The relative importance of species richness and functional diversity for ecosystem functions performed by dung beetles (Coleoptera: Scarabaeidae) in South Africa.

by

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Declaration

By submitting this dissertation electronically, I declare that the entirety of the work contained therein is my own, original work, that I am the sole author thereof (save to the extent explicitly otherwise stated), that reproduction and publication thereof by Stellenbosch University will not infringe any third party rights and that I have not previously in its entirety or in part submitted it for obtaining any qualification.

Date: August 2020

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I dedicate this dissertation to:

My Parents, Agnes Tinswalo and Philemon Nkhangweleni Simba, for giving me the best foundation in life, love and faith. The sacrifices and difficulties you endured while ensuring that my siblings and I get the best education will not be forgotten. All the greatness that we are to achieve was founded in your inspirational lives and unconditional love.

Audrey RareGold Raedani for inspiration and spiritual guidance. All the love you left with me, I will give to those around me in the way that you taught me. And I will make sure to continue the good that you started, with your works and your children. Rest in peace and Sail on my ship.

Overall Summary

The ongoing and accelerating loss of biodiversity due to anthropogenic activities has highlighted the effects of declining biodiversity on ecosystem functioning. In rangelands, livestock grazing along with variation in soil texture and climatic conditions can have significant impacts of biodiversity through alteration of habitat structure. In the semi-arid Karoo, South Africa, rangelands are extensive, and much of this ecosystem has been disturbed by livestock. This study aimed to determine how variation in land use (rangeland for livestock or protected area) and rainfall (100 to 520 mm.year^{-1} in the Nama Karoo and 20 to 290 mm.year^{-1} in the Succulent Karoo) influence the functionally important dung beetle diversity (i.e. species richness, abundance, functional diversity and body size, and their assemblage composition, and the ecosystem functions they provide in the semi-arid Karoo. Here, I investigate the relative importance of long-term (mean annual precipitation), medium-term (yearly difference from mean) and short-term (recent rains) on dung beetle species richness, abundance and assemblage composition.

First, I assessed whether variation in land use, herbivore stocking rates, vegetation cover, soil texture and rainfall affect dung beetle communities and functional diversity. Dung beetle abundance and functional diversity showed contrasting responses between protected areas (PAs) and livestock farms, with PAs having a significantly greater abundance of dung beetles and lower functional diversity. Neither species richness nor body size was influenced by land use, although richness and abundance increased with higher herbivore stocking rates and rainfall. Species richness was best predicted by short-term rainfall and abundance by long-term rainfall.

I further assessed whether variation in land use and rainfall affect dung beetle community composition. Dung beetle species composition varied between farms and PAs, and also varied with MAP, stocking rates, vegetation cover and rainfall season. I Identified 15 indicator species that explained this variation in dung beetle species composition which were associated with the different environmental variables, furthermore, four of these species were associated with two environmental variables. The response of dung beetle species to environmental variables was influenced by their functional traits, particularly reproduction capacity and dispersal ability. There was greater reproduction capacity for dung beetles in the PAs than on farms. Greater dispersal ability was also associated with PAs as well as the summer rainfall region and greater vegetation cover. I also assessed beta diversity across the rainfall gradient, and these analyses indicated that beta diversity is driven by assemblage nestedness, with all species at the driest sites being a subset of the assemblage in the wettest sites.

I then investigated the role of dung beetle communities (in terms of their abundance, species richness, body size and functional groups (rollers or tunnellers)) and the influence of environmental variables on the ecosystem functions that they provide. The rate at which dung was removed increased with increased species richness in both farms and PAs and increased with an increase in rainfall, with dung removal responding to medium-term rainfall. Different functional groups proved to be more efficient at different functions. Rollers and tunnellers efficiently facilitated the removal of dung and plant productivity, respectively. This demonstrated that the different functional groups made different contributions to different ecosystem functions (i.e. dung removal or nutrient cycling), and that conservation of a

functionally complete species assemblages is essential to maintain optimum ecosystem functioning.

Both dung beetle communities and their ecosystem functions showed varied responses to rainfall. This suggests that to fully understand dung beetle community structure and their contribution to ecosystem function, ecological studies need to include all species community attributes when assessing the impacts of land use and climate changes. Moreover, to fully grasp their contributions to ecosystem functions, these assessments should not rely on only one of their ecosystem functions.

Algehele opsomming

Die deurlopende en versnellende verlies van biodiversiteit as gevolg van menslike aktiwiteite het beklemtoonde effekte op ekosisteemwerking. In weidingslande, kan veewyding tesame met variasie van grondtekstuur en klimaatsomstandighede beduidende impakte hê op biodiversiteit, deur middel van veranderde habitatsstruktuur. Weidingslande neem groot areas in beslag in die halfdroeë Karoo van Suid-Afrika, en 'n groot deel van hierdie bioom is alreeds versteur deur veeboerdery. Die doel van hierdie studie was om te bepaal hoe verskillende grondgebruike (weidingslande vir vee of beskermde gebiede) en reënval (100 tot 520 mm.jaar-1 in die Nama Karoo en 20 tot 290 mm.jaar-1 in die Vetplant Karoo) die funksioneel-belangrike miskruier diversiteit (d.w.s. spesierykheid, veelheid, funksionele diversiteit en liggaamsgrootte), en hul spesiesamestelling, en die ekosisteemfunksies wat hul uitvoer in the halfdroeë Karoo, beinvloed. Hier ondersoek ek die relatiewe belangrikheid van langtermyn (gemiddelde jaarlikse reënval), mediumtermyn (jaarlikse verskille teenoor die gemiddeld) en korttermyn (onlangse reën) op miskruier spesierykheid, veelheid en spesiesamestelling.

Ek het eerstens geassesseer of variasie in grondgebruik, herbivoor aanvullingskoers, plantbedekking, grondtekstuur en reënval miskuier gemeenskappe en funksionele diversiteit affekteer. Miskuier veelheid en funksionele diversiteit het tussen beskermde gebiede (BGe) en veeplase teenstrydige reaksies getoon, waar BGe beduidend hoër miskruier veelheid en laer funksionele diversiteit getoon het. Spesierykheid en liggaamsgrootte was nie deur grondgebruik beïnvloed nie, alhoewel spesierykheid en veelheid toegeneem het tesame met vee-aanvullingskoers en reënval. Beste voorspellings vir spesierykheid was volgens

korttermyn reënval, terwyl die beste voorspellings vir veelheid volgens langtermyn reënval was.

Ek het verder geassesseer of variasie in grondgebruik en reënval miskruier gemeenskapsamestelling affekteer. Miskruier spesiesamestelling het gewissel tussen plase en BGe, asook MAP, aanvullingskoers, plantbedekking en reënvalseisoen. Ek het 15 aanwyserspesies geïdentifiseer wat hierdie variasie in miskruier spesiesamestelling verduidelik, wat geassosieer was met veskillende omgewingsveranderlikes. Verdermeer was vier van hierdie spesies geassosieerd met twee omgewingsveranderlikes. Die reaksies van miskruier-spesies teenoor omgewingsveranderlikes was beïnvloed deur funksionele karaktereienskappe, spesifiek voorplantingskapasiteit en verspreidingsvermoë. Daar was hoër voorplantingskapasiteit vir miskruiers in BGe in vergelyking met plase. Beter verspreidingsvermoë was ook geassosieer met BGe, asook die somerreënvalgebiede en hoër plantbedekking. Ek het ook beta-diversiteit oor die reënvalsgradiënt geassesseer, en hierdie analises het getoon dat beta-diversiteit aangedryf word deur genestheid van gemeenskappe, waar die gemeenskappe in droeë gebiede 'n onderafdeling van dié gemeenskappe in natter gebiede is.

Hierna het ek die rol van miskruier-gemeenskappe (in terme van spesierykheid, veelheid, liggaamsgrootte en funksionele groepe (rollers of tonnelgrouers)) en die invloed van omgewingsveranderlikes op die ekosisteemfunksies wat hul voorsien, ondersoek. Die koers waarteen mis verwyder was het toeneem met toenemende spesierykheid vir beide plase en BGe, asook toenemende reënval, waar misverwydering gereageer het op mediumtermyn reënval. Verskillende funksionele groepe was verantwoordelik vir verskillende

funksies. Rollers en tonnelgrouers het afsonderlik doeltreffende verwydering van mis en plantprodukte gehandhaaf. Dit dui aan dat verskillende funksionele groepe verskillende bydrae maak tot ekosisteemwerking (d.w.s. misverwydering en voedingstof-sirkulering), en dat die bewaring van 'n gemeenskap waar alle funksionele groepe ingesluit is van hoë belang is om optimale ekosisteemwerking te handhaaf.

Miskruier gemeenskappe en hul funksies in hul ekosisteme het verskeie reaksies getoon teenoor reënval. Dit dui aan dat ekologiese studies alle eienskappe van miskruier-gemeenskap moet insluit wanneer die impakte van grondgebruik en klimaatsverandering ondersoek word, om sodoende goeie verstand van miskruier gemeenskapstruktuur en hul bydrae tot ekosisteemfunksionering te kry. Om hul bydrae ten volle te verstaan, moet hierdie assesserings nie alleenlik op een ekosisteemfunksie staatmaak nie.

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Psalm 138:3

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CHAPTER 1: INTRODUCTION

1.1. Ecosystem functions facilitated by insects

Numerous studies are finding a link between biodiversity and ecosystem function (Anderson et al., 2009; Cardinale et al., 2012; Díaz et al., 2006; Faith et al., 2010; Haines-Young and Potschin, 2010; Mace et al., 2012). Ecosystem functioning or processes are a combination of biological, physical and geochemical mechanisms (Bengtsson et al., 2000). The subset of ecosystem functions that directly benefit humans is referred to as ecosystem services (Kremen, 2005). Insects facilitate a variety of these ecosystem services that provide social, environmental and economic benefits. These include the well-studied pollination by flower-visiting insect taxa such as bees, flies, beetles and ants (Öckinger and Smith, 2007; Ollerton et al., 2011), carbon and nutrient cycling by dung beetles and other soil fauna (Yang and Gratton, 2014), serving as a food source for many vertebrates, including humans (Ramos-Elorduy, 1997), and pest control in crop production (Kremen and Chaplin-Kramer, 2007) and livestock farming (Losey and Vaughan, 2006). These social, environmental and economic benefits of ecosystem services provided by insects, point to the importance of conserving insects (Hallmann et al., 2017).

Ecosystems are structured by biogeochemical pathways and networks of interactions occurring within and among species (Naeem et al., 2012). For example, plant productivity depends on the pollination of plant species by animal species (Traill et al., 2010), the vast majority of which are insects. Moreover, crop production depends not only on pollinators but also other plant species within agricultural lands and surrounding natural vegetation to support shared pollinators, by providing supporting resources when the crop is not in flower (Simba et al., 2018). These

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networks and the variety of ecosystem functions that rely on them are the reason why the decline in insect populations is of great global concern (Cardoso et al., 2020). Similarly, livestock forage on palatable plant species as food resource; however, the lingering presence of dung provides a substrate for parasites and pests, and dung beetles remove and decompose the dung, reducing fly and parasite loads (Bornemissza, 1976; Braga et al., 2012; Davis, 1994).

1.2.   Global insect decline

Biologists and ecologists have recently presented compelling evidence of insect population declines occurring at alarming rates (Fox, 2013; Hallmann et al., 2017; Nilsson et al., 2008; Ollerton et al., 2014; Potts et al., 2010; Sánchez-Bayo and Wyckhuys, 2019; Cardoso et al., 2020; Samways et al., 2020; van Klink et al., 2020). Like much biodiversity loss (Pardini et al., 2010; Valiente-Banuet et al., 2015), the decline of insects has been linked to anthropogenic activities that result in habitat loss, fragmentation and degradation, leading to loss of forage, nesting sites and opportunities for reproduction (Kearns et al., 1998; Kevan, 1999). A meta-analysis study showed a 45% decline in insect abundance across two-thirds of species evaluated globally (Dirzo et al., 2014). Although protected areas should help biodiversity conservation and ecosystem functioning by providing refuge for some species, over the 27 years between 1989 and 2016, the biomass of flying insects in German protected areas had declined by over 70% (Hallman et al., 2017). These authors argued that the decline in insect biomass could be a result of the effects imposed on the protected areas by the surrounding agricultural activities. Although these parks were close to cities, similar trends could be observed elsewhere.

One of the greatest threats posed by habitat degradation to biodiversity has been the increasing loss of specialist insect species with specific ecological functions (Kitahara et al., 2000). Many specialist insect species have diversified with vertebrates making them co-dependent and more prone to co-extinction (Dunn, 2005; Dunn et al., 2009; Cardoso et al., 2020). For example, dung beetles have been shown to decline with a decline in mammals in response to climate change, habitat degradation and hunting (Nichols et al., 2009; Bogoni et al., 2019). Plant-pollinator networks also experience co-extinctions, with insect pollinators that occupy narrower niches than their partner plants being more vulnerable to habitat loss than plant species (Taki and Kevan, 2007). Similarly, plant species that rely on a single pollinator species may be vulnerable to extinction (e.g., *Pterygodium* orchids, which rely on a single species of oil-collecting bee, *Rediviva peringueyi,* for pollination; Pauw, 2006). In some instances, declining insect species are replaced by more generalist species that are adapted to different ecological conditions (Sánchez-Bayo and Wyckhuys, 2019). However, even generalist and widespread species are undergoing precipitous declines (Gaston and Fuller, 2007; Habel and Schmit, 2018; Sánchez-Bayo and Wyckhuys, 2019; Hallman et al., 2020), resulting in uniform species composition within assemblages, with concomitantly reduced species and functional diversity (Houghton and Holzenthal, 2010).

Other threats to insect populations include the use of pesticides and herbicides. The increased need for food security associated with the increasing human population has driven agricultural production to rely on pesticides and herbicides to maximize production (Kohler and Triebskorn, 2013). Evidence shows that these pesticides and herbicides not only affect the targeted species but also negatively affect non-target species (Blacquiere et al., 2012, Sanchez-Bayo, 2011).

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These impacts have been noted for predatory insects (i.e. ants, beetles, parasitic flies and dragonflies) that prey on most targeted pest species (Butler et al., 2009). Herbicides negatively impact the survival of predatory insects (Ahn et al., 2001) and are also known to degrade habitats needed by insects (Pratt et al., 1997). Declines in dung-breeding insects have also been recorded owing to the residue of insecticides in mammal dung aimed at controlling ectoparasites (Floate et al., 2005).

Climate change also threatens insect populations, owing to changes in species phenology (particularly of species involved in insect-plant mutualisms), distribution ranges and reduction in body size (Scheffers et al., 2016). However, contrary to many studies that show climate change amongst the prime suspects for biodiversity loss, some recent studies on insect declines have found little to no contribution of climate change effect on this loss (Hallmann et al., 2017; Sánchez-Bayo and Wyckhuys, 2019). However, temperature and wind speed were the only climatic variables assessed in these studies, and changes in rainfall were not considered. The ongoing decline in biodiversity emphasises the need to consider all climatic variables to understand these patterns, particularly extreme events (e.g. droughts and flooding) which are expected to increase in frequency and severity (Pachauri et al., 2014).

1.3.   Effect of insect decline on ecosystem functions

Declines in insect abundance and species richness negatively impact the provision of important ecosystem functions (Larsen et al., 2005). For example, loss of insect pollinators has been shown to affect both the productivity of crops and plant diversity in natural ecosystems (Biesmeijer et al., 2006; Vanbergen and The Insect Pollinators Initiative, 2013). Similarly, declines in dung beetles have been associated with

reduced dung removal, and crucially, loss of functionally-efficient species sees far greater disruption of ecological function than random species loss (Larsen et al., 2005). Furthermore, a global assessment demonstrated that ecosystem functions that are not dependent on a single specialised species or insect group benefit from greater biodiversity (Sánchez-Bayo and Wyckhuys, 2019). Species loss does not necessarily equate to the loss of ecosystem functions, as systems have ecological resilience (Kremen, 2005). It has been reported that ecosystem functions performed by dung beetles may be facilitated by other ground-dwelling insects when dung beetles are lost from the system (Dangles et al., 2012). However, the extent to which ecosystems can retain their ecological resilience in this way is unknown (Memmott et al. 2004).

1.4.   Dimensions of biodiversity on ecosystem functions

To better understand the impacts of insect population declines, the contribution of species and functional diversity to ecosystem functioning must be assessed. The different dimensions of biodiversity (i.e., abundance, biomass, taxonomic diversity, functional diversity and phylogenetic diversity) have varied effects on ecosystem processes, thus each of these dimensions should be considered to explain the role of biodiversity on ecosystem functioning (Mouillot et al., 2011). Insect abundance can increase the provision of ecosystem services. For example, greater grasshopper densities were found to improve nutrient availability, which subsequently increased plant abundance (Belovsky and Slade, 2000). Greater pollinator abundance is crucial for the maintenance of pollination services in agricultural systems that experience high yearly variation in pollinator species composition, as this may result in a complementary mechanism where high abundance becomes beneficial in the

absence of the most efficient pollinator species (Lyons et al., 2005). Moreover, an abundance of natural enemies reduced the proportion of mined leaves and bored fruit in a coffee plantation by pests (Rezende et al., 2014).

Taxonomic structure (i.e.species richness) has been deemed less important in the provision of ecosystem services than functional diversity, however, it may have indirect effects through mediating the community's functional structure (Mouillot et al., 2011). Communities with more species are more likely to have different functional traits, and thus greater functional diversity, these communities are, therefore, more likely to perform more functions (Villeger et al., 2008). Therefore, to maintain ecosystem functions and ensure multifunctional communities, it is imperative that conservation strategies aim for greater biodiversity and thus functionally diverse communities.

Functional diversity is a better predictor of ecosystem functioning than species diversity (Díaz and Cabido, 2001; Gagic et al., 2015; Naeem et al., 2012) because a species' ability to perform ecological functions depends on its functional traits, be they morphological, physiological, phenological (Mouillot et al., 2011) or behavioural traits. Trait-based approaches are increasingly used to understand the role of biodiversity to ecosystem functioning (McGill et al., 2006). Functional diversity as well as phylogenetic diversity (phylogenetic information), which can be used as a proxy for functional diversity (Gerhold et al., 2015), are highly-relied upon measures when ecosystem services depend on facilitation or niche complementarity (Xie et al 2018).

1.5.   Dung beetles and their ecological functions

In this thesis, I focused on dung beetles for four reasons; firstly, because they are a species-rich (approximately 650 species in southern Africa; Brown et al. 2010) insect group found in most terrestrial ecosystems, with some habitat-specific species (Roslin and Viljanen, 2011). Secondly, because dung beetles have been recognised as both biological and ecological indicators (Halffter and Favila, 1993) mainly because of their sensitivity to disturbance and land use (Nichols et al., 2007; Pryke et al., 2013; Scholtz et al., 2009). Unlike ecologically robust species, sensitive species are often unable to meet their ecological requirements in transformed habitats (Saunders et al., 1991). Thirdly, amongst terrestrial invertebrates, dung beetles have suffered some of the most substantial declines in diversity, with declines in abundance evident for over 60% of species in Mediterranean countries (Sánchez-Bayo and Wyckhuys, 2019). The decline in dung beetle species is of major conservation concern (Nichols et al 2007). Like many insect groups, dung beetles are threatened by land degradation and habitat loss (Nichols et al., 2008). Alterations to soil temperature, moisture levels and vegetation densities by livestock grazing negatively impact dung beetle communities (Brown et al. 2010). The fourth and most important reason is that dung beetles are responsible for several ecosystem functions in terrestrial ecosystems; these services include dung removal, pollination, seed dispersal, bioturbation and nutrient cycling (Nichols et al., 2008). Dung removal in turn controls flies and livestock internal parasites (Gregory et al., 2015, Nichols and Gomez, 2014). Moreover, nutrient cycling and bioturbation by dung beetles have a positive influence on soil fertility (Amezquita and Favila, 2010), thereby increasing plant productivity.

1.6.   Thesis aims and objectives

This thesis aims to investigate how dung beetle abundance, diversity (measured in terms of species richness, functional traits and functional diversity) and species composition respond to environmental factors, and how dung beetle diversity, in turn, affects ecosystem functions in the semi-arid Karoo. The main research questions in this thesis are:

1. Do land use and rainfall affect dung beetle species richness, abundance, functional diversity and functional traits (collectively referred to as "community attributes", henceforth)? (Chapter 2)

2. Do land management and the associated impacts on habitat at finer scales (e.g. stocking rates, vegetation cover, soil texture and rainfall) influence dung beetle assemblage composition? (Chapter 3)

3. Are the effects of land management and the associated impacts on habitat evident on all dung beetle species, or are some species more sensitive than others? (Chapter 3)

4. How do land use, rainfall and their influence on dung beetle community attributes affect ecosystem function provided by dung beetles? (Chapter 4)

5. Are some dung beetle functional groups more efficient in performing some ecosystem functions than others? (Chapter 4)

1.7.   Breakdown of chapters

The thesis consists of five chapters, with chapters 2-4 written as separate scientific papers for publication, so some repetition within the introductory and method sections is unavoidable. Chapter 1 contains a general introduction and Chapter 5

summarises and discusses the findings of the chapters and makes recommendations based on these findings for conservation and future research.

Chapter 2. This chapter aims to investigate how dung beetle taxonomic and functional community attributes (abundance, species richness, functional diversity and functional traits) are affected by land-use type, herbivore stocking rates, habitat structure, and along a rainfall gradient (20 mm.year^{-1} to 520 mm.year^{-1}) in the semi-arid Karoo region of South Africa.

Chapter 3. Here, I investigate whether there is variation in dung beetle species composition between two land-use types, livestock farms and protected areas, in the semi-arid Karoo. I also assess whether variation in dung beetle species composition varies with herbivore stocking rates, vegetation cover, soil texture and rainfall. I investigate whether these factors affect all species equally or whether certain species are more sensitive and so may serve as indicator species in future assessments. I also investigate how functional traits of dung beetle species respond to these environmental factors.

Chapter 4. In this chapter, I determine how dung beetle community attributes (i.e. abundance, species richness, functional diversity and functional traits), and different land uses (rangeland for livestock vs protected areas) along a rainfall gradient (20 mm.year-1 to 520 mm.year-1) influence the ecosystem function of dung removal. To determine variation in the rate of dung removal with land use and rainfall, I ran *in situ* dung removal experiments on farms and in protected areas around the Karoo. I assessed how dung beetle attributes, land use, vegetation cover, soil texture and rainfall influence the rate of dung removal.

I also ran an *ex situ* experiment to determine the contribution of the different dung beetle functional groups and their interactive effects on dung removal and plant productivity. Dung beetles are most active after rainfall and the experiment required several beetles from different functional groups. For this reason, this study was conducted in Limpopo in summer where rainfall is more reliable than the Karoo. I manipulated dung beetle assemblages by varying functional groups (rollers and tunnellers) and biomass while keeping species richness and abundance constant. I assessed whether having more functional groups is more efficient in dung removal and whether this influenced plant productivity of seedlings planted in soils collected from the different treatments. I also investigated whether there were differences in relative investment by plants in above and below-ground biomass when planted in soils from the different treatments.

1.8. Study sites

The semi-arid Karoo, covering over 400 000 km^2 of land (Cowling, 1986), has undergone degradation as a result of irreversible vegetation change and soil erosion (Du Toit et al., 1991). Furthermore, much of the productive lands have shifted from periodic intense grazing by wild herbivores to constant grazing by livestock, dominated by sheep, resulting in lower plant species richness (Todd, 2006). Other threats to natural vegetation in the Karoo include alien invasive species and the most recent potential threat is the exploration for shale gas and possible subsequent exploitation, which may have negative impacts on the ecosystem (Christenson et al., 2017; Scholes et al, 2016; Todd et al., 2016; Vermeulen, 2012). Until recently, few studies have looked at biodiversity in arid areas because of the low productivity and

biomass associated with such environments (Davies et al., 2012), thus little is known about the species occupying these areas, and the Karoo is no exception.

The Karoo region is characterised by summer rainfall in the east and winter rainfall in the west and Mean Annual Precipitation (MAP) ranging from 500 mm in the east to well below 100 mm in the north-west (Venter et al., 1986). Many parts experience prolonged droughts with total rainfall received in 12 months falling up to 60% below the MAP (Venter 1986). Study sites in this research span a gradient of over 240 mm.year-1 MAP, with the driest site receiving ~137 mm/year-1 and the wettest ~381 mm.year-1). This variation in seasonal rainfall and drought events brings about shifts in biomass and species composition and thus influence species richness and vegetation cover (Dean et al., 1995). Climate projections predict changes in climatic conditions that may impact biodiversity in this area, with the Succulent Karoo expected to experience warmer and drier conditions (Musil et al., 2005), while an increase in summer rainfall along with greater rainfall variability is expected for the Nama Karoo (Altwegg and Anderson, 2009).

The primary study sites for this study were six livestock farms and five protected areas located in the Nama and Succulent Karoo biomes spread across the Western, Eastern and Northern Cape. The details of the primary sites are given in Table 1.1. and Fig. 2.2 and the details of other study sites used in this thesis are given in the relevant chapters.

Table 1. 1. The primary study sites (five protected areas (PA) and six livestock farms (Farm) found in the Western, Northern and Eastern Cape provinces in the Nama and Succulent Karoo, and their rainfall data recorded from nearest South African Weather services' stations, and stocking rates estimated from records supplied by the farm and park managers. These sites are mapped in Figure 2.2.

Site #	Site	Coordinates		Land use	Rainfall season	Rainfall	Stocking rate (LSU/ha)
		Latitude	Longitude			MAP (mm)	
1	Anysberg NR	-33.4715	20.63855	PA	Winter	225.1	0.019
2	Argentina	-33.1778	22.2229	Farm	Winter	184.9	0.017
3	Camdeboo NP	-32.2118	24.4965	PA	Summer	381.1	0.063
4	Good Luck	-33.0404	24.96755	Farm	Summer	242.3	0.062
5	Hopewell	-32.3214	23.11992	Farm	Winter	229.2	0.033
6	Karoo NP	-32.3546	22.43541	PA	Winter	316.5	0.028
7	Portugalsriver	-32.5109	20.87749	Farm	Winter	312.1	0.031
8	Rietvlei	-32.2122	21.85938	Farm	Winter	212.2	0.031
9	Rooidraai	-32.4832	23.61924	Farm	Summer	317.8	0.042
10	Tankwa Karoo NP	-32.2836	20.07266	PA	Winter	137.8	0.009
11	Tierberg LTER	-33.1718	22.26992	PA	Winter	184.9	0.007

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CHAPTER 2 SHORT-TERM CLIMATIC VARIABLES AND RANGELAND MANAGEMENT BOTH INFLUENCE DUNG BEETLE COMMUNITY RICHNESS

Abstract

Insects perform many ecosystem functions; however, relative to other taxa, they are understudied in disturbance research. Understanding the influence of environmental variables in transformed landscapes on biodiversity is essential for biodiversity monitoring, management and conservation. Dung beetles are sensitive to habitat structure (and therefore, land-use change) and climate (particularly rainfall variation). In this study, I assessed how dung beetle species richness, abundance, and functional diversity varied with habitat structure and rainfall on six livestock farms and five protected areas across a rainfall gradient of 138 to 381 mm/year in the semi-arid Karoo, South Africa. Arthropod body size and its variation within communities can vary with habitat structure and climatic variables, and this, in turn, can influence the efficiency and quality of ecological functions that arthropods perform. I therefore also assessed patterns in body size, assessing size inequality using the Gini coefficient. Species richness did not differ between rangelands and protected areas, but abundance was significantly greater in protected areas. Functional diversity was lower in protected areas and increased with an increase in vegetation cover but was not affected by rainfall nor soil content. Dung beetle species richness and abundance both increased significantly with increasing vegetation cover. Mean body length and the Gini coefficient did not vary significantly between the two land-use types. However, mean body length increased with an increase in soil clay content while the Gini coefficient decreased with an increase in vegetation cover and clay content, suggesting that the spread of beetle sizes was more even as vegetation cover and clay content increased. Species richness and

abundance both increased significantly with mammalian herbivore stocking rates and rainfall. Short-term rainfall was a better predictor of species richness than medium or long-term rainfall, but abundance was best explained by long term rainfall. The highly variable response of dung beetle communities to different aspects of habitat suggests that this group is sensitive to both land use and climate. Future climate projections indicate an extreme change in rainfall in this area, and my results here suggest that this would have dramatic impacts on dung beetle communities.

Keywords: Anthropogenic disturbance, body size, functional diversity, land-use, rainfall gradient, rangelands, Scarabaeidae, species richness,

2.1.   Introduction

Invertebrates, and insects, in particular, are intimately involved in many ecosystem functions. Some ecosystem functions performed by insects (i.e. pollination, nutrient cycling, pest control and provision of food) are considered ecosystem services, as they are directly beneficial to humans (Noriega et al., 2018). This makes the decline of insect diversity and abundance through habitat transformation and climate change concerning (Bommarco et al., 2011; Hallmann et al., 2017; Lobo, 2001; Shortall et al., 2009; Sanchez-Bayo and Wyckhukys, 2019; Cardoso et al., 2020; van Klink et al., 2020). Furthermore, insects have received relatively little attention in disturbance ecology research, compared to vertebrates and plants, and as such, they have not been considered in conservation strategies (Dunn, 2005).

While the majority of assessments on insects' response to disturbance have focused on the impacts of disturbance on abundance and species richness, trait-based approaches are beginning to be adopted in community ecology studies

(Lavorel and Garnier, 2002; McGill et al., 2006; Mouillot et al., 2013). These trait-based studies have improved the understanding of species' responses to environmental changes and how these responses influence community structures (McGill et al., 2006; Mouillot et al., 2013). For example, animal body size can change along gradients (Rodriguez et al., 2008; Brans et al., 2017), with some studies showing a decrease in body size with an increase in elevation (Classen et al., 2017; Brown and Maurer,1989). While large-bodied species are associated with greater strength and competitive ability in acquiring resources (Magura et al., 2006; Gianuca et al 2016; Tessier et al 2000), they have high per capita energy requirements and tend to have low population sizes (Brown et al., 2004). Body size is also associated with ecological functions such as species' dispersal capacity, reproduction rate and development time (Di Grumo and Lovei, 2016). Therefore, assessing the variation in body size along gradients may help us understand how insect communities may be affected by habitat transformation and climate change.

Dung beetles (Coleoptera: Scarabaeoidea) play a crucial role in terrestrial ecosystems. In their behaviour of using and burying dung as a food and nesting source, they perform a variety of ecosystem functions and services (Nichols et al., 2008). The burial (and thus removal) of dung control pest populations (particularly Diptera and intestinal parasites) that depend on dung for nesting or further transmission to other hosts (Gregory et al., 2015; Nichols and Gómez, 2014), and reduces the emission of greenhouse gases from dung into the atmosphere (Slade et al., 2016). Dung beetles improve plant productivity by burying the seeds that are embedded in the dung (Milotic et al., 2019; Nunes et al., 2018; Vulinec, 2002) and ensuring soil fertility and aeration through bioturbation (Amézquita and Favila, 2010).

The effects of disturbance and land-use change on dung beetles have been assessed in numerous studies focusing on species diversity and the tolerance of different species to disturbance (Braga et al., 2013; Louzada et al., 2010; Nichols et al., 2007; Nunes et al., 2018; Scheffler, 2005; De Castro Solar et al., 2016). Globally, dung beetles have exhibited a decline in both species richness and abundance (Brown et al., 2010; Davis et al., 2004; Lobo, 2001; Nichols et al., 2007; Pryke et al., 2016). Their sensitivity to disturbance, along with the variation in response to disturbance across species, makes them ideal biological indicators for monitoring anthropogenic impacts (Frank et al., 2017).

Anthropocene habitat degradation and fragmentation also have had marked adverse effects on mammals (Culot et al., 2013), whose dung serves as the primary food and nesting source for dung beetles (Hanski and Cambefort, 1991). Thus, anthropogenic disturbance affects dung beetles indirectly by changing the composition of mammal species (Estrada et al., 1999; Frank et al., 2017; Whipple and Hoback, 2012). The change in mammal composition is a result of habitat loss and steep declines in wild mammal species, which have been replaced by a few livestock species (Young et al., 2005), usually not native to areas in which they are farmed. This introduction of livestock and the greater rates in which they are stocked for agricultural purposes has adverse impacts on the landscapes as they mostly exceed the environmental capacity for grazing (Young et al., 2013). These effects include alteration of the vegetation composition, decrease in vegetation cover and increased soil erosion (Allsopp et al., 2007).

Dung beetles' reliance on dung would be expected to make them more abundant on farms, where stocking rates (numbers of herbivores/ha) tend to be higher than in protected areas. However, farmers might also use anthelmintic drugs

for parasite control and/or hormones to maximise production (Manning et al., 2017), which can negatively influence dung beetle abundance. Furthermore, the replacement of wild species may result in niche simplification of livestock vs native grazers (Pryke et al., 2016), which can negatively influence dung beetle diversity. Herbivores may also impact dung beetle communities through trampling dung and vegetation, reducing both the vegetation height and cover (Jankielsohn et al., 2001), which can in turn influence soil moisture; trampling also causes soil compaction, making digging for nesting sites more difficult.

Dung beetles are strongly influenced by changes in physical habitat structure (Doube, 1983; Nealis, 1977) and many species have specific preferences for vegetation and soil type (Scholtz et al., 2009). Vegetation defines the micro-habitat through the influence on factors such as temperature and soil moisture (Jankielsohn et al., 2001; Joseph et al. 2018), and also influences dung availability as a source of food for dung beetles. Moreover, morphological trait (i.e. body size) variation within and amongst dung beetle species can respond to resource availability (Moczek and Nijhout, 2004) and environmental changes (Alves and Hernández, 2017). Some studies have linked the sensitivity of dung beetles to these factors with changes in body size, nesting strategy, dispersal ability, activity period and diet preference (Barragán et al., 2011; Nichols et al., 2013; Da Silva & Hernández, 2014). For example, large-bodied dung beetles were excluded in a habitat where invasive tree species had created almost impenetrable thickets, but these dung beetles were more abundant in open savannah (Steenkamp and Chown, 1996). Moreover, small-bodied dung beetles have been recorded at higher elevations where temperatures are cooler while larger dung beetles were recorded in lower elevations (Herzog et al., 2013). Rainfall is associated with greater dung beetle diversity and abundance

(Andresen, 2005) and most dung beetle species emerge from the soil shortly after rainfall (Davis et al., 2008). Dung beetle communities tend to show declines in species richness and diversity across rainfall gradient (Tshikae et al., 2013). The question arises as to whether various measures of dung beetle diversity respond to rainfall at different time scales: for example, although we might expect dung beetle species richness to be dictated by long term rainfall, are other measures, like abundance, driven more by medium-term rainfall (i.e. that year's rainfall against the long term mean), or even short term rainfall (i.e., rainfall in the most recent rains)? There is also a considerable seasonal variation in the way dung beetles respond to disturbance. For example, dung beetle communities have been found to respond differently to fire in the wet season compared to their response in the dry season (De Andrade et al., 2011).

To my knowledge, this is the first study to assess differences of dung beetle communities across a rainfall gradient in the context of land use, rainfall season and their interactive effects. The research was conducted across a rainfall gradient in the winter and summer rainfall regions of the semi-arid Nama and Succulent Karoo, where much of the biodiversity is currently unknown. The study area falls in an area with a gap on dung beetle records (Animal Demography Unit, University of Cape Town, Fig.2.1). Rainfall variation and land use (i.e. stocking rates in farms vs protected areas) are responsible for most of the observed vegetation and soil structure of the Karoo. Recently, shale gas exploration has been proposed in the area, which may pose additional threats to the vegetation and soil structure (Christenson et al., 2017; Scholes et al., 2016; Todd et al., 2016). It is thus essential to understand the influence of land use, habitat structure and rainfall on dung beetles

to conserve dung beetle biodiversity, monitor community changes caused by future impacts and ensure the maintenance of ecosystem services.

In this study, I investigated the factors that influence dung beetle abundance, species richness and functional diversity within protected areas and rangelands in the Karoo. To do this, I asked how these measures are affected by land-use type, herbivore stocking rates, vegetation cover, soil texture, rainfall, and rainfall seasonality. Given that farms in this study had greater stocking rates compared to protected areas, I expected to find greater dung beetle abundance on farms.
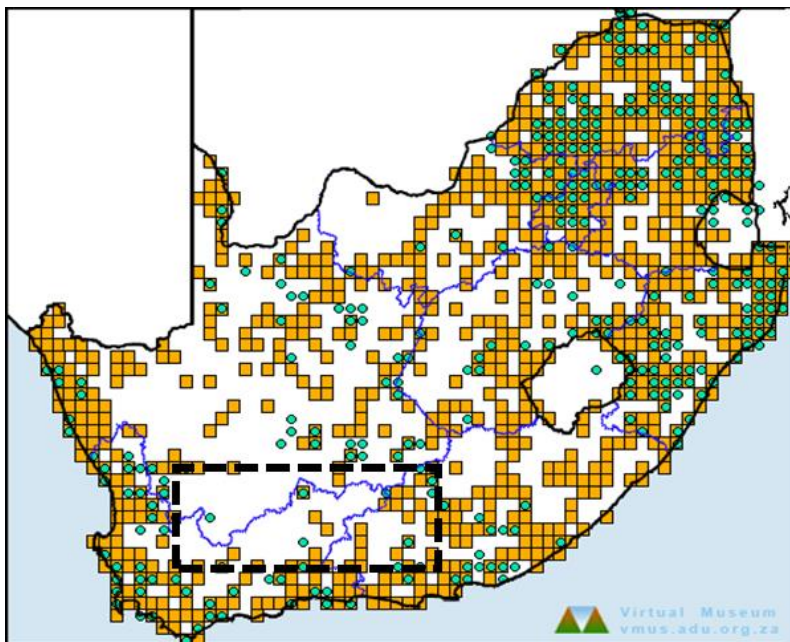
Figure 2.1. Dung beetle map from the ADU virtual museum showing where dung beetle surveys have been conducted (orange grids) and where there are no survey records (white grids). The dashed rectangle represents the current study area. Green dots represent records with photographic evidence on the virtual museum.

I also expected to find greater species richness and functional diversity in protected areas where there is a variety of dung types. Given that the quality and quantity of ecosystem services delivered by dung beetle assemblages should be influenced by body size, I also investigated changes in the distribution of dung beetle

body sizes across climatic gradients and between protected areas and rangelands. Variation in vegetation cover and soil type should provide more niches and thus not only influence the abundance and diversity but also the distribution of dung beetles body sizes (Steenkamp & Chown, 1996). Therefore, I asked how the distribution of body size changes across environmental gradients in these different land uses and expected to find large-bodied dung beetles and a wider array of sizes in habitats with less vegetation because larger dung beetles are restricted in movement in thicker vegetation cover (Steenkamp & Chown, 1996) and higher clay content because high clay content may restrict the ability of dung beetles to dig deep, particularly smaller dung beetles (Brown et al., 2010).

2.2. Methods

2.2.1. Study site

This study area was located in the Nama- and Succulent Karoo Biomes in South Africa (Mucina and Rutherford, 2006). The vegetation in these areas is characterised by a high diversity of perennial shrubs, geophytes, annual forbs, succulents, C3 and C4 grasses as well as scattered trees, with many of South Africa's endemic plant species nested in the Succulent Karoo (Mucina et al., 2006). Eleven study sites (Appendix 1), spanning about 500 km, were selected on six farms (Good Luck, Rooidraai, Hopewell, Reitvlei, Portugalsriver and Argentina), four protected areas (Anysberg Nature Reserve, Camdeboo, Karoo, Tankwa Karoo National Parks) and one long-term ecological research site, Tierberg LTER, managed by South African Environmental Observation Network (SAEON) and established in 1986 (Fig.2.2). The Tierberg LTER is mainly managed in a similar way to protected areas but has a lower density of wild herbivores. Rainfall declines from east to west, with Mean
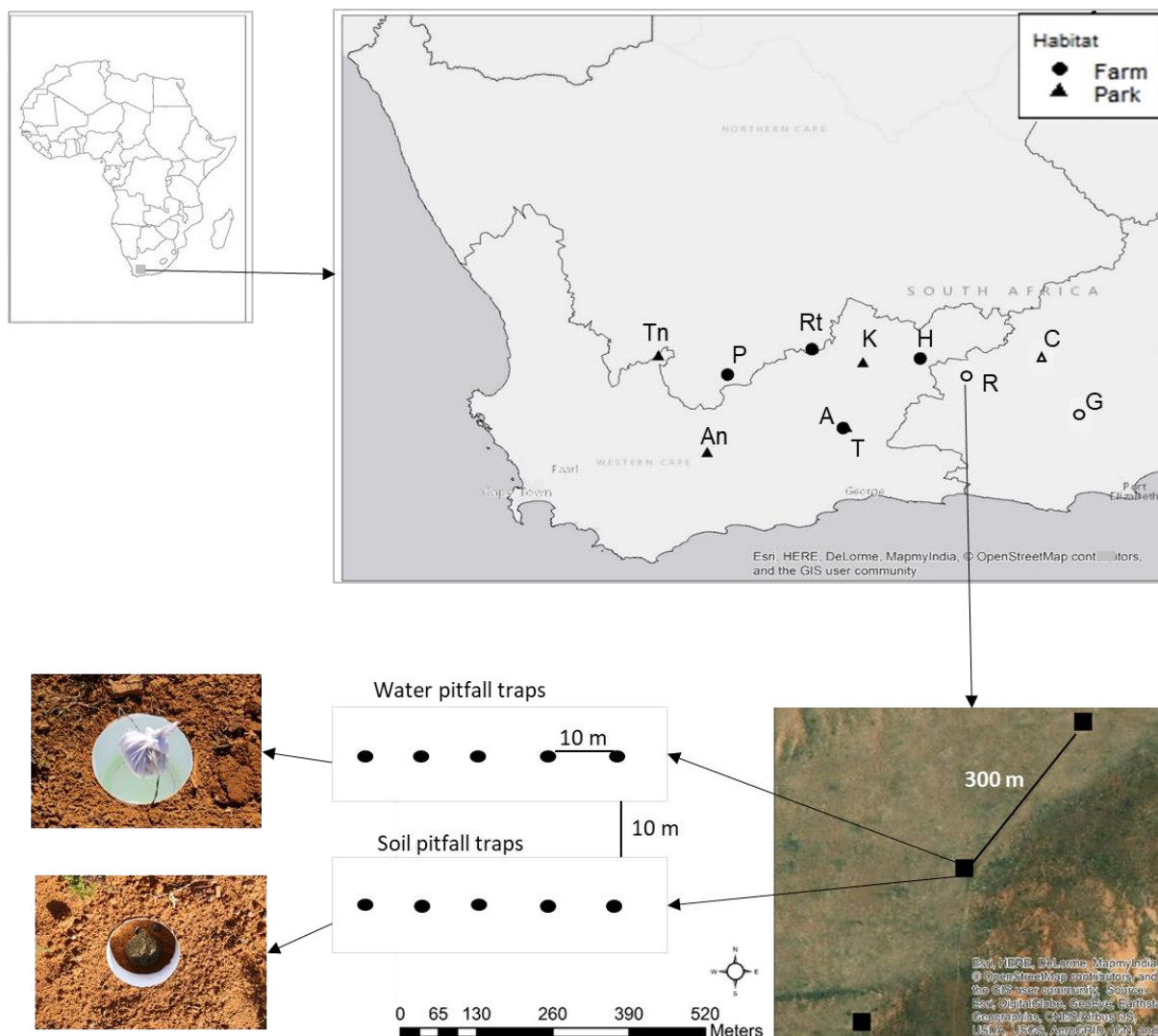
Figure 2.2. Site map showing A) the relative position of the 11 sampling sites; were open (summer rainfall) and closed (winter rainfall) circles depict six sites in livestock farms (A - Argentina; G – Good Luck; G - Hopewell; P - Portugalsriver; Rt- Rietvlei; R - Rooidraai), and the open (summer rainfall) and closed (winter rainfall) triangles depict five sites in protected areas (An – Anysberg Nature reserve; C – Camdeboo National Park; K – Karoo National Park; Tn – Tankwa-karoo National Park; T – Tierberg LTER)); and the sampling design with B) the 1 km^2 site and the three plots where the sampling was conducted, C) the two transects showing the relative positioning of the pitfall traps and D) the two pitfall trap types.

Annual Precipitation (MAP) varying from 138 mm/year in the western-most (winter rainfall) study site to 381 mm/year in the most eastern (summer rainfall) site (i.e.,

spanning a gradient of 243 mm/year (accessed from rainfall data over the years 1988 to 2017 obtained South African Weather Services)). Most of the region is rangeland under livestock grazing (hereafter referred to as 'farms'), hence much of it has been disturbed by current or historic grazing by domestic livestock (mostly sheep) with some low-density wild herbivores (primarily springbok (*Antidorcas marsupialis*), kudu (*Tragelaphus strepsiceros*) and klipspringer (*Oreotragus oreotragus*); Appendix 2). At each site (about 1 km^2), I established three sampling plots (50 x 10 m) separated by at least 300 m (Fig. 2.2) to ensure that the sampling replicates have homogenous internal conditions, however, still far apart enough that they are independent (Hernandez et al., 2014; Gotelli and Ellison, 2004).

2.2.2. Dung beetle sampling

I ran an intensive survey on the 11 sites accounting for temporal variation across two seasons (one dry and one wet season). Fieldwork was conducted in March of 2017 and then again in August of 2017, with each site visited once per sampling season. Within each of the three sampling plots at each site, ten pitfall traps were placed 10 m apart and baited with cow dung along two transects that were at least 10 m apart (Fig. 2.2). During a pilot study, I found that sheep (which is the most dominant in the area), goat and horse dung dried out within hours and was then not attracting as much dung beetles. Cow dung has been found to attract numerous species in farmlands and reserves in South Africa (Geyser, 1995). The pilot study also showed that roller dung beetle species were highly abundant in the water traps and dwellers and tunnellers were rare, suggesting that water traps might have created a bias in functional group representation. Therefore, in subsequent trapping surveys, and for the data used here, two trap types were used to try to ensure sampling of different

functional groups (i.e. different nesting behaviour), and the full complement of species. One of the transects had five soil-filled pitfall traps, and the other had five water-filled pitfall traps. The pitfall traps (2 L plastic containers: 14 cm deep with a 17 cm diameter) were buried at ground level and filled to about two-thirds capacity with water and a drop of dishwashing liquid for the water pitfall traps and soil for the soil pitfall traps. Two hundred grams of fresh cow dung was placed inside a white linen bag and suspended on a wire harp ca. 5 cm above the centre of the water pitfall trap (Pryke et al., 2013) (Fig.2.3. b). For the soil pitfall traps, 200 g of fresh cow dung was placed inside the trap on the soil (Fig.2.3. a). The locations of the traps were the same in March and August of 2017. Traps were set out between 08h00 and 09h30 and dung beetles were collected after 24 h. Dung beetle specimens were preserved in 95% ethanol and later identified to genus level, and where possible to species level using appropriate keys (Appendix 3). Voucher specimen collections are kept at the Entomology Museum at the Department of Conservation Ecology and Entomology, Stellenbosch University, South Africa.
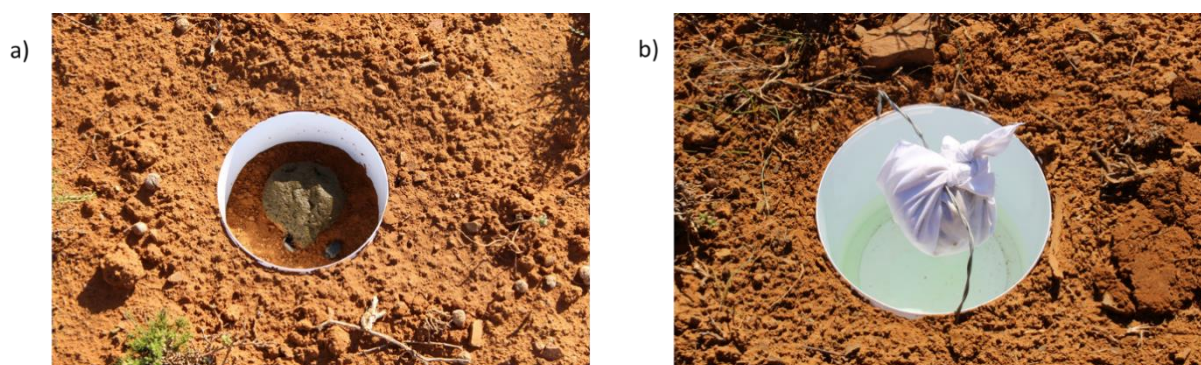
Figure 2.3. Pitfall trap techniques used; a) soil pitfall trap with a dung ball in the centre of a buried bucket, and b) water pitfall trap with a wire harp holding dung bait suspended above a buried bucket.

2.2.3. Dung beetle trait selection and measurements

To assess variation in body size structure and functional diversity between the two land uses and across this rainfall gradient, I measured seven dung beetle traits (1 functional and 6 morphometric measures (mm)) from 356 dung beetles representing the 20 dung beetle species (n = 5 to 23 individuals per species) that were represented by more than five individuals (Appendix 4). These individuals were selected randomly from 30 pitfall traps. I selected traits that influence the survival of dung beetle populations (i.e. dispersal ability to allow searching for food and suitable nest sites) and the provision of ecosystem functions (Raine et al., 2018). Body size was measured as dung beetle length (Marden, 2000) from the tip of the clypeus to the base of the elytra. Relative abdominal size, which gives a good indication of the reproductive capacity of individuals, was measured as a ratio of thorax to abdomen length (Srygley and Chai, 1990). Two measures, wing aspect ratio (Wing Width/Wing Length) and wing loading (Wing Area/Body Area (Body Area = Body Length × Thorax Width), were taken to capture some measure of dispersal ability (Berwaerts et al., 2002). I used morphometric measurements and behavioural traits to represent nesting behaviours. The morphometric measurements were taken as relative hind leg size (hind leg length/body length) and hind leg robustness (hind leg width/hind leg length) (Raine et al., 2018). Behavioural traits were classified according to whether the dung beetle species were rollers (species that make a ball, roll it and bury it at a distance from the dung pile), tunnellers (bury the dung directly under the dung pile) or dwellers (feed and nests on the dung pile) (Hanski and Cambefort, 1991). This, in turn, influences how they participate in ecosystem functions like dung removal and soil nutrient cycling.

To analyse the distribution of body size of dung beetles, I used the community weighted mean (CWM) of body length, which is the mean of trait values present in the community, weighted by the relative abundance of taxa bearing each value (Lavorel et al., 2008), and calculated using the dung beetle length measures. To analyse body size inequality, I used the Gini coefficient (G), usually used for economic disparities, but which also can be used to measure the diversity of sizes in a community (Gini, 1912). Unbiased estimates of the Gini coefficient can be calculated from data ordered by increasing body size as:

$$G = \frac{\sum_{i=1}^{N}(2i - N - 1)X_{[i]}}{N^2 \bar{x}} \, N(N-1) \, ,$$

Where N is the number of individuals; $x_{[i]}$ is the ordered body size of individuals i and $\bar{x}$ in the mean body size (Dixon et al., 1987; Glasser, 1962). The Gini coefficient has been instrumental in assessing changes in size distribution as a response to anthropogenic and climate factors (Belskaya and Zolotarev, 2017; Di Grumo and Lovei, 2016; Magura et al., 2006).

2.2.4. Environmental variables

I assessed the influence of rainfall, rainfall seasonality, stocking rates, soil texture and vegetation cover on dung beetle activity. Rainfall season was treated as a binary factor of summer or winter rainfall region. Rainfall data (daily rainfall record and Mean Annual rainfalls) were obtained from nearest South African Weather Services stations (Appendix 5). I used three different temporal measures of rainfall: Mean annual precipitation (MAP), Standardized precipitation index (SPI), and "raindex", a measure I created. I used these as measures of long-, medium- and short-term rainfall, respectively. MAP was calculated as the average rainfall for each site over

the years 1988 to 2017. SPI was calculated as the number of standard deviations that observed rainfall for the year differed from the MAP. I calculated "raindex" (Appendix 6) as the amount of rain received in the most recent downpours (days of rain not separated by more than five dry days) divided by the number of days since the last day of rain. This measure was to capture the effects of rainfall events that had occurred close to sampling times as a measure of recent rainfall, given that arid systems often respond quickly, and dramatically, to rain. Using this measure in analyses, I was able to give more weight to substantial rainfall events that occurred close to sampling times than to events that were either not very substantial, or that had occurred sometime before sampling.

Four soil samples were collected from each of the eleven sites and were sent to Bemlab (Pty) Ltd for particle size analyses (percentage of sand, silt and clay). To determine the relative rate of soil infiltration by water, I used a can (10 cm deep with a 7 cm diameter) opened at the top and bottom. The can was buried to 3 cm into the ground and filled with 50 ml of water in each sampling plot. I recorded the rate of water infiltration as the amount of time it took for the water to infiltrate into the soil. Vegetation cover was estimated visually as the percentage of vegetated area in each transect, with vegetation, bare ground and litter cover together totalling 100% (Delamater et al., 2012). The average percentage of vegetated area was calculated from three 1 m^2 plots that were randomly selected from each transect. Mammalian herbivore species richness and abundance, and stocking rate records for each site were collected from the farmers and park managers. Stocking rates included both livestock and wild herbivores and was measured as a number of equivalent large stock units per hectare (LSU/ha); although most farms were characterized by

monospecific assemblages of sheep with extremely low densities of wild herbivores (Appendix 2).

2.2.5. Data analysis

To test for sampling adequacy, I used the "*specaccum*" function in the vegan package (Oksanen et al., 2013). Dung beetles were not always present at all sites or in all traps. Hurdle models were therefore used first to determine which aspects of land use, environmental and climatic variables determine the presence of dung beetles, and where dung beetles were found, which factors influence relative dung beetle abundance (Zuur et al., 2009). The hurdle model is comprised of two parts, one that is a binary logit model which assesses whether the observed data takes a positive count or not. The second part of the hurdle model fits only positive counts of the data (Zuur et al., 2009). Initial data exploration showed that one site, Camdeboo National Park, was an outlier, with 5445 dung beetles caught in the traps in summer. A zero-inflated negative binomial (ZINB) hurdle model (with logit function) was used to account for overdispersion associated with outliers (Zuur et al., 2009) in the 'pscl' package of R (Zeileis et al., 2008). The ZINB models are able to handle overdispersion caused by excess zero counts and the presence of outliers (Usman and Oyejola, 2013; Tüzen et al., 2018). The dispersion parameter in these models accounts for unobserved heterogeneity in count data which allows the variance to exceed the mean (Tüzen et al., 2018).

Dung beetle presence and abundance were modelled per site as a function of land use (farm or protected area), rainfall (MAP, SPI and raindex), rainfall season, soil content, soil infiltration rates, mammalian species richness and stocking rates. The data from the three plots per site where pooled. Although rainfall measures assessed

long-, medium- and short-term rainfall, these and the soil content percentages (clay, sand and silt) were collinear and so could not be included in the same models. Therefore, I ran a series of models, each with a combination of different measures of rainfall (MAP, SPI and raindex) and soil content (silt, sand and clay), and then used an information-theoretic approach, using the Akaike Information Criterion (AIC) to choose the best fitting model (i.e. the model with the lowest AIC value; Akaike, 1973).

I employed the FD package in R (Laliberté et al., 2014) to calculate functional diversity (henceforth referred to as FD) and CWM of dung beetle length. To determine FD, I constructed a distance matrix for dung beetle species caught in the traps using Gower distances (Podani 1999), which allows the use of both quantitative and qualitative traits (De Bello et al., 2013). I used the measured dung beetle functional traits (i.e. body size, abdomen size, wing aspect ratio and loading, hind leg length and width) as quantitative traits and dung beetle functional guilds (i.e., whether they were rollers, tunnellers or dwellers) as qualitative traits to account for each species strategy in dung removal. As the hind leg length and width measurements reflected leg measurement, I down-weighted the effect of each to one-third (1/3) to not over-represent the importance of leg size in functional diversity. I standardised the mean of each trait to zero with a standard deviation of one so that the variation within each trait was treated equally (Petchey and Gaston, 2006). I used average pairwise distances to cluster the matrix because that gave the highest cophenetic correlation (0.93) between original and estimated distances of the dendrogram. I calculated FD by adding lengths of the dendrogram branches corresponding to the species assemblage for each transect (Petchey and Gaston, 2006; Seymour et al., 2015).

To obtain the standardised effect size of functional diversity (sesFD), which accounts for the increase in FD as species richness increases (Petchey and Gaston, 2002), I ran model simulations comparing the observed FDs against null distribution values. To obtain the expected FD in sites containing *n* species, the simulation models randomly select *n* species from the total species pool without replacement. Permutations of 1000 null values were created for each observed value by running the models 999 times. Then sesFD was calculated by subtracting the mean of this distribution from the observed FD value, which was then divided by the standard deviation of the null distribution. This sesFD measure represents the number of standard deviations that the observed community is above or below the mean (0) of the simulated communities from that null model (Gotelli and Rohde 2002).

To ascertain how species richness, sesFD, CWM size and Gini coefficient per site changed with land use and environmental variables I used Generalised Linear Mixed Models (GLMM) with poisson distribution (Zuur et al., 2009) using the package lme4 (Bates et al., 2014) for species richness and Linear Mixed Models (Lmer) for functional diversity, Gini coefficient and CWM of size. Species richness, sesFD and the CWM of dung beetle size were modelled using the same environmental explanatory variables as for the hurdle model above, with site, season and trap type as the random factors and the same data pooled from the three plots.

2.3.   Results

2.3.1. Factors influencing dung beetle presence

A total of 9 089 dung beetles were collected, representing 35 species, nine tribes and two subfamilies (Appendix 3). The species accumulation curves for sampling on both summer and winter season reached an apparent asymptote (Appendix 7), suggesting that sampling had been sufficient. Surprisingly, land use was not

significantly associated with the presence of dung beetles in the Karoo (Odds Ratio (OR) = 0.4, p = 0.09) and support for an effect of stocking rates on dung beetle presence was weak (OR = 1.0, p = 0.055). The chances of finding dung beetles in a trap in this study were 25.8%. This chance increased by 50% with increased vegetation cover (OR= 0.5, p = 0.0003) and higher MAP (OR = 0.5, p = 0.029), and decreased with increasing soil clay content (OR = 0.4, p = 0.044). Mean species richness per site was 1.99 (95% CI [1.77, 2.20]), but this was highly variable across sites, ranging from a minimum of 1 and a maximum of 25 in summer and a minimum of 2 to a maximum of 10 in winter. Abundances of dung beetles per site averaged 14.43 (95% CI [10.72, 18.13]), this was also highly variable across sites, ranging from a minimum of 1 and a maximum of 5445 in summer and ranging from a minimum of 2 and a maximum of 981 in winter.

2.3.2. Factors influencing dung beetle abundance, richness, functional diversity and body size

Land use had no significant influence on species richness, Gini coefficients or CWM of body length. Dung beetle abundance and functional diversity were significantly affected by land use, however (Table 2.1). Dung beetle abundance was greater in protected areas than farms (z = 4.3, p < 0.001, Fig. 2.4 a), but functional diversity was lower in protected areas than farms (t = - 2, p < 0.001, Fig. 2.4 b). Stocking rates significantly affected dung beetle abundance and species richness (Table 2.1). Both abundance and species richness increased with increasing stocking rates (z = 7.7, p < 0.001; z = 3.1, p = 0.002, Fig. 2.5, respectively).

Species richness and functional diversity increased with increasing vegetation cover (z = 3.9, p < 0.001, Fig. 2.6 a; t = 4.7, p < 0.001, Fig. 2.6 b, respectively). The Gini coefficient decreased with increased vegetation cover and clay content (t = - 11.4, p = 0.0001; t = -2.6, p = 0.01, respectively). Soil content also had a significant

effect on the CWM of body size, which increased with increase in clay content (t = 12.0, p < 0.001, Fig.2.7).

Rainfall seasonality did not affect any of the measures considered, i.e., dung beetle abundance, species richness, functional diversity or body size. Whereas functional diversity and CWM of dung beetle length were not affected by rainfall, dung beetle abundance was influenced by long-term rainfall (i.e. MAP; z = 2.6, p = 0.008, Fig. 2.8 a), and species richness was influenced by short-term rainfall (i.e. raindex; z = 3.6, p < 0.001, Fig. 2.8 b) (Table 2.1). Mammalian herbivore species richness and soil infiltration rates did not influence dung beetle communities.

Table 2.1. Best model summaries showing the effects of land use and rainfall on dung beetle abundance, species richness and body size. Where; R^2_m (Marginal R^2), R^2_c (Conditional R^2), M (MAP), Lp (Land use: Protected areas), Sr (Stocking rates), R (Raindex), Sa (Sand), V (vegetation cover), C (Clay content), ns (not significant)). Model types used are described in section 2.2.5. The model equations show the predictors included in the best models, predictors that were not significant are indicated with '*ns*'.

Response Variable	Model type	AIC (Best model)	ΔAIC (2nd best)	ΔAIC (Null)	R^2_m	R^2_c
a) Abundance	ZINB	3172.8	2	299.6		
b) Presence	a) Abundance model equation: $Y = e^{-1.99 + 0.98Lp + 57.41Sr - 0.01V\ (ns)\ +0.01M\ +0.01C(ns)}$ b) Presence model equation: $Y = e^{-1.06 - 0.39Lp(ns)+ 17.0Sr(ns) + 0.02V + 0.01M - 0.03C}$					
c) Species richness	GLMM (Poisson distribution) Model equation: $Y = e^{4.81 + 1.15Sr + 0.21V - 0.01Sa\ (ns)+ 0.24R}$	1846.6	3.1	36.1	0.41	0.83
d) CWM of dung beetle length	Lmer Model equation: $Y = 5.16 + 0.29C$	2503.0	3.3	115.4	0.36	0.72
e) SesFD	Lmer Model equation: $Y = 0.29 - 0.23Lp +0.07V$	- 202.7	2.5	11.4	0.18	0.58
f) Gini coefficient	Lmer Model equation: $Y = 0.63 -0.03V + 0.01C$	-2391.6	3	91.2	0.28	0.31
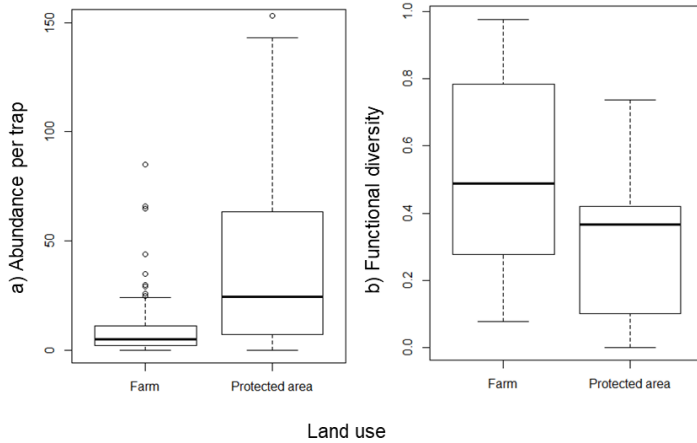
Figure 2.4. The effect of land use on a) dung beetle abundance (z = 4.3, p < 0.001) and b) standardised effect size of functional diversity (sesFD, t = - 2, p < 0.001). The solid black lines represent the median, boxes represent the first and third quartiles, and the error bars are standard errors. The circles represent outliers.
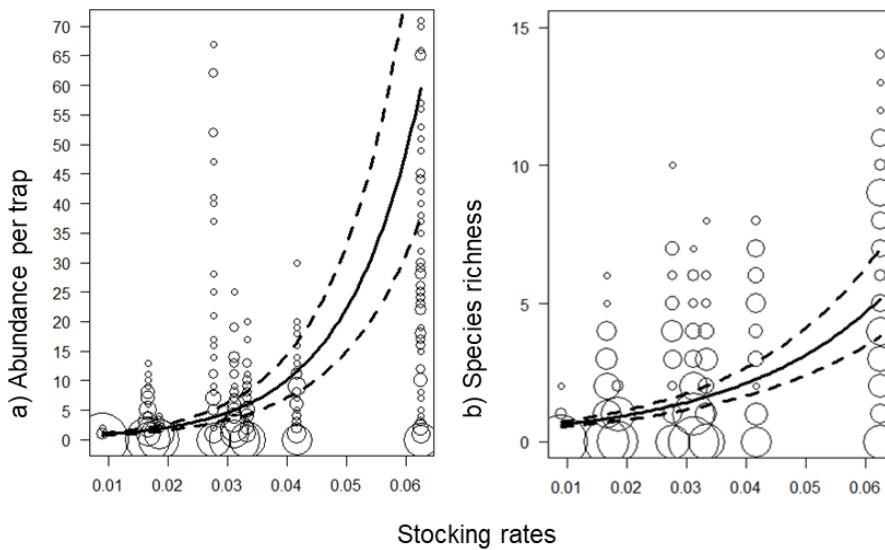
Figure 2.5. Size plot showing the effect of stocking rates (Large stock unit per hectare; LSU.ha) on a) dung beetle abundance (z = 7.7, p < 0.001) and b) species richness (z = 3.1, p = 0.002). Solid lines represent negative binomial glm fits of mean values ± 1 SE (dotted lines). Points are scaled according to the number of points with the same number of (a) dung beetles or (b) species (i.e. large plots represent data with repeated points).
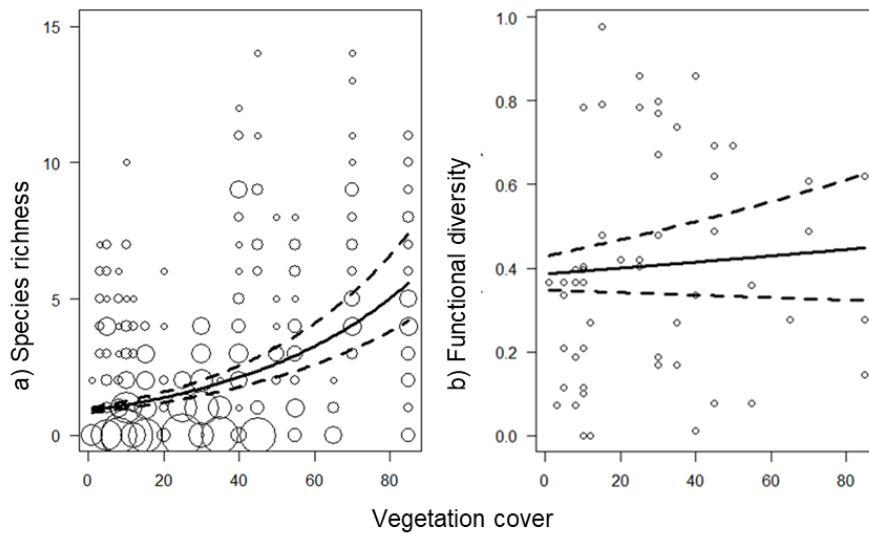
Figure 2.6. Sizeplot showing the effect of vegetation cover on a) species richness (z = 3.9, p < 0.001) and b) standardised effect size of functional diversity (sesFD, t = 4.7, p < 0.001). Points are scaled according to the number of points with the same number of species (i.e. large plots represent data with repeated points). Solid lines represent negative binomial glm fits of mean values ± 1 SE (dotted lines).
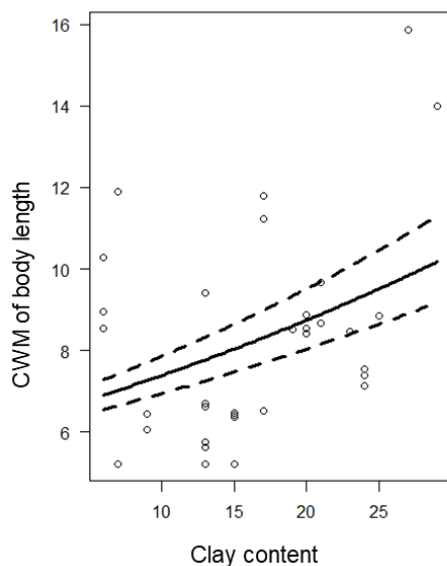
Figure 2.7. The effect of clay on the community weighted mean of body length (t = 12.0, p < 0.001). Solid lines represent negative binomial glm fits of mean values ± 1 SE (dotted lines).

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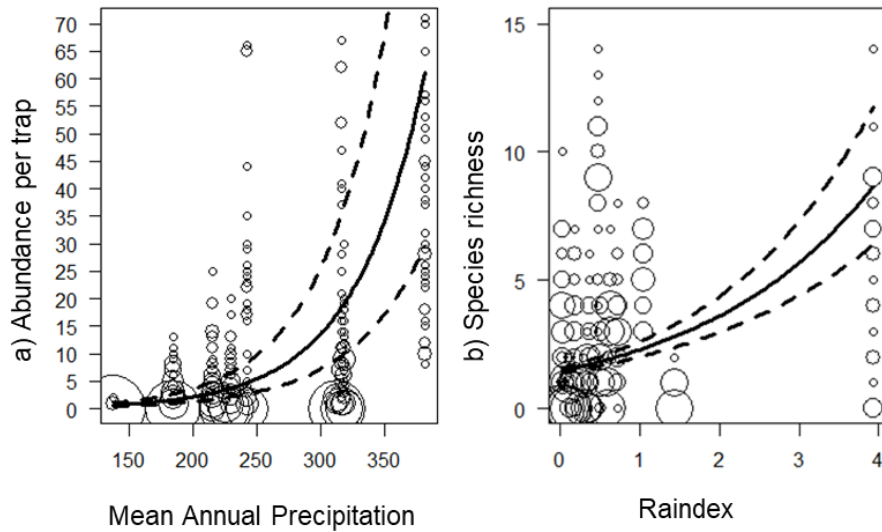
Figure 2.8. Size plot showing the effect of rainfall; a) MAP vs dung beetle abundance (z = 2.6, p = 0.008), b) Raindex vs species richness (z = 3.6, p < 0.001). Solid lines represent negative binomial glm fits of mean values ± 1 SE (dotted lines). Points are scaled according to the number of points with the same number of species (i.e. large plots represent data with repeated points).

2.4. Discussion

The present study is one of the first to assess dung beetle communities along a rainfall gradient and also assessing the role played by land use (PAs vs farms). Dung beetle abundance in the protected areas was significantly greater than in farms, despite farms generally having greater stocking rates than reserves. Surprisingly, the greater abundance of dung beetles in protected areas did not result in greater functional diversity, which was significantly lower in protected areas. Rainfall only influenced species richness and dung beetle abundance, and although abundance was correlated with long-term rainfall, species richness varied with short-term rainfall. One trap type could have caught more individuals than the other (i.e. soil vs water pitfall traps). Nevertheless, the same trapping method was used across the study, so trap data are comparable between sites.

2.4.1. Dung beetle communities on farms vs protected areas

Herbivore species composition is an essential factor influencing diversity and size of dung beetles present in an assemblage (Nichols et al., 2009). Body size of herbivores is strongly associated with the size of dung deposited (Blueweiss et al., 1978), with small-bodied mammals depositing small dung pats that may not be used by large-bodied dung beetles that prefer large dung pats (Peck and Howden, 1984). However, in this study, protected areas (with more dung producing species) and farms (with fewer species) did not differ in dung beetle presence or absence, species richness or the CWM of body length of the dung beetle species found. Nevertheless, dung beetle abundance was greater in protected areas than in farms. This was surprising as there was a positive correlation between dung beetle abundance and increased stocking rates in the farms. This may be because there were dung types more appropriate for breeding available in protected areas than in farms (i.e. larger dung pats than just the pelleted dung of sheep). The Nama and Succulent Karoo are grazed mainly by sheep, producing pellet-type dung that is very different from that of cattle dung. There were only two farms that had cattle and the protected areas in this study had few species with dung type similar to that of cattle (e.g. buffalo and wildebeest that are ruminants and larger animals that make larger dung pats in the wet season). A study investigating the variation of dung beetle species between the two land uses also found greater abundance in protected areas compared to cattle farms in the savanna biome (Jankielsohn et al., 2001). The difference in dung type may be another predictor of dung beetle abundance and may need to be investigated in further studies. It may also be that dung deposited by livestock competes with that used in pitfall traps, obscuring any clear patterns related to stocking rates. One possible reason for lower dung beetle abundance in the farms

may include the use of anthelmintics by farmers to reduce livestock parasite loads, which negatively affect the survival of dung beetles (Nichols and Gomez, 2014), however, further investigation is required to determine whether farmers in this area use anthelmintics or not. Another explanation could be that the cattle dung that was used as bait in this study may have failed to attract dung beetles that prefer other dung types (Tshikae et al., 2013).

Land use also had a significant effect on functional diversity (measured as sesFD); however, in this case, functional diversity was lower in protected areas compared to farms. This suggests that the species in these protected areas were more similar to each other, dividing up niches more finely, with greater competition between species (Tilman, 1994). It is therefore expected that with higher abundance, as observed in the protected areas in this study, there would more competition for dung resources. Another possible explanation for lower FD in protected areas may be either unfavourable biotic (i.e such as less dung resulting from lower stocking rates) and abiotic (i.e high rainfall as observed in the eastern summer rainfall sites) conditions that lower opportunities for niche differentiation (Gao et al., 2020). The extent of such interaction effects needs to be investigated further to fully understand these observed patterns.

As with the abundance of dung beetles, species richness was also strongly and positively correlated to higher stocking rates. However, it is not clear from this study whether this is a casual relationship or if it is influenced by ecosystem productivity. Livestock grazing in this region is primarily by a single species (i.e. sheep) with small dung pellets and constitutes a much simpler system than the multi-species natural system in protected areas with a host of different herbivores. Surprisingly, land use (i.e. farms or protected areas) did not affect dung beetle

species richness, probably because other factors, like rainfall, are far more important. These results highlight the importance of resource availability for maintaining dung beetle richness and abundance (Tshikae et al., 2013). Even though one protected area (Camdeboo National Park) was observed to have high dung beetle species richness and abundance with both high dung availability and diversity, the findings of this study show that dung beetle species richness in this region was driven by rainfall and the availability of dung (estimated using stocking rates in this study) and less so by dung diversity.

2.4.2. The effects of habitat structure on dung beetle communities

Dung beetle species richness and functional diversity were significantly affected by variation in habitat structure; this agrees with other studies that found a strong influence of vegetation cover (Boonrotpong et al., 2012) and soil texture (Beiroz et al., 2017) on dung beetle communities. The impacts of habitat structure are most apparent on abundance, size and functional role of the dung beetles (Davis, 1994; Jankielsohn et al., 2001). Although vegetation cover did not influence abundance or size of dung beetles in this study, it did have a positive effect on species richness and functional diversity. This can be explained by habitat type preferences and ability of species within different functional groups to compete for dung in these habitats (Jankielsohn et al., 2001; Scholtz et al., 2009). It may also be a result of enhanced grazing capacity by herbivores.

The study area was dominated by small-bodied dung beetles mainly from the *Aphodius* and *Onthophagus* genera. This was not surprising as small-bodied dung beetles are able to use most microhabitats and food resources (Jankielsohn et al., 2001; Nichols et al., 2009). The CWM of body length increased with an increase in

clay content. This could be because dung beetles require high moisture (which would tend to be greater with greater clay content) in the soil for broods to develop successfully (Sowig, 1995). Moreover, dung beetles emerging from moist soils tend to be larger in size than those emerging from dry soils (Sowig, 1996). Soils with high clay content hold water for longer (Lund, 1959), providing the most conducive microhabitat for successful breeding (Sowig, 1995; 1996). This may explain the positive influence of increased clay content on large-bodied dung beetles. Moreover, most of the large-bodied species surveyed in this study were roller species from the *Scarabaeus* genus that usually dig shallower nests than tunnellers (Davis et al., 2010). Body size inequality measured as the Gini coefficient was only significantly influenced by vegetation cover and clay content. While the Gini coefficient cannot be used to determine drivers of inequality in size (Lorenz, 1905), this parameter shows that body size inequality in dung beetle communities was larger in sites with low vegetation cover and clay content and smaller in high vegetation cover and clay content. Thus, in areas with high vegetation cover and clay content, the different size classes are represented more evenly.

2.4.3. Dung beetles across the rainfall gradient

Dung beetles, which are known to be most active after rain (Davis et al., 2004), responded positively to rainfall at different temporal scales. For example, dung beetle abundance was best explained by MAP, a long-term measure of rainfall, while species richness of the dung beetles caught in the traps correlated best with raindex, a measure of recent rainfall. These findings are consistent with other studies that found species richness to increase after rainfall (Davis, 2002; Hernández et al., 2014). The increase in dung beetle abundance with increasing MAP is consistent

with productive systems having higher species diversity, which may also affect stocking rate, and abundance (Chase, 2010), and greater MAP is likely associated with more events where conditions are sufficiently moist for dung beetle activity (Tshikae et al., 2013). Most adult dung beetle species stay dormant in soil during the dry season when conditions are unfavourable (Halffter and Matthews, 1966; Hernández et al., 2014). This aspect of dormancy may also explain increased species richness following recent rain, with many species emerging immediately after rainfall when conditions are suitable for breeding. This has been observed with *Khepher nigroaenes* which only emerges a few weeks after the first rainfall event at the beginning of the summer rainfall season (Edwards and Aschenborn, 1988). Interestingly, medium-term rainfall, i.e., the relative dryness or wetness of the rainfall of the preceding year compared to the long term mean, did not explain abundance or species diversity as well as long or short term rainfall. This study suggests that some species cannot tolerate very dry conditions and might have retreated further away from the dry areas during this drought.

2.5. Conclusion

These results suggest that while variation in land use, habitat structure and rainfall influence dung beetle communities across the Karoo, different measures of dung beetle assemblages respond in different ways to these variables. The effects of herbivore stocking rates and rainfall were only apparent and positively correlated with dung beetle species richness and abundance. However, short-term rainfall was the best predictor for species richness and long-term rainfall was the best predictor for abundance. There were no significant differences in dung beetle species richness and mean body length between the protected areas and farms, possibly because

other factors like rainfall and vegetation cover were more important in explaining these measures. However, protected areas had greater abundance and lower functional diversity. Species richness and functional diversity were affected by vegetation cover, but mean body length varied with soil texture. Overall, the findings of this study emphasise the importance of assessing all community attributes in order to determine how dung beetle communities are affected by specific changes. Furthermore, these different attributes yield different insights into community assemblages, and this might dictate their use in long-term monitoring of future land use and climatic changes.

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CHAPTER 3: THE RELATIVE IMPORTANCE OF RAINFALL, HABITAT STRUCTURE AND HERBIVORE STOCKING RATE ON DUNG BEETLE SPECIES COMPOSITION ALONG AND ARIDITY GRADIENT

Abstract

There is a need to understand how human activities impact the environment and how these impacts change the way ecosystems function and in turn, affect landscape resilience. To do this, we need insight into how functionally important organisms are influenced by land use. Here, I investigate whether and how dung beetle species composition along a rainfall gradient on livestock farms and protected areas in the Nama and Succulent Karoo region respond to different, herbivore stocking rates, habitat structure and rainfall gradients. To determine the importance of rainfall, I assessed whether dung beetle assemblage responded to long-term rainfall (mean annual precipitation), medium-term rainfall (standard precipitation index) or recent rainfall relative to sampling time. Eleven sites were sampled, representing six livestock farms and five protected areas, once in summer and once in winter. During the study, 35 species were caught. Most species were common in both land-use types, but two species were found only on farms and six species were found exclusively within the protected areas. Dung beetle species composition varied significantly with land use, rainfall, stocking rates, vegetation cover and rainfall seasonality. However, long-term rainfall was the best predictor for dung beetle assemblage composition, explaining the most variation compared to all the other measured environmental variables. Beta diversity as a measure of differentiation between habitats, here, was driven by the gain or loss of species and not turnover. The species composition in the drier sites was a subset of the assemblage in the

wetter sites, suggesting that species drop out as sites become drier, but new species are not added.

Keywords: Aridity gradient, dung beetle assemblage, rangelands, Scarabaeinae, soil arthropods, species vulnerability, species traits

3.1. Introduction

Different land-use practices are known to alter environmental conditions and species community structures (Kietzka et al., 2018; Stohlgren et al., 1998; Stohlgren et al., 2001). Understanding the impacts of human activities and climate variation on the environment and how these influence ecological communities and the services they provide is crucial in community ecology (De Castro-Arrazolla et al., 2018; Finn et al., 1999). This knowledge should give insights into how ecological communities may respond to environmental changes (Høye et al., 2017) and is thus essential in developing more effective conservation strategies.

Several studies have identified protected areas to serve as refuges for some sensitive species (Bhagwat et al., 2008; Fabricius et al., 2003; Gray and Rickard, 1989; Kietzka et al., 2018; Struebig et al., 2015). The relatively pristine nature of protected areas (PA), or at least the reduced disturbance from human activities, can provide suitable habitats for species that are sensitive to habitat fragmentation and degradation.

In semi-arid ecosystems, ground-dwelling insect communities and their activities are limited to a short period of sufficiently humid conditions (Lindsey and Skinner, 2001). The rainfall gradient span is 100 to 520 mm/year in the Nama Karoo and 20 to 290 mm/year in the Succulent Karoo (Mucina and Rutherfold, 2006). Furthermore, climate change projections for the Succulent Karoo indicate that

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biodiversity will be negatively influenced by extreme warmer and drier climate conditions with a potential loss of endemic plant species (Musil et al., 2005). However, knowledge of the actual tolerance of drought and heat of the species in this area is still lacking (Midgley et al., 2005). Rainfall projections in the Nama Karoo predict increased summer rainfall and more rainfall variability, which may potentially influence some species populations (Altwegg and Anderson, 2009).

Dung beetles (Coleoptera: Scarabaeidae) are sensitive to climatic changes (Estrada et al., 1999; Lumaret et al., 1992), including variations in rainfall gradients (Abdel-Dayem et al., 2016; Tshikae et al., 2013b). The impacts of climate change on species community structure (Emmerson et al., 2005; Høye et al., 2017; Walther, 2010), can be particularly damaging in arid areas, owing to their high level of unpredictability (McCluney et al., 2012). About 38% of the earth is described as drylands (Huang et al., 2016) with the most unpredictable rainfall (Cheng et al., 2011). This makes it crucial to understand the effects of aridity on dung beetle community composition, considering that availability of water is essential in shaping dung beetle communities (Abdel-Dayem et al., 2016; Labidi et al., 2012; Tshikae et al., 2013b; Hanski and Cambefort, 1991).

Dung beetle communities benefit greatly from grazing and browsing, given that livestock and wild herbivores provide dung (Lobo et al., 2006; Negro et al., 2011). Livestock and game farming change the relative diversity of available dung, and farms tend to stock (both livestock and game) at higher densities than PAs. While this could have a positive effect on dung beetles, with the provision of more dung for breeding and as a food source, it may also have negative effects by reducing the habitat structure either by overgrazing or soil trampling. Understanding how dung beetles respond to these two conflicting effects (increased availability of

dung vs reduced habitat structure) from higher stocking densities may give insights for conservation of biodiversity. Overgrazing reduces habitat structure, which has been associated with declines in some dung beetle species (Carpaneto et al., 2007; Negro et al., 2011), however, overgrazing may also lead to habitat encroachment which has also been shown to negatively influence dung beetle communities (Tocco et al., 2013). The losses of sensitive species, along with soil trampling through heavy stocking rates, both conspire to affect soil structure (Negro et al., 2011; van de Koppel et al., 1997). These changes can be ameliorated by reducing herbivore stocking rates (van de Koppel et al., 2002), which in turn lowers the grazing pressure and lessens the effect on the habitat structure.

With the exception of plants, biodiversity in the Karoo remains relatively poorly studied. This lack of baseline data makes it almost impossible to monitor potential effects of global change on ecological communities in these biomes. Dung beetles' sensitivity to both habitat and climatic changes make them ideal indicator species (Davis et al., 2001; Gollan et al., 2013). Here, I analysed the effects of land use, habitat structure and rainfall on dung beetle communities, at eleven sites across the Karoo, including livestock farms (the most common land use in the region), and PAs. The farms in this study areas had higher stocking rates (an average of 0.036 LSU/ha) than the PAs (average of 0.027 LSU/ha (Appendix 1)). The main objective was to understand dung beetle communities in a semi-arid area and identify environmental variables that may be correlated with changes in species assemblage composition. The questions asked were: (1) does species composition of dung beetle assemblages differ with land-use, rainfall gradient, soil texture, herbivore stocking rates and vegetation cover? (2) Are these effects evident for all species, or are there certain species which are more sensitive and could serve as indicator

species? 3) How do functional traits vary with land use, habitat structure and rainfall, and how does this affect species composition?

The question arises as to whether dung beetles in semi-arid areas are locally adapted, with assemblages found in the most arid areas merely a subset of the larger group, or whether dung beetles found in the most arid areas are completely different to those found in more mesic areas. In addition, the study area tends to have winter rainfall in the west, and summer rainfall in the east. This seasonality of rainfall might dictate two different groups of beetle species, with the arid sites within these two areas having subsets of the species found in their more mesic counterparts. I expected dung beetle species composition to differ between the two land-use types owing to higher herbivore stocking rates in the farms, and differences in dung type. I expected that the dung beetle communities in the drier parts of the gradient would be adapted to arid conditions or merely be a subset of the communities in the wetter part of the gradient, but that there might be an effect of rainfall seasonality (Davis 1990, 1993), with assemblages at drier sites in winter rainfall areas subsets of other winter rainfall areas, but quite different to the set of species at summer rainfall areas. Alternatively, dung beetle assemblages would differ completely, with a set of species specially adapted to dry areas on the one side of the gradient; however, this may also depend on recent rainfall relative to sampling date.

3.2. Methods

3.2.1. Study area

Dung beetle communities were studied in the Nama and Succulent Karoo region at 11 sites spanning over three provinces (Western Cape, Northern Cape and Eastern

Cape) in South Africa, over a distance of 429 km between the most western to most eastern sites (Fig. 3.1). Six sites were located in livestock farms, and five sites were located in protected areas. The Nama Karoo is dominated by grassy dwarf shrubland vegetation, with trees occurring along watercourses (Todd, 2006). The Succulent Karoo is dominated by dwarf succulent shrubs, geophytes and annual forbs (Todd and Hoffman, 2009), with much of South Africa's endemic plant species nested in the Succulent Karoo (Mucina et al., 2006b). Three sites are located within the summer rainfall region, and eight sites fall in the winter rainfall region (see Appendix 1). The dominant land use in the region is rangeland grazed by livestock (hereafter referred to as 'farms'), hence much of this landscape has been disturbed by current or historical grazing by domestic stock with some wild herbivores.
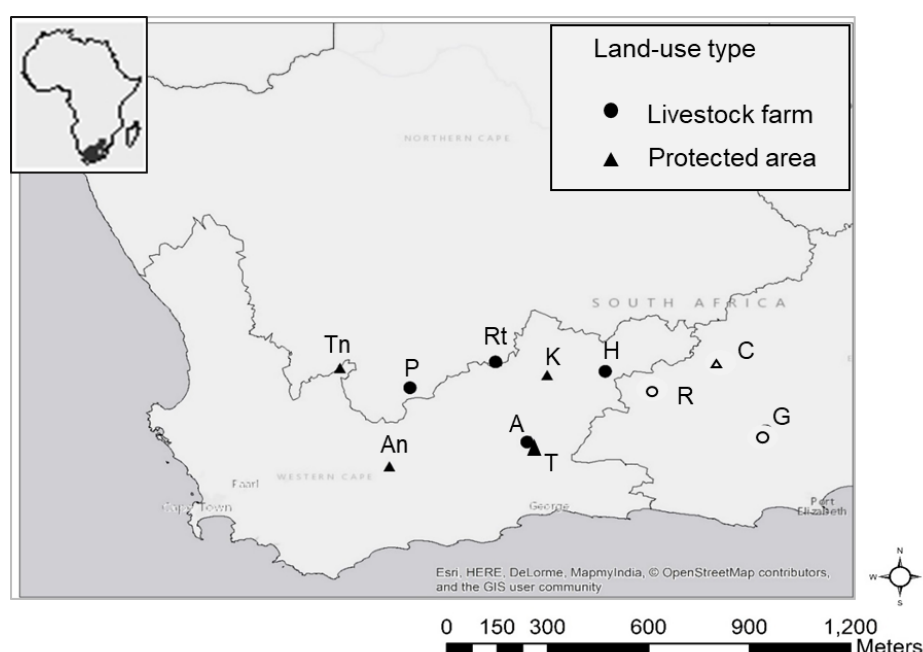
Figure 3.1. Study area in the Nama and Succulent Karoo showing the 11 study sites; where the open (summer rainfall sites) and closed (winter rainfall sites) circles depict six sites in livestock farms (A - Argentina; G – Good Luck; G - Hopewell; P - Portugalsriver; Rt- Rietvlei; R - Rooidraai), and the open (summer rainfall sites) and closed (winter rainfall sites) triangles depict five protected areas (An – Anysberg Nature reserve; C – Camdeboo National Park; K – Karoo National Park; Tn – Tankwa-karoo National Park; T – Tierberg LTER)).
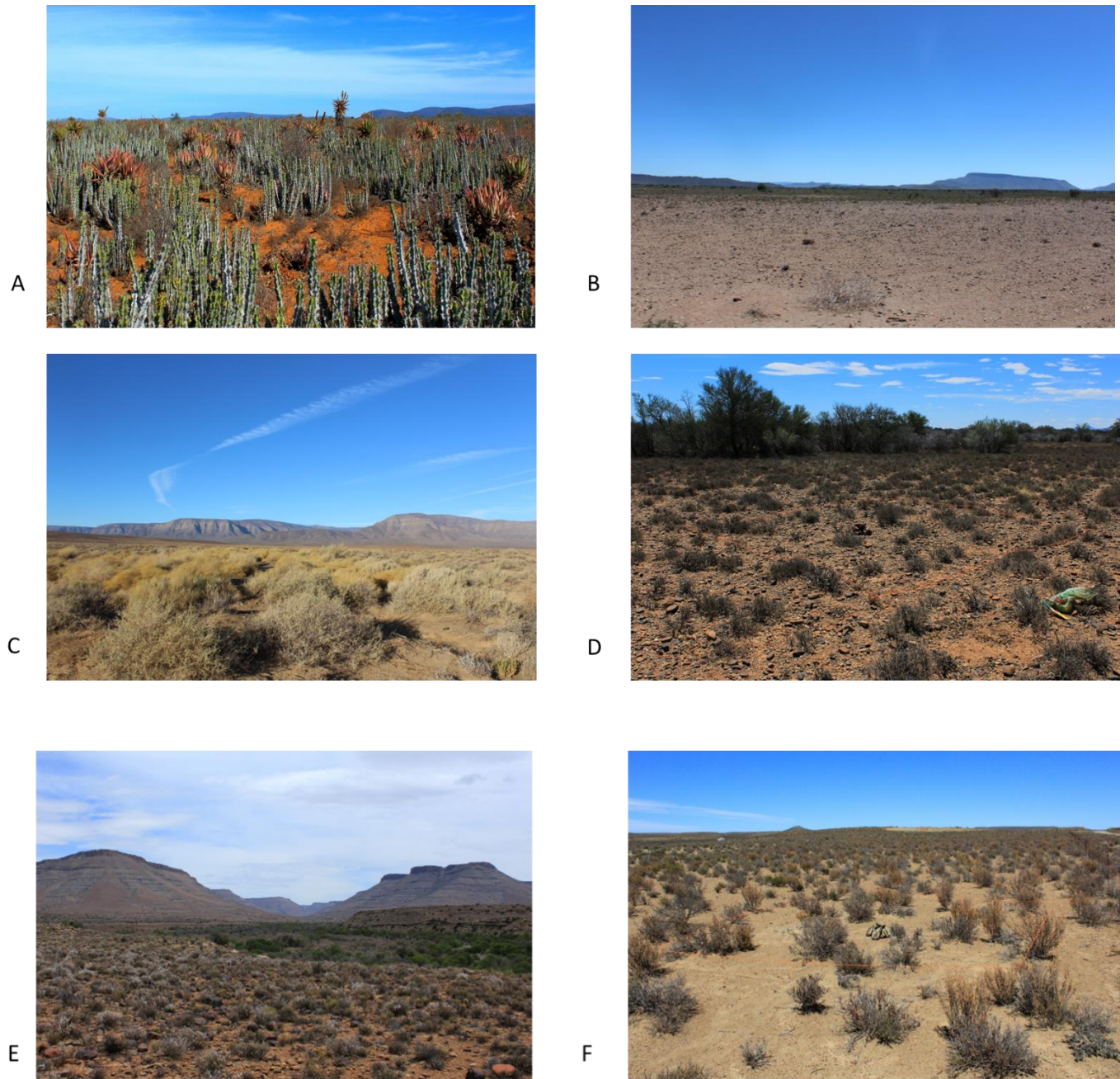
Figure 3.2. The livestock farms sites. A – Good luck, B – Hopewell, C – Argentina, D – Rooidraai, E – Rietvlei and F – Portugalsriver.

3.2.2. Data collection

Fieldwork was conducted at the end of the austral summer (March) of 2017 and then again in the winter (August) of 2017, with each site visited once per sampling season. Each site had three sampling plots separated by at least 300 m.
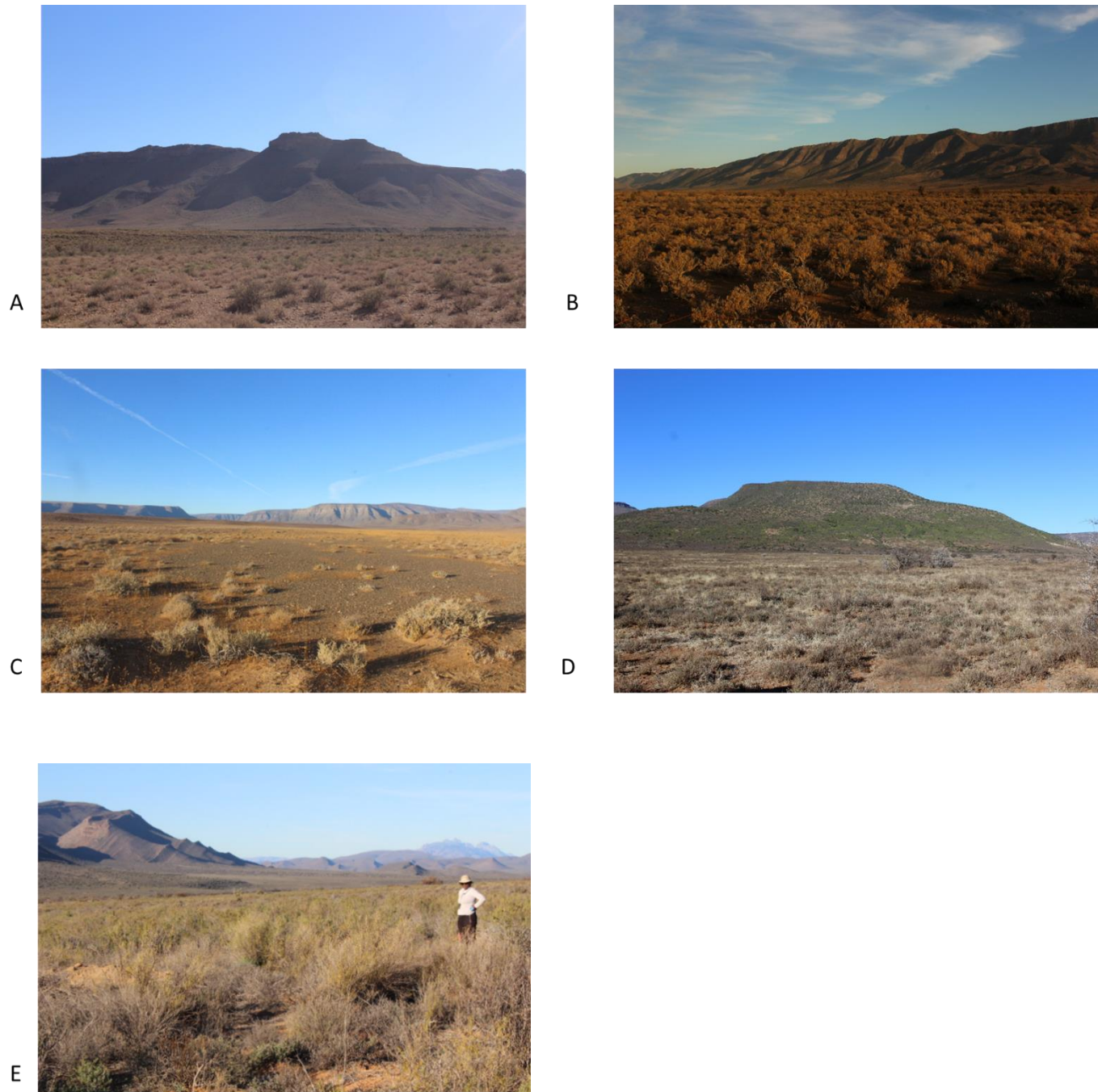
Figure 3.3. Protected area sites. A – Karoo National Park, B – Tierberg LTER, C – Tankwa Karoo National Park, D – Camdeboo National Park and E – Anysberg Nature Reserve.

Ten pitfall traps baited with cow dung were placed 10 m apart along two transects (that were 30 m apart) of five traps per transect within each of the three sampling plots at each site. Each transect had a different type of pitfall, one with

pitfalls filled with soil, and the other with pitfall traps filled with water. The pitfall traps (2 L plastic containers: 14 cm deep with a 17 cm diameter) were buried at ground level and filled to about two-thirds capacity. Two hundred grams of fresh cow dung was placed inside a white linen bag and suspended on a wire harp ca 5 cm above the centre of the water pitfall traps (Pryke et al., 2013). For the soil pitfall traps, 200 g of fresh cow dung was placed inside the trap on the soil. The locations of the traps were the same for both sampling visits. Traps were set out between 08h00 and 09h30 and dung beetles were collected after 24 h. Dung beetles were identified to genus level, and to species level where possible. Voucher specimen collections are kept at the Entomology Museum at the Department of Conservation and Entomology, Stellenbosch University.

3.2.3. Dung beetle functional trait measurement

Dung beetles used in trait measurements were randomly selected from the 30 pitfall traps in each of the 11 sites. I measured dung beetle traits that linked to relative body size (body length), reproduction capacity (abdomen size), nesting behaviour (hind leg size and hind leg robustness) and dispersal ability (wing aspect ratio and wing loading) (Raine et al., 2018), as detailed in Table 3.1. The functional traits were measured from 356 dung beetles (n = 5 – 23 individuals per species) from 20 species using digital callipers with an accuracy of 0.01 mm, measuring only the species with five or more sampled individuals. The mean of each functional trait was standardised to zero with a standard deviation of one so that the variation within each trait was treated equally (Petchey and Gaston, 2006).

Table 3.1. Dung beetle functional traits measured and a description of the morphometric measurements taken used to assess how functional traits vary with land use, habitat structure and rainfall.

Variable	Measured trait	Measurement	Description
Relative body size	Body length	Body length (mm)	Total length of beetle from the tip of the clypeus to the base of the elytra
Reproductive capacity	Abdominal size	Thorax length/abdomen length (mm)	Dorsal length of the pronotum disk's centre/ maximum abdomen's ventral length
Dispersal ability	Wing aspect ratio	Wing width/wing length (mm)	The maximum wing width and length
	Wing loading	Wing area (wing width x wing length) / body area (body area = body length × thorax width (mm))	Body length and thorax width same as described above
Nesting behaviour	Hind leg size	Hind leg length/body length (mm)	Maximum tibia length, excluding the spurs
	Hind leg robustness	Hind leg width/hind leg length (mm)	Tibia width taken one third from the trochanter/ hind leg length same as above

3.2.4. Environmental variables

I gathered data on land use, rainfall, season, soil type, and vegetation cover to understand their influence on dung beetle activity. Rainfall data were obtained from weather stations placed by the South African Weather Services nearest to each of the sites (maximum distance of 37.6 km; Appendix 5). Dung beetle communities

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might respond to recent rains or more long term rainfall. Therefore, I used three different measures of rainfall; Mean annual precipitation (MAP), Standardized precipitation index (SPI), and "raindex", which measures of long-, medium- and short-term rainfall, respectively. MAP was calculated as the average rainfall for each site over the years 1988 to 2017. SPI was calculated as the number of standard deviations that observed rainfall for the year differed from the long-term MAP. Raindex was the amount of rain received in the most recent downpours (days of rain not separated by more than five dry days) divided by the number of days since the last day of rain relative to dung beetle sampling (Appendix 6).

Table 3.2. Measured environmental variables measured and used for analyses.

Variable	Category	Units
Land use	1 – Farms	
	2 – Protected areas	
Rainfall seasonality	1 – Summer rainfall region	
	2 – Winter rainfall region	
Rainfall measure	1 – Mean annual precipitation (MAP)	mm/year
	2 – Standardized precipitation index (SPI)	
	3 – Raindex	mm
Soil content	1 – Clay	%
	2 – Sand	%
	3 – Silt	%
Stocking rates	Number of equivalent large stock units/ha	LSU/ha
Vegetation cover	Overall vegetation cover	% cover

The texture (percentage of sand, silt and clay) of the soil was assessed based on four soil samples collected from each of the sites, analysed by Bemlab (Pty) Ltd. I counted all plants found in each transect and then visually estimated overall

vegetation cover for each transect as the percentage of vegetated area, averaged from three 1 m^2 plots that were randomly selected in each of the transects; were vegetation, bare ground and litter cover sums to 100% (Delamater et al., 2012). Mammalian herbivore species richness and abundance, and stocking rates for each of the sites were sourced from the farmers and park managers.

3.2.5. Data analysis

I used a general linear model-based analysis of multivariate abundance, using the "manyGLM" function in the mvabund (Wang et al., 2012) package in R (R Core Team, 2018) to assess the variability of species composition across different land uses and environmental variables. Dung beetle abundance at Camdeboo National Park site was found to be an outlier during initial data exploration, with 6 426 dung beetles caught in the traps. Therefore, the data were square-root transformed to downweight the influence of the outlier (Loreau and Hector, 2001). The response variable was the square-root transformed abundance data of each dung beetle species on each of the sites per sampling season, modelled with a negative binomial distribution, which gave a better fit than Poisson. The explanatory variables were land use, amount of rainfall, measured as MAP, SPI or raindex, rainfall seasonality, stocking rate, vegetation cover and soil content (Table 3.2). I assumed that the influence of stocking rates might differ between the two land uses, so I included two-way interaction terms for land use and stocking rates. I also assumed that MAP and rainfall seasonality might influence species composition, and included an interaction between MAP and rainfall seasonality. The soil content and rainfall measures assessed long-, medium- and short-term rainfall, were collinear and so were not included in the same models. I ran a series of models, each with a different measure of rainfall and soil content, and then used the Akaike Information Criterion (AIC) to

choose the best fitting model (Akaike, 1973). I also tested for each species' response to these explanatory variables using post hoc univariate test with p values adjusted for multiple testing (Wang et al., 2012). Model residuals were inspected for normality, independence and constant mean-variance relationships.

To assess the influence of functional traits on the response of dung beetle communities to different environmental variables (land use, rainfall seasonality, rainfall, stocking rates, Herbivore species richness, vegetation cover and soil content), I used a model-based approach for the fourth-corner analyses (Brown et al., 2014). The fourth-corner approach produces model-based analyses of the relationships between species traits and environmental variables using a species abundance matrix (Legendre et al., 1997). I fitted fourth-corner models for species abundance, using square root transformed data, as a function of the species traits matrix, environmental variable matrix, and their interactions (environment x traits), using the traitglm function in the mvabund package (Wang et al., 2016) in R (R Core Team, 2018). Species abundances were count data; hence, the models were fitted using the negative binomial distribution. The interactions between environmental variables and species traits represent the fourth corner, which addresses how species traits influence environmental responses across taxa (Brown et al. 2014). Of the measured functional traits (Table 3.1), abdominal size and wing aspect ratio were both positively correlated to hind leg robustness, and body size was positively correlated to wing loading. Therefore, I ran the models with different trait combinations ensuring that variables that were correlated were not used simultaneously. I chose the best trait combination by selecting the model that explained the highest deviance.

I assessed the change in community composition amongst sites using beta diversity. Beta diversity can be classified as nestedness, which occurs when a lesser species-rich assemblage is a subset of a greater species-rich assemblage, and spatial turnover, which shows the replacement of some species by others as a result of constraints imposed by environmental characteristics (Baselga, 2010). To assess whether variations in dung beetle communities between sites are due to species replacement (i.e. species turnover) or richness difference (i.e. nestedness) I employed the beta function in the BAT package in R (Cardoso et al., 2015). This function calculates three matrices of beta diversity (β_{total} (total beta diversity), β_{repl} (dissimilarity explained by replacement of species) and β_{rich} (differences in richness)) measured between all pairs of sites and partitioning for multiple sites simultaneously (Cardoso et al., 2015).

3.3. Results

I collected a total of 9 089 dung beetle individuals representing 35 species; 29 species (1 645 individuals) were found on farms, with two species unique to farms, and 33 species (7 444 individuals) in protected areas, with six species found exclusively in the protected areas. Three species, *Aphodius* sp.5 (1 056 individuals), *Onthophagus fritschi* (3 025 individuals) and *Onthophagus albipennis* (1 767 individuals) accounted for 64.3% of all the collected dung beetles (Appendix 3).

3.3.1. Differences in dung beetle assemblage composition with land use, rainfall gradient, soil texture, herbivore stocking rates and vegetation cover

Dung beetle species composition differed significantly between farms and protected areas (Dev = 57.06, p = 0.015; Table 3.3), this was associated with *Aphodius* sp.2 which was most abundant in the parks compared to the farms. Herbivore stocking

rates also influenced dung beetle species composition (Dev = 107.3, p = 0.001, Table 3.3), with *Drepanocerus patrizii* and *Odontoloma pygidiale* being markedly more abundant in sites with high stocking rates. Together, these indicator species accounted for 26% of the variation in abundance with a change in stocking rates. As expected, there was an interaction between land use and stocking rates on dung beetle species composition (Dev = 105.4, p = 0.001; Table 3.3), associated with *Aphodius* sp.6 and *Euniticellus africanus* (Table 3.4), together accounting for 28% of the interaction effect. Both these species increased in abundance most steeply with an increase in stocking rates in protected areas and far less steeply on farms. Vegetation cover (Dev = 67.6, p = 0.006, Table 3.3) was associated with *Cheironitis audiens* (Table 3.4), which increased in abundance with increasing vegetation cover, accounting for 21% of the observed variation in assemblage composition. Surprisingly for a soil-dwelling group such as dung beetles, soil texture had no significant influence on dung beetle community composition (Table 3.3).

Mean annual precipitation was the best rainfall measure. The most influential variable of all the variables was MAP (Dev = 246.91, p = 0.001, Table 3.3), explaining 31% of the total variation. Eight indicator species varied significantly in abundance with change in MAP, and together they accounted for 46% of the deviance explained by the model (Table 3.4). Dung beetle species composition was also significantly influenced by the predominant period at which an area receives rainfall (Dev = 133.9, p = 0.001, Table 3.3). Species which differed consistently in their relative representation between rainfall regions were *Onthophagus fritschi, O. peringueyi, Phalops dregei* and *Scarabeaus viator,* all far more abundant in summer rainfall regions, and which together explained 25% of the variance (Table 3.4). The effect of MAP on dung beetle species composition differed between the summer and

winter rainfall areas (Dev = 90.4, p = 0.001, Table 3.3), was associated with *Euonthophagus vicarius* (Table 3.4) with increasing MAP in the summer rainfall regions and decreased in abundance with increasing MAP in the winter rainfall region.

Table 3.3. Model summary of the community analyses using multivariate generalised linear modelling showing the variation (Dev) in dung beetle species abundance data explained by the evaluated environmental variables. Bold values indicate significant P values; Res.df: Residual degrees of freedom; Dev: Deviance.

Variables	Res.Df	Dev	P-value
MAP	28	246.9	**0.001**
Rainfall seasonality	27	133.9	**0.001**
Land use	26	57.06	**0.015**
Stocking rates	25	107.6	**0.001**
Vegetation cover	24	67.55	**0.006**
Clay	23	39.9	0.155
MAP x Rainfall seasonality	22	61.50	**0.002**
Land use x Stocking rates	21	105.4	**0.001**

3.3.2. Variation in Beta diversity between sites.

Beta diversity (β_{total}) of dung beetles between sites was 0.5 (sd = 0.2), attributed more to differences in richness between sites (average β_{rich} = 0.4, sd = 0.2) than species turnover (average β_{repl} = 0.2, sd = 0.1) component. For almost two-thirds (36 out of 55; 65.5%) of site comparisons, beta-diversity was explained by β_{rich}, while 32.7% (18 out of 55 site comparisons) was explained by β_{repl} and 1.8% (1 out of 55 sites) of the beta-diversity was equally explained by both β_{rich} and β_{repl}. Beta-diversity

was greatest between the site with the highest MAP (381.1 mm in Camdeboo National Park) and the site with the lowest MAP (137.8 mm in Tankwa-Karoo National Park) (β_{total} = 0.83) and this was attributed completely to β_{rich}.

Table 3.4. Univariate test statistics with adjusted p values, showing the indicator species for each of the environmental variables and the deviance explained by each species. The asterisk symbol (*) represents an interaction term between two environmental variables.

Species	Deviance	p-value	Environmental variable
Aphodius sp.2	16.8	0.003	MAP
	17.1	0.004	Land use
Aphodius sp.5	16.5	0.003	MAP
Aphodius sp.6	20.7	0.002	Land use*Stocking rates
Cheironitis audiens	13.9	0.019	Vegetation cover
Drepanocerus patrizii	12.4	0.023	Stocking rates
Euniticellus africanus	9.2	0.038	Land use*Stocking rates
Euonthophagus vicarius	11.2	0.001	MAP* Rainfall seasonality
Neosisyphus macrorubus	14.5	0.003	MAP
Odontoloma pygidiale	15.7	0.006	Stocking rates
Onthophagus albipennis	19.6	0.002	MAP
Onthophagus fritschi	16.8	0.003	MAP
	16.8	0.001	Rainfall seasonality
Onthophagus peringueyi	9.7	0.025	MAP
	31.7	0.001	Rainfall seasonality
Phalops dregei	11.5	0.024	Rainfall seasonality
Phalops rufosignatus	10.3	0.025	MAP
Scarabaeus viator	11.6	0.015	MAP
	18.5	0.001	Rainfall seasonality

3.3.3. Variation in trait representation with variation in environmental variables.

A significant amount of variation in species response to environmental variables that was explained by species traits (Fourth corner analysis: Dev = 65.59, p = 0.01, Fig.3.4). Land use was significantly associated with the CWM of abdominal length and wing loading. Abdominal size and wing loading were larger for protected area sites (w = 2.22, p = 0.039, Fig.3.4; w = 2.25, p = 0.039, respectively, Fig.3.4).
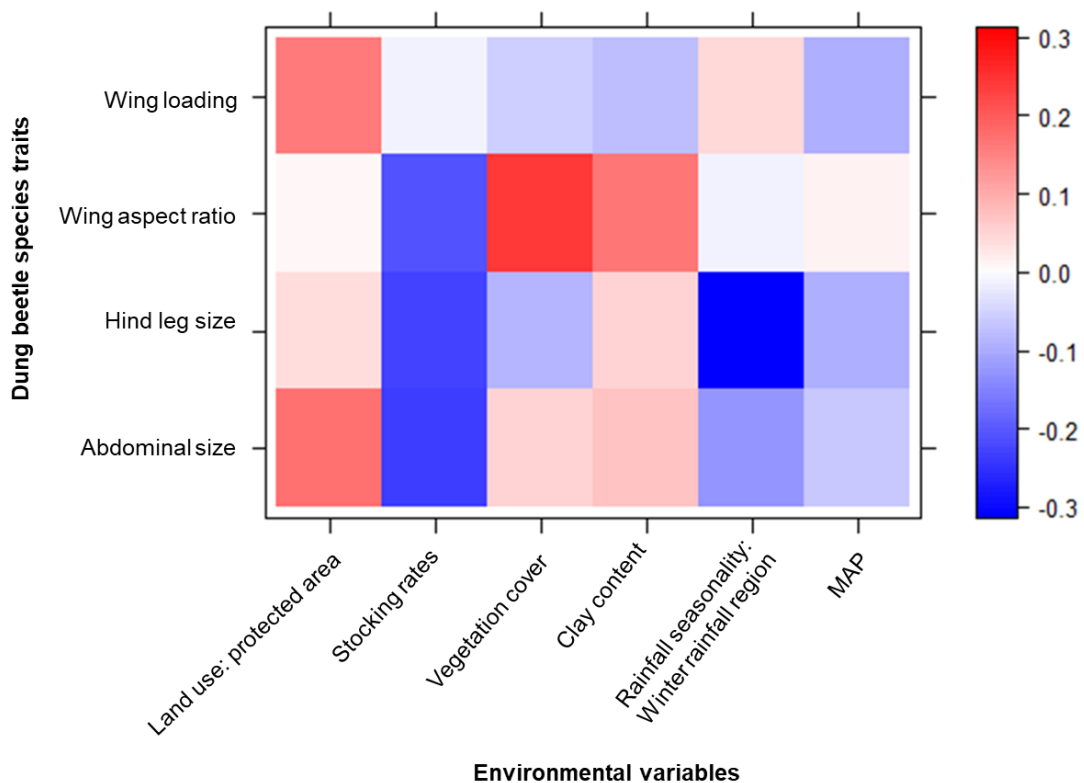
Figure 3.4. The fourth-corner biplot showing the relationships between species traits and environmental variables. Red represents positive relationships, and blue represents negative relationships; deeper colours represent stronger relationships. Column1 (Land use: protected area) shows the relative trait representation in protected areas vs. farms and Column 5 (Rainfall seasonality: winter rainfall region) shows the relative trait representation in winter rainfall sites vs. summer rainfall sites.

Hind leg size is negatively associated with stocking rates (w = 2.17, p = 0.044, Fig.3.4) and rainfall seasonality, with smaller hind leg size in sites in the winter region (w = 2.84, p = 0.006, Fig.3.4). Abdominal size was also negatively associated with stocking rates; however, this was not significant (w = 1.95, p = 0.057). Wing aspect ratio positively associated with vegetation cover (w = 2.71, p = 0.016, Fig.3.4). MAP and clay content had no significant associations with any functional traits considered here.

3.4. Discussion

The environmental variable explaining most variation in dung beetle species composition was long-term rainfall, MAP. Within that, dung beetle assemblage composition also varied with rainfall seasonality (summer or winter rainfall region), stocking rates, vegetation cover and management type (farmed or protected). The importance of rainfall on dung beetle communities was also apparent in Chapter 2, species richness responded to recent rainfall and abundance to long-term rainfall. The overriding importance of MAP on community composition is probably linked to rainfall, but could also be driven by spatial proximity: areas in this study with similar long-term rainfall tend to be closer to each other, as long term rainfall tends to follow a trend of increasing rainfall from west to east. Dung beetle abundance and beta diversity indicated that dung beetle assemblages in arid sites along the rainfall gradient were subsets of the species found at more mesic sites. In fact, the entire species assemblage of the driest site (Tankwa-Karoo National Park with low MAP, winter rainfall) was a subset of those found in the wettest site (Camdeboo National Park with high MAP, summer rainfall). This suggests that rainfall itself can explain

the variation in species assemblages with increasing MAP, and that seasonality of rainfall may not be highly influential.

3.4.1. The community structure of dung beetles of the Karoo

I collected 35 dung beetle species in the 11 sites during the two sampling periods, summer and winter seasons. Eighty-three percent of the sampled dung beetle species were from the Scarabaeinae subfamily, dominated by small tunneller dung beetles, mostly from the genus *Onthophagus*. This is perhaps unsurprising, given that *Onthophagus* is considered the most species-rich dung beetle genus in the world and species in this genus have diversified to adapt to various soil and dung types (Davis et al., 2008a). Large rollers and tunnellers were rare, with the exception of *Scarabaeus viator*, a roller species that was found in nine of the 11 sites. The other three large species were found only once, in the protected area (Camdeboo National Park); one roller beetle species (*Escarabaeus satyrus*) and two tunneller beetle species (*Metacatharsius vitulus* and *Onitis alexis*).

Farms are dominated by sheep, goats and small antelopes, with three also having cattle and one farm and one protected area having horses. The low number of large-bodied dung beetles in my study sites may thus be explained by the dominance of pellet-type dung and the absence of large mammals (Nichols et al., 2013b). Sheep, goats and antelopes have small pellet type dung that has low water quantity (Lumaret et al., 1992), which mostly supports small-sized beetles. Most large-sized dung beetles require large dung pats (Doube, 1990; Hanski and Camberfort, 1991; Peck and Howden, 1984; Tshikae et al., 2013c), although the use of pelletised dung by a large-sized dung beetle has been recorded for *Kheper nigroaeneus*, which has the ability to mash fresh pellet type impala dung (Edwards and Aschenborn, 1988).

Diet shifts may be possible, for example, *Circellium bacchus* which was known to specialise in large herbivore dung has now been shown to also use rodent dung (Kerley et al 2018).

3.4.2. Effects of land use, stocking rates and vegetation cover on dung beetle communities

Dung beetle assemblage composition was significantly different between farms and protected areas, which is perhaps unsurprising, given that dung beetles are sensitive to anthropogenic disturbances which lead to habitat fragmentation and degradation (Nichols et al., 2007; Pryke et al., 2016; Scheffler, 2005; Tocco et al., 2013). This sensitivity varies amongst species (Scholtz et al., 2009), however. Some dung beetle species have particular habitat preferences (Roslin and Viljanen, 2011). In this study, the main species responsible for differences in dung beetle assemblage composition was *Aphodius* sp.2, which was found in far higher abundances in protected areas than farms. I also found interesting patterns for *Aphodius* sp.6 and *Euniticellus africanus*, both these species increased with increase in stocking rates, especially in protected areas. One possible explanation for this variation might be a response to dung heterogeneity; while farms offer a much simpler system with an abundance of one species of herbivore, most of the parks have a mix of different herbivores ensuring a variety in dung type. Dung type preference (as in, species that specialise in the dung of very few or only one mammal species) is associated with very few dung beetle species, with slight evidence of preference observed through relative abundance of certain species across dung types (Finn and Giller, 2002; Gittings and Giller, 1998; Tshikae et al., 2013a). Species that specialise in a certain dung type may be rare in arid systems, where herbivores tend to occur at low densities,

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reducing the options for specialist species, which would need to survive with the dung that they find.

The composition and stocking rates of dung producing animals determine the occurrence of dung beetle species (Frank et al., 2017), especially in arid areas (Hanski and Cambefort, 1991). The preference for large amounts of dung by large-bodied dung beetles (Nichols et al., 2013b) makes them not only dependent on the availability of preferred dung types but also the quantity of the dung. In this study, the species that were associated with variation explained by stocking rates (*Drepanocerus patrizii and Odontoloma pygidiale)* were found almost exclusively in sites that had high stocking rates. In other studies, *Drepanocerus patrizii* has been considered a generalist that has been found in sites with a variety of domestic and wild mammals, however, that study was conducted in an area with an MAP of 501 mm (Gorgon and Barbero, 2008)*.* Furthermore, *Drepanocerus patrizii* becomes active and abundant in the wet season (Stronkhorst and Stronkhorst, 1997). It is, therefore, possible that in the arid Karoo, they are relatively rare and limited to areas with high stocking rates. The nesting habits of *Odontoloma pygidiale* are unknown (Davis et al., 2008b), although its association with high stocking rates may be due to its poor dispersal ability. *Odontoloma pygidiale* display phenotypic plasticity and this species may have wings that vary from well-developed to much reduced (Davis et al., 2008b), thus, the preference for sites with high stocking rates that will ensure access to dung resources may select for reduced wings and so result in low dispersal ability.

In this study, I found a strong influence of vegetation cover on dung beetle community structure. Vegetation cover influences microclimatic conditions (Joseph

et al., 2018), with greater vegetation cover increasing the rate of soil moisture loss (Ozkan and Gokbulak, 2017) and reducing surface temperatures (Hansen, 2000; Schaffers et al., 2008). In turn, this influences dung beetle composition through their response to these microclimate conditions, as recorded in several studies (Davis, 1996; Davis, 1994; Halffter and Arellano, 2002; Hill, 1996; Louzada et al., 2010; Tshikae et al., 2013b; Verdú et al., 2011). *Cheironitis audiens,* identified as an indicator species for vegetation cover in this study, shows sensitivity to reduced vegetation cover and was predominantly limited to high vegetation cover sites. Larger dung beetle species are more susceptible to extinction and may be excluded from dung beetle communities if the microclimatic conditions and trophic resources are not favourable (Larsen et al., 2005). Although in Chapter 2 I found that dung beetle body size increased with an increase in clay content, soil texture did not emerge as a significant factor influencing dung beetle community composition here. This likely indicates that body size alone is not the only trait shaping dung beetle species composition.

3.4.3. The effects of rainfall on dung beetle assemblage composition

Dung beetles are well known to be affected by timing and amount of rainfall, especially in dry climatic conditions where species tend to be more active at the beginning of the rain seasons (Andresen, 2005; Hanski and Cambefort, 1991). Long-term rainfall was the best predictor of dung beetle assemblage composition in this study. The response was reflected in the increase in abundance of dung beetles in sites with higher MAP, as seen in another study that showed an increase in dung beetle activity with rainfall (Davis, 2002). All eight indicator species (Table 3.4) associated with MAP were highly abundant in sites with mid-high MAP. The response of a dung beetle community along an aridity gradient has been recorded in

another study (Tshikae et al., 2013b), showing a decrease in species richness in arid areas compared to the mesic areas.

This study showed that rainfall seasonality was also a predictor of dung beetle communities, significantly affecting four dung beetle species that were abundant in the eastern summer rainfall sites. Total rainfall and rainfall seasonality are confounded, however, with the western sites (winter rainfall) tending to be more arid than the eastern sites (summer rainfall), thus making it difficult to separate the effect of seasonality from the amount of rainfall. Species loss was the main component influencing variation in dung beetle communities which suggest that while arid areas are characterised by species that are adapted to conditions with limited resources (De Castro-Arrazolla et al., 2018) some species may probably tolerate more aridity than others. Thus, perhaps the dung beetles that are found there are those that can "make do" with the dung that is there, given that mammals occur in low densities in these areas of aridity because of the relatively low productivity. Specialisation in this arid area may be an adaptation to saprophagy to enable exploitation of dry dung and other dead matter (Verdu and Galante, 2004).

The effect of MAP on dung beetle species composition varied with rainfall seasonality, mainly due to patterns in *Euonthophagus vicarious*. This species was found most commonly in summer, but it had the greatest abundance at winter rainfall sites that had the lowest MAP. This suggests either morphological or behavioural adaptation to the semi-arid conditions of the western sites in the Karoo. Adaptation to dry environments have been recorded in some studies for flightless dung beetles (Holter et al., 2009; Scholtz, 1989; Verdu and Galante, 2004; Verdu et al 2010), associating this flightlessness behaviour to using dry pellets for species that had

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modified mouthparts suitable to exploit dry pellets (Verdu and Galante, 2004). Such an adaptation eliminates interspecific competition with other dung beetles, as dry dung is unattractive to many dung beetle species (Scholtz, 1989). Further investigation of *E. vicarious'* resource preferences may shed a light as to whether this species has adapted to using dry pellets.

3.4.4. Functional traits and environmental variables interaction

I found that the representation of several dung beetle functional traits varied significantly with environmental variables. Land use, stocking rates and rainfall seasonality were the environmental variables influencing representation of dung beetle traits. Dung beetles with high reproductive capacity (greater relative abdomen size) and high dispersal ability (greater wing loading) were more common in protected areas. Dung beetles depend on dung as a food resource for both the adult and larval stages (Nichols et al., 2009). Protected areas in this study include three national parks and a nature reserve that have a greater variety of herbivore species than the livestock farms. This diversity in herbivores implies a variation in dung types and may provide the preferred dung required for reproduction, especially for most large-bodied dung beetles that may not be able to use the pellet type of dung found in the farms (Bogoni et al., 2016; Moczek, 1998; Nichols et al., 2013a; Pessôa et al., 2017).

The ability of animals to disperse is strongly influenced by the suitability of the habitat they occupy and the availability of resources (Gardner et al., 2008; Klein, 1989). In order to ensure successful foraging for dung resources, dung beetles have had to physically adapt to their environment (Caveney et al., 1995). Flight ability has been correlated with the response of beetle species to fragmentation; species most vulnerable to fragmentation are either flightless or live underground (Driscoll and

Weir, 2005). In the current study, protected areas had lower stocking rates compared to farms; thus, being in environments with fewer resources, there may have been selection for mobile species that are able to disperse. Although it was surprising that species at drier sites didn't have more traits or at least, a significant association of traits for mobility with low rainfall as would be expected for species that would need to get around to find dung.

I also found that the winter rainfall region was associated with beetles that had smaller wing loadings. This supports an observation in the winter rainfall climate of the Mediterranean, where dung beetles in habitats with limited dung availability (i.e. as a result of dry conditions) are flightless, either by loss or reduction in wings, to lower the energy spent on flying for acquiring resources (Davis et al., 2008b). Recent studies have noted that wing morphology variation is associated more with phylogenetic relatedness than habitat characteristics (Ospina-Garces et al., 2018), with wing aspect ratio and wing loading associated with diel activity (Tocco et al., 2019). Nocturnal dung beetles were found to have the lowest wing aspect ratio and wing loading, followed by crepuscular dung beetles and then diurnal dung beetles with the highest wing aspect ratio and wing loading (Tocco et al., 2019).

Food resource availability can have a strong influence on dung beetle functional groups (Bogoni et al., 2016). In support of this, I found that dung beetles exhibiting rolling nesting behaviour declined with increasing stocking rates. This trend may also be explained by land use, with farms having the highest stocking rates, characterised mostly by livestock (i.e. sheep). This would explain why there seemed to be a selection of tunnellers over rollers with an increase in stocking rates. While stocking rates may increase the availability of dung, this pellet dung type may

not be ideal for roller dung beetles. This preference for dung type was not investigated in this study.

3.5. Conclusions

The findings of this study show that variation in dung beetle species composition can be attributed to both land use and environmental variables in the semi-arid Nama and Succulent Karoo. However, the most important variables explaining species composition were stocking rates and MAP. Together these variables explained 44% of the variation in dung beetle species composition. Furthermore, the interaction term between land use and stocking rates may suggest the importance of diversity in dung types, an aspect that may need further investigation for these land uses. Rainfall seasonality also influenced the effect of MAP on dung beetle species composition. Further exploration of this interaction between MAP and rainfall seasonality suggests an adaptation of *Euonthophagus vicarius* to dry conditions.

The findings of this study may be used to help in designing the strategies for the conservation of dung beetles and their ecosystem functions in these areas. The 15 indicator species identified here may be used in future assessments or to predict the vulnerability of dung beetle communities to land use and climatic changes. The vegetation cover and stocking rate indicator species might be useful for management, MAP indicator species for monitoring programmes for climate change. Furthermore, functional traits may better explain the response of individual species to disturbance (Moretti et al., 2017), and yield more understanding of how dung beetles interact with and are influenced by, the environments in which they find themselves. Identifying these responses will help us understand the vulnerability of species based on their traits and predict important patterns that environmental changes may pose.

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CHAPTER 4: THE INFLUENCE OF DUNG BEETLES, RAINFALL AND LAND USE ON DUNG REMOVAL AND PLANT GROWTH.

Abstract

The decline in insect diversity and abundance due to habitat transformation and climate change may threaten the provision of ecosystem functions, emphasizing a need to understand how biodiversity loss might impact ecosystem functioning. Dung beetles have long been recognised for their contribution to several valuable ecosystem functions and services, including dung removal and nutrient cycling, which in turn contributes to plant growth enhancement. Here, I used an *in situ* experiment to determine the rate at which dung beetles perform the ecosystem function of dung removal, and the influence of dung beetle species richness, abundance, mean body length and functional diversity on dung removal. I further assessed the effects of the differences in land use (protected areas with low stocking rates vs livestock farms with higher stocking rates) across a rainfall gradient (mean annual precipitation of 138 mm to 381 mm) in the semi-arid Karoo of South Africa on dung removal rates. I also used an *ex situ* experiment to determine the performance of rollers versus tunnellers focusing on dung removal and plant productivity, using four dung beetle species representing the most locally abundant dung beetles, two species of rollers and two species of tunnellers. The findings of the *in situ* experiment showed that the rate at which dung was removed increased with increase in dung beetle abundance and species richness in both farms and protected areas. However, species richness was the best predictor for dung removal. Dung removal rates increased with increasing rainfall, with Standard Precipitation Index (SPI) being the best predictor. The findings of the *ex situ* experiment show that, in contrast to previous studies, rollers removed dung most efficiently, removing about 50% more

dung than tunnellers. However, total dry mass and above-ground mass of plants grown in soils in which tunnellers had been active were all significantly greater than for soils in which rollers had been active. This study demonstrates that there is a link between land use, rainfall gradient, dung beetles, and the importance of maintaining functionally-complete species assemblages for the ecosystem functions they provide.

Keywords: Ecosystem functioning, ecosystem services, livestock farming, land use, plant growth, protected areas, rainfall gradient, rate of removal.

4.1. Introduction

Ecological studies focusing on ecosystem functioning show a link between biodiversity and ecosystem functions and services (Barnes et al., 2018; Delgado-Baquerizo et al., 2020). Insects facilitate a variety of these ecosystem functions and services, including the well-studied pollination by a variety of flower-visiting insects (Öckinger and Smith, 2007; Ollerton et al., 2011), pest and disease control and nutrient cycling facilitated by dung beetles and other soil fauna species (Yang and Gratton, 2014), and as a source of food for many vertebrates, for example, birds (Morse, 1971).

Recently, great concern for ecosystem functioning has arisen from the alarming global decline of insects (Hallmann et al., 2017; Naeem et al., 2012; Nilsson et al., 2008; Ollerton et al., 2014; Potts et al., 2010; Sánchez-Bayo and Wyckhuys, 2019; Winfree et al., 2009) related mainly to anthropogenic activities (Barnosky et al., 2011; Valiente-Banuet et al., 2015). This decline in insect populations threatens multiple ecosystem functions and the ecosystem services that insects provide (Hallmann et al., 2017; Sánchez-Bayo and Wyckhuys, 2019;

Schmitz, 2009). Apart from pollination, for which numerous studies have demonstrated the impacts of a loss of biodiversity on function (Bartomeus et al., 2013; Carvalheiro et al., 2013; Fontaine et al., 2005; Garibaldi et al., 2013), understanding of how declines in diversity and abundance of insects might impact ecosystem functioning remains poorly studied.

The ongoing and accelerating loss of biodiversity through anthropogenic activities in recent decades has driven many studies to assess the effects of declining biodiversity on ecosystem functioning, yet relatively few of these have dealt with insect-delivered ecosystem functions. A major focus has been to determine how the decrease in species richness and changes in composition affect the provision of ecosystem functions. Most of these studies have found a correlation between biodiversity and maintenance of optimal ecosystem functioning (Beynon et al., 2012; Hooper et al., 2005; Milotic et al., 2019; O'Hea et al., 2010; Slade et al.,2007; Loreau et al., 2001). Much effort has been made to identify functionally important species and understand how functional traits and the associated ecosystem functions are affected by changes in habitat and climate (Hevia et al., 2017; Loboda et al., 2018; Naeem et al., 2012). Few studies have addressed the actual contribution of these functional traits to ecosystem functioning, however (Gagic et al., 2015; Slade et al., 2007).

Dung beetles (Coleoptera: Scarabaeoidea) are an ideal group of insects to investigate the contribution of functional traits to ecosystem functions for two reasons. Firstly, dung beetles have long been recognised for their provision of several valuable ecosystem functions and services (Anderson et al., 1984; Bornemissza, 1970; Fincher, 1973; Manning et al., 2016; Nichols et al., 2008). Perhaps the most famous of these is dung-removal, but dung beetles also contribute

to nutrient cycling, bioturbation, plant growth enhancement, secondary seed dispersal, trophic regulation, pollination, fly control, pest and parasite suppression, and greenhouse gas reduction (Nichols et al., 2008; Slade et al., 2007). By removing dung from the surface, dung beetles not only remove breeding sites for pests (Bornemissza, 1970; Doube, 1990; Horgan, 2005), but they also increase plant productivity through nutrient cycling into the soil (Yamada et al., 2007). Moreover, through digging tunnels where they bury dung, they promote soil aeration (Bang et al., 2005) and subsequently facilitate water infiltration and reduce soil compaction (Brown et al., 2010). To date, most research has focused on species richness and abundance and how these two affect the delivery of functions (Beynon et al., 2012; Horgan, 2005; Manning and Cutler, 2018; Yoshihara and Sato, 2015), leaving a knowledge gap on the contribution of different dung beetle functional groups to these ecosystem functions.

Secondly, dung beetles can be separated into functional groups based on morphological traits such as body size and behavioural traits such as diel activity and nesting behaviour. Dung beetles have four different nesting behaviours (rollers, tunnellers, dwellers and kleptocoprids) that are further classified into seven functional groups based on the rate of dung removal and their ability to compete for dung (Doube, 1990; Hanski and Cambert, 1991). These nesting behaviours together with the diel activity and size of the dung beetles can be used to distinguish between dung beetle functional groups (Doube, 1990; Feer and Pincebourde, 2005; Vulinec, 2002). The different techniques by which they move dung at different times and over different distances allows species that are likely to compete for resources to coexist (Doube, 1990; Feer and Pincebourde, 2005). These functional groups may also have varied responses to environmental change impacts. For example, alteration of soil

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type and moisture level may be detrimental to tunnellers due to their dung burying behaviour (Sowig, 1995), while increased temperatures will affect dwellers more than tunnellers or rollers by accelerating the rate at which dung pats dry out (Numa et al., 2012). In southern Africa, rollers and tunnellers are both effective competitors for dung; however, their competitiveness depends on each species' behaviour in relocating dung (Doube, 1990). While large fast-burying rollers and tunnellers take only a few hours to bury dung, some small slow-burying dung beetles take a couple of days (Doube, 1990). Furthermore, while several studies have examined the efficiency of dung beetles on plant productivity and their role in soil nutrient cycling (Badenhorst et al., 2018; Bang et al., 2005; Yamada et al., 2007), few assess whether the tunnellers and rollers have the same effect on plant productivity (Batilani-Filho and Hernandez, 2017).

The declines in dung beetle abundance, diversity and even mean body size, are attributed to alterations in environmental factors such as soil type and moisture levels (Sowig, 1995), vegetation cover (Lobo, 2001; Nichols et al., 2007), availability of resources (Davis et al., 2004; Nichols et al., 2008; Brown et al., 2010; Andresen, 2007), quality of resources (Dadour and Cook, 1996), use of anthelmintics (Wardhaugh and Mahon, 1991; Lumaret and Errouissi, 2002) and the removal of native mammalian herbivores (Nichols et al., 2009; Pryke et al., 2016). This decline in dung beetles also leads to declines in ecosystem functions and services provided by the action of dung removal (Frank et al., 2017; Manning and Cutler, 2018; Yoshihara and Sato, 2015). To date, most work on dung beetle activity has been conducted in mesic areas (Andresen, 2003; Nunes et al., 2018; Braga et al., 2013). The few studies that have focused on dung beetles in arid areas have investigated how rainfall influences dung beetle species richness (Tshikae et al., 2013b), species

distribution (Lobo et al., 2007), assemblage structure (Davis et al., 2008), metabolic rates (Davis et al., 2000) and food selection (Tshikae et al., 2013a). How dung beetle ecosystem functions (i.e., rate of dung removal) vary across a rainfall gradient in arid areas is currently unknown.

Dung beetle communities are affected by seasonal changes in temperature and rainfall (Andresen, 2005; Liberal et al., 2011, Chapter 2, 3), with increased dung beetle activity during warm and wet conditions and decreased dung beetle activity in cooler and dry conditions (Davis et al., 2008). The current study was carried out in a semi-arid environment (the Karoo, South Africa), where rainfall is central to the ebb and flow of biotic interactions (Noy-Meir, 1973). Climatic conditions in the Karoo are expected to become hotter and drier in the next 20 to 40 years, thus posing a great threat to the biodiversity of the region (DEA, 2014). Given expected changes to climate, we may gain insights into future changes in dung beetle communities if we understand patterns in their diversity and distribution along a rainfall gradient, and how this affects their ability to perform the ecosystem function of dung removal.

Globally, landscapes have been changed and transformed by agriculture and livestock grazing (Foley et al., 2005). This study is conducted partly in an area which is predominantly rangeland under grazing by domestic livestock (mostly sheep), and some wild herbivores (numerous species including springbok (*Antidorcas marsupialis*), kudu (*Tragelaphus strepsiceros*) and klipspringer (*Oreotragus oreotragus*); Appendix 2). Dung beetles respond negatively to intense land use through declines in species richness or shifts in community structures (Favila, 2005). For example, the expansion of pasture into Vicente Guerrero forest landscape in southern Mexico led to the reduction in the number of forest specialist species and infiltration by opportunistic dung beetles (Arellano et al., 2008).

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It has recently become evident that in order to understand the role of biodiversity in ecosystem functioning, we have to consider different dimensions of biodiversity (Mouillot et al., 2011). The use of functional diversity to predict ecosystem functioning has proven more effective than species diversity (Gagic et al., 2015; Naeem et al., 2012). Functional trait identity and dominance patterns explain the general mechanism that links biodiversity to ecosystem functioning more than species diversity (Gagic et al., 2015). It is thus essential to understand how functional traits may be affected by anthropogenic activities and variation in climatic conditions, and ultimately how these effects may influence ecosystem functions. For example, we might expect larger beetles to be more efficient at removing dung (Braga et al., 2013; Nervo et al., 2014), however, they may not be able to survive in arid settings. Moisture levels influence the size of dung beetles, with larger dung beetles more common in mesic compared to arid areas (Vessby, 2001). Furthermore, larger dung beetles may occur at far lower densities than smaller beetles in some habitats as dung beetle size decreases with increase in land-use intensity (Hidayat et al., 2010).

In light of documented declines in invertebrate diversity, the main objectives of this study were, firstly, to determine how the effects of dung beetle species richness, abundance, functional diversity and dung beetle size, different land uses (rangeland for livestock vs protected areas) and variations in habitat structure along a rainfall gradient influence the ecosystem function of dung removal by dung beetles. To assess variation in the rate of dung removal in relation to land use and rainfall, I ran an *in situ* dung removal experiment in farms and protected areas in the Nama and Succulent Karoo. I asked the following question: do dung beetles, land use, habitat structure and rainfall influence the rate of dung removal? I expected lower dung

removal rates in areas with lower dung beetle species richness and abundance (i.e. fewer individuals to remove dung). Also, I expected fewer and smaller dung beetles in the more arid areas, thus reduced dung removals.

The second objective was to determine the contribution and efficiency of two dung beetle functional groups (rollers vs tunnellers) of varying sizes on dung removal and plant productivity. To achieve this, I ran an *ex-situ* dung removal experiment in terrariums. I asked; do the two functional groups have the same or different effects on dung removal and plant productivity? I expected the two functional groups to differ in dung removal capacity, and for beetle sizes to affect dung removal capacity. Therefore, I measured the rate of removal per individual and the rate of removal per gram of dung beetle (wet mass). The productivity of plants was assessed by measuring above- and below-ground growth of radish plants (*Raphanus raphanistrum* subsp. *sativus*) measured as dry mass in the different dung beetle functional group treatments.

Abiotic influences on plant growth are often reflected in the relative investment in above- and below-ground biomass (Eghball and Maranville, 1993; Wardlaw, 1990; Wolfson and Tainton, 1999). As a rule, plants invest more biomass in the organ that is responsible for acquiring a limited resource (Harpole et al., 2011; Poorter et al., 2012). Thus, should nutrients be limited, there will be a decrease in the plants' relative investment in the above-ground biomass and an increase in the below-ground biomass (Freschet et al., 2015). Thus, I also ask if there is evidence of differences in plants' relative investment to above and below-ground biomass in response to nutrients recycling to the soil from dung buried by dung beetles. I predicted that the plants would invest more biomass in the roots (below-ground

mass) in soil treatments in which dung beetles had had relatively little effect on soil nutrient levels.

4.2. Methods

4.2.1. *In situ* dung removal experiment

4.2.1.1. Study site

This study was undertaken in the Nama- and Succulent Karoo Biomes in South Africa (Mucina and Rutherford, 2006). The vegetation is characterised by a high diversity of perennial shrubs, geophytes, annual forbs, succulents, C3 and C4 grasses with some scattered trees, with much of South Africa's endemic plant species found in the Succulent Karoo (Mucina et al., 2006).

Eleven study sites (1 km X 1 km areas, Figure 4.1), were selected on six farms (Good Luck, Rooidraai, Hopewell, Reitvlei, Portugalsriver and Argentina), four protected areas (Anysberg Nature Reserve, Camdeboo, Karoo, Tankwa Karoo National Parks) and one long term ecological research site, Tierberg LTER, managed by South African Environmental Observation Network (SAEON) and established in 1986 (Fig.4.1). The Tierberg LTER is essentially managed in a similar way to protected areas but has a lower density of herbivores. Mean annual precipitation (MAP) varies from 138 mm/year in the western-most study site to 381 mm/year in the most eastern site (i.e., spanning a gradient of 243 mm/year).
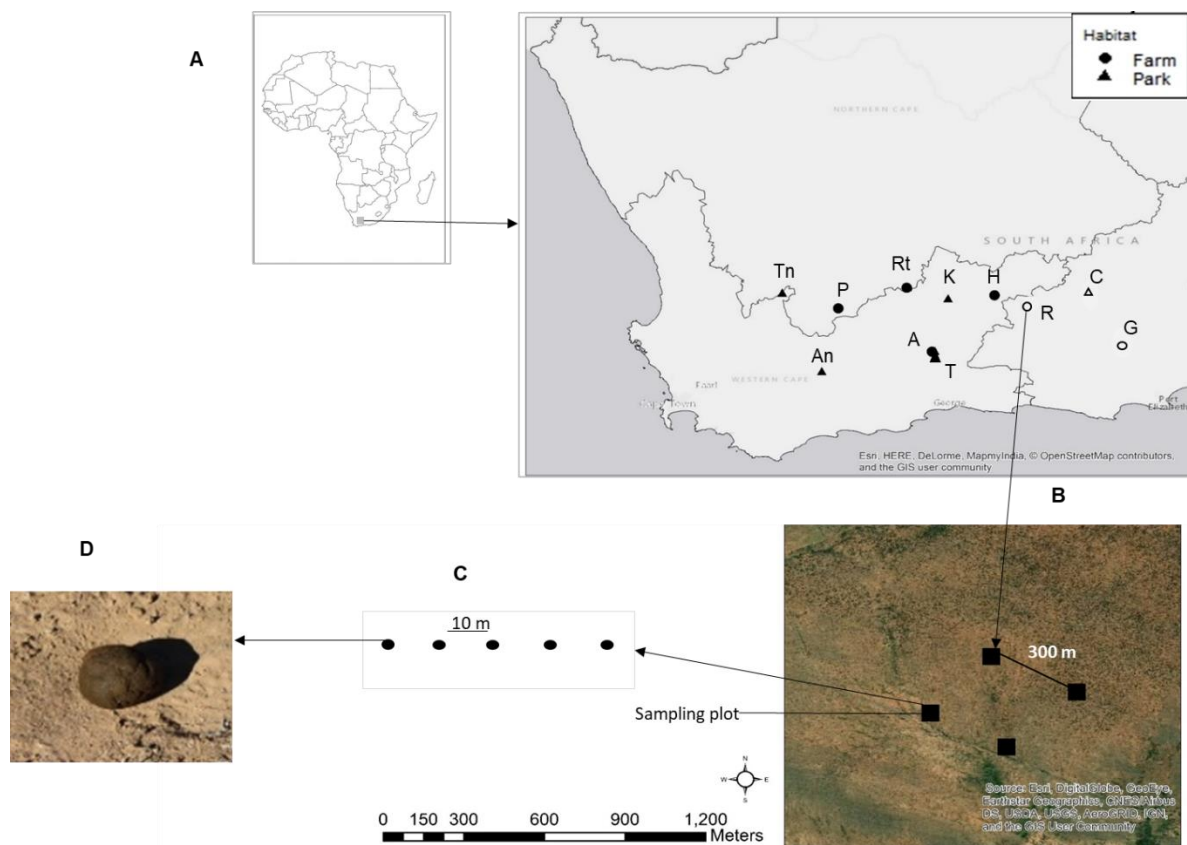
Figure 4.1. Site map showing A) the relative position of the 11 sampling sites; were open (summer rainfall) and closed (winter rainfall) circles depict six sites in livestock farms (A - Argentina; G – Good Luck; G - Hopewell; P - Portugalsriver; Rt- Rietvlei; R - Rooidraai), and the open (summer rainfall) and closed (winter rainfall) triangles depict five sites in protected areas (An – Anysberg Nature reserve; C – Camdeboo National Park; K – Karoo National Park; Tn – Tankwa-karoo National Park; T – Tierberg LTER)); and the sampling design with B) the 1 km² site containing four plots where the dung removal experiment was conducted, C) the experimental set up of the dung pats placed in each plot and D) 200 g of cow dung left for 24 hours.

4.2.1.2. Rate of dung removal

An *in situ* experiment was conducted to compare the rate of dung removal at each site. In a pilot study conducted prior to this study, I used 50 g dung pats. After eight to ten hours in the field, these dung pats were dry and no dung beetle activity was

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observed on the dung in that state. For this reason, I used 200 g of dung left in the plots for only 24 hours. Five cow dung pats (200 g) were placed on the ground, along four transects that were about 300 m apart from each other and 500 m from a set of pitfall plots that were used to assess dung beetle assemblages, between 09h00 and 09h30, with one pile every 10 m (20 dung pats per plot; Fig.4.1). A control dung pat (one for each site) of the same weight was kept in a freezer for comparison. The dung pats were collected after 24 h and a soft paintbrush was used to remove soil adhering to the dung pat (see also Doube et al., 1988). The remains of the dung pats were taken to the laboratory where they were dried, along with the controls, at 80 °C for 48 h. I determined this time based on a pilot study where I found that 48 hours of drying was sufficient for dung to reach a constant mass, suggesting that all water had been removed. Dung removed by dung beetles was recorded as the difference in post-drying mass between the control dung pats and the dung pats that were set out in the field (Appendix 8). The rate of dung removal was expressed as the amount of dung removed from the dung pat (in grams) after 24 h, i.e., g/day.

4.2.1.3. Environmental variables

Variation in rainfall, season, soil type, soil water infiltration rates and vegetation cover were used to understand the influence of environmental factors on dung beetle's ability to remove dung. Rainfall seasonality was treated as a binary factor of summer or winter rainfall regions. Rainfall data were obtained from the nearest weather stations placed by the South African Weather Services (see Appendix 5). To determine whether dung removal was influenced by recent or long-term rainfall, I calculated three measures of rainfall: mean annual precipitation (MAP), standardized precipitation index (SPI), and "raindex", a measure I created (Table 4.1). Raindex

was intended to capture the influence of recent rainfall and calculated as the amount of rain received in the most recent downpours divided by the number of days since the last day of that rain relative to the date of the dung removal experiment (Appendix 6).

Table 4. 1 Rainfall measures used for statistical analyses

Rainfall measure	Description
Mean annual precipitation (MAP)	Long-term measure - average rainfall over the years 1988 to 2017
Standardized precipitation index (SPI)	Medium-term measure - number of standard deviations that observed rainfall for the year differed from the MAP
Raindex	Short-term measure- the amount of rain received in the most recent downpours divided by the number of days since last rainfall (see Appendix 6)

At each sampling site, I collected four soil samples from which particle size (percentage of sand, silt and clay) analysis was conducted at Bemlab (Pty) Ltd. To determine relative soil infiltration rates, I used a can (10 cm deep with a 7 cm diameter) opened at the top and bottom. The can was buried to 3 cm into the ground (within 5 cm of each dung pile) and filled with 400 ml of water. The rate of soil infiltration was recorded as the amount of time it takes for water to infiltrate into the soil using a stopwatch. I measured vegetation cover as the percentage cover of vegetation at each experimental transect. Vegetation cover was taken visually for each transect, with vegetation, bare ground and litter cover totalling 100% (Delamater et al., 2012). I took the average percentage of vegetated area from three 1 m^2 plots that were randomly selected from each transect. Mammalian herbivore

species richness and abundance, and stocking rates records were collected from the farmers and park managers for each of the sites.

4.2.2. *Ex situ* dung removal and plant productivity experiment

4.2.2.1. Study area

The study area was the Granite Lowveld Savanna within the Kruger to Canyons Biosphere dominated by *Senegalia nigrescens* (Oliver) and *Sclerocarya birrea* (A. Rich) (Mucina and Rutherford, 2006), located near Hoedspruit, Limpopo province, South Africa (24°23'9.25" S and 30°56'19.92" E), in an area predominantly browsed and grazed by wildlife species, with no dipping for ectoparasites or treatment for internal parasites. The study took place over November and December 2018 when maximum temperatures ranged from 30.1 °C to 39.2 °C, and the total rainfall was 13.4 mm received on only two occasions in the experiment period (1.2 mm on day five and 12 mm on day seven of the eight days of the dung removal experiment).

4.2.2.2. Dung beetle collection

To collect dung beetles, I used eight pitfall traps baited with 200 g of cow dung. Fresh cow dung was used, mixed to make it of uniform consistency. The traps were plastic containers (2 L plastic containers: 14 cm deep with a 17 cm diameter) filled to one-third of their volume with soil, with the 200 g of the cow dung pat in the centre and buried with the rim at ground level. Each trap had a top cover with a hole in the middle to allow the beetles to enter the trap while preventing them from escaping. The traps were placed in the ground at 08h00 and dung beetles were collected the next day after 24 h. Collected individual dung beetles belonging to the species *Scarabeaus khepe nigroaeneus*, *Gymnopleurus aenescens*, *Neosisyphis* sp., *Copris*

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sp. and *Onthophagus* sp. were transferred to a terrarium until the start of the experiment within 8 hours of collection. In order to determine the contribution of each functional group to dung removal and plant productivity, I used a dung removal experiment and a subsequent plant productivity experiment using radish plants. I manipulated the dung beetle assemblage by varying functional groups and biomass while keeping species richness and abundance constant, using the five dung beetle species.

4.2.2.3. Dung removal experiment

I assessed the role of functional groups on dung removal by dung beetles using different combinations of four dung beetle species within two functional groups (rollers and tunnellers) with varied body sizes (Table 4.2). Endocoprids and kleptocoprids were not considered because their effect on dung removal after 24 hours has been described in other studies as minimal (Milotic et al., 2019; Nervo et al., 2014; Slade et al., 2007). Two functional groups (with four individuals each) were used in each treatment (i.e., a total of eight individuals per treatment). These beetles were weighed and added into a terrarium (30 L plastic containers: 53 cm in length x 37 cm in width x 18 cm in depth) half-filled with soil, with a 200 g of cow dung pat was placed in the centre. There were seven dung removal treatments: one treatment with large and small roller dung beetle species (rollers only), one treatment with small and large tunneller dung beetle species (tunnellers only) and four treatments with different combinations of large and small rollers and tunnellers (rollers and tunnellers) (Table 4.2). Each treatment had eight replicates and a control with dung but without dung beetles (Table 4.2). Each terrarium was covered by wire mesh to prevent beetles from escaping and others from entering. Each terrarium was placed under a 40% shade cloth to prevent the dung pat from drying out too quickly. The

eight replicates were all carried out on eight different days, using a randomised complete block design. The remaining dung pat was removed after 24 hours and any soil adhering to the dung removed using a soft paintbrush (Doube et al., 1988). The remaining dung pats were weighed to yield a measure of the dung removed (Appendix 9) and the control was used to adjust estimates of mass loss through evaporation. This time interval was selected because the preliminary study in this area showed that after 24 hours, the dung pat would have dried out to the point of not attracting roller and tunneller dung beetle activity. The soil in each terrarium replicate was set aside for the plant productivity experiment.

Table 4.2. The combinations of functional groups (with the mean total weight of the dung beetles, with standard deviations in brackets, representing each functional group) used in each transect, where R = rollers, T = tunnellers, LR = large rollers, SR =small rollers, LT = large tunnellers, ST = small tunnellers, C = control and D = dung.

Treatment	Replicates	Rollers		Tunnellers	
		S. nigroaeneus (large)	*G. aenescens* and *Neosisyphis* sp. (small)	*Copris* sp. (large)	*Onthophagus* sp. (small)
LR + ST	8	7.7 g (0.68)			0.4 g (0.04)
SR + LT	8		2.1 g (0.24)	2.5 g (0.65)	
LR + LT	8	7.4 g (0.85)		2.4 g (0.43)	
SR + ST	8		1.7 g (0.49)		0.4 g (0.04)
R	8	7.7 g (0.59)	1.8 g (0.57)		
T	8			2.1 g (0.41)	0.5 g (0.09)
C + D	8				
C (control used for the plant productivity experiment only)					

4.2.2.4. Experiment: Plant productivity

To assess how dung removal influences plant productivity, I planted radish seeds in black plant bags (75 x 50 x 150 mm) using the four soil treatments from the dung removal experiment with an additional control treatment with only soil (with neither dung nor dung beetles) (Table 4.2). Each of the six treatments had 12 replicates, with three seeds per bag that were watered an equivalent of 20 mm of rain a day for the entire growing period. The experiment also followed a complete block design with 12 blocks that were 30 cm apart with each replicate placed randomly in each block. All the blocks were placed under an 80% shade cloth. Plants were checked daily for invertebrate damage. Invertebrates (mostly caterpillars) were removed when seen. Nevertheless, sometimes plants sustained some invertebrate damage. When the plants were harvested, I estimated the percentage of above-ground biomass that had been removed by invertebrates and recorded this as percent invertebrate damage, estimated as an area of leaf lost per plant. The plants were harvested after four weeks, and the roots were washed thoroughly to remove soil. The plants were then air-dried, then oven-dried at 100 °C for 48 hours. I weighed the total, above-ground and the below-ground mass of the dried plants (Appendix 9).

4.2.5. Data analysis

4.2.5.1. Dung removal *in situ*

Dung removal, the dependent variable, was expressed as a proportion of dung removed. Therefore, to determine the factors that influence the rate of dung removal, I used linear mixed models with beta distribution for proportion data, using the betareg package in R (Zeileis et al., 2016). Dung beetle species richness, abundance, functional diversity and CWM of body size (see details of dung beetle

sampling, measurement of body length and calculation for functional diversity and CWM of body length in Chapter 2 of this thesis) along with land use, soil content, mammalian herbivore species richness, stocking rates, vegetation cover, soil infiltration and rainfall were treated as fixed explanatory effects. Dung beetle abundance data were square-root transformed to account for overdispersion caused by an outlier. Dung beetle abundance, species richness, CWM of body length and functional diversity are collinear, so were the three rainfall and soil content measures. Dung beetle species richness and abundance were also correlated to herbivore stocking rates. I did not include variables that were collinear in the same model, so I constructed a series of models, each with a different measure of rainfall (MAP, SPI and raindex), soil content (percent sand, clay and silt), and dung beetle measure (species richness, abundance, functional diversity and CWM of body size), and then used the Akaike information criteria (AIC) to choose the best fitting model (Akaike, 1973).

4.2.5.2. Dung removal and plant productivity in the *ex-situ* experiment

To determine how dung beetle functional groups affect dung removal rates, I used linear mixed models with Gaussian distribution within the lme4 package (Bates et al., 2014 in R (R Core Team, 2018). Dung removed per gram of dung beetle was calculated by dividing the amount of dung removed after 24 hours by the mass of dung beetles placed in each treatment in order to correct for the mass of dung beetles in each treatment. There were two rainfall events (2 separate days receiving 1.2 on day five and 12 mm on day seven) that occurred during the eight days of the dung removal experiment. For this reason, rainfall, as well as temperature, were included as predictors for dung removal in the statistical analysis. Dung removed per

gram of dung beetle was modelled as the dependent variable, with treatment (i.e., dung beetle functional groups), temperature and rainfall and an interaction term between these variables as fixed variables, and terrarium number as a random variable. The fixed variables were ranked based on their p-values, keeping variables with p < 0.05 for the best model (Zuur et al., 2009). When comparing models with different correlated variables, models were compared using AIC to choose the best fitting model (Akaike, 1973), the model with the lowest AIC value by more than two was preferred. A plot of residuals against fitted values showed that the model met assumptions of homogeneity and normality, and thus the data were left untransformed.

I used the lme4 (Bates et al., 2014) package in R (R Core Team, 2018) to construct linear mixed-effects models on the effects of functional groups on three different measures of plant productivity: total, above-, and below-ground plant mass, and generalised linear mixed models with binomial distribution for above to below ground ratio. Total plant, the above- and below-ground masses and the above/below ratio were modelled as dependent variables, with treatment and invertebrate damage as fixed effects, and block as a random effect.

4.3. Results

4.3.1. *In situ* experiment: effect of dung beetles, land use, rainfall and habitat structure on dung removal in the Karoo.

The only measures of dung beetle assemblages to significantly affect the rate of dung removal were abundance and species richness (SR) (z =14.5, P < 0.001; z = 15.5, P < 0.001, respectively, Table 4.3) in the *in situ* experiment. Of these, SR was the best predictor of dung removal, explaining 47 % of the variation (Pseudo R^2 =

0.47, Table 4.3). Rate of dung removal was significantly faster in protected areas than on farms (z = 3.3, P < 0.001), and also increased with SR and soil clay content (z = 2.2, P = 0.027, Fig. 4.4. Table 4.3). SPI (i.e., medium-term rainfall; z = 5.9, P < 0.001, Fig. 4.4.) was the best measure of rainfall explaining rate of dung removal. Furthermore, there was a significant interaction between species richness and land use. On farms, the rate of dung removal increased with increasing species richness faster than in protected areas (z = - 5.5, p < 0.001, Table 4.4, Fig. 4.3.). The model that included dung beetle abundance also found an interaction between abundance and land use (z = - 9.9, P < 0.001), with the rate of removal increasing faster with abundance on farms than it did in protected areas s (Fig. 4.3). Functional diversity, CWM of body length, stocking rate, soil infiltration and vegetation cover did not significantly influence rate of dung removal.

Table 4.3. Model summary showing the effects of land use and rainfall on the rate of dung removal. The best model equations show important explanatory predictors where; SR (species richness), S (Standard Precipitation Index), Lp (land use: protected areas), C (soil clay content), abu (abundance), FD (functional diversity), Sa (soil sand content), R (Raindex), CWM (community weighted mean of dung beetle length), ns (not significant).

Response variable	Community attribute used	AIC (Best model)	ΔAIC (2nd best)	ΔAIC (Null)	Pseudo R^2
Dung removal	**Species richness**	**- 472.1**	**2.4**	**270.4**	**0.47**
	Best model equation: $Y = e^{-1.79 + 0.15SR + 0.45Lp - 0.01C + 0.34S - 0.06SR:Lp}$				
	Abundance	- 429.1	15.4	227.4	0.41
	Best model equation: $Y = e^{-2.99 + 0.11abu + 0.47Lp - 0.28Sr + 0.03C + 0.32S - 0.08abu:Lp}$				
	Functional diversity	- 258.7	2.2	57	0.15
	Best model equation: $Y = e^{0.45 - 0.09FD(ns) - 0.01Sa(ns) + 0.37R}$				
	CWM of body length	- 259.0	5.3	57.3	0.15
	Best model equation: $Y = e^{-0.55 - 0.02CWM(ns) + 0.02C + 0.39R}$				
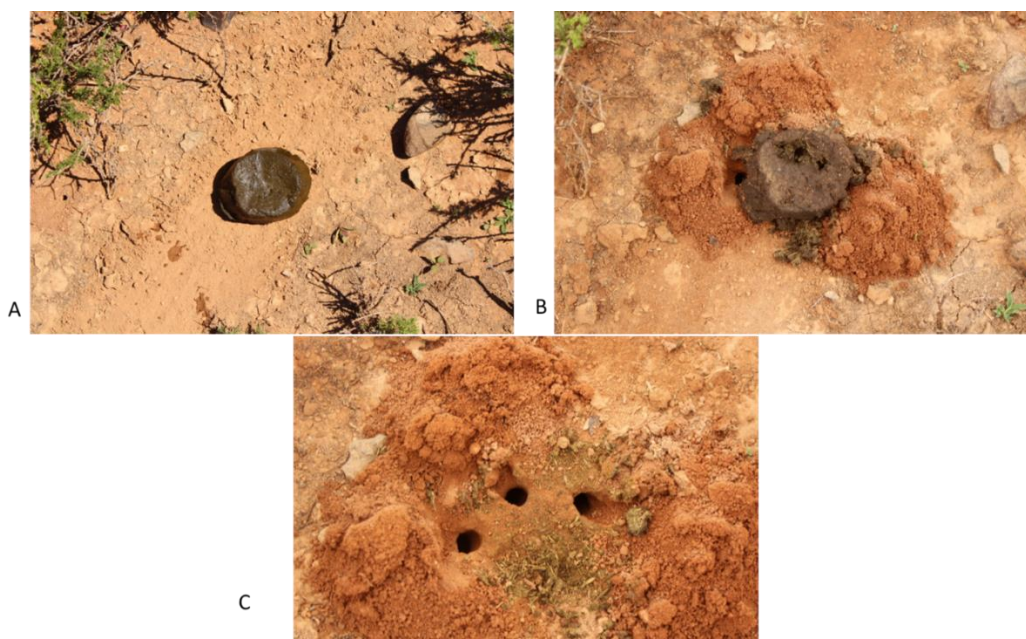
Figure 4.2. Dung removal experiment; showing A) fresh dung pat, B) dung pat after 24 h and C) tunnels dug by dung beetles beneath the dung pat.

A) Species richness
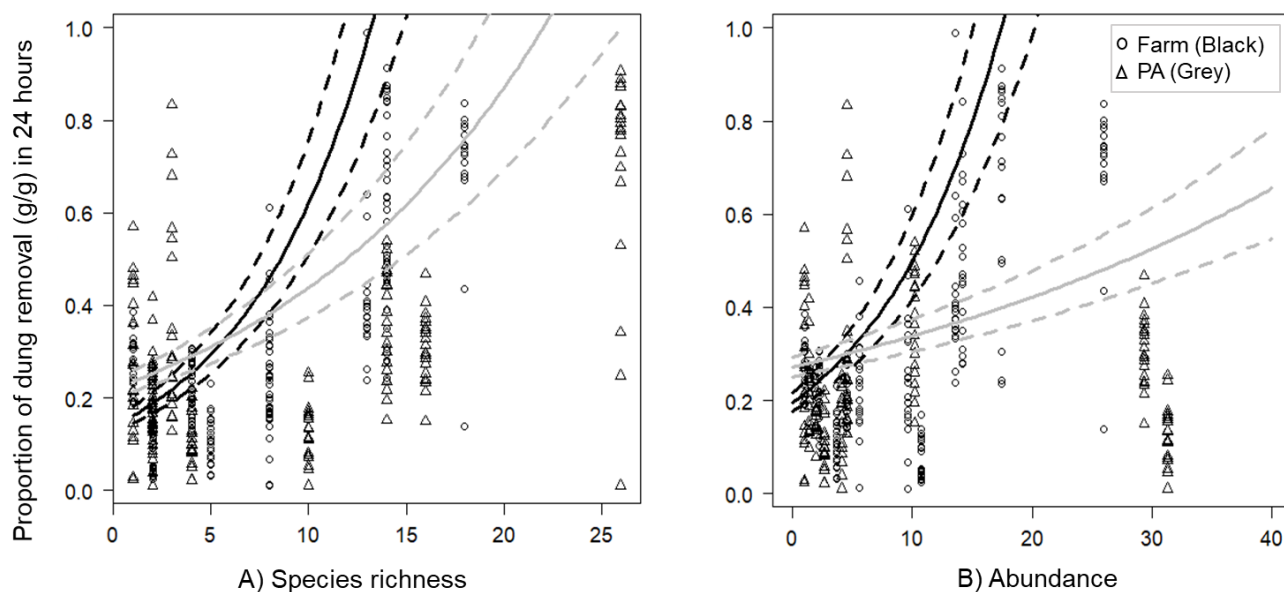
B) Abundance

Figure 4.3. Plot showing the proportion of dung removed in 24 hours as influenced by the interaction between A) dung beetle species richness and land use, and B) dung beetle abundance and land use, with an increase in dung removal as species richness abundance increases in both land uses. The black (for farms) and grey (for protected areas) lines represent negative binomial glm fits of mean values ± 1 SE (dotted lines).
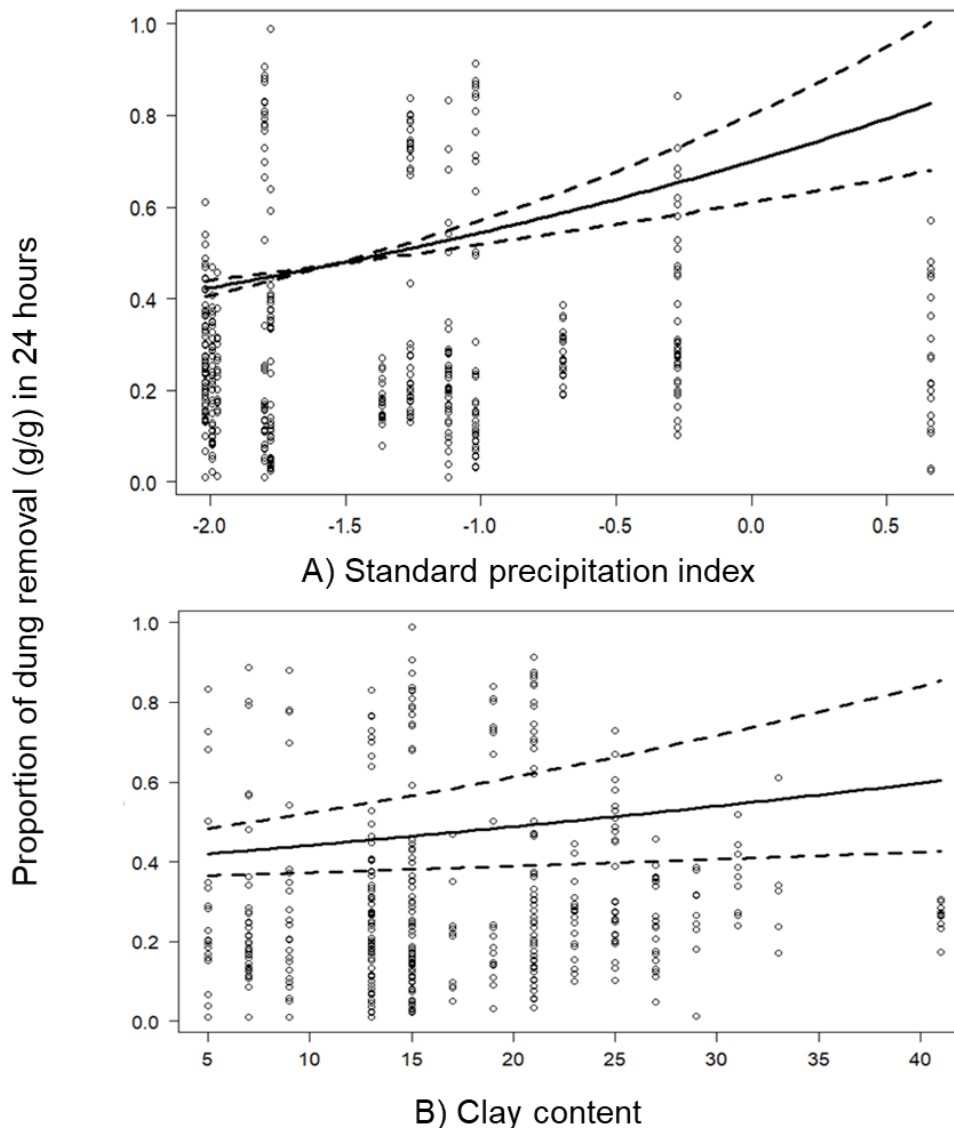
Figure 4.4. Plot showing the effect of A) SPI and B) clay content on the rate of dung removal, with an increase in dung removal as SPI and clay content increases in both land uses. Lines represent negative binomial glm fits of mean values ± 1 SE (dotted lines).

4.3.2. *Ex situ* experiment: The effect of dung beetle functional groups on dung removal

The amount of dung removed by dung beetles differed significantly between seven dung removal treatments (Table 4.4). The amount of dung removed per gram of dung beetle was significantly greater than all other treatments in the rollers treatment with an average of 14.7 g of dung removed (SD = 2.3, t = 5.8, P < 0.0001, Fig.4.5, Table 4.4).

Table 4.4. Model summary: the effects of treatment (with different functional groups) on dung removal per gram of dung beetle. R = Rollers; R + T = Rollers + Tunnellers; T = Tunnellers.

Factor	Estimate	Standard error	t value	P-value
Intercept	-0.1	1.9	-0.1	0.950
R	13.7	2.4	5.8	< 0.0001***
R+T	11.6	1.7	6.6	< 0.0001***
T	6.4	2.3	2.7	0.013*
Best model AIC = 360.3, Δ 2nd best model = 2.4, Δ Null model = 39.2, R^2_m = 0.40, R^2_c = 0.59; Model equation: y = - 0.12 + 13.73R + 11.58RT + 6.41T				

The treatment with both rollers and tunnellers were significantly lower than rollers-only treatment but greater than the tunnellers-only treatment, with an average of 9.8 g of dung removed per gram of dung beetle (SD = 6.2, t = 6.6, P < 0.001, Fig.4.5, Table 4.4). The tunneller-only treatment had the least dung removed compared to the roller-only and the roller and tunneller treatments, with an average of 6.2 g dung removed per gram of dung beetle (SD= 4.9, t = 2.7, P = 0.013, Fig.4.5, Table 4.4). Temperature and rainfall during the 24 hours of the experiment had no significant influence on dung removal. Dung beetle functional groups (fixed variable) explained 40% of the variation, whereas the terrarium number and date the experiments were performed (random variable) explained a further 19% of the variation (Table 4.4).

4.3.3. The effect of dung beetle functional groups on plant productivity

Dried plant average mass ranged from 0.003 to 0.146 g for the entire plant, 0.002 to 0.105 g for above-ground and 0.0002 to 0.102 g for below-ground biomass (Fig.4.6). Dung beetle functional group significantly influenced total plant and above-ground mass (Table 4.5). Both the total plant mass and above-ground mass were greatest in the treatments with soil from tunnellers only (t = 3.1, P = 0.003, Fig.4.6a; t = 2.7, P

= 0.009, Fig.4.6b, respectively, Table 4.5). The treatments with rollers and tunnellers and rollers only did not have a significant influence on plant productivity (Table 4.5). Below-ground mass was not significantly influenced by functional groups (t = 1.9, P = 0.05, Table 4.5), however.

The biomass of the total plant, above- and below-ground masses were significantly influenced by invertebrate damage (Table 4.5). Invertebrate damage negatively impacted all measures of plant biomass: total (t = -4.7, P < 0.0001), above (t = - 4.1, P < 0.0001, Table 4.5, see Appendix 10) and below-ground plant biomass (t = - 2.8, P = 0.006, Table 4.5, see Appendix 11). The ratio of above- to below-ground biomass was influenced by neither one of the fixed variables (Table 4.5).
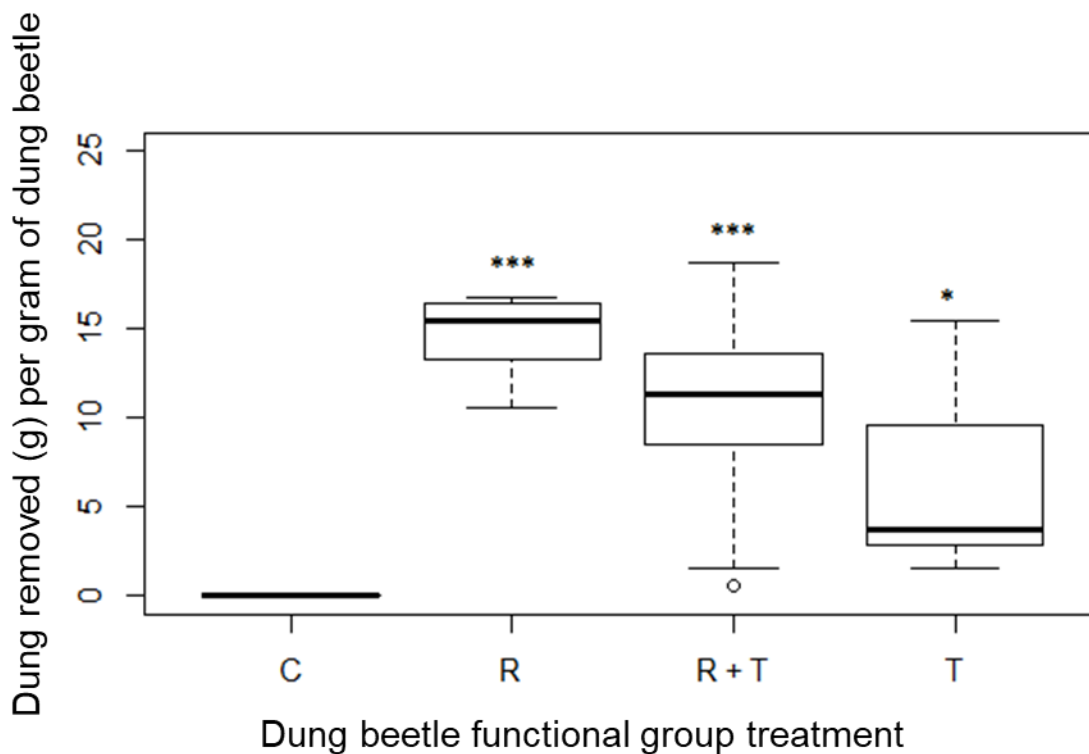
Figure 4.5. Dung removed per gram of dung beetle size in the different dung beetle functional group treatments with greater dung removal in the rollers-only treatment followed rollers and tunneller treatment. The tunnellers-only treatment showed the lowest dung removal. C = Control; R = Rollers; R + T = Rollers + Tunnellers; T = Tunnellers. [* p ≤ 0.01; *** p ≤ 0.0001]

Table 4.5. Model summary: the effects of treatment (with different functional groups) on plant productivity. FG = Functional groups, T = tunnellers, and D = damage by invertebrate.

Response	Model	AIC (Best model)	ΔAIC (2nd.best)	ΔAIC (Null)	R^2_m	R^2_c
Total mass	Best model ~ FG** + Damage***	560.5	4	41.6	0.15	0.28
	Model equation: Y = 0.15 + 0.69T – 0.01D					
Above ground	Best model ~ FG* + Damage***	559.3	3.3	34.3	0.11	0.28
	Model equation: Y = 0.1 + 0.61T – 0.01D					
Below ground	Best model ~ FG. + Damage***	610.9	6.7	12.5	0.07	0.09
	Model equation: Y = 0.15 + 0.52T – 0.01D					
Above/Below	Best model ~ Damage	1398.6	5	24.1	0.02	0.12
	Model equation: Y = 9.28 + 0.02D					
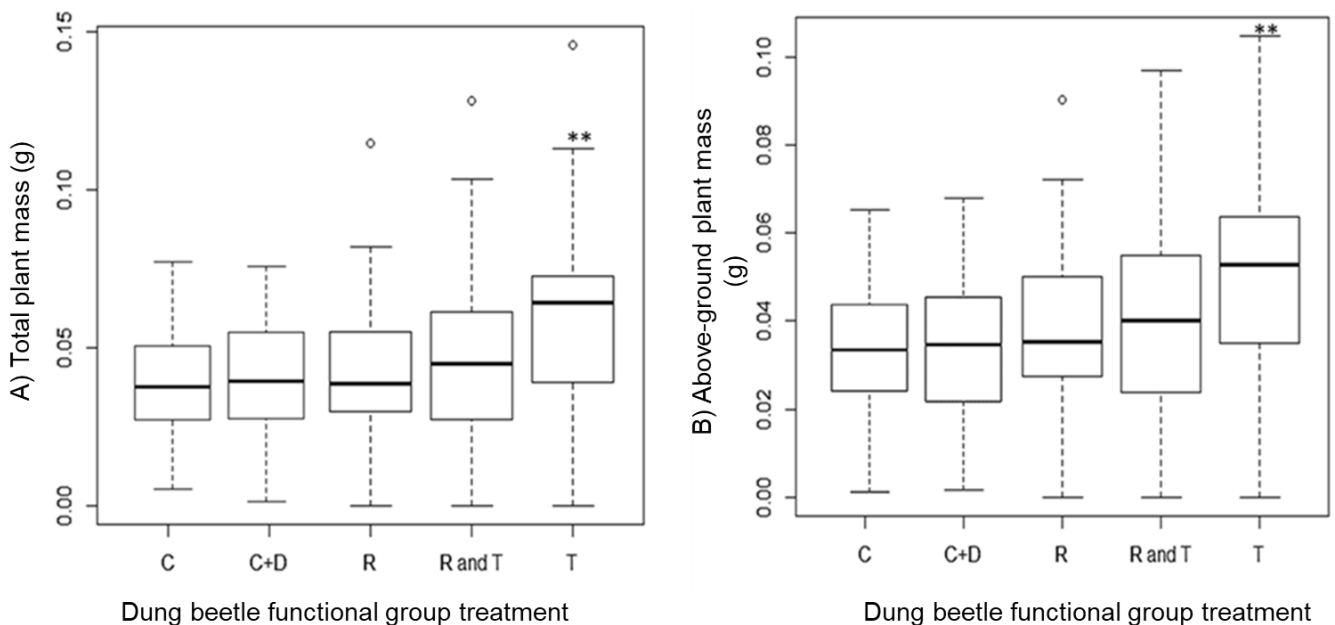
Figure 4.6 The dry weight of A) total plant mass and B) Above-ground plant mass in the different dung beetle functional group treatments; C = Control; C+ D = Control treatment with dung; R = Rollers; R + T = Rollers + Tunnellers; T = Tunnellers [p ≤ 0.001].**

4.4. Discussion

Ecosystem functioning can be significantly improved by greater biodiversity. The findings of this study indicate that a system containing more than one functional group is needed for the effective provision of different ecosystem functions. Recent studies have also found that having several functional groups promotes the provision of multiple ecosystem functions (Lahteenmaki et al., 2015; Manning et al., 2016; Penttila et al., 2013; Slade et al., 2016). While this study agrees with these findings, it also suggests that different functional groups contribute in differing proportions to the suite of ecosystem services provided by dung beetles. In this study, I highlight a functional complementarity, where tunnellers were more efficient in facilitating plant productivity while rollers were the most efficient in facilitating dung removal. This shows that tunnellers are very good at nutrient cycling in soils immediately under and around the dung pat, while rollers distribute the dung across a much broader scale.

This study further indicates that greater species richness with more chances of positive additive effects on dung removal would be better for ecosystem functions and services (e.g. fly control). More species increase the chances of having diurnal and nocturnal species and therefore more continuous dung removal. This complementarity mechanism on ecosystem functions due to greater species richness has also been noted for nutrient cycling facilitated by dung beetles, with greater species richness accelerating the transfer of nitrogen and carbon from dung to soil (Yoshihara and Sato, 2015). Another example of this phenomenon has been noted in agricultural systems where spatial complementarity between wild pollinators that pollinated the lower sections of crop trees and managed honey bees that visited the higher sections (Brittain et al., 2013; Hoehn et al., 2008).

4.4.1. *In situ* experiment: The effects of dung beetles on the rate of dung removal

Although dung removal was correlated with both dung beetle species richness and abundance, species richness was a better predictor. This link between species richness and dung removal corroborate that increased species richness facilitates ecosystem functions (Braga et al., 2013; Griffiths et al., 2016; Nunes et al., 2018; Santos-Heredia et al., 2018; Slade et al., 2011). However, this also contrasts with other studies that found that a decline in dung beetle abundance negatively affects dung removal more than the decline in species richness (Horgan, 2005; Manning and Cutler, 2018). Thus, other factors (e.g., how dung beetle species interact with dung) in the present study may have reduced the effects of dung beetle abundance. The greater abundance of dwellers and kleptocoprids observed in this study would not lead to improved dung removal, because they do not remove dung from the source (Doube, 1990). Although diel activity was not assessed in this study, it is also possible that the contribution of nocturnal and diurnal dung beetles on dung removal may differ (Batilani-Filho and Hernandez, 2017; Slade et al., 2007; Slade et al., 2011).

Elsewhere, functional group richness has been found to increase dung removal, with large nocturnal tunnellers playing the greatest role in dung removal (Slade et al., 2007). However, this was not the case in the current study as functional diversity did not influence dung removal. It is therefore possible that functional group richness may have other effects that could not be predicted by functional diversity. The most abundant dung beetle species in the samples were relatively small slow-burying tunnellers (an average of 3.4 mm in length) and dwellers, which cannot remove dung as quickly as large-bodied rollers (Amézquita and Favila, 2010). The

smaller slow-burying tunnellers and dwellers usually take several weeks to remove dung (Doube, 1990) and thus may make little contribution to the rate of dung removal in the 24 h period used in the study. Thus, dung beetle species play different roles in dung removal (Nervo et al., 2014); small tunnellers and dwellers may remove less dung just by virtue of their life cycle history and traits. Furthermore, the dung dries out in 24 hours suggesting that slow-burying tunnellers and dwellers possibly make little contribution to dung removal in this area. Therefore, the most benefit with regards to dung removal may be seen when there is high species richness, and possible diversity in functional guilds of different-sized dung beetles rather than an abundance of small-sized beetles (see also Braga et al., 2013). Alternatively, an abundance of roller dung beetles which seems to contribute more to dung removal than tunnellers as suggested by the ex situ experiment.

4.4.2. *In situ* experiment: The effects of environmental variables on the rate of dung removal

Dung beetle activity is favoured by warm and wet weather conditions (Davis et al., 2004). In the semi-arid Karoo, where weather conditions in the winter rainfall areas can be particularly extreme, varying from hot and dry to cold and dry (Mucina et al., 2006), the influence of weather is likely to have been quite marked. Rate of dung removal increased with the medium-term measure of rainfall (SPI). The combination of explanatory variables (land use, species richness, clay content and SPI) included in the models explained about 47% of the variation in the rate of dung removal. The rate at which dung beetles remove dung increased with increasing species richness in both farms and protected areas. However, this rate of increase was lower in protected areas than in farms. Species richness, however, was not influenced by land use (Chapter 2). Herbivore stocking rates were positively associated with

species richness and have also been linked to intense competition for dung (Doube, 1990), which explained why the rate of dung removal was significantly faster in farms with high stocking rates relative to protected areas.

Soil moisture also plays a role on dung beetle reproduction and dung removal (Nunes et al., 2018), as the depth in which dung beetles can burrow depends on soil moisture content (Edwards, 1986). However, high clay content, which allows retention of moisture, may restrict dung beetle activity (Brown et al., 2010). In Chapter 2 of this thesis, I found that dung beetle body size increased with increasing soil clay content. This exclusion of small-bodied dung beetle species did not affect dung removal as large-bodied dung beetles removed more dung compared to small dung beetles, thus positively influencing dung removal. This is expected because large-bodied dung beetles move more dung and dig deeper into the soil than smaller-bodied dung beetles are able to, thus possibly removing more dung (Halffter and Edmonds, 1982).

4.4.3. *Ex situ* experiment: The effects of different functional groups on dung removal

In general, the most effective functional group for dung removal was the rollers-only treatment followed by the treatment with rollers and tunnellers. The amount of dung removed in this study might be overestimated, considering that the removal of dung by dung beetles leaves smaller fragments of dung which may dry faster than larger dung piles. Nevertheless, because of the uniformity of experimental design between treatments, the results between the dung beetle functional groups are comparable. Total biomass of large tunnellers was less than that of the large rollers, which could explain why the rollers removed more dung in total. However, when measured as the mass of dung removed per gram of dung beetle per terrarium, tunnellers alone made

the lowest contribution to dung removal. The combination of tunnellers and rollers removed more dung than tunnellers alone, although not more than dung removed by rollers alone. The complementarity between dung beetle functional groups has been documented in some recent studies and may improve facilitation of ecosystem functions (Batilani-Filho and Hernandez, 2017; Menéndez et al., 2016); for example, greater functional group richness maximised dung removal (Dangles et al., 2012; Slade et al., 2007).

The findings here were surprising, given that in the majority of studies to date, tunnellers have been more efficient in dung removal than rollers (Davis, 1996; Estrada and Coates-Estrada, 1991; Rosenlew and Roslin, 2008; Slade et al., 2007). In some studies, rollers are slower than tunnellers in dung removal, owing to time spent on other interactions (i.e. fighting for the dung balls) while relocating dung (Andresen, 2003; Batilani-Filho and Hernandez, 2017; Chamorro-Florescano et al., 2011). Even though rollers were observed rolling a single brood ball around the terrarium for lengthy periods (2 hours or more) in this study, they were still able to remove 50% more dung than tunnellers. Therefore, the loss of roller dung beetles in this study area would likely have marked negative implications for dung removal. Several studies have recorded the loss of roller dung beetles including species in the *Scarabaeus* and *Gymnopleurus* genera (Barbero et al., 1999; Lobo, 2001; Lobo et al., 2001; Nervo et al., 2014). Habitat alteration and destruction by the use of insecticides, veterinary drugs given to livestock, urbanisation and tourism are the main threats driving the loss of these species (Lobo et al., 2001; Lumaret et al., 1992). It is not clear whether rollers are one of the first functional groups to disappear within these perturbations, and this requires investigation.

4.4.4. *Ex situ* experiment: Effects of the different functional groups on plant productivity

The interaction of dung beetles with dung was associated with greater plant productivity (total dry mass and above-ground mass). This was consistent with a study that also found an increase in above-ground plant biomass owing to the transfer of dung into the soil by dung beetles (regardless of their nesting behaviour) and earthworms (Borghesio et al. 1999). The behaviour of different functional groups, coupled with their distinct attributes, may lead to varied roles in dung decomposition (Horgan, 2008). While tunnellers burrow beneath the dung source to bury dung, roller dung beetles have to find suitable nesting sites to bury the dung (Halffter and Edmonds, 1982; Gill, 1991).

The tunneller-only treatment removed significantly less dung than rollers that move dung in larger balls (dependent on the dung beetle size). However, tunnellers break the dung into smaller bits that are transferred into the soil and thus they were able to incorporate nutrients from the dung into the soil, thus improving plant productivity. Although roller dung beetles removed large amounts of dung from the original dung pat, they may not have been able to incorporate this dung into the soil within the terraria. One possible explanation for this may be that rollers traded their ability to burrow for longer legs that give them competitive superiority at the dung source by making and rolling dung faster (Scholtz et al., 2009). Larger terrarium may have allowed the rollers to bury their balls, but that this would likely have had only local effects on soil nutrients, whereas the tunnellers might have a more diffuse effect on soil nutrients.

Although I expected plants to invest more on roots in treatments with relatively low dung removal, the ratio of above-ground to below-ground biomass of the plants

did not differ significantly between treatments. Although there was variation in total plant growth between treatments after four weeks of seeds being sown, had the experiment continued beyond this period, the results may have shown a variation in the investment in above- and below-ground tissues, as the seedlings grew to deplete nutrients in the soil, making the influence of dung beetles on nutrient cycling more influential. Another plausible explanation would be the balance between the available nutrients and water (Slade and Roslin, 2016). Future studies may benefit from analysing the nutrient in the soil to determine which functional group is efficient in transferring nutrients from the dung. Nevertheless, Dung beetles may have increased soil porosity and aeration, thus increasing the uptake of water and increasing plant growth. This would also explain why the treatment with tunnellers, which buried the dung into the soil, showed greater plant productivity.

4.5. Conclusion

The fast removal of dung with an increase in species richness observed in this study may lessen the chances of providing habitat for flies to breed in (Nichols et al., 2008). However, it is also possible that the response of one ecosystem function may not be related to another ecosystem function performed by the same species. Assessing dung removal alone may not reflect the full importance of dung beetles to all ecosystem functions in which they are involved. Although nutrient cycling, soil aeration and water infiltration are ecological functions linked to dung removal, the results of this study suggest that these functions are better facilitated by different functional groups. For example, in this study, the treatment with the least amount of dung removed was associated with the greatest plant productivity. It is impossible to draw any conclusions on whether other ecosystem functions facilitated by dung

beetles would also benefit from greater species richness from this study. Therefore, the contribution of each different dung beetle species and functional groups to the provision of the different ecosystem functions might be an interesting and rewarding field of research.

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CHAPTER 5: SYNTHESIS

This thesis aimed to assess the relative importance of dung beetle species richness and functional diversity for ecosystem functions across two land uses along an aridity gradient of the Nama and Succulent Karoo, and to assess whether different dung beetle functional groups perform different ecosystem functions similarly. To achieve this, I surveyed dung beetles from eleven sites within farms and protected areas using pitfall traps (Chapter 2 and 3) and conducted dung removal experiments at the same sites (Chapter 4: *in situ* experiment). I also conducted an experiment looking at the influence of functional traits on dung removal and plant productivity (Chapter 4: *ex situ* experiment). The latter experimental study was conducted in Hoedspruit, Limpopo, to assess the effects of dung beetles without the aridity gradient effect experienced in the Karoo. The study sites in the Karoo were relatively dry, with very few rainy occasions during the sampling periods. In fact, the study took place during a prolonged and severe drought, and the results of this study are useful in that they reveal what the system might be like in future droughts. Further research, in wetter periods, would also be useful to allow comparison with the dry period over which this study was conducted. In this chapter, I summarise my main findings addressing the aims and initial research questions and their implications for further research and our understanding of biodiversity and ecosystem functions.

Summary of the results

This study found that dung beetle communities respond to different environmental variables, acting at different spatial and temporal scales (Chapter 2). Moreover, one environmental variable can have a contrasting effect on different community

attributes. For example, while protected areas had a positive effect on dung beetle abundance, it influenced functional diversity negatively, possibly owing to low stocking rates. Stocking rates and variation in rainfall only affected species richness and abundance. Dung beetle abundance and species richness showed a consistent response to variation in stocking rates and rainfall, with an increase in both attributes as stocking rate and rainfall increased. However, different aspects of dung beetle communities responded to different temporal scales of rainfall. Species richness was best predicted by short-term rainfall (i.e. raindex) while abundance was best explained by long-term rainfall (i.e. MAP). Functional diversity, Community Weighted Mean (CWM) of body length and the Gini coefficient of size responded to soil content and vegetation cover. Vegetation cover also had a significant impact on species richness. The results showed that there were large-bodied dung beetles in sites with greater soil clay content. Both species richness and functional diversity increased with an increase in vegetation cover. These results indicate that the impacts of anthropogenic and climatic changes on dung beetle communities cannot be assessed only by species richness and abundance.

Dung beetle species composition varied significantly between farms and protected areas and also between the winter and summer rainfall regions (Chapter 3). All of the assessed environmental variables influenced dung beetle community composition, except for soil texture. Herbivore stocking rates had the greatest influence on dung beetle species composition; however, this effect varied significantly between farms and protected areas. As with abundance (Chapter 2), long-term rainfall was the best predictor for species composition. About 15 dung

beetle species were identified as potential bio-indicators for the different environmental variables.

The best predictor of dung removal, from the measured community variables, was species richness (Chapter 4). The rate at which dung was removed increased with increased species richness in both the farms and the protected areas. Dung removal also responded to the medium-term rainfall measure (SPI), with dung removal increasing with an increase in rainfall. Soil clay content was also a significant predictor for the ecosystem function of dung removal, as dung removal increased with an increase in clay content.

Dung beetle functional groups have different roles in the facilitation of ecological functions, contributing to the different ecosystem functions at different proportions (Chapter 4). The delivery of dung removal and plant productivity depends greatly on the diversity of functional groups. Roller dung beetles effectively facilitated dung removal, while dung beetles within the tunneller nesting group were most associated with greater plant productivity despite their smaller contribution to dung removal. While roller dung beetles were able to remove considerably large amounts of dung, compared to tunnellers, in this experiment, they were not able to incorporate this dung into the soil.

While I expected to see a difference in the investment of plant's above- and below-ground biomass as a result of the allocation of dung by dung beetles, this was not apparent in this study (Chapter 4). The ratio of above-ground to below-ground biomass of the plants did not differ significantly between treatments.

After exploring the relationships between the fixed variables (land use, stocking rates, rainfall, rainfall seasonality, vegetation cover and soil content) and all the dependent variables it was apparent that there may be confounding effects from stocking rates or rainfall. This effect could potentially distort the effects of other fixed variables on dung beetle activity and species assemblages. Further inspection of this hypothesis showed that there was only minor confounding effect for most variables, except there was a substantial confounding effect with stocking rates (Appendix 12). Owing to the semi-arid nature of the Karoo, it is highly likely that the stocking rates will be dependent on the land use type (thus, profit vs conservation), vegetation cover and rainfall. Therefore, it may seem that after all the other variables are accounted for, stocking rates becomes less important as a predictor for dung beetle activity. However, it cannot be concluded from this study that stocking rates are not as important predictors, hence further investigation of this confounding effect is recommended.

Dung beetle communities of the semi-arid Karoo

Dung beetle communities are mainly defined by environmental factors and variation between habitats (Lumaret and Kirk, 1987; Nealis, 1977). This study found that the dung beetle species composition varied significantly between livestock farms and protected areas (Chapter 3). Although dung beetles were more abundant in protected areas (Chapter 2), these dung beetles also had greater dispersal ability (Chapter 3). This may be a result of the scarcity in dung resources, as the protected areas in this study had lower herbivore stocking rates compared to farms. Thus, in order to survive in these conditions, there has perhaps been a selection for species with those wing loadings (i.e. species that can fly far can survive in reserves).

Mammal communities play a major role in the structure of dung beetle species composition through their provision of dung (Nichols et al., 2009). Dung beetles were more abundant in the protected areas (Chapter 2) which was surprising as the protected areas had low stocking rates compared to the farms. However, most dung beetles in these protected areas were small-bodied dweller and tunneller dung beetles from the *Aphodius* and *Onthphagus* genera, respectively (Chapter 3). A possible explanation for the abundance of dung beetles in protected areas, where the availability of dung might have been lower, is that small-bodied dung beetles have adapted to using most microhabitats and food resources (Jankielsohn et al. 2001). Although the successful development of adult dung-feeding insects depends on the quality of dung (Lumaret et al., 1992), some dung beetle species can use other food resources, including dry dung (Ocampo and Philips, 2017).

Dung beetle species composition also varied significantly between the winter and summer rainfall regions (Chapter 3). The winter rainfall region was generally more arid (i.e. MAP ranging from 137.8 – 316.1 mm per year) than the summer rainfall region (i.e. MAP ranging from 242.3 – 381.1 mm per year). This contrast makes it challenging to separate the effect of seasonality from the amount of rainfall. Variation in species composition was also influenced by MAP. This variable, however, was not associated with any indicator species.

Ecological functions

The role played by dung beetles on the ecosystem function of dung removal has been assessed by several studies, associating function to abundance (Horgan, 2005; Manning and Cutler, 2018), body size/ biomass (Slade et al., 2007) and

species richness (Nunes et al., 2018). However, in Chapter 4, I found that dung removal was best facilitated by dung beetle species richness. Moreover, the effects of dung beetle functional groups varied for dung removal and plant productivity (Chapter 4). While roller dung beetles removed more dung than tunnellers, these tunnellers were the most effective functional group for plant productivity. The results of Chapter 4 suggest that the effectiveness or contribution of each community attribute depends upon the ecological function being facilitated. Furthermore, in order to understand the effects of disturbance on ecosystem functions facilitated by dung beetles, we cannot depend on the response of one ecosystem function (i.e. dung removal) nor the effects of one community attribute (i.e. species richness).

Consideration for long-term monitoring

Dung beetles are sensitive to environmental changes, this along with their wide distribution and ease in which they can be sampled, makes them an ideal indicator species (Gardner et al., 2008; McGeoch et al., 2002; Nichols et al., 2007). This study revealed 15 indicator species from the semi-arid Karoo dung beetle communities, and these indicator species were associated with several environmental variables (Chapter 3). Some indicators were associated with more than one environmental variable. There was an apparent variation in the dung beetle community and species composition between farms and protected areas in this study. Furthermore, a great deal of this variation (30%) in species composition was associated with *Aphodius* sp.2. This species was more commonly found in the protected areas. Long-term rainfall (MAP), rainfall seasonality and stocking rates had the strongest influence on dung beetle communities. However, the most variation (30%) was explained by MAP which also had the most indicator species (8). The results also showed *Cheironitis*

audiens as an indicator species for variation in vegetation cover, which was mostly found in sites with high vegetation cover. Rainfall seasonality was associated with *Onthophagus fritschi, O. perngueyi, Phalops dregei* and *Scarabaeus viator*, which were more common in the eastern summer rainfall region. Future studies must narrow down the changes in rainfall and their prospective influence on biodiversity and ecosystem functioning, considering the influence of rainfall on dung beetle activity highlighted in this study and also the current prediction of an increase in summer rainfall and variation on rainfall.

In this study, I assessed the response of dung beetle species richness, abundance, functional diversity, CWM of body length and body size inequality (Gini coefficient) to variation in land use, habitat structure and rainfall (Chapter 2). The results showed that environmental changes have varied effects on these community attributes. Land use had a different influence on the abundance and functional diversity, with greater dung beetle abundance in the protected areas, while functional diversity was smaller. Abundance and species richness were the only attributes that responded to variation in stocking rates and rainfall. Species richness also positively responded to vegetation cover along with functional diversity. CWM of body length was the only variable to respond to soil texture. Furthermore, the fourth-corner analysis found a significant link between dung beetle functional traits and the effects of the variation in land use, habitat structure and rainfall seasonality on dung beetle species composition (Chapter 3). This emphasises the value of trait-based analysis in ecology studies focusing on the response of insect communities to disturbance (McGill et al., 2006; Mouillot et al., 2013; Raine et al., 2018).

Conservation implications and recommendations

Environmental variables also influenced the ecosystem functions of dung removal. This also emphasises the need to consider all community attributes and ecosystem functions in ecological assessments in order to develop better biodiversity conservation strategies. Particularly now, with global records showing ongoing insect declines and anthropogenic disturbances that may threaten the provision of these ecosystem functions. Species richness has been the most relied upon measure of biodiversity when evaluating impacts of disturbance (Barragán et al., 2011). However, the findings of this study suggest that in order to fully understand dung beetle community structures and their contributions to ecosystem functions, ecological studies need to include all species community attributes (i.e. taxonomic and functional attributes) simultaneously when assessing the impacts of anthropogenic and climate changes.

Limitations and Future Research

In this study, I used cow dung for both dung beetle sampling and dung removal experiment. Although this dung type was able to attract a diverse representation of dung beetle species, it may have excluded some smaller dung beetles that require pellet-type (i.e. sheep) dung (Lumaret et al., 1992). The reason for using cow dung in this study was because sheep (which dominate most farms), as well as goat and horse dung, dries too quickly in this area, thus, giving shorter suitable conditions for feeding and breeding. Also using one dung type allowed comparison between sites (see also Lumaret et al., 1992). The presence of dung beetles in the areas dominated by sheep and goats is an interesting finding, especially in this semi-arid

area where the harsh climatic conditions also influence the rate in which the dung dries. This could be an indication that dung beetle communities in this area are characterised by generalists. Future studies may shed more light in these dung beetle communities by assessing their tolerance and adaptation to these conditions.

The experiment assessing the effects of functional groups on dung removal and plant productivity clearly shows that different functional groups contribute to different ecosystem functions. Further studies may benefit from designing experiments which includes both species and functional group diversity to understand the interactions between different functional groups better. This could also be extended further to consider the vulnerability of each functional group and species to environmental change.

Finally, this study took place during a severe and fairly prolonged drought. The data and findings here are therefore useful as a snapshot of how dung beetles in the Karoo respond to dry periods. Further studies, in wetter periods, could provide rich material for comparison with the findings of this study.

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Appendix 1: Main environmental characteristics of the study site; NR – Nature Reserve, NP – National Park, LTER – Long-term ecological research site, PA – Protected area

Site #	Site	coordinates		Land use	Rainfall season	Rainfall		Stocking rate (LSU/ha)	Vegetation cover (%)	Soil Content (%)		
		Latitude	Longitude			MAP (mm)	SPI			Clay	Sand	Silt
1	Anysberg NR	-33.4715	20.63855	PA	Winter	225.1	-1.12	0.0185	23	6	89	5
2	Argentina	-33.1778	22.2229	Farm	Winter	184.9	-2.02	0.0167	30	20	75	5
3	Camdeboo NP	-32.2118	24.4965	PA	Summer	381.1	-1.79	0.0625	65	12	77	11
4	Good Luck	-33.0404	24.96755	Farm	Summer	242.3	-1.26	0.0621	42	17	72	11
5	Hopewell	-32.3214	23.11992	Farm	Winter	229.2	-0.27	0.0333	45	24	66	10
6	Karoo NP	-32.3546	22.43541	PA	Winter	316.5	-1.99	0.0278	6	12	74	8
7	Portugalsriver	-32.5109	20.87749	Farm	Winter	312.1	-1.98	0.0313	11	23	72	5
8	Rietvlei	-32.2122	21.85938	Farm	Winter	212.2	-1.78	0.0311	9	14	76	10
9	Rooidraai	-32.4832	23.61924	Farm	Summer	317.8	-1.02	0.0417	70	18	68	15
10	Tankwa Karoo NP	-32.2836	20.07266	PA	Winter	137.8	-1.36	0.0091	8	12	78	11
11	Tierberg LTER	-33.1718	22.26992	PA	Winter	184.9	-2.02	0.0067	45	23	71	6

Appendix 2: The mammal species list showing the occurrence of the different species found in the livestock farms and protected areas sites in the Nama and Succulent Karoo. Where An – Anysberg Nature reserve, A – Argentina farm, C – Camdeboo National Park, G – Good luck farm, H – Hopewell farm, K – Karoo National Park, P – Portugalsriver farm, Rt – Rietvlei farm, R – Rooidraai farm, Tn – Tankwa-karoo National Park, Tierberg long-term ecological research site.

Species		An	A	C	G	H	K	P	Rt	R	Tn	T
African wild cat	*Felis lybica*										x	
Angora goats	*Capra aegagrus hircus*				x	x						
Baboon	*Papio hyamadryas*			x			x				x	
Bat-eared fox	*Otocyon megalotis*			x							x	
Black rhinoceros	*Diceros bicornis*						x					
Black wildebeest	*Connochaetes gnou*			x								
Black-backed fox	*Canis mesomelas*										x	
Blesbok	*Damaliscus pygargus*			x								
Boer goats	*Capra aegagrus hircus*				x							
Buffalo	*Syncerus caffer*			x								
Caracal	*Caracal caracal*										x	
Cattle	*Bos taurus*				x	x			x			
Common duiker	*Sylvicapra grimmia*			x			x				x	x
Eland	*Taurotragus oryx*	x		x			x				x	
Gemsbok	*Oryx gazella*	x		x			x				x	
Giraffe	*Giraffa camelopardalis*		x									
Goats	*Capra aegagrus*										x	
Greater kudu	*Tragelaphus strepsiceros*	x		x	x		x				x	
Grey Rhebok	*Pelea capreolus*	x					x				x	
Horse	*Equus ferus*	x	x									
Black-backed Jackal	*Canis mesomelas*			x			x					
Klipspringer	*Oreotragus oreotragus*			x			x				x	

Common name	Scientific name											
Lion	*Panthera leo*						x					
Merino sheep	*Ovis aries*					x						
Mountain reedbuck	*Redunca fulvorufula*			x			x					
Mountain Zebra	*Equus zebra*	x		x			x				x	
Ostrich	*Struthio camelus*	x		x			x				x	
Plains zebra	*Equus quagga*						x					
Porcupine	*Hystrix africaeaustralis*						x				x	x
Red hartebeest	*Alcelaphus buselaphus*	x		x			x				x	
Sheep	*Ovis aries*				x			x	x	x		
Springbok	*Antidorcas marsupialis*	x		x	x		x				x	
Steenbok	*Raphicerus campestris*		x	x			x				x	

Appendix 3: Species composition and abundance of dung beetles trapped during the two sampling seasons at the 11 study sites within the farms and protected areas in the Nama and Succulent Karoo. FG – Functional group. D – Dweller, T – Tunneller, R – Roller, An – Anysberg, A – Argentina, C – Camdeboo, G – Good luck, H – Hopewell, K - Karoo, P – Portugalsriver, R – Rooidraai, Rt – Reitvlei, T – Tierberg, Tn – Tankwa Karoo.

Species	FG	DA	Protected areas					Livestock farms						Total
			AN	C	K	Tn	T	A	G	H	P	Rt	R	
Summer														
Aphodinae														
Aphodius sp1	D		0	0	5	0	2	1	15	0	0	17	0	**40**
Aphodius sp2	D		0	33	3	0	0	0	0	2	0	0	0	**38**
Aphodius sp3	D		0	0	1	0	0	0	0	1	0	2	0	**4**
Aphodius sp4	D		0	0	3	0	0	0	0	0	0	0	2	**5**
Aphodius sp5	D		6	470	326	0	1	5	2	93	0	20	25	**948**
Aphodius sp6	D		5	23	110	0	10	14	16	9	0	46	5	**238**
Scarabaeinae														
Cheironitis audiens	T		0	6	0	0	0	0	2	12	0	0	18	**38**
Cheironitis scabrosus	T	D	1	50	5	1	2	13	3	14	1	12	8	**110**
Digitonthophagus gazella	T	N	0	14	0	0	0	1	0	0	0	0	0	**15**
Digitonthophagus namaquensis	T		0	0	3	0	3	0	0	0	0	1	0	**7**
Drepanocerus patrizii	T		0	14	1	0	0	0	0	3	0	2	0	**20**
Eonthophagus carbonarius	T		0	0	0	0	0	0	0	0	0	1	0	**1**
Epirinus aeneus	R	D	0	3	0	0	1	0	7	0	0	0	1	**12**
Escarabaeus satyrus	R		0	1	0	0	0	0	0	0	0	0	0	**1**
Euniticellus africanus	T		0	10	9	0	0	0	7	1	0	15	4	**46**
Euonthophagus vicarius	T		0	15	1	0	57	13	0	0	0	12	2	**100**
Gymnopleurus andreaei	R		0	2	157	0	18	41	33	0	0	20	0	**271**
Metacatharsius marani	T	N	0	0	0	0	0	0	5	0	0	0	0	**5**

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Species	FG		AN	C	K	Tn	T	A	G	H	P	Rt	R	Total
Metacatharsius vitulus	T		0	1	0	0	0	0	0	0	0	0	0	**1**
Neosisyphus quadricollis	R	D	0	0	0	0	2	2	0	0	0	0	0	**4**
Neosisyphys macrorubus	R	D	0	16	4	0	0	0	2	2	0	2	7	**33**
Odontoloma pygidiale	R		0	1	0	0	0	0	15	0	0	0	0	**16**
Onitis alexi	T		0	1	0	0	0	0	0	0	0	0	0	**1**
Onitis caffer	T		0	1	0	0	0	0	0	0	0	0	0	**1**
Onthophagus albipennis	T		0	1389	198	0	2	2	80	19	0	13	64	**1767**
Onthophagus binodus	T		0	3	0	0	0	0	0	0	0	0	0	**3**
Onthophagus fritschi	T		0	2800	3	0	1	0	117	5	0	0	35	**2961**
Onthophagus nr. Discretus	T		0	1	0	0	0	0	0	0	0	0	0	**1**
Onthophagus peringueyi	T		0	197	2	0	1	0	83	2	0	0	50	**335**
Phalops dregei	T	D	0	94	1	0	0	0	11	1	0	1	3	**111**
Phalops rufosignatus	T	D	0	70	17	0	1	0	28	36	0	9	32	**193**
Scarabaeolus karrooensis	R		0	1	0	0	1	0	14	0	0	0	4	**20**
Scarabaeus viator	R		9	229	13	0	2	1	236	1	0	0	46	**537**

		Protected areas					Livestock farms							
Species	**FG**		**AN**	**C**	**K**	**Tn**	**T**	**A**	**G**	**H**	**P**	**Rt**	**R**	**Total**
Winter														
Aphodinae														
Aphodius sp2	D		6	848	3	2	0	0	1	1	2	0	3	**866**
Aphodius sp5	D		2	23	0	2	0	0	6	0	6	69	0	**108**
Aphodius sp6	D		9	6	1	0	1	0	7	2	0	54	8	**88**
Scarabaeinae														
Cheironitis scabrosus	T		0	5	1	0	0	0	2	0	1	0	1	**10**
Drepanocerus patrizii	T		0	1	0	0	0	0	0	0	0	0	0	**1**
Epirinus obtusus	R	D	0	0	2	0	0	0	0	1	6	0	1	**10**
Euniticellus africanus	T		0	1	0	0	0	0	0	0	0	0	0	**1**
Euonthophagus vicarius	T		0	0	0	0	0	0	0	0	0	2	0	**2**
Odontoloma pygidiale	R		0	1	0	0	0	0	0	0	3	0	0	**4**

Onthophagus cameloides	T	0	35	0	0	1	0	0	0	1	0	0	**37**
Onthophagus fritschi	T	0	58	0	0	0	0	5	1	0	0	0	**64**
Scarabaeolus karrooensis	R	0	0	0	0	0	0	0	0	2	0	0	**2**
Scarabaeus viator	R	0	3	0	0	0	0	0	0	10	0	0	**13**
Total		**38**	**6426**	**869**	**5**	**106**	**93**	**697**	**206**	**32**	**298**	**319**	**9089**

Appendix 4: The average values of functional traits measured from 356 dung beetles within 20 species.

Species	Body size	Abdominal size	Hind leg size	Hind leg robustness	Wing aspect ratio	Wing loading
Aphodius sp1	5.39	1.17	0.21	0.08	0.29	0.93
Aphodius sp2	4.98	1.23	0.23	0.09	0.34	1.33
Aphodius sp5	4.88	1.23	0.21	0.08	0.34	1.17
Aphodius sp6	4.79	1.37	0.23	0.08	0.33	1.36
Cheirontis audiens	13.77	1.68	0.23	0.25	0.46	0.65
Cheirontis scabrosus	11.90	1.42	0.21	0.20	0.34	0.49
Digitonthophagus gazella	11.02	1.98	0.26	0.20	0.34	0.64
Digitonthophagus namaquensis	9.08	1.98	0.24	0.27	0.35	0.89
Drepanocerus patrizii	5.98	1.61	0.27	0.07	0.26	0.59
Epirinus obtusus	8.13	1.22	0.39	0.08	0.28	0.59
Euniticellus africanus	7.62	1.43	0.24	0.15	0.31	0.39
Euonthophagus vicarius	8.88	2.39	0.25	0.17	0.33	0.70
Gymnopleurus andreaei	8.83	1.20	0.50	0.10	0.34	0.59

Neosisyphys macrobus	9.06	1.68	0.52	0.08	0.29	0.65
Odontoloma pygidiale	2.78	1.11	0.32	0.09	0.28	1.09
Onthophagus albipennis	5.28	1.65	0.22	0.15	0.30	0.65
Onthophagus fritschi	5.19	1.57	0.25	0.08	0.33	0.69
Onthophagus peringueyi	6.09	1.42	0.24	0.13	0.32	0.66
Phalops dregei	10.48	1.28	0.27	0.16	0.34	0.62
Phalops rufosignatus	10.15	1.65	0.26	0.20	0.33	0.59
Scarabaeolus karrooensis	11.50	1.34	0.43	0.09	0.31	0.56
Scarabeaus viator	21.09	1.66	0.48	0.08	0.33	0.64

Appendix 5: The South African Weather Stations that are nearest to the study sites in the Nama and Succulent Karoo where the rainfall data were obtained, also showing the distance from the corresponding study site. NR –Nature reserve, NP - National Park and LTER - long-term ecological research site.

Site #	Sampling sites	coordinates		SA weather station	coordinates		Distance from site (km)
		Latitude	Longitude		Latitude	Longitude	
1	Anysberg NR	-33.4715	20.63855	Ladismith Buffelsriver	-33.4715	20.63855	37.61
2	Argentina	-33.1778	22.2229	Zachariasfontein	-33.1778	22.2229	11.1
3	Camdeboo NP	-32.2118	24.4965	Winterhoek	-32.2118	24.4965	4.83
4	Good Luck	-33.0404	24.96755	Darlington dam	-33.0404	24.96755	25.18
5	Hopewell	-32.3214	23.11992	Kamerskraal	-32.3214	23.11992	11.33
6	Karoo NP	-32.3546	22.43541	Beaufort Wes Stolshoek	-32.3546	22.43541	5.58
7	Portugalsriver	-32.5109	20.87749	Sutherland Ginsfontein	-32.5109	20.87749	19.31
8	Rietvlei	-32.2122	21.85938	Tafelberg	-32.2122	21.85938	23.17
9	Rooidraai	-32.4832	23.61924	Walplaas	-32.4832	23.61924	30.29
10	Tankwa Karoo NP	-32.2836	20.07266	Tankwa Karoo NP	-32.2836	20.07266	5.25
11	Tierberg LTER	-33.1718	22.26992	Zachariasfontein	-33.1718	22.26992	13.43

Appendix 6: Rainfall data showing the days since the last rainfall event relative to sampling period in the two sampling season, the amount of rainfall received (days of rain not separated by more than five dry days) and raindex measure calculated as the amount of rain received in the most recent downpours divided by the number of days since the last day of rain relative to dung beetle sampling and dung removal experiment. NR –Nature reserve, NP - National Park and LTER - long-term ecological research site.

Season	Site	Days since last rainfall	Recent rainfall (mm)	Raindex
Summer	Anysberg NR	10	6	0.60
	Argentina	5	2.5	0.50
	Camdeboo NP	61	29	0.48
	Good luck	14	55	3.93
	Hopewell	9	6.5	0.72
	Karoo NP	126	2.2	0.02
	Portugalsriver	34	2	0.06
	Reitvlei	20	3.5	0.18
	Rooidraai	21	22	1.05
	Tankwa-karoo NP	126	2	0.02
	Tierberg LTER	7	2.5	0.36
Winter	Anysberg NR	24	7	0.29
	Camdeboo NP	48	30	0.63
	Good luck	153	3.7	0.02
	Hopewell	31	2.5	0.08
	Karoo NP	5	0.7	0.14
	Portugalsriver	15	5	0.33
	Reitvlei	18	2	0.11
	Rooidraai	7	10	1.43
	Tankwa-karoo NP	27	2.6	0.09
	Tierberg NP	128	4	0.03

Appendix 7: Rarefied species accumulation curve for the sampled dung beetles in A-Summer and B-Winter season.
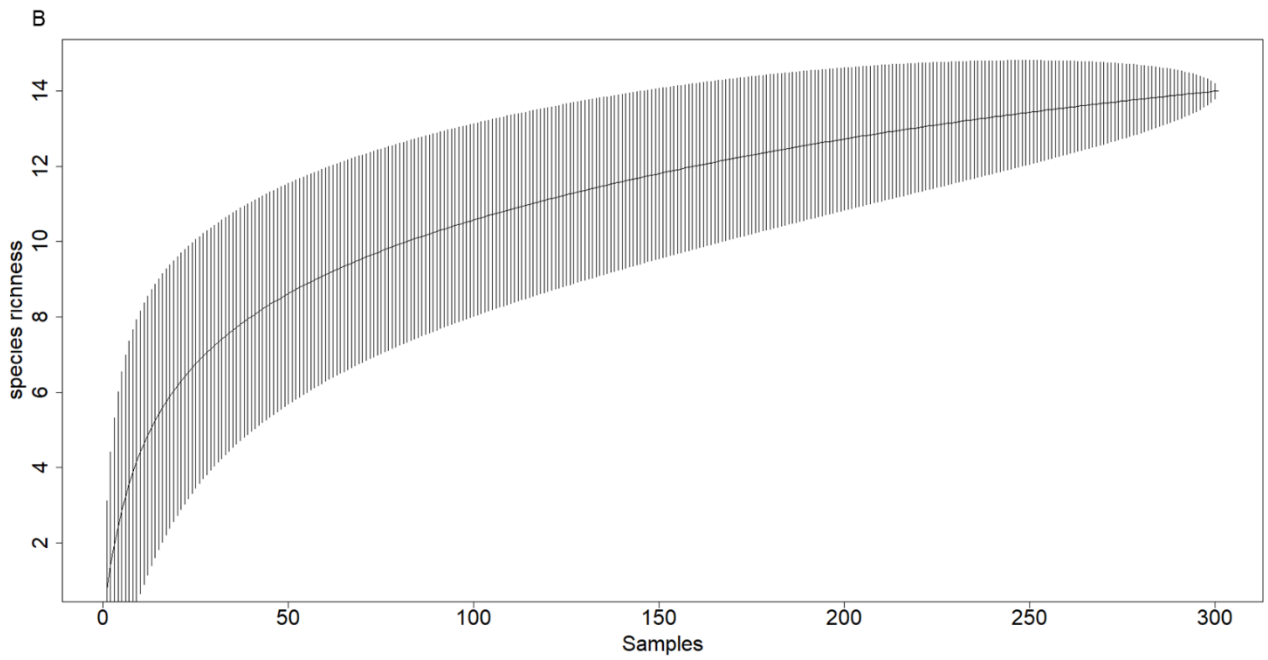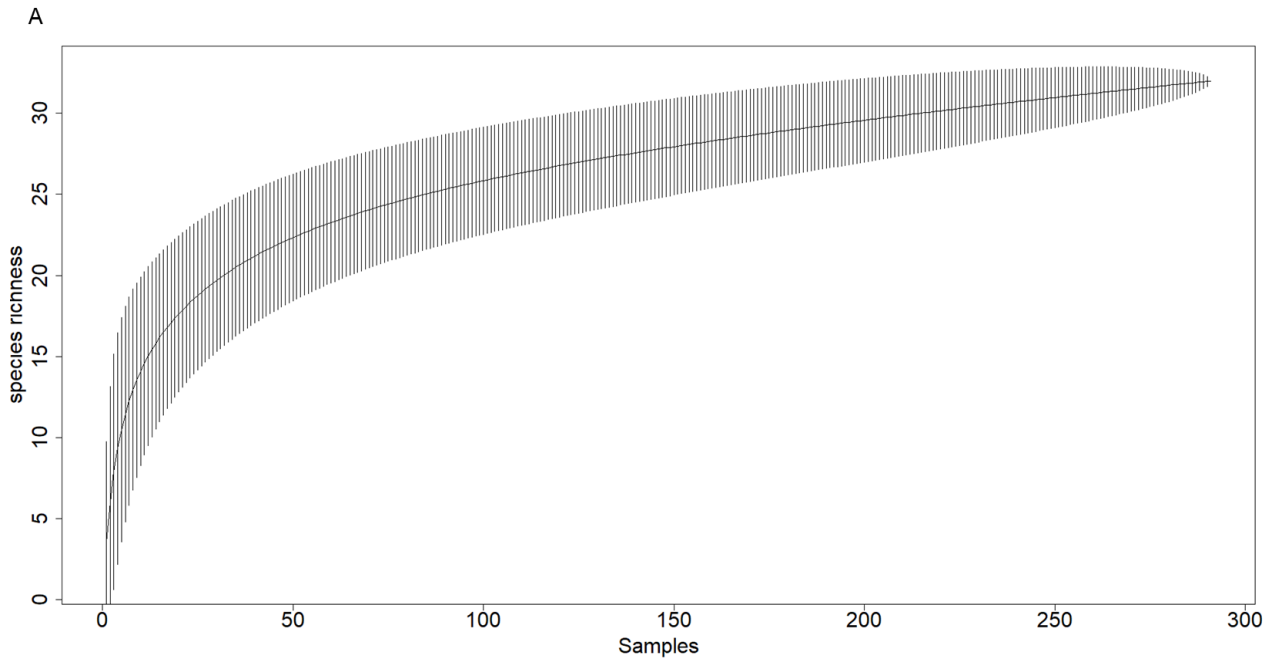
Appendix 8: Dung removal by dung beetles after a 200 g dung pat was left in the 11 study sites for 24 hours.

Season	Land use	Site	Plot	Proportion dung removed
Summer	Farm	Argentina	Ao1	0.25
Summer	Farm	Argentina	Ao2	0.19
Summer	Farm	Argentina	Ao5	0.31
Summer	Farm	Argentina	Ao6	0.17
Summer	Farm	Good Luck	Go1	0.73
Summer	Farm	Good Luck	Go2	0.58
Summer	Farm	Good Luck	Go8	0.74
Summer	Farm	Good Luck	Go9	0.75
Summer	Farm	Hopewell	Ho1	0.62
Summer	Farm	Hopewell	Ho3	0.30
Summer	Farm	Hopewell	Ho7	0.50
Summer	Farm	Hopewell	Ho9	0.57
Summer	Farm	Portugalsriver	Pf1	0.31
Summer	Farm	Portugalsriver	Pf2	0.26
Summer	Farm	Portugalsriver	Pf7	0.28
Summer	Farm	Portugalsriver	Pf8	0.27
Summer	Farm	Reitvlei	Rto3	0.42
Summer	Farm	Reitvlei	Rto4	0.42
Summer	Farm	Reitvlei	Rto8	0.34
Summer	Farm	Reitvlei	Rto9	0.49
Summer	Farm	Rooidraai	Ro1	0.52
Summer	Farm	Rooidraai	Ro2	0.59
Summer	Farm	Rooidraai	Ro7	0.82
Summer	Farm	Rooidraai	Ro8	0.73
Summer	Protected Area	Anysberg	Ano1	0.28
Summer	Protected Area	Anysberg	Ano2	0.27
Summer	Protected Area	Anysberg	Ano7	0.33
Summer	Protected Area	Anysberg	Ano8	0.54
Summer	Protected Area	Camdeboo	Co1	0.85
Summer	Protected Area	Camdeboo	Co2	0.63
Summer	Protected Area	Camdeboo	Co7	0.70
Summer	Protected Area	Camdeboo	Co8	0.61
Summer	Protected Area	Karoo	Ko1	0.30
Summer	Protected Area	Karoo	Ko2	0.32
Summer	Protected Area	Karoo	Ko7	0.30
Summer	Protected Area	Karoo	Ko8	0.31
Summer	Protected Area	Tankwa-Karoo	Tnf1	0.27
Summer	Protected Area	Tankwa-Karoo	Tnf2	0.21
Summer	Protected Area	Tankwa-Karoo	Tnf7	0.27

Summer	Protected Area	Tankwa-Karoo	Tnf8	0.33
Summer	Protected Area	Tierberg	To3	0.32
Summer	Protected Area	Tierberg	To6	0.31
Summer	Protected Area	Tierberg	To8	0.40
Summer	Protected Area	Tierberg	To9	0.41
Winter	Farm	Good Luck	Go1	0.18
Winter	Farm	Good Luck	Go2	0.21
Winter	Farm	Good Luck	Go8	0.19
Winter	Farm	Good Luck	Go9	0.23
Winter	Farm	Hopewell	Ho1	0.24
Winter	Farm	Hopewell	Ho3	0.22
Winter	Farm	Hopewell	Ho7	0.20
Winter	Farm	Hopewell	Ho9	0.23
Winter	Farm	Portugalsriver	Pf1	0.22
Winter	Farm	Portugalsriver	Pf2	0.25
Winter	Farm	Portugalsriver	Pf7	0.23
Winter	Farm	Portugalsriver	Pf8	0.25
Winter	Farm	Reitvlei	Rto3	0.07
Winter	Farm	Reitvlei	Rto4	0.08
Winter	Farm	Reitvlei	Rto8	0.12
Winter	Farm	Reitvlei	Rto9	0.06
Winter	Farm	Rooidraai	Ro1	0.11
Winter	Farm	Rooidraai	Ro2	0.15
Winter	Farm	Rooidraai	Ro7	0.08
Winter	Farm	Rooidraai	Ro8	0.11
Winter	Protected Area	Anysberg	Ano1	0.16
Winter	Protected Area	Anysberg	Ano2	0.19
Winter	Protected Area	Anysberg	Ano7	0.15
Winter	Protected Area	Anysberg	Ano8	0.13
Winter	Protected Area	Camdeboo	Co1	0.14
Winter	Protected Area	Camdeboo	Co2	0.13
Winter	Protected Area	Camdeboo	Co7	0.12
Winter	Protected Area	Camdeboo	Co8	0.12
Winter	Protected Area	Karoo	Ko1	0.10
Winter	Protected Area	Karoo	Ko2	0.1
Winter	Protected Area	Karoo	Ko7	0.11
Winter	Protected Area	Karoo	Ko8	0.10
Winter	Protected Area	Tankwa-Karoo	Tnf1	0.18
Winter	Protected Area	Tankwa-Karoo	Tnf2	0.15
Winter	Protected Area	Tankwa-Karoo	Tnf7	0.17
Winter	Protected Area	Tankwa-Karoo	Tnf8	0.21
Winter	Protected Area	Tierberg	To3	0.16
Winter	Protected Area	Tierberg	To6	0.25
Winter	Protected Area	Tierberg	To8	0.21

Winter	Protected Area	Tierberg	To9		0.29

Appendix 9: Dung removal (g) in different treatment of dung beetle functional groups along with the plant mass (dry mass (g) of the total, above- and below-ground mass of radish plants) planted in the soil with dung mixed by the dung beetles. As the plants were damaged by invertebrates, the percentage of plant damages is also presented. C = control; D = dung; LR = larger rollers; SR = small rollers; LT = large tunnellers; ST = small tunnellers.

Block	Treatment	Dung beetle mass	Dung removed	Wet weight	Total dry mass	Above-ground mass	Below-ground mass	Damage by invertebrates
6	C	0	0	0.8	0.0657	0.0623	0.0034	40
6	C	0	0	0.8	0.0611	0.056	0.0051	50
6	C	0	0	0.9	0.0661	0.0607	0.0054	30
9	C	0	0	0.6	0.0449	0.0425	0.0024	0
9	C	0	0	0.6	0.0318	0.0269	0.0049	0
10	C	0	0	0.7	0.0527	0.0475	0.0052	20
11	C	0	0	1.1	0.0501	0.0399	0.0102	10
11	C	0	0	0.8	0.008	0.0034	0.0046	10
11	C	0	0	0.8	0.023	0.0018	0.0212	20
1	C	0	0	0.7	0.029	0.0246	0.0044	20
1	C	0	0	0.6	0.027	0.0228	0.0042	20
1	C	0	0	1.1	0.0601	0.0525	0.0076	30
2	C	0	0	1.5	0.0572	0.0452	0.012	0
3	C	0	0	0.7	0.0607	0.0552	0.0055	10
3	C	0	0	0.6	0.0492	0.0436	0.0056	10
3	C	0	0	1.1	0.0679	0.0572	0.0107	10
7	C	0	0	0.9	0.032	0.029	0.003	30
7	C	0	0	0.9	0.0429	0.0393	0.0036	20
5	C	0	0	1.6	0.0648	0.058	0.0068	0
4	C	0	0	1.5	0.0919	0.0829	0.009	10
4	C	0	0	1.3	0.0849	0.068	0.0169	0
12	C	0	0	0.8	0.0406	0.0332	0.0074	0
12	C	0	0	0.8	0.0396	0.0352	0.0044	0
12	C	0	0	0.8	0.0347	0.0328	0.0019	0

8	C	0	0	0.8	0.0445	0.0426	0.0019	0
8	C	0	0	0.9	0.0459	0.0398	0.0061	0
8	C	0	0	0.6	0.0308	0.0276	0.0032	10
6	C+D	0	0	0.8	0.0467	0.044	0.0027	20
6	C+D	0	0	1	0.0702	0.0649	0.0053	10
9	C+D	0	0	0.6	0.0318	0.0288	0.003	0
9	C+D	0	0	0.5	0.0245	0.021	0.0035	10
9	C+D	0	0	0.6	0.0513	0.0475	0.0038	0
9	C+D	0	0	0.9	0.0714	0.0647	0.0067	0
10	C+D	0	0	0.8	0.0446	0.0412	0.0034	10
10	C+D	0	0	0.3	0.0032	0.0024	0.0008	90
10	C+D	0	0	0.6	0.027	0.0239	0.0031	40
11	C+D	0	0	0.4	0.013	0.0107	0.0023	20
1	C+D	0	0	1.4	0.0551	0.0529	0.0022	0
1	C+D	0	0	0.8	0.0304	0.0267	0.0037	0
1	C+D	0	0	1.5	0.0871	0.0837	0.0034	0
2	C+D	0	0	1.1	0.0376	0.0312	0.0064	20
3	C+D	0	0	1.9	0.0788	0.0731	0.0057	10
3	C+D	0	0	1.1	0.054	0.0462	0.0078	0
7	C+D	0	0	0.6	0.0276	0.0254	0.0022	20
7	C+D	0	0	0.6	0.0359	0.0218	0.0141	0
5	C+D	0	0	1.2	0.057	0.0455	0.0115	10
5	C+D	0	0	1.3	0.062	0.0509	0.0111	20
5	C+D	0	0	1.4	0.0902	0.086	0.0042	0
4	C+D	0	0	0.6	0.048	0.0349	0.0131	0
4	C+D	0	0	1.6	0.0714	0.0622	0.0092	0
8	C+D	0	0	1.2	0.0472	0.0389	0.0083	10
8	C+D	0	0	1.2	0.0418	0.0377	0.0041	0
12	C+D	0	0	1	0.0564	0.0508	0.0056	10
12	C+D	0	0	1.4	0.0754	0.0665	0.0089	10
6	LR+LT	9.86	132.9	0.9	0.0818	0.0769	0.0049	50
6	LR+LT	9.86	132.9	0.5	0.0436	0.0398	0.0038	70

6	LR+LT	9.86	132.9	0.7	0.0579	0.0541	0.0038	50
9	LR+LT	9.86	132.9	0.8	0.0453	0.0386	0.0067	10
9	LR+LT	9.86	132.9	0.7	0.0302	0.0286	0.0016	20
10	LR+LT	9.86	132.9	0.6	0.0269	0.0253	0.0016	70
10	LR+LT	9.86	132.9	0.8	0.0314	0.027	0.0044	60
11	LR+LT	9.86	132.9	1.3	0.0621	0.0593	0.0028	0
11	LR+LT	9.86	132.9	0.6	0.0212	0.02	0.0012	20
11	LR+LT	9.86	132.9	0.6	0.0192	0.0186	0.0006	30
1	LR+LT	9.86	132.9	1.4	0.0461	0.0442	0.0019	10
1	LR+LT	9.86	132.9	0.9	0.0187	0.0155	0.0032	10
1	LR+LT	9.86	132.9	0.9	0.0378	0.0338	0.004	20
2	LR+LT	9.86	132.9	0.5	0.0249	0.0231	0.0018	10
2	LR+LT	9.86	132.9	1.2	0.0411	0.0353	0.0058	10
2	LR+LT	9.86	132.9	1.4	0.0446	0.039	0.0056	10
3	LR+LT	9.86	132.9	1	0.0427	0.04	0.0027	10
3	LR+LT	9.86	132.9	1.3	0.045	0.0427	0.0023	10
3	LR+LT	9.86	132.9	1.4	0.0464	0.0351	0.0113	10
7	LR+LT	9.86	132.9	1	0.0558	0.0421	0.0137	0
7	LR+LT	9.86	132.9	1.2	0.0664	0.0522	0.0142	0
7	LR+LT	9.86	132.9	1.4	0.067	0.0553	0.0117	10
5	LR+LT	9.86	132.9	1.1	0.0681	0.0621	0.006	40
5	LR+LT	9.86	132.9	1.7	0.0775	0.0728	0.0047	20
4	LR+LT	9.86	132.9	0.6	0.0325	0.024	0.0085	10
4	LR+LT	9.86	132.9	1.3	0.0965	0.0895	0.007	10
8	LR+LT	9.86	132.9	1.3	0.0567	0.0518	0.0049	60
8	LR+LT	9.86	132.9	0.7	0.0314	0.0261	0.0053	50
12	LR+LT	9.86	132.9	0.6	0.0242	0.0183	0.0059	40
12	LR+LT	9.86	132.9	1.3	0.0549	0.0504	0.0045	30
12	LR+LT	9.86	132.9	0.6	0.0361	0.0328	0.0033	50
6	LR+ST	8.11	109.8	0.5	0.0245	0.0225	0.002	80
6	LR+ST	8.11	109.8	1.4	0.0958	0.0881	0.0077	30
6	LR+ST	8.11	109.8	0.7	0.0414	0.0381	0.0033	20

9	LR+ST	8.11	109.8	1.3	0.0783	0.0751	0.0032	10
9	LR+ST	8.11	109.8	0.9	0.0555	0.0495	0.006	30
9	LR+ST	8.11	109.8	0.9	0.0497	0.0467	0.003	40
10	LR+ST	8.11	109.8	0.4	0.016	0.0144	0.0016	80
10	LR+ST	8.11	109.8	0.6	0.0268	0.0198	0.007	60
10	LR+ST	8.11	109.8	0.7	0.0444	0.039	0.0054	60
11	LR+ST	8.11	109.8	0.4	0.0244	0.0214	0.003	10
1	LR+ST	8.11	109.8	1.4	0.0748	0.0722	0.0026	10
2	LR+ST	8.11	109.8	1.6	0.0546	0.0504	0.0042	20
2	LR+ST	8.11	109.8	2.1	0.0832	0.0721	0.0111	20
3	LR+ST	8.11	109.8	0.9	0.0584	0.0433	0.0151	10
3	LR+ST	8.11	109.8	2.2	0.1283	0.0944	0.0339	0
7	LR+ST	8.11	109.8	1	0.0482	0.0401	0.0081	10
7	LR+ST	8.11	109.8	1.9	0.0947	0.069	0.0257	30
5	LR+ST	8.11	109.8	0.8	0.0353	0.0283	0.007	10
4	LR+ST	8.11	109.8	0	0	0	0	0
8	LR+ST	8.11	109.8	1.1	0.0577	0.0528	0.0049	20
8	LR+ST	8.11	109.8	0.7	0.0262	0.0217	0.0045	10
12	LR+ST	8.11	109.8	1.3	0.0583	0.0524	0.0059	0
12	LR+ST	8.11	109.8	1.2	0.0571	0.0545	0.0026	10
12	LR+ST	8.11	109.8	0.4	0.0162	0.0117	0.0045	50
6	LT+ST	2.52	22.3	0.9	0.0956	0.0793	0.0163	0
6	LT+ST	2.52	22.3	1.6	0.1129	0.1048	0.0081	30
6	LT+ST	2.52	22.3	1.2	0.0766	0.0709	0.0057	20
9	LT+ST	2.52	22.3	1.2	0.0702	0.0668	0.0034	0
9	LT+ST	2.52	22.3	1.4	0.088	0.0813	0.0067	0
10	LT+ST	2.52	22.3	1	0.0506	0.0459	0.0047	30
10	LT+ST	2.52	22.3	0.7	0.1458	0.0434	0.1024	10
11	LT+ST	2.52	22.3	0.8	0.0381	0.0354	0.0027	20
11	LT+ST	2.52	22.3	0.9	0.0429	0.039	0.0039	50
11	LT+ST	2.52	22.3	0.6	0.0287	0.0256	0.0031	25
1	LT+ST	2.52	22.3	1	0.0397	0.0345	0.0052	30

1	LT+ST	2.52	22.3	1.3	0.0542	0.0491	0.0051	20
2	LT+ST	2.52	22.3	1.1	0.065	0.0529	0.0121	10
2	LT+ST	2.52	22.3	1.6	0.0682	0.0581	0.0101	10
2	LT+ST	2.52	22.3	2.5	0.0709	0.0574	0.0135	20
2	LT+ST	2.52	22.3	0.5	0.0213	0.0168	0.0045	10
3	LT+ST	2.52	22.3	0	0	0	0	
7	LT+ST	2.52	22.3	1	0.0641	0.0593	0.0048	0
7	LT+ST	2.52	22.3	0.8	0.0368	0.0328	0.004	40
7	LT+ST	2.52	22.3	0.9	0.0381	0.0301	0.008	30
5	LT+ST	2.52	22.3	1.9	0.0712	0.0628	0.0084	20
5	LT+ST	2.52	22.3	0.9	0.0607	0.0583	0.0024	10
5	LT+ST	2.52	22.3	1.3	0.0635	0.0529	0.0106	10
4	LT+ST	2.52	22.3	0	0	0	0	0
8	LT+ST	2.52	22.3	1.6	0.0744	0.0646	0.0098	40
8	LT+ST	2.52	22.3	1.2	0.0682	0.0602	0.008	40
12	LT+ST	2.52	22.3	1.2	0.082	0.0758	0.0062	10
6	SR+LR	9.41	120.9	1	0.0663	0.0563	0.01	20
6	SR+LR	9.41	120.9	0.4	0.0312	0.0295	0.0017	80
6	SR+LR	9.41	120.9	1.2	0.0818	0.0721	0.0097	40
9	SR+LR	9.41	120.9	0.7	0.0448	0.0415	0.0033	0
10	SR+LR	9.41	120.9	0.7	0.0392	0.0356	0.0036	70
11	SR+LR	9.41	120.9	0.2	0.0069	0.0067	0.0002	90
11	SR+LR	9.41	120.9	0.5	0.018	0.0158	0.0022	80
1	SR+LR	9.41	120.9	0.9	0.0338	0.0305	0.0033	30
1	SR+LR	9.41	120.9	0.9	0.0368	0.0317	0.0051	40
2	SR+LR	9.41	120.9	1.1	0.0261	0.0209	0.0052	30
3	SR+LR	9.41	120.9	1.1	0.0434	0.0403	0.0031	0
7	SR+LR	9.41	120.9	1.1	0.055	0.0502	0.0048	10
7	SR+LR	9.41	120.9	1	0.0477	0.0434	0.0043	10
7	SR+LR	9.41	120.9	0.7	0.0361	0.0325	0.0036	10
7	SR+LR	9.41	120.9	0.6	0.0288	0.0247	0.0041	0
5	SR+LR	9.41	120.9	1.5	0.0381	0.0347	0.0034	20

4	SR+LR	9.41	120.9	1.8	0.1145	0.0904	0.0241	0
4	SR+LR	9.41	120.9	1.6	0.079	0.0678	0.0112	40
8	SR+LR	9.41	120.9	1.2	0.0643	0.0592	0.0051	40
8	SR+LR	9.41	120.9	1	0.0535	0.0462	0.0073	50
8	SR+LR	9.41	120.9	0.6	0.0296	0.0274	0.0022	0
12	SR+LR	9.41	120.9	0	0	0	0	
6	SR+LT	4.6	34.6	1.4	0.1032	0.0971	0.0061	15
6	SR+LT	4.6	34.6	0.9	0.0717	0.0639	0.0078	0
6	SR+LT	4.6	34.6	0.2	0.014	0.0123	0.0017	90
9	SR+LT	4.6	34.6	0.4	0.0215	0.0192	0.0023	0
10	SR+LT	4.6	34.6	0.4	0.0251	0.0234	0.0017	70
10	SR+LT	4.6	34.6	0.7	0.0536	0.051	0.0026	80
11	SR+LT	4.6	34.6	0	0	0	0	
1	SR+LT	4.6	34.6	1.1	0.0268	0.0251	0.0017	20
1	SR+LT	4.6	34.6	0.7	0.0219	0.0195	0.0024	10
2	SR+LT	4.6	34.6	1.2	0.0333	0.0268	0.0065	30
2	SR+LT	4.6	34.6	1.3	0.0584	0.0467	0.0117	10
3	SR+LT	4.6	34.6	0.5	0.0179	0.0136	0.0043	20
3	SR+LT	4.6	34.6	0.8	0.0404	0.0365	0.0039	30
3	SR+LT	4.6	34.6	1.1	0.0767	0.0628	0.0139	10
3	SR+LT	4.6	34.6	0.8	0.0721	0.068	0.0041	0
7	SR+LT	4.6	34.6	1.1	0.0719	0.0613	0.0106	50
7	SR+LT	4.6	34.6	0.9	0.0608	0.0523	0.0085	10
7	SR+LT	4.6	34.6	1	0.0632	0.0502	0.013	50
5	SR+LT	4.6	34.6	1.1	0.0411	0.0363	0.0048	30
5	SR+LT	4.6	34.6	1.4	0.0447	0.0354	0.0093	20
4	SR+LT	4.6	34.6	1.4	0.0979	0.0696	0.0283	0
4	SR+LT	4.6	34.6	0.7	0.0672	0.0578	0.0094	10
4	SR+LT	4.6	34.6	1.3	0.081	0.073	0.008	20
8	SR+LT	4.6	34.6	1.4	0.0449	0.0415	0.0034	10
12	SR+LT	4.6	34.6	0.8	0.0478	0.0451	0.0027	10
12	SR+LT	4.6	34.6	0.6	0.0467	0.044	0.0027	60

12	SR+LT	4.6	34.6	1	0.0528	0.0445	0.0083	40
6	SR+ST	2.11	6.7	1.1	0.0803	0.0727	0.0076	20
6	SR+ST	2.11	6.7	0.7	0.0698	0.0657	0.0041	30
6	SR+ST	2.11	6.7	0.6	0.0591	0.055	0.0041	10
9	SR+ST	2.11	6.7	0.4	0.0182	0.0173	0.0009	10
9	SR+ST	2.11	6.7	0.7	0.0741	0.0677	0.0064	10
10	SR+ST	2.11	6.7	0.8	0.0423	0.0372	0.0051	0
10	SR+ST	2.11	6.7	0.4	0.0124	0.011	0.0014	70
10	SR+ST	2.11	6.7	0.3	0.0113	0.0108	0.0005	90
11	SR+ST	2.11	6.7	0.3	0.0106	0.0077	0.0029	90
11	SR+ST	2.11	6.7	0.2	0.008	0.0077	0.0003	80
11	SR+ST	2.11	6.7	0.2	0.0059	0.0055	0.0004	80
1	SR+ST	2.11	6.7	0.9	0.0407	0.0388	0.0019	30
1	SR+ST	2.11	6.7	1	0.0433	0.0421	0.0012	30
1	SR+ST	2.11	6.7	0.6	0.027	0.024	0.003	50
2	SR+ST	2.11	6.7	0.5	0.0253	0.0219	0.0034	70
2	SR+ST	2.11	6.7	0.7	0.0254	0.023	0.0024	10
2	SR+ST	2.11	6.7	2.1	0.0665	0.0601	0.0064	20
3	SR+ST	2.11	6.7	1.5	0.0592	0.0502	0.009	30
3	SR+ST	2.11	6.7	0.7	0.0587	0.0566	0.0021	20
7	SR+ST	2.11	6.7	0.9	0.0428	0.0398	0.003	10
7	SR+ST	2.11	6.7	1.4	0.0483	0.0357	0.0126	10
5	SR+ST	2.11	6.7	1	0.0676	0.0565	0.0111	0
5	SR+ST	2.11	6.7	1	0.0379	0.0352	0.0027	0
5	SR+ST	2.11	6.7	1.5	0.0817	0.0679	0.0138	0
4	SR+ST	2.11	6.7	0.6	0.0425	0.0384	0.0041	0
4	SR+ST	2.11	6.7	1.6	0.083	0.078	0.005	0
4	SR+ST	2.11	6.7	0.6	0.0275	0.0219	0.0056	20
8	SR+ST	2.11	6.7	0.9	0.0411	0.035	0.0061	60
8	SR+ST	2.11	6.7	0.5	0.028	0.0233	0.0047	60
8	SR+ST	2.11	6.7	0.5	0.0279	0.0233	0.0046	0
12	SR+ST	2.11	6.7	1.2	0.0605	0.0551	0.0054	30

| 12 | SR+ST | 2.11 | 6.7 | 1 | 0.0534 | 0.0478 | 0.0056 | 40 |
| 12 | SR+ST | 2.11 | 6.7 | 0.9 | 0.0473 | 0.0426 | 0.0047 | 30 |

Appendix 10: The dry weight of A) total plant and B) above-ground mass in the different dung beetle treatments; C = Control; R = Rollers; R + T = Rollers + Tunnellers; T = Tunnellers, as a function of damage by invertebrates.
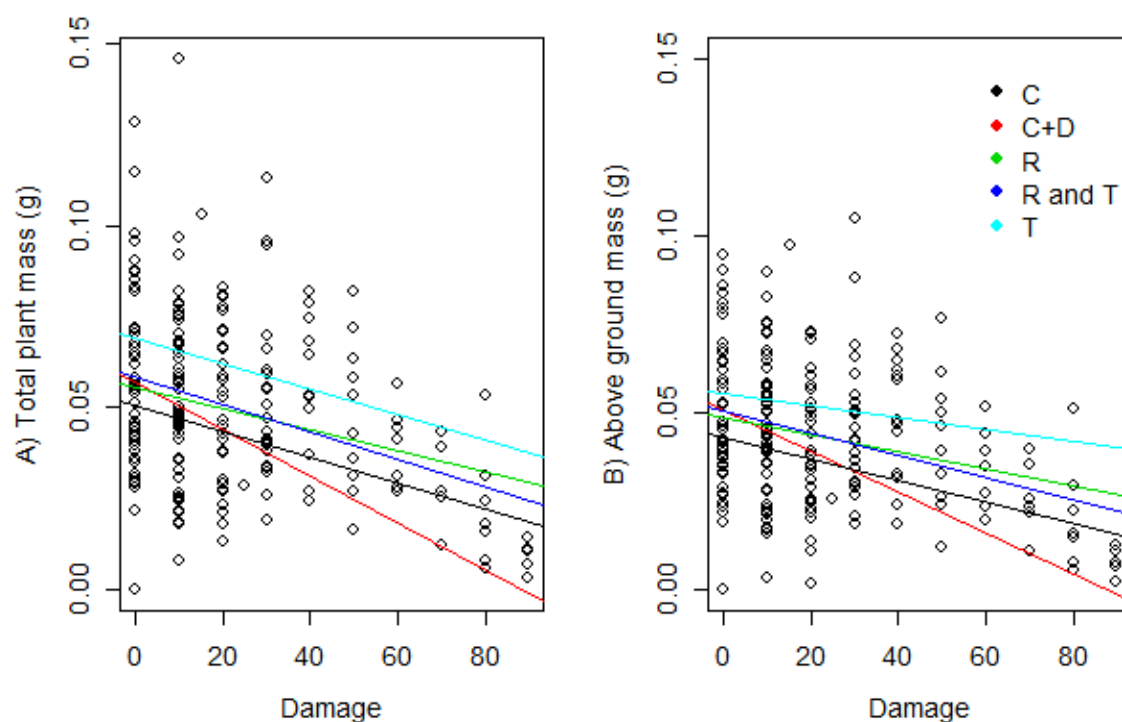
Appendix 11: The dry weight of the below-ground mass as a function of damage by invertebrates. This graph shows the decline in below-ground mass with an increase in invertebrate damage.
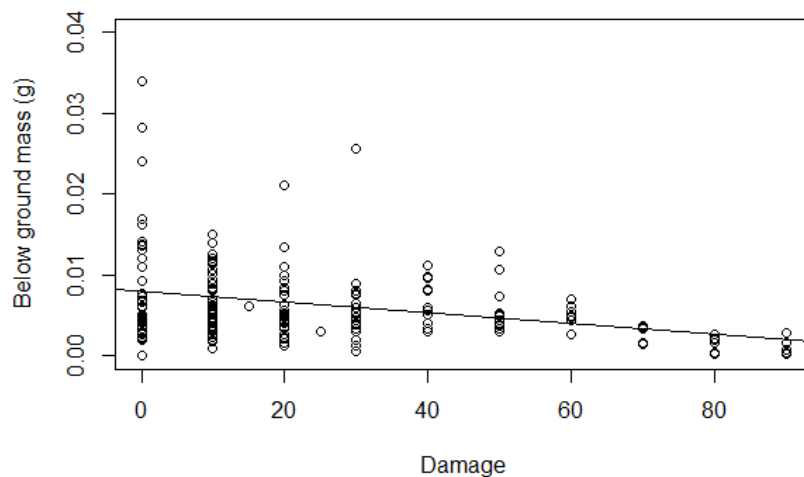
Appendix 12: Summary showing coefficients of multivariate and univariate analysis of the effects of fixed variables on dung beetle species richness and abundance. These analyses were performed to tease out any confounding variables from the fixed variables. This was done by comparing the multivariate analysis with all the fixed variables included in the multivariate model and a univariate analysis where the fixed variables were assessed individually. When the estimated difference was higher than 10%, then that variable was concluded to have a confounding effect. Of all the fixed variables assessed, stocking rates showed the most substantial confounding effect.

		Multivariate		Univariate	
Response	Fixed	Estimate	Std. error	Estimate	Std. error
Species	(Intercept)	4.813588	1.475962		
richness	Stocking rates	1.146342	0.373855	1.6254	0.3276
	Vegetation cover	0.208666	0.053364	0.18093	0.04920
	Sand	-0.011453	0.006715	-0.004151	0.006373
	Raindex	0.235876	0.064782	0.26230	0.06703
Abundance	(Intercept)	-1.055937	0.476899		
	Land use	-0.388884	0.227179	-0.5732	0.1624
	Stocking rates	17.001571	8.882502	45.2597	5.7339
	Vegetation cover	0.018524	0.005132	0.03082	0.00425
	MAP	0.003859	0.001778	0.008761	0.001274
	Clay	-0.031422	0.015599	-0.007984	0.012857