

Chapter 5 | Coastal Dune Topography as a determinant of Abiotic Conditions and Biological Community Restoration in Northern KwaZulu-Natal, South Africa

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Introduction

Ecological restoration is widely recognised as a conservation tool and aims to re-instate natural processes that sustain biological diversity (Dobson et al. 1997; MacMahon & Holl 2001). Such diversity is determined by both regional and local forces, the latter often as a function of topography due to cascading effects on microclimatic conditions, water retention, and nutrient availability (Larkin et al. 2006). These relationships are especially well-documented in mountainous regions (Burnett et al. 1998; Nichols et al. 1998; Tateno & Takeda 2003; da Silva et al. 2008), but less often for coastal sand dune ecosystems (e.g. Martínez et al. 2001; Acosta et al. 2007). The restoration of topography may be a priority (Weiss & Murphy 1990; Palik et al. 2000; Larkin et al. 2006), but difficult or costly to achieve. However, an approximation of the original topography may be sufficient to maintain desired ecological processes. This may well be the case in our study areas where succession drives forest regeneration, but where the full complement of species has not yet been regained (van Aarde et al. 1996b; Grainger 2012). This may be due to the micro-environmental needs of specialist species not being met due to constraints imposed by topography. Justification to restore terrain requires an assessment of the relevance of

topography for species and ecological processes. In this study, we assess the influence of dune topography on abiotic and biotic conditions (Table 5-1) in coastal dune forests regenerating in response to an ecological restoration program.

The aspect, elevation, and gradient of slopes are collectively referred to as dune morphology, while the relative position is described as the crest, slope, or valley. These variables of dune topography can influence habitat conditions in various ways (Larkin et al. 2006). For example, nutrients leaching from dune crests into valleys where plant-communities are light-limited results in nutrient-limited communities on crests, but greater nutrient availability in valleys (Tateno & Takeda 2003). Canopy structure changes with gradients in soil fertility and light (Nichols et al. 1998; Tateno & Takeda 2003), even with limited altitudinal variation (da Silva et al. 2008). This may explain patterns in plant species composition, abundance, and distribution (Chen et al. 1997; Oliviera-Filho et al. 1998). The aspect and gradient of dune slopes may amplify these differences as they also influence light availability (Oliviera-Filho et al. 1998; Bennie et al. 2008) and wind exposure (Chen et al. 1997; Acosta et al. 2007). Wind sculpts tree canopies (Kubota et al. 2004; Nzunda et al. 2007), hastens canopy gap formation (Ritter et al. 2005), and contributes to seed dispersal (Furley & Newey 1979). The windward slopes of coastal dunes have higher evaporation rates than leeward slopes and are more exposed to salt spray that increases salt concentrations in the soil, in turn influencing soil pH and the availability of nutrients (Furley & Newey 1979; Chen et al. 1997; Acosta et al. 2007). We therefore expected that dune morphology and position would influence microclimatic conditions (temperature, relative humidity, and light intensity) and that soil nutrient availability (C:N ratio) and soil pH would vary with dune morphology (see Table 5-1 for further details). Altered topographic profiles could therefore hinder the ecological restoration of new-growth

forests, or simply alter heterogeneity and rearrange the distribution of resources and hence that of species. Therefore, the structure and composition of biotic communities at locations with different dune morphologies should be assessed to determine the importance of restoring the topographic profile.

Table 5-1. Key questions and expectations of this study

| Key questions | General assumptions | Expectations | Examples from the literature |
|--|---|--|--|
| 1. Does dune topography influence abiotic conditions? | Microclimatic conditions vary with dune topography | Irradiation, temperature and humidity may increase or decrease, depending exposure to wind and sun that is facilitated or eased by dune aspect, elevation, and position | (Tateno & Takeda 2003; Bennie et al. 2008) |
| | Dune topography influences soil nutrient availability | Soil carbon-to-nitrogen ratio and soil pH will be greater in valleys and at low elevations | (Chen et al. 1997; Tateno & Takeda 2003) |
| 2. Does dune topography influence biotic conditions? | Dune topography influences woody plant community structure and distribution | <ul style="list-style-type: none"> Woody plant richness will depend on aspect, elevation and position depending on their exposure to wind Woody plant canopy structure will depend on gradient and position Species-specific woody plant abundances will differ based on dune morphology and position | (van Dyk 1996; Oliviera-Filho et al. 1998; da Silva et al. 2008; Laurance et al. 2010) |
| | Dune topography influences millipede community structure and distribution | <ul style="list-style-type: none"> Millipede richness, as well as taxon-specific density may be influenced by aspect, elevation, and position depending on their exposure to wind and sunlight Species-specific millipede abundances will differ based on dune morphology and position | (Weiss & Murphy 1990; Moir et al. 2009) |

Topography influences plant growth and species richness in old-growth forests (Tateno & Takeda 2003; da Silva et al. 2008), which has cascading effects on biota through the responses of microclimatic conditions to topography (Larkin et al. 2006). Physiological trade-offs associated with the small size and ectothermy of invertebrates, such as millipedes, renders them sensitive to microclimatic conditions

that dictate habitat preferences (Ashwini & Sridhar 2008; Loranger-Merciris et al. 2008; David & Gillon 2009). We therefore assessed the importance of the topographic profile in structuring millipede assemblages. We expected that within a seral stage, plant richness, canopy structure and species-specific abundances would respond to variability in dune morphology and position in regenerating stands of new-growth coastal dune forest, as would millipede richness, taxon-specific density and species-specific abundances (for details see Table 5-1). If millipedes respond to topography, changes in the topographic profile should result in changes in millipede diversity. If this is not the case, topography has a limited role to play, if any, in explaining millipede community structure. Although this study is based upon coastal dune forests, it may have implications for any disturbed dune system under restoration.

Methods

Study area

The study area was located north of Richards Bay town (between 28°46' and 28°34' south) on the sub-tropical north coast of Kwazulu-Natal, South Africa (Fig. 5-1). The climate is humid with a mean annual rainfall of 1458 ± 493.5 mm (mean \pm SD, $n = 34$ years between 1976 and 2009), peaking in February. The mean annual temperature was $23.79 \pm 3.40^\circ\text{C}$ ($n = 3$ years between 2006 and 2009). Winds of between 10 and $40 \text{ km}\cdot\text{h}^{-1}$ blew from the north-east for about 20% of the time, as did those from south-south west and south-west combined (data courtesy of Richards Bay Minerals).

The establishment of forests on the coastal dunes here occurred with the return of warm interglacial conditions between 6,500 and 4,000 years ago, making them among the highest vegetated dunes in the world (Weisser & Marques 1979; Lawes 1990).

These forests are therefore relatively young and harbour few endemic species (Lawes

1990; van Wyk & Smith 2001). Coastal dune forests are sensitive to disturbance but previous work has shown that they are relatively resilient and are thus able to recover (e.g. Wassenaar et al. 2005; Grainger et al. 2011).

Richards Bay Minerals (RBM) has leased this area since 1976 for the extraction of heavy metals from the coastal sands. Ahead of the dredging pond, all vegetation was cleared and the dunes were collapsed for mining. After mining, sand tailings were stacked to resemble pre-mining topography and were covered with topsoil (van Aarde et al. 1996c). A third of the mined area was set aside for the restoration of indigenous coastal dune forest and this area comprised known-aged stands that at the time of the study ranged in age from 1 year (in the northeast) to 33 years (in the southwest) (see Fig. 5-1). This age-range represented three seral stages based on those defined by Grainger (2012): seral stage one = 1-10 years, two = 11-25 years, and three >25 years. Adjoined by a coastal strip of unmined vegetation about 200 m wide, the stands were themselves no wider than 2 km, set in a mosaic of active mining areas, plantations, degraded woodland, and rural villages (Wassenaar et al. 2005).

Microclimatic data

Fifteen HOBO[®] 4-channel data loggers (Onset Computer Corporation, 470 MacArthur Blvd., Bourne, MA 02532, U.S.A.) were deployed in the 22-year old stand (see Fig. 5-1) on custom-made platforms placed 10 cm above the ground (five on the crest, five on a slope and five in the valley). We programmed these loggers to record ground-level temperature, relative humidity, and light intensity (see Table 5-2 for definitions) every 10 minutes between 08:00, 28 January and 05:00, 4 February 2011, yielding 14,850 records.

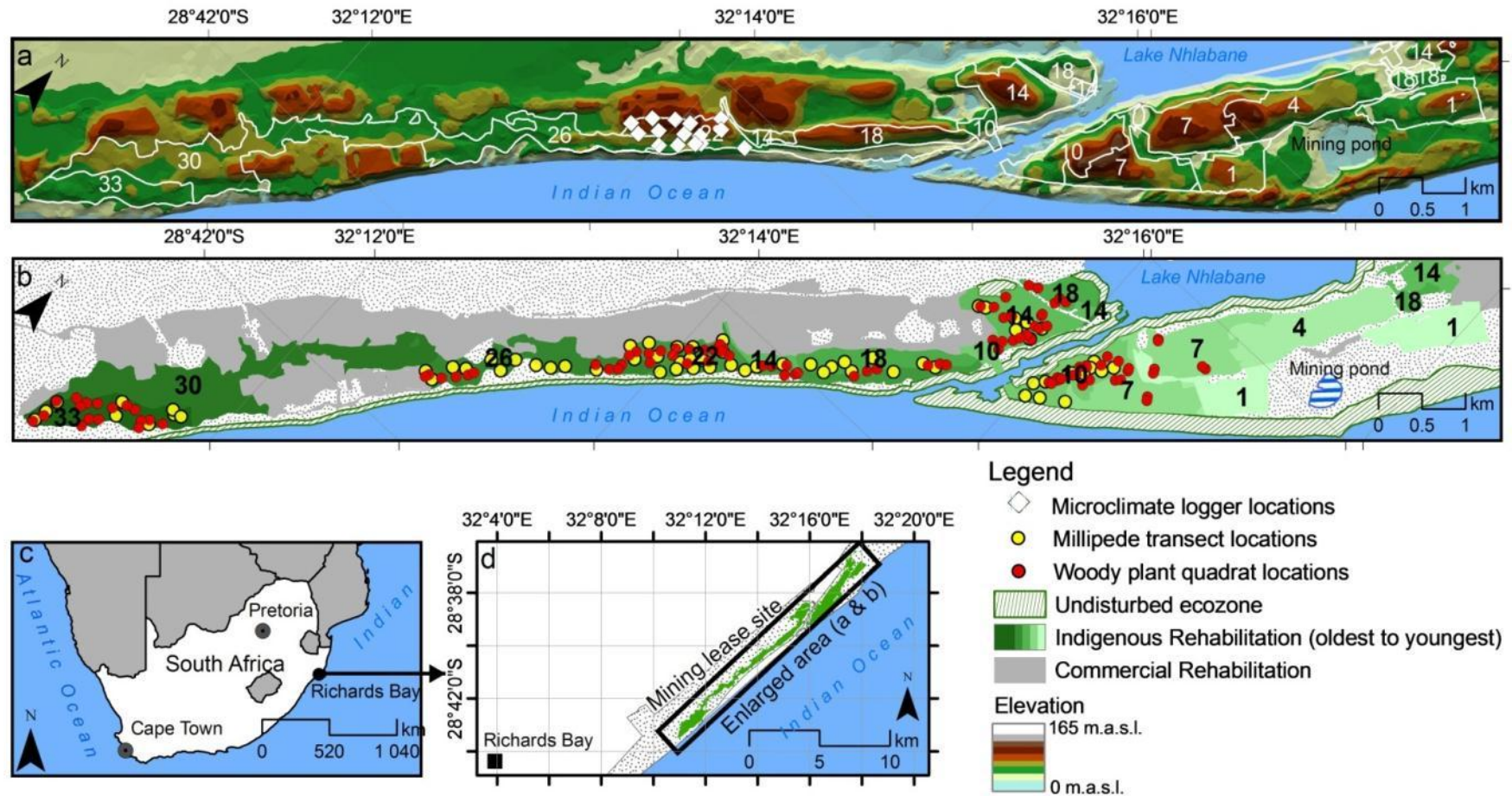


Figure 5-1. Digital elevation model of the study area also showing the delineation of rehabilitating stands according to age, and the sites where data loggers were deployed (a). The locations of woody plant quadrats and millipede transect surveys were conducted are shown in relation to stand age (b). Inset maps provide geographical context (c & d).

Soil surveys

An auger was used to collect soil samples to 20 cm depth at the corners and centre of each of the millipede survey transects (see below). These five samples were mixed into a single bag and consequently 65 bags were analyzed at the Department of Plant Production and Soil Science at the University of Pretoria using procedures described in van Aarde et al. (1998; see supplementary information for detailed chemical profile). We used Nitrogen and Carbon concentrations to calculate the carbon-to-nitrogen ratio (C:N, Table 5-2) and included the pH values of each sample in our analysis.

Table 5-2. Definitions of response variables

| Variable | Definition and units | |
|---------------------|----------------------|---|
| Microclimate | Temperature | Ambient temperature measured in degrees Celsius (°C) |
| | Relative humidity | The partial pressure of water vapor measured as a percentage (%) of the saturated vapor pressure |
| | Light intensity | Incident sunlight, measured as luminous power per area (illuminance) in lumens (lux) |
| Soil | Soil pH | Soil acidity |
| | Soil C:N | Carbon and nitrogen percentage content in soil samples presented as a ratio of carbon-to-nitrogen |
| Woody plants | Canopy tree species | Total number of species forming the canopy (height class 2-5, referred to as trees) per quadrat |
| | TH | Mean tree height (TH) class (2 [>2–4 m], 3 [>4–6 m], 4 [>6–8 m], and 5[>8 m]) of each quadrat |
| | CBH | Per-quadrat mean circumference at breast height (CBH), measurement carried out on all trees (height class 2-5) at ~1.4 m above ground |
| | Canopy tree density | Number of trees per 100 m ² , calculated for each quadrat |
| | Understory species | Total number of species making up the understory (height class 1 [0-2m], referred to as understory plants) per quadrat |
| | Understory density | Number of understory plants per 100 m ² calculated for each quadrat |
| Millipedes | Millipede species | Total number of millipede species per quadrat |
| | Cylindrical density | Number of <i>Centrobolus</i> spp., <i>Doratagonus</i> sp., <i>Spinotarsus anguiliferus</i> , and <i>Spirostreptidae</i> spp. per 100 m ² calculated for each quadrat |
| | Keeled density | Number of <i>Gnomeskelus tuberosus</i> individuals per 100 m ² calculated for each quadrat |
| | Pill density | Number of <i>Sphaerotheridae</i> spp. individuals per 100 m ² calculated for each quadrat |

Woody plant surveys

All woody plants taller than 0.2 m in 106 randomly placed quadrats (16×16-m, at least 100 m apart) in six stands of known regeneration age (10, 14, 18, 22, 26, and 33 years) were sampled between July and November 2010. Each plant was identified against reference material. We calculated six variables of woody plant community structure for each quadrat (see Table 5-2).

Millipede surveys

Millipede species occurring on the ground up to 3 m on plants were counted between 13 January and 4 February 2011 in 65 randomly placed transects within a 10, 14, 18, 22, 26, and 33 year-old stand (see Fig. 2). Each transect was 32 × 6-m wide and comprised 48 2 × 2-m cells. Surveys were conducted by three observers per transect, each responsible for a column of 16 cells. All millipedes found in a cell during five minutes were identified based on reference images and descriptions (Porter et al. 2007), counted, and removed to avoid recounting. We calculated the number of millipede species and the density of cylindrical, keeled, and pill millipedes (see Table 5-2) within each location-specific transect.

Topographic data

We used classified topographic data based on eight cardinal directions (aspect), seven elevation categories, and five gradient categories that had been extracted from a topographic map (see Fig. 5-1.) based on a Light Detection and Ranging (LIDAR) mission conducted in 2010 (post-mining). We used GIS overlay procedures to relate all of the sampling points and quadrat locations recorded in the field to location-specific variables of dune morphology based on the topographic maps.

Statistical analyses

We used stratified random sampling to extract one microclimate record (including the temperature, relative humidity, and light intensity readings) per hour, per logger for each sampling day (29 January – 3 February 2011), rendering 2,475 records to be included in analyses. We \log_{10} -transformed the light intensity data to meet assumptions for analyses of variance (ANOVA). To determine whether microclimatic conditions varied with topography, we conducted repeated measures ANOVA with hour and day as repeated measures factors, and categorized variables of dune morphology as between-groups factors.

We assessed the influence of dune morphological variables on soil C:N ratios and pH, as well as woody plant and millipede community variables in each of the three seral stages. We assessed these using generalized linear models with age as a covariate (Analyses of Covariance (ANCOVA) for all seral stages for woody plants and seral stages 2 and 3 for soil and millipedes. We used ANCOVA because the explanatory variables were continuous and categorical, while the response variable was continuous in each case. The Akaike Information Criterion (AIC) was used to test all terms to find the minimum adequate model. AIC is a penalised log-likelihood that measures the lack of fit by trading off model fit and degrees of freedom. When comparing two or more models the lowest number is 'best'. The lowest AIC value on the number line from plus to minus infinity represents the best-fit model. A large AIC value therefore means a poor-fitting model (Motulsky 2004). Millipede and soil data for seral stage 1 comprised too few cases and was therefore not assessed separately. All statistical analyses were conducted using STATISTICA 10 (Statsoft Inc., Tulsa, Oklahoma).

Woody plant and millipede species abundance data were \log_{10} -transformed and calculated the similarity between quadrats, with different dune morphological

characteristics using the Bray-Curtis index. Cluster analyses and non-metric multi-dimensional scaling (NMDS) were used to detect community clusters based on the four characteristics of dune morphology. Analyses of similarity (ANOSIM) allowed us to assess the significance of community groupings based on dune morphology within each successional stage. To identify the distinguishing species, we conducted similarity percentage (SIMPER) analyses (SIMPER) for those community groupings that differed significantly based on dune morphological characteristics. All multivariate techniques were conducted using PRIMER 6 software (Clarke 1993).

Results

Dune topography and abiotic variables

Temperature varied significantly with aspect and gradient when sampling day and time of day were taken into account (repeated measures ANOVA: $F_{(575, 1035)} = 1.33$, $p < 0.001$ and $F_{(230, 1380)} = 1.27$, $p = 0.007$, respectively). Similarly, relative humidity varied significantly with elevation ($F_{(345, 1265)} = 1.7632$, $p < 0.001$), gradient ($F_{(230, 1380)} = 1.69$, $p < 0.001$) and position ($F_{(230, 1380)} = 1.65$, $p < 0.001$), while light intensity was influenced by aspect ($F_{(575, 1035)} = 1.93$, $p < 0.001$) and position ($F_{(230, 1380)} = 1.38$, $p < 0.001$). Northern slopes were hotter and lighter than other slopes, although south-facing slopes were also relatively warm. Low-lying areas were relatively humid compared to higher dunes. Slopes with mid-range steepness were generally more humid, but cooler than comparatively gentle and steep slopes. Valleys were generally more humid and darker than crests and slopes. For illustrative purposes, we presented one day's data for these significant cases (see Fig. 5-2).

Variability in soil pH was best explained by age in seral stage 2, and a model including aspect, elevation, and position in addition to age in seral stage 3 (ANCOVA

and AIC; Table 5-3). However, none of the models significantly explained variability in soil C:N ratios (Table 5-3).

Dune topography and biotic variables

The 8,833 woody plants sampled in 106 quadrats comprised 7,122 canopy and 1,736 understory plants among 88 species. Variability in all woody plant variables was best explained by models that included age as a covariate within pooled seral stages, as was the case when seral stage 2 was treated separately (ANCOVA and AIC; Table 5-3). The number of tree canopy species in seral stage 1 was best explained by a model including aspect, elevation, gradient, and position, but not age. There were more species on west- and northwest-facing slopes compared to south- and southwest-facing slopes (Figure 5-3a), while relatively flat slopes had fewer species than other gradients (Figure 5-3b), as did crests relative to slopes (Figure 5-3c). However, canopy tree species richness varied little with elevation (Figure 5-3d). Tree density in seral stage 3 increased significantly with gradient (ANCOVA and AIC; Figure 5-3e).

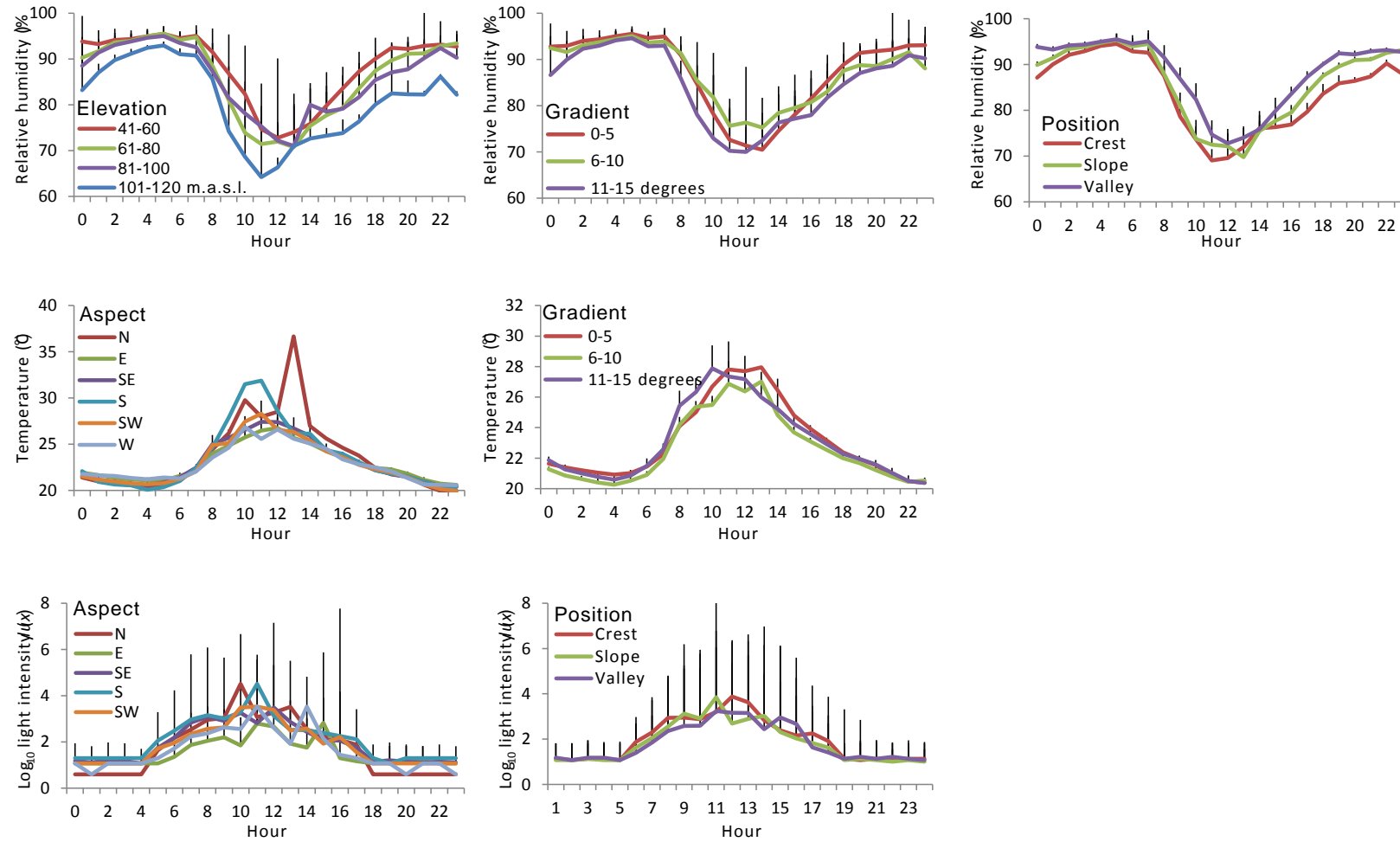


Figure 5-2. Mean ± one standard deviation of the mean of three microclimatic variables (relative humidity, temperature, and light intensity, from top to bottom, respectively) that showed significant responses to variables of dune morphology according to the repeated measures ANOVA, as recorded between 01h00 and 24h00 on the 29th of January 2011.

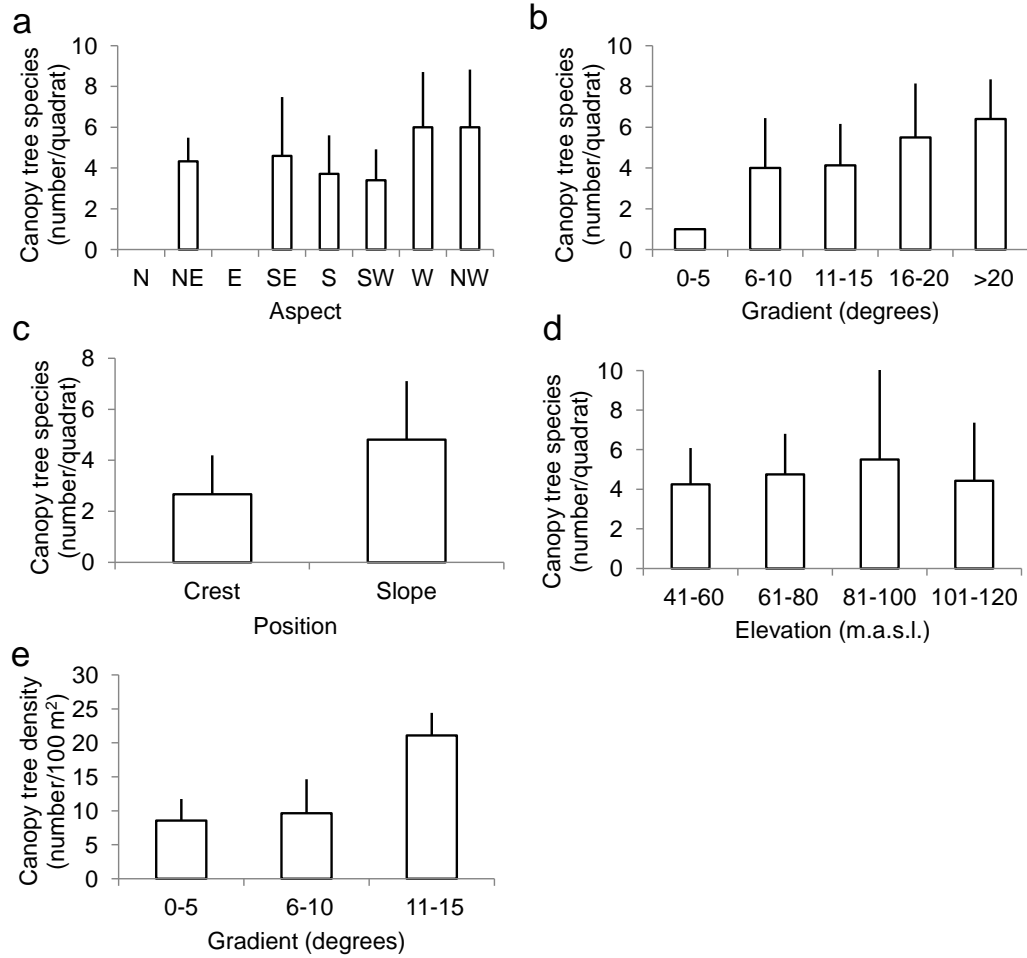


Figure 5-3. Mean \pm one standard deviation of the mean of woody plant response variables presented as a function of those variables that best-explained their variability significantly despite stand age (see Table 2).

Table 5-3. Dune morphological variables included in the most parsimonious models (based on Akaike Information Criteria (AIC) scores) explaining variance in abiotic and biotic variables for each of three seral stages and pooled stages, as well as the significance of the model ($p < 0.05$). Those response variables that were explained by dune morphological variables in the absence of age are highlighted in boldface text.

| Response variables | Seral stage | Explanatory variables | | | | | ANCOVA results | | | |
|-------------------------|---------------------------------|-----------------------|--------------------|----------|----------|----------|----------------|-----------|----------------|-------------------|
| | | Dune morphology | | | | | df | AIC | P | |
| | | Aspect | Elevation | Gradient | Position | Age | | | | |
| Soil | Soil pH | 1 | Insufficient cases | | | | | | | |
| | | 2 | | | | | X | 1 | 54.35 | 0.0005 |
| | | 3 | X | X | | | X | 12 | 13.73 | < 0.0001 |
| | | Pooled | | | | | X | 1 | 157.54 | < 0.0001 |
| | Soil C:N | 1 | Insufficient cases | | | | | | | |
| | | 2 | | | X | | | 4 | 284.46 | 0.119 |
| | 3 | | | | | X | 1 | 186.59 | 0.745 | |
| | Pooled | | | | | X | 1 | 542.26 | 0.778 | |
| Woody plants | Mean canopy height | 1 | X | X | | | X | 9 | 23.03 | < 0.0001 |
| | | 2 | | X | | | X | 5 | 23.77 | < 0.001 |
| | | 3 | X | | X | X | X | 12 | 46.27 | < 0.001 |
| | | Pooled | | X | | | X | 5 | 236.79 | 0.024 |
| | Mean canopy tree CBH | 1 | X | X | | | X | 10 | 158.23 | < 0.0001 |
| | | 2 | | | | | X | 1 | 280.81 | < 0.001 |
| | | 3 | X | | X | | X | 10 | 229.17 | < 0.001 |
| | | Pooled | X | X | X | | X | 16 | 787.49 | < 0.001 |
| | Number of species in canopy | 1 | X | X | X | X | | 13 | 125.49 | 0.002 |
| | | 2 | | X | | | X | 5 | 195.20 | < 0.001 |
| | | 3 | | | X | | X | 3 | 169.77 | 0.015 |
| | | Pooled | | X | | X | X | 7 | 528.67 | < 0.001 |
| | Mean canopy tree density | 1 | | | | | X | 1 | -10.80 | 0.009 |
| | | 2 | X | X | X | | X | 15 | -120.87 | < 0.001 |
| | | 3 | | | X | | | 2 | -120.89 | 0.0004 |
| | | Pooled | X | X | | X | X | 14 | -155.73 | < 0.001 |
| | Number of species in understory | 1 | X | X | X | X | X | 14 | 97.78 | 0.009 |
| | | 2 | | | X | | X | 5 | 105.12 | < 0.001 |
| 3 | | | | X | X | X | 5 | 57.26 | 0.0006 | |
| Pooled | | X | | X | | X | 12 | 289.13 | 0.0008 | |
| Mean understory density | 1 | | | | | X | 1 | 74.66 | 0.679 | |
| | 2 | X | X | X | | X | 15 | -171.69 | < 0.001 | |
| | 3 | | | | | X | 1 | -113.38 | 0.0005 | |
| | Pooled | | | | | X | 1 | -305.24 | 0.003 | |
| Millipedes | Number of species | 1 | Insufficient cases | | | | | | | |
| | | 2 | | | | X | | 2 | 126.00 | 0.016 |
| | | 3 | X | X | X | X | X | 14 | 83.35 | < 0.001 |
| | | Pooled | | | | X | X | 3 | 271.23 | < 0.001 |
| | Cylindrical millipede density | 1 | Insufficient cases | | | | | | | |
| | | 2 | | X | | | X | 6 | 92.18 | < 0.0001 |
| | | 3 | X | X | | X | X | 13 | -18.05 | < 0.001 |
| | | Pooled | X | X | X | X | X | 20 | 183.63 | < 0.001 |
| | Keeled millipede density | 1 | Insufficient cases | | | | | | | |
| | | 2 | X | X | X | X | X | 15 | -114.18 | < 0.0001 |
| | | 3 | X | X | | X | X | 12 | -96.33 | 0.0004 |
| | | Pooled | X | X | X | X | | 9 | -235.50 | < 0.001 |
| Pill millipede density | 1 | Insufficient cases | | | | | | | | |
| | 2 | X | X | X | | X | 14 | -221.88 | 0.004 | |
| | 3 | X | | X | X | X | 12 | -110.06 | 0.0001 | |
| | Pooled | X | X | X | | X | 18 | -400.40 | < 0.001 | |



Only 11% of the variability in tree species abundances was explained by gradient in seral stage 2, although the NMDS plot was unconvincing of this separation (ANOSIM, $p < 0.05$, Table 5-4). Nevertheless, SIMPER analysis revealed consistent dominance by *Acacia karroo* Hayne and *Celtis africana* Burm.f. (contributing more than 80% of the community) across all gradients (Table 5-4). However, the number of species increased with gradient so that in addition to these two species, *Allophylus natalensis* Sond. (Dune False Currant) characterized slopes ranging from 0 to 15° and *Brachylaena discolor* DC. (Coast Silver-oak) those of 11 to 15°. Slopes of more than 15° were characterised by the addition of *Grewia occidentalis* L. (Cross-berry), *Chaetachme aristata* Planch. (Giant Pock Ironwood) and *Teclea gerrardii* I. Verd. (Zulu Cherry-orange), though all with less than a 5% contribution to tree communities on these slopes (Table 5-4).

Table 5-4. Characteristic tree species (taller than 2 m) forming the canopies on slopes of different gradients in seral stage two based on similarity percentage analysis (SIMPER).

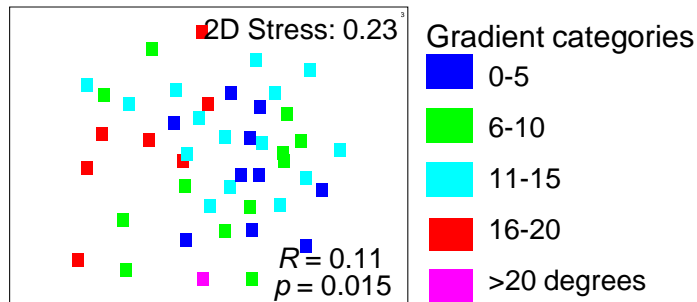
| Species | Family | Average abundance | Average similarity | Similarity SD | Percentage contribution | Cumulative percentage |
|-------------------------------------|-------------|-------------------|--------------------|---------------|-------------------------|-----------------------|
| 0-5 degree slope | | | | | | |
| Average similarity: 54.91 | | | | | | |
| <i>Acacia karroo</i> Hayne | Mimosaceae | 3.26 | 39.44 | 6.11 | 71.83 | 71.83 |
| <i>Celtis africana</i> Burm.f. | Celtidaceae | 0.92 | 7.70 | 1.12 | 14.02 | 85.85 |
| <i>Allophylus natalensis</i> Sond. | Sapindaceae | 0.76 | 4.90 | 0.88 | 8.93 | 94.78 |
| 6-10 degree slope | | | | | | |
| Average similarity: 48.96 | | | | | | |
| <i>Acacia karroo</i> | Mimosaceae | 3.39 | 35.83 | 2.44 | 73.18 | 73.18 |
| <i>Allophylus natalensis</i> Sond. | Sapindaceae | 0.70 | 4.41 | 0.98 | 9.01 | 82.19 |
| <i>Celtis Africana</i> Burm.f. | Celtidaceae | 0.99 | 3.32 | 0.78 | 6.78 | 88.97 |
| <i>Cestrum laevigatum</i> Schlttdl. | Solanaceae | 0.52 | 1.19 | 0.41 | 2.42 | 91.39 |
| 11-15 degree slope | | | | | | |
| Average similarity: 52.42 | | | | | | |
| <i>Acacia karroo</i> Hayne | Mimosaceae | 3.44 | 40.69 | 4.33 | 77.62 | 77.62 |
| <i>Celtis Africana</i> Burm.f. | Celtidaceae | 0.70 | 3.71 | 0.72 | 7.07 | 84.70 |
| <i>Brachylaena discolor</i> (DC.) | Asteraceae | 0.35 | 1.67 | 0.45 | 3.19 | 87.89 |
| <i>Allophylus natalensis</i> Sond. | Sapindaceae | 0.47 | 1.54 | 0.37 | 2.94 | 90.82 |
| 16-20 degree slope | | | | | | |
| Average similarity: 50.52 | | | | | | |
| <i>Acacia karroo</i> Hayne | Mimosaceae | 3.49 | 26.86 | 4.48 | 53.17 | 53.17 |
| <i>Celtis Africana</i> Burm.f. | Celtidaceae | 2.08 | 14.93 | 5.77 | 29.55 | 82.72 |
| <i>Grewia occidentalis</i> L. | Tiliaceae | 0.87 | 2.47 | 0.56 | 4.89 | 87.61 |
| <i>Chaetachme aristata</i> Planch. | Ulmaceae | 0.55 | 1.03 | 0.37 | 2.04 | 89.66 |
| <i>Tecklea gerrardii</i> I.Verd. | Rutaceae | 0.30 | 0.87 | 0.39 | 1.72 | 91.38 |
| >20 degree slope | | | | | | |
| Less than two samples in a group | | | | | | |

Elevation explained 32% of the variability in understory species abundances in seral stage 3 (ANOSIM, $p < 0.05$, Table 5-5). However, this was the result of most cases representing mid-elevations of 41–60 m.a.s.l, with very few cases for other elevation categories. Nevertheless, these mid-elevations were dominated (61% contribution) by *Rhoicissus revoilii* Planch. (Bushveld grape), followed by *Scutia myrtina* Burm.F (Cat-thorn) that contributed 28%, and the invasive alien species, *Chromolaena*

odorata L. (Triffid Weed), contributing 11% (Table 5-5). Elevations of 61–80 m.a.s.l. were dominated by *S. myrtina* alone (Table 5-5).

Seral stage 2

Species-specific canopy abundances



Seral stage 3

Species-specific understory abundances

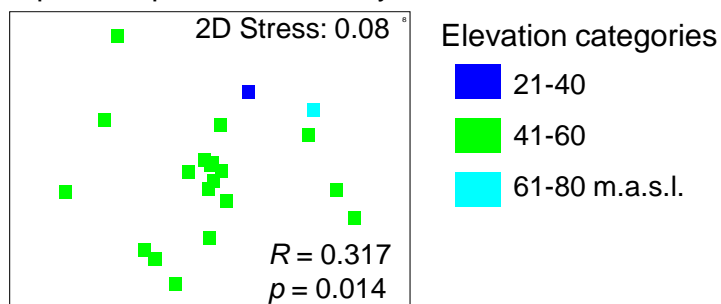


Figure 5-4. Non-metric multi-dimensional scaling (NMDS) plots of woody plant abundances in the canopy (top) and understory (bottom) where analysis of similarity revealed significant ($p < 0.05$) community separation attributable to dune morphological characteristics (elevation, gradient, position) according to seral stages two (11-25) and three (>25 years), respectively.

Table 5-5. Characteristic species occurring in the understory of each elevation category within seral stage three based on similarity percentage analysis (SIMPER).

| Species | Family | Average abundance | Average similarity | Similarity SD | Percentage contribution | Cumulative percentage |
|---|------------|-------------------|--------------------|---------------|-------------------------|-----------------------|
| 21-40 m.a.s.l. Less than 2 samples in group | | | | | | |
| 41-60 m.a.s.l. Average similarity: 44.51 | | | | | | |
| <i>Rhoicissus revoilii</i> Planch. | Vitaceae | 1.49 | 27.25 | 1.10 | 61.23 | 61.23 |
| <i>Scutia myrtina</i> Burm.F. | Rhamnaceae | 0.95 | 12.50 | 0.69 | 28.09 | 89.32 |
| <i>Chromolaena odorata</i> L. | Asteraceae | 0.57 | 4.75 | 0.46 | 10.68 | 100.00 |
| 61-80 m.a.s.l. Average similarity: 30.00 | | | | | | |
| <i>Scutia myrtina</i> Burm.F. | Rhamnaceae | 0.87 | 30.00 | 0.76 | 100.00 | 100.00 |

Millipede assemblages

We recorded 28,987 millipedes (28,351 cylindrical, 513 keeled, and 123 pill millipedes) from 16 species in 65 quadrats. The number of millipede species in the transects of seral stage 2 covaried with dune position (Table 5-3), whereby valleys had the most species, though that of slopes and crests did not differ from one another (Figure 5-5). Models including age as a covariate in addition to variables of dune morphology best explained the density of cylindrical millipedes for pooled and separated seral stages. Pill millipede density was very low and also driven by rehabilitating stand age in combination with dune morphological variables for pooled as well as separate seral stages. The density of keeled millipedes for pooled seral stages was best explained by a model including aspect, elevation, gradient, and position, but not age (Table 5-3). These millipedes were most prolific in valleys (Figure 5-5b), as well as east-facing slopes (Figure 5-5c) with gradients steeper than 10° (Figure 5-5d). However, we found little correlation between millipede

communities and elevation (Figure 5-5e), and when seral stages were separated age was included in the best-fit model (Table 5-3). Based on our ANOSIM analyses none of the variables of dune morphology significantly influenced species-specific millipede abundances.

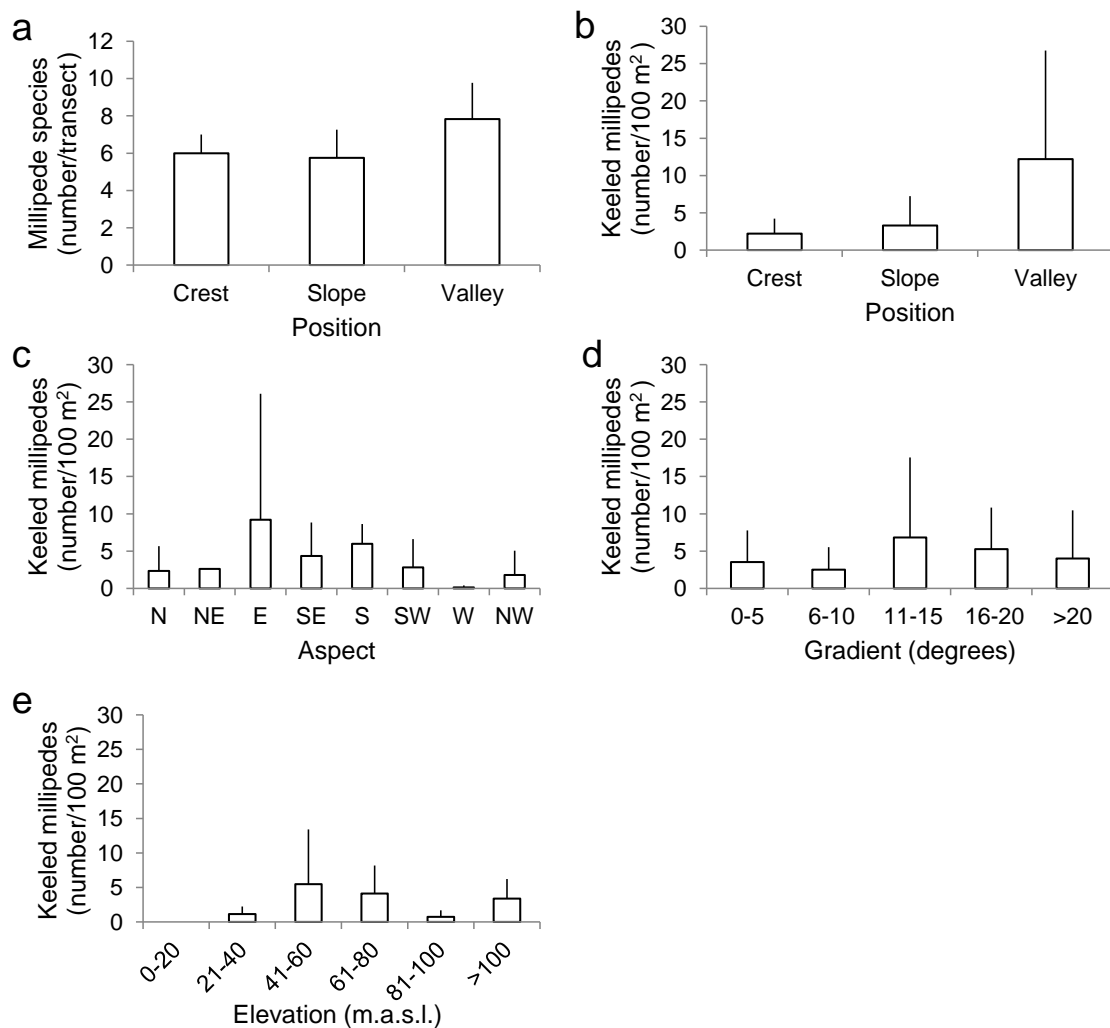


Figure 5-5. Mean \pm one standard deviation of the mean of millipede response variables presented as a function of those variables that best-explained their variability significantly despite stand age (see Table 5-2).

Discussion

As expected, microclimatic conditions varied with dune morphology (see Table 5-1). This finding was in line with those of other studies and similar to the findings of others (Tateno & Takeda 2003; Bennie et al. 2008). We acknowledge though that the conditions on each dune face are likely the product of conditions ameliorated or exacerbated by surrounding dunes that have consequences for wind channelling and shading, thus cumulatively influencing microclimatic conditions. Contrary to our expectations (see Table 5-1), soil nutrient concentrations did not vary with dune morphology, but with regeneration age. The processing of sand as part of the mining operation probably reshuffled soil nutrients and minerals that accumulate through natural processes. With only a few years of post-mining regeneration of biotic activity and mechanical processes (e.g. leeching) it is not surprising that soil fertility (C:N ratios) and pH levels are not yet conforming to expected spatially structured patterns induced by dune topography. Given the weak associations between topographic and abiotic variables, it is also not surprising that spatial variability in woody plant and millipede community structure could not be explained by topographic variables.

Species richness and density, as well as species-specific abundances of canopy trees and the understory varied with topography, as did millipede species richness, all in support of our expectations (see Table 5-1), though with the caveat of an overriding influence of regeneration age. Keeled millipedes, a group of invertebrates associated with forests, also responded to topography as expected, although cylindrical and pill millipedes did not (see Table 5-1). This suggests that forest specialists may be more sensitive to microhabitats induced by topography, but this requires further investigation.

As expected, the structure and distribution of woody plants responded to dune morphology (see Table 5-1), such that increasing slope steepness resulted in more dense woody plant canopies in stands older than 25 years and this finding was similar to that of van Dyk (1996) for earlier stages of regeneration in the study area. Laurance et al. (1999) also described a decrease in the number of large trees with increased tree density on steep slopes. Furthermore, although woody plant communities of different gradients in stands of 11-25 years were generally dominated by similar sets of forest tree species, species composition varied with the gradient of slopes. The majority of these dominant species have previously been identified as those that could colonize newly formed gaps in the woodland (Grainger 2012). This may be due to their ability to grow in low sunlight and high nitrogen levels (e.g. *Celtis africana* Gunton et al. 2010). This was likely due to their wide tolerance to irradiance, temperatures, and moisture that change along dune slopes with elevation and gradient (Ritter et al. 2005). Species abundances of canopy and understory communities responded to different gradients in stands of 11-25 years, and elevation in stands of >25 years, respectively. The number of canopy species, though not their abundances, was best explained by aspect, elevation, gradient, and position in stands younger than 11 years, suggesting that dune morphology may provide habitat conditions that support different species in the early stages of succession when conditions are likely to be most harsh.

Millipede variables also responded to dune morphology as expected (see Table 5-1). However, explanatory models for cylindrical and pill millipede density included age as a covariate. These relationships are likely the result of age-related increases in woodland complexity (Kritzing & van Aarde 1998), moisture-retention and nutrient accumulation associated with litter accumulation (van Aarde et al. 1998), as well as

the variation of microclimatic conditions with topography as discussed above. As in Greyling et al. (2001), two closely related cylindrical millipedes (Centrobolidae) dominated these new-growth forests. This may have obscured patterns in species-specific abundances related to topography. However, the number of millipede species covaried with position on the dune face in stands of 11-25 years, whereby valleys supported more millipede species than slopes and crests. When considering the microclimatic data, this likely relates to the moderate temperature and light intensities but relatively humid conditions that existed in the valleys in comparison with ambient conditions such as wind and high temperatures. Keeled millipedes responded to topographic variables independent of age and this likely relates to the provision of microhabitats for this relatively small, forest-associated species and justifies further study.

Despite the idiosyncratic responses by woody plants and millipedes, position on the dune, as well as aspect, elevation and gradient of the dune face contributed to age-related changes in community structure. Our study also suggests that variability in microclimatic conditions induced by dune topography provides habitats conducive to forest-associated species that have narrow climatic habitat tolerances. This suggests that even though these new-growth forests are in transition, topography may influence the structure and composition of biological communities of new-growth forests, especially when acting in concert with other site-level factors. Such factors are likely to include those previously identified as determinants of community structure and composition, such as landscape composition (Grainger et al. 2011), and age (Wassenaar et al. 2005; Grainger & van Aarde 2012a).

The role of dune morphology seems more obvious in well-established ecosystems (Chen et al. 1997; Oliviera-Filho et al. 1998; Tateno & Takeda 2003;



Larkin et al. 2006), than the new-growth forests that we studied, where age explained changes in assemblages better than topography. Dune topography shaped as part of the rehabilitation procedure provides for the topography that influences local conditions and therefore possibly for ecosystem patterns and processes in a set manner according to prevailing climatic conditions. Topographically, these dunes may differ from those shaped by natural forces (wind, water) which will probably affect patterns and processes. However, these differences may be negligible and therefore not be reflected in biological patterns, especially during the early stages of succession-driven forest regeneration where most community variables vary with regeneration age. For instance, age-related increases in habitat complexity provide an increasing variety of conditions that accommodate more animal species and associated ecological processes (Kritzing & van Aarde 1998; Wassenaar et al. 2005). For example, increased plant diversity, tree senescence and the associated development of a litter layer, increased soil water retention, and nutrient accumulation would presumably benefit millipede communities (e.g. Scheu & Schaefer 1998; Greyling et al. 2001; Berg & Hemerik 2004). In conclusion, topography matters, more so for specialists than generalists. Response to topographic variability is clearly species-specific and not necessarily reflected at the community level.

Chapter 6 | Synthesis

The coastal dune forests in northern KwaZulu-Natal are of high conservation priority, some portions of which were recently listed as critically endangered ecosystems ('Kwambonambi Dune Forest' and 'North Coast Dune forest', Department of Water and Environmental Affairs 2011). These forests are associated with a specific landform – coastal dunes (Berliner 2005; Mucina et al. 2006) and have a legacy as a mosaic of patches in various stages of regeneration as a result of historical disturbances by climatic shifts and people (see Chapter 2, Weisser & Marques 1979; Tinley 1985; Lawes et al. 1990; Watkeys et al. 1993; Finch & Hill 2008). In my study area, these forests comprise a few fragments of old-growth forest situated in a mosaic of various land uses, as well as patches in various stages of regeneration in response to a rehabilitation programme (Grainger et al. 2011, Chapter 2). My thesis provides an evidence-based summary of the role of some site- and landscape-level factors in determining the presence of species in regenerating patches. I aimed to quantify the spatial structure and underlying topographic profile of coastal dune forests and then assess the response of some biological communities to these and related habitat conditions. In this Chapter, I assimilate the findings of this thesis.

The regeneration of a coastal dune forest in response to indigenous ecological processes activated through a rehabilitation programme involves changes in the physical environment and biota over a range of spatial and temporal scales. Restoration failure is often ascribed to local and regional constraints (Suding 2011). The management of restoration programmes therefore involves identifying potential constraints to target outcomes (Holl et al. 2007; Brudvig 2011). The aim of the thesis

was to identify potential hindrances to restoration based on the response of biological communities to local habitat conditions.

Ecological restoration induced by rehabilitation hinges on the colonisation of species indigenous to the target ecosystem from source areas (Holl et al. 2007). While dispersal is largely dependent on regional conditions, colonisation depends on species-specific responses to local conditions here represented by landscape-level (Rutledge 2003; Ewers & Didham 2006), and site-level factors that comprise both abiotic (Marage & Gégout 2009; Laurance et al. 2010) and biotic components (Wardle et al. 2004; Hättenschwiler et al. 2005). Some argue that the so-called “*Field of Dreams*¹” approach is therefore risky because the species pool and environmental conditions that led to the development of the pre-disturbance ecosystem are likely to have changed (Hilderbrand et al. 2005; Wright et al. 2009). Prevailing conditions may cause the ecosystem to diverge from the target (Laurance et al. 2007; Suding 2011)², or even form a novel ecosystem (see Hobbs et al. 2009).

I have illustrated changes in local conditions (Chapters 2 and 3) of coastal dune habitats over time by assessing a few of the responses of some biological communities to landscape- and site-level factors (Chapters 4 and 5). This research therefore falls roughly within the model set out by Brudvig (2011), where, given the regional species pool, the ecologically restored system is the product of the historical context of the site, as well as factors operating at the site- and landscape-level. A

¹ The notion that all that is required to restore ecosystems is the physical structure, and biotic composition and function will self-assemble. Similarly, the restoration of a process (e.g. fire/hydrological regime) is expected to re-create pre-disturbance structure (Hilderbrand et al. 2005; Wassenaar et al. 2007)

² Recent studies accept “divergent” ecosystems as an ecological reality based on changes in species distributions and environmental conditions as a result of climate and land use change (Suding 2011). Such “novel” ecosystems are perhaps likely to become the norm rather than the exception, and perhaps represent a more sustainable outcome of restoration initiatives that require a completely different restoration outlook (Hobbs et al. 2009)

plethora of similar models exist to simplify complex ecological theories and research to understand and predict the outcomes of restoration activities (e.g. Bradshaw 1990b; Naveh 1994; Hobbs 1997; Palmer et al. 1997; Whisenant 2004; Lindenmayer et al. 2008). Brudvig (2011) showed that most research focuses on the restoration of site-level factors to promote species diversity, but the interplay between historical and landscape-level factors has largely been ignored, although site-level factors depend on both these sets of factors (see Figure 1-2). Indeed, I demonstrated that site- and landscape-level factors are in turn dependent on the historical context of a site (Chapters 2 and 3), but that different measures of community structure are better explained by site-level factors that change with the age of new-growth coastal dune forest (Chapters 4 and 5). This supports earlier work in the study area that showed how species assemblages recovered through succession (e.g. Wassenaar et al. 2005; Grainger & van Aarde 2012b).

In essence, I illustrate in this thesis that:-

- 1) Canopy cover differed between the lease and benchmark sites, before and after mining;
- 2) The restored topographic profile had changed little in comparison to the pre-mining profile;
- 3) Responses by animal communities to site-level factors were idiosyncratic and largely age-dependent and
- 4) Abiotic conditions varied little with dune topography and responses by plant and animal communities to variability in the topographic profile were similarly limited and once-again dependent on age.

The responses by woody plant, millipede, dung beetle and bird communities did not vary with topography and associated changes in habitat conditions.

The historical context of landscape- and site-level factors

Historical events influence soil condition, vegetation structure and therefore ecosystem functioning (e.g. Xu et al. 2009; Cristofoli et al. 2010). Changes in canopy cover before the start of mining reflected on the history of land-use by people in the area (Chapter 2). However, the physical environment is artificially ‘rebuilt’ after mining as topsoil is removed ahead of the mining face and spread over the rebuilt dunes to kick-start successional processes (van Aarde et al. 1996b; 1996d).

Furthermore, management interventions such as shade-netting and sowing the cover crop preclude further, more natural shaping of these dunes. The onset of rehabilitation therefore erases the historical context of these dunes.

In Chapter 2, I describe the changes in the spatial structure of indigenous tree canopies over time within the relatively pristine benchmark site and the mineral lease area at three intervals before mining began and three after the rehabilitation of mined areas. In the southern portion of the study area (the lease site), ~20% of canopy cover was made up of patches less than 10 ha in extent. These trends in canopy cover were consistent with historical accounts and other studies claiming that the area had been exposed to slash and burn agriculture and extraction since the Iron Age (Weisser 1980; Watkeys et al. 1993; Bourquin et al. 2000; Finch & Hill 2008). This legacy explains the fragmented nature of forests in the lease site before mining, where patches of forests occurred in a matrix of disturbed woodlands, secondary grasslands, wetlands, subsistence crops, and later on, plantations. Similarly, the increase in indigenous forest cover that I documented here between 1950 and 1970, may be due

to removing people from the area and stabilising the fore dunes by planting Beefwood trees (*Casuarina equisetifolia*) (Weisser & Marques 1979; Watkeys et al. 1993, see Chapter 1). However, the forests of the northern ‘benchmark’ area, were always more contiguous and this lends support to claims that the relatively steep dunes of this area and the prevalence of disease in the swampy valleys rendered it unsuitable for subsistence agriculture until portions were proclaimed as the St Lucia Game Reserve in 1897 (Weisser & Marques 1979; Watkeys et al. 1993).

The mining company has undertaken to restore coastal dune forest on one-third of the mining path (van Aarde et al. 1996c). Historically, the coastal dune topography may have contributed to the heterogeneity in conditions that supported the diverse species assemblages typical of these forests. Given that the topographic profile is destroyed as part of the mining process, the restoration thereof is arguably one of the more important steps of the rehabilitation programme. In Chapter 3, I found that rehabilitation simplifies dune topography. However, there are logistical constraints associated with restoring topographic heterogeneity. For example, steep slopes are difficult to rehabilitate due to sand movement and the number and size of dunes created is dependent on the availability of sand tailings. Although the mining company never undertook to build a facsimile of the topographic profile, these constraints likely led to the differences in topographic heterogeneity and dune morphology found here. The hierarchical link between topography, microclimate, soils, and biological communities is well documented elsewhere (e.g. Martinez et al. 2001; Bennie et al. 2008; da Silva et al. 2008; Laurance et al. 2010). The topographic profile could have other consequences in the short-and long-term; for example, although steep slopes may hinder the reestablishment of plants on the dune face due to moving sand, they are less accessible and may inadvertently protect biodiversity (e.g.

Laurance et al. 2010; Zhao et al. 2012). However, of more immediate concern is that these changes in topography impact on initial conditions in the new-growth forests (Parker 1997). As I have shown, microclimatic conditions vary with topography that in turn affects some species-related variables which is not reflected at the community level (Chapter 5). It is therefore imperative that although it is difficult to replicate the pre-mining topographic profile the mine continues to strive to restore the topographic heterogeneity of these dunes to generate microhabitats suitable for a variety of biological communities.

The response of biological communities to site- and landscape-level factors

As expected, period-specific rates of canopy cover loss with the onset of mining in 1976 increased slightly between 1990-1998 and 1998-2006 as the mine moved northwards into less fragmented areas (Chapter 2). These rates of loss will increase as mining activities continue northwards into relatively pristine forest to within ~4 km of the iSimangaliso Greater Wetlands Park boundary. This highlights the concern that as the mine moves northwards, the benchmark is becoming too isolated for dispersing forest species to reach regenerating areas in the south of the lease site. However, in contrast to Grainger et al. (2011), I found no support for this as none of the taxa that I investigated responded to my measure of isolation (Chapter 4). Several of the metrics that I used suggested trends of change. However, the lack in apparent trends for some of the metrics implies that analyses at a finer resolution are likely required to better assess the responses of different taxa and functional groups.

Grainger (2012) suggested that although successional theory has had an important role to play in guiding restoration ecology, it disregards factors that will filter the species pool, such as landscape composition and historical context (e.g. land-

use, changes in climate). Composition forms part of structure and changes in structure will have consequences for ecosystem function and vice versa (Hobbs 1997).

However, I found limited support for the notion that the variables of habitat structure and composition that I used played an important role in structuring biological communities of regenerating coastal dune forests. Grainger (2012) suggested that restoration success should be based on community composition, structure and function. However, rehabilitation adds structure and function but does not necessarily result in the restoration of community composition (Bradshaw 1984). Indeed, responses by biotic communities depend on species-, taxonomic-, population-level responses to factors that are in turn based on environmental tolerances and inter-specific interactions (Matthews et al. 2009). Most restoration efforts therefore rely on both landscape- and site-level factors of ecosystem structure to facilitate colonisation by target communities (Brudvig 2011).

In Chapter 4, I investigated the relative importance of the composition (woody plant diversity) and substrate (soil quality) of patches of regenerating coastal dune habitat in addition to spatial structure in explaining the composition and structure of animal species assemblages. There is much variability in the way that species perceive a site and I therefore assessed three taxa (millipedes, dung beetles and birds) to take into account different functional groups and dispersal abilities (Swihart et al. 2006; e.g. Barbaro et al. 2007; Golet et al. 2009). As expected, birds responded to the diversity of woody plants constituting a patch and this likely relates to the availability of resources like food and shelter (Kritzinger & van Aarde 1998; Grainger et al. 2011). However, millipedes did not respond to variables of habitat structure as had been expected. Dung beetles and birds responded to soil nitrogen, likely due to an association with regeneration age that increased from north to south. The trends

recorded here could therefore be an artefact of the linear nature of the study area: because mining moves towards the benchmark, the oldest regenerating patches (with the most developed soils) that presumably met habitat requirements more closely were also the furthest away from the benchmark. This suggests that the variables used here (largely an indication of habitat patchiness or heterogeneity), were inappropriate as surrogate or explanatory variables at the scale of assessment used here.

In Chapter 5, I assessed topography as a co-variate of abiotic conditions as well as biological community structure and composition to determine whether the topographic profile (quantified in Chapter 3) of the rebuilt coastal dunes influenced ecological processes. As in other studies based on old-growth forests (Chen et al. 1997; Tateno & Takeda 2003; da Silva et al. 2008), I found that temperature, relative humidity and light intensity within new-growth forests varied with aspect, elevation, gradient and position on the dune. However, as was the case in Chapter 4, age was a more important determinant of soil quality than topography. Given the relatively young age of the new-growth forests (<30 years), it is likely that there had been little time for topography to influence soil nutrient content or pH.

Most studies investigating the variation in habitat conditions with topography, assessed the response of plants (e.g. Tateno & Takeda 2003; Bohlman et al. 2008; da Silva et al. 2008; Laurance et al. 2010, but see Catterall et al. 2001). In addition to woody plants though, I also investigated the response of millipedes because of their known sensitivity to microhabitat conditions (Hopkin & Read 1992; David & Gillon 2009) and importance in processes such as nutrient cycling that facilitates the restoration of coastal forests on the regenerating dunes (Smit & van Aarde 2001). Age also interacted with topographic variables as a determinant of tree canopy density, woody plant species richness and millipede species richness. However, the density of

a keeled millipede species was dependent on all topographic variables regardless of age. The specialist nature of this species and its small size in comparison to the other millipede species may have rendered it more sensitive, but this requires further investigation in the future.

The importance of age

The development of regenerating ecosystems involves systematic changes in the physical environment (abiotic factors such as soil and topography) and biota (biomass, species diversity,) that inevitably lead to systematic changes in spatial structure over time (Cutler et al. 2008). Indeed, research has demonstrated these relationships for the regenerating coastal dune forests of this study site (e.g. van Aarde et al. 1996c; Ferreira & van Aarde 1997; Kritzinger & van Aarde 1998; van Aarde et al. 1998; Kumssa et al. 2004; Wassenaar et al. 2005; Grainger et al. 2011). The restoration of coastal dune forest is therefore age-related (Wassenaar et al. 2005), so that species diversity increases and habitat structure becomes increasingly complex with age, generating new niches for species to fill (Grainger et al. 2011). The correlations between age and habitat variables is not surprising though, 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). Therefore, age likely represents the best proxy of successional processes.

Into the future: Reality check

It is estimated that by 2050 there will be 30% more people to feed worldwide (Lutz & KC 2010). The associated increase in natural resource requirements will compromise biodiversity conservation (Godfray 2011; Phalan et al. 2011), as one-third of

terrestrial ecosystems have already been converted for human use, whilst a further third is heavily degraded (Millennium Ecosystem Assessment 2005). The conservation of landscapes will increasingly depend on the restoration of the degraded third and this realisation has led to increased popularity and viability of restoration initiatives (Suding 2011). Restoration ecology and conservation biology therefore share many goals relating to the maintenance of ecosystem services. Indeed, integrated land conservation, restoration and management requires a landscape perspective (e.g. Hobbs 1997; Fortin & Agrawal 2005; Wiens 2009). This is especially true in South Africa where land degradation continues unabated (Shackleton et al. 2011).

About one-third of the mined portion of the lease site is under rehabilitation at any time, while the rest is revegetated with *Casuarina equisetifolia* plantations in accordance with the land-use patterns prior to mining and in agreement with the then land owner – the State. The coastal dunes within and outside of the now-mining lease area remain under pressure from threats of development and subsistence expansion due to the proximity of Richards Bay town, the mine and other associated industries that continue to draw people into the area.

My study is based on the assumption that old-growth and new-growth coastal dune forest represented the only habitat in a hostile matrix. However, recent studies suggest that the quality of the matrix is more important than patch area and isolation as a determinant of dispersal and colonisation (see Prevedello & Vieira 2010; Turgeon & Kramer 2012). I therefore suggest that future research at this study area should consider the landscape mosaic. In addition, given the recent alarming trends in regional bird population structure (Trimble & van Aarde 2011), such studies should include forest remnants from across the region. In this study area, remnant old- and

new-growth forest patches alike have become increasingly surrounded by a transformed mosaic of sugarcane fields, mining, plantations, rural settlements, and peri-urban development (Wassenaar et al. 2005; Grainger et al. 2011). It is yet unknown to what extent other land-cover types can serve as habitat to species typical of coastal dune forests, but it is likely that the landscape is not binary (habitat/non-habitat), but rather a heterogeneous continuum from ideal habitat to hostile areas (Wiens 1995).

These forests form the narrow, southern-most distribution of the East African coastal forests and are expected to exhibit a peninsula effect (Simpson 1964), as well as distributional edge effects (Caughley et al. 1988). This means that with increasing latitude (from the benchmark to the lease site) the dune forests will comprise fewer northern forest specialists and probably more generalists, also common to adjacent savannah and grassland biomes (van Aarde et al. 2012). This suggests that future studies should consider the quality, context, boundary permeability and connectivity of patches in a landscape mosaic, thereby providing a more realistic approach to characterising the responses of biological communities to spatial structure (Wiens 1997). Such landscape-level factors will influence the dispersal of potential colonisers to the regenerating patches (Watson 2002; Bender & Fahrig 2005), thus impacting site-level biodiversity (Damschen et al. 2008; Mabry et al. 2010; Brudvig 2011) and the persistence of forest species within the region (e.g. Fernández-Juricic 2004; Sekercioglu et al. 2007; Hendrickx et al. 2007). Ecosystems do not function independently of their surroundings and, as is the case in this study area, sites under restoration are often too small to be self-sustaining and must be considered as part of the greater landscape or region (Parker 1997; Bradshaw 1997; van Diggelen 2005; Simenstad et al. 2006; Brudvig 2011). Future studies should therefore use a landscape



approach to quantify the movements of forest-associated species between old- and new-growth forest patches, as well as non-forest patches throughout the landscape to help build a better understanding of the role of spatial structure in the restoration of these forests.