Coastal dune topography as a determinant of abiotic conditions and biological community restoration in northern KwaZulu-Natal, South Africa

Theresia Ott • Rudi J. van Aarde

T. Ott (correspondence author) • R. J. van Aarde
Conservation Ecology Research Unit, Department of Zoology and Entomology, University of Pretoria, Pretoria, South Africa e-mail: tott@zoology.up.ac.za

R. J. van Aarde
e-mail: rjvaarde@zoology.up.ac.za

Abstract Topography is rarely considered as an independent goal of restoration. However, topography determines microenvironmental conditions and hence living conditions for species. Restoring topography may therefore be an important first step in ecological restoration. We aimed at establishing the relative importance of topography where coastal dunes destroyed by mining are rebuilt as part of a rehabilitation program. We assessed the response of (1) microclimatic and soil conditions, and (2) woody plant and millipede species richness and density, to location-specific topographic profiles. We enumerated the topographic profile using variables of dune morphology (aspect, elevation, and gradient) as well as relative position on a dune (crest, slope, and valley). Temperature, relative humidity, and light intensity varied with aspect, elevation, gradient, and position. However, regeneration age was a better predictor of soil nutrient availability than these topographic variables. Age also interacted with topographic variables to explain tree canopy density and species richness, as well as millipede species richness. The density of keeled millipedes (forest specialists) was best explained by topographic variables alone. The transient nature of these new-growth coastal dune forests likely masks topography-related effects on communities because age-related succession (increasing structural complexity) drives the establishment and persistence of biological communities, not habitat conditions modulated by topography. However, our study has shown that the microhabitats associated with topographic variability influence specialist species more than generalists.

Keywords Aspect · Dune morphology · Elevation · Gradient · Microclimate · Soil

Introduction

Ecological restoration is widely recognized as a conservation tool and aims to reinstate natural processes that sustain biological diversity (Dobson et al. 1997; MacMahon and Holl 2001; Rands 2012). 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 and 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). Restoration of topography may be a priority (Weiss and 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 and van Aarde 2012a). This may be due to the microenvironmental needs of specialist species not being met due to constraints imposed by topography. Justification of terrain restoration 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 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 modulate 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 and Takeda 2003). Canopy structure changes with gradients in soil fertility and light (Nichols et al. 1998; Tateno and 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), hastens canopy gap formation (Ritter et al. 2005), and contributes to seed dispersal (Furley and 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 and Newey 1979; Chen et al. 1997; Acosta et al. 2007). We therefore expected dune morphology and position would (1) modulate microclimatic conditions (temperature, relative humidity, and light intensity) and (2) influence soil nutrient availability (C:N ratio) and soil pH (Table 1). Disturbed or destroyed topographic profiles could therefore hinder the ecological restoration of plant and animal communities of new-growth forests, or simply alter heterogeneity and rearrange the distribution of resources. Thus, 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.

Topography influences plant growth and species richness in old-growth forests (Tateno and 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, render them sensitive to microclimatic conditions that dictate habitat preferences (Ashwini and Sridhar 2008; Loranger-Merciris et al. 2008; David and Gillon 2009). We therefore assessed the importance of the topographic profile in structuring millipede assemblages. We expected that, within a seral stage, dune morphology and position would (3) influence plant community structure and composition, and (4) millipede community structure and composition in regenerating stands of new-growth coastal dune forest (Table 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 regenerating coastal dune forests, it may have implications for any disturbed dune system under restoration.

Table 1 Key questions and expectations of this study

Key question	General assumptions	Expectations	Examples from the literature
1. Does dune topography influence abiotic conditions?	Dune topography modulates microclimatic conditions	Irradiation, temperature, and humidity may increase or decrease, depending on exposure to wind and sun that is facilitated or eased by dune aspect, elevation, and position	Tateno and 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 and Takeda (2003)
2. Does dune topography influence biotic conditions?	Dune topography influences woody plant community structure and distribution	• Woody plant richness will depend on aspect, elevation, and position, depending on their exposure to wind	van Dyk (1996), Oliviera-Filho et al. (1998), da Silva et al. (2008), Laurance et al. (2010)
		• Woody plant canopy structure will depend on gradient and position	
		• Species-specific woody plant abundances will differ based on dune morphology and position	
	Dune topography influences millipede community structure and distribution	• Millipede richness, as well as taxon-specific density, may be influenced by aspect, elevation, and position, depending on their exposure to wind and sunlight	Weiss and Murphy (1990), Moir et al. (2009)
		• Species-specific millipede abundances will differ based on dune morphology and position	

Methods

Study area

The study area is located north of Richards Bay Town (between 28°46′ and 28°34′ S) on the subtropical north coast of KwaZulu-Natal, South Africa (Fig. 1). The climate is humid with mean annual rainfall of 1458 ± 493.5 mm (mean ± SD, $n = 34$ years between 1976 and 2009), peaking in February. The mean annual temperature was 23.79 ± 3.40 °C ($n = 3$ years between 2006 and 2009). Winds of between 10 and 40 km h^{-1} blew from the northeast for about 20 % of the time, as did those from south–southwest and southwest 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 and Marques 1979; Lawes 1990). These forests are therefore relatively young and harbor few endemic species (Lawes 1990; van Wyk and 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 premining topography and were covered with topsoil (van Aarde et al. 1996c). A third of the mined area was set aside for 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) (Fig. 1). This age range represented three seral stages based on those defined by Grainger (2012): seral stage 1 (1–10 years), 2 (11–25 years), and 3 (>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, USA) were deployed in the 22-year-old stand (Fig. 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 2 for definitions) every 10 min between 0800 hours,
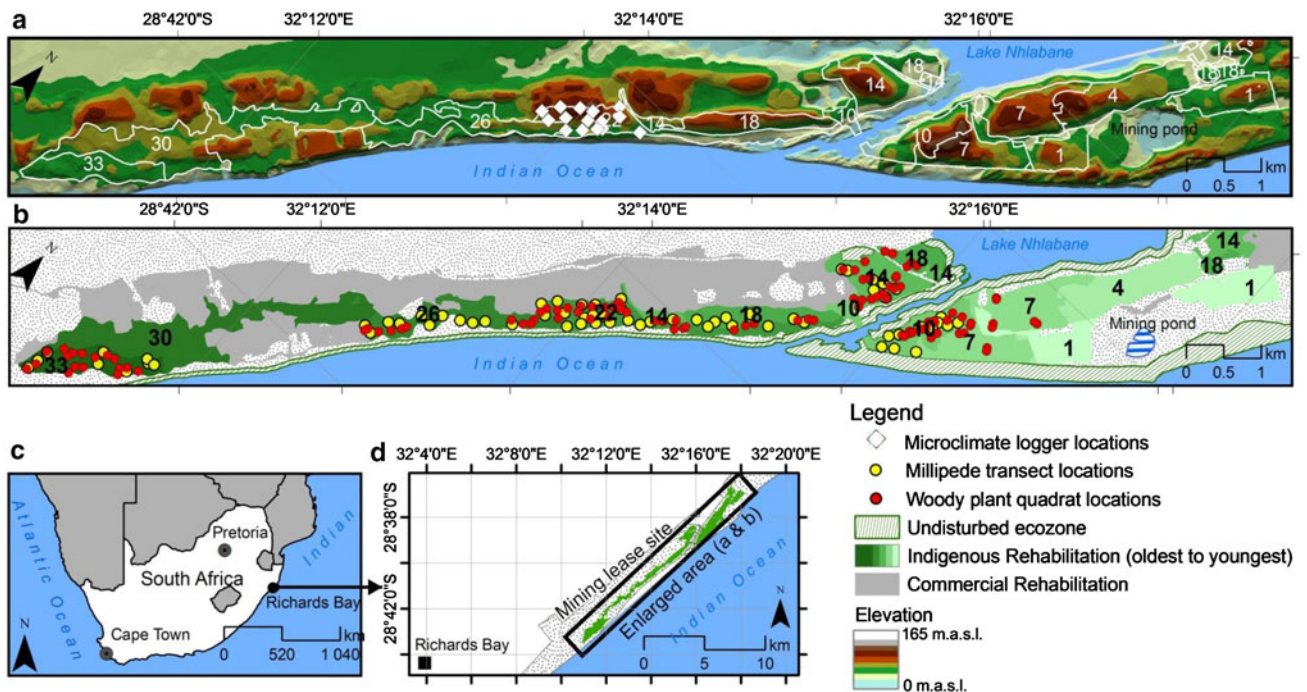

Fig. 1 Digital elevation model of the study area also showing the delineation of rehabilitating stands according to age, and the sites where data loggers were deployed (**a**). The locations of woody plant quadrats and millipede transect surveys are shown in relation to stand age (**b**). *Inset maps*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

Table 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 (0–2 m), 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 *Centrobolus* spp., *Doratogonus* sp., *Spinotarsus anguiliferus*, and Spirostreptidae spp. per 100 m^2 calculated for each quadrat
Keeled density	Number of *Gnomeskelus tuberosus* individuals per 100 m^2 calculated for each quadrat
Pill density	Number of Sphaerotheriidae spp. individuals per 100 m^2 calculated for each quadrat

28 January and 0500 hours, 4 February 2011, yielding 14,850 records.

Soil surveys

An auger was used to collect soil samples to 20 cm depth at the corners and center 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 2) and included the pH values of each sample in our analysis.

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 (Table 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 (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 5 min 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 (Table 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 (Fig. 1) based on a light detection and ranging (LIDAR) mission conducted in 2010 (post-mining). We used geographic information system (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.
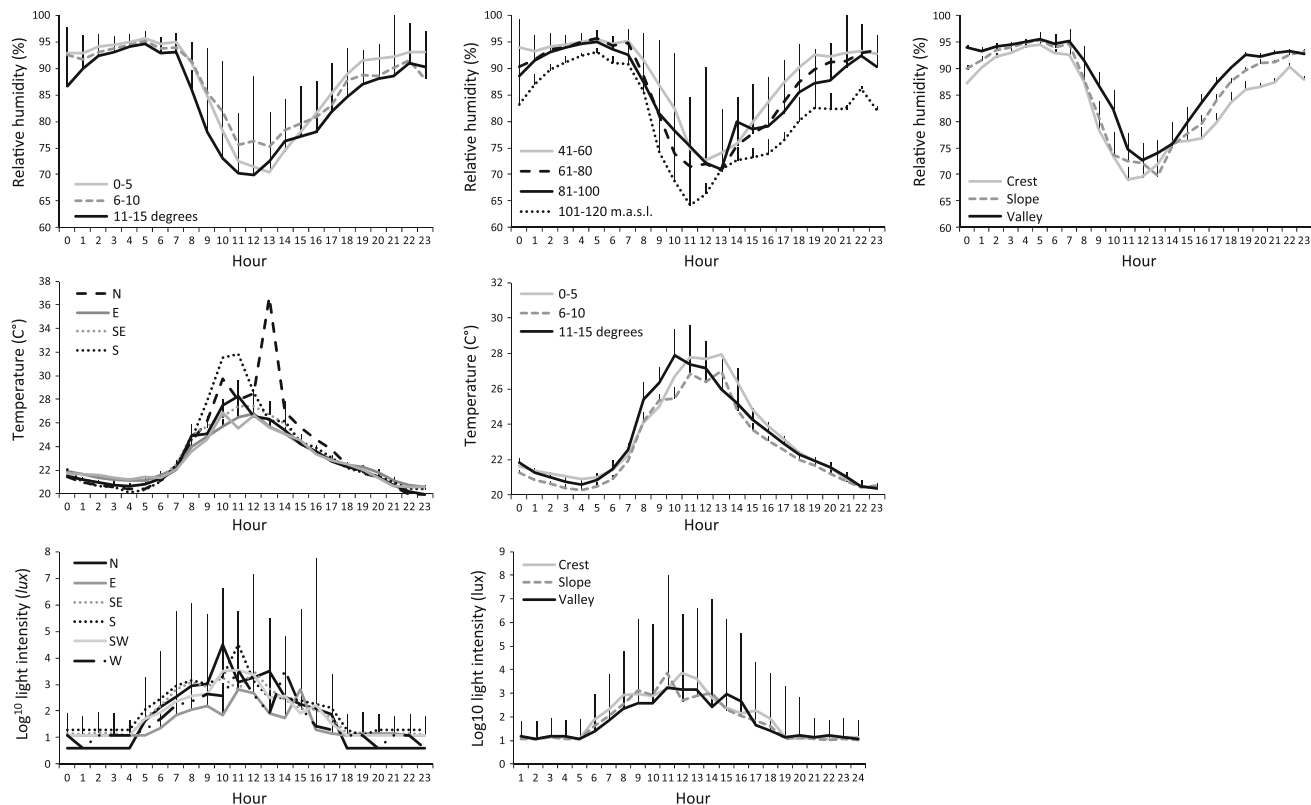
Fig. 2 Mean ± standard deviation of three microclimatic variables (relative humidity, temperature, and light intensity, from top to bottom, respectively) that showed significant responses to variables of dune morphology according to repeated-measures analysis of variance (ANOVA), as recorded between 0100 and 2400 hours on the 29 January 2011

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 to 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 were modulated by 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 by analyses of covariance (ANCOVA) for all seral stages for woody plants and seral stages 2 and 3 for soil and millipedes. Millipede and soil data for seral stage 1 comprised too few cases and were therefore not assessed separately. All statistical analyses were conducted using STATISTICA 10 (StatSoft Inc., Tulsa, OK, USA).

Woody plant and millipede species abundance data were $\log_{10}$-transformed, and we calculated the similarity between quadrats with different dune morphological characteristics using the Bray–Curtis index. Cluster analyses and nonmetric multidimensional 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 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 was significantly modulated by 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 was significantly modulated by 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 with 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 present 1 day's data for these significant cases in Fig. 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 3). However, none of the models significantly explained variability in soil C:N ratios (Table 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 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 with south- and southwest-facing slopes (Fig. 3a), while relatively flat slopes had fewer species than other gradients (Fig. 3b), as did crests relative to slopes (Fig. 3c). However, canopy tree species richness varied little with elevation (Fig. 3d). Tree density in seral stage 3 increased significantly with gradient (ANCOVA and AIC; Fig. 3e).

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, $p < 0.05$, Fig. 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 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 11–15°. Slopes of more than 15° were characterized 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 5 % contribution to tree communities on these slopes (Table 4).

Elevation explained 32 % of the variability in understory species abundances in seral stage 3 (ANOSIM, $p < 0.05$, Fig. 4). 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). Elevations of 61–80 m a.s.l. were dominated by *S. myrtina* alone (Table 5).

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 3), whereby valleys had the most species, though slopes and crests did not differ from one another in this regard (Fig. 5). Models including age as a covariate in addition to variables of dune morphology best explained the density of cylindrical millipedes for pooled and separate 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 3). These millipedes were most prolific in valleys (Fig. 5b), as well as east-facing slopes (Fig. 5c) with gradients steeper than 10° (Fig. 5d). However, we found little correlation between millipede communities and elevation (Fig. 5e), and when seral stages were separated, age was included in the best-fit model (Table 3). Based on our ANOSIM analyses, none of the variables of dune morphology significantly influenced species-specific millipede abundances.

Discussion

In line with our expectations, dune morphology modulated microclimatic conditions in a similar manner as reported in other studies (Tateno and Takeda 2003; Bennie et al. 2008). However, we acknowledge that the conditions on each dune face are likely the product of conditions ameliorated or exacerbated by surrounding dunes that have consequences for wind channeling and shading, thus cumulatively influencing microclimatic conditions.

Table 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 ($p < 0.05$)

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

Response variables that were explained by dune morphological variables in the absence of age are highlighted in bold

Fig. 3 Mean ± standard deviation of woody plant response variables presented as a function of those variables that best explained their variability significantly despite stand age (Table 2)
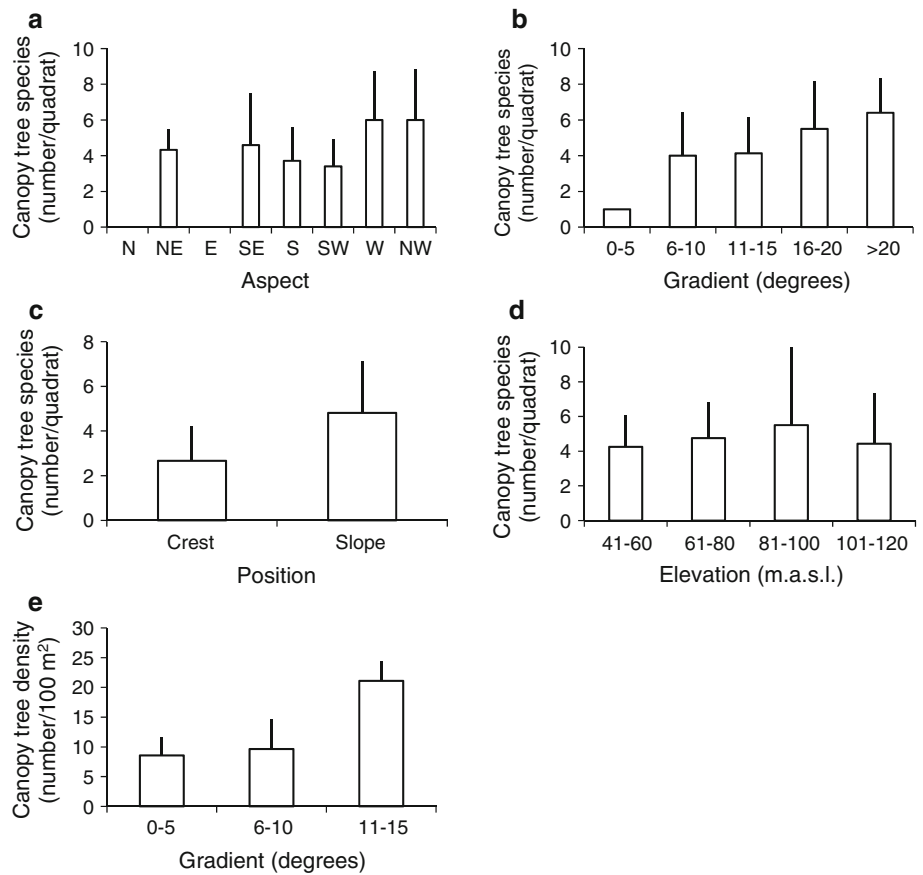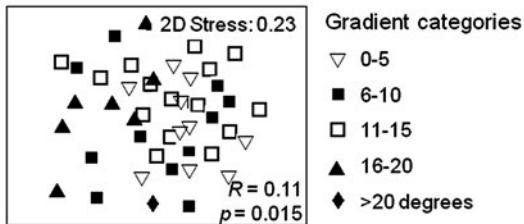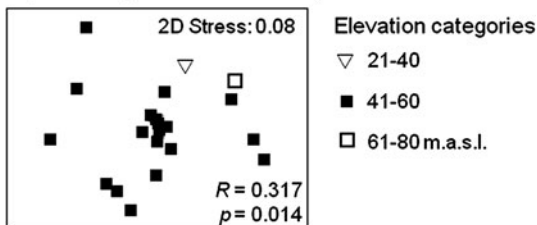

Fig. 4 Nonmetric multidimensional scaling (NMDS) plots of woody plant abundances in the canopy (*top*) and understory (*bottom*) where analysis of similarity revealed significant (*p* < 0.05) community separation attributable to dune morphological characteristics (elevation, gradient, and position) according to seral stages 2 (11–25) and 3 (>25 years), respectively

Contrary to our expectations, variability in soil nutrient concentrations was not explained by dune morphology, but rather by 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., leaching) it is not surprising that soil fertility (C:N ratios) and pH levels are not yet conforming to expected 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, though with the caveat of an overriding influence of regeneration age. Keeled millipedes, a group of invertebrates associated with forests, responded to topography regardless of regeneration age, though cylindrical and pill millipedes did not. This suggests that forest specialists may be more sensitive to microhabitats induced by topography, although this requires further investigation.

Increasing slope steepness resulted in denser woody plant canopies in stands older than 25 years, a finding

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

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

Table 5 Characteristic species occurring in the understory of each elevation category within seral stage 3 based on similarity percentage analysis (SIMPER)

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

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. 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. Incidentally, the majority of these

Fig. 5 Mean ± standard deviation of millipede response variables presented as a function of those variables that best explained their variability significantly despite stand age (Table 2)
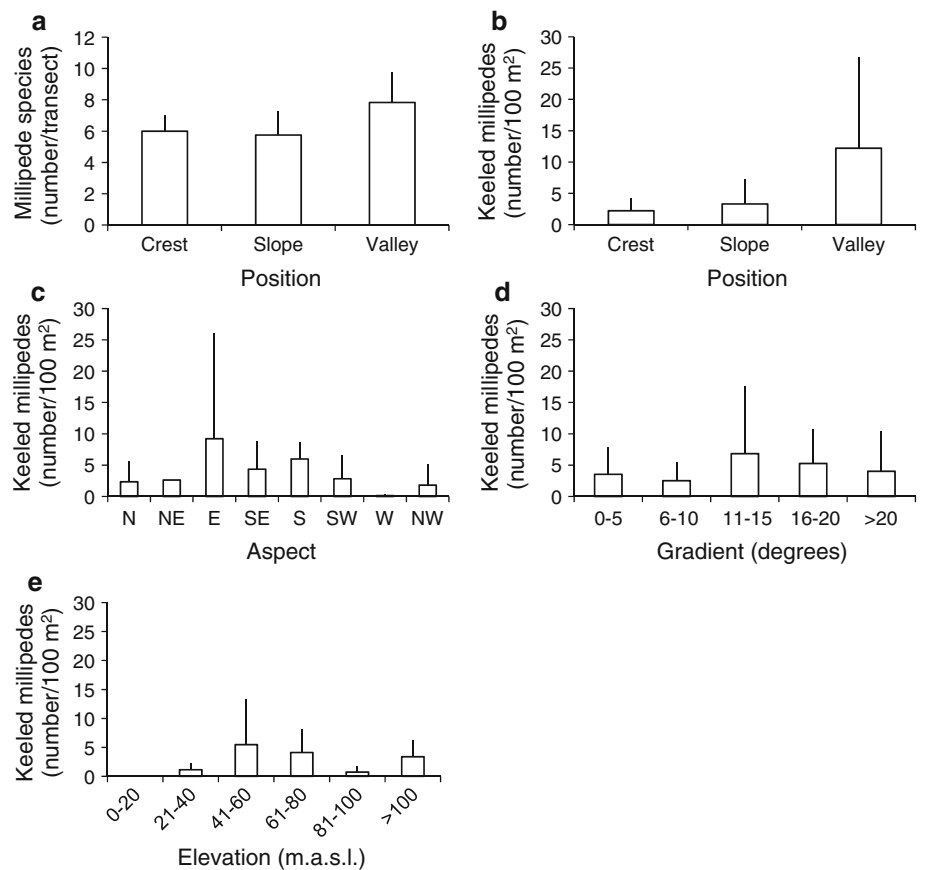
dominant species were identified by Grainger and van Aarde (2012b) as species that could colonize newly formed gaps in woodland. This was likely due to their wide tolerance to irradiance, temperatures, and moisture that change along dune slopes with elevation and gradient (Ritter et al. 2005). Species 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 harshest.

Millipede variables also responded to age and dune morphology. 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 (Kritzinger and van Aarde 1998), moisture retention, and nutrient accumulation associated with litter accumulation (van Aarde et al. 1998) and the modulation of microclimate by 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 independently 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, due to its modulation of microclimatic conditions, 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 and van Aarde 2012).

The role of dune morphology seems more obvious in well-established ecosystems (Chen et al. 1997; Oliviera-Filho et al. 1998; Tateno and Takeda 2003; Larkin et al. 2006) than in 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 (Kritzinger and 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 and Schaefer 1998; Greyling et al. 2001; Berg and 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.

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