Replacing wild grazers with domestic livestock: effect on dung beetle diversity, biomass, size and ecosystem function in a semi-arid Namibian savannah

by

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DECLARATION

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GENERAL SUMMARY

Anthropogenic activities have parcelled most native mammals into protected areas while cattle and other livestock replace them as the dominant grazers in the surrounding farmlands. This has severe consequences for biodiversity reliant on the resources provided and functions performed by native mammals. These effects can precipitate through multiple trophic levels and ultimately lead to changes in ecosystem processes. A taxon frequently used to measure these changes are dung beetles who are increasingly used as a study taxon—both as a model system for exploring ecosystem functioning and as bioindicators of environmental change. The advantages of using dung beetles are many: they are speciose, abundant in a wide range of terrestrial ecosystems, they respond to environmental gradients and sampling methods are straightforward. Despite their frequent use in land-use and habitat change studies, there is little research on the relationship between dung beetles and the mammals they rely on for dung. Few studies have evaluated both the response of this keystone taxa to land transformation associated with livestock farming and its consequences for ecosystem functions and services. Furthermore, no studies to this effect have been undertaken in the semi-arid Namibian savannahs despite being particularly rich in mammal species and experiencing ever-increasing anthropogenic pressures. Here, I aim to elucidate how land-use change (natural ecosystems into rangeland farming) and the accompanying loss of native vertebrates affects the diversity, development and ecosystem functions provided by dung beetles (Scarabaeidae: Scarabaeinae and Aphodinae). This was accomplished by comparing dung beetle diversity (richness, abundance and biomass), developmental attributes (individual size) and their main ecological functions (secondary seed dispersal and dung removal) between farmlands and protected areas in an area previously neglected in terms of dung beetle diversity studies: African savannahs. The region was very diverse with over a hundred dung beetle species and over 76 000 individuals collected in a relatively small area and during a few months of sampling. Amongst the species sampled, some were collected for the first time in decades and others well beyond their known geographic ranges. At a larger scale, I demonstrated that protected areas harbour far richer vertebrate communities compared to farmlands which had severe effects on dung beetle richness, abundance, biomass and community assemblage composition. Dung beetle species richness was positively correlated with vertebrate richness but not with stocking density, indicating that a rich native vertebrate assemblage is paramount in conserving natural dung beetle diversity. Numerous species were found on farmlands in high abundance, indicating an ability to adapt to these altered conditions, however, the individual development of many of these species was negatively affected due to diminished availability of native dung on farmlands. The native dung was therefore assumed to be of higher quality due to the lack of veterinary pharmaceutical use. Decreases in dung beetle diversity on farmlands lead to decreased ecosystem functioning particularly at the expense of the loss of larger, specialist species. This work, in keeping with the broader literature,

shows that rich native vertebrate diversity is not only important to support and promote diverse dung beetle communities but also for maintaining the ecosystem functioning of these threatened savannah landscapes.

OPSOMMING

Antropogeniese aktiwiteite het gelei daartoe dat inheemse soogdiere in beskermde gebiede verpak word, terwyl beeste en ander vee hulle as die dominante beweiders in die omliggende matriks vervang. Dit kan ernstige gevolge hê vir biodiversiteit wat afhanklik is van hulpbronne wat deur inheemse soogdiere voorsien word. Hierdie effekte kan deur verskeie trofiese vlakke presipiteer en uiteindelik tot veranderinge in ekosisteemprosesse lei. Slegs 'n paar studies het beide die reaksie van kern taxa op grondtransformasie beoordeel, asook die gevolge hiervan vir ekosisteemfunksies en -dienste. Geen studies hiroor is onderneem in die semi-droë Namibiese savanne nie, hoewel hierdie areas besondrs ryk aan soogdiere is, maar wat ook toenemende antropogeniese druk ondervind. Hierdie studie het ten doel gehad om te verstaan hoe verandering in grondgebruik, van natuurlike ekosisteme na landelike boerderye, en die gepaardgaande verlies van inheemse gewerwelde diere, 'n invloed het op diversiteit, ontwikkeling, ekosisteemfunksie en die dienste gelewer deur 'n kern takson, miskruiers (Scarabaeidae: Scarabaeinae en Aphodinae). Dit is bewerkstellig deur die veranderinge in die kenmerke van die miskruier-diversiteit (rykheid, getalle en biomassa), ontwikkelingskenmerke (individuele grootte) en hul belangrikste ekologiese funksies (sekondêre verspreiding van saad en misverwydering) tussen landbougrond en beskermde gebiede in die Namibiese savanne te bepaal. Ek het gewys dat die Namibiese savanne baie divers is in miskruiers aangesien meer as 100 spesies en meer as 76 000 individue binne 'n paar maande in 'n betreklik klein gebied versamel is. Talle spesies wat voorheen baie swak bekend was, of spesies wat nie voorheen van Namibië bekend was nie, is versamel. Hierdie studie dra dus aansienlik by tot die bewaring van oënskynlike skaars miskruierspesies. Op 'n groter skaal demonstreer ek dat beskermde gebiede baie ryker gewerwelde gemeenskappe het in vergelyking met landbougrond, en dit het 'n negatiewe uitwerking op die spesierykheid van miskruiers, hul getalle, biomassa en hul gemeenskapsamestelling. Spesiesrykheid was negatief gekorreleer met die werweldierrykheid, maar nie met veedigtheid nie, wat 'n aanduiding is dat 'n ryk inheemse werweldiergemeenskap belangrik is om natuurlike miskewerdiversiteit te bewaar. Talle spesies is in redelike hoë getalle op landbougrond versamel, wat 'n aanduiding is dat hulle by hierdie veranderde toestande kan aanpas. Ten spyte hiervan is die individuele ontwikkeling van baie van hierdie spesies negatief beïnvloed waarskynlik as gevolg van die lae beskikbaarheid van inheemse hoë gehalte mis op landbougrond. Veranderings in diversiteit lei ook tot afname in die funksionering en ekosisteem dienste (mis verwyder en sekondêre verspreiding van saad) wat deur miskruiers op plaasgrond voorsien word. Groter spesies wat oënskynlik gespesialiseerd was in mis van inheemse gewerwelde diere, was die meeste geraak, wat tot 'n aansienlike verlies aan hul funksies gelei het. Ek toon aan dat 'n ryk inheemse werweldierdiversiteit nie net belangrik is om die ongeskonde bioverskeidenheid van miskewers te handhaaf nie, maar ook vir die normale funksionering van hierdie bedreigde savanne-landskappe.

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DEDICATION

This thesis is dedicated to:

My parents Uaundja and Veenda Nependa

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General Introduction

Burgeoning human populations and pervasive anthropogenic disturbance have led to population declines of wild herbivores throughout much of the world (Dirzo and Raven 2003; Collen et al. 2009; Wilkie et al. 2011; Young et al. 2013). African savannahs and woodlands are among the few places on the globe where wild herbivores persist in high abundances. Even so, massive declines of megafauna are increasingly reported due to range contractions (Nichols et al. 2009; Malhi et al. 2016). This is driven by the high productivity of savannah landscapes that lends itself to the raising of domestic livestock (Young et al. 2014). Increases in agricultural practices in savannah landscapes also lead to increasing conflict between wildlife and humans (Malhi et al. 2016; Young et al. 2018).

The dramatic declines of native fauna have been particularly concerning, especially due to the strong effects mammalian herbivores exert on the vegetation physiognomy in savannahs (Scholes and Archer 1997; Bond 2008) and trophic structures in these ecosystems (Estes et al. 2011; Malhi et al. 2016). Populations have been diminished not only outside protected areas, but also within, resulting with species now vulnerable and some locally extinct (Western 1989; Georgiadis 2011; Young et al. 2014; Malhi et al. 2016). The effects of these disturbances on birds, vegetation and large charismatic mammals have been relatively well documented (Happold 1995; Newmark 2008). However, far less is known about the impacts of habitat modification on the entomofauna of the African savannah, one of the most diverse taxa in these systems (Stork 1988; Pryke et al. 2016; Hering et al. 2019). Research has also largely focused on direct impacts of anthropogenic activity on certain taxa, with cascading effects across multiple trophic levels receiving less attention (Brook et al. 2008, Tylianakis et al. 2008; Nichols et al. 2009). There is therefore and an urgent need for more research on the ecological consequences of land-use change on biodiversity and ecosystem functions when keystone resource providers such as megafauna are removed (Nichols et al. 2009; Culot et al. 2013; Bogoni et al. 2019; Raine et al. 2019).

1.1 Namibia, an exceptionally diverse African landscape facing strong anthropogenic threats

Namibia is a mainly arid land renowned for its deserts, the Namib and the Kalahari. However, it is also characterised by straddling woodland and savannah biomes which makes the country remarkably biodiverse, boasting ancient biotic communities rich in endemics (Barnard et al. 1998; de Klerk 2004; Midgley et al. 2005; Joubert et al. 2013). Many species ranges extend across its borders to the north, east and south (Angola, Botswana, Zambia and South Africa respectively) and the region has biogeographic affinities with the north-eastern arid montane landscapes of Africa (Barnard et al.

1998). These features make it an important region for conservation and a prime area for biodiversity research.

Namibia falls within the 17°S to 25°S latitudinal zone, the Sub-Tropical High-Pressure Belt. The overall climate is therefore mostly arid and shaped by a multitude of aridifying characteristics such as proximity to the Hadley cell and the cold Benguela current (Midgley et al. 2005). As a result, convectional rainfall in the interior of the country is restricted and shows immense inter-annual variability and droughts are common. Rainfall is sporadic thundershowers between the summer months of September and March which separated into two: the "small" rainy season from September to November and the "big" rainy season between February and April (Barnard 1998; Barnard et al. 1998; De Klerk 2004).

Climatic constraints have endowed the country with unique and rich environmental attributes and Namibia boasts an extraordinarily interesting and species-rich biotic community (Midgley et al. 2005). Namibia contains four major biomes namely: Succulent Karoo, Nama Karoo, tree and shrub savannah and the Namib Desert and they can further be partitioned into 14 distinctive ecoregions (Fig 1.1) Desert occupies the western coastal plains and the south while savannah occupies the central and north-central plateau and woodlands the more mesic north-east (Geiss 1971; Barnard 1998). The northern region of Namibia is primarily branded as shrub and thornbush savannah biome and comprises a narrow escarpment that delimits the ecoregion from the Kaokoveld and Namib Desert (Fig 1.1). The central district consists of Kartsveld and montane bushveld with dolomite, limestone and marble hills that are adjacent to the Otavi mountain range which comprises the unique mountain savannah (Maggs et al. 1998). The rest of the area is characterised by mopane savannah, semi-desert and savannah transition, and dwarf shrub savannah and some elements of Nama Karoo. The result: scenic juxtapositions of vast, open, arid regions dominated by low-shrub vegetation, promptly interrupted by savannah woodlands and impenetrable acacia bush (Dean and Milton 1999).

Faunal communities tend to correspond with the vegetation zones. The savannah expanse supports a rich and diverse array of plains game species all of which are impressively adapted to its climatic extremes, including several threatened species like the white (*Ceratotherium simum*) and black rhinoceroses (*Diceros bicornis).* Other important mammals include large herds of ungulates including black wildebeest (*Connochaetes gnou*), gemsbok (*Oryx gazella*) and mountain zebra (*Equus zebra hartmannae*). These large mammals maintain open grassy ecosystems through behaviour and foraging and provide a top-down-control of vegetation structure and architecture where they still exist (Vohland et al. 2005; Bond 2008).

Map 4: Biomes and vegetation types in Namibia

Vegetation type
- Caprivi Floodplains
- Caprivi mopane woodland
- Central Kalahari
- Central desert
- Central-western escarpment and inselbergs
- Cuvelai drainage
- Desert/dwarf shrub transition
- Dwarf shrub savanna
- Dwarf shrub/southern Kalahari transition
- Eastern drainage
- Etosha grass and dwarf shrubland
- Highland shrubland
- Karas dwarf shrubland
- Karstveld
- Mopane shrubland
- North-eastern Kalahari woodlands
- North-western escarpment and inselbergs
- Northern Kalahari
- Northern desert
- Okavango valley
- Omatako drainage
- Pans
- Riverine woodlands and islands
- Southern Kalahari
- Southern desert
- Succulent steppe
- Thornbush shrubland
- Western Kalahari
- Western highlands

Biomes in Namibia

Broad-leaved

Acacia

Namibian landscapes make up a mosaic of various land-use types which include pastoralism, commercial livestock production, subsistence dryland cropping and other forms of land management such as private nature reserves, national parks, game ranches and mining (Barnard et al. 1998). Approximately 46% of the total surface area is under some form of conservation management and formally protected areas make up 13.8% or roughly 114 080 km^2. These form the Protected Areas Network (PAN) with increasing amounts of land also protected by private nature reserves and wildlife conservancies (Figure 1.2). The rest forms part of the world-renowned community-based natural resource management (CBRNM) (Barnard 1998) further enabling conservation efforts.

Although biodiversity conservation seems well assured with the impressive size of the country and the areas protected, the assignment of conservation areas did not focus on the conservation of biological diversity. Rather they were designed with economic, veterinary and ideological considerations as a primary basis. As a result, the PAN delineation is more reflective of land that is unsuitable for agriculture, and of interest to tourists, making it dangerously insufficient as a basis for effective biodiversity conservation (Barnard 1998). The Namib Desert biome, for example, makes up 69% of the entire PAN while woodlands and savannahs only have 8.4% and 7.5% of their entire land areas protected (Fig 1.1; Figure 1.2) (Barnard et al. 1998) and mountain savannah, a vegetation type unique to Namibia is wholly unprotected (Maggs et al. 1998). Despite the PAN's haphazard origins and bias in ecological representation, it is still a reasonable scaffold on which to improve a representative assortment of informal and state-protected conservation areas. If augmented with novel and integrative conservation strategies, and more thoughtfully identified and designed sites, it may safeguard valuable biological diversity much more comprehensively (Kremen et al. 1993; Barnard et al. 1998).

The conservation strategy and efforts in Namibia have been much-admired over the last few decades and strides have been made to preserve the important and charismatic species of the country. This management strategy has helped revive populations of many species (Ministry of Environment and Tourism 2014). The PAN, although impressively sized and conservation well assured within its margins, has proven insufficient for safeguarding wildlife outside its delineation. The bias in ecological representation is a cause of great concern particularly for less charismatic species that don't receive any conservation attention but have keystone status and whose loss may have ruinous effects on the environment. There is, therefore, a need to assess existing conservation efforts for their efficacy in preserving all biodiversity (Barnard et al. 1998).

Around 40% are communal areas and 20% are national parks and restricted areas. Much of the wildlife outside protected areas are on private farmland. Namibian farmland, therefore, has a crucial role to play in the sustainable management and conservation of the country's wildlife and cheetahs in particular (Förster and Förster 2007). Agricultural landscapes in Namibia are largely modified due to the decline in megaherbivores, fire suppression and extensive large-scale farming have altered habitats while protected areas (hereafter PA(s)) have maintained structural complexity which helps maintain a more diverse species pool (Tscharntke et al. 2005). Private PAs are established primarily with scenic and biological diversity in mind with stringent restrictions on land-use activities (e.g. hunting) focusing on enhancing habitat for charismatic game species such as ungulates and gamebirds (Ashley and Barnes 1996). Therefore, private PAs take exceptional care when designing management

plans that are often bound by ecologically sensitive objectives such as managing stocking rates and water regimes (Barnes and de Jager 1996).

By contrast, livestock farming operates under very different objectives and often suffer from higher stocking rates and intensified water usage. Unfortunately, livestock species are now the most abundant herbivores in Namibian savannah ecosystems (Vohland et al. 2005; Bond 2008) with native mammal species goaded into PAs with cattle replacing them in the surrounding matrix (Barnard et al. 1998). Fences are a fundamental barrier between PAs and livestock farms and, although they have veterinary considerations in mind, impede the migratory routes of native ungulates and exclude important ecosystem functions that maintain diverse vegetation mosaics (Main 1987; Albertson 1998). Farms however still have a large and vital role to play in sustainable management and overall conservation of wildlife because *ca*. 90% of the Cheetah population lives on commercial farmland (Marker 2002) and *ca*. 80% of other commercially usable large game species roam through farmland (Brown 1992).

An assessment of the potential impacts of anthropogenic climate change on Namibian vegetation by Midgley et al. (2005) revealed that the warming projections for Namibia were higher than the current mean. Coupled with Namibia's inconsistent rainfall this places further pressure on natural resources (Thullier et al. 2006). This is exacerbated by increases in CO_2 that favour trees (C3 plants) compared to grasses (C4) leading to bush encroachment. Bush encroachment has adverse effects on land productivity and biodiversity, water-use efficiency and underground water tables and therefore negatively affects many mammals, birds and arthropods (de Klerk 2004; Bond 2008). Bush encroachment and thickening is a very large problem in Namibia with approximately 72% of farmers labelling it as the greatest threat to reaching their maximum outputs (McGranahan 2008). Climate change also extends to changes in rainfall variability and anthropogenic climate change has resulted in a greater frequency of very wet years followed by severe droughts however it remains unclear whether this pattern will promote bush encroachment (particularly in the wet years) (Bond 2008; O'Connor et al. 2014). All this results in considerable changes in ecosystem functioning, vegetation structure and species diversity. The severe changes in the climate make agriculture (an already difficult practice in Namibia) difficult and reduce the overall productivity due to fewer resources for livestock and wildlife (Thullier et al. 2006).
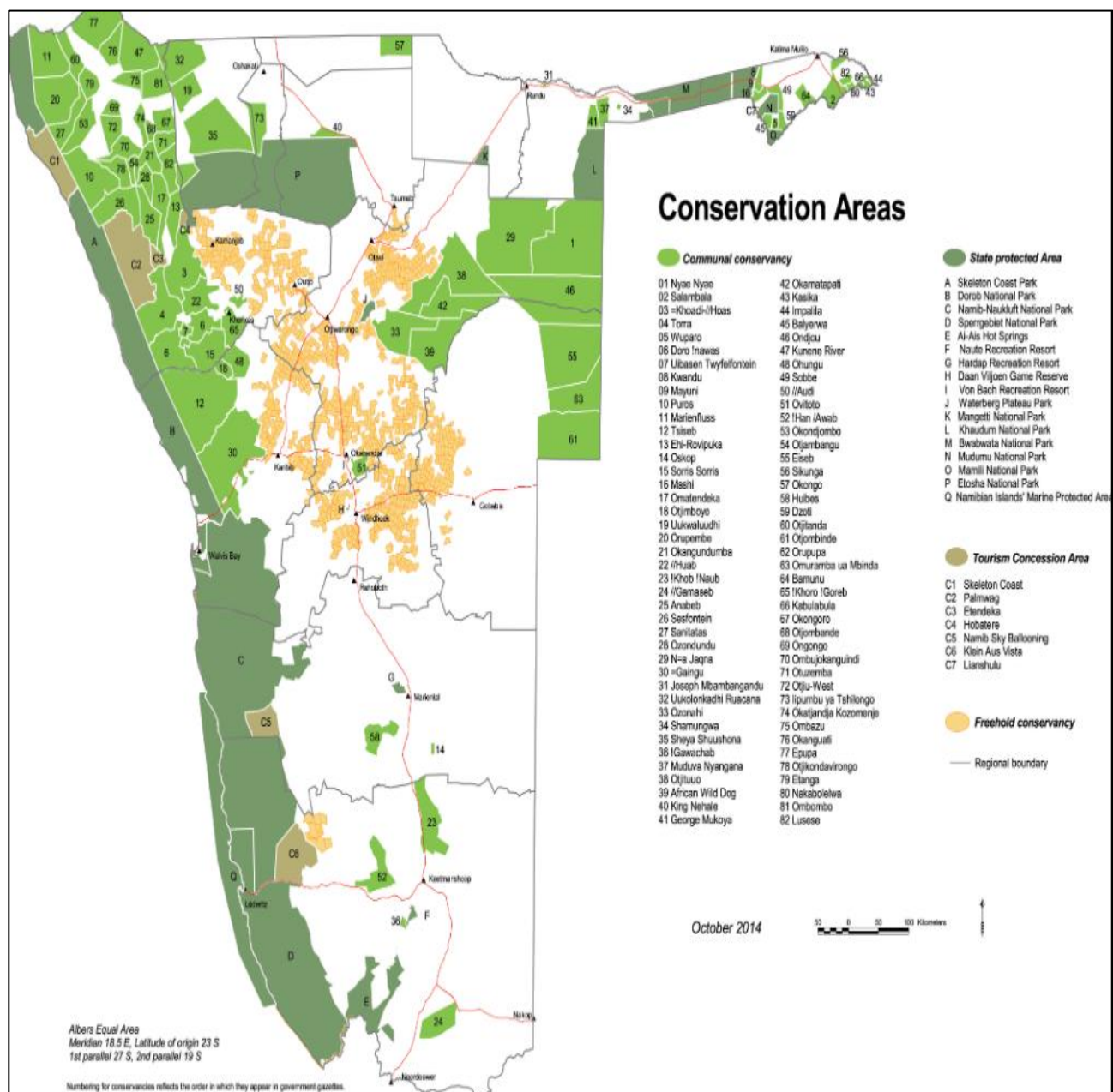
Figure 1.2 Map of land partitioning in Namibia with major conservation areas in green. Freehold conservancies and concession areas are also represented. The remaining area is private land either used for farming of livestock or as private protected areas. Source: NACSO at http://www.nacso.org.na/resources/map

1.2 Dung beetles, ecologically diverse keystone members of ecosystems

Dung beetles form part of the coleopteran subfamily Scarabaeinae (they are considered the "true" dung beetles) and are a largely coprophagous group specialized to feeding on the microorganism-rich liquid component of mammalian dung and show a range of associations and adaptations with regards to dung type, seasonality, soil type and vegetation (Davis et al. 2008; Nichols et al. 2008; Tshikae et al. 2008). Dung beetles exploited an unoccupied niche during the Tertiary that was punctuated by the opening of habitats and establishment of savannahs and grasslands, starting from the Miocene (Sole and Scholtz 2010). This era saw the subsequent evolution of large mammalian herbivores living

in herds that produced large quantities of moist dung (Hallfter and Edmunds 1982; Scholtz et al. 2009; Nichols et al. 2011). The most important trait that developed was the fast exploitation of dung, protecting it from drying and other climatic vagaries that ensured prolonged use of the precious resource. These food relocation strategies motivated the development of subterranean nests and brood care which, not only make dung beetles unique but also resulted in high fitness and low mortality during development (Scholtz et al. 2009). This highlights the strong relationship between mammals and dung beetles (Raine and Slade 2019).

Dung beetles construct tunnels ending in either spherical, pearl-shaped, oval or elongate broods that are encompassed by moulded masses of dung in which they lay their eggs. Each brood contains a single egg, although some contain several eggs in multiple brood masses and are kept separate from their neighbours. Broods are assembled from dung packed at the end of the tunnel each modified in a chamber in a manner and form representative of a particular species (Fig 2.3). Seven key variations of nesting have been identified (Davis et al. 2008). Davis et al. (2008) and Scholtz et al. (2009) describe four distinct variants of dung-exploitation behaviour and morphological traits: 1) Paracoprids are tunnellers and makeup approximately 70% of African species. They excavate tunnels directly under dung pads and dung is buried one small piece at a time. Tunnellers often relocate the most dung and produce the most offspring per event in many ecosystems and they bury their dung about 2-3 times deeper than rollers (Davis et al. 2008; Scholtz et al. 2009). 2) Telocoprids are ball-rollers and are perhaps the most popular even though they make up only 15% of African species. They either roll dung balls or portion some dung (up to 7-9cm in diameter in some species) some distance away from the dropping and bury it in tunnels. They are notably less adapted for burrowing than their paracoprid counterparts, a trait that they traded for fast dung removal and they subsequently also construct far shallower burrows. 3) Endocoprids are dwellers that breed in pits within chambers excavated within large droppings or at the dung-earth interface. 4) Kleptocoprids are scroungers that nest in dung balls of tunnellers and rollers (Fig 2.3) (Davis et al. 2008). The various patterns of faeces manipulation, consumption and relocation by dung beetles drives a series of ecological process including nutrient cycling, parasite suppression and biological pest control, soil fertilization, bioturbation and secondary seed dispersal. Dung beetles also play a role in plant growth enhancement, pollination and trophic regulation. These ecological functions instigate several ecosystem services making dung beetles integral members of many ecosystems and production landscapes (Davis et al. 2008; Nichols et al. 2008).

Telecoprids (rollers)

Large diurnal rollers spend ca. 2 hours in the dung pad. They move their dung balls several meters away from the dung pad

Smaller rollers are also diurnal and will spend upwards of 24 hours rolling dung balls. Rollers bury their dung up to 20cm

20 cm
40 cm
60 cm
80 cm
90 cm

Fast burying tunnellers create compound subterranean nests. They are crepuscular or diurnal and can spend between 6 and 24 hours removing dung

Endocoprids (dwellers)

Dwellers are diurnal and can stay in the dung deposit for many weeks after feeding with their brood balls

Small and slow burying and can be crepuscular, diurnal or nocturnal. They make shallow nests that they fill with brood balls and spend several weeks in dung pads

Paracoprids (tunnellers)

Large tunnellers that bury the dung slowly in compound subterranean nests with brood masses. They are usually nocturnal and can ca. 6 weeks under the dung pad

Figure 1.3 Nesting habitats of dung beetles representing each of the major functional groups, their removal behaviour and the various depths to which they bury their dung (Modified from Floate 2011)

Parasite and pest suppression

Adult and larval dung beetles control the abundance of dung-dispersed protozoa and nematodes dung-breeding hematophagous and detritivorous flies simply through their nesting and breeding activities. For example, Bryan (1973) found that dung beetles suppress parasites and pests by desiccating the dung soon after defecation which can dissuade the migration of helminth larvae to herbage. Dung beetles can also cause premature pupation of flies by diminishing their food source (Bryan 1973). These services have considerable implications for wildlife, human and livestock health and well-being (Bornemissza 1960, 1970; Nichols et al. 2008). This service is so important that a biological control measure was undertaken by Australia where four different South African dung beetle species attracted to ruminant dung were imported during the 1960s. These species have successfully established themselves and are now prominent features in Australia's livestock producing regions and have not only led to an increased gain in available grazing areas but also the significant suppression of bush fly populations (Bornemissza 1960, 1970; Waterhouse 1974).

Nutrient cycling

A substantial portion of nutrients consumed by vertebrates is voided in excreta and the extent to which these nutrients can be returned to plant growth cycle has strong implications for plant productivity (Nichols et al. 2008). Freshly deposited faecal matter is transferred below the soil surface by rolling and tunnelling dung beetles which allows for the relocation of nutrient-rich organic material into the soil which instigates micro-organismal and chemical changes in the upper soil layers (Steinfeld et al. 2006; Davis et al. 2008). This is particularly integral in agroecosystems and soil benefits from this fertilization. Nitrogen is presumably the most critically limiting factor structuring plant productivity, however, an FAO report estimated that of the 30 million tons of nitrogen excreted by livestock, 12 million is lost through ammonia NH_3 volatilization (Steinfeld et al. 2006). Dung beetles prevent this excessive loss of nitrogen by making nitrogen available for uptake by plants through mineralization (Nichols et al. 2008). Several authors have also reported the increase of soil nutrients due to dung beetle activity (Yamada et al. 2008).

Soil physical properties

Dung beetles affect soil structure in many advantageous ways particularly through bioturbation, the displacement and mixing of sediment particles. Bioturbation is facilitated by tunnellers through their burrowing activities. They move slabs of the earth to the soil surface through their various nesting styles where they construct long tunnels up to several meters deep with branching brooding chambers (Nichols et al. 2008). The effect of dung beetles on soil physical properties have been studied to a lesser extent however the tunnelling activity, in which macropores with a diameter ranging between 1-50mm are created, increase soil aeration and water porosity (Nichols et al. 2008). Bang et al. (2005) concluded that only large-bodied species had a positive significant effect on soil permeability as a minimum depth of 10 cm was necessary to have a meaningful impact.

Secondary seed dispersal

Dung beetles are also involved in secondary seed dispersal, thought to play a key role in plant recruitment (Andresen and Feer 2005). In many temperate and tropical regions, vertebrates are the primary seed dispersers because they typically swallow the seeds of the plants they are eating and later excrete the seeds, still viable and intact, in a different place. The seeds deposited in dung face numerous risks such as predation, pathogens and a harsh climate that may prevent seedling recruitment. Dung beetles play an important role in relocating and burying the seeds along with their dung which greatly reduces the risk of predation and pathogens and provides the seeds with a more moderate microclimate, all conducive to germination (Chambers and MacMahon 1994; Andresen and Feer 2005; Nichols et al. 2008; Milotić et al. 2017). Dung beetles bury between 6-95% of seeds found in a dung pad; however, these may range significantly depending on the beetle community present at

the dung deposit (Andresen 2002; Andresen and Levy 2004; Nichols et al. 2008; Milotić et al. 2017). The size of the dung beetle is also important, with larger dung beetles being more adept at seed removal because of the amount of excrement they are taking with them and larger beetles will bury seeds at greater depths (Andresen 2002; Slade et al. 2007). Vulinec (2000) found that tunnellers bury seeds better than their rolling counterparts. It is therefore unsurprising that a multitude of studies have contributed substantial increases in aboveground biomass, plant height, protein levels and nitrogen content to the actions of dung beetles (Bang et al. 2005; Yamada et al. 2007; Nichols et al. 2008).

1.3 Importance of the local environment and dung sources for dung beetle assemblages

Vegetation physiognomy rather than taxonomic composition affects surface and subsurface microclimate which in turn influences dung beetle habitat associations (Davis et al. 2008). The height of the vegetation determines the amount of shade consequently affecting light intensity, radiant heat, ambient temperature and humidity. Vegetation cover and density influences the surface temperature and the rate of subsurface/surface moisture loss which is elevated in areas where surface cover is sparse, resulting in only brief periods of dung beetle activity. Most dung beetles are quite malleable and will frequent partially unshaded or moderately shaded vegetation types however some are specialists with a bias towards the extremes (Davis 1996; Davis et al. 2008).

Beetle association with soil types is largely associated to soil particle size which is related to soil hardness (penetrability), drainage and water retention (Davis et al. 2008). Soil moisture is imperative for the effectiveness of brood ball production (Barkhouse and Ridsdill-Smith 1986). Some species are found on a mixture of clay and sand; however, most species are associated with sand because sands have the largest grain size, the greatest softness (least amount of rainfall to soften) and fastest drainage. Species-richness is lowest on stony soils which contain fewer soil particles and are strenuous to excavate (Davis et al. 2008).

Dung beetle assemblages are hugely complex and are made up of hundreds of species and thousands of individuals all dependant on a highly nutritious and desirable resource: dung. Virtually all types of dung are attractive to dung beetles, but they are predominantly attracted to mammalian dung and the two organisms share deep trophic associations. Ecological linkages between mammals and dung beetles have played a significant role in Scarabaeinae evolution and extant dung beetle assemblages for at least the last 40 million years (Nichols et al. 2008). The various dung types can conveniently be divided into four categories based on mammal body-size, diet and digestive processes which influence fibre content and bolus and dropping size. These categories are (a) large, course-fibred by large-bodied non-ruminants e.g. elephants and rhinoceros (b) large, moist, soft, fine-fibred pads by ruminants e.g. cattle, buffalo (c) pellets dropped by small– to medium-bodied herbivores e.g. rodents and some ungulates (d) small, odiferous droppings of omnivores and carnivores e.g. baboons and cats

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(Davis et al. 2008). Although most dung beetles are opportunistic feeders, some species are specialists. The selection is determined by physical and chemical components of dung and its "findability" (Gittings and Giler 1998).

The physical characteristics that might attract a dung beetle are the fibre and water content as well as the size of the dropping (Aschenborn et al. 1989; Davis et al. 2008). Dung beetles use their olfactory senses to locate dung and so this findability is linked to dung odour dispersion properties. These odour dispersion properties are correlated to the volatile substances found in dung and the chemical composition is therefore important (Dormont et al. 2007). Sixty-four compounds have been identified from dung emissions and dung volatiles which allows for olfactory discrimination by dung beetles (Dormont et al. 2010). Interestingly, larval feeding has no meaningful effect on dung selection, rather resource selection is seemingly based on innate olfactory preferences (Dormont et al. 2007; Whipple and Hoback 2012; Frank et al. 2017). Vertebrate dung has a high degree of diversity of chemical composition and some may be more attractive than others based on the volatiles contained in the dung (Hanski and Camberfort 1991; Dormont et al. 2007). Unsurprisingly, the stage of dung desiccation and decomposition is also very important during the selection process and the freshest excrements are favoured by most species (Holter and Scholtz 2007). Suitability is the physical dung environment for adults, larvae and eggs and the habitat predilection of the source species which makes some dung and habitat types more suitable for dung beetles than others.

Holter and Scholtz (2007) compared the nitrogen contents of different dung types and found that selective feeding by dung beetles may largely be due to differences in concentrate assimilable carbon in the dung. The nitrogen content is highly dependent on the diet of the herbivores and a comparison of Danish sheep grazing on luscious green pastures yielded higher nitrogen contents (3.3%) compared to say white rhinos (1.2%) or elephants (1.4%) (Holter and Scholtz 2007). The carbon to nitrogen ratio was more important for dung beetles than nitrogen alone. The optimal ratio in assimilated food is supposed to be twice that of the organism (approximately 5:7 in a typical insect) because the surplus carbon, not counting the carbon needed for tissue production, is meant to cover energy expenditure (Elser et al. 2000; Holter and Scholtz 2007). The ratio sampled by Holter and Scholtz (2007) was 7:13, which is not at an optimal range and that of assimilated food is then even lower. The reason – carbon is contained in the tiny indigestible plant fragments while nitrogen comes from the epithelial cells of the animal. The carbon is therefore likely also trapped in these epithelial cells meaning dung beetles need to ingest about twice the amount of nitrogen in order to reach merely adequate levels of carbon. This again is dependent on the type of herbivore and the herbivore's diet (Holter and Scholtz 2007; Scholtz et al. 2009) which all ultimately affect the quality of the dung and thus the development of the beetle (Dormont et al. 2004; Frank et al. 2017)

Water content is another important characteristic because this fluid component is a major source of nutrition for adult dung beetles, in fact, their mouthparts evolved for this purpose. Holter and his co-workers (Holter 2000; Holter et al. 2002; Holter and Scholtz 2005, 2007) conducted extensive research on this aspect and concluded that dung beetles use their maxillary palps to collect food and brush large particles with their filtration setae while the residual paste is squeezed by the molar lobes. The surplus liquid is led through the filtration channels away from the pharynx and the remaining concentrated minor particles are ingested (Holter and Scholtz 2005, 2007). Edwards (1991) reconnoitred the preference of higher water content dung compared to drier dung in *Euoniticellus intermedius* where no breeding took place in dung containing less than 65% water, regardless of nitrogen content. It is also very unlikely that any feeding or breeding would take place in dung with a low water content because the small particles that are consumed by dung beetles are largely suspended in dung fluids (Scholtz et al. 2009).

1.4 Effects of land-use change on dung beetle assemblages and their use as bio-indicators

The biggest threats that dung beetles face is habitat loss due to the anthropogenic habitat fragmentation, land-use change and habitat degradation. Overuse of medical veterinary products in livestock farming and the abandonment of grazing land are also major contributing threats (Nichols et al. 2008), but threats such as invasive species, vegetation amelioration and climate change magnify the effects of land-use change (Nichols et al. 2009). Numerous studies have shown that habitat loss has detrimental effects on biodiversity such as species richness and abundance, population distributions and changes in morphological, behavioural and genetic traits. Habitat loss also affects the interactions and interspecific social relationships as well as the movement of individuals (Hanski and Camberfort 1991; Scholtz et al. 2009). Tonelli (2018) found that there is an overall compositional shift towards more opportunistic species with a reduction on large-bodied specialists resulting in reduced trophic chain lengths. Other studies have reported severely reduced dung beetle biomass because of clearing and disturbance of forests in the Brazilian Amazon (Vuinec 2002) and reduced beetle abundance, species diversity and average beetle body size with decreasing forest fragment size (Nichols et al. 2008).

Livestock farming has had calamitous effects not only dung beetle assemblages but also overall habitat health and functioning. A survey by Horgan (2007) found that the expansion of cattle pastures and proliferation of domesticated species led to a regional decline of native dung beetle species. A study conducted in the Free State in South Africa comparing natural bushveld to cattle farms found that beetle assemblages differed between the two land-use types with higher diversity and biomass in natural habitats compared to altered habitats (Jankielsohn et al. 2001). Overgrazing and severe vegetation trampling by cattle were identified as the main contributing factors. The use of

anthelmintic veterinary drugs such as ivermectin has also long been known to impair dung beetle functioning, dung decomposition and overall guild structures on livestock farms (Errouissi and Lumaret 2010).

The loss of large native vertebrates is currently at crisis level and have been recorded across Africa (Nichols et al. 2009), Southeast Asia (Corlett 2007) the Amazon and in other regions (Nichols and Gardner 2011). The loss of these species is largely due to the intensification of cattle farming (Jankielsohn et al. 2001; Horgan 2007), habitat loss and over-hunting (Nichols et al. 2009). The changes in the mammal assemblage lead to an altered dung profile for dung beetles and reductions in dung specialists, while generalists may increase (Nichols et al. 2009). Despite this change, some studies posit that there is some compensation by smaller-bodied mammal species such as smaller ungulates, primates and rodents persisting in the altered environments (Nichols and Gardner 2011) or that livestock may replace the role of native large-bodied vertebrates (Samways and Kreuzinger 2001). This, however, does not entirely absolve the loss of native large-bodied vertebrates and their absence may instigate cascading negative effects beyond just resources for dung beetles. Dung beetles and native megafauna exist in co-evolved systems and the loss of even one species often instigates a torrent of downstream extinctions among taxa that are dependent on the now-extinct species. This may have dramatic implications for functional capacity and patterns of community structure (Koh et al. 2004; Nichols et al. 2009). The ecological penalties of these downstream impacts are particularly threatening in events where a functionally significant taxon is closely dependent upon the vanishing keystone resource providers (Nichols et al. 2009; Nichols and Gardner 2011; Bogoni et al. 2019; Raine and Slade 2019).

All the aforementioned interactions between vertebrates, vegetation, humans and dung beetles make these ideal bio-indicator taxa. They possess all the necessary traits for what constitutes a good bio-indicator. Dung beetles are a cosmopolitan group that have a well-established taxonomy and species delineation and they represent a distinct and rich guild structure that is fundamental to ecosystem functioning and structure (Halffter and Edmonds 1982; Halffter and Favila 1993). They are invariably conditioned by the natural environment being highly sensitive to plant composition, density and architecture. In addition, dung beetles and native ungulates have been tightly interacting over evolutionary time (Nichols et al. 2009). They are therefore useful in quantifying the effects of anthropogenic disturbance across many different scales (Samways and Kreuzinger 2001).

1.5 Dung beetles in Namibia and other arid regions

Dung beetle species richness, as well as day to day activity, is strongly related to rainfall incidences and vegetation cover that moderates surface temperature (Davis 1994, 2002). Davis (2002) observed

a decline in species richness of 386 species in the warmer northeast of South Africa to 68 species in the cooler southwest of the country and the decrease in species richness due to changes in climate has been observed in other regions as well. Aridity is associated with reductions in mammal diversity and abundance and therefore there is a reduction of resources particularly in the diversity of food types and these changes could also affect the quality of the resource (Tshikae 2008; Tshikae et al. 2013). An arid climate also means that there is complete faunal turnover and changes in temporal and spatial availability of dung resources making it a largely ephemeral resource (Holter and Scholtz, 2007). Diminished resources have a direct effect on dung beetle assemblage structure, decreases in species richness, abundances, alpha diversity and additionally could result in high species turnover (Tshikae 2013a, b). Despite a reduction in diversity, arid regions do show patterns of increasing endemism with increasing dryness in the southwest Kalahari in Botswana (Tshikae et al. 2008) and in the Iberian Peninsula (Verdu and Galante 2002), where many dung beetle species have modified their diet to that of fibrous dry pellets as well as other morphological and behavioural specializations considered to be secondary evolutionary changes.

There is very little known about diversity patterns of dung beetles in Namibia except for few studies focusing on unique relictual species of taxonomic importance (e.g. Frolov and Scholtz 2003; Frolov 2005; Sole et al. 2005; Deschodt et al. 2007, 2011, 2016; Harrison et al. 2010; Deschodt 2019). These dung beetles were sampled in the Namib Desert and the region is considered a centre of endemism for dung beetles with several genera exclusively found here. Dung beetles in this area are largely associated with rock hyrax middens, *Provacia capensis* (Pallas 1766) (Mammalia: Hyraocoidea) (Deschodt and Davis 2018). Davis et al. (2008) explored the functional implications of colour morphisms in Scarabaeine dung beetles (specifically *Gymnopleurus humanus*). Three other studies, Hull (1998), Vohland et al. (2005) and Hering et al. (2019) also mention dung beetles in their biodiversity surveys, but the focus of these papers was Buprestidae and Tenebrionidae respectively. The interior of the country should naturally have a higher number of species considering the vast agricultural landscape and a general increase in megafauna. Therefore, the Namibian dung beetle fauna is still very poorly documented even though it has a likely rich compliment.

1.6 Thesis outline and study aims

The primary goal of this work was to understand the impact of wildlife replacement with livestock in terms of dung beetle diversity and ecological function in the arid Savannah regions of northern Namibia. In the first data chapter (Chapter 2), I assess the effect of land-use change on the loss of native herbivores and on dung beetle biodiversity measures and physical development. Key questions addressed, centred on comparisons between protected areas and farmlands, included:

I. What is the effect of replacing native vertebrates with domestic livestock on dung beetle species richness, abundance, biomass and community composition?

II. Does the replacement of native vertebrates with domestic livestock affect the development of the remaining species?

The primary hypotheses tested were that 1) PAs will support greater diversity, abundance and biomass of dung beetles compared to farms, and 2) land-use change and the resulting reduction in the quality of dominant dung resources will negatively affect individual dung beetle development (size).

The second data chapter (Chapter 3) focuses on the effect that land-use change has on dung beetle ecological function as measured by their capacity for dung removal and secondary seed dispersal using manipulative field experiments. The key questions addressed here were:

I. What is the effect of replacing native vertebrates with domestic livestock on dung removal and secondary seed dispersal functions?

II. Which dung beetle functional groups are the most important and most severely impacted by the land-use change? Is there evidence for antagonism, facilitation or complementarity between the functional groups?

III. Which dung beetle biodiversity measures (richness, abundance or biomass) are most important for dung removal and secondary seed dispersal functions?

Dung removal and secondary seed dispersal were hypothesised to be lower in the farmland compared to the protected area due to reduced dung beetle richness, abundance and biomass. Tunnelling beetles were expected to have a more dominant effect compared to rollers and I expected to find evidence of strong competition between the two functional groups for resources. Finally, biomass was anticipated to be the most influential factor correlated with dung removal and secondary seed dispersal as the greater combined body size of all individuals in a community likely leads to greater dung removal and secondary seed dispersal.

Chapter 4 summarises the main conclusions of the study with some recommendations for biodiversity conservation particularly with regards to the selection and prioritisation of conservation areas in this region. Avenues for future work that would improve the experimental design and further disentangling the effects of anthropogenic disturbances on dung beetles and their functioning were also explored.

1.7 References

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

Andresen E, Feer F (2005) The role of dung beetles as secondary seed dispersers and their effect on plant regeneration in tropical rainforests. In: Forget PM, Lambert JE, Hulme PE, Vander Wall SB (ed) Seed fate. Predation, dispersal and seedling establishment. CABI, Oxon, UK, pp 331 – 349

Andresen E, Levey DJ (2004) Effects of dung and seed size on secondary dispersal, seed predation, and seedling establishment of rain forest trees. Oecologia 139:45 – 54

Ascehenborn HH, Loughnan ML, Edwards PB (1989) A simple assay to determine the nutritional suitability of cattle dung for coprophagous beetles. Entomologia Experimentalis Applicata. 53: 73 – 9

Ashley C, Barnes JI (1996) Wildlife use for economic gain: the potential for wildlife to contribute to development in Namibia. DEA Research Discussion Paper 12: 1 – 23. Windhoek: Directorate of Environmental Affairs

Bang HS, Lee JH, Kwon OS, Na YE, Jang YS, Kim WH (2005) Effects of paracoprid dung beetles (Coleoptera: Scarabaeidae) on the growth of pasture herbage and on the underlying soil. Applied Soil Ecology 29: 165 – 171

Barkhouse J, Ridsdill-Smith TJ (1986) Effect of soil moisture on brood ball production by *Onthophagus binodis* (Thunberg) and *Euoniticellus intermedius* (Reiche) (Coleoptera: Scarabaeinae). Journal of the Australian Entomological Society 25: 5 – 78

Barnard P (1998) Biological diversity in Namibia: a clash of sea and land, fog and dust. Biodiversity and Conservation 7: 415 – 417

Barnard P, Brown CJ, Jarvis AM, Robertson A (1998) Extending the Namibian protected area network to safeguard hotspots of endemism and diversity. Biodiversity and Conservation 7: 531 – 547

Barnes JI, de Jager JLV (1996) Economic and financial incentives for wildlife use on private land in Namibia and the implications for policy. South African Journal of Wildlife Res 26: 37 – 46

Bogoni JA, da Silva PG, Peres CA (2019) Co-declining mammal–dung beetle faunas throughout the Atlantic Forest biome of South America. Ecography 42: 1 – 16

Bond WJ (2008) What Limits Trees in C4 Grasslands and Savannas? Annual Review of Ecology, Evolution, and Systematics 39:641 – 59

Bornemissza G F (1960) Could dung eating insects improve our pastures? Journal of the Australian Institute of Agricultural Science 75: 54 – 56

Bornemissza G F, Williams C H (1970) The effect of dung beetle activity on plant yield. Pedobiologia 10: 1 – 7

Brook BW, Sodhi NS, Bradshaw CJA (2008) Synergies among extinction drivers under global change. Trends in Ecology and Evolution 8:453 – 460

Bryan RP (1973) The effects of dung beetle's activity on the numbers of parasitic gastrointestinal helminthic larvae recovered from pasture samples. Australian Journal of Agricultural Research 24: 161 – 168

Burke A (2003) Practical measures in arid land restoration after mining – a review for southern Namibia: Research in action. South African Journal of Science 99: 413 – 417

Burke A (2004) Range management systems in arid Namibia– what can livestock numbers tell us? Journal of Arid Environments 59:387 – 408

Chambers JC, MacMahon JA (1994) A day in the life of a seed: movements and fates of seeds and their implications for natural and managed systems. Annual Review of Ecology, Evolution and Systematics 25:263 – 292

Collen B, Loh J, Whitmee S, McRae L (2009) Monitoring changes in vertebrate abundance: the Living Planet Index. Conservation Biology 23:317 – 327

Corlett RT (2007) The impact of hunting on the mammalian fauna of tropical Asian forests. Biotropica 39: 292 – 303

Culot L, Bovy E, Vaz-de-Mello FZ, Guevarad R, Galetti M (2013) Selective defaunation affects dung beetle communities in continuous Atlantic rainforest. Biological Conservation 163: 79 – 89

Davis, ALV (1994) Associations of Afrotropical Coleoptera (Scarabaeidae, Aphodiidae, Staphylinidae, Hydrophilidae, Histeridae) with dung and decaying matter: implications for selection of fly-control agents for Australia. Journal of Natural History 28: 383 – 399

Davis ALV (1996) Seasonal dung beetle activity and dung dispersal in selected South African habitats: implications for pasture improvement in Australia. Agriculture, Ecosystems & Environment 58: 157 – 169

Davis ALV (2002) Dung beetle diversity in South Africa: influential factors, conservation status, data inadequacies and survey design. African Entomology 10: 53 – 65

Davis ALV, Frolov AV, Scholtz CH (2008) The African Dung Beetle Genera. Protea Book House, Pretoria

De Klerk JN (2004) Bush Encroachment in Namibia: Report on Phase 1 of the Bush Encroachment Research, Monitoring and Management Project. John Meinert Printing

Dean WRJ, Milton SJ (1999) The Karoo. Ecological patterns and processes. Cambridge University Press, Cambridge

Deschodt CM, Kryger U, Scholtz CH (2007) New taxa of relictual Canthonini dung beetles (Scarabaeidae: Scarabaeinae) utilizing rock hyrax middens as refuges in south-western Africa. Insect Systematics and Evolution 38: 361 – 376

Deschodt CM, Davis ALV (2018) New deltochiline (Coleoptera: Scarabaeidae: Scarabaeinae) taxa associated with hyrax dung in arid southwestern Namibia. Zootaxa 4450: 066 – 076

Deschodt CM, Davis ALV, Scholtz CH (2011) New dung beetle (Coleoptera: Scarabaeidae: Scarabaeinae) taxa from arid south-western Africa. Insect Systematics & Evolution 42: 277 – 294

Deschodt CM, Davis ALV, Scholtz CH (2016) A new monotypic genus, a species synonymy and nomenclatural corrections in the arid-adapted Canthonini (Scarabaeidae, Scarabaeinae) from the Succulent Karoo Biome of south-western Africa. Zootaxa 4147: 490 – 500

Deschodt CM, Davis AVL, Daniel GM, (2019) The endemic Southern African genus *Epirinus* Dejean, 1833 (Coleoptera: Scarabaeidae: Scarabaeinae) revisited: five new species and two new synonyms. Zootaxa 4603: 327–340

Dirzo R, Raven PH (2003) Global State of Biodiversity and Loss. Annual Review of Environmental Resources 28:137 – 67

Dormont L, Epinat G, Lumaret JP (2004) Trophic preferences mediated by olfactory cues in dung beetles colonizing cattle and horse dung. Environmental Entomology 33: 370 – 377

Dormont L, Rapior S, McKey DB, Lumaret JP (2007) Influence of dung volatiles on the process of resource selection by coprophagous beetles. Chemoecology 17:23 – 30

Dormont L, Jay-Robert P, Bessiere JM, Rapior S, Lumaret JP (2010) Innate olfactory preferences in dung beetles. Journal of Experimental Biology 213:3177– 3186

Edwards PB (1991) Seasonal variation in the dung of African grazing mammals, and its consequences for coprophagous insects. Functional Ecology 5: 617 – 628

Errouissi F, Lumaret JP (2010) Field effects of faecal residues from ivermectin slow-release boluses on the attractiveness of cattle dung to dung beetles. Medical and Veterinary Entomology 24: 433 – 440

Estes JA, Terborgh J, Brashares JS, Power ME, Berger J, Bond WJ, Carpenter SR (2011) Trophic downgrading of planet Earth. Science 333: 301–306

Floate KD (2011) Arthropods in cattle dung on Canada's grasslands. In: Floate KD ed. Arthropods of Canadian Grasslands (Volume 2): Inhabitants of a Changing Landscape. Ottawa: Biological Survey of Canada 71 – 8

Frank, K, Bruckner A, Hilpert A, Heethoff M, Bluthgen N (2017a) Nutrient quality of vertebrate dung as a diet for dung beetles. Scientific Reports 7:1214

Frank K, Hulsmann M, Assmann T, Schmitt T, Bluthgen N (2017b) Land-use affects dung beetle communities and their ecosystem service in forests and grasslands. Agriculture, Ecosystems and Environment 243:114 – 122

Frolov AV, Scholtz CH (2003) A new genus and species of dung beetle from southern Namibia (Coleoptera: Scarabaeidae: Scarabaeinae). African Entomology 11: 297 – 299

Frolov AV (2005) A New Species of the Dung Beetle Genus *Namakwanus* (Coleoptera, Scarabaeidae) from Namibia. Contributions to Systematics and Biology of Beetles 245 – 247

Giess W (1971) A preliminary vegetation map of South West Africa. Dinteria 4: 5 – 114

Georgiadis NJ (2011) Introduction: Conserving Wildlife in Kenya's Ewaso Landscape. Smithsonian Institution. Smithsonian Contributions to Zoology

Gittings T, Giller PS (1998) Resource quality and colonisation and succession of coprophagous dung beetles. Ecography 21: 581 – 592

Halffter G, Edmonds WD (1982) The nesting behaviour of dung beetles (Scarabaeinae): an ecological and evolutive approach. Instituto de Ecologia, Mexico

Halffter G, Favila ME (1993) The Scarabaeinae (Insecta: Coleoptera) an animal group for analysing, inventorying and monitoring biodiversity and tropical rain forest and modified landscapes. Biology International 27: 15 – 21

Hanski I, Cambefort Y (1991) Dung Beetle Ecology. Princeton University Press, Princeton

Happold DCD (1995) The interactions between humans and mammals in Africa in relation to conservation: a review. Biodiversity Conservation 4: 395 – 414

Harrison S, Damschen EI, Grace JB (2010) Ecological contingency in the effects of climatic warming on forest herb communities. Proceedings of the National Academy of Sciences USA 107:19362 – 19367

Hering R, Hauptfleisch M, Geißler K, Marquart A, Schoenen M, Blaum N () Shrub encroachment is not always land degradation: Insights from ground-dwelling beetle species niches along a shrub cover gradient in a semi-arid Namibian savanna. Land Degradation & Development 30:14 – 24

Holter P (2000) Particle feeding in Aphodius dung beetles (Scarabaeidae): old hypotheses and new experimental evidence. Functional Ecology 14: 631 – 637

Holter P, Scholtz CH (2005) Are ball-rolling (Scarabaeini, Gymnopleurini, Sisyphini) and tunnelling scarabaeine dung beetles equally choosy about the size of ingested dung particles? Ecological Entomology 30: 700 – 705

Holter P, Scholtz CH (2007) What do dung beetles eat? Ecological Entomology 32:690 – 697

Hull HE, Freitag S, Chown SL, Bellamy CL (1998) Identification and evaluation of priority conservation areas for Buprestidae (Coleoptera) in South Africa, Lesotho, Swaziland and Namibia. African Entomology 2:265 – 274

Jankielsohn A, Scholtz CH, Louw SV (2001) Effect of habitat transformation in the dung beetle assemblages: A comparison between a South African nature reserve and neighbouring farms. Environmental Entomology 30: 474 – 483

Joubert D, Smit G, Hoffman M (2013) The influence of rainfall, competition and predation on seed production, germination and establishment of an encroaching acacia in an arid Namibian savanna. Journal of Arid Environments 91:7 – 13

Koh LP, Dunn RR, Sodhi NS, Colwell RK, Proctor HC, Smith VS (2004) Species coextinctions and the biodiversity crisis. Science 305: 1632 – 1634

Kremen C, Colwell RK, Erwin TL, Murphy DD, Noss RF, Sanjayan MA (1993) Terrestrial arthropod assemblages: their use in conservation planning. Conservation Biology 7:796 – 808

Maggs GL, Craven, P, Kolberg, HH (1998) Plant species richness, endemism and genetic resources in Namibia. Biodiversity and Conservation 7:435 – 446

Malhi Y, Doughty CE, Galetti M, Smith FA, Svenning JC, Terborgh JW (2016) Megafauna and ecosystem function from the Pleistocene to the Anthropocene. PNAS 113:838 – 846

McGranahan DA (2008) Managing private, commercial rangelands for agricultural production and wildlife diversity in Namibia and Zambia. Biodiversity and Conservation 17: 1965 – 1977

Midgley G, Hughes G, Drew WTG, Foden W (2005) Assessment of potential climate change impacts on Namibia's floristic diversity, ecosystem structure and function. SANBI (For NNBP)

Milotić T, Quidé S, Van Loo T, Hoffmann M (2017). Linking functional group richness and ecosystem functions of dung beetles – An experimental quantification. Oecologia, 183:177 – 190

Ministry of Environment and Tourism (2014) Namibia's Second National Biodiversity Strategy and Action Plan 2013 – 2022. Directorate of Environmental Affairs, Windhoek, Namibia

Newmark WD (2008) Isolation of African protected areas. Frontiers in Ecology and the Environment. 6:321 – 328

Nicholas E, Spector S, Louzada J, Larsen T, Amezquita S, Favila ME, The Scarabaeinae Research Network (2008) Ecological Functions and ecosystem services provided by Scarabaeinae dung beetles. Biological Conservation 141: 1461 – 1474

Nichols E, Gardner TA, Peres CA, Spector S, The Scarabaeinae Research Network (2009) Co-declining mammals and dung beetles: an impending ecological cascade. Oikos 118:481 – 487

Nichols E, Gardner TA, 2011. Dung beetles as a candidate study taxon in applied biodiversity conservation research. In: Simmons, L.W., Ridsdill-Smith, J. (Eds.), Dung Beetle Ecology and Evolution. Wiley-Blackwell, Chichester UK, pp 267 – 291

O'Connor TG, Puttick JR, Hoffman MT (2014) Bush encroachment in southern Africa: changes and causes. African Journal of Range and Forage Science 31: 67 – 88

Pryke JS, Roets F, Samways MJ (2016) Wild herbivore grazing enhances insect diversity over livestock grazing in an African grassland system. PLoS One 11:1 – 15

Raine EH, Mikich SB, Lewis OT, Riordan P, Vaz-de– Mello FZ, Slade EM (2018) Extinctions of interactions: quantifying a dung beetle–mammal network. Ecosphere 9: e02491

Raine EH, Slade EM, (2019) Dung beetle–mammal associations: methods, research trends and future directions. Proceedings of the Royal Society B: Biological Sciences 286: 20182002

Samways MJ, Kreuzinger K (2001) Vegetation, ungulate and grasshopper interactions inside vs outside an African savanna game park. Biodiversity Conservation 10:1963 – 1981

Scholtz CH, Davis ALV, Kryger U (2009). Evolutionary Biology and Conservation of Dung Beetles. Pensoft Publishers. Sofia, Bulgaria

Slade E, Mann D, Villanueva J, Lewis O (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 76:1094 – 1104

Sole CL, Scholtz CH. (2010) Did dung beetles arise in Africa? A phylogenetic hypothesis based on five gene regions. Molecular Phylogenetics & Evolution 56: 631 – 641

Sole CL, Scholtz CH, Bastos ADS (2005) Phylogeography of the Namib Desert dung beetles Scarabaeus (Pachysoma) MacLeay (Coleoptera: Scarabaeidae). Molecular Phylogenetics and Evolution 56:631 – 641

Steinfeld H, Gerber P, Wassenaar T, Castel V, Rosales M, de Haan C (2006) Livestock's long shadow: environmental issues and options, Food and Agriculture Organization of the United Nations, Rome, p 414

Stork NE (1988) Insect diversity: facts, fiction and speculation. Biological Journal of the Linnean Society. 35:321 – 37

Thuiller W, Midgley GF, Hughes GO, Bastians B, Drew G, Rutherford MC, Woodward FI (2006) Endemic Species and ecosystem sensitivity to climate change in Namibia. Global Change Biology 12:759 – 776

Tonelli M, Verdú JR, Zunino ME (2018) Effects of the progressive abandonment of grazing on dung beetle biodiversity: body size matters. Biodiversity Conservation 27:189 – 204

Tscharntke T, Klein AM, Kruess A, Steffan-Dewenter I, Thies C (2005) Landscape perspectives on agricultural intensifications and biodiversity-ecosystem service management. Ecology Letters 8: 857 – 874

Tshikae BP, Davis ALV, Scholtz CH (2008) Trophic Associations of a Dung Beetle Assemblage (Scarabaeidae: Scarabaeinae) in a Woodland Savanna of Botswana. Environmental Entomology 37: 431-441

Tshikae BP, Davis AL, Scholtz CH (2013a) Species richness: energy relationships and dung beetle diversity across an aridity and trophic resource gradient. Acta Oecologica 49:71 – 82

Tshikae BP, Davis ALV, Scholtz CH (2013b) Does an aridity and trophic resource gradient drive patterns of dung beetle food selection across the Botswana Kalahari? Ecological Entomology 38:83 – 95

Tylianakis JM, Rand TA, Kahmen A, Klein AM, Buchmann N, Perner J, Tscharntke T (2008) Resource heterogeneity moderates the biodiversity-function relationship in real-world ecosystems. PLoS Biol. 6:947 – 956

Verdú JR, Galante E (2001) Larval morphology and breeding behaviour of the genus Pedaridium Harold (Coleoptera: Scarabaeidae). Annals of the Entomological Society of America 94: 596 – 604

Vohland K, Uhlig M, Marais E, Hoffman A, Zeller U (2005) Impact of different grazing systems on diversity, abundance and biomass of beetle (Coleoptera), a study from southern Namibia. Zoosystematics and Evolution 81:131 – 143

Vulinec K (2000) Dung beetles (Coleoptera: Scarabaeidae), monkeys, and conservation in Amazonia. Florida Entomologist 83: 229 – 241

Vulinec K (2002) Dung beetle communities and seed dispersal in primary forest and disturbed land in Amazonia. Biotropica 34: 297 – 309

Waterhouse DF (1974) The biological control of dung. American Scientist 230: 101–108

Western D (1989) Conservation without parks: wildlife in the rural landscape. In: Western, D., Pearl, M.C. (ed.), Conservation for the Twenty-first Century. Oxford University Press, Oxford, pp158 – 165

Whipple SD, Hoback WW (2012) A comparison of dung beetle (Coleoptera: Scarabaeidae) attraction to native and exotic mammal dung. Environmental Entomology. 41:238 –2 44

Yaacobi G, Ziv Y, Rosenzweig ML (2007) Effects of interactive scale-dependent variables on beetle diversity patterns in a semi-arid agricultural landscape. Landscape Ecology 22: 687 – 703

Yamada D, Imura O, Shi K, Shibuya T (2007) Effect of tunneller dung beetles on cattle dung decomposition, soil nutrients and herbage growth. Grassland Science 53:121 – 129.

Young HS, McCauley DJ, Castillo E, Goheen JR, Helgen KM, Palmer TM, Pringle RM, Young TP, Dirzo R (2013) Plant community response to changes in herbivore abundance and identity across abiotic gradients and experimental contexts. Journal of Ecology 101:1031 – 1041

Young TP, Porensky LM, Riginos C, Veblen KE, Odadi WO, Kimuyu DM, Charles GK, S. Young H (2018) Relationships between Cattle and Biodiversity in Multiuse Landscape Revealed by Kenya Long-Term Exclosure Experiment. Rangeland Ecology and Management 71:281 – 291

Chapter 2

Replacement of large native mammals by domestic livestock negatively affects dung beetle diversity and reduces dung beetle body mass

Abstract

Land transformation alters biotic communities with cascading effects on ecosystem function. Furthermore, the simplification of ecological process reduces heterogeneity such as the replacement of complex native megafauna with domestic livestock that amplifies these losses. Here I measure the response of dung beetle diversity and their biomass, for both the assemblage and individual species in response to land transformation in an African savannah. Dung beetles were sampled from three protected areas (PAs) and three adjacent cattle farms in northern Namibia. I first hypothesized that maintaining a diversity of large mammals is crucial for dung beetle diversity. Secondly, I hypothesized that dung beetles prefer the predominant resources in their environment. Finally, as the availability of high-quality dung resources directly influences larval development, I also hypothesized that livestock farming will lead to reductions in individual body mass of dung beetle on farms. Overall dung beetle richness increased with higher vertebrate richness but not stocking rate, demonstrating that a complex native vertebrate assemblage promotes high dung beetle richness. Dung beetles showed a preference for native mammal dung (wildebeest) on PAs but not farms, indicating possible conditioning towards available resources. However, functional guilds showed differential responses to land-use change and dominant grazer assemblage. Land-use change and vertebrate richness and abundance significantly influenced overall dung beetle assemblage composition. Overall dung beetle biomass was higher in PAs even though their abundance was unaffected by cattle farming. In addition, there was a significant difference in the 58 conspecifics commonly found between PAs and farms, with larger individuals in PAs. The results show that a high diversity of native vertebrates maintain a high diversity of dung beetles. I also demonstrate that a decrease in the availability of native dung resources on cattle farms leads to reduced body mass that will negatively impact ecological functions.

Keywords: dung beetles, biodiversity Scarabaeidae, interaction networks, mammals, African savannah

2.1 Introduction

Transformation of natural landscapes into urban and agricultural land changes both abiotic (e.g. temperature) and biotic (e.g. species assemblages) conditions (Newbold et al. 2015) is the most significant contributor to global biodiversity loss (Godfray et al. 2010; Beddington et al. 2012; Cardaso et al. 2019; Sim et al. 2019). The abundance of species that cannot adapt to the newly created

environmental conditions (i.e. mainly specialist species) will decrease or entirely disappear, while numbers of more adaptable species (mainly generalist species) will increase (Bengtsson et al. 2005; Winfree et al. 2005; Piccini et al. 2018). Such changes in populations and assemblages can have profound negative effects on ecosystem functions and services such as pollination, litter decomposition and seed dispersal (Nichols et al. 2009; Manning et al. 2016; Manning and Cutler 2018). This can form a negative feedback loop and may ultimately lead to ecological collapse (Koh et al. 2004; Eklof and Ebenman 2006).

Anthropogenic land transformation in the form of livestock grazing covers approximately 60% of the world's agricultural land and has severe consequences for native biodiversity (Alexandratos and Bruinsma 2012; Alkemade et al. 2013). Rangelands such as savannah ecosystems contribute the bulk of this forage (Lund 2007) and are home to a large diversity of wild browsers, grazers and mixed feeders (Kartzinel et al. 2015). These determine the relative dominance of grasses and trees (Midgley et al. 2005; Bond, 2008) and herbaceous biomass (Augustine and McNaughton 1998). A diverse assemblage of wild ungulates is important for maintaining overall vegetation structure and biodiversity in these systems (Tscharntke et al. 2005). Livestock in altered savannah landscapes consists mostly of grazers such as cattle (Coetzee et al. 2008), which can maintain some native biodiversity when stocking densities are well managed (Young et al. 2018). However, stocking densities are often too high (Veblen et al. 2016; Young et al. 2018) and domestic grazers usually replace larger herbivores on farmland (Fynn et al. 2016; Ranglack and du Toit 2016; Holechek and Valdez 2018; Young et al. 2018). Domestic livestock are also easy prey, necessitating the construction of fenced camps and the (often lethal) control of larger predators on farms (McGranahan 2008; Kreuter et al. 2010). Therefore, even when stocking densities are well managed, natural ecosystem processes are altered. The effects of these more subtle changes to ecosystems are not well understood (McGranahan 2008; Kreuter et al. 2010; Keesing and Young 2014).

Most studies on land transformation for cattle farming in African savannahs have focused on the effects on vertebrates (McGranahan 2008; Dona et al. 2013; Keesing and Young et al. 2014; Young et al. 2018) and vegetation (Bond 2008; Young et al. 2013; Sims et al. 2019). Research on arthropods remains scant even though they provide many essential ecosystem functions (Noreiga et al. 2018; Raine and Slade 2019) and are considered good indicators of environmental change (McGeoch 2002,2011; McGeoch et al. 2002). One of the most widely used biological indicator arthropod taxa are dung beetles (Hanski and Cambefort 1991; McGeoch 2002, 2011; Davis et al. 2008; Nichols et al. 2008; Scholtz et al. 2009). This is because of their mainly coprophagous feeding habits which make them closely associated with vertebrates (Hanski and Cambefort 1991; Davis et al. 2002). Dung beetles also have distinct associations with other biotas such as vegetation, but also respond to

differences in abiotic variables including climate and soils, making them highly sensitive to disturbances (McGeoch 2002, 2011; Slade et al. 2007; Verdú et al. 2007; Tonelli et al. 2018). This sensitivity coupled with their hyper-diversity and abundance (Philips et al. 2004; Spector 2006) makes dung beetles a keystone feature in various ecosystems (Slade et al. 2007; Nichols et al. 2008). They are an ideal focal taxon for exploring the effects of land transformation on biota (Andresen and Laurance 2007; Viljanen et al. 2010; Culot et al. 2013; Nichols et al. 2013; Raine et al. 2018b; Raine and Slade 2019).

Vertebrate species identity and stocking rates are important to preserve ecological integrity and to maintain rich biological communities in savannah ecosystems (Naeem and Wright 2003; Sugiura et al. 2013). However, only a few studies have explored how vertebrate species compositional changes affect dung beetle assemblages (Valiente-Banuet et al. 2015; Raine et al. 2018a; Raine and Slade 2019). Some dung beetle species are dung specialists or prefer dung from specific vertebrates (Larsen et al. 2006; Holter and Scholtz, 2007) however, most dung beetles are generalist dung feeders (Hanski and Cambefort 1991) and can utilize dung from both domestic and native species (Whipple and Hoback 2012).The selective defaunation of vertebrates therefore leads to co-extinctions (Kurten 2013; Nichols et al. 2009) and rapid ecosystem functional losses (Nichols et al. 2008; Culot et al. 2013).

Individual dung beetles develop from egg to larvae typically using resources available form a single dung pad (Nichols et al. 2008) and resources high in nitrogen benefit their reproductive performance (Davis 1989; Cambefort 1991). Mean percentage of nitrogen in the dung of herbivores in African savannah ecosystems varies between 2.7 and 1.7% (Codron et al. 2007), with the nitrogen content of carnivore dung being much higher (Al-Houty and Al-Musalam 1997). In contrast, the mean percentage of nitrogen in the dung of cows in African savannahs varies between 1.09 and 1.4% (Lekasi et al. 2001; Augustine 2003; Onduru et al. 2008). Dung quality from domestic livestock is reduced due to the use of veterinary medical products (Verdu et al. 1992; Bernal et al. 1994; Floate, 2006; Verdu et al. 2015; Hammer et al. 2016). Many studies, for example, have looked at the effects of ivermectin, an endectocides made up of macrocyclic lactones (e.g. Roncalli et al. 1989; Fincher 1992; Lumaret et al. 1993; Sommer et al. 1993; Bernal 1994; Krüger and Scholtz 1998a, b; Verdu et al. 2015, 2017). Fincher (1992) and Krüger and Scholtz (1997) found that when the endectocides were administered to adults it was lethal and reduced adult emergence in *Euoniticellus intermedius*. Furthermore, field studies by Krüger and Scholtz (1998a, b) found that use of the endectocide leads to diminished species richness and greater species dominance in the community however this was only the case in drier conditions. Namibia is a relatively arid country (Barnard et al. 1998) and the dung beetle communities may, therefore, be particularly vulnerable to veterinary pharmaceutical use

(Krüger and Scholtz 1998a). Therefore, the replacement of native vertebrates with domestic livestock would not only alter dung beetle populations and assemblages due to dung specialization or preferences but also due to differences in resource quality.

Altered dung beetle populations and assemblages can have cascading effects on ecological functions such as dung removal rates, seed dispersal and the regulation of pests and diseases (Andresen 2002; Nichols et al. 2009; Milotić et al. 2019). However, focussing on these population and assemblage parameters alone may mask some of the more subtle effects of land transformation on dung beetles and their function. For example, even when a species is present at both natural and altered biotopes in equal numbers, the body condition and health of an individual may be compromised as a result of the disturbances (Salomão et al. 2015). This can manifest in decreased body size and mass of adults in transformed landscapes (Salomão et al. 2015).

 Larger beetles are generally more fit than their smaller counterparts as they are better competitors for food resources and mates (Doube et al. 1988; Larsen et al. 2005; Slade et al. 2007; Nervo et al. 2014; Tonelli et al. 2018), especially for males where sexual armature is strongly correlated to body size (Emlen 1997; Hunt and Simmons 2002). Larger beetles also provide larger quantities of dung to offspring (Hunt and Simmons 2002). Resource quality, therefore, has multiple effects on the biology of individual dung beetles, and dung beetle body size (or mass) can be used as a proxy for the cumulative effects of changes in resource quality (Shafiei et al. 2001; Lobo et al. 2006; Jay-Robert et al. 2008; Treitler et al. 2017; Tonelli et al. 2018). As larger beetles can process larger quantities of dung, increased body size will also have positive impacts on ecosystem functions and services (Larsen et al. 2005; Scholtz et al. 2009; Tonelli et al. 2018). Despite the close link between dung beetle size, resource parameters (quantity and quality of dung) and ecosystem function (Emlen 1997; Holter and Scholtz, 2007; Kryger et al. 2006; Moczek, 1998), no studies have evaluated the impact of replacing wild herbivores with livestock grazers on dung beetle development. Also, the few studies that have incorporated differences in dung beetle individual size or mass in reaction to ecological parameters and has been evaluated in a very limited numbers of species (Slade et al. 2007, Manning et al. 2016; Tonelli et al. 2018; Milotić et al. 2019). General patterns of dung beetle development for an entire assemblage have yet to be assessed.

Here, I determined how the exclusion of indigenous large vertebrates influences dung beetle populations and assemblages, and whether domestic ungulates can act as surrogates for natural dung beetle populations and assemblages on pasturelands. To address this, I measured dung beetle richness, abundance, assemblage composition, total biomass and the developmental characteristics (mass) of individual species. I tested the hypothesis that less diverse natural vertebrate fauna on farms will lead to decreased dung beetle species richness and altered assemblage composition due to changes in dung

resources. I postulate that dung beetles will show a greater preference for dung originating from native grazers than for dung from domestic livestock, especially in PAs due to a long co-evolutionary history and possible selection for optimal resource quality. This effect will be diminished on farms due to resource conditioning (Davis 1994, Tshikae et al. 2008). Total dung beetle biomass was expected to be higher on farms (due to greater number of ungulates), but mean mass of individuals of shared species would be greater in PAs due to greater general quality of available dung resources.

2.2 Methods and Materials

2.2.1 Study area

Namibia is an arid yet diverse landscape that house some of Africa's most iconic megafauna (Barnard 1998; Barnard et al. 1998; Beerling and Osborne 2006). The widespread introduction of livestock into many of its ecosystems has led to the drastic decline of megafauna and livestock are now the predominant herbivores in the country (Barnard et al. 1998; Vohland et al. 2005). Only a few studies focused on the effects of land transformation on invertebrates in Namibia (Hull et al. 1998; Zeidler et al. 2002; Vohland et al. 2005) and studies on dung beetles are limited to taxonomic accounts only (Frolov and Scholtz, 2003; Frolov 2005; Sole et al. 2005; Deschodt et al. 2007, 2011, 2016, 2018, 2019; Harrison et al. 2010). This study was conducted within the central northern thornbush savannah expanse of Namibia, in a region characterised by a mosaic of cattle farms (Brahman and Simmentaler breeds) and wildlife ranches/protected areas (Fig. 2.1). Plant communities at the selected sites comprise either Central Western Plains or Khomas/Hochland Plateau vegetation types on mostly Regisols soils. Regional temperatures vary considerably daily, with minimum summer temperatures between 15 and 17 °C and maximums that often exceed 37 °C. Rainfall is restricted to summer but is highly erratic, with disparities of up to 250 mm between two successive rainy seasons. However, it usually ranges between 100 mm and 300 mm per annum (Barnard et al. 1998).

Protected areas (PAs) and farms are separated by a physical boundary, fences (Barnard et al. 1998, Samways and Kreuzinger 2001; van Schalkwyk et al. 2010), and this has created a complex cultural landscape that is under great anthropogenic pressure (Vohland et al. 2005; Engler et al. 2019). Fences exist largely for two reasons: 1) veterinary control to prevent the spread of disease between wild ungulates and domestic livestock (Barnard et al. 1998; van Schalkwyk et al. 2010; Engler et al. 2019) and 2) to prevent predators such as jackal (*Canis aureus*) and cheetah (*Acinonyx jubatus*) from crossing onto farms and kill livestock (Rust and Marker 2014). PAs maintain their natural complement of megaherbivores (e.g. elephant (*Loxodonta Africana)*, wildebeest (*Connochaetes taurinus)* and giraffe (*Giraffa giraffa)* and other iconic African fauna (e.g leopard (*Panthera pardus*) and pangolin (*Smutsia temmincki*) (Barnard et al. 1998; van Schalkwyk et al. 2010). Native wild fauna are largely excised on farms and domestic herds of cattle and smaller livestock such as domestic goats

(*Capra hircus*) and sheep (*Ovis aries*) have replaced them as the bulk grazers (du Toit and Cumming 1999; van Schalkwyk et al. 2010).

2.2.2 Sampling protocol

Dung beetles were sampled from three PAs (Okonjima Nature Reserve, N/a'an ku sê Lodge and Wildlife Sanctuary and Cheetah Conservation Fund) and three farms adjacent to these (Tottenham Farm, N/a'an ku sê Farms and Cheetah Conservation Fund Livestock Farm) (Fig. 2.1). The minimum distance between a farm and reserve pair was 17 km and a minimum distance between pairs was 70 km. Ten sites were selected at each farm/PA with the help of reserve managers, field guides and farmers that had intimate knowledge of the major soils, vegetation physiognomies and grazing intensities on the respective properties. These aspects were kept as consistent as possible to minimise their effect on dung beetles collected in the present study. Sites on each farm/PA were a minimum of 1 km apart to avoid pseudoreplication (Larsen and Forsyth 2005; Silva and Hernandez 2015b).

At each site, dung beetles were sampled using four baited pitfall traps (Larsen and Forsyth 2005) set at the corners of a square at 100 m apart. This spacing ensured that each catch would constitute an independent sample and would minimise trap interaction in attractiveness to beetles from the intermixing of bait odours (Larsen and Forsyth 2005). Traps consisted of a 2L plastic bucket with a diameter of 17 cm and a depth of 14 cm that was buried with the rim flush with the soil surface. Traps were half-filled with water containing a few drops of liquid detergent to capture beetles (Fletchman et al. 2008; Tshikae et al. 2008). Traps were baited with fresh dung balls (150 g) of either wildebeest, collected from Okonjima Nature Reserve, or cow, collected from Tottenham Farm, wrapped in fine nylon mesh that was suspended over the centre of the trap with steel wire (Pryke et al. 2013;Appendix K). All dung collected were first homogenised and then frozen (-20°C) until use to ensure consistency in attractiveness.

Two of the traps at opposite ends of the square per site were baited with wildebeest dung and the other two with cow dung. Traps were operational for 24 hours after which baits were replaced with fresh dung and left operational for another 24 hours. Hereafter all individuals within traps were preserved (frozen) for later sorting and identification (Fletchman et al. 2008). Since rainfall events are known to affect dung beetle assemblages and increase the numbers of active species and their abundances (Hanski and Cambefort 1991; Davis 2002; Andresen 2005), the entire sampling protocol was repeated in the early rainy season (December/January 2017) and in the middle/late rainy season (March/April 2018).

All collected dung beetles were sorted, counted and identified to the lowest taxonomic rank possible using available keys (d'Orbigny 1913; Janssens 1937; Balthasar 1963a,b, 1965; Zur Strassen 1967; Ferreira 1969, 1976, 1978; Nguyen-Phung and Cambefort 1986a, 1986b, 1987; Nguyen-Phung

1988a,b,c; Cambefort 1996; Barbero et al. 2003; Deschodt et al. 2007; Deschodt and Scholtz 2008; Zídek and Pokorný 2008; Krikken 2009; Branco 2010; Roggero et al. 2015; Génier 2017a,b; Deschodt and Davis 2018). Species were also assigned to a functional guild according to their method of dung use as either endocoprids (dwellers that remain within a dung pad or the dung ball of other dung beetle species for feeding and breeding), paracoprids (tunnellers that provision dung into brooding chambers below a dung pad) or telocoprids (rollers that translocate pieces of dung away from dung pads) (Doube 1990; Davis et al. 2008). A reference collection is housed in the Stellenbosch University Entomological Collection, Department of Conservation Ecology and Entomology, Stellenbosch, South Africa.
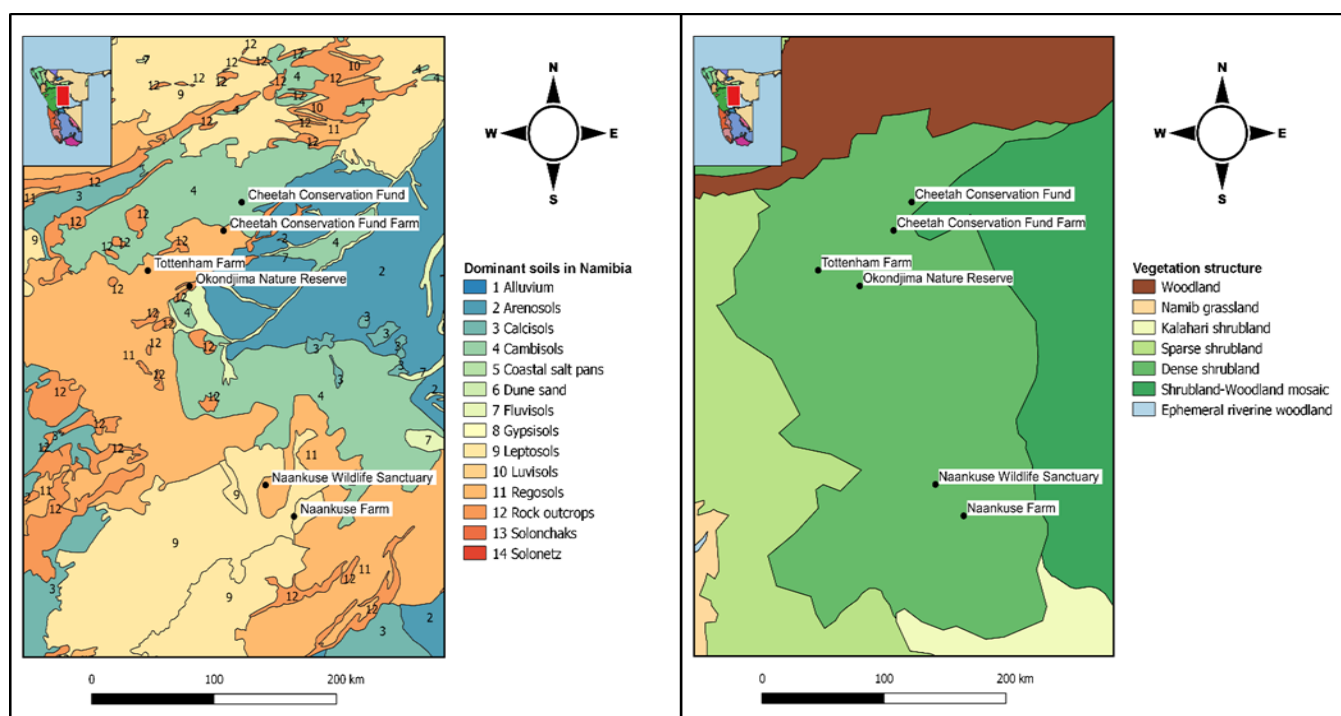
Figure 2.2.1 Map indicating the location of sites in relation to a) dominant soil profile and b) vegetation structure. The shapefiles for the maps are available online form the Digital Atlas of Namibia project at http://www.uni-koeln.de/sfb389/e/e1/download/atlas_namibia/main_namibia_atlas.html

Vertebrate richness and stocking rates

To gain a better understanding of the influence of resource availability on dung beetle assemblages, the identity and densities of medium to large animals (larger than a rabbit) at each site were determined. This delineation was made not because dung beetles do not utilise smaller mammal dung but because 1) Scarabaeinae species feed mostly on large herbivore dung in the region which is largely due to size of the deposit which makes the dung more attractive (Scholtz et al. 2009) 2) the study focuses on the effects of the replacement of native ungulates with domestic ungulates therefore a larger size class of vertebrates was used and 3) the methods used to sample vertebrate species were

adapted from Sensenig et al. (2010) and Marques et al. (2010) specifically recommended these methods for medium to large animals. Vertebrate presence was measured using dung transects which is a reliable measure for comparisons of relative abundance and has been recommended for surveying medium to large animal populations in savannah ecosystems (Sensenig et al. 2010; Marques et al. 2010). All dung piles (fresh and old faeces) were identified and counted (species and abundance) along a combined transect of 1 km long and 4 m wide, divided into four sub transects of 250 m that radiated in opposite directions from the sampling plot as a central point. Seven days later, newly deposited dung along these transects was recorded. The total number of species recorded per transect during both surveys were used as an estimate for vertebrate richness and the mean number of dung pads per transect between both surveys were used as an estimate of vertebrate stocking rates at each plot following Cromsigt et al. (2009). It is important to recognise that the vertebrate community observations are not exact and, irrespective of any method used, not all species present in the landscape will be recorded (Lyra-Jorge et al. 2008; Bogoni et al. 2016).

It is important to note that farmlands were expected to yield slightly lower stocking densities due to an ongoing drought in the region that resulted in many farmers (including the ones where the study was conducted) selling some of their cattle due to the lack of forage. The drought also led to the death of a significant number of livestock (pers. comm.). These effects were also present in protected areas however the landscapes are somewhat more resilient to drought because of management practices (Barnard et al. 1998; Maggs et al. 1998; Young et al. 2018) and had more resources to alleviate the more devastating effects of the drought.

Dung beetle mass

The mean wet biomass of each dung beetle species was determined per plot from a random selection of 10 individuals (where available, otherwise all available individuals). Their total body length was measured using digital callipers (linear distance between the pygidium and the clypeus) and their dry mass was calculated using the formula: Biomass $= 0.010864 \times$ Length $^{3.316}$ (Lobo 1993; Tonelli et al. 2018, 2019). The mean mass per species per site was then used to calculate the total mass of all dung beetles and the mass of dwellers, tunnellers and rollers, collected in each trap. Mean mass per species per site was also used for comparisons of mean individual dung beetle mass between PAs and farms.

2.2.3 Data analyses

All statistical analyses were conducted using R statistical software (version 3.5.1) (R Development Core Team 2019). Relative completeness of the species recorded in the current study was estimated using EstimateS version 9.1 (Colwell 2013). Completeness of the species record was measured for each of the six study areas using the default setting of 100 randomizations of the abundance data

tallied from the four traps at each site. The non-parametric abundance-based estimators Chao 2 and Jackknife 2 were used (Gotelli and Colwell 2001; Chao and Jost 2012; Colwell 2012; Chao et al. 2014). Results were visualised in the iNEXT package in R (Hsieh et al. 2016). Data on the vertebrate richness and stocking density were compared between farms and PAs using generalised mixed models and the *lme4* package with a Poisson error distribution (Bolker et al. 2009) and the region as a random variable (Bates et al. 2014; Sensenig et al. 2010; Zuur et al. 2009). The region here consisted of a farm and a reserve site that were paired based on their proximity.

Response of dung beetle richness, abundance and total biomass to differences in land-use, bait type, vertebrate richness and vertebrate stocking density

The effect of land-use type (farm or PA), bait type (wild or domestic = wildebeest or cow), vertebrate richness and vertebrate stocking density on dung beetle abundance, richness and biomass was tested using linear modelling (Tshikae et al. 2013b). All data was tested for normality using the Shapiro Wilks test (P<0.05) along with visual inspections of the frequency distributions to determine which model family would fit data the best (i.e. linear mixed models (*lmer*) for normal distributions and generalised linear mixed models (*glmer*) for non-normal distributions) (Bates et al. 2014). Data were also evaluated for spatial autocorrelation using the mantel test and region was subsequently used as a spatial random factor (Filgueiras et al. 2015). Species richness data were fitted using the *glmer* function in the *lme4* package with a Poisson error structure (Bolker et al. 2009) while abundance and biomass data were analysed using a linear mixed-effects model with the *lmer* function in the *nlme* package (Zuur et al. 2009; Pinheiro et al. 2015). Biomass, vertebrate richness and vertebrate stocking density values were scaled prior to the analyses in order to meet the requirements of a normal distribution of the residuals (Zuur et al. 2009). The effects of land-use, bait type, vertebrate richness, vertebrate stocking density and their interactions were evaluated from a multitude of candidate models with relative support for the candidate models tested using Akaike's Information Criterion for small sample sizes (AICc) that are compared through likelihood tests (Zuur et al. 2009). The AICc is used to obtain the most optimal and parsimonious model using a prior threshold of an AICc of Δ2 (Crawley 2013; Manning et al. 2016). The *AICcmodavg* package in R was used which ranks the candidate models from lowest to highest AICc which was used to select the best-suited model. In the case where the smallest AICc obtained was for the dummy model (intercept) it was assumed that none of the variables were able to significantly explain the variation of the diversity measures for the guilds (Burnham and Anderson 2004).

Response of dung beetle assemblages to differences in land-use, bait type, vertebrate richness and vertebrate stocking density

Compositional responses of dung beetle assemblages to differences in land-use type (farm or PA), bait type (wild or domestic = wildebeest or cow), vertebrate richness and vertebrate stocking density were assessed using the Mvabund package in R (Wang et al. 2012). The *manyglm* function was used to build multivariate GLMs to test the statistical significance of the candidate models. A negative binomial regression was used because it provided a more random structure and was, therefore, a better fit to the data (O'Hara and Kotze 2010). The *anova* and *summary* functions were used to assess community-environment hypotheses by making taxon-specific and community-level inferences about factors and environmental variables associated with the multivariate abundances, based on the resampling-based hypothesis. Data were visualised using the BORAL package that can fit a variety of models using a Bayesian Markov Chain Monte Carlo estimation (MCMC) by incorporating latent variables as a parsimonious method of modelling correlation between species. The package was used to implement a model-based approach (rather than a linear approach) through unconstrained ordination, by fitting a pure latent variable model. A Poisson distribution error structure was used to fit the latent variable model. Hereafter plots were constructed using the *lvsplot* function. After fitting the model, a summary was generated through the *fit.lvmp* function which returns posterior median estimates of the species-specific intercepts and latent variables. A residual analysis was performed using *plot (fit.lvmnb)* with a negative binomial distribution. An ordination plot was then constructed based on the pure latent variable model assuming negative binomial counts using *lsvplot (fit.lvmnb)* (Hui et al. 2016).

Response in the development of dung beetles to differences in land-use

I tested for differences in the mean mass of individual dung beetle species between farms and PAs for those species for which more than ten individuals were collected on farms and PAs respectively. Data on estimated individual mass for ten individuals from each land-use (n=20 individuals in total) was first tested for normality using the Shapiro Wilk's tests ($P<0.05$) where after either a Pearson chi-squared test or paired Welch t-test was performed with R software, depending on the distribution of the data. Hereafter all p-values were adjusted using a Bonferroni corrective model for multiple testing (Sokal and Rohlf 1995). Additionally, to determine if there was a general trend for dung beetles to differ in mass between farms and PAs, a likelihood ratio (G-test) was performed using the same candidate species evaluated above. For this analysis, species were scored as larger in either PAs or farms based on their mean mass and the ratio was tested against what was expected at random (50:50 ratio). These analyses were performed using the *DescTools* and *RVAideMemoire* packages in R (Mangiafico 2015).

2.3 Results

2.3.1 Sampling completeness

In total 70 540 individuals were collected representing 101 species and morphospecies from the Scarabaeinae (85 species) and Aphodiinae (16 species) (Appendix A; Table 2.1). This was in line with total species richness expected using the species estimators (Table 2.1), and the species accumulation curves reached asymptotes (Appendix D). Of the 70 540 individuals, 80.98% were represented by only seven species of Aphodiinae and *Onthophagus* (Appendix A). Ninety-eight species and 44 432 individuals were sampled from PAs while 75 species and 26 108 individuals were recorded on farms. Twenty-two of the species were considered rare with less than ten individuals collected (Colwell et al. 2012). PAs harboured 26 unique species while farms only had three species found there exclusively. Of the rare species, *Onitis bilobatus* (Ferreira) represents a species previously known only from the holotype specimen that was collected 43 years ago. *Epirinus flagellatus* (Fabricius), a species previously thought to be restricted to South Africa and Lesotho (Deschodt et al. 2019), was recorded in Namibia for the first time, some 1000 km from the closest other known locality. Other species whose assessment in Namibia is considered data deficient for Red Listing (Koch et al. 2002) include *Onitis deceptor* (Peringuey) and *Sarophorus cf. angolensis* (Klug) (Davis et al. 2019 (unpublished)).

Table 2.1 Observed and estimated richness and abundance of dung beetles collected from three PAs and three farms in the present study

Site	Index	Count
All sites	Abundance	70 540
	Observed richness	101
	Chao2	112.9 ±9.58
	Jackknife2	117.7
Protected areas	Abundance	44 432
	Observed richness	98
	Chao2	103.16±4.78
	Jackknife2	107.79
Farm	Abundance	26108
	Observed richness	75
	Chao2	78.92±3.5
	Jackknife2	83.09

2.3.2 Vertebrate richness and stocking density

There were a total of 23 vertebrate species identified at sites based on dung surveys (Appendix C). Seventeen species were present at sites in the PAs and mainly included large ruminant and non-ruminant ungulates as well a few carnivore species (all carnivore dung was grouped into one group even though it was representative of cheetah, leopard and hyena). There were only nine species present at sites on farms, however, only five of them were recurrent and present at all farm sites. These included mainly livestock and other domestic species with the dung of a few wild animals (e.g.

Kudu) occurring infrequently at a few of the sites. Both vertebrate richness and stocking density were significantly higher on PAs than on farms (vertebrate richness: $F_{(1,119)} = 3.392$, $p<0.001$; vertebrate stocking density: $F_{(1,119)} = 2.564$, $p<0.05$; Fig 2.2).
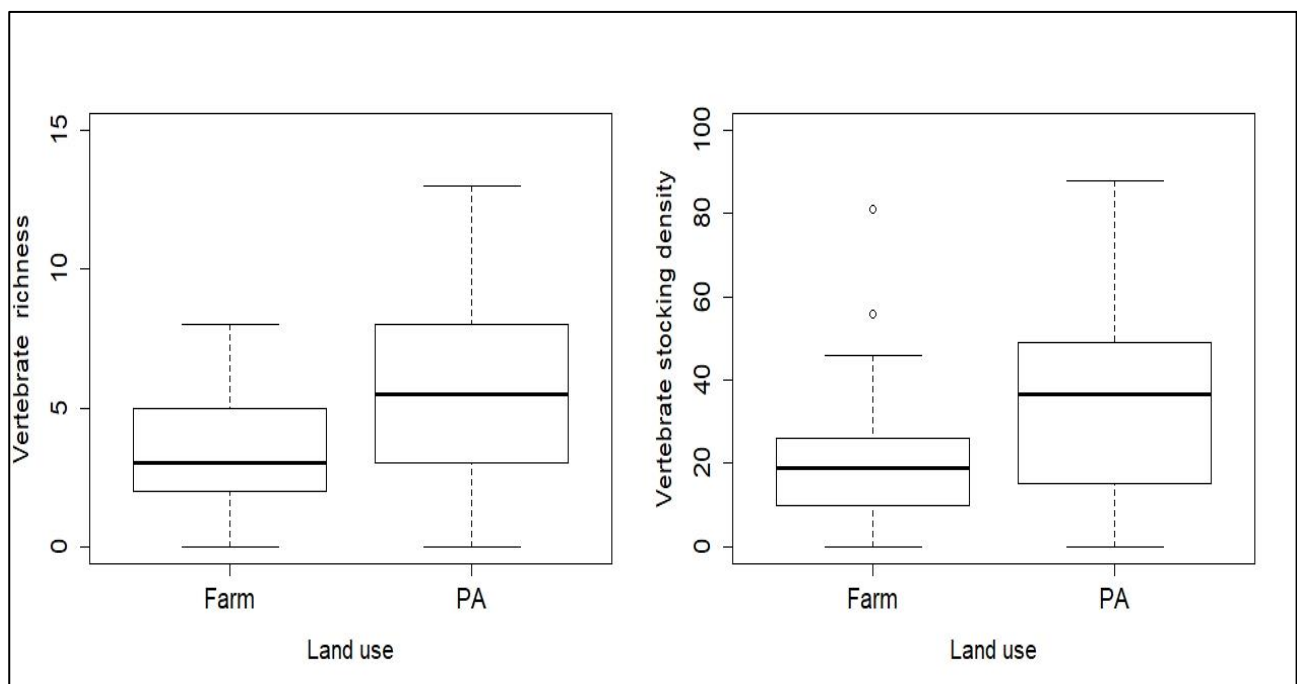
Figure 2.2 Overall a) vertebrate richness and b) vertebrate stocking density on farms and PAs. Graphs show significant results

2.3.3 Response of dung beetle richness, abundance and total biomass to differences in land-use, bait type, vertebrate richness and vertebrate stocking density

Best models selected in analyses are presented in Appendix F. Significant differences were found for dung beetle species richness in response to differences in land-use and changes in vertebrate richness (Appendix F), and there was a significant interaction between land-use and bait type (Appendix F; Fig 2.3). Significantly more dung beetle species were collected on PAs than on farms, and there was an increase in dung beetle species richness with increased vertebrate richness. Significantly more dung beetle species were attracted to wild dung (wildebeest) than to domestic dung (cow) on PAs, but this effect disappeared on farms (Fig 2.3). In terms of the different functional guilds, land-use also had a significant effect on tunneller and dweller richness, with significantly more species on PAs (Appendix F). Tunneller richness also increased significantly with an increase in vertebrate stocking rates. In addition to land-use, the richness of dweller species was influenced by differences in dung type, and these two variables significantly interacted.

Table 2.2 Summary results of the generalized linear mixed models for the effects of land-use, bait type, vertebrate richness and vertebrate stocking density on dung beetle richness, abundance and biomass and the effects on the dynamics of the three functional guilds. Only those variables retained after model selection procedure based on AICc (Appendix F) are shown

Response Variable	Predictor variable	F – value	P-value
Species richness	Land-use	3.395	<0.001
	Bait type	-0.231	0.817
	Vertebrate richness	2.995	0.003**
	Land-use * Bait type	3.876	<0.001
Abundance	Land-use	5.580	0.067
	Bait Type	1.849	0.333
	Land-use * Bait type	0.971	0.012*
Biomass	Land-use	2.729	0.007**
	Bait type	-0.829	0.409
	Vertebrate stocking density	0.634	0.527
	Bait type* Vertebrate stocking density	2.757	0.007**
Roller richness	Vertebrate richness	3.662	<0.001
Roller abundance	Land-use	2.164	0.033*
Roller biomass	Land-use	1.609	0.110
	Vertebrate stocking density	2.979	0.0035**
Tunneller richness	Land-use	4.410	<0.001
	Vertebrate stocking density	2.043	0.043*
Tunneller abundance	Land-use	2.282	0.024*
	Bait type	-0.607	0.544
	Vertebrate richness	-0.299	0.765
	Bait type * Vertebrate richness	2.250	0.026*
Tunneller biomass	Land-use	3.106	0.002**
	Vertebrate stocking density	2.125	0.035*
Dweller richness	Land-use	3.710	<0.001
	Bait type	-0.190	0.849
	Land-use * Bait type	2.534	0.013**
Dweller abundance	Land-use	1.524	0.130
	Bait type	0.146	0.883
	Land-use * Bait type	2.997	0.003**
Dweller biomass	Intercept	0	1

$P < 0.1$, * $P < 0.05$, **$P < 0.01$, ***$P < 0.001$
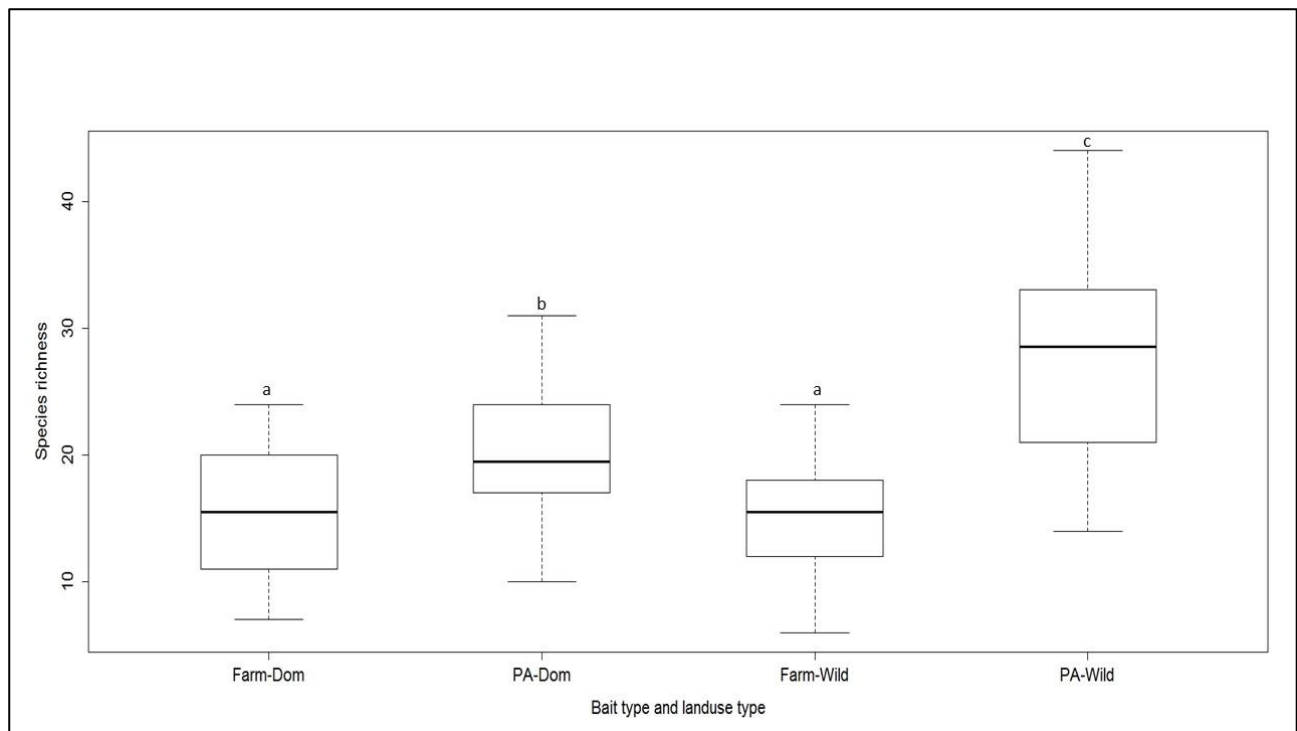
Figure 2.3 Boxplots showing dung beetle species richness response to bait type and land-use type. Box indicates 25%-75% data range, whiskers indicate the minimum and maximum values. The alphabetical letters indicate significant differences recorded using a GLMM followed by a Tukey post hoc test

Overall dung beetle abundance was significantly influenced by the interaction between land-use and bait type but not by either of these alone (Fig 2.4; Table 2.2). This effect was especially evident for the beetles that were attracted to the wild dung in the PAs, whereas wild and domestic dung attracted similar numbers of dung beetle individuals on farms (Fig 2.4; Table 2.2). Land-use had a significant effect on tunneller and roller abundance, with PAs hosting more individuals than farms. For dwellers, the overall effect of land-use was not significant but the interaction between land-use and dung type did yield a significant result (Table 2.2)
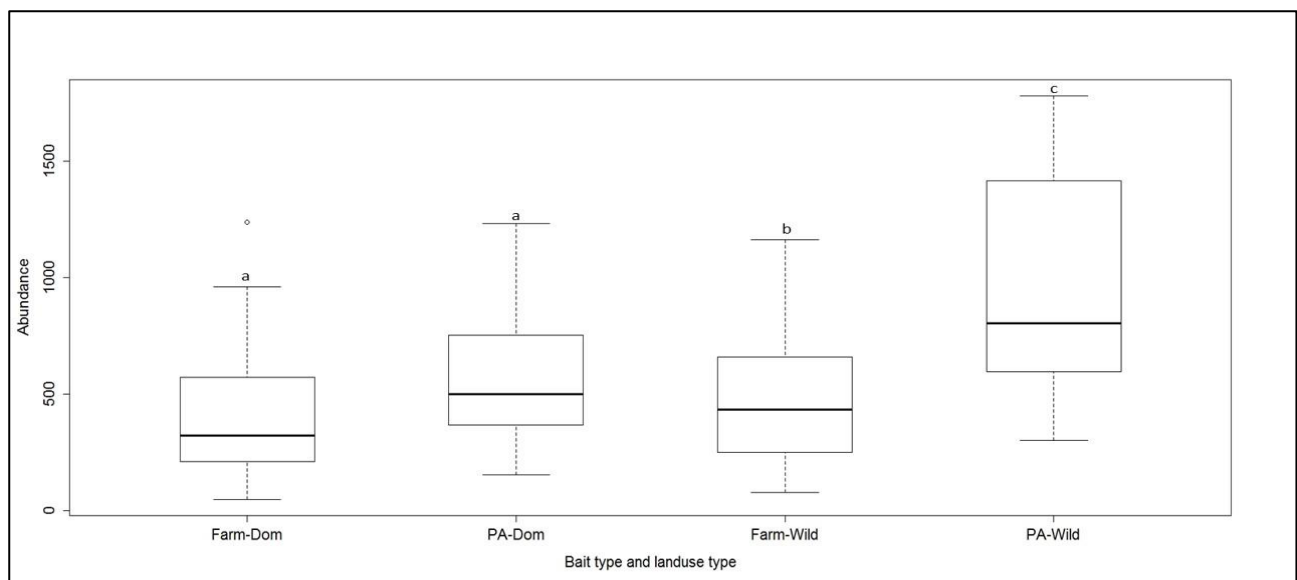
Figure 2.4 Boxplots of the dung beetle abundance response to dung type and land-use type. Box indicates 25%-75% data range, whiskers indicate the minimum and maximum values. The alphabetical letters indicate significant differences recorded using an LMM followed by a Tukey post hoc test

As expected, overall dung beetle biomass was significantly affected by land-use type, with higher biomass recorded on PAs, but the interaction between bait type and vertebrate stocking density also had a significant effect, with higher biomass in traps with wild dung in PAs (Fig 2.5; Table 2.2). Land-use type had similar effects on tunneller and roller biomass but had no effect on dweller biomass. For tunnelers and rollers, an increase in vertebrate stocking density also leads to an increase in dung beetle biomass (Table 2.2).
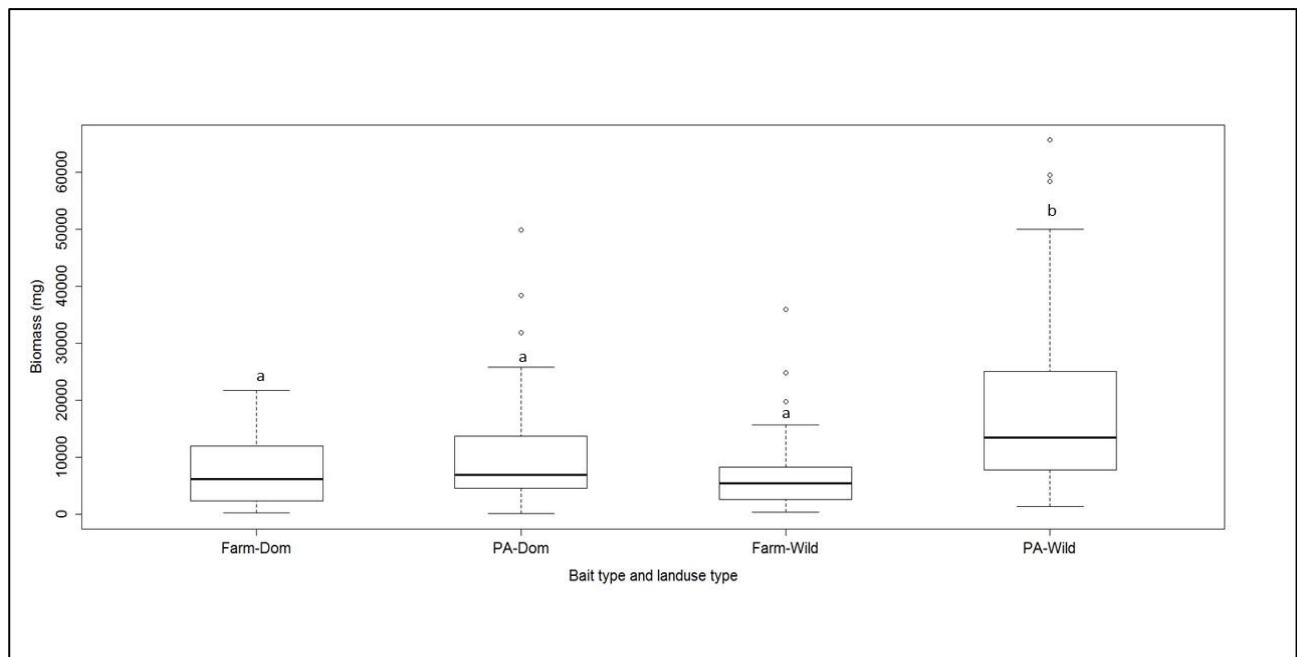
Figure 2.5 Boxplots of the dung beetle biomass response to dung type and land-use type. Box indicates 25%-75% data range, whiskers indicate the minimum and maximum values. The alphabetical letters indicate significant differences recorded using an LMM followed by a Tukey post hoc test

2.3.4 Response of dung beetle assemblages to differences in land-use, bait type, vertebrate richness and vertebrate stocking density

Dung beetle assemblage composition was significantly different between farms and PAs, between the two different bait types, and was significantly influenced by changes in vertebrate species richness and vertebrate stocking densities (Table 2.3) These effects are visualised in the model-based constrained and unconstrained ordination (Fig 2.6). Community assemblage composition was also significantly influenced by the interactive effect of land-use and bait type (Fig 2.6; Table 2.3) with most divergent assemblages found between the beetles collected with the different baits on the PAs. Other significant second-order interactive effects were found between bait type and vertebrate species richness (Table 2.3).

Univariate results for these analyses are reported in Appendix J and presents 'species-by-species' test statistics of the most abundant species that were significant indicators for both land-use and dung type. Only two species were significant for land-use type, *Onthophagus venustulus* (close to 2) and *Metacatharsius cf. dentinum*, while bait type had one species, *Pedaria cf. cylindrica*.

Table 2.3 ANOVA table summarising multivariate GLM results for the variables land-use, bait type, vertebrate richness and vertebrate stocking density on dung beetle community assemblage composition

Factor	Res.df	DF. diff	Val (DEV)	Pr(>DEV)
Land-use	118	1	356.5	0.001***
Bait type	117	1	163.6	0.005**
Vertebrate richness	116	1	148.2	0.011*
Vertebrate stocking density	115	1	174.9	0.002**
Land-use: Bait type	114	1	121.1	0.037*
Land-use: Vertebrate richness	113	1	99.1	0.089
Bait type: Vertebrate richness	112	1	126.7	0.050*
Land-use: Vertebrate stocking density	111	1	96.5	0.144
Bait type: Vertebrate stocking density	110	1	121.6	0.051
Vertebrate richness: Vertebrate stocking density	109	1	129.4	0.242
Land-use: Bait type: Vertebrate richness	108	1	109.8	0.045*
Land-use: Bait type: Vertebrate stocking density	107	1	59.4	0.183
Land-use: Vertebrate richness: Vertebrate stocking density	106	1	110.0	0.035*
Bait type: Vertebrate richness: Vertebrate stocking density	105	1	80.4	0.412
Land-use: Bait type: Vertebrate richness: Vertebrate stocking density	104	1	43.0	0.324

*P < 0.05, **P < 0.01, ***P < 0.001
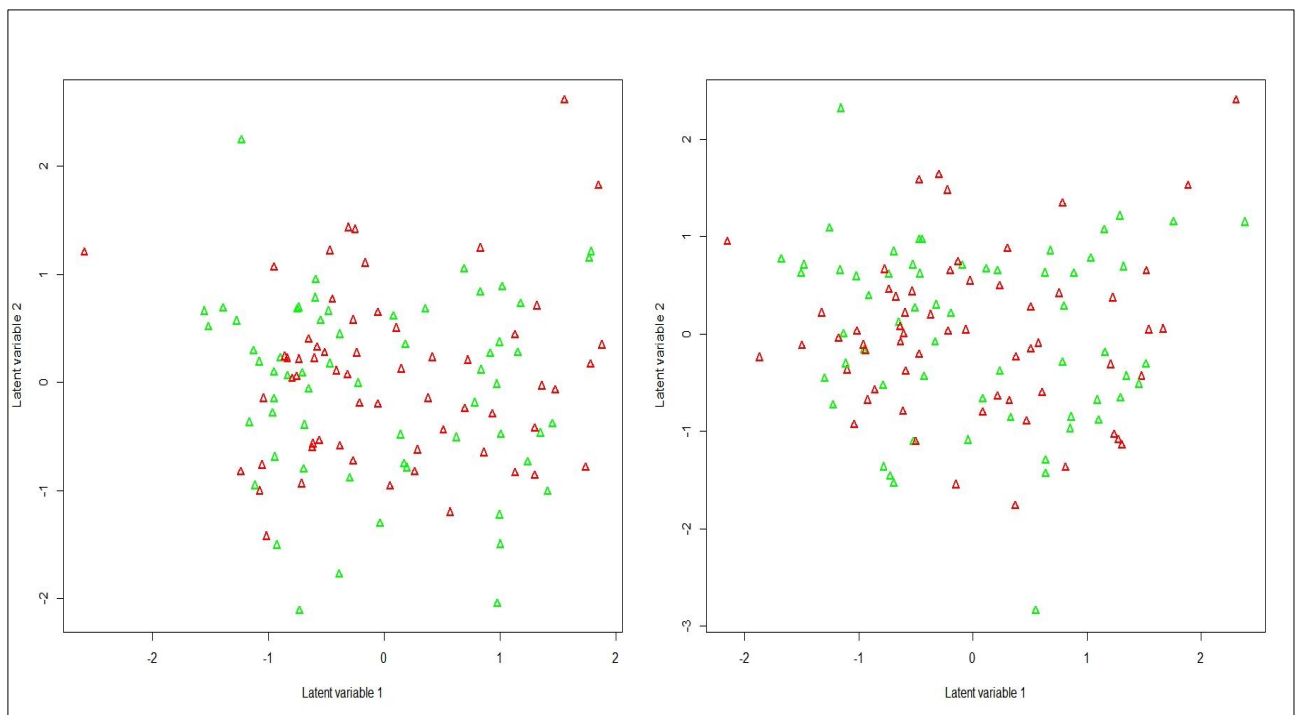
Figure 2.6 Model-based unconstrained ordination plot (right) and constrained plot (left)of dung beetle assemblages across the two land-use types. The colours show the categorical variables of land-use (in red) and species (in green) and the axes represent the latent variables

2.3.5 Response in the development of dung beetles to differences in land-use

Individual dung beetles of most of the 58 species commonly found on PAs and farms tended to be larger in PAs than their conspecifics on farms (Appendix A; Fig 2.7). Only 13 species were larger on farms than on PAs (four of them significantly so) while 45 species were larger on PAs (ten of them significantly so). Overall, dung beetle species tended to be larger in PAs than on farms (G = 12.081, df = 1, p = <0.001).

***Onthophagus sp3
**Aphodiinae sp8
Onthophagus semiflavus
*Aphodiinae sp10
Aphodiinae sp1
Aphodiinae sp3
Onthophagus suffusus
Onthophagus venustulus (close to 1)
Aphodiinae sp4
Aphodiinae sp7
Aphodiinae sp5
Onthophagus axillaris
Onthophagus aeruginsus
Onthophagus impressicollis
**Pedaria cf. cylindrica
Onthophagus sp2
Gymnopleurus pumilus
Scarabaeolus bohemani
Garreta nitens
Chalconotus convexus
**Scarabaeus vicinus
*Kheper cupreus
Phalops prasinus
Phalops rufosignatus
**Metacatharsius troglodytes
Copris gracilis
Metacatharsius exiguus
*Onitis setosus
Copris laioides

Farm vs Protected Area

2.4 Discussion

I found a remarkably rich diversity of species on both PAs and farms with species richness even exceeding numbers collected in tropical rainforests (Nichols et al. 2008; Slade et al. 2011; Audino et al. 2014; Dangles et al. 2012; Griffiths et al. 2017) and other African regions (Shepherd and Chapman 1998; Davis et al. 2002; Tshikae et al. 2008; Jacobs et al. 2010; Pryke et al. 2016). The richness of dung beetles was higher in PAs, and assemblages differed significantly between the two land-use types, indicating strong negative effects of land transformation for domestic livestock farming on dung beetle diversity. This echoes previous studies that show that more natural ecosystems support greater dung beetle diversity compared to transformed landscapes (Jankiesholn et al. 2001; Davis et al. 2005; Vohland et al. 2005; Manning et al. 2016). Dung beetle numbers and assemblage composition was also variably influenced by both changes in vertebrate richness and stocking densities and I show that a diverse assemblages of native vertebrates is necessary for the maintenance of a rich dung beetle assemblage (Pryke et al. 2016; Raine et al. 2018a, b; Raine and Slade 2019). Dung beetle biomass was higher in PAs than on farms even though abundances were similar. In addition, dung beetle taxa that were present on farms generally tended to be smaller than their conspecifics in PAs. These results demonstrate that dung resources on farms are generally suboptimal for normal beetle development, which may have negative effects on ecosystem functions and services.

2.4.1 A diverse natural vertebrate fauna maintains high dung beetle diversity

The most significant variable that influenced dung beetle diversity measures in the present study was land-use change. Dung beetle overall richness, abundance for most guilds, and biomass were significantly lower on farms than on PAs. Dung beetle assemblage composition was also significantly different between farms and PAs. Similar to other studies, I identified declining vertebrate species richness on farms as an important reason for declines in dung beetle species richness (Nichols et al. 2009; Raine and Slade 2019) and for changes in dung beetle assemblages. In my study, some dung beetle species were seemingly native dung specialists (e.g. *Onitis bilobatus*, *Onthophagus aequepubens* and *Pedaria* sp. 1) or preferred dung from native vertebrates (*Onitis uncinatus*, *Onthophagus venustulus* and allied taxa, and *Phalops pyroides*) and the decrease in species richness may be ascribed to the loss of these more specialist dung feeders (du Toit and Cumming 1999; Tshikae et al. 2008). As with other studies I found that the rollers were the guild most significantly affected by declines in vertebrate richness (Davis et al. 2008; McGranahan 2008). Rollers are quite closely associated with pellet dropping species like Duikers (*Sylvicapra grimmia*) and Kudu (*Tragelaphus strepsiceros*) (Davis 1994; Scholtz et al. 2009; Tshikae et al. 2013a, b; Davis et al. 2008), two species that are in rapid decline in the agricultural landscapes. Like with other studies I found that most of the relatively rare species (those with less than 20 individuals collected) were largely confined to the PAs and therefore are unable to adapt to land transformation pressures

(Nichols et al. 2013; Raine and Slade 2019). However, most species collected here were attracted to both native and domestic dung resources and bait type had little effect on overall richness and abundance of the beetles captured. Loss of dung beetle richness due to the intensification of agricultural practices (Manning et al. 2017) is often ascribed to the homogenisation of mammal communities despite generalist feeding habits (Nichols et al. 2009; Pryke et al. 2016). As vertebrate stocking density did not affect dung beetle richness, it is reasonable to assume those general reductions in resource quality on farms added to the reduction in dung beetle species richness. It is therefore probable that changes in mammal species composition instigates a highly complex reaction in dung beetle trophic guilds related to their degree of stenophagy (Gordon and Cartwright 1974), level of resource plasticity (quantity and quality) and vagility (Hanski 1980; Hanski et al. 2008), and their adaptations to changes in soil and vegetation characteristics associated with land transformation (Davis et al. 2008; McGranahan 2008; Tonelli et al. 2017, 2018).

The reduction in dung beetle species richness on farms may also be linked to the use of veterinary pharmaceuticals on farms. Cattle in the study region are routinely treated with veterinary pharmaceuticals such as SUPAVAX® and *Brucellla* S19 (pers. comm.). The use of medicines such as these on livestock have been known to impair sensory functions in dung beetles and can lead do declines in their diversity (Verdu et al. 2015, 2017). These substances can be excreted in dung for up to two weeks after treatment (Lumaret et al. 1993). Some dung beetle species may be more severely impacted by these chemicals than others and be removed from populations, leading to the dominance of only the more immune species. It is therefore often found that veterinary parasiticide free areas support a higher richness of dung beetles (Hutton and Giller, 2003; Bang et al. 2005).

Despite the lower richness of dung beetles on farms, overall dung beetle abundance was similar to those on PAs. This was an unexpected result because insect abundances typically respond negatively to agricultural intensification (Numa et al. 2012; Manning et al. 2017, 2018). Farms had only a few species unique to them and these were found in low abundance. Therefore, many taxa were still abundant on farms and may be readily able to utilise the dung of domestic grazers. This indicates that both farms and PAs have sufficient available resources to maintain populations of most dung beetle species (Hanski and Cambefort 1991; Davis et al. 2008) and that there exists a fairly high level of resource plasticity amongst many species (Hanski et al. 2008) collected here. However, dung beetle assemblage composition was significantly influenced not only by vertebrate richness but also by vertebrate stocking rates. This indicates general shifts in the relative abundances of most dung beetle species in relation to land-use change and the accompanying altered vertebrate assemblages. As with other studies, I identified shifts in the dominance of dung beetle guilds due to disturbance (Nichols et al. 2007; Korasaki et al. 2013) which will likely alter natural functions.

2.4.2 Resource conditioning

It is reasonable to expect some degree of resource conditioning where species will be attracted to a bait that is locally available (Davis 1994; Tshikae et al. 2008; Amézquita and Favila 2010). Therefore, I expected dung beetles to prefer dung resources from native vertebrates in the PAs where this resource is available, unlike farms where it has been replaced by domestic livestock dung. Similar to other studies, I found that most of the species that I collected were euryphagous with a majority of species attracted indiscriminately between the two dung types (Halffer and Matthews, 1966; Bogoni et al. 2014). However, this was evident only on farms where the two bait types collected similar richness, abundance and assemblages of dung beetles. On PAs, there were strong biases in richness and abundance for dung originating from the native vertebrate and here the assemblages collected by each dung type were significantly different. There are a plethora of possible reasons for this pattern, one being the long evolutionary history that dung beetles and native fauna share (Nichols et al. 2008; Raine and Slade 2019), with the removal of native fauna being from agricultural land, leading to the loss of specialist dung beetle species (Nichols et al. 2009; Raine et al. 2018a,b; Bogoni et al. 2019; Raine and Slade 2019). Even though dung beetles make choices based on olfactory cues (Dormont et al. 2007; Whipple and Hoback 2012), olfactory cues do not provide any nutritional information to dung beetles (Dormont et al. 2007; Whipple and Hoback 2012; Frank et al. 2017a). Therefore, the indiscriminate attraction of dung beetles on farms may be a result of the remaining dung beetles being opportunistic due to the general reduction in the variety of resources available on farms (Nichols et al. 2009; Raine et al. 2018a, b). Generalist feeding is often a corollary of resource scarcity (Al-Houty and Al-Musalam 1997; Dormont et al. 2004), which is highly likely in this arid region (Vohland et al. 2005) and seasonal migrations and mammal population fluctuations (Edwards 1991).

2.4.3 The negative effect of land transformation on dung beetle biomass and individual development

Overall dung beetle biomass was significantly higher on PAs than on farms. This was similar to findings by Al-Houty and Al-Musalam (1997) and Dormont et al. (2004) that indicated higher biomass in areas with more resources. Although there is usually a close correlation between dung beetle biomass and abundance (Manning et al. 2018), I found no difference in dung beetle abundance between farms and PAs. Protected areas likely had higher dung beetle biomass due to the exclusion of several large-bodied tunnelling species such as *Catharsius ulysses* and *Heliocopris atropos*, and lower abundance of large rolling species such as *Pachylomera femoralis* and *Scarabaeus goryi* on farms. This is similar to other studies that documented the loss of larger tunnelling and rolling dung beetle species due to habitat degradation and their comparatively longer generation times compared to smaller rolling and tunnelling beetles (Ribera et al. 2001; Larsen et al. 2005; Jelaska and Durbesic 2009). Predictably, reductions in resource quality on farms would also have the largest negative

impact on the development of the larger-bodied species (Frank et al. 2017a, b). Reductions in the numbers of large-bodied species on farms are concerning as dung beetle ecosystem function may be severely impaired (Slade et al. 2011; Braga et al. 2013; Gollan et al. 2013; Nervo et al. 2014; Raine and Slade 2019).

I found a general trend in the average mass of individuals of dung beetle species common on both farms and PAs to be smaller on farms. I believe that this is linked to greater resource quality in PAs than on farms. The average nitrogen content of dung resources on farms is expected to be lower than those on PAs (Al-Houty and Al-Musalam 1997; Lekasi et al. 2001; Augustine 2003; Codr0n et al. 2007; Onduru et al. 2008). Increased nitrogen content of dung will directly result in the production of larger-bodied individuals on PAs (Edwards 1991; Moczek 1998; Schwab et al. 2017). However, reductions in quality of dung of domestic livestock may also be due to the use of veterinary medical products (Verdu et al. 2015, 2017; Bernal et al. 1994; Floate, 2006; Hammer et al. 2016). Dung quality may also be affected by pasture quality (Edwards 1991) and livestock behaviour tends to have deleterious effects on vegetation and soil (Samways and Kreuzinger 2001; Vohland et al. 2005). Dung beetles are highly adapted to vegetation type and soil (Scholtz et al. 2009) and changing these parameters on farms will have unfavourable outcomes for the physiological condition of the dung beetles and their development (Sands and Wall 2017; Raine and Slade 2019). Furthermore, Krüger and Scholtz (1998a, b) found that dung beetles were more vulnerable to veterinary pharmaceuticals under drought conditions and seeing that the region sampled is a xeric savannah the dung beetles may very well be more susceptible to the use of these pharmaceuticals. Whatever the mechanism, the reduction in mean individual body mass on farms will have cascading effects on future populations. Larger beetles compete better for food resources (Doube et al. 1988; Larsen et al. 2005; Slade et al. 2007; Nervo et al. 2014; Tonelli et al. 2018) and provide larger quantities of dung to offspring (Hunt and Simmons 2002). Reductions in size will, therefore, reduce their competitive abilities, and lead to decreases in dung provision to offspring. This may form a negative feedback loop over many generations. The reduced amount of dung removed due to smaller beetles will also reduce positive ecosystem effects associated with dung removal (Larsen et al. 2005; Milotic et al 2019). The possible negative effect of veterinary medical products on dung beetle development may be antithetical given that one of the main services provided by dung beetles is the suppression of parasites (Davis 2004; Nichols et al. 2008; Sands and Wall 2017), an action that may be reduced because of its use.

2.5 Conclusion

Here I highlighted some of the ways in which land-use change and the wildlife-domestic animal divide in Namibia is impacting dung beetle ecology particularly in the context of their abundance, richness, assemblages, overall biomass and development, all of which had been affected adversely.

The degree to which these species attributes are affected varied with the most noteworthy changes detected in the loss of large-bodied species and the difference in the size of the beetle individuals between natural and agroecosystems. These changes may have major short- and long-term implications for the maintenance of important ecosystem processes (Nichols et al. 2009). This further attests to the fact that an amalgam of megaherbivores is essential because they create important niches not only for dung beetles but other invertebrate fauna (Pryke et al. 2016; Gomez– Cifuentes et al. 2018). The preservation of functionally complete dung beetle – mammal assemblages is essential to enable continued efficient ecosystem functioning (Manning et al. 2016) and the concomitant economic advantages they bring (de Klerk 2004; Beynon et al. 2015).

2.6 References

Alexandratos N, Bruinsma J (2012) World Agriculture towards 2030/2050: The 2012 revision. Rome: UN Food and Agricultural Organization (FAO)

Al-Houty W, Al-Musalam F (1997) Dung preference of the dung beetle *Scarabaeus cristatus* fab (Coleoptera-Scarabaeidae) from Kuwait. Journal of Arid Environments 35:511 – 516

Alkemade R, Reid RS, van den Berg M, de Leeuw J, Jeuken M (2013) Assessing the impacts of livestock production on biodiversity in rangeland ecosystems. Proceedings of the National Academy of Sciences of the United States of America 110: 20900 – 20905

Amezquita S, Favila ME, (2010) Removal rates of native and exotic dung by dung beetles (Scarabaeidae: Scarabaeinae) in a fragmented tropical rain forest. Environmental Entomology 39: 328 – 336

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

Andresen E, Feer F (2005) The role of dung beetles as secondary seed dispersers and their effect on plant regeneration in tropical rainforests. In: Forget PM, Lambert JE, Hulme PE, Vander Wall SB (e) Seed fate. Predation, dispersal and seedling establishment. CABI, Oxon, UK, pp 331 – 349

Andresen E, Laurance SGW (2007) Possible indirect effects of mammal hunting on dung beetle assemblages in Panama. Biotropica 39:141 – 146

Audino, LD, 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

Augustine DJ (2003) Long-term, livestock-mediated redistribution of nitrogen and phosphorus in an East African savannah. Journal of Applied Ecology 40:137 – 149

Augustine DJ, McNaughton SJ (1998) Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. Journal of Wildlife Management 62:1165 – 1183

Balthasar V (1963a) Neue arten der familie Scarabaeidae. Acta Societatis Entomologicae Cechosloveniae 60: 284 – 295

Balthasar V (1963b) Monographie der Scarabaeidae und Aphodiidae der palaearktischen und orientalischen Region (Coleoptera: Lamellicornia). Band 2. Coprinae (Onitini, Oniticellini, Onthophagini). Verlag der Tschechoslowakischen Akademie der Wissenschaften, Prague: pp 627

Balthasar V (1965a) Eine neue undergattung und neue arten der familie Scarabaeidae (121. Beitrag zur Kenntnis der Scarabaeoidea). Acta entomologica bohemoslovaca 62: 14 – 23

Balthasar V (1965b) Monographie der untergattung Metacatharsius Paulian. Entomologische Abhandlungen Staatlichen Museum für Tierkunde, Dresden 31:1– 48

Bang HS, Lee JH, Kwon OS, Na YE, Jang YS, Kim WH (2005) Effects of paracoprid dung beetles (Coleoptera: Scarabaeidae) on the growth of pasture herbage and on the underlying soil. Applied Soil Ecology 29: 165 – 171

Barnard P (1998) Biological diversity in Namibia: a clash of sea and land, fog and dust. Biodiversity and Conservation 7:415 – 417

Barnard P, Brown CJ, Jarvis AM, Robertson A (1998) Extending the Namibian protected area network to safeguard hotspots of endemism and diversity. Biodiversity and Conservation 7:531 – 547

Bates D, Mächler M, Bolker B, Walker S (2014) Fitting linear mixed-effects models using {lme4}. Journal of Statistical Software 67:1 – 48

Beerling DJ, Osborne CP (2006) The origin of the savanna biome. Global Change Biology 12:2023 – 2031

Bengtsson J, Angelstram P, Elmqvist T, Emanuelson U, Folke C, Ihse M, Moberg F, Nystrom M, (2003) Reserves, resilience and dynamic landscapes. Ambio 32:389 – 396

Beynon SA, Wainwright WA, Christie M (2015) The application of an ecosystem services framework to estimate the economic value of dung beetles to the UK cattle industry. Ecological Entomology 40:124 – 135

Bernal JL, Del Nozal MJ, Salas M, Galante E, Lumaret JP (1994) HPLC determination of residual ivermectin in cattle dung following subcutaneous injection. Journal of Liquid Chromatography 17: 2429 – 2444

Beynon SA, Wainwright WA, Christie M (2015) The application of an ecosystem services framework to estimate the economic value of dung beetles to the UK cattle industry. Ecological Entomology 40:124 – 135

Bogoni JA, Hernández MIM (2014) Attractiveness of native mammal's faeces of different trophic guilds to dung beetles (Coleoptera: Scarabaeinae). Journal of Insect Science 14:1 – 7

Bogoni JA, Graipel ME, de Castilho PV, Fantacini FM, Kuhnen VV, Luiz MR, Maccarini TB, Marcon CB, de Souza Pimentel Teixeira C, Tortato MA, Vaz-de-Mello FZ, Hernández MIM (2016) Contributions of the mammal community, habitat structure, and spatial distance to dung beetle community structure. Biodiversity Conservation 251: 661 – 1675

Bogoni JA, Pires JSR, Graipel ME, Peroni N, Peres CA (2018) Wish you were here: How defaunated is the Atlantic Forest biome of its medium– to large-bodied mammal fauna? PLoS ONE 13: e0204515

Bogoni JA, da Silva PG, Peres CA (2019) Co-declining mammal–dung beetle faunas throughout the Atlantic Forest biome of South America. Ecography 42: 1 – 16

Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White JSS (2008) Generalized linear mixed models: a practical guide for ecology and evolution. Trends Ecol Evol 2:127 – 135

Bond WJ (2008) What Limits Trees in C4 Grasslands and Savannas? Annual Review of Ecology, Evolution, and Systematics 39:641 – 59

Braga RF, 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 with biodiversity. PLoS ONE 8: e5778

Branco T (2010) Revision of the genera Tiniocellus Péringuey, 1901 and Nitiocellus gen. n. Boletin de la Sociedad Entomologica Aragonesa 47: 71 – 126

Burnham KP, Anderson DR (2004) Multimodel inference understanding AIC and BIC in model selection. Sociological Methods & Research 33:261 – 304

Cambefort Y (1991) Biogeography and evolution. In: Dung beetle ecology; Hanski I, Cambefort Y. (eds); Princeton University Press. Princeton, USA pp 51 – 68

Cambefort Y (1996) Une nouvelle espèce Afro-Tropicale d'Euoniticellus Janssens, 1953, avec une Phylogénie du genre. Revue française d'Entomologie (N.S.) Paris 18 115 – 119

Cardoso P, Erwin TL, Borges PAV, New TR (2011) The seven impediments in invertebrate conservation and how to overcome them. Biological Conservation 144:2647 2655

Chao A (2005) Species richness estimation. In: Balakrishnan, N., Read, C.B., Vidakovic, B. (Eds.), Encyclopedia of Statistical Sciences. Wiley, New York, pp 7909 – 7916

Chao A, Gotelli NJ, Hsieh TC, Sander EL, Ma KH, Colwell RK, Ellison AM (2014) Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. Ecol Monogr 84:45 – 67

Coetzee BWT, Tincani L, Wodu Z, Mwasi SM (2008) Overgrazing and bush encroachment by Tarchonanthus camphoratus in a semi-arid savanna. African Journal of Ecology 46:449 – 451

Colwell RK, Chao A, Gotelli NJ, Lin SY, Mao CX, Chazdon RL, Longino JT (2012) Models and estimators linking individual-based and sample-based rarefaction, extrapolation and comparison of assemblages. Journal of Plant Ecology, 5:3 – 21

Colwell RK (2013) EstimateS: Statistical estimation of species richness and shared species from samples

Codron D, Lee-Thorp JA, Sponheimer M, Codron J, De Ruiter D, Brink JS (2007) Significance of diet type and diet quality for ecological diversity of African ungulates. Journal of Animal Ecology 76:526 – 537

Crawley MJ (2013) The R Book, second ed. Wiley, West Sussex

Culot L, Bovy E, Vaz-de-Mello FZ, Guevarad R, Galetti M (2013) Selective defaunation affects dung beetle communities in continuous Atlantic rainforest. Biological Conservation 163: 79 – 89

Cromsigt JPG, Olaf H (2009) Resource partitioning among savanna grazers mediated by local heterogeneity: an experimental approach. Ecology 87: 1532 – 1541

Dangles O, Carpio C, Woodward G (2012) Size-dependent species removal impairs ecosystem functioning in a large-scale tropical field experiment. Ecology 93:2615 – 2625

Davis AL (1989) Nesting of Afrotropical Oniticellus (Coleoptera: Scarabaeidae) and its evolutionary trend from soil to dung. Ecological Entomology 14:11 – 21

Davis, ALV (1994). Associations of Afrotropical Coleoptera (Scarabaeidae, Aphodiidae, Staphylinidae, Hydrophilidae, Histeridae) with dung and decaying matter: implications for selection of fly-control agents for Australia. Journal of Natural History 28: 383 – 399

Davis ALV (2002) Dung beetle diversity in South Africa: influential factors, conservation status, data inadequacies and survey design. African Entomology 10: 53 – 65

Davis AVL, Deschodt CM, Scholtz CH (2019) Conservation Assessment of Scarabaeine DUNG BEETLES in South Africa, Botswana and Namibia: IUCN Red List Categories, Atlas and Ecological Notes (unpublished)

Davis ALV, Scholtz CH, Deschodt C (2005) A dung beetle survey of selected Gauteng nature reserves: implications for conservation of the provincial scarabaeine fauna. African Entomology 13: 1 – 16

Davis ALV, Frolov AV, Scholtz CH (2008) The African Dung Beetle Genera. Protea Book House, Pretoria

De Klerk JN (2004) Bush Encroachment in Namibia: Report on Phase 1 of the Bush Encroachment Research, Monitoring and Management Project. John Meinert Printing, Windhoek, Namibia

Deschodt CM, Kryger U, Scholtz CH (2007) New taxa of relictual Canthonini dung beetles (Scarabaeidae: Scarabaeinae) utilizing rock hyrax middens as refuges in south-western Africa. Insect Systematics and Evolution 38: 361 – 376

Deschodt CM, Davis ALV (2018) New deltochiline (Coleoptera: Scarabaeidae: Scarabaeinae) taxa associated with hyrax dung in arid southwestern Namibia. Zootaxa 4450: 066 – 076

Deschodt CM, Davis ALV, Scholtz CH (2011) New dung beetle (Coleoptera: Scarabaeidae: Scarabaeinae) taxa from arid south-western Africa. Insect Systematics & Evolution 42: 277– 29

Deschodt CM, Davis ALV, Scholtz CH (2016) A new monotypic genus, a species synonymy and nomenclatural corrections in the arid-adapted Canthonini (Scarabaeidae, Scarabaeinae) from the Succulent Karoo Biome of south-western Africa. Zootaxa 4147 (4): 490 – 500

Deschodt CM, Davis AVL, Daniel GM, (2019) The endemic Southern African genus *Epirinus* Dejean, 1833 (Coleoptera: Scarabaeidae: Scarabaeinae) revisited: five new species and two new synonyms. Zootaxa 4603: 327 – 340

Dormont L, Epinat G, Lumaret J (2004) Trophic preferences mediated by olfactory cues in dung beetles colonizing cattle and horse dung. Environmental Entomology 33:370 – 377

Dormont L, Rapior S, McKey DB, Lumaret JP (2007) Influence of dung volatiles on the process of resource selection by coprophagous beetles. Chemoecology 17:23 – 30

Doube BM (1990) A functional classification analysis of the structure of dung beetle assemblages. Ecol Entomol 15:371 – 383

Du Toit JT, Cumming DHM (1999) Functional significance of ungulate diversity in African savannas and the ecological implications of the spread of pastoralism. Biodiversity and Conservation 8:1643 – 1661

Edwards PB (1991) Seasonal variation in the dung of African grazing mammals, and its consequences for coprophagous insects. Functional Ecology 5:617 – 628

Eklof A, Ebenman B (2006) Species loss and secondary extinctions in simple and complex model communities. Journal Animal Ecology 75: 239 – 246

Emlen DJ (1997) Diet alters male horn allometry in the beetle *Onthophagus acuminatus* (Coleoptera: Scarabaeidae). Proceedings of the Royal Society of London 264: 567 – 574

Engler JO, Abson DJ, Feller R, Hanspach J, von Wehrden H (2018) A social-ecological typology of rangelands based on rainfall variability and farming type. Journal of the Arid Environment 148:65 – 73

Ferreira MC (1969) Contribuiçao para o conhecimento dos Escarabídeos de África. Descriçao de uma espécie nova de Scarabaeus s. str. Novos Taxa Entomológicos 68: 3 – 4

Ferreira MC (1976) A new species of *Platyonitis* Janssens from Angola. Navorsinge van die Nasionale Museum 3: 177 – 180

Ferreira MC (1978) The genus Onitis F. of Africa south of the Sahara. Memoirs van die Nasionale Museum 10: 1-410

Filgueiras BKC, Iannuzzi L, Leal IR (2011) Habitat fragmentation alters the structure of dung beetle communities in the Atlantic Forest. Biological Conservation 144:362 – 369

Fincher, G (1992) Injectable ivermectin for cattle: effect on some dung inhabiting insects. Environmental Entomology 21: 871 – 876

Fletchmann CAH, Tabet VG, Quinter I (2009) Influence of carrion smell and rebaiting time on the efficiency of pitfall traps to dung beetle sampling. Entomologia Experimentalis et Applicata 132:211 – 217

Floate KD (2006) Endectocide use in cattle and faecal residues: environmental effects in Canada. Canadian Journal of Veterinary Research 70:1 – 10

Frank, K, Bruckner A, Hilpert A, Heethoff M, Bluthgen N (2017a) Nutrient quality of vertebrate dung as a diet for dung beetles. Science Report 7:12 – 14

Frank K, Hulsmann M, Assmann T, Schmitt T, Bluthgen N (2017b) Land-use affects dung beetle communities and their ecosystem service in forests and grasslands. Agriculture, Ecosystems & Environment 243:114 – 122

Frolov AV, Scholtz CH (2003) A new genus and species of dung beetle from southern Namibia (Coleoptera: Scarabaeidae: Scarabaeinae). African Entomology 11: 297 – 299

Frolov AV (2005) A New Species of the Dung Beetle Genus Namakwanus (Coleoptera, Scarabaeidae) from Namibia. Contributions to Systematics and Biology of Beetles 245 – 247

Gittings T, Giller PS (1998) Resource quality and colonisation and succession of coprophagous dung beetles. Ecography 21: 581 – 592

Godfray HCJ, Beddington JR, Crute IR, Haddad L, Lawrence D, Muir JF, Pretty J, Robinson S, Thomas SM, Toulmin C (2010) Food security: the challenge of feeding 9 billion people. Science, 327: 812 – 818

Gollan JR, Reid CAM, Barnes PB, Wilkie L (2011) The ratio of exotic-to-native dung beetles can indicate habitat quality in riparian restoration. Insect Cons. & Divers 4:123 – 131

Gómez VC, Verdú JR, Alonso CBG, Zurita G A (2018) Relationship between land-uses and diversity of dung beetles (Coleoptera: Scarabaeinae) in the southern Atlantic forest of Argentina: which are the key factors? Biodiversity and Conservation 27:3201 – 3213

Gordon RD, Cartwright L (1974) Survey of food preferences of some North American Canthonini (Coleoptera: Scarabaeidae). Entomology News 85: 181 – 185

Gotelli NJ, Colwell RK (2001) Quantifying biodiversity: procedures and pit– falls in the measurement and comparison of species richness. Ecology Letters 4:379 – 391

Griffiths HM, Bardgett RD, Louzada J, Barlow J (2016) The value of trophic interactions for ecosystem function: dung beetle communities influence seed burial and seedling recruitment in tropical forests. Proceedings of the Royal Society B: Biological Sciences 283:20161634

Halffter G, Matthews EG (1996) The natural history of dung beetles of the subfamily Scarabaeinae (Coleoptera, Scarabaeidae). Folia Entomológica Mexicana 12:1 – 312

Hammer TJ, Fierer N, Hardwick B, Simojoki A, Slade EM, Taponen J, Viljanen H, Roslin, T. (2016) Treating cattle with antibiotics affects greenhouse gas emissions, and microbiota in dung and dung beetles. Proceedings of the Royal Society B: Biological Sciences 283: 20160150

Hanski I (1980) Spatial variation in the timing of seasonal occurrence in coprophagous beetles. Oikos 34: 311-321

Hanski I, Cambefort Y (1991) Dung Beetle Ecology. Princeton University Press, Princeton

Hanski I, Wirta H, Nyman T, Rahagalala P (2008) Resource shifts in Malagasy dung beetles: contrasting processes revealed by dissimilar spatial genetic patterns. Ecology Letters 11:1208 – 1215

Harrison S, Damschen EI, Grace JB (2010) Ecological contingency in the effects of climatic warming on forest herb communities. Proceedings of the National Academy of Sciences of the United States of America 107:19362 – 19367

Holechek J, Valdez R (2018) Wildlife conservation on the rangelands of eastern and southern Africa: past, present, and future. Rangeland Ecology & Management 71:245 – 258

Holter P, Scholtz CH (2007) What do dung beetles eat? Ecol Entomol 32:690 – 697

Hsieh TC, Ma KH, Chao A (2016) iNEXT: An R package for rarefaction and extrapolation of species diversity (Hill numbers). Methods in Ecology and Evolution 7:1451–1456

Hunt J, Simmons LW (2002) Behavioural dynamics of biparental care in the dung beetle Onthophagus taurus. Anim. Behav. 64:65 – 75

Hui FKC (2016) Boral – Bayesian ordination and regression analysis of multivariate abundance data in r. – Methods in Ecology and Evolution 7: 744 – 750

Hull HE, Freitag S, Chown SL, Bellamy CL (1998) Identification and evaluation of priority conservation areas for Buprestidae (Coleoptera) in South Africa, Lesotho, Swaziland and Namibia. African Entomology 2:265 – 274

Hutton SA, Giller PS. (2003) The effects of the intensification of agriculture on northern temperate dung beetle communities. Journal of Applied Ecology 40:994 – 1007

Jacobs C, Scholtz CH, Escobar F, Davis AL (2010) How might intensification of farming influence dung beetle diversity (Coleoptera: Scarabaeidae) in Maputo Special Reserve (Mozambique)? Journal of Insect Conservation, 14: 389 – 399

Jankielsohn A, Scholtz CH, Louw SVDM (2001) Effect of habitat transformation in the dung beetle assemblages: A comparison between a South African nature reserve and neighbouring farms. Environmental Entomology 30 (3): 474 – 483

Janssens A (1937) Révision des Onitides. Verhandelingen Koninklijk Natuurhistorisch Museum Belgie, Brussel 2: 1 – 200

Jay-Robert P, Niogret J, Errouissi F, Labarussias M, Paoletti E, Va´zquez Luis M, 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 141:2879 – 2887

Jelaska LS, Durbešić P (2009) Comparison of the body size and wing form of carabid species (Coleoptera: Carabidae) between isolated and continuous forest habitats. Ann la Société Entomol Fr 45:327 – 338

Kartzinel TR, Chen PA, Coverdale TC, Erickson DL, Kress WJ, Kuzmina ML, Rubenstein DI, Wang W, Pringle RM (2015) DNA metabarcoding illuminates dietary niche partitioning by African large herbivores. Proceedings of the National Academy of Sciences of the United States of America 112:8019 – 8024

Keesing F, Young TP (2014) Cascading consequences of the loss of large mammals in an African Savanna. Bioscience 64:487 – 495

Koch SO, Chown SL, Davis ALV, Endrödy – Younga S, Van Jaarsveld AS (2000) Conservation strategies for poorly surveyed taxa: a dung beetle (Coleoptera, Scarabaeidae) case study from southern Africa. Journal of Insect Conservation 4: 45 – 56

Koh LP, Dunn RR, Sodhi NS, Colwell RK, Proctor HC, Smith VS (2004) Species coextinctions and the biodiversity crisis. Science 305: 1632 – 1634

Korasaki V, Lopes J, Gardner B G, Louzada J (2013) Using dung beetles to evaluate the effects of urbanization on Atlantic Forest biodiversity. Insect Science 20:393 – 406

Krikken J (2009) Drepanocerine dung beetles: a group overview, with description of new taxa. Haroldius 4:3 – 30

Kreuter U, Peel M, Warner, E (2010) Wildlife Conservation and Community-Based Natural Resource Management in Southern Africa's Private Nature Reserves. Society and Natural Resources 23: 507 – 524

Krüger K, Scholtz CH (1998a) Changes in the structure of dung insect communities after ivermectin usage in a grassland ecosystem. I. Impact of ivermectin under drought conditions. Acta Oecologica 19:425 – 438

Krüger K, Scholtz CH (1998b) Changes in the structure of dung insect communities after ivermectin usage in a grassland ecosystem. II. Impact of ivermectin under high-rainfall conditions. Acta Oecologica 19: 439-451

Kryger U, Deschodt C, Davis ALV, Scholtz CH (2006) Effects of cattle treatment with a cypermethrin/cymiazol spray on survival and reproduction of the dung beetle species *Euoniticellus intermedius* (Coleoptera: Scarabaeidae). Bulletin of Entomological Research 96:597 – 603

Kurten EL (2013) Cascading effects of contemporaneous defaunation on tropical forests communities. Biological Conservation 163:22 – 32

Larsen TH, Lopera A, Forsyth A (2006) Extreme trophic and habitat specialization by Peruvian dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae). Coleopterists Bulletin 60:315 – 324

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

Larsen TH, Williams NM, Kremen C (2005) Extinction order and altered community structure rapidly disrupt ecosystem functioning. Ecology Letters 8:538 – 547

Lekasi JK, Tanner JC, Kimani SK, Harris PJC (2001) Manure Management in the Kenya Highlands: Practices and potential. HDRA. Kenilworth, UK

Lobo JM (1993) Estimation of dung beetle biomass (Coleoptera: Scarabaeoidea). European Journal of Entomology 90:235 – 238

Lobo JM, Hortal J, Cabrero-Sañudo FJ (2006) Regional and local influence of grazing activity on the diversity of a semi-arid dung beetle community. Diversity Distribution 12:111–123

Lumaret JP, Galante E, Lumbreras C, Mena J, Bertrand M, Bernal JL, Cooper JF, Kadiri N, Crowe D (1993) Field effects of ivermectin residues on dung beetles. Journal of Applied Ecology 30:428 – 436

Lund HG (2007) Accounting for the world's rangelands. Rangelands 29:3-10

Lyra-Jorge MC, Ciochetti G, Pivello VR, Meirelles ST (2008) Comparing methods for sampling large– and medium-sized mammals: camera traps and track plots. European Journal of Wildlife Research 54:739 – 744

Mangiafico SS (2015) An R companion for the handbook of biological statistics. Rutgers Cooperative Extension New Brunswick, NJ, USA

Manning P, Cutler GC (2018) Ecosystem functioning is more strongly impaired by reducing dung beetle abundance than by reducing species richness. Agriculture, Ecosystems & Environment 264: 9 – 14

Manning P, Slade EM, Beynon SA, Lewis OT (2016) Functionally rich dung beetle assemblages are required to provide multiple ecosystem services. Agriculture, Ecosystems & Environment 218:87 – 94

Manning P, Slade EM, Beynon SA, Lewis OT, (2017) Effect of dung beetle species richness and chemical perturbation on multiple ecosystem functions. Ecological Entomology 42:577 – 586

Marques FFC, Buckland ST, Goffin D, Dixon CE, Borchers DL, Mayle BA, Peace AJ (2001) Estimating deer abundance from line transect surveys of dung: sika deer in southern Scotland. Journal of Applied Ecology 38:349 – 363

McGeoch MA, Rensburg BJV, Botes A (2002). The verification and application of bioindicators: a case study of dung beetles in a savanna ecosystem. Journal of Applied Ecology 39: 661-672

McGeoch MA, Sithole H, Samways MJ, Simaika JP, Pryke JS, Picker M, Uys C, Armstrong AJ, Dippenaar-Schoeman AS, Engelbrecht IA, Braschler B, Hamer M (2011) Conservation and monitoring of invertebrates in terrestrial protected areas. Koedoe 53: 113

McGranahan DA (2008) Managing private, commercial rangelands for agricultural production and wildlife diversity in Namibia and Zambia. Biodiversity and Conservation 17: 1965 – 1977

Midgley G, Hughes G, Drew WTG, Foden W (2005) Assessment of potential climate change impacts on Namibia's floristic diversity, ecosystem structure and function. SANBI (For NNBP)

Milotić T, Baltzinger C, Eichberg C, Eycott AE, Heurich M, Müller J, Noriega J A, Menendez R, Stadler J, Ádám R, Bargmann T, Bilger I, Buse J, Calatayud J, Ciubuc C, Boros G, Jay-Robert P, Kruus M, Merivee E, Miessen G, Must A, Ardali E, Preda E, Rahimi I,Rohwedder D, Rose R,Slade EM, Somay L, Tahmasebi P, Ziani S, Hoffmann M, (2019) Functionally richer communities improve ecosystem functioning: Dung removal and secondary seed dispersal by dung beetles in the Western Palaearctic. Journal of Biogeography 46:70 – 82

Moczek AP (1998) Horn polyphenism in the beetle Onthophagus taurus: larval diet quality and plasticity in parental investment determine adult body size and male horn morphology. Behavioural Ecology 9:636 – 641

Naeem S, Wright JP (2003) Disentangling biodiversity effects on ecosystem functioning: deriving solutions to a seemingly insurmountable problem. Ecology Letters 6:567 – 579

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: e107699

Newbold T, Hudson LN, Hill SLL, Contu S, Lysenko I, Senior RA, Borger L, Bennett DJ, Choimes A, Collen B, Day J, De Palma A, Diaz S, Echeverria– Londono S, Edgar MJ, Feldman A, Garon M, Harrison MLK, Alhusseini, T, Ingram DJ, Itescu Y, Kattge J, Kemp V, Kirkpatrick L, Kleyer M, Correia DLP, Martin CD, Meiri S, Novosolov M, Pan Y, Phillips HRP, Purves DW, Robinson A, Simpson J, Tuck SL, Weiher E, White HJ, Ewers RM, Mace GM, Scharlemann JPW, Purvis A (2015) Global effects of land-use on local terrestrial biodiversity. Nature 520:45 – 50

Nicholas E, Spector S, Louzada J, Larsen T, Amezquita S, Favila ME, The Scarabaeinae Research Network (2008) Ecological Functions and ecosystem services provided by Scarabaeinae dung beetles. Biological Conservation 141: 1461 – 1474

Nichols E, Gardner TA, Peres CA, Spector S, The Scarabaeinae Research Network (2009) Co-declining mammals and dung beetles: an impending ecological cascade. Oikos 118:481 – 487

Nichols E, Gardner TA (2011) Dung beetles as a candidate study taxon in applied biodiversity conservation research. In: Simmons, L.W., Ridsdill-Smith, J. (Eds.), Dung Beetle Ecology and Evolution. Wiley-Blackwell, Chichester UK, pp 267 – 291

Nichols E, Uriarte M, Bunker DE, Favila ME, Slade EM, Vulinec K, Larsen T, Vaz de Mello FZ, Louzada J, Naeem S, Spector S (2013) Trait-dependent response of dung beetle populations to tropical forest conversion at local and regional scales. Ecology 93:180 – 189

Noriega JA, Hortal J, Azcárate FM, Berg MP, Bonada N, Briones M JI, Del Toro I, Goulson D, Ibanez S, Landis DA, Moretti M, Potts S G, Slade EM, Stout J C, Ulyshen MD, Wackers FL, Woodcock BASantos AMC (2018) Research trends in ecosystem services provided by insects. Basic Applied Ecology 26:8 – 23

Numa C, Verdú JR, Rueda C, Galante E (2012) Comparing dung beetle species assemblages between protected areas and adjacent pasturelands in a Mediterranean savanna landscape. Rangeland Ecology and Management 65:137–143

O'Hara RB, Kotze DJ (2010) Do not log-transform count data. Methods in Ecology & Evolution 1: 118 – 122

Onduru DD, Snijders P, Muchena F, Wouters B, De Jager A, Gachimbi L, Gachini GN (2008) Manure and Soil Fertility Management in sub-Humid and Semi-arid Farming Systems of sub-Saharan Africa: Experiences from Kenya. International Journal of Agricultural Research 3:166 – 187

Orbigny H d' (1913) Synopsis des Onthophagides d'Afrique. Annales de la Société Entomologique de France 82: 1 – 742

Philips K, Pretorius E, Scholtz CH (2004) A phylogenetic analysis of dung beetles (Scarabaeinae: Scarbaeidae) unrolling an evolutionary history. Invertebrate Systematics 18: 53 – 88

Piccini I, Nervo B, Forshage M, Celi L, Palestrini C, Rolando A, Roslin T (2018) Dung beetles as drivers of ecosystem multifunctionality: are response and effect traits interwoven? Science of the Total Environment 616:1440 – 1448

Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team. (2019). nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-131.https://CRAN.R-project.org/package=nlme 3rd July 2019

Pryke JS, Roets F, Samways MJ (2016) Wild herbivore grazing enhances insect diversity over livestock grazing in an African grassland system. PLoS One 11: e0164198

R Core Team (2019) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/

Raine EH, Mikich SB, Lewis OT, Slade EM (2018a) Interspecific and intraspecific variation in diet preference in five Atlantic forest dung beetle species. Ecological Entomology 44:436 – 439

Raine EH, Mikich SB, Lewis OT, Riordan P, Vaz-de– Mello FZ, Slade EM (2018b) Extinctions of interactions: quantifying a dung beetle–mammal network. Ecosphere 9: e02491

Raine EH, Slade EM, (2019) Dung beetle–mammal associations: methods, research trends and future directions. Proceedings of the Royal Society B: Biological Sciences 286: 20182002

Ranglack DH, du Toit JT (2016) Bison with benefits: towards integrating wildlife and ranching sectors on a public rangeland in the western USA. Oryx 50: 549 – 554

Ribera I, Doledec S, Downie IS, Foster GN (2001) Effect of land disturbance and stress on species traits of ground beetle assemblages. Ecology 82:1112 – 1129

Roggero A, Barbero E, Palestrini C (2015) Phylogenetic and biogeographical review of the Drepanocerina. Arthropod Systematics & Phylogeny 73: 153 – 174

Rust NA, Marker LL (2014) Cost of carnivore coexistence on communal and resettled land in Namibia. Environmental Conservation 41: 45 – 53

Salomão RP, Iannuzzi L. (2015) Dung beetle (Coleoptera, Scarabaeidae) assemblage of a highly fragmented landscape of Atlantic forest: from small to the largest fragments of north-eastern Brazilian region. Revista Brasileira de Entomologica 59:126 – 131

Samways MJ, Kreuzinger K (2001) Vegetation, ungulate and grasshopper interactions inside vs outside an African savanna game park. Biodiversity Conservation 10:1963 – 1981

Sands B, Wall R (2017) Dung beetles reduce livestock gastrointestinal parasite avail– ability on pasture. J. Appl. Ecol. 54:1180 – 1189

Sensenig RL, Demment MW Laca, EA (2010) Allometric scaling predicts preferences for burned patches in a guild of East African grazers. Ecology 91:2898 – 2907

Shafiei M, Moczec AP, Nijhout HF (2001) Food availability controls the onset of metamorphosis in the dung

Scholtz CH, Davis ALV, Kryger U (2009) Evolutionary Biology and Conservation of Dung Beetles. Pensoft Publishers. Sofia, Bulgaria

Schwab DB, Casasa S, Moczek AP (2017) Evidence of developmental niche construction in dung beetles: effects on growth, scaling and reproductive success. Ecology Letters 20:1353 – 1363

Shepherd VE, Chapman CA, (1998) Dung beetles as secondary seed dispersers: impact on seed predation and germination. Journal of Tropical Ecology 14:199 – 215

Silva PGd, Hernández MIM (2015a) Scale dependence of processes structuring dung beetle metacommunities using functional diversity and community deconstruction approaches. PLoS ONE 10: e0123030

Silva PGd, Hernández MIM (2015b) 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: e0126112

Sims RJ, Lyons M, Keith DA (2019) Limited evidence of compositional convergence of restored vegetation with reference states after 20 years of livestock exclusion. Austral Ecology 44:734 – 746

Slade E, Mann D, Villanueva J, Lewis O (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 76:1094 – 1104

Slade EM, Mann DJ, Lewis OT (2011) Biodiversity and ecosystem function of tropical forest dung beetles under contrasting logging regimes. Biological Conservation 144:166 – 174

Sokal RR, Rohlf FJ (1995) Biometry: The Principles and Practice of Statistics in Biological Research, 3rd edn. W.H. Freeman & Co., New York, NY

Sole CL, Scholtz CH, Bastos ADS (2005) Phylogeography of the Namib Desert dung beetles Scarabaeus (Pachysoma) MacLeay (Coleoptera: Scarabaeidae). Molecular Phylogenetics and Evolution 56:631 – 641

Sommer C, Gronvol J, Holter P, Nansen P (1993) Effects of ivermectin on two afrotropical dung beetles, *Onthophagus gazella* and *Diastellopalpus quinquedens* (Coleoptera: Scarabaeidae). Veterinary Parasitology 48: 171 – 179

Spector S (2006) Scarabaeine dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae): an invertebrate focal taxon for biodiversity research and conservation. Coleopterists Bulletin 5:71 – 83

Sugiura S, Tanaka R, Taki H, Kanzaki N (2013) Differential responses of scavenging arthropods and vertebrates to forest loss maintain ecosystem function in a heterogeneous landscape. Biological Conservation 159:206 – 213

Tonelli M, Verdú JR, Zunino ME (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 JR, Zunino ME (2018) Effects of the progressive abandonment of grazing on dung beetle biodiversity: body size matters. Biodiversity Conservation 27:189 – 204

Tonelli M, Verdú JR, Zunino ME (2019) Grazing abandonment and dung beetle assemblage composition: Reproductive behaviour has something to say. Ecological Indicators 96:361 – 367

Treitler JT, Buse J, Carpaneto GM, Zerbe S, Mantilla-Contreras J, (2017) Effects of dung-pad conditions and density on coprophagous beetle assemblages in a Mediterranean rangeland. Biodiversity Conservation 26:1431 – 1444

Tscharntke T, Klein AM, Kruess A, Steffan-Dewenter I, Thies C (2005) Landscape perspectives on agricultural intensifications and biodiversity – ecosystem service management. Ecology Letters 8: 857 – 874

Tshikae BP, Davis ALV, Scholtz CH (2008) Trophic Associations of a Dung Beetle Assemblage (Scarabaeidae: Scarabaeinae) in a Woodland Savanna of Botswana. Environmental Entomology 37: 431 – 441

Tshikae BP, Davis AL, Scholtz CH (2013a) Species richness: energy relationships and dung beetle diversity across an aridity and trophic resource gradient. Acta Oecologica 49:71 – 82

Tshikae BP, Davis ALV, Scholtz CH (2013b) Does an aridity and trophic resource gradient drive patterns of dung beetle food selection across the Botswana Kalahari? Ecological Entomology 38:83 – 95

Valiente-Banuet A, Aizen MA, Alcántara JM, Arroyo J, Cocucci A, Galett, M, García MB, García D, Gómez JM, Jordano P, Medel R, Navarro L, Obeso J R, Oviedo R, Ramírez N, Rey P J, Traveset A, Verdú M, Zamora R (2015) Beyond species loss: the extinction of ecological interactions in a changing world. Functional Ecology 29:1 – 8

Van Schalkwyk DL, McMillin W, Witthuhn RC, Hoffman LC (2010) The Contribution of Wildlife to Sustainable Natural Resource Utilization in Namibia: A Review. Sustainability 2:3479 – 3499

Veblen KE, Porensky L M, Riginos C, Young TP (2016) Are cattle surrogate wildlife? Savanna plant community composition explained by total herbivory more than herbivore type. Ecological Applications 26:1610 – 1623

Verdu JR, Cortez V, Ortiz AJ, Gonzalez-Rodriguez E, Martinez-Pinna J, Lumaret JP, Lobo JM, Numa C, Sanchez-Pinero F (2015) Low doses of ivermectin cause sensory and locomotor disorders in dung beetles. Science Report 5:13912

Verdú JR, Galante E (2001) Larval morphology and breeding behaviour of the genus Pedaridium Harold (Coleoptera: Scarabaeidae). Annals of the Entomological Society of America 94: 596 – 604

Verdú JR, Lobo MJ, Sánchez-Piñero F, Gallego B, Numa C, Lumaret JP, Cortez V, Ortiz A, Tonelli M, García-Teba Rey A, Rodriguez A, Durán J (2017) Ivermectin residues disrupt dung beetle diversity, soil properties and ecosystem functioning: an interdisciplinary field study. Sci Total Environ 618:219 – 228

Verdú JR, Moreno CE, 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 140:308 – 317

Viljanen H, Escobar F, Hanski I (2010) Low local but high beta diversity of tropical forest dung beetles in Madagascar. Global Ecology and Biogeography 19:886 – 894

Vohland K, Uhlig M, Marais E, Hoffman A, Zeller U (2005) Impact of different grazing systems on diversity, abundance and biomass of beetle (Coleoptera), a study from southern Namibia. Zoosystematics and Evolution 81:131 – 143

Wang Y, Naumann U, Wright ST, Warton DI, (2012) mvabund—an R package for model-based analysis of multivariate abundance data. Methods of Ecology & Evolution 3:471 – 474

Whipple SD, Hoback WW (2012) A comparison of dung beetle (Coleoptera: Scarabaeidae) attraction to native and exotic mammal dung. Environmental Entomology 41:238 – 244

Winfree R, Fox JW, Williams NM, Reilly JR, Cariveau DP, (2015) Abundance of common species, not species richness, drives delivery of a real-world ecosystem service. Ecology Letters 18:626 – 635

Young HS, McCauley DJ, Castillo E, Goheen JR, Helgen KM, Palmer TM, Pringle RM, Young TP, Dirzo R (2013) Plant community response to changes in herbivore abundance and identity across abiotic gradients and experimental contexts. Journal of Ecology 101:1031 – 1041

Young TP, Porensky LM, Riginos C, Veblen KE, Odadi WO, Kimuyu DM, Charles GK, S. Young H (2018) Relationships between Cattle and Biodiversity in Multiuse Landscape Revealed by Kenya Long-Term Exclosure Experiment. Rangeland Ecology and Management 71:281 – 291

Zeidler J, Kandjinga L, David A, Turpie J, Malema D (2012) Climate governance & development case study Namibia. Namibia: Heinrich Boll Stiftung

Zídek J, Pokorný S (2008) Illustrated keys to Palearctic Scarabaeus Linné (Scarabaeidae). Animma.X 27: 1 – 27

Zur Strassen, R. (1967) Arten-iibersicht der Gattung Scarabaeus Linnaeus (Scarabaeidae) mit besonderer Berucksichtigung der athiopischen Formen. Entomologisches Blätter 63:129 – 173

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed Effects Models and Extensions in Ecology with R. Springer, New York, USA

Chapter 3
Land-use change disrupts ecological function of dung beetles and their inter-guild interactions

Abstract

In many African savannah ecosystems, native large mammal species have been replaced with domestic livestock to the detriment of dung beetle diversity. How these changes influence their functional roles and inter-guild interactions (between tunnellers and rollers) remains unexplored. Here I used manipulative experiments to explore the relationship between dung removal and secondary seed dispersal and shifts in inter-guild interactions between a protected area (PA) and a nearby livestock farm. Dung removal and secondary seed dispersal were generally higher in the PA compared to the farm as a result of lower richness, abundance and biomass of dung beetles on the farm. Similar amounts of dung and numbers of seeds were removed by rollers and tunnellers with the highest removal when both were present. However, the interaction between guilds for dung removal changed from competitive on the PA to neutral on the farm. Generally, more seeds associated with native dung were removed than domestic dung. Roller abundance decreased in the presence of tunnellers, but tunneller abundance, richness and biomass increased when rollers were present, indicating that tunnellers were better competitors. Higher, species richness and biomass increased dung removal and secondary seed dispersal although this was correlated to abundance. Ecosystem functions on the farm were reduced due to the loss of species, especially the rollers (and their biomass), that are better adapted to the dung of native animals. These results highlight that functionally complete dung beetle taxonomic assemblages and guilds are crucial to maintaining ecosystem function and services in the rapidly changing savannah ecosystems of Africa. Conserving dung beetles and their functions require the maintenance of native vertebrate diversity.

Keywords: dung removal, secondary seed dispersal, ecosystem functioning, Scarabaeinae, guild interaction, mammals, the African savannah

3.1 Introduction

Livestock farming is the largest form of anthropogenic land transformation covering roughly 60% of the world's agricultural land (Alexandratos and Bruinsma 2012; Alkemade et al. 2013). A major consequence of this is the restriction of native herbivores to protected areas (PA) and domestic grazers (mainly cattle) replacing them in the surrounding matrix (Samways and Kreuzinger, 2001; Nichols et al. 2009; Bogoni et al. 2016; Pryke et al. 2016; Piccini et al. 2017; Raine et al. 2018a; Raine and Slade

2019). This selective defaunation has consequences for numerous ecological processes such as altering animal behaviour (Culot et al. 2013; Galetti and Dirzo 2013; Dirzo et al. 2014) and changes in plant reproductive performance (Nicholas et al. 2008; Bogoni et al. 2016). Agricultural management practices such as the use of veterinary pharmaceuticals creates additional to pressures on native fauna, which has cascading effects on many taxa (Verdu et al 2007, 2015, 2017; Tuck et al. 2014) and their associated ecological functions (Nichols et al. 2009; Whipple and Hoback 2012; Kurten 2013; Piccini et al. 2017; Raine et al. 2018a,b). This is particularly concerning in co-evolved systems where even the loss of a single species can have dramatic implications for dependent species groups, instigating downstream extinctions (Nichols et al. 2009), changing community dynamics (Koh et al. 2004; Manning et al. 2016) and functional capacity (Eklof and Ebenman 2006; Milotić et al. 2019). The contribution of biodiversity to ecosystem functioning has become a highly relevant and fundamental question in ecology (Isbell et al. 2011; Tilman et al. 2012; Manning et al. 2018; Noriega et al. 2018). Current consensus holds that functional shifts in communities are more disruptive to ecological functioning than biodiversity loss *per se*, especially when species with unique traits are lost (Milotić et al. 2019).

In this study, I used coprophagous dung beetles (Coleoptera: Scarabaeidae; Scarabaeinae) to study the effects of land-use change on ecosystem function. Their general obligatory use of vertebrate dung provides a series of epidemiologically and economic relevant ecosystem services that are highly relevant in agricultural systems (Zhang et al. 2007; Nichols et al. 2009; Gómez and Kolokotronis 2017). These include nutrient recycling (Steinfeld et al. 2006; Sitters et.al. 2014), bioturbation (Brown et al. 2010; Gregory et al. 2015; Dabrowski et al. 2019) and mediation of gas fluxes from dung pads (Penttilä et al. 2013). Dung beetles also act as biological pest control agents by dissuading the migration and pupation of harmful pests through faecal desiccation (Bryan, 1973). In addition, dung beetles inadvertently transfer seeds found in faecal matter of herbivores back into the earth (Feer 1999; Andresen 2002; Nathan et al. 2008; Nichols et al. 2008), which promotes the reproductive success of plants (Andresen 2002; Andresen and Levey 2004; Andresen and Feer 2005, Nichols et al. 2008; Milotić and Hoffman 2016) and enhances forage growth (Shepherd and Chapman 1998; Milotić et al. 2019).

A majority of studies investigating the ecological functioning of dung beetles are centred in tropical regions and in Europe with very few studies in Africa and African savannahs in particular (Slade et al. 2007; Manning et al. 2016; Noreiga et al. 2018; Tonelli et al. 2018; Milotic et al. 2019; Raine and Slade 2019). Another missing component form these surveys is the very important dung beetle – mammal network perspective which is what makes exploring this kind of research in an African savannah all the more appealing (Nichols et al. 2009; Sole and Scholtz 2010; Davis et al. 2017; Raine

et al. 2018a; Bogoni et al. 2019; Raine et al. 2019). African savannahs support the most impressive arrays of large mammals and subsequently an equally striking dung beetle diversity (Scholtz et al. 2009; Sole and Scholtz 2010). The megafauna of this region has experienced dramatic declines, having strong effects on trophic ecosystem structure (Estes et al. 2011; Malhi et al. 2016). Although these effects have been documented for certain taxa (Newmark 2008), invertebrates and dung beetles have received little attention particularly with regards to how it affects their ecosystem functioning (Nichols et al. 2009; Raine et al. 2019).

The provision of ecosystem functions and services by dung beetles can be positively related to species richness (Manning et al. 2016; Milotić et al. 2019), abundance, body size and biomass (Nervo et al. 2014), and complementarity of their different functional guilds (Slade et al. 2007). Low species richness has been linked to lowered productivity in pastures (Manning et al. 2017), reduced biological pest control (Snyder et al. 2006) and many other ecosystem functions and services (Cardinale et al. 2002; Slade et al. 2007; Manning et al. 2016; Milotić et al 2019). Increase in dung removal is also closely linked to increased beetle body size as larger beetles can manipulate larger quantities of dung than their smaller counterparts (Horgan and Fuentes 2005; Nichols et al. 2011). When total biomass of large beetles was matched by that of small beetles, the same removal capacity was observed, making the abundance of dung beetles an essential consideration (Dangles et al. 2012). Also, smaller dung beetles may be less efficient in secondary seed dispersal than larger species (Andresen and Feer 2005; Milotic et al. 2017). Therefore, body mass heterogeneity remains important as it promotes facilitation and resource partitioning resulting in more efficient resource usage. Larger species, although more functionally important, are also often highly sensitive to environmental degradation and are more prone to extinction (Larsen et al. 2005; Sugiura et al. 2013).

In Chapter 2 I found a marked decrease in dung beetle individual size due to land-use change with beetle size decreasing on farms. This result echoed previous research that re-counted the potentially deleterious effects of altered dung quality (Bernal et al. 1994; Floate, 2006; Verdu et al. 2015, 2017; Hammer et al. 2016; Frank et al. 2017; Schwab et al. 2017) on dung beetle development and physiological condition as well as detrimental effects on biotic interactions (Salomão et al. 2015; Sands and Wall 2018; Raine and Slade 2019). Dung quality may therefore negatively influence dung beetle assemblages with cascading effects on ecosystem functioning, which needs further exploration particularly in African savannah regions (Raine and Slade 2019).

Dung beetles are classified into three key functional groups centred on their direction of dung transport for nesting: dwellers/endocoprids simply reside within the original dung deposit, rollers/ telocoprids roll a dung ball and move it a certain distance away from the dung pad before shallowly burying it and tunnellers/paracoprids make shafts right beneath the dung pad transporting fragments

of dung with them (Doube 1990; Davis et al. 2008). An important element to understanding dung beetle functional change lies in unravelling the dynamics between the functional groups (Silva and Hernandez 2015a, b). Dung beetle species interactions can be separated into one of three relationships: antagonism (competition), facilitation/complementarity or a passive effect (Slade et al. 2007; Scholtz et al. 2009; Roslin and Viljanen 2011). These interactions are important as they may influence the per capita contributions of the three guilds to overall functioning, either diminishing it via competition or improving it via facilitation (Slade et al. 2007). Tunnellers are thought to contribute the most given their quarrying ability (Doube 1990), the size of the galleries they craft (Davis et al. 2008; Scholtz et al. 2009; Amézquita and Favila 2010; Braga et al. 2013) and their abundance (Arnaudin et al. 2014). Classic ecological theory, however, predicts that functional groups and individual species respond differently to different environmental stressors and in different regions due to variations in environmental preferences and functional traits (Siqueira et al. 2012; Alahunta et al. 2014; Silva and Hernández 2015a). As most previous studies are non-African savannah, it is difficult to predict ecosystem functional changes (Chapter 2).

Here, I used manipulative experiments to test the functional efficiency of dung beetles between farm and a PA in an African savannah ecosystem. I compared the dung and seed removal rates associated with both native and domestic dung and assessed whether a particular functional group had a dominant effect. Specifically, I asked three questions: How do dung removal and seed dispersal rates differ inside vs outside a PA and does this relate to variables related to surrounding mammal richness and numbers? How did dung removal and seed dispersal rates compare between dung beetle guilds and was there evidence for any antagonism, facilitation or complementarity? Which dung beetle biodiversity measure (richness, abundance or biomass) was most important for predicting dung removal and seed dispersal rates? Based on previous studies, I hypothesised that overall dung and seed removal, as well as species richness, abundances and biomass measures would be higher in the PA than on the farm (Jankielsohn et al. 2001; Jacobs et al. 2010; Nichols et al. 2011, 2013; Slade et al. 2011; Numa et al. 2012; Frank et al. 2017) and these would be positively correlated to one another. More native dung and seeds would be removed than domestic dung and the seeds, as dung beetles will prefer the native dung resource (Amezquita and Favila 2010; Chapter 2). Dung beetle species richness and biomass were expected to be the most important biodiversity measures affecting dung removal and secondary seed dispersal (Nervo et al. 2014; Numa et al. 2012; Milotic et al. 2019). Tunnellers were expected to perform better than rollers due to their high species diversity and abundance (Davis et al. 2008; Scholtz et al. 2009; Chapter 2). Lastly, the PA was expected to have a greater complementarity between guilds while on the farm I expected to see greater competition effect between guilds due to decreased resource diversity (Slade et al. 2007; Chapter 2).

3.2 Methods and Materials

3.2.1 Study area

The study was conducted in the north-central region of Namibia on a PA, Okonjima Nature Reserve (-20°85'02", 16°67'35"), and an adjacent farm, Tottenham Farm (-20°74'26", 16°36'73"), in the Namibian thornbush savannah biome (Fig 3.1). The PA features an impressive assortment of animals including abundant blue wildebeest (*Connochaetes taurinus*), African elephant (*Loxodonta africana*) and giraffe (*Giraffa giraffa*) and other rare and highly endangered iconic African fauna such as leopards (*Panthera pardus*) and pangolins (*Smutsia temmincki*) (Barnard 1998; Barnard et al. 1998; van Schalkwyk et al. 2010). Tottenham is a 3000 ha mixed cattle (*Bos taurus*), sheep (*Ovis aries*) and domestic goat (*Capra hircus*) farm. The regional climate is predominately warm (day-time highs of $35 - 40°C$) for most of the year, but this fluctuates considerably throughout the day, especially in winter. Rainfall in this region is very erratic but usually ranges between 150 mm and 300 mm during the summer rainy season (November to March). To minimise biases in my experimental results due to environmental variables not considered in the present study, the selection of sites was carefully considered with the help of landowners and field rangers to keep most parameters as constant as far as possible, i.e. vegetation architecture and cover (Davis et al. 2008), soil properties (Scholtz et al. 2009) and preceding rainfall evets (Lahteenmaki et al. 2015), whilst also considering accessibility of sites and personal safety (Skelly 2002; Lahteenmaki et al. 2015; Appendix L). Study sites were all selected on sandy soils, with low vegetation cover (<30%) consisting of ca. $40\% - 60\%$ trees. At the time sampling, both sites had received over 50 mm of rain in the preceding weeks (based on rain gauge readings made by PA manager and farm owner).

3.2.2 Sampling Protocol

Dung sources and bait preparation

Fresh (less than one-hour-old) and uncolonized (by beetles) wildebeest and cow dung was collected from the PA and farm and prepared for use one day prior to use in experiments. Dung was homogenised (separately for the two dung types) to ensure consistency of odours and moisture content between different experimental units (Feer 1999; Andresen 2002; Manning et al. 2016; Milotic et al. 2017, 2018). Hereafter each bait type was divided into 500 g (wet mass) portions, measured using a digital scale (accurate to 2 decimal places), which served as experimental bait units. In order to quantify secondary seed dispersal by dung beetles, bait units were amended with seed mimics. I used spherical plastic beads as seed mimics because they avert predation by rodents and other vertebrates, and these simplify recovery after the experiment, as they float on the surface of the water (Andresen 2002; Slade et al. 2007). To avoid biases due to differences in the volume of seed mimics added to each bait unit, I added a similar volume of large (12.0 mm diam.; n=6 per replicate),

medium (7.0 mm diam.; n=45) and small (2.8 mm diam.; n=330) beads and mixed into bait to ensure even distribution within.
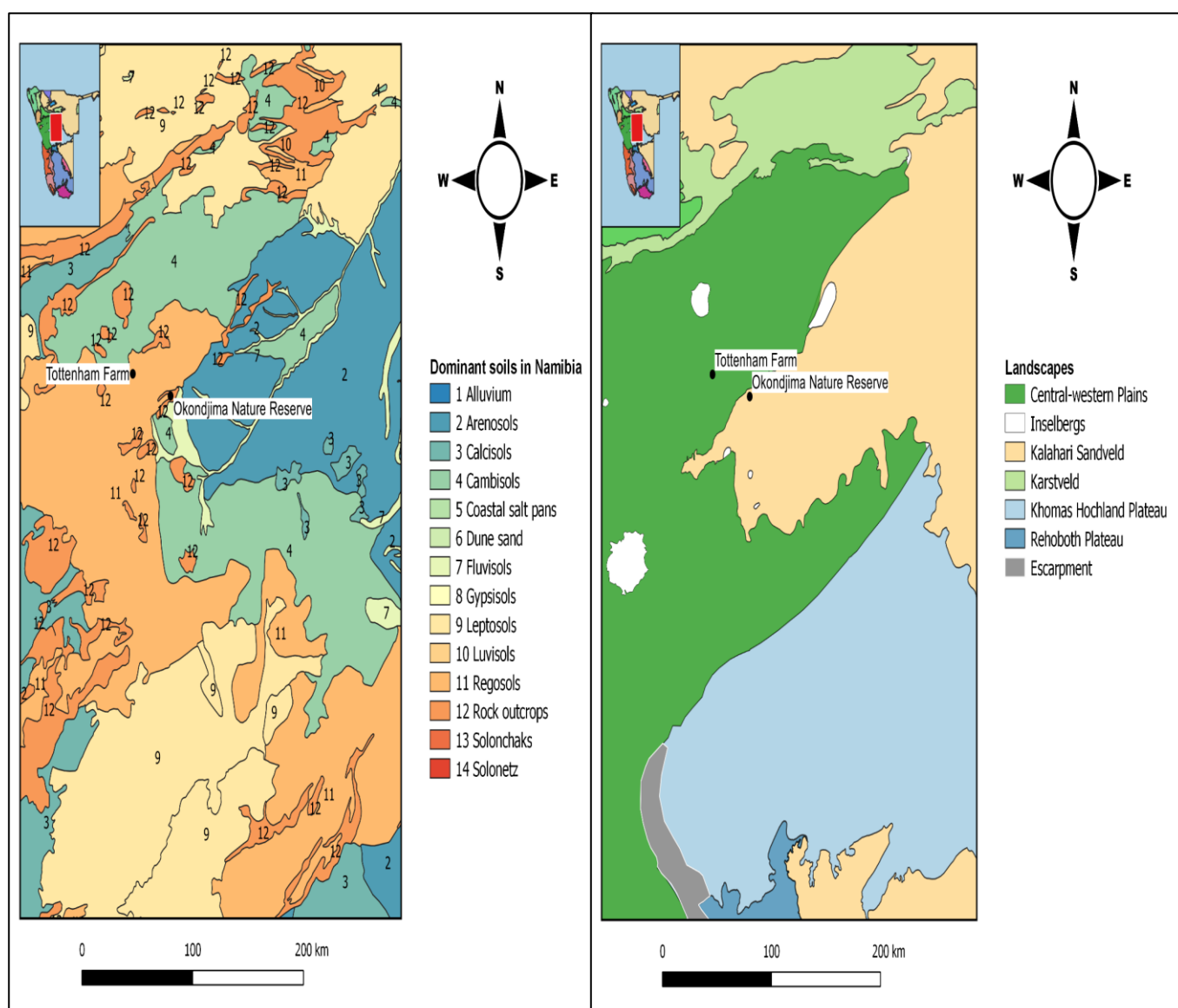
Arena design

Studies evaluating dung removal and seed dispersal usually estimate dung beetle species richness and abundance-based only on beetles captured close to but separated from the experimental units either in space or time (Slade et al. 2007; Manning et al. 2016; Milotić et al. 2019). For greater accuracy in the present study and reduce possible biases, I set out to capture the individuals that likely directly interacted with the bait, rather than to merely estimate the number of interacting individuals and species. I, therefore, used various combinations of exclusion and capturing techniques in experimental arenas to enumerate dung removal, secondary seed dispersal, and the numbers of species and

individuals of various dung beetle nesting guilds. Dung beetle experimental arenas were created to selectively restrict access to bait by different combinations of dung beetle functional groups (nesting guilds) like those employed by Milotić et al. (2016) and Slade et al. (2007). The experiment made use of three enclosure types (arenas) that served as different treatments and were designed to provide access to either only tunnellers (species that nest directly under dung pads), only rollers (species that translocate dung for nesting at some distance away from dung pads), or to individuals of both guilds (no exclusion positive control). Endocoprid dung beetles (those that nest within dung pads) were ignored in the current study as their role in dung removal and secondary seed dispersal are negligible (Davis et al. 2008; Batilani-Filho and Hernandez 2017). Negative controls, from which all dung beetles were excluded, were used to compute dung mass loss due to evaporation and other organisms not considered here.

Arena walls were constructed from polyvinyl chloride (PVC) piping (16 cm diameter) that was cut into 1 m^2 lengths. These were dug into the soil to a depth of 8 cm with the open side (the side that originally formed the inside of the pipe) orientated inwards towards the arena. The arena walls were therefore 8 cm high and had an overhang towards the inside of the arena that helped to prevent the escape of beetles that moved away from the centre of the arena. Bait was placed in the centre of the arena. Exclusion methods and traps within different arenas differed for the three treatments and were designed to selectively exclude or include particular nesting guilds of dung beetles (Fig. 3.2): *Treatment 1 (positive control)*: In this treatment, all tunnelling and rolling dung beetle individuals were allowed access to bait and were captured. This is a natural representative of beetles that would typically colonise dung in experimental arenas (Slade et al. 2007). To capture dung rollers that were attracted to the dung units, four pitfall traps were placed at the four corners of the arena. These consisted of 2L plastic buckets with a diameter of 17 cm and a depth of 14 cm that was buried with the rim flush with the soil surface. Pitfall traps were half-filled with water containing a few drops of liquid detergent to immobilise captured dung beetles (Fletchman et al. 2008; Tshikae et al. 2008). This allowed for the collection of all dung rollers from within the arena (and the translocated seeds in dung balls), irrespective of whether beetle individuals were involved in dung removal and may therefore slightly overestimate the numbers of roller individuals responsible for dung removal and seed translocation. However, it is also known that reduced numbers of rollers that initially visit dung in such experimental arenas are eventually trapped within pitfall traps (Slade et al 2007; Manning et al. 2016; Miltoć et al. 2016, 2019), which will negate some of these biases. To collect tunnelling dung beetles, the bait unit was placed in the centre on the surface of a soil-filled 10L bucket (30 cm diameter), buried with the rim flush with the soil surface in the centre of the arena. This allowed for normal burrowing activity of tunnelling dung beetles underneath the bait, and for the confinement of

individuals. To prevent biases based on using foreign soil, soil used to fill the bucket originated from the hole excavated in the middle of the arena. At the end of the experiment, the soil was placed in water and mixed to collect the tunnelling dung beetles and plastic seed mimics that floated to the surface. ***Treatment 2 (Tunneller exclusion):*** To prevent tunnellers from relocating dung into the soil, a 60 x 60 cm aluminium mesh of 1 x 1 mm, was placed directly underneath the bait in the centre of the arena (Fig. 3.2). The bait was left uncovered allowing rollers to construct brood balls and translocate these without immediate impediment. Pitfall traps were placed at the corners of the arena to collect the roller dung beetles, their dung and the seed mimics within balls, and all other beetles trapped (from other guilds) were ignored in the analyses. ***Treatment 3 (roller exclusion):*** The bait was placed on the surface of a 10L sand-filled bucket to collect tunnelling beetles as described above. Vertical walls were erected around the bait unit using a 30 cm diameter cylinder (15 cm high) constructed from the same aluminium insect screen used in treatment 2. This was placed along the rim of the bucket and held in place by the soil inside the bucket. This design allowed access to the bait unit to all flying species. However, rollers were prevented from removing any dung as they abandon their brood balls when incapable of moving it to a nesting site (Slade et al. 2007; Milotic et al. 2019). Therefore, all dung removed was assumed to be that of tunnelling species that were collected as described above. ***Negative control:*** For the negative control, all dung beetles were prevented from accessing baits by covering these with fine (0.8 mm aperture diameter) nylon mesh and placing on a 60 cm x 60 cm 2 cm aperture wire mesh screen in the centre of the arena. This unit served as a reference to estimate the percentage of bait mass loss due to evaporation and other causes (Slade et al. 2007; Milotic et al. 2019).

Experimental design

The study was replicated at ten sites at each location (farm and PA). Sites (Fig. 3.2) were at least 1 km apart and at each, eight sampling units were established along two 300 m transects lines that were separated by 100 m with an arena interspacing distance of 100 m in each transect. This spacing helps to minimise trap interference and maintains their spatial independence (Silva and Hernandez 2015b; Ortega-Martinez et al. 2016). Each transect consisted of four sampling units (the three treatments and the negative control) that were baited with either cow-based bait units (domestic) or wildebeest-based bait units (native) that were randomised per transect (Fig. 3.2). Arenas and traps were open for 24 hours to allow for the attraction of both day and night active dung beetle species, but before all bait was completely removed. Dung bait also loses most of its attractiveness to dung beetles if left longer than 24 h in arid regions (Davis et al. 2008). A month later, the entire experiment was repeated at the same sites, and data from the two seasons were combined per site before statistical analyses. After 24 h, all dung remaining on the surface in the arena was carefully collected and weighed to determine

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residual dung mass after being cleared of dung beetles (endocoprids), soil and plant material (Tixier et al. 2015). All dung beetle individuals from traps were recovered (as described above) and preserved in 80% ethanol for sorting in the laboratory. Remaining dung was placed in water to collect remaining seed-mimics whose combined weight was subtracted from that of the remaining dung. Vertebrate species richness and densities are known to be higher in PAs than on farms in Namibia (Chapter 2) and these variables could not be standardised in the present study. In addition to treatment and land-use, I therefore also included these as explanatory variables influencing dung removal and secondary seed dispersal. The vertebrate richness and stocking densities around each sampling plot were estimated following techniques described in Chapter 2.

3.2.4 Laboratory protocol

All dung beetles collected from the soil, pitfall traps and dung pads were transported to Stellenbosch University for identification. Beetles were sorted, counted and identified to the lowest taxonomic rank possible using available keys (d'Orbigny 1913; Janssens 1937; Balthasar 1963a,b, 1965; Zur Strassen 1967; Ferreira 1969, 1976, 1978; Nguyen-Phung and Cambefort 1986a, 1986b, 1987; Nguyen-Phung 1988a,b,c; Cambefort 1996; Barbero et al. 2003; Deschodt et al. 2007; Deschodt and Scholtz 2008; Zídek and Pokorný 2008; Krikken 2009; Branco 2010; Roggero et al. 2015; Génier 2017a,b; Deschodt and Davis 2018) and into their respective functional groups (Davis et al. 2008) with the aid of a dissecting microscope. All dung beetle functional groups were collected from the traps and remaining dung, although dwellers were excluded from all analyses (Davis et al. 2008). Only collected tunneller species were considered in the roller exclusion treatment and only roller species were considered in the tunneller exclusion experiment. Both were included in the positive control (no exclusion). For some species that are normally considered dwellers, I found evidence of tunnelling behaviour. These taxa were included in the appropriate treatments for analyses. Biomass was estimated for all species by measuring the total body length of 10 voucher specimens (in the case of sexual dimorphism 5 males and 5 females were measured) using digital callipers. The total body length was used to calculate the biomass for every individual using the biomass formula devised by Lobo (1993): Biomass $= 0.010864 \times \text{Length}^{3.316}$. Mean mass per species per site was then used to calculate the total mass of tunnellers and rollers collected in each experimental unit (Tonelli et al. 2018, 2019). Voucher specimens of all species are housed in the Stellenbosch University Entomological Collection, Department of Conservation Ecology and Entomology, Stellenbosch University, South Africa.

Top View

Side View

dung pad	aluminium mesh cylinder (1mm)	
sand filled bucket (10l)	direction of dung transport allowed	
pvc panel (8cm high)	direction of dung transport prohibited	
no pvc panel	pitfall trap	
dwellers	aluminium mesh (1mm)	
tunnellers	aluminium mesh (1mm)	
rollers	control unit	tunnellers only
	full guild	
	rollers only	
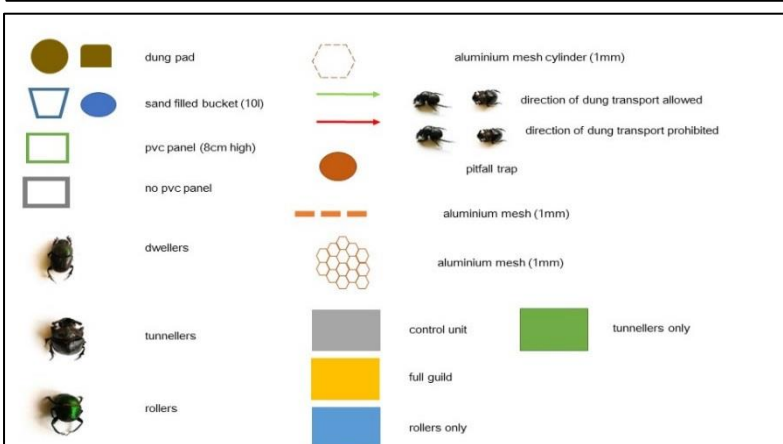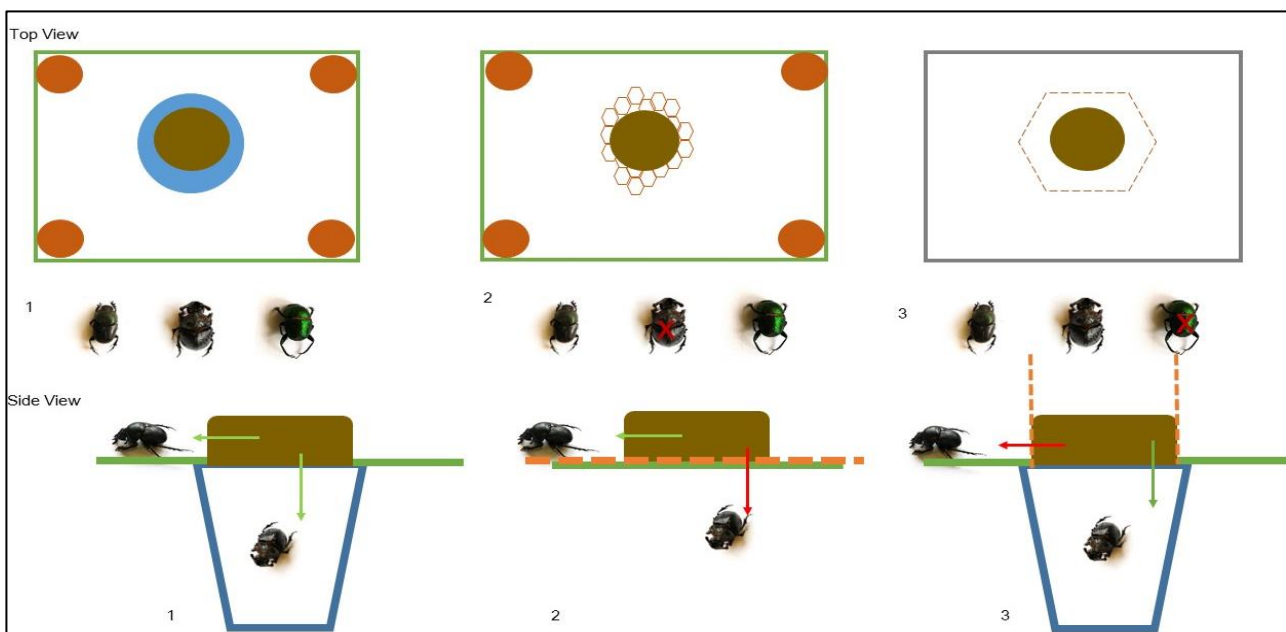
3.2.5 Data analyses

Completeness of species record

Completeness of the species record for the two sites sampled was calculated using EstimateS version 9.1 (Colwell 2013) and results were visualised using the iNEXT package in R (Hsieh et al. 2016). The default setting of 100 randomizations using abundance data pooled from the eight traps at each site was used for calculations of the estimated number of species collected at the 20 study sites. The non-parametric incidence-based estimators Chao2 and Jackknife2 were used (Gotelli and Colwell 2001; Chao and Jost 2012; Colwell 2012; Chao et al. 2014).

Calculating dung and seed removed

Dung removed and seed translocated from each bait unit was calculated using basic formulas by Milotić et al. (2016). Dung removal was calculated as $D_{removed} = \frac{\text{Dinitial} - \text{Dremaining}}{\text{Dinitial}} \times 100$ where $D_{initial}$ is the initial mass of the bait unit and $D_{remaining}$ is the mass of the bait unit at the end of the experiment. The negative control (all beetles excluded) was used to adjust the dung removal estimates according to evaporation at each site. Therefore, remaining dung mass was adjusted lower according to the percentage mass loss from the negative control bait units at the end of the experiment. Seed dispersal was calculated as $S_{dispersed} = \frac{\text{Sinitial} - \text{Sretrieved}}{\text{Sinitial}} \times 100$ with $S_{initial}$ and $S_{retrieved}$ representing the number of seeds in the dung pad at the beginning of the experiment and at the end of the experiment respectively. These numbers were verified by numbers of seeds recovered from soil traps and pitfall traps.

Environmental factors that influence dung removal and secondary seed dispersal

All statistical analyses for the functional group manipulation experiments were conducted using R statistical software (version 3.5.1) (R Development Core Team 2019). The data were first tested for normality using the Shapiro Wilks test ($P<0.05$) to determine which model family would be most appropriate, linear mixed models (lmm) for normal distributions and generalised linear mixed models (glmm) for non-normal distributions (Bates et al. 2014; Pinheiro et al. 2015). The property was included as a spatial random variable (Bates et al. 2014) and binomial distributions were implemented as the amount of dung removed and the number of seeds dispersed as ratios (Skaug et al. 2011). The effects of how land-use type (farm or PA), bait type (cow or wildebeest), treatment (no exclusion, roller exclusion or tunneller exclusion) and vertebrate richness and stocking densities affected dung removal and secondary seed dispersal were then tested in a multitude of candidate models using Akaike's Information Criterion correction for small sample sizes (AICc) (Burnham and Anderson 2004; Slade et al. 2007; Slade et al. 2016; Milotić et al. 2019). The models were compared through likelihood tests in the *AICcmodavg* package in R and the most parsimonious model using *a priori*

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threshold of delta two AICc (Crawley 2013; Manning et al. 2016). The *anova* function was used to obtain p – and F –values and significant overall effects were explored using the post hoc Tukey test using the *multcomp* package (Hothorn et al. 2008). The vertebrate richness and stocking density between the farm and PA were compared using generalised linear mixed models using the lme4 package with a Poisson error distribution (Bolker et al. 2009; Zuur et al. 2009; Sensenig et al. 2010; Bates et al. 2014).

Inter-guild interactions

In addition to comparing dung removal and secondary seed dispersal by 1) all dung beetles combined and 2) that removed when each functional guild acted alone (using the different treatments above), inter-guild interactions (competition, complementarity or facilitation) were investigated by comparing the abundance, richness and biomass of tunnellers and rollers separately (exclusion treatments where there was no competition with the opposite guild) to their respective numbers when both guilds were allowed access to bait (where there would be interaction with the opposite guild) (Manning et al. 2016; Menéndez et al. 2016). For example, in the case of tunneller abundance, the abundance of tunnellers in the roller exclusion (tunnellers only) treatment were compared to the abundance of tunnellers in the positive control treatment where both guilds had access to the bait unit. Generalized linear mixed models were used for species richness and abundance measures with a Poisson error distribution (Zuur et al. 2009; Bates et al. 2014) and linear mixed models were used for biomass measures (Bates et al. 2014). The functional group diversity measures were fixed effects (i.e. roller richness, abundance or biomass) and treatment (e.g. roller richness, abundance or biomass in the treatment where tunnellers were excluded), land-use type and bait type were used as the predictor variables. The property was used as a spatial random variable. Each model (including a single variable or interaction) was compared to a full model containing all the predictor variables through the *anova* function where the two AIC values were compared and the most parsimonious model was selected (Burnham and Anderson 2004; Manning et al. 2016; Menéndez et al. 2016) and the *anova* function was used to obtain p – and F–values.

Effect of dung beetle species richness, abundance and biomass on dung removal and secondary seed dispersal

The effects of dung beetle biodiversity measures (richness, abundance and biomass) on dung removal and secondary seed dispersal were explored using linear mixed models and generalized linear mixed models were Akaike's Information Criterion (AICc) was used to select the best-suited model using the *AICcmodavg* package in R (Burnham and Anderson 2004; Slade et al. 2007; Zuur et al. 2009). The spatial random variable used was property (Bates et al. 2014) and binomial distributions were implemented (Skaug et al. 2011). Dung removal and secondary seed dispersal were the response

variables and species richness, abundance and biomass were used as predictor variables. Dung removal by tunnellers and rollers only, as well as seed dispersal by tunnellers and rollers only, was also analysed separately to further compare the three treatments (Slade et al. 2016; Milotić et al. 2019). The *anova* function was used to obtain $p-$ and $F-$values. To explore the relationship between the various diversity indices (richness, abundance and biomass) for the overall assemblages and those of the separate functional guilds, I calculated the degree of collinearity using Spearman's correlations (Corder and Foreman 2014).

3.3 Results

3.3.1 Sampling completeness

A total of 5 769 specimens belonging to 51 species from the Scarabaeinae were collected. Of these 2 992 specimens belonging to 51 species were collected on the PA and 2777 specimens representing 35 species were collected on the farm. Therefore, the PA harboured 16 unique species. There were 13 rolling species with 519 individuals and 38 tunnelling species consisting of 5250 individuals. The species accumulation curve reached an asymptote for the farm and the PA (Appendix E) and the sample coverage estimators indicated that the inventories were >99% complete (Table 3.1).

Table 3.1 Summarised results of abundance and richness, including species estimates based on Chao2 and Jackknife2 calculations, reported for all sites combined and for the farm and PA separately

Site	Index	Count
All sites	Abundance	5769
	Observed richness	51
	Chao2	51.53±0.98
	Jackknife2	49.73±0
Protected areas	Abundance	2992
	Observed richness	51
	Chao2	51.45±0.86
	Jackknife2	49.7±0
Farmland	Abundance	2777
	Observed richness	35
	Chao2	35±0.52
	Jackknife2	32.87±0

3.3.2 Vertebrate profile

A total of 23 vertebrate species were identified in the dung surveys with seventeen species present in the PA and only nine species recorded on the farm (Appendix C). The PA hosted an assortment of species including non-ruminant ungulates and large ruminants as well as the occasional carnivorous species (all carnivore was grouped together and is representative of dung from leopards, cheetahs and hyena). Of the nine species present on farms, only three were recurrent throughout all the sites surveyed. These were mainly livestock and other domestic species with sporadic recordings of the dung of wild animals (e.g. kudu and duiker). Vertebrate richness and stocking densities were

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significantly higher in the PA compared to the farm (vertebrate richness: $F_{(1,119)} = 14.06$, $p < 0.001$; vertebrate stocking density: $F_{(1,119)} = 9.79$, $p < 0.001$).

3.3.3 Environmental factors that influence dung removal and secondary seed dispersal

Dung removal

The proportion of dung removed differed significantly between the two land-use types, with more dung removed in the protected area compared to the farm (Table 3.2). Dung removal was also significantly influenced by treatment, with the non-exclusion treatment having the greatest amount of dung removed (Fig. 3.3; Table 3.2). However, the interaction between land-use and treatment was significant for dung removal. The amount of dung removed by tunnellers and rollers respectively on the farm were similar, but dung removed when both were present was nearly double that. On the PA the respective contributions of tunnellers and rollers to dung removal was also similar, but when both guilds were present, dung removal remained the same (Fig 3.3).

Table 3.2 Results of the linear mixed models and generalized linear mixed models for the effects of land-use, bait type, vertebrate richness and vertebrate stocking density on dung removal and secondary seed dispersal. Only those variables retained after model selection procedure based on AICc (Appendix G) are shown. Tukey post hoc results are also shown

Variable	Predictor variable	F– value	P-value	Tukey post hoc
Dung removal	Land-use	15.39	<0.001	PA > FL
	Treatment	34.67	<0.001	AG >TO; AG>RO
	Land-use * Treatment	7.22	<0.01	PG≥FA; PT>FT; PR> FT
Small seeds	Land-use	181.57	<0.001	PA > FL
	Bait type	54.37	<0.001	WD>CD
	Treatment	5.46	<0.01	AG ≥TO; AG≥RO; RO≥TO
	Land-use * Bait Type	74.76	<0.001	PW>PC; PW>FW; PW>FC; FW ≥FC; PC >FC; PW>FC
Medium seeds	Bait type	0.86	0.357	
	Treatment	7.27	<0.01	AG >TO; AG≥RO; RO≥TO
	Vertebrate richness	4.50	<0.05	
	Bait type * Treatment	23.35	<0.001	WA>CA; WA>CT; WR>CT; WA>CR; WA>WR
Large seeds	Land-use	7.90	<0.01	PA > FL

PA= Protected Area, FL= Farmland, RO = Rollers only, TO = Tunnellers only, AG= All guilds (rollers and tunnellers), PA=Protected area all guilds, PR= Protected area rollers, PT= Protected area tunnellers, FA = Farmland all guilds, FR = Farmland rollers, FT = Farmland tunnellers, WD = Wildebeest dung, CD = Cow dung, PW=Protected area wildebeest dung, PC = Protected area cow dung, FW = Farmland wildebeest dung, FC = Farmland cow dung, WA = Wildebeest all guilds, WR = Wildebeest rollers only, WT = Wildebeest tunnellers only, CA = Cow all guilds, CR = Cow rollers only, CT = Cow tunnellers only. Tukey post hoc test results are arranged from the highest mean to lowest mean; ≥ indicates the specific variable was higher but non-significant; > indicates the means differ significantly for the specific variable.
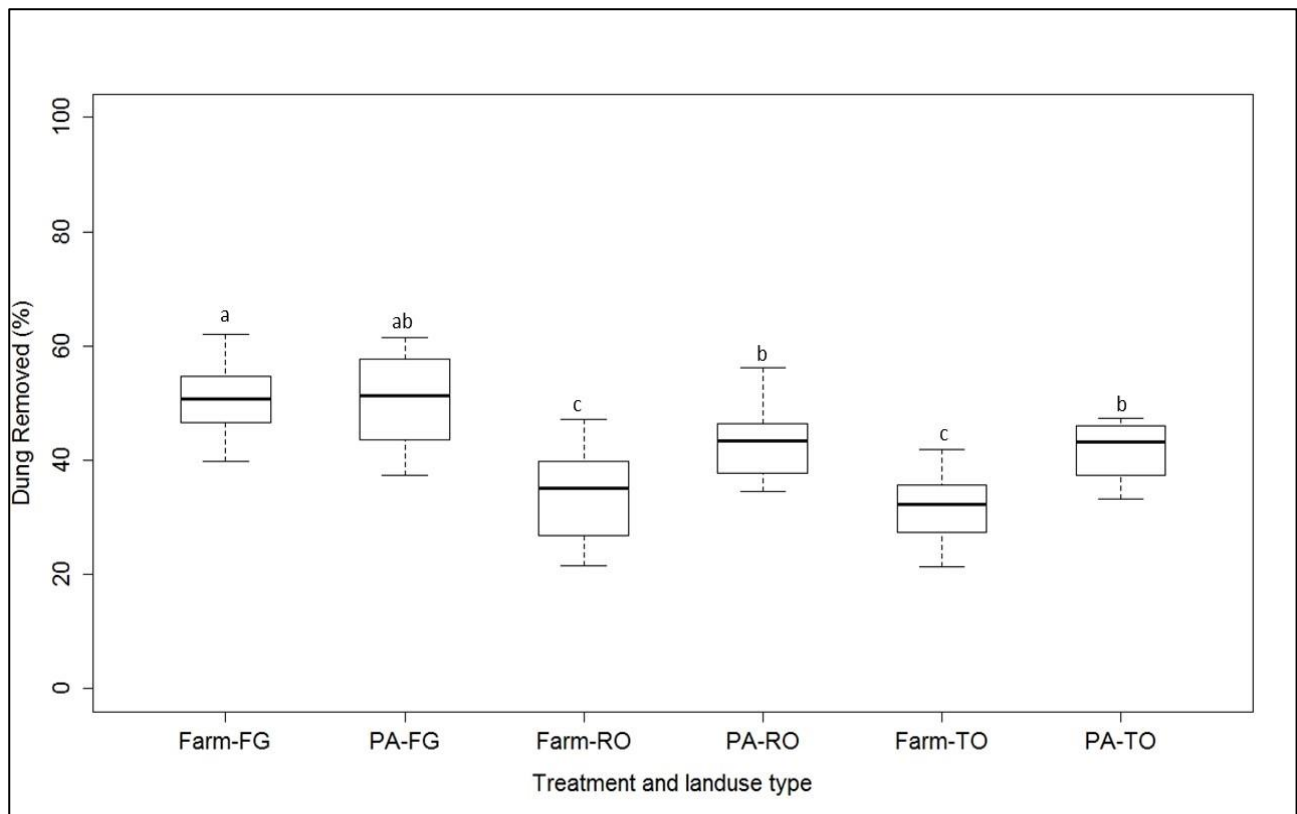
Figure 3.3 Proportion of dung removed in relation to treatment (functional group) and land-use type. The alphabetical letters indicate significant differences recorded using a GLMM followed by a Tukey post hoc test. Abbreviations used are protected areas (PA)

Seed dispersal

Land-use, bait type and treatment had significant effects on the relocation of small seeds by dung beetles. These were more effectively relocated on the PA and more seeds present in the native dung type were relocated (Fig 3.4; Table 3.2). However, a significant interaction between different land-uses and bait types was found for the relocation of small seeds (Fig 3.4; Table 3.2). Small seed dispersal was only higher for wildebeest dung on the PA and not the farm. The mixed guild of dung beetles removed more small seeds that either the rollers or tunnellers when acting alone (that removed similar numbers of small seeds), but this effect disappeared when performing the conservative Tukey post hoc test. (Table 3.2).

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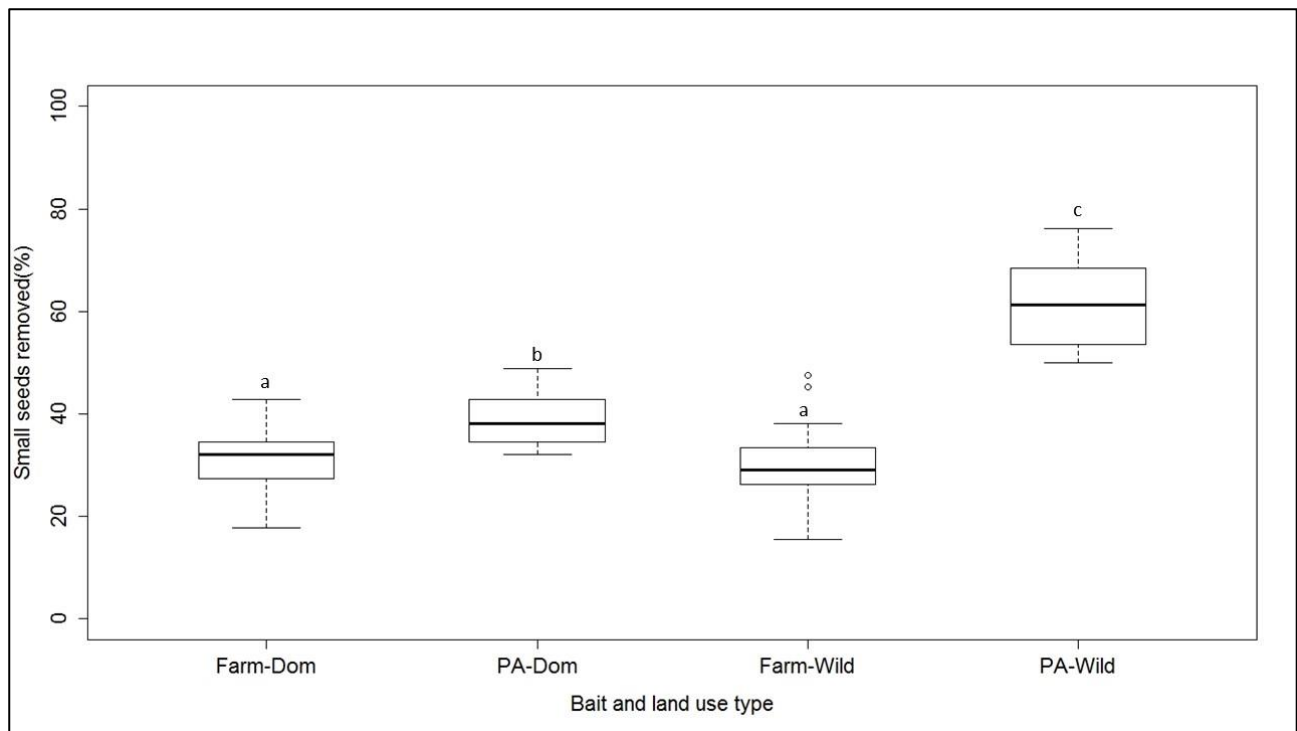
Figure 3.4 Proportion of small seeds dispersed in relation to bait type (domestic or wild) and land-use type. The alphabetical letters indicate significant differences recorded using a GLMM followed by a Tukey post hoc test. Abbreviations used are protected areas (PA), cow (domestic) dung (Dom) and wildebeest dung (Wild)

Medium-sized seed relocation was significantly affected by treatment and dung type, but not by land-use (Table 3.2). Instead, increased vertebrate richness had a positive influence on the relocation of medium-sized seeds (Table 3.2). More seeds were relocated when the full complement of beetles was present than when only tunnellers were present, but rollers relocated similar numbers of medium seeds than when the full complement of guilds was present (Table 3.2). Bait type did not significantly influence relocation of medium-sized seeds, but this variable significantly interacted with treatment (Fig. 3.5; Table 3.2). Treatment had no significant effect on the number of medium seeds relocated along with domestic dung (Fig. 3.5), but significantly more medium seeds were relocated when these were associated with wild dung and when the full complement of dung beetle guilds was present. However, this effect disappeared when these seeds were associated with wild dung in the presence of only one of the dung beetle guilds.
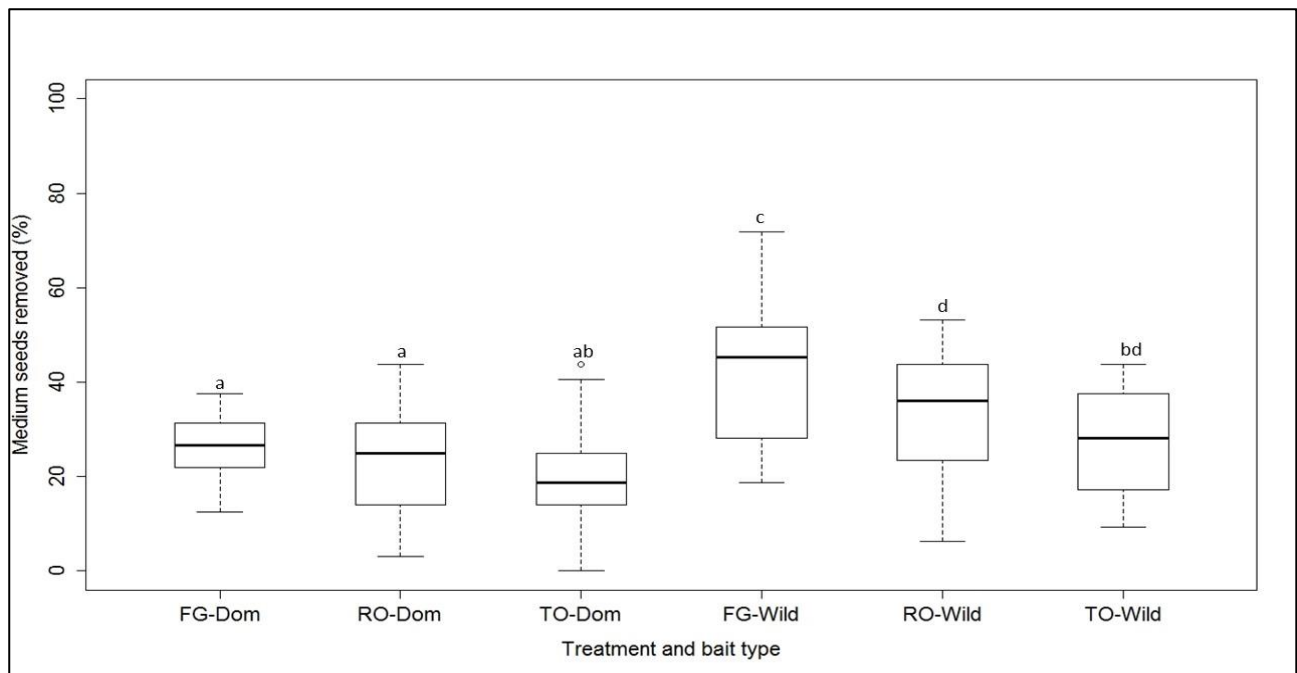
Figure 3.5 Proportion of medium seeds dispersed in relation to treatment (functional group) and bait type used. The alphabetical letters indicate significant differences recorded using a GLMM followed by a Tukey post hoc test. Abbreviations used are protected areas (PA), wildebeest dung (Wild) and cow (domestic) dung (Dom), rollers only (RO), tunnellers only (TO) and full guild (FG)

The relocation of large seeds was only significantly affected by land-use type (Table 3.2), with more relocated in the PA than on the farm (Fig 3.6; Table 3.2).
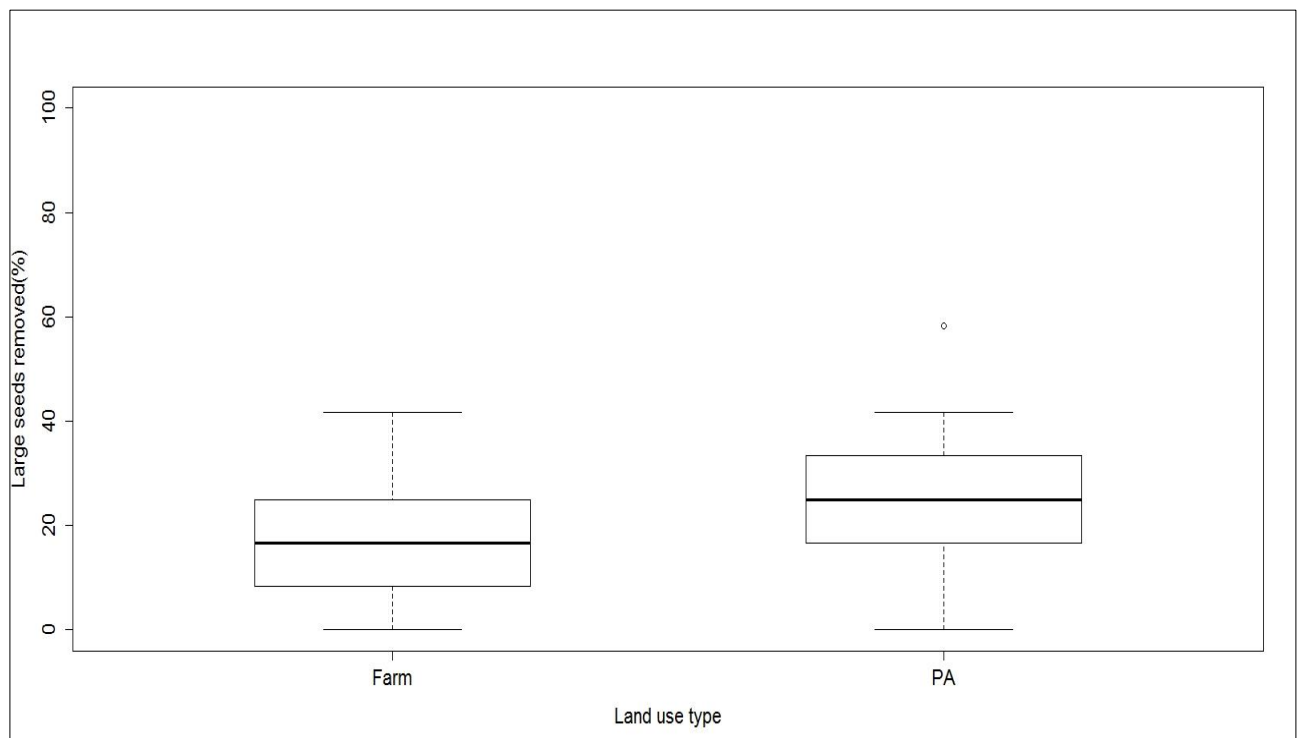
Figure 3.6 Proportion of large seeds dispersed in relation to land-use type. Abbreviations used are protected areas (PA)

3.3.4 Inter-guild interactions

Roller and tunneller richness, abundance and biomass were always significantly higher in the PA compared to the farm (Table 3.3). Higher roller abundance and biomass was attracted to the wildebeest dung, while more tunneller dung beetle individuals were attracted to the cow dung (Fig 3.7; Table 3.3). This was however context-dependent as land-use and bait type significantly interacted (Table 3.3). Roller richness and biomass were similar between the two bait types on farms, but wildebeest dung attracted significantly more species in the PA than cow dung (Fig. 3.7). Tunneller dung beetle richness and abundance was also context-dependent as the number of species attracted to cow and wildebeest dung on farms were similar, but again wildebeest dung attracted more species than cow dung in the PA (Fig. 3.8). The abundance of tunnellers attracted to cow dung was higher on farms compared to the wildebeest dung, but abundance was higher in wildebeest dung than cow dung on farms (Fig. 3.8).

The response of the two functional groups to treatment was measured for when only a single guild was present vs. when both guilds had access to the bait. Roller richness and biomass was unaffected by the presence of tunnellers, but roller abundance was significantly higher when no tunnellers were present (Table 3.3). For tunneller biomass, this effect was context-dependent. On the farm, tunneller biomass was similar between these two treatments, but on the PA tunneller biomass was increased when both guilds have access to the dung source vs. when rollers were excluded (Fig. 3.8).

Table 3.3 Model results of the linear mixed models and generalised linear mixed models for the two dung beetle guilds and their diversity indices as the fixed effects and treatment, bait type and land-use type modelled as the predictor variables The interactions between treatment and bait type and bait type and land-use type are also reported. The Wald chi-square values are reported.

Variable	Treatment	Land-use	Bait type	BT * TMT	LU * BT	TMT * LU
Roller richness	0	7.01**[PA]	3.42	0.02	10.87***	1.94
Roller abundance	9.66**[RO]	8.91** [PA]	77.84***[W]	12.13***	0.08	10.87***
Roller biomass	0.643	4.85* [PA]	6.91**[W]	0.73	7.69**	0.18
Tunneller richness	504.61***[FG]	5.08* [PA]	0.89	0	15.20***	0
Tunneller abundance	2642.30***[FG]	5.66* [PA]	5.04*[D]	0	329.72***	0
Tunneller biomass	8.93**[FG]	3.90* [PA]	2.08	2.14	3.04	5.42*

PA= Protected Area, FL= Farmland, D=Domestic (cow) dung, W=Wildebeest dung, RO = Rollers only, FG= All guilds (rollers and tunnellers). Asterisks denote significant chi square values $P < 0.1$, * $P < 0.05$, **$P < 0.01$, ***$P < 0.001$.
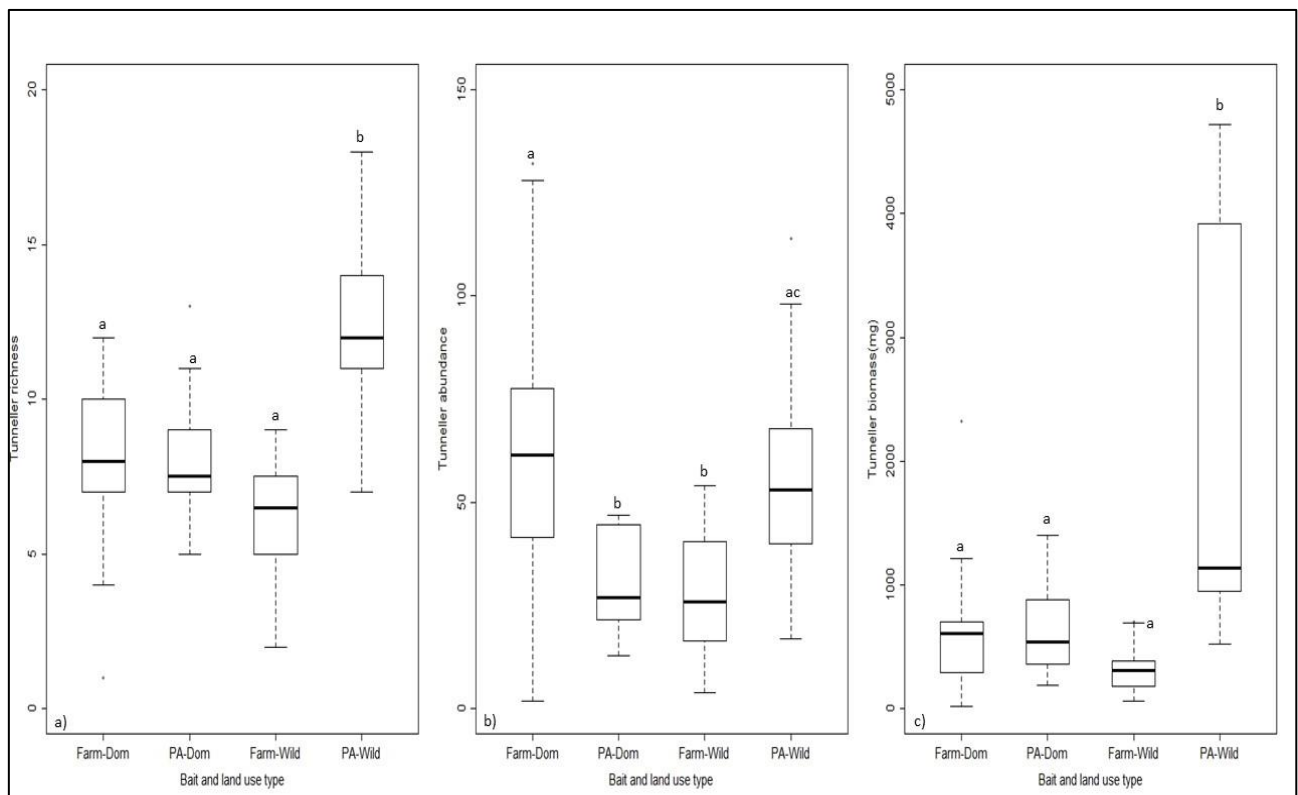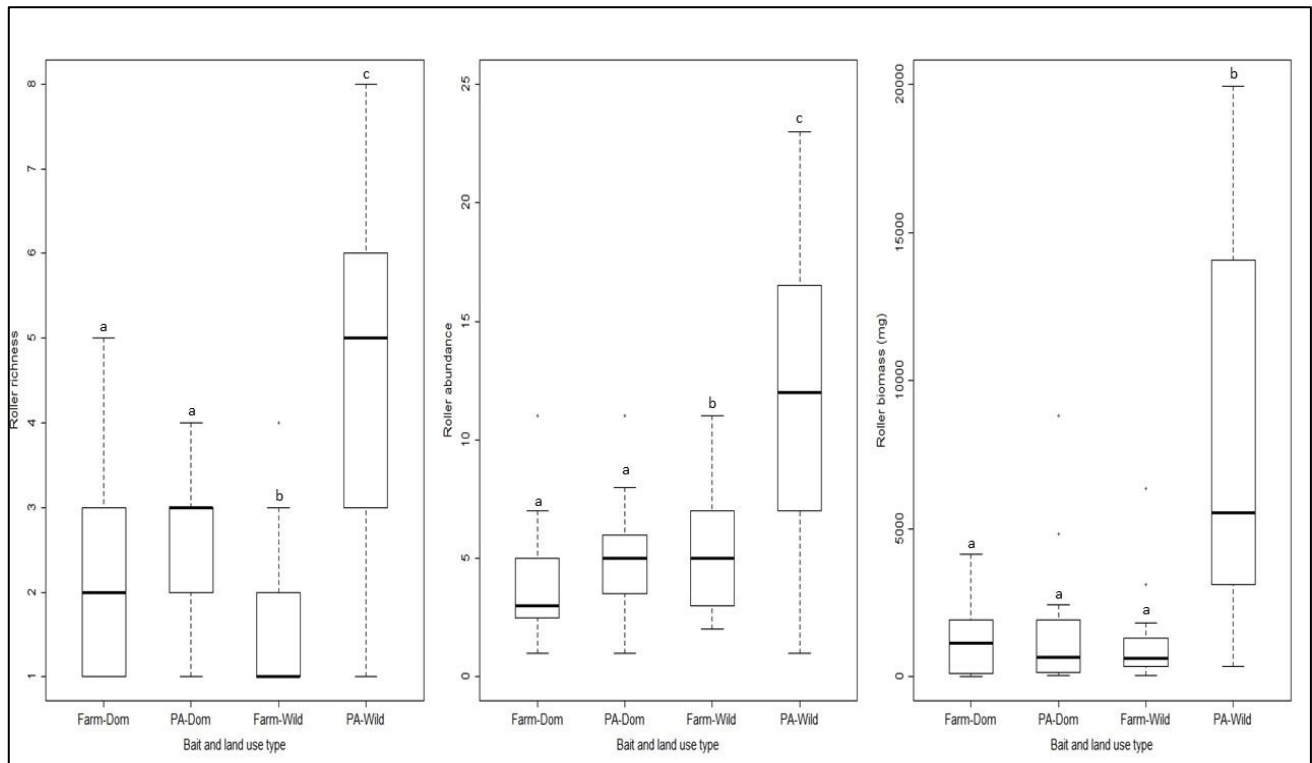
3.3.5 Effect of dung beetle species richness, abundance and biomass on dung removal and secondary seed dispersal

Dung removal

After the model selection procedure, the most important factors related to dung removal were species richness and biomass, although these factors were often strongly correlated to abundance (Table 3.4; Appendix I). When all guilds were present, dung removal was significantly increased by increased overall dung beetle species richness, the rollers in particular (Table 3.4). An increase in tunneller biomass also leads to increased dung removal (Table 3.4). However, overall species richness was significantly correlated to all other diversity indices (Appendix I). When only rollers were present, dung removal significantly increased with increased roller species richness and roller biomass. Roller biomass was significantly positively correlated to roller abundance, but roller richness was not correlated to any of the diversity measures. Dung removal in the presence of only tunnellers was significantly increased by increased tunneller species richness and tunneller biomass, but both measures were significantly correlated with each other and with tunneller abundance (Table 3.4; Appendix I).

Secondary seed dispersal

After model selection procedures, most important explanatory factors that increased dung removal and secondary seed dispersal were dung beetle species richness and biomass, although these factors were often strongly correlated to each other and/or abundance (Appendix I; Table 3.4;). Richness especially that of the rollers, most often produced the largest effect sizes (*F*-values) for dung removal and secondary seed dispersal (Table 3.4). When all guilds were present, the removal of small seeds was significantly increased with increased species richness, including the richness of the tunnellers and rollers and tunneller biomass (Table 3.4). However, overall species richness was significantly correlated to all other diversity indices (Appendix I). Dispersal of small seeds when only rollers were present was increased with increased roller richness only (Appendix I; Table 3.4). When only tunnellers were present, an increase in small seed dispersal was observed with an increase in tunneller richness, but this was significantly correlated also to tunneller abundance and biomass (Table 3.4; Appendix I). Medium seed dispersal was significantly increased with an increase in overall dung beetle abundance and an increase in roller richness (Table 3.4). Dispersal by tunnellers was affected by tunneller richness only. Dispersal, when only rollers were present, was increased with an increase in roller richness, but this was correlated with abundance and biomass (Appendix I; Table 3.4).

Large seed dispersal was significantly increased with an overall increase in species richness and increases in roller and tunneller biomass (Table 3.4) all three of which are strongly positively correlated. Dispersal of large seeds when only tunnellers were present was only increased with an

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increase in tunneller richness, but again this was positively correlated to tunneller abundance and biomass (Appendix I). When only rollers were present, an increase in their biomass led to an increase in large seed dispersal, but this was significantly positively correlated to their abundance (Appendix I; Table 3.4).

Table 3.4 Results of the linear mixed models and generalized linear mixed models for dung removal and secondary seed dispersal by dung beetles as the response variables. Dung removal and seeds dispersal were also separated based on guild involved to compare the contribution of the two guilds. The diversity indices were used as predictor variables – species richness, abundance, biomass for all and each guild separately. Only those variables retained after model selection procedure based on AICc (Appendix H) are shown.

Variable	Predictor variable	F– value	P– value
Dung removal (All)	Species Richness	9.751	<0.01
	Roller Richness	31.742	<0.001
	Tunneller Abundance	3.468	0.071
	Tunneller Biomass	5.015	<0.05
Small seeds (All)	Species Richness	0.301	<0.001
	Abundance	3.137	0.224
	Roller Richness	5.008	<0.05
	Tunneller Richness	3.097	<0.01
	Tunneller Abundance	0.359	0.052
	Tunneller Biomass	0.008	<0.05
Medium seeds (All)	Abundance	15.452	<0.001
	Roller Richness	10.291	<0.01
Large seeds (All)	Species Richness	14.9409	<0.001
	Roller Biomass	4.6632	<0.05
	Tunneller Biomass	10.2703	<0.01
Dung removal (Rollers)	Roller Richness	24.904	<0.001
	Roller Abundance	4.765	<0.05
Small seeds (Rollers)	Roller Richness	6.489	<0.001
Medium seeds (Rollers)	Roller Abundance	3.5006	0.069
	Roller Richness	18.050	<0.001
	Roller Biomass	3.185	0.083
Large seeds (Rollers)	Roller Biomass	14.498	<0.001
Dung removal (Tunnellers)	Tunneller Richness	21.731	<0.001
	Tunneller Biomass	3.130	<0.001
Small seeds (Tunnellers)	Tunneller Richness	5.720	<0.001
Medium seeds (Tunnellers)	Tunneller Richness	12.3839	<0.001
	Tunneller Biomass	2.502	0.122
Large seeds (Tunnellers)	Tunneller Richness	2.33	<0.05

3.4 Discussion

3.4.1 Negative effect of land transformation on dung beetle ecological function

I found a marked decrease in dung removal and secondary seed dispersal in the farmland area compared to the adjacent PA. This is in agreement with many other studies showing that dung beetle ecological function is adversely affected by anthropogenic disturbances particularly agricultural practices (Jankielsohn et al. 2011; Young et al. 2005, 2018; Nichols et al. 2008; Numa et al. 2012 Culot et al. 2013; Sugiura et al. 2013; Manning et al. 2016; Pryke et al. 2016; Raine et al 2018; Raine and Slade 2019; Chapter 2). Decreased functionality was strongly correlated to decreased overall dung beetle species richness, abundance and biomass, similar to studies in other parts of the world (Slade et al. 2011; Kenyon et al. 2016; Manning and Cutler 2018; Milotić et al. 2019). These parameters, in turn, are likely driven by two main factors: increased management intensity on farms (Frank et al. 2017b; Manning and Cutler 2018) and altered vertebrate composition (Raine and Slade 2019; Chapter 2). Land-use modification due to management intensity on farmlands alters micro-climatic conditions which in turn affect landscape characteristics such as vegetation physiognomy, temperature and moisture which alter dung beetle assemblages (Davis et al. 2002; Tscharntke et al. 2005, 2011; Williams-Guillén and Perfecto 2010; Korasaki et al. 2013). Increase in dung beetle function associated with native dung demonstrated the strong negative effects of changing vertebrate profiles from wild to domestic (Kenyon et al. 2016; Bogoni et al. 2018, 2019; Raine and Slade 2019) and the importance of maintaining representative populations of native vertebrates to promote the existence of the full assemblage of dung beetles to increase ecological function (Andresen and Feer 2005; Manning and Cutler 2018; Bogoni et al. 2019; Milotić et al. 2017, 2018, 2019). Also, seed predation by small rodents increases with the loss of predatory mammal populations (Andresen and Levy 2004; Galetti et al. 2015; Bogoni et al. 2019), which can result in a secondary deed dispersal bottleneck influencing both dung beetle diversity (Culot et al. 2013) and the ecological trajectory of transformed regions (Derhé et al. 2016).

Increases in dung beetle species richness are strongly related to an increase in the number of ecological niches used and therefore, an increased in ecosystem function (Nichols et al. 2008,2013; Scholtz et al. 2009; Manning et al. 2016; Noriega et al. 2018). It was therefore expected that dung beetle species richness would be strongly correlated to increased functions in the present study. Increased abundance of individuals also usually correlates positively to dung beetle functions, as more individuals can manipulate more of the resource (Manning and Cutler 2018). However, in the present study, I show that there was a stronger correlation between dung beetle biomass and their ecological functions than between abundance and their functions, even though these response variables are correlated. Differences in mean beetle size between the farm and the PA likely also

contributed to these disparities. Larger bodied beetles such as *Heliocopris andersoni*, *H. atropos, Scarabaeolus bohemani and Scarabaeus deludens* were far less common or absent on the farmland. Lowered average dung quality on farms have been shown to reduce the average size of most individuals remaining on farms (Chapter 2). Therefore, the PA maintained higher biomass not only due to higher abundance and richness of beetles but also due to larger average size of individuals, which will increase the average amount of dung removed per beetle in the PA (Amezquita and Favila 2010; Piccini et al. 2019).

As with previous studies, I show that seed size-class is important for their probability of secondary seed dispersal *via* dung beetles (Andresen and Feer 2005; Milotic et al. 2018, 2019). Relatively small seeds (e.g. 4 mm diam. in Andersen (2002) and 3.5 mm diam. in Slade et al. (2007)) are most likely to be dispersed than larger ones. In the present study, the smallest seed (2.8 mm) had nearly double the probability of being dispersed by dung beetles in this ecosystem than the medium (7.0 mm) and large seeds (12.0 mm). Seed dispersal by dung beetles is mostly serendipitous as they process dung for ovipositing and feeding (Halffter and Edmonds 1982). Some dung beetle species purposefully remove seeds and seed dispersal and this selection would be coupled to the size of beetles with large beetles only removing large seeds and smaller beetles removing both larger and smaller seeds, increasing the overall probability of smaller seeds to be dispersed (Andresen and Levey 2004; Andresen and Feer 2005; Culot et al. 2018; Urrea– Galeano et al. 2019). However, it should be noted that dung beetles may handle real seeds differently than the seed mimics used here, since these may differ in smell and morphological features (Andresen and Levey 2004; Hulme and Kollmann 2004 Milotić et al. 2019).

3.4.2 Altered inter-guild interactions

Tunnellers were expected to be competitively superior in terms of their functions than rollers because of higher abundance and richness in southern Africa (Davis et al. 2008). Furthermore, previous studies have found that rollers are less efficient dung removers and seed dispersers compared to tunnellers (Estrada and Coates– Estrada 1991; Shepherd and Chapman 1998; Andresen 2002; Slade et al. 2007). Contrary to these expectations, I did not find that different guilds differed in their dung removal and secondary seed dispersal capabilities in this African savannah system. Also, I could not detect complementarity effects between the two guilds for dung removal or seed dispersal as shown in a tropical rainforest (Slade et al. 2007). When both guilds were present in the PA, they had strong competitive interactions on dung removal, but on the farmland, they maintained their respective functional importance levels to a large degree. The interaction between the guilds, therefore, shifted from competitive in the PA, to neutral on the farmland, leading to a net decrease in dung removal. Greater competitiveness in the PA is likely due to higher species richness in both guilds (more inter-

species competition) and to increased abundance and biomass (i.e. increased intra-species competition) (Scholtz et al. 2009). Therefore, the loss of any feature of dung beetle biodiversity is problematic as it precipitates the loss of some functional capacity (Slade et al. 2007), especially when the most sensitive species that provide the greatest level of ecosystem functioning (e.g. larger tunnellers) are lost (Larsen et al. 2005; Piccini et al. 2018).

Roller richness and biomass were unaffected by the presence of tunnellers, however, their abundance increased considerably when not competing with tunnellers, indicating strong competitive exclusion by tunnellers (Scholtz et al. 2009). Similar to dung removal functions, this effect was strongest in the PA and on wild dung, suggesting larger tunnellers that were still present in the PA, in particular, are superior competitors in this African savannah ecosystem as also found in other biomes (Slade et al. 2007). Unexpectedly, tunneller richness, biomass and abundance increased when rollers were also present indicating possible facilitation (Slade et al. 2007). This contradicts previous studies that show that large tunnellers facilitate rollers and smaller tunnellers by breaking down the dung deposit into more corrigible portions (Slade et al. 2007; Mendez et al. 2016). The precise mechanism by which rollers can facilitate the numbers of tunnellers in this study is unknown but may include larger rollers facilitating smaller tunnelling beetles (Slade et al. 2007; Slade et al. 2011; Kenyon et al. 2007) and this is highly likely due to the high population of large rollers compared to that of large tunnellers on the farm and in the PA. Many studies exploring dung beetle functioning in different ecosystems alluded to facilitative behaviour between rollers and tunnellers (Cadotte et al. 2011; Kenyon et al. 2016; Menéndez et al. 2016). Whatever the reasons, the shift in dung beetle communities in the present study are largely due to land-use change and their inter-guild and ecological interactions change along with these shifts. Loss of keystone taxa such as the large tunnellers identified in this study results in interaction deficits which promote the emergence of new interactions (Quental and Marshall 2013; Valient – Banuet et al. 2015).

3.4.3 Effect of richness, abundance and biomass on ecosystem functioning

Manning and Cutler (2018) proposed that ecosystem functions of dung beetles are more strongly impaired by diminished abundances than species richness. The results of the present study seem to agree with other studies that show that communities richer in species provide more ecosystem functions and services (Hooper et al. 2005; Manning and Cutler 2018; Milotić et al. 2019). In consideration of the aforementioned, species abundances and species richness were positively correlated meaning both biodiversity measures are important in maintaining ecosystem function. Declines in species richness and abundances due to anthropogenic pressures will, therefore, have severe consequences for overall ecosystem functioning in this region. Biomass was also a very important factor that explained increased ecosystem function. The link between increased biomass

and increased function are well established, as greater biomass of beetles would manipulate greater biomass of resources (Nervo et al. 2014). It is also important to note that species richness and biomass was often correlated to abundance as in other studies (Nervo et al. 2014; Manning et al. 2016). These three factors, therefore, work synergistically in promoting dung beetle ecosystem function and services (Numa et al. 2012; Nervo et al. 2014; Griffiths et al. 2016; Piccini et al. 2019) and management options that tend to increase any one of these attributes of dung beetle communities in the African savannah will inevitably increase their functions and services.

3.5 Conclusions

This study contributes to the growing body of literature on the negative impact of anthropogenic change on dung beetle diversity and their ecosystem functioning to now also include African savannahs (Noriega et al 2018; Raine et al. 2019). It also adds knowledge of the value of quantifying the individuals involved in dung removal and seed dispersal studies (Slade et al. 2011; Kenyon et al. 2016; Manning et al. 2018; Milotić et al. 2018, 2019). For example, this region is known to be particularly rich in dung beetle species and abundance (Chapter 2) and generalizations on the specific roles of separate guilds would not have been possible if individuals were collected without having opportunities to interact with and without members of a different guild present. Like in other systems around the globe I show that a functionally complete mixture of dung beetle guilds is necessary for increased ecosystem function provided (Manning et al. 2016, 2018; Milotić et al. 2018), but that the relative importance of each guild can be severely impacted by land transformation. Functionally more complete dung beetle assemblages are linked to increased species richness, which is known to be correlated to the increased native vertebrate richness in this region (Chapter 2). Overall the findings show that a rich native vertebrate fauna is paramount to not only the co-occurring dung beetle assemblages but also for maintaining landscape heterogeneity and improving the productivity of landscapes.

3.6 References

Alahuhta J, Johnson LB, Olker J, Heino J (2014) Species sorting determines variation in the community composition of common and rare macrophytes at various spatial extents. Ecological Complex 20: 61 – 68

Alexandratos N, Bruinsma J (2012) World Agriculture towards 2030/2050: The 2012 revision. Rome: UN Food and Agricultural Organization (FAO)

Alkemade R, Reid RS, van den Berg M, de Leeuw J, Jeuken M (2013) Assessing the impacts of livestock production on biodiversity in rangeland ecosystems. Proceedings of the National Academy of Sciences 110: 20900 – 20905

Amezquita S, Favila ME, (2010) Removal rates of native and exotic dung by dung beetles (Scarabaeidae: Scarabaeinae) in a fragmented tropical rain forest. Environmental Entomology 39: 328 – 336

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

Andresen E, Feer F (2005) The role of dung beetles as secondary seed dispersers and their effect on plant regeneration in tropical rainforests. In: Forget PM, Lambert JE, Hulme PE, Vander Wall SB (ed) Seed fate. Predation, dispersal and seedling establishment. CABI, Oxon, UK, pp 331 – 349

Andresen E, Levey DJ (2004) Effects of dung and seed size on secondary dispersal, seed predation, and seedling establishment of rain forest trees. Oecologia 139:45 – 54

Balthasar V (1963a) Neue arten der familie Scarabaeidae. Acta Societatis Entomologicae Cechosloveniae 60: 284 – 295

Balthasar V (1963b) Monographie der Scarabeidae und Aphodiidae der palaearktischen und orientalischen Region (Coleoptera: Lamellicornia). Band 2. Coprinae (Onitini, Oniticellini, Onthophagini). Verlag der Tschechoslowakischen Akademie der Wissenschaften, Prague: pp 627

Balthasar V (1965a) Eine neue undergattung und neue arten der familie Scarabaeidae (121. Beitrag zur Kenntnis der Scarabaeoidea). Acta entomologica bohemoslovaca 62: 14 – 23

Balthasar V (1965b) Monographie der untergattung Metacatharsius Paulian. Entomologische Abhandlungen Staatlichen Museum für Tierkunde, Dresden 31: 1–48

Barbero E, Palestrini C, Roggero A (2003) Revision of the genus *Phalops*. Museo Regionale di Scienze Naturale Torino Monografia 38: 1 – 378

Barnard P (1998) Biological diversity in Namibia: a clash of sea and land, fog and dust. Biodiversity and Conservation 7:415 – 417

Barnard P, Brown CJ, Jarvis AM, Robertson A (1998) Extending the Namibian protected area network to safeguard hotspots of endemism and diversity. Biodiversity and Conservation 7:531 – 547

Bates D, Mächler M, Bolker B, Walker S (2014) Fitting linear mixed-effects models using {lme4}. Journal of Statistical Software 67:1 – 48

Batilani-Filho M, Hernández MIM (2017) Decline of Ecological Functions Performed by Dung Beetles in Areas of Atlantic Forest and Contribution of Rollers and Tunnellers in Organic Matter Removal. Community. Environmental Entomology 46: 4784 – 793

Bernal JL, Del Nozal MJ, Salas M, Galante E, Lumaret JP (1994) HPLC determination of residual ivermectin in cattle dung following subcutaneous injection. Journal of Liquid Chromatography 17: 2429 – 2444

Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White JSS (2008) Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology and Evolution 2:127 – 135

Bogoni JA, Hernández MIM (2014) Attractiveness of native mammal's faeces of different trophic guilds to dung beetles (Coleoptera: Scarabaeinae). J. Insect Sci. 14:1 – 7

Bogoni JA, Graipel ME, de Castilho PV, Fantacini FM, Kuhnen VV, Luiz MR, Maccarini TB, Marcon CB, de Souza Pimentel Teixeira C, Tortato MA, Vaz-de-Mello FZ, Hernández MIM (2016) Contributions of the mammal community, habitat structure, and spatial distance to dung beetle community structure. Biodiversity Conservation 251: 661 – 1675

Bogoni JA, Pires JSR, Graipel ME, Peroni N, Peres CA (2018) Wish you were here: How defaunated is the Atlantic Forest biome of its medium– to large-bodied mammal fauna? PLoS ONE 13: e0204515

Bogoni JA, da Silva PG, Peres CA (2019) Co-declining mammal–dung beetle faunas throughout the Atlantic Forest biome of South America. Ecography 42: 1 – 16

Braga RF, 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: e5778

Branco T (2010) Revision of the genera Tiniocellus Péringuey, 1901 and Nitiocellus gen. n. Boletin de la Sociedad Entomologica Aragonesa 47: 71 – 126

Brown J, Scholtz CH, Janeau J-L, Grellier S, Podwojewski P (2010) Dung beetles (Coleoptera: Scarabaeidae) can improve soil hydrological properties. Applied Soil Ecology 46: 9 – 16

Bryan RP (1973) The effects of dung beetle's activity on the numbers of parasitic gastrointestinal helminthic larvae recovered from pasture samples. Australian Journal of Agricultural Research 24: 161 – 168

Burnham KP, Anderson DR (2004) Multimodel inference understanding AIC and BIC in model selection. Sociological Methods & Research 33:261 – 304

Cadotte MW, Carscadden K, Mirotchnick N (2011) Beyond species: functional diversity and the maintenance of ecological processes and services. Journal of Applied Ecology 48:1079 – 1087

Cambefort Y (1996) Une nouvelle espèce Afro-Tropicale d'Euoniticellus Janssens, 1953, avec une Phylogénie du genre. Revue française d'Entomologie (N.S.) Paris 18: 115 – 119

Cardinale BJ, Duffy E, Gonzalez A Hooper D, Perrings C, Venail P, Narwani A, Mace GM, Tilman D, Wardle DA, Kinzig AP, Daily GC, Loreau M, Grace JB, Larigauderie A, Srivastava DS, Naeem S (2012) Biodiversity loss and its impact on humanity. Nature 486:59 – 67

Chao A (2005) Species richness estimation. In: Balakrishnan, N., Read, C.B., Vidakovic, B. (Eds.), Encyclopedia of Statistical Sciences. Wiley, New York, pp 7909 – 7916

Chao A, Jost L (2012) Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. Ecology 93: 2533 – 2547

Chao A, Gotelli NJ, Hsieh TC, Sander EL, Ma KH, Colwell RK, Ellison AM (2014) Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. Ecological Monographs 84:45 – 67

Colwell RK, Chao A, Gotelli NJ, Lin SY, Mao CX, Chazdon RL, Longino JT (2012) Models and estimators linking individual-based and sample-based rarefaction, extrapolation and comparison of assemblages. Journal of Plant Ecology 5:3 – 21

Colwell R (2013) EstimateS: Statistical estimation of species richness and shared species from samples. http://viceroy.ee– b.uconn.edu/estimates

Corder GW, Foreman DI (2014) Nonparametric Statistics: A Step-by-Step Approach. 2nd edn. Wiley, New York USA

Crawley MJ (2013) The R Book, second ed. Wiley, West Sussex

Culot L, Bovy E, Vaz-de-Mello FZ, Guevarad R, Galetti M (2013) Selective defaunation affects dung beetle communities in continuous Atlantic rainforest. Biological Conservation 163: 79 – 89

Dabrowski J, Venter G, Truter WF, Scholtz CH (2019) Dung beetles can tunnel into highly compacted soils from reclaimed mined sites in eMalahleni, South Africa. Applied Soil Ecology 134:116 – 119

Dangles O, Carpio C, Woodward G (2012) Size-dependent species removal impairs ecosystem functioning in a large-scale tropical field experiment. Ecology 93:2615-2625

Davis ALV (2002) Dung beetle diversity in South Africa: influential factors, conservation status, data inadequacies and survey design. African Entomology 10: 53-65

Davis ALV, Frolov AV, Scholtz CH (2008) The African Dung Beetle Genera. Protea Book House, Pretoria

Davis ALV, Scholtz CH, Sole CL (2017) Biogeographical and co-evolutionary origins of scarabaeine dung beetles: Mesozoic vicariance versus Cenozoic dispersal and dinosaur versus mammal dung. Biological Journal of the Linnean Society 120: 258 – 273

Derhé MA, Murphy H, Monteith G, Menéndez R (2016) Measuring the success of reforestation for restoring biodiversity and ecosystem functioning. Journal of Applied Ecology 53: 1714 – 1724

Deschodt CM, Kryger U, Scholtz CH (2007) New taxa of relictual Canthonini dung beetles (Scarabaeidae: Scarabaeinae) utilizing rock hyrax middens as refuges in south-western Africa. Insect Systematics and Evolution 38: 361 – 376

Deschodt CM, Davis ALV (2018) New deltochiline (Coleoptera: Scarabaeidae: Scarabaeinae) taxa associated with hyrax dung in arid south western Namibia. Zootaxa 4450: 066 – 076

Deschodt CM Scholtz CH (2008) Systematics of South African forest-endemic dung beetles: new genera and species of small Canthonini (Scarabaeidae: Scarabaeinae). African Entomology 16: 91 – 106

Dirzo R, Young HS, Galetti M, Ceballos G, Isaac NJB, Collen B (2014) Defaunation in the Anthropocene. Science 345:401 – 406

Doube BM (1990) A functional classification analysis of the structure of dung beetle assemblages. Ecological Entomology 15:371 – 383

Eklof A, Ebenman B (2006) Species loss and secondary extinctions in simple and complex model communities. Journal of Animal Ecology 75: 239-246

Estes JA, Terborgh J, Brashares JS, Power ME, Berger J, Bond WJ, Carpenter SR (2011) Trophic downgrading of planet Earth. Science 333: 301 – 306

Estrada A, Coates-Estrada R (1991) Howler monkeys (Alouatta palliata), dung beetles (Scarabaeidae) and seed dispersal: ecological interactions in the tropical rain forest of Los Tuxtlas, Mexico. Journal of Tropical Ecology 7:459 – 474

Feer F (1999) Effects of dung beetles (Scarabaeidae) on seeds dispersed by howler monkeys (A*louatta seniculus*) in the French Guianan rain forest. Journal of Tropical Ecology 15:129 – 142

Ferreira MC (1969) Contribuiçao para o conhecimento dos Escarabídeos de África. Descriçao de uma espécie nova de Scarabaeus s. str. Novos Taxa Entomológicos 68: 3–4

Ferreira MC (1976) A new species of *Platyonitis* Janssens from Angola. Navorsinge van die Nasionale Museum 3: 177–180

Ferreira MC (1978) The genus Onitis F. of Africa south of the Sahara. Memoirs van die Nasionale Museum 10: 1-410

Floate KD (2006) Endectocide use in cattle and faecal residues: environmental effects in Canada. Canadian Journal of Veterinary Research 70:1 – 10

Frank K, Bruckner A, Hilpert A, Heethoff M, Bluthgen N (2017a) Nutrient quality of vertebrate dung as a diet for dung beetles. Science Report 7:1214

Frank K, Hulsmann M, Assmann T, Schmitt T, Bluthgen N (2017b) Land-use affects dung beetle communities and their ecosystem service in forests and grasslands. Agriculture, Ecosystems & Environment 243:114 – 122

Galetti M and Dirzo R (2013) Ecological and evolutionary consequences of living in a defaunated world. Biological Conservation 163: 1 – 6

Galetti, M Bovendorp RS, Guevara R (2015) Defaunation of large mammals leads to an increase in seed predation in the Atlantic forests. – Global Ecological Conservation 3: 824 – 830

Génier F, Moretto P (2017a) Digitonthophagus Balthasar, 1959: taxonomy, systematics, and morphological phylogeny of the genus revealing an African species complex (Coleoptera: Scarabaeidae: Scarabaeinae). Zootaxa 4248: 1 –1 10

Génier F, Davis ALV (2017b) Digitonthophagus gazella auctorum: an unfortunate case of mistaken identity for a widely introduced species (Coleoptera: Scarabaeidae: Scarabaeinae: Onthophagini). Zootaxa 4221: 497 – 500

Gómez A, Kolokotronis S. (2017) Genetic identification of mammalian meal source in dung beetle gut contents. Mitochondrial DNA A 28:612 – 615

Gotelli NJ, Colwell RK (2001) Quantifying biodiversity: procedures and pit–falls in the measurement and comparison of species richness. Ecology Letters 4:379 – 391

Gregory N, Gómez A, Oliveira TMF, Nichols E (2015) Big dung beetles dig deeper: trait-based consequences for faecal parasite transmission. International Journal for Parasitology 45:101 – 5

Griffiths HM, Bardgett RD, Louzada J, Barlow J (2016) The value of trophic interactions for ecosystem function: dung beetle communities influence seed burial and seedling recruitment in tropical forests. Proceedings of the Royal Society B: Biological Sciences 283:16 – 34

Halffter G, Edmonds WD (1982) The nesting behaviour of dung beetles (Scarabaeinae): An ecological and evolutive approach. Instituto de Ecologia, Mexico

Hammer TJ, Fierer N, Hardwick B, Simojoki A, Slade EM, Taponen J, Viljanen H, Roslin, T. (2016) Treating cattle with antibiotics affects greenhouse gas emissions, and microbiota in dung and dung beetles. Proceedings of the Royal Society B: Biological Sciences 283: 1 – 50

Hooper DU, Chapin FSI, Ewel JJ, Hector A, Inchausti P, Lavorel S, Lawton JH, Lodge DM, Loreau M, Naeem S, Schmid B, Setala H, Symstad AJ, Vandermeer J, Wardle DA (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecological Monographs 75:3 – 35

Horgan FG, Fuentes RC (2005) Asymmetrical competition between Neotropical dung beetles and its consequences for assemblage structure. Ecological Entomology 30:182 – 193

Hsieh TC, Ma KH, Chao A (2016) iNEXT: An R package for rarefaction and extrapolation of species diversity (Hill numbers). Methods in Ecology and Evolution 7:1451 – 1456

Hulme P, Kollmann J (2004) Seed predator guilds, spatial variation in post-dispersal seed predation and potential effects on plant demography: A temperate perspective. In Forget P, Lambert J, Hulme P, Vander Wall S (ed) Seed Fate Wallingford, Oxfordshire: CAB International. pp 9 – 30

Isbell F, Calcagno V, Hector A, Connolly J, Harpole WS, Reich PB, Scherer-Lorenzen M, Schmid B, Tilman D, van Ruijven J, Weigelt A, Wilsey BJ, Zavaleta ES, Loreau M (2011) High plant diversity is needed to maintain ecosystem services. Nature 477:199 – 202

Jacobs C, Scholtz CH, Escobar F, Davis AL (2010) How might intensification of farming influence dung beetle diversity (Coleoptera: Scarabaeidae) in Maputo Special Reserve (Mozambique)? Journal of Insect Conservation 14: 389 – 399

Jankielsohn A, Scholtz CH, Louw SVDM (2001) Effect of habitat transformation in the dung beetle assemblages: A comparison between a South African nature reserve and neighbouring farms. Environmental Entomology 30: 474 – 483

Janssens A (1937) Révision des Onitides. Verhandelingen Koninklijk Natuurhistorisch Museum Belgie, Brussel 2:1 – 200

Kenyon T, Mayfield M, Monteith G, Menéndez R (2016). The effects of land-use change on native dung beetle diversity and function in Australia's Wet Tropics. Austral Ecology 41:797 – 808

Koh LP, Dunn RR, Sodhi NS, Colwell RK, Proctor HC, Smith VS (2004) Species coextinctions and the biodiversity crisis. Science 305: 1632 – 1634

Korasaki V, Lopes J, Gardner B G, Louzada J (2013) Using dung beetles to evaluate the effects of urbanization on Atlantic Forest biodiversity. Insect Science 20:393 – 406

Krikken J (2009) Drepanocerine dung beetles: a group overview, with description of new taxa. Haroldius 4: 3 – 30

Kurten EL (2013) Cascading effects of contemporaneous defaunation on tropical forests communities. Biological Conservation 163:22 – 32

Lähteenmäki S, Slade EM, Hardwick B, Schiffler G, Louzada J, Barlow J, Roslin T (2015) MESOCLOSURES – increasing realism in mesocosm studies of ecosystem functioning Methods in Ecology and Evolution 6:916 – 924

Larsen TH, Williams NM, Kremen C (2005) Extinction order and altered community structure rapidly disrupt ecosystem functioning. Ecology Letters 8:538 – 547

Lobo JM (1993) Estimation of dung beetle biomass (Coleoptera: Scarabaeoidea). European Journal of Entomology 90:235–238

Manning P, Van der Plas F, Soliveres S, Allan E, Maestre FT, Mace G, Whittingham MJ, Fischer M (2018) Redefining ecosystem multifunctionality. Nature Ecology and Evolution 2:427 – 436

Manning P, Cutler GC (2018) Ecosystem functioning is more strongly impaired by reducing dung beetle abundance than by reducing species richness. Agriculture, Ecosystems & Environment 264: 9 – 14

Manning P, Slade EM, Beynon SA, Lewis OT (2016) Functionally rich dung beetle assemblages are required to provide multiple ecosystem services. Agriculture, Ecosystems & Environment 218:87 – 94

Manning P, Slade EM, Beynon SA, Lewis OT, (2017) Effect of dung beetle species richness and chemical perturbation on multiple ecosystem functions. Ecological Entomology 42:577 – 586

Malhi Y, Doughty CE, Galetti M, Smith FA, Svenning JC, Terborgh JW (2016) Megafauna and ecosystem function from the Pleistocene to the Anthropocene. PNAS 113:838 – 846

Milotić T, Quide S, Van Loo T, Hoffman Maurice (2016) Linking functional group richness and ecosystems functions of dung beetles: an experimental quantification. Oecologica 183:177 – 190

Milotić T, Hoffmann M (2016) Reduced germination success of temperate grassland seeds sown in dung: consequences for post-dispersal seed fate. Plant Biology 18:1038 – 1047

Milotić T, Quidé S, Van Loo T, Hoffmann M (2017). Linking functional group richness and ecosystem functions of dung beetles – An experimental quantification. Oecologia 183:177 – 190

Milotić T, Baltzinger C, Eichberg C, Eycott AE, Heurich M, Müller J, Bargmann T (2018) Functionally complete communities result in better ecosystem functioning: Dung removal and secondary seed dispersal by dung beetles in the Western Palaearctic. Journal of Biogeography 46:70 – 82

Milotić T, Baltzinger C, Eichberg C, Eycott AE, Heurich M, Müller J, Noriega J A, Menendez R, Stadler J, Ádám R, Bargmann T, Bilger I, Buse J, Calatayud J, Ciubuc C, Boros G, Jay-Robert P, Kruus M, Merivee E, Miessen G, Must A, Ardali E, Preda E, Rahimi I, Rohwedder D, Rose R, Slade EM, Somay L, Tahmasebi P, Ziani S, Hoffmann M, (2019) Functionally richer communities improve ecosystem functioning: Dung removal and secondary seed dispersal by dung beetles in the Western Palaearctic. Journal of Biogeography 46:70 – 82

Menéndez R, Webb P, Orwin KH (2016) Complementarity of dung beetle species with different functional behaviours influence dung–soil carbon cycling. Soil Biology and Biochemistry 92: 142 – 148

Nathan R, Schurr FM, Spiegel O, Steinitz O, Trakhtenbrot A, Tsoar A (2008) Mechanisms of long–distance seed dispersal. TREE 23:638 – 47

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: e107699

Newmark WD (2008) Isolation of African protected areas. Frontiers in Ecology and the Environment 6:321 – 8

Nguyen-Phung T (1987) Révision des Copris afro-tropicaux V. Une nouvelle espèce du <groupe fidius Olivier>. [Col. Scarabaeidae]. Bulletin de la Société Entomologique de France 91: 271 – 273

Nguyen-Phung T (1988a). Révision des espèces Afrotropicales du genre Copris. IV. Le groupe fidius Müller, 1764 [Coleoptera, scarabaeidae]. Revue française d'Entomologie, Paris (N.S.) 10: 5 – 15

Nguyen-Phung T (1988b) Révision des espèces afro-tropicales du genre Copris Müller, 1764 VI. Le groupe bootes Klug (Coleoptera, Scarabaeidae). Nouvelle Revue d'Entomologie (N.S.) 5: 247 – 258

Nguyen-Phung T (1988c) Révision des espèces afrotropicales du genre Copris Müller, 1764, VII. Le groupe corniger Sahlberg. [Col. Scarabaeidae]. Bulletin de la Société Entomologique de France 92: 209 – 219

Nguyen-Phung T (1989). Révision des espèces afrotropicales du genre Copris Müller, 1764 (Coleoptera: Scarabaeidae). VIII. Le groupe orion Klug. Annales de la Société Entomologique de France (N.S.) 25: 199 – 208

Nguyen-Phung T, Cambefort Y (1986a). Révision des espèces afro-tropicales du genre Copris Müller, 1764. I. Le groupe integer Reiche (Coleoptera, Scarabaeidae). Nouvelle Revue d'Entomologie (N.S.) 3: 401 – 416

Nguyen-Phung T, Cambefort Y (1986b) Révision des espèces afro-tropicales du genre Copris Müller, 1764. III. Le groupe inhalatus Quedenfeldt [Coleoptera, Scarabaeidae]. Revue française d'Entomologie, Paris (N.S.) 8: 100 – 106

Nguyen-Phung T, Cambefort Y 1(987) Révision des espèces afro-tropicales du genre Copris Müller, 1764. II. Le groupe jacchus (Fabricius) (Coleoptera Scarabaeidae s. str.). Annales de la Société Entomologique de France (N.S.) 23: 67 – 75

Nicholas E, Spector S, Louzada J, Larsen T, Amezquita S, Favila ME, The Scarabaeinae Research Network (2008) Ecological Functions and ecosystem services provided by Scarabaeinae dung beetles. Biological Conservation 141: 1461 – 1474

Nichols E, Gardner TA, Peres CA, Spector S, The Scarabaeinae Research Network (2009) Co-declining mammals and dung beetles: an impending ecological cascade. Oikos 118:481 – 487

Nichols E, Gardner TA (2011) Dung beetles as a candidate study taxon in applied biodiversity conservation research. In: Simmons, L.W., Ridsdill-Smith, J. (Eds.), Dung Beetle Ecology and Evolution. Wiley-Blackwell, Chichester UK, pp 267 – 291

Nichols E, Uriarte M, Bunker DE, Favila ME, Slade EM, Vulinec K, Larsen T, Vaz de Mello FZ, Louzada J, Naeem S, Spector S (2013) Trait-dependent response of dung beetle populations to tropical forest conversion at local and regional scales. Ecology 93:180 – 189

Noriega JA, Hortal J, Azcárate FM, Berg MP, Bonada N, Briones M JI, Del Toro I, Goulson D, Ibanez S, Landis DA, Moretti M, Potts SG, Slade EM, Stout J C, Ulyshen MD, Wackers FL, Woodcock BASantos AMC (2018) Research trends in ecosystem services provided by insects. Basic Applied Ecology 26: 8 – 23

Numa C, Verdú JR, Rueda C, Galante E (2012) Comparing dung beetle species assemblages between protected areas and adjacent pasturelands in a Mediterranean savanna landscape. Rangeland Ecology and Management 65:137 –1 43

Orbigny H d' (1913) Synopsis des Onthophagides d'Afrique. Annales de la Société Entomologique de France 82: 1 – 742

Ortega-Martínez IJ, Moreno CE, Escobar F (2016) A dirty job: manure removal by dung beetles in both a cattle ranch and laboratory setting. Entomologica Experimentalis et Applicata 161:70 – 78

Penttilä A, Slade EM, Simojoki A, Riutta T, Minkkinen K, Roslin T, (2013) Quantifying beetle-mediated effects on gas fluxes from dung pats. PLoS One 8: e71454

Piccini I, Arnieri F, Caprio E, Nervo B, Pelissetti S, Palestrini C, Roslin T, Rolando A. (2017) Greenhouse gas emissions from dung pats vary with dung beetle species and with assemblage composition. PLoS ONE 12: e0178077

Piccini I, Nervo B, Forshage M, Celi L, Palestrini C, Rolando A, Roslin T, (2018) Dung beetles as drivers of ecosystem multifunctionality: are response and effect traits interwoven? Science of the Total Environment 616:1440 – 1448

Piccini I, Caprio E, Palestrini C, Rolando A (2019) Ecosystem functioning in relation to species identity, density, and biomass in two tunneller dung beetles. Ecological Entomology 1 -10

Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team. (2019). nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-131.https://CRAN.R-project.org/package=nlme 3rd July 2019

Pryke JS, Roets F, Samways MJ (2016) Wild herbivore grazing enhances insect diversity over livestock grazing in an African grassland system. PLoS One 11:1 – 15

Quental TB, Marshall CR (2013) How the Red Queen drives terrestrial mammals to extinction. Science 341:290 – 292

R Core Team (2019) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/

Raine EH, Mikich SB, Lewis OT, Riordan P, Vaz-de– Mello FZ, Slade EM (2018a) Extinctions of interactions: quantifying a dung beetle–mammal network. Ecosphere 9: e02491

Raine EH, Mikich SB, Lewis OT, Slade EM (2018b) Interspecific and intraspecific variation in diet preference in five Atlantic forest dung beetle species. Ecological Entomology 44:436 – 439

Raine EH, Slade EM, (2019) Dung beetle–mammal associations: methods, research trends and future directions. Proceedings of the Royal Society B: Biological Sciences 286:20182002

Roslin T, Viljanen H (2011) Dung beetle populations: structure and consequences. – In: Simmons, LW and Ridsdill– Smith TJ (ed) Ecology and evolution of dung beetles. Blackwell Publishing, pp 220 – 244

Salomão RP, Iannuzzi L. (2015) Dung beetle (Coleoptera, Scarabaeidae) assemblage of a highly fragmented landscape of Atlantic forest: from small to the largest fragments of north-eastern Brazilian region. Revista Brasileira de Entomologica 59:126 – 131

Samways MJ, Kreuzinger K (2001) Vegetation, ungulate and grasshopper interactions inside vs outside an African savanna game park. Biodiversity Conservation 10:1963 – 1981

Sands B, Wall R (2017) Dung beetles reduce livestock gastrointestinal parasite availability on pasture. Journal of Applied Ecology. 54:1180 – 1189

Scholtz CH, Davis ALV, Kryger U (2009). Evolutionary Biology and Conservation of Dung Beetles. Pensoft Publishers. Sofia, Bulgaria

Schwab DB, Casasa S, Moczek AP (2017) Evidence of developmental niche construction in dung beetles: effects on growth, scaling and reproductive success. Ecology Letters 20:1353–1363

Sensenig RL, Demment MW Laca, EA (2010) Allometric scaling predicts preferences for burned patches in a guild of East African grazers. Ecology 91:2898 – 2907

Shepherd VE, Chapman CA, (1998) Dung beetles as secondary seed dispersers: impact on seed predation and germination. Journal of Tropical Ecology 14:199 – 215

Skelly DK (2002) Experimental venue and estimation of interaction strength. Ecology 83: 2097-2101

Silva PGd, Hernández MIM (2015a) Scale dependence of processes structuring dung beetle metacommunities using functional diversity and community deconstruction approaches. PLoS ONE 10: e0123030

Silva PGd, Hernández MIM (2015b) 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: e0126112

Siqueira T, Bini LM, Roque FO, Marques Couceiro SR, Trivinho-Strixino S, Cottenie K (2012) Common and rare species respond to similar niche processes in macroinvertebrate metacommunities. Ecography35: 183 – 192

Sitters J, Maechler MJ, Edwards PJ, Suter W, Olde Venterink H (2014) Interactions between C: N: P stoichiometry and soil macrofauna control dung decomposition of savanna herbivores. Functional Ecology 28:776 – 786

Skaug H, Fournier D, Nielsen A, Magnusson A, Bolker B (2011) glmm ADMB: Generalized linear mixed models using AD model builder. R package version 0.6.6/r148

Slade E, Mann D, Villanueva J, Lewis O (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 76:1094-1104

Slade EM, Riutta T, Roslin T, Tuomisto HL (2016). The role of dung beetles in reducing greenhouse gas emissions from cattle farming. Scientific Report 6:18140

Snyder WE, Snyder GB, Finke DL, Straub CS (2006) Predator biodiversity strengthens herbivore suppression. Ecology Letters 9: 789 – 796

Sole CL, Scholtz CH. (2010) Did dung beetles arise in Africa? A phylogenetic hypothesis based on five gene regions. Molecular Phylogenetics & Evolution 56: 631 – 641

Steinfeld H, Gerber P, Wassenaar T, Castel V, Rosales M, de Haan C (2006) Livestock's long shadow: environmental issues and options, Food and Agriculture Organization of the United Nations, Rome pp 414

Sugiura S, Tanaka R, Taki H, Kanzaki N (2013) Differential responses of scavenging arthropods and vertebrates to forest loss maintain ecosystem function in a heterogeneous landscape. Biological Conservation 159:206 – 213

Tilman D, Reich, PB, Isbell F (2012) Biodiversity impacts ecosystem productivity as much as resources, disturbance, or herbivory. Proceedings of the National Academy of Sciences of the United States of America, 109: 10394 – 10397

Tixier T, Bloor JM, Lumaret JP (2015) Species-specific effects of dung beetle abundance on dung removal and leaf litter decomposition. Acta Oecologica 69:31 – 34

Tonelli M, Verdú JR, Zunino ME (2018) Effects of the progressive abandonment of grazing on dung beetle biodiversity: body size matters. Biodiversity Conservation 27:189 – 204

Tscharntke T, Clough Y, Bhagwat SA, Buchori D, Faust H, Hertel D, Hölscher D, Juhrbandt J, Kessler M, Perfecto I, Scherber C, Schroth G, Veldkamp E, Wanger T (2011) Multifunctional shade-tree management in tropical agroforestry landscapes – A review. Journal of Applied Ecology 48:619 – 629

Tuck SL, Winqvist C, Mota F, Ahnström J, Turnbull LA, Bengtsson J (2014) Land-use intensity and the effects of organic farming on biodiversity: a hierarchical meta-analysis. Journal of Applied Ecology 51:746 – 755

Urrea-Galeano LA, Andresen E, Coates Rosamond, Mora Ardila F, Díaz Rojas A, Ramos-Fernández G (2019) Horizontal seed dispersal by dung beetles reduced seed and seedling clumping but did not increase short-term seedling establishment. PLoS ONE 14: e0224366

Valiente-Banuet A, Aizen MA, Alcántara JM, Arroyo J, Cocucci A, Galett, M, García MB, García D, Gómez JM, Jordano P, Medel R, Navarro L, Obeso J R, Oviedo R, Ramírez N, Rey P J, Traveset A, Verdú M, Zamora R (2015) Beyond species loss: the extinction of ecological interactions in a changing world. Functional Ecology 29:1 – 8

van Schalkwyk DL, McMillin W, Witthuhn RC, Hoffman LC (2010) The Contribution of Wildlife to Sustainable Natural Resource Utilization in Namibia: A Review. Sustainability 2:3479 – 3499

Verdu JR, Cortez V, Ortiz AJ, Gonzalez-Rodriguez E, Martinez-Pinna J, Lumaret JP, Lobo JM, Numa C, Sanchez-Pinero F (2015) Low doses of ivermectin cause sensory and locomotor disorders in dung beetles. Scientific Report 5:13912

Verdú JR, Lobo MJ, Sánchez-Piñero F, Gallego B, Numa C, Lumaret JP, Cortez V, Ortiz A, Tonelli M, García-Teba Rey A, Rodriguez A, Durán J (2017) Ivermectin residues disrupt dung beetle diversity, soil properties and ecosystem functioning: an interdisciplinary field study. Science of the Total Environment 618:219 – 228

Verdú JR, Moreno CE, 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 Conservation140:308 – 317

Whipple SD, Hoback WW (2012) A comparison of dung beetle (Coleoptera: Scarabaeidae) attraction to native and exotic mammal dung. Environmental Entomology 41:238 – 244

Williams-Guillén K, Perfecto I (2010) Effects of agricultural intensification on the assemblage of leaf-nosed bats (Phyllostomidae) in a coffee landscape in Chiapas, Mexico. Biotropica 42:605 – 613

Young TP, Palmer TM, Gadd ME (2005) Competition and compensation among cattle, zebras, and elephants in a semi-arid savanna in Laikipia, Kenya. Biological Conservation 122:351–359

Young TP, Porensky LM, Riginos C, Veblen KE, Odadi WO, Kimuyu DM, Charles GK, S. Young H (2018) Relationships between Cattle and Biodiversity in Multiuse Landscape Revealed by Kenya Long-Term Exclosure Experiment. Rangeland Ecology and Management 71:281 – 291

Zhang W, Ricketts TH, Kremen C, Carney K, Swinton SM (2007) Ecosystem services and disservices to agriculture. Ecological Economics 64:253 – 260

Zídek J, Pokorný S (2008) Illustrated keys to Palearctic Scarabaeus Linné (Scarabaeidae). Animma.X 27: 1 – 27

Zur Strassen, R (1967) Arten-iibersicht der Gattung Scarabaeus Linnaeus (Scarabaeidae) mit besonderer Berucksichtigung der athiopischen Formen. Entomologisches Blätter 63:129 – 173

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed Effects Models and Extensions in Ecology with R. Springer, New York, USA

Chapter 4
Conclusions and recommendations

4.1 General discussion

Dung beetles are dependent on vertebrate waste for feeding and breeding and thus represent one of the most important expressions of detritivore food webs (Davis et al. 2002; Scholtz et al. 2009; Nichols and Gardner et al. 2011). This has made them indispensable features in many ecosystems across the globe and is the reason why they have been the subject of numerous research endeavours detailing their response to anthropogenic changes and the associated functional consequences (Nichols et al. 2008; Scholtz et al. 2009; Chapter 3). Dung beetle research had a shift in focus in the last years with more emphasis placed on their role in ecosystems and their functioning efficiency as well as their relationship with their mammal cohorts. Much of the research on dung beetle functioning, particularly dung removal and seed dispersal, has been focused in the tropical regions of the world with little research in Africa, particularly in the faunal rich savannahs (Noriega et al. 2018; Raine and Slade 2019). Savannahs of Africa are well suited for studies of ecosystem functioning because they are highly productive systems with higher mammal and dung beetle diversity compared to other regions in the world (Hanski and Cambefort 1991, du Toit and Cumming 1999; Davis et al. 2008; Scholtz et al. 2009; Davis et al. 2019 (unpublished)).

The overall aim of this study was to generate knowledge about dung beetle species richness, abundance and biomass, the effect on individual development and the effect on ecosystem function in light of the ongoing loss of native vertebrates in two of African savannahs' most important and productive landscapes: livestock rangelands (farms) and protected areas (PAs). These questions were all addressed against the premise of a long evolutionary history that dung beetles share with native vertebrate fauna, a complex interaction that has been grossly overlooked in many dung beetle surveys (Valiente-Banuet et al. 2015; Raine et al. 2018; Bogoni et al. 2019; Raine and Slade 2019). The loss of these large-bodied vertebrates has undoubtedly had deleterious effects on dung beetles (Nichols et al. 2009), their function and the structural complexity and productivity of landscapes (Barnes and de Jager, 1996; de Klerk 2004; Tscharntke et al. 2005). This remained to be tested in the savannah ecosystems of Africa and specifically in Namibia.

4.1.1 A taxonomic wellspring of dung beetles

A surprising but valuable result from this study was the remarkable diversity and abundance of dung beetles sampled, more so than expected for a semi-arid region. A total of 101 species and 76 309 individuals were collected in this study which is much higher than other studies in similar regions

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e.g. Tshikae et al (2008) where 69 075 specimens were collected comprising 67 species in Botswana. Compared with regions out of Africa, this is even more impressive considering Tonelli et al. (2018) collected 136,884 individuals comprising 56 species from their study in Italy and another extensive study across the western Palaearctic realm by Milotić et al. (2019) sampled 94 species. The beetles sampled in this study represented ca. 21% of the total African dung beetle genera and eight of the nine tribes (Davis et al. 2008). PAs harboured a host of important taxonomic relicts (e.g *Onitis bilobatus* (Ferreira) a species previously known only from a holotype collected 43 years ago), species whose distributions were not well known from this region (*Onitis deceptor* (Peringuey) and *Sarophorus cf. angolensis* (Klug)) and others that were recorded well beyond their previously reported biogeographic ranges (*Epirinus flagellatus* (Fabricius)) (Koch et al. 2002; Deschodt et al. 2019; Davis et al. 2019 (unpublished)). In addition, many species could not be confidently placed within existing species and may represent yet undescribed taxa such as *Caccobius* sp1, *Cleptocaccobius* sp1, *Onthophagus* sp2, *Onthophagus venustulus* (close to 2) and *Pedaria* sp1.

Documenting the dung beetles in this previously unexplored region is very important for bridging taxonomic gaps for species that have inadequate distribution data and whose assessment rationale is incomplete (Koch 2000). This is potentially momentous in uncovering the spatial distribution of southern African dung beetles and selecting the habitat ranges for taxonomically distinct and vulnerable species. Even more crucial is their role in conservation management and the delineation of conservation areas (Barnard et al. 1998; Koch et al. 2000; Socolar et al. 2016). Namibia's PAs are heavily biased towards the Namib biome due to its incapacity for agricultural production and are less reflective of values attached to conservation. The more productive landscapes like woodlands and the savannah biomes (where all the dung beetles were sampled) are terribly under-represented (Barnard et al. 1998). Furthermore, conservation prioritization in this region continues to be skewed towards charismatic vertebrate species (Hunter and Hutchinson 1994), however, the loss of the native fauna and their confinement to protected areas has further reduced dung beetle populations (Koch et al. 2002). Species of great taxonomic importance that are members of the key trophic network could increase their prospects for conservation in this region (Koch et al. 2002).

4.1.2 Land-use change and megafauna losses have severe consequences for dung beetle diversity and development

In Chapter 2, I explored some of the ways in which land-use, and the faunal divide it has created, impacted dung beetle diversity and individual development. These objectives were investigated through standardized pitfall trapping as well as dung transects that acted as proxies for vertebrate richness and stocking densities. I investigated how the megadiverse dung beetle assemblages of the region responded to land-use type (PA and farmland), bait type, vertebrate richness and stocking

densities in terms of richness, abundance and biomass measures. Species diversity was severely negatively affected by land-use change particularly with losses of the larger species (Larsen et al. 2005). This was consistent with dung beetle literature in many other parts of the world and is particularly concerning because larger species are often the most functionally efficient (Larsen et al. 2005; Slade et al. 2007; Nichols et al. 2009; Keynon et al. 2016; Dangles et al. 2017). This loss was attributed to the changing mammal composition on farmlands which not only has consequences for the resources dung beetles consume but also habitat quality (Finn 2001; Nichols et al. 2009; Bogoni et al. 2018). Livestock behaviour is known to have destructive effects on pasture quality with regards to vegetation physiognomy and soil bioturbation, both of which are fundamental to dung beetles (Edwards 1991; Vohland et al. 2005; Frank et al. 2018). Dung beetles, in turn, have hugely important roles in vegetation physiognomy and soil bioturbation (Tonelli et al. 2018; Dabrwoski et al. 2019) and land-use change, therefore, may result in a negative feedback loop that can result in eventual ecosystem collapse (Nichols and Gardner 2011; Milotić et al. 2019; Tonelli et al. 2019).

In addition to changes in dung beetle diversity measures associated with anthropogenic land-use change, I also uncovered a more subtle, yet noteworthy change in dung beetles. I found strong evidence that, even for dung beetles that are able to adapt to these anthropogenic changes, land-use change may negatively impact their normal development. I often found a difference in the sizes of beetles between the PAs and the agricultural sites, with smaller beetles recorded in farms. This I attributed to a decreased quality in their diet on the farmlands (Shepherd and Chapman 1998; Nichols et al. 2008; Milotic et al. 2019). This result echoed other dung quality surveys that documented the injurious effects that veterinary pharmaceuticals and low levels of nitrogen can have on dung beetle behaviour (Verdu et al. 2015) and physiology (Dormont et al. 2010; Frank et al. 2017; Villada-Bedoya et al. 2019). This trend is particularly concerning because dung beetle functional ability is strongly related to their size (Slade et al. 2007; Dangles et al. 2017) and large species are already excised from agricultural areas, further diminishing the functional capacity of dung beetle communities on farmlands (Manning et al. 2016; Noriega et al. 2018). How these morphological and physiological changes translate to dung beetle fecundity and ecosystem functions remains to be determined in these ecosystems.

The boundary between protected areas and farmlands was essentially created for large mammals however this does not extend to the more cryptic fauna, dung beetles in this case (Samways and Kreuzinger 2001), and introduced ungulates (cattle) evidently do not act as surrogates of native fauna making them unable to maintain dung beetle diversity (Barlow et al. 2007, 2010; Kuhn 2010; Bogoni et al. 2016). The conservation of megaherbivores is thus imperative because they create fundamental niches which preserve their diversity and integrity of dung beetles (Frank et al. 2018; Raine and Slade

2019). To increase the diversity (and probably also the functionality) of dung beetles in farmlands, it may be valuable to consider mixed farming practices that may be able to slowly increase the diversity of dung beetles with the increase of dung resources (Nichols et al. 2009; Young et al. 2018; Bogoni et al. 2018; Raine et al. 2018). The increase in vertebrate diversity will have positive effects on the landscape structure (Bond 2008; Young et al. 2013) created niches better suited to dung beetles that would increase their diversity and abundances (Scholtz et al. 2009).

4.1.3 Changes in land-use and faunal assemblages impair dung beetle functional efficiency

In Chapter 3 I explored the consequences of land-use change and the loss of native fauna by comparing dung beetle function between a livestock farm and a protected area. Manipulative experiments were adapted from other dung removal and seed dispersal studies in which I was able to quantify the particular individuals involved in dung removal and seed relocation (Andresen 2002; Slade et al. 2007; Slade et al. 2011; Manning et al. 2016; Noriega et al. 2012; Milotic et al. 2018, 2019). I demonstrated that there may be merit in collecting the specific individuals involved, rather than merely estimating their involvement based on traps set in proximity, as functional guilds may compete when at a resource. This study also contributes to the growing body of literature of dung beetle ecosystem functioning to now include African savannahs (Noriega et al 2018; Raine et al. 2019).

Dung beetle communities were highly altered as a result of changing faunal assemblages and this affected dung beetle functional efficiency with lower dung removal and secondary seed dispersal by dung beetles on farmlands compared to PAs. These changes were all ascribed to habitat transformation and the associated loss of megafauna and cascading effects accompanying their declines such as altered habitat quality (Frank et al. 2018) and resource quality (Finn 2001; Nichols et al. 2009; Bogoni et al. 2018). Notably, dung beetle species richness and biomass were the most important biodiversity measures for the dung removal and seed relocation, however, these were correlated to each other as well as species abundance. This was similar to a study by Larsen et al. (2005) who demonstrated a relationship between species richness and ecosystem functioning (e.g. plant regeneration and nutrient cycling) in South America.

The local extinction of larger tunnelling and rolling species seems to be closely linked to diminished ecosystem functions (Yoshihara and Sato 2015; Dangles et al. 2017). This implies that functional trait diversity, rather than just taxonomically based biodiversity measures, are more important for increasing ecosystem function (Cadotte et al. 2011) and that a functionally complete dung beetle guild is necessary for maximum ecosystem function and ecological services provided (Manning et al. 2016; Milotić et al. 2018). An important next step is to enumerate functional diversity measures based on combinations of morphological and behavioural traits and their influence on ecosystem function in

this region (Larsen et al. 2008; Audino et al. 2014; Bui et al. 2019; Correa et al. 2019). Valiente-Banuet et al. (2015) investigated the extinction of biotic interactions and emphasized the importance of these interactions as a key biodiversity component important in maintaining ecological integrity. The shift in dung beetle communities also altered interactions between the different dung beetle guilds with more competitive interactions observed in the PA and more neutral interactions on the farmlands (Valiente-Banuet et al. 2015; Raine et al. 2018). The preservation of these interactions may lead to greater ecosystem functioning and should, therefore, be encouraged in these systems.

The conservation of dung beetle communities in these cattle-raising areas is key for ecological and economic sustainability as they may potentially affect agricultural output (Bateman et al. 2010; Burkhard, Petrosillo and Costanza 2010; Balmford et al. 2011; Beynon et al. 2015; Toth et al 2016; Gómez – Cifuentes et al 2018). This is especially disquieting in a country reliant on this sector, where the agricultural practice is already challenging due to the hyper-arid climate (Barnard et al. 1998; de Klerk 2004; O'Connor et al. 2014; Kaereho and Tjizu 2019). The final conclusions were that the preservation of a functionally complete dung beetle assemblages is imperative and strongly relies on intact habitats and diverse faunal assemblages (Gómez Cifuentes et al. 2018; Raine et al. 2018; Bogoni et al. 2019). These changes will undoubtedly have major short– and long-term consequences for the maintenance of important ecosystem processes in these delicate systems (Larsen et al. 2008; Nichols et al. 2009; Slade et al. 2011; Nervo et al. 2017). Mixed farming that would incorporate wildlife into cattle dominated landscapes should be considered as it could potentially increase dung beetle diversity and has many other benefits for the environment (Lambrecht 1983; Ntiamoa-Baidu 1997; Bogoni et al. 2018; Raine and Slade 2019).

4.2 Study limitations and avenues for future work

Due to time constraints, the inclusion of other biotic and abiotic factors were not explored. This includes vegetation structure and soil type which are key local environmental factors that determine dung beetle occurrence (Davis et al. 2008, 2016; Nichols and Gardner 2011). These two factors are especially important because they can be highly modified in agricultural landscapes (Samways and Kreuzinger 2001; de Klerk 2004; Vohland et al. 2005; Bond 2008) and may have further elucidated the patterns of diversity that were observed especially because they determine the microclimate (Silva et al. 2016; Gómez-Cifuentes et al. 2017). These factors were, however, kept as consistent as possible given limitations in site availability and safety when working in the PAs that contain numerous large predators such as lions (*Panthera leo*) and leopards (*Panthera pardus*).

Clarifying the relationship between large herbivore diversity and dung beetles in savannah was the first step toward more comprehensively understanding the consequences of anthropogenic change on

ecosystem function and this relationship should further be explored. In fact, many recent studies have called for the incorporation of mammals into dung beetle studies as this relationship maintained over millennia is quickly eroding (Bogoni et al 2019; Raine and Slade 2019). Incorporating mammals into dung beetle studies is the first step and future efforts that could be considered are 1) exploring dietary switching and plasticity with the use of other dung resources (Culot et al. 2013; Halffter and Halffter 2009) 2) identifying important functional traits such as olfaction, flight capacity and digestion (Verdu et al. 2008; Frank et al. 2018; Holter and Scholtz et al. 2013) 3) exploring the evolutionary context to better understand how species could adapt in light of anthropic disturbance (Raine et al. 2018) 4) further investigating biotic interactions and how they are being affected by possible changes in dung beetle morphology (e.g. cephalic horns used in male-male competition) (Baena-Díaz et al. 2018) and 5) using molecular methods to unravel direct interactions between dung beetles and mammals (Calvignac– Spencer et al. 2013).

While this study focused on farmlands, the results cannot be extrapolated to other forms of land-use change. Mining, for example, presents a major threat to dung beetle diversity largely because unlike farms that still support an ungulate population that provides resources for dung beetles, mines do not (Sheoran et al. 2010; Dabrowski et al. 2019). Mining is one of the largest economic sectors in Namibia (Barnard et al 1998; de Klerk 2004; Thuiller et al. 2006) and presents many more quandaries for overall biodiversity including soil erosion, water, air pollution and loss of grazing areas for animals with the potential of geoenvironmental disasters (Sheoran et al. 2010). Badenhorst et al. (2018) and Dabrowski et al. (2019) conducted studies in South Africa focussing on their potential to improve herbaceous plant growth in reclaimed mined land and how dung beetle tunnelling activity could increase land-use potential. Dung beetles, therefore, have the proclivity to maintain landscapes other than agricultural and faunal rich sites and their role in these systems should be further explored. The present study forms a firm baseline for other studies aiming to understand the effect of changes in all Namibian ecosystems on interactions between plants, vertebrates and insects (Raine and Slade 2019).

4.3 References

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

Audino LD, 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

Badenhorst J, Dabrowski J, Scholtz CH, Truter WF (2018) Dung beetle activity improves herbaceous plant growth and soil properties on confinements simulating reclaimed mined land, South Africa. Applied Soil Ecology 132:53 – 59

Bang HS, Lee JH, Kwon OS, Na YE, Jang YS, Kim WH (2005) Effects of paracoprid dung beetles (Coleoptera: Scarabaeidae) on the growth of pasture herbage and on the underlying soil. Applied Soil Ecology 29: 165 – 171

Baena-Díaz F, Martínez-M I, Gil-Pérez Y, González-Tokman D (2018) Trans-generational effects of ivermectin exposure in dung beetles. Chemosphere 202:637 – 643

Barlow J, Gardner TA, Araujo IS, Ávila-Pires TC, Bonaldo AB, Costa JE, Esposito MC, Ferreira LV, Hawes J, Hernandez MIM, Hoogmoed MS, Leite RN, Lo-Man-Hung NF, Malcolm JR, Martins MB, Mestre LAM, Miranda-Santos R, Nunes-Gutjahr AL, Overal WL, Parry L, Peters SL, Ribeiro-Junior, MA, da Silva MNF, da Silva Motta, C, Peres CA (2007) Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. Proceedings of the National Academy of Sciences of the United States of America 104:18555 – 18560

Barnard P (1998) Biological diversity in Namibia: a clash of sea and land, fog and dust. Biodiversity and Conservation 7:415 – 417

Barnard P, Brown CJ, Jarvis AM, Robertson A (1998) Extending the Namibian protected area network to safeguard hotspots of endemism and diversity. Biodiversity and Conservation 7:531 – 547

Barnes JI, de Jager JLV (1996) Economic and financial incentives for wildlife use on private land in Namibia and the implications for policy. South African Journal of Wildlife Research 26:37 – 46

Beynon SA, Wainwright WA, Christie M (2015) The application of an ecosystem services framework to estimate the economic value of dung beetles to the UK cattle industry. Ecological Entomology 40:124 – 135

Bogoni JA, Hernández MIM (2014) Attractiveness of native mammal's faeces of different trophic guilds to dung beetles (Coleoptera: Scarabaeinae). Journal of Insect Science 14:1 – 7

Bogoni JA, Graipel ME, de Castilho PV, Fantacini FM, Kuhnen VV, Luiz MR, Maccarini TB, Marcon CB, de Souza Pimentel Teixeira C, Tortato MA, Vaz-de-Mello FZ, Hernández MIM (2016) Contributions of the mammal community, habitat structure, and spatial distance to dung beetle community structure. Biodiversity Conservation 251: 661 – 1675

Bogoni JA, Pires JSR, Graipel ME, Peroni N, Peres CA (2018) Wish you were here: How defaunated is the Atlantic Forest biome of its medium– to large-bodied mammal fauna? PLoS ONE 13: e0204515

Bogoni JA, da Silva PG, Peres CA (2019) Co-declining mammal–dung beetle faunas throughout the Atlantic Forest biome of South America. Ecography 42:1 – 16

Bond WJ (2008) What Limits Trees in C4 Grasslands and Savannas? Annual Review of Ecology, Evolution, and Systematics 39:641–59

Bui VB, Zieglerc T, Bonkowskia M (2019) Morphological traits reflect dung beetle response to land-use changes in tropical karst ecosystems of Vietnam. Ecological Indicators 108:105697

Burkhard B, Petrosillo I, Costanza R (2010) Ecosystem services – bridging ecology, economy and social sciences. Ecological Complexity 7:257 – 259

Cadotte MW, Carscadden K, Mirotchnick N (2011) Beyond species: functional diversity and the maintenance of ecological processes and services. Journal of Applied Ecology 48:1079 – 1087

Calvignac-Spencer S, Leendertz FH, Gilbert MTP, Schubert G. (2013) An invertebrate stomach's view on vertebrate ecology: certain invertebrates could be used as 'vertebrate samplers' and deliver DNA– based information on many aspects of vertebrate ecology. Bioessays 35:1004 – 1013

Correa CMA, Braga RF, Puker A, Korasaki V (2019) Patterns of taxonomic and functional diversity of dung beetles in a human-modified variegated landscape in Brazilian Cerrado. Journal of Insect Conservation 23:89 – 99

Culot L, Bovy E, Vaz-de-Mello FZ, Guevarad R, Galetti M (2013) Selective defaunation affects dung beetle communities in continuous Atlantic rainforest. Biological Conservation 163:79 – 89

Dabrowski J, Venter G, Truter WF, Scholtz CH (2019) Dung beetles can tunnel into highly compacted soils from reclaimed mined sites in eMalahleni, South Africa. Applied Soil Ecology 134:116 – 119

Dangles O, Carpio C, Woodward G (2012) Size-dependent species removal impairs ecosystem functioning in a large-scale tropical field experiment. Ecology 93:2615 – 2625

Davis ALV (2002) Dung beetle diversity in South Africa: influential factors, conservation status, data inadequacies and survey design. African Entomology 10: 53 – 65

Davis ALV, Frolov AV, Scholtz CH (2008) The African Dung Beetle Genera. Protea Book House, Pretoria, South Africa

Davis ALV, Scholtz CH, Sole CL (2017) Biogeographical and co-evolutionary origins of scarabaeine dung beetles: Mesozoic vicariance versus Cenozoic dispersal and dinosaur versus mammal dung. Biological Journal of the Linnean Society 120: 258 – 273

Davis AVL, Deschodt CM, Scholtz CH (2019) Conservation Assessment of Scarabaeine DUNG BEETLES in South Africa, Botswana and Namibia: IUCN Red List Categories, Atlas and Ecological Notes (unpublished)

De Klerk JN (2004) Bush Encroachment in Namibia: Report on Phase 1 of the Bush Encroachment Research, Monitoring and Management Project. John Meinert Printing, Windhoek, Namibia

Deschodt CM, Davis AVL, Daniel GM, (2019) The endemic Southern African genus *Epirinus* Dejean, 1833 (Coleoptera: Scarabaeidae: Scarabaeinae) revisited: five new species and two new synonyms. Zootaxa 4603: 327 – 340

Dormont L, Jay-Robert P, Bessiere JM, Rapior S, Lumaret JP (2010) Innate olfactory preferences in dung beetles. Journal of Experimental Biology 213:3177 – 3186

Edwards PB (1991) Seasonal variation in the dung of African grazing mammals, and its consequences for coprophagous insects. Functional Ecology 5: 617 – 628

Ferreira MC (1976) A new species of *Platyonitis* Janssens from Angola. Navorsinge van die Nasionale Museum 3: 177 – 180

Frank K, Hulsmann M, Assmann T, Schmitt T, Bluthgen N (2017) Land-use affects dung beetle communities and their ecosystem service in forests and grasslands. Agriculture, Ecosystems and Environment 243:114 – 122

Frank K, Krell, FT, Slade EM, Raine EH, Chiew LY, Schmitt T, Vairappan CS, Walter P, Blüthgen N (2018) Global dung webs: high trophic generalism of dung beetles along the latitudinal diversity gradient. Ecology Letters 21:1229 – 1236

Finn JA (2001) Ephemeral resource patches as model systems for diversity– function experiments. Oikos 92:363 – 366

Gómez A, Kolokotronis S. (2017) Genetic identification of mammalian meal source in dung beetle gut contents. Mitochondrial DNA A 28:612 – 615

Gómez VC, Verdú JR, Alonso CBG, Zurita G A (2018) Relationship between land-uses and diversity of dung beetles (Coleoptera: Scarabaeinae) in the southern Atlantic forest of Argentina: which are the key factors? Biodiversity and Conservation 27:3201 – 3213

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

Hanski I, Cambefort Y (1991) Dung Beetle Ecology. Princeton University Press, Princeton, USA

Kenyon T, Mayfield M, Monteith G, Menéndez R (2016). The effects of land-use change on native dung beetle diversity and function in Australia's Wet Tropics. Austral Ecology 41:797–808

Koch SO, Chown SL, Davis ALV, Endrödy – Younga S, Van Jaarsveld AS (2000) Conservation strategies for poorly surveyed taxa: a dung beetle (Coleoptera, Scarabaeidae) case study from southern Africa. Journal of Insect Conservation 4: 45 – 56

Kuhn K (2010) Kartierung der dungbewohnenden Kaferarten im Beweidungsgebiet des NSG Stadtwald Augsburg. Berichte des Naturwissenschaftlichen Vereins fur Schwaben 114:102 – 115

Lambrecht FL (1983) Game Animals: A Substitute for Cattle? Rangelands Archives 5:22-24

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

Larsen TH, Williams NM, Kremen C (2005) Extinction order and altered community structure rapidly disrupt ecosystem functioning. Ecology Letters 8:538 – 547

LaScaleia MC, Reynolds C, Magagula CN, Roets F, McCleery RA (2018) Dung beetle richness decreases with increasing landscape structural heterogeneity in an African savanna-agricultural mosaic. Insect Conservation and Diversity 4: 396 – 406

Manning P, Slade EM, Beynon SA, Lewis OT, (2016) Functionally rich dung beetle assemblages are required to provide multiple ecosystem services. Agriculture, Ecosystems and Environment 218:87 – 94

Milotić T, Quidé S, Van Loo T, Hoffmann M (2017). Linking functional group richness and ecosystem functions of dung beetles – An experimental quantification. Oecologia 183:177 – 190

Milotić T, Baltzinger C, Eichberg C, Eycott AE, Heurich M, Müller J, Noriega J A, Menendez R, Stadler J, Ádám R, Bargmann T, Bilger I, Buse J, Calatayud J, Ciubuc C, Boros G, Jay-Robert P, Kruus M, Merivee E, Miessen G, Must A, Ardali E, Preda E, Rahimi I, Rohwedder D, Rose

R, Slade EM, Somay L, Tahmasebi P, Ziani S, Hoffmann M, (2019) Functionally richer communities improve ecosystem functioning: Dung removal and secondary seed dispersal by dung beetles in the Western Palaearctic. Journal of Biogeography 46:70 – 82

Nervo B, Caprio E, Celi L, Lonati M, Lombardi G, Falsone G, Iussig G, Palestrini C, Said-Pullicino D, Rolando A (2017) Ecological functions provided by dung beetles are interlinked across space and time: evidence from 15N isotope tracing. Ecology 98:433 – 446

Nicholas E, Spector S, Louzada J, Larsen T, Amezquita S, Favila ME (2008) Ecological Functions and ecosystem services provided by Scarabaeinae dung beetles. Biological Conservation 141:1461 – 1474

Nichols E, Gardner TA, Peres CA, Spector S (2009) Co-declining mammals and dung beetles: an impending ecological cascade. Oikos 118:481 – 487

Nichols E, Gardner TA, 2011. Dung beetles as a candidate study taxon in applied biodiversity conservation research. In: Simmons LW, Ridsdill-Smith J (ed) Dung Beetle Ecology and Evolution. Wiley-Blackwell, Chichester UK, pp 267 – 291

Noriega JA, Hortal J, Azcárate FM, Berg MP, Bonada N, Briones M JI, Del Toro I, Goulson D, Ibanez S, Landis DA, Moretti M, Potts SG, Slade EM, Stout J C, Ulyshen MD, Wackers FL, Woodcock BASantos AMC (2018) Research trends in ecosystem services provided by insects. Basic Applied Ecology 26:8 – 23

Ntiamoa-Baidu Y (1997) Wildlife and food security in Africa (No. 33). Food & Agriculture Organization

O'Connor TG, Puttick JR, Hoffman MT (2014) Bush encroachment in southern Africa: changes and causes. African Journal of Range and Forage Science 31: 67 – 88

Raine EH, Mikich SB, Lewis OT, Riordan P, Vaz-de– Mello FZ, Slade EM (2018a) Extinctions of interactions: quantifying a dung beetle–mammal network. Ecosphere 9: e02491

Raine EH, Slade EM, (2019) Dung beetle–mammal associations: methods, research trends and future directions. Proceedings of the Royal Society B: Biological Sciences 286: 2018 – 2002

Samways MJ, Kreuzinger K (2001) Vegetation, ungulate and grasshopper interactions inside vs outside an African savanna game park. Biodiversity Conservation 10:1963 – 1981

Scholtz CH, Davis ALV, Kryger U (2009). Evolutionary Biology and Conservation of Dung Beetles. Pensoft Publishers. Sofia, Bulgaria

Shepherd VE, Chapman CA, (1998) Dung beetles as secondary seed dispersers: impact on seed predation and germination. Journal of Tropical Ecology 14:199 – 215

Sheoran V, Sheoran AS, Poonia P (2010) Soil reclamation of abandoned mine land by revegetation: a review. International Journal of Soil Sediment Water 3:1 – 20

Silva JA, Uchida R (2000) Plant Nutrient Management in Hawaii's Soils, Approaches for Tropical and Subtropical Agriculture. College of Tropical Agriculture and Human Resources. The University of Hawaii at Manoa

Silva RJ, Storck-Tonon D, Vaz-de-Mello FZ (2016) Dung beetle (Coleoptera: Scarabaeinae) persistence in Amazonian forest fragments and adjacent pastures: biogeographic implications for alpha and beta diversity. Journal of Insect Conservation 20: 549 – 564

Slade E, Mann D, Villanueva J, Lewis O (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 76:1094 – 1104

Slade EM, Mann DJ, Lewis OT (2011) Biodiversity and ecosystem function of tropical forest dung beetles under contrasting logging regimes. Biological Conservation 144:166 – 174

Socolar JB, Gilroy JJ, Kunin WE, Edwards DP (2016) How Should Beta-Diversity Inform Biodiversity Conservation? Trends in Ecology & Evolution 31: 67 – 80

Tonelli M, Verdú JR, Zunino ME (2018) Effects of the progressive abandonment of grazing on dung beetle biodiversity: body size matters. Biodiversity Conservation 27:189 – 204

Tóth E, Deák B, Valkó O, Kelemen A, Miglécz T, Tóthmérész B, Török P (2018) Livestock type is more crucial than grazing intensity: traditional cattle and sheep grazing in short-grass steppes. Land Degradation and Development 2:231 – 239

Tscharntke T, Klein AM, Kruess A, Steffan-Dewenter I, Thies C (2005) Landscape perspectives on agricultural intensifications and biodiversity-ecosystem service management. Ecology Letters 8: 857 – 874

Valiente-Banuet A, Aizen MA, Alcántara JM, Arroyo J, Cocucci A, Galett, M, García MB, García D, Gómez JM, Jordano P, Medel R, Navarro L, Obeso J R, Oviedo R, Ramírez N, Rey P J, Traveset A, Verdú M, Zamora R (2015) Beyond species loss: the extinction of ecological interactions in a changing world. Functional Ecology 29:1 – 8

Verdu JR, Cortez V, Ortiz AJ, Gonzalez-Rodriguez E, Martinez-Pinna J, Lumaret JP, Lobo JM, Numa C, Sanchez-Pinero F (2015) Low doses of ivermectin cause sensory and locomotor disorders in dung beetles. Scientific Report 5:13912

Verdú JR, Galante E (2001) Larval morphology and breeding behaviour of the genus *Pedaridium* Harold (Coleoptera: Scarabaeidae). Annals of the Entomological Society of America 94: 596 – 604

Verdú JR, Moreno CE, 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 140:308 – 317

Villada-Bedoya S, Córdoba-Aguilar A, Escobar F, Martínez-Morales I, González-Tokman D (2019) Dung beetle body condition: A tool for disturbance evaluation in contaminated pastures. Environmental Toxicology and Chemistry 00:1 – 13

Vohland K, Uhlig M, Marais E, Hoffman A, Zeller U (2005) Impact of different grazing systems on diversity, abundance and biomass of beetle (Coleoptera), a study from southern Namibia. Zoosystematics and Evolution 81:131 – 143

Yoshihara Y, Sato S (2015) The relationship between dung beetle species richness and ecosystem functioning. Applied Soil Ecology 88:21 – 25

Young HS, McCauley DJ, Castillo E, Goheen JR, Helgen KM, Palmer TM, Pringle RM, Young TP, Dirzo R (2013) Plant community response to changes in herbivore abundance and identity across abiotic gradients and experimental contexts. Journal of Ecology 101:1031 – 1041

Young TP, Porensky LM, Riginos C, Veblen KE, Odadi WO, Kimuyu DM, Charles GK, S. Young H (2018) Relationships between cattle and biodiversity in multiuse landscape revealed by Kenya long-term exclosure experiment. Rangeland Ecology and Management 71:281 – 291

Appendix

Appendix A

Appendix A Species table of all dung beetles, and their functional guild grouping, sampled from three PAs and three farms in Namibia. Their abundances are separated according to bait type (cow or wildebeest dung) and according to land-use (farm and reserve). Statistical values after species represent results of a Pearson chi-squared test or paired Welch t-test for differences in mean mass of individuals collected on farms and PAs (n=10 individuals per land-use category)

Species	Guild	PA	Farm	Cow	Wildebeest	W/X value	df	p-value
Allogymnopleurus splendidus (Bertolini 1849)	roller	295	233	140	388	0.569	17.823	0.576
Aphodiinae sp1	dweller	6676	3914	4820	5770	-0.019	14.022	0.985
Aphodiinae sp10	dweller	165	118	69	214	-2.271	16.713	0.036*
Aphodiinae sp11	dweller	6	3	2	7			
Aphodiinae sp12	dweller	36	9	13	32			
Aphodiinae sp13	dweller	0	6	6	0			
Aphodiinae sp14	dweller	4	0	1	3			
Aphodiinae sp15	dweller	0	1	1	0			
Aphodiinae sp16	dweller	0	1	1	0			
Aphodiinae sp2	dweller	3345	891	1655	2581	1.311	16.27	0.208
Aphodiinae sp3	dweller	295	89	77	307	40.5	18	0.496
Aphodiinae sp4	dweller	3015	2755	2574	3196	-0.807	17.978	0.43
Aphodiinae sp5	dweller	57	66	75	48	1.083	13.761	0.298
Aphodiinae sp6	dweller	506	228	220	514	0.321	17.858	0.752
Aphodiinae sp7	dweller	56	13	5	64	-1.553	16.976	0.139
Aphodiinae sp8	dweller	68	64	78	54	2.936	15.828	0.009**
Aphodiinae sp9	dweller	73	9	46	36			
Caccobius castaneus (Klug 1855)	dweller	332	71	146	257	-0.181	17.875	0.8588
Caccobius cf. histerinus (Fahraeus 1857)	dweller	2	0	0	2			

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Caccobius ferrugineus (Fahraeus 1857)	dweller	330	195	201	324	-4.071	13	0.001***
Caccobius sp1	dweller	745	208	476	477	0.555	16.741	0.586
Catharsius ulysses (Boheman 1857)	tunneller	25	3	16	12			
Catharsius cf. vitulus (Boheman 1857)	tunneller	17	1	8	10			
Chalconotus convexus (Boheman 1857)	roller	48	74	42	80	67.5	18	0.199
Cheironitis scabrosus (Fabricius 1776)	tunneller	7	0	4	3			
Cleptocaccobius sp1	dweller	2	0	0	2			
Cleptocaccobius sp2	dweller	1	0	0	1			
Copris elphenor (Klug 1855)	tunneller	16	9	7	18			
Copris gracilis (Waterhouse 1891)	tunneller	177	173	99	251	0.17	17.286	0.867
Copris laioides (Boucomont 1932)	tunneller	48	13	13	48	1.575	14.548	0.137
Copris subsidens (Péringuey 1901)	tunneller	23	0	9	14			
Digitonthophagus namaquensis (Génier 2017)	tunneller	88	9	38	59			
Digitonthophagus viridicollis (Génier 2017)	tunneller	374	148	183	339	0.786	17.385	0.442
Drepanocerus cf. patrizii (Boucomont 1923a)	tunneller	8	0	4	4			
Epirinus flagellatus (Fabricius 1775)	roller	16	0	0	16			
Euoniticellus intermedius (Reiche 1849)	tunneller	251	159	158	252	2.379	15.382	0.031*
Euonthophagus cf. carbonarius (Klug 1855)	dweller	12	0	8	4			
Garreta nitens (Olivier 1789)	roller	52	161	133	80	1.242	17.975	0.23
Gymnopleurus aenescens (Wiedemann 1821)	roller	132	120	135	117	-1.427	15.669	0.173
Gymnopleurus humanus (Macleay 1821)	roller	8	0	3	5			
Gymnopleurus pumilus (Reiche 1850)	roller	28	38	53	13	-1.138	16.578	0.272
Heliocopris andersoni (Bates 1868)	tunneller	1	0	0	1			
Heliocopris atropos (Boheman 1860)	tunneller	11	0	2	9			
Heliocopris faunus (Boheman 1857)	tunneller	18	9	11	16			

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Species	Type							
Heliocopris japetus (Klug 1855)	tunneller	10	3	6	7			
Kheper cupreus (Castelnau 1840)	roller	76	90	86	80	2.846	11.519	0.015*
Kurtops quadraticeps (Harold 1867c)	tunneller	1	0	0	1			
Metacatharsius cf. dentinum (Ferreira 1964b)	tunneller	44	4	20	28			
Metacatharsius exiguus (Boheman 1860)	tunneller	20	33	16	37	1.516	13.454	0.153
Metacatharsius opacus (Waterhouse 1891)	tunneller	170	19	91	98	2.569	15.615	0.021**
Metacatharsius troglodytes (Boheman 1857)	tunneller	58	38	34	62	12	18	0.005**
Odontoloma louwi (Howden and Scholtz 1987)	tunneller	37	12	21	28	1.293	14.645	0.216
Onitis alexis (Klug 1835)	tunneller	5	0	2	3			
Onitis bilobatus (Ferreira 1976a)	tunneller	4	0	0	4			
Onitis deceptor (Péringuey 1901)	tunneller	2	0	0	2			
Onitis obscurus (van Lansberge 1886)	tunneller	136	74	99	111	2.314	14.267	0.036*
Onitis setosus (van Lansberge 1875b)	tunneller	29	14	32	11	2.213	17.289	0.041*
Onitis uncinatus (Klug 1855)	tunneller	202	146	132	216	59.5	18	0.496
Onitis cf. viridulus (Boheman1857)	tunneller	1	0	0	1			
Onthophagus aequepubens (d'Orbigny 1905)	dweller	23	0	0	23			
Onthophagus aeruginosus (Roth 1851)	dweller	502	265	321	446	0.014	16.803	0.989
Onthophagus axillaris (Boheman 1860)	dweller	149	72	104	117	-0.361	17.861	0.722
Onthophagus cf. albipodex (d'Orbigny 1902)	dweller	49	3	23	29	3.781	17.906	0.001**
Onthophagus cf. apiciosus (d'Orbigny 1902)	dweller	16	11	14	13	0.206	17.643	0.839
Onthophagus cf. obtusicornis (Fahraeus 1857)	dweller	4	0	1	3			
Onthophagus cf. fugitivus (Péringuey 1901)	dweller	327	60	158	229	-1.746	17.728	0.098
Onthophagus impressicollis (Boheman 1860)	dweller	93	27	63	57	1.366	17.991	0.189
Onthophagus leucopygus (Harold 1867)	dweller	67	16	50	33	1.591	15.294	0.132
Onthophagus probus (Péringuey 1901)	dweller	1664	787	1005	1446	1.983	16.929	0.064

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Onthophagus semiflavus (Boheman 1857)	dweller	379	234	201	412	1.365	14.337	0.193
Onthophagus sp2	dweller	99	104	35	168	0.967	13.093	0.351
Onthophagus sp3	dweller	222	39	86	175	94	18	0.0003***
Onthophagus sp5	dweller	117	109	109	117	1.509	14.238	0.153
Onthophagus sp6	dweller	1	0	0	1			
Onthophagus suffusus (Klug 1855)	dweller	1373	945	815	1503	-0.742	12.621	0.472
Onthophagus tricorniger (Boheman 1860)	dweller	8	6	0	14			
Onthophagus venustulus (close to 1)	dweller	9703	6521	5160	11064	1.963	16.646	0.067
Onthophagus venustulus (close to 2)	dweller	367	9	166	210	0.556	13.561	0.588
Onthophagus venustulus (Erichson 1843)	dweller	8808	5593	6307	8094	0.455	17.376	0.655
Onthophagus verticalis (close to)	dweller	100	9	139	102			
Onthophagus verticalis (Fahraeus 1857)	dweller	165	76	20	89	0.158	17.905	0.876
*Onthophagus vinctus (*Erichson 1843)	dweller	299	129	183	245	-0.114	16.685	0.911
Pachylomera femoralis (Kirby 1828)	roller	109	21	48	82	0.812	13.604	0.431
Pedaria cf. cylindrica (Fahraeus 1857)	dweller	63	13	9	67	3.463	17.391	0.003**
Pedaria sp1	dweller	26	0	0	26			
Phalops cf. wittei (Harold 1867c)	tunneller	18	0	6	12			
Phalops cf. dregei (Harold 1867c)	tunneller	22	0	10	12			
Phalops pauliani (Barbero, Palestrini and Roggero 2003)	tunneller	111	9	28	92			
Phalops prasinus (Erichson 1843)	tunneller	81	47	75	53	-1.658	12.006	0.123
Phalops pyroides (d'Orbigny 1908)	tunneller	81	106	67	120	0.066	12.975	0.948
Phalops rufosignatus (van Lansberge 1885a)	tunneller	29	15	24	20	1.118	16.121	0.279
Proagoderus bicallosus (Klug 1855)	tunneller	2	0	0	2			
Proagoderus sapphirinus (Fahraeus 1857)	tunneller	5	1	1	5			
Sarophorus cf. angolensis (Frolov 2004)	dweller	13	0	2	11			

Scarabaeolus bohemani (Harold 1868b)	roller	170	42	34	178	0.248	17.376	0.807
Scarabaeolus flavicornis (Boheman 1860)	roller	3	0	1	2			
Scarabaeus ambiguus (Boheman 1857)	roller	733	341	549	525	2.579	17.486	0.019*
Scarabaeus deludens (zur Strassen 1961a)	roller	50	13	10	53	-0.56	15.655	0.583
Scarabaeus goryi (Castelnau 1840)	roller	98	8	41	65			
Scarabaeus vicinus (Janssens 1940b)	roller	64	34	19	79	3.384	16.587	0.004**
Scarabaeus zambesianus (Péringuey 1901)	roller	192	82	113	161	0.437	17.279	0.667

*P < 0.05, **P < 0.01, ***P < 0.001

Appendix B

Appendix B Species table for Chapter 3 of all dung beetles, and their functional guild groupings, sampled from PAs and farms in Namibia. Their abundances are separated according to bait type (cow or wildebeest dung) and according to land-use (farm and PA)

Species Name	Guild	PA	Farm	Cow	Wildebeest
*Allogymnopleurus splendidus (*Bertolini 1849*)*	roller	69	40	21	88
Catharsius ulysses (Boheman 1857)	tunneller	6	0	0	6
Catharsius vitulus (close) (Boheman 1857)	tunneller	5	0	0	5
Chalconotus convexus (Boheman 1857)	roller	27	9	10	26
Copris elphenor (Klug 1855)	tunneller	3	0	0	3
Copris gracilis (Waterhouse, 1891)	tunneller	46	12	8	50
Copris laioides (Boucomont 1932)	tunneller	28	7	6	29
Copris subsidens (Péringuey 1901)	tunneller	6	3	4	5
Digitonthophagus namaquensis (Génier 2017)	tunneller	33	16	20	29
Digitonthophagus viridicollis (Génier, 2017)	tunneller	63	32	24	71
Euoniticellus intermedius (Reich, 1849)	tunneller	193	116	199	110
Garreta nitens (Olivier 1789*)*	roller	49	7	18	38
Gymnopleurus aenescens (Wiedemann 1821*)*	roller	24	28	20	32
Gymnopleurus humanus (Macleay 1821*)*	roller	10	0	0	10
Gymnopleurus pumilus (Reiche 1850*)*	roller	39	31	51	19
Heliocopris andersoni (Bates 1868)	tunneller	1	0	0	1
Heliocopris atropos (Boheman 1860*)*	tunneller	2	0	0	2
Heliocopris faunus (Boheman 1857)	tunneller	3	0	0	3
Heliocopris japetus (Klug 1855)	tunneller	4	0	2	2
Kheper cupreus (Castelnau 1840)	roller	25	14	12	27
Metacatharsius opacus (Waterhouse 1891)	tunneller	25	12	11	26
Metacatharsius troglodytes (Boheman 1857)	tunneller	61	12	20	53
Onitis alexis (Klug 1835)	tunneller	2	0	0	2
Onitis obscurus (van Lansberge 1886)	tunneller	48	6	14	40
Onitis setosus (van Lansberge 1875b)	tunneller	25	0	3	22
Onitis uncinatus (Klug 1855)	tunneller	80	20	33	67
Onthophagus aeruginosus (Roth 1851)	tunneller	72	51	66	57
*Onthophagus cf. albipodex (*d'Orbigny 1902)	tunneller	88	48	63	73
Onthophagus impressicollis (Boheman 1860)	tunneller	1	0	0	1
Onthophagus probus (Péringuey 1901)	tunneller	217	284	244	257
Onthophagus semiflavus (Boheman 1857)	tunneller	124	42	43	123
Onthophagus suffusus (Klug 1855)	tunneller	103	311	200	214
Onthophagus venustulus (close to 1) (Erichson 1843)	tunneller	509	612	494	627
Onthophagus venustulus (close to 2) (Erichson 1843)	tunneller	15	99	86	28
Onthophagus venustulus (Erichson 1843)	tunneller	515	634	695	454
Onthophagus verticalis (Fahraeus 1857)	tunneller	117	140	71	186
Onthophagus vinctus (Erichson 1843*)*	tunneller	73	55	55	73
Pachylomera femoralis (Kirby 1828)	roller	30	4	9	25
Pedaria cf. cylindrica (Fahraeus 1857)	tunneller	23	5	7	21
Pedaria sp1	tunneller	13	0	0	13

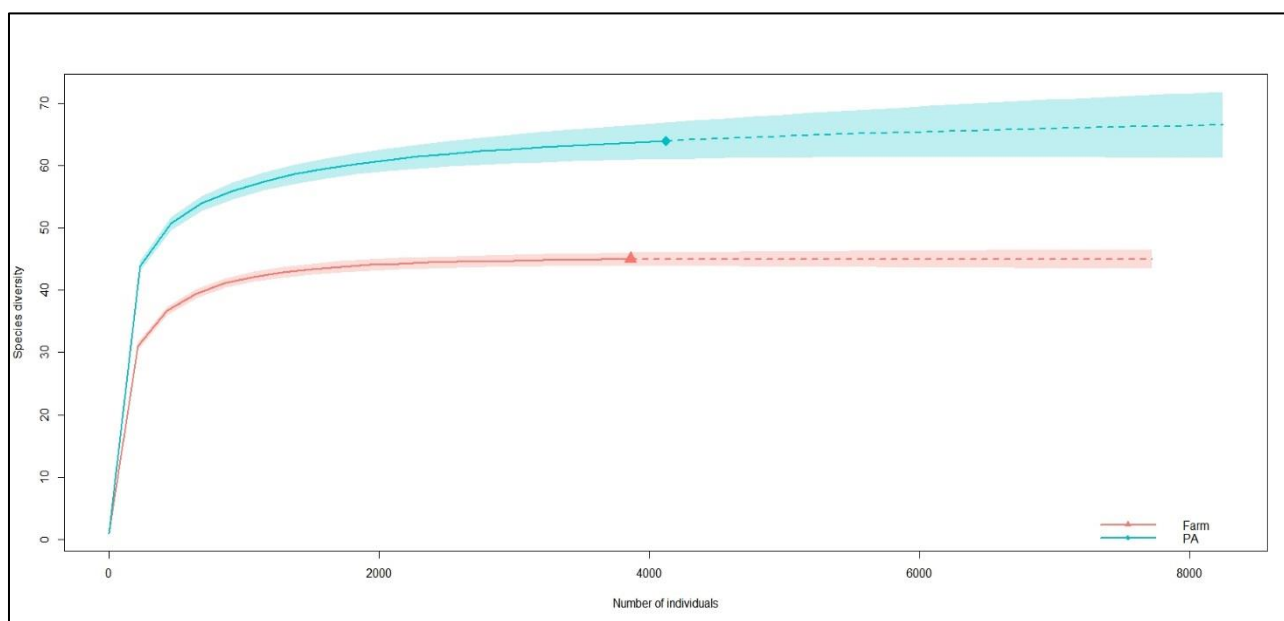| Species					
Phalops cf. wittei (Harold 1867c)	tunneller	6	0	0	6
Phalops dregei (close to) (Harold 1867c)	tunneller	1	0	0	1
*Phalops pauliani (*Barbero, Palestrini and Roggero 2003)	tunneller	35	12	22	25
Phalops prasinus (Erichson 1843)	tunneller	38	29	38	29
Phalops pyroides (d'Orbigny 1908)	tunneller	17	45	17	45
Phalops rufosignatus (van Lansberge 1885a*)*	tunneller	24	22	17	29
Scarabaeolus bohemani (Harold 1868b)	roller	10	0	0	10
Scarabaeus deludens (zur Strassen 1961a)	roller	8	0	0	8
Scarabaeus goryi (Castelnau 1840)	roller	4	4	4	4
Scarabaeus vicinus (Janssens 1940b)	roller	15	3	1	17
*Scarabaeus zambesianus (*Péringuey 1901)	roller	57	12	10	59

Appendix C

Appendix C Species table of vertebrate inventory including common name, species/genus name. Tick marks give an indication of mammal's presence on either the farm, reserve or both.

Species	Common name	PA	Farm
Aepyceros melampus (Lichtenstein, 1812)	Impala	√	
Alcelaphus buselaphus (Pallas, 1766)	Hartebeest	√	
Antidorcas marsupialis (Zimmermann, 1780)	Springbok	√	√
Aves	Birds	√	√
Bos taurus (Linnaeus, 1758)	Cow		√
Canidae	Dogs		√
Capra hircus aegagrus (Erxleben, 1777)	Goats		√
Carnivora	Carnivore	√	
Connochaetes taurinus (Burchell, 1823)	Wildebeest	√	
Equus (Equus) caballus (Linnaeus, 1758)	Horse		√
Equus quagga (Boddaert, 1785)	Zebra	√	√
Equus (Asinus) africanus (Heuglin and Fitzinger, 1866)	Donkey		√
Giraffa giraffa (von Schreber, 1784)	Giraffe	√	
Kobus ellipsiprymnus (Ogilby, 1833)	Waterbuck	√	
Oryx gazella (Linnaeus, 1758)	Oryx	√	√
Ovis aries (Linnaeus, 1758)	Sheep		√
Papio ursinus (Kerr, 1792)	Chacma Baboon	√	√
Phacochoerus africanus (Gmelin, 1788)	Warthog	√	√
Raphicerus campestris (Thunberg, 1811)	Steenbok	√	√
Rhinocerotidae	Large Non-Ruminant	√	
Sylvicapra grimmia (Linnaeus, 1758)	Duiker	√	
Taurotragus oryx (Pallas, 1766)	Eland	√	
Tragelaphus strepsiceros (Pallas, 1766)	Kudu	√	√

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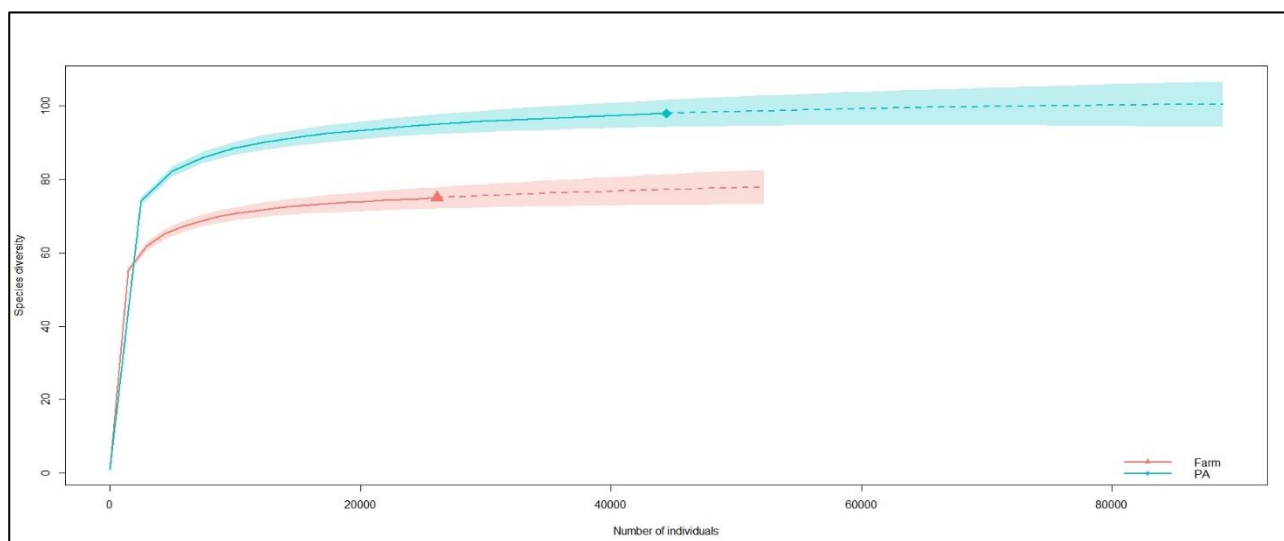
Appendix D

Appendix E

Appendix E Species accumulation cure for dung beetles collected on farms and PAs for the second data chapter (Chapter Three). The solid line shows interpolation and the dotted line shows the extrapolation

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Appendix F

Appendix F Model selection based on AICc (Akaike's Information Criterion for small sample sizes) for all dung beetles as well as the three dung beetle guilds with their three respective diversity indices: richness, abundance and biomass. The three top candidate models are presented where K = number of parameters, ΔAICc = difference in AICc scores between focal model and top-ranked model, AICc (weight) = model weight. LU=land-use, BT= bait type, VSR= vertebrate stocking density and VR= vertebrate richness. "*" denotes an interaction between the factors

Diversity Indices

Guild	Species Richness				Abundance				Biomass			
	Model	K	ΔAICc	AICc(weight)	Model	K	ΔAICc	AICc(weight)	Model	K	ΔAICc	AICc(weight)
Overall	LU+BT+ VR +LU* BT	6	0,00	0,99	LU+ BT +LU* BT	6	0,00	0,80	LU+ BT + VSR + VSR * BT	7	0,00	0,73
Rollers	VR	4	0,00	0,25	LU	4	0,00	0,14	LU+ VSR	5	0,00	0,21
Tunnellers	LU+ VSR	5	0,00	0,25	LU+ BT + VR + VR * BT	7	0,00	0,40	LU+ VSR	5	0,00	0,24
Dwellers	LU+ BT +LU* BT	6	0,00	0,67	LU+ BT +LU* BT	6	0,00	0,9	Intercept	3	0,00	0,15

Appendix G

Appendix G Model selection based on AICc (Akaike's Information Criterion for small sample sizes) for the two function measures, dung removal and seed dispersal and their response to the environmental variables – land-use, dung type, vertebrate richness and vertebrate stocking densities as well as how they responded to the different treatments. The top candidate model is presented where K = number of parameters, ΔAICc = difference in AICc scores between focal model and top-ranked model, AICc (weight) = model weight. SPR =species richness, AB = abundance, BM= biomass, RR= roller richness, RAB = roller abundance, RBM = roller biomass, TR = tunneller richness, TAB = tunneller abundance and TBM = tunneller biomass

Explanatory variable	Model	K	AICc	AICc(weight)
Dung removal	L U + TMT+ LU*TMT	8	1019.00	0
Small seeds	LU+DT+TMT+LU*DT	8	1008.30	0
Medium seeds	DT+TMT+VR+DT*TMT	8	1100.43	0
Large seeds	LU	5	1120.45	0

Appendix H

Appendix H Model selection based on AICc (Akaike's Information Criterion for small sample sizes) for the two function measures, dung removal and seed dispersal, for all dung beetles as well as the two dung beetle guilds with their three respective diversity indices: richness, abundance and biomass. The top candidate model is presented where K = number of parameters, ΔAICc = difference in AICc scores between focal model and top-ranked model, AICc (weight) = model weight. SPR =species richness, AB = abundance, BM= biomass, RR= roller richness, RAB = roller abundance, RBM = roller biomass, TR = tunneller richness, TAB = tunneller abundance and TBM = tunneller biomass

Explanatory variable	Model	K	AICc	AICc(weight)
Dung removal (All)	RR + SPR + TAB + TBM	6	385.43	0.00
Small seeds (All)	AB + SPR + RR + TR + TAB + TBM	8	423.18	0.00
Medium seeds (All)	AB + RR	4	428.65	0.00
Large seeds (All)	SPR + RBM + TBM	5	408.40	0.00
Dung removal (Rollers only)	RR + RAB	4	391.95	0.00
Small seeds (Rollers only)	RR	3	437.80	0.00
Medium seeds (Rollers only)	RR + RAB + RBM	5	431.47	0.00
Large seeds (Rollers only)	RBM	3	414.54	0.00
Dung removal (Tunnellers only)	TR + TAB	4	394.95	0.00
Small seeds (Tunnellers only)	TR	3	442.79	0.00
Medium seeds (Tunnellers only)	TR + TBM	4	436.25	0.00
Large seeds (Tunnellers only)	TR	3	422.13	0.00

Appendix I

Appendix I Spearman's correlation coefficients (rho values) of the diversity indices measured for overall dung beetle diversity and for the two guilds tunnellers and rollers

	1	2	3	4	5	6	7	8	9
1. Species richness	-								
2. Abundance	0.630***	-							
3. Biomass	0.752***	0.379*	-						
4. Roller richness	0.409**	0.185	0.427**	-					
5. Roller abundance	0.396*	0.403**	0.322*	0.026	-				
6. Roller biomass	0.552***	0.247	0.451**	0.269	0.478**	-			
7. Tunneller richness	0.568***	0.297	0.458**	0.392*	0.302	0.366*	-		
8. Tunneller abundance	0.438*	0.437**	0.293	0.081	0.474**	0.284	0.531***	-	
9. Tunneller biomass	0.616***	0.362*	0.595***	0.409**	0.118	0.449***	0.511***	0.577***	-

P < 0.1, * P < 0.05, **P < 0.01, ***P < 0.001.

Appendix J

Appendix J Univariate statistics from the multivariate GLM which recognizes what species significantly contributed to the difference in abundance between farms and PAs and between the two different bait types. The deviance explained by each species provided with its p-value reported

Land-use type			Bait type		
Species	**Dev**	**Pr(>DEV)**	**Species**	**Dev**	**Pr(>DEV)**
Garreta nitens	5.896	0.541	*Garreta nitens*	1.205	1.000
Onitis obscurus	2.803	0.981	*Onitis obscurus*	0.099	1.00
Allogymnopleurus splendidus	0.319	1.000	*Allogymnopleurus splendidus*	5.920	0.663
Scarabaeus zambesianus	2.351	0.996	*Scarabaeus zambesianus*	0.410	1.000
Scarabaeolus bohemani	1.854	0.999	*Scarabaeolus bohemani*	2.562	1.000
Onthophagus suffusus	0.550	1.000	*Onthophagus suffusus*	1.471	1.000
Onthophagus semiflavus	1.582	0.999	*Onthophagus semiflavus*	3.504	0.989
Onthophagus venustulus	3.494	0.920	*Onthophagus venustulus*	1.05	1.000
Onthophagus venustulus (close to 2)	22.513	0.001***	*Onthophagus venustulus (close to 2)*	0.11	1.000
Aphodiinae sp1	1.601	0.999	Aphodiinae sp1	0.302	1.000
Onthophagus probus	5.617	0.650	*Onthophagus probus*	1.323	1.000
Onthophagus axillaris	1.500	0.999	*Onthophagus axillaris*	0.04	1.000
Onthophagus aeruginosus	1.834	0.999	*Onthophagus aeruginosus*	0.488	1.000
Onthophagus vinctus	5.115	0.729	*Onthophagus vinctus*	0.618	1.000
Digitonthophagus viridicollis	9.059	0.152	*Digitonthophagus viridicollis*	3.995	0.976
Aphodiinae sp2	4.061	0.867	Aphodiinae sp2	0.474	1.000
Aphodiinae sp3	1.077	0.99	Aphodiinae sp3	1.42	1.000
Aphodiinae sp4	0.025	1.000	Aphodiinae sp4	0.142	1.000
Onthophagus venustulus (close to 1)	1.644	0.999	*Onthophagus venustulus (close to 1)*	6.065	0.647
Caccobius sp1	9.99	0.121	*Caccobius* sp1	0	1.000
Euoniticellus intermedius	1.174	0.999	*Euoniticellus intermedius*	1.228	1.000
Gymnopleurus aenescens	0.061	1.000	*Gymnopleurus aenescens*	0.138	1.000
Caccobius ferrugineus	2.199	0.997	*Caccobius ferrugineus*	1.811	1.000
Onthophagus verticalis	3.672	0.904	*Onthophagus verticalis*	0.587	1.000

Onitis uncinatus	1.109	0.999	*Onitis uncinatus*	2.554	1.000
Scarabaeus ambiguus	1.15	0.999	*Scarabaeus ambiguus*	0.004	1.000
Aphodiinae sp6	2.991	0.959	Aphodiinae sp6	3.386	0.990
Copris gracilis	0.003	1.000	*Copris gracilis*	4.755	0.867
Caccobius castaneus	9.539	0.133	*Caccobius castaneus*	1.309	1.000
Onthophagus sp2	0.008	1.000	*Onthophagus* sp2	8.186	0.338
Onthophagus sp3	8.275	0.240	*Pedaria cf. cylindrica*	12.424	0.041*
Onthophagus fugitivus (close)	7.033	0.407	*Onthophagus* sp3	1.428	1.000
Onthophagus sp5	0.006	1.000	*Onthophagus fugitivus (close)*	0.351	1.000
Metacatharsius cf. dentinum	12.717	0.038*	*Onthophagus* sp5	0.006	1.000
Aphodiinae sp10	0.18	1.000	Aphodiinae sp10	2.010	1.000

P < 0.1, * P < 0.05, **P < 0.01, ***P < 0.001

Appendix K

Appendix K Supporting photographs of trap methodology and study area