

## **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 & Mushinsky 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*:  $0.17 \pm 1.06$ ; *P. guajava*:  $0.61 \pm 3.54$ ; *C. limon*  $0.01 \pm 0.10$ ; mean  $\pm$  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; Kritzing & 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 managers 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 & Mushinsky 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 increasingly 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 19<sup>th</sup> 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 homogeneity, 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.



## Literature cited

Abreu, Z., L.L. Llambí and L. Sarmiento. 2009. Sensitivity of soil restoration indicators during Páramo succession in the high tropical Andes: Chronosequence and permanent plot approaches. *Restoration Ecology* **17**: 619–628.

Asquith, N. M., S. J. Wright and M. J. Clauss. 1997. Does mammal community composition control recruitment in neotropical forest forests? Evidence from Panama. *Ecology* **78**: 941–946.

Battaglia, L.L., D.W. Pritchett and P.R. Minchin. 2008. Evaluating dispersal limitation in passive bottomland forest restoration. *Restoration Ecology* **16**: 417–424.

Beard, K.H., K.A. Vogt, D.J. Vogt, F.N. Scatena, A.P. Covich, R. Sigurdardottir, T.G. Siccama, and T.A. Cowl. 2005. Structural and functional responses of a subtropical forest to 10 years of hurricanes and droughts. *Ecological Monographs* **75**: 345–361.

Blondel, J. 2003. Guilds or functional groups: does it matter? *Oikos* **100**: 223–231.

Boyes, L.J., R.M. Gunton, M.E. Griffiths and M.J. Lawes. *In press*. Causes of arrested succession in coastal dune forest. *Plant Ecology* DOI:10.1007/s11258-010-9798-6

Bradshaw, A.D. 1984. Ecological principles and land reclamation practice. *Landscape Planning* **11**: 35–48.

Bray, J.R., and J.T. Curtis. 1957. An ordination of the upland forest communities of Southern Wisconsin. *Ecological Monographs* **27**: 325–349.

Brown, J.H. and D.F. Sax. 2007. Do biological invasions decrease diversity. *Conservation Magazine* **8**(2). <http://www.conservationmagazine.org/2008/07/aliens-among-us/>. Accessed on 4<sup>th</sup> March 2011.

Castellón, T. D., and K. E. Sieving 2005. An experimental test of matrix permeability and corridor use by an endemic understory bird. *Conservation Biology* **20**: 135-145.

Chase, J. 2003. Community assembly: when should history matter? *Oecologia* **136**: 489-498.

Choi, Y.D. 2004. Theories for ecological restoration in changing environment: Toward ‘futuristic’ restoration. *Ecological Research* **19**: 75–81.

Choi, Y. D. 2007. Restoration Ecology to the Future: A Call for New Paradigm. *Restoration Ecology* **15**: 351-353.

Clements, F.E. 1916. *Plant succession: An analysis of the development of vegetation*. Washington, D.C.: Carnegie Institution of Washington, Washington D.C. United States of America.

Coates-Palgrave, K. 2002. *Trees of southern Africa*. Struik Publishers, Cape Town, South Africa.

Cordeiro, N. J., and H. F. Howe. 2003. Forest fragmentation severs mutualism between seed dispersers and an endemic African tree. *Proceedings of the National Academy of Sciences of the United States* **24**: 14052–14056.

Cortina, J., F.T. Maestre, R. Vallejo, M. J. Baeza, A. Valdecantos and M. Pe´rez-Devesa. 2006. Ecosystem structure, function, and restoration success: Are they related? *Journal for Nature Conservation* **14**: 152–160.

Danielsen, F. 2005. The Asian Tsunami: A Protective Role for Coastal Vegetation. *Science* **310**: 643.

Davis, A.L.V., R.J. van Aarde, C.H. Scholtz and J.H. Delpont. 2002. Increasing representation of localized dung beetles across a chronosequence of regenerating vegetation and natural dune forest in South Africa. *Global Ecology & Biogeography* **11**: 191–209.

Davis, A.L.V., R.J. van Aarde, C.H. Scholtz and J.H. Delpont. 2003. Convergence between dung beetle assemblages of a post-mining vegetational chronosequence and unmined dune forest. *Restoration Ecology* **11**: 29–42.

Díaz, S., J.G. Hodgson, K. Thompson, M.J. Cabido, J.H.C. Cornelissen, A. Jalili, G. Montserrat-Martí, J.P. Grime, F. Zarrinkamar, Y. Asri, S.R. Band, S. Basconcelo, P. Castro-Díez, G. Funes, B. Hamzehee, M. Khoshnevi, N. Pérez-Harguindeguy, M.C. Pérez-Rontomé, F.A. Shirvany, F. Vendramini, S. Yazdani, R. Abbas-Azimi, A. Bogaard, S. Boustani, M. Charles, M. Dehghan, L. de Torres-Espuny, V. Falczuk, J. Guerrero-Campo, A. Hynd, G. Jones, E. Kowsary, F. Kazemi-Saeed, M. Maestro-Martínez, A. Romo-Díez, S. Shaw, B. Siavash, P. Villar-Salvador, and M.R. Zak. 2004. The plant traits that drive ecosystems: Evidence from three continents. *Journal of Vegetation Science* **15**: 295–304.

Doube, B.M. 1990. A functional classification for analysis of the structure of dung beetle assemblages. *Ecological Entomology* **15**: 371–383.

Duncan, R. S., and V. E. Duncan. 2000. Forest succession and distance from forest edge in an Afro-tropical grassland. *Biotropica* **32**:33-41.

Ehrlich, P.R. and A.H Ehrlich .1981. Extinction. The Causes and Consequences of the Disappearance of Species. Random House, London, UK.

Ewel, J. J. 1990. Restoration is the ultimate test of ecological theory. Pages 31 to 34 in W. R. Jordan, editor. Restoration Ecology a synthetic approach to ecological research. Cambridge University Press, Cambridge, UK.

Ferreira, S.M. and R.J. van Aarde. 1996. Changes in community characteristics of small mammals in rehabilitating coastal dune forests in northern KwaZulu-Natal. African Journal of Ecology **34**: 113–130.

Ferreria, S. M. 1997. Determinants of small mammal community structure on rehabilitating dune forests in northern KwaZulu Natal, South Africa PhD thesis. University of Pretoria, Pretoria, South Africa.

Foord, S.H., R.J. van Aarde and S.M. Ferreira. 1994. Seed dispersal by vervet monkeys in rehabilitating coastal dune forests at Richards Bay. South African Journal of Wildlife Research **24**: 56-59.

Fox, B. 1987. Species assembly and the evolution of community structure. Evolutionary Ecology **1**: 201-213.

Fukami, T., M. Bezemer, S. R. Mortimer, and W.H. van der Putten. 2005. Species divergence and trait convergence in experimental plant community assembly. Ecology Letters **8**: 1283–1290.

Gibbon, G. 2006. Roberts' multimedia birds of southern Africa version 3.3, South African Birding, Westville, South Africa.

Gleason, H.A. 1927. Further views on the succession concept. *Ecology* **8**: 299 – 326.

Gleason, H.A. 1926. The individualistic concept of the plant association. *Bulletin of the Torrey Botanical Club* **53**:7–26.

Gómez, J. M. 2003. Spatial patterns in long-distance dispersal of *Quercus ilex* acorns by jays in a heterogeneous landscape. *Ecography* **26**:573-584.

Guariguata, M.R. and R. Ostertag. 2001. Neotropical secondary forest succession: changes in structural and functional characteristics. *Forest Ecology and Management* **148**: 185–206.

Halle, S. 2007. Science, art, or application – the “Karma” of restoration ecology. *Restoration Ecology* **15**:358-361.

Hobbs, R.J. 2007. Managing plant populations in fragmented landscapes: restoration or gardening? *Australian Journal of Botany* **55**: 371-374.

Holl, K.D., E.E. Crone and C.B. Schultz. 2003. Landscape restoration: Moving from generalities to methodologies. *Bioscience* **53**: 491–502.

Holl, K.D. 2002. Long-term vegetation recovery on reclaimed coal surface mines in the eastern USA. *Journal of Applied Ecology* **39**: 960-970.

Howe, H.F. and M.N. Miriti. 2000. No question: seed dispersal matters. *Trends in Ecology and Evolution* **15**: 434-436.

Hubbell, S.P. 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton, USA.

Jackson, S.T. and R.J. Hobbs. 2009. Ecological restoration in the light of ecological history. *Science* **325**: 567–569.

Janzen, D.H. 1970. Herbivores and the number of tree species in tropical forests. *The American Naturalist* **104**: 501-528.

Johnson, K.H., K.A. Vogt, H.J. Clark, O.J. Schmitz and D.J. Vogt. 1996. Biodiversity and the productivity and stability of ecosystems. *Trends in Ecology and Evolution* **11**: 372–377.

Khurana, E. and J.S. Singh. 2001. Ecology of seed and seedling growth for conservation and restoration of tropical dry forest: a review. *Environmental Conservation* **28**: 39-52.

King, A.W. and K. A. With. 2002. Dispersal success on spatially structured landscapes: when do spatial pattern and dispersal behaviour really matter? *Ecological Modelling* **23**: 23-39.

Kritzing & van Aarde 1998;

Lanta, V., and J. Lepš. 2009. How does surrounding vegetation affect the course of succession: A five-year container experiment. *Journal of Vegetation Science* **20**: 686–694.

Lavorel, S. and E. Garnier. 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology* **16**: 545–556.

Lawes, M.J., H. A. Eeley, N. J. Findlay and D. Forbes. 2007. Resilient forest faunal communities in South Africa: a legacy of palaeoclimatic change and extinction filtering? *Journal of Biogeography* **34**: 1246–1264.

Lawton, J.H. 1994. What do species do in ecosystems. *Oikos* **71**: 367–374.

Lebreton, J.D., J.E. Hines, R. Pradel, J.D. Nichols and J.A. Spendelov. 2003. Estimation by capture-recapture of recruitment and dispersal over several sites. *Oikos* **101**: 253-264.

Lubke, R.A. and A.M. Avis. 1998. A review of the concepts and application of rehabilitation following heavy mineral dune mining. *Marine Pollution Bulletin* **37**: 546–557.

MacArthur, R. 1955. Fluctuations of animal populations and a measure of community stability. *Ecology* **36**: 533–536.

Maggs, T. 1980. The Iron Age sequence south of the Vaal and Pongola Rivers: Some historical implications. *The Journal of African History* **21**: 1-15.

Manchester, S.J. and J.M. Bullock. 2000. The impacts of non-native species on UK biodiversity and the effectiveness of control. *Journal of Applied Ecology* **37**: 845 – 864.

Mason, T.J. and K. French. 2007. Management regimes for a plant invader differentially impact resident communities. *Biological Conservation* **136**: 246–259.

Matthews, J.W. and G. Spyreas. 2010. Convergence and divergence in plant community trajectories as a framework for monitoring wetland restoration progress. *Journal of Applied Ecology* **47**: 1128–1136.

McCann, K.S. 2000. The diversity-stability debate. *Nature* **405**: 228 – 233.

McCoy, E.D. and H.R. Mushinsky. 2002. Measuring the success of wildlife community restoration. *Ecological Applications* **12**: 1861 – 1871.

McGeoch, L., I. Gordon and J. Schmitt. 2008. Impacts of land use, anthropogenic disturbance, and harvesting on an African medicinal liana. *Biological Conservation* **141**: 2218-2229.

Midgley, J. A. Seydack, D. Reynell and D. McKelly. Fine-grain pattern in Southern Cape Plateau Forests. 1990. *Journal of vegetation Science* **1**: 539 – 546.

Morgan, P.A. and F.T. Short. 2002. Using Functional Trajectories to Track Constructed Salt Marsh Development in the Great Bay Estuary, Maine/New Hampshire, U.S.A. *Restoration Ecology* **10**: 461 – 473.

Mouchet, M.A. S. Villéger, N.W.H. Mason and D. Mouillot. 2010. Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. *Functional Ecology* **24**: 867–876.

Mpanza, T.D.E., P.F. Scogings, N.W. Kunene and A.M. Zobolo. 2009. Impacts of cattle on ecological restoration of coastal forests in KwaZulu-Natal, South Africa. *African Journal of Range and Forage Science* **26**: 1-7.

Neubert, M.G. and H. Caswell. 1997. Alternatives to resilience for measuring the responses of ecological systems to perturbations. *Ecology* **78**: 653–665.

Nichols, G. 2005. Growing rare plants – a practical handbook on propagating the threatened plants of southern Africa. Southern African Botanical Diversity Network Report No. 36. SABONET, Pretoria.



Norton, D.A. 2009. Species invasions and the limits to restoration: Learning from New Zealand experience. *Science* **325**: 569–571.

Ntshotsho, P. 2006. Carbon sequestration on the subtropical dunes of South Africa: a comparison between native regenerating ecosystems and exotic plantations. M.Sc. Thesis. University of Pretoria, South Africa.

Odum, E. 1969. The strategy of ecosystem development. *Science* **164**: 262–270.

Ott, T. and R.J. van Aarde. *In prep.* Spatio-temporal changes in forest canopies of a coastal dune forest.

Paul, M., C. Catterall, P. Pollard, and J. Kanowski. 2010. Recovery of soil properties and functions in different rainforest restoration pathways. *Forest Ecology and Management* **259**: 2083–2092.

Petchey, O.L., A. Hector and K.J. Gaston. 2004. How do different measures of functional diversity perform. *Ecology* **85**: 847–857.

Pimm, S.L. 1991. The balance of nature. Ecological issues in the conservation of species and communities. The University of Chicago Press, Chicago, Illinois, USA.

Pooley, E. 2003. Trees of Natal, Zululand and Transkei (4<sup>th</sup> edition). Natal Flora Publications Trust, Durban, South Africa.

Pooley, E. 1998. A Field Guide to Wild Flowers KwaZulu-Natal and the Eastern Region. Natal Flora Publications Trust, Durban, South Africa.

Potter, M.A. 1990. Movement of North Island brown Kiwi (*Apteryx australis mantelli*) between forest remnants. *New Zealand Journal of Ecology* **14**: 17-24.

Price, O.F. 2006. Movements of frugivorous birds among fragmented rainforests in the Northern Territory, Australia. *Wildlife Research* **33**: 521-528.

RBM .1995. Environmental Management Plan. Unpublished Report.

Redi, B.H., R.J. van Aarde and T.D. Wassenaar. 2005. Coastal dune forest development and the regeneration of millipede communities. *Restoration Ecology* **13**: 284–291.

Rey Benayas, J.M., A.C. Newton, A. Diaz and J.M. Bullock. 2009. Enhancement of biodiversity and ecosystem services by ecological restoration: A meta-analysis. *Science* **325**: 1121-1124.

Root, R. B. 1967. The niche exploitation pattern of the blue-gray gnatcatcher. *Ecological Monographs* **37**: 317–350.

Ruiz-Jaen, M.C. and T.M. Aide. 2005. Restoration success: How is it being measured? *Restoration Ecology* **13**: 569-577.

Shanley, P. and L. Luz. 2003. The impacts of forest degradation on medicinal plant use and implications for health care in Eastern Amazonia. *BioScience* **53**: 573-584.

Simberloff & Dayan 1991

Smit, A.M., and R.J. van Aarde. 2001. The influence of millipedes on selected soil elements: a microcosm study on three species occurring on coastal sand dunes. *Functional Ecology* **15**:51–59.

Society for Ecological Restoration International Science & Policy Working Group (SER). 2004. The SER International Primer on Ecological Restoration. [www.ser.org](http://www.ser.org), Tucson: Society for Ecological Restoration International.

Stoner, K.E., P. Riba-Hernández, K. Vulinec and J.E. Lambert. 2007. The role of mammals in creating and modifying seed shadows in tropical forests. Some possible consequences of their elimination. *Biotropica* **39**: 316-327.

Suding, K.N. and R.J Hobbs. 2009. Threshold models in restoration and conservation: a developing framework. *Trends in Ecology and Evolution* **24**: 271-279.

Sutherland, J.P. 1974. Multiple stable points in natural communities. *The American Naturalist* **108**: 859-873.

Sweeney, O.F. McD. 2005. Seed size and dispersal mechanism of trees as determinants of colonization of rehabilitating coastal dune forests in South Africa. M.Sc. Thesis. University of Pretoria.

Taylor, J.L.S., T. Rabe, L.J. McGaw, A.K. Jager, and J. van Staden. 2001. Towards the scientific validation of traditional medicinal plants. *Plant Growth Regulation* **34**: 23–37.

Temperton, V. M., and R. J. Hobbs. 2004. The search for ecological assembly rule and its relevance to restoration ecology. Pages 34–54 in V. M. Temperton, R. J. Hobbs, T. Nuttle, and S. Halle, editors. *Assembly rules and restoration ecology—bridging the gap between theory and practice*. Island Press, Washington, D.C.

The Mineral and Petroleum Resources Development Act. 2002. No. 28 of 2002. Republic Of South Africa, Cape Town.

Tilman, D. 2001. Functional diversity. Pages 109-120 in S. A. Levin, editor. Encyclopedia of biodiversity. Academic Press, San Diego, California, USA.

Tilman, D., P.B. Reich and J.M. H. Knops. 2006. Biodiversity and ecosystem stability in a decade long grassland experiment. *Nature* **441**: 629 – 632.

Trimble, M.J., and R.J. van Aarde. 2011. Decline of birds in a human modified coastal dune forest landscape in South Africa. *PloSONE*. **6**: e16176. doi:10.1371/journal.pone.0016176

van Aarde, R.J., A.M. Smit and A.S. Claassens. 1998. Soil characteristics of rehabilitating and unmined coastal dunes at Richards Bay, KwaZulu-Natal, South Africa. *Restoration Ecology* **6**: 102–110.

van Aarde, R.J., M. Coe, and W.A. Niering. 1996b. On the rehabilitation of coastal dunes of KwaZulu-Natal. *South African Journal of Science* **92**: 122-124.

van Aarde, R.J., S.M. Ferreira, and J.J. Kritzing. 1996a. Successional changes in rehabilitating coastal dune communities in northern KwaZulu-Natal, South Africa. *Restoration Ecology* **4**: 334 – 345.

van Aarde, R.J., S.M. Ferreira, and J.J. Kritzing. 1996c. Millipede communities in rehabilitating coastal dune forests in northern KwaZulu-Natal, South Africa. *Journal of Zoology* **238**: 703 – 712.

van Dyk, P.J. 1997. The population biology of the sweet thorn *Acacia karroo* in rehabilitating coastal dune forests in northern KwaZulu-Natal, South Africa. M.Sc. Thesis. University of Pretoria.

van Wyk, G.F., D.A. Everard, J.J. Midgley and I.G. Gordon. 1996. Classification and dynamics of a southern African subtropical coastal lowland forest. *South African Journal of Botany* **62**: 133–142.

Veblen, T.T., C. Donoso, Z. Federico, M. Schlegel, and B. Escobar. 1981. Forest dynamics in south-central Chile. *Journal of Biogeography* **8**: 211–247.

Walker, L.R. and R. del Moral. 2009. Lessons from primary succession for restoration of severely damaged habitats. *Applied Vegetation Science* **12**: 55–67.

Walker, B. H. 1992. Biodiversity and ecological redundancy. *Conservation Biology* **6**:18–23.

Walker, L.R., and R. del Moral. 2003. *Primary succession and Ecosystem Rehabilitation*. Cambridge University Press, Cambridge, United Kingdom.

Wang, B.C. and T.B. Smith. 2002. Closing the seed dispersal loop *Trends in Ecology and Evolution* **17**: 379-386.

Wassenaar, T. D., and R. J. van Aarde. 2001. Short-term responses of rehabilitating coastal dune forest ground vegetation to livestock grazing. *African Journal of Ecology* **39**:329-339.

Wassenaar, T. D., R. J. van Aarde, S. L. Pimm, and S. M. Ferreira. 2005. Community convergence in disturbed sub-tropical dune forest. *Ecology* **86**: 655-666.

Wassenaar, T. D., S. M. Ferreira, and R. J. van Aarde. 2007 Flagging aberrant sites and assemblages in restoration projects. *Restoration Ecology* **15**:68-76

Weiermans, J. and R.J. van Aarde. 2003. Roads as ecological edges for rehabilitating coastal dune assemblages in northern KwaZulu-Natal, South Africa. *Restoration Ecology* **11**: 43-49.

Weiher, E. 2007. On the status of restoration science: Obstacles and Opportunities. *Restoration Ecology* **15**: 340-343.

Weisser, P.J. and R. Muller. 1983. Dune vegetation dynamics from 1937 to 1976 in the Mlalazi-Richards Bay area of Natal, South Africa. *Bothalia* **14**:661–667.

Weisser P. J and F. Marques. 1979. Gross vegetation changes in the dune area between Richards Bay and the Mfolozi River, 1937–1974. *Bothalia* **12**:711–721.

West, A., W. Bond, and J.J. Midgley. 2000. Dune forest succession on old lands: implications for post-mining restoration. Pages 35-39 in: A.H.W. Seydack, W.J. Vermeulen, and C. Vermeulen, editors. *Towards Sustainable Management Based on Scientific Understanding of Natural Forests and Woodlands*. Department of Water Affairs and Forestry, Knysna, South Africa.

Wright, J.P. S. Naeem, A. Hector, C. Lehman, P. B. Reich, B. Schmid and D. Tilman. Conventional functional classification schemes underestimate the relationship with ecosystem functioning. *Ecology Letters* **9**: 111–120.

Wu, J. and O.L. Loucks. 1995. From balance of nature to hierarchical patch dynamics: A paradigm shift in ecology. *The Quarterly Review of Biology* **70**: 439-466.

Young, T. P., D. A. Petersen, and J. J. Clary 2005. The ecology of restoration: historical links, emerging issues and unexplored realms. *Ecology Letters* **8**:662-673.

Zedler, J.B. and J.C. Callaway. 2000. Evaluating the progress of engineered tidal wetlands. *Ecological Engineering* **15**: 211-225.



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.



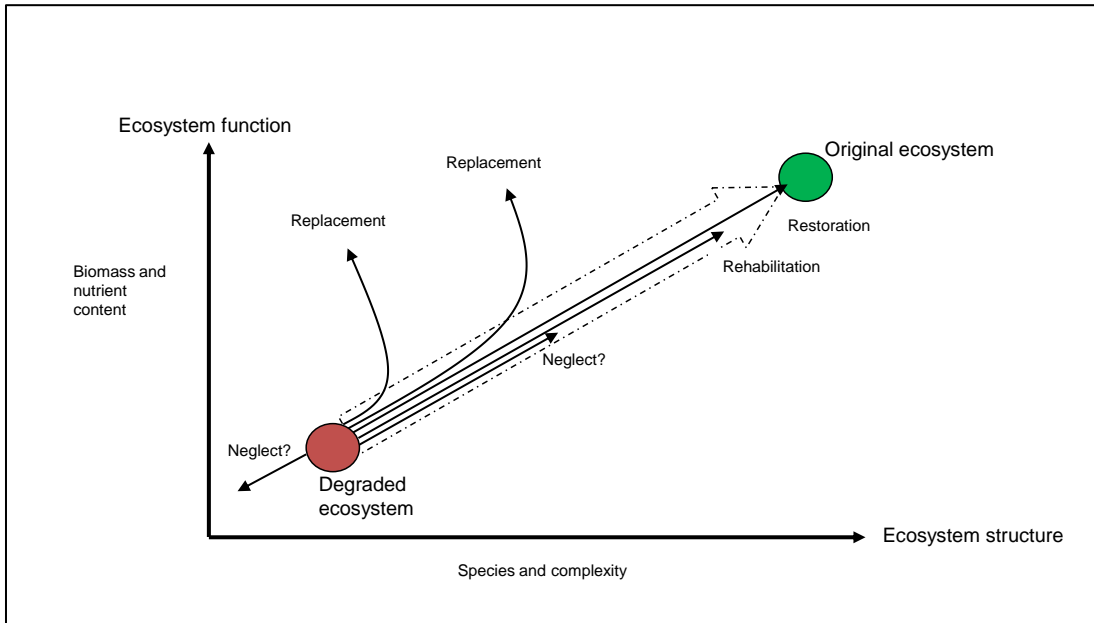


Figure 7-1. The structure – function model of Bradshaw (1984). The arrow with the dashed outline indicates normal ecosystem development.

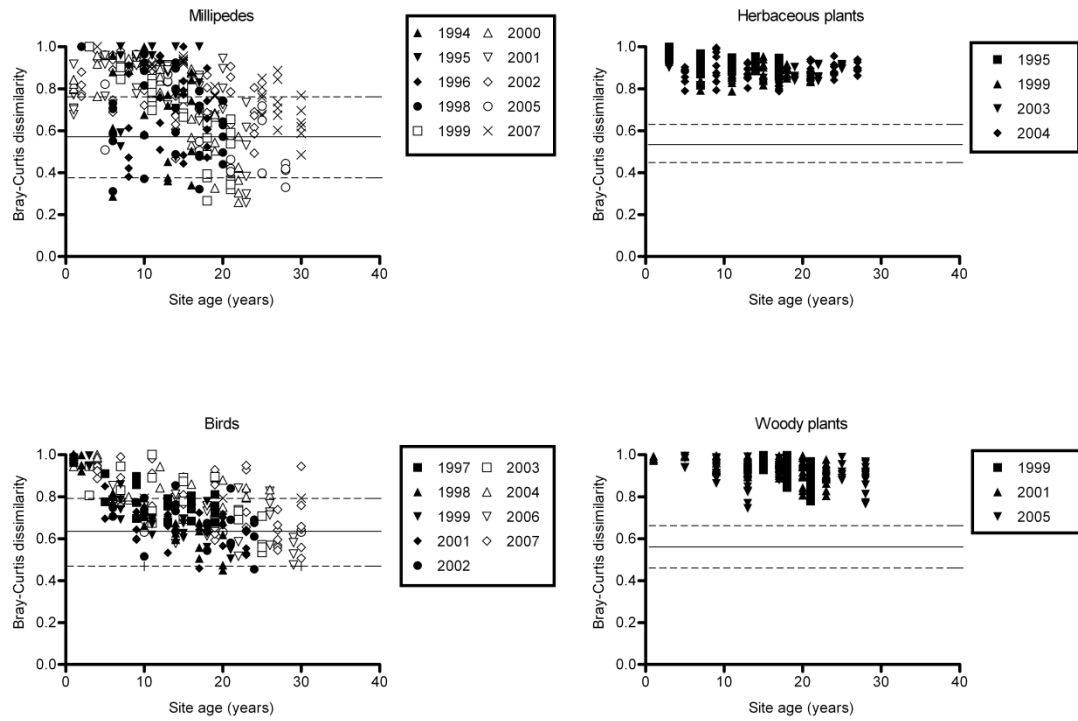


Figure 7-2. Bray-Curtis dissimilarity between rehabilitating coastal dune forest sites and the Sokhulu Forest reference site for four forest taxa. Solid horizontal lines indicate the mean Bray-Curtis dissimilarity value within the reference site and the dashed horizontal lines indicate the variation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

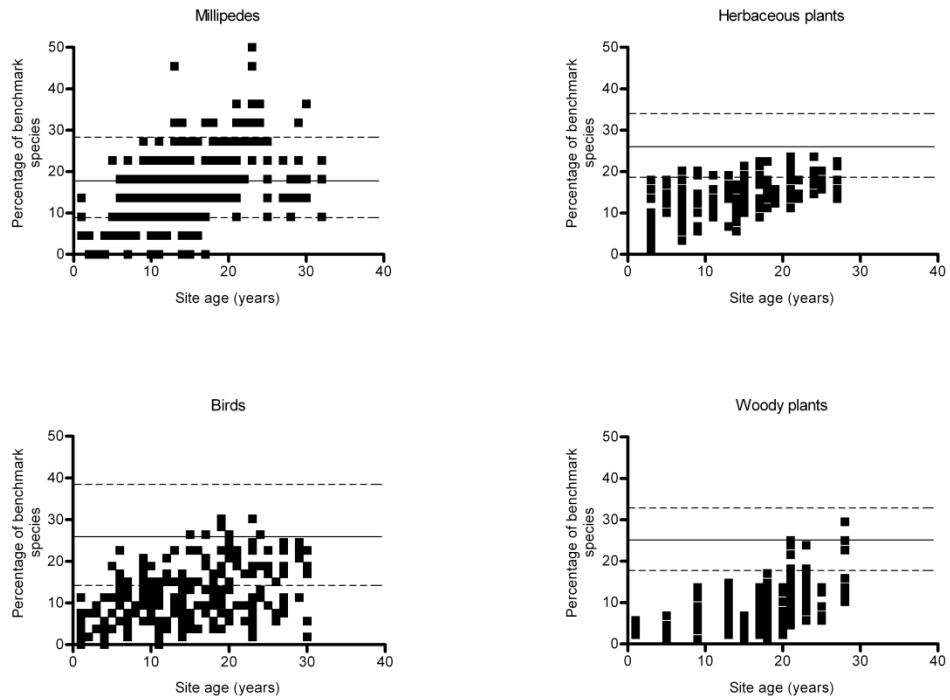


Figure 7-3. The percentage of species found within the reference site (benchmark) that are also found in the rehabilitating sites as they increase in age. Once again the solid horizontal lines indicate the mean Bray-Curtis dissimilarity value within the reference site and the dashed horizontal lines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

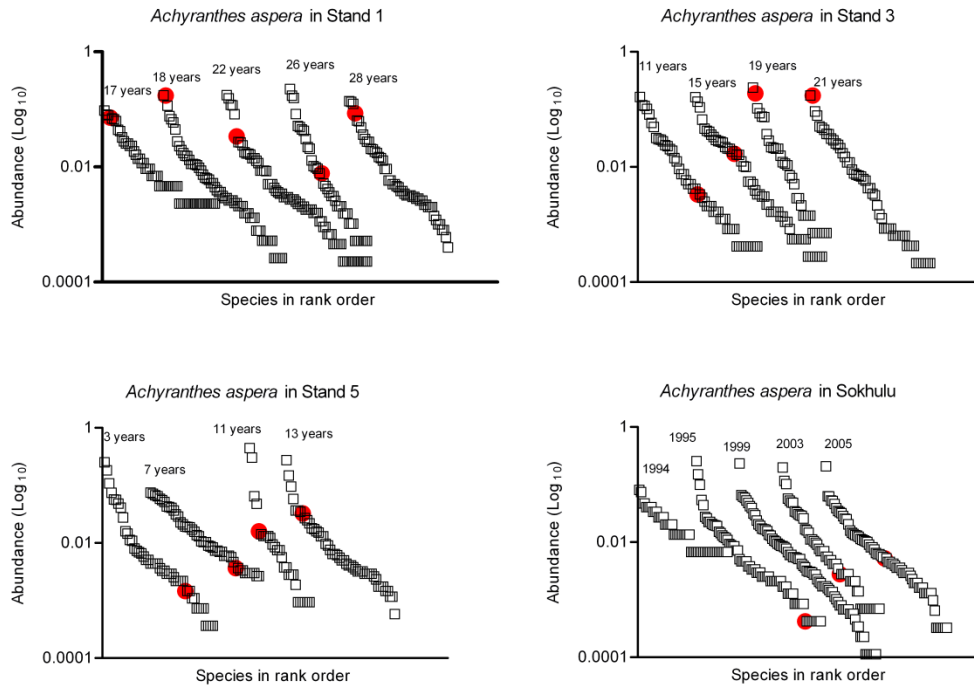


Figure 7-4. The change in rank abundance position for the non-indigenous species, *Achyranthes aspera*, in three rehabilitating coastal dune forests at different times post disturbance. The Sokhulu Forest reference site has also been invaded by this species; it was first recorded in the year 1995.

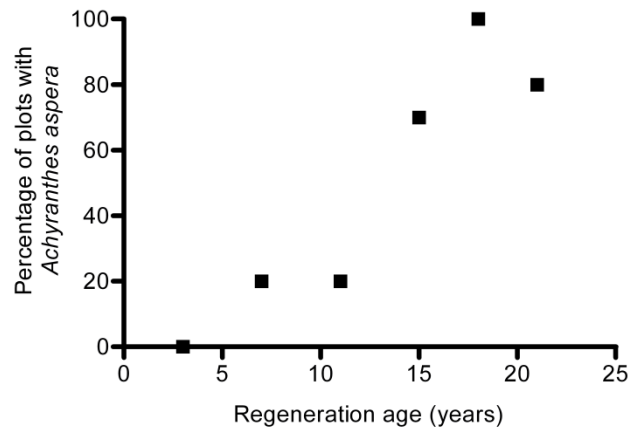


Figure 7-5. The percentage of sampling plots in rehabilitating coastal dune forest sites that contain *Achyranthes aspera*. The data presented here comes from the 2001 herbaceous plant chronosequence.

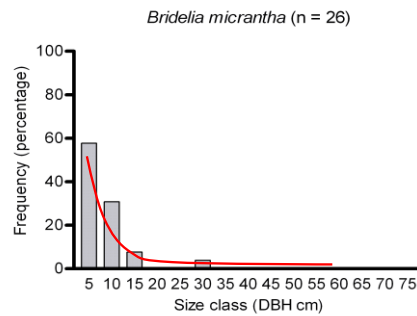
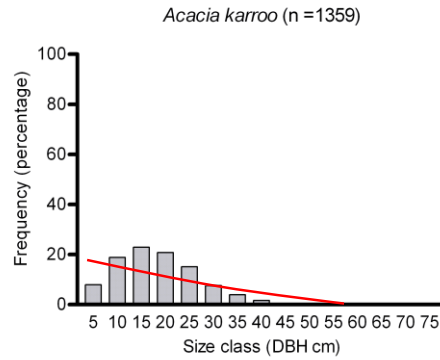


Figure 7-6. Size-class distributions for the pioneer tree species *Acacia karroo* and forest tree species *Bridelia micrantha*. The pioneer does not show the “reverse-J” pattern of a reproducing population where as the forest tree does. The line illustrates the negative exponential function.

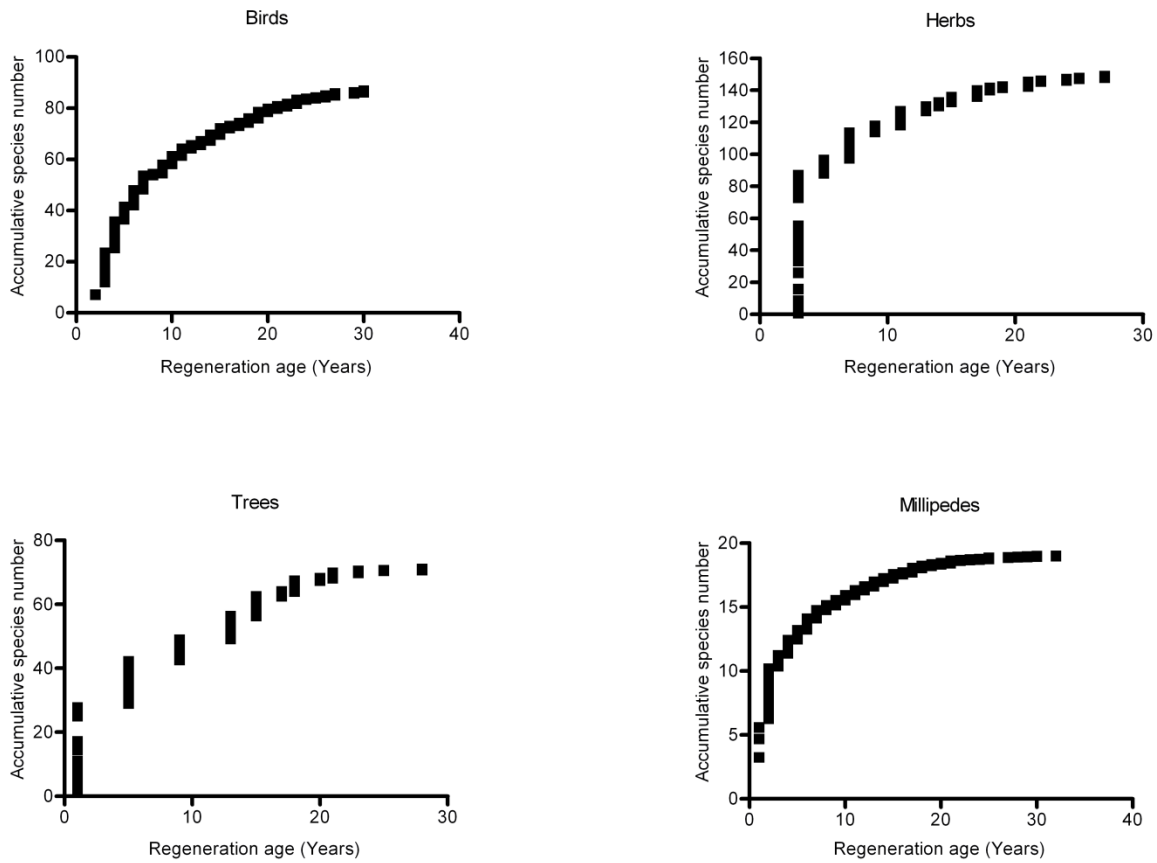


Figure 7-7. The accumulation of species across the rehabilitating coastal dune forest sere for four forest taxa.