RESEARCH ARTICLE

Increasing representation of localized dung beetles across a chronosequence of regenerating vegetation and natural dune forest in South Africa

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ABSTRACT

Aim Species assemblages with high proportions of localized taxa occur in regional islands with a history of strong eco-climatic separation from adjacent systems. Current disturbance in such islands of relictualism or endemism disrupts the distinctive local character in favour of regionally distributed taxa with a wider range of tolerances. However, rehabilitation of the system should restore the localized biota. Thus, we used biogeographical composition to assess progress towards restoration of the dung beetle fauna associated with such an island of endemism following dredge-mining.

Location The study was conducted in natural coastal dune forest and a 23-year chronosequence of regenerating dune vegetation in the Maputaland centre of endemism, KwaZulu-Natal, South Africa.

Methods Dung beetles were trapped in eight stands of regenerating vegetation of different ages (< 1 year to ~21 years) and in four stands of natural dune forest with differing ecological characteristics defined by measurements of vegetative physiognomy and microclimate. Species groups defined from multivariate analysis of biogeographical distribution patterns and vegetation associations were used to demonstrate quantitative compositional changes in the dung beetle assemblages across the chronosequence to natural forest.

Results Three biogeographical groups were defined. One group comprised species widespread in southern Africa or both southern and east Africa. The other two groups were endemic, one to the east coast and the other to Maputaland. There was a general trend from dominance by regionally distributed dung beetle taxa to dominance by locally distributed

taxa across the chronosequence of regenerating vegetation from grassland, to open *Acacia karroo* thicket, to dense *A. karroo*-dominated woodland. However, this trend was linked closely to the relative physiognomic and microclimatic similarity between the regenerating vegetation and natural forest. Thus, proportions of locally distributed taxa were lower in older chronosequence woodland (~18–~21 years) with its low canopy cover and open understorey than in dense early chronosequence woodland (~9–~12 years), which is physiognomically and microclimatically closer to species-diverse natural forest with its dense canopy and understorey. Overall, the present dung beetle community comprises five species groups. Single widespread (21 spp.) and endemic groups (14 spp.) showed similar patterns of association with early chronosequence grassland and open thicket stands. A single widespread (3 spp.) and two endemic shade-associated groups (3 and 11 spp.) showed differing patterns of association centred, respectively, in late chronosequence woodland, natural forest, or all shaded stands.

Main conclusions At 23 years, vegetative regeneration is still at an early stage, but abundant activity of most, although not all species recorded in natural forest, is recovered with the closure of the woodland canopy at ~9 years. Compositional differences with respect to natural forest vary closely with vegetative physiognomy and its effect on the microclimate. Therefore, full compositional recovery is dependent on the re-establishment of natural forest physiognomy and microclimate.

Key words chronosequence, dung beetles, ecosystem recovery, endemism, forest, localized species, Maputaland, restoration, widespread species.

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INTRODUCTION

On large land masses, the formation of natural regional islands is associated with the development of distinctive local climatic, edaphic and/or vegetative characteristics. These islands often contain species assemblages with high proportions of localized taxa (Catling, 1995; Willis *et al.*, 1996; Davis, 1997; Harding & Winterbourne, 1997; Lombard *et al.*, 1997; Simmons *et al.*, 1998; Schmiedal & Juergens, 1999). Localization may occur as a result of the region acting as an eco-climatically stable refuge for relict populations of old lineages or due to the region acting as an ecologically isolated centre of taxon divergence over evolutionary time (Cronk, 1997; Fjeldsá & Lovett, 1997; Fjeldsá *et al.*, 1999). At any point in time, the relative proportions of localized and widespread taxa may depend on the degree of ecological difference between the island and adjacent systems and the duration of the period over which this difference has persisted. Habitat fragmentation may disrupt the local ecological processes responsible for the occurrence of localized taxa by creating conditions through which some may be lost or replaced by widespread generalist taxa (Parsons, 1991; Davis *et al.*, 1999) with a wider range of ecological tolerances. A trend towards high proportions of localized taxa may, thus, change to one of dominance by regional generalists (Janzen, 1986; Davis, 1993). In order to reverse this trend towards a return to dominance by localized taxa, it is necessary to restore the local ecological character to which they are adapted. Therefore, the present study examines the effect of forest destruction and postmining vegetative regeneration on the biogeographical composition of local dung beetle assemblages (Coleoptera: Scarabaeidae: Scarabaeinae) on coastal sand dunes in the Maputaland centre of endemism which lies on the north-east, Indian Ocean coastline of South Africa.

The vegetative system of the Indian Ocean coastal belt (Moll & White, 1978) extends from the extreme south of Somalia to the southern edge of the subtropical climate type II(I)a (Walter & Lieth, 1964) near East London (33°01′S 27°58′E) in the Eastern Cape, South Africa. The vegetation of the coastal belt is distinctive since 40% of the larger woody plant species are confined to the region. Based on species turnover from north to south, Moll & White (1978) divided the system into two major phytochoria, the Zanzibar–Inhambane and the Tongaland–Pondoland Regional Mosaics. Recent work has divided the northern phytochorion into the Swahili Centre of Endemism and the Maputaland–Swahili transitional zone (Burgess *et al.*, 1998) which contains relatively few endemics (Moll & White, 1978). The southern phytochorion has been divided into the Maputaland (Tongaland) and Pondoland centres of endemism (van Wyk, 1990, 1994, 1996). For a combined outline map of the regions, see Davis *et al.* (2001).

The Maputaland centre of endemism (van Wyk, 1990) occupies a small east coastal range of *c.* 26 734 km² straddling the borders of Swaziland, Moçambique and South Africa. It marks the southernmost extent in range of many African plant species with tropical affiliations (van Wyk, 1996). The Maputaland vegetation has been classified into 15–21 ecotypes, most of which include many endemics associated with sandy soils (van Wyk, 1996). Most of these taxa must be considered neo-endemics since separation from relatives is mainly at infraspecific level. This is consistent with the recent Quaternary derivation of the low-lying coastal plain (Maud, 1980; Lawes, 1990) that comprises most of the region. However, a small part of Maputaland comprises both ancient and recent north–south-trending dunes. These dunes support two (sand and dune forest) of the five forest ecotypes (also lowland, swamp and riparian fringing or riverine forest) defined for the Maputaland portion of the east coast of South Africa by Moll & White (1978) and Eeley *et al.* (1999). The ancient, inland, dunes support sand forest, which is the most distinctive of the Maputaland plant ecotypes because it contains a significant number of endemics (van Wyk, 1996). The more recent coastal dunes receive higher rainfall (Dent *et al.*, 1989) and support dune forest, which differs in species composition from sand forest. It is very limited in extent as it forms no more than a narrow coastal fringing belt extending from Maputaland southwards, where it becomes patchy and floristically impoverished (Moll & White, 1978). It has been placed in the highest risk category of loss to fragmentation (Eeley *et al.*, 1999).

The coastal dune system around Richards Bay has been granted as a mining concession for the exploitation of minerals containing titanium dioxide. During the mining process, all original vegetation is cleared and all sand is removed to an on-site processing plant that separates the minerals. After processing the pile of discarded sand is reshaped according to the original dune configuration (van Aarde *et al.*, 1996a). In terms of the conditions set by the lease contract, the mining company (Richards Bay Minerals) is placing 65% of the mined dunes under *Casuarina* plantations for charcoal production and the other 35% is permitted to regenerate as natural forest. To assist regeneration, the original topsoil containing the seed bank is spread across the new dunes together with seeds of rapid-growing exotic grasses and herbs (millet, sunflowers). These exotics help to bind the surface and are succeeded by the indigenous grass, *Eragrostis curvula* within 6–8 months (van Aarde *et al.*, 1996a; van Dyk, 1997). Over a 2–3-year period, this grassland cover is replaced by *Acacia karroo* shrubland thicket (van Aarde *et al.*, 1996b; van Dyk, 1997). Further successional changes in physiognomy result in the development of *Acacia* woodland. These changes comprise the closure of the canopy, the separation of understorey and canopy height profiles and the gradual opening of the understorey after 6–9 years (van Dyk, 1997). Thus, although forest physiognomy is soon restored, the open understorey and dominance by *A. karroo* at 14 years (van Dyk, 1997) is quite different to the closed understorey and high species diversity of trees in natural forests (McKenzie, 1996; van Aarde *et al.*, 1996b).

Three questions were addressed in the present study. (1) How does vegetative physiognomy influence microclimate across a 23-year chronosequence of regenerating vegetation to natural forest and how does this affect dung beetle community composition in terms of biogeographical affiliation, habitat association and functional habit? (2) Is there a strong trend to endemism or localization in the dung beetle fauna in the natural dune forests? (3) Do the dung beetle assemblages change from dominance by regionally distributed taxa to dominance by locally distributed taxa across the chronosequence? If so, this would represent a trend towards re-establishment of a specialized endemic dung beetle fauna within their localized distributional range.

METHODS

Study area

The study was conducted on coastal sand dunes within two areas of mining concessions that occupy narrow coastal strips to the north of Richards Bay (28°48′S 32°05′E), KwaZulu-Natal, South Africa. The principal study area (28°38–43′S 32°10–17′E) (Fig. 1) was situated primarily in the Tisand mineral concession where mining commenced in 1977. This 20-km long coastal strip contains patches of exotic *Casuarina equisetifolia* plantations, a patch of indigenous regenerating coastal dune vegetation, and patches of natural dune forest, two of which were used as reference points (coastal and inland dune forests). In general, the regenerating patch forms a continuous north–south chronosequence with the youngest stand (< 1 year) to the north and the oldest stand (23 years) to the south. A second study area, comprising a further two reference points in natural forest, was situated some 15 km further north (28°30–31′S 32°23′E) in the Department of Water Affairs and Forestry, Sokhulu Forest Reserve, which straddles the northern edge of the Zulti North mineral concession (Fig. 1). The understorey and canopies of unmined forest patches harbour a greater variety of indigenous forest plant species than the regenerating patches that have been exposed to mining (van Aarde *et al.*, 1996b).

Study sites and trap placement

For sampling purposes, the chronosequence of regenerating vegetation across mined dunes was divided into eight stands. The youngest was < 1 year in age. The remaining seven each represented a 3-year period in the chronosequence ranging from a median age of ~3 years to a median age of ~21 years. A further four stands, occurring in three separate unmined patches, were selected in natural forest (Fig. 1, Table 1). In each of these 12 stands, three study sites were selected at the maximum possible distance from one another within the limitations imposed by the shape and size of each stand. At each

site, five pitfall traps were placed in a line at 10 m distance from one another. Thus, there were 180 traps in all (12 stands × 3 sites × 5 traps). In the < 1-year stand, only unshaded situations were available for placement of traps. Predominantly shaded situations were all that were available in stands ≥ 9 years. In the ~3 and ~6 years stands most, but not all, traps were placed in broad or narrow grassland/open shrubland patches between the *Acacia* thickets. Thickets were so dense as to be inaccessible without hacking pathways, which would modify the habitat. Precise placement of traps is described in Table 1.
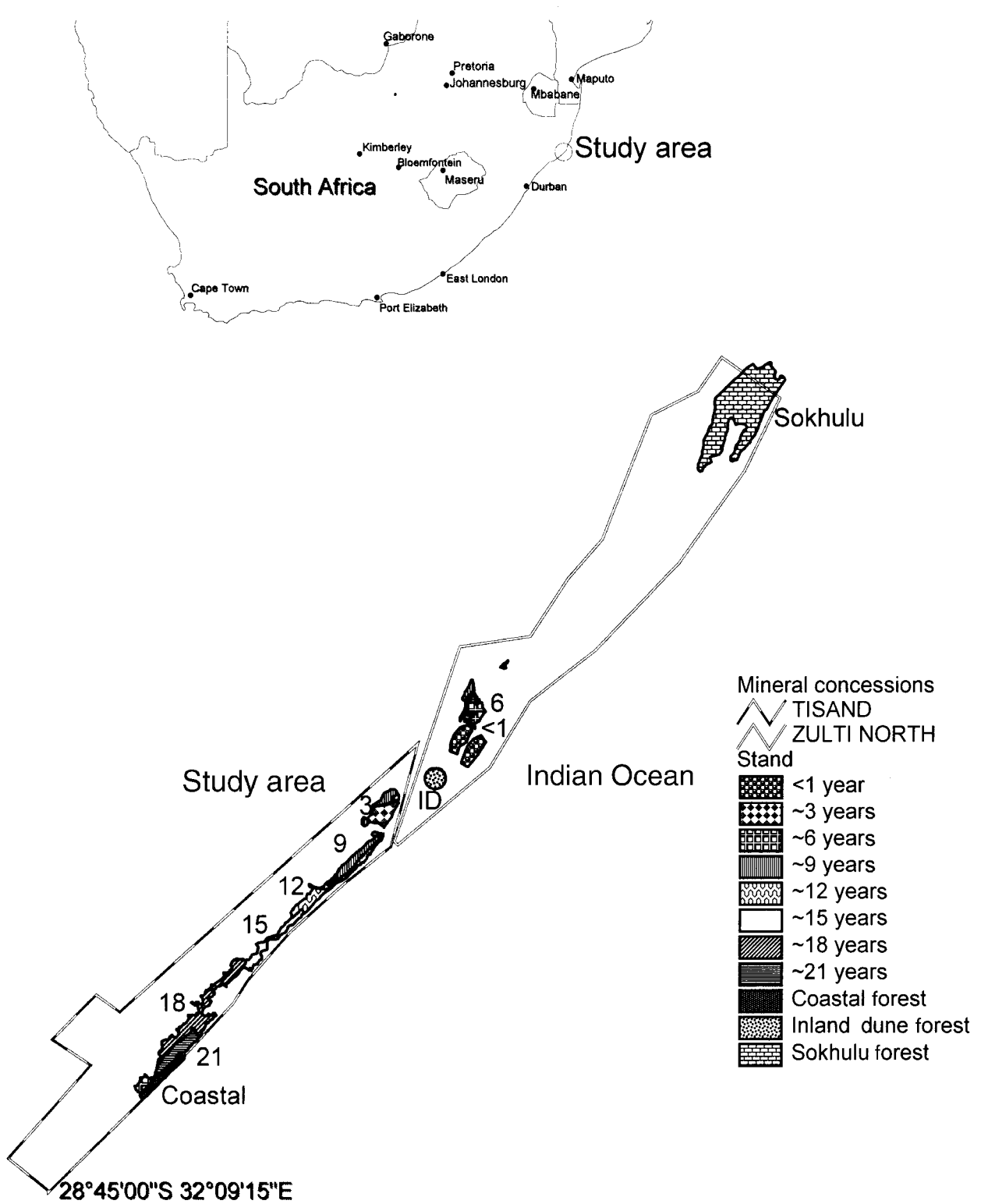
Trap description and trapping method

Each pitfall trap comprised a 5-litre plastic bucket sunk into the sand up to its rim. Traps were baited with a composite of 200 mL of cattle dung and 200 mL of pig dung wrapped in chiffon, which permitted dissemination of dung volatiles whilst excluding dung beetles. These two dung types acted as surrogates for the dung of larger mammal species represented in both past and present forest faunas (Lawes, 1990; Rowe-Rowe, 1994; pers. obs.). This was a necessary feature of the trapping design as dung type strongly influences species abundance composition of dung beetle assemblages (Fincher *et al.*, 1970; Davis, 1994). The baits were supported at ground level above each bucket using two lengths of strong galvanized wire. Beetles attracted to the pitfall traps were immobilized in several cm of water to which a little detergent had been added.

Trapping was conducted over 2 days from 25–27 January 2000 during the mid-summer seasonal peak in activity of dung beetles in the summer rainfall region of South Africa (Davis, 1996a, 1997). Traps were baited both in the late afternoon and the early morning to present fresh dung to both diurnally and nocturnally active species of dung beetles. Traps were emptied after 24 h and 48 h to provide 30 samples per stand and 360 samples in all. Material from the study, including voucher specimens of unnamed species, have been deposited in the reference collection of the Department of of Zoology and Entomology, University of Pretoria. This collection will ultimately become part of the National Collection of Insects, Pretoria, South Africa.

Vegetation data

Proportional cover of the tree canopy above each of 135 traps was estimated by eye in all forest stands with an age ≥ 9 years. Surface cover was measured at each of the 36 study sites by walking transects of 20–50 steps depending on accessibility within the vegetation type. Surface vegetation was scored as present or absent according to whether or not grass or woody stemmed herbs were touching the boot tip at each pace. The results were expressed as mean percentage canopy or surface cover per stand.

Fig. 1 Map showing the location of the study area and the location of stands of regenerating vegetation and natural dune forest near Richards Bay.

Table 1 Brief description of trapping sites at Richards Bay

Stand age (years)	Stand number	Years	Patch area (ha)	Site number	Year	GPS grid reference	Vegetation and number of traps (*n*)
< 1	8	1999	—	1	1999	28°38′ 52.9′S 32°16′ 11.7′E	Sparse grass tufts and herbs (5)
				2	1999	28°38′ 49.2′S 32°16′ 13.7′E	Sparse grass and sunflowers (5)
				3	1999	28°38′ 46.2′S 32°16′ 15.9′E	Millet and sunflowers (5)
~3	7	1996–98	51.55	1	1998	28°38′ 52.0′S 32°15′ 30.3′E	Dune top grassland (5)
				2	1998	28°38′ 52.1′S 32°15′ 26.2′E	Open shrubland (5), *Acacia* thicket
				3	1997	28°38′ 47.1′S 32°15′ 29.6′E	Open shrubl. (3), edge (1), thicket (1)
~6	6	1993–95	34.46	1	1995	28°37′ 07.4′S 32°17′ 34.1′E	Grassland patch in *Acacia* thicket (5)
				2	1995	28°36′ 57.6′S 32°17′ 35.4′E	Open shrubland corridor in thicket (5)
				3	1995	28°36′ 52.1′S 32°17′ 30.2′E	Grassland (3), edge (1), thicket (2)
~9	5	1990–92	84.25	1	1992	28°40′ 01.5′S 32°14′ 46.9′E	Dense canopy *Acacia* woodland (5)
				2	1992	28°39′ 29.1′S 32°15′ 19.2′E	Dense canopy *Acacia* woodland (5)
				3	1992	28°39′ 21.1′S 32°15′ 30.8′E	Dense canopy *Acacia* woodland (5)
~12	4	1987–89	34.89	1	1988	28°40′ 15.9′S 32°14′ 26.2′E	Dense canopy *Acacia* woodland (5)
				2	1988	28°40′ 21.8′S 32°14′ 15.0′E	Dense canopy *Acacia* woodland (5)
				3	1988	28°40′ 26.1′S 32°14′ 08.8′E	Dense canopy *Acacia* woodland (5)
~15	3	1984–86	38.1	1	1986	28°41′ 36.0′S 32°12′ 55.1′E	Open understorey *Acacia* woodland (5)
				2	1986	28°41′ 16.4′S 32°13′ 06.4′E	Open understorey *Acacia* woodland (5)
				3	1986	28°41′ 04.2′S 32°13′ 22.2′E	Open understorey *Acacia* woodland (5)
~18	2	1981–83	133.61	1	1983	28°43′ 00.3′S 32°11′ 00.8′E	Open understorey *Acacia* woodland (5)
				2	1982	28°42′ 40.1′S 32°11′ 31.9′E	Open understorey *Acacia* woodland (5)
				3	1981	28°41′ 49.0′S 32°12′ 22.8′E	Open understorey *Acacia* woodland (5)
~21	1	1977–79	53.09	1	1979	28°43′ 28.5′S 32°10′ 52.6′E	Open shrub understorey *Acacia* woodland (5)
				2	1977	28°43′ 11.3′S 32°10′ 18.4′E	Open shrub understorey *Acacia* woodland (5)
				3	1977	28°43′ 01.5′S 32°10′ 31.6′E	Open shrub understorey *Acacia* woodland (5)
Coastal	—	?	—	1	—	28°43′ 28.5′S 32°10′ 52.6′E	Opening in dense understorey forest (5)
				2	—	28°43′ 11.3′S 32°10′ 18.4′E	Opening in dense understorey forest (5)
				3	—	28°43′ 01.5′S 32°10′ 31.6′E	Dense shrubland understorey forest (5)
In Dune*	—	?	—	1	—	28°37′ 28.2′S 32°17′ 26.3′E	Dense shrubland understorey forest (5)
				2	—	28°37′ 39.5′S 32°17′ 24.8′E	Dense shrubland understorey forest (5)
				3	—	28°37′ 46.2′S 32°17′ 46.2′E	Dense shrubland understorey forest (5)
S. Top*	—	?	—	1	—	28°30′ 37.7′S 32°23′ 42.2′E	Old forest, dense shrub understorey (5)
				2	—	28°30′ 48.2′S 32°23′ 37.2′E	Old forest, dense shrub understorey (5)
				3	—	28°30′ 52.2′S 32°23′ 32.8′E	Old forest, dense shrub understorey (5)
S. Base*	—	?	—	1	—	28°31′ 42.1′S 32°23′ 33.7′E	Edge of clearing (4) in old forest (1)
				2	—	28°31′ 28.9′S 32°23′ 39.0′E	Old forest (3), dense shrubland (2)
				3	—	28°31′ 19.2′S 32°23′ 41.6′E	Old forest (3), dense shrubland (2)

* In Dune = inland dune, S Top = Sokhulu dune top, S. Base = Sokhulu dune base.

Microclimatic data

Measurements were made of shade air temperature, radiant temperature, relative humidity and background light intensity at one point in each of 10 stands using digital dataloggers (Onset, Hobo, 4-channel, H08-004–02, supplied by C.W. Price (Pty) Ltd, PO Box 5, Marlboro 2063, South Africa). For logistic reasons, it was not possible to measure microclimatic differences between the stands simultaneously with the beetle trapping programme. Therefore, the measurements were made between 7–9 March 2000 when diel temperature fluctuations were still similar to those in late January (Davis *et al.*, in press). In woodland and forest, mean canopy cover was calculated for each stand and microclimatic measurements were made at the one point out of 15 where canopy cover most closely approximated this stand mean. A single datalogger was placed in each of the eight stands of regenerating vegetation and in the two reference forest stands in Sokhulu Forest Reserve. In the coastal and inland dune forests, a single Onset Stowaway SRHA02 relative humidity logger and a single Onset Stowaway XT102 temperature logger were placed in each stand. Each 4-channel logger was mounted on a bracket

fixed to a wooden pole so that the recording face of the logger faced upwards. Each bracket was mounted on the pole approximately 1 m above the soil surface so the logger lay 10 cm below a 30-cm square of clear acrylic sheeting fixed to the top of the pole. This allowed the passage of light and most of the radiant heat while protecting the logger from rainfall. To standardize light intensity readings, each pole was positioned with the point of the bracket and the top side of the logger facing north. To measure ambient air temperature in the shade, a TMC6-HA remote temperature sensor was plugged into the fourth channel socket of each logger. The distal end of the 2-m sensor wire was fixed just behind its tip to a second supporting pole so that the thermister sensor protruded from the pole at approximately 1 m above the soil surface and 10 cm below a 26-cm diameter opaque plastic disc (providing shade and protection from rainfall) fixed to the top of the pole. In the coastal and inland dune forests, the relative humidity and temperature loggers were fixed directly to the supporting pole at 1 m above the soil surface and 10 cm below the 26 cm diameter opaque plastic disk. Data logging commenced at 1800 h on 7 March and ceased at 1800 h on 9 March. Microclimatic measurements were set at a frequency of 1 min 30 s for the 4-channel loggers and at a frequency of 1 min 36 s for the Stowaway loggers. Mean daytime data are calculated from the data points between 0630 h and 1745 h when background light intensity was maximal in unshaded situations. Mean dusk data are calculated from the data points between 1745 h and 1830 h when light intensity declined from near maximal to near minimal in unshaded situations. Mean night-time data are calculated from the data points between 1830 h and 0545 h when light intensity was minimal. Because dataloggers were dislodged on the first night in the ~21-year woodland and on the second night in Sokhulu dune base forest, only a single day's data were available for each of these stands.

Data analysis

Validity of data

The abundance-based coverage estimator (ACE) method (Chao *et al.*, 1993; Chadzon *et al.*, 1998) was used to assess the completeness of the species record. Calculations were made from a matrix of species abundance by the 30 samples from each vegetative stand using the EstimateS computer package, Version 5 (Colwell, 1997).

Environmental and dung beetle distribution patterns

Between-stand differences shown by the vegetational (percentage cover) and microclimatic (temperature, humidity, light) parameters were tested for statistical significance using one-way ANOVA. Correlation analysis was used to test for relationships between vegetative cover and microclimatic factors. All data were $\log_{10}(n + 1)$-transformed before ANOVA and correlation analysis. All multiple range tests were conducted using Tukeys's HSD or Tukey's HSD for unequal sample size (Spjotvoll/Stoline test) in cases where there were missing data (microclimatic records). Distributional trends are depicted by data points joined by lines. These lines are merely to guide the eye and are not intended to imply any statistical or biological trend. Rehabilitating stands are ordered in chronosequence. Reference forest stands are ranked according to degree of possible disturbance. The coastal forest immediately adjoins the oldest chronosequence site. The inland dune forest is 100 m from patches that 1937 aerial photographs show were completely cleared (Weisser & Marques, 1979). The Sokhulu forest is least disturbed but a few patches of secondary shrubland occurred at the road edge at the dune base.

Classification of dung beetle species distribution and habitat associations

Geographical distribution patterns were analysed for the 60 species recorded in the 12 stands. Five widespread species were represented by distinct varieties or subspecies restricted to Maputaland. Therefore, separate data were included for both the overall distributions of the five species and for the local distributions of the five varieties. Locality data for the 60 species and five varieties were obtained from published data (Davis *et al.*, 1999) and unpublished data from Itala Game Reserve and the Australian CSIRO reference collection of southern African dung beetles, which is lodged with the National Collection of Insects in Pretoria, South Africa. Presence or absence records for each taxon were plotted across the 249 degree squares of latitude and longitude from which the beetles were recorded in 31 climate types (Walter & Lieth, 1964) of southern and east Africa. Separate presence or absence records were made for each portion of a degree square cut by a climatic boundary. Presence records for each species were summed for each of the climate types. To standardize for variation in regional area, each summed number was divided by the total number of degree squares from which collections were made in its respective region. In most regions, presence records were patchy. Therefore, there was a tendency to over-emphasize the importance of presence records for five of the 31 climate types since they were each represented by a single degree square. Records for these five climate types were down-weighted by dividing the data by two. In the resulting data matrix, values for each species were given equal weighting by converting their cross-climatic distributions to a percentage scale. These percentages were then summed to reduce the number of climate types from 31 to 10, which had the effect of improving separation of clusters. These larger climatic regions comprised East Africa and seven

of the eight major climatic regions defined for southern Africa by Davis (1997) after Walter & Lieth (1964). For the purposes of this east coastal study, the eighth region, comprising east coastal climate, was divided into a southern part incorporating Maputaland and a more tropical northern part. The data matrix comprising percentage distribution of 65 dung beetle taxa between 10 climatic regions was subjected to $\log_{10}$ ($n + 1$) transformation. Cluster analysis was used to classify the geographical distribution patterns shown by these dung beetle taxa. The similarity matrix was calculated using the non-metric, Bray–Curtis similarity coefficient. This matrix was subjected to analysis by the agglomerative clustering technique, group average linking. The results were used to construct a dendrogram on which clusters of dung beetle species were defined at the 50% level of similarity. Multiple paired comparisons of clusters were conducted using the ANOSIM subroutine of the multivariate analytical computer package, *Primer* Version 4.0. Comparisons were conducted using the default setting of a maximum of 5000 permutations.

Habitat associations were also analysed for the 60 species recorded in the 12 stands. Data were arranged as a matrix of species abundances per stand. These data were converted to percentage abundance per stand to give equal weighting to each species. Eight species with low abundance showed outlier distributions in exploratory cluster analyses. Therefore, these species were deleted so that the final data matrix comprised percentage distributions of 52 dung beetle taxa between the 12 stands. This data matrix was subjected to $\log_{10}$ ($n + 1$) transformation, cluster analysis and multiple comparison of cluster pairs (defined at the 25% and 40% levels of similarity) as described for the classification of geographical distribution patterns.

These separate analyses at regional (three patterns) and local scales (two patterns) were combined to classify the Richards Bay dung beetle community into five groups based on both biogeographical distribution pattern and local vegetation association. Statistics generated during multiple regression (Statistica, 1995) were used to define relationships between proportional vegetative cover (canopy, surface) and each of the five species groups. The functional structure of the groups was described according to the classification system of Doube (1990).

## RESULTS

Validity of data

In total, 53 663 individuals were collected, representing 60 species. In most vegetative stands, observed species-richness was greater than 80% of predicted species-richness (Table 2). However, there were much greater discrepancies between observed and predicted species-richness in the < 1-year, ~12-year and coastal forest stands.

Vegetation and microclimate

Vegetative cover varied significantly across the chronosequence (surface cover – $F_{(11,24)}$ = 2.456, $P < 0.05$, tree canopy cover – $F_{(8,126)}$ = 8.937, $P < 0.001$) (Fig. 2). Surface cover dominated by grass was generally well-developed in open situations between thickets but disappeared under the dense, closed canopy of early *A. karroo* woodland (~9 years) to be replaced by a sparse cover of forest herbs. A dense cover of herbs occurred under the reduced canopy cover in older *A. karroo* woodland (~15–~21 years) but again was reduced

Table 2 Observed and predicted species richness (abundance-based coverage estimator (ACE) — Chadzon *et al.*, 1998) of dung beetles in each vegetative stand at Richards Bay

| Vegetative stand	Observed species richness	Predicted species richness	Percentage of species observed
Chronosequence			
< 1 years	22	35.1	62.7
~3 years	33	39.5	83.6
~6 years	41	47.8	85.6
~9 years	24	27.1	88.5
~12 years	22	32.8	67.1
~15 years	28	31.3	89.5
~18 years	28	34.8	80.5
~21 years	24	28.0	85.6
Natural forest			
Coastal	21	28.7	73.1
Inland dune	24	26.5	90.6
Sokhulu base	23	26.3	87.4
Sokhulu top	18	19.6	91.7
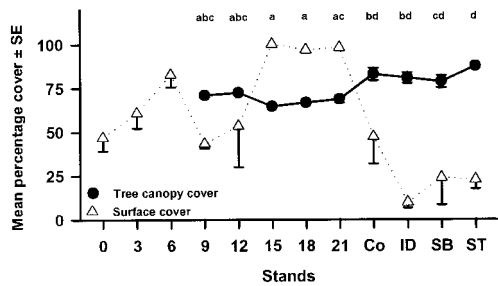
Fig. 2 Changes in vegetative cover across the chronosequence of regenerating vegetation to natural dune forest (stand age (year) depicted by numbers, Co = coastal, ID = inland dune, SB = Sokhulu dune base, ST = Sokhulu dune top forest (the line of letters reports the results for Tukey's HSD multiple range tests on tree canopy cover; pairs of data points with no letters in common differ significantly, $P < 0.05$).

to a very sparse cover under the dense canopy of natural forest stands. Although surface cover was generally highest where canopy cover is absent or lowest, the correlation between the two parameters was not significant overall ($r^2 = 0.07$, $F_{(1,34)} = 2.521$, $P = 0.12$). However, within woodland and

forest stands there was a strong correlation between proportional canopy cover and herbaceous surface cover ($r^2 = 0.39$, $F_{(1,25)} = 16.059$, $P < 0.001$). The validity of these estimates for vegetative cover (Fig. 2) is strongly supported by the complementary patterns shown by microclimatic measurements (Fig. 3) and the significant correlations shown between vegetative and microclimatic parameters (Table 3). These vegetative parameters are used in tests for correlation between environmental variables and dung beetle distribution patterns.

Regional and local spatial distribution of dung beetle species

Three main biogeographical species groups (A, B, C) are defined at the 50% level of similarity (Fig. 4). ANOSIM comparison of cluster pairs showed that these groups differed significantly (global $R = 0.861$; A:B – $R = 0.532$, A:C – $R = 0.928$, B:C – $R = 0.953$; all R numbers $P = 0.001$). Group B showed a widespread regional distribution (Fig. 5), predominantly in tropical climate types. Its local distribution was bimodal with significantly greater occurrence in unshaded stands, older *Acacia* woodland stands and coastal forest ($F_{(11,347)} = 36.49$, $P < 0.001$). However, multiple regression
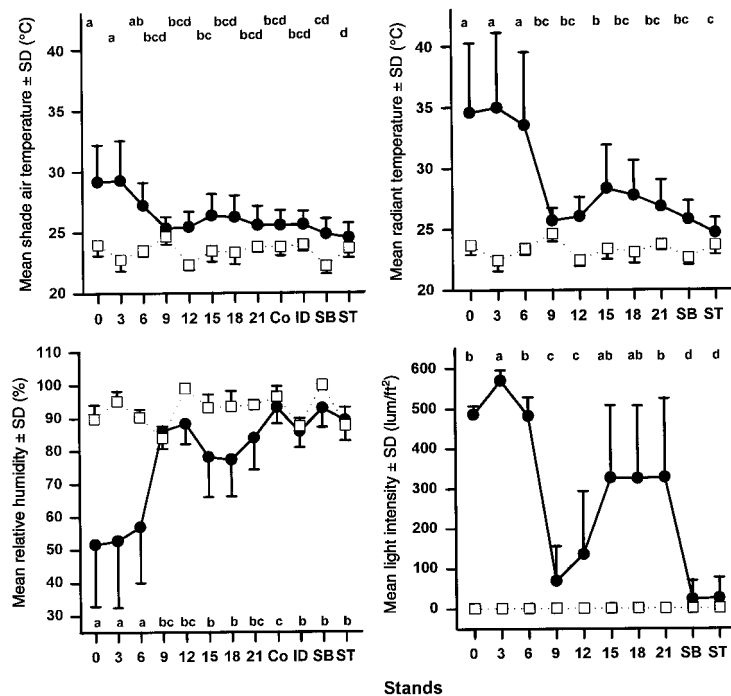
Fig. 3 Patterns of microclimatic variation across the chronosequence of regenerating vegetation to natural dune forest (stand age (year) depicted by numbers, Co = coastal, ID = inland dune, SB = Sokhulu dune base, ST = Sokhulu dune top forest; ● daytime data; □ night-time data (the lines of letters report the results for Tukey's HSD multiple range tests on day-time data; pairs of data points with no letters in common differ significantly, $P < 0.05$).

Table 3 ANOVA statistics for between-stand differences in microclimatic data and statistics for linear regression of mean microclimatic data on proportional cover of the tree canopy and surface vegetation at Richards Bay (all data $\log_{10} (n + 1)$ transformed before analysis)

Microclimatic variable	Tree canopy cover*			Surface cover*			ANOVA**
	r^2	F	P	r^2	F	P	F
Day							
Light intensity	0.41	5.55	< 0.05	0.70	18.46	< 0.01	61.53***
Radiant temperature	0.93	103.88	< 0.001	0.13	0.31	0.31	24.13***
Shade air temperature	0.81	42.93	< 0.001	0.12	1.41	0.26	14.23***
Relative humidity	0.94	157.60	< 0.001	0.12	1.32	0.28	36.80***
Dusk							
Light intensity	0.75	29.44	< 0.001	0.38	6.23	< 0.05	—
Radiant temperature	0.09	0.36	0.36	0.27	3.69	0.08	—
Shade air temperature	0.22	2.85	0.12	0.01	0.05	0.83	—
Relative humidity	0.42	7.25	< 0.05	0.01	0.06	0.81	—
Night							
Light intensity	0.91	84.80	< 0.001	0.004	0.86	0.86	—
Radiant temperature	0.02	0.71	0.71	0.000	1.00	1.00	16.13***
Shade air temperature	0.01	0.93	0.93	0.003	0.88	0.88	18.31***
Relative humidity	0.01	0.80	0.80	0.07	0.41	0.41	37.48***

* Degrees of freedom for linear regression are: 1, 8 for light intensity and radiant temperature and 1, 10 for shade air temperature and relative humidity. ** Degrees of freedom for one-way ANOVA are: 11, 264 for shade air temperature, 11, 252 for relative humidity and 9, 206 for radiant temperature and light intensity. *** $P < 0.001$.

indicated that this overall distribution pattern was not correlated with either tree canopy or surface cover ($r^2 = 0.36$, $F_{(2,9)} = 2.50$, $P = 0.14$). Group A showed a regional distribution restricted principally to tropical east coastal climates, although five species also occurred variously at points up the Limpopo, Save and Zambezi river valley systems, with one species penetrating into the Okavango Swamps in northern Botswana. The significant between-stand differences in local occurrence ($F_{(11,347)} = 12.70$, $P < 0.001$) followed no vegetational trend ($r^2 = 0.37$, $F_{(2,9)} = 2.63$, $P = 0.13$). Group C is largely restricted to the subtropical climate types in Maputaland. Its overall local distribution (Fig. 5) was significantly associated with forest stands ($F_{(11,347)} = 32.41$, $P < 0.001$) and tree canopy cover ($r^2 = 0.85$, $F_{(2,9)} = 25.04$, $P < 0.001$; canopy: $t = 6.82$, $P < 0.001$, surface cover: $t = -0.07$, $P = 0.95$).

The subgroups defined in Fig. 4 at the 75–77% levels of similarity also showed distinctive biogeographical associations. Group B2 showed a distribution across tropical, east coastal and Kalahari climates where sandveld was prominent. Group B3 comprised species widespread only in southern Africa while group B4 was widespread in southern and east Africa. These widespread subgroups were biogeographically more heterogeneous in the absence of the down-weighting process described in the methods. Group A1 occurs along the coastline from Maputaland to east Africa, while group A2 is

known primarily from the south-east African coast to the south of the Beira (19°50′S 34°52′E) region of central Moçambique. Group C1 is only known from Maputaland while group C2 is distributed from Maputaland to the foot of the coastal escarpment in Itala Game Reserve (27°32′S 31°16′E) and at least as far south as Vernon Crookes Nature Reserve (30°16′S 30°36′E) in southern KwaZulu-Natal.

Local vegetational associations of dung beetle species

Figure 6 shows that community associations may be classified into two groups at the 25% level of similarity. Group A represents species restricted primarily to woodland and forest stands, while group B is primarily recorded in unshaded situations. These clusters differed significantly (global $R = 0.761$, $P = 0.001$). Subgroups were defined at the 30% level of similarity. Woodland/forest subgroups showed either broad-based distribution (A1) or narrowly defined distribution (A2) in forests with low surface cover. Multiple paired comparisons of subgroups also showed significant differences (global $R = 0.772$, $P = 0.001$; A1:A2 – $R = 0.940$, $P = 0.01$, A1:B – $R = 0.754$, $P = 0.001$, A2:B – $R = 0.891$, $P = 0.01$). This comparison ignored group B1 as it comprised only four species with relatively low abundance, centred on the ~3-year open shrubland thicket stand.
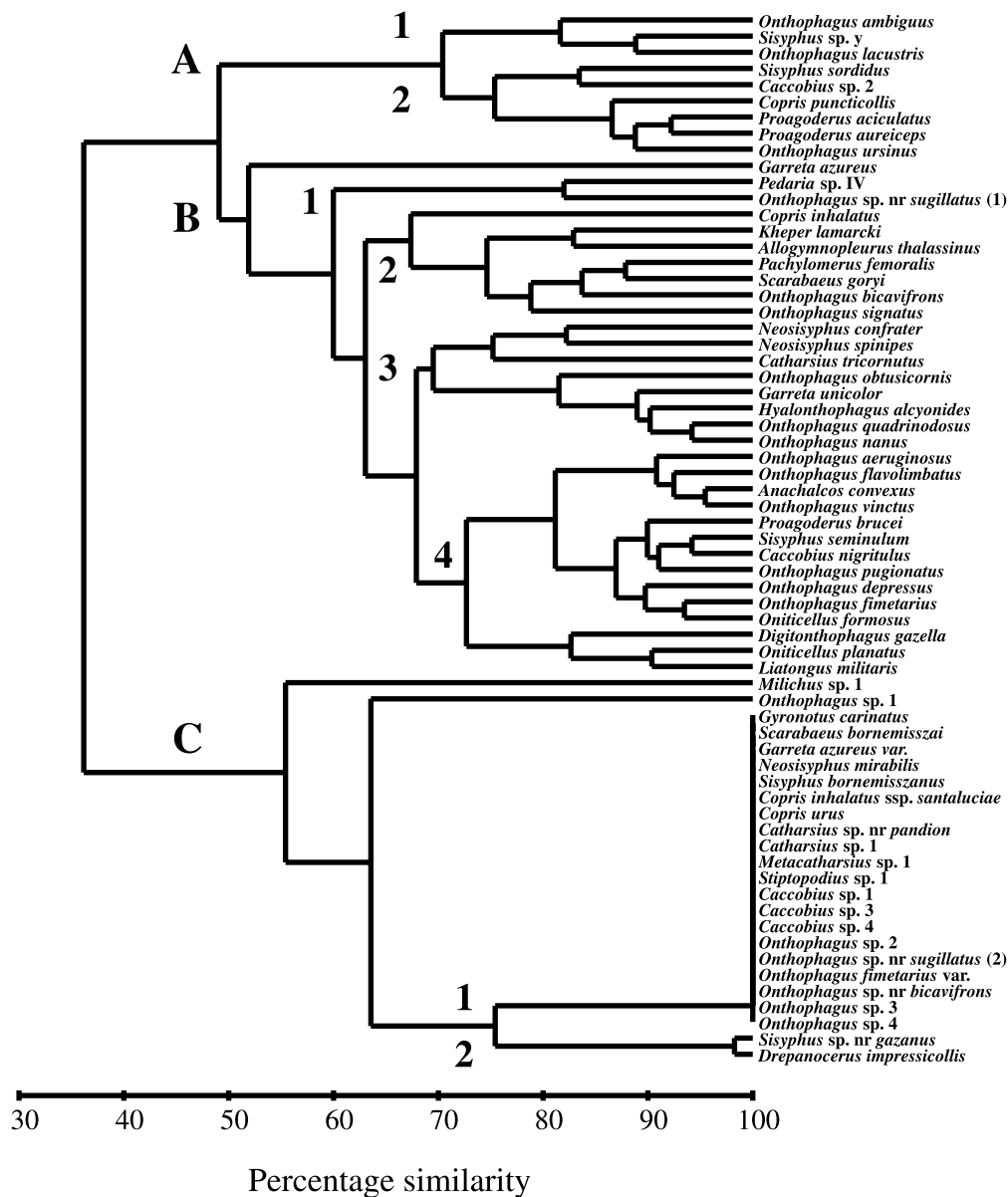
Fig. 4 Dendrogram showing the percentage similarity between the regional southern and east African distributions of 60 dung beetle species and those of five Maputaland varieties of these species recorded in the present study (similarity matrix constructed using Bray–Curtis similarity coefficient, clustering conducted using group average linking) (A = east coast-centred species, B = widespread species, C = Maputaland-centred species).

Community analysis

By combining classifications of regional (Fig. 4 — first hierarchical level) and local (Fig. 6 — second hierarchical level) species distribution, it is possible to define five main community distribution patterns (Fig. 7, Appendix I). Pattern C is characteristic of three widespread species with a bimodal distribution pattern, particularly in unshaded open shrubland thicket

and shaded older *A. karroo* woodland stands with high surface cover. However, this distinctive distribution is not correlated with either surface or tree canopy cover ($r^2 = 0.27$, $F_{(2,9)} = 1.69$, $P = 0.24$). It shows the greatest overall abundance of any group (21 790 individuals) owing to the inclusion of the panAfrican species, *Onthophagus vinctus*. Pattern A is characteristic of 11 endemic shade specialist species showing distributions restricted to Maputaland (8 spp., 12 805

Regional distribution

Local distribution
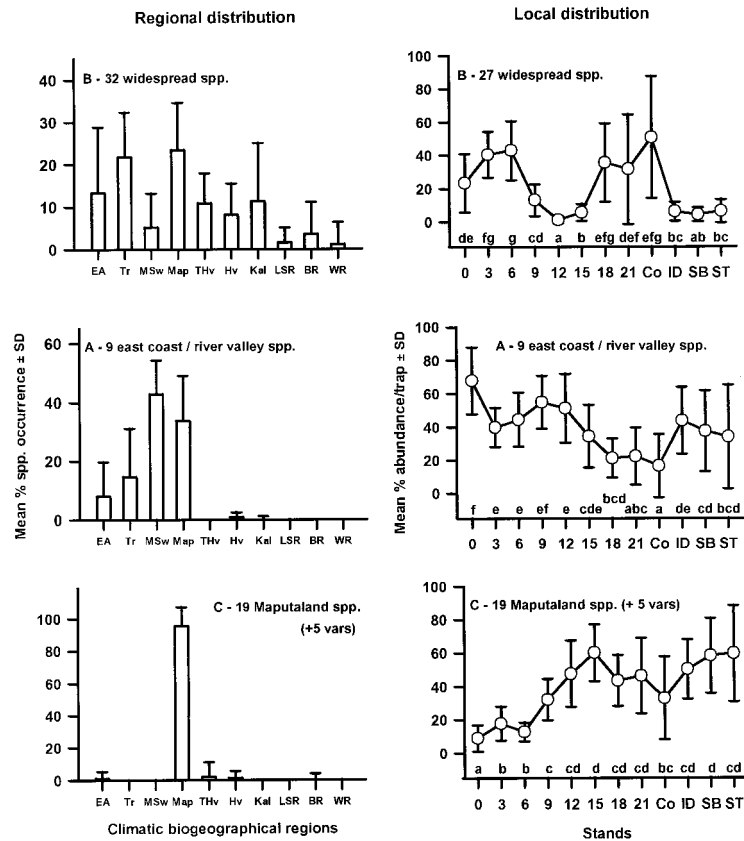
Fig. 5 Summaries of regional distribution between climatic regions shown by dung beetle species recorded at Richards Bay and their local distribution across the chronosequence of regenerating vegetation to natural dune forest (climatic regions: EA = east Africa, Tr = tropical climate, MSw = Maputaland–Swahili transitional region, Map = Maputaland (MSw and Map = east coast), THv = transitional highveld, Hv = highveld, Kal = Kalahari, LSR = late summer rainfall, BR = bimodal rainfall, WR = winter rainfall (see Davis, 1997 for map of climate types) — stand age (year) depicted by numbers, Co = coastal, ID = inland dune, SB = Sokhulu dune base, ST = Sokhulu dune top forest (the lines of letters report the results for Tukey's HSD multiple range tests; pairs of data points with no letters in common differ significantly, $P < 0.05$).

individuals) or to the east coast (3 spp., 11 809 individuals). The pattern shows a positive significant association with tree canopy cover ($r^2 = 0.83$, $F_{(2,9)} = 21.75$, $P < 0.001$; canopy cover: $t = 6.59$, $P < 0.001$, surface cover: $t = 1.87$, $P = 0.10$). Pattern B is characteristic of three Maputaland endemic species with a bimodal distribution, occurring in shaded situations with low-density surface cover. The pattern shows a significant negative association with surface cover although tree canopy cover was a nonsignificant influence despite complete restriction of the group to shaded situations ($r^2 = 0.83$, $F_{(2,9)} = 22.06$, $P < 0.001$; canopy cover: $t = 1.57$, $P = 0.15$, surface cover: $t = -5.83$, $P < 0.001$). Overall abundance is the lowest of the three forest groups (1239 individuals). Patterns D and E are very similar in occurring predominantly in the three unshaded stands of grassland or open shrubland thicket with increasing abundance across the chronosequence (Fig. 7). Pattern D is characteristic of 14 species showing either east coastal (5 spp., 2126 individuals) or Maputaland

endemism (9 spp., 2721 individuals). Pattern E is characteristic of 21 widespread species comprising a total of 1150 individuals numerically dominated by large-bodied taxa. Both patterns showed a significant negative association with tree canopy cover (pattern D – $r^2 = 0.86$, $F_{(2,9)} = 29.06$, $P < 0.001$; canopy cover: $t = -7.16$, $P < 0.001$, surface cover: $t = 0.69$, $P = 0.51$; pattern E – $r^2 = 0.69$, $F_{(2,9)} = 10.13$, $P < 0.01$, canopy cover: $t = -4.11$, $P < 0.01$, surface cover: $t = 0.70$, $P = 0.50$). Overall, there is a significant imbalance between the distribution of species richness at a local scale (classified according to vegetation association) relative to that at a regional scale (classified according to biogeographical distribution pattern) ($\chi^2_{(2)} = 7.23$, $P < 0.05$) (Table 4). On one hand, this pattern reflects the concentration of regionally distributed, open habitat species in the grassland and open shrubland thicket stands of the early stages of the chronosequence. On the other hand, it reflects the more equitable distribution of localized species between unshaded stands of the early
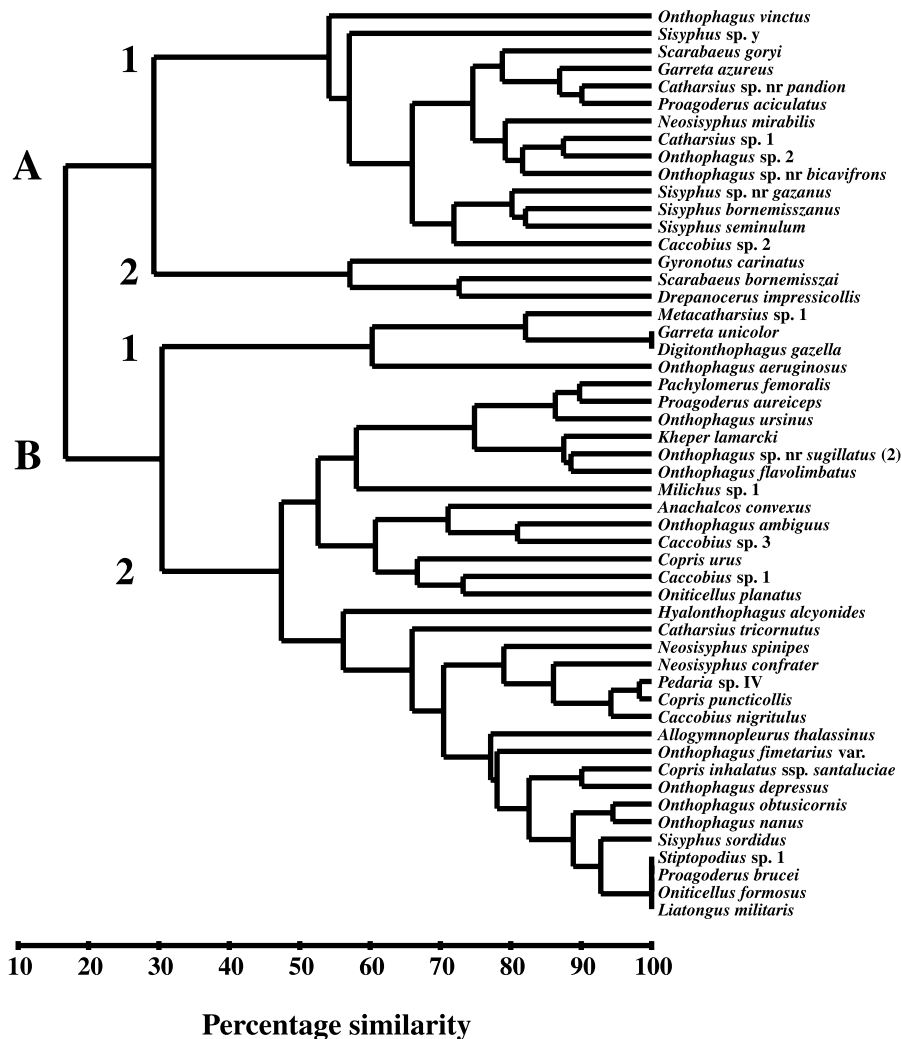
Fig. 6 Dendrogram showing percentage similarity between the local distributions of 52 dung beetle species across the chronosequence of regenerating vegetation to natural forest, which comprises both shaded and unshaded vegetation types (similarity matrix constructed using the Bray–Curtis similarity coefficient, clustering conducted using group average linking) (A = species centred in shaded situations, B = species centred in unshaded situations).

chronosequence and shaded stands of the later chronosequence and natural forest.

Trends in functional group composition are summarized in Table 5 and Appendix I. Ball rollers were proportionately much more prominent in grass/shrubland specialists (24.7% of abundance, 93.1% of biomass) and in grass/shrubland stands (18.6%, 79.5%) whereas tunnellers were proportionately much more prominent in shade specialists (95.9%, 76.7%) and in woodland or forest stands (95.9%, 79.8%). In any functional group, high abundance in endemic species was usually matched by much lower abundance in widespread species and vice versa. This held more or less true for both woodland/forest and shrub/grassland centred assemblages.

Widespread species with a grassland or open shrubland thicket centre of distribution (pattern E) include members of all seven functional groups described for dung beetles. However, both of the endemic unshaded and shade-centred species groups (patterns A, D) comprised only species in functional groups II–V. Two further woodland/forest-centred groups (patterns B, C), one widespead and the other endemic, each comprised three species with similar functional groups (I, II, V). These groups showed alternating patterns of low relative abundance in stands where the opposing group showed maximal relative abundance (Fig. 7). Large ball rollers in functional group I were largely drawn from widespread species as there was only a single large endemic ball roller, *Scarabaeus*
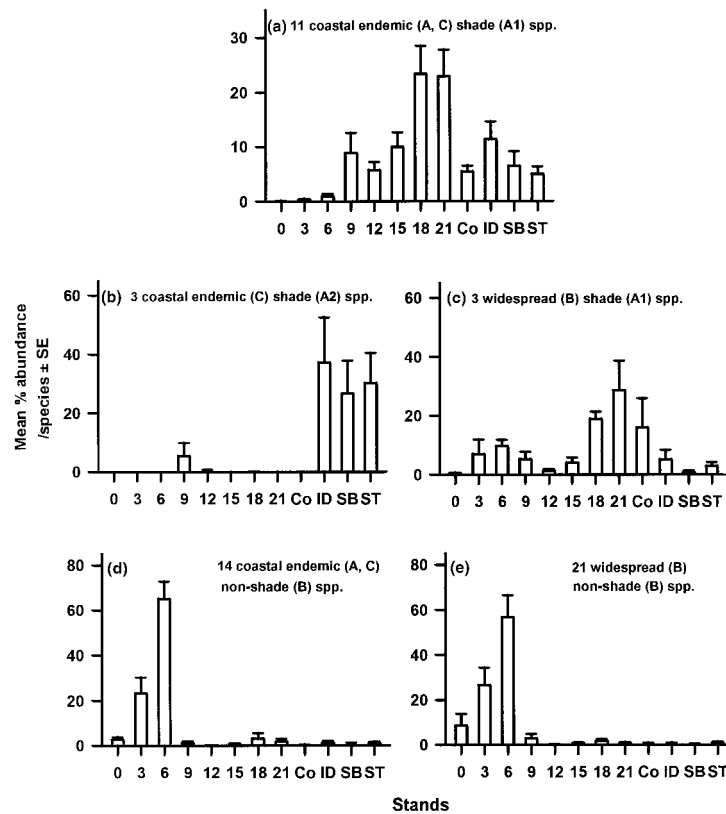
Fig. 7 Proportional distribution of abundance across the chronosequence of regenerating vegetation to natural dune forest in five species groups defined according to both their regional and local patterns of distribution (stand age (year) depicted by numbers, Co = coastal, ID = inland dune, SB = Sokhulu dune base, ST = Sokhulu dune top forest).

Table 4 Contingency table comparing the biogeographical distribution pattern vs. the vegetational associations of dung beetle species at Richards Bay

Vegetation association	Biogeographical distribution pattern			
	Widespread	East coast	Maputaland	Total
Forest	5	4	13	22
Grass/shrubland	22	5	11	38
Total	27	9	24	60

bornemisszai, which showed a distribution restricted to *A. karroo* woodland and natural forests with low surface cover. In unshaded situations, the functional groups represented by endemic species were numerically dominant over widespread species although it should be noted that 2300 individuals of *O. vinctus* were recorded in unshaded situations, boosting the total of widespread functional group V above that of endemic Vs.

DISCUSSION

Validity of data

The January trapping of dung beetles at Richards Bay coincided with the mid-summer peak in activity shown by dung beetles (Davis, 1996b) in the mid-summer rainfall region of north-eastern South Africa (Davis, 1997). Although the data were collected over only 2 days, the number of species observed exceeded 80% of estimated species richness at all but three study sites (Table 2), thus indicating that most species present were recorded. Simultaneous collection of data over a short period is perfectly adequate for comparing spatial differences between vegetative stands, particularly as the trapping yielded high numbers of individuals and provided 30 datasets for each stand. Although microclimatic measurements were made some 6 weeks after data collection, mean maximum and minimum temperatures showed minimal variation between occasions. In any case, microclimatic data were used to determine between-stand differences and were not used to interpret activity patterns or spatial occurrence of dung beetles.

Table 5 Summary of dung beetle community trends at Richards Bay (nb. total abundance of grass/shrubland elements has been multiplied by a factor of three to standardize for differences in trapping intensity in woodland and forest stands)

Functional group***	Total abundance (number of species) woodland/forest-centred species (270 traps)				Total abundance × 3 (number of species) Grass/shrub-centred species (3 × 90 traps)		
	Widespread C*	Endemic B*	Endemic A*	Total**	Endemic D*	Widespread E*	Total**
I	882 (1)	86 (1)		968 (2)		2169 (3)	2169 (3)
II	53 (1)	394 (1)	550 (5)	997 (7)	2133 (1)	138 (4)	2271 (5)
III			4264 (2)	4264 (2)	318 (4)	300 (1)	618 (5)
IV			11177 (2)	11187 (5)	6912 (5)	540 (7)	7452 (12)
V	20855 (1)	759 (1)	8623 (2)	30247 (6)	5178 (4)	111 (1)	5295 (7)
VI						123 (3)	126 (4)
VII						69 (2)	69 (2)

* Letters refer to distribution patterns defined in Fig. 7. ** Totals include eight species (23 individuals) deleted from the habitat analysis (Fig. 6).
*** Functional groups defined by Doube (1990): I = large ball rollers, II = small ball rollers of < 100 mg dry mass, III = fast-burying tunnellers, IV = slow-burying tunnellers, V = small, slow-burying tunnellers of < 10 mg dry body mass, VI = kleptocoprids, usually of < 10 mg dry body mass, which use dung buried by other species, VII = endocoprids, which breed within or immediately under droppings *in situ*.

Overview

Fragmentation and degradation of natural habitats is a global problem (Ehrlich, 1980; Soulé & Wilcox, 1980; Soulé, 1986). It leads to the numerical dominance of widespread species, which has raised fears of the homogenization of the world's fauna (Holmes, 1998; Lockwood *et al.*, 2000). However, it is possible to reverse this process through the ecological restoration of threatened habitats that harbour localized taxa, a policy which Young (2000) has suggested will be a major direction of future conservation effort. Although habitat destruction results in dominance by more widespread dung beetle species in the present study, this trend is quickly reversed towards recovery of dominance by localized taxa following restoration of forest physiognomy.

In the Maputaland centre of endemism, key historical and regional influences on the localized character of the dung beetle assemblages would stem from biogeographical expansion from the southern African interior or along the east coast coupled with periods of ecological isolation of Maputaland vegetative ecotypes. It is suggested that this isolation is responsible for the separation of endemic species and subspecies with inland relatives on Kalahari sands, e.g. *Copris inhalatus* ssp. *santaluciae* (Davis, 1997), or on the South African highveld, e.g. *Scarabaeus bornemisszai* (zur Strassen, 1980; Davis, 1997). Similar biogeographical origins account for the present dung beetle assemblage in the fragmented landscape at Richards Bay, which is composed of widespread species from the interior, east coastal endemics, and Maputaland endemics characteristic of both unshaded and shaded habitats (Figs 4, 6).

Historical and regional biogeographical influences on Maputaland

The origin of east coastal sands lies in marine incursions and regressions, which are linked to oscillations in polar glaciation. These have occurred cyclically from the late Miocene throughout the Plio-Pleistocene (Hendey, 1983). The comparatively young age of the region would account for the low taxonomic level of endemism to Maputaland shown by most plants (van Wyk, 1996) and dung beetles. This is only at species or subspecies level with some taxa represented only by morphologically distinctive local varieties. However, generic-level endemism has also been noted in three plant (van Wyk, 1996) and one dung beetle taxon (*Tropidonitis* Janssens). A number of dung beetle taxa show wider, endemic coastal distributions as far as central Moçambique, north-eastern Tanzania or Kenya, with additional records inland along major river valleys or within the coastal belt southwards to the southern border of KwaZulu-Natal. In plants, outliers of Maputaland endemics occur in tropical regions northwards to central Moçambique, inland to the edge of the escarpment, and southwards along the very narrow coastal strip to the southern border of KwaZulu-Natal (van Wyk, 1996). These distributions may be relicts of past climatic changes that created vegetational links between Maputaland and other regions now climatically isolated from one another (Lawes, 1990; Eeley *et al.*, 1999).

Maputaland is a coastal enclave of sandy soils (van Wyk, 1996) characterized in the north by the drier climate type, II3e, and in the south by the wetter climate type, II(I)a (Walter & Lieth, 1964). This climatic division results from a steep

north–south rainfall gradient along which mean annual precipitation doubles from Kosi Bay (700–850 mm) (26°58′S 32°50′E) to Richards Bay (1200–1500 mm) (28°48′S 32°05′E) (Dent *et al.*, 1989). The wettest part of the coastline (14–1500 mm p/a) stretches from the ~15-year-old stand in the middle of the Tisand Mineral concession to just north of the Sokhulu Forest Reserve. To the north of Sokhulu, rainfall is marginally lower (1200–1300 mm p/a) as far as the St Lucia Estuary (28°05′S 32°30′E) and lower still (1000–1100 mm p/a) to the edge of climate type II(I)a just north of Sodwana Bay (27°32′S 32°41′E). It is suggested that ecological differences across this climatic and rainfall gradient provide an explanation for the occurrence of northern and southern endemic Maputaland plant endemics (van Wyk, 1996). It is also suggested that this ecological and climatic gradient is responsible for Maputaland dung beetle endemics showing specialization to forest or relatively unshaded situations that are more characteristic of the drier northern climate type II3e. Furthermore, it is suggested that the present occurrence of both groups of endemics at Richards Bay may have been facilitated by extensive thinning or clearance of woody vegetation (Low & Rebelo, 1996), leading to southwards range expansion by these putative northern dung beetle elements.

It appears that endemic Maputaland dung beetles with the smallest ranges are restricted to the wet coastal dune forests between Kosi Bay and Mtunzini (28°57′S 31°46′E) (e.g. *Scarabaeus bornemisszai, Catharsius* sp. 1). Endemic species with wider ranges (*Catharsius* sp. nr *pandion, Sisyphus bornemisszanus*, large green variety of *Garreta azureus*) occur in both coastal dune forest and further inland in sand forest. They are prominent in species assemblages of Sileza sand forest (27°06′S 32°36′E) but are poorly represented in sand forest of Tembe Elephant Park (27°01′E 32°24′E) (van Rensburg *et al.*, 1999), which lies at the drier inland end of a rainfall gradient from the coastline (Dent *et al.*, 1989). Maputaland endemic species with a grassland and shrubland thicket occurrence (*Copris urus, Copris inhalatus* ssp. *santaluciae*) (Appendix I) also occur in the coastal regions and further inland. However, these species were relatively poorly represented in shaded dune and sand forest compared to more open mixed woodland in Sileza and Tembe (van Rensburg *et al.*, 1999). It is probable that some of the dung beetle forest endemics are distributed into the extreme south of Moçambique since sand forest outliers with Maputaland vegetation occur northwards almost as far as Maputo (25°59′S 32°42′E) (Moll & White, 1978).

The east coast represents one of the major biogeographical regions of southern Africa (Davis, 1997). Natural forest fragments on the south coast of KwaZulu-Natal are dominated by species with east coastal affiliations (Davis *et al.*, 1999). It was expected that with increasing age across the chronosequence, the Richards Bay dung beetle fauna would become less characterized by biogeographical generalists and more dominated by east coastal and Maputaland endemics. In the event, unshaded situations were dominated by east coastal endemics and widespread species (Fig. 5). Early chronosequence *A. karroo* woodland and most natural dune forests were indeed dominated by Maputaland and east coastal endemics. However, older chronoseqence *A. karroo* woodland and the adjacent natural coastal forest were dominated by Maputaland endemics and widespread species. Even so, as a general trend, the relative abundance of Maputaland endemics increased across the chronosequence with greatest proportional representation where vegetative physiognomy was closest to that in natural forest. Furthermore, in groups of species defined according to their biogeographical and habitat affiliations, widespread species declined in number from grassland to woodland and forest, whilst the numbers of endemic species remained similar but increased in woodland and forest in terms of proportional representation.

Community composition

The composition of the dung beetle fauna reflected both regional (biogeographical) and local influences (functional group, habitat association). Functionally different widespread (21 spp. of pattern E) and endemic groups (14 spp. of pattern D) of species showed congruent patterns of association with early chronosequence stages (< 1–~6 years), which are characterized by unshaded, hot, light conditions (grassland or gaps in *Acacia karroo* shrubland thicket). Other than for *Anachalcos convexus* and *Caccobius* sp. 3, the occurrence of group members in woodland and forest stands was probably related to edge effects. The endemic group in unshaded situations was numerically dominated by east coastal elements. An endemic, forest specialist group (11 spp. of pattern A) was distributed throughout all cooler, shaded stands irrespective of dominance by *A. karroo* in ~9–~21-year woodland or greater tree species diversity in natural dune forest. This group was numerically dominated by Maputaland endemics although the single most abundant species was an east coastal endemic. Functionally similar, endemic (3 spp. of pattern B) and widespread, shade-biased groups (3 spp. of pattern C) showed opposing distributional patterns with maximal abundance where the other was minimal. The endemic group showed maximal occurrence in early *A. karroo* woodland (dense canopy, low light, sparse surface cover, open understorey — low numbers of *Scarabaeus bornemisszai* only) and natural dune forests (dense canopy, low light, sparse surface cover, dense understorey) with their physiognomic similarities. The widespread group showed maximal occurrence in open shrubland thicket and, particularly, in older *A. karroo* woodland forest with its differing physiognomy (reduced canopy, greater light and temperature, dense surface cover, open understorey). It is this small group that is

responsible for the decline in localization of the dung beetle assemblages in the older *A. karoo* woodland. In conclusion, despite the decline, relative abundance of endemic Maputaland dung beetles does show a general increase across the chronosequence reaching *c.* 50–60% of total abundance in natural dune forest with the balance contributed primarily by east coastal endemics (*c.* 34–44%) (Fig. 5).

CONCLUSION

We found distinct cross-chronosequence differences in vegetative physiognomy, microclimate and dung beetle assemblages. Clearance of dune forest results in virtual replacement of shade elements by different suites of both widespread and endemic taxa adapted to relatively unshaded situations. However, within a few years the re-establishment of forest physiognomy is associated with the virtual replacement of the grass/shrubland elements by suites of specialist endemic shade taxa. The initial recovery of physiognomy and microclimate similar to natural dune forest is diminished by the subsequent opening of the understorey and thinning of the canopy. Assuming that the future direction of successional changes in physiognomy will be towards that in natural dune forest (increase in canopy density and reduction in light intensity due to replacement of *A. karroo* by other tree species, development of a dense shrubland understorey and virtual loss of surface cover), one would predict a gradual decline in abundance of the group of shade-adapted widespread species that is currently responsible for the proportional reduction in dung beetle endemism in older *Acacia* woodland. Such a prediction would be supported by the higher abundance of *O. vinctus* in younger (~6 years) and older stands (~18–~21 years) as opposed to its low abundance in the ~9-year and ~12-year stands (Davis *et al.*, in press) that are microclimatically closest to natural forest stands. Reduction in abundance of *O. vinctus* would strengthen the overall cross-chronosequence trend to greater localization in spatial relationships of the dung beetle fauna, which is already apparent. However, it will be several decades before the final outcome is known.

ACKNOWLEDGMENTS

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APPENDIX I

Summary of the attributes of the dung beetle species recorded across the chronosequence of regenerating vegetation to natural dune forest at Richards Bay (diel flight: D = diurnal, N = crepuscular or nocturnal; functional group: see Table 4 for group definitions)

Group	Total abundance†				Diel flight	Funct. group	Dry mass (mg)‡	Biogeo. group§
	Grass/ shrubland	Younger woodland	Older woodland	Dune forest				
Pattern B*								
East coastal endemic (C**)								
shade specialists (A2***)								
Drepanocerus impressicollis Boheman	0	0	1	758	D	V	10	M
Gyronotus carinatus Felsche	0	0	0	394	D	II	83	M
Scarabaeus bornemisszai zur Strassen	0	15	0	71	D	I	531	M
Pattern C*								
Widespread (B**)								
shade specialists (A1***)								
Onthophagus vinctus Erichson	2300	229	18259	67	N	V	9	EA (Pan)
Scarabaeus goryi Castelnau	308	156	237	181	N	I	1071	Sa (Pan)
Sisyphus seminulum Gerstaecker	3	7	40	3	D	II	4	EA
Pattern A*								
East coastal endemic (A, C**)								
shade specialists (A1***)								
Proagoderus aciculatus Fahraeus	824	3673	2631	4016	D	IV	55	EC
Onthophagus sp. 2	2	1495	5162	1338	D	V	5	M
Catharsius sp. nr *pandion*	68	1135	714	1072	N	III	660	M
Catharsius sp. 1	42	252	712	269	N	III	530	M
Caccobius sp. 2	1	27	584	14	D	V	2	EC
Neosisyphus mirabilis Arrow	3	41	144	83	D	II	40	M
Sisyphus sp. nr *gazanus*	0	13	73	7	D	II	14	M
Sisyphus bornemisszanus Endroedi	0	7	75	3	D	II	36	M
Garreta azureus (Fabricius) var.	0	17	13	32	D	II	360	M (Pan)
Sisyphus sp. y (*sensu* Paschalidis, 1974)	0	19	6	14	D	II	8	EC
Onthophagus sp. nr *bicavifrons*	0	14	16	3	D	IV	12	M (Sa)
Pattern D*								
East coastal endemic (A, C**)								
non-shade specialists (B1, B2***)								
Proagoderus aureiceps d'Orbigny	1341	89	2	2	D	IV	42	EC
Caccobius sp. 3	409	233	40	70	D	V	4	M
Sisyphus sordidus Boheman	706	4	1	0	D	II	21	EC

APPENDIX I *Continued*

Group	Total abundance†			Dune forest	Diel flight	Funct. group	Dry mass (mg)‡	Biogeo. group§
	Grass/ shrubland	Younger woodland	Older woodland					
Onthophagus ambiguus Péringuey	536	52	40	44	N	IV	8	EC
Onthophagus ursinus d'Orbigny	563	15	6	0	D	V	3	EC
Caccobius sp. 1	304	11	22	5	D	V	3	M
Onthophagus fimetarius Roth var.	189	2	1	1	N	IV	10	M (EA)
Onthophagus sp. nr *sugillatus* (2)	48	0	0	0	D	V	3	M (SA)
Copris inhalatus ssp. *santaluciae* Ferreira	42	0	0	0	N	III	169	M (Sa)
Copris urus Boheman	19	0	5	1	N	III	230	M
Copris puncticollis Boheman	22	0	0	0	N	III	80	EC
Metacatharsius sp. 1	17	0	0	0	N	III	20	M
Milichus sp. 1	4	0	0	0	?N	IV	10	EC (EA)
Stiptopodius sp. 1	1	0	0	0	?N	IV	3	M
Pattern E*								
Widespread (B**)								
non-shade specialists (B₁, B₂***)								
Pachylomerus femoralis (Kirby)	283	10	1	3	D	I	1507	Sa
Anachalcos convexus Boheman	99	34	16	100	N	I	668	EA (Pan)
Kheper lamarcki (M'Leay)	174	2	1	0	D	I	1216	Sa
Catharsius tricornutus de Geer	93	2	1	4	N	III	565	SA
Onthophagus obtusicornis Fahraeus	97	0	0	0	D	IV	21	SA
Onthophagus depressus Harold	58	0	1	0	N	IV	15	EA
Onthophagus nanus Harold	37	0	0	0	D	V	2	SA
Neosisyphus spinipes Gory	32	0	1	0	D	II	23	SA
Caccobius nigritulus Klug	23	0	0	0	D	VI	4	EA
Oniticellus planatus Castelnau	11	1	5	1	D	VII	29	EA (Pan)
Pedaria sp. IV (*sensu* Davis, 1996b)	14	0	0	0	N	VI	17	SA
Hyalonthophagus alcyonides (d'Orbigny)	7	1	1	0	D	IV	27	SA
Allogymnopleurus thalssinus Klug	9	0	0	0	D	II	85	Sa
Liatongus militaris (Castelnau)	7	0	0	0	D	IV	26	EA
Oniticellus formosus Chevrolat	5	0	0	0	D	VII	29	EA (Pan)
Onthophagus aeruginosus Roth	2	0	2	0	D	IV	11	EA
Onthophagus flavolimbatus d'Orbigny	4	0	0	0	D	VI	4	EA
Neosisyphus confrater Kolbe	2	0	0	0	D	II	15	SA
Proagoderus brucei Reiche	2	0	0	0	D	IV	98	EA
Digitonthophagus gazella (Fabricius)	2	0	0	0	N	IV	52	EA (Pan)
Garreta unicolor (Fahraeus)	2	0	0	0	D	II	264	SA
Deleted shade specialist species								
Onthophagus lacustris Harold	0	4	3	0	N	IV	35	EC
Onthophagus sp. 3	0	0	0	6	?D	V	5	M
Caccobius sp. 4	1	1	0	2	?N	V	4	M
Onthophagus pugionatus Fahraeus	0	1	1	0	N	IV	17	EA
Onthophagus quadrinodosus Fahraeus	0	0	1	0	N	IV	24‡	SA
Deleted non-shade specialist species								
Onthophagus sp. 4	1	0	0	0	N	IV	3	M
Onthophagus sp. 1	1	0	0	0	D	V	2	M (SA)
Onthophagus signatus Fahraeus	1	0	0	0	D	VI	4	Sa

† Total abundance in 90 traps in each column: (1) < 1–~6 year grassland/open *Acacia* shrubland thickets; (2) ~9–~15 year *Acacia* woodland; (3) ~18–~21 year *Acacia* woodland and adjacent coastal dune forest; (4) Inland dune and Sokhulu natural dune forests. ‡ Data from Doube (1991), Davis (1996b) or weighed material from Richards Bay. § Biogeographical group: (wider distributions of species represented as varieties or with distributions outside the group classification, Pan = PanAfrotropical distribution, EA = East African distribution, SA = Southern African distribution, Sa = deep sand specialist). * See Fig. 7 for classification of combined biogeographical and habitat associations. ** See Fig. 4 for biogeographical classification. *** See Fig. 6 for classification of habitat associations.