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Dung beetle conservation in a heterogeneous landscape of the Maputaland Centre of Endemism

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Background: Maputo Special Reserve (MSR) in Mozambique lays within the Maputaland Centre of Endemism (MCE) and protects the biota of a habitat mosaic dominated by coastal dune forest and inland sand forest patches of different sizes surrounded by natural grassland.

Objectives: To determine the importance of woody versus grassland vegetation for supporting endemic east coast versus widespread savanna dung beetles in the MCE in the face of increased accessibility and exploitation of woody vegetation in southern Mozambique, especially by charcoal burners.

Method: We used general linear mixed models, additive partitioning of diversity and ordination to analyse species abundance and occurrence across a mosaic of three major habitats in the MSR (grassland, sand and dune forest).

Results: High compositional heterogeneity was found between habitat types and study sites so that beta diversity was mostly higher than alpha diversity. Three distinct scarabaeine dung beetle assemblages defined from ordination were largely centred on the three habitat types. Out of a total of 61 species, greater numbers were associated with grassland (38) than sand (17) and dune forest (6) although abundance was greater in both dune forest and grassland than in sand forest. Biogeographical classification indicated that >40% of the species are endemic to the east coast of southern Africa with the remainder centred in adjacent savanna. Endemic east coast species were well represented in both forest (15) and grassland (11). Savanna species were better represented in grassland (27) than forest (8). Proportions of grassland species and their abundance declined across increasing patch sizes of sand forest becoming lowest in dune forest.

Conclusions: Conservation of endemic, east coast dung beetle species requires the preservation of both natural grassland and sizeable patches of forest in an undisturbed habitat mosaic. As the east coastal system is relatively small in extent with the MCE widely transformed in South Africa, the MSR is an important contributor to regional conservation of endemic species.

Keywords: conservation; dung beetles; endemism; Maputo Special Reserve; Maputaland; Mozambique; Scarabaeinae, South Africa.

Introduction

The southeast coastal region of Mozambique and South Africa is biogeographically distinct and may be divided into southern (Pondoland) and northern (Maputaland) centres of endemism based on floral and vertebrate distribution (van Wyk 1994; Perera et al. 2011). The southeast coast also comprises the smallest of six regional centres of dung beetle distribution defined for southern Africa (Davis & Scholtz 2020) in an area characterised by rain falling mainly during summer (60–80%). The greatest numbers of summer rainfall dung beetle species restricted to the southeast coast are concentrated in the MCE in northeast KwaZulu-Natal and southeast Mozambique (Davis & Scholtz 2020) where they are known primarily from quaternary deep coastal sands (Davis et al. 2020). Some past (Davis et al. 2003, 2013; Jacobs et al. 2010) and present studies on these sands have recorded from 57 to 63 species in each local assemblage of which ± 42–52% were endemic to the east coast with some restricted to Maputaland.

A variable degree of protection is offered to endemic species of the deep coastal sands in the MCE. In South Africa, a narrow coastal strip is formally protected southwards from the Mozambique border as the Kosi Bay Nature Reserve, iSimangaliso World Heritage Site and Mapelane Nature Reserve. At the inland edge of the coastal sands on the South African border with Mozambique, the Tembe Elephant Park and Sileza Nature Reserve also protect mixed savanna woodland and patches of sand forest as well as dung beetles (van Rensburg et al. 1999; Botes et al. 2006). However, the remainder of the region is unprotected farmland or local conservancy. Furthermore, the coastal dunes to the south of Mapelane have been subjected to dredge mining for titanium bearing sands although 33% of this area is under restoration as dune forest (van Aarde et al. 1996). Within Mozambique to the south of Maputo, the MSR protects grassland, dune and sand forest patches from the coast to approximately 20 km inland. Although the extreme southeast corner of the country remains formally unprotected, the inland edge of MSR continues southwards as a corridor for elephant movement along the Futi River as far as the South African border where it abuts Tembe Elephant Park. As a result, the area of protected coastal belt vegetation on deep sands of the MCE is much larger in southeast Mozambique than in South Africa where its conservation status (Maputaland Coastal Belt – CB1; Maputaland Wooded Grassland – CB2) is rated as vulnerable to endangered (Mucina & Rutherford 2006).

The dung beetle fauna on deep sands of the MCE has been well studied in South Africa (van Rensburg et al. 1999; Davis et al. 2002, 2003, 2013; Botes et al. 2006) but only to a lesser extent in southeast Mozambique (Jacobs et al. 2010). Since composition of dung beetle assemblages shows clear differences in response to habitat disturbance by elephants and humans in and around Tembe Elephant Park (Botes 2006), the study of Jacobs et al. (2010) suggested further research should address questions on the effects of relative habitat continuity, isolation, patch size, and levels of disturbance in and around MSR. This is now more urgent as threats to the region around the reserve have recently increased along with greater accessibility (Makhaye & Mkhize 2019), development (Peace Parks Foundation 2020), and in particular, clearance of sand forest by farmers and charcoal burners (Tokura et al. 2020). Therefore, we examined: (1) differences in species abundance patterns, diversity and rarity of dung beetles between grassland, dune forest and three patch sizes of sand forest (large, medium, small) for the entire, heterogeneous, habitat mosaic of a study area in the MSR; (2) associations of species assemblages with each of the five habitat/patch sizes; (3) bias in associations of species with each of the five habitat/patch sizes; (4) patterns resulting from the overlay of biogeographical affiliations (east coast, savanna or sandy savanna) onto species habitat associations; (5) how habitat type and forest patch size influenced the occurrence of both east coast endemics and species also found in the adjacent savanna. This approach was designed to demonstrate the importance of the reserve and its environmental mosaic for conservation of the forest and endemic, east coast component of the dung beetle fauna given the greater transformation of the MCE in South Africa.

Methods

Study area

The MCE is roughly consistent with both the Maputaland Coastal Forest Mosaic ecoregion of Olson et al. (2001) and the northern part of the Indian Ocean Coastal Biome of Mucina and Rutherford (2006) including the edge of the adjoining Savanna Biome. Although the biomes of Mucina and Rutherford (2006) were defined for just South Africa, they continue over the border into southeast Mozambique. In northeast KwaZulu-Natal, South Africa, the sandy coastal part of the MCE comprises the eastern part of the Savanna Biome (vegetation unit: Tembe Sandy Bushveld – SVl18) and the northern part of the Indian Ocean Coastal Biome (dominant vegetation units: Maputaland Coastal Belt – CB1; Maputaland Wooded Grassland – CB2; with embedded patches of Northern Coastal Forest – FOz7) (Mucina & Rutherford 2006). The dominant mixed woodland savanna of the Tembe Sandy Bushveld continues northwards into Mozambique and surrounds the protected Licuati sand forests to the west of MSR that is, itself (Figure 1), situated within a 35 km wide coastal strip representing a northern continuation of the Indian Ocean Coastal Biome from South Africa (Mucina & Rutherford 2006).

Proclaimed in 1960, the MSR (800 km^2 from 1960 to 2011; ± 1500 km^2 from 2011 to present by addition of the Futi corridor) protects the flora and fauna in a region characterised by a mosaic of habitats (Smith & Leader-Williams 2006). Within the original 800 km^2 reserve, these habitats are dominated by hygrophilous or woody grassland with patches of sand forest and sand thicket plus water bodies. In particular, the naturally fragmented sand forest and sand thicket comprises patches of different sizes (<1 ha to ± 2000 ha) immersed mainly in a matrix of natural grassland. Other

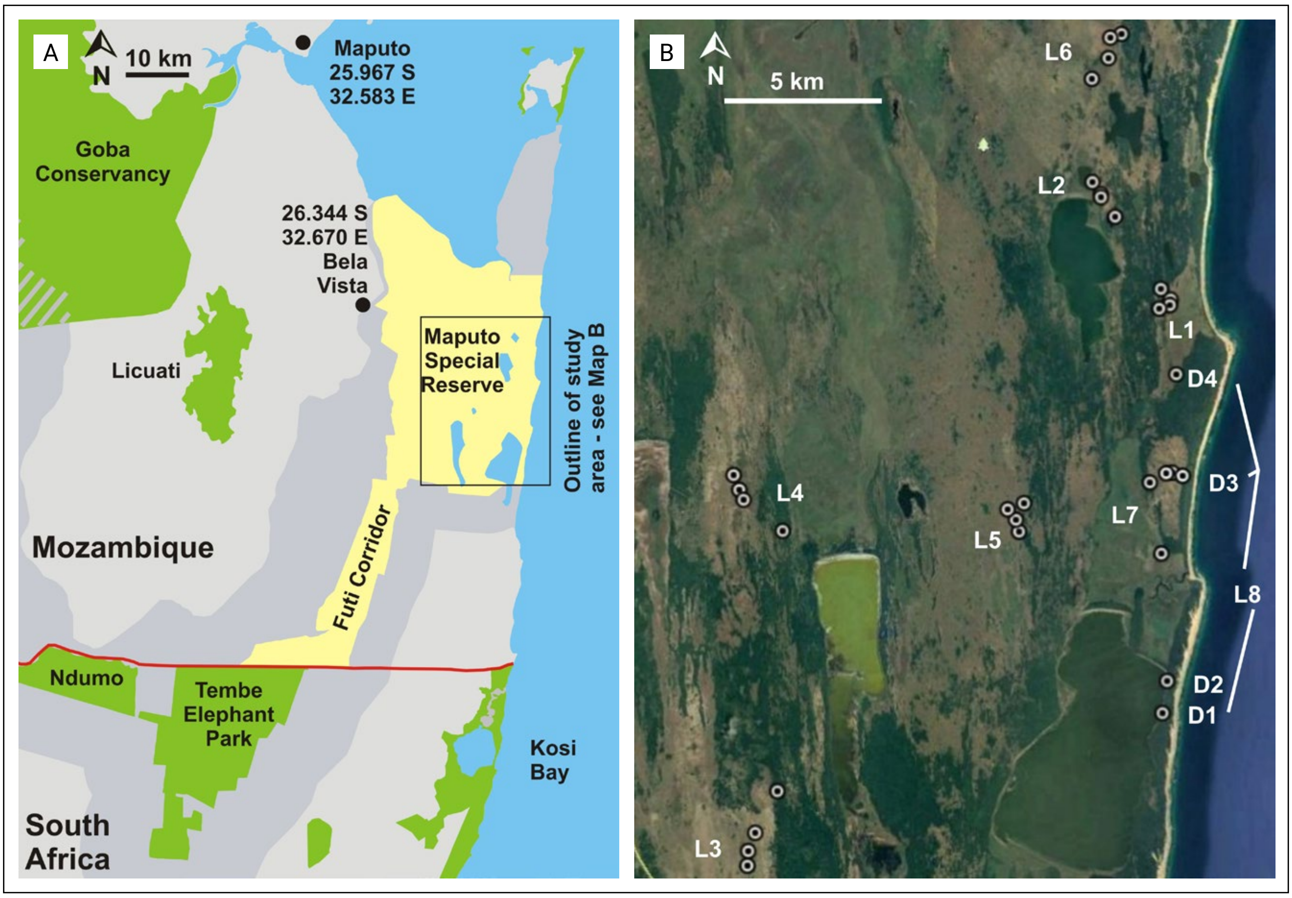

Figure 1. A, map outlining the study area and showing the position of Maputo Special Reserve (MSR) in relation to land usage in the surrounding area of southeast Mozambique and northeast KwaZulu-Natal, South Africa (nature and game reserves are marked by green and yellow, darker grey outlines the Lubombo Conservancy, unprotected areas are pale grey, Indian Ocean, inlets and lagoons are blue) (redrawn from Peace Parks Foundation 2020); B, position of sampling localities in MSR plotted onto Google Earth; L1–L7 = study sites at each locality in large, medium and small sand forest patches plus grassland; L8, DF1–DF4 = dune forest study sites. Position of most forest sites was measured at the point of entry as the GPS could not detect satellites under the canopy.

habitats are more limited in extent and include fringing coastal dune forest, *Terminalia* woodland, grass and sedge swamp in addition to plantations (Smith & Leader-Williams 2006).

Sampling protocol

Sampling was conducted in three major habitats (grassland, sand forest/thicket, dune forest) and in three patch sizes of sand forest/thicket (large, medium, small) within the confines of the original 800 km^2 reserve. This combination of habitats and patch sizes is, hereafter, considered as five different habitat types. To determine habitat associations, dung beetles were sampled at eight localities across the reserve (Figure 1). Each of localities 1–7 included single study sites in grassland, plus small (< 3.8 ha), medium (8 to 53 ha) and large (> 137 ha) patches of sand forest/thicket (= 28 study sites in total separated by 2.30 to 0.10 km at each locality; sand forest at localities 3 and 4; sand thicket at the other localities; hereafter, all cited as sand forest). Locality 8 was defined from widely scattered study sites in a 10.35 km, more-or-less continuous band of dense dune forest (0.35 to 1.25 km wide at sampling points) along the coastline (= 4 study sites in total separated by 1.0 to 6.3 km). At each of the 32 study sites, four pitfall traps were placed at least 50 m apart with distances from forest edges dictated by patch size (dune forest 200 m; large, medium and small sand forest patches: 100 m, 50 m and ±25 m, respectively). This amounted to a total of 128 traps, 16 in dune forest (Locality 8) and 28 in each of the more extensive grassland plus large, medium and small sand forest patches (localities 1–7).

Pitfall traps comprised five-litre plastic buckets (top diameter, 23 cm; depth, 17.5 cm) dug into the sand so that the rims were level with the soil surface. Pig dung was selected as bait since it was readily available and is a good attractant for many dung beetle species (Marsh et al. 2013). Each bait comprised ± 200 ml of fresh pig dung wrapped in thin cloth that was supported at ground level across the top of the buckets by two strong wires. Water plus detergent was placed at the bottom of each pitfall to immobilise the catch.

Sampling was conducted on a single 48 h occasion at each locality between 08 and 24 November 2006.

Samples were collected every 24 h and placed in 99% ethanol for later identification. Fresh baits were placed on the traps at the beginning of sampling and then replaced three times with fresh baits after ± 12 h, either early in the morning or late in the afternoon. This protocol presented fresh dung for attracting both diurnal and nocturnal fliers and yielded a total of 256 samples (32 study sites × 4 traps × 2 days). Representative material was originally deposited in the reference collection at the University of Pretoria that has now been donated to the IZIKO South African Museum, Cape Town.

Data analysis

Completeness of sampling

Coverage-based rarefaction (Chao & Jost 2012) was used to estimate if sampling effort at each study site was sufficient to provide a complete inventory of the species assemblage represented within the whole community. This was determined using the equation: $\hat{C}n = 1 - f_1 / n\ [(n - 1)f_1 / (n - 1)f_1 + 2f_2]$, where f_1 and f_2 are, respectively, the numbers of species with one (singletons) and two individuals (doubletons) in the sample and n is the number of individuals. Sample completeness ($\hat{C}n$) indicates the proportion of the entire community represented by the trapped species (Chao & Jost, 2012). When $\hat{C}n \approx 100\%$ (or '1' on a 0–1 scale), sampling is complete in terms of the effort and capture technique used. Therefore, the diversity values can be compared directly (Chao & Jost 2012). Sample coverage was calculated using the iNEXT package for R (Hsieh et al. 2016).

Species abundance patterns

General linear mixed effects models (GLMM) with poisson error distributions were used to examine how numbers of species and abundance were affected by habitat type and between–study site heterogeneity within each habitat. Due to high over-dispersion detected for abundance, the quasi-poisson error distribution was used (Crawley 2013). Habitat type was considered as a fixed factor and study sites as a random factor. Traps (128 in total) were nested within study sites; study sites were the replicates. For analyses of deviance and tests of contrasts, we used the Type II Wald Chi square test. For the adjustment of P values in the contrasts, we used the Tukey method. Analyses were carried out using the 'lme4' (Bates et al. 2020), 'multcomp' (Hothorn et al. 2017), and 'MASS' (Ripley et al. 2019) packages in R v. 3.5.3 (R Core Team 2019).

Diversity and rarity

Additive partitioning of total species richness (gamma - γ) (Veech et al. 2002; Crist et al. 2003) was used (1) to determine the proportion of species occurring within (alpha – α) and between study sites (beta – β_1) in each of the five habitats ($\gamma = \alpha + \beta_1$ study sites) and (2) to determine overall proportion of diversity occurring within (α) and between study sites (β_1) and between habitat types (β_2) ($\gamma = \alpha + \beta_1$ study sites $+\ \beta_2$ habitat types). This approach permitted a direct comparison between numbers of species attributable to the alpha and beta components of gamma diversity.

We calculated a species rarity index based on species distribution across sampling sites. This was calculated as $1 - (n_i / N)$, where n_i is the number of sites at which species i was present, and n is the total number of sites ($N = 32$). Based on the index values, frequency of species occupation at the 32 sites determines the proportion of species with restricted occurrence across the study area.

Habitat and biogeographical associations

Factor analysis and hierarchical analysis of oblique factors (Tibco Software Inc. 1987–2014 – Statistica 13.3.) were used to analyse local distribution patterns across the 32 study sites. The 32 × 61 data matrix represented mean abundance per sample at 32 study sites for each of 61 species of dung beetles. The data were 4th root transformed before factor analysis using varimax-normalised rotation of factors. Hierarchical analysis of oblique factors was used to identify clusters of sites with similar faunal composition (default setting of 0.7) and determine the amount of shared and unique variance between clusters represented by extended factors.

Non-metric multi-dimensional scaling (NMDS) (Tibco Software Inc. 1987–2014 – Statistica 13.3.) and a minimum spanning tree (MST) were used to analyse bias in spatial distribution of dung beetle species between five habitat types. The 61 × 5 data matrix represented mean abundance per sample of 61 species in grassland, dune forest and the three different patch sizes of sand forest. The data were square root transformed and converted to a correlation matrix before NMDS analysis. The distance matrix was used to fit a minimum spanning tree to the ordination biplot for dimensions 1 and 2. Distances between species pairs were first placed in rank order. A search then determined the shortest distances between each species pair until all data points were connected by a complete tree. Dotted lines were used to represent the greatest distances (> 0.7) on the MST to assist defining clusters with similar habitat bias.

Habitat bias was combined with measurements of biogeographical bias. That shown by 50 of the 61 species was defined using the classification in Davis and Scholtz (2020 – three patterns, east coast, savanna or sandy savanna). Biogeographical bias shown by *Onthophagus juvencus* Klug and ten unnamed or undescribed species

Table 1. Species numbers and abundance of dung beetles in three habitats and three patch sizes of sand forest in Maputo Special Reserve (f_1 / f_2 = number the numbers of species with one (singletons) and two individuals (doubletons) in the sample; $\hat{C}n$ = sampled coverage (Chao and Jost 2012)

Diversity data and coverage	Dune forest	Sand forest			Grassland	All habitats
		Large	Medium	Small		
Total species ± 95% CI	21 ± 4.3	33 ± 2.9	30 ± 2.9	40 ± 3.9	49 ± 4.8	61 ± 4.2
Total abundance	13873	8405	9500	5172	20177	57127
f_1 / f_2	5 / 1	3 / 1	3 / 2	9 / 4	8 / 4	8 / 2
$\hat{C}$n	0.9996	0.9996	0.9983	0.9997	0.9996	0.9996

also conformed to these three patterns according to known distribution patterns (pers. obs. ALVD).

Results

Completeness of sampling

A total of 57 127 individuals, belonging to 61 species and 23 genera, was captured in the five habitat types. In all cases, completeness of sampling ($\hat{C}$n) was close to '1' with a sampling deficit of less than 0.2% (Table 1). These results indicate that our comparisons of richness species, abundance and species composition are reliable. Overall, nine species (15%) accumulated around 74% of total abundance: *Proagoderus aciculatus* (Fahraeus) (27%) more typical of dune forest; followed by three species biased to grassland, *Mimonthophagus ambiguus* (Péringuey) (13%), *Proagoderus aureiceps* (d'Orbigny) (7%), *Kurtops signatus* (Fahraeus) (6%); and five species biased to sand forest, *Sisyphus oralensis* Daniel & Davis (5%), *Onthophagus lacustris* Harold (5%), *Catharsius pandion* Harold (4%), *Onthophagus* sp. 1 (4%), *Onthophagus giuseppecarpanetoi* Tagliaferri & Moretto (3%) (Table S1). However, about 23% of the total species (14) were restricted to less than two study sites and about 59% (36) to less than eight sampling sites (Figures 2, S1).

Species abundance patterns

GLMM indicated differences in species numbers and abundance between habitat types ($\chi^2_{\text{species number}}$ = 75.31, df = 4, P <0.001; $\chi^2_{\text{abundance}}$ = 63.39, df = 4, P <0.001) and significant spatial heterogeneity between study sites within habitats ($\chi^2_{\text{species number}}$ = 11.44, df = 5, P = 0.041; $\chi^2_{\text{abundance}}$ = 11.78, df = 5, P = 0.037). The median number of species was significantly higher in grassland than in dune forest and sand forest patches of different sizes where values were relatively similar and did not differ significantly (Figure 3A). The greatest, between-site heterogeneity in number of species was found within grasslands and small sand forest patches (Figure S2A). Median abundances in dune forest and grassland did not differ significantly but were significantly higher than those in sand forest patches (Figure 3B). The greatest, between-site variation in abundance, was found within grasslands followed by dune forest (Figure S2B).

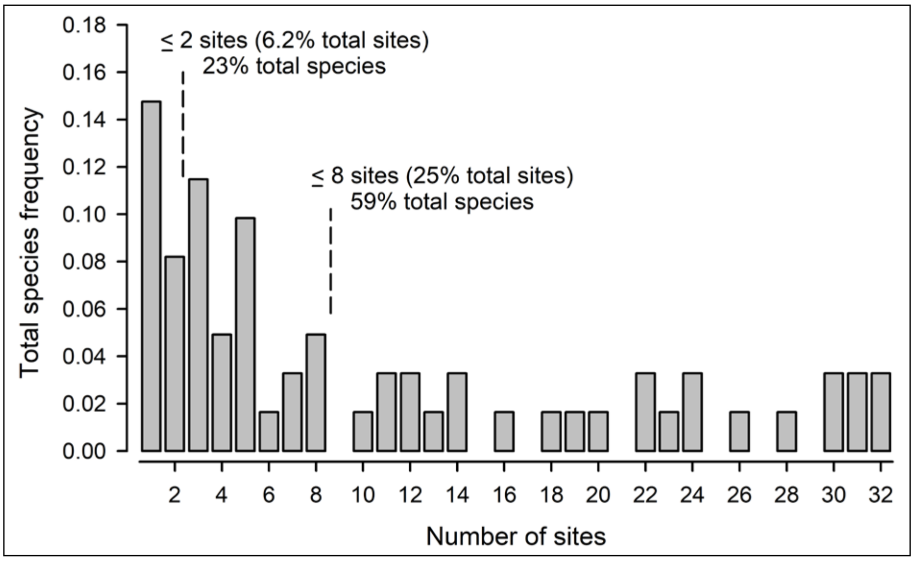

Figure 2. Frequency distribution for proportions of species recorded at 32 study sites in MSR (n = 4 in dune forest; n = 7 in grassland and each of three patch sizes of sand forest). Dotted lines delineate the relative incidence of rarer species at study sites. Note that a high percentage of the total species are found only in 25% of the sampled sites. See Figure S1 for values of the species rarity index.

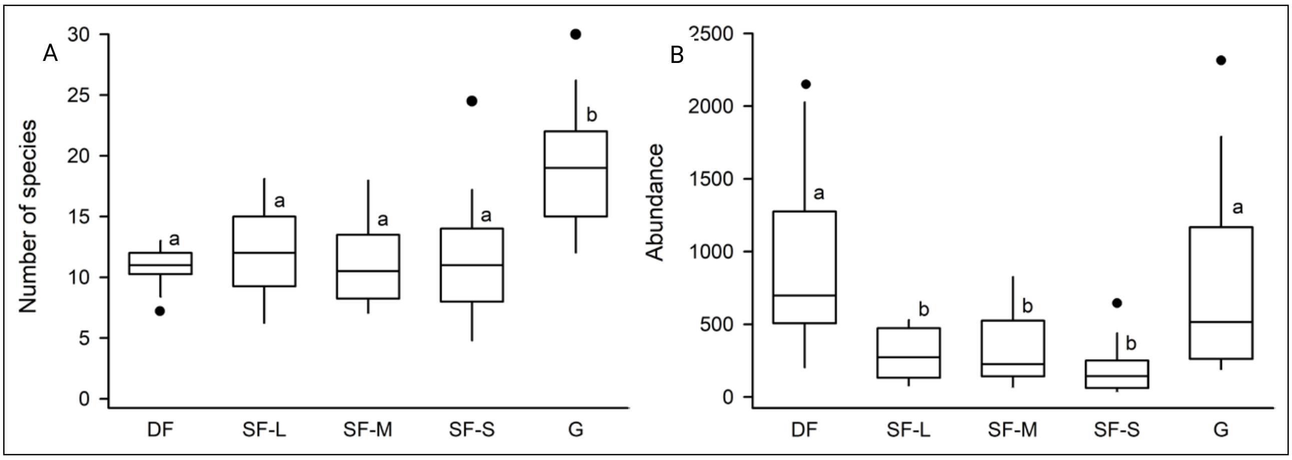

Figure 3. Box plots comparing number of species (A) and abundance (B) in each habitat type (DF = dune forest, SF-L, SF-M, SF-S = large, medium and small sand forest patches, G = grassland). Within each box, the mid-line represents the median whereas the lower and upper extents of the box represent the interquartile range Q_1 = 25th percentile and Q_3 = 75th percentile, respectively. Whiskers are minimum and maximum values. Black points represent outliers. Different letters indicate statistical differences at $P < 0.05$.

Relative proportions of total species and individuals (Table 1) also differed between habitats. The overall highest proportions of species (80.3% of 61) and individuals (36.3% of 57127) was found in grasslands. Although the lowest proportion of individuals (9.1%) was recorded in small sand forest patches, species richness was relatively higher (65.7%) than in the medium and large patches (49.1%, 54.1%) with relative abundance of 16.6% and 14.7%, respectively. Dune forest showed the lowest proportions of species (34.5%) but higher relative abundance (24.3%) than other forest habitats despite the lower number of study sites.

Several other trends in heterogeneity were noted across the reserve. These include a decline in abundance northwards along the coastline in dune forest (Locality 8: study sites 1–4) and higher species numbers and abundance in grassland at inland localities 3 and 4 plus coastal Locality 7 that are partly paralleled in sand forest at those localities (Figure S2). Mostly lower numbers were recorded at study sites in localities 1, 2, 5 and 6.

Diversity and rarity

In an additive manner, gamma diversity (γ) across the study area in MSR was expressed as: 61 = 15.6 [α within study sites] + 34.6 [β_1 between sites] + 11.1 [β_2 between habitat types] (Figure 4). Proportionally, overall diversity was divisible into only 25% generated by alpha diversity within study sites and 57% generated by beta diversity between study sites at different localities with 18% generated by beta diversity between habitats. On the habitat scale, sand forest and grassland accounted for the highest values of beta diversity between study sites at different localities (55 to 62%) while dune forest showed the lowest beta diversity values between study sites (40%). The slightly greater contribution of beta diversity in small sand forest and grassland (62% and 57%, respectively) is reflected by greater numbers of rarer species (larger f_1 / f_2 values – Table 1) and the higher contribution of alpha diversity in dune forest is reflected by dominance of a single species (*Proagoderus aciculatus*, 70.1% – Table S1).

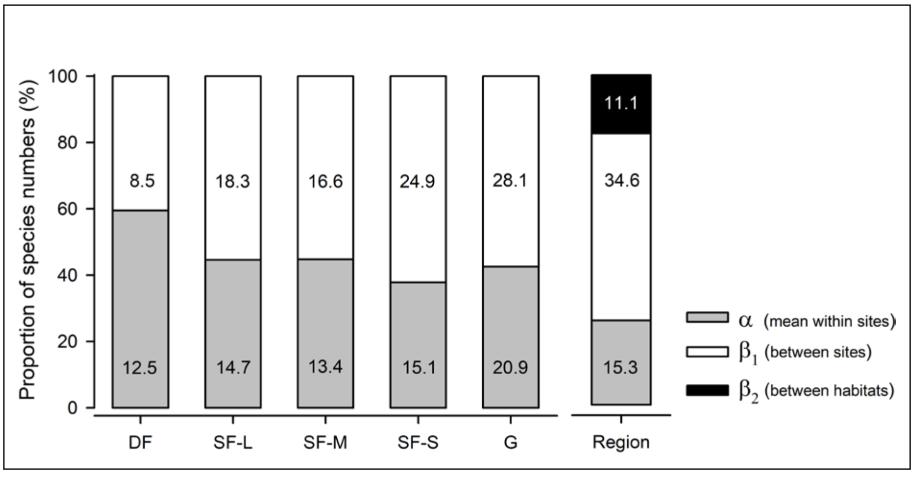

Figure 4. Contribution of each spatial component (habitat and patch size) to total species numbers sampled in the entire reserve (gamma diversity, n = 61 species); alpha (α) = diversity contributed by study sites; beta (β_1) = diversity between study sites; beta (β_2) = diversity between habitats. Proportions contributed by alpha and beta diversity are shown by the divisions within the bars whereas numbers of species are shown inside the bars (see methods). DF = dune forest; SF-L, SF-M, SF-S = large, medium and small sand forest patches; G = grassland.

Habitat and biogeographical patterns

Factor analysis and hierarchical analysis of oblique factors defined three differing spatial patterns in MSR accounting for 84.7% of the overall variance between mean species abundance data at 32 study sites (Figure 5A). The dung beetle faunas of grassland sites (93% unique variance) showed strong differences to those at forest study sites. The dung beetle faunas of dune and sand forest sites were structurally close (83% or 77% shared variance). There was some inconsistency in initial habitat classification as the 'sand forest faunas' at Locality 7 (large, medium and small patches) and Locality 5 (medium patch) were classified with the dune forest study sites. However, no difference was detected between most sand forest and sand thicket faunas.

NMDS ordination and a MST indicated three groups of species showing a local bias to either dune forest (6 spp.), patches of sand forest (17 spp.) or grassland (38 spp.) (Figure 5B, Table S1). These species groups also showed differing degrees of bias to either east coast, savanna or sandy savanna distribution patterns at biogeographical scale. Species with distributions centred on the east coast (26 spp.) occurred in all three studied habitat types although there were slightly more in natural forest (15 spp.) than in natural grassland (11 spp.). Species with distributions centred in sandy savanna and savanna were heavily biased to grassland (27 spp.) as opposed to forest occurrence (8 spp.) although this was less true of small sand forest patches (Table 1). Overall endemism to the east coast amounted to 42.6% in terms of total species numbers and 80.6% in terms of mean abundance per sample, of which 61.3% comprised abundance contributed by east coast forest endemics.

Penetration of grassland species into sand forest varied according to patch size, which accounted for the

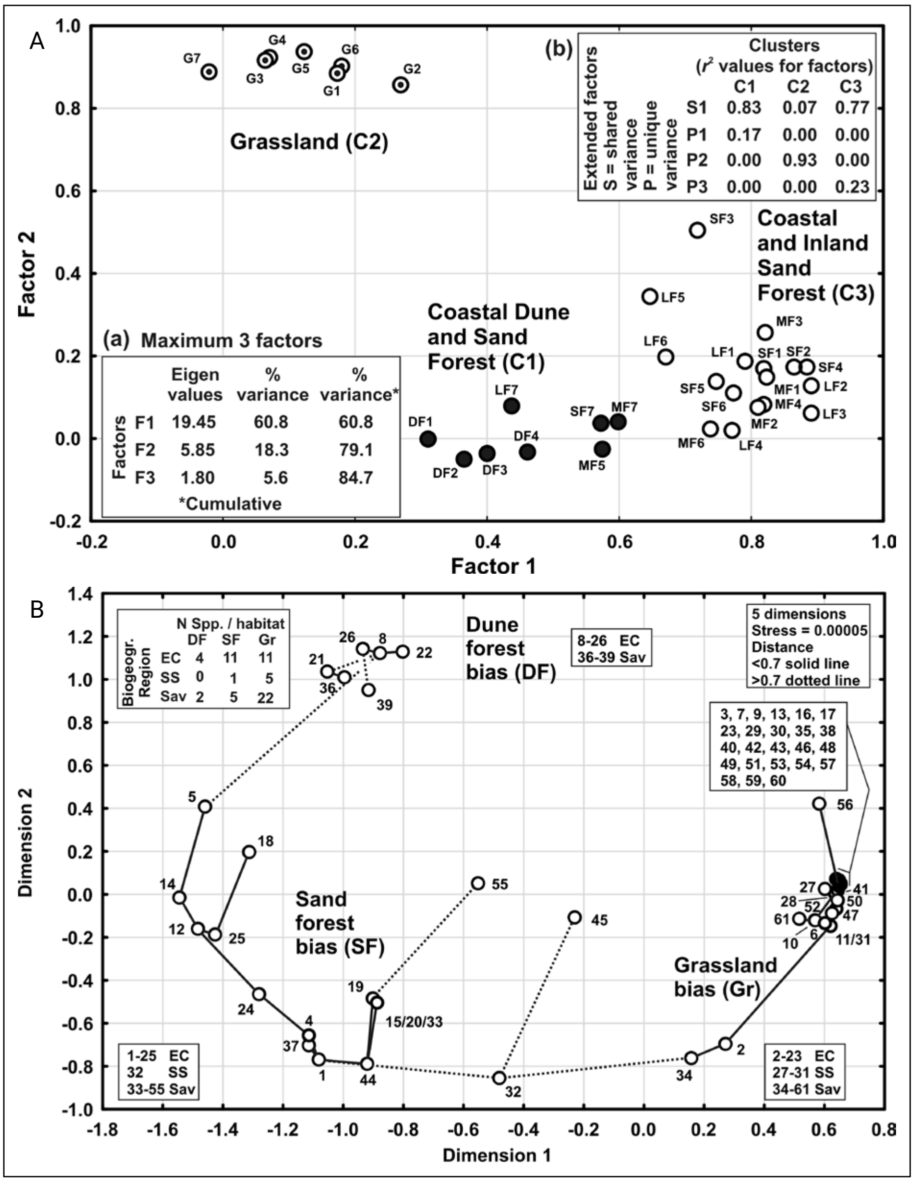

Figure 5. A, factor analysis ordination biplot showing three statistically defined clusters with, (a) a table of eigenvector values for each factor with proportional contribution to variance, and (b) r^2 values for the relationship between clusters and secondary (S) or primary (P) extended factors derived from hierarchical analysis of oblique factors (data points for study sites: G = grassland, DF = dune forest, LF, MF, SF = large, medium and small sand forest patches); B, NMDS ordination biplot with minimum spanning tree representing the habitat and biogeographical bias of 61 dung beetle species from Maputo Special Reserve (See Table S1 for key to species; EC = east coast species, SS = sandy savanna species, Sav = savanna species).

Table 2. Dung beetle species numbers, abundance, and proportions of grassland species in three habitats and three patch sizes of sand forest in Maputo Special Reserve.

Habitat associations	Dune forest	Sandforest			Grassland
		Large	Medium	Small	
Total N forest species ^	14	20	18	19	12
Total N grassland species ^	7	13	12	21	37
% N grassland species ^	33.3	39.4	40.0	52.5	75.5
Average. abundance/sample forest spp. ^	430.5	133.5	135.2	71.3	9.2
Average abundance/sample grass spp. ^	3.0	16.6	34.5	21.1	357.7
% abundance grassland species ^	0.7	11.1	20.3	22.9	97.5

^ See Figure 5 and SI plus Table 1 for classification of species habitat associations.

greater total numbers in small patches compared with medium and large patches (Tables 1, 2). Proportional representation by grassland species increased from dune forest across large and medium patches of sand forest becoming much larger in small sand forest patches (Table 2). Proportional average abundance of grassland species per sample also increased from dune forest to large sand forest patches becoming appreciably greater in both medium and small patches but much lower than in unshaded grassland.

Discussion

We first discuss some peripheral problems associated with defining scale of endemism along the east coast as well as outlining some of the climatic and faunal variation within the deep sand region of the MCE. We then discuss influences on species abundance patterns, associations with habitat and patch size, as well as outlining how recent threats illustrate the importance of MSR for conservation of east coast endemics, particularly in the light of current clearance of forest outside and within other nearby reserves.

Endemism on the east coast

Centres of endemism have been recognised along the east coast of southern Africa for various biota including flora, mammals and dung beetles (van Wyk 1996; Perera 2011; Davis et al. 2003, 2013; Jacobs et al. 2010). Although many dung beetle species are currently considered to be endemic to either the Pondoland or Maputaland centres (Davis et al. 2020), biogeographical classification relies on the quality of survey data. Whilst the dung beetle fauna of the MCE has been well studied (Davis et al. 2002, 2003, 2013; Jacobs et al. 2010) that to the south in Pondoland is less well studied and that to the north in the Southern Zanzibar–Inhambane Coastal Mosaic is very poorly known. Thus, although some papers have defined species distributions as widespread savanna and Maputaland or east coast endemics (Davis et al. 2003, 2013; Jacobs et al. 2010), the known distributional extent of some species has subsequently changed. For instance, *Sisyphus neobornemisszanus* cited as *S. bornemisszanus* is not restricted to the MCE as it is now known from Pomene further north along the east Mozambique coast in the Southern Zanzibar–Inhambane Coastal Mosaic. Furthermore*, Sisyphus* (*Neosisyphus*) *mirabilis* cited as *Neosisyphus mirabilis* is, also, not restricted to the MCE as it is now also known from far to the south in the Eastern Cape, South Africa. Thus, in the present work the most recent classification developed by Davis and Scholtz (2020) is used to describe biogeographical patterns shown by most of the dung beetle fauna of MSR (savanna, sandy savanna or east coast distribution). Unnamed and possibly undescribed species were also allotted to these three categories according to known distributions (pers. obs. ALVD).

Within the area encompassed by the Maputaland Coastal Forest Mosaic of Olson et al. (2001), annual rainfall is lower inland (± 600–650 mm) compared to the moister coastal band where annual temperature and rainfall vary from the warm but dryer centre around MSR (± 22.4ºC, 760–800 mm) to a little cooler and moister at the southern extreme (± 21.5ºC, 900–950 mm) and a little warmer and moister at the northern extreme (± 22.8ºC, 830–860 mm). Of 93 species recorded by four quantitative studies along the coastal part of the MCE (Davis et al. 2002, 2003, 2013; Jacobs 2010; present study), 28 are known only from the east coast. Of these, 25 are protected in the MSR with three recorded only to the south. However, six species recorded in the reserve were not recorded to the south in studies conducted in natural dune forest or in early succession grassland and woodland that replaced cleared dune forest after dredge-mining around Richards Bay (Davis et al. 2002, 2003, 2013). Notably, the reserve does not protect two flightless forest endemics showing restricted east coast distributions. One has been recorded at the northern edge of its range near Richards Bay, South Africa (*Gyronotus carinatus* (Boheman)), in the south of the MCE. The other is known from only four museum specimens and is, apparently, restricted to the moist area at the unprotected northern edge of the MCE in Mozambique (*Canthodimorpha lawrencei* Davis, Scholtz & Harrison).

Species abundance patterns in the MSR

GLMM results and high beta diversity indicate extensive variation in species abundance composition between study sites and habitats, which may be ascribed to a complex of spatial and temporal factors. These include: (1) different microclimates in grassland sand forest and dune forest habitats; (2) different patch sizes of forests, possibly with increased effects of edges in smaller patches; (3) day-to-day weather variation during sampling; (4) variability in local availability of suitable dung types for feeding and breeding; and (5) possibly, different levels of disturbance by elephants influencing habitat microclimate. Some of these factors may be responsible for trends in spatial patterns.

Differences in species abundance composition in unshaded grassland and shaded woodland or forest habitats of the MCE are known to be strongly correlated to microclimatic factors including light intensity, radiant and ambient temperature (Davis et al. 2002, 2003, 2013). Presumably, these factors were responsible for the three main assemblage structures recorded in MSR. Grassland and forest assemblages showed extreme differences that would parallel extreme differences in microclimate. Differences in assemblage structure between dune and sand forest were limited but significant. However, the driving factors are unclear as no measurements were made of likely differences in percentage canopy cover and underlying microclimate, nor of possibly greater edge effects in smaller patches of sand forest. Nevertheless, it is clear that differences in patch size of sand forest influences the numbers of species and individuals but has not driven any consistent differences in species abundance composition. However, it is unknown if the configuration of patches of different sizes had any effect, particularly after 14 years since data collection.

It is known that weather influences day-to-day variation in activity by dung beetles (Davis 1995, 2002; Davis et al. 2014), primarily the effects of sunshine, cloud or incidence of rainfall on diel temperatures and light intensity although wind may also be a factor, particularly in some coastal regions. Although there were clear differences in Day 1 and Day 2 results at many study sites that were possibly due to weather variation, microclimatic parameters could not be monitored at the 32 study sites for logistical reasons. Furthermore, as the workload demanded that sampling at some localities should be conducted on different days to that at others, it was not possible to standardise weather effects for the entire data set. However, this omission is not thought to have adversely influenced reliability of principal results for diversity and composition.

Over 400 elephants were recorded by the last census in the ± 1 500 km^2 of MSR (Peace Parks Foundation 2020), up from an earlier census of 180 (de Boer et al. 2000) when the reserve comprised just 800 km^2. Although no measurements are available for the effects of past or present elephant damage in the forests of the reserve, past research on dung beetles in Tembe Elephant Reserve and Sileza Nature Reserve showed that assemblage structure in elephant-disturbed sand forest differed to that in undisturbed sand forest (Botes et al. 2006). In and around the reserves, assemblage structure showed even greater differences in human-disturbed sand forest and the surrounding matrix of mixed woodland savanna (Botes et al. 2006), to which sand forest is converted after excessive disturbance (van Rensburg et al. 1999). Thus, size and effect of the elephant population should be monitored in MSR, particularly as sand forest harbours many neo-endemic plant species (van Wyk & Smith 2000).

Although frequency distribution of dung is known to influence local species abundance composition of dung beetle assemblages (Lobo et al. 2006), distribution of dung types and their amounts remain unknown for the sampling period in MSR. However, close to this time, tracking the movement of five elephants showed that they were primarily utilising the sand forest and hygrophilous grassland along the Futi floodplain (Ntumi et al. 2005) in the northeast of the current reserve, a similar pattern to that recorded from earlier tracking and dung counts (de Boer et al. 2000). The Futi floodplain is closest to localities 3 and 4 where large samples of dung beetles were recorded in sand forest and woody grassland. Observations of elephants and their dung during sampling also indicated that elephants visit some sand thicket patches closer to the coastline whereas, currently, frequent observations are made of elephants on the floodplains and in dense dune forest (Peace Parks Foundation 2020). Such differences in the concentration of elephant distribution in relation to water and forage availability could contribute to the differences in local abundance of dung beetles that were recorded across the overall landscape of the reserve.

Biogeographical plus habitat and patch size patterns in MSR

Within the MSR, biogeographical affiliations, associations with habitat and effects of patch size may be considered to reflect those for dung beetles across the entire region of coastal sands within the MCE. The reserve does not protect all of the east coastal sand species in the region but does include the bulk of the known endemics (see above). Ordination of site data suggests that classification into either dune or sand forest faunas was not entirely accurate as those in all patch sizes of sand forest' at Locality 7 clustered with dune forest. This probably reflects its greater proximity to the coastline and coastal dune forest than other sites that clustered as sand forest. Nevertheless, the clusters showed limited but significant differences in structure that are reflected by habitat bias to either sand (17 spp.) or dune forest (6 spp.) in 23 species of which 15 are east coast endemics. Despite the heterogeneity in abundance and species data between localities, study sites and sampling days, results suggest that small sand forest patches are less effective in conserving the forest dung beetle fauna. This owes to lower overall abundance than larger patches and greater penetration of species biased to grassland habitat, which is also true of medium patches based on proportional abundance data. Furthermore, the greater representation of savanna taxa in natural grassland suggest that reduction in the extent of forest areas would result in greater prominence of savanna taxa in the east coastal zone. Although 11 out of 38 grassland-biased species were identified as having east coastal centres of distribution, it should be noted that two of these 11 species showed a wider but unique distribution pattern from the east coast into savanna up the Zambezi valley to the Okavango delta and north Namibia (*Copris puncticollis*, *Mimonthophagus ambiguus*).

Endemism, threats and conservation

Within MSR, some clear trends shown by analyses of local habitat and species distribution data suggest that protection of natural grassland and both large patches of dune and sand forest would be necessary to adequately conserve the endemic east coastal dung beetle fauna. Threats to this fauna were limited at the time of data collection in 2006 when the southeast corner of Mozambique was only accessible by 4×4. However, a new tarmac road was officially opened in November 2018. This reduced the travel time from Kosi Bay (South Africa) to Maputo (capital of Mozambique) from 6 hours via 4×4 tracks to only 90 minutes. Although the new road skirts the entrance to MSR, which has been upgraded (Peace Parks Foundation 2020), the ease of regional access on tarmac has generated a much greater volume of traffic (Makhaye & Mkhize 2019), which may lead to increased future regional disturbance. For instance, the new road cuts across the Futi corridor, proclaimed as part of the reserve in 2011 to protect elephant movement along the Futi River towards South Africa. Also, a recent report describes increased deforestation for production of charcoal and agricultural lands around and, even within, the nearby Licuati sand forest (Tokura et al. 2020). Furthermore, the road system of MSR has been upgraded and new lodges on the coastline have been created or are under construction for development of ecotourism from which local communities will benefit (Peace Parks Foundation 2020). Nevertheless, under such management, the results suggest that MSR should remain a valuable asset for conservation in the MCE as long as the large patches of sand and dune forest remain preserved within a natural grassland matrix.

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Competing interests

The authors declare that they have no financial or personal relationships that may have inappropriately influenced them in writing this article.

Authors' contributions

Design and field execution of the research (FE, CMD), identification of samples (ALVD), data analysis and writing (FE, ALVD), input into writing (CMD, CHS).

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Supplementary Material

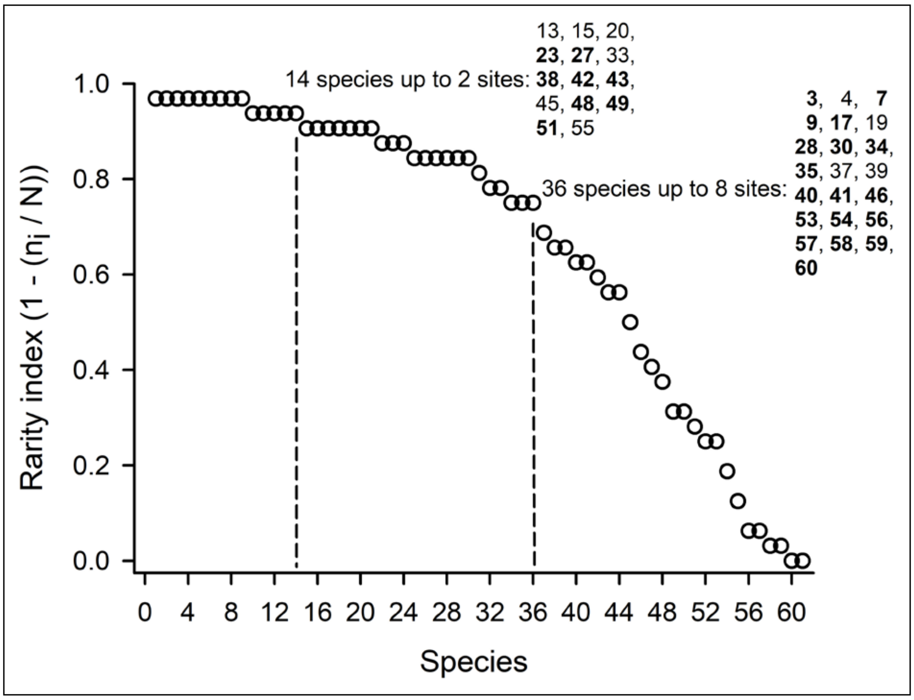

Figure S1. Rarity index values for each species ranked from highest to lowest. Dotted lines show rare species found at up to two sites and indicate the high proportion of the total species (~60%) found at eight sites or less (key to blocks of species numbers in Table S1; species in bold biased to grassland occurrence).

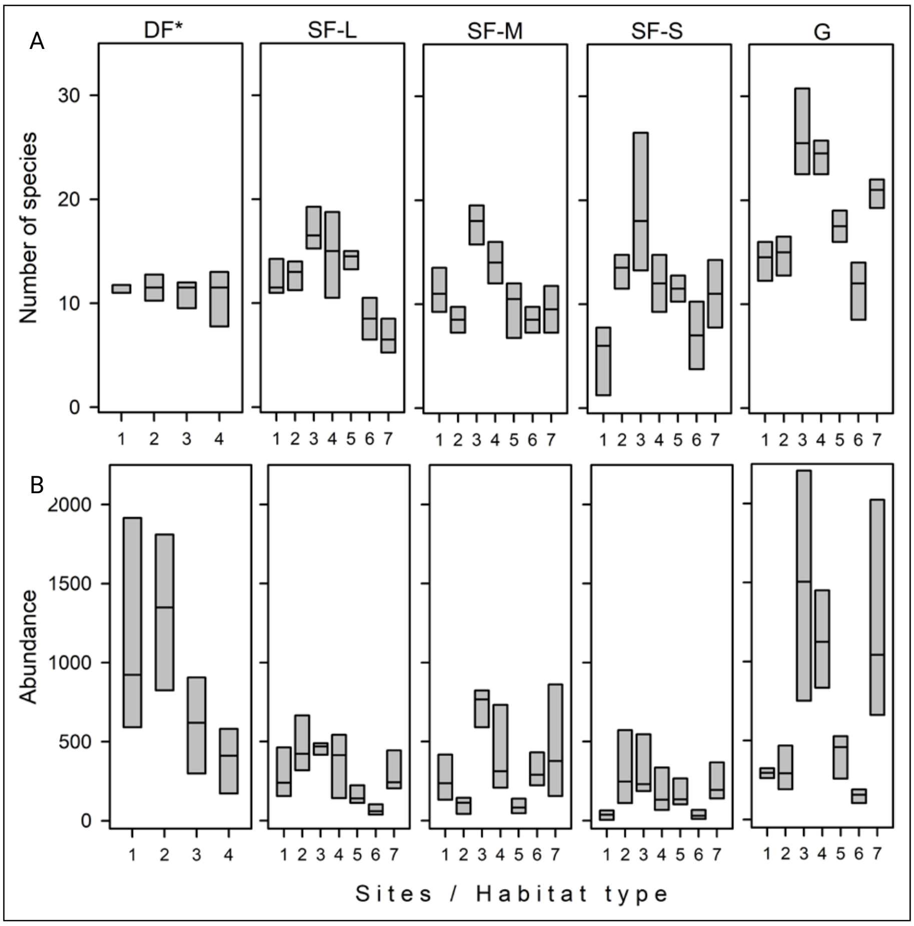

Figure S2. Box plots comparing number of species (A) and abundance (B) at each study site (1–7, except DF* = 1–4) within each habitat type. Within each box, the mid-line represents the median whereas the lower and upper extents of the box represent the interquartile range: Q_1 = 25th percentile and Q_3 = 75th percentile, respectively. DF = dune forest, SF-L, SF-M, SF-S = large, medium and small sand forest patches, G = grassland.

Table S1. Average numbers of 61 dung beetle species in three different habitats (DF = dune forest, SF = sand forest, G = grassland) and three patch sizes of sand forest in Maputo Special Reserve with a classification of biogeographical (see Davis and Scholtz 2020) and habitat bias (see Figure 5 and methods*) with rarity index values (see SI Figure 1 and methods**) for wide (0) or restricted (1) coverage

N	Biogeographical centre* and species		Average abundance / sample				Habitat	Rarity
		Dune forest	Sand forest			Grass-land	Bias*	Index**
			Large	Medium	Small			
	EAST COAST CENTRE							
1	*Caccobius* sp. 1^ (M)	0.47	15.52	8.59	5.02	0.98	SF	0.063
2	*Caccobius* sp. 3^ (M)	0.03	5.89	3.54	3.29	11.76	G	0.125
3	*Catharsius harpagus* Harold (M)	0	0	0	0	3.49	G	0.875
4	*Catharsius laticeps* Boheman (M)	0	1.18	0.75	0.05	0	SF	0.844
5	*Catharsius pandion* Harold (M)	15.78	13.75	9.91	4.54	0.65	SF	0.031
6	*Copris inhalatus* Quedenfeldt ssp. *sanctaluciae* Ferreira (M)	0	0.09	0.11	0.04	2.71	G	0.625
7	*Copris puncticollis* Boheman	0	0	0	0.04	1.16	G	0.906
8	*Garreta caffer* (Fahraeus)	24.59	0.52	0.95	0.11	0	DF	0.500
9	*Metacatharsius zuluanus* (Balthasar)	0	0	0	0	1.33	G	0.813
10	*Mimonthophagus ambiguus* (Péringuey)	1.81	4.68	23.02	7.91	97.71	G	0.031
11	*Onthophagus giuseppecarpanetoi* Tagliaferri & Moretto (M)	0.03	1.09	1.86	2.70	30.55	G	0.313
12	*Onthophagus lacustris* Harold	6.59	16.43	19.59	7.18	0	SF	0.250
13	*Onthophagus ursinus* d'Orbigny	0	0	0	0	0.02	G	0.969
14	*Onthophagus* sp. 1^ (M)	9.72	16.71	14.43	7.66	0.09	SF	0.188
15	*Onthophagus* sp. 2^ (M)	0	0.02	0	0	0	SF	0.969
16	*Onthophagus* sp. 3^ (M)	0.03	0.09	0.02	0.41	24.85	G	0.594
17	*Onthophagus* sp. 4^ (M)	0	0	0	0	3.44	G	0.906
18	*Onthophagus* sp. 5^ (M)	2.34	1.41	6.54	2.54	0.02	SF	0.281
19	*Onthophagus* sp. 6^ (M)	0	0.05	0	0.04	0	SF	0.906
20	*Onthophagus* sp. 7^ (M)	0	0.45	0	0	0	SF	0.938
21	*Proagoderus aciculatus* (Fahraeus)	303.8	41.23	38.68	24.25	2.25	DF	0.000
22	*Scarabaeus bornemisszai* zur Strassen (M)	16.81	0.43	0.20	0.05	0.04	DF	0.656
23	*Sceliages gagates* Shipp (M)	0	0	0	0	0.04	G	0.969
24	*Sisyphus (Neosisyphus) mirabilis* (Arrow)	0.53	4.43	4.04	0.70	0.05	SF	0.438
25	*Sisyphus oralensis* Daniel & Davis (M)	4.97	12.66	21.20	11.14	0	SF	0.250
26	*Sisyphus neobornemisszanus* Daniel & Davis	34.75	0.38	3.57	1.88	0	DF	0.406
	SANDY SAVANNA CENTRE							
27	*Allogymnopleurus splendidus* (Bertolini)	0	0	0	0.02	0.09	G	0.938

^ Species with biogeographical pattern derived from observations. Endemic east coast species, currently, still known only from Maputaland marked by '(M)' although some may have wider distributions.

Table S1. Average numbers of 61 dung beetle species in three different habitats (DF = dune forest, SF = sand forest, G = grassland) and three patch sizes of sand forest in Maputo Special Reserve with a classification of biogeographical (see Davis and Scholtz 2020) and habitat bias (see Figure 5 and methods*) with rarity index values (see SI Figure 1 and methods**) for wide (0) or restricted (1) coverage (continued)

N	Biogeographical centre* and species		Average abundance / sample				Habitat	Rarity
		Dune forest	Sand forest			Grass-land	Bias*	Index**
			Large	Medium	Small			
SANDY SAVANNA CENTRE (continued)								
28	*Kheper lamarcki* (Macleay)	0	0	0.09	0.04	2.27	G	0.781
29	*Kurtops signatus* (Fahraeus)	0	0.05	0	0.64	58.35	G	0.563
30	*Metacatharsius troglodytes* (Boheman)	0	0	0	0	2.18	G	0.781
31	*Pachylomera femoralis* (Kirby)	0	0.57	1.07	1.21	21.36	G	0.313
32	*Scarabaeus goryi* (Castelnau)	0.03	0.71	1.05	0.52	0.49	SF	0.375
SAVANNA CENTRE								
33	*Afrodrepanus impressicollis* (Fahraeus)	0	0.04	0	0	0	SF	0.938
34	*Caccobius histerinus* (Fahraeus)	0	0.02	0.02	0.02	0.04	G	0.844
35	*Caccobius nigritulus* (Klug)	0	0	0	0	1.07	G	0.906
36	*Chalconotus convexus* Boheman	9.94	6.20	5.32	5.23	4.56	DF	0.000
37	*Cleptocaccobius postlutatus* (d'Orbigny)	0	0.20	0.05	0.02	0	SF	0.844
38	*Catharsius tricornutus* DeGeer	0	0	0	0	0.18	G	0.938
39	*Copris fidius* (Olivier)	0.09	0	0.02	0.07	0	DF	0.906
40	*Gymnopleurus virens* Erichson	0	0	0	0.02	0.40	G	0.750
41	*Metacatharsius opacus* (Waterhouse)	0	0.02	0	0.07	6.82	G	0.750
42	*Onitis viridulus* Boheman	0	0	0	0	0.02	G	0.969
43	*Oniticellus planatus* Castelnau	0	0	0	0	0.02	G	0.969
44	*Onthophagus aeruginosus* Roth	0	1.18	0.18	0.25	0.04	SF	0.688
45	*Onthophagus beiranus* Péringuey	0	0	0.09	0	0.02	SF	0.938
46	*Onthophagus juvencus* Klug^	0	0	0	0.02	7.56	G	0.750
47	*Onthophagus obtusicornis* Fahraeus	0	0.07	0.16	0.55	7.96	G	0.656
48	*Onthophagus pullus* Roth	0	0	0	0	0.02	G	0.969
49	*Onthophagus* sp. 8^	0	0	0	0	0.02	G	0.969
50	*Pedaria segregis* Péringuey	0	0.07	0.04	0.41	10.91	G	0.625
51	*Pedaria* sp. 1^	0	0	0	0	0.02	G	0.969
52	*Proagoderus aureiceps* (d'Orbigny)	1.03	3.48	4.55	3.61	55.75	G	0.063
53	*Proagoderus bicallosus* (Klug)	0	0	0	0	0.24	G	0.906
54	*Proagoderus chalcostolus* Péringuey	0	0	0	0.02	0.35	G	0.844
55	*Proagoderus dives* (Harold)	0	0	0	0.02	0	SF	0.969

^ Species with biogeographical pattern derived from observations. Endemic east coast species, currently, still known only from Maputaland marked by '(M)' although some may have wider distributions.

Table S1. Average numbers of 61 dung beetle species in three different habitats (DF = dune forest, SF = sand forest, G = grassland) and three patch sizes of sand forest in Maputo Special Reserve with a classification of biogeographical (see Davis and Scholtz 2020) and habitat bias (see Figure 5 and methods*) with rarity index values (see SI Figure 1 and methods**) for wide (0) or restricted (1) coverage (continued)

N	Biogeographical centre* and species		Average abundance / sample				Habitat	Rarity
		Dune forest	Sand forest			Grass-land	Bias*	Index**
			Large	Medium	Small			
SAVANNA CENTRE (continued)								
56	*Scarabaeus geminogalenus* Davis & Deschodt	0.03	0	0	0	0.27	G	0.906
57	*Scarabaeolus clanceyi* (Ferreira)	0	0	0	0.07	0.91	G	0.844
58	*Scarabaeolus planipennis* (Davis & Deschodt)	0	0	0	0.02	0.31	G	0.875
59	*Sisyphus* (*Neosisyphus*) *confrater* (Kolbe)	0	0	0	0	0.35	G	0.875
60	*Sisyphus* (*Neosisyphus*) *fortuitus* (Péringuey)	0	0	0	0	0.24	G	0.844
61	*Sisyphus sordidus* Boheman	0.06	0.48	0.04	0.02	2.91	G	0.563

^ Species with biogeographical pattern derived from observations. Endemic east coast species, currently, still known only from Maputaland marked by '(M)' although some may have wider distributions.