Chapter 3

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

Abstract

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

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

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

Introduction

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Methods

Study sites and restoration process

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

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

Data collection

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

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

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

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

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

Analysis

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

Structural Trends

Change in life-history traits

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

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

Species turnover

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

Trends in species richness, diversity and evenness

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

Functional Trends

Trends in soil minerals and organic matter

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

Influence of function on structure

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

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

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

Results

Structural Trends

Species turnover

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

Change in life-history traits

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

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

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

Trends in species richness, diversity and evenness

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

Functional trends

Trends in soil minerals and organic matter

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

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

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

Interactions between functional and structural changes

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

Discussion

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

Species turnover

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

Change in life-history traits

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

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

Trends in species richness, diversity and evenness

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

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

Trends in soil minerals and organic matter

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

Interactions between functional and structural changes

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

Succession drives coastal dune forest restoration

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

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

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

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

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

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

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

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

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

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

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

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

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

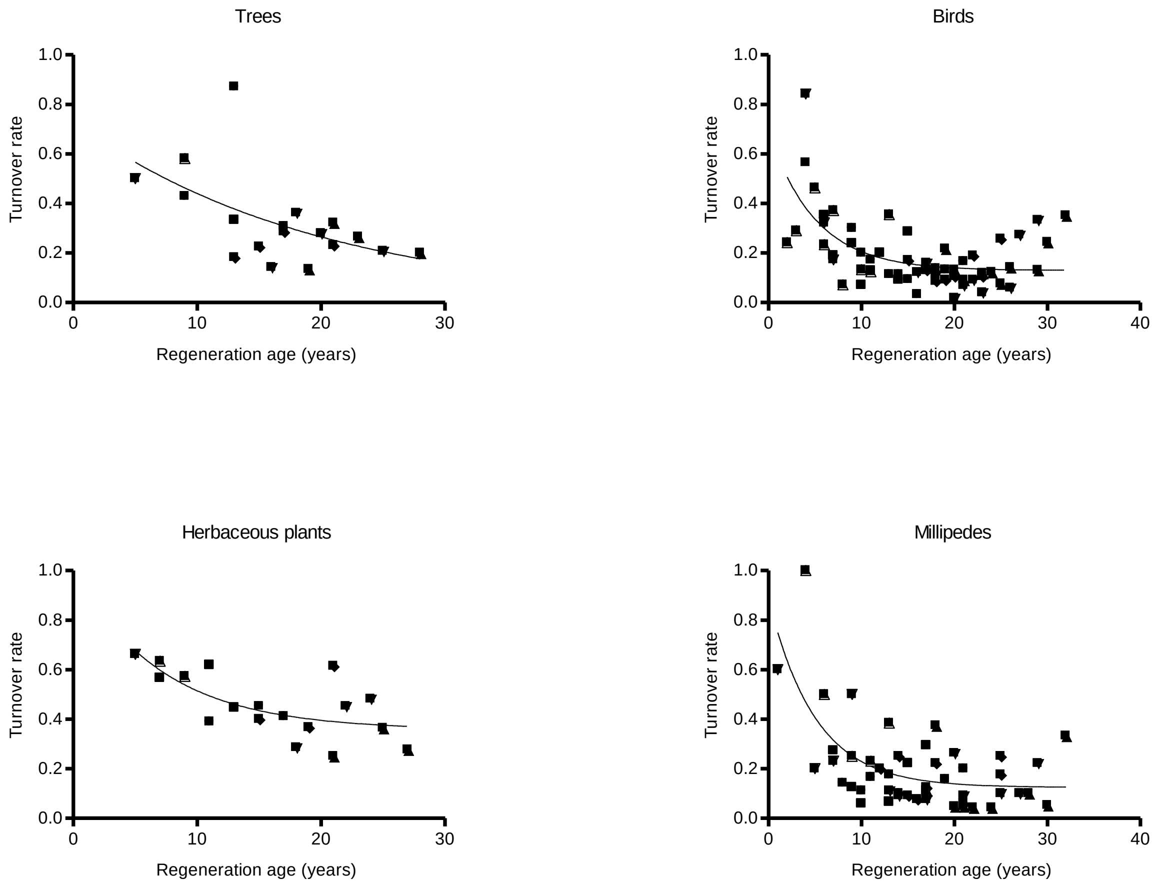


Figure 3-1. The rate of species turnover in regenerating coastal dune forest for the tree, bird, herbaceous plants and millipede communities.

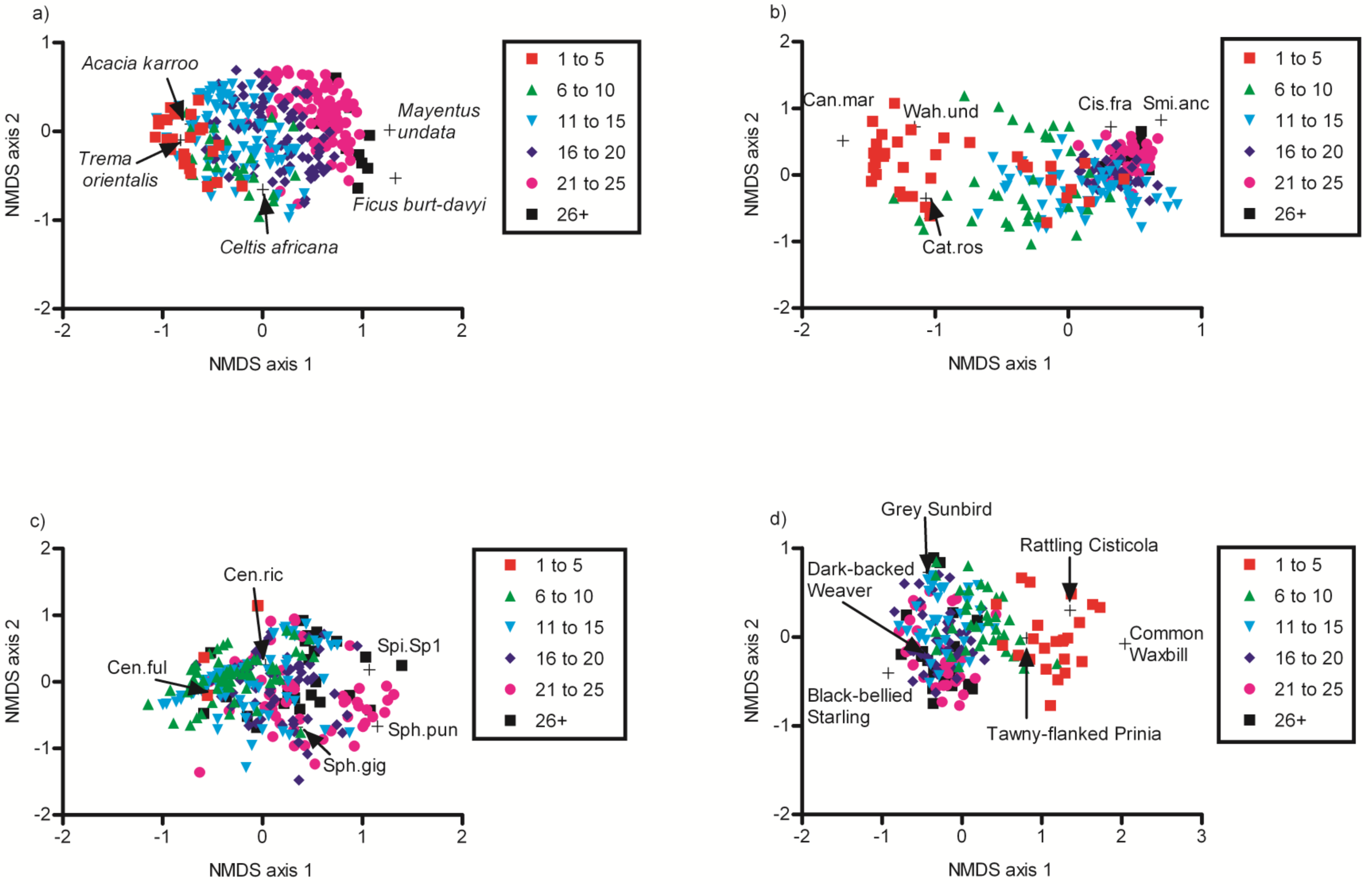
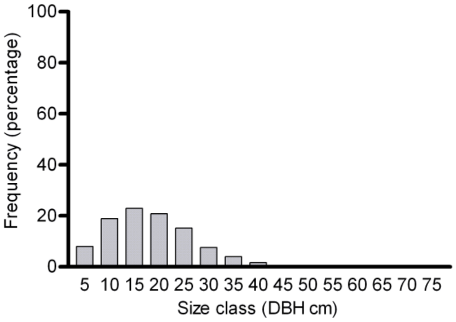
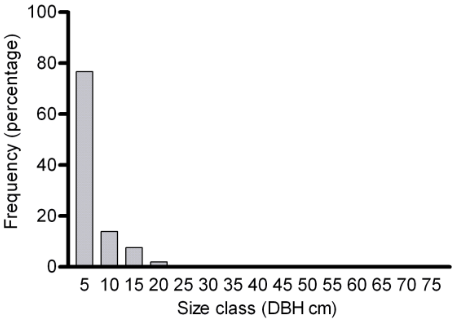

a)
Acacia karroo
Mayentus undata
Trema orientalis
Ficus burt-davyi
Celtis africana
NMDS axis 1
NMDS axis 2
1 to 5
6 to 10
11 to 15
16 to 20
21 to 25
26+
b)
Can.mar
Wah.und
Cis.fra
Smi.anc
Cat.ros
NMDS axis 1
NMDS axis 2
c)
Cen.ric
Spi.Sp1
Cen.ful
Sph.pun
Sph.gig
NMDS axis 1
NMDS axis 2
d)
Grey Sunbird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

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

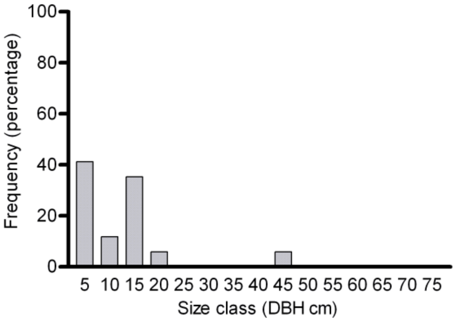
Acacia karroo (n =1359)



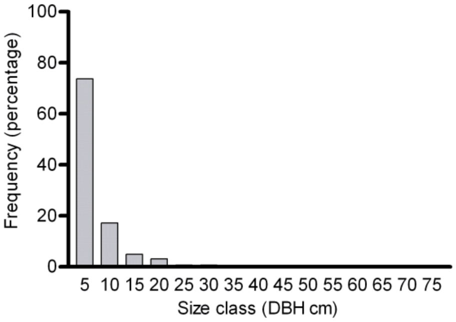
Allophylus natalensis (n= 158)



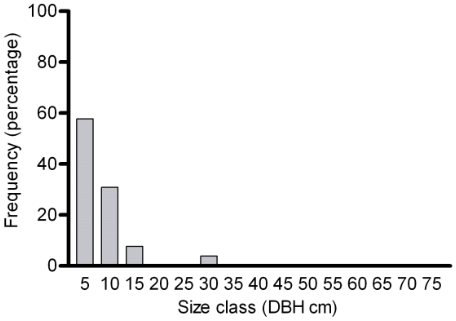
Antidesma venosum (n = 17)



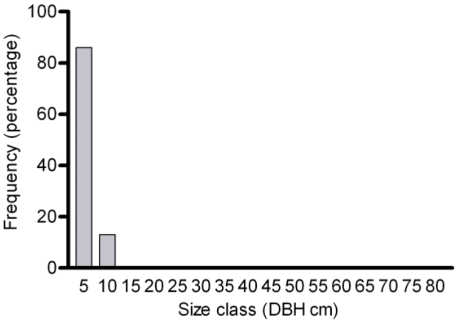
Brachlaena discolour (n= 163)



Bridelia micrantha (n = 26)



Canthium inerme (n =200)



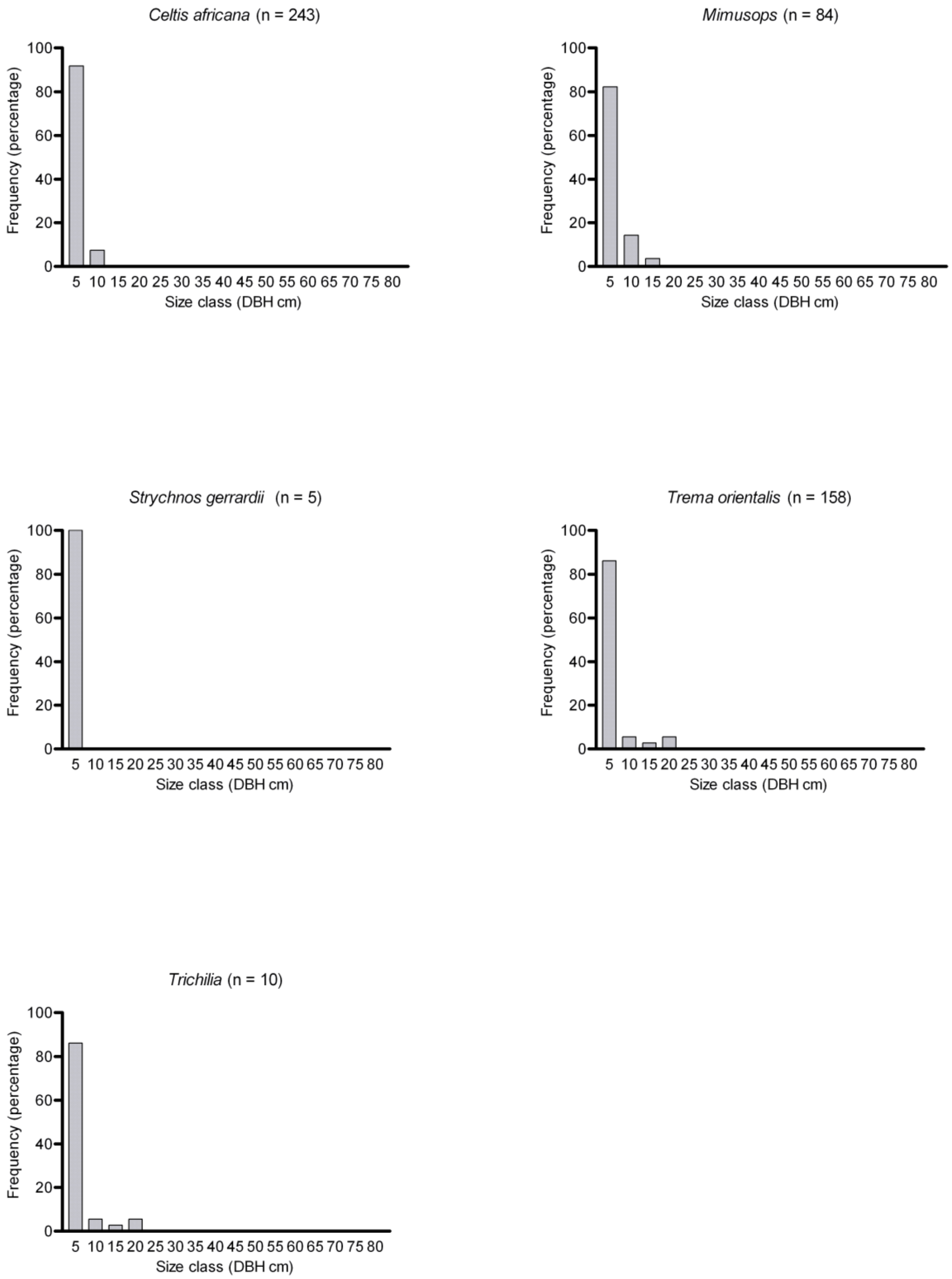


Figure 3-3. Size class distributions of the dominant pioneer tree *Acacia karroo*, and the most abundant ten other tree species. The only tree that did not show a regenerating population is the pioneer *Acacia karroo*.

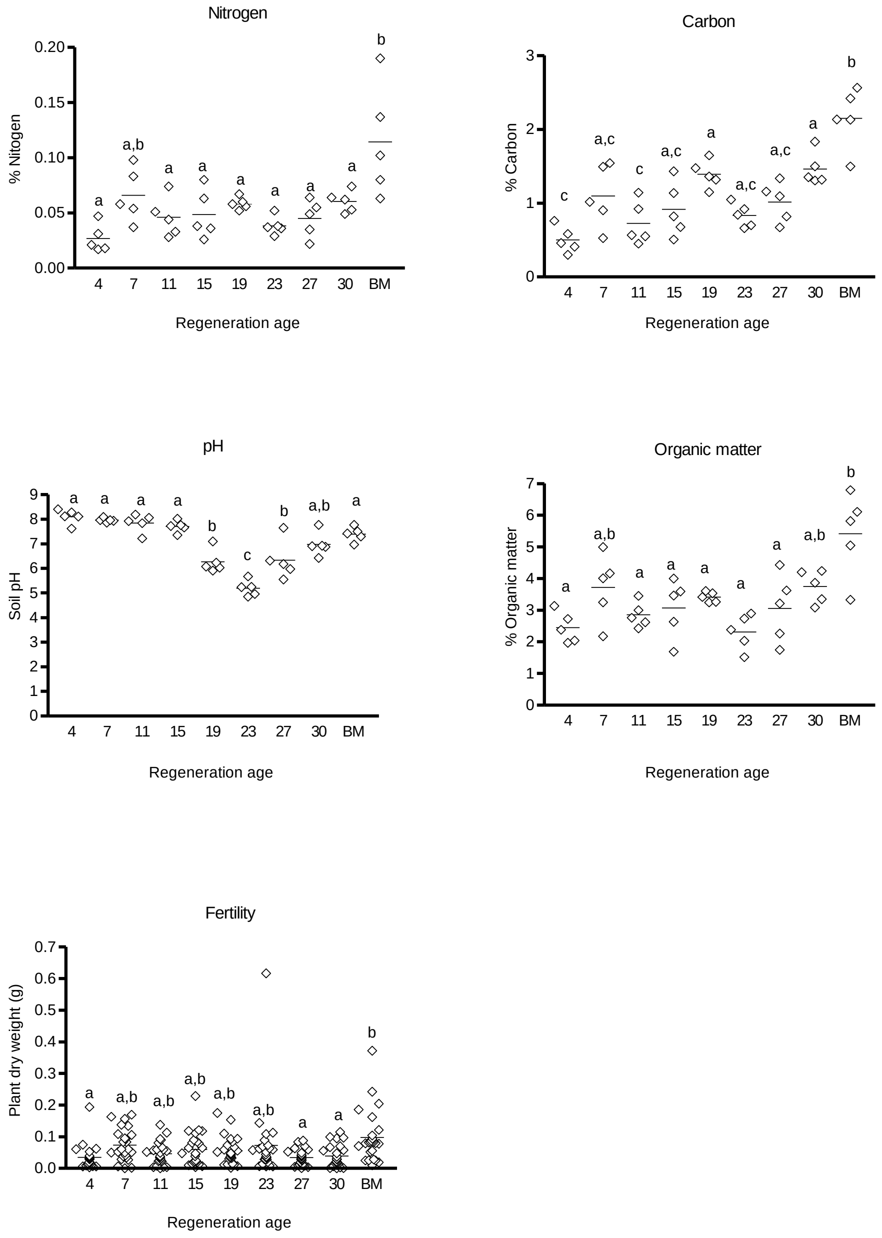


Figure 3-4. Results of an analysis of soil Nitrogen, Carbon, organic matter, pH, and fertility for 8 regenerating coastal dune forests of various ages and an undisturbed reference site of unknown age. Horizontal black lines indicate the mean value. Letters indicate groupings based on the

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