
Convergence Between Dung Beetle Assemblages of a Post-Mining Vegetational Chronosequence and Unmined Dune Forest

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Abstract

In Maputaland, South Africa vegetative and microclimatic changes on mined dunes drive the composition of the dung beetle fauna toward convergence with that in natural dune forest on unmined dunes. We assessed the pattern of these changes using a 23-year vegetational chronosequence on mined dunes, which passes from grassland (approximately 1 year) to open *Acacia* shrubland thicket to *Acacia karroo*-dominated woodland (approximately 9 years). Across this sequence, which represents successional stages in the restoration of dune forest, there was a sequential trend toward convergence in dung beetle species composition in both the entire species complement and, particularly, in shade specialist species. However, species abundance patterns showed a trend toward convergence only in early chronosequence *Acacia* woodland, followed by a decline in similarity between dung beetle assemblages of older *Acacia* woodland and unmined natural forest. This trend toward divergence

was common both to the entire species complement, which includes widespread taxa, and to species endemic to Maputaland or the east coast. These trends in similarity and dissimilarity between dung beetle assemblages closely parallel the greater physiognomic and microclimatic similarity between early *Acacia* woodland and natural forest and the relative dissimilarity of older *Acacia* woodland. In conclusion, although percentage similarities between dung beetle assemblages of approximately 12-year woodland and natural forests were comparable with those between each natural forest stand, decline in similarity in older woodland stands suggests that lasting convergence in dung beetle species abundance will only be attained once the *Acacia* woodland is replaced by secondary natural forest.

Key words: *Acacia*, assemblages, convergence, dune, dung, forest, post-mining, restoration, South Africa.

Introduction

It is predicted that as relatively pristine habitat contracts into ever smaller fragments due to exploitation, restoration of degraded patches will come to dominate future conservation efforts (Young 2000). This will, perhaps, stem from the recognition that it is better to consolidate and expand the fragments saved by conservation (Young 2000) than to squander effort in blanket attempts to prevent further habitat degradation. Restoration ecology is already experiencing rapid growth in terms of numbers of publications, but it is currently still perceived as botanically biased (Morrison 1998; Young 2000), even though faunal restoration has now been well studied in some regions (Majer 1989). The present study examines links between patterns in the restoration of both forest and associated animals in South Africa. Specifically, it examines changes in dung beetle community composition across a

vegetative chronosequence from disturbed to undisturbed sand dunes along the Indian Ocean coastline at the southern end of the Maputaland center of endemism, northeastern South Africa. This chronosequence of coastal dune vegetation is the result of an ongoing, post-mining, dune rehabilitation program aimed at restoring an indigenous coastal dune ecosystem typical of the region.

The Indian Ocean coastal belt supports a vegetational system that is distinctive by virtue of the 40% endemism in woody plants (Moll & White 1978). The two coastal belt phytochoria defined by Moll and White (1978) are now divided into four regions, comprising the northerly Swahili center of endemism, the central Maputaland-Swahili transitional zone with little endemism, and the southerly Maputaland and Pondoland centers of endemism (van Wyk 1990, 1994, 1996; Burgess et al. 1998). The Maputaland center occupies a small east coastal range of approximately 26,734 km², straddling the borders of Swaziland, Moçambique, and South Africa. The Maputaland vegetation has been classified into 15 to 21 ecotypes, most of which include many endemic or localized plants that are mostly associated with sandy soils (van Wyk 1996). One of these ecotypes comprises dune forest that occupies a narrow belt along the coastline (Moll & White 1978; Eeley et al. 1999) from Maputaland southward, where it becomes patchy and floristically impoverished (Moll & White 1978).

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Since 1977 dredge mining for titanium-bearing mineral sands has been conducted in the coastal dunes around Richards Bay. Mining is preceded by the complete clearance of dune vegetation and is followed by rehabilitation of indigenous vegetation across one-third of the mined area (van Aarde et al. 1996b). Over the first 14 years of rehabilitation vegetative regeneration passes from bare dunes, to seeded surface-binding exotic herbs and grasses, to endemic grassland (within 6–8 months), to shrubland thickets dominated by *Acacia karroo* (Mimosaceae) (after 2–3 years), and finally to an *A. karroo*-dominated woodland (after approximately 9 years) (van Aarde et al. 1996a, 1996b; van Dyk 1997). Across this chronosequence both dune vegetation and the associated fauna mostly show an increase in species richness and diversity, accompanied by high species turnover and a decrease in species-specific abundances. There are indications that this flora and fauna are converging toward those in natural dune forest (Majer & de Kock 1992; van Aarde et al. 1996a, 1996b; Ferreira & van Aarde 1997; van Dyk 1997), which comprises many tree species dominated by *Mimusops caffra* (Mimosaceae), *Diospyros rotundifolia* (Ebenaceae), *D. inhacensis* (Ebenaceae), and *Euclea natalensis* (Ebenaceae) (Moll & White 1978). However, it is predicted that full restoration of dune forest will require many more years (Mentis & Ellery 1998).

The present assessment examines further progress toward the restoration of biota associated with dune forest after 23 years. The study compares age-related differences in vegetative physiognomy and microclimate with the species composition and abundance of dung beetle assemblages (Coleoptera: Scarabaeidae: Scarabaeinae). Specifically, it investigates whether or not the cross-chronosequence com-

position of dung beetle assemblages is converging toward those in four selected reference points in unmined natural forest, each with differing ecological characteristics.

Methods

Study Area

The principal study area (28°38–43'S, 32°10–17'E) was situated along a 20-km long coastal strip just to the north of Richards Bay (28°48'S, 32°05'E), KwaZulu-Natal, north-eastern South Africa, where mining commenced in 1977, some 23 years before the present survey. This area comprises a mosaic of *Casuarina* (Casuarinaceae) plantations, natural forest patches (including the coastal and inland dune forest reference points), and regenerating vegetation of various ages. The regenerating vegetation follows a continuous north–south chronosequence, with the youngest (<1 year) to the north and the oldest (23 years) to the south. A smaller study area comprising the other two reference points in natural forest (dune top and dune base) was situated some 15 km further north (28°30–31'S, 32°23'E) in the Sokhulu Forest Reserve (see Davis et al. 2002 for map).

Study Stands, Sites, and Trap Placement

Twelve vegetational stands were selected from within the study area (Table 1). Eight comprised regenerating vegetation of known age and four comprised older natural forest remnants. Across the chronosequence, the youngest regenerating stand was less than 1 year old, whereas the remaining seven stands each represented a 3-year period

Table 1. Dominant vegetation, physiognomy, and microclimate in each study stand near Richards Bay (15 trapping points per stand).

Stand	Vegetation	Mean ± SD		Mean ± SD Daytime Measurements (0630–1745 hr)			
		Canopy Cover (%)	Surface Cover (%)	Ambient Temperature (°C)	Radiant Temperature (°C)	Relative Humidity (%)	Light Intensity (lum/sq.ft)
<i>Regenerating vegetation</i>							
<1 yr	Millet, sunflowers, sparse grass Grassland, open shrubland,	0.0	46.8 ± 13.1	29.1 ± 3.1	34.6 ± 5.7	51.6 ± 18.7	486.0 ± 20.5
3 yr	<i>Acacia</i> thicket Grassland, open shrubland,	0.0	60.7 ± 14.9	29.2 ± 3.3	35.0 ± 6.2	52.7 ± 20.1	569.8 ± 25.2
6 yr	<i>Acacia</i> thicket	0.0	82.7 ± 12.4	27.2 ± 1.9	33.5 ± 6.0	56.9 ± 16.9	481.7 ± 47.0
9 yr	Dense canopy <i>Acacia</i> woodland	70.8 ± 3.1	43.3 ± 4.7	25.4 ± 0.9	25.7 ± 1.0	86.1 ± 5.4	69.6 ± 86.3
12 yr	Dense canopy <i>Acacia</i> woodland	72.3 ± 23.1	53.3 ± 40.5	25.4 ± 1.3	26.0 ± 1.6	88.3 ± 6.1	135.7 ± 157.4
15 yr	Open understory <i>Acacia</i> woodland	64.5 ± 22.6	100.0 ± 0.0	26.4 ± 1.8	28.3 ± 3.6	78.1 ± 12.2	326.6 ± 180.9
18 yr	Open understory <i>Acacia</i> woodland	66.5 ± 23.1	96.7 ± 2.7	26.2 ± 1.8	27.7 ± 2.9	77.3 ± 11.1	325.2 ± 180.5
21 yr	Open shrub understory <i>Acacia</i> woodland	68.5 ± 28.0	98.0 ± 2.8	25.6 ± 1.6	26.8 ± 2.2	83.9 ± 9.6	327.7 ± 197.2
<i>Natural forest patches</i>							
Coastal	Openings in dense understory forest	82.7 ± 14.0	47.0 ± 26.4	25.6 ± 1.2	—	93.2 ± 4.9	—
In. dune	Dense shrubland understory forest	80.5 ± 11.9	9.8 ± 5.5	25.6 ± 1.1	—	85.8 ± 4.8	—
S. top	Old forest, dense shrub understory	87.2 ± 4.9	22.6 ± 9.1	24.5 ± 1.2	24.7 ± 1.2	89.2 ± 6.2	25.5 ± 51.3
S. base	Old forest, dense shrubland patches	78.3 ± 13.3	23.7 ± 26.5	24.8 ± 1.3	25.8 ± 1.5	92.9 ± 5.7	23.5 ± 47.0

In. dune, inland dune; S. top, Sokhulu dune top; S. base, Sokhulu dune base.

in the chronosequence, ranging from a median of approximately 3 years to a median of approximately 21 years since mining. Vegetation in regenerating stands differed both taxonomically and physiognomically from that in the four natural forest stands, which were selected from three separate unmined patches.

Three sites were selected in each stand. At each site five pitfall traps were placed in a line at a 10-meter distance from one another. Thus, there were 180 traps in all (12 stands \times 3 sites \times 5 traps). In the stand less than 1 year old only unshaded situations were available for placement of traps, whereas predominantly shaded situations were all that was available in regenerating stands older than approximately 9 years. In the approximately 3- and 6-year-old stands, most but not all traps were placed in broad or narrow grassland/open shrubland patches between the *Acacia* thickets. Davis et al. (2002) provide a more detailed description of the study area and trapping sites.

Trap Description and Trapping Method

Each pitfall trap comprised a 5-liter plastic bucket (diameter 20 cm at the top) sunk into the sand up to its rim. On trapping occasions these traps were baited with a composite of 200 mL of cattle dung and 200 mL of pig dung wrapped in brown chiffon. 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; A. Davis, personal observation, 2000). 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 centimeters of water to which a little detergent had been added. Trapping was conducted over 2 days from 25 to 27 January 2000 during the mid-summer seasonal peak in activity of dung beetles for this summer rainfall region of South Africa (Davis 1996a, 1997). Traps were baited on the afternoon of 25 January 2000 and rebaited with fresh dung approximately every subsequent 12 hr. Traps were emptied after 24 hr and again after 48 hr, thus providing 30 separate samples per stand and 360 samples in all (180 traps \times 2 days).

Vegetation and Microclimatic Data

A brief description of the vegetation, physiognomy, and microclimate in each stand is provided in Table 1. Vegetative physiognomy was assessed by visually estimating percentage canopy cover above each trap and by measuring percentage surface cover along walking transects in which scores were made according to whether or not vegetation was in contact with the boot tip at each of 20 to 50 steps (20 steps in dense natural forest stands, 50 steps in more open stands). These data were supported by measurements of radiant heat, ambient shade air temperature, relative humidity, and light intensity in 10 stands and of shade temperature and relative humidity in 2 stands (coastal and inland dune forest). Microclimatic measure-

ments were made at 1 meter above the soil surface using digital data-loggers (10 \times Onset, Hobo, 4 channel, H08-004-02 with TMC6-HA remote temperature sensor, 2 \times Onset Stowaway SRHA02 relative humidity loggers, and 2 \times Onset Stowaway XT102 temperature loggers, supplied by C.W. Price Ltd., Marlboro, South Africa). For logistic reasons it was not possible to measure microclimatic differences between the stands simultaneously with the beetle-trapping program. Therefore, the measurements were made from 7 to 9 March 2000 when temperature conditions were still similar (mean maximum, $28.8 \pm 0.1^\circ\text{C}$; mean minimum, $22.8 \pm 0.1^\circ\text{C}$) to those in late January (mean maximum, $29.6 \pm 0.1^\circ\text{C}$; mean minimum, $22.9 \pm 1.5^\circ\text{C}$). Microclimatic measurements were made at a frequency of 1 minute, 30 seconds for the four-channel loggers and at a frequency of 1 minute, 36 seconds for the Stowaway loggers. Mean daytime data are calculated from the data points between 0630 hr to 1745 hr when background light intensity was maximal in unshaded situations. Davis et al. (2002) provide more detailed descriptions of physiognomic and microclimatic measurements.

Validity of Data

To assess the completeness of the species record, cumulative species curves were constructed for the six data points yielded by trap day (2) \times number of sites (3) in each stand. Cumulative species numbers for each data point were the average for the six possible site sequences on day 1 plus the same for day 2.

Relative contribution of spatial (stands, sites) and temporal factors (trap days) to the variance shown within the data set was tested using multifactor analysis of variance (ANOVA). For the ANOVA design, sites were nested in stands and the data for days 1 and 2 were treated as repeated measures. All data were $\log_{10}(n + 1)$ transformed before analysis.

Classification of Stands Using Vegetative and Microclimatic Data

Cluster analysis and multidimensional scaling (MDS) were used to define similarities between plant physiognomy and microclimate in regenerating stands and natural forest. Data were arranged as a matrix of vegetation cover and microclimatic measurements in each stand. These data were $\log_{10}(n + 1)$ transformed before cluster analysis. The similarity matrix was calculated using the nonmetric Bray-Curtis similarity coefficient. This matrix was analyzed using the agglomerative clustering technique, group average linking. The results were used to construct a dendrogram on which clusters of stands were defined at the 95% level of similarity. Multiple paired comparisons of clusters were conducted using the ANOSIM subroutine of the multivariate analytical computer package, PRIMER Version 4.0 (Plymouth Marine Laboratory, 1994). Comparisons were conducted using the default setting of a maximum of 5,000 permutations. The similarity matrix from cluster analysis

was used to conduct the MDS. The default setting of six random starts gave the same configuration stress of 0.01 in each case. Results for the first two dimensions were used to construct an ordination plot.

Classification of Stands Using Dung Beetle Data

Cluster analysis was used to define similarities between dung beetle assemblages across the chronosequence from regenerating to natural forest stands. Data were arranged as a matrix of mean species abundance per trap in each stand over the entire trapping period. These data were $\log_{10}(n + 1)$ transformed before analysis. Clustering was conducted as for the classification of stands using vegetative and microclimatic data. The results were used to construct a dendrogram on which clusters of dung beetle assemblages were defined at the 40% and 68% levels of similarity. Multiple paired comparisons of clusters were conducted as for the classification of stands using vegetative and microclimatic data.

Assessment of Faunal Convergence

The degree of faunal similarity between stands of regenerating vegetation and each of the four reference points in

natural forest was measured both for dung beetle species composition and for relative abundance of species. Plotting these data in chronosequence allowed an assessment as to whether or not the dung beetle fauna is converging toward that of each unmined forest stand. Species composition was compared according to the presence or absence of taxa from pairs of stands (x, y) using the percentage disagreement measure of distance, dissimilarity coefficient (Statsoft, Inc. 1995). This is expressed as distance (x, y) = $100 (\sum |x_i \neq y_i| / I)$, in which I is the total number of species and $\sum |x_i \neq y_i|$ is the number of instances in which a species is present in one stand and absent from the other. The results are expressed as percentage similarity ($100 - \text{distance } [x, y]$). Analyses were conducted for the entire fauna and also for shade-specialist species, as defined by Davis et al. (2002). Similarity between relative abundances of species in pairs of stands was compared using the Steinhaus similarity index: $S = 2W / (A + B)$, in which W is the sum of the smaller numbers in pairs of species abundance data converted to decimal proportions for each stand and in which $A (=1)$ and $B (=1)$ are the total proportional density of the two stands (=2), that is, if $A = B = 1$, $S = W$ (Legendre & Legendre 1983). Analyses were conducted for the entire fauna, which includes widespread species, and also for species endemic to the east coast or Maputa-

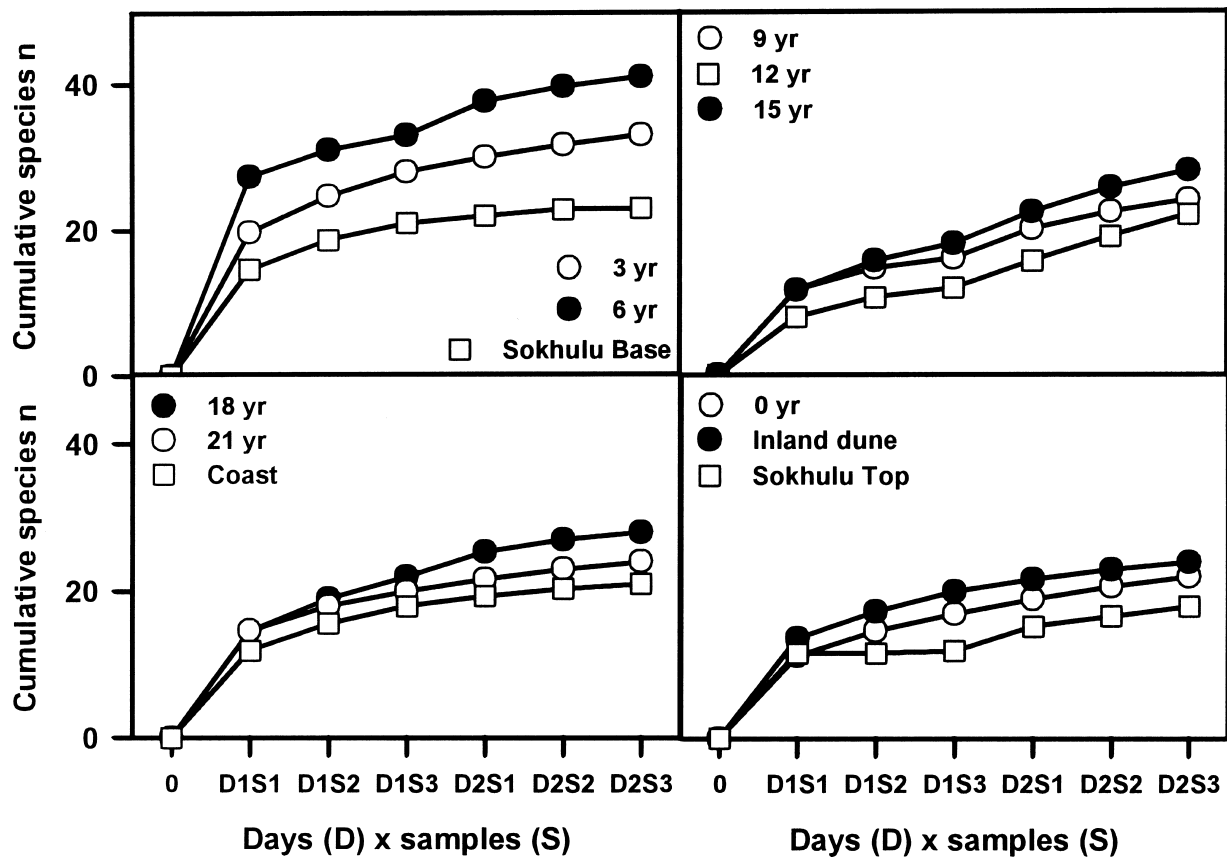


Figure 1. Cumulative numbers of dung beetle species trapped at three sites over 2 days in each of eight stands across the vegetational chronosequence and four stands in natural dune forest (see Methods).

land (Appendix) (Davis et al. 2002). The series of indices developed by these analyses were tested for correlation with physical parameters (canopy cover, surface cover, radiant heat, light intensity) across the post-mining chronosequence of stands. All data were $\log_{10}(n + 1)$ transformed before analysis.

Results

Validity of Data

Figure 1 shows average cumulative numbers of species recorded at each site from day 1 to day 2 (see Methods). Cumulative species richness in each sequence is clearly at or close to asymptote except, perhaps, for the approximately 9-, 12-, and 15-year stands.

Classification of Stands Using Vegetation and Microclimate Data

Cross-chronosequence variation in vegetative physiognomy and microclimate is summarized in Table 1. The dendrogram derived from cluster analysis of these data indicates four principal groups of stands (Fig. 2). These clusters comprise unshaded stands (Table 1) with hot light conditions and variable surface cover (cluster A); shaded stands with dense canopy, low light intensity, and low surface cover either dominated by *A. karroo* (cluster B) or by species-diverse tree cover (cluster D); and shaded stands with lower canopy cover of *A. karroo*, high subcanopy light intensity, and high surface cover (cluster C). Whereas the dendrogram shows that the five *Acacia* woodland stands are physiognomically and microclimatically closer to one

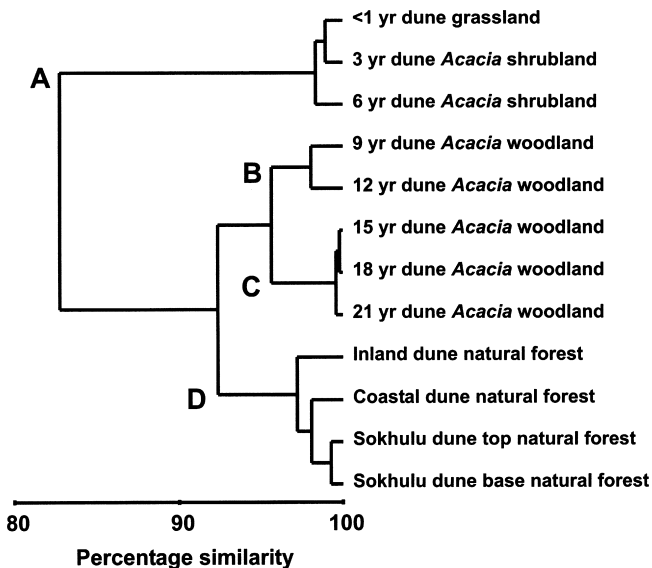


Figure 2. Dendrogram showing between-stand similarities in terms of vegetative cover (canopy, surface) and microclimate (shade temperature, radiant temperature, relative humidity, light intensity) (clusters defined at the 95% level of similarity).

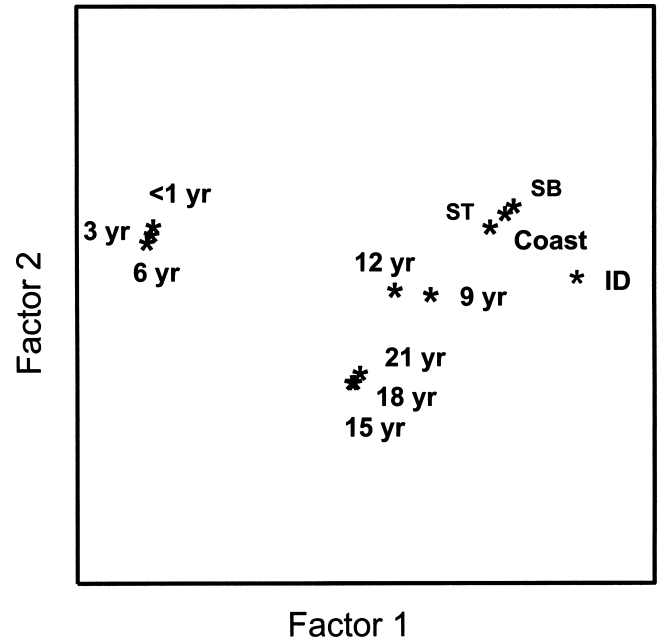


Figure 3. Multidimensional scaling ordination showing between-stand distance in terms of vegetative cover (canopy, surface) and microclimate (shade temperature, radiant temperature, relative humidity, light intensity). Chronosequence stand age (yr) depicted by numbers, natural forest stands depicted by Coast, coastal; ID, inland dune; SB, Sokhulu dune base; ST, Sokhulu dune top.

another than to the four natural forest remnants, the MDS ordination shows that early *Acacia* woodland (approximately 9–12 years) is closer to unmined natural forest than to older *Acacia* woodland (approximately 15–21 years) (Fig. 3). This latter result is supported by ANOSIM comparison of the cluster pairs, which showed that physiognomy and microclimate of the natural forest cluster differed significantly to both the youngest (unshaded, <1 to approximately 6 years) and oldest (shaded, approximately 15–21 years) stands of regenerating vegetation (D:A and D:C, 35 permutations; $R = 1.000$, $p = 0.029$) but not to shaded stands in the middle of the early chronosequence (approximately 9–12 years) (D:B, 15 permutations; $R = 1.000$, $p = 0.067$). None of the cluster pairs of stands comprising regenerating vegetation differed significantly from one another (A:B, A:C, and B:C, 10 permutations; $R = 1.000$, $p = 0.10$). However, overall variation was highly significant (global $R = 0.988$, $p < 0.001$).

Classification of Stands Using Dung Beetle Data

Cross-chronosequence variation in species richness and abundance of dung beetles is summarized in Figure 4 and Table 2. Between-stand differences accounted for most of the variance in species richness (71.4%) and abundance (69.3%) (Table 2). Stand area had no significant effect on either total species richness ($r^2 = 0.39$, $t_{(3)} = 1.39$, $p = 0.26$) nor mean numbers of species per trap ($r^2 = 0.41$, $t_{(3)} =$

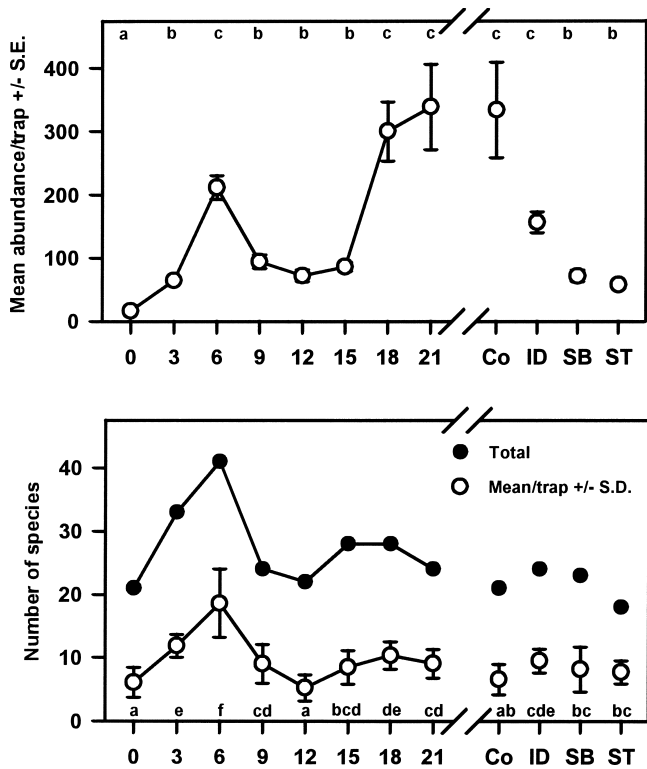


Figure 4. Overall patterns of dung beetle species richness and abundance across the vegetational chronosequence to natural forest. Chronosequence stand age (yr) depicted by numbers, natural forest stands depicted by Co, coastal; ID, inland dune; SB, Sokhulu dune base; ST, Sokhulu dune top. Different letters denote significant differences between data points, $p < 0.05$, Tukey's HSD.

1.46, $p = 0.24$) in woodland stands. Species abundance composition of dung beetles (Fig. 5) differed significantly between unshaded (cluster A) and shaded (cluster B) stands (global $R = 0.979$, $p = 0.05$). Whereas dung beetle faunas of all *Acacia* woodland and natural forest stands

Table 2. Contribution of spatial and temporal factors to variance in $\log_{10}(n + 1)$ transformed abundance and species richness of dung beetles across the chronosequence from grassland to forest (see Methods for multifactor ANOVA design).

Factor	df	MS	F	p
Abundance				
Stands	11, 143	3.471	42.13	<0.001
Sites	24, 143	0.440	5.33	<0.001
Days	1, 143	0.022	0.38	0.537
Stands \times days	11, 143	0.823	14.35	<0.001
Sites \times days	24, 143	0.252	4.39	<0.001
Species richness				
Stands	11, 143	0.680	37.85	<0.001
Sites	24, 143	0.055	3.05	<0.001
Days	1, 143	0.074	5.25	<0.05
Stands \times days	11, 143	0.110	7.75	<0.001
Sites \times days	24, 143	0.034	2.40	<0.001

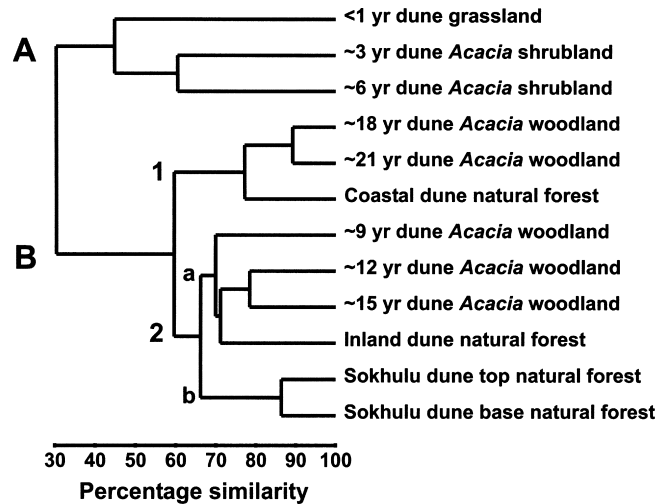


Figure 5. Dendrogram showing similarities between dung beetles species abundance composition in chronosequence and natural forest stands. Clusters are defined at the 40% and 65% levels of similarity. A, unshaded stands; B, shaded stands.

were relatively similar (cluster B), those of older *Acacia* woodland and natural coastal forest (cluster B1) included large numbers of the dung beetle, *Onthophagus vinctus*, and were more dissimilar to natural inland forests than those of younger *Acacia* woodland stands (included in cluster B2). The least disturbed Sokhulu natural forest faunas (cluster B2b) showed a measure of dissimilarity to all other woodland and natural forest faunas. However, differences between the faunas of three clusters of shaded stands were mostly nonsignificant (global $R = 0.877$, $p = 0.01$. B1:B2a, 35 permutations; $R = 0.852$, $p = 0.03$. B1:B2b, 10 permutations; $R = 1.000$, $p = 0.10$. B2a:B2b, 15 permutations, $R = 0.714$, $p = 0.07$).

Faunal Convergence Between Stands

Figures 6 and 7 show the degree of similarity between the dung beetle faunas of each stand of regenerating vegetation and each natural forest stand. These data show clear patterns of increase and decline in similarity to the natural forest fauna when ordered in chronosequence. Comparison of species composition (percentage similarity) (Fig. 6) yields different patterns when compared with proportional species abundance composition (Steinhaus indices) (Fig. 7). The degree of similarity between assemblages in reference natural forest stands (Inland dune, Sokhulu dune base, Sokhulu dune top) was similar to those between these forests and the approximately 12-year *Acacia* woodland stand (Table 3).

Over the first few years of the chronosequence (<1 to approximately 6 years) species composition of dung beetles increases in similarity to that in all natural forest stands (Fig. 6). However, an asymptote is reached at the earliest shaded chronosequence stage of approximately 9

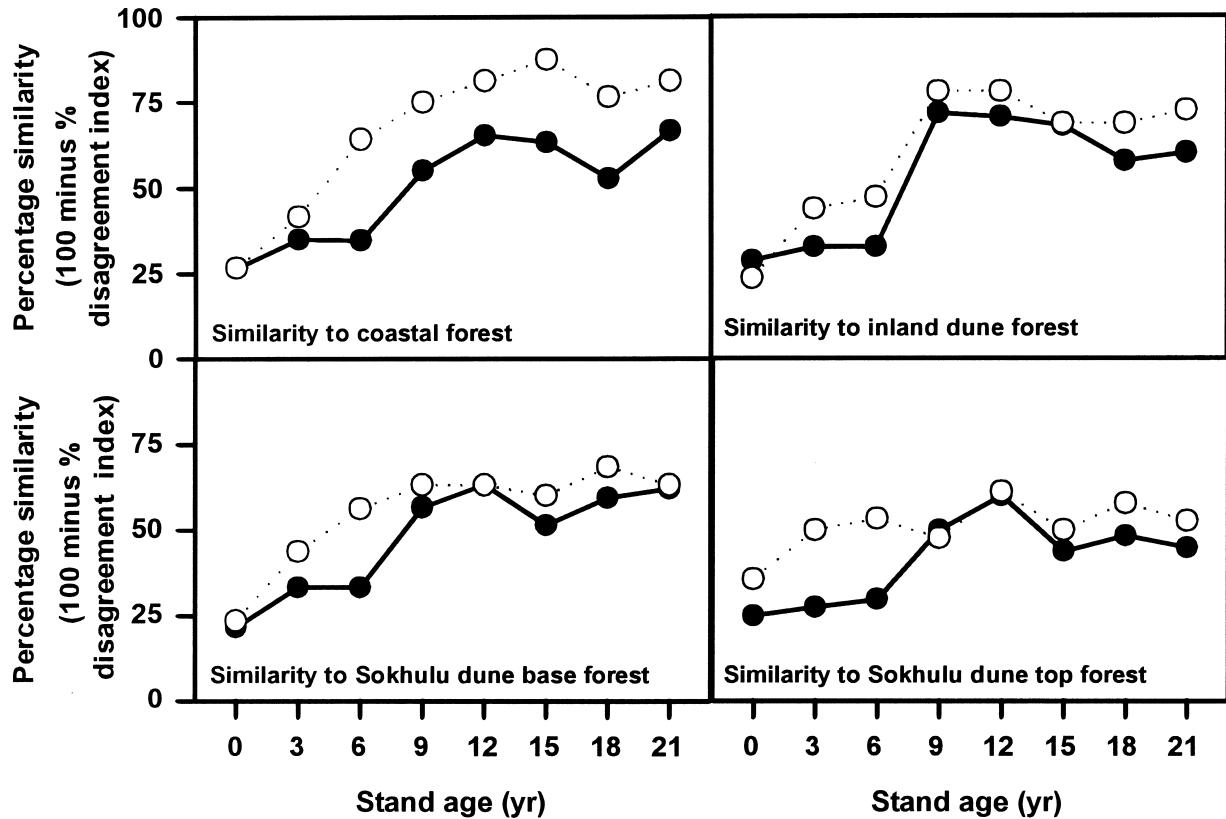


Figure 6. Cross-chronosequence patterns of similarity between dung beetle species composition in regenerating and natural forest stands. ●, all species; ○, shade specialist species defined by Davis et al. (2002).

years. Across the chronosequence, proportional similarity to the natural forest faunas is greater in the shade specialist fauna than in the entire fauna. However, the correlation between similarity indices and physical parameters is stronger for the entire fauna than for shade specialists (Table 4). The positive correlations to canopy cover and the negative correlations to radiant temperature were mostly significant in each comparison. The negative correlations to light intensity and surface cover were mostly nonsignificant.

Across the chronosequence Steinhaus indices for stands of regenerating vegetation showed similar patterns of increase or decrease in faunal similarity to natural forest stands in three cases (Fig. 7). In these three cases (the inland dune and the Sokhulu forests) unshaded stands of the early chronosequence (<1 to approximately 6 years) showed a trend toward increasing dissimilarity with natural forest faunas, followed by a steep trend toward increasing similarity that coincided with the closure of the woodland canopy at approximately 9 years. However, this progression was followed by a trend toward increasing dissimilarity in older *Acacia* woodland stands (Fig. 7), where canopy cover decreased (Table 1) (approximately 15–21 years). This decline in similarity remained, even after deleting the data for widespread species, although it was less pronounced. The correlation between similarity indices and physical parameters was stronger for the endemic species than for the entire

fauna (Table 5). The positive correlations to canopy cover and the negative correlations to radiant temperature and light intensity were significant in most comparisons.

Across the chronosequence Steinhaus indices for stands of regenerating vegetation showed two quite different patterns of increase in faunal similarity to coastal forest (Fig. 7). The entire fauna showed low similarity to that of coastal forest over most of the chronosequence, with a steep trend toward increased similarity in the two oldest *Acacia* woodland stands (approximately 18 and approximately 21 years). This pattern is presumably related to the superabundance of *Onthophagus vinctus* in the adjoining approximately 18- and approximately 21-year stands and coastal forest stands where it comprised, respectively, 44.70%, 58.85%, and 84.54% of total numbers. This superabundance was not correlated with any physical factor (Table 5). The pattern of similarity changed radically with the removal of data for widespread species. The dominant trend for endemic species was a steady cross-chronosequence increase in similarity between the faunas of *Acacia* woodland stands and coastal forest. This pattern did show a strong correlation with canopy cover and radiant temperature, but the correlations were mostly weaker than those shown for the other natural forest comparisons. These different patterns emphasize the broad differences between the structure of dung beetle assemblages in coastal forest and the three other dune forests (Fig. 5).

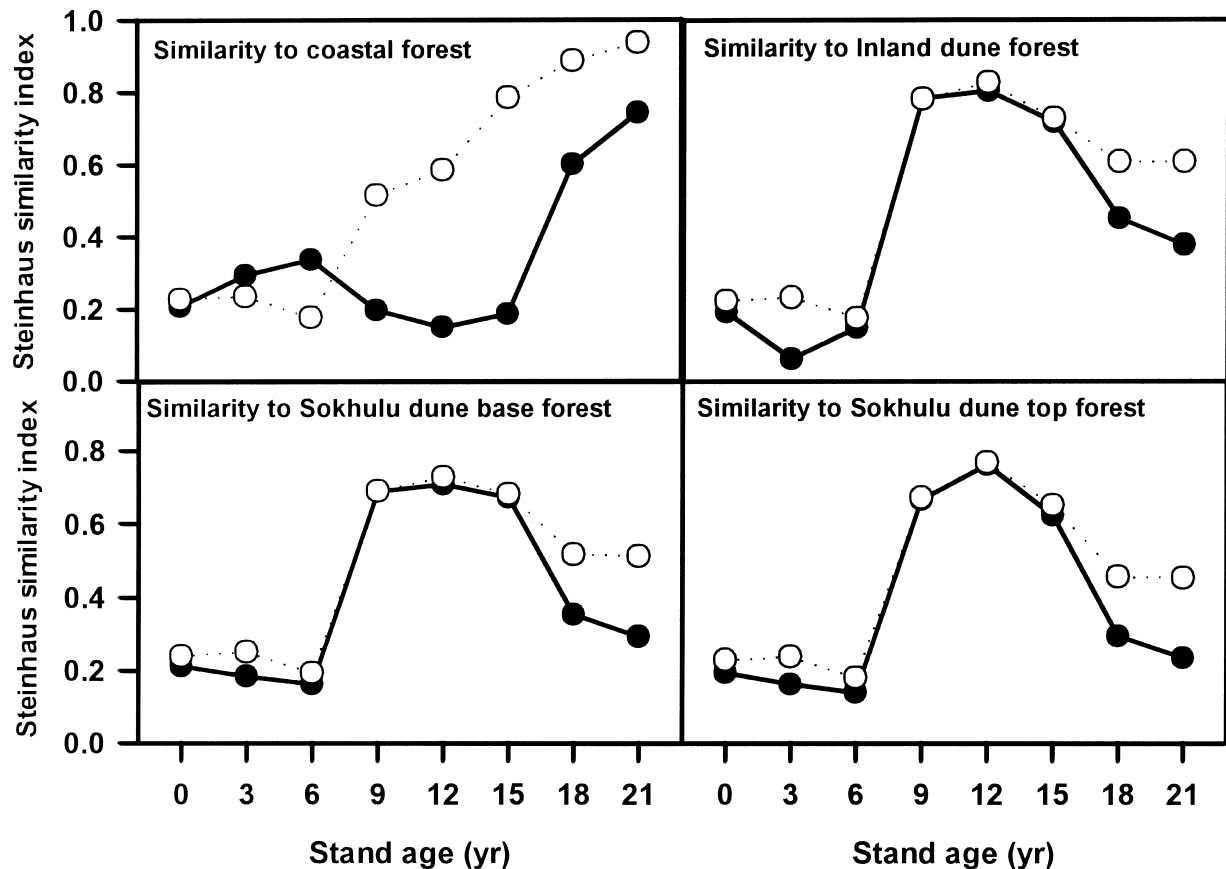


Figure 7. Cross-chronosequence patterns of similarity between proportional dung beetle species abundance in regenerating and natural forest stands. ●, all species; ○, species endemic to Maputaland and the east coast defined by Davis et al. (2002).

Discussion

Validity of Data and Analyses

The January trapping of dung beetles at Richards Bay coincided with the mid-summer peak in activity shown by dung beetles (Davis 1996a) in the mid-summer rainfall region of northeastern South Africa (Davis 1997), and the species record compares favorably with reference material

Table 3. Percentage similarity of dung beetle assemblages between natural forest and ~12-yr *Acacia* woodland stands.

Comparison	% Similarity in Species Composition ^a	% Similarity in Proportional Species Abundance ^b
Inland dune : Sokhulu top	55.6	71.8
Inland dune : Sokhulu base	67.9	76.5
Sokhulu top : Sokhulu base	64.0	82.7
Sokhulu base : ~12-yr stand	60.0	70.8
Sokhulu top : ~12-yr stand	63.3	76.8
Inland dune : ~12-yr stand	70.4	80.4

^a100 - Percentage disagreement index.

^bSteinhaus index \times 100.

for the region. Although the data were collected over only 2 days, cumulative species richness plots are close to asymptote at most study sites, which suggests that most species present were recorded. Collection of dung beetle data over a short period is perfectly adequate for comparing spatial differences between vegetative stands. Overall, the 360 samples captured a total of 53,663 individuals belonging to 60 species. These samples provided 30 dung beetle data sets for each stand, and statistical tests clearly demonstrated significant between-stand differences in species richness and abundance. Although species richness and abundance of insects fluctuate according to year to year (Doube 1987), seasonal (Wolda 1988), and day to day weather-mediated effects (Davis 1995), the present dung beetle data were collected simultaneously and are therefore a valid reflection of between-stand differences under the same warm sunny weather conditions. Furthermore, a recent study on Australian forest Lepidoptera shows that although species composition and ordinal position change with season, ordinal pattern and statistical distances between each habitat remain similar (Kitching et al. 2000). Although microclimatic measurements were made some 6 weeks after dung beetle data collection, both data sets reflect similar between-stand differences, because overall

Table 4. ANOVA statistics and coefficients of determination from linear regression of physiognomic and microclimatic parameters (Table 1) on indices of percentage faunal similarity between stands of regenerating vegetation and natural forest (Fig. 6).

Forest Stand	Statistic	Physical and Microclimatic Parameters			
		Canopy Cover	Surface Cover	Radiant Temperature	Light Intensity
<i>All species</i>					
Coastal	r^2	0.89	0.14	0.85	0.34
	$F_{(1,6)}$	49.35***	0.96	32.87**	3.10
Inland dune	r^2	0.96	0.03	0.94	0.58
	$F_{(1,6)}$	129.68***	0.18	97.80***	8.11*
Sokhulu top	r^2	0.86	0.12	0.86	0.39
	$F_{(1,6)}$	38.22***	0.79	36.24***	3.82
Sokhulu base	r^2	0.90	0.02	0.94	0.58
	$F_{(1,6)}$	52.73***	0.11	89.30***	8.27*
<i>Shade species</i>					
Coastal	r^2	0.67	0.26	0.66	0.26
	$F_{(1,6)}$	12.17*	0.20	11.75*	2.08
Inland dune	r^2	0.75	0.11	0.77	0.42
	$F_{(1,6)}$	18.12**	0.70	20.44**	4.27
Sokhulu top	r^2	0.53	0.23	0.54	0.22
	$F_{(1,6)}$	6.79*	1.82	7.13*	1.72
Sokhulu base	r^2	0.27	0.21	0.27	0.06
	$F_{(1,6)}$	2.17	1.56	2.25	0.38

All data were $\log_{10}(n + 1)$ transformed before analysis.

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Units for physical and microclimatic parameters are as for Table 1.

mean maximum and minimum temperatures showed minimal variation between occasions in this subtropical coastal system. Thus, it is acceptable to conduct regressions of between-stand differences in dung beetle data on between-stand differences in microclimatic data.

Restoration of Forest and Associated Fauna

Although there is little difference between the early vegetational succession on mined or unmined but completely devegetated coastal sand dunes in the study area (Mentis & Ellery 1994), there are differences in the vegetational succession elsewhere in the region where the pattern of disturbance differs (Lubke et al. 1992). However, irrespective of the disturbance pattern on unmined dunes, the successional end point is secondary forest. Predictions indicate that in secondary forest, recovery of maximum dune forest species richness occurs between 28 and 40 years after clearance of dune vegetation with full compositional convergence at 54 to 70 years (Mentis & Ellery 1998). This compares favorably with predictions made for restoration of tropical rain forest in Mexico after 73 years (Hughes et al. 1999) and in Nigeria 100 years (Osho 1996) after deforestation. It may be concluded that although forest may be restored on mined dunes in the future, this will be a long-term process that may depend on the restitution of a forest soil profile that has been disturbed by the mining process. Although mineral and organic soil content is mostly lower

Table 5. ANOVA statistics and coefficients of determination from linear regression of physiognomic and microclimatic parameters (Table 1) on Steinhaus indices of faunal similarity between stands of regenerating vegetation and natural forest (Fig. 7).

Forest Stand	Statistic	Physical and Microclimatic Parameters			
		Canopy Cover	Surface Cover	Radiant Temperature	Light Intensity
<i>All species</i>					
Coastal	r^2	0.04	0.43	0.02	0.09
	$F_{(1,6)}$	0.23	4.43	0.12	0.61
Inland dune	r^2	0.78	0.004	0.81	0.70
	$F_{(1,6)}$	21.07**	0.03	25.09**	13.72*
Sokhulu top	r^2	0.54	0.06	0.59	0.68
	$F_{(1,6)}$	7.12*	0.38	8.51*	12.91*
Sokhulu base	r^2	0.63	0.03	0.65	0.67
	$F_{(1,6)}$	10.19*	0.17	11.11*	12.36*
<i>Endemic species</i>					
Coastal	r^2	0.83	0.30	0.65	0.11
	$F_{(1,6)}$	28.46**	2.57	11.33*	0.73
Inland dune	r^2	0.94	0.004	0.92	0.61
	$F_{(1,6)}$	95.94***	0.03	72.49***	9.27*
Sokhulu top	r^2	0.82	0.003	0.82	0.65
	$F_{(1,6)}$	26.67**	0.02	27.97**	11.18*
Sokhulu base	r^2	0.90	0.001	0.87	0.61
	$F_{(1,6)}$	51.73***	0.01	41.38***	9.40*

All data $\log_{10}(n + 1)$ transformed before analysis.

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Units for physical and microclimatic parameters are as for Table 1.

in chronosequence stands than in natural forest (van Aarde et al. 1998), millipede activity may accelerate the release of such elements (Smit & van Aarde 2001). However, it is still too early to determine the final outcome as, at 23 years, the oldest chronosequence woodland still represents an early successional stage in forest ecosystem regeneration.

Trends toward recolonization of mined dunes by all natural forest biota may be examined by measuring changes in habitat structure and species composition across the chronosequence and by assessing their relative statistical distance from natural forest biota (van Aarde et al. 1996b). Across the chronosequence from grass to younger and older *Acacia* woodland, species richness and diversity of several plant (trees, herbs) and animal (birds, millipedes, beetles) groups is increasing with time (van Aarde et al. 1996b; van Dyk 1997; Kritzing & van Aarde 1998), and this trend is accompanied by a clear turnover in species composition (Kritzing & van Aarde 1998). Although there is also a clear turnover from open to shade specialist dung beetle taxa, overall species richness declines across the chronosequence. This phenomenon is presumably linked to the greater dung beetle diversification in open habitats. Such animals may benefit from the open habitat created in the early stages of rehabilitation, compared with detritus feeding millipedes and many of the beetle taxa swept from woody vegetation by van Aarde et al. (1996b). Relative densities of all taxa decrease across the chrono-

sequence from 0 to 16 years (van Aarde et al. 1996b), including dung beetles. However, in older stands of regenerating vegetation (approximately 18 and approximately 21 years) and in the adjoining coastal forest there was a vast increase in dung beetle density, primarily influenced by one species, *O. vinctus*.

Previous measurements of similarity in diversity between chronosequence stages and natural forest using other biota suggest that convergence will occur at some point in the future, because stands of older regenerating vegetation are closer in character to natural forest than younger stands (van Aarde et al. 1996a, 1996b; Ferreira & van Aarde 1997; van Dyk 1997). However, because of the degree of variation in biological assemblages it is unrealistic to expect 100% convergence in species richness and abundance. In the present study on dung beetles percentage similarities between inland dune and Sokhulu dune forest assemblages were similar to those shown between these natural forest assemblages and the approximately 12-year *Acacia* woodland stand. Thus, in terms of proportional assemblage structure, the dung beetle community is restored fairly rapidly with the reestablishment of vegetation offering shade. However, the early convergence in relative abundance of species populations is succeeded by a trend toward dissimilarity in the oldest stands of regenerating vegetation.

Because dung beetle distribution is closely linked to vegetative physiognomy (Cambefort 1982; Doube 1983; Davis 1996b), patterns of faunal similarity between stands of regenerating vegetation and natural forest were closely linked to vegetational and microclimatic changes across the chronosequence. Most dung beetle species at Richards Bay showed relatively extreme specialization to either shaded or unshaded situations (Davis et al. 2002). Thus, the species convergence curve reached asymptote at approximately 9 years after reestablishment of forest physiognomy and showed little further variation. However, in the case of relative species abundance, the initial convergence with dung beetle faunas in natural dune forest after approximately 12 years was followed by a trend toward dissimilarity in older *Acacia* woodland stands. The trends were strongly correlated with vegetative physiognomy and microclimate, which are similar to natural forest in early post-mining *Acacia* woodland stages (approximately 9 and approximately 12 years) but more dissimilar in older stages of *Acacia* woodland (approximately 18 and approximately 21 years). The trend toward lower similarity in older regenerating woodland is strongly influenced by the abundance of widespread species (particularly *O. vinctus*). However, this trend remained evident even with the removal of data for widespread species, although it is less strongly expressed. Differences to natural forest may be related to the presence of cattle droppings in all rehabilitating stands, particularly in older *Acacia* woodland stands (approximately 15–21 years) (T. D. Wassenaar, Conservation Ecology Research Unit, University of Pretoria, personal communication, 2001). This factor might be ex-

pected to influence relative abundance of both widespread and endemic dung beetle species. However, differences between relative abundance patterns of dung beetles in approximately 15-year stands and natural forest were less extreme than for approximately 18-year and approximately 21-year stands despite similar vegetative physiognomy in all three age groups. It is unknown whether or not this result could be related to between-stand differences in density of droppings or due to other reasons.

As members of the ground fauna population dynamics of the dung beetles at Richards Bay are primarily influenced by microclimatic factors related to vegetative physiognomy rather than to the taxonomic composition of the vegetation. Similar relationships to physiognomy of native or replanted vegetation were seen in ground-dwelling beetles in New Zealand (Watts & Gibbs 2002). However, factors other than vegetation and dung type may also influence the present data set. It has been noted that the distribution pattern of population size across ecological or successional gradients is “humped,” best fitting a quadratic curve (Andersen 1992). In ants it has been noted that where a single species is superabundant across such a distribution, relative abundance of other species is lower. This observation has been interpreted as an example of competitive suppression (Andersen 1992). Dung beetle assemblages are also organized in a competitive hierarchy (Doube 1990; Hanski & Cambefort 1991). This hierarchy is based on body size, manner of dung exploitation, and rate of dung burial, which varies with soil type. Despite these observations we would urge caution in interpretation of the results on the humped population distribution patterns and the superabundance of *O. vinctus* in the present dung beetle data set. Whereas the populations of some shade-specialist dung beetle species are relatively lower where *O. vinctus* is superabundant, those of others are greatest in those stands (Appendix). Furthermore, *O. vinctus* is probably a small slow-burying tunneler (average dry body mass, 9 mg) and is considered competitively inferior to large, fast-burying, shade-specialist tunnelers such as *Catharsius* sp. 1 (530 mg) and *Catharsius* sp. nr *pandion* (660 mg). As regards competition for dung from the large populations of ants that are known from some chronosequence stands (Majer & de Kock 1992), although ants are known to colonize dung (personal observation) this is not a common occurrence. Ants were not noted as a dominant component in most pitfall traps.

Lack of connectivity between undisturbed and regenerating patches of vegetation also strongly influences biotic diversity (Metzger 1997; Dewenter & Tscharnke 1999) and metapopulation persistence (Swart & Lawes 1996). These factors are probably not an extensive problem in the study area, because the unmined coastal strip and the shaded chronosequence stands are contiguous (Davis et al. 2002). Therefore, shade specialist species are easily able to recolonize regenerating vegetation, thus accounting for the occurrence of most species throughout all shaded stands. However, there are some notable absences, particularly

that of the vulnerable flightless relict, *Gyronotus carinatus* (Davis et al. 2001), which is absent not only from *Acacia* woodland but also from the coastal and inland dune forests. It is unclear whether its absence is related to habitat unsuitability, disturbance, or the lack of connectivity between the dune forest remnants and relatively undisturbed dune forest at Sokhulu Forest Reserve where *G. carinatus* still occurs. Temperatures in the lower lying inland dune forest are only marginally higher than at Sokhulu, whereas annual rainfall is similar (>1,400 mm) (Dent et al. 1989). However, past and present disturbance is likely to have been much greater, because trigonometric survey photographs from 1937 indicate patchy but complete forest clearance within 100 meters of the inland dune trapping sites (Weisser & Marques 1979).

Like the flora (van Wyk 1996) much of the dung beetle fauna of natural dune forest is endemic to Maputaland or the east coast (Appendix) (Davis et al. 2002). However, the post-mining dung beetle assemblage is dominated by species with wider biogeographical associations and specialization to unshaded situations (Appendix) (Davis et al. 2002). With the reestablishment of forest physiognomy at approximately 9 years, there is high species turnover and restoration of a shade specialist dung beetle fauna with more localized climatic ranges (Davis et al. 2002) and high similarity to the fauna of natural forest. However, this convergence does not persist because in older *Acacia* woodland stands, the population dynamics of both widespread and endemic dung beetle species are driven toward decreasing similarity with those in natural forest. This decrease may be due to either decline in physiognomic and microclimatic similarity to natural forest (reduced trunk density and canopy cover with increased light intensity, virtual absence of shrubs leading to an open understory with dense surface cover) or other factors such as differences in the density of cattle dung between older woodland stands and natural forest. Although older stands of regenerating vegetation remain dominated by *A. karroo*, which has a potential lifespan of 40 years (van Dyk 1997), there are indications that physiognomy is continuing to converge with that in natural dune forest (Davis, A. L. V., R. J. van Aarde, C. H. Scholtz, and J. H. Delpont, unpublished data). The current decline in similarity between the dung beetle assemblages of older *Acacia* woodland and natural forest may therefore move back toward convergence in similarity as the vegetation in rehabilitating stands converges toward that of primary natural dune forest. This trend would be characterized by increased tree species diversity, increased canopy density with reduced light intensity, and a reestablishment of a dense shrub understory with little surface cover that is unsuitable for cattle grazing.

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Appendix 1. Average numbers of dung beetle species per trap in each vegetational stand near Richards Bay with a classification of their biogeographical distributions (Distr.) and habitat associations (hab.).

Species	Distr.	Hab.	<1 yr	~3 yr	~6 yr	~9 yr	~12 yr	~15 yr	~18 yr	~21 yr	Coastal	ID	ST	SB
<i>Anachalcos convexus</i> Boheman	W	NS	0.00	0.37	2.93	0.80	0.07	0.27	0.53	0.00	0.00	1.47	0.90	0.97
<i>Gyronotus carinatus</i> Felsche	M	S	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	7.00	6.13
<i>Pachylomerus femoralis</i> (Kirby)	W	NS	0.37	2.30	6.77	0.13	0.03	0.17	0.00	0.03	0.00	0.07	0.00	0.03
<i>Kheper lamarcki</i> (M'Leay)	W	NS	0.43	3.43	1.93	0.00	0.00	0.07	0.03	0.00	0.00	0.00	0.00	0.00
<i>Scarabaeus bornemisszai</i> zur Strassen	M	S	0.00	0.00	0.00	0.47	0.03	0.00	0.00	0.00	0.00	1.70	0.50	0.17
<i>Scarabaeus goryi</i> Castelnau	W	S	0.30	5.60	4.37	3.30	0.60	1.30	3.97	2.24	1.77	3.87	0.67	1.50
<i>Garreta azureus</i> (Fabricius), coastal var.	M	S	0.00	0.00	0.00	0.23	0.20	0.13	0.10	0.21	0.13	0.33	0.60	0.13
<i>Garreta unicolor</i> (Fahraeus)	W	NS	0.00	0.07	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Allogymnopleurus thalassinus</i> Klug	W	NS	0.03	0.00	0.27	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Neosisyphus confrater</i> Kolbe	W	NS	0.00	0.03	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Neosisyphus mirabilis</i> Arrow	M	S	0.00	0.03	0.07	0.07	0.27	1.03	2.43	2.10	0.33	0.13	1.30	1.33
<i>Neosisyphus spinipes</i> Gory	W	NS	0.03	0.17	0.87	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00
<i>Sisyphus bornemisszanus</i> Endroedi	M	S	0.00	0.00	0.00	0.17	0.00	0.07	0.77	1.72	0.07	0.07	0.00	0.03
<i>Sisyphus seminulum</i> Gerstaecker	W	S	0.00	0.00	0.10	0.07	0.03	0.13	0.43	0.90	0.03	0.03	0.00	0.07
<i>Sisyphus sordidus</i> Boheman	M	NS	0.00	0.03	23.50	0.00	0.00	0.13	0.00	0.00	0.03	0.00	0.00	0.00
<i>Sisyphus</i> sp. nr <i>gazanus</i>	M	S	0.00	0.00	0.00	0.23	0.03	0.17	1.83	0.62	0.00	0.07	0.00	0.17
<i>Sisyphus</i> sp. y (<i>sensu</i> Paschalidis 1974)	EC	S	0.00	0.00	0.00	0.57	0.03	0.03	0.00	0.14	0.07	0.47	0.00	0.00
<i>Pedaria</i> sp. IV (<i>sensu</i> Davis 1996b)	W	NS	0.00	0.03	0.43	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Copris inhaletus</i> ssp. <i>santaluiciae</i> Ferreira	M	NS	0.00	0.03	1.37	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Copris puncticollis</i> Boheman	EC	NS	0.00	0.07	0.67	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Copris urus</i> Boheman	M	NS	0.00	0.53	0.10	0.00	0.00	0.00	0.10	0.03	0.03	0.00	0.00	0.03
<i>Catharsius tricornutus</i> de Geer	W	NS	0.00	0.07	3.03	0.00	0.00	0.07	0.00	0.03	0.00	0.13	0.00	0.00
<i>Catharsius</i> sp. nr <i>pandion</i>	M	S	0.17	1.23	0.87	9.30	13.97	14.57	8.77	9.41	5.93	13.97	11.60	10.17
<i>Catharsius</i> sp. 1	M	S	0.00	0.10	1.30	0.47	3.27	4.67	14.27	7.86	1.87	5.97	1.43	1.57
<i>Metacatharsius</i> sp. 1	M	NS	0.00	0.53	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Stiptopodius</i> sp. 1	M	NS	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Proagoderus aciculatus</i> Fahraeus	EC	S	2.50	6.63	18.33	51.83	41.47	29.13	43.10	33.79	11.93	78.70	26.37	28.80
<i>Proagoderus aureiceps</i> d'Orbigny	EC	NS	2.57	9.13	33.00	1.67	0.20	1.10	0.07	0.00	0.00	0.07	0.00	0.00
<i>Proagoderus brucei</i> Reiche	W	NS	0.00	0.00	0.07	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Hyalonthophagus alcyonides</i> (d'Orbigny)	W	NS	0.00	0.00	0.23	0.03	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00
<i>Digitonthophagus gazella</i> (Fabricius)	W	NS	0.00	0.07	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Onthophagus aeruginosus</i> Roth	W	NS	0.00	0.07	0.00	0.00	0.00	0.00	0.07	0.00	0.00	0.00	0.00	0.00
<i>Onthophagus ambiguus</i> Péringuey	EC	NS	2.60	5.93	9.33	1.60	0.03	0.10	0.97	0.14	0.23	0.10	0.57	0.80
<i>Onthophagus depressus</i> Harold	W	NS	0.00	0.03	1.90	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00
<i>Onthophagus fimetarius</i> Roth, coastal var.	M	NS	0.10	0.00	6.20	0.03	0.00	0.03	0.03	0.00	0.00	0.03	0.00	0.00
<i>Onthophagus flavolimbatus</i> d'Orbigny	W	NS	0.03	0.07	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Onthophagus lacustris</i> Harold	EC	S	0.00	0.00	0.00	0.03	0.07	0.03	0.07	0.00	0.03	0.00	0.00	0.00
<i>Onthophagus nanus</i> Harold	W	NS	0.03	0.00	1.20	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Onthophagus obtusicornis</i> Fahraeus	W	NS	0.03	0.00	3.20	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Onthophagus pugnatus</i> Fahraeus	W	S	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.03	0.00	0.00	0.00	0.00
<i>Onthophagus quadrimodosus</i> Fahraeus	W	S	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00
<i>Onthophagus signatus</i> Fahraeus	W	NS	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

(continued)

Appendix 1. Continued

Species	Distr.	Hab.	<1 yr	~3 yr	~6 yr	~9 yr	~12 yr	~15 yr	~18 yr	~21 yr	Coastal	ID	ST	SB
<i>Onthophagus ursinus</i> d'Orbigny	EC	NS	3.30	3.97	11.50	0.23	0.03	0.23	0.07	0.10	0.03	0.00	0.00	0.00
<i>Onthophagus vinctus</i> Erichson	W	S	2.50	14.40	59.77	4.77	0.10	2.77	134.00	199.14	282.13	1.73	0.23	0.27
<i>Onthophagus</i> sp. nr <i>bicavifrons</i>	M	S	0.00	0.00	0.00	0.00	0.10	0.38	0.23	0.24	0.07	0.07	0.03	0.00
<i>Onthophagus</i> sp. nr <i>sugillatus</i> , coastal var.	M	NS	0.10	1.27	0.23	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Onthophagus</i> sp. 1	W	NS	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Onthophagus</i> sp. 2	M	S	0.00	0.03	11.17	10.87	10.87	27.80	78.97	69.34	26.07	32.63	3.73	8.23
<i>Onthophagus</i> sp. 3	M	S	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.13	0.00	0.07
<i>Onthophagus</i> sp. 4	M	NS	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Milichus</i> sp. 1	EC	NS	0.10	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Caccobius nigriventris</i> Klug	W	NS	0.00	0.13	0.63	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Caccobius</i> sp. 1	M	NS	0.13	1.23	8.77	0.07	0.03	0.27	0.20	0.38	0.17	0.03	0.03	0.10
<i>Caccobius</i> sp. 2	EC	S	0.00	0.00	0.03	0.00	0.10	0.80	7.67	9.45	2.67	0.00	0.10	0.37
<i>Caccobius</i> sp. 3	M	NS	0.80	5.07	7.77	6.83	0.33	0.60	0.97	0.28	0.10	1.27	0.23	0.83
<i>Caccobius</i> sp. 4	M	S	0.03	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.00
<i>Drepanocerus impressicollis</i> Boheman	M	S	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	13.23	2.37	9.67
<i>Oniticeilus formosus</i> Chevrolat	W	NS	0.00	0.00	0.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Oniticeilus planatus</i> Castelnau	W	NS	0.00	0.07	0.03	0.00	0.00	0.03	0.03	0.14	0.00	0.00	0.00	0.03
<i>Liatongus militaris</i> (Castelnau)	W	NS	0.00	0.00	0.23	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

ID, inland dune; ST, Sokhulu dune top; SB, Sokhulu dune base; W, widespread; EC, east coastal distribution; M, Maputaland distribution; NS, centered in unshaded situations; S, centered in shaded situations.