



Coastal dune forest regeneration:
The response of biological communities to rehabilitation

by

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I exhort you, o Celtis, let me walk in the soil with you, let me breathe the humid air. Do you remember the shopkeeper, hands full of glowing embers, playing artist, more, God? Letting words climb like plants, like monkeys from the north, swinging from the slender branches of trees, vicariously placed on this spot. What say do they have, Celtis, in their allotted time and place, in how they are used and discarded upon the ancient carbon soils, as if they are droppings from a sub-tropical bird? Such is the forest life. Humans, often, are blind to the sinuous movement of words up the mouldy lichen-mottled stems of trees, chasing a tree agama, this way, that way, flashes of blue consonants as its sheer beauty is shouted in pure natural, silent breath. Oh, that was him, there he was, the shopkeeper, he was a sight to see, cloaked in the heavy early-morning air. Celtis! You have the better of us, you do.

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Abstract

Human appropriation of natural resources, and the consequent loss of habitats, means that ecological restoration may in the future become a vital conservation tool. For this to happen, we have to understand the processes and factors that govern community assembly, and their management. Here I analyze data on community structure (richness, evenness, diversity, composition) of assemblages (millipedes, spiders, dung beetles, plants, birds, rodents), and on soil chemical and physical properties, to describe and evaluate post-disturbance dune forest regeneration patterns. Data were collected from undisturbed “climax” coastal dune forests (the benchmarks for the ecological restoration

program of a dune mining company), from post-mining rehabilitating dune forests, and from self-regenerating dune forests in northern KwaZulu-Natal.

Both succession theory and community assembly theory predict that a species' niche will determine when it will colonize new sites, and by extension, what the eventual species composition will be. This type of control should result in deterministic regeneration patterns for a community. In support of this view, I found that the majority of habitat-age related changes in community structure and ecosystem function were either towards benchmark values (and will reach these values in less than 65 years post-disturbance), or were already equal to the benchmark. Age-related trajectories were repeatable between surveys and post-mining sites were changing as fast or faster than spontaneously regenerating sites. Moreover, detailed analysis of changes in community composition of millipedes, dung beetles, herbs, trees, birds and rodents showed that all of the taxa were also regaining the benchmark's species composition.

However, community change was dependent on how it was measured – dung beetles recovered only species presence, but others relative abundances as well. Changes were almost never exponential, suggesting that colonization and extinction are not the orderly events foreseen by equilibrium biodiversity theory. Furthermore, the average abundances of birds, trees and millipedes in undisturbed dune forest patches were correlated with colonization success, suggesting that post-disturbance recovery through colonization may be controlled from outside the local community, rather than by species interactions. The recovery of the spider community appeared to be towards the benchmark forest community, but spider species composition was critically linked to microhabitat structure. Because microhabitat is not necessarily restored concurrently with forest community structure, the spider assemblage (and possibly other invertebrates) may not recover the desired pre-disturbance structure or composition.

Dune forests thus seem to be resilient to mining disturbances, since most taxa were recovering structure and composition. However, classic successional and community assembly theories are unlikely to fully explain these community recovery mechanisms. More likely, post-disturbance recovery occurs because a new habitat passively “samples” the rain of dispersing propagules and individuals, leading to a high probability of capturing the average species composition of the region. A conceptual model of dispersal in the landscape suggested that species composition of new habitats might equilibrate to the composition of the closest habitat undergoing the least amount of species compositional change, although this may not apply to all taxa. This model may serve as the basis for directing future research and restoration management.

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Disclaimer

The present dissertation includes four paper manuscripts, prepared for submission to four different scientific journals. Style and formatting in these chapters are according to journal requirements. Consequently, some aspects of style and formatting differ between the different chapters and there is some unavoidable duplication in the descriptions of study site and methods. The lists of references pertaining to the general introduction and synthesis were prepared according to the requirements of the *Journal of Biogeography*.

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Chapter 1

General Introduction

Humanity is rapidly changing the ecological character of the earth (Vitousek 1994, Pimm *et al.* 1995, Pimm 2001). One of our worst legacies has been the systematic destruction of natural habitat, with obviously negative consequences for biodiversity. Without doubt, the most effective way to prevent further habitat loss and the concurrent extinction of species is to preserve them in formal conservation areas, but our future options here are decreasing rapidly (Mittermeier *et al.* 2003, Rosenzweig 2003). In the future, there will thus be an obvious need for an alternative to formal conservation, for some technique that we can use to moderate or reverse our negative effects on nature.

One possible alternative is to restore the ecological character of human-disturbed habitats through ecological rehabilitation. The sharp increase in the number of restoration projects and studies conducted worldwide (Ormerod 2003) is evidence that ecological restoration is increasingly being seen as a valid supportive tool for biodiversity conservation. However, success is not automatic nor is it obvious. Can restoration succeed in re-creating the structure (the diversity and composition) of a complex system, given that this structure is the result of what appears to be a frustratingly intractable scale-dependent mix of structuring forces (Lawton 1999)? Ecological theory (or the lack thereof) and empirical experience give many reasons why we should fail in this attempt and, in fact, why we should fail even to measure our progress (Lawton 1999). This is borne out by many reported restoration failures (Lockwood & Pimm 1999) and sometimes by the awkward apologetic suggestion to accept degraded system states as restoration targets (for example Stanturf *et al.* 2001). If the criterion for success is thus the recovery of both biodiversity and composition

(which, in the context of conservation management, it should be), there is unfortunately not much evidence so far that we are onto a true conservation alternative. Ecological restoration is nothing more than the assisted recovery of a disturbed ecosystem (SER 2002) and such assistance can take many forms from passive (allowing natural processes to repair the system) to active (single or multiple species introductions) (Bradshaw 2002). If ecological restoration is indeed meant to play a major role in replacing lost biodiversity (Young 2000), we clearly have to understand more about the processes and factors that govern community assembly, even where the community consists of a single species, and about how we can manage these to increase the chances for success (Lockwood 1997).

For Richards Bay Minerals, a company that mines the sand dunes north of Richards Bay, KwaZulu-Natal, for a variety of minerals, these issues are more than theoretical musings. Their dune forest rehabilitation program, which commenced in 1976, aims to restore forest on one third of the mined lease area (van Aarde *et al.* 1996b). The question of whether a disturbed community can be restored, and of what determines the outcome, are thus also of practical importance.

In this thesis, I analyze an ecological database on the community structure of assemblages from undisturbed forests, as well as those of chronosequences of rehabilitating and self-regenerating coastal dune forests in KwaZulu-Natal, to describe and evaluate dune forest regeneration patterns. The assemblages covered as many trophic levels and taxa as possible, from invertebrates such as dung beetles, millipedes and spiders, to vertebrates (rodents and birds) and plants (herbs and trees). Disturbance, from natural or human origin, is an ecological reality (Bradshaw 2000). But how a specific taxon, or even a whole ecosystem, responds to such a disturbance is not always self-evident. Succession theory (Rees *et al.* 2001) predicts that ecosystem recovery should be

a highly ordered process because species' niches will determine when they can colonize a newly disturbed habitat. In this thesis, I show that the question posed above, whether ecological restoration can re-create a complete ecosystem, can be broken down into parts which deal broadly with pattern and process in community assembly: Are community developmental patterns stable over time and space, and is there a clearly definable endpoint (suggesting stabilizing structuring forces at work)? Are there correlates of community regeneration that can explain developmental patterns? In other words, what are the cues that colonizing species respond to? If there are such cues, to what extent do they influence the outcome of the community assembly process?

The thesis is loosely divided into three parts. The first three chapters introduce the study (this chapter), the study area (Chapter 2) and the methods (the database on species distribution and abundance in regenerating and undisturbed forests, Chapter 3). These are followed by four chapters that each consists of a manuscript prepared for submission to scientific journals for publication. The first two of these (Chapters 4 and 5) describe and evaluate community structural and compositional regeneration patterns across up to seven taxa from four trophic levels. In the following two chapters (Chapters 6 and 7), I analyze the effects of regional abundance and microhabitat structure on colonization of new habitats by four different taxa. The third part (Chapter 8) comprises a synthesis of the results of Chapters 4 to 7, and proposes a conceptual, neutral community model as a basis for future evaluation and analysis of community regeneration. (By neutral I mean that species are ecologically equivalent in terms of their probability of establishing at a site).

The study was conducted on the southern tip of what is broadly defined as the Maputaland Centre of Endemism (van Wyk 1996), a globally recognized diversity hotspot. Evolutionary, geological and biogeographical factors have created a unique mix

of habitats and species associations here, of which coastal dune forest is one ecotype (van Wyk 1996). Site and study area descriptions pertaining to each study are provided in Chapters 4 to 7. I included a chapter on the history, biogeography and forest distribution of Maputaland and specifically of the Richards Bay-St Lucia area (Chapter 2) because I believe that results from any ecological research on dune forests have to be interpreted with this information as background knowledge.

For example, anthropogenic disturbance, and the subsequent regeneration of forests, has been a feature of this landscape for thousands of years (Hall 1984). This places the efforts of Richards Bay Minerals to restore a specific habitat type into historical and ecological contexts and allows us to evaluate the ecological restoration program on a more abstract level. More recent landscape changes are also pertinent. For example, by the start of mining in 1976, much of the current mining lease area was covered by secondary forests that had regenerated since the time of the earliest aerial photographs in 1937 (Weisser & Muller 1983, Fig. 1.1). Furthermore, mature forest was limited to a few large patches (at Mapelane, St Lucia and Cape Vidal) and to narrow strips on the coastal foredunes and along watercourses (Weisser & Muller 1983, own records).

The importance of these historical changes lie in the implication that dune forests have an inbuilt response mechanism that allows ecosystem recovery, even after disturbances on the scale of the dune mining operation of Richards Bay Minerals (RBM) (see Camp 1990 and van Aarde *et al.* 1996b for a description of the mining operation). Indeed, earlier work on the rehabilitation of mined dune forests by RBM (van Aarde *et al.* 1996a, b, Van Dyk 1997, Kritzinger & van Aarde 1998), as well as studies on post-disturbance changes in disturbed dune forests in the region (Weisser 1978, Weisser & Muller 1983, Mentis & Ellery 1994, von Maltitz *et al.* 1996, West *et al.* 1999), have

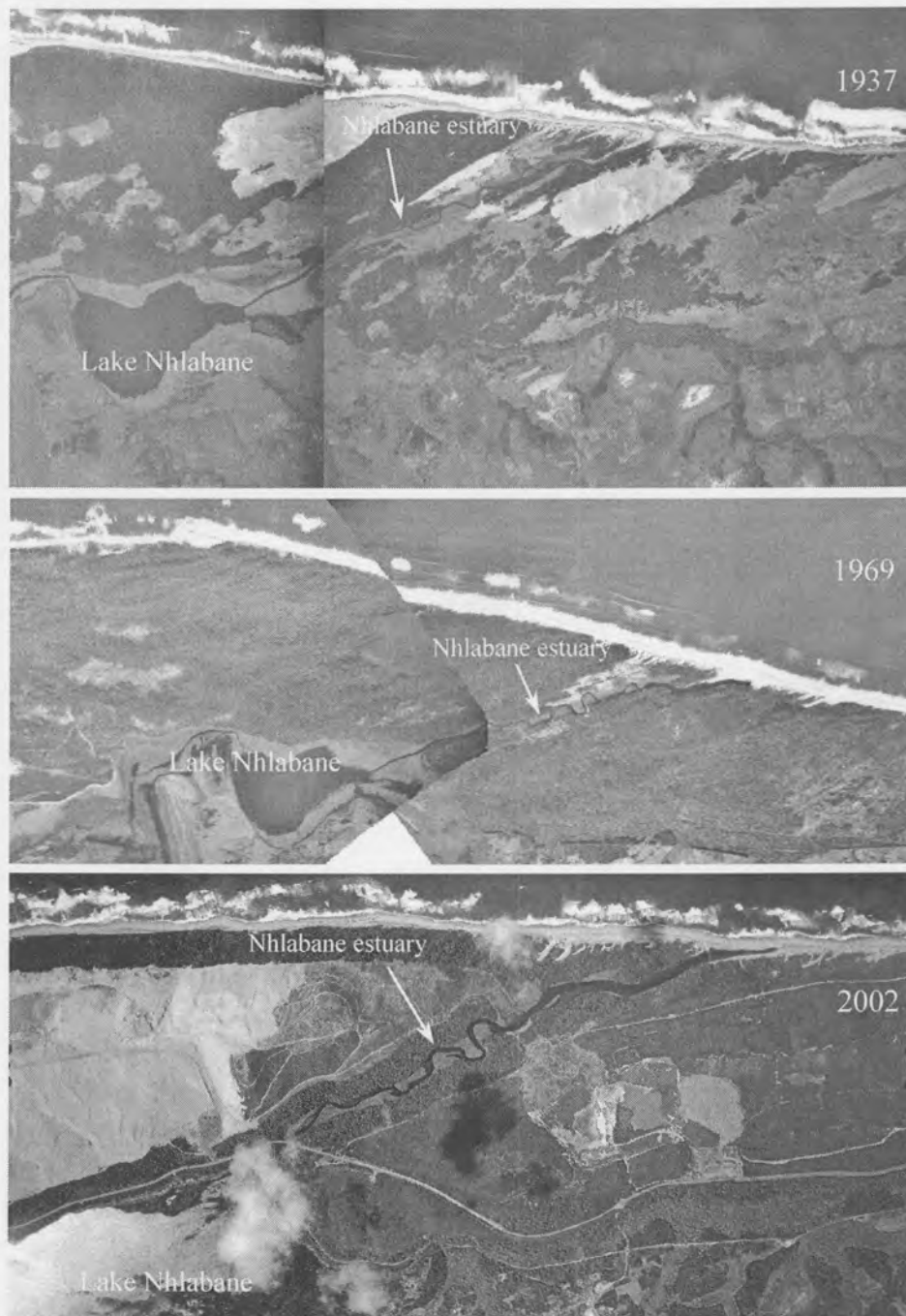


Figure 1.1. Mosaiced aerial photographs of the Lake Nhlabane estuary. The top photograph was taken in 1937, the middle one 1969 (this was taken 7 years prior to the start of mining in the Tisand lease area north of Richards Bay, mining at this point only commenced in the early to mid 1990's), and the bottom one in 2000. The relictual forest patches are clearly present in the 1937 photograph (the scattered dark vegetation patches). By 1969 most of the area was covered in secondary woodlands and forests. The dredge mining operation is visible in the 2002 photograph, showing the extent and location of mining *vis a vis* the historical forest and woodland cover. By 2002 the area to the right of the estuary had largely already been mined and rehabilitated. Scale is approximately 1:10000 (the photographs are not on the same scale).

described patterns that suggested successional changes leading to a climax dune forest state. Results from Chapters 4 and 5 confirm this observation, in the sense that most of the seven assemblages I (we) studied showed the species replacement sequence and the inexorable march of species assemblages towards an equilibrium composition that are typical of successional processes (although there were detailed differences between taxa).

This is a defining aspect of succession – sequential, deterministic and directional species replacement over time inexorably and predictably leads to well-defined endpoints. Such a scheme has obvious appeal in ecological restoration (Parker 1997). Yet, we know from mathematical-analytical (May 1977) and laboratory studies (Drake 1990, Drake *et al.* 1993), and from computer simulation studies on the assembly of interactive assemblages after a disturbance (Luh & Pimm 1993, Lockwood 1997, Lockwood *et al.* 1997), that a single persistent state (an equilibrium) should be the exception rather than the norm. These studies show that many persistent states are possible and that the particular group of species that survives the assembly process is a function of the colonization sequence (Lockwood *et al.* 1997). Because invasion sequence is a stochastic event, priority effects (competitive exclusion of particular species or groups of species by an early-colonizing competitor) may be common in regenerating communities.

Succession models and assembly rules share an important assumption – they both assume that community structural patterns are produced by niche-based (or otherwise species-interactive), stabilizing forces. This is essentially an “inside-out” view of community organization, because these stabilizing forces, which control the ordered return to one or more equilibrium states, are internal to the community. A ball in a depression on a plane is a good analogy for an ecosystem in an equilibrium state (see for

example May 1977, Ives *et al.* 2003). It can be nudged out of this stable resting condition by some disturbing force, and, depending on the severity of the perturbation, will more than likely tend to return to its original position, or to the bottom of another depression. Isaac Newton would undoubtedly have ascribed this tendency for the ball to move to a lower position to the effects of gravity on its mass. By ascribing community regeneration patterns exclusively to the effects of species interactions, we are essentially doing the same for disturbed ecosystems.

This touches on the decades old argument about whether community structure is the result of predictable relationships between species, or an unpredictable function of random events (Ward & Thornton 2000). In Chapter 6, I show that the rate and sequence of invasion (and hence the bias in the development towards a persistent state) are largely, but not completely, a function of metacommunity species characteristics. There is therefore an inbuilt tendency for particular invasion rates and sequences to re-occur, but enough uncertainty in some species to allow for some variability in eventual species composition. In Chapter 7 I furthermore show that, for a typical invertebrate group, the spiders, the apparently ordered successional patterns on closer inspection turn out to be more like a fine-scale habitat species sorting.

Results from Chapters 6 and 7 lead me to believe that the analogy of the ball on a plane, and by association the assumptions of niche-assembly views of community structure, is not at all a good one for the structural and compositional changes that occur in a dune forest after disturbance. Without getting ahead of results, I feel that niche-assembly theory ignores the most obvious, and to my mind the most important, aspect of post-disturbance dynamics: in the real world there is a metacommunity full of dispersing species on the outside, and all of these species will attempt to colonize any suitable, newly opened habitat space. Although all niche-assembly models incorporate the concept

of colonization in some form (for instance, community assembly models predict that persistent states will disappear with high invasion rates – Luh & Pimm 1993, Lockwood *et al.* 1997), it is rarely if ever seen as the principal controlling factor. Deterministic patterns may theoretically be produced as the consequence of local stochastic dispersal interacting with life history “invariance rules” (Hubbell 2001), without invoking competition mechanisms directly (Hurtt & Pacala 1995, Bell 2001, Hubbell 2001, Higgins & Cain 2002). Indeed, results from my study suggest that, if anything, “successional” patterns are probably determined by forces from outside the community, rather than from within.

It is difficult to think of strongly deterministic regeneration patterns as being produced by open, non-equilibrial species collections, but I discuss in Chapter 8 how and why such an “outside-in” view is a more reasonable framework for post-disturbance community development than the classical models of succession and community assembly. From that point of view, successional, or other post-disturbance patterns are produced by an interaction between the same stochastic forces that influence species coexistence (Chesson 1986). Community regeneration could thus perhaps more correctly be seen as a special case of dynamical diversity theory (Hubbell 2001). Such a view of post disturbance dune forest community regeneration holds promise as a basis for future research and a framework for management decision-making.

In summary, apart from the introductory chapters on the study, the area and the database, this thesis consists of a collection of four papers dealing with different aspects of post-disturbance community development in coastal dune forest, arranged around a central theme of describing developmental patterns, and suggesting (and evaluating) a few possible mechanisms that could generate these patterns. Inevitably, developmental patterns reflect on the broad ecological themes outlined above, but not exclusively on

one or the other. Thus, results from Chapters 4 and 5 suggest mostly stabilizing forces in community assembly, but leave no clues to the mechanisms responsible for these patterns. On the other hand, results from Chapters 6 and 7 suggest that deterministic patterns are probably largely (but not exclusively) the consequence of regional species characteristics and very fine-scale habitat suitability, and leave the door open for a neutral view of ecosystem regeneration. In the final chapter (Chapter 8), I discuss the meaning of these results for the rehabilitation program and for future research, in the context of a conceptual model of post-disturbance ecosystem regeneration.

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Chapter 2

Study area: History, Biogeography and Forest Distribution

Historical and climatic determinants of forest distribution

The distribution and extent of forest cover on the eastern coastal lowlands of southern Africa is the product of two factors (Lawes [1990] reviewed forest biogeographical history in southern Africa and particularly that of the east coast of southern Africa; much of my description here is taken from that work). Pleistocene global climate fluctuations probably played the most important role in determining large-scale forest extent in Africa (Lovett 1993). For instance, climate modeling studies suggest that the extent of forest cover in KwaZulu-Natal at the time of the last glacial maximum (~18,000 yr BP) was probably a fraction of what it is today, and was mostly limited to refugial pockets of montane and scarp forest (Lawes 1990, Eeley *et al.* 1999).

Climatic shifts during the last glacial, including the glacial maximum, brought dry summer conditions at a time when the sea level dropped, resulting in widespread dune formation on the Mozambique coastal plains (Tinley 1985). The geological substrate of coastal dune forests is thus relatively young (<20,000 yrs) (see references in Lawes 1990). However, the forests themselves are probably considerably younger than that, since climatic conditions were unsuitable for forest establishment for at least 10,000 yrs after the glacial maximum (Lawes 1990). Warm interglacial conditions returned by the mid Holocene (7,000-4,000 yrs BP) after an arid period at about 10,000-8,000 yrs BP (Tinley 1985) and resulted in raised sea levels and the characteristic truncated dune fields of northern KwaZulu-Natal. During this period forest range expanded in southern Africa as a whole (Scott *et al.* 1997, Eeley *et al.* 1999) and coastal dune forests were established in its present range on the eastern seaboard (see references in Lawes 1990).

Climate has therefore been a major determinant of forest distribution and anthropogenic climate change is set to play a crucial role in the future (Malhi & Grace 2000). However, on a smaller scale the extant coastal dune forest cover and distribution is more likely a product of human influence over almost two millennia, with a particularly severe impact over the last five decades (Hall 1984, Thompson 2002). The coast of KwaZulu-Natal and Mozambique have some of the earliest Iron Age sites south of the Limpopo River, dating back to about 200 AD (Hall 1983). The exact chronology of these earliest sites is unclear (Hall 1983), but it means that the coastal lowlands of southern Africa have been continuously occupied by humans for at least 1500 years, perhaps more. Permanent settlement by farming communities here predates settlement in the rest of South Africa, where farming communities appeared only in about 1000 AD (Hall 1983). This occupation had lasting effects on the coastal environment, to the point that forest distribution and extent in Maputaland/KwaZulu-Natal lowlands before 1950 AD was most likely a direct result of traditional human agricultural and cultural practices (Hall 1984, Avis 1992, Thompson 2002).

However, despite almost hundred years of British colonial rule, the environmental landscape of coastal KwaZulu-Natal, created and maintained by Iron Age agriculturalists, only changed fundamentally after the Second World War (Dominy 1992, Thompson 2002). By 1937, most of the area between Mtunzini and Cape Vidal consisted of grasslands (probably maintained for livestock grazing through fire), with scattered forest patches (Weisser & Muller 1983, Avis 1992). In the 1950s, a major change came about in agricultural practice, with subsistence agro-ecosystems that had existed for hundreds of years being replaced by industrial-scale commercial monocultures (Thompson 2002). Furthermore, in the mid 1950s, the Directorate of Forestry initiated large-scale afforestation programs, mainly in old grasslands with little

impact on the existing forests (Avis 1992, Dominy 1992). These afforestation and agricultural programs necessitated the displacement of many human settlements (Avis 1992).

Up to that stage (1950 to 1960), the landuse patterns have a simple and chronosequential history. However, over the next 40 years modern developments, such as urban expansion and town development, industrial expansion, mining, and small-scale commercial forestry, gave rise to a complex landscape of disturbed and regenerating patches. The net result was that after almost 2000 years of a fire-maintained grass-forest mosaic, forest cover began increasing as many old grasslands reverted to woody cover and eventually to secondary forest (Avis 1992). Some of these modern disturbed and subsequently abandoned sites are the spontaneously regenerating sites used in this thesis as a “trajectory control” (see Chapter 4) for regeneration patterns on the rehabilitation sites.

Biogeographical determinants of forest distribution

The study area is located on the northern broad sandy plain of the Tongaland-Pondoland Phytogeographical Region, which consists of a vegetation mosaic of generally small subtropical forest patches, thickets, savanna and grasslands (Cowling & Hilton-Taylor 1997). Coastal dune forests occur on poorly developed soils on deep, consolidated, calcareous Quaternary sands (composed of Cretaceous and Cenozoic marine sediments), overlying ancient Precambrian rocks (Tinley 1985, Lubke & McKenzie 1996).

Floristically and faunistically, these subtropical forests are related to the forests of the Zanzibar-Inhambane and Guineo-Congolian Regions (Cowling & Hilton-Taylor

1997, Midgley *et al.* 1997, De Klerk *et al.* 2002). The southeastern African coastal plain represents the furthest southern limits to the distribution of many tropical plant and animal species (Cooper 1980, Poynton 1961, van Wyk 1996). In southern Africa, forests occur in frost-free areas (Low & Rebelo 1996), with the largest distinction in tree species composition and physiognomy being between the coastal plain and montane forests (Everard *et al.* 1994, Midgley *et al.* 1997). The vegetation of the Maputaland Centre of Endemism (MCE) is characterized by high numbers of neo-endemic species (Davis *et al.* 1994, van Wyk 1996), but these are mostly associated with unique habitats such as the woody grasslands and sand forest (van Wyk & Smith 2001). Furthermore, although van Wyk (1996) is of the opinion that the vegetation of Maputaland is more closely related to Afrotropical flora than to Afromontane, there has also been extensive regional mixing of “temperate” (Afromontane) and “tropical” (lowland) forest flora (Midgley *et al.* 1997). In contrast to eastern African coastal forests (Burgess *et al.* 1998), the plant species complement of the northern KwaZulu-Natal dune forests is consequently not particularly unique or rich in endemics (Cowling & Hilton-Taylor 1997).

De Klerk *et al.* (2002) analyzed the biogeography of birds endemic to the Afrotropical mainland. Their Tongaland-Pondoland Biogeographical Province, part of a Southern Savanna Subregion that includes the Indian Ocean coastal belt and all miombo woodlands, coincides roughly with the MCE. About 0.14% of Afrotropical birds are endemic to the greater Tongaland-Pondoland Province and the coastal forests here show an endemism peak for birds (De Klerk *et al.* 2002). However, as in plants (although much less distinct), the largest distinction for birds are between Afromontane and east coast tropical regions (Allan *et al.* 1997), with most of the endemism in birds in MCE associated with sand forest (van Rensburg *et al.* 2000). In general, bird assemblages of

forests and woodlands are likely to be fairly similar because of similarities in habitat structure (van Rensburg *et al.* 2000).

It is not clear whether the endemism of plants and vertebrates in the MCE is mirrored by all invertebrates (Poynton 1961, Hamer & Slotow 2002). For instance, in general Diplopoda tend to have restricted ranges (Hamer & Slotow 2002), which can translate into high endemism in relictual forest patches (Hoffmann 1993). However, Maputaland has not been identified as a centre of endemism for millipedes (Hamer & Slotow 2002), perhaps because forest fragmentation here is a relatively recent phenomenon (or perhaps because species information is still inadequate). On the other hand, many dune forest-associated dung beetle species tend to be restricted to Maputaland (Davis 1997, Davis *et al.* 2002).

Clearly, fine-scale biogeographical patterns in plants and animals, and the relationship of these patterns with regeneration ecology, require further study. For instance, Davis *et al.* (2002) illustrated that vegetation regeneration is associated with an increased representation of dung beetle species restricted to smaller biogeographical regions. These macroecological factors will play a role in local colonization and extinction processes (Cornell & Lawton 1992) and I touch on one such a relationship in this thesis in the chapter on the relationship between abundance and colonization (Chapter 6).

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Chapter 3

Database

For the analyses in this thesis, I relied heavily on species abundance and distribution data collected in several postgraduate and non-degree related projects since 1991; here I provide the background and overall description of this database. Specific data collection techniques and analytical methods are described in Chapters 4 to 7. The ecological research program here commenced in 1991 with a study on the small mammal community, but descriptions of community structure in several taxa¹, as well as the physical properties of soils, were completed in the course of the program (Table 3.1). Data from all of the studies that recorded species presence and abundance in replicated sampling units per site, as well as some data on soil properties, were used for the analyses in the current thesis. Where field surveys were conducted over two or more seasons, data from only the summer season (November to February) were used because all other monitoring related surveys were conducted in summer.

Furthermore, a formal ecological evaluation program, which monitors changes in tree, herb, millipede and bird community structure, was initiated in 2001 (Wassenaar & van Aarde 2001a, b). The evaluation program for the first time included a developmental control trajectory (a chronosequence of previously disturbed self-regenerating sites in the region), as well as all undisturbed dune forest patches between Cape Vidal and Richards Bay. This allowed a comparison of developmental trajectories on the post-mining rehabilitation sites with presumably “natural” trajectories, and allowed a comprehensive

¹ I refer to assemblages of species as taxa where applicable. However, in some cases soil physical and chemical properties were included in an analysis, here I refer to the taxa and soil properties together as groups.

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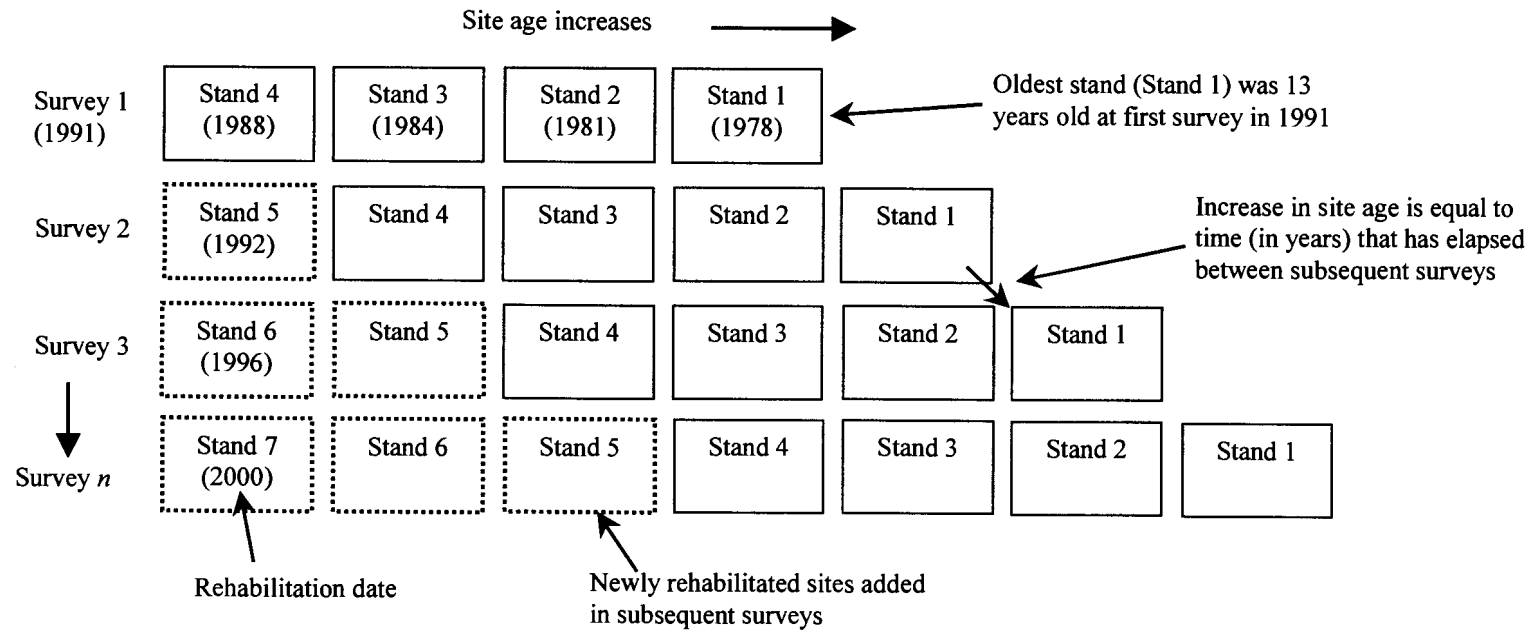
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Table 3.1. Summary of the sampling effort expended in collecting data on taxon and group-specific variables, used in the analyses for this thesis. The number of surveys completed to date was summed across different projects and repeat surveys conducted for the Ecological Evaluation Program. For simplicity only the year in which each survey commenced is given. The absolute number of sites and site surveys involved, the number of sampling units completed, and the amount of labor (in man-days) spent on each taxon were summed across all years and all sites. The absolute number of sites is the number of different sites involved in all years. The total number of site surveys was summed across years, thus if a particular site was re-surveyed in any subsequent year, it was treated as two different sites. The number of man-days was calculated based on an average of three sampling units completed per day.

Taxon / group	Number of surveys (Calendar years)	Absolute number of sites	Number of site surveys	Total number of sampling units	Number of man-days‡
Soil physical properties	2 (1995, 2001)	10	15	74	24.7
Herbs	3 (1994, 1995, 1999)	10	20	209	69.7
Trees	4 (1993, 1997, 1999, 2001)	39	53	865	288.3
Dung beetles	1 (1999)	10	10	33	11
Millipedes	6 (1993, 1998-2002)	21	55	343	114.3
Spiders	1 (1996)	5	5	25	8.3
Small mammals	8 (1991-1996, 1998, 1999)	7	47	148	49.3
Birds	5 (1993, 1997-2000, 2002)	20	51	199	66.3
Totals	30	122	256	1896	631.9

‡ This refers only to those data used in the current thesis. Several of these groups (millipedes, birds, spiders, small mammals) were studied for longer periods during some of these years. However, only summer data were used for all my analyses, hence this estimate does not represent complete sampling effort. Furthermore, it refers *only* to field and specimen handling time and does not include the data capturing and manipulation time or any further analyses and/or reporting.

a) Rehabilitating sites



b) Spontaneously regenerating sites

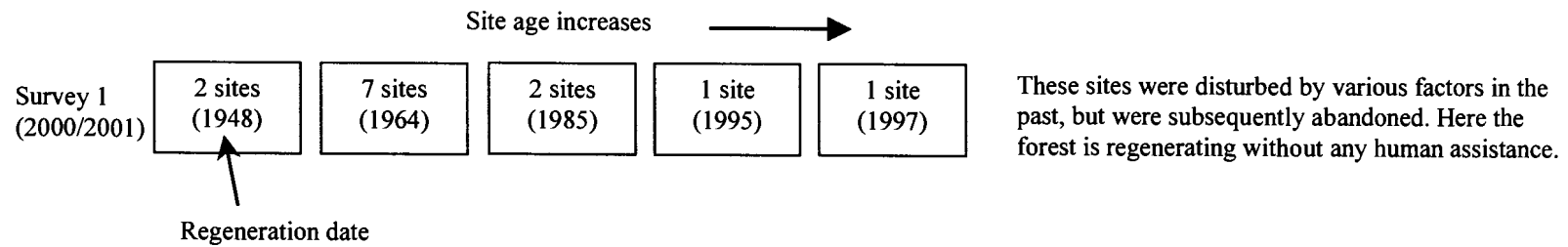


Figure 3.1. Continued on next page.

c) Undisturbed benchmark sites

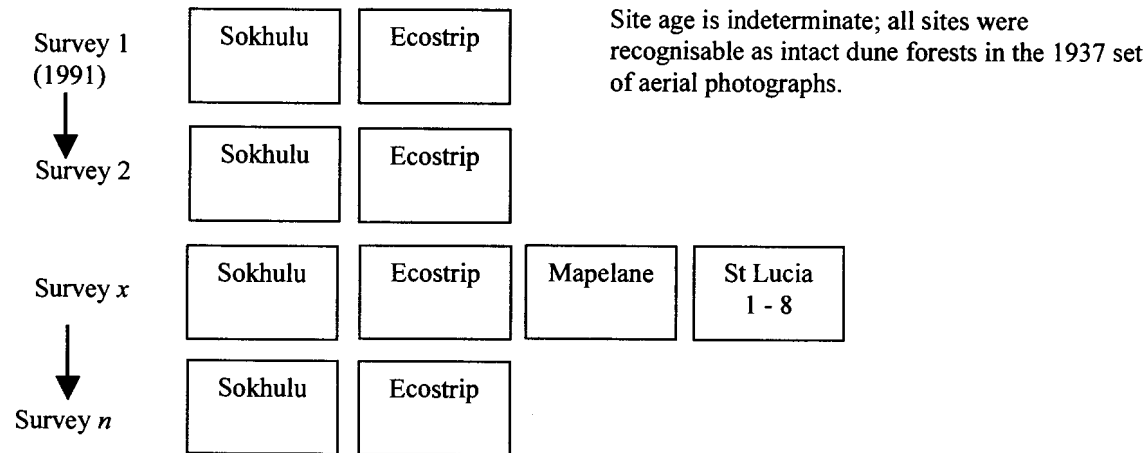


Figure 3.1. A graphical representation of the sampling design and site layout used in the study. Different sites (i.e. definable patches of vegetation separated in space) are represented by rectangular blocks. On these sites, surveys of up to seven taxa (millipedes, dung beetles, spiders, herb layer plants, trees, birds, small mammals) and soil chemical and physical properties were conducted during the course of the study. The sites are grouped into three distinct sets. **a)** Rehabilitating sites, the product of the post-mining rehabilitation process, are located adjacent to each other in a ~2km wide strip along the coast. These sites form a man-made chronosequence, a set of sites of chronosequential post-disturbance ages that, when surveyed simultaneously, can represent changes over time on any particular site. The chronosequence was surveyed several times at different frequencies for the different taxa. New sites were added as they became available after rehabilitation. **b)** The spontaneously regenerating sites, which are scattered widely in a ~2km-wide strip along the coast and were disturbed at different times in the past, are regenerating without human assistance. These sites were surveyed once only, in either 2000 or 2001 for different taxa. For each site, post-disturbance age was calculated by subtracting the regeneration date (the median date between chronological aerial photographs with only grass or bare surface visible on the first and a woody cover on the second photograph) from the survey date. **c)** Undisturbed forest patches, the benchmarks for restoration, were identified on the 1937 aerial photographs (the earliest available for the region). On these photographs, several patches of forest are clearly visible in a mostly grass-covered matrix. The closest of these benchmarks is the so-called “Ecostrip”, a strip of fore-dune and forest vegetation between the beach and the dredge path, left unmined under the conditions of the mining lease contract. Sokhulu is contiguous with the Mapelane Dune Forest Reserve, but falls within the lease area so that we had unlimited access to it. The St Lucia sites consist of 8 patches on the Eastern Shores of Lake St Lucia. Sokhulu and the Ecostrip were surveyed at different times and frequencies for different taxa, but Mapelane and St Lucia were surveyed only once in either 2000 or 2001 for the different taxa.

comparison of predicted developmental endpoints against regional variability in undisturbed dune forest structure.

Over the whole period, more than 35 people were involved in some aspect of data collection, either as the principal investigator for a project, or as field assistant. The total number of surveys, number of sites involved, number of site surveys, total number of sampling units, and the amount of sampling effort expended per taxon are given in Table 3.1. Assuming an average of three replicate sampling units completed per day, about 632 days of labor was involved in data collection pertaining to this thesis alone (Table 3.1). By far the largest effort (46%) has gone into collecting data on tree species abundance and distribution, followed by the millipedes (18%), herbs (11%) and birds (10%). Data transformations and manipulations for each of the analyses in this thesis are described in Chapters 4, 5, 6 and 7, and a summary of the numbers of replicate sampling units per site per taxon per year is given in Table 4.1.

Collection methods for most of the taxa and groups were standardized across years and sites, but the tree community was sampled using two different methods. In 1993 and 1997 a point-centre-quarter (Barbour *et al.* 1987) method on six randomly located line transects per site was used, while all surveys since then utilized variable numbers (depending on species accumulation curves) of randomly located 16 m x 16 m quadrates per site. For the analyses in this thesis that incorporated the earlier tree data (Chapter 5), I used relative rather than absolute abundance per species. Moreover, in all cases only the simplest measure of abundance, the number of individuals per species per sampling unit, was used to minimize observer and data manipulation error. For instance, the bird survey was designed as a distance sampling method (Krebs 1999), where density is routinely calculated. However, I used the simple measure of number of individuals seen per transect instead. In the same way, where appropriate I used the number of species recorded per

sampling unit (i.e. species density) as an index of species richness, rather than the more complicated extrapolation methods such as rarefaction (Krebs 1999). Species density has obvious disadvantages as a true biodiversity index (Magurran 2004), but is adequate as a standardized measure of changes in species numbers across sites or years. Although species density is technically not richness, for simplicity the term “species richness” is used throughout this thesis.

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Chapter 4
Manuscript

Evaluating restoration success – post-mining coastal dune forest rehabilitation in South Africa.

Theo D. Wassenaar & Rudi J. van Aarde

Summary

1. Although the potential of ecological restoration for the conservation of biodiversity is widely recognised, relatively few restoration projects are assessed in clear ecological terms. Moreover, restoration projects often fail to achieve even modest ecosystem structural goals. Clearly, there is a need for both an unequivocal evaluation of restoration, as well as for a success story.
2. We designed an ecological evaluation program to evaluate the coastal dune forest rehabilitation program of a company mining coastal sand dunes on the northeast coast of South Africa.
3. We sampled soil (for C, N, organic content and C:N ratio) and herb, tree, millipede, and bird community structure (richness, evenness, similarity to a benchmark, proportion of benchmark species and number of rare forest specialists) on several benchmark undisturbed forest patches and on two chronosequences, one post-mining and another consisting of regional spontaneously regenerating sites. We used least squares linear regression and t-tests to evaluate the absolute value, the direction of development, and the temporal and spatial stability in regeneration trajectories of the functional and community structural variables.
4. Our results show that the majority of the cases (21 of 24) had either reached the benchmark value, or were on a trajectory towards it. With few exceptions, the trajectories were stable over time and in most cases the mined sites were regenerating faster than spontaneously regenerating sites.
5. *Synthesis and applications.* These results are encouraging for the concept of restoration for biodiversity. We ascribe the evidently successful rehabilitation to the judicious use of a well-established natural process of succession, the presence of

several intact source areas, as well as to a financial and philosophical commitment to restoration for conservation. There are caveats, however. Apart from the continuing visual difference between the oldest sites and the benchmarks, increased fragmentation of source areas (due to amongst others the mining itself) will probably have a significant negative impact on colonisation in the future. There is thus a need, both for a better mechanistic understanding of dispersal and colonisation in such a fragmented landscape, and for future mine planning to take cognizance of distance to source areas for new rehabilitation sites.

Key words: dune mining, rehabilitation, community structure, ecosystem function

Introduction

Ecological restoration of degraded habitats is, for various reasons, set to become a major component of natural resource management (Ormerod 2003). Many forests already exist in a degraded state, with recent estimates putting the loss of tropical forests alone at 21 million ha per year (Laurance 1999). Consequently, many authors have pointed out that ecological restoration may in the future become the only option through which we can replace such lost biodiversity (Dobson, Bradshaw & Baker 1997; Young 2000; Cairns 2002; Suding, Gross & Houseman In Press).

In South Africa, the subtropical coastal dune forests of northern KwaZulu-Natal, an ecotype in the Maputaland centre of endemism, have a history of human disturbances going back to the early Iron Age (Hall 1984). More recently, town development and industrial activities, particularly mining for titanium and ferric

minerals in the coastal dunes northeast of Richards Bay by Richards Bay Minerals (RBM), has contributed to the increased fragmentation of the ecotype. However, a continuing rehabilitation program by RBM, initiated soon after mining commenced in 1976, aims to restore at least part of the mined area to indigenous coastal dune forest (van Aarde *et al.* 1996b). Full restoration of this dwindling and increasingly fragmented ecotype will benefit the maintenance of these forests as a unique ecotype of an important biome of southern Africa.

The primary long-term objective of RBM's restoration program is the recovery of a coastal dune forest that is similar to undisturbed dune forests in the region. This implies that the regenerating system must attain a state that is within the range of natural variability for a particular variable from an undisturbed benchmark site (see Sprugel 1991; White & Walker 1997). At the very heart of post-disturbance regeneration is a return (implying a dynamic process) of ecosystem structure and function (Ormerod 2003). From a conservation point of view, the importance of a complete ecological evaluation, including structure *and* function, cannot be overstressed (Ellison 2000; Ormerod 2003). Indeed, it is essentially worthless to espouse restoration as a biodiversity conservation option if a restoration project is not evaluated in these terms, or if, as Stanturf *et al.* (2001) advocated recently, restoration of function alone is accepted as a sufficient measure of success. Much of our previous research here (Foord, van Aarde & Ferreira 1994; Ferreira & van Aarde 1996; van Aarde *et al.* 1996a,b; Ferreira & van Aarde 1997; Kritzing & van Aarde 1998; Ferreira & van Aarde 2000; Greyling, van Aarde & Ferreira 2001; Wassenaar & van Aarde 2001; Davis *et al.* 2002, 2003) have focused on the development of community structure and ecosystem function as a result of successional processes. We used these

data and results as a basis to design an ecological evaluation and monitoring program to continually evaluate the outcome of the rehabilitation program.

The two most basic questions we can ask of a recovery process in a post-disturbance regenerating ecosystem are: has the regenerating variable (structural or functional) recovered fully and, if not, is it on its way there? Furthermore, considering the implicit assumption of determinism in any rehabilitation effort (Davy 2002), we would like to know whether regeneration patterns are stable – are they the same over time and over space? Accordingly, we set four simple but logical criteria for dune forest restoration success. We evaluate each group or variable (soil variables, diversity and composition) separately against the following criteria:

1. At the end of the post-disturbance regeneration process, the value for any ecological variable must be similar to that of the benchmark. Thus, if values on the oldest rehabilitating site are not significantly different from the benchmark, restoration for that particular variable is complete.
2. The overall trend on the regenerating sites must be towards a benchmark. Here we hypothesise that the age-related trajectory of change in an ecological variable on a rehabilitating chronosequence must be significantly different from zero in order to reach the benchmark value.
3. Regeneration patterns on the rehabilitation site must mimic natural patterns. Our hypothesis here is that if linear age-related trends on a chronosequence of regional, spontaneously regenerating sites are not significantly different from the rehabilitating (mined) chronosequence, restoration is succeeding because it has reinstated natural processes.

4. Age-related trends on the chronosequence of mined, regenerating sites must be stable over time. Thus, if a chronosequence is sampled in successive years, there must be no significant difference in the slopes of the different trajectories between years.

Methods

SITE DESCRIPTION

The study area, part of the Maputaland Centre of Endemism (MCE) (van Wyk & Smith 2001), is situated in the region between Cape Vidal (28°8.02' S, 32°32.85' E) and Richards Bay (28°47.27' S, 32°06.57' E) (Fig. 4.1). It is characterised by intact and regenerating forest patches, degraded and continuously disturbed grasslands, woodlots and commercial plantations, bare sand dunes where active mining is occurring, and township and rural residential areas. The climate is subtropical with most rain falling from January to March (peak in February), extended droughts are uncommon and about 70% of the annual precipitation of ~1292mm occurs in the summer (Wassenaar & van Aarde 2001). Mean annual temperature is 21.5°C (Wassenaar & van Aarde 2001).

We surveyed two sets of forest patches regenerating after disturbance, and several undisturbed forest patches typical of the coastal dune forest ecotype in the MCE. The first set of regenerating forest patches, consisting of seven closely situated sites ranging between 1 and 24 years old, is a post-mining chronosequence that is developing in response to RBM's rehabilitation program (Fig. 4.1). Here we surveyed all groups and variables between two and seven times during the period 1993 to 2002 (Table 4.1).

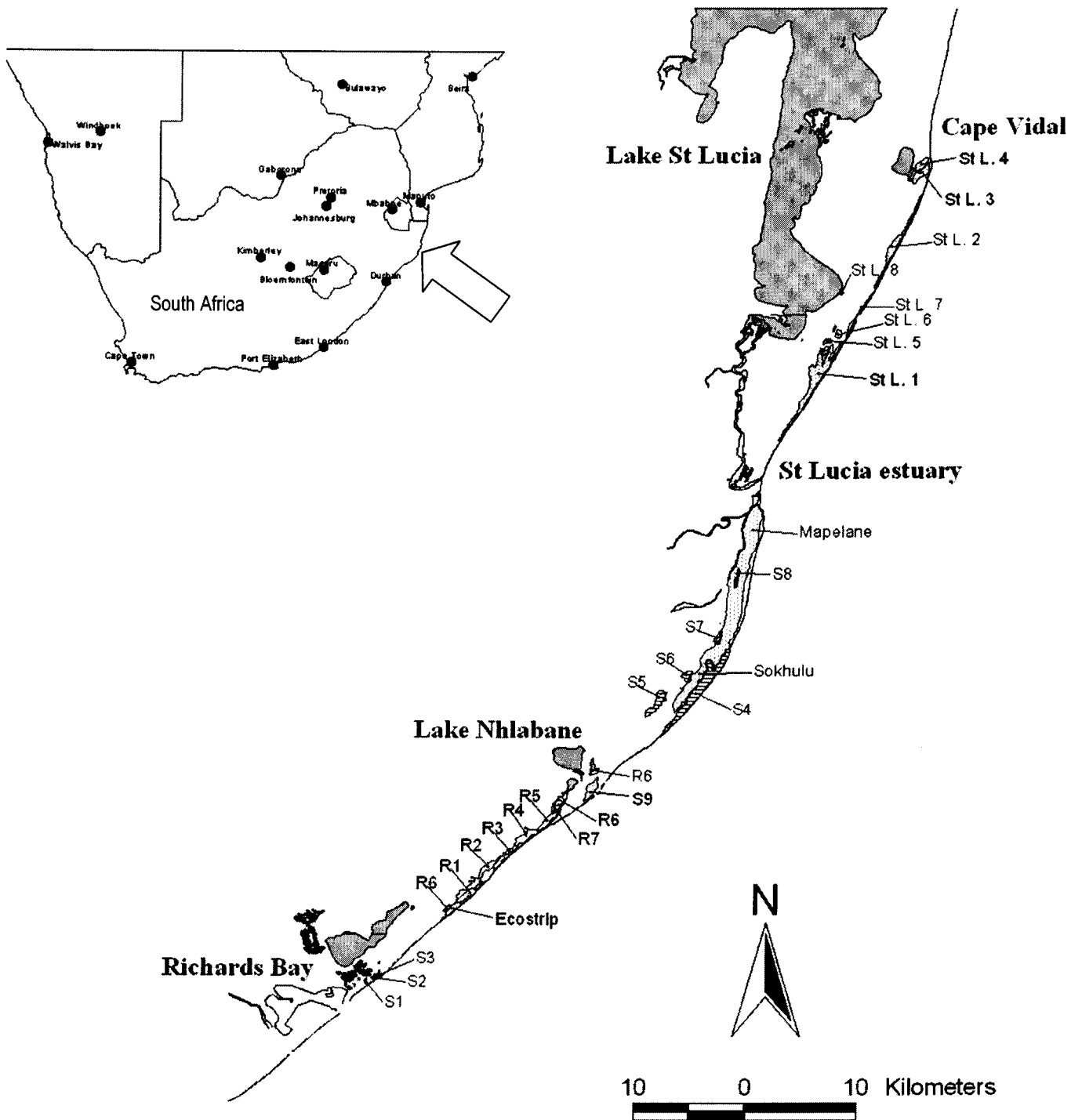


Figure 4.1. Map of the study area, showing the location of the different regenerating forest patches (R1-7; S1-9, for rehabilitating and spontaneously regenerating sites respectively) and the undisturbed benchmark sites (Sokhulu, Mapelane, St L.1-8 and Ecostrip). See text for detail on study sites.

Table 4.1. The number of sampling units per survey year per site for each group, followed by the number of sites in brackets. “Regenerating” is the collective term for between 5 (in 1993) and 8 (by 2002) mined rehabilitation sites (m) and 10 spontaneously regenerating sites (s). “Benchmark” refers to 4 sets of undisturbed forest patches: the Ecostrip (E, 1 patch), Mapelane Forest (Map, 1 patch) and Sokhulu Forest (Sok, 1 patch), and the St Lucia Nature Reserve (StL, up to 8 patches). See also Fig. 4.1.

Survey year	Soil		Herbs		Trees		Millipedes		Birds	
	<i>Regenerating</i>	<i>Benchmark</i>	<i>Regenerating</i>	<i>Benchmark</i>	<i>Regenerating</i>	<i>Benchmark</i>	<i>Regenerating</i>	<i>Benchmark</i>	<i>Regenerating</i>	<i>Benchmark</i>
1993					3-5 (x 4: m)	-	5 (x 2: m)	-	1-3 (x 5: m)	3 (x 1: E)
1994			10 (x 3: m)	4 (x 1: Sok)						
1995			10 (x 5: m)	10 (x 1: Sok)						
1996										
1997					2-4 (x 4: m)	6 (x 1: Sok)			2-4 (x 6: m)	2 (x 1: Sok)
1998	4-5 (x 4: m)	5 (x 1: Sok)					6 (x 5: m)	6 (x 1: Sok)	3-4 (x 6: m)	2 (x 1: E)
1999			10 (x 6: m)	25 (x 1: Sok)	40-70 (x 3: m)	40 (x 1: Sok)	6 (x 6: m)	6 (x 1: Sok)	3-4 (x 6: m)	8 (x 1: Sok)
2000							6 (x 7: m)	6 (x 1: Sok)		4 (x 1: E)
2001	5 (x 7: m)	5 (x 1: Sok)			10-40 (x 7: m)	20 (x 1: Sok)	6 (x 7: m)	6 (x 1: Sok)	2-4 (x 6: m)	4 (x 1: Sok)
					9-20 (x 7: s)	20 (x 1: E)		6 (x 1: E)	1- 10 (x 10: s)	20 (x 1: Map)
						22 (x 1: Map)				4 (x 1: E)
						13-20 (x 8: StL)				
2002							6 (x 7: m)	6 (x 1: Sok)		
							6 (x 6: s)	4 (x 1: Map)		
								6 (x 5: StL)		
								6 (x 1: E)		

The second set of sites, identified using sequential sets of aerial photographs of the area taken between 1937 and 1996 and surveyed during the summers of 2001 and 2002 for the presence and abundance of millipede, bird and tree species (Table 4.1), is a chronosequence sites regenerating spontaneously after disturbance between 4 and 54 years ago. Disturbances were caused by slash and burn agriculture dating back up to 1500 years (Hall 1984), as well as by more recent urban and industrial developments (the younger sites) (Thompson 2002). Abandonment of some of the modern disturbed sites, and a suppression of fire that was historically used to maintain grasslands (Hall 1984) in the older sites, has caused a general increase in cover of woody vegetation (Thompson 2002). Together these disturbances have resulted in a mosaic of dune forest patches of different ages, left to regenerate on their own accord with minimal intervention. Their ages were calculated by subtracting the regeneration date (the median calendar year between the time of the last aerial photographs showing only bare sand or grassland and the first photograph showing a tree- or shrub cover) from the survey year. We included these spontaneously regenerating sites as a natural control for the successional pattern on the mined sites.

The undisturbed sites (the benchmarks for restoration) consist of three different groups of forest patches. These were all recognizably intact and undisturbed on the earliest (1937) set of aerial photographs. The first of these benchmark groups, the so-called Ecostrip, consists of a single ~200 m wide and ~3.5 km long strip immediately adjacent to the seaward side of the mined chronosequence (Fig. 4.1), left un-mined under the conditions of the mining lease (Camp 1990). The vegetation here consists of foredune salt-spray and wind-pruned communities (approximately the first 100 m from the beach) and dune forest (the next 100 m) and was left intact to stabilize dune faces, but also to serve as a corridor for colonizing forest species. Here we

surveyed millipede, tree and bird assemblages between two and three times during the 10-year study period (Table 4.1).

We also surveyed two further groups of benchmark sites in the neighbourhood, one at the Mapelane Dune Forest Reserve and the other on the Eastern Shores of Lake St Lucia (Fig. 4.1). These sites were included to ensure that the restoration target is as typical of dune forests in the region as possible. The Mapelane Forest and its associated Sokhulu Forest, which together represent the largest contiguous dune forest patch left in South Africa (together ~2000 ha), are located immediately south of the Umfolozi/Lake St Lucia estuary and are about 20 km northeast of the mined sites. Here we surveyed soil variables and millipede, bird, herb and tree assemblages between one and seven times during the study period (Table 4.1). The final group of eight benchmark sites is situated about 20 km northeast of the Mapelane-Sokhulu group between the town of St Lucia and Cape Vidal in the St Lucia Nature Reserve (Fig. 4.1). Here we surveyed tree, millipede and bird assemblages once only (Table 4.1).

MINING AND REHABILITATION

The procedure used by RBM to extract the titanium and iron-based minerals ilmenite, rutile and zircon, as well as the rehabilitation process, have been described in detail elsewhere (van Aarde *et al.* 1996b). Here we summarise the salient aspects. The dredge mining is limited to the mineral-bearing top layers of a ~2 km wide strip, with the mining path dictated by the shape and form of the sand dunes (van Aarde *et al.* 1996b). After the gravitational extraction of minerals (~5% per volume), unused sand (the tailings) is stacked behind the dredger and shaped to resemble the pre-mining

topography as closely as possible. Pre-mining collected topsoil is then spread over the bare dunes and seeded with various annuals to stabilise the substrate.

The nitrogen-fixing pioneer *Acacia kosiensis* dominates the vegetation biomass from about 2 years post-rehabilitation. Over the course of the following 20 years its density decreases from a maximum of 20,000.ha⁻¹ to about 500.ha⁻¹ through self-thinning (Van Dyk 1997). Seeded annual species do not survive after two years when the shading effect of the young *A. kosiensis* plants is at its maximum, but several broad-leaved forest tree species start colonising from about 8 years post-rehabilitation (van Aarde *et al.* 1996b). In general, the number of species increases, the number of pioneers decreases, and the number of climax species increases with site age across several groups (van Aarde *et al.* 1996b).

GROUPS, VARIABLES AND FIELD METHODS

We measured soil variables (see Table 4.2 for a summary of all functional and structural variables) as a surrogate of ecosystem function. For ecosystem structure we measured or calculated five variables that represent the diversity and community composition of four biological groups across three trophic levels (Table 4.2). We chose millipedes to represent the decomposer group, herbs (all plant species below 1m) and trees the primary producers, and birds as the primary and secondary consumers.

Detailed surveying methods for soil variables are given by van Aarde, Smit & Claassens (1996), for birds by Kritzinger & van Aarde (1998) and Niemand (2001), for millipedes by van Aarde *et al.* (1996a), and for trees by Theron (2001) and Van

Table 4.2. The functional (soil) and community structural variables used for the monitoring of ecological development in post-disturbance regenerating coastal dune forests.

Factor	Variable	Description	Reference
<i>a) Ecosystem function</i>			
Soil nutrients:	% C	The percentage of the soil sample that consists of carbon.	van Aarde <i>et al.</i> 1996c Moore & Chapman 1986 Non-affiliated Soil Analysis Working Committee 1990
	N (mg/kg)	Total nitrogen concentration. Soil N is related to biological processes such as N-fixation and decomposition of organic matter.	
	C : N ratio	Ratio of % carbon to % nitrogen. Rough indicator of soil maturity. In natural environments with stable soil profile and organic activity, C:N ratio should range between 10 and 20.	
	Organic matter	The proportion of a sample that consists of macroscopic organic matter. It includes all organic material such as plant litter and soil micro-fauna, and is therefore an indication of both the level of biological activity and functional maturity of the system.	
<i>b) Ecosystem structure and composition</i>			
Biodiversity	Richness	The number of species per unit area (species density), an estimate of the total number of species per site.	Magurran 2004
	Evenness	A measure of how evenly abundances are distributed amongst species at a given site. If species in a site have similar abundances, this index would be high. Here we use the $E_{[var]}$ measure, which is independent of richness.	Smith & Wilson 1996
Composition	Bray-Curtis Distance D (BCD)	D is calculated as $1-S$, where S is the Bray Curtis measure of similarity. BCD is a one-dimensional measure of how dissimilar a rehabilitating site and the benchmark are in terms of the species present and their abundances.	Legendre & Legendre 1998
	Proportion of benchmark species	The proportion of species, from the total number of species in the benchmark site (i.e. the source pool), present at a particular rehabilitating site.	
	Number of rare species	The number of benchmark forest specialist species (species usually associated with forests or thickets) from the 75% least abundant group of species (herbs, trees, birds), or the number of benchmark species, regardless of their forest specialisation, from the 75% least abundant set (millipedes) per sampling unit.	

Dyk (1997). The numbers of sampling units per group per site per year are given in Table 4.1.

Soil variables: Soil samples, consisting of six 1000 cm³ cores (mixed and sub-sampled), were taken from the upper 10 cm of the soil profile. Soil carbon content, organic content, and total nitrogen were determined using the procedures described by van Aarde *et al.* (1996c).

Herbs and trees: Herbs were surveyed by recording all plant species providing cover below 1 m in ten 1 m² quadrates located at 5 m intervals on the periphery of a 25 m x 7 m rectangular survey plot. Abundance per survey plot was calculated as the number of these quadrates where a species was recorded. For trees, the first two surveys used the Point-Centre-Quarter method and subsequent surveys used randomly located 16 m x 16 m quadrates per site as in Theron (2001).

Millipedes and Birds: Millipede species were counted in 6m x 30m transects where three observers recorded all individuals from the ground up to 3m by each scanning 2m wide belts. Transects were randomly located for each survey. Birds were surveyed on ~100m long line transects, separated by at least 200 m. Line transects were initially randomly located, but were then fixed between years. An observer walked each transect for 2 hours, recording all perching birds within sighting distance.

NUMERICAL ANALYSIS

In order to get as comprehensive an estimate of the benchmark target value as possible and because the benchmark sample was necessarily unbalanced (some benchmark sites were sampled more than once – Table 4.1), we calculated the target

value for each variable as the average across all benchmark sites and across all surveys. This was the most logical way to ensure an unbiased estimate of the target. For the same reason we calculated the variability in the benchmark value as the average of the standard deviations of each site, rather than as the standard deviation across all surveys or means. We used ordinary least squares regression analyses to determine trends over site age.

To evaluate the temporal stability of ecological development on the mined sites, we used an F-test to test for difference in the slopes of developmental trajectories across site age (i.e. along the chronosequence) between different survey years. No significant differences indicated that there was no variability in the pattern across the chronosequence over time. We compared developmental trajectories across the chronosequence to “natural” trajectories on spontaneously regenerating sites by testing for differences between the slopes (F-test) of the common trajectory for all surveys on the mined sites and the spontaneously regenerating trajectory.

The requirement of development towards the benchmark was met if the common slope for all sites across all surveys was significantly different from zero (according to an F-test) and in the right direction. Regression equations for all the variables are reported in Table 4.3. We also calculated the predicted age at which the trajectory on the mined sites will converge with the benchmark mean. Finally, we compared the values on the oldest mined sites with the values on the benchmark site using a student’s t-test. No significant difference here indicated that the oldest mined site has already reached the target value.

There are a number of obvious assumptions in these criteria, chief amongst which is the implication that all variables will start out far from the benchmark target

value and then linearly develop towards it. Indeed, some variables are likely to be relatively similar to benchmark values from early on and then change so slowly over time that the linear trend is not significantly different from zero. We therefore have to accept some measure of disparity between the outcomes of the different criteria, and a certain amount of subjective interpretation is unavoidable.

Moreover, even if development is strongly deterministic, simple linear regeneration patterns across all variables are unlikely, given the scope of our study and the ubiquity of non-linear patterns in ecology (Pimm 1991). If the rate of change for a particular variable is not inherently linear, convergence times (habitat age at which the benchmark value will be reached) may be over- or underestimated. However, we are here mainly interested in whether developmental *trends* imply a return to former structure and function, and do not wish to imply that underlying processes are themselves linear, or indeed simple. Predicted convergence times are also intended to serve as an indication of habitat regeneration rate should there be a linear process driving it.

Results

Ecosystem Function

With the exception of the carbon to nitrogen (C:N) ratio, all soil variables tended to increase with site regeneration age (Fig. 4.2). Both total nitrogen and the C:N ratio were characterised by high variability in regenerating as well as benchmark sites (Fig. 4.2). However, the rate of increase with site age was only significant for percentage carbon and organic content and only if the high values in early post-rehabilitation sites were omitted (Table 4.3). These high values were probably the result of carbon and

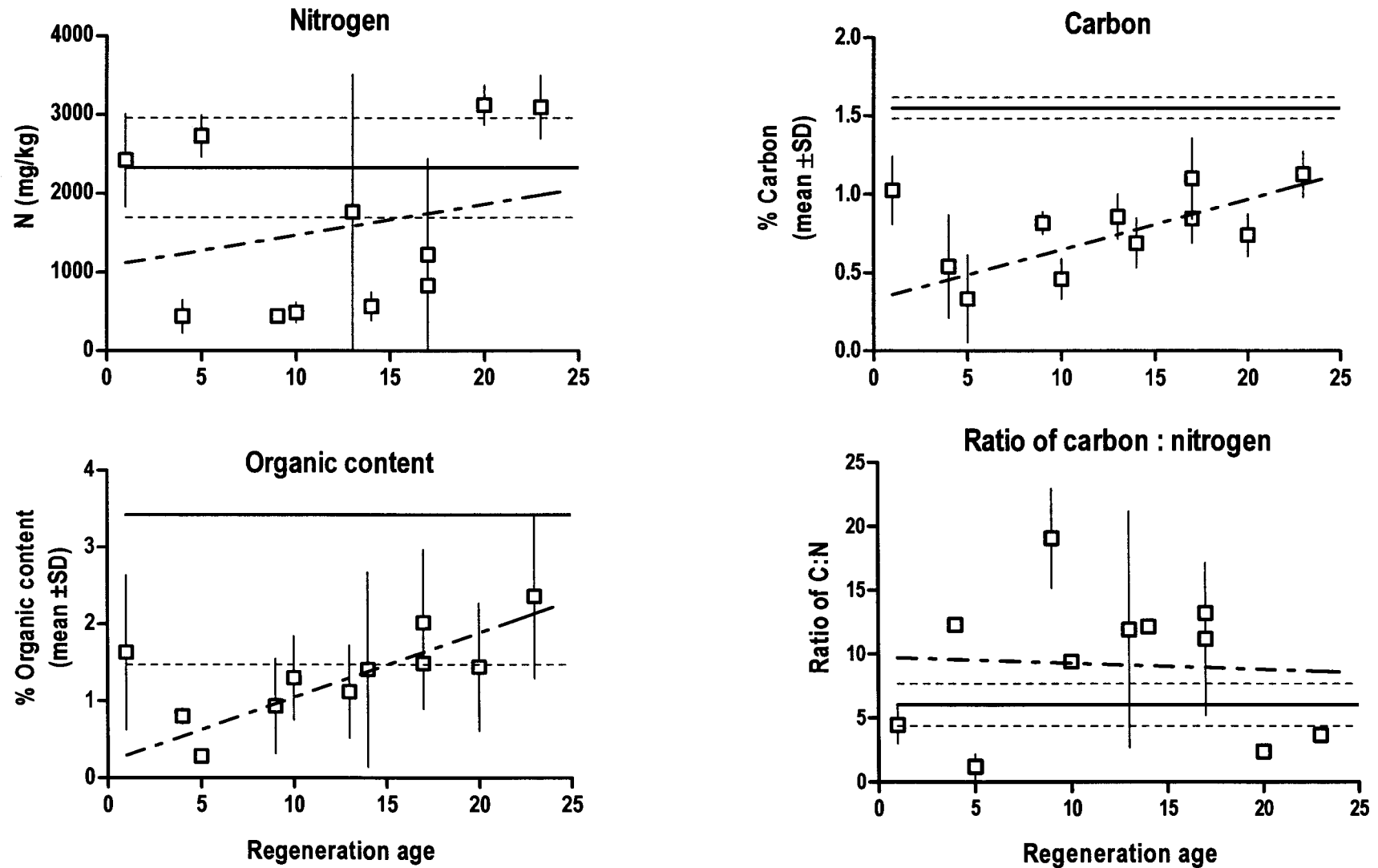


Figure 4.2. Soil nitrogen concentrations, percentage carbon values, percentage organic content and the C:N ratio as a function of dune forest regeneration age. Two early outliers for organic content and carbon were omitted for the regression analyses. Horizontal lines: average benchmark target value \pm SD. Regression equations are reported in Table 4.3.

Table 4.3. Summary statistics of regeneration trends in communities and soil variables on post-disturbance regenerating dune forest chronosequences. The criteria are described in detail in the text. Convergence is the estimated time to when the value of a variable on the mined rehabilitating site will be equal to a benchmark target value. The common linear regression equation describes the linear change in the variable across all survey years together, regardless of whether trends differed significantly between survey years. There are not currently any regional data available for soil variables, nor for herb community structure or composition.

<i>Criteria</i>						
	1 Regenerating site = benchmark?	2 Overall* trend towards benchmark?	3 Trend on mined = natural trend?	4 Trends same between survey years?	Convergence (years post-mining ^b)	Common linear regression equation for mined sites
<i>Ecosystem function</i>						
Nitrogen	Yes ($t_8 = 0.25, P > 0.05$)	No ($F_{1,9} = 0.59, P > 0.05$)	–	Yes ($F_{1,7} = 0.0005, P > 0.05$)	No convergence	$y = 1083.00 + 39.16x$
% Carbon	No ($t_8 = 5.81, P = 0.0004$)	Yes ($F_{1,8} = 12.19, P = 0.008$)	–	Yes ($F_{1,6} = 0.17, P > 0.05$)	38.2	$y = 0.33 + 0.03x$
Organic content	Yes ($t_8 = 1.06, P > 0.05$)	Yes ($F_{1,8} = 28.15, P < 0.001$)	–	Yes ($F_{1,6} = 0.6, P > 0.05$)	38.3	$y = 0.21 + 0.08x$
Carbon : Nitrogen	No ($t_8 = 3.19, P = 0.01$)	No ($F_{1,9} = 0.03, P > 0.05$)	–	Yes ($F_{1,7} = 0.03, P > 0.05$)	No convergence	$y = 9.75 - 0.05x$
<i>Ecosystem structure: Species richness</i>						
Herbs	Yes ($t_{11} = 0.14, P > 0.05$)	No ($F_{1,12} = 3.74, P = 0.08$)	–	Yes ($F_{2,8} = 2.18, P > 0.05$)	No convergence	$y = 12.83 + 0.40x$
Trees	No ($t_{29} = 2.41, P = 0.02$)	Yes ($F_{1,16} = 17, P < 0.001$)	No ($F_{1,19} = 5.85, P = 0.03$)	Yes ($F_{3,9} = 3.09, P = 0.08$)	40.7	$y = 1.93 + 0.39x$
Millipedes	Yes ($t_8 = 0.46, P > 0.05$)	Yes ($F_{1,33} = 49.99, P < 0.001$)	No ($F_{1,37} = 4.24, P = 0.04$)	Yes ($F_{4,23} = 0.29, P > 0.05$)	35.2	$y = 0.87 + 0.21x$
Birds	Yes ($t_7 = 1.51, P > 0.05$)	Yes ($F_{1,27} = 6.55, P = 0.02$)	Yes ($F_{1,30} = 3.11, P = 0.09$)	Yes ($F_{4,19} = 1.23, P > 0.05$)	57.7	$y = 7.81 + 0.17x$
<i>Ecosystem structure: Evenness</i>						
Herbs	No ($t_{10} = 3.35, P = 0.01$)	No ($F_{1,7} = 49.05, P < 0.001$)	–	Yes ($F_{1,7} = 0.01, P > 0.05$)	No convergence	$y = 0.46 - 0.008x$
Trees	No ($t_{29} = 3.07, P = 0.005$)	Yes ($F_{1,15} = 14.83, P = 0.002$)	No ($F_{1,18} = 11.68, P = 0.003$)	Yes ($F_{3,9} = 1.80, P > 0.05$)	29.1	$y = 0.17 + 0.02x$
Millipedes	No ($t_8 = 3.07, P = 0.02$)	No ($F_{1,31} = 8.60, P = 0.006$)	Yes ($F_{1,35} = 2.98, P > 0.05$)	Yes ($F_{4,21} = 1.52, P > 0.05$)	No convergence	$y = 0.68 - 0.02x$
Birds	Yes ($t_7 = 0.26, P > 0.05$)	No ($F_{1,27} = 3.07, P = 0.09$)	Yes ($F_{1,30} = 1.83, P > 0.05$)	No ($F_{3,19} = 3.96, P = 0.02$)	No convergence	$y = 0.52 + 0.005x$

<i>Criteria</i>						
	1 Regenerating site = benchmark?	2 Overall* trend towards benchmark?	3 Trend on mined = natural trend?	4 Trends same between survey years?	Convergence (years post-mining [#])	Common linear regression equation for mined sites
<i>Ecosystem composition: Bay-Curtis dis-similarity</i>						
Herbs	No ($t_{11} = 8.90, P < 0.001$)	Yes ($F_{1,12} = 33.42, P < 0.001$)	–	Yes ($F_{2,8} = 2.71, P > 0.05$)	62.3	$y = 1.00 - 0.006x$
Trees	No ($t_{29} = 3.12, P = 0.004$)	Yes ($F_{1,16} = 25.53, P < 0.001$)	No ($F_{1,19} = 7.56, P = 0.01$)	Yes ($F_{3,10} = 1.52, P > 0.05$)	39.1	$y = 0.99 - 0.007x$
Millipedes	Yes ($t_8 = 1.06, P > 0.05$)	Yes ($F_{1,31} = 24.63, P < 0.001$)	No ($F_{1,35} = 20.66, P < 0.001$)	Yes ($F_{4,21} = 1.29, P > 0.05$)	32.3	$y = 0.91 - 0.01x$
Birds	Yes ($t_7 = 1.14, P > 0.05$)	Yes ($F_{1,27} = 107.7, P < 0.001$)	No ($F_{1,30} = 43.51, P < 0.001$)	No ($F_{4,19} = 3.06, P = 0.04$)	24.9	$y = 0.94 - 0.02x$
<i>Ecosystem composition: Proportion of benchmark species</i>						
Herbs	Yes ($t_{11} = 1.10, P > 0.05$)	Yes ($F_{1,12} = 30.45, P < 0.001$)	–	Yes ($F_{2,8} = 1.54, P > 0.05$)	27.4	$y = 0.03 + 0.006x$
Trees	No ($t_{29} = 2.48, P = 0.02$)	Yes ($F_{1,16} = 18.84, P < 0.001$)	No ($F_{1,19} = 6.23, P = 0.02$)	No ($F_{3,10} = 4.02, P = 0.04$)	38.6	$y = 0.01 + 0.003x$
Millipedes	Yes ($t_8 = 0.70, P > 0.05$)	Yes ($F_{1,33} = 49.03, P < 0.001$)	Yes ($F_{1,37} = 4.04, P = 0.05$)	Yes ($F_{4,23} = 0.27, P > 0.05$)	35.5	$y = 0.04 + 0.009x$
Birds	Yes ($t_7 = 1.86, P > 0.05$)	Yes ($F_{1,27} = 39.53, P < 0.001$)	No ($F_{1,30} = 17.29, P < 0.001$)	Yes ($F_{4,19} = 2.31, P = 0.09$)	40.5	$y = 0.05 + 0.005x$
<i>Ecosystem composition: Colonisation by rare species</i>						
Herbs	Yes ($t_{11} = 0.95, P > 0.05$)	Yes ($F_{1,12} = 14.41, P = 0.003$)	–	Yes ($F_{2,8} = 0.72, P > 0.05$)	33.5	$y = -0.25 + 0.12x$
Trees	No ($t_{29} = 5.86, P < 0.001$)	Yes ($F_{1,16} = 5.57, P = 0.03$)	Yes ($F_{1,19} = 1.61, P > 0.05$)	Yes ($F_{3,10} = 0.76, P > 0.05$)	54.6	$y = 0.04 + 0.03x$
Millipedes	Yes ($t_8 = 1.56, P > 0.05$)	Yes ($F_{1,33} = 28.8, P < 0.001$)	Yes ($F_{1,37} = 0.03, P > 0.05$)	Yes ($F_{4,23} = 0.93, P > 0.05$)	56.3	$y = -0.38 + 0.10x$
Birds	Yes ($t_7 = 1.84, P > 0.05$)	Yes ($F_{1,27} = 14.95, P < 0.001$)	Yes ($F_{1,30} = 0.81, P > 0.05$)	No ($F_{4,19} = 3.00, P = 0.04$)	64.6	$y = -0.12 + 0.05x$

* This evaluates whether the slope of the common regression equation (across all survey years) is significantly different from zero.

Predicted by common regression.

other organic matter carried over in the topsoil that is spread over the dunes prior to seeding as part of the rehabilitation program. Percentage carbon drops after the first year of vegetation establishment as fast-growing annual plants probably take up more organic carbon than what they produce. Both total nitrogen and organic content values on the oldest site were equal to the benchmark (Table 4.3).

Soil variable development was stable over time – slopes for the two survey years did not differ from each other for any of the variables (Table 4.3). Soil variables were not surveyed in regional sites, so that we could not evaluate whether their development was similar to natural developmental trends. The two variables that were developing significantly towards the benchmark (carbon and organic matter) should converge with the benchmark value by about 38 years post-disturbance.

Community structure

SPECIES RICHNESS

Species richness in all four groups increased with site regeneration age (Fig. 4.3), but this was not significant for herbs (Table 4.3). The oldest rehabilitating site had the same numbers of herb, millipede and bird species as the benchmark (Table 4.3), but all four groups were fairly variable and millipedes apparently increased non-linearly on both the mined and regional sites (Fig. 4.3). Trends were the same over time for all groups (Table 4.3). Tree and millipede richness changed significantly faster on the mined sites than on the spontaneously regenerating sites (Table 4.3). All groups except the herbs will converge with benchmark values before about 58 years post-disturbance.

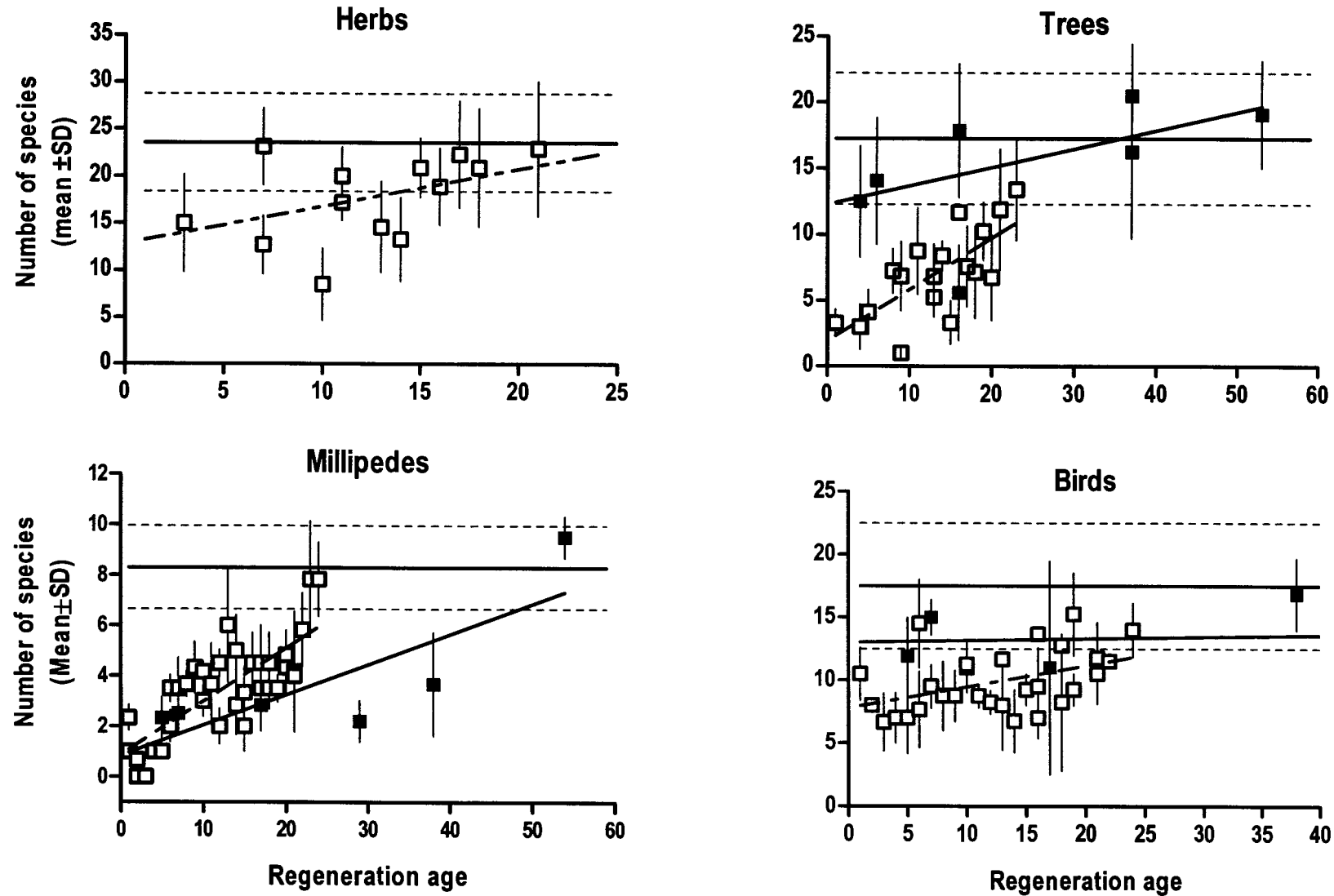


Figure 4.3. The change with regeneration age in the number of species per sampling unit in regional, spontaneously regenerating sites (—■—) and mined, rehabilitating sites (—□—), for four groups. Note that these values are considerably lower than the total number of species recorded on a site of a given age. Herbs were not surveyed in spontaneously regenerating sites. Horizontal lines: average benchmark target value \pm SD. Regression equations are reported in Table 4.3.

EVENNESS

In general, abundances should be more evenly apportioned in older communities, but the overall trend in the herb and millipede communities of the mined rehabilitating sites was the opposite of that (Fig. 4.4). Consequently, although the rates of change for these two groups were significant, they were both essentially moving away from the benchmark (Fig. 4.4). Evenness on the oldest rehabilitation site for both millipedes and herbs was significantly different from the benchmark (Table 4.3).

The rate of change in bird evenness was not stable over time, nor was the common rate of change significant, but the assemblage on the oldest site was already equal to the benchmark and the trajectory on the mined sites was the same as on the spontaneously regenerating sites (Table 4.3). On the other hand, the tree evenness trajectory on the mined sites was not the same as on the spontaneously regenerating sites, nor was the oldest site equal to the benchmark, but trajectories were the same over time and increasing significantly towards benchmark values (Table 4.3). Tree evenness on the mined sites will reach benchmark values by about 29 years post-disturbance.

Species composition

BRAY-CURTIS DISTANCE

Bray-Curtis Distance is a fairly conservative measure of the return of species composition because it measures the dis-similarity between two sites in terms of both species presence and abundance. Clearly, all four groups were becoming significantly more similar to the benchmark as the site grew older (Fig. 4.5) and in both millipedes

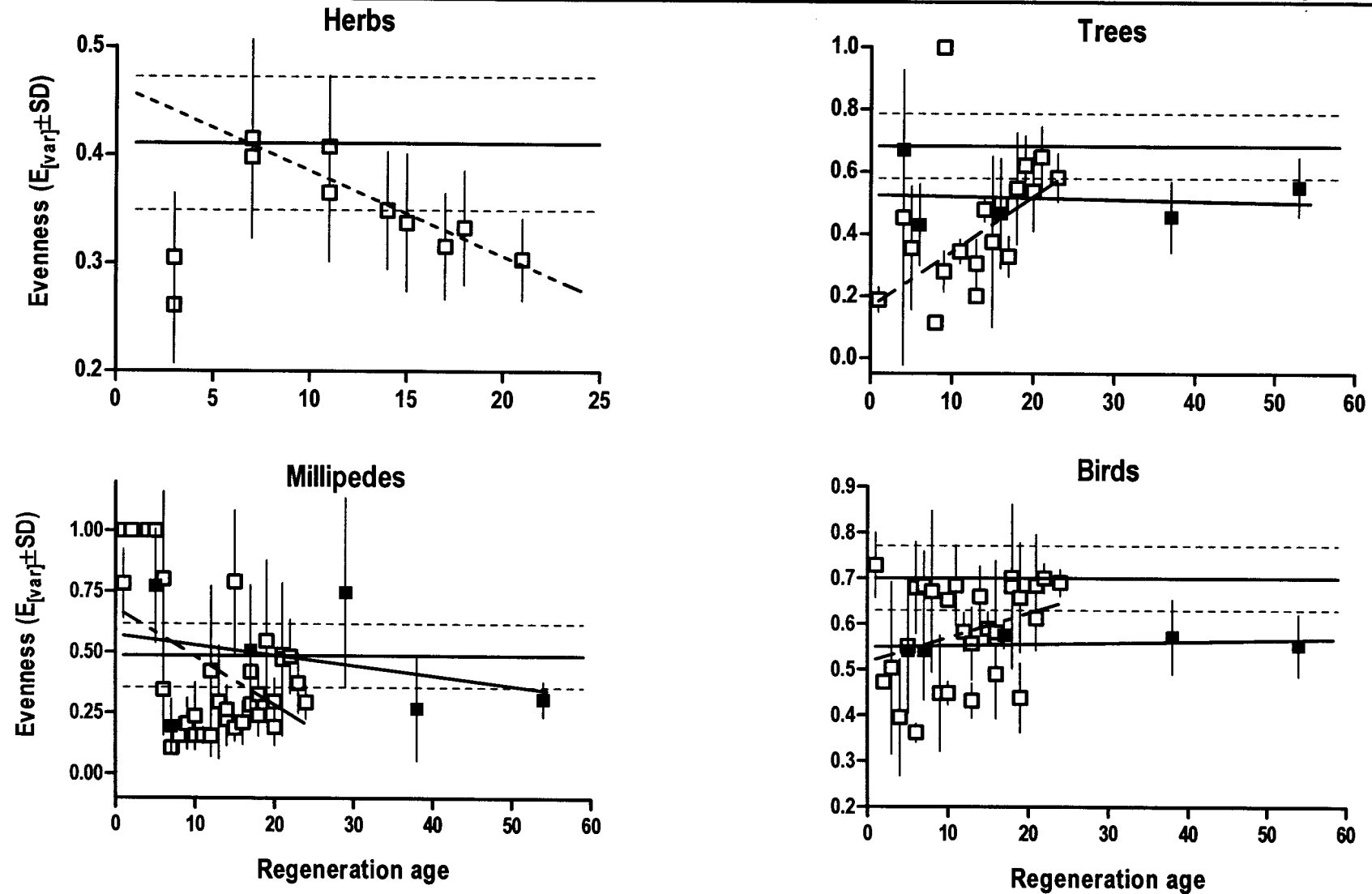


Figure 4.4. The change in Evenness ($E_{[var]}$) with regeneration age in regional spontaneously regenerating sites (—■—) and mined rehabilitating sites (—□—) for four groups. Herbs were not surveyed in spontaneously regenerating sites. Horizontal lines: average benchmark target value \pm SD. Regression equations are reported in Table 4.3. For trees the single outlier at 9 years (a single species) was omitted for the regression analysis.

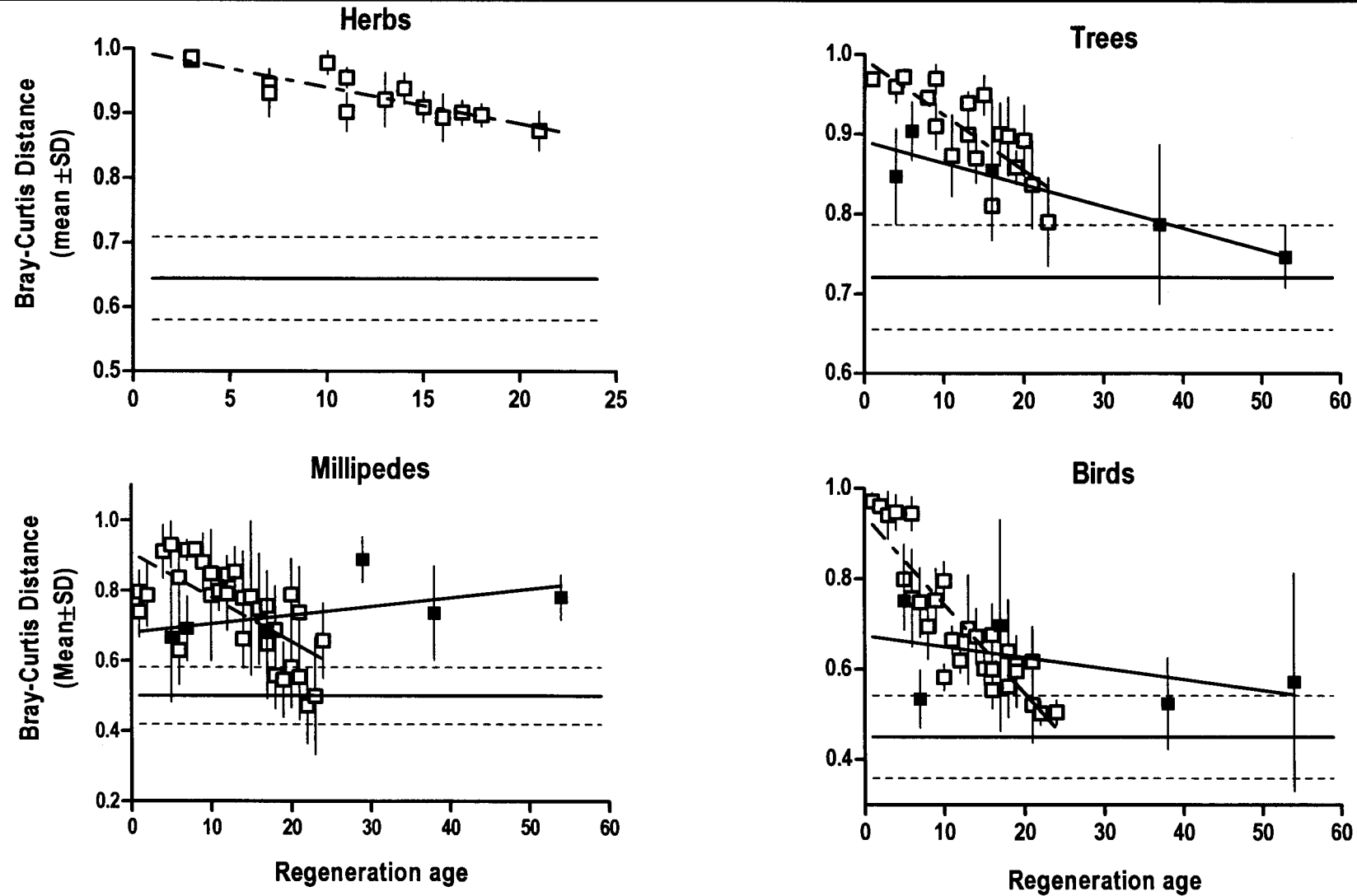


Figure 4.5. The change, over regeneration age, in Bray-Curtis Distance between four assemblages from spontaneously regenerating sites (—■—) and mined rehabilitating (—□—) sites on the one hand, and a composite species composition of their respective benchmark communities on the other hand. Herbs were not surveyed in spontaneously regenerating sites. Horizontal lines: average benchmark target value \pm SD. Regression equations are reported in Table 4.3.

and birds the assemblages on the oldest mined site were already as similar to the composite benchmark composition as were any transect on the benchmark itself (Table 4.3).

With the exception of birds, which were marginally significantly different between years, trends were the same over time in all groups (Table 4.3). In all three groups where a comparison was possible, assemblages on the mined sites were returning significantly faster than those on the spontaneously regenerating sites (Table 4.3). Herb assemblages will take relatively long (about 62 years) to converge with the benchmark composition, but convergence in the other three groups will take less than 40 years post-disturbance (Table 4.3).

PROPORTION OF BENCHMARK SPECIES

The rate of increase over site age in the proportion of benchmark species (see Table 4.2) is an indication of colonization dynamics. In all four groups the proportion of benchmark species increased with site age (Fig. 4.6). This rate of increase was significant in all four groups and was also faster on the mined sites than on regional sites in trees and birds (Table 4.3). As in species richness, the pattern in millipedes was non-linear on both the mined and spontaneously regenerating sites (Fig. 4.6). Only trees differed between years and between the oldest mined sites and the benchmark (Table 4.3). With the exception of the herbs, all groups will have converged with the benchmark between 35 and 40-odd years post-disturbance (Table 4.3).

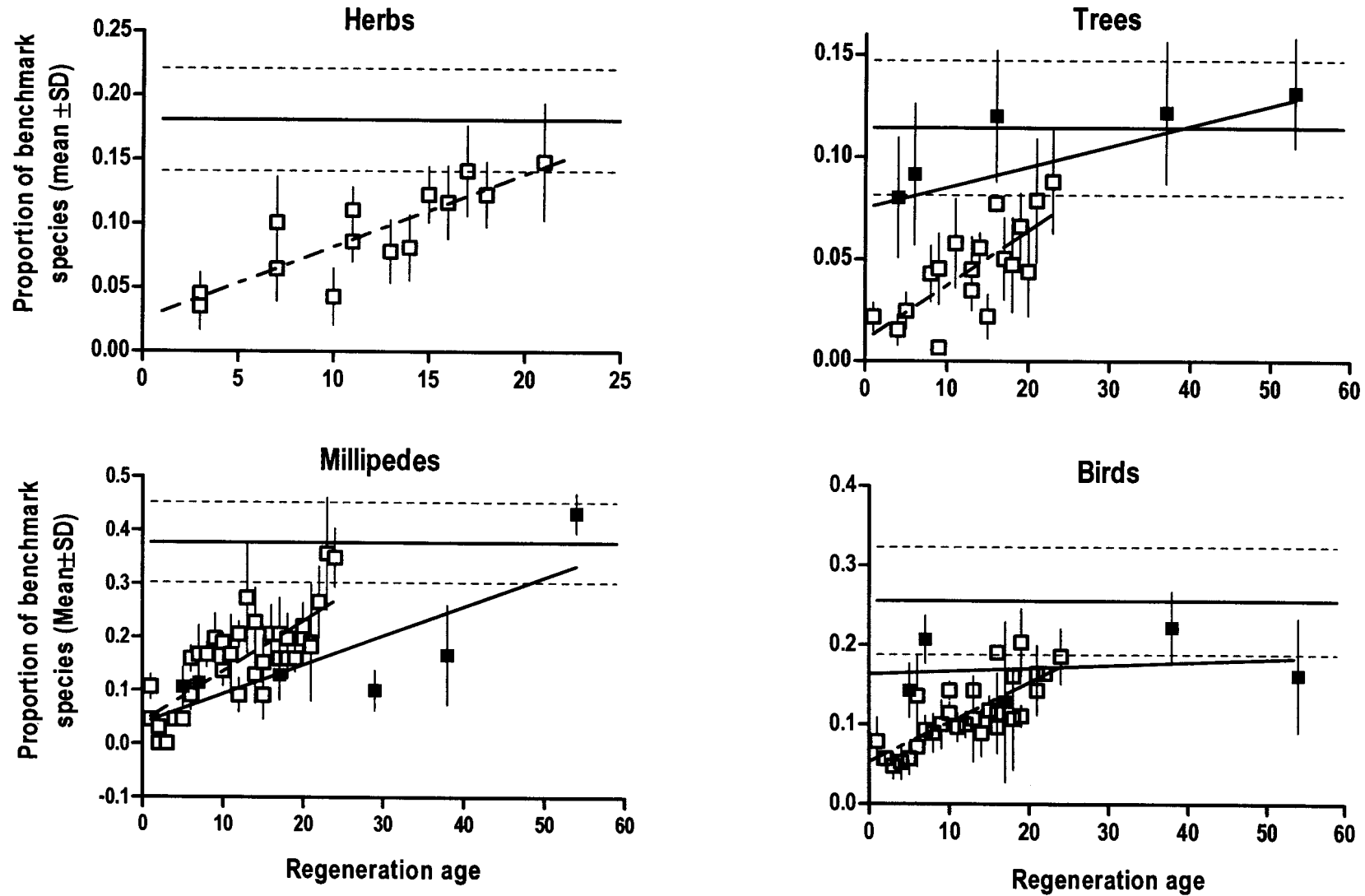


Figure 4.6. The mean proportion of all benchmark species present on any particular sampling site in both the spontaneously regenerating sites (—■—) and the mined rehabilitating sites (---□---), for herbs, trees, millipedes and birds. Herbs were not surveyed in spontaneously regenerating sites. Horizontal lines: average benchmark target value \pm SD. Regression equations are reported in Table 4.3.

COLONISATION BY RARE SPECIES

Rare forest specialist species increased significantly with site age in all four groups (Table 4.3). In trees and birds there was also a concurrent increase in variability, but in both cases this was matched by high variability in the benchmark as well (Fig. 4.7). Millipedes again showed a non-linear, almost stepped increase in both chronosequences, but this occurred much sooner after disturbance in the mined than in the regional sites (Fig. 4.7). Only in trees was the oldest mined site not equal to the benchmark (Table 4.3), but some of the slightly younger sites apparently were (Fig. 4.7). In all groups, the trajectories were the same on the mined and spontaneously regenerating sites and, with the exception of birds, were also the same between successive surveys (Table 4.3). Restoration of rare forest specialist species will take relatively long, with convergence in trees, millipedes and birds all predicted to take more than 50 years post-disturbance (Table 4.3).

Discussion

The scope of our study, in the number of assemblages, trophic levels and variables, as well as in the time and spatial scale on which we studied them, is larger than most published restoration assessment studies. Moreover, although it is possible to employ many other criteria to assess ecosystem development (Holl & Cairns 2002; Grant & Loneragan 2003), the ones we used are composite summaries of whole-community development, and are stricter than those based simply on the presence and absence of species. Yet, our results show that the post-mining restoration of coastal dune forests here are in general succeeding.

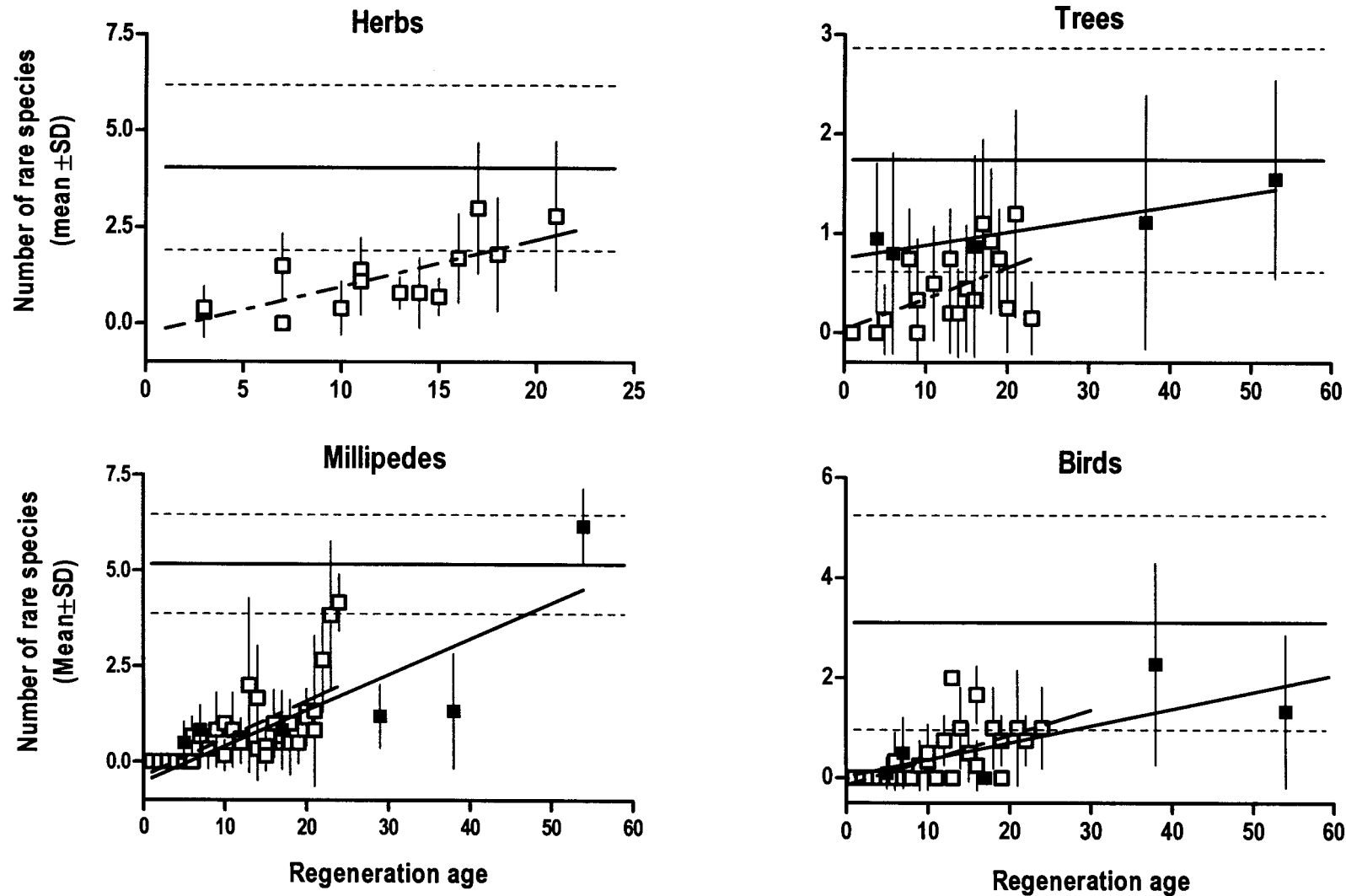


Figure 4.7. The change, over regeneration age, in the number of rare, forest specialist benchmark species (herbs, trees and birds) and the number of rare benchmark species, regardless of their habitat specialisation (millipedes), in the spontaneously regenerating sites (—■—) and the mined rehabilitating sites (—□—). Rare species are defined here as the 75% rarest species from the total, abundance-ranked species list for all benchmark sites. Herbs were not surveyed in spontaneously regenerating sites. Horizontal lines: average benchmark target value \pm SD. Regression equations are reported in Table 4.3.

Table 4.3 shows that the majority of the 24 cases (i.e. group and variable combinations) have either reached the benchmark values (14), or are developing significantly towards it (18). Only three of ten cases not equal to the benchmark (the C:N ratio and millipede and herb evenness) are not developing significantly towards it. In three of the six cases not developing towards the benchmark (nitrogen, herbs richness and birds evenness) values on the oldest sites, and indeed many of the younger sites, are already equal to the benchmark.

With only a few exceptions (bird evenness, Bray-Curtis Distance and rare species colonisation, and tree proportion of benchmark species) developmental trends were stable over time. Surprisingly, the mined regenerating sites were mostly regenerating faster than the spontaneously regenerating sites, perhaps because of the overt protection against continuous disturbance that is afforded by the rehabilitation management program.

Although predicted convergence times under the linear model are uncertain, our results suggest that most ecosystem structure and function (13 of 18 rehabilitating variables) will return before 50 years and the rest before about 70 years post-disturbance. On average the rare forest specialists will take the longest to be restored, but even here the predicted convergence times are not unreasonably long, given the inherent handicap of rarity (Maina & Howe 2000). These regeneration times are relatively fast compared to many estimated or measured regeneration times for temperate forests (Reay & Norton 1999; Holl 2002; Thom, Zeigler & Borde 2002; Vallauri, Aronson & Barbero 2002), but compare well with those for tropical and subtropical forests (Mentis & Ellery 1994; Aide *et al.* 2000; but see West, Bond & Midgley 1999; Kammesheidt, Köhler & Kuth 2002).

These results are encouraging for biodiversity restoration. So many of the variables are either already there, or are on track to reach the benchmark value, that it would be wrong to conclude differently. Why is this rehabilitation program apparently successful where so many others are failing (see Lockwood & Pimm 1999)? No doubt the company's scientific approach and financial commitment to rehabilitation has helped. But in our view, the most important biological reason is the interaction between the many natural disturbances characteristic of the region (Weisser 1978; von Maltitz, van Wyk & Everard 1996), and a relatively high primary productivity because of the high annual rainfall (~1300 mm). Under these conditions the coastal dune forests have developed strongly deterministic successional developmental pathways (Weisser & Muller 1983; Mentis & Ellery 1994; von Maltitz *et al.* 1996) and the rehabilitation program has made judicious use of one of them in its rehabilitation program, the *A. kosiensis* woodland pathway (van Aarde *et al.* 1996b). *A. kosiensis* woodlands are a natural feature on most denuded sites in the region (Weisser 1978) and although this pathway has been criticised as being slower than the so-called bush-clump pathway (von Maltitz *et al.* 1996; West *et al.* 1999), it is the most cost efficient one on an industrial scale. Related to these factors is the presence, thus far, of several intact and undisturbed source areas within reasonable distance from the rehabilitation sites.

However, at this point we have to introduce a number of important caveats and exceptions, which should be enough warning against using our results as justification for the destruction of ecosystems. Visually the mined rehabilitation sites in our study are still far from being a coastal dune forest, with the multiple layers of a typical forest only starting to appear in the oldest rehabilitation sites. The pioneer tree species *A. kosiensis* is still the dominant canopy species (own unpublished data; van Aarde *et*

al. 1996b; Van Dyk 1997). Indeed, much of the decrease in Bray-Curtis Distance for the tree assemblage was probably driven by the decrease in density of *A. kosiensis* as a result of self-thinning.

There is a second aspect that may influence the outcome of the developmental process, particularly in trees. Beyond the cutoff of 1.7m that we employed in the field survey, none of our criteria takes the age of individual trees into account. Since very few of these individuals in the regenerating sites are reproductively mature, local population dynamics must still be determined by colonization from outside. The dominance structure may therefore still change considerably as individuals mature and local reproduction start to dominate population dynamics.

Although the majority of the cases were converging, there were enough exceptions to warrant attention. In herbs and millipedes for instance, development in one of the most important community variables, evenness, was actually away from the benchmark. Moreover, our assumption of linear development in all groups and variables may be misplaced, and many trajectories may still turn out to be different 25 years from now. More practically, mining (and some other related activities) has increased the fragmentation of colonisation source areas. The resultant impact on dispersal and colonisation rates of forest species may only become apparent in the next few years, but it is likely to have a negative effect on regeneration rates.

Much more could and should therefore be done to improve the chances for success. Mine and rehabilitation planning should take cognizance of the distance to source areas, for instance. Also, most of the success of a minimal intervention rehabilitation program is ultimately dependent on natural colonisation and extinction. A more mechanistic understanding of these two processes in a landscape context

(Bell, Fonseca & Motten 1997) is a prerequisite if ecologists are to be of any use in increasing the likelihood of successful restoration. Together with a comprehensive and committed monitoring program as an integral part of any restoration action (Cooke & Johnson 2002; SER 2002), such a scientific approach should make the restoration of indigenous biodiversity as a conservation action possible.

Acknowledgements

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Chapter 5
Manuscript

Community convergence in disturbed coastal dune forests

T.D. Wassenaar, R.J. van Aarde, S.L. Pimm and S.M. Ferreira

Abstract

Do communities return to their former state when we disturb them? The answer is “surely not always,” since some disturbances may be so devastating that recovery will be impossible. If communities do recover, then how fast is that recovery? Do different subsets of species return at the same rate? Is that rate a simple exponential recovery — meaning that the change towards the original state is fastest when the community is furthest away and it slows as the community converges? Or is recovery a more dynamically complex process? These questions are theoretically interesting and practically important. The theoretical questions are whether there is a particular state — some exact composition — to which a community is likely to return, might there be several (or many) possible such states, or is community composition essentially haphazard. The practical implication is that if disturbed ecological communities do not tend to return to a previous state, it may be impossible to undo human impacts on natural ecosystems.

We follow the fate of species assemblages following the removal of vegetation for mining. We show that these assemblages in restored sub-tropical coastal dune forests do converge with a regional equilibrium state and that convergence is possible within a reasonable period. However, changes in assemblages from different trophic levels were idiosyncratic – the convergence in trees and birds did not mirror convergence for the dung beetle assemblage, for example. Few of the assemblages converged exponentially – the simplest shape for the decay function. Furthermore, trends were sometimes different for different indices of community dissimilarity, suggesting that whether one accepts convergence depends, in part, on exactly what one measures.

Keywords: restoration, community organization, resilience, convergence, coastal dune forests, mining



Introduction

Do communities return to their former state when we disturb them? The answer is surely “not always,” since some disturbances may be so devastating that recovery will be impossible. If communities do recover, then how fast is that recovery? Do different subsets of species return at the same rate? Is that rate a simple exponential recovery — meaning that the change towards the original state is fastest when the community is furthest away and it slows as the community converges? Or is recovery a more dynamically complex process?

These questions are practically important. If disturbed ecological communities do not tend to return to a previous state, it may be impossible to undo human impacts on natural ecosystems. No doubt, the most effective way of saving ecosystems threatened by human actions is to conserve them. However, restoration, not conservation, is the only option across tens of millions of square kilometers of already damaged natural ecosystems (Pimm 2001).

These questions are also theoretically challenging. The theoretical question of what *is* an ecological community has long been a central — and controversial — theme in ecology. Is there a “climax community”, a particular state involving some exact species composition, to which a community is likely to return? Might there be several (or many) such possible states, or is community composition essentially haphazard? Put in other words: is community composition persistent or fleeting?

The idea of a climax community has a long and controversial history in ecology, one that has not been resolved completely. (See, for example, Clements 1928, Gleason 1939, Horn 1974, Hubbell 1979, Christensen and Peet 1984 and references therein, Condit et al. 1992, Terborgh et al. 1996, Wilson et al. 1996, Phillips et al. 1997, Sheil 1997, Wilson et al. 2000). We know that species composition is seldom constant in natural communities (Sprugel 1991, Inouye 1995) and is often dependent on stochastic changes across various scales of space and

time in factors such as climate (Tilman 1987, Sprugel 1991, Davis et al. 2000, Ford et al. 2000). Such changes, however, do not deny the existence of some state towards which a community will tend to return.

Theoretically, there are numerous possibilities. There can be more than one persistent state — perhaps many more (Drake 1990). The invasion sequence determines the persistent, state obtained (Lockwood et al. 1997, Pimm 1991). Theory also suggests a “Humpty-Dumpty” effect: it may be impossible to re-assemble a community from its constituent species (Drake et al. 1993, Law and Morton 1993, Pimm 1991, Luh and Pimm 1993). Present day communities may have obtained their present states through an assembly that necessarily used species no longer present. The practical significance of these speculations is that it may be statistically unusual to find a community returning to its original state following disturbance. The failure of ecological restorations to restore desired species composition (Palmer et al. 1997, Lockwood and Pimm 1999, Stanturf et al. 2001) is evidence in favor of such a view.

Conversely, there are a number of factors that constrain what a persistent community state might be. The dependence of local communities on regional processes (Cornell and Lawton 1992, Blackburn and Gaston 2001) implies that only a small number of species combinations are possible. Local communities are seldom completely random draws from a regional species pool (Law 1999). Rather they depend on large-scale factors such as species’ geographic range size or abundance (Maurer 1999, Blackburn and Gaston 2001). In short, nature constrains the sequence of species re-colonizing a disturbed community in ways that models do not.

Recognizing a persistent state is not trivial (Connell and Sousa 1983). A direct way is to determine if the community tends to return to its former composition if the species mix is altered (Hubbell and Foster 1986, Wilson et al. 1996). Terborgh et al. (1996) used such a

directional development of tree assemblages on a chronosequence of tropical rain forest sites towards an undisturbed benchmark site as evidence for the operation of biological mechanisms and the existence of a persistent state.

We follow the fate of species assemblages following the removal of vegetation for mining. We show that these assemblages in restored sub-tropical coastal dune forests do converge to a regional benchmark state and do so within a reasonable period. However, changes in assemblages from different trophic levels were idiosyncratic – the convergence in trees and birds did not mirror convergence for the dung beetle assemblage, for example. Few of the assemblages converged exponentially – the simplest shape for the decay function. Furthermore, trends were sometimes different for different indices of community dissimilarity, suggesting that whether one accepts convergence depends, in part, on exactly what one measures (Rodriguez 1994).

Here we evaluate the trajectories of species assemblages across three trophic levels and one set of abiotic factors, relative to a benchmark undisturbed forest in the region. Initially different biological communities converge if there is a continuous shift in composition of the one community (the regenerating community) towards another (the undisturbed benchmark) in the identity or the relative abundances of their constituent species over time (Grover and Lawton 1994). We therefore expect a continuous decrease (decay) in some multivariate dissimilarity index (d), based on species composition or species abundance, between benchmark sites and regenerating sites with increasing time since initial disturbance.

The rate of change in community composition is unlikely to be similar near and far away from a stable equilibrium (Ludwig et al. 1997). For resilient, disturbed systems that are reasonably close to a persistent community state (i.e. still within that state's domain of attraction), the simplest trajectory is an exponential decay of d (Pimm 1991). More complex

dynamics are possible, of course, and we use the exponential decay in d over time only as a reference.

Methods

Study area

We studied two separate locations at the southern end of the Maputaland-Pondoland regional centre of plant diversity (van Wyk 1996). In one location, we surveyed regenerating coastal dune forest sites (the Tisand lease area of Richards Bay Minerals, RBM), northeast of Richards Bay, KwaZulu-Natal, South Africa. RBM have mined coastal sand dunes here for ilmenite, iron and rutile since 1976 (van Aarde et al. 1996b). The pond-based mining process is followed by a rehabilitation process during which reshaped sand tailings are covered with pre-mining harvested topsoil, re-vegetated with a cover crop of annuals and grasses and then left to regenerate naturally (van Aarde et al. 1996b). Post-rehabilitation management is limited to the removal of alien vegetation and re-seeding of die-offs in the first two years.

The rehabilitation process has created a series of known-aged regenerating areas. They are arranged in a narrow strip on the second and third dune ranges from the coast from Nhlabane in the northwest to about 10km northeast of Richards Bay (Fig. 5.1). They do not exceed more than 2km in width at any point along the coast and are bordered variously by bare sandy mining areas, un-mined forest, commercial plantations of beefwood (*Casuarina equisetifolia*), rural dwellings and crops, as well as highly disturbed and scrubby areas dominated by exotic invasive plants. The adjacent un-mined forest patches consist of a ~200 m wide strip on the seaward side of the rehabilitating areas as well as a number of small (<1 ha) patches scattered around the mining area.

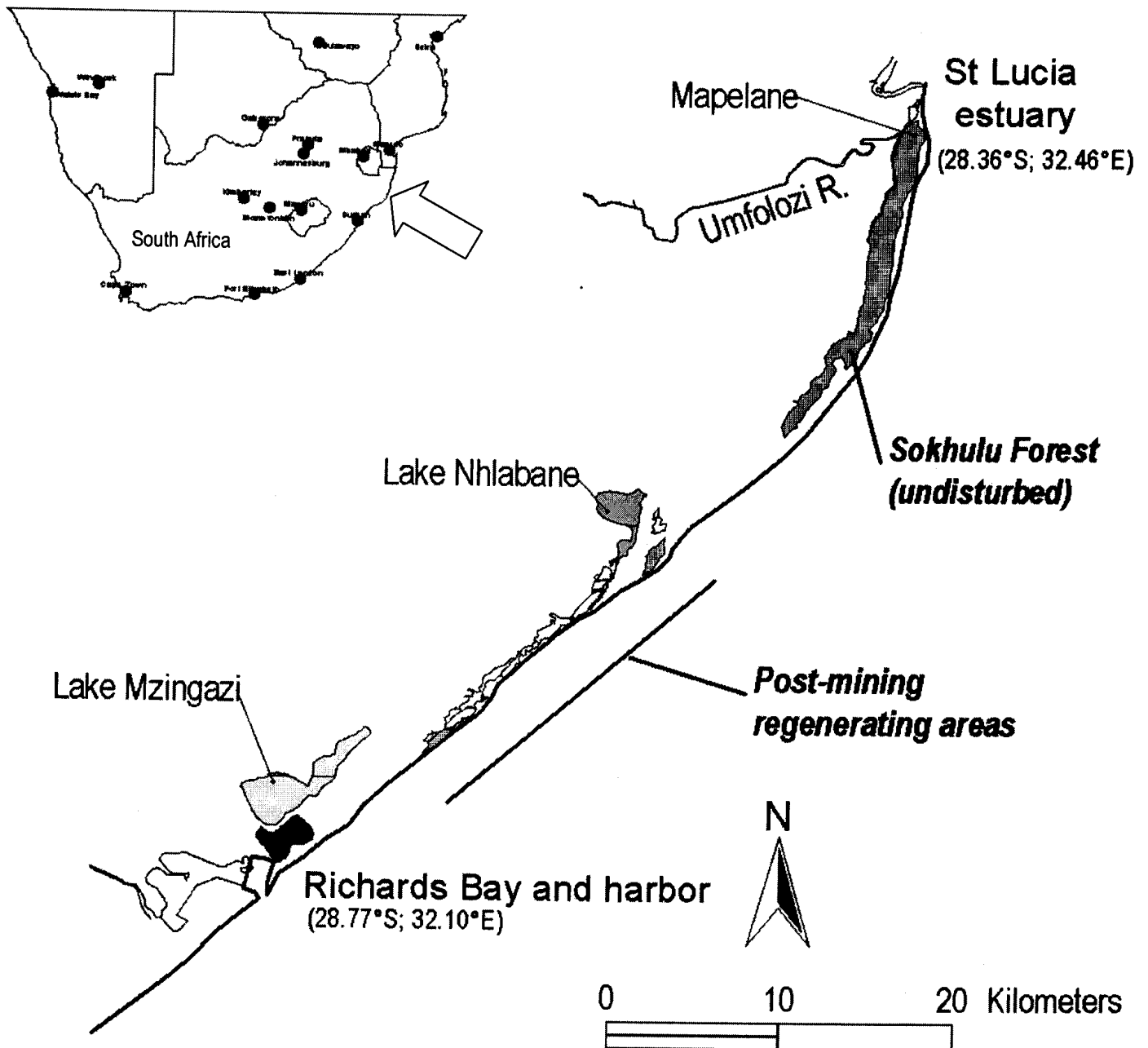


Figure 1. Map of the study area. The study site (the post-mining regenerating areas) is located on the coast about ten kilometers northeast of the town Richards Bay. Sokhulu is an undisturbed forest used as benchmark for our study and is contiguous with the Mapelane Coastal Dune Forest Nature Reserve to the northeast.

We used a second location (Sokhulu), an un-mined coastal dune forest situated about 20 km northeast of the rehabilitating sites, as a benchmark. Sokhulu is ~500 ha in size and is contiguous with the Mapelane Coastal Dune Forest Nature Reserve (~1500 ha). Aerial photographs show that the Mapelane-Sokhulu forest patch has been intact since before 1937. The Sokhulu forest patch is typical of coastal dune forests in the region and is the closest relatively large patch of undisturbed forest to the mining lease area.

Mentis and Ellery (1994) and Van Aarde et al. (1996b) described the abiotic (topography, climate and soils) and biotic (vegetation) characteristics of both mined and un-mined areas. Here, we provide descriptions of only the most salient aspects of the vegetation physiognomy on our study site. In the early stages, the rehabilitating sites are essentially scrubby grasslands dominated by weedy annuals, several grass species and seedlings of the pioneer tree, *Acacia kosiensis*. By about 4 years, *A. kosiensis* forms a dense, monoculture stand about 3 m high with very little undergrowth (typically < 30% ground cover). Over the next 16-18 years, *A. kosiensis* continues to dominate while it increases in height to about 12 m. By 12 years, a number of other old-forest tree species has started to colonize and a dense undergrowth, consisting mainly of stoloniferous grasses, climbers, and scandent plants develops. Vegetation cover on the forest floor is then > 100% but a true sub-canopy layer is still absent. At the time of our last surveys, the oldest sites were ~22 years old and were still dominated by ~15 m high *A. kosiensis*. A sub-canopy layer consisting of emergent 2-4 m high forest tree species and lianas is also beginning to appear in places.

The Sokhulu forest site is an undisturbed moist sub-tropical coastal dune forest (12 to >15 m) with relatively high tree diversity. Dominant tree species are *Celtis africana*, *Mimusops caffra* and *Ziziphus mucronata*. The undergrowth is patchy and of varying height (10 cm to 2 m) and there is a true sub-canopy layer consisting of specialist shade-adapted species such as

Psychotria capensis and *Dracaena alectrifomis*, as well as several lianas (e.g. *Cyphostemma* sp.) and erect woody forbs (e.g. *Isoglossa woodii*).

Data collection

We collated data from published and unpublished sources for six biological assemblages and one abiotic group that have all been studied on the site. We deliberately selected groups to reflect one inorganic resource and three trophic levels (primary producers, decomposers and consumers). Details on methods employed in surveying some of the assemblages and abiotic variables can be found in the following publications: soil: van Aarde et al. (1998); dung beetles: Davis et al. (2003); millipedes: van Aarde et al. 1996a; trees: Theron (2001); small mammals: Ferreira and van Aarde (2000); birds: Kritzinger and van Aarde (1998).

Soil elements: Soil was sampled using a 1000 cm³ square soil-corer. Samples were taken from the upper 10 cm of the soil profile in five randomly located points per site (Table 5.1). Each sample consisted of six core sub-samples that were later mixed together and sub-sampled for the chemical analyses. In our analysis, we chose the variables of pH, %Carbon and concentrations of the minerals P, Ca, Mg, K and Na.

Millipedes: Millipedes were sampled in randomly located 6 x 35 m transects per site (Table 5.1). For the current analysis, only data collected during the spring and summer were used. Three to four observers searched the transect from one side to the next and recorded all millipedes seen up to a height of 3 m. We calculated abundance as the number of individuals per species per transect as a proportion of the total number of individuals per transect.

Beetles: Eight rehabilitating sites and one benchmark site were surveyed for dung beetles during 2000. Pitfall traps (in three groups of five traps per sampling site) using pig dung as bait were randomly located in the different sites (Table 5.1). Trapping was conducted over two days

Table 5.1. The number of replicates per year per area for each group. Numbers in brackets refer to the number of rehabilitating areas that existed for that year. A new area is rehabilitated about once every three years, thus in 1991 there were only four rehabilitation sites increasing to eight by 2000. “Rehab” is the collective term for the rehabilitation areas and “Sokhulu” is the benchmark area. Thus, in birds for instance, in 1998 four transects were surveyed in *each* of the six rehabilitating areas that existed at that stage, and eight transects were surveyed in Sokhulu. For birds in 1997 this resulted in a total of 32 transects.

Survey year	Soil		Herbs		Trees		Millipedes		Dung beetles		Birds		Mammals	
	<i>Rehab</i>	<i>Sokhulu</i>	<i>Rehab</i>	<i>Sokhulu</i>	<i>Rehab</i>	<i>Sokhulu</i>	<i>Rehab</i>	<i>Sokhulu</i>	<i>Rehab</i>	<i>Sokhulu</i>	<i>Rehab</i>	<i>Sokhulu</i>	<i>Rehab</i>	<i>Sokhulu</i>
1991													1-2 (x4)	2
1992													1 (x4)	1
1993											3 (x5)	-	1 (x5)	1
1994			10 (x3)	4			5 (x4)	-					6 (x5)	-
1995	4-5 (x4)	5	10 (x5)	10			5 (x5)	5					6 (x5)	3
1996							6 (x5)	6					3 (x5)	2
1997							6 (x5)	6			2-4 (x6)	2	3 (x6)	3
1998											4 (x6)	8		
1999			10 (x6)	25	40-70 (x3)	40	6 (x6)	6			3-4 (x6)	4	3 (x6)	3
2000							6 (x7)	6	3 (x8)	6	3-4 (x6)	4	3 (x6)	3
2001					10-40 (x7)	-								

during the mid-summer seasonal activity peak. We calculated abundance as the number of individuals per species per trapping grid as a proportion of the total number of individuals per grid.

Herbs: Forest floor herbaceous vegetation (< 1 m) was surveyed in 1994, 1995 and 1999. The number of sampling plots in the rehabilitating sites was the same in all survey years but differed between years in the benchmark site (Table 5.1). Sampling plots were randomly located per site and consisted of ten 1m² quadrates laid out in a 2 x 5 pattern with 5 m between each quadrate. Quadrates were subdivided into ten sub-quadrates (1995 and 1999), and species present recorded per quadrate (1994) and per sub-quadrate (1995, 1999). We calculated abundance as the number of quadrates (1994) or the number of sub-quadrates (1995, 1999) per plot per species as a proportion of the total number of quadrates or sub-quadrates per species per plot.

Trees: Self-supporting woody plants taller than shoulder height (about 1.7 m) were counted during 1999 and 2001 in 16 m x 16 m randomly located quadrates (Table 5.1). Abundance was calculated as the number of rooted individuals per species per quadrate as a proportion of the total number of individuals per quadrate.

Birds: Line transects (different numbers of transects per year and per site – Table 5.1) were used to survey birds in 1993 and from 1997 to 2000. Transects were randomly located per site and were separated by at least 200 m. Each transect was walked until at least thirty individuals were observed. We calculated abundance as number of individuals per species per transect as a proportion of the total number of individuals per transect.

Small mammals: Small mammals (rodents and shrews) were surveyed using Sherman live traps in permanent trapping grids. The numbers of grids per stand varied between years (Table

5.1). Abundance was calculated as the minimum number of animals alive on the grid per species as a proportion of the total number in the grid.

Data Analysis

Calculating site age

We define “site age” to be the median post-rehabilitation age at the time of the first survey, plus the number of intervening years between the first and each subsequent survey. Each survey is deemed an independent sample representing the composition of the community at a particular habitat age.

Calculating dissimilarity and defining the benchmark using Euclidean distances

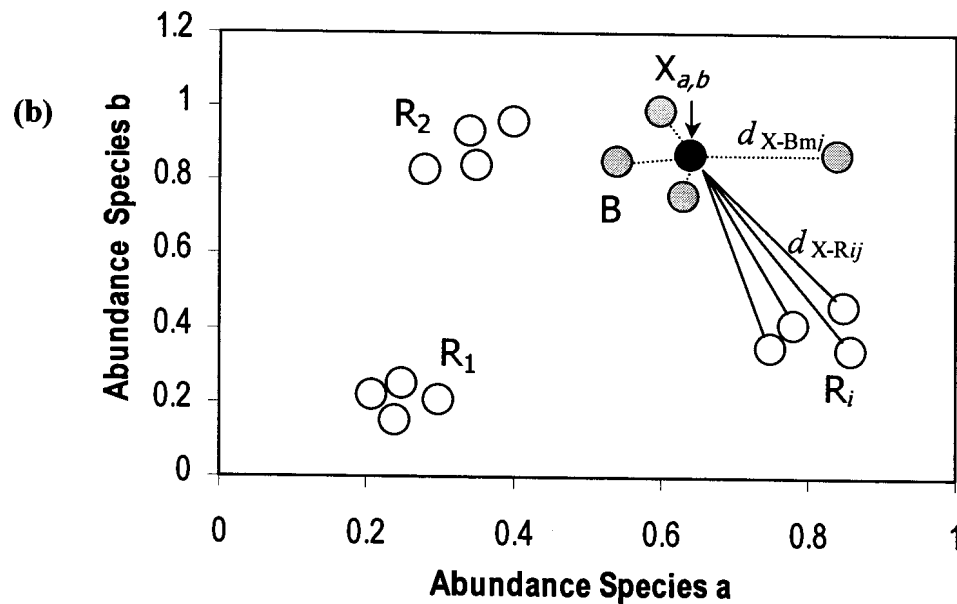
The data for one survey consist of the proportional abundances of all the species ($a, b \dots z$) at each of several sites (Fig. 5.2a). One set of sites was disturbed (mined) at different times in the past, resulting in regenerating sites of different ages ($R_1, R_2 \dots R_i$), while another site, the “Benchmark” (B_m), was undisturbed (Fig. 5.2a). In each site, we surveyed the plants and animals in several sampling plots or transects ($R_{11}, R_{12} \dots R_{ij}; B_{m1}, B_{m2} \dots B_{mj}$) (Fig. 5.2a).

We created a “reference vector” ($X_{a..z}$) by taking the average benchmark proportional abundance for each species (Fig. 5.2a). The dissimilarity of the different benchmark samples to this reference vector then defines a range of “natural” states (i.e. the natural variability in species composition) around the reference vector.

The expectation is that the species composition of the regenerating sites will be much less similar to the reference vector than what the different benchmark sites will be, but their dissimilarity will decrease over time as benchmark species colonize these new habitats. To

(a)

	Sites												Reference Vector						
	Disturbed (mined and rehabilitated)						Undisturbed												
	Regenerating area 1			Regenerating area 2			Regenerating area i			Benchmark									
Species	R_{11}	R_{12}	...	R_{1j}	R_{21}	R_{22}	...	R_{2j}	...	R_{i1}	R_{i2}	...	R_{ij}	B_{m1}	B_{m2}	...	B_{mj}	δ	$X_{a..z}$
Species a	a_{11}	a_{12}	...	a_{1j}	a_{21}	a_{22}	...	a_{2j}	...	a_{i1}	a_{i2}	...	a_{ij}	A_1	A_2	...	A_j	-	μ_A
Species b	b_{11}	b_{12}	...	b_{1j}	b_{21}	b_{22}	...	b_{2j}	...	b_{i1}	b_{i2}	...	b_{ij}	B_1	B_2	...	B_j	-	μ_B
...	-	...
Species z	z_{11}	z_{12}	...	z_{1j}	z_{21}	z_{22}	...	z_{2j}	...	z_{i1}	z_{i2}	...	z_{ij}	Z_1	Z_2	...	Z_j	-	μ_Z
Multivariate distance (d)	d_{X-R11}	d_{X-R12}	...	d_{X-R1j}	d_{X-R21}	d_{X-R23}	...	d_{X-R2j}	...	d_{X-Ri1}	d_{X-Ri2}	...	d_{X-Rij}	d_{X-Bm1}	d_{X-Bm2}	...	d_{X-Bmj}	$\mu_{d_{X-Bmj}}$	$d_{X-X} = 0$



Euclidean distance (ED):
$$d = \sqrt{\sum_{i=1}^z (y_{1k} - y_{2k})^2}$$
, where

y_{1k} is the proportional abundance of the k^{th} species in site 1, and z is the number of species in both sites

Figure 5.2. Legend on next page.

Figure 5.2. A graphical summary of data structure and calculation of Euclidean distance. (a) Proportional species abundances were tabulated per site for the mined regenerating areas ($a..z_{ij}$) and the undisturbed benchmark area ($A..Z_j$). The reference vector ($X_{a..z}$) is the average proportional abundance of each species in the undisturbed benchmark. Dissimilarity (d) was calculated as the multivariate distance between the reference vector $X_{a..z}$ and each sample site. The target is represented by δ , the mean of the group of distances $d_{X-Bm1..j}$ between the benchmark sites and $X_{a..z}$. (b) Here the multivariate distance measure Euclidean distance is the distance between two points on the two-dimensional plane defined by the proportional abundance of species **a** and **b** in each site. Replicate sites within a regenerating or benchmark area appear as clusters ($R_1, R_2...R_i, Bm$). The average distance between any regenerating area and the reference vector (the solid lines d_{X-Rij} connecting each replicate regenerating site with the centroid $X_{a..b}$) should over time decrease to become, on average, equal to the distance between the benchmark replicates and the reference vector (the dotted lines d_{X-Bmj} connecting each replicate benchmark site with the centroid).

evaluate the relative dissimilarity of the sites to the reference vector, we calculated the “distance” between each regenerating sample and the reference vector ($d_{X-R11} \dots d_{X-R21} \dots d_{X-Rij}$), as well as between each benchmark sample and the reference vector ($d_{X-Bm1} \dots d_{X-Bmj}$) (Fig. 5.2a). Finally we calculated $\mu_{d_{X-Bm1..j}}$, which is the mean of the distances between the benchmark samples and the reference vector and is also our target value δ (Fig. 5.2a). Quite what we mean by “distance,” we shall explain in the following paragraph.

To illustrate the calculation of the multivariate distance measure, in this case Euclidean distance, we can represent these data as a two-species simplification, plotting the proportional abundance of species **b** versus species **a** (Fig. 5.2b). In this two-dimensional example, Euclidean distance is the simple linear distance, in units of proportional abundance, between any two points on this plane. For our data, the several replicate plots for each site age appear as a cluster of points in the graph (R_1 is a site age cluster, as is R_2 , R_i is a cluster, etc.) (Fig. 5.2b). The benchmark samples also form a cluster around the centroid $X_{a,b}$, which is the reference vector represented as a point in two-dimensional space in Fig. 5.2b. The average proportional abundances of this two-species community on a regenerating area should change over time to become more similar to the average proportional abundances on the benchmark area. Hence the distances between each replicate site on a regenerating area and the reference vector $X_{a,b}$ (solid lines, d_{X-Rij}) should decrease, until it is on average equal to the distances between the benchmark replicates and the reference vector (dotted lines, d_{X-Bmj}) (Fig. 5.2b). The two-dimensional distance from our example is easily extended to a multi-dimensional space defined by the proportional abundances of all species in all the sites through the equation for Euclidean

$$\text{distance (ED): } d_{(ED)} = \sqrt{\sum_{i=1}^z (y_{1k} - y_{2k})^2}, \text{ where } y_{1k} \text{ is the proportional abundance of the } k^{\text{th}}$$

species in site 1, and z is the number of species in both sites (see also Fig. 5.2b).

Calculating dissimilarity and defining the benchmark using Ochiai's distance

“Distance” can also be measured in a number of other ways. Euclidean distance will mostly be affected by differences in species proportional abundances and will be relatively insensitive to local colonizations and extinctions unless such species have high proportional abundances.

However, communities can also change over time due only to species turnover, independently of finer changes in relative abundances. In such a case, two sites sharing many species (Figure 3; these are the species in the shaded region) relative to the number of species unique to each site will be more similar to each other than two that share few species. We therefore calculated an alternative distance measure, Ochiai's distance (OD) (Legendre and Legendre 1998), which is the geometric mean of the ratios of the number of shared species to the total number of

species in each site: $d_{(OD)} = 1 - \frac{a}{\sqrt{(a+b)(a+c)}}$, where a is the number of shared species

between two sites, and b and c is the number of species unique to the respective sites (see also Fig. 5.3). Ochiai's distance is sensitive only to species presence and absence and was therefore not appropriate for the soil elements.

Model of multivariate distance decay.

In Fig. 5.4, we show the hypothetical relationship between the distances calculated above (using either of the two methods), and the age of the site. At the right are the distances between the benchmark samples and the reference vector (grey diamonds). The mean of these, our target value δ , is represented by a horizontal dotted line. At the left (open diamonds), we show the distances for each site plotted against the age in years of the site. The reference vector has, trivially, a distance d_{X-X} of zero to itself (the solid diamond in the lower right of Fig. 5.4).

	Site R_{ij} / Bm_j	$X_{a..z}$	
Species <i>a</i>	1 ←	0	Species unique to R_{ij} / Bm_j (<i>b</i>)
Species <i>b</i>	1	0	
Species <i>c</i>	1	1	Shared species (<i>a</i>)
Species <i>d</i>	1	1 ←	
Species <i>e</i>	1	1	
Species <i>f</i>	0	1	Species unique to $X_{a..z}$ (<i>c</i>)
Species <i>g</i>	1	0	
Species <i>h</i>	0	0	
Species <i>i</i>	0	1 ←	
Species <i>j</i>	1	0	
Species <i>k</i>	1	0	
Species <i>l</i>	0	1	
Species <i>m</i>	0	1	

Ochiai's distance (OD): $d = 1 - \frac{a}{\sqrt{(a+b)(a+c)}}$, where *a* is the number of shared species between two sites, and *b* and *c* : the number of species unique to the respective sites

Figure 5.3. A graphical representation of how the dissimilarity measure Ochiai's distance is calculated. Only species presence (bold 1's) is used. Ochiai's distance is the geometric mean of the ratio of the number of shared species (shaded grey) to the total number of species in both sites.

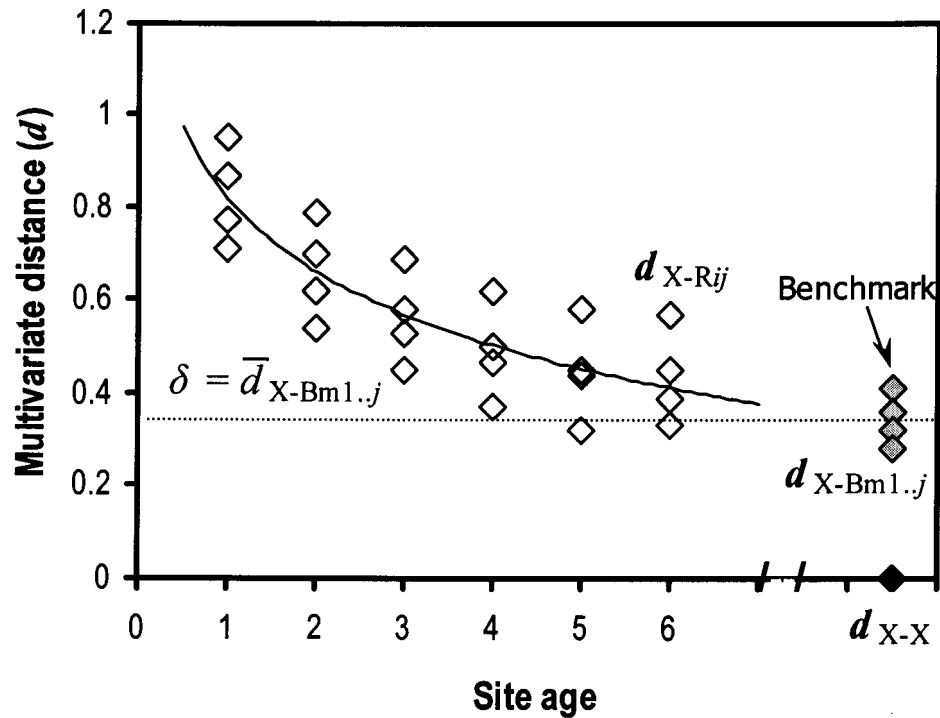


Figure 5.4. A graphical representation of the relationship between dissimilarity and site age. Multivariate distance (d), calculated as Euclidean and Ochiai's distance between regenerating sites of different ages (the open diamonds) and the reference vector $X_{a..z}$, should decay exponentially with site age until it approaches δ , which is the mean distance between the benchmark sites (grey diamonds) and $X_{a..z}$ and is here represented by a dotted line. The centroid of $X_{a..z}$ (where $d = 0$) is represented by the solid diamond d_{X-X} .

In this hypothetical example, convergence is an exponential decay described by the equation $d_t = d_0 e^{-kt}$, where d_t is the distance index after t years since disturbance, d_0 its initial value, and k is a rate constant that measures resilience (Pimm 1991, 1999) (Fig. 5.4).

Convergence is complete when the samples from a regenerating site are, on average, as different from the reference vector as are the benchmark samples.

Were the distances indeed decaying exponentially, then the logs of the distances would decay linearly as the age of the site increases. The test for convergence is that the slope of the log-linear regression line is significantly less than zero. Furthermore, if the relationship between log distances and site age is linear, then convergence is exponential. Since there are multiple observations for each site age, we test for linearity by partitioning the residual variance about the linear regression into within-age variance (“pure error”) and the remaining lack of fit variance. If the latter is sufficiently large (as measured by an F-test), we reject the linear decline in log distance.

To estimate the time it will take to complete convergence we used the regression model to calculate the predicted site age at which differences between the rehabilitating sites and the reference vector are, on average, as different as the sites within the benchmark.

Results

With the exception of the relative species abundances of dung beetles (measured by Euclidean distance, ED) and the species composition of the small mammals (measured by Ochiai’s distance, OD), the community abundances and composition converged significantly towards the benchmarks as the time after disturbance increased (Table 5.2; Fig. 5.5).

Only two of the cases, the relative abundances (ED) of herbs and dung beetles, were predicted to take longer than 41 years after disturbance to converge (Table 5.2). Indeed, a number of the

Table 5.2. Results of an analysis of post-disturbance changes in species composition and species presence of six assemblages and one functional group (soil), as measured by Euclidean distance (ED) and Ochiai's distance (OD; not done in soil) respectively. After disturbance, the \log_e of distance should decay linearly as the new assemblage changes to become progressively more similar to a benchmark, undisturbed community. Here we present the results of a least squares linear regression on \log_e OD and \log_e ED, and an F-test for slope significance (significant F-values are in bold). "Years to converge" is the number of years, as predicted from the regression, that a disturbed community will take to become as similar to an average benchmark community as replicate benchmark sites are themselves. The "Lack of Fit test" tests for linearity in the relationship between \log_e and site age. F-values for groups where the relationship is significantly different from linear are in bold.

Group	Distance index	Convergence regression			Years to converge	Lack of Fit test	
		Log-linear model	F (df)	P		F (df)	P
Soil	ED	$d_t = -0.81 - 0.08t$	26.61 _(1,17)	<0.001	25.4	7.85 _(2,15)	0.005
Herbs	ED	$d_t = -0.67 - 0.01t$	15.31 _(1,108)	0.0002	105	4.15 _(6,102)	0.0009
Herbs	OD	$d_t = -0.06 - 0.01t$	200.5 _(1,108)	<0.001	32.9	2.49 _(6,102)	0.03
Trees	ED	$d_t = 0.28 - 0.04t$	145.4 _(1,172)	<0.001	38.7	18.83 _(8,170)	< 0.0001
Trees	OD	$d_t = -0.02 - 0.01t$	124.4 _(1,172)	<0.001	40.5	13.54 _(8,170)	< 0.0001
Dung beetles	ED	$d_t = -0.89 - 0.002t$	0.03 _(1,22)	0.86	no convergence	12.57 _(5,17)	< 0.0001
Dung beetles	OD	$d_t = -0.30 - 0.02t$	51.56 _(1,22)	<0.001	26.8	2.32 _(5,17)	0.09
Millipedes	ED	$d_t = -0.47 - 0.03t$	19.97 _(1,138)	<0.001	21.6	2.39 _(14,124)	0.006
Millipedes	OD	$d_t = -0.12 - 0.02t$	47.51 _(1,138)	<0.001	14.31	2.99 _(14,124)	0.0006
Small mammals	ED	$d_t = -0.35 - 0.01t$	13.22 _(1,106)	0.0004	24.5	1.24 _(17,89)	0.25
Small mammals	OD	$d_t = -0.36 + 0.004t$	1.00 _(1,106)	0.32	no convergence	2.47 _(17,89)	0.003
Birds	ED	$d_t = -0.48 - 0.04t$	91.61 _(1,77)	<0.001	32.4	1.71 _(16,61)	0.07
Birds	OD	$d_t = -0.07 - 0.01t$	180.4 _(1,77)	<0.001	37.6	0.38 _(16,61)	0.98

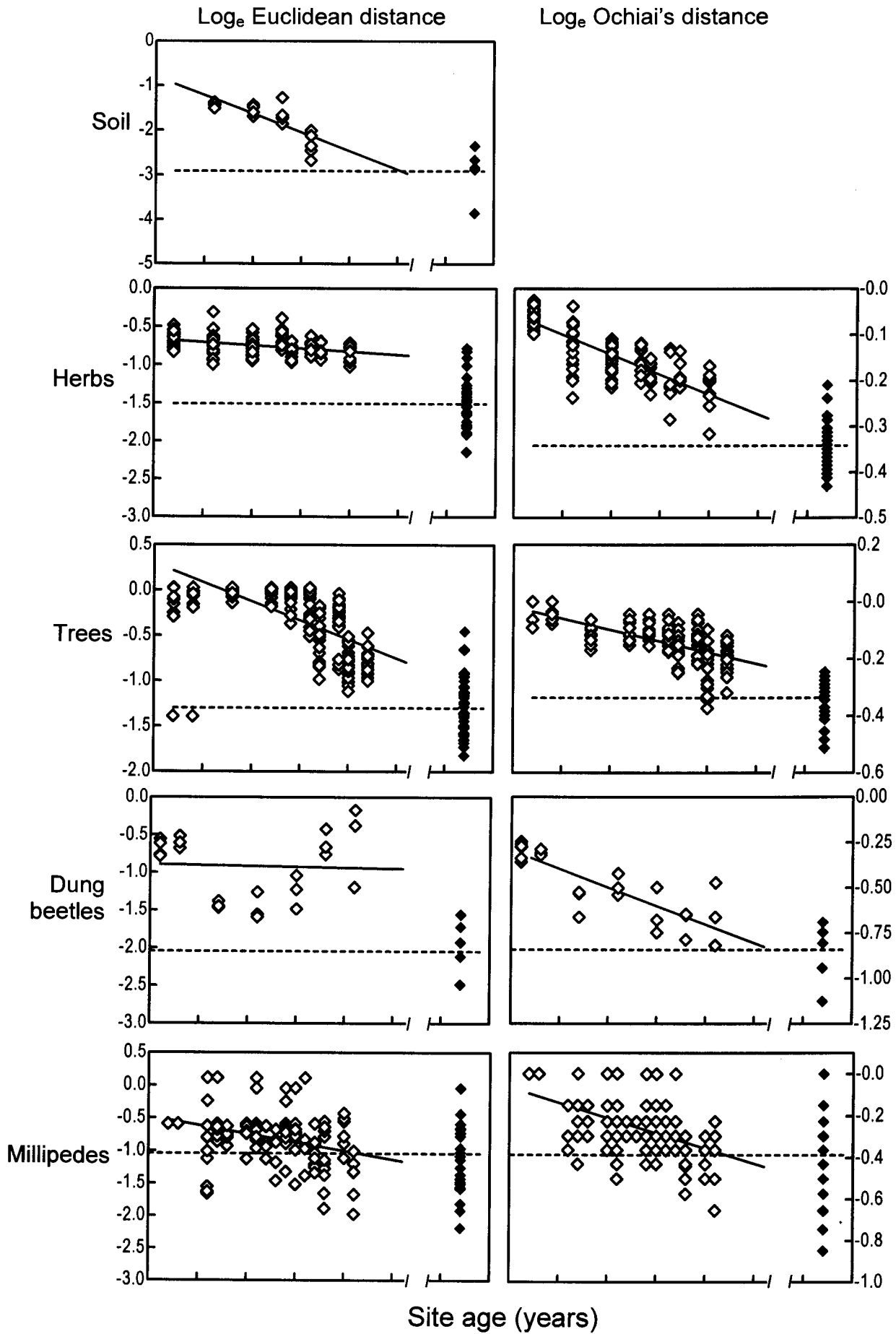


Figure 5.5

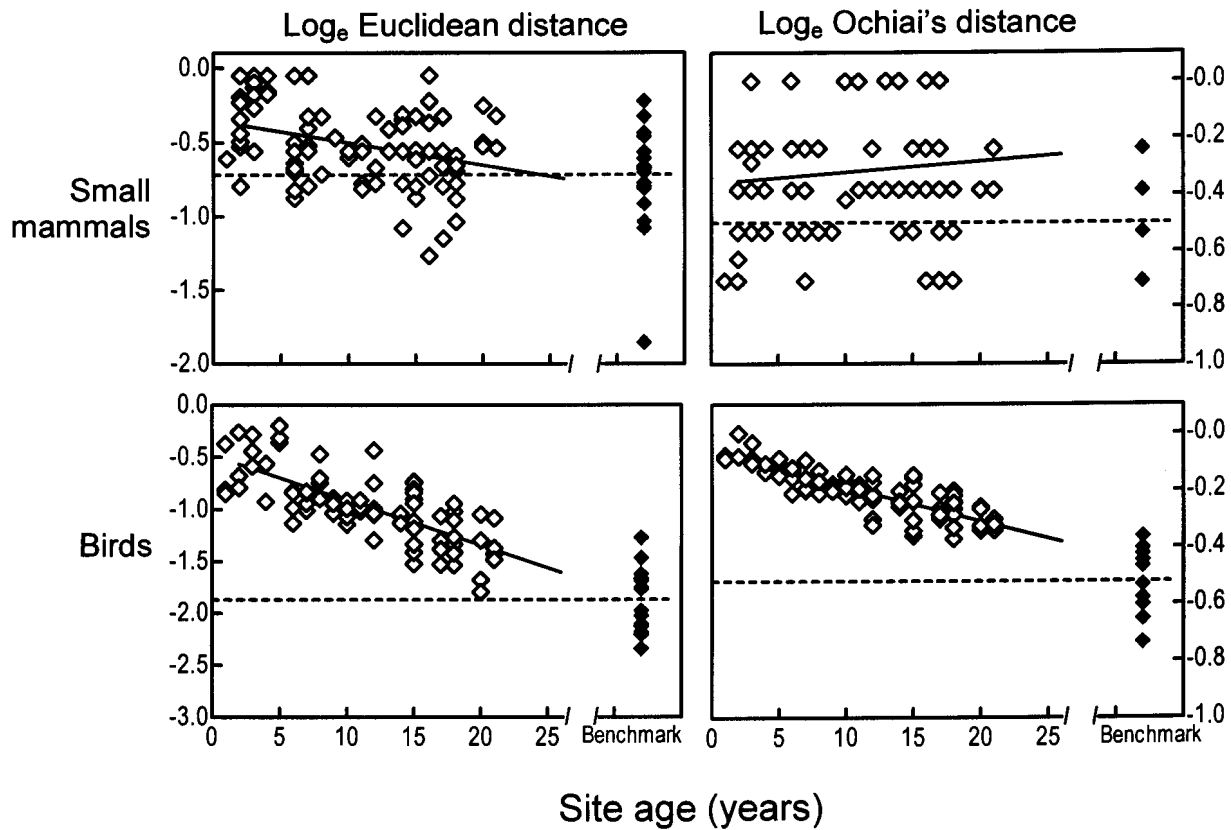


Figure 5.5 (continued). The change in assemblages of herbs, trees, millipedes, dung beetles, small mammals and birds, as well as a group of soil elements (pH and a variety of minerals), after disturbance (mining) and subsequent rehabilitation of coastal dune forests, compared to the same assemblages on an undisturbed area. Here we regress the logs of two dissimilarity indices, Euclidean distance (on the left), which is sensitive to species relative abundances, and Ochiai's distance (on the right), which is sensitive only to species presence, on site age. The solid diamonds on the right in each graph, which are not of any particular age, represents the variability in either species relative abundance (Euclidean distance), or composition (Ochiai's distance) on the undisturbed benchmark area. The mean of these, the dotted horizontal line in each graph, is the target value at which the regenerating area will become as similar to the average benchmark assemblage as the benchmark is itself. Ochiai's distance was not used for the soil group.

groups, including composition (OD) of the soil elements (pH and a variety of minerals), dung beetle species composition (OD), millipedes relative abundance (ED), and small mammal relative abundance (ED) and composition (OD) had already converged, or were about to converge at the time of our study (Table 5.2).

The relationship between site age and log distance was linear (i.e. convergence was exponential) in only three of the 13 cases: dung beetles species composition (OD), and birds composition (OD) and relative abundance (ED) (Table 5.2; Fig. 5.5). Non-exponential convergence is particularly evident in the soil elements (ED), trees (both OD and ED) and dung beetles (ED) (Fig. 5.5). Both trees and soil elements remained at or near their initial values for between 12 and 15 years before decreasing, while dung beetle relative abundances diverged after the first 15 years of convergence (Fig. 5.5). However, in most of the rest, decay trajectories were apparently exponential, although particularly small mammals and millipedes were characterized by a large amount of variability (Fig. 5.5). Indeed, in the majority of the cases, variability in the benchmark area exceeded that of the regenerating areas, even the oldest ones (Fig. 5.5). Over all, the pattern produced by relative abundances (ED) was remarkably similar to that of composition (OD) for the herbs, trees and birds, but very different in dung beetles, millipedes and small mammals (Fig. 5.5).

Two outliers at 1 and 4 years post-disturbance in tree relative abundances (ED) actually consisted of six sites that had no trees (Fig. 5.5). We omitted these data, which were the result of a peculiarity of the Euclidean distance index (see Legendre and Legendre 1998), from the regression analysis.

Discussion

We found that with the exception of two cases, species composition (measured here by Ochiai's d) and relative abundance (measured with Euclidean d) became significantly more similar to a reference system as the assemblage's age increases. Moreover, convergence was reasonably fast – with the exception of herbs (Euclidean d), all predicted convergence times were less than 41 years. This amounts to no more than a few generations for any of the groups in our study and is less than the lifespan of most of the tree species. Our results are not evidence for (or against) any specific community assembly mechanisms, but do suggest that real communities must experience some type of structuring during the assembly process.

Much of the argument around the existence of persistent states, and hence the probability of community recovery, may lie in the ecological detail that models often ignore. For instance, we found a disparity between relative abundance (Euclidean d) and species presence (Ochiai's d) for both small mammals and dung beetles. One community may therefore recover only its species composition, while another may recover both. A persistent state may thus be in the eye of the beholder – using a distance index that measures only presence or only abundance may lead to a different conclusion.

Furthermore, in small mammals (relative abundance or Euclidean d) and millipedes (both distance indices) the pattern was variable, yet the rate of convergence was still highly significant. This variability may thus be seen as implying that the occurrence, and relative abundance, of species is random across the age gradient, but it may also be influenced by the sampling technique (live-trapping of mobile animals is not nearly as efficient at sampling a community as quadrat sampling of sessile plants). The absence of convergence in small mammal species composition (Ochiai's d) implies that this assemblage is not returning to a persistent state, but an equivalent variation in the

benchmark forest's assemblage suggests that "persistent state" is perhaps a misnomer for small mammals.

If colonization and extinction rates on a new habitat decrease over time as a function of diversity (MacArthur and Wilson 1967, Manne et al., 1998), dissimilarity should also decay exponentially. From our results it appears that colonization and extinction (and the concomitant change in relative abundances) are anything but the orderly events foreseen by equilibrium biodiversity theory – only in dung beetles (Ochiai's d) and birds (Euclidean d) was the decay in dissimilarity exponential. In some of the groups, the rate of decay was apparently either faster (dung beetles) or slower (trees) than exponential in the initial stages. For trees, this may be explained by simple successional dynamics (Finegan 1996)– the presence of a long-lived set of pioneer species will result in a lag period in the decay of dissimilarity. Dung beetle population levels are probably influenced by non-linear changes in microclimatic variables across the chronosequence (Davis et al. 2003), but external disturbances such as the presence of cattle dung at certain times of the year may play a role.

In at least three of the groups (herbs, trees and birds), the variability on the regenerating sites was much smaller than on the benchmark. This suggests that the regenerating assemblages have so far managed to assemble only a portion of the possible species combinations present across the range of undisturbed forest. The regenerating sites have converged, on average, but have attained only a portion of the undisturbed forest's beta diversity. Complete convergence here may thus critically depend on colonization by a subset of species that are either simply very rare, or require the presence of dispersal agents (Richardson et al. 2000), or a particular habitat component (such as large old trees for nesting holes).



In conclusion, we have demonstrated that real communities may return to a persistent state within at the most a few generations. Indeed, with only a few exceptions convergence seems to be a common type of post-disturbance change, at least in these dune forests. In the debate over whether stabilizing mechanisms, internal to the community or not, exists (Hubbell 1979, 2001, Wilson et al. 1996, Clark and McLachlan 2003), we conclude that there are such mechanisms. In a real regenerating forest community, resilience is a demonstrable fact and the number of possible end-states is at best small for various, perhaps even opposing, reasons.

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Chapter 6
Manuscript

Are abundant species better at colonizing new sites?

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ABSTRACT

Empirical studies on invasions, and macroecological theory, suggest that abundant species in an undisturbed habitat will be superior colonizers of new habitats, either because they are better dispersers, or have wider niches. On the other hand, late-successional dominants (the abundant species in an undisturbed habitat) should be poor colonizers because they are adapted to be good competitors rather than good dispersers. The issue of whether a species' abundance in a source area may influence its ability to colonize new habitats is practically important for the management of ecological restoration, but also theoretically interesting because colonization is integral in many models of community assembly and metapopulation dynamics. We surveyed undisturbed, mature coastal dune forest patches, and two sets of post-disturbance regenerating forest patches for the presence and abundance of millipede, bird, and tree species. We found that bird and tree species that are abundant in a source area were more likely to colonize regenerating forests than rare species were. Abundant species from all three groups colonized soon after disturbance (i.e. they were recorded in the youngest regenerating sites), but rare species colonized at any stage. Abundant bird and tree species had larger founder populations than rare ones, but abundance at the point of colonization was always less than source area abundance for forest specialists and late-successional species. Post-disturbance community re-assembly is therefore at least partially deterministic, most likely because of a simple passive dispersal advantage for abundant species. Our results suggest 1) that the role of abundance in colonization is likely to be complex and different for different groups, and 2) that local colonization and extinction can never be evaluated outside the specific regional landscape context.



INTRODUCTION

To colonize disturbed sites, a species has to overcome a number of obstacles. Once it has solved the set of obstacles associated with dispersal, which is more difficult the further a source area is from a colonizable site (MacArthur and Wilson 1967), it has to find a foothold in an environment that is not necessarily large enough (MacArthur and Wilson 1967), or suitable for it (Pacala and Rees 1998). Which species will make it and which not? To what extent is colonization (and hence also the template for community assembly) deterministic or stochastic? To what extent does a species' regional abundance determine local processes such as colonization?

The question of which species colonize, and which not, is clearly very important in ecological restoration (and for other conservation management issues) (Bradshaw 2000). However, it is also theoretically interesting. For instance, colonization is central to all community assembly models (Drake 1990, 1991, Gitay and Wilson 1995), yet most treat colonization as a constant and invariable background process. Is the picture sketched by these community assembly models a good approximation of what happens in a real, regenerating community?

Although island biogeography tradition has it that colonization is influenced only by distance to source area and patch size (MacArthur and Wilson 1967), whether a species is rare or abundant in a source area may play a fundamental role (Gaston and Kunin 1997; Williamson and Fitter 2002). Numerous studies on invasive species have shown that the more abundant a species is in its country of origin, and the more often it is introduced (i.e. a high dispersal rate by analogy), the more likely it is that it will successfully colonize (Williamson and Fitter 1996; Kolar and Lodge 2001).

The mechanisms that link abundance with colonization, which may be from one to many operating simultaneously, do not necessarily influence the process directly, in

the same direction, or even in the same way across groups. For example, abundant species may have a statistically better chance of finding and colonizing a new habitat because they have more dispersing individuals (a mass effect *vide* Shmida and Ellner 1984), or they may just be better at exploiting a larger variety of habitat types (Brown 1984). On the other hand, later-successional, dominant species (i.e. the abundant species in an undisturbed habitat) may be poor colonizers because species that are competitively dominant in stable environments rarely disperse to new habitats (Tilman 1994; Hurtt and Pacala 1995), or because they are not adapted to conditions in new habitats (Pacala and Rees 1998; Stanton et al. 2002).

In sum, there are several reasons to expect that abundance will influence colonization, but it is less clear how or in what direction this influence will be. In this paper, we use a chronosequence of regenerating post-disturbance sites to find evidence for the effect of source area abundance on colonization success. A chronosequence consists of spatially separated sites of increasing regeneration age and increasing habitat suitability for colonizing forest species. A simultaneous survey of all sites can thus provide a snapshot of the whole ecosystem regeneration process from the beginning to the time of the oldest site. Because all developmental stages exist alongside each other, colonization could theoretically occur at any regeneration age, dependent only on a species' ability to disperse and then to endure conditions there.

We use data collected over 11 years on the abundance of tree, millipede and bird species to test for the effect of a species' source area abundance on colonization of chronosequences of regenerating coastal dune forests. We ask three specific questions: (i) are abundant species in general more likely to colonize new habitats?, (ii) do abundant species colonize sooner after disturbance than rare ones?, and (iii) do abundant species have larger founder populations in their new habitat?

METHODS

Study site

The eastern coast of South Africa, in particular the dune cordon occupied by tropical coastal forests of KwaZulu-Natal, has had a long and continuous history of human occupation and varied disturbances (Thompson 2002). This has created a mix of undisturbed forest patches (ranging from 1 ha to a few thousand ha in size) and patches of regenerating forests of different post-disturbance age in the same area. Our study, which centered on the coastal region between Richards Bay (28° 47.27' S, 32° 06.57' E) and Cape Vidal (28° 8.02' S, 32° 32.85' E) in South Africa (Fig. 6.1), focuses on two chronosequences (sets of post-disturbance regenerating sites of sequential age), one natural, and one man-made.

The man-made chronosequence is the result of a minimal intervention post-mining rehabilitation process (van Aarde et al. 1996). Mining for aeolian heavy minerals in the strip of high, forested coastal dunes (< 2 km from the sea), results in the destruction of all vegetation cover. However, subsequent rehabilitation of post-mining dunes by the mining company over a period of ~24 years, has created a chronosequence of regenerating forest patches (van Aarde et al. 1996). No active seeding or planting occurs after the initial topsoil and cover seeding treatment during the rehabilitation process (van Aarde et al. 1996), so that the directional successional trends in the vegetation, soil, and faunal communities (van Aarde et al. 1996; Kritzinger and van Aarde 1998) rely on an entirely unassisted process of colonization by forest species.

The natural chronosequence consists of patches of regenerating forest between 4 and ~53 years old scattered within and close to the town of Richards Bay (Fig. 6.1).

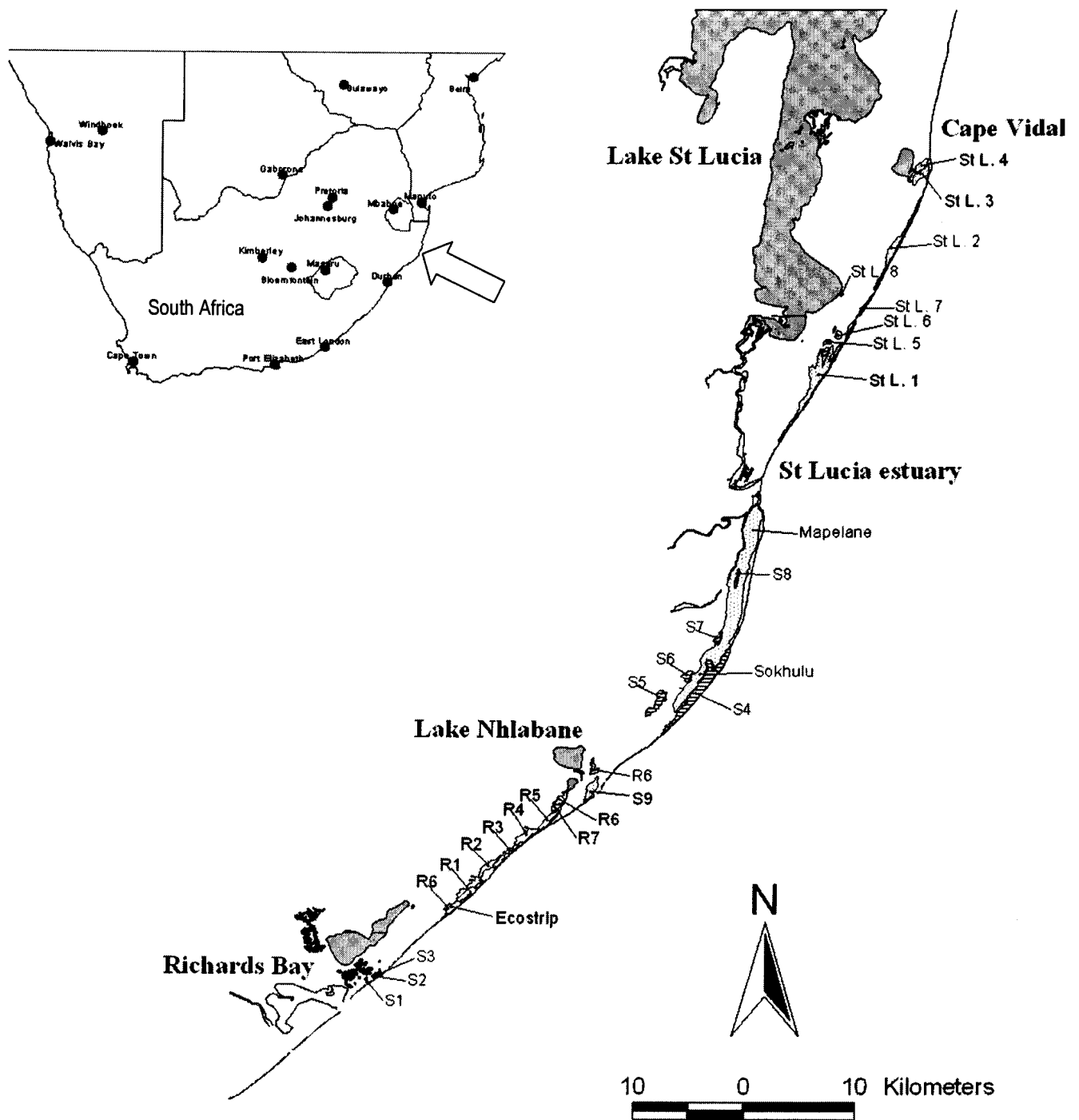


Figure 6.1. The study area northeast of Richards Bay, showing the location of the different regenerating forest patches (R1-7; S1-9, for rehabilitating and spontaneously regenerating sites respectively) and the undisturbed benchmark sites (Sokhulu, Mapelane, St Lucia1-8 and Ecostrip). See text for detail on study sites.

Here natural processes have resulted in well-established successional changes (Weisser and Muller 1983) leading ultimately to the typical moist evergreen subtropical forests of the region. We identified these spontaneously regenerating sites as well as the undisturbed sites (the colonization source areas) by comparing historical series of aerial photographs (series from 1937, 1957, 1978, 1985, 1996) with the current landscape.

The undisturbed sites consist of three different groups of forest patches. These were all recognizably intact and undisturbed on the earliest (1937) set of aerial photographs. The first of these groups, the so-called Ecostrip, consists of a single ~200 m wide and ~3.5 km long strip immediately adjacent to the seaward side of the mined chronosequence (Fig. 6.1), left unmined under the conditions of the mining lease (van Aarde et al. 1996). The vegetation here consists of fore dune salt-spray and wind-pruned communities (about 100 m) and dune forest (about 100 m) and was left intact to stabilize dune faces, but also to serve as a corridor for colonizing forest species. The Mapelane Dune Forest Reserve and its associated Sokhulu Forest represent the largest contiguous dune forest patches left in South Africa (together ~2000 ha) and are located immediately south of the Umfolozi-Lake St Lucia estuary (Fig. 6.1). The final group of eight benchmark sites is situated in the St Lucia Nature Reserve, about 20 km northeast of the Mapelane-Sokhulu group (Fig. 6.1).

The study area is surrounded by commercial beefwood (*Casuarina equisetifolia* Forst. and Forst.) plantations, rural dwellings, woodlots, subsistence agriculture and mining areas. Soils, including those of the undisturbed forest patches, are simple and undifferentiated and relatively uniform throughout the study area.



Data collection

Each site was re-surveyed during each survey year for millipedes and birds as part of an ongoing ecological monitoring program. Site age was taken as the number of years between the start of regeneration and the survey. In the case of the mined chronosequence, regeneration date was determined by the date of rehabilitation, while for the natural chronosequence, regeneration date was taken as the median calendar year between the time of the last aerial photographs showing only bare sand or grassland and the first photograph showing a tree- or shrub cover.

Birds were surveyed during the austral summers of 1994, 1997, 1999, 2000 and 2001 using randomly located line transects (between 2 and 4 per site), separated by at least 200 m between transects. Annual abundances were calculated as the mean number of individuals per species per transect. Millipedes were sampled annually in the spring and summer of 1992 and from 1996 to 2002 (except 1998) using six randomly located 6 x 35m transects per site. Surveying was done by three observers who systematically searched the transect and recorded all millipedes seen, up to a height of 3m. Trees were surveyed during 2001 using between 15 and 40 16m x 16m randomly located quadrates per site, in which all rooted individuals of each species were recorded. Abundance in millipedes and trees was calculated as the number of individuals per transect or quadrate. The replicated millipede and bird surveys meant that some sites could appear more than once in the database, at different ages. Although not all sites were surveyed in all years, each regeneration age class was represented at least once in the database.

Numerical analysis

Dealing with pioneer species: Essentially our interest in colonization is about the true forest specialist species. Several so-called pioneer tree species (species adapted to early successional stages) persisted in the undisturbed sites in our study, either as long-lived leftovers of previous successional changes, or as remnants in old treefall gaps. These species, and their functional analogs for millipedes and birds, may mask the effect of abundance amongst forest specialist species. We therefore repeated the analysis for only the non-pioneer species, using two methods to identify and remove pioneer species.

Firstly, for all three groups, we defined pioneers as those species whose mean *relative* abundances in all the undisturbed forests were lower than in all the regenerating chronosequence sites, on the assumption that pioneer species will tend to have relatively higher population sizes in earlier successional stages (see for example Dalling et al. 2002). Secondly, for trees and birds only, we categorized species as being either forest specialist or not, based on descriptions of their habitat affinity in Coates Palgrave (1993), Pooley (1993), Newman (1996), Sinclair and Hockey (1996), and van Wyk and van Wyk (1997).

In total, 72 of 144 tree and 21 of 70 bird species from the undisturbed forest sites were categorized as forest specialists. The removal of pioneer species from the set yielded a decreased species list for the undisturbed sites: trees decreased from 144 to 109, birds from 70 to 49 and millipedes from 22 to 20 species.

Statistical tests: The relationship between abundance in the source area and abundance of the founder population was tested using ordinary least squares regression. Because absolute abundance values were not normally distributed for any of the three groups, these values were log-transformed before regression analysis. The

relationship between source and founder abundance may be driven by particular sets of species. We therefore tested whether the slope for this relationship differs significantly from unity (perfect relationship) using a t-test (Sokal and Rohlf 1995), and evaluated the position of pioneer and non-pioneer species vis-à-vis the unity line.

We used a two-dimensional Kolmogorov-Smirnov test (Garvey et al. 1998) to test for a significant relationship between abundance and the habitat age at which a species was first recorded (i.e. colonization habitat age). This non-parametric test evaluates the dependence between two variables under the null hypothesis of random spatial arrangement of data points on a bivariate (i.e. 2-dimensional) scatterplot. The method assumes neither a linear relationship between the two variables, nor equal variances (Garvey et al. 1998). This technique is especially suitable for our analysis, since the larger number of rare than abundant species constrains variation at the upper end of abundance. For this test, the maximum difference (D_{BKS}) between observed and expected proportions of points in four quadrants around each point (i.e. a pair of x - y coordinates) on a bivariate plot is calculated. Significance is then assessed by randomly rearranging the points on the bivariate plot a 1000 times. We used a macro in a spreadsheet program (Microsoft Excel version 9) to do the permutations.

Finally, if abundant species are more likely to colonize anywhere along the chronosequence than rare ones, there should be a difference in the abundance ranks of species that have colonized compared to those that have not. We tested this hypothesis using a Mann-Whitney U test (Sokal and Rohlf 1995).

RESULTS

The set of undisturbed forest patches share 69% of their tree species, 83% of their bird species and 86% of their millipede species with all the regenerating sites. Abundant

tree and bird species were more likely to colonize any of the new habitats, regardless of regeneration stage, than rare ones were, but millipedes not (Fig. 6.2).

In all three of these groups the relationship between abundance and habitat age at first colonization was almost triangular, so that very abundant species apparently always colonize early, but rare species colonize at any habitat age (Fig. 6.3). The tendency for these abundant species to colonize early was significant across all species (including pioneers and non-forest specialists) for millipedes and birds, but for trees only if the obvious set of species that colonized by 37 years was omitted (Table 6.1). The relationship was not significant for either the set of forest specialists or mature forest species on their own, for any of the three taxa (Table 6.1).

On the other hand, tree and bird species with high abundance in the source area had a significant tendency to have large founder populations, but not millipedes (Table 6.2, Fig. 6.4). The slopes for all three groups were significantly less than unity (millipedes: $t_{17} = 4.36$, $P < 0.001$; birds: $t_{56} = 9.72$, $P < 0.001$; trees: $t_{97} = 9.59$, $P < 0.001$) implying that the abundance effect is not perfect, regardless of the positive relationship between source and founder abundance. These results did not change for any of the three groups, either when we removed pioneer species from the analysis, or when we tested only the bird and tree forest specialist species.

DISCUSSION

If species rank-abundance patterns tend to recur, which will happen if regional abundance determines the order of colonization and the founder abundance in new habitats, local communities will effectively have a regional “bauplan” for post-disturbance recovery. Our results suggest that this is at least partially the case, and that regional abundance will have a variable amount of influence on the extent to

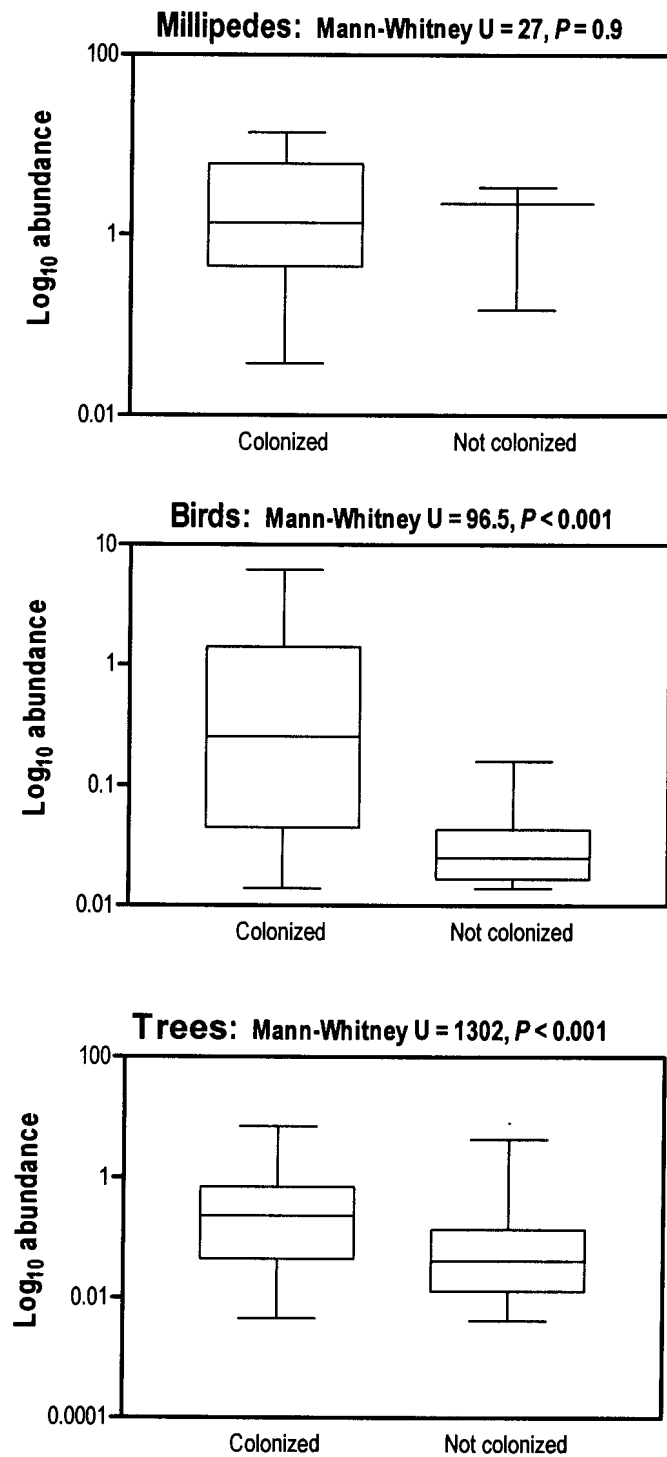


Figure 6.2. The median abundance rank of species that have colonized any one or more of eight mined and seven spontaneously regenerating sites of different post-disturbance age, compared to the median rank of those that have not. The box represents the median, quartile and range. The two sets differed for the trees and birds, but not for millipedes.

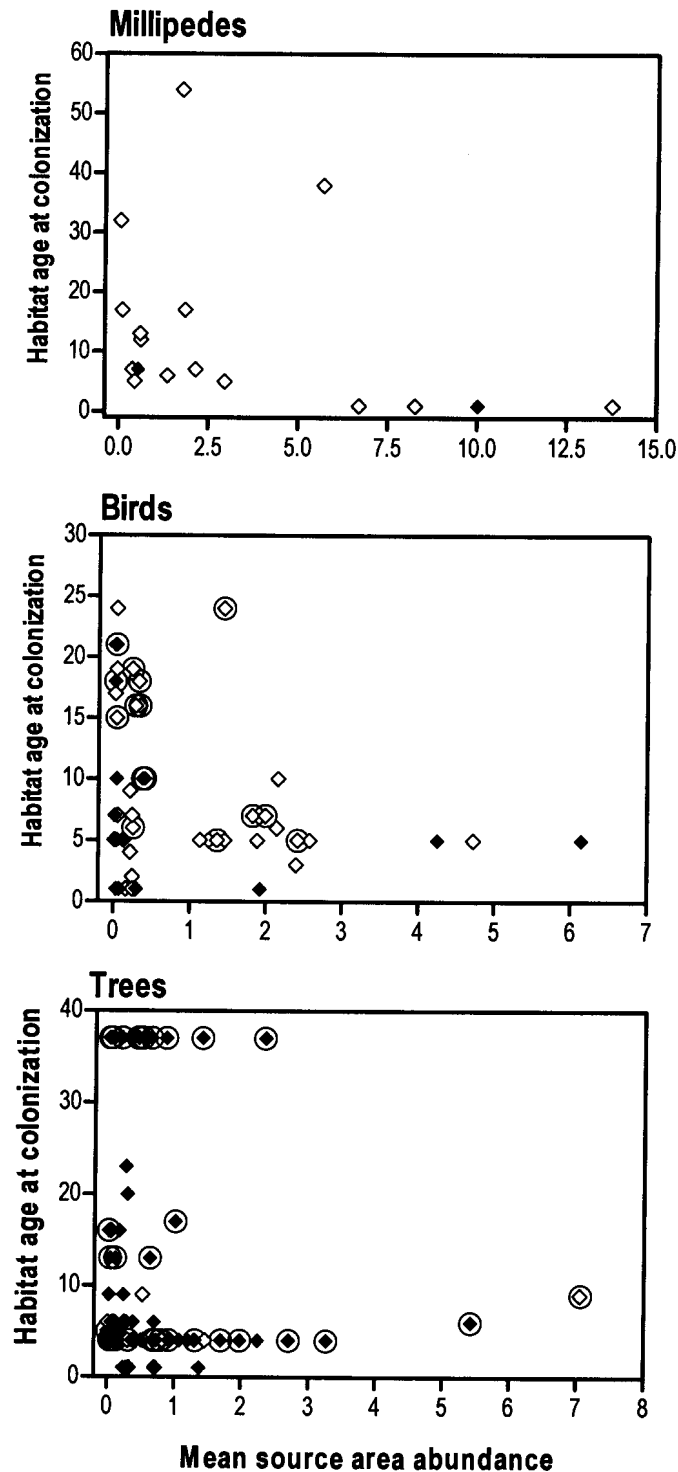


Figure 6.3. The relationship between the mean abundance of millipede, bird and tree species in all undisturbed source areas and the age of the youngest post-disturbance regenerating site where it was first recorded. Shaded data points indicate pioneer species (species with higher relative abundance in all the regenerating sites than in all the source areas combined). Circled data points indicate forest specialist species, identified on the basis of independent habitat affinity descriptions (see text). No information on habitat affinity is available for millipedes. The relationship was significant for birds and millipedes, but for trees only if the group of late colonizers at 37 years was removed (see text).

Table 6.1. Results of a two-dimensional Kolmogorov-Smirnof test (Garvey et al. 1998) testing for a significant relationship between abundance in the source area and habitat age at first colonization. “ D_{BKS} ” is the maximum difference between the expected and observed distributions, “Species” is the species responsible for the maximum difference (see also Fig. 3) and “P” is the probability of finding a larger value of D_{BKS} at random, calculated from a 1000 random draws (significant values in bold). “All species” denotes the complete set of species shared by the undisturbed and regenerating sites, “Forest specialists” denotes the data set including only species with high affinity to undisturbed forest, and “Mature forest species” denotes the full data set with pioneer species (higher relative abundance in regenerating than undisturbed forest) removed.

	All species	Forest specialists	Mature forest species	
<i>Millipedes</i>				
D_{BKS}	0.167	–	0.155	
Species	<i>Sphaerotherium punctulatum</i>	–	<i>Sphaerotherium</i> sp2	
P	0.047	–	0.11	
<i>Birds</i>				
D_{BKS}	0.097	0.177	0.079	
Species	<i>Sylvia borin</i> (Garden Warbler)	<i>Tockus alboterminatus</i> (Crowned Hornbill)	<i>Tockus alboterminatus</i> (Crowned Hornbill)	
P	0.03	0.11	0.56	
<i>Trees</i>				
D_{BKS}	0.062	0.076 [§]	0.084	0.079
Species	<i>Phoenix reclinata</i>	<i>Phoenix reclinata</i>	<i>Erythrococca berberidea</i>	<i>Albizia adianthifolia</i>
P	0.12	0.048	0.41	0.34

[§] The test was repeated for trees with the data for the 37-year old site removed.



Table 6.2. Results of linear regressions of the relationship between source area abundance and abundance at point of colonization (i.e. founder population size) for three taxa.

Taxon	Regression model	Is slope significantly different from zero?			
		df	F	P	R ²
Millipedes	$y = -0.25 + 0.09x$	1, 17	0.21	0.65	0.01
Birds	$y = -0.21 + 0.31x$	1, 56	19.15	<0.001	0.26
Trees	$y = -0.4 + 0.22x$	1, 97	7.18	0.009	0.07

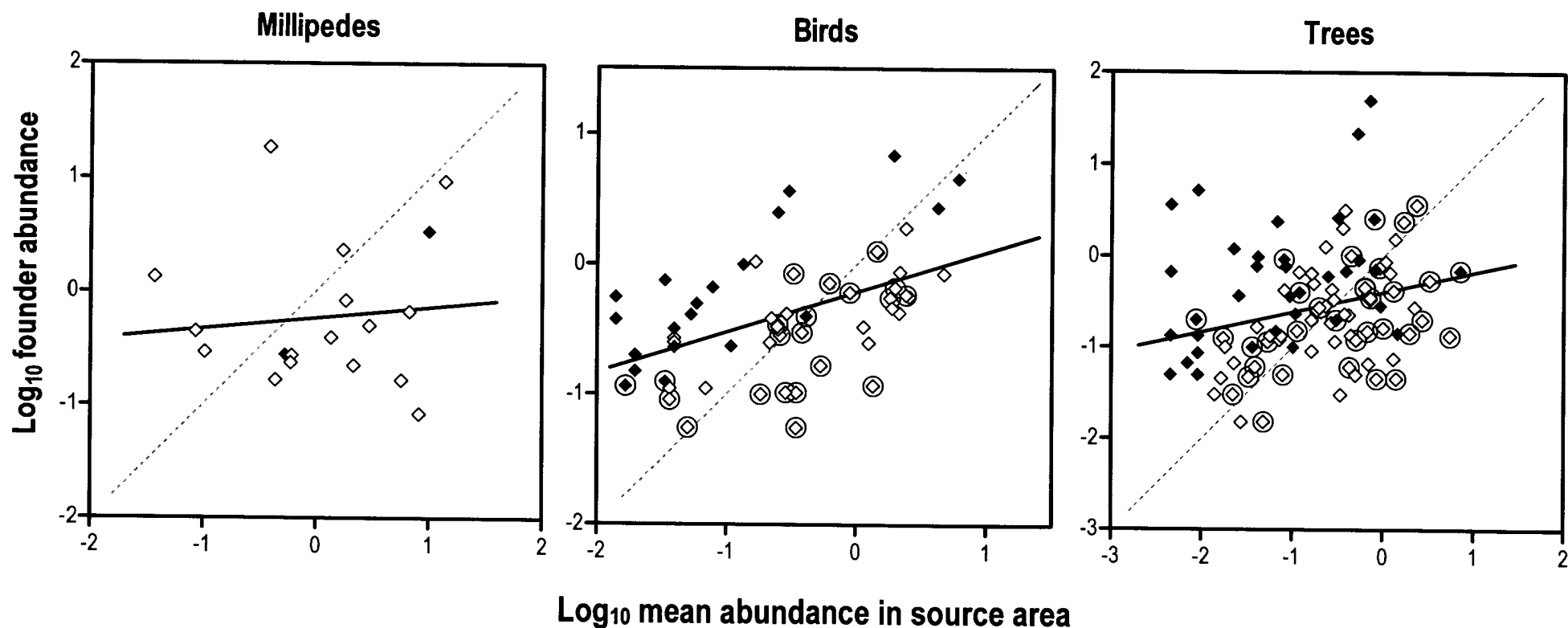


Figure 6.4. The relationship between a species' \log_{10} mean abundance in the undisturbed source areas and its \log_{10} mean abundance where it first colonizes a new habitat (solid lines). Shaded data points indicate pioneer species (species with higher relative abundance in all the regenerating sites than in all the source areas combined). Circled data points indicate forest specialist species, identified on the basis of independent habitat affinity descriptions (see text). No information on habitat affinity was available for millipedes. Dotted lines are the unity line for each group, indicating a perfect relationship. All three groups differed from unity and birds and trees differed from zero (Table 6.2).

which it can happen. We found that abundance is related to colonization ability in the form of a “constraint” boundary (preventing the occurrence of abundant late colonizers, but allowing rare early colonizers) and that abundant species have an overall higher probability of colonizing than what rare species do. For birds and trees, this effect was fairly straightforward and significant (although there was some ambiguity in the pattern of timing of colonization in trees), and even in millipedes abundant species were more likely to colonize early than late.

However, the effect of abundance on timing of colonization was not perfect. A large number of rare species from all groups managed to colonize from relatively early on and there was no obvious difference in this pattern for forest specialists, pioneers or the rest (see Fig. 6.3). The abundance effect, even where it was clearly present, was also not smooth – we found that the relationship between source area abundance and habitat age at colonization was significant for trees only if the set of species that colonized at 37 years post-disturbance was omitted. Abundant source area species did not manage to immediately recover their abundance in the new community: the relationship between source and founder abundance was less than unity, even in the birds and trees where the overall relationship was significant (see Fig. 6.4). Moreover, forest specialist species (trees and birds) tended to have lower founder abundances than expected from the empirical relationship, lending some support to the notion that late-successional species are poor colonizers.

Many confounding factors may influence the effect of abundance on colonization and lead to such an imperfect relationship. For instance, colonization may occur in stages, perhaps because some critical threshold value is reached during autogenic succession, leading to a type of “chronological clustering” (Legendre et al. 1985). In such a case, the abundance effect will only be visible within each stage and not across

all stages. In addition, rare source area species are often (but not exclusively) pioneers, which can be expected to have higher founder abundances than would be predicted from their source area abundance.

Nevertheless, although at least part of the explanation may therefore lie in the detail about species biology, overall we found clear evidence that regional abundance must be playing a crucial role in the way a new community will recover. What is more, our results suggest that this is not because abundant species have wider niches or are more tolerant of a wider set of habitat conditions (Brown 1984). If that was the case, we would not have found rare early colonizers, yet many rare species from all three groups managed to colonize early in the chronosequence. In our study, it is much more likely that the regenerating sites were passively sampling the rain of propagules and individual animals that are dispersing from all other sites in the region. A large population in a source area may simply mean more dispersing individuals, more instances of long-distance dispersal events (Johst et al. 2002; Nathan et al. 2002) and, for plants, more chance of being dispersed by vertebrate frugivores (Stanley and Lill 2002).

Species-specific biological and ecological factors, such as dispersal constraint in many plant species (Verheyen and Hermy 2001), or niche width (Thompson et al. 1999), could thus independently influence colonization, to the point that even rare forest specialists colonize early or that some forest specialists simply won't colonize at all. Ultimately, however, on a community scale these factors must be overwhelmed by the effect of large numbers that will ensure that abundant species colonize and that they do so early (Dalling et al. 2002; Hewitt and Kellman 2002). This regional influence on local populations also implies that colonization of post-disturbance habitats can partially be viewed as a metapopulation problem (Gotelli 1991, Freckleton and Watkinson 2002), superimposed on classic successional facilitation.

Our results have interesting practical and theoretical implications. For one, restoration managers need to be aware that the re-creation of a naturally variable community will most likely be a complex function of species' regional abundances and will be dependent on trophic level. On the other hand, our results also suggest that the strength of the so-called rescue effect (Hanski 1982) in metapopulation models will be more variable the lower a species' mean regional abundance, regardless of the number of sites occupied (Gotelli 1991). Moreover, many community assembly studies have concluded that end-state community composition will be determined by chance because of strong priority effects early in the invasion sequence (for instance Drake 1990, 1991, Gitay and Wilson 1995). However, it appears from our results that invasion sequence itself is not necessarily a product of chance and historical factors; it may at least partially be a deterministic (although imperfect) function of regional species characteristics. In sum, on both a theoretical and practical level, local colonization and extinction cannot be evaluated outside a specific landscape context.

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Chapter 7
Manuscript

Developmental trends in the community structure of coastal dune forest ground-dwelling spiders (Arachnida: Araneae)

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Abstract

Fragmentation of the dune forests of Maputaland, a recognized centre of biodiversity and endemism in northeastern South Africa, has the potential to negatively impact the diversity of many taxa, with some invertebrate groups being particularly susceptible. However, recent attempts by a mining company to restore dune forests on part of their lease area has raised the hope that the recovery of many plant and animal assemblages may offset this negative effect. We surveyed three rehabilitating sites (2, 8 and 16 years post-mining), one previously disturbed site (approximately 40 years post-disturbance), and an undisturbed mature dune forest site, for the presence of ground-dwelling spiders and measured several aspects of their microhabitat (litter structure, vegetation cover, vegetation growth form). We hypothesized that previously described successional processes will lead to deterministic habitat age-related patterns of recovery in spider microhabitat architecture and community structure. We found that species composition on disturbed sites becomes more similar to the undisturbed dune forest as the sites get older, and that there is an age-related change in spider microhabitat structure over the series, suggesting deterministic successional development in community structure. However, Canonical Correspondence Analysis showed that the change in habitat is not a simple monotonic function of site age, but rather equates to three different habitats, separated in terms of their litter structure and low-level vegetation cover. Multiple regression confirmed the importance of particularly litter structure and vegetation cover for community structure. The negative effects of fragmentation will only be offset if dune forest restoration concurrently manages to restore spider microhabitat structure.

Key-words: Araneae, spiders, conservation, dune forest, rehabilitation, succession, age-related pattern, microhabitat structure

Introduction

Over the past 50 years the sub-tropical dune forests of the Maputaland centre of endemism in southern Africa have been severely fragmented, mostly due to human activities (Weisser and Muller, 1983; van Wyk, 1994; Woolley, 2003). Such fragmentation and the associated habitat loss must have had detrimental effects on a number of taxa, but perhaps none more so than on invertebrates that are often characterized by disjunct distributions and small range sizes (Poynton, 1961, Margules et al., 1994, Burgess et al., 1998, Slotow and Hamer, 2000, Hamer and Slotow, 2002). The conservation implications of the effect of such habitat fragmentation on genetic isolation (Vandergast, 2002), species diversity (Miyashita, et al. 1998), metapopulation dynamics (Topping, 1999) and species composition (Gibb and Hochuli, 2002) in small isolated arachnid communities are obvious.

On the other hand, dune forests are apparently highly resilient to large-scale disturbances (Weisser and Muller, 1983; Woolley, 2003), with the result that much of the invertebrate biodiversity may be recovered during vegetation succession. For instance, dune forest millipede community structure is fairly quickly restored in response to active rehabilitation after disturbance by mining (van Aarde, et al. 1996a). In general, some invertebrate assemblages, including arachnids, show clear successional patterns in response to disturbance (Duffey, 1968; Huhta, 1971; Bultmann et al., 1982; Bonte et al., 2002). Others, because of responses to microhabitat structure and fine-scale differences in microclimate, don't (Hurd and Fagan, 1992; Bradley, 1993; Davis et al., 2003). We use the opportunity afforded us by the dune forest rehabilitation program of the mining company Richards Bay Minerals to evaluate whether an arachnid community can recover its structure after disturbance and thus counteract the deleterious effects of forest fragmentation and habitat loss.

Ground spiders are a diverse group of predators, perhaps the most important such group in many forest ecosystems, capable of indirectly exerting some effect on plant productivity and litter decomposition (Wise et al., 1999; Lawrence and Wise, 2000). They are mostly cursorial, but many species of the forest floor are specialized retreat web-builders, or trapdoor hunters, or utilize other specialized forms of hunting (Dippenaar-Schoeman and Jocqué, 1997). Moreover, the spiders of the Maputaland forests are still poorly known, because sampling and taxonomic research do not keep pace with their functional and phylogenetic diversity.

How will such a diverse group respond to a disturbance? For instance, will ground spider diversity increase over time and will the species composition of the whole assemblage change in a deterministic (predictable) way, becoming more similar to the species composition of an undisturbed site? The questions we therefore ask in the present article are: (i) How does spider habitat for ground-dwelling spiders change over a successional coastal dune forest sere? (ii) How is the ground-dwelling spider community related to their habitat? (iii) Is there a successional development of spider assemblages (meaning is there some age-related community development independent of variation in microhabitat structure)?

Materials and methods

Site description

Spiders were sampled from three mined, rehabilitating sites with median ages of 2, 8, and 16 years, one unmined but disturbed site which is approximately 40 years old and an unmined, undisturbed coastal dune forest site (Sokhulu) in KwaZulu-Natal, South Africa (Fig. 7.1). The rehabilitating sites were established by Richards Bay Minerals

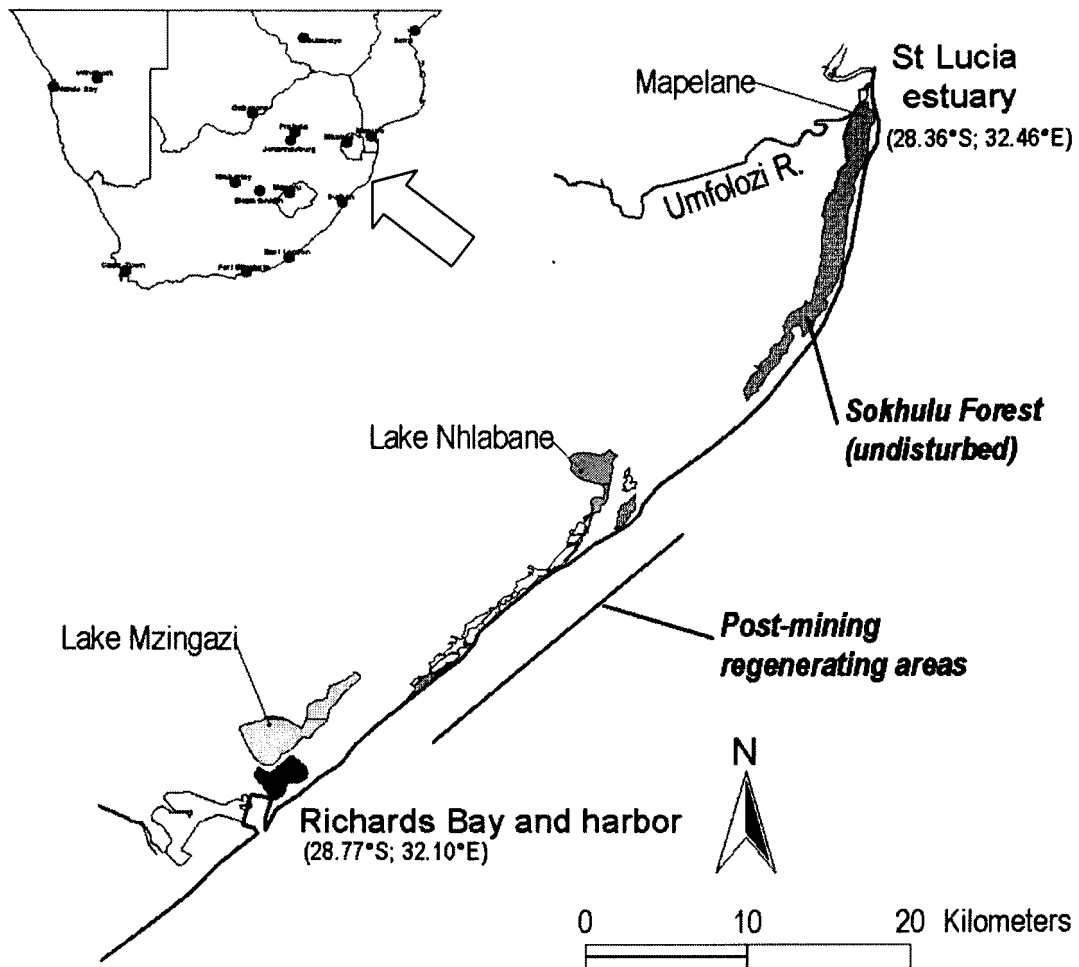


Figure 7.1. A map of the study area, showing the undisturbed Sokhulu Forest and the regenerating sites.

shortly after mining northeast of Richards Bay (Fig. 7.1). The area is situated at the southern end of the Maputaland centre of plant endemism (van Wyk, 1994).

Abiotic (topography, climate and soils) and biotic (vegetation) characteristics of both mined and unmined areas are described in Mentis and Ellery (1994), and van Aarde et al. (1996b). The rehabilitating sites (in total ~450 ha) are arranged in a narrow strip (≤ 2 km wide) on the second and third dune ranges from the coast. They are bordered either by bare sand dunes where mining is taking place, by unmined forest (a thin strip on the seaward side of the rehabilitating areas), by commercial plantations of beefwood (*Casuarina equisetifolia*), rural dwellings and crops, as well as highly disturbed and scrubby areas dominated by exotic invasive plants. The two unmined forest sites are situated about 5 km (40-year old site) and 20 km (Sokhulu) northeast of the rehabilitating sites. The ~500 ha Sokhulu site is contiguous with the Mapelane Coastal Dune Forest Nature Reserve (~1500 ha) (Fig. 7.1).

Trapping

The spider assemblages were sampled with pitfall traps consisting of clear plastic containers (10 cm diam, 12 cm height), which were placed in the ground flush with the soil surface. A funnel was placed over the opening leading to a smaller plastic bottle containing a mixture of 7 parts 96% ethanol, 1 part glycerol and 2 parts water (to a depth of 5 cm). Gurdebeke and Maelfait (2002) considered this funnel type of pitfall trap to be superior to other designs. A polystyrene cover (5 cm from the soil surface) protected each trap from rain and falling debris. Pitfall trapping records species density activity (Bultmann et al., 1982) and is considered a biased sampling method (Lang, 2000; Bonte et al., 2003; Wagner et al., 2003). Nevertheless, it remains the least labor-

intensive method and is reasonably effective as long as trapping is done over a sufficiently long period (Riecken, 1999).

Five grids consisting of nine traps each (in a 3 x 3 pattern with traps 5 m apart) were randomly located in each site, giving a total of 225 traps over the whole area. Sampling took place in four trapping sessions: August 1996, December 1996, February 1997 and May 1997. Each session lasted five days, at the end of which trap contents were collected and the traps closed. Contents were first sorted under a dissection microscope after which spiders were identified to species level wherever possible, or assigned to morphospecies where not. No differentiation was made between adult and immature, or between male and female specimens. Voucher specimens are stored in the National Collection of Arachnology (NCA) at the ARC-Plant Protection Research Institute in Pretoria, South Africa. A checklist of species recorded is available in Dippenaar-Schoeman and Wassenaar (2002)

Habitat variables

We recorded 13 presumed microhabitat variables at five points on each grid during the second trapping session (December, 1996) (Table 7.1). A 1-m² quadrat was placed in the middle and on each of the four corners of the grid. This quadrat was used to estimate vegetation ground cover (%) in three height classes, as well as the biomass/volume (a type of importance value [IV_{al}]) of different vegetation growth form classes per quadrat. All litter in a 20 x 20 cm area in the middle of each quadrat was collected in a paper bag and later dried at 60°C for 48 hours in a drying oven. The contents of the five litter samples from each grid were pooled before weighing on a DB600 Digital Balance (Clover Scales Pty Ltd, Northriding, Johannesburg).

Table 7.1. Habitat variables recorded at each sampling grid. Acronyms in parentheses refer to the habitat variable codes used in the CCA diagram (see Fig. 7.2).

Variable	Description
Vegetation growth form-specific IVal (8 variables)	Estimate (on scale of 1 - 10) of the biomass/volume (\approx an importance value), within a 1.5 m ³ volume above the quadrat, of each of the following vegetation growth form classes: woody plants not part of the canopy (IVwood), scandent shrub (IVscandshrub), erect forb (IVforb), decumbent herb (IVdecherb), woody herb (IVwoodherb), fern (IVfern), vine (IVvine), and graminoid (IVgrass)
Litter weight (2 variables)	Dry weight of: small litter particles: <5 cm length and/or <2 cm diameter (LWs) and large litter particles: \geq 5 cm length and/or \geq 2 cm diameter (LWI)
Ground cover (3 variables)	Estimated percentage vegetation ground cover in three height classes: <10 cm (GC10), 10-50 cm (GC50), and 50-100 cm (GC100)

Community structural variables

We used the following diversity and composition variables as community macro structure parameters: (i) average abundance (average number of individuals per grid over the four trapping sessions), (ii) species richness (number of species recorded per grid over four trapping sessions), (iii) Shannon diversity ($H = -\sum_{i=1}^q p_i \log p_i$, where q = number of species and p_i is the proportion of species i), (iv) Evenness (the E_{var} measure of Smith and Wilson (1996) which is insensitive to richness), and (v) Bray-Curtis distance, the Bray-Curtis dis-similarity of each sampling grid with all Sokhulu sampling grids. Bray-Curtis distance is calculated as $1 - 2W/(A+B)$, where W is the sum of the minimum abundances of the various species in two samples, and A and B are the sums of the abundances of species in each of the two sites respectively. For each trapping session, the contents of the nine traps in each grid were pooled and considered as one sample.

Numerical analysis

Statistical analyses were performed using STATISTICA (Statsoft 2001), and CANOCO (ter Braak and Smilauer, 2002). We used Kruskal-Wallis tests and Dunn's multiple comparisons (Sokal and Rohlf, 1995) to test for differences between sites in those habitat variables where variances were heterogeneous even after \log_{10} transformation (see Table 7.2). For the other habitat variables and all community structure variables (which were all homogeneous either before or after log transformation), we used one-way ANOVA with Tukey's multiple comparisons to test for differences between sites.

We also correlated the habitat variables (and abundance), and community structural variables with site age, using Spearman rank and Pearson's correlations respectively.

We tested for a relationship between spider community structure and their habitat using forward stepwise multiple linear regression ($F = 2.0$ to enter, $F = 1.9$ to remove) on each of the five community structure variables separately. However, the responses of individual species are arguably more important and meaningful than overall community variables. We therefore also investigated the relationship of spider species with their habitat with canonical correspondence analysis (CCA- ter Braak, 1986). This technique identifies the linear combination of explanatory (habitat) variables that maximizes the dispersion of species scores on several canonical axes. We performed CCA with CANOCO, which includes a forward selection Monte-Carlo test for the significance of habitat variables in determining the dispersion of species or sites along two (or more) ordination axes (ter Braak and Smilauer, 2002).

The program allows many permutations of samples, species and habitat variables to be included. We used species-conditional biplot scaling, which arranges species in a sample space, so that each species is located at the centroid of all the plots in which it occurs. Habitat variables may further be included as supplementary or as a covariable. Including it as a supplementary variable means that it is not assessed for its contribution to the variance during the analysis, but is plotted together with the rest of the variables to illustrate its main direction of influence. When a variable is included as a covariable, the program first regresses each habitat variable on the covariable and then performs the ordination on the residuals (a type of partial correlation, holding the covariable constant). We did both these types of ordination, first including site age as a supplementary variable, and secondly as a covariable. If successional developmental patterns are strong and deterministic, holding site age constant in this way should

account for all the variability in the species-habitat associations. In both ordinations we log-transformed species abundances prior to analysis, but did not down-weight rare species further.

Results

Habitat

The importance values (IV_{al}) of erect forbs, decumbent herbs, woody herbs, ferns and graminoid plants all differed significantly across sites, as did the weight of litter particles (small and large) and vegetation cover below 10 cm and 100 cm (Table 7.2). Generally, these differences were most often between, rather than within, the three regenerating and the two unmined forest sites (Table 7.2). In particular, in the three rehabilitation sites the highest percentage vegetation cover was below 10 cm, while in the two older unmined forest sites, this layer had the least plant cover (although only the oldest rehabilitating site differed from the rest) (Table 7.2). In both unmined forest sites the percentage ground cover 10-50 cm and more than 50 cm high were roughly equal, while in the group of rehabilitating sites percentage ground cover decreased with height above the ground (Table 7.2). The IV_{al}'s for erect forb, woody herb and graminoid plants were also relatively similar within each group of sites, but not across groups (Table 7.2). The undisturbed Sokhulu forest differed from the rest in the weight of small and large litter particles (Table 7.2). Six of the habitat variables correlated significantly with site age. The importance value of woody herbs, vines, the weight of small and large litter particles and vegetation ground cover 50 – 100 cm increased significantly in older sites, while vegetation cover below 10 cm decreased (Table 7.2).

Table 7.2. Habitat structure (mean \pm SD) for ground dwelling spiders in three mined rehabilitating (R) sites and two unmined forest (F) sites, one of which (Sokhulu) is undisturbed. Sites are identified on the basis of their post-disturbance age. Habitat variables are explained in Table 1. Each variable is followed by the results of Kruskal-Wallis (H) and ANOVA (F) tests between sites. Weight of large litter particles was log-transformed before analysis. The results of post-hoc comparisons are denoted as superscript letters; means with different superscript letters are significantly different. Correlation is the strength and significance of the Spearman rank correlation between site age and each habitat variable.

Variable	Site					Correlation
	2 year (R)	8 year (R)	16 year (R)	~40 year (F)	Sokhulu (F)	
(a) Vegetation growth form (mean importance values for vegetation in eight growth form classes)						
Woody plant F = 2.6; P = 0.07	3.8 \pm 2.72	0.44 \pm 0.59	1.84 \pm 1.66	2.32 \pm 1.34	1.68 \pm 1.36	-0.01
Scandent shrub F = 2.7; P = 0.06	0	0	0.88 \pm 1.06	0.24 \pm 0.43	0.04 \pm 0.09	-0.23
Erect forb H = 11.8; P = 0.02	1.48 \pm 1.30 ^{ab}	0.24 \pm 0.17 ^{ab}	0.16 \pm 0.36 ^a	4.08 \pm 2.61 ^b	3.96 \pm 3.21 ^{ab}	0.35
Decumbent herb H = 16.5; P = 0.002	2.00 \pm 2.31 ^{ab}	1.12 \pm 1.03 ^{ab}	8.44 \pm 1.34 ^a	0.12 \pm 0.27 ^b	0.12 \pm 0.11 ^b	-0.37
Woody herb F = 3.8; P = 0.02 [‡]	0.04 \pm 0.09	0	0	1.76 \pm 1.19	2.36 \pm 2.67	0.68 ***
Fern F = 2.7; P = 0.06	0	1.00 \pm 1.3	0	1.04 \pm 1.01	0.08 \pm 0.11	0.21
Vine F = 1.8; P = 0.17	0.48 \pm 0.64	0.64 \pm 0.46	1.28 \pm 0.64	1.00 \pm 0.62	1.20 \pm 0.55	0.44 *
Graminoid H = 15.8; P = 0.003	1.00 \pm 2.13 ^{ab}	4.76 \pm 2.19 ^a	2.20 \pm 2.17 ^{ab}	0.08 \pm 0.11 ^b	0.24 \pm 0.54 ^b	-0.37
(b) Litter weight (mean mass in g)						
Small particles F = 11.4; P < 0.001	8.94 \pm 6.67 ^a	18.02 \pm 6.16 ^a	20.20 \pm 5.32 ^a	16.04 \pm 7.88 ^a	34.18 \pm 3.91 ^b	0.67 ***
Large particles F = 19.1; P < 0.001	9.60 \pm 3.34 ^{ac}	7.42 \pm 2.81 ^a	16.47 \pm 7.23 ^{cd}	21.21 \pm 5.70 ^d	52.92 \pm 19.25 ^e	0.82 ***
(c) Vegetation ground cover (estimated percentage vegetation cover in three height classes)						
0 - 10 cm H = 20.6; P < 0.001	43.20 \pm 16.77 ^{ab}	59.60 \pm 27.11 ^{ab}	86.00 \pm 7.75 ^a	13.60 \pm 5.90 ^b	12.80 \pm 4.15 ^b	-0.58 **
10 - 50 cm ns	32.00 \pm 13.19	26.40 \pm 26.51	50.00 \pm 3.16	40.80 \pm 7.16	40.80 \pm 9.23	0.22
50 - 100 cm H = 11.3; P = 0.02	28.00 \pm 27.13 ^{ab}	2.80 \pm 3.35 ^a	18.00 \pm 14.76 ^{ab}	44.80 \pm 17.92 ^b	38.40 \pm 8.41 ^{ab}	0.43 *

* P < 0.05; ** P < 0.01; *** P < 0.001

‡ Post-hoc tests did not show any significant differences

Community structure

A total of 834 spiders belonging to 25 families, 39 genera and 48 species were caught over the whole study period (see Dippenaar-Schoeman and Wassenaar, 2002). Family and species-specific differences between sites, and spider guilds and their ecological roles are described in Dippenaar-Schoeman and Wassenaar (2002). The sites differed significantly in average abundance, Shannon diversity, evenness, and Bray-Curtis distance (Table 7.3). Abundance and evenness mirrored each other: abundance increased from the 2-year old site to the 8-year old site, but declined after that, while evenness (and to an extent also Shannon diversity) declined to a minimum in the 8-year old site and thereafter increased significantly to reach a maximum in the two unmined sites (Table 7.3). Again, most of the significant differences were between the three rehabilitating and the two forest sites, rather than within (Table 7.3). Three variables correlated significantly with site age: abundance and Bray-Curtis distance decreased and evenness increased in older sites (Table 7.3).

Relationship of community structure with habitat structure

All community structure variables were significantly related to the habitat, with habitat variables explaining between 39% and 89% of the variation in community structure (Table 7.4). Overall, litter and vegetation cover were the most influential in determining community structure. Weight of small and large litter particles (LWs and LWI respectively) and the percentage vegetation cover <10 cm (GC10) were each significant in at least two community variables and were retained for the model in others (Table 7.4). These three habitat variables played a particularly large role in the three diversity measures (richness, Shannon and evenness) (Table 7.4). Abundance was also related to

Table 7.3. The structural variables of the spider communities of rehabilitating (R) and unmined forests (F). The Bray Curtis distance is the dis-similarity between each sampling grid and the sampling grids in the completely undisturbed Sokhulu Forest. Sites are identified on the basis of their post-disturbance age. Each variable is followed by the result of an ANOVA test for differences between sites. Abundance was log-transformed before analysis. The results of post-hoc comparisons are denoted as superscript letters; means with different superscript letters are significantly different. Correlation is the strength and significance of the Spearman rank correlation (for abundance) and Pearson's correlation (for the rest) between site age and each community variable.

Variable	Site					Correlation
	2 year (R)	8 year (R)	16 year (R)	~40 year (F)	Sokhulu (F)	
Abundance F = 34.94; P < 0.001	6.90 ±0.74 ^a	16.70 ±4.15 ^b	8.50 ±1.79 ^a	6.65 ±1.53 ^a	2.95 ±1.18 ^c	-0.57 **
Species richness F = 1.93; P = 0.14	8.00 ±3.67	6.60 ±2.30	5.00 ±1.00	7.40 ±2.51	4.60 ±1.52	-0.34
Shannon diversity F = 4.01; P = 0.02	1.31 ±0.77 ^{ab}	0.72 ±0.39 ^a	0.65 ±0.28 ^a	1.56 ±0.27 ^b	1.09 ±0.19 ^{ab}	0.11
Evenness F = 11.67; P < 0.001	0.52 ±0.20 ^{ac}	0.29 ±0.06 ^b	0.33 ±0.07 ^{ab}	0.63 ±0.08 ^c	0.65 ±0.07 ^c	0.48 *
Bray-Curtis F = 41.13; P < 0.001	0.84 ±0.04 ^a	0.77 ±0.08 ^{ab}	0.75 ±0.06 ^{ab}	0.66 ±0.06 ^b	0.42 ±0.04 ^c	-0.87 **

* P < 0.05; ** P < 0.01

Table 7.4. Forward stepwise multiple regression ($F = 2.0$ to enter, $F = 1.9$ to remove) results for the relationship between spider habitat variables and five spider community structural variables (the response variables). Community variables are each followed by their respective F-tests for the overall regression, the final model and the proportion of variation accounted for by the model (R^2). Codes for the habitat variables (in square brackets) are explained in Table 1. Significant habitat variables ($P < 0.05$) are in bold.

Response variable	Model	R²
Abundance $F_{3,21} = 13.6; P < 0.001$	$y = 11.50 + 1.16[\mathbf{IVgrass}] - 0.10[\mathbf{LWI}] - 0.08[\mathbf{GC50}]$	0.66
Species richness $F_{2,22} = 6.9; P = 0.004$	$y = 10.42 - 0.16[\mathbf{LWs}] - 0.02[\mathbf{GC10}]$	0.39
Shannon diversity $F_{2,22} = 8.9; P = 0.001$	$y = 2.0 - 0.01[\mathbf{GC10}] - 0.03[\mathbf{LWs}]$	0.45
Evenness $F_{2,22} = 12.5; P < 0.001$	$y = 0.55 - 0.004[\mathbf{GC10}] + 0.003[\mathbf{GC50}]$	0.53
Bray-Curtis $F_{5,19} = 30.8; P < 0.001$	$y = 0.97 - 0.003[\mathbf{LWI}] - 0.03[\mathbf{IVherb}] - 0.007[\mathbf{LWs}] - 0.01[\mathbf{IVgrass}] - 0.02[\mathbf{IVwherb}]$	0.85

the amount of grass (IVgrass) and vegetation cover 10-50 cm (GC50), while Bray-Curtis distance was related to the amount of herb (IVherb), grass (IVgrass) and woody herb (IVwherb) material present (Table 7.4), over and above their relationship with litter weight.

The first CCA diagram (Fig. 7.2a) shows the results of a CCA performed using site age as a supplementary variable. Only the significant variables ($P < 0.05$), and weight of large litter particles (LW1) ($P = 0.06$) are illustrated (Table 7.5). The clear gradient on the first axis ($\lambda = 0.65$) was mostly related to LW1, and on the second axis ($\lambda = 0.47$) to vegetation cover <10 cm (GC10). Together the first two axes explained 25% of the variance in the species data, and 40% of the variance in the species-environment relationship (Table 7.6). The direction of the site age gradient suggests that it was associated with changes in both litter weight (LW1 and LWs) and GC10 (see Table 7.2), but all three of these variables changed in other directions as well (Fig. 7.2a), to the point that the variance associated with GC10 was almost orthogonal to the site age effect (Fig. 7.2a). The GC10 gradient clearly separates out the species of rehabilitating wooded sites (the 8- and 16-year old rehabilitating sites with high vegetation cover) from those of the two unmined sites (with low cover) (Fig. 7.2a). Species of the youngest scrubby grassland sites were intermediate on this gradient and hence not associated with changes in vegetation cover. The LWs gradient distinguished between the species from the earliest grassland sites (low litter values) and all wooded sites (high values), while LW1 separated the species from the older unmined sites (high litter values) from the rehabilitating wooded sites (8- and 16-year old sites with low litter values) (Fig. 7.2a). Species from the grassland sites were again intermediate on the LW1 gradient.

Table 7.5. Results of a forward selection procedure in CCA, using Monte Carlo permutations (500) to test for the relationship of habitat variables with spider species. CCA was first performed with site age included as a composite habitat variable and then with site age held constant as a covariable, in which case the relationship is between spider species and the residuals of habitat variables regressed on site age. Only significant habitat variables are shown.

Habitat variable	Marginal effect	Conditional effect	
	λ	Extra fit	P
<i>Site age = supplementary variable</i>			
GC10	0.48	0.36	0.002
LWs	0.34	0.33	0.004
LWI	0.42	0.25	0.06
<i>Site age = covariable</i>			
GC10	0.36	0.36	0.002
LWI	0.25	0.24	0.04
LWs	0.24	0.24	0.03

Table 7.6. Summary of a canonical correspondence analysis (CCA) on spider communities and their habitat in post-disturbance regenerating and undisturbed coastal dune forest. CCA was first performed with site age included as a composite habitat variable and then with site age held constant as a covariable, in which case the relationship is between spider species and the residuals of habitat variables regressed on site age. The cumulative percentage variance of the species environment relationship is the variance explained after fitting species to the habitat variables.

	Axes				Total inertia	Sum of eigenvalues
	1	2	3	4		
Site age = supplementary variable						
Eigenvalue	0.67	0.47	0.34	0.31	4.52	
Cumulative % variance of species data explained	14.4	24.7	32.3	38.8		4.52
Cumulative % variance of species-environment relationship explained	23.5	40.4	52.8	63.5		2.77 *
Site age = covariable						
Eigenvalue	0.48	0.37	0.37	0.26	4.52	
Cumulative % variance of species data explained	12.3	21.6	31	37.7		3.94
Cumulative % variance of species-environment relationship explained	20	35.2	50.4	61.3		2.42 *

* Sum of canonical eigenvalues

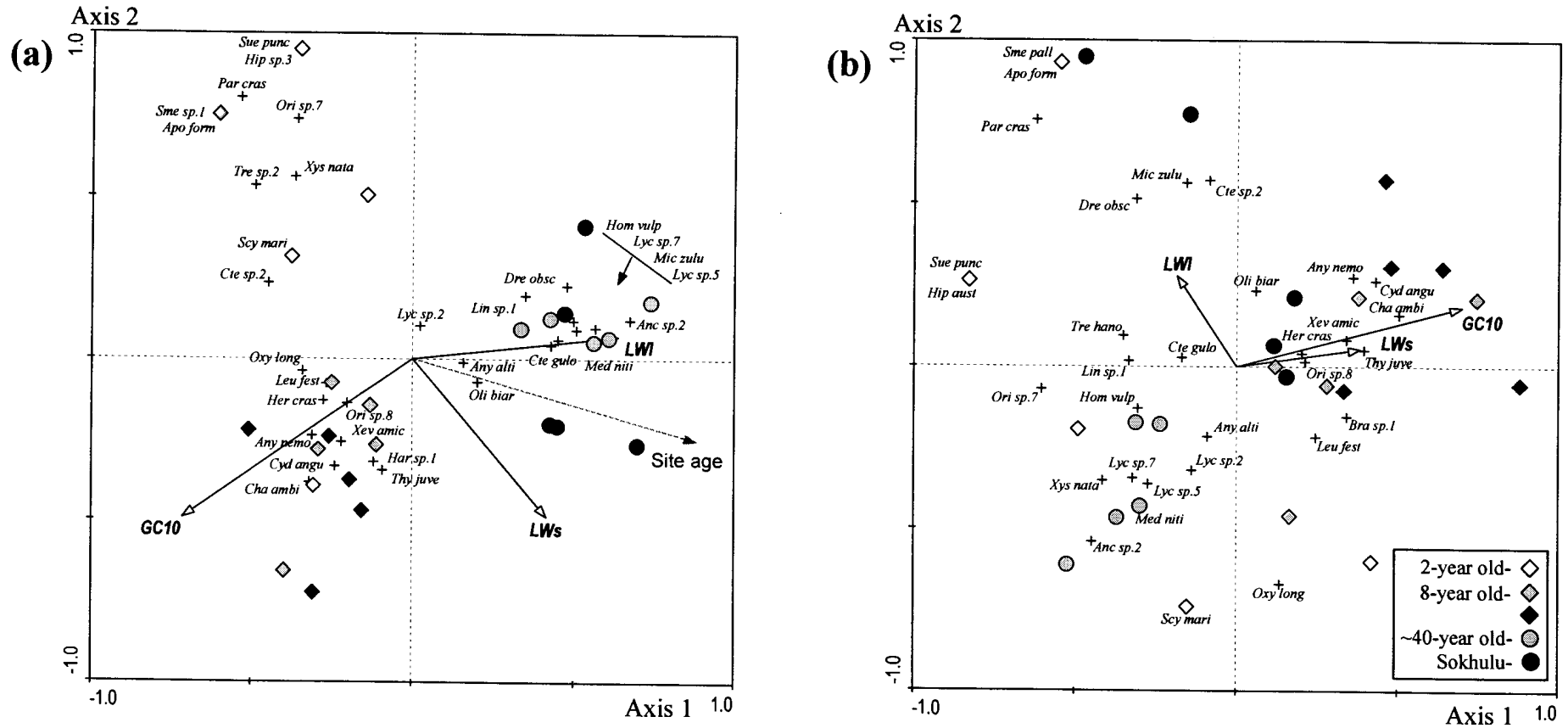


Figure 7.2. Figure legend on next page

Figure 7.2. A species-conditional Canonical Correspondence Analysis (CCA) diagram of the relationship between ground-dwelling spiders and the principal variables that describe their habitat. Only significant habitat variables ($P < 0.05$, Monte Carlo forward selection permutation test) and in (a) the marginally non-significant LWI ($P = 0.06$), and species recorded more than once are shown. Diamonds and circles represent the different sampling grids in the five sites and crosses represent species. In (a), site age was treated as a supplementary habitat variable. Here the two axes explain 25% of the total variance in the dataset and 40% of the species-environment relationship. The eigenvalue for axis 1 (horizontal) is 0.67 and for axis 2 (vertical) 0.47. In (b), site age was included as covariable (i.e. the relationship between spider species and their habitat after correcting for site age). Here the two axes explain 22% of the remaining variance (after correcting for site age), and 35% of the remaining species-environment relationship. The eigenvalues are 0.48 and 0.37 for axis 1 and 2 respectively. Codes for habitat variables are explained in Table 7.1 and species codes are as follows: Apo form: *Apochinomma formicaeforme*; Med niti: *Medmassa nitida*; Cte gulo: *Ctenus gulosus*; Cte sp.2: *Ctenus* sp.2; Anc sp.2: *Ancylotrypa zuluensis*; Hom vulp: *Homostola vulpecula*; Dre obsc: *Dresserus obscurus*; Tre hano: *Trephopoda hanoveria*; Lin sp.1: Linyphiidae sp.1; Lyc sp.2: *Lycosa* sp.2; Hip aust: *Hippasa australis*; Par cras: *Pardosa crassipalpis*; Lyc sp.5: Lycosidae sp.5; Lyc sp.7: Lycosidae sp.7; Ori sp.8: *Orinocosa cf trochosa*; Ori sp.7: *Orinocosa* sp.7; Mic zulu: *Microstigmata zuluense*; Oxy long: *Oxyopes longispinosus*; Sue punc: *Suemus punctatus*; Sme pall: *Smeringopus pallidus*; Xev amic: *Xevioso amica*; Cha ambi: *Charminus ambiguus*; Thy juve: *Thyenula juvenca*; Scy mari: *Scytodes maritima*; Any alti: *Anyphops alticolus*; Any nemo: *Anyphops nemorensis*; Oli biar: *Olios biarmatus*; Leu fest: *Leucauge festiva*; Bra sp.1: *Brachionopus robustus*; Her cras: *Heriaeus crassispinus*; Xys nata: *Xysticus natalensis*; Cyd angu: *Cydrela anguiculata*

A large amount of variation in species occurrence could not be explained by site age, as is evident from Fig. 7.2b. Here the effect of variance due to site age is partialled out resulting in a strong gradient related mostly due to vegetation cover on the first axis ($\lambda = 0.48$) and weight of large litter particles on the second axis ($\lambda = 0.37$). Species associated with high values of vegetation cover and weight of small litter particles tended to occur in the 8- and 16-year old rehabilitating sites (Fig. 7.2b). Together these two axes accounted for 21.6% of the variance in species data and 35.2% of the variance in the species-environment relationship. Sampling grids on the rehabilitating sites associated much more closely with the Sokhulu grids, and grassland sampling grids with the ~40-year old grids, than in the first CCA (Fig. 7.2).

Discussion

Evidently, the spider community of a coastal dune forest can recover its structure during post-disturbance vegetation succession. The strong correlation of changes in community species composition (Bray-Curtis distance between regenerating communities and an undisturbed forest) with site age suggests that over time forest species are sequentially added to the regenerating communities. Moreover, site age apparently summarizes the combined effect of changes in litter structure and vegetation cover over the successional sere. This is in agreement with a number of studies that have shown spider community composition changes related to vegetation succession (Duffey, 1968; Bultmann et al., 1982; Bonte et al., 2003). We also showed previously for the same study area that there is a dominance reversal in line with known family – habitat associations, with some lycosids dominating in the early post-disturbance stages and ctenids in the later stages (Dippenaar-Schoeman and Wassenaar, 2002). These are all hallmarks of deterministic successional change, leading to the conclusion that the effects of forest fragmentation on



spider communities may eventually be reversed. Such a clear and predictable successional trend is a comforting phenomenon, particularly where the outcome of a post-mining rehabilitation program is in question.

On the other hand, site age was not closely related to the individual species, as was evident from the amount of unexplained variation left after correcting for site age in a CCA. The first two axes still explained 35% of the variation in species-environment relationship, meaning that species variation was still strongly related to microhabitat variables beyond what can be summarized by site age. This suggests that proximate habitat factors control the spider community as a whole, rather than the composite “habitat” variable of site age (and notwithstanding the significant correlations of some of these habitat variables with site age). The patterns produced by both CCA ordinations imply that, from an individual spider’s point of view, the change in habitat is not a simple monotonic function of site age. It should perhaps rather be seen as three completely different habitats defined by the amount of litter and vegetation cover in each. A multiple regression analysis showed that even the more complex variables that measure community structure responded strongly to the litter and vegetation cover gradients, as well as to vegetation growth form. Spiders are sensitive to habitat complexity, litter depth and atmospheric and soil humidity (Bultmann et al., 1982; Bultmann and Uetz, 1982; Abraham, 1983; Downie et al., 1999; New, 1999; Bonte et al., 2002; Whitmore et al., 2002) and here we essentially confirm these results.

However, our results also suggest that this critical dependency of spider species to their habitat may disrupt successional patterns in the spider community. The link between spiders and fine-scale plant physiognomy is a mixture of direct (web-anchoring, shelter from predators) and indirect (prey availability linked to plants) effects (Whitmore et al., 2002). Some species need patches of dense and litter-rich vegetation for their

juvenile development and/or retreat during unfavorable periods in their mature life-stage (Uetz, 1979; Bonte et al., 2002). Although the predominance of wanderers in our study area (96%) (Dippenaar-Schoeman and Wassenaar, 2002) precluded a detailed analysis of spider guilds, these habitat characteristics will obviously differentiate between spiders that employ different hunting strategies (Uetz, 1979; Canard, 1990).

Spider community recovery may thus depend on more than macro vegetation successional patterns; it may be closely linked to restoration of microhabitat. The similarities between the ~40-year old forest site and the undisturbed forest in microhabitat and in spider species composition suggest that microhabitat on the mined sites may eventually develop in the right direction, given enough time. However, dune forest undergrowth may recover slower than the tree community, may end up in a different stable state and are apparently more sensitive to small-scale disturbances (Wassenaar and van Aarde, 2001). Clearly, described dune forest vegetation succession pathways (Weisser and Muller, 1983; Mentis and Ellery, 1994; van Aarde et al., 1996b; von Maltitz et al., 1996), are unlikely to guarantee the deterministic recovery of the arachnid community unless their microhabitat structure is recovered as well.

Some widespread species (such as the salticid *Thylenula juvenca* (Simon, 1902)) apparently colonize new sites as easily as old forest (Dippenaar-Schoeman and Wassenaar, 2002). However, the real conservation issue is about the recovery of populations of range restricted and rare species, as well as those taxa with strong habitat affinities (such as some of the lycosids and ctenids- Dippenaar-Schoeman and Wassenaar, 2002). These are the species most likely to be affected by fragmentation (see for instance Gibb and Hochuli, 2002) and for them it may not be good enough to establish macro-scale vegetation structure.



Our data show that fragmentation, and the consequent habitat loss, will have negative conservation implications for forest spiders if spider microhabitat structure is not restored during vegetation succession. Future research should consequently be directed at enumerating the change in microhabitat over a longer time scale, at establishing the relationships between particularly the rare and range-restricted forest species and their microhabitat structure, and at determining the need for management intervention (such as species re-introductions).

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Chapter 8

Synthesis

Introduction

What do the papers presented here (Chapters 4 to 7) imply? As a first approximation, I have to conclude that, notwithstanding some variability around the main patterns, and with one or two exceptions, rehabilitation is succeeding in restoring community structure, composition and function for a wide array of taxa. I say this because so many of the variables that I used to measure the recovery of community structure and function changed predictably across habitat regeneration age and over time. Moreover, some of the trajectories of change (Chapters 4 and 5) confirmed what could have been expected from successional theory: not only was there a consistent age-related increase in the number of climax (benchmark) species in a typical regenerating site, but community structure and composition converged on the benchmark. Inter-annual repeatability in most (83%) of the trajectories (Chapter 4) further suggest that changes over time on a particular patch of disturbed forest may be reliably repeated in other instances and on any other disturbed site.

Taken together, these results are hard to argue against and suggest that change in community structure and function is not a capricious interaction between the environment and contingent history. There must thus be some stabilizing factor that moderates and influences the direction of change. Such results are extremely attractive for a restoration ecologist, because it obviously implies that rehabilitation may have predictable endpoints. It should come as no surprise then that the deterministic concept of succession has been, implicitly and explicitly, the philosophical basis of a large part of

the previous research on RBM's rehabilitation of dune forests (Mentis & Ellery 1994, van Aarde *et al.* 1996, Van Dyk 1997, van Aarde *et al.* In press).

Traditionally, such stabilizing forces have been ascribed to species interactions (Holling 1973, Moulton & Pimm 1986, Lawton 1987, Terborgh *et al.* 1996). In this view of community structure, each species is assembled into the community according to its niche, chiseled out over millennia of adaptation to its environment and to the effects of historical competition with other species and modified by limitations placed on resource use by the effects of current competition (Hutchinson 1957). Niche-assembly theory has had a long, and often controversial, history in community ecology (Diamond 1975, Connor & Simberloff 1979, Simberloff & Connor 1981, Diamond & Gilpin 1982, Gilpin & Diamond 1982) and has contributed greatly to our understanding of how structure may evolve in assemblages of trophically equivalent species. However, in spite of its intuitive appeal, there has been little empirical support for the niche as an important driver of community structure (Cornell & Lawton 1992, Loreau 2000, Roxburgh & Wilson 2000, Watkins & Wilson 2003). Most importantly, it remains difficult to reliably detect species interactions from patterns alone (Bell 2001).

Nevertheless, aside from all the arguments, the utility of niche-based models as a predictive framework for research and application, beyond a *post hoc* interpretation of suggestive patterns, will be limited because so much species-specific information is needed. In short, although it will be difficult to completely exclude it as an important mechanism, the weight of evidence is firmly against the niche and it would be wrong to use it as the philosophical basis for the analysis of dune forest regeneration patterns.

However, this begs the question: if niche-based community organization is rare in nature and in any case difficult to detect, how can we explain the deterministic regeneration patterns of assemblages from the coastal dune forests of my study area?

Indeed, on what alternative theoretical grounds should we then evaluate the rate and direction of regeneration? The last two papers in this thesis (Chapters 6 and 7) are important clues that change in community structure may be controlled on both a larger and smaller scale than predicted by niche-based theories. Perhaps the two most important findings from the present study are therefore that mean regional abundance, a macro-ecological characteristic, is highly correlated with the order and timing of colonization and with founder abundance for three disparate taxa (Chapter 6), and that the effects of microhabitat structure in a typical invertebrate group, the spiders, overshadow (or simply masks) successional development in community structure (Chapter 7).

The patterns I described in Chapters 4 and 5 are undoubtedly important in their own right, because they suggest that rehabilitation can lead to community recovery, irrespective of particular mechanisms. However, results from Chapters 6 and 7 hold many implications for how we should view ecological restoration, for the questions that we should be asking, and for how we should manage rehabilitation. The analysis of regeneration patterns on these regenerating dune forests has so far probably been too heuristic. The absence of a theoretical model of community regeneration to underpin research means that even though most trajectories appear to be stable over time and in the direction of the benchmark, even major changes in the trajectories are possible, but will remain unpredictable. Equally important, however, a theoretical model supported by empirical results will be able to guide management decisions more effectively. In the following section, I will describe a conceptual model that I propose as a basis for developing a theoretical model of community regeneration. The mechanics of the model means that it can serve as a type of null model against which other types of post-disturbance community changes may be compared. It is closer to how a plant community will regenerate, but the overall principles may be more widely applicable.

A conceptual model for post-disturbance regeneration

Earlier, I contrasted an “inside-out” with an “outside-in” view of the development of structure. To begin with, it is fitting to consider the differences between these two views. Fig. 8.1 is a simple illustration of succession on a patch released from disturbance. Here successional, niche-assembly processes dictate a predetermined sequence of colonization by species to produce a directional change in species composition (Glenn-Lewin *et al.* 1992). The “force” that drives directional changes in species composition is internal to the successional patch, in such a way that species composition moves from pioneer, through mid-successional stages to the only persistent stage, the climax. Importantly, the colonizing species are only implicitly present in the environment as part of an undefined regional species pool. The successional process is therefore essentially uncoupled from the landscape. This basic concept has been qualitatively adapted to a degree by acknowledging that pioneer species constantly require the presence of newly disturbed patches where they can survive (see Rees *et al.* 2001). However, no matter how many individuals of a species arrive at a regenerating patch, or from where they arrive, if it is not their allotted time to colonize, they are not allowed to colonize (Glenn-Lewin & van der Maarel 1992).

Contrast this with Fig. 8.2 where landscape-related factors are integral to both the rate of change and the endpoint for any given patch. In Fig. 8.2, two situations are illustrated. In Box A, the focal ecosystem (i.e. the undisturbed or “climax” ecosystem), in solid grey, and the stippled grey disturbed surroundings form the two major habitats. Apart from the disturbed landscape, smaller disturbed patches (*a-c*) can also occur within the larger focal system. Some factors, principally disturbance, prevent colonization (Glenn-Lewin & van der Maarel 1992) and hence prevent changes in species composition on such a disturbed patch. Therefore, when the disturbance agent is

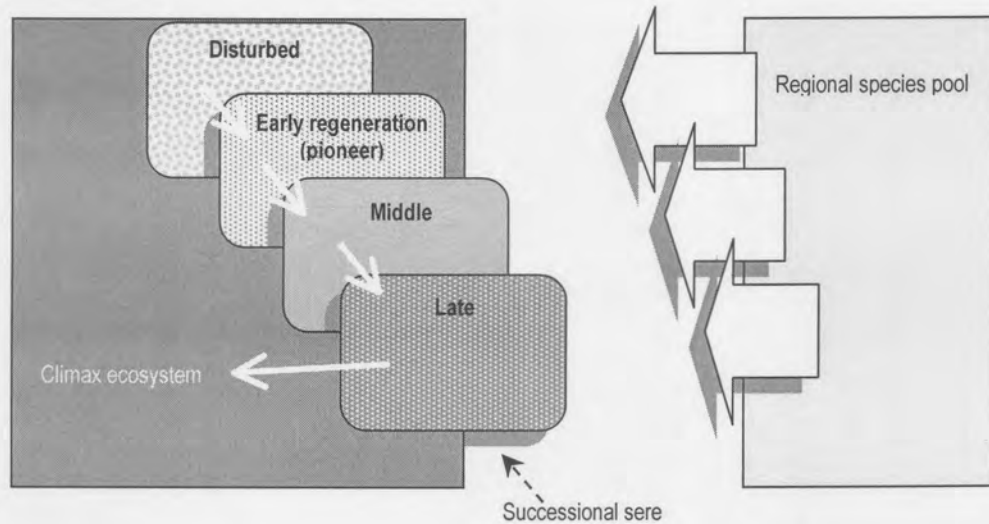


Figure 8.1. A graphic model of ecological succession. Here a climax ecosystem is disturbed, followed by succession in the disturbed area. Changes from early (“pioneer”) communities, through mid- and late-successional stages to the inevitable “climax” endpoint occur primarily through facilitation. Species adapted to early, middle, late and climax stages colonize when conditions are suitable, dispersing from an undefined regional species pool. The successional process is thus essentially uncoupled from the landscape, with dispersal and colonization only implied or qualitatively incorporated.

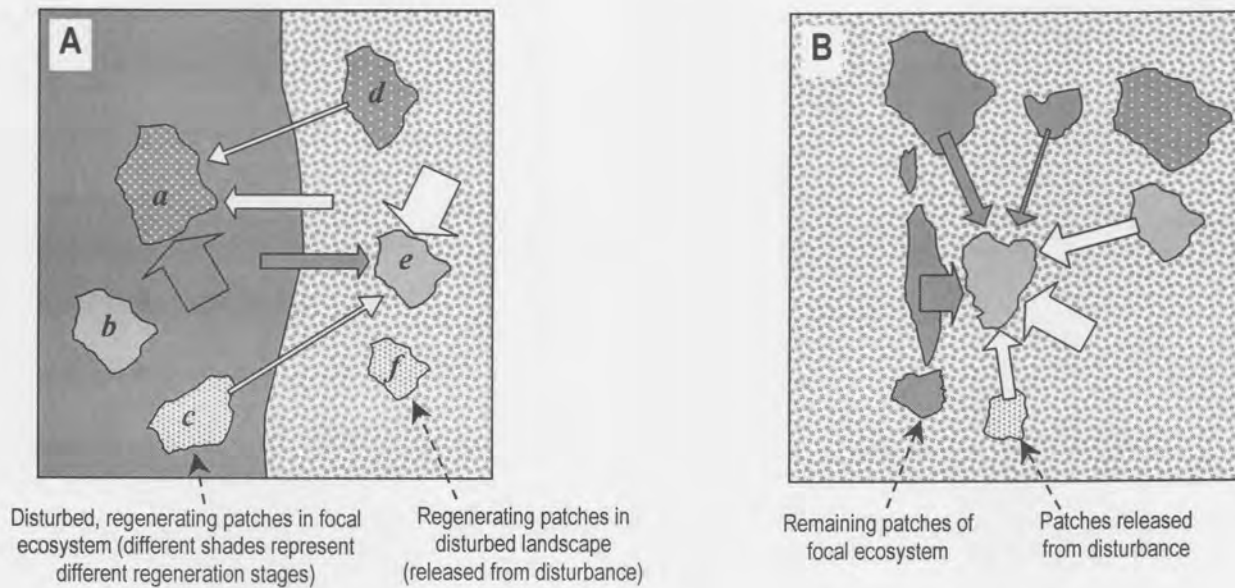


Figure 8.2. A graphic model of ecosystem disturbance and regeneration. In **Box A**, the undisturbed or “climax” (focal) ecosystem in solid grey and the disturbed surroundings form the two major habitats. Apart from the disturbed landscape, smaller disturbed patches (*a-c*) can also occur within the larger focal system. Provided the initial disturbance is removed, a patch (here represented by patches *a-b* and *d-f*) will undergo change in species composition because of colonization by species from other patches. Immigration can potentially occur from any patch in any stage of regeneration or stasis (white and grey arrows), but the two dominant habitats will dictate the outcome of most colonization events (the two thick arrows), because they are in such close proximity to all regenerating patches. The situation described in **Box B** is a more general form of Box A. The focal system is now reduced to patches of the same size as all other disturbed patches in the environment, so that not only the proximity of source areas, but also their relative sizes play a role in colonization rate for any particular regenerating patch.

removed, species composition in a particular patch changes over time, as in patches *a-b* and *d-f*. Immigration is primarily a function of dispersal, so that the structure of the landscape now plays a crucial role in the direction of species composition changes. Dispersal can potentially occur from any patch in any stage of regeneration or stasis, but the two dominant habitats will dictate the outcome of most immigration events (the two thick arrows in Fig. 8.2), because they are in such close proximity to all regenerating patches. For instance, the endstage species composition in patches *a-c* will be biased to be more similar to the focal ecosystem than to any other habitat, because of the overwhelming number of species colonizing from there. In patches *d-f*, species from the disturbed landscape itself will be more likely to colonize, but because the landscape is being disturbed and is also species poor, the net result will still be colonization from the focal system, albeit slower than in patches *a-c*.

The situation described in Box B of Fig. 8.2 is a more general form of Box A. The focal system is now reduced to patches of the same order of magnitude as all other disturbed patches in the environment, so that not only the proximity of source areas (McLachlan & Bazely 2003), but also their relative sizes play a role in colonization rate for any particular regenerating patch. The landscape effect is illustrated by the different-sized arrows leading to a patch. This model of post-disturbance regeneration posits that the bias in endstage species composition will be dependent on the composition of the propagule rain arriving at a given patch, which is a function of the species composition in and physical arrangement of habitats in the landscape (Dalling *et al.* 2002). The crucial influence of invasion rate (i.e. the number of arriving propagules) in determining colonization success and the identity of the eventual persistent state has been shown in many studies (Williamson 1996, Williamson & Fitter 1996, Lockwood 1997, Lockwood *et al.* 1997, Kolar & Lodge 2001, Hewitt & Huxel 2002, Brown & Fridley 2003,

Schreiber & Rittenhouse In Press, Chapter 6 this thesis). The mean and variance of the probability of colonization for a species will thus be a function of the mean and variance of its abundance in all patches in the landscape (Hubbell 2001, Boughton & Malvadkar 2002, Hewitt & Kellman 2002, Chapter 6). Similarly to succession, species composition change is inevitable if the disturbance is removed, but crucially, the reason is different: the driving force for change (dispersal and colonization) is now external to the successional patch. The decades-old concept of initial floristics in vegetation succession already foresaw the importance of dispersal and colonization in determining the subsequent direction of development (Glenn-Lewin & van der Maarel 1992, see also Finegan 1996 for a recent example). However, although some metacommunity effect (the “neighbouring sites”) has always been recognized (see for instance DeSteven 1991, Augustin *et al.* 2001), these were always seen as important, but never as the controlling factors (but see Maina & Howe 2000).

Fig. 8.2 clearly illustrates the central assumption of this model – that dispersal and colonization is inevitable and will relentlessly cause a change in species composition as soon as a patch is released from disturbance. Concurrently, only continued disturbance can prevent compositional change. However, there is a limitation on the number of individuals that can occur on a given patch (what Hubbell [2001] calls the “zero-sum game”, see also Brown *et al.* 2001a,b, Gómez de Silva & Medellín 2002), so that we can also assume that as a regenerating patch gradually “fills up” with individuals, overall colonization rate will decrease. Change in species composition will thus decrease as the total colonization rate decreases and when this change approaches zero, something that we can call a persistent state will be reached. Regionally abundant species will have a finite but low probability of extinction, both because its local abundance will tend to be high, leading to long average times to stochastic extinction (Hubbell 2001), and because

it will continuously be rescued (Gotelli 1991, Hanski 1999). Species change will thus never be zero, but without further disturbances, it may hover close to zero.

However, it is important to note that from this point of view a persistent state is a relative concept. As long as change in species composition on a particular patch is lower than in the regenerating state, the species composition here will act as a type of attracting state (Grover & Lawton 1994) for the regenerating system because it will be able to contribute most to the propagule rain. The most important prediction from this conceptual model is therefore that regionally there will be an equilibration to the species composition of the (largest) patch undergoing the least change in composition. The larger the total area of this habitat type and the less change it undergoes, the faster species composition on a disturbed patch will converge to it. This has been my primary aim in designing a conceptual model of community regeneration: to be able to explain convergent patterns such as those I (we) have found in Chapters 4 and 5, without falling back on the analytically intractable concept of the niche. Although difficulty of use is hardly a good enough reason to abandon a particular mechanism, I am convinced from my data and from personal observations that resilience is primarily (I would like to say almost exclusively) a function of dispersal and colonization from the metacommunity.

This model is firmly based on a neutral community model (Bell 2001). It is neutral because all species have identical per capita probabilities of colonizing and going extinct, modified by their abundance in the metacommunity, and because they obey the rules of the “zero-sum game”. However, it is unlikely that a completely neutral model can capture all typical regeneration patterns. For instance, a recovery of the species composition of the focal system implies that any non-focal system species must go locally extinct during the time it takes for a representative number of focal system species to colonize, otherwise a persistent state other than the focal system may be

reached too quickly and too often. There must therefore be some factor that can increase the probability of extinction for non-focal species much sooner than for focal system species, because they don't universally colonize a newly disturbed site sooner than focal species do (see Chapter 6). Moreover, results from Chapter 4 (dung beetles and millipedes) and Chapter 7 (spiders) indicated that colonization in some groups might be critically dependent on habitat suitability on such a fine scale that the effects of the metacommunity may be impossible to measure.

This deviation from neutrality stems from two factors. First is the observation that late-successional and forest specialist species are more likely to increase than to decrease after colonization (Fig. 6.4). This is contrary to one of the central assumptions of Hubbell's (2001) neutral theory, namely that all species are equally likely to decrease or increase in abundance (i.e. they undergo a random walk in densities). Second is the fact that pioneer species occupy an ephemeral habitat that is quite different from the persistent state. One of the main shortcomings of neutral community models is indeed that they cannot account for dynamics across habitats (Bell 2001, Hubbell 2001).

In a successional sequence, the per capita probability of colonization is therefore probably not equal across species, but influenced by species-specific autecological tradeoffs. It can also be argued that neutral community models are unlikely to apply to invertebrates in any case, because invertebrate communities are seldom "filled" in the sense implied by Hubbell (2001) for closed-canopy forest trees (see for instance Lawton & Hassell 1981, Mouillot *et al.* 2003). However, it should be possible to include this successional gradient into a working neutral model, since its real effect will equate to a temporal modification of colonization and extinction probabilities. It will be an interesting exercise to determine whether species-specific adaptations and facilitation-

inhibition over the successional sequence overwhelms the effects of the metacommunity, and if so, whether such an influence is relaxed under particular circumstances.

In summary, I feel that the conceptual model I proposed here is enough to qualitatively explain the deterministic return to equilibrium, which I have shown for several assemblages at Richards Bay, without invoking problematic niche mechanisms. It does not deny the presence of competition, or the relevance of priority effects for determining species composition locally (Ward & Thornton 2000). Competition may for instance be very important in stable communities (Moulton & Pimm 1986). Neither does it deny the negative effect that environmental constraints can place on colonization (see for instance Ejrnæs *et al.* 2003, Fernandez-Illescas & Rodriguez-Iturbeg 2003, McLachlan & Bazely 2003). But it does predict that on a metacommunity scale, the probabilistic nature of dispersal, colonization and extinction will decrease their importance (perhaps to a greater and smaller extent in different habitat or ecotypes).

Invertebrates may or may not fit into this picture all that well. For example, regional abundance may determine colonization success to some extent in millipedes (Chapter 6), but on the other hand, dung beetles showed a very atypical return trajectory (Chapter 5, Fig. 5.5). In spiders, the sequence and rate of colonization may theoretically still be influenced by the regional abundance of a species, while habitat suitability only acts as a type of filter. On the other hand, it is also entirely possible that a different set of colonization and assembly rules pertain to invertebrates and that the model is more applicable to larger organisms.

The model's potential utility for restoration is that it predicts that variables that have the largest influence on colonization and extinction probabilities will have the largest influence on rehabilitation success and will thus in general be the most effective for management manipulation (Bradshaw 2000, Ellison 2000, Puyravaud 2003). It also

means that benchmark source areas must be protected from disturbance; otherwise colonization from there will be reduced. To be really of any theoretical and practical utility, it of course has to be developed mathematically, but it does make a number of testable predictions that can serve to guide future research. In the next section, I will summarize what I believe are the most important predictions.

Future research

The presumed overwhelming importance of dispersal and colonization as drivers of species composition change means that whatever constrains or misdirects dispersal will play a crucial role in preventing recovery of a particular combination of species. For instance, many plant species are dispersal-limited (Hubbell *et al.* 1999, Ehrlén & Eriksson 2000, Verheyen & Hermy 2001), so that their colonization probability may be close to zero even though there are significant source populations in the landscape. Dispersal constraint is an important aspect of some diversity theories (see for instance Hurtt & Pacala 1995 and references therein, Hubbell 2001) and will be just as important in regeneration dynamics (Hubbell *et al.* 1999, Dalling *et al.* 2002, Wang & Smith 2002). Related to this, but applicable across all groups, the average distance between source areas and a regenerating patch will be of crucial importance.

Indeed, the model predicts a large effect of landscape structure, because the spatial arrangement of patches in relation to each other will ultimately determine from which patch most colonization will occur (see for instance Augustin *et al.* 2001, Berggren *et al.* 2001, de Blois *et al.* 2002, Vellend 2003). Colonization probabilities in general will probably decrease exponentially with distance away from a benchmark source area, and the critical distance where it is too low to ensure regeneration in a rehabilitating patch,

will be a function of the community's (as opposed to a species') dispersal kernel, as well as the landscape structure (see Dupré & Ehrlén 2002, Higgins & Cain 2002, Johst *et al.* 2002). Rehabilitation may thus be relatively easy when it is done close to a source area, but extremely difficult if it is further away than some critical distance.

Because abundance is predicted to play a large role in modifying colonization probabilities, most differences between patches of the focal system will be in the composition of the rare set of species (say the 75% rarest species), and recovery of species composition will be faster for the abundant set. This is a relatively easy factor to investigate and will provide much insight into colonization dynamics in general. A corollary prediction is that alternative states will be relatively rare or ephemeral, because most of the abundant species will be found in most of the sites. Alternative states, where they occur, will only be recognized in differential occurrence of particular moderate to low abundance species. This is contrary to most predictions from niche-assembly models (see for instance May 1977, Drake *et al.* 1993, Grover & Lawton 1994, Ludwig *et al.* 1997) and is supported by Lockwood *et al.*'s (1997) observation that alternative persistent states may disappear when invasion rates are high.

The patch-mosaic nature of the model predicts that for particularly middle to low abundance species, metapopulation dynamics will influence the probability of arriving at a newly created habitat (Maina & Howe 2000). It may thus be profitable to investigate the influence of variables that control metapopulation dynamics on colonization probability for particular species (see for instance Hanski *et al.* 2002, Johst *et al.* 2002). Indeed, a metapopulation approach may be very fruitfully combined with a neutral, metacommunity approach.

Aside from these immediate questions, undoubtedly many more secondary questions can be formulated. Moreover, all the central assumptions, principally the

dominant role that abundance and dispersal play in biasing the endpoint for development, have to be evaluated. However, these will have to await a formal mathematical treatment of the model, which is beyond the scope of this thesis.

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Summary

Coastal dune forest regeneration: the response of biological communities to rehabilitation

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Notwithstanding mixed successes in the past, ecological restoration may become a vital conservation tool if the principles and mechanisms that control post-disturbance ecosystem regeneration are understood. This thesis analyzes community data on disturbed, regenerating dune forests, and on undisturbed forests, to determine whether communities, and ecosystem function, can recover in response to rehabilitation.

In most cases (83%), community structure (richness, evenness, proportion of benchmark species) of trees, herbs, millipedes and birds, and ecosystem function (soil N, C, C:N ratio, organic content) either changed towards benchmark values with habitat age (and will reach these values in less than 70 years post-disturbance), or were already equal to the benchmark. The slopes of regression lines depicting age-related changes in community characteristics for different years were similar. In 50% of the cases, the rehabilitating chronosequence was recovering faster than the spontaneously regenerating chronosequence.

Ordinary least squares regression showed that most groups (84%) were regaining the benchmark's species composition (presence and abundance), but dung beetles

recovered only species presence, and small mammals only relative abundance. A Lack-of-Fit test showed that changes were seldom exponential (only birds, small mammals and dung beetles were), suggesting that colonization and extinction are not the orderly events foreseen by equilibrium biodiversity theory.

Average abundance in undisturbed dune forest patches were correlated with colonization success for birds and trees, but not entirely for millipedes, suggesting that post-disturbance recovery may be controlled from outside the local community. Spider habitat changes predictably with site age, as does community structure. However, Canonical Correspondence Analysis and Multiple Regression showed that spider species are associated with litter weight and vegetation cover, variables that do not themselves correlate well with site age. Spiders probably perceive three distinct habitats – grassland, woodland, and forest – rather than a smooth successional change in habitat structure.

Coastal dune forests thus appear to be resilient to mining disturbances, since most groups were recovering structure and composition. I ascribe this to a passive “sampling” of the rain of dispersing propagules and individuals by the new habitat, leading to a high probability of capturing the average species composition of the region.