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Is microclimate-driven turnover of dung beetle assemblage structure in regenerating coastal vegetation a precursor to re-establishment of a forest fauna?

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Abstract We questioned the capability of post-mining rehabilitation and successional changes in coastal vegetation to achieve restoration of dune forest, dung beetle assemblages in the Maputaland Centre of Endemism, South Africa. A repeat 2010 study of structural turnover between dung beetle assemblages across a 33 year successional sere of rehabilitating vegetation and old-growth forest (>73 years) produced comparable results to an earlier study across the 23 year chronosequence of 2000. Despite overlap, three structural patterns along the 33 year chronosequence were associated with specific stages of vegetation succession and their characteristic microclimates as in 2000. Although species biased to unshaded habitat dominated the earliest succession, there was rapid re-establishment of dominance by shade-associated forest species. In concert with progression from unshaded, post-mining vegetation to strongly shaded, early successional, *Acacia* shrub-woodland, there was an initial increase in similarity of the dung beetle fauna (species-poor, low abundance) to that in strongly-shaded forest (also species-poor, low abundance). However, in concert with decreasing shade cover in late successional woodland, the dung

beetle fauna became species-rich with high abundance so that the early successional trajectory of increasing similarity to forest fauna either levelled off to a plateau (species in 2000; abundance in 2010) or declined (species in 2010, abundance in 2000). It remains to be seen if gaps forming in the oldest *Acacia* woodland permit forest tree saplings of the exposed understorey to recreate a forest canopy that would be tracked by dung beetles to re-establish a typically species-poor, deep shade, forest assemblage with low abundance.

Keywords *Acacia karroo* woodland · Chronosequence · Dung beetle · Dune forest · Patchiness · Restoration · Richards Bay · Scarabaeinae · Succession

Introduction

Ecological succession drives vegetation recovery after disturbances (Townsend 2007; Grainger and van Aarde 2012a). In general, secondary succession follows a predictable pattern of turnover where community composition and structure change with time as plant and animal species that dominate early seral stages give way to species typical of later seral stages (Wang 2002; Hopp et al. 2010; Taki et al. 2010). Efforts to determine the precise nature, time-scales, and processes responsible for successional changes have generated a multitude of restoration studies in different ecotypes. These include long-term monitoring of post-mining, dune forest restoration at Richards Bay in South Africa where various patterns have been demonstrated for progression towards or away from convergence with the biota of old-growth forest (Wassenaar et al. 2005). Results for different taxa may vary according to the quality of the resource that they are tracking across the succession.

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The diversity of insect species that feed on plants may increase in a unimodal linear progression towards convergence with those in old-growth forest in concert with the increased species richness of woody plants recorded across the succession by van Aarde et al. (1996a). Other vegetative qualities such as density of shade cover may show a bimodal linear progression across the succession, i.e. unshaded grassland; dense, strongly shaded shrub-woodland; less shaded woodland; dense, strongly shaded, old-growth forest. Therefore, in insects that respond to shade cover rather than plant species composition, this may generate patterns of early successional faunal response that progress towards then away from convergence such as those yielded by a study on dung beetles across a 23 years chronosequence in 2000 (Davis et al. 2003). Such variability in patterns led to questions on the capability of successional processes to achieve restoration of dune forest dung beetle assemblages. Therefore, the present repeat study examines patterns after 33 years at a time when there is further decline in canopy cover.

The study area is located in the Maputaland Centre of Endemism (van Wyk 1996). This ecologically diverse region (~26,734 km²) straddles the borders of Swaziland, southern Mozambique, and northeast KwaZulu-Natal, South Africa. One of the regional ecotypes comprises dune forest, which is very limited in extent as it is restricted to a narrow coastal fringe. In places this forest is intensely disturbed through clearing for forestry, development for tourism and informal settlements, or mining for minerals, which entails the removal of all forest vegetation (van Aarde et al. 1996a). At present mining is the only regional disturbance event that is followed by a forest rehabilitation programme (van Aarde et al. 1996b). This provides a platform for studying the regeneration of dune forest and associated assemblages at a range of trophic levels.

Earlier studies across the successional sere of rehabilitating coastal vegetation suggested age-related convergence towards old-growth dune forest in both compositional and structural properties of tree, herb, millipede and bird assemblages (van Aarde et al. 1996b, c; Kritzinger and van Aarde 1998; Redi et al. 2005; Wassenaar et al. 2005). By contrast, trends in small mammal and dung beetle assemblages were contradictory in suggesting either convergence or non-convergence (Ferreira and van Aarde 1997; Davis et al. 2003; Wassenaar et al. 2005). The predicted time scales for compositional convergence with old-growth forest also varied greatly between biota (Wassenaar et al. 2005) and there was aberrant variation in assemblage structure in some regenerating patches (Wassenaar et al. 2007). Despite this variability, Grainger and van Aarde (2012a) concluded that succession does provide a valid explanation for the restoration of forest plant assemblages. However, the spatial configuration of the landscape is also

influential as it comprises a mosaic of patches of differing ages, sizes, and degrees of isolation so that limitations on dispersal and habitat suitability may result in the failure of some forest specialist species to colonize and establish in small and/or distant patches (Grainger et al. 2011).

The present study re-examines successional patterns shown by dung beetles in 2010 and compares them with the findings recorded 10 years earlier (Davis et al. 2003). Our previous study showed a partial progression of species composition towards convergence with that in old-growth dune forest, which is negated by the divergence of species abundance structure after an initial strong trend towards convergence. In view of these conflicting results, the 2010 study determines if the post-mining vegetation produces similar responses in assemblage structure to those recorded during 2000. Furthermore, the present study analyzes structural composition of assemblages, identifies points of temporal transition between dominant faunal components, and investigates the degree of structural variation between habitat patches. It also re-examines if these patterns are consistent with the successional age of vegetation and how they are influenced by the development of dense shade cover, its subsequent decline, and the associated microclimatic changes. Given that microclimate was again found to drive dung beetle assemblage structure, it was concluded that despite non-convergent trajectories of similarity between forest and regenerating vegetation, a typical forest assemblage could still be re-established if secondary forest is the end point that follows the current structural changes in late chronosequence vegetation (Grainger and van Aarde 2012b).

Methods

Study area

In both 2000 and 2010, sampling was restricted to a narrow 31 km long coastal strip of dunes north of the port of Richards Bay (28°48'S 32°05'E), KwaZulu-Natal, South Africa. Some 17 km (28°36'24"–28°43'30"S; 32°10'56"–32°18'24"E) of this area comprised rehabilitating vegetation patches of known age representing consecutive windows in chronosequential time that pass from grassland to shrubland to woodland with all woody cover dominated by *Acacia karroo* (Ferreira and van Aarde 1997; Appendix 1, 2). The old-growth Sokhulu Forest (28°30'34"–28°31'38"S; 32°23'33"E–32°23'42"E), used as a benchmark reference, is situated 12.5–14 km to the north of the nearest sampled part of the rehabilitating area. The exact age of Sokhulu Forest is unknown although aerial photographs show that it was present in 1937 (Weisser and Marques 1979).

In 2000, three study sites were selected in each of four forest patches (12 study sites) and in each of eight age

windows across a 23 year chronosequence of rehabilitating vegetation (24 study sites) (Davis et al. 2002; 2003). In the present 2010 survey, six original study sites in two surviving forest patches were re-sampled (Sokhulu Forest) whereas in 10 age windows across a 33 year chronosequence of rehabilitating vegetation, 18 original study sites were re-sampled (Windows 2–6), six original sites had to be relocated due to re-mining (Window 1) or lack of access (Window 7), and six new, younger sites were added (Windows 9, 10) (Appendix 1).

Sampling and pitfall trap emplacement

For purposes of comparison, the present survey followed a similar design to that used in 2000 (Davis et al. 2002; 2003). The 2010 survey sampled dung beetles from 36 study sites in the two forest patches and ten age windows of rehabilitating vegetation, three study sites per window. As in 2000, five, 5 L pitfall traps were placed at each study site (top diameter: 20 cm; depth: 19 cm). Sampling was conducted over 48 h from January 21st till January 23rd 2010 and samples were collected at the end of each 24 h period. Traps were baited at circa 12 h intervals, with 200–250 mL composite baits of 50 % pig and 50 % cattle dung, which acted as surrogates for dung dropped by the indigenous mammal fauna (Rowe–Rowe 1994). This method provided 360 samples comprising five samples per study site per day and 30 per chronosequence age window or forest patch.

Compared to the earlier survey (Davis et al. 2002; 2003), trap emplacement was the same at all study sites and age windows except in the early succession where, in 2010, traps were placed along pathways cut into the edge of the dense shrubland (Window 9) or woodland (Window 7) rather than primarily in spaces between patches of dense shrubland as in 2000 (Windows 6y, 6o). Despite recommendations for a minimum between-trap distance of 50 m (Larsen and Forsyth 2005), traps were emplaced 10 m apart to be consistent with the methods used in 2000. However, no comparisons were made below the scale of study sites, which were a minimum of 0.11 km and a maximum of 0.96 km apart within each age window.

Microclimatic and vegetation data

Microclimate was measured in each of the 12 age windows or forest patches simultaneously with sampling. In eight windows, radiant temperature, relative humidity, background light intensity, and shade (ambient) air temperature were measured using Onset, Hobo H08-004-02 four channel data loggers that were mounted face up, 1 m above the soil surface, on support poles. In the two forest patches (Sokhulu Top and Base) and Windows 3 and 5, only

relative humidity and ambient temperature were measured using Onset, Hobo H08-007-02 data loggers. These loggers were also attached to support poles, 1 m above the soil surface.

Microclimatic measurements were made at a frequency of 90 s for all loggers. Mean daytime data (light intensity, radiant temperature) were calculated from 525 measurements made between 05h27 and 18h33, which were the first and last readings that registered background light intensity of >0 lux on day 1 in unshaded vegetation. Mean values for relative humidity and ambient temperature were based on 960 measurements recorded during each 24 h trapping period. Proportional shade cover offered by woody vegetation was estimated by eye at each study site except in Window 10, which lacked tall shrubs or trees.

Analysis of dung beetle successional patterns

Ordination was used to classify changes in faunal structure across the successional sere. The analysis was conducted on a 63 × 36 data matrix comprising the mean abundances/trap/day of 63 species at 36 study sites. This data matrix was square root transformed and converted to a 36 × 36 correlation matrix. As data for most of the 36 variables (30) did not deviate significantly from normal distributions (Kolmogorov–Smirnov tests), the matrix was subjected to Factor Analysis using Principal Components to extract factors (Statistica 10—StatSoft Inc 2011). A maximum of four factors was extractable.

As oblique factors are often difficult to interpret, a Hierarchical Analysis of Oblique Factors was conducted (Wherry 1984). Clusters of study sites were defined at the default factor score level of 0.7 and subjected to varimax-normalized factor rotation through clusters, which enhances patterns of high and low factor loadings, thus maximizing between-cluster separation. A 36 × 36 correlation matrix was created for rotated, oblique factor loadings and a second Factor Analysis was conducted to generate extended orthogonal factors. Correlations (r^2) between extended orthogonal and oblique factors were used to determine the proportion of unique character contributed by primary (P) extended factors within each cluster, and the proportion in common with other clusters, due to shared secondary (S) factors.

Parallels between dung beetle successional patterns, vegetation physiognomy, and microclimate

We used GLM one-way ANOVA to compare differences in factor loadings, species richness, abundance, percentage shade cover, and microclimatic factors between clusters. Tests on microclimatic factors were based on mean values

recorded during each hour of daylight (light intensity, radiant temperature) or during each hour over 24 h periods (humidity, ambient temperature).

Patterns of habitat association and biogeographical representation across the succession

Changes in dung beetle representation across the successional sere were determined with regard to their habitat associations and biogeographical distribution patterns. Bias of the species to either unshaded or shaded vegetation was classified using Non-Metric Multidimensional Scaling (NMDS). The data matrix comprised 63 species by their mean abundances/trap/day in each of the four ordination clusters. The results were used to determine proportional bias of species abundance to shade or non-shaded conditions in each cluster. With modifications, the biogeographical classification of Davis et al. (2002) was used to determine proportional bias within each cluster to three different biogeographical patterns. Modifications were necessary as, during the course of the 2010 study, several species formerly classified as Maputaland endemics (Davis et al. 2002) were discovered to have wider distributions, either northwards along the Mozambique coastline (e.g. *Sisyphus* sp. cited as *S. bornemisszanus* Endrödi), or in shaded localities to the south (e.g. *Neosisyphus mirabilis* (Arrow)) (see Appendices in Supplementary Information).

Comparing dung beetle successional patterns in 2000 and 2010

For dung beetle data recorded in both 2000 (Appendix in Davis et al. 2003) and 2010 (Appendix 3), paired comparisons were made between species composition and species abundance structure in each age window of regenerating vegetation and each of two forest patches. Species composition was compared using the percentage disagreement measure of distance (Statsoft Inc 2011): 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 window and absent from the other. The results are expressed as percentage similarity $(100 - \text{distance } [x, y])$. Species abundance structure was compared using the Steinhaus similarity index (Legendre and Legendre 1983): $S = 2W / (A + B)$, in which W is the sum of the smaller numbers in pairs of species abundance data converted to decimal proportions for each window and in which $A (=1)$ and $B (=1)$ are the total proportional density of the two windows $(=2)$. The results are expressed as percentage similarity $(S \times 100)$. These paired comparisons were plotted in chronological order to test for similarity in patterns between windows of similar age in 2000 and 2010.

Results

Vegetational changes during succession

Figure 1 summarizes the post-mining successional changes in shade cover offered by woody vegetation at sampling sites. Within a few years, the unshaded grassland of the youngest sites gave way to a dense shrubland cover and then a dense woodland cover, both providing strong shade. Shade cover declined somewhat as the shrubs grew into trees, trunk density thinned, and the canopies of surviving trees expanded over the open understorey. At some sites >25 years old, shade cover became much reduced by tree fall exposing the open shrubland of the understorey. These vegetational changes are described in more detail in Appendix 2.

Ordination and faunal successional patterns

The ordination of species abundance patterns (63 species, 50,606 individuals) classified the study sites into a maximum of four different clusters (Table 1, Fig. 2). These clusters accounted for 91.8 % of overall variance and represented four different structural patterns that occur in chronosequence although there is temporal overlap and uneven progressions, suggesting some differences in structure between habitat patches (Fig. 3). Each comprised a proportion of unique faunal structure (P1, P2, P3 or P4) and a greater or lesser proportion of two shared faunal influences that either increased (S2) or decreased (S1) from shaded to less shaded vegetation types (Table 2). Greatest unique faunal structure occurred at the endpoints in the unshaded vegetation of the earliest succession (P1) and the oldest shaded vegetation in natural forest (P3), with the intervening successional sere dominated by shared faunal influences (Table 2).

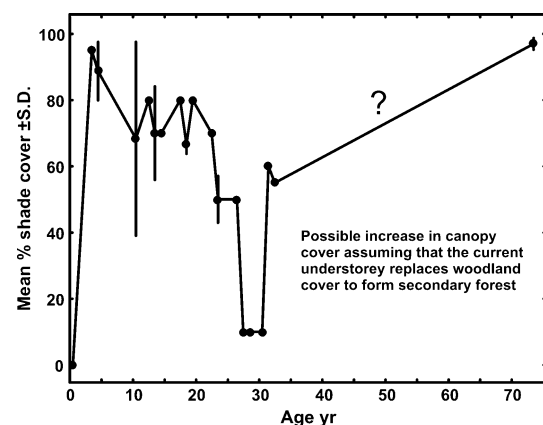


Fig. 1 Percentage shade cover offered by woody vegetation across the 33 year chronosequence and in natural forest

Table 1 Ordination factor loadings for clusters of study sites with similar dung beetle assemblage structure and GLM one-way ANOVA results for between and within cluster comparisons

	Mean factor loadings ± S.D. (ranked in successional sequence)				F	df
	Factor 2	Factor 4	Factor 1	Factor 3		
Cluster 2	0.902 ± 0.025^a	0.132 ± 0.163 ^b	0.085 ± 0.027 ^{bc}	−0.060 ± 0.034 ^c	115.812***	F _{3,13}
Cluster 4	0.241 ± 0.219 ^b	0.748 ± 0.062^a	0.407 ± 0.158 ^b	0.231 ± 0.158 ^b	18.361***	F _{3,28}
Cluster 1	0.086 ± 0.088 ^c	0.332 ± 0.131 ^b	0.847 ± 0.090^a	0.251 ± 0.093 ^b	155.087***	F _{3,56}
Cluster 3	−0.063 ± 0.038 ^c	0.231 ± 0.125 ^b	0.290 ± 0.109 ^b	0.870 ± 0.083^a	101.339***	F _{3,20}
Cluster 2	a	c	c	c		
Cluster 4	b	a	b	b		
Cluster 1	c	b	a	b		
Cluster 3	c	bc	b	a		
F _{3,29}	55.347***	34.017***	75.942***	73.179***		

*** P < 0.001. Values followed by a different letter differed significantly along rows (between factor within cluster comparisons—upper table) or along columns (between cluster comparisons—lower table) (Tukey's HSD, P < 0.05)

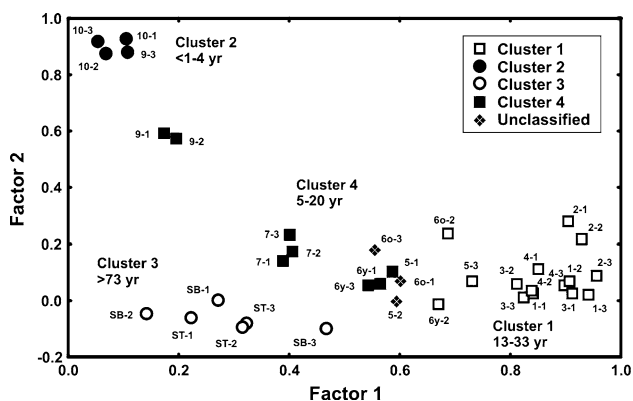


Fig. 2 Ordination plot showing the relative distance between data points representing dung beetle species abundance structure at 36 study sites in 12 vegetation age windows. In sequence, data point labels represent the window identifier (rehabilitating vegetation: 10-1; Sokhulu Forest: ST, SB) and study site number (1–3)

GLM ANOVA tests on ordination loadings suggest that the clusters were well defined (Table 1). All study sites of Window 10 (<1 year—Cluster 2), Window 7 (10–11 years—Cluster 4), Windows 4–1 (18–33 years—Cluster 1), and Sokhulu Forest (>73 years—Cluster 3) were placed within single clusters (Fig. 2). Early successional seres of intermediate age (Window 9—4–5 years) were classified in either Cluster 2 or 4. Later succession seres of intermediate age (Windows 6y, 6o, 5—12–20 years) were classified in Clusters 4 or 1, or remained unclassified owing to lack of dominance in loadings along any one factor (Factor 2: 0.081 ± 0.093; Factor 4: 0.604 ± 0.032; Factor 1: 0.585 ± 0.025; Factor 3: 0.370 ± 0.063). Greatest dominance of loadings along factors occurred within windows for which all study sites were classified in the same cluster (Fig. 3).

Cluster 2 was characteristic of unshaded, herbaceous vegetation (<1 years) with minor overlap into the youngest

shrubland patch (3–4 years) (Fig. 2). Coefficients of determination (Table 2) suggest high proportions of unique (P4) and shared elements characteristic of open vegetation (S2). Shared fauna characteristic of shaded vegetation (S1) was poorly represented.

Cluster 4 represented various shrubland and early to mid-successional woodland sites (5–20 years) (Fig. 2). Proportional variation defined by coefficients of determination (Table 2), suggest limited unique faunal composition (P2). However, there was relatively strong representation by shared elements characteristic of shaded vegetation (S1), particularly at woodland sites (>10 years) where Factor 1 loadings were higher. There was also appreciable representation by shared elements characteristic of open vegetation (S2), particularly at shrubland sites (4–5 years) where Factor 2 loadings were higher (Fig. 3).

Cluster 1 comprised closed to open canopy woodland (13–33 years), whereas Cluster 3 comprised the Sokhulu Forest (>73 years) (Fig. 2). Proportional variation defined by coefficients of determination, suggest limited unique faunal composition (P1) or appreciable unique faunal composition (P3), respectively (Table 2). However, both clusters included high proportions of shared faunal elements typical of shaded vegetation (S1) and poor representation of those characteristic of unshaded vegetation (S2). Despite the further opening of the late succession woodland canopy at sites >26 years, only two (Window 2: sites 1, 2) showed greater proximity to dominant faunal structure at unshaded sites (Factor 2) and greater distance from that at forest sites (Factor 3) (Fig. 3).

Parallels between successional patterns in dung beetles, vegetation physiognomy, and microclimate

The clusters defined by ordination showed clear trends in dung beetle species richness and abundance that paralleled

Fig. 3 Patterns of dung beetle assemblage structure across the vegetation chronosequence to natural forest defined by ordination factor loadings. Data points are coded according to the four clusters defined in Fig. 2. As far as possible, data points are plotted in chronosequence from Windows 10-1 to Sokhulu Top (ST) to Sokhulu Base (SB). Within windows, sites are plotted in the order: Sites 1, 2, and 3

changes in shade cover and microclimate (Table 3). Species richness showed a significant bimodal trend of high values in the less shaded vegetation of the early and late chronosequence (Clusters 2 and 1) and lower values in the more strongly shaded vegetation of the intermediate chronosequence and benchmark forest (Clusters 4 and 3). Abundance showed a significant unimodal trend with values in the late chronosequence (Cluster 1) much higher than those in all other clusters. Differences in light intensity and temperature paralleled variation in shade from woody vegetation. They were highest in the unshaded early chronosequence (Cluster 2), next highest in the moderately shaded late chronosequence (Cluster 1), much or somewhat lower in the intermediate chronosequence (Cluster 4), and lowest in the benchmark forest (Cluster 3). Humidity was the exception in that the significantly highest and lowest values were recorded in the strongly shaded natural forest and strongly shaded intermediate chronosequence, with equally high values in the unshaded early and moderately to poorly shaded, late chronosequence.

Patterns of habitat association and biogeographical representation across the succession

Habitat association and biogeographical affiliation are shown by Fig. 4. Species with a bias to less shaded habitat show negative loadings along Dimension 1 and those with a bias to more shaded habitat show positive loadings along Dimension 1. Clear changes in habitat bias and biogeographical composition occurred across the successional sere (Fig. 4, Table 4).

There were similar numbers of non-shade (29) and shade-associated species (34) (Fig. 4). However, non-shade association was dominated by widespread species (19) and far outnumbered East Coastal (8) and Maputaland endemics (2). By contrast, shade associated species showed similar numbers of widespread (16) or Maputaland (12) endemics and fewer East Coastal species (6). Proportional representation of widespread species was comparatively high in chronosequence clusters (C1, C2, C4) but extremely low in the forest cluster (C3). Although proportional representation of Maputaland endemics increased in ranked clusters across the successional sere, it remained similar for the East Coastal species.

In terms of abundance, non-shade species outnumbered shade species by two to one in primarily unshaded early

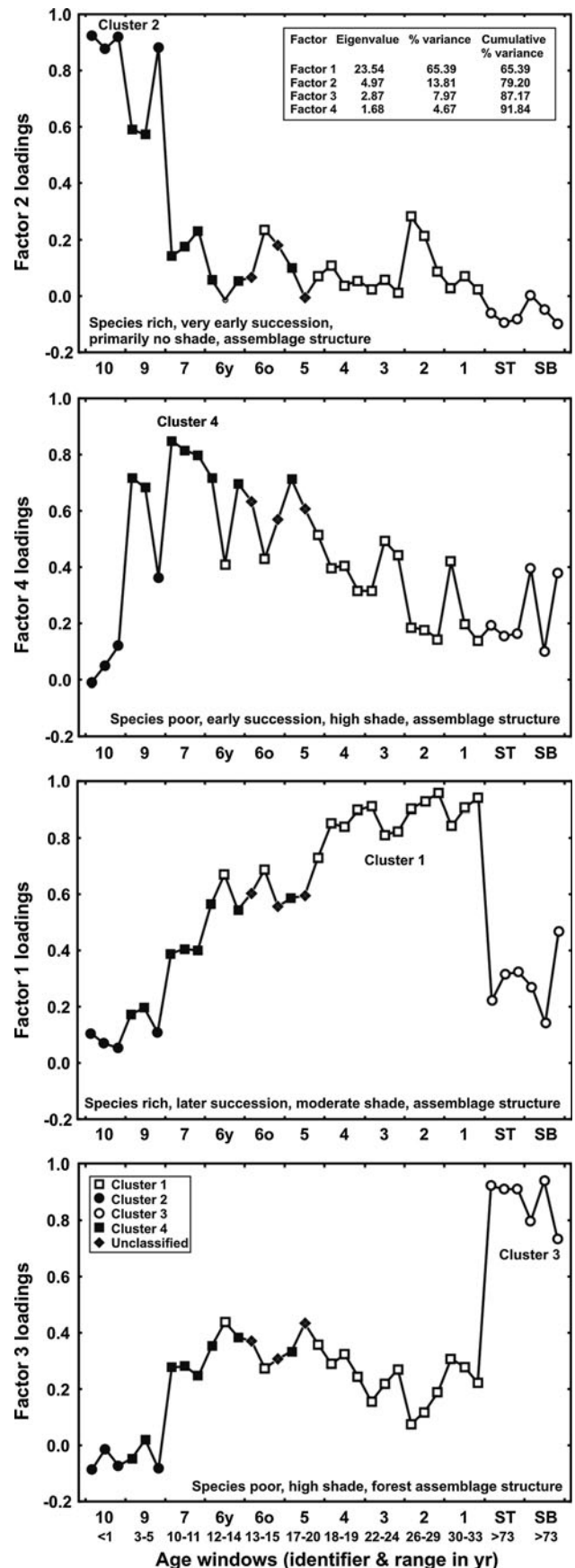


Table 2 Correlations of variable oblique factors with secondary (S) and primary (P) extended orthogonal factors (Figs 2, 3) ranked in chronological sequence across the succession (*Pearson's r and Coefficient of Determination (r^2))

Extended Factors	Correlation statistics, r (r^2)* Oblique factors (clusters)			
	Cluster 2 Grass/shrub ^a <1–4 years	Cluster 4 Shrub/wood ^b 5–20 years	Cluster 1 Open wood ^c 13–33 years	Cluster 3 Shaded forest >73 years
S1	0.05 (0.003)	0.75 (0.57)	0.84 (0.70)	0.77 (0.59)
S2	0.65 (0.42)	0.50 (0.25)	0.27 (0.07)	–0.13 (0.02)
P2	0.76 (0.57)	0	0	0
P4	0	0.42 (0.18)	0	0
P1	0	0	0.48 (0.23)	0
P3	0	0	0	0.62 (0.39)

^a Three, unshaded, grassland sites and one, 1.3–2 m tall, shrubland site

^b Dense, strongly shaded

^c Open herbaceous to shrubland understorey and moderate shade to much reduced shade through tree fall

Table 3 Mean species richness and abundance for clusters of dung beetle assemblages defined by ordination (Fig. 2) with mean values for associated vegetative shade cover and microclimatic measurements derived from hourly means

Variables	Mean ± S.D.				GLM ANOVA $F_{3,29}$
	Cluster 2 Grass/shrub ¹ <1–4 years	Cluster 4 Shrub/wood ¹ 5–20 years	Cluster 1 Open wood ¹ 13–33 years	Cluster 3 Shaded forest >73 year	
Species richness/site	25.0 ± 4.9 ^a	14.3 ± 4.2 ^b	24.7 ± 5.2 ^a	10.3 ± 2.0 ^b	21.971***
Abundance/trap/day	34.2 ± 7.0 ^b	39.4 ± 23.9 ^b	262.2 ± 110.7 ^a	42.7 ± 21.4 ^b	22.088***
% shade or canopy cover	23.8 ± 47.5 ^b	77.8 ± 18.2 ^{ac}	53.0 ± 24.3 ^{bc}	97.0 ± 1.8 ^a	9.085***
<i>Data during daylight</i>					$F_{2,179}$
Radiant temperature, °C	32.8 ± 6.8 ^a	26.4 ± 3.9 ^b	30.8 ± 7.7 ^a	–	14.156***
Light intensity, lux	43.4 ± 9.0 ^a	18.9 ± 15.6 ^c	29.7 ± 22.4 ^b	–	19.088***
<i>24 h data</i>					$F_{3,535}$
Ambient temperature, °C	25.2 ± 3.5 ^a	24.1 ± 2.7 ^a	24.6 ± 3.5 ^a	23.7 ± 1.6 ^b	3.310*
% humidity	79.8 ± 26.1 ^b	60.0 ± 25.5 ^c	86.7 ± 20.3 ^b	97.7 ± 4.6 ^a	77.649***

* $P < 0.05$, *** $P < 0.001$; along each row, values followed by a different letter differed significantly, Tukey's HSD

¹ See notes under Table 2

Microclimatic data:- Cluster 2: site 10-1; Cluster 4: sites 9-1, 7-1, 6y-1; Cluster 1: sites 6o-2, 5-3, 3-3, 2-2, 1-3; Cluster 3: sites ST3, SB3

Fig. 4 Ordination plot showing the distances between 63 data points representing dung beetle species abundance distributions between four ordination factors (Appendix 3). The corner table shows the percentage vegetation bias and biogeographical compositions of species in different clusters (C1–C4) (biogeographical classification from Davis et al. (2002) with minor modifications: *m* Maputaland, *ec* East Coastal, *w* widespread distributional bias) (key to species code numbers in Supplementary data, Appendix 3)

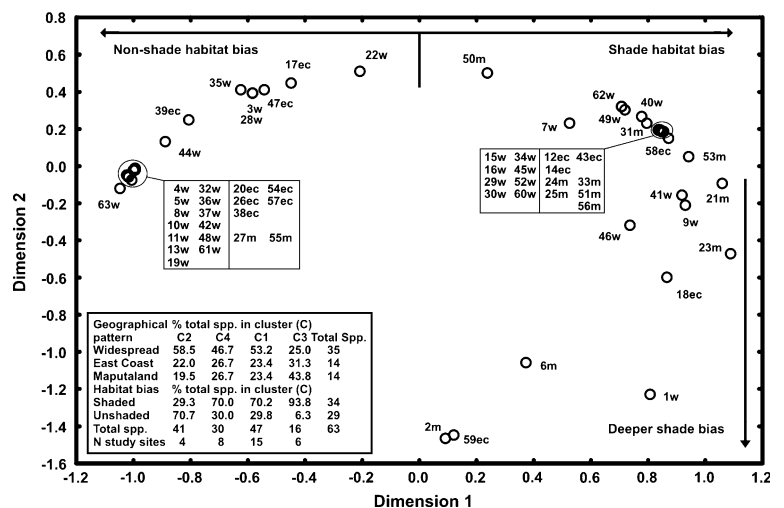


Table 4 Proportional biogeographical composition and habitat bias of ordination clusters (Fig. 2) in terms of abundance and results of GLM one-way ANOVA on square root-transformed data

Distributional pattern	% abundance/study site \pm S.D.				$F_{3, 29}$
	Cluster 2 Grass/shrub ¹ <1–4 years	Cluster 4 Shrub/wood ¹ 5–20 years	Cluster 1 Open wood ¹ 13–33 years	Cluster 3 Shaded forest >73 years	
<i>Biogeographical</i>					
Widespread	31.3 \pm 5.6 ^a	8.9 \pm 4.9 ^b	15.2 \pm 7.9 ^b	1.4 \pm 1.6 ^c	24.493***
East Coastal	59.9 \pm 5.0 ^a	54.9 \pm 13.7 ^a	20.3 \pm 8.3 ^b	39.3 \pm 13.9 ^a	23.427***
Maputaland	8.8 \pm 4.4 ^c	36.3 \pm 17.9 ^b	64.5 \pm 9.9 ^a	59.3 \pm 13.1 ^a	30.617***
<i>Habitat bias</i>					
Shade	30.8 \pm 12.2 ^b	93.3 \pm 9.8 ^a	98.1 \pm 2.6 ^a	99.9 \pm 0.1 ^a	114.600***
Non-shade	69.2 \pm 12.2 ^a	6.7 \pm 9.8 ^b	1.9 \pm 2.6 ^b	0.1 \pm 0.1 ^b	114.600***

*** $P < 0.001$; along each row, values followed by a different letter differed significantly, Tukey's HSD

¹ See notes under Table 2

successional stages (Cluster 2) (Table 4). By contrast, shade species showed extreme dominance in clusters of later successional stages and the benchmark forest. Proportional abundance of Maputaland endemics increased across the ranked clusters for the successional sere, whereas that of East Coastal species showed a shallow decline, with an appreciably lower value in the late succession woodland (Cluster 1). Proportional abundance of widespread species also declined but followed a bimodal pattern with peaks in the least shaded early and late succession (Clusters 2 and 1).

Similarities between dung beetle faunas of rehabilitating vegetation and natural forest in 2000 and 2010

Paired comparisons were made between dung beetle faunas (species composition (spp.), abundance (ab.)) in benchmark forest and each age window of rehabilitating vegetation in both 2000 and 2010 (Fig. 5). On both occasions, early successional faunas of grassland and low canopy shrubland showed very low similarity to forest faunas followed by increase to moderate (spp. in 2000, ab. in 2010) or high similarity (spp. in 2010, ab. in 2000) in shaded shrub/woodland. Late successional patterns in relatively less shaded woodland were variable leveling out (2000 spp., 2010 ab.), declining and then leveling out (2010 spp.), or showing a steep decline (2000 ab.). Thus, overall, similarities (Fig. 5), suggest that early succession-associated patterns are age specific, irrespective of the year of study, although later successional patterns were inconsistent, both between years of study and between species composition and abundance.

Discussion

Successional processes and ecological restoration

Over time following complete clearance of vegetation, primary successional processes are considered to lead to restoration of the original ecotype (Townsend 2007; Grainger and van Aarde 2012a). However, the lengthy time-scales predicted for the full restoration of forest (Osho 1996; Hughes et al. 1999; Aide et al. 2000; Wassenaar et al. 2005; Liebsch et al. 2008) suggest that, after 33 years, the chronosequence at Richards Bay remains at an early successional stage. Following turnover from grassland to densely shaded woodland to less shaded open woodland, there is currently extensive canopy loss due to tree fall (Grainger and van Aarde 2012b), which is consistent with the known longevity of 30–40 years for *Acacia karroo* (Gourlay et al. 1996) that dominates the early succession. A general pattern of primary succession in forest restoration in the Neotropics involves a three stage turnover from grassland to a forest canopy dominated by early successional trees unable to germinate under shade, to a forest canopy dominated by later successional trees able to germinate under the shade of the early succession (Guariguata and Ostertag 2001). In view of this observation, the existence of both convergent and non-convergent trajectories of similarity between forest and age windows of regenerating vegetation shown by various taxa at our study site (Wassenaar et al. 2005), does not necessarily preclude the restoration of dune forest. Similar results for invertebrates of a mined area in Western Australia that track vegetation types, either towards or away from convergence with assemblages in unmined areas (Majer et al. 2007), suggest that such variable trends are a widespread phenomenon.

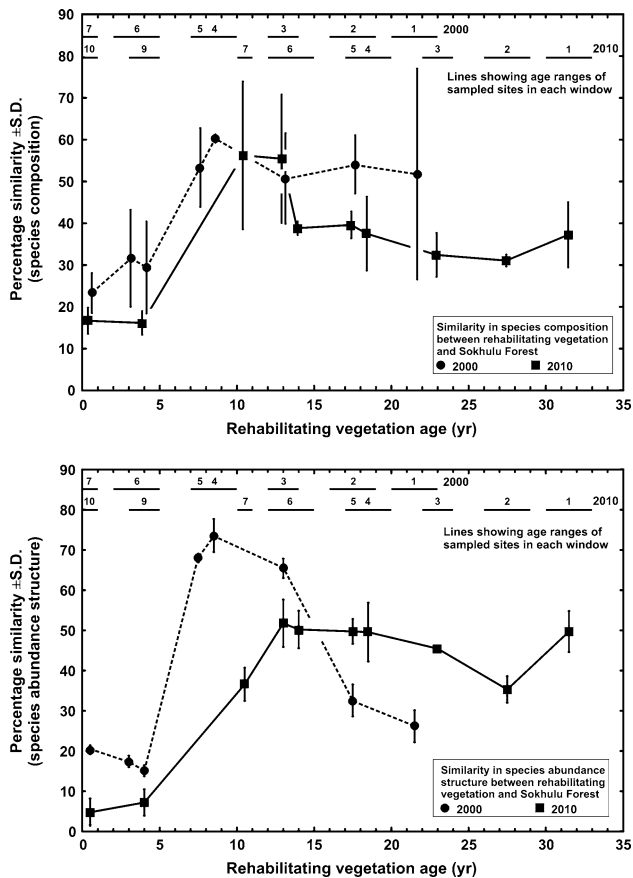


Fig. 5 Similarity of patterns between 2000 and 2010 described by paired comparisons between dung beetle assemblages of age windows in rehabilitating vegetation and each of two reference points in Sokhulu natural forest plotted in chronosequence

Potential drivers of dung beetle successional patterns at Richards Bay

From work elsewhere we know that soil texture and vegetation cover (Nealis 1977; Cambefort 1982; Davis 1996), dung type (Davis 1994; Tshikae et al. 2008), dung density (Lobo et al. 2006) and gross amounts available (Lumaret et al. 1992) influence the composition and abundance of dung beetle assemblages. In our 2000 (Davis et al. 2003) and 2010 studies, cross-chronosequential turnover in dung beetle assemblages on deep sands was especially consistent with progressive differences in vegetation structure and their associated microclimates. Trophic variables were probably of lesser importance as coastal dune forest is not ideally suited for mammalian herbivores. However, mammalian dung is available from monkeys, small antelope, and cattle that are illegally herded into the new growth vegetation.

Recovery of forest species at Richards Bay

All dung beetle species recorded in old-growth dune forest were also recorded within regenerating vegetation with a

shaded understorey, bar for one uncommon *Onthophagus* species, and *Gyronotus carinatus*, which belongs to a genus with ancient ancestry (Sole and Scholtz 2010). This flightless Maputaland endemic was also absent from a relatively isolated, probably formerly disturbed, forest patch studied by Davis et al. (2002; 2003). Due to flightlessness, it may not be able to re-colonize rehabilitated sites if they are isolated from an undisturbed source forest by disturbed terrain.

Comparisons between cross-chronosequence patterns in 2000 and 2010

Despite progressive thinning of the 22–33 year *Acacia* woodland canopy due to tree fall and the creation of gaps in the canopy (Grainger and van Aarde 2012b), largely similar results were generated by both the 2000 (Davis et al. 2003) and 2010 studies on dung beetle assemblages across, respectively, 23 year and 33 year chronosequences of regenerating vegetation. Although overall similarity in patterns reflects similar responses to similar microclimate in vegetation windows of similar age, there were differences in population structure that were possibly partly related to inter-annual differences in weather conditions. During sampling, beetles active under cooler conditions were more favoured in 2010 (mean ambient temperatures in Window 10: Jan. 21–22 = 23.2 °C, Jan. 22–23 = 26.8 °C) whereas beetles active under warmer conditions were more favoured in 2000 (mean ambient temperatures at Richards Bay: Jan. 25 = 31.7 °C, Jan. 26 = 26.1 °C, Jan. 27 = 27.8 °C). As the local distribution of dung beetles varies with the location of dung and the amounts available (Lobo et al. 2006), their proximity to pitfalls and their likelihood of attraction could also drive differences in population structure between 2000 and 2010.

However, patterns of species richness and abundance were generally comparable. In 2010, species richness followed a bimodal pattern from high to low to high richness across the chronosequence ending in low species richness in forest. This paralleled the bimodal changes in relative shade cover across the successional sere from unshaded to strongly shaded to less shaded chronosequence vegetation to strongly shaded dune forest. By contrast, abundance showed a unimodal pattern from low to high values across the 33 year chronosequence followed by a decrease to low values in natural forest. In 2000, both species richness and abundance followed a bimodal pattern (Davis et al. 2003) although it was less clearly defined than in 2010.

On each occasion, three groups of age windows were defined from dung beetle assemblage structure, representing early succession unshaded vegetation, early succession dense shrub-woodland, and later succession open woodland, all of which differed to structure in a fourth age window represented by natural forest. These four groupings of assemblages result from differences in proportional

contribution by four faunal components demonstrated by analysis of the 2010 data. Turnover between dominant components mostly overlapped in time because of environmental patchiness across the chronosequence represented by uneven linear progression between values (Fig. 3). In both 2000 and 2010, changes in dung beetle assemblages were correlated (Davis et al. 2003) or consistent with progressive structural changes in regenerating vegetation and the associated significant changes in microclimate (Davis et al. 2002; Table 3).

There is an initial steep increase in similarity of dung beetle assemblages in chronosequence age windows to those in forest as unshaded vegetation gives way to dense shade but this is followed by declining shade. As natural forest is characterized by dense shade, this decline would be responsible for the plateaux or declines in the trajectories of lines connecting chronosequential values for similarity between dung beetle assemblages of forest and age windows of regenerating vegetation that were variously recorded in 2000 and 2010. However, the lack of a uniform increase in shade cover over time is not necessarily evidential that neither forest nor forest dung beetle faunas will be re-established in the future given that time periods of 70 to >100 years have been predicted for recovery in forest ecosystems (Osho 1996; Hughes et al. 1999; Liebsch et al. 2008). Currently, tree fall in the oldest age windows of *Acacia* woodland is resulting in further reductions in shade-cover. Whilst gaps within age windows from 22 to 33 years are increasing in size, they also show greater stem density of forest tree saplings than under the surviving *Acacia* canopy (Grainger and van Aarde 2012b). It remains to be seen what future vegetation structure will result from this continuing succession.

Patterns recorded during the 2010 study are probably a better reflection of dung beetle responses to early successional changes than in 2000 as the pitfalls were all placed within the dominant shrubland vegetation (windows 7, 9) rather than partly within shrubland and partly in intervening spaces (windows 6y, 6o, cited as ~3 years and ~6 years old shrubland in 2000) (Davis et al. 2003). However, irrespective of trap placement, early successional faunas showed low similarity to those in natural dune forest in both 2000 and 2010. Thereafter, the rapid re-establishment of dense shaded vegetation drove a relatively steep increase in compositional similarity with the dung beetle faunas of natural forest, similar to patterns observed for dung beetle assemblages in fragmented Neotropical forest (Quintero and Roslin 2005). The late successional decline in shade cover that variously led to plateaux or declines in faunal similarity to forest assemblages may be due to between-occasion differences in beetle population dynamics. In 2000, decline in species abundance similarity resulted primarily from high numbers of a single widespread species, *Onthophagus vinctus*, in the

two oldest age windows. In 2010, relatively fewer *O. vinctus* were recorded in late successional windows and the overall pattern of similarity to forest hardly declined at all. However, in 2010, tree fall in window 2 resulted in extensive exposure of the understorey, which would increase light intensity. This may be responsible for a slight reduction in similarity between the faunas of Window 2 and densely-shaded, old-growth forest. Even so, ordination loadings for the dung beetle assemblages of these gaps in the canopy (window 2, sites 1, 2) show only limited increase in proximity to those characteristic of unshaded habitats (Factor 2) and only limited increase in distance from those of old-growth forest (Factor 3). Despite the increased abundance of some open area, dung beetle species in these gaps (e.g. *Mimonthophagus ambiguus*, *Onthophagus ursinus*), the dense understorey shrubland may provide sufficient shade to exclude most. This minor increase in open area dung beetle species may prove to be a transitory response to decreased shade cover if the canopy is restored by growth of forest tree saplings occupying the gaps.

Comparisons between habitat and biogeographical associations in 2000 and 2010

Biogeographical composition in different habitats were largely comparable in 2000 (60 spp.) and 2010 (63 spp.). On both occasions, species abundance representation of Maputaland endemics increased across the chronosequence to natural forest, decreased in east coastal taxa, and showed a bimodal pattern in widespread species with peaks in the unshaded early succession and the moderately shaded later succession (Davis et al. 2002; Table 4). Species patterns were only analyzed in this manner in 2010, and showed essentially similar trends except for east coastal taxa which were equally represented across the entire chronosequence. After the re-establishment of woody vegetation, there was a strong turnover from species of unshaded habitat to those characteristic of shaded habitat with an increasing decline in both species representation and abundance of open area taxa towards natural forest. Assemblages from strongly shaded sites with dense *Acacia* woodland or dense canopy, old-growth forest are both characterized by low species richness and abundance. However, as the classification currently stands, Maputaland endemics are better represented than east coastal species in the cooler forest that is highly humid with moist surface litter. By contrast, east coastal species are better represented than Maputaland endemics in the warmer, early-succession shrub-woodland that is characterized by low humidity and little surface litter. The warmest and least shaded early succession grassland and late succession open woodland showed the greatest concentrations of widespread species.

Conclusions

The local species pool at our study site north of Richards Bay comprises species with widespread, east coastal or endemic Maputaland distributions. Occurrence and relative abundance of these species in dung beetle assemblages varies according to their responses to microclimate (light intensity, temperature, humidity). Changes in microclimate and dung beetle assemblage structure are induced by differing vegetation structure with increasing age across the chronosequence. Thus, the trajectory of similarity to forest fauna does not proceed as a gradual increase but rather as an increase followed by a decrease that is consistent with transitions from unshaded grassland to dense and deeply shaded shrub/woodland, to less shaded open *Acacia* woodland, to exposure of the shrubland understorey after the fall of senescent *Acacia* trees. This non-convergent trajectory does not exclude the re-establishment of a typical dune forest fauna, as most forest species are also present in the woody regenerating vegetation. Therefore, recovery of forest species abundance structure would be dependent only on the re-establishment of forest microclimate. It remains to be seen if young forest trees in the exposed shrubland understorey grow to establish secondary forest.

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