

How might intensification of farming influence dung beetle diversity (Coleoptera: Scarabaeidae) in Maputo Special Reserve (Mozambique)?

Carmen T. Jacobs · Clarke H. Scholtz ·
Federico Escobar · Adrian L. V. Davis

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Abstract There are concerns over the increasing encroachment of humans, domestic livestock, and farming onto Maputo Special Reserve because of the potential for habitat modification. Therefore, differences between an undisturbed area of the reserve and a neighbouring farming area are assessed using dung beetle as indicators. In each of the two areas, pig-dung-baited pitfall traps were used to sample dung beetle assemblages in two contrasting habitats, grassland and forest. Distributional analysis of the 57 species and 36 942 individuals that were captured, showed that species richness, species turnover, relative abundance patterns, and biogeographical composition differed strongly between both habitats and areas under different land usage. However, in analyses that apportion variation, the greatest amounts were related to habitat rather than land usage. Even so, in both habitats, the total and mean number of species per trap was higher in the farmed area than in the reserve although this was a significant trend only in grassland. Furthermore, in grassland, widespread species were better represented in the farmed area than in the reserve whereas in forest, widespread species were poorly represented compared to grassland. Also in forest, Maputaland endemics were better represented in the reserve than in the farmed area. Further work is necessary to separate the different geographical, ecological, and land

usage factors responsible for the patterns detected in this preliminary study. Even so, there are clearly differences between the Maputo Special Reserve and the farmed area.

Keywords Farming · Conservation · Diversity · Dung beetle · Indicator · Maputaland centre of endemism · Maputo Special Reserve · Mozambique

Introduction

The Maputaland Centre of Endemism (26,734 km²) is situated on the southeast coast of Africa where it straddles the borders of Mozambique, South Africa and Swaziland. It is floristically varied comprising numerous vegetation ecotypes and endemic taxa (van Wyk 1996). Towards the northern end of the Centre of Endemism, the Maputo Special Reserve (MSR) currently protects some of the least disturbed patches of coastal vegetation in the region (Mucina and Rutherford 2006) as well as a number of dung beetle species that are endemic to the southern tip of Mozambique and the adjoining northeast KwaZulu-Natal, South Africa (Davis et al. 2003). As the encroachment of farming onto the reserve is of concern for conservation of flora and fauna, the present study examines some potential effects of such changes in land usage using dung beetles as indicators.

Dung beetles are an excellent indicator taxon for examining interactions between human disturbance and community structure (Spector 2006) as they are an integral part of any grazing ecosystem (Nichols et al. 2008). Furthermore, they are good bio-indicators of pasture health due to their narrow habitat tolerances, complex assemblage structure, and sensitivity to habitat disturbance. Therefore, it is possible to use them to characterise or monitor changes

C. T. Jacobs (✉) · C. H. Scholtz · F. Escobar · A. L. V. Davis
Scarab Research Group, Department of Zoology & Entomology,
University of Pretoria, Lynnwood Rd, Pretoria 0002, South
Africa
e-mail: ctjacobs@zoology.up.ac.za

F. Escobar
Departamento de Biodiversidad y Ecología Animal, Instituto de
Ecología, A.C., Apartado Postal 63, 91000 Xalapa, Veracruz,
Mexico

in habitats (Halfpter and Favila 1993; van Rensburg et al. 1999; Davis et al. 2004; Spector 2006).

In any landscape, habitat selection by dung beetles is influenced primarily by climate, soil type, vegetation structure, and mammal dung type (Cambefort 1982; Davis 1994, 1996; Davis et al. 2008). Of the four main influences, both vegetation and dung type availability are susceptible to short term modification (Jankielsohn et al. 2001; Escobar et al. 2007; Verdú et al. 2007). Species composition, species richness and abundance of dung beetles may exhibit a wide variety of rapid, graded responses to changes in landscape vegetation physiognomy whether natural or due to anthropogenic disturbances (Escobar et al. 2007; Nichols et al. 2007). In addition, due to their dependence on vertebrate dung, beetle assemblages may be influenced by changes in mammal assemblages, which are, themselves, affected by landscape alterations (Nichols et al. 2007). Understanding how the components of natural communities respond to the different landscape features in natural and farmed areas can be useful in the design of land management strategies for these environments (Escobar 2004). Thus, the present preliminary study investigates if and how such changes might influence the MSR.

Before the MSR was gazetted in 1932, people living inside the present park boundaries fished, hunted and gathered wild foods. Thereafter, they were forcibly relocated and encouraged to farm along the park borders (Osborn 1998). More recently, increasing human demand for farmland is converting parts of the MSR into cultivated areas and pasturage for grazing of domestic livestock. Therefore, the present study uses dung beetles as indicators of possible collective effects induced by such changing land usage. Specifically, it compares the dung beetle fauna of a relatively undisturbed area of the MSR with an adjoining farming area. For logistic reasons, the comparison was made only between grassland and forest habitats, even though the MSR and adjoining areas comprise a wide variety of vegetation types, which include forest, savanna woodland, grassland, and wetland habitats (De Boer and Baquette 1998).

Methods

Study area

The study was conducted during November 2007 about 50–70 km south of Maputo on the southeast coast of Africa (Fig. 1). Dung beetles were sampled both in the Maputo Special Reserve (MSR) and in a farming area bordering the southern side of the MSR. These two areas were separated by a distance of 19 km across the coastal plain that lies at an altitude of 20–120 m a.s.l. This plain mainly comprises

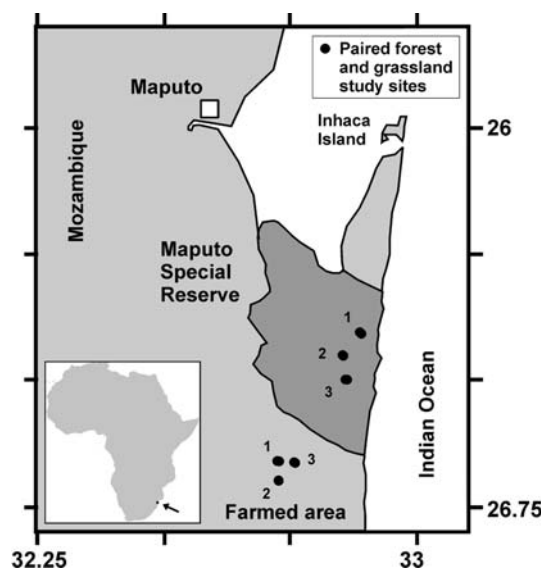


Fig. 1 Map of southern Mozambique showing the locations of Maputo Special Reserve (dark grey) and study sites (black circles)

redistributed sands from Quaternary marine sediments. It supports a coastal vegetation belt up to 35 km wide that extends from Mtunzini in South Africa continuing into Southern Mozambique. Formerly, the region was probably densely forested but it now comprises a mosaic of dry-adapted, moisture-adapted, and palm-velv grasslands together with pockets of forest (Mucina and Rutherford 2006). At 3–15 km inland, both study areas in southern Mozambique were observed to fall within this coastal vegetation zone. Across this landscape, the extensive palm-velv grasslands would be characterized, as in South Africa, by grass species in the genera *Aristida*, *Eragrostis*, *Themeda*, and *Perotis* with raised areas supporting northern coastal forest patches with typical trees species comprising, *Drypetes natalensis* J. Hutch, *Englerophytum natalense* (Sonder) T.D.Pennington, *Albizia adianthifolia* (Schumacher) W.Wight, and *Diospyrus inhacaensis* F. White (Mucina and Rutherford 2006). The area of well-preserved coastal vegetation is much larger in southern Mozambique than in South Africa where most of this zone has been transformed (Mucina and Rutherford 2006).

The study sites in the MSR and farmed area were at similar altitude and were subject to similar rainfall and temperature regimes. In the farmed area, spot altitude at study sites was 43–67 m, and in 5 × 5 km polygons surrounding the sites, average annual rainfall was 747–762 mm and average annual temperature (max. + min./2) was 22.3°C. This is comparable to the reserve where spot altitude at study sites was 25–60 m, whereas in 5 × 5 km polygons surrounding the sites, average annual rainfall was 765–768 mm, and average annual temperature was 22.4–22.45°C. Whilst every effort was made to chose forest

patches of similar size, those in the farmed area tended to be smaller than those in the reserve (C. Deschodt personal communication).

Sampling design

Dung beetles were sampled according to a hierarchical design. Level one comprised the farmed area and the MSR. Level two comprised three study sites in each of the two areas. Level three comprised a single forest and grassland plot at each of the six study sites. Five pitfall traps were placed 50 m apart in each of the six forest patches and six grassland plots. Thus, the design comprised: 2 study areas under different land usage \times 3 study sites \times 2 habitats \times 5 traps = 60 sets of species assemblage data.

Five-litre plastic buckets were used as pitfall traps (top diameter, 23 cm; depth, 17.5 cm). The traps were buried in the ground up to the rim, half-filled with a mixture of detergent and water and baited with \sim 250 ml of fresh domestic pig dung, which usually attracts more species than other bait types (Davis 1994) and is useful for species diversity inventories. The baits were wrapped in chiffon to permit the release of dung volatiles while excluding dung beetles, and each was placed on two supporting wires directly above the trap. The traps were operated for 48 h, samples were removed every 24 h, and traps were re-baited every 12 h to present fresh dung to both diurnally as well as nocturnally active species of dung beetles. The sampled beetles were stored in 99% ethanol for later identification in the laboratory. To assist in the process of identification, a reference collection was made for the MSR. This is currently held at the Department of Zoology and Entomology, University of Pretoria but will ultimately become part of the National Collection of Insects, Pretoria, South Africa.

Data analysis

As recommended by Gotelli and Colwell (2001), we used rarefaction curves to evaluate species accumulation relative to the number of recorded individuals (individual-based rarefaction). This approach avoided bias in the comparisons that might result from differences in overall abundance among sites. The smoothed accumulation curves were obtained by repeated, random reordering of the samples (100 times) using EstimateS v. 8.0.0 (Colwell 2006). We also used two non-parametric estimators to predict total expected species richness as an evaluation of sampling efficiency. These estimators, Chao1 and Chao2, are the most appropriate for small sample sizes (Colwell and Coddington 1994). Completeness of the species inventory was measured as the percentage of observed species with respect to the number of species predicted by the estimators.

To quantify the contribution of each component of the landscape (Reserve Forest, Farmed Forest, Reserve Grassland and Farmed Grassland) to total diversity, we calculated the average number of species absent from each site (beta diversity) defined as $\beta = \gamma - \alpha$, where γ is the number of species sampled in the entire landscape (gamma diversity) and α is the average number of species present in a given habitat (alpha diversity) (Lande 1996). In addition we calculated the additive partitioning of beta diversity for the entire landscape by dividing it into that due to habitat and that related to land usage, $\gamma = \alpha + \beta_{\text{habitat}} + \beta_{\text{land usage}}$. This approach allows for a direct comparison between alpha and beta diversities in terms of numbers (or percentage) of species (Veech et al. 2002; Crist et al. 2003).

To compare between-trap differences in species richness and abundance between habitats and land usage, we used a two-way ANOVA derived from a generalised linear model (GLM). As suggested for discrete count-dependent variables we selected a Poisson error distribution with a log link-function, and corrected for over-dispersion (Crawley 2002). In all cases, the model was verified by examining the standardised residuals versus the fitted values, in addition to the graphed distribution of errors.

Changes in community structure were analyzed by comparing the distribution patterns of species abundance (Magurran 2004). For each possible combination of habitat type and land use (Reserve Forest, Farmed Forest, Reserve Grassland, Farmed Grassland), we plotted the \log_{10} rank abundance of each species ordered from the most to the least abundant. Additionally, in order to evaluate the differences in diversity, we calculated Simpson's index (Magurran 2004). Although this index represents the probability that two individuals randomly selected from a sample belong to different species, in the present study, we used the reciprocal of this index ($1/D$), which is a measure of dominance (Magurran 2004). The value of the indices for Farmed Forest versus Reserve Forest and Farmed Grassland versus Reserve Grassland were compared statistically using the null model developed by Solow (1993) that is included in the Species Diversity and Richness program v.3.0 (Henderson and Seaby 2002). In Solow's test (1993), the absolute observed change (δ) in $1/D$ is compared with the values obtained from 10,000 random partitions of the total sample of individuals in a set of samples similar in size to that observed.

To define the overall differences in species abundance composition between habitats and land usage categories, we used ordination of a triangular Q-mode matrix of similarity between species abundance at each sampling site. We chose the Bray–Curtis similarity coefficient as it is an effective index to use with raw values of species abundance. The index ranges from 0 (no species in common

between samples) to 1 (identical species composition and abundance). For ordination, we used non-metric multidimensional scaling (NMDS). We chose NMDS because neither normality nor linearity of data is required (Kruskal and Wish 1978). To evaluate how many dimensions are needed to reproduce similarity between sites, we calculated a stress value. The smaller the stress value, the better the fit of the reproduced similarity matrix to the observed similarity matrix. In order to test statistical differences in community composition among sites according to habitat and land use we performed a non-parametric, two-way analysis of similarity (ANOSIM, Clarke and Warwick 1994). ANOSIM is a permutation procedure applied to (rank) similarity or dissimilarity matrices. The R_{ANOSIM} statistic values, generated by ANOSIM in PRIMER v. 5.2.4, are a relative measure of separation of a priori-defined groups. A zero (0) indicates that there is no difference among groups, while a one (1) indicates that all samples within groups are more similar to one another than to any samples from different groups (Clarke and Gorley 2001).

Finally, the species were classified according to their biogeographical distribution based on Davis et al. (2002) or general knowledge. Three groups were defined: Maputaland endemics, east coastal endemics and species with widespread savanna distribution. We used a contingency table and a goodness-of-fit test to examine if the proportion of species abundance in each group varies significantly between landscape components (Reserve Forest, Farmed Forest, Reserve Grassland, and Farmed Grassland). To determine if group proportions differed significantly between the same habitats under different land usage, we subdivided the contingency table and reanalysed the data using the same test (Zar 1996).

Results

At landscape scale, we captured 36,942 individuals belonging to a total of 57 species of dung beetles (Table 1). At habitat and land usage scales, total species richness was greater in grassland (43; 36) than in forest (29; 27), and greater in the farmed area (grass: 43; forest: 29) than in the reserve (MSR) (grass: 36; forest 27). In all four habitat/land usage combinations, the species accumulation curves (individual-based rarefaction) approached asymptote (Fig. 2). Irrespective of land usage, it appears that the species record was close to complete in forest as it was predicted that more than 90% of the species had been captured. However, the species record in grassland may have been less complete as predictions suggest that only 75–82% of the species were captured (Table 1). For the whole study area the non-parametric richness estimates

indicate that around 88% of the expected maximum numbers of species were trapped (Table 1).

The gamma diversity $[\gamma]$ of the entire landscape expressed in an additive form was: $57 [\gamma] = 26.3 [\alpha] + 21.7 [\beta_{\text{habitat}}] + 9.0 [\beta_{\text{land usage}}]$ (Fig. 3). This amounts to 46.1% contributed by alpha diversity, 38.1% by beta diversity between habitats and 15.8% by beta diversity between types of land usage. At habitat scale, the proportional contribution of beta diversity was higher for forest patches (reserve 66%; farm 61%) than for grassland (reserve: 51%; farm 37%). These results also showed a pronounced difference between land usage categories in grassland that was not duplicated in forest. Overall, the proportional contribution of beta diversity is lower in the farmed area (forest: 61%; grass: 37%) than in the reserve (forest: 66%; grass: 51%).

As with total species numbers (Table 1), there were differences in the number of species per trap according to habitat type and land usage (Fig. 4). Out of 69% of total variation explained by a model (GLM), 57.8% was significantly associated with habitat type whereas a much smaller proportion (6.7%) was significantly related to land usage (Table 2). There were negligible differences between mean species richness per trap under different land usage in forest (Fig. 4). Therefore, the significant variation contributed by land usage must have emanated primarily from the much greater mean species richness per trap in farmed grassland compared to that in grassland of the reserve. For unknown reasons, in the case of numbers of individuals, the model explains only 4% of total variation (Table 2) and neither habitat nor land usage contributed significantly to differences in mean abundance per trap.

Although similar slopes were shown by rank species abundance graphs for all four habitat and land usage categories, neither distribution pattern of species abundance nor the hierarchical order of the species were similar (Fig. 5). When comparing the reciprocal of Simpson's diversity index between land usage categories (reserve vs. farmed area), we found that differences (δ) in dominance deviated significantly from a random distribution in both forest (Simpson's index $(1/D) \pm \text{CI } 95\%$: Reserve forest = 5.03 ± 0.26 , Farmed forest = 5.50 ± 0.26 , $\delta = -0.46$, simulated $\delta < \text{observed } \delta = 1$, $P = 0.0001$) and grassland (Simpson's index $(1/D) \pm \text{CI } 95\%$: Reserve grassland = 7.20 ± 0.31 , Farmed grassland = 5.97 ± 0.35 , $\delta = 1.22$, simulated $\delta > \text{observed } \delta = 0$, $P < 0.0001$). However, with respect to land usage there were opposite trends in different habitats in that dominance was significantly higher in Reserve grassland than in Farmed grassland and significantly lower in Reserve forest than in Farmed forest.

The NMDS ordination (stress value = 0.04) revealed four different groups separated according to habitat type

Table 1 Abundance and biogeographical centres of 57 dung beetle species captured in forest and grassland in southern Mozambique under two different land usage regimes represented by Maputo Special Reserve and a neighbouring farmed area

Species and biogeographical classification*	Abundance forest		Abundance grassland	
	Reserve	Farm	Reserve	Farm
Maputaland endemics				
<i>Scarabaeus bornemisszai</i> zur Strassen	27	6	0	0
<i>Scarabaeus galenus</i> Westwood (coastal variety) ¹	2	1	0	1
<i>Neosisyphus mirabilis</i> (Arrow)	32	0	0	1
<i>Sisyphus natalensis</i> Balthasar	0	49	0	0
<i>Pedaria</i> sp. III (sensu Doube 1991) ¹	1	1	259	187
<i>Catharsius harpagus</i> Harold ¹	0	0	1	5
<i>Catharsius mossambicanus</i> Ferreira	237	231	7	17
<i>Catharsius</i> sp. 1	0	0	1	0
<i>Copris inhalatus</i> Quedenfeldt ssp. <i>santaluciae</i> Ferreira	1	5	6	29
<i>Metacatharsius zuluanus</i> Balthasar	0	0	34	99
<i>Caccobius</i> sp. 3	204	725	489	296
<i>Onthophagus</i> sp. nr <i>asperulus</i>	2,555	690	1	0
<i>Onthophagus</i> sp. nr <i>fmietarius</i>	624	43	1,250	74
<i>Onthophagus</i> sp. nr <i>vincius</i> ¹	1	0	332	37
East Coastal endemics				
<i>Scarabaeus</i> (<i>Scarabaeolus</i>) <i>clanceyi</i> Ferreira ¹	0	0	0	109
<i>Scarabaeus</i> (<i>Scarabaeolus</i>) <i>xavieri</i> Ferreira ¹	0	0	1	16
<i>Sisyphus sordidus</i> Boheman**	0	0	1,573	7
<i>Sisyphus</i> sp. y (sensu Paschalidis 1974)	527	1,537	0	0
<i>Copris puncticollis</i> Boheman	0	0	0	102
<i>Caccobius</i> sp. 2	11	156	0	0
<i>Mimonthophagus ambiguus</i> (Péringuey)	0	0	190	378
<i>Onthophagus lacustris</i> Harold	736	1,504	0	0
<i>Proagoderus aciculatus</i> (Fahraeus)	3,250	2,557	219	136
<i>Proagoderus aureiceps</i> d'Orbigny	360	15	2,667	1,902
Widespread savanna distribution				
<i>Anachalcos convexus</i> Boheman	246	134	55	129
<i>Pachylomera femoralis</i> (Kirby)	11	5	1,118	776
<i>Scarabaeus</i> (<i>Kheper</i>) <i>lamarcki</i> Macleay	7	11	37	38
<i>Allogymnopleurus thalassinus</i> Klug	0	0	0	111
<i>Garreta azureus</i> (Fabricius)	24	10	0	0
<i>Gymnopleurus virens</i> Erichson ¹	0	0	113	77
<i>Neosisyphus confrater</i> (Kolbe)	59	2	3	76
<i>Neosisyphus fortuitus</i> (Péringuey) ¹	16	2	11	7
<i>Neosisyphus spinipes</i> (Thunberg)	0	2	3	23
<i>Catharsius tricornutus</i> Degeer	0	8	1	3
<i>Metacatharsius opacus</i> (Waterhouse) ¹	0	0	16	30
<i>Metacatharsius troglodytes</i> (Boheman) ¹	0	0	14	8
<i>Onitis deceptor</i> Péringuey ¹	0	0	0	5
<i>Onitis viridulus</i> Boheman ¹	0	0	1	0
<i>Caccobius cavatus</i> d'Orbigny ¹	0	0	0	20
<i>Caccobius nigrifulus</i> Klug	11	14	13	448
<i>Cleptocaccobius viridicollis</i> (Fahraeus) ¹	0	0	0	5
<i>Hyalonthophagus?</i> <i>alcyonides</i> (d'Orbigny) ¹	0	0	0	5
<i>Onthophagus aeruginosus</i> Roth ¹	302	57	47	2

Table 1 continued

Species and biogeographical classification*	Abundance forest		Abundance grassland	
	Reserve	Farm	Reserve	Farm
<i>Onthophagus flavolimbatus</i> d'Orbigny	0	0	0	1
<i>Onthophagus juvenicus</i> Klug ¹	0	0	4	0
<i>Onthophagus obtusicornis</i> Fahraeus	2	2	284	189
<i>Onthophagus</i> sp. nr <i>pullus</i> ¹	0	1	0	79
<i>Onthophagus signatus</i> Fahraeus	0	1	1,851	2,448
<i>Onthophagus stellio</i> Erichson ¹	0	0	3	5
<i>Proagoderus bicallosus</i> Klug ¹	0	0	6	0
<i>Proagoderus chalcostolus</i> (d'Orbigny)	0	0	41	0
<i>Euoniticellus triangulatus</i> (Harold) ¹	0	0	0	1
<i>Oniticellus planatus</i> Castelnau	0	0	0	1
Unclassified				
<i>Odontoloma pauxillum</i> Boheman	3	0	0	0
<i>Caccobius</i> sp. 1	197	28	134	4
<i>Onthophagus</i> sp. 2	0	0	94	240
<i>Onthophagus</i> sp. 3	281	492	0	0
Total abundance	9,727	8,289	10,879	8,047
Total number of species observed	27	29	36	43
Estimated number of species—Chao ₁	28.1	31.0	51.0	50.7
Estimated number of species—Chao ₂	28.7	33.2	48.0	57.0
Mean completeness of species record (% ±SD)	94.1 ± 2.6	90.0 ± 4.8	75.0 ± 6.3	82.5 ± 10.0
Maputaland endemics (%) M*	37.9	21.1	21.9	9.2
East coastal endemics (%) EC*	50.2	69.6	42.7	32.6
Widespread distribution in African savannas (%) W*	7.0	3.0	33.3	55.2

The Chao₁ and Chao₂ estimators are used to predict the total number of species expected for each habitat and land use category. Completeness of the inventory is expressed by the average percentage (±SD) of observed compared to predicted numbers of species

* Classification of biogeographical distribution based on Davis et al. (2002) or general knowledge¹

** Currently erroneously synonymised with *S. caffer* Boheman

and land usage (Fig. 6). An ANOSIM comparison between the groups indicated that there are significant statistical differences in species composition between both habitat type (Forest vs. Grassland; $R = 0.96$, $P < 0.001$) and land use category (Reserve vs. Farmed area; $R = 0.76$, $P < 0.001$). Study sites in the farmed area clustered closely together whereas those in the reserve were well separated from one another, particularly along dimension 2. This reflects the greater variability in species composition between both forest and grassland sites in the reserve.

The proportion of individuals in each biogeographical group varied significantly between landscape components ($\chi^2 = 9180.7$, $P < 0.0001$, $df = 6$, Table 1). The forest habitat comprised primarily Maputaland and east coastal endemics with Maputaland endemics more prominent in the forest of the reserve than in the farmed area ($\chi^2 = 1674.4$, $P < 0.0001$, $df = 3$). The grassland habitat comprised much greater proportions of elements with widespread distributions in African savannas, particularly

in the farmed area where the proportion of the endemic Maputaland component was particularly low ($\chi^2 = 6084.5$, $P < 0.0001$, $df = 3$). A small unreported percentage in each habitat/land usage type comprised unclassified species.

Discussion

The present study has demonstrated clear differences in dung beetle assemblage structure between the MSR and the farmed area as well as between habitats within each area. To account for the differences, the discussion focuses on the possible influence of a complex of factors. These include the possibility of climatic and ecological differences between the MSR and the farmed area; the influence of differing vegetative physiognomy between habitats (forest vs. grassland); how differing land usage may have modified both the vegetative physiognomy and dung fauna

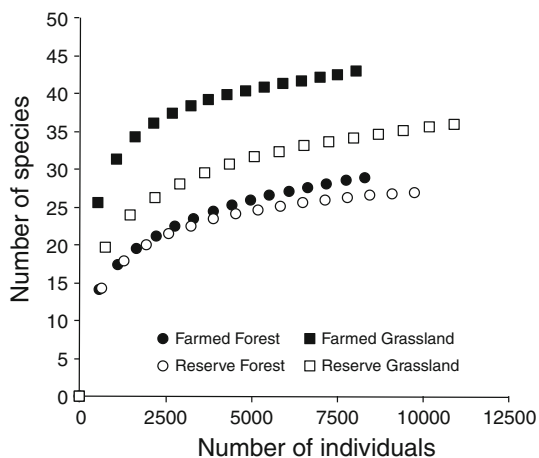


Fig. 2 Species accumulation curves (individual-based rarefaction) for dung beetle assemblages in each habitat (forest, grassland) and land usage category (reserve, farmed area) in southern Mozambique

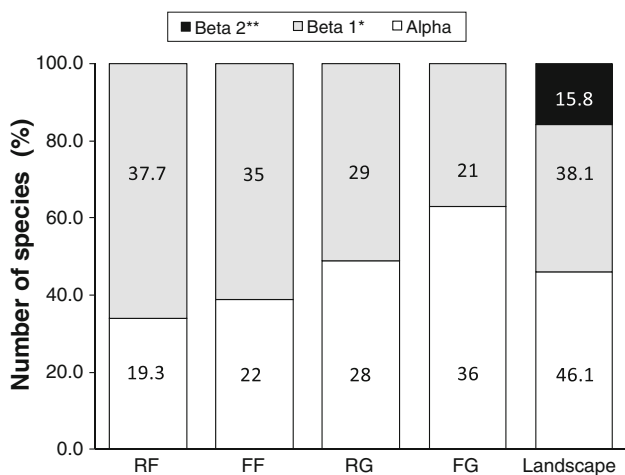


Fig. 3 Contribution of each component of the landscape (RF = Reserve Forest, FF = Farmed Forest, RG = Reserve Grassland, and FG = Farmed Grassland) to the proportions and numbers of species sampled in the entire landscape (gamma diversity, $n = 57$ species) (see methods) (Alpha = diversity contributed by habitat, Beta 1* = diversity between habitats, Beta 2** = diversity between land usage types). Proportions contributed by alpha and beta diversity are shown by the divisions within the bars whereas numbers of species are shown inside the bars

of these habitats (possible effects of elephants on conserved vegetation in MSR versus those of the combined effects of elephants, human activity, and livestock-grazing in the farmed area); differences induced by differing dung type arrays (MSR vs. farmed area); and the validity of results generated using domestic pig dung as bait. These possible climatic, ecological, land usage, and methodological factors are discussed with reference to their relative influence on results and to observations that have been made elsewhere both on a global (Jankielsohn et al. 2001; Escobar et al. 2007; Verdú et al. 2007) or regional scale in

the Maputaland Centre of Endemism (van Rensburg et al. 1999; Botes et al. 2006).

Species abundance structure of the dung beetle fauna in the cooler coastal dune forest of the MSR is known to show some differences to that of forest patches situated a little further inland (F. Escobar, unpublished data). It is unclear if the closer proximity to the coast of the MSR sites might have influenced the present results. However, each of the two study areas comprises similar mosaics of forest patches in grassland on deep sand. None of the sites is in coastal dune forest and they show negligible differences in overall altitude, average annual temperature, and average annual rainfall.

Although the Maputaland Centre of Endemism includes various vegetation types (van Wyk 1996), for logistic reasons, comparisons were made only between two well-represented ecotypes comprising the physiognomic extremes of forest (shaded) and grassland (unshaded). These habitat types show quite different microclimates as regards radiant heat, light intensity, ambient temperatures and humidity, and harbour quite different dung beetle faunas (Davis et al. 2002). In the present study clear differences have, again, been shown between dung beetle assemblages in shaded forest patches and surrounding unshaded grassland habitats of Maputaland.

Over time, farming practices, including cattle-grazing, may lead to modification of a natural ecosystem due to changes in vegetative physiognomy (Jankielsohn et al. 2001; Escobar et al. 2007). As habitat associations in the Maputaland Centre are highly correlated with microclimatic factors induced by vegetative physiognomy (Davis et al. 2002), changes in vegetative physiognomy related to such farming practices or cattle-grazing would induce strong changes in overall dung beetle assemblage structure. Dense populations of both humans and elephants may also induce changes to woody vegetation in the Maputaland region as evidenced by disturbances in sand forest both within and outside the borders of Tembe Game Reserve (South Africa) (Botes et al. 2006) leading to differences in dung beetle assemblage structure (van Rensburg et al. 1999). Although in general appearance, the MSR and farmed area remain similar at the present time, observations suggest that the forest patches are smaller and somewhat more opened out in the farmed area, possibly by the grazing activity of cattle (C. Deschodt, personnel communication) as opposed to activity by elephants. Further degradation might have serious implications given the strong associations of many endemic Maputaland species with shaded forest habitat.

To some degree, available trophic resources may have influenced differences in species richness at study sites since the farmed area and the MSR are characterized by different arrays of large mammal dung types. Studies of

Fig. 4 Number of dung beetle species per trap in each habitat type (forest, grassland) and land usage category (reserve, farmed area) in southern Mozambique

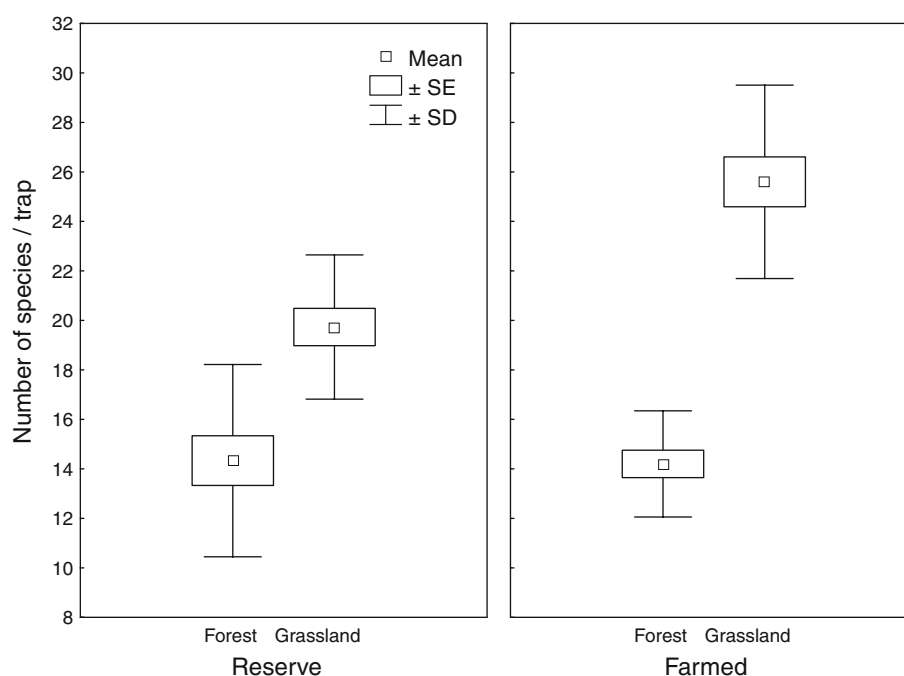


Table 2 Summary of the results for a two-way ANOVA that analyzes species richness and abundance patterns between habitat and land usage categories (see Fig. 4)

Factor	<i>df</i>	Richness deviance	<i>P</i> (χ^2 approx.)	Abundance deviance	<i>P</i> (<i>F</i>)
Habitat	1	57.82	<0.0001	22.42	0.76
Farmed area	1	6.68	0.009	494.66	0.16
Habitat x Farmed area	1	4.75	0.029	45.60	0.67
Error	57	34.74		13313.79	
Total	60	103.98		13876.47	

Results were generated from a Generalised Linear Model (GLM) with a Poisson error distribution (link function = Log). Deviance values are given as a measure of the model's fit. Because abundance showed a high value of over-dispersion, we used *F* to compare the effect of factors (Crawley 2002). In both cases, the fitted model was $Y = \mu + \text{Habitat} + \text{Land use} + \text{Habitat} \times \text{Land use} + \varepsilon$

dung type associations suggest that important categories of dung type comprise: the large, coarse-fibred droppings of monogastric herbivores (e.g., elephant, equines); the large pads of some ruminant herbivores (e.g., buffalo, cattle); the small, strong-odoured droppings of omnivores or carnivores (e.g., pigs, monkeys, humans); and the pellets dropped by smaller herbivores (Davis and Scholtz 2001). Many African dung beetle species are attracted to wide range of droppings and although they often show a bias in distribution towards particular dung types, or dung type categories, this is only extreme in a few cases (Davis 1994; Tshikae et al. 2008). The MSR protects 340 species of mammals, including elephants, bushpigs, and monkeys (Simango and Vervet), but does not include buffalo (R Guldmond and J. Fourie, personnel communication). Although the farming area is not separated from the MSR by fences, and one observes passing elephants, it shows different character to the study area in the reserve,

particularly due to the presence of humans, and cattle. Thus, in terms of the above classification, there might be a greater diversity of dung types in the farming area.

For logistic reasons, only a single bait type was used in the present study. Even so, it should reflect the local conditions relating to differences in habitat and land usage to provide valid comparative results. Domestic pig dung has been shown to be a good attractant for African dung beetles as it tends to capture more species and individuals than most other dung types (Davis 1994; Tshikae et al. 2008) albeit in different relative abundances. In the few studies that compare both dung type attractiveness in Africa and provide species level data, pig dung has attracted all but one of the scarabaeine species recorded on other bait types near Pretoria (Davis 1994) and 51 out of 67 species recorded by all bait types used in Chobe National Park, Botswana (Tshikae et al. 2008). In the Botswana study, all but three of those species not trapped to pig dung were

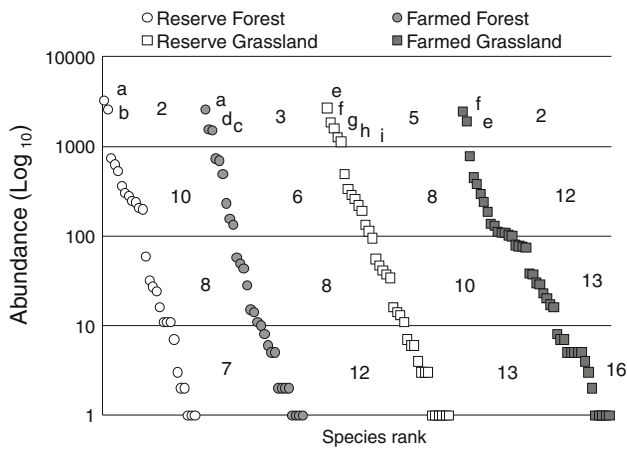


Fig. 5 Rank-abundance plots showing species dominance within dung beetle assemblages in two different habitat types (forest, grassland) and two different land usage categories (reserve, farmed area). Numbers of species are shown for each of four hierarchical levels and species with an abundance > 1,000 are indicated by letters (a = *Progoderus aciculatus*, b = *Onthophagus* sp. nr. *asperulus*, c = *Onthophagus lacustris*, d = *Sisyphus* sp., e = *Progoderus auriceps*, f = *Onthophagus signatus*, g = *Sisyphus sordidus*, h = *Onthophagus* sp. nr. *fimetarius*, i = *Pachylomerus femoralis*)

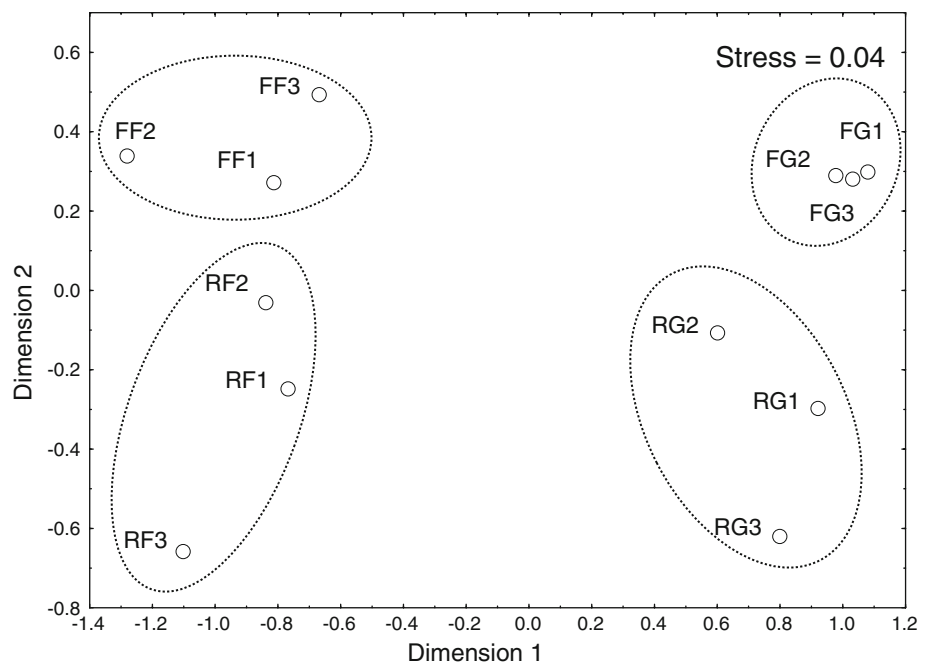
present in very low abundance. The exceptions were three relatively abundant carrion specialists.

Results have, indeed, shown clear differences between forest, grassland, the MSR, and the farmed area with principal trends related, variously, to species richness, species turnover, and species assemblage structure. It is likely that a complex of local ecological factors have influenced these results. These would include the possible influence of relative continuity in grassland versus

patchiness and patch size in forest as well as factors discussed above that include natural microclimatic differences associated with physiognomy of forest and grassland habitats, and combined effects of land usage in terms of disturbed vegetation and modified dung type arrays. Lower predicted completeness of the species record in grassland and greater turnover in forest than in grassland might be associated with patch isolation/habitat continuity factors. In the farmed area, greater species richness at several scales could, conceivably, be related to the greater local diversity of dung types that is discussed above. A similar link between resource availability and species richness in the Maputaland Centre of Endemism was noted by Botes et al. (2006) in the Tembe Elephant Reserve, South Africa, where reduced resources led to decreased species richness. Also in the farmed area, there was greater similarity in species abundance structure that was reflected by tighter clustering of study sites in ordination space and lower beta diversity. This could reflect a more disturbed and homogeneous environment than in the reserve. Biogeographical composition also differed strongly between habitats and study sites under different land usage. The reasons for the differences are unclear and could potentially be related, variously, to historical patterns of endemism, ecological responses to climate, and variables related to land usage.

In conclusion, as in other studies in Maputaland, the present study in southern Mozambique shows strong differences in dung beetle assemblage structure between forest and grassland habitats. It also shows differences between the MSR and the farmed area. In combined analyses of the relative influence of habitat versus land

Fig. 6 NMDS (nonmetric multi-dimensional scaling) ordination plots showing the relative statistical distance between dung beetle assemblages in each habitat type and each land usage category in southern Mozambique (FG = Farmed Grassland, FF = Farmed Forest, RG = Reserve Grassland, RF = Reserve Forest)



usage (species richness and turnover, ANOSIM results from species abundance ordination), habitat was much the greater influence. Thus, although there were clear differences between the farm area and the MSR, land usage would be the lesser contributor to variation at present. As increasing disturbance could become more important in the future, further research would be useful in order to determine the relative contribution of different ecological influences leading to the observed results. For instance, it would be helpful to focus on dung association studies to better understand the effects of different dung type arrays in the MSR and the farmed area. A transect from coastal to inland forest in the MSR and the farmed area would help to determine if there is a climatic gradient. A study of influential local ecological factors comprising relative habitat continuity, isolation, patch size, and levels of disturbance would also be useful.

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References

- Botes A, McGeoch MA, van Rensburg BJ (2006) Elephant- and human-induced changes to dung beetle (Coleoptera: Scarabaeidae) assemblages in the Maputoland Centre of Endemism. *Biol Conserv* 130:573–583
- Cambefort Y (1982) Les coléoptères Scarabaeidae *s. str.* de Lamto (Côte d'Ivoire): structure des peuplements et rôle dans l'écosystème. *Ann Soc Entomol Fr* 18:433–459
- Clarke RK, Gorley RN (2001) Primer v5 for windows: user manual/tutorial. PRIMER-E Ltd, Plymouth
- Clarke K, Warwick R (1994) Similarity-based testing for community pattern: the two-way layout with no replication. *Mar Biol* 118:167–176
- Colwell RK (2006) EstimateS: statistical estimation of species richness and shared species from samples. Version 8. Persistent. <http://purl.oclc.org/estimates>
- Colwell RK, Coddington JA (1994) Estimating terrestrial biodiversity through extrapolation. *Philos T Roy Soc B* 345:101–118
- Crawley MJ (2002) Statistical computing. J. Wiley, Oxford
- Crist TO, Veech JA, Summerville KS, Gering JC (2003) Partitioning species diversity across landscapes and regions: a hierarchical analysis of alpha, beta, and gamma diversity. *Am Nat* 162:734–743
- Davis ALV (1994) Associations of Afrotropical Coleoptera (Scarabaeidae, Aphodiidae, Staphylinidae, Hydrophilidae, Histeridae) with dung and decaying matter: implications for selection of fly-control agents for Australia. *J Nat Hist* 28:383–399
- Davis ALV (1996) Habitat associations in a South African, summer rainfall, dung beetle community (Coleoptera: Scarabaeidae, Aphodiidae, Staphylinidae, Histeridae, Hydrophilidae). *Pedobiologia* 40:260–280
- Davis ALV, Scholtz CH (2001) Historical versus ecological factors influencing global patterns of scarabaeine dung beetle diversity. *Divers Distrib* 7:161–174
- Davis ALV, van Aarde RJ, Scholtz CH, Delpont JH (2002) Increasing representation of localized dung beetles across a chronosequence of regenerating vegetation and natural dune forest in South Africa. *Glob Ecol Biogeogr* 11:191–209
- Davis ALV, van Aarde RJ, Scholtz CH, Delpont JH (2003) Convergence between dung beetle assemblages of a post-mining chronosequence and unmined dune forest. *Restor Ecol* 11:29–42
- Davis ALV, Scholtz CH, Dooley PW, Bham N, Kryger U (2004) Scarabaeine dung beetles as indicators of biodiversity, habitat transformation and pest control chemicals in agro-ecosystems. *S Afr J Sci* 100:415–424
- Davis ALV, Scholtz CH, Deschodt C (2008) Multi-scale determinants of dung beetle assemblage structure across abiotic gradients of the Kalahari-Nama Karoo ecotone, South Africa. *J Biogeogr* 35:1465–1480
- De Boer WF, Baquette DS (1998) Natural resource use, crop damage and attitudes of rural people in the vicinity of the Maputo Elephant Reserve, Mozambique. *Environ Conserv* 25:208–218
- Doube BM (1991) Dung beetles of southern Africa. In: Hanski I, Cambefort Y (eds) *Dung beetle ecology*. Princeton University Press, Princeton, pp 133–155
- Escobar F (2004) Diversity and composition of dung beetle (Scarabaeinae) assemblages in a heterogeneous Andean landscape. *Trop Zool* 17:123–136
- Escobar F, Halfpeter G, Arellano L (2007) From forest to pasture: an evaluation of the influence of environment and biogeography on the structure of dung beetle (Scarabaeinae) assemblages along three altitudinal gradients in the Neotropical region. *Ecography* 30:193–208
- Gotelli NJ, Colwell RK (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecol Lett* 4:379–391
- Halfpeter G, Favila ME (1993) The Scarabaeinae (Insecta: Coleoptera): an animal group for analysing, inventorying and monitoring biodiversity in tropical rainforest and modified landscapes. *Biol Int* 27:15–21
- Henderson PA, Seaby RM (2002) Species diversity and richness v. 3.0. Pisces Conservation, Pennington
- Jankielsohn A, Scholtz CH, Louw S VDM (2001) Effect of habitat transformation on dung beetle assemblages: a comparison between a South African nature reserve and neighbouring farms. *Environ Entomol* 30:474–483
- Kruskal JB, Wish M (1978) *Multidimensional scaling*. Sage Publications, Beverly Hills
- Lande R (1996) Statistics and partitioning of species diversity, and similarity among multiple communities. *Oikos* 76:5–13
- Magurran AE (2004) *Measuring ecological diversity*. Blackwell Publishing Company, Oxford
- Mucina L, Rutherford MC (eds) (2006) *The vegetation of South Africa, Lesotho and Swaziland*. Strelitzia, vol 19, pp 1–807, South African National Biodiversity Institute, Pretoria
- Nichols E, Larsen T, Spector S, Davis AL, Escobar F, Favila M, Vulinec K, The Scarabaeine Research Network (2007) Global dung beetle response to tropical forest modification and fragmentation: a quantitative literature review and meta-analysis. *Biol Conserv* 137:1–19
- Nichols E, Spector S, Louzada J, Larsen T, Amezcua S, Favila ME (2008) Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. *Biol Conserv* 141:1461–1474
- Osborn L (1998) *Elephant/human conflict around Maputo elephant reserve, Mozambique*. Department of Zoology, University of Cambridge, IUCN, Maputo
- Paschalis KM (1974) *The genus Sisyphus Latr. (Coleoptera: Scarabaeidae) in Southern Africa*. Unpublished M.Sc. Thesis, Rhodes University, Grahamstown, South Africa

- Solow AR (1993) A simple test for change in community structure. *J Anim Ecol* 62:191–193
- Spector S (2006) Scarabaeine dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae): an invertebrate focal taxon for biodiversity research and conservation. *Coleopt Bull* 60:71–83
- Tshikae BP, Davis ALV, Scholtz CH (2008) Trophic associations of a dung beetle assemblage (Scarabaeidae: Scarabaeinae) in a woodland savanna of Botswana. *Environ Entomol* 37:431–441
- Van Rensburg BJ, McGeoch MA, Chown SL, van Jaarsveld AS (1999) Conservation of heterogeneity among dung beetles in the Maputoland Centre of Endemism, South Africa. *Biol Conserv* 88:145–153
- Van Wyk AE (1996) Biodiversity of the Maputoland centre. In: van der Maesen LJG, van der Burgt XM, van Medenbach de Rooy JM (eds) *The biodiversity of African plants. Proceedings XIVth AETFAT Congress, 22–27 August 1994, Wageningen*. Kluwer Academic Publishers, Dordrecht, pp 198–207
- Veech JA, Summerville KS, Crist TO, Gering JC (2002) The additive partitioning of diversity: recent revival of an old idea. *Oikos* 99:3–9
- Verdú JR, Moreno CE, Sánchez-Rojas G, Numa C, Galante E, Halfpeter G (2007) Grazing promotes dung beetle diversity in the xeric landscape of a Mexican Biosphere Reserve. *Biol Conserv* 140:308–327
- Zar J (1996) *Biostatistical analysis*, 3rd edn. Prentice Hall, Upper Saddle River