THE FUNCTIONAL ECOLOGY OF EASTERN RÛENS SHALE RENOSTERVELD

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THIS THESIS IS DEDICATED TO THE MEMORY OF MY FATHER WHO PASSED AWAY MIDWAY THROUGH ITS COMPLETION AND HAS BEEN MISSED EVERY DAY SINCE.

WILLIAM DOUGLAS COWAN

1952-2017

"It seems to me that the natural world is the greatest source of excitement; the greatest source of visual beauty; the greatest source of intellectual interest. It is the greatest source of so much in life that makes life worth living."
- **David Attenborough**

"I cannot separate the aesthetic pleasure of seeing a butterfly and the scientific pleasure of knowing what it is."
– **Vladimir Nabokov**

Declaration

This thesis comprises original research undertaken by myself, Oliver Cowan, and has not previously been submitted for a degree or diploma at any university or institution. To the best of my knowledge and belief, this thesis contains no material previously published or written by another person except where due reference is made in the thesis itself.

The Introduction section of this thesis details the contributions of fellow authors to the four data chapters accepted, or under review, for publication. Non-author contributions to this thesis are detailed in the acknowledgements section of each data chapter.

Signed by candidate

Oliver Sølve Cowan June 2019

Declaration: Inclusion Of Publication

I confirm that I have been granted permission by the University of Cape Town's Doctoral Degrees Board to include the following publications in my PhD thesis, and where co-authorships are involved, my co-authors have agreed that I may include the publications:

A) Cowan OS, Anderson PML, Meadows ME (2019) Taxonomic Diversity, Functional Diversity and Functional Composition in a Critically Endangered Vegetation Type within the Cape Floristic Region, South Africa (Submitted and in review at Journal Of Vegetation Science).

B) Cowan OS, Anderson PML (2019) Litter decomposition variation across a degradation gradient and two seasons in a critically endangered vegetation type within the Fynbos biome, South Africa. South African Journal of Botany 121: 200-209.

C) Cowan OS, Janion-Scheepers C, Anderson PML (2019) Springtail communities in a critically endangered vegetation type in South Africa (Submitted and in review at Soil Biology and Biochemistry).

D) Cowan OS, Anderson PML (2019) Three complete plant-pollinator networks anlong a secondary successional gradient in critically endangered renosterveld, South Africa. Journal of Pollination Ecology 25: 24-35.

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Oliver Sølve Cowan June 2019

ABSTRACT

Globally, ecosystems are under mounting pressure as biodiversity is lost at an ever increasing rate due to drivers such as habitat destruction and climate change. The systematic degradation of natural habitats witnessed today is often accompanied by a loss of ecosystem functioning and services which not only endangers the future of humankind but has consequences for all life on earth. To manage the ecological challenges facing us there is an urgent need to increase our understanding of how ecosystems function, the relation/ship between biodiversity and ecosystem functioning, and the effect habitat degradation can have on this relationship. Eastern Rûens Shale Renosterveld, located in the Overberg region of South Africa, is a vegetation type both critically endangered and poorly understood. Centuries of agricultural activity in the region has resulted in a landscape typified by fragments of pristine vegetation, in addition to communities in various states of degradation, embedded in an agricultural matrix. The current quantities of pristine vegetation are inadequate to meet conservation goals and conservation efforts are further challenged by the fact that little is known of the functional ecology of not only pristine fragments of Renosterveld, but the degraded communities in various stages of secondary succession.

The overarching aim of this thesis is to better understand the relationship between biodiversity and ecosystem functioning across a degradation gradient in critically endangered Renosterveld vegetation within an agricultural landscape in South Africa. To achieve this, a variety of methods were employed using different lenses of analysis. In Chapter 2, I studied the components of biodiversity to assess the relationship between taxonomic and functional diversity indices and investigate the effect of habitat degradation. In Chapters 3 and 4, I used litter traps to investigate the effect of plant litter type, season and habitat degradation on litter decomposition rates and Springtail (Collembola) community dynamics, respectively. Finally, in Chapter 5, I constructed three high-resolution plant-pollinator networks from sites with distinct land-use histories and with different above-ground vegetation communities.

The results revealed a complex association between different taxonomic and functional diversity indices, influenced by habitat degradation, with potential ecological and conservation implications. Particularly, the loss of functional redundancy in degraded sites is likely to reduce resilience to future environmental perturbations which may reduce ecosystem functions. Conversely, the similarities in both taxonomic and functional diversity indices between pristine and moderately degraded sites may be cautiously interpreted as the occurrence of successful passive restoration. Litter decomposition rates were shown to be variable with litter type and season revealed as important controlling factors. Although degradation did not appear to significantly affect decomposition rates, the initial nutrient content of litter appears to correlate with decomposition rate and it can be expected this ecosystem function will be accelerated where habitat degradation results in shifts in above-ground vegetation and subsequent litter input, specifically where the cover of non-native, nitrogen-rich annual species is increased. There was found to be a significant impact of litter type on community composition, and of sampling day on species richness, abundance and community composition, in Springtail communities. Despite the overall lack of effect of degradation on Springtail community dynamics, the abundance of the non-native *Entomobrya multifasciata* in degraded sites, and its absence from pristine sites, raises the intriguing possibility of its suitability as a bioindicator for habitat degradation. Comparisons to similar global studies revealed the Renosterveld networks to be highly functionally specialized. Assessing network dynamics across a degradation gradient showed the impact of above-ground vegetation structure on network properties with the more open and diverse vegetation structure and floral resources provided by the highly degraded site resulting in network indices more similar to that of the pristine site when compared to the relatively structurally uniform moderately degraded site.

Although this thesis has enhanced our understanding of the functional ecology of Renosterveld, it has also highlighted knowledge gaps which still exist. Creating and collating a database of functional trait data can provide the building blocks for future ecological work. Furthermore, to truly gain a mechanistic understanding of the biodiversity-ecosystem function relationship one needs to utilise an integrated analysis which considers different facets of biodiversity, particularly functional diversity, across multiple trophic levels while simultaneously acknowledging the legacy effects that distinct land-use histories can impose at the community level.

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Chapter 1

Introduction

1.1 Introduction

Globally, ecosystems are under increasing pressure as biodiversity is lost at an ever increasing rate due to drivers such as habitat destruction and climate change (Cardinale et al., 2012; IPBES, 2018). The systematic degradation of natural habitats witnessed today is often accompanied by a loss of ecosystem functioning and services which not only endangers the future of humankind but has consequences for all life on earth (Millennium Ecosystem Assessment, 2005; IPBES, 2018). To overcome the ecological challenges facing us there is an urgent need to increase our understanding of how ecosystems function, the relationship between biodiversity and ecosystem functioning, and the effect habitat alteration can have on this relationship (for definitions of relevant terminology see Box 1.1) (Tilman, 1999; Sala et al., 2000; Loreau et al., 2002; Balvanera et al., 2006; Hooper et al., 2012; IPBES, 2018).

One development towards improving our understanding in recent years is the refinement and use of functional diversity in ecological studies (Villéger et al., 2008; Kleyer et al., 2012; Mouillot et al., 2013; Chao et al., 2018). Traditionally, biodiversity has focused on taxonomic richness and abundance; however these indices can fail to capture the full complexity of ecosystem dynamics (Díaz and Cabido, 2001; McGill et al., 2006). Functional diversity provides a mechanistic link between biodiversity and ecosystem functioning (Petchey and Gaston, 2006) and is increasingly used in the study of a wide range of ecological processes (Villéger et al., 2012; Violle et al., 2014; Garcia et al., 2015). Understanding the effect of disturbance on ecosystem functioning through the alteration of community structure is a key element in the conservation of ecological resources and functional diversity has proved an important tool in exploring this relationship (Mayfield et al., 2005; Flynn et al., 2009; Sasaki et al., 2009; Mouillot et al., 2013; Derhé et al., 2016). Nevertheless, the rate and extent of habitat alteration are such that, particularly at the landscape level, the relationship between biodiversity loss and ecosystem functioning remains poorly resolved (Pecl et al., 2017), and in certain communities has not been explored at all.

Renosterveld, an endemic vegetation type in the Cape Floristic Region, South Africa, remains under-researched. Due to substantial agricultural transformation less than 10% of this critically endangered vegetation type remains, persisting in pockets of natural vegetation embedded within a surrounding agricultural matrix (Newton and Knight, 2005; Rebelo et al., 2006; Topp and Loos, 2018). Aside from these fragments of relatively pristine vegetation, variety in land-use history and subsequent abandonment has resulted in communities in various states of degradation (Heelemann et al., 2013; Cowan and Anderson, 2014; Ruwanza, 2017). As such, Renosterveld provides an ideal location to explore the relationship between biodiversity and ecosystem functioning across a gradient of habitat alteration from pristine vegetation to degraded communities of various ages following agricultural abandonment. In addition to enhancing the theoretical understanding of this fundamentally important relationship, the outcomes of this research may have real-world implications for conservation and management of this imperilled vegetation, and the provision of valuable ecosystem services for an agricultural landscape in an economically important region of South Africa (Davis-Reddy and Vincent, 2017).

The overarching aim of this thesis is to better understand the relationship between biodiversity and ecosystem functioning across a degradation gradient in critically endangered Renosterveld vegetation within an agricultural landscape in South Africa. In this chapter, I provide an overview of the literature touching on the themes of functional ecology, the relationship between species richness and functional diversity, the relationships between biodiversity, ecosystem function and habitat degradation, and introduce Renosterveld vegetation through an appraisal of its history, current extent, and key conservation concerns. This review contextualises and affords background to the research undertaken in this thesis, and explicitly shows how the work presented here contributes towards the advancement of knowledge while providing data potentially relevant to enhancing conservation management of this highly threatened vegetation type. Following the review, I restate the project aim and link it to the key objectives of the thesis. Finally, as this thesis contains four empirical chapters presented as stand-alone journal articles, I provide a note on the structure and format of the thesis as a whole.

1.2 Setting The Scene: Contextualizing The Concept Of Functional Ecology

Biodiversity can be defined as the variety in all living things (MEA, 2005) and is measurable from the scale of genetics to ecosystems (Gaston, 2000). In ecology, biodiversity has traditionally focussed on taxonomic diversity, that is to say the identity and abundance of species (Díaz and Cabido, 2001), with indices of measurement typically encompassing species richness and evenness for a given geographical area and a certain scale (Whittaker, 1972; Magurran, 1988). More recently, the use of alternative measures of biodiversity, such as phylogenetic (Srivastava et al., 2012) and functional diversity (Laliberté and Legendre, 2010), have gained traction due to their ability to provide a link between diversity and ecosystem function (Díaz et al., 2013). The focus of this thesis is functional ecology thus, although phylogenetic diversity has on occasion been advocated as a proxy for function (Winter et al., 2013), functional diversity is used to address ecological concepts.

Box 1.1: Glossary*

Biodiversity: The variability among living organisms. It includes diversity within and among species and diversity within and among ecosystems (MEA, 2005).

Community Assembly: The processes that shape the identity and abundance of species within ecological communities (Kraft and Ackerly, 2014).

Ecosystem: A dynamic community of plant, animal and microorganism communities and their non-living environment interacting as a functional unit and linked by energy and nutrient flows (adapted from MEA, 2005).

Ecosystem Functioning: The joint effects of all functions that sustain an ecosystem (Reiss et al. 2009).

Ecosystem Functions or Processes: The fluxes of matter and energy over time and space through biological activity (Reiss et al. 2009).

Ecosystem Services: The benefits people obtain from ecosystems. These include provisioning services such as food and water; regulating services such as flood and disease control; cultural services such as spiritual, recreational, and cultural benefits; and supporting services, such as nutrient cycling, that maintain the conditions for life on Earth (MEA, 2005).

Effect Traits: Traits which determine how a species contributes to ecosystem processes and functioning (Violle et al., 2007).

Functional Diversity: The extent of functional differences among the species in a community. It quantifies trait variation or multivariate trait differences within a community (Tilman, 1997; Cadotte et al., 2011).

Functional Redundancy: Occurs when species have functional traits in common and therefore perform similar functions (Rosenfeld, 2002; Ricotta et al., 2016).

Functional Traits: Any measurable feature of an individual that potentially affects fitness or performance, whether physical, behavioural or temporal/phenological (Cadotte et al., 2011).

Habitat Degradation: A decline in habitat quality, generally as a result of direct or indirect human activities, that leads to reduced survival and/or reproductive success in some, but not necessarily all, species and affects ecosystem functioning (adapted from IUCN, 2006).

Habitat Filtering: Ecological filters select individual species from a regional pool because they possess traits suitable for a given habitat, thus compelling species to converge toward an optimum trait value and become functionally similar (Keddy, 1992; Maire et al., 2012).

Niche Differentiation: Process through which co-occurring species differ in their resource-acquisition traits, decreasing the intensity of interspecific competition and promoting the complementarity of resource use in space and time (Gross et al., 2007; Carroll et al., 2011).

Response Traits: Traits which determine how a species responds to changes in abiotic conditions and biotic pressures (Díaz et al., 2013).

*Terms have been variably defined within the literature. Presented here are commonly used definitions and their respective sources. Where appropriate, terminology is further defined in more detail in relevant sections in the text.

Below I review the genesis of functional diversity, from the building blocks of functional traits, to the refinement of metrics of measurement, its relationship with traditional diversity measures such as species richness, its link to ecosystem functioning, and the effect that habitat degradation has on the biodiversity - ecosystem function relationship with reference to the particular ecosystem functions which form a topic of study in this thesis.

1.3 Functional Traits: The Building Blocks Of Community Assembly And Functional Ecology

Functional diversity is intrinsically linked to species' traits as it is a measure of the value and range of these traits (Díaz and Cabido, 2001). A trait can be defined as any measurable feature of an individual that potentially affects fitness or performance, whether physical, behavioural or temporal/phenological (Cadotte et al., 2011). Traits, which are the outcome of natural selection (Reiss et al., 2009), in turn determine where a species can live (Lavorel et al., 1997), how they interact (Davies et al., 2007), how they respond to environmental change (Violle et al., 2007), and their contribution to ecosystem functioning (Lavorel et al., 2011). Hooper et al. (2005) define a functional trait more succinctly as 'those traits that influence ecosystem properties or species' responses to environmental conditions'. At a community level, trait-based approaches can thus provide a mechanistic way by which to better understand how communities assemble (Weiher and Keddy, 1995), and likely ecosystem-level responses at a level not tied to taxonomy (Webb et al., 2010). Essentially, there is a shift in focus to what an organism does, rather than what it is (Reiss et al., 2009); although, as discussed in section 1.5 and investigated in **Chapter 2**, a relationship can exist between species identity and function.

The diversity of potential traits that can be measured is huge (Cornelissen et al., 2003), ranging from whole-organism traits such as plant growth form (which are used in this thesis to classify plant species in **Chapters 3** and **5**), to traits at a finer scale such as antennae length (used in **Chapter 4**). Some traits are continuous (e.g. leaf area, body length) while others are categorical (e.g. petal presence or absence).

Functional traits are typically classified as either response traits or effect traits (Lavorel and Garnier, 2002; Naeem and Wright, 2003; Suding et al., 2008). Response traits are those traits which determine how a species responds to changes in abiotic conditions and biotic pressures (Díaz et al., 2013). Shifts in ecological drivers, such has habitat degradation, often change the suite of functional trait properties within an ecosystem (Allan et al., 2015) and response traits are central to understanding this change (Díaz et al., 2013). Particular environmental conditions which pose specific challenges to organism colonization, establishment and persistence in a given habitat are defined as habitat filters (Díaz et al., 1999; Maire et al., 2012). Habitat filtering imposes ecological conditions which select individual species from a regional pool due to their possession of traits which are suitable for a given habitat (Keddy, 1992). Habitat filtering constrains the trait values possible within a community, affecting community assembly as species are forced to converge to an optimum trait value and functional similarity (Grime, 2001; Maire et al., 2012). Species that are functionally dissimilar to those suited to those ecological conditions are excluded as they cannot survive the local environmental stress (Mayfield and Levine, 2010). For example the habitat suitable for soil microfauna, the focus of study in **Chapter 4**, can be limited by soil pH level (Vilkamaa and Huhta, 1986). Thus, only those species from the regional species pool with traits suited to those particular conditions survive to procreate; species with traits unsuited to handle the soil pH within a particular environment are filtered out of the community. Habitat filters can also impact variably at the different life stages of an organism. For example, many of the insect pollinator species recorded in **Chapter 5** have larval stages which may have significantly different habitat requirements compared to their adult stage (Céréghino, 2006).

Biotic interactions can also play an important role in community assembly (Diamond, 1975; Mayfield and Levine, 2010; Breitschwerdt et al., 2018). Competition may arise where species compete for the same limited resources and species that have a functional strategy complimentary to that utilised by neighbouring species may be at an advantage (MacArthur and Levins, 1967). This can result in the divergence of trait values and niche differentiation (Kraft et al., 2008). For example, two plant species may benefit from different floral traits or by flowering at different times of year to enhance pollinator visits (Blüthgen and Klein, 2011). Despite their apparent opposing effects on community-level trait distribution, both habitat filtering and biotic interactions shape community assembly simultaneously (MacAarthur and Levins, 1967; Gross et al., 2013), although their relative importance may change with environmental degradation (Mason et al., 2013) and along successional gradients (Böhnke et al., 2014). Where habitat filtering dominates it is expected that few similar response traits, which most successfully respond to the filters, will dominate (Ordoñez et al., 2009). Conversely, in communities where high levels of competition drive niche differentiation, it is expected that the dominant, co-existing response traits would be divergent and complimentary in resource acquisition (Thompson et al., 2010). Furthermore, in the same community, some traits can show convergence while others exhibit divergence and the scale of analysis may also affect both processes with habitat filtering dominant at a larger scale and niche differentiation more prevalent at a smaller scale (Gross et al., 2013).

Effect traits are those traits which determine how species contribute to ecosystem processes (Violle et al., 2007), whether or not such traits represent an adaptive advantage to an organism itself (Díaz et al., 2013), and are central in understanding the relationship between biodiversity and ecosystem functioning (Grime, 2001). Response and effect trait categories are not mutually exclusive (Suding et al., 2008) as traits can simultaneously influence how species respond to a disturbance or a change of environment (functional response traits) and the effect of species on ecosystem processes and properties (functional effect traits) (Chapin et al., 1996; Weiher et al., 1999; Díaz and Cabido, 2001). For example the functional trait of litter quality, the key trait of consideration in **Chapter 3**, may be a *response* to stress tolerance or nutrient enrichment in addition to *affecting* fire frequency and litter decomposition (Funk et al., 2008).

The increased movement towards a functional approach to answering ecological questions has resulted in a strong demand for standardised methods to measure ecologically meaningful traits (Pérez-Harguindeguy et al., 2016) and a rapid expansion of regional and, to a lesser extent, global trait databases (e.g. Díaz et al. 2004; Wright et al. 2004; Kleyer et al. 2008; Cornwell et al. 2008; Chave et al. 2009; Baraloto et al. 2010; Zanne et al. 2010; Fortunel et al. 2012). Despite this, data remains conspicuously lacking from less studied regions, particularly in the global south, predominantly due to the under-studied nature of many of these locales in addition to financial and/or logistic constraints (Kattge et al., 2011). It is beyond the scope of this review to detail the protocols for the standardized measurement of functional traits (see Cornelissen et al. (2003); Pérez-Harguindeguy et al. (2016)) but certain factors are worthy of mention. In particular, it is important to highlight that study objectives and logistics determine the selection of traits measured, species selected, and number of replications. Furthermore, an important consideration is the potential of intra-specific trait variation where certain traits may vary considerably within a species depending on abiotic conditions, biotic constraints or even temporally. Despite these caveats, with adequate precautions the use of functional traits has proven to be fundamental in understanding how functional diversity in the broad sense underpins ecosystem functioning (Chapin et al., 2000; Díaz et al., 2007).

1.4 Functional Diversity: A Vital Component Of Biodiversity

Functional diversity, defined by Tilman (2001) as the extent of functional differences among the species in a community, quantifies functional trait variation or multivariate functional trait differences within a community (Cadotte et al., 2011). A functional approach to biodiversity can thus allow ecological understandings that go beyond taxa and biogeographical regions, and can reveal how communities assemble, how species coexist, how they may respond to environmental change, and how they might affect multiple ecosystem processes (Tilman et al., 1997; Mason and De Bello, 2013). In the past two decades, numerous indices of functional diversity have been developed (see Petchey and Gaston, 2006; Villéger et al., 2008; Laliberté and Legendre, 2010; Chao et al., 2018). Although it is beyond the scope of this chapter to deliver an exhaustive review of all indices, a brief overview is provided in the following two paragraphs.

Until relatively recently, functional diversity was only measured by functional group richness (Hooper et al., 2002) where groups of species were assigned according to *a priori* classification schemes such as plant growth form (Flynn et al., 2009). While potentially useful (Lavorel et al., 1997), this method was found to be inadequate due, most notably, to extensive biological variation within functional groups and arbitrary cut-off points (Petchey et al., 2004; Wright et al., 2006). Subsequently, the need for continuous metrics to measure functional diversity was highlighted (Petchey and Gaston, 2002; Villéger et al., 2008) and studies which utilised dendrogram-based methods to calculate functional diversity values became more frequent (Petchey and Gaston, 2002; Flynn et al., 2009, 2011). In these methods, Euclidean distances are calculated from a matrix of functional traits to create a dendrogram, thereafter the sum of branch lengths of the dendrogram is used as a multivariate measure of functional diversity (Petchey and Gaston 2002; Podani and Schmera, 2006). However, the value of the dendrogram-based method has also been questioned, primarily due to an inability to take into account trait abundance and the difficulty in choosing the correct distance-cluster method to create a dendrogram, and this method is rarely used today (Podani and Schmera, 2006; Mouchet et al., 2008; Maire et al., 2015). Contemporary studies incorporating functional diversity measurements typically use a distance-based approach based on functional pairwise distance matrices computed using trait values and a measure of species abundance (Mouchet et al., 2010; Schleuter et al., 2010).

Generally, functional diversity cannot be expressed as a single number (Mason et al., 2005), since it describes the range, evenness and divergence of functional trait values within a community (see Box 1.2 for definitions) (Van der Plas et al., 2017). Mason et al. (2005) developed three independent indices, namely functional richness, functional evenness, and functional divergence, to provide more detail in examining the mechanisms linking biodiversity to ecosystem function and community assembly processes. The aforementioned indices were initially derived using single traits and consequently deemed unsuitable for a multi-trait approach. The indices were subsequently further developed by Villéger et al. (2008) to allow for the measurement of species in multivariate functional trait space, in addition to being independent of species richness and each other. Villéger et al.'s (2008) framework was mostly limited to quantitative trait data without missing values and was yet further developed by Laliberté and Legendre (2010) by increasing flexibility and allowing the indices to measure any number and type (i.e. categorical and/or continuous) of traits while tolerating missing trait values and allowing for the weighting of individual traits. Laliberté and Legendre (2010) additionally proposed a new multidimensional index, namely functional dispersion, which indicates the distribution of abundances in functional trait space relative to an abundance weighted centroid, and the volume of space occupied. Functional dispersion, along with functional entropy (also known as Rao's Q (Botta-Dukát, 2005)), are occasionally used in studies as singular measures of functional diversity (Mouchet et al., 2010). Because functional diversity is a multifaceted framework that can be divided into three main categories (functional richness, functional evenness and functional divergence), it is recommended to investigate each functional component separately with an appropriate index (Mouchet et al., 2010). As the indices are independent of each other, the majority of contemporary studies use a combination of functional richness, evenness, divergence, dispersion, and/or entropy. This allows for an accurate and more comprehensive assessment of functional diversity and the establishment of its relationships with ecosystem functioning, community assembly and habitat disturbance (Mouchet et al., 2010; Mouillot et al., 2013). These relationships form an important focus of **Chapter 2**.

Box 1.2: Functional Diversity Indices

Functional Trait Space: a multidimensional space where the axes are functional traits along which species are placed according to their functional trait values (Mouillot et al., 2013).

Functional Richness: The range of traits in a community quantified by the volume of functional trait space occupied (Derhé et al., 2016). Functional richness only takes into account the species with the most extreme trait values and ignores potential trait variation between the extremes (Mouchet et al., 2010).

Functional Evenness: Shows how species' abundances are distributed throughout the occupied functional trait space (Derhé et al., 2016). Functional Evenness will be maximized by an even distribution of both species and abundances in the functional space and lower when some parts of the functional space are empty while others are densely populated (Mouchet et al., 2010).

Functional Divergence: the proportion of total abundance supported by species with the most extreme trait values within a community (Mouillot et al., 2013) **OR** the variation in the distribution of species abundances with respect to the centre of functional trait space (Derhé et al., 2016). High functional divergence is associated with a high degree of niche differentiation among species within communities - the most abundant species are very dissimilar and weakly compete (Mouchet et al., 2010).

Functional Dispersion: The distribution of abundances in functional trait space relative to an abundance weighted centroid, and the volume of space occupied (Laliberte and Legendre, 2010).

Rao's Quadratic Entropy: The degree of divergence in the abundance distribution of species functional traits (Botta-Dukat, 2005). It depends both on the range of functional space occupied and on the similarity between species with the highest abundance (Mouchet et al., 2010).

1.5 Species Richness vs. Functional Diversity: A Complex And Non-Linear Association

While there is an inherent connection between species richness and functional diversity (Cadotte et al., 2011), the precise nature of this relationship remains uncertain (Díaz and Cabido, 2001; Naeem, 2002; Hooper et al., 2005; Rodrigues-Filho et al., 2017) and forms the topic of study in **Chapter 2**. Simply put, the functional identity of species matters in functional diversity. For example, a community of five functionally different species would exhibit much higher functional richness than a community of five functionally identical species. Similarly, where species richness remains static because colonization matches extinction, functional diversity may fluctuate independently of species richness depending on the functional traits which characterize the old and new communities (Mayfield et al., 2010). This relationship is covered in more detail in section 1.7.

Niche differentiation theory implies that functional characteristics of co-occurring organisms must differ at some level, such that greater species richness should lead to increased functional diversity (Weiher and Keddy, 1999). Alternatively, habitat filters may restrict community composition to a relatively limited range of functional characteristics which, in turn, constrain the degree of functional diversity present (Díaz et al., 1998; Loreau et al., 2001). In such instances, greater species richness results in a finer division of the available niche space instead of increased functional diversity (Díaz and Cabido, 2001). Where species converge into relatively discrete functional strategies, a positive linear relationship between functional diversity and species richness has been reported with the latter exceeding the former (Díaz and Cabido, 2001).

In many ecosystems, species richness exceeds functional richness as a result of functional redundancy whereby species have functional traits in common (Rosenfeld, 2002; Ricotta et al., 2016). Functional redundancy is a mechanism which increases an ecosystem's resilience, providing an insurance against loss of function as species are lost (Loreau, 2000). Of course, redundancy changes depending on the number and identity of traits examined and there are many possible permutations of a species richness-functional diversity relationship within a single community (Naeem and Wright, 2003). For example, plant species may have identical growth forms and leaf sizes but differ remarkably in palatability, or response to fire (Cowling et al., 1994). The more traits used to assess functional diversity, the greater the likelihood to detect functional differences between species (Petchey and Gaston, 2002). However, care should be taken to not include traits which are positively correlated as this may cause artificial convergence of functional diversity and species richness (Naeem and Wright, 2003). Conversely, negatively correlated traits may inflate functional diversity (Cadotte et al., 2011).

The relationship between species richness and functional diversity is also sensitive to the metric used to measure functional diversity (Cadotte et al., 2011), another key aspect investigated in **Chapter 2**. For example, consider a community dominated by functional redundant species but with a rare, functionally distinct species present. A significant reduction in the number of the functionally redundant species may not affect functional richness, but functional evenness will change. Conversely, loss of the functionally distinct species would reduce functional richness and increase functional evenness. Functional diversity indices based on both species traits and relative abundance (e.g. functional evenness and dispersion) do not even require a loss of species, merely a change in abundance, to show change (Villéger et al., 2010) and unlike species richness, may provide an early warning signal of habitat disturbance (see section 1.7) (Mouillot et al., 2013).

1.6 The Biodiversity-Ecosystem Function Relationship

Universal driving forces of matter and energy cause biotic and abiotic components of ecosystems to interact in complex ways resulting in a multitude of natural processes (Figure 1.1) (de Groot et al., 2002). Ecosystem functions, such as litter decomposition (**Chapter 3**) and pollination (**Chapter 5**), are attributes of one or many of these natural processes (Lovett et al., 2006) which can have both intrinsic and potential anthropocentric values (Petter et al., 2013). Where ecosystem functions result in direct or indirect benefits to humans they are defined as ecosystem services and provide economic benefit to humankind (Costanza et al., 1997; MEA, 2015), while a strong movement also exists to conserve natural systems for ethical reasons and for the less easily defined benefits they can provide to human well-being (Ridder, 2008; Jax et al., 2013).

The unprecedented loss of biodiversity across the globe due to unsustainable human activity is pushing many of the planet's natural systems that are supporting life on Earth to the brink of collapse (Dirzo et al., 2014; IPBES, 2018). As a result, understanding of the relationship between biodiversity and ecosystem function has become increasingly important (Figure 1.1) (Loreau et al., 2001). In the early 2000s, in particular, numerous reviews were published synthesizing the findings of empirical studies on this relationship (Loreau et al., 2001; Hector et al., 2001; Hooper et al., 2005; Balvanera et al., 2006; Worm et al., 2006) and the topic continues to elicit much interest today (Thompson et al., 2018). In addition, it has proved a fertile ground for the growth of functional diversity studies as this particular component of biodiversity provides a mechanistic relationship with ecosystem functioning (Cadotte et al., 2011). Overall trends disseminated from multiple reviews found that losing diversity in an assemblage tends to reduce the ecosystem process rates carried out by these assemblages (Hooper et al., 2005), both diversity loss and reduction of ecosystem processes becomes stronger over time (Cardinale et al., 2007), and reduction in diversity affects certain aspects of ecosystem stability (Balvanera et al., 2006). The majority of the studies included in the aforementioned reviews used species richness as a measure of biodiversity (Hillebrand and Matthiessen, 2009); however species richness alone can be a poor measure of biodiversity (Wilsey et al., 2005), particularly in how it is associated with ecosystem function (Weisser et al., 2017). Firstly, species richness fails to take into account relative dominance or rarity of species within communities (Hillebrand et al., 2008), and secondly ignores the concept of functional traits which control how a species responds to and affect ecosystem functions (Figure 1.1) (Díaz and Cabido, 2001). As such, functional diversity, which measures the distribution and range of what species *do* in communities and ecosystems (Petchey and Gaston, 2006), is commonly acknowledged to be a better predictor of ecosystem function than species richness (Tilman et al., 1997; Díaz and Cabido, 2001). For example, studies have linked increased above-ground biodiversity (and thus a more diverse litterfall) to increased decomposition rates (Hector et al., 2000; Hättenschwiler et al., 2005; Handa et al., 2014). However, without knowledge of the functional diversity within these communities it is impossible to know how this phenomenon occurs.

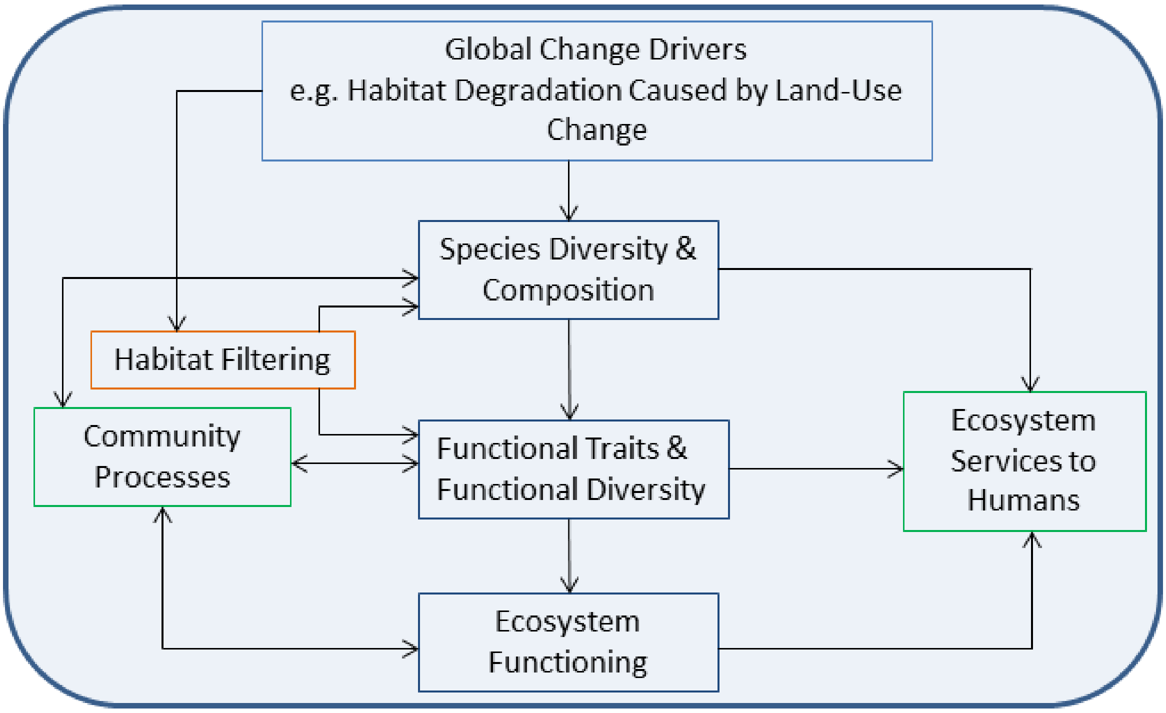

Figure 1.1: A conceptual framework showing biotic controls, habitat filtering, and feedbacks on ecosystem function. Habitat filtering results in a community consisting of a particular assemblage of species diversity and composition. This community contains a set of functional traits in varying abundance which affect both community processes (e.g. competition) and ecosystem functions (e.g. nutrient cycling). Community processes themselves provide feedback affecting species composition and diversity, functional traits, and ecosystem function. Ecosystem function can, in turn, affect community processes. Humans derive benefits at all scales of this cycle from species composition, functional traits and ecosystem functions. Finally, global change drivers such has land-use change-induced habitat degradation can rapidly alter habitat filters resulting in shifts in community composition and diversity (Adapted from Chapin et al., 1997; Slingsby et al., 2014).

Ecosystem function is often dependent on the trait values of the dominant species in the assemblage (Smith and Knapp, 2003; Garnier et al., 2004), or can be greatly affected by rare species that act as biotic modifiers through their role as ecosystem engineers, keystone species, or niche constructors (Lyons and Schwarts, 2001; Linder et al., 2012). For example, the presence of a nitrogen-fixing species in an ecosystem can have profound effects on litter decomposition by altering soil chemistry (Mack and D'Antonio, 2003). As discussed in section 1.5, species richness and functional diversity are inherently linked (Cadotte et al., 2011). As such, greater diversity in trait range and values, as a result of increased species richness, may enhance ecosystem functioning by allowing more complete and efficient use of available resources through resource partitioning and/or by promoting positive species interactions such as facilitation (Cardinale et al., 2012; Slingsby et al., 2014).

When several species share traits which influence ecosystem functioning, the 'effect traits' referred to in section 1.3, they are labelled, as mentioned previously, as functionally redundant (Rosenfeld, 2002). This is a misnomer however, as functional redundancy is not the equivalent of functional superfluousness (Loreau, 2000); rather, it is a mechanism of enhancing stability and resilience to ecosystem processes when faced with species loss (Ricotta et al., 2016). High functional redundancy may also explain the weak relationship observed on occasion between species richness and ecosystem functioning (Wardle et al., 1997; Cardinale et al., 2006). It is clear that the functional traits of a species are more important than species richness in determining ecosystem functioning and, where functional redundancy occurs, the relationship between species richness, functional diversity and ecosystem function, is not linear (Flynn et al., 2009; Guerrero et al., 2014).

Ecosystem functioning is ensured by a range of processes. Some of these processes will be driven by a species deemed redundant, whereas others may be ensured by a single or a few species. Thus, whether an ecosystem can be considered functionally redundant as a whole, and thus more stable, resistant and resilient, will depend upon the ratio between the number of species and their functions which is never constant (Micheli and Halpern, 2005). Ecosystem functioning therefore depends on the strength and nature of the relationship between functional and species diversity, however for many ecosystems this relationship remains poorly understood (Naeem, 2002; Guillemot et al., 2011; Rodrigues-Filho et al., 2017) as is highlighted by the dearth of knowledge on the functional role of indigenous Springtails in **Chapter 4** .

1.7 Degradation: Habitat Alteration Impacts On The Biodiversity-Ecosystem Function Relationship

Land use change is one of the most fundamental and persistent environmental drivers world-wide with habitat destruction and degradation one of the chief causes of biodiversity loss in the majority of ecosystems (Plieninger and Gaertner, 2011; Maxwell et al., 2016). Although it comes in many forms, habitat degradation is most prominent following the increase in land-use intensification associated with agricultural activity (Kleijn et al., 2011). Agricultural intensification and expansion is a multifactorial process (Chamberlain et al., 2000) which acts at a scale from individual agricultural fields to the entire landscape, affecting habitat structure and composition (Guerrero et al., 2014). As a result, agricultural intensification and subsequent habitat degradation is often associated with complex and detrimental effects on biodiversity and ecosystem functioning (Kremen et al., 2002; Stoate et al., 2009). Degradation can exist along a gradient from almost complete destruction of an ecosystem to more subtle effects, such as the selective loss of certain elements impacting on ecosystem functioning.

There is an inherent link between the gradient of habitat degradation as a result of disturbance, and secondary succession (Pickett et al., 1987). Simply put, secondary succession is the ecological succession that occurs after a pre-existing community or ecosystem has been disrupted and some plants and animals still exist. In agricultural lands, the cessation or significant reduction in human land-use is followed by some form of secondary succession (Debussche et al., 1999). Indeed, habitat degradation and secondary succession can be viewed as different directions along the same axis with degradation causing community disassembly (but see Figure 1.2 for exceptions), and secondary succession causing community reassembly (Sanders et al., 2003). Subsequently, the same ecological processes which influence communities which undergo habitat degradation, namely environmental filtering and niche differentiation due to biotic interactions, play an important role in community dynamics during reassembly (Tate and Battaglia, 2013). An additional factor which influences the trajectory of secondary succession are the initial conditions at the point of cessation of disturbance (Chazdon, 2008). These conditions are heavily controlled by the nature of the land-use activity and not only determine the point of departure for secondary succession but may have longer lasting legacy effects (Rees et al., 2001). Finally, secondary succession generally involves a migration of species to the previously disturbed community and is thus influenced by landscape dynamics; particularly the landscape structure (e.g. highly fragmented remnant patches of natural vegetation), and dispersal abilities within the regional species pool (e.g. highly mobile animals and wind-dispersed plants are more likely to colonize a previously degraded environment compared to more sedentary species) (Cook and Crisp, 2005; Myers and Harms, 2009; Lohbeck et al., 2014)

A specific ecosystem, or community within an ecosystem, could be described either through the lens of degradation or through that of secondary succession. In this thesis I use the term degradation to describe the current state of individual study sites as I believe that in agricultural landscape it is a more accurate descriptor of what has resulted in the communities seen today. In the following chapters, sites which until recently were subject to agricultural activity are labelled ‘highly degraded’ while abandoned lands where activity ceased some time ago are described as ‘moderately degraded’; however I fully acknowledge that these sites could be described using secondary successional nomenclature (e.g. early successional and late successional, respectively). I keep this in mind throughout the thesis, particularly in discussion points surrounding future conservation implications as processes such as the dispersal abilities of species within the regional species pool, and land-use legacy effects are important factors controlling the future trajectories of communities.

The growing concern on how habitat degradation-induced biodiversity loss will impact on the ecosystem functions and processes provided by natural communities has resulted in increased empirical and theoretical work in an attempt to enhance our understanding of this relationship (Díaz et al., 2007). Initially, the general consensus was that land-use intensification simply causes a loss of species and a subsequent reduction in functional diversity with concurrent impacts on ecosystem functions (Mayfield et al., 2010). The logic was that habitat degradation affects species in a non-random sequence due to their possession of vulnerable functional response traits causing a decline and eventual loss of species and the vulnerable traits they possess (Zavaleta et al., 2009; Mouillot et al., 2013). However, as discussed in section 1.6, the relationship between species richness, functional diversity and ecosystem functioning is complex, non-linear, and for the most part poorly understood or rarely described (Naeem and Wright, 2003). Empirical studies have, on occasion, reported no decrease in either species or functional diversity of plants in conjunction with agricultural intensification (Flynn et al., 2009). In addition, in degraded habitats the rate of non-native species introductions can exceed the rate of species loss (Sax et al., 2002; Ellis et al., 2011) and habitat degradation can lead to novel ecosystems (see Hobbs et al., 2006, 2009 for a review). Indeed, ecosystem response to habitat degradation is controlled at least as much by which species and functional traits are lost (or gained) as by how many species are lost or gained (Hooper et al., 2005).

As illustrated in Figure 1.2, a key factor in determining the effect degradation has on the relationship between species and functional diversity is the level of functional redundancy within a community (Ricotta et al., 2016). Habitat degradation can increase the prominence of habitat filters or introduce new filters but, in communities with high functional redundancy, if species loss is evenly distributed across functional types there is no concurrent loss of functional diversity (Mayfield et al., 2010). However, where degradation processes disproportionally remove certain functional traits (e.g. longer-lived, slow-growing species (Pakeman, 2011)) this pattern is unlikely and functional diversity will decrease (Flynn et al., 2009).

In agricultural landscapes empirical evidence suggests with decreasing species richness a decrease in functional diversity is the most likely outcome as traits vulnerable to activities such as ploughing and intense grazing are filtered out of the community (Quétier et al., 2007). Conversely, functional diversity may decrease, even though species richness remains the same, if degradation causes the extinction of functionally unique species from a community and a simultaneous influx of new species with similar functional traits to those species unaffected by the degradation may occur (Mayfield et al., 2010).

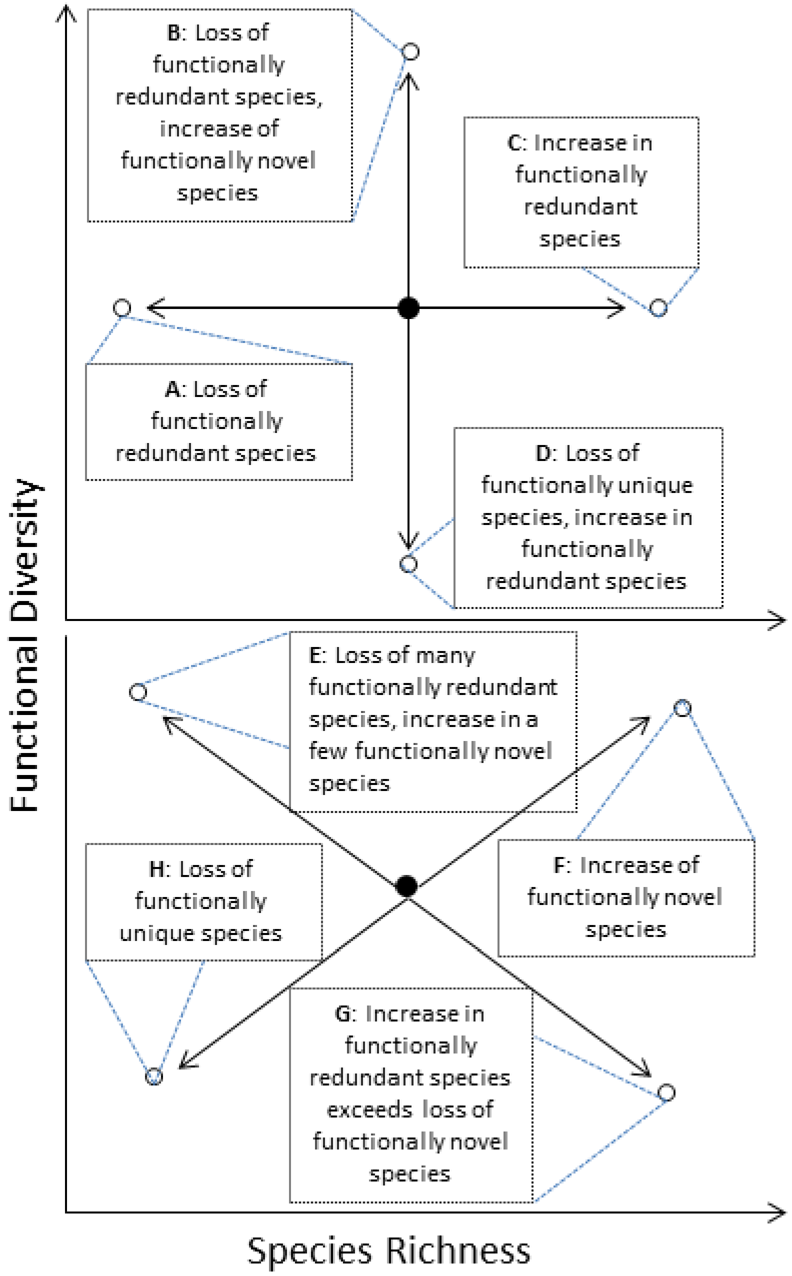

Figure 1.2: Theoretically feasible changes in species richness and functional diversity following degradation as a result of habitat alteration. Filled circles represent undisturbed communities and open circles represent communities following degradation. Circle positions are relative and not exact locations on the axes. Note: Relationships not necessarily linear as depicted here e.g. functionally unique species loss preceding functionally redundant loss will result in curved relationship (Adapted from Mayfield et al. (2010).

This scenario, where functional diversity decreases but species richness remain the same, is feasible e.g. in a situation where a pristine community has both tall, long-lived species and herbaceous annuals present and degradation filters out the former and new, herbaceous annual species arrive to supplement the species pool which persisted post-disturbance (McIntyre and Lavorel, 1994). If, in a similar situation, functionally redundant species are filtered out and replaced by species with novel functional traits, functional diversity will increase but species richness will remain the same (Mayfield et al., 2010). A less likely, but still theoretically plausible, scenario is an increase in species richness accompanied by static functional diversity where disturbance reduces competitive interactions and allows an increase in functionally redundant species to persist within a community (Mayfield et al., 2010). If this same unlikely scenario is accompanied by an increase in functionally unique species, both functional diversity and species richness will increase within a community.

If one accepts that functional effect traits directly affect ecosystem functions (Violle et al., 2007; Suding et al., 2008), and that habitat degradation influences the abundance and presence of certain traits through habitat filtering (Mouillot et al., 2013), it naturally follows that degradation will impact on ecosystem functioning (Chapin et al., 1997). Of course, certain ecosystem processes respond directly to human modification, however the effect of degradation-induced shifts in functional diversity and thus ecosystem functioning is an important, non-trivial factor (Pakeman, 2011; Venn et al., 2011). The link between biodiversity, particularly functional diversity, and ecosystem function has been covered in section 1.5. Similarly, the various manners in which habitat degradation can cause shifts in biodiversity have been discussed in this section and illustrated in Figure 1.2. The most salient point here is that there is wide variation in the manner in which ecosystem functioning may change in relation to shifts in biodiversity as a result of habitat degradation (Díaz et al., 2006). While agricultural intensification frequently filters out species of both plants and animals with vulnerable traits thus reducing species richness, functional diversity and reducing ecosystem function (Pakeman, 2011), many exceptions to this pattern are possible and the relationship is highly context dependent, influenced by the amount of functional redundancy, the type and intensity of habitat degradation, the specific ecosystem function in question (Mayfield et al., 2010).

A prime example of the complexity surrounding the relationship between biodiversity, ecosystem function, and degradation can be found in pollination, the focus of study in **Chapter 5**. The aftermath of degradation can often lead to an influx of alien plant species, particularly in agricultural landscapes (Early et al., 2016). The presence of alien vegetation can prove beneficial for indigenous pollinator communities and thus even benefit native flora (Moragues and Traveset, 2005), particularly where initial degradation has severely reduced floral resources. However, the opposite is also true if alien vegetation reduces insect visitation to native plants resulting in pollinators utilising alien plant species at the expense of indigenous species (Morales and Traveset, 2009). Clearly, context is important, just as is how an ecosystem function is measured. In the latter case, pollination may appear fully functional from one perspective (e.g. if pollinator communities have sufficient access to floral resources), but inadequate from an alternate perspective (e.g. pollination success of indigenous flora is severely reduced).

Functional diversity metrics can provide an important mechanism to reveal the complex nature of change within degraded communities, both in terms of functional community structure and associated ecosystem functioning (Pakeman, 2011; Mouillot et al., 2013). The rationale behind using functional diversity indices, rather than traditional taxonomic measurements, to reveal the impact of disturbance on community structure is that they are suggested to be more likely to show consistent monotonic relations along a disturbance gradient (Cornwell et al., 2006). Conversely, taxonomic diversity indices generally show idiosyncratic or unimodal responses to disturbance (Villéger et al., 2010; Mouillot et al., 2013). The functional richness component of functional diversity, which is linked to species richness, is likely to decrease at high levels of habitat degradation as species are filtered out the community (but see Figure 1.2 and associated text for alternate scenarios). On the other hand, functional diversity indices which take into account both trait values and abundance (e.g. functional evenness and functional divergence) do not require the local extinction of species to change along a degradation gradient and can thus act as an early warning of habitat degradation despite no change in species or functional richness (Mouillot et al., 2013). Through the calculation and comparison between functional diversity indices, ecologists can assess the effect of disturbances on the functional structure of communities and potential changes to ecosystem functioning (Mouillot et al., 2013). Comparing functional diversity indices requires statistical tests, often with the use of null models, to account for strong correlations which may occur between the functional and taxonomic structure of communities (Flynn et al., 2009; Mouillot et al., 2013). Although more detailed accounts of how a functional approach can be used to assess community responses to degradation is provided in Kleyer et al. (2012) and Moulliot et al. (2013), a key point to distil from the literature is how the different components of functional diversity can track changes to community functional structure after habitat degradation in different ways.

Another mechanism to measure and monitor degradation of communities is the use of bioindicators (Parmar et al., 2016). These indicators of biodiversity are generally species, or groups of species, which are sensitive to changes in environmental health, thus their presence or abundance can used to assess habitat degradation (Teder et al., 2007). As is the case with most ecological concepts, bioindicators have historically been based on taxonomic identification (Breure et al., 2005) but in the last decade a more functional approach has been developed using species traits and functional groups (Feld et al., 2009; Vandewalle et al., 2010). The taxonomic identity and/or the functional composition of plant (Hodgson et al., 2005), benthic invertebrate (Charvet et al., 1998), soil fauna

(Van Straalen, 1998), above-ground insect (Vanbergen et al., 2005), and bird (Douglas et al., 2009) communities are examples of some of the organisms which have been used successfully as bioindicators. Soil fauna in particular have been frequently used as bioindicators in measuring the impact of degradation as a result of agricultural land-use (Volz, 1962; Van Straalen, 1998; Kennedy, 1999; Parisi, 2001; Lindberg and Bengtsson, 2005; Ponge et al., 2006). Among soil fauna, Springtails, the organism of study in **Chapter 4**, have great potential for use in integrated biodiversity monitoring schemes (Van Straalen et al., 2008) due to their abundance, diversity and functional role in soils (Hopkin, 1997). Indeed, their use as bioindicators for ecosystem health has already been explored (Lindberg and Bengtsson, 2005; Cassagne et al., 2006; Ponge et al., 2006; Frampton and van den Brink, 2007; Greenslade, 2007; Errington et al., 2018). However, the current state of knowledge concerning the impact of disturbance on functional traits, functional diversity, and Springtail community dynamics remains limited in many locations such as South Africa, in part due to a lack of empirical data for multiple species (Lindberg and Bengtsson 2005; Van Straalen et al. 2008).

1.8 Renosterveld: Understudied And Critically Endangered

1.8.1 History

Renosterveld is a species-rich, highly transformed and critically endangered vegetation type located within the Cape Floristic Region of South Africa. Although subdivided into a number of different types, Renosterveld is generally found growing on the relatively fertile and clay-rich soils derived from underlying shale (Rebelo et al, 2006). Unlike the adjacent Fynbos vegetation, this relative fertility and grassier nature most likely supported native herbivore communities (Krug et al., 2004). Due to its accessibility and its relatively nutrient-rich soils, Renosterveld was the first vegetation type to be converted for agriculture by the early European settlers who reached the shores of the Western Cape post 1652 (Newton and Knight, 2004). Additionally, sustained hunting by the settlers would have severely depleted the native fauna (Rebelo, 1995). Even prior to European colonisation, the indigenous inhabitants of the region had influenced Renosterveld for their benefit. The Khoi pastoralists arrived in the region approximately 2 000 years ago and they undoubtedly burnt areas of Renosterveld to promote vegetation more suitable for their cattle and sheep to graze on (Deacon, 1992). Prior to the Khoi, the San hunter-gatherers may have used fire to flush out game species from Renosterveld; however their impact on Renosterveld is negligible when compared to the initiation of agriculture (Deacon, 1992). The manipulation of Renosterveld ecosystems for millennia, particularly since the arrival of European settlers, has made it complicated to know what a fully functional natural Renosterveld ecosystem looks like and how drivers interact within it (Radloff et al., 2014) and several authors have incorrectly postulated that Renosterveld originated, at least in part, from anthropogenic disturbances (Acocks, 1953; Boucher and Moll, 1981). However, the presence of endemic taxa indicates an independent and potentially long history (Bergh et al., 2014).

1.8.2 Extent, Definitions And Threats

Renosterveld extends over approximately 20 000 km^2 of the Cape Floristic Region. It is the most poorly defined vegetation type in South Africa (Milton, 2007) and many contemporary descriptions and definitions of Renosterveld are ambiguous or complicated resulting in a lack of consensus on what the distinguishing features of Renosterveld are (Walton, 2006). The main reasons for this ambiguity surrounding Renosterveld are the lack of accurate baseline data and the considerable variation in the community composition across a gradient of rainfall quantity and seasonality (Milton, 2007). In addition, the phytochorologically transitional nature of Renosterveld, with its floristic links to Fynbos, Subtropical Thicket and Succulent Karoo, may explain why in some instances it is not straightforward to classify communities as Renosterveld (Bergh et al., 2014). In the wake of numerous ecological studies on the adjacent Fynbos in the last century, Renosterveld has often been erroneously relegated to "transitional" (Cowling, 1984), "derived" (Boucher, 1987) or "disclimax" (Specht and Moll, 1983) and on occasion not distinguished from Fynbos at all (e.g. Pole-Evans, 1936). But now, following an increased level of study in recent years (Topp and Loos, 2018), and refined use of phylogenetics, Renosterveld is widely acknowledged as a unique and important component of the Cape Floristic Region (Bergh et al., 2014).

Renosterveld typically comprises a low shrub layer (1-2 m tall) of predominantly fine-leaved, well-branched woody shrubs (usually with one dominant species at a site) with a ground layer of seasonally active bulbs and grasses (Cowling, 1983; Bergh et al, 2014). Unlike Fynbos, which is partly defined by the presence of members of the Ericaceae, Restionaceae and Proteaceae, these families are almost entirely lacking in Renosterveld, though they may occur in low abundances (Cowling, 1983; Bergh et al, 2014). Renosterveld is generally restricted to the fine-grained, shale-derived soils of the coastal plains and inland valleys, predominantly where an annual rainfall of between 300 and 650 mm falls (of which at least 30% falls in winter) (Boucher and Moll, 1981; Rebelo, 1998). It usually occurs on the ecotone between Fynbos and Succulent Karoo with varying proportions of perennial grasses, succulents, geophytes and re-sprouting and re-seeding evergreen shrubs (Rebelo et al., 2006).

Despite the evident value in the biodiversity of Renosterveld (Turpie et al. (2003) estimate the monetary value of biodiversity in the CFR as R10 billion per annum), there are multiple issues facing Renosterveld conservation currently. Chief among these threats is habitat degradation and loss but the threat of invasive alien species, inappropriate disturbance regimes and climate change all pose significant challenges (Rebelo, 1992; Rouget et al., 2014). Habitat loss through crop cultivation in particular over the past 150 years has led to the majority of Renosterveld being converted into agricultural land (Kemper et al., 1999), much of which is still farmed for grain and artificial pasture (and increasingly vineyards) today. Even formerly ploughed areas which are no longer in use, so called 'old fields', are generally invaded by alien grasses or other weedy species (Ruwanza, 2017). Less than 10% of the natural Renosterveld vegetation remains (Curtis, 2013) and most of the remaining Renosterveld is in fragmented remnants surrounded by cereal crops and artificial pasture (Kemper et al., 1999; Donaldson et al., 2002). Less than 3% of Renosterveld is formally conserved (Low and Rebelo, 1998) and the majority of fragments are found within private property where they are in danger of mismanagement (Curtis, 2013). Often the smaller fragments (<10 ha) have persisted because they are situated in positions where ploughing is difficult, for instance on rocky outcrops, steeper slopes and road verges. Farmers occasionally allowed larger fragments to remain to provide grazing for sheep; however these would be frequently burnt to encourage grass growth (Donaldson et al., 2002). A more recent study has reported that there are only 12,296 patches of Renosterveld remaining, of which only 72 are greater than 80 hectares in size (Curtis, 2013).

1.8.3 Overberg Renosterveld

Overberg Renosterveld, largely synonymous with South Coast Renosterveld (Cowling et al., 1986; Curtis, 2013), consists of four dominant vegetation types: Western-, Central- and Eastern-Rûens Shale Renosterveld which span the relatively fertile lowlands of the Overberg and south-eastern Cape, and Rûens Silcrete Renosterveld which largely occurs in a thin strip along the Breede River (Figure 1.3). Although all types are broadly similar in vegetation composition, Western Rûens Renosterveld is distinguished from other Rûens Renosterveld types by the absence of *Hermannia flammea* and rare occurrence of *Aloe ferox* and *Vachellia karroo* in addition to having a higher mean annual precipitation. Central Rûens Renosterveld is distinguished from Eastern Rûens Shale Renosterveld by the absence of *Aloe ferox* (Rebelo et al., 2006). Only 12% of the original extent of Overberg Renosterveld remains (SANBI, 2009) although other estimates are as low as 4-6% (Curtis, 2013) and all Renosterveld types are classified as critically endangered (Rebelo et al., 2006).

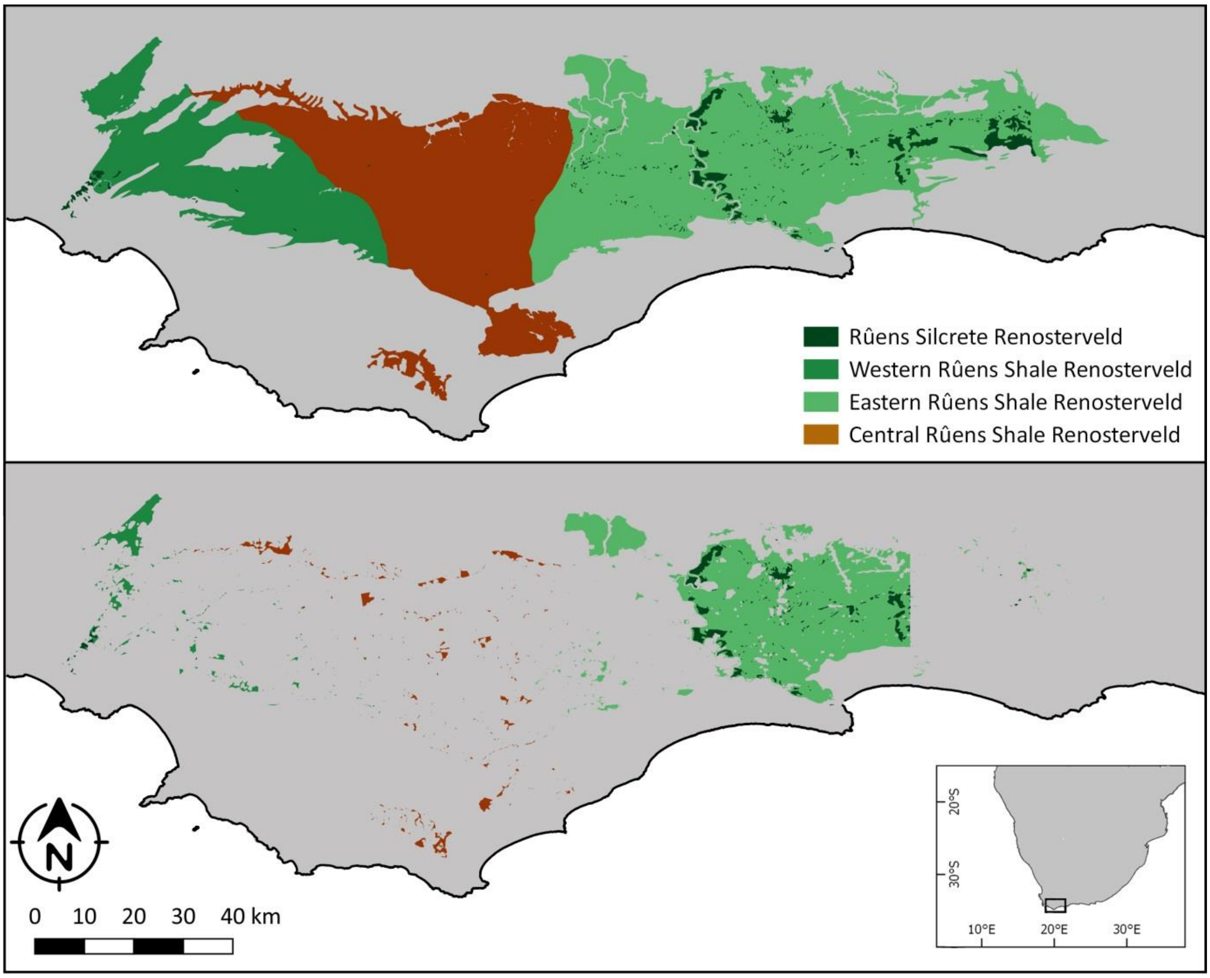

Figure 1.3: The original extent and delineation of Renosterveld types within the Overberg region of South Africa (top) and the remaining fragments (below). Data sourced from Mucina and Rutherford (2006).

There is a paucity of research on Overberg Renosterveld although this has been somewhat ameliorated by Curtis (2013) who focussed her PhD research on the area. Her findings suggest the natural vegetation was more than likely a grassy-shrubland rather than a 'shrubby grassland', although historically a higher proportion of palatable C3 and C4 grasses existed in the region. In addition, the system is fire dependent and sensitive to grazing regimes, with a fire return interval equal or slightly lower than that of Fynbos (approximately 4-12 years). The more intact patches were shown to have high alpha, beta and gamma diversity with alpha diversity comparable to, if not higher, than that of adjacent Fynbos. As a result of the highly fragmented nature, altered disturbance regimes, and substantial habitat degradation, many aspects of the functional ecology of Overberg Renosterveld may be at risk of extinction (Krug et al., 2004, Curtis, 2013). Indeed, a general lack of knowledge regrading functional ecology could impede current and future conservation efforts (Topp and Loos, 2019).

1.8.4 Conservation

The biggest threat facing Overberg Renosterveld is the continued agricultural expansion for pasture and crops (Curtis et al., 2013), augmented by the risk of alien invasion as a result of poor management of land not currently used for agriculture (Topp and Loos, 2019). A vital step in counteracting this is to change the opinion of farmers who do not see Renosterveld as economically advantageous (Winter et al., 2005). Collating data which show the importance of biodiversity towards ecosystem functions, particularly ecosystem services which are beneficial to farmers themselves, is important motivation to the majority of farmers who are unwilling, or financially unable, to conserve remnant patches of Renosterveld within privately owned lands purely for the sake of conservation (Winter et al., 2007). Effective conservation the world over is underpinned by improved understanding of ecological functioning, however Overberg Renosterveld remains understudied (Topp and Loos, 2019). To safeguard and conserve this critically endangered vegetation a network of reserves and the motivation of land-owners to manage their remaining fragments is crucial (Curtis, 2013). Although notable success has been achieved by the Overberg Renosterveld Conservation Trust (www.overbergrenosterveld.org.za) to do this effectively, it is vital to enhance our knowledge of the functional ecology of the region and explore the relationship between biodiversity and ecosystem function, and what effect habitat degradation may have on it.

The restoration of degraded habitats is a critical tool for conservation both globally (Dobson et al., 1997), and in Renosterveld where so little pristine vegetation remains (Krug and Krug, 2007) and where remnants fall far below national conservation targets (Rebelo et al., 2006). The restoration of ecosystem function is a fundamental goal for restoration practitioners but, although considerable progress has been made in recent years (Temperton et al., 2004; Falk et al., 2006), the understanding of the ecological processes underlying successful restoration of the ecosystem services provided by biodiversity often remains incomplete (Montoya et al., 2012). To successfully restore ecosystem function it is vital to have an understanding of the relationship between taxonomic diversity, functional diversity and ecosystem functioning (Mayfield et al., 2005). Similarly, as restoration is essentially the amelioration and reversal of habitat degradation (SER, 2004), understanding the effect degradation has on the aforementioned relationship can be an important part of restoration endeavours (Temperton et al., 2004). Degradation imposes environmental filters on communities but these filters may vary according to the type and intensity of the degradation (Weiher and Keddy, 1995). Understanding how this gradient of degradation affects community disassembly and ecosystem functions may provide instructive information on how best to reassemble communities and efficiently restore lost functionality (Hobbs et al., 2013). Similarly, the resistance of degraded systems to restoration will vary along these degradation gradients resulting in different 'thresholds' to be overcome (Hobbs and Harris, 2001). By understanding how these thresholds, both biotic and abiotic (Whisenant, 1999), may vary in accordance with disturbance history, restoration practitioners can refine their actions to best utilise their available resources and maximise their chance of success (Hobbs and Norton, 2004).

Essentially, to maximize conservation we need to ensure successful restoration of degraded ecosystems. This requires a robust understanding of the relationship between biodiversity (both taxonomic and, in particular, functional diversity components), ecosystem function, and the effects of degradation to inform us what we need to restore and when. Currently, this knowledge is lacking for Renosterveld and it is through this lens that the more practical applications of this thesis are addressed.

1.9 Thesis Aim, Objectives And Structure

Current debates in literature presented above emphasize the importance of developing a detailed understanding of the relationship between biodiversity and ecosystem function for the successful conservation of endangered vegetation types such as Renosterveld.

As such, the overarching aim of this thesis is to explore the relationship between biodiversity and ecosystem functioning across a degradation gradient in critically endangered Renosterveld vegetation within an agricultural landscape in South Africa. Five specific objectives were formulated to address this aim. The objectives of this thesis are to:

1. Explore the relationship between taxonomic diversity, functional diversity, and functional composition along a degradation gradient.
2. Determine the effect of plant functional types, season, and habitat degradation on plant litter decomposition.
3. Determine the effect of season, plant litter type and habitat degradation on Springtail (Collembola) community composition.
4. Evaluate the effect of degradation on plant-pollinator networks.
5. Synthesize the data reported in the project to assess the relationship between biodiversity and ecosystem function across a degradation gradient and reflect on potential practical recommendations.

Objectives 1-4 are addressed in **Chapters 2**, **3**, **4**, and **5** which are formatted as journal articles. Each journal article has more detailed and specific objectives presented within, but all are informed by the overall aim of this thesis (see Table 1.1). **Chapter 6** is written as a general discussion and serves to address objective 5, synthesizing the empirical data collected and addressing the overarching project aim. Although formatting a PhD thesis this way comes with many benefits, there is some unavoidable repetition in the four research papers, particularly in providing details on the study site, and at times an overlap exists with the literature reviewed in this chapter and that presented in the journal article introductions. Additionally, the peer-review process necessarily implemented by all respected journals impacted on the final content presented here. At the behest of reviewers, certain materials presented in the original submitted manuscripts were recommended to be cut for the purpose of streamlining the final published articles. These edits were implemented; however, some of the materials removed are directly relevant to the broader thesis narrative, despite understandably being deemed superfluous to the individual journal articles. Where relevant, I refer to this expurgated material in **Chapter** 6 and, in the appendices of **Chapter** 6, include details on the corresponding methodology and data. Finally, different peer-reviewed journals have different formatting requirements but, for the sake of continuity and consistency, I have re-formatted the articles, numbering all tables and figures consecutively, and standardizing article structure, ecological terminology and citation style. Certain pictures have also been included in this thesis which are absent from the submitted articles but hopefully add context and insight to the thesis as a whole.

Figure 1.4 positions each chapter within the larger ecological framework presented in Figure 1.1 and disseminated within the literature review above. **Chapter 2** addresses the relationship between taxonomic diversity and species diversity of above-ground vegetation, a critical component of the biodiversity-ecosystem function relationship. **Chapter 3** investigates the drivers controlling the ecosystem function of litter decomposition, before **Chapter 4** focuses on the factors influencing Springtail (functionally important, soil-dwelling microinvertebrates) community dynamics, both in terms of taxonomic diversity and through functional trait data. **Chapter 5** studies the ecosystem function of pollination through the analysis of three complete plant-pollinator networks.

A common thread throughout the four research papers is the impact the level of habitat degradation, as a result of historical land-use, has on communities, ecosystem functions, and their relationship. Theoretically, this allows the thesis to address conceptual issues surrounding community assembly and disassembly processes, functional redundancy, how the relationship between the different facets of biodiversity may change, and whether this affects the relationship between biodiversity and ecosystem function. In practical terms, not only does the thesis add to the current limited number of functional ecology studies in Renosterveld, but in addressing the biodiversity-ecosystem function relationship through the lens of a degradation gradient, it provides data and insights to optimize future conservation and restoration work in this critically endangered vegetation type.

All data collection, analysis, interpretation, and writing of this thesis have been undertaken by me, but there have been collaborators who have assisted in various ways. Co-authors and their respective roles are detailed in Table 1.2; all other assistance is noted in the acknowledgment section of each chapter and at the outset of this thesis.

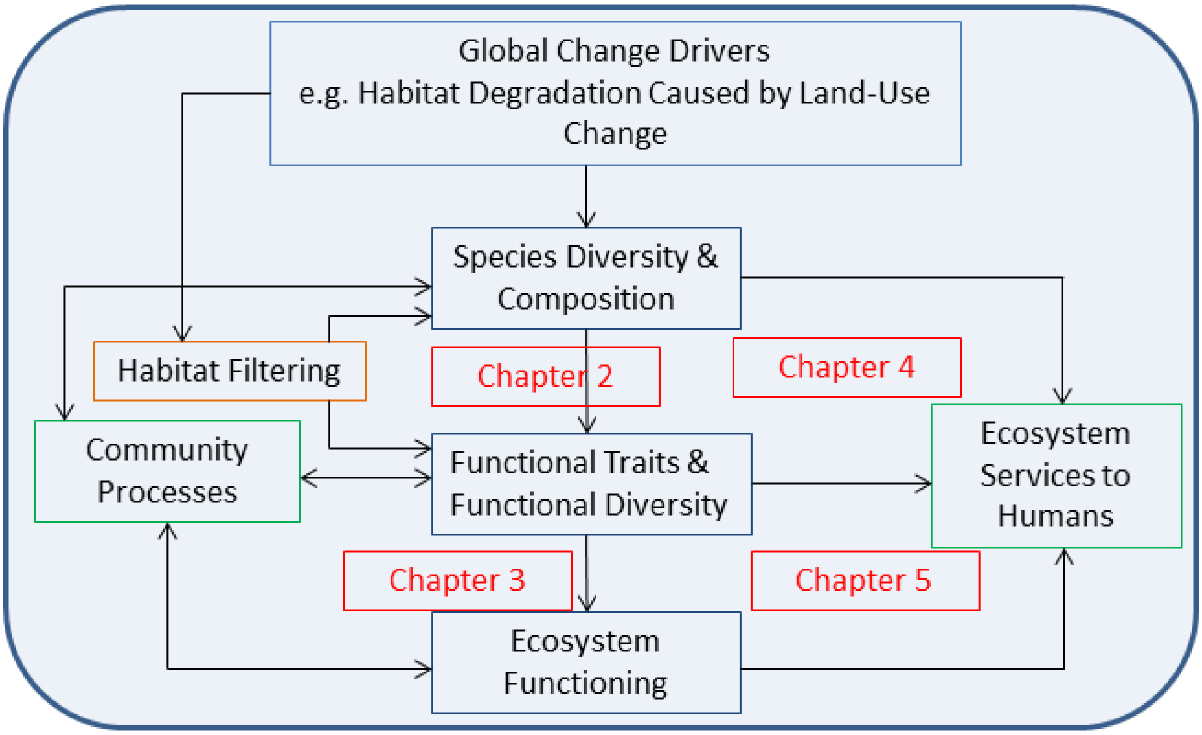

Figure 1.4: A reproduction of Figure 1.1 giving a graphic representation of the approximate position of the four empirical data chapters in relation to the conceptual framework of the feedbacks affecting ecosystem function.

Table 1.1: Structure of the thesis in relation to thesis chapters, key objectives and journal submission details

Chapter	Central Purpose	Submission Details
Chapter 1 **Introduction**	Chapter 1 serves to introduce the project through a detailed literature review which contextualizes and provides rationale to the research. The overarching aim and research objectives are presented and details of the thesis structure provided.	
Chapter 2 **Taxonomic Diversity, Functional Diversity and Functional Composition in a Critically Endangered Vegetation Type within the Cape Floristic Region, South Africa**	Through the use of vegetation surveys, functional trait data and statistical analysis Chapter 2 investigates the relationship between taxonomic and functional diversity indices of vegetation across a degradation gradient, and the effect of degradation on community composition.	Under Review In: *Journal of Vegetation Science*
Chapter 3 **Litter decomposition variation across a degradation gradient in a critically endangered vegetation type within the Fynbos biome, South Africa**	Through the use of litterbags and generalized linear mixed models Chapter 3 investigates the effect of species identity, plant functional traits, time, season, and habitat degradation on the ecosystem function litter decomposition.	Published in: *South African Journal of Botany*
Chapter 4 **Springtail communities in a critically endangered vegetation type in South Africa**	Chapter 4 investigates the taxonomic and functional distribution of a functionally important yet understudied microinvertabrate through the assessment of the effect of litter type, level of landscape degradation, and season on Springtail community dynamics.	Submitted to: *Soil Biology and Biochemistry*
Chapter 5 **Three complete plant-pollinator networks along a secondary successional gradient in critically endangered Renosterveld, South Africa**	In Chapter 5, three complete plant-pollinator networks are used to assess the critical ecosystem process of pollination with the reported network structure from the pristine site compared to that of a similar study from the adjacent Fynbos and global studies. Network indices are additionally used to explore the effect of habitat degradation on network structure, diversity and specialization.	Published in: *Journal of Pollination Ecology*
Chapter 6 **Discussion**	Chapter 6 serves to synthesize the key findings and link them to the overarching thesis aim through the discussion of theoretical concepts introduced in Chapter 1, and more practically data relevant for future conservation work	

Table 1.2: Author contributions to chapters in this thesis

Chapter	Authors	Author Contribution
1	OS Cowan	OSC wrote all text
2	OS Cowan, PML Anderson, ME Meadows	OSC & PMLA conceived and designed study. OSC collected and analysed all data and wrote manuscript. PMLA and ME edited manuscript and provided feedback
3	OS Cowan, PML Anderson	OSC & PMLA conceived and designed study. OSC collected and analysed all data and wrote manuscript. PML edited manuscript and provided feedback
4	OS Cowan, PML Anderson, CL Janion-Scheepers	OSC, PMLA & CLJ-S conceived and designed study. OSC collected and analysed data and wrote manuscript. CLJ-S assisted with data analysis. PMLA and CLJ-S edited manuscript and provided feedback.
5	OS Cowan, PML Anderson	OSC & PMLA conceived and designed study. OSC collected and analysed all data and wrote manuscript. PML edited manuscript and provided feedback
6	OS Cowan	OSC wrote all text

1.10 References

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Chapter 2

Taxonomic Diversity, Functional Diversity and Functional Composition in a Critically Endangered Vegetation Type within the Cape Floristic Region, South Africa

Paul Godard

Taxonomic Diversity, Functional Diversity and Functional Composition in a Critically Endangered Vegetation Type within the Cape Floristic Region, South Africa

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Abstract

Although there is an implicit connection between taxonomic and functional diversity, the precise nature of this relationship remains uncertain, particularly where habitat degradation alters environmental filters. In Renosterveld, a critically endangered vegetation type within the Cape Floristic Region of South Africa, this relationship remains understudied. Here, our aim is to explore the relationship between taxonomic diversity and functional diversity along a degradation gradient in an attempt to not only provide information on community assembly and disassembly processes, but deliver important data towards conservation and restoration of biodiversity and ecosystem functioning. Twenty one sites were assigned into three degradation classes with the use of historical aerial photographs of the region, current satellite imagery, and local expert knowledge. We conducted vegetation surveys and compiled functional trait data on identified species. Taxonomic indices, functional diversity indices, and community-weighted means were calculated from abundance data collected during vegetation sampling. We used explored the relationship between taxonomic and functional diversity, and analysis of variance on community-weighted mean values to assess the effect of degradation on community functional composition. The nature and degree of correlation between taxonomic and functional diversity was shown to be inconsistent across indices and degradation gradient. Significant differences in functional composition were shown to exist between highly degraded sites compared to pristine sites; however moderately degraded sites and pristine sites were found to be functionally similar. The relationship between taxonomic and functional diversity indices in Eastern Rûens Shale Renosterveld is complex and may be influenced by the functional redundancy which has evolved to provide resilience to stochastic population shifts.

Habitat degradation can alter this relationship with potential ecological and conservation implications. Reduction in functional diversity in highly degraded communities may increase their vulnerability to environmental perturbations and reduce ecosystem functioning. Conversely, the similarity in functional composition between pristine and moderately degraded sites may provide a more positive indication of passive restoration, however further studies are advocated.

2.1 Introduction

Globally, biodiversity loss is occurring at an unprecedented rate as a result of direct and indirect human alterations to the natural environment (Cardinale et al., 2012). As species' abundance and their distributions shift, there is a concurrent change to ecosystems and their functions (Weed et al., 2013). The well-being of human societies is intrinsically linked to the multitude of ecosystem goods and services provided by these ecosystem functions (Millennium Ecosystem Assessment, 2005). The nature, extent and rate of recent environmental changes are such that the evolving relationship between biodiversity alteration and ecosystem functioning at the community level is poorly resolved (Pecl et al., 2017).

Functional diversity is now widely regarded as a key determinant in understanding ecosystem processes and response to environmental disturbance (Tilman et al., 1997; Díaz and Cabido, 2001; Flynn et al., 2009; Cadotte et al., 2011; Mouillot et al., 2013; van der Plas et al., 2017). As the realization grows that traditional measures of diversity (e.g. species richness) fail to capture the complexities of ecosystem dynamics (McGill et al., 2006), the more complex concept of functional diversity has become extensively used to understand and address biogeographical patterns (Violle et al., 2014), assembly processes along environmental gradients (Villéger et al., 2012), and the impacts of disturbance (Flynn et al., 2009; Sasaki et al., 2009) and restoration (Derhé et al., 2016) on ecosystem functioning. Functional diversity measures are typically based on species functional traits - those traits which respond to environmental drivers and determine ecosystem functioning (Lavorel and Garnier, 2002) - and species abundance (Díaz and Cabido, 2001; Chao et al., 2018). Unlike traditional measures of species richness and diversity, functional diversity presupposes a mechanistic link between diversity and ecosystem function (Cadotte et al., 2011) and it is therefore critical that traits under consideration are those actually responsible for ecosystem function (Violle et al., 2007). As trait measurement methods become standardized (Cornelissen et al., 2003), global trait databases grow (Tavsanoglu and Pausas, 2018), and statistical tools continue to be developed (Chao et al., 2018), functional diversity promises to be an even more useful tool for biodiversity-ecosystem function studies at this critical juncture in environmental conservation and restoration.

Functional diversity cannot generally be expressed as a single number (Chao et al., 2018), since it describes the range, evenness, divergence and dispersion of functional trait values within a community (van der Plas et al., 2017). Earlier studies utilised dendrogram-based methods to calculate functional diversity values (Petchey and Gaston, 2002), however the value of these methods has been questioned (Mouchet et al., 2008) and is rarely used today. Subsequent studies incorporating functional diversity measurements have used a distance-based approach based on functional pairwise distance matrices computed using trait values (see Schleuter et al., 2010, for an overview). Of these, functional richness, functional evenness, functional divergence (Villéger et al., 2008), Rao's quadratic entropy (Botta-Dukát, 2005), and functional dispersion (Laliberté and Legendre, 2010) have become the indices most frequently used in recent years. However, the field of study is advancing rapidly and new functional diversity measures are being refined (Chao et al., 2018).

While there is an implicit connection between species richness, functional diversity and ecosystem functioning, the precise nature of this relationship remains uncertain (Díaz and Cabido, 2001; Hooper et al., 2005). The theories of niche differentiation and limiting similarity imply that functional characteristics of co-occurring organisms must differ at some level, such that greater species richness should lead to increased functional diversity (Weiher and Keddy, 1999). Alternatively, environmental filters may restrict community composition to a relatively limited range of functional characteristics which, in turn, constrain the degree of functional diversity influencing various ecosystem properties (Díaz et al., 1998). In such instances, greater species richness results in a finer division of the available niche space instead of increased functional diversity (Díaz and Cabido, 2001). A single, or a select few species, may be predominantly responsible for any given ecosystem process or property (Hooper et al., 2005), thus increasing species richness increases the chances that those species responsible for a specific ecosystem process are present (Loreau, 2000). A single species may be dominant within an assemblage thus strongly influencing ecosystem function (Garnier et al., 2004), although, certain species (so-called keystone species), while relatively rare or of low biomass, can act as the most important biotic modifiers, ecosystem engineers, niche constructors or facilitators (Power et al., 1996; Linder et al., 2012). In many ecosystems, species richness exceeds functional richness as a result of functional redundancy (Ricotta et al., 2016), a mechanism which increases an ecosystem's resilience, providing an 'insurance policy' against loss of function as species are lost (Loreau, 2000). The greater the number of functionally similar species in an assemblage, the greater the probability that at least some of the species will survive environmental changes and maintain ecosystem functioning (Chapin et al., 1996). Essentially, the losses or gains of particular species have far greater functional implications than others (Isbell et al., 2017) and affect functional diversity and ecosystem functioning differently (Cadotte et al., 2011).

Biodiversity loss (both taxonomic and functional) is generally accompanied by a shift in functional composition as the trait expression of a community shifts simultaneously with change in community structure (Allan et al., 2015) with subsequent effects on numerous ecosystem functions (Lavorel and Grigulis, 2012). For example, an increase in agricultural land-use intensification has shown to favour fast-growing, acquisitive species over slow growing species (De Vries et al., 2012) which in turn increases biomass production and nutrient cycling. By analysing the relationship between taxonomic diversity, functional diversity, and composition, unique insights into the origin and maintenance of biodiversity can be provided (Edie et al., 2018) which, in turn, can deliver powerful data for environmental conservation and restoration of threatened habitats (Petchey and Gaston, 2006). The relationship between biodiversity and ecosystem functioning is particularly pertinent in threatened ecosystems such as Renosterveld, which forms the focus of this study.

Renosterveld is a species rich, highly transformed and critically endangered vegetation type located within the Cape Floristic Region of South Africa (Rebelo et al., 2006), a global diversity hotspot (Myers et al., 2000). Once covering approximately 30% of the Cape Floristic Region, the relatively nutrient rich underlying soils and gentle topography associated with this vegetation type resulted in large swathes of Renosterveld being converted for agriculture (Kemper et al., 1999). Today less than 10% of the original extent remains (Newton and Knight, 2005) with fragments of critically endangered natural vegetation found embedded within an agricultural matrix (Kemper et al., 1999). Due to differences in historical land-use and current management practices (e.g. local extinction of native herbivores, historical ploughing, grazing intensity of domestic livestock, controlled burning regimes etc.), patches of natural vegetation can occur side-by-side along a degradation gradient from pristine vegetation, variably grazed rangelands, to old fields in variable stages of secondary succession and states of degradation (Heelemann et al., 2013). Despite the recent advances in understanding functional ecology in the Cape Floristic Region (see Slingsby et al., 2014), there remains a dearth of studies into the relationship between taxonomic diversity and functional diversity. Furthering our understanding of the relationship between taxonomic and functional diversity and the impact of degradation on this relationship, allows us to better infer the effect of degradation and habitat alteration on ecosystem processes and functioning, and is vital to future conservation and restoration-related decisions in this critically endangered Renosterveld vegetation. Previous ecological studies in Renosterveld have highlighted high species richness and functional redundancy; however these studies focused either solely on taxonomic diversity or used plant functional types as a surrogate for functional diversity (Kemper et al., 1999; van der Merwe and van Rooyen, 2011; Cowan and Anderson, 2014; Radloff et al., 2014; Cousins et al., 2018). Plant functional types, while useful (Lavorel et al., 1997), are limited in the scope of functional data they provide (Wright et al., 2006).

In this paper, we aim to (i) provide data towards exploring the relationship between taxonomic diversity and functional diversity along a degradation gradient, and (ii) assess the implications for biodiversity management and ecosystem functioning, through the following objectives: (i) calculate taxonomic diversity indices using abundance data from vegetation sampling at multiple sites from three different degradation states based on historic land-use, (ii) calculate functional diversity indices and express the structure of trait values using abundance data and trait measurements from vegetation sampling at multiple sites from three different degradation states based on historic land-use, (iii) explore the relationship between taxonomic and functional diversity indices, (iv) use community weighted mean trait values to assess community functional composition between degradation states, and (v) use NMDS plots to assess differences in community composition and explore which environmental variables and functional traits are associated with observed differences.

2.2 Materials And Methods

2.2.1 Study Area

Eastern Rûens Shale Renosterveld is critically endangered vegetation type located within the Overberg region of the Western Cape Province of South Africa (Rebelo et al., 2006). The geology of the region comprises clays and loams derived from Bokkeveld Group Shales (Curtis, 2013). Rebelo et al. (2006) describe Eastern Rûens Shale Renosterveld as occurring on moderately undulating hills and plains which supports cupressoid and small-leaved, low to moderately high grassy shrubland dominated by Asteraceae shrubs. Centuries of agricultural activities and altered disturbance regimes in the region have resulted in a decimation of natural vegetation and currently pockets of pristine vegetation (less than 10% of the original extent (Curtis, 2013)) are found embedded within a matrix of agricultural land (Kemper et al., 1999), consisting predominantly of grain fields (wheat, barley, oats, canola), artificial pasture (lucerne), and grazing for livestock (Curtis, 2013). Eastern Rûens Shale Renosterveld has an altitudinal range of 40-320 metres above sea level and an average rainfall of 384 mm per annum with an essentially even distribution (Rebelo et al., 2006). Mean daily temperatures range from a 5.9 °C minimum in July to a 26.9 °C maximum in January (Rebelo et al., 2006).

2.2.2 Site Selection And Sampling Procedure

Using historical aerial photographs of the region, current satellite imagery, ground-truthing and local expert knowledge, 21 sites were identified and assigned into one of three degradation states (Figure 2.1). Namely, Pristine (n=11) – characterised by no evidence of historical agriculture; Moderately Degraded (n=5) – characterised by evidence of historical agricultural use but none within the last 10 years; and Highly Degraded (n=6) – characterized by evidence of agricultural use within the last 10 years. It was not possible to set equivalent sample sizes for each degradation state due to limited suitable sites and accessibility.

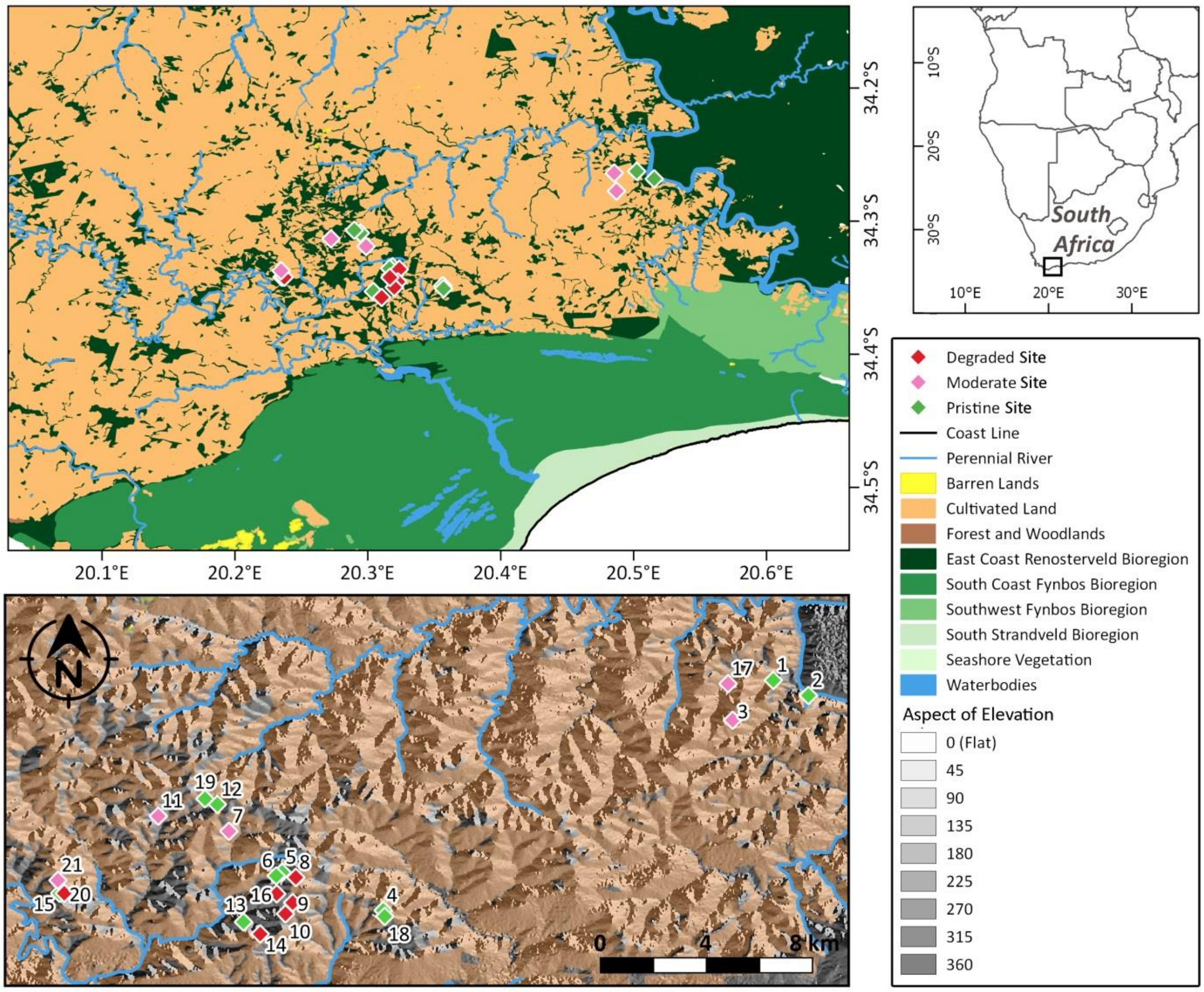

Figure 2.1: The location of the 21 study sites within the greater study area.

Vegetation sampling was conducted at each site, standardized to 1000 m^2, using the modified Whittaker nested vegetation sampling method (Stohlgren et al., 1995) during the austral spring of 2014. Species were identified *in situ* where possible or, alternatively, samples were taken and identified at a later date using expert knowledge and herbarium specimens where necessary.

2.2.3 Environmental Variables

At each site, a composite soil sample (approximately 500 g) was taken from four random locations at depths down to 15 cm (Bohn et al., 2001) and sent to an external accredited laboratory (Bemlab Pty Ltd., Somerset West, South Africa) where the following soil characteristics were measured: pH (KCl; see Mclean, 1982, Phosphorus (Bray II) (mg/kg; see Bray and Kurtz, 1945), Potassium (mg/kg), Exchangeable Sodium, Potassium, Calcium and Magnesium cations (cmol(+)/kg; see Chapman, 1965), organic Carbon (%; see Nelson and Sommers, 1982). In addition, slope aspect and site elevation were recorded using a handheld compass and a GPS device respectively. Finally, the distance from the centre of each site to the nearest agricultural crop field was measured using the measurement function on Google Earth. Although unintentional, highly degraded sites tended to occur on flat lands compared to pristine and moderately degraded sites which typically occurred on sloped gradients.

2.2.4 Functional Trait Selection And Measurement

Trait selection was limited by an absence of an exhaustive trait data repository for flora of the region and restricted by time and financial constraints. Nevertheless 13 traits of known importance to species' ecological functioning, and conservation status in the case of IUCN Redlist data, were recorded (Supplementary Data Table S2.1). Flower colour for each species was assigned based on the literature or direct observation. Where flowers consisted of more than one colour category, such as flowers with visible nectar guides, the dominant colour was used for categorization. Onset of flowering season data was sourced from the literature or from direct observation. Pollination method for each species was sourced from the literature or from expert knowledge. Where a species fell into more than one category the pollination vector with the greatest range of movement (e.g. bird > insect) was chosen. This logic was also used to record dispersal mechanism (e.g. anemochory > myrmecochory). Dispersal mechanism categories were taken from Cornelissen et al. (2003). Species' life form was simplified into either annuals or perennials based on information sourced from the literature. Plant growth form categories follow those of Cornelissen et al. (2003). Data were sourced from the literature and, where measurements such as height or leaf length were required, measured *in situ*. Plant height is defined as the shortest distance between the upper boundary of the main photosynthetic tissues on a plant and the ground level (Cornelissen et al., 2003). As plant height can vary according to populations, direct measurements using a measuring rule of at least 10 individuals per species were taken and averaged. In the case of rare species where n<10, heights of all individuals were recorded and averaged. For leaf area, the average from a minimum of 10 (usually 20) healthy, photosynthetically active leaves per species were used. The area of each individual leaf was calculated using the Easy Leaf Area^{tm} app on a smart phone (Easlon and Bloom, 2014). For minute or narrow needle-like leaves, a magnifying glass and a millimetre grid were used, whereas for large leaves, leaves were cut into smaller pieces before measurement and subsequently summed to obtain a whole-leaf area. For succulence and spinescence (categories taken from Cornelissen et al. (2003)), direct observations were used. Re-sprouting ability and photosynthetic pathway data for each species was sourced from the literature or directly from expert knowledge. Finally, IUCN Redlist status data for each species was sourced from the South African Biodiversity Institute's Redlist of South African Plants (SANBI, 2017) and definitions for each category can be found at http://redlist.sanbi.org.

2.2.5 Data Analyses

Taxonomic and functional diversity indices were calculated for each study site using abundance data collected during vegetation sampling. Taxonomic diversity comprises of two separate components, namely richness and evenness. Although single indices such as the Shannon Diversity index take into account both species richness and evenness and are commonly used, many ecological studies use two distinct indices to avoid confounding the effects of richness and evenness (Magurran, 1988). As our primary aim was to explore the relationship between taxonomic and functional diversity in our study area, we evaluated three species-based taxonomic diversity measures to provide a comprehensive description of taxonomic diversity: species richness (S); species evenness, calculated using Pielou's J (J'); and species diversity, calculated with Shannon's Diversity Index (H). J' is an index constrained between 0 and 1 with lower J' values indicative of low evenness whereas H takes into account both species richness and evenness with the index increasing as both the richness and evenness of a community increases. All taxonomic indices were calculated using the Vegan package for R (R Core Team, 2015).

The functional structure of communities embraces three distinct yet complementary components, namely functional richness, evenness and divergence. Functional diversity thus cannot be summarized using only one index (Villéger et al., 2008). Nevertheless, some synthetic indices, which ostensibly combine some, or all, three facets of functional diversity, exist (Botta-Dukát, 2005; Laliberté and Legendre, 2010). To allow for the most comprehensive understanding of functional diversity, and to aid comparisons with studies which used different functional diversity measurements, the FD package for R (R Core Team, 2015) was used to calculate five measures of functional diversity which describe different functional aspects of biological communities. As defined by Derhé et al. (2016) and Májeková et al. (2016): (i) functional richness (FRic) is the range of traits in a community quantified by the volume of functional trait space occupied; (ii) functional evenness

(FEve), which summarizes how species’ abundances are distributed throughout the occupied functional trait space; (iii) functional divergence (FDiv), which describes the variation in the distribution of species abundances with respect to the centre of functional trait space (Villéger et al., 2008); (iv) Rao’s quadratic entropy (Q), which captures the degree of divergence in the abundance distribution of species functional traits (Botta-Dukát, 2005); and, (v) functional dispersion (FDis), which indicates the distribution of abundances in functional trait space relative to an abundance weighted centroid, and the volume of space occupied (Laliberté and Legendre, 2010). Rao’s Q is conceptually similar to FDis, and simulations have shown high positive correlations between the two indices (Laliberté and Legendre, 2010); however as both are widely used in functional diversity studies we chose to calculate both indices to allow comparison to other studies. In addition, we computed community level weighted means (CWM) which expresses the structure of trait values in the community (Lavorel et al., 2008). For continuous traits, CWM is the mean trait value of all species present in the community weighted by their relative abundances, while for categorical traits the abundance of each individual category is returned.

Diversity indices were illustrated graphically and used to explore the relationship between taxonomic and functional diversity indices through the fitting of linear regression lines and the calculation of Pearson’s correlation coefficient. Values from the CWMs were used for analysis of functional composition across the three degradation levels. To test for significance of trait values between degradation levels, Kruskal-Wallis tests and pairwise comparisons using a Wilcoxon rank sum tests were performed.

Differences in community composition were examined by Non-metric Multidimensional Scaling (NMDS) using the Vegan package in R (R Core Team, 2015). To run the NMDS a Bray-Curtis dissimilarity index was used on square-root transformed abundance data with the number of iterations set at 1000 and a solution reached when the stress was minimized. Using the function *envfit* in Vegan (R Core Team, 2015), environmental variables and functional traits with $p < 0.05$, and species with $p < 0.01$ were overlaid onto the ordinations. A higher significance level was chosen for the species overlay due to large numbers of species found to be significant at $p < 0.05$ which cluttered the ordination.

2.3 Results

2.3.1 Taxonomic Diversity

A total of 286 different plant species were identified in this study, 101 of which were found in only one study site, 231 in five study sites or less and only 21 found in more than 10 study sites. Only a single species, *Dicerothamnus rhinocerotis***,** was present at all sites. In the 10 pristine sites, 243 species were recorded of which 201 were found recorded in three or less sites. In the five moderately degraded sites, 156 species were recorded with 122 species found in two or less of those sites. In the six highly degraded sites, 77 species were recorded with 55 found in three or less of those sites. In total 20 non-native alien species were recorded with 17 of these found in highly degraded sites, 10 in moderately degraded sites and seven in pristine sites. In terms of taxonomic diversity indices (Table 2.1), pristine and moderately degraded sites are similar (mean S = 55.8 for both, mean J' = 0.69 and 0.73, and mean H = 2.77 and 2.93 respectively) and uniformly higher in comparison to the highly degraded sites (mean S = 32.5, mean J' = 0.59, and mean H = 2.08).

Table 2.1: Mean values (±standard deviation) of taxonomic and functional diversity indices for the three degradation states (Values sharing the same superscripts are not significant different. * = *p*<0.05, ***p*<0.01, ****p*<0.001).

	S	**J'**	**H**	**Fric**	**Feve**	**Fdiv**	**RaoQ**	**Fdis**
Pristine	55.80 (8.95)^{a}	0.69 (0.05)^{a}	2.77 (0.23)^{a**}	0.010 (0.004)^{ab}	0.76 (0.05)^{a}	0.79 (0.08)^{a}	0.06 (0.01)^{a}	0.23 (0.02)^{a}
Moderately Degraded	55.80 (7.46)^{a}	0.73 (0.13)^{a}	2.93 (0.05)^{ab}	0.013 (0.005)^{a*}	0.76 (0.02)^{a}	0.81 (0.10)^{a}	0.07 (0.02)^{a}	0.25 (0.02)^{a}
Highly Degraded	32.50 (6.41)^{b***}	0.60 (0.16)^{a}	2.09 (0.62)^{b**}	0.07 (0.001)^{b*}	0.69 (0.06)^{a}	0.75 (0.16)^{a}	0.06 (0.03)^{a}	0.22 (0.08)^{a}

2.3.2 The Relationship Between Taxonomic And Functional Diversity Indices

In terms of the relationship between taxonomic and the various functional diversity indices (Figures 2.2-2.4), we analysed all study sites together and separated the pristine sites from the moderately and highly degraded sites in an attempt to discern any meaningful differences that habitat disturbance may have on the aforementioned relationship. Overall, FRic is moderately correlated to S (Figure 2.2A1) and H (Figure 2.3A1) but more weakly correlated to J' (Figure 2.4A1). When assessing the degraded sites separately (Figures 2.2C1, 2.3C1, 2.4C1) a much stronger correlation emerges, with more than twice the strength of correlation than that observed in the pristine sites (Figures 2.2B1, 2.3B1, 2.4B1). The overall relationship between FRic and J' is weak (Figure 2.4A1), although, in the degraded sites it is substantially stronger (Figure 2.4C1). No strong relationship exists between FEve and H and J', however a tighter fit exists between S and FEve overall and in pristine sites (Figure 2.2B2). FDiv shows a strong negative correlation with S in pristine sites (Figure 2.2B3). Rao's Q shows a moderate negative correlation to S in pristine sites (Figure 2.2B4), but there is no correlation between the two indices overall (Figure 2.2A4) or in the degraded sites (Figure 2.2C4). The opposite is true when analysing the relationship between Rao's Q and J' and H. Here there is moderately tight fit observed overall (Figures 2.3A4, 2.4A4) and in the degraded sites (Figures 2.3C4, 2.4C4), but not in the isolated pristine sites (Figures 2.3B4, 2.4B4). This pattern is repeated for FDis, although in all cases the corresponding correlation is slightly stronger than that for Rao's Q and the taxonomic diversity indices.

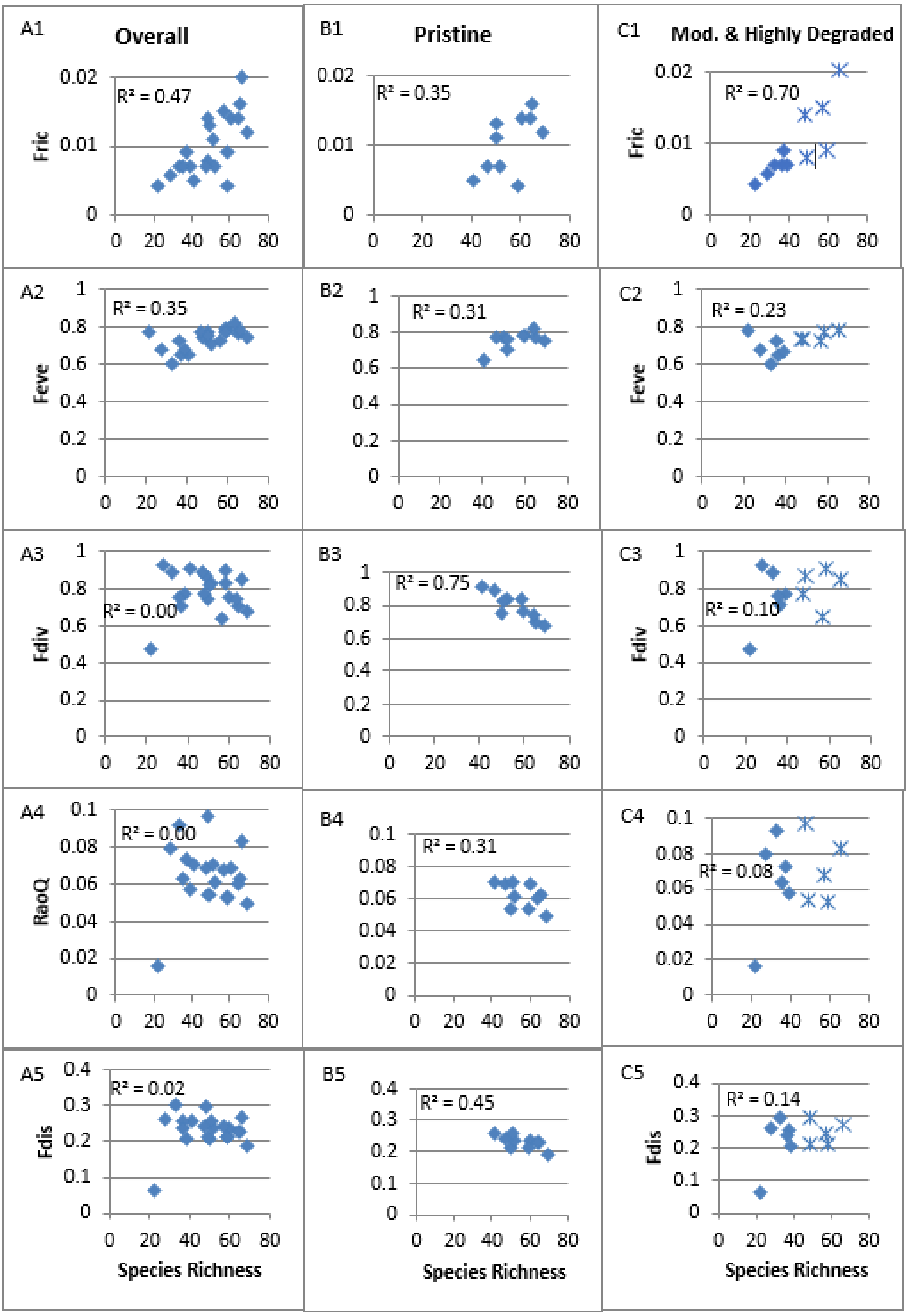

Figure 2.2: Scatter plots showing the relationship between Species Richness and functional diversity indices in a) overall sites b) pristine sites c) moderately (stars) and highly (diamonds) degraded sites.The square of Pearson's R is provided. Fric=Functional Richness; Feve=Functional Evenness; Fdiv=Functional Divergence; FDis=Functional Dispersion.

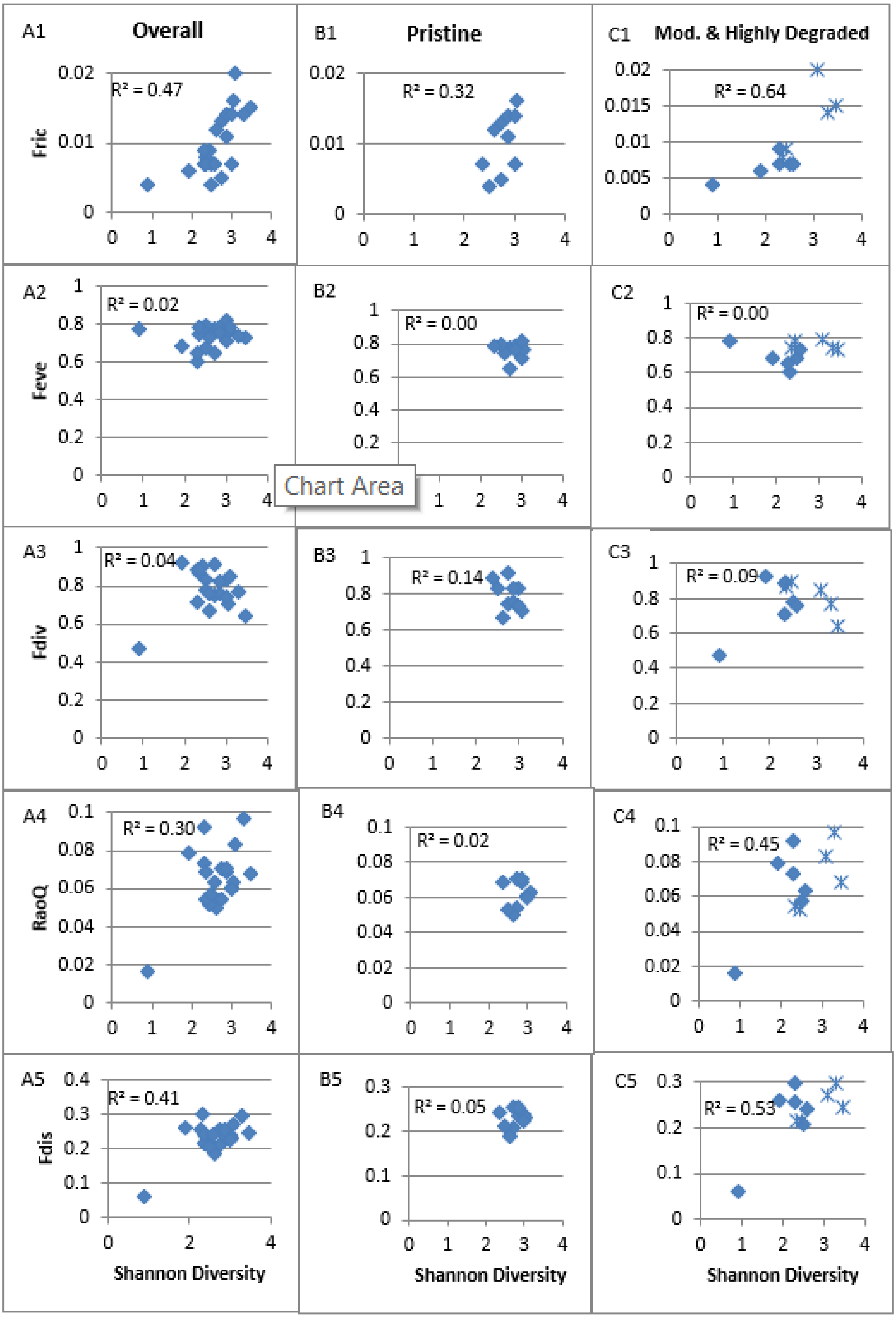

Figure 2.3: Scatter plots showing the relationship between Shannon Diversity and functional diversity indices in a) overall sites b) pristine sites c) moderately (stars) and highly (diamonds) degraded sites.The square of Pearson's R is provided. Fric=Functional Richness; Feve=Functional Evenness; Fdiv=Functional Divergence; FDis=Functional Dispersion.

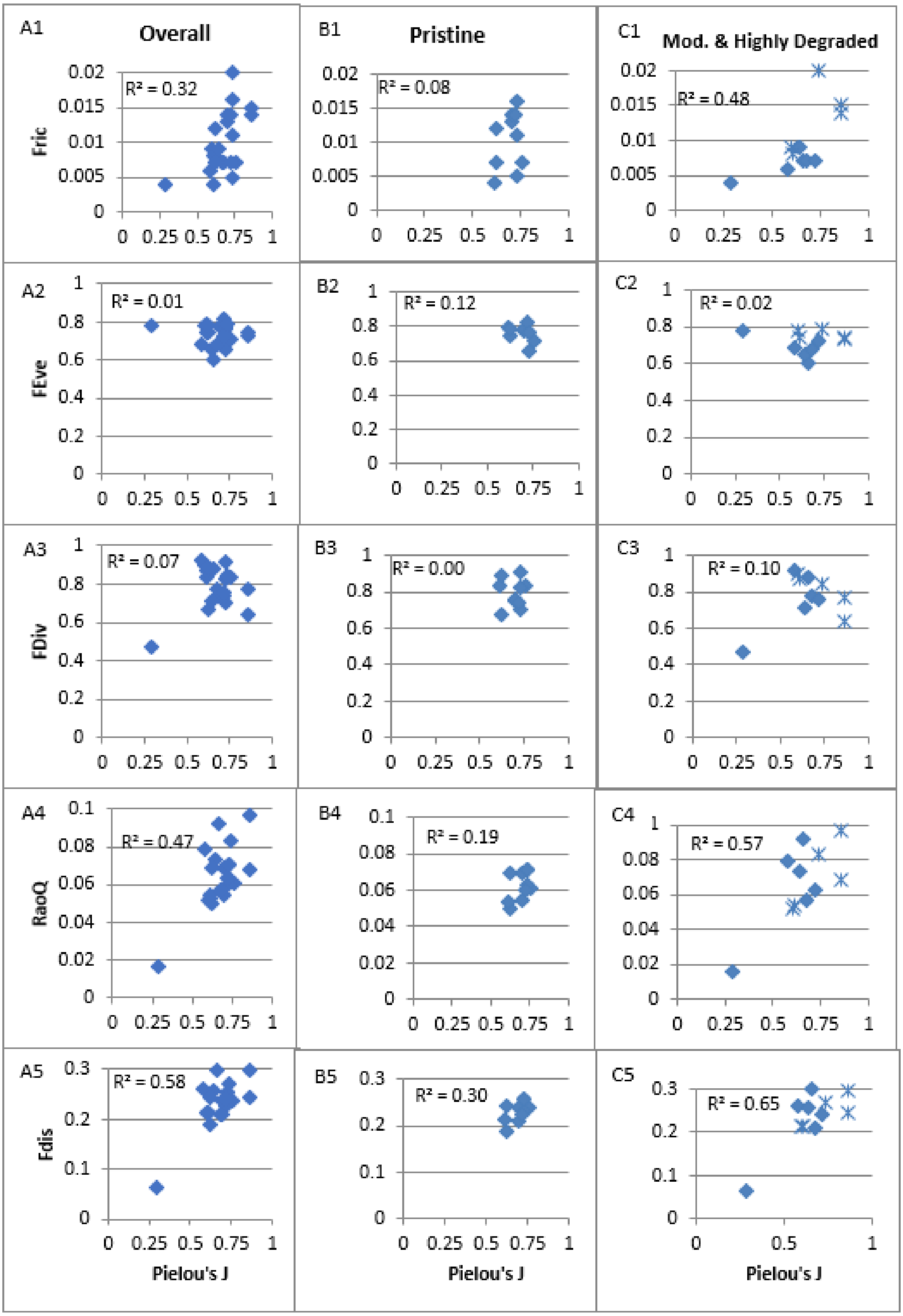

Figure 2.4: Scatter plots showing the relationship between Pielou's J and functional diversity indices in a) overall sites b) pristine sites c) moderately (stars) and highly (diamonds) degraded sites.The square of Pearson's R is provided. Fric=Functional Richness; Feve=Functional Evenness; Fdiv=Functional Divergence; FDis=Functional Dispersion.

2.3.3 Community Composition

The NMDS ordinations related to species space (Figure 2.5), environmental variables (Figure 2.6), and functional traits (Figure 2.7) indicate that the pristine and highly degraded sites are clearly separated along Axis 1. Moderately degraded sites, while more randomly scattered along this axis, tend to cluster towards the pristine sites. In regards to Axis 2, pristine sites exhibit a dispersed pattern. The environmental factors that significantly correlate with study site distribution show an association between highly degraded sites and flatter habitats with increased soil phosphorus levels (Figure 2.6). Conversely, pristine and moderately degraded sites are associated with sloped land, although aspect is not a distinguishing factor (Figure 2.6). In terms of functional traits, non-native alien annuals are strongly aligned with the highly degraded sites whereas “least-concern” (i.e. common indigenous) species are associated with pristine sites (Figure 2.7). The species overlay in Figure 2.5 shows which species are responsible for this with alien annuals such as *Anagallis arvensis*, *Trifolium angustifolium*, *Taraxacum officinale* and *Conyza bonariensis* all favouring the highly degraded sites. Sites 8, 9 and 10 (all highly degraded) are associated with the indigenous shrub *Galenia africana* which is toxic to lifestock. The species associated with the pristine sites are less well grouped but all are indigenous species. Species associations for these sites are more site-limited – e.g. *Asparagus lignosus* and *Ledebouria revoluta* are associated only with sites 1 and 2, and *Thesium strictum* associated only with site 15 (Figure 2.5).

The functional traits represented in the ordination analysis (Figure 2.6) are typically those of the dominant species across the sites and this may obscure more subtle differences in functional composition across the degradation gradient. In depicting these traits graphically and by performing statistical analysis on each individual trait category, differences across degradation states are more clearly evident. There is a significant increase in proportion of autumn flowering in pristine sites and an increase in winter flowering in highly degraded sites (Figure 2.8A). In terms of flower colour, highly degraded sites have a significantly higher proportion of yellow flowers compared to moderately degraded sites, although all sites are dominated by yellow and inconspicuous flowers (Figure 2.8B). All three degradation states are dominated by insect and wind-pollinated species (Figure 2.8C), and also by those species whose seeds are wind dispersed (Figure 2.8D). In the highly degraded sites there is an increased proportion of exo-zoochory but a significantly decreased proportion of myrmecochory, hydrochory and unassisted dispersal (Figure 2.8D).

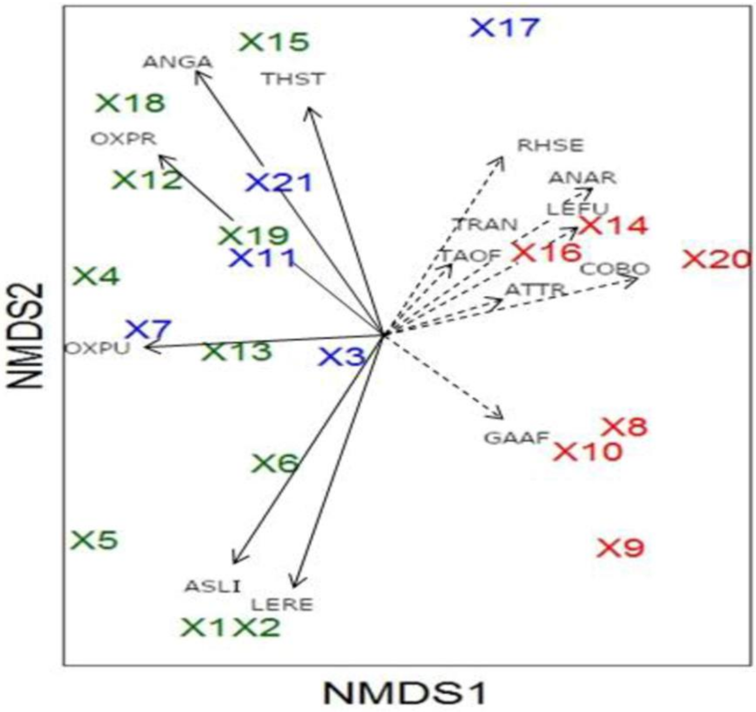

Figure 2.5: Non-metric multidimensional scaling (nMDS) plots of the 21 study sites with species vectors overlay where $p<0.01$. Red labels = Degraded Sites; Blue Labels = Moderately Degraded Sites; Green Labels = Pristine Sites. (OXPU=*Oxalis punctata*; OXPR=*O. purpurea*, ANGA=*Anthospermum galioides*; THST=*Thesium strictum*; RHSE=*Rhynchopsidium sessiliflorum*; ANAR=*Anagallis arvensis*; LEFU=*Lessertia frutescens*; COBO=*Conyza bonariensis*; TRAN=*Trifolium angustifolium*; TAOF=*Taraxacum offinale*; ATTR=*Athanasia trifurcat*; LERE=*Ledebouria revoluta*; ASLI=*Asparagus lignosus*;). Dashed arrows are for ease of interpretation and do not denote anything.

Figure 2.9A reveals that all degradation states are dominated by species considered of “least concern” for conservation purposes, although the highly degraded sites have a significantly increased proportion of alien species. Species of greater conservation concern are present in both moderately degraded and pristine sites but only in extremely small proportions (Figure 2.9A). Annuals are far more dominant in degraded sites (Figure 2.9B). Little difference is evident in the proportion of re-seeders to re-sprouters between the pristine and moderately degraded sites, although highly degraded sites are much more strongly dominated by re-seeders (Figure 2.9D).

Both spinescence and succulence are rare in general across the sites, but especially so in degraded sites (Figures 2.10A, 2.10B). In terms of photosynthetic pathway, C3 is the dominant trait across all sites (Figure 2.10C). Mean maximum height is greatest in pristine sites and lowest in highly degraded sites (Figure 2.10D), although the differences are not statistically significant. This trend is also evident for leaf area, although in this instance, the difference between pristine and highly degraded sites is significant (Figure 2.10E).

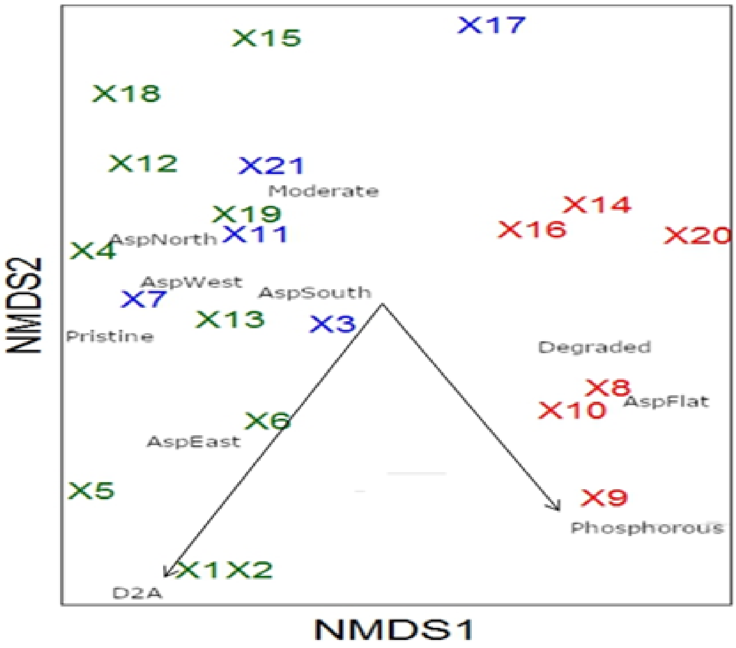

Figure 2.6: Non-metric multidimensional scaling (nMDS) plots of the 21 study sites. Environmental factors with $p<0.05$ are overlain. Continuous factors are represented by vector arrows and categorical factors by text labels. . Red labels = Degraded Sites; Blue Labels = Moderately Degraded Sites; Green Labels = Pristine Sites. D2A=distance to nearest agricultural field; AspNorth=north-facing slopes; AspEast=East-facing slopes; AspSouth=south-facing slopes; AspWest=west-facing slopes; AspFlat=flat slopes.

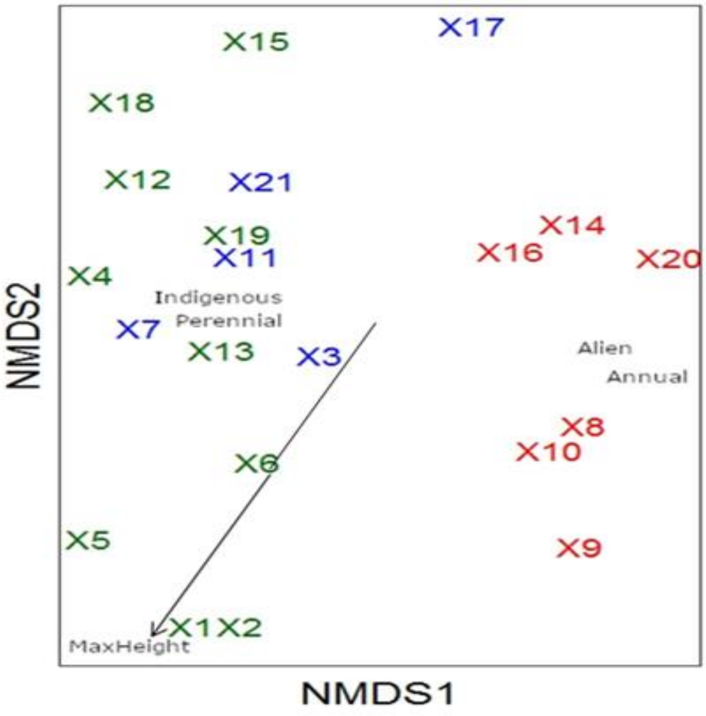

Figure 2.7: Non-metric multidimensional scaling (nMDS) plots of the 21 study sites. Functional Traits are overlain where traits are significant at $p<0.05$. Continuous traits are represented by vector arrows and categorical factors by text labels. . Red labels = Degraded Sites; Blue Labels = Moderately Degraded Sites; Green Labels = Pristine Sites.

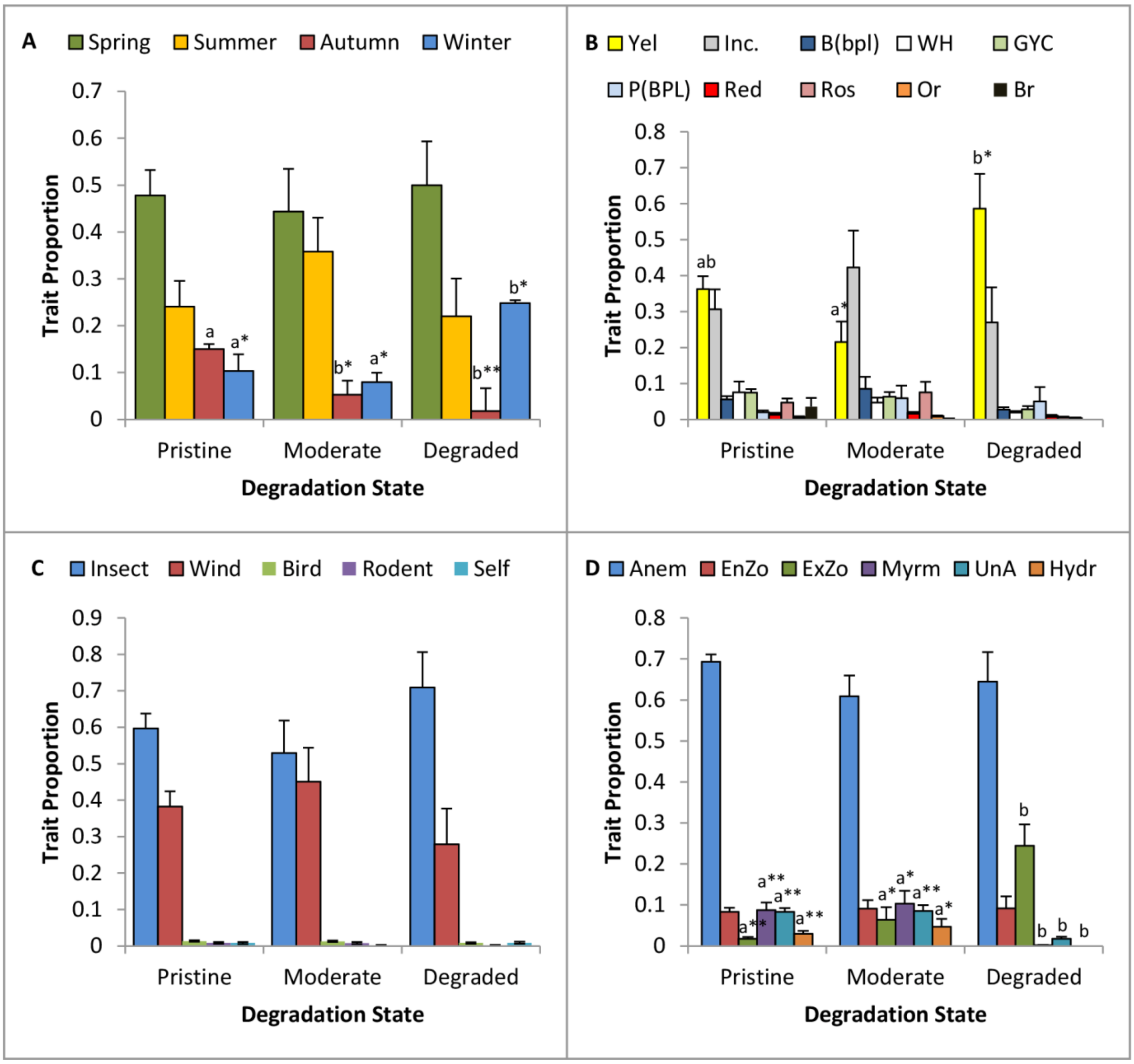

Figure 2.8: Mean trait proportions across degradation state for A) Flowering Onset Season B) Flower Colour C) Pollination Method and D) Maximum Dispersal Method. (Yel=Yellow; Inc.=Inconspicuous; B(bpl)=Bright blue/purple/lilac; WH=White; GYC=Green/Yellow/Cream; P(bpl)=Pale blue/purple/lilac; Ros=Rose; Or=Orange; Br=Brown. Anem=Anemochory; EnZo=Endo-Zoochory; ExCo=Exo-Zoochory; Myrm=Myrmecochory; UnA=Unassisted; Hydr=Hydrochory. Trait categories with different letters above bar indicate significant differences. * $p<0.05$, ** $p<0.01$.

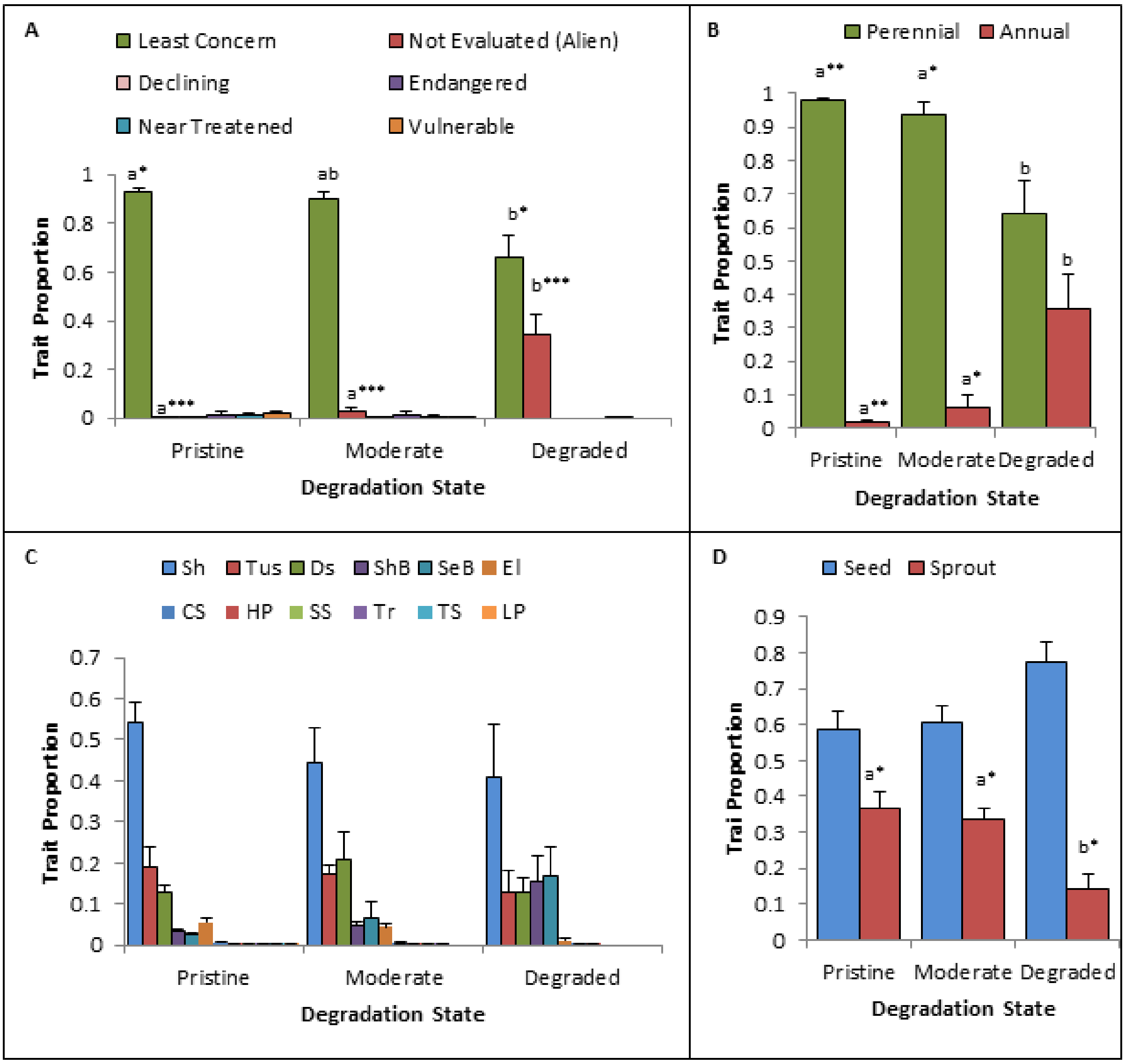

Figure 2.9: Mean trait proportions across degradation state for A) National Conservation Status B) Life Form C) Growth Form and D)Resprouting Ability. (Sh=Shrub; Tus=Tussock; Ds=Dwarf Shrub; ShB=Short Basal; SeB=Semi Basal; El=Erect Leafy; CS=Climbers & Scramblers; HP=Hemi-parasite; SS=Short Succulent; Tr=Tree; TS=Tall Succulent; LP=Leafless Parasite). Trait categories with different letters above bar indicate significant differences. * *p*<0.05, ** *p*<0.01, ****p*<0.001.

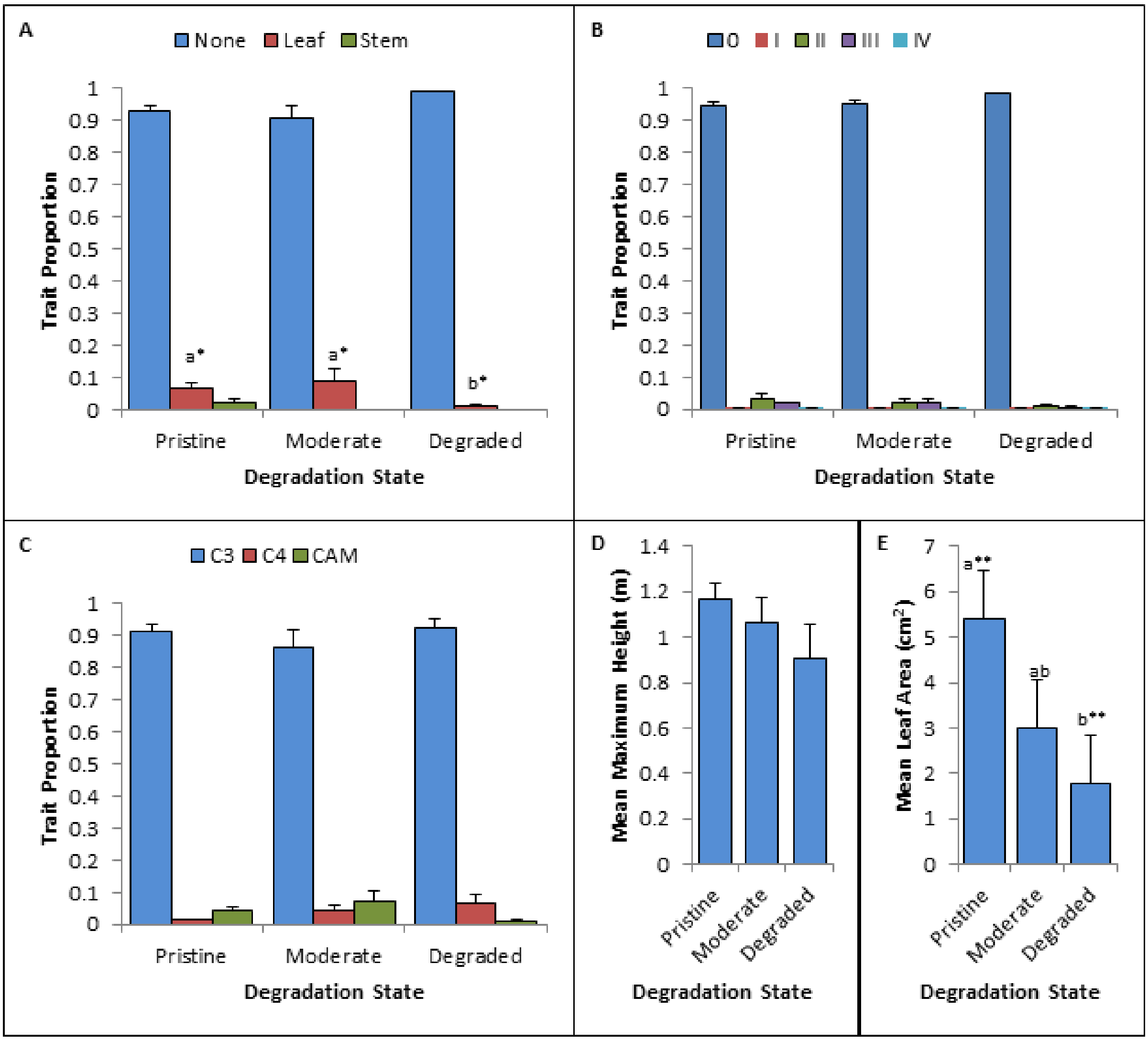

Figure 2.10: Mean trait proportions across degradation state for A) Succulence B) Spinescence and C) Photosynthetic Pathway and mean trait values across degradation gradient for D) Maximum Plant Height and E) Leaf Area. (0-IV=Increasing levels of spinescence – see table S1). Trait categories with different letters above bar indicate significant differences. * $p<0.05$, ** $p<0.01$.

2.4 Discussion

2.4.1 Taxonomic Diversity vs. Functional Diversity

Plant functional types and taxonomic diversity have been shown to change along degradation or disturbance gradients in Renosterveld (van der Merwe and van Rooyen, 2011; Cowan and Anderson, 2014; Heelemann et al., 2013; Radloff et al., 2014; Cousins et al., 2018) and, globally, disturbance or degradation has been reported to influence the relationship between taxonomic and functional diversity (Mayfield et al., 2005; Flynn et al., 2009; Sasaki et al., 2009; Derhé et al., 2016). Species richness and functional richness in this study indeed reveal a positive linear relationship overall

(Figure 2.2A1), consistent with the theory that increasing the number of species present in a community increases the number of functional traits within that community (Hooper et al., 2005). The slope is steeperand the correlation is considerably tighter between the two variables in the moderately and highly degraded sites (Figure 2.2C1) which suggests functional redundancy in pristine sites whereby additional species may not add to the number of functional traits present (Ricotta et al., 2016). However, functional richness should not be considered in isolation (Villéger et al., 2008) and assessing the responses of complementary indices (functional evenness and functional divergence) to species richness displays an opposing trend. A strong negative correlation is present in pristine sites between species richness and functional divergence (Figure 2.2B3). Functional divergence measures the degree to which the abundance of a community is distributed towards the extremities of occupied trait space (Mouillot et al., 2013), that is to say a high functional divergence is indicative of the most abundant species in a community occupying extremely dissimilar trait space (Mouchet et al., 2010). Increasing species richness in pristine sites appears to favour the accumulation of species with similar traits, thus decreasing functional divergence and further strengthening the hypothesis that functional redundancy is characteristic of pristine Renosterveld vegetation. There is no strong correlation between species richness and Rao's quadratic entropy Q (Figure 2.2A4) and the closely associated functional dispersion (Figure 2.2A5), a result of how the two indices are constructed to be unaffected by species richness (Laliberté and Legendre 2010).

The overall relationship between Pielou's J, an index of species evenness, with Rao's Q (Figure 2.4A4) and functional dispersion (Figure 2.4A5) is positive, although, considering degraded sites separately, the correlation is stronger (Figures 2.4C4, 2.4C5)). As Rao's Q and functional dispersion are directly related to relative species abundance, increasing species evenness within communities results in increased Rao's Q and functional dispersion. This correlation is much stronger in the degraded sites (Figures 2.4C4, 2.4C5) due to the presence of one instance of significantly lower species evenness, Rao's Q, and functional dispersion values. Where species evenness values display a narrower range, as in the pristine sites (Figures 2.4B4, 2.4B5), the correlation is less clear.

The Shannon Diversity index takes into account both species richness and evenness, so that a similar relationship with Rao's Q and functional dispersion to that observed for species evenness is evident (Figures 2.3A4, 2.3A5). In addition, the species richness component of the index results in a strong positive correlation with functional richness in the degraded sites (Figures 2.3C4, 2.3C5) – the increase in species richness in the degraded sites increases the number of functional traits present in the community.

2.4.2 Functional Composition

Although secondary succession of abandoned agricultural land remains poorly understood in semi-arid Mediterranean ecosystems, it is an important source of information which may inform future management decisions and conservation planning (Martínez-Duro et al., 2010). Functional composition considers changes in each of the traits displayed by species in the community (Tilman et al., 1997). Data of mean values (for continuous traits) or proportions (for categorical traits) for each trait are provided for each site and, by grouping them according to degradation state, the extent to which habitat degradation reduces (or removes) functional traits can be assessed, along with what this implies for secondary succession, ecosystem functioning and conservation. Flowering onset (Figure 2.8A), flower colour (Figure 2.8B), dispersal (Figure 2.8D), conservation status (Figure 2.9A), life form (Figure 2.9B), re-sprouting ability (Figure 2.9D), succulence (Figure 2.10A) and leaf area (Figure 2.10E) all show some significant differences in abundance across degradation states traits.

The significant difference in functional composition between highly degraded sites compared to pristine sites is as expected, and has indeed been reported elsewhere in Renosterveld vegetation (Cowan and Anderson, 2014; Radloff et al., 2014), neighbouring vegetation types in South Africa (Holmes and Richardson, 1999) and globally (Díaz et al., 1999; Flynn et al., 2009). Agricultural activities tend to filter out species with a suite of traits unsuitable to persistence and favour smaller, herbaceous annuals and/or species with long-distance dispersal mechanisms and rapid growth rates as observed here (Figures 2.8D, 2.9B, 2.9C) and recorded elsewhere in Renosterveld (van der Merwe and van Rooyen, 2011; Cowan and Anderson, 2014).

With the exception of an increased proportion of autumn flowering flowers (Figure 2.8A), there are no significant differences in functional composition between pristine and moderately degraded sites; highly degraded sites are however, more strongly differentiated. This pattern is similar to that reported by van der Merwe and van Rooyen (2010) for Mountain Renosterveld and has intriguing implications for conservation, as it would appear that passive restoration over time may allow functional traits that were significantly reduced or removed by agricultural activities to return. Contrary to our findings, other studies have reported slow succession and recovery of indigenous vegetation in old fields within West Coast and Swartland Renosterveld (Midoko-Iponga et al., 2005; Heelemann et al., 2013). Disturbance history is an important component in explaining current vegetation dynamics (Díaz et al., 1994; McIntyre et al., 1999) and even within a preordained disturbance state, variables such as grazing intensity (both from indigenous fauna and domestic livestock) or ploughing and/or fertilizer application during cultivation may have long-lasting effects (Snapp et al., 2010; Jangid et al., 2011). For example, pristine Renosterveld often has a significant geophyte component (Rebelo et al., 2006) along with numerous species which have evolved to re-sprout after above-ground disturbance (Kemper et al., 1999). Historical ploughing may result in the contemporary absence or significant reduction of such species, whereas sites subject to only heavy grazing may have retained geophytes in the relatively undisturbed below-ground environment (McIntyre et al., 1995). The absence of detailed data on disturbance regimes across the moderately and highly degraded sites makes it impossible to confidently predict whether the currently highly degraded sites will shift in community trajectory towards the moderately degraded and pristine sites over time, or remain functionally similar with no passive recovery such as reported in old fields studied by Heelemann et al. (2013). Heelemann et al.'s (2013) study reported significantly increased phosphorus levels in old fields compared to neighbouring pristine Renosterveld and a similar association between elevated phosphorus levels in the highly degraded sites in this study is evident; farmers in Renosterveld are known to apply phosphates to augment crop yield (O'Farrell et al., 2010). Phosphorus generally occurs in extremely low concentrations in pristine Renosterveld soil (Witkowski and Mitchell, 1987) and the increased nutrient levels may favour the establishment and maintenance of annual grasses and agricultural weeds in old fields which in turn inhibit re-colonization from native species (Milton, 2004). No significant difference is evident in phosphorus levels in soils from moderately degraded and pristine sites, either because no phosphate fertilizers have been added in the past, or because it has been leached from the soil. Given that the moderately degraded sites are generally on sloping topography, the loss of soil nutrients may be somewhat higher than on the highly degraded sites, which are located on flatter ground. Additional factors which influence post-disturbance recovery include the regional species pool dynamics (Zobel et al., 1998), site fragmentation (Hanski, 2015), and dispersal dynamics (Ozinga et al., 2005).

The dominance of anemochoric (wind-dispersed) plants present in the pristine sites suggests that the majority of species have the potential to recolonize disturbed sites provided there are no abiotic constraints such as soil degradation. The similarity in functional composition of other dispersal syndromes may be the result of landscape arrangement where the majority of moderately degraded sites are located in close proximity to pristine vegetation, thereby facilitating dispersal of these species over time. Habitat fragmentation was not considered explicitly in this study but has been shown to influence community composition and, in turn, ecosystem functions in Renosterveld (Kemper et al., 1999).

2.4.3 Functional Redundancy

The decrease in functional diversity indices such as Rao's Q and functional dispersion with increasing species richness observed in the pristine sites is indicative of functional redundancy (Ricotta et al., 2016). Functional redundancy occurs when some species share analogous functional traits and play similar roles in ecosystem functioning, thus providing resilience to loss of function if species are removed (Loreau, 2000). Cowling et al. (1994) reported substantial functional redundancy within plant functional groups in Renosterveld and, at a regional scale, redundancy is common throughout vegetation types of the Cape Floristic Region (Aiello-Lammens et al., 2017). In Renosterveld, communities have evolved with fire and grazing as naturally occurring ecological driver (Curtis, 2013). Due to the stochastic nature of fire as a disturbance (van Wilgen, 2013), functional redundancy provides an 'insurance policy' (Loreau, 2000) to changes in disturbance frequency, timing and severity thus promoting long-term community structure stability and maintaining ecosystem function (Cowling et al., 1994). However, species may appear functionally analogous in respect of their more prominent traits yet possess subtle differences in others such as post-fire regeneration strategy (e.g. *Hermannia saccifera* and *H. holosericea* are functionally analogous in many respect, but the former re-sprouts after fire while the latter regenerates from seed). Furthermore, subtle differences may exist between species traits which determine certain ecosystem functions (e.g. *Oederra squarrosa* and the functionally similar *O. uniflora* coexist in communities, but the former flowers during spring while the latter flowers during summer).

Conversely, the moderately degraded and highly degraded sites exhibit a strong, steep positive correlation between increased taxonomic diversity and functional diversity suggesting reduced functional redundancy. This may diminish the ability of these communities, especially in highly degraded sites with significantly reduced richness, to adapt to perturbations in environmental conditions without a reduction or loss of ecosystem function, although this may be moot if these degraded environments have already lost ecosystem function. In a subsample of the study sites studied here, Cowan and Anderson (2019) showed that certain processes, such as litter decomposition and nutrient recycling, were comparable across degradation states, thus our results here suggest that ecosystem functions may be at risk in the degraded sites due to reduced functional redundancy.

2.4.4 Conservation Implications

Changes to biodiversity have traditionally been assessed using measures of species richness and evenness (Villéger et al., 2008) without considering how different, or similar, these species are to one another (McGill et al., 2006). Although protecting biodiversity is a worthy goal in itself, conserving ecosystems to protect the services and functions they provide is of paramount importance (Cadotte et al., 2011). The use of functional diversity metrics allows us to link changes in biodiversity to community assembly, functioning and, importantly, may provide advanced warning of ecosystem disturbance as they do not require a loss of species to be reactive (Moillot et al., 2013). This intrinsic link suggests that functional diversity should be included in conservation decision-making, particularly where the goal is to manage habitats to promote healthy and functioning ecosystems (Cadotte et al., 2011).

The reduced functional diversity in highly degraded sites compared to pristine sites observed in this study is unsurprising as agricultural activity has been shown to greatly reduce functional diversity (Lin et al., 2011). Furthermore, the complex nature of the relationship between taxonomic and functional diversity across degradation states indicates that using species richness is not an adequate surrogate for functional diversity. The fact that in the pristine sites an increase in species richness is less strongly correlated with increased functional diversity than the correlation reported in degraded sites indicates that functional redundancy is an important component of vegetation structure within natural Renosterveld and most likely a mechanism of providing ecological resilience in the face of natural perturbations such as fire and grazing (Cowling et al., 1994). The similarities in functional diversity indices between pristine and moderately degraded sites has important implications for conservation and suggests, given enough time, secondary succession may allow habitat previously under the yoke of agriculture to recover. However, caution should be applied to this tentative conclusion and further studies are required. In particular, avenues of future research would benefit from a more in-depth functional trait database, especially for traits related to important ecosystem functions such as palatability and response to fire. Moreover, the implementation of conservation efforts would be greatly enhanced by an increased understanding of the effect of type and intensity of historic land-use on current ecological patterns. While our study provides novel data on the relationship between taxonomic diversity, functional diversity and functional composition, it is limited by a lack of precision of land-use history. We advocate further studies which control for type, intensity, and period of land-use as unpacking the effect of degradation on ecosystem dynamics into finer details will be hugely beneficial in guiding future conservation efforts. Finally, empirically testing how changes in biodiversity effect specific ecosystem functions is a logical next step in the optimization of management of ecological resources in this critically endangered vegetation type.

2.4.5 Conclusion

This study has shown that the relationship between taxonomic and functional diversity indices in Eastern Rûens Shale Renosterveld is diverse. Vegetation degradation as a result of historic land-use intensity can alter this relationship with potential ecological and conservation implications. The functional redundancy which has evolved in Renosterveld provides resilience to stochastic population shifts in response to fire and grazing disturbance and thus safeguards ecosystem functioning. The reported functional redundancy reduction apparent in degraded communities increases their vulnerability to environmental perturbations and means they are less likely to recover. Conversely, the similarity in functional composition between pristine and moderately degraded sites is a more positive indication of passive restoration, although the absence of high resolution historic land-use data from the various degraded sites, combined with the increased levels of soil phosphorus in the highly degraded sites, suggest this assumption should be treated with caution. Future research into the relationship between taxonomic and functional diversity indices and the effect on ecosystem functioning in the region would benefit greatly from enhancing our knowledge of trait expression, particularly in traits linked to the two main ecological drivers (fire and grazing). Furthermore, a higher resolution of historic land-use data would greatly enhance our ability to quantify and predict the effect of future disturbances on ecological processes and guide conservation efforts.

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2.7 Supplementary Data

Table S2.1: Functional trait name, type, range of values and example of ecologically significance used in this study.

	Type	Range of Values	Ecological Significance
Flower Colour	Categorical	Red; Yellow; Orange; Green/Yellow/Cream; Pale Blue/Purple/Lilac; Bright Blue/Purple/Lilac; Rose; Brown; White; Inconspicuous	Pollination[1]
Flowering Onset Season	Categorical	Spring; Summer; Autumn; Winter	Pollination[2]
Pollination Method	Categorical	Wind; Bird; Insect; Rodent; Self	Pollination[3]
Maximum Dispersal Method	Categorical	Anemochory (wind); Hydochory (water); Endo-Zoochory (internal animal); Exo-Zoochory (external animal); Myrmecochory (Ant); Unassisted	Dispersal[4]
Life Form	Categorical	Annual; Perennial	Life History[5]
Growth Form	Categorical	Tree; Shrub; Dwarf Shrub; Tall Succulent; Short Succulent; Tussock; Semi-Basal; Short-Basal; Erect Leafy; Climbers & Stragglers; Hemi-Parasite; Leafless Parasite	Ecophysiological Adaption[5]
Maximum Plant Height	Continuous	0.01 – 1.4 metres	e.g. Competitive Vigour; Whole Plant Fecundity[5]
Leaf Area	Continuous	0 – 7 cm2	Ecophysiological Adaption[5]
Succulence	Categorical	None; Leaf; Stem	Ecophysiological Adaption[5]
Spinescense	Categorical	0-none; 1-low density, soft spines; 2-high density, soft spines; 3-intermediate/high density hard spines <20mm; 4-high density, hard spines>20mm	Anti-Herbivore Defence[5]
Resprouting Ability	Categorical	Reseeder; Resprouter	Post-Disturbance Persistence[5]
Photosynthetic Pathway	Categorical	C3; C4; CAM	Ecophysiological Adaption[5]
National Conservation Status	Categorical	Not Evaluated (Alien); Least Concern; Declining; Near Threatened; Vulnerable; Endangered	Conservation Implications[6]

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Chapter 3

Litter decomposition variation across a degradation gradient and two seasons in a critically endangered vegetation type within the Fynbos biome, South Africa

Litter decomposition variation across a degradation gradient and two seasons in a critically endangered vegetation type within the Fynbos biome, South Africa

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Abstract

Litter decomposition is an ecosystem function essential for nutrient cycling; however until very recently it was considered of minor importance within the fire-prone Fynbos Biome. To investigate decomposition rate and litter nutrient dynamics, litterbags containing materials from three plant species from different functional types were placed in sites across a degradation gradient and over two seasons. Litterbags were removed after three and six months for both seasons to determine decomposition rates and change in nutrient concentration. Decomposition varied greatly among the species and was strongly correlated to initial nutrient values of the litter. The most nutrient rich litter type, the alien herbaceous *Medicago sp.*, lost 65% of its original mass after six months while the most nutrient poor, the indigenous grass *Pentameris eriostoma*, lost 18%. Litter from *Dicerothamnus rhinocerotis*, an indigenous shrub, lost 27% of its original mass. For all litter types, the majority of the loss occurred during the first three months of the experiment. Season was found to significantly affect litter decomposition; however the exact mechanism behind this is unclear. Degradation level, at least defined by the metrics of this study, did not significantly affect litter decomposition rate. The faster decomposition rate shown in *Medicago sp.* suggests that in degraded areas where significant proportions of the species invade, nutrient cycling will be accelerated in comparison to pristine land; however broadening the species of study to include additional plant functional types, such as indigenous annuals, would help give insight into this hypothesis. This study affirms the notion that litter decomposition is an important ecosystem function within the Fynbos Biome with litter type acting as a strong controlling variable.

3.1 Introduction

Habitat degradation is driving unprecedented changes in biodiversity, ecosystem structure and function across the globe, representing one of the most pressing environmental issues of our time (Krauss et al., 2010; Maxwell et al., 2016). Nevertheless, degradation can be difficult to define with the term used to describe everything from major habitat destruction to relatively minor habitat alteration. Evidently a gradient exists and the severity of degradation may vary depending on the particular metric used to assess a habitat. The intricate relationship between land degradation, biodiversity and ecosystem function remains contentious (Breitbach et al., 2012; Winfree et al., 2015); however furthering our understanding of the relationship is essential for human and environmental wellbeing (Naeem et al., 2016).

Litter decomposition - a biogeochemical process essential to the cycling of nutrients, Carbon and energy both within and between ecosystems – is one such ecosystem function (Wardle, 2002; Aerts, 2006; Schlesinger and Bernhardt, 2013). Understanding the controlling factors of litter decomposition is a vital component in informing models linking the biosphere and atmosphere (Bonan et al., 2013; Todd-Brown et al., 2014). In light of global climate change, generating robust models which take into account the role litter decomposition plays in Carbon cycling in terrestrial systems is a valuable resource (Cornelissen et al., 2007; Wieder et al., 2013).

Habitat degradation can alter above-ground vegetation and the composition of litter fauna (Gonzalez and Seastedt, 2001; Kamau et al., 2017). In addition, abiotic factors can be changed through direct alteration to soil properties (Souza-Alonso et al., 2017) and indirectly through changes in the microenvironment as a result of changes in vegetation cover (e.g. canopy reduction or the introduction of alien species (Galloway et al., 2017)). Some or all of these factors may interact to impact litter decomposition rates; however the effect of habitat degradation has been poorly studied (Paudel et al., 2015).

At the global and regional scale litter decomposition rates are controlled by climate and litter quality (Meentemeyer, 1978; Parton et al., 1988; Aerts, 1997). While the aforementioned factors impact soil microorganism activity, and thus the deconstruction of litter into simpler forms, more recent research has shown that the number of factors regulating litter decomposition are now hypothesized to extend beyond climate and litter quality - for example, photodegradation has been shown to play a significant role in drylands (Austin and Vivanco, 2007; Almagro et al., 2017). The influence of any single factor will be strongly context dependent even at the regional scale (Bradford et al., 2016) and a combination of several factors generally serves as a more accurate indicator of what is controlling the rate of litter decomposition (Zhang et al., 2008).

At a local scale decomposition rates may also vary seasonally as soil temperature and moisture fluctuate (Rigobelo and Nahas, 2004; Eviner et al., 2006). In addition, litter quality and quantity may change as the above-ground floral community varies through the year which, in conjunction with soil conditions, affects decomposer activity (Paudel et al., 2015). The microbial communities themselves are specific to different stages of decomposition as the physical and chemical properties of litter change through time (Bergh and McClaugherty, 2014). Thus, changes in decomposition rates linked to seasonal climate variation may interact with the effects of the seasonal fluctuation in litter properties and phase of decomposition (Paudel et al., 2015; Wu and Wang, 2018). It is thus probable that the decomposition rate in any given ecosystem, while broadly controlled by regional climate (Parton et al., 2007), will vary according to seasonal variation in temperature and precipitation, type and quality of litter present, the nature and abundance of decomposer organisms, and severity of habitat degradation (Couteaux et al., 1995; Xu et al., 2009; Zhao et al., 2011; Paudel et al., 2015).

Plant functional types have been widely used to describe patterns of plant responses to the environment (Chapin et al., 1996) and have been used frequently and with success in bridging the gap between plant physiology and community and ecosystem processes (Díaz and Cabido, 1997). In litter decomposition studies functional leaf traits have provided a basis for predicting the decomposition rate of leaf litter (Pérez-Harguindeguy et al., 2000; Cornwell et al., 2008). Linking plant functional types, and their associated leaf traits, to litter decomposition rates can provide predictive tools for modelling decomposition rates under different vegetation types (Cornelissen, 1996; Cornelissen and Thompson, 1997).

The Western Cape of South Africa is characterized by the megadiverse vegetation of the Fynbos Biome (Linder, 2003; Rebelo et al., 2006; Allsopp et al., 2014). True Fynbos vegetation is fire adapted (Kruger and Bigalke, 1984), occurs on nutrient poor, stony or sandy soils (Cowling, 1983; Rebelo et al., 2006), and is characterized by the presence of Proteaceae and Ericaceae shrubs in addition to reed-like Restionaceae (Bergh et al., 2014). All three of the dominant plant types are typically low in nutrients and produce litter which tends to decompose slowly (Mitchell et al., 1986; Witkowski, 1991). These slow decomposition rates led to the assumption that fire was the key process in nutrient cycling in this biome (Mitchell et al., 1986; Stock and Lewis, 1986; Stock and Allsopp, 1992). More recent studies have shown an eight-fold difference in decomposition rates between Fynbos species indicating that litter decomposition may be more important for nutrient cycling and certainly more subtle than previously thought (Bengtsson et al., 2012).

This particular study was performed in Renosterveld, a broad term used to describe a floristically and ecologically distinct vegetation type within the Fynbos Biome (Curtis et al., 2013; Bergh et al., 2014). Renosterveld is found on predominantly shale-derived soils which are richer, finer-grained and further developed compared to true Fynbos (Bergh et al., 2014). Although similarly fire-prone, unlike true Fynbos, Renosterveld generally lacks Proteoids, Ericoids and Restioids and tends to be dominated by asteraceous shrubs and C3 grasses with a rich geophyte and herbaceous annual understory (Cowling, 1983, 1990; Rebelo, 1995; Procheş et al., 2006). Once covering approximately 30% of the Fynbos Biome, the relatively nutrient rich underlying soils and gentle topography resulted in large swathes of Renosterveld being converted to agriculture (Kemper et al., 1999; Cowan and Anderson, 2014). Today less than 10% of the original extent remains (Newton and Knight, 2005; Rebelo et al., 2006) with fragments of critically endangered natural vegetation found embedded within an agricultural matrix (Kemper et al., 1999; Rebelo et al., 2006). Due to differences in historical land-use and current management practices (e.g. historical ploughing, grazing intensity, controlled burning etc.), patches of natural vegetation can occur side-by-side along a degradation gradient from pristine vegetation to old fields in variable states (Heelemann et al., 2013; Ruwanza, 2017). Compared to true Fynbos, ecological processes in Renosterveld are understudied (Curtis, 2013), with below-ground processes particularly under-represented (but see: Bengtsson et al., 2011). In addition, possible differences in ecological processes in Renosterveld fragments due to variable land-use history and current management regimes remain largely untested (but see: Cowan and Anderson, 2014).

In this study, we compared litter decomposition of three species from different plant functional types across a degradation gradient in a Renosterveld type subject to non-seasonal rainfall. A grass and a shrub species common throughout the region were chosen to represent the indigenous flora in addition to an introduced annual herb which represented non-native, agriculturally introduced species. Study sites were designated a degradation level after being subjected to a vegetation survey and historical land-use analysis. Although rainfall in the region is purportedly non-seasonal, temperatures are Mediterranean with distinct warm and cold seasons (Belda et al., 2014). Both seasons were investigated in an attempt to understand the role litter type, degradation and season have on decomposition rates in this critically endangered vegetation type.

3.2 Materials And Methods

3.2.1 Study Site

Haarwegskloof Nature Reserve (34°20’17.9”S; 20°19’34.1”E) is situated within the Overberg lowlands of the Western Cape Province of South Africa (Figure 3.1). The indigenous vegetation of the Overberg region includes four different types of Renosterveld (Western, Central, Eastern Rûens Shale Renosterveld and the less frequent Rûens Silcrete Renosterveld), all of which are considered critically endangered (Driver et al., 2012) with less than 10% of the original extent remaining (Curtis, 2013). The vegetation types exist as fragmented islands within an agricultural matrix of privately owned land (Kemper et al., 1999) - predominantly grain fields (wheat, barley, oats, canola) and artificial pasture (lucerne) (Curtis et al., 2013). The reserve itself is situated within the Eastern Rûens Shale Renosterveld and was purchased by the World Wildlife Fund-South Africa and the Overberg Renosterveld Conservation Trust in 2013. It consists of approximately 500 hectares of land, 80% of which is virgin Renosterveld while the remaining area is old lands of varying age, portions of which may have been previously ploughed and/or used as grazing pasture. Eastern Rûens Shale Renosterveld has an altitudinal range of 40-320 metres above sea level and an average rainfall of 384 mm per annum with an essentially even distribution (Rebelo et al., 2006; Curtis et al., 2013). Mean daily temperatures range from a 5.9 °C minimum in July to a 26.9 °C maximum in January (Rebelo et al., 2006). Rebelo et al. (2006) describe Eastern Rûens Shale Renosterveld as occurring on moderately undulating hills and plains which supports cupressoid and small-leaved, low to moderately high grassy shrubland dominated by renosterbos (*Dicerothamnus rhinocerotis*).

Vegetation sampling was conducted in the reserve at six sites of 1000 m^2 using the modified Whittaker nested vegetation sampling method (Stohlgren et al., 1995). Vegetation data, combined with historical aerial photograph analysis and expert knowledge identified two sites each in three degradation ‘states’ (Figure 3.1). Namely, Pristine – characterised by high species richness, low alien species cover and no evidence of historical agriculture; Moderately degraded – characterised by moderate to low diversity, dominance of common, early successional shrubs (e.g. *D. rhinocerotis*, *Oedera squarrosa*) and evidence of historical agricultural use; and Highly Degraded – characterized by low diversity, high alien species cover (e.g. *Medicago* species and alien grasses) and evidence of recent agricultural use (Table 3.1).

3.2.2 Plant Species Selection And Litter Collection

The three plant species used in this study were chosen as they represent common but different plant functional types which differ in dominance across the landscape according to level of

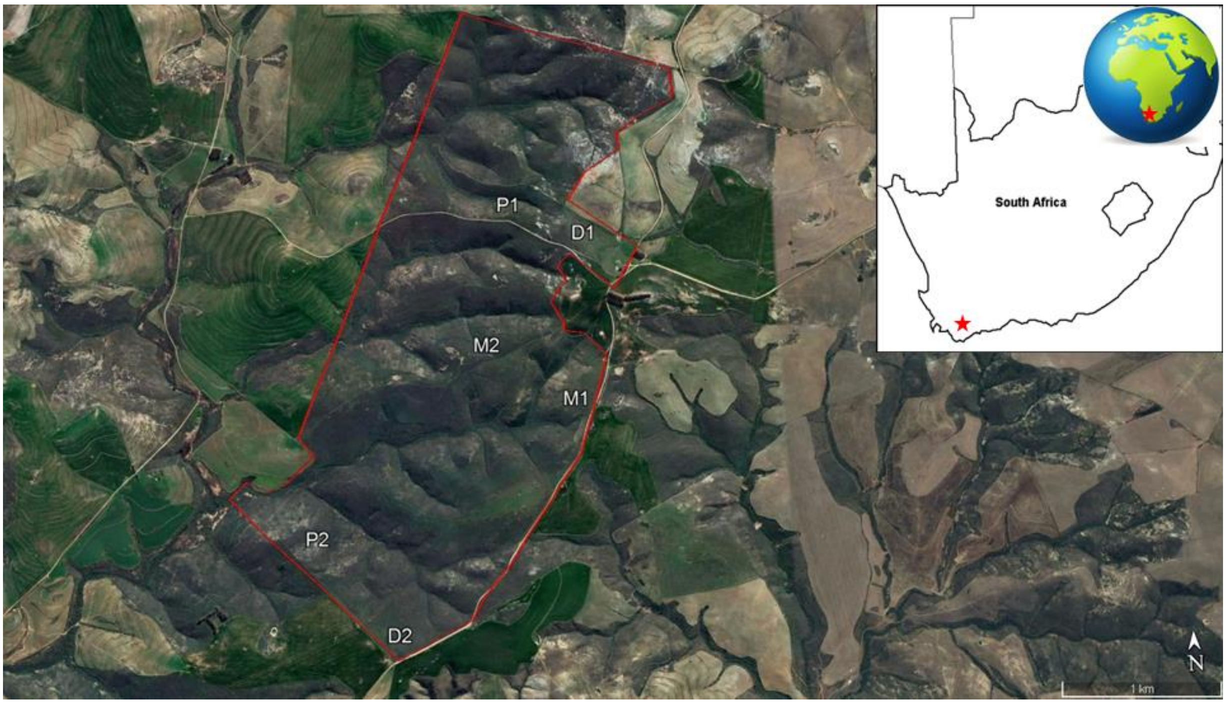

Figure 3.1: The location of the six study sites within Haarwegskloof Nature Reserve, South Africa.

degradation. *Pentameris eriostoma (Nees) Steud.* is an indigenous, densely tufted, erect, perennial, C3 grass common throughout Haarwegskloof and the surrounding Renosterveld remnants. It flowers in winter and grows to 0.9 m in height. It does not appear to be particularly palatable (J. Groenewald, 2016 pers comm) and its blades are quite tough and wiry often with an almost woody base closely covered by the remains of the sheaths. In the pristine parts of the reserve *P. eriostoma* is frequent, at times providing up to 20% of the cover. It was recorded in the moderately degraded areas of the reserve but at much lower densities (<1% cover) and was absent from the highly degraded fragments surveyed. *Dicerothamnus rhinocerotis (L.f.) Less*. is a common, evergreen, resinous shrub which grows up to 2 m in height. It is rich in phenolics and exhibits anti-herbivore properties (Proksch et al., 1982). While present in healthy Renosterveld, its weedy nature allows it to dominate disturbed land. *D. rhinocerotis* was recorded on all sites surveyed on the reserve and at times dominated the moderately and highly degraded areas. *Medicago* is a genus of flowering plant in the legume family. A forb that is generally annual, it is an alien species in Renosterveld vegetation often associated with agriculture. Indeed, fields of the forage crop Lucerne (*Medicago sativa)* are a frequent sight in the Overberg. A few species of *Medicago* were present in the reserve – including *M. sativa*, *M. polymorpha* and *M. lanciniata* and no distinction was made during the collection, however it is likely that a larger proportion of *M. sativa* was present during the collection of material used in the winter season. No *Medicago* was present in any of the pristine sites surveyed while it occurred in varying amounts in the moderately and highly degraded sites.

Plant material for the summer season was collected on the 6 and 7 August 2016 and for the winter season on the 22 March 2017. For *D. rhinocerotis* and *P. eriostoma* the outer branches/leaf blades (~10 cm) were removed from healthy individuals with secateurs, stored separately in plastic bags before being dried in a laboratory oven at 40 °C for 48 hours and thereafter cut into 1-3 cm pieces. The litter was then mixed separately and stored in open containers at room temperature. *Medicago sp*. was collected by hand and dried at room temperature for 7 days before being cut into small pieces where necessary and mixed thoroughly. To ascertain initial nutrient content 5 samples for each litter type were sent for analysis at an external accredited laboratory (Bemlab Pty Ltd., Somerset West, South Africa) where Nitrogen (N), Phosphorus (P), Potassium (K), Calcium, Magnesium, Sodium, Manganese (all %) and Iron, Zinc, Copper, Boron (all mg/kg) were determined (see Supplementary Data Table S3.1). In addition, 10 samples of each species were weighed, placed in a furnace at 550 °C for 3 hours and weighed again and used to calculate the ash-free dry weight for each sample.

The litterbags were individually numbered plastic cylinders with removable lids. Each cylinder was 8 cm high with a diameter of 7 cm. The bottom of the cylinders consisted of stainless steel mesh with an aperture of 0.55 mm while the lids consisted of stainless steel mesh with an aperture of 1.5 mm. Litter for each individual bag was weighed to the nearest 0.01 g before being placed in the litterbags without compression, allowing the litter to preserve its normal density and volume. Litterbags were placed in the field on the 17 August 2016 for the summer season and on the 10 April 2017 for the winter season.

3.2.3 Experimental Design

To investigate the differences in litter decomposition and nutrient dynamics of the three litter types across a degradation gradient, three sets of three litterbags were placed in two 'groupings' in each of the six study sites (see Supplementary Figure S3.1 for study site example). Each set contained one litterbag of each litter type. Litterbags were submerged in the soil with the lids at ground level. Litterbags within a set were placed within 10 cm of each other while sets within a grouping were approximately 100 cm apart. Each grouping within a study site was at least 15 m apart and every effort was made to ensure environmental homogeneity between groupings in terms of slope, aspect and shade cover

During the summer season a single litterbag was lost and during the winter season three litterbags were dug up by animals. All were excluded from analysis thus the final data set consists of 212 litterbags (Summer Season-107; Winter Season-105).

Table 3.1: Vegetation data from the six study sites showing species richness, alien cover and the dominant three species at each site. Values (with the exception of Species Richness) are the percentage of above-ground cover.

	Pristine 1	Pristine 2	Moderate 1	Moderate 2	Degraded 1	Degraded 2
Species Richness	70	65	22	39	28	35
Alien Cover (%)	0	0.5	7	20	30	40
Dominant Species 1	*Oedera squarrosa* 65(%)	*Oedera squarrosa* 40(%)	*Oedera squarrosa* 95(%)	*Oedera squarrosa* 40(%)	*Dicerothamnus rhinocerotis* 60(%)	*Medicago sp.* 50(%)
Dominant Species 2	*Anthospermum spathulatum* 10(%)	*Dicerothamnus rhinocerotis* 15(%)	*Medicago sp.* 7(%)	*Dicerothamnus rhinocerotis* 35(%)	*Medicago sp.* 30(%)	*Helichrysum anomalum* 45(%)
Dominant Species 3	*Pentameris eriostoma* 10(%)	*Pentameris eriostoma* 12(%)	*Dicerothamnus rhinocerotis* 3(%)	*Medicago sp.* 20(%)	*Cynodon dactylon* 25(%)	*Pteronia incana* 10(%)

3.2.4 Soil Analysis

To assess whether above ground vegetation and land-use history influenced edaphic conditions soil analysis was performed. At each site a composite soil sample (approximately 500 g) was taken from four random locations at depths up to 15 cm (Bohn et al. 2001) and sent to an external accredited laboratory (Bemlab Pty Ltd., Somerset West, South Africa) where the following soil characteristics were measured: pH (KCl; see Mclean, 1982), electrical resistance (ohms; see, Richards 1969), Hydrogen (cmol(+) /kg), stone volume (%), P (Bray II) (mg/kg; see Bray and Kurtz, 1945), K (mg/kg), Exchangeable Sodium, K, Calcium and Magnesium cations (cmol(+)/kg; see Chapman, 1965), organic Carbon (%; see Nelson and Sommers, 1982), soluble Sulphur (mg/kg), clay, silt and sand content (%), and waterholding capacity mm/m).

3.2.5 Litter Collection And Treatment

To ascertain a broad temporal view of litter degradation and nutrient dynamics litterbags were sampled twice during each season. During the summer season, one randomly selected set from each grouping was removed on the 9 November 2016 while the remaining litterbags were removed on the 20 February 2017 (84 and 187 days *in situ* respectively). This process was repeated for the winter season where the initial sets were removed on the 18 July 2017 and the remaining sets on the 25 October 2017 (98 and 197 days *in situ* respectively). After the litterbags were removed they were immediately wrapped in aluminium foil, sealed inside plastic bags, and transported back to the laboratory in thermally insulated boxes. Mass loss was determined as a loss of organic matter from each litterbag as the accumulation of inorganic matter in the litterbags had to be accounted for. To calculate dry weight, samples were weighed before and after heating at 100 °C for 24 hours in an oven. Ash-free dry weight was calculated after placing samples in a furnace at 550 °C. The difference between ash-free dry weight and dry weight was used as the amount of organic content for each sample. Sub-samples were sent to an external accredited laboratory (Bemlab Pty Ltd., Somerset West, South Africa) for nutrient analysis. There was a processing error for the first set of litterbags from the winter season and their nutrient analysis could not be included in the analysis.

3.2.6 Statistical Analysis

Mass loss of the litter was measured using the decomposition constant k which was calculated assuming Olson's (1963) exponential decomposition model where $W_t = W_0e^{-kt}$ with W_0 the mass of organic matter at the beginning of the experiment and W_t the organic matter mass at time t. The constant k has the unit day^{-1} and was calculated for each litterbag. In addition, litter half-life ($0.693k^{-1}$) was calculated (Olson, 1963).

Litter decomposition was analysed with a General Linear Mixed Model using the R packages lme4 and lmertest (R Core Team, 2015). After initial data exploration, the fixed effects chosen in the model were Litter Type, Removal Day, Site Type, and Season, whereas the random effects chosen were Litterbag Set and Site. Degrees of freedom were estimated with the Satterthwaite method.

ANOVAs were performed on soil chemistry data between site types, initial litter nutrient contents between seasons, and six month litter nutrient content across site type.

3.3 Results

3.3.1 Decomposition

Litter type was the factor that best explained variation in litter decomposition rate, measured as loss of organic matter, followed by removal day and then the interaction between the two (Table 3.2). *Medicago sp.* decomposed the quickest with >50% of the original mass lost after the first removal day in both seasons. This slowed dramatically thereafter with <10% of the original weight lost in the following three months. In contrast, *P. eriostoma* decomposed the slowest with only 15% of the original mass lost after the first removal date. Similar to *Medicago sp.*, decomposition subsequently slowed and <5% of the original mass was lost thereafter. *D. rhinocerotis* demonstrated a similar decomposition across the two seasons at the first withdrawal date with the summer season recording 23% of original mass lost and the winter season 21% lost. There was a significant difference in mass loss thereafter however with only a further 2% lost during summer season and 10% in winter season (Figure 3.2). Litter half-life ranged from 110 days for *Medicago sp.* to 702 days for *P. eriostoma (*Table 3.3).

Table 3.2: GLMM results in relation to fixed factors Litter Type, Removal Day, Site Type and Season. (Degrees of Freedom estimated with the Satterthwaite Method. Significance levels: *** p<0.001; ** p<0.01).

Factor	df	F	P
Litter Type	165.82	1923.48	<0.001***
Removal Day	172.89	510.07	<0.001***
Site Type	33.24	2.53	0.09
Season	180.85	62.12	<0.001***
Litter Type x Removal Day	167.16	175.18	<0.001***
Litter Type x Site Type	165.79	1.01	0.40
Removal Day x Site Type	172.87	0.02	0.98
Litter Type x Season	165.69	45.91	<0.001***
Removal Day x Season	117.71	26.66	<0.001***
Site Type x Season	180.50	1.72	0.18
Litter Type x Removal Day x Site Type	167.15	0.32	0.87
Litter Type x Removal Day x Season	167.65	6.73	0.001**
Litter Type x Site Type x Season	165.67	1.43	0.23
Removal Day x Site Type x Season	117.22	0.33	0.72
Litter Type x Removal Day x Site Type x Season	167.61	1.64	0.17

Season was also shown to be a significant factor influencing decomposition. Evaluating the climate data from the two seasons shows the non-seasonal nature of rainfall and the higher temperatures in the summer months. Only one month had rainfall over 100 mm while the majority of months recorded rainfall considerably less than half this amount. The highest average monthly temperatures were recorded in the last three months of the summer season where temperatures reached just below 30°C (Figure 3.3). Monthly evapotranspiration rates were consistently higher for the summer season (Figure 3.4). Although the interaction between litter type and season significantly influenced decomposition, there was no consistent pattern observed. Decomposition of *Medicago sp.* was faster in the summer season while the opposite was true for *P. eriostoma*. For *D. rhinocerotis*, after the first removal day the decomposition was faster in the summer season but the inverse was true during the final three months.

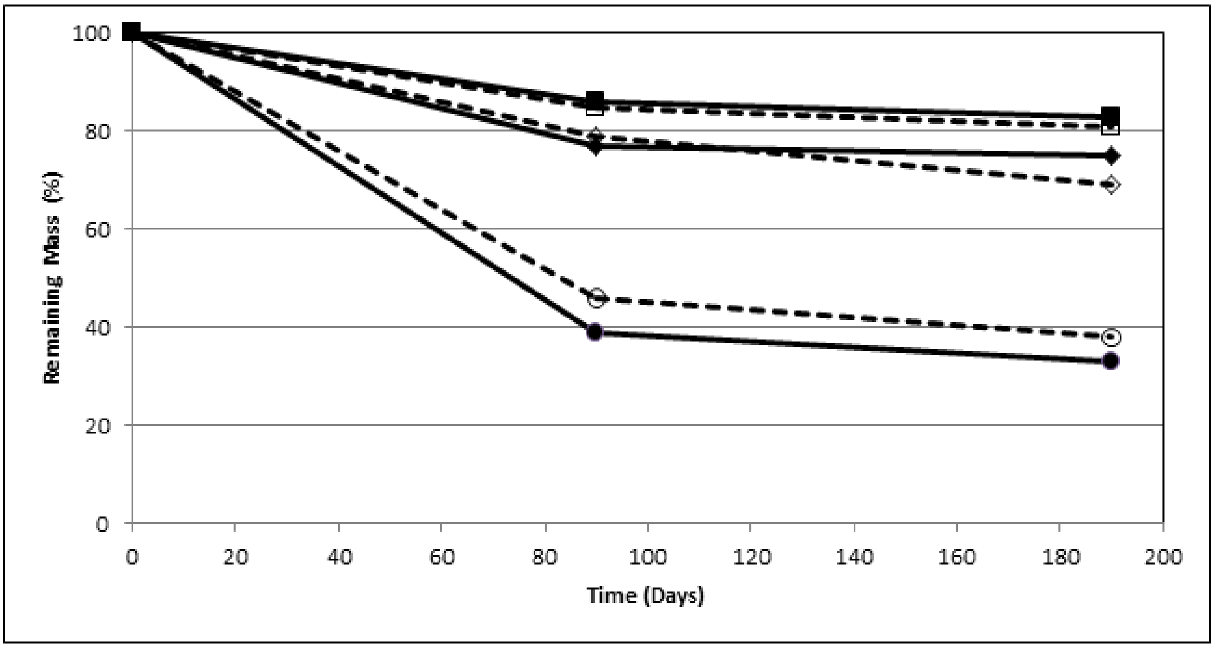

Figure 3.2: Mass loss measured as percentage of remaining litter through time. (*P. eriostoma*=squares; *D. rhinocerotis*=diamonds; *Medicago sp*=circles. Summer Season = black, Winter Season=white).

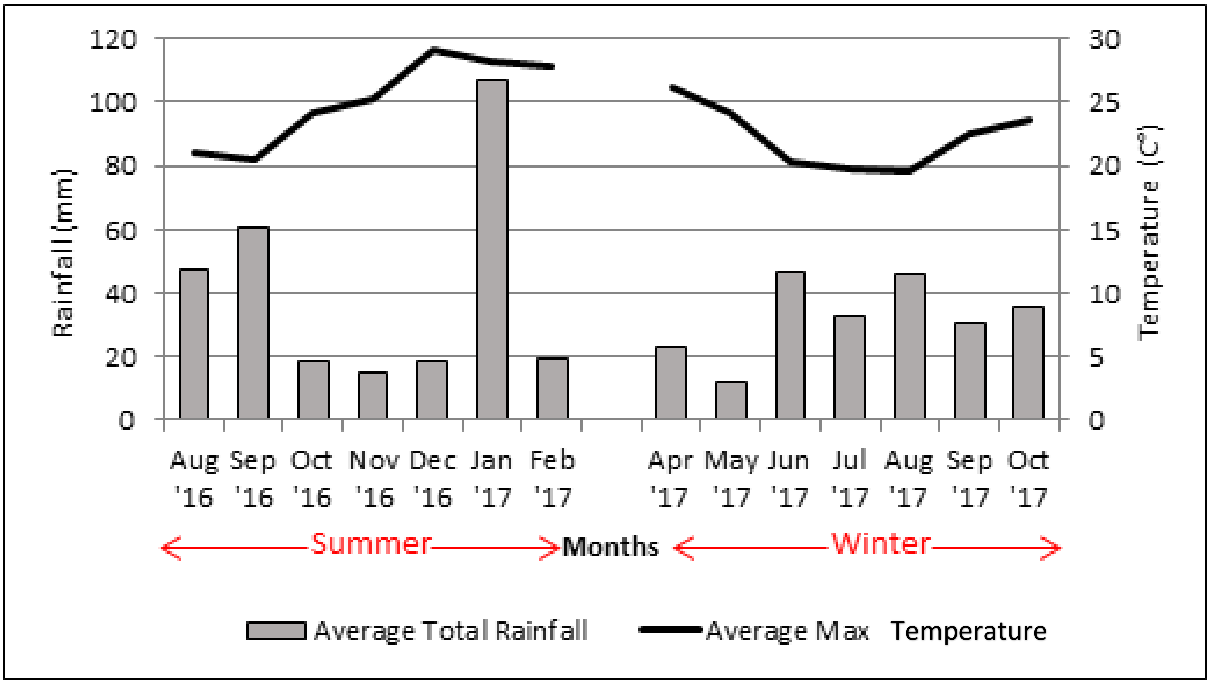

Figure 3.3: Climate data from the study area for the study period. Summer Season: August 2016-February 2017; Winter Season: April 2017-October 2017 (Data courtesy of the Agricultural Research Council).

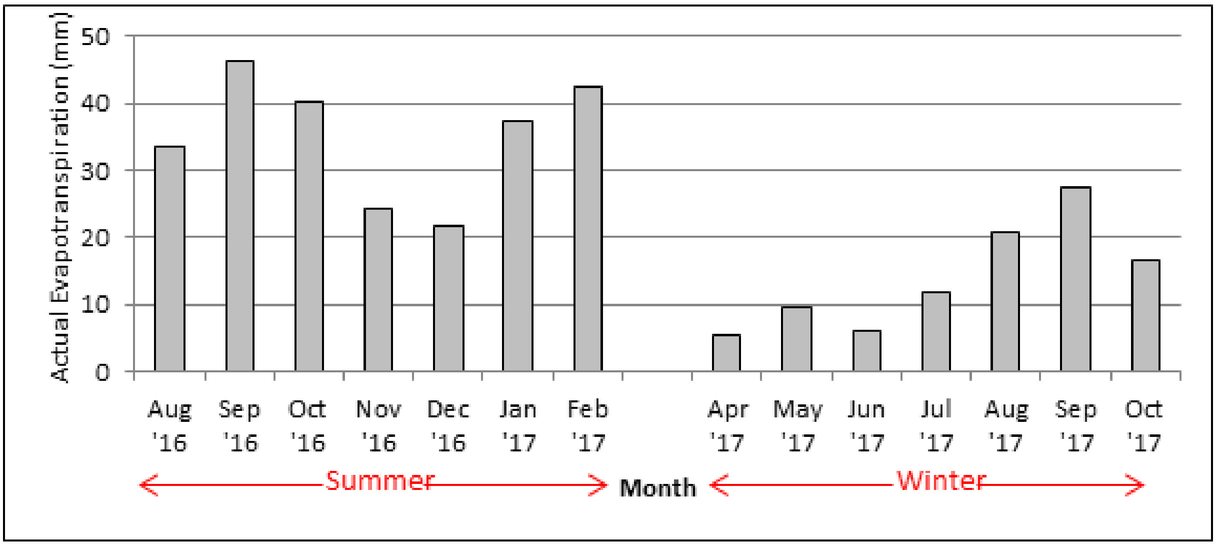

Figure 3.4: Actual **e**vapotranspiration levels from the study area for the study period. Summer Season: August 2016-February 2017; Winter Season: April 2017-October 2017 (Satellite-derived data from MODIS (Running et al., 2017). See also Mu et al., (2011)).

There was no significant difference in decomposition rate found between site types nor any of the factors which included site type. Despite clear differences in land-use history and current above-ground vegetation, ANOVAs performed on soil chemical and physical values between study site types (e.g. Pristine, Moderate and Degraded) showed no significant differences (the exception being Potassium values which were significantly higher in Degraded sites-see Supplementary Table S3.2).

Table 3.3: Mean Decomposition rates (*k*-value) and half–lives with standard errors of the three study species. Only the effect of litter type is shown as it was by some distance the most influential factor (Table 2).

Litter Type	k value (day-1)	SE	n	Half-life (day)	SE	n
D. rhinocerotis	0.00207	0.00008	72	367	12.74	72
P. eriostoma	0.00125	0.00005	72	702	89.73	72
***Medicago* sp.**	0.00699	0.00031	68	110	4.07	68

3.3.2 Litter Nutrients

The proportion of remaining N for *Medicago sp.* decreased quite uniformly across the two seasons (summer season – 36% loss; winter season – 29% loss). The processing error means that first removal day values are missing for the winter season but the values from the summer season actually show most of this N loss happened in the first few months and proportion of remaining N increased by 2% from the first removal day to the second. For *D. rhinocerotis*, both seasons showed an 8% increase in N after six months. After the first removal day however, the summer season showed a 7% decrease in overall N. In the summer season *P. eriostoma* showed 15% loss of N after six months, conversely in the winter season this value was recorded as a 3% net gain (Figure 3.5A).

Results were similarly haphazard for the proportion of remaining P in the litter, although the summer season P loss was consistently significantly greater across all three litter types after six months (Figure 3.5A).

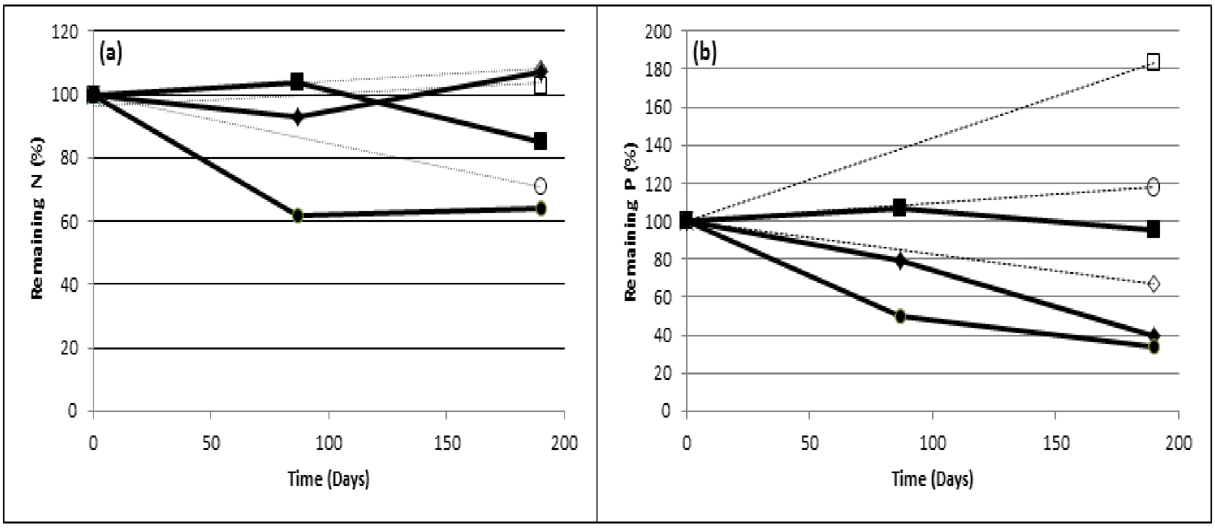

Figure 3.5: Percentage of remaining nutrients (a) N and (b) P. (*P. eriostoma*=squares; *D. rhinocerotis*=diamonds; *Medicago sp*=circles. Summer Season=black, Winter Season=white). Note: processing error resulted in no litter nutrient values for winter season samples removed after three months.

Plotting proportion of remaining mass after six months for the three litter types against initial N, P and K values consistently showed a strong correlation between initial nutrient values and litter decomposition (r^2=0.97(N); 0.82(P); 0.90(K)). Initial values of the aforementioned nutrients were similar across seasons for *P. eriostoma* and *D. rhinocerotis* but in *Medicago sp.* P and K were significantly higher in the summer season (Figure 3.6). There was no significant difference found in litter nutrient values after six months across site type for either the summer or the winter season.

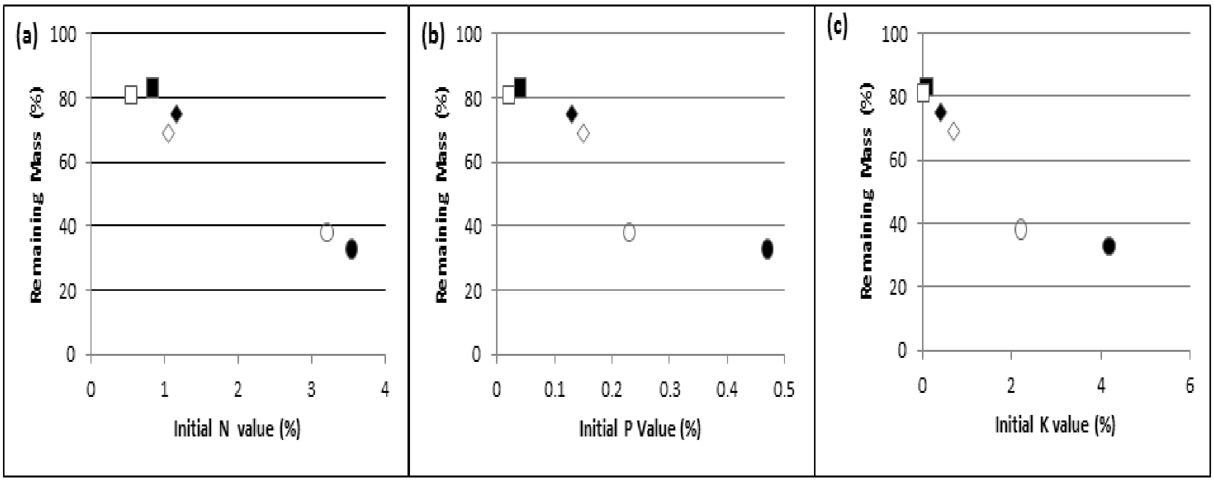

Figure 3.6: Mass loss after six months measured as percentage of litter remaining against initial nutrient concentrations (a) N, (b) P, and (c) K. (*P. eriostoma*=squares; *D. rhinocerotis*=diamonds; *Medicago sp*=circles. Summer Season=black, Winter Season=white).

Table 3.4: Comparison of decomposition rates and half-lives between this and other studies conducted in the Fynbos Biome ([1]-this study; [2]-Bengtsson et al., 2011; [3]-Bengtsson et al. 2012; [4]-Mitchell et al., 1986).

Species-source	**Vegetation**	***k* value(day^{-1})**	**Half-Life (day)**
D. rhinocerotis[1]	Eastern Rûens Shale Renosterveld	0.00207	367
P. eriostoma[1]	Eastern Rûens Shale Renosterveld	0.00125	702
Medicago sp[1]	Eastern Rûens Shale Renosterveld	0.00699	110
D. rhinocerotis[2]	Swartland Shale Renosterveld	0.00222	308
Galenia africana[2]	Swartland Shale Renosterveld	0.00674	101
Watsonia borbonica[2]	Swartland Shale Renosterveld	0.00029	2032
Galenia africana[3]	Fynbos	0.00642	108
Protea exima x P. susannae[3]	Fynbos	0.00233	297
Erica multumbellifera[3]	Fynbos	0.00150	462
Restio multiflorus[3]	Fynbos	0.00060	1136
Leucospermum parile[4]	Lowland Fynbos	0.00080	887

3.4 Discussion

Previous studies into ecosystem function within the Fynbos biome postulate that due to fire dependence and the extremely slow decomposition rate of a select number of species, litter decomposition plays a minimal role in nutrient cycling (Mitchell et al., 1986; Witkowski, 1991; Stock and Allsopp, 1992). However, more recent work has shown 8- to 20- fold differences between species decomposition rates in Fynbos and Renosterveld respectively, suggesting that litter decomposition in the Fynbos Biome may play an important role in nutrient and Carbon cycling between fire events (Bengtsson et al., 2011, 2012). This current study supports Bengtsson et al.'s (2011, 2012) assertion with a 5½-fold difference in decomposition rates recorded between plant functional types in the Eastern Rûens Shale Renosterveld of the Overberg. This study goes a step further however, including consideration of an indigenous grass species and an introduced annual herb. In addition, a degradation gradient and seasonal variation provide further insights.

3.4.1 Litter Decomposition

Although the decomposition rate of *D. rhinocerotis* was almost identical to that recorded for the same species by Bengtsson et al. (2011) (Table 3.4), the rate for *P. eriostoma* was, perhaps unexpectedly, half this value. No grass decomposition rates have been studied in the Fynbos biome before, however grasses, C3 grasses in particular (Barbehenn et al., 2004), are frequently associated with elevated nutrient content (van Oudtshoorn, 1999) which often indicate increased decomposition rates (Enríquez et al., 1993; Sterner and Elser, 2002; Bengtsson et al., 2011). *P. eriostoma* is not highly palatable (J. Groenewald, 2016 pers com) with low initial nutrient concentrations and tough, wiry leaf blades. In addition, *P. eriostoma* individuals tend to retain their sheath remains creating an almost woody base. Leaf toughness, generally associated with elevated fibre, lignin (Wright and Illius, 1995) and Silicon content (Epstein, 1994), has previously been correlated with lower decomposition rates in graminoids (Cornelissen and Thompson, 1997). It would appear that it cannot be assumed that graminoids have higher decomposition rates within the Fynbos biome. Instead traits such as apparent physical toughness and nutritional quality, often associated with palatability (Cornelissen and Thompson, 1997), need to be taken into account when assessing graminoid litter decomposition. Indeed, the lack of data on litter quality variables such as lignin content is a limitation in this study and we advise future studies to include it in analysis.

Medicago sp. recorded similar decomposition rates to those reported for the indigenous weedy shrub *Galenia africana* (Table 3.4). This elevated decomposition rate is typical of nutrient-rich annual herbs (Cornwell et al., 2008) and an influx of *Medicago sp*. into a Renosterveld system may accelerate the natural rate of nutrient cycling. However, as *G. Africana* proves, there are indigenous species with analogous decomposition rates and pristine Renosterveld has a rich understory of annual herbs and geophytes (Rebelo et al., 2006). No litter decomposition studies have been done on any indigenous annuals but it would be interesting to see how the rates compared to alien annuals and alternative indigenous plant functional types as invasive species can change decomposition rates within an ecosystem (Ashton et al., 2005). In terms of geophytes, the only species studied, *Watsonia borbonica*, exhibited the slowest decomposition rate yet recorded for any species in the Fynbos biome (Bengtsson et al., 2011; Table 3.4), however until a wider variety of geophytes have been investigated it would be unwise to make any generalisations.

The observed pattern of largest proportion of mass loss occurring in the first three months of decomposition is consistent with other studies (Bengtsson et al., 2011; Bergh and McClaugherty, 2014) and is a characteristic of the exponential decay curves used to estimate decomposition rates. The initial mass loss was probably the result of the decay of the more labile components of the litter and from abiotic leaching following the first rain event (Vossbrinck et al., 1979).

3.4.2 Initial Nutrient Content And Stoichiometry

In general, our results support the notion that decomposition rate in the Fynbos biome can be estimated by initial nutrient content of litter (Bengtsson et al., 2011, 2012) with a clear gradient showing increased initial values of N, P and K correlating strongly with increased decomposition rates (Figure 3.6). We do recommend expanding the data with a wider pool of species studied to make this assertion more robust and gather information on as yet untested functional types such as palatable indigenous grasses, indigenous annuals and geophytes, and invasive grasses. This would help in understanding what effect, if any, an increased cover of fast decomposing alien annual herbs would have on decomposition, nutrient cycling, and the local ecology in general.

In terms of stoichiometry (Figure 3.5), litter types varied in the dynamics of N and P. *D. rhinocerotis* accumulated N after six months for both seasons, possibly due to fungal activity (Lindahl and Olsson, 2004) or passive transportation from the surrounding soil (Bengtsson et al., 2011). This slight accumulation was also recorded for *P. eriostoma* during the winter season but in the summer season, and in both seasons for *Medicago*, N was mineralized and lost into the soil. Patterns were similarly haphazard for P, with mineralization occurring during both seasons for *D. rhinocerotis* and in the summer season for *P. eriostoma* and *Medicago*. However, a net accumulation of P was recorded after six months during the winter season for *P. eriostoma* and *Medicago*. As nutrient accumulation may play a role in delayed litter decomposition (Bengtsson et al., 2011), further studies are required to discern the role litter quality, climate and decomposer organisms play in litter stoichiometry.

3.4.3 Degradation Gradient

Considering the different land-use histories and dissimilarities in the current standing vegetation it is perhaps surprising that site type was not a significant factor in determining decomposition rate. As sites were classified according to a degradation gradient, it was expected that decomposition rates would differ between site types. Studies have linked increased above-ground biodiversity (and thus a more diverse litterfall) to increased decomposition rates (Hector et al., 2000; Hättenschwiler et al., 2005; Handa et al., 2014), while decomposition rate was found to decrease along a degradation gradient in a Chinese forest system (Paudel et al., 2015); however this was not observed during this study. Despite being grouped according to above-ground vegetation and land-use history, there was no significant difference in soil chemistry and structure across the sites. Agricultural activities have been shown to increase soil nutrients both in the Fynbos biome (Rebelo, 1992) and globally (Vitousek et al., 1997) thus the similarities in edaphic conditions across the degradation gradient are somewhat unexpected. While the limited replication may have influenced the statistical analysis (n=2 for each site type), the similarities in soil across sites may be a result of uncertainty surrounding the sites' land-use histories. While historical aerial photographs do provide some limited land use history information, the lack of archived records from the study area makes it near impossible to know exactly what kind of agricultural activities were taking place in the moderate and degraded sites in the past. For instance, crop type, application of fertilizer or whether the land was solely managed for grazing and at what stocking rate would all have different impacts on edaphic conditions and soil microbial communities (Snapp et al., 2010; Jangid et al., 2011). Another potential explanation for edaphic similarities may lie in previous grazing and management regimes in the 'pristine' sites prior to the first historical aerial photograph. Ecosystem characteristics such as soil nutrients and attributes do not necessarily return to their original state despite the return of above-ground species composition (Forsythe, 2013) and this may be an example of that phenomenon. It may be illuminating to test the role edaphic conditions play on litter decomposition rates by selecting sites based on an *a priori* soil analysis.

3.4.4 Season

Although climate is no longer considered the most important factor controlling litter decomposition rates (Zhang et al., 2008; Bradford et al., 2016), it has been shown to be influential (Aerts, 1997; Parton et al., 2007). As such, it is not surprising that season was a significant factor influencing decomposition rate in this study. Although climate in the Fynbos biome is described as Mediterranean with dry, hot summers and cold, wet winters, this is an oversimplification. In the east of the Fynbos biome where this study was conducted rainfall is non-seasonal as illustrated by the climate data for the period of study (Figure 3.3). *D. rhinocerotis* litter displayed marked difference in mass loss in the last three months across the two seasons. This pattern of a decreased mass loss was present, although to a lesser degree, in the other two litter types. The significantly reduced loss in summer season coincided with the three hottest months of the study while the evapotranspiration rates for the final two months for the summer season were significantly higher than the final two months of the winter season (Figure 3.4). It is feasible that the high temperatures and high evapotranspiration rates reduced activity of soil micro-organisms (Franken et al., 2018; Janion-Scheepers et al., 2018). Microbial activity has also been inversely correlated to desiccation (West et al., 1992); however the year-round precipitation in the study area (albeit often in low quantities) obscured any evidence of this. Indeed, the slower decomposition rates recorded for the final three months of the summer season coincided with the month of highest rainfall recorded across both seasons. In certain semi-arid ecosystems abiotic factors have been shown to control litter decomposition rates in the form of photodegradation (Austin and Vivanco, 2006; Almagro et al., 2017) and it is not inconceivable that this process may play a role during the hot summer months. Further studies would need to be conducted to confirm this. Understanding the exact role climate plays in litter decomposition in the study area is confounded by other factors; however it is possible that elevated summer temperatures reduce the rate of decomposition somewhat.

Difference in climate may not be the main reason for the variance in litter decomposition rate across seasons as the initial nutrient content of the litter for all three litter types differed significantly for certain elements . This can be explained by the different time of year that the litter was harvested as plant species' nutrient levels may fluctuate throughout the year (Chapin et al., 2002; Cramer et al., 2014). *Medicago sp*. in particular exhibited highly increased P and K values in the summer season. We did not distinguish between species within the genus and the litter collected for the summer season had a larger proportion of *M. polymorpha* compared to the winter season which was dominated by *M. sativa* which is a somewhat hardier species. The supply of nutrients and their availability to decomposers influences the rate of decomposition (Knorr et al., 2005; Manning et al., 2008; Güsewell and Gessner, 2009) and this may in part explain the difference in rates observed between seasons of study.

3.4.5 Conclusion

In conclusion, our results concur with Bengtsson et al.'s (2011) assertion that litter decomposition in the Fynbos biome is more variable than previously thought and, in Renosterveld in particular, may play a more significant role in nutrient cycling between fire events than previously speculated. Initial litter nutrient values may be a good indication of the rate of a species' decomposition, however, additional species need to be analysed to make this assertion more robust. While season was a significant factor influencing decomposition rates, the exact mechanism behind this is still unclear and may be a combination of climatic conditions and seasonal change in litter quality. Although degradation level did not significantly affect litter decomposition rate, we recommend further testing in sites with known differences in edaphic conditions as the significantly faster decomposition rate shown for the alien annual *Medicago sp.* does suggest that in degraded lands and old fields, where significant proportions of the species invade, nutrient cycling will be accelerated in comparison to pristine Renosterveld. However, Renosterveld can possess a rich understorey of indigenous herbaceous annuals, geophytes and palatable grasses and we recommend investigating the decomposition rates of typical species for comparison. In addition, investigating the role of more litter quality variables (e.g. lignin content) and decomposer activity would enhance our knowledge of litter decomposition dynamics.

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3.7 Supplementary Data

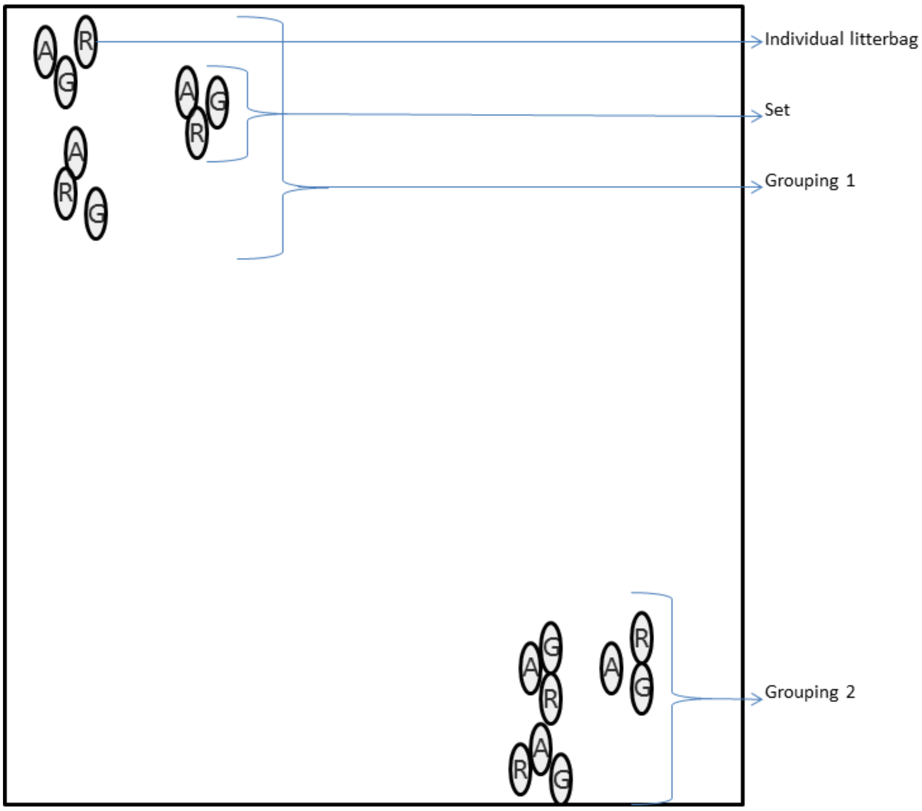

Figure S3.1: Study site example (Each set contains: A=individual *Medicago* sp. litterbag; G=individual *P. eriostoma* litterbag; R=individual *D. rhinocerotis* litterbag). Three sets per grouping; two groupings per site.

Table S3.1: Please see overleaf.

Table S3.2: Mean soil chemical and physical properties across site types. Standard deviations given in brackets. (x=exchangeable cations; *= p significant at p<0.05).

	Pristine	**Moderate**	**Degraded**
Soil	Loam	Loam	Loam
pH	4.7 (0.10)	4.9 (0.10)	5.2 (0.35)
Resistance	370 (270)	595 (375)	330 (190)
H+	1.69 (0.26)	1.11 (0.20)	0.90 (0.10)
Stones	28.50 (5.5)	29 (5)	32.50 (0.50)
Phosphorus	17.50 (1.5)	44 (12)	96.50 (74.50)
Potassium	236.50 (5.5)	185.50 (22.5)	330.50 (29.50)*
xSodium	2.79 (2.41)	0.58 (0.36)	1.29 (0.73)
xPotassium	0.60 (0.01)	0.47 (0.05)	0.84 (0.07)
xCalcium	4.72 (0.77)	4.89 (0.82)	6.76 (2.57)
xMagnesium	4.15 (0.58)	2.49 (0.69)	4.48 (1.63)
Carbon(%)	4.30 (0.11)	3.16 (0.45)	3.43 (0.99)
Soluble Sulphur	114.51 (92.44)	45.32 (25.25)	210.42 (188.20)
Cation Exchange Capacity	9.18 (0.58)	10.37 (0.67)	11.34 (3.20)
CLAY(%)	15 (3)	23 (7)	26 (2)
SILT(%)	18 (8)	24 (0)	27 (1)

Table S3.1: Mean initial nutrient values for season 1 (summer) and season 2 (winter) of the three species. Standard deviations given in brackets.

	D. rhinocerotis				***P. eriostoma***				***Medicago sp.***			
	Season 1		**Season 2**		**Season 1**		**Season 2**		**Season 1**		**Season 2**	
	Initial	**Final**	**Initial**	**Final**	**Initial**	**Final**	**Initial**	**Final**	**Initial**	**Final**	**Initial**	**Final**
N	1.16 (0.04)	1.25 (0.12)	1.05 (0.04)	1.13 (0.14)	0.83 (0.07)	0.71 (0.04)	0.54 (0.08)	0.56 (0.05)	3.54 (0.08)	2.25 (0.64)	3.21 (0.35)	2.27 (0.47)
P	0.13 (0.01)	0.05 (0.01)	0.15 (0.01)	0.10 (0.02)	0.04 (0.00)	0.04 (0.01)	0.02 (0.00)	0.03 (0.01)	0.47 (0.03)	0.16 (0.07)	0.23 (0.02)	0.28 (0.08)
K	0.41 (0.02)	0.16 (0.11)	0.70 (0.02)	0.30 (0.11)	0.09 (0.01)	0.08 (0.03)	0.05 (0.01)	0.07 (0.04)	4.18 (0.16)	0.17 (0.04)	2.21 (0.10)	0.26 (0.23)
Ca	0.43 (0.02)	0.38 (0.05)	0.35 (0.02)	0.45 (0.04)	0.10 (0.02)	0.12 (0.12)	0.03 (0.02)	0.14 (0.01)	1.22 (0.03)	0.91 (0.33)	1.06 (0.11)	1.29 (0.28)
Mg	0.22 (0.01)	0.25 (0.02)	0.22 (0.01)	0.23 (0.02)	0.03 (0.00)	0.11 (0.08)	0.04 (0.00)	0.11 (0.06)	0.37 (0.00)	0.33 (0.08)	0.26 (0.02)	0.24 (0.07)
Na	2042 (97)	727 (492)	3180 (93)	1262 (480)	153 (15)	257 (64)	961 (118)	286 (140)	3249 (125)	285 (45)	1625 (82)	313 (151)
Mn	27 (0.71)	59 (29.04)	21.40 (0.71)	60 (13.56)	19.40 (2.30)	63.75 (33.23)	8 (2.00)	49.33 (36.40)	41.60 (2.30)	120.25 (29.17)	30.80 (5.40)	92.17 (36.55)
Fe	394.40 (43.25)	10223 (8648)	387 (43)	9354 (3827)	373 (87)	17546 (16526)	515 (206)	17916 (17051)	270 (49)	26650 (1531)	305 (173)	15696 (10008)
Cu	6.20 (0.45)	7 (0.82)	6 (0.45)	8 (1.55)	3.20 (1.10)	5.25 (1.89)	1.80 (0.45)	4.50 (2.07)	10.80 (0.45)	10.25 (1.50)	6.40 (0.55)	8 (1.41)
Zn	24.80 (1.64)	41.25 (9.29)	20.80 (1.64)	52.83 (7.36)	37.40 (34.03)	52 (4.76)	5.80 (1.79)	47.50 (7.04)	40.60 (13.69)	101.75 (21.72)	18.80 (2.17)	80.33 (22.96)
B	51.40 (1.14)	31.25 (13.84)	49.20 (1.14)	37.33 (3.27)	3.20 (0.45)	4 (1.41)	4.80 (0.84)	6.67 (1.75)	63 (3.94)	15.25 (6.45)	36.60 (4.04)	19.50 (6.47)

Chapter 4

Springtail communities in a critically endangered vegetation type in South Africa

Dann Thombs

Springtail communities in a critically endangered vegetation type in South Africa

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Abstract

Springtails (Collembola) are important components of soil biota and contribute to a variety of ecosystem functions. Despite an increase in studies in recent years, Springtail ecology is still poorly understood in South Africa and the ability of Springtails to be utilised as a bioindicator, as they have been successfully used elsewhere, has not been explored. Here, we investigate the community dynamics of Springtails in Renosterveld, a critically endangered vegetation type in South Africa. For the first time, we measure the effect of litter type and season on Springtail species richness, abundance and community composition across a degradation gradient with the use of litter traps. Litter type and degradation level were found to have no significant effect on Springtail richness or abundance; however season, in the form of litter trap removal day, strongly affected community dynamics with litter traps removed after three months containing more diverse and abundant communities than those removed after six months. Community composition was also significantly affected by season with certain species more abundant after six months, possibly due the possession of functional traits which allow them to better exploit resources at this time. Although habitat degradation did not have an overall significant impact on Springtail dynamics, the non-native *Entomobrya multifasciata* was found in significantly higher numbers in degraded sites compared to sites within pristine vegetation. Our study has shown the dynamic nature of Springtail community dynamics within Renosterveld, improving our ecological understanding of an organism with a crucial role in ecosystem functioning. Our findings also suggest that Springtails may be suitable to use as a bioindicator for habitat degradation due to the abundance and identity of certain species in degraded sites in comparison to pristine sites.

4.1 Introduction

Soils are a critical and dynamic regulatory resource which delivers a variety of ecosystem services and provide enormous economic benefit to humankind (Costanza et al., 1997; Pascual et al., 2015; Adhikari and Hartemink, 2016). Soil health and functionality are fundamentally linked to soil biota and understanding the ecology of biotic soil communities and the relationship between soil biota biodiversity to ecosystem functioning is of critical importance (Bardgett and van der Putten 2014; Wagg et al., 2014). A significant constituent of soil biota are Springtails (Collembola) due to their abundance, ubiquity and functional role (Peterson and Luxton, 1982; Bardgett et al., 2005). Springtails contribute to ecosystem functioning in a myriad of ways, for example, through the facilitating of litter decomposition, nutrient cycling, and the formation of soil microstructure (Peterson and Luxton, 1982; Hopkin, 1997; Rusek, 1998). Springtail community dynamics are controlled at a local scale by environmental parameters such as soil conditions (moisture, acidity, temperature, and structure), litter layer composition, and fungal community (Addison et al., 2003a; Alerding and Hunter 2013; Hashimoto and Tamura, 1994; Kovác, 1994; Ponge et al., 1993; Raymond-Léonard et al., 2018). Landscape factors such as vegetation cover fragmentation, land-use history, and contemporary vegetation structure exert controls on more localized parameters. However, despite an increase in studies in recent years (Chust et al., 2003; Da Silva et al., 2012; Da Silva et al., 2016; Ponge et al., 2006; Querner et al., 2013; Sousa et al., 2004; Vanbergen et al., 2007), the precise relationship between Springtails and landscape-level factors remains poorly understood (Querner et al., 2018).

Part of this uncertainty is the result of the multiplicity of interacting factors which control Springtail community dynamics. Springtails feed directly on both plant matter and the fungae which colonize decomposing litter (Rusek, 1998; Chahartaghi et al., 2005); however the relationship is complex with certain fungivorous species highly specific in their choice of sustenance (Chen et al., 1995), while other species may switch their diet according to environmental conditions or their developmental stage (Filser et al., 2002; Jensen et al., 2006). Additionally, Springtail species differ in their tolerance to temperature and moisture (Makkonen et al., 2011), dispersal ability (Berg et al., 1998) and their ability to aggregate and synchronise behaviour through chemical communication (Leinaas, 1983; Widenfalk et al., 2018). It is clear that the chemical and physical nature of both litter input and environmental parameters governed by the above-ground vegetation of a habitat influence Springtail community dynamics (Adderson et al., 2003b; Raymond-Léonard et al., 2018). It is therefore unsurprising that factors which alter above ground vegetation structure and environmental conditions, such as disturbance in the form of fire, degradation, alien plant invasion, and landscape management affect Springtail communities (Brand and Dunn, 1998; Bedano et al., 2006; Barbercheck et al., 2009; Alerding and Hunter, 2013; Janion-Scheepers et al., 2016a; Leinaas et al., 2015; Pollierer and Scheu, 2017; Errington et al., 2018). Enhancing our understanding of how Springtails respond to environmental disturbances may allow us to utilise them as bioindicators for ecosystem health (Neher et al., 1999; Parisi et al., 2005), the possibility of which is already being explored (Cassagne et al., 2006; Frampton and van den Brink, 2007; Greenslade, 2007; Errington et al., 2018).

Despite an increase in attention in recent years (Janion et al., 2011; Liu et al., 2012; Janion-Scheepers et al., 2015; Leinaas et al., 2015; Janion-Scheepers et al., 2016a), compared to Europe, Springtails in South Africa remain under studied with their ecological significance particularly poorly understood (Janion-Scheepers et al., 2016b). Recent studies however, while limited, have shown Springtail assemblages in South Africa to be highly diverse (Liu et al., 2012; Janion-Scheepers et al., 2015) and ecologically significant (Leinaas et al., 2015; Janion-Scheepers et al., 2016a) with introduced European species forming a significant component in habitats such as suburban gardens and agricultural lands (Janion-Scheepers et al., 2015). The rapid progress in taxonomic expertise witnessed in the country is expected to advance the field of research in coming years (Janion et al., 2011) and the potential exists to use Springtails as an indicator of environmental change, habitat disturbance and soil health (Janion-Scheepers et al., 2016b), as has been done elsewhere (Cassagne et al., 2006; Greenslade, 2007). For this to be successful a greater depth of understanding is needed on the factors which affect Springtail community dynamics.

In light of the global environmental crisis (Dirzo et al., 2014; IPCC, 2018), understanding the ecology of ecosystem functioning, and in turn how this relates to the delivery of ecosystem services is vitally important (Pettorelli et al., 2018). This is particularly so in South Africa, where agriculture is one of the most important economic contributors to the GDP (Davis-Reddy and Vincent, 2017) and ecosystem services associated with healthy soil are fundamental to this contribution. Despite this, many aspects of the role of soil fauna remain poorly understood (Janion-Scheepers et al., 2016b). The Overberg region of the Western Cape Province of South Africa has a long history of agricultural activity and the current landscape ranges from small pockets of pristine vegetation to agricultural fields (see section 4.2.1). It thus provides an ideal location to further our understanding of the ecological significance of Springtails by investigating how Springtail community dynamics respond to localized factors such as litter type; landscape parameters such as level of degradation; and how these may change through time. In particular, we will test: 1) the effect of litter type on Springtail communities, 2) The effect of landscape level degradation on Springtail communities, and 3) the effect of season on Springtail communities within an understudied and critically endangered vegetation type.

4.2 Materials And Methods

4.2.1 Study Area And Site Selection

Haarwegskloof Nature Reserve (34°20’17.9”S; 20°19’34.1”E) is situated within the Overberg lowlands of the Western Cape Province of South Africa (Figure 4.1). The indigenous vegetation of the Overberg region includes four different types of Renosterveld all of which are considered critically endangered (Driver et al., 2012) with less than 10% of the original extent remaining (Curtis, 2013). The vegetation types exist as fragmented islands within an agricultural matrix of privately owned land (Kemper et al., 1999) - predominantly grain fields (wheat, barley, oats, canola) and artificial pasture (lucerne/alfalfa) (Curtis et al., 2013). The reserve itself is situated within the Eastern Rûens Shale Renosterveld which was purchased by the World Wildlife Fund-South Africa and the Overberg Renosterveld Conservation Trust in 2013. Rebelo et al. (2006) describe Eastern Rûens Shale Renosterveld as occurring on moderately undulating hills and plains which supports cupressoid and small-leaved, low to moderately high grassy shrubland. The reserve consists of approximately 500 ha of land, 80% of which is described as virgin Renosterveld while the remaining area is lands of varying age, portions of which may have been previously ploughed and/or used as grazing pasture. Eastern Rûens Shale Renosterveld has an altitudinal range of 40-320 m above sea level and an average rainfall of 384 mm per annum with an essentially even distribution (Rebelo et al., 2006; Curtis et al., 2013). Mean daily temperatures range from 5.9 °C minimum in July to 26.9 °C maximum in January (Rebelo et al., 2006).

Vegetation sampling combined with historical aerial photograph analysis identified two sites of each in three degradation ‘states’ (Figure 4.1). First, ‘Pristine’ – characterised by high species richness, no alien species presence and no evidence of historical agriculture; second ‘Moderately Degraded’ – characterised by moderate to low diversity, dominance of early successional species and evidence of historical agricultural use; and third ‘Highly Degraded’ – characterized by moderate to low diversity, substantial alien species presence and evidence of recent agricultural use.

4.2.2 Plant Species Selection And Litter Collection

The three plant species used in this study were chosen as they represent common but different plant functional types which differ in dominance across the landscape according to level of degradation. *Pentameris eriostoma* is an indigenous, densely tufted, erect, perennial, C3 grass common throughout Haarwegskloof and the surrounding Renosterveld remnants. It flowers in

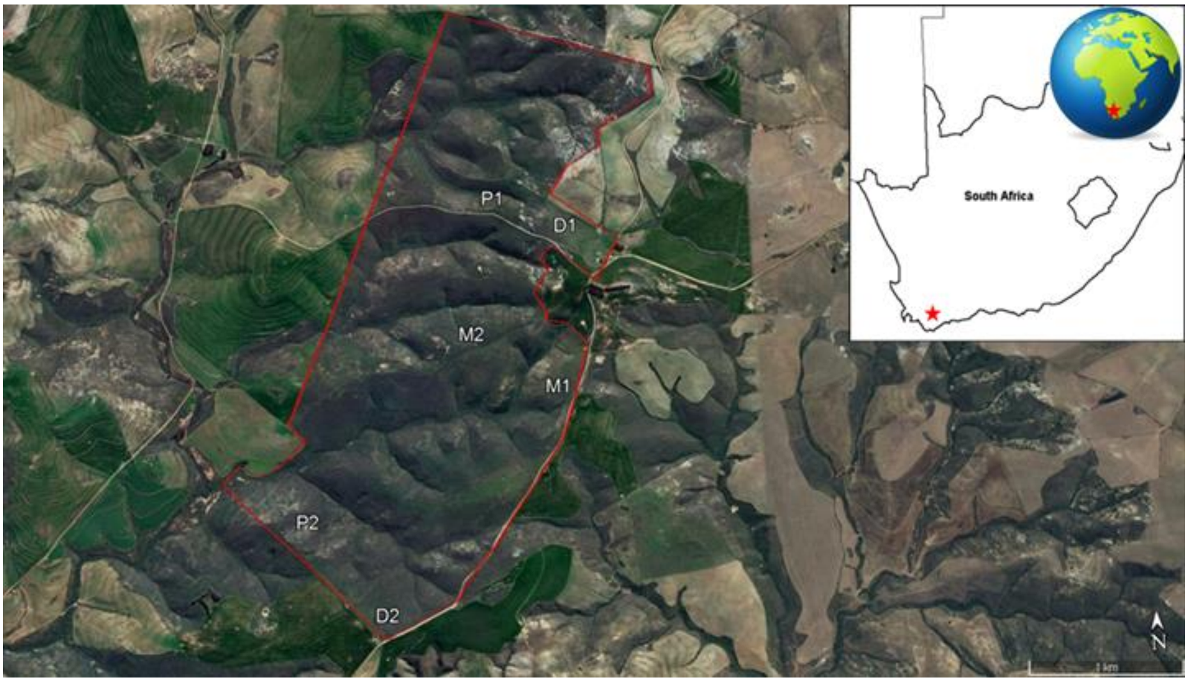

Figure 4.1: The location of the six study sites within Haarwegskloof Nature Reserve, South Africa.

winter and grows to 0.9 m in height. It does not appear to be particularly palatable (J. Groenewald 2016 pers. comm.) as its blades are tough and wiry, often with an almost woody base closely covered by the remains of the sheaths. In the pristine parts of the reserve *P. eriostoma* is common, at times providing up to 20% of the cover. It was recorded in the moderately degraded areas of the reserve but at much lower densities (<1% cover) and was absent from the highly degraded fragments surveyed. *Dicerothamnus rhinocerotis* (renosterbos) is the defining species in Renosterveld. It is a common, evergreen, resinous shrub which grows up to 2 m in height. It is rich in phenolics and exhibits anti-herbivore properties (Proksch et al., 1982). While present in healthy Renosterveld, its weedy nature allows it to dominate disturbed land. *Dicerothamnus rhinocerotis* was recorded on all sites surveyed on the reserve and at times dominated the moderately and highly degraded areas. *Medicago sativa* (lucerne/alfalfa) is a perennial herb from the Fabaceae family. It is an alien species in Renosterveld, introduced into the Western Cape by the agriculture industry in the 1860s, but now widely used as a fodder crop. Managed fields of lucerne were only found in the surrounding landscape; however small pockets of lucerne, and the closely related alien annual herbs *Medicago polymorpha* and *M. lanciniata,* were present in the reserve, occurring in varying amounts in the moderately and highly degraded sites.

Plant material was collected on 22 March 2017. For *D. rhinocerotis* and *P. eriostoma* the outer branches/leaf blades (~10 cm) were removed from healthy individuals with secateurs, stored separately in bags before being dried in a laboratory oven at 40 °C for 48 hours and thereafter cut into 1-3 cm pieces. The litter was then mixed separately and stored in open containers at room temperature. *Medicago sativa* fodder was sourced from local farmers, dried at room temperature for seven days before being cut into small pieces and mixed thoroughly. To ascertain initial nutrient content, five samples for each litter type were analysed for Nitrogen (N), Phosphorus (P), Potassium (K), Calcium, Magnesium, Sodium, Manganese (all %) and Iron, Zinc, Copper, Boron (all mg/kg) (Bemlab Pty Ltd., Somerset West, South Africa).

Due to the rocky nature of the Renosterveld, traditional quantitative sampling of microarthropods by means of a standard soil corer (O'Connor, 1957), is not possible. To calculate decomposition rates and collect Springtails, litter traps were used. Litter traps or litterbags are used globally to investigate the role of soil fauna in decomposition (see Wall et al., 2008). In this study, litter traps consisted of individually numbered plastic cylinders with removable lids which were filled with litter (design based on Bengtsson et al., 2011). Each cylinder was 8 cm high with a diameter of 7 cm. The bottom of the cylinders consisted of stainless steel mesh with an aperture of 0.55 mm while the lids consisted of stainless steel mesh with an aperture of 1.5 mm. Litter for each individual trap was weighed to the nearest 0.01 mg before being placed in the litter traps. Litter traps were placed in the field on 10 April 2017.

4.2.3 Experimental Design

The experiment was set up to simultaneously investigate litter decomposition and nutrient dynamics (see Bengtsson et al., 2011, 2012, Cowan and Anderson, 2019), but has also been used previously to investigate the abundance and diversity of Collembola in different litter types (Leinaas et al., 2015). As such, three sets of three litter traps each were placed in two 'groupings' in each of the six study sites. Each set contained one litter trap of each litter type. Litter traps were submerged in the soil with the lids at ground level. Litter traps within a set were placed within 10 cm of each other while sets within a grouping were approximately 100 cm apart. Each grouping within a study site was at least 15 m apart and every effort was made to ensure environmental homogeneity between groupings in terms of slope, aspect and shade cover (Supplementary Data Figure S4.1).

A total of 108 litter traps were deployed, although the final data set consists of 102 litter traps, as three litter traps were disturbed by animals and a further three compromised in the laboratory and thus excluded from the analysis.

4.2.4 Soil Analysis

To assess whether above ground vegetation and land-use history influenced edaphic conditions soil analysis was performed. At each site a composite soil sample (approximately 500 g) was taken from four random locations at depths up to 15 cm (Bohn et al., 2001) and sent to an external accredited laboratory (Bemlab Pty Ltd., Somerset West, South Africa) where the following soil characteristics were measured: pH (KCl; see Mclean, 1982), electrical resistance (ohms; see Richards, 1969), Hydrogen (cmol(+) /kg), stone volume (%), P (Bray II) (mg/kg; see Bray and Kurtz, 1945), K (mg/kg), Exchangeable Sodium, K, Calcium and Magnesium cations (cmol(+)/kg; see Chapman, 1965), organic Carbon (%; see Nelson and Sommers, 1982), soluble Sulphur (mg/kg), clay, silt and sand content (%), and waterholding capacity mm/m).

Hygrochron^{TM} DS1923 iButtons (Maxim Integrated, San Jose, USA) were placed in a subset of litter traps at each study site to record soil temperature. Temperature data were only reliably obtained for the first three months (Supplementary Data Figure S4.2), due to equipment failure, thus soil temperatures were excluded from analysis.

4.2.5 Trap Collection, Treatment, Springtail Extraction And Functional Traits

To ascertain a broad temporal view of Springtail community dynamics litter traps were sampled twice. One randomly selected set from each grouping was removed on 18 July 2017 and the remaining sets on 25 October 2017 (98 and 197 days *in situ* respectively – hereafter referred to as three months and six months). After the litter traps were removed they were immediately wrapped in aluminium foil, sealed inside bags, and transported back to the laboratory in thermally insulated boxes. Springtails were extracted using a modified open extraction method where litter traps were inverted and placed in funnels for seven days in the laboratory. Microfauna fell through the funnel into beakers below containing 75% ethanol. Beaker contents were then transferred to labelled, sealable vials. Springtails were separated under a microscope, counted and sorted into morphospecies to the lowest taxonomic level possible using taxonomically significant morphological characteristics, local taxonomic expertise and identification keys (Fjellberg, 1998, 2007; Bretfield, 1999; Potapov, 2001; Hopkin, 2007). As much of the Springtail fauna of South Africa is not well described (Janion et al., 2011), the morphospecies approach is widely used (Liu et al., 2012; Janion-Scheepers et al., 2015; Leinaas et al., 2015; Janion-Scheepers et al., 2016a) and is sufficient to provide confidence that morphospecies are representative of the assemblage investigated. The litter samples were subsequently analysed for litter decomposition and chemical alterations (see Cowan and Anderson (2019) for details).

Functional traits have been used to better understand and compare community assembly and species diversity patterns in the study of terrestrial invertebrate communities (Moretti et al., 2017) and have been used extensively in Springtail studies (Krab et al., 2010; Makkonen et al., 2011; Bokhorst et al., 2012; Da Silva et al., 2012; Malmström, 2012; Van Dooremalen et al., 2013;

Widenfalk et al., 2015). To assess whether there was a relationship between Springtail community composition and functional traits, three traits which have previously been used in the aforementioned studies to explain shifts in Springtail composition across time, space and environmental gradients were recorded. Traits were measured from each morphospecies using the measurement function of Leica Application Suite software on a Leica DM4B or a Leica Z16 APO (Leica Microsystems, Wetzlar, Germany). Body length (maximum length from head to tip of abdomen) is connected to dispersal ability, lifeform and ecophysiology (Berg et al., 1998). Antenna-to-body ratio (antennal length divided by body length) is assumed to be linked to sensory ability and active dispersal (Da Silva et al., 2012; Widenfalk et al., 2016). Antenna length was measured and used in conjunction with body length to calculate antenna-to-body ratio. Life form is trait complex composed of number of ommatidia, length of body and intensity of colouration (Gisin, 1943) and is a proxy for vertical stratification, ecophysiology and dispersal ability (Ponge et al., 2006). Life form for the morphospecies were determined from their morphological characteristics and classified into one of the following groups: Euedaphic refers to soil dwelling species; hemi-edaphic to litter dwelling species; and atmobiotic to free living species in the vegetation (Gisin, 1943; Janion-Scheepers et al., 2016a).

4.2.6 Data Analysis

To investigate how species richness and species abundance were affected by litter type, degradation gradient, sampling day, and their interactions we used Generalized Linear Models (GLMs) to model the data (R Core Team, 2015). For the species richness analysis count data were used, a Poisson GLM was run with a Chi-Squared test to attain p values. Species abundance data varied from 1-352 individuals per litter trap and the decision was made to log-transform the data prior to analysis. The transformed data were approximately normally distributed (visually assessed using a qqplot in R) thus a Gaussian GLM was run with an F-test to attain p-values.

Differences in Springtail community composition were examined by Non-metric Multidimensional Scaling (nMDS) and analysis of similarity (ANOSIM) using the Vegan package in R (R Core Team, 2015). To run the nMDS a Bray-Curtis dissimilarity index was used on square root transformed abundance data with the number of iterations set at 1000 and a solution reached when the stress was minimized. Using the function *envfit* in Vegan (R Core Team, 2015), environmental variables and controlled experimental factors with $p < 0.05$ were overlaid onto the ordination. Species with $p < 0.05$ were overlaid onto the ordination using modified version of the *envfit* function. ANOSIM is used to test statistically whether there are significant differences between two or more groups of a sampling unit. The function generates a P value (significance) and R value which is scaled to lie between 0 (indistinguishable) and 1 (complete separation). ANOSIM was performed on all factors and species to assess which were statistically significant. Analysis was repeated using presence absence data, however no noticeable differences were found and it was decided to only present results for analysis run on Springtail abundance data.

4.3 Results

4.3.1 Species Richness And Abundance

A total of 2,838 Springtails comprising 26 species from nine families were found in this study (Supplementary Data Table S4.1) with *Symphypleona* sp. 1 (1,190), *Entomobrya multifasciata* (435), *Tullbergia* sp. (255), *Seira* sp. 1 (185) and *Seira* sp. 3 (272) the most abundant (Figure 4.2). These five species, along with *Parisotoma* sp. and *Sminthurinus* sp. 1 and 2, were also the most ubiquitous (Figure 4.3). Seven species were only found in litter traps removed after three months whereas two species were only found in litter traps removed after six months (Figure 4.3). Removal day significantly affected both species richness and abundance with more diverse and numerous Springtail assemblages found in samples removed after three months compared to those samples removed after six months (Table 4.1).

Table 4.1: Results from Generalized Linear Model (GLM) analyses of the effects of degradation state (Pristine, Moderately Degraded, Highly Degraded), litter type (*D. rhinocerotis*, *P. eriostoma*, *M. sativa*), and removal day (three months, six months) on Springtail A) species richness and B) log abundance. Factors with $p < 0.05$ are shown in bold.

Effect	DF	P value
A) Species Richness		
Litter Type	2	0.983
Site Type	2	0.420
Removal Day	1	**< 0.001**
Litter Type*Site Type	4	0.946
Litter Type*Removal Day	2	0.171
Site Type*Removal Day	2	0.920
Litter Type*Site Type*Sampling Day	4	0.765
B) Log Abundance		
Litter Type	2	0.210
Site Type	2	0.100
Removal Day	1	**< 0.001**
Litter Type*Site Type	4	0.223
Litter Type*Removal Day	2	0.362
Site Type*Removal Day	2	0.252
Litter Type*Site Type*Sampling Day	4	0.275

This pattern was consistent across site (Figure 4.4) and litter type (Figure 4.5) but not all species were more abundant after the first removal day with *Seira* sp. 3, *E. multifasciata*, *Brachystomella* sp. and *Pseudosinella* sp. having a larger mean abundance in litter traps removed after six months than after three months (Figure 4.2). Litter type and site type (i.e. degradation level) had no significant effect on species richness and overall abundance (Table 4.1 and Figure 4.6); however *E. multifasciata* were found in significantly higher numbers in highly degraded (313) and moderately degraded (112) sites compared to pristine sites (10).

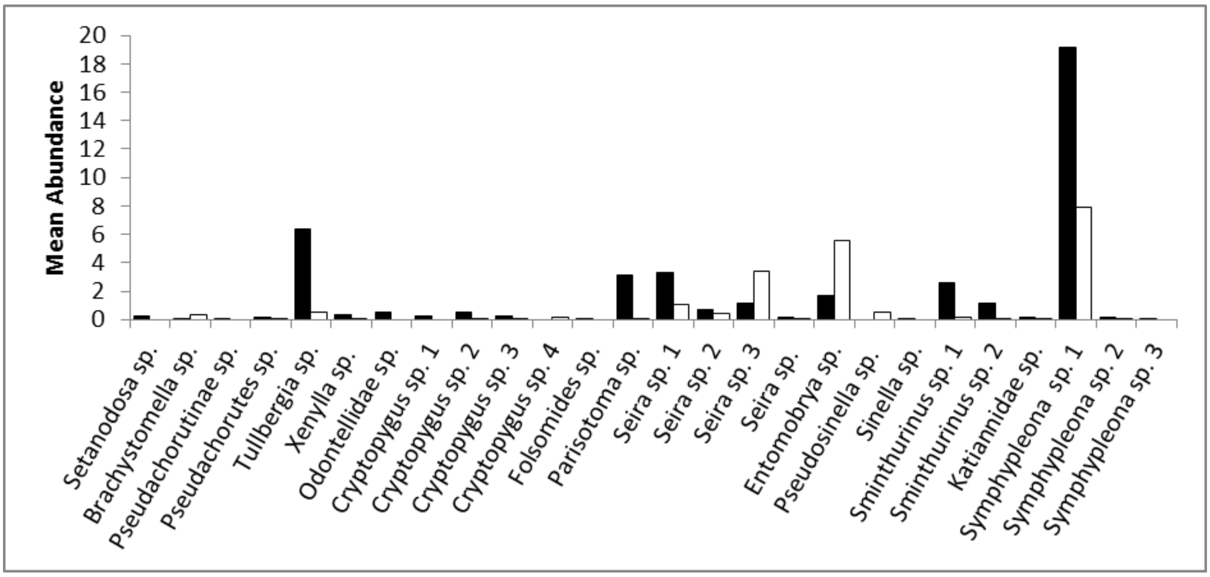

Figure 4.2: Mean abundance per litter trap of the species found during the study period. Black bars represent mean abundances after three months; white bars represent mean abundances after six months.

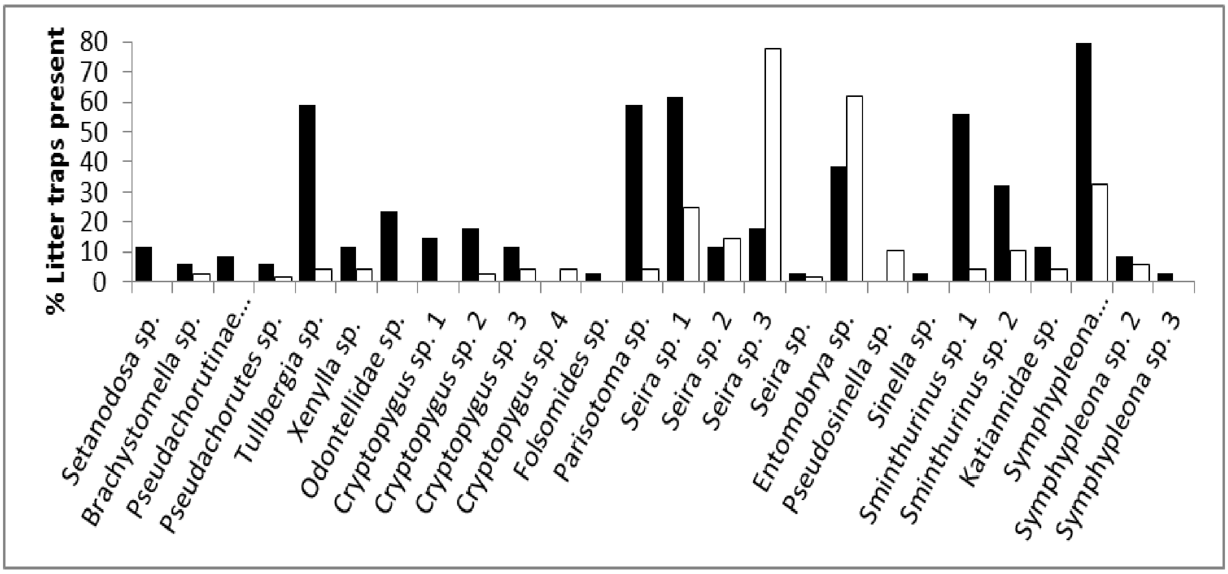

Figure 4.3: Percent of total litter traps in which species were found. Black bars represent litter trap percent after three months; white bars represent litter trap percent after six months.

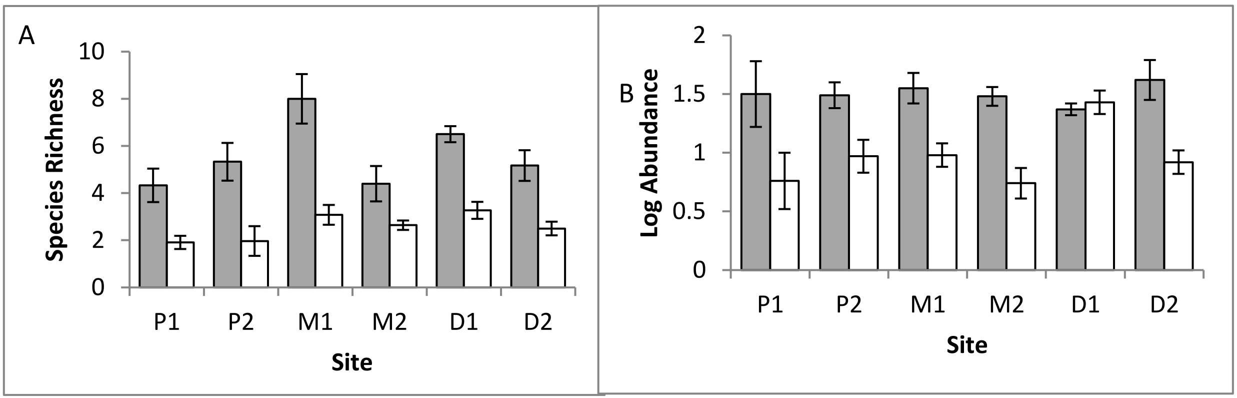

Figure 4.4: Springtail mean ± SE species richness (A) and Log Abundance (B) for each study site at both removal days. (Light Grey=Three Months; White=Six Months. P=Pristine; M=Moderately Degraded; D=Highly Degraded).

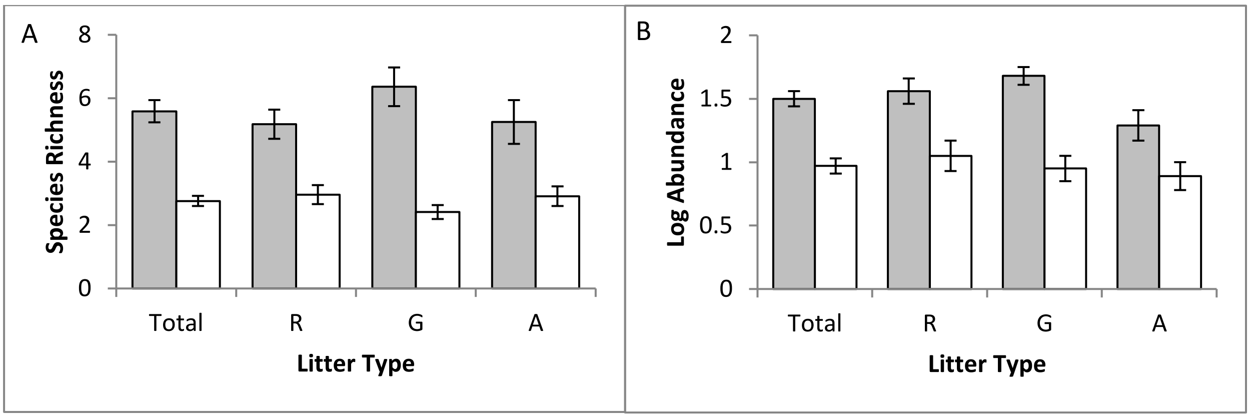

Figure 4.5: Springtail mean ± SE Species Richness (A) and Log Abundance (B) for total and each litter type for all sites combined at both removal days. (Light Grey=Three Months; White=Six Months. R= *D. rhinocerotis* G= *P. eriostoma*; A= *M. sativa*).

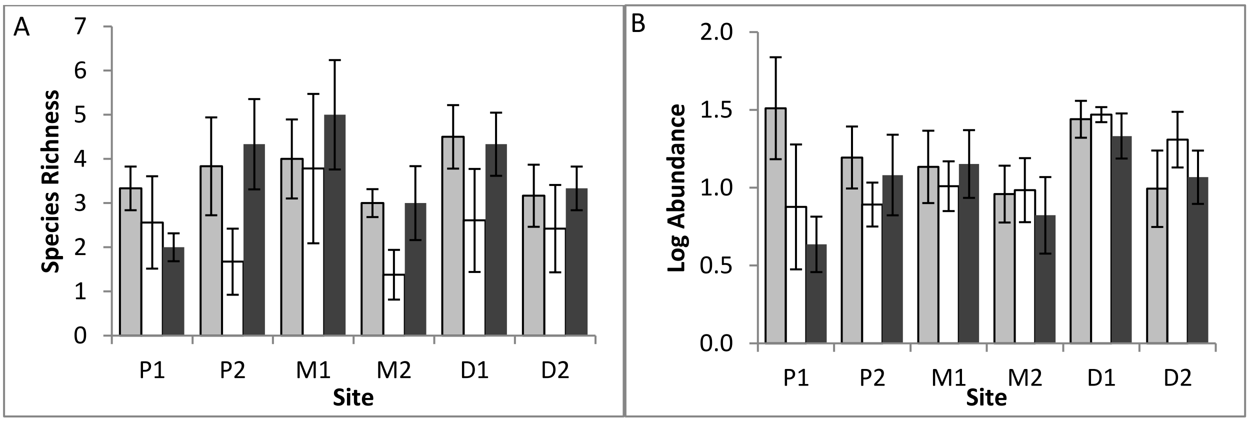

Figure 4.6: Springtail mean ± SE species richness (A) and Log Abundance (B) for each litter type at each study site. (Light Grey=*D. rhinocerotis*; White=*P. eriostoma*; Dark Grey=*M. sativa*. P=Pristine; M=Moderately Degraded; D=Highly Degraded).

4.3.2. Assemblage Composition

Significant differences in Springtail assemblage composition were found across litter traps. This was predominantly correlated with sampling day although litter type, litter decomposition rate, initial Nitrogen and Potassium litter values were also significant. Of the species with significant correlation to the ordination grouping of $p < 0.05$, *Seira* sp. 3, *E. multifasciata* and *Pseudosinella* sp. were correlated with litter traps removed after six months, while *Setanodasa* sp., *Pseudochorutinae* sp., *Pseudochorutes* sp., *Tullbergia* sp., *Odontellidae* sp. *Parisotoma* sp., *Seira* sp. 1., *Seira* sp., *Pseudosinella* sp., *Sminthurinus* sp. 1 and 2, *Symphypleona* sp. 1 and 2, *Katiannidae* sp. and *Cryptopygus* sp. 1 were all correlated to litter traps removed after three months. In terms of litter type, *E. multifasciata* and *Pseudosinella* sp. were correlated with litter traps containing *M. sativa* while *Seira* sp. 3, *Setanodosa* sp. and *Symphypleona* sp. 1 were correlated with litter traps containing *D. rhinocerotis* (Figure 4.7).

NMDS ordinations are primarily visual aids for interpreting community data thus to test for statistical significance ANOSIM was performed (Tables 4.2 and 4.3). The ANOSIM results largely correlated with the ordination with all five factors highlighted significantly affecting assemblages. Seven were found to be statistically significant in explaining differences in assemblage composition, namely *Tullbergia* sp., *Parisotoma* sp., *Seira* sp. 1 and 3, *E. multifasciata*, *Sminthurinus* sp. 1 and *Symphypleona* sp. 1. These seven species were both the most abundant and ubiquitous Springtails found in the study whereas the remaining 10 species reported in the ordination were less numerous and found in far fewer litter traps (Figure 4.2 and 4.3).

Table 4.2: Results from Analysis of Similarities (ANOSIM) on factors which may affect community composition of Springtails within litter traps. Only factors with $p < 0.05$ are shown.

Factor	**Global R value**	**p-value**
Decomposition Rate (k)	0.55	0.002
Sampling Day	0.42	<0.001
Initial Litter Nitrogen content	0.13	<0.001
Initial Litter Potassium content	0.13	<0.001
Litter Type	0.13	<0.001

The two species associated with Springtail assemblages after six months, *Seira* sp. 3 and *E. multifasciata*, are both relatively large, atmobiotic species with large antenna-to-body ratios. The species associated with assemblages after three months show more trait variation: *Seira* sp. 1, *Sminthurinus* sp. 1 and *Symphypleona* sp. 1 are also atmobiotic species but vary from minute (*Symphypleona* sp. 1) to medium sized (*Seira* sp. 1), while *Tullbergia* sp. is euedaphic with a small body and minute antennae and the medium-sized *Parisotoma* sp. is hemiedaphic (Table 4.4).

Table 4.3: Results from Analysis of Similarities (ANOSIM) on species which significantly affect community composition of Springtails within litter traps. Only factors with p < 0.05 are shown. Roman numerals in brackets are the species codes on Figure 4.6.

Species	**Global R value**	**p-value**
Tullbergia sp.	0.30	0.02
Symphypleona sp. 1 (xiv)	0.19	<0.001
Sminthurinus sp. 1 (xii)	0.17	0.002
Parisotoma sp. (vi)	0.14	0.02
Entomobrya multifasciata	0.12	0.02
Seira sp. 3 (viii)	0.11	0.02
Seira sp. 1 (vii)	0.10	0.03

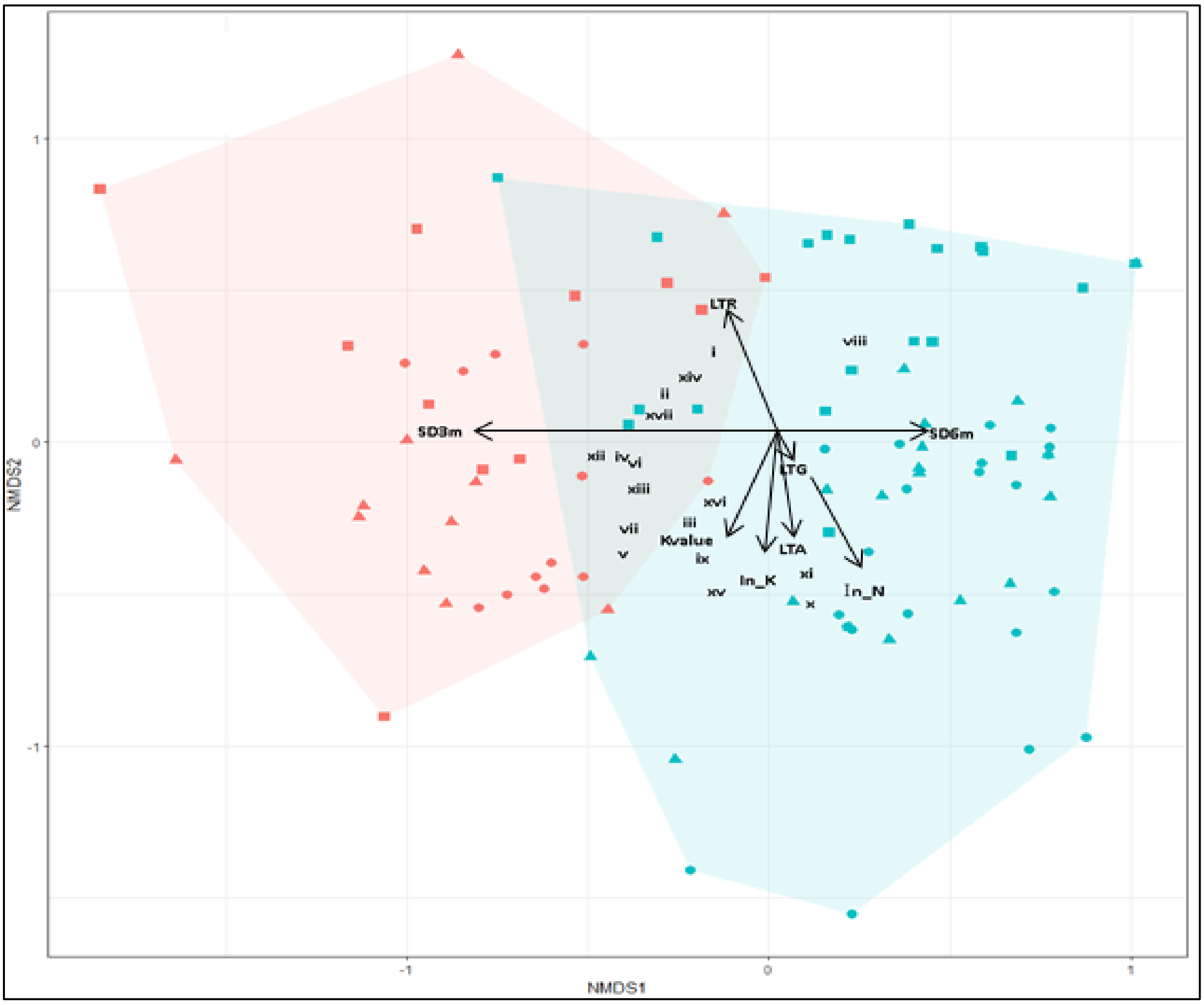

Figure 4.7: Non-metric multidimensional scaling (nMDS) plots of Springtail assemblages of the 102 litter traps using species abundance data (Red symbols=litter traps removed after three months; blue symbols=litter traps removed after six months. Squares=*D. rhinocerotis* litter traps; Triangles=*P. eriostma* litter traps; Circles=*M. sativa* litter-traps). Overlaid black arrows represent potential explanatory parameters with p < 0.05 and arrow length indicating strength of correlation (SD3=Sampling Day at three months; SD6=Sampling Day at six months. LTR=*D.rhinocerotis* litter; LTG=*P. eriostoma* litter; LTA=*M. sativa* litter. In_N=Initial Nitrogen content of litter; In_K=Initial Potassium content of litter; Kvalue=litter decomposition rate (see Cowan and Anderson, 2018)). Roman numerals i-xvii represent species with p < 0.05 (i-*Setanodosa sp.*; ii-*Pseudachorutinae sp.*; iii-*Pseudachorutes sp.*, iv-*Tullbergia sp.*; v-*Odontellidae sp.*; vi-*Parisotoma* sp.; vii-*Seira* sp. 1; viii-*Seira* sp. 3; ix-*Seira* sp.; x-*Entomobrya* sp.; xi-*Pseudosinella* sp.; xii-*Sminthurinus* sp. 1; xiii-*Sminthurinus* sp. 2; xiv-*Symphypleona* sp. 1; xv-*Symphypleona* sp. 2; xvi-*Katiannidae* sp.; xvii-*Cryptopygus* sp. 1).

Table 4.4: Functional trait data for the Springtail species recorded during the study period

	Body Length (mm)	**Antenna to Body Length Ratio**	**Life Form**
Setanodosa sp.	3	0.1	Hemiedaphic
Brachystomella sp.	0.8	0.12	Hemiedaphic
Pseudachorutinae sp.	3	0.1	Hemiedaphic
Pseudachorutes sp.	1.5	0.12	Hemiedaphic
Tullbergia sp.	0.75	0.09	Euedaphic
Xenylla sp.	0.5	0.12	Hemiedaphic
Odontellidae sp.	1.2	0.18	Hemiedaphic
Cryptopygus sp. 1	1	0.2	Hemiedaphic
Cryptopygus sp. 2	1.3	0.23	Hemiedaphic
Cryptopygus sp. 3	0.8	0.2	Hemiedaphic
Cryptopygus sp. 4	0.6	0.18	Hemiedaphic
Folsomides sp.	0.6	0.2	Euedaphic
Parisotoma sp.	1	0.2	Hemiedaphic
Seira sp. 1	1.2	0.2	Atmobiotic
Seira sp. 2	1.9	0.4	Atmobiotic
Seira sp. 3	2.1	0.46	Atmobiotic
Seira sp.	1.8	0.4	Atmobiotic
Entomobrya multifasciata	1.3	0.4	Atmobiotic
Pseudosinella sp.	0.5	0.19	Hemiedaphic
Sinella sp.	1.1	0.4	Hemiedaphic
Sminthurinus sp. 1	1	0.35	Atmobiotic
Sminthurinus sp. 2	0.5	0.45	Atmobiotic
Katiannidae sp.	0.8	0.8	Atmobiotic
Symphypleona sp. 1	0.3	0.25	Atmobiotic
Symphypleona sp. 2	0.6	0.25	Atmobiotic
Symphypleona sp. 3	0.5	0.25	Atmobiotic

4.3.3 Environmental Variables And Litter Dynamics

Environmental variables such as temperature, precipitation, actual evapotranspiration and soil temperature all varied in the preceding months prior to the two removal days, however no data was taken to evaluate if soil chemistry varied through time with soil chemistry values established at the onset of the project only. Average monthly rainfall ranged from a low of 12.9 mm in May to a high of 47 mm in June with the values for the remaining months of the study period ranging between 23 mm and 45 mm (Figure 4.8a). Actual evapotranspiration showed a significant increase in the months following the first removal (Figure 4.8b). Soil temperature data (Supplementary Data Figure S4.2) largely tracked the ambient temperature - decreasing from the onset of the experiment in April through to a low in the austral winter (June, July and August) before rising in spring (September and October).

Despite sites being categorized according to land-use history and above-ground vegetation composition, site type did not affect species richness or abundance. This may be related to the soil chemistry which showed no significant differences between degradation levels (Supplementary Data Table S4.2). Similarly, litter type had no effect on species richness and abundance despite the variation in nutrient composition of the three litter types (Supplementary Data Table S4.3). No correlation was found between litter decomposition rate (k) and species richness and abundance (Supplementary Data Figure S4.3).

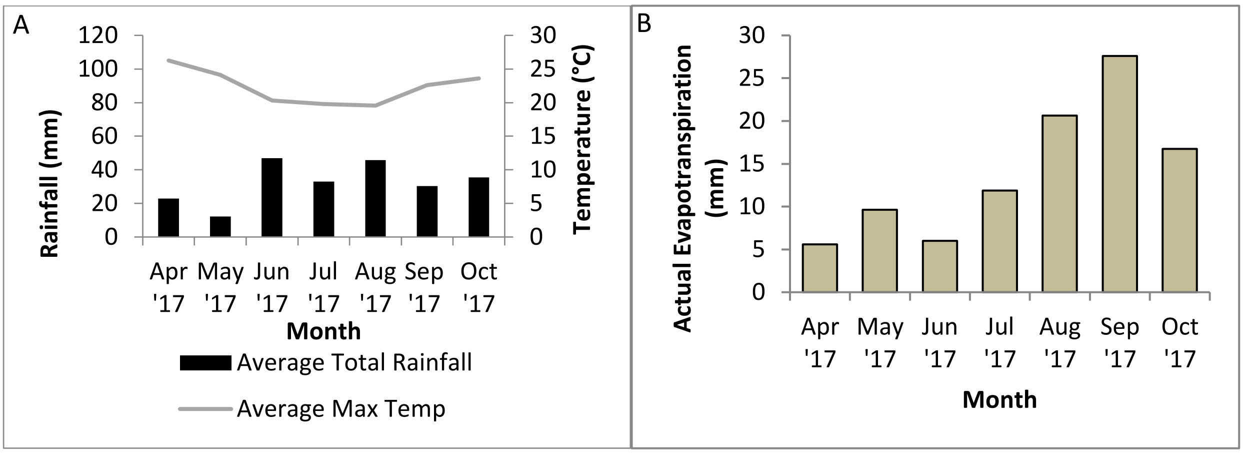

Figure 4.8: Climate data for the study area over the period of study A)**:** Average monthly rainfall and temperature (Data provided by the Agricultural Research Council); B) Actual evapotranspiration levels (Satellite-derived data from MODIS (Running et al., 2017)). Litter traps were placed in ground on April 10th 2017 with sampling occurring after three months on July 18th 2017 and six months on October 25th 2017.

All three litter types lost the largest proportion of its mass during the first three months of the study with a significantly smaller proportion of mass lost thereafter. *Medicago sativa* litter lost a significantly greater proportion of mass (62%) compared to *D. rhinocerotis* (30%) and *P. eriostoma* (20%) after six months (Figure 4.9).

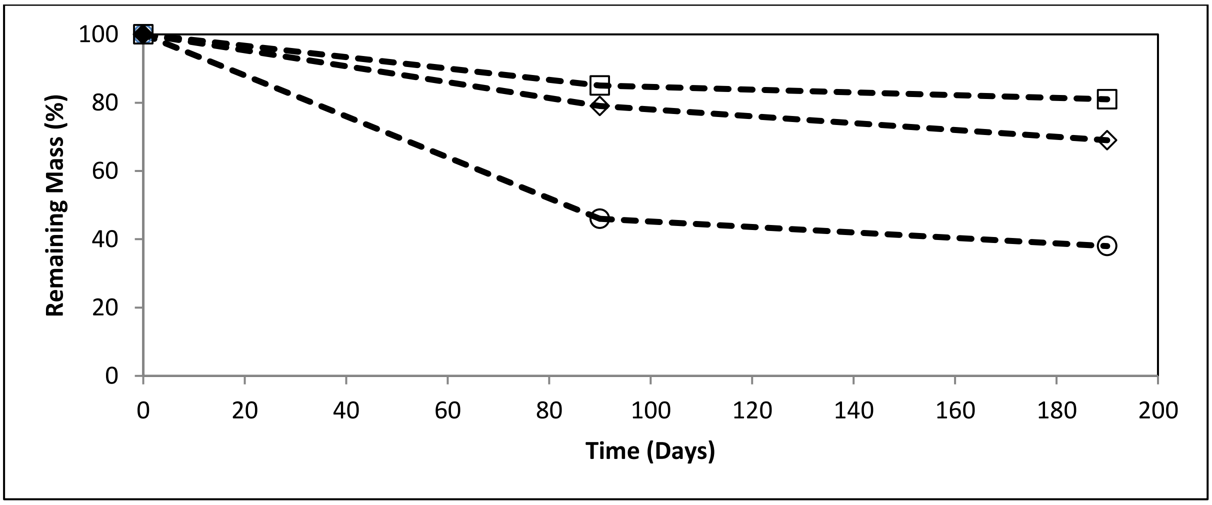

Figure 4.9: Mass loss measured as percentage of remaining litter through time (*P. eriostoma*=squares; *D. rhinocerotis*=diamonds; *Medicago sativa*=circles - data taken from Cowan and Anderson, 2019).

4.4 Discussion

This study provided the opportunity to investigate how landscape factors, such as habitat degradation, and local factors, such as litter type, affect Springtail community composition across a season in a critically endangered vegetation type embedded in an agri-environment matrix in a region of the world often overlooked and under sampled.

4.4.1 Litter Type

As Springtails have been reported to be selective over their food resources (Chen et al., 1995, Filser et al., 2002; Jensen et al., 2006) it was expected that litter type would impact Springtail assemblages. However, litter type had no effect on species richness or abundance and the patterns of community composition were mainly driven by that of removal day. The three litter types varied greatly in initial chemical composition with the alien annual herb *M. sativa* containing significantly higher Nitrogen and Potassium levels compared to *D. rhinocerotis* and *P. eriostoma* (Supplementary Data Table S4.3). In a litter trap experiment in highly fragmented and disturbed Renosterveld, Leinaas et al. (2015) found that litter traps containing litter from the nutrient-rich Yellowbush (*Galenia africana*) contained significantly higher numbers of the invasive Springtail (*Hypogastrura manubrialis*) compared to the litter traps containing less nutrient rich litter. This agrees with the logical assumption that litter of highest nutritional quality would support a higher density of Springtails (e.g. Hertzberg et al., 2000; Salamon et al., 2004; Terauds et al., 2011). Conversely, there have been reports of comparatively lower quality litter supporting more Springtails (Badejo et al., 1998), although this may be attributable to the effect the litter had on reducing soil temperature and increasing soil moisture rather than being attributable solely to litter nutrients. It is a possibility that after three months all three litter types had lost their more labile nutrients or the fungal communities they hosted homogenized. Although nominally similar vegetation types, Leinaas et al.'s (2015) study occurred approximately 250 km away from our study area in a heavily overgrazed and fragmented landscape. *Hypogastrura manubrialis* was not present in the Springtail community in Overberg Renosterveld, at least within Haarwegskloof. In fact, only a small proportion of the total number of Springtails found in this study are invasive species (*E. multifasciata* and *Folsomides* sp. - a total of 437 specimens). Sampling litter traps more frequently would help in determining if the lack of effect of litter type on Springtail abundance and richness is an effect of the ecology of the study area or an artefact of sampling procedure.

4.4.2 Degradation Level

Considering the different land-use histories and resultant variation in contemporary above-ground vegetation composition and structure between site types, it is perhaps surprising that no significant relationship was found between degradation level and Springtail richness or abundance. Janion-Scheepers et al. (2016a) reported differences in Springtail community composition following a fire in two sites with different dominant above-ground Fynbos vegetation, while Leinaas et al. (2015) postulated that Springtail assemblages in Renosterveld are significantly affected by differential litter input resulting from above-ground vegetation dynamics. The impact of vegetation structure – often as a result of degradation or land management policy - on Springtail assemblages has been documented elsewhere. For example, in Nigeria, agroforestry tree stands contained more Springtails than secondary forest and grass plots (Badejo et al. 1998), while similar trends were reported in old growth temperate forests compared to regenerating forest in Canada (Addison et al. 2003a), managed and natural forests in the Pyrenees (Cassagne et al. 2006), and an agroforestry landscape in France (Heiniger et al. 2014). In agricultural landscapes in the United States (Barbercheck et al. 2009) and Argentina (Bedano et al. 2006) disturbance was found to reduce Springtail richness and abundance.

Conversely, degradation has also resulted in an increase in Springtail abundance in certain circumstances such as Garlic Mustard (*Alliaria petiolata*)-invaded pine forest in the United States (Alerding and Hunter 2013) and overgrazed Renosterveld in South Africa (Leinaas et al. 2015). It should be noted that in both these cases the increased abundance was a result of a population expansion of one or two species only and in the latter case the Springtail responsible was itself an alien species.

Although there was no overall significant effect of degradation on Springtail abundance, the impact on *Entomobrya multifasciata* numbers is worthy of elucidation. One of only two non-indigenous species found in the study, *E. multifasciata* was abundant in the moderately degraded and highly degraded sites yet almost absent in the pristine sites. The species, probably introduced accidently during historical agricultural activity, appears well adapted to degraded land often dominating assemblages within arable croplands (Frampton, 2002), increasing with sheep density (King et al., 1976), and resistant to desiccation (Davies, 1928). The discord between the abundance of *E. multifasciata* in pristine and degraded sites suggests it may have the potential to act as a bioindicator in Renosterveld for land that has previously been farmed previously, a role previously suggested as suitable for the species in European agricultural lands (Frampton and van den Brink, 2007).

The general lack of impact on Springtail assemblages caused by habitat disturbance recorded in this study is not completely unprecedented as studies into landscape level factors influencing Springtail communities such as different wheat farming strategies (Alvarez et al., 2001) and forest management intensities (Pollierer and Scheu, 2017) found little to no effect on Springtail diversity and abundance, despite these parameters influencing litter input. Springtails occupy a continuum of trophic positions from herbivores, to primary and secondary decomposers (Chahartaghi et al., 2005), and predators (Heidemann et al., 2014). Landscape factors such as degradation are often complex and may alter biotic controls in a variety of ways thus changes to litter input would directly affect herbivorous Springtails, particularly if they are specialist feeders, and indirectly affect fungivorous Springtails as litter properties influence fungal communities (Beare et al., 1992). Predatory Springtails may also be affected by shifting prey abundances if the prey is affected by litter input.

Abiotic factors such as soil chemistry, soil temperature and moisture can also exert strong effects on Springtail communities (Loranger et al., 2001; Petersen, 2011) with niche compatibility varying between species (Makkonen et al., 2011). Abiotic factors can be directly affected by habitat degradation (e.g. fertilization (Zhou et al., 2014)) or indirectly through changes in above-ground vegetation which may in turn change soil chemistry, moisture and temperature (Yelenik et al., 2004). In our study, despite distinct land-use histories and current above-ground vegetation communities, no significant differences existed in soil chemistry across degradation level (Supplementary Data Table S4.2). While the limited replication may have influenced the statistical analysis (n=2 for each site type), the similarities in soil across sites may be a result of uncertainty surrounding the sites' land-use histories. Historical aerial photographs provide an idea of when natural vegetation was converted to agricultural land (and *vice versa*) but a lack or archived data makes it near impossible to know precisely the types and intensity of agricultural activity which occurred. Crop type, fertilizer application, ploughing and grazing intensity would all have different effect on abiotic conditions (Snapp et al., 2010; Jangid et al., 2011). Soil temperature values varied between sites but not consistently between degradation levels (Supplementary Data Figure S4.2) and were likely the result of differences in microhabitat. The similarities in soil chemistry between sites and the lack of significant differences between Springtail communities, despite the differences in above ground vegetation, suggests that in this study area, abiotic conditions rather than biotic controls through differential litter input govern Springtail diversity and abundance. To test this conclusion it would be illuminating to replicate this study following an *a priori* soil analysis to select sites with differing soil chemistries.

4.4.3 Temporal Changes

Litter traps removed after three months had significantly increased species richness and overall abundance compared to those traps removed after six months. Litter mass and quality for all litter types declined through time with the majority of the loss occurring in the first three months and the rate of decomposition slowing significantly thereafter. Thus, the greater amount and quality of food directly available to herbivorous Springtails and indirectly available to microbial-feeding Springtails at three months may explain the higher diversity and abundance observed. A similar trend was observed in degraded Renosterveld where litter traps removed after four months contained higher abundances of Springtails compared to traps removed after six months (Leinaas et al., 2015).

As previously discussed, abiotic factors also exert strong controls on Springtails and they may change through time. Soil chemistry was not measured through the study period following the initial recording however climate data was available and showed certain trends which may have affected Springtail community dynamics. The study area has year-round rainfall; however the temperatures are distinctly Mediterranean with hot summers and cool winters. During the study period the first removal of litter traps after three months coincided with significantly colder temperatures (July) compared to the second removal after six months (October). Although months when removals occurred had similar mean levels of precipitation, the week prior to removal of litter traps in October was rain-free whereas a rain event occurred three days prior to the first removal in July (Pers. Obs.). Additionally, the month prior to the first removal (June) had an actual evapotranspiration rate of nearly a fifth of that recorded in the month prior to the second removal (September). Springtail abundance and richness have been shown to be positively correlated with soil moisture (Makkonen et al., 2011) due to their soft bodies and the difference in environmental conditions prior to the two removal days may have affected Springtail numbers. Establishing the relative importance of litter quality and quantity, and abiotic conditions is a logical next step in understanding the controlling factors on Springtail abundance and species richness.

4.4.4 Community Composition

Community composition can be more sensitive to disturbance than abundance or calculated diversity (Pietikäinen et al., 2003), however in this study neither the ordination nor ANOSIM results revealed a relationship between degradation level and community composition. Like the lack of relationship between degradation level and Springtail abundance and richness, this may be due to the similarity in soil chemistry across the landscape which may exert a stronger control than changes in litter input from distinct above-ground vegetation communities. Conversely, community composition was affected by litter type, with *D. rhinocerotis* associated with *Seira* sp. 3, *Setanodosa* sp. and *Symphypleona* sp. 1 and *M. sativa* correlating most strongly with *E. multifasciata*, *Pseudosinella* sp. and *Symphypleona* sp. 2. Springtail species showing a preference is for litter type is not uncommon (Chahartaghi et al., 2005) and may be a result of herbivorous species exploiting different litter types directly or microbial-feeding species gravitating to litter which supports fungi suitable for their dietary preference. For example, the nutrient rich and more labile *M. sativa* may provide substrate for a different microbial community to the hardier and nutrient-poor *D. rhinocerotis* litter.

Sampling day had a strong effect on community composition however the effect was not consistent across all species with *Seira* sp. 3, *E. multifasciata*., *Brachystomella* sp. and *Pseudosinella* sp. all with a larger mean abundance in litter traps removed after six months (as opposed to the remaining 22 species which had greater mean abundances after three months). ANOSIM results showed *Seira* sp. 3 and *E. multifasciata* to be significantly correlated to litter traps removed after six month whereas *Tullbergia* sp., *Parisotoma* sp., *Seira* sp. 1, *Sminthurinus* sp. 1 and *Symphypleona* sp. 1 were correlated to litter traps removed after three months. Both *Seira* sp. 3 and *E. multifasciata* are relatively large, atmobiotic species with large antenna-to-body ratios which suggests these traits give them a competitive advantage as litter decomposition progresses. The two species may also possess hitherto unmeasured traits allowing them to utilise the less labile litter contents available after six months or the associated shift in microbial communities. Alternatively, size may potentially result in a reduced dispersal ability which prevents them from escaping the litter traps as litter is reduced in quality and quantity.

There is also a possibility that environmental factors are influencing community composition. *Seira* sp. 3 and *E. multifasciata* may possess traits which allow them to survive in drier conditions. Makkonen et al. (2011) found that drought tolerance was correlated to larger body size in sub-Arctic Springtail communities and Davies (1928) reported *E. multifasciata* to be relatively resistant to experimental desiccation. As previously discussed, the month preceding the removal of litter traps after six months had higher actual evapotranspiration rates and the week prior to removal was rain-free. Morphological trait differences between species allows for niche differentiation and it is possible that *Seira* sp. 3 and *E. multifasciata* possess traits – such as their large body size - which allow them to flourish in drier conditions. Determining the precise mechanism controlling the community dynamics observed in this study would require thermalphysiological experiments and gut content analysis of Springtail species.

4.4.5 Conclusion

This was the first study in pristine, critically endangered Renosterveld vegetation and adds to the steadily increasing body of work on the ecological significance of Springtails in Southern Africa and imparts some important findings while highlighting potential departure points for future work. The absence of *H. manubrialis* from this study despite prevalent habitat disturbance in the study area is a positive and may indicate the robustness of the biotic soil community. More generally, the lack of effect of habitat degradation on Springtail richness, abundance and community composition can be cautiously interpreted similarly; however we recommend further research across sites with known differences in soil chemistry. Despite the overall lack of effect on degradation on Springtail community dynamics, the abundance of the non-indigenous *E. multifasciata* in degraded sites, and its absence from pristine sites, may make it a suitable bioindicator for habitat disturbance. The significant effect of litter type on community composition, and of sampling day on species richness, abundance and community composition, are indicative of dynamic Springtail communities. We recommend combining further field experiments with controlled laboratory experiments to test gut content, feeding preferences and response to changes in climatic conditions across multiple species. In general, improving our knowledge of the functional roles of different Springtail species is an important next step in understanding their ecological role and how environmental change may impact on soil communities and subsequent ecosystem services.

4.5 Acknowledgements

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4.7 Supplementary Data

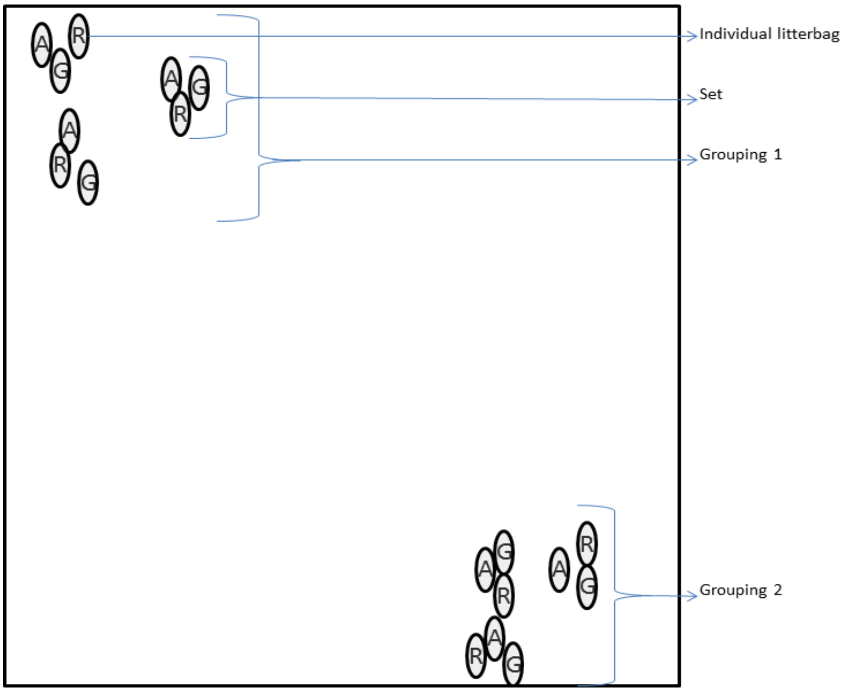

Figure S4.1: Study site example (Each set contains: A=individual *Medicago* litterbag; G=individual *P. eriostoma* litterbag; R=individual *D. rhinocerotis* litterbag). Three sets per grouping; two groupings per site.

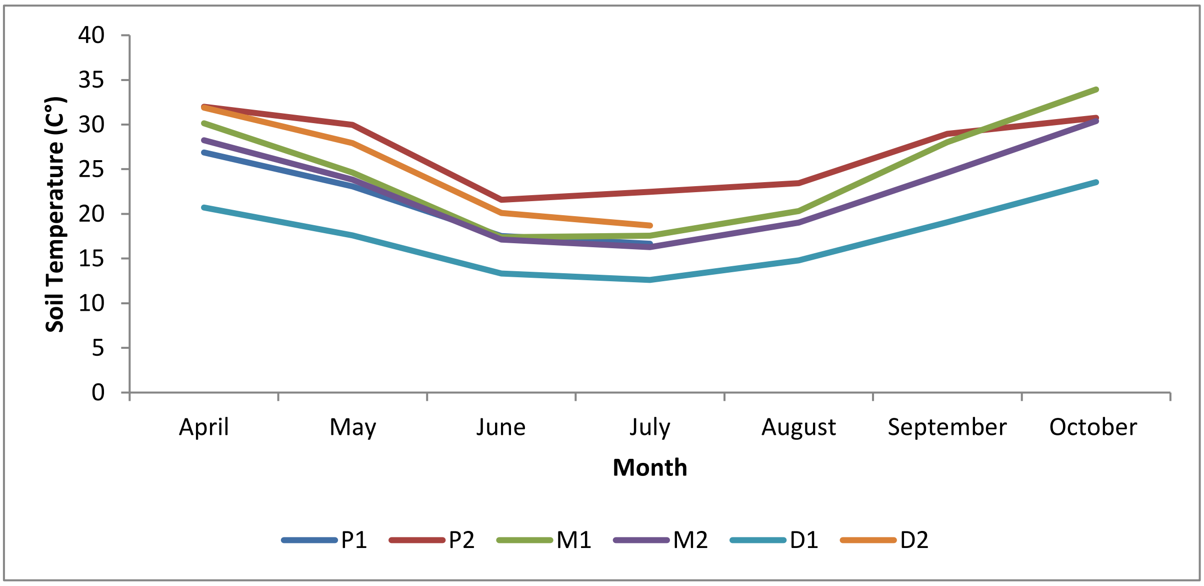

Figure S4.2: Average monthly soil temperatures recorded daily at 15:45pm for subsamples of litter traps at each study site (P=Pristine; M=Moderately Degraded; D=Highly Degraded). *note* equipment error resulted in no data for the final three months for sites P1 and D2.

Table S4.1: Total abundance, mean abundance at three and six months, and functional trait values for all Springtail species recorded in the study

	Total Abundance	**Mean Abundance at 3 months**	**Mean Abundance at 6 months**	**Body Length (mm)**	**Antenna to Body Ratio**	**Life Form**
Setanodosa sp.	7	4	0	3	0.1	Unknown
Brachystomella sp.	25	2	2	0.8	0.12	Hemiedaphic
Pseudachorutinae sp.	3	3	0	3	0.1	Hemiedaphic
Pseudachorutes sp.	7	2	1	1.5	0.12	Hemiedaphic
Tullbergia sp.	255	20	3	0.75	0.09	Euedaphic
Xenylla sp.	15	4	3	0.5	0.12	Hemiedaphic
Odontellidae sp.	19	8	0	1.2	0.18	Hemiedaphic
Cryptopygus sp. 1	9	5	0	1	0.2	Hemiedaphic
Cryptopygus sp. 2	20	6	2	1.3	0.23	Hemiedaphic
Cryptopygus sp. 3	12	4	3	0.8	0.2	Hemiedaphic
Cryptopygus sp. 4	8	0	3	0.6	0.18	Hemiedaphic
Folsomides sp.	2	1	0	0.6	0.2	Euedaphic
Parisotoma sp.	111	20	3	1	0.2	Hemiedaphic
Seira sp. 1	185	21	17	1.2	0.2	Atmobiotic
Seira sp. 2	52	4	10	1.9	0.4	Atmobiotic
Seira sp. 3	272	6	53	2.1	0.46	Atmobiotic
Seira sp. 4	13	1	1	1.8	0.4	Atmobiotic
Entomobrya multifasciata	435	13	42	1.3	0.4	Atmobiotic
Pseudosinella sp.	38	0	7	0.5	0.19	Hemiedaphic
Sinella sp.	1	1	0	1.1	0.4	Hemiedaphic
Sminthurinus sp. 1	97	19	3	1	0.35	Atmobiotic
Sminthurinus sp. 2	44	11	7	0.5	0.45	Atmobiotic
Katiannidae sp.	7	4	3	0.8	0.8	Atmobiotic
Symphypleona sp. 1	1190	27	22	0.3	0.25	Atmobiotic
Symphypleona sp. 2	10	3	4	0.6	0.25	Atmobiotic
Symphypleona sp. 3	1	1	0	0.5	0.25	Atmobiotic

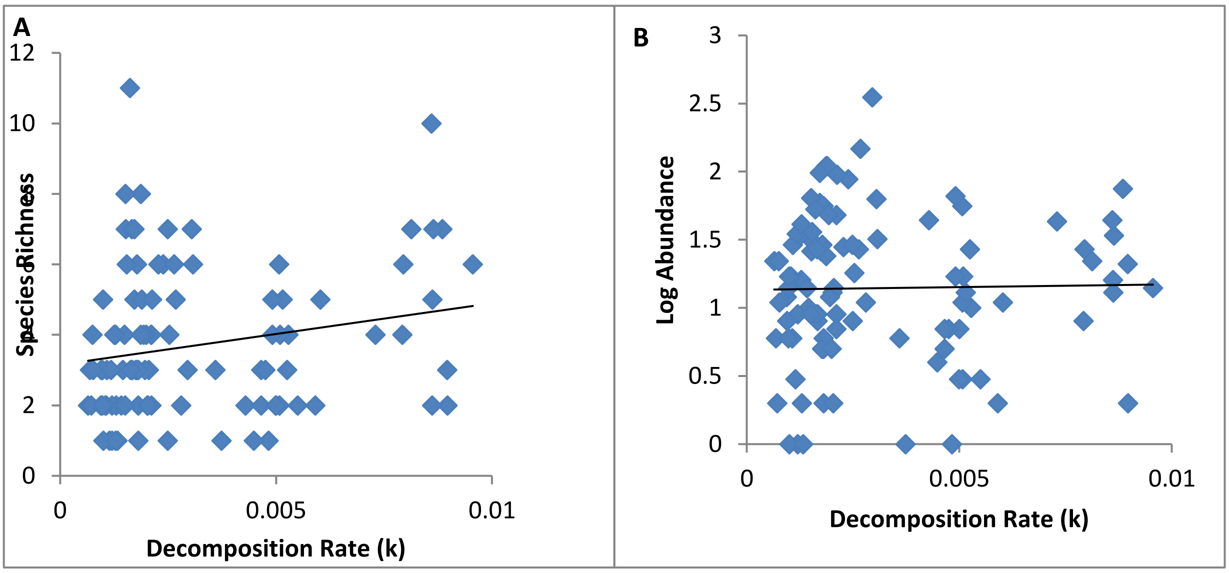

Figure S4.3: Relationship between decomposition rate (k) and A) Species Richness, and B) Log Abundance. Regression lines: A) y = 174.4x + 3.1517; r^2-0.0415 B) y = 4.0377x + 1.1322; r^2-0.0003 (Decomposition rates taken from Cowan and Anderson (2019)).

Table S4.2: Mean soil chemical and physical properties across site types. Standard deviations given in brackets. (x=exchangeable cations; *= significant at p < 0.05).

	Pristine	**Moderate**	**Degraded**
Soil	Loam	Loam	Loam
pH	4.7 (0.10)	4.9 (0.10)	5.2 (0.35)
Resistance	370 (270)	595 (375)	330 (190)
H+	1.69 (0.26)	1.11 (0.20)	0.90 (0.10)
Stones	28.50 (5.5)	29 (5)	32.50 (0.50)
Phosphorus	17.50 (1.5)	44 (12)	96.50 (74.50)
Potassium	236.50 (5.5)	185.50 (22.5)	330.50 (29.50)*
xSodium	2.79 (2.41)	0.58 (0.36)	1.29 (0.73)
xPotassium	0.60 (0.01)	0.47 (0.05)	0.84 (0.07)
xCalcium	4.72 (0.77)	4.89 (0.82)	6.76 (2.57)
xMagnesium	4.15 (0.58)	2.49 (0.69)	4.48 (1.63)
Carbon(%)	4.30 (0.11)	3.16 (0.45)	3.43 (0.99)
Soluble Sulphur	114.51 (92.44)	45.32 (25.25)	210.42 (188.20)
Cation Exchange Capacity	9.18 (0.58)	10.37 (0.67)	11.34 (3.20)
CLAY(%)	15 (3)	23 (7)	26 (2)
SILT(%)	18 (8)	24 (0)	27 (1)
SAND(%)	67 (11)	53 (7)	47 (3)
Waterholding Capacity	97.22 (10.11)	84.99 (0.40)	80.53 (1.43)

Table S4.3: Mean initial (t=0) and final (t=187 days) nutrient values of the three litter types. Standard deviations given in brackets. (Data taken from Cowan and Anderson (2019)).

	D. rhinocerotis		***P.eriostoma***		***M. sativa***	
	Initial	**Final**	**Initial**	**Final**	**Initial**	**Final**
N	1.05 (0.04)	1.13 (0.14)	0.54 (0.08)	0.56 (0.05)	3.21 (0.35)	2.27 (0.47)
P	0.15 (0.01)	0.10 (0.02)	0.02 (0.00)	0.03 (0.01)	0.23 (0.02)	0.28 (0.08)
K	0.70 (0.02)	0.30 (0.11)	0.05 (0.01)	0.07 (0.04)	2.21 (0.10)	0.26 (0.23)
Ca	0.35 (0.02)	0.45 (0.04)	0.03 (0.02)	0.14 (0.01)	1.06 (0.11)	1.29 (0.28)
Mg	0.22 (0.01)	0.23 (0.02)	0.04 (0.00)	0.11 (0.06)	0.26 (0.02)	0.24 (0.07)
Na	3180 (93)	1262 (480)	961 (118)	286 (140)	1625 (82)	313 (151)
Mn	21.40 (0.71)	60 (13.56)	8 (2.00)	49.3 (36.40)	30.80 (5.40)	92.2 (36.55)
Fe	387 (43)	9354 (3827)	515 (206)	17916 (17051)	305 (173)	15696 (10008)
Cu	6 (0.45)	8 (1.55)	1.80 (0.45)	4.50 (2.07)	6.40 (0.55)	8 (1.41)
Zn	20.80 (1.64)	52.83 (7.36)	5.80 (1.79)	47.50 (7.04)	18.80 (2.17)	80.33(22.96)
B	49.20 (1.14)	37.33 (3.27)	4.80 (0.84)	6.67 (1.75)	36.60 (4.04)	19.50 (6.47)

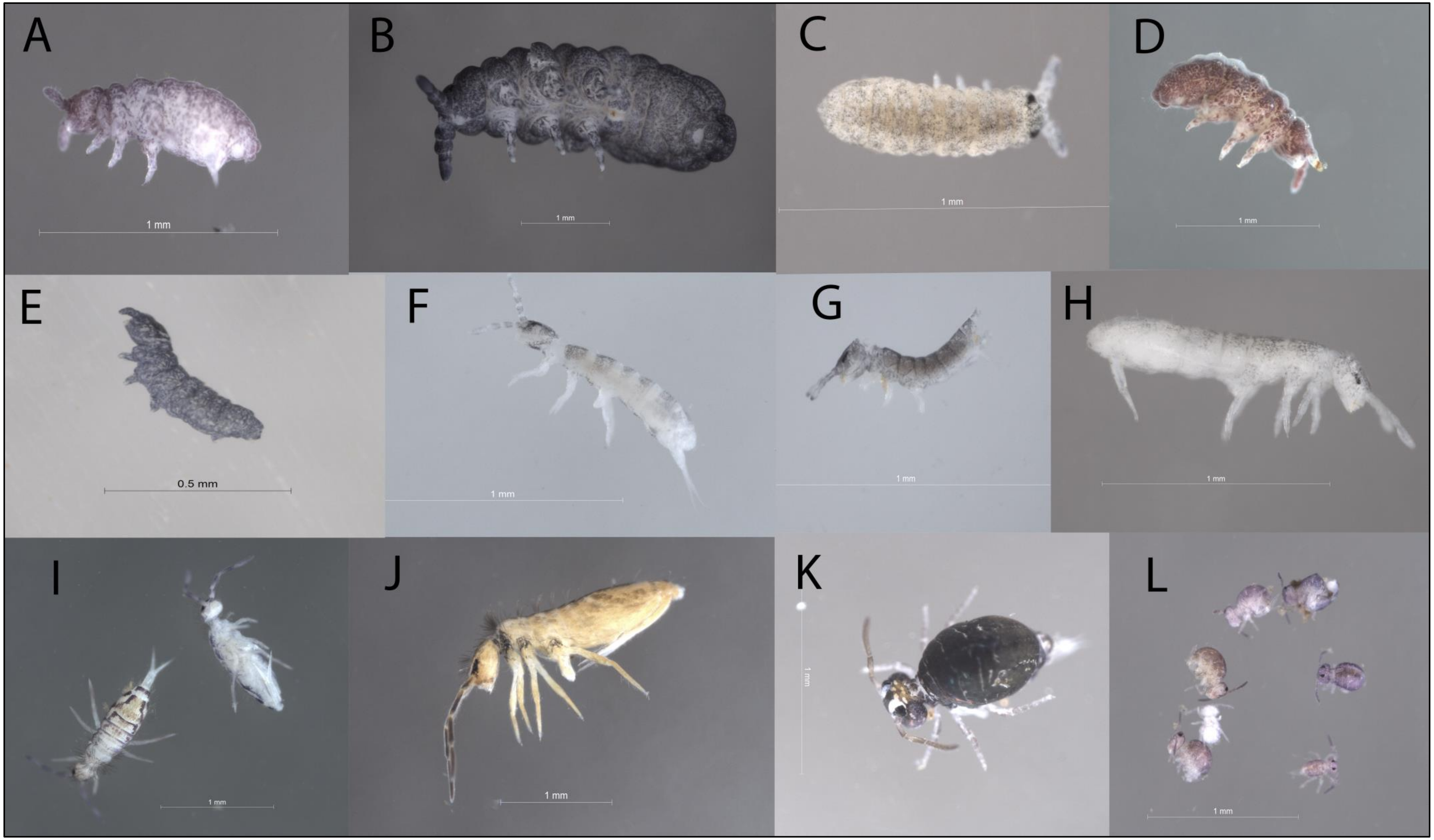

Figure S4.4: Examples of Springtails found in this study from the Order Poduromorpha: A) *Brachstomella* sp., (B) Pseudachorutinae sp., (C) *Odontella* sp., (D) *Setanodosa* sp., (E) *Xenylla* sp., Order Entomobryomorpha: (F) *Parisotoma* sp., (G, H) *Cryptopygus* spp., (I) *Entomobrya multifasciata*, (J) *Seira* sp., Order Symphypleona: (K) Katiannidae sp. and (L) *Sphaeridia* sp. [As seen through a Leica DM4B microscope].

Chapter 5

Three complete plant-pollinator networks along a degradation gradient in critically endangered Renosterveld, South Africa


Martin Heigan

Three complete plant-pollinator networks along a degradation gradient in critically endangered Renosterveld, South Africa

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Abstract

Despite the global recognition of the importance of pollination as an ecosystem function, there remains a dearth of community level studies on the African continent. Here we present three complete pollination networks, along a secondary successional gradient, in critically endangered Renosterveld vegetation within an agri-environment, South Africa. Site selection was based on historical land-use and contemporary vegetation data resulting in a pristine site, a moderately degraded site where agriculture was halted >15 years ago, and a highly degraded site where agriculture was halted <five years ago. In total, 240 hours of pollinator-plant observations were recorded over a single flowering season. The pristine site was highly specialised in comparison to global datasets – most likely as a result of relative climatic stability through the Quaternary which allowed specialisation to manifest and persist. Both non-pristine sites showed noticeable differences in characteristics when expressed through network indices; however, the highly degraded site was closer in nature to the pristine site as a result of vegetation structure. Notwithstanding a lack of replication across the degradation gradient precluding robust statistical analyses, this study provides important data which allows for the comparison of pollination dynamics in an understudied and vulnerable vegetation type, to plant-pollinator networks at the global and regional scale. In addition, apparent changes to network indices as a result of habitat alteration, suggest that successional trajectory following degradation plays an important role in pollination dynamics.

5.1 Introduction

Global insect populations are in peril due in part to intensive agriculture and habitat degradation (IPBES, 2016; Sanchez-Bayo and Wyckhuys, 2019). The potentially catastrophic effects on key ecosystem functions such as pollination (Kevan and Viana 2003; Brown and Paxton 2009; Potts et al., 2010) will not only have dire ecological implications (Vanbergen et al., 2013) but huge economic consequences (Costanza et al., 1997; Gallai et al., 2009). Yet the drivers influencing insect populations and pollination that relate to habitat change remain poorly understood at the community and landscape level (Hallmann et al., 2017; Redhead et al., 2018), and in many instances, particularly on the African continent, remain undescribed (Vizenti-Bugani et al., 2018).

Fuelled largely by developments in complex network analysis (Proulx et al., 2005), an increasingly popular way of assessing pollination functioning is through pollination network analysis (Bascompte, 2009; Vizentin-Bugoni et al., 2018). Community pollination networks can be defined both visually, in the form of quantitative flower visitation webs, and numerically through indices which describe network properties (Dormann et al., 2009). Pollination networks across diverse habitats, species assemblages, and time have shown similar structural properties (Jordano et al., 2003; Vazquez et al., 2009). Networks tend to exhibit low connectance (i.e. only a small fraction of possible interactions are observed), are nested (i.e. specialist species predominantly interact with a core group of generalist species), and species are significantly more specialized than expected given the availability of potential mutualistic partners (Jordano et al., 2003, Blüthgen et al., 2008, Dupont et al., 2009). Indices calculated from qualitative interactions, while useful (Jordano, 1987), tend to be less sensitive to change than quantitative indices which take into account the frequency of pollinator-plant interaction and thus are better suited for revealing changes to network structure and are more robust to sampling effects (Blüthgen et al., 2008, Almeida-Neto and Ulrich, 2011). Despite a need for caution when using network indices to interpret biologically meaningful patterns due to the effect sampling limitations can impart on analyses (Blüthgen, 2010; Chacoff et al., 2012), pollination network analysis has been successfully used to identify and assess factors influencing biodiversity maintenance (Bascompte et al., 2006; Albrecht et al., 2010; Valdovinos et al., 2013), to predict consequences of disturbances such as extinction (Memmott et al., 2004; Kaiser-Bunbury et al., 2010; Saavedra et al., 2011), inform the restoration of degraded ecosystems (Menz et al., 2011; Kaiser-Bunbury et al., 2017), and establish the impact alien species have in disturbed ecosystems (Bartomeus et al., 2008; Valdovinos et al., 2009).

Abandonment of agricultural land for economic or ecological reasons is common practice in contemporary times (Villa-Galaviz et al., 2012). During the secondary succession which follows the cessation of the initial disturbance, environmental variability influences pollinator population dynamics (Steffan-Dewenter and Tscharntke, 2001) and plant community structure (Garnier et al., 2004). However, the subsequent changes in interaction networks at the community level such as pollination are poorly understood (Albrecht et al., 2010) and may be affected by land-use history and ecological drivers such as fire regime (Potts et al., 2003; Brown et al., 2017) or grazing intensity (Vanbergen et al., 2014). A change in habitat as a result of environmental degradation and subsequent secondary succession can alter the structure of pollination networks, and thus network indices, through changes in species richness and the functional composition of the community (Tylianakis et al., 2007). For example, higher values of nestedness reflect the prevalence of specialist species that predominantly interact with a core group of generalist species (Grass et al., 2018). However, nestedness changes with the number of interacting species e.g. a loss of rare species which interact with abundant generalists would reduce nestedness (Spiesman and Inouye, 2013). Shifts in functional composition, such as floral size thresholds (Stang et al., 2009), may further modify community nestedness as the number of possible interactions are altered (Vazquez et al., 2009). Similarly, specialization indices may change following the removal or influx of certain species. For example, homogenization of above-ground vegetation alters the spectrum of resources available to pollinators which may lead to local extinction or re-wiring of the network (Kaiser-Bunbury et al., 2010; CaraDonna et al., 2017). It is clear that any shifts in the number of interacting species or the functional composition of a community caused by habitat alteration, either through natural succession, restoration or habitat degradation, can have cascading effects on network structure and ecosystem functioning (Albrecht et al., 2010; Ferreira et al., 2013; Vanbergen et al., 2014; Ponisio et al., 2017). Understanding how these shifts occur and what impact they have on network properties can provide important information towards understanding the underlying ecological processes (MacFadyen et al., 2009; Vanbergen et al., 2017) and is a powerful tool in conservation (Devoto et al., 2012; Kaizer-Bunbury and Blüthgen, 2015).

Renosterveld is an ecologically distinct vegetation type within the Cape Floristic Region of South Africa (Bergh et al., 2014). Only 10% of the original extent remains due to intensive agricultural conversion (Newton and Knight, 2005) with critical endangered remnant fragments of natural vegetation found embedded within an agricultural matrix (Kemper et al., 1999). Differences in historical land-use and current management practices has resulted in patches of natural vegetation occurring side-by-side along a degradation gradient from pristine vegetation to old fields in various stages of secondary succession (Heelemann et al., 2013; Cowan and Anderson, 2014; Ruwanza, 2017). The ecological workings of Renosterveld remain understudied (Curtis, 2013) and there is a dearth of community-level pollination network analyses and pollination studies in general (but see

Donaldson et al., 2002; Pauw, 2007; Kehinde and Samways, 2014; Pauw and Hawkins, 2011). To our knowledge, only one comprehensive study exists from neighbouring pristine Fynbos (Pauw and Stanway, 2015). Notably, Pauw and Stanway (2015) reported globally unrivalled functional specialization in their study, attributing it to the long-term climatic stability in the region which they argue allowed phenotypic and functional specialization to manifest and persist. Renosterveld has similar floral diversity levels to that of Fynbos (Bergh et al., 2014) but due to its comparatively fertile underlying soils has undergone significantly greater agricultural transformation (Kemper et al., 1999) with the relevance of this transformation largely untested on ecological functioning.

Here, for the first time, we present three fully quantitative pollination networks along a degradation gradient from recently abandoned agricultural land to pristine Renosterveld and ask the following questions. (1) What are the characteristics of these plant-pollinator networks when expressed through network indices?, (2) Are the indices of the studied networks similar to the indices of a published pollination network in adjacent Fynbos vegetation?, (3) How do the indices of the studied networks compare to the indices of pollination networks published globally?, (4) How is the degree of habitat alteration as a result of initial degradation and subsequent secondary successional vegetation shifts related to (a) the richness, evenness and diversity of species and interactions?, and (b) the degree of interaction network-level, and species-level, specialization?

5.2 Materials And Methods

5.2.1 Study Area, Site Selection And Vegetation Characteristics

Haarwegskloof Nature Reserve (34°20’17.9”S; 20°19’34.1”E) is situated within the Overberg lowlands of the Western Cape Province of South Africa (Figure 5.1). Renosterveld, the indigenous vegetation of the Overberg region, is classified as critically endangered (Rebelo et al., 2006) with less than 10% of the original extent remaining (Curtis, 2013). The vegetation type exists as fragmented islands within an agricultural matrix of privately owned land (Kemper et al., 1999) and the cover is predominantly grain fields (wheat, barley, oats, canola) and artificial pasture (lucerne/alfalfa) (Curtis et al., 2013).

The reserve itself is situated within the Eastern Rûens Shale Renosterveld and was purchased by the WWF-SA and the Overberg Renosterveld Conservation Trust in 2013. It consists of approximately 500 hectares of land, purportedly 80% of which is virgin Renosterveld while the remaining area is old lands of varying age, portions of which may have been previously ploughed and/or used as grazing pasture. Eastern Rûens Shale Renosterveld has an altitudinal range of 40-320 m.a.s.l. and an average rainfall of 384 mm per annum with an essentially even distribution (Rebelo et al., 2006, Curtis et al., 2013).

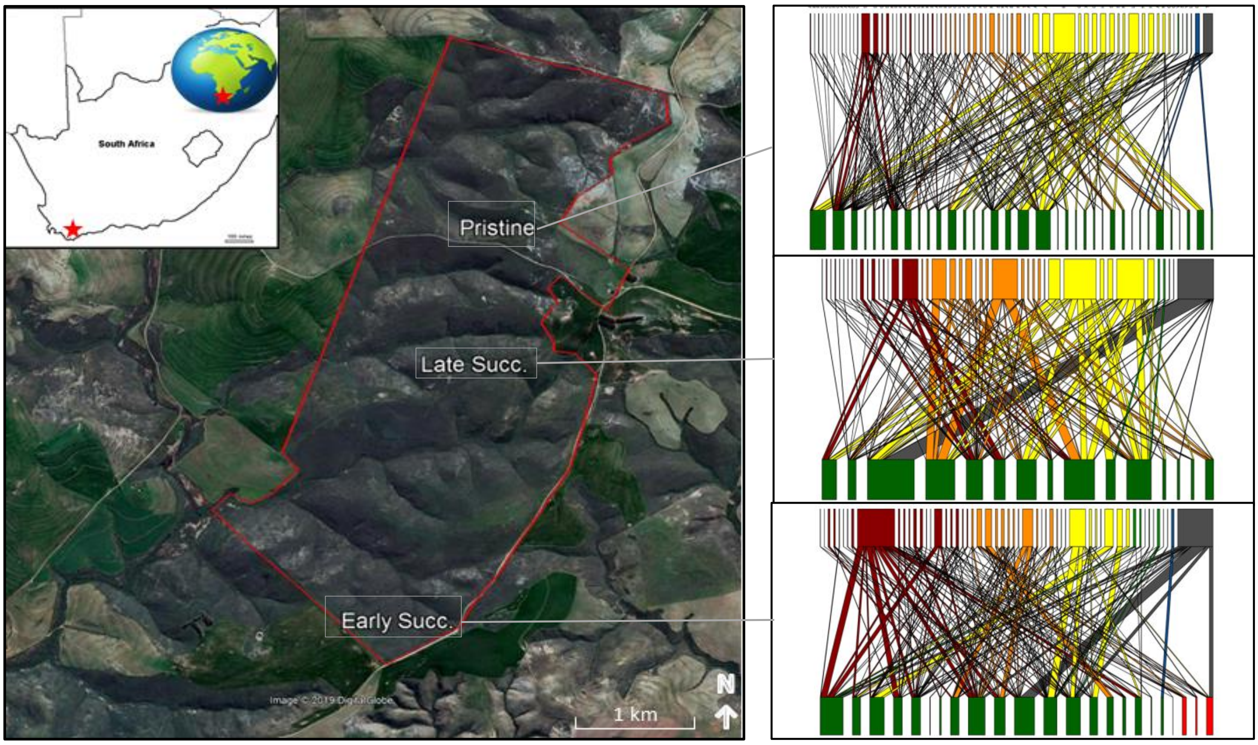

Figure 5.1: Study area showing the three study sites within Haarwegskloof Reserve (red polygon) and their associated quantitative plant-pollinator networks. Late Succ. refers to the moderately degraded site and Early Succ. refers to the highly degraded site. Pollinators are shown as rectangles at the top (Red=Coleoptera, Orange=Diptera, Yellow=Hymenoptera, Green=Lepidoptera, Blue=Avis, Grey=Thysanoptera) and plants as rectangles at the bottom (red rectangles depict alien plant species). Detailed networks with species names are supplied as Supplementary Data Figure S5.1.

Mean daily temperatures range from a 5.9°C minimum in July to a 26.9°C maximum in January (Rebelo et al., 2006). Natural Eastern Rûens Shale Renosterveld occurs on moderately undulating hills and plains which support a cupressoid and small-leaved, low to moderately high grassy shrubland (Rebelo et al., 2006). Historical aerial photograph analysis, combined with expert local knowledge, was utilised to select three sites situated along a degradation gradient: pristine vegetation, a site where agriculture ceased approximately 15 years ago, and a site where agricultural activities ceased less than five years ago. At each site vegetation sampling and abundance was conducted using the modified Whittaker nested vegetation sampling method (Stohlgren et al., 1995). With the aid of expert knowledge and herbarium records over 80% of the species encountered were identified to species level and over 90% to genus level. Thus we worked in three study sites of 1000 m^2: Pristine – characterised by high species richness, the absence of alien species and no evidence of historical agriculture; Moderately Degraded – characterised by moderate to low diversity, dominance of shrub species and evidence of historical agricultural use; and Highly Degraded – characterized by moderate to low diversity, high alien species cover and evidence of recent agricultural use. According to management records of the reserve and personal observation, none of the sites had experienced a fire event, a natural disturbance within Renosterveld, within the last ten years. The moderately degraded site was situated 1 km from the pristine site with the highly degraded site a further 1.8 km away. Each study site had a buffer zone (> 250 m) of vegetation of similar composition and structure to the site in question with the exception of the highly degraded site which was abutted by a wheat field on one side.

Using the literature, each plant species recorded during sampling was assigned a growth form under the categories: Hemiparasite; Semi Basal; Short Basal; Short Succulent; Climbers and Scramblers; Tussock; Erect Leafy; Dwarf Shrub (<0.8m); Shrub (> .8m); Trees (sensu Cornelissen et al., 2007). While no causal relationship is inferred in this study between growth form and pollination, the data was used to assess differences in vegetation structure between sites which in turn can affect pollinator communities (Ferreira et al., 2013).

Each plant species had its flower colour assigned to one of seven categories based on direct observation: Red; Orange; Green/Yellow/Cream; Rose; Yellow; White; Blue/Purple/Lilac. Where flowers consisted of more than one category the dominant category was chosen. The exact role of flower colour, particularly how it is perceived by humans and its relative importance to different pollinator guilds, has been debated in pollination biology (Vorobyev and Brandt, 1997; Arnold et al., 2009; Bukovác et al., 2017); however here we use it as an additional tool for assessing differences in vegetation characteristics between study sites and no further assumptions are made on its impact on pollinator communities.

5.2.2 Pollinator Observations

Pollinator-plant interaction observations were undertaken during the austral spring (August-November) of 2016, the peak flowering season in Renosterveld, with methods adapted from Pauw and Stanway (2015). Observations were carried out during clear, warm, relatively wind-free days between 8am and 5pm during the first two weeks of August, September, October and November. Flowering plant species were initially selected at random and observed in 30 minute periods. Subsequently, species were selected so that each species at each site was observed at least twice during a morning observation session (8-12am) and twice in an afternoon observation session (12-5pm) for a minimum total observation period of 2 hrs per species per site. All three sites were observed during each two week block, alternating each site between morning and afternoon observation periods to ensure equal coverage (approximately four morning and four afternoon sessions at each site per two week block). In total 240 hours of observations were recorded across all three sites. On some occasions, plant species occurring close together were observed simultaneously. Observations typically occurred from between two and five metres away from the plant(s) whereas birds were observed from a distance of >10 m with the use of binoculars. During each observation period, flower visitors were identified and each individual flower visit recorded. Where possible, only visitors that made contact with flower reproductive organs were recorded and composite inflorescences were treated as single flowers. Pollination activity was expressed as visits.flower^{-1}.hour^{-1}. At the first observation of an unidentified pollinator species, the insect was caught and included in a reference collection to aid species identification. Whenever possible, pollinators were caught outside of the observation period. Invertebrate pollinators were killed humanely, stored in ethanol, and identified to lowest taxonomic level possible using the collections at the South African Museum, Cape Town.

Similarly to Pauw and Stanway (2015), we took a plant-centric approach where each flowering plant present received equal sampling effort rather than a “representative” transect approach which would have under-sampled species due to the heterogeneous landscape (Gibson et al., 2011).

5.2.3 Data Analysis

Plant growth form and flower colour data were used in conjunction with vegetation cover data to construct figures illustrating a) the proportional cover of growth forms at each site and b) the proportion of flower colours present in spring-flowering species at each site. Quantitative pollination networks were illustrated as bipartite visitation graphs using matrices of visitation rates for every plant species from each study site. Two rows of rectangles representing pollinator and plant species are connected by lines, with a thickness proportional to the interaction strength. The presence of individual species (both plants and pollinators) at each site were used to calculate the proportion of species occurring in all three sites, shared between two sites, and found solely in a single site.

The following qualitative network parameters were calculated for each network: Number of plant species (p), number of pollinators (a), species richness (r = p+a), network size (s = p*a), total number of interactions recorded (i), connectance (c = i/s): the realized proportion of possible links (Blüthgen et al., 2006), web asymmetry (w = (p-a)/(p+a)): the balance between pollinator and plant numbers, mean number of links per pollinator, and mean number of links per plant. Although these indices by and large provide an indication of the size of the networks, they can allow for basic comparisons between network characteristics not only within this study but from other pollination network studies.

In addition, we computed the following quantitative indices which take into account the magnitude of the interaction: WeightedNODF – a quantitative value for nestedness where higher values indicate increased nestedness (Almeida-Neto and Ulrich, 2011), weighted connectance – linkage density divided by number of species in the network (Tylianakis et al., 2007), interaction evenness - homogeneity of interaction frequencies across all links in the network, with higher values reflecting a more uniform spread of interaction among the species in the community (Tylianakis et al. 2007), Interaction Diversity – Shannon's diversity of interactions, H_2' – a network level of specialisation where 0 equates to no specialisation and 1 complete specialisation (Blüthgen et al., 2006). To detect whether the observed results were due to ecological mechanisms rather than sampling artefacts, observed values were compared to those generated by a null model. For each network of study, 1000 randomly generated matrices of the same size were created using the r2d method. Standardized z-scores were calculated for each metric ($z = [\text{observed} - \text{null mean}]/\text{null } \sigma$) to test for significant differences.

The lack of replication of site type prevents any statistical comparison of network-level indices, thus our interpretations are merely descriptive; however they do allow for discussion on the effect of land-use history and contemporary vegetation dynamics on the richness, evenness, diversity and specialization observed in plant-pollinator interactions while providing a means of comparison between this and other similar studies and a baseline for future work.

Statistical analysis could be, and was, performed on species-level specialization. The Kullback-Leibler distance (d') expresses how strongly a species deviates from interacting with species in proportion to their overall importance in the community (Blüthgen et al., 2006). Values range from 0 (no specialization) to 1 (complete specialization). Additionally, mean number of links per species for both plants and pollinators were calculated. One-way ANOVAs and Tukey Multiple Pairwise Comparisons (normally distributed data) and Kruskall-Wallis and pairwise comparisons using Wilcoxon rank sums (non-parametric data) tests were combined to test for significant differences between the aforementioned indices for species (both plant and pollinator) occurring in all three sites and for pollinator groups (e.g. Hymenoptera, Diptera etc.) between sites.

All analyses were conducted with the statistical package BIPARTITE in R (Dormann et al., 2018; R Core Team, 2015).

5.3 Results

5.3.1 Ecological Composition

In total 62 flowering plant species were observed across the three sites however there were no recorded visitors for 11 of these species. Of the 51 species which were present in the pollination web analyses only six species (12%) were found in all three study sites with a further 11 (22%) occurring in two of the three sites. Most species - 34 (66%) - were found in one site only of which 24 were found solely in the pristine site (Figure 5.2A). Species and family richness were higher in the pristine site compared to the moderately and highly degraded sites; however the highly degraded site, supplemented by increased alien species numbers, was more diverse than the moderately degraded site. With respect to alien plant species, none were recorded in the pristine site while the three flowering species of aliens in the moderately degraded site were not observed receiving visitors. In the highly degraded site only one out of the five flowering alien species did not receive visitors (Table 5.1A).

A total of 99 pollinator species were observed across the three sites. Coleoptera (43%) was the most diverse order followed by Diptera (24%), Hymenoptera (19%) and Lepidoptera (10%). In terms of total pollinator species recorded, numbers mirrored those observed for plant species with the most recorded in the pristine site and the least in the moderately degraded site. Proportionally, the number of Coleoptera species remained fairly constant (~40% of total species), however the pristine site had a lower proportion of recorded Diptera species (23%) compared with the highly degraded site (Diptera: 29%) which, in turn, had fewer than the moderately degraded site (Diptera: 35%). There was a noticeably higher proportion of Hymenoptera species recorded in the pristine site (25% of species recorded) while the highest proportion of Lepidoptera was found in the highly degraded site (15% of species recorded). In the pristine site three species, all red-flowered and containing large volumes of nectar, were visited by birds. No bird pollination was observed in the moderately degraded site despite the presence of species that conform to the bird pollination syndrome (Table 5.1B). Of the 99 pollinator species recorded, only 16 were observed across all three sites with 25 solely recorded in the pristine site, and six and 18 observed exclusively in the moderately degraded and highly degraded sites respectively (Figure 5.2b).

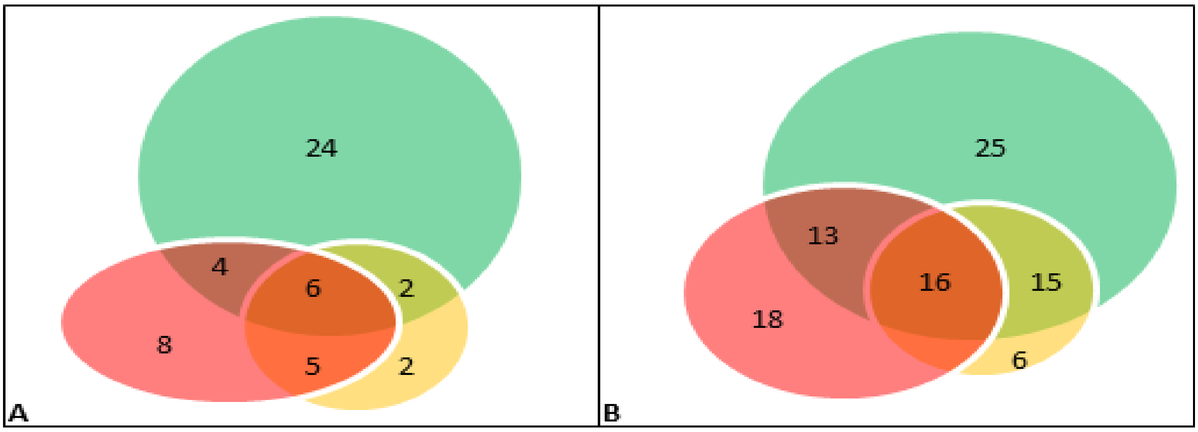

Figure 5.2: Venn diagram illustrating the number of (a) plant species, and (b) pollinator species found exclusively and in common across the three sites. Green Ovals=Pristine; Yellow Ovals=Moderately Degraded; Red Ovals=Highly Degraded.

Table 5.1: A) Floral, and B) Pollinator composition of the three study sites.

A) Plants	**Pristine**	**Moderately Degraded**	**Highly Degraded**	**B) Pollinators**	**Pristine**	**Moderately Degraded**	**Highly Degraded**
Total Species	56	28	36	**Total Species**	69	43	53
Total Families	27	11	12	**Coleoptera**	29	17	21
Total Alien Species (Flowering)	0(0)	3(0)	10(5)	**Diptera**	16	15	15
Spring Flowering Species	43	22	27	**Hymenoptera**	17	6	7
Spring Flowering Families	21	8	9	**Lepidoptera**	5	4	8
Spring Flowering Cover (%)	80	50	70	**Aves**	1	0	1
Flowering Species With No Visits	7	7	4	**Thysanoptera**	1	1	1

In all three sites yellow was the dominant flower colour present. While all seven flower colour categories were represented in the pristine and highly degraded sites, only red, yellow, white and blue flowers were present in the moderately degraded site (Figure 5.3A).

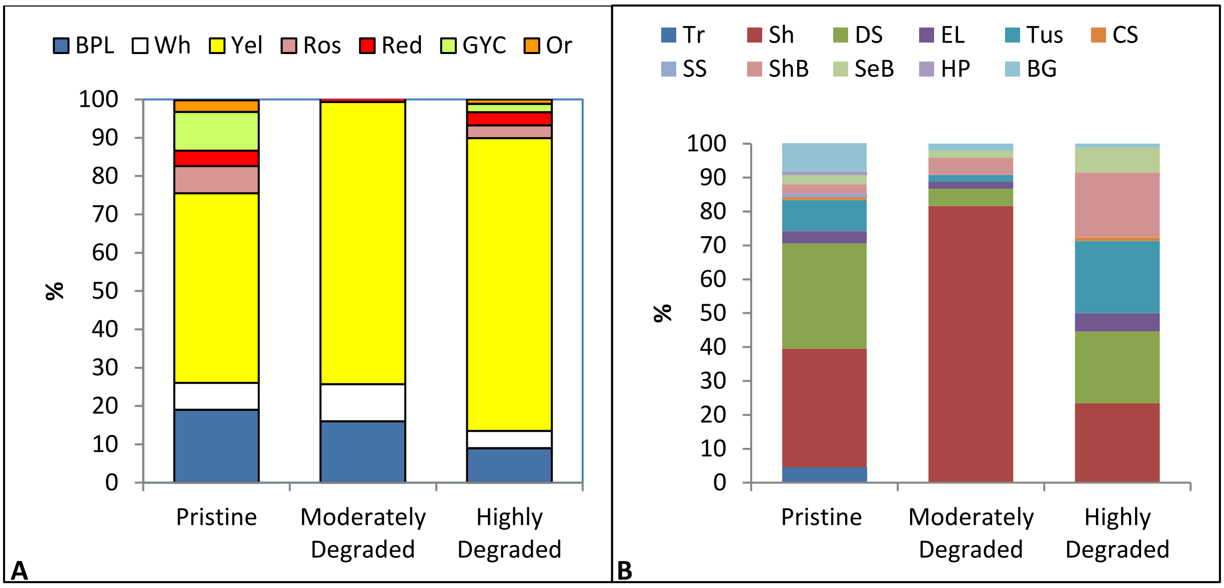

Figure 5.3: A) Proportion of Flower Colours of the Spring Flowering Plant Cover across the three study sites, and B) Proportion of plant growth forms across the three study sites. (Or-Orange; GYC-green/yellow/cream; Ros-Rose; Yel-Yellow; Wh-White; BPL-Blue/Purple/Lilac). (BG-Bare Ground; HP-Hemiparasites; SeB-Semi Basal; ShB-Short Basal; SS-Short Succulent; CS-Climbers & Scramblers; Tus-Tussock; EL-Erect Leafy; DS-Dwarf Shrub (< 0.8m); Sh-Shrub (> 0.8m); Tr-Trees (sensu Cornelissen et al. (2003)).

In terms of vegetation structure, the overall communities of both pristine and moderately degraded sites were dominated by shrubs (75% and 85%, respectively) whereas the highly degraded site had only 40% shrub cover with a higher cover of herbaceous basal (25%) and tussock (20%) species. Diversity of plant growth forms was greatest in the pristine site (11) compared to the moderately and highly degraded sites (seven and eight growth forms, respectively) (Figure 5.3B).

5.3.2 Network Analyses

The pollination networks show visible differences between study sites (Supplementary Data Figure S5.1). In the highly degraded site 36% of all recorded interactions were from Coleoptera, double the proportion recorded elsewhere. Diptera accounted for 30% of interactions in the moderately degraded site, markedly higher than the highly degraded (20%) and pristine (16%) sites. In the pristine site over half of all interactions (55%) were Hymenoptera, a noticeably higher proportion in comparison to the moderately (37%) and highly degraded (20%) sites. Of all Hymenoptera interactions, the proportion of Cape Honey Bee (*Apis mellifera capensis*) visits were distinctly lower at the pristine site (9%) compared to the moderately (37%) and highly degraded (43%) sites. Lepidoptera and Avian interactions were a consistently low proportion of total visits at all three sites (Supplementary Data Figure S5.1).

With regard to network indices (Tables 5.2 and 5.3), the pristine site recorded lower nestedness, connectance, and mean number of links per species compared to the moderately degraded site.

Indices for the highly degraded site fell between the two. The exception to this pattern was mean links per pollinator where highly degraded site values were higher than those calculated for the moderately degraded site. For nestedness and connectance, values for the highly degraded site tended to be closer to those of the pristine site; however for mean numbers of link per plant species values for moderately and highly degraded sites were similar. The opposite was true for network specialisation (H’) where the highest values were recorded for the pristine site, and the lowest for the moderately degraded site. For mean species specialization (d’), both plants and pollinators had higher values than those calculated for the moderately and highly degraded sites; however for this index the latter two sites had equivalent values. All calculated indices were significantly different when compared to the generated null models ($p < 0.001$).

Table 5.2: Qualitative pollination network indices for the three study sites

	Pristine	**Moderately Degraded**	**Highly Degraded**
Number of Plant Species (P)	36	15	23
Number of Pollinator Species (A)	69	43	55
Species Richness (R)	105	58	78
Network Size (S)	2484	645	1265
Total Number of Recorded Interactions (I)	203	131	188
Connectance (C)	0.08	0.20	0.15
Web Asymmetry (W)	0.31	0.48	0.42
Mean Links per Pollinator(SD)	2.94(2.04)	3.04(2.28)	3.47(2.93)
Mean Links per Plant(SD)	5.64(6.53)	8.73(5.11)	8.17(6.07)

Of the six plant species found in all three sites, specialization (d’) was found to be significantly higher in the pristine site compared to the highly degraded site (Figure 5.4a). This difference was not evident when comparing the mean links per species for these six plant species (Figure 5.4b). Specialization (d’) (Figure 5.5a), and mean links per species (Figure 5.5b), of the 16 pollinator species found in all three sites were not found to be significantly different. In terms of pollinator groups, Hymenoptera were significantly more specialized (d’) in the pristine site compared to the moderately degraded site (Figure 5.7a). No significant difference was found for Hymenoptera mean links per pollinator across sites (Figure 5.7b) or d’ values and mean links per species for the other pollinator groupings across sites (results not shown).

Table 5.3: Quantitative pollination network indices for the three study sites

	Pristine	Moderately Degraded	Highly Degraded
WeightedNODF	12.32	19.53	17.50
Weighted Connectance	0.04	0.09	0.07
Interaction Evenness	0.59	0.63	0.62
Shannon Diversity	4.63	4.10	4.42
H2'	0.66	0.49	0.55
Mean d' Pollinator(SD)	0.41(0.25)	0.34(0.17)	0.34(0.20)
Mean d' Plant(SD)	0.62 (0.15)	0.46(0.12)	0.46(0.23)

It is worth re-iterating that due to the nature of this study we were precluded from replicating sites along the gradient of degradation. Thus, apart from comparisons between d' values and mean links per plant and pollinators, no statistically robust comparisons between sites were possible. Nevertheless, indices calculated here are suitable for answering our research questions and allow for comparison with datasets from other studies. Moreover, Renosterveld is a fragmented vegetation type facing a conservation crisis and furthering our understanding of the role vegetation state and structure play in pollination dynamics is a worthwhile task.

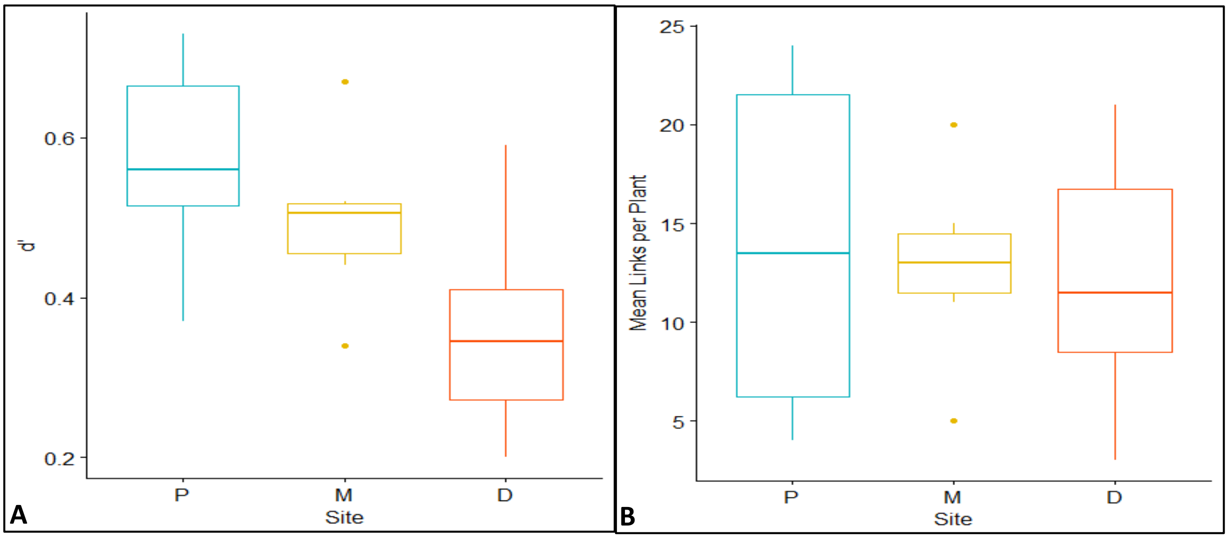

Figure 5.4: Box plots for (a) species-level specialization values (d'), and (b) mean links per plant for the six plant species found in all three sites. P=Pristine; M=Moderately degraded; D=Highly degraded. P and D are significantly different at $p < 0.05$ in (a).

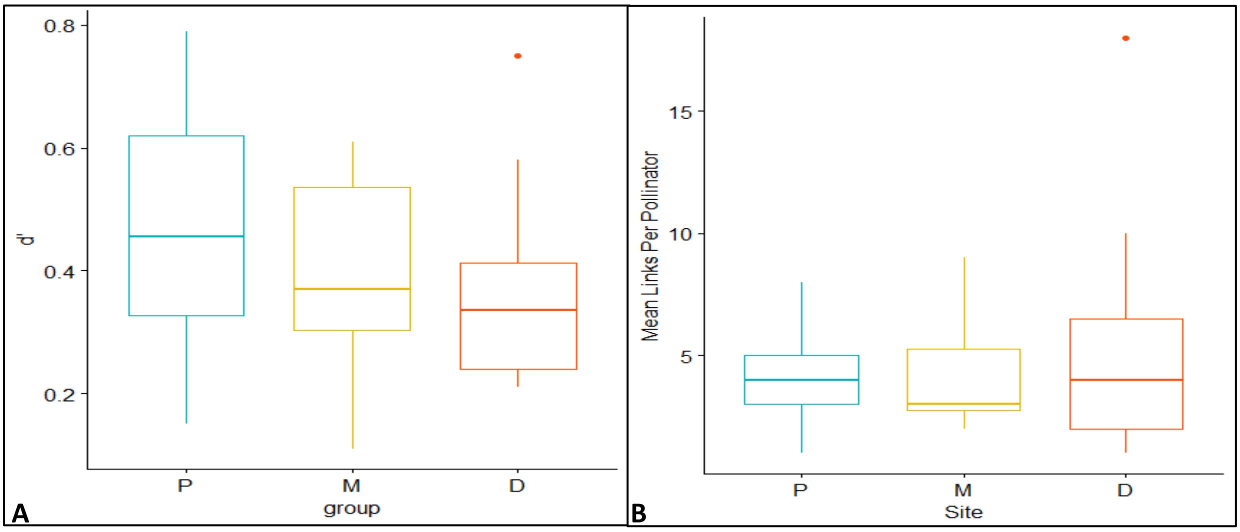

Figure 5.5: Box plots for (a) species-level specialization values (d'), and (b) mean links per pollinator for the 16 pollinator species found in all three sites. P=Pristine; M=Moderately degraded; D=Highly degraded. No significant differences were found.

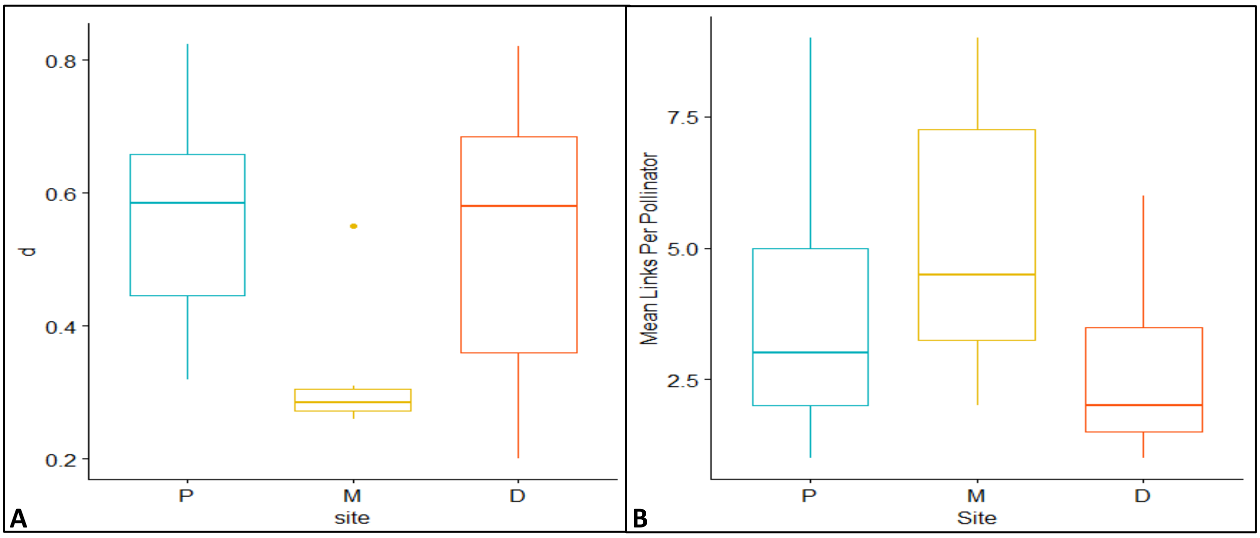

Figure 5.6: Box plot showing (a) species-level specialization (d'), and (b) mean links per pollinator for Hymenopteran pollinators between the three sites. P=Pristine; M=Moderately degraded; D=Highly degraded. P is significantly different to M at p< 0.001.

5.4 Discussion

This study presents three complete plant-pollinator networks along a degradation gradient in a highly disturbed, critically endangered vegetation type and adds to the scarce data on community-level pollination in Southern Africa and the African continent in general. Here, we discuss the characteristics of the networks as expressed through network indices; how the indices from pristine vegetation compare to i) a similar study conducted in the region and ii) global pollination networks; and, finally, how vegetation change, as a result of initial degradation followed by secondary succession, is related to i) the richness, evenness and diversity of interactions and ii) the degree of specialization of interactions.

The low connectance value reported for the pristine vegetation pollinator network is typical of large networks (Olesen and Jordano, 2002). The large number of unobserved links may be the result of under-sampling. However, it is more likely the result of forbidden interactions due to species possessing certain traits resulting in phenotypic specialization (Ollerton et al., 2007), or size thresholds between interacting pairs (Stang et al., 2009), which restrict pairwise interactions (Kaiser-Bunbury et al., 2014). The probable proportion of forbidden interactions is also suggested by the high H2' value reported from the pristine site. Indeed, in comparison to global specialisation data collated from 58 pollination networks (Schleuning et al., 2012), the pristine site in our study ranks as the second highest. Assessing species-level indices shows a similar trend, particularly for plants, with the mean d' value for plants comparable to the higher values collated by Schleuning et al. (2012). The mean d' value for pollinators was less noticeably specialized although still positioned in the upper half when compared to Schleuning et al.'s (2012) dataset. Conversely, compared to the aforementioned dataset (Schleuning et al. 2012), the average number of links per plant is relatively high which would appear to indicate generalised interactions.

This apparent paradox can be understood by considering the difference between the average number of links per species and specialization indices (H2' and d') which take the scope of the available interaction partners into account. A plant species may only have a single pollinator species visit it but, if this pollinator is common within the community, the plant species would have a low d' value i.e. a visit from this particular pollinator is not unexpected in comparison to its presence within the community. In contrast, a plant species may have interactions with numerous pollinator species but if these pollinators are not recorded on other plant species the d' value would be high (Pauw and Stanway, 2015). High d' despite relatively low number of visitors per plant species is indicative of functional specialization (Fenster et al., 2004) as floral traits select for pollinator species with complementary traits.

There have been no other comprehensive plant-pollinator network studies performed in pristine Renosterveld for comparison; however Pauw and Stanway (2015) reported unparalleled specialization in a pollination network analysis performed in adjacent Fynbos vegetation despite similarly high mean links per plant species. Whilst a distinct vegetation type, Renosterveld has similar levels of diversity to Fynbos and numerous plant families in common (Bergh et al., 2014), Pauw and Stanway's (2015) Fynbos site was substantially larger than that of our pristine Renosterveld site and considerably more diverse (62 plants and 217 pollinators), however both networks are characterized by low connectance and high specialization despite relatively high values of mean links per plant compared to global pollination networks (Schleuning et al., 2012). Increased specialization as indicated by the H2 and d’ indices in the Fynbos and pristine Renosterveld networks, supports the notion that pollination networks in the region are functionally specialized in comparison to the majority of global studies, perhaps as a result the relative climatic stability through the Quaternary (Chown et al., 2004) which has allowed specialization to manifest and persist (Pauw and Stanway, 2015).

Although compared to the possible range of values for each of the studied indices the differences among the three networks were generally relatively small, consistent patterns were evident and are worthy of discussion. The pristine site was more diverse, had lower connectance, lower asymmetry, lower nestedness, and higher levels of network-level specialisation compared to the moderately and highly degraded sites. Interestingly, indices calculated for the highly degraded site were closer to those of the pristine site compared to indices from the moderately degraded site. While network characteristics as expressed through indices may be artefacts of sampling intensities (Blüthgen, 2010), the sampling intensity at each site was equal which suggests these differences can be attributed to the nature of the above-ground vegetation. The moderately degraded site, while free from agricultural activities for over 15 years and dominated by indigenous vegetation, was fairly homogenous with large stands of the shrub *Dicerothamnus rhinocerotis* present. While present in healthy Renosterveld vegetation, *D. rhinocerotis* is an early successional species which can dominate degraded veld. It is a drab shrub with inconspicuous, wind-pollinated flowers, and of no use as a floral resource to foraging pollinators. In contrast, the highly degraded site with its recent agricultural activity was far more open with numerous annual flowering species, both indigenous and alien. The more common shrubs, scattered throughout the site, included species of *Pteronia* and *Oederra* – indigenous Asteraceae species with high densities of yellow flowers. The increased diversity in vegetation structure and availability of flowering species in the highly degraded site in the earlier stage of secondary succession provides superior habitat and floral resources for pollinator populations. The presence of alien vegetation can be beneficial for indigenous pollinator communities and even benefit native flora (Moragues and Traveset, 2005), however the opposite is also true and affects may change through time with changes in community composition (Morales and Traveset, 2009). A lack of replication across the degradation gradient prevents any robust conclusions to be drawn on differences in plant-pollinator network structure; however our results indicate that above ground vegetation characteristics are important drivers. The reduced nestedness and lower connectance in pristine site indicate that plants and pollinators are not as highly linked to each other in comparison to the moderately and highly degraded sites. This, combined with the higher level of network specialization observed in the pristine site, suggests that the pristine site is less resilient to future stress as network generalization has been associated with increased robustness to perturbation (Memmot et al., 2004). It may seem counterintuitive that agricultural activity has resulted in subsequent degraded systems that are more resilient to future perturbations; however this relationship can be explained if one considers what habitat degradation can do to a community. More vulnerable and specialized species may go extinct while resistant, generalized species are favoured due to the possession of traits which make them more tolerant to disturbance (Vinebrooke et al., 2004, Redhead et al., 2018). A similar trend was observed in a landscape-level study in Great Britain where agricultural land-cover was positively correlated with generalization and robustness to extinction (Redhead et al., 2018).

For species that occurred across all sites, significant differences were found (i) in specialization (d’) for plant species which were present at all three sites, and (ii) between certain pollinator groups. Four of the six shared plants were Asteraceae shrubs with solitary Scrophulariaceae and Aizoaceae species, and the mean d’ values were only significantly higher in the pristine compared to the highly degraded site with no significant difference in mean d’ found between these shared species elsewhere. This implies that in the pristine site, these plant species are attracting a more select number of pollinators compared to the same species in the moderately degraded and highly degraded sites. Whether this is a sampling artefact due to the increase in pollinator species present in the pristine site or evidence of niche partitioning is hard to say. The fact that six of the species are Asteraceae shrubs with floral traits which do not discriminate against pollinator functional groups (with the possible exception of birds) would suggest the former, as does the lack of significant differences in mean links per plant.

The only significant difference found in species-level specialization of species across pollinator orders between the sites was a higher mean d’ value for Hymenoptera in the pristine site, compared to the moderately degraded site. A quarter of all pollinator species recorded in the pristine site were Hymenoptera many of which were found on a select number of plant species. Conversely, less than 15% of pollinator species recorded in the moderately degraded site were Hymenoptera, the majority of which visited numerous plant species. The structural heterogeneity of the pristine site may provide more favourable nesting opportunities for a wider array of Hymenoptera (Gess and Gess, 2014) and the increased floral resources present may additionally allow for greater niche partitioning within Hymenoptera. Similarly, increasing insect diversity could also enhance competition resulting in smaller realized niches for insects. Steffan-Dewenter and Tscharntke (2001) found that the succession of bee (Hymenoptera) communities in fallowed land was related to changes in vegetation. They reported a correlation between both increased species richness of flowering species and increased bee species, and increased cover of flowering plants and bee abundance (Steffan-Dewenter and Tscharntke, 2001).

5.5 Conclusion

This study has provided the first insights into plant-pollinator networks within critically endangered Renosterveld vegetation, despite a lack of site replication precluding in depth statistical analysis on network-level indices. Similar to a network described by Pauw and Stanway (2015) from the adjacent Fynbos vegetation, Renosterveld pollination networks appear highly specialized when compared to global network studies – potentially as a result of climatic stability through the Quaternary which has allowed functional specialization to manifest and persist. In a region vastly transformed by agriculture, variation in above-ground vegetation composition due to habitat alteration as a result of degradation and subsequent secondary succession has resulted in changes to pollination network structure. In this study, the moderately degraded site was less diverse, with network indices more dissimilar to that of the pristine site, when compared to the indices of the highly degraded site. This was probably the result of the dominance of the wind pollinated shrub, *D. rhinocerotis*, at the moderately degraded site reducing floral resources and homogenizing vegetation structure. The trajectory of secondary succession following the cessation of agricultural activity in Renosterveld is not necessarily fixed however, with historical land-use activities (e.g. ploughing) and disturbance events post initiation of secondary succession (e.g. fire season, grazing intensity) affecting vegetation dynamics. With regards to pollination, it does appear that more diverse vegetation, both in terms of floral resources and structure, result in more diverse and specialized plant-pollinator interaction networks. Although further studies are required, acknowledging this in future management decisions may aid the safeguarding of a crucial ecosystem service in a critically endangered vegetation type.

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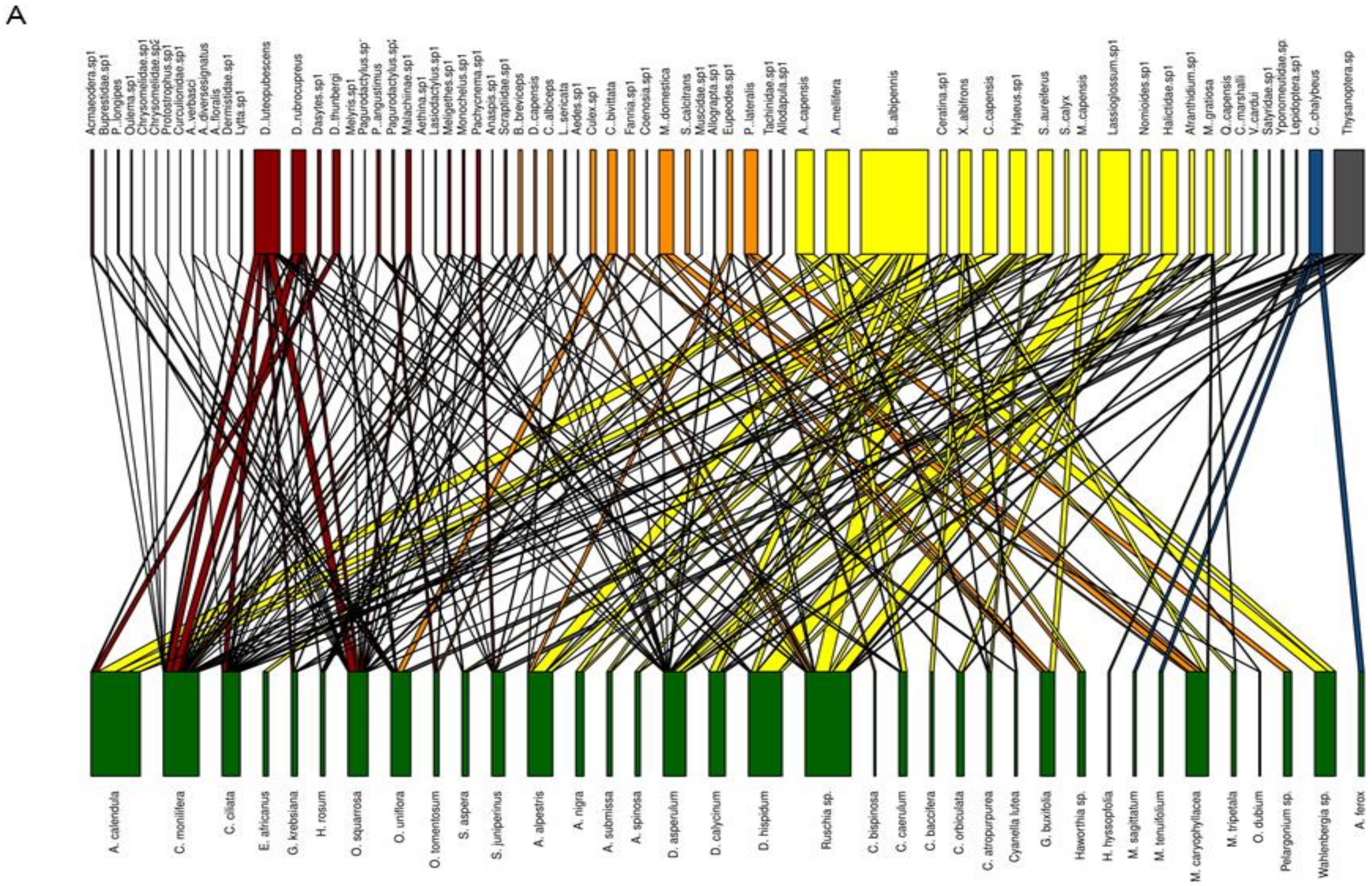
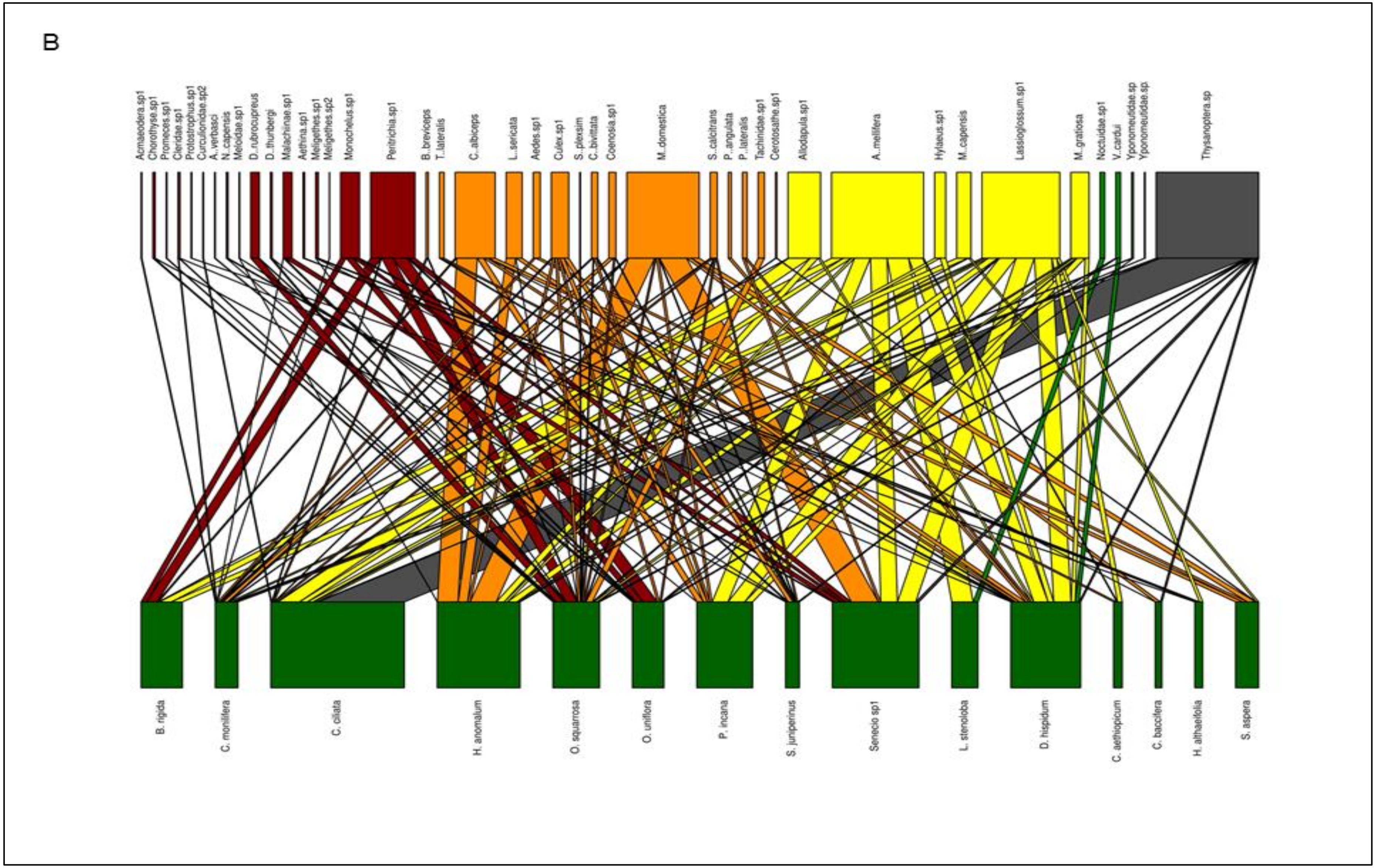
5.8 Supplementary Data

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Chorothyse.sp1
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Protostrophus.sp1
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N..capensis
Meloidae.sp1
D..rubrocupreus
D..thunbergi
Malachinae.sp1
Aethina.sp1
Meligethes.sp1
Meligethes.sp2
Monochelus.sp1
Peritrichia.sp1
B..breviceps
T..lateralis
C..albiceps
L..sericata
Aedes.sp1
Culex.sp1
S..plexsim
C..bivittata
Coenosia.sp1
M..domestica
S..calcitrans
P..angulata
P..lateralis
Tachinidae.sp1
Cerotosathe.sp1
Allodapula.sp1
A..mellifera
Hylaeus.sp1
M..capensis
Lassioglossum.sp1
M..gratiosa
Noctuidae.sp1
V..cardui
Yponomeutidae.sp
Yponomeutidae.sp.
Thysanoptera.sp
B. rigida
C. monilifera
C. ciliata
H. anomalum
O. squarrosa
O. uniflora
P. incana
S. juniperinus
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C. aethiopicum
C. baccifera
H. althaeifolia
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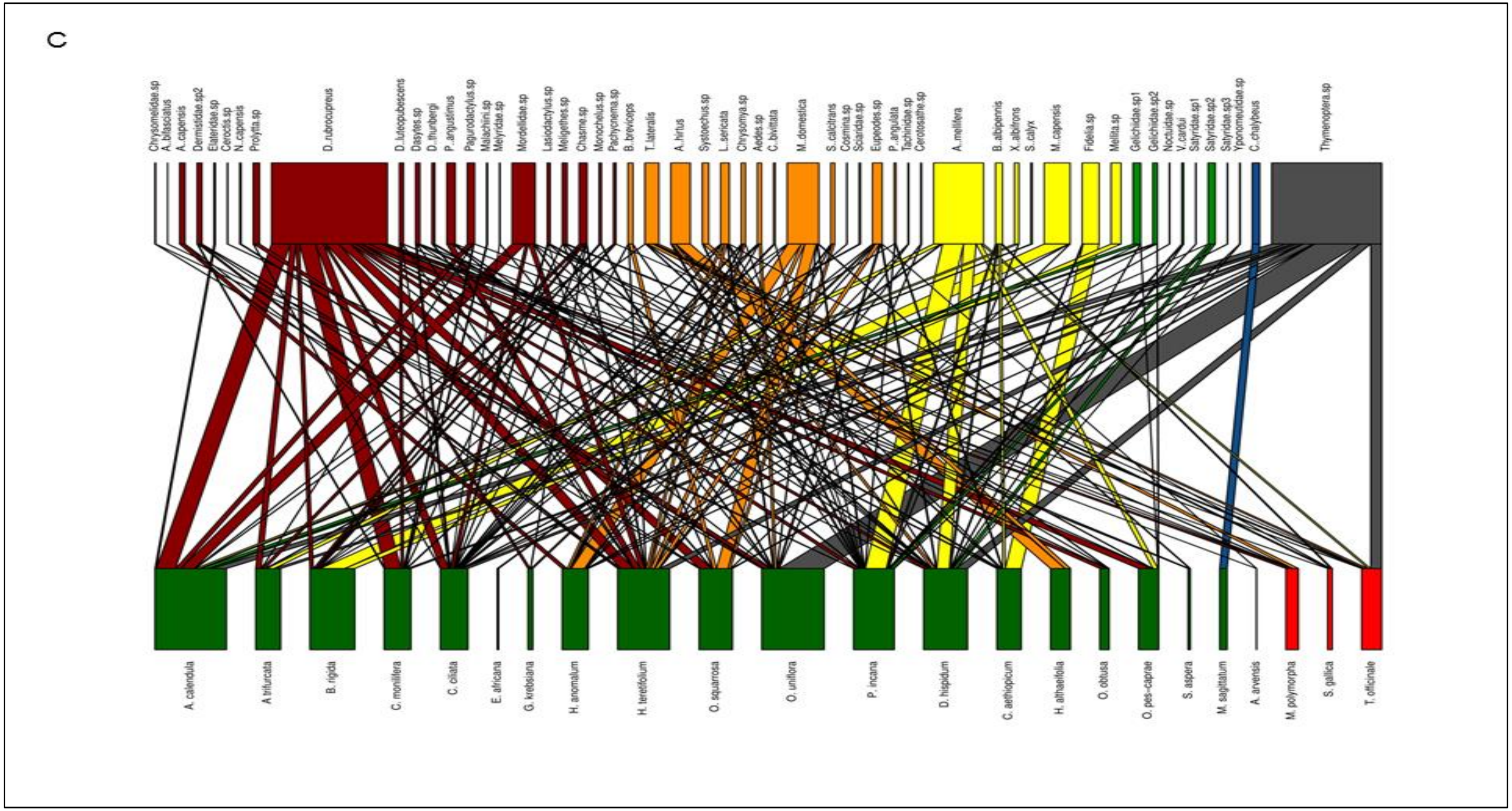

Figures S5.1A-C: Quantitative pollination networks of plant-pollinator communities at (A) Pristine Site, (B) Moderately degraded Site and (C) Highly degraded Site. Pollinators are shown as rectangles at the top (Red=Coleoptera, Orange=Diptera, Yellow=Hymenoptera, Green=Lepidoptera, Blue=Avis, Grey=Thysanoptera) and plants as rectangles at the bottom (red rectangles depict alien plant species). Rectangle width reflects the relative abundance of pollinators and plants.Links represent interactions between species with the width depicting the relative quantitative visitation rate between interacting pairs.

Chapter 6

Discussion

6.1 Synthesis

This thesis has explored the relationship between biodiversity and ecosystem functioning across a degradation gradient in the critically endangered Overberg Renosterveld vegetation. With the use of historical aerial photographs of the region, current satellite imagery, ground-truthing and local expert knowledge, 21 sites were identified and assigned into one of three designated degradation states. These were namely, Pristine – characterised by no evidence of historical agriculture; Moderately Degraded – characterised by evidence of historical agricultural use but none within the last 10 years; and Highly Degraded – characterized by evidence of agricultural use within the last 10 years. Various methods were applied, and lenses considered, in an effort to address the effect of degradation on the relationship between biodiversity and ecosystem functioning from a number of different angles.

In **Chapter 2**, detailed vegetation sampling and collation of functional trait data allowed for an analysis of the relationship between taxonomic diversity and functional diversity through the use of various indices across a degradation gradient. The results showed a complex association influenced by habitat degradation with potential ecological and conservation implications. The loss of functional redundancy in degraded sites is likely to reduce resilience to future environmental perturbations which may reduce ecosystem functions. Conversely, the similarities in both taxonomic and functional diversity indices between pristine and moderately degraded sites may be cautiously interpreted as the occurrence of successful passive restoration.

In **Chapter 3**, the ecosystem process of plant litter decomposition was investigated and the importance of its role in nutrient cycling between fire events was interrogated. Litter decomposition rates were shown to be variable with litter type and season revealed as important controlling factors. Although degradation did not appear to significantly affect decomposition rates, the initial nutrient content of litter appears to correlate with decomposition rate and it can be expected this ecosystem function will be accelerated where habitat degradation results in shifts in above-ground vegetation and subsequent litter input, specifically where the cover of non-native, nitrogen-rich annual species is increased.

Chapter 4 provided the first study of Springtails (functionally important, soil-dwelling organisms) in Renosterveld vegetation, while exploring the effect habitat degradation, litter type and sampling day may have on Springtail community dynamics. The significant impact of litter type on community composition, and of sampling day on species richness, abundance and community composition, are indicative of dynamic Springtail communities. Despite the overall lack of effect of degradation on

Springtail community dynamics, the abundance of the non-native *Entomobrya multifasciata* in degraded sites, and its absence from pristine sites, raises the intriguing possibility of its suitability as a bioindicator for habitat degradation.

Finally, **Chapter 5** provided the first comprehensive plant-pollinator interaction networks from Renosterveld vegetation, and only the second for the Cape Floristic Region. Comparisons to similar global studies revealed the Renosterveld networks to be highly functionally specialized. Assessing network dynamics across a degradation gradient showed the impact of above-ground vegetation structure on network properties with the more open and diverse vegetation structure and floral resources provided by the highly degraded site resulting in network indices more similar to that of the pristine site when compared to the relatively structurally uniform moderately degraded site.

This thesis seeks to address my overarching aim of interrogating the effect of degradation on the biodiversity-ecosystem function relationship in Renosterveld. In doing so, I have performed four relatively distinct studies, albeit all of which fall under the broad umbrella topic of functional ecology, culminating in four distinct publications. As highlighted in section 1.9 when describing the thesis structure, certain materials which I believe to be relevant to the central thesis were recommended to be removed during the peer review process of the four papers. In this chapter, in addition to the findings of each of the papers (**Chapters 2-5**), I pick up on, and address, some of these supplementary elements where I feel they provide additional insights to the more generalized discussion presented here. In this final chapter, I address certain theoretical aspects, first brought forward in the literature review in **Chapter 1**, in consideration with findings from **Chapters 2-5**. The structure of this thesis has resulted in certain segments of the individual discussion sections addressing particular theoretical concepts which are both necessary in addressing the specific objectives of the paper in question, and relevant to central aim of this thesis. As such, there is some unavoidable repetition in this chapter, particularly when discussing certain ecological concepts. I have decided occasional repetition to be a superior option (and kinder on the reader) than cross-referencing back to previous chapters. Following the appraisal of the theoretical considerations, I reflect on the practical applications which emerge from my results that may prove relevant for management and conservation decision makers. Although there has been an increase in the number of studies relevant to the functional ecology of Renosterveld in recent years, many questions remain only partially answered or completely unaddressed. This thesis addresses many aspects of functional ecology within the vegetation type; however it has also highlighted where gaps within our knowledge persist. As such, in both the theoretical and practical discussions, I attempt to flag where our understanding may benefit from further research. Finally, before concluding this chapter, I collate these suggestions and highlight potential future points of departure for ecological work in the hope that it proves a valuable resource for future ecological studies into this critically endangered vegetation type.

6.2 Theoretical Considerations

6.2.1 The Relationship Between Taxonomic Diversity And Functional Diversity

Biodiversity has been widely accepted as a major driver of ecosystem function (Balvanera et al., 2006, Midgley, 2012). As discussed in the literature review in **Chapter 1**, biodiversity is a multifaceted construct although a single facet, species richness, has frequently been used as its dominant measure despite the many drawbacks associated with the use of this metric (Díaz and Cabido, 2001). The most pertinent of these drawbacks is that taxonomic indices do not take into account the biological identity and differences amongst species (Villéger et al., 2010). In other words, merely providing the number of unique species present in a community reveals little about the ecological properties of said community. Functional diversity on the other hand is a component of biodiversity which provides a mechanistic link to ecosystem function (McGill et al., 2006). By analysing the relationship between taxonomic diversity and functional diversity unique insights into the origin and maintenance of biodiversity can be provided (Edie et al., 2018) which, in turn, can deliver powerful data for environmental conservation and the restoration of threatened habitats (Petchey and Gaston, 2006). **Chapter 2** opened the study into the functional ecology of Overberg Renosterveld by demonstrating that species richness, and taxonomic diversity in general, do not uniformly correlate with functional diversity indices for plant communities in the study area and is therefore inadequate as a reliable surrogate for functional diversity (Díaz and Cabido, 2001). Not only did the relationship vary according to which index of taxonomic or functional diversity was used, but even when they were kept constant, the nature of the relationship would differ depending on the level of site degradation.

The overall species richness and functional richness in the study area revealed a positive linear relationship, consistent with the theory that increasing the number of species present in a community increases the number of functional traits within that community (Schmid et al., 2002). This correlation is considerably stronger with a steeper slope in the moderately and highly degraded sites compared to the pristine sites. The disparity between species richness and functional diversity is due to the functional redundancy which exists within Renosterveld communities, as has been reported in many other vegetation types (Naeem, 1998; Sasaki et al., 2009; Guerrero et al., 2014). Species are considered redundant with respect to an ecosystem function when the loss of one or more of those species does not affect that ecosystem function in a significant way (Díaz and Cabido, 2001). Theoretically, the larger the number of functionally similar species in a community, the greater the probability that at least some of these species will survive changes in the environment (Chapin et al., 1996). Renosterveld evolved as a fire-prone system subject to stochastic population shifts (Cowling et al., 1994) and constant grazing pressure from a variety of herbivores drawn to its relative fertility (Krug et al., 2004). As such, it is logical that functional redundancy is an important mechanism in Renosterveld to maintain ecosystem function in the face of variation in these ecological drivers.

Chapter 2 also clearly illustrated how the relationship between taxonomic and functional diversity indices may produce variable results depending on the indices used for its assessment. Functional diversity itself is separated into three unique components (functional richness, evenness, and divergence), and can also be measured through synthetic indices which purportedly take into account some, or all, of the three facets of functional diversity (e.g. Rao’s Q, functional dispersion). The correlation between functional richness and species richness has been covered previously in this section but a strong correlation was also found between species evenness and the two synthetic functional diversity measures, Rao’s Q and functional dispersion. This is logical as species evenness describes how close in numbers each species in an environment is. Evenness is low when one or a few species are dominant and the remaining species present are rare. If these dominant species are functionally similar, one would expect low functional dispersion as there is little dispersion in trait abundance (i.e. similar trats are the most abundant in the community). As species evenness increases, those traits associated with rarer species increase in abundance resulting in an increase in functional dispersion. That this correlation is strongest in the moderate and highly degraded sites further strengthens the idea that the environmental filters imposed on communities through habitat degradation results in trait convergence (i.e. species with similar traits which allow them to despite or because of the habitat degradation).

Interestingly, Shannon’s diversity, which takes into account both species richness and evenness, correlated well with both functional richness and the two synthetic functional diversity indices. Despite correlating well with Rao’s Q and functional dispersion, neither species evenness nor Shannon’s diversity had similar relationships with all three separate components of functional diversity. Clearly, the relationship between taxonomic diversity and functional diversity indices in my study area, even without the separation of study sites according to land-use history, is neither simple nor consistent. It would thus be inappropriate to use taxonomic diversity as a surrogate for functional diversity with any confidence. This is particularly true when one takes into account the disparity in many of the relationships when looking at the pristine sites and the degraded sites separately.

Assessing how degradation, and the subsequent secondary succession which may follow, impacts on community composition and structure can provide insight into the processes of community disassembly and reassembly respectively (Zavaleta et al., 2009; Bhaskar et al., 2014). Here, the concept of functional response traits, and functional diversity in general, greatly aids in understanding how these ecological processes occur. While it is true that degradation often leads to a reduction in species richness, it is by addressing these changes in communities through the lens of functional ecology that allows us a mechanistic understanding of why these shifts occur and provide valuable data for conservationists. Essentially, habitat degradation affects species in a non-random manner due to their possession of vulnerable functional response traits causing a decline and eventual loss of species and the vulnerable traits they possess (Zavaleta et al., 2009; Mouillot et al., 2013).

Of course, habitat degradation is a broad description for the outcome of numerous potential ecosystem-altering disturbances. Even within the spectrum of agricultural land-use, a major focus of this thesis, not all activities are equal with the type and intensity of activities imposing different habitat filters. For instance ploughing may leave an indelible mark on communities by destroying the underground storage organs of geophytes, a growth form Renosterveld is particularly rich in (Procheş et al., 2006), thus removing that specific growth form from local assemblages. On the other hand, intensive grazing filters out highly palatable species and favours the proliferation of toxic or unpalatable species but may allow geophytes to remain locally extant. Indeed, even the role of grazing as an ecosystem driver in Renosterveld is a matter of debate with some authors arguing that the local extinction of indigenous herbivores following the expansion of European settlers has resulted in a marked reduction in palatable grasses (Krug et al., 2004). If this is true, then what we consider pristine contemporary Renosterveld is in fact already degraded in some ways and potentially not even in a stable state but rather in a state of flux as it adapts to missing drivers (Krug et al., 2004).

Figures 2.8-2.10 in **Chapter 2** illustrate how habitat filtering as a result of degradation favours certain traits at the expense of others. The community weighted means demonstrate that highly degraded sites where agricultural activity had ceased within the past five years had a significantly increased proportion of winter flowering, yellow flowered, exozoochorous, non-native, and annual life form traits compared to the pristine and moderately degraded sites. Traits which were significantly reduced in the degraded sites included the ability to re-sprout, indigeneity, and ant, water and unassisted dispersal. The reduction in species with the ability to re-sprout suggests that ploughing has occurred historically in the highly degraded sites. The majority of geophyte species are re-sprouters and have underground storage organs, allowing them to flower opportunistically before dying back to persist in the soil until conditions are favourable again (McIntyre et al., 1995). Geophyte species have been reported to produce seeds which appear to be adapted to short distance dispersal, for example through splashing water, unassisted, or via myrmecochory (Goldblatt and Manning, 2002). Clearly, these are vulnerable traits most at risk from agricultural activity in the region. Another major driver in amplified agricultural activity is the increase in grazing activity by domestic livestock. The analysis here was hamstrung by a lack of trait data, particularly with regard to plant palatability. With palatability data missing for approximately three quarters of all recorded species the trait could not be included in the analysis. Vegetation sampling did highlight the frequent occurrence of *Galenia africana*, an indigenous but highly unpalatable shrub which is reportedly toxic to livestock (Van Der Lugt et al., 1992), in highly degraded sites whereas it was generally absent in pristine sites. *Galenia africana* is a frequent indicator of over-grazed land throughout the Western Cape as livestock avoid eating it and it appears to thrive in nitrogen-enriched soil (Allsopp, 1999). Although this anecdotal evidence needs to be supplemented with more robust palatability trait data, it would appear likely that intensive grazing filters out the more palatable species from impacted communities.

The increase in certain community-level trait proportions (e.g. reseeding) in highly degraded sites may appear counterintuitive on the surface but can occur via two plausible scenarios. Firstly, the elimination of species with vulnerable traits under agricultural activity may reduce biotic pressure (e.g. competition) on species with traits hitherto sparsely represented within the assemblage, thus allowing them to increase in dominance. Secondly, agricultural intensification is often associated with an influx of non-native species, either through deliberate introduction (e.g. Canola, Wheat, Barley), or accidentally (e.g. agricultural weeds). Although both processes can occur simultaneously, the increased proportion of non-native species in the highly degraded sites suggests that it is the latter process which is the dominant factor. These non-native agricultural weeds tend to be annual reseeding species suited to disturbed environments. The increase in external animal dispersal as a strategy is also a trait associated with agricultural activity, in this case livestock farming (Malo and Suarez, 1997). Seeds, or the capsules containing them, have evolved morphological traits which can increase the likelihood of attachment to the hides or wool of cattle and sheep, and are thus dispersed through the landscape (Johansson et al., 2011).

The similarity between the trait composition, as measured by community weighted means, of moderately degraded sites (i.e. those sites where agricultural activity ceased > 15 years ago) and pristine sites, is of interest. Because of the practical implications of this apparent passive restoration, this finding is dealt with more extensively in section 6.3, however a few pertinent points that relate to community reassembly are highlighted here. It would appear that after a sufficient period of time the removal or cessation of habitat filters initially imposed by agricultural activity allows the vulnerable traits which were absent in the highly degraded sites to reappear in communities. Either the species in possession of these vulnerable traits have persisted in the degraded communities at much lower densities and subsequently increased in number during secondary succession, or species immigrated back into the depleted communities from the regional species' pool. In sites where ploughing has occurred it is likely that both the indigenous seedbank and underground storage organs of re-sprouting species would be mechanically damaged to such an extent as to preclude the first scenario. Similarly, limited dispersal distance in traits such as unassisted or ant dispersal may not be conducive to replenishing the local community from the wider regional species pool particularly in a highly fragmented landscape such as the Overberg.

Another plausible explanation exists which is based on potential different points of departure for the moderately degraded and highly degraded sites. The use of chronosequences has been successfully applied to address post-disturbance community assembly (Walker and del Moral, 2003; Albrecht et al., 2010); however it is imperfect for a number reasons. As highlighted earlier not all agricultural activity is equal and although historical data and local knowledge can provide broad scale information on the type, intensity, and period of agricultural activity, the resolution of this data can be coarse, inaccurate or missing entirely. Habitats that have been intensively ploughed will have significantly different points of departure for subsequent secondary succession compared to habitats that have only experienced grazing as a disturbance factor. Additionally, land-use type and intensity can leave behind vastly different "legacy effects" (D'antonio and Meyerson, 2002). Presuming therefore that the natural trajectory of the highly degraded sites is towards the composition and structure currently exhibited by the moderately degraded sites in this study is fraught with assumptions. It is entirely possible that the initial habitat filters implemented by different levels of agricultural activity were different across degraded sites, creating different species assemblages and legacy effects at the time the respective activities ceased. Renosterveld is renowned for its high levels of beta diversity (Curtis, 2013), thus regional species pools may vary considerably across the landscape. To avoid these assumptions and have a clearer understanding of the trajectory of secondary succession either high-resolution land-use data is required, or one needs to initiate long-term monitoring of sites where the exact nature of the previous land-use is known.

A key inference from the literature reviewed in **Chapter 1** was the potential for functional diversity as a valuable tool for measuring and monitoring habitat degradation (Mouillot et al., 2013). In this study, the highly degraded sites had lower functional richness, evenness and divergence than the pristine sites. Conversely, the moderately degraded sites displayed higher values for functional richness and divergence, and the equivalent value for functional evenness to that of the pristine sites. Figure 6.1 illustrates conceptually a possible mechanism as to how this may have occurred.

Figure 6.1 illustrates how the three facets of functional diversity may change between the three degradation states. Here, agricultural activity introduces habitat filters which eliminate species with vulnerable traits. Non-native species, introduced into the landscape either deliberately or accidentally, possess novel traits adapted to the agriculturally-associated habitat filters. Despite this, overall the functional richness (illustrated by the surface area of the outline (Cornwell et al., 2006) in Figure 6.1B), is reduced in the highly degraded sites due to the significant loss of indigenous species. After the habitat filters are lifted following the cessation of agricultural activity, indigenous species return to the assemblage in the moderately degraded sites from the regional species pool and/or the soil seedbank. This is accompanied by a reduction (but not complete removal) of non-native species due to biotic interactions such as competition or the introduction of new habitat filters. The new community now has a functional richness equal to, or slightly higher, than that of the pristine sites. Functional evenness, which measures the regularity of abundance distributions within the functional space, is depicted in Figure 6.1C as the shortest minimum-spanning tree linking all the species (Villéger et al., 2008).

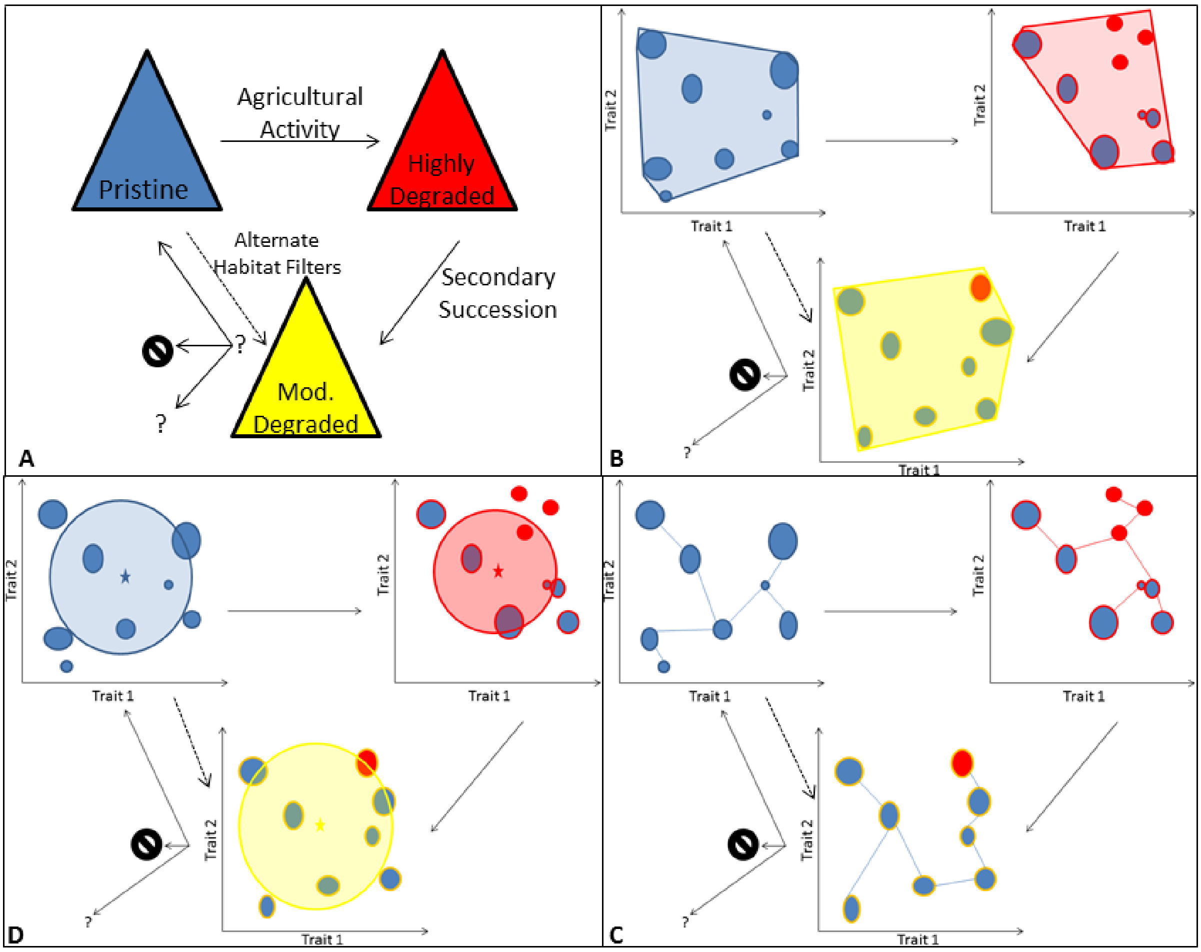

Figure 6.1: A conceptual illustration of the hypothetical changes to functional richness (**B**), functional evenness (**C**), and functional divergence (**D**) which may occur as a result of initial degradation and subsequent secondary succession (**A**). NB: Here species (represented by circles) are found within the functional space of two traits (i.e. axis 1 and axis 2). In reality, the functional space is multidimensional with all measured traits affecting placement of species. Blue circles represent indigenous species; red circles represent non-native species. Circle size is approximately proportional to abundance. For more information on diagram see discussion in text. Concept adapted from Mouillot et al. (2013).

The highly degraded sites exhibit reduced functional evenness as a result of the distribution and abundance of species within the trait space; however, in the moderately degraded sites, the new community increases in functional evenness to match that of the pristine sites. Finally, changes to functional divergence, which is measured by the proportion of the total abundance that is supported by the species with the most extreme functional traits (Villéger et al., 2008), is illustrated in Figure 6.1D. The circles in Figure 6.1D represent the mean functional distance from the centre (indicated by stars) for each community. Similar to functional richness, agricultural activity alters community structure and composition reducing functional divergence in highly degraded sites; however this trend is reversed in moderately degraded sites where functional divergence marginally exceeds that of the pristine sites. Under this scenario, there are three possible scenarios accounting for the moderately degraded sites. The trajectory of secondary succession can return the communities to the state they were in pre-degradation as defined functional diversity indices; they can remain as they are currently; or they can follow a trajectory towards a different end-point i.e. a novel system distinct from the remnant patches of pristine Renosterveld.

The scenario described above applies only if the moderately degraded sites fall along the natural secondary successional trajectory of the highly degraded sites. However, as hypothesized earlier, the possibility exists that the moderately degraded sites were subject to less intense habitat filters which resulted in more 'intact' communities when agricultural activity ceased. This scenario is depicted by the dotted lines in Figure 6.1. Here, the functional trait space would conceivably be augmented by the addition of a limited number of non-native species without the substantial loss of indigenous species. Finally, Figure 6.1 illustrates how functional evenness and divergence could potentially provide an indication of habitat degradation which may not be detected using species richness or functional richness. Whereas functional richness is intrinsically linked to species richness, more subtle habitat disturbance can diminish the population of species with vulnerable traits without a change in species numbers (Mouillot et al., 2013). Thus, changes to functional evenness and divergence can flag habitat degradation before it results in local extinction of species or traits, prompting action.

So far, the discussion in this chapter has dealt with above-ground plant communities. Biodiversity, and the relationship between its different aspects, is just as important at other levels even if the organisms of study may appear at first cryptic to the human eye as is the case with soil microfauna. One such important component of soil fauna is Springtails, the organism of study in **Chapter 4**. Springtails contribute to ecosystem functioning in a myriad of ways, including through the facilitation of litter decomposition, nutrient cycling, and the formation of soil microstructure (Peterson and Luxton, 1982; Hopkin, 1997; Rusek, 1998). Springtails in South Africa remain understudied with their ecological significance particularly poorly understood (Janion-Scheepers et al., 2016) resulting in a lack of knowledge surrounding how traits may be associated with responses to habitat change and effects on ecosystem function. This lack of fine-scale data on the functional traits, and their ecological role, of the species recorded in the study also resulted in the exclusion of functional diversity analysis in the journal article at the recommendation of the reviewers who suggested the article would benefit from a more streamlined approach. Outside of the constraints of that chapter, I choose to reflect here on the broader functional implications in addition to the material covered within **Chapter 4** itself.

To maintain the structure of this chapter as a discussion, a more detailed description and outcome of the functional diversity analysis of the Springtail communities is provided in Appendix I. However, here I provide a brief summary to contextualize the subsequent discussion. Community Weighted Trait Means (CWMs) were calculated for the two quantitative traits (body length and antennae to body length ratio) for each Springtail community. CWMs of Springtail functional traits for the different levels of one (or multiple) of the controlling factors in **Chapter 4** (i.e. litter type, site degradation state, removal day) were used as categories to assess whether these factors significantly affect the CWMs. In addition, functional richness, evenness, divergence, and dispersion were calculated for each littertrap (i.e. Springtail community). These values were used to perform regression analysis on the relationship between species richness and functional diversity indices in an approach similar to that implemented for above-ground vegetation in **Chapter 2**. The limited number of functional traits used (i.e. body length, antennae to body length ration, life form) reduced the robustness of functional diversity indices. Functional richness can only be calculated where the number of species is larger than the number of traits therefore littertraps containing less than three Springtail species were excluded for analysis. Similarly, functional evenness and functional divergence could not be calculated for communities where less than two species were recorded. Of the controlling factors, only sampling day showed significant differences in CWMs for both body length and antennae to body length ratio. Litter type and site degradation level had no significant effect on overall CWMs. This was also the case when littertraps that were removed after three months and six months were analysed separately. Regression analysis showed an overall correlation between functional richness and species richness. This correlation was much stronger in Springtail communities from litter traps removed after six months compared to those after three months. A similar pattern emerged when using regression analysis to assess the relationship between functional dispersion and species richness, although in this case the correlation was less strong overall. Again, the correlation was weaker in Springtail communities from littertraps removed after three months. No correlation was found between species richness and functional evenness or functional divergence.

The results suggest that that much like the vegetation data from **Chapter 2**, the relationship between Springtail functional diversity and species richness is complex. The overall correlation between species richness and functional richness suggests that the more species in a community the greater the number functional traits that are present. The logarithmic shape of the correlation may possibly be indicative of functional redundancy at higher species richness; however with such limited traits included in analysis this should be interpreted with caution.

The lack of impact that designated site degradation appeared to have on species richness and abundance has been covered in depth in **Chapter 4**. Here, further analysis shows that neither CWMs, nor functional diversity, are affected by site degradation. Litter type had an effect of community composition (**Chapter 4**) but not functional composition, at least not when considering the few functional traits that could be measured. Sampling day had a significant effect on both species richness, abundance (**Chapter 4**) and CWMs of both body length and antennae to body length ratio. *Seira* sp. 3 and *Entomobrya multifasciata*, the two species shown to be significantly correlated to litter traps removed after six months, are relatively large, atmobiotic species with large antenna-to-body ratios which suggests these traits give them a competitive advantage as litter decomposition progresses. The two species may also possess hitherto unmeasured traits allowing them to utilise the less labile litter contents available after six months or the associated shift in microbial communities. Alternatively, it is possible that environmental factors are influencing the functional composition of Springtail communities. *Seira* sp. 3 and *E. multifasciata* may possess traits which allow them to survive in drier conditions. Makkonen et al. (2011) found that drought tolerance was correlated to larger body size in sub-Arctic Springtail communities and Davies (1928) reported *E. multifasciata* to be relatively resistant to experimental desiccation. As detailed in **Chapter 4**, the month preceding the removal of litter traps after six months had higher actual evapotranspiration rates and the week prior to removal was rain-free. Morphological trait differences between species allow for niche differentiation and it is possible that the two species possess traits, such as their large body size, which allow them to flourish in drier conditions whereas species with more vulnerable traits may be filtered out the community.

It is clear that Springtail communities in Renosterveld are dynamic entities, influenced by biotic and abiotic factors. Linking the biodiversity of Springtails to changes in ecosystem function however will require substantially improving our knowledge of the functional roles of different Springtail species and which traits account for the diversification of functional roles. This will allow for a greater understanding of their ecological roles and how environmental change, particularly through habitat alteration, may impact on Springtail community structure and subsequent ecosystem functioning.

To conclude this section, the relationship between taxonomic and functional diversity indices is neither simple nor constant across the designated degradation gradient. Although the limited functional trait data for Springtails makes me hesitant to draw any definitive theoretical conclusions with regard to the organism, this is not the case with the above-ground vegetation communities. Clearly, habitat filters as a result of agricultural activity filter out species with vulnerable traits while there is a simultaneous increase in non-native species. In the highly degraded sites the significant reduction in certain traits suggests that ploughing is the chief mechanism of initial disturbance. The similarity in diversity indices in the moderately degraded and pristine sites may either indicate successful passive restoration from sites which previously had similar community composition and structure to that of highly degraded sites, or that moderately and highly degraded sites underwent distinct agricultural activities and are thus on separate trajectories. In this latter scenario, moderately degraded sites may have had less severe habitat filters imposed on them (e.g. grazing rather than ploughing), allowing species vulnerable to ploughing to persist. The concept of natural ecosystem trajectories is tricky in Renosterveld, due to the role of fire which is stochastic in nature. The type, frequency, extent, and intensity of fire may vary, which impacts on Renosterveld vegetation structure as species respond variably in accordance to their suite of functional response traits. As such, two communities with identical land-use history in terms of agricultural activity could support very different assemblages depending on the fire history. Fire has been conspicuous by its absence in the discussion so far, predominantly because it was untenable to include it as a controlled topic of study in any of the four empirical data chapters. I therefore cannot, with any certainty, predict the role fire will play on the theoretical concepts discussed above. Evidently it is an important factor with regard to community assembly acting almost as an indiscriminate ‘herbivore’ (Bond and Keeley, 2005). Following a fire event, Renosterveld communities reassemble either through re-sprouting species which persist, or reseeders whose progeny emerge from the seedbank or migrate from the wider regional species pool. Indeed, if the scenario in which the moderately degraded sites were subject to habitat filters without the apparent decimation brought about through ploughing is true, the adaption of Renosterveld communities to rejuvenate after fire may go some way to explaining the similarities in diversity indices between the pristine and moderately degraded sites. Further work into Renosterveld functional ecology should include fire as a key ecological driver.

6.2.2 The Biodiversity-Ecosystem Function Relationship

As highlighted in **Chapter 1**, the relationship between biodiversity and ecosystem function is of critical importance in light of the substantial loss of biodiversity globally and the uncertainty on the effects this may have on ecosystem functioning (IPBES, 2018). A key finding from my study of the relationship between taxonomic and functional diversity was the presence of apparent functional redundancy. Functional redundancy, which occurs when species have functional traits in common and therefore perform similar functions (Rosenfeld, 2002), is a crucial factor to consider when addressing the biodiversity-ecosystem function relationship.

The distinction between functional response and effect traits has profound implications for the role functional redundancy plays in the biodiversity-ecosystem functioning relationship. Species which share functional effect traits should by definition contain some degree of redundancy in how they influence certain ecosystem functions (Díaz and Cabido, 2001). However, within these apparent redundant species, variation in functional response traits may exist. An example to illustrate this point is two co-occurring species of *Hermannia*: *Hermannia saccifera* and *Hermannia holosericea*, both found within the study area. The species share almost identical leaf traits, floral traits, and growth forms. These shared traits result in the two species having a redundant role in ecosystem processes such as litter decomposition and pollination. However, where the two species differ profoundly is in their regenerative strategy: *H. saccifera* is a re-sprouter whereas *H. holosericea* is a reseeder. After a fire event, a re-sprouter regenerates from a storage organ beneath the ground quicker than a re-seeder which may take more than a year to reach maturity (Bond and Midgley, 2001). By having unique response traits nested within redundant effect traits, ecosystem processes such as pollination are safeguarded and ecological resilience increased. Species will appear redundant, or functionally unique, depending on which traits are measured. The more traits taken into account, the higher the likelihood that subtle differences, even between seemingly functionally identical species, will be detected**.** Similarly, although potentially less important in the short-term, subtle differences in seemingly functionally redundant species may be crucial for the longer-term resilience of ecosystem functions at the larger landscape scale (Oliver et al., 2015).

The level of influence measured of functional effect traits on ecosystem function is also dependent on the function being studied. Litter decomposition, the ecosystem process studied in **Chapter 3**, is a prime example of the complexity possible within the biodiversity-ecosystem function relationship. Litter decomposition is controlled both at the biotic level, driven by a vast diversity of organisms that are structured in complex food webs (Gessner et al., 2010), and by abiotic factors (Meentemeyer, 1978). Additionally, both biotic and abiotic factors may interact and influence each other (Paudel et al., 2015). At the global and regional scale decomposition is controlled by climate (abiotic) and leaf traits (biotic) (Meentemeyer, 1978; Aerts, 1997). Although climate influences the distribution of all organisms on earth and most ecological processes (Wall et al., 2008), within biomes the effect of leaf traits has been shown to be stronger than climatic controls on litter decomposition (Cornwell et al., 2008). Leaves with higher Nitrogen, lower lignin and low tannin content have been reported to decompose more rapidly across numerous ecosystems (Parton et al., 2007; Garcia-Palacios et al., 2013) including Renosterveld (Bengtsson et al., 2011; **Chapter 3**). Additional biotic drivers of litter decomposition at the local scale include soil-dwelling invertebrates and microbial activity which themselves may be influenced by physical and chemical soil attributes, and seasonal fluctuations in climate and substrate supply (Gonzalez and Seastedt, 2001; Wall et al., 2008; Garcia-Palacios et al., 2013). General principles of the effects of biodiversity on litter decomposition have proved elusive and key questions remain as to when and how biodiversity affects litter decomposition (Handa et al., 2014).

The study conducted in **Chapter 3** included sites with major differences in both taxonomic and functional diversity of above-ground vegetation as a result of habitat degradation. Data reporting a uniform alteration in litter decomposition for litter types in degraded sites compared to pristine sites would have provided evidence of degradation impacts on decomposer organisms and/or the abiotic conditions which influence litter decomposition; however no significant effects of site type on decomposition rate were recorded. Despite this, it would be premature to assert that differences in above-ground vegetation communities have no effect on decomposition rates in Renosterveld as the litter was controlled for across all study sites. Of the three species used as litter, initial leaf nutrient content was a key factor determining decomposition rate. Logically, a community dominated by the nutrient-rich *Medicago* would provide litter input which would result in a substantially higher decomposition rate than a community dominated by *D. rhinocerotis* which, in turn, would have a higher decomposition rate than a *P. eriostoma*-dominated community. Clearly, functional traits matter for litter decomposition, thus a functional approach to studying the biotic controls affecting litter decomposition is important moving forward.

In terms of diversity effects, Handa et al. (2014) found that, across a range of biomes, mixing leaf litter from various plant functional types together (i.e. increasing functional diversity) resulted in accelerated decomposition rates. Similarly, in adjacent Fynbos vegetation, Bengtsson et al. (2012) reported that mixed litter of *Protea* and *Erica* leaves decomposed faster compared to litter bags containing a single species. A possible cause of this is the mechanism by which nutrients move among litters with higher quality litter stimulating the decomposition of a lower quality litter, either by biological processes or leaching (Gartner and Cardon, 2004). It would be intriguing to test decomposition rates of litter mixtures within the study area to assess whether this holds true within Renosterveld. It does not necessarily follow that increased species richness in litter input increases decomposition. Rather litter decomposition dynamics are affected by the presence of particular plant functional traits, supporting the idea that the functional diversity within a community underlies the effects of species richness on ecosystem functions (Garnier et al., 2004; Cadotte et al., 2011).

Vegetation is not the only biotic facet of litter decomposition which is of relevance to exploring the biodiversity-ecosystem function relationship. Soil-dwelling invertebrates and microbial decomposers are integral to the process of litter decomposition (Powers et al., 2009; Garcia-Palacios et al., 2013), yet are rarely considered in large-scale studies (Handa et al., 2014) and the ecological consequences of their diversity little understood (Hättenschwiler et al., 2005). Handa et al. (2014) reported that reducing the functional diversity of decomposer organisms slowed down the cycling of Carbon and Nitrogen in litter. No strong correlation was found when plotting Springtail community functional diversity against litter decomposition rates (Appendix II); however this may be attributed to the limited Springtail trait data. Once our understanding of the functional role soil microfauna plays in litter decomposition improves, it would be instructive to study how functional diversity within decomposer communities impacts on litter decomposition rates.

Pollination, the focus of study in **Chapter 5**, is an ecosystem function of great importance due to the extremely valuable and essential service it provides to humankind (Eilers et al., 2011) and its role in maintaining biodiversity (Ollerton et al., 2011). It is also a subject of attraction to ecologists due to its role in facilitating the understanding of numerous complex ecological concepts such as specialization, niche differentiation and complementarity, interspecific competition, ecological filtering, resilience, extinction cascades, and evolution (Faegri and van der Pijl, 2013). Many of these ecological concepts are at the heart of the biodiversity-ecosystem function relationship and the plant-pollinator networks presented in **Chapter 5** provide a template to explore this relationship further. Three main hypotheses have been proposed to explain how an increase in biodiversity may lead to an increase in pollination service, as reported in numerous studies (e.g. Klein et al., 2003, 2008; Fontaine et al., 2005; Hoehn et al., 2008; Martins et al., 2011). Firstly, selection or sampling effects can result in diverse communities which are more likely to include highly effective species (Loreau and Hector, 2001). Secondly, some community members may enhance the effectiveness of other members through the process of functional facilitation (Cardinale et al., 2002). Finally, niche complementarity is a mechanism by which niche partitioning through space and time results in diverse communities enhancing pollination (Fontaine et al., 2006). It is this latter hypothesis which is the most commonly invoked mechanism to explain how pollination services may increase in diverse communities (Hoehn et al., 2008; Tylianakis et al. 2008; Blitzer et al., 2016).

A key concept in understanding how niche complementarity may enhance pollination is the functional niche, a subset of the ecological niche, and defined as the niche dimensions of a species which represent ecosystem functions (Blüthgen and Klein, 2011). Where functional niche overlaps occur (i.e. different species doing the same thing), species can be considered functionally redundant and interspecific competition is possible (Brittain et al., 2013). Conversely, where multiple species differ in their functional niche, functional niche complementarity can occur (Loreau and Hector, 2001). It is this latter process which supports the theory that increased diversity will lead to increased ecosystem functioning: multiple species with different functional niches contribute more to ecosystem function then any one of them alone. This can occur through a number of mechanisms, some of which are set out below. From the pollinator's point of view, differences in flower phenology and/or variation in the nutrition of floral resources may explain the complementary role of functionally diverse flowering species. For plants, environmental or temporal variation in pollinator species' activities may increase pollination success and thus ecosystem function (Blüthgen and Klein, 2011).

The breadth of the functional niche is closely linked to the level of specialization exhibited by a species: a narrow functional niche breadth is associated with specialist species and a broad niche breadth with generalist species (Waser et al., 1996). However, a continuum exists from fully generalist species to fully specialist species (Waser and Ollerton, 2006) and individual species may shift along this continuum in response to temporal and environmental dynamics (Dupont et al., 2009). This is particularly true of pollinator species who may adapt their foraging strategies to maximise resource acquisition (Valdovinos et al., 2013). Nevertheless, 'forbidden interactions' exist within plant-pollinator networks as a result of trait mismatches resulting in morphological barriers (e.g. long, narrow tubes that are inaccessible to visitors that are either too large or have a short proboscises (Stang et al., 2009)).

The increased ecosystem function as a result niche complementarity and high levels of specialization may come at the cost of increased fragility as specialized interactions are more at risk of extinction due to either natural or anthropogenic-induced environmental fluctuations (Montoya et al., 2006). Conversely, functional redundancy provides ecosystem stability as the loss of a single species is offset by other species which occupy the same functional niche (Naeem, 1998). Species may appear to be redundant under particular environmental conditions, or at a specific time, but differ in their response to environmental changes (Chapin et al., 1997). Furthermore, most studied plant-pollinator networks have reported a high degree of nestedness, a network property where specialist species mainly interact with generalists, thus conferring resilience to pollination services in the face of perturbations such as species extinctions (Bascompte et al., 2003).

Overall, the Renosterveld pollination networks presented in **Chapter 5** appear highly specialized when compared to global network studies. This supports the hypothesis put forward by Pauw and Stanway (2015), who described a high-resolution network in adjacent Fynbos vegetation, that the relative climatic stability of the region through the Quaternary (Chown et al., 2004) allowed specialization to manifest and persist. The networks also exhibited low connectance values which typically occur when numerous unobserved links exist (i.e. a pollinator is not recorded visiting a plant). This is as a result of 'forbidden interactions' due to species possessing certain traits resulting in phenotypic specialization (Ollerton et al., 2007), or size thresholds between interacting pairs (Stang et al., 2009), which restrict pairwise interactions (Kaiser-Bunbury et al., 2014). A high level of specialization and differences in the functional niche breadth of species in Renosterveld suggests that functional complementarity is an important mechanism in maximising pollination. In theory, increased functional diversity in both plants and pollinators in Renosterveld should be associated with increased pollination efficiency as species (assuming they are not functionally identical) occupy different functional niches.

Theory also suggests that increased specialization as a result of functional complementarity may result in increased network fragility. However, it is important to bear in mind what functional specialization actually equates to. For instance, a plant species may have interactions with numerous pollinator species but if these pollinators are not recorded on other plant species the species specialization value for this plant would be high (Pauw and Stanway, 2015). This is because specialization indices (H’ and d’ – see **Chapter 5**) take into account the scope of available interaction partners. For example, a plant species may be pollinated by multiple species of rodent but if these rodents are not recorded in abundance on other plant species in the community the plant species in question will be considered highly specialized. For the plant this provides a degree of insurance against the loss of a rodent pollinator as other ‘redundant’ species will continue to pollinate it. For the rodent species in this scenario, their existence is more fragile. It is for this reason that one-to-one pollination interactions are rare in nature (Johnson and Steiner, 1995); rather, pollination guilds are formed where pollinator species with similar functional traits visit plant species which share similar traits. Traits can be phylogenetically conserved, such as numerous bird species with elongated beaks who visit red, nectar-rich flowers (Geerts and Pauw, 2009), or through convergent trait evolution such as where minuscule beetle and fly species pollinate minute-flowered plants (Pauw and Stanway, 2015).

In **Chapter 5** I reported on three plant-pollination networks, each from a site with a unique land-use history, ranging from pristine vegetation to a site where agricultural activity occurred up until five years before the study occurred. Although a lack of duplication prevented any robust statistical analysis, network indices were shown to be variable across the degradation gradient. Globally, anthropogenic disturbance, particularly the degradation and loss of natural and semi-natural habitats, is regarded as a primary cause of pollinator decline (Goulson et al., 2008). Agricultural intensification, and the assorted pressures associated with it (e.g. fragmentation, introduced non-native plants, agro-chemicals, and disease) may have both direct and indirect effects on pollination (Steffan-Dewenter and Westphal, 2008). From the pollinator’s viewpoint, habitat alteration may not only reduce the diversity and abundance of floral resources but also that of nesting habitats (Potts et al., 2010). Homogenization of the landscape, a common result of increased agricultural intensity, reduces the diversity of floral resources limiting plant-pollinator interaction diversity, particularly in networks which are naturally specialized and exhibit a degree of niche complementarity (CaraDonna et al., 2017). For plants, in addition to direct effects of habitat alteration on community structure, the concurrent reduction in pollinator assemblage can result in reduced seed-set and, in the worst case scenario, their local extinction if they are not self-compatible (Wilcock and Neiland, 2002). Clearly shifts in the number of interacting species or the functional composition (i.e. the biodiversity) of a community caused by habitat alteration can have cascading effects on the structure of plant-pollinator networks which will likely result in changes to pollination efficiency (Ponisio et al., 2017).

Although it was unfeasible to implement seed-set experiments to assess pollination efficiency in my pollination network study, with the use of data from **Chapters 2** and **5** I can assess how changes in taxonomic and functional diversity of plant communities as a result of habitat degradation impacted on the associated pollinator communities. There was a correlation between higher plant species richness and the number of pollinators recorded. This resulted in the more diverse sites having a higher number of plant-pollinator interactions, larger network sizes, increased levels of network specialization, and lower connectance values. In terms of plant functional diversity, higher functional richness and evenness was associated with increased pollinator species richness. Of course, the traits used to calculate functional diversity indices in **Chapter 2** were not all related to pollination. It would be informative to calculate the functional diversity of plant communities from the study sites using pollination-specific traits such as corolla length, nectar volume, flower size and shape in addition to the traits already measured (i.e. flower colour and flowering phenology). Similarly, calculating functional diversity indices for the pollinator communities would provide further insight into the relationship between pollinator taxonomic and functional diversity indices, the biodiversity-ecosystem relationship, and allow for a comparison of the relationship between the functional diversity of both plants and pollinators. Finally, the three sites chosen here to represent the different degradation states were outliers when compared to the overall trend reported for communities along the degradation gradient in **Chapter 2**. Here, the highly degraded site had higher plant species richness and functional diversity compared the moderately degraded site as it was supplemented by a number of flowering non-native species. In addition, the indigenous shrubs present at the highly degraded site possessed floral traits which made them more attractive to pollinators when compared to the indigenous shrub species dominant in the moderately degraded site. The implications of this are addressed in more detail in section 6.3

6.3 Practical Implications

In this thesis I have shown that species richness, in isolation, is inadequate as a descriptor of biodiversity in above-ground vegetation. In Renosterveld, where functional redundancy is an important mechanism ensuring ecosystem resilience, information on how a species responds to environmental shifts and affects ecosystem processes, as governed by its functional traits, is of more value to land managers than taxonomic descriptors. Replacing, or better yet supplementing, taxonomic indices with functional diversity indices can provide information which results in a better understanding how ecosystems function and their resilience or vulnerability to environmental perturbations.

Functional diversity is a multifaceted entity and the results from **Chapter 2** revealed that each facet responded differently to changes in taxonomic diversity thus, for a holistic representation of the functional diversity of a community, it is recommended that all three components are calculated. Functional richness is inherently linked to species richness and is most suited for analysing the level of functional redundancy within a community. A strong and steep linear correlation between functional richness and species diversity would be indicative of limited functional redundancy as the addition of species introduces new traits into the functional space. Conversely, a less steep or a logarithmic-shaped correlation is indicative of functional redundancy as increasing the number of species does not introduce new traits into the functional space. In the former case, the reduced redundancy may be indicative of community in danger of compromised ecosystem function as any loss of species results in a loss of functional traits. Functional richness does not take into account the abundance or evenness of trait distribution within the functional space, therefore additionally utilising both functional evenness and divergence are recommended, particularly in the monitoring of community health as it may provide an early warning signal of habitat degradation (Villéger et al., 2010). Disturbance or ecosystem degradation can change the distribution of traits within a community without necessarily the extirpation or local extinction of species. Even low disturbance intensity can diminish the population of species with vulnerable traits without reducing species richness or affecting functional richness (Mouillot et al., 2013). Land managers and conservationists can use this information to act pre-emptively in an attempt to firstly identify the cause of the degradation, and secondly stave off more severe damage to ecosystem health through appropriate remedial actions.

Understanding how habitat filters and biotic interactions affect community disassembly and reassembly during degradation and subsequent secondary succession is important in informing management decisions. The findings of this thesis suggest that an understanding of the disturbance history of individual habitats is a central starting point for evaluating the potential trajectory of degraded communities. The most common forms of historical agricultural land-use in the region are crop farming and livestock grazing. In the former, ploughing, either solely at the onset of land conversion or more frequently, appears to impose particularly strong habitat filters which notably affect geophytes and re-sprouting species. In these communities remedial action will need to be taken to re-introduce the plant functional types that are locally extinct. Intensive grazing on the other hand, favours the persistence of non-palatable species such as *Galenia africana* and *Dicerothamnus rhinocerotis* over more palatable species. Unlike ploughing, grazing would presumably leave the seedbank and underground storage organs of geophytes and other re-sprouters undisturbed, resulting in an increased likelihood of these populations rejuvenating once the grazing pressure is alleviated. However, if over-grazing has occurred over a multi-year period, more platable species may have gone locally extinct and require re-introduction. Both ploughing and livestock grazing activity are associated with the introduction of non-native species, particularly annual grasses and herbaceous growth forms. Furthermore, in previously ploughed land, non-native species establishment and success may be enhanced by a lack of competition from the decimated indigenous plant community. An understanding of the functional compostion of the non-native species present in a community will hep inform land managers on whether they require active removal or whether their impact on environmental health is more understated.

A further important factor to consider when assessing potential ecosystem trajectory is the general structure of the landscape. A major process in community reassembly is the immigration of species from the regional species pool. In the study area, natural remnants of vegetation are highly fragmented thus dispersal ability is a key determinant in governing which species are capable of immigrating to degraded communities, particularly if those communities are isolated. For wind or bird-dispersed species the fragmented structure of the landscape is not particularly troublesome, however in the case of species with shorter dispersal mechanisms (e.g. myrmecochorous species), fragmentation can prevent their reestablishment in degraded habitats where they underwent local extinction. Short dispersal distances may be less of a hurdle for community reassembly if the degraded community is contiguous or in close proximity to pristine vegetation.

Finally, community reassembly may be heavily influenced by natural occurring perturbations such as fire. Renosterveld vegetation has evolved in conjunction fire and is adapted to a fire return interval hypothesized to be between 7-15 years (Kraaij, 2010), although there is virtually no peer-reviewed literature on this matter (Bond et al., 2004). Obligate re-seeders are at risk if subjected to extreme fire regimes. Too frequent fires before re-seeders can set seed can lead to local population collapse.

On the other hand, if fire is excluded, species may senesce and no longer produce viable seeds (van Wilgen, 2013). Fire regime also interacts with other ecological drivers such as grazing. Over-grazing following a fire can halt the natural successional trajectory resulting in community dominated by unpalatable species. Of course, Renosterveld evolved with natural grazing pressure from indigenous herbivores however the historical landscape would have been continuous and vast enough to sustain healthy levels of grazing intensity. Nevertheless, pristine Renosterveld is suited to being grazed at an appropriate level. Despite a dearth of empirical data on what this acceptable level may be, approximate guidelines are available from local conservationists and local government structures who liaise with farmers where possible. Renosterveld patches on privately owned land are routinely used as supplementary grazing by livestock farmers. Where this is managed correctly, it should be a boon rather than a bane for ecosystem health. Indeed, this particular service provided by Renosterveld can provide an important motivation to encourage private land-owners to invest in conservation. However, where this ecological know-how is lacking, or ignored, the use of recovering or pristine land for grazing can be hugely detrimental.

In summary, taxonomic diversity is an inadequate metric of biodiversity in Renosterveld. Replacing or preferably supplementing it with functional diversity metrics allows for a more robust, mechanistic understanding of vegetation dynamics. The relationship between species richness and functional richness can provide a useful measure of redundancy (or lack thereof), while functional evenness and functional divergence can be utilised to monitor degradation, providing an early warning signal without the loss of species. In terms of management of previously disturbed habitats, detailed knowledge of land-use history can be highly beneficial for conservation planning. Community assembly following the cessation of agricultural activity may occur organically if the land-use was limited to grazing, and the presence of non-palatable shrubs (e.g. *Galenia africana* and *Dicerothamnus rhinocerotis*) does not prevent species joining the community either through resprouting from underground stock, or emigrating from the regional species pool. Conversely, habitats which have undergone ploughing and are not contiguous with pristine vegetation, may struggle to return to a community structure containing the entire suite of functional traits ordinarily found in healthy Renosterveld vegetation. Here, active measures may need to be taken to introduce resprouting, dispersal limited, and palatable species back into the community. Finally, natural ecosystem drivers such as fire and grazing need to be considered during secondary succession.

As alluded to earlier, private land owners, which in the study area are predominantly commercial farmers, need to be motivated to conserve remaining pristine fragments or restore degraded habitats on their land. If farmers believe that Renosterveld provides value to the overall functioning of their farms they may be encouraged to be active participants in its conservation. Relating ecosystem functioning of healthy Renosterveld to tangible beneficial ecosystem services is one such method. However, to achieve this one needs to know that what is considered healthy Renosterveld does indeed enhance ecosystem functioning.

Pollination is one such ecosystem function that provides direct benefit to the agriculture industry. Although plant-pollinator network analysis may not provide seed set data and thus empirical proof of pollination efficacy, certain inferences can still be made. Network structure varied across the three study sites, seemingly as a result of the above-ground community structure and functional composition. Numerous examples exist in the literature showing how historical landscape modification as a result of agricultural land-use has led to a decrease in pollinator diversity and subsequent reduction in seed set (Aguilar et al., 2006; Klein et al., 2012; Burkle et al., 2013; Clough et al., 2014). The fact that the pristine site supported the most diverse network suggests that undisturbed habitats improve pollination functioning. For farmers who grow crops which have been shown to benefit from pollinator diversity, such as Canola (Morandin and Winston, 2006) and Lucerne (Cane, 2002), conserving patches of pristine Renosterveld within the broader agricultural matrix is therefore a valuable undertaking with tangible benefits.

As highlighted in section 6.2.2, compared to the moderately degraded site, the highly degraded site was more similar in network properties to the pristine site. In **Chapter 5** I attributed the lack of pollinator diversity in the moderately degraded site to the uniform nature of the plant community and the characteristics of its dominant species, *Dicerothamnus rhinocerotis*. *D. rhinocerotis* is an early successional species which can dominate degraded veld, particularly where over-grazing has occurred (Krug and Krug, 2007) and is wind-pollinated. In contrast, the highly degrade site was more open with more increased levels of functional richness and functional divergence with indigenous insect-pollinated shrubs supplemented by non-native, flowering, herbaceous species. Clearly the habitat structure of this relatively novel system provided a wider range of resources for the pollinator community, as has been reported elsewhere (Moragues and Traveset, 2005). However, non-native species can also reduce the pollination of indigenous species through competition (Morales and Traveset, 2009). The results from **Chapter 5** suggest that increased functional diversity of above-ground vegetation is recommended for promoting more diverse plant-pollinator networks, even if the floral community contains non-native species, but I would suggest controlled seed set experiments to ensure that we better understand how the abundance of non-native plants affect the pollination efficiency in indigenous plant species.

Unlike pollination the ecosystem function of litter decomposition is less likely to capture the attention of private land owners. Although it is essential to the cycling of nutrients, Carbon and energy both within and between ecosystems (Aerts, 2006; Parton et al., 2007) these are not necessarily primary concerns for farmers despite the importance global importance attached to informing robust models linking the biosphere and atmosphere. In Renosterveld, the role of litter decomposition has historically been underestimated due to the natural occurrence of fire (Kruger and Bigalke, 1984, Mitchell et al., 1986; Witkowski, 1991). However, this study supports more recent findings by Bengtsson et al. (2011) that litter decomposition is an important process between fire events and that decomposition rates vary significantly between species and that leaf traits, particularly initial nutrient content, are a good predictor of species decomposition rate. This thesis also provided the first study into the decomposition of a non-native species in Renosterveld and *Medicago* sp. litter, the species in question, was found to decompose significantly faster than the other studied species. An influx of *Medicago* sp. into a Renosterveld system may accelerate the natural rate of nutrient cycling. Interestingly, in a previous study, *Galenia africana* was found to have a similar decomposition rate to that reported for *Medicago* sp. in this study (Bengtsson et al., 2011). *Galenia africana*, although indigenous, is associated with highly disturbed over-grazed land thus, in disturbed Renosterveld where either one or both species are dominant, the rate of nutrient cycling through litter decomposition may be accelerated. What effect this would have on other ecosystem properties, such as soil fauna composition, is unknown and would require further investigation.

As an important component of soil fauna, it is encouraging that the results from **Chapter 4** reported that litter type and degradation level were found to have no significant effect on Springtail richness or abundance. Without more detailed knowledge on their functional ecology it is perfidious to make any practical recommendations; however the intriguing possibility of Springtails to act as bioindicators, as they have been used elsewhere (Van Straalen, 1998; Greenslade, 2007; Vandewalle et al., 2010), is worth exploring further. *Entomobrya multifasciata*, a non-native species, was found in significantly higher numbers in degraded sites compared to sites with pristine vegetation. Expanding the range of study of Springtails to assess the distribution of *E. multifasciata* at a larger scale, and investigating potentially relevant functional response and effect traits would be an important first step in establishing the viability of using the species as an indicator of soil quality and ecosystem health particularly in relation to land-use disturbance (Siepel, 1995; Van Straalen et al., 2008).

6.4 Future Gazing: Points Of Departure For Functional Ecology In Overberg Renosterveld

Despite an increase in interest in recent years (Topp and Loos, 2019), this thesis is one of the few studies into the functional ecology of Overberg Renosterveld. Functional ecology is such a broad topic that this thesis could never comprehensively investigate the numerous ecosystem functions and relationships which fall under its banner. Although significantly advancing our understanding in many ways, the nature of this approach is that it raises just as many questions as answers. Below, I detail some key knowledge gaps and suggest points of departure for future work.

Firstly, compared to the Northern Hemisphere, we still lag behind when it comes to detailed trait databases. Functional traits are the building blocks upon which functional ecological studies are made yet for too many species, trait data is unavailable. In a system influenced by fire and grazing, it is imperative we improve our knowledge on traits related to these stochastic ecological drivers. Similarly, the fragmented nature of the landscape means that improving our knowledge of dispersal and establishment capability is essential for understanding community dynamics. For many species, dispersal vectors and seed traits remain absent. While I acknowledge that the initial compilation of such data is time-consuming and potentially costly in such a diverse vegetation type, the accumulation and collation of information in an accessible database would allow and encourage further work on ecosystem functionality within the region.

Controlling for land-use history is another factor which would benefit future studies. In this thesis a lack of high-resolution land-use history data prevented any robust comparisons to be made between the effect of historical ploughing and intensive grazing. Alternatively, long term monitoring of sites with known disturbance histories would provide powerful data into secondary successional dynamics. Similarly, the history of ecological drivers is an important factor in determining habitat structure and composition. Studies which include high-resolution fire history and grazing intensity data would be informative. Alternatively, long-term monitoring where these drivers are controlled for (e.g. grazing enclosures or controlled burns) would also be instructive in detailing community disassembly and reassembly dynamics.

For Springtails, there is more that we do not know than what we do. While improving our taxonomic knowledge of endemic species is important, to relate Springtails to functional ecology it is essential we improve our understanding of their functional traits and how they respond to environmental conditions and affect ecosystem functioning. Laboratory experiments which link morphological features to both diet and habitat preference are important next steps. In addition, this thesis has highlighted the possibility of using *Entomobrya multifasciata* as a bioindicator of degraded habitats.

Before this can be effectively used, the population pattern recorded in this study needs to be assessed on larger scale to ensure it is a consistent rather than an idiosyncratic finding. Additionally, an understanding of the ecological filters and/or biotic interactions which allow the species to thrive in degraded lands but remain absent from pristine environments would be informative.

Despite clear differences existing in the above-ground vegetation of the study sites used for litter decomposition investigation, soil chemistry was found to be similar. As litter decomposition takes place in or above the soil, it would be interesting to study whether differences in soil chemistry impact decomposition rate. For this *a priori* soil analysis would be required prior to site selection. Furthermore, differentiating between the importance of biotic and abiotic factors may be informative. This would require inoculation of litter prior to initiation of the study and preventing faunal access to a select number of samples. Finally, to address whether functionally diverse litter decomposes faster than its individual constituents, including a litter mixture alongside individual species would be instructive.

With regards to pollination, it is important that future work takes into account pollination success through the utilisation of seed set experiments. Within this remit, various other focuses of pollination studies exist. Enhancing our knowledge of pollinator efficiency is important as different species possess different functional and behavioural traits. Indeed, assessing plant-pollinator interaction networks through the lens of functional traits is advocated to link diversity to function. Finally, how plant-pollinator network dynamics change after a fire event has yet to be explored in Renosterveld, however it is crucial in understanding the effect of disturbance on biodiversity which is directly related to a measurable ecosystem function.

6.5 Conclusion

Considering the results generated from this study into the functional ecology of a highly localized and critically endangered vegetation type in relation to global debates, a few conclusions can be drawn. Firstly, taxonomic diversity is clearly an inadequate measure of ecosystem functionality in Renosterveld and to truly gain a mechanistic understanding of the biodiversity-ecosystem function relationship one needs to utilise measures of functional diversity. Secondly, the biodiversity-ecosystem function relationship is highly complex with different measures revealing different facets of the relationship. Diversity can be found, measured and impact on different levels of an ecosystem and the lens one chooses to look through to study the biodiversity-ecosystem function relationship is important. From the community (e.g. Springtails or above-ground plant communities), to ecosystem outcomes (e.g. litter decomposition) and functions (e.g. pollination), each aspect is controlled by the functional composition of the organisms present. But nothing in nature acts alone. The abiotic environment interacts with the biotic environment and, within the biotic environment, feedbacks exist across multitrophic levels. To gain the most holistic understanding of the functional ecology of a landscape it is important to acknowledge all these aspects and feedback mechanisms. Finally, what we see at any given point is merely a snapshot in time. Understanding the land-use history of an environment not only aids in explaining the current communities present, but is influential in understanding what the future may hold and what, if any, actions are required to maintain or increase ecosystem integrity and resilience. To conserve, one must understand. Although this thesis has started to address the issue, there is still plenty of work to be done in Renosterveld from increasing the data available on the building blocks of functional traits to landscape-level multitrophic processes.

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Appendix 1

Methodology

To assess the functional composition of the Springtail assemblages and test whether there was a correlation between species richness* and functional diversity, three traits were measured from each identified morphospecies using the measurement function of Leica Application Suite software on a Leica DM4B or a Leica Z16 APO (Leica Microsystems, Wetzlar, Germany). Body length (maximum length from head to tip of abdomen) is connected to dispersal ability, lifeform and ecophysiology (Berg et al., 1998). Antenna-to-body ratio (antennal length divided by body length) is assumed to be linked to sensory ability and active dispersal (Da Silva et al., 2012; Widenfalk et al., 2016). Antenna length was measured and used in conjunction with body length to calculate antenna-to-body ratio. Life form is trait complex composed of number of ommatidia, length of body and intensity of colouration (Gisin, 1943) and is a proxy for vertical stratification, ecophysiology and dispersal ability (Ponge et al., 2006). Life form for the morphospecies were determined from their morphological characteristics or from records in the literature and classified into one of the following groups: Euedaphic refers to soil dwelling species; hemi-edaphic to litter dwelling species; and atmobiotic to free living species in the vegetation (Gisin, 1943; Janion-Scheepers et al., 2016a**).

It should be noted here the limited number of functional traits used (i.e. body length, antennae to body length ration, life form) reduced the robustness of functional diversity indices. Functional richness can only be calculated where the number of species is larger than the number of traits therefore littertraps containing less than three Springtail species were excluded for analysis. Similarly, functional evenness and functional divergence could not be calculated for communities where less than two species were recorded.

Using the FD package in R (R Core Team, 2015), I computed community level weighted means (CWMs) of the Springtail assemblage within each littertrap. CWMs express the structure of trait values in the community (Lavorel et al., 2008). For continuous traits, the CWM is the mean trait value of all species present in the community weighted by their relative abundances. In addition, I calculated four measures of functional diversity which describe different functional aspects of biological communities. As defined by Derhé et al. (2016) and Májeková et al. (2016): (i) functional richness (FRic) is the range of traits in a community quantified by the volume of functional trait space occupied; (ii) functional evenness (FEve), which summarizes how species' abundances are distributed throughout the occupied functional trait space; (iii) functional divergence (FDiv), which describes the variation in the distribution of species abundances with respect to the centre of functional trait space (Villéger et al., 2008); (iv) functional dispersion (FDis), which indicates the distribution of abundances in functional trait space relative to an abundance weighted centroid, and the volume of space occupied (Laliberté and Legendre, 2010).

Each littertrap/Springtail assemblage had an associated category for litter type, site where it was placed, and number of days it was in the ground for. CWM data was used to create Figures S6.1-S6.3 and Kruskal-Wallis tests and pairwise comparisons using a Wilcoxon rank sum tests were performed to test for significant differences between factors.

Functional diversity indices were plotted against species richness data from the littertraps to create Figures S6.4-S6.7 to explore the relationship between taxonomic and functional diversity indices through the fitting of regression lines.

*see methods section in Chapter 4

**all references cited in Appendix I and II can be found in section 2.6 or section 4.6.

Results

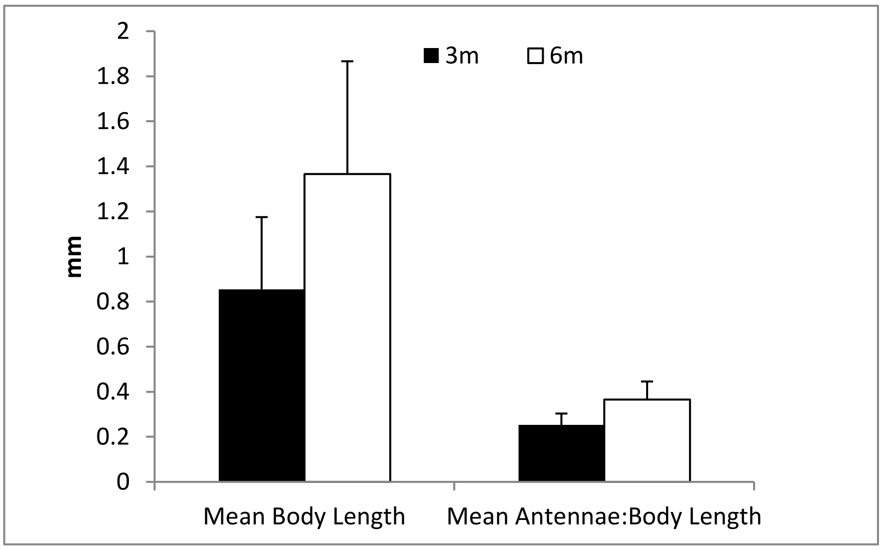

Figure S6.1: Community weighted means (plus standard deviation) for two quantitative functional traits for Springtail communities removed after three and six months. Mean body length was significantly different for communites removed after 3 months and those removed after 6 months at p<0.001. The same was true for mean antennae:body length ratio but at p<0.01.

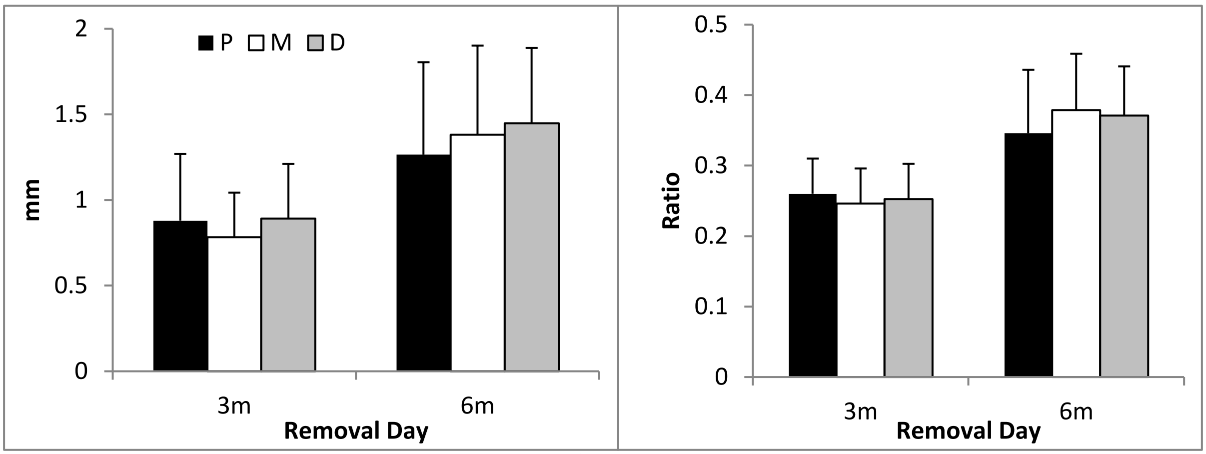

Figure S6.2: Community weighted mean values (plus standard deviations) for Springtail assemblages from littertraps located in 3 different site types and across the 2 removal days. The figure on the left illustrates mean body length and the figure on the right mean antennae:body length ratio. No significant differences were reported. P=Pristine; M=Moderately Degraded; D=Highly Degraded.

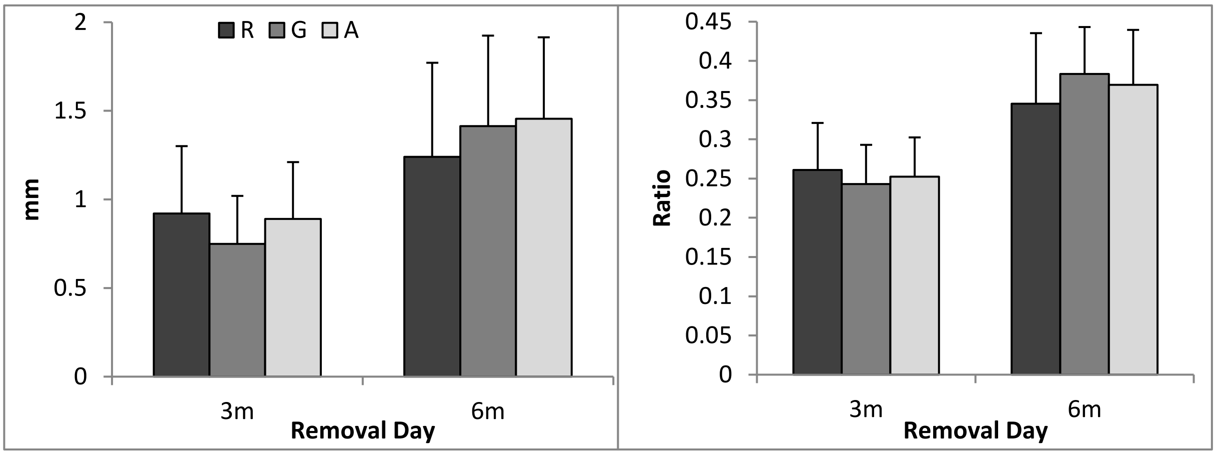

Figure S6.3 Community weighted mean values (plus standard deviations) for Springtail assemblages from littertraps containing 3 litter types and across the 2 removal days. The figure on the left illustrates mean body length and the figure on the right mean antennae:body length ratio. No significant differences were reported. R=Renosterbos; G=*P. eriostoma*; A=*Medicago* sp.

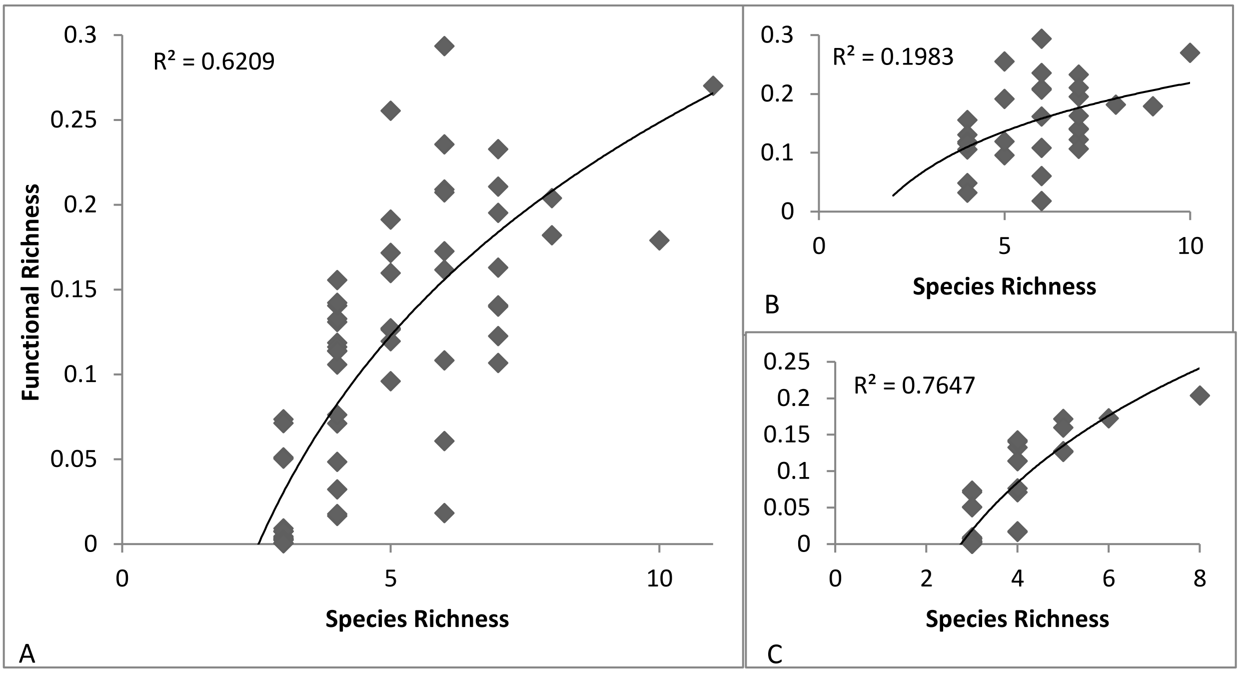

Figure S6.4: Scatter plots showing the best fitted relationship between species richness and functional richness in a) overall littertraps b) littertraps removed after 3 months c) littertraps removed after 6 months.

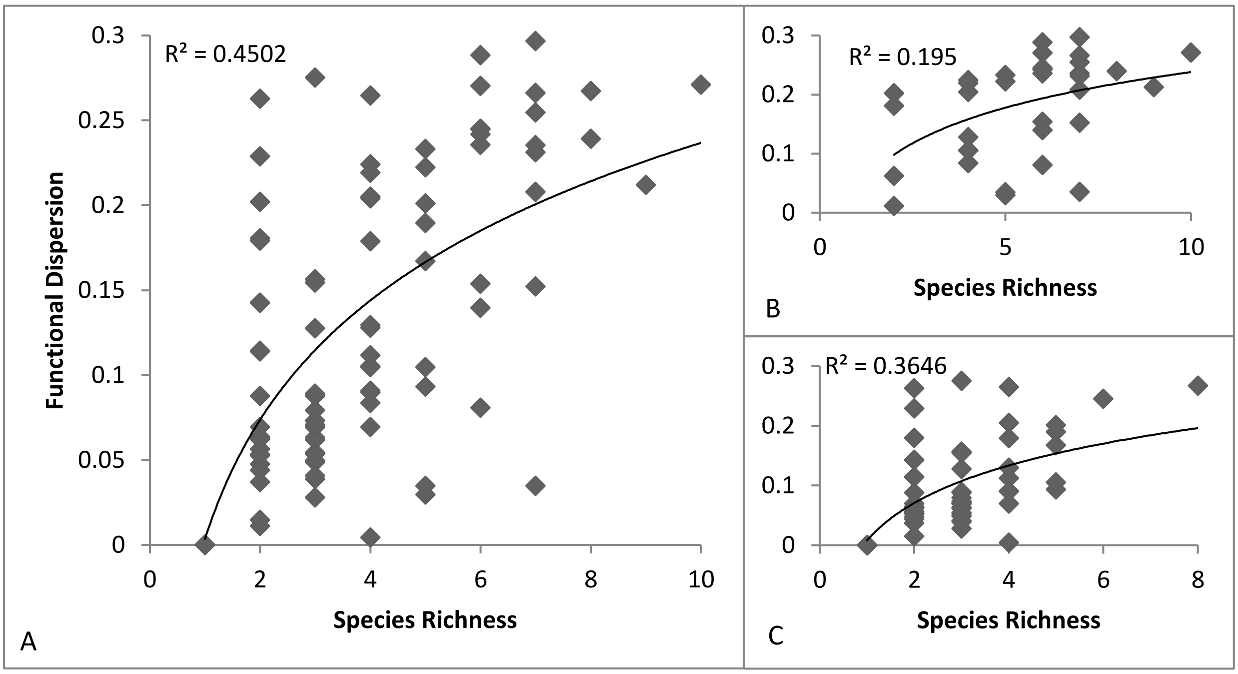

Figure S6.5: Scatter plots showing the best fitted relationship between species richness and functional dispersion in a) overall littertraps b) littertraps removed after 3 months c) littertraps removed after 6 months.

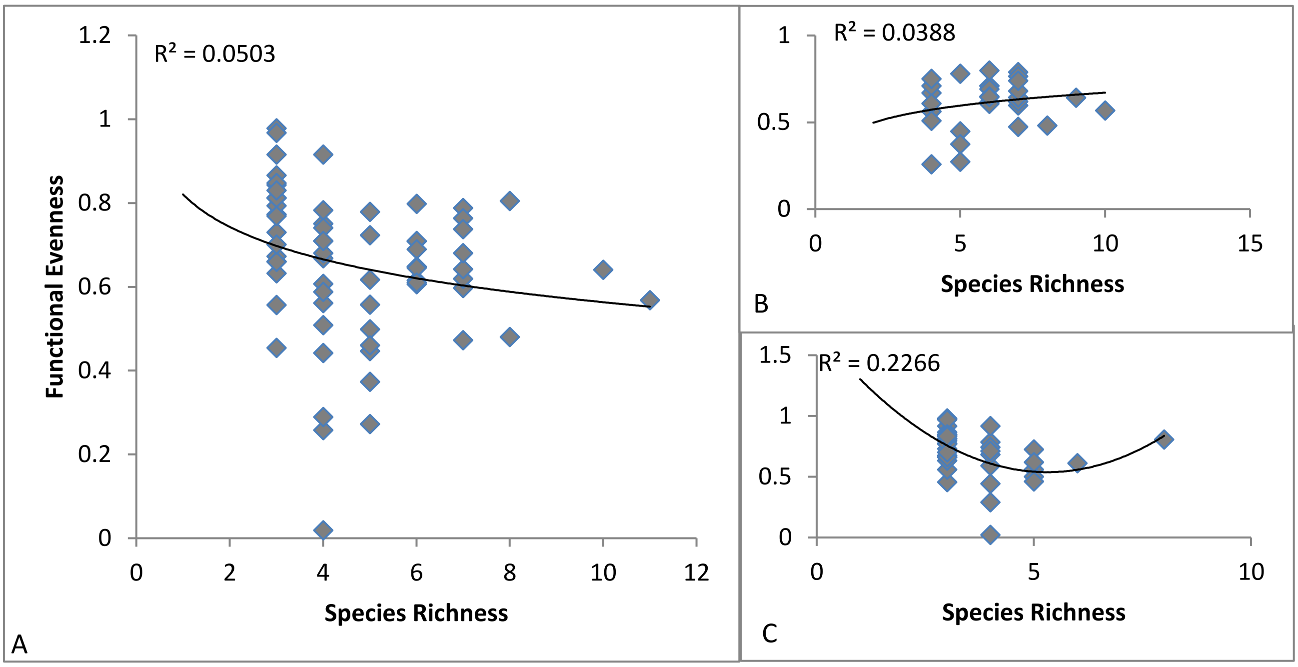

Figure S6.6: Scatter plots showing the best fitted relationship between species richness and functional evenness in a) overall littertraps b) littertraps removed after 3 months c) littertraps removed after 6 months.

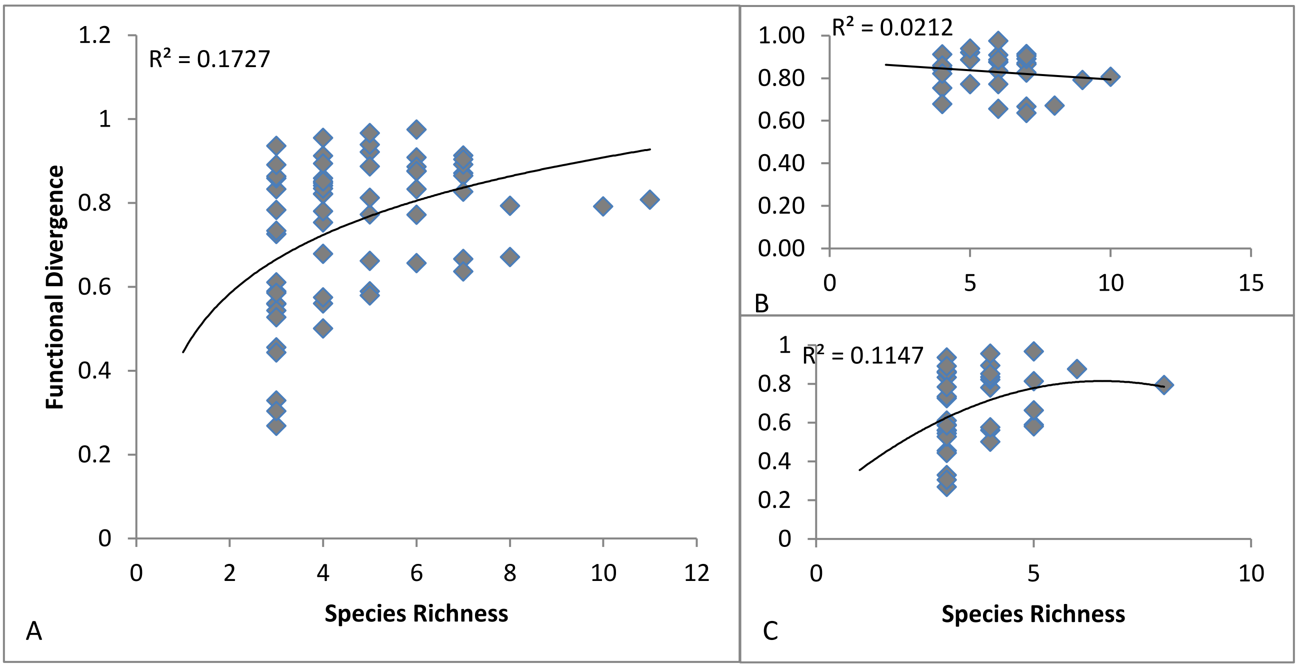

Figure S6.7: Scatter plots showing the best fitted relationship between species richness and functional divergence in a) overall littertraps b) littertraps removed after 3 months c) littertraps removed after 6 months.

Appendix II

Table S6.1 combines data taken from the functional diversity conducted in Chapter 2 with species richness and specialization indices taken from Chapter 5.

Table S6.1: Taxonomic diversity, functional diversity and specialization indices from three pollination network study sites.

	Plant Species Richness	Pollinator Species Richness	Functional Richness	Functional Evenness	Functional Divergence	Network Specialization
Pristine	36	69	0.016	0.748	0.681	0.66
Moderately Degrade	15	43	0.005	0.700	0.590	0.49
Highly Degraded	23	55	0.009	0.651	0.811	0.55