

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.

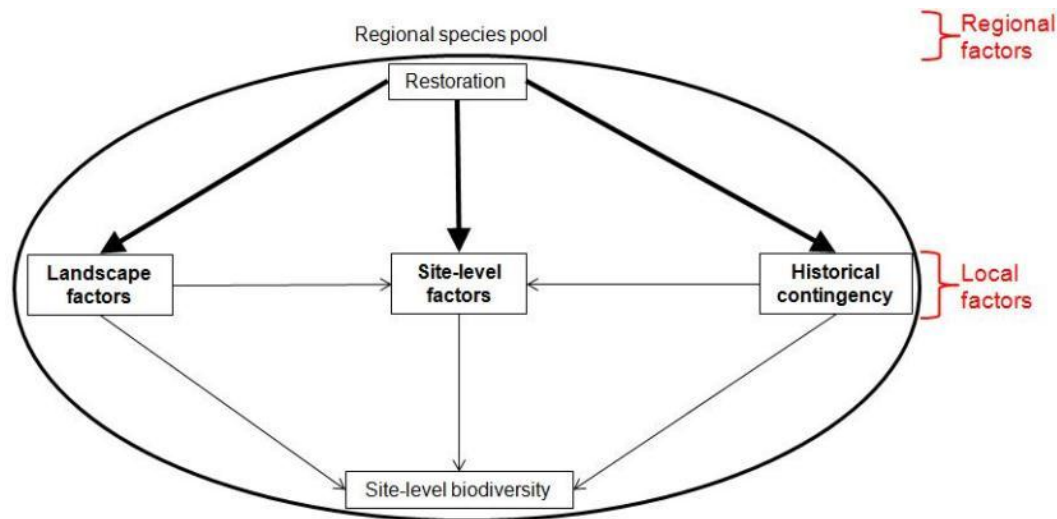


Figure 1-1. Conceptual model of biodiversity restoration as proposed by Brudvig (2011) whereby biodiversity at a site is the result of landscape, site-level, and historical factors. In this study though, historical contingency is referred to as historical context. Regional and local factors are indicated 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 (Riitters 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 world¹ (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

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 km², 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; Kritzing & 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 (Guldmond & 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.

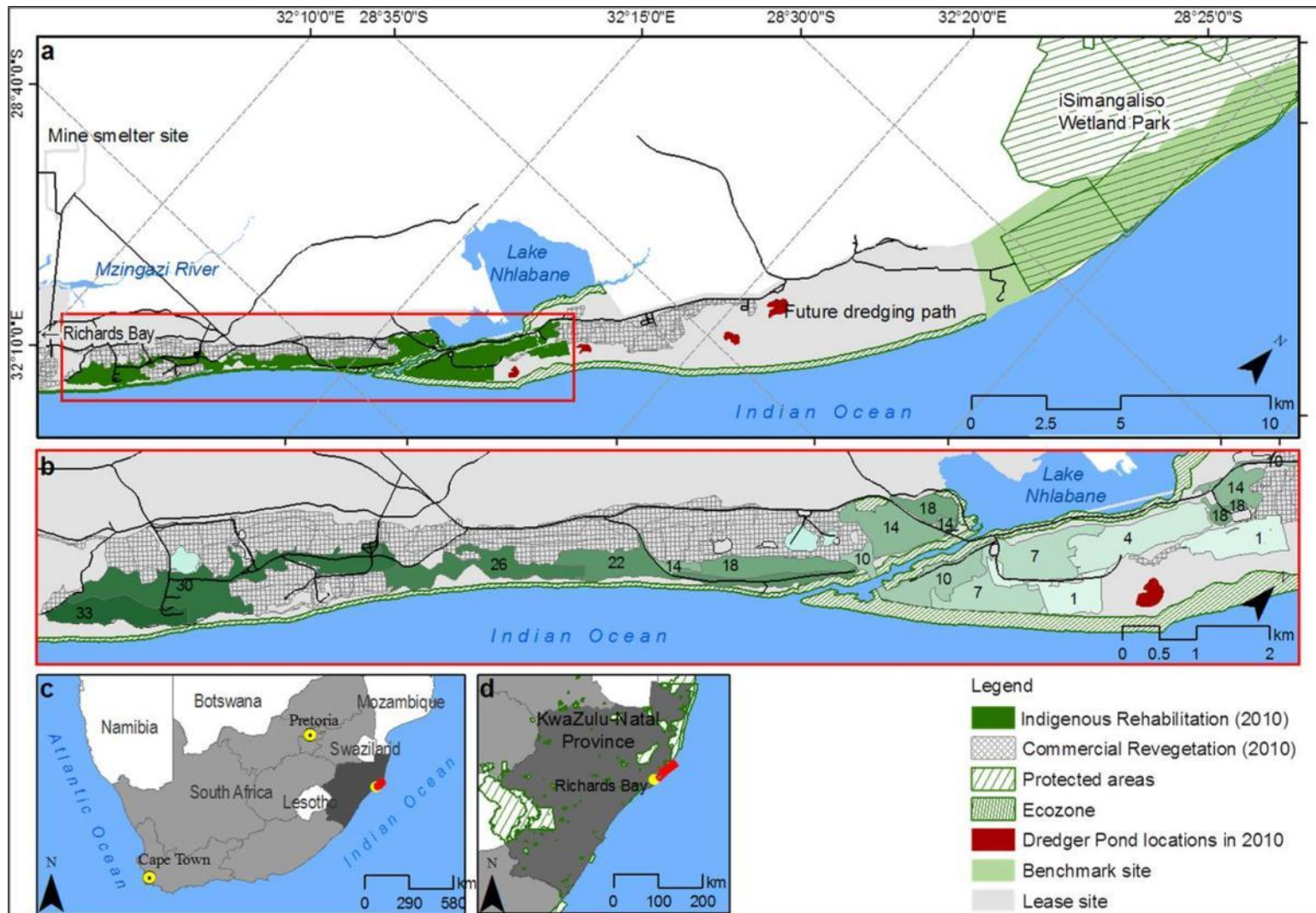


Figure 1-2. Map of study area showing benchmark and lease sites, as well as position of mining ponds in 2010 (a). The area in the red box is magnified to show the extent of stands of new-growth vegetation responding to rehabilitation, and their ages in 2010 (b). The context of the study area in South 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

* 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; Kritzingner & 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 & China 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 & China 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.itvis.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)

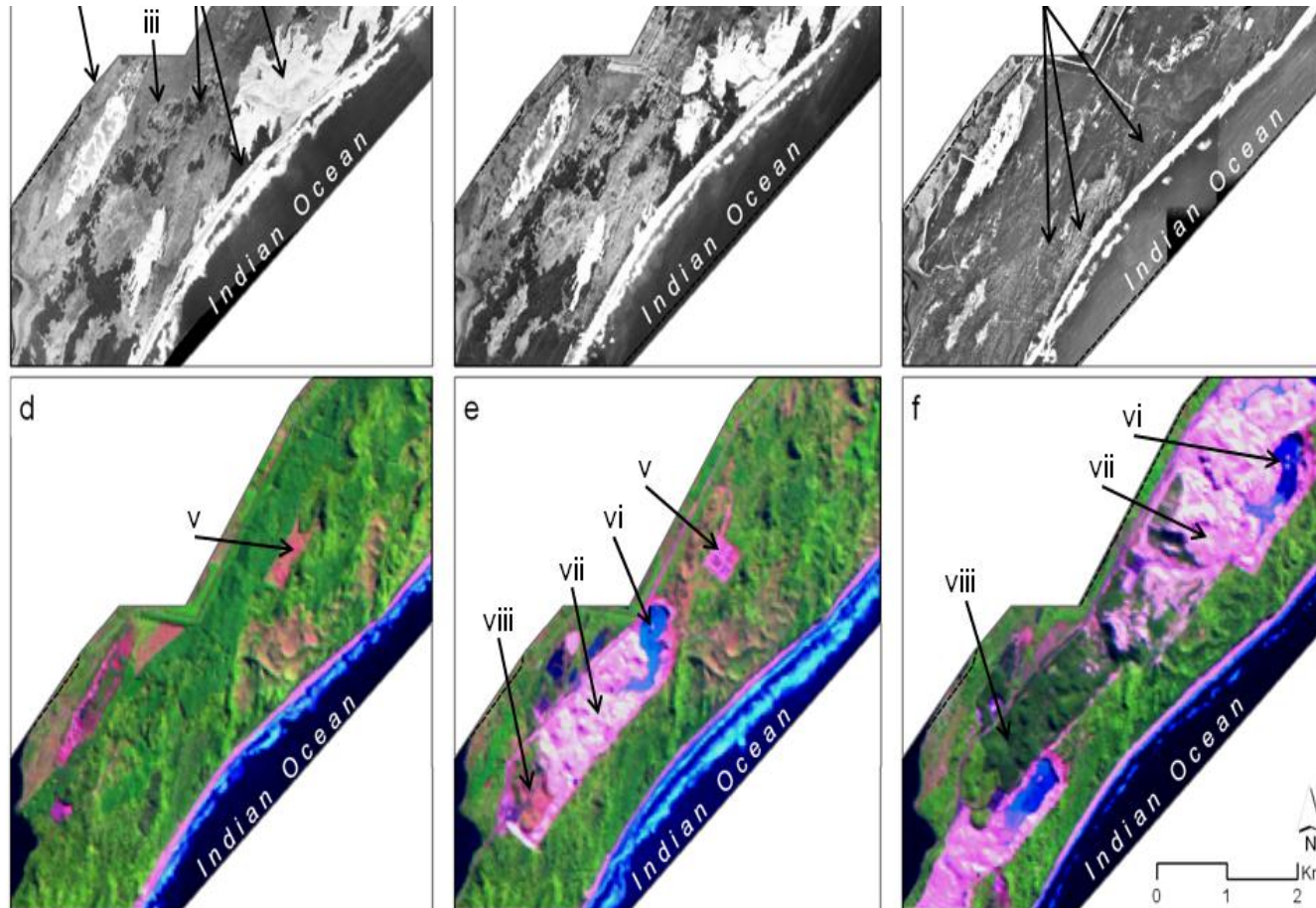


Figure 2-1. An enlarged portion of the lease site north-east of Lake Nhlabane, shown by aerial photographs taken during 1937 (a), 1957 (b), and 1970 (c), as well as Landsat 5 Thematic Mapper images from 1990 (d), 1998 (e), and 2006 (f). Arrows point to tracts of drift sand (i), patches of indigenous 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.

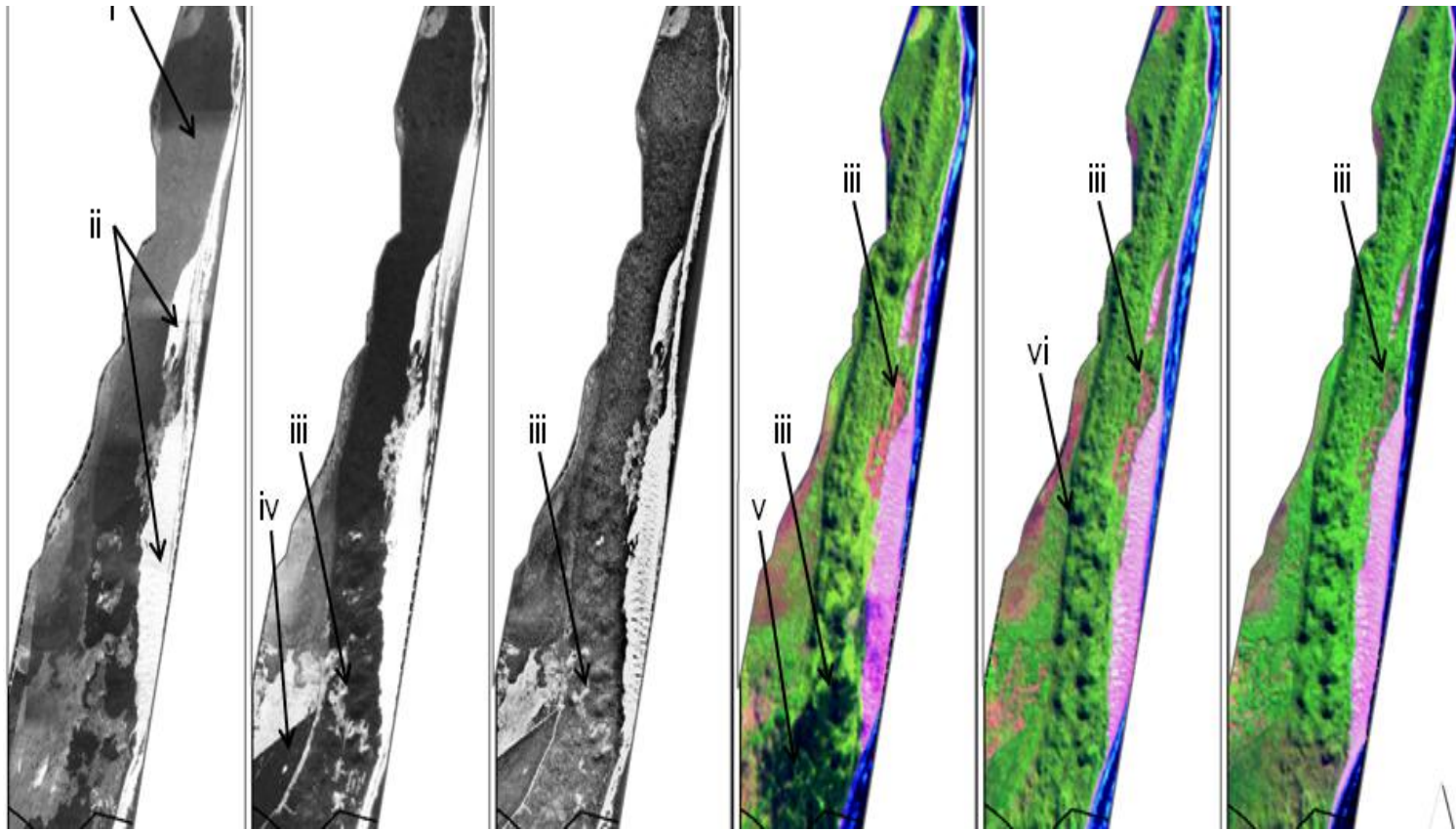


Figure 2-2. The benchmark site shown by aerial photographs taken during 1937 (a), 1957 (b), and 1970 (c), as well as Landsat 5 Thematic Mapper images from 1990 (d), 1998 (e), and 2006 (f). The arrows denote the largest (>1,000 ha) patch of coastal dune forest known as Sokhulu forest (i), drift sands 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).

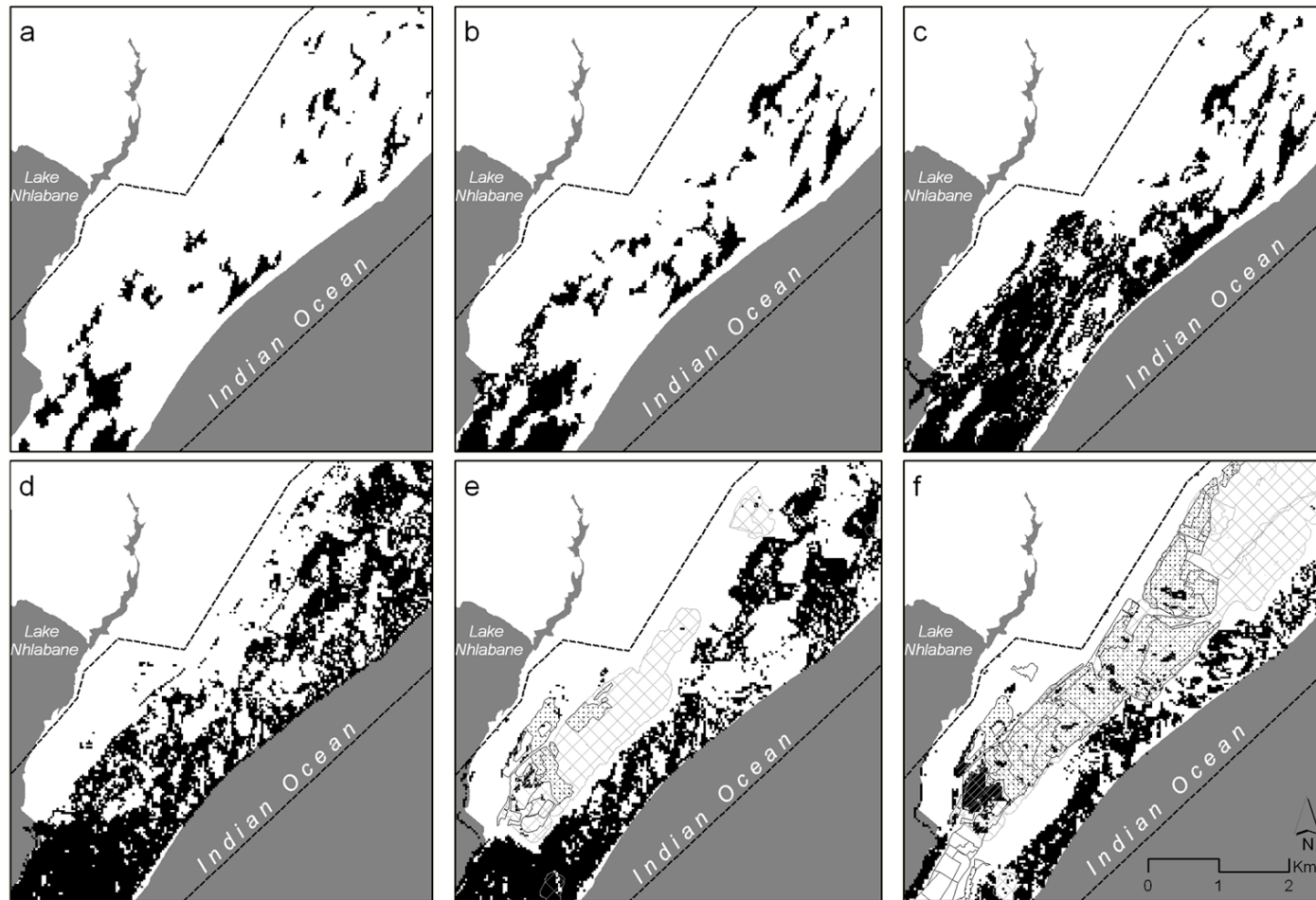


Figure 2-3. A portion of the lease site enlarged in (Fig. 2-1), for each year (1937 (a), 1957 (b), 1970 (c), 1990 (d), 1998 (e), and 2006 (f)), but showing tree-cover extracted as patches for the analysis of landscape structure (shaded black). Cross-hatched areas indicate mined sites and those delineated 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.

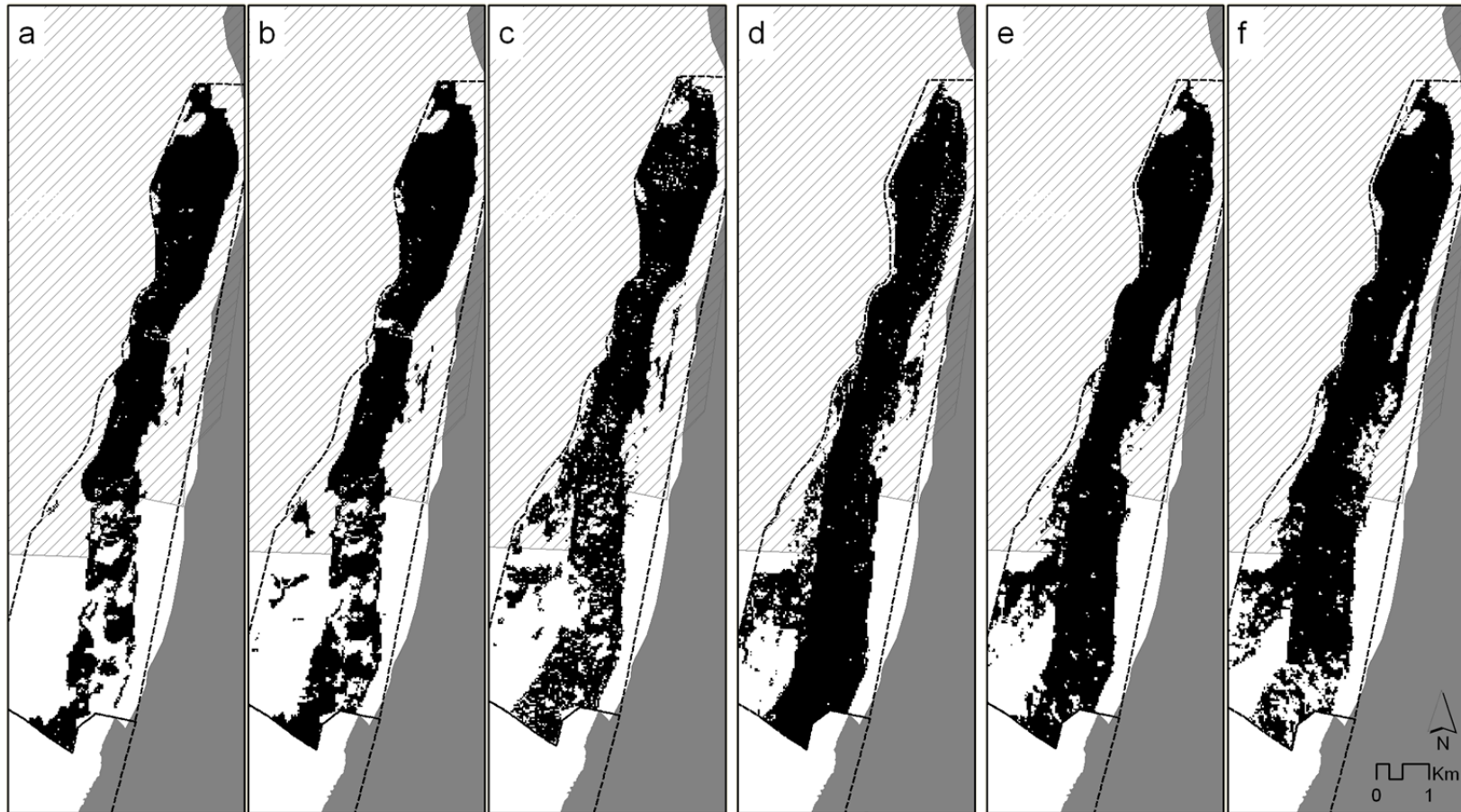


Figure 2-4. The benchmark site enlarged and represented by year as in (Fig. 2-2) (1937 (a), 1957 (b), 1970 (c), 1990 (d), 1998 (e), and 2006 (f)), but showing tree-cover extracted as patches for the analysis of landscape structure (shaded black). Hatched areas indicate the iSimangaliso Wetlands Park.



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 \pm one standard deviation (mean \pm 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).

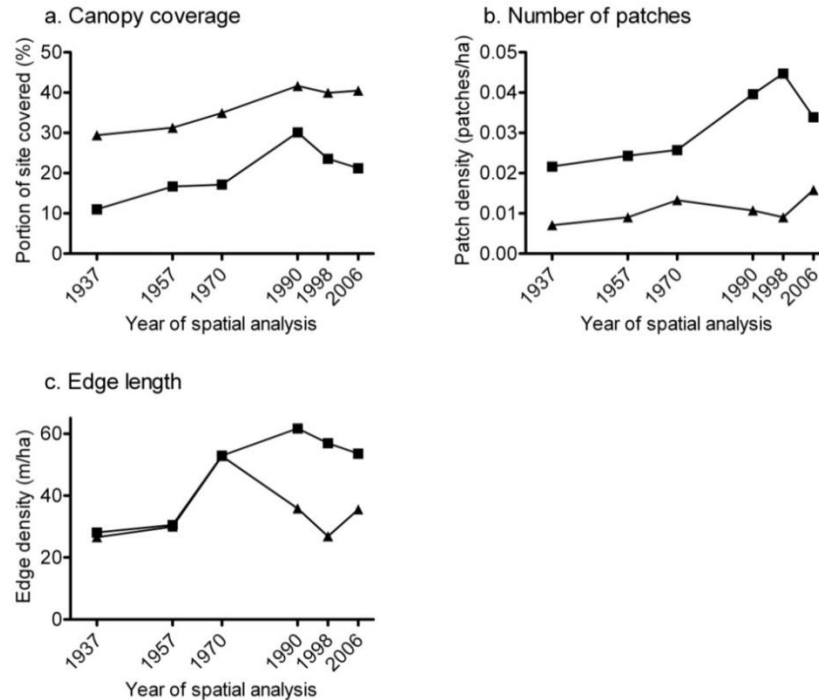


Figure 2-5. Site-scale metrics summarizing changes in the extent of canopy cover (a), patch density (b) as a measure of the number of patches, and edge density as an indication of edge length (c) across the benchmark (▲) and lease (■) sites.

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	<i>U</i>	<i>Z</i>	<i>p</i> -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

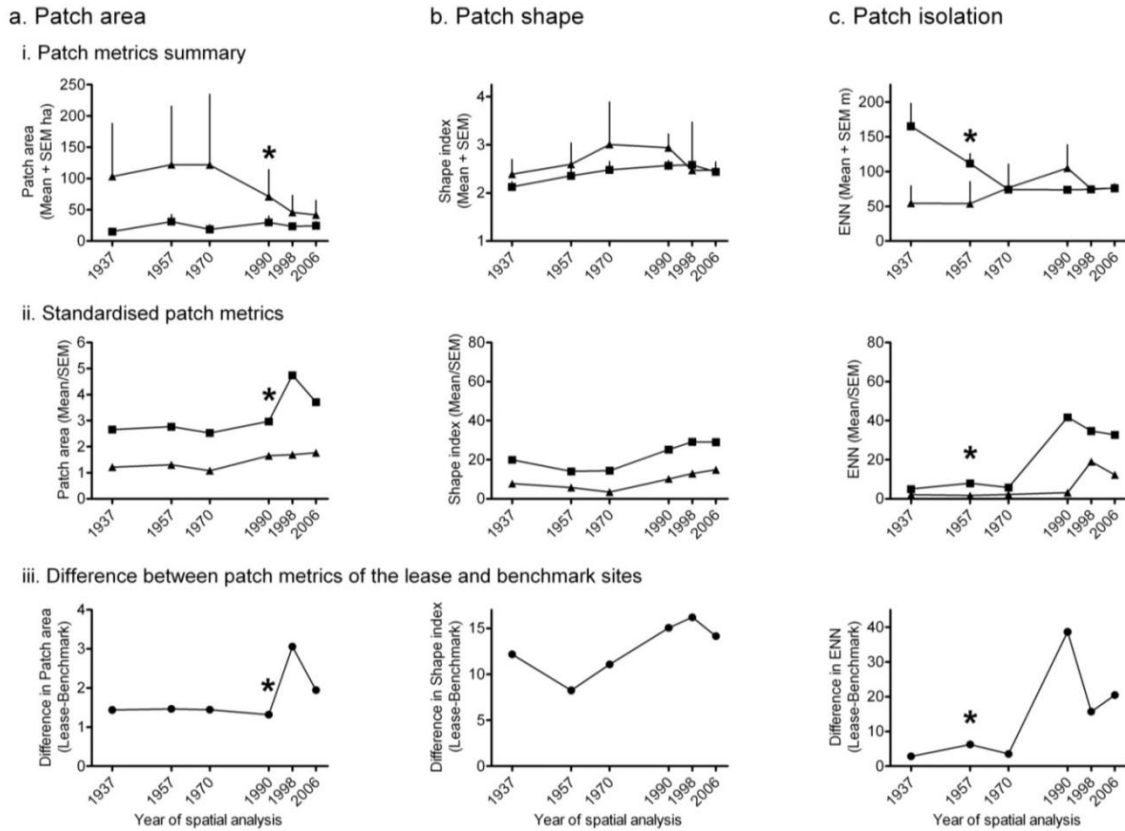


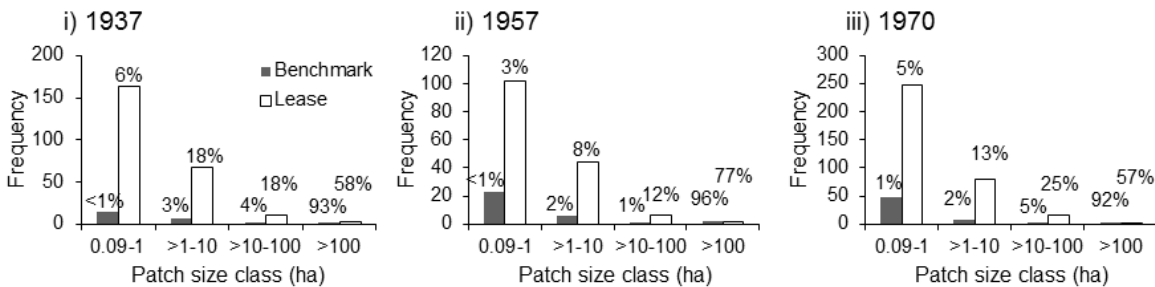
Figure 2-6. Patch-scale metrics of patch structure: patch area (a), shape (b), and isolation (c) presented as a function of the year for which spatial analysis was conducted. A summary of the patch metrics (mean +SEM (standard error of the mean)) for the benchmark (▲) and lease (■) sites (i), standardized 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).

a. Pre-mining



b. Post-mining

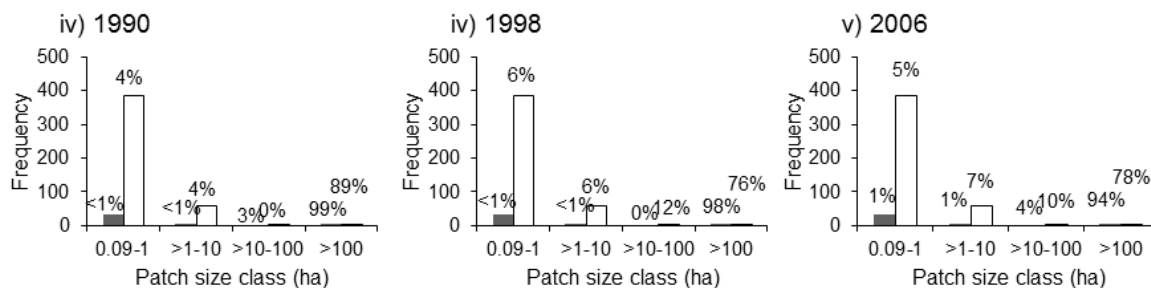


Figure 2-7. Frequency distributions of patch sizes within four size classes for the lease and benchmark sites, prior to- and after mining (a and b, respectively). The percentage contribution of each class to the total canopy cover is indicated above the bar of each year.



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 >10 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.

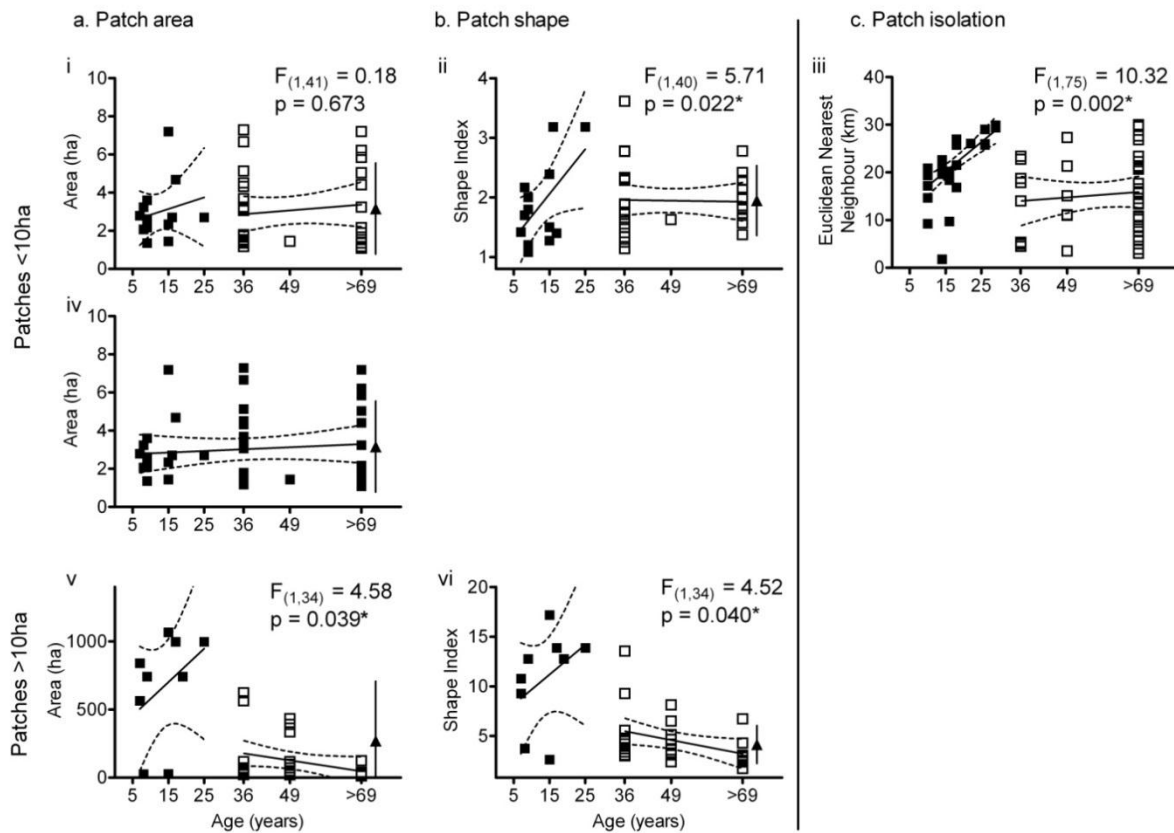


Figure 2-8. Patch area (a); shape (b), and isolation (c) of regenerating patches (■) and unmined patches (□) in the lease site regressed on patch age. Patch area and shape are separated into two size classes, <10 ha (i-iv) and >10 ha (v-vi). P-values presented with an asterisk indicate the where slopes 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.

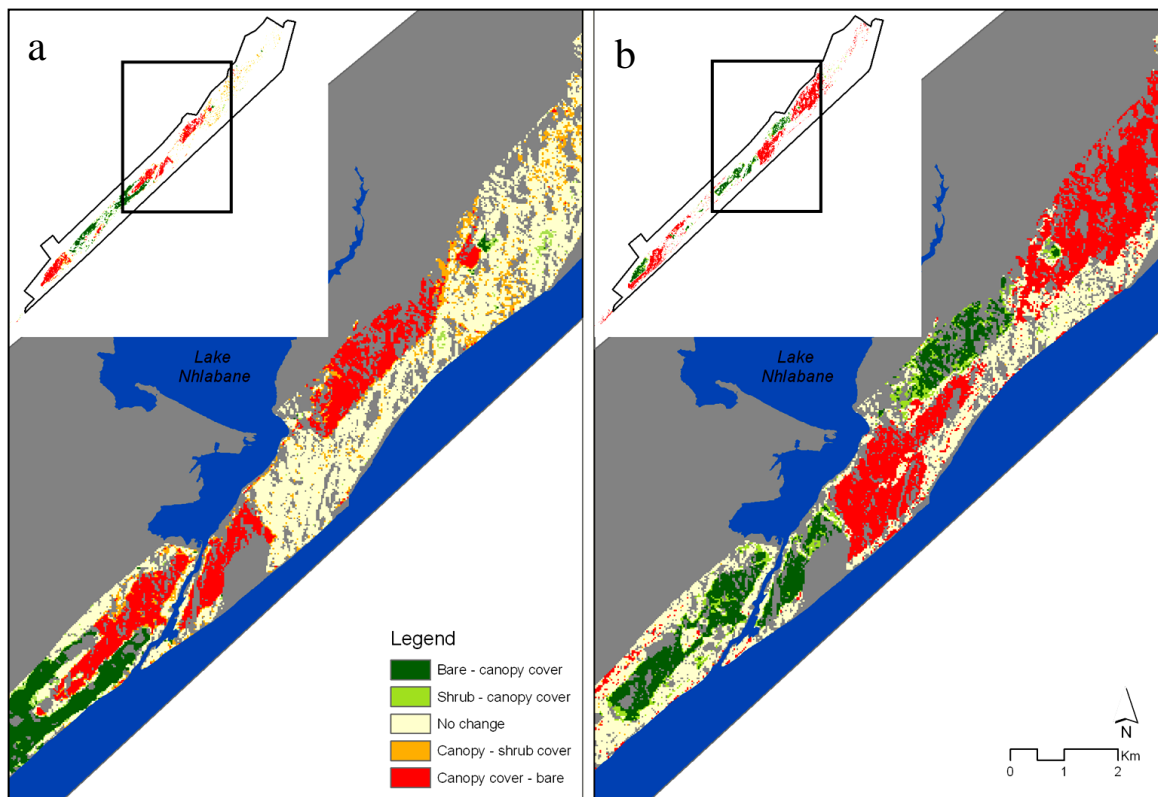


Figure 2-9. The lease site illustrating areas of change between 1990 – 1998 (a), and 1998 – 2006 (b), enlarged areas are indicated by the rectangle in the inset. Areas in red and orange highlight tree-cover loss and those in different shades of green indicate areas of tree-cover gain, whilst those in 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).

a. Increased in extent after mining

b. Decreased in extent after mining

c. Beyond the mining path

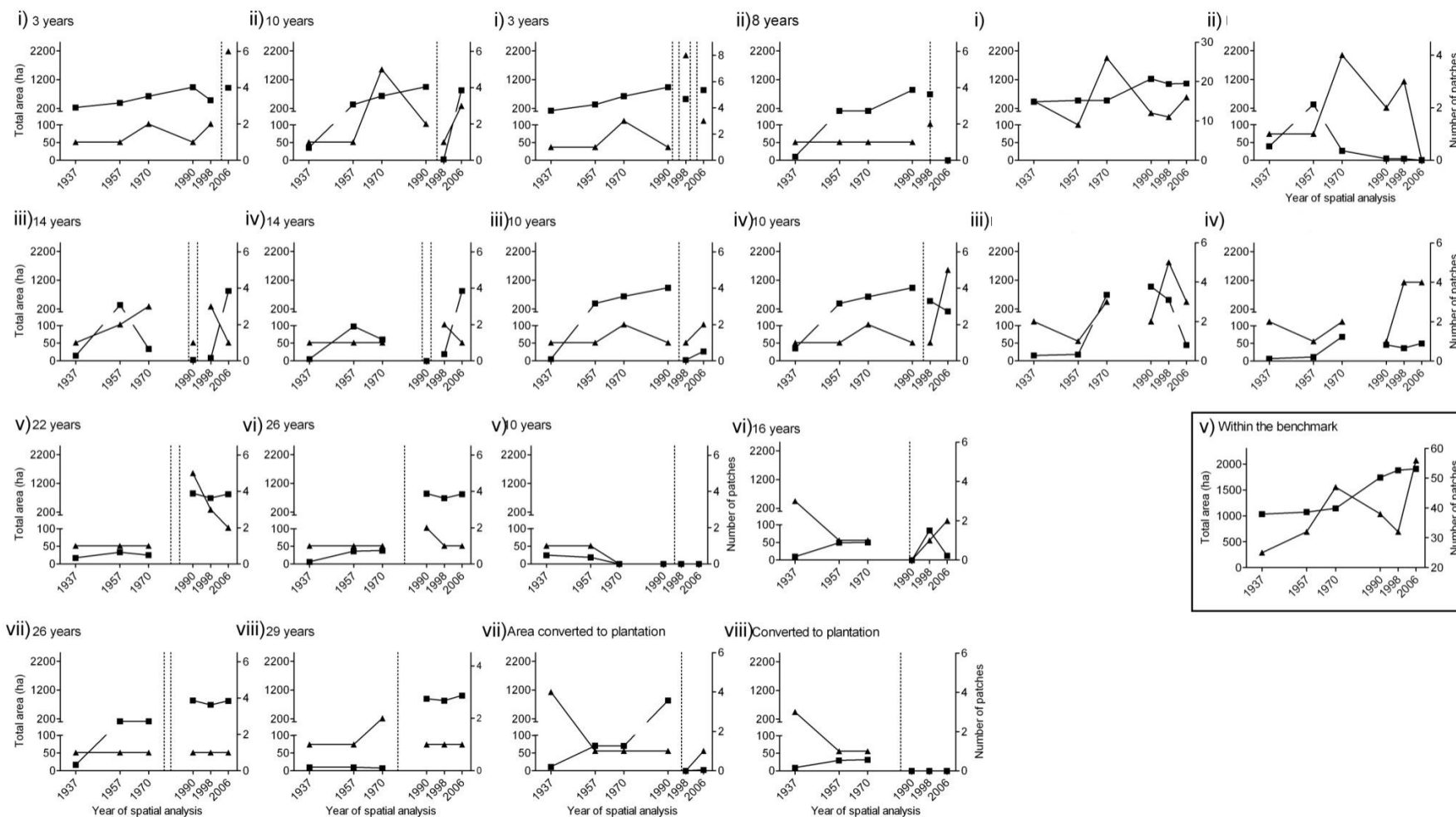


Figure 2-10. Summary of the size (■) and number (▲) of patches that occupied an area as tracked during each sampling year, separated into those that increased in extent (a), or decreased in extent following mining (b), and those that were not directly impacted by mining (c) – including the patches of 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.