Chapter 3 Assessing the Restoration of Coastal Dune Topography after Mining

Introduction

Natural forces shape beach sediments into coastal dunes, some of which are colonised by region-specific dune vegetation. Coastal dunes vary in height, aspect, and slope that result in microclimatic variability and ultimately spatially heterogeneous habitats. For example, variability in incident light and ambient temperature (Tateno & Takeda 2003; Bennie et al. 2008; da Silva et al. 2008), water retention (e.g. Pachepsky et al. 2001; Arbel et al. 2005), as well as nutrient and mineral accumulation in the soil (Chen et al. 1997; Oliviera-Filho et al. 1998; Tateno & Takeda 2003; da Silva et al. 2008). Spatial heterogeneity of these variables may contribute to species turnover and hence diversity (Larkin et al. 2006). Habitat variability related to topographic heterogeneity may therefore improve colonisation opportunities for species.

The restoration of topography should thus precede restoration efforts that aim at the recovery of biological diversity (Weiss & Murphy 1990; Lubke & Avis 1999; Palik et al. 2000; Larkin et al. 2006). However, I could find no example where the landscape engineering of the topographic profile of any ecosystem had been evaluated as a restoration goal. I posit that the topography of coastal dune ecosystems is core to their multi-functionality and therefore assess the restoration of the topographic profile after mining.

In this study area, mining destroys the coastal dune forest vegetation and the topographic profile of dunes (van Aarde et al. 1996c). Reshaping the sand tailings after

mining forms part of the restoration programme and the resultant topographic profile had not been investigated until now. I used historical and recent remote sensing data to assess how closely the restored dunes match the topographic profile of the dunes before mining. Although the mining company does make efforts to rebuild the dunes, I expected the topographic profile (as characterized by the elevation, aspect and gradient of dune slopes) of post-mining dunes would be dissimilar from that of their pre-mining counterparts. Furthermore, fewer dunes would characterize the post-mining landscape and it was therefore expected that topographic heterogeneity would be reduced following mining and rehabilitation.

Methods

Study area

The study area consists of coastal sand dunes between 28°46' and 28°34' south. These parabolic-shaped dunes comprise porous, leached aeolian sand deposits left by a regressing Indian Ocean during the end of the last glacial maximum (Tinley 1985). These dunes run parallel to the shoreline and range in height between the Umlalazi River (80 m), southwest of the study area and the Umfolozi River (188 m) (Weisser & Marques 1979).

During mining, the dunes are collapsed ahead of the dredging pond where heavy minerals are extracted. After mining, sand tailings are stacked and bulldozed to resemble pre-mining topography, after which they are covered with a layer of topsoil salvaged from the mining face (van Aarde et al. 1996c).

Topographic data

Dune topography may be quantified or categorized at specific geographic locations according to the aspect, elevation, and gradient of slopes (Table 1). I used topographic layers from geographical surveys done during 1971 (pre-mining) and data products from a Light Detection and Ranging (LIDAR) mission conducted in September 2010 (post-mining). Using inverse-distance-weighting interpolation in ArcMap Desktop 9.3.1 (ESRI Inc., Redlands, California) (see Woolard and Colby 2002), I generated digital elevation models (DEMs) of matching extent and resolution (cell size) for the pre-mining (Figure 3-1a) and post-mining landscapes (Figure 3-1b). I used these to generate pre- and post-mining surface models of aspect and gradient using three-dimensional analyst tools in ArcGIS. I classified these models based on eight cardinal directions (aspect), seven elevation categories, and five gradient categories (see Table 3-1).

Table 3-1. Definitions of variables describing the topographic profile of coastal dunes

Variable		Definition and units	Explanatory variable categories
Dune position		The relative position on the dune face	Crest, slope, valley
Dune morphology	**Aspect**	The cardinal direction in which the dune slope faces	Eight cardinal directions: N, NE, E, SE, S, SW, W, NW
	Elevation	The height of the dune surface, measured in meters above sea level (m.a.s.l.).	Binned into seven height categories: 1 (0-20), 2 (21-40), 3 (41-60), 4 (61-80), 5 (81-100), 6 (101-120, 7 (>120 m.a.s.l.)
	Gradient	The angle of the dune slope, measured in degrees	Binned into four gradient categories: 1 (0-5), 2 (6-10), 3 (11-15), 4 (16-20), 5 (>20°)

Statistical analyses

To calculate topographic heterogeneity I used the Zonal Statistics tool of ArcGIS to calculate the area covered by each elevation category and then used Shannon's Diversity Index to estimate pre- and post-mining topographic heterogeneity for the study area (see Nichols et al. 1998). I also made this comparison for individual regenerating stands. I calculated diversity as the $\sum p_i \log p_i$ for each elevation class, where p_i is the proportion of the total area of the stand covered by elevation class *i*. A low diversity index indicates that a stand comprised little variability in elevation (low topographic heterogeneity), whilst a stand of similar size with more elevation classes will yield a high diversity index. A negative value for topographic heterogeneity (TH´) therefore suggests a reduction in topographic heterogeneity following mining.

To identify areas of change between pre- and post-mining dune morphology, I conducted an image differencing exercise, subtracting values of the post-mining DEM from that of the pre-mining (Figure 3-1c). I used GIS overlay procedures to sample dune morphological variables (aspect, elevation and gradient) at 161 geographically random locations (>100 m apart) from the pre- and post-mining datasets (Figure 3-1d). I calculated the frequency distributions of these random locations based on the eight aspect categories (cardinal directions), while the categories for elevation were widened to 25-m intervals (0-25, 26-50, 51-75, and >75 m.a.s.l.), and those for gradient to four categories (0-5, 6-10, 11-15, and > 15°) to avoid frequencies of less than five. I assessed differences in these pre- and post-mining frequency distributions using contingency table analyses for each feature of dune morphology. All statistical analyses were conducted in STATISTICA 10 (© 2011, Statsoft Inc., Tulsa, Oklahoma).
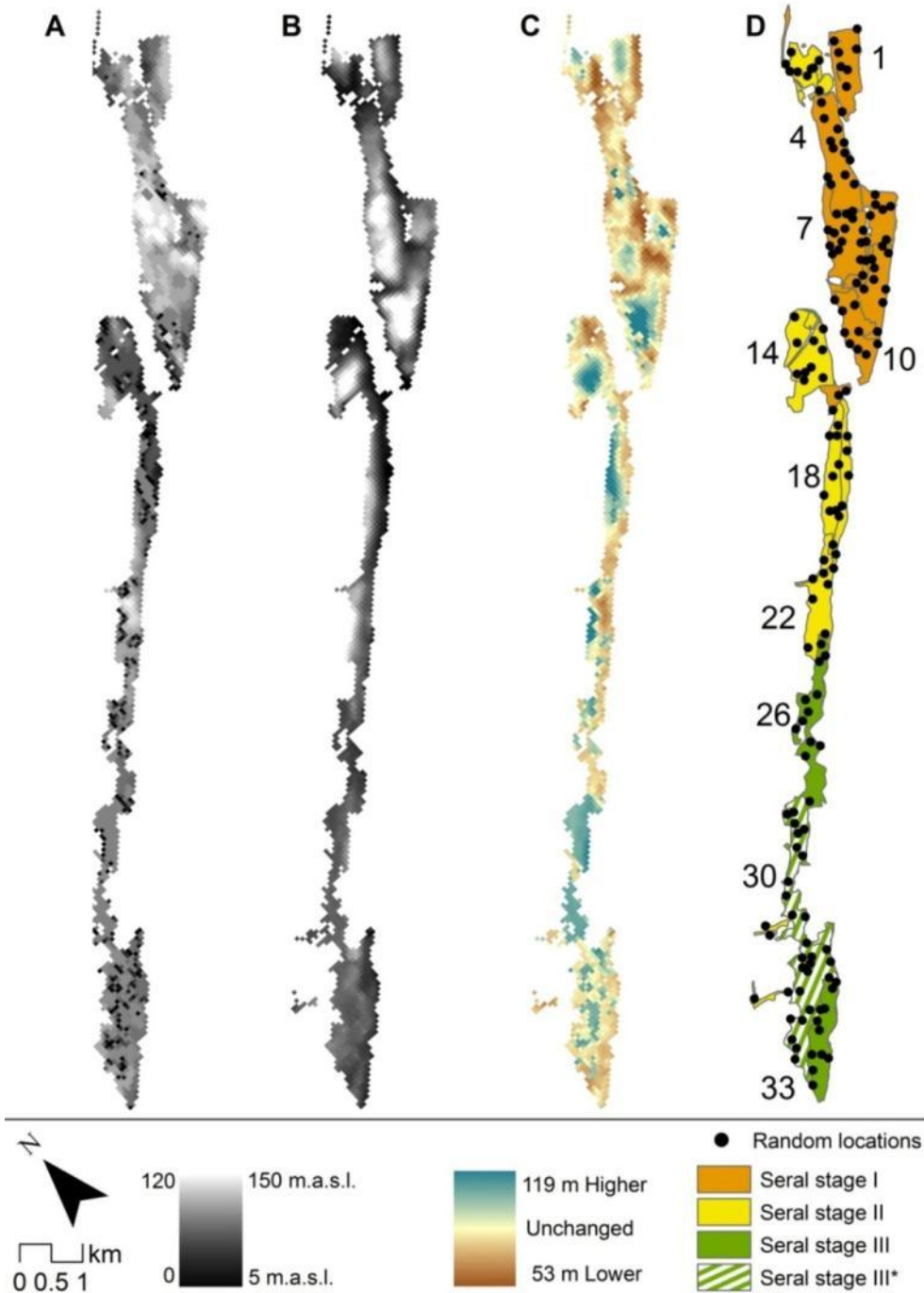
Figure 3-1. Digital elevation models of the study area prior to the start of mining (1971, A), and after mining and rehabilitation (2010, B). The difference in elevation between these two periods is indicated by C, where turquoise represents areas that were higher after mining than before mining, with the reverse true for areas in brown (see legend). The random locations used to sample dune morphology within the rehabilitating stands are shown in D, which also indicates the delineations of rehabilitating stands and their respective ages shown in years.

Results

Restored topographic heterogeneity was lower than pre-mining heterogeneity for the study site, but on an age-specific basis, five stands were less heterogeneous and five were more heterogeneous (Figure 3-2). However, cases where the topographic heterogeneity of stands was reduced after mining and rehabilitation were slightly more pronounced (max = -2.9) than those where heterogeneity had increased (max = 2.3).
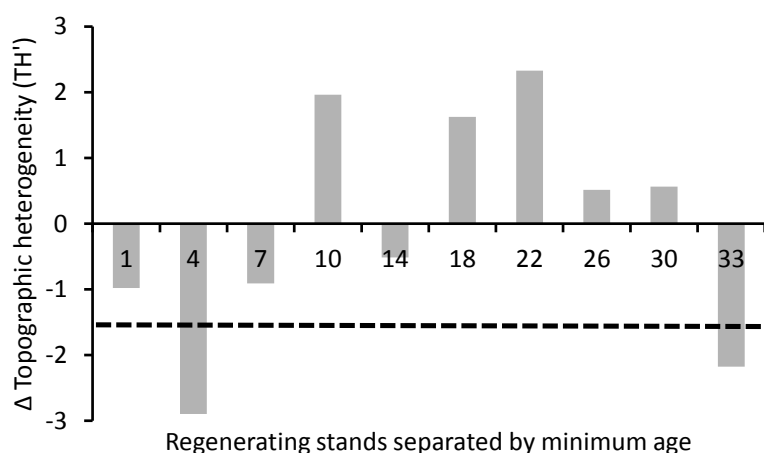

Figure 3-2. Change in topographic heterogeneity of age-specific rehabilitating stands calculated as the difference in Shannon's Diversity Index before mining (1971) and after topographic restoration (2010). Negative values therefore indicate a decrease, whilst positive values indicate an increase in topographic heterogeneity. The dashed line represents the change in topographic heterogeneity for the whole study site.

The morphology of dunes after restoration differed from that before mining and, as indicated by the frequency distributions of random locations recorded within categories of aspect, elevation and gradient before and after mining (contingency tables: $\chi^2 = 45.16$, $df = 7$, $p < 0.0001$, $\chi^2 = 84.12$, $df = 3$, $p < 0.0001$, and $\chi^2 = 24.69$, $df = 3$, $p < 0.0001$, respectively) (Figure 3-3). After mining, more of the random locations were

recorded on southeast- and north-facing slopes than before mining, though fewer fell on slopes facing all other aspects. There were also fewer random locations on elevations below 25 m, but more of the random locations were recorded on elevations of greater than 51 m after than before mining. Fewer random locations were recorded on slopes steeper than 15°, but there were more on gradients of between 0 and 10° after mining, than before mining.
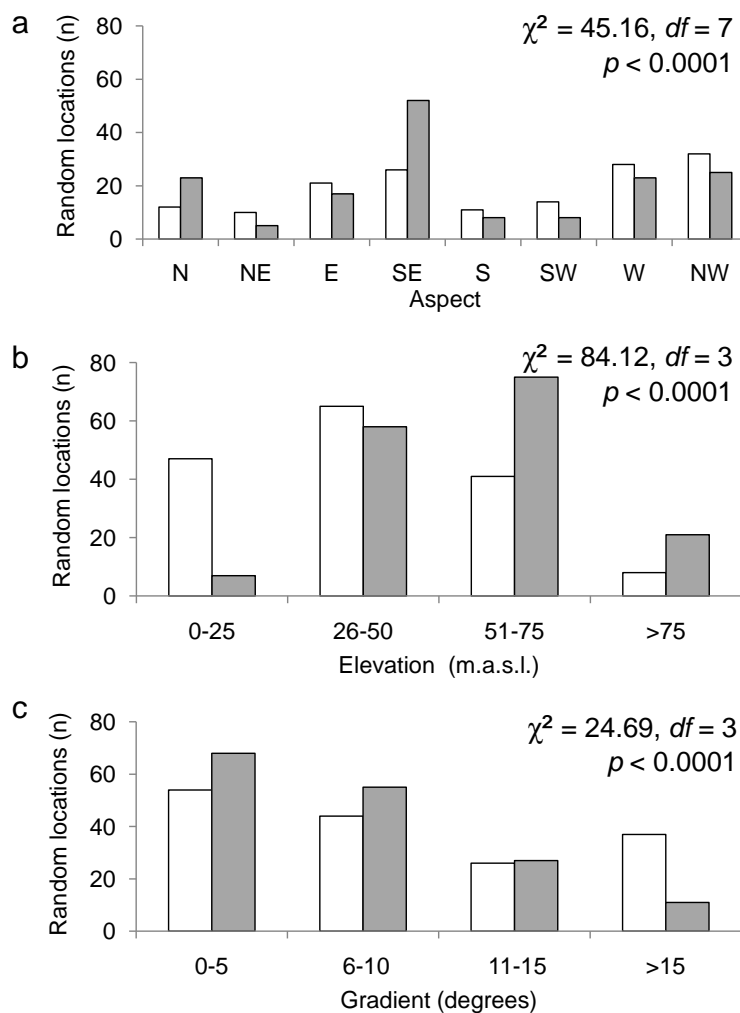

Figure 3-3. Frequency distributions of randomly placed locations that were used to sample aspect (a), elevation (b), and gradient (c) across rehabilitating stands of the study area before (1971, clear) and after (2010, shaded) mining

Discussion

Topography may have a fundamental role to play in restoration given its well-documented influence on ecological processes and therefore community composition (e.g. Weiss & Murphy 1990; Tateno & Takeda 2003; Larkin et al. 2006; Laurance et al. 2010). The association of the indigenous forests of this area with coastal dunes suggests that the topographic profile played a role in the establishment of these forests by sheltering them from prevailing winds and fires, as has been documented for forests elsewhere (see Geldenhuys 1994). Restoring the topographic profile may be an important step in the rehabilitation programme, as it essentially erases the historical context of these dunes.

In the study and in line with the expectations, there was a reduction in topographic heterogeneity across the study site and restored dunes were in places taller and their slopes somewhat gentler than prior to mining. This suggests that there were fewer dunes in the same area than before mining began. There are several logistical constraints to building dunes with mine tailings. For example, building more dunes in the same area will require steeper slopes; however, this increases the risk of dune slumping, while sand movement and increased run-off will hinder plant growth. These constraints could explain the post-mining reduction in topographic heterogeneity.

The morphology of sand dunes is related to topographic heterogeneity, and is known to influence the spatial heterogeneity of habitat conditions as a result of the modulation of wind, water, light and soil conditions in much the same way as for other topographically variable ecosystems (Oosting & Billings 1942; Martinez et al. 2001). For example, the aspect of slopes in relation to the prevailing wind direction or the sun, can

influence incident light and ambient temperatures (Tateno & Takeda 2003; Bennie et al. 2008; da Silva et al. 2008). Similarly, valleys may provide relatively moist micro-environments that are protected from the wind and sunlight relative to dune crests (Martinez et al. 2001). The topographic profile of restored dunes differed from that of the pre-mining landscape. Exceptions included large increases in the number of locations falling on north- and southeast-facing dunes and areas over 50 m.a.s.l., as well as decreases in relatively steep slopes (>15°) and low-lying areas (<25 m.a.s.l.). However, it is important to note that these comparisons were relatively strict as they are based on the same set of geographic locations that sampled dune morphological variables before and after mining and restoration. These changes therefore represent either a change in dune morphology, or the 'shift' of dunes across the landscape, or a combination of the two scenarios. The topographic profile has been shown elsewhere to influence biological diversity (Nichols et al. 1998; Martinez et al. 2001). Nevertheless, the implications of this increase in relatively warm and steep slopes requires further investigation by assessing the responses of biological communities, if any (see Chapter 5).

The topographic profile may also have implications for the long-term management of an area. For example, high-lying areas are more exposed and therefore could comprise harsher climates (e.g. Tateno & Takeda 2003), while steep slopes may even afford natural protection from disturbance (see Laurance et al. 2010). Therefore, by increasing the topographic heterogeneity, the amount of exposed area would decrease in favour of the relatively protected , nutrient-rich environments of valleys (Oosting & Billings 1942; Tateno & Takeda 2003; Laurance et al. 2010).

In a landscape in the throes of regeneration such as the study area though, topography is likely to interact with other site- and landscape-level factors, such as those previously identified as determinants of community structure and composition in ecosystems under restoration, for example, landscape composition (Grainger et al. 2011), and age (Wassenaar et al. 2005). It is therefore important to understand how the topographic profile has changed as a result of mining and rehabilitation.

The topographic profile is relatively easy to monitor provided starting conditions are available. The morphology of coastal dunes presumably influences habitat heterogeneity and initial conditions required to mimic natural conditions conducive to the regeneration of forests. Rebuilding coastal dune topography may therefore represent an important part of rehabilitation projects where topography has been altered. However, the level of importance of the topographic profile can only be ascertained when its influence on other abiotic, and biotic components in a regenerating landscape is understood, and some of this will be investigated in Chapter 5.

Chapter 4 The Response of Millipede, Dung Beetle and Bird Communities to the Patch Substrate, Composition and Spatial Structure of Regenerating Coastal Dune Forest Canopies

Introduction

Succession drives regeneration, as is the case in this study area (Grainger 2012; Grainger & van Aarde 2012b) where the post-disturbance recovery of coastal dune forests depends on colonisation from old-growth forests (Grainger 2012). However, succession also depends on many other processes (e.g. topsoil development, nutrient cycling, and dispersal, e.g. Walker & del Moral 2003; Holl et al. 2007) and is therefore difficult to study. By comparison, the interpretation of satellite images is relatively easy and cost effective.

Satellite imagery provides an aerial perspective of landscape features, which, through classification protocols can yield measures of the spatial structure of habitat patches (e.g. Stuart et al. 2006). The spatial structure of such patches is a scale-specific abstraction of habitat distribution that is widely accepted as an important determinant of colonization and persistence (Watson 2002; Ewers & Didham 2006). Generally, such patches are delineated according to scale-dependent[1] spatial information, such that in the case of forests a patch may be represented as a contiguous clump of tree canopies (Forman & Godron 1981; Forman 1995; Turner et al. 2001; Glossary of terms) comprising different species growing in response to other local conditions (e.g. soil nutrient content). Given the continuum of regenerating coastal dune vegetation at this

---

[1] Most metrics of spatial structure are scale-dependent, that is, results may differ depending on the resolution at which the spatial analysis was conducted (e.g. Wu, J. 2004. Effects of changing scale on landscape pattern analysis: scaling relations. *Landscape Ecology* **19:** 125–138).

study site, earlier research here has instead delineated patches as age-specific stands of regenerating coastal dune vegetation dominated by the pioneer species, *Acacia karroo* (see Grainger et al. 2011). Here, variability in the assemblages of several taxa has been attributed to the spatial structure of these patches (Weiermans & van Aarde 2003; Redi et al. 2005; Grainger et al. 2011). However, the colonisation and persistence of species in these new-growth forests is only possible if their habitat requirements are met by local habitat conditions. Such habitat requirements differ between species but measuring large suites of habitat variables as surrogates of resource availability for many taxa would be excessively time consuming and expensive. I aimed to find a surrogate for habitat applicable to different trophic levels, improving the cost-efficiency of monitoring and provide a more accurate assessment of regeneration trends rather than focal species or taxa. This may be over-ambitious but might enable the identification of potential shortcomings in local conditions that impair successional development and therefore detract from restoration success.

The spatial structure of tree canopies is hardly a comprehensive indication of habitat conditions within a forest patch, but associated features such as woody plant diversity and soil fertility may well be (e.g. Vanbergen et al. 2007; Leyequién et al. 2010). The close relationships between the biological communities of forests and features of their environment are well-documented (Cueto & de Casenave 1999; Atauri & de Lucio 2001; Watson 2002; Wethered & Lawes 2003; Tews et al. 2004; Wethered & Lawes 2005; Smith & Gehrt 2009; Wallis de Vries & Ens 2009; Grainger et al. 2011). Age-related increases in woody plant diversity are linked to increased habitat complexity (Kritzinger & van Aarde 1998) that has been shown elsewhere to increase the resource

base (Poulsen 2002) and niche availability (Kritzinger 1996; Poulsen 2002) for animals. Similarly, soil fertility can often explain variability in the community structure and composition of plants and animals (Dzwonko & Gawronski 1994; Oliviera-Filho et al. 1994; Bohlman et al. 2008). However, van Aarde et al. (1998) showed that soil fertility increases with regeneration age, and Boyes et al. (2010) later showed that soil fertility was not responsible for arrested succession in coastal dune forests.

In combination, the spatial structure of patches, plant diversity and soil nutrient content, quantify the patchiness or spatial heterogeneity of regenerating coastal dune forests that may be indicative of the amount and quality of resources available to animals. By inference then, such changes could also serve as surrogates for cascading effects on the colonisation and persistence of animal communities (Gustafson & Gardner 1996) and may therefore serve as surrogates of their presence and numbers.

Habitat features such as soil fertility, woody plant richness and diversity, as well as the structure of forest patches may be easier to quantify at various scales than animal community composition and structure. Measures of the former to evaluate restoration success may thus be more appropriate than measuring animal community variables. With a relatively large database on potential surrogates of habitat variables and species abundance data on which to assess them, I here have the opportunity to assess whether any of these could serve as surrogates of age-related changes, some of which may give an indication of restoration success. After all, we know that taxon-specific responses to habitat features likely indicate the availability of essential resources (Atauri & de Lucio 2001; Wassenaar et al. 2005; Golet et al. 2009). I selected multiple taxa to account for

intra- and inter-taxonomic differences in life history, dietary guild, and functional traits that would influence their response to habitat features (e.g. Golet et al. 2009).

From earlier work in the study area, we know that as saprophytes, millipedes and dung beetles contribute to (Teuben & Verhoef 1992; Smit & van Aarde 2001; Nichols et al. 2008), but also benefit from soil nutrients (Hopkin & Read 1992; Redi et al. 2005). The nutrient availability and water retention of soils are enhanced by succession-related enrichment of soils and the development of a litter layer (van Aarde et al. 1998). These changes further facilitate the activity of decomposers such as fungi and saprophytic arthropods (Hopkin & Read 1992; van Aarde et al. 1998; Smit & van Aarde 2001; Redi et al. 2005), having cascading effects on the ecosystem (Wardle et al. 2004). For these reasons, soil nutrient content is often used to assess restoration (van Aarde et al. 1998; Abreu et al. 2009; Zuo et al. 2009; Piqueray et al. 2011).

Bird communities at the study area are associated with age-related increases in vertical canopy complexity (Kritzinger & van Aarde 1998) that is presumably brought about by increased plant species diversity. This increase in plant species diversity provides essential resources such as nesting sites, shelter and food, important for the persistence of forest-associated species in regenerating patches (Kritzinger & van Aarde 1998; Sekercioglu et al. 2007; Leyequién et al. 2010). Birds are therefore expected to respond to changes in the diversity of woody plants present (patch composition). Dung beetles on the other hand, depend on the availability and quality of dung (Davis et al. 2003; Arellano et al. 2008; Nichols et al. 2008), but also on the dung types available, microclimatic conditions, soil nutrients, soil pH and rainfall (Fincher et al. 1970; Gittings & Giller 1998).

In contrast to dung beetles, millipedes have relatively poor dispersal abilities (Moir et al. 2009) and their sensitivity to microclimatic conditions (Dangerfield & Telford 1991; David 2009) may render them responsive to landscape-level changes in forest patch area, edge and isolation (Weiermans & van Aarde 2003). Birds, particularly forest-associated species, are sensitive to the spatial structure of forest patches, such as the area (e.g. Wethered & Lawes 2003; 2005; Bowen et al. 2009; Shanahan & Possingham 2009), edge (e.g. Robinson et al. 1995; Kruger et al. 1997; Weiermans & van Aarde 2003; Watson et al. 2004; Leyequién et al. 2010), and isolation (Watson et al. 2004; Grainger et al. 2011).

I evaluated three sets of potential surrogates for community composition and structure: i) the spatial structure of tree canopies (from here on referred to as patch structure) quantified as the area and shape (relating to patch edge) of patches, as well as distances between them (isolation), ii) the composition of patches, defined as the diversity and richness of woody plants constituting the patches, and iii) substrate as the nutrient content (carbon and nitrogen) and pH of soils. Using these habitat features, I aimed to determine 1) if the substrate, composition and structure of patches interact and 2) whether species abundance and community composition for three taxa of different trophic levels respond to these features.

Methods

Study area

The study took place on a narrow belt of coastal vegetation along South Africa's north-eastern coastline between Richards Bay (28°46′ south) and the St Lucia estuary (28°24′

south) (see Figure 1-2). This vegetation was nested within a relatively transformed mosaic of land-cover and land-use types andrural development and forestry along the inland boundary isolated the dune forest cordon from the hinterland (see Chapter 1).

Some 2 300 ha of coastal dunes have been mined since 1976, a third of which was subjected to continuous post-mining rehabilitation (van Aarde et al. 1996b). About 800 ha of sand dunes have therefore been set aside for rehabilitation to date, resulting in known-aged stands of new-growth forest that develop through succession (van Aarde et al. 1996b; Wassenaar et al. 2005; Grainger 2012). In 2006, these stands varied in area from 50 to 140 ha and in age from 1 to 30 years (Figure 1-2), but stands younger than six years had no tree canopy and were excluded from this study. Canopy cover changes from even to relatively heterogeneous along this successional sere as gaps formed where pioneer trees grew senescent (Grainger 2012). Based on their physiognomy and following Grainger & van Aarde , these stands could be classified as early- (6 to 10 years old), mid- (11 to 24 years old), and late- (25 to 29 years old) successional stages (seral stages 1, 2, and 3).

Explanatory variables

Rehabilitation behind the mining path is progressive such that the difference in age between adjacent regenerating stands is less than a two years. With the assumption that biological communities are unlikely to recognise the transitions between these stands, I defined patches in the present study as contiguous indigenous tree canopies discernible on Landsat TM 5 remote sensing imagery from 1998 and 2006 (sourced from the Satellite

Applications Center, CSIR, Hartebeeshoek, South Africa)[1]. These were I cross-referenced

with the age-specific stand data from mining records. This definition therefore differs

from that of Grainger et al. (2011), where patches were defined based on their age alone.

I delineated patches using classification routines conducted in spatial analysis software

(ENVI version 4, ITT Visual Information Solutions, www.ittvis.com and ArcMap version

9.3, 2009 © ESRI Inc., Redlands, California). I quantified the area, shape and isolation of

these patches using a spatial analysis program (FRAGSTATS version 3.3, McGarigal et

al. 2002).

I overlaid the woody plant abundance data and soil mineral content data from

surveys conducted within two years of either of the remote sensing images over these

patches in a GIS. The woody plant and soil survey methods are described elsewhere (van

Aarde et al. 1998; Theron 2001). Soil pH, nitrogen, and carbon reflected on substrate

quality, while tree species richness and diversity characterized the composition of tree

canopies (see Table 4-1).

---

[1] See Chapter 2 for detailed description of classification routines.

Table 4-1. Variables of habitat used to characterise regenerating patches (see Chapter 2)

		Variable	Description
Explanatory variables	Patch structure	Patch area	Geographical area (ha) covered by the woody canopy, defining the extent of a regenerating patch. Measured using "patch area" metric of FRAGSTATS v3.3.
		Patch shape	Patch shape complexity of the patch corrected for area, an indication of the amount of edge. Measured using "shape index" metric of FRAGSTATS v3.3.
		Patch isolation	Distance between a patch of tree canopies and any patch older than itself (potential source patches). Quantified using Edit Tools Geo Wizards version 9.8 (© Ianko Tchoukanski, www.ian-ko.com) extension for ArcMap v9.2 (ESRI, California, USA).
	Patch composition	Woody plant richness	An estimate of the number of woody plant species per site
		Woody plant diversity	Abundance-weighted index of woody plant diversity per site calculated using the Shannon-Wiener diversity index ($\acute{H} = -\sum P_i(\ln P_i)$, where P_i is the proportion of each species in the sample), therefore combining species evenness with richness (Krebs 1999).
	Patch substrate	Soil C	Organic carbon (%) present in the soil, determined using the Walkley-Black method (van Aarde et al. 1998).
		Soil N	Organic nitrogen (mg/kg) present in the soil, quantified using the Kjeldahl method (van Aarde et al. 1998).
		Soil pH	Acidity of soil measured in water solution using pH metre (van Aarde et al. 1998)
Response variables		Species richness	Mean number of species recorded within a patch for each taxon
		Forest-associated species richness	Mean number of forest-associated species recorded within a patch for each taxon. Forest-associated species were those that are typically dependent on forest habitats and are defined in Table 4-6 (millipedes), Table 4-7 (dung beetles), and Table 4-8 (birds).
		Proportion of old-growth forest species	The proportion of species found within a patch also present in the old-growth forest
		Beta diversity	Calculated between sampling sites per patch using the second modification of Whittaker's measure suggested by Harrison et al. (*sensu* Magurran 2004), $$\beta = \left\{ \frac{\left[\left(\frac{S}{\alpha_{max}} \right) - 1 \right]}{N-1} \right\} \times 100$$

Response variables

I extracted location-specific abundances of millipedes, dung beetles, and birds from data collected during two sampling seasons (1997 to 1999 and 2005 to 2007 to match the explanatory data as close as possible) under the auspices of the Conservation Ecology Research Unit (CERU, see Appendix II for list of species). Descriptions of the relevant survey methods are provided elsewhere (van Aarde et al. 1996a; Kritzinger & van Aarde 1998; Davis et al. 2002). I used these abundances to calculate taxon-specific community variables including species richness, forest-associated species richness, the proportion of species present that were also present in the old-growth forest, and beta diversity as defined in Table 4-1.

Relating community variables to habitat features

The patch structure, composition, substrate, and community response variables were overlaid in a Geographical Information System (GIS). I tested for correlations between the explanatory variables of habitat features (patch age, structure, composition and substrate) using a Spearman rank correlation test at the $p < 0.05$ level. Uncorrelated variables served as explanatory variables in further analyses as part of the requirements for assumptions of the RDA analysis. I also used a Spearman rank correlation as a first assessment of relationships between variables of community composition and patch variables (patch structure, composition, substrate), before conducting univariate and multivariate statistics.

I assessed the associations between patch variables and community composition and structure. I assessed whether the species richness, forest-associated species richness, the proportion of species present that were also present in the old-growth forest, and beta

diversity of three taxa (millipedes, dung beetles and birds) responded to patch variables using a forward stepwise multiple regression for each response variable within each taxon. This would determine the usefulness of patch structure as a surrogate for community structure and composition.

For the second level of assessment, I used a multivariate approach to assess apparent relationships between species-specific abundances and patch composition and substrate. I did this using a separate redundancy analysis (RDA) for each taxon as described by Zuur, Ieno, & Smith (RDA, see Zuur et al. 2007) to identify which of the habitat features (patch composition and substrate) best explained community structure within patches using the abundance data for millipedes, dung beetles, and birds. Species abundances were subjected to an RDA, rather than canonical correspondence analysis because they comprised detrended correspondence analysis gradient lengths less than 3 (ter Braak & Smilauer 2002). I applied the Chord distance transformation on species abundance data to rescale the data and so prevent the arch-effect caused by double zeros (Zuur et al. 2007). I also applied a square-root transformation prior to analysis to reduce the influence of high abundances on overall assemblage structure (ter Braak & Smilauer 2002). A stepwise Monte-Carlo permutation test (999 permutations, Novák & Konvicka 2006) was used to examine the significance of the relationship between each habitat variable and species abundances for the three taxa. Significant ($p < 0.05$) variables were then used to generate a dimensionless species-environment biplot (ter Braak & Smilauer 2002). Only those species for which more than 10% of the variance was explained by the axes, were included in the biplots (ter Braak & Smilauer 2002). I interpreted these biplots by examining the sign and angle of variable-specific eigenvectors. Angle was interpreted

as the strength of the correlation with species abundance. Species positioned near the arrow-head of the eigenvector were positively correlated with the metric, and near the tail, negatively (ter Braak & Smilauer 2002; Zuur et al. 2007).

Results

Interactions between patch structure, composition and substrate

Plant species richness, plant diversity, as well as soil carbon were positively correlated with patch age (Spearman rank test, $p < 0.05$, Table 4-2). Canopy patch area and shape were highly correlated with each other. Woody plant species richness, diversity, and soil carbon were highly correlated with one another and with age. I therefore excluded age, patch shape, soil carbon, and woody plant species diversity from the multiple regression analyses.

Table 4-2. A matrix of Spearman rank correlation coefficients for the relationship between explanatory variables of patch structure, composition, and substrate. Bold values indicate significance at $p < 0.05$.

Variable	Patch age	Patch area	Patch shape	Isolation	Woody plant richness	Woody plant diversity	Soil carbon	Soil nitrogen	Soil pH
Age	1.00								
Patch area	0.03	1.00							
Patch shape	0.06	**0.97**	1.00						
Isolation	0.32	-0.21	-0.17	1.00					
Woody plant richness	**0.69**	-0.11	-0.03	0.58	1.00				
Woody plant diversity	**0.63**	0.06	0.09	0.47	**0.93**	1.00			
Soil carbon	**0.68**	-0.27	-0.28	0.45	**0.65**	**0.67**	1.00		
Soil nitrogen	0.04	-0.06	-0.15	-0.43	-0.33	-0.26	0.01	1.00	
Soil pH	-0.42	-0.05	-0.03	0.44	-0.20	0.17	-0.06	-0.31	1.00

Interactions between habitat features on community composition

Spearman rank correlations between habitat features and community variables for all taxa were significant in only 12 of the 108 cases (Table 4-3). For millipedes, species richness and the number of forest-associated species increased with isolation and woody plant richness. Millipede species richness was also positively correlated with patch age and plant diversity, but decreased with increased patch area, as did millipede beta diversity with increased soil carbon. Dung beetle species richness was negatively associated with soil carbon, while dung beetle beta diversity was positively associated with soil nitrogen. Forest-associated bird species richness and the proportion of benchmark bird species present were positively associated with patch age, while forest-associated species richness also increased with patch area. The beta diversity of bird communities decreased with increased soil carbon.

Table 4-3. Spearman rank correlation coefficients for the relationship between patch features and community variables for each taxon. Bold values indicate significance at $p < 0.05$.

Community variables	Taxon	Patch age	Patch area	Patch shape	Isolation	Woody plant richness	Plant diversity	Soil carbon	Soil nitrogen	Soil pH
Species richness	Millipedes	**0.68**	**-0.07**	-0.03	**0.83**	**0.78**	**0.72**	0.57	-0.20	-0.32
	Dung beetles	-0.28	0.16	0.07	-0.55	-0.60	-0.57	**-0.62**	0.34	-0.24
	Birds	0.29	-0.11	-0.19	-0.19	-0.04	-0.19	0.05	0.58	-0.32
Forest-associated species richness	Millipedes	0.43	0.19	0.18	**0.69**	**0.62**	0.60	0.48	-0.21	-0.30
	Dung beetles	-0.01	-0.46	-0.44	0.09	-0.06	-0.37	0.21	0.27	-0.04
	Birds	**0.78**	**0.31**	0.01	0.00	0.41	0.30	0.34	0.30	-0.30
Proportion old-growth forest species	Millipedes	0.15	0.40	0.49	0.05	0.100	0.08	-0.14	-0.15	-0.22
	Dung beetles	0.03	0.51	0.45	0.18	-0.19	0.29	-0.27	-0.43	0.12
	Birds	**0.66**	-0.02	0.10	0.10	0.46	-0.22	0.26	0.14	-0.22
Beta diversity	Millipedes	0.31	0.36	0.42	0.43	0.54	**0.63**	0.17	-0.31	0.15
	Dung beetles	-0.43	-0.23	-0.18	-0.37	-0.52	-0.59	-0.32	**0.63**	-0.04
	Birds	-0.35	0.47	-0.14	-0.14	-0.19	-0.25	**-0.80**	-0.26	0.15

Multiple regression analyses confirmed that millipede and bird species richness were best predicted by patch isolation and soil nitrogen, respectively (Table 4-4). Forest-associated bird species richness, the proportion of old-growth forest species present and the beta diversity of the bird community covaried with variability in woody plant richness and patch area, although the models accounting for overall variability in these response variables were not significant. Changes in beta diversity for the dung beetle community were best explained by variability in soil nitrogen (Table 4-4).

Table 4-4. Coefficients of determination and *p*-values for stepwise multiple regressions with community variables of millipedes, dung beetles and birds as response, and patch features (patch area, patch isolation, woody plant richness, soil pH and soil nitrogen) as explanatory variables. Significant regressions ($p < 0.05$) are indicated in bold print.

Community variables	Taxon	*r*	*r²*	*p*	Patch feature	Beta in	*r*	*r²*	*p*
Species richness	**Millipedes**	**0.93**	**0.86**	**0.002**	**Isolation**	**0.70**	**0.82**	**0.42**	**0.007**
					Woody plant richness	0.36	0.29	0.38	0.082
					Soil pH	-0.20	-0.19	0.10	0.221
	Dung beetles	0.65	0.42	0.115	Woody plant richness	-0.44	-0.48	0.09	0.157
	Birds	**0.61**	**0.37**	**0.046**	**Soil nitrogen**	**0.61**	**0.61**	**0.00**	**0.046**
Forest-associated species richness	Millipedes	0.86	0.74	0.054	Woody plant richness	0.45	0.57	0.38	0.138
					Soil pH	0.28	0.47	0.10	0.240
					Patch area	0.31	0.52	0.03	0.185
					Patch isolation	0.35	0.46	0.43	0.250
	Dung beetles				No variables in the regression equation				
	Birds	0.64	0.41	0.124	**Woody plant richness**	**0.81**	**0.64**	**0.38**	**0.047**
					Patch isolation	-0.51	-0.46	0.38	0.181
Proportion old-growth forest species	Millipedes	0.53	0.28	0.097	Patch area	0.53	0.53	0.00	0.097
	Dung beetles	0.67	0.45	0.220	Soil nitrogen	-0.20	-0.22	0.33	0.577
					Patch area	0.46	0.50	0.10	0.167
					Patch isolation	0.37	0.38	0.32	0.312
	Birds	0.68	0.46	0.082	**Woody plant richness**	**0.86**	**0.68**	**0.38**	**0.030**
					Soil pH	-0.51	-0.48	0.38	0.156
Beta diversity	Millipedes	0.60	0.37	0.162	Patch area	0.52	0.55	0.01	0.102
					Woody plant richness	0.36	0.41	0.01	0.237
	Dung beetles	**0.67**	**0.45**	**0.024**	**Soil nitrogen**	**0.67**	**0.67**	**0.00**	**0.025**
	Birds	0.70	0.49	0.067	**Patch area**	**0.63**	**0.66**	**0.00**	**0.037**
					Soil pH	0.29	0.38	0.00	0.285

Habitat features and community variables

The species abundance data included 14 467 millipedes among 19 species, 13 835 dung beetles of 53 species, and 6 682 bird sightings among 148 species (see Appendix II). Monte Carlo permutations revealed significant responses by dung beetle and bird community variables to habitat features, but this did not hold for millipede variables (Table 4-5). The conditional effects were consistently, though slightly larger than the marginal effects, suggesting that patch variables collectively explained more about the changes in community variables than independently[1]. For illustrative purposes, only those species with a proportional explained variance >10% were plotted (Figures 4-1, 4-2 & 4-3).

Table 4-5. Total explained variance for the RDA model applied to each taxon, as well as the explained partitioned variance (λ) with the results of the Monte Carlo test for significance for each patch feature. Boldface type indicates significance at the $p < 0.05$ level.

Variable	Millipedes			Dung beetles			Birds		
	F	*p*	λ (%)	*F*	*p*	λ (%)	*F*	*p*	λ (%)
Woody plant richness	0.13	0.958	0	**3.97**	**0.001**	**12**	**1.77**	**0.035**	**6**
Soil nitrogen	1.84	0.159	6	**2.64**	**0.015**	**8**	**3.02**	**0.005**	**9**
Soil pH	2.15	0.117	8	**2.08**	**0.040**	**5**	1.08	0.326	3
Total conditional effect			14			25			18
Total marginal effect			12			23			17

Millipede species abundance was best explained by soil pH and nitrogen, but the RDA model was not significant (Table 4-6). Three millipede species (*Doratagonus sp., Centrobolus richardii*, and *Orthoporoides sp.*) had >10% of the variation in their abundances accounted for by the RDA model (27, 19, and 35%, respectively).

---

[1] The conditional effect is the variation explained by the whole set of habitat variables after their jointly explained variation is removed, whilst the marginal effect is the total variation explained by all three habitat variables (Cushman & McGarigal 2004)

Orthoporoides sp. and *C. richardii* increased in abundance with soil pH, while woody

plant richness explained variation in *Doratagonus* sp. abundance (Figure 4-1).

Table 4-6. List of millipede species included in RDA model, those with >10% of their variance explained are highlighted in boldface. The code used for the RDA biplot is given along with if they were considered forest-associated species (•), the habitat they were sampled in (0 = not used, 1 = important, 2=secondary, based on abundances). In addition, their morphometric class groupings are noted from Porter et al. (2007).

| Species	Species code	Forest-associated species	Morphometric class	Habitat		
				Ground	Shrubs	Trees
Doratogonus sp.	**Dor sp.**		**Cylindrical**	**2**	**0**	**1**
Centrobolus fulgidus	*Cen ful*		Cylindrical	2	1	2
Centrobolus richardii	**Cen ric**		**Cylindrical**	**2**	**2**	**1**
Centrobolus rugulosus	*Cen rug*		Cylindrical	1	0	0
Gnomeskelus tuberosus	*Gno tub*	•	Keeled	1	2	2
Orthroporoides sp.	**Ort sp.**		**Cylindrical**	**2**	**0**	**1**
Orthroporoides pyrocephalus	*Ort pyr*		Cylindrical	0	0	1
Sphaerotherium giganteum	*Sph gig*	•	Pill	1	0	0
Sphaerotherium punctulatum	*Sph pun*	•	Pill	1	0	2
Sphaerotherium sp. B	*Sph spB*	•	Pill	1	0	2
Sphaerotherium sp. C	*Sph spC*	•	Pill	1	0	0
Sphaerotherium sp. D	*Sph spD*	•	Pill	2	0	1
Spinotarsus anguliferus	*Spi ang*		Cylindrical	1	0	0
Spirostreptidae sp. Imm.	*Spi sp. I*		Cylindrical	1	0	0
Spirostreptidae sp. Imm. 2	*Spi sp. 2*		Cylindrical	0	1	0
Ulodesmus micramma zuluensis	*Ulo zul*	•	Keeled	1	0	0
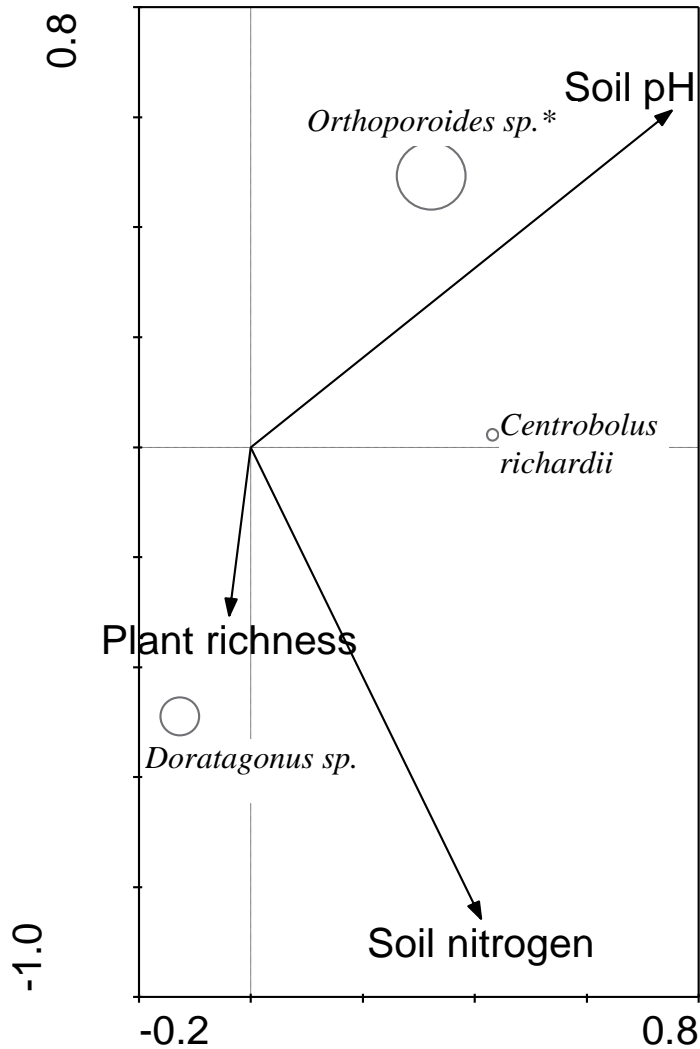
Figure 4-1. Correlation biplot of the redundancy analysis for millipedes using woody plant richness, soil nitrogen, and soil pH. Symbol size corresponds to the proportion of explained variance of a species' abundance accounted for by the ordination (Ter Braak & Šmilauer 1998). Only those with >10% are displayed and these values ranged between 19 and 35%). Length of vectors (arrows) indicates their relative importance along their steepest direction of increase. Species near a particular vector arrow head are positively correlated with that variable, and those on the opposite end, negatively correlated. Asterisks indicate forest-associated species. See Table 4-6 for all millipede species and habitat associations.

Variability in the abundances of all (53) dung beetle species was best explained by woody plant richness, followed by soil nitrogen and pH (Table 4-7). Thirty-eight of these

species had more than 10% of the variation in abundance explained by these variables (Figure 4-2). Of these, 10 were woodland and forest-associated species, while the remaining 28 species were widespread open-habitat associated species, according to the groupings suggested by Davis et al. (2002). More than 34 % (range: 34 – 50%) of the variation in shade-dependent forest endemic ("Group A" of Davis et al. 2002) abundances were associated with decreased soil nitrogen and woody plant richness. Widespread open habitat-associated species ("Groups D" & "E" of Davis et al. 2002) were positively influenced by these variables (Figure 4-2). Increasing abundance of forest-associated species that seek out sunlit areas (three species; *Scarabaeus bornemisszai, Onthophagus pugionatus,* and *Afrodrepanus impressicollis*) as well as that of one forest-associated species that prefers shaded areas (*Sisyphus sp. y*) was associated with increasing soil pH. Every functional group was represented, but there was no clear pattern in the response of these groups to the variables of habitat (see Table 4-7).

Table 4-7. List of dung beetle species included in RDA model that had >10% of their variance accounted for by the RDA model. The code used for the RDA biplot is given along with if they are considered endemic widespread forest-associated species (•), endemic forest-associated species dependent on shaded habitat (••), or endemic forest-associated species dependent on sunlit habitat (•••), as well as the habitat they were sampled in (1= most important, 4 = least important, based on abundances. In addition, their functional groupings and biogeographic associations are noted from Davis et al. (2002).

Latin name	Species code	Forest-associated species	Habitat‡				Functional group*	Biogeo-graphic group§
			Open	Young woodland	Older woodland	Unmined dune forest		
Afrodrepanus impressicollis	*Afr imp*	•••			2	1	V	M
Allogymnopleurus thalassinus	*All tha*		1				II	Sa
Anachalcos convexus	*Ana con*		2	3	4	1	I	EA(Pan)
Caccobius nigritulus	*Cac nig*		1				VI	EA
Caccobius sp. 1	*Cac sp. 1*		1	3	2	4	V	M
Caccobius sp. 2	*Cac sp. 2*	••	4	2	1	3	V	EC
Caccobius sp. 3	*Cac. sp. 3*		1	2	4	3	V	M
Catharsius sp. 1	*Cat sp. 1*	••	4	3	1	2	III	M
Catharsius tricornutus	*Cat tri*		1	3	4	2	III	SA
Copris inhalatus ssp santaluciae	*Cop inh*		1				III	M(Sa)
Copris puncticollis	*Cop pun*		1				III	EC
Copris urus	*Cop uru*		1		2	3	III	M
Hyalonthophagus alcyonides	*Hya alc*		1	2	2		IV	SA
Kheper lamarcki	*Khe lam*		1	2	3		I	Sa
Liatongus militaris	*Lia mil*		1				IV	EA
Neosisyphus spinipes	*Neo spi*		1		2		II	SA
Oniticellus formosus	*Oni for*		1				VII	EA(Pan)
Oniticellus planatus	*Oni pla*		1	3	2	3	VII	EA(Pan)
Mimonthophagus ambiguous	*Mim amb*		1	2	4	3	IV	EC
Onthophagus depressus	*Ont dep*		1		2		IV	EA
Onthophagus fimetarius (coastal var.)	*Ont fim*		1	2	3	3	IV	M(EA)
Onthophagus flavolimbatus	*Ont fla*		1				VI	EA
Onthophagus nanus	*Ont nan*		1				V	SA
Onthophagus obtusicornis	*Ont obt*		1				IV	SA
Onthophagus pugionatus	*Ont pug*	•		1	1		IV	EA
Onthophagus sp. 2 (v. small endemic)	*Ont sp. 2*	••	4	2	1	3	V	M
Onthophagus sp. nr bicavifrons	*Ont bic*	••	4	2	1	3	IV	M
Onthophagus sp. nr sugillatus (coastal var.)	*Ont sug*		1				V	M(SA)
Onthophagus ursinus	*Ont urs*		1	2	3		V	EC
Pachylomerus femoralis	*Pac fem*		1	2	4	3	I	Sa
Pedaria sp. IV	*Ped sp. IV*		1				VI	SA
Proagoderus aciculatus	*Pro aci*	••	4	2	3	1	IV	EC
Proagoderus aureiceps	*Pro aur*		1	2	4	3	IV	EC
Proagoderus chalcostolus	*Pro cha*		2				IV	EA
Scarabaeus bornemisszai	*Sca bor*	•••		2		1	I	M
Sisiphus sp.nr gazanus	*Sis gaz*	••	4	2	1	3	II	M
Sisyphus sordidus	*Sis sor*		1	2	3		II	EC
Sisyphus sp y	*Sis sp. y*	••		1	3	2	IV	M(Sa)

‡Habitat descriptions: Open = < 1–~6 year old grassland/open Acacia shrubland thickets; Young woodland = ~9–~15 year Acacia woodland; Older woodland = ~18–~21 year Acacia woodland and adjacent coastal dune forest; Unmined dune forest = Inland dune and Sokhulu natural dune forest. *Functional group: I) large ball rollers; II) small ball rollers (<100g dry body mass); III) fast-burying tunnelers; IV) slow burying tunnelers; V) small, slow-burying tunnelers (<10mg dry body mass); VI) kleptocoprids (<10mg dry body mass); VII) endocoprids. § Biogeographical group: Pan = PanAfrotropical distribution, EA = East African distribution, SA = Southern African distribution, Sa = deep sand specialist).
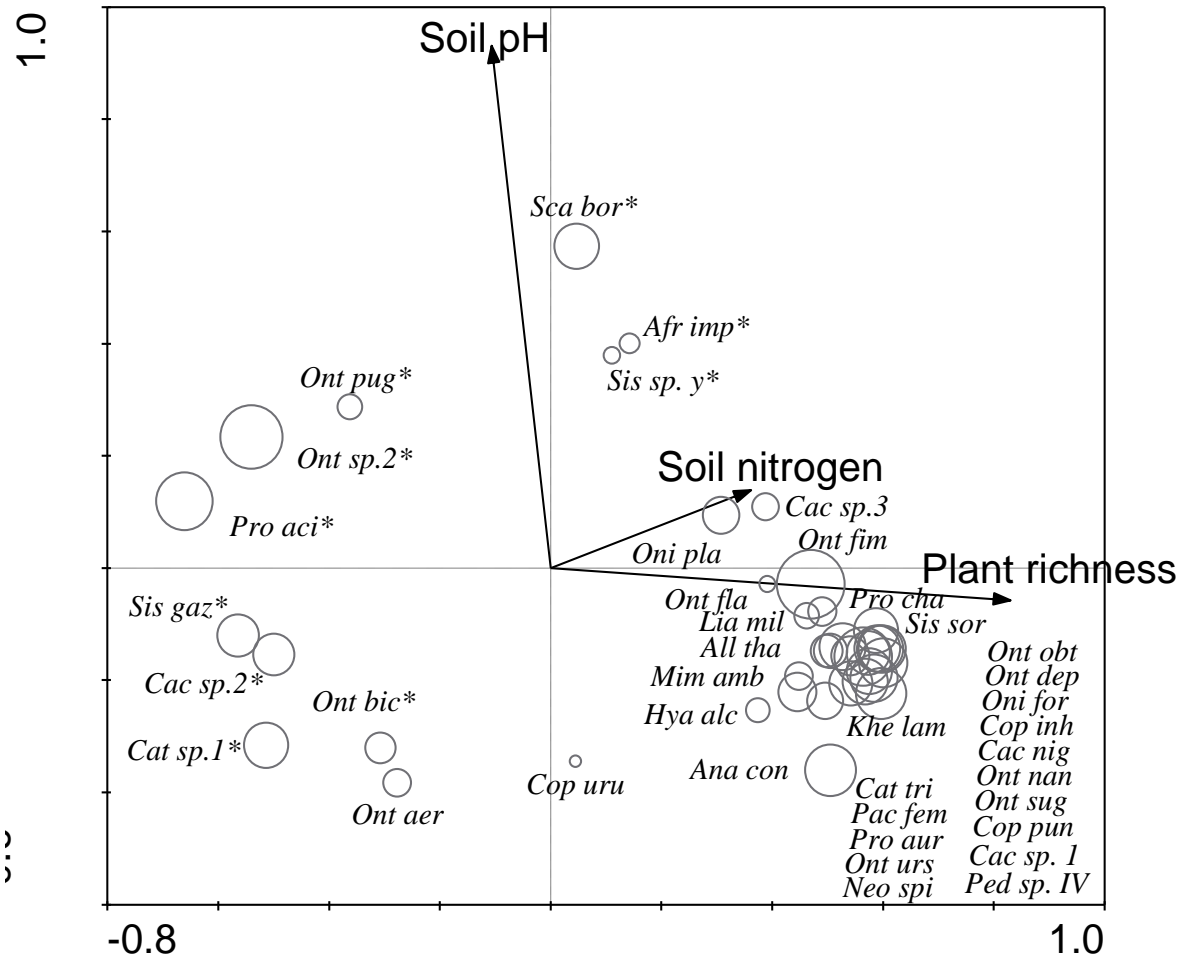
Figure 4-2. Correlation biplot of the redundancy analysis for dung beetles using woody plant richness, soil nitrogen, and soil pH. Symbol size corresponds to the proportion of explained variance of a species' abundance accounted for by the ordination (Ter Braak & Šmilauer 1998). Only those with >10% are displayed and these values ranged between 12 and 50 %). Length of vectors (arrows) indicates their relative importance along their steepest direction of increase. Species near a particular vector arrow head are positively correlated with that variable, and those on the opposite end, negatively correlated. Asterisks indicate forest-associated species from groups "A" and "B" (Davis et al. 2002). Abbreviated species names used here for display purposes (see Table 4-7 for full species names and habitat associations).

The abundances of 45 of 148 bird species were explained by three habitat features (soil pH, soil nitrogen, and woody plant richness, see Table 4-8), but only 17 of these had more than 10% of the variance in their abundances explained by these habitat features

(range: 12-46%, see Figure 4-3). Soil nitrogen was the most important predictor of variability in abundance, followed by woody plant richness. These two variables explained the abundances of three forest-associated species (Olive sunbird (*Cyanomitra olivacea*), Square-tailed drongo (*Dicrurus ludwigii*)*,* and African Emerald Cuckoo (*Chrysococcyx cupreus*), (Figure 4-3). The abundances of two woodland species, Rudd's Apalis (*Apalis ruddi*) and Lesser Masked Weaver (*Ploceus intermedius*) were strongly negatively correlated with increasing soil nitrogen and woody plant richness, along with the open-habitat associated species Tawny-flanked Prinia (*Prinia subflava*).

Table 4-8. List of bird species with >10% of their variance accounted for by the RDA model. The code used for the RDA biplot is given, as well as their preferred habitat and whether they are used by nest parasites (•) and preferred food items (1 = most important, 2 = secondary).

Latin Name	Common Name	Species code	Forest-associated	Parasitized	Food					Habitat					
					Invertebrates	Vertebrates	Fruit	Flowers	Seeds	Woodlands	Forest	Forest edge	Thicket	Near water	Grassland
Apalis flavida	Yellow-breasted Apalis	*Apa fla*		•	1		2	2		•	•			•	
Apalis ruddi	Rudd's Apalis	*Apa rud*		•	1		2	2		•*					
Ceuthmochares aereus	Green Malkoha	*Ceu aer*	•		1	1	2			•	•	•	•		
Chrysococcyx caprius	Diderick cuckoo	*Chr cap*			1					•		•			
Chrysococcyx cupreus	African Emerald Cuckoo	*Chr cup*	•		1		2					•			
Chlorocichla flaviventris	Yellow-bellied Greenbul	*Chl fal*		•	2		1	2	2	•	•	•			
Cisticola chiniana	Rattling Cisticola	*Cis chi*		•	1					•*					•
Cisticola juncidis	Zitting Cisticola	*Cis jun*		•	1										•
Cyanomitra olivacea	Eastern Olive Sunbird	*Cya oli*	•	•	1		2	1		•	•				
Dicrurus ludwigii	Square-tailed Drongo	*Dic lud*	•	•	1			2			•	•			
Dryoscopus cubla	Black-backed Puffback	*Dry cub*			1		2	2		•	•				
Halcyon albiventris	Brown-hooded Kingfisher	*Hal alb*			1	2				•		•			
Lanius collaris	Common Fiscal	*Lan col*		•	1	2			2	•					
Muscicapa caerulescens	Ashy Flycatcher	*Mus cae*	•	•	1		2			•	•				
Ploceus intermedius	Lesser Masked Weaver	*Plo int*		•	1			1	2	•*			•	•	
Prinia subflava	Tawny-flanked Prinia	*Pri sub*		•	1			2						•	•
Zosterops virens	Cape White-eye	*Zos vir*			1		2	2		•	•		•		

* indicates species especially associated with *Acacia* species
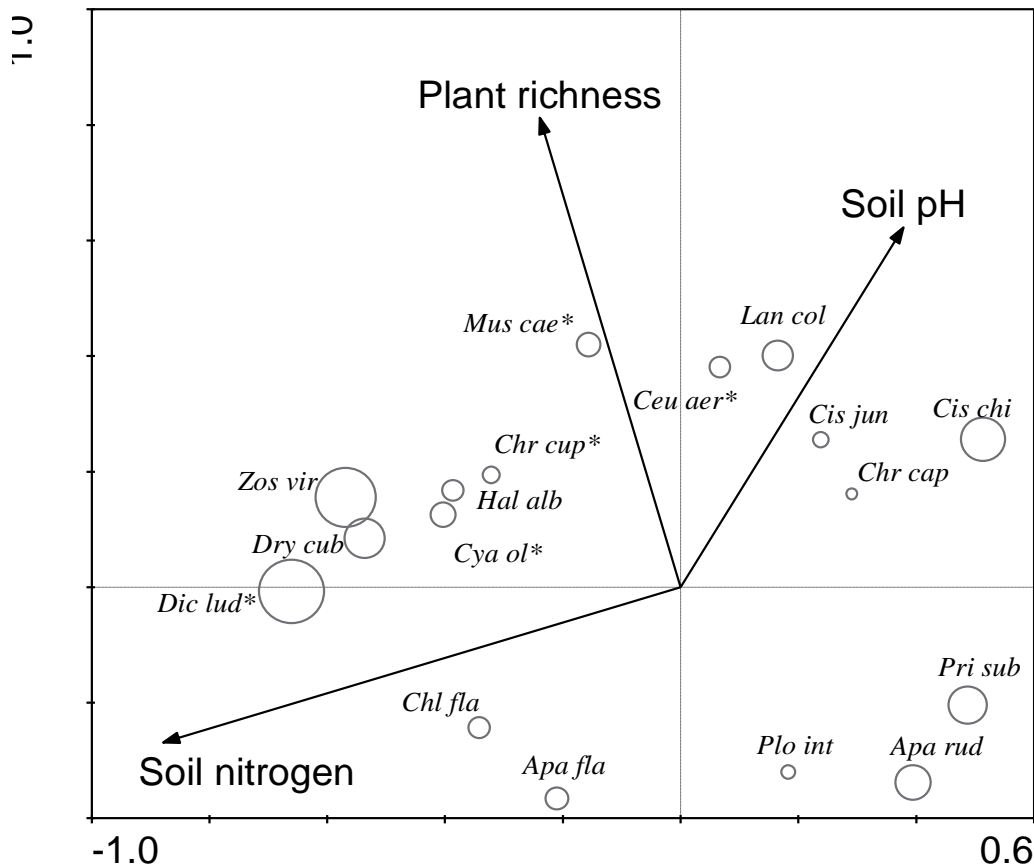
Figure 4-3. Correlation biplot of the redundancy analysis for birds, where only those habitat variables that had significant influence on species abundance are shown. Symbol size corresponds to the values of the fit of species into the ordination space (range 13-75%). See interpretation explanation in the caption of Figure 3. Asterisks indicate forest-associated species. Abbreviated species names used here for display purposes (see Table 4-8 for full species names and habitat associations).

Discussion

I investigated the relative importance of the spatial structure, composition and substrate in explaining the structure and composition of millipede, dung beetle, and bird communities. I expected the animal communities to respond to variables of the substrate, composition and spatial structure of patch of forest, as they were indicative of habitat patchiness or heterogeneity. Furthermore, I expected that taxa would respond differently to these habitat variables based on their resource requirements.

Indeed, I found that millipedes responded to isolation, dung beetles to soil nitrogen and birds to patch area, soil nitrogen and woody plant species richness. However, responses were idiosyncratic and in most cases could be related to age-related increases in habitat complexity.

Interactions between habitat features

As in other studies (Novák & Konvicka 2006; Grainger et al. 2011), age served as a mere proxy for a number of habitat variables, and I therefore excluded age, patch shape, soil carbon, and woody plant species diversity from the stepwise multiple regression analyses. These correlations between age and habitat variables was not surprising because although age itself is not indicative of habitat quality, it is an axis along which habitat variables change as a result of successional processes and later, patch dynamics (Grainger 2012). Previous work in the study area also documented age-related increases in carbon, plant species diversity, and richness through succession in the study area (van Aarde et al. 1996b; van Aarde et al. 1998; Wassenaar et al. 2005; Wassenaar et al. 2007; Grainger et al. 2011; Grainger 2012). Soil nutrients play an important role in the distribution and structure of plant communities (e.g. Chen et al. 1997; van Aarde et al. 1998) that also show age-related increases in richness and diversity (Grainger 2012), in turn relating to increased heterogeneity (e.g. Kritzinger & van Aarde 1998). Nutrient availability in regenerating patches of forest therefore increases gradually with age as a result of increasing ecosystem functionality (e.g. the development of a litter layer and decomposition, van Aarde et al. 1998).

Interactions between habitat features and community variables

Community composition and structure showed idiosyncratic inter- and intra-taxon responses to habitat features. Patch isolation was positively associated with millipede

community composition and soil nitrogen with that of dung beetle composition. Bird communities covaried with soil nitrogen as well as patch area. This idiosyncrasy suggests not only that trait-specific habitat requirements drive responses to the variables assessed here, as has been shown in many other studies – the very reason we use multiple taxa for such assessments (e.g. Golet et al. 2009) – but also suggests that none of the variables used here could serve as a definitive surrogate for the changes in community assemblages associated with succession.

Habitat selection or preferences are not a feature of the community, but rather the consequences of selective pressures on individuals. However, in considering the community as comprising a number of co-occurring species, it may be argued that considerable overlap exists in their habitat requirements. The justification for seeking such convenient relations stems from the need for practical and surrogate approaches to deduce successional patterns and hence, additional surrogate measures of restoration success.

Community variables such as species richness, turnover rates etc., are mere convenient units of study and statistical abstracts, and as such may not reflect the operational scale of ecosystems in question (e.g. Harrison et al. 1992; Kraft et al. 2011). In much the same way, the spatial structure of canopy cover is an abstraction of the extent of the new-growth forests that may be too broad to discern signals required to generate a meaningful surrogate of successional processes taking place beneath the tree canopies. Although in half the cases variability in community variables could be explained by habitat variables, the total explained variation in abundances of dung beetle and bird species was relatively low (25 and 18%, respectively) compared to that of other studies (Jeanneret et al. 2003; Hutchens et al. 2009). Furthermore, millipede abundances could not be explained by any of the

habitat variables. Furthermore, patch area explained neither the composition of millipede nor dung beetle communities, but did explain species turnover in bird communities. It seems that the resolution at which I delineated patches, did not match the extent of patches as perceived by invertebrates (see Grand & Mello 2004). Indeed, mismatches in scale may well explain the lack of a pattern, as millipede species abundances did not respond to any of the variables of habitat aside from isolation. Abiotic factors such as rainfall (David 2009), topography (Moir et al. 2009), microclimate (Weiermans & van Aarde 2003; Moir et al. 2009) may provide better predictors of millipede abundance than those that I included in the present study.

Differences in beta diversity for bird communities were best explained by patch area, though neither patch edge nor isolation significantly explained bird community composition. There is much literature describing the importance of patch area as a determinant of bird community composition through the greater availability of resources supposedly associated with larger patches, such as shelter and food (e.g. Coppedge et al. 2001; Bowen et al. 2009; Leyequién et al. 2010). Nevertheless, larger patches also relate to decreased edge effects such as brood parasitism and predation (see Watson et al. 2004). With at least eight species of brood parasites present in the new-growth forests, this may also contribute toward explaining the importance of patch area to beta diversity (see species susceptible to brood parasitism in Table 4-8). This finding, as well as the lack of a negative association with patch isolation, were in contrast to that of Grainger et al. (2011), who found no species-area effect and suggested that this was due to the low contrast between rehabilitating and adjacent patches (plantation, woodland, old-growth forest), allowing birds to obtain resources from adjacent patches (Wethered & Lawes 2003). My definition of a patch based on a contiguous stretch of indigenous tree canopies likely resulted in a greater contrast

between patches and the matrix, but may have been too broad to capture differences in faunal assemblages, highlighting the scale-dependent nature of such metrics of patch structure. Future studies here should incorporate a multi-scale approach to properly extract patterns of response by biological communities (Wu 2004).

Increased nitrogen content in soils was associated with greater dung beetle species turnover and abundances, as well as bird species richness and abundances. Dung beetles are known to increase soil pH and nitrogen content through bioturbation of the soil (Nichols et al. 2008). So do millipedes (Smit & van Aarde 2001), and I therefore ascribe covariation at this scale of assessment to age-related regeneration that includes increases in soil nitrogen and organic content (van Aarde et al. 1998), increased heterogeneity in vertical structure (Grainger 2012), and therefore a greater resource base. For example, variability in the majority of forest-associated dung beetle species that prefer shaded habitats (e.g. *Onthophagus* sp. 2*, Proagoderus aciculatus, Sisphus natalensis, S. gazanus* and *Catharsius* sp.1, Davis et al. 2002) was negatively associated with soil nitrogen and woody plant richness. On the other hand, *Scarabaeus bornemisszai*, a forest-associated species dependent on sunlit habitats was associated with soils with relatively higher soil pH. One could also argue that the canopy gaps in older patches have an understory and grass that attract cattle, and with them, open-habitat dung beetle species to the area (see Arellano et al. 2008). This suggestion is in line with Davis et al. (2012), who noted that dung beetle assemblages found in regenerating patches were related to changes in canopy structure and thus shade. However, all dung beetles aside from a flightless species (*Gyronotus carinatus*) were found in the patches, suggesting that their presence may be an artefact of the sampling procedure used to attract dung beetles here. Similarly, Purtauf et al. (2004), who also used pitfall traps, found that the colonization of post-disturbance habitat by

carabid beetle species was independent of their dispersal abilities. However, by sampling cow pats rather than providing an artificial food source in the form of pitfall traps, Roslin and Koivunen (2001) found that the distribution of species among guilds with different habitat specificity was related to patch structure, although there was no relationship between this and the proportion of the regional source pool represented. The ability of most dung beetle species to rapidly seek out transient food resources perhaps therefore renders them a poor taxon on which to base an analysis testing potential surrogates of succession.

Despite the multivariate model explaining so little of the variability in bird abundances, patterns related to the habitat preferences of species – as was the case in other studies (e.g. Bowen et al. 2009; Leyequién et al. 2010; Grainger et al. 2011). As expected, forest-associated species, as well as those species that use both forest and woodland habitats were positively influenced by increasing woody plant richness. The same was true for the number of forest-associated and the proportion of old-growth forest bird species present, which increased with woody plant richness. This could again be explained by age-related increases in shelter (increased vertical complexity) and food resources with increased woody plant species richness (Kritzinger & van Aarde 1998; Watson et al. 2004; Leyequién et al. 2010). However, in line with a study also using a multivariate approach on the effect of woody encroachment on grassland bird species in the Southern Great Plains, USA (Coppedge et al. 2001), open habitat species were negatively associated with woody plant richness. At the very least then, woody plant richness appears a relatively good predictor of successional processes for birds, because it was associated with bird community composition and abundances.

It is dangerous to use a single species as an effective 'indicator' or 'umbrella' species (Ozaki et al. 2006; Cushman et al. 2010), and therefore a potential surrogate

of restoration success. However, some authors claim that the variables important to birds may serve as good indicators for other faunal groups because of the niche breadth of this taxon, as well as their sensitivity to a wide range of environmental factors, including habitat fragmentation and climate change (see Gregory et al. 2005). Finding cost-efficient means of assessing the relative importance of habitat features to successional processes would be an important contribution to the monitoring of restoration programmes. One way of doing this would be to identify a suite of habitat variables that are relatively easy to quantify and a range of taxa representing different functional groups on which to test them. However, my study demonstrated the obscurity of such a suite of metrics.

Previous work in the study area has demonstrated that many forest species have colonized the regenerating patches and that community assembly is age-related (Kritzinger & van Aarde 1998; Wassenaar et al. 2005). Some species, however, remain absent, particularly forest-associated species (Grainger et al. 2011). Results here showed that forest-associated bird species covaried with woody plant richness, suggesting that, as previously argued (Kritzinger & van Aarde 1998) the recovery of bird assemblages, could be a factor of increased habitat heterogeneity. However, future assessments need to be conducted so that the requirements of species that operate at finer scales, such as millipedes, are also considered. As such, this study is an important reminder that in providing for the apparent needs of one guild, functional group, taxon, or single species, does not necessarily facilitate the return or persistence of others to the site. However, here the development of soil and woody plant richness appear the best predictors of community structure and composition, while birds may be the best taxa on which to assess such surrogates of habitat conditions. It therefore

seems that the components assessed here are better explained by site-level factors that

change with the age of new-growth coastal dune forest.