

Beta diversity in a regenerating coastal dune forest in KwaZulu-Natal,  
South Africa

By

Jelena Reljic

Submitted in partial fulfilment of the requirements for the degree

*Magister Scientiae (Zoology)*

In the Faculty of Natural and Agricultural Sciences

University of Pretoria

Pretoria

South Africa

February 2018

I dedicate this thesis to my mum, Stacey Anastopoulos.

Beta diversity in a regenerating coastal dune forest in KwaZulu-Natal,  
South Africa

Student: Jelena Reljic

Supervisor: Professor Rudi J. van Aarde

Conservation Ecology Research Unit

Department of Zoology and Entomology

University of Pretoria

Pretoria, 0002

South Africa

Email: [rjvanaarde@zoology.up.ac.za](mailto:rjvanaarde@zoology.up.ac.za)

## **ABSTRACT**

Beta diversity, defined as the variation or turnover in species composition, is important to the understanding of how ecological communities assemble. Studies of beta diversity during secondary forest succession may thus afford the chance to understand community assembly from a known onset. This study examined the relationship between regeneration age and beta diversity within and between seral stages along a coastal dune forest successional sere for three taxa (trees, millipedes, and birds). These taxa represent different trophic levels and have different dispersal abilities. Niche-based processes (e.g. environmental filtering and niche diversification) and dispersal-based processes (e.g. dispersal limitation), or a mixture of the two, can influence beta diversity over the course of regeneration. However, stochastic community assembly processes (e.g. sampling and priority effects) can influence beta diversity in an unpredictable way. To determine whether these dune forest communities are developing deterministically (i.e. through environmental selection and/or dispersal limitation) or stochastically (i.e. via sampling and priority effects) with succession, a null model of beta diversity was also used. Beta diversity responses to regeneration age based on classical measures of compositional dissimilarity varied among taxa (e.g. tree beta diversity increased while millipede and bird beta diversity decreased). The choice of dissimilarity index (presence-absence vs. abundance) also had important consequences on beta diversity responses. The results of this study showed that deterministic processes such as niche diversification generally increased with increasing regeneration age, leading to greater compositional dissimilarity. However, this varied depending on whether presence-absence or abundance information was included. The null model for species turnover suggested that species-poor communities were not rarefied samples of species rich communities in older seral stages, but these communities experienced some degree of species turnover. Again, this differed among taxa. This leads to the conclusion that the post-mining development of coastal dune forest largely follows

deterministic assembly rules and that stochastic sampling effects are of minor importance. However, there is apparent taxonomic and abundance dependency of beta diversity and inferred processes. Future studies that aim to clarify community assembly processes ought to adopt a null model approach and include species relative abundances. If not, inferences made about the processes driving beta diversity may be misleading.

## **ACKNOWLEDGEMENTS**

I would above all like to thank my Supervisor, Professor Rudi van Aarde, for granting me the opportunity to be part of the Conservation Ecology Research Unit (CERU) three years ago. Under this program, Professor Rudi van Aarde has guided me and provided me with immense knowledge to achieve my intellectual objectives. Without his investment (intellectually and financially), none of this would be have been possible and I am sincerely thankful. I would also like to thank post-doctoral fellows, Victor Rolo and Pieter Olivier, for their time, patience, and valuable input.

To my fellow peers, Andrew Purdon and Marc Freeman, I would like to extend many thanks. From statistical modelling to ecological theory, they have helped me immensely. I would also like to thank everyone who assisted in the fieldwork to collect the data since 2012 used in this study.

I would also like to thank the National Research Foundation (NRF), the Conservation Ecology Research Unit (CERU), Richards Bay Minerals (RBM), and the University of Pretoria (UP) for their financial support.

I would like to extend many thanks to my friends, who have motivated and believed in me throughout this study. Special thanks go to my mum, Stacey, who dedicated 25 years of her life to me and supported me emotionally throughout my academic career. My mum gave me the strength, encouragement, and perseverance to complete this study.

## **DISCLAIMER**

I, Jelena Reljic, declare that this thesis, which I hereby submit for the degree *Magister Scientiae* (Zoology) at the University of Pretoria, is my own research and I have not previously submitted it for a degree at this or any other institution of higher education.

Jelena Reljic

February 2018

## TABLE OF CONTENTS

<b>ABSTRACT.....</b>	<b>iv</b>
<b>ACKNOWLEDGEMENTS.....</b>	<b>vi</b>
<b>DISCLAIMER.....</b>	<b>vii</b>
<b>TABLE OF CONTENTS.....</b>	<b>viii</b>
<b>LIST OF TABLES.....</b>	<b>x</b>
<b>LIST OF FIGURES.....</b>	<b>xii</b>
<b>LIST OF APPENDICES.....</b>	<b>xiv</b>
<b>CHAPTER 1 – GENERAL INTRODUCTION.....</b>	<b>1</b>
1.1. BACKGROUND AND RATIONALE.....	1
1.2. BETA DIVERSITY AND COMMUNITY ASSEMBLY.....	5
1.3. AIM OF THE STUDY.....	11
<b>CHAPTER 2 – MATERIALS AND METHODS.....</b>	<b>12</b>
2.1. STUDY AREA.....	12
2.2. STUDY TAXA.....	16
2.3. DATA COLLECTION.....	17
2.4. DATA ANALYSIS.....	18
<b>CHAPTER 3 – TEMPORAL PATTERNS IN BETA DIVERSITY FOR TREE, MILLIPEDE, AND BIRD ASSEMBLAGES.....</b>	<b>23</b>
3.1. INTRODUCTION.....	23
3.2. MATERIALS AND METHODS.....	26
3.3. RESULTS.....	28
3.4. DISCUSSION.....	30
<b>CHAPTER 4 –DETERMINISTIC PROCESSES PRIMARILY SHAPE BETA DIVERSITY DURING COASTAL DUNE FOREST SUCCESSION</b>	
4.1. INTRODUCTION.....	43
4.2. MATERIALS AND METHODS.....	46
4.3. RESULTS.....	48
4.4. DISCUSSION.....	50



<b>CHAPTER 5 – SYNTHESIS.....</b>	<b>65</b>
5.1. CAVEATS AND CONSIDERATIONS.....	69
<b>REFERENCES.....</b>	<b>71</b>
<b>APPENDICES.....</b>	<b>96</b>

## LIST OF TABLES

**Table 2.1.** The number of replicates per survey period per seral stage for trees, millipedes, and birds.

**Table 3.1.** Number of sampling sites in seral stages of increasing regeneration age for analysis of beta diversity within seral stages for trees, millipedes, and birds.

**Table 3.2.** Results from binomial log-linear GLM fits of turnover along the gradient of age based on the Bray-Curtis ( $d_{BC}$ ) and Jaccard ( $d_J$ ) similarity measures for trees, millipedes, and birds.

## LIST OF FIGURES

**Figure 2.1.** Map of the study area northeast of Richards Bay. Ten rehabilitating stands of known age currently exist since the time of establishment in 1976 to present-day.

**Figure 3.1.** Mean Bray-Curtis (closed squares) and Jaccard (open squares) dissimilarity ( $\pm$  SD) among all pairs of survey sites within seral stages as a function of regeneration age for tree communities (N=120). The solid black line denotes the regression line. The goodness of fit ( $r^2$ ) and the intercept and slope coefficients ( $a$  and  $b$ , respectively), as well as the P value ( $p$ ), from the least squares nonlinear regression model are shown here. For each data set, I analysed 840 pairwise dissimilarity values (not shown here, but see Supplementary material Appendix III).

**Figure 3.2.** Mean Bray-Curtis (closed squares) and Jaccard (open squares) dissimilarity ( $\pm$  SD) among all pairs of survey sites within seral stages as a function of regeneration age for millipede communities (N=50). The black lines represent the regression lines. The goodness of fit ( $r^2$ ) and the intercept and slope coefficients ( $a$  and  $b$ , respectively), as well as the P value ( $p$ ), from the least squares nonlinear regression model are shown here. Results from least squares nonlinear regression based on the Bray-Curtis dissimilarity index ( $d_{BC}$ ) are at the bottom left corner while results based on Jaccards' index ( $d_J$ ) are at the top right corner. For each data set, I analysed 142 dissimilarity values (not shown here, but see Supplementary material Appendix III).

**Figure 3.3.** Mean Bray-Curtis (closed squares) and Jaccard (open squares) dissimilarity ( $\pm$  SD) among all pairs of survey sites within seral stages as a function of regeneration age for bird communities (N=100). The black line represents the regression line. The goodness of fit ( $r^2$ ) and the intercept and slope coefficients ( $a$  and  $b$ , respectively), as well as the P value ( $p$ ), from the least squares nonlinear regression model are shown here. I analysed 450 pairwise dissimilarity values for each data set (not shown here, but see Supplementary material Appendix III).

**Figure 4.1.** Mean compositional dissimilarity ( $\pm$  SD) among survey sites within seral stages of increasing regeneration age based on  $\beta_{RC}$  (open squares) and  $\beta_{RC-abund}$  (closed squares) for tree communities (N=120). The dotted horizontal line represents a mean value of zero, which

indicates community assembly that is predominantly stochastic relative to the regional species pool. A mean values close to -1 implies deterministic processes that favour less dissimilar community composition than expected by chance, while a mean value close to 1 implies deterministic processes that favour more dissimilar community composition than expected by chance..

**Figure 4.2.** Mean compositional dissimilarity ( $\pm$  SD) among survey sites within seral stages as a function of regeneration age based on  $\beta_{RC}$  (open squares) and  $\beta_{RC-abund}$  (closed squares) for millipede communities (N=50). The dotted horizontal line represents a mean value of zero, which indicates stochastic community assembly. A mean values close to -1 or 1 implies deterministic community assembly processes that favour less or more dissimilar community composition than expected by chance, respectively.

**Figure 4.3.** Mean compositional dissimilarity ( $\pm$  SD) among survey sites within seral stages of increasing regeneration age based on  $\beta_{RC}$  (open squares) and  $\beta_{RC-abund}$  (closed squares) for bird communities (N=100). The dotted horizontal line indicates stochastic community assembly, while a mean value close to or approaching -1 or 1 implies deterministic community assembly.

**Figure 4.4.** Mean  $\beta_{RC}$  ( $\pm$  SD) between survey sites in the youngest successional stage and sites in older successional stages as a function of regeneration age for tree communities (N=120). Here, there were 105 dissimilarity values from which to calculate the mean. Closed circles represent the mean dissimilarity values. Open circles represent the dissimilarity values.

**Figure 4.5.** Mean  $\beta_{RC}$  ( $\pm$  SD) between survey sites in the youngest successional stage and sites in older successional stages as a function of regeneration age for millipede communities (N=50). Here, there were 41 dissimilarity values from which to calculate the mean. Closed circles represent the mean dissimilarity values. Open circles represent the dissimilarity values.

**Figure 4.6.** Mean  $\beta_{RC}$  ( $\pm$  SD) between survey sites in the youngest successional stage and sites in older successional stages (i.e. species turnover) as a function of regeneration age for

bird communities (N=100). Here, there were 90 dissimilarity values from which to calculate the mean. Closed circles represent the mean dissimilarity values. Open circles represent the dissimilarity value.

## LIST OF APPENDICES

**Appendix I.** Standard errors for the binomial log-linear GLM fits obtained using the leave-one-out jack-knife method based on the Bray-Curtis ( $d_{BC}$ ) and Jaccard ( $d_J$ ) similarity measures for trees, millipedes, and birds.

**Appendix II.** Appendix II. Mean number of species per survey site within a seral stage ( $\pm$ SD) (a) and the total number of species per seral stage (b) with increasing regeneration age for trees (closed squares) (N=120), millipedes (open triangles) (N=50), and birds (open squares) (N=100).

**Appendix III.** Pairwise Bray-Curtis and Jaccard dissimilarities (beta diversity) within seral stages of increasing regeneration age for tree (N=120), millipede (N=50), and bird communities (N=100). For trees, there were 840 pairwise dissimilarity values for each data set. For millipedes, there were 142 dissimilarity values for each data set. Lastly, there were 450 values for each data set for birds.

**Appendix IV.** The decay in similarity of millipede communities with increasing age distance for the 2012-2013 survey period, as measured using the Bray-Curtis (a) and Jaccard similarity index (b). The grey lines denote the fitted curves from the binomial GLM with a log-link function. Here, there were 1225 similarity values from 50 sites for each data set.

**Appendix V.** The decay in similarity of millipede communities with increasing age distance for the 2012-2013 survey period, as measured using the Bray-Curtis (a) and Jaccard similarity index (b). The grey lines denote the fitted curves from the binomial GLM with a log-link function. Here, there were 1225 similarity values from 50 sites for each data set.

**Appendix VI.** The decay in similarity of bird communities with increasing age distance for the 2014-2015 survey period, as measured using the Bray-Curtis (a) and Jaccard similarity index (b). The grey lines denote the fitted curves from the binomial GLM with a log-link function. Here, there were 4950 similarity values from 100 sites for each data set.

# CHAPTER 1

## GENERAL INTRODUCTION

### 1.1. BACKGROUND AND RATIONALE

What are the restraints on assembling communities? This question is the core component of community ecology and has been the source of debate since the beginning of the twentieth century (Clements 1916; Gleason 1926; McIntosh 1983; Connell & Sousa 1983; Samuels & Drake 1997; Belyea & Lancaster 1999; Chase 2003). Diamond (1975) suggested that a set of ‘Assembly Rules’ typifies community composition. These rules, in sense determinants of community composition, may include the size of the regional species pool, the abiotic environment, and biotic interactions (Diamond 1975). The underlying premise is that the environment acts as an ecological filter selecting only species suitable for persisting under certain local environmental conditions (Keddy 1992).

The principles that govern community assembly and succession are similar, but succession is primarily concerned with the assembly processes (i.e. filters) that drive community change over time after a disturbance (Young et al. 2001; Chang & HilleRisLambers 2016). In line with classic successional theory, compositional changes within a community are often directional and predictable based on the life history traits of species (Egler 1954; Connell & Slatyer 1977; Pulsford et al. 2016). Different ‘filters’ allow some species from the regional pool to arrive while acting as a barrier to unsuitable species as they enter and try to establish in a community. Noble & Slatyer (1980) were first in describing such filtering effects during succession. If only some species can establish at a given time and if local colonisations and extinctions take place in identifiable and repeatable stages (i.e. early vs. late succession), then it might be possible to identify a set of rules governing community reassembly.

Processes that control the assembly of species into local communities can be stochastic or deterministic in nature (Stegen et al. 2013; Zhou et al. 2014; Püttker et al. 2015; Silva et al. 2015; Ulrich et al. 2017). Deterministic processes may include abiotic and dispersal filtering, as well as biotic interactions such as facilitation and competition. Conversely, stochastic processes may include unpredictable disturbance, chance dispersal, and random births and deaths (Chase & Myers 2011). While no single process governs community assembly (Chase 2007; Chase & Myers 2011), the relative importance of each may differ over the course of succession (Zhou et al. 2014).

With the application of novel methods (Meiners et al. 2015), recent studies have started to test hypotheses about which deterministic processes are more important during succession and when (Purschke et al. 2013; Zhou et al. 2014; Li et al. 2016). For instance, theory predicts that dispersal and abiotic filters will play a more important role early in succession, while biotic interactions (e.g. competition) will become increasingly more important late in succession (Purschke et al. 2013; Chang & HilleRisLambers 2016). Knowing the processes that drive succession can facilitate to predict how ecological communities will respond to human-induced recovery. This is particularly important for deciding the kind of approach to use and when, when the aim is to recover locally indigenous plant and animal populations.

Ecological restoration by definition is the “process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed” (SER 2004). The SER recognises that restoration facilitates a process of recovery steered by species themselves, while taking into account the surrounding landscape (McDonald et al. 2016). This process may be accelerated with greater levels of human intervention (McDonald et al. 2016). Intervention by practitioners to initiate recovery may either be intentional (e.g. direct species introductions to degraded sites) or limited (i.e. natural regeneration). The latter approach is usually the most desirable and cost-effective, but the kind of approach used depends to a large extent on the



resilience of species and/or ecosystems, as well as the severity of degradation (McDonald et al. 2016).

Coastal dune forest in South Africa forms part of the Maputaland centre of plant endemism and supports high biodiversity (van Wyk & Smith 2001). These dunes are also an important source of minerals such as rutile, ilmenite, and zircon, and as a result have been subject to intense strip-mining. Every three to four years, mined sand dunes are stabilised according to specified management procedures. Thereafter, the native vegetation is allowed to regenerate naturally. This has resulted in the development of a narrow strip of known-aged seral stages along the eastern seaboard, north of the coastal town Richards Bay in the KwaZulu-Natal province. If succession leads to predictable community development, inferences from space-for-time substitution studies can predict temporal changes in restoring ecosystems (Pickett 1989; Rolo et al. 2016).

Previous work along the successional sere of coastal dune forest has shown increasing species richness and diversity for various taxa, including trees, millipedes, and birds (van Aarde, Ferreira, Kritzing, et al. 1996; van Aarde, Ferreira & Kritzing 1996a; van Aarde, Ferreira & Kritzing 1996b; Kritzing & van Aarde 1998; Grainger & van Aarde 2012). Community composition in regenerating forest is also becoming more similar to that in unmined forest (van Aarde, Ferreira & Kritzing 1996a; Kritzing & van Aarde 1998; Redi et al. 2005; Wassenaar et al. 2005). However, compositional changes differed among taxa (Ferreira & van Aarde 1997; Davis et al. 2003; Wassenaar et al. 2005; Davis et al. 2013), and some sites developed aberrantly (Wassenaar et al. 2007). Despite these idiosyncrasies, the findings of Grainger & van Aarde (2012) suggest that succession is a valid approach for coastal dune forest restoration.

Restoring indigenous fauna and flora that is typical of coastal dune forest is the main goal of post-mining restoration in Richards Bay. To do this, the restoration program has relied

on successional processes (Grainger & van Aarde 2012). Restoration outcomes, however, may be unpredictable and restoration actions could result in multiple stable states that differ to and support less biodiversity than the pre-disturbance state (Handa & Jefferies 2000; Pywell et al. 2002; Suding et al. 2004). Restoration contingent on successional processes may thus be impractical. Successful restoration therefore depends on our understanding of the processes generating and maintaining biodiversity over time (Chase 2007).

Niche-based environmental filters (e.g. canopy openness) and dispersal-based filters (e.g. habitat size and connectivity) can collectively influence diversity and abundance patterns through space and/or time. Chase & Myers (2011) provide a detailed review of these interacting processes. Inferences about the relative importance of niche- and dispersal-based processes usually come from the correlation of beta diversity with environmental and/or spatial variables known to influence community assembly (Stegen et al. 2013). For instance, in coastal dune forest, Olivier & van Aarde (2014) found that spatial factors mostly explained tree beta diversity, whereas environmental factors largely explained bird beta diversity. From this, Olivier & van Aarde (2014) were able to infer that dispersal-based processes most likely drive tree community assembly, while niche-based processes most likely drive the assembly of bird communities.

Stochastic sampling and priority effects, however, may confound inferences made about the ecological processes driving community assembly when comparing patterns among localities that differ in the number of species (Stegen et al. 2013). Such sampling effects may occur when there is stochastic recruitment of individuals into local communities from the regional species pool or because of sampling errors (Socolar et al. 2016). Null models can help to distinguish the relative influence of stochastic sampling processes from ecological processes associated with species' niches or dispersal (Chase & Myers 2011). Statistical null models randomise community data to generate a pattern in the absence of a specific process (Gotelli &

Graves 1996). So, by randomly shuffling species into sites, null models can mimic stochastic community assembly processes (Colwell & Winkler 1984; Gotelli & Graves 1996).

While several studies on succession have evaluated the relative importance of deterministic and stochastic processes in shaping community assembly (Thompson & Townsend 2006; Chase 2007; Ellwood et al. 2009), few studies have measured restoration in this way (Chai et al. 2016; Li et al. 2016). Resolving if community assembly in regenerating coastal dune forest is developing deterministically or stochastically is important if we want to predict the outcomes of restoration. If stochasticity drives restoration, then restoration outcomes such as beta diversity will be unpredictable.

## **1.2. BETA DIVERSITY AND COMMUNITY ASSEMBLY**

### *The concept of beta diversity*

The turnover or variation in species composition broadly describes beta diversity (Anderson et al. 2011), and is a central concept in community ecology (Melo et al. 2011). Robert Whittaker first introduced the concept of beta diversity in 1960. It has since received growing attention, in part, because of the ongoing debate concerning the processes that govern community assembly (Hubbell 2006; Chase et al. 2011). In his paper, ‘Vegetation of the Siskiyou Mountains, Oregon and California’, Whittaker (1960) defined beta diversity as the “extent of change of community composition” and classified it as one of three features of biodiversity. The other two features encompass alpha diversity (defined as the “richness in species of a particular stand or community”) and gamma diversity (defined as the “species diversity of a number of community samples”) (Whittaker 1960). While alpha and gamma diversity indices are useful for describing biodiversity, indices of beta diversity offer greater explanatory power and can provide insight into the processes that generate and maintain biodiversity (Chase & Myers 2011; Avolio et al. 2015; Socolar et al. 2016). Current methods to investigate the factors

that generate and maintain beta diversity have unlocked a new path for the study of community assembly (Melo et al. 2011; Meiners et al. 2015).

For instance, some studies have tested hypotheses regarding the drivers of beta diversity (Balvanera et al. 2002; Condit et al. 2002; Guillem et al. 2006; Wang et al. 2012; Stegen et al. 2013), while others have assessed the distance decay of similarity in ecological communities (Steinitz et al. 2006; Astorga et al. 2012; Fitzpatrick et al. 2013). To a lesser extent, the concept of beta diversity has been applied in studies of biotic homogenization (Villéger et al. 2011; Villéger et al. 2014; Villéger et al. 2015; Toussaint et al. 2014) and conservation (Olivier & van Aarde 2014; Bishop et al. 2015). Furthermore, Martin et al. (2005) used beta diversity to quantify and evaluate restoration success. The number of methods available to measure beta diversity and test potential drivers however may hinder comparisons made between the findings of different studies. Currently, a plethora of beta diversity indices exists. This is an issue several authors have tried to address (Jurasinski et al. 2009; Anderson et al. 2011; Tuomisto 2010b; Tuomisto 2010c). Nevertheless, beta diversity remains an important focus in biodiversity research, conservation, and management, as it quantifies the spatial and temporal distribution of species (Legendre et al. 2005).

### *Measures of beta diversity*

Whittaker (1960, 1972) first suggested a way of quantifying beta diversity by partitioning beta diversity into multiplicative components of gamma diversity, where beta diversity results from the division of gamma diversity by the mean alpha diversity. In other words, beta diversity is the ratio of the total species richness observed in a region and the mean species richness observed at a site, given by:

$$\beta = \gamma/\alpha$$

(Melo et al. 2011) also refers to this as hierarchical beta diversity. This equation does not measure exact compositional dissimilarity, but rather the proportion of species richness found in an average sample (Jurasinski et al. 2009). MacArthur et al. (1966) and Levins (1968) later proposed a partition of beta diversity into additive components of gamma diversity, where beta diversity results from the subtraction of the mean alpha diversity from gamma diversity, given by:

$$\beta_A = \gamma - \alpha$$

This formula explains the average amount of diversity not recorded in a sample unit, and does not account for differences among samples (Veech et al. 2002). Since multiplicative and additive partitioning both compute beta diversity directly from alpha and gamma diversity, they are ideal for relating alpha and gamma diversity (Socolar et al. 2016), but not for comparing beta diversity among sites within a region (Chase et al. 2011).

Baselga (2010) proposed a partition of beta diversity into its turnover and nestedness-resultant components, which offers a greater explicatory way of measuring beta diversity than multiplicative and additive partitioning. Turnover involves the replacement of species from one sampling unit to another, whereas nestedness reflects species richness differences among sample units (Baselga 2010). Baselga (2010) showed that partitioning beta diversity into two additive components, reflective of species turnover and nestedness, could elucidate the mechanisms that influence community composition and structure along environmental, spatial, or temporal gradients. The application of beta diversity partitioning has since been positively applied (Azeria et al. 2011; Bishop et al. 2015; Murray et al. 2015), but criticised by a few authors (Almeida-Neto et al. 2012; Carvalho et al. 2012; Podani & Schmera 2011). Carvalho et al. (2012) proposed an alternative method for partitioning beta diversity into its species turnover and nestedness components, but computing beta diversity between more than two samples is not feasible using this approach.

When comparing beta diversity among several samples, it may be more practical to estimate beta diversity using pairwise dissimilarities (Anderson et al. 2011; Socolar et al. 2016). Pairwise beta diversity computes the mean dissimilarity across all pairs of sampling sites within a given area, and is useful for identifying environmental or spatial variables that influence beta diversity by correlating beta diversity with between-site differences in these factors (Olivier & van Aarde 2014; Stegen et al. 2013).

Whether one employs partitioning methods or employs pairwise dissimilarities, beta diversity will still depend to some extent on alpha or gamma diversity (Socolar et al. 2016). By definition, any two of the three diversity components are statistically dependent on each other (Chase et al. 2011; Chase & Myers 2011). This means that if, for example, there is a large difference in alpha diversity (local species richness) between two sites, there will be an associated increase in beta diversity just because species richness is concentrated in one locality (Koleff et al. 2003). Null models of beta diversity take into account these differences in local species richness. Therefore, inferences made about the ecological processes driving beta diversity from null models may be stronger than inferences made from classical measures of beta diversity such as Bray-Curtis and Jaccard (Anderson et al. 2011).

#### *Beta diversity and null models*

Null models are an effective approach for revealing ‘true’ changes in beta diversity that are not caused by random fluctuations in local species richness (Chase 2007; Vellend et al. 2007; Anderson et al. 2011; Chase et al. 2011; Azeria et al. 2011; Avolio et al. 2015). This approach assumes that ecological (i.e. deterministic) processes do not shape community composition (Ulrich & Gotelli 2010), but rather stochastic sampling processes. If stochastic sampling processes play a greater role in shaping community composition, then observed beta diversity would be statistically indistinguishable from the null expectation, which assumes that ecological niches or species traits are unrelated to patterns of beta diversity (Chase & Myers

2011). Any deviation from the null expectation provides an estimate from which to compare the relative influence of deterministic processes among localities that differ in any factor of interest such as regeneration age, which may inherently cause random fluctuations in alpha diversity (Chase & Myers 2011). A large deviation signifies a strong role for deterministic processes, while a small deviation signifies the dominance of stochastic processes (Chase & Myers 2011). The type of deterministic processes may be inferred from the direction of change in beta diversity. Lower beta diversity than the null expectation may suggest deterministic processes such as environmental and/or dispersal filtering, which tend to produce similar community composition (Chase et al. 2011). Alternatively, greater beta diversity than the null expectation may suggest deterministic processes such as competition and/or niche complementarity, which may generate dissimilar community composition (Chase et al. 2011).

#### *Patterns of beta diversity*

Numerous studies have documented patterns of beta diversity, but these may be taxon specific within a given system (Avolio et al. 2015; Socolar et al. 2016). For example, in the Great Basin of North America, Mac Nally et al. (2004) found that the beta diversity of resident butterflies was higher than that of breeding birds. Si et al. (2015) documented a similar pattern for breeding birds and lizards in China. Beta diversity patterns may therefore depend on the life history traits of taxa, such as dispersal ability, niche breadth, and body size (Soininen et al. 2007; Barton et al. 2013). Inferences about the relative importance of niche- and dispersal-based processes may therefore also depend on the life history traits of taxa (Olivier & van Aarde 2014).

For instance, birds have shown a stronger relationship between beta diversity and environmental variables, indicating niche-based community assembly (Driscoll & Lindenmayer 2009; Özkan et al. 2013; Baselga et al. 2015). In contrast, trees have shown a stronger relationship between beta diversity and spatial variables, which indicates dispersal

limitation (Balvanera et al. 2002; Guillem et al. 2006; but see Davidar et al. 2007). Invertebrates (e.g. snails) have also shown a stronger relationship between beta diversity and spatial variables (Steinitz et al. 2006). It is thus hypothesised that dispersal limitation will play a more important role in influencing the beta diversity of taxa with poor dispersal ability (e.g. trees and invertebrates) compared with more vagile taxa, i.e. birds (Soininen et al. 2007; da Silva et al. 2017).

Although many studies have investigated the relationship between beta diversity and specific factors (e.g. environmental heterogeneity, spatial variation, and dispersal mode), few have examined the relationship between these factors through both space and time (Stegen et al. 2013; Lamy et al. 2015). Beta diversity across space and beta diversity across time may result from different processes. For instance, beta diversity across time can be the result of deterministic selection by particular environmental variables or stochastic variation in immigration history (Baselga et al. 2015). Since space links communities, beta diversity can also be the result of spatial heterogeneity in species responses or environmental filtering (Lamy et al. 2015). As a result, inferences regarding the drivers of beta diversity may differ across space and time. Thus, it is important to assess both temporal and spatial beta diversity if we want to inform conservation and restoration managers about appropriate actions.

Again, differences in local species richness (alpha diversity) can influence beta diversity patterns. A change in alpha diversity because of a change in some factor is likely to cause a concomitant change in beta diversity (Chase et al. 2011; Chase & Myers 2011). For instance, if local species richness decreases due to habitat fragmentation, then beta diversity may increase owing to isolation effects (Maaß et al. 2014).



### **1.3. AIM OF THE STUDY**

The direction, magnitude, and predictability of community change during the post-mining recovery of coastal dune forest depends on the underlying processes shaping community assembly. Predicting how ecological communities will respond to restoration is difficult if we do not recognise the processes behind patterns of diversity, as well as how different communities respond over time. If community assembly is primarily stochastic, coastal dune forest restoration contingent on successional processes may be impractical. Using data collected over a period of 26 years from a 40-year old coastal dune forest sere, I aimed to assess the relationship between the beta diversity of three coastal dune forest assemblages (trees, birds, and millipedes) and regeneration age. I also aimed to investigate how deterministic and stochastic processes interact during coastal dune forest development to structure these communities by applying a statistical null modelling approach, which also accounts for differences in local species richness.

## CHAPTER 2

### GENERAL MATERIALS AND METHODS

#### 2.1. STUDY AREA

The study area comprises ten rehabilitating stands of varying age that represent different seral stages of a successional sere, stretching along coastal dunes situated northeast of the town Richards Bay (28°43' S, 32°12' E) in the Province of KwaZulu-Natal, South Africa (Fig. 2.1). Coastal dune forests form part of the southern African Indian Ocean Coastal Belt (IOCB) forests (Mucina et al. 2006). This region stretches approximately 800 km along the eastern coastline of the Indian Ocean between southern Mozambique and the northern half of South Africa, including the KwaZulu-Natal and Eastern Cape Provinces (Mucina et al. 2006).

The IOCB represents a unique vegetation biome separated into four distinct regions (northern Swahili Centre of Endemism, central Maputaland-Swahili Transitional Zone, and southern Maputaland and Pondoland Centres of Endemism) with differing levels of plant endemism (van Wyk 1996). Coastal dune forests are one of the many vegetation types (about 15-21) found in the southern Maputaland Centre of Endemism (van Wyk 1996; Eeley et al. 1999; van Wyk & Smith 2001). While the vegetation in this region contains many endemic plant species, coastal dune forests are limited in this regard (McLachlan 1991). Despite this, dune forests have many plant species (Mucina et al. 2006).

For instance, the Conservation Ecology Research Unit (CERU) has identified 85 species of tree (woody plants higher than 1.7 m) in unmined coastal dune forests (Sokhulu Forest and Mapelane Nature Reserve) (van Aarde et al. 2014). Four tree species were very common, six species were common, and 13 were rare, whereas 62 species were very rare (Grainger 2011). The most dominant shrub species in these two forests include *Dracaena*

*aletriformis* (Large-leaf Dragon Tree) and *Psychotria capensis* (Black Bird-berry). The most dominant (canopy) tree species include *Diospyros natalensis* (Acorn Jackal-berry), *Erythroxylum emarginatum* (African Coca-tree), *Teclea gerrardi* (Zulu Cherry-orange), *Drypetes natalensis* (Dune Soap-berry), *Euclea race-mosa* subsp. *sinuate* (Sea Guarri), *Peddiea africana* (Poison Olive), and *Chionanthus peglerae* (Giant Pock Ironwood).

Coastal dune forests also support high levels of vertebrate diversity (McLachlan 1991). For instance, CERU has recorded at least 135 species of birds in coastal dune forests (van Aarde et al. 2014). Of the bird species recorded yearly since 1993 (39 to 90 per year), only three (*Chlorocichla falciventris* [Yellow-bellied Greenbul] *Camaroptera brachyuran* [Green-backed Camaroptera], *Hedydipna collaris* [Collared Sunbird]) are considered very common. Six species are considered common (*Apalis flavila* [Yellow-breasted Apalis], *Ploceus bicolor* [Dark-backed Weaver], *Phyllastrephus terrestris* [Terrestrial Brownbul], *Dryoscopus cubla* [Black-back Puffback], *Cyanomitra olivacea* [Eastern Olive Sunbird], *Pogoniulus bilineatus* [Yellow-rumped Tinkerbird]), eight are considered rare while 70 are considered very rare (Grainger 2011). Three bird species are considered vulnerable (*Columba delegorguei* [Eastern Bronze-naped Pigeon], *Halcyon senegaloides* [Mangrove Kingfisher], *Circaetus fasciolatus* [Southern Banded Snake Eagle]), while one species, *Zoothera guttata* (Spotted Ground Thrush), is listed as endangered (van Aarde et al. 2014).

Coastal dune forests are also rich in invertebrate species (van Aarde et al. 2014). For example, CERU has recorded 21 millipede species in these forests. Similar to birds, there are few common and many rare species, with one very common, 1 common, 2 rare, and 12 very rare species (Grainger 2011). Two of the most common millipede species include *Centrobolus fulgidis* and *Centrobolus richardii*. There is also one species, *Doratogonus zuluensis*, listed as endangered.

Coastal dunes formed after the last glacial maximum (18 000 BP) (Lawes 1990). During the last glacial period (about 10000 years ago), sand deposits left by the retreat of the Indian Ocean established the littoral dunes (Eeley et al. 1999). Strong winds and arid conditions have subsequently influenced the shape of the dunes (Tinley 1985). The warm interglacial period between 4000 and 6500 BP headed forest formation (Lawes 1990). Eeley et al. (1999) have approximated the period of coastal dune forest establishment to about 8000 years ago. Geologically, this places the dune forests of KwaZulu-Natal on Pleistocene and Recent sands (Tinley 1985). At present, the regional climate is humid and subtropical (van Aarde et al. 2014). Long-term mean annual rainfall (1976-2015) was  $1366 \pm 117$  mm/year since restoration (Rolo et al. 2017).

Since the Iron Age (circa AD 400), anthropogenic activities such as agricultural production and iron smelting in the region have influenced the nature of coastal dune forest (West et al. 2000). It has been noted that the earliest anthropogenic impact on coastal dune forest was the exploitation of natural resources such as iron and wood during the establishment of Zulu settlements circa 1670 (Grainger 2011). Past actions have translated recently into livestock grazing, sugarcane farming, wood plantations, urbanisation, and tourism expansion, thereby reducing the historical range of coastal dune forest and transforming the region into a mosaic of different land use types (Mucina et al. 2006). A recent study suggests that an estimated 82% of coastal forests (e.g. lowland, dune, and swamp forest) in South Africa have been replaced, assuming that the environmental conditions that favour coastal forests are still similar today, which will most likely result in the extinction of some species (Olivier et al. 2013). Other threats undoubtedly include the increasing human population and the resultant increasing demand for natural resources (Grainger 2011). Urban development and silviculture (wood plantations) is probably the greatest threat to coastal dune forest conservation today, as

they do not make allowances for restoration. Understanding the post-mining restoration of coastal dune forest is therefore essential to conserve and recover indigenous forest.

#### *Dune mining in KwaZulu-Natal, South Africa*

Dredge mining of coastal dunes for heavy minerals such as rutile, ilmenite, and zircon has been occurring since 1977 (Camp 1990). Mining involves the removal of vegetation along the dunes. Topsoil is then stored and sand is extracted and deposited into an artificial pond. A floating dredger pumps the sand into a gravity separator, which separates the minerals from the sand. The machine then pumps the sand tailings back behind the dunes. The dunes are then reshaped with purified sand tailings and preserved topsoil is spread over the tailings (a 10-15 cm thick layer) to resemble the original dune topography.

The sowing of a mixture of seeds (e.g. *Sorghum* spp., *Pennisetum americanum* [Pearl Millet], *Crotalaria juncea* [Sunn Hemp]) in the topsoil, which serves as a seed bank for relatively slow growing native plant species, initiates the natural regeneration of indigenous coastal dune vegetation (Camp 1990). Once these crops die off, the pioneer tree species, *Vachellia karroo* (this is the new scientific name given to the *Acacia karroo* species) (Dyer 2014), dominates the canopy early in succession (van Aarde, Ferreira, Kritzing, et al. 1996). These trees may facilitate the establishment of non-pioneer species through their ability to fix nitrogen, thereby enhancing soil fertility (Lubke et al. 1993). Being senescent, the eventual collapse of *Vachellia karroo* individuals, and the subsequent creation of canopy gaps may further promote the establishment of secondary forest tree species (Grainger & van Aarde 2013).

Restoration management allows vegetation to develop naturally, either from the seedbank or through seed dispersal, and is restricted mostly to invasive species control. For instance, frugivorous birds and vervet monkeys (*Cercocepithecus aethiops*) most likely disperse

secondary tree species (Foord et al. 1994). Richards Bay Minerals (RBM) have designated over 1000 hectares of land for the restoration of coastal dune forest (RBM 2014). This has resulted in the formation of a successional sere from which several studies have explained patterns of succession in various plant and animal communities (van Aarde, Ferreira, Kritzing, et al. 1996; van Aarde, Ferreira & Kritzing 1996a; van Aarde, Ferreira & Kritzing 1996b; Kritzing & van Aarde 1998; Redi et al. 2005; Grainger & van Aarde 2012). Landscape composition and structure, however, may constrain the dispersal of plants and animals into older sites (Grainger et al. 2011). Dispersal is thus also an important process in restoration which management needs to consider.

The landscape comprises a successional sere of regenerating coastal dune forest (the study area), stripped mining areas, *Casuarina equisetifolia* (Beefwood) plantations, densely populated areas, disturbed areas dominated by a mix of native and non-native species, and unmined forest fragments (van Aarde, Ferreira, Kritzing, et al. 1996). The Sokhulo forest (28°27'S, 32°25'E) and Mapelane Nature Reserve (32°25'S, 28°27'E) represent old growth forest and are used as benchmark sites for regenerating coastal dune forest (van Aarde, Ferreira, Kritzing, et al. 1996; Grainger & van Aarde 2012).

## **2.2. STUDY TAXA**

In this study, I examined successional patterns in beta diversity in restored coastal dune forest for three different taxa (trees, millipedes, and birds). These taxa have distinct life history traits and represent three different trophic levels: primary producers (trees), decomposers (millipedes), and consumers (birds) (Olivier et al. 2017).

### 2.3. DATA COLLECTION

CERU's research initiatives began in 1991. Table 2.1 provides the number of replicates per seral stage per survey period for trees, millipedes, and birds since 1994. For the purpose of this study, I collated data which was surveyed by research assistants at CERU during the survey periods 2012-2013 (millipedes) and 2014-2015 (trees and birds). These seral stages represent over 35 years of coastal dune forest succession. For both birds and millipedes, 10 seral stages were surveyed, but only 8 seral stages were surveyed for trees. This is because the two youngest seral stages (aged 5 and 9 years at the time of the tree survey) are densely occupied by the pioneer species, *Vichellia karroo*, which imposed a sampling constraint when using the quadrat-based method for tree surveys.

#### *Trees*

We surveyed tree plots during the summer season (November-February) in eight seral stages using a quadrat-based method (Theron 2001). Survey plots were 16x16m and randomly located along the successional sere. We recorded and identified all trees above shoulder height (approximately 1.7m) within each quadrat.

#### *Millipedes*

Millipede surveys also took place during the summer period (November-February) in ten seral stages. Randomly located transects (6x16m in size) were surveyed between 0500h and 1000h as millipedes are most active during this time (Greyling et al. 2001). Trained observers collected all millipedes observed on the ground and on foliage that was within hands' reach (< 3m), and then used reference material from the Natural Science Museum to identify millipede species. The soil layer was not included in the search as it mostly contains juveniles, which are not easily identifiable.

## *Birds*

Similar to trees and millipedes, we conducted bird surveys during the summer season (November-February) in ten seral stages using a point-based method (Olivier & van Aarde 2014). We surveyed point counts between 0500h and 0900h during clear and non-windy conditions. For 10 minutes per point and within a ~60m radius, skilled observers recorded all birds seen and heard, excluding largely aerial species, such as swifts and swallows, and birds that flew above the forest canopy. A pair of observers ‘shared’ survey points (Olivier & van Aarde 2014). Given the terrain and habitat characteristics of coastal dune forests (e.g. thick undergrowth, large canopy trees), the point-based method is preferred, as any birds that may have been disturbed when reaching the survey point are allowed to resettle within a couple of minutes (Olivier & van Aarde 2014).

## **2.4. DATA ANALYSIS**

Quantifying and predicting biodiversity change over time is a major concern in the field of ecology (Magurran & Dornelas 2010; Dornelas et al. 2012; Avolio et al. 2015). It also has real world applications, particularly when the aim is to recover locally indigenous fauna and flora. For instance, in the case of South African coastal dune forest, which has been destroyed by mining, investigating, describing, and quantifying temporal changes in ecological communities over the course of natural regeneration is imperative for the success of restoration, as well as the for the future conservation of this native forest.

A number of metrics exist to describe and quantify the different aspects of biodiversity over time. These include species richness (the total number of species), evenness (the relative abundance of species), species diversity (a combination of richness and evenness), functional diversity (the variety of species traits), phylogenetic diversity (the evolutionary breadth of the community), or beta diversity indices (compositional variability, species turnover). While



species diversity, richness, and evenness indices are useful for describing biodiversity, beta, functional, and phylogenetic diversity indices are more orientated towards the quantification of biodiversity and provide stronger potential evidence for ecological processes.

Repeated surveys (time) and chronosequences (space-for-time substitution) are two potential sources of information from which to infer temporal trends in biodiversity change. Less contemporary sources include historical and fossil records.

The present study examines patterns of beta diversity across a coastal dune forest successional sere to infer successional processes. Due to the 3-4 year period it takes to stabilise mined sand dunes before natural regeneration can take place, we used the modal age (in years) of regenerating sites to explain changes in beta diversity. I used non-linear regression analysis and generalised linear models (GLMs) to assess the relationship between beta diversity and regeneration age.

#### *Space-for-time substitution*

Space-for-time substitution uses a series of different aged sites to infer temporal trends (Pickett 1989). This approach can overcome the research limitations associated with the cost of collecting data and the extent of time needed to monitor community development on one site (Gratzer et al. 2004; Wassenaar et al. 2007; Rolo et al. 2016).

Previous work in the study region has relied mostly on space-for-time substitution to infer temporal trends in species composition and diversity (van Aarde, Ferreira & Kritzing 1996a; van Aarde, Ferreira & Kritzing 1996b; Ferreira & van Aarde 1997; Kritzing & van Aarde 1998; Davis et al. 2003; Redi et al. 2005; Wassenaar et al. 2005; Grainger & van Aarde 2012). While this approach has several drawbacks (e.g. initial site conditions, persistence of pioneers, the establishment of dominant species, random dispersal, and chance colonization),

Wassenaar et al. (2005) as well as Rolo et al. (2016) have tested the validity of space-for-time substitution in the study area.

### *Beta diversity*

I used two dissimilarity metrics (Bray-Curtis and Jaccard) to estimate beta diversity. The Bray-Curtis metric uses count data to compute beta diversity while Jaccard's index uses presence-absence information. Analyses emphasising different aspects of the community can yield different insights into whether/how communities changed over time (Anderson et al. 2006).

I estimated beta diversity among sites 'within' each of the seral stages. In other words, all species within a seral stage (pooling of sites) comprise a single local community. This is the same as variation (Vellend 2001; Anderson et al. 2011) or differentiation beta diversity (Tuomisto 2010a). I also estimated beta diversity among sites 'between' consecutive time steps. This is the same as turnover beta diversity (Vellend 2001; Anderson et al. 2011) or species turnover (Tuomisto 2010a).

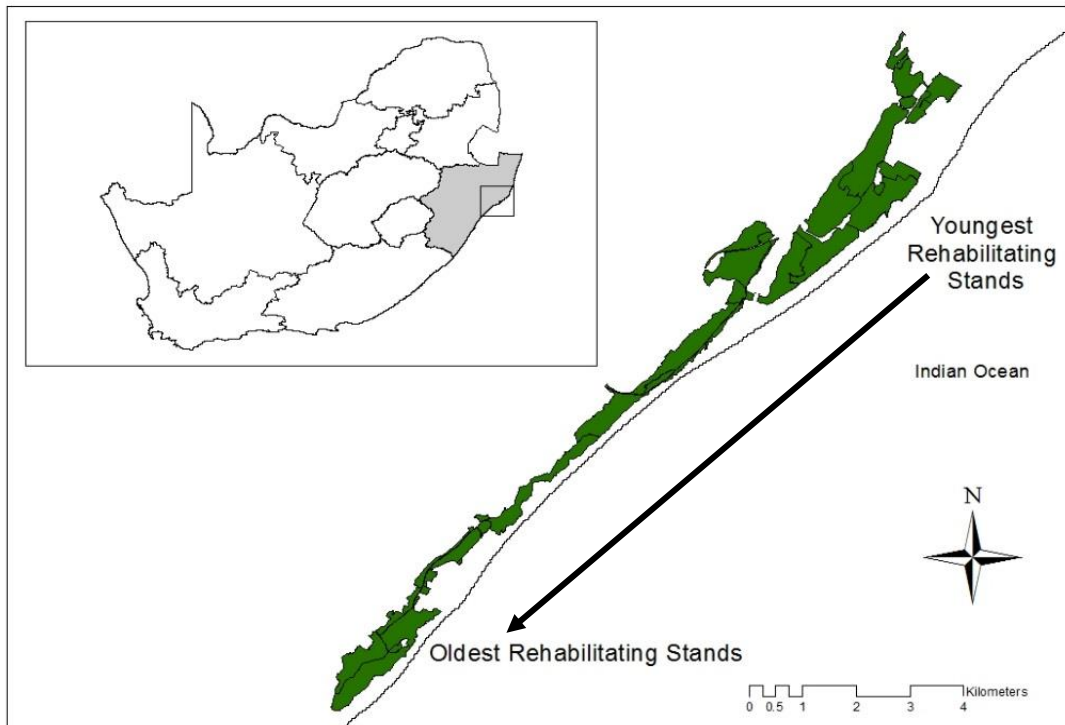
### *Null model analysis*

Given that alpha diversity may influence beta diversity metrics in the absence of a particular ecological gradient, especially metrics based on presence-absence data (e.g. Jaccard), I used a null modelling approach similar to the one described in Chase et al. (2011) to account for observed differences in alpha diversity. This allowed me to test whether changes in beta diversity resulted from deterministic selection by regeneration age or stochastic sampling processes.

**Table 2.1.** The number of replicates per survey period per seral stage for trees, millipedes, and birds.

Survey period	Trees	Millipedes	Birds
1993-1994	X	9-18 (×4)	3-4 (×5)
1997-1998	X	X	2-4 (×6)
1998-1999	X	6 (×6)	3-4 (×6)
1999-2000	40 (×3)	6 (×6)	3-4 (×6)
2000-2001	X	4-6 (×7)	X
2001-2002	10-40 (×7)	6 (×6)	2-4 (×6)
2002-2003	X	6 (×6)	2-4 (×6)
2003-2004	X	X	2-4 (×7)
2004-2005	X	X	2-4 (×8)
2005-2006	6-12 (×7)	X	X
2006-2007	X	4-6 (×7)	3-5 (×8)
2007-2008	X	X	3-11 (×9)
2008-2009	X	6 (×8)	4-7 (×8)
2009-2010	X	10-12 (×8)	4-7 (×9)
2010-2011	12-18 (×8)	7-16 (×6)	X
2011-2012	X	3-23 (×4)	X
2012-2013	X	3-9 (×10)	4-6 (×10)
2013-2014	X	X	4-6 (×10)
2014-2015	15 (×8)	X	10 (×10)

*Numbers in parentheses refer to the number of seral stages that we surveyed for that period. For example, we surveyed 15 sampling sites in the 2014-2015 period in each of the eight seral stages for trees.*



**Figure 2.1.** Map of the study area northeast of Richards Bay. Ten rehabilitating stands of known age currently exist since the time of establishment in 1976 to present-day.

## **CHAPTER 3**

# **TEMPORAL PATTERNS IN BETA DIVERSITY FOR TREE, MILLIPEDE, AND BIRD ASSEMBLAGES**

### **3.1. INTRODUCTION**

Ecological succession, which is the sequential change in species composition following a disturbance (Clements 1916), is a fundamental concept in community ecology (Walker & del Moral 2003), and provides the conceptual framework for restoration ecology (Young et al. 2005; Prach & Walker 2011). Restoration is essentially the manipulation of succession to achieve desired goals (Prach & Walker 2011). These goals include mirroring natural processes (Luken 1990; Davy 2002; Hobbs 2007), maintaining or extending desired states, and restoring original development trajectories (Perrow & Davy 2002; Walker & del Moral 2003).

Restoration contingent on successional principles, however, is not always practical. Some studies have reported the failure of successional trajectories in achieving restoration targets (Zedler & Callaway 1999; Suding et al. 2004). This may be because restoration projects only last a few decades, whereas succession is on an ecological time scale greater than 100 years (Dobson et al. 1997). In addition, other factors such as priority effects (Belyea & Lancaster 1999), year effects (Vaughn & Young 2010), landscape factors (Grainger et al. 2011), and site-specific characteristics (Bakker et al. 2003; Matthews et al. 2009) may all render restoration outcomes unpredictable (Grman et al. 2013).

Accepting that succession is a valid model for coastal dune forest restoration, regeneration processes should generate clear patterns of diversity and abundance (Grainger & van Aarde 2012). Temporal trends in species composition, diversity, and turnover should be predictable (Grainger & van Aarde 2012) and, given enough time, communities should

converge towards that of intact forests in the identity of species and/or their relative abundances (Wassenaar et al. 2005). In addition, the traits of species should converge early in succession and diverge late in succession, as specialist species replace pioneers (Rolo et al. 2016). These patterns are consistent with trait-based theories of succession (Gleason 1917; Gleason 1927; MacArthur & Wilson 1967; Drury & Nisbet 1973; Connell & Slatyer 1977; Noble & Slatyer 1980; Tilman 1985), where a species' life-history traits dictate where it occurs on environmental gradients (Pulsford et al. 2016).

Perhaps the most well studied successional pattern is the temporal trend in species diversity (i.e. richness and evenness). Theory predicts that species diversity will increase during succession (Odum 1969). Prior work in my study area has reported an increase in species richness and evenness during coastal dune forest succession for numerous taxa (van Aarde, Ferreira, Kritzing, et al. 1996; van Aarde, Ferreira & Kritzing 1996a; van Aarde, Ferreira & Kritzing 1996b; Kritzing & van Aarde 1998; Redi et al. 2005; Grainger & van Aarde 2012). Moreover, community convergence may take less than 70 years, but this varied among taxa (Wassenaar et al. 2005).

The rate of change during succession (species turnover) is also an important deterministic trend. This pattern is usually convex, with changes occurring most rapidly early in succession (Anderson 2007). In my study area, Grainger & van Aarde (2012) found that species turnover showed a decelerating decrease, with early successional stages experiencing the most rapid turnover. Of much less interest, however, are successional trends in beta diversity. Anderson et al. (2011) identified two types of measures of beta diversity: i) compositional dissimilarity among a set of sample units *within* a given spatial or temporal extent and ii) *turnover*, which is the change in community composition from one sampling unit to another along a particular spatial or temporal gradient.

In what way is beta diversity an appropriate index of diversity? As beta diversity reflects heterogeneity (dissimilarity) in the identity of species and/or their relative abundances, it may also reflect heterogeneity in local environmental conditions (Whittaker 1960). This may in turn provide some insight into ecological succession. For example, processes such as environmental filtering and/or dispersal limitation may reduce species diversity and increase the functional space (i.e. broad and overlapping niche breadths) early in succession (Peet & Christensen 1988). As a result, beta diversity in early successional stages may be low. As succession ensues (local conditions change), niche specialisation may cause species diversity to increase (Odum 1969). This may in turn lead to an increase in beta diversity (Peet & Christensen 1988). We can therefore identify specific trends in compositional dissimilarity over the course of succession.

Changes in the intensity of inter-specific competition may also produce clear temporal trends in species turnover. Competition is usually minimal during the early stages of forest development and many species may establish and spread quickly (Peet & Christensen 1988). In advanced stages of succession, the community may become saturated and competition may intensify, which may prevent further colonisation (Tilman 1997). It is frequently empirically observed that communities that are more diverse in terms of species have low temporal turnover, while communities that are less diverse have high turnover (Shurin 2007). This is a common phenomenon observed in plant and arthropod communities (Anderson 2007). There are two possible explanations for this pattern (Shurin 2007). First, if the range of species tolerances to environmental conditions and the size of the species pool depend on the degree of environmental heterogeneity, reduced heterogeneity can lead to lower species diversity and higher turnover. Second, higher species diversity can enable colonization by different species or decrease extinction of existing species. The pattern of diminishing species turnover with time may be related with Connell & Slatyer's tolerance model (1977), Gleason's model of

succession (1917), and the fugitive species concept (Elton 1927; Hutchinson 1951), which all predict an increase in the intensity of competition over time (Pulsford et al. 2016). We can therefore test different hypotheses regarding the ecological processes during succession using beta diversity indices.

In this study, I aimed to examine patterns of beta diversity, both as compositional dissimilarity (i.e. beta diversity within seral stages) and as species turnover (i.e. beta diversity between seral stages) along a 38-year old coastal dune forest successional sere for three taxa (trees, millipedes, and birds). I tested if regeneration age could explain beta diversity patterns for each of these three taxa. I predicted i) an increase in beta diversity within seral stages with increasing regeneration age, as the environment becomes more heterogeneous and ii) a decay in similarity between seral stages with increasing age distance, as competition strengthens and/or the regional species pool becomes depleted.

### **3.2. MATERIALS AND METHODS**

Using data collated from the Conservation Ecology Research Unit (CERU), I examined the relationship between regeneration age and beta diversity both within and between regenerating coastal dune forest sites that represent a seral stage along the successional sere for trees, millipedes, and birds. I used both abundance (count) and presence-absence (incidence) data to compute beta diversity (i.e. compositional dissimilarity among sites). Each site represents a sampling unit. Chapter 2 of the thesis provides a description of the survey methods used for each taxa.

#### *Beta diversity 'within' seral stages*

Here, I estimated beta diversity as the mean pairwise dissimilarity among sampling sites *within* each seral stage, using both the Bray-Curtis ( $d_{BC}$ ) and Jaccard ( $d_J$ ) indices. The former measures



compositional dissimilarity in the relative abundance of species, while the latter measures dissimilarity in the presence-absence of species. Table 3.1 provides the number of sites sampled in each seral stage for each of the three taxa.

To model the relationship between beta diversity within seral stages and regeneration age, I used least squares non-linear regression in the programme, GraphPad Prism. This analysis is the same as linear regression, but allows the user to apply specific weights. Therefore, I was able to take into account both the number of pairwise dissimilarities (N) and the standard error of the mean (SE), which may influence simple linear regression results. This allowed me to test the first hypothesis that beta diversity within seral stages would increase with increasing regeneration age.

*Beta diversity 'between' seral stage (i.e. turnover)*

I measured turnover as the pairwise similarity among sites *between* seral stages, using both the Bray-Curtis ( $d_{BC}$ ) and Jaccard ( $d_J$ ) similarity measures. The Bray-Curtis index measures turnover in the relative abundance of species, whereas Jaccard's index measures turnover in the presence-absence of species. I then plotted the similarities as a function of Euclidean distance, which measures variance in univariate sample data such as regeneration age.

To test the second hypothesis that species turnover will diminish along the gradient of age, I fitted a distance-decay curve to the points using a binomial generalised linear model (GLM) with a log link function (Millar et al. 2011). This method allows data to have many zero values (i.e. a random distribution), but it may produce false standard errors and significance values. I therefore used the leave-one-out jack-knife method to estimate model parameters (Millar et al. 2011; Anderson et al. 2013). I then used a Mantel test based on the Spearman rank correlation ( $\rho$ ), with 9999 permutations, to test the significance of the relationship between similarity and regeneration age (Anderson et al. 2013). I also calculated

the similarity at zero age distance, which is interpretable as the similarity of a pair of sites at similar ages. I also computed the halving distance, which Whittaker (1960) interprets as the distance along the gradient that produces a halving in similarity (Anderson et al. 2013). Millar et al. (2011) give the equation as follows:

$$d_{0.5} = -\log(0.5)/\beta = 0.693/\beta.$$

For all statistical analyses, I used the *vegan* (Oksanen et al. 2016) and *MASS* (Venables & Ripley 2002) packages developed under R (R Core Team 2016). Millar et al. (2011) provide the R script needed to fit the distance-decay curves using a GLM, and estimate the standard errors using the jack-knife method. To visualise patterns of beta diversity, I used the computer program GraphPad Prism 6.

### 3.3. RESULTS

We recorded a total of 75, 17, and 115 species for trees, millipedes, and birds, respectively. The mean number of species per sampling site (Supplementary material Appendix IIa) and the total number of species per seral stage (Supplementary Appendix IIb) was generally highest in advanced seral stages and lowest in early seral stages. This distinction was less sharp for millipedes compared with birds and trees.

#### *Beta diversity 'within' seral stages*

##### *Trees*

Compositional dissimilarity, as measured using the Bray-Curtis index ( $d_{BC}$ ), generally increased with increasing regeneration age (Fig. 3.1). There was an initial increase in mean  $d_{BC}$  with age, which then decreased slightly at intermediate ages (between 19 and 27 years). Mean values then increased again. In contrast with analysis based on abundance data, dissimilarity in

the presence-absence of species, as measured using Jaccard's index ( $d_J$ ), did not change significantly with age. However, mean  $d_J$  values were high (Fig. 3.1).

### *Millipedes*

Compositional dissimilarity in both the relative abundance of species ( $d_{BC}$ ) and their presence-absence ( $d_J$ ) decreased significantly with increasing regeneration age (Fig. 3.2). However, regeneration age explained very little of the change in beta diversity (Fig. 3.2). Mean  $d_{BC}/d_J$  values were high to moderate.

### *Birds*

Compositional dissimilarity in the relative abundance of species ( $d_{BC}$ ) did not change with increasing regeneration age, but dissimilarity in the presence-absence of species ( $d_J$ ) decreased significantly, although age explained little to no variation in beta diversity (Fig. 3.3). Mean  $d_{BC}/d_J$  values were moderate to low.

### *Beta diversity 'between' seral stages (i.e. turnover)*

### *Trees*

The distance-decay in Bray-Curtis similarity was clearly stronger than the distance-decay in Jaccard similarity (Table 3.2, Supplementary Material Appendix IV). The relationship between turnover and regeneration age, as measured using the Spearman Rank Correlation  $\rho$  (rho) and associated P-value for a Mantel test, was significant for both similarity metrics (all P values < 0.001, Table 3.2).

### *Millipedes*

Distance-decay was low across the gradient of age, regardless of whether I used the Bray-Curtis or Jaccard similarity index (Table 3.2, Supplementary Material Appendix V). Spearman's Rank Correlation of turnover with age was weak and there were no significant relationships based on the Mantel Test (all P values >0.9, Table 3.2).

## *Birds*

Decay of similarity with increasing age distance was not apparent for either of the two indices (Table 3.2, Supplementary Material Appendix VI). There were no significant relationships between turnover and age based on the Mantel Test (all P values >0.9, Table 3.2).

Table 3.2 shows the halving distance and estimated Bray-Curtis/Jaccard similarity at zero (age) distance for all three taxa. For example, tree communities of similar recovery age are likely to share ~56% of their composition in terms of species' abundances, but only ~30% of their composition in terms of species present. See Supplementary material (Appendix I) for the results of the jack-knife procedure for the three taxa.

### **3.4. DISCUSSION**

#### *Does beta diversity 'within' seral stages increase with increasing regeneration age?*

According to Clements (1916), succession is a predictable process of community change over time driven by autogenic environmental modification (Christensen & Peet 1981). If environmental conditions become more heterogeneous, then beta diversity within seral stages may increase (Astorga et al. 2014; Grman et al. 2015). This is because environments that are more heterogeneous may provide more suitable conditions for a larger number of species with different ecological niches, which may increase the effective species pool (Allouche et al. 2012; Brown et al. 2013). Contrary to this expectation, beta diversity within seral stages did not increase with increasing regeneration age in all but one case for trees, when abundance-based beta diversity within seral stages increased.

Temporal heterogeneity in environmental conditions may influence heterogeneity in tree species composition through local niche-based processes. Greater heterogeneity in environmental conditions may in turn lead to an increase in tree beta diversity within seral

stages. Age-related changes in forest canopy cover most likely drive changes in tree community composition (Grainger & van Aarde 2013). Mature regenerating sites tend to have large canopy gaps due to the collapse of *Vachellia karroo* individuals, which are senescent by about 30 to 40 years (Gourlay et al. 1996). Most tree species on average had higher abundance in these large canopy gaps (Grainger & van Aarde 2013). Perhaps trees regenerate with greater abundance due to increased light availability (Rüger et al. 2009; Grainger & van Aarde 2013). Increased heterogeneity in soil (van Aarde et al. 1998) and microhabitat conditions with age (Ott & van Aarde 2014) may also explain these patterns in tree communities. Ferreira & Aarde (2000) also proposed that gaps forming at different times might create patches of varying age within a given seral stage, which may influence the local recruitment of species, thereby potentially increasing heterogeneity. Few studies, however, have specifically tested this in regenerating coastal dune forest in our study area. However, Lawes et al. (2007) found that most species in coastal forests in my study region do not replace themselves in disturbed forest patches, but this was dependent on patch area size (larger patches had more self-replacement).

In contrast with the first hypothesis, beta diversity within seral stages in both the presence-absence of species and their relative abundances decreased with increasing regeneration age for millipedes (Fig. 3.2). For birds, only compositional dissimilarity in the presence-absence of species decreased with age (Fig. 3.3). A high degree of vertical and horizontal (open layer) heterogeneity early in succession may explain higher observed beta diversity in early successional stages compared with late stages (Bazzaz 1975; Kappelle et al. 1995). This may create greater variation in microclimate conditions, forest composition and structure, and other environmental conditions. As succession ensues, the open layer may become more characteristic of old-growth forest, which may favour fewer species that are better adapted. This may in turn lead to a decrease in beta diversity within seral stages.

It is likely that differences in reproduction and dispersal would lead to divergent patterns of compositional dissimilarity for diverse taxonomic groups (Anderson et al. 2005). Patterns of beta diversity within taxonomic groups may also be strongly affected by stochastic sampling effects (e.g. random inability to detect some species in a sampling site), resulting from variation in local species richness or alpha diversity (Chase & Myers 2011; Myers et al. 2015). This may be especially true for pairwise metrics such as Jaccard, which use presence-absence data to measure beta diversity (Koleff et al. 2003). For instance, within a given species pool, beta diversity is likely to decrease as alpha diversity increases (i.e. as the number of species in local communities approaches the total number of species in the regional pool), owing simply to sampling effects in species-rich communities. Conversely, beta diversity is likely to increase as alpha diversity decreases relative to the species pool (Chase & Myers 2011).

However, estimates of beta diversity in the presence-absence of species for trees were generally the highest, followed by incidence-based estimates for millipedes, and then birds. Moreover, birds generally had the lowest abundance-based beta diversity estimates compared with millipedes and trees. Taxonomic groups with poor dispersal ability (e.g. trees and millipedes) may present higher beta diversity compared with taxa that are more mobile, i.e. birds (da Silva et al. 2017). This is because taxa with superior dispersal ability such as birds tend to spread more easily and may thus have communities that are more similar (Korhonen et al. 2010; Soininen 2010). Differences in dispersal ability therefore most likely explain higher beta diversity estimates observed for tree and millipede communities compared with bird communities, as birds are active dispersers and can travel far distances to reach sites (Van Houtan et al. 2007).

In instances where age had no significant effect on beta diversity within seral stages, this may be because some species respond better to microhabitat conditions as opposed to

regeneration age. For example, forest associated species of millipede (e.g. keeled millipedes) seem to respond to topography independently of regeneration age (Ott & van Aarde 2014). Millipedes may also respond behaviourally to fine-scale temperature and moisture conditions (Hopkins & Read 1992; Olivier et al. 2017). For instance, millipede activity generally decreases during dry conditions and under high temperatures, which may result in undersampling (Bailey & Kovaliski 1993) and influence observed species richness (Olivier et al. 2017). This may in turn influence observed beta diversity. Different bird and tree species also seem to respond differently to explanatory variables. For example, some tree and bird specialists respond better to landscape variables such as distance to source forest than regeneration age (Grainger et al. 2011). This is in line with hypotheses that spatial variables are more likely to influence species with narrow-ranges (i.e. habitat specialists) while environmental variables are more likely to influence species with wider-ranges, i.e. habitat specialists (Wang et al. 2012).

Ontogenetic variation in habitat selection among age classes may also explain weak relationships observed between beta diversity and regeneration age. For example, one study showed that forest age was a strong predictor of adult tree species distribution during succession, whereas environmental variables such as soil explained the distribution of tree species in more juvenile classes (Schurman & Baltzer 2012). In this case, future studies on beta diversity should incorporate species-specific traits such as range size and age class. Functional and phylogenetic indices of beta diversity may thus be more enlightening on the effects of environmental heterogeneity during succession than taxonomic indices, which include only species identity (Chai et al. 2016).

Most community variables (e.g. species richness, density, and evenness) appear to respond well to succession-based coastal dune forest regeneration. For instance, greater heterogeneity in local environmental conditions such as soil (van Aarde et al. 1998), canopy

cover (Grainger & van Aarde 2013), and topography (Ott & van Aarde 2014) may provide more ecological niches for more species to occupy (Kritzing & van Aarde 1998; Wassenaar et al. 2005). This may in turn cause beta diversity to vary with succession. In my study, I only found partial support for the first hypothesis that beta diversity would increase with age. Instead, the beta diversity of millipedes and birds decreased. Further, this trend in compositional dissimilarity contrasted based on whether I included presence-absence or abundance information. Beta diversity is thus likely a function of regeneration age, but trends may differ depending on the taxonomic group under study and the inclusion of abundance information. If we want to make inferences regarding succession that are more comprehensive, it may be more useful to include multiple taxa and beta diversity indices that take into account the relative abundances of species. This may shed some light on the temporal changes in dominant species, as opposed to more rare species, to which beta diversity indices such as Jaccard are more sensitive.

A potential limitation in my study that may have influenced observed beta diversity trends may be incomplete sampling and/or the use of an inappropriate scale to estimate beta diversity. Undersampling may lead to bias and inaccurate results with low correlations and greater chance effects, especially for incidence-based measures (Beck et al. 2013). The latter is more likely given that previous work in the study region has shown that beta diversity patterns differ at coarse and fine sampling scales (Olivier & van Aarde 2014). In my study, analysis of beta diversity took place at the inter-site level. Each site yields a unique beta diversity value that may not represent beta diversity within a seral stage as such. Averaging pairwise dissimilarities across sites (Lennon et al. 2001; Vellend 2001; Anderson et al. 2013) may further lead to erroneous conclusions (Chen 2013). This is because pairwise estimates of beta diversity tend to be correlated (Diserud & Odegaard 2007). In addition, pairwise beta diversity cannot fully describe compositional dissimilarity when multiple sites share certain



species (Chao et al. 2008). There is now an emergent trend to quantify beta diversity at community (or multiple-site) level (Chen 2013).

*Does turnover (beta diversity 'between' seral stages) diminish with increasing regeneration age?*

In line with the second hypothesis, turnover (similarity between successive stages) in tree communities was high initially and then dwindled with increasing age distance (Table 3.2). This pattern is consistent with Connell & Slatyer's tolerance model (1977), Gleason's model of succession (1917), and the fugitive species concept (Elton 1927; Hutchinson 1951). Temporal changes in local species richness, which may influence similarity indices, may also explain the pattern of decaying similarity with increasing age distance for trees. This phenomenon describes the famous species–time relationship, where the number of species increases simply as a function of time (Rosenzweig 1995). As a result, species-poor communities may experience high turnover (high similarity) while those that are species-rich may experience low turnover (low similarity) (Shurin 2007). Thus, changes in species composition should be greater early in succession than resultant changes late in succession.

Similar with observed compositional dissimilarity, the amount of turnover observed in my study contrasted based on whether I measured similarity using abundance or presence-absence information. For all taxa, distance-decay in similarity was greater when I included abundance information, and the correlation of abundance-based turnover with age was stronger, but this was only significant for trees. Li et al. (2016) also found contrasting patterns of turnover during post-agricultural plant succession. They found that abundance-based turnover diminished with time, whereas turnover in the presence-absence of species did not change. In this case, the occurrence of a long-lived set of pioneers may impede compositional turnover in plant communities (Wassenaar et al. 2005; Meiners et al. 2015).

Theory predicts that dispersal-limited taxa will experience greater distance-decay in similarity than taxa that are mobile (Araújo & Pearson 2005; Qian et al. 2009; Lenoir et al. 2012; Fitzpatrick et al. 2013). My results are in line with this expectation, whereby turnover in tree communities was apparently more rapid than turnover in millipede and bird communities, with birds experiencing the least rapid turnover. Moreover, the halving distance was greatest for birds compared with millipedes and trees. A large halving distance indicates that turnover changed little with increasing temporal (i.e. age) distance, while a short halving distance implies that species turnover is highly time dependent. Short halving distances for trees and millipedes is also consistent with predictions that the halving distance will be smaller for taxa with poor dispersal ability (Soininen et al. 2007).

Little to no decay in similarity with increasing age distance, on the other hand, suggests that rates of colonization and mortality may not be a simple function of increasing diversity over time, as suggested by some authors (MacArthur & Wilson 1967; Manne et al. 1998). Instead, colonization and mortality rates, and thus turnover, may depend on other factors, such as microclimate, distance from source area, taxon-specific life history traits, and the availability of suitable habitat. Distance from source area can delay turnover if species are unable to disperse to sites due to either spatial obstructions or poor mobility (Soininen 2010). This factor may be less important for birds as opposed to millipedes, which are generally poor dispersers (Hopkins & Read 1992; Hamer & Slotow 2002; Redi et al. 2005). Alternatively, the temporal scale at which I measured species turnover may be too small to detect relevant changes in species composition between successive stages. Soininen et al. (2007) indeed predicted that the halving distance would be shorter for smaller study extents. Millipede communities may thus be showing a prolonged response to regeneration.

Taken together, my results suggest that regeneration age does drive changes in beta diversity within seral stages, but this may not lead to an increase in beta diversity for some

taxa. Rather, beta diversity within seral stages decreased with age for birds and millipedes. This is in line with recent predictions that beta diversity will respond differently for different taxa (Soininen et al. 2007). Where beta diversity within seral stages was comparable across the gradient of age, this may be because species itself may respond differently to regeneration age. The use of beta diversity indices based solely on species identity or relative abundances may thus be inappropriate. This approach does not take into account ecological differences between species (Ricklefs 2006), which may result in bias trends along successional gradients and the ecological processes underlying community assembly (Cornwell et al. 2006; Villéger et al. 2008; Chai et al. 2016). Likewise, regeneration age explained turnover only for trees, whereas millipedes and birds showed little to no change in species turnover along the successional sere.

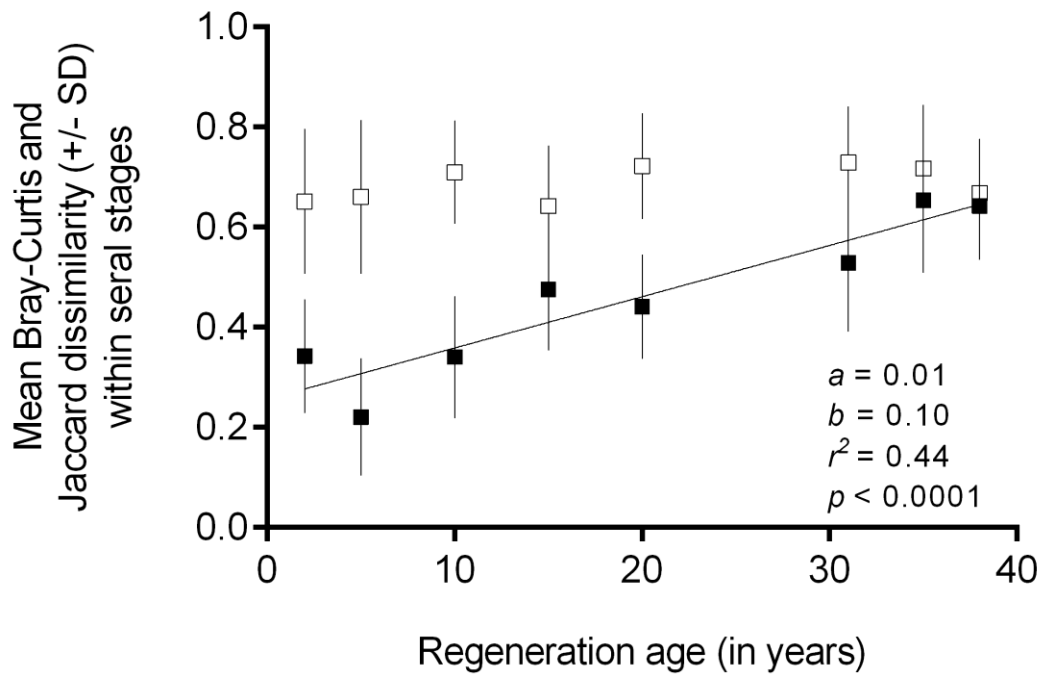
Further, patterns of beta diversity may not only depend on the taxa under study, but also the inclusion of abundance information (Li et al. 2016). My study showed that the inclusion of abundance information influenced observed temporal changes in community composition within seral stages, as well as observed turnover trends. It is therefore important to include abundance information over and above presence-absence information when analysing beta diversity, as succession may be operating on different aspects of the community, which may go unnoticed when using solely presence-absence data. Alternatively, other deterministic factors may be driving beta diversity in regenerating coastal dune forest. The use of other gradients relating with landscape (Grainger et al. 2011), management (Rehounková & Prach 2006), or climate (De Luis et al. 2001) may thus be more revealing than regeneration age (Rolo et al. 2016). Again, no change in beta diversity may also be the result of incomplete sampling or the use of an inappropriate scale to measure beta diversity, most likely being the latter.

**Table 3.1.** Number of sampling sites in seral stages of increasing regeneration age for analysis of beta diversity within seral stages for trees, millipedes, and birds.

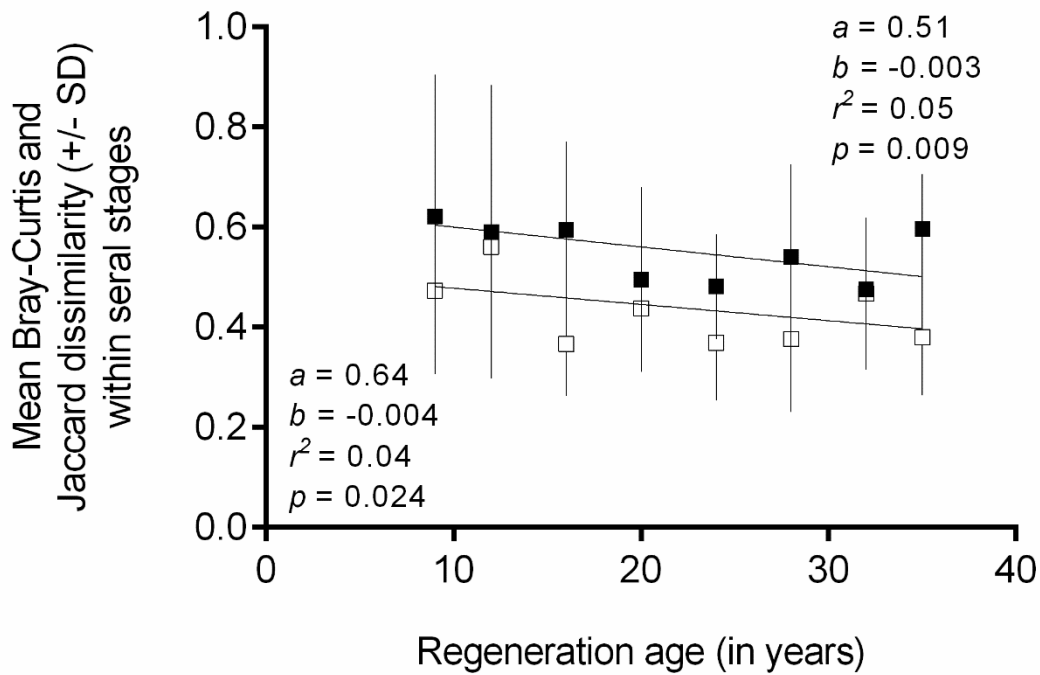
Regeneration age	Trees	Millipedes	Birds
5	X	X	10
9	X	9	10
12	15	6	10
15	15	X	10
16	X	4	X
19	15	X	10
20	X	4	X
23	15	X	10
24	X	6	X
27	15	X	10
28	X	7	X
31	15	X	10
32	X	8	X
35	15	X	10
38	15	6	10

**Table 3.2.** Results from binomial log-linear GLM fits of turnover along the gradient of age based on the Bray-Curtis ( $d_{BC}$ ) and Jaccard ( $d_J$ ) similarity measures for trees, millipedes, and birds.

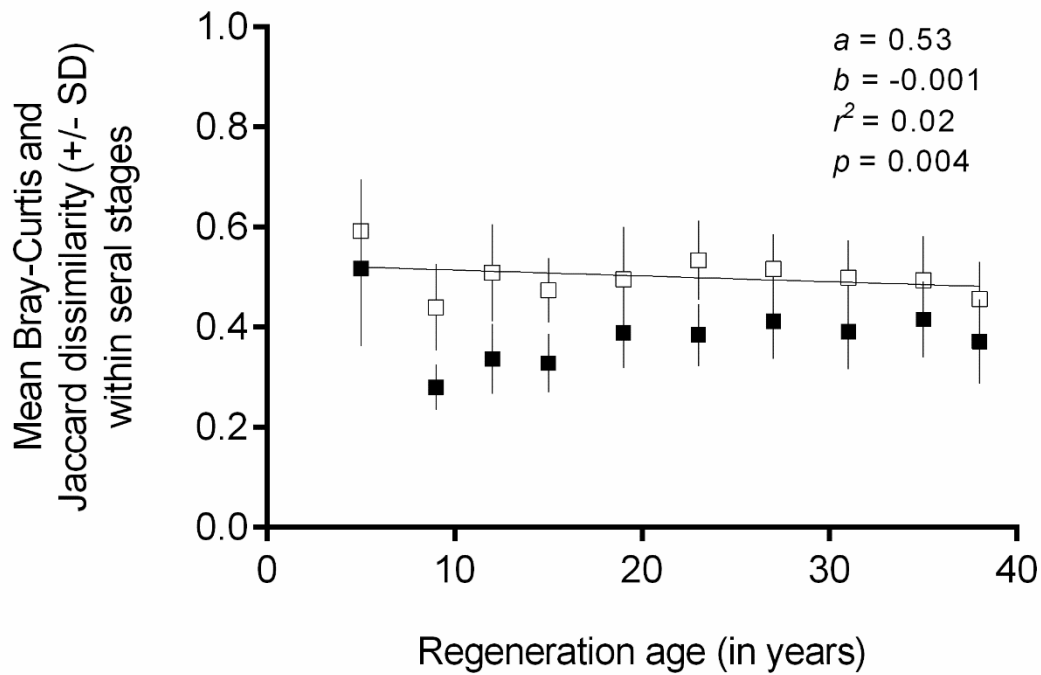
Taxa	Years of regeneration	$d_{BC}$					$d_J$				
		Intercept	Slope	Similarity at zero distance	Halving distance (years)	Mantel $\rho$	Intercept	Slope	Similarity at zero distance	Halving distance (years)	Mantel $\rho$
Trees	12 to 38	-0.58	-0.05	0.56	13.98	-0.63	-1.22	-0.03	0.30	26.52	-0.38
Millipedes	9 to 35	-0.81	-0.03	0.70	16.05	-0.17	-0.58	-0.02	0.56	42.55	-0.16
Birds	5 to 38	-0.79	-0.03	0.46	27.62	-0.47	0.08	0.01	0.04	6.64	-0.41



**Figure 3.1.** Mean Bray-Curtis (closed squares) and Jaccard (open squares) dissimilarity ( $\pm$  SD) among all pairs of survey sites within seral stages as a function of regeneration age for tree communities (N=120). The solid black line denotes the regression line. The goodness of fit ( $r^2$ ) and the intercept and slope coefficients ( $a$  and  $b$ , respectively), as well as the P value ( $p$ ), from the least squares nonlinear regression model are shown here. For each data set, I analysed 840 pairwise dissimilarity values (not shown here, but see Supplementary material Appendix III).



**Figure 3.2.** Mean Bray-Curtis (closed squares) and Jaccard (open squares) dissimilarity ( $\pm$  SD) among all pairs of survey sites within seral stages as a function of regeneration age for millipede communities (N=50). The black lines represent the regression lines. The goodness of fit ( $r^2$ ) and the intercept and slope coefficients ( $a$  and  $b$ , respectively), as well as the P value ( $p$ ), from the least squares nonlinear regression model are shown here. Results from least squares nonlinear regression based on the Bray-Curtis dissimilarity index ( $d_{BC}$ ) are at the bottom left corner while results based on Jaccards' index ( $d_j$ ) are at the top right corner. For each data set, I analysed 142 dissimilarity values (not shown here, but see Supplementary material Appendix III).



**Figure 3.3.** Mean Bray-Curtis (closed squares) and Jaccard (open squares) dissimilarity ( $\pm$  SD) among all pairs of survey sites within seral stages as a function of regeneration age for bird communities (N=100). The black line represents the regression line. The goodness of fit ( $r^2$ ) and the intercept and slope coefficients ( $a$  and  $b$ , respectively), as well as the P value ( $p$ ), from the least squares nonlinear regression model are shown here. I analysed 450 pairwise dissimilarity values for each data set (not shown here, but see Supplementary material Appendix III).



# **CHAPTER 4**

## **DETERMINISTIC PROCESSES PRIMARILY SHAPE BETA DIVERSITY DURING COASTAL DUNE FOREST SUCCESSION**

### **4.1. INTRODUCTION**

Broadly, two ecological processes control the assembly of species into local communities, the first being niche-based processes and the second being dispersal limitation processes. Niche-based processes include local abiotic and biotic factors, which with species traits, determine the distribution of species (Tilman 1982; Chase & Leibold 2003). Energy (Currie 1991), water availability (Francis & Currie 2003; O'Brien 2006), climatic variability (Stevens 1989; Currie & Low 2001), disturbance (Fang et al. 2006; Nogués-Bravo et al. 2008), and habitat heterogeneity (Kerr & Packer 1997) are all abiotic factors that may affect species distributions (Wang et al. 2012). Biotic factors, on the other hand, may include competition and predation (Srivastava et al. 2008; Gilbert et al. 2009). The second mechanism is associated with dispersal limitation (Hubbell 2001; Vellend 2010; Chase & Myers 2011). Dispersal limitation induced by species traits or landscape barriers is an important constraint on assembling communities (Verheyen & Hermy 2001; Verheyen & Hermy 2004; Flinn & Vellend 2005; Grainger et al. 2011).

Dispersal-based processes such as dispersal limitation may be more important than environmental filtering immediately after a disturbance, as dispersal constraints may determine which species can disperse to disturbed sites. As species propagules attempt to colonise disturbed sites, environmental filtering effects, along with the competitive displacement of

species, may become increasingly more important. Yet, the relative importance of dispersal limitation and environmental filtering is not that straightforward, and may depend on various factors such as the life stage of species (Yang et al. 2016), type of disturbance (Chase 2007), and habitat connectivity (Chase 2003). While the relative importance of these processes may differ during community assembly, both dispersal- and niche-based processes can alter beta diversity in a stochastic or deterministic way (Chase et al. 2009; Chase & Myers 2011; Segre et al. 2014).

Community assembly and succession share similar concepts (Chang & HilleRisLambers 2016). Succession describes the recovery of communities and trajectories over time after a disturbance (Clements 1916), while community assembly describes the rules and processes shaping local diversity patterns within a region (Diamond 1975; Connell & Slatyer 1977; Weiher & Keddy 1995). Both succession and community assembly recognise the importance of dispersal, the abiotic and biotic environment, and random events, however, the former posits assembly processes in a temporal framework and highlights the importance of priority effects (Chang & HilleRisLambers 2016), i.e. the order in which species arrive (Grman et al. 2013; Zhou et al. 2014). Studies of succession may thus afford the chance to understand community assembly from a known onset (Meiners et al. 2015; Chang & HilleRisLambers 2016).

Null models combined with beta diversity indices can provide insight into the importance of deterministic and stochastic community assembly processes during succession (Zhou et al. 2014; Jonsson et al. 2016; Li et al. 2016; Mi et al. 2016). Theory predicts that community composition will be similar early in succession simply owing to dispersal and environmental filtering effects (Connell & Slatyer 1977; Weiher & Keddy 1995; Douma et al. 2012; Chang & HilleRisLambers 2016). This may result in low beta diversity, as wide-ranged species (habitat generalists) usually respond first to disturbance and establish populations early in succession (Hadly & Maurer 2001) while narrow-ranged species (habitat specialists) largely

depend on specific habitat features associated with forest age (DeGraaf & Yamasaki 2003; Wilson et al. 2006). For instance, birds recorded in regenerating coastal dune forest sites are typically generalist species (e.g. weavers). While some forest specialists such as Narina Trogon and Blue-mantled Crested-flycatcher occur in regenerating sites, most specialist species such as forest weaver only occur in mature forest (Kritzinger & van Aarde 1998). As succession ensues, environmental conditions may change and interspecific competition may increasingly play a more important role in influencing community composition (Callaway & Walker 1997; Chang & HilleRisLambers 2016). Environmental responses and biotic interactions therefore may, according to theory, lead to increasingly more dissimilar community composition, or high beta diversity. Stochastic forces such as priority and sampling effects may however make communities more dissimilar, regardless of environmental conditions (Chase 2003). In this case, the outcomes of forest succession may be unpredictable (Mi et al. 2016), leading to random beta diversity (Chase 2003).

In this study, I aimed to assess the relative importance of deterministic and stochastic community assembly processes in influencing beta diversity patterns during coastal dune forest succession for three taxa (trees, millipedes, and birds). To do this, I used a null model approach (Chase et al. 2011). Püttker et al. (2015) used a similar approach to determine the relative influence of stochastic and deterministic processes in influencing patterns of beta diversity across a gradient of habitat loss (Püttker et al. 2015). They found that deterministic processes primarily structure mammal communities. As found in recent studies, environmental filtering and/or dispersal limitation govern community assembly during early succession, while interspecific competitions control assembly late in succession (Letcher 2010; Ding et al. 2012; Purschke et al. 2013; Rolo et al. 2016). Niche complementarity becomes increasingly more important with time (Cardinale et al. 2007; Fargione et al. 2007). This theory states that there are different types of habitat niches that species can exploit in complementary ways (Fargione

et al. 2007). I therefore expect ecological processes such as environmental filtering and/or dispersal limitation to be more important early in succession, while niche complementarity become increasingly more important late in succession, leading to an increase in beta diversity within seral stages. I also expect changes in species composition (i.e. species turnover) to be a function of regeneration age. Here, I defined species turnover as the dissimilarity in species composition (presence-absence) between the earliest successional stage and later stages (i.e. between consecutive time steps). Further, I expect that taxa will respond similarly to restoration.

## **4.2. MATERIALS AND METHODS**

### *Null model of beta diversity*

Here I used the Raup-Crick metric (Raup & Crick 1979) modified by Chase et al. (2011) to estimate beta diversity *within* and *between* seral stages. For the purpose of this study, I mainly used the Raup-Crick metric to gauge the relative importance of deterministic and stochastic community assembly processes during coastal dune forest succession. This metric also accounts for differences in species richness among survey sites. Treating species frequencies as weights, the Raup-Crick function calculates compositional dissimilarity between a pair of sites through repeated random draws of the observed number of species in each site, and compares the pairwise similarity between these random sites to the observed similarity between communities. The function then returns a dissimilarity value ranging from -1 to 1. These values represent the proportion of random sites that results in the same or greater number of shared species compared to the observed. Negative values indicate community dissimilarity less than would be expected by chance, while positive values indicate community dissimilarity more than would be expected by chance. A value close to 0 indicates random community assembly.

The group of species observed across sites within a region usually represents the regional species pool (Chase et al. 2011). I therefore defined the regional pool as all species observed across the successional sere for a given taxa. This metric originally only used presence-absence data, but now it can be adapted to abundance data ( $\beta_{RC-abun}$ ) (Püttker et al. 2015). For the abundance-based null model, counts of species were included instead of just species identity. To define the regional pool, I used the total number of individuals per species observed across the successional sere (all seral stages).

I ran 9999 random draws for each pair of sites in both sets of analyses. I then calculated the mean  $\beta_{RC}$  and  $\beta_{RC-abun}$  ( $\pm$  SD) of survey sites *within* seral stages and the mean  $\beta_{RC}$  ( $\pm$  SD) *between* survey sites in the earliest seral stage and sites in successive stages (i.e. species turnover). A positive mean value (close to 1) implies deterministic processes such as dispersal limitation and/or environmental filtering that tend to favour more similar community composition or lower beta diversity than expected by chance. A negative mean value (close to -1) on the other hand implies deterministic processes such as niche specialisation and competition that tend to favour more dissimilar community composition or higher beta diversity than expected by chance. A mean value close to 0 implies stochastic community assembly that may lead to unpredictable beta diversity. I compared mean  $\beta_{RC}/\beta_{RC-abun}$  within seral stages across the gradient of age to assess the first hypothesis. To assess the second hypothesis, I compared mean  $\beta_{RC}$  between the earliest stage and successive stages (i.e. between time steps). Sample size (i.e. the number of sites within a seral stage) may influence the precision of probabilistic metrics such as Raup-Crick, but having a different number of sites does not pose any problems when comparing estimates. I used R, version 3.3.1, to run the null model analysis (R Core Team 2016). I calculated  $\beta_{RC}$  using the R-script supplied by Chase et al. (2011). To calculate  $\beta_{RC-abun}$ , I obtained the R-script from the first author of Püttker et al.

(2015). To visualise patterns of mean  $\beta_{RC}/\beta_{RC-abun}$  along the age gradient, I used GraphPad Prism 6.

### 4.3. RESULTS

The total number of species per seral stage generally increased with increasing regeneration age (Supplementary material Appendix II). Of the 75 species of tree, we recorded 19 species in the earliest stage and 42 in the oldest stage. Of the 17 millipede species, we recorded 8 species in the youngest stage and 12 in the oldest. We recorded 43 birds in the youngest stage and 55 in the oldest stage (out of 115 bird species). Likewise, mean species richness per survey site was lowest in the youngest seral stage compared with the oldest stage for all taxa (Supplementary material Appendix II).

#### **Do deterministic processes increase with increasing regeneration age, leading to an increase in beta diversity ‘within’ seral stages?**

##### *Trees*

There was no discernible trend in mean  $\beta_{RC}$  within seral stages with increasing regeneration age (Fig. 4.1). Mean values were negative and comparable across the gradient of age (-0.55 to -0.88). This suggests that beta diversity was lower than expected by chance, which may imply the greater importance of environmental and/or dispersal filtering, as these processes tend to produce similar community composition by reducing the functional space that species may occupy. In contrast, mean  $\beta_{RC-abun}$  showed a distinct trend with age (Fig. 4.1). Mean values generally increased with increasing regeneration age, as well as deterministic processes that favour high beta diversity (compositional dissimilarity). Mean  $\beta_{RC-abun}$  values were negative and close to -1 early in succession, which may imply a environmental filtering and/or dispersal

filtering effects. Late in succession, mean values were positive and close to 1 late in succession, which may imply deterministic processes such as niche complementarity which may increase the functional space in a community. Values were close to 0 at intermediate stages of succession, indicating stochastic community assembly.

### *Millipedes*

Similar to tree communities, there was no discernible trend in mean  $\beta_{RC}$  within seral stages of increasing age (Fig. 4.2). Mean values were all negative (-0.22 to -0.62), suggesting the dominance of environmental filtering and/or dispersal limitation during succession. Mean  $\beta_{RC-abund}$  within seral stages, however, showed an increasing trend across the gradient of age, but mean values were all positive (0.38 to 0.97) (Fig. 4.2). This suggests the greater importance of niche complementarity in influencing millipede communities.

### *Birds*

Similar to trees and millipedes, mean  $\beta_{RC}$  within seral stages did not show a clear trend with age (Fig. 4.3). Mean values were negative and comparable across the age gradient (-0.75 to -1), suggesting strong environmental and/or dispersal filtering. When including abundance information, however, mean  $\beta_{RC-abund}$  within seral stages increased with increasing regeneration age (Fig. 4.3). Mean values were generally close to or approaching -1 early in succession (with one potential outlier) and positive late in succession. Deterministic processes were still important late in succession for birds but mean values were closer to 0 than 1. This suggests the weaker influence of deterministic processes late in succession for birds compared with trees.

## **Are changes in species composition functions of successional age?**

### *Trees*

Mean  $\beta_{RC}$  values between consecutive stages were all negative (-0.16 to -0.62) (Fig. 4.4). However, mean  $\beta_{RC}$  was close to -0.5 early in succession and then increased abruptly at intermediate stages of succession, approaching 0 towards the end of succession (Fig. 4.4). This suggests that changes in species composition increased abruptly (i.e. high species turnover) at intermediate stages of succession.

### *Millipedes*

Mean  $\beta_{RC}$  values between consecutive stages were all negative (-0.20 to -0.53) (Fig. 4.5). Mean  $\beta_{RC}$  between the youngest stage and later stages were comparable and close to -0.5, but increased slightly late in succession (Fig. 4.5). This suggests that there was little to no turnover in species composition for millipedes.

### *Birds*

Mean  $\beta_{RC}$  between successive stages increased abruptly early in succession and came close to or approached 0 at intermediate stages of succession (Fig. 4.6). Thereafter, mean  $\beta_{RC}$  between successive stages were comparable. This suggests that changes in species composition were more abrupt early in succession, accompanying low levels of species richness observed in early successional stands, plateauing towards the end of succession.

## **4.4. DISCUSSION**

A recent study by Rolo et al. (2016) suggests that deterministic processes associated with niche complementarity replaced those associated with environmental filtering and/or dispersal limitation as coastal dune vegetation in my study area developed. The results of my study support this notion in trees, but also show that inferences made about the processes driving



dune forest development may depend on the actual abundance of species and the taxa under study.

Community assembly during succession may be predictable due to deterministic processes such as dispersal limitation and environmental filtering, as well as niche specialisation and biotic interactions such as facilitation and competition (Chang & HilleRisLambers 2016). This may lead to predictable patterns of beta diversity over the course of succession. For example, theory predicts that dispersal limitation and/or environmental filtering will lead to similar community composition or low beta diversity early in succession (Hypothesis 1) while niche specialisation and/or competition will lead to increasingly more dissimilar community composition or higher beta diversity as succession progresses (Hypothesis 2). Contrary to these expectations, and even though species richness appeared to increase with successional age, compositional dissimilarity (beta diversity) was lower than expected by chance in all seral stages for all taxa when including only presence-absence information.

This would suggest that community assembly during coastal dune forest succession is an artefact of environmental and/or dispersal filtering, regardless of seral stage. Given the approach I used in this study, which focused on three taxonomic groups with varying dispersal ability, dispersal limitation is most likely an important factor generating patterns of beta diversity. The importance of environmental filtering, on the other hand, is less clear, but separating the joint effects of multiple environmental and spatial variables may help to overcome this problem (Stegen et al. 2013). In the case of regenerating coastal dune forest in my study area, these results may reflect dispersal constraints associated with more narrow-ranged species and the surrounding landscape (Redi et al. 2005; Grainger et al. 2011). Dispersal limitation usually favours wider-ranged species, which may disperse far and establish large populations early in regeneration. This may lead to more homogenous community composition

within seral stages of varying age if some species are unable to colonise regenerating sites (Vellend et al. 2007; Chase 2007).

However, the strength of environmental and/or dispersal filtering effects, as implied by the size of Raup-Crick estimates of the mean, was generally weaker for trees and millipedes compared with birds. The size of the local community may have influenced the strength of environmental/dispersal filtering effects (Chase & Myers 2011). For instance, if the ‘realised’ species pool is very low or very high relative to the regional pool, beta diversity will be as dissimilar as expected by chance. Earlier studies indeed show that some species that were highly dominant in young seral stages became less abundant in mature stages, while uncommon species became more abundant (van Aarde, Ferreira & Kritzing 1996a; Kritzing & van Aarde 1998; Redi et al. 2005; Davis et al. 2013; Grainger & van Aarde 2012). This suggests that during regeneration the likelihood of occurrence is disparate among species and linked with species abundance (Grainger & van Aarde 2013). Several studies indeed show that community responses in regenerating coastal dune forest are largely species-specific (Ott & van Aarde 2014; Grainger et al. 2011) and functionally-related (Rolo et al. 2017). Deterministic processes, in this case probably associated with species traits (e.g. dispersal ability, feeding guild), most likely influence coastal dune forest regeneration.

When including abundance information, there was a clear shift from environmental and/or dispersal filtering early in succession to niche complementarity late in succession, leading to an increase in abundance-based beta diversity within seral stages. However, this was only apparent for trees and birds. This result is in agreement with the first hypothesis and may result from increasing environmental complexity with increasing regeneration age (Kritzing & van Aarde 1998; van Aarde et al. 1998; Grainger & van Aarde 2013; Ott & van Aarde 2014). Many studies have shown a positive relationship between environmental heterogeneity and beta diversity in both terrestrial (Veech & Crist 2007; Questad & Foster 2008; Crandall & Platt

2012; Stegen et al. 2013) and aquatic ecosystems (Anderson et al. 2013; Astorga et al. 2014; Heino et al. 2015). Greater environmental heterogeneity over the course of succession can cause beta diversity to increase deterministically as environments that are more heterogeneous provide suitable conditions for a larger number of species with different ecological niches, thereby increasing the realised species pool (Allouche et al. 2012; Brown et al. 2013). Environmental heterogeneity can also have an opposing effect on different species (Dornelas et al. 2009). For instance, previous work has encountered a positive effect of environmental heterogeneity on the abundance of rare species (Benedetti-Cecchi et al. 2008). Density-dependent processes, in this case apparently favouring rare species, may thus drive community changes over time (Chesson & Warner 1981; Volkov et al. 2005; Azaele et al. 2006; Benedetti-Cecchi et al. 2008).

Successional changes may also occur via shifts in the most dominant species (Li et al. 2016). A few species may spread rapidly and persist temporally, but may gradually lose dominance in favour of better competitors or as abiotic conditions change due to changes in the forest structure. Collectively, these findings suggest that ecological processes associated with niche complementarity and/ or competition may replace those associated with environmental filtering and/or dispersal limitation during succession (Rolo et al. 2016), even though beta diversity was already higher than expected by chance for millipede communities throughout succession. Functional diversity indices may provide a more informative way to measure the influence of niche complementarity on community composition. For instance, Rolo et al. (2016) used functional diversity indices to test whether the traits of species converged or diverged over the course of coastal dune forest regeneration in my study area. Trait divergence or high functional diversity may indicate niche complementarity as more specialised forest species gradually replace generalists and there is less niche overlap. Dune forest restoration, driven by succession, may thus impose strong ecological filtering, leading to

greater compositional dissimilarity in species abundances within seral stages, but not their presence-absence. Given that rare species are sensitive to environmental variation, they may play an important role during succession (Benedetti-Cecchi et al. 2008).

Although bird and tree communities experienced a similar shift in community assembly processes, mean estimates for birds late in succession indicate that the influence of deterministic processes such as niche complementarity may be weaker for birds than trees. Zhou et al. (2013) proposed that, in a highly connected, “fluidic”, system, ecological filtering would lead to more predictable beta diversity after disturbance, but as succession ensued, stochasticity would increase because of higher dispersal rates and/or ecological drift. Even though Zhou et al. (2013) applied this theory to microbial communities, the response of birds, which are active dispersers, is consistent with this idea. Local conditions that are more similar to old-growth forest levels could also lead to a stronger effect of stochastic processes. Rolo et al. (2017) found that, as regenerating coastal dune forest matured, the number of bird species and their abundances, except for large frugivorous birds, developed towards old-growth forest levels. These findings, along with the results of Kritzing and van Aarde (1998), suggest that birds can make use of undeveloped forest and probably recover faster than trees (Crouzeilles et al. 2016; Rolo et al. 2017).

Previous studies that followed a similar analytical approach than the one I used also found a discrepancy when using presence-absence versus abundance information (Püttker et al. 2015; Li et al. 2016; Jonsson et al. 2016). This may be because presence-absence data cannot produce reliable relationships between community variables (i.e. beta diversity) and local factors (i.e. regeneration age), as all species may extend their distributions away from typical locales where their populations numerically dominate other species (Roff et al. 2011). Additionally, abundance-based beta diversity includes more information, i.e. individuals rather than species. As a result, mean values tend to be greater by increasing the likelihood of pairwise

dissimilarity (Püttker et al. 2015). In other words, even if species occur at all sites it is unlikely that the number of individuals will be the same across sites, which probably explains higher beta diversity late in succession. Lower beta diversity early in regeneration is most likely due to the dominance of a few species, typically generalists. For example, *V. karroo* was the most abundant tree species in young rehabilitating stands. The use of presence-absence data alone to make inferences about the ecological processes that shape beta diversity may thus be inappropriate.

When including only presence-absence information, beta diversity within seral stages did not change across the gradient of age, but beta diversity between seral stages increased. However, there were some inconsistencies among taxa. Bird species composition in the youngest stage was highly dissimilar relative to species composition in the oldest stage (Fig. 4.3c). Of the 115 bird species, we recorded only 43 species in the youngest stage compared with over 65 in more mature stages. Some of CERU's previous work has observed an increase in bird species richness with increasing regeneration age (Kritzing & van Aarde 1998). My results further suggest that changes in species composition increase quickly early in succession and then level off in advanced stages. This pattern is in line with former predictions (Drury & Nisbet 1973), and may arise because the number of available niches decreases and interspecific competition intensifies late in succession (Peet & Christensen 1988). A reduction in the regional species pool as more species enter the local community and establish may also generate this pattern (Tilman 1997). However, my findings suggest that bird communities in the earliest stage are not nested subsets of species-rich communities in advanced stages, but experience high species turnover.

Furthermore, habitat specificity may also induce changes in species composition with regeneration or successional age. For instance, Zitting Cisticola (*Cisticola juncidis*) only occurred in the earliest seral stage in my study area. This species is very widespread and

common in both natural (e.g. grasslands and wetlands) and anthropogenic habitats (e.g. croplands). The Yellow-throated Warbler (*Phylloscopus ruficapilla*), a forest specialist, however, was exclusive to the oldest seral stage. Turnover is therefore most likely the result of habitat differences between successive seral stages (Kritzing & van Aarde 1998). Furthermore, the development of vegetation from grassland to woodland to forest during regeneration may enable bird species with narrower ranges to establish, as well as promote an increase in forest specialists (Kritzing & van Aarde 1998; Wilson et al. 2006).

Tree species composition in the youngest seral stage differed from the oldest stage (Fig. 4.4). However, changes in species composition increased abruptly at intermediate stages of succession as opposed to early in succession. This pattern was less apparent for millipedes, but still similar. For instance, *Orthoporoides pyrocephalus*, a species of millipede, was exclusive to the oldest stand. This species is associated with forest and mostly prefers trees (field observation). Another millipede species, *Centrobolus rugulosus*, was found exclusively late in succession, and is a forest specialist. While there are some new species present at advanced stages (i.e. *O. pyrocephalus* and *C. rugulosus*), most millipede species, including forest specialists, are present in most stands, regardless of successional stage, and without much replacement. Changes in forest canopy cover may explain high species turnover between intermediate and advanced successional stages. As vegetation progresses from completely unshaded to shaded early in succession and then decreasing shade cover late in succession (Davis et al. 2013), interspecific competition may increase (Sousa 1979). Large openings in the canopy very early in regeneration become a mosaic of small openings as succession ensues, so that mid- to late-successional species can make use of habitat better than early successional species (Grainger & van Aarde 2013; Davis et al. 2013).

My results suggests that tree and millipede communities may not have reached equilibrium (Connell 1978), as previously suggested (Gleason 1926; Egler 1954; Anderson

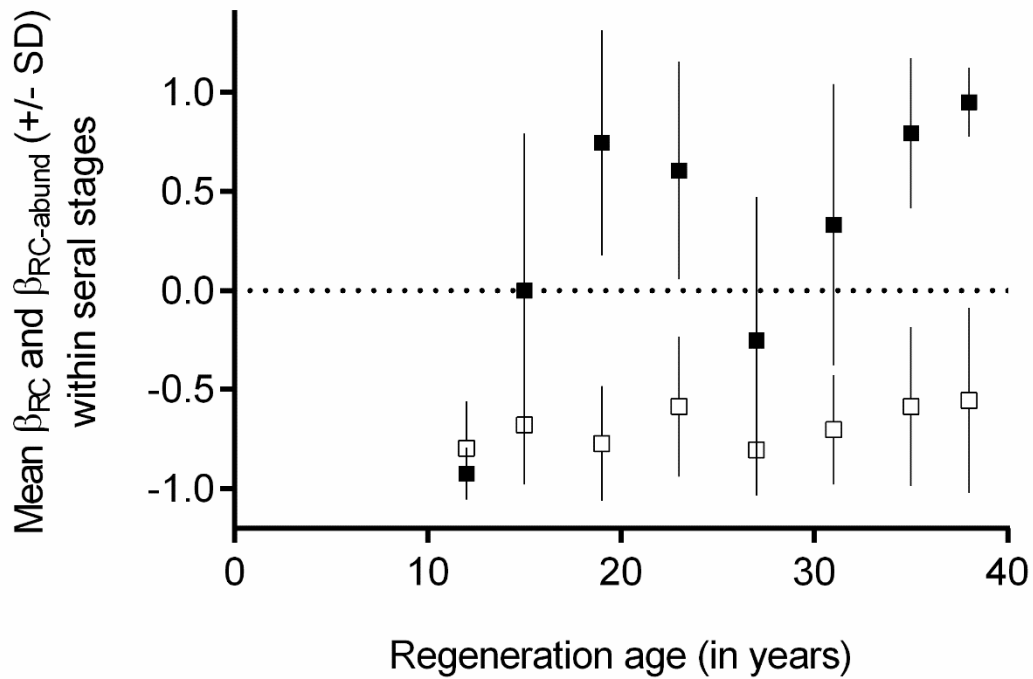
2007). However, the temporal scale (40 years) of this study may be too short. Forest succession may last centuries compared with the timescale used in this study (Finegan 1996; Olander et al. 1998; Bruelheide et al. 2011). Alternatively, stochastic community assembly processes associated with demography, immigration, and dispersal may strongly influence early successional species (Bruelheide et al. 2011; Mi et al. 2016; Li et al. 2016). On the other hand, early colonisers may inhibit the establishment of later colonisers (Fukami et al. 2005). For example, *V. karroo* may develop monospecific stands and arrest succession in regenerating coastal forests elsewhere (Boyes et al. 2011). However, forests in my study area are likely regenerating through the expiration of this pioneer (Grainger & van Aarde 2013). This pattern is consistent with a mechanism of facilitation, and not one of inhibition (Connell & Slatyer 1977). In addition, the formation of canopy gaps due to the eventual collapse of *V. karroo* trees may promote heterogeneity in light conditions, which may increase the importance of deterministic, niche-based processes (Grainger & van Aarde 2013). Little-to-no species turnover early in succession may also be because some species do not completely replace other species. Instead, differences in abundance may drive changes in community composition and structure during succession (Sarmiento et al. 2003). For instance, species present in older sites may not entirely replace species that are typically dominant in young sites, but may occur in larger numbers. Sarmiento et al. (2003) found a similar pattern during forest succession in tropical mountains. This is likely given that regeneration age had a positive effect on abundance-based beta diversity within seral stages.

Compositional changes in animal communities are likely to reflect successional changes in vegetation (Kritzinger & van Aarde 1998). Despite a few idiosyncrasies, my findings attest to this. There might be a specific association between trees and birds. The corresponding period (11 to 25 years of age) when beta diversity within seral stages became more deterministic than stochastic is particularly important. This shift may reflect improved

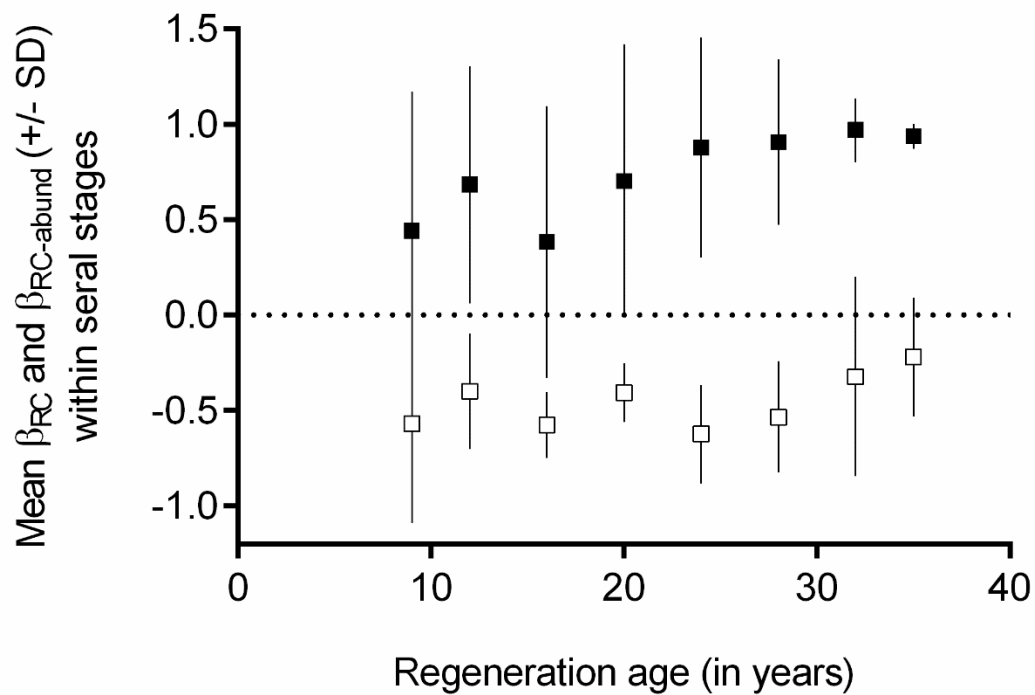
local environmental conditions (e.g. soil and light conditions for trees). Earlier studies that focus on trees and birds also detected similarities in beta diversity patterns (Jankowski et al. 2013).

Idiosyncrasies show the taxonomic dependency of beta diversity estimates and inferred processes (Soininen & Hillebrand 2007), and provide evidence against the notion that community responses are uniform along environmental gradients (Fukami et al. 2005; Chase 2010). Taken together, my results suggest that environmental filtering and/or dispersal limitation is prevalent throughout dune forest succession for all taxa, although the effect of deterministic processes may be weaker for birds than trees or millipedes. Ecological filtering could in turn lead to homogenous community composition (low beta diversity), which may pose a problem for forest specialists. When abundance information was included, however, the importance of deterministic processes increased with increasing regeneration age, so that, late in succession, communities were more heterogeneous in terms of species abundances. Furthermore, early successional stages are disproportionately dissimilar in terms of species composition from mature stages, and not merely a product of species richness differences.

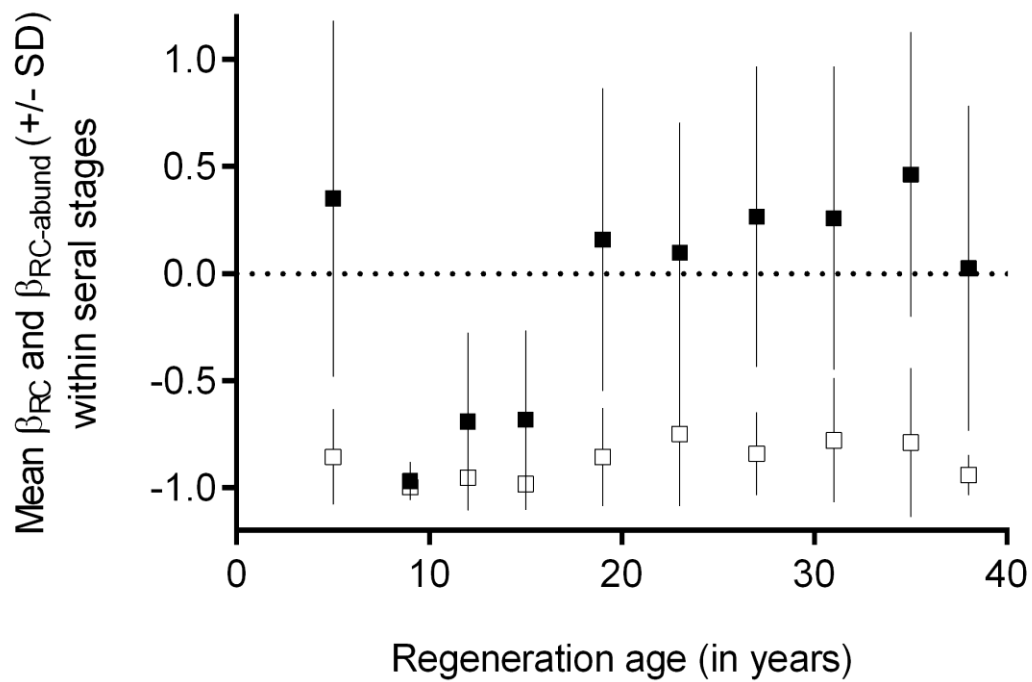




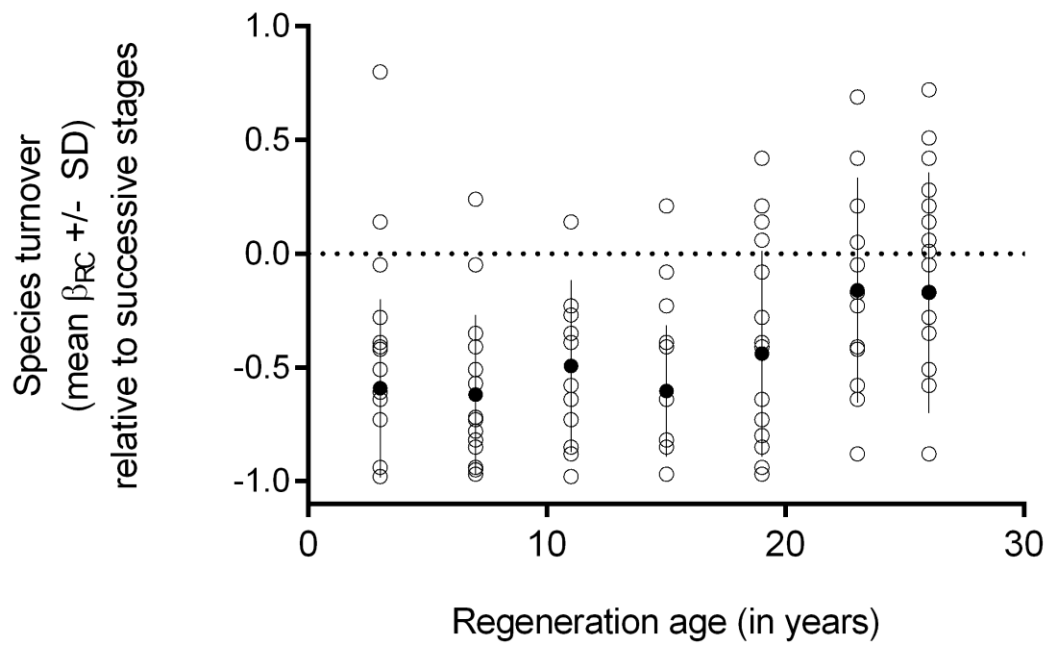
**Figure 4.1.** Mean compositional dissimilarity ( $\pm$  SD) among survey sites within seral stages of increasing regeneration age based on  $\beta_{RC}$  (open squares) and  $\beta_{RC-abund}$  (closed squares) for tree communities (N=120). The dotted horizontal line represents a mean value of zero, which indicates community assembly that is predominantly stochastic relative to the regional species pool. A mean values close to -1 implies deterministic processes that favour less dissimilar community composition than expected by chance, while a mean value close to 1 implies deterministic processes that favour more dissimilar community composition than expected by chance.



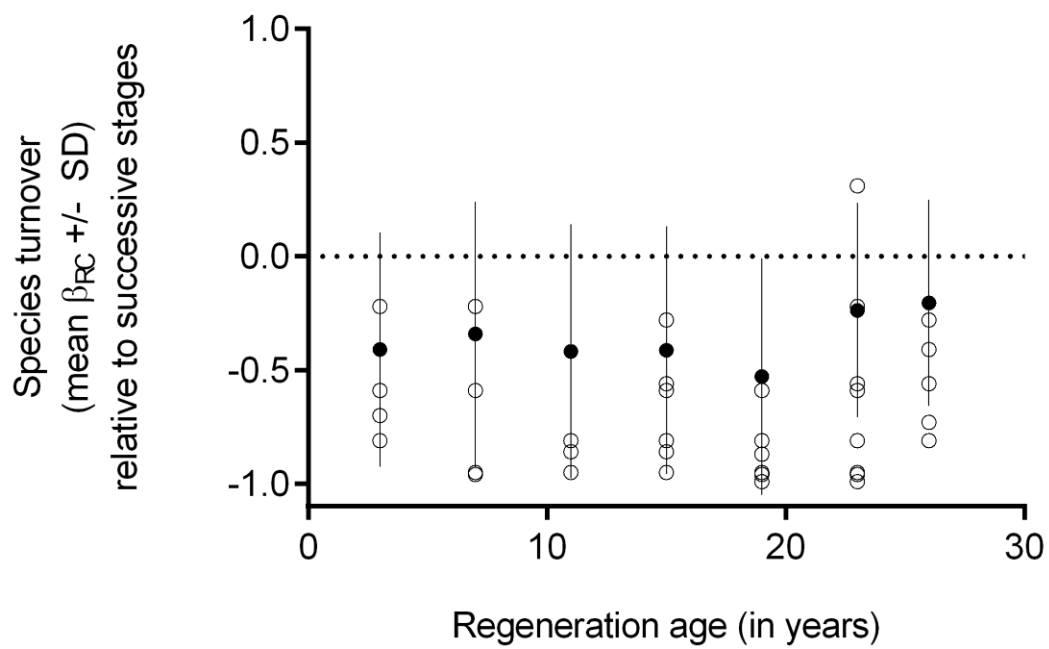
**Figure 4.2.** Mean compositional dissimilarity ( $\pm$  SD) among survey sites within seral stages as a function of regeneration age based on  $\beta_{RC}$  (open squares) and  $\beta_{RC-abund}$  (closed squares) for millipede communities (N=50). The dotted horizontal line represents a mean value of zero, which indicates stochastic community assembly. A mean values close to -1 or 1 implies deterministic community assembly processes that favour less or more dissimilar community composition than expected by chance, respectively.



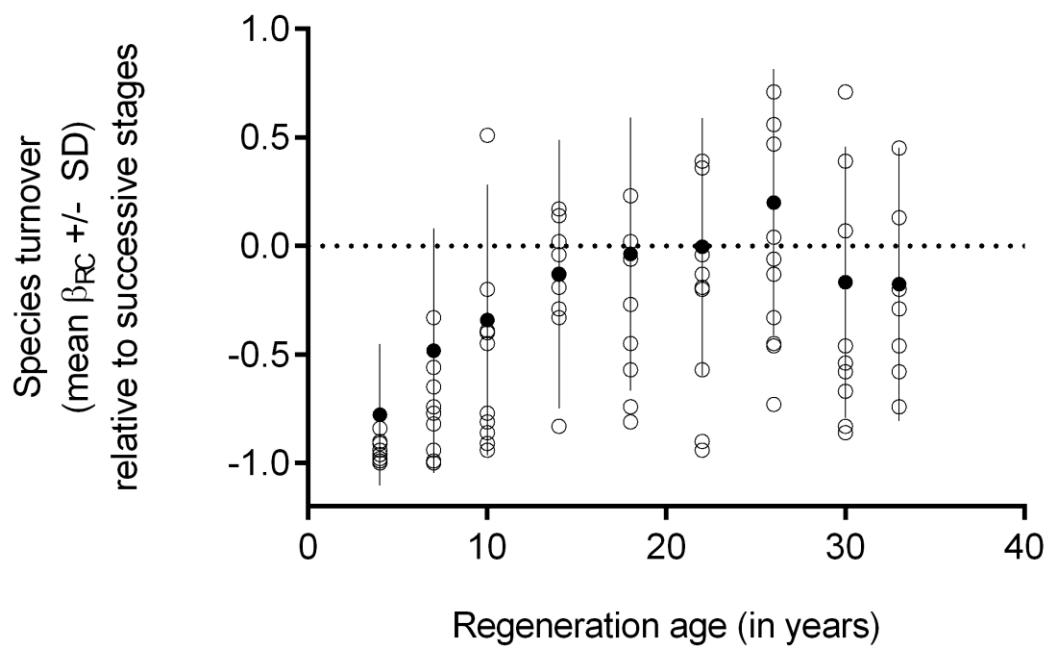
**Figure 4.3.** Mean compositional dissimilarity ( $\pm$  SD) among survey sites within seral stages of increasing regeneration age based on  $\beta_{RC}$  (open squares) and  $\beta_{RC-abund}$  (closed squares) for bird communities (N=100). The dotted horizontal line indicates stochastic community assembly, while a mean value close to or approaching -1 or 1 implies deterministic community assembly.



**Figure 4.4.** Mean  $\beta_{RC}$  ( $\pm$  SD) between survey sites in the youngest successional stage and sites in older successional stages as a function of regeneration age for tree communities (N=120). Here, there were 105 dissimilarity values from which to calculate the mean. Closed circles represent the mean dissimilarity values. Open circles represent the dissimilarity values.



**Figure 4.5.** Mean  $\beta_{RC}$  ( $\pm$  SD) between survey sites in the youngest successional stage and sites in older successional stages as a function of regeneration age for millipede communities (N=50). Here, there were 41 dissimilarity values from which to calculate the mean. Closed circles represent the mean dissimilarity values. Open circles represent the dissimilarity values.



**Figure 4.6.** Mean  $\beta_{RC}$  ( $\pm$  SD) between survey sites in the youngest successional stage and sites in older successional stages (i.e. species turnover) as a function of regeneration age for bird communities (N=100). Here, there were 90 dissimilarity values from which to calculate the mean. Closed circles represent the mean dissimilarity values. Open circles represent the dissimilarity values.

## CHAPTER 5

### SYNTHESIS

Does succession drive ecological responses to restoration efforts? Can restoration of human-disturbed ecosystems prompt and/or produce successional processes? Resolutions may lie in our understanding of the patterns and processes underlying community responses to ecosystem restoration.

One way to recognise ecological processes is through indices of compositional dissimilarity and similarity, which quantify the variation or turnover in species composition (beta diversity). Ecologists often apply these indices to studies of biotic homogenisation or diversification following a natural or anthropogenic disturbance (Vellend et al. 2007; Püttker et al. 2015; Avolio et al. 2015; Grman et al. 2015). However, differences in local species richness can influence indices of beta diversity, leading to erroneous conclusions about the ecological processes that may be driving beta diversity (Chase & Myers 2011; Stegen et al. 2013). The combination of null models with beta diversity indices is one current approach used to distinguish random sampling effects from beta diversity that results from community assembly processes such as dispersal limitation or environmental filtering (Chase et al. 2011).

According to successional theory, dispersal limitation and environmental filtering will have the strongest effect early in succession, controlling the types of species that are able to colonise first (Chang & HilleRisLambers 2016). Early colonisers are usually weak competitors (i.e. habitat generalists/wide-ranged species), which may establish and spread quickly. As succession progresses, biotic interactions such as competition and facilitation will increasingly become more important, thereby allowing species with more specialised traits (i.e. habitat specialists/narrow-ranged species) to enter, owing to feedback loops between the abiotic and

biotic environment (Purschke et al. 2013; Rolo et al. 2016). This switch in community assembly processes may reveal itself in deterministic patterns of community change in both species richness and beta diversity across different seral stages (Peet & Christensen 1988).

In the present study, I hypothesised that compositional dissimilarity (beta diversity) within seral stages would increase with increasing regeneration age for tree, millipede, and bird assemblages as the environment becomes more heterogeneous, and that, as the intensity of competition is likely to increase, community similarity between seral stages (turnover) would diminish (Chapter 3). In addition, I applied a null model approach to test if tree, millipede, and bird beta diversity was convergent (suggestive of environmental filtering and/or dispersal limitation) or divergent (suggestive of niche diversification) per seral stage (Chapter 4).

Does compositional dissimilarity (beta diversity) within seral stages increase with increasing regeneration age? Regeneration age generally had a weak effect on compositional dissimilarity. Moreover, taxonomic group influenced the degree of compositional dissimilarity, as trees with poor dispersal ability showed the highest beta diversity than more mobile taxa, i.e. millipedes and birds. Taxonomic group also influenced the direction of community change, whereby the beta diversity of trees increased while that of millipedes and birds decreased. Patterns of compositional dissimilarity also differed between abundance and presence-absence data.

Does community similarity between seral stages (species turnover) diminish with age? Again, regeneration age was a poor predictor of beta diversity, and the degree of species turnover varied among taxa. Decay in community similarity with age was more rapid for tree communities compared with millipede or bird communities. This leads to the conclusions that while age-related changes in local conditions (e.g. light availability and soil fertility) may be driving changes in some communities, i.e. trees (Grainger & van Aarde 2013), successional changes are not uniform across taxonomic groups. This has important consequences for



understanding how different dune forest assemblages respond to restoration and how resilient these assemblages are toward restoration, post-mining. It may be that regional (dispersal-based) as opposed to local forces (niche-based) are driving community responses to coastal dune forest restoration (Redi et al. 2005; Grainger et al. 2011), or unmeasured local environmental variables. For instance, microhabitat variation may override the importance of regeneration age for some millipede species in my study area (Ott & van Aarde 2014). It may also be a simple matter of spatial (Olivier & van Aarde 2014) or temporal scale (Korhonen et al. 2010). My findings further suggest that forest regeneration may act through the relative abundances of species rather than the types of species present, which was found in another similar study (Li et al. 2016). Beta diversity (as both compositional dissimilarity and species turnover) thus does not only depend on the taxonomic group under study, but also the choice of dissimilarity index used.

The null model of beta diversity within different seral stages largely supported these findings, whereby beta diversity differed depending on whether I included abundance or presence-absence information, and the taxonomic group under study. While the null model based on presence-absence information indicated the presence of environmental and/or dispersal filters across the gradient of regeneration age, the abundance-based null model suggested that these processes were more important early in succession, and that deterministic processes favouring high compositional dissimilarity became more important late in succession. This is in line with previous hypothesis regarding successional processes (Connell & Slatyer 1977; Weiher & Keddy 1995; Callaway & Walker 1997; Douma et al. 2012; Chang & HilleRisLambers 2016). However, this shift in community assembly processes was more apparent for trees and birds compared with millipedes.

The null model of species turnover showed that turnover in bird species was more rapid early in regeneration and then plateaued towards the end of regeneration, with is in line with

previous predictions (Li et al. 2016). Tree and millipede communities, however, showed little to no species turnover with age when applying the null model. Nevertheless, the null model of species turnover showed that early successional communities are not merely rarefied samples of species-rich communities in later successional stages. Instead, these communities experience some degree of environmental filtering and/or dispersal limitation.

While this study generally supports the notion that coastal dune forest regeneration is deterministic, the choice of dissimilarity measure had important consequences for interpreting results. Furthermore, patterns of beta diversity, as well as inferences made about the processes that generate and maintain diversity, may depend on the actual taxa under study. Furthermore, differences between presence-absence- and abundance-based null models suggest that community assembly processes operate differently not only across the successional sere, but also for different aspects of the community (i.e. the types of species present vs. the relative abundances of species). Differences between classical measures of beta diversity (Jaccard/Bray Curtis) and probabilistic measures of beta diversity (Raup-Crick) highlight the importance of combining the use of null models in statistical analyses of beta diversity, especially when making inferences about the processes that shape beta diversity (Püttker et al. 2015). This discrepancy between observed and ‘null’ beta diversity may be in part due to the sensitivity of presence-absence metrics such as Jaccard to rare, uncommon species (Chase & Myers 2011).

There is ever more evidence to suggest that, as regenerating coastal dune forests develop, deterministic processes fostering assemblage diversification do replace assembly processes that tend to homogenise community composition, such environmental filtering and/or dispersal limitation (Rolo et al. 2016). The results here and the findings of others (Li et al. 2016) suggest however that successional changes may occur via shifts in the most dominant species as opposed to just the types of species present. It is likely that a few species spread

rapidly and persist temporally, but gradually lose dominance in favour of better competitors, as local conditions (e.g. canopy cover, light availability, temperature, and moisture) change, or as the regional species pool becomes depleted. As a result, it may be better to focus on the responses of dominant and/or rare species.

## **5.1. CAVEATS AND CONSIDERATIONS**

A possible caveat to this study is the inability to discern the relative roles of environmental filtering from dispersal limitation in shaping beta diversity. Unravelling the joint effects of multiple environmental and spatial variables may help to overcome this problem (Stegen et al. 2013). As different groups of species may respond differently to environmental and spatial variables (Wang et al. 2012), the inclusion of species functional (and phylogenetic) traits in future studies of beta diversity may also be more forthcoming. Another potential caveat is the use of space-for-time substitution, which assumes that seral stages only differ in age. While Rolo et al. (2016) validated its general utility for coastal dune vegetation, we do not know if this approach is valid for birds and millipedes. The use of an inappropriate scale to measure beta diversity is another potential caveat. Scale may influence beta diversity estimates and inferred processes through both sampling grain and sampling extent (Mac Nally et al. 2004; Barton et al. 2013; Olivier & van Aarde 2014). In addition, presence-absence data may not produce reliable relationships between community variables and local factors (Roff et al. 2011). In this case, it may be better to use abundance information. Furthermore, using a single indicator group to measure restoration success may be inappropriate given that different taxonomic groups seem to respond differently to regeneration processes.

As suggested by my findings, differences in the relative abundances of species most likely drive changes in regenerating coastal dune forest. This does not mean however that most of the species able to colonise regenerating coastal dune forests in my study area have already

done so. There are still some clear differences in the compositional and structural properties of assemblages in regenerating forests compared with unmined, old-growth forests. For instance, some forest specialists, particularly large-canopy trees, pill and keeled millipedes, and large frugivorous birds, are absent or rare in regenerating forests (van Aarde, Ferreira & Kritzing 1996a; Kritzing & van Aarde 1998; Grainger & van Aarde 2013; Rolo et al. 2017). As a result, restoration practitioners ought to focus on both enhancing local conditions and maximising dispersal across the region, as this would ensure the successful colonisation and establishment of forest-associated species.

## REFERENCES

- Allouche, O. et al., 2012. Area-heterogeneity tradeoff and the diversity of ecological communities. *Proceedings of the National Academy of Sciences*, 109(43), pp.17495–17500.
- Almeida-Neto, M., Frensel, D.M.B. & Ulrich, W., 2012. Rethinking the relationship between nestedness and beta diversity: a comment on Baselga (2010). *Global Ecology & Biogeography*, 21, pp.772–777.
- Anderson, K.J., 2007. Temporal patterns in rates of community change during succession. *The American Naturalist*, 169(6), pp.780–793.
- Anderson, M.J. et al., 2005. Consistency and variation in kelp holdfast assemblages: Spatial patterns of biodiversity for the major phyla at different taxonomic resolutions. *Journal of Experimental Marine Biology and Ecology*, 320(1), pp.35–56.
- Anderson, M.J. et al., 2011. Navigating the multiple meanings of  $\beta$  diversity: A roadmap for the practicing ecologist. *Ecology Letters*, 14(1), pp.19–28.
- Anderson, M.J., Ellingsen, K.E. & McArdle, B.H., 2006. Multivariate dispersion as a measure of beta diversity. *Ecology Letters*, 9(6), pp.683–693.
- Anderson, M.J., Tolimieri, N. & Millar, R.B., 2013. Beta Diversity of demersal fish assemblages in the north-eastern Pacific: Interactions of latitude and depth. *PLoS ONE*, 8(3), pp.1–15.
- Araújo, M.B. & Pearson, R.G., 2005. Equilibrium of species' distributions with climate. *Ecography*, 28(5), pp.693–695.
- Astorga, A. et al., 2012. Distance decay of similarity in freshwater communities: Do macro- and microorganisms follow the same rules? *Global Ecology and Biogeography*, 21(3),

pp.365–375.

Astorga, A. et al., 2014. Habitat heterogeneity drives the geographical distribution of beta diversity: The case of New Zealand stream invertebrates. *Ecology and Evolution*, 4(13), pp.2693–2702.

Avolio, M.L. et al., 2015. A framework for quantifying the magnitude and variability of community responses to global change drivers. *Ecosphere*, 6(12), pp.1–14.

Azaele, S. et al., 2006. Dynamical evolution of ecosystems. *Nature*, 444(7121), pp.926–928.

Azeria, E.T. et al., 2011. Towards a better understanding of beta diversity: Deconstructing composition patterns of saproxylic beetles breeding in recently burnt boreal forests. In D. I. Pavlinov, ed. *Research in Biodiversity: Models and Applications*. InTech, pp. 75–94.

Bailey, P.T. & Kovaliski, J., 1993. Summer quiescent behaviour of the millipede *Ommatoiulus moreleti* (Julida: Julidae). *Journal of Zoology*, 231(4), pp.523–532.

Bakker, J.D. et al., 2003. Contingency of grassland restoration on year, site, and competition from introduced grasses. *Ecological Applications*, 13(1), pp.137–153.

Balvanera, P. et al., 2002. Patterns of  $\beta$ -diversity in a Mexican tropical dry forest. *Journal of Vegetation Science*, 13(2), pp.145–158.

Barton, P.S. et al., 2013. The spatial scaling of beta diversity. *Global Ecology and Biogeography*, 22(6), pp.639–647.

Baselga, A., 2010. Partitioning the turnover and nestedness components of beta diversity. *Global Ecology & Biogeography*, 19, pp.134–143.

Baselga, A., Bonthoux, S. & Balent, G., 2015. Temporal beta diversity of bird assemblages in agricultural landscapes: Land cover change vs. stochastic processes. *PLoS ONE*, 10(5),

pp.1–14.

- Bazzaz, F.A., 1975. Plant species diversity in old-field successional ecosystems in southern Illinois. *Ecology*, 56(2), pp.485–488. Available at: <http://www.jstor.org/stable/1934981>.
- Beck, J., Holloway, J.D. & Schwanghart, W., 2013. Undersampling and the measurement of beta diversity. *Methods in Ecology and Evolution*, 4(4), pp.370–382.
- Belyea, L.R. & Lancaster, J., 1999. Assembly rules within a contingent ecology. *Oikos*, 86(3), pp.402–416.
- Benedetti-Cecchi, L. et al., 2008. Neutrality and the response of rare species to environmental variance. *PLoS ONE*, 3(7), pp.21–26.
- Bishop, T.R. et al., 2015. Contrasting species and functional beta diversity in montane ant assemblages. *Journal of Biogeography*, 42(9), pp.1776–1786.
- Boyes, L.J. et al., 2011. Causes of arrested succession in coastal dune forest. *Plant Ecology*, 212(1), pp.21–32.
- Brown, C. et al., 2013. Multispecies coexistence of trees in tropical forests: spatial signals of topographic niche differentiation increase with environmental heterogeneity. *Proceedings of the Royal Society B: Biological Sciences*, 280(20130502).
- Bruelheide, H. et al., 2011. Community assembly during secondary forest succession in a Chinese subtropical forest. *Ecological Monographs*, 81(1), pp.25–41.
- Callaway, R.M. & Walker, L.R., 1997. Competition and facilitation: a Synthetic approach to interactions in plant communities. *Ecology*, 78(7), pp.1958–1965.
- Camp, P.D., 1990. Rehabilitation after dune mining at Richards Bay Minerals. *South African Mining World*, pp.34–37.
- Cardinale, B.J. et al., 2007. Impacts of plant diversity on biomass production increase

- through time because of species complementarity. *Proceedings of the National Academy of Sciences*, 104(46), pp.18123–18128.
- Carvalho, J.C., Cardoso, P. & Gomes, P., 2012. Determining the relative roles of species replacement and species richness differences in generating beta-diversity patterns. *Global Ecology and Biogeography*, 21(7), pp.760–771.
- Chai, Y. et al., 2016. Patterns of taxonomic, phylogenetic diversity during a long-term succession of forest on the Loess Plateau, China: insights into assembly process. *Scientific Reports*, 6(27087), pp.1–10.
- Chang, C. & HilleRisLambers, J., 2016. Integrating succession and community assembly perspectives. *F1000Research*, 5(2294), pp.1–10. Available at: <http://f1000research.com/articles/5-2294/v1>.
- Chao, A. et al., 2008. A two-stage probabilistic approach to multiple-community similarity indices. *Biometrics*, 64(4), pp.1178–1186.
- Chase, J.M., 2003. Community assembly: When should history matter? *Oecologia*, 136(4), pp.489–498.
- Chase, J.M., 2007. Drought mediates the importance of stochastic community assembly. *Proceedings of the National Academy of Sciences*, 104(44), pp.17430–17434.
- Chase, J.M. et al., 2009. Predators temper the relative importance of stochastic processes in the assembly of prey metacommunities. *Ecology Letters*, 12(11), pp.1210–1218.
- Chase, J.M. et al., 2011. Using null models to disentangle variation in community dissimilarity from variation in  $\alpha$ -diversity. *Ecosphere*, 2(2), pp.1–11.
- Chase, J.M. & Leibold, M.A., 2003. *Ecological niches: linking classical and contemporary approaches*, University of Chicago Press.



- Chase, J.M. & Myers, J.A., 2011. Disentangling the importance of ecological niches from stochastic processes across scales. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366(1576), pp.2351–2363.
- Chen, Y., 2013. MBI: an R package for calculating multiple-site beta diversity indices. *Computational Ecology and Software*, 3(2), pp.26–32.
- Chesson, P.L. & Warner, R.R., 1981. Environmental Variability Promotes Coexistence in Lottery Competitive Systems. *The American Naturalist*, 117(6), pp.923–943. Available at: <http://www.journals.uchicago.edu/doi/10.1086/283778>.
- Christensen, N.L. & Peet, R.K., 1981. Secondary forest succession on the North Carolina Piedmont. In D. C. West, H. H. Shugart, & D. B. Botkin, eds. *Forest Succession: Concepts and Application*. New York, NY: Springer New York, pp. 230–245.
- Clements, F.E., 1916. *Plant succession: an Analysis of the development of vegetation*, Washington, DC: Carnegie Institution of Washington Publication.
- Colwell, R.K. & Winkler, D.W., 1984. A null model for null models in biogeography. In D. R. Strong Jr et al., eds. *Ecological communities: conceptual issues and the evidence*. Princeton, NJ: Princeton University Press, pp. 344 – 359.
- Condit, R.S. et al., 2002. Beta-diversity in tropical forest trees. *Science*, 295(5555), pp.666–669.
- Connell, J.H., 1978. Diversity in tropical rain forests and coral reefs. *Science*, 199(4335), pp.1302–1310.
- Connell, J.H. & Slatyer, R.O., 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *The American Naturalist*, 111(982), pp.1119–1144.

- Connell, J.H. & Sousa, W.P., 1983. On the evidence needed to judge ecological stability or persistence. *The American Naturalist*, 121(6), pp.729–824.
- Cornwell, W.K., Schilck, D.W. & Ackerly, D.D., 2006. A trait-based test for habitat filtering: Convex hull volume. *Ecology*, 87(6), pp.1465–1471.
- Crandall, R.M. & Platt, W.J., 2012. Habitat and fire heterogeneity explain the co-occurrence of congeneric resprouter and reseeder *Hypericum* spp. along a Florida pine savanna ecocline. *Plant Ecology*, 213(10), pp.1643–1654.
- Crouzeilles, R. et al., 2016. A global meta-analysis on the ecological drivers of forest restoration success. *Nature Communications*, 7, p.11666.
- Currie, D.J., 1991. Energy and large-scale patterns of animal- and plant-species richness. *The American Naturalist*, 137, pp.27–49.
- Currie, D.J. & Low, 2001. Projected effects of climate change on patterns of vertebrate and tree species richness in the Conterminous United States. *Ecosystems*, 4(3), pp.216–225.
- Davidar, P. et al., 2007. The effect of climatic gradients, topographic variation and species traits on the beta diversity of rain forest trees. *Global Ecology and Biogeography*, 16(4), pp.510–518.
- Davis, A.L. V et al., 2003. Convergence between dung beetle assemblages of a post-mining vegetation chronosequence and unmined forest. *Restoration Ecology*, 11(1), pp.29–42.
- Davis, A.L. V et al., 2013. Is microclimate-driven turnover of dung beetle assemblage structure in regenerating coastal vegetation a precursor to re-establishment of a forest fauna? *Journal of Insect Conservation*, 17(3), pp.565–576.
- Davy, A.J., 2002. Establishment and manipulation of plant populations and communities in terrestrial systems. In M. R. Perrow & A. J. Davy, eds. *Handbook of Ecological*

- Restoration I*. Cambridge, UK: Cambridge University Press, pp. 223–241.
- DeGraaf, R.M. & Yamasaki, M., 2003. Options for managing early-successional forest and shrubland bird habitats in the northeastern United States. *Forest Ecology and Management*, 185, pp.179–191.
- Diamond, J.M., 1975. Assembly of species communities. In J. M. Diamond & M. L. Cody, eds. *Ecology and Evolution of Communities*. Boston: Harvard University Press, pp. 342–344.
- Ding, Y. et al., 2012. Disturbance regime changes the trait distribution, phylogenetic structure and community assembly of tropical rain forests. *Oikos*, 121(8), pp.1263–1270.
- Diserud, O.H. & Odegaard, F., 2007. A multiple-site similarity measure. *Biology Letters*, 3(1), pp.20–22.
- Dobson, A.P., Bradshaw, A.D. & Baker, A.J.M., 1997. Hopes for the future: Restoration ecology and conservation biology. *Science*, 277, pp.515–522.
- Dornelas, M. et al., 2012. Quantifying temporal change in biodiversity: Challenges and opportunities. *Proceedings of the Royal Society B-Biological Sciences*, 280(20121931), pp.1–10.
- Dornelas, M. et al., 2009. Species abundance distributions reveal environmental heterogeneity in modified landscapes. *Journal of Applied Ecology*, 46(3), pp.666–672.
- Douma, J.C. et al., 2012. Succession-induced trait shifts across a wide range of NW European ecosystems are driven by light and modulated by initial abiotic conditions. *Journal of Ecology*, 100(2), pp.366–380.
- Driscoll, D.A. & Lindenmayer, D.B., 2009. Empirical tests of metacommunity theory using an isolation gradient. *Ecological Monographs*, 79(3), pp.485–501.

- Drury, W.H. & Nisbet, I.C.T., 1973. Succession. *Journal of the Arnold Arboretum*, 54(3), pp.331–368.
- Dyer, C., 2014. New names for the African Acacia species in *Vachellia* and *Senegalia*. *Southern Forests: a Journal of Forest Science*, 76(4), pp.iii–iii.
- Eeley, H.A.C., Lawes, M.J. & Piper, S.E., 1999. The influence of climate change on the distribution of indigenous forest in KwaZulu-Natal, South Africa. *Journal of Biogeography*, 26(3), pp.595–617.
- Egler, F.E., 1954. Vegetation science concepts I. Initial floristic composition, a factor in old-field vegetation development. *Vegetatio*, 4(6), pp.412–417.
- Ellwood, F.M.D., Manica, A. & Foster, W.A., 2009. Stochastic and deterministic processes jointly structure tropical arthropod communities. *Ecology Letters*, 12, pp.277–284.
- Elton, C., 1927. *Animal Ecology*, London: Sidgwick and Jackson.
- Fang, J. et al., 2006. Biodiversity changes in the lakes of the Central Yangtze. *Frontiers in Ecology and the Environment*, 4(7), pp.369–377.
- Fargione, J. et al., 2007. From selection to complementarity: Shifts in the causes of biodiversity-productivity relationships in a long-term biodiversity experiment. *Proceedings of the Royal Society B: Biological Sciences*, 274(1611), pp.871–876.
- Ferreira, S.M. & van Aarde, R.J., 1997. The chronosequence of rehabilitating stands of coastal dune forests: Do mammals confirm it. *South African Journal of Science*, 93, pp.211–214.
- Ferreira, S.M. & Aarde, R.J. Van, 2000. Maintaining diversity through intermediate disturbances : evidence from rodents colonizing rehabilitating coastal dunes. , pp.286–294.

- Finegan, B., 1996. Pattern and process in neotropical secondary rain forests: The first 100 years of succession. *Trends in Ecology and Evolution*, 11(3), pp.119–124.
- Fitzpatrick, M.C. et al., 2013. Environmental and historical imprints on beta diversity: insights from variation in rates of species turnover along gradients. *Proceedings of the Royal Society B: Biological Sciences*, 280(1768), pp.1–8.
- Flinn, K.M. & Vellend, M., 2005. Recovery of forest plant communities in post-agricultural landscapes. *Frontiers in Ecology and the Environment*, 3(5), pp.243–250.
- Foord, S.H., van Aarde, R.J. & Ferreira, S.M., 1994. Seed dispersal by vervet monkeys in rehabilitating coastal dune forests at Richards Bay. *South African Journal of Wildlife Research*, 24(3), pp.56–59.
- Francis, A.P. & Currie, D.J., 2003. A globally consistent richness-climate relationship for angiosperms. *The American Naturalist*, 161(4), pp.523–536.
- Fukami, T. et al., 2005. Species divergence and trait convergence in experimental plant community assembly. *Ecology Letters*, 8(12), pp.1283–1290.
- Gilbert, B., Turkington, R. & Srivastava, D.S., 2009. Dominant species and diversity: Linking relative abundance to controls of species establishment. *The American naturalist*, 174(6), pp.850–862.
- Gleason, H.A., 1927. Further views on the succession-concept. *Ecology*, 8(3), pp.299–326.
- Gleason, H.A., 1926. The individualistic concept of the plant association. *Bulletin of the Torrey Botanical Club*, 53(1), pp.7–26.
- Gleason, H.A., 1917. The structure and development of the plant association. *Bulletin of the Torrey Botanical Club*, 44(10), pp.463–481.
- Gotelli, N.J. & Graves, G.R., 1996. *Null Models in Ecology*, Washington DC: Smithsonian

Institution Press.

- Gourlay, I.D., Smith, J.P. & Barnes, R.D., 1996. Wood production in a natural stand of *Acacia karroo* in Zimbabwe. *Forest Ecology and Management*, 88, p.289–295.
- Grainger, M.J., 2011. *An evaluation of coastal dune forest restoration in northern KwaZulu-Natal, South Africa*. University of Pretoria.
- Grainger, M.J. & van Aarde, R.J., 2012. Is succession-based management of coastal dune forest restoration valid? *Ecological Restoration*, 30(3), pp.200–208.
- Grainger, M.J. & van Aarde, R.J., 2013. The role of canopy gaps in the regeneration of coastal dune forest. *African Journal of Ecology*, 51(1), pp.11–20.
- Grainger, M.J., van Aarde, R.J. & Wassenaar, T.D., 2011. Landscape composition influences the restoration of subtropical coastal dune forest. *Restoration Ecology*, 19, pp.111–120.
- Gratzer, G. et al., 2004. Spatio-temporal development of forests: Current trends in field methods and models. *Oikos*, 107(1), pp.3–15.
- Greyling, M.D., van Aarde, R.J. & Ferreira, S.M., 2001. Seasonal changes in habitat preferences of two closely related millipede species. *African Journal of Ecology*, 39, pp.51–58.
- Grman, E. et al., 2015. Altered beta diversity in post-agricultural woodlands: Two hypotheses and the role of scale. *Ecography*, 38(6), pp.614–621.
- Grman, E., Bassett, T. & Brudvig, L.A., 2013. Confronting contingency in restoration: Management and site history determine outcomes of assembling prairies, but site characteristics and landscape context have little effect. *Journal of Applied Ecology*, 50, pp.1234–1243.
- Guillem, C. et al., 2006. Determinants and spatial modeling of tree  $\beta$ -diversity in a tropical

- forest landscape in Panama. *Journal of Vegetation Science*, 17, pp.83–92.
- Hadly, E. & Maurer, B., 2001. Spatial and temporal patterns of species diversity in montane mammal communities of western North America. *Evolutionary Ecology Research*, 3, pp.477–486.
- Hamer, M.L. & Slotow, R.H., 2002. Conservation application of existing data for South African millipedes (Diplopoda). *African Entomology*, 10(1), pp.29–42.
- Handa, I.T. & Jefferies, R.L., 2000. Assistent revegetation trials in degraded salt-marshes. *Journal of Applied Ecology*, 37, pp.944–958.
- Heino, J., Melo, A.S. & Bini, L.M., 2015. Reconceptualising the beta diversity-environmental heterogeneity relationship in running water systems. *Freshwater Biology*, 60(2), pp.223–235.
- Hobbs, R.J., 2007. Integrating restoration and succession. In L. R. Walker, J. Walker, & R. J. Hobbs, eds. *Linking Restoration and Ecological Succession*. Springer, pp. 168–179.
- Hopkins, S. & Read, H., 1992. *The Biology of Millipedes*, New York: Oxford University Press.
- Hubbell, S.P., 2006. Neutral theory and the evolution of ecological equivalence. *Ecology*, 87(6), pp.1387–1398.
- Hubbell, S.P., 2001. *The Unified Neutral Theory of Biodiversity and Biogeography*, Princeton, NJ: Princeton University Press.
- Hutchinson, G.E., 1951. Copepodology for the Ornithologist. *Ecology*, 32(3), pp.571–577.
- Jankowski, J.E. et al., 2013. The relationship of tropical bird communities to tree species composition and vegetation structure along an Andean elevational gradient. *Journal of Biogeography*, 40(5), pp.950–962.

- Jonsson, M. et al., 2016. Divergent responses of  $\beta$ -diversity among organism groups to a strong environmental gradient. *Ecosphere*, 7(10), pp.1–13.
- Jurasinski, G., Retzer, V. & Beierkuhnlein, C., 2009. Inventory, differentiation, and proportional diversity: a Consistent terminology for quantifying species diversity. *Oecologia*, 159, pp.15–26.
- Kappelle, M., Kennis, P.A.F. & de Vries, R.A.J., 1995. Changes in diversity along a successional gradient in a Costa Rican upper montane *Quercus* forest. *Biodiversity and Conservation*, 4(1), pp.10–34.
- Keddy, P.A., 1992. Assembly and response rules: Two goals for predictive community ecology. *Journal of Vegetation Science*, 3(2), pp.157–164.
- Kerr, J.T. & Packer, L., 1997. Habitat heterogeneity as a determinant of mammal species richness in high-energy regions. *Nature*, 385(6613), pp.252–254.
- Koleff, P., Gaston, K.J. & Lennon, J.J., 2003. Measuring beta diversity for presence-absence data. *Journal of Animal Ecology*, 72(3), pp.367–382.
- Korhonen, J.J., Soininen, J. & Hillebrand, H., 2010. A quantitative analysis of temporal turnover in aquatic species assemblages across ecosystems. *Ecology*, 91(2), pp.508–517.
- Kritzinger, J.J. & van Aarde, R.J., 1998. The bird communities of rehabilitating coastal dunes at Richards Bay, KwaZulu-Natal. *South African Journal of Science*, 94, pp.71–78.
- Lamy, T. et al., 2015. Understanding the spatio-temporal response of coral reef fish communities to natural disturbances: Insights from beta-diversity decomposition. *PLoS ONE*, 10(9), pp.1–18.
- Lawes, M.J., 1990. The distribution of the Samango Monkey (*Cercopithecus mitis erythrarchus* Peters, 1852 and *Cercopithecus mitis labiatus* I. Geoffroy, 1843) and forest



- history in Southern Africa. *Journal of Biogeography*, 17(6), pp.669–680.
- Lawes, M.J. et al., 2007. The effect of the spatial scale of recruitment on tree diversity in Afromontane forest fragments. *Biological Conservation*, 139(3–4), pp.447–456.
- Legendre, P., Borcard, D. & Peres-neto, P.R., 2005. Analyzing beta diversity: Partitioning the spatial variation of community composition data. *Ecological Monographs*, 75(4), pp.435–450.
- Lennon, J.J. et al., 2001. The geographical structure of British bird distributions: Diversity, spatial turnover and scale. *Journal of Animal Ecology*, 70(6), pp.966–979.
- Lenoir, J. et al., 2012. Dispersal ability links to cross-scale species diversity patterns across the Eurasian Arctic tundra. *Global Ecology and Biogeography*, 21(8), pp.851–860.
- Letcher, S.G., 2010. Phylogenetic structure of angiosperm communities during tropical forest succession. *Proceedings of the Royal Society B: Biological Sciences*, 277(1678), pp.97–104.
- Levins, R., 1968. *Evolution in Changing Environments*, Princeton: Princeton University Press.
- Li, S.P. et al., 2016. Convergence and divergence in a long-term old-field succession: the Importance of spatial scale and species abundance. *Ecology Letters*, 19(9), pp.1101–1109.
- Lubke, R.A., Moll, J.B. & Avis, A.M., 1993. Rehabilitation Ecology. In C. E. Services, ed. *Environmental Impact Assessment, Eastern Shores of Lake St. Lucia (Kingsa/Trojan Lease Area)*. Pretoria: CSIR, pp. 251–302.
- De Luis, M. et al., 2001. Climatic trends, disturbances and short term vegetation dynamics in a Mediterranean shrubland. *Forest Ecology and Management*, 147, pp.25–37.

- Luken, J.O., 1990. *Directing Ecological Succession* 1st ed., New York: Chapman and Hall.
- Maaß, S. et al., 2014. Disturbance, neutral theory, and patterns of beta diversity in soil communities. *Ecology and Evolution*, 4(24), pp.4766–4774.
- MacArthur, R., Recher, H. & Cody, M., 1966. On the relation between habitat selection and species diversity. *The American Naturalist*, 100(913), pp.319–332.
- MacArthur, R.H. & Wilson, E.O., 1967. *The Theory of Island Biogeography*, Princeton, NJ: Princeton University Press.
- Magurran, A.E. & Dornelas, M., 2010. Biological diversity in a changing world. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1558), pp.3593–3597.
- Manne, L.L. et al., 1998. The form of the curves: a Direct evaluation of Macarthur and Wilson's classic theory. *Journal of Animal Ecology*, 67(5), pp.784–794.
- Martin, L.M., Moloney, K.A. & Wilsey, B.J., 2005. An assessment of grassland restoration success using species diversity components. *Journal of Applied Ecology*, 42(2), pp.327–336.
- Matthews, J.W. et al., 2009. Relative influence of landscape vs. local factors on plant community assembly in restored wetlands. *Ecological Applications*, 19(8), pp.2108–2123.
- Mcdonald, T. et al., 2016. *International standards for the practice of ecological restoration – including principles and key concepts*, Washington DC: Society for Ecological Restoration (SER).
- McIntosh, R.P., 1983. Excerpts from the work of L. G. Ramensky. *Bulletin of the Ecological Society of America*, 64(1), pp.7–12.

- McLachlan, A., 1991. Ecology of coastal dune fauna. *Journal of Arid Environments*, 21(2), pp.229–243.
- Meiners, S.J. et al., 2015. Is successional research nearing its climax? New approaches for understanding dynamic communities. *Functional Ecology*, 29(2), pp.154–164.
- Melo, A.S. et al., 2011. Focusing on variation: Methods and applications of the concept of beta diversity in aquatic ecosystems. *Acta Limnologica Brasiliensia*, 23(3), pp.318–331.
- Mi, X. et al., 2016. Stochastic assembly in a subtropical forest chronosequence: Evidence from contrasting changes of species, phylogenetic and functional dissimilarity over succession. *Scientific Reports*, 6(32596), pp.1–10.
- Millar, R.B., Anderson, M.J. & Tolimieri, N., 2011. Much ado about nothings: Using zero similarity points in distance-decay curves. *Ecology*, 92(9), pp.1717–1722.
- Mucina, L. et al., 2006. Indian Ocean Coastal Belt. In L. Mucina & M. C. Rutherford, eds. *The Vegetation of South Africa, Lesotho and Swaziland*. Pretoria, South Africa: SANBI, pp. 569–583.
- Murray, K.A. et al., 2015. Global biogeography of human infectious diseases. , 112(41), pp.12746–12751.
- Myers, J.A. et al., 2015. Disturbance alters beta-diversity but not the relative importance of community assembly mechanisms. *Journal of Ecology*, 103(5), pp.1291–1299.
- Mac Nally, R. et al., 2004. Comparative influence of spatial scale on beta diversity within regional assemblages of birds and butterflies. *Journal of Biogeography*, 31(6), pp.917–929.
- Noble, I.R. & Slatyer, R.O., 1980. The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. *Vegetatio*, 43(1), pp.5–21.

- Nogués-Bravo, D. et al., 2008. Scale effects and human impact on the elevational species richness gradients. *Nature*, 453(7192), pp.216–219.
- O'Brien, E.M., 2006. Biological relativity to water-energy dynamics. *Journal of Biogeography*, 33(11), pp.1868–1888.
- Odum, E.P., 1969. The strategy of ecosystem development. *Science*, 164(3877), pp.262–270.
- Oksanen, J. et al., 2016. vegan: Community Ecology Package. Available at: <https://cran.r-project.org/package=vegan>.
- Olander, L.P., Scatena, F.N. & Silver, W.L., 1998. Impacts of disturbance initiated by road construction in a subtropical cloud forest in the Luquillo Experimental Forest, Puerto Rico. *Forest Ecology and Management*, 109(1–3), pp.33–49.
- Olivier, P.I. & van Aarde, R.J., 2014. Multi-scale sampling boosts inferences from beta diversity patterns in coastal forests of South Africa. *Journal of Biogeography*, 41, pp.1428–1439.
- Olivier, P.I., van Aarde, R.J. & Lombard, A.T., 2013. The use of habitat suitability models and species-area relationships to predict extinction debts in coastal forests, South Africa. *Diversity and Distributions*, 19(11), pp.1353–1365.
- Olivier, P.I., Rolo, V. & van Aarde, R.J., 2017. Pattern or process? Evaluating the peninsula effect as a determinant of species richness in coastal dune forests. *PLoS ONE*, 12(4), pp.1–15.
- Ott, T. & van Aarde, R.J., 2014. Coastal dune topography as a determinant of abiotic conditions and biological community restoration in northern KwaZulu-Natal, South Africa. *Landscape and Ecological Engineering*, 10(1), pp.17–28.
- Özkan, K., Svenning, J.C. & Jeppesen, E., 2013. Environmental species sorting dominates

- forest-bird community assembly across scales. *Journal of Animal Ecology*, 82(1), pp.266–274.
- Peet, R.K. & Christensen, N.L., 1988. Changes in species diversity during secondary forest succession on the North Carolina Piedmont. In W. W. Murdoch, F. C. Evans, & C. H. Peterson, eds. *Diversity and pattern in plant and insects*. The Hague, The Netherlands: SPB Academic Publishing, pp. 233–245.
- Perrow, M.R. & Davy, A.J., 2002. *Handbook of Ecological Restoration I*, Cambridge, UK: Cambridge University Press.
- Pickett, S.T.A., 1989. Space-for-time substitution as an alternative to long-term studies. In G. E. Likens, ed. *Long-term studies in ecology*. New York: Springer-Verlag, pp. 110–135.
- Podani, J. & Schmera, D., 2011. A new conceptual and methodological framework for exploring and explaining pattern in presence-absence data. *Oikos*, 120, pp.1625–1638.
- Prach, K. & Walker, L.R., 2011. Four opportunities for studies of ecological succession. *Trends in Ecology and Evolution*, 26(3), pp.119–123.
- Pulsford, S.A., Lindenmayer, D.B. & Driscoll, D.A., 2016. A succession of theories: Purging redundancy from disturbance theory. *Biological Reviews*, 91(1), pp.148–167.
- Purschke, O. et al., 2013. Contrasting changes in taxonomic, phylogenetic and functional diversity during a long-term succession: Insights into assembly processes. *Journal of Ecology*, 101(4), pp.857–866.
- Püttker, T. et al., 2015. Ecological filtering or random extinction? Beta-diversity patterns and the importance of niche-based and neutral processes following habitat loss. *Oikos*, 124(2), pp.206–215.
- Pywell, R.F. et al., 2002. Restoration of species-rich grassland on arable land: Assessing the

- limiting processes using a multi-site experiment. *Journal of Applied Ecology*, 39(2), pp.294–309.
- Qian, H., Badgley, C. & Fox, D.L., 2009. The latitudinal gradient of beta diversity in relation to climate and topography for mammals in North America. *Global Ecology and Biogeography*, 18(1), pp.111–122.
- Questad, E.J. & Foster, B.L., 2008. Coexistence through spatio-temporal heterogeneity and species sorting in grassland plant communities. *Ecology Letters*, 11(7), pp.717–726.
- R Core Team, 2016. R: A Language and Environment for Statistical Computing. Available at: <https://www.r-project.org/>.
- Raup, D.M. & Crick, R.E., 1979. Measurement of faunal similarity in paleontology. *Journal of Paleontology*, pp.1213–1227.
- RBM, 2014. *Responsible Beyond Mining*, Richards Bay.
- Redi, B.H., van Aarde, R.J. & Wassenaar, T.D., 2005. Coastal dune forest development and the regeneration of millipede communities. *Restoration Ecology*, 13(2), pp.284–291.
- Rehounková, K. & Prach, K., 2006. Spontaneous vegetation succession in disused gravel-sand pits: Role of local site and landscape factors. *Journal of Vegetation Science*, 17, pp.583–590.
- Ricklefs, R., 2006. Time, species, and the generation of trait variance in clades. *Systematic Biology*, 55(1), pp.151–159.
- Roff, J., Zacharias, M. & Day, J., 2011. *Marine Conservation Ecology*, Taylor and Francis.
- Rolo, V. et al., 2016. Validating space-for-time substitution in a new-growth coastal dune forest. *Applied Vegetation Science*, 19(2), pp.235–243.
- Rolo, V., Olivier, P.I. & van Aarde, R.J., 2017. Tree and bird functional groups as indicators

- of recovery of regenerating subtropical coastal dune forests. *Restoration Ecology*, 25(5), pp.1–10.
- Rosenzweig, M.L., 1995. *Species diversity in space and time*, Cambridge University Press.
- Rüger, N. et al., 2009. Response of recruitment to light availability across a tropical lowland rain forest community. *Journal of Ecology*, 97(6), pp.1360–1368.
- Samuels, C.L. & Drake, J.A., 1997. Divergent perspectives on community convergence. *Trends in Ecology and Evolution*, 12(11), pp.427–432.
- Sarmiento, L. et al., 2003. Vegetation patterns, regeneration rates and divergence in an old-field succession of the high tropical Andes. *Plant Ecology*, 16(9), pp.793–796.
- Schurman, J.S. & Baltzer, J.L., 2012. Environmental correlates of tree species distributions vary among age classes in a northern temperate forest. *Plant Ecology*, 213(10), pp.1621–1632. Available at: <https://doi.org/10.1007/s11258-012-0117-2>.
- Segre, H. et al., 2014. Competitive exclusion, beta diversity, and deterministic vs. stochastic drivers of community assembly. *Ecology Letters*, 17(11), pp.1400–1408.
- Shurin, J.B., 2007. How is diversity related to species turnover through time? *Oikos*, 116(6), pp.957–965.
- Si, X., Baselga, A. & Ding, P., 2015. Revealing beta-diversity patterns of breeding bird and lizard communities on inundated land-bridge islands by separating the turnover and nestedness components. *PLoS ONE*, 10(5), pp.1–19.
- Silva, J.L.A. et al., 2015. Community assembly in harsh environments: the prevalence of ecological drift in the heath vegetation of South America. *Ecosphere*, 6(7), p.18.
- da Silva, V.X. da et al., 2017. Taxonomic groups with lower movement capacity may present higher beta diversity. *Iheringia. Série Zoologia*, 107(e2017005), pp.1–20.

- Society for Ecological Restoration Science and Policy Working Group., 2004. The Society for Ecological Restoration Primer. *Ecological Restoration* (GMT) *Ecological Restoration*, 29(3), pp.207–20809. Available at:  
[https://muse.jhu.edu/article/448452%5Cnhttp://www.ser.org/reading\\_resources.asp](https://muse.jhu.edu/article/448452%5Cnhttp://www.ser.org/reading_resources.asp).
- Socolar, J.B. et al., 2016. How should beta-diversity inform biodiversity conservation? *Trends in Ecology and Evolution*, 31(1), pp.67–80.
- Soininen, J., 2010. Species turnover along biotic and biotic gradients: Patterns in space equal patterns in time? *BioScience*, 60(6), pp.433–439.
- Soininen, J. & Hillebrand, H., 2007. Disentangling distance decay of similarity from richness gradients: Response to Baselga (2007). *Ecography*, 30(6), pp.842–844.
- Soininen, J., McDonald, R. & Hillebrand, H., 2007. The distance decay of similarity in ecological communities. *Ecography*, 30(1), pp.3–12.
- Sousa, W.P., 1979. Disturbance in marine intertidal boulder fields: the Nonequilibrium maintenance of species diversity. *Ecology*, 60(6), pp.1225–1239.
- Srivastava, D.S. et al., 2008. Why are predators more sensitive to habitat size than their prey? Insights from Bromeliad insect food webs. *The American Naturalist*, 172(6), pp.761–771.
- Stegen, J.C. et al., 2013. Stochastic and deterministic drivers of spatial and temporal turnover in breeding bird communities. *Global Ecology and Biogeography*, 22(2), pp.202–212.
- Steinitz, O. et al., 2006. Environment, dispersal and patterns of species similarity. *Journal of Biogeography*, 33(6), pp.1044–1054.
- Stevens, G.C., 1989. The latitudinal gradient in geographical range: How so many species coexist in the tropics. *The American Naturalist*, 133(2), pp.240–256.



- Suding, K.N., Gross, K.L. & Houseman, G.R., 2004. Alternative states and positive feedbacks in restoration ecology. *Trends in Ecology and Evolution*, 19(1), pp.46–53.
- Theron, L.-J., 2001. *Distribution and abundance of rodents, millipedes and trees in coastal dune forests in northern KwaZulu-Natal*. University of Pretoria.
- Thompson, R. & Townsend, C., 2006. A truce with neutral theory: Local deterministic factors, species traits and dispersal limitation together determine patterns of diversity in stream invertebrates. *Journal of Animal Ecology*, 75, pp.476–484.
- Tilman, D., 1997. Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology*, 78, pp.81–92.
- Tilman, D., 1982. *Resource competition and community structure*, Princeton, NJ: Princeton University Press.
- Tilman, D., 1985. The resource ratio hypothesis of plant succession. *The American Naturalist*, 125(6), pp.827–852.
- Tinley, K., 1985. *Coastal dunes of South Africa*, Pretoria.
- Toussaint, A. et al., 2014. Historical assemblage distinctiveness and the introduction of widespread non-native species explain worldwide changes in freshwater fish taxonomic dissimilarity. *Global Ecology and Biogeography*, 23(5), pp.574–584.
- Tuomisto, H., 2010a. A consistent terminology for quantifying species diversity? Yes, it does exist. *Oecologia*, 164, pp.853–860.
- Tuomisto, H., 2010b. A diversity of beta diversities: Straightening up a concept gone awry. Part 1. Defining beta diversity as a function of alpha and gamma diversity. *Ecography*, 33, pp.2–22.
- Tuomisto, H., 2010c. A diversity of beta diversities: Straightening up a concept gone awry.

- Part 2. Quantifying beta diversity and related phenomena. *Ecography*, 33, pp.23–45.
- Ulrich, W. et al., 2017. Environmental filtering triggers community assembly of forest understorey plants in Central European pine stands. *Scientific Reports*, 7(274), pp.1–9.
- Ulrich, W. & Gotelli, N.J., 2010. Null model analysis of species associations using abundance data. *Ecology*, 91(11), pp.3384–3397.
- van Aarde, R.J., Ferreira, S.M., Kritzing, J.J., et al., 1996. An evaluation of habitat rehabilitation on coastal dune forests in northern KwaZulu-Natal, South Africa. *Restoration Ecology*, 4(4), pp.334–345.
- van Aarde, R.J., Ferreira, S.M. & Kritzing, J.J., 1996a. Millipede communities in rehabilitating coastal dune forests in northern KwaZulu/Natal, South Africa. *Journal of Zoology, London*, 238, pp.703–712.
- van Aarde, R.J., Ferreira, S.M. & Kritzing, J.J., 1996b. Successional changes in rehabilitating coastal dune communities in northern KwaZulu/Natal, South Africa. *Landscape and Urban Planning*, 34, pp.277–286.
- van Aarde, R.J., Guldmond, R.A.R. & Olivier, P.I., 2014. Biodiversity status of coastal dune forests in South Africa. In B. Maslo & J. L. Lockwood, eds. *Coastal Conservation*. Cambridge, UK: Cambridge University Press, pp. 161–179.
- van Aarde, R.J., Smith, A.-M. & Claassens, A.S., 1998. Soil Characteristics of Rehabilitating and Unmined Coastal Dunes. *Restoration Ecology*, 6(1), pp.102–110.
- Van Houtan, K.S. et al., 2007. Dispersal of Amazonian birds in continuous and fragmented forest. *Ecology Letters*, 10(3), pp.219–229.
- Vaughn, K.J. & Young, T.P., 2010. Contingent conclusions: Year of initiation influences ecological field experiments, but temporal replication is rare. *Restoration Ecology*, 18,

pp.59–64.

Veech, J.A. et al., 2002. Nordic Society Oikos The Additive Partitioning of Species

Diversity : Recent Revival of an Old Idea. *Oikos*, 99(1), pp.3–9.

Veech, J.A. & Crist, T.O., 2007. Habitat and climate heterogeneity maintain beta-diversity of

birds among landscapes within ecoregions. *Global Ecology and Biogeography*, 16(5),

pp.650–656.

Vellend, M., 2010. Conceptual synthesis in community ecology. *The Quarterly Review of*

*Biology*, 85(2), pp.183–206.

Vellend, M., 2001. Do commonly used indices of  $\beta$ -diversity measure species turnover?

*Journal of Vegetation Science*, 12(4), pp.545–552.

Vellend, M. et al., 2007. Homogenization of forest plant communities and weakening of

species-environment relationships via agricultural land use. *Journal of Ecology*, 95(3),

pp.565–573.

Venables, W.N. & Ripley, B.D., 2002. *Modern Applied Statistics with S* Fourth., New York:

Springer.

Verheyen, K. & Hermy, M., 2004. Recruitment and growth of herb-layer species with

different colonizing capacities in ancient and recent forests. *Journal of Vegetation*

*Science*, 15(1), pp.125–134.

Verheyen, K. & Hermy, M., 2001. The relative importance of dispersal limitation of vascular

plants in secondary forest succession in Muizen Forest, Belgium. *Journal of Ecology*,

89(5), pp.829–840.

Villéger, S. et al., 2015. From current distinctiveness to future homogenization of the world's

freshwater fish faunas. *Diversity and Distributions*, 21(2), pp.223–235.

- Villéger, S. et al., 2011. Homogenization patterns of the world's freshwater fish faunas. *Proceedings of the National Academy of Sciences*, 108(44), pp.18003–18008.
- Villéger, S., Grenouillet, G. & Brosse, S., 2014. Functional homogenization exceeds taxonomic homogenization among European fish assemblages. *Global Ecology and Biogeography*, 23(12), pp.1450–1460.
- Villéger, S., Mason, N.W.H. & Mouillot, D., 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology*, 89(8), pp.2290–2301.
- Volkov, I. et al., 2005. Density dependence explains tree species abundance and diversity in tropical forests. *Nature*, 438(December), pp.658–661.
- Walker, L.R. & del Moral, R., 2003. *Primary Succession and Ecosystem Rehabilitation*, Cambridge, UK: Cambridge University Press.
- Wang, Z., Fang, J. & Shi, L., 2012. Geographical patterns in the beta diversity of China's woody plants: the Influence of space, environment and range size. *Ecography*, 35, pp.1092–1102.
- Wassenaar, T.D. et al., 2005. Community convergence in disturbed subtropical dune forests. *Ecology*, 86(3), pp.655–666.
- Wassenaar, T.D., Ferreira, S.M. & van Aarde, R.J., 2007. Flagging aberrant sites and assemblages in restoration projects. *Restoration Ecology*, 15(1), pp.68–76.
- Weiher, E. & Keddy, P.A., 1995. Assembly rules, null model, and trait dispersion: New questions from old patterns. *Oikos*, 74(1), pp.159–164.
- West, A.G., Midgley, J.J. & Bond, W.J., 2000. Regeneration failure and the potential importance of human disturbance in a subtropical forest. *Applied Vegetation Science*, 3,

pp.223–232.

Whittaker, R.H., 1972. Evolution and measurement of species diversity. *Taxon*, 21(2), pp.213–251.

Whittaker, R.H., 1960. Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs*, 30(3), pp.279–338.

Wilson, M.W. et al., 2006. Effects of growth stage and tree species composition on breeding bird assemblages of plantation forests. *Bird Study*, 53(3), pp.225–236.

van Wyk, A.E., 1996. Biodiversity of the Maputaland Centre. In L. J. G. van der Maesen, X. M. van der Burgt, & J. M. van Medenbach de Rooy, eds. *The Biodiversity of African Plants*. Springer, Dordrecht, pp. 198–207.

van Wyk, A.E. & Smith, G.F., 2001. *Regions of Floristic Endemism in Southern Africa: a Review with Emphasis on Succulents*, Pretoria: Umdaus Press.

Yang, Q.S. et al., 2016. Detangling the effects of environmental filtering and dispersal limitation on aggregated distributions of tree and shrub species: Life stage matters. *PLoS ONE*, 11(5).

Young, T.P., Chase, J.M. & Huddleston, R.T., 2001. Community succession and assembly: Comparing, contrasting and combining paradigms in the context of ecological restoration. *Ecological Restoration*, 19(1), pp.5–18.

Young, T.P., Petersen, D.A. & Clary, J.J., 2005. The ecology of restoration: Historical links, emerging issues and unexplored realms. *Ecology Letters*, 8(6), pp.662–673.

Zedler, J.B. & Callaway, J.C., 1999. Tracking wetland restoration: Do mitigation sites follow desired trajectories? *Restoration Ecology*, 7(1), pp.69–73.

Zhou, J. et al., 2014. Stochasticity, succession, and environmental perturbations in a fluidic

ecosystem. *Proceedings of the National Academy of Sciences*, 111(9), pp.E836–E845.

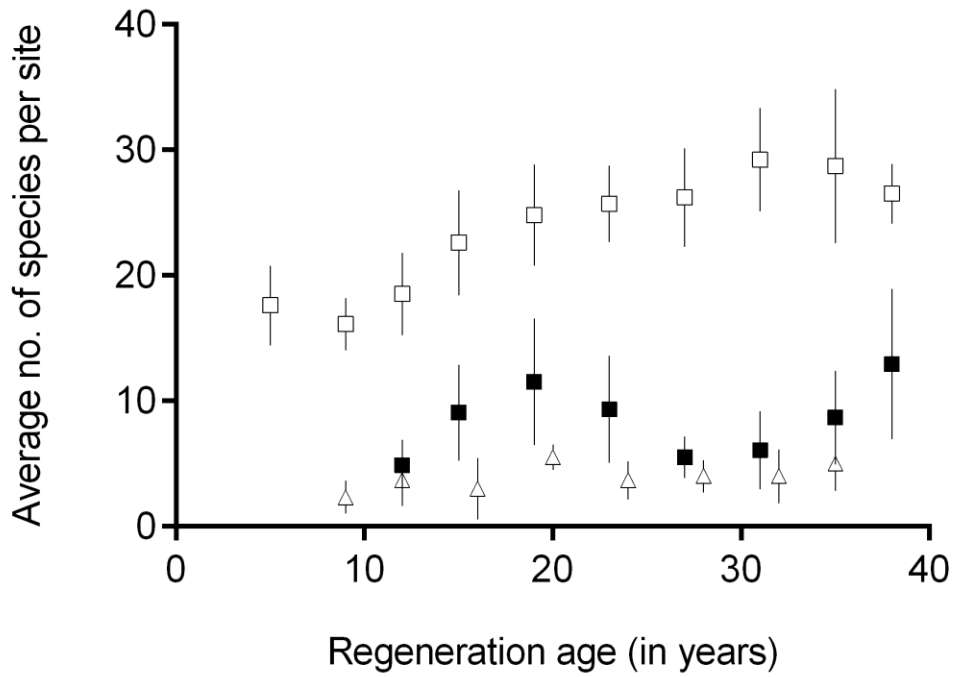
## **APPENDICES**

Appendix I. Standard errors for the binomial log-linear GLM fits obtained using the leave-one-out jack-knife method based on the Bray-Curtis ( $d_{BC}$ ) and Jaccard ( $d_J$ ) similarity measures for trees, millipedes, and birds.

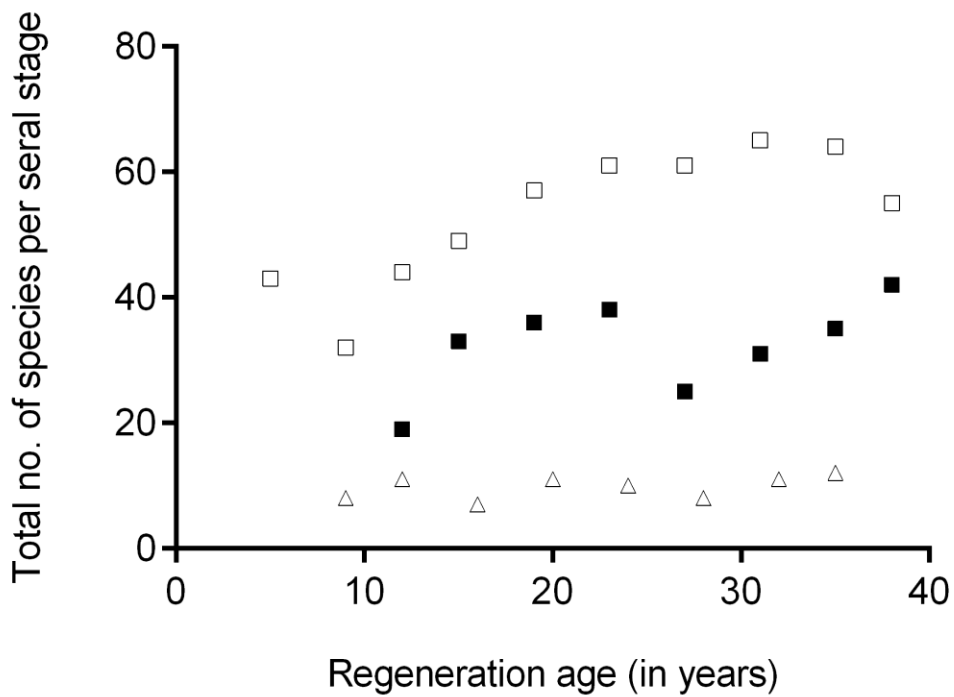
Taxa	Years of regeneration	$d_{BC}$				$d_J$			
		Intercept	Slope	Similarity at zero distance	Halving distance (years)	Intercept	Slope	Similarity at zero distance	Halving distance (years)
Trees	12 to 38	0.0040	0.0476	0.0266	1.1092	0.0029	0.0345	0.0102	2.9280
Millipedes	9 to 35	0.0520	0.0046	0.0363	19.482	0.0646	0.0057	0.0361	15.556
Birds	5 to 35	0.0014	0.0163	0.0098	7.8710	0.0016	0.0194	0.0093	8.0003



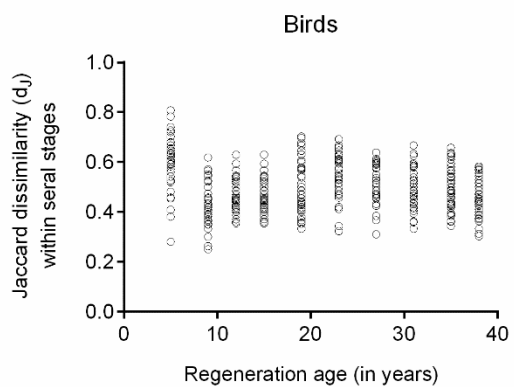
a)



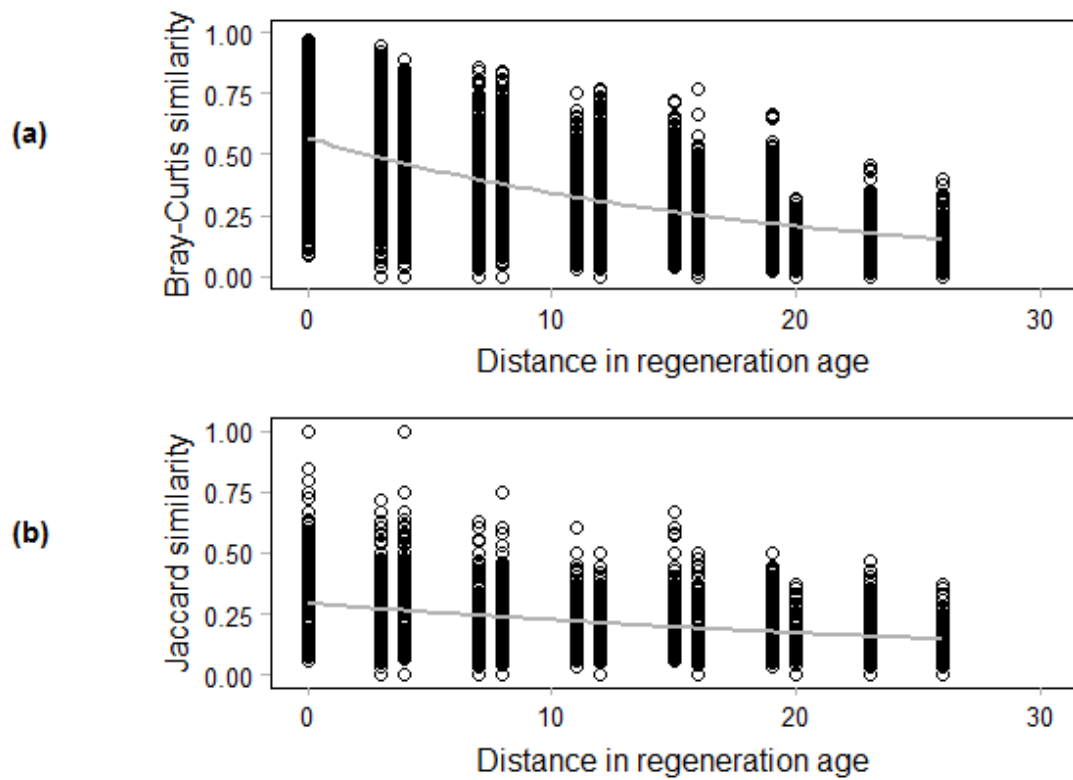
b)



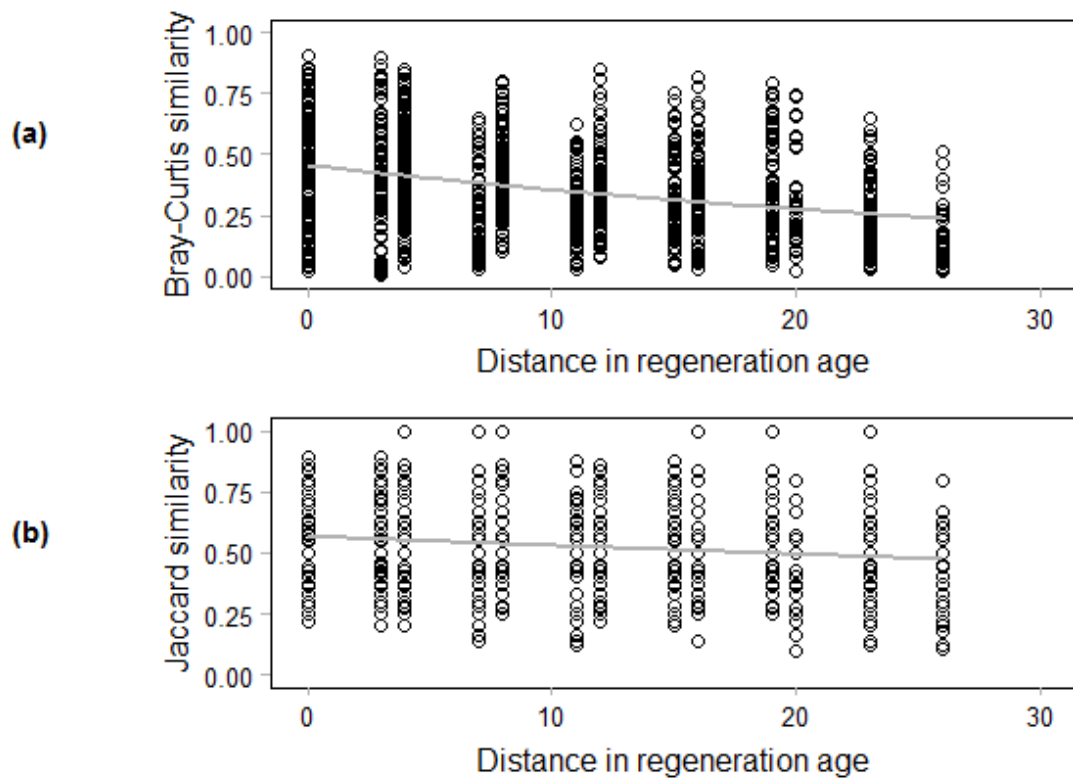
Appendix II. Mean number of species per survey site within a seral stage ( $\pm$ SD) (a) and the total number of species per seral stage (b) with increasing regeneration age for trees (closed squares) (N=120), millipedes (open triangles) (N=50), and birds (open squares) (N=100).



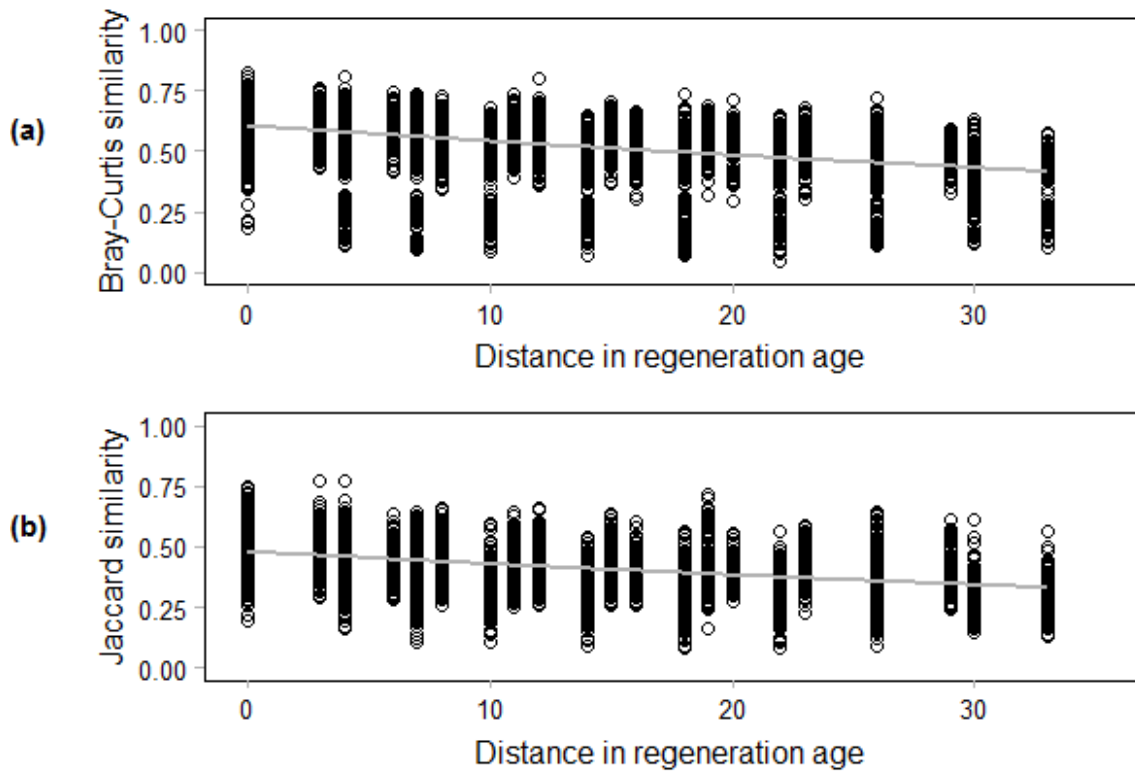
Appendix III. Pairwise Bray-Curtis and Jaccard dissimilarities (beta diversity) within seral stages of increasing regeneration age for tree (N=120), millipede (N=50), and bird communities (N=100). For trees, there were 840 pairwise dissimilarity values for each data set. For millipedes, there were 142 dissimilarity values for each data set. Lastly, there were 450 values for each data set for birds.



Appendix IV. The decay in similarity of tree communities with increasing age distance for the 2014-2015 survey period, as measured using the Bray-Curtis (a) and Jaccard similarity index (b). The grey lines denote the fitted curves from the binomial GLM with a log-link function. Here, there were 7140 similarity values from 120 sites for each data set.



Appendix V. The decay in similarity of millipede communities with increasing age distance for the 2012-2013 survey period, as measured using the Bray-Curtis (a) and Jaccard similarity index (b). The grey lines denote the fitted curves from the binomial GLM with a log-link function. Here, there were 1225 similarity values from 50 sites for each data set.



Appendix VI. The decay in similarity of bird communities with increasing age distance for the 2014-2015 survey period, as measured using the Bray-Curtis (a) and Jaccard similarity index (b). The grey lines denote the fitted curves from the binomial GLM with a log-link function. Here, there were 4950 similarity values from 100 sites for each data set.