

**The effect of farmland abandonment on dung beetle diversity and
function in the Nama-Karoo, Northern Cape, South Africa.**

By

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Science (Conservation Ecology) in the Faculty of Agricultural Science at
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DECLARATION:

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GENERAL SUMMARY

Agricultural land abandonment has cascading effects on native biota. When badly managed, pressures on native biota can increase leading to reduced ecosystem function. Conversely, increased ecosystem function can result after decreasing anthropogenic pressures. This phenomenon has received little attention in the often-overexploited arid rangeland areas of the world. Here, I used a keystone taxon, dung beetles, as a bioindicator of the effect of farmland abandonment in the Nama-Karoo of South Africa. I documented changes in dung beetle abundance, richness, community assemblage composition, and their functional diversity as a result of ceasing large-scale sheep farming and evaluated differences in these factors across different biotopes. Dung beetles were sampled using baited pitfall traps on farms that were abandoned a long time ago (>10 years), recently (ca. 1 year ago) and on active farms, as well as from three dominant biotopes (hills, flatlands and ephemeral riparian zones) using three dung types (omnivore = pig; ruminant non-pelleted = cow; and ruminant pelleted = sheep). In general, riparian systems and flatlands had greater dung beetle richness, abundance, biomass and functional richness in comparison with hills, and each had a unique assemblage composition. Therefore, the flatland and ephemeral riparian areas that are generally most severely impacted by anthropogenic actions (since rocky slopes inhibit grazing activities) are particularly important for conserving dung beetle ecosystem functions and services. Dung beetle richness, abundance, and functional richness was higher in abandoned farmland areas due to greater dependence on omnivore and cow dung than on sheep dung, and reduced pressures on remaining native vertebrates. However, large-bodied dung beetles became rare after farmland abandonment. I therefore strongly encourage the reintroduction of native meso-herbivores to enhance dung resources in these abandoned areas, which will support higher dung beetle diversity, greater ecosystem function and increased ecosystem services.

OPSOMMING

Die staking van veeboerdery kan 'n effek hê op inheemse biota. Indien dit sleg bestuur kan die druk op inheemse biota toeneem tot 'n verminderde ekosisteenfunksie. Tog kan 'n verhoogde ekosisteenfunksie ontstaan na so 'n afname in antropogeniese druk. Hierdie verskynsel het min aandag geniet in die dikwels oorbenutte droë gebiede van die wêreld. Hier het ek 'n sleutelsteen takson, miskruiers, as bioindikator gebruik om die effek van landbougrondverlating in die Nama-Karoo van Suid-Afrika te bestudeer. Ek het veranderinge in die volopheid van miskruiers, spesies-rykheid, samestelling van gemeenskappe asook hul funksionele diversiteit gedokumenteer as gevolg van die staking van grootskaalse skaapboerdery en die verskille tussen hierdie faktore oor verskillende biotope geëvalueer. Ek het miskruiers gevang deur gebruik te maak van lokvalle op plase wat al 'n geruime tyd gelede (> 10 jaar) ontruim is, onlangs ontruim is (ongeveer 1 jaar gelede) of steeds aktief is, en dan ook in drie dominante biotope (klipkoppies/heuwels, platvlaktes en efemerale oewersones) met behulp van drie soorte mis (omnivore = vark; herkouer = koei; en nie-herkouer = skaap). Oor die algemeen het oewerstelsels en platvlaktes groter miskruier rykheid, volopheid, biomassa en funksionele rykdom in vergelyking met klipperige heuwels gehad, elkeen met 'n unieke spesies samestelling. Daarom is die plat vlaktes en efemerale oewergebiede, wat meestal die ergste geraak word deur antropogeniese optrede (aangesien klipperige hellings weidingsaktiwiteite belemmer) veral belangrik vir die behoud van ekosisteenfunksies en dienste van miskruiers. Interessant genoeg was die rykheid, oorfloed en funksionele rykheid van miskruiers hoër in verlate landbougebiede as gevolg van 'n groter afhanklikheid van herkouer mis as van nie-herkouer (skaap) mis, asook druk op die inheemse soogdiere wat verminder het. Die grootste miskruiers het egter skaars geword ná die verlating van landbougrond. Ek moedig die herinvoering van inheemse meso-herbivore sterk aan om mis kwaliteit in hierdie verlate gebiede te bevorder, wat 'n groter diversiteit van miskruiers, groter ekosisteenfunksie en verhoogde ekosisteedienste sal ondersteun.

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TABLE OF CONTENTS

DECLARATION.....	i
GENERAL SUMMARY.....	ii
OPSOMMING.....	iii
ACKNOWLEDGEMENTS.....	iv
List of Figures.....	viii
List of Tables.....	x
Abbreviations.....	xi
CHAPTER 1.....	1
GENERAL INTRODUCTION AND OBJECTIVES.....	1
1.1 Land-use change in the 21 st Century.....	1
1.2. Effects of Land Abandonment on Ecosystems.....	3
1.3. Effect of Land-use change and Land Abandonment on Arthropods.....	5
1.4. Arthropods as Biological Indicators.....	7
1.4.1. The Use of Dung Beetles as Bioindicators.....	8
1.5. Arthropod Functional Diversity.....	10
1.5.1. Using Dung Beetle Functional Diversity in Conservation Planning.....	11
1.6. The Present Study.....	12
1.6.1. Setting the Scene: The Nama Karoo Drylands in Flux.....	12
1.6.2. Study Rationale.....	13
1.6.3. The SKA Radio Astronomy Observatory: Ideal for Natural Experiment.....	14

1.6.4. Study Aim and Objectives.....	15
1.7. References.....	15
CHAPTER 2.....	37
CEASING LIVESTOCK GRAZING POSITIVELY AFFECTS DUNG BEETLE DIVERSITY IN A DRYLAND ECOSYSTEM.....	34
2.1 Abstract.....	34
2.2 Introduction.....	36
2.3 Materials and Methods.....	40
2.3.1 Study Area.....	40
2.3.2 Sampling Design and Dung Beetle Collection.....	42
2.3.3 Statistical Analyses.....	43
2.4 Results	44
2.4.1 The Effect of Land Use on Dung Beetle Assemblages.....	48
2.4.2 The Effect of Dung Type on Dung Beetle Assemblages	50
2.4.3 The Effect of Biotope on Dung Beetle Assemblages.....	52
2.5 Discussion.....	55
2.5.1. Land-use change and dung beetle diversity.....	56
2.5.2. Biotope diversity begets dung beetle diversity.....	58
2.5.3. Single large or several small? A look at dung beetle biomass.....	59
2.6. Conclusion.....	60
2.7. References.....	61

CHAPTER 3.....	72
THE EFFECT OF FARMLAND ABANDONMENT ON DUNG BEETLE FUNCTIONAL DIVERSITY IN THE NAMA-KAROO BIOME OF SOUTH AFRICA.....	72
3.1. Abstract.....	72
3.2. Introduction.....	73
3.3. Materials and Methods.....	76
3.3.1. Study Area.....	76
3.3.2. Sampling Design.....	77
3.3.3. Functional Traits	79
3.3.4. Statistical Analyses.....	80
3.4. Results.....	82
3.5. Discussion.....	86
3.6. Conclusions.....	89
3.7. References.....	90
CHAPTER 4	107
GENERAL DISCUSSION AND CONCLUSIONS.....	107
4.1. Exploring the dung beetle communities of a Nama Karoo dryland ecosystem....	107
4.2. The effect of biotope on dung beetles.....	108
4.3. The effects of ceasing livestock farming.....	109
4.4. References.....	111

LIST OF FIGURES

Figure 2.1 - Map showing the extent of my study area containing the 72 sampling sites.....	41
Figure 2.2 - Canonical analysis of principal coordinates ordination of the dung beetle assemblage for three different land use types.....	48
Figure 2.3 - Boxplots of the numbers (abundance, species richness and biomass) of dung beetles found within the different land use types.....	49
Figure 2.4 - Canonical analysis of principal coordinates ordination of the dung beetle assemblage for three different dung types.....	50
Figure 2.5 - Boxplots of the numbers (abundance, species richness and biomass) of dung beetles found within the different dung types.....	51
Figure 2.6: Canonical analysis of principal coordinates ordination of the dung beetle assemblage for three different biotopes.....	52
Figure 2.7: Boxplots of the numbers (abundance, species richness and biomass) of dung beetles found within the different biotopes.....	53
Figure 3.1 - Boxplots of the functional richness between different dung types, biotopes and land-use types.....	84
Figure 3.2: Boxplots of the functional dispersion between the different biotopes.....	85

Figure 3.3: Boxplots of the RaoQ between different biotopes.....85

LIST OF TABLES

Table 2.1 - Species table comprising the total abundance of individuals collected using different land use types, dung types and biotopes.....	46
Table 2.2 - Observed (Sobs) and estimated overall dung beetle species richness and species richness associated with the different environmental variables.....	47
Table 2.3 - Table showing effect of land use, dung type sheep and biotope on the abundance, species richness and biomass of dung beetles.....	54
Table 2.4 - Comparisons between assemblage compositions of dung beetles at sites that differ in land use, biotope and dung type (bait).....	55
Table 3.1 - Significance of variables (biotope, land use, and dung type) for explaining functional diversity indices (FRic—functional richness, FEve—functional evenness, FDiv—functional divergence, FDis—functional dispersion, RaoQ—Rao’s quadratic entropy (Q))...	83

ABBREVIATIONS

G: grazed areas

NG: non-grazed areas

RNG: recently non-grazed areas

P: pig dung

C: cow dung

S: sheep dung

F: flatlands

M: mountainous areas

R: riparian zones

FD: Functional diversity

FRic: functional richness

FEve: functional evenness

FDiv: functional divergence

FDis: functional dispersion

RaoQ: Rao's quadratic entropy (Q)

Chapter 1

GENERAL INTRODUCTION AND OBJECTIVES

1.1. Land-Use Change in the 21st Century

Worldwide changes to landscapes and ecosystems are driven by the need to provide basic human needs to more than six billion people (DeFries *et al.* 2004, 2007; Foley *et al.* 2005; Matson *et al.* 1997; Vitousek *et al.* 1997). Several papers have demonstrated the direct effects of land-use alteration on diverse environments worldwide (Dale *et al.* 1993; Sala *et al.* 2000; Tolba 1992). Changes in an environment often leads to biodiversity loss (Baldi and Batary 2011; Hanski 2005; Queiroz *et al.* 2014; Shackelford *et al.* 2015; Uchida and Ushimaru 2014). This decline is not isolated to particular taxonomic groups and therefore involves all biodiversity of an area (Donald *et al.* 2001; Tschamntke *et al.* 2005). Hence, there is a tremendous challenge to manage the demand of human consumption and conserve the health of our ecosystems to supply for the ever-growing human population now, as well as for future generations (Houghton 1994). Little wonder then that research on biodiversity decline due to land-use change has developed into a central issue in conservation (Billeter *et al.* 2008; Krebs *et al.* 1999; McNeely *et al.* 1995).

Land-use change is defined as human activities that either modify the way land is utilized or influences the amount of biomass in that land (Pitesky *et al.* 2009). Land-use alteration comprises of two key processes. The driving system behind land-use change is the development or reduction of an area that has changed its land cover for diverse reasons (Lambin *et al.* 2003). The other key process is the transformation of the kind of management that the remaining land cover uses (Lambin and Geist 2008). Land-use change can occur in many ways, such as urbanisation, agricultural expansion, deforestation, land abandonment, etc. (Benayas *et al.* 2007). The impacts of land-use change include soil degradation, global climate change, desertification, damage to natural environments and many more (Munroe *et al.* 2013). These impacts also lead to alterations in ecosystem functions and the capacity of

ecological structures to sustain human life on earth (Munroe *et al.* 2013; Vitousek *et al.* 1997). It is expected that by 2100 the damage done to biodiversity due to the impacts caused by land-use change will surpass the damage caused by climate change (Sala 2000; Young 2009).

Land-use change plays a huge role in ecosystems and how they function, which could cause biodiversity loss or recovery depending on how well the process is monitored and managed (Turner *et al.* 2007). The process of land-use change varies worldwide, but in many cases, agricultural boundaries are further expanded, which negatively affects natural habitats through deforestation, freshwater contamination, loss of carbon and rises in infectious disease (Verstegen *et al.* 2019). However, the expansion of agricultural boundaries also provides food security, which is a basic human need, and this apparent dichotomy needs to be managed with extreme care (Lambin and Meyfroidt 2011). In contrast to expansion, land abandonment is another form of land-use change and is created by rural exodus, and with the increase in urbanisation, these land-use changes could potentially benefit ecosystems via rehabilitation and the recovery of fauna and flora (Foley *et al.* 2005; van Vliet *et al.* 2015; Verstegen *et al.* 2019).

However, farmland abandonment, which is the opposite of agricultural expansion, often leads to further degradation of ecosystems. For example, Acha *et al.* (2015) showed how a rural exodus during tough economic times in Spain led to poor management of these areas, which severely impacted the local ecosystem. Thus, if farmland abandonment is not managed correctly, the potentially positive effects of shifting from horizontal agricultural expansion to the more vertical urban expansion would decrease against the backdrop of landscape degradation (Godinho *et al.* 2016; Turner *et al.* 2007; Wang *et al.* 2019). The sustainable organization of abandoned agricultural land entails a complete understanding of the process of abandonment, which includes the drivers and consequences of farmland abandonment, as well as the interaction between local, international, environmental and human influences (Allison and Hobbs 2006; Haines-Young 2009; Tonelli *et al.* 2018).

1.2. Effects of Land Abandonment on Ecosystems

Land abandonment is one of the more significant systems of land-use change. Land abandonment is defined as the process whereby humans abandon or release a previously controlled piece of land (e.g. agricultural or forestry land) and leave it to naturally recover over time (Diaz *et al.* 2011). Research has shown that land abandonment can disturb areas that have important ecological value and that certain farming practices should likely be sustained in these systems (Fischer *et al.* 2012). Other studies indicated that land abandonment can be positive when more natural environments are restored and their biodiversity is conserved (Chazdon 2008; Li *et al.* 2018). These two conflicting views have made land abandonment a progressive topic in worldwide debates and have attracted many researchers from different fields of study (Cramer *et al.* 2008; Gellrich and Zimmermann 2007; MacDonald *et al.* 2000; Sluiter and de Jong 2007). Therefore, abandoned land is a transformational phase, which can lead to a number of outcomes that have various, often conflicting or contradictory consequences, such as natural regeneration of an area, as well as rehabilitation and conservation or degradation of an area through increases in invasive species or desertification.

Land abandonment may have numerous negative consequences to the habitat and if not managed properly, can cause environmental destruction (Lasanta *et al.* 2015). Farming can create significantly unique biological populations and environments, which may even support more species diversity than that of pristine habitats (Li *et al.* 2018; MacDonald *et al.* 2000). When farmland abandonment occurs, organisms that are supported by these agricultural environments will decline slowly (Anthelme *et al.* 2001; Doxa *et al.* 2010; Li *et al.* 2018). Habitat degradation after land abandonment can produce decreases in species richness and a growth in abundance of more generalist species, as well as an increase in invasive plants (Scholts *et al.* 2009; Simmons and Ridsdill-Smith 2011). This will affect interspecific interactions and intraspecific social relationships and movements of individuals within the ecosystem (Plieninger *et al.* 2014; Scholts *et al.* 2009). Farmland abandonment may therefore also have negative results on the preservation of ecological systems, which include services and

functions (Munroe *et al.* 2013; Pausas 1999), such as disruptions to the nutrient cycle (Plieninger *et al.* 2014), that are not fully understood. Land abandonment can reduce the biodiversity of an area (Laiolo *et al.* 2004), due to many factors such as an increase in invasion by non-native species (Schneider and Geoghegan 2006), altered fire regimes (Benayas *et al.* 2007), changes in water availability (López-Moreno *et al.* 2008; Schneider & Geoghegan 2006; Tonelli *et al.* 2018; Zavala and Burkey 1997) and bush encroachment (Manroe *et al.* 2013). It can also have extreme negative impacts on food availability, which may greatly affect local human populations, specifically in poor regions (Khanal and Watanabe 2006). Farmland abandonment and the severe degradation of arable farmland therefore increases pressures to expand agriculture, thus forming a feedback loop (Beilin *et al.* 2014; Benayas *et al.* 2007; Lasanta *et al.* 2017; Lasanta *et al.* 2015; Plieninger *et al.* 2014; Sirami *et al.* 2008).

Agricultural land abandonment can also have benefits for the environment and local populations. These benefits include restoration and vegetation regrowth if managed properly, which will allow ecosystem services to recover, and increase in the recovery of native plants and animals (Benayas *et al.* 2007; Correia 1993; Lasanta *et al.* 2015; Munroe *et al.* 2013; Navarro and Pereira 2012). Benefits of this regeneration includes promoting biodiversity (Navarro *et al.* 2012), improved global regulation of heat and gas exchange, as well as better carbon sequestration (Houghton *et al.* 1999; Batlle-Bayer *et al.* 2010; Benayas 2007). Other benefits include increased soil infiltration rates, enhanced water-holding capacity (Bruijnzeel 2004) and decreased surface run-off, and, in doing so, decreases in soil erosion and water loss (Molinillo *et al.* 1997).

1.3. Effect of Land-Use Change and Land Abandonment on Arthropods

Many studies on the impacts of land-use change, and land abandonment in particular, have studied the effects of these disturbances on more prominent taxa such as plants and vertebrates (Blood 2006; Pauw *et al.* 2018; Pais and Varanda 2010; Plieninger *et al.* 2013; Prevosto *et al.* 2011). This is surprising, as invertebrates often play key ecological roles such as pollination and nutrient cycling, and perform many other key ecosystem functions which maintains ecosystem health (Lei *et al.* 2016). They often also be a vital link in creating create the base of food webs and support a large diversity of species at higher trophic levels, as well as occupying specialised niches (Longcore 2003; Majer and Beeston 1996; Steed *et al.* 2018). Therefore, arthropods are very important for sustaining ecosystem function and services; however, the overall understanding of their responses to human activities remains limited. Due to land-use change, including land abandonment, a reduction in arthropod species pools in agricultural landscapes worldwide over the past few decades has been documented (Sala *et al.* 2000; Uchida and Ushimaru 2015). For example, a few studies have shown a decrease in plant and herbivore insect diversity as a result of this land-use change (Kruess and Tscharntke 2002; Poyry *et al.* 2009; Uchida and Ushimaru 2014, 2015). Insects have smaller home ranges and weaker dispersal capabilities compared to vertebrates, are more effected by the isolation effect of fragmentation (Tscharntke *et al.* 2002), but yet remain overlooked all too often in studies or policies on habitat disturbance (Dunn 2004; Samways 1993). This despite that they amount to more than 50% of all living species and impact more strongly on terrestrial ecosystems than any other animal group (Kruess and Tscharntke 1994).

Arthropods are vital when it comes to ecosystem functions and processes, and arthropod loss could create cascading negative impacts all the way through the different trophic communities (Coleman and Hendrix 2000). For example, in South Africa's drylands, insects like *Apis mellifera* (honeybee) and *Messor capensis* (harvester ant) are just some of the species that perform a cardinal function in the dispersal of plants and pollination of seeds and, without these species, this already water- and heat-stressed ecosystem would be severely damaged

(Dean and Yeaton 1993). The impact of land transformation on these taxa and the ecosystems in which they abound are, however, unknown. The effects of farmland transformation on arthropod diversity are expected to be severe. For example, a recent study showed that global arthropod numbers are rapidly declining, most likely due to landscape alterations (Grubisic *et al.* 2018), which has many cascading negative effects. A study in Brazil used ants as bioindicators to assess disturbance impacts caused by mining and found that these provided reliable feedback on the effects of habitat alteration (Majer and Beeston 1996). Increases in the management intensity of grazing lands, as well as modifications to landscape structure in terms of plant heterogeneity and cover presumably decreases, caused a reduction in the overall species richness of arthropods in temperate Europe (Hendrickx *et al.* 2007).

Research conducted in other parts of the world has also investigated the increase in management intensity of agriculture and demonstrated that this is a central cause of species richness decline (Bengtsson *et al.* 2005; Dauber *et al.* 2005). It is, therefore, often the case that more traditional management systems support greater arthropod diversity than more modern systems (Marini *et al.* 2009; Pykälä 2000, Mykkestad and Setersdal 2004). This is because traditional farming practices help maintain biodiversity (Foley *et al.* 2011; Hahn and Orrock, 2015; Kleijn *et al.* 2011; Uchida and Ushimaru 2014) by conserving plant diversity, and subsequently insect diversity (Kleijn *et al.* 2011; Tscharrntke *et al.* 2005; Uchida and Ushimaru 2015; Uchida *et al.* 2016). Therefore, actions like overgrazing and other forms of active management may have many negative impacts on arthropod biodiversity, suggesting that farmland abandonment could lead to a growth in these communities (Bell *et al.* 2001, Morris 2000; Poyry *et al.* 2006; Swengel 2001). However, arthropod diversity may also decrease after land abandonment; for example, even though the numbers of a threatened butterfly species in England declined after land abandonment (Thomas 1991), whole butterfly communities benefited from advanced stages of abandonment (Balmer and Erhardt 2000).

1.4. Arthropods as Biological Indicators

Land-use change has many different outcomes and effects. To understand these completely, monitoring and management is necessary to evaluate ecosystem health and this is best done with a bioindicator (Wang *et al.* 2011; Cristescu *et al.* 2012). Bioindicators have been extensively recognized as valuable tools to observe and identify the well-being of an environment (Dufrene and Legendre 1997). Bioindicators have the potential to be used to evaluate the effect that humans have on the ecosystem, instead of monitoring the whole environment (Spellerberg 1993). Therefore, a bioindicators' reaction to changes in the environment or degree of disturbance should be a reflection of the response of many species in that ecosystem (Noss 1990; Pearson and Cassola 1992). A good bioindicator must fulfil several criteria and provide an early warning of changes: an indicator species should be a species that is well-known, sensitive to environmental changes and easy as well as cost effective to survey (Blood 2006; Cairns *et al.* 1993). The group should be widespread and abundant, with a well-resolved taxonomy, functionally important and sensitive to disturbances to the community (Scholts *et al.* 2009; Simmons and Ridsdill-Smith 2011). Generalist species are better bioindicators than more specialized species because generalist species occupy a wide distribution and demand less specific environmental characteristics (Dufrene and Legendre 1997). Arthropods are good bioindicators because they are more intensely affected by environmental disturbance than vertebrates; for example, arthropods have weaker dispersal abilities with smaller home ranges (Tscharrntke *et al.* 2002). They are also extremely diverse and occupy a wide range of microhabitats and functional niches (Kremen *et al.* 1993). In semi-arid and disturbed areas in South Africa, arthropods have been shown to be very useful as bioindicators to monitor the success of environmental change and the rehabilitation success after drastic ecosystem degradation (Kremen *et al.* 1993; Steed *et al.* 2018).

1.4.1. The Use of Dung Beetles as Bioindicators

One of the most commonly used terrestrial bioindicator taxa are dung beetles (Scarabaeidae: Scarabaeinae and Aphodiinae), as they meet all the requirements of an ideal bioindicator (Halffter and Favila 1993; McGeoch 2002; Scholtz *et al.* 2009; Shahabuddin 2005; Simmons and Ridsdill-Smith 2011; Slade 2011, 2010; Spector 2006). Dung beetles have diverse and abundant populations, which are distributed widely across the globe. For example, there are more than 5000 species worldwide and nearly 800 species found in southern Africa (Scholtz *et al.* 2009; Simmons and Ridsdill-Smith 2011). They are also easily sampled with low-cost trapping methods and their taxonomy and ecological/economic importance are well established (Spector 2006). Dung beetles play a key role in the environment, as well as being important to humans as they carry out numerous ecosystem functions and deliver many services due to dung transport and removal (Scholtz *et al.* 2009; Simmons and Ridsdill-Smith 2011; Manning *et al.* 2016; Nichols *et al.* 2008). For example, they are intricately involved with ecological processes such as secondary seed dispersal (Andresen 2001, 2002; Andresen and Feer 2005; Andresen and Levey 2004; Beynon *et al.* 2012; Shepherd and Chapman 1998), soil amelioration, soil fertility (Brown *et al.* 2010; Scholtz *et al.* 2009; Simmons and Ridsdill-Smith 2011) and, in a few cases, even pollination (Ratcliffe 1970) as well as preying on herbivore insects (Nichols *et al.* 2008). Many studies indicate a positive relationship between dung beetle diversity and an increase in vegetation growth (Bang *et al.* 2005; Lastro 2006; Scholtz *et al.* 2009), plant height (Galbiati *et al.* 1995; Scholtz *et al.* 2009; Simmons and Ridsdill-Smith 2011), and for nitrogen and protein content in the soil (Bang *et al.* 2005). Dung beetles also effectively control dung-related diseases and parasites through the removal of dung resources (Scholtz *et al.* 2009; Simmons and Ridsdill-Smith 2011; McKellar 1997).

In addition to abovementioned characteristics, dung beetles are also sensitive to various forms of ecosystem change and disturbance (Nichols *et al.* 2008). For example, grazing intensity, overgrazing and grazing abandonment are notorious in affecting dung beetle biodiversity and community structure (Lobo 2001; Nichols *et al.* 2007; Scholtz *et al.* 2009; Simmons and

Ridsdill-Smith 2011; Smith 2011; Tonelli *et al.* 2017, 2018; Verdu *et al.* 2007). Several studies show a severe impact on dung beetle biodiversity in tropical and temperate systems due to habitat change (Nicholas *et al.* 2008; Scholtz *et al.* 2009; Simmons and Ridsdill-Smith 2011). Alterations in the structure of the vegetation and fluctuations in the accessibility of dung resources greatly affect dung beetle populations (Halffter *et al.* 1992; Nichols 2007, 2008; Scholtz *et al.* 2009; Simmons and Ridsdill-Smith 2011). Even slight changes in the availability of heat and solar energy can affect the activity of adults (Chown *et al.* 2001). In addition, changes in soil parameters can affect their populations through larval development (Sowig 1995). Their sensitivity to environmental change has led to their extensive use as biological indicators in ecological impact assessments (EIA) and studies of farm health, as well as in conservation research, showing the impacts of habitat modification, habitat fragmentation and loss of mammals (Scholtz *et al.* 2009; Simmons and Ridsdill-Smith 2011). Unfortunately, numerous species are presently facing threats from land-use change in farmland practices, which include the abandonment of agricultural lands (Nichols *et al.* 2007; Kryger 2009; Scholtz *et al.* 2009; Simmons and Ridsdill-Smith 2011; Tonelli *et al.* 2017). Farmland abandonment creates a biological cascade effect that stems from the loss of trophic resources (mammals and their dung resources), and dung beetle communities could be negatively affected through this process (Nichols *et al.* 2009).

Research shows that dung beetles that depend on native wild animal faeces may struggle to sustain communities in agricultural environments, due to the fact that in these environments there are more domestic animals which create problems for dung beetles (Jay-Robert *et al.* 2008), as there are limited numbers of species that can survive on dung from domestic animals (Carpaneto *et al.* 2005). Research conducted in South Africa has shown that dung beetles occurred in higher abundance and biomass in natural habitats as opposed to disturbed habitats (Jankielsohn *et al.* 2001). This study proposed that trampling and overgrazing by cattle in the disturbed habitats has led to changes in vegetation structure and made it difficult for the larger dung beetle species to be successful competitors (Scholtz *et al.* 2009; Simmons

and Ridsdill-Smith 2011). Therefore, farmland used for grazing can affect dung beetle diversity negatively. However, in the absence of wild animals, domestic livestock may be important surrogate dung donors for dung beetles (Nichols and Gardner 2009, 2011). Papers by Jay-Robert *et al.* (2008) and Carpaneto *et al.* (2005) examined the impact of farmland abandonment on dung beetle communities, but there is still a deficiency of studies on this topic. It seems that generally, abandoned areas lose a substantial amount of the total dung beetle biomass due to diminished resources, which is why low to moderate intensity grazing is beneficial for the persistence of many species (Larsen *et al.* 2005; Nervo *et al.* 2014; Slade *et al.* 2007). Livestock like cattle and sheep, etc., are declining in certain areas, particularly in abandoned lands, and this creates a decrease in dung beetle numbers, in some cases virtually to extinction (Scholts *et al.* 2009; Simmons and Ridsdill-Smith 2011). This decrease in dung beetle numbers can cause extreme shifts in these environments, such as increased diseases and parasites, as well as soil degradation and decreased seed dispersal (Scholts *et al.* 2009; Simmons and Ridsdill-Smith 2011). The causes and consequences of land abandonment usually interact with a set of ecological (vegetation degradation), social (rural community) and economic (agricultural decline) drivers at diverse scales e.g. (Plieninger *et al.* 2014).

1.5. Arthropod Functional Diversity

The community characteristics of arthropod taxa, including species richness, abundance, biomass and composition, have been linked to ecological services and processes within their natural habitats (Beynon *et al.* 2012; Braga *et al.* 2013; Gollan *et al.* 2013; Kudavidanage *et al.* 2012; Larsen *et al.* 2005; Slade *et al.* 2007). But changes in these characteristics due to land abandonment remains understudied in South Africa. In recent years, studies have suggested that these ecological services and processes are generally dependent on the functional diversity of the populations. Functional diversity is defined by Diaz *et al.* (2007) as “the type, variety and comparative abundance of functional traits present in the populations”.

The functional traits being “any, physical, biological or behavioural factor, that can be measured”. Functional traits are typically also ones that impact on, or play a function in, an ecosystem and this makes them valuable. In terms of dung beetles, different size classes, different nesting methods, different functional traits (morphological and behavioural) can define functional diversity, but these can also include any measurable trait from the cell level to the whole-organisms level (Tonelli *et al.* 2017). Ecological studies should include functional diversity measures because these are connected to ecosystem processes, services and composition assemblage patterns (Díaz and Cabido 2001; Spasojevic and Suding 2012). Functional diversity would, therefore, greatly inform conservation planning in a given environment.

1.5.1. Using Dung Beetle Functional Diversity in Conservation Planning

A paper by Griffiths *et al.* (2015) tested dung beetle diversity and functioning in a field experiment in the Brazilian Amazon. They used experiments to establish how different soil conditions will affect seed dispersal and the biodiversity–ecosystem functioning connections of dung beetle functional diversity. These interactions were measured using functional diversity metrics, which were calculated by the measurement of dung beetle morphological traits (pronotum area, front tibia and femur area, as well as front and back leg length, pronotum height and dry biomass). This study showed that dung beetle functional diversity has an important impact on seed burial and seed dispersal across the different soil types. They promote the use of functional diversity metrics over taxonomic approaches in dung beetle-focused investigations related to seed dispersal and seed burial across different soil types.

A paper by Barragan *et al.* (2011) tested the functional diversity of copro-necrophagous beetles under multiple situations of land use in three Mexican biosphere reserves. They allocated dung beetle functional groups based on food preferences, beetle size, activity period and food relocation. They found that functional evenness and function dispersion did not differ

in comparison across fragment size or habitat types. Functional richness was poor in small forest fragments and rich in continuous forests and larger fragments. Functional diversity is thus necessary when investigating the impacts of land-use change. A paper by Edwards *et al.* (2014) used morphological and behavioural traits, which included diet preference, body size, behavioural guild, and diet breadth and diel activity to measure variation of functional diversity across a change of disturbance. Logging to a decrease in nocturnal individuals, an increased number of smaller dung beetles and a complete loss of roller species. This shows that there is a decline in functional diversity with increased disturbance. A study by Tonelli *et al.* (2017) reported the effects of progressive grazing abandonment, which is the abandonment of grazing lands in order to progress or improve human development, on dung beetle functional diversity, as well as the repercussions of grazing abandonment on dung beetle ecological processes. The authors used 24 different traits to analyse functional diversity and showed that the abandonment process acts as a filter, from well-structured rich communities in the moderate grazing areas to a decline of functional diversity mechanisms in low grazing areas due to generalist species filling the niches. Once areas were totally abandoned, habitat changes and availability of dung resources created a well-structured and functional unique community. Changes in functional diversity are clearly an important consideration in studies aiming to measure the responses of biological communities to land-use changes, yet this has not received much research attention.

1.6. The Present Study

1.6.1. Setting the Scene: The Nama Karoo Drylands in Flux

The Nama-Karoo is a semi-arid biome located in South Africa (Dean and Milton 1999; Mucina and Rutherford 2006). Limited water resources coupled with harsh temperatures produce young soils with low biomass, restricting agricultural and industrial developments both spatially and temporally. Nevertheless, this sparsely populated biome maintains a large proportion of the

meat and wool industry in South Africa (Pierce and Cowling 1997). However, during the past decade or so, the Nama-Karoo has been inundated by companies prospecting for shale gas (De Wit 2011) and uranium (Scholtz *et al.* 2006), as well as for sites for constructing and operating large solar energy farms (e.g., see Rudman *et al.* 2017). These renewable energy developments already cover 4% of the Karoo drylands and is likely to increase given the vast open skies and ample flat space to harvest solar energy. In addition to mining and energy-related developments, a large-scale technological development, the South African chapter of the Square Kilometre Array (SKA) radio astronomy observatory, has also changed the business-as-usual façade of the Nama-Karoo (Walker *et al.* 2018). Clearly, the Nama-Karoo is in flux (Walker *et al.* 2018), suggesting conservation planning must be reviewed for this historically understudied area.

1.6.2. Study Rationale

Much of the Nama-Karoo is suggested to have been over utilised for domesticated livestock farming (Roux and Vorster 1983). The result is that many of the floral components have become increasingly unpalatable woody plants (Todd and Hoffman 1999; Milton *et al.* 1994; Kraaji and Milton 2005). Regarding native fauna, an estimated mammal species richness of 38 is predicted for the Karoo biome, with an incline in richness as one moves from the drier western region to the wetter eastern region (Woodgate *et al.* 2018). This includes animals such as Jackal and Caracal, as well as smaller antelope, Aardvark and porcupine. Some authors suggest that farms in the region don't have important effects on mammal species richness but may limit the presence and abundance of especially larger predators that are actively hunted to protect livestock (Drouilly and O'Riain 2019). However, very little is known about insect diversity, given variable land uses and their effects on trophic cascades.

Dung beetles are tremendously complex arthropods and are exceptionally sensitive to ecosystem change and changes in the availability of dung resources. Therefore, many

important ecological processes could be monitored by assessing changes in their diversity (Nichols *et al.* 2008). For example, it is known that farmland abandonment impacts dung beetle conservation worldwide (Lobo *et al.* 2006; Tonelli *et al.* 2018). Thus, given that livestock grazing has become the main anthropogenic practice of many landscapes in this region, the question remains that if livestock were to be permanently removed, due to increasing land-use change, would this aid recovery or lead to localised extinction of certain fauna or flora in the area that had become adapted to their presence. Conversely, the diversity of dung beetles within the semi-arid rangelands of the Karoo are relatively poorly known and unstudied. Davis *et al.* (2008) showed that climate and soil characteristics are significant multi-scale influencers of dung beetle spatial patterns. Therefore, dung beetle assemblages are expected to be diverse across the various biotopes of the Northern Cape (Davis *et al.* 2010). However, the influence of environmental change, such as land abandonment, on their communities are also unknown in the region.

1.6.3. The SKA Radio Astronomy Observatory: Ideal for Natural Experiments

Recently, the South African Radio Astronomy Observatory (SARAO) acquired c. 130,000 hectares of land in the Bushmanland region of the Nama-Karoo biome (Walker *et al.* 2018). This area, named the Square Kilometre Array (SKA), will eventually become a formally protected area. As a protected area, the majority of commercial livestock, conservatively estimated to be around 13,000 ewes, will be removed from these dryland ecosystems (Walker *et al.* 2018). This sudden exclusion of livestock and thus grazing pressure might represent optimal conditions for landscape rehabilitation. As biodiversity continues to suffer declines due to agricultural expansion, the setting aside of land for conservation purposes is highly valued from an ecological viewpoint. On the other hand, removing a key dung-producer from the area may also impact dung beetle diversity patterns at the landscape scale, who might have become accustomed to the abundance of sheep dung in the area (Walker *et al.* 2018). The predecessor to the SKA, MeerKAT, had already removed livestock from two farms right in the

centre of their circle of properties in 2007. This core has thus been devoid of sheep and goats for >10 years. The properties subsequently bought around this core had livestock cleared approximately 1 year ago. In turn, the matrix of the SKA radio astronomy observatory remains to be intensively farmed. This makes the SKA area an ideal natural scientific experiment to study the effects of livestock release on dung beetle diversity (Walker et al. 2018). As this landscape also has marked biotope heterogeneity, it further provides for a chance to test for other ecological parameters that could also help predict dung beetle diversity—now and in the future. This biotope heterogeneity could provide scientists with variables to see how dung beetles act and move in a semi-arid area, and how they are affected by changes in the environment.

1.6.4. Study Aim and Objectives

My main aim is to determine how historical and more recent farmland (grazing by mainly sheep) abandonment affects the structure and function of dung beetle assemblages, using the natural experiment that arose due to the SKA development of the past decade in the Nama-Karoo, South Africa. My specific objectives are:

1. To understand the impacts of farmland (grazing) abandonment on dung beetle biodiversity, which includes abundance, biomass, species richness and assemblage composition.
2. To determine the influence of dung type (source animal) as a trophic resource on dung beetle biodiversity, which includes abundance, biomass, species richness and assemblage composition.
3. To understand the effects of differences in biotopes on dung beetle biodiversity (abundance, richness, biomass, and assemblage composition).
4. To determine the impacts of land abandonment on dung beetle communities from a functional perspective.

References

Acha, A., & Newing, H. S. (2015). Cork oak landscapes, promised or compromised lands? A case study of a traditional cultural landscape in Southern Spain. *Human ecology*, 43(4), 601-611.

Allison, H. E., & Hobbs, R. J. (2006). *Science and policy in natural resource management: Understanding system complexity*. Cambridge University Press.

Andresen, E. (2001). Effects of dung presence, dung amount and secondary dispersal by dung beetles on the fate of *Micropholis guyanensis* (Sapotaceae) seeds in Central Amazonia. *Journal of Tropical Ecology*, 17(1), 61-78.

Andresen, E. (2002). Dung beetles in a Central Amazonian rainforest and their ecological role as secondary seed dispersers. *Ecological Entomology*, 27(3), 257-270.

Andresen, E., & Levey, D. J. (2004). Effects of dung and seed size on secondary dispersal, seed predation, and seedling establishment of rain forest trees. *Oecologia*, 139(1), 45-54.

Andresen, E., & Feer, F. (2005). The role of dung beetles as secondary seed dispersers and their effect on plant regeneration in tropical rainforests. *Seed fate: Predation, dispersal and seedling establishment*, 331-349.

Anthelme, F., Grossi, J. L., Brun, J. J., & Didier, L. (2001). Consequences of green alder expansion on vegetation changes and arthropod communities' removal in the northern French Alps. *Forest Ecology and Management*, 145(1-2), 57-65.

Baldi, A., & Batary, P. (2011). Spatial heterogeneity and farmland birds: different perspectives in Western and Eastern Europe. *Ibis*, 153(4), 875-876.

Balmer, O., & Erhardt, A. (2000). Consequences of succession on extensively grazed grasslands for central European butterfly communities: rethinking conservation practices. *Conservation Biology*, 14(3), 746-757.

Bang, H. S., Lee, J. H., Kwon, O. S., Na, Y. E., Jang, Y. S., & Kim, W. H. (2005). Effects of paracoprid dung beetles (Coleoptera: Scarabaeidae) on the growth of pasture herbage and on the underlying soil. *Applied Soil Ecology*, 29(2), 165-171.

Barragán, F., Moreno, C. E., Escobar, F., Halffter, G., & Navarrete, D. (2011). Negative impacts of human land use on dung beetle functional diversity. *PloS One*, 6(3), e17976.

Batlle-Bayer, L., Batjes, N. H., & Bindraban, P. S. (2010). Changes in organic carbon stocks upon land use conversion in the Brazilian Cerrado: a review. *Agriculture, ecosystems & environment*, 137(1-2), 47-58.

Beilin, R., Lindborg, R., Stenseke, M., Pereira, H. M., Llausàs, A., Slätmo, E, et al. (2014). Analysing how drivers of agricultural land abandonment affect biodiversity and cultural landscapes using case studies from Scandinavia, Iberia and Oceania. *Land use policy*, 36, 60-72.

Bell, G. (2001). Neutral macroecology. *Science*, 293(5539), 2413-2418.

Benayas, J. R., Martins, A., Nicolau, J. M., & Schulz, J. J. (2007). Abandonment of agricultural land: an overview of drivers and consequences. *CAB reviews: Perspectives in agriculture, veterinary science, nutrition and natural resources*, 2(57), 1-14.

Bengtsson, J., Ahnström, J., & WEIBULL, A. C. (2005). The effects of organic agriculture on biodiversity and abundance: a meta-analysis. *Journal of Applied Ecology*, 42(2), 261-269.

Bernaldez, F. G. (1991). Ecological consequences of the abandonment of traditional land use systems in central Spain. *Options Méditerranéennes*, 15, 23-29.

Beynon, S. A., Mann, D. J., Slade, E. M., & Lewis, O. T. (2012). Species-rich dung beetle communities buffer ecosystem services in perturbed agro-ecosystems. *Journal of Applied Ecology*, 49(6), 1365-1372.

Billeter, R., Liira, J., Bailey, D., Bugter, R., Arens, P., Augenstein, et al. (2008). Indicators for biodiversity in agricultural landscapes: a pan-European study. *Journal of Applied Ecology*, 45(1), 141-150.

Blood, J. R. (2006). *Monitoring rehabilitation success on Namakwa Sands heavy minerals mining operations, Namaqualand, South Africa* (Doctoral dissertation, Stellenbosch: University of Stellenbosch).

- Borghesio, L., Luzzatto, M., & Palestrini, C. (1999). Interactions between dung, plants and the dung fauna in a heathland in northern Italy. *Pedobiologia*, 43(2), 97-109.
- Braga, R. F., Korasaki, V., Andresen, E., & Louzada, J. (2013). Dung beetle community and functions along a habitat-disturbance gradient in the Amazon: a rapid assessment of ecological functions associated to biodiversity. *PLoS One*, 8(2), e57786.
- Brown, J., Scholtz, C. H., Janeau, J. L., Grellier, S., & Podwojewski, P. (2010). Dung beetles (Coleoptera: Scarabaeidae) can improve soil hydrological properties. *Applied Soil Ecology*, 46(1), 9-16.
- Bruijnzeel, L. A. (2004). Hydrological functions of tropical forests: not seeing the soil for the trees? *Agriculture, ecosystems & environment*, 104(1), 185-228.
- Cairns, J., McCormick, P. V., & Niederlehner, B. R. (1993). A proposed framework for developing indicators of ecosystem health. *Hydrobiologia*, 263(1), 1-44.
- Chazdon, R. L. (2008). Beyond deforestation: restoring forests and ecosystem services on degraded lands. *Science*, 320(5882), 1458-1460.
- Chown, S. L., Rodrigues, A. S., Gremmen, N. J., & Gaston, K. J. (2001). World heritage status and conservation of southern ocean islands. *Conservation Biology*, 550-557.
- Correia, T. (1993). Land abandonment: changes in the land use patterns around the Mediterranean basin. *Cahiers Options Méditerranéennes*, 1(2), 97-112.
- Cramer, V. A., Hobbs, R. J., & Standish, R. J. (2008). What's new about old fields? Land abandonment and ecosystem assembly. *Trends in Ecology & Evolution*, 23(2), 104-112.
- Cristescu, R. H., Frère, C., & Banks, P. B. (2012). A review of fauna in mine rehabilitation in Australia: current state and future directions. *Biological Conservation*, 149(1), 60-72.

- Dale, V. H., O'Neill, R. V., Pedlowski, M., & Southworth, F. (1993). Causes and effects of land-use change in central Rondônia, Brazil. *Photogrammetric engineering and remote sensing*, 59(6).
- Dauber, J., Purtauf, T., Allspach, A., Frisch, J., Voigtländer, K., & Wolters, V. (2005). Local vs. landscape controls on diversity: a test using surface-dwelling soil macroinvertebrates of differing mobility. *Global Ecology and Biogeography*, 14(3), 213-221.
- Davis, A. L., Scholtz, C. H., & Deschodt, C. (2008). Multi-scale determinants of dung beetle assemblage structure across abiotic gradients of the Kalahari–Nama Karoo ecotone, South Africa. *Journal of Biogeography*, 35(8), 1465-1480.
- Davis, A. L., Scholtz, C. H., Kryger, U., Deschodt, C. M., & Strümpher, W. P. (2010). Dung beetle assemblage structure in Tswalu Kalahari Reserve: responses to a mosaic of landscape types, vegetation communities, and dung types. *Environmental Entomology*, 39(3), 811-820.
- De Wit, M. J. (2011). The great shale debate in the Karoo. *South African Journal of Science*, 107(7-8), 02-10.
- Dean, W. R. J., & Milton, S. (Eds.). (1999). *The Karoo: ecological patterns and processes*. Cambridge University Press.
- Dean, W. R. J., & Yeaton, R. I. (1993). The influence of harvester and *Messor capensis* nest-mounds on the productivity and distribution of some plant species in the southern Karoo, South Africa. *Vegetatio*, 106(1), 21-35.
- DeFries, R. S., Foley, J. A., & Asner, G. P. (2004). Land-use choices: Balancing human needs and ecosystem function. *Frontiers in Ecology and the Environment*, 2(5), 249-257.
- DeFries, R., Hansen, A., Turner, B. L., Reid, R., & Liu, J. (2007). Land-use change around protected areas: management to balance human needs and ecological function. *Ecological Applications*, 17(4), 1031-1038.

- Díaz, S., & Cabido, M. (2001). Vive la difference: plant functional diversity matters to ecosystem processes. *Trends in Ecology & Evolution*, *16*(11), 646-655.
- Díaz, S., Lavorel, S., Chapin, F. S., Tecco, P. A., Gurvich, D. E., & Grigulis, K. (2007). Functional diversity—at the crossroads between ecosystem functioning and environmental filters. *Terrestrial ecosystems in a changing world* 81-91.
- Donald, P. F., Green, R. E., & Heath, M. F. (2001). Agricultural intensification and the collapse of Europe's farmland bird populations. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *268*(1462), 25-29.
- Doxa, A., Bas, Y., Paracchini, M. L., Pointereau, P., Terres, J. M., & Jiguet, F. (2010). Low-intensity agriculture increases farmland bird abundances in France. *Journal of Applied Ecology*, *47*(6), 1348-1356.
- Drouilly, M., & O'Riain, M. J. (2019). Wildlife winners and losers of extensive small-livestock farming: a case study in the South African Karoo. *Biodiversity and Conservation*, *28*(6), 1493-1511.
- Dufrêne, M., & Legendre, P. (1997). Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs*, *67*(3), 345-366.
- Dunn, R. R. (2004). Recovery of faunal communities during tropical forest regeneration. *Conservation Biology*, *18*(2), 302-309.
- Edwards, D. P., Gilroy, J. J., Woodcock, P., Edwards, F. A., Larsen, T. H., Andrews, D. J., et al. (2014). Land-sharing versus land-sparing logging: reconciling timber extraction with biodiversity conservation. *Global Change Biology*, *20*(1), 183-191.
- Foley, J. A., DeFries, R., Asner, G. P., Barford, C., Bonan, G., Carpenter, S. R., et al. (2005). Global consequences of land use. *science*, *309*(5734), 570-574.
- Foley, J. A., Ramankutty, N., Brauman, K. A., Cassidy, E. S., Gerber, J. S., Johnston, M., et al. (2011). Solutions for a cultivated planet. *Nature*, *478*(7369), 337.

Galbiati, C., Bensi, C., Concciação, C. H. C., Florcovski, J. L., Calafiori, M. H., & Tobias, A. C. T. (1995). Estudo comparativo entre besouros do esterco *Dichotomius analypticus* (Mann, 1829). *Ecossistema*, 20, 109-118.

Gellrich, M., & Zimmermann, N. E. (2007). Investigating the regional-scale pattern of agricultural land abandonment in the Swiss mountains: a spatial statistical modelling approach. *Landscape and Urban Planning*, 79(1), 65-76.

Godinho, S., Guiomar, N., Machado, R., Santos, P., Sá-Sousa, P., Fernandes, J. P, et al. (2016). Assessment of environment, land management, and spatial variables on recent changes in montado land cover in southern Portugal. *Agroforestry Systems*, 90(1), 177-192.

Gollan, J. R., de Bruyn, L. L., Reid, N., & Wilkie, L. (2013). Monitoring the ecosystem service provided by dung beetles offers benefits over commonly used biodiversity metrics and a traditional trapping method. *Journal for Nature Conservation*, 21(3), 183-188.

Grubisic, M., van Grunsven, R. H., Kyba, C. C., Manfrin, A., & Hölker, F. (2018). Insect declines and agroecosystems: does light pollution matter?. *Annals of Applied Biology*, 173(2), 180-189.

Hahn, P. G., & Orrock, J. L. (2015). Land-use history alters contemporary insect herbivore community composition and decouples plant–herbivore relationships. *Journal of Animal Ecology*, 84(3), 745-754.

Haines-Young, R. (2009). Land use and biodiversity relationships. *Land use policy*, 26, S178-S186.

Halffter, G., Favila, M. E., & Halffter, V. (1992). A comparative study of the structure of the scarab guild in Mexican tropical rain forests and derived ecosystems. *Folia Entomológica Mexicana*, 84(13), 155.

Hanski, I. (2005). Landscape fragmentation, biodiversity loss and the societal response. *EMBO reports*, 6(5), 388-392.

Hendrickx, F., MAELFAIT, J. P., Van Wingerden, W., Schweiger, O., Speelmans, M., Aviron, S, et al. (2007). How landscape structure, land-use intensity and habitat diversity affect components of total arthropod diversity in agricultural landscapes. *Journal of Applied Ecology*, 44(2), 340-351.

Houghton, R. A. (1994). The worldwide extent of land-use change. *BioScience*, 44(5), 305-313.

Houghton, R. A., Hackler, J. L., & Lawrence, K. T. (1999). The US carbon budget: contributions from land-use change. *Science*, 285(5427), 574-578.

IUCN, 2016. The IUCN Red List of Threatened Species. Version 2016-1. <http://www.iucnredlist.org>. Downloaded on 11 August 2016.

Jankielsohn, A., Scholtz, C. H., & Louw, S. V. (2001). Effect of habitat transformation on dung beetle assemblages-a comparison between a South African nature reserve and neighboring farms. *Environmental Entomology*, 30(3), 474-483.

Jay-Robert, P., Errouissi, F., & Lumaret, J. P. (2008). Temporal coexistence of dung-dweller and soil-digger dung beetles (Coleoptera, Scarabaeoidea) in contrasting Mediterranean habitats. *Bulletin of Entomological Research*, 98(3), 303-316.

Khanal, N. R., & Watanabe, T. (2006). Abandonment of agricultural land and its consequences. *Mountain Research and Development*, 26(1), 32-41.

Kleijn, D., Rundlöf, M., Scheper, J., Smith, H. G., & Tscharntke, T. (2011). Does conservation on farmland contribute to halting the biodiversity decline?. *Trends in Ecology & Evolution*, 26(9), 474-481.

Koh, L. P., Dunn, R. R., Sodhi, N. S., Colwell, R. K., Proctor, H. C., & Smith, V. S. (2004). Species coextinctions and the biodiversity crisis. *Science*, 305(5690), 1632-1634.

- Kraaij, T., & Milton, S. J. (2006). Vegetation changes (1995–2004) in semi-arid Karoo shrubland, South Africa: effects of rainfall, wild herbivores and change in land use. *Journal of Arid Environments*, 64(1), 174-192.
- Krebs, J. R., Wilson, J. D., Bradbury, R. B., & Siriwardena, G. M. (1999). The second silent spring?. *Nature*, 400(6745), 611.
- Kremen, C., Colwell, R. K., Erwin, T. L., Murphy, D. D., Noss, R. A., & Sanjayan, M. A. (1993). Terrestrial arthropod assemblages: their use in conservation planning. *Conservation Biology*, 7(4), 796-808.
- Kruess, A., & Tscharntke, T. (1994). Habitat fragmentation, species loss, and biological control. *Science*, 264(5165), 1581-1584.
- Kruess, A., & Tscharntke, T. (2002). Grazing intensity and the diversity of grasshoppers, butterflies, and trap-nesting bees and wasps. *Conservation Biology*, 16(6), 1570-1580.
- Kryger, U. (2009). Conservation of Dung beetles. *Evolutionary biology and conservation of dung beetles. Pensoft, Sofia*, 387-480.
- Kudavidanage, E. P., Qie, L., & Lee, J. S. H. (2012). Linking biodiversity and ecosystem functioning of dung beetles in South and Southeast Asian tropical rainforests. *The Raffles Bulletin of Zoology*, 25, 141–154.
- Laiolo, P., Dondero, F., Ciliento, E., & Rolando, A. (2004). Consequences of pastoral abandonment for the structure and diversity of the alpine avifauna. *Journal of Applied Ecology*, 41(2), 294-304.
- Lambin, E. F., & Geist, H. J. (Eds.). (2008). *Land-use and land-cover change: local processes and global impacts*. Springer Science & Business Media.
- Lambin, E. F., & Meyfroidt, P. (2011). Global land-use change, economic globalization, and the looming land scarcity. *Proceedings of the National Academy of Sciences*, 108(9), 3465-3472.

- Lambin, E. F., Geist, H. J., & Lepers, E. (2003). Dynamics of land-use and land-cover change in tropical regions. *Annual review of environment and resources*, 28(1), 205-241.
- Larsen, T. H., & Forsyth, A. (2005). Trap spacing and transect design for dung beetle biodiversity studies 1. *Biotropica: The Journal of Biology and Conservation*, 37(2), 322-325.
- Lasanta, T., Arnáez, J., Pascual, N., Ruiz-Flaño, P., Errea, M. P., & Lana-Renault, N. (2017). Space–time process and drivers of land abandonment in Europe. *Catena*, 149, 810-823.
- Lasanta, T., Nadal-Romero, E., & Arnáez, J. (2015). Managing abandoned farmland to control the impact of re-vegetation on the environment. The state of the art in Europe. *Environmental Science & Policy*, 52, 99-109.
- Lastro, E. (2006). Dung beetles (Coleoptera: Scarabaeidae and Geotrupidae) in North Carolina pasture ecosystem. PhD Thesis submitted to North Carolina State University.
- Li, S., Li, X., Sun, L., Cao, G., Fischer, G., & Tramberend, S. (2018). An estimation of the extent of cropland abandonment in mountainous regions of China. *Land degradation & development*, 29(5), 1327-1342.
- Lobo, J. M., Hortal, J., & Cabrero-Sañudo, F. J. (2006). Regional and local influence of grazing activity on the diversity of a semi-arid dung beetle community. *Diversity and Distributions*, 12(1), 111-123.
- Lobo, J. M. (2001). Decline of roller dung beetle (Scarabaeinae) populations in the Iberian peninsula during the 20th century. *Biological Conservation*, 97(1), 43-50.
- Longcore, T. (2003). Terrestrial arthropods as indicators of ecological restoration success in coastal sage scrub (California, USA). *Restoration Ecology*, 11(4), 397-409.
- López-Moreno, J. I., Beniston, M., & García-Ruiz, J. M. (2008). Environmental change and water management in the Pyrenees: Facts and future perspectives for Mediterranean mountains. *Global and Planetary Change*, 61(3-4), 300-312.

- Lovegrove, B., & Siegfried, R. (1993). *The living deserts of southern Africa*. Fernwood Press.
- MacDonald, D., Crabtree, J. R., Wiesinger, G., Dax, T., Stamou, N., Fleury, P, et al. (2000). Agricultural abandonment in mountain areas of Europe: environmental consequences and policy response. *Journal of Environmental Management*, 59(1), 47-69.
- Majer, J. D., & Beeston, G. (1996). The biodiversity integrity index: an illustration using ants in Western Australia. *Conservation Biology*, 10(1), 65-73.
- Manning, P., Slade, E. M., Beynon, S. A., & Lewis, O. T. (2016). Functionally rich dung beetle assemblages are required to provide multiple ecosystem services. *Agriculture, Ecosystems & Environment*, 218, 87-94.
- Marini, L., Fontana, P., Klimek, S., Battisti, A., & Gaston, K. J. (2009). Impact of farm size and topography on plant and insect diversity of managed grasslands in the Alps. *Biological Conservation*, 142(2), 394-403.
- Matson, P. A., Parton, W. J., Power, A. G., & Swift, M. J. (1997). Agricultural intensification and ecosystem properties. *Science*, 277(5325), 504-509.
- McGeoch, M. A., Van Rensburg, B. J., & Botes, A. (2002). The verification and application of bioindicators: a case study of dung beetles in a savanna ecosystem. *Journal of Applied Ecology*, 39(4), 661-672.
- McKellar, Q. A. (1997). Ecotoxicology and residues of anthelmintic compounds. *Veterinary Parasitology*, 72(3-4), 413-435.
- McNeely, J. A. (1995). *How traditional agro-ecosystems can contribute to conserving biodiversity* (pp. 20-40). Cambridge: IUCN Publishing Unit.
- Milton, S. J., & Hoffman, M. T. (1994). The application of state-and-transition models to rangeland research and management in arid succulent and semi-arid grassy Karoo, South Africa. *African Journal of Range & Forage Science*, 11(1), 18-26.

- Molinillo, M., Lasanta, T., & García-Ruiz, J. M. (1997). Managing mountainous degraded landscapes after farmland abandonment in the Central Spanish Pyrenees. *Environmental Management*, 21(4), 587-598.
- Morris, A. V., Roberts, C. M., & Hawkins, J. P. (2000). The threatened status of groupers (Epinephelinae). *Biodiversity & Conservation*, 9(7), 919-942.
- Mucina, L., & Rutherford, M. C. (2006). *The vegetation of South Africa, Lesotho and Swaziland*. South African National Biodiversity Institute.
- Munroe, D. K., van Berkel, D. B., Verburg, P. H., & Olson, J. L. (2013). Alternative trajectories of land abandonment: causes, consequences and research challenges. *Current Opinion in Environmental Sustainability*, 5(5), 471-476.
- Myklestad, Å., & Sætersdal, M. (2004). The importance of traditional meadow management techniques for conservation of vascular plant species richness in Norway. *Biological Conservation*, 118(2), 133-139.
- Navarro, L. M., & Pereira, H. M. (2015). Rewilding abandoned landscapes in Europe. In *Rewilding European Landscapes* (pp. 3-23). Springer, Cham.
- Navarro, L. M., Proença, V., Kaplan, J. O., & Pereira, H. M. (2015). Maintaining disturbance-dependent habitats. In *Rewilding European Landscapes* (pp. 143-167). Springer, Cham.
- Navarro-Perez, M., & Tidball, K. G. (2012). Challenges of biodiversity education: A review of education strategies for biodiversity education. *International Electronic Journal of Environmental Education*, 2(1), 13-30.
- Nervo, B., Tocco, C., Caprio, E., Palestrini, C., & Rolando, A. (2014). The effects of body mass on dung removal efficiency in dung beetles. *PLoS One*, 9(9), e107699.
- Nichols, E. S., & Gardner, T. A. (2011). Dung beetles as a candidate study taxon in applied biodiversity conservation research. *Ecology and evolution of dung beetles*, 267-291.

Nichols, E., Gardner, T. A., Peres, C. A., Spector, S., & Scarabaeinae Research Network. (2009). Co-declining mammals and dung beetles: an impending ecological cascade. *Oikos*, 118(4), 481-487.

Nichols, E., Larsen, T., Spector, S., Davis, A. L., Escobar, F., Favila, M, et al. (2007). Global dung beetle response to tropical forest modification and fragmentation: a quantitative literature review and meta-analysis. *Biological Conservation*, 137(1), 1-19.

Nichols, E., Spector, S., Louzada, J., Larsen, T., Amezquita, S., Favila, M. E., & Network, T. S. R. (2008). Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. *Biological Conservation*, 141(6), 1461-1474.

Noss, R. F. (1990). Indicators for monitoring biodiversity: a hierarchical approach. *Conservation Biology*, 4(4), 355-364.

Ojima, D. S., Galvin, K. A., & Turner, B. L. (1994). The global impact of land-use change. *BioScience*, 44(5), 300-304.

Pais, M. P., & Varanda, E. M. (2010). Arthropod recolonization in the restoration of a semideciduous forest in southeastern Brazil. *Neotropical Entomology*, 39(2), 198-206.

Pausas, J. G. (1999). Response of plant functional types to changes in the fire regime in Mediterranean ecosystems: a simulation approach. *Journal of vegetation Science*, 10(5), 717-722.

Pauw, M. J., Esler, K. J., & Le Maitre, D. C. (2018). Assessing the success of experimental rehabilitation on a coastal mineral sands mine in Namaqualand, South Africa. *African Journal of Range & Forage Science*, 35(3-4), 363-373.

Pearson, D. L., & Cassola, F. (1992). World-wide species richness patterns of tiger beetles (Coleoptera: Cicindelidae): indicator taxon for biodiversity and conservation studies. *Conservation Biology*, 6(3), 376-391.

Pierce, S. M., & Cowling, R. M. (Eds.). (1997). *Vegetation of southern Africa*. Cambridge University Press.

Pitesky, M. E., Stackhouse, K. R., & Mitloehner, F. M. (2009). Clearing the air: Livestock's contribution to climate change. In *Advances in agronomy* (Vol. 103, pp. 1-40). Academic Press.

Plieninger, T., Dijks, S., Oteros-Rozas, E., & Bieling, C. (2013). Assessing, mapping, and quantifying cultural ecosystem services at community level. *Land use policy*, 33, 118-129.

Plieninger, T., Hui, C., Gaertner, M., & Huntsinger, L. (2014). The impact of land abandonment on species richness and abundance in the Mediterranean Basin: a meta-analysis. *PloS One*, 9(5), e98355.

Pöyry, J., Luoto, M., Heikkinen, R. K., Kuussaari, M., & Saarinen, K. (2009). Species traits explain recent range shifts of Finnish butterflies. *Global Change Biology*, 15(3), 732-743.

Pöyry, J., Luoto, M., Paukkunen, J., Pykälä, J., Raatikainen, K., & Kuussaari, M. (2006). Different responses of plants and herbivore insects to a gradient of vegetation height: an indicator of the vertebrate grazing intensity and successional age. *Oikos*, 115(3), 401-412.

Prévosto, B., Kuiters, L., Bernhardt-Römermann, M., Dölle, M., Schmidt, W., Hoffmann, M., ... & Klotz, S. (2011). Impacts of land abandonment on vegetation: successional pathways in European habitats. *Folia Geobotanica*, 46(4), 303-325.

Pykälä, J. (2000). Mitigating human effects on European biodiversity through traditional animal husbandry. *Conservation Biology*, 14(3), 705-712.

Queiroz, C., Beilin, R., Folke, C., & Lindborg, R. (2014). Farmland abandonment: threat or opportunity for biodiversity conservation? A global review. *Frontiers in Ecology and the Environment*, 12(5), 288-296.

Ratcliffe, B. C. (1970). Dung feeders, jeweled pollinators, and horned giants. *University of Nebraska News*, 59, 1-4.

Romero-Calcerrada, R., & Perry, G. L. (2004). The role of land abandonment in landscape dynamics in the SPA 'Encinares del río Alberche y Cofio, Central Spain, 1984–1999. *Landscape and Urban Planning*, 66(4), 217-232.

Roux, P. W., & Vorster, M. (1983). Vegetation change in the Karoo. *Proceedings of the annual congresses of the Grassland Society of Southern Africa*, 18(1), 25-29.

Rudman, J., Gauché, P., & Esler, K. J. (2017). Direct environmental impacts of solar power in two arid biomes: An initial investigation. *South African Journal of Science*, 113(11-12), 1-13.

Sala, O. E., Chapin, F. S., Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., et al. (2000). Global biodiversity scenarios for the year 2100. *Science*, 287(5459), 1770-1774.

Samways, M. J. (1993). Insects in biodiversity conservation: some perspectives and directives. *Biodiversity & Conservation*, 2(3), 258-282.

Schneider, L., & Geoghegan, J. (2006). Land abandonment in an agricultural frontier after a plant invasion: the case of bracken fern in southern Yucatán, Mexico. *Agricultural and Resource Economics Review*, 35(1), 167-177.

Scholtz, C. H., Davis, A. L. V., & Kryger, U. (2009). *Evolutionary biology and conservation of dung beetles* (pp. 1-567). Sofia-Moscow: Pensoft.

Scholtz, N., Scholtz, O. F., & Potgieter, G. P. (2006). Potential environmental impact resulting from inadequate remediation of uranium mining in the Karoo Uranium Province, South Africa. In *Uranium in the Environment* (pp. 789-799). Springer, Berlin, Heidelberg.

Shackelford, G. E., Steward, P. R., German, R. N., Sait, S. M., & Benton, T. G. (2015). Conservation planning in agricultural landscapes: hotspots of conflict between agriculture and nature. *Diversity and Distributions*, 21(3), 357-367.

Shahabuddin, G., & Kumar, R. (2005). Linkages Between Human Use of Forests and Biodiversity Indicators in Sariska Tiger Reserve, Rajasthan. In *seminar on 'Making*

Conservation Work: Attempting Solutions to Biodiversity Loss in India. Council for Social Development, March (pp. 11-12).

Shahabuddin, G., & Rao, M. (2010). Do community-conserved areas effectively conserve biological diversity? Global insights and the Indian context. *Biological Conservation*, 143(12), 2926-2936.

Shepherd, V. E., & Chapman, C. A. (1998). Dung beetles as secondary seed dispersers: impact on seed predation and germination. *Journal of Tropical Ecology*, 14(2), 199-215.

Simmons, L. W., & Ridsdill-Smith, T. J. (Eds.). (2011). *Ecology and evolution of dung beetles*. John Wiley & Sons.

Slade, E. M., Mann, D. J., & Lewis, O. T. (2011). Biodiversity and ecosystem function of tropical forest dung beetles under contrasting logging regimes. *Biological Conservation*, 144(1), 166-174.

Slade, E. M., Mann, D. J., Villanueva, J. F., & Lewis, O. T. (2007). Experimental evidence for the effects of dung beetle functional group richness and composition on ecosystem function in a tropical forest. *Journal of Animal Ecology*, 76(6), 1094-1104.

Sluiter, R., & de Jong, S. M. (2007). Spatial patterns of Mediterranean land abandonment and related land cover transitions. *Landscape Ecology*, 22(4), 559-576.

Smith, R. M., & Ward, P. D. (2001). Pattern of vertebrate extinctions across an event bed at the Permian-Triassic boundary in the Karoo Basin of South Africa. *Geology*, 29(12), 1147-1150.

Sodhi, N. S., Koh, L. P., Brook, B. W., & Ng, P. K. (2004). Southeast Asian biodiversity: an impending disaster. *Trends in Ecology & Evolution*, 19(12), 654-660.

Sowig, P. (1995). Habitat selection and offspring survival rate in three paracoprid dung beetles: the influence of soil type and soil moisture. *Ecography*, 18(2), 147-154.

Spasojevic, M. J., & Suding, K. N. (2012). Inferring community assembly mechanisms from functional diversity patterns: the importance of multiple assembly processes. *Journal of Ecology*, *100*(3), 652-661.

Spector, S. (2006). Scarabaeine dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae): an invertebrate focal taxon for biodiversity research and conservation. *The Coleopterists Bulletin*, *60*(mo5), 71-83.

Spellerberg, I. F., & Sawyer, J. W. (1993). *Biodiversity in plantation forests: Increasing levels and maintaining standards*. Centre for Environmental Science.

Steed, A., Swart, R., Pauw, M. J., & Roets, F. (2018). Response of arthropod communities to plant-community rehabilitation efforts after strip mining on the semi-arid west coast of South Africa. *African Journal of Range & Forage Science*, *35*(3-4), 375-385.

Swengel, A. B. (2001). A literature review of insect responses to fire, compared to other conservation managements of open habitat. *Biodiversity & Conservation*, *10*(7), 1141-1169.

Thomas, C. D. (1991). Habitat use and geographic ranges of butterflies from the wet lowlands of Costa Rica. *Biological Conservation*, *55*(3), 269-281.

Todd, S. W., & Hoffman, M. T. (1999). A fence-line contrast reveals effects of heavy grazing on plant diversity and community composition in Namaqualand, South Africa. *Plant Ecology*, *142*(1-2), 169-178.

Tolba, M. K. (1992). *Saving our planet: challenges and hopes*. Springer Science & Business Media.

Tonelli, M., Verdú, J. R., & Zunino, M. (2018). Effects of the progressive abandonment of grazing on dung beetle biodiversity: body size matters. *Biodiversity and Conservation*, *27*(1), 189-204.

- Tonelli, M., Verdú, J. R., & Zunino, M. E. (2017). Effects of grazing intensity and the use of veterinary medical products on dung beetle biodiversity in the sub-mountainous landscape of Central Italy. *PeerJ*, 5, e2780.
- Tscharntke, T., Klein, A. M., Kruess, A., Steffan-Dewenter, I., & Thies, C. (2005). Landscape perspectives on agricultural intensification and biodiversity–ecosystem service management. *Ecology Letters*, 8(8), 857-874.
- Tscharntke, T., Steffan-Dewenter, I., Kruess, A., & Thies, C. (2002). Characteristics of insect populations on habitat fragments: a mini review. *Ecological Research*, 17(2), 229-239.
- Turner, B. L., Lambin, E. F., & Reenberg, A. (2007). The emergence of land change science for global environmental change and sustainability. *Proceedings of the National Academy of Sciences*, 104(52), 20666-20671.
- Uchida, K., & Ushimaru, A. (2014). Biodiversity declines due to abandonment and intensification of agricultural lands: patterns and mechanisms. *Ecological Monographs*, 84(4), 637-658.
- Uchida, K., & Ushimaru, A. (2015). Land abandonment and intensification diminish spatial and temporal β -diversity of grassland plants and herbivorous insects within paddy terraces. *Journal of Applied Ecology*, 52(4), 1033-1043.
- Uchida, K., Takahashi, S., Shinohara, T., & Ushimaru, A. (2016). Threatened herbivorous insects maintained by long-term traditional management practices in semi-natural grasslands. *Agriculture, Ecosystems & Environment*, 221, 156-162.
- van Vliet, J., de Groot, H. L., Rietveld, P., & Verburg, P. H. (2015). Manifestations and underlying drivers of agricultural land-use change in Europe. *Landscape and Urban Planning*, 133, 24-36.

Verdú, J. R., Moreno, C. E., Sánchez-Rojas, G., Numa, C., Galante, E., & Halffter, G. (2007). Grazing promotes dung beetle diversity in the xeric landscape of a Mexican Biosphere Reserve. *Biological Conservation*, 140(3-4), 308-317.

Verstegen, J. A., van der Laan, C., Dekker, S. C., Faaij, A. P., & Santos, M. J. (2019). Recent and projected impacts of land use and land cover changes on carbon stocks and biodiversity in East Kalimantan, Indonesia. *Ecological Indicators*, 103, 563-575.

Vitousek, P. M., Aber, J. D., Howarth, R. W., Likens, G. E., Matson, P. A., Schindler, D. W., ... & Tilman, D. G. (1997). Human alteration of the global nitrogen cycle: sources and consequences. *Ecological Applications*, 7(3), 737-750.

Vitousek, P. M., Mooney, H. A., Lubchenco, J., & Melillo, J. M. (1997). Human domination of Earth's ecosystems. *Science*, 277(5325), 494-499.

Wang, J., Li, Z., Hu, X., Wang, J., Wang, D., & Qin, P. (2011). The ecological potential of a restored abandoned quarry ecosystem in Mt. Mufu, Nanjing, China. *Ecological Engineering*, 37(6), 833-841.

Wang, C., Siriwardana, M., & Meng, S. (2019). Effects of the Chinese arable land fallow system and land-use change on agricultural production and on the economy. *Economic Modelling*, 79, 186-197.

Woodgate, Z., Distiller, G., & O'Riain, J. (2018). Variation in mammal species richness and relative abundance in the Karoo. *African Journal of Range & Forage Science*, 35(3-4), 325-334.

Young, K. R. (2009). Andean land use and biodiversity: humanized landscapes in a time of change. *Annals of the Missouri Botanical Garden*, 492-507.

Zavala, M. A., & Burkey, T. V. (1997). Application of ecological models to landscape planning: the case of the Mediterranean basin. *Landscape and Urban planning*, 38(3-4), 213-227.

Chapter 2

CEASING LIVESTOCK GRAZING POSITIVELY AFFECTS DUNG BEETLE DIVERSITY IN A DRYLAND ECOSYSTEM

2.1 Abstract

Farmland abandonment may have a wide range of impacts on local biodiversity. Positive effects can stem from natural regeneration of previously well-maintained ecosystems, or from good post-abandonment management practices. However, when abandoned rangelands were severely degraded due to poor management, this abandonment can lead to increased pressure on biodiversity and ecosystem health. This may be especially relevant in arid regions where overexploited land, for example through extensive livestock grazing, may take decades to recover. Here, I used dung beetles as bioindicators of land-use change to assess the effect of land abandonment on biodiversity in the semi-arid Nama-Karoo of South Africa. Dung beetles were sampled using baited pitfall traps on farms that were abandoned ten years ago (>10 years), on recently abandoned farms (ca. 1 year ago) and on active farms. Since these areas have never been studied before, I firstly hypothesised that dung beetle diversity, biomass and assemblage composition would differ between different Karoo landscape features (hills, flatlands and ephemeral riparian zones). Then, I tested whether the removal of livestock would have a damaging impact on dung beetle diversity, due to resource dependencies in the absence of prolific native meso-herbivores. Flatlands and ephemeral riparian systems generally had higher dung beetle richness, abundance and biomass compared to the rockier hills, and each had a unique assemblage composition. Contrary to my expectations, dung beetle richness and abundance was generally higher in abandoned areas, likely due to greater dependence of the beetles on native omnivore and non-pelleted ruminant dung than on drier pelleted domestic sheep dung. Despite this, dung beetle biomass was still high at actively grazed sites and recently non-grazed sites compared to non-grazed sites, indicating that relatively large dung beetle species can become locally rare after

farmland abandonment. I conclude that land abandonment in this semi-arid ecosystem can improve conditions for numerous dung beetle species and their associated ecosystem functions, as a result of decreased pressures on native animals on abandoned farms. I advocate the reintroduction of native meso-herbivores, especially wildebeest (*Connochaetes taurinus*), to ameliorate diminished dung resources in these abandoned landscapes, which will promote dung beetle diversity and ecological function.

Key words: biodiversity conservation, land-use change, Nama-Karoo, SKA, South Africa

2.2 Introduction

Farmland abandonment usually occurs on less profitable land, which can be due to changes in global markets or local mismanagement of resources (Gellrich and Zimmermann 2007). However, it may also follow much needed developments to sustain growing human populations (Baumann *et al.* 2011; Benayas 2007; Hatna and Bakker 2011; Hartter *et al.* 2010; MacDonald *et al.* 2000; Radel and Schmook 2008). A more recent African example is the abandonment of large areas of rangelands in the semi-arid Nama-Karoo region of South Africa for the development of the Square Kilometre Array (SKA) project. The SKA will eventually form part of the world's largest radio telescope, greatly promoting global scientific collaborative work on the African continent (Taylor 2012). Despite this, the impacts of farmland abandonment associated with its development on native biota and ecosystem functions are unknown. For example, a conservative estimate would be that ca. 13,000 ewes will no longer be grazing the ca. 130,000 ha of land necessary for the SKA development, and this after centuries of farming activity (Taylor 2012).

The short- and long-term outcomes for native biodiversity on abandoned rangelands can be quite unpredictable and depend on the pre-abandonment level of use and on post-abandonment management practices (Munroe *et al.* 2013). In many cases, conditions for native biota can improve, with subsequent increases in local biodiversity (Chazdon 2008; Li and Li 2017). However, when abandoned land is incorrectly managed, the negative impacts on native biota can become severe (Scholtz *et al.* 2009; Lasanta *et al.* 2015; Simmons and Ridsdill-Smith 2011). This is due to a wide variety of influences, which includes increases in populations of invasive species after release from their management (Schneider and Geoghegan 2006), altered fire regimes (Benayas *et al.* 2007), reductions in water availability (López-Moreno *et al.* 2008; Schneider and Geoghegan 2006; Tonelli *et al.* 2018; Zavala and Burkey 1997), and increased bush encroachment (Munroe *et al.* 2013). Therefore, land abandonment not only affects biodiversity, but also changes how an ecosystem functions

(Sala *et al.* 2000). Proper management and monitoring of abandoned land is therefore extremely important (Munroe *et al.* 2013).

Pressures on natural resources in arid and semi-arid regions are often unsustainably high (Ludwig *et al.* 1999; Twine *et al.* 2003). These areas are therefore often overexploited for resources such as fodder for livestock grazing, with devastating consequences for native biodiversity (Darkoh 2003; McCown *et al.* 1979; Williams 1998). The recovery of plant communities after degradation in these regions can often take decades (Allen *et al.* 1995; Aronson *et al.* 1993; Suding *et al.* 2004). However, when arid and semi-arid rangelands are well managed, recovery of vegetation and its associated biota can be much quicker (Pauw *et al.* 2018; Steed *et al.* 2018; Verdoodt *et al.* 2010). Land abandonment of rangelands in arid and semi-arid regions may therefore have positive effects on native biota (Benayas *et al.* 2007; Correia 1993; Munroe *et al.* 2013), but abandonment of properly managed rangelands may also have negative impacts on biota that were dependent on actions provided during farming (MacDonald *et al.* 2000; Li and Li 2017). For example, the removal of meso-herbivore livestock, such as sheep and cattle, can alter grazing regimes from more natural levels with cascading effects on other biota (Charles 2018; Vavra *et al.* 2007). The exclusion of livestock in the absence of replacement with native meso-herbivores also has direct implications for other organisms dependent on the resources that they provided. This includes dung resources needed for sustaining dung-associated biota such as dung beetles. Indirect effects include the release of pressure on populations of native herbivores and release of control of larger predators that used to prey on livestock, with cascading effects on their associated biota and their functions (Berger *et al.* 2001; Bruno and Cardinal 2008).

A prominent example of a taxon that is directly associated with herbivorous vertebrates is the dung beetles. Most dung beetle species rely strongly on dung resources for sustaining their populations, which make them good indicators of changes in vertebrate populations (Nichols and Gardner 2011). In fact, dung beetles are considered an excellent bioindicator of various forms of environmental change, such as in disturbance ecology (Braga *et al.* 2013; Halffter

and Arellano, 2002; McGeoch *et al.* 2002) and landscape ecology (Halffter and Favila 1993; Numa *et al.* 2009; Spector 2006; Verdú *et al.* 2011), as they possess all the necessary characteristics (Saleh *et al.* 2014). These characteristics include their high diversity (Audino *et al.* 2014), their sensitivity to environmental gradients (Blood 2006; Viegas *et al.* 2014) and their ease of sampling (Gardner *et al.* 2008; Nichols *et al.* 2007; Spector 2006). They are also directly responsible for many fundamental ecosystem processes, such as parasite and pest control, secondary seed dispersal, nutrient cycling and vegetation development, also in often resource-limited semi-arid regions (Nichols *et al.* 2008). Regardless of their important role in the environment, many dung beetle species are presently facing pressures stemming from land transformation, such as the abandonment of grazing areas (Carpaneto *et al.* 2005; Jay-Robert *et al.* 2008; Verdú *et al.* 2000; Tonelli *et al.* 2017). Yet, this has not been studied in semi-arid ecosystems in Africa.

Different dung beetle species have preferences towards the dung of different vertebrate groups. For example, many species are preferentially attracted to the dung from ruminants, such as cattle and buffalo, non-ruminants, such as horse and zebra, or omnivores, such as pigs and warthogs (Simmons and Ridsdill-Smith 2011). Therefore, replacing diverse groups of wild vertebrates with more homogenous populations of livestock, such as sheep, could negatively impact species that are adapted to other dung types (Beynon 2012; Simmons and Ridsdill-Smith 2011; Tonelli 2019). In contrast, species adapted to the use of this plentiful non-native resource will increase in numbers (Simmons and Ridsdill-Smith 2011; Tonelli 2019). This will ultimately lead to shifts in assemblage composition and in functional roles (Simmons and Ridsdill-Smith 2011).

In addition to vertebrate identity and densities, the occurrence and movement of dung beetles are also affected by numerous environmental influences such as soil type, vegetation cover, temperature regimes and rainfall (Barkhouse and Ridsdill-Smith 1986). The interactions between dung beetles, vertebrates and these environmental factors can be complex (Roslin and Koivunen, 2001). The outcome of these interactions is that different landscape elements

often house different communities of dung beetles (Edwards *et al.* 2014). In the case of the semi-arid karoo ecosystems, the most prominent landscape features are usually valleys or flatlands, hills or mountain slopes, and riparian systems dominated by dry riverbeds (Dean and Milton 1999). As vegetation, moisture, soil and other characteristics differ between these landscape features, affecting vertebrate movements and numbers, cascading effects are expected to reach the dung beetle assemblages (Dean and Milton 1999; Simmons and Ridsdill-Smith 2011). This remains to be assessed in African semi-arid systems.

The semi-arid rangelands of the Nama Karoo in South Africa are severely understudied and large areas remain completely devoid of data on any biota (see, e.g., the SANBI Karoo BioGaps Project at <https://www.sanbi.org/karoo-biogaps-project>). Furthermore, very little information is available on the dung beetle taxa, their distribution and the factors that influence their assemblages (Simmons and Ridsdill-Smith 2011). Consequently, not much is known about the outcome that an environmental change such as farmland abandonment will have on dung beetle communities. Therefore, the main aims of the current study were to increase our present knowledge on the diversity and distribution of dung beetle species in the Nama-Karoo biome, to determine how their assemblages are influenced by different landscape features in this semi-arid landscape, and define the effects that land abandonment due to a large-scale change in land use would have on their numbers, biomass and assemblage structure. I predicted that 1) dung beetle richness, abundance, biomass and assemblages will differ between different landscape features (biotopes) and 2) the removal of livestock will have harmful impacts on dung beetle richness and abundance, and will change their assemblage composition due to resource dependencies.

2.3 Materials and Methods

2.3.1 Study Area

The Northern Cape Province of South Africa is dominated by the semi-arid Nama Karoo biome, a dryland ecosystem naturally poor in plant diversity and cover (Mucina and Rutherford 2006). Landscapes typically consist of a mosaic of flat sandy or stony plains, shale and dolerite hills (koppies), as well as dry (ephemeral) riverbeds. Precipitation is extremely seasonal, and rainfall occurs between December and March and ranging between 100 mm to 500 mm (Palmer and Hoffman 1997). Rainfall decreases from east to west and from north to south (Palmer and Hoffman 1997). Native meso-herbivores in the area historically included large migrating herds of wildebeest (*Connochaetes taurinus*), blesbok (*Damaliscus dorcas*), quagga (*Equus quagga*), eland (*Taurotragus oryx*) and springbok (*Antidorcas marsupialis*) (Lovegrove and Siegfried 1993), providing an array of dung types (pelleted or not) and dung consistencies (moister vs. dry). But these, and many other animals, have largely been replaced by farming with domestic sheep, providing a more homogenous dung type (small, dry pellets), with only scattered farming of cattle. However, low numbers of native meso-herbivore species, such as kudu (*Tragelaphus strepsiceros*), as well as smaller mammals, such as porcupine (*Erethizon dorsatum*), grey duiker (*Sylvicapra grimmia*) and steenbok (*Raphicerus campestris*), remain present on farms (see Woodgate *et al.* 2018; Michelle Blanckenberg, *pers. comm.*). In addition, farms still have numerous smaller omnivores present, such as various mongoose species, honey badger (*Mellivor capensis*) and baboon (*Papio ursinus*), as well as carnivores, such as jackal (*Canis mesomelas*) and caracal (*Caracal caracal*), although the latter two species are often hunted to protect livestock. Dung beetle assemblages that remain in the region are therefore expected to rely heavily on dung provided by the most dominant domestic grazers—sheep.

The SKA (Square Kilometre Array) radio astronomy observatory will be the world's largest radio telescope, and will eventually occupy vast areas (>130,000 ha) in the Nama-Karoo, ca.

90 km northeast from the small town of Carnarvon. To fulfil radio-silence and other regulatory and safety requirements, large areas surrounding the radio telescopes have been bought and the livestock subsequently removed. In fact, farmland abandonment in the core of the SKA area has already begun in 2007 with the acquisition of land for building the infrastructure and telescopes for the SKA predecessor, MeerKAT. The remainder of the land necessary to complete the project was acquired more recently, in 2017, and subsequently abandoned by farmers and other land users. The area therefore comprises a mosaic of land use practices, the core of which was abandoned by livestock farming more than 10 years ago, surrounded by recently abandoned farms (one year abandoned) and, in the latter's matrix, land still used for livestock farming (Fig. 2.1).



Figure 2.1: Map showing the extent of my study area containing the 72 sampling sites (the minimum distance between traps was 1 kilmoeter). These sampling sites straddle the different biotopes (R = riverbed, M = mountainous or hilly, and F = flat plains) and the different land abandonment criteria (core area in red = not grazed by livestock for more than 10 years (NG);

area in purple = recently not grazed land (RNG); and the remaining sites comprise farms still actively grazed by livestock (G), particularly sheep).

2.3.2 Sampling Design and Dung Beetle Collection

The highest local diversity of dung beetles is usually encountered after precipitation and declines as surface circumstances become drier and warmer (Pienaar 2002). However, different dung beetle species are active during different seasons of the year and, for more complete sampling, effort should be staggered throughout the year. Therefore, sampling was repeated twice, first during spring (August–September 2018) and thereafter during winter (June 2019). It has to be mentioned that the region has experienced an ongoing drought for the past couple of years. Although the rainfall in 2018 was average, rainfall was below average during the preceding years. Three different levels of land abandonment were selected within the study area, including areas currently grazed by livestock, areas recently abandoned (ca. 1 year prior to first sampling) and areas abandoned a long time ago (10 years or longer before the first sampling). Within each of these different land use areas, 24 study plots were selected, each separated by at least 1 km to reduce the effect of pseudo replication. These 24 plots consisted of eight sites in each of the three different predominant biotopes for each land use type. The three biotopes included plains/flatlands, rocky hills (where all plots were placed on the cooler and wetter southern slopes) and in dry riverbeds.

At each plot, four pitfall traps were placed in a line with at least 100 m separation to minimize trap interference (Larsen and Forsyth 2005). This form of baited pitfall trapping is a basic trapping method to deliver quantifiable data for dung beetles across many ecological gradients (Davis *et al.* 2008). Traps consisted of plastic cups with opening of 5.7 cm and depth of 9.0 cm that were buried to the rim and level with the soil surface (Pryke *et al.* 2016). Each trap per plot was baited with a different bait source as different taxa are attracted to different sources, which can give an indication of functional diversity in the ecosystem (Davis *et al.* 2008). Baits included pig dung (omnivore), cow dung (moist pats), sheep dung (pellets) and rotten chicken livers (carrion) (Davis *et al.* 2010). Bait balls consisted of ca. 150 g of dung or carrion, which were acquired from single sources, and then thoroughly mixed before being made into bait balls to create consistency in volatiles which were then placed into a breathable material

bag. These were frozen to kill pathogens and placed onto traps while frozen to ensure freshness and consistency in dung volatiles, between different sampling days. Baits were suspended over the pitfall traps using wire (Pryke *et al.* 2016).

Traps were half filled with soapy water to capture beetles and left operational for 24 hours. All individuals collected were frozen, separated into different species, counted and assigned to one of three functional guilds (tunnelers, dwellers and rollers, and depending on nesting category as paracoprid, endocoprid or telocoprid, respectively). Species were identified using a taxonomic key provided for testing purposes (Deschodt, unpublished) by an expert and five randomly dried individuals of each species (where available, otherwise all individuals) were weighed to obtain mean dry mass per species, which was used to calculate the mean dry mass of the individuals collected in each trap. A reference collection of all species is housed in the Stellenbosch University Entomological Collection, Stellenbosch, South Africa.

2.3.3 Statistical Analyses

Due to the rotten chicken livers (carryon) not attracting any dung beetle species in either sampling season, we removed this bait type from statistical analyses. Two non-parametric species estimators (Chao2 and Jackknife2) were calculated to assess sampling coverage for overall assemblages and those separated by land use, dung type and biotope (Colwell and Coddington 1994). These indices were calculated using PRIMER 6 (PRIMER-E, Plymouth, UK, 2008).

Before analyses, all data sets were first tested for normality using a Shapiro–Wilks test in R version 3.0.1 (R Development Core Team 2015). Dung beetle abundance and species richness best fitted a Poisson distribution by a Laplace approximation (Bolker *et al.* 2009) and biomass best fitted a negative binomial distribution because the data was over dispersed count data. The influence of land use, dung type and biotope (as fixed effects) on dung beetle species richness, abundance, and biomass for overall assemblages and for assemblages

consisting of the rollers, tunnelers and dwellers were tested using generalized linear mixed-effect models (GLMMs), using the positions of sites, which were in clusters, as a spatial random variable (sites were in clusters) (Fig. 2.1) in the lme4 package (Bates *et al.* 2014; Braga *et al.* 2013) in R (R Core Team 2018). Due to this clustering, I separated sites into four different clusters and used these four different clusters as spatial variables: Cluster A—these grazed sites situated outside of the SKA site on privately owned land; Cluster B—sites situated just north of the SKA core; Cluster C—non-grazed sites situated in the SKA core; and D—sites situated south of the SKA core. All three biotopes were found at each site. Best fit models were determined with a stepwise forward selection method based on AIC values using the AICcmodavg package (Mazerolle and Mazerolle 2017) in R (R Core Team 2018). Significant main effects were further separated using conservative Tukey post-hoc tests in R, which allows for multiple comparisons between means and that generates p-values for these comparisons.

To determine the effect of the environmental variables on dung beetle assemblage composition, I used 9999 permutations of permutational multivariate analyses of variance (PERMANOVA; Anderson 2001) on Bray–Curtis similarity matrices constructed from square-root-transformed abundance data (to reduce the effect of common species) in PRIMER 6 (2009 by PREMIER Biosoft International). This was done separately for land use, dung type and biotope and visualized with the use of CAP analyses in PRIMER 6. Significant groupings based on PERMANOVA were further analysed using post-hoc pairwise tests in PRIMER.

2.4 Results

A total of 2584 dung beetle individuals, comprising fifteen species, were sampled (Table 2.1). Species estimates for dung beetles neared observed species richness (Chao2 = 17.00 ± 3.74 ; second-order Jackknife = 17.99) (Table 2.2). Some 601 dung beetle individuals were collected in grazed areas representing twelve species, 899 dung beetle individuals were collected in

non-grazed areas consisting of thirteen species, and 1084 dung beetle individuals were collected in recently non-grazed areas representing thirteen species. There were 1205 dung beetle individuals collected using pig dung, 1322 dung beetle individuals collected using cow dung and 57 dung beetle individuals collected using sheep dung (Table 2.1). There were 1275 dung beetle individuals collected in the flatlands, 429 dung beetle individuals collected in the mountainous areas and 880 dung beetle individuals collected in the riparian zones (Table 2.1). There were six roller species, five dweller species and four tunneller species. Observed overall species richness was greatest at recently non-grazed and non-grazed sites (Table 2.2). Observed and estimated overall species richness was greatest using the pig dung bait (Table 2.2). Cow dung collected the second highest observed and estimated number of species. Sheep bait collected much lower observed and estimated number of species in comparison to the other dung types. Observed and estimated overall species richness was greatest within the flatland biotope (Table 2.2). Riparian zones had the second highest observed and estimated dung beetle species richness. Mountainous areas had the lowest observed and estimated species richness in comparison to the other biotopes (Table 2.2).

Table 2.1: Species table comprising the total abundance of individuals collected using different land use types (G—grazed, NG—non-grazed, RNG—recently non-grazed), different dung types (P—pig, C—cow, and S—sheep) and from different biotopes (F—flatlands, M—mountainous areas, and R—riparian zones)

Species	Abundance	Land use			Dung type			Biotope			Guild
		G	NG	RNG	P	C	S	F	M	R	
<i>Aphodinae</i> sp.1	2	0	1	1	1	1	0	1	0	1	Dweller
<i>Aphodinae</i> sp.2	406	96	131	179	125	279	3	242	50	114	Dweller
<i>Aphodinae</i> sp.3	84	38	20	26	58	23	0	16	33	35	Dweller
<i>Aphodinae</i> sp.4	160	27	110	23	55	105	43	54	59	47	Dweller
<i>Cheironitis scabrosus</i>	54	7	32	15	19	35	0	23	10	21	Tunneller
<i>Epirinus aeneus</i>	1177	122	533	522	550	584	0	479	202	496	Roller
<i>Euoniticellus intermedius</i>	1	1	0	0	1	0	0	1	0	0	Tunneller
<i>Escarabaeus satyrus</i>	48	9	23	16	33	15	2	33	3	12	Roller
<i>Euonthophagus vicarius</i>	5	1	0	4	5	0	0	5	0	0	Tunneller
<i>Onitis confusus</i>	1	0	1	0	1	0	0	0	1	0	Tunneller
<i>Onthophagus cf. fugitivus</i>	191	16	20	155	115	76	0	51	65	75	Dweller
<i>Scarabaeus busuto</i>	4	0	2	2	3	1	4	3	0	1	Roller
<i>Scarabaeolus damarensis</i>	16	4	6	6	6	10	0	14	1	1	Roller
<i>Scarabaeolus karrooensis</i>	102	32	9	61	38	60	0	87	1	14	Roller
<i>Scarabaeus viator</i>	333	248	11	74	195	133	5	266	4	63	Roller
Total:	2584	601	899	1084	1205	1322	57	1275	429	880	

Table 2.2: Observed (Sobs) and estimated overall dung beetle species richness and species richness associated with the different environmental variables. Values in parentheses are the SE.

	Sobs	Chao2(SE)	Jackknife2
Overall	15	17.00 (3.74)	17.99
Land use			
Recently non-grazed	13	13.25 (0.73)	15.96
Non-grazed	13	15.00 (3.74)	15.94
Grazed	12	12.00 (2.86)	15.92
Dung type (bait)			
Pig	15	15 (5.83)	20.88
Cow	12	13 (3.08)	18.88
Sheep	5	9.5 (7.19)	9.92
Biotope			
Flatlands	14	15 (5.77)	20.87
Riparian zone	12	12 (2.64)	17.88
Mountainous areas	11	15.5 (7.19)	15.92

2.4.1 The Effect of Land Use on Dung Beetle Assemblages

Overall dung beetle abundance and richness was lowest at the currently grazed sites (Table 2.3, Fig. 2.3). Recently non-grazed and non-grazed sites had similar richness and abundance of dung beetles. This was similar for most functional guilds except for the richness of tunnellers and rollers that were unaffected by differences in land use. Dweller species richness was higher at recently non-grazed and non-grazed sites. In contrast to abundance and richness, overall dung beetle biomass was the highest at grazed and recently non-grazed sites, with non-grazed sites carrying a significantly lower biomass. This did, however, not extend to the different guilds as all had similar biomass between the three land use types (Table 2.3, Fig. 2.3). In terms of assemblage composition, dung beetle assemblages differed between all three land use types (Table 2.4, Fig. 2.2). Dung beetle assemblages from non-grazed and recently non-grazed areas were, however, slightly more similar than either were to those on grazed sites (Fig. 2.3).

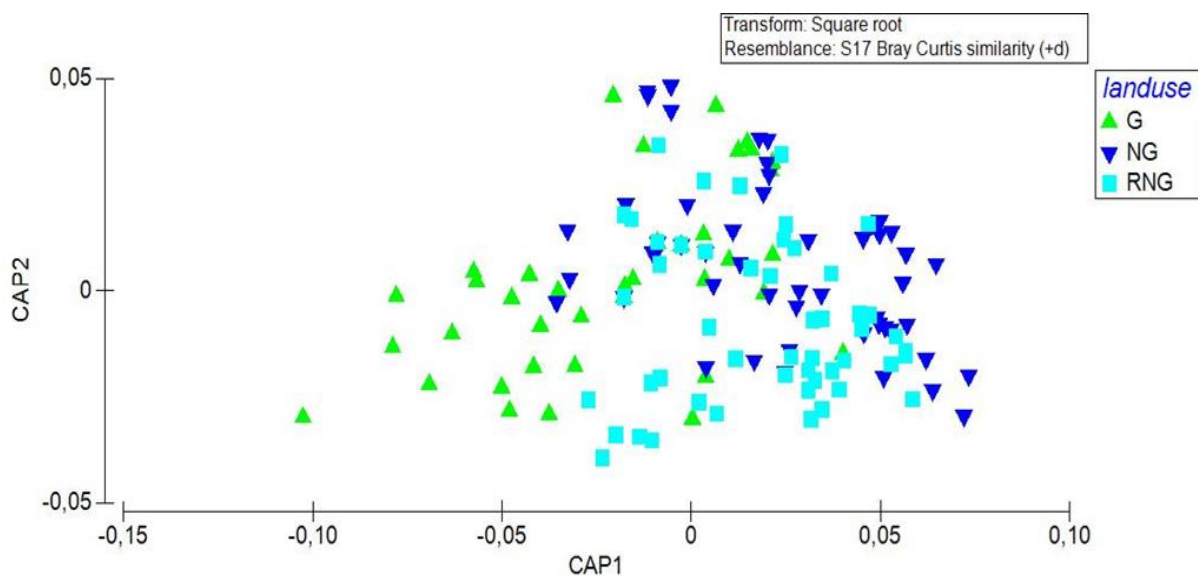


Figure 2.2: Canonical analysis of principal coordinates (CAP) ordination of the dung beetle assemblage for three different land use types (G—grazed, NG—non-grazed, and RNG—recently non-grazed).

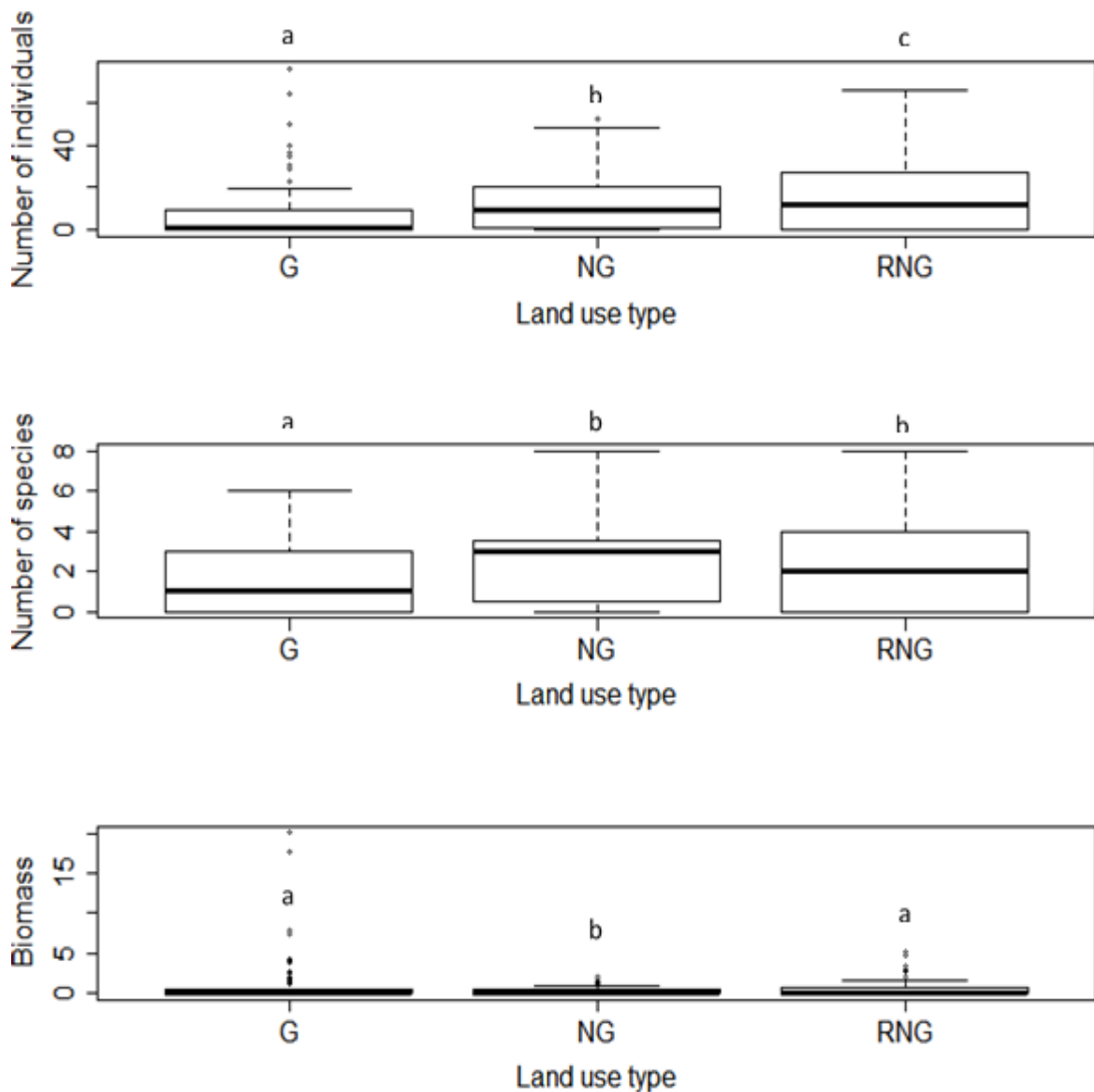


Figure 2.3: Boxplots of the numbers (abundance, species richness and biomass) of dung beetles found within the different land use types (G—grazed, RNG—recently non-grazed and NG—non-grazed). Different letters above bars indicate significant differences ($p < 0.05$). Box indicates 25–75% data range, whiskers indicate 1.5 times the interquartile range, dots represent outliers.

2.4.2 The Effect of Dung Type on Dung Beetle Assemblages

Sheep dung always attracted fewer dung beetle species and numbers of individuals as well as for the different guilds (Table 2.3, Fig. 2.5). Cow dung and pig dung attracted similar number of species and individuals collected overall, and for the different guilds. The biomass of dung beetles collected using the different baits showed a similar pattern for beetles overall and for the roller guild (Table 2.3, Fig. 2.5). The biomass of other guilds did not differ according to the different dung types. Community assemblage composition of dung beetles did not differ between those collected using pig dung and those collected using cow dung (Table 2.4, Fig. 2.4). Sheep dung collected a unique dung beetle assemblage, different from that collected by both the pig and the cow dung.

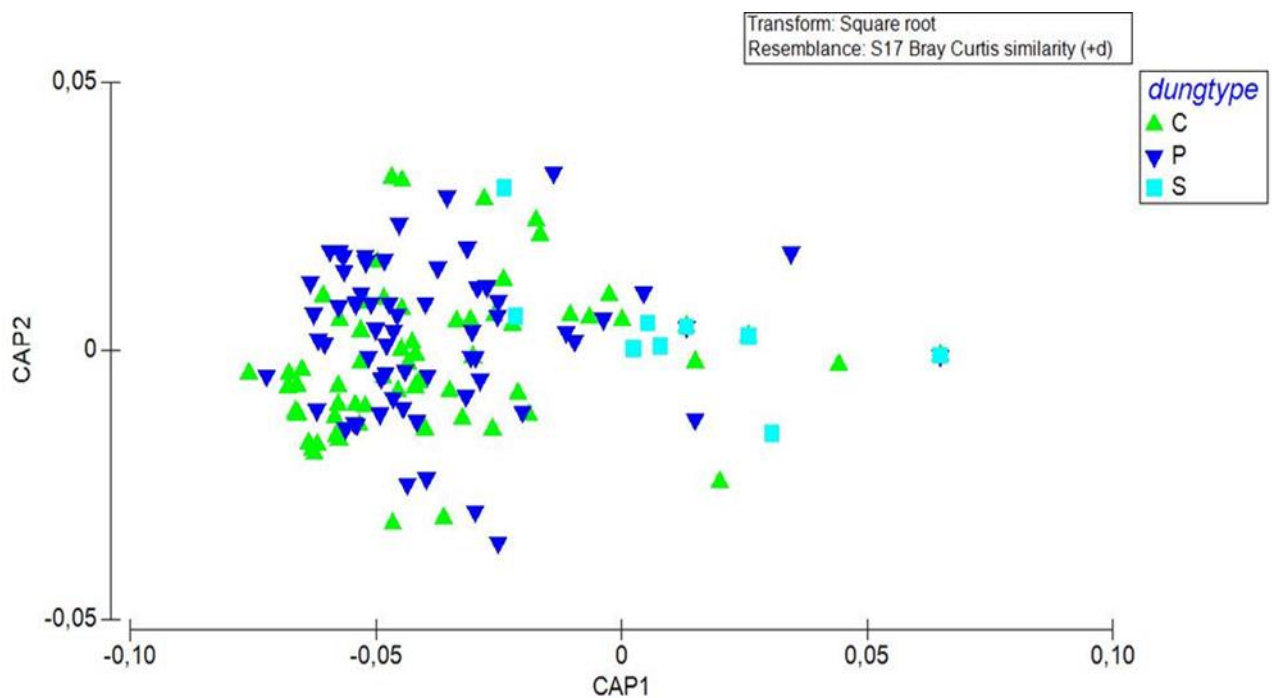


Figure 2.4: Canonical analysis of principal coordinates ordination of the dung beetle assemblage for three different dung types (C—cow dung, P—pig dung, S—sheep dung).

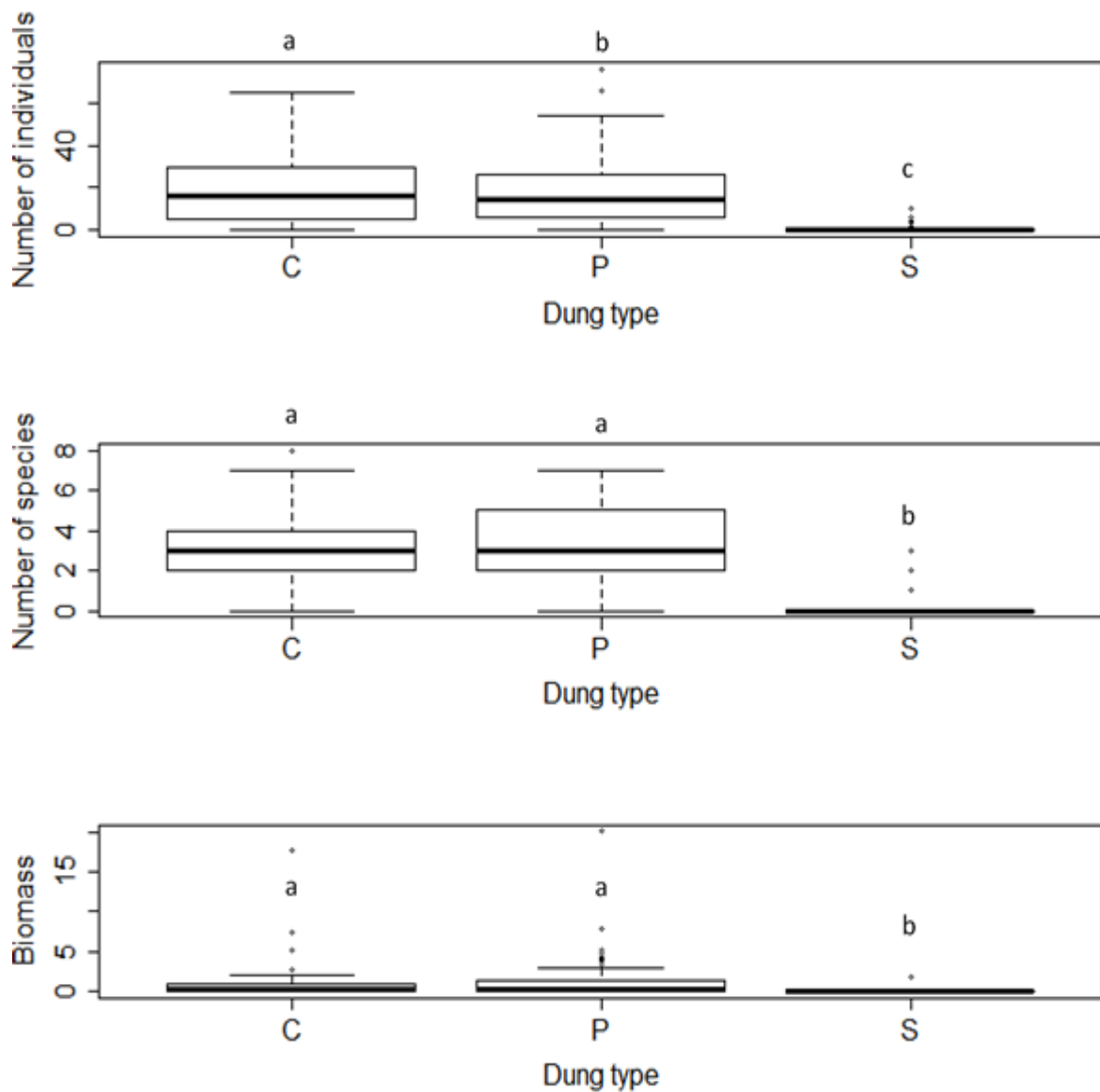


Figure 2.5: Boxplots of the average numbers (abundance, species richness and biomass) of dung beetles found overall using the different dung types (C—cow dung, P—pig dung, S—sheep dung). Different letters above bars indicate significant differences ($p < 0.05$). Box indicates 25–75% data range, whiskers indicate 1.5 times the interquartile range, dots represent outliers.

2.4.3 The Effect of Biotope on Dung Beetle Assemblages

Flatlands always had the highest dung beetle species richness, abundance and biomass, although not always significantly so for the tunneller and dweller groups (Table 2.3, Fig. 2.7). The overall abundance of dung beetles collected, as well as those from different guilds, were second highest in the riparian sites, and these were significantly higher than the abundance of dung beetles collected in mountainous sites. This was similar for overall dung beetle biomass. However, these patterns were not reflected in the richness of the dung beetles collected (overall and for the different guilds) from the different biotopes, or from data on the biomass of beetles of the different guilds, as riparian sites and those in mountainous areas did not differ significantly (Table 2.3, Fig. 2.7). For community assemblage composition, flatlands had a unique assemblage, different to both mountainous and riparian biotopes (Table 2.4, Fig. 2.6). Mountainous and riparian biotopes were statistically similar to one another in terms of dung beetle assemblage composition (Fig. 2.6).

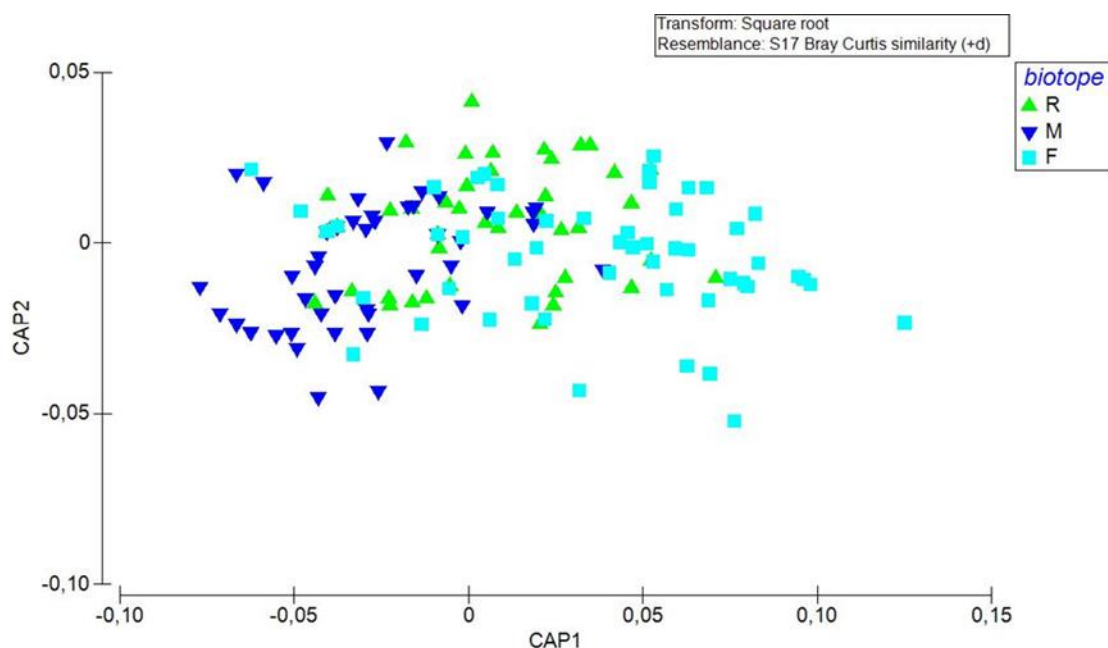


Figure 2.6: Canonical analysis of principal coordinates ordination of the dung beetle assemblage for three different biotopes (R—riparian zones, M—mountainous areas, F—flatlands).

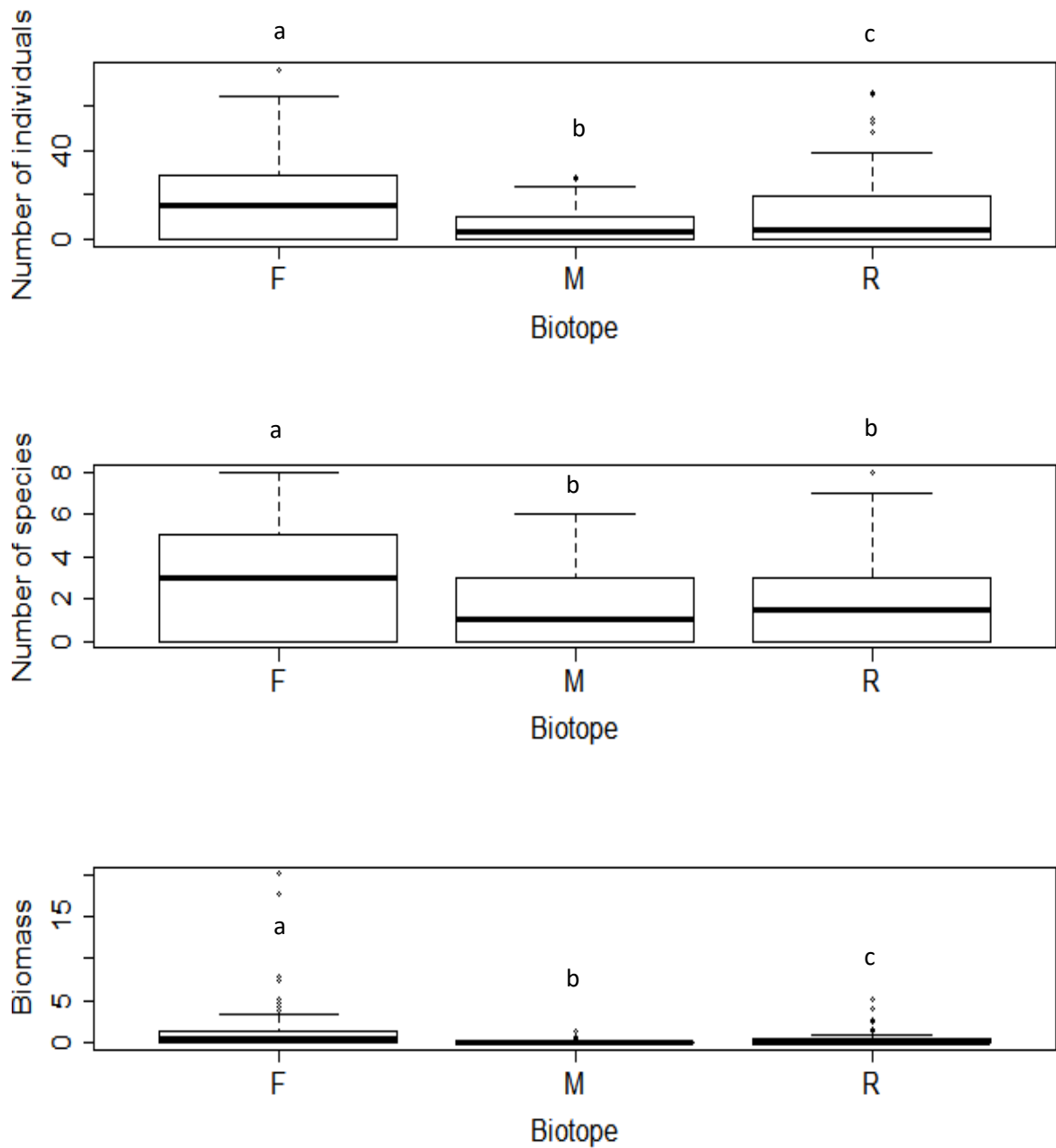


Figure 2.7: Boxplots of the numbers (abundance, species richness and biomass) of dung beetles found within the different biotopes (R—riparian zones, M—mountainous areas, F—flatlands). Different letters above bars indicate significant differences ($p < 0.05$). Box indicates 25–75% data range, whiskers indicate 1.5 times the interquartile range, dots represent outliers.

Table 2.3: Table showing the effect of land use (NG—non-grazed, RNG—recently non-grazed, G—grazed), dung type (bait; P—pig, C—cow, and S—sheep) and biotope (F—flatlands, M—mountainous areas, and R—riparian zones) on the abundance, species richness and biomass of dung beetles (** $p < 0.01$, * $p < 0.05$), (NA—data deficient).

	Abundance		Species Richness		Biomass	
	χ^2	Pairwise	χ^2	Pairwise	χ^2	Pairwise
Land use						
Overall	148.46 ***	NG=RNG>G	15.022 ***	NG=RNG>G	6.2832 *	G=RNG>NG
Roller	75.19 ***	NG=RNG>G	2.0516	G=NG=RNG	6.658 *	G=NG=RNG
Tunneller	8.4999 *	NG=RNG≥G	3.3053	G=NG=RNG	0.4729	G=NG=RNG
Dweller	69.012 ***	RNG>NG>G	19.182 ***	NG=RNG>G	0.5402	G=NG=RNG
Dung type						
Overall	1786.6 ***	C>P>S	248.57 ***	C=P>S	64.928 ***	C=P>S
Roller	1132.7 ***	C=P>S	106.28 ***	C=P>S	61.09 ***	C=P>S
Tunneller	(NA)	C=P>S	(NA)	C=P>S	1.3234	C=P=S
Dweller	627.08 ***	C>P>S	122.38 ***	C=P>S	2.1309	C=P=S
Biotope						
Overall	434.71 ***	F>R>M	36.746 ***	F>M=R	60.516 ***	F>R>M
Roller	430.89 ***	F>R>M	45.18 ***	F>M=R	61.172 ***	F>R=M
Tunneller	7.5072 *	F=R>M	2.7184	F=M=R	0.1749	F=M=R
Dweller	49.463 ***	F>R>M	1.934	F=M=R	0.0387	F=M=R

Table 2.4: Comparisons between community assemblage composition of dung beetles at sites that differ in land use, biotope and dung type (bait) and including the interactions between them (***p* < 0.05).

Diversity Index	df	Pseudo-F	Pairwise
Land use	2	10.561 ***	all different
Dung type	2	62.54 ***	P=C≠S
Biotope	2	9.1765 ***	F≠R=M
Dung type x Land use	4	2.5813 ***	
Dung type x Biotope	4	3.1145 ***	
Land use x Biotope	4	2.2622 ***	
Dung type x land use x biotope	8	0.9984	

2.5 Discussion

In the present study, I set out to examine the influence of land-use change and biotope type on dung beetle assemblages in the semi-arid Nama-Karoo region of South Africa. I found a fairly low number of species and these were found at low abundances in this region. Only 15 species were collected here in an extensive area and over multiple seasons. Low arthropod diversity is, however, not unusual for semi-arid regions like this in South Africa and abroad (Dean and Milton 1999; Liberal *et al.* 2011). Indeed, the relatively low species richness recorded here can be linked to the current drought conditions in the region, as species richness is known to decline over time after precipitation (Davis 1996; Davis *et al.* 2010). This, and other studies, show that maintaining a mosaic of different landscape features is important for maintaining dung beetle diversity in this region, as different landscape features can differ

in their dung beetle assemblage composition. Moreover, and contrary to expectations, dung beetle richness and abundance were generally significantly higher in areas where commercial livestock activities are no longer practiced (non-grazed and recently non-grazed, largely sheep). Farmland abandonment therefore has a net positive effect on dung beetle communities in the region.

2.5.1. Land-use change and dung beetle diversity

There are multiple reasons for increased dung beetle diversity after land abandonment, although my data suggest a major reason might be that very few dung beetle species are actually attracted to the dry, pelleted sheep dung—the main dung resource on active farms, where stocking rates are typically one adult ewe per 8–10 ha. Indeed, here the highest numbers of species and individuals were attracted to cow and pig (omnivore) dung, both of which are non-pelleted and wetter in consistency. Reductions in sheep grazing will therefore not negatively influence dung beetle diversity, most likely due to greater dependence of the beetles on omnivore and other ruminant dung types. Although not measured here, increases in availability are likely to result in increased abundance (Liberal et al. 2011). Large native herbivores like eland and kudu, which have non-pelleted dung, are still largely excluded in non-grazed areas, but the availability of dung resources from carnivores (e.g., jackal and caracal) and omnivores (e.g., baboons) are likely higher due to decreased pressures on their populations in non-grazed areas. Therefore, patterns of increased dung beetle diversity in abandoned farmland in this region seems to be driven by increased resource availability due to decreased pressures on native vertebrates (Liberal et al. 2011).

My results differ from Liberal *et al.* (2011), which focussed on how habitat change and rainfall affect dung beetle diversity in Caatinga, a Brazilian semi-arid ecosystem. They found that dung beetle communities in undisturbed areas (no tree cutting or livestock grazing) were species poor in comparison to those in the actively used, disturbed areas (cattle and corn

farming). Lobo *et al.* (2006) also analysed the impact of resource accessibility (i.e., sheep dung) on dung beetle communities in an arid region of central Spain. They propose that grazing intensity and the growth in trophic resources is a vital influence in defining native differences in the diversity and composition of dung beetle assemblages. They stated that the abandonment of traditional pastoral systems, ending grazing, and the increase of livestock fed with imported products, are causing decreases in the diversity of dung beetle assemblages. A study by Verdu *et al.* (2007) stated that grazing encourages dung beetle diversity in the arid regions of a Mexican biosphere reserve. Their outcomes specify that livestock grazing sustains a diverse land mosaic, and these ranges maintain more diverse dung beetle assemblages than the homogenous zones of closed, shrubby vegetation. They suggest that livestock grazing could positively benefit the conservation of dung beetle biodiversity and increase ecosystem functioning by preserving dung decomposition rates. In turn, dung produced by newly introduced livestock, mainly cattle, horses and goats, increased dung beetle diversity in Mexico because they were capable of exploiting this exotic resource (Favila 2014). Because I found greater dung beetle diversity associated with abandoned sites (suggesting that abandonment of sheep grazing in particular improved the conservation of dung beetle assemblages) dung quality and not quantity is most likely key to disentangle these contrasting patterns.

This greater dung beetle diversity found at the abandoned sites could be due to the large-scale removal of sheep in particular, possibly leading to a more continuous supply of more appropriate dung forms (native dung) for the dung beetles. Indeed, sheep dung was by far the least attractive dung form. Reductions in dung beetle diversity on farms can be due to a reduction in the quality of the dung resource on farms, as well as modifications to the habitat structure, which include the erection of fences, over grazing and use of veterinary products (Tonelli *et al.* 2017). Individuals found in previously grazed sites were able to maintain viable populations, despite the perception that the area has scarce resources due to sudden sheep removal. Thus, they are most likely consuming other dung types, such as kudu, aardvark,

jackal, rabbits, etc., mammals known to frequent the SKA area (Woodgate *et al.* 2018). And although these animals could also occur on actively managed farms, many are likely to avoid them, especially jackal and other meso-predators, which are actively hunted by land users as they prey on the livestock. Increased dung provision from allowing a diversity of native mammals to return would therefore increase the population maintenance of species diversity when traditional sheep grazing vanishes.

2.5.2. Biotope diversity begets dung beetle diversity

Dung beetles are influenced by several environmental characteristics, including, elevation, and vegetation structure as well as, soil type and moisture (Carpaneto *et al.* 2005; Davis 1996, 2000; Davis *et al.* 2010; Doube 1983; Halffter and Matthews 1966; Jay-Robert *et al.* 2008; Kanda *et al.* 2005; Mocogna 2009). I tested different biotopes in this study, all of which differ with regard to vegetation cover and edaphic conditions. The existence of unique communities associated with the different biotopes were thus not unexpected. Here, Flatlands had the highest number of dung beetle individuals, species and biomass. These plains are the areas that are most intensively grazed by livestock, followed by riverbeds. Following extensive land-use change, carnivores move towards mountainous environments due to the alteration of appropriate habitat for farming and human occupation in the lower areas of their landscape (Grey *et al.* 2013). This could be a reason for low dung beetle numbers in the mountainous areas; native herbivores possibly avoid the mountains due to high risk of predators, leading to less dung resources. Another possible reason for low dung beetle individuals and species numbers in the mountainous areas could be because these dolerite hills are rocky and hard to dig for the dung beetles, which would prefer the softer, less rocky soils of the flat lands and riparian zones (Dean and Milton 1999).

2.5.3. Single large or several small? A look at dung beetle biomass

Despite generally low richness and abundance of dung beetles at sites that are still grazed, dung beetle biomass was still high at grazed sites, indicating that relatively larger dung beetle species can become locally rare after land abandonment (Tonelli *et al.* 2018). Large-sized dung beetle numbers are being artificially inflated in grazed landscapes, with relapse to smaller species in "more natural" systems. I suppose this is contingent on how well sheep dung approximates the resource niche provided by the larger herbivores in the landscape before European extirpation. This could be because larger dung beetles need more dung resource for feeding, as well as for nesting and reproduction (Taco 2013). Once sheep are removed, dung beetle species with smaller biomass increased in numbers, because they need less dung resources to survive and reproduce, which make them more opportunistic and less vulnerable when there is a change in quality and quantity of dung resource (Nichols *et al.* 2007; Tonelli *et al.* 2017). Reduction in average size will affect the functional roles that the dung beetle community performs, as there is a strong correlation between body size and dung burial (Doube *et al.* 1988; Larsen *et al.* 2005; Nervo *et al.* 2014; Slade *et al.* 2007).

Relatively larger species, such as *Scarabaeus viator* and *Scarabaeolus karrooensis*, were still common in the grazed areas in the present study. They were highly attracted to the cow dung, which could mean that they currently have a source of such ruminant dung on the farm or that they settle for sheep dung when it is the only available resource. Indeed, a few of these larger species were also attracted to sheep dung. Therefore, in order to maintain larger dung beetle species, and their associated ecological functions, numbers of native herbivores providing an array of dung types should be increased in abandoned farmland areas. Ideal candidates for reintroductions at the sites evaluated in the present study include wildebeest (*Connochaetes taurinus*), blesbok (*Damaliscus dorcas*), eland (*Taurotragus oryx*) and springbok (*Antidorcas marsupialis*) (Lovegrove and Siegfried 1993). Not only will these increase the availability of key dung resources for dung beetles, but they will also increase the resources for carnivorous and omnivorous mammals, creating a positive feedback loop between vertebrate functions

and dung beetle functions in this sensitive ecosystem (Estrada *et al.* 1998, Feer and Hingrat 2005, Nichols *et al.* 2009). Areas with more available trophic energy can also maintain more individuals, which creates an ecosystem that can sustain higher population sizes as well as enhance species richness and decrease extinction rates (Evans *et al.* 2005; Lumaret *et al.* 1992).

2.6. Conclusion

This present analysis highlighted that ceasing sheep farming has had an overall positive effect on dung beetle diversity within this semi-arid landscape, arguably linked to decreasing pressure on native animals that provide a dung type more preferred to dung beetles. Thus, dung beetle abundance, diversity and ecological function would benefit, and be maintained spatially and temporally, should native animals be conserved or even reintroduced into these abandoned areas. Nonetheless, there were fewer large dung beetles found at the non-grazed sites, since these heavier beetles have different ecological functions and need more dung resources to survive as well as to reproduce. In order to attract and maintain large dung beetle numbers at these abandoned sites, the reintroduction of native animals (in line with the carrying capacity the area can sustain) would indeed promote a comprehensive dung beetle conservation plan for these drylands. Finally, biotope diversity begets dung beetle diversity, which has implications for future studies on and monitoring protocols for this group. Indeed, a heterogeneous landscape (Pryke *et al.* 2013), in addition to a diversity of native dung producers, will increase dung beetle diversity and hence their and other species' conservation in the Nama Karoo.

References

- Allen, E. B., Roundy, B. A., McArthur, E. D., Haley, J. S., & Man, D. K. (1995). Restoration ecology: limits and possibilities in arid and semiarid lands. In *Proceedings of the Wildland Shrub and Arid Land Restoration Symposium, Roundy, BA; McArthur, ED* (pp. 7-15).
- Anderson, M. J. (2001). A new method for non-parametric multivariate analysis of variance. *Austral Ecology*, 26(1), 32-46.
- Aronson, J., Floret, C., Le Floc'h, E., Ovalle, C., & Pontanier, R. (1993). Restoration and rehabilitation of degraded ecosystems in arid and semi-arid lands. I. A view from the south. *Restoration Ecology*, 1(1), 8-17.
- Audino, L. D., Louzada, J., & Comita, L. (2014). Dung beetles as indicators of tropical forest restoration success: Is it possible to recover species and functional diversity? *Biological Conservation*, 169, 248-257.
- Barkhouse, J., & Ridsdill-Smith, T. J. (1986). Effect of soil moisture on brood ball production by *Onthophagus binodis* Thunberg and *Euoniticellus intermedius* (Reiche)(Coleoptera: Scarabaeinae). *Australian Journal of Entomology*, 25(1), 75-78.
- Bates, D., Maechler, M., Bolker, B., & Walker, S. (2014). lme4: Linear mixed-effects models using Eigen and S4. *R package version*, 1(7), 1-23.
- Baumann, M., Kuemmerle, T., Elbakidze, M., Ozdogan, M., Radeloff, V. C., Keuler, N. S., et al. (2011). Patterns and drivers of post-socialist farmland abandonment in Western Ukraine. *Land Use Policy*, 28(3), 552-562.
- Benayas, J. R., Martins, A., Nicolau, J. M., & Schulz, J. J. (2007). Abandonment of agricultural land: an overview of drivers and consequences. *CAB reviews: Perspectives in agriculture, veterinary science, nutrition and natural resources*, 2(57), 1-14.

- Berger, J., Stacey, P. B., Bellis, L., & Johnson, M. P. (2001). A mammalian predator–prey imbalance: grizzly bear and wolf extinction affect avian neotropical migrants. *Ecological Applications*, 11(4), 947-960.
- Blood, J. R. (2006). *Monitoring rehabilitation success on Namakwa Sands heavy minerals mining operations, Namaqualand, South Africa* (Doctoral dissertation, Stellenbosch: University of Stellenbosch).
- Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., & White, J. S. S. (2009). Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution*, 24(3), 127-135.
- Braga, R. F., Korasaki, V., Andresen, E., & Louzada, J. (2013). Dung beetle community and functions along a habitat-disturbance gradient in the Amazon: a rapid assessment of ecological functions associated to biodiversity. *PLoS One*, 8(2), e57786.
- Bruno, J. F., & Cardinale, B. J. (2008). Cascading effects of predator richness. *Frontiers in Ecology and the Environment*, 6(10), 539-546.
- Carpaneto, G. M., Mazziotta, A., & Piattella, E. (2005). Changes in food resources and conservation of scarab beetles: from sheep to dog dung in a green urban area of Rome (Coleoptera, Scarabaeoidea). *Biological Conservation*, 123(4), 547-556.
- Charles, G. (2018). *Herbivore-mediated Trophic Cascades in an East African Savanna*. University of California, Davis.
- Chazdon, R. L. (2008). Beyond deforestation: restoring forests and ecosystem services on degraded lands. *Science*, 320(5882), 1458-1460.
- Colwell, R. K., & Coddington, J. A. (1994). Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 345(1311), 101-118.

- Correia, T. (1993). Land abandonment: changes in the land use patterns around the Mediterranean basin. *Cahiers Options Méditerranéennes*, 1(2), 97-112.
- Darkoh, M. B. K. (2003). Regional perspectives on agriculture and biodiversity in the drylands of Africa. *Journal of Arid Environments*, 54(2), 261-279.
- Davis, A. L., Scholtz, C. H., & Swemmer, A. M. (2012). Effects of land usage on dung beetle assemblage structure: Kruger National Park versus adjacent farmland in South Africa. *Journal of Insect Conservation*, 16(3), 399-411.
- Davis, A. J., Holloway, J. D., Huijbregts, H., Krikken, J., Kirk-Spriggs, A. H., & Sutton, S. L. (2001). Dung beetles as indicators of change in the forests of northern Borneo. *Journal of Applied Ecology*, 38(3), 593-616.
- Davis, A. L. V. (1996). Habitat associations in a South African, summer rainfall, dung beetle community (Coleoptera: Scarabaeidae, Aphodiidae, Staphylinidae, Histeridae, Hydrophilidae). *Pedobiologia*, 40(3), 260-280.
- Davis, A. L., Scholtz, C. H., & Deschodt, C. (2008). Multi-scale determinants of dung beetle assemblage structure across abiotic gradients of the Kalahari–Nama Karoo ecotone, South Africa. *Journal of Biogeography*, 35(8), 1465-1480.
- Davis, A. L., Scholtz, C. H., Kryger, U., Deschodt, C. M., & Strümpher, W. P. (2010). Dung beetle assemblage structure in Tswalu Kalahari Reserve: responses to a mosaic of landscape types, vegetation communities, and dung types. *Environmental Entomology*, 39(3), 811-820.
- Dean, W. R. J., & Milton, S. (Eds.). (1999). *The Karoo: ecological patterns and processes*. Cambridge University Press.
- Doube, B. M., Giller, P. S., & CSIRO, F. M. (1988). Dung burial strategies in some South African coprine and onitine dung beetles (Scarabaeidae: Scarabaeinae). *Ecological Entomology*, 13(3), 251-261.

- Doube, B. M. (1983). The habitat preference of some bovine dung beetles (Coleoptera: Scarabaeidae) in Hluhluwe Game Reserve, South Africa. *Bulletin of Entomological Research*, 73(3), 357-371.
- Edwards, F. A., Edwards, D. P., Larsen, T. H., Hsu, W. W., Benedick, S., Chung, A., et al. (2014). Does logging and forest conversion to oil palm agriculture alter functional diversity in a biodiversity hotspot? *Animal Conservation*, 17(2), 163-173.
- Estrada, A., Coates-Estrada, R., Dadda, A. A., & Cammarano, P. (1998). Dung and carrion beetles in tropical rain forest fragments and agricultural habitats at Los Tuxtlas, Mexico. *Journal of Tropical Ecology*, 14(5), 577-593.
- Evans, K. L., Warren, P. H., & Gaston, K. J. (2005). Species–energy relationships at the macroecological scale: a review of the mechanisms. *Biological Reviews*, 80(1), 1-25.
- Favila, M. E. (2014). Historical, biogeographical and ecological factors explain the success of some native dung beetles after the introduction of cattle in Mexico. *Pastos*, 42(2), 161-181.
- Feer, F., & Hingrat, Y. (2005). Effects of forest fragmentation on a dung beetle community in French Guiana. *Conservation Biology*, 19(4), 1103-1112.
- Gardner, T. A., Hernández, M. I., Barlow, J., & Peres, C. A. (2008). Understanding the biodiversity consequences of habitat change: the value of secondary and plantation forests for neotropical dung beetles. *Journal of Applied Ecology*, 45(3), 883-893.
- Gellrich, M., & Zimmermann, N. E. (2007). Investigating the regional-scale pattern of agricultural land abandonment in the Swiss mountains: a spatial statistical modelling approach. *Landscape and Urban Planning*, 79(1), 65-76.
- Grey, J. N. C., Kent, V. T., & Hill, R. A. (2013). Evidence of a high density population of harvested leopards in a montane environment. *PloS One*, 8(12), e82832.
- Halffter, G., & Mathews, E. G. (1966). Folia Entomologica Mexicana. *The natural history of dung beetles of the sub family Scarabaeinae (Coleoptera, Scarabaeidae)*, 12, 1-132.

Halffter, G., & Arellano, L. (2002). Response of Dung Beetle Diversity to Human-induced Changes in a Tropical Landscape 1. *Biotropica*, 34(1), 144-154.

Halffter, G. (1993). The Scarabaeinae (Insecta: Coleoptera) an animal group for analyzing, inventorying and monitoring biodiversity in tropical rainforest and modified landscapes. *Biology International*, 27, 15-21.

Hartter, J. (2010). Resource use and ecosystem services in a forest park landscape. *Society and Natural Resources*, 23(3), 207-223.

Hatna, E., & Bakker, M. M. (2011). Abandonment and expansion of arable land in Europe. *Ecosystems*, 14(5), 720-731.

Jay-Robert, P., Niogret, J., Errouissi, F., Labarussias, M., Paoletti, É., Luis, M. V., & Lumaret, J. P. (2008). Relative efficiency of extensive grazing vs. wild ungulates management for dung beetle conservation in a heterogeneous landscape from Southern Europe (Scarabaeinae, Aphodiinae, Geotrupinae). *Biological Conservation*, 141(11), 2879-2887.

Kanda, N., Yokota, T., Shibata, E. I., & Sato, H. (2005). Diversity of dung-beetle community in declining Japanese subalpine forest caused by an increasing sika deer population. *Ecological Research*, 20(2), 135-141.

Larsen, T. H., & Forsyth, A. (2005). Trap spacing and transect design for dung beetle biodiversity studies 1. *Biotropica: The Journal of Biology and Conservation*, 37(2), 322-325.

Larsen, T. H., Williams, N. M., & Kremen, C. (2005). Extinction order and altered community structure rapidly disrupt ecosystem functioning. *Ecology Letters*, 8(5), 538-547.

Li, S., & Li, X. (2017). Global understanding of farmland abandonment: A review and prospects. *Journal of Geographical Sciences*, 27(9), 1123-1150.

Liberal, C. N., de Farias, Â. M. I., Meiado, M. V., Filgueiras, B. K., & Iannuzzi, L. (2011). How habitat change and rainfall affect dung beetle diversity in Caatinga, a Brazilian semi-arid ecosystem. *Journal of Insect Science*, 11(1), 114.

- Lobo, J. M. (2001). Decline of roller dung beetle (Scarabaeinae) populations in the Iberian peninsula during the 20th century. *Biological Conservation*, 97(1), 43-50.
- Lobo, J. M., Hortal, J., & Cabrero-Sañudo, F. J. (2006). Regional and local influence of grazing activity on the diversity of a semi-arid dung beetle community. *Diversity and Distributions*, 12(1), 111-123.
- López-Moreno, J. I., Beniston, M., & García-Ruiz, J. M. (2008). Environmental change and water management in the Pyrenees: Facts and future perspectives for Mediterranean mountains. *Global and Planetary Change*, 61(3-4), 300-312.
- Lovegrove, B., & Siegfried, R. (1993). *The living deserts of southern Africa*. Fernwood Press.
- Ludwig, J. A., Tongway, D. J., & Marsden, S. G. (1999). Stripes, strands or stipples: modelling the influence of three landscape banding patterns on resource capture and productivity in semi-arid woodlands, Australia. *Catena*, 37(1-2), 257-273.
- Lumaret, J. P., Kadiri, N., & Bertrand, M. (1992). Changes in resources: consequences for the dynamics of dung beetle communities. *Journal of Applied Ecology*, 29(2), 349-356.
- MacDonald, D., Crabtree, J. R., Wiesinger, G., Dax, T., Stamou, N., Fleury, P., et al. (2000). Agricultural abandonment in mountain areas of Europe: environmental consequences and policy response. *Journal of Environmental Management*, 59(1), 47-69.
- McCown, R. L., Haaland, G., & de Haan, C. (1979). The interaction between cultivation and livestock production in semi-arid Africa. In *Agriculture in semi-arid environments* (pp. 297-332). Springer, Berlin, Heidelberg.
- McGeoch, M. A., Van Rensburg, B. J., & Botes, A. (2002). The verification and application of bioindicators: a case study of dung beetles in a savanna ecosystem. *Journal of Applied Ecology*, 39(4), 661-672.

- Mucina, L., Rutherford, M. C., Palmer, A. R., Milton, S. J., Scott, L., Lloyd, J. W., et al. (2006). Nama-Karoo Biome. *The vegetation of South Africa, Lesotho and Swaziland. Strelitzia*, 19, 324-47.
- Munroe, D. K., van Berkel, D. B., Verburg, P. H., & Olson, J. L. (2013). Alternative trajectories of land abandonment: causes, consequences and research challenges. *Current Opinion in Environmental Sustainability*, 5(5), 471-476.
- Nervo, B., Tocco, C., Caprio, E., Palestrini, C., & Rolando, A. (2014). The effects of body mass on dung removal efficiency in dung beetles. *PLoS One*, 9(9), e107699.
- Nichols, E. S., & Gardner, T. A. (2011). Dung beetles as a candidate study taxon in applied biodiversity conservation research. *Ecology and Evolution of Dung beetles*, 267-291.
- Nichols, E., Gardner, T. A., Peres, C. A., Spector, S., & Scarabaeinae Research Network. (2009). Co-declining mammals and dung beetles: an impending ecological cascade. *Oikos*, 118(4), 481-487.
- Nichols, E., Larsen, T., Spector, S., Davis, A. L., Escobar, F., Favila, M., et al. (2007). Global dung beetle response to tropical forest modification and fragmentation: a quantitative literature review and meta-analysis. *Biological conservation*, 137(1), 1-19.
- Nichols, E., Spector, S., Louzada, J., Larsen, T., Amezcuita, S., Favila, M. E., & Network, T. S. R. (2008). Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. *Biological conservation*, 141(6), 1461-1474.
- Numa, C., Verdú, J. R., Sánchez, A., & Galante, E. (2009). Effect of landscape structure on the spatial distribution of Mediterranean dung beetle diversity. *Diversity and Distributions*, 15(3), 489-501.
- Palmer, A. R., Hoffman, M. T., Cowling, R. M., Richardson, D. M., & Pierce, S. M. (1997). *Vegetation of Southern Africa. Cambridge: The Press Syndicate of the University of Cambridge.*

Pauw, M. J., Esler, K. J., & Le Maitre, D. C. (2018). Assessing the success of experimental rehabilitation on a coastal mineral sands mine in Namaqualand, South Africa. *African Journal of Range & Forage Science*, 35(3-4), 363-373.

Pienaar, E. (2002). *Vegetation on and adjacent to mesas in the Nama-Karoo, South Africa: characteristics and comparisons* (Doctoral dissertation, Stellenbosch: Stellenbosch University).

Pryke, J. S., Roets, F., & Samways, M. J. (2013). Importance of habitat heterogeneity in remnant patches for conserving dung beetles. *Biodiversity and Conservation*, 22(12), 2857-2873.

Pryke, J. S., Roets, F., & Samways, M. J. (2016). Wild herbivore grazing enhances insect diversity over livestock grazing in an African grassland system. *PloS One*, 11(10), e0164198.

Radel, C., & Schmook, B. (2008). Male transnational migration and its linkages to land-use change in a southern Campeche ejido. *Journal of Latin American Geography*, 59-84.

Roslin, T., & Koivunen, A. (2001). Distribution and abundance of dung beetles in fragmented landscapes. *Oecologia*, 127(1), 69-77.

Sala, O. E., Chapin, F. S., Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., et al. (2000). Global biodiversity scenarios for the year 2100. *Science*, 287(5459), 1770-1774.

Schneider, L., & Geoghegan, J. (2006). Land abandonment in an agricultural frontier after a plant invasion: the case of bracken fern in southern Yucatán, Mexico. *Agricultural and Resource Economics Review*, 35(1), 167-177.

Scholtz, C. H., Davis, A. L. V., & Kryger, U. (2009). *Evolutionary biology and conservation of dung beetles*. Sofia-Moscow: Pensoft.

Simmons, L. W., & Ridsdill-Smith, T. J. (Eds.). (2011). *Ecology and evolution of dung beetles*. John Wiley & Sons.

Slade, E. M., Mann, D. J., Villanueva, J. F., & Lewis, O. T. (2007). Experimental evidence for the effects of dung beetle functional group richness and composition on ecosystem function in a tropical forest. *Journal of Animal Ecology*, 76(6), 1094-1104.

Spector, S. (2006). Scarabaeine dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae): an invertebrate focal taxon for biodiversity research and conservation. *The Coleopterists Bulletin*, 60(mo5), 71-83.

Steed, A., Swart, R., Pauw, M. J., & Roets, F. (2018). Response of arthropod communities to plant-community rehabilitation efforts after strip mining on the semi-arid west coast of South Africa. *African Journal of Range & Forage Science*, 35(3-4), 375-385.

Suding, K. N., Gross, K. L., & Houseman, G. R. (2004). Alternative states and positive feedbacks in restoration ecology. *Trends in Ecology & Evolution*, 19(1), 46-53.

Taylor, A. R. (2012). The square kilometre array. *Proceedings of the International Astronomical Union*, 8(S291), 337-341.

Toco, C., Negro, M., Rolando, A., & Palestrini, C. (2013). Does natural reforestation represent a potential threat to dung beetle diversity in the Alps? *Journal of Insect Conservation*, 17(1), 207-217.

Tonelli, M., Verdú, J. R., & Zunino, M. (2018). Effects of the progressive abandonment of grazing on dung beetle biodiversity: body size matters. *Biodiversity and Conservation*, 27(1), 189-204.

Tonelli, M., Verdú, J. R., & Zunino, M. (2019). Grazing abandonment and dung beetle assemblage composition: Reproductive behaviour has something to say. *Ecological Indicators*, 96, 361-367.

Tonelli, M., Verdú, J. R., & Zunino, M. E. (2017). Effects of grazing intensity and the use of veterinary medical products on dung beetle biodiversity in the sub-mountainous landscape of Central Italy. *PeerJ*, 5, e2780.

Tshikae, B. P., Davis, A. L., & Scholtz, C. H. (2013). Species richness–Energy relationships and dung beetle diversity across an aridity and trophic resource gradient. *Acta Oecologica*, 49, 71-82.

Twine, W., Moshe, D., Netshiluvhi, T., & Siphugu, V. (2003). Consumption and direct-use values of savanna bio-resources used by rural households in Mametja, a semi-arid area of Limpopo province, South Africa. *South African Journal of Science*, 99(9), 467-473.

Vavra, M., Parks, C. G., & Wisdom, M. J. (2007). Biodiversity, exotic plant species, and herbivory: the good, the bad, and the ungulate. *Forest Ecology and Management*, 246(1), 66-72.

Verdoodt, A., Mureithi, S. M., & Van Ranst, E. (2010). Impacts of management and enclosure age on recovery of the herbaceous rangeland vegetation in semi-arid Kenya. *Journal of Arid Environments*, 74(9), 1066-1073.

Verdú, J. R., Moreno, C. E., Sánchez-Rojas, G., Numa, C., Galante, E., & Halffter, G. (2007). Grazing promotes dung beetle diversity in the xeric landscape of a Mexican Biosphere Reserve. *Biological Conservation*, 140(3-4), 308-317.

Verdú, J. R., Crespo, M. B., & Galante, E. (2000). Conservation strategy of a nature reserve in Mediterranean ecosystems: the effects of protection from grazing on biodiversity. *Biodiversity & Conservation*, 9(12), 1707-1721.

Verdú, J. R., Numa, C., & Hernández-Cuba, O. (2011). The influence of landscape structure on ants and dung beetles diversity in a Mediterranean savanna—forest ecosystem. *Ecological Indicators*, 11(3), 831-839.

Viegas, G., Stenert, C., Schulz, U. H., & Maltchik, L. (2014). Dung beetle communities as biological indicators of riparian forest widths in southern Brazil. *Ecological Indicators*, 36, 703-710.

Williams, T. O. (1998). Multiple uses of common pool resources in semi-arid West Africa: a survey of existing practices and options for sustainable resource management. *Natural Resource Perspectives*, 38(10).

Woodgate, Z., Distiller, G., & O'Riain, J. (2018). Variation in mammal species richness and relative abundance in the Karoo. *African Journal of Range & Forage Science*, 35(3-4), 325-334.

Zavala, M. A., & Burkey, T. V. (1997). Application of ecological models to landscape planning: the case of the Mediterranean basin. *Landscape and Urban Planning*, 38(3-4), 213-227.

Chapter 3

THE EFFECT OF FARMLAND ABANDONMENT ON DUNG BEETLE FUNCTIONAL DIVERSITY IN THE NAMA-KAROO BIOME OF SOUTH AFRICA

3.1. Abstract

Abandoning rangelands without the reintroduction of wild herbivores often leads to declines in the diversity of organisms that depends on dung resources such as dung beetles. This can have profound negative effects on their ecosystem functions and services. Here, I investigate how land abandonment affects the functional diversity of dung beetles in the semi-arid Nama-Karoo of South Africa. Specifically, I investigated changes in dung beetle functional diversity in terms of functional richness, evenness, dispersion, divergence and Rao's quadratic entropy (Q) due to progressive land abandonment and differences between different biotopes. Dung beetles were sampled using baited pitfall traps on farms that were abandoned a long time ago (>10 years), on recently abandoned farms (ca. 1 year ago) and on active farms. I hypothesised that dung beetle functional diversity would be negatively affected by the removal of livestock (sheep). Furthermore, I expected that functional diversity of dung beetles would differ between the three dominant landscape features (hills, flatlands and riparian zones). Contrary to my expectations, recently non-grazed and non-grazed areas had the highest functional richness, suggesting land abandonment had a positive effect on functional richness. This was likely driven by a low functional richness of dung beetles associated with sheep dung compared to cow and omnivore pig dung. Dung beetle functional richness and dispersion was lowest in mountainous areas indicating that flatlands and riparian systems are particularly significant for sustaining greater functional diversity. I promote the re-establishment of indigenous ruminant meso-herbivores in abandoned areas to encourage even greater dung beetle functional diversity. Similarly, on farms, expansion of meso-herbivore richness (wild or domestic) will greatly improve dung beetle functional diversity and increase their ecosystem services.

Keywords: functional diversity, semi-arid, conservation, SKA, land-use change

3.2. Introduction

Dung beetles (Scarabaeidae: Scarabaeinae and Aphodinae) perform many ecological functions (Nichols *et al.* 2008), which make them essential to the normal functioning of ecosystems (Neita and Escobar 2012). Some of these processes include controlling of vertebrate parasites (Bishop *et al.* 2005; Fincher, 1975), encouraging secondary seed dispersal (Andresen 2001, 2002; Bardgett and Wardle 2010; Braga *et al.* 2013; Slade *et al.* 2007) and promoting nutrient cycling in soils (Brown *et al.* 2010; De Deyn and Van der Putten 2005; Korasaki *et al.* 2013; Nichols *et al.* 2008). Furthermore, the process of dung burial also leads to improved plant growth and vegetation cover (Gómez-Cifuentes *et al.* 2017). Dung beetles are therefore considered a keystone species of many ecosystems (Steinfeld *et al.* 2006). Dung beetles are also renowned for their bio-indicator potential as they are intimately reliant on vertebrate dung, as well as being very diverse and abundant with a worldwide distribution (Nichols *et al.* 2007, Simmons and Ridsdill-Smith 2011). Dung beetles furthermore display a large diversity of behavioural and morphological traits that have been linked to multiple ecological roles (Hanski and Cambefort 1991), they are well documented and their taxonomy is well resolved (Philips *et al.* 2004), and they are easily and cost-effectively sampled using standardized and simple trapping methods (Gardener *et al.* 2008, Larsen and Forsyth 2005; Pryke *et al.* 2016).

Despite their importance, dung beetles are under threat worldwide as they are extremely sensitive to ecological change (Duraes *et al.* 2005; Gardner *et al.* 2009; Halffter *et al.* 2007; Hogan 2005; Korasaki *et al.* 2012, Nichols *et al.* 2007; Rodrigues *et al.* 2013, Salomão and Iannuzzi 2015; Simmons and Ridsdill-Smith 2011; Spector and Ayzama 2003), such as habitat fragmentation (Filgueiras *et al.* 2011; Klein 1989), pasture and grazing land abandonment (Tonelli 2017; Chapter 2 in this thesis), urbanisation, medicinal veterinary substances used for

farm animals (IUCN, 2016), and land use intensification (Davis *et al.* 2010; Gardner *et al.* 2008; Jacobs *et al.* 2010; Korasaki *et al.* 2013; Shahabuddin *et al.* 2010). In fact, most environmental disturbances cause a decline in abundance, species richness, and creates a compositional shift toward more opportunistic species (Kryger 2009; Nichols *et al.* 2007; Tonelli 2017). Pasture abandonment leads to a loss of dung resources, which is known to negatively affect dung beetle numbers and community composition due to their dependence on this resource (Carpaneto *et al.* 2005; Nichols *et al.* 2009). In contrast, farmland abandonment may also positively affect dung beetle diversity. This is thought to be linked to a low dependence on domestic dung sources and subsequent reduced pressures on remnant native vertebrates (Chapter 2). Additionally, the resulting changes in vegetation cover and structure can also change dung beetle assemblages after land abandonment (Hanski and Cambefort 1991).

Biodiversity is closely linked to ecosystem health and functioning (Cardinale *et al.* 2006, 2007, 2012; Hooper *et al.* 2005; Jiang and Pu 2009; Loreau 2000; Loreau *et al.* 2001; Tilman 1999), and the loss of biodiversity through land abandonment may have a negative impact on the environment (Cardinale *et al.* 2012). However, little is currently known about land abandonment and the effect it has on ecological functions, as well as how this affects the functional diversity in an ecosystem (Berragan *et al.* 2011). The study of land-use change and its ecosystem effects are usually investigated using species richness, abundance, biomass, and assemblage composition of biotic communities, but this approach assumes that every species contributes equally to processes and functions (Berragan *et al.* 2011; Flynn *et al.* 2009; Lindenmayer *et al.* 2012; MacDonald *et al.* 2000; Newbold *et al.* 2015). Ecological studies should therefore ideally include measures of functional diversity because these can be quantified as differential functional performance (Díaz and Cabido 2001; Spasojevic and Suding 2012). Ecosystem services, processes, and resilience to environmental change are all known to be driven by functional diversity (Botta-Dukát 2005; Diaz *et al.* 2007; Folke *et al.* 2004; Hooper *et al.* 2005; Petchey and Gaston 2002). Therefore, when monitoring alterations

to an environment, we should include the diversity of ecological roles and functional traits of the different species within the ecosystem (Barragan *et al.* 2011; Diaz and Cabido 2001; Chapin *et al.* 200; Perrings *et al.* 2010; Purvis 2000; Tilman 2001).

Functional diversity (FD) is defined as “the type, variety and comparative abundance of functional traits present in a population” (Díaz *et al.* 2007), which can be comprised of any physical, biological, or behavioural factor directly associated with a particular species of interest (Violle *et al.* 2007). Few studies have investigated the impact of human activity on functional diversity in the field. The majority of the information available is from experimental studies conducted under controlled conditions (e.g., Barragan *et al.* 2011). Most of these show that human activity results in changes in species with specific functional traits, consequently changing the function of an ecosystem (Kremen 2005). There is also a distinct possibility that functional diversity affects ecological processes more than species richness (Díaz and Cabido 2001; Hooper *et al.* 2005; Hillebrand and Matthiessen 2009; Scherer-Lorenzen 2009; Tilman 2001).

Most studies that investigated the influence of land-use change in terms of functional diversity and species have focused on intensification processes (Dorrough and Scroggie, 2008, Flynn *et al.* 2009, Laliberté *et al.* 2010). Land abandonment, which is the opposite to intensification, has received far less attention (Castro *et al.* 2010, MacDonald *et al.* 2000, Pakeman and Marriot 2010, Peco *et al.* 2005, 2012). The present study therefore sets out to examine the effect of farmland abandonment on dung beetle functional diversity using a number of species traits that are linked to their ecosystem function (Peco *et al.* 2012). I test the hypothesis that land abandonment through removal of livestock without active replacement with wild grazers will have negative effects on dung beetle diversity and ecological function as is the case in other systems studied to date (Tonelli *et al.* 2018).

3.3. Materials and Methods

3.3.1. Study Area

This study took place in the Nama-Karoo, a semi-arid biome covering ca. 20% of South Africa. This rangeland is a mosaic of deep and stony soils, hills and usually dry river beds (Cowling and Roux 1987; Dean and Milton 1999; Hanks 2009) best described as a desert shrub land that is dominated by succulent dwarf shrubs and grasses (Cowling and Roux 1987; Dean and Milton 1999; Hanks 2009). The Nama-Karoo is characterised by low rainfall and high summer temperatures and receives less than 500 mm of rainfall per year (ca. 200 mm average at my study site), with droughts often being long and extreme (Desmet and Cowling 1999; Palmer and Hoffman 1997; Pienaar 2000). The landscape is flat to gently undulating with many low, flat-topped hills and ridges (Cowling and Roux 1987; Dean and Milton 1999; Hanks 2009). Plant diversity in this biome is considered low compared to other South African biomes, with only 2147 species, of which 386 are endemic (Cowling and Roux 1987; Dean and Milton 1999; Hanks 2009). Threats to the environment include invasive alien plants, land-use change and drought (Cowling and Roux 1987; Dean and Milton 1999; Hanks 2009).

Study sites were selected in the area of the SKA (Square Kilometre Array), a large-scale radio telescope project, which is currently tasked with building hundreds of telescopes across $\pm 130,000$ ha in the Northern Cape Province of South Africa, ca. 90km from the town of Carnarvon. The SKA forms part of the world's largest radio telescope (Morris 2018; Hoffman *et al.* 2018) and also aims to provide much needed work for thousands of people in an area of low socio-economic development (Schilizzi 2011). Land abandonment in the core of the SKA area started ca. 10 years ago with the acquisition of the first land for building of the radio telescopes. However, recently (since 2016) numerous farms have been abandoned for the expansion of this project. The area therefore comprises a mosaic of land that has been abandoned and some land that is still used for grazing of sheep and to a lesser extent cattle and goats (Fig. 2.1, Chapter 2).

3.3.2. Sampling Design

Dung beetles are most active following rainfall events, which is the best time to sample them, and their activity decreases once an area becomes drier and warmer (Lobo *et al.* 1997; Simmons and Ridsdill-Smith 2011). To maximise dung beetle sampling, the 1st sampling took place during spring, October 2018, and the 2nd sampling took place during winter, June 2019. Sampling was conducted under prevailing drought conditions. Three different land-use types were chosen within the study area: non-grazed, which was abandoned a long time ago (10 years or longer); only recently non-grazed, which was abandoned recently (1 year ago); and grazed, which is currently still being grazed by livestock. This mosaic of different land uses provided a good opportunity to compare and monitor the effects of land abandonment over time in this arid ecosystem. In each of these land-use types 24 study sites were selected, separated by at least 1 km to reduce the possible effect of pseudo replication. These 24 study sites were arranged into 3 separate groups of 8, each group representing a different biotope within the land-use type ($n = 8$, 3 biotopes surveyed per each of the three impact levels) as this has been shown to influence dung beetle assemblages in the region (Chapter 2). The three different biotopes included dry riverbeds/riparian areas, which are characterised by sandy soils and the presence of shrub-trees on the riverbanks; rocky hills/mountainous areas (sites selected on the cooler and wetter southern sides for standardization) that are characterised by shallow soils and dolerite rocks; and plains/flatlands that are usually characterised by deep sandy-loamy soils with a flat slope. These three biotopes were selected based on their frequency throughout this region, and the different effects they may have on dung beetle functional diversity; i.e., different biotopes may consist of variable abiotic elements and biotic communities to which dung beetles may have different responses.

At each of these sites four pitfall traps were placed in a line at least 100 m apart (to minimize trap interference) (Larsen and Forsyth 2005). This method of baited pitfall trapping is an easy and effective way to provide quantitative data for dung beetles across many environmental gradients (Davis *et al.* 2008). Each trap within study sites was baited with a different bait

source, as different taxa are attracted to different sources, which can give a good indication of functional diversity within this ecosystem (Davis *et al.* 2008). Dung bait types included pig dung (omnivore); cow dung (moist pats); sheep dung (pellets); and rotten chicken livers (carryon) (Davis *et al.* 2010). Due to the rotten chicken livers (carryon) not attracting any dung beetle species within the first and second sampling season, the chicken liver traps were excluded from statistical analyses. Trapping methods, trap operating times, and trap design followed those set out by Pryke *et al.* (2016) and in Chapter 2. Dung bait was sourced from Worcester Abattoir, processed, and placed in the field as outlined in Chapter 2.

All individuals collected in the traps were sorted to species (morpho-species when species identity was not known) and frozen. Thereafter they were assigned to one of three functional guilds (tunnellers, dwellers, and rollers, depending on their nesting behaviour as paracoprid, endocoprid, or telocoprid, respectively). Species were identified using a taxonomic key (Deschodt, unpublished) by an expert. Five dried individuals of each species (where available) were kept for the reference collection. Hereafter five individuals from each species (here available) otherwise all individuals, were used to measure nine different functional traits and then the average of these five measurements per species were used for analyses (Tonelli *et al.* 2018). A reference collection of all species is housed in the Stellenbosch University Entomological Collection, Stellenbosch, South Africa.

3.3.3. Functional Traits

Nine traits were used to determine functional identity of guilds or species collected here: 1) The first trait was associated with food relocation: the telecoprids or rollers, which roll dung into a ball and then translocate this at some distance from the dung pad for burial; the paracoprids or tunnellers that bury pieces of dung in tunnels constructed directly under the dung pad; and the endocoprids or dwellers that live and nest inside the dung (Halffter and Edmonds 1982; Hanski and Cambefort 1991). This information was sourced from literature (Davis *et al.* unpublished); 2) bigger beetles process more dung than smaller counterparts (Barragan *et al.* 2011). The second trait included was therefore the total length of the beetle (mm) measured from the tip of the abdomen to the tip of the clypeus using digital callipers (Navarrete and Halffter 2008); 3) the third trait measured was dry mass of the beetle measured using a digital scale after air drying for three weeks; 4) time of day that the beetle is active, nocturnal or diurnal, was recorded from literature (Davis *et al.* unpublished) or from own observations and was coded as 1—diurnal or 0—nocturnal for analyses; 5) diet preferences of dung beetles in the region can be separated into coprophagous (dung), necrophagous (carrion) or generalists that will utilise more than one source (Halffter and Halffter 2009). Coprophagous taxa can be further subdivided into those that prefer dung from carryon, non-ruminal vertebrates, ruminal vertebrates or omnivorous vertebrates. Species were scored as 1—carryon, 1—ruminal, 1—omnivorous, and 1—non-ruminant, and then depending how many sources the dung beetle species utilized, I created a score (1–4) for each species. Emended according to my trap catches; 6) a larger head area vs. body size indicates that a beetle can manipulate relatively larger quantities of dung for its size (Tonelli *et al.* 2016). I therefore calculated the ratio of the head area vs. total body area (mm²) of each dung beetle species, using Image J software (ImageJ2 - National Institutes of Health) after taking photos of dismembered beetles on a background with a standardised grid of 1 mm x 1 mm; 7) species with longer legs can generally move faster and roll larger dung balls than species with shorter legs (Inward *et al.* 2011). I therefore measured hind tibia length (mm) using digital callipers; 8)

dispersal ability of dung beetles strongly affected by wing load (Barnes *et al.* 2014; Howden and Nealis, 1975, 1978; Larsen *et al.* 2008; Silva and Hernández 2015; Peck and Forsyth 1982). I therefore calculated wing load from dry mass data and the area of the hind wings determined using Image J software (mg/mm^2). Moreover, this trait is also strongly linked to dung beetle thermoregulatory performance and 9) dung beetles can partition behaviour into distinct seasons (Merrick and Smith 2004). The final trait included was therefore phenology (seasonal activity). Phenology information was sourced from the literature (Davis *et al.* unpublished) and my own collections and coded as outlined by Tonelli (2017) for analyses.

3.3.4. Statistical Analyses

I calculated functional traits across the different land uses, dung types, and biotopes using the FD package (Laliberté *et al.* 2015) in R version 3.0.1 (R Development Core Team 2015). The FD package can compute different multidimensional functional diversity (FD) indices by implementing a distance-based framework to measure FD using any number and type of functional trait, whilst also considering species relative abundances (Laliberte *et al.* 2014). Functional diversity indices assessed in the present study were calculated for each trap and included FRic (functional richness), which reflects the entire range of functional niches present in the community (Villegger *et al.* 2008) as it takes only the species with most extreme traits in account (irrespective of abundance). It is therefore a reflection of the size of the trait-space cloud (Mason *et al.* 2005). FEve (functional evenness) measures how regularly species and their abundances are spaced in trait space (Villegger *et al.* 2008). The more skewed abundances of taxa are in trait space, the lower the value, and this measure can therefore be used to evaluate how evenly ecological niches are occupied. FDis (functional dispersion) is the average distance of individual species to the centroid of all species in the community trait space (rescaled based on abundance data). A low value will indicate a community with little difference in function of all the constituent taxa, while a higher value will indicate greater dissimilarity in functional diversity between taxa. FDiv (functional divergence) is a measure of

how the abundances behave (while controlling for FRic) on the outer margins of the functional space, which can be used to identify if the resource is evenly exploited by the functional niches of the community (Mason *et al.* 2005; Mouchet *et al.* 2010). Comparatively low levels of FDiv indicates a low level of niche differentiation among the most abundant species within communities (traps) (Laliberté and Legendre 2010; Laliberte *et al.* 2015; Mason *et al.* 2005; Tonelli *et al.* 2019). RaoQ (Rao's quadratic entropy (Q); Botta-Dukát 2005) is a calculation of the abundance-weighted variance of the dissimilarities between all species pairs (Botta-Dukát 2005; Champely and Chessel 2002; Rao 1982; Ricotta 2005).

Before analyses, all data sets were first tested for normality using a Shapiro–Wilks test in R (R Development Core Team 2015). Where possible, data that were not normal were transformed using the arcsine transformation, as was the case for functional evenness and functional divergence data. If not, data were analysed untransformed, as was the case for functional richness, functional dispersion and RaoQ. To compare differences in functional diversity indices with regard to land use, biotope, and dung type, I used linear modelling procedures. Best fit models were determined with a stepwise forward selection method based on AIC values using the AICcmodavg package (Mazerolle and Mazerolle 2017) in R. For data that could not be transformed (FRic, FDis and RoaQ) I calculated generalized linear models (GLM) with a gamma distribution and log link function using the lme4 package (Bates *et al.* 2014, Braga *et al.* 2013). For transformed data (FEve and FDiv), I used linear models (LMs). Data were not over-dispersed. Significance of variables retained after model forward selection procedures were tested using the anova() function in R. Hereafter, significant main effects were separated using conservative Tukey post-hoc tests, which allows for multiple comparisons between means and that generates t- and p-values for these comparisons.

3.4. Results

Dung beetle species and numbers are reported in Chapter 2. A total of 2584 dung beetle individuals, comprising fifteen species, were sampled (Chapter 2, Table 2.1). The highest abundance and species richness were found in the recently non-grazed areas representing 1084 dung beetle individuals and thirteen species (Chapter 2, Table 2.1). For FRic, the variables biotope, land use and dung type were retained after forward selection procedures (Table 3.1). For FEve no variables were retained and for FDiv and FDis only biotope was retained. For RaoQ, biotope and dung type were retained in the model after forward selection procedures (Table 3.1). Functional evenness, functional divergence, functional dispersion, and RaoQ were not affected by dung type so it was excluded from further analyses.

Differences in land-use type and dung type had no effect on functional evenness (FEve) or functional divergence (FDiv) of dung beetles, FDiv was affected by biotope as a whole, but the post-hoc testes couldn't pick up which level of the factor was responsible for this (Table 3.1). Except for FRic, dung beetle communities were similar between different land-use types for all functional diversity indexes examined here. Recently non-grazed sites had the highest FRic and grazed sites the lowest, with non-grazed sites with intermediate FRic (Table 3.1, Fig. 3.1). Biotopes differed significantly in terms of dung beetle FRic (Fig. 3.1), functional dispersion (FDis, Fig. 3.2) and Rao's quadratic entropy (RaoQ, Fig. 3.3) (Table 3.1). Of all, flatlands and riparian zones had dung beetle communities with similar functional values, and significantly higher than for dung beetle communities on mountainous areas (Table 3.1, Figs. 3.1—3.3). Dung beetle functional diversity was similar between the different dung types in terms of all diversity indexes except for FRic (Table 3.1, Fig. 3.1). Here, dung beetles attracted to pig dung and cow dung were similar in terms of FRic, but these were significantly higher than for the dung beetles attracted to the sheep dung (Table 3.1, Fig. 3.1).

Table 3.1: Significance of variables (biotope, land use, and dung type) for explaining functional diversity indices (FRic—functional richness, FEve—functional evenness, FDiv—functional divergence, FDis—functional dispersion, RaoQ—Rao’s quadratic entropy (Q). For post hoc analyses variables were arranged from highest to lowest median values and with > meaning the preceding factor(s) is significantly larger than those that follow, = factors are equal, and ≥ indicates that the last factor is significantly larger than the first, but equal to the second. N/A – not enough data.

Functional diversity index	Variables retained after forward selection	F/X ²	P	Post hoc
FRic	Dung type	125.661	0.0166	P=C>S
	Biotope	108.709	<0.001	F=R>M
	Land use	93.205	<0.001	RNG=NG≥G
FEve	N/A	N/A	N/A	N/A
FDiv	Biotope	3.1548	0.047	F=R=M
FDis	Biotope	6.7043	0.002	F=R>M
RaoQ	Dung type	2.5989	0.080	N/A
	Biotope	8.3529	<0.001	F=R>M

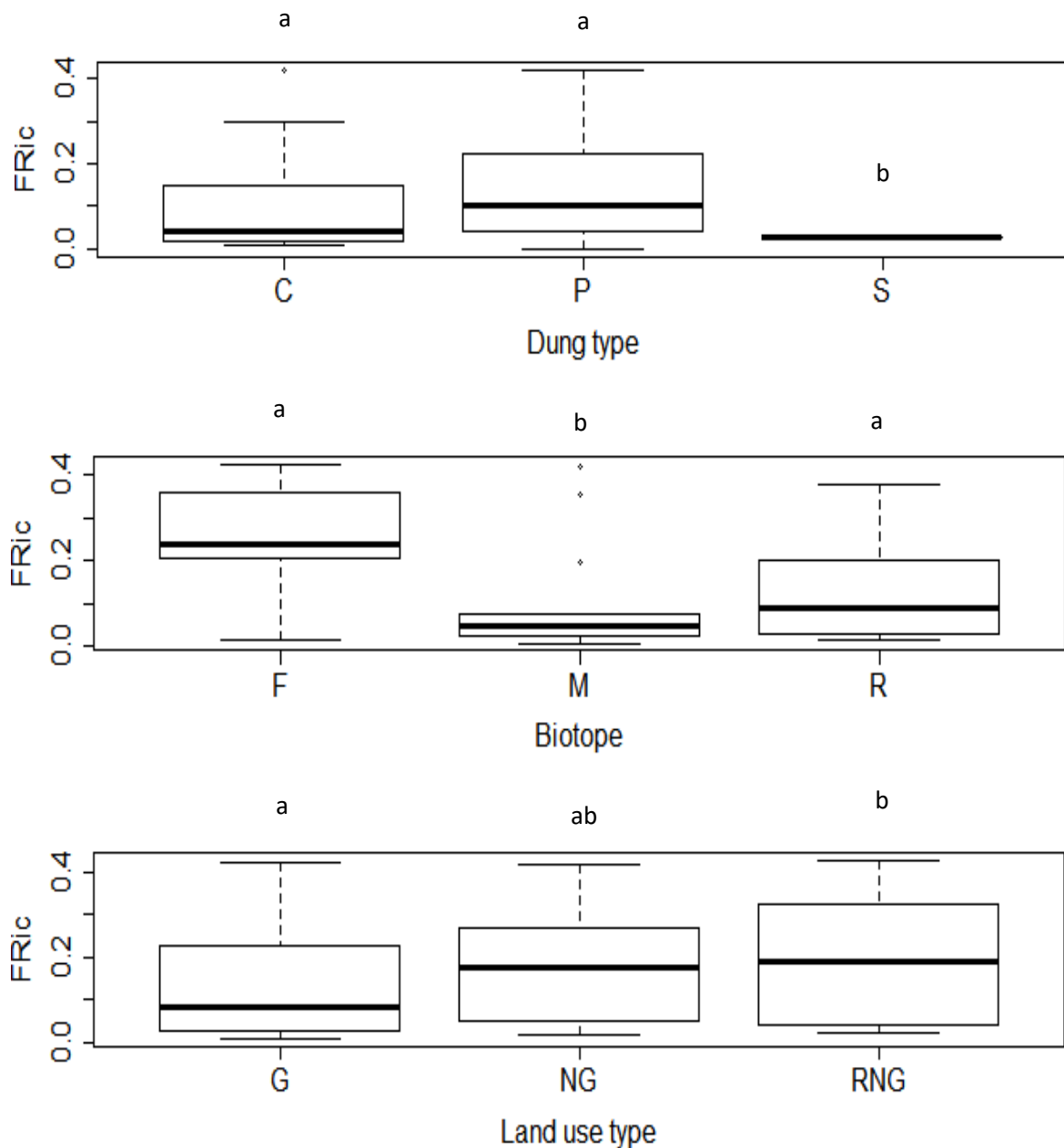


Figure 3.1: Boxplots of the functional richness between different dung types (P—pig dung, C—cow dung, and S—sheep dung), biotopes (F—flatlands, M—mountainous zone, and R—riparian zone), and land-use types (G—grazed, NG—non-grazed, and RNG—recently non-grazed). Different letters above bars indicate significant differences ($p < 0.05$). Box indicates 25–75% data range, whiskers indicate 1.5 times the interquartile range, dots represent outliers.

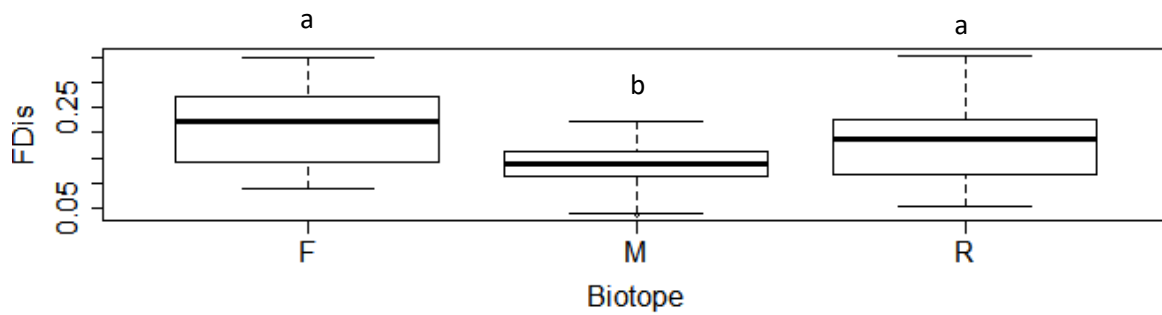


Figure 3.2: Boxplots of the functional dispersion between the different biotopes (F—flatlands, M—mountainous zone, and R—riparian zone). Different letters above bars indicate significant differences ($p < 0.05$). Box indicates 25–75% data range, whiskers indicate 1.5 times the interquartile range.

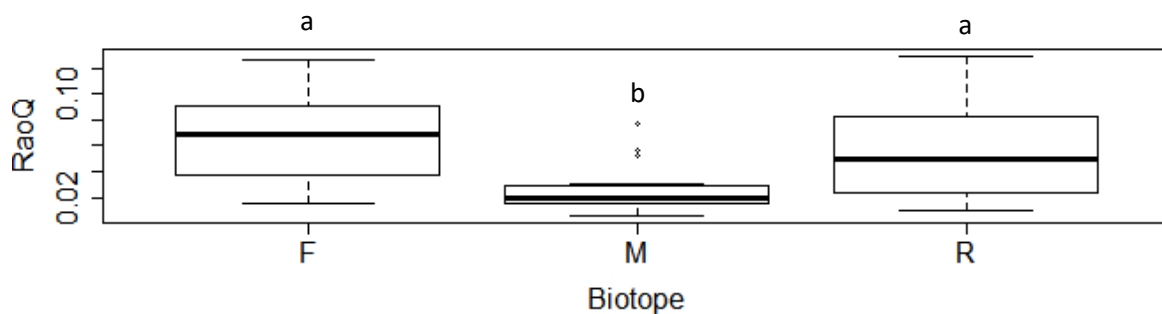


Figure 3.3: Boxplots of the RaoQ (Rao's quadratic entropy (Q)) between different biotopes (F—flatlands, M—mountainous zone, and R—riparian zone). Different letters above bars indicate significant differences ($p < 0.05$). Box indicates 25–75% data range, whiskers indicate 1.5 times the interquartile range, dots represent outliers.

3.5. Discussion

In this study I set out to assess the impact of land abandonment, and the subsequent removal of livestock (sheep) without active replacement with wild grazers, on dung beetle functional diversity in the Nama-Karoo biome of South Africa. I found that dung beetle functional richness was generally higher in areas that were abandoned (non-grazed and recently non-grazed) due to livestock removal (mainly sheep) than in areas that are currently still grazed by livestock (grazed areas). Land abandonment therefore has a positive effect on both dung beetle communities (Chapter 2) and their ecological function, which include dung reallocation, seed dispersal and dung burial in this region. This is similar to a study by Tonelli *et al.* (2019) that found progressive land abandonment acts as an environmental filter with moderately grazed sites still having functionally rich and well-structured communities. With low grazing areas losing their functional diversity due to niches being filled by opportunistic species and when totally abandoned, a functionally rich, unique and well-structured community developed, which we see in my study. In my study we saw how land abandonment acts as an environmental filter, where currently grazed areas had lower overall functional richness but still had a functional community. Similarly as the abandonment process takes place, we see a growth in overall functional richness, with recently non-grazed areas having higher functional diversity than grazed and no longer grazed areas forming a unique, well-structured community with functional richness higher than that of the currently grazed areas.

Functional richness can either remain unchanged or increase with an increase in species richness (Petchey and Gaston 2002). The increase in functional richness detected here goes hand-in-hand with an increase in species richness at abandoned sites (Chapter 2). This is likely because a higher number of species fills more niches when there is not considerable niche overlap between taxa (Tonelli 2017). Thus, ultimately, increased functional richness in abandoned areas will improve ecological buffering against environmental fluctuations (Manson *et al.* 2005; Tilman 1996). Indeed, this high functional richness also implies that

invasion resistance to other dung beetle species at these sites should be higher because there are fewer niches currently unoccupied (Dukes 2001).

Functional richness of dung beetle communities attracted to sheep dung was considerably lower than those attracted to the non-pelleted ruminant and omnivore dung types. Again, this reflects a much-reduced species richness associated with sheep dung (Chapter 2). Therefore, very few dung beetle species and a low functional diversity is expected on farms where sheep dung flourishes, and where native omnivorous and ruminant animals are actively managed by farmers in terms of hunting and control through fences. As no native animals have been reintroduced in the abandoned landscapes, the increase in functional richness in non-grazed and recently non-grazed areas is likely due to the decreased pressure on native animals compared to farmlands. To improve conditions for enriched dung beetle functional richness in the abandoned areas further, reintroductions of native ruminants and omnivores could be considered. Wildebeest (*Connochaetes taurinus*) should benefit dung beetles as they have a similar dung type to cow and pig dung; perhaps also non-ruminant species like zebra to diversify dung sources (*Equus quagga*). These species were known to historically occupy the region (Lovegrove and Siegfried 1993). However, functional richness is also of benefit to current farming areas as dung beetles provide numerous ecosystem functions, such as vegetation development, nutrient cycling, parasite and pest control, and secondary seed dispersal (Nichols *et al.* 2008). Thus, increasing the presence of omnivores and ruminants on farms would increase dung beetle functional diversity and may include various domestic ((e.g., cattle (*Bos taurus*) and pigs (*Sus scrofa domestica*)) and wild herbivores.

Functional richness cannot incorporate relative abundance, and this means rare species with extreme trait values can greatly inflate functional richness. This is also evident in the present study where rare and functionally divergent taxa, such as *Euoniticellus intermedius*, *Euonthophagus vicarius* and *Onitis confusus*, added considerably to increased functional richness. Diversity measures that did account for abundance (FEve, FDiv, FDis, RaoQ) showed no difference between the different land-use types. Most ecological niches across

these land-use types are therefore fairly regularly filled, functional diversity is fairly similar between land-use types when these rare taxa are not present, and resources are evenly exploited by the community. However, rarity in the taxa that drive divergence between sites are likely caused by rarity in favoured resources linked to diminished numbers of native mammals and reintroductions should lead to increases in their numbers (Laliberté and Legendre 2010). For example, all three above mentioned species were attracted to omnivore dung, a resource that is particularly limited due to hunting and the control of animals, such as mongoose species, honey badger (*Mellivor capensis*), baboon (*Papio ursinus*), and Jackal (*Canis mesomelas*).

Functional richness followed a similar trend to what was found for abundance and species richness of dung beetles in the region with regards to biotope (Chapter 2). Highest functional richness was found in the flatlands and riverine areas with diminished functional richness in the mountainous regions. This same trend was seen for functional dispersion. Therefore, more ecological niches are available in the flatlands and riparian systems and ecological function of dung beetles would be most important here. Unfortunately, these are also the areas that are most severely impacted by farming activities as these areas are often overstocked, leading to overgrazing by sheep. As sheep dung is not a favoured resource, larger ecosystem impacts (e.g., decreased secondary seed dispersal) and decreased ecosystem services (reduced clearing of pest breeding sites) will result, forming a negative feedback loop.

A strong correlation between functional dispersion and RaoQ can be expected (Laliberté and Legendre 2010), given that both of these indices estimate the dispersion of species in trait space, weighted by their relative abundance. RaoQ was highest in flatlands and riparian zones and lowest at mountainous areas. This means that the functional distance between individuals in flatlands and riparian areas was greater than those in mountainous areas. Consequently, it can be expected that species that occur in these flatlands and riparian zones occupy more divergent niches and that there is likely less competition for these niches available in these areas. Also, the mountainous areas have rocky soils, which makes these areas less habitable

to dung beetles leading to less availability of niches in this biotope. Only certain dung beetle species, probably those with similar adaptations to these rocky areas, would be able to survive here, which causes less functional distance between species.

3.6. Conclusions

Results of the present study highlight that land abandonment and the subsequent cessation of large-scale sheep farming has an overall positive effect on dung beetle diversity. Ecological function within this semi-arid landscape, arguably linked to increased availability of native animal dung resources that provides a higher quality resource. Preserving a mosaic of different landscape structures is significant for sustaining dung beetle diversity (Chapter 2) and may also promote greater functional diversity as is shown here. There are multiple possible reasons for the increase in dung beetle functional diversity after land abandonment and these need further study. For example, it is possible that only generalist and functionally similar dung beetles thrive on actively managed farms. Relatively functionally dissimilar taxa may also require specialist dung resources not currently present in high densities in the landscape. Future studies should therefore aim to assess the diversity and functional richness of dung beetles in well stocked (with wildlife) protected areas of the Nama-Karoo biome. Whether functional diversity measures assessed in this study correlates well with functions and services, such as dung removal and secondary seed dispersal, should also receive focused attention in future studies.

References

- Anderson, M. J. (2001). A new method for non-parametric multivariate analysis of variance. *Austral Ecology*, 26(1), 32-46.
- Andresen, E. (2002). Dung beetles in a Central Amazonian rainforest and their ecological role as secondary seed dispersers. *Ecological Entomology*, 27(3), 257-270.
- Andresen, E., & Feer, F. (2005). The role of dung beetles as secondary seed dispersers and their effect on plant regeneration in tropical rainforests. *Seed fate: Predation, dispersal and seedling establishment*, 331-349.
- Bardgett, R. D., & Wardle, D. A. (2010). *Aboveground-belowground linkages: biotic interactions, ecosystem processes, and global change*. Oxford University Press.
- Barragán, F., Moreno, C. E., Escobar, F., Halffter, G., & Navarrete, D. (2011). Negative impacts of human land use on dung beetle functional diversity. *PloS One*, 6(3), e17976.
- Bates, D., Maechler, M., Bolker, B., & Walker, S. (2014). lme4: Linear mixed-effects models using Eigen and S4. *R package version*, 1(7), 1-23.
- Benayas, J. R., Martins, A., Nicolau, J. M., & Schulz, J. J. (2007). Abandonment of agricultural land: an overview of drivers and consequences. *CAB reviews: Perspectives in agriculture, veterinary science, nutrition and natural resources*, 2(57), 1-14.
- Beynon, S. A., Mann, D. J., Slade, E. M., & Lewis, O. T. (2012). Species-rich dung beetle communities buffer ecosystem services in perturbed agro-ecosystems. *Journal of Applied Ecology*, 49(6), 1365-1372.
- Bilsborrow, R. E., & DeLargy, P. F. (1990). Land use, migration, and natural resource deterioration: The experience of Guatemala and the Sudan. *Population and Development Review*, 16, 125-147.

- Botta-Dukát, Z. (2005). Rao's quadratic entropy as a measure of functional diversity based on multiple traits. *Journal of Vegetation Science*, 16(5), 533-540.
- Braga, R. F., Korasaki, V., Andresen, E., & Louzada, J. (2013). Dung beetle community and functions along a habitat-disturbance gradient in the Amazon: a rapid assessment of ecological functions associated to biodiversity. *PLoS One*, 8(2), e57786.
- Brown, J., Scholtz, C. H., Janeau, J. L., Grellier, S., & Podwojewski, P. (2010). Dung beetles (Coleoptera: Scarabaeidae) can improve soil hydrological properties. *Applied Soil Ecology*, 46(1), 9-16.
- Cardinale, B. J., Srivastava, D. S., Duffy, J. E., Wright, J. P., Downing, A. L., Sankaran, M., & Jouseau, C. (2012). Effects of biodiversity on the functioning of trophic groups and ecosystems. *Nature*, 443(7114), 989.
- Carpaneto, G. M., Mazziotta, A., & Piattella, E. (2005). Changes in food resources and conservation of scarab beetles: from sheep to dog dung in a green urban area of Rome (Coleoptera, Scarabaeoidea). *Biological Conservation*, 123(4), 547-556.
- Chapin III, F. S., Eugster, W., McFadden, J. P., Lynch, A. H., & Walker, D. A. (2000). Summer differences among arctic ecosystems in regional climate forcing. *Journal of Climate*, 13(12), 2002-2010.
- Cowling, R. M., & Roux, P. W. (1987). *Karoo biome: a preliminary synthesis. Part 2-vegetation and history*. National Scientific Programmes Unit: CSIR.
- da Silva, P. G., & Hernández, M. I. M. (2015). Scale-dependence of processes structuring dung beetle metacommunities using functional diversity and community deconstruction approaches. *PLoS One*, 10(3), e0123030.
- da Silva, P. G., & Hernández, M. I. M. (2015). Spatial patterns of movement of dung beetle species in a tropical forest suggest a new trap spacing for dung beetle biodiversity studies. *PLoS One*, 10(5), e0126112.

- Davis, A. L., Scholtz, C. H., & Deschodt, C. (2008). Multi-scale determinants of dung beetle assemblage structure across abiotic gradients of the Kalahari–Nama Karoo ecotone, South Africa. *Journal of Biogeography*, *35*(8), 1465-1480.
- Davis, A. L., Scholtz, C. H., Kryger, U., Deschodt, C. M., & Strümpher, W. P. (2010). Dung beetle assemblage structure in Tswalu Kalahari Reserve: responses to a mosaic of landscape types, vegetation communities, and dung types. *Environmental Entomology*, *39*(3), 811-820.
- Dean, W. R. J., & Milton, S. (Eds.). (1999). *The Karoo: ecological patterns and processes*. Cambridge University Press.
- Desmet, P. G., & Cowling, R. M. (1999). The climate of the Karoo—a functional approach. *The Karoo: ecological patterns and processes*, 3-16.
- Dormont, L., Epinat, G., & Lumaret, J. P. (2004). Trophic preferences mediated by olfactory cues in dung beetles colonizing cattle and horse dung. *Environmental Entomology*, *33*(2), 370-377.
- Dorrough, J., & Scroggie, M. P. (2008). Plant responses to agricultural intensification. *Journal of Applied Ecology*, *45*(4), 1274-1283.
- Durães, R., Martins, W. P., & Vaz-de-Mellos, F. Z. (2005). Dung beetle (Coleoptera: Scarabaeidae) assemblages across a natural forest-cerrado ecotone in Minas Gerais, Brazil. *Neotropical Entomology*, *34*(5), 721-731.
- Fincher, G. T. (1975). Effects of dung beetle activity on the number of nematode parasites acquired by grazing cattle. *The Journal of Parasitology*, *61*(4), 759-762.
- Foley, J. A., DeFries, R., Asner, G. P., Barford, C., Bonan, G., Carpenter, S. R., et al. (2005). Global consequences of land use. *science*, *309*(5734), 570-574.

Gardner, T. A., Barlow, J., Chazdon, R., Ewers, R. M., Harvey, C. A., Peres, C. A., & Sodhi, N. S. (2009). Prospects for tropical forest biodiversity in a human-modified world. *Ecology Letters*, 12(6), 561-582.

Gardner, T. A., Hernández, M. I., Barlow, J., & Peres, C. A. (2008). Understanding the biodiversity consequences of habitat change: the value of secondary and plantation forests for neotropical dung beetles. *Journal of Applied Ecology*, 45(3), 883-893.

Gómez-Cifuentes, A., Munevar, A., Gimenez, V. C., Gatti, M. G., & Zurita, G. A. (2017). Influence of land use on the taxonomic and functional diversity of dung beetles (Coleoptera: Scarabaeinae) in the southern Atlantic forest of Argentina. *Journal of Insect Conservation*, 21(1), 147-156.

Halffter, G., & Edmonds, W. D. (1982). The nesting behavior of dung beetles (Scarabaeinae). An ecological and evolutive approach. *The nesting behavior of dung beetles (Scarabaeinae). An ecological and evolutive approach*. 170-178.

Halffter, G., & Halffter, V. (2009). Why and where coprophagous beetles (Coleoptera: Scarabaeinae) eat seeds, fruits or vegetable detritus. *Boletín de la Sociedad Entomológica Aragonesa*, 45, 1-22.

Hanks, K. (2009). *Exploring Our Biomes: The succulent Karoo and Nama-Karoo biomes* (Vol. 5). Jacana Media.

Hanski, I., & Cambefort, Y. (1991). Competition in dung beetles. *Dung beetle ecology*, 305-329.

Hidayat, P., Manuwoto, S., Noerdjito, W. A., Tschardtke, T., & Schulze, C. H. (2010). Diversity and body size of dung beetles attracted to different dung types along a tropical land-use gradient in Sulawesi, Indonesia. *Journal of Tropical Ecology*, 26(1), 53-65.

Hillebrand, H., & Matthiessen, B. (2009). Biodiversity in a complex world: consolidation and progress in functional biodiversity research. *Ecology Letters*, 12(12), 1405-1419.

Timm Hoffman, M., Skowno, A., Bell, W., & Mashele, S. (2018). Long-term changes in land use, land cover and vegetation in the Karoo drylands of South Africa: implications for degradation monitoring. *African Journal of Range & Forage Science*, 35(3-4), 209-221.

Holter, P., Sommer, C., Grønvold, J., & Madsen, M. (1993). Effects of ivermectin treatment on the attraction of dung beetles (Coleoptera: Scarabaeidae and Hydrophilidae) to cow pats. *Bulletin of Entomological Research*, 83(1), 53-58.

Hooper, D. U., Chapin, F. S., Ewel, J. J., Hector, A., Inchausti, P., Lavorel, S., et al. (2005). Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs*, 75(1), 3-35.

Horgan, F. G., & Fuentes, R. C. (2005). Asymmetrical competition between Neotropical dung beetles and its consequences for assemblage structure. *Ecological Entomology*, 30(2), 182-193.

Howden, H. F., & Nealis, V. G. (1978). Observations on height of perching in some tropical dung beetles (Scarabaeidae). *Biotropica*, 10(1), 43-46.

Inoue, T. (2005). Causes of butterfly decline in Japan. *Japan Journal of Entomology*, (NS), 8, 43-64.

Jacobs, S., Burkhard, B., Van Daele, T., Staes, J., & Schneiders, A. (2015). 'The Matrix Reloaded': A review of expert knowledge use for mapping ecosystem services. *Ecological Modelling*, 295, 21-30.

Jay-Robert, P., Niogret, J., Errouissi, F., Labarussias, M., Paoletti, É., Luis, M. V., & Lumaret, J. P. (2008). Relative efficiency of extensive grazing vs. wild ungulates management for dung beetle conservation in a heterogeneous landscape from Southern Europe (Scarabaeinae, Aphodiinae, Geotrupinae). *Biological Conservation*, 141(11), 2879-2887.

Jiang, L., & Pu, Z. (2009). Different effects of species diversity on temporal stability in single-trophic and multitrophic communities. *The American Naturalist*, 174(5), 651-659.

Kinzig, A. P., Pacala, S. W., & Tilman, D. (Eds.). (2001). *The functional consequences of biodiversity: empirical progress and theoretical extensions* (Vol. 33). Princeton University Press.

Korasaki, V., Braga, R. F., Zanetti, R., Moreira, F. M., Vaz-de-Mello, F. Z., & Louzada, J. (2013). Conservation value of alternative land-use systems for dung beetles in Amazon: valuing traditional farming practices. *Biodiversity and conservation*, 22(6-7), 1485-1499.

Kosmas, C., Kairis, O., Karavitis, C., Acikalin, S., Alcalá, M., Alfama, P., et al. (2015). An exploratory analysis of land abandonment drivers in areas prone to desertification. *Catena*, 128, 252-261.

Kremen, C. (2005). Managing ecosystem services: what do we need to know about their ecology? *Ecology Letters*, 8(5), 468-479.

Kryger, U., 2009. Conservation of dung beetle. In: Scholtz, C.H., Davis, A.L.V., Kryger, U., (Eds.) *Evolutionary biology and conservation of dung beetles*, Pensoft, Sofia, Bulgaria, pp 387-480.

Scholtz, C. H., Davis, A. L. V., & Kryger, U. (2009). *Evolutionary biology and conservation of dung beetles* (pp. 1-567). Sofia-Moscow: Pensoft.

Laiolo, P., Dondero, F., Ciliento, E., & Rolando, A. (2004). Consequences of pastoral abandonment for the structure and diversity of the alpine avifauna. *Journal of Applied Ecology*, 41(2), 294-304.

Laliberté, E., & Legendre, P. (2010). A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, 91(1), 299-305.

Laliberté, E., Lambers, H., Burgess, T. I., & Wright, S. J. (2015). Phosphorus limitation, soil-borne pathogens and the coexistence of plant species in hyperdiverse forests and shrublands. *New Phytologist*, 206(2), 507-521.

Larsen, T. H., Lopera, A., & Forsyth, A. (2008). Understanding trait-dependent community disassembly: dung beetles, density functions, and forest fragmentation. *Conservation Biology*, 22(5), 1288-1298.

Larsen, T. H., & Forsyth, A. (2005). Trap spacing and transect design for dung beetle biodiversity studies 1. *Biotropica: The Journal of Biology and Conservation*, 37(2), 322-325.

Larsen, T. H., Williams, N. M., & Kremen, C. (2005). Extinction order and altered community structure rapidly disrupt ecosystem functioning. *Ecology Letters*, 8(5), 538-547.

Lindenmayer, D. B., Northrop-Mackie, A. R., Montague-Drake, R., Crane, M., Michael, D., Okada, S., & Gibbons, P. (2012). Not all kinds of revegetation are created equal: revegetation type influences bird assemblages in threatened Australian woodland ecosystems. *PLoS One*, 7(4), e34527.

Lindenmayer, D., Prober, S., Crane, M., Michael, D., Okada, S., Kay, G., et al. (2014). Temperate eucalypt woodlands. *Biodiversity and Environmental Change: Monitoring, Challenges and Direction*, 283-334.

Lobo, J. M. (2001). Decline of roller dung beetle (Scarabaeinae) populations in the Iberian peninsula during the 20th century. *Biological Conservation*, 97(1), 43-50.

Lobo, J. M., Hortal, J., & Cabrero-Sañudo, F. J. (2006). Regional and local influence of grazing activity on the diversity of a semi-arid dung beetle community. *Diversity and Distributions*, 12(1), 111-123.

Lobo, J.M., 1993. Estimation of dung beetle biomass (Coleoptera: Scarabaeoidea). *European Journal of Entomology*, 90: 235-238.

Lobo, J. M., Lumaret, J. P., & Jay-Robert, P. (1998). Sampling dung beetles in the French Mediterranean area: effects of abiotic factors and farm practices. *Pedobiologia*, 42(3), 252-266.

Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J. P., Hector, A., et al. (2001). Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science*, 294(5543), 804-808.

Loreau, M. (2000). Biodiversity and ecosystem functioning: recent theoretical advances. *Oikos*, 91(1), 3-17.

Lumaret, J. P., Kadiri, N., & Bertrand, M. (1992). Changes in resources: consequences for the dynamics of dung beetle communities. *Journal of Applied Ecology*, 349-356.

Lumaret, J. P. (1987). Ecology of dung beetles in the French Mediterranean region (Coleoptera: Scarabaeidae). *Acta Zoologica Mexicana*, 24, 1-55.

Lumaret, J-P., Kirk, A.A., 1991. South temperate dung beetles. In: Hanski, I., Cambefort, Y. (Eds.), *Dung beetle ecology*, Princeton University Press, Princeton, New Jersey, pp 97-115.

Macagno, A. L. M., & Palestrini, C. (2009). The maintenance of extensively exploited pastures within the Alpine mountain belt: implications for dung beetle conservation (Coleoptera: Scarabaeoidea). *Biodiversity and Conservation*, 18(12), 3309.

MacDonald, D., Crabtree, J. R., Wiesinger, G., Dax, T., Stamou, N., Fleury, P., et al. (2000). Agricultural abandonment in mountain areas of Europe: environmental consequences and policy response. *Journal of Environmental Management*, 59(1), 47-69.

Marini, L., Fontana, P., Klimek, S., Battisti, A., & Gaston, K. J. (2009). Impact of farm size and topography on plant and insect diversity of managed grasslands in the Alps. *Biological Conservation*, 142(2), 394-403.

Mason, N. W., & De Bello, F. (2013). Functional diversity: a tool for answering challenging ecological questions. *Journal of Vegetation Science*, 24(5), 777-780.

McGeoch, M. A., & Chown, S. L. (1998). Scaling up the value of bioindicators. *Trends in Ecology & Evolution*, 13(2), 46-47.

Morris, A. V., Roberts, C. M., & Hawkins, J. P. (2000). The threatened status of groupers (Epinephelinae). *Biodiversity & Conservation*, 9(7), 919-942.

Naeem, S., & Wright, J. P. (2003). Disentangling biodiversity effects on ecosystem functioning: deriving solutions to a seemingly insurmountable problem. *Ecology Letters*, 6(6), 567-579.

Navarrete, D., & Halffter, G. (2008). Dung beetle (Coleoptera: Scarabaeidae: Scarabaeinae) diversity in continuous forest, forest fragments and cattle pastures in a landscape of Chiapas, Mexico: the effects of anthropogenic changes. *Biodiversity and Conservation*, 17(12), 2869-2898.

Negro, M., Palestini, C., Giraud, M. T., & Rolando, A. (2011). The effect of local environmental heterogeneity on species diversity of alpine dung beetles (Coleoptera: Scarabaeidae). *European Journal of Entomology*, 108(1), 91.

Neita, J. C., & Escobar, F. (2012). The potential value of agroforestry to dung beetle diversity in the wet tropical forests of the Pacific lowlands of Colombia. *Agroforestry Systems*, 85(1), 121-131.

Nervo, B., Tocco, C., Caprio, E., Palestini, C., & Rolando, A. (2014). The effects of body mass on dung removal efficiency in dung beetles. *PLoS One*, 9(9), e107699.

Newbold, T., Hudson, L. N., Hill, S. L., Contu, S., Lysenko, I., Senior, R. A., et al. (2015). Global effects of land use on local terrestrial biodiversity. *Nature*, 520(7545), 45.

Nichols, E., Spector, S., Louzada, J., Larsen, T., Amezquita, S., Favila, M. E., & Network, T. S. R. (2008). Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. *Biological Conservation*, 141(6), 1461-1474.

Nichols, E., Larsen, T., Spector, S., Davis, A. L., Escobar, F., Favila, M., et al. (2007). Global dung beetle response to tropical forest modification and fragmentation: a quantitative literature review and meta-analysis. *Biological Conservation*, 137(1), 1-19.

- Nichols, E., Gardner, T. A., Peres, C. A., Spector, S., & Scarabaeinae Research Network. (2009). Co-declining mammals and dung beetles: an impending ecological cascade. *Oikos*, 118(4), 481-487.
- Numa, C., Verdú, J. R., Sánchez, A., & Galante, E. (2009). Effect of landscape structure on the spatial distribution of Mediterranean dung beetle diversity. *Diversity and Distributions*, 15(3), 489-501.
- Pakeman, R. J., & Marriott, C. A. (2010). A functional assessment of the response of grassland vegetation to reduced grazing and abandonment. *Journal of Vegetation Science*, 21(4), 683-694.
- Palmer, A. R., & Hoffman, M. T. (1997). Nama-karoo. *Vegetation of southern Africa*, 167, 186.
- Peck, S. B., & Forsyth, A. (1982). Composition, structure, and competitive behaviour in a guild of Ecuadorian rain forest dung beetles (Coleoptera; Scarabaeidae). *Canadian Journal of Zoology*, 60(7), 1624-1634.
- Peco, B., Carmona, C. P., De Pablos, I., & Azcárate, F. M. (2012). Effects of grazing abandonment on functional and taxonomic diversity of Mediterranean grasslands. *Agriculture, Ecosystems & Environment*, 152, 27-32.
- Peco, B., Sánchez, A. M., & Azcárate, F. M. (2006). Abandonment in grazing systems: consequences for vegetation and soil. *Agriculture, Ecosystems & Environment*, 113(1-4), 284-294.
- Perrings, C., Naeem, S., Ahrestani, F., Bunker, D. E., Burkill, P., Canziani, G., et al. (2010). Ecosystem services for 2020. *Science*, 330(6002), 323-324.
- Petchey, O. L., & Gaston, K. J. (2002). Functional diversity (FD), species richness and community composition. *Ecology Letters*, 5(3), 402-411.
- Petchey, O. L., & Gaston, K. J. (2007). Dendrograms and measuring functional diversity. *Oikos*, 116(8), 1422-1426.

- Petchey, O. L. (2003). Integrating methods that investigate how complementarity influences ecosystem functioning. *Oikos*, *101*(2), 323-330.
- Pineda, E., Moreno, C., Escobar, F., & Halffter, G. (2005). Frog, bat, and dung beetle diversity in the cloud forest and coffee agroecosystems of Veracruz, Mexico. *Conservation Biology*, *19*(2), 400-410.
- Pryke, J. S., Roets, F., & Samways, M. J. (2016). Wild herbivore grazing enhances insect diversity over livestock grazing in an African grassland system. *PloS One*, *11*(10), e0164198.
- Poschlod, P., Bakker, J. P., & Kahmen, S. (2005). Changing land use and its impact on biodiversity. *Basic and Applied Ecology*, *6*(2), 93-98.
- Purvis, A., & Hector, A. (2000). Getting the measure of biodiversity. *Nature*, *405*(6783), 212.
- Reidsma, P., Tekelenburg, T., Van den Berg, M., & Alkemade, R. (2006). Impacts of land-use change on biodiversity: an assessment of agricultural biodiversity in the European Union. *Agriculture, Ecosystems & Environment*, *114*(1), 86-102.
- Renwick, A., Jansson, T., Verburg, P. H., Revoredo-Giha, C., Britz, W., Gocht, A., & McCracken, D. (2013). Policy reform and agricultural land abandonment in the EU. *Land Use Policy*, *30*(1), 446-457.
- Rodrigues, E. T., Lopes, I., & Pardal, M. A. (2013). Occurrence, fate and effects of azoxystrobin in aquatic ecosystems: a review. *Environment International*, *53*, 18-28.
- Rosenmeier, M. F., Hodell, D. A., Brenner, M., Curtis, J. H., & Guilderson, T. P. (2002). A 4000-year lacustrine record of environmental change in the southern Maya lowlands, Petén, Guatemala. *Quaternary Research*, *57*(2), 183-190.
- Rudel, T. K. (2009). Tree farms: Driving forces and regional patterns in the global expansion of forest plantations. *Land Use Policy*, *26*(3), 545-550.

Saleh, S., Hasanah, U., & Eljonnahdi, E. (2014). Effectiveness of Dung Beetles as Bioindicators of Environmental Changes in Land-use Gradient in Sulawesi, Indonesia. *BIOTROPIA-The Southeast Asian Journal of Tropical Biology*, 21(1), 48-58.

Rodriguez V, Moreno C, Tabarelli M (2010) Edge-related loss of tree phylogenetic diversity in the severely fragmented Brazilian Atlantic Forest. *PLoS One*, 5, e12695.

Schleuter, D., Daufresne, M., Massol, F., & Argillier, C. (2010). A user's guide to functional diversity indices. *Ecological Monographs*, 80(3), 469-484.

Schulze, E. D., & Mooney, H. A. (Eds.). (2012). *Biodiversity and ecosystem function*. Springer Science & Business Media.

Sierra, R., & Russman, E. (2006). On the efficiency of environmental service payments: a forest conservation assessment in the Osa Peninsula, Costa Rica. *Ecological Economics*, 59(1), 131-141.

Simmons, L. W., & Ridsdill-Smith, T. J. (Eds.). (2011). *Ecology and evolution of dung beetles*. John Wiley & Sons.

Slade, E. M., Mann, D. J., Villanueva, J. F., & Lewis, O. T. (2007). Experimental evidence for the effects of dung beetle functional group richness and composition on ecosystem function in a tropical forest. *Journal of Animal Ecology*, 76(6), 1094-1104.

Slade, E. M., Riutta, T., Roslin, T., & Tuomisto, H. L. (2016). The role of dung beetles in reducing greenhouse gas emissions from cattle farming. *Scientific Reports*, 6, 18140.

Spasojevic, M. J., & Suding, K. N. (2012). Inferring community assembly mechanisms from functional diversity patterns: the importance of multiple assembly processes. *Journal of Ecology*, 100(3), 652-661.

Spector, S. (2006). Scarabaeine dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae): an invertebrate focal taxon for biodiversity research and conservation. *The Coleopterists Bulletin*, 60(mo5), 71-83.

Spector, S., & Ayzama, S. (2003). Rapid Turnover and Edge Effects in Dung Beetle Assemblages (Scarabaeidae) at a Bolivian Neotropical Forest-Savanna Ecotone. *Biotropica*, 35(3), 394-404.

Tilman, D., Isbell, F., & Cowles, J. M. (2014). Biodiversity and ecosystem functioning. *Annual Review of Ecology, Evolution, and Systematics*, 45, 471-493.

Toco, C., Negro, M., Rolando, A., & Palestirini, C. (2013). Does natural reforestation represent a potential threat to dung beetle diversity in the Alps? *Journal of Insect Conservation*, 17(1), 207-217.

Tonelli, M., Verdú, J. R., & Zunino, M. (2018). Effects of the progressive abandonment of grazing on dung beetle biodiversity: body size matters. *Biodiversity and Conservation*, 27(1), 189-204.

Tonelli, M., Verdú, J. R., & Zunino, M. (2019). Grazing abandonment and dung beetle assemblage composition: Reproductive behaviour has something to say. *Ecological Indicators*, 96, 361-367.

Tonelli, M., Verdú, J. R., & Zunino, M. E. (2017). Effects of grazing intensity and the use of veterinary medical products on dung beetle biodiversity in the sub-mountainous landscape of Central Italy. *PeerJ*, 5, e2780.

Verdú, J. R., Crespo, M. B., & Galante, E. (2000). Conservation strategy of a nature reserve in Mediterranean ecosystems: the effects of protection from grazing on biodiversity. *Biodiversity & Conservation*, 9(12), 1707-1721.

Verdú, J. R., Numa, C., & Hernández-Cuba, O. (2011). The influence of landscape structure on ants and dung beetles diversity in a Mediterranean savanna—forest ecosystem. *Ecological Indicators*, 11(3), 831-839.

Verdú, J. R., Moreno, C. E., Sánchez-Rojas, G., Numa, C., Galante, E., & Halffter, G. (2007). Grazing promotes dung beetle diversity in the xeric landscape of a Mexican Biosphere Reserve. *Biological Conservation*, *140*(3-4), 308-317.

Villéger, S., Mason, N. W., & Mouillot, D. (2008). New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology*, *89*(8), 2290-2301.

Vulinec, K., Lima, A. P., Carvalho Jr, E. A., & Mellow, D. J. (2008). Dung beetles and long-term habitat fragmentation in Alter do Chão, Amazônia, Brazil. *Tropical Conservation Science*, *1*(2), 111-121.

Webb, L., Beaumont, D. J., Nager, R. G., & McCracken, D. I. (2010). Field-scale dispersal of *Aphodius* dung beetles (Coleoptera: Scarabaeidae) in response to avermectin treatments on pastured cattle. *Bulletin of Entomological Research*, *100*(2), 175-183.

CHAPTER 4

GENERAL DISCUSSION AND CONCLUSIONS

4.1. Exploring the dung beetle communities of a Nama Karoo dryland ecosystem

This study represents a first account of dung beetle assemblages (Chapter 2) and functional diversity (Chapter 3) in the Nama-Karoo biome of South Africa and their responses to land-use change and different biotopes. I collected 2584 Individual dung beetles in two different collection seasons, using multiple bait types, and over a wide area. These belonged to fifteen different dung beetle species, consisting of five dweller species, four tunneller species and six roller species. Species diversity and abundance of dung beetles are therefore very low compared to other systems in South Africa (Hanski and Cambefort 1991; Pryke *et al.* 2013) and abroad (Jay-Robert *et al.* 1997; Jay-Robert 2008; Verdu and Galante 2004). This is likely due to the aridity of the region and the fact that it is currently experiencing a prolonged drought as dung beetle numbers and precipitation are usually closely correlated. Regions in which sampling was conducted in the present study also devoid of historically occurring large mammals to which local populations of dung beetles would have been adapted to. Therefore, future studies should consider comparing sites in the Nama-Karoo that still contain these mammals to experimental sites as these can serve as reference sites towards which conservation managers should aim to restore. However, the Nama-Karoo in South Africa seems to be generally quite depauperate in dung beetles (Davies *et al.* unpublished) and the numbers collected here may well be a true reflection on most of the diversity at these sites. Notwithstanding, the current study was conducted in an area for which there were no previous information on dung beetle species occurrence available. As such, I provide much needed data that will be invaluable for future conservation decisions (for example, potentially useful for Karoo biogas projects; see <https://www.sanbi.org/karoo-biogaps-project/>).

All of the true dung beetle species (Scarabaeinae) collected here are widely dispersed generalist feeders (Davis *et al.* unpublished), a feature that seems common for this taxon within arid ecosystems. This is likely due to the scarcity of dung resources in this environment which promotes the use of multiple resources. It was therefore surprising that the carrion bait used in the study did not attract any dung beetles, even more so as some of the species collected here (e.g., *Euoniticellus intermedius* and *Scarabaeolus damarensis*) are known carrion feeders (Davis *et al.* unpublished). Also surprising was the relatively few taxa that were attracted to the sheep dung, especially as this resource would be very common on the active farms. Instead, most individuals were attracted to the pig and cow dung, showing strong connections between dung beetles and non-pelleted, moister dung types. Reintroductions of native ruminants and omnivores would therefore go a long way in restoring dung beetle numbers and functional diversity. However, it is possible that the sampling design followed here resulted more in a “buffet-style” choice experiment than a true reflection of the exploitation of dung sources in general. Traps were set at ca. 100 meters apart as this spacing allows for little trap interference as defined by (Larsen and Forsyth 2005; Pryke *et al.* 2016). Even though this standard is maintained for numerous studies on dung beetle diversity (Larsen and Forsyth 2005) it is based on collections of beetles in a vastly different biome, (primary forests) than the one focused on in the present study. Therefore, in the present study there were far fewer obstacles in the form of vegetation to interfere with beetle flight patterns and with the distribution of dung volatiles in the air. This may result in the beetles being able to detect all of the different dung types present in the experimental area. They were then able to choose the one that they were most attracted to, rather than using the closest source. This may be a general issue with dung beetle diversity studies in other open environments and should be investigated in future studies.

4.2. *The effect of biotope on dung beetles*

A total of 1275 individual dung beetles were collected in flat lands (fourteen species), 880 individual dung beetles were found in riparian zones (twelve species) and 429 individual dung beetles were found in mountainous areas (eleven species). Different biotopes therefore differed substantially in their dung beetle communities as is known from other systems (Pryke *et al.* 2016). This highlights the importance of maintaining the integrity of as many different biotopes as possible to maintain local dung beetle communities and their functions. It also indicated that flatlands and riparian areas in the Nama-Karoo are particularly valuable for maintaining dung beetle diversity. However, these are also the areas that are under most significant pressures from overgrazing and other anthropogenic threats. For farmers, maintaining good ecological integrity in the flatlands to the benefit of dung beetles would not only benefit the beetles themselves, but also their associated ecosystem services. For example, dung beetles remove dung from the soil surface resulting in reduced pest and parasite populations (Simmons and Ridsdill-Smith 2011). They also enrich the soil, increasing the growth vigour of plants (Munroe *et al.* 2013). In addition, they are responsible for secondary seed dispersal and bury seeds at a depth that is more conducive to germination and less overcrowding and above-ground seed predation (Nichols *et al.* 2008). Increasing the activity of dung beetles would therefore lead to a positive feedback loop that will increase plant growth and the carrying capacity of the system. Although this has been well researched in other systems (Carpaneto *et al.* 2005; Jay-Robert *et al.* 2008; Tonelli *et al.* 2017; Verdú *et al.* 2000), the degree to which dung beetles are involved in soil enrichment and secondary seed dispersal. This has positive effects on vegetation has received no attention in this arid region and may therefore prove to be a fruitful field for future study.

4.3. *The effects of ceasing livestock farming*

There were 601 individual dung beetles found in currently grazed areas (twelve species), 1084 individual dung beetles found in recently non-grazed areas (thirteen species) and 899 individual dung beetles (thirteen species) found in non-grazed areas. This showed the positive impact that grazing abandonment (mainly by sheep) had on dung beetle diversity and the community assemblage, also an increase in their diversity as time progresses from the point of abandonment. This was contrary to other studies on the subject where (Liberal *et al.* 2011).

In other systems the decrease in dung beetle diversity was related to a decrease in the available dung resources. Here, the most dominant resource on farms (sheep dung) was not readily attractive to dung beetles and, therefore, with the removal of sheep there was little effect on dung resources for the beetles. Instead, their numbers increased after sheep removal likely due to greater availability of dung sources from native animals whose numbers would increase in areas that were abandoned. On these managed farms, predators were being killed and pushed for safety of the sheep, as well as herbivores were being hunted and pushed out of farming areas to protect grazing lands. Thus, the SKA radio astronomy observatory appears to already provide a reserve for dung beetle community conservation in what is essentially a livestock farming matrix. However, dung beetle biomass was still high at actively grazed sites. Large dung beetles, which included *Scarabaeus viator* and *Scarabaeolus karrooensis* in this study, were still common in grazed areas, indicating that relatively large dung beetle species that probably play comparatively large roles in ecosystem functions can become rare after land abandonment, as is known in other systems (Larsen *et al.* 2005; Tonelli *et al.* 2018). In essence, apart from those mammals naturally returning to abandoned farmlands, promoting an increase in dung beetle numbers by introducing appropriate native mesoherbivores, such as wildebeest (*Connochaetes taurinus*)—to increase the appropriate dung resources in these abandoned landscapes—would increase their functional roles in abandoned areas. For active

farmers, and of course only those that have the ability to do so, also introducing a greater mix of mesoherbivores with their sheep farming would help conserve a wider array of dung beetles in the landscape.

Functional richness was also usually higher in the abandoned landscapes than in the currently grazed areas (Chapter 3). This effect is closely linked to an increase in species richness. The link between species richness and increased functional roles is well-established as different species fill different niches in ecological systems. This often translates to increased functions in ecosystems (Petchey and Gaston 2002; Tonelli *et al.* 2017). However, whether the increases reported in the current study translates to increased functions such as dung removal and secondary seed dispersal is not known. There is therefore a strong need for future studies to incorporate more functional measures related to changes in dung beetle diversity as a result of anthropogenic change on ecosystem processes.

References

- Carpaneto, G. M., Mazziotta, A., & Piattella, E. (2005). Changes in food resources and conservation of scarab beetles: from sheep to dog dung in a green urban area of Rome (Coleoptera, Scarabaeoidea). *Biological Conservation*, 123(4), 547-556.
- Hanski, I., & Cambefort, Y. (1991). Competition in dung beetles. *Dung Beetle Ecology*, 305-329.
- Jay-Robert, P., Niogret, J., Errouissi, F., Labarussias, M., Paoletti, É., Luis, M. V., & Lumaret, J. P. (2008). Relative efficiency of extensive grazing vs. wild ungulates management for dung beetle conservation in a heterogeneous landscape from Southern Europe (Scarabaeinae, Aphodiinae, Geotrupinae). *Biological Conservation*, 141(11), 2879-2887.

- Jay-Robert, P., Lobo, J. M., & Lumaret, J. P. (1997). Altitudinal turnover and species richness variation in European montane dung beetle assemblages. *Arctic and Alpine Research*, 29(2), 196-205.
- Larsen, T. H., & Forsyth, A. (2005). Trap spacing and transect design for dung beetle biodiversity studies 1. *Biotropica: The Journal of Biology and Conservation*, 37(2), 322-325.
- Larsen, T. H., Williams, N. M., & Kremen, C. (2005). Extinction order and altered community structure rapidly disrupt ecosystem functioning. *Ecology Letters*, 8(5), 538-547.
- Liberal, C. N., de Farias, Â. M. I., Meiado, M. V., Filgueiras, B. K., & Iannuzzi, L. (2011). How habitat change and rainfall affect dung beetle diversity in Caatinga, a Brazilian semi-arid ecosystem. *Journal of Insect Science*, 11(1), 114.
- Munroe, D. K., van Berkel, D. B., Verburg, P. H., & Olson, J. L. (2013). Alternative trajectories of land abandonment: causes, consequences and research challenges. *Current Opinion in Environmental Sustainability*, 5(5), 471-476.
- Nichols, E., Spector, S., Louzada, J., Larsen, T., Amezcuita, S., Favila, M. E., & Network, T. S. R. (2008). Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. *Biological Conservation*, 141(6), 1461-1474.
- Petchey, O. L., & Gaston, K. J. (2002). Functional diversity (FD), species richness and community composition. *Ecology Letters*, 5(3), 402-411.
- Pryke, J. S., Roets, F., & Samways, M. J. (2013). Importance of habitat heterogeneity in remnant patches for conserving dung beetles. *Biodiversity and Conservation*, 22(12), 2857-2873.
- Pryke, J. S., Roets, F., & Samways, M. J. (2016). Wild herbivore grazing enhances insect diversity over livestock grazing in an African grassland system. *PloS One*, 11(10), e0164198.
- Simmons, L. W., & Ridsdill-Smith, T. J. (Eds.). (2011). *Ecology and evolution of dung beetles*. John Wiley & Sons.
- Tonelli, M., Verdú, J. R., & Zunino, M. E. (2017). Effects of grazing intensity

and the use of veterinary medical products on dung beetle biodiversity in the sub-mountainous landscape of Central Italy. *PeerJ*, 5, e2780.

Tonelli, M., Verdú, J. R., & Zunino, M. (2018). Effects of the progressive abandonment of grazing on dung beetle biodiversity: body size matters. *Biodiversity and conservation*, 27(1), 189-204.

Verdú, J. R., Díaz, A., & Galante, E. (2004). Thermoregulatory strategies in two closely related sympatric *Scarabaeus* species (Coleoptera: Scarabaeinae). *Physiological Entomology*, 29(1), 32-38.

Verdú, J. R., Crespo, M. B., & Galante, E. (2000). Conservation strategy of a nature reserve in Mediterranean ecosystems: the effects of protection from grazing on biodiversity. *Biodiversity & Conservation*, 9(12), 1707-1721.