Glossary of Terms

Term	Definition
Benchmark	A reference site that can serve as a model or target for planning and evaluating an ecological restoration project (SER 2004).
Dune morphology	The topographic profile of sand dunes based on the aspect, elevation and gradient of their slopes.
Ecological restoration	The process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed (SER 2004).
Historical context	Also known as the historical contingency, land-use legacy or historical landscape of a site, this considers year-on-year effects. In this thesis, I illustrated the land-use legacy and its effect on the historical landscape.
Landscape-level factors	Factors such as the habitat mosaic, inter-patch connectivity and patch structure that influence the dispersal and colonisation of species at the local scale (Watson 2002; Brudvig 2011). This thesis focuses on the structure (area, shape and isolation) of old- and new-growth forest patches.
Lease site	The land leased by the mining company from the landowner for mining activities until mine closure (mineral lease area).
New-growth forest	Regenerating coastal dune forest.
Old-growth forest	Relatively undisturbed indigenous coastal dune forest.
Patch	A continuous indigenous tree canopy that may differ in species composition.
Patch structure	The spatial structure of patches of indigenous tree canopies determined using spatial analysis procedures to quantify patch area, shape, and isolation.
Post-mining	Refers to the period from the end of mining at a defined area in the lease site until 2006, within which patch structure for 1990, 1998 and 2006 (13, 21 and 29 years after mining and rehabilitation, respectively) was assessed.
Pre-mining	Refers to the phase prior to the onset of mining on the lease site in 1976, within which I assessed patch structure for 1937, 1957 and 1970 (40, 20 and 7 years prior to mining, respectively).
Regional factors	Factors that impact whole regions, (where a region is defined as an area composed of landscapes with the same macroclimate and tied together by human activities (Forman 1995) that are usually associated with climatic shifts and anthropogenic land transformation leading to large-scale changes to landscapes.
Seral stage	An intermediate stage of ecological succession, but progressing towards a climax state. In this study three seral stages were recognised according to Grainger (2012), based on the age of regenerating stands one = 1-10, two = 11-25, and three >25 years.
Site	Portions of the study area delineating either the mineral lease areas (directly exposed to disturbances associated with mining) or the relatively undisturbed benchmark.

Site-level factors	Abiotic and biotic factors operating within a site that filter biological diversity and are often monitored and manipulated as part of rehabilitation programs.
Spatial structure	A collective term used in this thesis that refers to canopy coverage, patch area, shape and the isolation of patches.
Stand	Regenerating area of known age.

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Chapter 1 General Introduction

'*If you build it, they will come*' – the Field of Dreams Hypothesis, as it has become known by some restoration ecologists, epitomizes the assumption that the rehabilitation of local habitat structure will result in the restoration of biological communities through natural processes (Palmer et al. 1997). However, unforeseen biophysical filters induced by historical disturbances, the surrounding landscape, or the reconstruction of the physical environment can hinder ecological restoration (Bradshaw 1997; Holl et al. 2007). Ecological research that identifies such filters will help to pre-empt impacts that these factors may have on the restoration of ecosystems (Harper 1990; SER 2004). Furthermore, due diligence given to any rehabilitation programme comes down to practicability and economics, and costs are presumably substantially reduced with a better understanding of the ecosystem under restoration (Bradshaw 1990a; van Andel & Aronson 2005). In this thesis, it is postulated that changes in the biophysical features of regenerating coastal dune habitats on the northeast coast of South Africa could present filters to the restoration of biological communities. To test this, the response of biological communities to spatial changes in coastal dune habitat over time is investigated.

Brudvig et al. (2011) proposed a conceptual model of ecological restoration that illustrates the restored system as a product of the historical context, as well as landscape-, and site-level factors that filter regional biodiversity (Figure 1-1). Despite the simplicity of this model, it merely echoes other frameworks (e.g. Palmer et al. 1997; Holl et al. 2007) in that it encapsulates the importance of both regional and local factors that in turn represent a suite of features that drive restoration. However, there is more to restoration than a simple framework as is made clear by recent work

(e.g. Lessard et al. 2013). In this thesis, local factors (see Figure 1-1) that may explain the distribution and abundances of species and communities from selected taxa in a coastal dune forest were assessed.
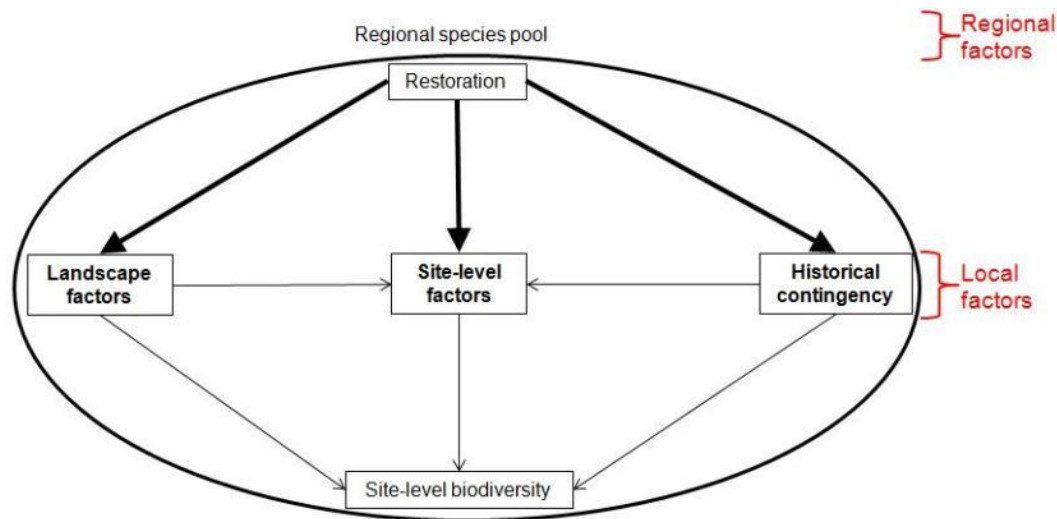
Figure 1-1. Conceptual model of biodiversity restoration as proposed by Brudvig (2011) whereby biodiversity at a site is the result of landscape, site-level, and historical factors. In this study though, historical contingency is referred to as historical context. Regional and local factors are indicated in red. Reproduced and modified with permission from the *American Journal of Botany*.

This thesis comprises five chapters. In Chapters 2 to 5, four case-studies that consider features of rehabilitated coastal dunes that may facilitate or hinder the restoration of coastal dune forest habitat are presented. Each of these chapters deals with at least one of the three so-called filters in Brudvig's (2011) model – historical context, as well as landscape- and site-level factors. The final chapter (Chapter 6) focuses on the management and conservation implications of my study.

Historical context

Geomorphological and climatic processes that operate over millennia determine the distribution and extent of ecosystems (Swanson et al. 1988; Bridge & Johnson 2000). However, the structure and composition of biological communities within these ecosystems is also the product of a history of local processes, as are the interactions between members of the species pool (Parker 1997; Jacquemyn et al. 2003; Fukami 2010; Lessard et al. 2012). Disentangling these processes that ultimately determine the role of regional, landscape and site-level processes requires research at a range of temporal and spatial scales (see Lessard et al. 2012).

Humans though, are an integral part of the landscape (Szabó & Hédl 2011) and unrivalled in their ability to modify or destroy habitat (Vitousek et al. 1997) and our practices therefore form part of the historical context of a landscape (Jacquemyn et al. 2003; Lindenmayer et al. 2006). Studies investigating related changes in community composition over time and in relation to land-use histories are imperative to restoration ecology as they provide insight into the successional processes operating within a site (e.g. Xu et al. 2009; Lessard et al. 2012) and the proximate forces driving land-cover and land-use change (e.g. Arroyo-Mora et al. 2005). Such studies therefore help to define realistic targets for rehabilitation programmes (SER 2004; Ehrenfeld 2000; Suding 2011). In addition, the temporal patterns of land-cover change may have implications for the presence of species as a result of changes in the distribution of habitat.

Landscape-level factors

It is widely acknowledged that a landscape perspective is required to develop an integrated approach to land conservation and management (e.g. Hobbs 1997; Fortin &

Agrawal 2005; Wiens 2009). Landscapes are heterogeneous – and some areas complement the resource, shelter and reproductive requirements of certain species better than others (i.e. optimal foraging theory, Emlen 1966; MacArthur & Pianka 1966). The structure of habitat patches across a landscape is therefore an important determinant of colonisation and persistence (e.g. Chave 2001; Ewers & Didham 2006; Sekercioglu et al. 2007). Given the growing concerns surrounding habitat loss and fragmentation, a plethora of metrics were developed to quantify just three features of habitat patches: their composition (number and size), shape (edge to core ratio) and configuration (isolation/connectivity) (Forman & Godron 1981; Gustafson 1998; McGarigal et al. 2002; Rutledge 2003). Many of these metrics are highly correlated (Riiters et al. 1995; Rutledge 2003), but effective measures of landscape pattern that can be related to ecological processes (Li & Reynolds 1994; 1995). For example, larger patches with more regular shapes relate to more core habitat with less edge that may support more forest-associated species (e.g. Watson et al. 2004; Ewers & Didham 2006). Isolation, or fragmentation lead to losses in habitat connectivity and therefore influence the occupancy and persistence of biotic assemblages in a habitat patch (Baguette et al. 2003; Ewers & Didham 2006; Wallis de Vries & Ens 2009; Grainger et al. 2011). Therefore, taking metapopulation theory into account, the greatest contribution of a landscape ecological approach is likely the characterisation and management planning of fragmented landscapes allowing for a broad-scale approach to conservation issues that recognises spatial complexity and dynamics (Turner et al. 2001; Wiens 2009).

Site-level factors

Site-level factors represent a series of filters to potential colonisers of habitat patches (Mabry et al. 2010; Brudvig 2011). Such filters include local abiotic and structural

conditions often influenced by historical, regional and landscape-level factors (Brudvig 2011). For example, microclimatic conditions such as temperature, relative humidity, and incident light are generally associated with a climatic region, but are influenced by patch structure (Weiermans & van Aarde 2003; Rutledge 2003) and topography (Tateno & Takeda 2003; Laurance et al. 2010) within a site. As such, site-level factors include any number of cascading effects present in regenerating landscapes including relationships between abiotic factors (e.g. Crooks et al. 2002; Chen et al. 2005; Ritter et al. 2005; Grainger et al. 2011) or between abiotic and biotic factors (Smit & van Aarde 2001; Xiong et al. 2003; Ottermanns et al. 2011; Lessard 2012).

Coastal Dune Habitats of the Northeast Coast of South Africa

A combination of climatic and oceanic conditions during the last glacial maximum (approximately 20,000 years ago) led to aeolian coastal dune formation on South Africa's northeastern seaboard (Tinley 1985; Eeley et al. 1999). The return of warm interglacial conditions between 6,500 and 4,000 years ago marked the establishment of forests on these dunes to form some of the highest vegetated dunes in the world[1] (Weisser & Marques 1979). Specifically associated with these dunes, the coastal dune forests of northern KwaZulu-Natal comprised a naturally patchy and narrow distribution as a result of these geomorphological and climatic episodes (see Lawes 1990; Eeley et al. 1999). Further fragmentation occurred during the early Iron Age because of slash-and-burn shifting agriculture and iron smelting for Zulu spears (Moll 1978; Finch & Hill 2008). Historical accounts suggest that in the northern section of the study area larger patches possibly persisted because of the much taller, steep

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[1] These dunes range in height from 80 m at the Umlalazi River southwest of the study area to 188 m at the Umfolozi River, northeast of the study area (Weisser & Marques 1979; Weisser & Muller 1983; Lawes 1990).

dunes and swampy valleys that harboured tsetse flies (*Glossina* sp.) and *Anopheles* mosquitoes, precluding cattle herding and other agricultural activities (Weisser & Marques 1979; Bruton & Cooper 1980; Watkeys et al. 1993). In addition, grasslands were transformed to commercial plantations that often encroached on indigenous forests (Bourquin et al. 2000).

The coastal dune forests of KwaZulu-Natal form part of the southern portion of the Maputaland Centre of floristic endemism (Moll 1978; van Wyk 1996) and the globally recognised Maputaland-Pondoland-Albany biodiversity hotspot (Bredenkamp et al. 1996). Approximately 36% of coastal dune forests are protected (Berliner 2005). Forests north of the Umfolozi are afforded protection by the iSimangaliso Wetland Park, a UNESCO world heritage site (Smith et al. 2006). However, coastal dune forests have come under increasing threat and now cover less than 124 km^2, whilst ~ 56% are transformed (Berliner 2005). These forests were recently listed as critically threatened by the National Environmental Management: Biodiversity Act, 2004 ("Kwambonambi dune forest" and "North Coast dune forest"; Act No. 10 of 2004, Department of Environmental Affairs, 9 December 2011). This highlights the importance of the restoration of these forests in addition to conservation actions.

Study area

My research focused on the coastal dune forests north of Richards Bay (28°45' S, 32°00' E) and south of the Umfolozi River (28°48' S, 32°24' E) on the north-east coast of South Africa. This area comprises two adjacent mineral lease areas (referred to from here on as the lease site) in the south, adjacent to undisturbed coastal dune forest to the north (see Figure 1-2).

Rehabilitation program

Dredge mining of coastal sand dunes for heavy minerals represents a discrete disturbance within the lease site, whereby all vegetation and the associated topography is destroyed ahead of the dredger pond (Grainger & van Aarde 2012a). Sand tailings, constituting about 96% of the original volume of sand were stacked behind the mining face to approximate the pre-mining topographic profile. In line with statutory requirements, a third of the mining path was committed to restoring coastal dune forest typical of the area and this entails a kick-start process (Grainger & van Aarde 2012a; see Appendix I for photographic account). Topsoil was collected ahead of the mining path and spread over these newly built dunes (van Aarde et al 1996b; Wassenaar et al. 2005) where it was sown with annuals and indigenous grass seeds to stabilise the surface (Wassenaar et al. 2005; Grainger et al. 2011; Grainger & van Aarde 2012a). Within a few months, these seeds germinate and the sand is covered by a green carpet. The topsoil also contained a seedbank of the pioneer tree species *Acacia karroo* (Sweet thorn) that was augmented with additional *A. karroo* seed that germinated within a year. These grew into a thick shrubland within three years, *A. karroo*-dominated woodland within 10 years, and a regenerating forest within 20 years (Grainger et al. 2011). At this point the *A. karroo* had begun to senesce and later (>25 years), died standing or fell over (van Aarde et al 1996b; Grainger 2012). Forest canopy species had begun to appear within 15 years and by 20 years, the understory was well-developed with forest species colonising gaps (Grainger & van Aarde 2012). After this initial kick-start rehabilitation, mine management minimizes external disturbances that may derail the restoration of these forests, such as invasive alien plants, fire, and cattle grazing (Wassenaar et al. 2005; Grainger et al. 2012a).

This facilitation of ecological processes has left a successional sere of known-aged stands where coastal dune forest plant and animal assemblages are regenerating in the wake of the north-eastward advance of the mining plants (see van Aarde et al. 1996c; Ferreira & van Aarde 1997; Wassenaar et al. 2005; Grainger & van Aarde 2012a). The relatively undisturbed old-growth forest adjacent to the lease site in the north forms the buffer zone of the iSimangaliso Wetland Park and this served as a benchmark for the monitoring and evaluation of the rehabilitation programme (e.g. Wassenaar et al. 2005).

Regeneration through ecological succession

The Conservation Ecology Research Unit has conducted more than twenty years of ecological research on the new- and old-growth coastal dunes of northern KwaZulu-Natal. The modelling of regeneration trajectories suggests that soil conditions (van Aarde et al. 1998; Smit & van Aarde 2001), soil microfauna (Kumssa et al. 2004), as well as plant and animal assemblages (e.g. van Aarde et al. 1996a; van Aarde et al. 1996c; Kritzinger & van Aarde 1998; van Aarde et al. 2004; Wassenaar et al. 2007; Grainger & van Aarde 2011) are likely to converge with the benchmark within 68 years (Wassenaar et al. 2005). However, rates of recovery may slow due to local or regional factors (Parker 1997) so that succession appears arrested as shown here (Guldemond & van Aarde 2009) and elsewhere in the region (Boyes et al. 2010, 2011). For example, a recent study demonstrates that almost 50% of the bird species recorded 15 years ago no longer occur in the Maputaland region (see Trimble & van Aarde 2011). Human-induced disturbances could result in aberrant site conditions that could in turn hamper colonization (Wassenaar et al. 2007). Furthermore, as the species pool of regenerating patches becomes more similar to that of the regional species pool with age, there are simply fewer species available and species

accumulation slows (Wassenaar et al. 2005). Given the integral role that landscape-(e.g. Gustafson & Gardner 1996; Lindenmayer et al. 1999; Fernández-Juricic 2004; Grainger et al. 2011) and site-level (e.g. Burke et al. 1999; Ritter et al. 2005; Bohlman et al. 2008; Laurance et al. 2010) factors play in dispersal and colonization, this thesis will investigate the response of biological communities to some of these factors in old- and new-growth coastal dune forests.
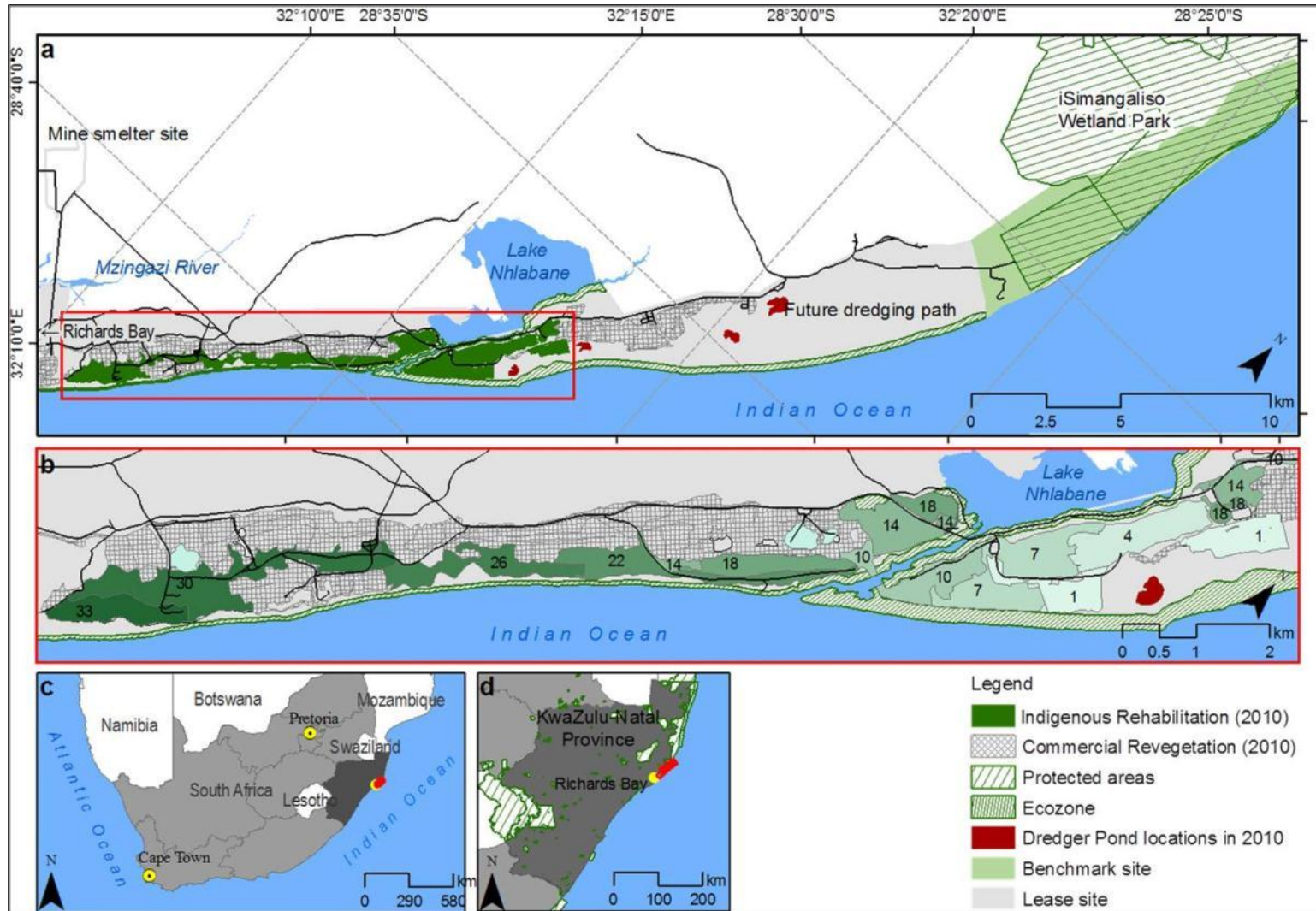
Figure 1-2. Map of study area showing benchmark and lease sites, as well as position of mining ponds in 2010 (a). The area in the red box is magnified to show the extent of stands of new-growth vegetation responding to rehabilitation, and their ages in 2010 (b). The context of the study area in South Africa and KwaZulu-Natal Province are also provided in the inset maps, (c, and d, respectively).

Investigating the Response of Biological Communities to Spatial and Temporal Changes in Regenerating Coastal Dune Forest Habitats

Given the history of the area, the known-aged stands and the proximity of a benchmark habitat, this study area presents an opportunity to explore the value of historical context, as well as site- and landscape-level factors to understand the outcomes of post-mining restoration. To do this the following key questions were posed and investigated:

Key question 1: Did the spatial structure of indigenous canopy cover differ between the benchmark and lease site before, and after mining (Chapter 2)?

Key question 2: Did the topographic profile of restored coastal dunes differ from that of their pre-mining profile (Chapter 3)?

Key question 3: Do the presence of some animal communities in the new-growth forests co-vary with variables indicative of habitat conditions (Chapter 4)?

Key question 4: Do i) microclimatic and, ii) soil conditions, as well as the structure and composition of iii) plant and iv) animal communities vary with the topographic profile of restored coastal dunes within new-growth forests (Chapter 5)?

Investigating Spatial changes in Coastal Dune Habitats through time

Proposed targets for regenerating landscapes are often based on preconceived ideas or surrounding landscapes and as a result, landscapes that develop from rehabilitation programmes may not represent natural or pre-disturbance landscapes (Bell et al. 1997; Tong et al. 2006).

The landscape-divergence hypothesis[*] may also explain such anomalies in landscape development due to differing initial conditions or disturbance patterns (Laurance et al. 2007). For these reasons, the historical context of a site is increasingly recognised as a pivotal determinant of its biodiversity (Arroyo-Mora et al. 2005; Kardol et al. 2007; Brudvig 2011). In Chapter 2, the spatial structure (patch area, shape and isolation) of patches of indigenous forest canopies in the mining lease and benchmark sites before mining began in 1976 and after the initiation of the rehabilitation programme was assessed. This assessment was based on the expectation that the spatial structure of canopy cover differed i) between pre- and post-mining periods and ii) between the benchmark and lease sites. Therefore, in Chapter 2, changes in the spatial structure of these patches at three intervals before, and three after mining and rehabilitation are described.

The effects of topography on ecosystems are well-documented and suggest that restoring the topographic profile is an imperative step in any rehabilitation programme to ensure the regeneration of associated communities (Larkin et al. 2006). Indeed, at this study area, the first step of the mining company's rehabilitation programme is shaping the sand tailings to mimic the pre-mining topographic profile of the coastal dunes (van Aarde et al. 1996c). Given that coastal dune forests are associated with the coastal dune cordon (Mucina et al. 2006), the restoration of the topographic profile was assessed in Chapter 3. The pre-mining profile of these dunes was the result of wind and sand movement during

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[*] Converse to the principle of nested subsets (Patterson 1990), which predicts that the composition of habitat fragments across a region will converge, the landscape divergence hypothesis predicts that the composition of habitat fragments with different disturbance histories will diverge as a result of variable edge-effects (Laurance et al. 2007). This may explain the lack of nestedness in patches of coastal dune forests in Maputaland (see Guldemond & van Aarde 2010).

the regression of the Indian Ocean coastal plain over thousands of years (Tinley 1985). I therefore expected that mechanical rebuilding of these dunes would not restore the topographic profile similar to that of pre-mining conditions. I therefore hypothesised that the topographic profile of restored coastal dunes as measured by dune elevation, aspect and gradient, would differ from that of their pre-mining topographic profile and the landscape would be characterised by a lower topographic heterogeneity. I therefore compared the topographic heterogeneity and dune displacement as well as the pre- and post-mining aspect, elevation and gradient of specific geographic locations.

Assessing Biotic Responses to Spatial changes in Coastal Dune Habitats through Time
Successional theory is used to predict the outcome of the ecological restoration of coastal dune forests at least in the early stages of regeneration, after which patch dynamics is expected to play a more important role (Grainger & van Aarde 2012b. Assuming the regional species pool is adequate, the first concern then is whether or not plant and animal species are able to colonise new-growth areas from remnant source patches, and once there, are conditions sufficient for them to persist (Jacquemyn et al. 2003; Wallis de Vries & Ens 2009; Suding 2011). However, such processes are dependent on the structure of the new-growth forest habitats, which includes among others, their spatial structure, topography, microclimate, soil quality and woody plant composition (e.g. Yates et al. 2000; Bohlman et al. 2008; Grainger et al. 2011).

The long-term stability of populations in patchy landscapes depends on the rate of dispersal and colonisation among patches. Gustafson and Gardner (1996) suggested that 89% of the variability in dispersal success can be accounted for by differences in size and isolation of forest patches, although more recent studies suggest that these effects can be

overridden by matrix quality (Kupfer et al. 2006; Prevedello & Vieira 2010). The geometry and arrangement of habitat patches influences population dynamics and species persistence (Ewers & Didham 2006), while conditions within each patch may influence the probability or rate of regeneration through cascading effects on colonising biota (Matthews et al. 2009; Brudvig 2011). For example, soil fertility, soil fauna, vegetation diversity, and productivity are co-dependent (Reynolds et al. 2003; Wardle et al. 2004; Vanbergen et al. 2007). Previous research at the study site has shown that soil quality (fertility, pH, and nutrient content), vegetation structure and composition increase with age (van Aarde et al. 1996b; van Aarde et al. 1996c; van Aarde et al. 1998). Soil quality (e.g. Bradshaw 1997; Wardle et al. 2004), vegetation structure and composition (e.g. Rotenberry 1985; Cutler et al. 2008; Smith & Gehrt 2009) may therefore represent important site-level factors that influence biota.

In Chapter 4, I considered the spatial structure (patch size, shape and arrangement), composition (woody plant diversity), and substrate (soil Nitrogen, Carbon and pH) of regenerating coastal dune forest patches as landscape- and site-level factors that may determine the structure and composition of biotic communities. Biological communities presumably respond to age-related increases in resource availability and therefore patchiness within regenerating stands. I therefore hypothesised that variables indicative of the i) spatial structure ii) composition and iii) substrate of canopy patches could explain the presence of millipede, dung beetle, and bird communities in the new-growth forests.

Much ecological research has recognized the hierarchical link between topography, soils, microclimatic conditions, and biological diversity (e.g. Chen et al.

1997; Dorner et al. 2002; Bennie et al. 2008), and thus the importance of topography in ecological restoration (Weiss & Murphy 1990; Palik et al. 2000; Rozé & Lemauviel 2004; Larkin et al. 2006). Just as soil is central to the regeneration of vegetation, and both presumably have cascading effects on biological communities, topographic features mediate abiotic conditions to create microhabitats of varying microclimates and soil quality (e.g. Tateno & Takeda 2003; Acosta et al. 2007). Topographic features include the relative position on the dune (crest, slope, or valley), aspect (cardinal direction in which the dune slope faces), gradient (angle of the slope) and elevation (height of the dune). All of these features influence the amount of sunlight, and wind to which localities on a dune are exposed, as well as the distribution of soil nutrients and rates of soil development (Chen et al. 1997; da Silva et al. 2008; Laurance et al. 2010). Therefore, increased topographic heterogeneity causes increased microhabitat availability, presumably increasing species diversity (Nichols et al. 1998; Atauri & de Lucio 2001; Wallis de Vries & Ens 2009).

Vegetation is the focus of most research on the influence of topography on biota, particularly that of coastal dunes (e.g. Nichols et al. 1998; Martínez et al. 2001; Tateno & Takeda 2003; Acosta et al. 2007; Bennie et al. 2008). However, such studies are also needed on animals, especially due to their sensitivity to microhabitats that varies with topography. Therefore in Chapter 5, I hypothesised that i) microclimate and ii) soil nutrient status would vary with the topographic profile of dune slopes (as qualified by aspect, gradient, elevation, dune position). Furthermore, due to cascading effects I also hypothesised that the structure and composition of iii) plant and iv) animal communities would co-vary with topography.

The model for the restoration of biodiversity presented by Brudvig (2011) outlines three themes that encompass potential filters or obstacles to the dispersal and colonisation of species to regenerating habitats. The findings of this thesis are synthesised in this chapter based on this framework (Chapter 6).

Conclusion

The ultimate goal of ecological restoration is the development of a self-sustaining ecosystem through the facilitation of ecological processes (Bradshaw 1990a; SER 2004; Suding 2011). Ecological processes are driven by factors operating and interacting at a variety of spatial and temporal scales, thus influencing the trajectory and rate of restoration. In this thesis, I investigated the historical context of, and changes in site- and landscape-level factors and the implications for the restoration of coastal dune forests. The identification and understanding of biophysical features operating at either the site- or landscape-level that hinder or facilitate the restoration of these communities would allow for their management and the concomitant improvement in the efficiency and efficacy of the associated rehabilitation programme.

Chapter 2 Temporal Changes in the Spatial Structure of Coastal Dune Forest Canopies

Introduction

A pressing question to restoration ecologists is whether ecosystems that develop in response to restoration programmes represent the natural state (Bell et al. 1997). Consequently, targets against which to evaluate restoration efforts are often derived from reference or benchmark sites (SER 2004). Two types of targets are used, namely, contemporary reference sites considered analogous to the disturbed site (e.g. Wassenaar et al. 2005; Grainger et al. 2011), and/or historical information on the disturbed site (e.g. Xu et al. 2009; Cristofoli et al. 2010). However, historical context may influence landscapes under restoration (e.g. Xu et al. 2009; Cristofoli et al. 2010; Fukami 2010). This also holds for my study area where anthropogenic disturbances dating back to the mid-1880's may have reduced once-continuous stretches of coastal dune forest to a collection of relatively small fragments (see Fourcade 1889; Lawes 1990). These fragments are now embedded in a matrix of formal and informal land use types such as sugar cane fields, plantations, subsistence agriculture, as well as rural and suburban villages (Wassenaar et al. 2005).

The rehabilitation programme along a third of the area of a mining path north of Richards Bay in KwaZulu-Natal province aims to restore coastal dune vegetation (van Aarde et al. 1996b). Research on soil properties, microfauna, millipede, dung beetle, small mammal and bird communities in the resultant new-growth forests demonstrates convergence with those of a relatively undisturbed old-growth dune forest on its northern boundary (van Aarde et al. 1996c; Kritzinger & van Aarde 1998; Davis et al. 2003;

Kumssa et al. 2004; Redi et al. 2005; Wassenaar et al. 2005). However, a number of forest specialist species remain absent from these new-growth forests (Grainger & van Aarde 2012b), probably due to a combination of local and regional factors that determine their likelihood of occurrence in new-growth forests. For instance, in the regenerating forests, local conditions may be underdeveloped, thus hampering succession (e.g. many forest birds rely on the availability of nesting sites in hollows provided by old trees, fruiting trees and refuges; Grainger et al. 2011). However, in the older patches (>20 years) the pioneer species, the Sweet thorn (*Acacia karroo*), begins to senesce and self-thin, forming gaps in the canopy that are colonised by broad-leaved tree species that include some forest specialists (Grainger & van Aarde 2012b). The establishment of these species may change the spatial structure of the regenerating canopies to more closely resemble the structure of old-growth forests, where localised disturbances lead to a shifting mosaic of patches at different stages of succession (i.e. patch dynamics, Cutler et al. 2008).

In addition to regional and local factors that drive dispersal, colonisation and establishment (Grainger et al. 2011; Trimble & van Aarde 2011; van Aarde et al. 2012), the historical context of the site may explain aberrant regeneration trends (see Brudvig 2011). For instance, historical differences in land-use at the study area led to a gradient of increasing disturbance of coastal dune forests from north to south (Weisser & Marques 1979). Therefore, the community composition of the new- (southern) and old-growth (northern) forests may have differed even before mining began. Relying on old-growth forests as benchmarks for new-growth forest may therefore be unrealistic (e.g. White & Walker 1997; SER 2004). Given the historical context and previous research comparing

assemblages present in the new- and old-growth forests of the mining lease and benchmark sites, this chapter assesses temporal trends in the spatial structure of forest canopies of the mining lease and benchmark sites.

Due to historical human disturbances being greater in the southern portion of the study area, I set out to investigate the following four expectations:- (i) Before mining, patches of the benchmark site were larger, comprised less edge and were less isolated than those of the lease site. Furthermore, due to mining progressing faster than rehabilitation, both in a northerly direction, I expected that ii) the spatial structure of canopy cover in the lease site to continue to differ from that of the benchmark site, but (iii) would increasingly resemble the benchmark with age. Due to the increased rate of mining, an increase in the rate of mining, I expected (iv) increased rates of loss in indigenous canopy cover over time.

I therefore quantified and compared the spatial structure of indigenous tree canopies within the lease and benchmark sites at irregular intervals over 69 years using historical remote sensing imagery and spatial analysis tools to enumerate change in the two-dimensional structure of these canopies. Metrics such as patch area, edge, and isolation enumerated spatial structure as the extent, shape, and distribution of tree canopies (Table 2-1). These metrics are ecologically meaningful because the spatial structure of habitat, conceivably corresponds to patches of tree canopies, plays a role in structuring communities (e.g. Jeanneret et al. 2003; Watson et al. 2004; Kappes et al. 2009) and ecological processes (e.g. Saunders et al. 1991; Bender & Fahrig 2005). The spatial structure of tree canopies may present a relatively robust measure of reference conditions that may have existed before disturbance. Such structure changes little within

a year, but represents suitable patches of forest habitat. For instance, Grainger et al. (2011) found that patch area, edge, and isolation explain the presence of at least half of the tree and bird species found in new-growth forests, highlighting the relevance of these landscape-related features for restoration. However, their delineation of patches relies on age, while I defined patches as distinct, contiguous indigenous tree canopies visible on remote sensing imagery. Forman (1995) also used this definition of a patch, here referred to as a canopy patch (see Glossary).

Table 2-1. Definitions and applications of metrics used to quantify the spatial structure of indigenous tree canopies, as well as the studies that used the relevant metric.

Metric name (unit)	Site	Patch	Description	Reference
Canopy cover (%)	●		Total coverage of indigenous trees in a site, represented as a percentage of the site's total area	(Robinson et al. 1995; Kemper et al. 2000; Endress & Chinea 2001; Turner et al. 2003)
Patch density (Patches/ha)	●		Number of patches within each site†, corrected for area	(Watson et al. 2004)
Edge density (edge length/ha)	●		Edge length of each site, corrected for area	(Southworth et al. 2004; Watson et al. 2004; Hartter & Southworth 2009)
Patch area (ha)		●	Extent or coverage of each patch	(Robinson et al. 1995; Endress & Chinea 2001; Turner et al. 2003; Lawes et al. 2004)
Shape Index (none, ≥1)		●	Complexity of patch shape, the closer to 1, the more compact the shape and the less edge.	(Crk et al. 2009)
Isolation (km)		●	Mean distance from stand edge to nearest potential source patch this was calculated both at intra-site and inter-site levels	(Lawes et al. 2004; Watson et al. 2004)

† benchmark or lease site

Methods

Study area

The study area included an area of land along South Africa's northeast coastline, approximately 2 km wide and 50 km long, extending between Richards Bay (28°46′ south) and the St Lucia estuary (28°24′ south) (Figure 1-2). The coastal dune forest included in this area is no wider than 1.9 km (van Wyk & Smith 2001; van Aarde et al. 2004), but fragmented through anthropogenic disturbances such as slash-and-burn agriculture, tourism, forestry, and mining since 1976.

Mining of the coastal sand dunes entails the removal of all vegetation and therefore represents a discrete disturbance event. Following mining, an active rehabilitation programme is initiated to facilitate ecological succession and has resulted in areas of known-aged regenerating vegetation (van Aarde et al. 1996b; Wassenaar et al. 2005; Grainger et al. 2011). Relatively undisturbed forest of unknown age (intact since before 1937) lay north of the mining lease site and is presumably the source of potential coastal dune forest species and is used as a benchmark to monitor restoration progress (e.g. van Aarde et al. 1996b; Wassenaar et al. 2005; 2007; Grainger & van Aarde 2012b. Old-growth forests of the benchmark comprised at least 150 tree species (Grainger 2012), while the new-growth forests of rehabilitating areas were dominated by a single pioneer species, *Acacia karroo*, that declines in density and relative contribution to the canopy with increasing age (Wassenaar et al. 2005). This chronosequence of coastal dune forests in various stages of succession provides the opportunity to evaluate trends in the spatial structure of indigenous canopies over time.

Spatial data

I used digitally scanned and geometrically rectified monochromatic aerial photographs of the entire study area for the years 1937, 1957 and 1970. On the aerial images, forest patches were clearly distinguishable from plantations due to their uneven and irregular patch structure (see Figure 2–1 & 2–2). The inability to distinguish between grasslands, wetlands and shrublands, especially in older images precluded a maximum-likelihood classification procedure typically used in spatial analysis software. I therefore digitized the extent of the forests for each year and then reduced the resolution of the resultant images to match that of the Landsat 5 TM imagery (30×30–m pixels). Landsat images were georeferenced using a georectified 2006 SPOT Image mosaic (SAC, CSIR, Hartebeesthoek, South Africa) as a reference. I used an unsupervised classification procedure using ENVI (ITT Visual Information Solutions, www.ittvis.com) to distinguish indigenous tree canopy cover from any other vegetation type in these images. However, to distinguish plantations from indigenous forests, I based a supervised classification on (i) ground-truthing carried out during April 2008, (ii) the presence of a patch in question in the aerial photographs pre-dating plantations, and (iii) mining records that showed the extent of plantations prior to mining. Cloud shadows in the 1990 image and shadows from high dunes required manual reclassification using the reference material, particularly the SPOT mosaic. In this way, I generated raster images depicting patches of indigenous forest tree canopies for 1990, 1998, and 2006 (Figs 2-3 & 2-4)
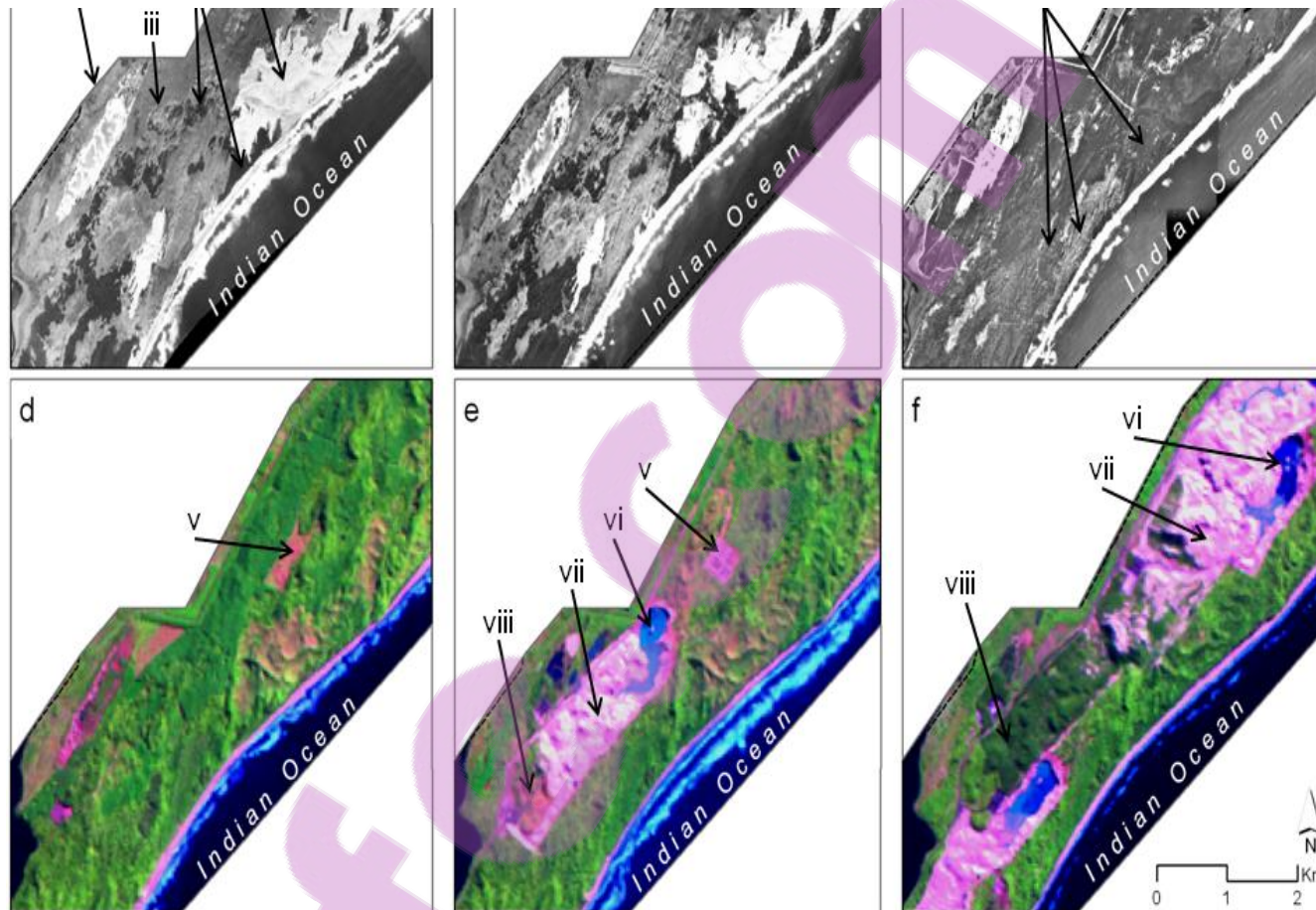
Figure 2-1. An enlarged portion of the lease site north-east of Lake Nhlabane, shown by aerial photographs taken during 1937 (a), 1957 (b), and 1970 (c), as well as Landsat 5 Thematic Mapper images from 1990 (d), 1998 (e), and 2006 (f). Arrows point to tracts of drift sand (i), patches of indigenous canopy cover (ii), grassland areas (iii), *Casuarina equisetifolia* plantations established to eliminate drift sands (iv), areas cleared of vegetation prior to the onset of mining activities (v), ponds where dredge-mining took place (vi), mined out areas of bare sand (vii) and stands in various phases of rehabilitation following mining.
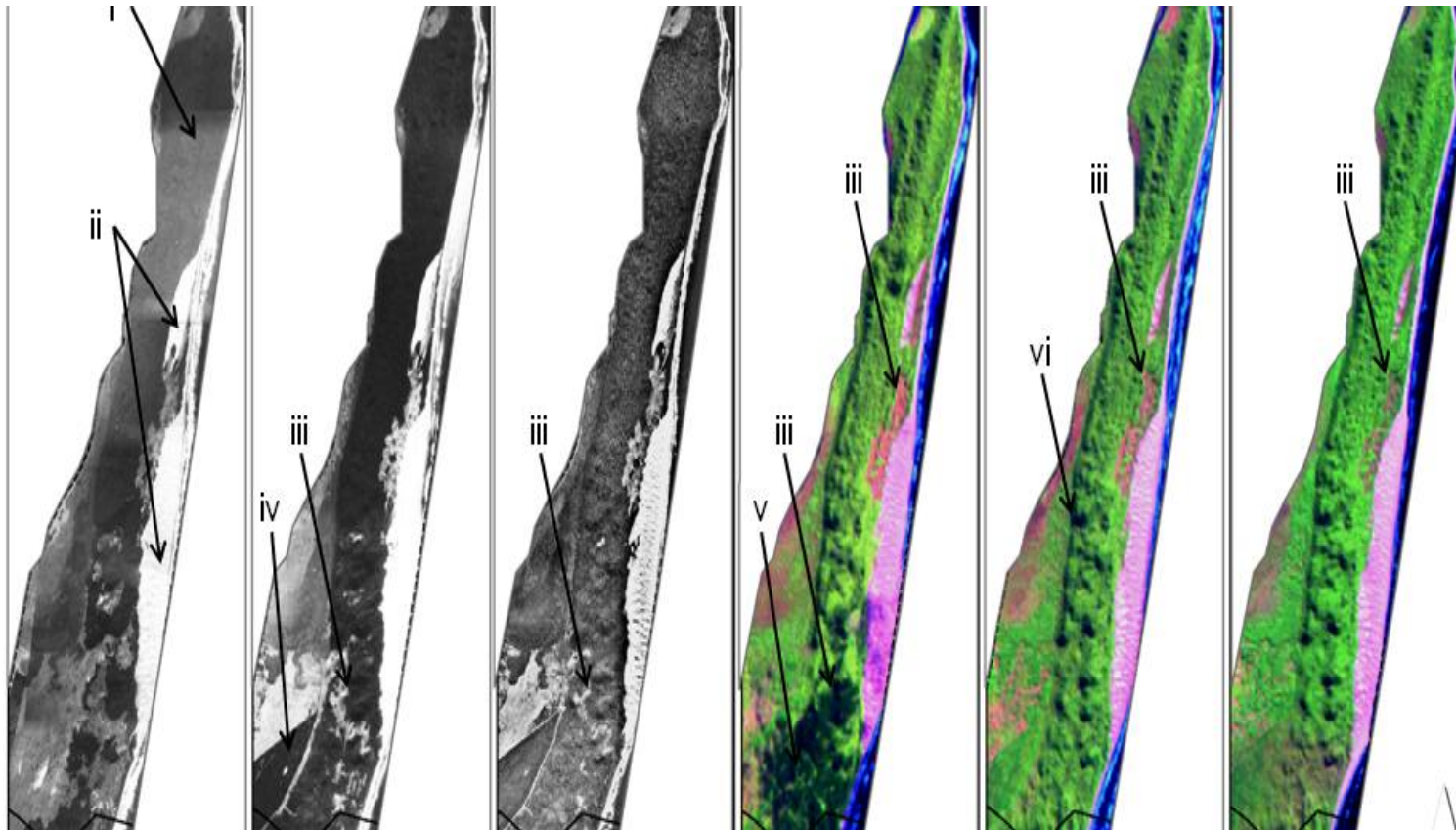
Figure 2-2. The benchmark site shown by aerial photographs taken during 1937 (a), 1957 (b), and 1970 (c), as well as Landsat 5 Thematic Mapper images from 1990 (d), 1998 (e), and 2006 (f). The arrows denote the largest (>1,000 ha) patch of coastal dune forest known as Sokhulu forest (i), drift sands on the seaward side of the dunes (ii), smaller bare areas that were gradually wooded (iii), a plantation that extends into the benchmark from 1957 onwards (iv) and shadows caused by clouds (v) and high dunes (vi).
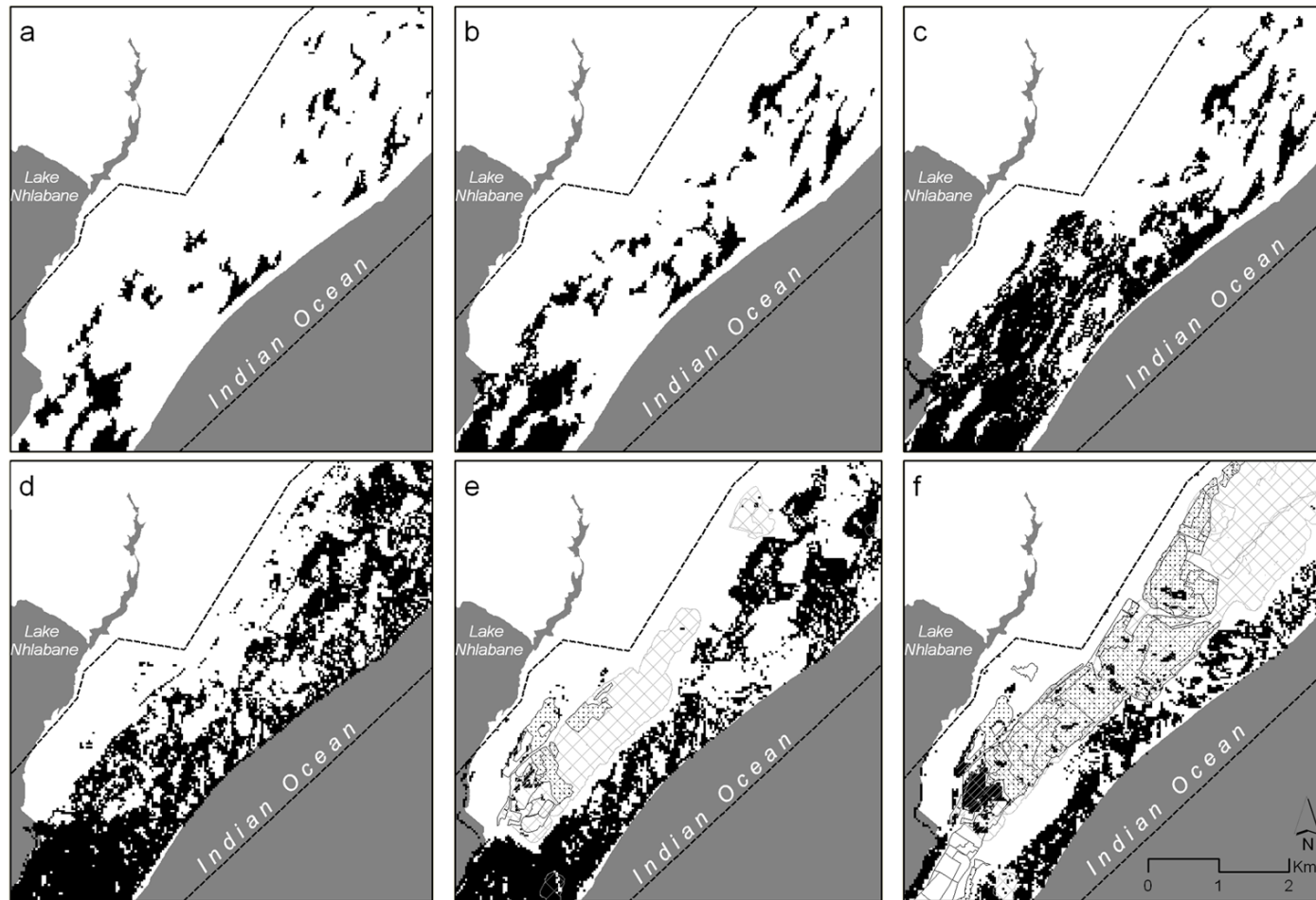
Figure 2-3. A portion of the lease site enlarged in (Fig. 2-1), for each year (1937 (a), 1957 (b), 1970 (c), 1990 (d), 1998 (e), and 2006 (f)), but showing tree-cover extracted as patches for the analysis of landscape structure (shaded black). Cross-hatched areas indicate mined sites and those delineated by stipples indicate areas revegetated with commercial timber species. Areas where the rehabilitation of indigenous vegetation was under way, are outlined without shading. Such areas that were captured as patches of canopy cover are indicated in black overlaid with white cross-hatching.
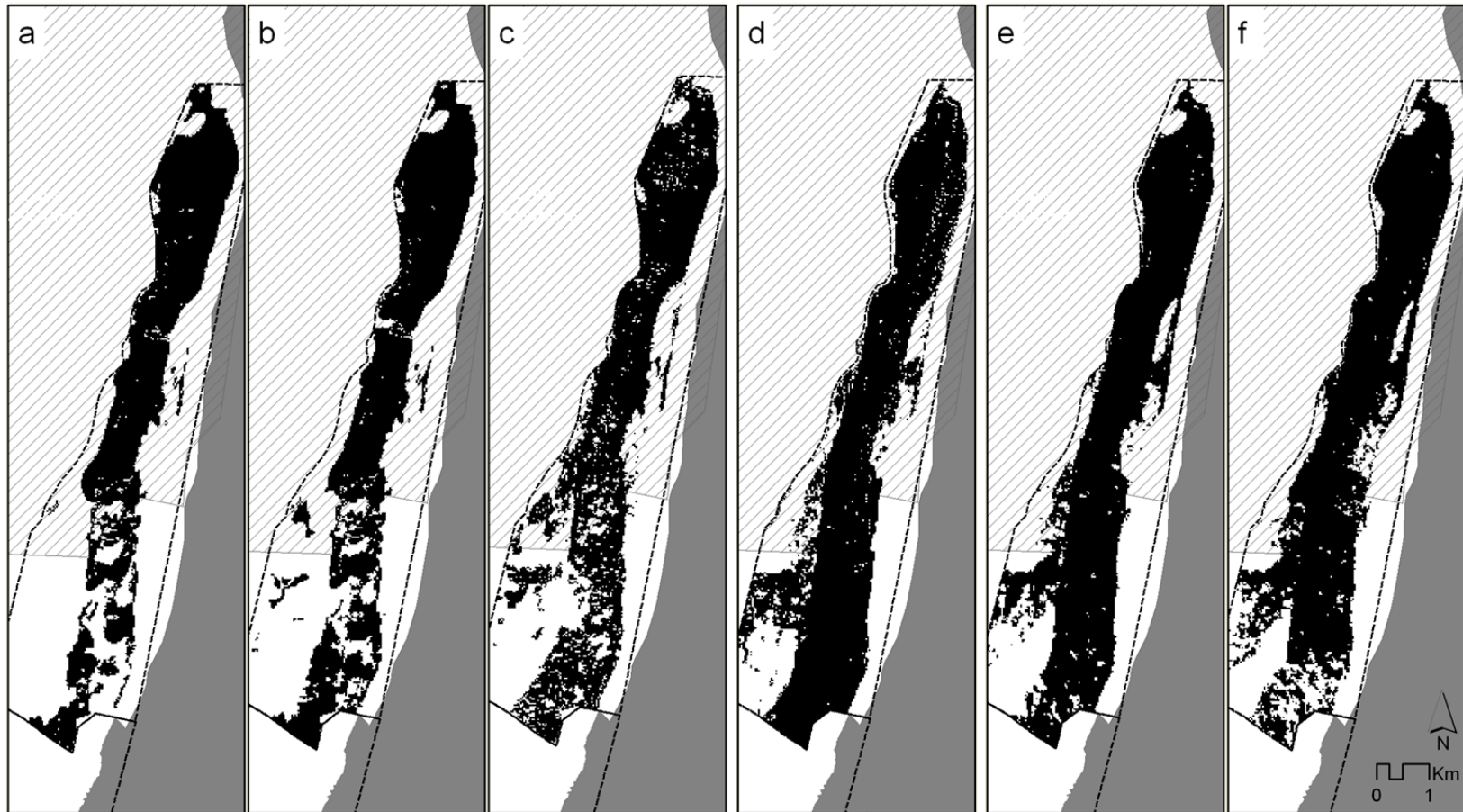
Figure 2-4. The benchmark site enlarged and represented by year as in (Fig. 2-2) (1937 (a), 1957 (b), 1970 (c), 1990 (d), 1998 (e), and 2006 (f)), but showing tree-cover extracted as patches for the analysis of landscape structure (shaded black). Hatched areas indicate the iSimangaliso Wetlands Park.

Patch structure

For each of the years (1937, 1957, 1970, 1990, 1998, and 2006), I calculated three landscape metrics with FRAGSTATS version 3.3 (McGarigal et al. 2002) to assess site-scale changes in total canopy cover, patch density, and edge density (Table 2-1.). I also quantified the spatial structure of tree canopies (patch area, perimeter, shape, and isolation) within the lease and benchmark sites for each sampling year (Table 2-1.). Because patch perimeter was more strongly correlated with patch area (Spearman rank correlation $r = 0.93$, $p < 0.05$) than shape index (Spearman rank correlation $r = 0.71$, $p < 0.050$ (Table 2-2), I used the patch shape to quantify edge. This metric gives an indication of the complexity of the patch – a more complex shape has a greater perimeter-to-area ratio. Patch area and shape were calculated using Fragstats, whilst the Edit Tools Geo Wizards version 9.8 (© Ianko Tchoukanski, www.ian-ko.com) extension for ArcMap version 9.2 (ESRI, Redlands, California, U.S.A.) was used to calculate Euclidean nearest neighbour (edge to centre) distance within and between the benchmark and lease sites (Table 2-1.). The site-scale metrics for the lease and benchmark sites were plotted as a function of the sampling year to allow for a comparative assessment of changes in canopy cover in the lease and benchmark sites, within and between pre- and post-mining phases. To draw comparisons within and between lease and benchmark sites for pre- and post-mining phases, values were plotted as the mean ± one standard deviation (mean ± SD) for patch area, shape, and isolation as a function of the sampling year.

Table 2-2. Spearman rank order correlations between patch-level metrics. Boldface correlations are significant at p < 0.05.

	Area	Perimeter	Shape Index	Euclidean Nearest Neighbour
Area	1.000			
Perimeter	**0.935**	1.000		
Shape Index	**0.706**	**0.897**	1.000	
Isolation	**-0.305**	**-0.297**	**-0.243**	1.000

      High variability in benchmark values for all metrics indicated that the single large patch, the Sokhulu forest, dominated trends here. To correct for this, I standardized the data for all three metrics by dividing the mean by the standard error of the mean and plotted these values (Johnson & Wichern 2002). To compare inter-site values of the benchmark and lease sites, I plotted the difference between the standardized lease and benchmark site values. As a result of small sample-sizes for the benchmark, unequal sample sizes between the benchmark and lease site, and lack of normality for all three metrics, I used the non-parametric Mann-Whitney U test for two independent samples using STATISTICA version 9 (© 2009, Statsoft, Inc., Tulsa, Oklahoma) to compare the spatial structure of tree canopies between sites within years.

Fragmentation

To compare the extent of fragmentation within the pre- and post-mining phases as well as between sites, I plotted the frequency distribution of patches falling within four size classes (0.09-1; >1-10; >10-100; >100 ha) for the lease and benchmark site for each year. The first class was truncated at 0.09, as this was the size of a single pixel and therefore minimum sampling unit, I excluded patches smaller than 1 ha from further analyses. The

largest class was established by combining classes (>100-1000 ha and >1000 ha) to eliminate any zero frequencies. I used contingency tables to assess differences within and between the lease and benchmark site during pre- and post-mining phases, respectively.

Age-related trends in the spatial structure of tree canopies

The age of unmined patches in the lease site was calculated as the difference between the sampling year when they were first identified and the final sampling year (2006). Patches present in the 1937 imagery were assigned an age of 69 years. Area, shape and isolation of the regenerating and unmined patches were regressed against their assigned ages to compare the slopes of the linear regression lines for regenerating patches and unmined patches.

Rates of change in canopy cover

To identify areas of change in canopy cover of the lease site as a direct result of mining, I conducted a change detection analysis for the area in the mining path of Normalised Difference Vegetation Index (NDVI) image differencing (see Hayes & Sader 2001) between pairs of Landsat images: 1990-1998, and 1998-2006. In addition to the spatial agreement between images, any shadows and dark areas that appeared in any one of the images were also removed from all images before the method was applied. This method entailed the calculation of NDVI for each image followed by subtracting the older image from the younger image (1998-1990 and 2006-1998). This resulted in two thematic images for which I identified and classified four categories of interest by referencing the 2006 SPOT image, the 1990, 1998 and 2006 raw and classified images, as well as ground-truthed locations, as described in detail by Hayes & Sader (2001). These categories included: (1) canopy cover that changed to shrubland; (2) canopy cover that

became bare; (3) no change, (4) shrubland areas that became covered by trees, and bare areas that became covered by trees. Following this classification, I combined and tabulated the two loss (1 & 2) and two gain (3 & 4) clusters.

Patch development

I described changes in the spatial structure of tree canopies over time by overlaying the year-specific images in ascending (1937, 1957, 1970, 1990, 1998, 2006) and descending order (*vice versa*) to ensure that all patches were included in the assessment. It was possible to record zeros if there was no patch in the area in a particular sampling year. I used mining records to determine the ages of regenerating patches and I was therefore able to plot the age-related size and number of specific patches. Using the same method, I also tracked the largest patch in the benchmark for comparative purposes. After plotting the size and number of patches occupying an area against the sampling year, I categorized the areas based on whether they were directly impacted by mining and rehabilitation, or not.

Results

The lease site did not resemble the benchmark during any of the sampled years. Canopy cover was consistently greater in the benchmark than in the lease site, though in both cases, cover increased until 1990. Following this, cover in the benchmark stabilized with relatively small losses and gains. By contrast, canopy cover decreased in the lease site between 1990-1998 and 1998-2006 (Figure 2-5a). Furthermore, the lease site consistently comprised more patches than the benchmark and this difference increased after the onset of mining. Patch density remained relatively stable in the benchmark, but increased

between 1998 and 2006 (Figure 2-5b). Edge was similar in the benchmark and lease site

until 1970, but after mining began, edge decreased and increased in the benchmark and

lease site, respectively (Figure 2-5c).
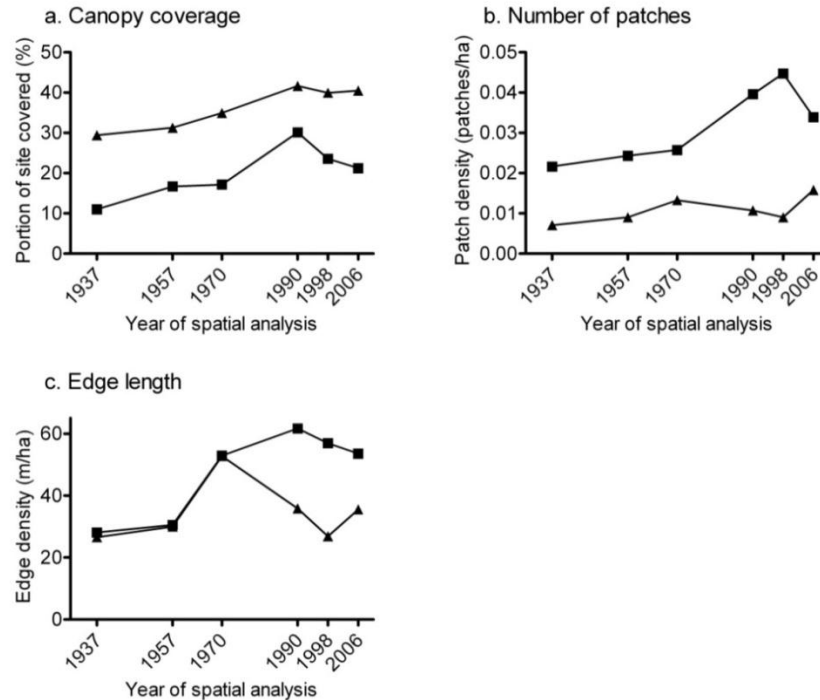
Figure 2-5. Site-scale metrics summarizing changes in the extent of canopy cover (a), patch density (b) as a measure of the number of patches, and edge density as an indication of edge length (c) across the benchmark (▲) and lease (■) sites.

Spatial structure of tree canopies

Spatial structure measured at the patch-scale differed in the lease from that of the

benchmark site before mining began (1937, 1957, and 1970). On average the lease site

had smaller, less complex patches that were more isolated than the benchmark (Figure

2-6i). However, from 1990 onwards the lease site became more similar to the benchmark,

but the high variability of the benchmark, particularly for patch area, and the difference in

the number of patches suggested that trends were influenced by the dominance of the

Sokhulu forest (>1000 ha). I therefore standardized values by dividing the mean by the

standard error of the mean (see Figure 2-6ii). In most cases this clarified, but reversed

trends; patches in the lease site were larger, comprised more edge (greater shape index),

and were more isolated than those of the benchmark. These trends were even more

noticeable when the standardized benchmark values were subtracted from those of the

lease (Figure 2-6iii). However, these differences were only significant for patch area

during 1990, and patch isolation during 1957 (Mann-Whitney non-parametric U-test for

independent samples by groups, Table 2-3.). Different to expectations, most comparisons

yielded statistically insignificant differences (Table 2-3).

Table 2-3. Mann-Whitney non-parametric U-tests comparing the area, shape and isolation of patches within the benchmark and lease for each sampled year. Significant values at p < 0.05 are highlighted in boldface.

Year of spatial analysis	Patch-scale metric	*U*	*Z*	*p*-value
1937	Area	268.5	1.59	0.111
	Shape	298.5	1.20	0.233
	Isolation	254.0	-1.78	0.075
1957	Area	216.5	0.88	0.381
	Shape	240.5	0.44	0.656
	Isolation	**156.0**	**-1.97**	**0.047**
1970	Area	421.0	0.73	0.473
	Shape	472.5	0.18	0.855
	Isolation	440.0	0.52	0.605
1990	**Area**	**4525.0**	**2.43**	**0.015**
	Shape	5385.5	1.06	0.289
	Isolation	5978.0	-0.12	0.907
1998	Area	10591.0	1.33	0.183
	Shape	11315.0	-0.61	0.543
	Isolation	11502.0	0.42	0.673
2006	Area	11616.5	0.98	0.327
	Shape	11932.0	0.64	0.522
	Isolation	11922.5	-0.68	0.497
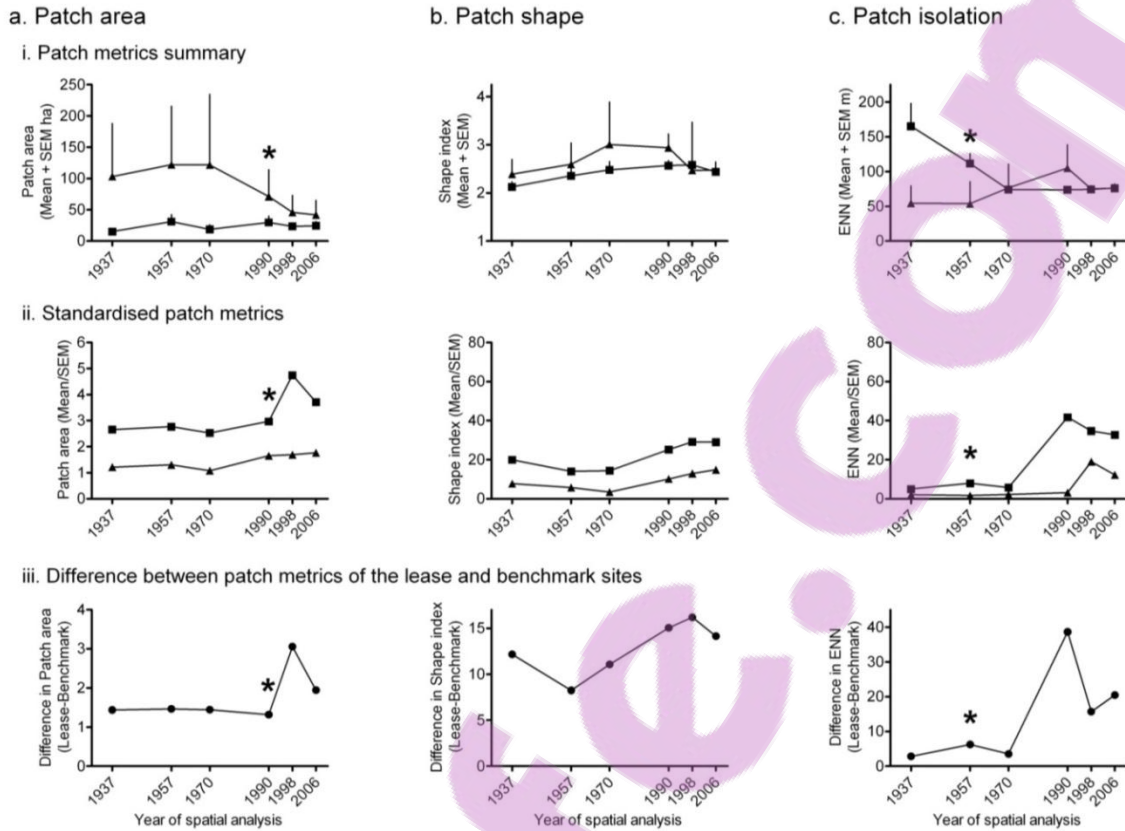
Figure 2-6. Patch-scale metrics of patch structure: patch area (a), shape (b), and isolation (c)) presented as a function of the year for which spatial analysis was conducted. A summary of the patch metrics (mean +SEM (standard error of the mean)) for the benchmark (▲) and lease (■) sites (i), standardized values of these metrics calculated as the mean by the SEM (ii), and the difference between the standardized metrics of the benchmark and lease (●) sites (iii). Instances where the patches of the lease were significantly different from those of the benchmark for a metric within a year are indicated with an asterisk.

Fragmentation

Frequency distribution of patch sizes as a measure of fragmentation differed significantly between the lease and benchmark sites during the pre-mining years (2×4 contingency table, $\chi^2 = 10.38$, $df = 3$, $p = 0.016$), but were similar during post-mining years (2×4

contingency table, $\chi^2 = 4.68$, $df = 3$, $p = 0.197$) for all size classes (Figure 2-7). However,

fragmentation was similar between the pre- and post-mining phases in the benchmark (2

× 4 contingency table, $\chi^2 = 4.02$, $df = 3$, $p = 0.260$), but significantly different within the

lease site (2 × 4 contingency table, $\chi^2 = 66.87$, $df = 3$, $p < 0.0001$. Both the lease and

benchmark sites were dominated by small patches (<10 ha), however, these only made up

<25% and <5% of the total canopy cover in these sites, whilst larger patches made up

>70% and >90%, respectively (Figure 2-7).
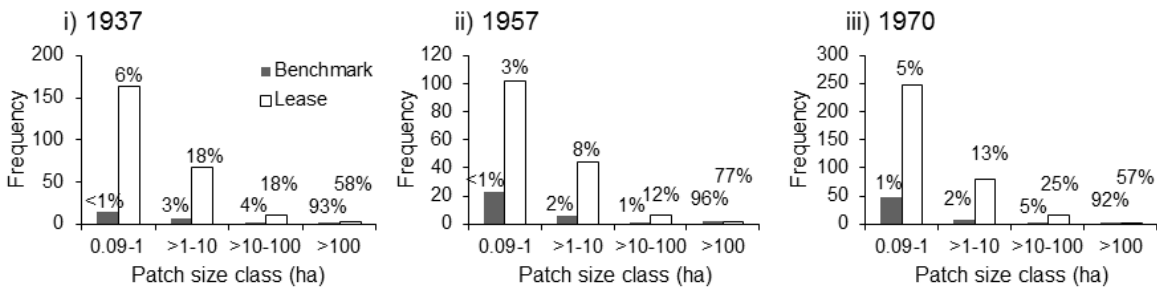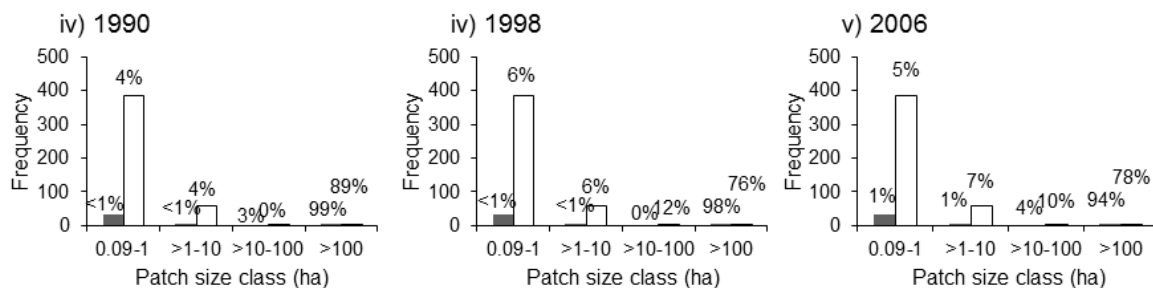
Figure 2-7. Frequency distributions of patch sizes within four size classes for the lease and benchmark sites, prior to- and after mining (a and b, respectively). The percentage contribution of each class to the total canopy cover is indicated above the bar of each year.

Age-related trends in patch structure

Patch area and patch shape showed two clearly disparate trends for small (<10 ha) and large (>10 ha) patches when plotted against age and I therefore conducted separate linear regression analyses on these two size classes (Figure 2-8a & 2-8b). I used 10 ha as a cut-off because it coincided with the classes of the frequency distribution, where patches >1 ha and <10 ha made up less than 20% of the total canopy cover in any particular sampling year. Patch area and edge (as measured by patch shape) of rehabilitating patches increased with age, becoming more dissimilar from unmined patches of the lease and benchmark sites. The slope of this increase was barely significant for the shape of patches smaller than 10 ha (F = 5.08, *df* = 11, *p*= 0.046), but not for small or large patches (F = 0.49, *df* = 11, *p*= 0.498, F = 1.26, *df* = 7, *p*= 0.299, respectively), nor the shape of large patches (F = 1.25, *df* = 7, *p*= 0.300). The slopes of the regression of unmined patches were not significantly different from zero, except for the shape of patches larger than 10 ha as well as the isolation of all patches. The slopes of regression lines for rehabilitating patches differed significantly from those of unmined patches in the lease site, except the area of small patches, (Figure 2-8a). This suggested that the spatial structure of canopy cover differed between unmined and regenerating patches through time. This was not the case for patch isolation that did not show such a dissimilar trend and was plotted on a single graph (Figure 2-8c) that showed a significant increase in isolation with increasing age (F = 34.43, *df* = 39, *p* < 0.0001). The area of small regenerating patches and unmined patches could be regressed using a single model because they were so similar. However, this was not the case for the area or shape of larger patches, nor patch isolation. For all variables the range of values recorded for

unmined patches were similar to those noted for the benchmark, but the rehabilitating

patches were not.
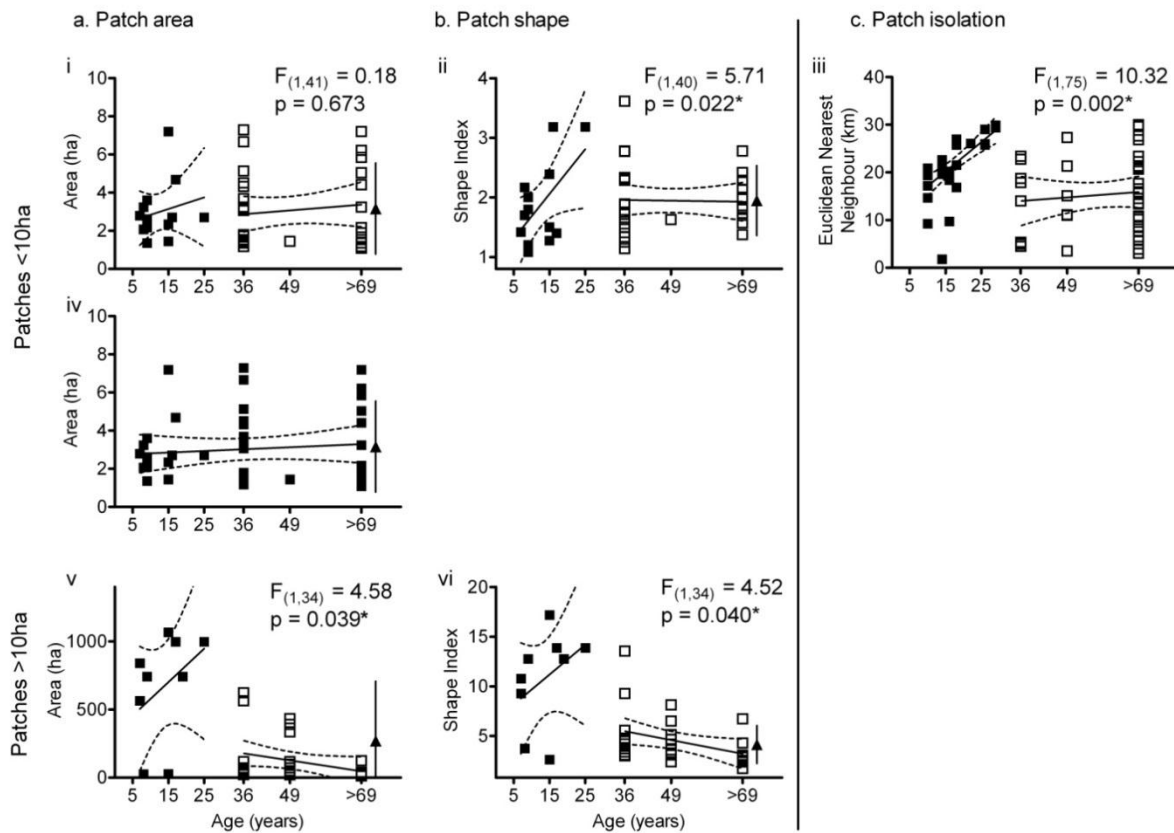
Figure 2-8. Patch area (a); shape (b), and isolation (c) of regenerating patches (■) and unmined patches (□) in the lease site regressed on patch age. Patch area and shape are separated into two size classes, <10 ha (i-iv) and >10 ha (v-vi). P-values presented with an asterisk indicate the where slopes of regenerating and unmined patches were significantly different from one another. This was not the case for the relationship between patch area and age for small patches (i) these were therefore modelled using a single regression (iv). Mean metric values and their standard deviations of benchmark patches (▲) are given for comparative purposes to assess whether patch structure was tending towards the benchmark.

Rates of change in canopy cover

Indigenous tree canopy cover lost as a direct result of mining amounted to 27% between 1990 and 1998, and 33% between 1998 and 2006 (Figure 2-9). However, there was a 15% increase in canopy cover between 1990 and 1998, and a 17% increase between 1998 and 2006. These trends were different from those recorded by site-scale metrics of the lease site, where loss between 1990 and 1998 was greater than that between 1998 and 2006.
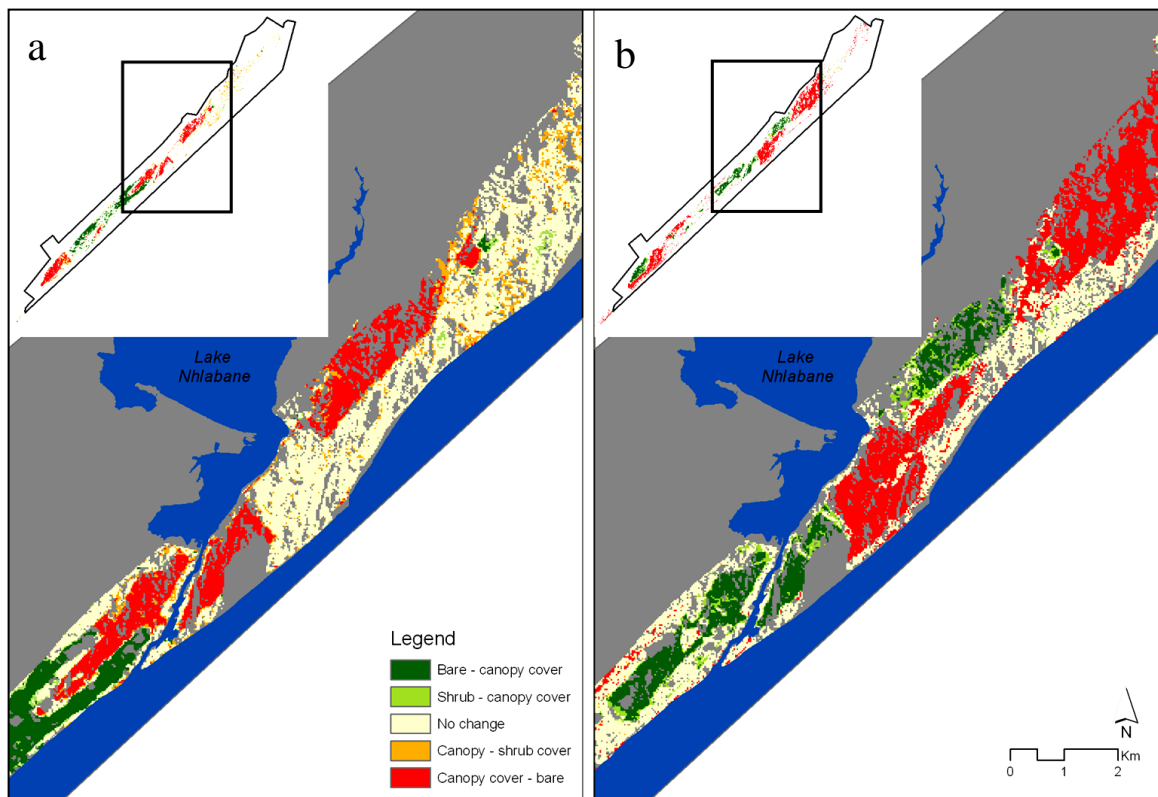
Figure 2-9. The lease site illustrating areas of change between 1990 – 1998 (a), and 1998 – 2006 (b), enlarged areas are indicated by the rectangle in the inset. Areas in red and orange highlight tree-cover loss and those in different shades of green indicate areas of tree-cover gain, whilst those in beige denote areas of no change.

Patch development

The areas occupied by patches that were tracked through time revealed flux in the spatial structure of patches even before mining began. Some of these areas comprised a single patch that changed in size over time (Figure 2-10a, vii), whilst others disappeared before mining began (Figure 2-10b, v), or after mining where the area was revegetated with commercial plantations (Figure 2-10b, vii-viii). However, in most cases that I assessed, rehabilitation resulted in increases in patch size and decrease in numbers (Figure 2-10a, ii-viii). Areas that were not mined, but were within the boundaries of the lease site (Figure 2-10c, i-iv), fluctuated more similarly to those that were mined, rather than those of the benchmark site (Figure 2-10c, v).
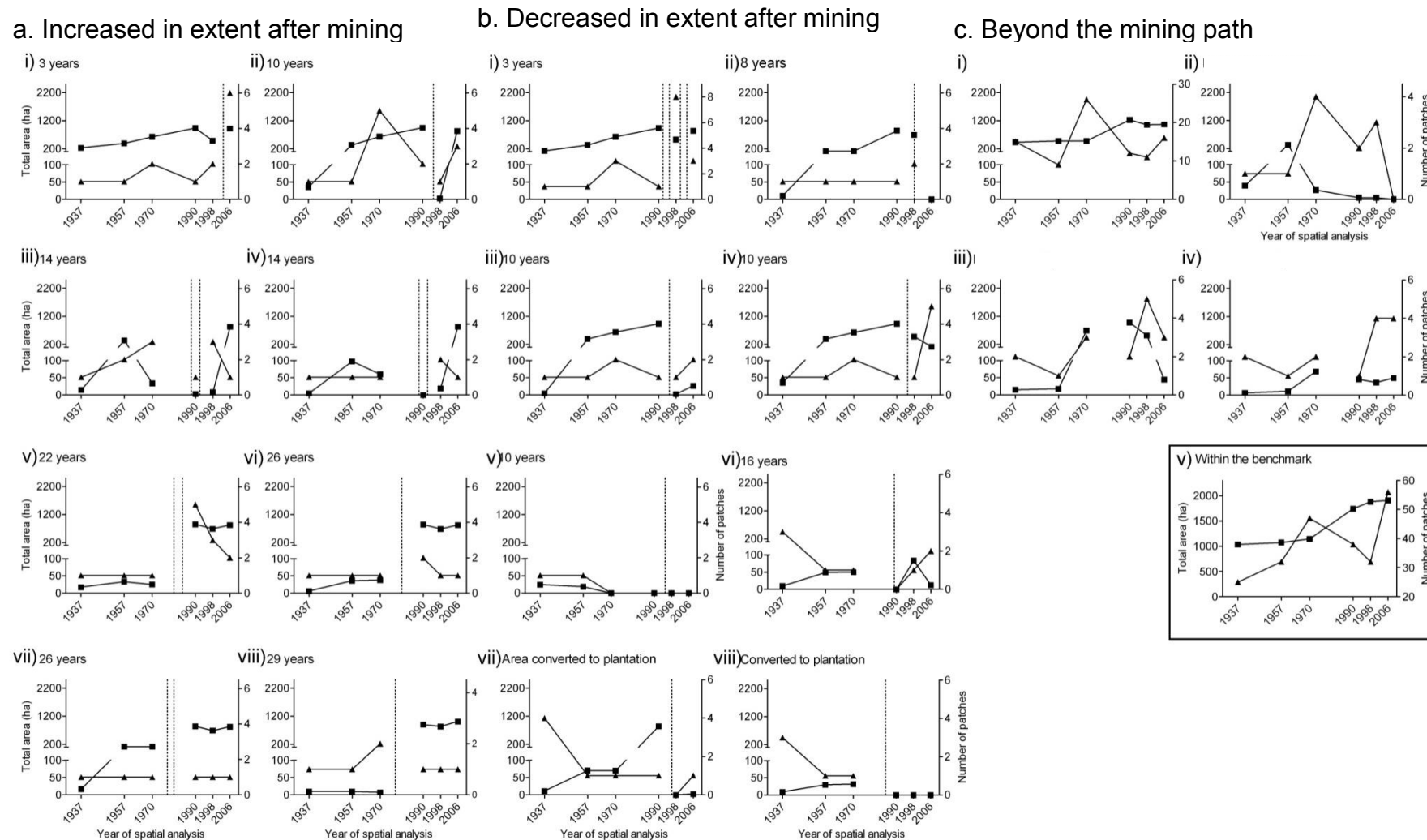
Figure 2-10. Summary of the size (■) and number (▲) of patches that occupied an area as tracked during each sampling year, separated into those that increased in extent (a), or decreased in extent following mining (b), and those that were not directly impacted by mining (c) – including the patches of the benchmark in the box. Titles of each graph indicate the age of regenerating patches if applicable, or the location of the area tracked. The vertical stippled lines denote instances of mining. The number of years refer to the age of the patch in 2006.

Discussion

In this study, the historical context of a rehabilitated landscape was characterized and its development by rehabilitation after disturbance tracked and compared to both a relatively undisturbed reference site and itself prior to disturbance.

Human-associated disturbances were higher in the lease site than the benchmark site prior to mining (see Chapter 1, Weisser & Marques 1979), and I therefore did not expect indigenous forest canopies of the lease site to resemble those of the benchmark before mining – the lease site having smaller, more isolated and fragmented patches with more edge. Little forest cover remained in the area forming the lease site before the onset of mining, and that which remained was highly fragmented. This supports my expectation that canopy cover of the lease site did not resemble that of the benchmark for years preceding mining. Similarly, the lease site was more fragmented and had smaller patches than the benchmark.

There are several shortcomings in the methods that I used. Although I did my utmost to standardise the two sets of imagery, inherent differences between the aerial and satellite imagery that may have resulted in classification inaccuracies were likely the cause of the inconsistent results. However, I noted an increase in canopy cover in both the lease and benchmark sites in the 1957 and 1970 imagery that implied a phase of spontaneous dune forest regeneration. This period coincided with the establishment of *Casuarina equisetifolia* (beefwood) plantations to help stabilize drift sands during the early 1950's (visible in the 1937 imagery, see Figure 2-2, Weisser & Marques 1979). These provided the protection from wind and fire required for the regeneration of forests

(Weisser & Marques 1979). In the benchmark, this increase in canopy cover continued after 1970, whilst in the lease site, mining began and cover began to decrease again, diverging from the benchmark.

My expectation that the spatial structure of indigenous canopies in sites rehabilitated after mining differed from that of the benchmark, was also supported. Fragmentation of the lease site was consistently greater than that of the benchmark, such that patches were smaller and more isolated than those of the benchmark were, although less-so after rehabilitation.

The target of the rehabilitation programme is the restoration of coastal dune vegetation typical of the region (see van Aarde et al. 1996b). The location, initial size and shape of rehabilitating stands are determined by the Company's mining office – these stands are large and simple in shape, quite unlike the unmined patches or those of the benchmark. Following this and in line with my expectations, the spatial structure of these patches was age-related. Decreases in patch size and increased shape complexity after initial increases in patch size, suggest that the formation of gaps in older regenerating patches (Grainger & van Aarde 2012b) results in a more natural spatial structure that appears to become more similar to that of the benchmark with time. This also explains why relatively young (<12 years) regenerating patches comprised similar edge (measured by shape index) to that of unmined patches and the benchmark, but with the increased thinning of *Acacia* trees with age, edge increased as gaps formed in the canopy (van Aarde et al. 1996c; Grainger & van Aarde 2012b). In addition, the isolation of regenerating patches increased with age, but this was due to the elongated nature of the

study area, with the oldest patches being the furthest from the benchmark. Rates of canopy loss were relatively similar across years after mining began.

Tracking particular areas of the lease site through time to assess the changes in spatial structure lent further support to these interpretations. Cases where patch area increased and the number of patches decreased prior to the onset of mining implied that the gradual increase in patch size led to 'clumping' of patches. In contrast, areas regenerating in response to the rehabilitation programme formed single, very large patches of *Acacia* woodland that then broke up to form many patches covering a smaller area. Following years of successional development shown by earlier work, the regenerating forest has now entered a phase of patch dynamics (Grainger & van Aarde 2012b) that may either stimulate or inhibit further development of these forests. Whatever the situation, the diversification of the spatial structure of tree canopies of rehabilitating areas towards structures similar to those I noted in the benchmark implies that regeneration may continue. Differences between the patch structure of regenerating patches and unmined patches of the benchmark (particularly in terms of patch edge and isolation) may therefore merely be due to the relatively short time that has elapsed since the onset of regeneration. The coastal dune forest of the benchmark is present in the 1937 photographs and therefore older than 69 years; however, the lease site comprised a highly disturbed mosaic of various stages of degradation, regeneration, and small forest patches when mining began. In 2006, the oldest regenerating area was 30 years old and given more time, the spatial structure of patches within the site may become more similar to that of the benchmark site.

Wassenaar et al. (2005) noted that despite imminent convergence between assemblages, the benchmark remained more variable than the new-growth forest suggesting that only a portion of the possible combinations of species across the range of undisturbed forest had been assembled in regenerating stands. Similarly, I noted that the spatial structure of patches in the benchmark site was more variable through time than that of the lease site. This highlights the interplay between the processes that underpin ecological succession (colonization and extinction), and variables of patch structure, as noted in many other studies (e.g. MacArthur & Wilson 1967; Pickett & Cadenasso 1995; Gustafson & Gardner 1996; von Maltitz 1996; Lindenmayer et al. 1999; Viña et al. 2007; Chazdon 2008). Patch formation and spatial structure is thus dynamic and highly dependent on local and regional disturbances.

Management Implications

Across the years studied here, indigenous tree canopies in the lease never comprised more than ~30% of the area. My work reinforced the findings of Grainger et al. (2011) who found regenerating patches were becoming more isolated from the benchmark, in that as mining advanced northwards, new regenerating patches were also becoming more isolated from older regenerating patches in the south that could serve as source patches. Although more regenerating patches are added following the removal of existing patches at the mining face, these regenerating patches cannot serve as sources for patches older than themselves. This may isolate all but the youngest regenerating patches from potential source patches, as dispersing individuals have to cross ever-larger tracts of hostile matrix or unfavourable habitat. Such a loss of connectivity is known to influence species assemblages (Bjørnstad et al. 1998; Acosta et al. 2000; Lindborg & Eriksson

2004) and could well explain slowed rates of recovery and missing specialists in the regenerating patches. Patch isolation from the benchmark may therefore pose a serious threat to the success of the restoration programme and further research is required to assess the role of the oldest regenerating patches as sources of colonizers for the younger regenerating patches in the middle of the lease. However, a potential solution would be to leave more intact patches in the wake of mining to serve as stepping-stones.

The relatively constant state of canopy cover in the benchmark throughout pre- and post-mining phases relative to the lease site suggests that the canopy has not been disturbed for at least 70 years. Future rehabilitation incentives may consider minimizing disturbances of potential source areas.

Chapter 3 Assessing the Restoration of Coastal Dune Topography after Mining

Introduction

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

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

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

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

Methods

Study area

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

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

Topographic data

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

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

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

Statistical analyses

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

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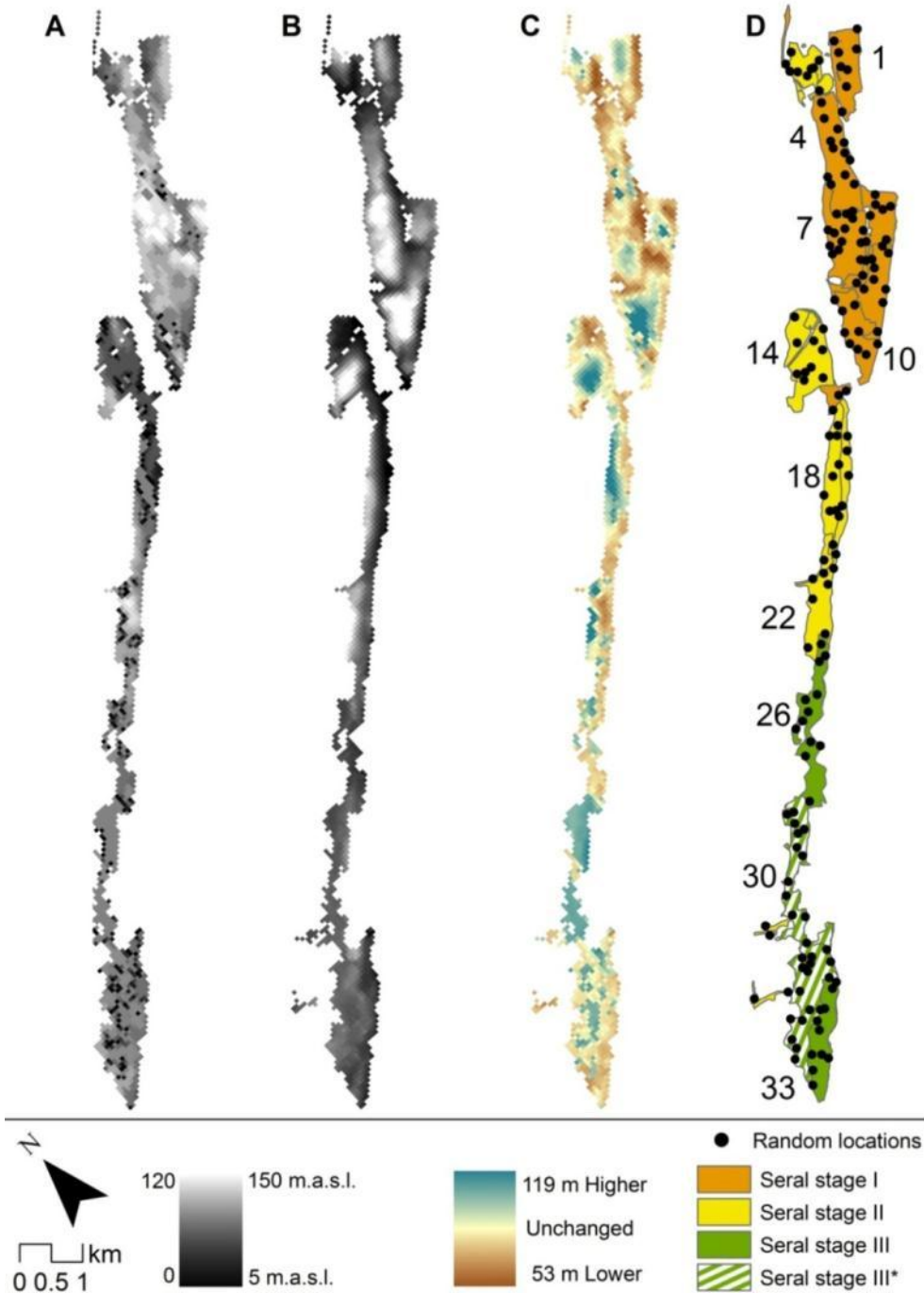
Figure 3-1. Digital elevation models of the study area prior to the start of mining (1971, A), and after mining and rehabilitation (2010, B). The difference in elevation between these two periods is indicated by C, where turquoise represents areas that were higher after mining than before mining, with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

Results

Restored topographic heterogeneity was lower than pre-mining heterogeneity for the study site, but on an age-specific basis, five stands were less heterogeneous and five were more heterogeneous (Figure 3-2). However, cases where the topographic heterogeneity of stands was reduced after mining and rehabilitation were slightly more pronounced (max = -2.9) than those where heterogeneity had increased (max = 2.3).
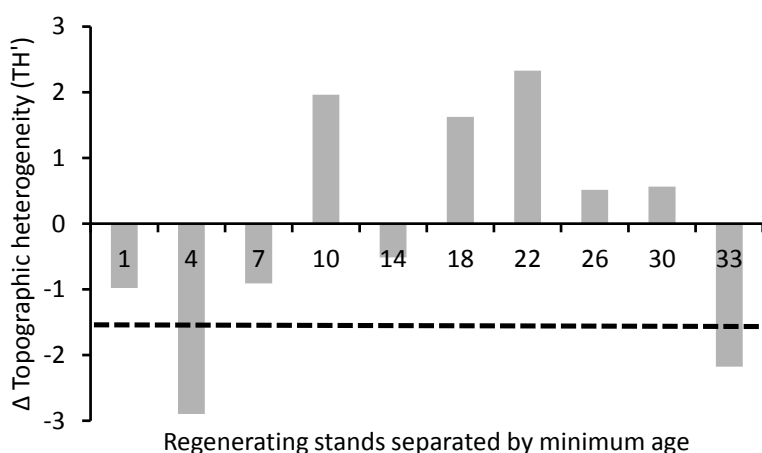
Figure 3-2. Change in topographic heterogeneity of age-specific rehabilitating stands calculated as the difference in Shannon's Diversity Index before mining (1971) and after topographic restoration (2010). Negative values therefore indicate a decrease, whilst positive values indicate an increase in topographic heterogeneity. The dashed line represents the change in topographic heterogeneity for the whole study site.

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

recorded on southeast- and north-facing slopes than before mining, though fewer fell on slopes facing all other aspects. There were also fewer random locations on elevations below 25 m, but more of the random locations were recorded on elevations of greater than 51 m after than before mining. Fewer random locations were recorded on slopes steeper than 15°, but there were more on gradients of between 0 and 10° after mining, than before mining.
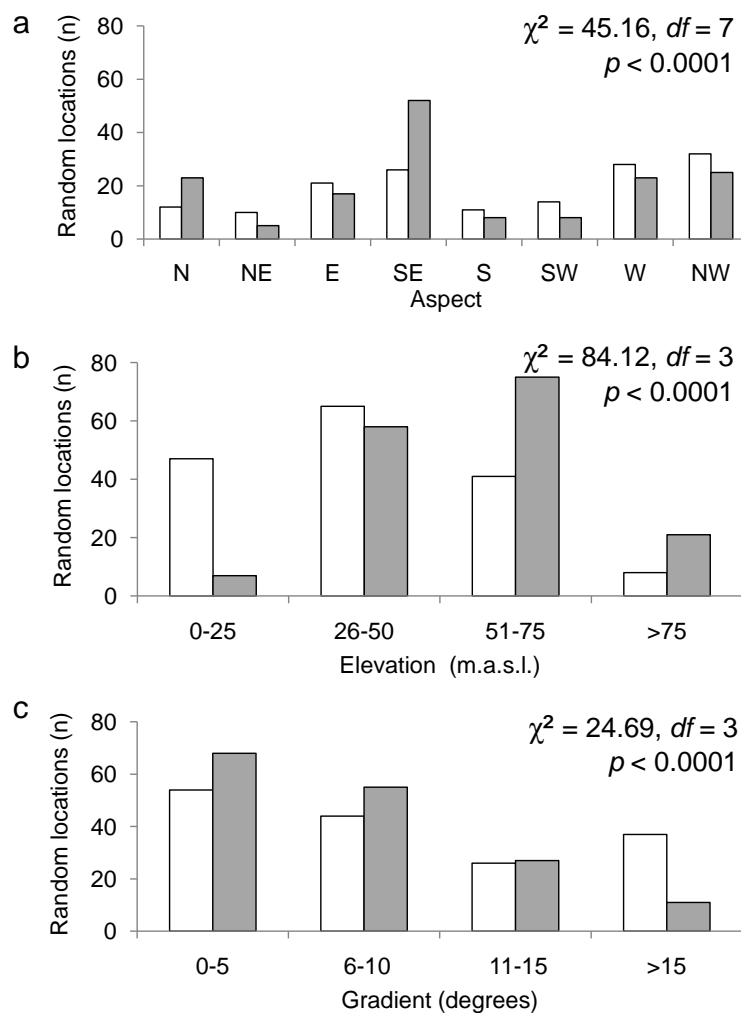
Figure 3-3. Frequency distributions of randomly placed locations that were used to sample aspect (a), elevation (b), and gradient (c) across rehabilitating stands of the study area before (1971, clear) and after (2010, shaded) mining

Discussion

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

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

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

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

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

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

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

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

Introduction

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

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

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

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

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

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

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

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

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

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

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

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

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

Methods

Study area

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

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

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

Explanatory variables

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

Applications Center, CSIR, Hartebeeshoek, South Africa)[1]. These were I cross-referenced with the age-specific stand data from mining records. This definition therefore differs from that of Grainger et al. (2011), where patches were defined based on their age alone. I delineated patches using classification routines conducted in spatial analysis software (ENVI version 4, ITT Visual Information Solutions, www.ittvis.com and ArcMap version 9.3, 2009 © ESRI Inc., Redlands, California). I quantified the area, shape and isolation of these patches using a spatial analysis program (FRAGSTATS version 3.3, McGarigal et al. 2002).

I overlaid the woody plant abundance data and soil mineral content data from surveys conducted within two years of either of the remote sensing images over these patches in a GIS. The woody plant and soil survey methods are described elsewhere (van Aarde et al. 1998; Theron 2001). Soil pH, nitrogen, and carbon reflected on substrate quality, while tree species richness and diversity characterized the composition of tree canopies (see Table 4-1).

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

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

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

Response variables

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

Relating community variables to habitat features

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

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

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

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

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

Results

Interactions between patch structure, composition and substrate

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

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

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

Interactions between habitat features on community composition

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

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

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

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

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

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

Habitat features and community variables

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

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

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

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

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

Orthoporoides sp. and *C. richardii* increased in abundance with soil pH, while woody plant richness explained variation in *Doratagonus* sp. abundance (Figure 4-1).

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

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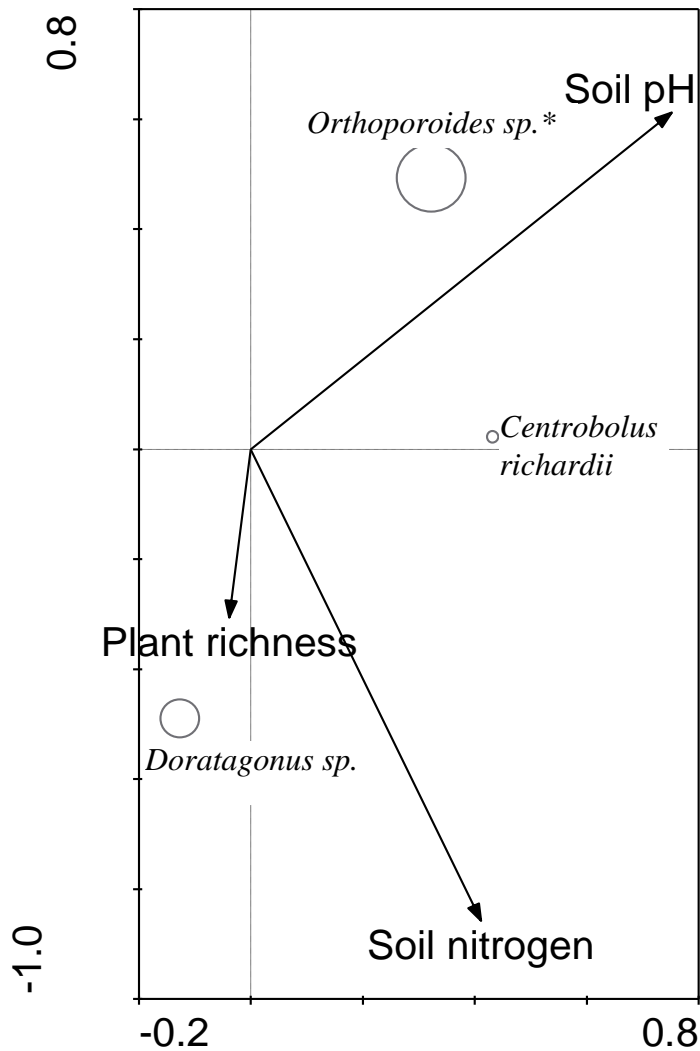
Figure 4-1. Correlation biplot of the redundancy analysis for millipedes using woody plant richness, soil nitrogen, and soil pH. Symbol size corresponds to the proportion of explained variance of a species' abundance accounted for by the ordination (Ter Braak & Šmilauer 1998). Only those with >10% are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

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

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

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

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

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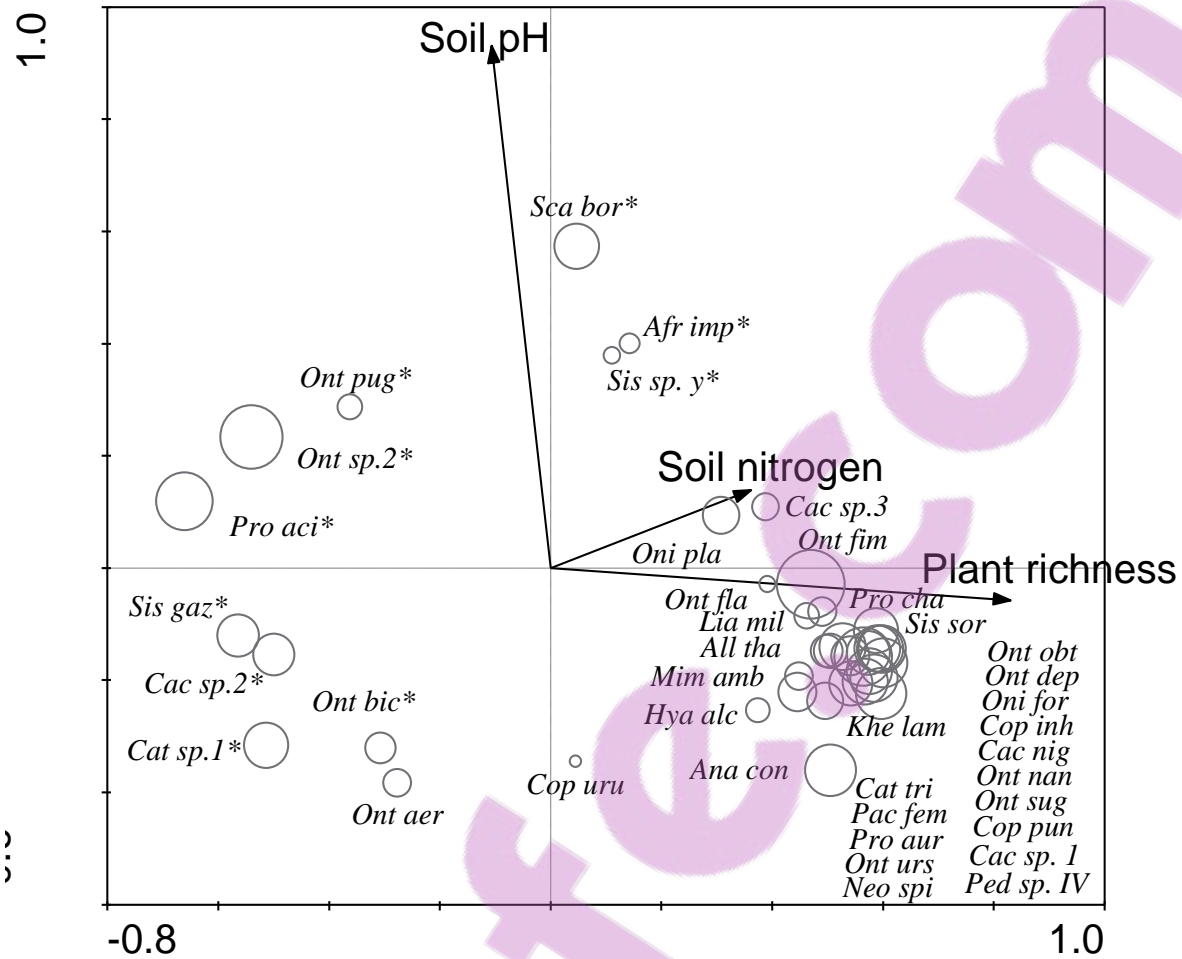
Figure 4-2. Correlation biplot of the redundancy analysis for dung beetles using woody plant richness, soil nitrogen, and soil pH. Symbol size corresponds to the proportion of explained variance of a species' abundance accounted for by the ordination (Ter Braak & Šmilauer 1998). Only those with >10%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

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

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

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

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

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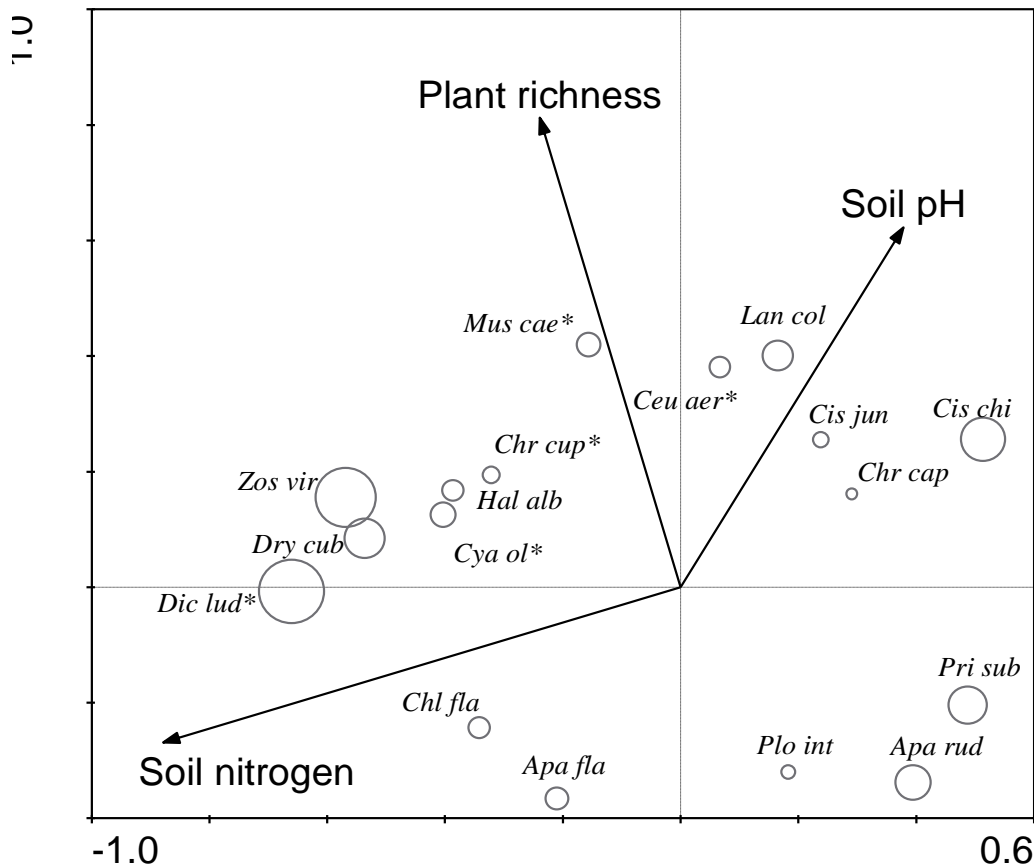
Figure 4-3. Correlation biplot of the redundancy analysis for birds, where only those habitat variables that had significant influence on species abundance are shown. Symbol size corresponds to the values of the fit of species into the ordination space (range 13-75%). See interpretation explanation in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

Discussion

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

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

Interactions between habitat features

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

Interactions between habitat features and community variables

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

This chapter was submitted to Landscape and Ecological Engineering for publication and is therefore presented according to that journal's specifications. It has since been reviewed and was accepted for publication on 23 January 2013, DOI: 10.1007/s11355-013-0211-1 (see Appendix III).

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	• 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	• 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
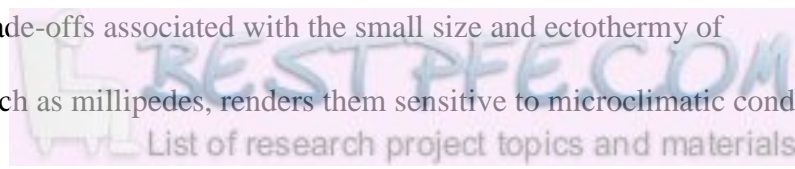
that dictate habitat preferences (Ashwini & Sridhar 2008; Loranger-Merciris et al. 2008; David & Gillon 2009). We therefore assessed the importance of the topographic profile in structuring millipede assemblages. We expected that within a seral stage, plant richness, canopy structure and species-specific 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 amd 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 ± 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 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.
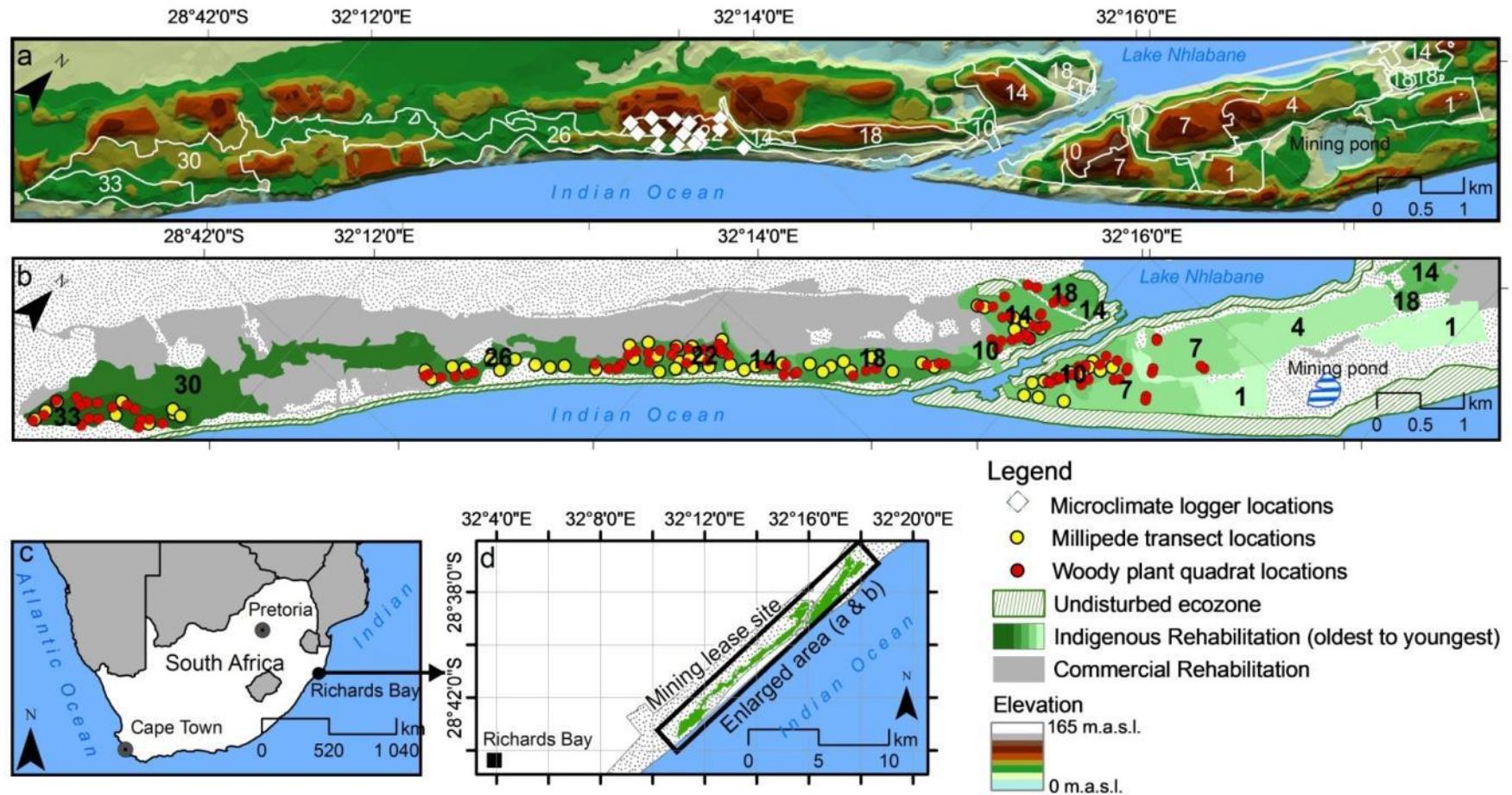
Figure 5-1. Digital elevation model of the study area also showing the delineation of rehabilitating stands according to age, and the sites where data loggers were deployed (a). The locations of woody plant quadrats and millipede transect surveys were conducted are shown in relation to stand age (b). 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 per100 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 per100 m^2 calculated for each quadrat
Millipedes	Millipede species	Total number of millipede species per quadrat
	Cylindrical density	Number of *Centrobolus* spp*., Doratagonus* 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 *Sphaerotheridae* 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).
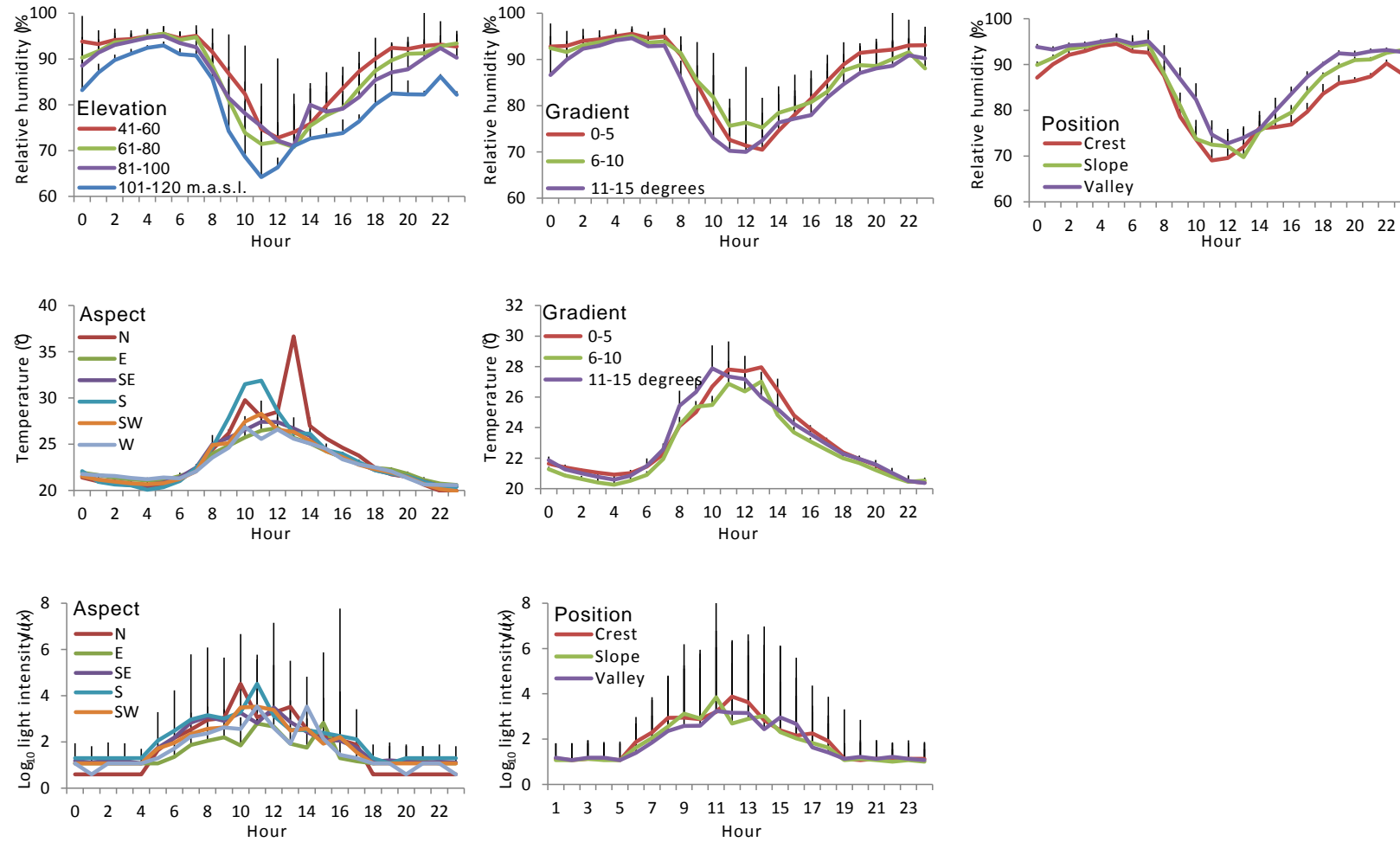
Figure 5-2. Mean ± one standard deviation of the mean of three microclimatic variables (relative humidity, temperature, and light intensity, from top to bottom, respectively) that showed significant responses to variables of dune morphology according to the repeated measures ANOVA, as recorded between 01h00 and 24h00 on the 29th of January 2011.

Figure 5-3. Mean ± 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 | Dune morphology | | | | | ANCOVA results | | |
		Aspect	Elevation	Gradient	Position	Age	df	AIC	P
Soil									
Soil pH	1	Insufficient cases							
	2					X	1	54.35	0.0005
	3	X	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	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**						
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 degree 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 degree 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 discolour (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 degree 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 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).
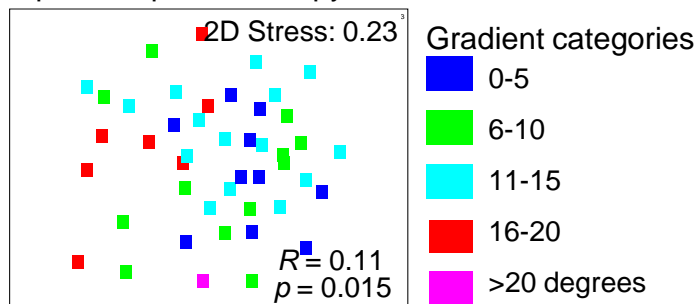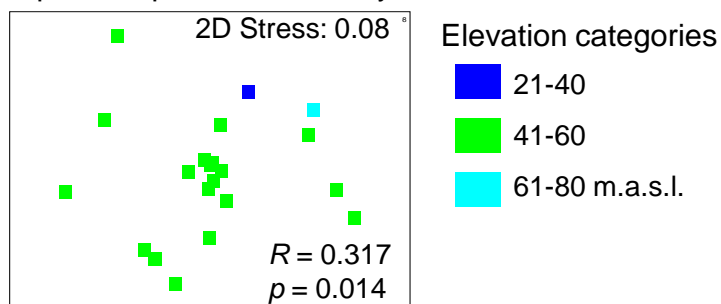
Figure 5-4. Non-metric multi-dimensional scaling (NMDS) plots of woody plant abundances in the canopy (top) and understory (bottom) where analysis of similarity revealed significant ($p < 0.05$) community separation attributable to dune morphological characteristics (elevation, gradient, position) according 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**						
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

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.
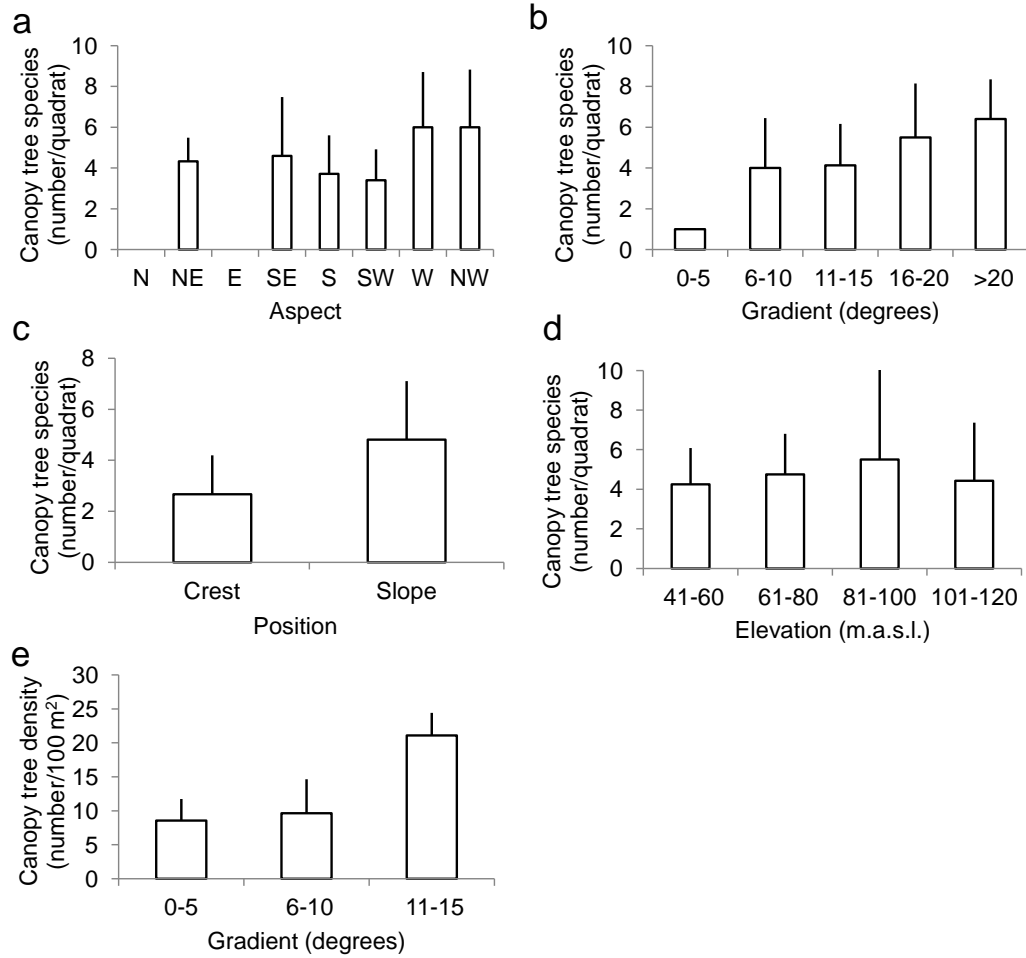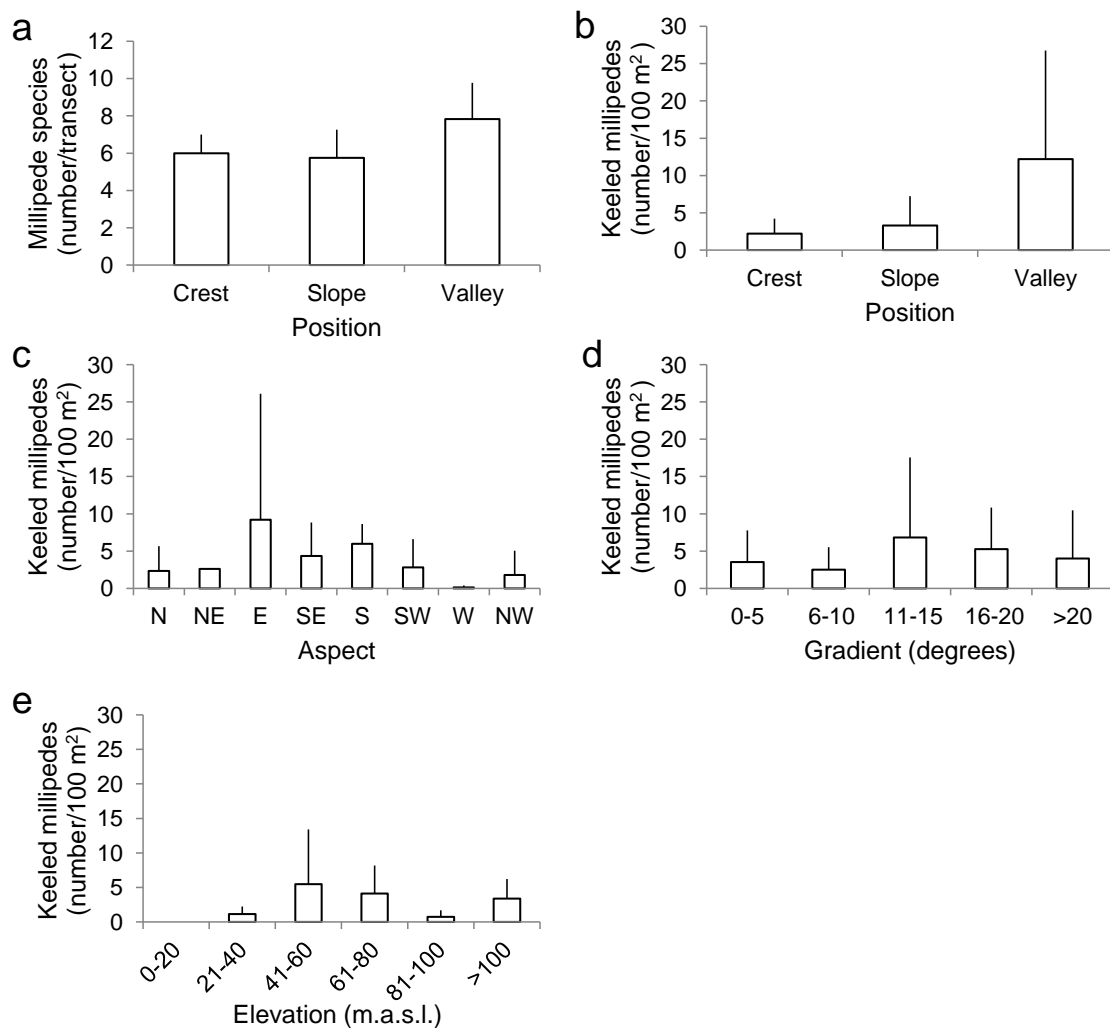

Figure 5-5. Mean ± one standard deviation of the mean of millipede response variables presented as a function of those variables that best-explained their variability significantly despite stand age (see Table 5-2).

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. Futhermore, 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 (Kritzinger & van Aarde 1998), moisture-retention and nutrient accumulation associated with litter accumulation (van Aarde et al. 1998), as well as

the variation of 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 (Kritzinger & 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 though 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; Hãttenschwiler 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

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[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 equisitefolia*) (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.

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Appendix I: Images that illustrate mining and rehabilitation of coastal dunes along the northeast coast of KwaZulu-Natal, South Africa.

Plate 1. Heavy machinery is used to clear vegetation from the coastal dunes prior to the extraction minerals from the sand.

Plate 2. The mine works as an open-cast dredging system whereby dune sand is taken up by a bucket wheel and separated from the heavy minerals (~4% of the sand) by means of a cyclonic system on the mining plant. This heavy mineral concentrate is taken to the smelter site for further processing where the rutile, zircon and ilmenite are further separated and prepared.

Plate 3. Once separated from the heavy minerals, the sand is stacked into shapes that mimic the pre-mining topographic profile.

Plate 4. Topsoil collected from cleared areas ahead of the mine is brought and spread over the newly stacked dunes. This is then sown with annuals and indigenous to stabilize the dune as soon as possible with a cover crop. Shade-netting is erected to prevent wind erosion, as well as shade and protect seedlings.

Seral stage 1

Plate 5. The cover crop grows up within months and between these annuals and grasses, Acacia karroo seedlings begin to germinate (insert picture).

Plate 6. Within three years an impenetrable *Acacia karroo* shrubland has formed (at three years there are 20724±2143 trees/ha (van Dyk 1996)).

Seral stage 2

Plate 7. Within 11 years the *Acacia karroo* still dominates but has thinned to 737±35 trees/ha by the age of 14 (van Dyk 1996). Forest canopy species are beginning to emerge, although the understory is not well-developed

Plate 8. After about 20 years of age the *Acacia karroo* trees begin to senesce and fall over or die standing (inset), forming canopy gaps of varying sizes. Although *A. karroo* remain dominant, the understory has become more developed and forest canopy species are more common.

Seral stage 3

Plate 9. After 30 years gaps of all sizes have formed as *Acacia karroo* continue to fall down. The forest is multi-layered and forest canopy trees are in excess of 8m tall.

Plate 10. In these oldest stands (35 years) *Acacia karroo* has thinned to 141±11 trees/ha (van Dyk 1998), larger gaps comprise grassy patches and clumps of forest tree species. Importantly, these gaps are not recolonized by *A. karroo* (Grainger 2012).

Appendix II: List of species from three taxa recorded in the study area

Table A-1. List of woody plant species identified in the regenerating and unmined forests, third column indicates species associated with forest habitats (●).

Species	Family	Forest-associated species
Acalypha glabrata	Euphorbiaceae	
Acacia karroo	Mimosaceae	
Acacia kraussiana	Mimosaceae	
Acokanthera oppositifolia	Apocynaceae	
Albizia adianthifolia	Mimosaceae	
Allophylus africanus	Sapindaceae	
Allophylus natalensis	Sapindaceae	
Annona senegalensis	Annonaceae	
Antidesma venosum	Euphorbiaceae	
Apodytes dimidiata	Icacinaceae	
Artabotrys monteiroae	Annonaceae	
Barringtonia racemosa	Lecythidaceae	
Bauhinia tomentosa	Caesalpiniaceae	
Bersama lucens	Melianthaceae	
Brachylaena discolor	Asteraceae	
Bridelia cathartica	Euphorbiaceae	
Bridelia micrantha	Euphorbiaceae	
Canthium inerme	Rubiaceae	
Capparis sepiaria	Capparaceae	
Capparis tomentosa	Capparaceae	
Carissa bispinosa	Apocynaceae	●
Carissa macrocarpa	Apocynaceae	
Casuarina equisetifolia	Casuarinaceae	
Cassine eucleiformis	Celastraceae	
Cassipourea gummiflua	Rhizophoraceae	
Cassipourea malosana	Rhizophoraceae	
Cassine tetragona	Celastraceae	
Cassinopsis tinifolia	Icacinaceae	
Catunaregam spinosa	Rubiaceae	
Celtis africana	Ulmaceae	
Cestrum laevigatum	Solanaceae	
Chaetacme aristata	Ulmaceae	●
Chionanthus battiscombei	Oleaceae	
Chionanthus foveolatus	Oleaceae	
Chionanthus peglerae	Oleaceae	●
Chrysanthemoides monilifera	Asteraceae	
Citrus lemon	Rutaceae	
Clausena anisata	Rutaceae	

Clerodendrum glabrum	Verbenaceae	
Clerodendrum myricoides	Verbenaceae	
Cola natalensis	Sterculiaceae	
Commiphora neglecta	Burseraceae	
Cordia caffra	Boraginaceae	●
Croton sylvaticus	Euphorbiaceae	
Cussonia sphaerocephala	Araliaceae	
Dalbergia armata	Fabaceae	
Deinbollia oblongifolia	Sapindaceae	
Dichrostachys cinerea	Mimosaceae	
Diospyros inhacaensis	Ebenaceae	
Diospyros lycioides	Ebenaceae	
Diospyros natalensis	Ebenaceae	●
Dodonaea angustifolia	Sapindaceae	
Dovyalis longispina	Flacourtiaceae	●
Dovyalis rhamnoides	Flacourtiaceae	
Dracaena aletriformis	Dracaenaceae	
Drypetes natalensis	Euphorbiaceae	
Drypetes reticulata	Euphorbiaceae	
Ekebergia capensis	Meliaceae	●
Elaeodendron croceum	Celastraceae	
Englerophytum natalense	Sapotaceae	
Ephippiocarpa orientalis	Apocynaceae	
Erythrococca berberidea	Euphorbiaceae	●
Erythroxylum emarginatum	Erythroxylaceae	
Erythrina lysistemon	Fabaceae	
Euclea natalensis	Ebenaceae	
Euclea racemosa subsp. sinuata	Ebenaceae	●
Eugenia capensis	Myrtaceae	
Eugenia natalitia	Myrtaceae	●
Ficus burtt-davyi	Moraceae	
Ficus craterostoma	Moraceae	
Ficus lutea	Moraceae	
Ficus natalensis	Moraceae	
Ficus polita	Moraceae	
Ficus sur	Moraceae	
Ficus sycomorus	Moraceae	
Ficus trichopoda	Moraceae	
Garcinia livingstonei	Clusiaceae	
Gardenia thunbergia	Rubiaceae	
Grewia caffra	Tiliaceae	
Grewia occidentalis	Tiliaceae	
Halleria lucida	Scrophulariaceae	
Harpephyllum caffrum	Anacardiaceae	
Hibiscus tiliaceus	Malvaceae	

Hymenocardia ulmoides	Euphorbiaceae	
Inhambanella henriquesii	Sapotaceae	
Keetia gueinzii	Rubiaceae	
Kiggelaria africana	Flacourtiaceae	
Kraussia floribunda	Rubiaceae	
Lagynias lasiantha	Rubiaceae	
Lantana camara	Verbenaceae	
Macaranga capensis	Euphorbiaceae	
Maesa lanceolata	Myrsinaceae	
Maerua nervosa	Capparaceae	
Manilkara concolor	Sapotaceae	
Manilkara discolor	Sapotaceae	
Maytenus cordata	Celastraceae	
Maytenus heterophylla	Celastraceae	
Gymnosporia mossambicensis	Celastraceae	
Gymnosporia nemorosa	Celastraceae	
Maytenus procumbens	Celastraceae	
Gymnosporia senegalensis	Celastraceae	
Maytenus undata	Celastraceae	
Melia azedarach	Meliaceae	
Mimusops caffra	Sapotaceae	
Mimusops obovata	Sapotaceae	
Monanthotaxis caffra	Annonaceae	
Myrica serrata	Myricaceae	
Mystroxylon aethiopicum	Celastraceae	
Ochna arborea	Ochnaceae	
Ochna natalitia	Ochnaceae	
Olea capensis	Oleaceae	●
Olea woodiana	Oleaceae	
Osyris compressa	Santalaceae	
Oxyanthus speciosus	Rubiaceae	
Ozoroa obovata	Anacardiaceae	
Pancovia golungensis	Sapindaceae	●
Parinari capensis subsp. incohata	Chrysobalanaceae	
Passerina rigida	Thymelaeaceae	
Pavetta lanceolata	Rubiaceae	
Pavetta natalensis	Rubiaceae	
Pavetta revoluta	Rubiaceae	
Pavetta Sp01	Rubiaceae	
Peddiea africana	Thymelaeaceae	●
Persea americana	Lauraceae	
Phoenix reclinata	Arecaceae	
Pinus elliotti	Pinaceae	
Pisonia aculeata	Nyctaginaceae	
Protorhus longifolia	Anacardiaceae	

Psidium guajava	Myrtaceae	
Psychotria capensis	Rubiaceae	●
Psydrax obovata	Rubiaceae	
Rapanea melanophloeos	Myrsinaceae	
Rauvolfia caffra	Apocynaceae	
Rhoicissus digitata	Vitaceae	
Rhoicissus revoilii	Vitaceae	
Rhoicissus rhomboidea	Vitaceae	●
Rhoicissus tomentosa	Vitaceae	
Rhoicissus tridentata	Vitaceae	
Rhus natalensis	Anacardiaceae	
Rhus nebulosa	Anacardiaceae	
Ricinus communis	Euphorbiaceae	
Rothmannia globosa	Rubiaceae	
Salacia gerrardii	Celastraceae	
Sapium integerrimum	Euphorbiaceae	
Schinus terebinthifolius	Anacardiaceae	
Schefflera umbellifera	Araliaceae	
Sclerocarya birrea	Anacardiaceae	
Scolopia zeyheri	Flacourtiaceae	
Scutia myrtina	Rhamnaceae	
Senna pendula	Caesalpiniaceae	
Sideroxylon inerme	Sapotaceae	
Solanum mauritianum	Solanaceae	
Strychnos gerrardii	Loganiaceae	●
Strychnos henningsii	Loganiaceae	
Strychnos madagascariensis	Loganiaceae	
Strychnos mitis	Loganiaceae	
Strelitzia nicolai	Strelitziaceae	
Strychnos spinosa	Loganiaceae	
Strychnos usambarensis	Loganiaceae	
Syzygium cordatum	Myrtaceae	
Syzygium cumini	Myrtaceae	
Tarenna junodii	Rubiaceae	
Tarenna littoralis	Rubiaceae	
Tarenna pavettoides	Rubiaceae	
Tecomaria capensis	Bignoniaceae	
Teclea gerrardii	Rutaceae	●
Thespesia acutiloba	Malvaceae	
Trema orientalis	Ulmaceae	
Tricalysia delagoensis	Rubiaceae	
Trichilia dregeana	Meliaceae	
Trichilia emetica	Meliaceae	
Tricalysia lanceolata	Rubiaceae	
Tricalysia sonderiana	Rubiaceae	

Turraea floribunda	Meliaceae	●
Turraea obtusifolia	Meliaceae	
Uvaria caffra	Annonaceae	
Vangueria cyanescens	Rubiaceae	
Vangueria infausta	Rubiaceae	
Vangueria randii	Rubiaceae	
Vepris lanceolata	Rutaceae	
Voacanga thouarsii	Apocynaceae	
Xylotheca kraussiana	Flacourtiaceae	
Zanthoxylum capense	Rutaceae	
Ziziphus mucronata	Rhamnaceae	

Table A-2. List of millipede species identified in the regenerating and unmined forests, third column indicates species associated with forest habitats (●).

Species	Family	Forest-associated species
Doratogonus sp.	Spirostreptidae	
Centrobolus fulgidus	Spirobolidae	
Centrobolus richardii	Spirobolidae	
Centrobolus rugulosus	Spirobolidae	●
Gnomeskelus tuberosus	Dalodesmidae	●
Orthroporoides sp.*	Spirostreptidae	●
Orthroporoides pyrocephalus	Spirostreptidae	●
Sphaerotherium giganteum	Sphaerotheridae	●
Sphaerotherium punctulatum	Sphaerotheridae	●
Sphaerotherium rotundatum	Sphaerotheridae	●
Sphaerotherium sp. B	Sphaerotheridae	●
Sphaerotherium sp. C	Sphaerotheridae	●
Sphaerotherium sp. D	Sphaerotheridae	●
Sphaerotherium sp. E	Sphaerotheridae	●
Sphaerotherium sp. F	Sphaerotheridae	●
Spinotarsus anguliferus	Odontopygidae	
Spirostreptidae sp. Imm.	Spirostreptidae	●
Spirostreptidae sp. Imm. 2	Spirostreptidae	●
Ulodesmus micramma zuluensis	Dalodesmidae	

Table A-3. List of dung beetle species identified in the regenerating and unmined forests, third column indicates species associated with forest habitats (●).

Species	Forest-associated species
Allogymnopleurus thalassinus	●
Anachalcos convexus	
Caccobius nigritulus	
Caccobius obtusus	
Caccobius sp. 1	●
Caccobius sp. 2	
Caccobius sp. 3	●
Caccobius sp. 4	
Caccobius sp. 5 = Caccobius cavatus	
Catharsius sp 1 (endemic)	
Catharsius mossambicanus	
Catharsius tricornutus	●
Cleptocaccobius viridicollis	
Copris inhalatus ssp santaluciae	
Copris puncticollis	
Copris urus	
Digitonthophagus gazella	
Drepanocerus impressicollis (now Afrodrepanus impressicollis)	
Drepanocerus kirbyi	
Euoniticellus intermedius	
Garreta azureus	●
Garreta unicolor	●
Gyronotus carinatus	
Heliocopris hamadryas	
Hyalonthophagus alcyonides	
Kheper lamarcki	●
Liatongus militaris	●
Metacatharsius sp. 1 (=zuluanus)	●
Milichus sp. 1	
Neosisyphus confrater	
Neosisyphus mirabilis	●
Neosisyphus spinipes	
Odontoloma sp.	
Oniticellus formosus	●
Oniticellus planatus	
Onthophagus aeruginosus	●
Onthophagus ambiguus (now Mimonthophagus ambiguus)	
Onthophagus bicavifrons	
Onthophagus depressus	
Onthophagus fimetarius (coastal var.) possibly new	
Onthophagus flavolimbatus	
Onthophagus lacustris	
Onthophagus nanus	
Onthophagus obtusicornis	
Onthophagus pugionatus	
Onthophagus quadrinodosus	●
Onthophagus signatus	●
Onthophagus sp 1 (=horned pullus)	
Onthophagus sp. 2 (v. small endemic)	

Onthophagus sp 3 (=sp. e George)	
Onthophagus sp 4	
Onthophagus sp nr bicavifrons	●
Onthophagus sp. nr sugillatus (coastal var.) possibly new	
Onthophagus ursinus	●
Onthophagus vinctus	●
Onthophagus stellio or variegatus gp??	
Onthophagus sp - mottled tail	
Onthophagus sp A	
Pachylomerus femoralis	
Pedaria sp. IV	●
Pedaria sp. III	
Proagoderus aciculatus	
Proagoderus aureiceps	
Proagoderus brucei (now P. chalcostolus)	
Scarabaeus bornemisszai	
Scarabaeus goryi	●
Sisyphus natalensis (cited as the syn. S. bornemisszanus)	●
Sisyphus seminulum	
Sisyphus sordidus	●
Sisyphus sp nr gazanus	●
Sisyphus sp y	
Stiptopodius sp. 1	

Table A-4. List of bird species identified in the regenerating and unmined forests, third column indicates species associated with forest habitats (●).

Species	Common Name	Forest-associated species
Acrocephalus palustris	Eurasian Marsh Warbler	
Alcedo cristata	Malachite Kingfisher	
Amblyospiza albifrons	Thick-billed Weaver	
Andropadus importunus	Sombre Greenbul	
Anthus cinnamomeus	African Pipit	
Apalis flavida	Yellow-breasted Apalis	
Apalis ruddi	Rudd's Apalis	
Apalis thoracica	Bar-throated Apalis	
Apalpderma narina	Narina Trogon	●
Aplopelia larvata	Lemon Dove	●
Ardea melanocephala	Black-headed Heron	
Batis capensis	Cape Batis	
Batis fratrum	Woodwards' Batis	●
Bostrychia hagedash	Hadeda Ibis	
Bradornis pallidus	Pale Flycatcher	
Bycanistes bucinator	Trumpeter Hornbill	●
Calendulauda sabota	Sabota Lark	
Camaroptera brachyura	Green-backed Camaroptera	
Campephaga flava	Black Cuckooshrike	
Campethera abingoni	Golden-tailed Woodpecker	
Caprimulgus europaeus	European Nightjar	
Centropus burchellii	Burchell's Coucal	
Cercotrichas leucophrys	White-browed Scrub-Robin	
Cercotrichas quadrivirgata	Bearded Scrub-Robin	
Cercotrichas signata	Brown Scrub-Robin	
Ceuthmochares aereus	Green Malkoha	●
Chalcomitra amethystina	Amethyst Sunbird	
Chalcomitra senegalensis	Scarlet-chested Sunbird	
Chlorocichla falviventris	Yellow-bellied Greenbul	
Chrysococcyx caprius	Diederik Cuckoo	
Chrysococcyx cupreus	African Emerald Cuckoo	●
Chrysococcyx klaas	Klaas's Cuckoo	
Cinnyris bifasciata	Purple-banded Sunbird	
Cisticola chinianus	Rattling Cisticola	
Cisticola cinnamomeus	Pale-crowned Cisticola	
Cisticola fulvicapilla	Neddicky	
Cisticola juncidis	Zitting Cisticola	
Cisticola natelensis	Croaking Cisticola	
Clamator jacobinus	Jacobin Cuckoo	
Coccopygia melanotis	Swee Waxbill	

Colius striatus	Speckled Mousebird	
Columba delegorguei	Eastern Bronze-naped Pigeon	●
Coracias caudata	Lilac-breasted Roller	
Coracias garrulus	Eurasian Roller	
Coracina caesia	Grey Cuckooshrike	
Corvus albus	Pied Crow	
Cossypha caffra	Cape Robin-Chat	
Cossypha dichroa	Chorister Robin-Chat	
Cossypha natalensis	Red-capped Robin-Chat	
Coturnix coturnix	Common Quail	
Cuculus canorus	Common Cuckoo	
Cuculus gularis	African Cuckoo	
Cuculus solitarius	Red-chested Cuckoo	
Cyanomitra olivacea	Eastern Olive Sunbird	●
Cyanomitra veroxii	Grey Sunbird	●
Dendropicos fuscescens	Cardinal Woodpecker	
Dendropicos griseocephalus	Olive Woodpecker	
Dicrurus adsimilis	Fork-tailed Drongo	
Dicrurus ludwigii	Square-tailed Drongo	●
Dryoscopus cubla	Black-backed Puffback	
Estrilda astrild	Common Waxbill	
Estrilda perreini	Grey Waxbill	
Euplectes axillaris	Fan-tailed Widowbird	
Euplectes orix	Southern Red Bishop	
Eurystomus glaucurus	Broad-billed Roller	
Guttera edouardi	Crested Guineafowl	
Halcyon albiventris	Brown-hooded Kingfisher	
Hedydipna collaris	Collared Sunbird	
Hippolais icterina	Icterine Warbler	
Indicator minor	Lesser Honeyguide	
Indicator variegatus	Scaly-throated Honeyguide	
Ispidina picta	African Pygmy-Kingfisher	
Lagonosticta rubricata	African Firefinch	
Lamprotornis corruscus	Black-bellied Starling	●
Laniarius ferrugineus	Southern Boubou	
Lanius collaris	Common Fiscal	
Lanius collurio	Red-backed Shrike	
Lanius minor	Lesser Grey Shrike	
Lonchura cucllata	Bronze Mannikin	
Lonchura nigriceps	Red-backed Mannikin	
Lybius torquatus	Black-collared Barbet	
Macronyx croceus	Yellow-throated Longclaw	
Malaconotus blanchoti	Grey-headed Bush-Shrike	
Mandingoa nitidula	Green Twinspot	

Megaceryle maxima	Giant Kingfisher	
Melaenornis pammelaina	Southern Black Flycatcher	
Merops pusillus	Little Bee-eater	
Mirafra africana	Rufous-naped Lark	
Monticola rupestris	Cape Rock-Thrush	
Motacilla aguimp	African Pied Wagtail	
Motacilla capensis	Cape Wagtail	
Muscicapa adusta	African Dusky Flycatcher	●
Muscicapa caerulescens	Ashy Flycatcher	●
Muscicapa striata	Spotted Flycatcher	
Musophaga porphyreolopha	Purple-crested Turaco	●
Myioparus plumbeus	Grey Tit-Flycatcher	
Nicator gularis	Eastern Nicator	
Oriolus larvatus	Black-headed Oriole	
Oriolus oriolus	Eurasian Golden Oriole	
Passer domesticus	House Sparrow	
Phyllastrephus terrestris	Terrestrial Brownbul	
Phylloscopus trochilus	Willow Warbler	
Platysteira peltata	Black-throated Wattle-eye	●
Plectropterus gambensis	Spur-winged Goose	
Ploceus	Weavers	
Ploceus bicolor	Dark-backed Weaver	●
Ploceus cucullatus	Village Weaver	
Ploceus intermedius	Lesser Masked-Weaver	
Ploceus ocularis	Spectacled Weaver	
Ploceus subaureus	Yellow Weaver	
Pogoniulus bilineatus	Yellow-rumped Tinkerbird	●
Pogoniulus pusillus	Red-fronted Tinkerbird	
Pogonocichla stellata	White-starred Robin	
Prinia subflava	Tawny-flanked Prinia	
Pycnonotus tricolor	Dark-capped Bulbul	
Rhinopomastus cyanomelas	Common Scimitarbill	
Sarothrura elegans	Buff-Spotted Flufftail	
Saxicola torquata	African Stonechat	
Serinus canicollis	Cape Canary	
Serinus mozambicus	Yellow-fronted Canary	
Serinus sulphuratus	Brimstone Canary	
Sigelus silens	Fiscal Flycatcher	
Smithornis capensis	African Broadbill	
Stactolaema leucotis	White-eared Barbet	●
Streptopelia capicola	Cape Turtle Dove	
Streptopelia semitorquata	Red-eyed Dove	
Sylvia borin	Garden Warbler	
Sylvietta rufescens	Long-billed Crombec	

Tauraco corythsix	Knysna Turaco	●
Tauraco livingstonii	Livingstone's Turaco	●
Tchagra australis	Brown-crowned Tchagra	
Tchagra senegala	Black-crowned Tchagra	
Telophorus olivaceus	Olive Bush-Shrike	
Telophorus quadricolor	Gorgeous Bush-Shrike	
Telophorus sulfureopectus	Orange-breasted Bush-Shrike	
Terpsiphone viridis	African Paradise-Flycatcher	
Tockus alboterminatus	Crowned Hornbill	●
Trachyphonus vallantii	Crested Barbet	
Treron calva	African Green-Pigeon	
Trochocercus cyanomelas	Blue-mantled Crested Flycatcher	●
Turdus libonyanus	Kurrichane Thrush	
Turtur chalcospilos	Emerald-spotted Wood-Dove	
Turtur tympanistria	Tambourine Dove	●
Uraeginthus angolensis	Blue Waxbill	
Urocolius indicus	Red-faced Mousebird	
Vidua macroura	Pin-tailed Whydah	
Zoothera guttata	Spotted Ground-Thrush	
Zosterops virens	Cape White-eye	

1 Appendix III: Manuscript accepted for publication at *Landscape and Ecological*

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5

6 **Title**: Coastal dune topography as a determinant of abiotic conditions and biological

7 community restoration in northern Kwazulu-Natal, South Africa

8

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14

17

18 **Abstract**

19 Topography is rarely considered as an independent goal of restoration. Yet, topography

20 determines micro-environmental conditions and hence living conditions for species.

21 Restoring topography may therefore be an important first step in ecological restoration. We

22 aimed at establishing the relative importance of topography where coastal dunes destroyed by

23 mining are rebuilt as part of a rehabilitation programme.

24   We assessed the response of 1) microclimatic and soil conditions, and 2) woody plant

25 and millipede species richness and density, to location-specific topographic profiles. We

26 enumerated the topographic profile using variables of dune morphology (aspect, elevation

27 and gradient) as well as relative position on a dune (crest, slope, valley).

28   Temperature, relative humidity and light intensity varied with aspect, elevation,

29 gradient and position. However, regeneration age was a better predictor of soil nutrient

30 availability than these topographic variables. Age also interacted with topographic variables

31 to explain tree canopy density and species richness, as well as millipede species richness. The

32 density of keeled millipedes (forest specialists) was best explained by topographic variables

33 alone. The transient nature of these new-growth coastal dune forests likely masks

34 topography-related effects on communities because age-related succession (increasing

35 structural complexity) drives the establishment and persistence of biological communities,

36 not habitat conditions modulated by topography. However, our study has shown that the

37 microhabitats associated with topographic variability influence specialist species more than

38 generalists.

39

40

41   **Introduction**

42   Ecological restoration is widely recognised as a conservation tool and aims to re-instate

43   natural processes that sustain biological diversity (Dobson et al. 1997; MacMahon & Holl

44   2001; Rands 2012). Such diversity is determined by both regional and local forces, the latter

45   often as a function of topography due to cascadal effects on microclimatic conditions, water

46   retention, and nutrient availability (Larkin et al. 2006). These relationships are especially

47   well-documented in mountainous regions (Burnett et al. 1998; Nichols et al. 1998; Tateno &

48   Takeda 2003; da Silva et al. 2008), but less often for coastal sand dune ecosystems (e.g.

49   Martínez et al. 2001; Acosta et al. 2007). The restoration of topography may be a priority

50   (Weiss & Murphy 1990; Palik et al. 2000; Larkin et al. 2006), but difficult or costly to

51   achieve. However, an approximation of the original topography may be sufficient to maintain

52   desired ecological processes. This may well be the case in our study areas where succession

53   drives forest regeneration, but where the full complement of species has not yet been

54   regained (van Aarde et al. 1996b; Grainger 2012). This may be due to the micro-

55   environmental needs of specialist species not being met due to constraints imposed by

56   topography. Justification to restore terrain requires an assessment of the relevance of

57   topography for species and ecological processes. In this study, we assess the influence of

58   dune topography on abiotic and biotic conditions (Table) in coastal dune forests regenerating

59   in response to an ecological restoration program.

60   The aspect, elevation, and gradient of slopes are collectively referred to as dune

61   morphology, while the relative position is described as the crest, slope, or valley. These

62   variables of dune topography can modulate habitat conditions in various ways (Larkin et al.

63   2006). For example, nutrients leaching from dune crests into valleys where plant-

64   communities are light-limited results in nutrient-limited communities on crests, but greater

65   nutrient availability in valleys (Tateno & Takeda 2003). Canopy structure changes with

66 gradients in soil fertility and light (Nichols et al. 1998; Tateno & Takeda 2003), even with

67 limited altitudinal variation (da Silva et al. 2008). This may explain patterns in plant species

68 composition, abundance, and distribution (Chen et al. 1997; Oliviera-Filho et al. 1998). The

69 aspect and gradient of dune slopes may amplify these differences as they also influence light

70 availability (Oliviera-Filho et al. 1998; Bennie et al. 2008) and wind exposure (Chen et al.

71 1997; Acosta et al. 2007). Wind sculpts tree canopies (Kubota et al. 2004), hastens canopy

72 gap formation (Ritter et al. 2005), and contributes to seed dispersal (Furley & Newey 1979).

73 The windward slopes of coastal dunes have higher evaporation rates than leeward slopes and

74 are more exposed to salt spray that increases salt concentrations in the soil, in turn

75 influencing soil pH and the availability of nutrients (Furley & Newey 1979; Chen et al. 1997;

76 Acosta et al. 2007). We therefore hypothesized that dune morphology and position would 1)

77 modulate microclimatic conditions (temperature, relative humidity, and light intensity) and 2)

78 influence soil nutrient availability (C:N ratio) and soil pH (see Table). Disturbed or

79 destroyed topographic profiles could therefore hinder the ecological restoration of plant and

80 animal communities of new-growth forests, or simply alter heterogeneity and rearrange the

81 distribution of resources. Thus the structure and composition of biotic communities at

82 locations with different dune morphologies should be assessed to determine the importance of

83 restoring the topographic profile.

84   Topography influences plant growth and species richness in old-growth forests

85 (Tateno & Takeda 2003; da Silva et al. 2008), which has cascadal effects on biota through the

86 responses of microclimatic conditions to topography (Larkin et al. 2006). Physiological trade-

87 offs associated with the small size and ectothermy of invertebrates, such as millipedes,

88 renders them sensitive to microclimatic conditions that dictate habitat preferences (Ashwini

89 & Sridhar 2008; Loranger-Merciris et al. 2008; David & Gillon 2009). We therefore assessed

90 the importance of the topographic profile in structuring millipede assemblages. We

91   hypothesized that within a seral stage, dune morphology and position would 3) influence

92   plant community structure and composition, and 4) millipede community structure and

93   composition in regenerating stands of new-growth coastal dune forest (Table). If millipedes

94   respond to topography, changes in the topographic profile should result in changes in

95   millipede diversity. If this is not the case, topography has a limited role to play, if any, in

96   explaining millipede community structure. Although this study is based upon coastal dune

97   forests, it may have implications for any disturbed dune system under restoration.

98   **Methods**

99   *Study area*

100   The study area was located north of Richards Bay town (between 28°46' and 28°34' south) on

101   the sub-tropical north coast of Kwazulu-Natal, South Africa (Fig. 1). The climate is humid

102   with a mean annual rainfall of 1458 ± 493.5 mm (mean ± SD, n = 34 years between 1976 and

103   2009), peaking in February. The mean annual temperature was 23.79 ± 3.40°C (n = 3 years

104   between 2006 and 2009. Winds of between 10 and 40 km.h^{-1} blew from the north-east for

105   about 20% of the time, as did those from south-south west and south-west combined (data

106   courtesy of Richards Bay Minerals).

107   The establishment of forests on the coastal dunes here occurred with the return of

108   warm interglacial conditions between 6,500 and 4,000 years ago, making them among the

109   highest vegetated dunes in the world (Weisser & Marques 1979; Lawes 1990). These forests

110   are therefore relatively young and harbour few endemic species (Lawes 1990; van Wyk &

111   Smith 2001). Coastal dune forests are sensitive to disturbance but previous work has shown

112   that they are relatively resilient and are thus able to recover (e.g. Wassenaar et al. 2005;

113   Grainger et al. 2011).

114   Richards Bay Minerals (RBM) has leased this area since 1976 for the extraction of

115   heavy metals from the coastal sands. Ahead of the dredging pond, all vegetation was cleared

116   and the dunes were collapsed for mining. After mining, sand tailings were stacked to

117   resemble pre-mining topography and were covered with topsoil (van Aarde et al. 1996c). A

118   third of the mined area was set aside for the restoration of indigenous coastal dune forest and

119   this area comprised known-aged stands that at the time of the study ranged in age from 1 year

120   (in the northeast) to 33 years (in the southwest) (see Fig. 1). This age-range represented three

121   seral stages based on those defined by Grainger (2012): seral stage one = 1-10 years, two =

122   11-25 years, and three >25 years. Adjoined by a coastal strip of unmined vegetation about

123   200 m wide, the stands were themselves no wider than 2 km, set in a mosaic of active mining

124   areas, plantations, degraded woodland, and rural villages (Wassenaar et al. 2005).

125   *Microclimatic data*

126   Fifteen HOBO[®] 4-channel data loggers (Onset Computer Corporation, 470 MacArthur Blvd.,

127   Bourne, MA 02532, U.S.A.) were deployed in the 22-year old stand (see Fig. 1) on custom-

128   made platforms placed 10 cm above the ground (five on the crest, five on a slope and five in

129   the valley). We programmed these loggers to record ground-level temperature, relative

130   humidity, and light intensity (see Table **2** for definitions) every 10 minutes between 08:00, 28

131   January and 05:00, 4 February 2011, yielding 14,850 records.

132   *Soil surveys*

133   An auger was used to collect soil samples to 20 cm depth at the corners and centre of each of

134   the millipede survey transects (see below). These five samples were mixed into a single bag

135   and consequently 65 bags were analyzed at the Department of Plant Production and Soil

136   Science at the University of Pretoria using procedures described in van Aarde et al. (1998;

137   see supplementary information for detailed chemical profile). We used Nitrogen and Carbon

138 concentrations to calculate the carbon-to-nitrogen ratio (C:N, Table 2) and included the pH

139 values of each sample in our analysis.

140 *Woody plant surveys*

141 All woody plants taller than 0.2 m in 106 randomly placed quadrats (16×16–m, at least 100 m

142 apart) in six stands of known regeneration age (10, 14, 18, 22, 26, and 33 years) were

143 sampled between July and November 2010. Each plant was identified against reference

144 material. We calculated six variables of woody plant community structure for each quadrat

145 (see Table 2).

146 *Millipede surveys*

147 Millipede species occurring on the ground up to 3 m on plants were counted between 13

148 January and 4 February 2011 in 65 randomly placed transects within a 10, 14, 18, 22, 26, and

149 33 year-old stand (see Fig. 2). Each transect was 32×6–m wide and comprised 48 2×2–m

150 cells. Surveys were conducted by three observers per transect, each responsible for a column

151 of 16 cells. All millipedes found in a cell during five minutes were identified based on

152 reference images and descriptions (Porter et al. 2007), counted, and removed to avoid

153 recounting. We calculated the number of millipede species and the density of cylindrical,

154 keeled, and pill millipedes (see Table 2) within each location-specific transect.

155 *Topographic data*

156 We used classified topographic data based on eight cardinal directions (aspect), seven

157 elevation categories, and five gradient categories that had been extracted from a topographic

158 map (see Fig.1.) based on a Light Detection and Ranging (LIDAR) mission conducted in

159 2010 (post-mining). We used GIS overlay procedures to relate all of the sampling points and

160 quadrat locations recorded in the field to location-specific variables of dune morphology

161 based on the topographic maps.

162   *Statistical analyses*

163   We used stratified random sampling to extract one microclimate record (including the

164   temperature, relative humidity, and light intensity readings) per hour, per logger for each

165   sampling day (29 January – 3 February 2011), rendering 2,475 records to be included in

166   analyses. We $\log_{10}$-transformed the light intensity data to meet assumptions for analyses of

167   variance (ANOVA). To determine whether microclimatic conditions were modulated by

168   topography, we conducted repeated measures ANOVA with hour and day as repeated

169   measures factors, and categorized variables of dune morphology as between-groups factors.

170   We assessed the influence of dune morphological variables on soil C:N ratios and pH,

171   as well as woody plant and millipede community variables in each of the three seral stages.

172   We assessed these using generalized linear models with age as a covariate (Analyses of

173   Covariance (ANCOVA) for all seral stages for woody plants and seral stages 2 and 3 for soil

174   and millipedes. Millipede and soil data for seral stage 1 comprised too few cases and was

175   therefore not assessed separately. All statistical analyses were conducted using STATISTICA

176   10 (Statsoft Inc., Tulsa, Oklahoma).

177   Woody plant and millipede species abundance data were $\log_{10}$-transformed and

178   calculated the similarity between quadrats, with different dune morphological characteristics

179   using the Bray-Curtis index. Cluster analyses and non-metric multi-dimensional scaling

180   (NMDS) were used to detect community clusters based on the four characteristics of dune

181   morphology. Analyses of similarity (ANOSIM) allowed us to assess the significance of

182   community groupings based on dune morphology within each successional stage. To identify

183   the distinguishing species, we conducted similarity percentage (SIMPER) analyses

184   (SIMPER) for those community groupings that differed significantly based on dune

185   morphological characteristics. All multivariate techniques were conducted using PRIMER 6

186   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 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. 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

208   case when seral stage 2 was treated separately (ANCOVA and AIC;
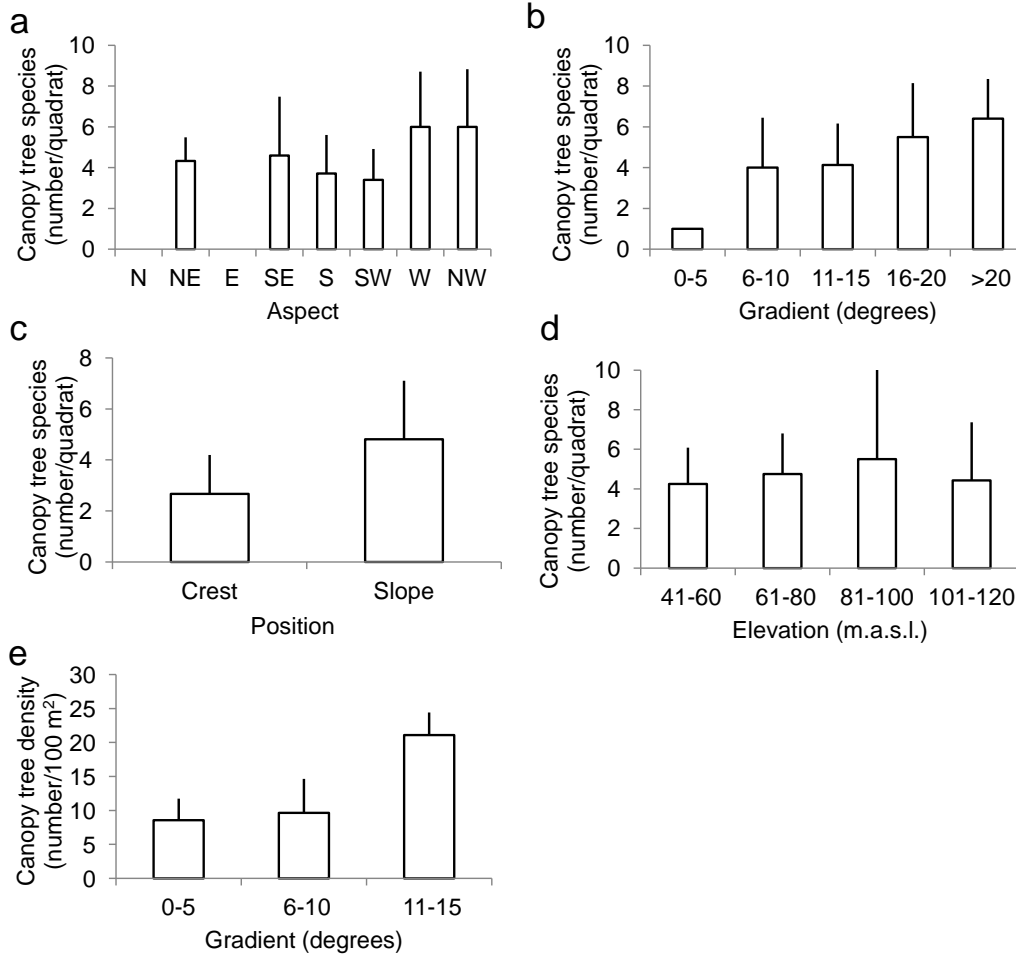
209

210   Figure 5-3. Mean ± one standard deviation of the mean of woody plant response variables

211   presented as a function of those variables that best-explained their variability significantly

212   despite stand age (see Table 2).

213   Table 5-3). The number of tree canopy species in seral stage 1 was best explained by a model

214   including aspect, elevation, gradient, and position, but not age. There were more species on

215   west- and northwest-facing slopes compared to south- and southwest-facing slopes (Fig. 3a),

216   while relatively flat slopes had fewer species than other gradients (Figure 5-3b), as did crests

217   relative to slopes (Fig. 3c). However, canopy tree species richness varied little with elevation

218   (Fig. 3d). Tree density in seral stage 3 increased significantly with gradient (ANCOVA and

219   AIC; Fig. 3e).

220   Only 11% of the variability in tree species abundances was explained by gradient in

221   seral stage 2, although the NMDS plot was unconvincing of this separation (ANOSIM, p <

222   0.05, Fig.). Nevertheless, SIMPER analysis revealed consistent dominance by *Acacia karroo*

223   Hayne and *Celtis africana* Burm.f. (contributing more than 80% of the community) across all

224   gradients (Table 4). However, the number of species increased with gradient so that in

225   addition to these two species, *Allophylus natalensis* Sond. (Dune False Currant) characterized

226   slopes ranging from 0 to 15° and *Brachylaena discolor* DC. (Coast Silver-oak) those of 11 to

227   15°. Slopes of more than 15° were characterised by the addition of *Grewia occidentalis* L.

228   (Cross-berry), *Chaetachme aristata* Planch. (Giant Pock Ironwood) and *Teclea gerrardii*

229   I.Verd. (Zulu Cherry-orange), though all with less than a 5% contribution to tree communities

230   on these slopes (Table 4).

231   Elevation explained 32% of the variability in understory species abundances in seral stage 3

232   (ANOSIM, *p* < 0.05, Fig.). However, this was the result of most cases representing mid-

233   elevations of 41–60 m.a.s.l, with very few cases for other elevation categories. Nevertheless,

234   these mid-elevations were dominated (61% contribution) by *Rhoicissus revoilii* Planch.

235   (Bushveld grape), followed by *Scutia myrtina* Burm.F (Cat-thorn) that contributed 28%, and

236   the invasive alien species, *Chromolaena odorata* L. (Triffid Weed), contributing 11% (Table

237   5). Elevations of 61–80 m.a.s.l. were dominated by *S. myrtina* alone (Table 5).

238   *Millipede assemblages*

239   We recorded 28,987 millipedes (28,351 cylindrical, 513 keeled, and 123 pill millipedes) from

240   16 species in 65 quadrats. The number of millipede species in the transects of seral stage 2

241   covaried with dune position (Table 3), whereby valleys had the most species, though that of

242   slopes and crests did not differ from one another (Fig. 5). Models including age as a covariate

243   in addition to variables of dune morphology best explained the density of cylindrical

244   millipedes for pooled and separated seral stages. Pill millipede density was very low and also

245   driven by rehabilitating stand age in combination with dune morphological variables for

246   pooled as well as separate seral stages. The density of keeled millipedes for pooled seral

247   stages was best explained by a model including aspect, elevation, gradient, and position, but

248   not age (Table 3). These millipedes were most prolific in valleys (Fig. 5b), as well as east-

249   facing slopes (Fig. 5c) with gradients steeper than 10° (Fig. 5d). However, we found little

250   correlation between millipede communities and elevation (Fig. 5e), and when seral stages

251   were separated age was included in the best-fit model (Table 3). Based on our ANOSIM

252   analyses none of the variables of dune morphology significantly influenced species-specific

253   millipede abundances.

254   **Discussion**

255   In line with our hypotheses, dune morphology modulated microclimatic conditions in a

256   similar manner as reported for other studies (Tateno & Takeda 2003; Bennie et al. 2008). We

257   acknowledge though, that the conditions on each dune face are likely the product of

258   conditions ameliorated or exacerbated by surrounding dunes that have consequences for wind

259   channelling and shading, thus cumulatively influencing microclimatic conditions. Contrary to

260   our hypotheses, variability in soil nutrient concentrations was not explained by dune

261   morphology, but rather by regeneration age. The processing of sand as part of the mining

262   operation probably reshuffled soil nutrients and minerals that accumulate through natural

263   processes. With only a few years of post-mining regeneration of biotic activity and

264   mechanical processes (e.g. leeching) it is not surprising that soil fertility (C:N ratios) and pH

265   levels are not yet conforming to expected spatially structured patterns induced by dune

266   topography. Given the weak associations between topographic and abiotic variables, it is also

267   not surprising that spatial variability in woody plant and millipede community structure could

268   not be explained by topographic variables.

269   Species richness and density, as well as species-specific abundances of canopy trees

270   and the understory varied with topography, as did millipede species richness, all in support of

271   our formulated hypotheses, though with the caveat of an overriding influence of regeneration

272   age. Keeled millipedes, a group of invertebrates associated with forests, also responded to

273   topography, although cylindrical and pill millipedes did not. This suggests that forest

274   specialists may be more sensitive to microhabitats induced by topography, but this requires

275   further investigation.

276   Increasing slope steepness resulted in more dense woody plant canopies in stands

277   older than 25 years, a finding similar to that of van Dyk (1996) for earlier stages of

278   regeneration in the study area. Laurance et al. (1999) also described a decrease in the number

279   of large trees with increased tree density on steep slopes. Although woody plant communities

280   of different gradients in stands of 11-25 years were generally dominated by similar sets of

281   forest tree species, species composition varied with the gradient of slopes. Incidentally, the

282   majority of these dominant species were identified by Grainger (2012) as species that could

283   colonize newly formed gaps in the woodland. This was likely due to their wide tolerance to

284   irradiance, temperatures, and moisture that change along dune slopes with elevation and

285   gradient (Ritter et al. 2005). Species abundances of canopy and understory communities

286   responded to different gradients in stands of 11-25 years, and elevation in stands of >25

287   years, respectively. The number of canopy species, though not their abundances, was best

288   explained by aspect, elevation, gradient, and position in stands younger than 11 years,

289   suggesting that dune morphology may provide habitat conditions that support different

290   species in the early stages of succession when conditions are likely to be most harsh.

291   Millipede variables also responded to age and dune morphology. Explanatory models

292   for cylindrical and pill millipede density included age as a covariate. These relationships are

293   likely the result of age-related increases in woodland complexity (Kritzinger & van Aarde

294   1998), moisture-retention and nutrient accumulation associated with litter accumulation (van

295   Aarde et al. 1998) and the modulation of microclimate by topography as discussed above. As

296   in Greyling et al. (2001), two closely related cylindrical millipedes (Centrobolidae)

297   dominated these new-growth forests. This may have obscured patterns in species-specific

298   abundances related to topography. However, the number of millipede species covaried with

299   position on the dune face in stands of 11-25 years, whereby valleys supported more millipede

300   species than slopes and crests. When considering the microclimatic data, this likely relates to

301   the moderate temperature and light intensities but relatively humid conditions that existed in

302   the valleys in comparison with ambient conditions such as wind and high temperatures.

303   Keeled millipedes responded to topographic variables independent of age and this likely

304   relates to the provision of microhabitats for this relatively small, forest-associated species and

305   justifies further study.

306   Despite the idiosyncratic responses by woody plants and millipedes, position on the

307   dune, as well as aspect, elevation and gradient of the dune face contributed to age-related

308   changes in community structure. Our study also suggests that due to its modulation of

309   microclimatic conditions, dune topography provides habitats conducive to forest-associated

310   species that have narrow climatic habitat tolerances. This suggests that even though these

311   new-growth forests are in transition, topography may influence the structure and composition

312 of biological communities of new-growth forests, especially when acting in concert with

313 other site-level factors. Such factors are likely to include those previously identified as

314 determinants of community structure and composition, such as landscape composition

315 (Grainger et al. 2011), and age (Wassenaar et al. 2005; Grainger & van Aarde 2012a).

316 The role of dune morphology seems more obvious in well-established ecosystems (Chen et

317 al. 1997; Oliviera-Filho et al. 1998; Tateno & Takeda 2003; Larkin et al. 2006), than the new-

318 growth forests that we studied, where age explained changes in assemblages better than

319 topography. Dune topography shaped as part of the rehabilitation procedure provides for the

320 topography that influences local conditions and therefore possibly for ecosystem patterns and

321 processes in a set manner according to prevailing climatic conditions. Topographically, these

322 dunes may differ from those shaped by natural forces (wind, water) which will probably

323 affect patterns and processes. However, these differences may be negligible and therefore not

324 be reflected in biological patterns, especially during the early stages of succession-driven

325 forest regeneration where most community variables vary with regeneration age.

326   For instance, age-related increases in habitat complexity provide an increasing variety

327 of conditions that accommodate more animal species and associated ecological processes

328 (Kritzinger & van Aarde 1998; Wassenaar et al. 2005). For example, increased plant

329 diversity, tree senescence and the associated development of a litter layer, increased soil

330 water retention, and nutrient accumulation would presumably benefit millipede communities

331 (e.g. Scheu & Schaefer 1998; Greyling et al. 2001; Berg & Hemerik 2004). In conclusion,

332 topography matters, more so for specialists than generalists. Response to topographic

333 variability is clearly species-specific and not necessarily reflected at the community level.

334

335

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344

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461
462

463 **Tables**

464 **Table 1** Key questions and hypotheses of this study

Key question	General assumptions	Hypotheses	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 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	• 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	• 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)

465

466 **Table 2** Definitions of response variables

Variable		Definition and units
Response variables	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 per100 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 per100 m^2 calculated for each quadrat
	Millipedes — Millipede species	Total number of millipede species per quadrat
	Cylindrical density	Number of *Centrobolus* spp.*, Doratagonus* 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 *Sphaerotheridae* spp. individuals per 100 m^2 calculated for each quadrat

467

468 **Table 3** Dune morphological variables included in the most parsimonious models (based on Akaike

469 Information Criteria (AIC) scores) explaining variance in abiotic and biotic variables for each of

470 three seral stages and pooled stages, as well as the significance of the model (p < 0.05). Those

471 response variables that were explained by dune morphological variables in the absence of age are

472 highlighted in boldface text.

	Response variables	Seral stage	Aspect	Elevation	Gradient	Position	Age	df	AIC	P
				Dune morphology					ANCOVA results	
Soil	Soil pH	1	Insufficient cases							
		2					X	1	54.35	0.0005
		3	X	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	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

Variable									
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

	Variable									
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

473

474 **Table 4** Characteristic tree species (taller than 2 m) forming the canopies on slopes of different

475 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						
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 degree 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 degree 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 discolour (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 degree 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 degree slope

Less than two samples in a group

476

477

478   **Table 5** Characteristic species occurring in the understory of each elevation category within seral

479   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						
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

480

Figures

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 were conducted are shown in relation to stand age (b). Inset maps provide geographical context (c & d).
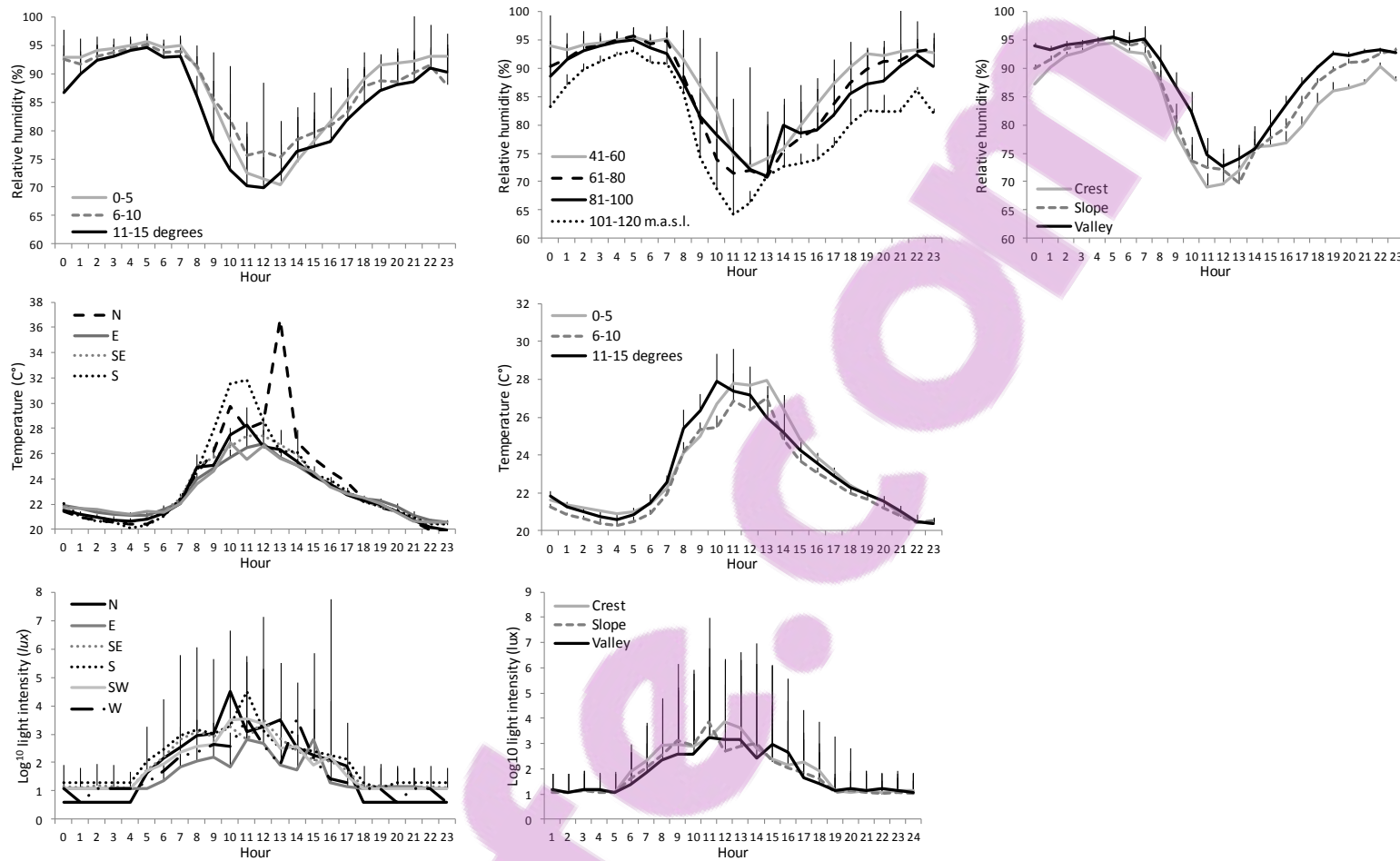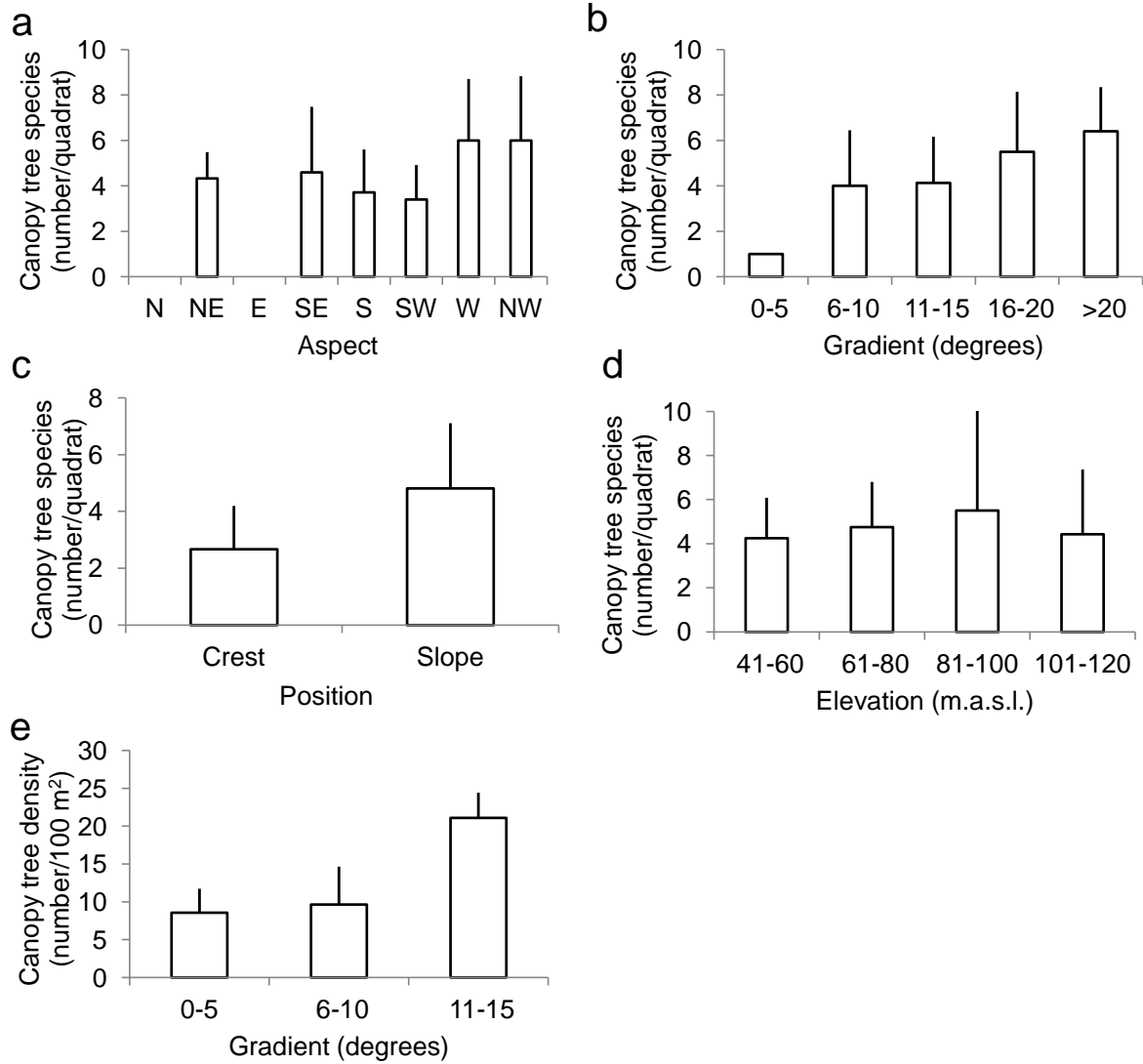
Fig. 2 Mean ± one standard deviation of the mean of three microclimatic variables (relative humidity, temperature, and light intensity, from top to bottom, respectively) that showed significant responses to variables of dune morphology according to the repeated measures ANOVA, as recorded between 01h00 and 24h00 on the 29th of January 2011.
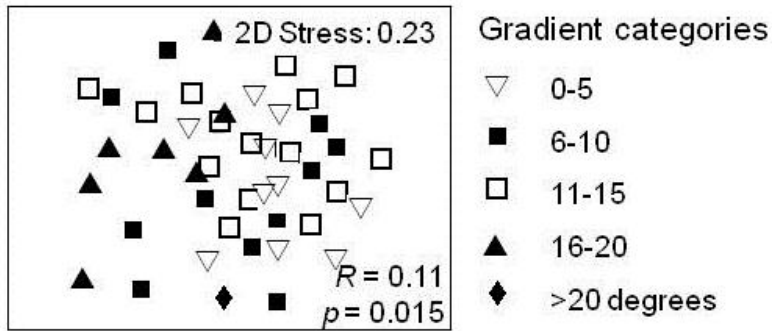
1

Fig. 3 Mean ± one standard deviation of the mean of woody plant response variables

presented as a function of those variables that best-explained their variability significantly
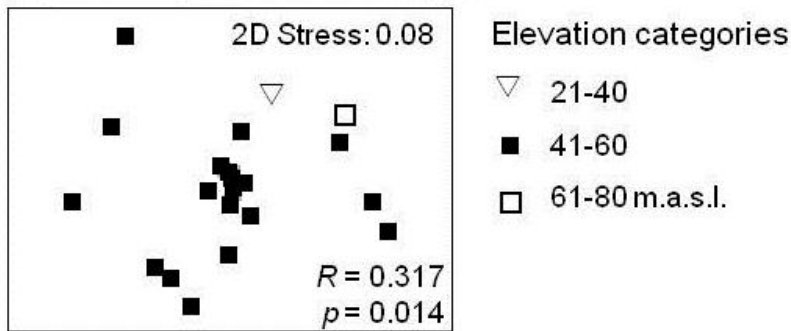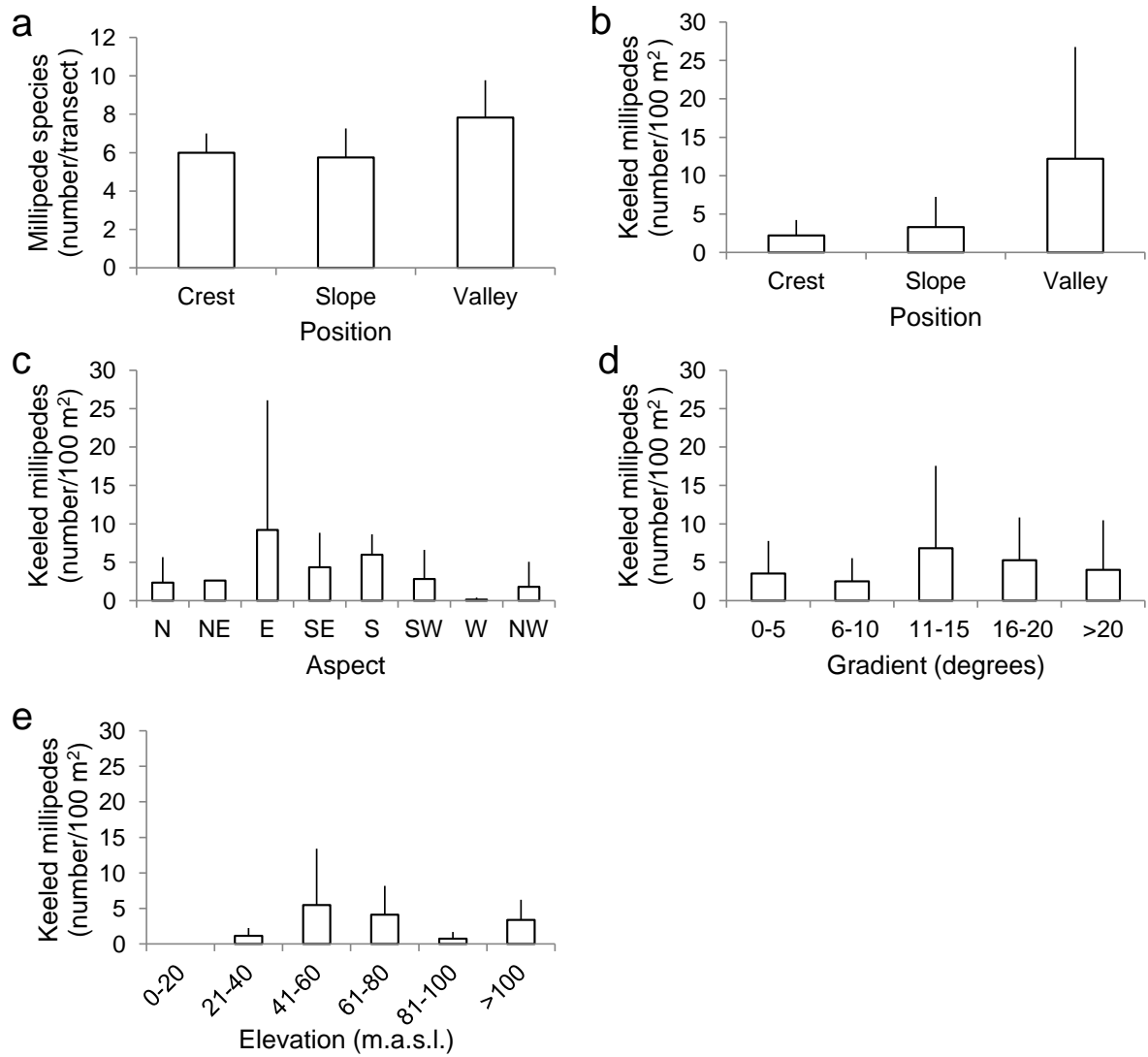
despite stand age (see Table 2).

Fig. 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.

5

6

7   **Fig. 5** Mean ± one standard deviation of the mean of millipede response variables presented

8   as a function of those variables that best-explained their variability significantly despite

9   stand age (see Table 2).