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An evaluation of coastal dune forest restoration in northern KwaZulu-Natal, South Africa

by

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An evaluation of coastal dune forest restoration in northern KwaZulu-Natal, South Africa

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"One should always have a definite objective… it is so much more satisfying to reach a target by personal effort than to wander aimlessly. An objective is an ambition, and life without ambition is…well, aimless wandering." A.W. Wainwright 1973

Abstract

Ecological restoration has the potential to stem the tide of habitat loss, fragmentation and transformation that are the main threats to global biological diversity and ecosystem services. Through this thesis, I aimed to evaluate the ecological consequences of a 33 year old rehabilitation programme for coastal dune forest conservation. The mining company Richards Bay Minerals (RBM) initiated what is now the longest running rehabilitation programme in South Africa in 1977. Management of the rehabilitation process is founded upon the principles of ecological succession after ameliorating the mine tailings to accelerate initial colonisation.

Many factors may detract from the predictability of the ecological succession. For example, if historical contingency is a reality, then the goal of restoring a particular habitat to its former state may be unattainable as a number of alternative stable states can result from the order by which species establish. Succession appears to be a suitable conceptual basis (at this stage in regeneration at least) for the restoration of coastal dune forest. Patterns of community characteristics observed in rehabilitating coastal dune forest sites were similar to those predicted by ecological succession, with few exceptions.

Changes in the species pool such as the establishment of strong dominants may lead to divergence of regenerating trajectories away from the desired endpoints. The species composition of herbaceous plants in regenerating coastal dune forest sites became increasingly uniform as the time since disturbance increased. Despite initially becoming more similar they deviated away from an undisturbed reference site. Contrary to our expectations, non-native species did not contribute the most to dissimilarity. The deviation from the reference forest is attributable to the higher abundance of a native forest specialist in the reference site and the higher abundances of native woodland adapted species in the rehabilitating sites.

Changes in the disturbance regime under which species have evolved may lead to arrested succession. The rehabilitation of coastal dune forest relies on the *Acacia karroo* successional pathway which, has been criticised because *Acacia* dominated woodlands may stagnate succession. The patterns of species composition within regenerating coastal dune forest are a response to the canopy characteristics and represent an early stage in forest succession. Succession did not appear to be stagnant.

Ecological succession does not pay much heed to the role that the surrounding landscape composition can play in the assembly of communities. The theory of Island biogeography provides predictions about how landscape composition influences community assembly. Landscape spatial parameters, measuring edge, isolation, and area explained the patch occupancy of the several bird and tree species, however, responses to patch characteristics were varied and idiosyncratic. For restoration to succeed, managers need to consider the spatial configuration of the landscape to facilitate colonization of rehabilitating patches.

From this thesis and previous work, it appears that processes are in place that will lead to the reassembly of dune forest communities. As the rehabilitating sites are at an early stage of regeneration this may take some time to give rise to these coastal dune forest communities, and the management of rehabilitating coastal dune forest must allow for this. In addition, it is

important to remember that time may be interacting with the landscapes spatial attributes, which may limit the presence of certain species.

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Disclaimer

The present dissertation includes four paper manuscripts, prepared for submission to different scientific peer-reviewed journals. Styles and formatting of these chapters follow the respective journal requirements. This results in some duplication in the study site description and methods between chapters. Chapters 3, 4, and 6 follow the format requirements for the journal *Restoration Ecology*, whereby Chapter 5 follows the requirements for the *Journal of Vegetation Science*. Chapter 6 has already been published in Restoration Ecology as "Grainger, M.J., R.J. van Aarde and T.D. Wassenaar (2011). Landscape Composition Influences the Restoration of Subtropical Coastal Dune Forest. Restoration Ecology **19**: 111 – 120 (DOI: 10.1111/j.1526-100X.2009.00630.x)". I hereby declare all the work to be my own and that I have acknowledged all those that helped me and contributed to producing this dissertation.

Matthew James Grainger

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Chapter 1 General Introduction

An evaluation of coastal dune forest rehabilitation through ecological succession

Across the globe, the attainment of natural resources (such as minerals and timber) for human-use has similar consequences; namely, habitat loss, habitat fragmentation and habitat degradation (Foley et al. 2005). It is intrinsically evident that where the amount of habitat that can support biological diversity is reduced, the number of species will also decline. Habitat loss, fragmentation and transformation are thought to be one of the main threats to global biological diversity and ecosystem services (Fahrig 1997; Bender et al. 1998; Gaston et al. 2004; Goldewijk & Ramankutty 2004; Hoekstra et al. 2005). Traditional conservation practices (for example, conserving nature in parks) have not yet stemmed the tide of habitat change and species loss.

Several authors have heralded the activity of ecological restoration as a potential panacea to this trend of global habitat loss (Wilson 1992; Dobson et al. 1997; Young 2000). Ecological restoration according to the Society for Ecological Restoration International (SER 2004) is "an intentional activity that initiates or accelerates the recovery of an ecosystem with respect to its health, integrity and sustainability." The eminent scientist E.O. Wilson believed that ecological restoration was "…the means to end the great extinction spasm…" and that "the next century will… be the era of restoration in ecology" (Wilson 1992). Ecological restoration has quickly become integral to biological diversity conservation and sustainable development, and is often a legally binding requirement of mining permission (Tischew et al. 2010). In addition to the conservation ethos, ecological restoration may be valuable to scientists who wish to test ecological theories that address the assembly of biological communities (Bradshaw 1983). Palmer et al. (1997) and Young et al. (2005) suggest that restoration ecology (the science of ecological restoration) is well equipped to address scientific questions with regard to community development, species diversity and its role in ecosystem function, seed limitation and the role of soil micro-biota in facilitating community assembly. In addition, the role of the landscape in restoration, metapopulations, niche theory, as well as many other areas of ecology offer unique opportunities to test key theoretical questions in ecology (Young et al. 2005).

However, some authors have suggested that restoration ecology is failing to live up to its potential with regard to scientific endeavour (Halle 2007; Weiher 2007). In addition, others have suggested that the conservation value of ecological restoration is overstated (Elliot 1982; Davis 2000; Katz 2003). In reality, the current practice of ecological restoration probably falls somewhere between these two polar views (panacea to an over-statement of conservation value). Ecological restoration always comes second to preservation, but it can enhance conservation (Young 2000; Rey Banayas et al. 2009). The extent to which ecological restoration enhances conservation is probably dependent on the goals, techniques, and locale of individual projects, and perhaps the views of individual restoration practitioners. Ecological restoration is characterised by intentional actions that facilitate ecosystem recovery (SER 2004). These intentional actions implemented by managers may vary between relatively passive approaches relying mostly on natural community assembly through to management intensive approaches where species are introduced directly in to disturbed sites (Prach & Hobbs 2008).

The reliance on natural community assembly has been criticised by some, as it is unpredictable and can result in multiple stable states that differ to and support less biodiversity than the pre-disturbed state (Handa & Jefferies 2000; Pywell et al. 2002; Suding et al. 2004). However, others have promoted passive approaches over technical interventions because they result in a more natural species composition and greater biological diversity (Hodačová & Prach 2003). Prach & Hobbs (2008) suggest that ecological succession is preferable to technical interventions but adaptive management can be implemented to direct succession if required. Whatever the management action taken it is important to monitor the biotic (and abiotic) responses within rehabilitating sites and to evaluate the success of the technique in ensuring progress toward stated objectives or targets.

In South Africa, the restoration target for mining companies is stipulated in the Mining and Petroleum Resources Development Act (2002; South Africa). This act states that mining companies (other land uses are not bound by this legal requirement): "…must as far as it is reasonably practicable, rehabilitate the environment affected by the prospecting or mining operations to its natural or predetermined state or to a land use which conforms to the generally accepted principle of sustainable development." The mining company Richards Bay Minerals (RBM) initiated what is now the longest running rehabilitation programme, in South Africa in 1977. The programme aims to restore indigenous coastal dune vegetation to one third of its lease area. The mining company relies on ecological succession after ameliorating the mine tailings to accelerate initial colonisation (see below for further details). Through this thesis, I wish to evaluate the ecological consequences of this programme for coastal dune forest.

From 1977 to the present day, RBM continues to mine the minerals zircon, ilmenite, and rutile through a dredging process (van Aarde et al. 1996a). The mining process involves the clearing of dune forest and topsoil, and then dredging of the underlying sand (see Plate 1-1). After removal of the minerals from the sand, the "tailings" (the stockpiled sand that has been through the dredging process) are shaped to reform dunes. Post-mining habitat rehabilitation is directed in one of two pathways, either to commercial land-use, which has historically been commercial *Casuarina equisetifolia* plantations, or to indigenous coastal dune vegetation. For sites earmarked for indigenous forest rehabilitation, topsoil, seeded with annuals, is returned to the dune (Plate 1-2). Topsoil is further stabilised by wind-breaking fences (Plate 1-3). After this process, management is limited to the removal of non-native plant and animal species, and the prevention of fires. Continuous mining and subsequent restoration has resulted in a sere of regenerating patches in the landscape (van Aarde et al. 1996a, Wassenaar et al. 2005, see Plates 1-4 to 1-7).

Through the amelioration of stressors associated with the establishment of species at disturbed sites and later the control of other potential disturbances (in the form of fires and non-indigenous plants and herbivores) the RBM rehabilitation programme aims to “kick-start” and facilitate the processes involved in ecological succession (van Aarde et al. 1996a). Our previous research on the rehabilitation of coastal dune forest has been explicitly founded on the theoretical predictions of succession (for example, van Aarde et al. 1996b; Kritzinger & van Aarde 1998), and this is common in the restoration ecology literature (for example, Jansen 1999; Fagen et al. 2010; Gould *In press*, see also Prach & Hobbs 2008 and references therein).

I have divided this thesis in to 7 chapters. In Chapters 1 and 2, I provide a general introduction and more detail on the context of coastal dune forest ecology within South Africa. In Chapters 3 through 6, I present four papers, all of which address the consequences of the use of a succession-based approach to the restoration of coastal dune forest destroyed after strip-mining. In the final Chapter, I assess the ecological consequences of the succession-based approach for the likelihood of restoration.

We can only really evaluate the restoration of coastal dune forest by comparing the desired outcomes of restoration with the actual outcomes. As community reassembly is a dynamic process, we cannot rely on a single snap-shot evaluation, but need to repeatedly monitor and evaluate progress. The long-term monitoring and research of rehabilitating coastal dune forest provides a case study to investigate the outcomes of rehabilitation. In keeping with other rehabilitation projects, the ultimate goal of coastal dune forest rehabilitation is the recovery of functioning communities and the ecological processes associated with them (Young et al. 2005). Restoration ecology is fundamentally about the spatial and temporal influences on the process of how plants and animals reach a disturbed site and survive there. Therefore, it is hardly surprising that restoration ecology has as its conceptual foundation, theories that address the assembly of communities (Young 2000). The theory of ecological succession appears to have had the most influence on restoration ecology (Young et al. 2005). Successional theory has been an important part of the history of ecology for over a century (Walker & del Moral 2008). This theory in its most basic form suggests that the recovery of ecosystem structure, composition and function after a disturbance event is largely predictable and progressive (Clements 1916). The basic premise is that all sites that share a regional climate will also eventually acquire the same stable set of species. As succession offers several predictions of the trends in species composition and other community properties that can be expected after a disturbance event, the outcomes of rehabilitation actions should be predictable (Van Andel & Aronson 2006).

However, many factors may detract from the predictability of the reassembly of disturbed communities. For example, the order in which species colonise the disturbed site may be important in determining community composition (Connell & Slatyer 1977). This assembly theory was alluded to by both Gleason (1926) and Egler (1954) who pre-empted Diamond (1975) in suggesting that the timing of species colonisation can lead to alternative stable states (Chase 2003). This is the key difference between the two approaches. Successional theory predicts that species composition will be similar in sites with similar climatic conditions recovering from disturbance. In contrast, assembly theory predicts that if all species in the regional pool have equal access to disturbed sites, but the order by which species colonise the sites differs, so will the eventual stable community composition (Chase 2003; see also Young et al. 2001). Obviously, these two theories have different consequences for restoration ecology. If the historical contingency is a reality then the goal of restoring a particular habitat to its former state may be unattainable (even with intensive management intervention) as a number of alternative stable states can result from the order by which species establish (Young et al. 2001). In Chapter 3, I evaluate if succession is a suitable conceptual basis for the restoration of coastal dune forest. I compare patterns of community characteristics observed in rehabilitating coastal dune forest sites with those predicted by theory.

Many other factors may compromise the efficacy of succession-based restoration management (Suding et al. 2004). For example, changes in the species pool such as the establishment of strong dominants (Walker & del Moral 2003; Matthews & Spyreas 2010) may lead to divergence of regenerating trajectories away from the desired endpoints. Non-indigenous species may also influence the re-assembly of communities by out-competing native species for limited resources (Hartman & McCarthy 2004; Suding et al. 2004), consuming or infecting native species with novel diseases (D’Antonio & Meyerson 2000) as well as altering the nutrient inputs in to the ecosystem (Vitousek et al. 1990). This forms the theme of Chapter 4, which addresses the role of non-native plant species in the rehabilitation of the herbaceous plant community.

Changes in the disturbance regime under which species have evolved may lead to arrested succession. For example, Chapman et al. (1999) showed that large-scale (unnatural) disturbances led to arrested succession in Ugandan forests. This was due to the lack of pioneer tree species adapted to survive in large logging gaps (Chapman et al. 1999). The restoration of coastal dune forest relies on the *Acacia karroo* successional pathway (see von Maltitz et al. 1996). This pathway has been criticised because *Acacia* dominated woodlands may stagnate succession (West et al. 2000). In Cape Vidal, to the north of the RBM lease area, *A. karroo* is replacing itself in the canopy suggesting arrested succession (Boyes et al. 2010). According to the gap-dynamics theory (Whitmore 1989), large gaps in the canopy promote shade intolerant species, such as *A. karroo*, which may lead to self-replacement. In Chapter 5, I test this theory in three of the oldest rehabilitating sites, and evaluate the role that canopy gaps play in the regeneration of coastal dune forest.

Neither succession nor assembly theory pay much heed to the role that the surrounding landscape composition can play in the assembly of communities. The theory of Island Biogeography (MacArthur & Wilson 1967), one of the most influential theories in ecology, provides predictions about how landscape composition influences community assembly. It predicts that the biological diversity of an island is determined by the outcome of two fundamental ecological processes: colonisation and extinction. Colonisation is the sum of all events that culminate in a species finding and occupying a new island habitat. Local extinction, the opposite of colonisation, is the disappearance of a species from an island habitat because of competitive interactions, or simply not finding enough resources there. These two processes are in turn determined by how large an island is and how far from the mainland it is. In general, the theory of Island Biogeography predicts that larger islands will suffer less extinction than smaller islands and hence will support a higher biodiversity. In the same way, islands that are closer to a mainland source will experience higher colonisation rates, and thus support more species than islands further away. This theory and its more modern extensions to terrestrial ecosystems in the form of mainland island, metapopulation and metacommunity theories, predicts that landscape pattern will be the major determinant of not only the number of species that a discrete habitat patch can support, but also its species composition.

This theory has profound consequences for the restoration of disturbed habitat. If the landscape is a dominant driver of community assembly processes after disturbance, it should form a distinct part of rehabilitation management planning. The relative position of rehabilitating sites to source areas may be an important and often manageable factor. This forms the theme of the next chapter in the thesis (Chapter 6). In this chapter, I evaluate the role that landscape composition has for the rehabilitation of coastal dune forest. In particular, I relate patch occupancy for forest associated birds and trees, and relate the probability of patch occupancy to the patch age, isolation from the largest intact forest, patch area, and patch shape in rehabilitating, regenerating and remnant forest patches.

In the final Chapter (7), I provide a synthesis of my findings and an evaluation of the rehabilitation of coastal dune forest in terms of the ecological consequences and threats that stem from the rehabilitation efforts of the last 33 years. This final evaluation includes discussion on the measurement of restoration success and assesses the progress that the rehabilitating coastal dune forests of KwaZulu-Natal have made toward a successful outcome.

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Plate 1-1. Mining operations at Richards Bay Minerals result in the removal of all vegetation and topsoil in front of the mining pond. Topsoil is stockpiled for use on rehabilitating sites. Immediately post-mining sand is formulated to an approximation of the dunes previous topography. The photograph was taken by Prof. R.J. van Aarde and is used with his permission.

Plate 1-2. This plate shows a rehabilitating site at less than 1 year old. Topsoil stockpiled prior to mining is replaced on re-shaped dunes and wind-breaking fences are erected to limit soil erosion. The soil is seeded with exotic annual seeds that provide a cover crop, further stabilising the soil. The photograph was taken by Prof. R.J. van Aarde and is used with permission.

Plate 1-3. This rehabilitating site is around 1 year old. Here the dune has a layer of topsoil and wind-breaking fences have been erected. In the foreground, a cover crop of exotic annual herbaceous plants has established. In the background, there are active mining operations, adjacent to previously rehabilitated coastal dune forest.

Plate 1-4. This rehabilitating site is around 3 years old. Various graminoids have established alongside the pioneer tree species *Acacia karroo*, which is shown in the foreground. The photograph was taken by Prof. R.J. van Aarde and is used with permission.

Plate 1-5. This ~8 year old site is dominated by *A. karroo*, with a developing herbaceous layer. Self-thinning of *A. karroo* potentially allows secondary species to colonise the site. The photograph was taken by Prof. R.J. van Aarde and is used with permission.

Plate 1-6. At ~28 years old, *A. karroo* is still the dominant canopy tree species. However several forest-associated species have established in the site, and there is a developed herbaceous layer. The photograph was taken by Prof. R.J. van Aarde and is used with permission.

Plate 1-7. At ~32 years old, individuals of *A. karroo* are beginning to reach senescence and the death and subsequent collapse of these canopy individuals may allow broadleaved secondary species to replace them in the canopy. The photograph was taken by Prof. R.J. van Aarde and is used with his permission.

Chapter 2 Coastal dune forest in context

The study area (between Richards Bay town and the Umfolozi River mouth) and the mining process are described in the methods sections of each of the following chapters (3 to 6). A map of the mining lease is available in Chapter 6 (Figure 6-1). To avoid repetition I limit this chapter to a characterisation of coastal dune forest and its historic and current threats.

Characterisation of Coastal dune forest

Broadly, there are two types of forest in South Africa, Afrotemperate Forests (also referred to as Afromontane Forest) and Indian Ocean Coastal Belt Forests, with an intermediate (in terms of species composition and geography) coastal scarp forest situated between the two groups (Lawes et al. 2004). Forests occur along the southern and eastern seaboard of South Africa and extend a short distance in to the interior across the Great Escarpment, mountain ranges, and coastal plains (Mucina et al. 2006). Approximately 7 % of South Africa’s land surface is climatically suitable for the development of forests, however forests comprise as little as 0.1 to 0.56 % (Mucina et al. 2006). Forests are generally fragmented and patches are very small (<100 hectares; Midgley et al. 1997). The threats to these forest patches include timber extraction, fuel-wood extraction, over-exploitation of plants and animals for food and traditional medicines, clearance for agriculture, clearance for housing, commercial plantations and mining (Lawes et al. 2004; Mucina et al. 2006). Therefore, an understanding of forest regeneration after disturbances is imperative to conserve and restore the disproportionate levels of biological diversity housed within South African forests (Lawes et al. 2004).

Coastal dune forest falls within the Indian Ocean Coastal Belt biome, which is one of the nine biomes in South Africa recognised by Rutherford et al. (2006). The biome covers the eastern seaboard of the Indian Ocean between the northern half of the Eastern Cape Province and extends through the KwaZulu-Natal Province northwards into Mozambique (Mucina et al. 2006). Burgess et al. (1998) suggest that coastal dune forest forms the southern most example of East African Tropical Coastal Forest, which extends along the Mozambican, Tanzanian, Kenyan and Southern Sudanese coast, although in east Africa, the forests generally have a larger inland extent than that seen in South Africa.

The Indian Ocean Coastal Belt formed in relatively recent (geological) times after the last glacial maximum (Lawes 1990). Sand dunes were formed from deposits left by the regression of the Indian Ocean during the last glacial period (8000-10000 years ago), and subsequently climatic forces (strong winds and arid periods) shaped the dunes in to their present day parabolic shape (Tinley 1985; von Maltitz et al. 2003).

The present-day climate is subtropical with rainfall occurring year-round but peaking in the summer months (southern hemisphere summer: November to February; see Figure 2-1). The temperature is hot and humid, the mean temperature between 2006 and 2009 was 23.79 ± 3.40 °C (mean ± standard deviation, n = 3 years) and peaked in February at 28.56 ± 0.72 °C (Figure 2-2). Thirteen of the last 18 years have been below the long-term mean rainfall (Figure 2-3).

Coastal dune forest is an eco-region within a biodiversity hotspot as it falls within the southern-most part of the Maputaland Centre of Endemism (van Wyk & Smith 2001; Küper et al. 2004). Endemism is rare within coastal dune forest itself, but a number of trees and birds do reach their southern-most limit within this eco-region (von Maltitz et al. 2003; Gibbon 2006). The Conservation Research Unit (CERU) have only assessed patterns of endemism in the dung beetle community (Davis et al. 2003). However, this is a taxon that I do not assess (directly) in this thesis. Hamer & Slotow (2002) report that the millipede community exhibits endemism within the forests of northern KwaZulu-Natal although a list of these endemics is not given and therefore one should be cautious when making conclusions based on this.

In general, coastal dune forest is rich in plant species (Mucina et al. 2006) and has a canopy of 12 – 16 m (Ferreira & van Aarde 2000; Wassenaar et al. 2005). There are several distinct vertical strata and well developed understory that is between 0.2 m and 2 m high (Ferreira & van Aarde 1999; Wassenaar et al. 2005). Over the last 18 years of research CERU have identified 103 species of tree (woody plants >1.7 m high), 60 species of herbaceous plant, 88 species of birds and 21 species of millipedes in the undisturbed Sokhulu Forest and the contiguous Mapelane Nature Reserve that serve as “reference” or “benchmark” sites for the present study. Some additional species have been recorded in surveys that have taken place further north in the iSimangaliso Wetland Park (formally The Greater St Lucia Wetlands World Heritage site; see Redi et al. 2005), to the south of Richards Bay Town, adjacent to the Richards Bay Nature Reserve, as well as in the Umlalazi Nature Reserve (CERU unpublished data). I have only included plots surveyed in the Sokhulu Forest and Mapelane Nature Reserve for the calculation of species number and the characterisation of common species (below) for three reasons: these sites are the closest in geographical distance to the rehabilitating sites; are not separated by physical barriers (the Umfolozi River to the north and Mhlatuze River to the South); and have been repeatedly surveyed for all taxa unlike the other dune forest sites.

Previous published work has highlighted typical or dominant species found in mature coastal dune forest (for example, van Aarde et al. 1996; Kritzinger & van Aarde 1998; Ferreira & van Aarde 1999; Wassenaar et al. 2005). However, since these papers were published CERU has amassed further data on the community composition of mature coastal dune forest in our study region. Therefore, in order to characterise the species composition of the coastal dune forest community I have calculated the mean abundance of each species across all survey plots and identified those species that cumulatively make up the four quartiles of abundance. "Very common" species account for >75 % of mean cumulative abundance, "common species" account for 50 – 74 %, "rare species" account for 25 – 49 % of cumulative abundance, whereas "very rare" species account for <25 %. In the tables below (Table 2-1 to Table 2-4) I have assigned all recorded and identified species in each taxa one of these four criteria.

From Tables 2-1 to 2-4, one can describe the most typical species in the Sokhulu Forest and Mapelane Nature Reserve as those species contributing more than 50 % to mean total abundance per survey unit (very common and common species as defined above). The most dominant species in the tree community include the understorey trees *Dracaena aletriformis* and *Psychotria capensis*, as well as the subcanopy and canopy species *Diospyros natalensis*, *Erythroxylum emarginatum*, *Teclea gerrardii*, *Drypetes natalensis*, *Euclea racemosa subsp. sinuata*, *Deinbollia oblongifolia*, *Peddiea africana* and *Chionanthus peglerae*. Common species in the herbaceous plant community include the patchily distributed *Isoglossa woodii*, which is characteristic of coastal dune forest throughout the study region and further to the north as well (Ferreira & van Aarde 1999; Griffiths et al. 2007). Other herbaceous species include *Asparagus falcatus*, *Laportea peduncularis* and *Pupalia lappacea*. The climber *Pyrenacantha scandens* is also a common species in mature coastal dune forest. Common bird species include Yellow-bellied Greenbul (*Chlorocichla falviventris*), Green-backed Camaroptera (*Camaroptera brachyura*), Collared Sunbird (*Hedydipna collaris*), Yellow-breasted Apalis (*Apalis flavida*), Dark-backed Weaver (*Ploceus bicolour*), Terrestrial Brownbul (*Phyllastrephus terrestris*), Black-backed Puffback (*Dryoscopus cubla*), Eastern Olive Sunbird (*Cyanomitra olivacea*) and the Yellow-rumped Tinkerbird (*Pogoniulus bilineatus*). Finally, the most common millipedes are *Centrobolus fulgidus* and *C. richardii*.

It is important to note that these species although dominant may not be specific to mature coastal dune forest as they are found throughout the region and can tolerate a wide variety of habitats including grasslands, woodlands and mature forest. For example, the millipede species C. *fulgidus* and *C. richardii* are present in all but the very youngest (< 6 years old) rehabilitating dune forest as well as dominating mature stages (Grayling et al. 2001; Redi et al. 2005). In order to determine the species that characterise a coastal dune forest one may also need to know which species are exclusive to mature coastal dune forest. These species include, for trees, *Chionanthus foveolatus*, *Pavetta natalensis*, *Acalypha glabrata*, *Ficus lutea*, *Allophylus africanus*, *Cassipourea malosana*, *Olea woodiana*, *Tecomaria capensis*, *Ficus polita*, *Pisonia aculeata*, *Drypetes reticulata*, *Ficus sycomorus*, *Tarenna pavettoides*, *Keetia gueinzii*, *Manilkara discolor*, *Tarenna junodii*, *Artabotrys monteiroae*, *Chionanthus battiscombei*, *Hymenocardia ulmoides*, *Ephippiocarpa orientalis* and four currently unknown species awaiting identification.

Herbaceous species exclusively recorded in mature coastal dune forest sites include *Aneilema dregeanum*, *Chlorophytum comosum*, *Combretum kraussii*, *Cryptocarya woodii*, *Cussonia arenicola*, *Eugenia woodii*, *Pavetta gerstneri*, *Pollichia campestris*, *Rawsonia lucida*, *Scadoxus membranaceus*, *Scolopia flanaganii*, *Solanaceae sp.*, *Sonchus sp.*, and 11 unconfirmed species. The birds exclusively found in mature coastal dune forest sites are Blackheaded Oriole (*Oriolus larvatus*), Bluebilled firefinch (*Lagonosticta rubricata*), Buffspotted Flufftail (*Sarothrura elegans*), Cape Wagtail (*Motacilla capensis*), Chorister Robin (*Cossypha dichroa*), Crested Barbet (*Trachyphonus vallantii*), Croaking Cisticola (*Cisticola natelensis*), Fantailed Flycatcher (*Myioparus plumbeus*), Fiscal Flycatcher (*Sigelus silens*), Grey Cuckooshrike (*Coracina caesia*), Greyheaded Bush Shrike (*Malaconotus blanchoti*), Olive Bush Shrike (*Telophorus olivaceus*), Orangebreasted Bush Shrike (*Telophorus sulfureopectus*), Pallid Flycatcher (*Bradornis pallidus*), Purplecrested Turaco (*Musophaga porphyreolopha*), Scimitarbilled Woodhoopoe (*Rhinopomastus cyanomelas*), Spotted Thrush (*Zoothera guttata*) and Threestreaked Tchagra (*Tchagra australis*). Finally, the millipede species include *Ulodesmus micramma zuluensis*, two unidentified members of the genus *Sphaerothrium*, and a further unidentified species.

A certain amount of caution is required in taking the above approach, as species may be present in rehabilitating sites but at low densities or in the edges of the site (where we do not survey) so are effectively undetectable. The bird species Narina Trogon (*Apaloderma narina*) has been seen in rehabilitating coastal dune forest sites but never recorded in a sampling plot. Without knowledge of species habitat requirements, it is difficult to draw many sound conclusions with regard to which species characterise coastal dune forest entirely. Assessing species typical in and species exclusive to mature coastal dune forest may only provide some insight.

Past and current threats to coastal dune forest

Coastal dune forest has a long history of human disturbance; iron-age man (around AD 400) may have influenced the regeneration dynamics of modern forests in the region by large-scale deforestation for agriculture and eventually for the production of charcoal to fuel the iron smelting process (West et al. 2000). The biggest impact probably coincided with the arrival of the Zulu people in the year 1670. The local clan, the Mbonambi, became well known as iron workers, due to the wealth of natural resources (iron ore and wood) in the area (Knight 1989).

In modern times as throughout history, impacts and threats stem from the increasing human population and their requirements for resources. The Province of KwaZulu-Natal has the second highest population in South Africa (10,650,000 people, which equates to 21.3 % of the total population; Statistics South Africa (2010)). In addition, it has high species richness and diversity (Fairbanks et al. 2001; Wessels et al. 2002) and encompasses 9351 km^2 (total area 17000 km^2) of the Maputaland centre of endemism (van Wyk & Smith 2001; Smith et al. 2006). The Maputaland centre of endemism forms a part of the Maputaland-Pondoland-Albany hotspot of biological diversity (Steenkamp et al. 2004). Where areas of high species richness coincide with areas of high human density, one expects conservation conflict (Balmford et al. 2001). This is particularly evident along the coastline of KwaZulu-Natal where large-scale habitat transformation has meant that less than 50 % of native vegetation remains (Wessels et al. 2002). In the large urban centres along the north coast (Durban and Richards Bay), the remaining natural vegetation is as little as 0 to 20 % (Wessels et al. 2002). Coastal dune forest historically, would have been the dominant vegetation along this coastline. Currently, 64-68 % of coastal dune forest is under statutory protection within nature reserves (Mucina et al. 2006; Wooley 2003). The original extent of dune forest has diminished through anthropogenic actions that have transformed forest in to land uses such as livestock grazing, agriculture (sugarcane), timber plantations, urbanisation, and tourism developments (Mucina et al. 2006). Presently, mining is considered as the largest threat to coastal dune forest conservation (Mucina et al. 2006). Wooley (2003) estimated that, of the total area of coastal dune forest within the Maputaland Centre of Endemism mining activities threatened 20.33 %.

Lawes et al. (2004) consider coastal dune forest to be resilient to disturbances. Weisser & Marques (1979) illustrate this clearly in their review of the changes in dune vegetation between Richards Bay Town and the Umfolozi River from 1937 to 1974. In 1937, there were high levels of degradation due to the clearance of vegetation for grazing and cultivation. The remaining forest habitat was patchily distributed. Between 1937 and 1974, there was commercial reforestation with plantations of *Eucalyptus* spp., *Pinus* spp., and *Casuarina equisetifolia*. A by-product of forestry management, the control of fire, allowed *Acacia karroo* to invade secondary dune grasslands, and eventually to develop as secondary dune forest. Therefore, there was defragmentation of forest as open areas reverted to closed woodland and forest habitat.

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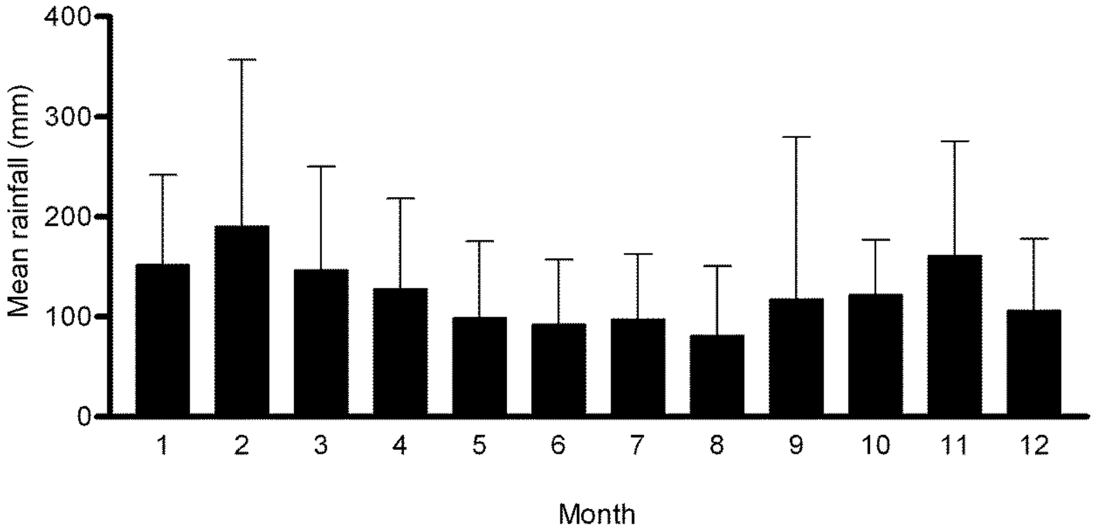

Fig.2-1. Mean monthly rainfall with standard deviation (error bars) calculated as a long term mean between 1976 and 2009 (data courtesy of RBM).

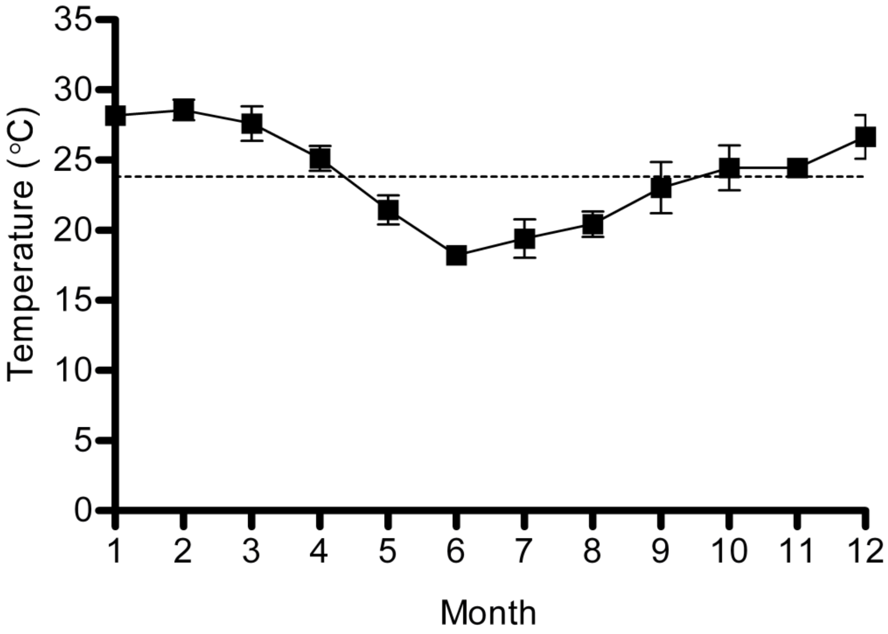

Fig.2-2. Mean (± Standard deviation) monthly temperature between 2006 and 2009 (data courtesy of RBM). The dotted line indicates the long-term mean temperature.

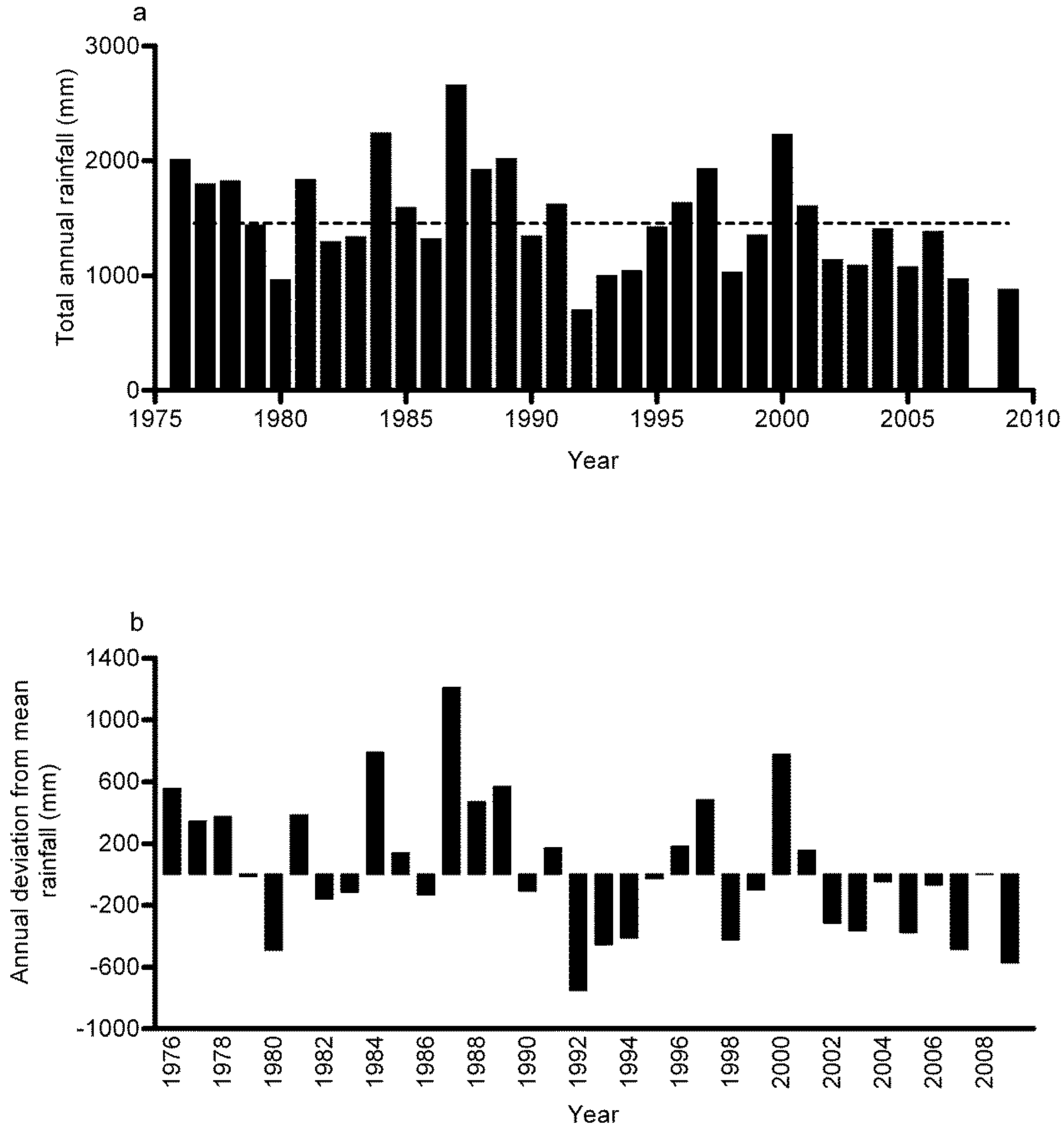

Fig.2-3. Total rainfall (a) per year between 1976 and 2009 (data courtesy of RBM). The dotted line indicates the long-term mean yearly rainfall. The annual deviation from the long-term mean annual rainfall is shown in (b).

Table 2-1. The tree species recorded in the Sokhulu Forest and Mapelane Nature Reserve between 1997 and 2005.

Latin name	Quartile >75 % = "Very Common"; 50 % to 74 % = "Common"; 25 % to 49 % ="Rare"; <25 % "Very Rare"
Dracaena aletriformis	Very Common
Diospyros natalensis	Very Common
Erythroxylum emarginatum	Very Common
Teclea gerrardii	Very Common
Drypetes natalensis	Common
Psychotria capensis	Common
Euclea racemosa subsp. sinuata	Common
Deinbollia oblongifolia	Common
Peddiea africana	Common
Chionanthus peglerae	Common
Pavetta revoluta	Rare
Celtis africana	Rare
Mimusops caffra	Rare
Dovyalis longispina	Rare
Acacia kraussiana	Rare
Ochna natalitia	Rare
Scutia myrtina	Rare
Englerophytum natalense	Rare
Scolopia zeyheri	Rare

Euclea natalensis	Rare
Diospyros inhacaensis	Rare
Clausena anisata	Rare
Carissa bispinosa	Rare
Rhoicissus tridentata	Very Rare
Eugenia natalitia	Very Rare
Pancovia golungensis	Very Rare
Tricalysia sonderiana	Very Rare
Erythrococca berberidea	Very Rare
Sideroxylon inerme	Very Rare
Gymnosporia nemorosa	Very Rare
Kraussia floribunda	Very Rare
Apodytes dimidiata	Very Rare
Ekebergia capensis	Very Rare
Strychnos gerrardii	Very Rare
Catunaregam spinosa	Very Rare
Allophylus natalensis	Very Rare
Turraea floribunda	Very Rare
Canthium inerme	Very Rare
Dalbergia armata	Very Rare
Elaeodendron croceum	Very Rare
Strelitzia nicolai	Very Rare
Grewia occidentalis	Very Rare
Monanthotaxis caffra	Very Rare
Capparis sepiaria	Very Rare
Pavetta Sp.	Very Rare

Mystroxylon aethiopicum	Very Rare
Ziziphus mucronata	Very Rare
Landolphia kirki	Very Rare
Ficus burtt-davyi	Very Rare
Eugenia capensis	Very Rare
Trichilia emetica	Very Rare
Ochna sp.	Very Rare
Psydrax obovata	Very Rare
Turraea obtusifolia	Very Rare
Brachylaena discolor	Very Rare
Chaetacme aristata	Very Rare
Clerodendrum glabrum	Very Rare
Olea capensis	Very Rare
Cola natalensis	Very Rare
Grewia caffra	Very Rare
Rhus natalensis	Very Rare
Vangueria randii	Very Rare
Ephippiocarpa orientalis	Very Rare
Acacia karroo	Very Rare
Capparis tomentosa	Very Rare
Cordia caffra	Very Rare
Cussonia sphaerocephala	Very Rare
Rhoicissus rhomboidea	Very Rare
Rhoicissus digitata	Very Rare
Acokanthera oppositifolia	Very Rare
Maytenus undata	Very Rare

Salacia gerrardii	Very Rare
Trichilia dregeana	Very Rare
Keetia gueinzii	Very Rare
Maerua nervosa	Very Rare
Antidesma venosum	Very Rare
Vepris lanceolata	Very Rare
Strychnos henningsii	Very Rare
Ficus craterostoma	Very Rare
Garcinia livingstonei	Very Rare
Pavetta Sp.	Very Rare
Bauhinia tomentosa	Very Rare
Maytenus procumbens	Very Rare
Uvaria caffra	Very Rare
Gardenia thunbergia	Very Rare

Table 2-2. The herbaceous plant species recorded in the Sokhulu Forest and Mapelane Nature Reserve in 2005.

Latin name	Quartile >75 % = "Very Common"; 50 % to 74 % = "Common"; 25 % to 49 % ="Rare"; <25 % "Very Rare"
Isoglossa woodii	Very Common
Asparagus falcatus	Common
Laportea peduncularis	Common
Pupalia lappacea	Common
Pyrenacantha scandens	Common
Clausena anisata	Rare
Commelina benghalensis	Rare
Cynanchum ellipticum	Rare
Dactyloctenium australe	Rare
Microsorium scolopendrium	Rare
Tragia glabrata	Rare
Acalypha villicaulis	Very Rare
Achyranthes aspera	Very Rare
Achyropsis avicularis	Very Rare
Ancylobotrys petersiana	Very Rare
Aneilema aequinoctiale	Very Rare
Asparagus setaceus	Very Rare
Asparagus sp.	Very Rare
Asplenium prionitis	Very Rare

Asystasia gangetica	Very Rare
Canthium sp.	Very Rare
Chlorophytum bowkeri	Very Rare
Chromolaena odorata	Very Rare
Cissampelos torulosa	Very Rare
Coccinia variifolia	Very Rare
Commelina eckloniana	Very Rare
Cyperus albostriatus	Very Rare
Cyphostemma hypoleucum	Very Rare
Cyphostemma woodii	Very Rare
Digitaria diversinervis	Very Rare
Dioscorea sylvatica	Very Rare
Drimiopsis maculata	Very Rare
Eragrostis sp.	Very Rare
Eugenia woodii	Very Rare
Flagellaria guineensis	Very Rare
Ipomoea ficifolia	Very Rare
Krauseola mosambicina	Very Rare
Mariscus macrocarpus	Very Rare
Menispermaceae sp.	Very Rare
Mikania natalensis	Very Rare
Neonotonia wightii	Very Rare
Oplismenus hirtellus	Very Rare
Panicum maximum	Very Rare
Rhynchosia caribaea	Very Rare
Sansevieria hyacinthoides	Very Rare

Scadoxus membranaceus	Very Rare
Secamone filiformis	Very Rare
Senecio deltoideus	Very Rare
Senecio quinquelobus	Very Rare
Senecio tamoides	Very Rare
Solanaceae sp.	Very Rare
Thunbergia dregeana	Very Rare
Tinospora caffra	Very Rare
Vernonia angulifolia	Very Rare
Vernonia aurantiaca	Very Rare
Zehneria parvifolia	Very Rare

Table 2-3. Bird species recorded in the Sokhulu Forest and Mapelane Nature Reserves between 1997 and 2009. I have added in the common name to ease identification.

Common name	Latin name	Quartile >75 % = "Very Common"; 50 % to 74 % = "Common"; 25 % to 49 % ="Rare"; <25 % "Very Rare"
Yellow-bellied Greenbul	*Chlorocichla falviventris*	Very Common
Green-backed Camaroptera	*Camaroptera brachyura*	Very Common
Collared Sunbird	*Hedydipna collaris*	Very Common
Yellow-breasted Apalis	*Apalis flavida*	Common
Dark-backed Weaver	*Ploceus bicolor*	Common
Terrestrial Brownbul	*Phyllastrephus terrestris*	Common
Black-backed Puffback	*Dryoscopus cubla*	Common
Eastern Olive Sunbird	*Cyanomitra olivacea*	Common
Yellow-rumped Tinkerbird	*Pogoniulus bilineatus*	Common
Sombre Greenbul	*Andropadus importunus*	Rare
Red-capped Robin-Chat	*Cossypha natalensis*	Rare
Dark-capped Bulbul	*Pycnonotus tricolor*	Rare
Square-tailed Drongo	*Dicrurus ludwigii*	Rare
White-eared Barbet	*Stactolaema leucotis*	Rare
Cape White-eye	*Zosterops virens*	Rare
Rudd's Apalis	*Apalis ruddi*	Rare
Southern Boubou	*Laniarius ferrugineus*	Rare
Livingstone's Turaco	*Tauraco livingstonii*	Very Rare

Woodwards' Batis	*Batis fratrum*	Very Rare
Blue-mantled Crested Flycatcher	*Trochocercus cyanomelas*	Very Rare
Grey Sunbird	*Cyanomitra veroxii*	Very Rare
Black-bellied Starling	*Lamprotornis corruscus*	Very Rare
Lemon Dove	*Aplopelia larvata*	Very Rare
Trumpeter Hornbill	*Bycanistes bucinator*	Very Rare
Tawny-flanked Prinia	*Prinia subflava*	Very Rare
Black-throated Wattle-eye	*Platysteira peltata*	Very Rare
Crowned Hornbill	*Tockus alboterminatus*	Very Rare
Green Malkoha	*Ceuthmochares aereus*	Very Rare
Eastern Nicator	*Nicator gularis*	Very Rare
Tambourine Dove	*Turtur tympanistria*	Very Rare
Thick-billed Weaver	*Amblyospiza albifrons*	Very Rare
Ashy Flycatcher	*Muscicapa caerulescens*	Very Rare
Burchell's Coucal	*Centropus burchellii*	Very Rare
Green Twinspot	*Mandingoa nitidula*	Very Rare
Red-fronted Tinkerbird	*Pogoniulus pusillus*	Very Rare
Red-backed Mannikin	*Lonchura nigriceps*	Very Rare
Zitting Cisticola	*Cisticola juncidis*	Very Rare
Pale Flycatcher	*Bradornis pallidus*	Very Rare
Purple-banded Sunbird	*Cinnyris bifasciata*	Very Rare
Eastern Bronze-naped Pigeon	*Columba delegorguei*	Very Rare
Golden-tailed Woodpecker	*Campethera abingoni*	Very Rare
African Paradise-Flycatcher	*Terpsiphone viridis*	Very Rare

Yellow Weaver	*Ploceus subaureus*	Very Rare
Brown-hooded Kingfisher	*Halcyon albiventris*	Very Rare
Red-eyed Dove	*Streptopelia semitorquata*	Very Rare
Woolly-necked Stork	*Ciconia episcopus*	Very Rare
Cape Wagtail	*Motacilla capensis*	Very Rare
Gorgeous Bush-Shrike	*Telophorus quadricolor*	Very Rare
African Green-Pigeon	*Treron calva*	Very Rare
Speckled Mousebird	*Colius striatus*	Very Rare
Willow Warbler	*Phylloscopus trochilus*	Very Rare
Yellow-fronted Canary	*Serinus mozambicus*	Very Rare
Amethyst Sunbird	*Chalcomitra amethystina*	Very Rare
Buff-Spotted Flufftail	*Sarothrura elegans*	Very Rare
Cape Canary	*Serinus canicollis*	Very Rare
Purple-crested Turaco	*Musophaga porphyreolopha*	Very Rare
Barn Swallow	*Hirundo rustica*	Very Rare
Black-crowned Tchagra	*Tchagra senegala*	Very Rare
Black-headed Oriole	*Oriolus larvatus*	Very Rare
Cape Rock-Thrush	*Monticola rupestris*	Very Rare
Common Waxbill	*Estrilda astrild*	Very Rare
African Emerald Cuckoo	*Chrysococcyx cupreus*	Very Rare
Fork-tailed Drongo	*Dicrurus adsimilis*	Very Rare
Grey Cuckooshrike	*Coracina caesia*	Very Rare
Grey Waxbill	*Estrilda perreini*	Very Rare
Hadeda Ibis	*Bostrychia hagedash*	Very Rare
Little Bee-eater	*Merops pusillus*	Very Rare
Scaly-throated Honeyguide	*Indicator variegatus*	Very Rare

Scarlet-chested Sunbird	*Chalcomitra senegalensis*	Very Rare
Bar-throated Apalis	*Apalis thoracica*	Very Rare
Olive Woodpecker	*Dendropicos griseocephalus*	Very Rare
Crested Guineafowl	*Guttera pucherani*	Very Rare
Bearded Scrub-Robin	*Cercotrichas quadrivirgata*	Very Rare
African Firefinch	*Lagonosticta rubricata*	Very Rare
Cardinal Woodpecker	*Dendropicos fuscescens*	Very Rare
African Dusky Flycatcher	*Muscicapa adusta*	Very Rare
European Nightjar	*Caprimulgus europaeus*	Very Rare
Grey Tit-Flycatcher	*Myioparus plumbeus*	Very Rare
Fiscal Flycatcher	*Sigelus silens*	Very Rare
Klaas's Cuckoo	*Chrysococcyx klass*	Very Rare
Narina Trogon	*Apalpderma narina*	Very Rare
Orange-breasted Bush-Shrike	*Telophorus sulfureopectus*	Very Rare
Rufous-naped Lark	*Mirafra africana*	Very Rare
Spotted Ground-Thrush	*Zoothera guttata*	Very Rare
Brown Scrub-Robin	*Cercotrichas signata*	Very Rare
Weavers[1]	*Ploceus*	Very Rare
Malachite Kingfisher	*Alcedo cristata*	Very Rare

[1] Yellow weavers (*Ploceus subaureus*) and Lesser masked weavers (*P. intermedius*) were considered as a morpho-species because females are difficult to distinguish in the field

Table 2-4. Millipede species recorded in the Sokhulu Forest and Mapelane Nature Reserves between 1997 and 2009.

Latin name	Quartile >75 % = "Very Common"; 50 % to 74 % = "Common"; 25 % to 49 % ="Rare"; <25 % "Very Rare"
Centrobolus fulgidus	Very Common
Centrobolus richardii	Common
Spinotarsus anguiliferous	Rare
Doratogonus sp.	Rare
Ulodesmus micramma zuluensis	Very Rare
Spirostreptidae sp. 1	Very Rare
Centrobolus rugulosus	Very Rare
Sphaerotherium punctulatum	Very Rare
Spirostreptidae sp. 2	Very Rare
Sphaerothrium sp. E	Very Rare
Gnomeskelus tuberosus	Very Rare
Juliaformia sp. 3	Very Rare
Sphaerotherium rotundatum	Very Rare
Orthroporoides sp.	Very Rare
Sphaerotherium giganteum	Very Rare
Sphaerotherium sp. D	Very Rare

Chapter 3

Is succession-based management of coastal dune forest restoration valid?

Abstract

Habitat restoration and the theory of ecological succession are linked intrinsically. However, restoration management does not always rely on successional principles. This separation between the theory and practical application may stem from the failure of succession to achieve restoration targets. Here we test the predictions of succession in a restoration context to ascertain the validity of succession-based management. Specifically we answer the following six questions; (1) Does the rate of species turnover decrease as coastal dune forest develops?; (2) Is there a sequence of changing species “types” from pioneer species adapted to harsh conditions to species adapted to high levels of competition?; (3) Is this sequence of “types” directional and the same across all sites with similar climatic conditions?; (4) Does species diversity increase or decrease, or both?; (5) Does soil increase in organic content and the concentration of organic minerals as rehabilitated coastal dune forest develops?; and (6) Do soil properties determine patterns of plant and animal turnover?

Patterns in turnover for all animal taxa showed a decelerating decrease contradicting Clements’s classical theory of succession. Changes in composition followed patterns predicted by the individualistic model of succession. Trends in species diversity measures did not always match predictions with bird numbers declining in most sites over time. Regional disturbances may explain this. Soils became increasing acidic with site age, indicating increased organic content, although there were no significant linear trends in the percentage of organic matter found in soils. Trends in soil content may take longer to emerge than our relatively short chronosequence represents. Turnover in the tree, millipede, herbaceous plants and birds was significantly correlated with soil properties. In addition, for both the animal taxa turnover correlated significantly with tree diversity. Succession-based management is a valid approach to dune forest rehabilitation as long as restoration managers recognize disturbance as an ecological reality.

Keywords: Birds, Chronosequence, Herbaceous plants, Rehabilitation, Soil, Trees

Introduction

The theory of succession has been a fundamental concept in ecology for over 100 years (at least since Cowles' publication in 1901), and is perhaps the most enduring of all ecological theories (Walker & del Moral 2008). This theory describes the progressive and deterministic change in species composition and dynamics over time and forms the conceptual basis of restoration ecology (Young et al. 2005). Successional theory may be ideal as a basis for restoration as it is conceptually simple and encapsulates the ability of ecosystems to recover from disturbances. The manipulation of that ability is a fundamental concern of restoration ecology (Walker et al. 2007).

The use of successional theory to frame restoration management is common, but testing the assumptions of this theory in a restoration setting is not (Walker & del Moral 2008; but see Prach & Pyšek 2001 and Řehounková & Prach 2008). The practice of restoration often relies more upon horticulture, agronomy and engineering than on succession (Hodačova & Prach 2003; Young et al. 2005). Hobbs et al. (2007) posit that this separation stems from cultural and conceptual differences between restoration practitioners and those studying succession. Many aspects of succession make it unattractive to restoration practitioners. For example, successional studies are often on a time scale of hundreds or thousands of years, whereas a restoration project may only last 20 or 30 years (Dobson et al. 1997). Importantly, there have been a number of examples of the failure of succession to achieve restoration goals (for example, Zedler & Callaway 1999; Suding et al. 2004).

Many factors may render succession unpredictable, including priority effects (Connell & Slatyer 1977), edaphic and topographical heterogeneity (Cutler 2009), propagule availability, species dispersal (Lanta & Lepš 2009), persistence of pioneers (Tsuyuzaki 2009), herbivory (Baniya et al. 2009), and the sporadic establishment of strong dominants (Walker & del Moral 2003). In addition, the structure, composition, and connectivity of the landscape may also have strong effects on species composition (Grainger et al. 2011). All these factors and many more, may compromise the efficacy of succession-based restoration management (Suding et al. 2004).

Succession, however, offers several predictions of the trends in species composition and other community properties that can be expected after a disturbance event. The outcomes of restoration actions should thus be predictable using successional theory (Van Andel & Aronson 2006). Temporal trends expected from succession include the progressive development of soil, sequential and directional changes in species composition, increased species diversity (in early succession at least; Connell 1978) and increased stability (Dobson et al. 1997).

Perhaps the most alluring aspect of succession for restoration ecology is the concept that after a disturbance event, habitats will predictably recover their former structure and function (Walker & del Moral 2007). Accordingly, there will be a directional progression in species composition, which becomes more similar over time to an undisturbed community (Pickett et al. 1987; Wassenaar et al. 2005). The traits of species should also be predictable so that immediately after the disturbance, species with life histories that are adapted to survive in harsh conditions colonize the site (Dobson et al. 1997). Increasingly, competitive interactions will structure the community, whereby pioneer species are replaced by species that are superior competitors

(Dobson 1997). This increased competition should eventually lead to community stability (Anderson 2007).

However, the definition of stability is ambiguous in the context of succession (Drury & Nisbet 1973), however, many authors have equated stability with compositional turnover (e.g. Anderson 2007). The rate of species turnover is predicted to be greatest at the earliest stages of succession (Drury & Nisbet 1973). This pattern occurs as the regional species pool becomes exhausted and the rate of competition increases as a community assembles, making it more difficult for new species to colonize (Tilman 1997). There are different responses of turnover expected for different theories of succession; the classical theory of Clements (1916) predicts spikes in turnover rate at each discrete community transition. However, if species are independent units (Gleason 1926) then turnover will be high initially and then decline to a continuous low level (a decelerating decrease). Anderson (2007) showed this response to be common in plant and arthropod successions.

Species diversity may follow one of three possible successional trends; classical theory predicts an increase in structural heterogeneity and thus an increase in species richness and diversity (Odum 1969). Egler's (1954) initial floristic composition model (also applied to faunal assemblages) predicts that all the components of the species assemblage are present at the beginning of succession and therefore diversity and richness are maximized in the early stages of succession. Connell's (1978) intermediate disturbance hypothesis, however, predicts an initial increase in species richness and diversity and then in the later stages of succession a decline, in the absence of further disturbance. Superior competitors at the later stages of succession are thought to exclude their inferiors. Thus, the mid-stages of succession are stages at which the species that are capable of establishing have done so, but competition has not yet filtered the species assemblage, leading to the highest levels of diversity (see Howard & Lee 2003).

Soil nutrients and minerals, and the species composition of vegetation are intrinsically linked (Sýkora et al. 2004; Wardle & Peltzer 2007). As generations of plants and animals die, their remains are incorporated into the soil (Drury & Nisbet 1973). Furthermore, not only does the presence of different plant species alter the resource input of the soil (Wardle & Peltzer 2007), but the composition of the soil minerals can also influence plant composition (Sýkora et al. 2004). Plant composition and structure then has a role in determining the composition of higher taxa, for example birds (Kritzinger & van Aarde 1998). Therefore, changes in soil minerals over time may be the mechanism that underlies patterns of succession.

Here we report on a restoration program that relies on successional processes to restore coastal dune forests destroyed by mining (see van Aarde et al. 1996a). The program began in 1977, and our research initiatives commenced during 1991. Several of our earlier papers (for example, Ferreira & van Aarde 1996; van Aarde et al.1996a,, 1996b; Kritzinger & van Aarde 1998et al. 2005; Grainger et al. 2011) implied that the recovery of communities on these sub-tropical dune forests is driven by succession. However, none of these papers focused on evaluating succession as the primary driving force of forest regeneration following rehabilitation, as practiced here. In this paper, we wish to ascertain if the assumption that succession is a valid model for the restoration of coastal dune forest is correct and if so which model of succession best describes the trends in community composition observed over time. We therefore assess six community level trends expected to result from ecological succession. Several of our previous papers have addressed the convergence of regenerating coastal dune forest with an undisturbed reference forest so we will not address this aspect of succession herein (for example van Aarde et al. 1996b; Davis et al. 2003; Redi et al. 2005; Wassenaar et al. 2005). We used data on soil nutrients and minerals, trees, herbaceous plants, millipedes, and birds from regenerating coastal dune forests to address the following questions:

1) *Does the rate of species turnover decrease as coastal dune forest develops?*

2) *Is there a sequence of changing species "types" from pioneer species adapted to harsh conditions to species adapted to high levels of competition?*

3) *Is this sequence of "types" directional and the same across all sites with similar climatic conditions?*

4) *Does species diversity increase or decrease, or both?*

5) *Does soil increase in organic content and the concentration of organic minerals as rehabilitated coastal dune forest develops?*

6) *Do soil properties determine patterns of plant and animal turnover?*

(See Table 3-1 for a summary of our expectations).

Methods

Study sites and restoration process

The study area included circa 60 km of coastline between Richards Bay Town (28°43'S, 32°12'E), and the Sokhulu forest (28°27'S, 32°25'E) in KwaZulu-Natal, South Africa. Here the climate is humid and subtropical, with mean annual rainfall of 1488 ± 447.3 mm (mean ± SD, *n* = 34 years between 1976 and 2009; data courtesy of Richards Bay Minerals). Rainfall peaks in February and the mean (± standard deviation) temperature is 23.8 ± 3.50 °C (monthly temperature between 2006 and 2009 (data courtesy of RBM)). These coastal dunes have been mined for minerals since 1977 (see van Aarde et al. 1996a).

The mining company Richards Bay Minerals' (RBM) aims to return indigenous coastal dune vegetation to one third of its mined area. The mining process (described in full in van Aarde et al. 1996a) destroys all vegetation in front of the mine-pond. Prior to mining, the topsoil is removed and stockpiled. Immediately post mining, sand dunes are mechanically re-shaped and topsoil replaced. The topsoil is then stabilized using drift-fencing, and seeded with exotic annual plants (sunhemps and sunflowers). We refer to this stabilization of dunes and return of topsoil as the "kick-start" to succession (van Aarde et al. 1996a, van Aarde et al. 1996c). After this, there is minimal management intervention (removal of non-native plant species and herbivores) and the restoration relies on natural successional processes (van Aarde et al. 1996a; van Aarde et al. 1996b).

Data collection

Our data comes from a number of published and unpublished sources. Soil was collected in 2007 in eight regenerating coastal dune forest sites of different ages (Table 3-2). Within each site at five randomly located sampling plots, we took six core subsamples from the top 10 – 20 cm of the soil profile using a soil auger. The subsamples were later mixed together and sampled for chemical analysis as described by van Aarde et al. (1998). For this study, we used the variables pH, percentage Carbon, organic matter and Nitrogen. We also assessed soil fertility using the method described in van Aarde et al. (1998). For each sample, five polystyrene cups were filled with 300 g of soil. Four randomly selected seeds of *Raphanus sativus* were placed in each cup at a depth of 1 cm. Only the first sprout per cup was retained with subsequent sprouts removed as soon as they emerged. Each cup was provided with 25 ml of distilled water daily and kept at a temperature of ~ 28°C. After 27 days, each plant was removed from the cup cleaned in distilled water and then oven dried at 60°C for 48 hours. After this, the whole plant (inclusive of root, tuber, stem and leaf) was weighed. The dry weight of the plant (g) was then used as an indicator of soil fertility.

Trees surveys were carried out in 1999, 2001 and 2005 in seven (six in 1999) rehabilitating sites. We followed the methods described by Wassenaar et al. (2005) whereby self-supporting woody plants greater than 1.7 m in height were identified in seven 16 x 16 m quadrats per site. In 2009, we used the Point-Centre Quarter method (PCQ) along randomly located transects that traversed the rehabilitating sites perpendicular to the sea (Cottam & Curtis 1956).

Bird surveys took place in summer (December, January, and February) in the years 1993, 1997 to 1999, 2001 to 2004, and 2006 to 2008 (see Table 3-2 for site ages) and followed the method described by Wassenaar et al. (2005). Experienced observers walked a number of 300 m line-transects separated by 200 m and recorded all birds seen within 60 m of either side of the transect. The exact number of transects varied between survey years and sites.

Millipede surveys took place in the summer and followed the methods described by van Aarde et al. (1996d). In each site, six randomly located transects 16 m x 6 m were used to record all millipedes found on vegetation and on the ground. Data were collected in 1993 to 1996, 1998 to 2002, 2005, 2007, and 2008. The sites established in 1984 and 1988 were not surveyed in 1993, and the site established in 1992 was first surveyed in 1998 (see Table 3-2).

For the herbaceous plant community surveys all plant species below 1 m in height were identified and counted in 10 randomly located (five in 2003) plots in each rehabilitating site and in the undisturbed reference forest (Wassenaar et al. 2005). A plot consisted of 10, 1 m^2 quadrats placed in a 2 x 5 m pattern with 5 m separating each quadrat. Data were collected in 1995, 1999, 2003 and 2005 (see Table 3-2). Tree seedlings were not included in the analyses.

Analysis

Previous work in the study region has relied on the chronosequence approach (for example, Ferreira & van Aarde 1997; Davis et al. 2003; Wassenarr et al. 2005). This approach has been criticized because it ignores site-specific effects (Chazdon et al. 2007; Johnson & Miyanishi 2008). In order to determine if tends in successional patterns were not just artifacts of the chronosequence we identified trends (where data allowed) within individual sites across several survey events. We compared these to trends across a chronosequence (substituting space for time). We used data from all of our 16 (at most) survey years to produce each chronosequence. We could not use data from the same site at different ages because this would violate the assumptions of a chronosequence. Instead, we constructed simulated chronosequences by a stratified random sampling procedure, whereby within each chronosequence a site was only included once. The data could come from any one of the survey years. This procedure was repeated 1000 times and the mean values used in the chronosequence.

Structural Trends

Change in life-history traits

To test the assumption that sites of a similar age would have similar composition we used Non-metric multidimensional scaling (NMDS) using the function 'metaMDS' of the package 'VEGAN' (v.1.15-3; Oksanen et al. 2008) in the R statistical software (v. 2.8.1; R Core Team Development 2008). We used Bray-Curtis as the similarity index and set the 'zerodist' argument to "add" a small positive value to zero dissimilarities. Patterns of community composition shown in the NMDS were confirmed using ANOSIM, analysis of similarity (using the function 'anosim' in R's VEGAN package). Further, to test if changes in species composition were related to the age of sites we used a Mantel test using the function 'mantel' once again in the 'VEGAN' package. This test measures concordance between two distance matrices - community similarity versus time in this instance. Species habitat associations were determined from published sources (Appendix 3-1 to 3-3) for herbaceous plants, trees and birds. No independent sources of information exist for millipede habitat associations.

To test the assumption that pioneers do not replace themselves we used diameter at breast height measurements from the 2009 tree survey to create size class distribution plots for all sites combined. We only show data for some of the tree species recorded, these include; *A. karroo*, the most abundant tree in the rehabilitating sites as well as the next top-ten abundant species. We combined data for *Mimusops caffra* and *M. obovata* as well as data for *Trichilia emetica* and *T. dregeana* as distinction between these related species is difficult.

Species turnover

We calculated species turnover simply as the average of species gains and losses between survey events, expressed as a proportion of the mean species richness during the survey period (Anderson 2007). Gains were defined as the number of new species added to the community and losses were defined as the number of species lost from the community. We did not consider the reappearance of a previously present species in the community as ecologically significant; rather we assumed that this was an artifact of sampling or a stochastic event. Therefore, these were not counted in the calculation of turnover. We used regression analysis to assess how much variation in turnover could be attributed to regeneration age.

Trends in species richness, diversity and evenness

Species richness was calculated as the number of species per transect/plot. We calculated species diversity using the Shannon index of diversity and evenness using the Smith and Wilson evenness index (E_{var}; Smith & Wilson 1996). The regression slopes of individual sites were compared to those predicted by randomized chronosequences using the method described by Zar (1984) and calculated in the program GraphPad Prism 3.0.

Functional Trends

Trends in soil minerals and organic matter

Trends in soil pH, percentage Nitrogen, Carbon and organic matter, and soil fertility were assessed across the 2007 soil chronosequence. We tested if the mean value for each site (and the reference site) differed significantly using an Analysis of Variance (ANOVA; or the non-parametric Kruskal-Wallis test). We then used two post-hoc tests, the Bonferroni test and Post-test for a linear trend (using the method described in Altman, 1991, and calculated in GraphPad Prism 3.0). Data was tested for departure from linearity with a runs test (calculated in GraphPad Prism 3.0) prior to running the post-test for a linear trend. We did not include the benchmark in this analysis as it is of unknown age. We also assessed the trends in the variation of the samples within a site using coefficient of variation.

Influence of function on structure

To test if the soil composition was a potential causal variable of successional patterns, we included the soil analysis data as environmental vectors within a NMDS using the function ‘envfit’ in the package ‘VEGAN’. This function reports the squared correlation coefficient (r^2) and significance is determined by random permutations of the data; we set the number of permutations to 1000.

We used the nearest survey year to the 2007 soil analysis for each taxon. The 2005 chronosequence for trees and herbaceous plants, millipedes in 2007 and birds in 2006 were included. Prior to our analysis, we tested for correlations between environmental variables using Pearson’s correlation coefficient. We expected turnover in the animal communities (birds and millipedes) to be influenced more by vegetation than by soil properties so we added both tree and herbaceous plant diversity to the environmental variables. The percentage Nitrogen was strongly correlated with the percentage Carbon in the soil samples (Pearson's r = 0.83). In addition, both soil Nitrogen and soil Carbon were correlated with the percentage of organic matter in the soil (Pearson's r = 0.93, 0.82 respectively). Regeneration age was strongly correlated with pH (Pearson's r = 0.73) and tree and herbaceous plant diversity (Pearson's r = 0.94; -0.97 respectively).

Consequently, in the analysis of environmental vectors, we only included the percentage organic matter, with the proviso that this can represent the percentage Nitrogen and percentage Carbon. We removed site age from the analysis, as we reason that site age is a proxy for a number of potential environmental variables.

Results

Structural Trends

Species turnover

Species turnover for all taxa followed the expected pattern of a decelerating decline in turnover rate with increased regeneration age (Fig.3-1). Regeneration age explained at least 30 % of the variation in turnover rate (non-linear regression, trees: R^2 = 0.31, birds: R^2 = 0.36, herbaceous plants: R^2 = 0.50 and millipedes: R^2 = 0.41).

Change in life-history traits

The stress of the NMDS ordinations was relatively high (>20 %) with a two-dimensional ordination (i.e., k = 2), however the results of the ANOSIM confirmed that community composition for all taxa differed between site ages (herbaceous plants: R = 0.31, P<0.001; birds:

R = 0.34, P<0.001; trees: R = 0.47, P<0.001; millipedes: R = 0.52, P<0.001; Fig.3-2). For the herbaceous plants, plots in sites aged between 1 and 5 years old, and plots in sites between 6 and 10 years old were separated from the plots in older sites (>11 years old) which overlapped considerably (Fig.3-2; NMDS, stress = 17.25, k = 3, non-metric fit r^2 = 0.95, linear fit r^2 = 0.83). The ordination of the bird community showed a similar pattern with transects in the youngest sites (1 to 5 years old) separating from those in the older sites (Fig. 3-2; NMDS, stress = 18.43, k = 3, non-metric fit r^2 = 0.96, linear fit r^2 = 0.88). The tree community ordination showed clearer convergence between the plots in sites of a similar age (Fig.3-2; NMDS, stress = 19.00, k = 3, non-metric fit r^2 = 0.98, linear fit r^2 = 0.93). Overlap in the millipede community ordination was considerably greater than in the other taxa (Fig.3-2; NMDS, stress = 19.00, k = 3, non-metric fit r^2 = 0.98, linear fit r^2 = 0.91). The results of the Mantel test confirm these changes in species composition with regeneration age for all taxa, with the plant taxa showing stronger concordance than the animal taxa (Mantel test; trees: r = 0.48, herbaceous plants: r = 0.38, millipedes: 0.27, and birds: r = 0.26 all P values <0.001). For all taxa, with the exception of millipedes, species identity appears to broadly shift from species adapted to harsh environments to those more typical of forests (Fig.3-2 & Appendices 3-1, 3-2 & 3-3). We had no reliable and independent information on the habitat associations of millipedes (Appendix 3-4) and were therefore, unable to assess changes in life history types with age.

Of the 11 tree species for which we show size class distributions only *Acacia karroo* and *Antidesma venosum* did not show the reverse-J pattern indicative of active recruitment (Fig.3-3.).

Trends in species richness, diversity and evenness

Site and taxon specific chronosequential trajectories for richness, diversity and evenness were idiosyncratic (see Table 3-3). The richness and diversity of herbaceous plants decreased in the youngest site with increased age, while in older sites it increased. This pattern was also evident in the youngest site for millipede diversity and tree evenness (Table 3-3). Bird richness decreased with age in all but the youngest site where there was no significant trend (Table 3-3).

Functional trends

Trends in soil minerals and organic matter

The percentage of soil Nitrogen differed significantly between sites (ANOVA; $P>0.001$; Fig. 3-4). Bonferroni's multiple comparison test highlighted significant differences (alpha = 0.05) between all sites and the reference site, except the second youngest site (established in 2000) being 7 years old at the time of the soil survey. The post-hoc test for a linear trend was not significant ($r^2 = 0.21$; $P = 0.21$).The percentage of soil Carbon also differed significantly between sites (ANOVA; $P<0.001$; Fig. 3-4). All sites had significantly lower percentage Carbon than the reference site and there was no significant linear trend ($r^2 = 0.01$; $P = 0.30$).

Soil pH differed significantly between sites (ANOVA; $P<0.001$; Fig. 3-4). The post-hoc test for a linear trend was significantly linear and age explained 62.44 % of the variation in soil pH (slope = 0.35; $R^2 = 0.62$; $P<0.001$), suggesting that soil became more acidic with regeneration age. Mean soil organic matter differed significantly (ANOVA; $P<0.05$; Fig. 3-4) between sites, and Bonferroni's multiple comparison test showed that all sites except the oldest regenerating site (30 years old) and the second youngest (7 years old) differed significantly from the reference forest. Once again the post-test for a linear trend was significantly linear and age explained 90 %

of the variation in mean soil organic matter (slope = -0.33; $R^2 = 0.91$; $P<0.05$) suggesting that mean soil organic matter increased with increasing regeneration age. Soil fertility (measured as the dry weight of *R. sativus*), differed significantly between sites (Kruskal-Wallis test; $P<0.001$; Fig. 3-4). The Dunn's multiple comparison test showed significant differences (alpha = 0.05) between the reference forest and the 30, 27 and 4 year old sites. We could not assess linear trend for the soil fertility because it was non-normally distributed. Only soil pH showed any significant change in variability (coefficient of variation) with regeneration age and the pH of samples became more heterogeneous with increased regeneration age.

Interactions between functional and structural changes

Environmental vectors from the soil analysis fitted to the tree data for 2005 showed that the variation in the NMDS is significantly and strongly correlated with soil fertility and the percentage organic matter in the soil ($r^2 = 0.30$ $P<0.05$; $r^2 = 0.37$ $P<0.05$). The ordination of herbaceous plants correlated with both soil pH and soil fertility ($r^2 = 0.45$, $P<0.05$; $r^2 = 0.34$, $P<0.05$). The millipede community ordination correlated with soil fertility and tree diversity ($r^2 = 0.71$, $P<0.001$; $r^2 = 0.36$, $P<0.05$), and the ordination of the bird chronosequence of 2006 correlated with soil fertility, soil pH and tree diversity ($r^2 = 0.34$, $P<0.05$; $r^2 = 0.45$, $P<0.05$; $r^2 = 0.74$, $P<0.05$).

Discussion

In our study, general patterns of community stability (species turnover), changing species composition, and species diversity followed patterns expected from the individualistic theory of succession (Gleason 1926). Regenerating coastal dune forest soils became more acidic and soil properties partially explained patterns of plant and animal turnover. These findings suggest that succession is a valid model of coastal dune forest restoration.

Species turnover

The rate of succession (species turnover) exhibited by all the taxa showed a decelerating decrease; sites that have recently undergone disturbance had a greater compositional turnover. As communities aged, the number of available micro-sites apparently declined and inter-specific competition may have increased (see Gross 1980; Tilman 1997). Compositional stability is a key concept in the theory of succession (McCook 1994; Anderson 2007). The declining decrease in the rate of turnover fits with Egler's (1954) theory of initial floristics, Gleason's (1926) individualistic theory of succession and Connell's (1978) intermediate disturbance hypothesis. This pattern does not support Clements's (1916) classical theory of succession.

Change in life-history traits

The shift in species composition from species adapted to harsh environments to those species that are superior competitors appears to be ubiquitous in forest succession (for example see, Kardol et al. 2005; Cutler et al. 2008; Lebrija-Trejos et al. 2008). However, Chazdon et al. (2007) and Johnson & Miyanishi (2008) suggest that this trend in the change in species composition is an artifact of the chronosequence approach. Our results dispute this. As we have shown here, sites of a similar age shared a similar species composition of coastal dune forest trees, herbaceous plants, birds and millipedes. This change in species composition may be driven by differences in species longevity, tolerance to shade (for plants), eventual size (a competitive advantage for forest trees), timing of colonization, and patterns of recruitment (Fajardo & González 2009). It is evident from the tree community in particular, that recruitment of *A.*

karroo, the first tree to colonize regenerating sites, is limited under a canopy consisting of adults of the same species; whereas, other longer-lived pioneer and forest species were actively recruiting. This pattern fits the predictions of Connell & Slayter's (1977) facilitation mechanism of succession. Without empirical knowledge of species tolerance to shade, it is difficult to conclude that light-intensity is driving the replacement of plant species in coastal dune forest. However, this is a plausible driver of plant species replacement (Woods 2000; Fajardo & González 2009; but see Dietze & Clarke 2008 for counter arguments to this paradigm) and changes in the tree community may influence changes in the other taxa (Kritzinger & van Aarde 1998).

Trends in species richness, diversity and evenness

Trends in species richness and diversity for all taxa, except the birds, appeared to match expectations overall; as sites aged, they increased in the number and diversity of species. For the herbaceous plants, the youngest site included in our survey (established in 2000, 3 to 5 years old) decreased in species richness as it aged, which could be consistent with Egler's (1954) initial floristics model. However, this is unlikely, as older sites still gained species with time. This loss in species was more possibly the result of a change in habitat type from grassland to scrub and woodland. In contrast, the bird community appeared to lose species in most sites even though the chronosequence predicted an increase in richness. Recently, Trimble & van Aarde (2011) showed a decrease in the number of bird species and their abundance over the last 15 years within our study region in both rehabilitating and pristine forest. Rainfall was one of the drivers of this decline, with drought conditions prevailing over the last ten years (Trimble & van Aarde (2011; see Table 2-3b also). This regional change in species may have detrimental effects on restoration success because birds disperse the seeds of many dune forest trees (Coates-Palgrave 2003).

The differences in chronosequence predictions and observed dynamics, although small, highlight an important proviso when using the chronosequence approach. Both regional scale climatic perturbations, such as drought, and site specific differences in the response to disturbance may obscure trends in diversity and richness (Foster & Tilman 2000; Svensson et al. 2009).

Trends in soil minerals and organic matter

Soils became more acidic although the percentage of organic matter in the soil did not increase with increasing regeneration age as expected. The process of acidification may be evidence of the development of soil organic matter (Sýkora et al. 2004), but trends in percentage organic matter may be undetectable at the relatively short time span of our chronosequence. Nitrogen concentration was lower in the youngest site than the second youngest, confirming the findings of van Aarde et al. (1998). They ascribe this phenomenon to its depletion by fast growing annual herbs and by grasses that have colonized the site. Soil Carbon was considerably lower in the regenerating sites than the reference site. This difference in Carbon levels may relate to different vegetation types that dominate the rehabilitating and reference sites (Paul et al. 2010). In contrast to van Aarde et al. (1998), we could not find any evidence that the concentration of Nitrogen and Carbon increased with regeneration age. However, soil Nitrogen or Carbon may not be good indicators of soil rehabilitation as they can take centuries to accumulate to pre-disturbance levels (Knops & Tilman 2000). Abreu et al. (2009) showed pH to be a more sensitive indicator of soil rehabilitation.

Interactions between functional and structural changes

It is common, as we have done here, to use time as a variable to describe successional patterns. However, as McCook (1994) affirms, "…time is a dimension, not a process" and therefore is not a causal mechanism for successional patterns. Changes in soil nutrients and minerals, which correlate to changes in vegetation and structure, may underpin the temporal changes that are expressed as the pattern of succession (Sýkora et al. 2004). Tree species turnover correlated with the percentage organic matter in the soil and soil fertility, and herbaceous plant turnover correlated with soil pH and soil fertility. However, it is difficult to ascertain the causal variable in these correlations, because soil nutrients and minerals can also be affected by plant species composition. Millipedes are known to affect soil elements (Smit & van Aarde 2001), and the significant correlation with soil fertility we found may reflect this. For the bird and millipede community, succession may be dependent on the physical structure of the tree community and the resources (shelter, food, nesting materials etc.) it provides rather than on the actual plant species composition (Kritzinger & van Aarde 1998). Our findings provide indirect evidence of this, as bird and millipede composition was correlated significantly to tree species diversity.

Succession drives coastal dune forest restoration

The patterns of age-related species turnover, trends in species "type", richness, diversity and evenness within regenerating coastal dune forest, followed the trends expected from Gleason's (1926) individualistic model of successional theory. Gleason's model follows many of the same predictions of trends in communities over time as Clements's (1916) classical model. The difference is that in Gleason's (1926) model community properties are the sum of individual species and these species will appear and disappear in a successional sere as independent units. The herbaceous plant, tree, and bird communities showed these trends more clearly than the millipede community did. The characteristics of the soil appeared to be driving changes in species composition of the plant taxa although as discussed above the casual variable in this relationship is difficult to ascertain. Our study is an observational one and as such, we can only hint at the mechanisms of change in species composition over the course of succession. To identify the mechanism that is driving these changes we may have to change the focus of our research from the observational to the experimental. Successional theory does provide hypotheses that can be tested experimentally, for example, Connell & Slayter’s (1977) three pathways of community succession: facilitation, inhibition, or tolerance (although see McCook 1994, for a critique of these three models being considered mechanistic). This must be an avenue of future research at the study site. In addition, we need to gather more information on the natural history of species in the regenerating coastal dune forest (in particular the millipedes) in order to fully understand the processes of forest regeneration.

Based on our assessment, succession (Gleason’s 1926 individualistic model) is a valid model for the restoration of tropical coastal dune forests. However, departures from the expected patterns do occur, which are likely the result of global, regional, or local scale disruptions and disturbance (see Trimble & van Aarde 2011), and landscape composition (see Grainger et al. 2011 and Chapter 6 of this thesis). It is imperative that any restoration project that relies on successional-based management must allow for and expect these external disruptions to the pattern of succession (Walker & del Moral 2003). In fact, continued disruption and disturbance should be embraced as a natural part of ecosystem dynamics.

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Table 3-1. Trends expected in structural and functional community characteristics of regenerating sites undergoing ecological succession

Community characteristics	**Expected trends**				**Analysis**	
Structural	Classical Theory (Clements 1916)	Initial Floristics or Faunistics (Egler 1954)	Individualistic (Gleason 1926)	Intermediate disturbance (Connell 1978)		
Species turnover	Turnover spikes at each community transition	Turnover will show a decelerating decrease over time (Anderson 2007)			Turnover rate	Regression analysis
Change in species life history traits	Pioneer species (those adapted to survive harsh conditions) will be the first to establish after disturbance. As resources are limited, competitive species will replace them. Pioneers cannot replace themselves	All components are present - but some are only there as seeds (plants) - therefore a compositional turnover (in adults) may be expressed as in classical	As Classical	As Classical	Change in species composition along a gradient of age	Mantel test
					Histograms of size class distribution to illustrate recruitment patterns	Visual Interpretation of reverse-J pattern
Species richness	Increase habitat complexity leads to increased available niche-space which leads to increases richness,	All components of the community are present in the beginning of succession and therefore richness, diversity, and evenness	As Classical	Early stages of succession are structured by resource availability and later by competitive interactions. At intermediate stages	Trends in species richness (expressed as number of species per plot/transect) as a function of site age (both chronosequence and site specific)	Regression analysis

Species Diversity	diversity, and evenness to a maximum at climatic climax	progressively decrease as species are filtered from the community		of succession the structural components are maximized. After this intermediate stage competitive interactions increasingly structure the community and lesser competitors are removed from the assemblage	Trends in diversity (Shannon index) as a function of site age(both chronosequence and site specific)	Regression analysis
Species evenness					Trends in evenness (Smith & Wilson Index) as a function of site age(both chronosequence and site specific)	Regression analysis
Functional						
Trends in soil minerals and organic matter	Soil minerals and organic matter should increase with time as plants and animals die				Trends in soil N,C, organic matter & pH as a function of site age	Analysis of variance
Interactions between functional and structural changes						
Soil minerals and plants	Soil minerals/organic matter determines plant community composition				Soil attributes plotted as an environmental variable in tree and herb NMDS plots	NMDS environmental fit
Plants community on animal community	Plant diversity drives animal diversity				Plant (trees and herbaceous plants) diversity used as an environmental variable in bird and millipede NMDS plots	

Table 3-2. Survey years and site ages for each rehabilitating coastal dune forest site, indicated by the year of establishment 1977 to 2003. Surveys for herbaceous plants, millipedes, birds, trees and soil took place in different survey years. Highlighted in grey are the survey years for each taxon.

Survey year	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009
Herbs			■				■				■		■				
Millipedes	■	■	■	■		■	■	■	■	■			■		■	■	■
Birds	■				■	■	■		■	■	■	■		■	■	■	■
Trees							■		■				■				■
Soil															■		
1977	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
1980	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
1984	9[1]	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
1988	5[1]	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
1992[2]	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1996	X	X	X	X	1	2	3	4	5	6	7	8	9	10	11	12	13
2000	X	X	X	X	X	X	X	X	1	2	3	4	5	6	7	8	9
2003	X	X	X	X	X	X	X	X	X	X	X	1	2	3	4	5	6

[1] No survey in the sites established in 1984 and 1988 in 1993; [2] The site established in 1992 was first surveyed for millipedes in 1998

Table 3-3. The slope of the regression lines for species richness, diversity and evenness for herbaceous plants, trees, millipedes and birds. The randomized chronosequence is the expected trend and the individual sites the observed trend. Asterisks (*) indicate a significant (alpha = 0.05) difference between the slope of the expected and observed regression line.

	Expected		Observed	
	Slope of the regression line	Significantly non-zero (alpha = 0.05)	Slope of the regression line	Significantly non-zero (alpha = 0.05)
Herbaceous plants – species per transect				
Randomized chronosequence	-0.06 ± 0.20	No		
18 to 28 years of regeneration			0.34 ± 0.14	Yes
15 to 25 years of regeneration			0.61 ± 0.16*	Yes
11 to 21 years of regeneration			0.50 ± 0.12*	Yes
7 to 17 years of regeneration			0.99 ± 0.12*	Yes
3 to 13 years of regeneration			0.17 ± 0.17	No
3 to 9 years of regeneration			1.25 ± 0.34*	Yes
3 to 5 years of regeneration			-2.82 ± 0.94*	Yes
Trees – species per transect				
Randomized chronosequence	0.42 ± 0.07	Yes		
14 to 28 years of regeneration			0.64 ± 0.15	Yes
11 to 25 years of regeneration			0.058 ± 0.15*	No
8 to 21 years of regeneration			0.64 ± 0.14	Yes
4 to 17 years of regeneration			0.58 ± 0.12	Yes
9 to 13 years of regeneration			0.81 ± 0.40	Yes
5 to 9 years of regeneration			1.02 ± 0.30	Yes
1 to 5 years of regeneration			0.71 ± 0.19	Yes
Millipedes – species per transect				
Randomized chronosequence	0.14 ± 0.04	Yes		
15 to 32 years of regeneration			0.12 ± 0.06	Yes

12 to 29 years of regeneration			0.15 ± 0.03	Yes
10 to 25 years of regeneration			0.18 ± 0.04	Yes
6 to 21 years of regeneration			0.23 ± 0.05	Yes
6 to 17 years of regeneration			0.02 ± 0.04*	No
2 to13 years of regeneration			0.31 ± 0.03	Yes
1 to 9 years of regeneration			0.22 ± 0.06	Yes
Birds – species per transect				
Randomized chronosequence	0.57 ± 0.21	Yes		
15 to 30 years of regeneration			-0.44 ± 0.12*	Yes
12 to 27 years of regeneration			-0.33 ± 0.12*	Yes
9 to 23 years of regeneration			-0.42 ± 0.11*	Yes
5 to 19 years of regeneration			-0.40 ± 0.08*	Yes
1 to 15 years of regeneration			-0.63 ± 0.14*	Yes
1to 11 years of regeneration			-0.65 ± 0.22*	Yes
3 to 7 years of regeneration			0.044 ± 0.48	No
Herbaceous plants – diversity				
Randomized chronosequence	0.02 ± 0.00	Yes		
18 to 28 years of regeneration			0.03 ± 0.01	Yes
15 to 25 years of regeneration			0.04 ± 0.01	Yes
11 to 21 years of regeneration			0.03 ± 0.01	Yes
7 to 17 years of regeneration			0.06 ± 0.01*	Yes
3 to 13 years of regeneration			0.02 ± 0.02*	No
3 to 9 years of regeneration			0.13 ± 0.03	Yes
3 to 5 years of regeneration			-0.13 ± 0.05	Yes
Trees – diversity				
Randomized chronosequence	0.08 ± 0.02	Yes		
14 to 28 years of regeneration			0.03 ± 0.02*	No
11 to 25 years of regeneration			0.04 ± 0.04*	No
8 to 21 years of regeneration			0.21 ± 0.02	Yes

4 to 17 years of regeneration			0.12 ± 0.03	Yes
9 to 13 years of regeneration			0.17 ± 0.05	Yes
5 to 9 years of regeneration			0.05 ± 0.05*	No
1 to 5 years of regeneration			0.06 ± 0.02	Yes
Millipedes – diversity				
Randomized chronosequence	0.97 ± 0.40	No		
15 to 32 years of regeneration			0.54 ± 0.25	Yes
12 to 29 years of regeneration			1.25 ± 0.31*	Yes
10 to 25 years of regeneration			2.53 ± 0.48*	Yes
6 to 21 years of regeneration			1.52 ± 0.32	Yes
6 to 17 years of regeneration			0.36 ± 0.29*	No
2 to13 years of regeneration			0.16 ± 0.55*	No
1 to 9 years of regeneration			-0.51 ± 0.20*	Yes
Birds – diversity				
Randomized chronosequence	0.04 ± 0.01	Yes		
15 to 30 years of regeneration			0.04 ± 0.01	Yes
12 to 27 years of regeneration			0.04 ± 0.01	Yes
9 to 23 years of regeneration			0.04 ± 0.01	Yes
5 to 19 years of regeneration			0.04 ± 0.01	Yes
1 to 15 years of regeneration			0.04 ± 0.01	Yes
1to 11 years of regeneration			0.03 ± 0.01	Yes
3 to 7 years of regeneration			0.01 ± 0.02*	No
Herbaceous plants – evenness				
Randomized chronosequence	0.00 ±0.01	No		
18 to 28 years of regeneration			-0.00 ± 0.00	No
15 to 25 years of regeneration			-0.01 ± 0.00	No
11 to 21 years of regeneration			-0.01 ± 0.00*	Yes
7 to 17 years of regeneration			-0.00 ± 0.00	No
3 to 13 years of regeneration			0.00 ± 0.01	No

3 to 9 years of regeneration			-0.00 ± 0.01	No
3 to 5 years of regeneration			0.03 ± 0.02	No
Trees – evenness				
Randomized chronosequence	0.03 ± 0.01	Yes		
14 to 28 years of regeneration			0.01 ± 0.00	Yes
11 to 25 years of regeneration			-0.01 ± 0.01*	No
8 to 21 years of regeneration			-0.00 ± 0.01*	No
4 to 17 years of regeneration			0.00 ± 0.01*	No
9 to 13 years of regeneration			0.00 ± 0.00*	No
5 to 9 years of regeneration			-0.00 ± 0.01*	No
1 to 5 years of regeneration			-0.01 ± 0.00*	Yes
Millipedes – evenness				
Randomized chronosequence	0.00 ± 0.01	No		
15 to 32 years of regeneration			0.01 ± 0.01	No
12 to 29 years of regeneration			-0.01 ± 0.01*	Yes
10 to 25 years of regeneration			0.01 ± 0.01	No
6 to 21 years of regeneration			-0.01 ± 0.01	No
6 to 17 years of regeneration			0.00 ± 0.01	No
2 to13 years of regeneration			0.01 ± 0.02	No
1 to 9 years of regeneration			-0.09 ± 0.02*	Yes
Birds – evenness				
Randomized chronosequence	-0.01 ± 0.00	No		
15 to 30 years of regeneration			0.02 ± 0.00*	Yes
12 to 27 years of regeneration			0.01 ± 0.00*	Yes
9 to 23 years of regeneration			0.02 ± 0.00*	Yes
5 to 19 years of regeneration			0.03 ± 0.00*	Yes
1 to 15 years of regeneration			0.02 ± 0.01*	Yes
1to 11 years of regeneration			0.02 ± 0.01*	Yes
3 to 7 years of regeneration			0.01 ± 0.01	No

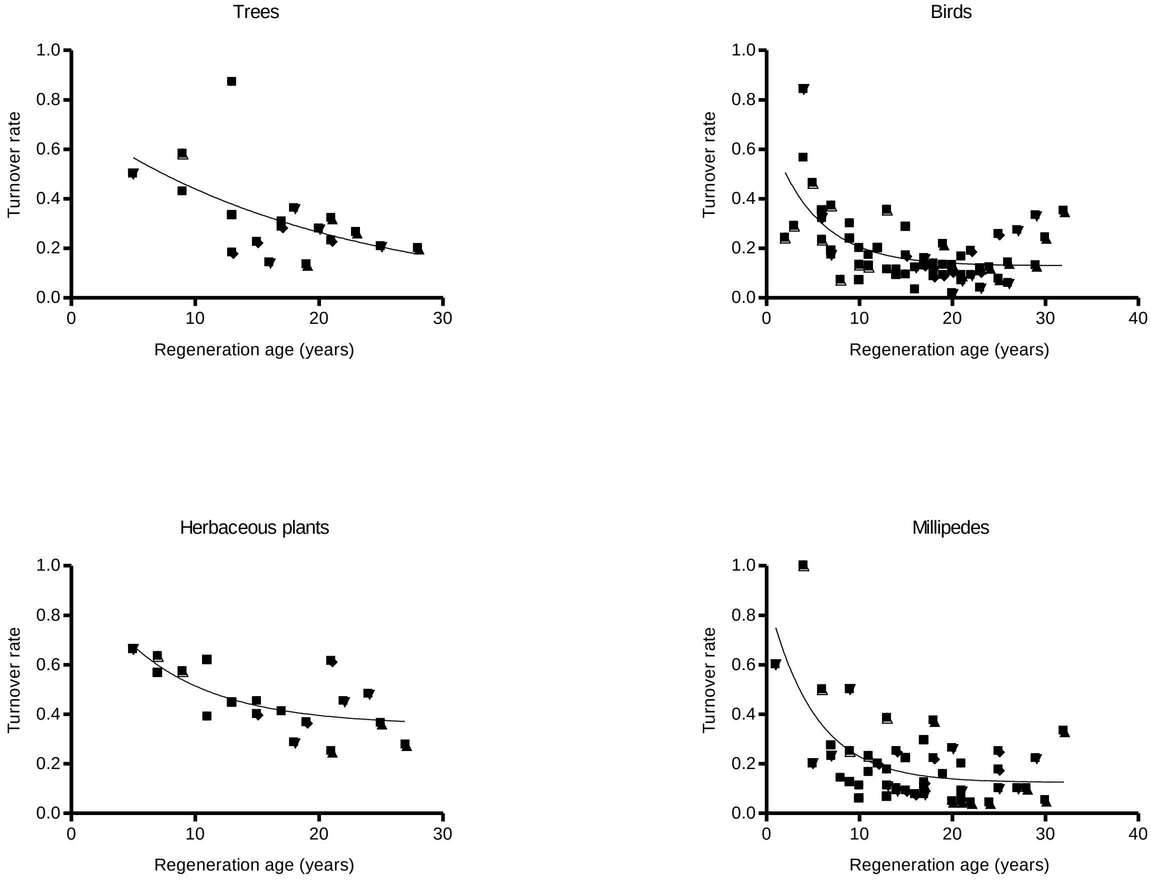


Figure 3-1. The rate of species turnover in regenerating coastal dune forest for the tree, bird, herbaceous plants and millipede communities.

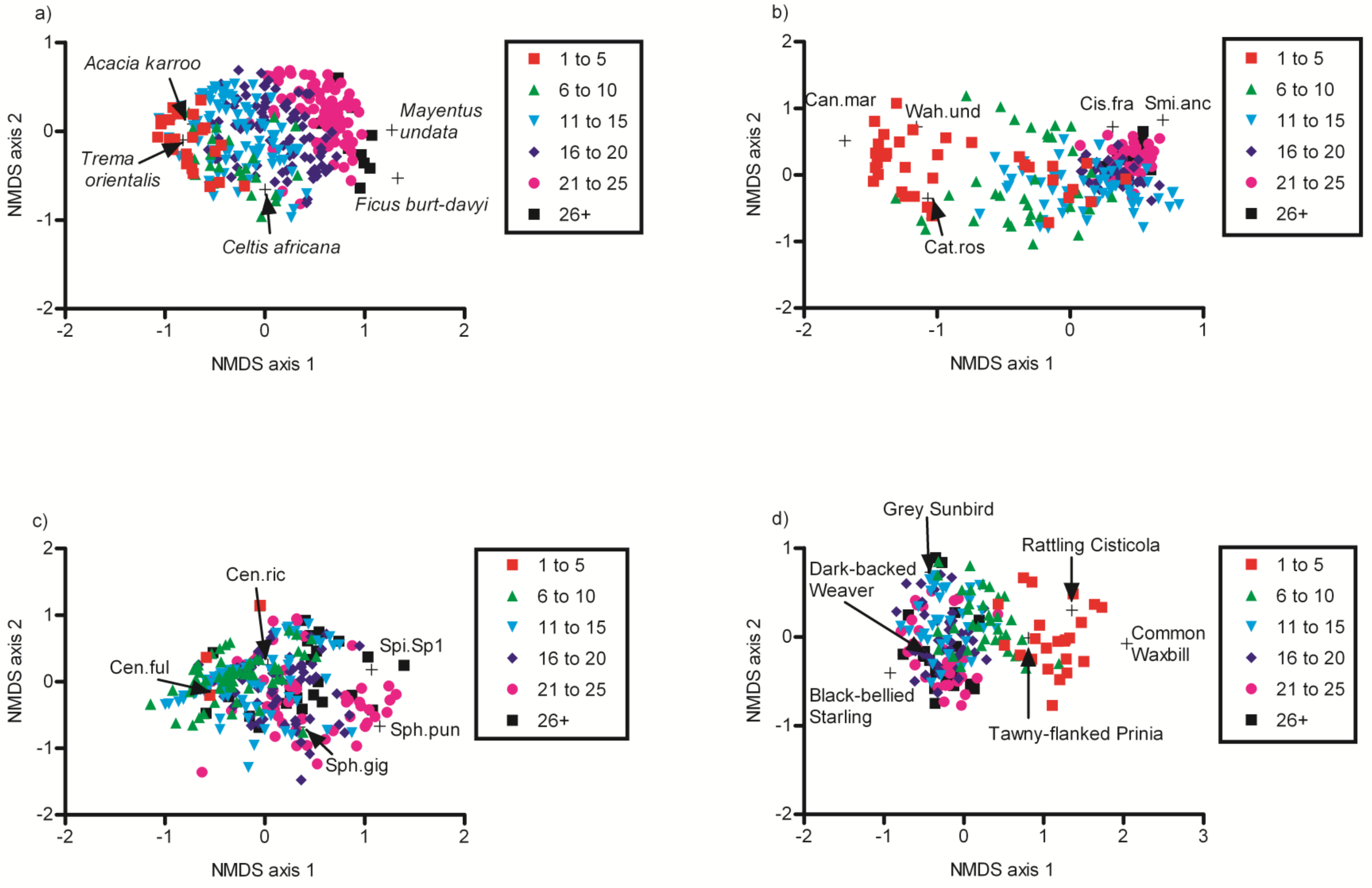
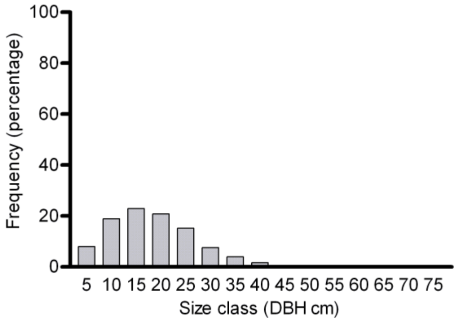
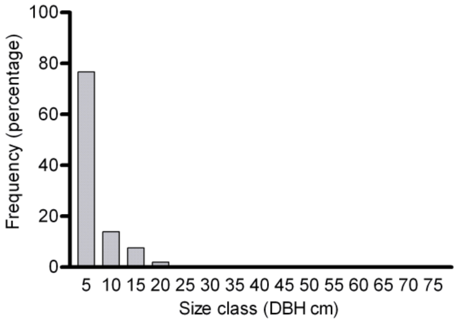

a)
NMDS axis 2
NMDS axis 1
1
0
-1
-2
-2
-1
0
1
2
Acacia karroo
Trema orientalis
Celtis africana
Mayentus undata
Ficus burt-davyi
■ 1 to 5
▲ 6 to 10
▼ 11 to 15
◆ 16 to 20
● 21 to 25
■ 26+
b)
NMDS axis 2
NMDS axis 1
2
1
0
-1
-2
-2
-1
0
1
Can.mar
Wah.und
Cis.fra
Smi.anc
Cat.ros
■ 1 to 5
▲ 6 to 10
▼ 11 to 15
◆ 16 to 20
● 21 to 25
■ 26+
c)
NMDS axis 2
NMDS axis 1
2
1
0
-1
-2
-2
-1
0
1
2
Cen.ric
Cen.ful
Spi.Sp1
Sph.pun
Sph.gig
■ 1 to 5
▲ 6 to 10
▼ 11 to 15
◆ 16 to 20
● 21 to 25
■ 26+
d)
NMDS axis 2
NMDS axis 1
1
0
-1
-2
-2
-1
0
1
2
3
Grey Sunbird
Rattling Cisticola
Dark-backed Weaver
Common Waxbill
Black-bellied Starling
Tawny-flanked Prinia
■ 1 to 5
▲ 6 to 10
▼ 11 to 15
◆ 16 to 20
● 21 to 25
■ 26+

Figure 3-2. Ordination of regenerating coastal dune forest communities of known age using Non-metric multidimensional scaling (NMDS). Sites of similar age (grouped together in 5 year categories) are indicated by the same symbol. Species are indicated by small black crosses (+) for the (a) trees; b) herbaceous plants; c) millipedes and d) bird communities. Labels for the herbaceous plants (b) refer to “Can.mar” = *Canavalia maritima*, “Cat.ros” = *Catharanthus roseus*, “Cis.fra” = *Cissus fragilis*, “Smi.anc” = *Smilax anceps* and “Wah.und” = *Wahlenbergia undulata*. For the millipede community “Cen.ful” = *Centrobolus fulgidus*, “Cen.ric” = *Centrobolus richardii*, “Sph.gig” = *Sphaerotherium giganteum*, “Sph.pun” = *Sphaerotherium punctulatum* and “Spi.Sp1” = *Spirostreptidae* spp.

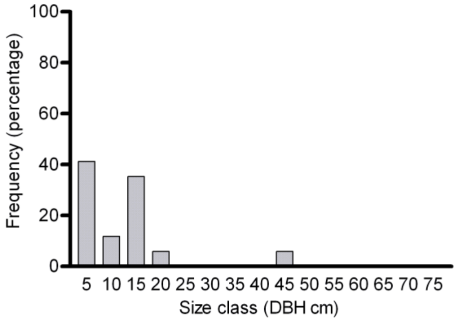
Acacia karroo (n =1359)



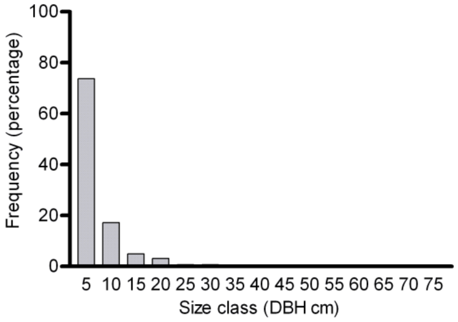
Allophylus natalensis (n= 158)



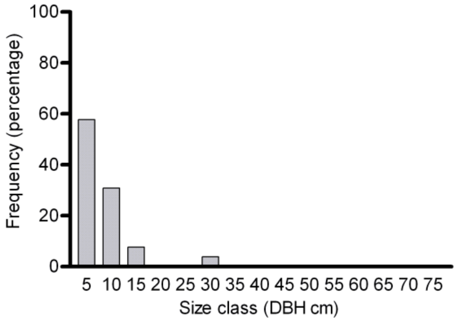
Antidesma venosum (n = 17)



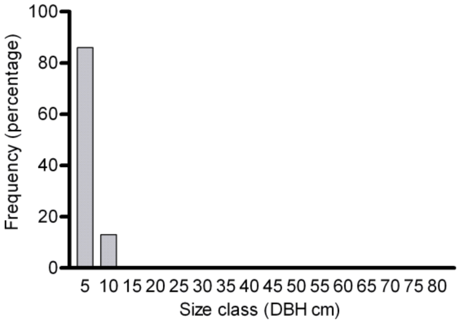
Brachlaena discolour (n= 163)



Bridelia micrantha (n = 26)



Canthium inerme (n =200)



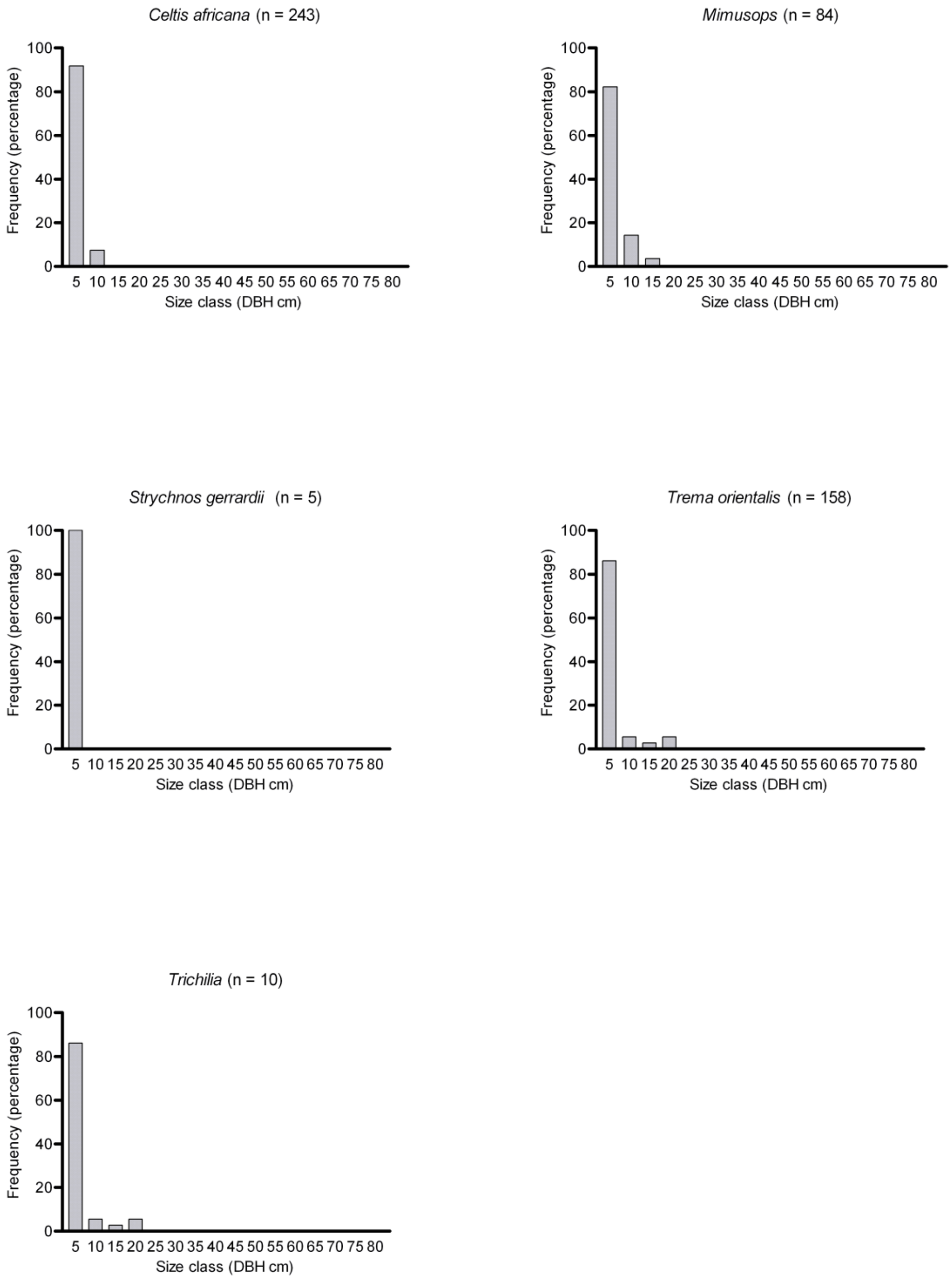


Figure 3-3. Size class distributions of the dominant pioneer tree *Acacia karroo*, and the most abundant ten other tree species. The only tree that did not show a regenerating population is the pioneer *Acacia karroo*.

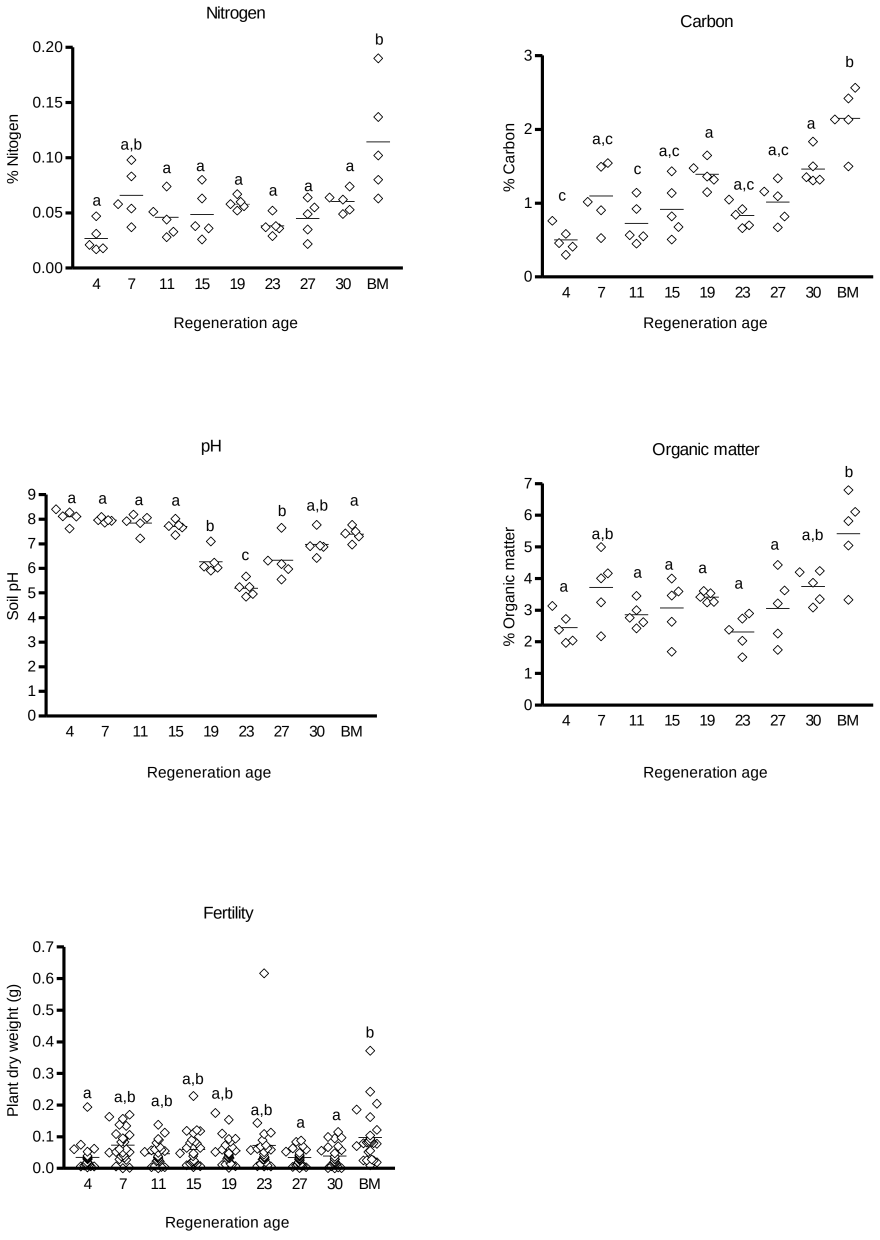


Figure 3-4. Results of an analysis of soil Nitrogen, Carbon, organic matter, pH, and fertility for 8 regenerating coastal dune forests of various ages and an undisturbed reference site of unknown age. Horizontal black lines indicate the mean value. Letters indicate groupings based on the

Bonferroni’s multiple comparison test (for soil fertility we used Dunn’s multiple comparison test), the same letter indicates no significant differences between sites.

Chapter 4

Can non-native species explain patterns of convergence and deviation in the herbaceous layer of regenerating coastal dune forest?

Abstract

The successful restoration of disturbed habitat is influenced by many factors; not least of which is the introduction of non-native species in to the regional species pool. These species may preclude native colonisation and deflect regeneration trajectories away from restoration targets. The success of restoration (commonly measured against reference sites) may therefore be an unobtainable goal.

We determined if non-native species divert the regenerating trajectories of coastal dune forest. Specifically, using measures of ecological distance we first determined if successional trajectories of the herbaceous plant community in rehabilitating coastal dune forest sites were convergent. We then determined if rehabilitating coastal dune forest sites became more similar to an undisturbed reference site as they aged and which species contributed the most to dissimilarity between the reference site and rehabilitating sites.

The composition of herbaceous species in regenerating coastal dune forest plots became increasingly convergent as the time since disturbance increased. However, species composition appeared to deviate from that within an undisturbed reference site. Contrary to our expectations, non-native species did not contribute the most to dissimilarity, and thus not to the recorded deviation. The deviation from the reference forest is attributable to the higher abundance of 1) a native forest specialist in the reference site, and 2) the higher abundances of native woodland adapted species in the rehabilitating sites. This deviation of the species composition in regenerating sites from that in the undisturbed reference site may therefore be indicative of successional changes and is not attributable to the presence of non-native species.

Keywords: Exotics plants, habitat restoration, herbaceous plants, regeneration trajectories, succession.

Introduction

Restoration success is typically measured against reference sites that represent the biological diversity characteristic of a region (for example, McLachlan & Bazely 2001; Wilkins et al. 2003; Redi et al. 2005; Wassenaar et al. 2005; Wong et al. 2010). These sites are usually high quality, minimally disturbed remnants of historic natural areas and constitute the desired endpoint of restoration (McLachlan & Bazely 2001; Wassenaar et al. 2005). If the species composition of rehabilitating sites becomes increasingly similar to that of the reference sites as the time since disturbance increases then restoration is considered successful (Wassenaar et al. 2005).

There are two linked assumptions that one makes when evoking reference sites within a restoration context. The first is that sites undergoing restoration represent early ecological stages of the reference habitat (SER 2004). The second is that sites undergoing restoration will become increasingly similar to the reference sites in terms of their species composition, abundance, and ecological processes (SER 2004; Wassenaar et al. 2005; 2007). However, these assumptions face several confounding factors, not least is that reference sites are a product of specific historic conditions that may no longer exist (Hobbs & Norton 1996; Jackson & Hobbs 2009). Changes in the disturbance regime, in landscape connectivity (which influences dispersal), and in the species pool (through local extinctions and by invasion of non-native species) may all hinder the reassembly of disturbed or destroyed communities (West et al. 2000; Suding et al. 2004; Jackson & Hobbs 2009; Matthews & Spyreas 2010; Grainger et al. 2011).

Here we investigate the regeneration of the herbaceous plant community in a post-mining restoration program on the east coast of South Africa. The mining company Richards Bay Minerals (RBM) aims to restore coastal dune vegetation to a third of its lease area (van Aarde et al. 1996). This programme aims to recover the community composition of coastal dune forest through successional processes (see van Aarde et al. 1996 for a full account of the rehabilitation). In the past, we have assessed the trajectory of regeneration against "benchmark" values within undisturbed coastal dune forest sites (for example, van Aarde et al. 1996; Weiermans & van Aarde 2003; Kumssa et al. 2004; Redi et al. 2005; Wassenaar et al. 2005). Latterly, we have used the Sokhulu forest as our reference site. This forest is a relatively undisturbed patch of forest to the north of our study site, which covers approximately 500 hectares. It is contiguous with the Mapelane Nature Reserve making the effective size of this forest patch approximately 1500 hectares.

There is no doubt that our study region has undergone changes since the herbaceous plant community in the Sokhulu forest (our reference site) developed (see Weisser & Marques 1979). One of the most important changes is the introduction of non-native species into the regional species pool. The eastern coastal belt of South Africa is one of the most invaded areas (in terms of species number and abundance) within the Southern African region (Henderson 2007). Invasion of non-native species is known to cause the failure of regeneration trajectories to progress toward undisturbed reference sites (for example, Matthews & Spyreas 2010; Tognetti et al. 2010). Wassenaar et al. (2005) identified a slow rate of recovery in the herbaceous plant community of regenerating coastal dune forest sites when compared to the Sokhulu forest, but they did not offer any possible explanations for this. Here we identify whether the presence of non-native species in the regional pool does divert regenerating trajectories of coastal dune forest. If so, then the successful restoration of a coastal dune forest may be an unobtainable goal, or at least require increased management intervention to curb the establishment of non-native species.

Recently, Matthews & Spyreas (2010) developed a framework for monitoring ecological restoration projects, which assesses community convergence, and progression using measures of community dissimilarity and ordination distance (see Fig. 4-1). Here we use the terms “convergence” and “progression” with specific meanings. “Convergence” (the antonym of which is “divergence”) is the increased similarity, in terms of species composition, between regenerating sites within a region as the time since disturbance increases. “Progression” (the antonym of which is “deviation”) is the trend in the species composition in regenerating sites within a region to become increasingly similar to an undisturbed reference site as the time since disturbance increases.

We use the conceptual framework of Matthews & Spyreas (2010) to ask the following three questions (1) Are successional trajectories of the herbaceous plant community convergent in rehabilitating coastal dune forest sites? (2) Are rehabilitating coastal dune forest sites becoming more similar to a reference site as they increase in age? (3) Which species contribute the most to dissimilarity between reference sites and rehabilitating sites?

Methods

Study site

The coastal sand dunes north of Richards Bay (28°43’S and 32°12’E) have been mined since 1977 for the minerals rutile, zircon, and ilmenite (van Aarde et al. 1996). Here mining uses a dredging process that follows on the removal of all vegetation and topsoil in front of the dredge-pond, and the topsoil is stock-piled for use in the rehabilitation process. The rehabilitation process takes place immediately behind the dredge-pond, where sand dunes are re-shaped and the previously stored topsoil returned to the dune. The topsoil is stabilised with drift-fencing (1.5 m high) and seeded with exotic annuals (sunflowers, sun-hemp, and millet). After this initial management intervention, the site regenerates naturally (van Aarde et al. 1996). The restoration process has led to the development of known-age (determined from mining records) regenerating coastal dune forest. Shortly after the initiation of rehabilitation, sites resemble grasslands; the exotic annuals have been replaced by species typical of grassland and the pioneer tree species *Acacia karroo* has established (Wassenaar et al. 2005). By 12 years of regeneration, trees typical of old-growth forest have colonized sites and dense undergrowth develops. By 22 years, a sub-canopy develops consisting of forest tree species and lianas, and by 30 years old *A. karroo* begins to senesce and secondary broadleaved species increase in abundance (Wassenaar et al. 2005).

The climate in the study area is humid and sub-tropical, with mean annual rainfall of 1488 ± 447.3 mm (mean ± SD, n = 34 years between 1976 and 2009; data courtesy of Richards Bay Minerals). Rainfall peaks in February and the mean (± standard deviation) temperature is 23.8 ± 3.50 °C (monthly temperature between 2006 and 2009 [data courtesy of RBM]).Following the methodology of Wassenaar et al. (2005) all plant species below 1 m in height were identified and counted in 5 to 10 randomly located plots in six known-age sites regenerating after mining disturbance and rehabilitation (see Appendix 4-1). In addition, we surveyed the vegetation within an undisturbed coastal dune forest (Sokhulu Forest) which has been intact since at least 1937 according to aerial photographs. A plot consisted of 10 1 m^2 quadrats placed in a 2 x 5 pattern with 5 m separating each quadrat. Data were collected in 1995, 1999, 2003 and 2004 (see Appendix 4-1). In 1995, only five known-age sites were sampled, and in 2003, only five plots per site were sampled.

As taxonomic uncertainties abound in the identification of non-native species, only those species listed on the Conservation of Agricultural Resources Act – South Africa (1983) or the South African Plant Invaders Atlas (listed in Henderson 2007) were considered non-native. This yielded a species pool of 15 non-natives from 10 families; these are listed in Appendix 4-2.

To address our first question with regard to the convergence of herbaceous plant communities in rehabilitating coastal dune forest sites we grouped survey plots into five age categories: 3 to 5, 6 to 10, 11 to 15, 16 to 20, and 21 to 27 years old. We do not include data from the first two years of regeneration because this stage is influenced by the initiation of restoration and the exotic annual species deliberately seeded by management are present in the species community. After three years, these species are no longer present in the community. As the number of plots per age category varied, we randomly selected 100 pairs of plots in each age category and assessed the amount of compositional dissimilarity between them using the Bray-Curtis dissimilarity measure. Bray-Curtis returns a value between 0 and 1, where a value of 0 means that the two plots share the same species at the same abundance, and a value of 1 means that the two plots do not have any species in common. We used Analysis of Variance (ANOVA) with Tukey's multiple comparison post-hoc test to assess differences in the mean similarity between age categories.

We used Bray-Curtis dissimilarity to assess progression between regenerating sites and the regional reference site. We first calculated the mean abundance of all species recorded in the undisturbed Sokhulu forest. We then assessed dissimilarity between all plots in the regenerating sites and these mean abundance values. The relationship between site age and the Bray-Curtis dissimilarity was tested using the Spearman's rank correlation coefficient. The mean dissimilarity between plots within the regional reference site was also calculated to provide an indication of the variation inherent in it. For a rehabilitating site to be considered successfully rehabilitated it must consistently fall within this range of dissimilarity (see Chapter 7 of this thesis).

To visualise patterns of species composition in regenerating and the reference site we used Non-Metric Multidimensional Scaling (NMDS). We used the “MetaMDS” function in the “VEGAN” package (Oksanen et al. 2008) using the R statistical software (v. 2.8.1; R Core Team Development 2008). We used the mean species abundance values for each site per survey year for the NMDS and joined survey years for each regenerating site together with a line for ease of visual interpretation. Patterns of community composition shown in the NMDS were confirmed using ANOSIM, analysis of similarity (using the function ‘anosim’ in R’s VEGAN package).

In order to identify which species contribute the most to dissimilarity between regenerating sites and the regional reference site we used SIMPER analysis (Similarity percentages) in Primer version 5.0. This analysis determines the percentage contribution by each species to dissimilarity between samples. We wished to identify which species are contributing the most to the dissimilarity to determine if non-native species divert regenerating trajectories of coastal dune forest.

Results

We recorded 150 species in the herbaceous layer of regenerating coastal dune forest, 15 of which were non-natives.

Are successional trajectories convergent?

The herbaceous plant community within regenerating coastal dune forest appears to differ greatly at early stages of regeneration, but as sites age the composition becomes increasingly similar but is still approximately at 60 % dissimilarity in the oldest plots. Mean dissimilarity differed significantly between age categories (ANOVA, $P<0.05$; Fig. 4-2). Plots in the youngest age category (3 to 5) shared on average 20 % of species in common. This did not differ significantly from the mean value in the 6 to 10 and 11 to 15 year categories, where plots shared 17 % and 24 % of species respectively (Tukey's post hoc test; $P>0.05$; Fig. 4-2). Plots in the 16 to 20 year category shared 29 % of species, this was significantly different from all but the 11 to 15 year category (Tukey's post hoc test; $P<0.05$; Fig. 4-2). In the oldest category (21 to 27 years old) plots shared 46 % of species and this was significantly different from all other age categories (Tukey's post hoc test; $P>0.05$; Fig. 4-2).

The NMDS plot illustrates the convergence between rehabilitating sites (Fig. 4-3). The stress of the NMDS ordination was relatively high (>20 %) with a two-dimensional ordination (i.e., $k = 2$) we therefore increased the number of axes to three ($k = 3$; Zuur et al. 2007; Fig. 4-3). Sites at younger stages of regeneration are found on the left-hand side of the plot and do not overlap with one another suggesting that they have few species in common. As the sites age (trend toward the right-hand side of the plot) they increasingly overlap suggesting species composition is similar and convergent.

Are rehabilitating sites progressing toward the reference site?

The species composition of all but the oldest rehabilitating site (Site 1) progressed towards that of the Sokhulu forest as sites increased in age (Fig. 4-4; Spearman's Rank Correlation test; Site 1: rs = 0.07, n = 35, $p>0.05$; Site 2: rs = -0.44, n = 34, $p<0.05$; Site 3: rs = -0.44, n = 35, $p<0.05$; Site 4: rs = -0.78, n = 35, $p<0.05$; Site 5: rs = -0.76, n = 35, $p<0.05$; Site 6: rs = -0.43, n = 24, $p<0.05$). However, none of the sites shared greater than 15 % of species that are found in plots in the Sokhulu forest, so whatever progression there was, appeared to be slow. The oldest sites (Site 1 and Site 2) become even more dissimilar in the last two surveys (i.e. they deviate from the reference site). The mean Bray-Curtis dissimilarity within the reference site was quite high at 0.57 ± 0.13 (± standard deviation, Fig 4-4). The NMDS plot (Fig. 4-3) confirmed the pattern of deviation away from the Sokhulu forest. The ANOSIM showed that there was a significant difference in composition between plots in the rehabilitating sites and the regional reference site ($R = 0.62$; $P<0.001$).

Which species contributes the most to dissimilarity?

Species responsible for the greatest amount of dissimilarity between regenerating sites and the reference site appear to represent successional changes in the younger age categories (Table 4-1). Species adapted to high salt concentrations (such as *Dactyloctenium geminatum*) and grassland species were responsible for the greatest amount of dissimilarity in the youngest age categories.

As categories increased in age, the species that were responsible for the greatest amount of dissimilarity between regenerating plots and the Sokhulu forest reference site were those adapted to open woodland (such as *Asystasia gangetica* and *Ipomoea ficifola*), then species adapted to more closed woodland (*Pupalia lappacea* and *Laportea peduncularis*; Table 4-1). The lack of *Isoglossa woodii* in the regenerating coastal dune forest plots contributed the most or second most to dissimilarity between the undisturbed forest and all except the oldest age category (Table 4-1). Only three non-native species contributed to dissimilarity between rehabilitating sites and the Sokhulu forest reference site. These included *Commelina benghalensis*, which contributed 3.18 % of dissimilarity between the 3 to 5 year old age category and Sokhulu forest (Table 4-1). *Achyranthes aspera* contributed 9.88 and 10.09 % to dissimilarity in the 16 to 20 and 21 to 27 year categories, respectively (Table 4-1). *Chromolaena odorata* contributed 2.19 % to dissimilarity between the 21 to 27 year old category (Table 4-1).

Discussion

The herbaceous plant community of rehabilitating coastal dune forest appeared to converge (i.e. become increasingly uniform as sites increased in age). Despite appearing to initially progress toward the undisturbed reference site, the trajectory of the rehabilitating sites was deviant (i.e. they did not progress toward the undisturbed reference site). This confirms the slow rate of progression found by Wassenaar et al. (2005) who used a chronosequence approach to assess the regeneration of the herbaceous layer in coastal forest. Patterns of convergence and deviation from progression as observed here are often attributed to the invasion and dominance of non-native species in regenerating sites (for example, Matthews & Spyreas 2010; Tognetti et al. 2010). In rehabilitating coastal dune forests, however, non-native species did not contribute the most to dissimilarity between plots in rehabilitating sites and the undisturbed Sokhulu forest. Although, the non-native species *Achyranthes aspera* did contribute second most to similarity in the 21 to 27 year old category. We therefore, need to ascertain the plausible causes of convergence between rehabilitating sites and deviation away from the Sokhulu forest.

Causes of convergence

Convergence may occur where regional species pools are small because sites quickly exhaust the available species and therefore become increasingly similar in species composition (Cutler 2010). This is unlikely, however, to be contributing toward convergence in our study. The species pool of the coastal dune forest herbaceous plant community is not small (150 species) when compared to those in far northern latitudes, the number of species, for example, was three times that of volcanic primary successions in Iceland (Cutler 2010).

Convergence between rehabilitating sites may occur where the factors that determine species composition in the early stages of regeneration are stochastic and those that determine composition in the later stages of regeneration are homogeneous (Lepš & Rejmanek 1991). For example, the species composition in the early stages of succession may be determined by the proximity of seed sources (Lanta & Lepš 2009). Later in succession habitat factors (such as soil depth) may supersede the initial chance factors as determinants of species composition (Lepš & Rejmanek 1991). The pattern of convergence within rehabilitating sites matches this scenario. There were high levels of dissimilarity between plots in the youngest age categories. In the older categories dissimilarity decreased, meaning that the composition of plots in these later stages of succession were more uniform. The homogeneous factor is currently unknown, but we can assume that the canopy structure influences the composition of the herbaceous layer. After the first 5 years of succession the species responsible for similarity within age categories were similar in all the age categories. These species were *Digitaria diversinervis*, *Laportea* *peduncularis* and *Asystasia gangetica*, which are all adapted to woodland or forest edge habitats (Pooley 1998). The canopy conditions across all sites may be similar, leading to homogenization of the species community and, therefore, convergence.

Dispersal and disturbance also may have attributed to the convergence of rehabilitating sites. Where there are few barriers to dispersal, convergence is likely as all sites can potentially share the same set of species (Lepš & Rejmanek 1991). The majority of species in the herbaceous layer of regenerating coastal dune forests are wind or bird dispersed, so one would expect that seeds would be spread across all sites. In addition, sites are in close proximity to one another and therefore, species that rely on relatively shorter distance dispersal, such as ballistic dehiscence (for example *Asystasia gangetica*), may reasonably be expected to have few barriers to dispersal. However, we still need to investigate the dispersal constraints of the herbaceous layer. Disturbance may also contribute to convergence, and one of the main forms of disturbance within rehabilitating sites is tree fall (see Chapter 5). Light gaps being created within the canopy in the later stages of rehabilitation may facilitate the persistence of the woodland or forest edge species and be the ultimate cause of convergence.

Causes of deviation

Deviation in the trajectory of rehabilitating sites from the Sokhulu forest can also be explained in terms of the habitat affinities. *Dactyloctenium geminatum* contributed to the most dissimilarity between the rehabilitating sites and the Sokhulu forest in the youngest plots (3 to 5 years old). This grass species is adapted to harsh environments such as those found on the seashore (Pooley 1998). It is, therefore, not surprising that this species is not found in mature forest. *Isoglossa woodii* contributed the most or second most to dissimilarity between all but the oldest age category and the Sokhulu forest. This species was at higher abundance in the Sokhulu forest and is actually yet to establish within the regenerating sites. *Isoglossa woodii* is the dominant understorey plant species in coastal dune forest and plays an important role in forest dynamics (Griffiths et al. 2007). The reasons for the absence of this species in regenerating coastal dune forest needs to be investigated. The species may have not been able to disperse to the regenerating sites as it is a dehiscent only spreading its seed a small distance from the parent plants. The Sokhulu forest is far from the rehabilitating sites, but other populations of *Isoglossa woodii* are found in remnant forest adjacent to some of the rehabilitating sites, albeit at much lower abundances (Conservation Ecology Research Unit, University of Pretoria unpublished data). Additionally, conditions in the regenerating sites may not yet be suitable for its establishment. The higher abundances of *Digitaria diversinervis*, *Laportea peduncularis*, and *Asystasia gangetica* in the regenerating sites also contributed to the deviation from the Sokhulu forest. Canopy conditions in regenerating sites may be ideal for these woodland adapted species explaining their dominance, where as in the Sokhulu forest, canopy conditions suit forest adapted species.

The role of non-native species

The only non-native species to contribute any dissimilarity were *Commelina benghalensis*, *Achyranthes aspera*, and *Chromolaena odorata* (Henderson 2007). *Commelina benghalensis* contributed to dissimilarity between the youngest plots and the Sokhulu forest. This species occurs in disturbed areas, and is particularly associated with cultivated land but can be found along forest edges (Pooley 1998). *Commelina benghalensis* is shade tolerant so it is surprising that it does not continue to contribute to dissimilarity between the older regenerating plots and the Sokhulu forest. The contribution of *A. aspera* to dissimilarity between regenerating plots and Sokhulu forest increased from 5 to 10 % in the two oldest age categories. This species has wide tolerances to shade, but prefers open woodland sites (Sager et al. 2008). Another species with wide shade tolerance is *C. odorata* which only contributed 2.19 % to dissimilarity between the oldest age category and the Sokhulu reference site. This species may be inhibited by closed canopies (De Rouw 1991). The oldest regenerating coastal dune forests resemble open woodland at this stage in their redevelopment, which may explain the high abundance of these species when compared to the Sokhulu forest reference site. The persistence of non-natives is not necessarily a precursor to a loss of native biological diversity and at present, non-natives do not appear to be the main drivers of deviation from progression between rehabilitating sites and the undisturbed Sokhulu forest. It is important, however, that we continue to monitor the situation.

The future of coastal dune forest rehabilitation

In answer to the three questions we originally posed, successional trajectories in the herbaceous plant community in rehabilitating coastal dune forest sites were convergent. Rehabilitating coastal dune forest sites, however, despite initially appearing to do so, did not progress towards the undisturbed reference site. Contrary to our expectations, non-native species did not contribute the most to dissimilarity. The deviation from the reference forest is attributable to the higher abundance of a native forest specialist in the Sokhulu forest and the higher abundances of native woodland or forest edge adapted species in the rehabilitating sites. Throughout a successional sere, one would expect that species' relative abundances would shift as the habitat conditions become optimal. The diversion from the undisturbed reference site may therefore be only temporary. Successional trajectories may be non-linear (Matthews & Spyreas

2010). We cannot be certain of the factors driving the convergence/deviation pattern we have observed here, but we continue to monitor the community composition of rehabilitating sites with reference to the Sokhulu forest. Using a process of adaptive management we can react to continued deviation through management action. Presently, we can initiate research initiatives to investigate questions of dispersal and habitat affinities of some key herbaceous plants.

Restoration managers must be aware that although idealized trajectories (as those indicated on Fig.4-1) are linear, changes in the abundance of species across successional time may cause non-linear trajectories to be a reality. It is therefore difficult to decide if and when to invoke more intensive management (such as restoration plantings), which aim to force regeneration trajectories back on course toward reference sites. Perhaps one way to decide if intensive management is required is to identify the species responsible for driving deviant trajectories as we have done here. Only if these species are new additions to the species pool (i.e. after the assembly of the reference community) should management be considered.

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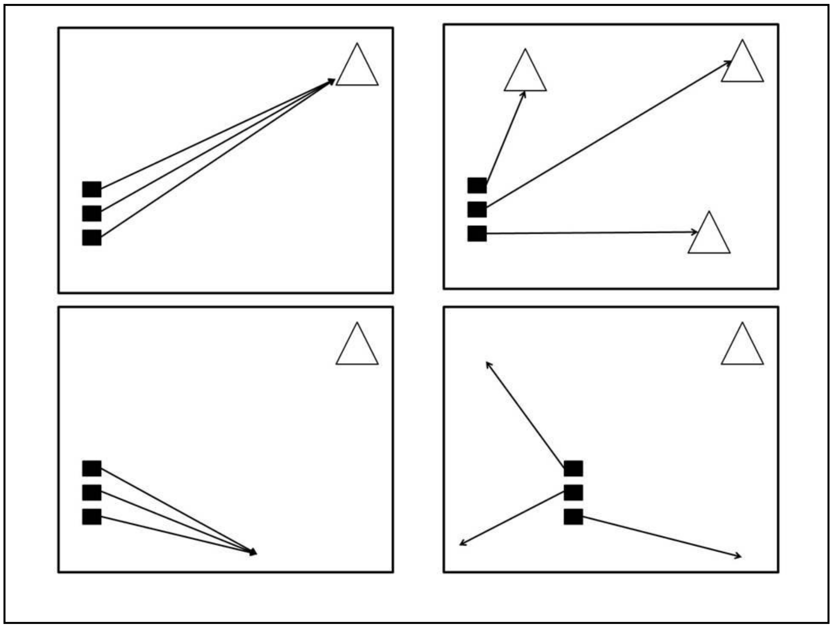


Figure 4-1. The conceptual model of convergence and progression of Matthews & Spyreas (2010). The top-left panel illustrates the convergence of the rehabilitating sites (black squares) and progression toward an undisturbed reference site (open triangles). The top-right panel illustrates divergence between the rehabilitating sites but progression toward a series of acceptable reference sites. The bottom-left panel illustrates convergence between rehabilitating sites but progression away from the reference site to an entirely novel species composition. Finally, the bottom-right panel which shows divergence between rehabilitating sites each of which heads away from the reference site. Reproduced with permission from John Wiley and Sons (License Number 2758771123540, 30th September).

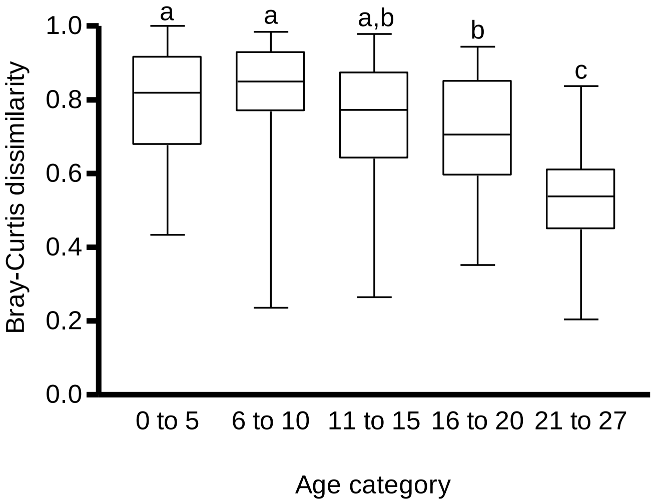
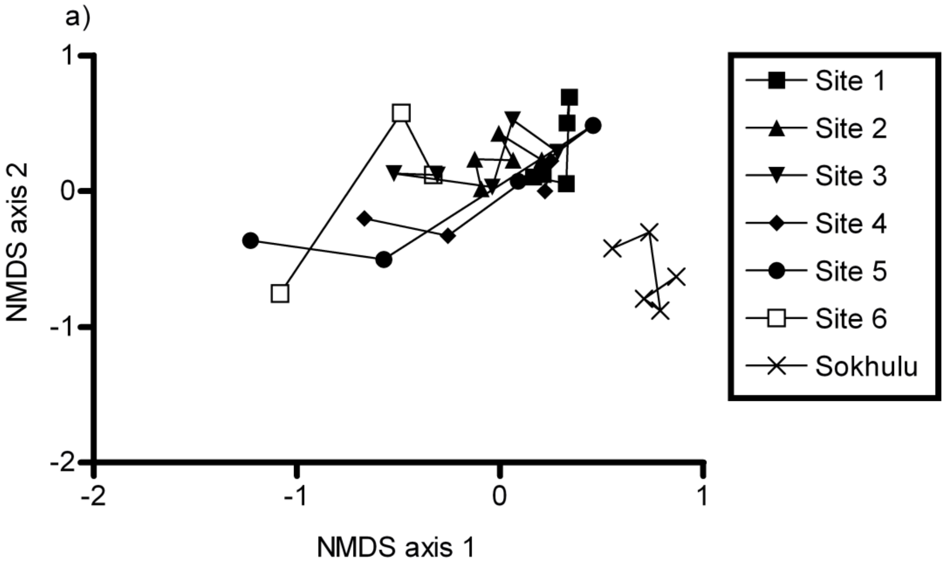


Figure 4-2. Box and whisker plot showing the mean Bray-Curtis dissimilarity between plots within age categories. Letters indicate the results of a Tukey's post hoc test, the same letter indicates age categories whose means do not differ significantly.



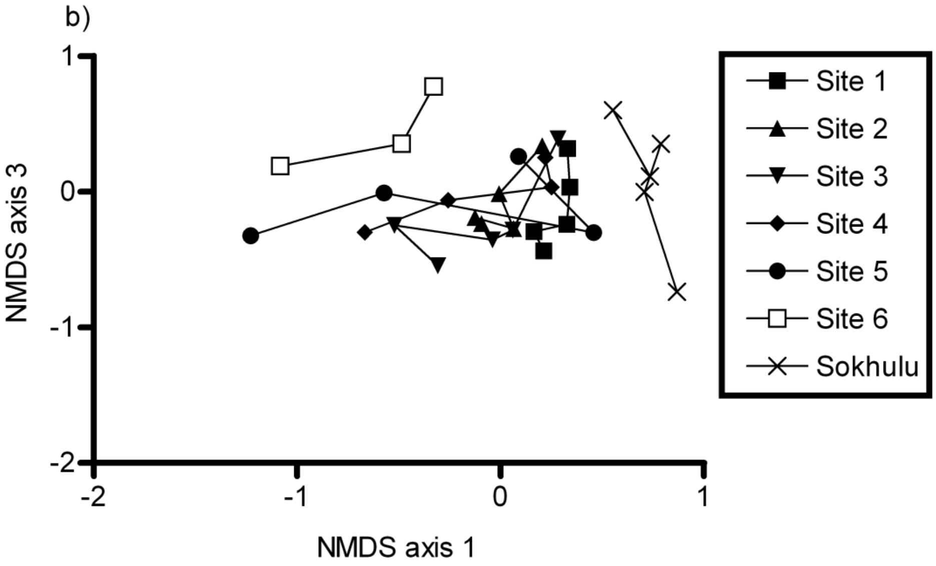


Figure 4-3. Non-metric Multidimensional Scaling (NMDS; stress = 11.70; non-metric fit r^2 = 0.99; linear fit r^2 = 0.95) plot (showing axis 1 versus 2 (a) and axis 1 versus axis 3 (b)). Survey events are linked within sites using a line.

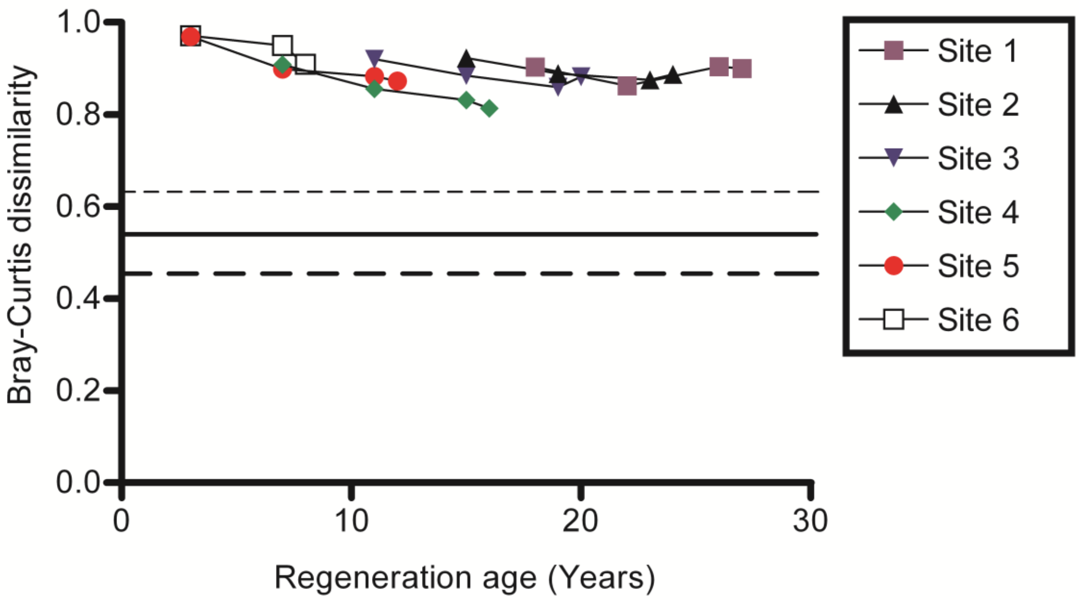


Figure 4-4. Bray-Curtis dissimilarity between regenerating sites and the reference site (Sokhulu forest). The points shown are the mean dissimilarity values per survey year for each site (for clarity of visual interpretation). The solid horizontal line indicates the mean dissimilarity within the regional reference site and the dotted horizontal lines indicate the variation about this mean.

Table 4-1. Results of a SIMPER analysis showing the 10 species with the highest contribution to Bray Curtis dissimilarity between each age category and the undisturbed Sokhulu forest.

Age category (years)	Species	Mean Abundance	Reference site mean abundance	Mean Dissimilarity	Standard deviation	Percentage contribution to dissimilarity	Cumulative percentage
3 to 5	*Dactyloctenium geminatum*	38.82	0	10.01	0.95	10.39	10.39
	Isoglossa woodii	0	7.78	9.09	0.98	9.44	19.83
	Panicum maximum	21.85	0	5.4	0.76	5.61	25.44
	Pupalia lappacea	0.68	6.87	3.9	1.07	4.05	29.49
	Senecio sp.	13.62	0	3.27	0.79	3.4	32.89
	Digitaria diversinervis	12.91	0.93	3.1	0.55	3.21	36.1
	Commelina benghalensis	11.79	2.35	3.06	0.67	3.18	39.28
	Pyrenacantha scandens	0	1.65	2.84	1.09	2.94	42.22
	Cyphostemma woodii	0	0.74	2.78	0.68	2.88	45.1
	Conyza albida	10.53	0.02	2.63	0.59	2.73	47.83
6 to 10	*Isoglossa woodii*	0	7.78	10.55	0.86	11.11	11.11
	Digitaria diversinervis	28.23	0.93	6.23	0.89	6.56	17.67
	Pupalia lappacea	3.56	6.87	4.75	0.99	5	22.67
	Asystasia gangetica	22	0.76	4.34	0.73	4.57	27.24
	Pyrenacantha scandens	0.1	1.65	3.31	0.92	3.49	30.73

	Cyphostemma woodii	0.23	0.74	3.31	0.61	3.48	34.21
	Ipomoea ficifolia	11.49	2.22	3.2	0.69	3.36	37.57
	Dactyloctenium australe	7.41	3.02	2.85	0.54	3	40.57
	Mariscus dregeanus	9.95	0	2.81	0.55	2.96	43.53
	Aneilema aequinoctiale	10.15	0.7	2.65	0.63	2.79	46.32
11 to 15	*Isoglossa woodii*	0	7.78	9.98	0.88	10.77	10.77
	Laportea peduncularis	37.1	8.44	8.46	1.05	9.14	19.91
	Dactyloctenium australe	33.5	3.02	8.08	0.94	8.72	28.63
	Digitaria diversinervis	29.13	0.93	7.17	0.83	7.74	36.37
	Pupalia lappacea	4.23	6.87	4.21	0.98	4.55	40.92
	Pyrenacantha scandens	0.11	1.65	3.12	0.94	3.37	44.29
	Cyphostemma woodii	0.47	0.74	3.11	0.62	3.35	47.64
	Panicum maximum	10.24	0	2.8	0.48	3.02	50.66
	Ipomoea ficifolia	10.13	2.22	2.57	0.7	2.77	53.43
	Asystasia gangetica	10.41	0.76	2.53	0.55	2.73	56.16
16 to 20	*Isoglossa woodii*	0	7.78	9.32	0.82	10.2	10.2
	Digitaria diversinervis	46.07	0.93	9.03	1.22	9.88	20.08
	Laportea peduncularis	43.73	8.44	8.24	1.27	9.01	29.09
	Achyranthes aspera	26.36	0.39	5.38	0.95	5.89	34.98
	Dactyloctenium australe	24.36	3.02	5.03	0.77	5.51	40.49
	Asystasia gangetica	25.16	0.76	4.93	0.8	5.39	45.88
	Pupalia lappacea	15.42	6.87	4.47	1.02	4.89	50.77

	Pyrenacantha scandens	0.11	1.65	2.93	0.87	3.2	53.97
	Cyphostemma woodii	0.2	0.74	2.9	0.58	3.18	57.15
	Secamone filiformis	12.11	0.52	2.52	0.87	2.76	59.91
21 to 27	*Digitaria diversinervis*	70.63	0.93	12.05	2.36	13.13	13.13
	Asystasia gangetica	53.29	0.76	9.49	1.3	10.34	23.47
	Achyranthes aspera	53.27	0.39	9.26	1.58	10.09	33.56
	Laportea peduncularis	51.86	8.44	8.14	1.51	8.87	42.43
	Isoglossa woodii	0	7.78	6.42	1	6.99	49.42
	Dactyloctenium australe	22.33	3.02	3.94	0.83	4.29	53.71
	Aneilema aequinoctiale	20.69	0.7	3.6	0.95	3.93	57.64
	Pupalia lappacea	22.14	6.87	3.6	1.08	3.92	61.56
	Chromolaena odorata	11.22	0	2.01	0.53	2.19	63.75
	Pyrenacantha scandens	0	1.65	1.99	1.11	2.17	65.92

Chapter 5

The role of canopy gaps in the regeneration of coastal dune forest

Abstract

Question: Are gap-dynamics determining the composition of coastal dune forest regenerating after strip-mining?

Location: Regenerating coastal dune forests, Richards Bay, KwaZulu-Natal Province, South Africa

Methods: The proportion of the canopy in gap-phase was estimated from 20 m wide strip-transects in three known-age regenerating coastal dune forest sites. For each gap, we measured the area, the species responsible for gap creation (gap-maker), the species most likely to reach the canopy (gap-taker) and the composition of adults, seedlings and saplings. We paired each gap with an adjacent plot of the same area that was entirely under intact canopy sampled in the same way.

Results: The majority of species had higher abundances under canopy gaps and in the largest canopy gaps. *Acacia karroo* was the most abundant gap-maker, but the probability of replacement was low even in the largest gaps. The most abundant gap-takers were forest pioneers with wide tolerances for light. Shade tolerant species were rare in the community.

Conclusions: The patterns of species composition within regenerating coastal dune forest are a response to the canopy characteristics and represent an early stage in forest succession. Gap-dynamics did not fully explain regeneration dynamics in coastal dune forest as canopy disturbance punctuated succession rather than resetting it. The future composition of the canopy should favour shade tolerant species.

Keywords: *Acacia karroo*, gap dynamics, habitat restoration, niche differentiation, shade tolerance, succession.

Introduction

Whitmore (1989) proposed that forest trees could be categorised in to two major groups of species, those whose seeds can germinate under intact canopy known as “climax” or more recently “shade-tolerant” species and those whose seeds cannot germinate under intact canopy, but require full sunlight, known as “pioneer” or “shade-intolerant” species. The maintenance of these two groups of species in the forest canopy is, according to gap-dynamics theory, the result of gap-phase regeneration, a small scale successional sequence that results in a new tree replacing the original canopy individual (Schnitzer & Carson 2001). This leads to a shifting mosaic of intact canopy and gaps over time as different individuals take advantage of a canopy gap, then eventually die allowing another individual to take its place in the canopy. Where small gaps in the canopy occur, shade tolerant species can recruit to the canopy from the sub-canopy (saplings) or the gap can close through lateral infilling (Rebertus & Veblen 1993; West et al. 2000). In large gaps, the change in light availability promotes the persistence of shade intolerant species allowing them to recruit to the canopy (Huston & Smith 1987).

The gap-dynamics paradigm has been questioned repeatedly, with some authors suggesting that it is irrelevant in determining composition of forest communities. In some mature tropical and sub-tropical forests, there is little niche separation and species have wide tolerances for light availability (for example, South African Plateau Forest, Midgley et al. 1995; South African Coastal Scarp Forest, Obiri & Lawes 2004; Panamanian Tropical Rainforest, Hubbell et al. 1999). In these forests, the composition of the tree community is unpredictable. The stochastic nature of canopy gap availability and recruitment limitation means that chance plays a greater role than determinism (see the review by Brokaw & Busing 2000). However, recently Chambers et al. (2009) showed that neutral or chance processes become less important and niche processes more important in determining species composition in central Amazonian forest along a gradient of increasing gap size.

Our interest in gap-dynamics stems from our experiences in a sere of regenerating coastal dune forest undergoing restoration after strip-mining (see study site description below and van Aarde et al. 1996a, b, c; Wassenaar et al. 2005). Mature coastal dune forest is characterised mainly by shade tolerant canopy and sub-canopy, but with some shade intolerant canopy species suggesting that a number of large disturbances do occur (Everard et al. 1995). In regenerating coastal dune forests, the pioneer species, *Acacia karroo*, currently dominates the canopy. As these individuals are senescent by about 30 or 40 years of age (Gourlay et al. 1996), we increasingly observe them falling and creating gaps in the canopy. If these large gaps promote the persistence of shade-intolerant pioneer species to the detriment of shade-tolerant forest species then the end-goal of a restored coastal dune forest could take a lot longer than we have previously predicted (between 38.7 and 40.5 years; Wassenaar et al. 2005). In addition, if large gaps do promote shade intolerant pioneers then *A. karroo* may replace itself leading to a stagnation of succession. The use of the *A. karroo* successional pathway post-mining has been criticised in the past for exactly this reason (West et al. 2000).

Here we intend to investigate if the gap-dynamics paradigm is relevant to the restoration of coastal dune forest. In particular, we wish to ascertain if tree species composition and richness differs significantly between canopy gaps and intact canopy and across a gradient of gap sizes. In addition, we wish to ascertain the probability that *A. karroo* will replace itself in the canopy. See Table 5-1 for a summary of our assumptions and expectations.

Methods

Study area

The study area was located to the north of the town of Richards Bay (28°43'S, 32°12'E) in the province of KwaZulu-Natal in the North-East of South Africa. Here the climate is humid and subtropical, with mean annual rainfall of 1458.0 ± 493.53 mm (mean ± SD, *n* = 34 years between 1976 and 2009; data courtesy of Richards Bay Minerals, RBM). Rainfall peaks in February and the mean temperature was 23.79 ± 3.40 °C (*n* = 3 years between 2006 and 2009; data courtesy of RBM). The mining company RBM aims to return indigenous coastal dune vegetation to one third of its mined area. The mining process (described in full in van Aarde et al. 1996a) destroys all vegetation in front of the mine-pond. Prior to mining topsoil is removed and stockpiled. Immediately after mining, sand dunes are mechanically re-shaped and the topsoil (seeded with exotic annual plants; sunhemps and sunflowers) is replaced and then stabilised using drift-fencing. After this initial kick-start, management is limited to the removal of non-native plant species and herbivores and restoration relies on natural successional processes (van Aarde et al. 1996a, c). Sampling took place in three regenerating coastal dune forest sites aged 33, 26, and 22 years old. Sites younger than this did not have a sufficient number of canopy gaps to allow analysis.

Gap sampling procedure

Strip-transects 20 m wide and separated by 50 m were walked in a North-South direction across the three regenerating coastal dune forest sites. Where we encountered a canopy gap (see definition below) which had its central point within the 20 m strip we recorded its size and sampled vegetation within it (see below for sampling description). This gap-centre method avoids a potential sampling bias toward larger canopy gaps (Nakashizuka 1984). We calculated the fraction of the site that was under canopy gap as the sum of the areas of all gaps sampled divided by the total area of the strip transects (Runkle 1992).

Defining and measuring a canopy gap

A canopy gap was defined as an opening in the canopy stratum formed by the death of a part of a tree, a single tree or a group of trees in which no trees are greater than two-thirds the height of the canopy (Runkle 1981). In each gap, we identified and measured the longest axis of the gap, and a number of equally spaced "offset" lines that bisected the longest axis. We then summed the length of the "offset" lines and multiplied this figure by the distance between the "offset" lines. Therefore, canopy gap area (*A*) was calculated as: $A = I^* (C+D+E)$, where I is the interval between offset lines and *C*, *D*, *E etc* are the lengths of the offset lines.

Sampling within canopy gaps and intact canopy plots

We paired each gap with an adjacent plot that was entirely under intact canopy, these plots were the same area as the canopy gap and sampled in the same way. We identified and counted all tree species in each gap and intact canopy plot. In addition, we measured the height and diameter at breast height (DBH) of each individual. We recorded trees as belonging to one of three size classes; we refer to these size classes as "seedlings" (<15 cm in height), "saplings" (>15 cm and <5 cm DBH) and "adults" (>15 cm and >5 cm DBH but <2/3 canopy height). It is important to note that we used these terms nominally and made no assumptions with regard the age of individual trees, but rather their size; these two traits are not necessarily related.

Gap-makers & gap-takers

The cause of a canopy gap was categorised as being either a fallen tree, a crown-collapse, or a standing dead tree. We recorded the species that had caused the gap (through its death) and the tallest seedling/sapling/adult in the gap that may replace the gap-maker (the gap-taker). An individual was only considered a gap-taker if it had the potential to reach the canopy.

Data Analysis

For each gap and intact canopy plot, we calculated species richness (using rarefaction), the abundance of stems and density of stems (per m^2). We used linear regression to assess the correlation between species richness, abundance and density of stems with gap area. In order to assess if the size of a canopy gap influenced species composition we first categorised the size of canopy gaps in to one of four size classes. We used the quartiles of the range of gap areas to define these gap size classes - small gaps were <94 m^2, medium gaps were between 94 and 156 m^2, large gaps were between 156 and 286 m^2 and very large gaps were >286 m^2. Our data did not allow for the use of Canonical Correspondence Analysis so we followed the advice of Zuur et al. (2007) and used the Analysis of Similarities (ANOSIM). We used ANOSIM to test for differences in the species composition between four size classes, and between canopy gaps and intact canopy plots. Replacement probabilities were estimated by counting the number of gap-takers of a particular species expressed as a proportion of gap-makers replaced (Midgley et al. 1995). All analyses except linear regression were carried out in the R programme (R foundation for Statistical Computing, Vienna, Austria, URL http://www.R-project.org). We used Graphpad Prism (version 3.03, Graphpad Software, San Diego, California, US, URL http://www.graphpad.com) for the linear regression analyses.

Results

Gap characteristics and causes

Gap characteristics for each site are described in Table 5-2. Median gap size differed significantly between the three sites (Kruskal-Wallis test; $P<0.001$). The post-hoc test showed that gaps in the 33 year old site were significantly larger than in the other two sites, but gap size in the 26 and 22 year old sites were similar. The percentage of the site canopy composed of gaps increased with increasing regeneration age. The largest gaps were found in the 33 and 22 year old sites. The 26 year old site did not have any gaps larger than 450 m^2 (Figure 5-1).

Five species were responsible for the creation of canopy gaps; *A. karroo*, *Allophylus natalensis*, *Apodytes dimidiata*, *Brachylaena discolor*, and *Casuarina equisetifolia*. However, *A. karroo* was by far the most abundant gap-maker composing 99.00 % of all gap-makers (n = 402). The mean number of gap-makers per gap was 2.83 trees. There was no significant difference between the number of gap-makers in each site (Kruskal-Wallis test; $P>0.05$). The median gap-makers in all sites were 2 trees per gap. The number of gap-makers per gap increased with increased gap area (linear regression; $P<0.05$). There was at least one fallen tree in each canopy gap, and fallen trees made up 89.80 % of all gap-makers (n = 402). Crown-collapse made up 8.45 % of gap-makers and the remainder (1.74 %) were standing dead.

Only 11 species made up the 165 gap-takers recorded, these were as follows; *A. karroo*, *Albizia adianthifolia*, *A. natalensis*, *A. dimidiate*, *Bridelia micrantha*, *Celtis africana*, *Clerodendrum glabrum*, *Ekebergia capensis*, *Mimusops caffra*, *Psydrax obovata* and *Trichilia* *emetica*. The most abundant gap-takers were *M. caffra* (25.45 %), *C. africana* (21.21 %) and *E. capensis* (12.12 %). The probability that the gap-taker would be the same species as the gap-maker was zero in the smallest and medium sized canopy gaps (<94 m^2 and between 94 and 156 m^2 respectively). In large (156 to 286 m^2) and very large (>286 m^2) canopy gaps the probability was 0.10 and 0.16 respectively. The probability that *C. africana* being the gap-taker decreased with increased gap size (0.33, 0.31, 0.23, and 0.13 in order from the smallest to very large gap sizes). The probability of *M. caffra* being the gap-taker increased with increasing gap size, but was lower in the very large gaps (0.17, 0.28, 0.33, and 0.21 respectively). Finally, the probability of *E. capensis* being the gap-taker increased with increased gap size (0.0, 0.03, 0.13, and 0.19 respectively).

Tree species richness, abundance, and density

In total, we recorded 53 species, 38 of these were present in both canopy gaps and under intact canopy. Five species (*Diospyros natalensis*, *Dovyalis caffra*, *Maytenus sp.*, *Turraea floribunda*, *Xylotheca kraussiana*) were found uniquely in canopy gaps and nine (*Antidesma venosum*, *Diospyros rotundifolia*, *Drypetes gerrardii*, *Dovyalis zeyheri*, *Acacia sp.*, *Harpephyllum caffrum*, *Margaritaria discoidea*, *Memecylon natalensis*, *Pavetta revoluta*) uniquely under intact canopy. However, all these species were relatively rare (<10 individuals recorded).

For both adults and saplings in canopy gaps and under intact canopy, species richness (per stem), abundance and density significantly increased with gap size (linear regression, $P<0.05$). Seedlings however, showed no significant relationship between sample area and richness, abundance, or density (linear regression, $P>0.05$).

The richness (species per stem), abundance and density of adults did not differ significantly between canopy gaps and under intact canopy (Wilcoxon rank – sum test, $P>0.05$). In contrast, sapling richness, abundance and density were all significantly greater in canopy gaps than under intact canopy (Wilcoxon rank – sum test, $P<0.05$). For the seedlings, species richness was greater in canopy gaps than under intact canopy (Wilcoxon rank – sum test, $P<0.05$), however abundance and density were not significantly different (Wilcoxon rank – sum test, $P>0.05$).

Species composition – gap area

We considered species with abundances of less than 10 individuals as rare and these were excluded from subsequent analysis. The composition of both adults and saplings differed significantly between gap size categories (ANOSIM, $P<0.05$). Of the nine adult species recorded, five species were equally abundant in all canopy-gap size classes (Kruskal-Wallis test, $P>0.05$). These included *Canthium inerme*, *C. africana*, *Grewia occidentalis*, *Teclea gerrardii* and *Trema orientalis* (see Table 5-3). The remaining four were all significantly more abundant in large or very large gaps (Kruskal-Wallis test, $P<0.05$). These included *B. discolour*, *A. natalensis*, *M. caffra* and the non-native *Cestrum laevigatum* (Table 5-3). Only one individual adult *A. karroo* was recorded in a canopy gap. Most (17 out of 23) of the saplings species recorded in canopy gaps were recorded in all gap sizes, and half (12 out of 23) showed significant differences in the mean number of stems (per 100 m) across the gradient of gap sizes (Kruskal-Wallis test, $P<0.05$). Five species were not recorded in the smallest gap size category (<94 m^2), these were *A. karroo*, *E. capensis*, *C. laevigatum*, *Peddia africana*, and *Psychotria capensis*. Seedling composition showed no significant difference between gap size categories (ANOSIM, $P>0.05$).

Seedlings were not found in the smallest gap size category (<94 m^2) and we did not find seedlings in the 22 year old site.

The composition of adults differed significantly between canopy gaps and intact canopy plots in the 33 year old site only (ANOSIM, P<0.05). Of the 9 adult species, 6 had significantly greater abundances in plots in canopy gaps (Wilcoxon rank – sum test, P<0.05). These were *C. inerme*, *B. discolour*, *A. natalensis*, *M. caffra*¸ *C. laevigatum* and *G. occidentalis* (Table 5-3). The 33 and the 22 year old site showed significant difference in the composition of saplings in canopy gaps compared to intact canopy plots (ANOSIM, P<0.05). There was no significant difference in composition in the 26 year old site (ANOSIM, P>0.05). Ten of the 23 sapling species were equally abundant in canopy gaps and in intact canopy plots. The remaining 13 species were more abundant in canopy gaps than under intact canopy.

There was no significant difference in the seedling composition between canopy gaps and under intact canopy in all sites (ANOSIM, P>0.05). However, only one species (*Zanthoxylym capense*) had seedlings in both canopy gaps and under intact canopy.

Discussion

In regenerating coastal dune forest, the canopy consists almost exclusively of a single species, *A. karroo*, and the death of these trees effects the species composition of dune forest and may shape the future success of restoration. The majority of species (15 out of 23) showed niche-differentiation mostly having higher abundance in canopy gaps, particularly large or very large gaps. Shade intolerant species dominate the regenerating sites. This may be considered alarming in the context of a restoration project that aims to restore coastal dune forest, especially considering that mature coastal dune forest is characterised by shade tolerant species in its canopy and sub-canopy layers. Shade intolerant species are rare in mature coastal dune forest, relying on infrequent large scale disturbances to reach the canopy (Everard et al. 1995). However, as we shall show here this predominance of shade intolerant species appears to be a primary stage in the succession of coastal dune forest.

An individual *A. karroo* rarely dies alone and the resultant large multi tree-fall gaps promote the persistence of shade intolerant species (Everard et al. 1995). The majority of canopy gaps in regenerating coastal dune forest formed through tree-fall. Fallen trees cause a larger disturbance in the canopy than standing dead trees or branch-fall due to the physical action of the tree falling, which can damage understorey vegetation. In addition, a fallen tree will no longer intercept light. The short lifespan of *A. karroo* may mean that gaps and multi-tree gaps open more readily in regenerating coastal dune forest than in mature forests. The proportion of canopy under gap and the mean gap area were both relatively large when compared to other forests (see Table 5-4), with the exception of boreal forests. Boreal forests are similar to regenerating coastal dune forest in that they have few canopy dominant species and are characterised by large scale disturbance such as fire, timber extraction, and insect outbreaks (see Table 5-4). These characteristics of the canopy of regenerating coastal dune forest may explain the predominance of shade intolerant trees.

In the 26 and 22 year old regenerating sites, the adult size class did not differ significantly between intact canopy and canopy gaps. This suggests that the adult size class is the same as the sub-canopy prior to the creation of the canopy gap. However, in the 33 year old regenerating site, the adult size class differed significantly between intact canopy and canopy gaps. Despite ensuring that an intact gap-maker was present in each recorded gap it appears that in the oldest site, gaps are old enough to have influenced the adult tree composition. Gap expansion may explain this phenomenon. The original gap maker may have decomposed, and subsequent trees fallen in to the gap. This cascading disturbance is characteristic of some forests where the probability of mortality is greater at the edge of a canopy gap when compared to those in intact canopy (Vepakomma et al. 2010). The greater mean gap size in the oldest site may also be a result of this gap expansion.

Sapling composition differed significantly between intact canopy and canopy gaps for both the 33 and 22 year old sites. This difference fits with the gap-dynamics paradigm. Most species were present in both intact canopy and under canopy gaps, but abundances between the two canopy types differed significantly. Very few species were more abundant under intact canopy at any size class. This finding agrees with Ruger et al. (2009) who showed that in tropical rainforest the majority of the tree community regenerate better in higher light. Very few species (20 %) regenerated under light conditions lower than the typical tropical forest understorey conditions. Species in regenerating coastal dune forest appear to have wide tolerances for light conditions but regenerate with greater abundance under increased light conditions, as is indicated by the higher abundances in larger canopy gaps for the majority of species.

Interestingly, the 26 year old site did not show any difference between canopy gaps and intact canopy. One plausible explanation for this may stem from the frequency distribution of gap sizes in this site compared to the other two sites. The 26 year old site had fewer large gaps and no gaps greater than 425 m^2. Recently, Chambers et al. (2009) suggested that in small gaps (typical of most forest types) neutral or stochastic processes (e.g. recruitment limitation) determine species composition. In large gaps however (defined as >1000m^2 by Chambers et al. 2009), pioneer species have a competitive advantage over other species. In our regenerating sites, the smaller gaps may have had similar light conditions to intact canopy where species tended to have similar abundances in both gap and intact canopy suggesting that conditions were similar and tolerances wide. However, in the largest gaps situated in the 22 and 33 year old sites, there was a greater differentiation and more pioneer species (such as *A. karroo*, *C. inerme*, and *C. laevigatum*).

In regenerating coastal dune forest seedlings were most abundant in canopy gaps. They were absent from small gaps, and with the exception of *P. africana* and *Z. capense*, were absent from intact canopy. This again suggests that the majority of species in the regenerating coastal dune forest tree community are shade intolerant and very few can tolerant low light levels.

This apparent lack of shade tolerant species is indicative of the characteristics of the current canopy. This canopy, dominated by *A. karroo*, will not replace itself after its senescence. *Acacia karroo* is a typical pioneer species as it has small and numerous wind dispersed seeds (Coates-Palgrave 2003). This species had low abundance of seedlings, saplings, and adults under intact canopy, confirming its pioneer status. The probability of *A. Karroo* replacing itself was zero in small and medium sized canopy gaps. In large and very large canopy gaps, the probability increased but was still very low (0.10 to 0.16). Therefore, there is only a small probability that this pioneer species will replace itself within the canopy. Unless gaps become increasingly larger *A. karroo* will not replace itself and therefore will not remain the dominant tree species, countering previous criticisms of RBM's rehabilitation process (West et al. 2000).

Contrary to our expectations, there were no shade intolerant gap-takers. The most abundant gap-taker was *M. caffra*. This species has a wide tolerance for environmental conditions; it can survive and grow within the salt-spray zone but is also a dominant canopy species within mature coastal dune forest (Coates-Palgrave 2003). The second most abundant gap-taker was *C. africana*, which is often described as a forest pioneer species (Midgley et al. 1995b; Coates-Palgrave 2003). In our study, *C. africana* seedlings were more abundant in canopy gaps than under intact canopy, and were only found in the largest canopy gaps. However, at the sapling size class, *C. africana* were more abundant in small and medium sized gaps. This suggests once again that this species has wide tolerances for light. It appears that the changes in the canopy of regenerating coastal dune forest are deterministic with the longer living pioneer species with wide environmental tolerances replacing the short-lived *A. karroo*. In the future *M. caffra* and *C. africana* may fundamentally alter the light penetration in to regenerating coastal dune forest. Both *M. caffra* and *C. africana* are broadleaved species whilst *A. karroo* has small compound leaves that are smaller in surface area. These may provide more suitable conditions for shade-tolerant species typical of forest than under the present *A. karroo* canopy.

The unit of coastal dune forest regeneration and replacement patterns in this early stage of succession is larger than that generally described by gap-phase dynamics (Yavitt et al. 1995). Gap-phase dynamics may give way to patch dynamics at this scale. However, in reality this is purely semantics. Both paradigms suggest that disturbances lead to a resetting of the successional process. We have shown here that the dominant early pioneer of regenerating coastal dune forest, *A. karroo*, is replaced by other shade intolerant (but with wider tolerances) species. The probability of self-replacement was low even in the largest gaps. Canopy gaps in regenerating coastal dune forest punctuates succession but does not reset it.

Our previous work has predicted that the composition of regenerating coastal dune forest will be similar to an undisturbed coastal dune forest within 40 years (Wassenaar et al. 2005). However, we have shown here that even if predicted changes in composition do occur the structure of the forest may take a longer time to mimic an undisturbed coastal dune forest. Regenerating coastal dune forest is currently undergoing the first phase of succession with forest pioneers with wide environmental tolerances replacing the dominant canopy species. The nature of these forest pioneer species (broadleaved) and stochastic generation of canopy gaps should lead to greater heterogeneity in light conditions allowing greater niche space available for shade tolerant species to establish in regenerating sites and lead to the successful regeneration of dune forest.

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Table 5-1. A summary of our assumptions and expectations

Variable		Assumptions	Expectations		Analysis
			Shade intolerant trees	Shade tolerant trees	
Tree species composition, richness and abundance	In gaps of various sizes	Tree species exhibit niche differentiation in terms of shade-tolerance	Shade intolerant species will proliferate in large gaps as there is greater available sunlight	Shade tolerant species will be fewer in larger gaps because they are out-competed by shade intolerants	Linear regression (for richness, abundance, and density) ANOSIM
	Between gaps and paired non-gaps (under closed canopy)	Gaps and intact canopy differ in the available light that reaches trees under the canopy	Shade intolerant trees will be more abundant (with greater species richness) in gaps because of high light availability	Shade tolerant trees will be more abundant and with greater species richness under canopy (non-gap)	ANOSIM
Replacement probabilities – the probability that a gap-maker is replaced by an individual of the same species	In gaps of various size	The tallest individual of a canopy species will be the first to take over the canopy position of the gap-maker	The probability that a shade intolerant tree will be replaced by an individual of its own species will increase with increased gap size	The probability that a shade tolerant will replace a shade intolerant will decrease with increased gap size	Calculation of probability

Table 5-2. Gap characteristics in three regenerating coastal dune forest sites

	33 year old site	26 year old site	22 year old site
Number of gaps measured	46	40	53
Area of smallest gap (m^2)	98	28	16
Area of largest gap (m^2)	732	405.5	778
Mean gap size (m^2 ± standard deviation)	352 ± 211	149 ± 81	150 ± 149
Percentage of site canopy composed by gaps (%)	27	17	13

Table 5-3. Differences in the abundance of each species in canopy gaps and intact canopy, as well as in each canopy gap size class (Small, Medium, Large or Very Large) for the three size classes (Adult, Sapling and Seedlings). A significant difference is indicated in the table by the labels "Canopy gap" or "Intact Canopy" indicating where the abundance of each species was significantly greater. The size classes where species had significantly greater abundance are labelled. The label "ns" indicates a non-significant difference.

Species	Size class					
	Adult		Sapling		Seedling	
	Canopy gap vs. Intact canopy	Gap size	Canopy gap vs. Intact canopy	Gap size	Canopy gap vs. Intact canopy	Gap size
Acacia karroo			Canopy gap	Large/Very Large	Canopy gap	Large/Very Large[1]
Allophylus natalensis	Canopy gap	Large/Very Large	Canopy gap	Small/Medium	Canopy gap	Very Large[1]
Apodytes dimidiata			ns	ns		
Brachylaena discolor	Canopy gap	Medium/Large/Very Large	Canopy gap	ns		
Bridelia micrantha			ns	ns		
Canthium inerme	Canopy gap	Ns	Canopy gap	ns		
Celtis africana	ns	Ns	ns	Small/Medium	Canopy gap	Very Large[1]
Cestrum laevigatum	Canopy gap	Very Large	Canopy gap	Large/Very Large		
Ekebergia capensis			ns	Large/Very Large		
Grewia occidentalis	Canopy gap	Ns	ns	ns		
Kraussia floribunda			Canopy gap	Medium/Large/Very Large		
Mimusops caffra	Canopy gap	Very Large	ns	ns		

Peddia africana			ns	Medium/Large	Intact Canopy	Not in gaps[2]
Psychotria capensis			Canopy gap	ns		
Psydrax obovata			ns	Small		
Rhus natalensis			Canopy gap	Very Large		
Rhus nebulosa			Canopy gap	Very Large		
Scutia myrtina			Canopy gap	ns	Canopy gap	Medium/Large/Very Large
Teclea gerrardii	ns	Ns	ns	ns		
Trema orientalis	ns	Ns	ns	ns		
Tricalysia sonderiana			ns	Small/Very Large		
Trichilia emetic			ns	Large/Very Large		
Zanthoxylym capense			ns	ns	Intact Canopy	Large[3]

[1] *A. karroo* seedlings were only found in large and very large canopy gaps, there was no significant difference in abundance between these two gap size classes (Mann-Whitney test, P>0.05). *A. natalensis* and *C. africana* seedlings were only found in very large gaps and therefore we could not assess significant differences between size classes.

[2] *P. africana* seedlings were not found in canopy gaps.

[3] Most *Z. capense* seedlings were found under intact canopy.

Table 5-4. Reported gap proportion and gap area from a variety of forest types, “N/A” indicates where information was not available.

Forest type	Location	Gap proportion (%)	Gap area (m^2)	Reference
Laurel Forests	Anga National Park, Tenerife	0.4 – 0.6[1]	77.62 ± 37.22[2]	Arévalo & Fernández-Palacios 1998
Plateau Forest	Knysna Forest, South Africa	2 – 10	124.1 ± 72.0 72.1 ± 46.3	Midgley et al. 1995
Coastal Scarp Forest	Mount Thesiger Reserve, South Africa	7.8	87.8 ± 7.4	Oribi & Lawes 2004
Red oak mixed hardwood Forest	Pennsylvania, USA	0.16	N/A	Pedersen & Howard 2004
Mangrove	Kosrae, Micronesia	2.3	64.4 ± 79.5	Pinzón et al. 2003
Mangrove	Los Haitizes National Park, Dominican Republic	1.9	724	Sherman et al. 2000
Neo-tropical Forest	Barro Colorado Island, Panama	4.3	79	Yavitt et al. 1995
Boreal Forest	Lake Duparquet Training and Research Forest, Canada	38[3] (1998) 32[4] (2003)	156.4[3] (1998) 202.3[4] (2003)	Vepakomma et al. 2010
Boreal Forest	Gaspé Peninsula, Canada	N/A	40	Reyes et al. 2010
Subalpine Forest	Yatsugatake Mountains, Japan	11.2 11.3	84.3 ± 78.6 64.7 ± 84.4	Narukawa & Yamamoto 2001
Boreal Forest	Lake Duparquet Training and Research Forest, Canada	7.1[5] 40.4[6]	N/A	Kneeshaw & Bergeron 1998
Juniperus-Laurus Forest	Terceira Island, Portugal	N/A	25.1 ± 4.8	Elias & Dias 2009
Tropical Wet Evergreen Forest	Namdapha National Park, India	N/A	59.90 ± 38.64	Deb & Sundriyal 2007
Boreal Forest	Gaspé Peninsula, Canada	42	70	De Römer et al. 2007
Atlantic Montane Rain Forest	Carlos Botelho State	N/A	88.28 ± 11.38[2]	de Lima & de Moura 2008

	Park, Brazil			
Quercus Forest	Dobbs Natural Area, USA	34	295	Cowell et al. 2010
Mangrove	Cape York Peninsula and Hinchinbrook Island, Australia	N/A	756 253	Clarke & Kerrigan 2000
Old-growth Subalpine Forest	Baldwin Basin	15[7] 48[8]	161[7] 222[8]	Battles & Fahey 2000
	Bowl Research Natural Area	41[7] 23[8]	106[7] 174[8]	
Subalpine Forest	Whiteface Mountain, USA	15	N/A	Battles et al. 1995
Boreal Forest	British Columbia, Canada	50.4	92	Bartemucci et al. 2001
Sub-Boreal Forest		57.4	173	
Subalpine Forest		73.2	196	
Northern Temperate Forest		32.2	148	

[1] The lower figure excludes gaps less than 10m^2,

[2] Expanded gap area

[3] Surveyed in the year 1998

[4] Surveyed in the year 2003

[5] Aspen dominated site

[6] Fir dominated site

[7] Spruce – Fir zone

[8] Transition zone

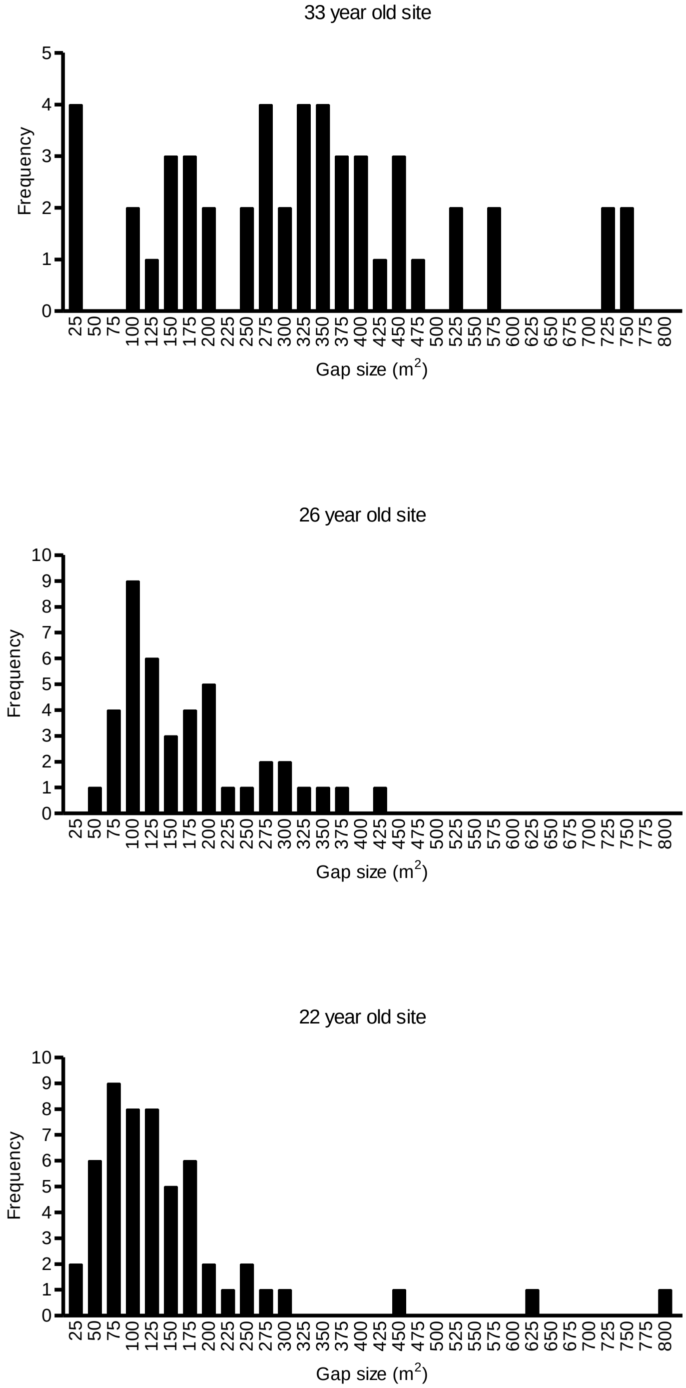

Figure 5-1. The gap size frequency distribution for the three regenerating coastal dune forests sites.

Chapter 6

Landscape composition influences the restoration of subtropical coastal dune forest

Abstract

Successional processes should increase habitat complexity, and increase resources available for forest associated species. However, according to the theory of Island Biogeography, the size, amount of edge, and isolation of a habitat patch will influence the probability of successful colonization. If this is true for restoring patches of coastal dune forest, then restoration managers need to mitigate for spatial characteristics.

We used patch occupancy models to assess correlations between the probability of forest birds and trees being present in a patch and patch characteristics that measured age, area, isolation and the amount of edge. We surveyed birds and trees in an un-mined coastal dune forest, remnant patches within the mine lease, and regenerating patches, some of which were being rehabilitated by a mining company.

Contrary to expectations patch age only explained the patch occupancy of six of 21 birds and eleven of 25 woody plant species. Landscape spatial parameters, measuring edge, isolation, and area explained the patch occupancy of the remaining 15 bird and 14 woody plant species. However, responses to patch characteristics were varied and idiosyncratic. These varied responses may be related to species habitat affinities, dispersal abilities, and establishment constraints. For restoration to succeed, managers need to consider the spatial configuration of the landscape to facilitate colonization of rehabilitating patches.

Keywords: birds, dune forest, mining, patch occupancy, rehabilitation, woody plants

Introduction

Restoration of the ecological character of disturbed land is a legitimate way of managing a mine's environmental impact (Cooke & Johnson 2002). However, the challenge of doing this successfully, at least in unambiguous ecological terms, remains large. Several factors, ranging from political to climatic, may influence success at restoring ecological structure and function. The relative importance of many of these factors is likely to differ among projects, but some factors may be more general. Here, we are concerned with one such factor that has the potential to be a common determinant in many projects: the landscape and its ecological configuration. The term "landscape" encompasses the structure, composition and spatial arrangements of habitat patches that may have an ecological influence on the success of a restoration project.

In keeping with the current understanding of ecological concepts, there has been an increasing call to include landscape or spatial components when managing habitat restoration (Huxel & Hastings 1999; Scott et al. 2001; Choi 2004; Miller & Hobbs 2007). Solid theoretical foundations form the basis of this call – a large part of what we know about how communities are structured rests on ideas about how landscape might influence assembly processes. For instance, Island Biogeography Theory (MacArthur & Wilson 1963), and its subsequent incarnations suggest that patch characteristics, such as the area of a discrete habitat patch, its isolation from other patches, and various properties of its edge influence its species composition and abundance (Brittingham & Temple 1983; Andrén & Angelstam 1988; Saunders et al. 1991).

The importance of the landscape for restoration is perhaps immediately obvious, but the mechanisms that link landscape characteristics to community structure may not be. There may be many such mechanisms, for instance, small habitat patches may have fewer species than large patches, because larger patches are more heterogeneous and therefore have more potential habitats, and consequently more species (Harner & Harper 1976). Also, as the distance between a "mainland" (or a large undisturbed patch) and another patch increases, the probability of successful dispersal from the source patch decreases (MacArthur & Wilson 1963). The relative size of a habitat's edge may influence species persistence through a number of abiotic and biotic interactions between the patch inhabitants and the non-patch matrix. For birds, these include increased nest predation (Andrén & Angelstam 1988) and nest parasitism (Brittingham & Temple 1983). For other taxa, changes in microclimate at the edge of a patch may lead to changes in the resources available for a species, or fall outside its climatic threshold (Murcia 1995).

We have been conducting research on post-mining restoration of coastal dune forests in South Africa since 1992 (see van Aarde et al. 1996). Restoration here depends on natural colonization of rehabilitating sites from adjacent forested areas (see van Aarde et al. 1996). This is ecological recovery sensu MacMahon & Holl (2001). The premise behind this approach is that as a site ages it is exposed to a greater number of potential colonizers dispersing from undisturbed (or minimally disturbed) forests (Wassenaar et al. 2005). This increased diversity presents a greater number of niches and distinct niches for species to utilize, leading to a successional pattern as pioneer species are gradually replaced by species characteristic of mature forests (van Aarde et al. 1996; Kritzinger & van Aarde 1998; Wassenaar et al. 2005).

Although the ecological recovery approach has been criticized, as its outcomes can be highly unpredictable (MacMahon & Hall 2001), it is still considered valid restoration practice (Scott et al. 2001; Young et al. 2005; Halle 2007). However, this approach does not provide for spatial limitations that may be imposed by the landscape and assumes an unhindered, unlimited and stable source of species beyond the areas targeted for recovery through ecological processes.

Our interest in the landscape's potential influence on restoration success stems from land use changes that the study region has experienced since the inception of the rehabilitation program in 1977. Influxes of people stimulated by industrial development, extensive transformation of grasslands and forests to commercial plantations, and the extending reach of mining collectively fragmented the landscape into an unnaturally diverse mosaic of forested patches. A changing landscape might influence restoration through changing dispersal and colonization rates due to changes in the nature of the inter-patch matrix. In addition, a changing landscape may increase the number of sink habitat patches relative to the number of source habitat patches (Keagy et al. 2005).

We are interested in this for practical reasons: if the landscape is a dominant driver of community assembly processes after disturbance, it should form a distinct part of rehabilitation management planning. The relative position of rehabilitating sites to source areas suddenly becomes an important and often manageable factor.

To gauge the influence of landscape on restoration, we assessed the probability of patch occupancy for both forest associated birds and woody plants as a function of patch area, isolation (a measure of distance), and edge. We further included in to our analysis patch age as earlier studies on species addition and replacement with increasing age point to succession taking place (see Wassenaar et al. 2007). We sampled un-mined forests as well as forests regenerating along a successional sere imposed by known-age mining and non-mining related disturbances. We reasoned that if the presence of typical forest species in these patches is strongly related to landscape properties, the likelihood of restoring these species in rehabilitating areas through successional processes alone would be low, unless the landscape itself is managed.

Methods

Study site

The coastal dune forests north of Richards Bay, KwaZulu-Natal, South Africa, fall within the southern most part of the Maputaland centre of plant endemism (van Wyk & Smith 2001). The climate is humid and subtropical, with mean annual rainfall of 1513 ± 449 mm (mean ± SD, *n* = 32 years between 1976 and 2008; data courtesy of Richards Bay Minerals). Rainfall peaks in February and during summer and the mean temperature was 23.79 ± 3.40 °C (*n* = 3 years between 2006 and 2009; data courtesy of RBM).

The study site included circa 60 km of coastline between Richards Bay Town (28°43’S, 32°12’E), and the Sokhulu forest (28°27’S, 32°25’E; see Fig. 6-1). Here dune forest (in its undisturbed state) formed a narrow strip of vegetation along the coast no wider than 1.9 km at its widest point (van Aarde et al. 2004). Within this area, Richards Bay Minerals have been mining for zircon, ilumenite, and rutile since 1976. The dredge-mining process involved the removal of vegetation; the topsoil was collected and stored for use in subsequent dune forest restoration. Post-mining, the sand was re-shaped in to dunes (resembling pre-mining topography) and for indigenous restoration topsoil seeded with annuals was spread over them. From then on restoration relied on the natural successional process (see van Aarde et al. 1996). The pioneer tree species, Sweet thorn (*Acacia karroo*) dominated, to form closed-canopy woodlands. After 12 years, typical mature forest species that have successfully dispersed to the site began to appear, and as it aged the woodland became more similar to a coastal dune forest in terms of species composition and abundance (Wassenaar et al. 2005). Richards Bay Minerals is committed to restoring one third of its mined area to indigenous coastal dune forest, and the remainder to commercial plantations (van Aarde et al. 1996).

Bird and woody plant surveys

As the target for restoration is an assemblage similar (within natural variation) to that of an un-mined coastal dune forest, we limited our analysis of both birds and woody plants to forest associated species (according to Gibbon 2006 for birds, and Coates-Palgrave 2002, and Pooley 2003, for woody plants). The term forest associated species is a qualitative judgment of which species are more closely associated with forest (inclusive of forest edge). Species recorded in the Sokhulu forest, and nearby Mapelane Coastal Dune Forest Nature Reserve consistently during our 18 years of fieldwork were considered forest associated.

Bird surveys took place in January and February 2008 at three different types of patch and the Sokhulu forest (see Fig. 6-1). These were “Rehabilitating patches” which were regenerating after mining disturbance (nine sites), “Spontaneous regenerating patches” were regenerating after non-mining related disturbance (without management intervention; 10 sites). “Forest patches” were remnant forests within the lease that are surrounded by exotic plantations and mining operations (four sites). The “Sokhulu forest” was the largest undisturbed patch of forest in the study region. Forest patches and spontaneous regenerating patches were located using historical aerial photographs. Patches that had vegetation cover in the earliest set of photographs available for assessment (1937), and were still comprised of forest in the 2005 photographs were classified as primary forest patches. Those patches that were bare sand in 1937 but that were covered with vegetation in subsequent images in the time series (1957, 1960, 1970, 1992, 2002, and 2005) were identified as spontaneously regenerating patches of known age.

Rehabilitating patches were defined from mining records; a patch was an area where rehabilitation was initiated within a four year period grouped together as one patch (Wassenaar et al. 2005), and where natural features (such as a river or estuary), exotic plantations, or roads adjoined or surrounded the patch.

For bird surveys, experienced observers walked five 300 m long line-transects that were separated by 200 m and recorded all birds seen within a distance of 60 m either side of the transect line and all birds heard at each patch. In total data were available for 24 patches.

Woody plant surveys were carried out in 2005 in three types of sites, rehabilitating sites (seven sites), spontaneous regenerating sites (six sites) and the Sokhulu forest. Self supporting woody plants greater than 1.7 m in height were identified in seven 16 x 16–m quadrats per patch. Tree surveys were carried out at rehabilitating patches, spontaneously regenerating patches, and at Sokhulu forest. Data were available for 14 patches.

We assume that in both rehabilitating and spontaneously regenerating coastal dune forest that trees have colonized by dispersal from elsewhere. Dune forest trees generally have recalcitrant seed, meaning that they do not remain viable in topsoil for very long because of desiccation (Nichols 2005). In addition, our previous monitoring and research has only recorded wind dispersed pioneer species occurring in the earliest stages of rehabilitation.

Patch parameters

For rehabilitating patches, age was determined from mining records. For spontaneously regenerating patches age was determined from digitized geo-referenced aerial images from 1937, 1957, 1960, 1970, 1992, 2002, 2005.

Patch isolation from the largest intact forest (Sokhulu forest) was measured in ArcMap version 9.2 (Environmental Systems Research Institute [ESRI], Redlands, Ca, U.S.A.). Distances were taken as edge to edge measurements. The other patch parameters (patch area, and patch shape index) were determined using metrics within the program FRAGSTATS (McGarigal & Marks 1995).

As correlations between patch variables can potentially confound the interpretation of patch occupancy results, we tested for correlation between patch variables using Pearson’s correlation coefficient.

Patch occupancy probability

We used patch occupancy models in PRESENCE version 2.2 (Hines 2006) to determine if patch parameters (estimated patch age, patch area, distance from the largest forest patch [which in this case was Sokhulu forest], and patch shape index) affected the probability that a patch was occupied by a species. The patch occupancy model assumes (1) that the focal species cannot colonize (or immigrate to) or go locally extinct at a patch during the survey period, (2) species are not falsely detected, and (3) that detection at one patch is independent of detection at other patches (Donovan and Hines 2007).

Patch occupancy models use the logit link and a maximum likelihood approach to estimate ψ, the probability of patch occupancy and p_i, the probability of detecting the species of interest on transect *i* (given that it is present in the patch) as a function of patch specific covariates. We used the global model : ψ ($P_{age}+P_{area}+P_{isolation}+P_{shape}$) p (T.), where p (T.) is the detection probability across all transects (p1, p2, p3, p4, etc.) and P denotes the patch characteristics: estimated patch age (P_{age}), patch area (P_{area}), distance from Sokhulu ($P_{isolation}$) and patch shape index (P_{shape}).

Our candidate model set consisted of the global model and all combinations of patch characteristics. The global model fit was tested using the MacKenzie and Bailey Goodness of Fit test, where the observed data and a simulated dataset are subjected to Pearson’s Chi-square tests. If the chi-square of the observed data divided by the average of the test statistics from 1000 parametric bootstraps is about 1, the model was considered a “good fit” (MacKenzie et al. 2006). Models were ranked using Akaike’s criterion, corrected for small sample size (AICc). However, where over-dispersion was detected in the global model ($\hat{c} > 1.0$) the small-sized quasi-AIC (QAIC) was used instead (Burnham & Anderson 2002; MacKenzie et al. 2006). AICc and QAICc are calculated as follows:

$$\text{AICc} = -2 \log \text{Likelihood} + 2K + 2K(K+1)/(n-K-1)$$

$$\text{QAICc} = -2 \log \text{Likelihood}/\hat{c} + 2K + 2K(K+1)/(n-K-1)$$

where K is the number of parameters in the model and n is the effective sample size. The determination of the effective sample size is conceptually difficult in patch occupancy modeling (MacKenzie et al. 2006). We used the number of sites as our effective sample size ensuring the maximum penalty in AICc and QAICc calculation. AIC values are relative and therefore a more intuitive way to view them is as ΔAIC. This was calculated as $AIC_i - AIC_{min}$, where the best ranked model is ΔAIC = 0. These values allowed models to be categorized as having substantial support (<2), less support (2-7), and no support (>10) (Burnham & Anderson 2002). We then calculated Akaike weights (w_i) which approximated the probabilities that model *i* was the best model in the set (Burnham & Anderson 2002). A single model with a weighting greater than 0.9 was considered to be the best model overall. We also calculated the relative variable importance, the sum of all w_i's of all models in the set containing the variable of interest (Burnham & Anderson 2002).

Results

Patch characteristics

Rehabilitating patches were more isolated from the largest intact forest, than the spontaneous regenerating patches (with the exception of two). Rehabilitating patches and forest patches had a greater amount of edge when compared with spontaneous regenerating forest patches (Fig. 6-1). None of the patch characteristics were significantly correlated to each other.

Bird and woody plant surveys

We recorded 39 bird and 36 woody plant forest associated species. Fourteen of the birds and eight of the woody plants were considered "rare" as they were recorded fewer than four times during the surveys; these species were excluded from further analysis. Models for 25 bird and 28 woody plant species fitted to the observed data.

For four of the 25 bird species the probability of patch occupancy was one in all patches but the youngest, which resembled grassland. For these ubiquitous species the determination of correlations to patch characteristics was impossible – these include the Green-backed Camaroptera (*Camaroptera brachyuran*), Yellow-bellied Greenbul (*Chlorocichla flaviventris*), Olive Sunbird (*Cyanomitra olivacea*), and Yellow-breasted Apalis (*Apalis flavida*). For the woody plants, three species were near ubiquitous (Dune false current, *Allophylus natalensis*, Large-leaved dragon tree, *Dracaena aletriformis* and Quar, *Psydrax obovata*). We therefore discarded these species from the rest of the analysis.

Patch occupancy models

Distance from Sokhulu

For both taxa the probability of patch occupancy decreased with increasing distance from Sokhulu (Fig. 6-2a & 6-2b). Distance from Sokhulu was the most parsimonious model for eight of the 25 woody plant species (Table 6-1). Five of these had distance from Sokhulu as the only plausible model (Natal apricot, *Dovyalis longispina*; Septee tree, *Cordia caffra*; Zulu cherry-orange, *Teclea gerrardii*; False ironwood, *Olea capensis*; and Coastal goldleaf, *Bridelia micrantha*). Wild honeysuckle (*Turraea floribunda*), had patch age as a plausible secondary model, but given the data and candidate models, distance from Sokhulu was 1.70 times more plausible than patch age. The Thorny elm (*Chaetachme aristata*), and the Dune soap-berry (*Deinbollia oblongifolia*), had patch area as their most plausible secondary model (the Thorny elm had high model uncertainty so had all variables as plausible alternatives). Distance from Sokhulu was 1.10 and 2.11 times more plausible for Thorny elm and Dune soap-berry respectively (Table 6-2).

Two birds (out of 21) had distance from Sokhulu as their top-ranked model, the White-eared Barbet (*Stactolaema leucotis*) and the Eastern bronze-naped Pigeon (*Columba delegorguei*; Tables 6-1 & 6-2). For the Eastern bronze-naped Pigeon distance to Sokhulu was the only plausible model. The White-eared Barbet had patch shape index, distance from Sokhulu + patch shape index, and patch age as alternative models.

Distance from Sokhulu was 1.08 times more plausible than the next most important variable patch shape index.

Patch area

Patch area was the most parsimonious model for three of the 25 woody plant species (Table 6-1), the Cape ash (*Ekebergia capensis*), Giant pock ironwood (*Chionanthus peglerae*), and the Sea guarri (*Euclea racemosa* ssp. *sinuata*). The Sea guarri had distance from Sokhulu and patch age as plausible alternatives, but patch area was 27.10 times more plausible than distance from Sokhulu. The Giant pock ironwood tree and the Sea guarri bush had a probability of patch occupancy of 0 in any patch below 300 ha and a probability of one above 300 ha. For the Cape ash probability of patch occupancy decreased with increased patch size (Table 6-2; Fig. 6-2g).

Two of the 21 bird species had patch area as top-ranked model (Table 6-1). The Eastern Nicator (*Nicator gularis*) was only present in sites greater than 20 ha. In contrast, the Green Malkhoa’s patch occupancy probability decreased with increasing patch area (Fig. 6-2h).

Patch shape index

Three of the 25 woody plants (Black bird-berry, *Psychotria capensis*; Coastal red milkwood, *Mimusops caffra*; and Poison olive; *Peddiea Africana*) had patch shape index as their top-ranked model (Tables 6-1 & 6-2). For the Poison olive and Coastal red milkwood, as patch shape complexity increased so did the probability of patch occupancy (Fig. 6-2c), whereas the opposite relationship was true for the Black bird-berry. The coastal red milkwood had patch area as a plausible alternative model, but patch shape index was 10.58 times more plausible (Table 6-2).

For 6 out of 21 birds patch shape index was the most parsimonious model (Table 6-1). For the Black-backed Puffback (*Dryoscopus cubla*), Tambourine Dove (*Turtur tympanistria*), Crowned Hornbill (*Tockus alboterminatus*) and Square-tailed Drongo (*Dicrurus ludwigii*) the probability of occurrence increased with patch shape complexity. The Red-capped Robin-chat (*Cossypha natalensis*), and Tawny-flanked Prinia (*Prinia subflava*) showed the opposite relationship (as patch shape complexity increased the probability of patch occupancy decreased; Fig. 6-2d). The Tambourine Dove had patch area, distance from Sokhulu and patch age as plausible alternative models. Patch shape index was 1.50 times more plausible than any of the other variables for this species (Table 6-2).

Estimated patch age

For both taxa the probability of patch occupancy increased with increasing estimated patch age (Fig. 6-2e & 6-2f). Estimated patch age was the top-ranked model for 11 of 25 woody plants (Table 6-1). For nine of these, patch age was the only possible model considering the data and candidate model set (Table 6-2). These were the Acorn diospyros, *Diospyros natalensis*; False soap-berry, *Pancovia golungensis*; Forest num-num, *Carissa bispinosa*; Prickly red-berry, *Erythrococca berberidea;* Black monkey orange, *Strychnos gerrardii*; White forest spike-thorn, *Gymnosporia nemorosa*; Common coca tree, *Erythoxylum emarginatum*; and the Coast coffee, *Tricalysia sonderiana*). The Glossy forest grape (*Rhoicissus rhomboidea*) had high model uncertainty with distance from Sokhulu, patch area, and patch shape index being supported as alternative models. The Dune bride’s bush (*Pavetta revoluta*) had patch shape index as an alternative. For the Glossy forest grape patch age was 1.50 times more plausible than distance from Sokhulu, whereas for the Dune bride's bush patch age was 2.40 times more plausible than patch shape index.

Five of 21 birds (Lemon Dove, *Aplopelia larvata*; Trumpeter Hornbill, *Bycanistes bucinator*; Yellow-rumped Tinkerbird, *Pogoniulus bilineatus*; Black-bellied Starling, *Lamprotornis corruscus*; and Collared Sunbird, *Hedydipna collaris*) had patch age as the only plausible model in the set (Tables 6-1 & 6-2).

Multivariate models

Multivariate models were the top-ranked in six of the 21 birds and none of the woody plant species (Table 6-1). The Scaly-throated Honeyguide (*Indicator variegates*), Dark-capped Bulbul (*Pycnonotus tricolor*), and the Blue-mantled crested Flycatcher (*Trochocercus cyanomelas*) all had models that included distance from Sokhulu as a variable (distance from Sokhulu + patch shape index, patch area + distance to Sokhulu + patch shape index, patch age + distance from Sokhulu, respectively). Distance from Sokhulu was more important than the next most important variable shape for both the Scaly-throated Honeyguide (distance from Sokhulu was 1.81 times more plausible) and the Dark-capped Bulbul (distance from Sokhulu was 1.03 times more plausible; Table 6-2). Both decreased in the probability of occupancy with increasing distance from Sokhulu. For the Blue-mantled crested Flycatcher patch age was 1.06 times more important than distance to Sokhulu; Table 6-2). The probability of patch occupancy increased with patch age and decreased with increased distance from Sokhulu.

Where patch area was a variable in multivariable models it was the most important in three out of four cases (Table 6-1). Both the Goldentailed Woodpecker (*Campthera abingoni*) and Red-fronted Tinkerbird (*Pogoniulus pusillus*) had patch age +

patch area as their top-ranked models, patch area was 1.10 and 1.50 times more plausible than patch age respectively (Table 6-2). For both of these species as patch area increased the probability of patch occupancy decreased. For the Brown-hooded Kingfisher (*Halcyon albiventris*) patch area + patch shape index was the top-ranked model (Table 6-1). Patch shape index was 1.10 times more plausible than patch area. For this species, as patch shape became more complex, the probability of patch occupancy decreased.

Discussion

Previous work on the community assembly of disturbed coastal dune forest has demonstrated age-related trends in both bird and woody plant community composition (van Aarde et al. 1996; Kritzinger & van Aarde 1998; Wassenaar et al. 2005). We therefore expected that patch age would be a major correlate of the probability of patch occupancy for coastal dune forest woody plants and birds. However, contrary to this expectation, patch age was not a variable in the plausible models for the majority of species assessed. Landscape structure (size, shape, and spatial arrangement of habitat patches) correlated better with the probability of patch occupancy of the remaining 15 birds and 14 woody plants. However, we found that this response was idiosyncratic and variable. Although the woody plants and birds broadly conformed to the expected differences resulting from differences in vagility (i.e. woody plants correlated better to isolation than birds), all species were not equally affected, nor did the different landscape structure parameters have the same influence.

For birds, the species-specific responses could be partly explained by their habitat affinity. Occupancy by forest-edge associated species such as the Crowned Hornbill (*Tockus alboterminatus*) and Black-backed Puffback (*Dryoscopus cubla*) was explained best by patch shape. Both these species are classified as forest-edge species (Gibbon 2006) and they conformed to this classification by responding positively to edge. Surprisingly, the Square-tailed Drongo (*Dicrurus ludwigii*) a forest core species (Gibbon 2006), showed increased patch occupancy with increased edge. Habitat-edge dogma suggests that birds which normally inhabit the forest core will be negatively affected by interactions with matrix inhabitants, through predation and nest-parasitism for example, when exposed to increased edge habitat (Brittingham & Temple 1983; Andrén & Angelstam 1988; but see Kotze & Lawes 2007). This appears not to be the case for this species. As it is an insectivore it may benefit from insect emergences that occur after rainfall along the sand roads that surround patches (M. Grainger, personal observation).

Bird species with high affinity to forests are notoriously loathe to cross open areas (Gómez 2003; Moore et al. 2008). However, only four birds, the White-eared Barbet (*Stactolaema leucotis*), Dark-capped Bulbul (*Pycnonotus tricolor*), Scaly-throated Honeyguide (*Indicator variegates*) and the Eastern bronze-naped Pigeon (*Columba delegorguei*), responded best to patch isolation. Species-isolation relationships may only become apparent where matrix habitat constrains movement (Wethered & Lawes 2003; Castellón & Sieving 2005; Watson et al. 2005). Our results suggest that the majority of forest birds in the study areas can cross the non-forest matrix, or make use of potential corridors such as the 200 m wide strip of vegetation on seaward side of the mining lease. This strip however, has never been assessed as a potential movement corridor. Of the species whose patch occupancy was described best by the distance from Sokhulu the White-eared Barbet and Dark-capped Bulbul have successfully colonized the rehabilitating sites. The Eastern bronze-naped Pigeon and Scaly-throated Honeyguide have not colonized the rehabilitating sites. The Eastern bronze-naped Pigeon is a forest associated species important in the dispersal of several large seeded trees, as well as the pioneer species Pigeon wood (*Trema orientalis*; Gibbon 2006). The further investigation of the effect of isolation on this species may therefore be important to ensure restoration success.

The nature of the matrix may also negate species-area relationships. Wethered & Lawes (2003) showed that in a high contrast landscape (forest and grassland), the species-area relationship was apparent. Whereas, in a low contrast landscape (forest and plantation) the relationship was not, this may have been because species could gain resources from the plantation matrix and were therefore not constrained by patch area. The contrast between some of landscape elements of the mining lease area are low, forest and secondary woodland or commercial forestry for example. This might explain why an increased patch area corresponded to an increase in patch occupancy in only two species (Eastern Nicator, *Nicator gularis* and Brown-hooded Kingfisher, *Halcyon albiventris*).

The differential responses of woody plants to measures of landscape structure for some species may also be attributed to habitat affinity. For example, woody plant species may respond positively to edge in response to abiotic variables, such as light intensity (Saunders et al. 1991). This may help explain the probability of occupancy of the Poison olive which increased with increased edge. This species is typical of forest margins (Coates-Palgrave 2002). It is found in deep shade which is associated with the forest edge. Forest edges may become dense with vegetation over time (Didham & Lawton 1999).

Woody plants may be exposed to increased seed and seedling predation at the edge of forests as seedlings or seeds are exposed to a greater number of matrix dwelling herbivores (del-Val et al. 2007). In our study area, this still requires investigation, but is a plausible mechanism for the positive correlation to patch area and patch edge demonstrated by Giant pock ironwood tree (*Chionanthus peglerae*), the Sea guarri bush (*Euclea racemosa* ssp. *sinuata*), and the Black bird-berry (*Psychotria capensis*).

The success of woody plant dispersal may be limited in tropical forests by distance (isolation effects) and dispersal vector availability (Duncan & Duncan 2000; Cordeiro & Howe 2001; Gómez 2003). Distance from Sokhulu was the top-ranked model for more woody plants in our study than any other patch variable except patch age, and all trees decreased patch occupancy with increased distance from Sokhulu. In patches closer to the un-mined Sokhulu forest, these species had a higher probability of occupancy, and as the distance from this un-mined area increased the probability of occupancy decreased. This may reflect a rescue effect where propagules can disperse to nearby patches and bolster the local population from extinction (Brown & Kodric-Brown 1977). As this distance increases, the probability of successful dispersal also decreases thus reducing the overall population size in isolated patches. Of course, the forest fragments that are closer to the rehabilitating patches may act as source for these species and we cannot rule out source populations other than those patches we surveyed (for example within the 200 m strip of vegetation along the coast).

Here we have shown a correlation between the presence of typical forest species in rehabilitating, spontaneous regenerating and remnant forest patches, and patch spatial characteristics. This means the success of a restoration program that relies upon successional processes alone may be jeopardized by the spatial characteristics of rehabilitating patches, such as their edge, and isolation from potential source. In these circumstances, managers may need to consider assisting the colonization of those species most affected by patch characteristics. It is crucial that any study of fragmentation effects also looks at the age of patches alongside traditional spatial factors (Ross et al. 2002), because both space and time may be interacting (Jacquemyn et al. 2001).

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Table 6-1. The number of species whose patch occupancy was best explained by each model, the numbers in brackets indicate the number of species that have each model as a plausible alternative.

Model	Birds	Trees
Ψ (Page)	5 (3)	11 (3)
Ψ (Pisolation)	2 (3)	8 (2)
Ψ (Page + Parea + Pisolation)	0 (2)	0
Ψ (Page + Parea + PShape)	0 (1)	0
Ψ (Page + Parea)	2 (0)	0
Ψ (Page + Pisolation + PShape)	0 (1)	0
Ψ (Page + Pisolation)	1 (0)	0
Ψ (Parea + Pisolation + PShape)	1 (0)	0
Ψ (Parea + PShape)	1 (0)	0
Ψ (Pisolation + PShape)	1 (2)	0
Ψ (PShape)	6 (1)	3 (3)
Ψ (Parea)	2 (3)	3 (4)

Table 6-2. Results of model selection for 25 forest associated tree species and 21 forest associated bird species. The variables included in the model selection include patch age (1), patch area (2), distance from Sokhulu (3), and patch shape index (4).

Species	**Latin Name**	**Best Model Fit**	**Number of parameters**	**AICc or QAICc**	***w_i***	**Other models with substantial support (ΔAICc between 0-2)**	**Importance value**			
Trees							**1**	**2**	**3**	**4**
Acorn diospyros	*Diospyros natalensis*	1	9	71.52	0.98		***0.98***	0.01	0.01	0.00
False soap-berry	*Pancovia golungensis*	1	9	67.57	0.98		***0.98***	0.01	0.01	0.00
Forest num-num	*Carissa bispinosa*	1	9	89.18	0.73		***0.75***	0.12	0.13	0.03
Prickly red-berry	*Erythrococca berberidea*	1	9	91.97	0.80		***0.82***	0.02	0.14	0.04
Black monkey orange	*Strychnos gerrardii*	1	9	79.24	0.62		***0.63***	0.09	0.19	0.10
Glossy forest grape	*Rhoicissus rhomboidea*	1	9	57.30	0.35	3,2,4	***0.35***	0.22	0.24	0.20
Natal ironplum	*Drypetes natalensis*	1	9	101.46	0.55		***0.55***	0.14	0.17	0.14
White forest spike-thorn	*Gymnosporia nemorosa*	1	9	125.94	0.72		***0.72***	0.06	0.05	0.16
Common coca tree	*Erythroxylum emarginatum*	1	9	98.68	0.99		***1.00***	0.00	0.00	0.00

Dune bride's bush	*Pavetta revoluta*	1	9	151.35	0.56	4	***0.56***	0.12	0.09	0.23
Coast coffee	*Tricalysia sonderiana*	1	9	175.47	0.89		***0.89***	0.04	0.03	0.04
Cape ash	*Ekebergia capensis*	2	9	58.11	0.74		0.05	***0.74***	0.03	0.18
Giant pock ironwood	*Chionanthus peglerae*	2	9	55.89	0.95		0.01	***0.95***	0.04	0.01
Sea guarri	*Euclea racemosa* ssp. *sinuata*	2	9	55.89	0.95	4,1	0.01	***0.95***	0.04	0.01
Natal apricot	*Dovyalis longispina*	3	9	111.79	0.73		0.13	0.09	***0.73***	0.06
Septee tree	*Cordia caffra*	3	9	85.96	0.89		0.02	0.02	***0.89***	0.07
Wild honeysuckle	*Turraea floribunda*	3	9	88.41	0.59	1	0.35	0.03	***0.59***	0.03
Zulu cherry-orange	*Teclea gerrardii*	3	9	115.64	0.83		0.05	0.06	***0.83***	0.06
Thorny elm	*Chaetachme aristata*	3	9	87.45	0.27	2,4,1	0.23	0.26	***0.27***	0.24
False ironwood	*Olea capensis*	3	9	80.27	0.90		0.02	0.02	***0.90***	0.06
Coastal goldleaf	*Bridelia micrantha*	3	9	108.08	0.89		0.03	0.04	***0.89***	0.04
Dune soap-berry	*Deinbollia oblongifolia*	3	9	164.88	0.52	2	0.15	0.25	***0.52***	0.09
Black bird-berry	*Psychotria capensis*	4	9	132.49	0.41		0.22	0.13	0.23	***0.41***
Coastal red	*Mimusops caffra*	4	9	187.44	0.78	2	0.07	0.07	0.07	***0.78***

milkwood										
Poison olive	*Peddiea africana*	4	9	112.50	0.61		0.08	0.23	0.08	***0.61***
Birds										
Lemon Dove	*Aplopelia larvata*	1	7	53.67	0.54		***0.89***	0.07	0.29	0.24
Trumpeter Hornbill	*Bycanistes bucinator:*	1	7	86.52	0.69		***0.99***	0.09	0.17	0.09
Yellow-rumped Tinkerbird	*Pogoniulus bilineatus*	1	7	151.46	0.68		***0.99***	0.16	0.10	0.09
Blackbellied Starling	*Lamprotornis corruscus*	1	7	56.46	0.31		***0.68***	0.30	0.35	0.23
Collared Sunbird	*Hedydipna collaris*	1	7	144.93	0.47		***0.68***	0.25	0.19	0.15
Eastern Nicator	*Nicator gularis*	2	7	112.36	0.82		0.09	***0.99***	0.09	0.04
Green Malkhoa	*Ceuthmochares aereus*	2	7	92.74	0.56		0.22	***0.76***	0.14	0.14
White-eared Barbet	*Stactolaema leucotis*	3	7	104.15	0.22	4, 3+4, 2	0.26	0.14	***0.52***	0.48
Eastern bronze-naped Pigeon	*Columba delegorguei*	3	7	21.00	0.56		0.22	0.20	***0.74***	0.20
Goldentailed Woodpecker	*Campethera abingoni*	1+2	8	126.34	0.80		0.92	***0.98***	0.08	0.07
Red-fronted Tinkerbird	*Pogoniulus pusillus*	1+2	8	142.46	0.34	2, 1+2+4	0.58	***0.86***	0.14	0.27

Blue-mantled crested Flycatcher	*Trochocercus cyanomelas*	1+3	8	86.50	0.48	1+2+3	***0.93***	0.43	0.88	0.10
Black-backed Puffback	*Dryoscopus cubla*	4	7	59.54	0.75		0.09	0.09	0.09	***0.78***
Red-capped Robin-chat	*Cossypha natalensis*	4	7	122.56	0.59		0.15	0.15	0.15	***0.63***
Square-tailed Drongo	*Dicrurus ludwigii*	4	7	138.11	0.99		0.00	0.00	0.00	***0.99***
Tambourine Dove	*Turtur tympanistria*	4	7	138.30	0.31	2, 3, 1	0.25	0.25	0.25	***0.37***
Tawny-flanked Prinia	*Prinia subflava*	4	7	164.63	0.54		0.17	0.17	0.16	***0.59***
Crowned Hornbill	*Tockus alboterminatus*	4	7	47.53	0.39		0.20	0.26	0.22	***0.59***
Brown-hooded Kingfisher	*Halcyon albiventris*	2+4	8	93.44	0.28	2, 3,1,4	0.25	***0.52***	0.23	0.48
Scaly-throated Honeyguide	*Indicator variegatus*	3+4	8	57.83	0.45	3	0.12	0.21	***0.90***	0.49
Dark-capped Bulbul	*Pycnonotus tricolor*:	2+3+4	9	152.25	0.37	1+3+4, 3+4	0.33	0.43	***0.92***	0.89

Italicised values indicate the most important variable for each species

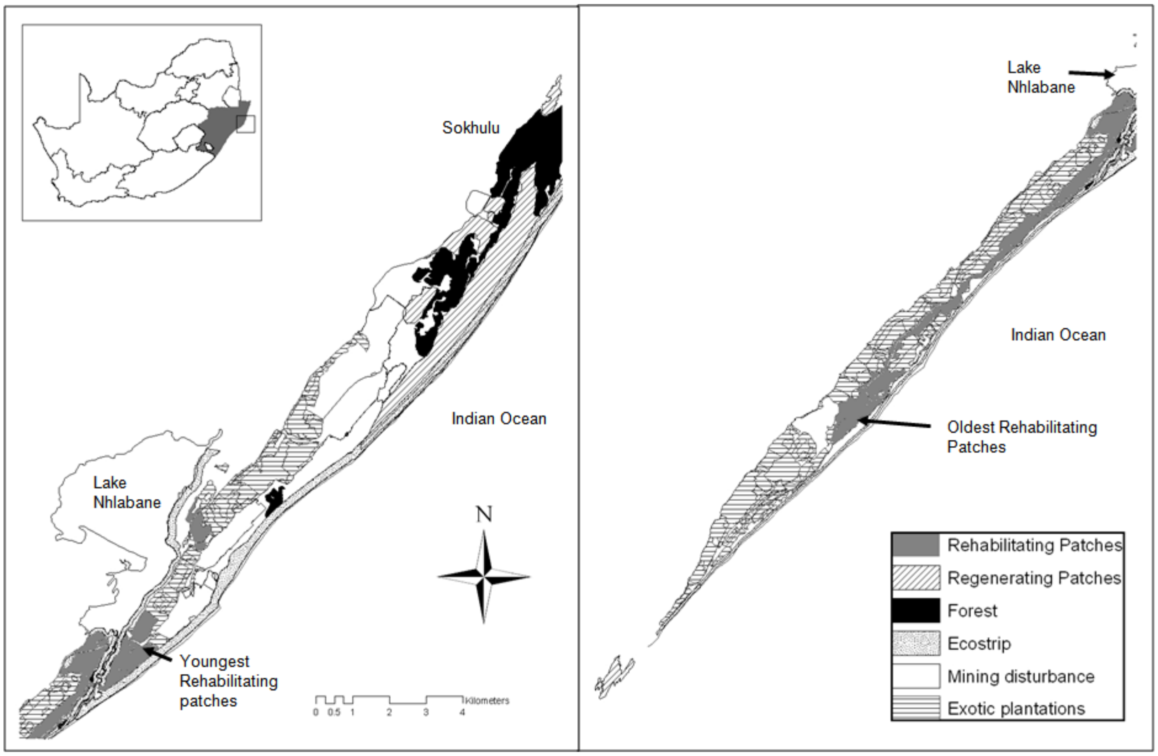

Figure 6-1. A map of the study area showing in the left hand insert the political map of South Africa, with the province KwaZulu-Natal highlighted, and the study area boxed. In the left panel the northern section of the lease (from Lake Nhlabane to Sokhulu) is displayed showing the Sokhulu forest as well as some of the youngest rehabilitating patches, the majority of spontaneous regenerating patches, and all forest patches. The right panel shows the southern section of the lease (from Lake Nhlabane to Richards Bay Town), showing the older rehabilitating patches and the remaining spontaneous regenerating sites. In-land from the lease the landscape is dominated by human habitation and exotic plantations.

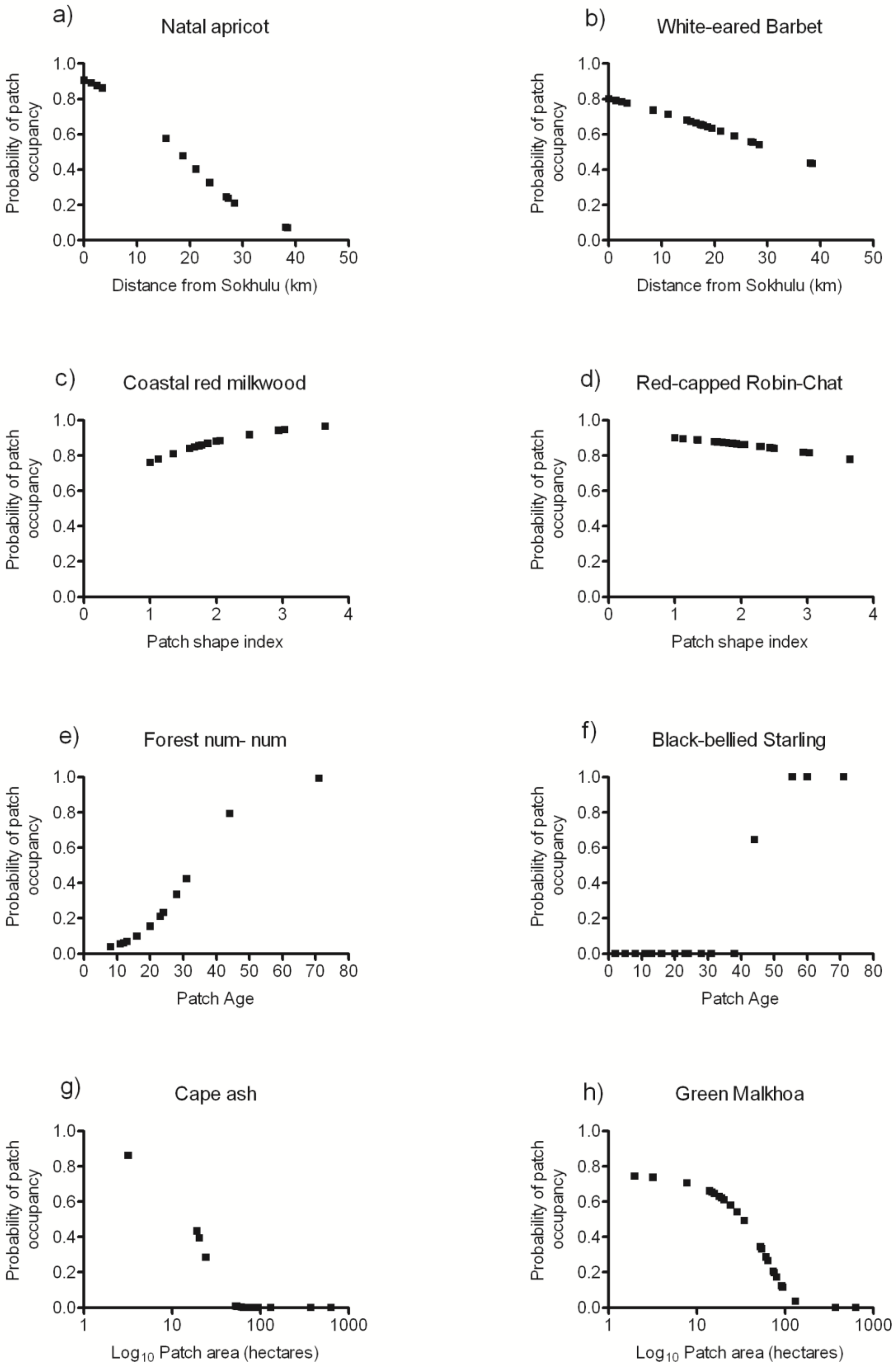
a)
Natal apricot
Probability of patch occupancy
1.0
0.8
0.6
0.4
0.2
0.0
0
10
20
30
40
50
Distance from Sokhulu (km)
b)
White-eared Barbet
Probability of patch occupancy
Distance from Sokhulu (km)
c)
Coastal red milkwood
Probability of patch occupancy
0
1
2
3
4
Patch shape index
d)
Red-capped Robin-Chat
Probability of patch occupancy
Patch shape index
e)
Forest num- num
Probability of patch occupancy
0
10
20
30
40
50
60
70
80
Patch Age
f)
Black-bellied Starling
Probability of patch occupancy
Patch Age
g)
Cape ash
Probability of patch occupancy
1
10
100
1000
Log$_{10}$ Patch area (hectares)
h)
Green Malkhoa
Probability of patch occupancy
Log$_{10}$ Patch area (hectares)

Figure 6-2. The probability of patch occupancy as a function of the patch characteristics distance from Sokhulu (a & b), patch shape index (c & d), patch age (e & f) and patch area (g & h). Here we show data for the trees a) Natal apricot (*Dovyalis longispina*), c) Coastal red milkwood (*Mimusops caffra*), e) Forest num – num (*Carissa bispinosa*), g) Cape ash (*Ekebergia capensis*), and the birds b) White-eared Barbet (*Stactolaema leucotis*), d) Red-capped Robin-Chat (*Cossypha natalensis*), f) Black-bellied Starling (*Lamprotornis corruscus*), and h) Green Malkhoa (*Ceuthmochares aereus*).

Chapter 7 – Synthesis and an evaluation of the success of coastal dune forest rehabilitation

This thesis addresses aspects relevant to coastal forest regeneration in response to rehabilitation after disturbances stemming from the strip-mining of coastal dunes in KwaZulu-Natal, South Africa. It questions and evaluates ecological succession as a primary driver of apparent regeneration in response to rehabilitation (Chapter 3), assesses the impact of non-indigenous species on the trajectory this regeneration follows (Chapter 4), assesses the role of canopy disturbances in regeneration dynamics (Chapter 5) and finally, evaluates the consequences of landscape variables (isolation and area) for the presence of species (Chapter 6). None of these chapters focuses specifically on restoration success and thus I will direct my synthesis at this topic.

Ecological restoration is an intentional activity that initiates or accelerates the recovery of an ecosystem in respect to its health, integrity and sustainability; an ecosystem is recovered or restored when it contains sufficient biotic and abiotic resources to continue its development without further assistance (SER 2004). Restoration has a strong historical focus as is evidenced by Bradshaw's (1984) conceptual structure – function model (Fig. 7-1). This model describes an ecological trajectory (an ecosystems developmental pathway through time, SER 2004), from a degraded state (on the bottom left of the diagram) toward the original state (on the top right of the diagram). This mirrors the supposed development of ecosystems through ecological succession, from a simple state towards a more complex one (indicated by a dotted arrow on Fig. 7-1). Ecosystem development, according to the model, can differ following one of several different management interventions. "Neglect" may lead to a further loss of both ecosystem function and structure or alternatively may lead to increased function and structure through spontaneous succession. “Replacement”, for example a change in land-use to a commercial plantation, may add some structure and function to a degraded ecosystem but not to the same extent as the original or undisturbed ecosystem. “Rehabilitation” adds structure and function, but does not necessarily result in restoration of the historic ecosystem composition and structure, but is a progression toward restoration (Bradshaw 1984; SER 2004). “Restoration” is the action of regaining the original composition, structure and function through the maintenance of indigenous self-sustaining ecological processes. Often the terms “rehabilitation” and “restoration” are used synonymously and the conceptual differences are ignored in practice (SER 2004).

According to the structure – function model (Fig. 7-1; Bradshaw 1984) success is achieved when the function and structure of a recovering ecosystem matches that of the original ecosystem. In reality, it is a daunting task to determine success, perhaps because restoration projects are generally short-term endeavours, rarely lasting longer than 5 years and the regeneration of ecosystem processes can take many years, extending past the lifespan of most research projects and even researchers (Ruiz-Jaen & Aide 2005a). Zedler & Callaway (2000) suggest that a “yes/no” term is inappropriate for assessing the gradual process of restoration, and that a term such as “progress” may be more appropriate. Despite this, the term “success” is still widely used, for example, in a recent issue of *Restoration Ecology*, (Volume 18 Issue 6, November 2010) 12 of the 16 research based articles (i.e. from the “Set-backs and Surprises” and “Research Article” sections) contained the term “success” in the context of evaluating the outcomes of restoration actions.

Restoration success, or any other success for that matter, is dependent on the goals one sets. The stated goal of the rehabilitation of coastal dune forest is 1) that “the area will be rehabilitated in accordance with prevailing legislation and to as near to its original condition as is practical", and 2) "the areas affected by the operations will be made safe to [sic] humans and animals" (RBM Environmental Management Plan, EMP, RBM 1995). The prevailing legislation in South Africa is the Mineral and Petroleum Resources Development Act (2002). This act states that mining companies "…must as far as it is reasonably practicable, rehabilitate the environment affected by the prospecting or mining operations to its natural or predetermined state or to a land use which conforms to the generally accepted principle of sustainable development…". It is clear from this goal that the focus of the coastal dune forest rehabilitation programme is rehabilitation and not restoration *per se*. This view highlights ecosystem function and structure more than the historic species composition (SER 2004). Although it is important to note here that neither the EMP or legislation defines the term "rehabilitate(d)".

There are no measures of ecosystem attributes prior to mining and, as such, one cannot divine the original condition. However, past work on rehabilitating coastal dune forests has assumed that intact or relatively undisturbed coastal dune forest sites close to and on the mining lease were representative of the original condition (van Aarde et al. 1996a; Redi et al. 2005; Wassenaar et al. 2005). One may dispute this assumption, especially given the recent work of Ott & van Aarde (*in prep*) and the work of Weisser & Marques (1979), which show that much of these sites were grassland or secondary woodland in the very recent past. However, without focused and structured assessment of the suitability of these sites as references and for the purposes of this synthesis, I will accept that these reference sites are appropriate.

To assess the success of rehabilitating coastal dune forest one must assess differences in ecosystem attributes between the rehabilitating and reference sites and decide if these differences are acceptably small (McCoy & Mushinksy 2002). Many authors have listed attributes of an ecosystem that indicate restoration success. Odum (1969) suggested successional traits that characterise a developing and mature ecosystem, and these have formed the basis of the assessment of restoration success (Choi 2004). Odum (1969, see Table 1 page 265 in his publication) listed 24 attributes in six categories, which address various aspects of an ecosystems development. These six categories include community energetics, community structure, life history, nutrient cycling, selection pressure and overall homeostasis. Odum (1969) considers that as an ecosystem develops toward maturity, it becomes increasingly complex. Ewel (1990) suggests 5 criteria by which managers may assess restoration success. Lubke & Avis (1998) further qualified these criteria. These include, “sustainability” which implies that the rehabilitating or restored site no longer needs management to perpetuate itself (Lubke & Avis 1998). “Productivity” implies that the rehabilitating site is equally as productive as the original or reference ecosystem. The third criteria “Invasibility” implies (importantly) that the site must be open to invasion (colonisation) at early stages of development, but become increasingly closed to invasion as the site develops over time (Lubke & Avis 1998). “Nutrient retention” relates to the ability of the sites to retain nutrients in the soil for use within the rehabilitating ecosystem. “Biotic interaction” implies the development of community interactions, such as predation, pollination, herbivory, mutualism, parasitism, etc. Ruiz-Jean & Aide (2005) reviewed the measures of restoration success used in 468 published articles. They grouped these measures in to three ecosystem attributes, diversity, vegetation structure and ecosystem processes.

There are a whole host of ecosystem attributes that can be measured to assess if a site is successfully rehabilitated. For the restoration manager, this ever expanding list of ecosystem attributes that one may utilise for the assessment of restoration success may be disconcerting. The SER (2004) provide restoration managers with a list of nine attributes that characterise a restored ecosystem (see below). Ruiz-Jaen & Aide (2005) suggest that these "…attributes could provide an excellent assessment of restoration success…" although few studies have the financial resources and detailed long-term studies to address some of these attributes adequately. In my study area, however, there has been 20 years of concerted research, the findings of which are available in 33 published papers and 28 postgraduate dissertations. This body of work has generated a considerable catalogue on several potential measures of restoration success (progression). Most of these research initiatives focused on compositional and structural elements of selected forest communities (herbs, trees, soil invertebrates, millipedes, dung beetles, small mammals and birds), with repeated enumeration over the study period. Information from these studies primarily reflects on compositional and structural aspects at a given time and across chronosequences of forest regeneration. Benchmark values from relatively intact "reference" forests are also available. There have been however, few data accumulated over the study period on functional properties of this ecosystem. These few have addressed soil fertility, the accumulation of soil minerals and the accumulation of biomass and carbon sequestration (van Dyk 1997; van Aarde et al. 1998; Ntshotsho 2006). This wealth of information provides an opportunity to ask whether disturbed coastal dune forest is progressing along a desired trajectory, i.e. gaining structure, composition and function typical (within natural variation) of the mature or undisturbed dune forests of the region.

Here I address the SER's (2004) attributes of a restored ecosystem in reference to the last 20 years of coastal dune forest rehabilitation. My aim is twofold, (1) to assess how useful these attributes are for restoration managers, and (2) to assess if the rehabilitation of coastal dune forest is heading toward a successful outcome. It is important to reiterate that the SER attributes are for a restored ecosystem, and that rehabilitating coastal dune forests appears some way from restoration *per se* (see Wassenaar et al. 2005, 2007, Chapter 3). Despite this, one can use these attributes as potentially desirable targets so that one knows when an ecosystem is restored.

SER (2004) attributes of a restored ecosystem

Attribute 1: "The restored ecosystem contains a characteristic assemblage of the species that occur in the reference ecosystem and that provide appropriate community structure".

This attribute addresses the species composition of the restoring ecosystem and compares it to that in a reference ecosystem. Its use of the term "characteristic" is ambiguous. The term "community structure" in this context has a definition that includes the physiognomy or architecture of the community (SER 2004). This attribute illustrates the most simplistic way to assess restoration success. Crudely, the attribute is suggesting that if the restored community "looks" like the reference ecosystem, in terms of species and architecture then it has been restored successfully. Ewel (1990) cautions against this superficial approach because the rehabilitating community may, in the longer term, collapse. He suggests that managers use ecological criteria that are more robust to assess restoration success. However, managers may need to find a balance between strict ecological criteria, which may be difficult to assess, and less rigorous criteria such as this that are easier and quicker to assess (Lubke & Avis 1998).

The Conservation Ecology Research Unit (CERU) has monitored the rehabilitation of coastal dune forest using this method. One may re-word the first attribute as follows: "In terms of species composition, the restored ecosystem is indistinguishable from that of the reference ecosystem, and it encompasses a similar amount of heterogeneity". Expressed in these terms, this is a less ambiguous approach to assess the compositional similarity between rehabilitating and reference sites. Restoration managers can use this approach to assess not only whether ecosystems are restored but also whether rehabilitating sites are progressing toward successful recovery.

This approach does not assume (as Bradshaw's structure – function model does) that the reference site is a static entity. A "characteristic" community is in reality a moving target, because fluctuations in regional factors (such as climate), small-scale disturbances and other local factors leads to shifts and changes in the species composition of the reference site. A potential method to account for this shifting composition is to use a similarity measure such as Bray-Curtis dissimilarity (Bray & Curtis 1957), to address the variation in species composition and abundance within the reference site. Bray-Curtis dissimilarity assigns a value to pairs of samples that falls between 0 and 1; a value of 0 indicates that the two samples share the same species with the same abundance, whereas a value of 1 indicates that the two samples do not share any species. By comparing the sampling units within the reference site against the mean species abundance values across all sampling units in the reference site one can express the mean compositional dissimilarity (and the variation about the mean value) within the reference site. Figure 7-2 illustrates this approach for four taxa (millipedes, birds, herbaceous and woody plants) in rehabilitating coastal dune forests. In the figure (7-2), the solid horizontal line indicates the mean Bray-Curtis dissimilarity between sampling units within the reference site, and the dashed horizontal lines indicate the variation about this mean. For all of our sampling years, it is evident that there is a great deal of compositional variation in this reference site. For all taxa assessed in Figure 7-2, the mean Bray-Curtis dissimilarity within the reference site was approximately 0.6. In other words, sampling units within the Sokhulu Forest tended to share 40 % of species (at similar abundances). For the millipede and bird communities as rehabilitating sites increase in age, their composition increasingly becomes more similar (or less dissimilar as expressed by Bray-Curtis dissimilarity in Fig. 7-2) to the “mean” species composition in the Sokhulu Forest. Eventually, the sampling units in the oldest rehabilitating sites, in terms of their species composition, have become indistinguishable from those in the Sokhulu Forest. In contrast, the herbaceous and woody plant communities do not appear to be heading toward convergence with the composition of the Sokhulu Forest as the rehabilitating sites age. Sampling plots in the oldest rehabilitating sites are still clearly distinguishable from plots within the Sokhulu Forest reference site as they fall outside of the mean compositional variation found in the reference site. I have suggested some reasons for this pattern in this thesis, such as dispersal limitation, establishment limitation, and the early stage of succession that we are addressing (see Chapters 2 to 6).

This method could be extended to other indicators of the composition (or even structure and function) of reference and recovering ecosystems, such as the proportion of species that occur in the reference ecosystem that are also found in the recovering ecosystem. If the recovering ecosystem is on a trajectory of development toward similarity with the reference ecosystem (benchmark) then the proportion of shared species should increase over time. Figure 7-3, illustrates the change in the percentage of species found in the reference site that are also found in the rehabilitating sites as they age. For all taxa, rehabilitating sites increased in the proportion of benchmark species (per sampling unit) as the sites increased in age. Sampling units in the older rehabilitating sites were indistinguishable from those in the Sokhulu Forest in terms of the proportion of benchmark species. The herbaceous and woody plants increased in the proportion of benchmark species indicating the importance of using more than one method to address changes in composition over time. This finding, taken in conjunction with the Bray-Curtis dissimilarity, indicates that although the species found in Sokhulu forest are increasingly present in the rehabilitating coastal dune forest sites, they are not yet at similar abundances. What both of these figures (7-2 & 7-3) demonstrate is that the reference site (Sokhulu Forest) is typically variable in its composition between sampling units and sampling years, suggesting that the emulation of this heterogeneity in the reference site may be an important goal for restoration managers to aim for.

The attribute in its original form has little practical use for the assessment of restoration success or rehabilitation progression. The adjustment to the wording of the attribute that I have suggested, would allow a more robust assessment of restoration success. The rehabilitating coastal dune forest in terms of species composition is becoming increasingly similar to the reference site as the time since disturbance increases. Some of the older sites have a species composition that is indistinguishable from that of the reference site. This suggests that coastal dune forest sites rehabilitated after mining disturbance are progressing toward restoration success.

Attribute 2: "The restored ecosystem consists of indigenous species to the greatest practicable extent. In restored cultural ecosystems, allowances can be made for exotic domesticated species and for non-invasive ruderal and segetal species that presumably co-evolved with them. Ruderals are plants that colonize disturbed sites, whereas segetals typically grow intermixed with crop species." (SER 2004).

This attribute also addresses the species composition of restored ecosystems. The exclusion of non-indigenous species is motivated by the historical focus of restoration, which attempts the recovery of "historical authenticity" (SER 2004). In addition, non-indigenous species are perceived to be competitively superior and have the potential to alter or deviate ecological trajectories, and therefore negatively influencing restoration success (Matthews & Spyreas 2010). However, the presence of non-indigenous species is not necessarily a precursor to negative ecological effects; many non-indigenous species are benign (Brown & Sax 2007). In addition, the eradication of all non-indigenous species is an expensive strategy and may be impossible (Mason & French 2007; Norton 2009). The SER (2004) recognise this reality in the text of their Primer on Ecological Restoration. They suggest that the highest priority should be to remove those species that pose the greatest threat. Perhaps this is what they mean by the term "…to the greatest practicable extent". This attribute needs to be qualified before it becomes a useful or obtainable measure by which restoration managers can determine restoration success.

How do we recognise the species that are of the greatest threat? One may expect that non-indigenous species become increasingly problematic where they are increasing in abundance, spread to an increasing number of localities within recovering sites and remain persistent throughout succession. Where species fulfil any or all of these criteria managers may wish to investigate the effect they have on native species or ecosystem functions.

Research in my study area on effects of non-indigenous plant species in the rehabilitating sites is limited to that shown within this thesis. In Chapter 4, I demonstrated a potential method by which managers may identify which species are responsible for the most dissimilarity between rehabilitating and reference sites. If these species are non-indigenous, then management can target their removal. Few herbaceous, non-indigenous plants were persistent and all were at relatively low abundances throughout the successional sere (less than 7 % of the total abundance of the herbaceous plants is non-indigenous in sampling plots; see also Chapter 4). However, I did identify one species that appeared to be increasing in abundance and increasing in its contribution to the Bray-Curtis dissimilarity between rehabilitating sites and the reference site.

This species was *Achyranthes aspera*, which appears to be becoming increasingly important (i.e. contributes a greater amount to the total abundance of sampling plots, Fig. 7-4) and appears to be spreading to more localities within sites as they age (Fig. 7-5). *Achyranthes aspera* is also increasing in relative abundance in the Sokhulu Forest reference site (Fig. 7-4). All of this suggests that it may be important for managers investigate whether this species has any negative impacts on indigenous species. In addition, *A. aspera* is listed as a 'Category 1' species in the Conservation of Agricultural Resources Act – South Africa (1983), which means landowners are legally obliged to control it through mechanical, biological or chemical methods.

In the woody plant community there are also non-indigenous species including *Cestrum laevigatum*, *Psidium guajava* and *Citrus limon*. These species do not contribute more than 1 % to the total abundance of woody plants in sampling plots (*C. laevigatum*: 0.17 ± 1.06; *P. guajava*: 0.61 ± 3.54; *C. limon* 0.01 ± 0.10; mean ± standard deviation, n = 324 plots). Interestingly, despite being dispersed by cattle, *P. guajava* was not persistent. The relatively high standard deviation reflected a peak in *P. guajava* relative abundance in 5 year old sites. There were no apparent age-related trends in the non-indigenous woody plants.

Few mammalian herbivores, other than cattle occur in coastal dune forests (Ferreira 1997). Indigenous herbivores forced through management practises (fencing and stocking of game reserves for example) to use this ecoregion have known destructive consequences for coastal dune forest regeneration (Boyes et al. *In press*). Both Wassenaar & van Aarde (2001) and Mpanza et al. (2009) addressed the influence of cattle (the most abundant non-indigenous mammal) on the plant community in rehabilitating sites. Cattle had several potential impacts on the rehabilitating coastal dune forest, such as the alteration of species richness, composition and cover through grazing, browsing and trampling (Wassenaar & van Aarde 2001; Mpanza et al.

2009). In addition, the cattle were apparently dispersing the seeds of the non-indigenous plant species, *Psidium guajava* (although *P. guajava* does not increase in abundance over time – as shown above). Therefore, restoration managers at RBM have decided to reduce the threat cattle pose by actively discouraging them from entering rehabilitating sites.

To date, rehabilitating coastal dune forest appears to be free of persistent non-indigenous species, with the exception of *A. aspera*, which is also increasing in the reference site. This species needs to be the target of a scientific investigation to ascertain its potential to influence the forest ecosystem negatively. The potential impact of non-indigenous mammals means that management solutions need to be investigated to ensure that the future of coastal dune forest post-mine closure is self-sustainable.

The historical focus of attribute 2 (SER 2004) means that in areas where non-indigenous species have colonised (I use this term to avoid the pejorative term “invaded”) the attainment of restoration *per se* would involve extensive management intervention. The eradication of non-indigenous species may be impossible; even where conservation bodies are well funded, there have been few successful eradication programmes (for example in the United Kingdom, see Manchester & Bullock 2000). The reality appears to be that eradication of all non-indigenous species is difficult (if not impossible) in areas where human-transformed landscapes dominate. If managers are to adhere to the letter of this attribute, then restoration will become a “gardening” discipline, by which I mean that there will be a need to continually control and remove non-indigenous species (Norton 2009). This contravenes attribute nine, which highlights the importance of self-sustainability in a restored ecosystem. As Norton (2009) states “ecological restoration in the face of biological invasion needs to be adaptable in the manner in which it sets outcome targets." Restoration ecologists may need to accept that native species can be sustained along with non-indigenous species in novel assemblages.

This attribute once again requires qualification prior to becoming useful for restoration managers. Species that degrade or cause detraction from the desired ecosystem trajectory need to be assessed and managed for. This attribute could be reworded to reflect this as such; "The restored ecosystem consists of species whose presence or actions do not detract from the desired trajectory of recovery. These could be non-indigenous or indigenous species."

Attribute 3: "All functional groups necessary for the continued development and/or stability of the restored ecosystem are represented or, if they are not, the missing groups have the potential to colonise by natural means." (SER 2004).

This attribute attempts to reconcile species composition and ecosystem functioning. A functional group, according to the SER primer (2004), is a subset of the species assemblage that can be recognised by their functional role in the ecosystem, for example, primary producers, herbivores, carnivores, decomposers, nitrogen fixers, and pollinators. Species may fall into one of these groups regardless of their phylogenetic groupings. Functional groups are components of biological diversity that influence how an ecosystem operates (Tilman 2001). Postulates on the assembly of communities after disturbance suggest species composition is influenced by historical contingency (Gleason 1927), but the composition of functional groups of species is determined by environmental factors (Fox 1987). This postulate was untested until recently, but Fukami et al. (2005) showed that although species identities in experimental grassland communities were divergent, species traits converged. For restoration ecology, this concept is applicable to projects that are following a process of rehabilitation (sensu SER 2004). The recovery of ecosystem function is not reliant on the return of the historical biotic community (which may be impossible) but is reliant on the colonisation of species that are functionally equivalent of the historical community.

Research on the rehabilitating coastal dune forest has not explicitly addressed functional groups. Where the term "functional group" has been used, it has been actually describing the related concept of "guilds". These two terms are often used synonymously (Simberloff & Dayan 1991), but the basis of their definition is different. Guilds are "a group of species that exploit the same class of environmental resources in a similar way" (Root 1967). A functional group, however, is defined on the basis of similarity in ecosystem function (Blondel 2003). The approaches differ in that the guild concept explicitly relates to the structural component of an ecosystem whereas the functional group concept relates to ecosystem function (Blondel 2003). Davis et al. (2002) suggest that the restoration of dung beetle functional groups will be achieved with the closure of the forest canopy. Functional groups in the dung beetle community in Davis et al.'s (2002) study are partitioned on traits related to how they utilise and disrupt dung (according to Doube 1990). This clearly relates to resource use and not ecosystem function and is therefore a guild description. A functional group defined on their role in nutrient cycling could include both dung beetles and millipedes, which also play a functional role in nutrient cycling (Smit & van Aarde 2001).

A major constraint with the functional group (and guild) approach is that the researcher arbitrarily selects the traits that define a particular group *a priori* (Petchey et al. 2004). This approach assumes that traits of importance are discrete, whereas evidence suggests that most traits are actually continuous (Diaz et al. 2004; Wright et al. 2006). The result of these arbitrary groupings is that the diversity of functional groups is no better than species richness in accurately predicting ecosystem function (Petchey et al. 2004). Wright et al. (2006) showed that *a priori* functional group classifications were no better than random group classifications at predicting ecosystem function.

In the past decade, many authors have developed methods to reduce bias in group characterisation (these have been recently described by Mouchet et al. 2010). These rely on information regarding species traits that relate to the function of interest, for example, root depth, canopy architecture and Nitrogen concentration are all related to growth rate, which is in turn related to the ecosystem level effect, primary productivity (Lavorel & Garnier 2002). The methods define functional diversity without the reliance on the researcher. These methods offer a potential for ecologists to link species composition and function in rehabilitating ecosystems. The potential value and application of these methods to coastal dune forests awaits assessment. However, one of the major limitations of the catalogue of information that has resulted from the 20 years of research on the rehabilitation of coastal dune forest is a lack of information on species traits. Sweeny (2005) did address seed size in dune forest trees and how this influences colonisation, but there have been few other traits that have been identified that can be used to assess functional groupings. This short-coming needs to be redressed.

This attribute in its current state is not particularly useful for the assessment of restoration success. The use of functional diversity as a measure of restoration success should be encouraged, but the functional group concept may be too arbitrary to be of use (see Petchey et al. 2004; and Wright et al. 2006). This attribute should be simplified as follows; “the restored ecosystem has an acceptably small difference in functional diversity when compared to the reference ecosystem.” The concept of acceptably small difference could be assessed in a similar way to that shown above for ecosystem composition.

Attribute 4: "The physical environment of the restored ecosystem is capable of sustaining reproducing populations of the species necessary for its continued stability or development along the desired trajectory." (SER 2004).

I will address this structural attribute in two sections. First, I will address the term "reproducing populations" and then I will attempt to address the phrase "… for its continued stability…" The latter phrase was also used in attribute 3. An indicator of restoration progression in a redeveloping ecosystem, such as the rehabilitating coastal dune forest, would be a reproducing population of late successional species. Conversely, an indicator of restoration failure or regression would be a reproducing population of a pioneer species. How would a manager recognise a reproducing population? Quite obviously, the presence of offspring of some species may be an indicator of reproducing individuals but not necessarily of reproducing populations. However, if we assume that size is a proxy for age, we can use size class distributions to assess the age-range within a population, this is a common method adopted in the study of forest tree dynamics (e.g. Midgley et al. 1990; van Wyk et al. 1996; West et al. 2000). A reproducing population would contain more saplings and seedlings and fewer adults. In this case, the size class distribution would fit a negative exponential function (also known as the "reverse J" distribution; Veblen 1981; Midgley et al. 1990; See Figure 7-6).

Within this study, I showed that typical early-colonising forest trees (*Celtis africana*, *Ekebergia capensis* and *Mimusops caffra*) were replacing the canopy dominant pioneer species *Acacia karroo* (Chapter 5), and I showed that the ten most abundant tree species in rehabilitating coastal dune forests displayed the typical "reverse J" size distribution pattern associated with a recruiting population (Chapter 3). The pioneer, *A. karroo*, did not show this pattern as there were few saplings and seedlings when compared to adults (see Figure 7-6). Therefore, it appears that the rehabilitating sites are providing a physical environment capable of sustaining reproducing populations of forest tree species. For other taxa, we can surmise that reproducing populations of later successional species are replacing early successional species from the patterns of turnover that we have observed over the last 20 years (see Chapter 3).

The attribute calls for reproducing populations of species that are "necessary" for the restored sites' "continued stability" or the "development" of a recovering site along an ecological trajectory. What does this mean? Ecosystem stability as defined by the SER (2004) is the ecosystems ability to maintain its trajectory in spite of stress; they state that this is a dynamic equilibrium and not a static state. Stability is achieved through resistance, the ability of an ecosystem to maintain its structure and function in the face of disturbance, and through resilience, its ability to regain structure and function after disturbance (Pimm 1991). Does this phrase mean that the rehabilitating site must show an increase in species richness or that certain species are more important in provisioning stability than others, which are both thought to correlate with increased stability (McCann 2000; Tilman et al. 2006)? Johnson et al. (1996) describes four hypotheses that address the relationship between species diversity (richness) and ecosystem stability.

The diversity-stability hypothesis, proposed by MacArthur (1955), suggests that any deletion of species from the community will increase the susceptibility of the ecosystem to disturbances (increased instability). Alternatively, only few species in the community may be important for ecosystem stability. The rivet hypothesis (Ehrlich & Ehrlich 1981) suggests that like the rivets holding an aeroplane's wing to the body, the rest of the community absorbs the loss of a few species, however, there is a threshold at which the cumulative loss of species can no longer be absorbed and the ecosystem collapses. Conversely, the redundancy hypothesis (Walker

1992) suggests that species in the same functional group can compensate for the loss of species from the same group. Finally, there may be no relationship or indeterminate relationship between species richness and function (Lawton 1994).

The rehabilitating coastal dune forests do increase in richness (and diversity) as they increase in age (Ferreira & van Aarde 1996; van Aarde et al. 1996b; van Dyk 1997; Kritzinger & van Aarde 1998; and see Chapter 3). However, the bird populations have been shown to be declining (Trimble & van Aarde 2011). What effect richness has on the stability or development of the rehabilitating coastal dune forest is currently unknown. Our data does not lend itself well to the measure of ecosystem stability, as we do not have controlled experimental plots for example. However, previous work has demonstrated that the development trajectory (species composition, abundance and diversity) of rehabilitating coastal dune forest is heading toward that found in the reference site (van Aarde et al. 1996c; Davis et al. 2003; Redi et al. 2005; Wassenaar et al. 2005). We can only assume that this will bring about similar levels of "stability" as those found in the reference site (which are also unknown).

This and the previous attributes' use of undefined terms makes it difficult for one to assess restoration success. The increase in reproducing populations is important – it shows that the ecosystem is functioning. However, the phrase "…necessary for its [the ecosystem's] continued stability or development…" may mean at least two related but different things, that restoration managers should promote species richness, or that they should promote certain subsets of the community to ensure stability. Rather than addressing this limited and confusing attribute, restoration managers may be better suited to assess the turnover of species from those with life histories adapted to early successional stages to those suited to late successional stages. Chapter 3 shows this type of analysis and as rehabilitating sites increase in age species with life histories suited to late successional stages have replaced those suited to early stages. So phrased in a similar way to the SER attribute one may expect that; “The physical environment of the restored ecosystem is capable of sustaining reproducing populations of species with life histories adapted to late successional stages such as the reference site.”

Attribute 5:”*The restored ecosystem apparently functions normally for its ecological stage of development, and signs of dysfunction are absent.” (SER 2004).*

What are the “normal” functions of an ecosystem? These could include things such as biomass accumulation, nutrient accumulation, carbon sequestration, primary productivity, mutualism and so on (see Odum 1969). There are a large number of potential ecosystem functions and an equally large number of possible responses that these functions may display across a sere of development. Past research on functional aspects of the rehabilitating coastal dune forest ecosystem have been restricted to soil nutrient accumulation, soil fertility and biomass accumulation with its associated carbon sequestration (van Dyk 1997; van Aarde et al. 1998; Ntshotsho 2006; see also Chapter 3). Nutrient accumulation is a commonly assessed functional aspect of ecosystem recovery (for example; van Aarde et al. 1998; Abreu et al. 2009; Paul et al. 2010). Mature systems are thought to have a greater capacity for the retention of nutrients than young systems (Odum 1969; although see Guariguata & Ostertag 2001 and references within); therefore, the assumption is that across a sere of rehabilitating or regenerating sites, soil nutrient retention (and hence nutrient concentrations) will increase to similar levels to that found in undisturbed reference ecosystems. This is exactly what happens on rehabilitating coastal dune forest sites (van Aarde et al. 1998). The accumulation of biomass also follows expected trends in rehabilitating coastal dune forests (Chapter 3). The pioneer tree, *Acacia karroo* increases in biomass resulting in increased competition between individuals and consequently, self-thinning. This is a potential mechanism by which niche-space is opened for the colonisation of secondary tree species (van Dyk 1997; Ntshotsho 2006).

This attribute addresses one of the three components of an ecosystem – its function. This component may be the first to recover after a disturbance event (depending on which aspect of function one addresses). For example, soil stability is increased by the development of plant roots; however, the species identity of the plants involved is irrelevant. In restoration, the function of an ecosystem is assumed to be linearly related to its structure, as shown on Bradshaw's (1984) structure – function model (Figure 7-1). However, the relationship between function and structure may be non-linear, and restoration ecologists need to be aware of this (Cortina et al. 2006). Rehabilitating coastal dune forest shows progression (toward levels in the reference sites) in two functional aspects, soil nutrient cycling and biomass accumulation (van Dyk 1997; van Aarde et al. 1996; Ntshotsho 2006). Future work may need to assess the relationship between species composition, structure and function in the rehabilitating and reference sites. This will allow one to highlight which species or groups of species play the most important functional roles and, therefore, need to be important targets for rehabilitation.

There is nothing wrong with the functional focus of this attribute, but once again, the undefined and ambiguous terms make it difficult to assess. Odum (1969) provides a much clearer list of expectations for the changes expected in functional aspects of an ecosystem after a disturbance event. These include nutrient and mineral cycling, biomass accumulation and productivity. Once again, these functional aspects could be compared with the reference site and an assessment made as to whether or not the difference is acceptably small (sampling units in rehabilitating and reference sites are indistinguishable).

Attribute 6: *"The restored ecosystem is suitably integrated into a larger ecological matrix or landscape, with which it interacts through abiotic and biotic flows and exchanges."* SER (2004).

This attribute recognises that the restored or rehabilitating ecosystem is not a closed system. Abiotic and biotic interactions and exchanges occur between the rehabilitating site and the surrounding landscape. These could include such factors as water flow, nutrient leeching, dispersal of biota, movement of herbivores, dispersal of non-indigenous plants, movement of predators and so on (Holl et al. 2003). The results of these exchanges could be both positive and negative for restoration success.

Early in succession, immediately after disturbance, one may expect that biotic interactions and exchanges are generally unidirectional; species disperse to and colonise the rehabilitating site. We can infer from compositional and structural data on the rehabilitating coastal dune forest sites that species are dispersing to the rehabilitating sites. We know from horticultural work that many trees found in coastal dune forest have seeds that are recalcitrant (Nichols 2005), meaning that these species in the rehabilitating sites have dispersed there and have not just germinated from the topsoil. The accumulation of species of all taxa is further evidence that the rehabilitating sites in this study are suitably integrated with the surrounding landscape (Figure 7-7). Another line of evidence comes from work on millipedes by Redi et al. (2005). They showed that the millipede community was more similar to that in reference sites that were geographically closer to the rehabilitating site. One can infer that the millipede community in rehabilitating sites is supplied by the nearest source population.

The composition of the landscape surrounding rehabilitating sites may act as a barrier to the dispersal of some species and to their dispersal vectors (Holl 2002; Chapter 6). Dispersal limitation is considered a threat to the success of rehabilitating sites (Holl 2002; Young et al. 2005; Battaglia et al. 2008;Walker & del Moral 2009). Earlier work, in my study area showed that vervet monkeys (*Chlorocebus pygerythrus*) move from remnant forest patches into the rehabilitating sites and bring with them the seeds of broadleaved forest species (Foord et al. 1994). From work in progress, it appears that birds (and bats) also bring in these seeds from outside of rehabilitating sites (I assume this because reproductive populations of the species have not been recorded in the sites).

Rehabilitating coastal dune forest sites appear to be integrated with the landscape in terms of biotic flows coming in. CERU's research has not addressed abiotic flows between the rehabilitating sites and the surrounding landscape. The attribute highlights the importance of recognising that the rehabilitating (or restored) site is an integrated component of a larger ecosystem. It is difficult for one to imagine a site that is not receiving biotic and abiotic flows from the surrounding landscape in reality, so this may only be a useful attribute for conceptual thinking and planning of rehabilitation.

Attribute 7: *"Potential threats to the health and integrity of the restored ecosystem from the surrounding landscape have been eliminated or reduced as much as possible." SER (2004).*

The attribute is similar to the previous, but addresses the negative impacts that potentially emanate from the surrounding landscape. Potential threats to health and integrity from surrounding landscape include the presence of non-indigenous species (as addressed above in attribute 2) dispersing from outside of the rehabilitating sites, and pollutants entering the rehabilitating sites from external sources (such as water courses, road runoff etc.). I have dealt with non-indigenous species above, and there is no information on abiotic negative impacts on rehabilitating coastal dune forest sites.

This attribute appears superfluous as the aspects it addresses could be incorporated into the previous attribute without reducing its effectiveness for assessing restoration success. The regenerating coastal dune forests are integrated into the matrix but may receive both undesirable and desirable consequences of this integration (Wassenaar et al. 2007).

Attribute 8: *"The restored ecosystem is sufficiently resilient to endure the normal periodic stress events in the local environment that serve to maintain the integrity of the ecosystem." SER (2004).*

The resilience of an ecosystem relates to the rate of its return to an equilibrium state after perturbation (Neubert & Caswell 1997). Measures of resilience used in restoration ecology compare values between rehabilitating and reference sites. These values include compositional, structural or functional aspects of the ecosystem as discussed above. Wassenaar et al. (2005) modelled the convergence rate between community composition in rehabilitating and reference sites in my study area. This illustrated that coastal dune forest is highly resilient. Resilient communities may have experienced past disturbances that lead to the extinction of species sensitive to disturbances (Lawes et al. 2007). The high levels of disturbance in the recent past may have inferred resistance on the coastal dune forest (Weisser & Muller 1983). Alternatively, the coastal dune forest is a relatively young (geologically) so it may not have had the opportunity to develop specialist species that are sensitive to disturbance events. A combination of both these factors may be the reality.

The attribute is a re-iteration of some of the previous attributes. Resilience is an important attribute of a community for restoration manages as it measures the rate at which recovery occurs. However, it is important to note that the rate at which disturbed sites recover ecosystem composition, structure and function may not be linear (or unidirectional) and therefore managers cannot rely on predictions based on linear assumptions. Routine evaluation of restoration based on measures of resilience may thus be fraught with complications and the attribute may do little else but pay irrelevant lip-service.

Attribute 9: *"The restored ecosystem is self-sustaining to the same degree as its reference ecosystem, and has the potential to persist indefinitely under existing environmental conditions. Nevertheless, aspects of its biodiversity, structure and functioning may change as part of normal ecosystem development, and may fluctuate in response to normal periodic stress and occasional disturbance events of greater consequence. As in any intact ecosystem, the species composition and other attributes of a restored ecosystem may evolve as environmental conditions change" SER (2004).*

This attribute addresses the key aim of restoration ecology, which is a self-sustaining community. The attribute does not contain any measurable aspect, and as such may only be useful as an aspiration for restoration managers. This attribute is the first to highlight that an intact ecosystem is a dynamic entity and may change with environmental conditions. This is an important conceptual consideration when one is assessing restoration success.

The rehabilitating coastal dune forest sites represent a successional sere (Chapter 3), which has undergone limited management, except the initial "kick-start" process (see Chapter 2 and Plate 7-1). Despite 34 years of regeneration, the oldest sites are still at an early stage of succession (Chapter 5). As such, we cannot yet address long-term self-sustainability. However, my predecessors and I have shown that key biotic and abiotic aspects of the rehabilitating community are progressing toward similar levels as that found in reference sites. This follows the predictions of theory (Chapter 3). We have identified some potential barriers to the success of this rehabilitation programme, such as the landscapes composition (Chapter 6) and regional climatic changes (Trimble & van Aarde 2011); however, overall research indicates that the rehabilitating community will eventually be self-sustaining to the same degree as the reference ecosystem.

Are the SER attributes fit for purpose?

The nine attributes proposed by the SER (2004) to describe a restored ecosystem are difficult for restoration managers to use towards assessing restoration success/progression. The reason I say this is that they are variously ambiguous, contradictory, repetitive, difficult to measure, superficial, and based on a static entity and not on processes. The use of undefined terms such as “characteristic”, “normal” and “greatest practicable extent” makes it difficult for managers to assess if their actions are leading toward restoration success. The definition of ecological restoration may encompass a variety of different activities, including technical measures such as planting of seeds and seedlings through to the reliance on spontaneous ecological processes after amelioration of initial (post-disturbance) conditions. This may explain the ambiguous and contradictory nature of some of the attributes; however, it does not excuse it.

The attributes have a strong historical focus. The first two attributes relate to the return of the historic composition of the reference site, which may be an unobtainable goal (Jackson & Hobbs 2009). The strong focus on ecosystem function that is apparent in the remaining attributes is a positive aspect of these attributes. Functional aspects are possibly the easiest aspect of an ecosystem to recover, followed by structure and then composition (Beard et al. 2005). However, functional aspects are likely the most difficult aspects of an ecosystem to measure because they may take the longest amount of time to recover (Morgan & Short 2002). Structural and compositional aspects of an ecosystem may be easier for managers to measure and monitor, but restoration ecologists need to link these aspects to the function of the ecosystem to ensure a complete assessment of rehabilitation success.

The SER (2004) attributes of a restored ecosystem do not appear "…to provide an excellent assessment of restoration success…" as suggested by Ruiz-Jaen & Aide (2005). Some, such as the last attribute, clearly reflect only inspirational statements of restoration and not measurable and robust descriptors of a recovered ecosystem. The lack of clearly defined ecology, and the use of ambiguous terms such as "characteristic" and "continued stability", makes it very difficult for restoration managers to use these attributes to assess success even when there is 20 years worth of data.

A framework for the assessment of success or progression in rehabilitating coastal dune forest

I have suggested that the SER (2004) attributes are not fit for purpose, so it is important that I provide alternatives. I provided an alternative wording for four of the attributes above. These attributes address aspects of the ecosystem that can be measured and that I feel are important in the assessment of the progression of rehabilitating coastal dune forest. However, these attributes are made redundant if one assesses restoration success as I suggest below.

An ecosystem is made up of three components: composition, structure and function. The focus of rehabilitation is on functional aspects (SER 2004) but these are linked to compositional and structural factors. Any assessment of the success of rehabilitating coastal dune forest must address all these three components. Progression or success can only be determined by addressing the differences in these three components between the rehabilitating and reference sites. One then needs to decide if this difference is "acceptably small" (McCoy & Mushinksy 2002). This can be achieved by addressing the inherent variation in reference sites in terms of these three components. Restoration success is therefore achieved when the rehabilitating site is indistinguishable from the reference site in terms of composition, structure and function. Progression would be evident where these values increasingly become more similar to those (inclusive of variation) in the reference site over time.

One could assess success (or progress) very simply with a single statement that addresses the three components that make an ecosystem; composition, structure, and function;

In terms of species composition, structure and function the restored ecosystem is indistinguishable from that of the reference ecosystem, and it encompasses a similar amount of heterogeneity.

To assess progression one would simply reword these statements to reflect a trend over time. The exact measures of composition, structure and function one addresses may be decided by 1) the specific goals of the project, 2) the budget of the project and 3) the timescale of the project. For example, some aspects of ecosystem function, such as soil nutrient content, may take several decades to recover and extrapolation of short-term monitoring may be inaccurate. Any of the above measures of the attributes of an ecosystem may be useful in determining restoration success, as long as they are compared to reference sites (relatively mature or undisturbed sites). This approach would benefit from an understanding of how these three components (composition, structure and function) are linked. Once one understands this for coastal dune forest then the monitoring of progression may be limited to the easiest aspects of the ecosystem to measure: structure and composition.

Obviously, this approach relies on reference ecosystems or values from the sites prior to disturbance. The validity of reference sites needs to be assessed. The goal of rehabilitation in my study area is that disturbed areas are rehabilitated "…to as near to its original condition as is practical" (RBM 1995). Therefore, some measure of "original condition" is needed. By addressing a current reference site rather than the pre-disturbance conditions however, one would avoid the incorrect assumption that an ecosystem is a static entity, and one can account for the variation in ecosystem attributes over time.

Is "restoration" of coastal dune forest obtainable?

Can we expect the return of all the species that make up the community in undisturbed sites? Of course not, the processes that give rise to a community assembly after disturbance events do not reproduce a facsimile of the previous community. Many factors limit the ability or potential for species to establish populations after disturbance. These include historical contingency, changes in the species pool, extinction debt, changes in the landscape composition, removal of sources and many more. A restoration practitioner may be able to mitigate for some of these factors but not others. For example, in Chapter 6, I defined "forest associated species" as those recorded in the Sokhulu forest, and nearby Mapelane Coastal Dune Forest Nature Reserve, consistently (present in the majority of survey years) during our 18 years of fieldwork. As well as being listed as inhabiting forests in well-known field-guides (Gibbon 2006 for birds, and Coates-Palgrave 2002 and Pooley 2003 for trees). The term "forest associated species" is a qualitative judgment of which species are more closely associated with forest (inclusive of forest edge). I showed that for some of these species the composition of the landscape (patch area and isolation) was more important in determining their presence at a site than the age of the site alone. This suggests that for some species the landscape composition presents a barrier to their successful colonisation of rehabilitating sites.

For other species, the age of sites was more important than patch variables (Chapter 6), which suggest that, given time, the composition of the rehabilitating sites will become more populated with forest associated species. Rehabilitation of coastal dune forest is increasingly giving rise to conditions that are suitable for forest species; these could include the availability of light or other such resources.

Given all of the above, can we now say if rehabilitation of coastal dune forest is successful? By this I mean, are the consequences of the combined effects of a kick-start process (soil amelioration) and natural colonisation giving rise to (or progresses toward) a self-sustaining coastal dune forest ecosystem? It appears that rehabilitating coastal dune forests become increasing similar to undisturbed forests typical of the region in terms of productivity (for example van Dyk 1997) and nutrient retention (van Aarde et al. 1998). In addition, the rehabilitating sites show that they are open to invasion at an early stage, and patterns of turnover show that they become less so as they age (Chapter 3). Questions of sustainability still need to be addressed; although, the obvious increase in abundance of species typical of late succession at the expense of early successional species, for example, give the impression that the sites are currently progressing toward self-sustainability. One key area of research that I feel we still need to address is the functional diversity that is present within the rehabilitating coastal forest.

Community composition also becomes increasingly similar to the undisturbed reference sites as rehabilitating sites age (for example, Wassenaar et al. 2005). This is an important finding, but one that I feel we should not wholly base our assessment of success on. If we accept that historical contingency and other factors that limit the return of historical community composition are a reality, then by basing success on the return of composition to a site we are setting ourselves impossible targets.

Rehabilitating coastal dune forest appears at this early stage of development to be progressing toward restoration success. However, as the rehabilitating sites are at such an early stage of succession, it is important that monitoring continues because threats that may detract from success (such as regional declines in species, Trimble & van Aarde 2011) may occur. Only through monitoring can we implement adaptive management to ensure future sustainability of the rehabilitated coastal dune forests.

Is the conceptual basis of coastal dune forest restoration the correct one?

We can place theories on the assembly of biological communities in to three stables, the deterministic assembly (stable equilibrium, Clements 1916), stochastic assembly (unstable equilibrium, Gleason 1926; Hubbell 2001) and alternative stable states (multiple stable equilibriums, Sutherland 1974). The deterministic assembly models (succession) suggest that species composition is determined by the environmental conditions prevalent within a region and that a community will re-assemble in a predictable manner toward the same end-point typical of the region. The stochastic assembly models suggest that random processes, such as the order of species arrival, determine the assembly of communities. Therefore, there is no unified end-point to the assembly process. The alternative stable states model represents the middle ground

(Temperton & Hobbs 2004). Deterministic community assembly is mediated by random events (the availability of species, historic events, timing of species arrival etc), and this leads to one of several possible alternative stable states. Currently, many ecologists are inclined to believe that the alternative stable states model is the most accurate description of natural systems (Temperton & Hobbs 2004).

Given the understanding of historical contingencies and the role of stochastic events in the re-assembly of communities, it is surprising that the theory of succession has provided such a sound basis by which we can assess the redevelopment of coastal dune communities destroyed by mining activities. Chapter 3 demonstrates the predictable assembly of species on these rehabilitating sites up until ~30 years of age. In Chapter 4, despite being initially dissimilar, the rehabilitating sites became increasing uniform in composition as they aged; although they still differed from the benchmark forest. Deterministic processes, therefore, initially seem to be driving the re-assembly of coastal dune forest. However, we must not rule out the alternative stable states model, as we are only at a very early stage of community assembly (Chapter 5).

The question of why coastal dune forest re-assembly is so predictable up until 34 years of regeneration needs to be addressed. Several others have addressed aspects relevant to this topic. For instance, Chase (2003) suggested that where there are few barriers to dispersal, high rates of disturbance, a small regional species pool and low productivity, one could expect community convergence. Lanta & Lepš (2009) show that the availability of propagules is important in determining the trajectory of succession; sites that share the same source become more similar in terms of community composition. What does this mean for the rehabilitating coastal dune forest sites? My assessment in Chapter 6 suggests that the probability of colonisation depends on the composition of the landscape - so some species may not be able to reach rehabilitating sites without assistance or a greater length of time. Currently, the rehabilitating coastal dune forest is made up of grassland (in the youngest stages) and woodland (in the oldest stages) adapted species. These species may be able to disperse freely from adjacent woodland and grassland areas of the rehabilitating sites and so-called “eco-strip” (a narrow unmined belt of vegetation along the coast). Forest species may be dispersal limited, and this may be due to the configuration of the landscape (Chapter 6). Therefore, the species composition of rehabilitating sites may be a product of the surrounding landscape, and those “missing species” are the ones that are not present (or not reproductive) in the adjacent landscape but are only present in the Sokhulu forest. The Sokhulu forest may be too remote for the dispersal capabilities of some species, or the matrix between it and the rehabilitating stands may form a distinct barrier. This dispersal limitation may lead to rehabilitating sites developing towards an alternative stable state (see Suding & Hobbs 2009). Currently, this is purely speculation, but research on issues of how a local community forms are important for restoration and interesting for ecologists to answer.

The equilibrium view of succession is largely disputed; one reason is that it ignores the patchiness of natural communities (Wu & Loucks 1995). The patch dynamics model suggests that small-scale disturbances reset succession and lead to a shifting mosaic of patches at different stages of succession (Wu & Loucks 1995). The mature stages of patch dynamics are, therefore, in non-equilibrium. Chapter 5 describes the collapse of the *A. karroo* dominated canopy, which led to patchiness in the rehabilitating sites. Patch-dynamics may be a better description of the mature stages of coastal dune forest regeneration and, therefore, a better conceptual basis. Again, this patchiness in the landscape and its role in determining community composition (at different scales) is an important avenue for future research.

What are the implications for conservation?

The question of whether there will be a net gain in conservation value because of this rehabilitation programme is fundamentally the most important question that we need to answer. Some species undoubtedly gain from the heterogeneity currently represented across the mining lease area; different successional stages support different sets of species. Recently, Rey-Benayas (2009) reviewed 87 restoration projects across the world and showed that these projects increased biological diversity and ecological services.

The work of Weisser & Marques (1979) and recent work by Ott & van Aarde (*in prep*) show that the pre-mining landscape was a mosaic of bare sand, coastal grassland, and small fragmented patches of secondary coastal dune vegetation. Therefore, the programme of coastal dune forest rehabilitation is actually attempting to recreate an assumed historical landscape prior to the large-scale exploitation of these forests for charcoal production in the 19th Century (Maggs 1980). The current rehabilitation programme has, therefore, probably added a large amount of biological value to these coastal dunes compared to their degraded state immediately prior to mining. However, we have no information of the pre-mining species richness and abundances of species, so the above has to remain a speculation.

In addition, the rehabilitating sites have at least two important socio-economic benefits. Firstly, the reassembly of coastal vegetation provides protection for the inland human communities from the negative effects of storm surges that have the potential to cause flooding, which could damage crops and livelihoods (Danielsen 2005). The second is the provision of medicinal plants. In South Africa, an estimated 60 % of the population use traditional medicines and in the province of KwaZulu-Natal the figure rises to 80 % of the population (Taylor et al. 2001). One of the main threats to the diversity of medicinal plants in Africa comes from habitat loss (McGeoch et al. 2008), and the degradation of these medicinal resources may negatively affect the healthcare of local people (Shanley & Luz 2003). Therefore, the assembly of at least 109 woody plant species and 62 herbaceous plants that have some medicinal value to humans and their livestock (Pooley 1998; Coates-Palgrave 2003) is of direct value.

Rare and specialised species are often the focus of conservation management, and if restored sites do not provide for these species, then restoration fails as a conservation initiative. The absence of forest species (Chapters 4 and 6) and the role that the landscape composition plays in the probability of occupancy for some forest species may question the conservation value of coastal dune forest restoration. However, as the rehabilitating coastal dune forests are at such an early stage of succession this may be a very premature judgement.

The contribution to conservation, however, can not be measured only in terms of providing ‘niche space’ for rare and specialist species as these may only account for a fraction of the biological diversity (genetic, species and systems) at which conservation should be directed.

What are the implications for management?

The findings of this thesis suggest that succession is a valid driver of the early regeneration of tropical coastal vegetation (Chapter 3). It appears that processes are in place that will lead to the reassembly of coastal dune forest communities, as long as internal and external disturbances are mitigated (if research shows this is needed). As the rehabilitating sites are at an early stage of regeneration (Chapter 5), these processes may take some time to give rise to these coastal dune forest communities, and the management of rehabilitating coastal dune forest must allow for this. In addition, it is important to remember that time may be interacting with the landscapes spatial attributes, which may limit the presence of certain species (Chapter 6). If these species play important functional roles in the forest ecosystem, they may need assistance in achieving colonisation and establishment. However, a thorough investigation of this subject is required, and any discussion of management techniques to assist colonisation needs to await such.

In Chapter 4, I used a methodology that has the potential to advance our monitoring of coastal dune forest. By identifying the species responsible for the differences between rehabilitating and undisturbed sites, managers may target either problem species or species that may be in need of assisted dispersal. This method is applicable to all our study taxa. For example, the non-indigenous herbaceous plant species *Achyranthes aspera*, although not contributing to the most dissimilarity between Sokhulu and the older rehabilitating sites, has increased in its contribution across the chronosequence. This species may be an important target for chemical control to remove it from the rehabilitating community; it is not currently controlled by RBM despite being on Appendix 1 of the Conservation of Agricultural Resources Act (1983). The species contributing the most dissimilarity was *Isoglossa woodii*, which is a native forest specialist and may require assisted dispersal to reach rehabilitating sites. By identifying this problem, managers can now instigate research into the species life history and its role in dune forest functioning. However, recently, this species has been observed on the edges of some rehabilitating coastal dune forest sites (personal observation). Therefore, it seems to have recently colonised these sites and may not need assistance.

Future research

Restoration ecology is often lambasted for not furthering the scientific understanding of community assembly (Halle 2007; Weiher 2007; Choi 2007; Hobbs 2007). The restoration of coastal dune forest is a long way from the “gardening” approach of many restoration programmes, i.e. the artificial and unsustainable creation of biological communities (Hobbs 2007). We have tested ecological succession with a mensurative experimental approach (Underwood 2000), but have not taken a true experimental approach. This may be because of logistical problems that one may face in an area where local people interfere with experimental plots (for example; Mpanza et al. 2009). In the future, carefully designed experiments could allow CERU to further the understanding of the mechanisms behind succession and community assembly. My opinion is that there is also an opportunity to assess theories, other than succession, that address how communities are assembled; this is something CERU have not touched on previously (with the exception of Weiermans & van Aarde 2003 and Chapter 6 of this thesis, which addressed aspects of the effect of the landscapes composition). For example, “assembly rules” have huge relevance for restoration ecology (Temperton & Hobbs 2004). One such rule is that the environment determines the type of species that can persist in a community, but the actual species identity is historically contingent (Fukami et al. 2005). This would mean that the return of specific species is irrelevant to the functioning of forest communities.

One of the main constraints of my work was the lack of basic ecological knowledge on the species that inhabit rehabilitating and undisturbed coastal dune forest sites and on the abiotic conditions in these sites. Without this knowledge, we cannot identify the processes that cause apparent dispersal and establishment constraints. If the aim of coastal dune forest restoration is to assemble a community representative of coastal dune forests in the region (or at least to restore a similar species assemblage), then we must investigate why species that are not present in the rehabilitating sites but are in the reference sites have failed to establish. Colonisation and extinction dynamics are influenced by both landscape-scale and local-scale factors. Two important components of colonisation are dispersal and establishment, and an understanding of these two processes is imperative for successful habitat restoration.

What are the consequences of the rehabilitation of coastal dune forest for dispersal and establishment? I have hinted that the landscape composition is a driver of species occupancy in coastal dune forest sites. What still needs to be known is what the mechanisms of these occupancy patterns are. For example, does the intervening matrix between sites influence how species move and where species disperse? There is a huge practical problem in obtaining data on how individuals disperse across a landscape, and as a result, there is a lack of empirical data and a dependence on models (e.g. King & With 2002; Lebreton et al 2003). However, radio-telemetry has been used to investigate how landscape effects the movement of dispersers (Potter 1990; Castellion & Sieving 2005; Price 2006). These studies use movement as a surrogate for dispersal. The majority of these studies do not incorporate the effect of different matrix habitat, with one notable exception. Castellion & Sieving (2005) showed that a forest understory bird was able to move equally fast across wooded corridors and shrub-land but was constrained by open habitat. The patchiness at the landscape level of the RBM lease (i.e. remnant forest patches, bare sand patches, active mining patches, rehabilitating and regenerating patches), may alter the way species disperse and therefore the probability that they will reach rehabilitating sites.

Seed dispersal is the main process by which trees can colonise new habitats (Howe & Miriti 2000). Where dispersal vectors deposit seed has an influence on plant population dynamics across the landscape (Wang & Smith 2002). The removal or reduction in a vector’s population will influence the trees population distribution. For example, habitat fragments in the Eastern Usambara Mountains of Tanzania have fewer trees of *Leptonychia usambarensis* and fewer seedlings greater than 10 m away from an adult tree (Cordeiro & Howe 2003). This led to reduced recruitment of *L. usambarensis* in forest fragments. In addition, the behaviour of vectors may influence where a seed is deposited. The distribution of oak, *Quercus ilex*, is affected by the avoidance of open habitat by European jays, *Garrulus glandarius* (Gómez 2003). Where fragmentation and habitat loss have increased the amount of open habitat surrounding a fragment, seed dispersal may be severely inhibited by these behavioural patterns. The study of seed dispersal, like that of bird dispersal, is inhibited by the ability to follow the fate of individual seed, some knowledge about the dispersal process can be gleaned from investigating patterns of distribution, but the factors that influence establishment also have a major role in determining species distribution. However, there are a number of new techniques involving plant genetics, radioactive labelling and fluorescent markers that maybe promising for the future (Wang & Smith 2002).

Once a species arrives at a site, there are a number of constraints to establishment. For example prior to germination, seeds are vulnerable to predation and secondary dispersal. Secondary dispersal by rodents and insects is increasingly recognised as an important determinate of seedling distribution, for example seed hoarding behaviour in rodents results a clumped distribution (Wang & Smith 2002). Seed predation can have large effects on species distribution; predators and parasites are more abundant nearer to parent plants (Janzen 1970). Where seed predators are controlled (by predation), a greater number of seeds germinate; in the absence of control, over 60 % of seeds may suffer predation (Asquith et al 1997). A number of abiotic factors, such as soil moisture, light, temperature and fire influence germination. Biotic factors such as genetics, seed size and handling by dispersal vectors can also have an affect. The requirements for soil moisture, light and temperature vary depending on species (there is also a great deal of inter-specific variation). Dispersal vectors can help induce germination, whereby the act of swallowing the seed allows stomach acids to remove the seeds husk stimulating germination once deposited. As an added benefit, faeces may provide nutrients for seedling growth (Stoner et al 2007). Soil moisture, light, predation and parasites also affect seedling survival to adulthood. Soil nutrients are a very important determinate of seedling growth, and numerous nutrient addition experiments have shown that N, P, and K are all limiting (see Khurana and Singh 2001).

The future of research at Richards Bay should focus on the mechanisms behind the patterns that we observe. Patterns of abundance and occupancy only tell half the story of the re-assembly of communities. The constraints of restoration are the constraints that species face in moving across the landscape and surviving at rehabilitating sites.

The final evaluation

The theory of ecological succession and the discipline of restoration ecology have had a fruitful partnership. Restoration has gained a theoretical basis, and succession has gained a new lease of life as its predictions are tested in applied scenarios (Young et al. 2005; Walker & del Moral 2003). Where the theory of succession lets restoration down is that it does not allow for factors that will alter or filter the species pool, such as the landscape composition and historical changes in the species pool. It also predicts that the “balance of nature” exists, and a disturbance will lead inexorably to a homogenous community composition that is typical of a regions climatic condition. In this thesis, I have shown that the landscape can play a role in the assembly of disturbed communities; although, changes in the species pool did not appear to have much of an impact on community re-assembly presently, but this situation may change in the future. In addition, I have shown that after initially appearing to head to a homogenous species composition, patch dynamics may lead rehabilitating coastal dune forest to a heterogeneous community composition across sites. Rather than striving for homogeny, restoration may have to strive for heterogeneity. Patch dynamics theory offers an extension to successional theory to account for patchiness.

Of course, restoration ecology has also let succession down; restoration ecology is an impatient practice carried out over a very short time-scales. Succession is a process that occurs on the time-scale of hundreds or even thousands of years. The succession of coastal dune forest appears quite rapid, but at 30 years, rehabilitating sites are still in the first stage of succession. The restoration of coastal dune forest, therefore, may well be just a matter of time. To accelerate the succession of coastal dune forest further (which is a main aim of restoration ecology) the barriers to successful colonisation of species need to be investigated and mitigated. In addition, the functions of coastal dune forest that are important for both human and biological communities need to be identified and promoted in order to ensure the eventual success of coastal dune forest restoration.

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Plate 7-1. Post-mining dunes are re-shaped and then previously stored topsoil is placed on the dune and spread evenly across the site. The erection of shade-netting fences, acts to reduce soil erosion resulting from the action of the wind. Exotic annual herbaceous plants are seeded to further ensure soil stability. The above plate shows a 1 year old site. The photograph was taken by Prof. R.J. van Aarde and is used with permission.

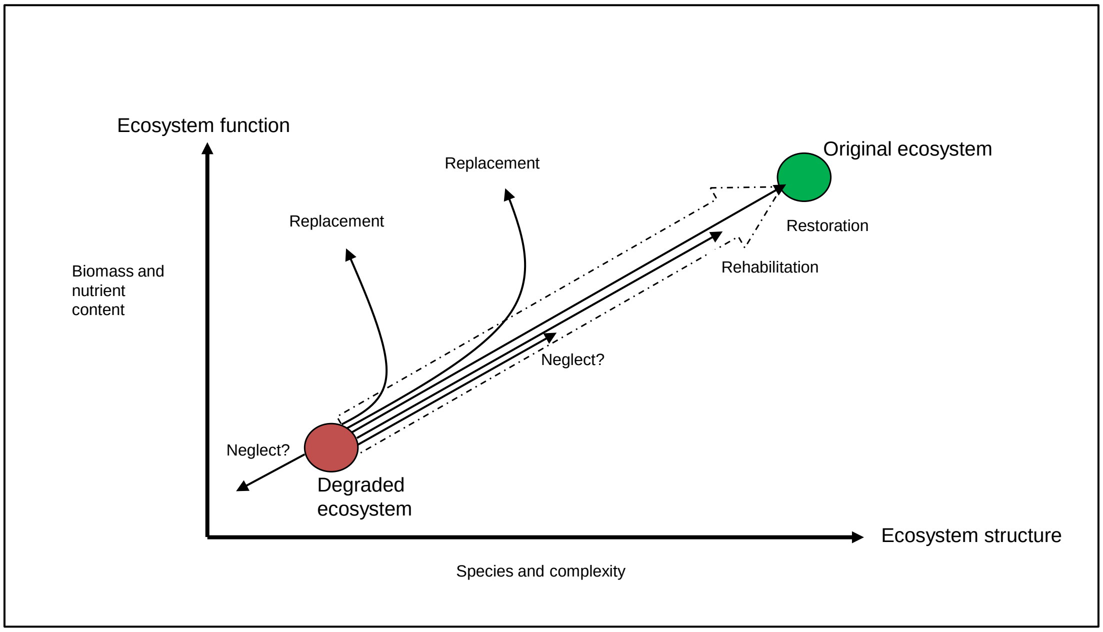


Figure 7-1. The structure – function model of Bradshaw (1984). The arrow with the dashed outline indicates normal ecosystem development.

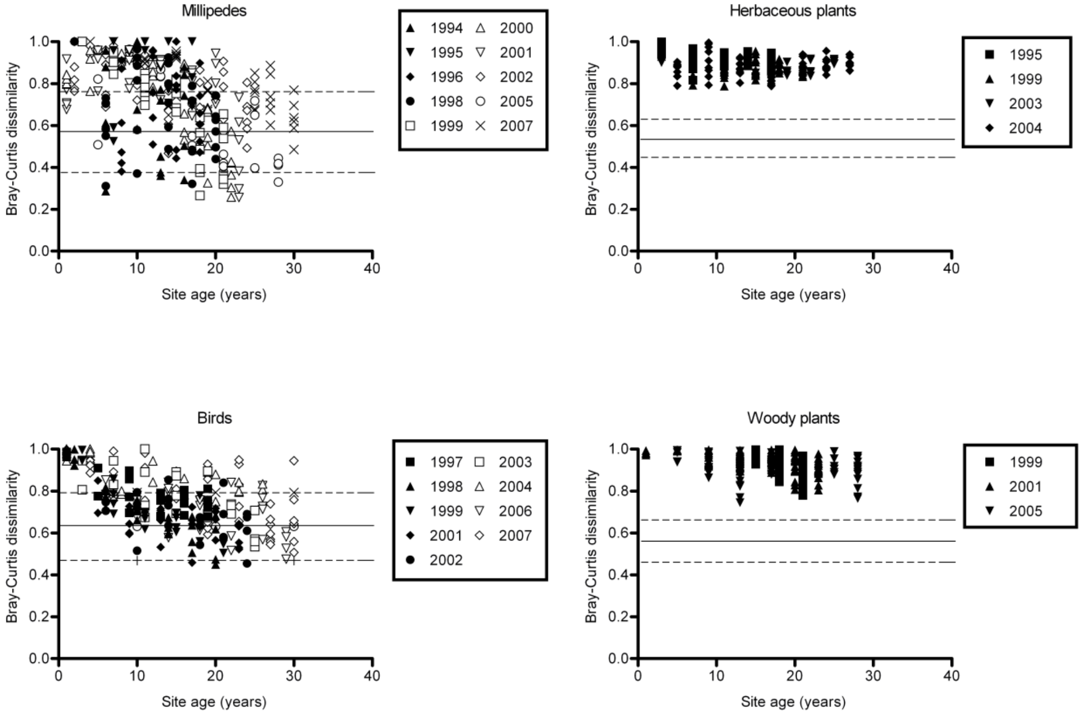


Figure 7-2. Bray-Curtis dissimilarity between rehabilitating coastal dune forest sites and the Sokhulu Forest reference site for four forest taxa. Solid horizontal lines indicate the mean Bray-Curtis dissimilarity value within the reference site and the dashed horizontal lines indicate the variation about this mean (SD). See text for further description.

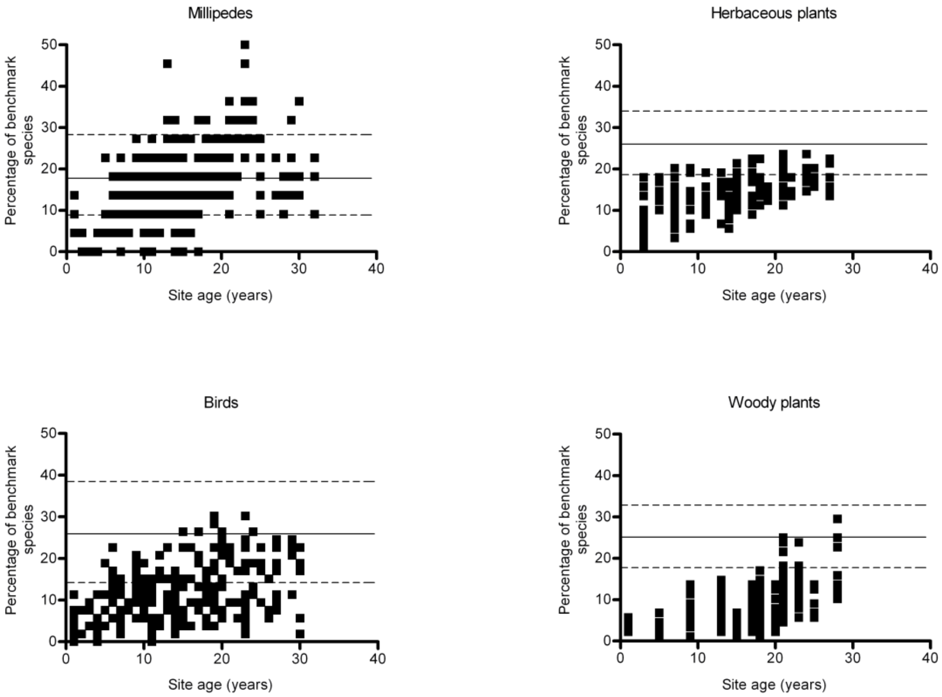


Figure 7-3. The percentage of species found within the reference site (benchmark) that are also found in the rehabilitating sites as they increase in age. Once again the solid horizontal lines indicate the mean Bray-Curtis dissimilarity value within the reference site and the dashed horizontal lines indicate the variation about this mean (SD).

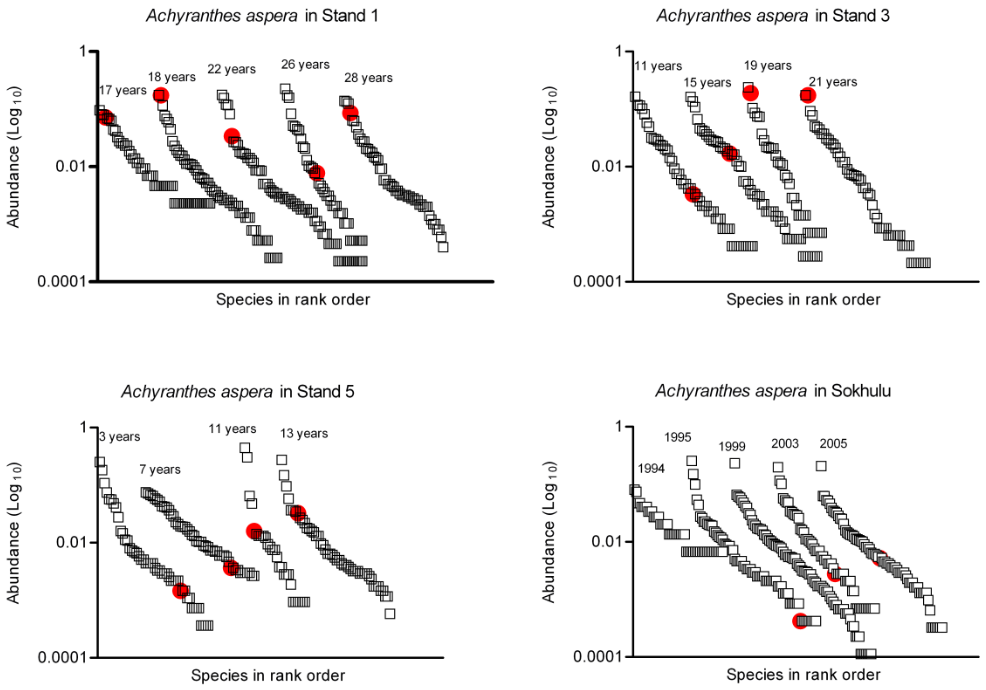


Figure 7-4. The change in rank abundance position for the non-indigenous species, *Achyranthes aspera*, in three rehabilitating coastal dune forests at different times post disturbance. The Sokhulu Forest reference site has also been invaded by this species; it was first recorded in the year 1995.

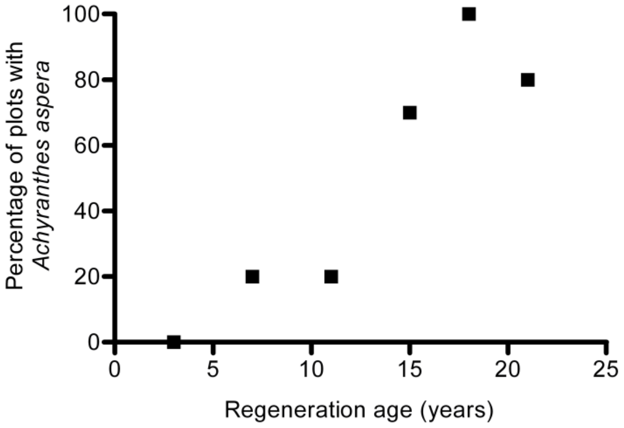
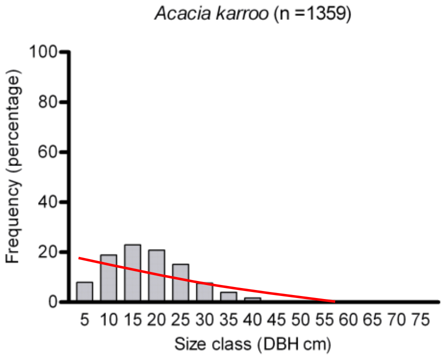


Figure 7-5. The percentage of sampling plots in rehabilitating coastal dune forest sites that contain *Achyranthes aspera*. The data presented here comes from the 2001 herbaceous plant chronosequence.



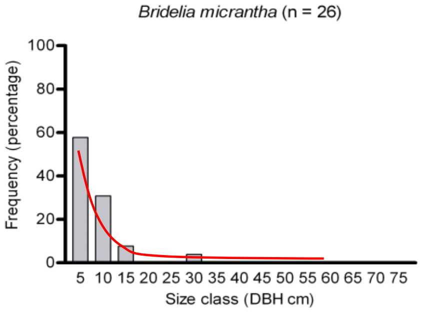


Figure 7-6. Size-class distributions for the pioneer tree species *Acacia karroo* and forest tree species *Bridelia micranthra*. The pioneer does not show the “reverse-J” pattern of a reproducing population where as the forest tree does. The line illustrates the negative exponential function.

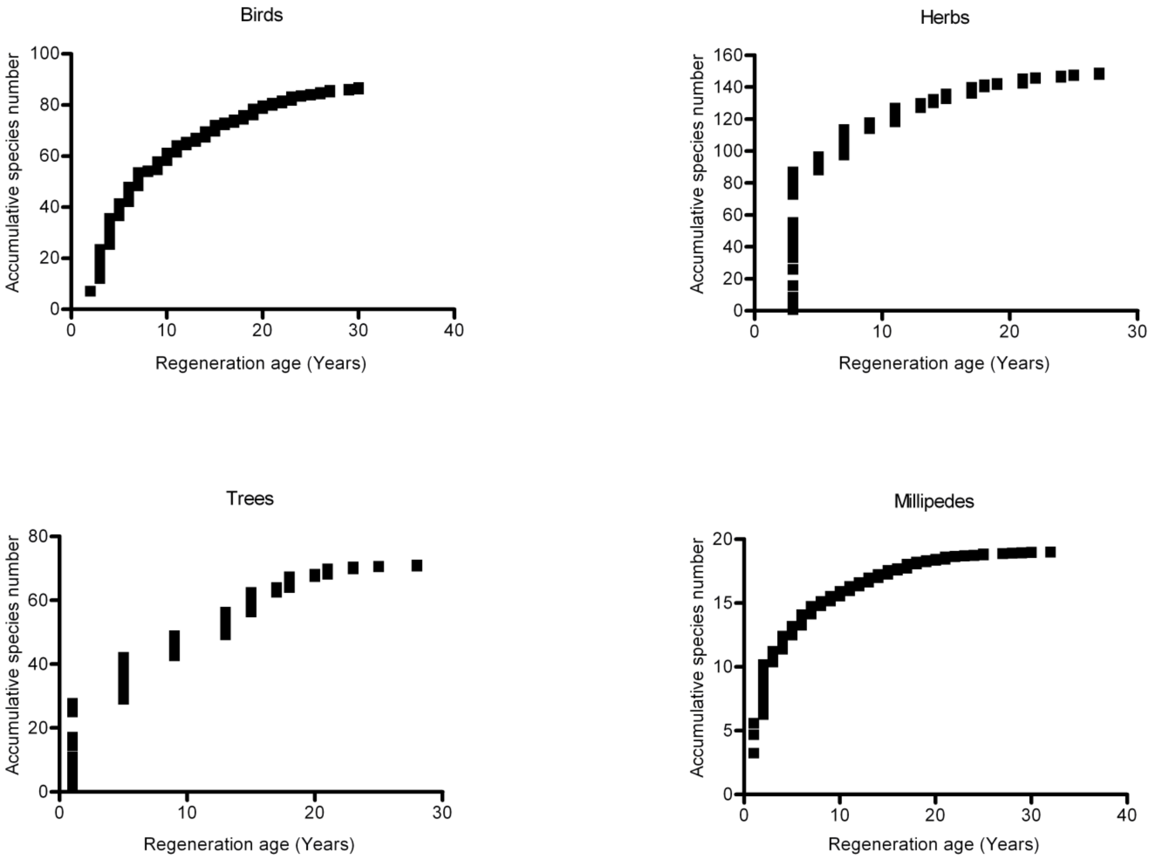


Figure 7-7. The accumulation of species across the rehabilitating coastal dune forest sere for four forest taxa.

Appendices

Appendix 3-1. Herb species and their Non-metric Multidimensional Scaling (NMDS) scores for axis 1 to 3 and their habitat associations according to Pooley (1998). Species are listed in order of their NMDS axis 1 score.

Latin name	Axis1	Axis 2	Axis 3	Habitat
Abrus precatorius	-1.216	-0.480	-0.861	Open woodland
Abutilon grantii	-0.413	-0.298	0.231	Open sandy areas
Abutilon sonneratianum	0.330	-0.314	0.917	Coastal bush in light shade
Acalypha villicaulis	0.039	0.631	0.325	Woodland and grassland
Achyranthes aspera	0.526	0.154	-0.007	Widespread (some shade tolerance)
Achyropsis avicularis	0.625	0.359	0.226	Forest
Adenia gummifera	0.452	0.035	-0.687	Forest margins
Ageratum conyzoides	-1.625	-0.587	-0.582	Forest
Aneilema aequinoctiale	0.278	0.118	0.031	Forest margins
Anthericum saundersiae	0.148	-0.448	-0.230	Grassland and open areas
Aristida junciformis	-1.241	-0.654	0.403	Grassland, forest clearings
Asparagus falcatus	-0.408	0.438	0.089	Forest and forest margns
Asystasia gangetica	0.266	0.383	-0.007	Forest edge

Bidens pilosa	-1.323	-0.065	-0.179	Widespread (some shade tolerance)
Brachiaria chusqueoides	0.199	-0.561	-0.041	Scrub, coastal bush and forest
Canavalia maritima	-1.693	0.514	1.126	Salt-spray zone
Carpobrotus dimidiatus	-1.585	-0.214	0.920	Thickets in dune vegetation
Catharanthus roseus	-1.072	-0.350	-0.151	Forest (climber)
Centella asiatica	0.127	0.355	0.183	Swampy areas
Cheilanthes viridis	-0.291	-0.130	-0.261	Scrub and leaf-litter of evergreen forest
Chlorophytum bowkeri	0.238	-0.289	0.848	Forest margins
Chromolaena odorata	0.391	0.339	0.395	Woodland and forest edge (non-native)
Cissampelos torulosa	0.558	0.514	0.232	Forest edge
Cissus fragilis	0.319	0.723	0.548	Forest (climber)
Coccinia variifolia	0.585	-0.046	-0.363	Forest (climber)
Commelina benghalensis	-0.228	-0.201	0.229	Disturbed areas and forest margins
Commelina eckloniana	-0.218	0.032	-0.217	Woodland
Commelina sp.	-0.612	0.802	0.081	Forest edge
Conyza albida	-1.445	0.328	0.264	Forest
Crassula expansa	-0.780	-0.951	-0.339	Shaded areas
Crotalaria capensis	-1.717	0.057	0.686	Coastal bush and forest margins
Cuscuta campestris	-0.899	2.042	-0.280	Riverine vegetation

Cynanchum ellipticum	-1.859	0.480	1.047	Edge of coastal scrub
Cynodon dactylon	0.179	-0.207	-0.029	Open areas and common in disturbed areas
Cyperus albostriatus	0.096	-0.381	0.407	Moist areas
Cyperus macrocarpus	0.551	-0.026	-0.902	Swampy grasslands
Cyperus natalensis	-1.009	0.061	-0.204	Grassland (sandy soils)
Cyperus sphaerospermus	-1.779	0.469	0.980	Swampy areas
Cyphostemma hypoleucum	0.473	0.134	0.785	Wooded slopes (climber)
Dactyloctenium australe	0.087	-0.571	-0.319	Grassland and bushveld
Dactyloctenium geminatum	0.323	-0.401	-0.124	Coastal bush near sea
Desmodium incanum	-1.662	0.466	0.192	Open woodland
Digitaria diversinervis	-0.212	0.054	-0.030	Forest margins
Digitaria natalensis	-1.047	2.171	-0.241	Dune forest
Dioscorea quartiniana	-1.602	-0.034	0.280	Forest, thickets and woodland (climber)
Dioscorea retusa	0.772	0.993	0.764	Woodland and forest (Climber)
Dioscorea sylvatica	-0.041	0.056	-0.914	Forest edge
Drimiopsis maculata	0.601	0.754	0.085	Forest margins
Eragrostis ciliaris	-0.014	-0.688	0.324	Woodland

Eriosema psoraleoides	-0.708	1.698	-0.171	Sandy coastal areas (open)
Flagellaria guineensis	-1.222	-0.554	-1.371	Open areas (wide tolerance)
Gymnosporia arenicola	-0.985	-0.788	0.304	Grassland
Helichrysum decorum	-1.316	-0.664	0.118	Forest edge
Helichrysum kraussii	-1.360	-0.458	-0.135	Dune slacks
Hibiscus surattensis	-0.414	0.214	0.589	Disturbed areas
Imperata cylindrica	-0.058	0.656	0.128	Open sandy areas
Indigofera trita	-0.418	-0.743	-0.165	Forest edge
Ipomoea ficifolia	-1.483	0.043	-0.518	Riverine forest and grasslands
Juncus kraussii	-0.350	-0.492	0.287	Grassland and forest
Krauseola mosambicina	-0.889	1.724	-0.114	Open scrub on coastal dunes
Kyllinga alba	0.440	-0.099	0.429	Sand dunes, open areas
Lagenaria sphaerica	-0.799	1.450	0.003	Forest and woodland (climber)
Lantana camara	0.562	0.189	0.361	Grassland and open woodland
Laportea peduncularis	-0.348	0.213	1.133	Coastal forest
Melinis repens	-0.277	-0.176	0.211	Open woodland and coastal forest

Microsorium scolopendrium	-1.086	1.643	-0.232	Forest and woodland (fern)
Neonotonia wightii	0.631	1.064	-0.530	Forest (vine)
Oldenlandia affinis	-0.913	-0.152	-0.609	Woodland , grassland, and scrub
Oxalis corniculata	-0.164	-0.040	-1.559	grasslands and disturbed areas
Panicum laticomum	-0.160	0.078	-0.060	Woodland (shaded)
Panicum maximum	-0.279	1.280	-0.116	Open woodland and bushveld
Passiflora subpeltata	-0.758	0.237	-0.764	Forest and woodland (non-native)
Phyllanthus parvulus	0.548	0.736	0.146	Forest
Priva meyeri	-1.750	1.965	0.267	Woodland and forest margin
Pupalia lappacea	-0.120	1.110	0.090	Widespread (some shade tolerence)
Pyrenacantha scandens	0.471	0.076	0.063	Forest (Liana)
Rhynchosia caribaea	-0.511	-0.250	-0.033	Forest margins
Richardia brasiliensis	-0.035	0.132	0.388	Disturbed areas
Rivina humulis	-0.253	-0.163	-0.495	Forest (non-native)
Sansevieria hyacinthoides	0.464	0.202	-0.277	Woodland
Sarcostemma viminale	0.344	-0.406	0.595	Savanna
Scadoxus puniceus	0.292	0.126	-0.375	Subtropical thicket

Secamone filiformis	0.366	-0.249	-0.695	Shaded riverine and swampy areas
Senecio conrathii	0.497	0.070	-0.432	Grassland
Senecio deltoideus	0.306	0.105	-0.297	Open woodland and bushveld
Senecio helminthioides	0.301	0.157	0.153	Forest (climber)
Senecio quinquelobus	-1.067	-0.474	0.006	Forest margins
Senecio tamoides	0.469	0.373	0.413	Evergreen forest margins (climber)
Sida cordifolia	0.545	0.390	-0.603	Grassland
Smilax anceps	-1.146	1.432	-0.031	Secondary forest
Solanum macrocarpon	0.693	0.826	0.970	Grassland and woodland
Solanum rigescens	0.574	0.262	0.413	Littoral zone
Sporobolus africanus	-1.494	0.863	-0.026	Sandy coastal areas (open)
Stenotaphrum secundatum	0.597	0.228	0.728	Swampy areas, close to seashore
Tinospora caffra	0.726	1.044	0.912	Forest and woodland
Tragia glabrata	0.660	0.547	0.434	Grassland
Triumfetta rhomboidea	-1.073	0.760	-0.192	Disturbed areas
Vernonia angulifolia	-0.177	0.239	1.943	Dune and coastal forest margins
Vernonia aurantiaca	0.134	0.276	-0.426	Woodland and riverine vegetation

Wahlenbergia undulata	-0.339	0.741	1.243	Wasteland, disturbed area
Zehneria parvifolia	-1.155	0.725	0.423	Woodland and forest (Climber)

Appendix 3-2. Bird species, their Non-metric Multidimensional Scaling (NMDS) scores for axis 1 to 3 and their habitat associations according to Gibbon (2006).

Species	Latin name	Axis 1	Axis 2	Axis 3	Habitat
African Pipit	*Anthus cinnamomeus*	1.888	-0.750	-1.092	Grassland
Ashy Flycatcher	*Muscicapa caerulescens*	-0.284	-0.192	0.231	Edge of evergreen forest
Black-backed Puffback	*Dryoscopus cubla*	-0.369	-0.048	0.240	Canopy of woodland and forest
Black-bellied Starling	Lamprotornis corruscus	-0.924	-0.407	0.696	Canopy of evergreen forest
Brown-hooded Kingfisher	*Halcyon albiventris*	-0.530	-0.760	-0.020	Woodland and savanna
Cape White-eye	*Zosterops virens*	-0.296	-0.069	0.270	Forest and woodland
Collared Sunbird	*Hedydipna collaris*	-0.342	-0.040	-0.361	Coastal bush
Common Waxbill	*Estrilda astrild*	2.040	-0.076	-0.707	Grassland
Dark-backed Weaver	*Ploceus bicolor*	-0.545	-0.187	0.170	Middle and upper strata of evergreen forest
Dark-capped Bulbul	*Pycnonotus tricolor*	0.362	-0.230	0.411	Woodland and forest edge
Eastern Nicator	*Nicator gularis*	-0.108	-0.246	-0.625	Forest and thickets
Eastern Olive Sunbird	*Cyanomitra olivacea*	-0.377	-0.400	0.180	Evergreen forest
Fork-tailed Drongo	*Dicrurus adsimilis*	-0.140	-0.260	0.560	Woodland and savanna

Green-backed Camaroptera	*Camaroptera brachyura*	-0.181	0.352	0.054	Forest edges
Grey Sunbird	*Cyanomitra veroxii*	-0.416	0.730	0.259	Coastal bush and forest
Hadeda Ibis	*Bostrychia hagedash*	0.391	-0.135	-0.861	Grasslands, savanna, bush, and forest edge
Livingstone's Turaco	*Tauraco livingstonii*	-0.051	1.094	-1.459	Evergreen forest
Long-billed Crombec	*Sylvietta rufescens*	0.232	-0.298	-0.314	Woodland and savanna
Rattling Cisticola	*Cisticola chinianus*	1.354	0.301	0.025	Acacia savanna and open woodland
Red-capped Robin-Chat	*Cossypha natalensis*	-0.304	-0.294	-0.474	Evergreen forest and thickets
Rudd's Apalis	*Apalis ruddi*	-0.066	0.618	-0.499	Coastal bush and woodland
Sombre Greenbul	*Andropadus importunus*	0.061	0.181	-0.754	Forest, coastal bush and thickets
Southern Boubou	*Laniarius ferrugineus*	-0.080	-0.467	-0.600	Thicket
Square-tailed Drongo	*Dicrurus ludwigii*	-0.351	-0.548	0.289	Middle strata of evergreen forest
Tambourine Dove	*Turtur tympanistria*	-0.341	-0.511	-0.300	Evergreen forest
Tawny-flanked Prinia	*Prinia subflava*	0.807	-0.010	-0.293	Grassland and savanna
Terrestrial Brownbul	*Phyllastrephus terrestris*	-0.217	-0.860	-0.274	Evergreen forest

Thick-billed Weaver	*Amblyospiza albifrons*	1.365	-0.356	0.395	Reed-beds (breeding) and forest (non-breeding)
Weavers[1]	*Ploceus species*	1.340	-0.233	1.311	Acacia savanna and open woodland
White-browed Scrub-Robin	*Cercotrichas leucophrys*	0.238	0.391	-0.400	Woodland and thickets
White-eared Barbet	*Stactolaema leucotis*	-0.179	-0.817	0.472	Evergreen Forest
Willow Warbler	*Phylloscopus trochilus*	0.290	0.431	0.070	Woodland and forest edge
Yellow-bellied Greenbul	*Chlorocichla falviventris*	-0.352	-0.101	-0.044	Coastal bush
Yellow-breasted Apalis	*Apalis flavida*	-0.219	0.341	0.145	Mixed woodland or bush
Yellow-fronted Canary	*Serinus mozambicus*	1.690	-0.023	-0.117	Bush and woodland
Yellow-rumped Tinkerbird	*Pogoniulus bilineatus*	-0.354	-0.321	0.182	Coastal forest
Zitting Cisticola	*Cisticola juncidis*	1.638	-0.289	0.293	Grassland

[1] Yellow weavers (*Ploceus subaureus*) and Lesser masked weavers (*P. intermedius*) were treated as a morphospecies because females are difficult to distinguish in the field (Kritzinger and van Aarde (1998).

Appendix 3-3. Tree species, their Non-metric Multidimensional Scaling (NMDS) scores for axis 1 to 3 and their habitat associations according to Coates-Palgrave (2003).

Species	Latin name	Axis 1	Axis 2	Axis 3	Habitat
Sweet-thorn Acacia	Acacia karroo	-0.719	0.081	0.039	Dune forest (pioneer)
Scented-pod Acacia	Acacia kraussiana	-0.341	-0.833	0.312	Scrub and forest
Dune false current	Allophylus natalensis	0.410	-0.374	-0.029	Coastal dune forest and bush
Tassleberry	Antidesma venosum	0.095	0.399	0.583	Forest margins and woodland
White Pear	Apodytes dimidiata	0.222	0.162	0.493	Forest and forest margins
Coast silver Oak	Brachylaena discolor	-0.005	0.546	-0.037	Coastal dunes and bush
Blue sweet-berry	Bridelia cathartica	-0.093	-0.009	0.571	Forest margins, open woodland and riverine forest
Common turkeyberry	Canthium inerme	0.377	0.295	-0.026	Forest, forest margin, bushveld and dune forest
Natal Plum or Large num-num	Carissa macrocarpa	1.176	0.458	-0.248	Coastal forest margin
Emetic nut	Catunaregam spinosa	-0.367	-0.624	0.761	Bushveld, forest margin and dune forest
White Stinkwood	Celtis africana	0.002	-0.655	-0.016	Forest (widespread - pioneer)
Inkberry	Cestrum laevigatum	-0.087	-0.306	-0.004	Forest margins (non-native)
Giant Pock Ironwood	Chaetacme aristata	-0.079	-1.426	-0.327	Coastal forest and scrub
Horsewood	Clausena anisata	0.542	-0.466	-0.287	Bushveld thicket and forest margins
Tinderwood	Clerodendrum glabrum	-0.303	-0.357	-0.382	Widespread in coastal dunes, forest margins, bushveld, thicket and riverine forest

Dune Soapberry	Deinbollia oblongifolia	-0.224	-0.567	0.407	Forest, scrub, bushveld and dune bush
Natal Apricot	Dovyalis longispina	1.034	-0.899	0.082	Forest and bushveld
Large-leaved dragon tree	Dracaena aletriformis	0.137	-0.239	0.193	Coastal dune forest and shaded ravines
Dune myrtle	Eugenia capensis	0.683	0.219	0.572	Seaward side of coastal dunes
Veld fig	Ficus burtt-davyi	1.331	-0.529	0.558	Bushveld and open woodland
Climbing Raisin bush	Grewia caffra	0.954	0.298	0.726	Bushveld, woodland, riverine forest and forest margin (can be a climber)
Cross-berry	Grewia occidentalis	-0.064	-0.449	0.174	Forest, forest margins, bushveld and thicket
White forest spike-thorn	Gymnosporia nemorosa	0.665	-0.053	-0.429	Forest, forest margins, bushveld and coastal dunes
Rhino-coffee	Kraussia floribunda	0.895	0.307	-0.380	Forest margins, riverine vegetation, and swamp forest
Koko tree	Maytenus undata	1.272	0.016	-0.396	Forest, forest margins a in bushveld along watercourses
Coastal red milk-plum	Mimusops caffra	0.434	0.409	0.165	Coastal dune forest
Poison olive	Peddiea africana	0.920	0.484	0.381	Forest and forest margins
Senegal date-palm	Phoenix reclinata	0.983	0.147	0.188	Open-forest and savanna (palm)
Guava	Psidium guajava	-1.364	0.191	-0.887	Forest (in natural range), grasslands, disturbed areas (Non-native)
Bird berry	Psychotria capensis	0.868	0.104	0.662	Forest and forest margins
Quar	Psydrax obovata	-0.040	0.236	-0.006	Forest and forest margins
Natal rhus	Rhus natalensis	0.807	0.297	-0.162	Coastal scrub and dune forest
Dune current	Rhus nebulosa	0.234	0.420	-0.236	Dune scrub and forest margins
Cat-thorn	Scutia myrtina	0.191	-0.048	0.504	Coastal forest, scrub forest and forest margins (climber)
White milkwood	Sideroxylon inerme	0.732	-0.425	-0.495	Coastal forest, woodland and scrub

Strelitzia or Crane flower	Strelitzia nicolai	0.648	0.099	0.526	Coastal dunes (Palm)
Zulu Cherry-orange	Teclea gerrardii	0.074	-0.505	0.144	Coastal dune bush, forest, and riverine forest
Pigeon wood	Trema orientalis	-0.823	-0.099	-0.291	Forest-edge (pioneer tree)
Jackal-coffee	Tricalysia lanceolata	0.686	0.565	-0.670	Coastal areas, riverine vegetation and open woodland
Coast-coffee	Tricalysia sonderiana	0.310	0.000	0.815	Forest, dune forest, and bushveld
Natal mahogany	Trichilia emetica	0.801	0.141	-0.429	Coastal areas, riverine vegetation and open woodland (widespread)
White Ironwood	Vepris lanceolata	0.329	-0.008	-0.404	Forest, riverine bush and scrub (widespread)
Small Knobwood	Zanthoxylum capense	0.223	-0.401	-0.561	Dry scrub bushveld and forest margins
Buffalo Thorn	Ziziphus mucronata	-0.718	-0.703	-0.148	Bushveld and forest

Appendix 3-4. Millipede species and their Non-metric Multidimensional Scaling (NMDS) scores for axis 1 to 3. There are no independent sources of information on their habitat associations.

Species	Axis 1	Axis 2	Axis 3
Centrobolus fulgidus	-0.54125	-0.12669	-0.06438
Centrobolus richardii	0.030092	0.256443	-0.35567
Centrobolus rugulosus	-0.33464	-1.28212	-0.01779
Doratogonus sp.*	0.74758	0.179887	-0.16997
Gnomeskelus tuberosus	0.093001	-0.51086	0.138415
Juliaformia sp.*	0.989596	-0.56878	-0.08981
Orthroporoides pyrocephalus	1.553339	0.90054	0.411473
Orthroporoides sp.*	0.506975	-1.29529	-0.69268
Sphaerotherium giganteum	0.344149	-0.67968	0.777536
Sphaerotherium punctulatum	1.149382	-0.66832	0.281929
Sphaerotherium rotundatum	0.677715	-1.4181	0.917772
Sphaerotherium sp.*	-1.46338	-1.03666	1.41567
Sphaerotherium sp.B*	0.578288	0.927759	-1.14289
Sphaerotherium sp.C*	0.585378	-0.70302	0.726205
Sphaerotherium sp.D*	1.215584	0.711891	-1.50355
Spinotarsus anguiliferous	-0.05474	0.523816	0.475629
Spirostreptidae sp.1*	1.069355	0.184503	-0.15242
Spirostreptidae sp.2*	1.177639	0.328197	0.159555

* Some species are yet to be officially identified past the genus level

Appendix 4-1. The year of establishment and mean elevation (meters above sea level) for each rehabilitating coastal dune forest site.

Site name	Year of establishment	Elevation (meters above sea level; mean ± standard deviation)
Site 1	1977	50.67±5.06
Site 2	1980	56.86±5.72
Site 3	1984	51.42±8.56
Site 4	1988	49.32±21.03
Site 5	1992	56.82±18.72
Site 6	1996	51.98±21.60

Appendix 4-2. The 15 non-native species recorded in the rehabilitating coastal dune forests. All species listed in the Conservation of Agricultural Resources Act (1983) are in category 1; species that are prohibited weeds in need of control in all situations. Species authorities are sourced from the International Plant Names Index (http://www.ipni.org/index.html).

Latin Name	Common Name(s)
Achyranthes aspera (L.)	Burweed[1]
Ageratum conyzoides (L.)	Invading ageratum[1,2]
Bidens bipinnata (L.)	Spanish Blackjack[2]
Bidens pilosa (L.)	Blackjack[2]
Catharanthus roseus (G. Don)	Madagascar periwinkle[2]
Chromolaena odorata (L.), R.M.King & H.Rob.	Trifid weed[1,2]
Commelina benghalensis (L.)	Benghal wondering Jew[2]
Lantana camara (L.)	Lantana, Tickberry, Cherrypie[1,2]
Oxalis corniculata (L.)	Creeping oxalis[2]
Passiflora subpeltata (Ortega)	Passion fruit[2]
Rivina humilis (L.)	Bloodberry[1,2]

Sonchus oleraceus (L.)	Sowthistle[2]
Tagetes minuta (L.)	Khaki-weed, Mexican marigold[2]
Cuscuta campestris (Yunk.)	Common dodder[1]
Richardia brasiliensis (Gomez)	Tropical Mexican clover, White-eye[2]

[1] Conservation of Agricultural Resources Act (1983)

[2] Henderson (2007)

Summary

Coastal dune forest is an eco-region within a biodiversity hotspot as it falls within the southern-most part of the Maputaland Centre of Endemism. Mining is the largest threat to coastal dune forest conservation. However, for the last 34 years the mining company Richards Bay Minerals has been engaged in a rehabilitation programme that aims to facilitate the recovery of coastal dune forest through ecological succession. Through this thesis, I aimed to evaluate the ecological consequences of this programme for the conservation of these coastal dune forests.

To begin with, I evaluated if succession is a suitable conceptual basis for the restoration of coastal dune forest. Patterns of community characteristics observed in rehabilitating coastal dune forest sites fitted with those predicted by theory. I then assessed three factors that could potentially compromise the efficacy of succession-based restoration management. The first of these was the establishment of non-native species. Non-native plants did not contribute the most to dissimilarity between rehabilitating and reference sites and deviation of the regeneration trajectory was due to higher abundances of a native species. The second factor was disturbance in the form of canopy-gap formation. Rehabilitation of coastal dune forest is reliant on the pioneer species, *Acacia karroo* and in other studies self-replacement by this species has been hypothesized to be responsible for the stagnation of succession. The most abundant gap-takers were secondary forest species suggesting that succession had not stagnated. The final factor was the role that the surrounding landscape played in community assembly. I correlated the probability of patch occupancy with patch age, area, isolation and edge. Patch age only explained the occupancy of six of 21 birds and eleven of 25 trees.

Finally, I provide a synthesis of my findings and an evaluation of the rehabilitation of coastal dune forest in terms of the ecological consequences and threats that stem from the

rehabilitation efforts of the last 33 years. This final evaluation includes discussion on the measurement of restoration success and assesses the progress of the coastal dune forests of KwaZulu-Natal toward successful rehabilitation.