	0	0	0	3	0
<i>Onitis</i> sp. 1		0	0	0	0	2	0
<i>Onitis tortuosus</i>	Houston, 1983	1	0	0	0	0	0

Onthophagini

<i>Caccobius cavatus</i>	(d'Orbigny, 1908)	466	37	83	120	1037	0
<i>Caccobius nigritulus</i>	Klug, 1855	0	95	0	0	43	0
<i>Caccobius</i> sp. 1		777	23	248	28	2234	0
<i>Caccobius</i> sp. 2		0	0	134	324	0	427
<i>Caccobius</i> sp. 3		0	0	12	607	0	144
<i>Cleptoaccobius viridicollis</i>	(Fåhraeus, 1857)	0	0	1	5	0	19
<i>Euonthophagus carbonarius</i>	(Klug, 1855)	2	86	0	26	290	15
<i>Hyalonthopagus alcyonides</i>	(d'Orbigny, 1913)	0	0	0	0	0	111
<i>Onthophagus acquepubens</i>	d'Orbigny, 1905	0	29	0	0	94	0
<i>Onthophagus aeruginosus</i>	Roth, 1851	115	561	0	2	61	154
<i>Onthophagus bicavifrons</i>	d'Orbigny, 1902	0	0	0	0	1	0
<i>Onthophagus fimetarius</i>	Roth, 1951	82	529	0	2	957	15
<i>Onthophagus flavolimbatus</i>	Klug, 1855	0	2	0	0	9	0
<i>Onthophagus juvencus</i>	Klug, 1853	37	8	58	31	160	6
<i>Onthophagus lacustris</i>	Harold, 1877	302	7	387	38	129	0



<i>Onthophagus lamelliger</i>	Gerstaecker, 1871	0	1	0	0	0	0
<i>Onthophagus obtusicornis</i>	Fåhraeus, 1857	0	1	7	0	266	0
<i>Onthophagus plebejus</i>	Klug, 1855	6	8	0	0	94	0
<i>Onthophagus pullus</i>	Roth, 1851	4	42	43	81	4	168
<i>Onthophagus rasipennis</i>	d'Origny, 1905	0	0	0	0	1	0
<i>Onthophagus signatus</i>	Fåhraeus, 1857	18	13	3	13	1747	19
<i>Onthophagus stigmosus</i>	(d'Origny, 1902)	403	31	121	140	103	100
<i>Onthophagus sugillatus</i> sp. A	Klug, 1855	227	1615	15	6	423	0
<i>Onthophagus sugillatus</i> sp. B	Klug, 1855	0	548	159	26	81	7
<i>Onthophagus sugillatus</i> sp. C	Klug, 1855	87	692	51	5	119	2
<i>Onthophagus ursinus</i>	(d'Origny, 1902)	69	266	5	10	251	151
<i>Onthophagus vinctus</i>	Erichson, 1843	3	393	166	134	168	344
<i>Phalops boschas</i>	Klug, 1855	0	2	0	0	2	0
<i>Phalops flavocinctus</i>	Klug, 1855	0	0	0	0	1	0
<i>Proagoderus aciculatus</i>	(Fåhraeus, 1857)	2278	40	403	502	316	721
<i>Proagoderus bicallosus</i>	(Klug, 1855)	0	0	0	0	40	8
<i>Proagoderus brucei</i>	(Reiche, 1849)	0	3	0	0	0	0
<i>Proagoderus dives</i>	(Harold, 1877)	918	1624	180	765	6851	1307
Scarabaeini							
<i>Kheper lamarcki</i>	(MacLeay, 1821)	0	0	1	3	13	35
<i>Pachylomerus femoralis</i>	(Kirby, 1828)	72	12	38	50	304	85
<i>Scarabaeus galenus</i>	(Westwood, 1847)	0	0	0	0	17	0
<i>Scarabaeus goryi</i>	Castelnau, 1840	7	0	1	9	6	6
<i>Scarabaeus</i> cf. <i>xavieri</i>		0	0	1	1	7	0
<i>Scarabaeus zambesianus</i>	Péringuey, 1900	0	0	0	0	5	11
Sisyphini							
<i>Neosisyphus fortuitus</i>	Péringuey, 1900	27	0	1	34	4	17
<i>Neosisyphus mirabilis</i>	Arrow, 1927	65	0	3	0	11	0
<i>Neosisyphus rubrus</i>	Paschalidis, 1974	0	0	0	0	43	4
<i>Sisyphus bornemisszanus</i>	Endrödi, 1983	66	1	6	5	0	0
<i>Sisyphus sordidus</i>	Boheman, 1857	34	4	14	92	1421	184
<i>Sisyphus</i> sp. Y <i>sensu</i> Paschalidis		558	207	25	22	3	2
<i>Sisyphus spinipes</i>	Thunberg, 1818	38	0	0	0	22	0

APPENDIX B

Functional group classification (Doube 1990), dung preference (Davis 1994b) and body mass (g) (Chown and Scholtz in prep.) of dung beetles collected in Tembe Elephant Park.

Species and functional group	Dung preference	Body mass (g)
FG I: Large telecoprids		
<i>Anachalcos convexus</i>	Omnivore	1.169
<i>Kheper lamarcki</i>	Omnivore	5.114
<i>Pachylomerus femoralis</i>	Omnivore	4.789
<i>Scarabaeus galenus</i>	Omnivore	2.667
<i>Scarabaeus goryi</i>	Omnivore	2.871
<i>Scarabaeus xavieri</i>	Omnivore	0.347
<i>Scarabaeus zambesianus</i>	Omnivore	1.258
FG II: Small telecoprids		
<i>Allogymnopleurus consocius</i>	Herbivore	0.264
<i>Gareta azureus</i>	Omnivore	1.124
<i>Gymnopleurus virens</i>	Omnivore	0.178
<i>Neosisyphus fortuitus</i>	Herbivore	0.234
<i>Neosisyphus mirabilis</i>	Herbivore	0.171
<i>Neosisyphus rubrus</i>	Herbivore	0.108
<i>Sisyphus bornemiss-zanus</i>	Omnivore	0.084
<i>Sisyphus sordidus</i>	Omnivore	0.078
<i>Sisyphus</i> sp. Y <i>sensu</i> Paschalidis	Omnivore	0.028
<i>Sisyphus spinipes</i>	Omnivore	0.191
FG III: Fast-burying paracoprids		
<i>Catharsius harpagus</i>	Omnivore	1.355
<i>Catharsius heros</i>	Omnivore	5.384
<i>Catharsius</i> sp. near <i>pandion</i>	Omnivore	1.482
<i>Catharsius tricornutus</i>	Omnivore	1.476
<i>Copris denticulatus</i>	Herbivore	2.382
<i>Copris fdius</i>	Herbivore	0.368



<i>Copris inhalatus</i> prob. <i>sanctaeluciaae</i>	Herbivore	0.554
<i>Copris mesacanthus</i>	Herbivore	1.263
<i>Copris puncticollis</i>	Herbivore	0.018
<i>Copris</i> sp. 1	Herbivore	0.351
<i>Copris urus</i>	Herbivore	0.821
<i>Heliocopris japedus</i>	Herbivore	10.529
<i>Metacatharsius exiguus</i>	Omnivore	0.319
<i>Metacatharsius pseudoopacus</i>	Herbivore	0.259

FG IV: Large slow-burying paracoprids

<i>Euonthophagus carbonarius</i>	Omnivore	0.097
<i>Hyalonthopagus alcyonides</i>	Herbivore	0.126
<i>Liatongus militaris</i>	Omnivore	0.124
<i>Onitis deceptor</i>	Herbivore	1.294
<i>Onitis</i> sp. 1	Herbivore	0.357
<i>Onitis tortuosus</i>	Herbivore	0.782
<i>Onthophagus acquepubens</i>	Omnivore	0.016
<i>Onthophagus aeruginosus</i>	Omnivore	0.050
<i>Onthophagus bicavifrons</i>	Omnivore	0.320
<i>Onthophagus fimetarius</i>	Omnivore	0.018
<i>Onthophagus juvencus</i>	Omnivore	0.051
<i>Onthophagus lacustris</i>	Omnivore	0.068
<i>Onthophagus obtusicornis</i>	Omnivore	0.066
<i>Onthophagus plebejus</i>	Omnivore	0.163
<i>Onthophagus signatus</i>	Omnivore	0.038
<i>Onthophagus stigmosus</i>	Omnivore	0.062
<i>Phalops boschas</i>	Omnivore	0.184
<i>Phalops flavocinctus</i>	Omnivore	0.151
<i>Proagoderus aciculatus</i>	Omnivore	0.184
<i>Proagoderus bicallosus</i>	Omnivore	0.479
<i>Proagoderus brucei</i>	Omnivore	0.178
<i>Proagoderus dives</i>	Omnivore	0.177
<i>Tiniocellus spinipes</i>	Herbivore	0.064

FG V: Small slow-burying paracoprids

<i>Drepanocerus impressicollis</i>	Herbivore	0.023
<i>Drepanocerus kirbyi</i>	Herbivore	0.018
<i>Onthophagus flavolimbatus</i>	Omnivore	0.008
<i>Onthophagus lamelliger</i>	Omnivore	0.036

FG VI: Kleptocoprids

<i>Caccobius cavatus</i>	Omnivore	0.007
<i>Caccobius nigrifulus</i>	Omnivore	0.011
<i>Caccobius</i> sp. 1	Omnivore	0.014
<i>Caccobius</i> sp. 2	Omnivore	0.017
<i>Caccobius</i> sp. 3	Omnivore	0.025
<i>Caccobius</i> sp. 4	Omnivore	0.016
<i>Onthophagus pullus</i>	Omnivore	0.008
<i>Onthophagus rasipennis</i>	Omnivore	0.025
<i>Onthophagus sugillatus</i> sp. A	Omnivore	0.022
<i>Onthophagus sugillatus</i> sp. B	Omnivore	0.016
<i>Onthophagus sugillatus</i> sp. C	Omnivore	0.019
<i>Onthophagus ursinus</i>	Omnivore	0.012
<i>Onthophagus vinctus</i>	Omnivore	0.035
<i>Pedaria</i> sp. III <i>sensu</i> Davis	Omnivore	0.065
<i>Pedaria</i> sp. IV <i>sensu</i> Davis	Omnivore	0.077

FG VII: Endocoprids

<i>Cyptochirus ambiguous</i>	Herbivore	0.142
<i>Oniticellus formosus</i>	Herbivore	0.157
<i>Oniticellus planatus</i>	Herbivore	0.123

Telecoprids = rollers; Paracoprids = tunnelers; Endocoprids = beetles that feed and breed in the dung pat; Kleptocoprids = beetles breeding in dung buried by other beetles (Doube 1990).